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Seed Orchards

R Faulkner

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Seed Orchards

A joint production by specialist members of the International Union of Forest Research Organization's Working Party on Seed Orchards (S2.03.3)

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EDITOR'S PREFACE

There is an urgent world-wide need to raise the production of wood in future afforestation schemes. This need can only be achieved on any given site through the correct choice of species, seed source and silvicultural treatment.

Most of the world's current planting programmes are still based on plants derived from seed collected from unselected populations, although in the last two decades there has been a decided trend towards the increased use of phenotypically superior stands as seed sources.

Since the late 1940's some countries have advanced their thinking on future seed supplies and have embarked on tree breeding programmes, based on the selection of superior phenotypes. These are vegetatively propagated and brought together on a suitable site for the creation of clonal seed orchards. At a later stage, orchards, based entirely on progeny tested clones, are developed. There are now many thousands of hectares of clonal seed orchards throughout the world. As an alternative, seedling seed orchards, which are based on selected seedling progenies, have also been established but only on a limited scale.

Understandably, there is now a considerable literature on all aspects and problems of seed orchard design, establishment, management and protection, and certification of the end product—seed. Much of the published information is superficial and already out-dated; and during the 1971 Congress of the International Union of Forest Research Organisations (I.U.F.R.O.) in Florida the Working Party on Seed Orchards decided that one of its primary functions in the immediate future should be the production of an authoritative book on seed orchards.

It was my honour and privilege as Chairman of the I.U.F.R.O. Seed Orchard Working Party and in consultation with my co-chairman Dr Robert Kellison, in the U.S.A. and Dr Sung Ok Hong, in South Korea, to draw up a list of potential contributors for such a publication and in early 1973 letters inviting contributions on specific topics were issued. The response was extremely gratifying and by August 1974 the last of the contributions was received.

The task of editing the texts has not been an easy one since the style of writing and presentation quite understandably varied between authors; for this reason each chapter can be regarded as a separate essay. There has been no intent to impose the style of the editor upon the contributing authors. In some chapters material which is perhaps outside the scope of the title of this book has been included since it provides a valuable link to other important aspects of tree breeding. Wherever important contributions to the literature have been published since the original texts were received, these have been included, often without consulting the authors.

This book is intended to provide a useful source of reference for practising orchardists and as a general textbook for university forestry courses which include tree breeding as a subject in their curriculum.

Finally, I must express my sincere gratitude to all the authors in particular and to the numerous practising orchardists and research workers who have contributed much by generously responding to several questionnaires which enabled many of the authors to provide up-to-date accounts of their subjects.

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CHAPTER 1

HISTORICAL REVIEW OF SEED ORCHARDS

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Terminology

In many early publications any plantation primarily established for producing seed for the reproduction of forest trees was described as a seed orchard. Forest tree breeders gave the term a more precise meaning when they linked it with the production of genetically improved seed.

In 1956 C. Syrach Larsen presented his ideas on the matter as: "The term 'seed-garden' (seed-orchard, seed-plantation, or seed-source-garden) should be used only for establishments which are laid down with improved seed-production in view. Broadly speaking that will mean that it ought to be applied only to plantations in which plants vegetatively reproduced (clones) or seedlings are used which have been raised after controlled pollination and have most frequently been the subject of selection. Although existing growing stands can be particularly valuable for seed-production, they ought not to be included under the name, but should always be referred to as 'seed-stands'. The same applies to plantations for which seed has been used from selected trees derived from free, uncontrolled pollination. However valuable and satisfactory they may be, it seems to me, nevertheless, to approach very near to ordinary good afforestation. Seed-gardens, as well as forest-tree breeding as a whole, ought to have their roots in reliable knowledge obtained from controlled pollination and vegetative reproduction in clones. That may perhaps only seem to be a splitting of hairs, but it is more than that."

Bruce Zobel *et al* in 1958 provided a definition which has since been widely used: "A seed orchard is a plantation of genetically superior trees, isolated to reduce pollination from genetically inferior outside sources, and intensively managed to produce frequent, abundant, easily harvested seed crops. It is established by setting out clones (as grafts or cuttings) or seedling progeny of trees selected for desired characteristics". He also warned of the dangers of confusing seed orchards with seed production areas (seed stands) when he continued . . . "care must be taken to distinguish seed orchards from seed production areas, which are good natural or planted stands from which the phenotypically inferior trees are removed and which are specially managed to increase seed production. As such stands are not originally established for production of genetically improved seed, the selection of the trees they contain is much less intensive than in the case of seed orchards, and their genetic worth is therefore usually problematical."

The genetical superiority of the end-product from an orchard is a condition in this definition, although Sarvas (1970) stresses the usefulness of seed orchards as a tool for supplying forestry with otherwise unavailable seed "even though no greater genetic demand is made". This viewpoint and Zobel's definition seem to have merged in the following definitions now adopted by the Organisation for Economic Co-operation and Development (O.E.C.D.) "Scheme for the Control of Forest Reproductive Material Moving in International Trade"; "A seed orchard is a plantation of selected clones or progenies which is isolated or managed to avoid or reduce pollination from outside sources, managed to produce frequent, abundant and easily harvested crops of seed."

Introduction

Seed collection is one of man's oldest occupations and probably began when seeds were first harvested for food. Subsequently part of the harvest was retained to provide a basis of a crop for the following year: this step provided the transition from "hunters and food gatherers" to agriculture.

In forestry the establishment of artificially planted trees crops derived from specially harvested seed was a silvicultural method seldom practised before the start of the eighteenth century. With the growing general acceptance of plantations as a better alternative to natural regeneration in most parts of the world a growing demand for tree seed has simultaneously arisen.

The idea of plantations specifically established for the production of forest seed appeared in the literature as early as 1787, when F. A. L. von Burgsdorf in Germany suggested using vegetatively propagated material for the purpose (v. Hassenkamp, 1952).

According to Schreiner (1962) clonal seed orchards were formed about 1880 by the Dutch in Java in attempts to increase the quinine content of *Cinchona ledgeriana*. Clonal seed orchards have been used in Malaya for breeding rubber (*Hevea brasiliensis*) since 1919 (Keiding, 1972).

In European forestry the idea of producing genetically improved seed by means of seed orchards has been discussed since the beginning of this century. In 1906 Gunnar Andersson (Andersson, 1963) in Sweden suggested the use of vegetative propagation in forest tree breeding. Shortly afterwards W. Johannsen (1909), referring to A. Oppermann, H. Hesselmann and G. Andersson, advocated the idea of establishing small "elite stands" in which progeny from selected individual trees were to be kept separate. These stands were to be rogued on the basis of progeny tests and the seed from them was to be used for establishing much larger plantations from which greater amounts of seed could be obtained for forestry purposes.

In 1918 N. Sylvén suggested that seed be produced in stands especially planted for the purpose with seedlings of known good origin, and in 1922 L. Fabricius included seed orchards in his proposal for a breeding programme with forest trees. A. Oppermann in 1923 suggested seedling seed orchards for the production of hybrid larch (*Larix eurolepis*) seed and C. G. Bates (1928) in the U.S.A. published an article on tree "seed farms" in which he discussed seedling seed orchards.

According to R. Faulkner (1965) the first forest tree seed orchard actually established in Britain was planted in 1931 by J. Scrymgeour-Wedderburn, Esq, on his Birkhill Estate in Fife, Scotland. This orchard was based on selected European larch and hybrid larch seedlings and was designed with the intention of producing back-cross hybrids having most of the hybrid larch vigour and the better wood qualities of the European larch parents. This orchard is still in production.

Following the early research in forest tree breeding in the 1930's the need arose to develop the results commercially. In 1934 C. Syrach Larsen, in his paper on "forest tree breeding", referred to Oppermann's earlier proposal and further suggested that vegetative propagation be used in the following recommendation: "I strongly urge, therefore, taking up vegetative propagation and, in conjunction with experiments of artificial pollinations, the establishment of seed plantations for the supply of seeds for practical use". This idea of using vegetative propagation as a simple method leading to the production of genetically improved seed smoothed the way for the application of forest genetics in practical forestry and in Europe and south-eastern U.S.A. in particular. It may also account for the use of grafted clonal seed orchards for those species where the advantages of the method are less obvious.

To obtain an up-to-date, accurate and comprehensive account of the history of seed orchard development throughout the world is now too daunting, if not an impossible, task. For this reason the authors have only surveyed the available literature and accept that the results must be less than complete. In the text more attention has been given to those countries with long-standing and extensive orchard programmes than others which have limited orchard experiences or programmes which have only recently begun.

EUROPE

In Europe the establishment of seed orchards for the mass-production of improved seed began shortly after the end of World War II. (Table 1).

Sweden

In Sweden forestry is of major importance to the national economy and is mainly based on two indigenous conifers, Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). A growing concern for the quantities and the quality of timber resources in Sweden, combined with the difficulties in procuring seed from acceptable sources, were expressed by Jensen (1943). According to Jensen's plan the country should be divided into climatic zones in which orchards were to be established and based on grafts from "élite" trees selected within each zone. (Jensen, 1949). Two private tree breeding societies were engaged in work with seed orchards from the late 1940's (Johnsson *et al*, 1950). The tree improvement work of the private and state tree breeding organisations was co-ordinated in 1950. The country was divided into sixteen plantation zones for pine and ten for spruce, and the area of private- and state-owned orchards increased steadily from the early 1950's onwards. In 1970 it had reached a total of 700 hectares of which two-thirds were Scots pine and the remainder mainly Norway spruce. (Andersson, 1960, 1963, 1966; Hadders *et al*, 1970).

The pine orchards began to produce commercial quantities of seed from about their tenth year onwards. Seed production increases rapidly until age 30 and seems likely to stabilise at around the age of 40–50 years at about 10 kilogram/hectare/year (Hadders *et al*, 1970). The experience with Norway spruce orchards has been less encouraging and the regular production of commercial seed crops has still to materialise.

Denmark

A successful early Danish example is the "Fårefolden" seed orchard. This was established in 1946–47 and was designed for the production of hydrid larch seed. It is based on a single European larch (*Larix decidua*) mother clone and several inbred, full-sib Japanese larch (*L. kaempferi*) seedling pollinators. This 1 hectare orchard was designed by C. Syrach Larsen (1956) and established at Humlebaek. Annual collections of seed from 1948–72 have ranged from 0.0 to 72.8 kilograms

TABLE 1

BRIEF HISTORICAL DETAILS OF SOME EUROPEAN SEED ORCHARD PROGRAMMES

(*See text for details of work in Sweden, Denmark, Finland and Hungary*)

Country	Main species	Seed Orchards: Approx total area and date hectares		Seed Orchards: Year of starting the programme	Authority
Belgium	*Pinus sylvestris; Larix eurolepis*	10	(1971)	1960	Nanson (1974)
Czechoslovakia	*Larix decidua; Pseudotsuga menziesii*	51	(1971)	1958	Šindelář (1974)
Federal Republic of Germany (Hessen)	*Pinus sylvestris; Picea abies; Fagus sylvatica*	35	(1967)	1955	Frölich *et al* (1967)
France	*Pinus pinaster* Various conifers	30 64	(1971) (1971)	early 1960's	Lacaze (1974)
German Democratic Republic	*Larix decidua* and other conifers	?	?	1957	Hoffmann (1955) Curschmann (1958)
Great Britain	*Pinus sylvestris; P. contorta; Larix eurolepis*	64	(1971)	1931	Faulkner (1974)
Holland	*Pinus sylvestris*	?	(1971)	early 1970's	Heybroek (1974)
Norway	*Picea abies; Pinus sylvestris*	150	(1971)	1963	Dietrichson (1974)
Lithuania	*Pinus sylvestris; Picea abies*	3½	(1967)	1964	Ramanauskas *et al* (1967)
Poland	Ten species	20	(1969)	1960	Korczyk (1969)
Republic of Ireland	*Pinus contorta; Pseudotsuga menziesii; Larix kaempferi*	56	(1971)	1955	O'Driscoll (1974)
Romania	*Pinus sylvestris; Picea abies*	35	(1966)	1961	Enescu (1966)
U.S.S.R. (including Asian areas)	*Larix decidua; Picea abies; Pinus sylvestris; Larix sibirica; Quercus robur*	10 670	(1971)	1962	Chebotaryov (1972)
Yugoslavia	*Larix decidua; Pinus nigra; Picea abies*	30	(1970)	early 1970's	Vidacović (1971)

(average 12.6 kilograms) and offspring have been established in many parts of the world; results have been sufficiently encouraging to create a demand for seed which cannot be met.

In 1946 the state forest service founded a tree improvement station at Humlebaek; private estates in south-east Sjaelland formed a tree breeding society in 1951; and the Danish Seed Society set up a forest seed and tree improvement centre in 1954. By 1972 and in mutual co-operation with the Hørsholm Arboretum these organisations had established commercial seed orchards totalling 96.5 hectares and covering 21 species, 16 species and 80 hectares of which were conifers.

Finland

Finland adopted a national seed orchard programme about 1960. The climate in north Finland adversely affects seed production and planned natural regeneration of Scots pine and gave impetus to the scope and time-scale of the scheme. A national goal of 3 738 hectares of clonal orchards was set. Work began in the mid-1960's, and by 1971 almost 2 500 hectares had been planted with 10^6 grafts at a spacing of 5×5 metres. Scots pine account for 90 per cent of the area, and Norway spruce 10 per cent. In recent years birch (*Betula pendula*) has also attracted the attention of Finnish tree breeders and orchards of this species have been established under green-house conditions (see Chapter 13 A).

Hungary

Hungary has been actively engaged in the breeding of black locust (*Robinia pseudoacacia*) since 1930. After World War II it was planned to increase the forest area of the country and the production of fast-growing conifers in particular. An orchard programme, chiefly based on Scots pine, was initiated in 1951 and in 1954 the first experimental seed orchards were planted. Two types were established; one for testing the clones and for assessing their seed production capacity; the others were based on small management units composed of tested clones—these were designed for testing differences in planting patterns and ground treatment. Forty-five hectares of these experimental orchards had been established by 1971.

In the production seed orchards, the first of which were planted in 1967, only clones which produce a minimum of 33 grams of seed per ramet are used. By 1971 about 108 hectares of production seed orchards had been established, 81 hectares of which were of Scots pine. The remainder were European larch, Austrian pine (*Pinus nigra*), and Norway spruce. Approximately 10 per cent of the originally selected plus trees are included in the production orchards (Bánó, 1970; Anonymous (b), 1971).

Other European Countries

Brief details of orchard programmes are presented in Table 1.

NORTH AMERICA

United States of America

As early as 1909 Ness (Schreiner, 1937), working at the Texas Agricultural College, artificially hybridised *Quercus lyrata* and *Q. virginiana*. In 1924 a planned breeding programme for poplar arose from collaboration between the Oxford Paper Company and the New York Botanic Garden. In the same year James G. Eddy established the Eddy Tree Breeding Station in Placerville, California.

The United States Forest Service began a basic research programme in forest tree breeding in 1936 and by 1968 24 orchards, totalling 478 hectares, had been established by the National Forest Service (Schreiner, 1937, 1970).

However, the development of orchards has been most vigorous in the south and south-eastern States and in North Carolina, Texas and Florida in particular. In 1956 the North Carolina State College together with twelve wood-using industries in North and South Carolina, Tennessee, Virginia and Georgia founded the "North Carolina State-Industry Co-operative Forestry Tree Improvement Program". This had a widely based programme and included theoretical, practical and education aspects of tree improvement. The co-operative was arranged by Dr Bruce Zobel and its outstanding success owes much to his leadership, determination, drive and ability to promote team-work. The establishment of clonal seed orchards for the supporting companies was started in 1957–58 and by 1962 200 hectares had been established. Ten years later the orchard area had increased to 1 200 hectares and the number of co-operating industries had grown to 23 in addition to the forest services of three states (Schreiner, 1970). The orchard work has been followed up by progeny testing of clones, and a number of investigations have been made including studies of the genetics of wood properties. During the first decade the programme was dominated by *Pinus taeda*, *P. elliottii* and *P. echinata*. More recently *Liriodendron tulipifiera*, *Liquidambar styraciflua*, *Eucalyptus* species and other hardwoods have been added.

The first commercial seed collections were reported in 1964, and in 1971 7 000 kilograms of seed were harvested. Insect damage to cones and seed has lowered the potential seed yields in later years (Anonymous (a), 1957–1973).

In Texas and Florida similar co-operatives have also established large areas of clonal seed orchards. By 1973 about 2 500 hectares of predominantly pine orchards had been established in the south and south-eastern states of the U.S.A. (Abbott, 1973).

In the Pacific north-west 114 hectares of Douglas fir seed orchards had been established by 1968—most are owned by the larger lumber companies. Breeding for white pine blister-rust resistance has led to the establishment of over 100 hectares of seed orchards in Idaho (Bingham, 1963), and in California seed orchards have been made for the production of pine hybrids (*P. attenuata* x *P. radiata*, *P. jeffreyi* x (*P. jeffreyi* x *P. coulteri*)) (Klaehn *et al*, 1961; Schreiner, 1970; Abbott, 1973).

Canada

An intensive tree breeding programme started in Petawawa, Ontario, in 1935 under the guidance of C. Heimburger. After World War II tree breeding began in British Columbia, and in 1966 it was agreed at the Quebec National Forestry Conference to intensify tree breeding in Canada. Subsequently the Canadian federal and provincial forest services, as well as private industries and universities, have contributed to the work.

In British Columbia Douglas fir has been the main interest and before 1969 40 hectares of orchards of this species had been established and a further 30 hectares were planned. In Ontario 45 hectares of orchards had been established by 1971 including 10 hectares for producing blister-rust resistant white pine. In other Canadian provinces tree breeding programmes have been initiated but so far orchards have not been established (Wang *et al*, 1969; Lane, 1970; Carlisle, 1970; Dyer, 1970).

SOUTH AMERICA

Argentina

A programme on forest tree breeding was initiated in 1960 by the Forest Tree Improvement working group at the National Institute of Agricultural Technology. A programme of seed orchards for *Pinus elliottii* and *Pinus taeda* is planned but has not yet started. (Barrett, 1974).

Brazil

Approximately 20 hectares of clonal seed orchard of *Pinus oocarpa*, *P. kesiya* and varieties of *P. caribaea* had been established by 1970. The orchard programme began in 1966 (Nikles, 1973).

ASIA

Japan

The first selection and breeding project, for the improvement of pine for pulpwood, began in 1950 although clonal selection of *Cryptomeria japonica*, *Thujopsis dolobrata* and *Chamaecyparis obtusa* and mass-production of rooted cuttings for forestry purposes had been practised since 1917. Seed orchards were first introduced on a prefectural basis in 1962 with the aid of government subsidies. By 1970 the area of established state-owned orchards was 418 hectares with a further 1 003 hectares under private or community ownership. The principal species in the orchard programme are: *Cryptomeria japonica*, *Pinus densiflora*, *P. thunbergii*, and *Abies sachalinensis* (Toda, 1974).

Korea

Forest tree breeding research was undertaken after 1953 at the government funded Forest Tree Breeding Laboratory at the Seoul National University in Suwon. In 1956 this laboratory became the Institute of Forest Genetics and became an independent government institute in 1964. It was intended to complete the establishment of 750 hectares of orchards by 1973. These will consist of *Pinus densiflora*, *P. rigida*, *P. koraiensis*, *Larix kaempferi*, *Chamaecyparis obtusa*, *Cryptomeria japonica* and the x *P. rigitaeda* hybrid. (Hyun, 1974).

Thailand

Teak breeding began in Thailand in 1959. In 1971 the area of clonal orchard had reached 100 hectares; 60–80 hectares annual extensions are planned.

India

A small seed orchard programme for teak has begun in two states (Venkatesh, 1974).

AFRICA

A *Eucalyptus camaldulensis* seed orchard planted in Morocco in 1956 was probably the first orchard to be established in Africa (Franclet, 1957).

Tree breeding in South Africa started at the D. R. de Wet Tree Breeding Station in 1958 and since then a number of orchards of both pine and *Eucalyptus* species have been established (Denison, 1968).

A summary of conifer orchards and clone banks was produced by Nikles (1973) details of which are presented in Table 2. Information on African tropical hardwood orchards is presented elsewhere in Chapter 13, B.

OCEANIA

Australia

Eldridge (1974) provided details of 447 hectares of seed orchards planted in Australia (and Papua New Guinea) before 1972. The first orchard of *Pinus elliottii* was established in 1953. By 1967 all *Pinus elliottii* seed used was derived from seed orchards. The main species being bred is *Pinus radiata*, the first

TABLE 2

ABSTRACT OF INFORMATION ON AFRICAN CONIFER SEED ORCHARDS

(*From Nikles, 1973*)

Country	Species	Period of establishment	Total Area hectares
East Africa (Kenya, Uganda, Tanzania)	*Cupressus lusitanica; Pinus caribaea* var. *hondurensis; P. patula; P. radiata*	1965–71	34
Madagascar	*Pinus kesiya; P. patula*	1967–70	8
Malawi*	*Cupressus lusitanica; P. caribaea;* var. *hondurensis; P. elliottii; P. patula*	1966–70	15
Rhodesia	*Pinus elliottii; P. kesiya; P. patula; P. taeda*	1961–69	18
South Africa	*Pinus caribaea* var. *bahamensis* and var. *hondurensis; P. elliottii; P. kesiya; P. oocarpa; P. palustris; P. patula; P. taeda*	1962–69	165
Zaire	*Pinus caribaea* var. *caribaea*	1962–69	2
Zambia	*Pinus kesiya; P. merkusii; P. oocarpa*	1962–69	40

*and from Paterson (1974)

orchard of which was planted in Queensland during 1957; by 1972 a total of 325 hectares of orchards had been established. Other conifer orchard programmes are concerned with *Pinus pinaster* and *Araucaria cunninghamii*. There were also 9 hectares of *Eucalyptus* spp. orchard in Australia and 16 hectares of teak in Papua New Guinea.

New Zealand

A breeding programme was begun in 1953 with *Pinus radiata* and in 1973 238 hectares of clonal seed orchards had been established. Commercial seed crops have been collected since 1968 (Thulin 1969) and in 1973 350 kilograms of seed were produced (Anonymous 1973).

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CHAPTER 2

THE PLANNING AND STRATEGY OF SEED ORCHARD PROGRAMMES, INCLUDING ECONOMICS

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Introduction

Taking extreme viewpoints the topic can be regarded in two ways: how has planning actually been done, and how could it be done using the more sophisticated methods presently available? This chapter mainly relates towards the second question.

To supplement the published literature letters were sent to investigators responsible for tree breeding programmes in about twenty different countries, raising the following questions. How are the objectives defined? How are the resources provided? How are the cost-benefit calculations made? What is the timing of the orchard programmes in relation to provenance studies and progeny tests and what are the time-scales for different species? What are the expected gains from different approaches to tree improvement? What are the pro's and con's of co-operative programmes. The response was extremely generous and resulted in about 1,000 pages of information, partially in the form of letters and partially as off-prints of publications. This chapter summarises the answers to the above six questions.

Many techniques such as the introduction of exotics, hybridisation, selection within species, mutation breeding and polyploid breeding are now available in addition to various methods of advanced-generation breeding. At the same time tools of economic analysis such as cash-flow analysis, investment-return calculations, net discounted returns, linear programming, goal programming and dynamic programming are available to evaluate the various methods. A lack of reliable basic information is one of the major obstacles to effective planning and the wide variety of possible options is now emerging as both an asset and a liability.

Since planning can be done at both national and regional levels and by industry and by government, it is necessary to define its scope somewhat further. Geographically the *basic unit*, for which a plan needs to be developed, is the area which can be served by a single improved strain of a particular species. This corresponds to the zone in which the seed can be moved freely and remains adapted to local variations of soil and climate. Such a zone could be served by one seed-production unit, as a seed orchard, or a nursery producing rooted cuttings, although for practical reasons it may have to be served by several such units. The organisation having responsibility for developing the plan could be a government organisation, for example a province, a state or a nation, or an industry either working at the regional or a higher corporate level. When the organisation is smaller than the basic geographic unit, the possibility of co-operation with other similar organisations is possible and often very fruitful. If the organisation is larger than the basic geographic unit planning may involve the integration of activities in several units. Integration primarily involves the summation and co-ordination of the "unit programmes"; unit programmes still form the core of the overall planning. In the following discussion planning for the basic unit is the main concern, since this is the level at which fundamental issues have to be resolved.

It is necessary to take a long-term view which includes more than one cycle of selection in the planning operation. Advanced-generation breeding is a most important part and should be included in all plans from the beginning.

With long-term goals in mind an orderly development of a programme can take place much more rapidly (Libby, 1973). Although a number of different approaches are feasible the following scheme provides an example of an orderly development of a programme starting in the complete absence of knowledge on a given species: the establishment of species site-tests; variability studies in the most promising species; the production of a first-generation improved population; the establishment of a breeding population for second-generation selections; production of the second-generation improved populations; a repitition of the last two steps for the next cycle. A critical path analysis can be made of all the stages and their component parts in a tree improvement programme in order to establish a realistic time-scale. The method of critical path analysis is fully described by Lockyer (1970).

How Are the Objectives Defined?

Although this is the most critical step, little information is recorded in the literature about it. At least the objectives are given without much indication as to how they were arrived at. The British Forestry Commission has given much thought to the matter and appears to be well organised in this respect (Morgan, 1970; Fletcher *et al*, 1972). The first step is to determine the needs in terms of species, area to be regenerated, numbers of improved seed and seedlings needed and the period in which they will be needed. The second step is to determine the properties to be improved and to evaluate their economic and biological importance. Further, some knowledge is required about the expected gain in response to selection and the nature and degree of correlated responses in other traits that might result. Finally it must be considered whether or not it might be more advantageous to obtain the desired improvement through improved silvicultural methods or by a combination of silvicultural and genetic techniques.

The procedure for arriving at the general objectives will vary greatly between organisations. Specific objectives are generally defined by the research and development workers, but the depth and nature of the review will vary greatly. In East Africa the forestry research programmes are reviewed annually by a specialist committee for forestry research (Dyson, 1973). Their recommendations are reviewed by higher committees at the department-head and ministerial levels. In the case of one American industry, International Paper Company (Blair, 1973), objectives which are proposed by the staff are then reviewed by the research directorate, consisting of the woodlands general and regional managers and a representative of the southern kraft division, the final decision is taken by the woodlands general manager.

Heybroek (1973) emphasised that plans should be flexible and allow for change with time. Ideally this is correct, but stable policies over half the rotation age or more are essential if waste of previous effort is to be avoided (Dyson, 1974). Specific objectives naturally vary between organisations. There is a basic difference in orientation between industry and state organisations (Jett, 1973). An industry normally has quite specific goals whereas a state often has a diverse clientele and must therefore adopt broader objectives. A mission-oriented programme must often move ahead without much information to support it. If there is less urgency then thorough and careful testing can be done prior to the orchard stage.

Specific objectives include, seed production, adaptation, higher seed-weight, fast growth, greater volume and dry-weight yield, straightness, regular branching, stem quality, wood quality, disease-resistance, frost-resistance, adaptation to marginal sites, and branching habits such as multinodal or uninodal whorls (Bánó *et al*, 1971; Dietrichson, 1972; Dyson, 1973; Einspahr, 1972a; Einspahr, 1973; Eldridge, 1973; Fletcher, *et al* 1972; Giertych, 1973; Goddard, 1973; Heybroek, 1973; Jett, 1973; Nikles, 1963; Shelbourne, 1970; Slee *et al*, 1967; Swofford, 1973).

In general, countries in which the forests are state-owned can do the most thorough job of planning since they have more control over the whole forestry operation. This contrasts sharply with countries where forests are largely privately owned and where forest ownership and the demand for forest products can change dramatically even over rather short time-intervals.

Formulation of Alternative Breeding Strategies

In this context a strategy is defined as an ingenious combination of breeding methods to achieve specific goals. It is recognised that different goals usually have different priorities associated with them. Some frequently chosen goals are; improvement in growth-rate, yield, wood quality, disease-resistance, form, the preservation of germplasm, the formation of adequate basis for long-term improvement, and the provision of an adequate supply of raw materials for a particular product, range of products, or industry.

Major factors which have to be considered in formulating a breeding strategy, in which orchards are often but not exclusively a part are: the biology of the species, the choice of breeding method; the use of combined or separate breeding- and production-populations; the manner in which the advanced generations are to be produced and the extent to which inbreeding is acceptable.

Biology of the Species

Some of the major considerations: Is the species monoecious or dioeceous? Is the species wind- or insect-pollinated? Can the species be readily propagated vegetatively either by grafting or by rooting cuttings? At what age does the species flower? Can the species be effectively propagated by means of controlled pollination? What is the production of viable seed in terms of yield from one cross and from one tree? How much variation is present in the species? Is the genetic variation in the desirable traits largely additive or does a substantial amount of non-additive variation exist? Does the species possess the genes for the desired trait or is inter-specific hybridisation desired? Can the species be grown in plantations? How long does it take to adequately test for the desired properties?

Other factors may be important, but those listed above are the commonest having a bearing on the choice of breeding methods.

What Breeding Method is Most Suitable?

The following breeding methods are amongst those most frequently used.

A. *Clonal Propagation.*

Clonal propagation has two different possible rôles in a tree improvement programme: first the establishment of seed orchards or scion banks for the production of seed for breeding purposes or for commercial forestry; secondly, for the establishment of plantations for the commercial production of wood. In the latter case clonal propagation is a breeding method while in the former it is merely a means of producing seed in large quantities.

Clonal selection and propagation is essentially a dead-end breeding method which should not be ruled-out, because extremely large gains can sometimes be made in this way—as demonstrated particularly with *Populus* species. After the very rapid initial gain, however, it is necessary to cross selected clones among each other to establish a new breeding population within which further clonal selections can be made. In the long-term the clonal method always has to be used in conjunction with other breeding methods.

B. *Selection.*

Selection is most suitable in those instances where substantial amounts of additive genetic variation are present. Selection can take the form of individual-tree selection, family selection, or combined selection. Individual-tree selection is most advantageous when heritabilities are relatively high. In contrast family selection is more effective when heritabilities are low. Combined selection is always as good or better then the other two methods, but the differences are never great (Falconer, 1960). For the majority of tree species this method appears to be very well suited.

C. *Hybridisation.*

There are several ways of creating hybrids, three of which appear to be potentially important in forest tree breeding. If a species can be readily self-pollinated hybrids can be developed between inbred lines in much the same way as for commercial hybrid maize (corn) production. This method will be valuable where a relatively large amount of non-additive variation is present. This does not appear to be the case now, but as more advanced generations are produced it could become more important. Andersson *et al* (1974) present evidence that under some circumstances the use of inbred material may be advantageous even in the absence of specific combining-ability. A somewhat simpler version of the same idea is to produce specific crosses in which a high degree of specific combining-ability exists. Seed production would be obtained in two-clone orchards.

Secondly, hybridisation may be arranged between crosses among widely separated geographic seed-sources. Namkoong (1974) has some rather interesting ideas on this. Local races are not always optimal for commercial forestry purposes and instead there appears to exist a theoretical optimal environment within which the best races for certain areas occur. Plotting the results of geographic seed source tests against the climatic variables of the sources often shows that the optimum environment does not exist. In such cases a suitable combination of seed sources should produce a hybrid, which in a sense could be regarded as the product of a synthetic theoretically optimal environment. A study by Woessner (1972) has shown that such an approach shows promise.

Inter-specific hybridisation can be useful in a number of cases. Perhaps its greatest scope is for the introduction of disease-resistance. The occurrence of true hybrid vigour is less common although frequent enough to be of real interest (Fielding, 1962). The method does not appear to hold much promise for improving wood properties (van Buijtenen, 1970).

If the process is to be continued for more than one generation all forms of hybridisation need to be combined with some form of selection and the maintenance of separate breeding-populations. It will necessarily be a rather complicated system, but may have great merit especially in the case of resistance breeding.

D. *Polyploidy.*

This method has been successfully applied to improve *Populus tremula* (Einspahr, 1972a). Faster growth, greater fibre-length and increased wood specific gravity have been the main responses to increasing the normal chromosome number. For long-term continuous improvement it must be combined with selection or hybridisation to obtain further gains. In the case of triploids this requires maintaining and improving both diploid and tetraploid populations for the production of triploids by crossing; the triploids can then be propagated vegetatively for the mass-production of plants.

Are the Breeding- and Production-Populations the Same or Separate?

Namkoong (1974) examined this question and concluded that either approach can be appropriate. Maintaining separate breeding- and production-populations will necessarily entail extra cost and it is therefore necessary to consider the advantages which would otherwise be missed in order to justify the extra cost. It is, for example, necessary to maintain at least two separate populations for the production of hybrids; this has already been discussed above.

Another strong argument for separating the two types of population is to avoid the conflict between increasing genetic gain by increasing the selection differential, (by selecting a very small proportion of the present population) and maintaining an adequate genetic base for future breeding. By separating the two types of population it is possible to maintain a very broad base in the breeding population and yet get a greater gain by only using the very top families for the commercial production of improved seed or clonally propagated material. This is a key point that is often overlooked (see also Chapter 12). Without a broad-based breeding population a severe loss of germplasm can be expected. It is also advantageous to separate the breeding and the production populations in order to reduce the risk of inbreeding within a few generations. This allows not only the inclusion of a greater number of genotypes but also the adoption of crossing schemes which minimise future inbreeding risks.

Production of Advanced Generations and Rate of Inbreeding

Advanced-generation breeding and the avoidance of inbreeding are best discussed together. It is desirable to both maintain an effective breeding population and obtain a rapid advance by selection. When cost is a limiting-factor these two objectives are mutually exclusive so that a compromise is necessary. Twenty selections as a base for a breeding population appears to be the absolute minimum (Rawlings, 1970). Approximately 1,000 appears to be the maximum attempted so far but is too large for most organisations to handle. A compromise may also be necessary when deciding the mating design. Advanced-generation populations serve many purposes (Burley, 1972; Anderson, 1960) such as: the evaluation of families for the purpose of roguing an orchard, or establishing a new orchard from the best clones; providing the population of the next generation; providing estimates of genetic parameters such as additive and non-additive genetic variation, heritabilities and gain prediction; demonstrating realised gain; and producing the commercial end-product.

Although separate tests could be set up for each objective, limitations on cost and manpower generally require that the tests are combined in some way. Preferably one test should serve all purposes. The following summary is based largely on Namkoong's (1974) analysis:

A. *Mass-selection.*

Allow the selections to mate at random, use all seed commercially and consider the entire production of seedlings as the next population. Although this system is simple, random sampling variations will cause some families to be over-represented and others to be completely omitted, thus leading to a future higher risk of inbreeding and loss of favourable genes.

B. *Single Pair-mating schemes.*

Different systems have been reviewed by Namkoong (1974), Cockerham (1970) and Kimura and Crow (1963). There appears to be an inverse relationship between the early avoidance of inbreeding and eventual inbreeding reached after many generations of using the same mating scheme.

In an initial population of n individuals inbreeding can be avoided for k generations if $n = 2^k$. Thereafter inbreeding increases rapidly. Systems studied include: maximum avoidance of inbreeding, circular matings, and circular pair-matings (Kimura and Crow, 1963). The circular mating-systems would develop inbreeding sooner (since $n = 8$ after two generations) but will lead to lower inbreeding levels in the long-run.

C. *Multiple Crosses Among Parents.*

Crossing patterns which have been advocated include: (1) Factorial mating designs such as, for example, the four-tester scheme in which all clones are tested with the same four tester-clones; this quickly leads to high levels of inbreeding. (2) Complete or modified half diallels. The complete diallels includes all the possible crosses including reciprocals and selfs. The modified half diallel omits the reciprocal crosses and the selfs. Complete diallels provide the maximum amount of flexibility, but are the most costly and where many clones are involved the number of controlled crosses becomes impracticable to handle. Some organisations use modified half diallels among the best parents (as proved by open-pollinated tests) to produce the next breeding generation (Stonecypher, 1968). (3) A series of disconnected small partial diallels (Anon, 1973). This is a very flexible system and fairly easy to handle in practice since each part-diallel can be handled separately. It produces limited test-information because the parents involved in the different partial diallels cannot be compared. (4) Other partial diallel schemes can also be used (Zsuffa, 1973; Anon, 1972) which allow considerable flexibility but suffer from the disadvantage that in practice it is impossible to complete the whole crossing scheme in a short period of time. Consequently the crosses have to be separated into different sets which are planted out in different years. The same problem also occurs with the tester schemes. Many of these crossing schemes allow alternate sets of single pair-matings to be made and, therefore, advantage can be taken of both family and individual tree selections. In such cases some families will be eliminated and a faster rate of inbreeding will be expected.

Some Examples of Strategies

Stonecypher (1969) in discussing various forms of recurrent selection provided a rather simplified but nevertheless complete strategy for a continuing breeding programme. He named this particular

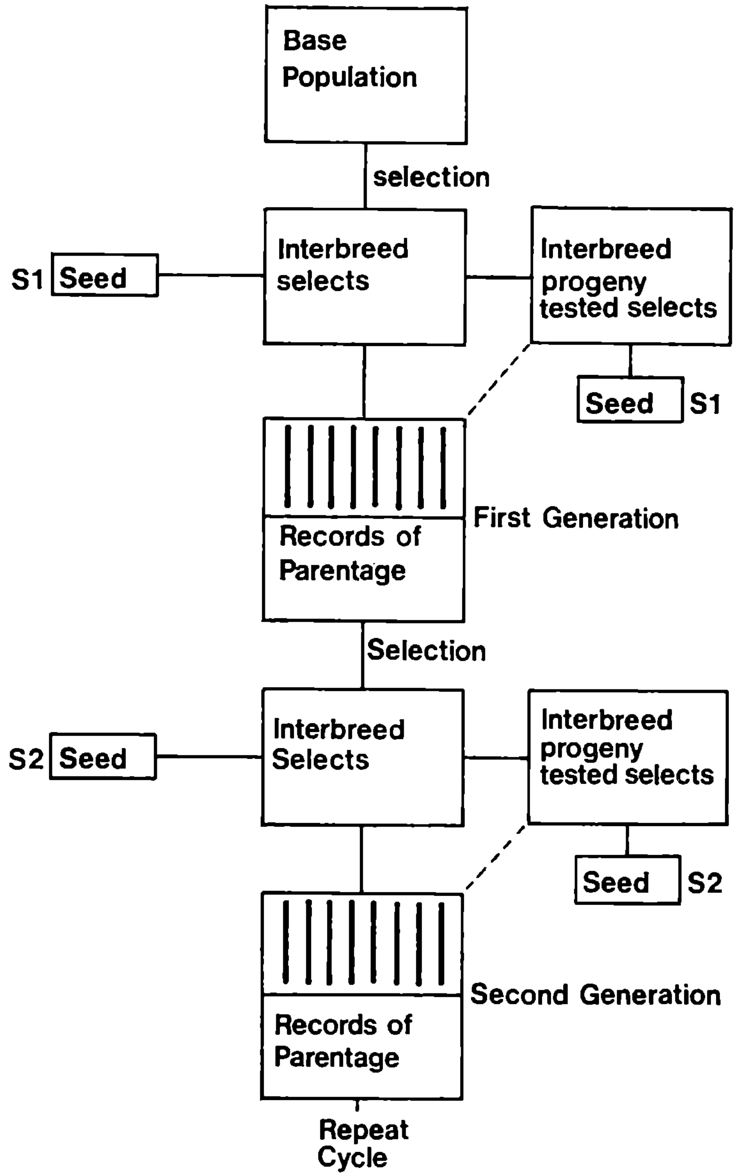

Figure 1. Diagrammatic representation of genotypic recurrent selection.

procedure "genotypic recurrent selection" (Figure 1) and defined this as a type of recurrent selection in which the identity of the families is maintained. The important distinction with phenotypic selection is that in the example shown not only the phenotypic value of the individual but also the phenotypic values of relatives are taken into account in determining the breeding value of the individual. In this particular example the production- and the breeding-population are the same, and the same selections are interbred to produce both commercial seed and the next generation for selection. The difference is, however, that the commercial seed may be randomly interbred and at the same time records are kept for the population from which the next generation is produced.

This of course is a very generalised scheme and no discussion is made of the mating design used for producing the progeny generations. Burdon *et al* (1971) went into considerably more detail and developed a number of strategies for different conditions. An example is given in Figure 2. Nothing was implied with regard to the production population, and the production orchard could be comprised of either all or only part of the selections, or could even include some trees not included in the breeding population. Chapter 12 contains a description of a breeding strategy for the North Carolina Cooperative Program.

Since situations vary widely it is impossible to present an ideal strategy; these examples provide suggestions on how suitable strategies leading to soundly based orchards might be developed.

How are Cost-benefit Calculations Made?

Many techniques are available for making economic evaluations, those most frequently used include: cash-flow analysis, investment-return analysis, net

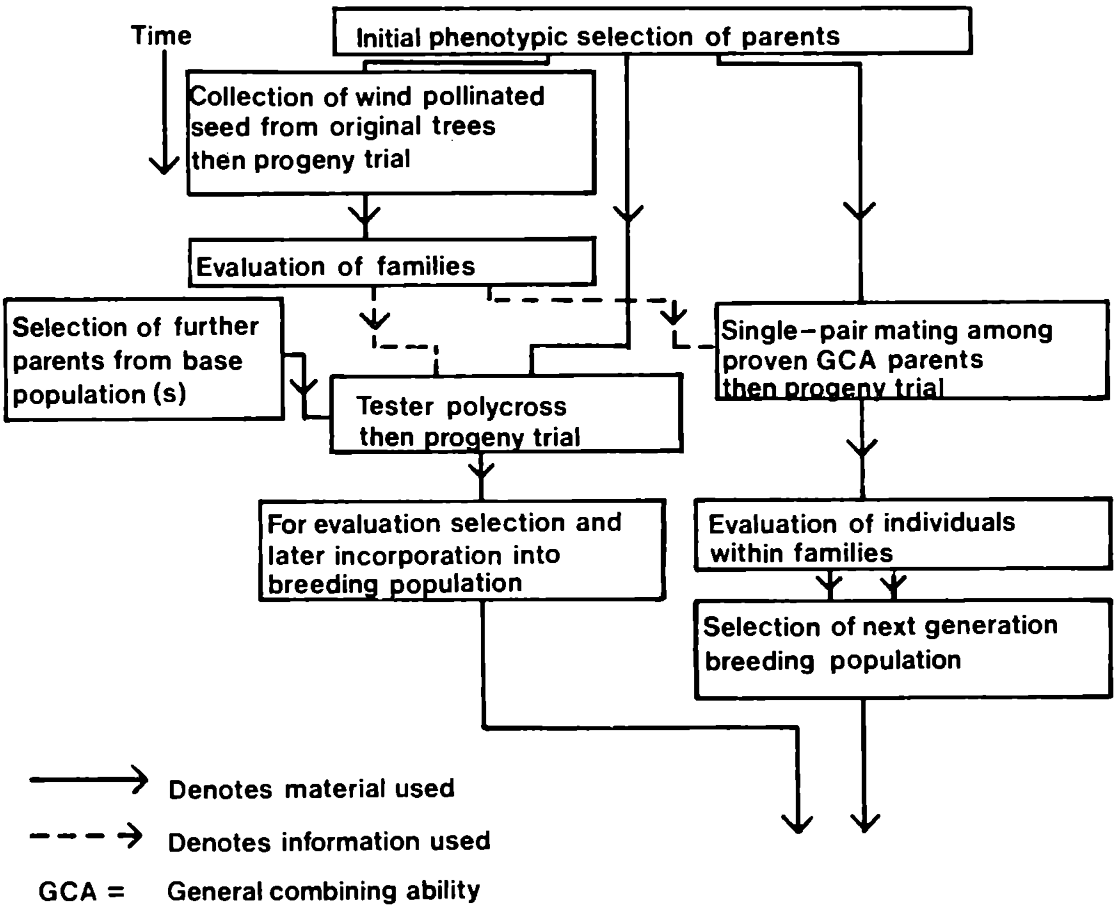

Figure 2. Diagrammatic illustration of one breeding strategy (after Burdon *et al*, 1971).

discounted revenue, linear programming and goal programming. Although other methods exist these are the main ones and discussion is limited to them. Good cost figures are now becoming increasingly available in many areas (Bánó *et al*, 1971; Bánó *et al*, 1972; Danbury, 1971; Wilson, 1965).

Gain estimates are less accurate but are also becoming available (see Table 3), thus making it possible to make some valid cost-benefit studies. Seed production is a factor which is often overlooked; increased seed yield reduces the seed cost and this can partially compensate for some degree of loss in the genetic improvement of other traits (Bergman, 1968; Danbury, 1972). Carlisle *et al* (1970) have published one of the few comprehensive works on costs and benefits applied to a model for a complete selection and breeding programme for *Picea glauca*.

Cash-flow Analysis

This is the simplest method and surprisingly has not been reported in the literature although it certainly must have been used by some organisations. It consists simply of tabulating anticipated expenses and income on a year by year basis (or any suitable time interval). It is useful as a planning tool since it alerts an organisation to future major items of expenditure and it presents a readily grasped indication of the approximate costs of the programme. Its main limitation is that it does not take into account the interest chargeable to the investment and therefore it cannot give a reliable indication of the breakeven selling price of the orchard seed. Figure 3 provides a simplified example based on Texas Forest Service data.

Benefit-cost Ratio

This is a sophisticated economic tool which has been discussed by Walsh *et al* (1969). Applied to forest trees it means discounting all costs and anticipated returns to a common date at a predetermined discount rate and calculating the ratio of the discounted returns divided by the discounted investment. Interpretation of the ratio is difficult but it

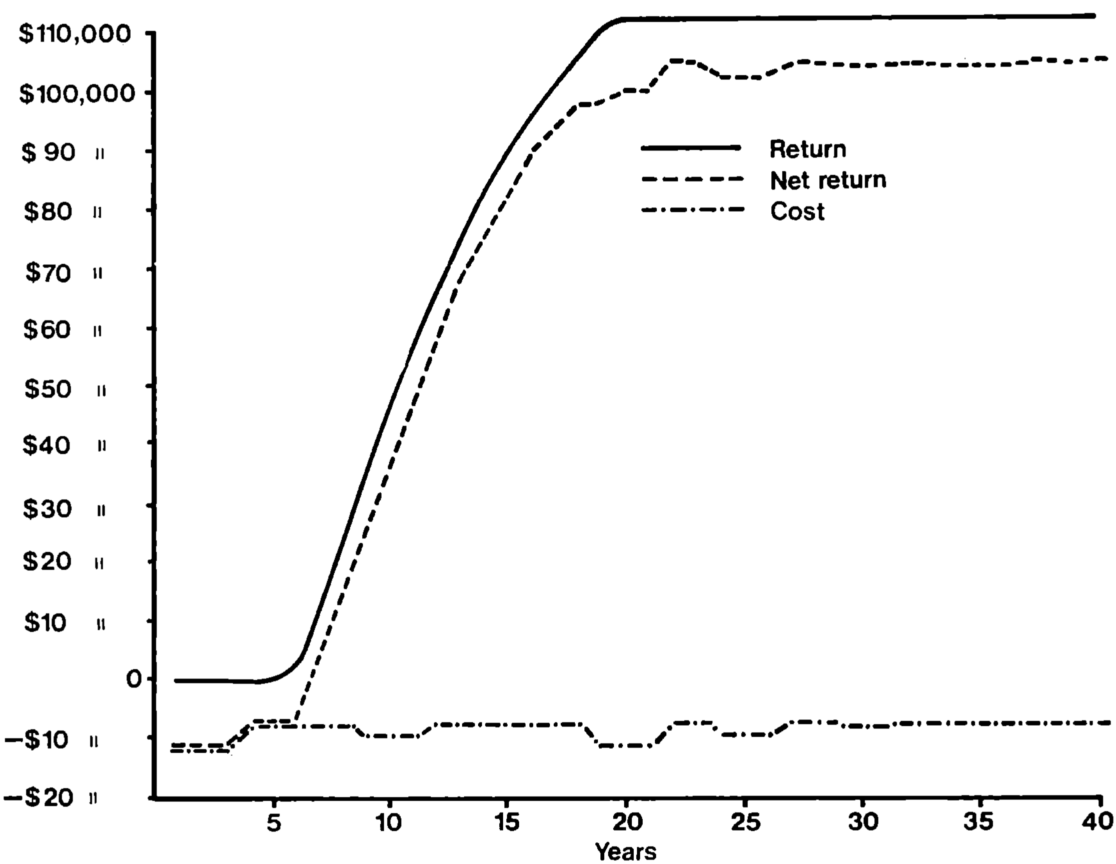

Figure 3. Cash-flows for a simple breeding programme based on Texas Forest Service data.

does enable a forest manager with limited funds to compare different choices of investment, for example tree breeding investments for different species, or between say the use of fertilizers and site cultivation treatment. If the ratio is much larger than unity an investment is obviously sound. Questions about the proper interest rate to use, the future inflation rate and future revenues make any evaluation at the best rather tentative. Nevertheless it does provide a fair basis for making comparisons between investments providing the same time-scales and fixed interest rates are used. The procedure can be carried one step further by adjusting the discount rate to make the ratio equal to 1. This discount rate is the internal rate-of-return. Again opinions vary as to the value of this figure and what constitutes an acceptable internal rate-of-return. Both measures are strongly affected by uncertainties in the estimated costs.

Net Discounted Revenue

This simply is the difference between the discounted revenue and the discounted costs rather than the ratio. The advantage of this measure is that it is less sensitive to assumptions made on the fixed costs (Morgan, 1970; Faulkner, 1973). It is therefore a slightly more reliable indicator but is still subject to the considerable uncertainties of future inflation rates and market prices.

TABLE 3

LINEAR PROGRAMMING SOLUTION FOR A HYPOTHETICAL PULP MILL AND SEED ORCHARD LOCATED IN THE NORTH CAROLINA PIEDMONT AREA.

This is a control case assuming no more than basic silviculture practices

(van Buijtenen *et al*, 1974)

Forestry Option	Rotation age	Total hectares needed to support mill	Volume/hectares cubic metres	Specific gravity
No genetic improvement; minimum site preparations; regeneration by planting	20	154,447	170	0.43

Mill Process Options Chosen
Reduce refining as much as possible.
Add 0.9 kg of starch per ton of pulp to meet strength requirements.

TABLE 4

LINEAR PROGRAMMING SOLUTION FOR THE SAME HYPOTHETICAL MILL, WHEN ALLOWED TO CHOOSE BEST OPTIONS AND ASSUMING AN 8 PER CENT INTEREST RATE.

Note the much smaller area required to support the mill.

(van Buijtenen *et al*, 1974)

Forestry Options	Rotation Age	Total hectares needed to support mill	Volume/hectares cubic metres	Specific gravity
Breed for volume and high wood specific gravity; regenerate by planting; site preparation and fertilize.	20	121,013	213	0.43

Mill Process Options Chosen
Reduce refining as much as possible.
Add 1.12 kg of starch per ton of pulp to meet strength requirements.

Linear Programming

Linear programming is a tool which has much wider application than economic evaluation alone, but it does yield some figures of considerable economic interest. Basically the procedure consists of developing a mathematical model of the operation to be studied describing its products and the limited resources needed in their production. The model seeks the best solution to the most advantageous allocation of the scarce resources. The approach can be particularly useful in defining breeding objectives. In addition it provides estimates of the costs incurred by not using the best possible solution. This can be a very sensitive indicator of the values of different approaches to tree improvement. An example of the results of such an analysis is given in Tables 3 and 4. This was developed by the T.A.P.P.I. Forest Biology Committee and based on actual data obtained from various forestry organisations throughout the southern United States.

Goal Programming

In linear programming the computer model will either maximise the profit or minimise the cost; it will thus essentially satisfy only one condition. Goal programming is an extension of this method in which the computer programme attempts to satisfy several goals simultaneously. This may not always be possible and may call for compromise. In order to achieve this the various goals have to be assigned priorities and the model is used for attempts to satisfy as many of the goals as possible in the given order of priority. As an example some work done by Porterfield (1973) is shown in Table 5.

What is the Timing of Seed Orchard Programmes?

This is an impossible question to answer categorically since so many variables are involved and because different pressures arise between different programmes. If large-scale planting programmes are in progress time will be of the utmost importance. If, on the other hand, extensive planting programmes are not planned until twenty years after the start of a breeding programme then the pace can be slower.

Responses to this question were limited and rather than produce a summary of historical facts from different countries data is given in Table 6 which provides a good estimate of practical schedules for a variety of species and which can be achieved by the sensible use of available technology. The data, therefore, do not represent the fastest possible schedule nor do they assume that everything goes right and that the speed is pushed to the limit. Instead they represent a more realistic situation using satisfactory acceptable techniques and take

TABLE 5

SELECTION INTENSITIES, GENETIC GAINS, AND ECONOMIC RETURNS FROM A GOAL PROGRAMMING MODEL.

In *Solution A* all traits were free to enter the solution at any level. In *Solution B* only trees free of fusiform rust were allowed to enter the solution.

(Porterfield, 1973)

Solution	Trait	Select. Intens. (std. dev.)	Gain %	Goal %	Diff. %	Coastal plain region
A	Straight	1.61	9.6	10.0	−0.4	B/C @ 6% = 8.2
	Crown	1.48	6.5	5.0	+1.5	IRR = 12%
	Sp. Gr.	0.19	4.5	3.0	+1.5	Cost/clone = $312
	Volume	1.98	10.0	10.0	0.0	Infection = medium
	Fusiform	0.10	2.7	1.3	+1.4	
	T. Volume		12.7			
B	Straight	1.48	9.3	10.0	−0.7	B/C @ 6% = 9.5
	Crown	1.41	6.4	5.0	+1.4	IRR = 12%
	Sp. Gr.	0.76	5.5	3.0	+2.5	Cost/clone = $312
	Volume	1.74	10.0	10.0	0.0	Infection = medium
	Fusiform*	0.80	4.4	1.3	+3.1	
	T. Volume		14.4			

* selection intensity 0.80
B/C = Benefit-cost ratio
IRR = Internal rate of return

TABLE 6

TIMING OF SEED ORCHARD PROGRAMMES

Completion of stages in years from start of programme

	Pinus taeda / *Pinus elliottii* — Barrett (1973), Blair (1973), Bowyer (1974)	*Pinus radiata* — Dyson (1973), Eldridge (1973), Pederick (1963), Shelbourne (1973)	*Pinus patula* — Dyson (1974)	*Pinus caribaea* — Dyson (1974)	*Pinus pinaster* — Butcher (1974)	*Pinus sylvestris* — Lindgren (1974), Andersson *et al* (1971)	*Picea abies* — Lindgren (1974), Andersson *et al* (1971)	*Pinus banksiana* — Yeatman (1973)	*Araucaria cunninghamia* — Gould (1974)	*Cupressus lusitanica* — Dyson (1974)	*Juglans nigra* clonal orchard — Masters *et al* (1972)	*Juglans nigra* seedling orchard — Masters *et al* (1972)	*Tectona grandis* — Dyson (1974)	*Liquidambar styraciflua* — Stonecypher (1968)	*Plantanus occidentalis* — Stonecypher (1968)
Establishment of species-site trials		1–3	1	1						1			1		
Assessment of species-site trials		10–15	10–15	11						10			15		
Establishment of provenance trials	3–5	5–20	1	1	10	1	1			1			1		
Assessment of provenance trials		20–25	15–25	20		15–40	10–30			17			20		
Mass-selection in unimproved stands	2–6	2–25			12	28	23	1	2		2	1		2	2
Seed Orchard establishment	2–8	2–35	15–30	20	13–14	30	25	2	6	20	4	2	20–25		
Time to commercial-scale seed production	10–20	10–45			21–24	45	50	20	16–20						
Field establishment of F_1 population	7–18	7–41	21–40	30	18–20	45	40	10	7–10	25	12	17	25–30	3	3
Roguing of seed orchards or selection of élite clones	12–23	12–46	28–47			57	48								
Initial selection in F_1 population	12–23	12–46	28–47			65	60	15		32	17	22	29–35	8	8
Establishment of new orchard	14–25	14–42						20			18	23		8	8
Establishment of F_2 population	19–35	19–62	35–54			67	70	28		37	30	38	34–40	15	15

into account some of the "normal" delays associated with an improvement programme.

The assumption is made that species-site trials are started first, followed by provenance tests and variation studies and then a tree selection programme, without awaiting the final results of provenance tests—in the knowledge that the programme will be improved as results become available. On the other hand if it is necessary to await the final results of the species-site trials and provenance tests the start of the selection programme will inevitably be delayed.

There are two further ways in which a programme can be accelerated. Earlier field planting of the F_1 generations can be made if the F_1 seed is obtained from parent tree selections themselves rather than from grafts which is assumed in Table 6. Selections can also be made earlier in the F_1 population if reliable early-testing procedures are available. The traits under selection also have important effects since some can be evaluated at a much earlier age than others.

How Are the Resources Provided?

Financial resources

In most cases finance is provided through ordinary budgeting procedures. In the case of government organisations this is usually in the form of appropriations channeled through the national or state forestry organisation. Funds can also be provided through experiment stations and universities. Where industries are involved, financing is through corporate funds which are also subject to normal budgeting procedures. Whether a tree improvement programme is classified as research or a normal forest operation can considerably influence the amount of money made available.

Land

In the case of a government programme, state, or nationally owned land is usually made available for orchard purposes. Occasionally exchanges or leases may be specially arranged to secure an area of land which is particularly suitable for an orchard. Where universities are concerned, land may sometimes be available through a university-owned farm or forest, otherwise alternative arrangements are made. In the case of industries, corporately owned woodlands are normally used for orchard sites and progeny tests. If suitable sites are not available on company land, land which meets the requirement of the species, isolation against contaminant pollen, and future management should be obtained by special purchase.

Personnel

This is a particularly critical matter which receives too little attention. Arrangements vary widely depending on the size and character of the organisation involved. Ideally a full-time staff is recruited specifically for the purpose but full-time staff can only be justified on economic grounds for a large-scale operation. In many cases existing personnel are given part-time responsibility for an orchard programme. If these responsibilities are added to a normal load of other activities and are given second priority to other work then the orchard programme must suffer. Orchard programmes need continuous detailed attention and even if the responsibility is part-time they will only be successful if the orchard work is given top priority.

What are the Expected Gains?

Einspahr (1972a) presented a comprehensive review of expected genetic gains. Additional data are presented in Table 7. Under favourable circumstances hybridisation can give the most spectacular gain. Clonal propagation can also give some large gains in a relatively short time. Polyploid breeding is uncommon, but seems particularly suited for increasing fibre length. Straight-forward selection normally produces slower gains but is the method which has to be used to maintain genetic gain over the long-term. Gain per unit-of-time is the most significant measure of effectiveness rather than gain per generation. Squillace *et al* (1972) have considered this and have calculated the value of early-testing in *Pinus elliottii* from this point-of-view. The correlation between early measurements and performance at harvesting age progressively decreases with younger material. The generation-span, however, is also reduced and as a consequence the gain per unit-of-time reaches an optimum at a certain age. This age will differ for different species and different methods of evaluation. In the case of *P. elliottii* Squillace *et al* (1972) suggests the optimum age to be about eight years. Such accelerated selection schemes can be very attractive. At least one major industry is putting a great deal of effort into developing such a scheme in which early selection heavily depends on measurements of physiological properties at the seedling stage.

Such accelerated selection schemes appear to be especially useful in connection with short-rotation fibre production (Einspahr, 1972b).

Factors For and Against Co-operative Programmes

The value of co-operative programmes is highest when the organisational unit is smaller than the basic geographic tree improvement unit discussed in the introduction, because the exchange of breeding

TABLE 7

EXAMPLES OF GENETIC GAINS EXPECTED FROM DIFFERENT METHODS OF GENETIC IMPROVEMENT

GAINS OBTAINED OR EXPECTED FROM VARIOUS SELECTION METHODS

Trait	Expected Gains, %	Species	Authors
Height	4–14	*Pinus taeda*	Stonecypher *et al* (1973), Swofford *et al* (1971), Zobel *et al* (1971)
	6–7	*Pinus elliottii*	Goddard (1973), Zobel *et al* (1971)
	17	*Pinus radiata*	Griffin (1970)
	46	*Pinus pinaster* (among provenances)	Hopkins (1960)
	6–32	*Pinus sylvestris*	Samuelson (1972)
	7–22	*Cupressus lusitanica*	Dyson (1969), Paterson (1966)
	6–24	*Eucalyptus* spp.	Castro Pasztor *et al* (1967), Castro Pasztor (1973)
Diameter	5–7	*Pinus taeda*	Stonecypher *et al* (1973), Zobel *et al* (1971)
	8–12	*Pinus elliottii*	Goddard (1973), Zobel *et al* (1971)
	4–20	*Pinus radiata*	Paterson (1966), Griffin (1970)
	6–26	*Cupressus lusitanica*	Dyson (1969), Paterson (1966)
Basal Area	18	*Pinus taeda*	Stonecypher *et al* (1973)
	11	*Pinus pinaster* (among provenances)	Hopkins (1960)
Volume	2–25	*Pinus taeda*	Stonecypher *et al* (1973), Zobel *et al* (1971), Swofford *et al* (1972)
	8–15	*Pinus elliottii*	Goddard (1973)
	10–15	*Pinus radiata*	Paterson (1966), Shelbourne (1973)
	38	*Pinus sylvestris*	Samuelson (1972)
	13	*Cupressus lusitanica*	Paterson (1966)
	10	*Pseudotsuga menziesii*	Silen (1969)
Survival	28	*Pinus sylvestris* (among provenances)	Koster *et al* (1971), Krick *et al* (1971)
Straightness	28	*Cupressus lusitanica*	Dyson (1969)
Fusiform rust infection	18–42	*Pinus taeda*	Stonecypher *et al* (1973)
Wood specific gravity	10	*Pinus taeda*	Stonecypher *et al* (1973)

GAINS OBTAINED OR EXPECTED FROM HYBRIDISATION			
Height	9–15	*Larix decidua* × *leptolepis* (*kaempferi*)	Langner *et al* (1966), Gothe (1967)
	29–79	*Pinus rigida* × *taeda* (gain over *P. rigida*)	Ahn (1963)
Diameter	9–18	*Larix decidua* × *leptolepis* (*kaempferi*)	Langner *et al* (1966), Gothe (1967)
	25–76	*Pinus rigida* × *taeda* (gain over *P. rigida*)	Ahn (1963)
Volume	125	*Populus glandulosa* × *alba*	Son *et al* (1972)
	123	*Populus koreana* × *nigra*	Son *et al* (1972)
	27	*Larix decidua* × *leptolepis* (*kaempferi*)	Langner *et al* (1966)
	3	*Larix decidua* × *leptolepis* (*kaempferi*)	Langner *et al* (1966)
Wood specific gravity	0.7	*Populus glandulosa* × *alba*	Son *et al* (1972)
	0	*Populus koreana* × *nigra*	Son *et al* (1972)
	−9	*Eucalyptus maideni* × *rabida*	Pryor *et al* (1964)
Fibre length	2	*Eucalyptus maideni* × *rabida*	Pryor *et al* (1964)
GAINS OBTAINED BY CLONAL PROPAGATION OF SELECTED INDIVIDUALS			
Height	6–21	*Populus deltoides*	Woessner (1973), Cooper *et al* (1973), Randall *et al* (1969), Farmer (1970)
	28	*Juglans nigra*	Beineke *et al* (1973)
	17–55	*Pinus radiata*	Burdon (1971)
Diameter	10–24	*Populus deltoides*	Randall *et al* (1969), Farmer (1970)
	37	*Juglans nigra*	Beineke *et al* (1973)
	7–86	*Pinus radiata*	Burdon (1971)
Stem weight	22	*Populus deltoides*	Farmer (1970)
Specific gravity	16	*Populus deltoides*	Farmer (1970)
GAINS OBTAINED BY POLYPLOID BREEDING			
Volume	12–22	Triploid *Populus tremuloides*	Einspahr (1972b), Einspahr (1974)
	101	Triploid *Populus tremuloides* × *P. tremula* hybrids	Einspahr (1974)
Fibre length	12–32	Triploid *Populus tremuloides* and *P. tremuloides* × *P. tremula* hybrids	Einspahr (1970), Einspahr (1972b)
Wood specific gravity	−3 to 20	Triploid *Populus tremuloides* and hybrids	Einspahr (1970), Einspahr (1972b)

materials will be largely limited to such an area. Beyond this area the value of co-operative programmes is more dependent upon the exchange of information and the development of techniques.

In the following sections a few specific advantages are discussed in more detail.

Exchange of Information and Plant Material

Everyone has his own way of doing things and the sharing of techniques and experiences of many people can be of great benefit (Zobel, 1973; Goddard, 1973; Blair, 1973). Information can be exchanged between university and industry and *vice versa* and also among industries.

Through co-operation many organisations can pool their parent tree selections and thus greatly enrich the store of materials available in a certain region. By the same token through the exchange of materials the number of selections required by any single co-operator can be reduced (Goddard, 1973; Blair, 1973).

Broad-scale Development Research

By co-ordinating the efforts over a large region the effectiveness of such programmes is greatly increased. For instance, effective fertilizer and irrigation schedules and insect control measures can be determined more quickly and for about the same amount of effort which would be required for a single individual (Goddard, 1973).

Technical Assistance

By pooling financial resources it is possible for co-operators to secure high-level technical assistance which would otherwise be unavailable (Zobel, 1973). A small or medium-sized organisation could not fully employ a trained geneticist or breeder but a number of organisations with a combined land area of a million hectares, for example, could very well justify the expenditure.

Co-operative Provenance Tests

This is probably the most outstanding example of an effort where co-operation can be extremely successful. The International Union of Forest Research Organisations (I.U.F.R.O.) provenance trials of Scots pine and larch and the south-wide seed source study in the United States are three of many good examples. Eldridge (1973) quotes similar success obtained by co-operative provenance testing in Australia.

Reduction of Genetic Diversity

Potential disadvantages of co-operative programmes are those relating to the exchange of plant material which, although they can result in increased genetic diversity, alternatively may result in a reduction of diversity (Goddard, 1973) if the material is too widely exchanged within a geographic area, and if individual co-operators do not contribute an equable and sufficiently large number of tree selections. For instance, if twenty co-operators serving an area of 4 million hectares each select one tree and exchange these among themselves, the individual orchard would have a reasonable genetic base. The fact that only twenty genotypes will provide all the future germplasm for such a huge area does not bear thinking about!

People Problems

When many people become involved in a single effort, "people problems" always arise and it is difficult to ensure that everyone works together and carries their full weight (Zobel, 1973). Fortunately in most areas a true spirit of co-operation has been engendered and most programmes have been quite successful.

Over-dependence on Outside Assistance

Especially where a large organisation is part of a co-operative programme it is possible to become over-dependent on the technical guidance provided through the co-operative programme, particularly where the scope of its own operation is adequate to support an individual approach. By necessity co-operative programmes encourage the use of standardised procedures to facilitate data collection, statistical analysis, and the smooth running of the co-operative. If over-done, however, the uniform approach will discourage and stifle innovation.

Conclusion

Every organisation which undertakes an orchard programme must develop its own strategy from the wide array of available choices in order to meet its own peculiar problems. Success rarely comes as the result of a moment of grand inspiration, but rather from the careful completion of each step leading to the final result. For a project to be successful each step must be well done and only if a high standard of professionalism and workmanship are maintained over several decades will satisfactory achievements be made.

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CHAPTER 3

SEED ORCHARD DESIGNS

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Introduction

This chapter is concerned with aspects of seed orchard planning related to initial planting distances; planting patterns; number of clones or families; type of planting material—clones or seedlings; and the planting design. Information has been obtained from 50 co-workers representing 21 countries throughout the world and to whom I am most grateful. Additional information on the number of ramets used per clone, the size of specific orchards and the total area under orchards in different countries has been excluded, since these are primarily economic rather than design considerations. The number of ramets per clone, unless required by a particular design, is generally a function of the number of clones, between-plant spacings, and the area of the site; and when limiting only affects the orchard size.

Matters concerned with the isolation of orchards from external contaminant pollen sources and thinning are dealt with in Chapter 5.

Initial Planting Distance

Clonal Seed Orchards

Planting distances of between 2 metres and 16 metres in both directions have been reported and both extremes have been experimentally tested with Scots pine (*Pinus sylvestris*) in Hungary. However, an initial spacing of five to six metres has been used in most orchard work throughout the world. This "normal" planting distance appears to reflect the ground-cover management practices in most countries and is more often related to the available equipment for tending the ground between rows than to the vigour and general habit of growth of the species.

At present there is a trend towards wider initial spacings since it is now generally accepted as being more economic in the longer-term to accept lower early seed-yields than to systematically thin expensively raised grafts before they are fully productive. This growing trend has been accelerated since it is seldom feasible or worthwhile to shape and keep the plants small by crown-pruning. Furthermore, because reliable progeny-test and flowering data, on which to base a programme of early roguing, is rarely available, many orchards would have to be thinned in the absence of this basic guidance information. (See also p. 124).

Seedling Seed Orchards

In seedling seed orchards the initial planting distances are normally much less than in clonal orchards; they range from 0.6 metres to 6 metres in both directions with the majority at 1½ metres to 2 metres. As in clonal orchards the spacings are often linked to the working widths of available inter-row, ground-tending machinery. Because the available number of seedlings from each family is seldom limiting, it is common practice to use large numbers of individuals per family-plot; thus providing better opportunities for within-plot roguing at a later stage.

Some orchards have narrow spacings within the family plots and wider ones between plots as, for example, in an Australian *Pinus elliottii* orchard which is based on 4-plant plots having a within- and between-plot spacing of 1.8 metres and 6 metres respectively.

Planting Pattern

A square or rectangular arrangement of plants is often used. A rectangular arrangement provides access for machinery between the more widely-spaced rows and the lines of plants with narrow inter-row spacings are sometimes aligned in an east to west direction to take full advantage of the sun. Square patterns are more common, they follow the long established traditions of commercial fruit growers and are well adapted for mechanical between-row tending in two directions.

A triangular arrangement (see Diagram 7) was recommended by Langner (1952/1953) because of the theoretical advantage of a graft in the middle of a hexagon having more crown-space than that provided in the centre of a square. However, this arrangement has not been adopted on any scale.

Number of Clones or Families

Most clonal orchard designs are based on between 20 and 50 clones. Quite frequently the recommended numbers are higher than those actually used in practice because of difficulties associated with finding sufficient plus trees, or clonal failures which occur during propagation and to permit roguing on the basis of progeny test results. At present there is a general world-wide trend towards using larger numbers of clones due to the increased awareness of the dangers associated with having too narrow a genetic base at the outset. However, in most countries these ideas have still to be translated into practice. Recently Lindgren (1974) has argued on theoretical grounds that orchards composed of selected progeny tested clones can be satisfactorily based on fewer than ten clones.

In certain cases the acceptable number of clones may be lower as, for example, in certain orchards designed for the production of hybrid seed. These may be designed on the basis of using one clone as the female parent and several pollinator clones. In Britain there are plans to establish several bi-clonal orchards using highly selected clones with well-matched flowering periods and high specific-combining-abilities; it is the intention to pool the seed from all of these orchards to provide seed mixtures with a broad genetic base.

Orchards with much larger numbers of clones have been reported, with up to 700 in Norway; these usually serve also as clone archives (*Syn.* tree banks).

Perhaps due to the scarcity of progenies derived from controlled crosses, most of the seedling seed orchards established before 1973 have been based on open-pollinated families in which 100 to 200 families are represented. So-called "seedling seed orchards" based on commercially obtained seed, or special provenance collections, should really be regarded as seed stands or "seedling seed stands"; the term "orchard" is deprecated and should be discouraged in these cases.

Clonal or Seedling Planting Material

The great majority of orchards established before 1973 are based on clonal material but there is a growing trend towards using seedling material, and particularly for those species which flower at an early age, despite the fact that the opinion of most breeders is towards favouring clonal orchards. A large part of Volume 13 of *Silvae Genetica* (1964) was devoted to a discussion of the relative merits of the two approaches. Toda (1964), who acted as moderator for this discussion, finally recommended clonal orchards mainly on the grounds that the success of seedling seed orchards largely depends on the value of early-selection which is made at a time when juvenile-mature correlations may be low. This recommendation is supported by more recent evidence (Wilusz and Giertych, 1973), although Nanson (1972) claims advantages for seedling orchards for species of unknown genetic composition and for which breeding programmes have begun with inferior material. The genetic gain is similar from both methods when the heritability of a trait is high and according to Toda (*op. cit.*) only very high vegetative propagation costs, in comparison with artificially controlled pollination costs, together with very low heritabilities could justify the use of seedling seed orchards.

Shelbourne (1969), in a detailed paper, showed the relative expected theoretical genetic gains from various tree improvement strategies using relative time-scales and heritability data for *Pinus radiata* in New Zealand for the basis. The greatest gains for characters with high or low heritabilities, for example, stem straightness and stem diameter respectively, were predicted for second-stage clonal orchards. Shelbourne expects that clonal orchards, combined with a programme of progeny testing, are as valuable as seedling orchards based on plants derived from artificial pollinations, and that untested clonal orchards are as valuable as seedling orchards based on plants derived from open-pollinations. Both costs, the associated benefits, and the time factors are very important considerations when choosing the best method for a given species. The use of highly selected progenies results in relatively more genetic gain for traits which have a low rather than a high heritability. Shelbourne particularly stresses the value of clonal tests based on rooted cuttings; when non-additive variance, topophytic, and propagation interaction effects are low, clonal tests provide a short-cut method for tests of general-combining-ability. The predicted high gains to be derived from breeding outstanding clones suggests that renewed and greater efforts should be made to solve outstanding problems associated with vegetative propagation so that these methods can be fully exploited. This trend, which is already evident in *P. radiata*, could, as in the case of *Populus* species, eventually eliminate the need for seed orchards. For the present, however, progeny-tested clonal orchards appear to be the cheapest and the most effective method for most tree improvement programmes.

More recently Masters and Beineke (1973) have returned to the controversy in connection with black walnut (*Juglans nigra*) orchards. Reviewing literature on the subject they similarly conclude that clonal orchards are more advantageous in spite of the fact that black walnut is difficult and expensive to graft, and that seedlings flower very early. They list the following advantages of clonal orchards:

1. Preservation of good genotypes.
2. Maximum genetic and profit gains.
3. Dealing with known genetic material and combining-ability.
4. Grafts flower earlier.
5. Easier to manage for increased crown growth and flowering control.
6. Pressures to rogue for early seed production are less.
7. Problems with related matings are less.

8. Full-sib progeny tests will eventually be available to verify any early roguing.
9. Improved seed is available before progeny testing is completed.
10. Clone archives combined with an orchard eliminate the initial need for large numbers of clones.
11. None of the problems associated with combining a seed orchard and a progeny test exist.

However, it is really item 11 which still keeps the option for seedling seed orchards open, because it is necessary to progeny test the components of clonal orchards and since the progeny test can, at little extra cost, be eventually converted into a seedling seed orchard simply by removing the poorer within-family plot trees (or, the poorer families entirely), during normal thinning operations, it seems highly probable that the number of such orchards will increase in parallel with the establishment and testing of further clonal orchards.

Designs

In this section the term "clone" or "ramet", as applied in clonal seed orchards, are used for descriptive purposes. Similar designs can be used for seedling seed orchards, in which case the word "progeny" should be substituted for "clone" and "family-plot" for ramet. Family-plots can consist of a single tree or groups composed of several trees.

Pure Rows

In some of the earlier orchards, and occasionally even today, the design is based on planting pure rows of individual clones. The design has several disadvantages, notably: the increased risk of inbreeding within clones; and the obvious problems of very uneven spacing which result if undesirable clones are later detected and have to be removed.

Chessboard

A chessboard arrangement for bi-clonal orchards can be obtained simply by alternating the two selected clones in each row and column of the orchard. Their main value lies in the production of hybrid seed when previous observation of flowering behaviour and progeny tests have revealed male-sterility in one clone and high advantageous specific-combining-ability from the only feasible cross.

Completely Random

The complete randomisation of all the available ramets of all clones between all the available planting positions on the site is the simplest of all designs to plan on paper; it can, however, pose practical management difficulties associated with planting, or, on-site grafting, and the re-location of individual ramets at a later stage and particularly when the orchard is large and contains many clones. If systematic thinning is to be practiced, as in Sweden, by removing every second tree or every second row, the design can be further refined by making separate randomisations for the ramets which are to remain and for those to be removed in thinning.

Quite frequently certain restrictions are imposed on the randomisation, for example, that no two ramets of the same clone may be planted in adjacent positions within rows or columns, or where they will occur in adjacent diagonal positions; or, that at least two different ramets must separate ramets of the same clone. These restrictions are usually arranged by manipulating the positions of the ramets on the plan, thus making the design no longer truly random, however, such deviations from randomness are seldom great. These designs have been employed, among other places, in Australia, Canada, Nigeria, Poland, South Africa, Sweden and the U.S.A.

At one time in the U.S.S.R. the scions were completely randomised before grafting and records of the clonal origin of each graft were not kept. Sometimes several scions from different clones were grafted on to a single stock. These procedures are no longer recommended or practiced in more recent times.

Randomised Complete-block

For this design the area is first divided into equal blocks each sufficient in size to contain one ramet of each clone or a multiple of that number; the ramet positions within each block are completely randomised and then manipulated to avoid having similar ramets in adjacent planting positions. Each block is randomised independently, taking care that the restrictions imposed hold true along the interfaces of the block edges. As with the completely random design this design can be adapted for systematic thinnings by superimposing several randomisations within the same block. The design is commonly used in Australia, Canada, Denmark, Norway, South Africa, U.S.A., U.S.S.R., West Germany, Yugoslavia, and elsewhere.

Fixed-block

Some orchardists have used a systematic layout in which a fixed single-block design is replicated over the entire area as, for example, in North Carolina, U.S.A. The value of the design largely depends upon the size of the basic block, its content of ramets per clone and their arrangement within the block.

Rotating-block

To avoid replicating the same arrangement of ramets in consecutive blocks a systematic shifting of the clonal arrangements within each replication of the block can be used as in North Carolina and Georgia, U.S.A.; and in British Columbia, Canada. This design, which is illustrated in Diagram 1, provides for limited changes in the composition of neighbourhoods around each ramet. It was first proposed by B. F. Malac (1962)

(*a*)
Original block

1	2	3	4
5	6	7	8
9	10	11	12
13	14	15	16
17	18	19	20

(*b*)
First repetition with first systematic shift

16	1	2	3
20	4	6	7
5	9	8	11
10	13	14	12
15	17	18	19

Diagram 1. Rotating-block design. Provided by R. J. Weir, U.S.A.

Reversed-block

Yet another modification of this approach is to use paired blocks with a reversed sequence of clones within them and with a different randomisation for each block pair. This is used for the elm species *Ulmus carpinifolia*, in the Netherlands, which is a self-sterile species and therefore does not require any isolation between ramets of the same clone. The design allows for systematic thinnings. (See Diagram 2).

7	11	4	3	2	1	8	7	12	3	
6	12	5	7	10	8	6	4	10	5	
5	12	6	9	5	5	9	1	11	2	
4	11	7	6	8	10	7	2	11	1	
3	10	8	1	1	2	3	5	10	4	
2	9	9	2	11	4	12	3	12	7	8
1	8	10	3	12	4	11	6	9	9	6

Diagram 2. Reversed-block design. Provided by W. Kriek, Holland.

Unbalanced Incomplete-block

Sometimes the random block arrangement is used with a fixed number of grafts per block, as for example, twenty grafts in Hungary, and regardless of the number of clones available for the orchard. In this arrangement the same set of clones is not always planted in each block and, therefore, the blocks cannot be treated as replicates for experimental comparisons of orchard treatments which is one of the main advantages of the complete block design.

A second approach to the unbalanced incomplete-block design is to use blocks in which any clone used is represented by one or several ramets but with the blocks varying in size according to the availability of clones with a sufficient number of ramets. A similar design has been recommended for *seedling* seed orchards of *Pinus pinaster* in France (Baradat *et al*, 1970).

Balanced Incomplete-block

This design, which was recommended by Langner and Stern (1955), provides the opportunity for randomly mixing the clones and also the possibility of comparing the performance of the various clones most effectively. The mathematical principle behind the method is that where: t = number of treatments (clones); k = number of ramets per block; b = number of blocks; and r = number of replicates (ramets per clone), a block is considered incomplete if $k < t$ in the design. The design is considered balanced when any two clones occur together in the same number (n) of blocks.

In a balanced incomplete-block design the following relationships hold:

$$n(t-1) = r(k-1) \tag{1}$$

and

$$rt = bk \tag{2}$$

***(a)* Theoretical plan**

1	2	3	2	4	10	3	8	9
1	2	4	2	5	8	3	9	10
1	3	5	2	5	9	4	5	9
1	4	6	2	6	7	4	5	10
1	5	7	2	7	9	4	6	9
1	6	8	2	8	10	4	7	8
1	7	9	3	4	7	5	6	10
1	8	10	3	4	8	5	7	8
1	9	10	3	5	6	6	7	10
2	3	6	3	7	10	6	8	9

***(b)* After randomisation within and between blocks**

2	3	1	10	6	5	10	8	1
5	9	4	2	9	7	3	9	10
7	6	10	8	3	4	2	5	8
3	1	5	9	6	8	10	4	2
8	4	7	3	10	7	5	1	7
5	9	2	4	1	2	8	9	3
1	6	8	5	6	3	4	6	1
3	4	7	2	8	10	7	5	8
10	9	1	10	4	5	6	9	4
7	2	6	9	7	1	2	3	6

Diagram 3. A Balanced Incomplete-block Design where $t = 10$; $k = 3$; $r = 9$; b = 30; $n = 2$. From Langner and Stern (1955).

The number of incomplete block designs that can be constructed for a given set of t, k, b, and r values is equal to the number of possible solutions of the above relationships (1) and (2). Solutions to these can be obtained from most published comprehensive collections of statistical tables.

The positions of ramets within blocks and of blocks within an area can be randomly assigned, but in practice the randomisation has usually been modified in order to satisfy restrictions on the proximity of ramets of the same clone.

The designs have the following advantages: provision is made for the permutation of neighbourhoods within blocks, thus favouring panmixis; they are better-suited for experimental comparisons of seed orchard treatments and for comparative clonal studies. Their main disadvantages are: they are only suitable for certain fixed combinations of clone numbers and number of ramets per clone (replicates), thus they have to be repeated several times over the orchard area; they are unsuitable for systematic thinnings which would spoil the design. An example of such a design from West Germany is illustrated in Diagram 3.

Cyclic Balanced Incomplete-block

A special case of the balanced incomplete-block design is the one in which there are four ramets per block ($k = 4$) planted in a square and in which the blocks are developed from each other in a cyclic way by adding or subtracting a fixed value from the clonal number. Freeman (1969) has provided solutions for such designs with clone numbers (t) = 17–22, 24, 25, 28, 29, and 31–34. An example is illustrated in Diagram 4. The designs have the advantage that neighbourhood combinations can occur in any direction with a more or less similar frequency.

5	15	9	27	24	8	20	29	6	2
4	12	1	3	10	30	16	17	18	23
6	16	20	28	25	9	21	30	7	4
5	13	2	4	11	31	17	18	19	24
7	17	11	29	26	10	22	31	8	5
6	14	3	5	12	1	18	19	20	25

↓ etc.

Diagram 4. A Cyclic Balanced Incomplete-block Design where $t = 31$; $k = 4$; $r = 20$; $b = 155$; and $n = 2$. From Freeman (1969).

Directional Cyclic Balanced Incomplete-block

During the pollination period of *Cupressus lusitanica*, in East Africa, the wind-direction is governed by the predictable tropical wind-system. Under these circumstances a special modification of the balanced incomplete-block design was developed which aimed at permutating all the up-wind neighbours. Balanced incomplete-block designs with three ramets per block ($k = 3$) exist for a number of clone numbers (t) and Freeman (1967) has adapted these for seed orchards, using a layout with three rows and as many columns as needed. Designs have been constructed for 5–20, and 22, 25, 28, 31, 34, 37, and 40 clones in which each fulfils the conditions that every pollen parent should occur once in positions to the north-east, east, and south-east of a given seed tree parent in regions where a predictable prevailing wind comes from the east. (Freeman (1967), Dyson and Freeman (1968)). An example of such a layout for 13 clones is illustrated in Diagram 5, in which only the central rows are considered as seed parents. The design is cyclic since consecutive columns of three clones are constructed from the adjacent ones by adding or subtracting a fixed number.

Seed to be collected from these rows

9	7	5	3	1	12	10	8	6	4	2	13	11	9
→ 12	10	8	6	4	2	13	11	9	7	5	3	1	12
8	6	4	2	13	11	9	7	5	3	1	12	10	8
11	10	9	8	7	6	5	4	3	2	1	13	12	11
→ 13	12	11	10	9	8	7	6	5	4	3	2	1	13
5	4	3	2	1	13	12	11	10	9	8	7	6	5
7	9	11	13	2	4	6	8	10	12	1	3	5	7
→ 3	5	7	9	11	13	2	4	6	8	10	12	1	3
6	8	10	12	1	3	5	7	9	11	13	2	4	6
10	11	12	13	1	2	3	4	5	6	7	8	9	10
→ 2	3	4	5	6	7	8	9	10	11	12	13	1	2
4	5	6	7	8	9	10	11	12	13	1	2	3	4

Wind direction →

Diagram 5. Directional Cyclic Balanced Incomplete-block Design when $t = 13$; $k = 3$, $r = 12$, $b = 52$ and $n = 2$. From Freeman (1967).

This design can be used for orchards which are only three rows wide and planted parallel to the prevailing wind direction. It can be readily adapted for use on a wide range of irregular-shaped sites but it is very wasteful since seed can only be collected from about thirty per cent of the ramets.

Balanced Lattice

A special case of the balanced incomplete-block design, known as the balanced lattice, arises when $t = k^2$. In it the following relationships hold:

$$b = k(k + 1)$$
$$r = k + 1$$
$$\text{and } n = 1$$

Balanced lattice designs can only be used when the number of clones is a square of a whole number. The advantage over the balanced incomplete-block designs is that randomisations can also be made of blocks within replicates, and that simple orthogonal Latin squares can be used in the basic design. An example is shown in Diagram 6. These designs have been tried in the U.S.A. and West Germany.

Permutated Neighbourhood

La Bastide (1967) has developed a computer programme which provides a design, if feasible, for a set number of clones, ramets per clone, and ratio of rows to columns. There are two constraints; first, that there is a double ring of different clones to isolate each ramet of the same clone (which are planted in staggered rows); second, that any combination of two adjacent clones should occur in any specific direction once only—see Diagram 7. The production of the design by computer is very expensive on computer time, but already several

1	2	3	4	5	1	6	11	16	21	1	7	13	19	25
6	7	8	9	10	2	7	12	17	22	21	2	8	14	20
11	12	13	14	15	3	8	13	18	23	16	22	3	9	15
16	17	18	19	20	4	9	14	19	24	11	17	23	4	10
21	22	23	24	25	5	10	15	20	25	6	12	18	24	5
1	12	23	9	20	1	17	8	24	15	1	22	18	14	10
16	2	13	24	10	11	2	18	9	25	6	2	23	19	15
6	17	3	14	25	21	12	3	19	10	11	7	3	24	20
21	7	18	4	15	6	22	13	4	20	16	12	8	4	25
11	22	8	19	5	16	7	23	14	5	21	17	13	9	5

Diagram 6. An example of a Balanced Lattice Design when $t = 25$; $k = 5$; $r = 6$; $b = 30$ and $n = 1$. From Cochran and Cox (1950).

designs have been obtained for small blocks, for example, composed of 30 clones and having 10 ramets per clone; which can then be replicated over the seed orchard area. When this is done the two constraints may not always apply at the inter-face between blocks.

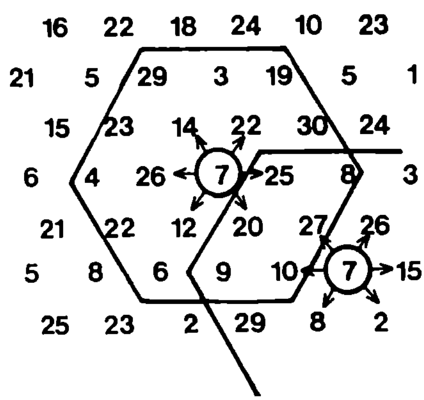

Diagram 7. A fragment of a Permutated Neighbourhood Design for 30 clones. With the restrictions on randomness employed by la Bastide (1967) in his computer design, viz., (i) 2 rings of different clones isolate each ramet, and, (ii) any combination of two adjacent clones must not occur more than once in any specific direction.

Ideally the design should be constructed for $r = t - 1$ which would ensure that every clone has every other clone as a neighbour once in each of the six possible directions. Thirty clones would, therefore, require 29 ramets per clone or a total of 870 grafts; whether such a large and complicated design has been created is unknown. Even so, the small blocks which have been developed are, at the moment, the best designs available for ensuring, at least in theory, the maximum permutation of neighbourhood combinations and the minimum production of full-sibs in the orchard progeny. These designs, which have been used in Holland and Ireland and have been recommended in several other countries, are available from J. G. A. La Bastide, Forest Research Station "De Dorschkamp", Wageningen, Holland.

A less-demanding design, but based on a similar principle, is used by Pawsey in Australia. In this case the restriction on randomness is confined only to the three up-wind neighbours of any ramet; these three are permutated to give each possible combination an equal chance of being obtained—see Diagram 8.

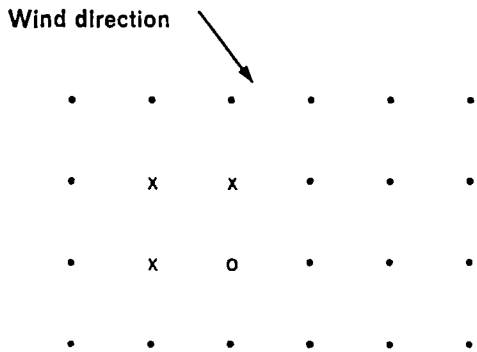

Diagram 8. Part of a Permutated Neighbourhood Design with the constraint on randomness that the three up-wind neighbours (x) of any ramet (o) are permutated. Used by C. K. Pawsey, Australia.

Systematic Designs

The first systematic design was proposed by Langner (*op. cit.*) for ten clones, and is based on a maximum distance of separation between the ramets of each clone equal to $\sqrt{10}$ multiplied by the planting distance. The method simply involves running the clones consecutively by numbers down a row and repeating the process in each succeeding row but always re-starting the process under a given clone in the preceding row. The design is unsuitable for systematic thinnings, but even so it is still occasionally employed in its original form (van Buijtenen, 1971). The present author has expanded the scheme to cover any number of clones between 9 and 65, and has specified the clone under which clone No. 1 is to be positioned in each consecutive row; the arrangements ensure that systematic thinnings are possible (Giertych, 1965). The clone numbers, which provide a quadratic scatter of ramets and are all odd sums of two squares, are the ones recommended for use (see Diagram 9).

Subsequently the system was further expanded for all such numbers between 5 and 313 (Giertych, 1971). The design: fits any orchard size or shape; rows or plots of the orchard can easily be used as replicates for experiments on the value of treatments; facilitates the location of clones during cone collection; maximises the separation of ramets of a clone ($\sqrt{t}$ planting distances); maintains the even representation of clones, and the optimum scatter, after any number of systematic thinnings; leaves a systematic distribution of the undesirable gaps after clones have been rogued; permits the pairing of compatible clones, or, those having useful combining-abilities when such information is available; and is very easy to lay out.

The only major disadvantages of the design are that: by having fixed neighbourhoods, it does not favour panmixis; and that it produces more full-sibs in the progeny than most other designs—but less than from a general collection of seed from a stand based on a number of trees equal to the number of clones in the orchard. The closer relationship of the progenies may raise the subsequent inbreeding risks between them and therefore it could be more dangerous to collect seed from plantations derived from orchards of this kind. However, a similar but smaller risk occurs to some extent with all seed orchard seed.

This design has been used in Australia, Canada, Japan, Poland, U.S.A., and U.S.S.R.

1	2	3	4	5	6	$\underline{7}$	8	9	10	11	12	13	1	2	3
6	$\underline{7}$	8	9	10	11	12	13	1	2	3	4	5	6	$\underline{7}$	8
11	12	13	1	2	3	4	5	6	$\underline{7}$	8	9	10	11	12	13
3	4	5	6	$\underline{7}$	8	9	10	11	12	13	1	2	3	4	5
8	9	10	11	12	13	1	2	3	4	5	6	$\underline{7}$	8	9	10
13	1	2	3	4	5	6	$\underline{7}$	8	9	10	11	12	13	1	2
5	6	$\underline{7}$	8	9	10	11	12	13	1	2	3	4	5	6	$\underline{7}$

Diagram 9. A Systematic Design for 13 clones. It is suitable for expansion in all directions and for any number of systematic thinnings. From Giertych (1965) and (1971).

Miscellaneous Notes

Polycross and Topcross Designs

Many tree breeders use the term "polycross" to describe the design of their orchards when they use a complete-block design in which there are as many blocks as clones ($t = b$) or some other system which aims to give each clone an equal chance to cross-fertilise with all the other clones. Several of the designs described above attempt to achieve this. To be precise a polycross design is one in which each clone is actually pollinated by a *balanced* mixture of pollen from all the other clones in the orchard. By this definition "polycross" only applies to artificial hybridisation studies in which all clones are tested by a balanced mixture of pollen from several clones. It is in this context that the term "polycross" was first proposed and its introduction into seed orchard terminology was unfortunate. Perfect polycross designs are impossible to construct and could never fully achieve a result which satisfies the definition. The term "polycross" should now be abandoned in the context of seed orchard designs; it should be replaced by a more accurate description.

Similarly a "topcross" design is one in which several maternal clones are fertilised with pollen from a single male parent, or, several paternal clones are used for the pollination of one maternal clone. Some bi-clonal or hybrid orchard designs approach this definition, but again it is preferable to restrict the use of this term to artificial hybridisation studies.

Hybrid Orchards

Orchards designed to produce hybrid seed commonly use a single female clone either, distributed systematically throughout the orchard area with several pollinator clones surrounding them, or, have the maternal clones in rows and the paternal clones randomised in the two adjacent rows. The latter practice has been used in Denmark and Holland.

Where hybrids are mass produced by artificial pollination, as in South Korea, the layout of the parental clones is obviously immaterial.

Outbreeding Orchards

Klein (1973) describes a Canadian *Pinus banksiana* seedling seed orchard which was established with the aim of maximising outbreeding. Twenty unrelated open-pollinated families from each of eleven geographic sources provided the basic material for the orchard which consisted of 24 blocks each containing eleven 20-tree plots. Each of the 20 trees are derived from a different family but from the same source and it is the intention that successive selection thinnings will eventually reduce each block to a single tree. Selection will, therefore, be amongst trees of the same geographic source but of little or no co-ancestry. Since each source is represented by only one plot in each block the mating within blocks will be predominantly between sources.

In Sweden, "provenance" orchards have been established for Norway spruce (*Picea abies*) and Scots pine based on clonal material from distant origins, the aim being to obtain heterosis in the resultant out-bred progenies (Andersson, 1960). As in most Swedish orchards a completely random design is used with a provision of a uniform residual number of ramets per clone after a systematic thinning.

Pollinator Clones

Scots pine grafts frequently produce regular female flower crops from the time of grafting onwards but pollen production is rarely achieved until after the seventh year. In order to take advantage of the potential early- and easily-harvested cone crops, tree breeders in Hungary have established temporarily an early male-flowering clone between the rows of the main orchard trees in one of their orchards. These pollinator trees will be removed as soon as the clones in the main orchard produce flowers of both sexes in abundance (E.R.T.I., 1970).

Van Buijtenen (1971) proposes to introduce several good pollinator clones into a systematic design on a permanent basis in order to ensure an abundant pollen supply.

Mixed Clonal and Seedling Seed Orchard

A Swedish orchard has been established composed of ten grafted clones of Swedish, Norway spruce plus trees, spaced at 8 metres × 8 metres intervals and inter-planted with seedlings from Central European provenances selected for frost-hardiness, and planted in rows between the grafts at 1.6 metre intervals (Andersson and Andersson, 1962).

Partial Planting in Second-generation Seed Orchards

To avoid the unnecessary cost of planting, and the later removal, of expensive clonal material in thinnings before full productivity is achieved, Weir (1973) has proposed that a quarter of the planting positions be left vacant. Alternate rows having alternate blank planting positions would be staggered so that each ramet would be surrounded by no more than three immediately adjacent neighbours (see Diagram 10). This procedure will delay the first orchard thinning for several years and with no adverse effect on the total seed production due to overcrowding.

x	x	x	x	x	x	x	x	x	x
x	–	x	–	x	–	x	–	x	–
x	x	x	x	x	x	x	x	x	x
–	x	–	x	–	x	–	x	–	x
x	x	x	x	x	x	x	x	x	x
x	–	x	–	x	–	x	–	x	–

Diagram 10. Staggered alternate half-filled rows in a seed orchard to delay the need for thinnings. From Weir (1973).

Evaluations of Designs

Various authors have stressed different aims as being of primary importance in the preparation of a seed orchard design. The two most commonly mentioned are: minimising self-fertilisation risks; and a provision for the maximum number of cross-fertilisation combinations. There are, however, other considerations and these are listed in Table 8 which summarises the advantages and disadvantages of the designs which have been described in this chapter.

Most orchards have been established using completely random, or random complete-block, designs modified by some transpositions of ramets to satisfy the need to ensure that ramets of the same clone do not occur in near proximity to each other. More recently there has been a trend towards the use of more refined designs, such as the balanced-lattice, the systematic and permutated neighbourhood designs. Table 8 should help when choosing the best design for any given set of local conditions or sequence of priorities.

TABLE 8

COMPARISONS OF THE SUITABILITY OF SEED ORCHARD DESIGNS FOR VARIOUS AIMS

	Design													
	In rows	Chessboard	Completely Random	Random Complete-block	Fixed-block	Rotating-block	Reversed-block	Unbalanced Incomplete-block	Balanced Incomplete-block	Cyclic Balanced Incomplete-block	Directional Cyclic Balanced Incomplete-block	Balanced Lattice	Permutated Neighbourhoods	Systematic
To avoid selfing	—	+	+	+	+	+	—	+	+	+	+	+	+	++
To favour panmixis	—	—	+	+	—	—	—	+	+	++	++	+	++	—
To permit systematic thinning without altering clonal composition	+	—	—	—	+	—	+	—	—	—	—	—	—	++
To permit use of orchard segments as replicates for other experiments	—	+	—	+	+	+	+	—	—	—	—	+	—	+
To permit comparisons of clone performance	—	+	—	+	—	—	+	—	+	+	—	+	+	—
To facilitate the re-location of clones for special cone collections	+	+	—	—	+	—	—	—	—	+	+	—	—	+
To permit expansion	+	+	+	+	+	+	+	+	—	+	+	+	—	+
To fit any orchard shape	+	+	+	—	—	—	—	—	—	—	+	—	—	+
To fit any number of clones and ramets	+	—	+	+	+	+	+	—	—	—	—	—	+	+
To utilise information on compatibilities, flowering times and combining abilities	+	+	—	—	+	—		—	—	—	—	—	—	+
Simplicity of design for non-mathematicians	+	+	+	+	+	+	+	—	—	—	—	—	—	+
Low design cost	+	+	+	+	+	+	+	+	+	+	+	+	—	+

Note: ++ = Highly suitable; + = Suitable; — = Unsuitable.

Most existing orchards have been established on the assumption that each clone and ramet, or, family-plot and seedling tree, in the orchard will: flower during the same period; will have the same cycle of periodic heavy flower production; be completely inter-fertile with all its neighbours and yield identical numbers of viable seed per plant; have the same degree of resistance to self-incompatibility; and will have a similar rate-of-growth and crown-shape as all other plants. It is common experience that this is never the case and it is not likely to ever be so. The successful breeder will be the one who diligently observes and assiduously collects all essential information on clonal behaviour, compatibilities and combining-abilities, and *translates* this information into practical terms by employing it in the next and subsequent generations of seed orchards. Such designs will make maximum use of the available data.

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VEGETATIVE PROPAGATION OF PLANT MATERIAL FOR SEED ORCHARDS WITH SPECIAL REFERENCE TO GRAFT-INCOMPATIBILITY PROBLEMS

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INTRODUCTION

Vegetative propagation of fruit, nut and ornamental plants has been successfully practised for over 2,000 years. In contrast, the practice has been used for the establishment of clonal seed orchards of forest tree species only during the last half-century.

Orchards of most tree species have been established with grafts although rooted cuttings have been used for a few other species (Libby *et al*, 1972). This chapter describes practical methods of vegetative propagation which have been used for the establishment of seed orchards of forest trees; no attempt is made to review all the methods of vegetative propagation which have been attempted by tree improvement workers. Graft-incompatibility, which has seriously hindered the establishment and management of some grafted seed orchards, is also discussed.

GRAFTING

Preparation of Rootstocks and Scions

Rootstock plants can be grown in pots, nursery beds or on the orchard site. Potted seedlings are convenient to handle for the mass-production of grafts and also, when raised in a glasshouse, for extending the grafting-season. They have the limitation that a pot-bound root system may develop and if corrective action is not taken the trees may later become vulnerable to wind-throw several years after out-planting in the orchard. Seedlings grown in nursery beds for *in situ* grafting are also well suited for mass-production grafting programmes and particularly where supervision is limited; they have the disadvantage that death following transplanting may be high. Seedlings established at pre-determined positions for subsequent grafting on the orchard site have the advantage that the successful grafts do not have to be transplanted and therefore both death and planting shock are reduced. However, grafting on the orchard site is very time-consuming and costly and the chances for error are greater than for the other alternatives because ramets of each clone are randomly dispersed over the site. Since each type of rootstock has advantages and disadvantages the planner must choose the system best suited to his needs with great care.

The condition of both the scion and rootstock at the time of grafting is an important factor for grafting success. Usually dormant scions and actively growing stocks are used, although for many pine species best results are achieved by grafting dormant scions onto dormant stocks. Freshly-collected scions normally give the best success rate but where such collections are impractical dormant scions, collected under dry weather conditions, can be collected several weeks in advance and stored in sealed plastic bags at temperatures of 1°–2° C until grafting time. Any surface water on scions collected during wet weather should be removed before cold-storage. For soft-tissue (soft-wood) grafting, in which the scion and grafting site on the rootstock are of the current year's growth, it is essential that the scions are freshly collected. Soft-tissue grafting has given variable results under orchard conditions, but has been very successful under the semi-controlled environment of glass- or plastic-houses. The principal value of soft-tissue grafting under glass-house conditions is that it allows the normal nursery and on-site season to be extended; an important consideration where there are few skilled propagators.

Ideally, the stock plants should be about 450 millimetres tall (range 300 to 600 millimetres) and it is essential that plants are healthy. Suitable nursery stocks are generally 1 + 1 transplants or 2 + 0 seedlings, and in northern temperate regions 1 + 1 + 1 transplants or 1 + 1 plants potted for a further year are more common. Obviously the size and age of plant is dependant upon species and the type of rootstock required, that is, whether for orchard or for green-house grafting.

Healthy scion material is also needed to achieve good grafting success. It is generally obtained from the upper crown of the ortet where shoots are more vigorous. In conifers, which bear terminal female flowers, scions from this position of the crown often contain female flower buds whereas scions from the lower crown, are less vigorous and often contain buds which include immature staminate strobili. However, observations have shown that pine grafts established with scions derived from the lower crown will, after about two years, produce numbers of ovulate strobili similar to those collected from the upper crown (R. C. Kellison per. comm.). Experiments have shown that better grafting results can be obtained when both rootstocks and the parent trees have been given fertilizers beforehand (Goddard *et al*, 1972).

Time of Grafting

The best period of the year for grafting is dependent upon the method of grafting, the species, and environmental factors at the place of grafting. Bench- or glass-house-grafting is less dependent on season than grafting on the orchard site or in the open nursery because rootstock growth can be manipulated. In all situations the success or failure of a grafting programme is highly dependent upon the co-ordination of the grafting operation with the optimum stage of plant activity. Out-of-door grafting in winter should be avoided since low, and particularly continuously low, temperatures adversely affect graft survival. Grafting success falls rapidly both as the time between grafting and the spring flush-of-growth increases, and also with increases in the number of excessively cold days to which grafts are exposed (Webb, 1961). For some species temperatures as low as $-1°$ C are not always fatal to grafts if they occur before the union of stock and scion cambial cells has taken place, but temperatures just below freezing point can be fatal when the contact layer between stock and scion is just forming. After a graft union has formed, freezing temperatures have a decreased effect on graft survival.

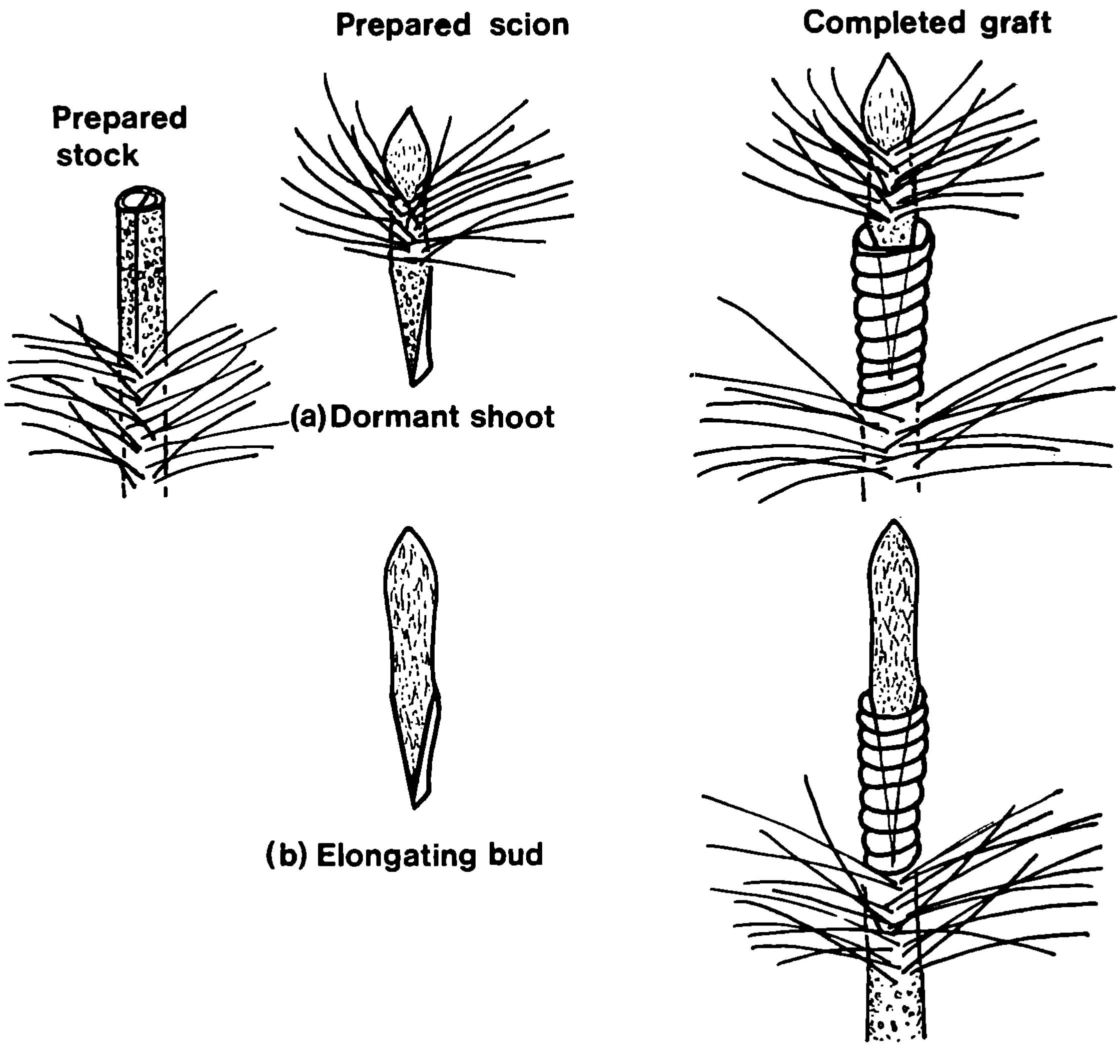

Figure 4. Steps in making a tip-cleft graft.

Normally the best period for grafting dormant scions and active stocks out-of-doors begins when the buds of the stock plants start to swell and continues throughout late-spring. When dormant scions are to be used on dormant stock, the period of grafting extends from about one month before bud-break to the time of bud-break on the stock. Soft-wood grafting is normally practised from late-spring to early summer; budding is generally done in mid-summer.

Types of Grafting

A wide variety of grafting methods have been described by Garner (1950); and many of these have been tried by workers in the field of tree improvement (Nienstaedt *et al*, 1958) for the establishment of seed orchards. Of them the most commonly used methods are cleft, side and bark grafts. Procedures for making these three types of grafts, together with the modified nurse-seed graft, which was developed for some large-seeded species, are described below.

Cleft Grafting

Cleft grafting is one of the oldest and most widely used methods of vegetative propagation. Grafts for seed orchards of many conifers (Copes, 1969; Kim, 1969; Magini, 1966; Mirov, 1940; Thulin and Faulds, 1966); pines, Douglas fir, larches, spruces, and some hardwood species (Kim, 1969; Thulin and Faulds, 1962) have been produced by "tip-cleft" grafting. The basic steps in making a tip-cleft graft are described below and are illustrated for pine in Figure 4.

(1) The tip of the leading shoot of a stock plant is removed and a straight, smooth split is cut vertically through the centre of the pith. (Top left, Figure 4.)

(2) The scion is prepared by making tapering cuts, of similar length to the vertical cut in the rootstock, on opposite sides of the basal part of the scion to form a wedge-shaped segment. Dormant shoots (a) or buds are commonly used as scions but elongating buds of pines (b) and new shoots of hardwood species are used as scions for soft-tissue grafting. (See Figure 4, two centre items.)

(3) The scion is inserted into the split so that the cambium layers of both scion and stock are well-matched; the scion is firmly and carefully bound in this position using a rubber band or vinyl tape (or "Scotch" tape) in order to avoid disturbing the contact layer. The cut surfaces are protected with a coating of grafting wax or other similar compound. (See Figure 4, two right-hand items.)

(4) Where necessary, and particularly in hot and sunny climates, the grafts can be covered with a polyethylene bag, in order to maintain high humidity, and/or given shade inside a lath-house. Alternatively, shade may be obtained by providing a second cover using a calico bag, a kraft paper bag with water-resistant glued seams, or an aluminium-foil chimney (Hearne, 1973).

(5) For pines, the polyethylene bags are removed about two to three weeks after grafting when the needles on the new shoot of the graft are about 6 millimetres long. Shading is gradually reduced from the same time onwards; the grafted plants should be fully hardened-off six weeks after grafting (Webb, 1961). Procedures for other species are similar to those for pines.

Side Grafting

Side grafting is a modification of the veneer grafting technique (see Figure 5, bottom) and has particular application to situations where the stock and scion have different diameters. Seed orchards of pines and yellow poplar in the United States (Zak, 1955; Webb, 1961; Churchwell, 1965; McAlpine, 1965), and of a number of hardwood and conifer species in many countries of Europe (Dormling, 1964; Fletcher and Faulkner, 1972; Laffers, 1960) have been established by this method. The procedures for side grafting are described below and are illustrated in Figure 5.

(1) A tapering downward cut from bark to pith is made in the rootstock at a point where the diameter of the rootstock most closely matches that of the scion. The cut is normally about 50 millimetres in length. (Figure 5, top left.)

(2) The scion is prepared by making tapering cuts on each side and culminating at the base of the scion to form a wedge-shaped segment. The length of the cut should be similar to that in the stock. (Figure 5, top centre.)

(3) The scion is inserted into the stock and at least one pair of exposed cambial layers is aligned. Then the union is securely held with rubber or vinyl tape. (Figure 5, top right.)

(4) Where necessary the grafts are covered with polyethylene bags and shaded as described for cleft grafting.

(5) Release procedures are similar to those described for cleft *except* that the upper part of the rootstock is gradually removed so that the scion eventually becomes the dominant part; in fast-growing species this may be as early as the time of final release.

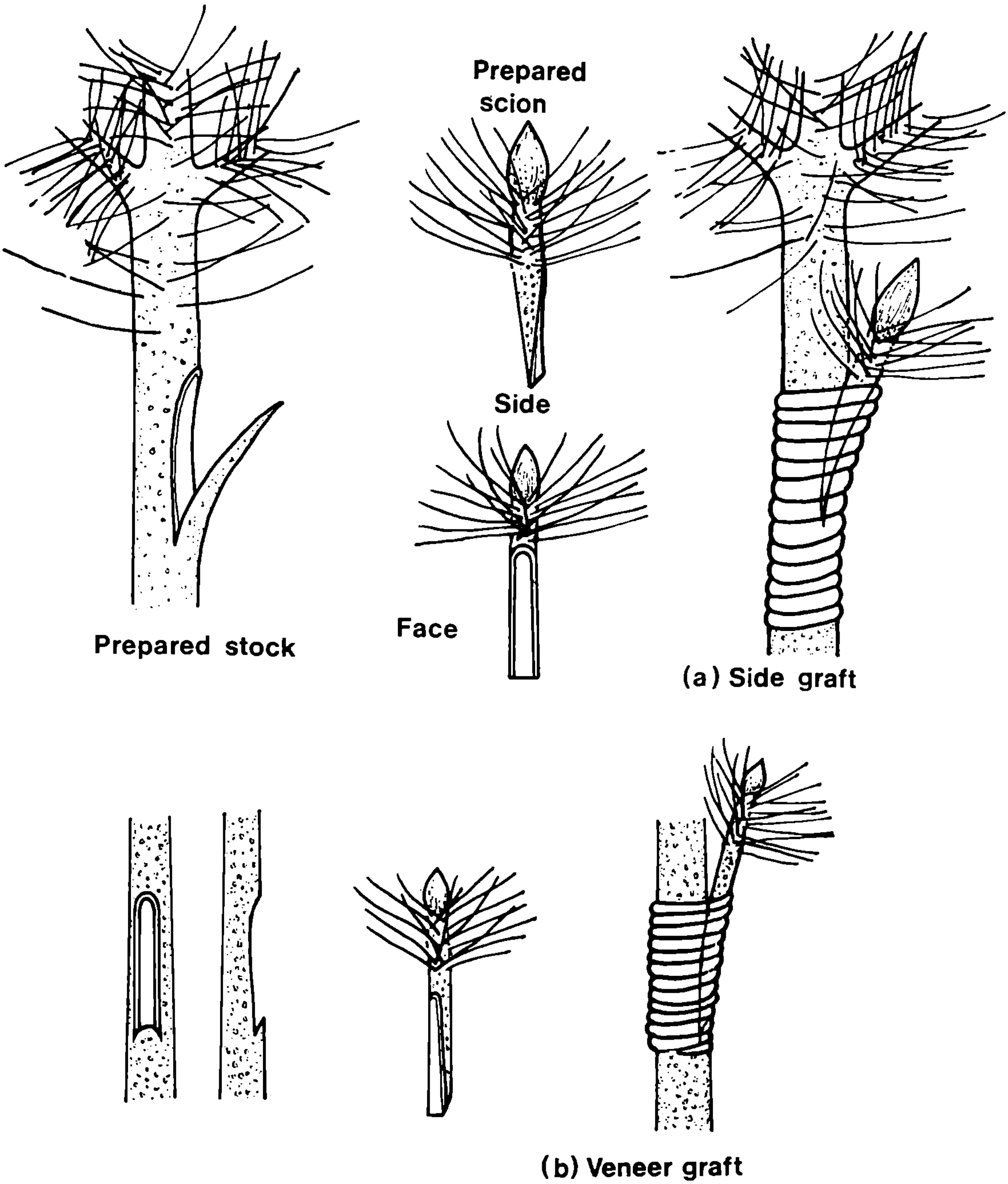

Figure 5. Steps in making side- and veneer-grafts (Webb, 1961).

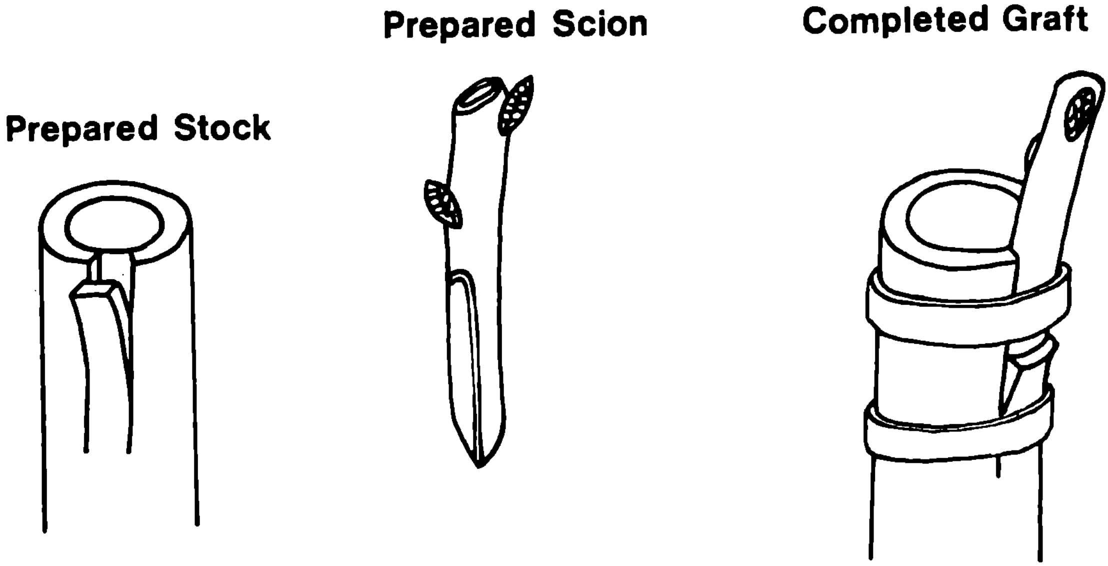

Figure 6. Steps in making a bark-inlay graft (Lowe and Beineke, 1969).

Bark Grafting

Bark grafting is rapid and simple and gives a high percentage of success particularly when used for hardwood species such as walnut and chestnut (Lowe and Beineke, 1969). The bark inlay-graft, which is a modified bark graft, is described below and is illustrated in Figure 6.

(1) Tops of rootstocks are normally removed just before grafting although in some species, for example, walnut, the cut is made 10 to 14 days before grafting in order to allow time for the stocks to "bleed" and so reduce graft failure due to excessive sap flow. At the time of grafting the tops of such stocks are again cut back to expose live wood.

(2) Two vertical, parallel cuts, 25 to 50 millimetres long, are made through the bark of the stock; the distance between cuts being equal to the width of the scion. (Figure 6, left.)

(3) The sliver of bark between the cuts should be carefully lifted back and the end two-thirds removed.

(4) The scion is prepared with a long sloping cut, 25 to 50 millimetres long, on one side and a second shorter cut is made on the opposite side at the basal end. (Figure 6, centre.)

(5) The scion is inserted into the groove, made by the removal of the bark, with the longer cut on the inside; the basal end of the scion is slipped under the remaining flap of bark.

(6) The scion is secured in position with a rubber or vinyl tape and the cut stub is given a protective coat of wax. (Figure 6, right.)

Modified Nurse-seed Grafting

The idea of nurse-seed grafting was originally developed by Moore (1963, 1964), for use with nut-tree species such as chestnuts, walnuts, oaks and pecans (Jaynes, 1965; Moore, 1966; Park, 1967a, b). Because of its general utility for propagating these species the method is now used on an operational scale (Goggans and Moore, 1967; Park, 1968). The procedures of the modified nurse-seed graft are as follows and are illustrated in Figure 7.

(1) Stratified seeds are sown in beds of moist peat-moss inside a glass-house at 21–27° C until well germinated.

(2) Using the seedlings as stocks, and just before the first leaves unfold, the plumule is removed immediately above the point where the cotyledons are attached. (Figure 7, left.)

(3) The hypocotyl is vertically and centrally split for about 13 millimetres, taking care not to damage the cotyledon petioles. (Figure 7, centre.)

(4) The scion, which should match the hypocotyl in diameter, is trimmed to form a thin wedge and is inserted into the split. Dormant or soft-wood scions having two or three buds and which are approximately 100 millimetres in length are used. (Figure 7, centre and right.)

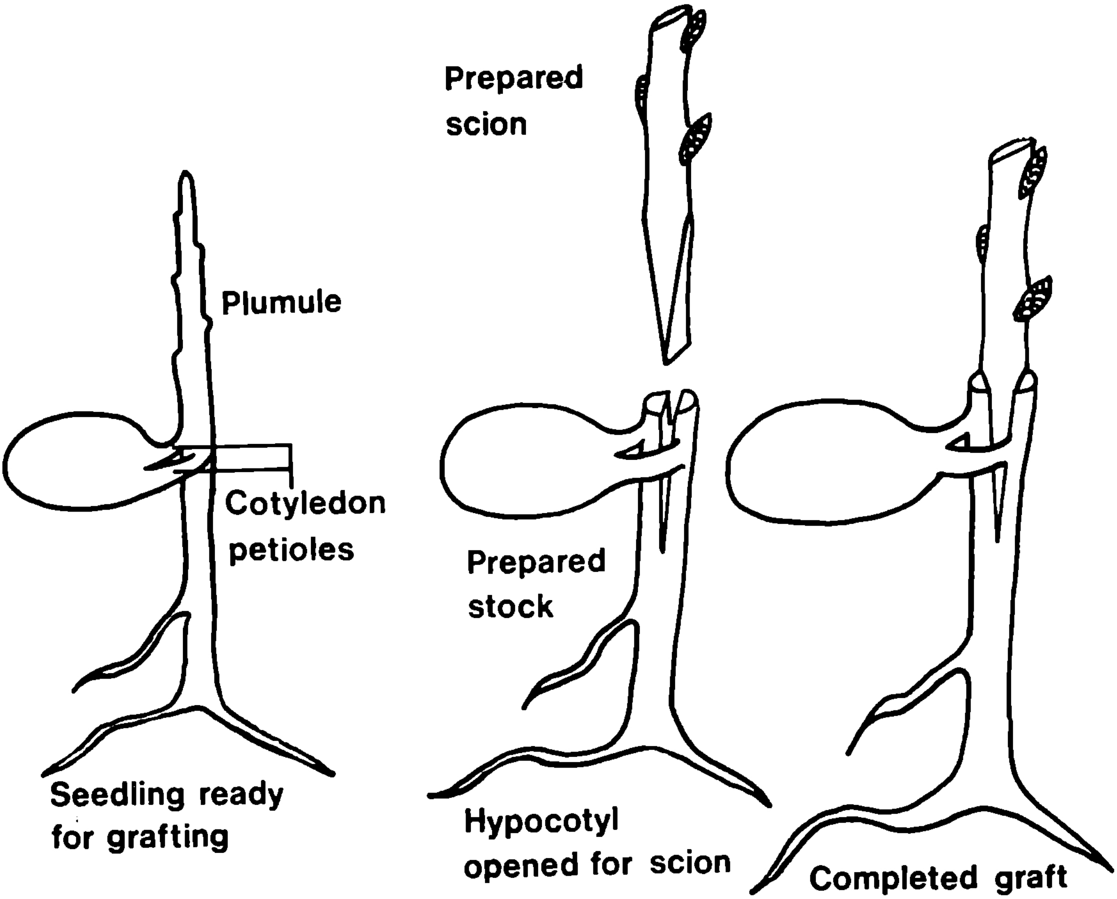

Figure 7. Steps in making a modified nurse seed-graft (Goggans and Moore, 1967).

(5) The graft union is firmly wrapped with ordinary untreated cotton twine taking care not to crush the tender hypocotyl.

(6) The graft is planted sufficiently deep, to ensure that the graft union is well covered, in a pot or frame containing moist potting soil or *Sphagnum* peat-moss. The plants are covered with a polyethylene bag, suitably supported to prevent damage to the growing-point. Shade is required and a temperature of 20° C is ideal.

(7) Grafts are released, by gradually removing the polyethylene cover, after leaves have developed.

After-care of Grafts

The tying materials used for binding the scions in position are released, to prevent stem-girdling, after removing any protective overhead covers. These operations are followed by periodically pruning back any side branches on the stock plant in order to avoid suppressing the development of the scion. Any branches or shoots directly competing with the scion are pruned first and side branches are gradually removed later. However, if growth of the rootstock, in comparison with that of the scion, is retarded, some branches should be left on the stock as an aid to the production of photosynthates. It may be necessary to support, with stakes, conifer grafts which have a tendency to a plagiotropic habit-of-growth, and until the plant can support itself in an upright position (Nienstadt *et al*, 1958); this is often the case with spruce and larch species and particularly where scion wood has been collected from horizontal or downward pointing branches.

Depending upon circumstances, spraying with insecticides and fungicides may be necessary to control any insects and diseases.

Transplanting Grafts

Generally pot- or nursery-raised grafts are transplanted as soon after the formation of a graft union as possible. This reduces both mortality and transplanting shock associated with delayed transplanting. However, if transplanting is delayed for management or other reasons the grafts should be pruned severely, or, sprayed with an anti-desiccant, both of which reduce plant water-stress after transplanting and until a balanced root system has been reestablished. Under severe drought conditions both watering and the erection of sun-shades and wind breaks may be necessary to promote survival.

To avoid the development of malformed root systems any root-ball which has developed on pot-raised grafts should, at the time of planting, be slashed vertically at four roughly equidistant points around its circumference; any curled taproot should also be severed at its point of contact with the pot base. Later deaths of plants in the orchards by root-girdling, or wind-throw may result if these precautions are ignored. Transplanting is usually carried-out with hand-tools but in large-scale operations it can be partially mechanised by using powered post-hole diggers for excavating the planting holes. Special tools attached to the front-end loader or the drawbar of a wheeled-tractor can be used for lifting nursery-bed grafts. Care must be exercised in maintaining a root-ball for some species, whereas other species, such as *Pinus radiata*, can be bare-root planted.

In many tropical and sub-tropical countries rootstocks are raised and grafted in thin plastic-film or wood-veneer containers and after "hardening-off" the whole plant is transported to the orchard site in the container; the container sides are slashed open before planting. This practice of raising containerised grafting planting stock is now being more widely used in temperate regions since it avoids transplanting-shock and leads to rapid orchard establishment.

Stock-scion Relationship

Horticulturists frequently use special rootstocks in order to control the final size and the rate-of-growth of grafts, and to induce early and prolific flowering in many fruit trees (Hartmann and Kester, 1964). Suitable clonal dwarfing-rootstocks, developed at the East Malling Research Station in England, provide a good practical example of the value of controlled scion growth by the correct choice of rootstock. If similar control of growth and flowering on grafts could be obtained by using special rootstocks for forest trees, both seed production and collection costs would be greatly lowered.

Although marked dwarfing effects from selected rootstocks have not been reported for commercial forest trees other rootstock effects on scion behaviour have been reported for several pine species. Shortleaf pine (*Pinus echinata*) grafted onto loblolly pine (*P. taeda*) rootstocks produced many more flowers, conelets and cones than others grafted onto slash pine (*P. elliottii*) or shortleaf pine rootstocks (Schmidtling, 1969). However, no height differences were found among shortleaf pine grafts established on rootstocks of different pine species (Allen, 1967).

The age of rootstock may affect graft survival and female flower production. In white pine (*Pinus strobus*) the survival was higher on grafted younger rootstocks and the production of female flowers was markedly higher on grafted older rootstocks (Ahlgren, 1962). Age of scion has also been reported to affect the growth of grafts. Grafts made with scions from 10-year-old trees grew much more rapidly than those made with scions from 30- to 35-year-old trees (Sweet, 1964).

The rootstock-scion inter-relationship of forest trees has not yet been critically studied and deserves much more consideration.

Graft-incompatibility

Graft-incompatibility, which manifests itself in several ways, has seriously impaired the establishment and management of clonal seed orchards of some forest tree species. Some trees of an otherwise graft-compatible species are extremely difficult or impossible to graft successfully. Other species exhibit early graft-incompatibility symptoms, often characterised by chlorotic, malformed foliage and an over-growth of the scion at the graft union, or by stem-fluting and the development of resin-filled bark blisters on both stock and scion. Others show good early development after grafting and only succumb to failure of the graft union and abnormal development several years later. The latter type is very common in Douglas fir (*Pseudotsuga menziesii*) where graft-incompatibility was 25 per cent by the fourth year, with an increase to 46 and 67 per cent respectively, by the eighth and ninth years after grafting (Copes, 1967a, 1968, 1970). Though losses of orchard trees by delayed graft-incompatibility was thought to be less in pines than in Douglas fir, severe problems have recently been encountered in seed orchards of *Pinus radiata* where up to 50 per cent of the 14-year-old trees are severely affected (Sweet and Thulin, 1973). Late incompatibility is also common to southern American pine species although not to the extent encountered with *P. radiata*.

The commonest external symptoms in Douglas fir is overgrowth of the scion above the graft union.

Originally this was thought to be due to the gradual development of a blockage in the phloem system, which impeded carbohydrate transport to the root system, eventually leading to death (Duffield and Wheat, 1964). However, later anatomical investigations have shown that incompatible grafts have wound-xylem areas in graft union zones, resulting from suberin development in the inner phloem of the cambium (Copes, 1970).

In *P. radiata* three typical forms of graft incompatibility were reported where neither suberin zones or wound-xylem areas were found: these were; xylem pitting occurring only below the graft union (most common type); xylem pitting present both above and below the union, and showing some overgrowth of scion; and a combination of the above two types with the rootstock xylem showing a number of resin pockets. For all types, the xylem pitting causes narrowing of functional phloem which results in translocation incompatibility (Sweet and Thulin, 1973).

Graft-incompatibility varies both within and among clones, some clones die as early as the autumn of the year of grafting, whereas others show good early survival without external incompatibility symptoms but develop incompatibility in later years. Such clones or trees offer more problems than those which show the symptoms early since they may occur in orchards which are in commercial seed production. Therefore, it has been an important task for seed orchardists to detect delayed incompatibility as early as possible and to substitute incompatible clones with compatible ones at an early stage. A simple method for the early detection of graft-incompatibility was developed in 2-year-old Douglas fir plants by Copes (1967b). In this an anatomical examination reveals the presence or absence of wound-xylem areas in the union at the start of the second year after grafting. He also found that a delay in the development of vegetative buds is also correlated with developing internal incompatibility in Douglas fir, suggesting that external screening methods could provide a valuable tool for Douglas fir seed orchardists (Copes, 1969).

Two practical methods which have been suggested for meeting incompatibility problems in Douglas fir and are now in use. The first is to check for incompatibility by microscopically examining the unions of ten to twelve grafts from each parent, only the compatible clones are used in seed orchards. The second is to make two grafts of each parent on a single rootstock. After the graft unions have formed one graft is sacrificed for an anatomical investigation (Copes, 1968). If found to be compatible, the second graft is maintained for the orchard but if incompatibility symptoms are observed then the clone is abandoned. Inter-stock grafting trials, using compatible clones as bridges between incompatible scions and nursery rootstocks, failed to reduce graft-incompatibility probably because of a three-way interaction among scion, interstock and rootstock (Copes, 1971).

The early detection method for incompatibility cannot be applied to *P. radiata* clones because any incompatibility symptoms occur in the phloem and not in the xylem and, therefore, an easy and early method of detecting incompatibility in this species is not available. Accordingly, serious consideration is now being given to raising clonal material from rooted cuttings (Sweet and Thulin, 1973), a method of propagation which is relatively easy to use on *P. radiata*. Root grafting (Hong, 1973), is an alternative promising technique which can solve some graft-incompatibility problems, In it the scions are grafted onto the excavated lateral roots of the same tree. Thus, it is possible to produce compatible grafts which have genetically identical roots and tops.

Denison (1973) has reported that stock-scion incompatibility in pines can be overcome to a certain degree by grafting incompatible clones onto rootstocks raised from seed derived from the same clone.

CUTTINGS

The age of the parent tree frequently has an overriding influence on the rootability of cuttings; rooting normally becomes progressively more difficult with increased age of the parent tree and many trees are impossible to root after they are 10–15 years old. Also there is usually a great between-tree variation in rootability.

Preparation of Cuttings

Hard-wood (dormant-wood) cuttings are collected during the dormant season from lignified shoots of the last season's growth. This type of cutting is most often used in the propagation of conifers and broadleaved plants because a high degree of success can be obtained without elaborate care being given to collection, storage, and preparation of the material. Success can also often be obtained from soft-wood cuttings which are obtained from the succulent, unlignified new shoots with leaves. Soft-wood cuttings generally root faster and more easily than hard-wood cuttings but require more care in collection and preparation and the rooting facilities generally have to be more elaborate than for hard-wood cuttings. Soft-wood cuttings are usually preferred for the propagation of difficult-to-root deciduous or evergreen woody-plants.

Shoots to be used as cuttings may have to be pretreated in some cases. In *P. radiata*, for example, the shoots of difficult-to-root trees are girdled about six weeks before removal from the tree. This interrupts the movement of photosynthates and growth substances, and callus tissue forms at the base of the cuttings from which the roots originate (Thulin and Faulds, 1968). In pines, shearing-off ("hedging") the terminal parts of shoots in early spring stimulates latent fascicular buds to develop into shoots for the production of brachyblast cuttings (fascicle shoot-cuttings) (Isakawa and Kusaka, 1959; Rudolph and Niestaedt, 1964; Hong, 1969), or to maintain juvenility of the ortet and to yield more cuttings (Libby *et al*, 1971).

Cuttings are normally collected from healthy lower-crown branches since, especially in conifers, these root better than cuttings collected from the upper crown (Toda, 1953; Yim, 1962). The length of cuttings varies with species; 50–150 millimetres for conifers and 150–300 millimetres for hardwoods. Extremely thin or stout cuttings should be discarded. Removing the needles from the base of cuttings of many conifers does not usually affect rooting but some leaves of broadleaved species must be removed from the basal part of cuttings (especially soft-wood cuttings) in order to reduce severe transpiration.

Hormone Treatment

Effects of hormone on the rooting of cuttings vary with the species, the environment provided for rooting and the physiological condition of the cuttings. Because of the variable results obtained to-date, no specific hormone or method of application can be recommended to the exclusion of others. Those most commonly used and from which some positive results have been obtained are: 3-indole acetic acid (I.A.A.), 3-indole butyric acid (I.B.A.), and 1-naphthalene acetic acid (N.A.A.). These root-promoting substances are usually applied either in a powder form, by soaking in a dilute solution, or, by quickly dipping the cuttings into a concentrated solution (Hartmann and Kester, 1964).

Fresh preparations of hormones should be used whenever possible. Dilute solutions are likely to lose their activity in a few days, whereas the chemical in talc powder can remain active for several months; the concentrated solution-dip can be kept active even longer because it contains higher percentages of alcohol than the diluted solutions.

Environmental Factors Affecting Rooting

Rooting medium, humidity, temperature, and light conditions are the main factors which influence the rootings of cuttings in rooting beds.

The rooting medium has four functions: to hold the cuttings in place; to retain and supply moisture for the cuttings; to provide air at the base of cuttings; and to provide warmth at the base of cuttings. Thus, an ideal rooting medium is one that provides sufficient porosity to allow good aeration and a high water-holding capacity but with good drainage. The medium should be free from such harmful organisms as fungi, bacteria, and nematodes, especially for soft-wood cuttings. Sand, peat-moss, vermiculite, perlite, *Sphagnum* moss, and combinations of these are satisfactory rooting media, but the most common and cheapest are sand and peat.

Humidity must be maintained at a high (above 70 per cent) relative humidity around the cuttings, otherwise desiccation will inhibit root formation. Therefore, it is necessary to supply an ample amount of water through the medium and to maintain a high atmospheric humidity around the tops of the cuttings. Atomisation or "misting", obtained by passing water at high pressure through very fine nozzles, provides a satisfactory means of raising the ambient humidity. Intermittent misting can be mechanised by using an "electronic-leaf", or a timer connected to a solenoid valve.

Increasing the temperature of the medium to about 4° to 5° C higher than that of the air surrounding the cuttings often hastens rooting. The temperature of the medium is raised above that of the atmosphere by using a thermostat-controlled soil-warming cable buried a few inches below the surface of the medium. Air temperatures can to some extent be controlled by the use of shades or exhaust fans. As a general rule, the optimum temperature of the medium is that of the mean noon air temperature during the growing period.

Light is necessary for cuttings to synthesise carbohydrates and hormones. The cuttings of some species root better when exposed to a "long-day" treatment obtained by the use of artificial lights; long-day treatments, however, are not universally effective.

Following the development of roots the plants are gradually hardened-off over a period of several weeks, after which they may be potted-up for a period, or, lined-out directly into well prepared and manured nursery beds. In the nursery the roots may be wrenched or pruned both laterally and horizontally. When large enough the rooted cuttings are planted out in the orchard.

CONCLUSIONS

With few exceptions, grafts have been used exclusively for establishing clonal seed orchards. Because of the ease and speed of establishment, this trend is not expected to change greatly in the near future. However, graft-incompatibility, which has been a nuisance in many tree improvement programmes and an absolute barrier in others, now appears to be an even greater problem than previously recognised, by the onset of stock-scion rejection, in later stages of orchard development; often after trees have already started to produce commercial quantities of seed.

For species where graft-incompatibility is a major problem during any stage of the life of the seed orchard and which are suited to the production of vegetative propagules by rooted cuttings, it seems certain that the use of grafts will gradually decline. For those species where graft-incompatibility is not a serious problem, grafting will continue to be the method of propagation if only for the reason that little is yet known about the relationship of cuttings and seed production over a long period of time. These factors have an overriding effect on seed orchard programmes where time is all important. Furthermore, it is difficult to root cuttings of many important forest tree species and particularly from trees selected for breeding which are normally so old that, with present technology at any rate, the prospects of rooting are poor. For this reason the time taken and the costs for producing rooted cuttings are generally much higher than for grafts.

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LOCATION, ESTABLISHMENT AND MANAGEMENT OF SEED ORCHARDS

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INTRODUCTION

Location, establishment and management of seed orchard matters are all concerned with maximising the production of seed of high genetic and physiological quality, as soon as possible, and at an acceptable price.

An analysis of the literature has high-lighted a surprisingly large variation in the amount of research and accounts of procedures on the numerous matters relating to the location, establishment and management of seed orchards. For this reason information for some of the following parts of this chapter has been obtained by personal communication with many experienced and helpful colleagues to whom I am most grateful. The lack of literature on certain aspects of the work is possibly due to a lack of scientific attraction; many of the problems being regarded as essentially practical and answerable by observation, intuition or empiric research. Despite this many of the problems cannot be regarded as being unimportant. The aim of the text is to indicate the main factors to be considered, rather than to provide a series of recommendations, and the selected literature references are provided to give supporting examples.

LOCATION OF SEED ORCHARDS

The siting of a seed orchard is determined firstly on a regional and then on a local basis. Climate, local site characteristics and isolation from undesirable pollen sources all affect flower and seed production, seed quality and orchard management practices, and must be given very careful thought.

Regional Criteria

Very favourable conditions are essential for the continuous and regular high production of orchard seed. Sarvas (1970) recommends, from a purely administrative point of view, that the location of a seed orchard should be within its normal area of use, but that a transfer outside this area to a warmer climate can be advantageous for seed maturation, earlier flowering and the physical isolation of the orchard from undesirable pollen sources. Sarvas has developed a model for the transfer of Scots pine (*Pinus sylvestris*) clones in Scandinavia based upon the requirements of different races; it utilises information on the temperature sum and the variation in annual heat sum between localities. For the *maturation* of seed it has been shown that the temperature sum requirement is much higher for southern races than for northern ones, but even so, the most northerly races have to be transferred southwards in order to meet the full maturation requirements of the seed. The greatest potential increase in *flowering intensity* for a clone by transfer seems to be about 160 per cent more than in the natural habitat. This is obtained if the difference in temperature sum between the natural habitat and the locality of the seed orchard is 200–230 degree-days. Sarvas does not recommend transfers over very large distances because of expected harmful effects. His recommendations have been supported by Johnsson (unpublished), who has shown that a transfer of Scots pine within Sweden of more than 1 200 kilometres to the south results in a marked decrease in both the yield of cones and the number of filled seed per cone; there is, however, an increase in seed weight and viability. The model of Sarvas has also been used in Canada for *Pinus contorta* var. *latifolia*, *Picea glauca* and *Picea engelmanni* (Meagher, per. comm.).

Transfers from high to lower elevations might be used with similar effects in countries where there are appreciable differences in altitude. Helleberg-shaugem (1970) in Norway, in studies with Scots pine, has related the cone and seed yields of mother trees at 650–700 metres above sea level with yields from the same clones in a seven-years-old seed orchard at 320 metres above sea level. The results show that the seed yield per kilogram of cones, the percentage of full seeds and the 1,000-grain weight were significantly greater in the seed orchard, although part of the effect may have been due to grafting effects and differences in soil fertility. Transfers of seed orchard plants are also used for Douglas fir (*Pseudotsuga menziesii*) on the west coast of the U.S.A. where seed orchards based on all elevation zones are located below 300 metres because of the risk of damage to flowers by late-frosts (Wheat, per, comm.). However, beneficial transfers in the opposite direction have also been recorded by Sijde and Denison (1967) and Sijde (per, comm.) who report that good seed crops of *Pinus patula* can only be expected at altitudes above 1 500 metres in Eastern Transvaal. On the contrary, *Pinus elliottii* produces more seed in the coastal sand plains of

Zululand when compared with the more fertile sites in Eastern Transvaal at altitudes of 1 000 metres.

Transfers may also affect photoperiodic responses to flowering and Wareing and Longman (1959) have summarised earlier work in which they found that long-day conditions are favourable for the formation of female flowers in Scots pine and *Betula* species. In *P. contorta* short-day conditions favoured female flowering, but in *Fagus* species and *Larix kaempferi* no effects of day-length could be detected. Vidaković (1962) suggests the need for further research into photoperiodic responses since for a number of species he has detected more favourable conditions for flowering in south Jugoslavia than in other parts of the country.

There are many reports concerned with beneficial climatic effects on seed production for numerous species. Beckers (1972) in Belgium reports that moist and cloudy conditions in March and April followed by warm sunny conditions in June and July promote good seed production in Douglas fir. Matyas (1969) found in the continental arid climate of Hungary that warm weather in June and July favours male flowering in *Fagus sylvatica* and that a cool October and mild November stimulate the development of female flower buds. Yanagihara *et al* (1960) have studied climatic records covering a 49 year period and found that sunshine, high temperatures and low rainfall in late June and early July favour good *Larix kaempferi* seed crops in the following year.

Frost, drought and wind may all have an adverse effect on the establishment of orchard trees, and/or flower crops and seed setting, and the local topography and aspect may all influence any of these factors. Zavadil (1969a) describes losses of Douglas fir grafts within five plots established in Czechoslovakia at altitudes between 280 and 590 metres above sea level. One of the main reasons for the losses was *early-spring frosts* and Zavadil, therefore, stresses the importance of site selection especially for seed orchards outside the natural range of the species. Zasada (1971) describes serious damage to *Picea glauca* flowers after a mild late May frost in the interior of Alaska. Frost damage is not necessarily detrimental and Eriksson *et al* (1972) describe an interesting way of increasing the frequency of hybrid larch seed by selecting for climatic male-sterility. Developing pollen mother cells of *Larix sibirica* grown in the maritime climate of south Sweden, are highly susceptible to frost damage and complete male sterility is obtained; similar damage to the better adapted *Larix decidua* is very low. The risk of frost damage to the embryo sac mother cells is very low for both species and consequently pure hybrid seed can be harvested from the *L. sibirica* with a high degree of confidence.

Severe drought may reduce the yield of seed. Pawsey (1960) reported a loss of 23 per cent of the cones in *Pinus radiata* in south Australia due to summer drought. However, mild early-summer droughts, which occur before the formation of flower bud initials, are frequently regarded as predisposing causes for the stimulation of flower crops in the following year and, therefore, it could be argued that localities subject to periodic abnormally dry early-summer conditions should be favoured for seed orchard sites. This hypothesis is shared by Dyson (per. comm.) who reports that *Pinus patula* and *Pinus radiata*, growing in East Africa at elevations above 2 000 metres in regions with a pronounced dry season, seem to favour early seeding in comparison with orchards in milder climates.

A serious adverse factor for the formation of good seed crops in conifers is a *constant wind direction* during the time of pollen dispersal. Sarvas (1962) found a marked concentration of pollen on the windward side of the female strobili on Scots pine; this seriously reduced the total number of fertilised ovules and where this fell to less than twenty ovules per strobilus the developing conelets aborted.

Local Climatic and Site Requirements

There is general agreement that above-average soil fertility is essential for good orchard tree development and regular fruiting. For Scots pine, Sarvas (1962) recorded heavier and better seed crops with increased site fertility. At least medium quality sites are recommended by Bánó *et al* (1972), for seed orchards of Scots pine in Hungary. Faulkner (1964) recommends arable or old pasture agricultural ground and has used good loams for most of his seed orchard programme. Limstrom (1965) recommends well-drained fertile soils for Central U.S.A.

Wheat (per. comm.) working with Douglas fir suggests that sites which are subject to moisture stress are desirable and this is the opinion shared for *Picea abies* orchards in Scandinavia.

Shelter from strong winds and good air and soil drainage are also basic requirements. Local topographic or artificial features which provide wind funnels should be avoided, as should level ground from which cold air cannot escape, and slopes on the edges of plateaux from which there is a constant downward movement of cold air.

The likelihood of attack by root pathogens should also be borne in mind and sites which have previously carried hardwood crops should not be used for conifers susceptible to *Armillaria mellea*. Similarly old conifer sites may carry a high risk of infection from *Fomes annosus* and particularly if the soil pH value is high.

As a seed orchard programme progresses it is essential to attempt to analyse the cause of failures and successes for different sites and species. Large differences in seed production between sites have been shown for Scots pine by Johnsson (1967), and Bergman (1968) working with *Pinus taeda* has evidence of a cone crop variation between two locations of 400 per cent within the same clone.

Where basic information on site selection is lacking it should be possible to identify potentially good sites from observations of flowering and seed production in local stands. This has been attempted by Geary (1966, office report) for *Pinus patula* and *P. elliottii* in Zambia, and for a number of species in Canada (Meagher, per, comm.). Sweet and Bolman (1972) have studied regional variation in Douglas fir seed yields in New Zealand and have found areas particularly suitable for seed orchard purposes. If, however, seed orchards are located within areas of good flowering of the same or compatible species then good isolation against pollen may be hard to obtain.

Isolation from Undesirable Pollen Sources

Ideally all seed orchards, and of wind-pollinated species in particular, should be established on sites where contamination by pollen of the same or related species is likely to be negligible or low. Complete isolation is probably impossible to obtain because many investigations have shown that wind-borne pollen travels great distances. However, local pollen sources are generally the most important. Sarvas (1970) describes *physiological isolation* through the transfer of clones to a warmer climate, but points out that under Finnish conditions the transfer of Scots pine clones over very large distances can be disadvantageous because the flowering of this species then coincides with the flowering of *Picea abies*. Silen (1963), working in western Oregon and Washington showed that the transfer of Douglas fir clones from 700 metres to 180 metres elevation only delayed the flowering by eight to ten days. As the local period of pollen shedding lasts for 20 to 30 days, the transferred clones were still receptive when local pollen was still abundant. A somewhat similar study by Strand (1957) on *Picea abies* showed differences in the time of pollen dispersal of two to five days for every 100 metres interval down a hillside. Hadders (1972) emasculated all trees in a Scots pine seed orchard which was established 2000 metres away from any pine stand, but in spite of this 78 per cent of the female strobili developed into cones, each of which contained an average of 14.7 filled seeds. The total number of contaminant pollen grains within the orchard was estimated to be 86.10^{10}; to ensure that 90 per cent of the total available pollen within the seed orchard is derived from the grafts it was calculated that each ramet should bear at least 750 male strobili. Hadders, therefore, proposes to delay cone collections until there is an abundant pollen supply within the orchard. Wang *et al* (1960) and Squillace (1967) studied pollen dispersion in *P. elliottii* orchards surrounded by 120 metres wide isolation barriers. Data on pollen dispersion has been reported by Wright (1953) for several species and from which he calculated the expected contamination associated with different widths of isolation strips and for varying proportions of internally and externally produced pollen. His data shows that heavy production of pollen within a seed orchard is most important for diluting outside contamination effects. Orchard *size* is also important since contamination decreases very rapidly from the edge rows towards the centre. Wright found very little pollen on the uphill sides of source trees but noted that wind direction and topography was often confounded.

Sarvas (1956) studied the dispersion of birch, *Betula* species, within a Scots pine seedling area surrounded with birch stands and in which the distance from the centre of the pine area to the birch was approximately 400 metres. He calculated that if a birch orchard had been established in the centre of the pine only five per cent of the seeds would have resulted from outside pollination.

Andersson (1955) studied the dispersal of pollen from local sources of Scots pine and *Picea abies*. For most transects there was a very rapid decrease in pollen density within 400–600 metres from the edge of the pollen source, beyond which the pollen frequency was fairly constant; because the calculated inbreeding risk was high, Andersson proposed that pine seed orchards be rotated within spruce areas and *vice versa*. In pollen dispersion studies on Douglas fir during a year of very heavy flowering, Silen (1962) found that most of the pollen from single trees was dispersed within a very short distance, even so considerable amounts were found 610 metres away. About half the amount was foreign pollen and for this reason Silen recommends on-site counts of pollen during years of heavy flowering on which to base decisions on the choice of sites. On this basis Schmidt and Hamblett (1962) located one out of three possible Douglas fir orchard sites with very little extraneous pollen; the site was over 1.6 kilometres from the nearest Douglas fir tree and was surrounded by other species. Quite obviously where there are predictable prevailing winds during the period of pollen release, as in the case of *Pinus keysia* and *P. patula* in Zambia, orchards should be located on the windward side of plantations (Geary, 1970).

A novel method of obtaining good isolation is described by Silen and Keane (1969) who found that the development of Douglas fir flowers can be delayed by up to twelve days. This technique could offer a practical solution for very small-seeded species which crop heavily.

Where good isolation is very difficult to attain, it seems likely that the most effective future method of reducing contamination will be to develop chemical methods for either hastening or delaying the flowering processes.

Not all species are wind-pollinated and Klaehn (1960) has made a useful classification of seed orchards according to their type and method of pollination.

Management Considerations

It is desirable to plan as large an area of orchards as possible in a single district in order to develop and fully utilise expertise to the best advantage; to keep overheads to the minimum; and to get maximum use of specially purchased machinery for ground maintenance, chemical spraying and cone collections etc.

Communications should be good; a water supply is essential and an electricity supply is very desirable.

Orchard work is seasonal and sources of reliable labour must be available when needed and organised well in advance of requirements. Similarly an orchard scheme must be properly costed and funded at the outset and there must be reasonable assurances that the estimated annual running costs will be met.

ESTABLISHMENT OF SEED ORCHARDS

The cost of producing seed orchard planting stock is high and it is therefore essential to achieve high standards of general site preparation and planting. Basic site work, including tree and scrub clearance and drainage, should be conducted at least one year ahead of planting. This is particularly important for drainage work since checks can be made on its effectiveness before planting. Compacted soils, or old agricultural soils which have a plough-pan, should be sub-soiled at regular intervals to promote better drainage and firmer rooting conditions.

The type of ground management must be decided; this may be clean cultivation, clean cultivation combined with a catch crop or swards. Clean cultivation involves initial ploughing followed by regular disc-harrowing or applications of weed-killers. It may be practiced over the entire area, or over strips of varying widths alongside lines of plants (Limstrom, 1965); the main disadvantage is that the strips in particular are readily re-invaded by wind-borne seeds or rhizomes from weeds from the uncultivated strips.

The combination of raising several successive catch crops on cultivated ground between the trees is a traditional and normal practice in many tropical afforestation schemes and provides a cheap method of keeping the trees weed-free during the early years. In some temperate countries a catch crop of Xmas trees is raised in a similar way (Gramada and Butol, 1972) and there is no reason why similar schemes which involve the short-term integration of soft-fruit, potato or other vegetable crops with widely spaced orchard plants cannot be used for practical and financial advantage. Alternatively swards can either be specially sown or obtained by repeatedly cutting the existing vegetation in the area to produce a "tumble-down" sward. Clover (*Trifolium* species) is often sown in mixture with the grasses to provide an on-site source of nitrogen but very regular cutting of the grass/clover mixture is needed to retain the latter over several years. Crops of lupins (*Lupinus* species) are often grown in European seed orchards to provide both ground-cover and soil nitrogen and they can improve Scots pine flowering (Azinev, 1970). On the other hand Nilsson (1955) reports better flowering of *Picea abies* on cleanly cultivated ground in comparison with a grass cover.

The need for fertilizers should be determined on the basis of a soil analysis. Potassium and phosphorous levels should be artificially raised to those associated with medium quality pastures in the district in order to ensure that these two elements are not limiting. Checks for specific element deficiencies are probably not worthwhile unless certain elements are known to be limiting factors in the district.

Protection against large game animals and other undesirable ground vermin should be provided by adequate fences before planting. Where necessary, shelter-belts for wind protection should be established as required. These belts should be composed of a mixture of short-lived fast-grown species and longer-lived, shade tolerant species. In Britain mixtures of *Populus* species, *Sorbus intemedia* and *Fagus sylvatica* have proved to be satisfactory.

An accurate map of the area should be produced on which to base the layout of the planting positions, internal roads, water points etc.

Planting

Plant positions should be accurately marked out on the ground. An easy way to do this on even ground, and where a square planting pattern is used, is to set-up a "dumb-Tam" on a tractor. This consists of a long rigid horizontal arm set at right-angles to the side of the tractor; it has a downward-pointing scribe on the end and this is used to quickly mark-out parallel planting lines in two directions.

The planting positions, normally about 60 × 60 centimetres in size, at the line intersects, should be thoroughly cultivated and marked with a stake bearing an appropriate label for identification purposes. If required peat or other organic supplements can be cultivated into the planting positions at this time. On completion the labelled stakes should be checked against the layout plan. Labels on the plants from the nursery should be checked against those on the stakes before planting.

Pot-raised stocks often have curled root systems and these may create serious later problems (Zobel *et al*, 1958 and Hoffman, 1960); attempts should be made to loosen the roots before planting. Plants grown in pots made from slowly decomposable or very light plastic materials although expensive to raise and transport often survive better than bare-rooted stocks; they also suffer less from post-planting check and can be safely planted over a longer period. Insecticidal dips, or dips of anti-transpirants should be given where necessary before planting.

In temperate regions grafts more than one-year old often survive better than one-year-old plants; the growth and survival of plants is often similar between those established on cultivated strips and isolated, prepared, planting positions (Zadavil, 1969a and 1969b). Nursery-grafted planting stock or rooted cuttings are not always used for clonal orchards and in many countries rootstocks are established and grown on the orchard site for several years before grafting (Larsen, 1956; Kieding *et al*, 1964). Irrigation may be required after planting (Zobel *et al*, 1958) and in dry areas an organic, or plastic sheet, mulch may be helpful and improve survival.

After planting the labelled stakes should be driven into their final position and any grafts with pendulous leaders should be tied with the leader in an upright position.

Similar procedures should be followed for replacing failures, but since replacement plants seldom grow sufficiently fast to grow level with trees established in the first year, it is seldom worthwhile replacing losses after the fourth season.

In orchards designed for hybrid seed production, and where the two parent-species have different growth-rates, it is often necessary to plant the faster-growing species several years after the slower-growing components in order to ensure that the final orchard trees have similar crown sizes during the flowering period.

Mitchel (1959) gives a very good description of the establishment procedures for a hybrid larch seed orchard and this is recommended as a good basic reference for all procedures connected with the establishment of an orchard.

MANAGEMENT OF SEED ORCHARDS

Management procedures should be directed towards the early establishment and healthy development of grafted trees and the promotion of sustained and regular fruiting. Costs incurred in achieving these objectives should be kept as low as possible.

Ground and Ground-cover Management

Weeds and cover-crops should be kept under strict control within a ½ metre radius of each plant until it is well established and growing vigorously (Bánó *et al*, 1972). Compeltely cultivated ground should be harrowed, or treated with a suitable weed killer as an alternative. Grass crops should be removed regularly but when the trees approach the flowering age it may be possible to encourage water-stress on the site, through transpiration losses, by leaving the ground cover to grow tall during the period of flower formation.

Fertilizers

Fertilizers containing nitrogen, phosphorous, or potassium, are commonly used and many publications provide data on both positive and negative effects of fertilizers on female flowers and cone production on many species. From the available evidence, however, it is not possible to provide reliable rules and prescriptions for general guidance on their use (Bergman, 1968). From the literature it is quite clear that a more critical approach to fertilizer effects and better records of the basic site site parameters are needed; in particular more information is needed on the effects of fertilizers on pollen production, female flower *and* cone production *and* seed yields in terms of viable seed rather than weight. Faulkner (1966) presents conflicting results from a number of experiments but overall he recommends fertlization as a treatment of general value. One important factor discussed by Faulkner is the need for complete grass control if the seed trees are to benefit from the fertilizers. Good flowering responses to fertilization and cultivation have been shown for *Pinus taeda* (Schmidtling, 1971), and the positive effects on flowering and improved seed yields have been published for *Pinus densiflora* (Takayana, 1967); *Pinus echinata* (Brinkman, 1962); and for Douglas fir by Steinbrenner *et al* (1960), and Harry *et al* (1968). Moderate increases in female flowering of Scots pine after fertilization was found by Kozubov (1969). A negative effect of fertilizer was shown by Mejnartowicz (1970) in a *Larix decidua* orchard.

Seed weights and germinative energy are commonly increased by fertilizers e.g. in *Pinus elliottii* (Mergen and Voigt, 1960), and *Larix gmelini* (Krečetova, 1962). Estimates of the amount of nutrient removed by seed crops from orchards and stands has been made by Hoffman (1968) who reported very small losses from pine and larch orchards when compared with losses from *Fagus* species.

Thinning

The initial espacement of orchard trees should be sufficiently wide to encourage the full development of the crowns for a period long enough to ensure that cone or fruit crops will be obtained for several years before thinning is needed. Thus narrower spacings can be used for species which flower precociously than for species which are slower to start general flowering. In an orchard the tree crowns should always be kept isolated to admit sunshine and to permit the easy movement of cone or seed harvesting equipment.

In orchards composed of trees which have not been progeny-tested at the time of establishment, it will be necessary to remove those which are shown, from progeny-tests, to be genetically inferior and as soon as evidence of inferiority is available; groups of remaining trees are then thinned on a systematic basis to permit full crown development as and when required. Very early- or late-flowering clones should be removed from poly-clonal orchards when reliable flowering data has been obtained; from a practical point of view clones which produce very low seed yields should also be felled; and the number of ramets of the remaining clones should be removed in inverse proportion to their contribution to the final seed-mix.

In orchards composed entirely of proven good genotypes a systematic approach can be adopted such as that proposed by Asakawa and Fujita (1966). They calculated the spacing on the basis of sun exposure on the crowns and after thinning they obtained a substantial increase in seed production. In attempts to determine the optimum density for young seed orchards Pronier and Castaing (1970) thinned a young stand of *Pinus pinaster*. After thinning they found a reduction of the scatter of values for numbers of cones per tree. Reukena (1961) describes a Douglas fir thinning experiment over a span of ten years; his results are typical of what, as a rule, can be achieved by thinning. Thinning did not affect the frequency of viable seed, nor did it stimulate seed production in poor seed-years, but in good seed-years thinned stands produced more seed than unthinned ones.

Many publications describe the influence of the combined effects of cultivation, fertilizers and thinning of seed stands from which guidance can be obtained. Cooley (1970) working with *Pinus resinosa* found that the quality of the site and the age of the stand strongly affected the response to treatment. Krasnjuk (1959) found a response to all three factors on acorn yields and Enescu (1968) demonstrated the benefits of both thinning and fertilizers on *Larix decidua* and Scots pine. At present the literature on thinning seed orchards is scanty but it is a common experience that orchards in which thinnings have been neglected show a marked decrease in seed production which can last for several years even after thinnings are made.

Irrigation

The question of irrigation in seed orchards has been discussed by Grigsby (1967). Beneficial effects of irrigation on the growth of grafts of *Pinus sibirica* have been reported by Golomazova and Kolegova (1968), and Bergman (1968) provides evidence of clonal responses in the cone production of *Pinus taeda* after irrigating a seed orchard. It is of course logical to expect that irrigation will have a beneficial effect on seed production on dry sites. Irrigation from overhead lines can be used to reduce frost damage to Douglas fir flowers (Silen and Keane, 1969).

Crown Pruning and Shaping

For ease of seed collection the crowns of orchard trees should be treated in a way which will encourage the development of a short, wide and bushy habit except for those species, e.g. oak and beech, where fallen seeds are collected from the ground. The idea stems from established practices in the management of fruit-tree orchards and which, among other things, improves crop yields. However, Nilsson and Wiman (1967) have showed that severe pruning in Norway spruce reduces cone production; similar effects have been demonstrated on Scots pine by Retkes (1969). Varnell (1969) reported a reduction in the number of branches bearing female strobili, and thus a reduction in the number of cones a year after pruning *Pinus elliottii* and remarked that pruning may favour natural selfing if the height of the tree is reduced by pruning. Kellison (1969) states that pruning techniques have never been successful with the southern pines in the U.S.A. An increase of mainly male flowers, after pruning young grafts of Scots pine, was observed by Melchior and Heitmüller (1961), and Melchior (1962), which supports earlier work by Wareing (1953) in which only buds were removed. An important aim of pruning is to retard height growth, and thus make seed harvesting simple and cheaper. Suggested ways of achieving this for a variety of coniferous and hardwood species described by Johnsson (1950), Kiellander (1956) and Henseler (1967). A combination of pulling and tying-down branches to obtain low-growing seed-trees of *Eucalyptus* species is described by Nel (1965). A standard practice in South African pine orchard management is to artificially bend both the main stem and branches (Sijde, 1969), a method shown to be more effective than pruning alone. In removing the top of a conifer many future potential flowering points are lost and the proportion of male to female flowers is increased within a zone of the crown where selfing is likely to occur; this has consequential harmful effects on seed yield and quality. Furthermore it is not long before one of the remaining upper branches in the crown asserts dominance over the others and the pre-pruning situation is restored. This can be delayed in pine by applying a lanoline paste containing eight per cent I.A.A. to the cut surface of the topped trees; this prevents the development of upward-curving branches below the cut for several years (Toda *et al*, 1963) and (Toda and Akasi, 1965).

Root and Stem Treatments

Shock treatments including root pruning, stem girdling and strangulation and chemical sprays have all been used for inducing early and heavier than normal flowering; these are described in Chapter 7.

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CHAPTER 6

PROTECTION OF SEED ORCHARDS

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INTRODUCTION

Seed orchards are essentially monocultures and as such are highly vulnerable to damaging agents; however, they have characteristics which permit protective measures to be taken fairly easily. Both establishment costs and crop values are high and managers can usually adopt measures that are impractical or unnecessary under normal forest conditions. When orchards are concentrated and intensively managed at one location, a constant and close surveillance is possible, and any remedial action can be quickly taken. The comparatively small areas of an orchard, its normally good isolation from the public, and easy access to each ramet or tree by motor-vehicle, all contribute towards safe and effective protection. The availability of trained staff allows a variety of, and often sophisticated, protective measures to be used.

The need for forward planning cannot be overemphasised. Plans must be made to detect damage, both from expected and unexpected causes at an early stage. All necessary materials and equipment should be on hand and staff should be trained how to use them safely and effectively. Records should be kept of the incidence of damage and of the nature and effectiveness of any control measures.

It is equally important, however, that decisions concerned with protection should only be made after a careful assessment of any damage and the expense and probable effectiveness of any action. Time and money have often been wasted on hastily planned and ill-considered measures. Identification of the causal agents and prescriptions for control should, whenever possible, be made by specialists. Disease problems are especially complex and accurate identification often requires the use of laboratory facilities.

The best method of protection is usually achieved by avoiding or minimising the risk and in this connection choice of orchard location is most important. Ideally, orchards should be established on sites suited to the species but well-isolated from stands of the same or closely related species (see Chapter 5). The prevalence of known and potentially damaging agents should be assessed before a site is finally chosen and the probability of damage should be weighed against other factors. Seemingly inocuous agents should also be considered, and even these may later become troublesome under seed orchard conditions. Potential orchard damage is often minimised, if not prevented, by locating orchards away from forests and other vegetation which provide natural habitats for alternate hosts of troublesome fungi, insects, birds, and mammals. Other risks to be considered are migrating birds, or very heavy snowfall, glazed frosts and tornadoes. When it is impossible to avoid the risk of certain serious hazards then at least one reserve orchard should be established for insurance.

Each orchard is subject to its own particular damaging agents. In this chapter discussion is limited to the most widespread and important problems chosen from approximately 150 individuals and agencies throughout the world with active orchard programmes who replied to a questionnaire. Recent forestry literature has also been consulted. Where feasible, the damaging agents or species have been grouped according to the type of damage they cause and a representative of each group has been chosen for discussion. In general, measures which are applicable to an agent attacking a species can be extended to related tree species or damaging agent.

Protection problems have been further grouped into two general categories, namely losses and damage resulting from injury to vegetative parts, and from direct damage to flowers, cones, fruits or seeds. Damage to the latter cause the greatest concern and both cone and seed insects appear to be the most widespread pests. Vigilance and preparedness are therefore necessary during every phase of orchard development.

The sequence and extent of discussion in the text does not imply importance or priority. On subjects where published information was unavailable measures suggested on returned questionnaires have been included. These are indicated as personal communication (p.c.) to distinguish them from published information.

Regulations concerned with protective measures, especially pesticide applications, vary between governments and are subject to continual revision. Hence, mention of control methods and materials, including trade names, is solely for the information and convenience of readers. Mention does not imply world-wide legality or constitute endorsement of any product, service, or method to the exclusion of others which may be suitable.

INSECTS

General

Insects are the most important pests of seed orchards, sometimes causing seed losses of over 50 per cent. Illustrated guides concerning the biology and identification of seed and cone insects are available (Bakke, 1969; Ebel, 1963; Goolsby *et al*, 1972; Hard, 1964; Keen, 1958; Kinzer *et al*, 1972; Ghani and Cheema, 1973; Hedlin, 1974). Barcia and Merkel (1972) have cross-referenced the North American literature on cone and seed insects by insect and host species.

Insect problems can be diagnosed by the recognition of characteristic damage signs or by trapping. Black-light traps (Plate 1, central inset) are used to determine the prevalence of lepidopterous insects which attack orchard trees (Powers, 1969; Merkel and Fatzinger, 1971; Yates, 1973; Yates and Ebel, 1970, 1972). Records of seasonal flight-activity (Plate 2), based on daily counts of trapped insects, provide a guide for timing control measures.

X-ray photographs, which do not destroy the seed, are useful for detecting insect-damaged seed (De Barr, 1970; Johnson and Hedlin, 1967).

Insecticides are widely used for controlling most insect pests. Systemic insecticides, which often have higher mammalian toxicities than many contact insecticides, have shown particular promise. Soil applications or implantations into trees are safer than more conventional spraying methods. Absorbed "systemics" are translocated within the tree to the shoots and cones; generally they remain effective for longer periods than insecticides applied as foliar sprays. Pest control methods for insect pollinated species include selective insecticides, repellants, attractants and traps. The introduction of parasites or predators may also be considered.

D.D.T. was the most widely used contact insecticide in the past, but its use is now prohibited in many countries and its place has been taken by several other chemicals of which B.H.C. (benzine hexachloride) is one of the more effective ones.

Insects Attacking Vegetative Structures

Defoliators

Defoliating insects attack orchards of all species at all ages. They reduce tree vigour, and repeated attacks may cause death. In the U.S.A., the sawfly, *Neodiprion pratti pratti* (Bramlett and Hutchinson, 1965), the geometrid moth, *Nepytia semiclusaria* (Ebel and DeBarr, 1973), and the budworm, *Choristoneura occidentalis* (Dewey, 1970), are primarily defoliators, which also feed directly on male and female strobili of pines and Douglas-fir (*Pseudotsuga menziesii*).

Some contact insecticides used against defoliators include carbaryl, lindane, and trichlorfon (p.c.).

In Canada, strobili and cones are protected from the spruce budworm, *C. fumiferana*, and spruce coneworm (*Dioryctria reniculella*) during controlled pollination work by placing 1 × 1 × 0.5 centimetre chips of dichlorvos-impregnated poly-vinyl-chloride inside the pollination bags (Fowler, 1971).

Sucking Insects

Aphids and scale insects may be found on orchard trees at almost any season. They have sucking mouthparts and may weaken or defoliate trees by feeding on the sap.

In Britain, the green spruce aphid, *Elatobium abietinum*, attacking Sitka spruce (*Picea sitchensis*), and *Adelges* species attacking Scots pine, Douglas-fir and larches are sprayed with 0.1 per cent malathion (p.c.). The scale, *Leucaspis knemion*, on pine in Cyprus is controlled by spraying with a mixture of 20 grams white oil and 100 millilitres of 50 per cent parathion mixed in 11 litres of water (p.c.). In Kenya, *Pineus sylvestris* is controlled by spraying a mixture of 0.5 per cent B.H.C., 1 per cent endosuflan, and a wetting agent. Repeat sprays of 0.5 per cent endosulfan are made at 3-week intervals. In Japan, 10–20 grams of granular disulfoton are applied to soil around young trees to reduce damage by scale, *Cinara* species (p.c.).

Stem Borers

Orchard trees weakened by poor management, natural disaster, or other pests may be attacked by bark beetles, *Ips*, *Tomicus*, and *Dendroctonus* species. In Australia, infested trees are felled and destroyed or sprayed with a 5 per cent B.H.C. solution in diesel fuel (p.c.). In the U.S.A., a 1 per cent solution of lindane in diesel oil is recommended. Thinning, or felling nearby woodlands or roguing within orchards may provide centres for bark beetle outbreaks; felled trees should, therefore, be removed as soon as possible.

A debarking weevil, *Hylobius abietis*, attacking young conifers in Britain is controlled by dipping plants in 1.5 per cent lindane prior to planting, or by spraying with 0.3 per cent lindane where the need for protection becomes apparent after planting. Though primarily attacking cones, larvae of *Dioryctria* species also damage pine stems, particularly those infected with the fusiform rust, *Cronartium fusiforme*. Preventive measures include pruning cankered branches and spraying the wounds with 1 per cent lindane in a non-phytotoxic oil.

Larvae of the swift moth, *Phassus excrescens*, attack stems and branches in *Cryptomeria*, *Chamaecyparis*, *Populus*, and *Alnus* orchards in Japan. Removal of underbrush and application of a 3 per cent Sumithion® powder on the soil around trees has given control. Larvae which bore into trees, can be controlled by pouring 10–20 millilitres of a 0.1 per cent solution of Sumithion® into the bore holes (p.c.).

Insects Attacking Reproductive Structures

Cone Borers

Cone borers provide the most serious threat to conifer orchards. Among numerous species, the most damaging are the cone moths, *Dioryctria* species and *Eucosma* species, and the cone beetles, *Conophthorus* species and *Pissodes* species, each of which may have from one to several generations per year.

Dioryctria larvae attack many tree organs, but damage to first- and second-year cones is especially important. After boring into second-year cones, for example, the larvae eat the seed and eventually kill the entire cone. Damage by *Eucosma* species is similar.

Scolytid beetles, *Conophthorus* species, bore into the base of the cone stalk and make a gallery down the cone axis in which to lay eggs. Developing larvae feed on the interior of the cone. Although most attacks occur on second-year cones, first-year conelets and new shoots may also be killed and occasionally cones are killed by girdling the stalk.

On *Pinus elliottii* in the southern U.S.A., at least three *Dioryctria* species are controlled by three or four sprays per year of either 0.2 per cent azinphosmethyl or 0.5 per cent lindane in water (Merkel, 1964). A fourth late-July spray only slightly decreased further damage. The azinphosmethyl formulation has been especially registered for slash pine. Late-May and mid-June sprays of 0.5 per cent tetrachlorvinphos in water protected *Pinus taeda* cones from *Dioryctria* species in Virginia (Copony, 1972). Three mist-blower applications of 1.0 per cent azinphosmethyl in the middle of April, May and June were effective on second-year longleaf pine (*P. palustris*) cones, (DeBarr and Merkel, 1971).

Granular formulations of phorate applied in three slash pine orchards at rates of 0.05, 0.23, and 0.45 kilograms per tree gave inconsistent control of *Dioryctria* species. The compound was broadcast under the tree crowns in early April (DeBarr *et al*, 1972). Trunk implantations of dicrotophos, at rates of 0.8 to 2.0 grams of actual insecticide per 10 millimetres of tree diameter, reduced cone larval infestation in slash pine (Merkel and DeBarr, 1971).

Pre- and post-flowering sprays of any of three insecticides, lindane 0.5 per cent, dimethoate 0.4 per cent, and oxydemeton-methyl 0.4 per cent, substantially reduced *D. abietella* damage to spruce cones in Finland (Annila, 1973). In Norway, *D. abietella* attacking *Picea abies* is controlled by applying systemic sprays soon after pollination is completed. Additionally, all cones are removed annually. Spraying immature cones with dimethoate in late-June is effective in Finland. This same cone moth, attacking Scots pine in Hungary, is controlled by spraying during the second half of June with trichlorphon, dimethoate, or formothion (p.c.).

The fir cone moth, *D. abietivorella* and the Douglas-fir cone moth, *Barbara colfaxiana* are controlled on Douglas-fir with sprays of 0.5 per cent dimethoate oxydemeton-methyl, or dicrotophos (Johnson and Hedlin, 1967). Sprays should be applied after the conelets become pendant.

In Finland, larvae of the European cone-boring weevil, *Pissodes validirostris* are controlled by spraying the bases of pines with lindane in early spring. The method is proven but not yet in common use. Spraying with trichlorfon, formothion, or dimethoate during the second half of June has been effective in Hungary (p.c.).

Seed Feeders

Eggs of seedworms, *Laspeyresia* species, are deposited on cones in spring or early summer, and the larvae bore directly into the cones leaving no external evidence of attack. Feeding is confined to developing seeds until the cones mature, after which the larvae migrate to the cone axis to overwinter and pupate.

The overwintering habit suggests that complete removal of mature cones each year might suppress seedworm populations in orchards not subject to reinvasion from neighbouring host stands. Such sanitation programmes are recommended for *L. strobilella* attacking spruce in Norway (Bakke, 1969) and Rumania (Tudor and Marcu, 1969).

The pests are vulnerable to contact insecticides only during the adult and egg stages, and for a brief time before newly hatched larvae bore into cones. Careful timing of sprays is essential.

Seedworms have been controlled on pines in the U.S.A. with soil applications of granular phorate (DeBarr *et al*, 1972), trunk implantation of dicrotophos or oxydemeton-methyl (Merkel, 1969, 1970; Merkel and DeBarr, 1971), mist-blower and drench applications of azinphosmethyl (Merkel, 1964; DeBarr and Merkel, 1971), and tetrachlorvinphos, monocrotophos, and fenthion (Merkel, 1968). The slash pine seedworm, *L. anaranjada*, has been controlled by a 0.2 per cent drench or 1.0 per cent mist-blown spray of azinphosmethyl applied during the peak period of moth emergence (Merkel, 1971; DeBarr and Merkel, 1971).

In Russia, damage to spruce seed crops by *L. strobilella* was reduced by helicopter applications of dimethoate (Elizarov, 1970); elsewhere in Europe, 0.2 per cent drench sprays of this chemical or oxydemetonmethyl have been effective (Annila, 1973). In Canada. *L. youngana* has been controlled by mid-June drench applications of 0.5 per cent to 1.0 per cent dimethoate (Hedlin, 1973).

Seed wasps *Megastigmus picea*, and *M. albifrons* in North America, and *M. spermotrophus* in Europe, are common pests of spruce, *Pinus ponderosa*, and Douglas-fir. Each larva destroys only one seed, but losses of more than 50 per cent of the crop have been recorded. In England, losses were reduced with a 0.3 per cent malathion spray applied three times at 10-day intervals during June (Stoakley, 1973). The systemics dimethoate, oxydemeton-methyl, and dicrotophos were effective in Canada when sprayed just after Douglas-fir conelets became pendant. Dimethoate was effective at a 0.5 per cent to 1.0 per cent concentration (Johnson and Hedlin, 1967; Hedlin, 1973). By contrast, Annila (1973) found that dimethoate and oxydemeton-methyl applications increased the number of *Megastigmus* larvae. Apparently, these systemics killed seed-destroying midges (*Plemeliella abietina*), thereby enabling the surviving wasps to deposit more eggs than normally. Spraying spruce cones in late-June with dimethoate or oxydemeton-methyl is, nevertheless, an operational control in Finnish seed orchards.

Trunk implantations of either dicrotophos or phorate reduced the proportion of acorns weeviled by *Curculio* species (Dorsey, 1967). In Russia, two crown-sprays of Fozalon® or methiocarb (0.2 per cent) at 50-day intervals, or three crown-sprays of trichlorfon (2 per cent) at 20- to 25-day intervals, controlled weevils on oaks (*Quercus* species). Repeated spraying with azodrin (0.5 per cent) at 20-day intervals was also effective (Zemkova, 1972).

The true beetles (Hemiptera) *Leptoglossus corculus*, *L. occidentalis*, and *Tetyra bipunctata* cause serious conelet abortion (DeBarr and Ebel, 1974) and seed losses in the U.S.A. (DeBarr, 1970; Krugman and Koerber, 1969). The insects feed externally using their stylets to penetrate the cones. Salivary enzymes are secreted into the seed and digested substrates are then extracted through the stylets. Attacks are therefore difficult to detect. Applications of granular 10 per cent phorate at 1.1 kilograms and 5.5 kilograms per tree (8 metres tall) have reduced damage (DeBarr *et al*, 1972).

Dipterous Cone and Seed Pests

These insects cause several types of damage. The cone-boring maggots, for example *Hylemya anthracina*, tunnel around the cone axis and destroy seed; seed-destroying midges such as *Plemeliella abietina* deposit eggs in female flowers and the larvae enter and eat the seed; gall midges, for example *Contarinia oregonensis*, lay eggs in female flowers and the larvae cause galls to develop by feeding on or near the seed; seed is then usually fused to a cone scale, preventing extraction. Cone midges such as *Thomasianiana* species feed in or on developing cones, causing necrotic patches or outright death. Cones which mature are difficult to extract.

Dimethoate (0.25 per cent), applied when conelets are closed and pendant, is effective against *C. oregonensis* on Douglas-fir (Buffam and Johnson, 1966). This species overwinters in the leaf litter and the emergence of adults can be prevented by applications of lindane in oil to the ground in March (Koerber, 1963).

Contact insecticides have little effect on the midge *P. abietina*, but sprays of dimethoate (0.4 per cent) have proved useful (Annila, 1973). This chemical and oxydemeton-methyl are used in Finnish spruce orchards (p.c.). To increase effectiveness, Bakke (1969) recommends collecting and burning cones each year.

The cone-boring maggot, *H. anthracina*, is a pest of spruce and larch throughout the world. Sprays of 0.1 per cent dimethoate, 0.1 per cent oxydemeton-methyl, and 0.2 per cent lindane (Annila, 1973), or 0.5 per cent to 1.0 per cent dimethoate (Hedlin, 1973) have been effective when applied during the flowering period. In Finland, *Plemeliella* and *Hylemya* species are controlled by spraying with dimethoate or oxydemeton-methyl in late-June (p.c.).

Flower and Conelet Feeders

Tip moths are common pests in pine orchards; they destroy shoots bearing newly-formed or developing strobili (Yates and Ebel, 1972). The larch shoot borer, *Argyresthia* species, can be a serious pest in very young orchards, (p.c.).

The Nantucket pine tip moth, *Rhyacionia frustrana*, is controlled in the U.S.A. by soil applications of granular phorate. 20 grams of the 10 per cent granules per tree are sufficient to protect loblolly pines up to 2.5 metres tall (Rauschenberger *et al*, 1969; Yates, 1970). Success depends on applications made in February to ensure translocation to the terminal shoots by the time larvae start to feed. Dimethoate, applied as a drenching foliar spray at 0.12 per cent concentration, is also recommended (Yates and Beal, 1971). Sprays should be timed to coincide with the end of egg hatching.

In Japan, the shoot moths, *Evetria cristata* and *R. duplana*, are controlled with sprays of 0.05 per cent to 0.1 per cent Bysit®. Carbaryl (10 per cent) is used in Cyprus (p.c.).

In Britain, damage by the pine shoot beetle, *Tomicus piniperda*, is minimised by locating orchards away from sources of infestation and by pruning all infested material (p.c.).

In the U.S.A., a thrips, *Gnophothrips fuscus*, feeds on female slash pine flowers and reduces seed yields by causing cone death or malformation. Control has been effected with drench sprays of 0.5 per cent heptachlor (Ebel, 1965) and mist-blower applications of either 0.25 per cent heptachlor or 0.75 per cent malathion (DeBarr and Matthews, 1971). Sprays are applied after the strobili begin to emerge, but before pollination.

DISEASES

Though usually not so severely damaging or widespread as insects, diseases affect orchards of many species and at every stage of orchard development.

Diseases of Vegetative Structures

Root Rots

Among root rots, those caused by *Armillaria*, *Fomes*, *Phytophthora*, and *Helicobasidium* species have been particularly threatening and they may even kill newly-established ramets or rootstocks. Infection also reduces vigour and seed productivity, and may predispose trees to wind-throw.

Throughout the world, *Armillaria mellea*, the honey fungus, is perhaps most damaging. Signs and symptoms are illustrated in the British Forestry Commission Leaflet (1971), Leaphart (1963), and Pawsey (1973). Many conifer and hardwood species are susceptible and greatest losses follow the establishment of conifer orchards on former hardwood sites.

The fungus can persist in stumps and roots for many years, spreading from these infection centres through the soil. Agricultural or other non-forested land is therefore preferred for orchard establishment. When forested land must be used, all stumps, roots, and debris should be removed several years before establishment. In tropical countries, standing trees should be girdled at least one growing-season before clearing (Leaphart, 1963).

The removal of infected materials also restricts the spread of *Armillaria* in established orchards. Disinfection of stump holes with carbon disulphide (Pawsey, 1973) or carbam (p.c.) is further advised. Similar approaches have been used against *Helicobasidium mompa* and several troublesome species of *Phytophthora* (p.c.).

Though not widespread in seed orchards, *Fomes annosus* attacks numerous conifers and causes limited damage to hardwoods. Signs and symptoms are illustrated in British Forestry Commission Leaflet (1967), and by Powers and Hodges (1970).

The fungus can persist for decades in stumps and roots, passing to living trees by root contact. Airborne spores infect freshly exposed wood. Orchards should not be established on sites which are known to be infected, or where fellings have recently occurred. Stumps and main roots should always be removed.

Losses in established orchards most frequently follow thinning, and selective fellings. In conifer orchards new stumps should be removed or their exposed surfaces immediately protected with solutions of borate compounds, sodium nitrite, or urea (British Forestry Commission Leaflet, 1967; Garrett, 1970). Dry, granular borax sprinkled liberally on freshly cut stumps has been an effective protection treatment in the U.S.A. (Powers and Hodges, 1970).

Protection of pines has also been achieved by stump inoculation with *Peniophora gigantea*, a common and effective competitor of *F. annosus* (Rishbeth, 1963); in some countries an inoculum is commercially available.

For maximum effectiveness, any protectant must be applied copiously to all exposed wood within 30 minutes of felling.

Foliage Diseases

Fungus-caused defoliation reduces growth and seed production but seldom causes death. One example is the needle blight, caused by *Dothistroma pini*, which severely infests *Pinus radiata* in particular. This species is highly susceptible when young, but becomes resistant with age (Gibson, 1971). Damage, therefore, is not as severe in grafted orchards as it has been in commercial plantings or might be in seedling orchards. The age at which resistance develops varies with climate, and is delayed longest in moist areas. Proper siting thus provides one means of protection. Inclusion of blight-resistant clones also lessens the need for direct control. Where such measures are inapplicable, copper fungicides can be employed. Two ground or aerial sprays of fungicide (50 per cent Cu) per year at approximately 4.4 kilograms/hectare, are effective in young plantings (Gibson *et al*, 1969).

Other troublesome foliage diseases include needle-casts or -blights caused by *Naemacyclus niveus* and *Lophodermium pinastri* on pines, *Rhizosphaera kilkoffii* on spruces, and *Mycosphaerella laricileptolepis* on *Larix kaempferi*. Where defoliation is severe or danger from secondary agents exists, removing susceptible clones, maintaining vigorous growth by cultivation and fertilization, and burning infected litter may prove helpful (p.c.). Four applications of Bordeaux mixture per growing-season have been successful against *Mycosphaerella* outbreaks (p.c.).

Anthracnose, caused by *Gnomonia leptostyla* is considered the most serious foliage disease of black walnut (*Juglans nigra*) (Berry, 1973). Premature defoliation reduces both growth and seed-yield. Controls include destruction of infected foliage (Berry, 1970) and spray applications of zineb or maneb (80 per cent) at 9 kilograms per 3 800 litres of water (Berry, 1973); Benomyl (50 per cent) at 4.5 kilograms per 3 800 litres of water is also effective (p.c.).

Branch and Stem Diseases

Walnut bunch disease, caused by a mycoplasm-like organism, adversely affects form, growth, and seed production of *Juglans* species (Berry, 1973). Black walnut is less susceptible than other species. Good sanitation practices, including pruning and burning infected materials, may be helpful (Berry, 1973) and any diseased trees should be eliminated from the vicinity of orchards.

A shoot dieback affecting *Larix* species and caused by *Guignardia laricini* is troublesome in Poland and Japan (p.c.). Trees often die within three years after symptoms are first observed. Some control has been obtained in Japan with mist-blower applications of cyclohexamide (5 ppm) at a rate of 300 litres/hectare (p.c.).

Stem-rusts, for example, those caused by *Cronartium fusiforme* and *C. quercuum* weaken branches and stems (Plate 3), thereby predisposing ramets to wind-break or attack by secondary agents. Infections on rootstocks or new ramets cause malformation or death.

Orchards should not be established in areas with high rust-incidence, climatic conditions favourable for infection, or abundant alternate hosts. Resistant clones should be chosen for new orchards, and progenies of only the most resistant clones should be used for rootstocks.

Where resistant clones are unavailable, some artificial protection can be given to rootstocks or young ramets. Weekly sprays, from March to mid-June, with 900 grams of ferbam or ziram (76 per cent wettable powder) and 5 litres of spreader-sticker in 285 litres of water, have been effective against *C. fusiforme* in forest nurseries (Czabator, 1971; Verall and Czabator, 1970). Unusually favourable conditions for infection can be forecast and additional sprays to those which are regularly scheduled can be applied (Davis and Snow, 1971).

In established orchards, pruning branches having galls 7 centimetres or more from the stem can prevent stem damage (Czabator, 1971). When branch galls are closer than 7 centimetres, infection has probably already entered the stem. Early efforts to kill stem galls with antibiotics were discouraging (Davis and Luttrell, 1967), but soil drenches with systemic fungicides appear to be effective in seedlings (Hare, 1973). Where laws permit, direct surface application of arsenite at 0.5 kilograms of arsenic trioxide equivalent per litre of water may be useful (Brown and Rowan, 1967).

Removing infected tissue from and adjacent to galls (Davis and Luttrell, 1967; Verall and Czabator, 1970) has proved to be reasonably effective, except on galls which completely girdle the stem; best results have been obtained on recently formed galls. In practice the infected area is outlined with a sharp knife by making a cut down to the wood and parallel to, but at least 5 centimetres outside, the obvious swelling. All bark and tissues within this area and down to the wood are then cut away and the wood is scraped clean to deny any remaining fungus access to surrounding cambial tissues. The application of a wound-dressing compound is advisable.

Wounds frequently occur as a result of pruning, operation of machinery, or breakage by snow and ice. Damaged branches should be removed, and any exposed wood protected with a wound-dressing compound to prevent fungal infection.

Diseases of Reproductive Structures

Cones

The southern cone-rust, caused by *C. strobilinum* Hedgc. & Hahn, damages slash and longleaf pine cones in the southern United States. Infected cones provide favourable habitats for *Dioryctria* species (Merkel, 1958). Infection can be minimised by locating orchards away from concentrations of evergreen oaks which are the alternate hosts. Control can otherwise be obtained by spraying with 900 grams of ferbam (76 per cent wettable powder) and 0.25 litre of spreader-sticker in 380 litres of water (Hepting and Matthews, 1970). Applications should be made at 5-day intervals after the emergence of female flowers and until natural pollination is complete.

Other cone-rusts of actual or potential importance affect *Picea* species. They include *Pucciniastrum padi* on *P. abies* in Norway (Lilja, 1967), and *Thecopsora areolata* on several *Picea* species in Japan (Saho and Takahashi, 1970); the respective alternate hosts are *Prunus padus* and *P. ssiori*. Near-total loss of *P. abies* cone crops by *P. padi* has been experienced in certain parts of Norway (p.c.). Damage varies directly with the frequency and proximity of alternate hosts. Recommended counter-measures include, locating orchards outside risk-areas, or, eliminating alternate hosts from the vicinity of established orchards (p.c.). Destruction of infected cones is also recommended.

MAMMALS

Mammals damage orchards on every continent by girdling roots, fraying or browsing stems, and destroying flowers.

Mammals Attacking Vegetative Structures

Mice, Voles, and Gophers

The field vole, *Microtus agrestis*, damages orchards of most species in north-west Europe and provides a good example of troublesome small rodents. It partially or completely girdles stems or roots particularly in winter. Newly-established plants are most vulnerable, but older plants are also killed. Voles are credited with damaging or destroying approximately 22,500 ramets in Finnish orchards during a single winter (Kanervo and Myllymaki, 1970).

Brambell (1965) and Myllymaki (1970) summarise the considerable research on vole ecology. The enormous numbers encountered during times of peak populations greatly complicate control. Application of endrin to surface vegetation is highly effective, but its use is restricted in many countries (Myllymaki, 1970). Also, rapid restoration of *Microtus* species, populations following endrin treatment in North American fruit orchards was attributed to the simultaneous killing of pests, predators, and parasites (Driggers, 1971). Myllymaki (1970) reported that stem applications of repellents or poisons were of little value, but that poisons in combination with certain cultural practices migh be more effective. Increased feeding was observed around manured ramets, thus when spot applications of nutrients are applied, only the small treated areas need be poisoned. The utility of poisoned baits is limited by difficulties associated with acceptability, placement, and safety. Many small mammals, particularly voles, take green forage in preference to small, dry grains. Apples have proven acceptable, even in winter (Myllymaki, 1970). Frequency of encounter and attractiveness may be increased by placing baits in mechanically made burrows; this approach has been used against pocket gophers (Geomyidae) in North America (Ward and Hansen, 1962), and may be useful against other rodents, including voles. Non-repellant and safe, but effective, poisons must yet be developed (Myllymaki, 1970). Anti-coagulants are perhaps the most suitable despite their low effectiveness outdoors.

So-called ecological countermeasures, for example, the removal of food and cover or the manipulation of microclimate, often work in specific situations but give inconsistent results. Two such approaches, however, have potential for use in orchards (Myllymaki, 1970). Clean-cultivation reduces vole survival and reproduction, particularly where the potential for invasion is minimal and snow-falls are light. Losses have also been reduced by compacting snow to restrict movement (Christiansen, 1971), but the utility of this technique varies among orchards (Myllymaki, 1970).

The most reliable protection is obtained by protecting individual stems with sleeves of aluminium foil (Myllymaki, 1970). Such sleeves, as used in Finland, have an apparent cost-advantage (Myllymaki, 1970) over similar guards of wire-netting used in Sweden (Hadders, 1968; Stenmark, 1967). For maximum protection, sleeves must cover stems to a point above the greatest expected snow accumulation. Entire orchards can be effectively fenced, provided the materials are sunk 15–20 centimetres into the soil to prevent tunnelling beneath the fence.

Rabbits

In many parts of the world, winter feeding by rabbits and hares (Leporidae) results in partial or complete girdling of stems and branches. Newly-established ramets are particularly vulnerable.

Shooting and trapping are expensive and of limited value unless re-invasion of the orchard is checked. Where regulations permit, some protection can be obtained with poisoned baits, such as apples, carrots, and grain treated with strychnine or sodium fluoroacetate (p.c.).

The extensive research on repellants has been summarised by Armour (1963). Older, simpler repellants, including bone oil, wood- and coal-tar products, and lime-sulphur solutions, are still used. Sulphurised oil and rosin/ethanol mixtures are useful and inexpensive. Repellants containing T.N.B.A., ziram, or thiram, give protection for a year or longer. Other preparations are described by Radwan and Dodge (1965), Szukiel (1972), and Tigner and Besser (1962).

Guards of wire-netting, mesh-size 31 millimetres or less, encircling stems to a height of at least 1 metre provide reliable protection. Another useful approach involves winding ribbons of metal foil or durable plastic around vulnerable portions of individual stems (Plate 4). Such guards also protect against fraying by roe deer, *Capreolus capreolus* (British Forestry Commission, 1964).

For areas over four hectares, Pepper and Tee (1972) indicate that the costs of protecting individual stems may exceed that of fencing. Their recommended design for rabbit fencing incorporates galvanised wire-netting 1 metre wide (hexagonal mesh: 31 millimetres size, 18 gauge) and strung top and bottom on 12-gauge spring steel wire. Some practitioners advise sinking the fence netting 30 centimetres into the soil (p.c.).

Deer, Elk, and Moose

Deer and their relatives (Cervidae) may browse shoots and buds of hardwoods and conifers or gnaw or strip bark for food. In addition, antler rubbing may fray the bark or break stems, particularly of newly-established ramets or seedlings. Attempts to reduce numbers by occasional or indiscriminate shooting are largely ineffective. Co-operation with game management agencies should therefore be sought to reduce populations in the vicinity of orchards, by legal means, to levels compatible with both conservation and tree improvement goals. Guidelines for reducing roe deer numbers to tolerable levels in woodlands are summarised in British Forestry Commission Leaflet (1964).

Repellants are abundant, but their efficiency is limited. Fraying is not deterred, and the need for repeated application greatly increases cost. Even so, traditional preparations containing slaked lime and kerosene, blood albumen, or bone tar-oil are used (Armour, 1963). Ziram formulations have also shown promise. Burlap strips or rags saturated with bone tar-oil and hung on temporary fencing has reduced damage to *Populus deltoides*, a much preferred food in North America (Denton *et al*, 1969).

Individual stems can be protected against roe deer with sleeves of wire-netting, firmly staked, and 1.2 metres high (British Forestry Commission, 1964), and by plastic tree-guards (see Plate 4). Larger animals, however, may not be so easily deterred.

For properties the size and value of seed orchards, fencing is the most practical alternative, especially when combined with some means of co-operative population control. Fences must be sturdy, tight, and continuous and constructed of wire-netting rather than separate strands. Designs vary among managers as well as with the size and behaviour of the animal species. One design uses two widths of wire-netting, each 1 metre wide, strung at top, centre, and bottom on 12-gauge spring steel wire (Pepper and Tee, 1972). Replacing the lower width with one of hexagonal 31 millimetres mesh will also exclude rabbits.

Primates

An unusual problem, at least to most orchardists, confronts those improving *Pinus patula* and *P. radiata* in East Africa. Sykes monkeys strip the bark for food (Omar and de Vos, 1970) and baboons break branches and leaders (p.c.). Greatest damage occurs in newly-established orchards, particularly those near indigenous forests. Shooting and chasing are neither desirable nor effective. Losses, however, can be reduced by exploiting the reluctance, of at least the monkeys, to cross grassy isolation-strips approximately 100 metres wide (p.c.). Fencing provides protection, but at considerable expense since individual ramets must be ringed extensively with barbed wire.

Mammals Attacking Reproductive Structures

Squirrels

Light to moderate losses of pine and spruce cones are occasionally caused by squirrels. Certain species not only reduce the current crops but also affect future productivity. *Tamiasciurus* species, for example, sever entire cone-bearing shoots of ponderosa pine (Shearer and Schmidt, 1971). Damage varies from year to year, but destruction is greatest in poor cone-years (Larson and Schubert, 1970). Asher (1963) observed a preference for cones from fertilized trees. The potential losses should not be underestimated since even a few squirrels can destroy significant numbers of cones. Other seed-eating mammals may become troublesome should seed collection methods, dependent upon cone opening *in situ*, become practical.

Live- or kill-traps in and around orchards may be useful and should be placed just before cone-feeding begins. Warfarin poisoning provides a less expensive alternative but requires great care (Rowe, 1973).

Aluminium sleeves placed around the stems of individual ramets are perhaps the most effective method of reducing losses. Sleeves should extend at least 0.5 metres in the vertical direction, be smooth-surfaced, and allow for expansion with radial growth. The bottom edge should be at least 1.5 metres above the ground. Materials, dimensions, and procedures for construction are described by Krugman and Echols (1963).

Opossums

The opossum, *Trichosurus volpecula*, has become a serious pest in Monterey pine orchards in New Zealand (p.c.). The pest was introduced from Australia and has few, if any, natural enemies. The animals eat large quantities of pollen shortly before anthesis. Of greater importance, they consume or damage female strobili during the interval between pollination and fertilisation. As much as 40 per cent of unprotected cone-crops have been destroyed.

Shooting and poisoning are not considered sufficiently reliable. Protection of individual ramets with metal sleeves fastened around their stems may prove effective since the pest is not particularly agile (p.c.). Fences of wire-netting are also being tested. These are 1.5 metres high and bent near the top to create a flange or lip extending outwards for

0.3 metres. An electrified wire can be strung along the outer edges of this flange as a further deterrent (p.c.).

BIRDS

Many species of birds visit seed orchards while feeding, mating, and migrating. Some break new grafts or elongating leaders and branches by perching; others feed on developing reproductive structures or seed.

Birds Attacking Vegetative Structures

Perching is mainly a serious problem in newly-established orchards. The responsible birds vary from common songbirds to large scavengers, and no tree species is unmolested or immune. Damage may be severe where orchards are along the route of a migrating species, or, when the surrounding vegetation provides an ideal habitat for nesting or feeding. The problem is transitory, however, and diminishes as the orchard plants increase in size.

Perching can be discouraged by scaring, shooting, or chemical repellants (Armour, 1963; Keil, 1968). Scaring is a popular method, but noise-making devices and even dummy predators become ineffective in a short time. Recorded alarm or distress calls are more useful, although cost may not be justified unless damage is especially severe or frequent. The killing of large numbers of birds is neither practical nor desirable. While few chemical repellants are effective (Armour, 1963) a recently developed flock-alarming repellant, "Avitrol", may be worth testing in seed orchards. The first birds to eat this repellant move about nervously and sound alarm-calls, and frightening away the rest (Anonymous, 1974).

Other protection can be obtained by providing wooden perches throughout the orchards. The stakes should be of a sturdy, durable wood and 15 to 30 centimetres taller than ramets. When flocks are large or visits frequent, it is necessary to stake each ramet (Otterbach, 1963). Staking young ramets will also support them and prevent wind-breakage. Seven to ten metres tall perches provide useful vantage and temporary resting places for hawks and falcons and these birds, if attracted to an orchard site, will scare away small birds and also reduce the local populations of mice and voles.

In Norway the eradication of other vegetation which provides food for thrushes, *Turdus* species, has discouraged perching on young Norway spruce ramets (p.c.).

Birds Attacking Reproductive Structures

Bird damage to reproductive structures mainly occurs in conifer orchards. It is usually worse when the pest or tree species, or both, have been introduced into a country.

A serious example involves the chaffinch, *Fringella coelebs*, and Monterey pine which were both introduced into New Zealand. These birds unerringly locate any developing female strobili before emergence, slit the bud scales, and extract the strobili for food (p.c.). In some orchards over 50 per cent of the potential strobili are eaten. The crimson rosella parrot, *Platycerus elegans*, causes similar problems of equal or greater magnitude in Australia (p.c.). There are no known methods of control.

FROST, ICE, AND SNOW

Seed orchard problems caused by low temperatures *per se* range from such subtle effects as altered reproductive phenology and reduced pollen fertility, to actual destruction of reproductive structures. Branches and stem breakage is a common result of excessive snow and ice accumulation.

The relationship of low temperatures and their duration to damage has been determined for numerous fruit varieties. Judgements concerning the location of fruit orchards, choice of protective devices, and their application, are based upon critical temperatures and the frequency of occurrence. The critical temperature for a given variety is defined as: that which material, in a particular developmental stage, can endure for 30 minutes or less without damage (Ballard, 1972; Rogers and Swift, 1970).

Critical temperatures or other measures of sensitivity are only now being determined for forest trees. Moreover, the concept is more difficult to apply to forest tree orchards than to fruit orchards. Among other factors, differences in spacing and size complicates protection. Also, the nature and extent of damage can be expected to vary among developmental stages (Hutchinson and Bramlett, 1964; Eriksson, 1968; Zasada, 1971), among structures on individual ramets, and especially among clones or families. The number and diversity of genotypes represented in seed orchards is a particularly complicating factor. The influence of weather conditions preceding and following periods of potentially damaging temperatures has also to be considered.

Avoidance of high-risk sites is the best protection. Other measures are difficult and expensive. The probability of low temperatures on given dates can be calculated from local weather records where these exist, and any prospective site can then be evaluated by comparing these with the forecasted timing and sensitivity of the different developmental stages. Full advantage should be taken of all existing local knowledge on known frosty pockets and the phenology of the species. Long-established procedures for choosing nursery sites provide additional guidelines. Where risks cannot be avoided, the same information should be used for choosing any system for protection, planning its installation, and applying it.

In general, two conditions give rise to potentially damaging temperatures. The first, radiation frost, occurs when air temperatures surrounding vegetation fall to 0° C or lower on clear, calm nights, as a result of rapid local heat-loss by radiation; air temperature-inversions may also occur. The second, advective frost, occurs when air temperatures over a large area remain at or below 0° C for several days. The major controlling influence is the inflow of a cold, dry, air mass (advection), as opposed to a localised radiation loss. Cold day-temperatures and moderate to strong night-winds are common. Quite frequently, temperatures drop below those against which most protective measures, other than proper siting, are effective. Further descriptions and definitions are given in Ballard (1972), Geiger (1957), Hervett (1971), and Rogers and Swift (1970).

On frosty nights, air at higher levels may remain warmer than that near the ground. This phenomenon (inversion) can be used for devising systems to protect against frost damage. Large fans or wind-machines have now been developed to mix the higher warm air with the colder air in and around crops. Detailed information concerning vertical temperature-distributions is necessary and procedures and equipment for detecting and measuring inversions are described by Ballard (1972), and Rogers and Swift (1970). As a general rule, wind-machines are likely to be effective when temperatures at 12 metres are 5° to 8° C warmer on the majority of nights that 0° C is recorded at 1.4 metres (Rogers and Swift, 1970). Ballard (1972) indicates that differentials of only 1.7° C may be sufficient and that a single wind-machine can protect 2.4 hectares of fruit orchard. Wind-machines are also valuable supplements to heating systems.

Heating is probably the most reliable means of protection. An adequate system should be capable of raising temperatures throughout an orchard by at least 3.9° C (Ballard, 1972). Heaters must be distributed uniformly around the orchard. Rogers and Swift (1970) suggest approximately 87 units/hectares for a typical fruit orchard, but suitable numbers can be determined only by experience. An effective system uses fuel that ignites easily, burns as smokelessly as possible and, above all, is readily obtainable in quantity at reasonable cost. Smoke has no value in preventing heat-loss and is a liability from the standpoint of pollution. Heating systems and operating procedures are reviewed by Ballard (1972), Hervett (1971), and Rogers and Swift (1970).

Systems burning oil are used most widely. Individual heaters are popular as a result of their low cost and flexibility. Three preferred models are described by Rogers and Swift (1970). Despite higher initial costs, pressurised central systems are considered easier to regulate, more efficient, and less expensive to operate.

Systems using natural or liquified petroleum gas are cleanest and most convenient (Ballard, 1972). Operating costs are low and heat output can be adjusted easily. Disadvantages include high installation costs and possible difficulties with access to gas supplies at reasonable rates. The capabilities of gas heating were demonstrated by Valli (1970).

Fruit orchardists have used various solid fuels, many of which are now considered impractical (Rogers and Swift, 1970). Petroleum coke blocks are a recent introduction (Gerber *et al*, 1969; Valli, 1969). As with other solid fuels, output peaks shortly after ignition, heat cannot be regulated, and burning continues until the fuel is exhausted. Heating can be increased or prolonged by igniting additional blocks. The effect of numerous small fires is desirable. As the small blocks (each weighing approximately 2 kilograms) are self-contained, they are easy to handle, ignite, and store; the fuel is stable over long periods of storage. These features make petroleum coke especially useful in emergencies, or where heating is required only a few times each year, but the cost will exceed that of oil heaters if it has to be used frequently.

Heating will also minimise damage by snow and ice accumulations. Though only applicable in specific situations, other methods of reducing snow-breakage include: the use of resistant clones; blowing with helicopters or by manual shaking. Supporting newly established orchard plants with stakes has also been helpful.

Although expensive, wooden props have also been used to prevent the breakage of stems and branches heavily laden with snow and ice.

FIRE

Seed orchards demand the highest priority for fire protection.

Isolation strips should be cleared of all inflammable vegetation and the ground cover on these areas and within the orchard should be mowed frequently. The immediate orchard boundary should consist of a fire-break, 10–15 metres wide, kept free of vegetation by annual or semi-annual cultivation or weedkillers. Fire-breaks should also surround individual sections within very large orchards or divide them at conveniently spaced intervals. Motorised equipment should be fitted with spark-arresting exhaust systems and the entry of visitors and the public should be controlled, particularly during hazardous periods. Workers should be alerted to conditions of high hazard and be trained to prevent and combat fires. In very large high-risk orchards both mechanised and manual fire-fighting equipment, along with communication facilities, should be provided.

PESTICIDE SAFETY

Until alternative pest-management systems are developed, the protection of seed orchards will require the purchase, storage, and use of a wide variety and considerable quantities of pesticides. Dangers associated with materials currently in use, including those discussed in this chapter, cannot be over-emphasised.

Regardless of the chemical or target organism, improper use of any pesticide can be injurious to man, animals, and plants. It is imperative therefore that orchard personnel be trained thoroughly in all phases of pesticide handling. Orchard managers, in particular, must have a detailed knowledge of each product and its safe use. The pesticide with the lowest mammalian toxicity should always be employed when a choice among several is possible. A reference concerning the safe use of insecticides is available (DeBarr and Merkel, 1969).

The most important safety rule is: Read the label. *Follow the directions, and heed all precautions.* Labels provide the name and formula of the pesticide and its toxicity, as well as instructions for mixing, requirements for protective clothing, procedures for application, and antidotes to be used in the event of an accident. The address of the manufacturer is usually provided to facilitate access to professional help.

Pesticides must be stored in their original containers, under lock and key and out-of-reach of children and animals, and away from food and feed supplies.

Before applying pesticides, the orchard manager must know the location and telephone number of the nearest medical facility (some hospitals are designated as poison control centres) where assistance can be obtained.

Pesticides should be applied in ways which do not endanger humans, livestock, crops, beneficial insects, fish, or wildlife. Their use should be avoided when there is danger of drift, when pollinating insects are active, or where they may contaminate water, or leave harmful residues.

When pesticides are applied, inhalation of spray or dust should be avoided, and protective equipment specified on the label should be worn. Each worker should be provided with a clean towel, bar of soap, and container of water. If spillage occurs, contaminated clothing should be removed immediately and the affected skin thoroughly washed.

THIS ACTION DOES NOT NECESSARILY NEGATE THE NEED FOR MEDICAL ATTENTION.

If a pesticide is swallowed or gets in the eyes, first-aid instructions on the label should be followed and the individual referred promptly to a physician. As an added precaution, personnel should wear emergency identification tags identifying the individual, his supervisor, a physician, the pesticide, and pertinent information about its toxicity, symptoms of poisoning, and antidotes. Tags should be worn for at least 12 hours after exposure, as the effects of pesticide poisoning usually appear within that time.

To further guard against contamination, containers or equipment should not be cleaned, and excess solutions should not be released near ponds, streams, or wells. Empty containers should be deeply buried in an approved dumping area or in a level, isolated place.

The protection provided by pesticides is necessary and beneficial, but is obtained only at some risk. Safety procedures must be meticulously observed.

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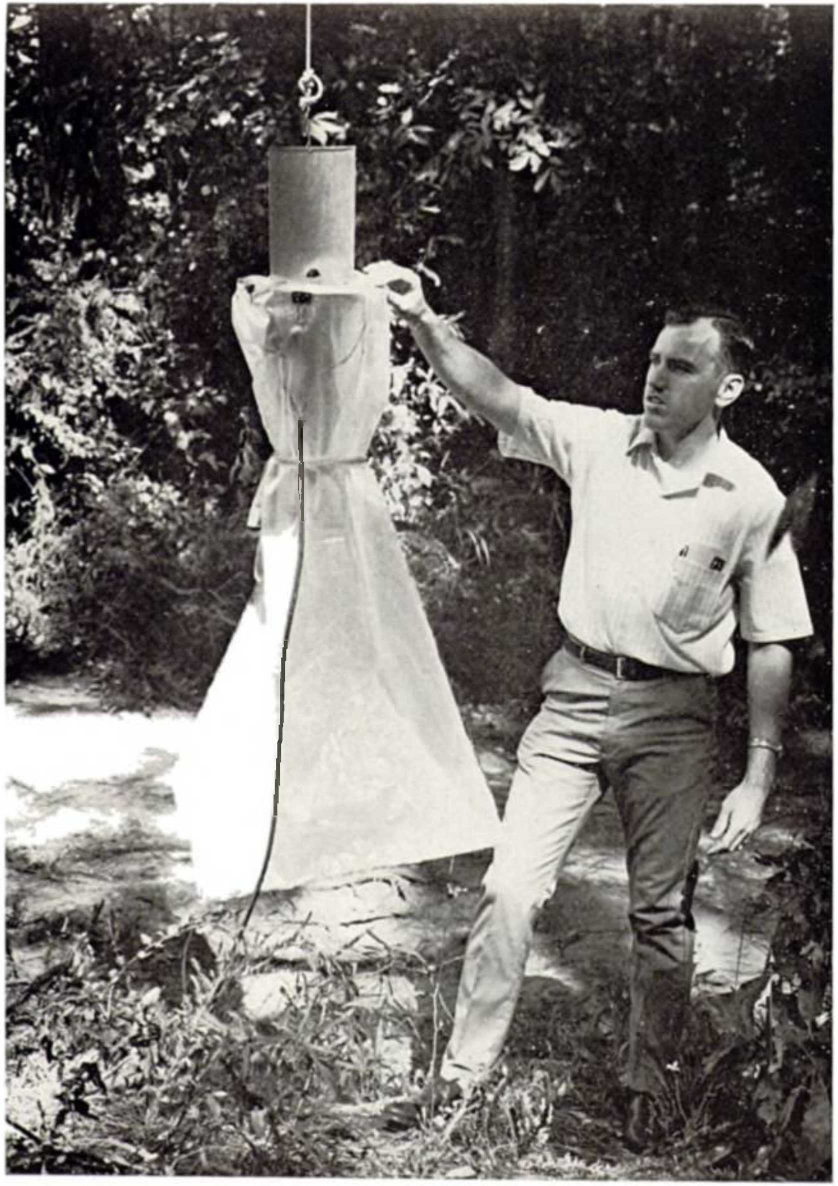

Plate 1. Dinus and Yates: Protection of Seed Orchards (p. 59). Black-light insect trap. A screen bottom allows rainwater to drain from the plastic collecting bag. The trap is lifted to the base of the tree crown by a rope and pulley arrangement.

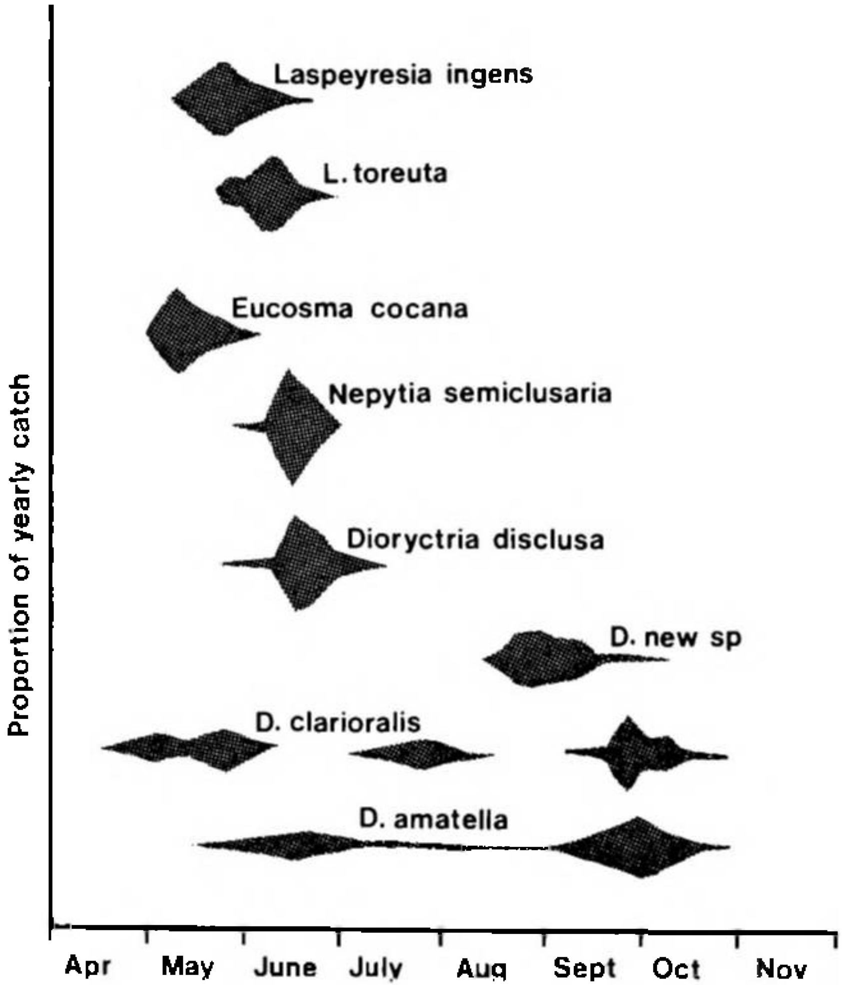

Plate 2. Dinus and Yates: Protection of Seed Orchards (p. 59). Species and proportions of lepidopterous orchard insects captured in a black-light trap during one season in northeast Georgia, U.S.A.

Plate 3. Dinus and Yates: Protection of Seed Orchards (p. 63). Stem rusts are important diseases in seed orchards of conifers. When they do not kill the tree outright, they often make it vulnerable to breakage in storms, or attack by secondary organisms. This tree is a loblolly pine in the Southern U.S.A., and has been cankered by the rust fungus *Cronartium fusiforme*.

Plate 4. Dinus and Yates: Protection of Seed Orchards (p. 65). Plastic spiral guards protect individual ramets or trees against girdling by rabbits and hares. If entwined around the stem and lower branches such a guard also prevents bark fraying by small deer.

Plate 5. Kellison: Cone and Seed Harvesting (p. 102). A knuckle-boom elevating platform and a truck-mounted scaffold in position for cone collection in the loblolly pine seed orchard of International Paper Co., Georgetown, South Carolina, U.S.A. Note the cone hooks being used by the men on the scaffold.

Plate 6. Kellison: Cone and Seed Harvesting (p. 102). Trailer-mounted aluminium extension ladder for access to the crowns of seed orchard trees. During transport the ladder is pivoted to a horizontal position to rest in the cradle-frame.

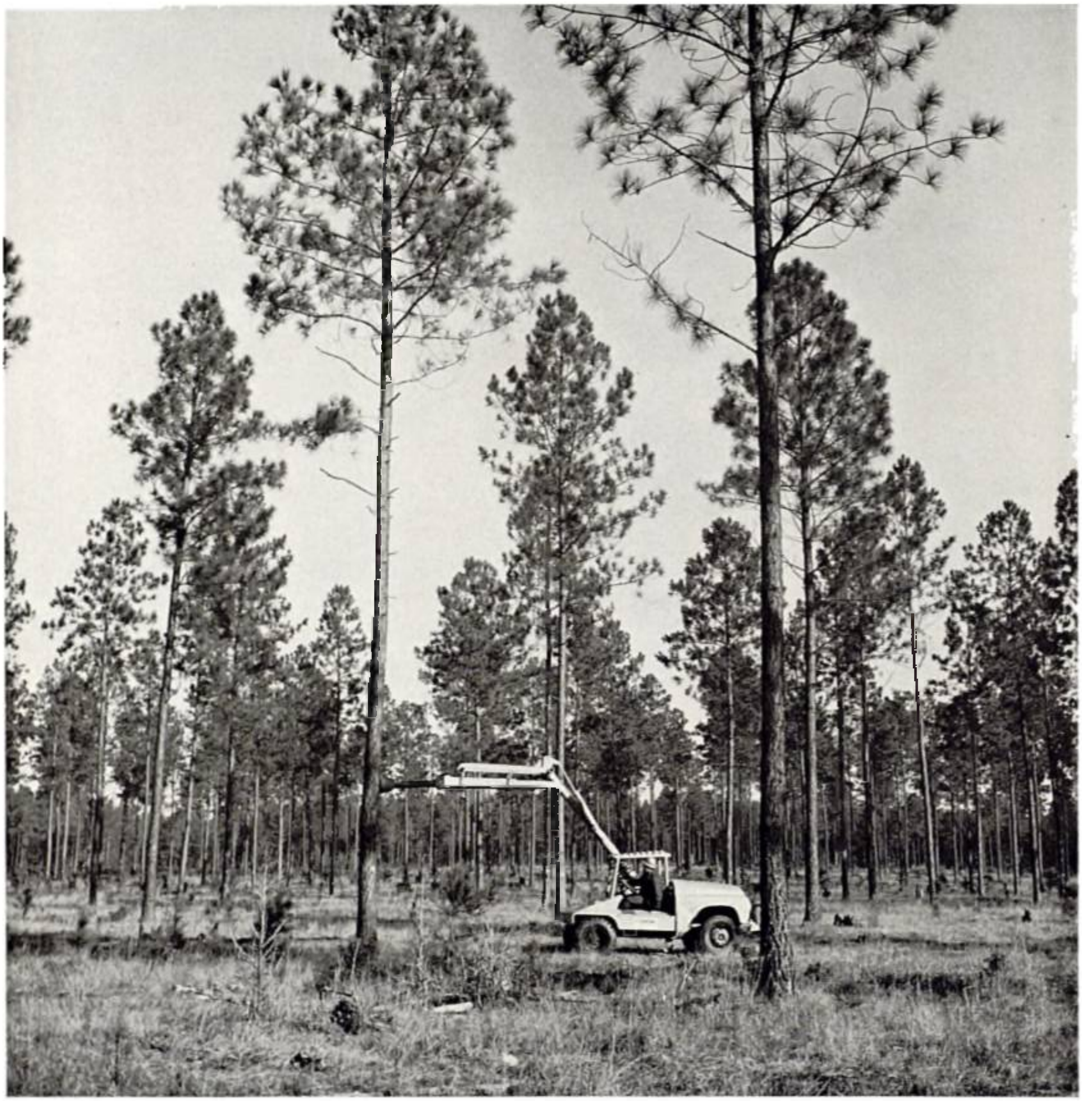

Plate 7. Kellison: Cone and Seed Harvesting (p. 103). General view of a shock-wave shaker at work in a slash pine seed stand (Photo: United States Department of Agriculture: Forest Service).

Plate 8. Kellison: Cone and Seed Harvesting (p. 103). The shaking head of a shock-wave shaker in action on a slash pine in the southern United States (Photo: United States Department of Agriculture: Forest Service).

Plate 9. Kellison: Cone and Seed Harvesting (p. 105). A prototype vacuum seed harvester at work in the loblolly pine seed orchard of Weyerhaeuser Co., Washington, North Carolina, U.S.A. Later modifications have significantly altered the appearance but not the principle of the machine.

Plate 10. Kellison: Cone and Seed Harvesting (p. 105). Part of a "harvest" of pine seeds, needles and debris caught by a temporary nylon netting seed orchard floor cover after trees have been mechanically shaken. The net and its contents are wound in by the machine; a second machine (not shown) sorts the seeds from the debris. (Photo: Georgia Forestry Commission).

Plate 11. Kellison: Cone and Seed Harvesting (p. 102). Truck-mounted scaffold for access to the crowns of seed orchard trees. Dual rear wheels give the truck greater stability.

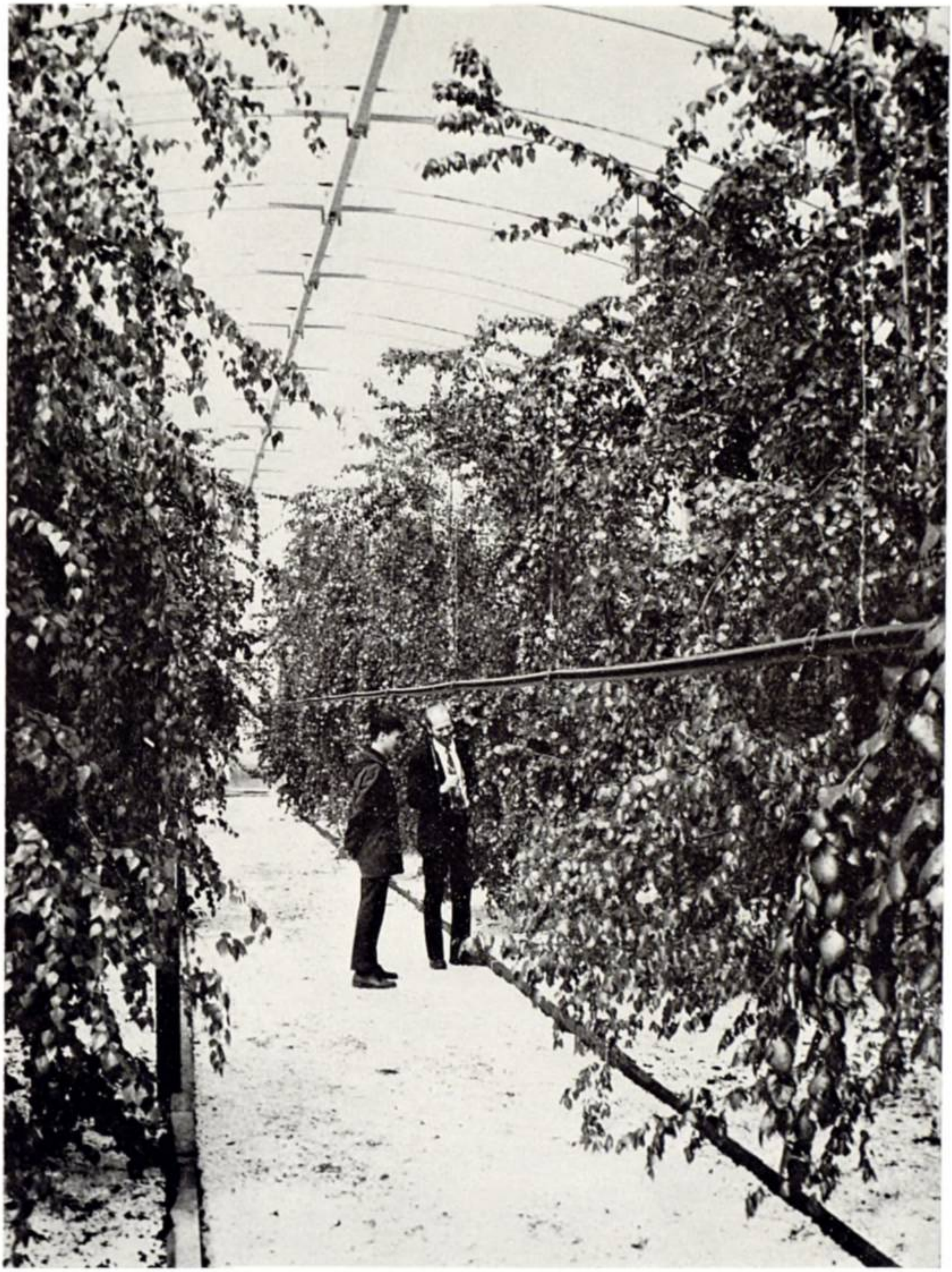

Plate 12. Koski: Broadleaved Seed Orchards (p. 108). A general view of a seed orchard of *Betula pendula* under plastic cover in spring 1973.

Plate 13. Koski: Broadleaved Seed Orchards (p. 108). Abundant seed crop of *Betula pendula* in summer 1972 under plastic cover.

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CHAPTER 7

FLOWERING AND SEED PRODUCTION

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INTRODUCTION

The main function of a seed orchard is to produce seed of improved genetic quality on a regular and sustained basis. In many forest tree species, particularly those which display periodicity in flowering, lack of flower initiation constitutes a major limitation to seed production. However, in nearly all species there is also a major loss of potential seed between the time of flower initiation and seed maturity, and thus it is important that seed orchard managers be concerned with *all* phases of seed production.

This chapter is presented as a "state of the art" report with the emphasis on seed orchard management rather than on flowering and seed production research. Several extensive reviews of the research literature have been published in recent years and are listed in Section 1 of the References at the end of this chapter: the older of these should not be neglected since some of the more recent ones have passed quickly over material well presented at an earlier date. The text of this chapter contains a few references only, but in addition to these a number of papers are listed (in Section 2 of the References) which have been published since the latest review papers were written.

FLOWER INITIATION

Introductory

A minor but annoying problem which affects writers on this subject is that the normally accepted definition of a flower excludes the strobili of gymnosperms. To overcome this Jackson and Sweet (1972) proposed a simplified definition of a flower as "a determinate sporogenous shoot", thus making it possible to use the term coniferous flower. This chapter uses that definition.

Although foresters have managed to influence flower initiation in forest trees with some success their methods to date have been largely empirical, and there is little doubt that in the future a more detailed understanding of the physiology of flowering will be needed. Some understanding may be gained from a knowledge of other species, but since the literature is extensive there are obvious practical difficulties in determining how much is relevant to the forester. In the past one of the major criteria has been to assume that while the woody-plant literature is useful, herbaceous plant literature is less so. Jackson and Sweet (*ibid*), however, have suggested that a more valid criterion might be to differentiate between perennial and annual plants. They suggest that while the annual plant literature (which forms the major part of the total literature on flowering) is of limited value to the forester, the literature on perennial species may be important regardless of whether or not the species are trees.

Recent review papers on flowering have stressed that to influence flower initiation on other than an empirical basis one needs to have a detailed understanding of the nature of floral buds, their location within the tree and the time at which they are initiated.

Flower buds in trees can be produced terminally (as in the Cupressaceae and Taxodiaceae) or laterally in the axils of leaves, as in *Betula, Populus, Eucalyptus*, and coniferous genera such as *Pinus* and *Pseudotsuga*. Generally they have a protective cover of bracts and scales from the time of initiation. The buds may be initiated while the vegetative shoot is still actively elongating (e.g. *Eucalyptus*) or while extension growth is inactive (e.g. most species of *Pinus*). Once initiation has started, development of the flower may be rapid and uninterrupted (e.g. *Cupressus* and *Eucalyptus*) or slow, often with the interruption of a dormant period (e.g. *Pseudotsuga* and *Pinus*). There is a considerable amount of evidence that in conifers such as Douglas-fir where floral development is slow, there may be a lengthy period of time between the formation of a potentially floral organ (initiation) and its irreversible commitment to become floral (flower determination). This is probably not universal in trees since it does not seem to occur in the Cupressaceae and Taxodiaceae for example, or in many species of *Eucalyptus*, but it may be an attribute of the majority of forest tree species. It is thus important that seed orchard managers be aware not only of the need to provide conditions suitable for the initiation of potential flowers, but also of the need to maintain the trees in the flowering condition for the necessary period of time.

The fact that potential flowers may not develop florally, or that they may cease growth and abort or revert to the vegetative condition, has been known for some years. Only very recently, however, has it been shown that potential vegetative buds can fail to develop vegetatively, and instead be switched to the floral condition well after their time of initiation (Silen, 1973a). The literature suggests that many flower-inducing treatments may operate by influencing the plant during the period between the initiation of potential floral organs, and their irrevocable commitment to flowering. Clearly this is pertinent to the timing of flower-inducing treatments, and thus it is necessary for seed orchard managers to have a good knowledge of the time of flower initiation, period of determination, and subsequent developmental processes for both the species and sites on which they are working. Puritch (1972) has reviewed much of the data on the time of flower initiation and development for a number of Pacific-coast conifers: Hashizume (1973) has comparable data for nine species used in Japan and has details of the influences of year to year effects, regional effects, and of tree to tree differences and the effect of position in the tree.

In many tree species the timing of flower initiation can be fairly precisely defined, but in species of *Pinus* which are polycyclic (i.e. having several clusters of flowers on the same annual shoot) flower initiation must occur over a wide time range. Unpublished data from two separate workers investigating *Pinus radiata* in New Zealand, for example, suggests a four- to six-week time interval between the initiation of two successive clusters of flowers. Since it is not uncommon for *P. radiata* to produce three clusters of flowers in the same year (see e.g. Sweet, 1973, Figure 9), there may be a two- to three-month time span between the initiation of the first and last clusters. Such a situation requires some consideration when timing the application of flower-inducing treatments.

Endogenous Factors Affecting Flower Initiation

1. Juvenility and Maturation

In the past there has been a tendency for workers in different disciplines to define a plant as mature or juvenile on the basis of a single criterion—its ability to flower for example, or its inability to root as a cutting. However, there is now a growing awareness that the relatively large number of criteria, which change with the process of maturation, cannot be looked at in isolation, and several scientists now believe that the juvenility or maturation status of a plant should be defined in terms of how far generally it has moved through the maturation process—i.e. on the basis of a number of factors in combination.

Large genetic differences exist between species, provenances and clones both in the age at which maturation is complete and in the age at which the first flowers are normally initiated (Zimmerman, 1972). Examples of the normal age of first flower initiation in the literature range from one year in *Pinus contorta* to 30 to 40 years in *Fagus sylvatica*. A number of treatments are known to promote precocity of flowering: most of these are shock treatments such as girdling, drought, root-pruning, heat treatment, excessively heavy fertilizing, etc. However in the Cupressaceae and Taxodiaceae the application of gibberellins has been successfully used to induce precocious flowering in a number of species.

The genetic component of precocity appears to be high, and there seems little doubt that breeders can incorporate this factor successfully into selection programmes. Currently there is a great deal of interest from tree breeders in reducing the period of time from seed germination to flowering in any one generation, in order to obtain the maximum number of cycles of genetic selection in the shortest possible time. It is thus likely that both genetic and manipulative methods to obtain early flowering will be used more extensively in the future than at present, and that research will continue to be active in this area.

2. Factors Associated with Shoot Growth

The majority of woody plants do not initiate flower buds while making active shoot extension growth and in some fruit and forest tree species flowers are borne on spur shoots which make only minimal annual extension growth. Facts such as these, together with the observation that many manipulative treatments which increase flowering (e.g. bending-down branches) also restrict shoot growth, lead to the conclusion that there may often be a causal relationship between flowering and restricted shoot growth. Supporting data come from the fact that many species appear to flower best on sites which are sub-optimal for growth. Also in a number of fruit-tree species the application of gibberellic acid, which promotes stem elongation, inhibits flowering and conversely the application of growth inhibitors increase flowering. Unfortunately little is known about the natural growth-substance levels in forest trees at the time of flower initiation, although in *Cryptomeria japonica* one result of flower-inducing treatments has been to increase the level of inhibitors in the shoots (Hashizume, 1973).

However, there are opposing philosophies: thinning, fertilizer applications and irrigation of seed stands and orchards all increase flowering, and these are treatments which also increase growth. For many years there has been a widely accepted rule-of-thumb that if a fertilizer application will increase growth it will probably also increase seed production. These apparent contradictions need to be understood much more clearly, but there is some evidence that the explanation lies partly in the timing of the treatments. Although flower initiation and the period of determination may be closely linked to periods of restricted vegetative growth in many species, this does not imply that the whole tree must have a slow growth-rate at all times. Also the subsequent development of a heavy fruit and seed crop from a heavy flower-crop almost certainly requires a high general level of health in the trees, and obviously there is some parallel between general health and growth-rate.

3. Periodicity in Flowering and Seed Bearing

Trees that bear heavy crops of flowers in one year and then bear sparsely or not at all for several years are said to show periodicity of flowering. If this occurs biennially, as in many fruit trees, it is termed biennial bearing. As a generalisation periodicity is common in many broadleafed tree species and in the Abietaceae, but is less common in the Pinaceae, Cupressaceae and Taxodiaceae.

Development of a heavy flower and cone crop appears to reduce the general level of nutrients available for tree growth. In many species this is shown by a reduction in the width of the annual rings of the stem in years of heavy seed production. Thus a general theory of biennial bearing suggests that it is the reduction in the supply of nutrients to the developing buds which results in a reduction of flowering the following year. There are, however, reasons to query this explanation in forest trees, and it is also questionable whether nutrient levels in forest trees take several years to recover after a heavy flowering year, as would be necessary to explain periodic flowering in these terms. In support of the explanation, however, is the fact that periodicity is much reduced on certain sites, and these may well be ones on which maximum carbohydrate production occurs. Certainly at present the most practical method of combating periodicity of flowering in seed orchards is the correct choice of location (see pages 49–52).

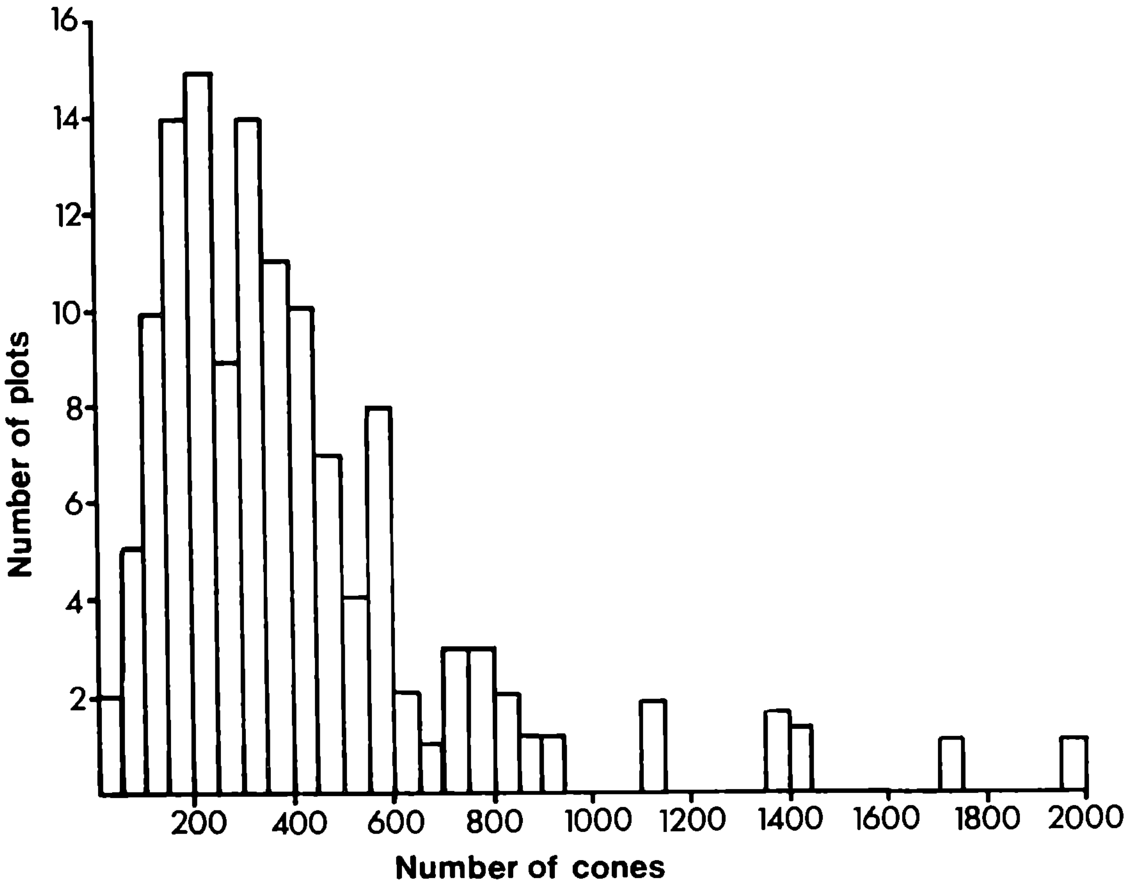


Figure 8. Frequency distribution histogram of cone production of Monterey pine, *Pinus radiata*, on 129 sites in New Zealand. Each plot consisted of 7 trees × 5 years of cones per tree. From unpublished data of D. S. Jackson, Forest Research Institute, Rotorua, New Zealand.

4. Levels of Mineral Nutrients

The levels of nitrogen, phosphorus, and potassium and a number of other elements including trace elements have been shown to influence flower production in different forest tree species. The exact nature of their role, however, is still unclear. In 1918, Kraus and Kraybill proposed that a high carbohydrate: low nitrogen ratio favoured flower initiation, and despite considerable subsequent data which threw doubt on the hypothesis, there is still recent supportive evidence. Hashizume (1973), for example, after summarising a great deal of experimental data reports that "the induction of flower bud formation in conifers is closely connected with the *decrease* of water, nitrogen and phosphorous contents, and the *increase* of insoluble carbohydrate (starch) content in shoots".

Conflicting with this is the very clear-cut and unarguable effect of fertilizer application, principally nitrogen, in increasing flowering (see page 77). Currently it is not possible to reconcile this conflicting evidence, but perhaps a clue may come from the fact that nitrogen *per se* does not appear to be important in increasing flower yields: to be useful it apparently has to be in a form which will promote some rather specific biochemical effects in the plant (see page 78). Clearly there is an important need for the role of mineral nutrients in flowering, and some of the conflicts concerning this role, to be resolved.

External Factors Affecting Flower Initiation

Since the establishment of seed orchards has become a common practice, foresters have become increasingly aware that a high proportion of the regional variability in seed production in a species is environmental rather than genetic in origin. Further information on this point has come from countries growing exotic species on a wide range of sites. Figure 8, for example, (from unpublished data by D. S. Jackson) shows a frequency distribution histogram for cone production of *Pinus radiata* on 129 different sites in New Zealand. From available knowledge of the genetic base of *P. radiata* in New Zealand it is likely that most of the variation shown in the Figure is due to environment, and such data provides immediate information on favourable seed orchard locations. Regression analyses of the data should also provide generalised information for the species concerning the climatic and soil factors which are important to flowering and seed production.

In countries where forestry practice is based on indigenous tree populations, between which there are genetical differences, it is not easy to obtain such precise information without first establishing clonal trials on a wide range of sites; but the returns from trials could well be great. Because environmental effects are so important it is necessary to review the available information on those external factors which affect flower initiation.

1. Temperature and Rainfall

Most of the information on this subject has been derived from studies which relate good flowering-years to past weather records, although some has been obtained from growth-room experiments. The weather record studies provide a pattern which seems to hold true for a large number of species which show periodic flowering. An example of this is provided in Figure 9 (from la Bastide and van Vredenburch, 1970) where cone-crop ratings for beech (*Fagus sylvatica*) and Douglas-fir (*Pseudotsuga menziesii*) grown in the Netherlands are shown to have very similar patterns over a 37-year period.

The general finding of such studies is that a warm dry summer in any year favours flower initiation and determination in that year; this knowledge is probably one of the prime factors influencing the siting of seed orchards in the Pacific north-west region of the U.S.A. today. Growth-room and moisture-stress experiments support these findings and emphasise the importance of the timing of the moisture-stress requirement (see page 77). With regard to the relationship between warm temperature and flowering it should be noted that some fruit trees have an additional winter-chilling requirement for flowering; this is almost certainly true for a number of forest tree species also.

2. Light and Photoperiod

There is considerable evidence which equates flowering with cumulatively large levels of light energy. The evidence comes from observations that it is usually the edge, open-grown, or dominant trees in a stand, with well-lit crowns, that flower; and that within these trees flowering is often heaviest on the sun-facing side of the crown. Thinning and shading experiments have confirmed this. Quantitatively the amount of light falling on a tree crown affects the rate of photosynthesis and thus the carbohydrate levels in the crown; and for at least 50 years there has been a general acceptance (in one form or another) that carbohydrate levels are important for flower initiation. In its best known form this represents the belief that the C:N (carbohydrate:nitrogen) ratio needs to be high for good flower initiation (see page 75, para 1).

In general the photoperiod affects flowering in annual species more than in perennial species. Within the Coniferae, the Cupressaceae and Taxodiaceae appear to be the only families in which flowering can be clearly influenced by photoperiod,

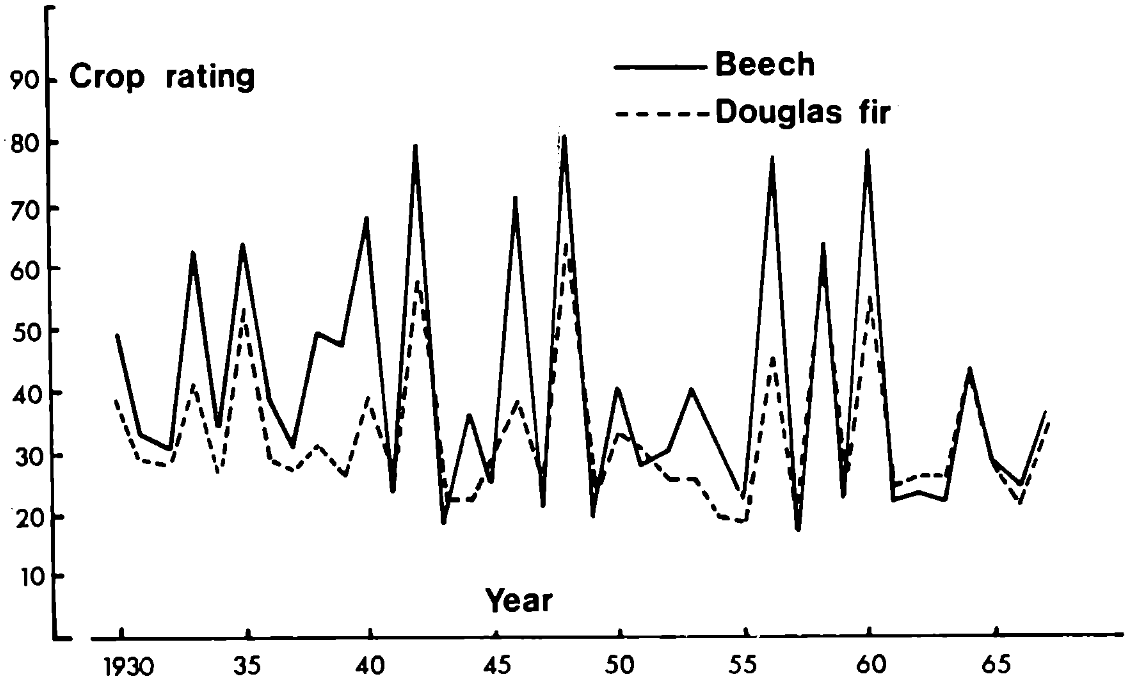


Figure 9. Cone crop ratings of Douglas-fir *Pseudotsuga menziesii*, and beech *Fagus sylvatica* in the Netherlands over a 37-year period. From la Bastide and van Vredenburch, 1970.

and until recently this had been demonstrated only when flowering was gibberellin-induced. More recently Longman *et al* (1972) have reported a striking temperature: photoperiod interaction in flower initiation in *Thuja plicata*, with maximum male and female flowering occurring under a combination of high temperature and long photoperiod.

Treatments Applied to Seed Orchards

Flower-promoting treatments which are applied to seed orchards are usually based on a knowledge of the endogenous and exogenous factors which influence flowering. They are examined here under five headings:

1. Selection of Site

This is regarded as a treatment because it is now widely accepted that the site usually contributes more to flowering than any other single factor. Several beliefs are beginning to emerge from observations on regional differences in flower yields: (i) that high annual flower yields and reduced periodicity frequently go together; (ii) that areas with hot dry summers are frequently associated with good flowering; and (iii) that good-flowering sites are frequently not the highest-quality sites in terms of vegetative growth and may not even be sites which the species occupies naturally. The site is also important to subsequent cone and seed development (see page 78). Thus there is a real need for those responsible for establishing new seed orchards to site them with maximum care and with a full understanding of the site factors which influence flower and seed development for the species.

2. Fertilizer Application

Despite some inconsistencies, failures, and a lack of understanding as to how it influences flowering, fertilizer application currently provide the success story of artificially increasing flower initiation and raising seed production in orchards. Fertilizers are now applied routinely in large areas of tree seed orchards in U.S.A. (see e.g. North Carolina State University, 1973) and in some other parts of the world.

Research into fertilizer effects on flowering has shown nitrogen to be the most important single element: phosphorus, potasssium and certain other elements have also been beneficial on some sites. Puritch (1972) provides an Appendix to his review which lists the results of a number of fertilizer experiments aimed at the improvement of flower and seed yields. These and other reports from the general literature when broadly summarised suggest; (i) that orchards must be kept adequately supplied with all the main and trace elements necessary for growth; and (ii) that orchards should, at the time of flower initiation receive an added application of nitrogen to stimulate flower determination. The timing of the nitrogen application (to coincide with flower initiation) and the type of nitrogen applied (Ebell, 1972a, b) are both important factors. Nitrogen applied in nitrate form is successful in promoting flowering in Douglas-fir whereas ammonium nitrogen forms are not, although both forms equally increase tree growth. With *Pinus* there is less information available, but ammonium nitrate is clearly a very effective fertilizer with *P. taeda* and *P. elliottii* in the eastern U.S.A. (see e.g. North Carolina State University, 1971, 1972, 1973). The available evidence suggests that the effectiveness of a nitrogen source is likely to be linked to its ability to increase the proportion of arginine and other guanidines in the soluble nitrogen pool of the shoot at the time of flower initiation (Ebell and McMullan, 1970).

The North Carolina State Co-operative Tree Improvement Programme has gone much further than the maintenance of adequate levels of nitrogen, phosphorous and potassium in the soil (R. C. Kellison, pers. comm.). Heavy annual fertilizer applications are made, first to develop vigorous trees with a framework of branching which is capable of carrying heavy cone crops, and secondly to induce flowering on those trees. The nutrient levels are based on horticultural crop needs and vary according to the soils. They include an early spring application of up to 1 100 kilograms/hectare of a 10–10–10 N P K general fertilizer plus other nutrients as required, followed by a heavy application (up to 600 kilograms/hectare) of ammonium nitrate just prior to flower initiation. Applications of this type are repeated annually until soil nutrient levels are considered optimal for heavy seed production (on the basis of horticultural experience). Thereafter maintenance applications of fertilizer are made; (i) to maintain these levels; and (ii) to provide a nitrogen boost at the time of flower initiation. The success of these treatments is evident from recent annual reports from the Co-operative.

Cultivation of the soil with a ripping tool is also used in conjunction with fertilizer application by the North Carolina Co-operative. There is little doubt that this contributes substantially to the vigour of the trees, and visual observations suggest that it may also benefit flower initiation (North Carolina State University, 1973).

3. Irrigation

There is a considerable weight of evidence to show that moisture-stress when coincident with the time of flower initiation will promote flowering, and in the light of this it may seem odd that a number of organisations now irrigate their orchards to increase seed yields. It is possible that the beneficial effects of irrigation are closely related to the timing of the operation. Thus while a degree of moisture-stress at exactly the right time promotes flower initiation, a greater availability of moisture is required prior to initiation, and for seed development. Reports by Schultz (1971) and Grano (1973) support this interpretation. Most irrigation treatments of which the author is aware, take place in the very late-summer and autumn, well after flower determination has occurred. If the understanding of these processes is correct, it would be sensible to deliberately choose orchard sites which enjoy dry summers, and to irrigate following flower determination. In some places there appears to be a strong interaction between irrigation and fertilizer applications: the combination of treatments being more effective than either alone in terms of cone production. In south-eastern U.S.A. a side benefit of irrigation, when applied prior to anthesis, is that flower emergence can be delayed for up to two weeks which can avert cold-damage to the developing flowers (R. C. Kellison, pers. comm.).

4. Root, Stem and Crown Treatments

These fall into two categories: (i) treatments such as root-pruning, stem-girdling or banding, shoot-pruning and shoot-bending; and (ii) crown-release treatments. Both have been practised in horticulture for many years and are aimed generally at creating high carbohydrate levels which are believed to be conducive to flowering.

The literature on application of the treatments under (i) has been reviewed by Matthews (1963) and Puritch (1972), and in the horticultural field by Zimmerman (1972). Additionally, Faulkner (1966), has reported on numerous experiments carried out in Great Britain. There is an obvious and major objection to some of the treatments on the grounds of the long-term effects they have on the health and condition of the trees, but in the short-term there is no doubt that they can often be very effective in stimulating flowering. A consensus of the reviews suggests stem- and branch-girdling to be very effective techniques, particularly if applied at the correct time. In many species this appears to be the time of bud initiation (Puritch, 1972; Hashizume, 1973). Root- and shoot-pruning treatments have been less consistent in their effects.

Crown-release clearly falls into a different category from those discussed under (i) in that there is no adverse long-term effect. On the contrary it is beneficial to the general health of the tree. Wide initial spacing and subsequent thinning are generally regarded as crucial in seed orchards if heavy flower-crops are to be obtained.

Application of Plant Growth-substance

The use of gibberellins to induce flowering in the Cupressaceae and Taxodiaceae has been an outstanding success, and gibberellic acid is now applied as a standard seed orchard treatment in many Japanese orchards (R. Toda, pers. comm.). The Cupressaceae and Taxodiaceae produce their flowers terminally on the branches, and appear to differ in a number of respects from other coniferous species which produce flowers in leaf axils. The prospects of obtaining similar results from gibberellin applications in genera without terminal flowers had until recently been considered unpromising. However, preliminary results from applications of very large amounts of gibberellins to Douglas-fir and Lodgepole pine indicate that there may be possibilities with these species (Ross and Pharis, 1973; Pharis *et al*, 1974).

Because flower initiation is often associated with a reduction in shoot extension, plant growth-inhibitors have been applied to induce flowering in a number of fruit tree species. Frequently this has been successful, but there are a few encouraging examples with forest trees. Plant growth-substances, however, have been successfully used both outside as well as within the Cupressaceae and Taxodiaceae for changing the sex of developing flowers. In *Pinus* there is evidence that a high auxin level may be associated with the development of female flowers, and a lower level with the development of male flowers.

Treatments other than auxin applications which change the male to female flower ratios in *Pinus* have been defoliation, bud removal, bagging with different coloured paraffin-waxed bags, stem-bending and applications of nitrogen and phosphorous fertilizer. Reversal from a male to a female flowering condition has been more common, but changes in the opposite direction have also been obtained. In addition to the review papers, considerable data on this subject are presented by Hashizume (1973).

In general all flower-promoting treatments which increase flowering at all, do so in clones (or provenances or species) which have some capacity to flower without treatment. The fact that treatment is essentially unhelpful to poorly flowering clones is of major importance when the wide range of clonal variability in flower initiation in many orchards is considered. Figure 10 (from Eriksson *et al*, 1973) illustrates this variability with male and female flower-production data for 22 clones of *Picea abies* in Sweden. These data are typical of the clonal variation shown in a number of orchards of different forest tree species.

The prospects for markedly altering such a pattern by flower-inducing treatments do not appear to be good; and this being so it should be accepted that one of the most important ways of increasing the total flower production in an orchard is to use only those clones which (while being desirable on growth and/or other counts) are capable of heavy flowering.

Acceptance of this concept implies a need for the very early recognition of clones with a high flowering potential, and raises the question as to whether this can be done on the basis of correlated non-reproductive features. A search for such features could be valuable.

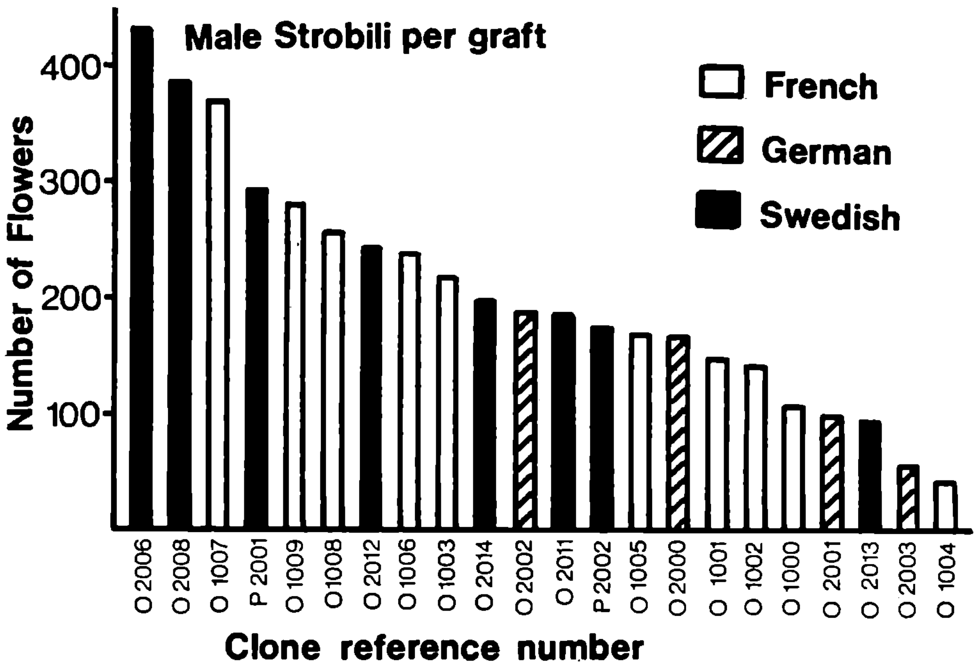
Flowering Records

Most seed orchard theory is based on the assumptions that panmixis will occur and that selfing will not be a serious problem. Panmixis is dependent, among other things, upon each clone producing similar numbers of ovules, similar numbers of viable pollen grains, completely random fertilization and perfectly synchronised flowering times. However, in practice each clone in an orchard behaves differently, some clones being predominantly male or female, or very late or early in developing flowers. Thus wherever possible it is important for the orchardist to record both the quantity of male and female production, and also the period of female flower receptivity and pollen shedding. These factors may then be considered along with other criteria when "roguing" of the orchard is planned. A simple method of recording flowering dates is illustrated by Larsen (1956, page 176) and detailed methods of recording amounts of flowering, by date, are given by Eriksson *et al* (1973).

CONE AND SEED DEVELOPMENT

Many of the factors affecting the development of flowers in forest trees, from the time of determination until seed collection, have been recently reviewed (Sweet, 1973). This section, as the previous one, essentially summarises an existing review to which the reader is referred for documentation of the statements made.

Throughout the plant kingdom generally the loss of reproductive material is very high between flower initiation and seed maturity; forest trees are no exception. On some sites many of the losses may be due to damage from insects, fungi, birds and mammals and these are dealt with in Chapter 6.



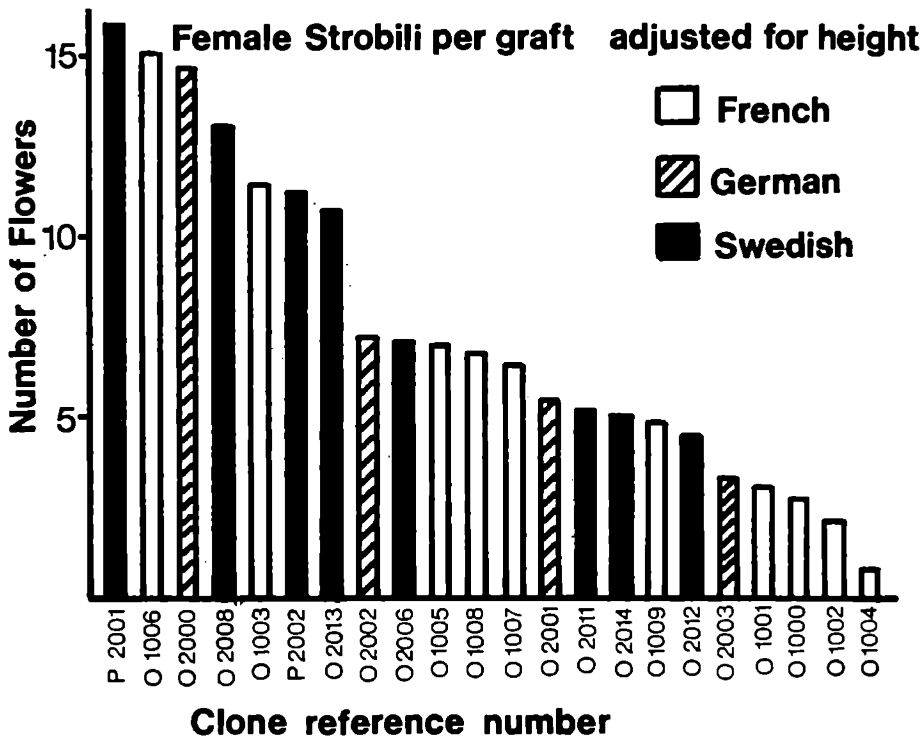


Figure 10. Male and female flower production per graft for 22 clones of Norway spruce, *Picea abies*, in Sweden. The counts have been adjusted on the basis of a standard tree height of 214 centimetres. From Eriksson *et al*, 1973.

This section is concerned solely with that proportion of the loss which is due to factors which may be classified as physiological and/or climatic in origin; quantitatively they are important. In *Pinus* for example, some 50 per cent of potential seed is lost for these reasons, and in *Quercus* a 90 per cent loss has been recorded. In *Eucalyptus* the loss has been recorded of a potential 40 million viable seeds per hectare in a year when the actual seed crop was only 6 million (Grose, 1960).

1. Loss During the Period between Initiation and Anthesis

As mentioned in the previous section there is in many species a time lag between flower initiation and an irreversible commitment to flowering. There is no doubt that much flower "loss" results from the "decision" of structures with floral potential to abort or to develop vegetatively rather than florally; and, as stated previously, many of the effects of flower promoting treatments may be to keep these structures in the floral condition.

In many species there seems to be little subsequent loss of male or female flowers from the time when the commitment to flower is irreversible until after anthesis. Some *Eucalyptus* species are exceptions, with, for example, the pre-anthesis abscission of flowers causing the major loss of reproductive material in *Eucalyptus pilularis* (Florence, 1964).

In terms of individual ovules and pollen grains however, as distinct from whole flowers, there may be problems during the period between determination and anthesis. There is a considerable Swedish literature (see e.g. Eriksson *et al*, 1972) which reports the effects of low temperatures on pollen meiosis in a number of conifers. It seems clear that cold-damage during this extended period can lead to wide-spread meiotic irregularities and a subsequent inability of the pollen grains to effect fertilization. Ovule development occurs in a number of conifers during the winter, and there is evidence that the percentage of ovules which develop to a stage where they are functional and capable of pollination can be influenced quite strongly by climate and site. As yet there is no reliable information on which climatic factors influence the number of deficient ovules, but clearly seed orchards should not be established on sites which are susceptible to very severe frosts.

2. Loss During the Period between Anthesis and Seed Maturity

During the period in which pollen germination, fertilization and seed development occur, loss of potential seed may take place at a number of different developmental stages and in a number of different ways.

1. Ovule Abortion

Data from Sarvas (1962) show a 25 per cent abortion of fully functional ovules in *Pinus sylvestris* in Finland. Developmentally the first ovules to abort are generally those which are not pollinated, and only a few forest tree species can develop viable seed from unpollinated ovules (agamospermy) it is particularly rare for gymnosperms to do so. In genera such as *Pinus* where ovule growth and development is slow, the seed coats of non-pollinated ovules fail to develop: in *Pseudotsuga* and *Picea*, however, seed development is considerably more rapid, and non-pollinated, aborted ovules develop to form empty seeds. Pollinated ovules also may abort prior to fertilization, and there is some evidence that this abortion results from the failure of ovules to compete successfully with other ovules for metabolites.

2. Drop of Developing Flowers and Cones

This is a widespread phenomenon in most species of forest trees, and in *Pinus* generally it is the major cause of loss of potential seed. In data published for a large range of pine species, the drop of flowers after pollination averages about 40 per cent. Two reasons have been put forward to explain this drop: (i) that it results from a high incidence of ovule abortion following poor pollination; and (ii) that it results from competition between developing flowers, and between flowers and vegetative shoots, for carbohydrates, mineral nutrients and water. Almost certainly both these factors are causal in different species and in different environments, but it is also possible that other factors may be causal in other species. Certainly the problem is not a simple one and there is a major research need for techniques to solve it (see page 81).

3. Embryo Abortion

Many forest tree species have multiple archegonia which, after fertilization, produce a number of pro-embryos. In these species empty seeds may be produced either, (i) by all of the pro-embryos failing to develop, or (ii) by one becoming dominant and developing normally for a time and then dying at a later stage. Embryo abortion reaches a high level after self-fertilization when it has an obvious genetic function, however, it can also occur following climatic damage (Andersson, 1965). The latest stage at which embryo abortion occurs is during seed germination (Ching and Simak, 1971). Sarvas (1962, 1968) presents typical figures for embryo abortion in Finland of 14 per cent for *Pinus sylvestris* and 20 to 40 per cent for *Picea abies*.

Seed Orchard Management Procedures Aimed at Reducing Potential Seed Loss

1. Selection of Site and Clones

Choice of site is one of the most important management procedures, and in *Pinus* and *Pseudotsuga* geographic location and site have been shown to influence both the total number of ovules present in a cone, and the percentage of these which develop and become fertile. It is probable that site affects other genera in a similar way. There is a real need for this type of information to be categorised and used for guidance in the selection of orchard sites.

One factor influencing ovule abortion is the quantity of pollen available, and pollen production of *Pinus sylvestris* in Finland has been shown to be greatly influenced by site. Damage to pollen by low temperatures at the time of meiosis is obviously avoidable by the correct choice of seed orchard location, and there is some evidence also that the abortion of pollinated ovules may be influenced by site. Site has a profound effect on the incidence of conelet-drop in *Pinus radiata* in New Zealand where the correct choice of site can reduce drop from more than 90 per cent to about 40 per cent. This effect does not relate to pollen levels and in part reflects the timing of vegetative shoot extension vis-a-vis flower development; conelet-drop is at a maximum when shoot extension occurs at a time close to anthesis. Embryo abortion, to the extent to which it is affected by adverse climatic conditions, is also influenced by site.

Clonal differences are observed in all these respects and may either reinforce or offset clonal differences in flowering. Thus a heavy flower-initiating clone with a high incidence of conelet-drop may contribute less seed to the orchard than a moderate cone-producer with a low level of drop. Clonal differences in seed yield per clone may also be striking: a report by the North Carolina State University (1973), for example, refers to one southern pine clone which contributed nearly 50 per cent to the volume of cones from an orchard, but produced only six sound seeds per cone compared with well over 100 for the average clone.

2. Applied Treatments

The application of treatments such as fertilizer, irrigation and sub-soiling, on other than extreme sites has not been particularly successful in reducing conelet-drop and embryo abortion. The treatments may, however, influence the abortion of pollinated ovules to some degree. Reports on extensive tests of various chemical sprays indicate that these too are seldom effective. It is certain that further research will continue into these and other treatments (see e.g. North Carolina State University, 1973), but at present it appears that prevention of losses of potential seed during development lies mainly in the careful selection of orchard sites and clones.

CONCLUSIONS AND SUMMARY

The seed orchard manager faces a two-pronged problem: (i) to obtain the maximum number of flowers possible in his orchard, and (ii) to manage the orchard in a way which ensures the minimal loss of potential seeds from these flowers.

Choice of site cannot be over-emphasised. Favourable sites for most species will have dry warm summers, and soils which are both suited to plant growth and also physically capable of being cultivated, fertilized and irrigated; they may well be in areas which are sub-optimal for vegetative growth of the species. To maximise seed yields the orchard should be composed of clones with a high capability to flower and to set a large number of full seeds. There is a need to identify early and eliminate clones which will not make effective contributions of seed (or pollen) within a reasonable length of time. There is also a most important need to keep the orchards thinned to an extent where all the tree crowns receive adequate amounts of light.

Of all orchard treatments, other than thinning, which are applied to increase seed yields, by far the most successful to date has been fertilizer application, with nitrogen being the most important element when applied at the right time and superimposed on a good general soil level of all other essential elements. The effects of fertilizers have sometimes been improved by cultivation, and on dry sites by irrigation. The literature suggests a clear need for orchardists using these techniques to identify precisely the time of flower initiation and determination for their particular sites and species and to time their applications carefully with respect to these. In particular, timing appears to be important for irrigation treatments.

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CHAPTER 8

NATURAL POLLINATION IN SEED ORCHARDS WITH SPECIAL REFERENCE TO PINES

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Introduction

Seed orchards are now being established on a considerable scale and in the U.S.S.R. almost 21 000 hectares of pine, spruce and larch orchards are planned for completion by 1980 (Chebotariev, 1972). Finland plans to have 3 400 hectares of Scots pine orchards and Sweden 600 hectares.

The mode of pollinating the female strobili affects both the amount of the seed crop and its genetic value. Light pollination perceptibly reduces the seed crop (Sarvas, 1962) and pollen from outside an orchard may reduce the genetic gain by a half and produce seed of questionable value. Pollination processes within a seed orchard pose much greater problems than were anticipated when orchards were first established on matters concerning pollen dispersal in wind-pollinated forest tree species and orchards (Koski, 1970; McElwee, 1970; Schmidt, 1970; Hadders, 1972; Stern, 1972). The present position is still confused and results and opinions from these studies are often contradictory and particularly with regard to the isolation of the orchards from foreign pollen. This raises the question of possibilities of error in the methods of measurement, the interpretation of results and, perhaps, insufficient attention to the fact that the studies dealt with different species and extremely variable conditions.

It is obvious that the orchard and its surrounding area affect pollination. Conditions vary widely between orchards and therefore problems associated with pollination patterns must be resolved separately for each orchard. However, where there are many orchards, as in Scandinavia for instance, it is impracticable to study each orchard individually by measuring the pollen levels in different years. What is often required, therefore, is some method of assessing the situation in an orchard with the help of fairly easily obtained basic information. This chapter suggests possible ways in which this might be done on the basis of experimental studies. It has particular relevance to countries similar to Finland where most of the country is under 200 metres and where almost 60 per cent of the area is under forest.

The problems associated with pollination in orchards are: inbreeding; amount and composition of cross-pollination within the orchard; and pollination from sources outside the orchard. Inbreeding is discussed in Chapter 11.

Pollination Within a Seed Orchard

Successful wind-pollination in a forest stand requires large quantities of pollen and Sarvas (1962, page 50) states that 20–30 kilograms of pollen per hectare is needed in a large Scots pine (*Pinus sylvestris*) stand for average pollination. In years when male flowering is profuse the amount of pollen exceeds 100 kilograms/hectare in south Finland. It can be assumed, therefore, that tens of kilograms of pollen are required to achieve really satisfactory pollination in pine orchards. Smaller quantities of pollen will result in inadequate pollination regardless of whether there are numerous or few female flowers. The probability of any air-borne pollen grain impacting a female strobilus is in any case very small and the probability of pollinating a female strobilus must depend on the density of the pollen cloud.

Both pine seedlings and grafts usually pass through a period when only female flowering occurs; male flowering first begins several years later. Thus if the female strobili on the grafts on young orchards develop into cones which contain sound seeds, pollination must have occurred from pollen sources outside the orchard. Male flowering in young orchards remains light for many years and is completely insufficient for adequate open-pollination purposes.

Direct measurement of the pollen crop from an orchard at different stages of development is difficult to perform but it is a simple and fairly easy operation to measure the amount of male flowering on the basis of the traces of male flowers which remain on the shoots. Pine male flowers occur around the basal end of the current annual shoot. The stamina fall after flowering to leave a measurable space between the base of the shoot and the first needle fascicles beyond the flowering zones. By collecting all the pollen from sample branches and then measuring the combined length of those parts of the shoot which produce male flowers it is easy to calculate the weight of pollen produced per 1 centimetre of pollen-bearing shoot. On the basis of samples from 27 Scots pine clones it has been calculated that 1 centimetre of male flower-bearing shoots yield an average of 0.028 grams of pollen. The variation between clones ranged from 0.013 grams to 0.072 grams.

The length of the male flower-bearing shoots was measured on 220 grafts together with the height

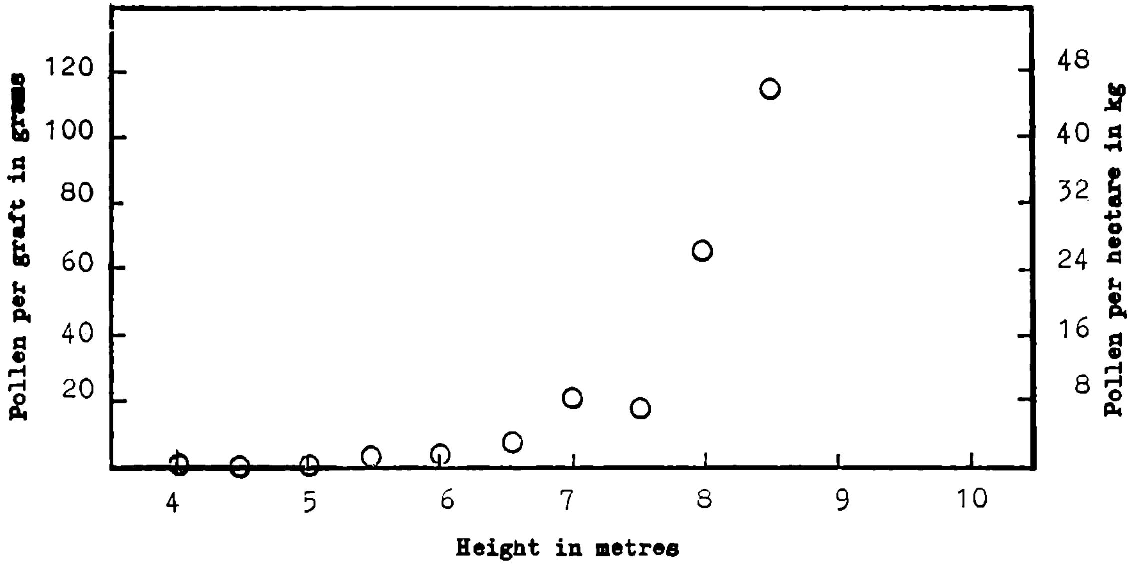

Figure 11. Average annual pollen crop from free-grown grafts of Scots pine of various heights.

and breast-height diameter of the same grafts and by simple calculation estimates were obtained of the quantity of pollen produced per graft. Figure 11 is a graph showing the expected pollen crop from individual grafts of different heights and the pollen production from 400 grafts per hectare.

Figure 12 provides similar data for grafts of different breast-height diameters. The grafts on which Figures 11 and 12 were based were not identical. Grafts used to provide data for Figure 11 had not been topped whereas the grafts used to provide data for Figure 12 had been topped to limit height growth.

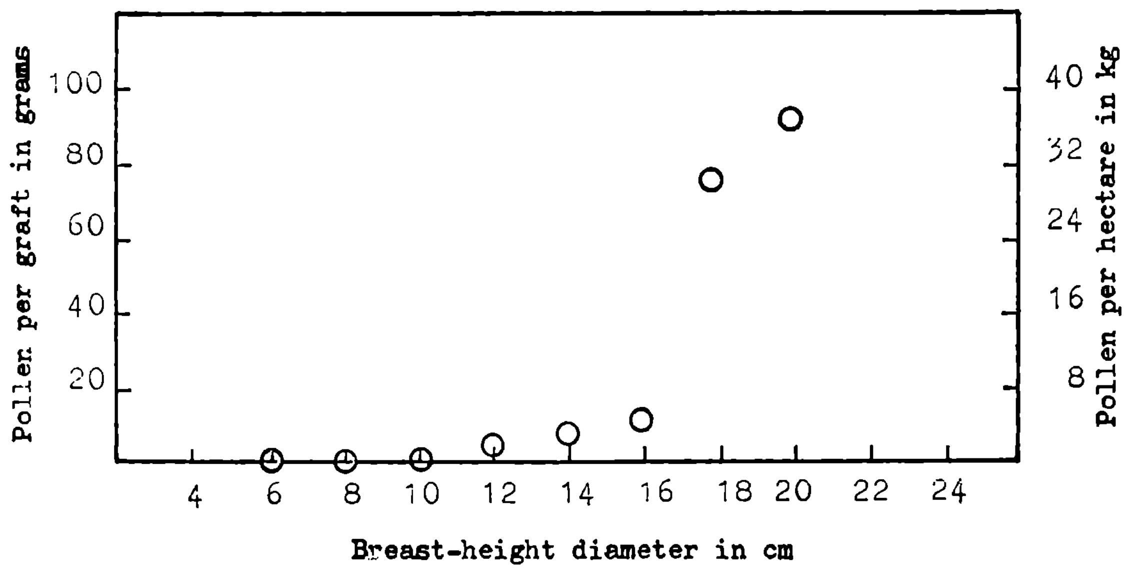

Figure 12. Average annual pollen crop from Scots pine grafts of different breast-height diameter classes. (A proportion of the grafts had had their tops removed.)

From this information it can be seen that Scots pine grafts should be allowed to grow to over 7 metres or to breast-height diameters of over 16 centimetres before the amount of pollen exceeds 20 kilograms/hectare. It is the author's opinion that in the early years the pollen crop is closely correlated with crown size rather than the age of the grafts, although small grafts can be made to flower profusely by certian treatments, for instance, drought or strangulation, the total pollen crop per hectare will still remain relatively small since the total number of flower-bearing branches remains the chief limiting factor.

Pollen which is shed during the pollen migration phase is mixed with a large volume of air and borne rapidly away from its launching site. For this reason the density of the pollen cloud is low in a small stand and the female strobili are poorly pollinated even when male flowers are abundant. This phenomenon is very manifest in small-sized plantations of exotic species, where quite commonly only individual pollen grains are caught in pollen samples. However, when the same species occurs in the neighbourhood of an orchard, pollen will obviously infiltrate from the outside sources and the scarcity of internally-generated pollen may be overlooked.

The importance of orchard size on the amount of pollination is difficult to assess. First, there is the difficulty of collecting empirical data from the orchards themselves and if satisfactory comparisons are to be made pollen-catch data should be collected in mature orchards of different sizes, including some which are too small for effective pollination. In the absence of suitable orchards data has been collected from Scots pine stands. Much data on the abundance of flowering and the pollen-catch has been accumulated during Sarvas' long-term and extensive studies (1955, 1962, 1968, 1972) from which it was found that the measured pollen-catch in relation to the pollen crop is much less in small stands than in large stands. For a more accurate analysis of the phenomenon Koski (1970) calculated ratios for the measured catch and the quantity of pollen produced. The values were calculated by dividing the measured catch value (grains/square millimetre) by the pollen yield (kilograms/hectare). The ratios were multiplied by 10^{-10}, the product of which was termed the *pollen-catch equivalent*. The size of each stand was described by the radius of the largest circle which fitted into the stand. Regression analysis showed that an equation of the form

$$y = ae^{\frac{b}{x}}$$

explained best the dependence of the pollen-catch equivalent on stand size. Measurements were continued in the same stands and the new means were calculated for the pollen-catch equivalents. The results are presented in Table 9.

TABLE 9

POLLEN CATCH EQUIVALENT IN SCOTS PINE STANDS OF DIFFERENT SIZES

Location and Stand No.	Period of observations	Radius metres	Pollen-catch equivalent
Bromarv 40	1965–1966		
	1968–1971	16	11.7
Punkaharju 306	1965–1971	20	4.7
Punkarkarju 100	1964–1972	30	18.7
Punkaharju I	1964–1972	46	34.3
Bromarv III	1965–1972	58	38.9
Kerimäki XX	1965–1971	70	32.9
Punkaharju	1964–1971	80	52.6
Kuorevesi XXIII	1964–1971	85	49.2
Vilppula 2a	1965–1969	120	53.1
Rovaniemi XXVII	1964–1971	130	43.7
Bromarv II	1964–1969	135	52.8
Heinola 566	1965–1971	140	60.4
Tuusula XXXII	1964–1969	155	54.1
Kerimäki XXXIII	1965–1971	170	69.5

The regression curve, drawn on the basis of the calculation, is satisfied by the equation

$$\log_e y = 4.26 - 38.5 \cdot \frac{1}{x}$$

The observed values, the regression curve and the asymptote of the equation are given in Figure 13 from which it may be seen that as long as the stand radius is less than 80–100 metres the regression curve rises fairly sharply.

From this it may be deduced that there is little merit in establishing pine orchards less than 3–4 hectares in area.

The pollination process presupposes that pollen grains impact female strobili when borne by the wind and the higher the wind velocity the greater the quantity of pollen that impacts a female strobilus in a given time interval. Koski (1970, page 18) noted that the pollen-catch, measured at a height of 1 metre above the ground in a stand, is only a fraction of the catch measured simultaneously at canopy-level in the same stand. Even greater catch figures were recorded 100–200 metres above ground-level. Later measurements of the density of pollen grains in the atmosphere, however, have allayed

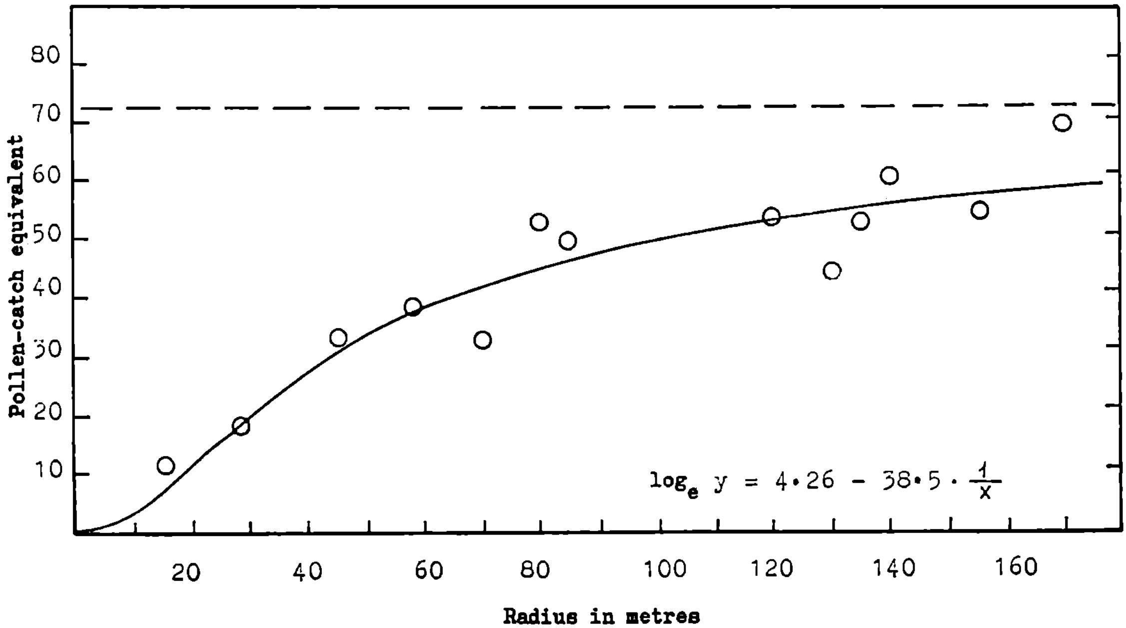

Figure 13. Correlation between the pollen-catch-equivalent and stand size for Scots pine. The values are denoted by small circles. The regression curve (unbroken line) plotted from the regression equation and the asymptote (broken line). The regression model explains 84 per cent of the variation in the pollen-catch-equivalent.

the fear that pollen density increases from the ground upwards. The density of pollen grains was measured in a single stand in 1970–1973 at 2 metres and 25 metres above ground-level with the aid of spore traps and globe-samplers together with recording meters placed at canopy-level for the measurement of pollination time. Apparatus was unavailable for recording wind velocity. The results are summarised in Table 10. The results from the pollen densitometers (spore traps) indicate the number of pollen grains sucked into a device per square millimetre of the aperture. The number of pollen grains per square millimetre of the cross-section of the globe-sampler was calculated to provide comparative data. The table shows that the pollen density was generally slightly higher at 2 metres than at 25 metres, however, the catch measured at 2 metres was only about one-fifth of that measured at 25 metres. Wind velocity was measured on two different days during the study at heights of 2 metres and 25 metres above ground level. On the first occasion the recorded wind speeds varied from 2–4 metres/second and 4–8 metres/second at 2 metres and 25 metres height respectively. On the second occasion the respective wind speeds were 2–3 metres/second and 5–10 metres/second. The difference in wind speed between 2 metres and 25 metres was, therefore, approximately two- to three-fold and fully explains the differences established in the pollen-catch.

TABLE 10

SCOTS PINE, PUNKAHARJU: POLLEN DENSITY AND POLLEN CATCH AT DIFFERENT HEIGHTS: GRAINS PER SQUARE MILLIMETRE

Time of measurement	Density of pollen		Pollen catch	
	2 metres	25 metres	2 metres	25 metres
1970, June 6–19	458	316	102	522
1971, June 5–20	115	98	146	692
1972, June 6–24	357	300	98	421
1973, June 1–18	232	238	882	348

Wind speed and the associated turbulence effects are of practical importance in orchards and in Chapter 11 it is reported that cones collected from the lower crowns of grafts contain more empty seed as a result of self-fertilization than those collected from the upper crown. This is often due partly to the occurrence of male flowering in the lower crown and partly to the smaller total pollination in the lower crown where wind velocities are much lower. A different phenomenon has been noted in a young pine orchard on top of a high hill in central Finland. The orchard is surrounded by spruce forest which was expected to provide good isolation against foreign pollen. The orchard was too young to produce significant amounts of pollen yet higher pine pollen-catches were made than those associated with catches made at canopy height in pure pine stands, and the high frequency of full seeds provided confirmation of abundant pollination. The greater exposure to pollen-bearing winds moving over the high hill provides a possible explanation.

Once an orchard is well established the natural wind movement within it cannot be influenced to any appreciable extent unless it is under thinned or surrounded by dense plantations.

The pollen composition within an orchard is affected by the clonal variation in pollen production and period of release and the distribution and positioning of ramets of the different clones. The period of pollen shedding and female flower receptivity also influence the crossing pattern between clones. In practice information on the flowering habit is seldom available at the time of establishment of an orchard but it is recognised as desirable that each clone in an orchard should be given an equal opportunity to out-cross with all the other component clones. In the absence of reliable information on flowering with regard to amounts, proportions by sex and period the following guidelines should be followed when establishing an orchard.

1. Use only clones which are likely to have well-matched flowering periods. In practice this usually means that the component clones are derived from a limited geographical area.

2. Use a great many clones and certainly not less than fifty, to minimise self-pollination and to ensure that clones which produce large quantities of pollen do not dominate the pollination.

3. Use equal numbers of ramets of each clone. This is often very difficult to achieve particularly when grafting successes are variable in the nursery and, therefore, for practical reasons alone, some flexibility must be allowed. A preponderance of a few clones in the orchard-mix can lead to higher self-pollination and higher proportions of cones from the commonest clones. In Finland variation within maximum limits of $\pm$ 30 per cent of the *average* number of grafts per clone is regarded as acceptable.

4. Use a planting design which ensures that the clones are evenly distributed within the orchard (see Chapter 3). This again ensures that self-fertilisation risks are minimised; McElwee (1970) calculated that related individuals should be kept at least 30 metres apart to avoid inbreeding.

Pollination from Outside Sources

In an ideal orchard, cross-pollination will occur only within the orchard. In practice, however, wind-borne pollen from outside sources will enter an orchard and such pollen must be given due consideration since it may participate in the pollination of orchard flowers.

Pollen which reaches an orchard from an outside source is a straightforward case of migration of one population to another. The effect of migration on the gene frequency of the receiving population is expressed by

$$\Delta q = m \cdot (q^2 - q^1)$$

in which m denotes the proportion of immigrants, q^1 the gene frequency in the acceptor population and q^2 the gene frequency of the donor population. Pollen dispersal always involes gamete migration and hence the maximum value that m may obtain is 0.50, when all the pollen comes from outside. A transient phase of development like this often occurs in young orchards which bear female flowers but which are not themselves producing pollen. Cone crops from orchards in such a state of development are usually ignored for practical purposes.

Pollen from outside an orchard, referred to as background pollen, is mainly derived from local forests of the species in question and it is obvious that the amount of background pollination will reflect the size of any local source. Koski (1970) examined the magnitude of background pollination in the pollination of normal forest stands of different species. In his analysis the magnitude of background pollination was compared with pollination measured in a pure, tended stand of each species. The ratio was called the *background pollination index*. To describe the abundance of each tree species a product, the *indicative product*, was calculated on the basis of the percentage of forest land and the percentage of the tree species in question as represented by its basal area. Figure 14 shows the abundance of the tree species studied and the background pollen index which is surprisingly high for Finland's commonest tree species Norway spruce and Scots pine. It also shows that the background pollination index is in linear correlation with the abundance of the tree species.

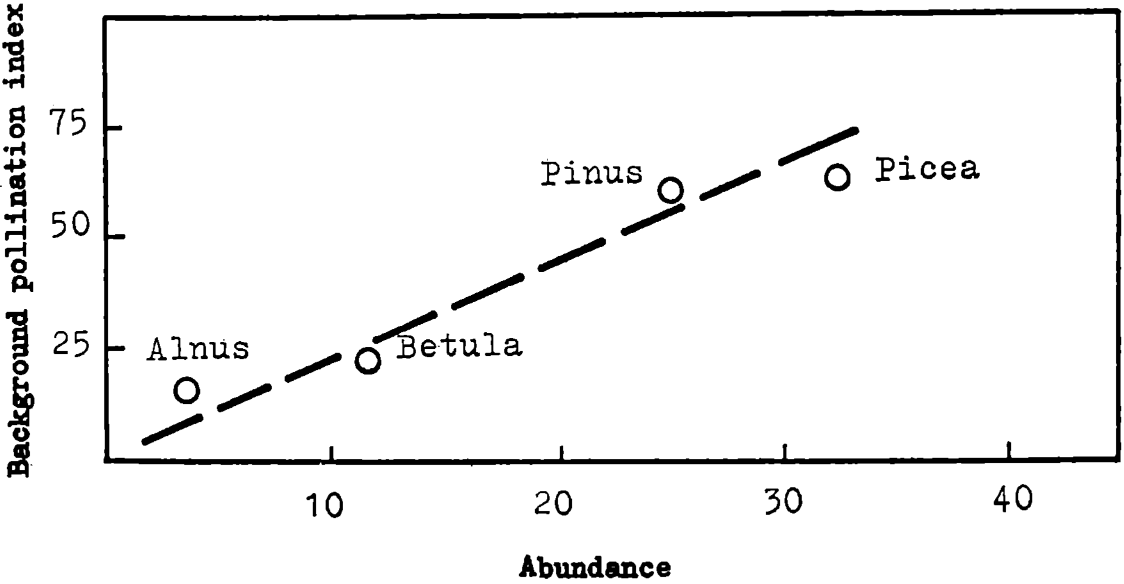

Figure 14. Abundance of some tree species and their background pollination indices in south Finland.

This indicative product can be used for the evaluation of the size-class of background pollination in orchards and even for other tree species.

If a species is common in an area the background pollination cannot be reduced significantly by an isolation zone of, for example, 50 metres but, if the species is relatively uncommon, then clearing a surround to the orchard will significantly reduce background pollination to very low levels. To assess the significance of background pollination with the aid of Figure 14 a figure, denoting the abundance of a tree species, within a radius of 50–100 kilometres must be taken into consideration.

In practice the significance of background pollination in an orchard may be much less than calculated since the pollen yield in well-tended orchards, greatly increases with age in comparison with normal stands. Seed orchards are often greater in area than the stands on which the values in Figure 14 are based. Furthermore, even a small time difference in flowering between an orchard and the surrounding forest greatly improves the situation.

When plant material is transferred over considerable distances, as is often the case in the establishment of an orchard, there is a change in the time of flowering in comparison with the original source. In natural populations the timetable of the annual cycle of development is genetically adapted to the climate and seasonal changes of the particular area. Flowering occurs at the start of the growth-period and it follows that differences in flowering times between material of different origins growing in the area cannot be very great in absolute terms. Even transfers over long distances usually fail to induce flowering at completely different times to the period of general flowering of the surrounding forests. In conifers the female strobili open a few days before the male flowers shed pollen and this factor, coupled with the limited volume of the ovule pollen chambers, reduces the significance of delayed background pollination in the orchards. Time differences of this kind can be extended by establishing orchards in areas which have an earlier and warmer spring period than in the natural habitat of the parent plus trees.

For successful wind-pollination it is essential that the periods of receptivity of the female strobili and pollen shedding are well synchronised. Sarvas (1967, 1970) reported that if flowering is related to a temperature-sum scale then flowering in Scots pine will occur in both single trees and over an entire forest exactly in the middle of the period when the male flowers are open. It is known, morevoer, that the temperature-sum of the median of the flowering period is a constant 17 per cent of the duration of the whole growth period in all years (Sarvas, 1967b). From this it is possible to predict by measurement and calculation the mutual time-relationship of an orchard's own pollen and background pollination. The procedure can best be illustrated by an example.

Scots pine in northern Finland has the shortest possible growth-period which can be expressed as a temperature-sum (above a + 5°C threshold) of

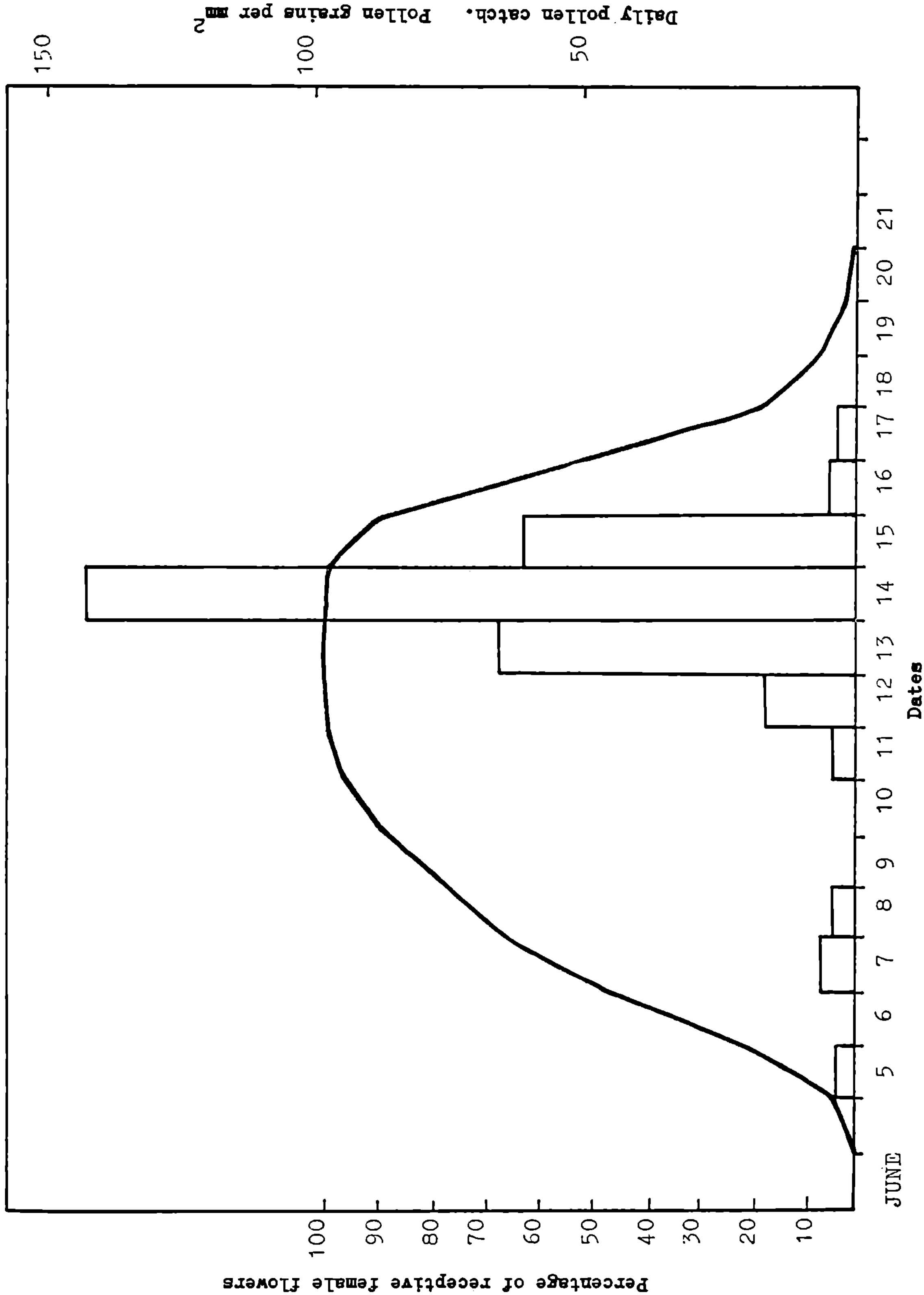

Figure 15. 1968 timetable showing the period of female flower receptivity (curve) and amounts of foreign pollen (columns) in the clonal Finnish Scots pine Seed Orchard No. 22.

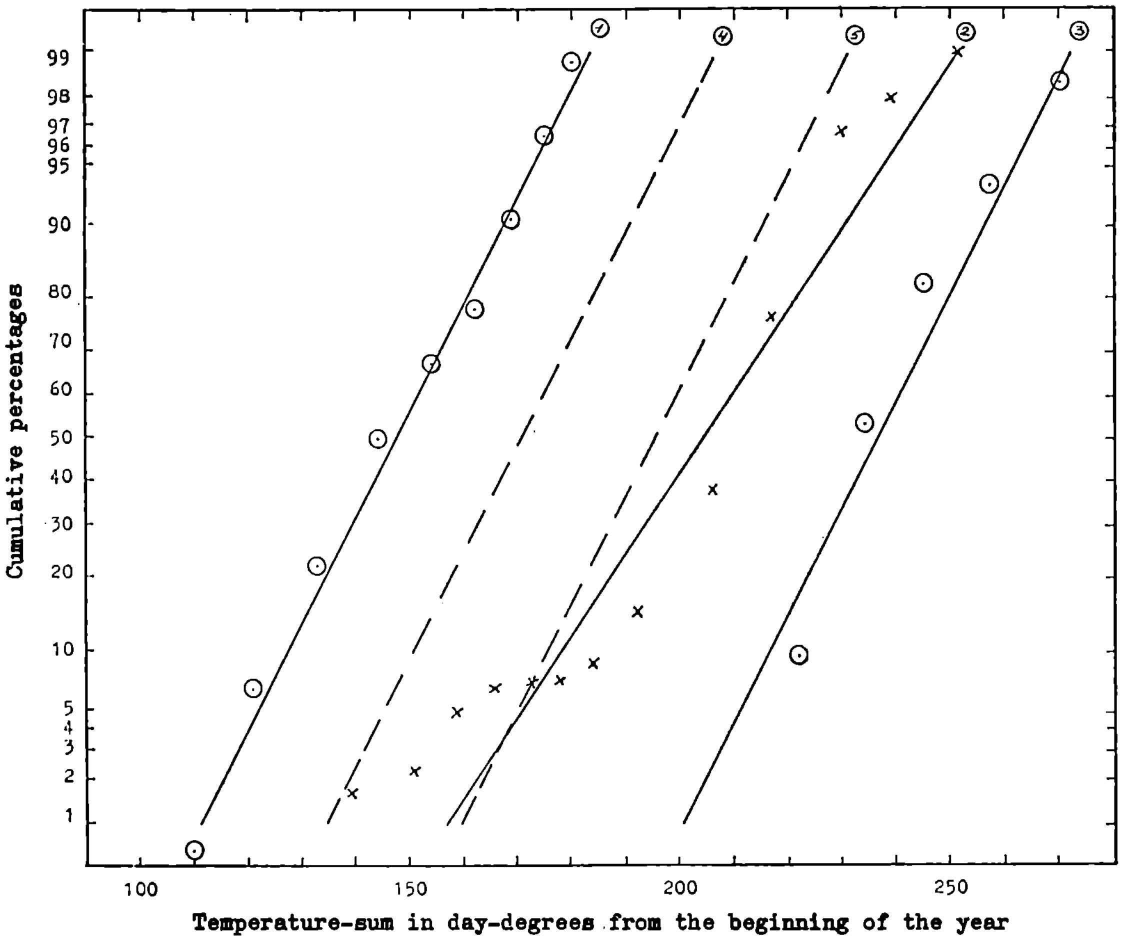

Figure 16. Analysis based on 1968 data collected in Scots pine Orchard No. 22 showing the significance of temporal isolation of Scots pine seed orchard material moved 500 kilometres to the south. Curves are numbered at the top of each.

1. Opening of female strobili; small circles denote the observed values,
2. Background pollination; the crosses denote the observed values.
3. Closure of female strobili.

N.B.—All lines have been drawn free-hand.

4. The broken line shows the time of anthesis of orchard grafts when pollen production has begun.
5. The broken line shows the expected timetable of female strobili closure when within-orchard pollination is adequate.

about 950 day-degrees. Grafts of northern pines have been transferred to central Finland where the mean temperature-sum of the growing period is about 1,100 day-degrees. The duration of the growth period in central Finland is, therefore, approximately 15 per cent longer than in the north. This difference should be discernible in the time of flowering and pollination in orchards. Since 1968 observations have been made in some orchards on the period of pollen-shedding and the period and magnitude of background pollination have been measured. The measurements were made in young orchards pollinated entirely by background pollen. The development of female strobili was judged daily by eye from a permanent set of grafts taken at random. Each time the number of strobili which had passed the stage of opening or closure were counted and their proportion of the sample was calculated. The cumulative percentage of open *versus* closed was then plotted against dates (or daily temperature sums) so that the mean could easily be found by graphical methods. Receptiveness was regarded as the time between flower opening and closure. The pollination timetable was studied with the aid of pollen samplers which collected pollen grains which drifted into them (see Sarvas, 1962 and 1968; Koski, 1970b). Since female strobili are wind-pollinated this method of assessing flowering gives a good indication of the time of pollination. The total amount of pollen was measured more accurately by 30 millimetre diameter globes. Figure 15 shows the daily timetable in 1968. In Figure 16 the same data are presented in a different manner.

It can be seen from Figure 15 that a relatively long-distance transfer of material (about 500 kilometres to the south) did not induce complete temporal isolation since all the female strobili were open when most of the background pollination arrived. However, it should be noted that the period of female strobili receptivity is prolonged in the absence of pollen at the normal time. Under normal conditions for pollination the earliest female strobili to open close before the latest ones become receptive and the total period of receptivity is shorter. There is every reason to assume that the female flowering in an orchard follows the same pattern once the orchard generates sufficient pollen. The broken lines in Figure 16 indicate the predicted timetable of flowering within a seed orchard and the normal closure time of female strobili on the basis of observations on flowering behaviour in adult pine stands (Sarvas, 1970 and unpublished material). It is expected that matters will improve, from the point of view of increased within-orchard cross-fertilisation, when the grafts achieve heights of over 7 metres (c.f. Figure 11). Thus although the absolute volume of background pollination does not decrease, its proportion is reduced and, more importantly, it lags behind the mean period of receptivity. Whole or partial exclusion of background pollen is especially important since the effect on the difference between the gene frequencies is quite important. When pollination takes place entirely or chiefly from outside an orchard the resultant seed is obviously of uncertain genetic merit.

Temporal isolation appears to be possible in conditions of heavy background pollination arising from an abundance of outside pollen sources of the same species. For biological reasons it is best to arrange the time difference so that orchards flower before the surrounding forests by transfers to warmer climates which will also increase rate-of-growth and flowering. If this arrangement is reversed the time difference will have to be greater; and this would not only be more difficult to achieve but it would also result in having to contend with a cooler climate which would inevitably hamper the development of the grafts. Slowing down the annual development by semi-artificial freezing, as proposed by Silen and Keane (1969), although correct in theory, would be very difficult to implement in practice on a large scale.

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CHAPTER 9

POLLEN MANAGEMENT

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The Concept

Pollen management is the manipulation of pollen sources for a seed orchard to accomplish dilution, isolation, and application in order to increase the quantity and genetic quality of the seed crop. Pollen management is essential if maximum genetic gains are to be obtained from a seed orchard and is, therefore, basic to even the least sophisticated orchard management system. The concept of pollen management is not new. Almost all orchards have a surrounding pollen dilution zone and most orchards are designed to maximise the distance between related orchard trees. While these practices may be sufficient in some cases, other practices based on new technologies should prove to be economically rewarding in most orchards. It is convenient to combine discussions of pollen dilution and isolation because dilution is often obtained by practices which could lead to isolation if totally effective. A discussion of the spectrum of methods of pollen application is followed by a summary of results obtained by some of the more intensive methods of pollen management.

Methods for Pollen Dilution and Isolation

The goals of pollen dilution and isolation are, respectively, to minimise or prohibit the fertilisation of trees by pollen of unknown or undesirable genetic quality. Methods for accomplishing these goals can be conveniently considered under three headings: geographical, physical and physiological.

Geographical Methods

Geographical isolation (see also Chapters 5 and 8) is obtained by the establishment of a seed orchard in a region where pollen of undesirable genetic quality is unable to reach the orchard and accomplish fertilisation. It is important to draw a sharp contrast between isolation and dilution because methods of orchard management vary depending on whether complete isolation or dilution of foreign pollen sources is obtained. Pollen isolation is an absolute prohibition of contaminating pollen, and thus is almost impossible to accomplish with most genera of commercial forest trees. The frequently used pollen isolation zones around the seed orchard are, therefore, more properly termed "dilution zones". Geographical isolation is possible in those circumstances where pollen distribution is quite limited, as with some insect pollinated species, or, where the introduction of an exotic species has been made on a controlled and limited basis. Unfortunately, such circumstances are rather rare.

One method of achieving geographical isolation is to locate a seed orchard in a geographical region where it can flourish but where flower (see page 72 for definition of conifer flowers) receptivity is phenologically out of phase with the neighbouring pollen sources. Unfortunately, in most areas within the range of a particular species the application of this method usually results in dilution rather than isolation. Nevertheless, dilution accomplished by this method can be significant in seed orchard management as illustrated by observations at the U.S. Forest Service's Dennie Ahl Seed Orchard near Shelton, Washington, where Silen (1963) observed that native Douglas-fir trees (*Pseudotsuga menziesii*) flowered eight to ten days earlier than grafted material from higher elevations. Even though pollen from outside the orchard area was still abundant when the clones in the orchard were receptive, the peak limits had been passed; thus significant dilution of ambient pollen was accomplished. Although often difficult to achieve there are numerous other examples of pollen dilution having been obtained simply by careful selection of the geographical location of the orchard.

Physical Methods

Physical methods for pollen isolation and dilution involve the use of physical barriers of various types to either prevent or retard the introduction of pollen of undesirable or unknown quality into an orchard. Such methods may be applied to individual flowers, individual or groups of trees such as a seed orchard. Obviously, the type and size of the barrier must be suited to the intended application.

Bags of various types have been used for isolating flowers. Rohmeder and Eisenhut (1959) investigated in detail the microclimate inside pollen isolation bags of various types and outlined the advantages and disadvantages of polyethylene film, cloth and pergamine bags. In general, the material of the bag must be suited to the climate and species for which it is intended. In the Republic of South Africa, the polyethylene bag proved quite satisfactory for slash (*Pinus elliottii*) and loblolly (*P. taeda*) pines. It is, however, quite unsuited for use with patula pine (*P. patula*) because the flowers generally abort when polyethylene film is used. The probable reason is that patula pine flowers late in the season when temperatures and humidity are much higher. Such conditions in the United States have led to the general use of cellulose sausage casing as a material for isolation bags because this material is freely permeable to gaseous moisture and thus, is self-cooling to some extent.

Choice of materials for physically isolating individual trees or groups of trees may be less critical than in the case of flowers but considerations of temperature and humidity control are just as important. Therefore, it is frequently necessary to control certain aspects of the environment in such large enclosures (see Chapter 13, Part A). Use of some type of physical isolation is necessary for all types of control-pollination and may have some utility on a limited basis for supplemental mass-pollination if individual trees or groups of trees are isolated.

The physical design of the seed orchard and surrounding areas is one of the most important methods of pollen dilution available to the seed orchard manager. This is reflected in the fact that virtually all orchards have pollen dilution zones around them and most orchards are designed to ensure wide distances between ramets of the same clone, or, between siblings in the case of seedling seed orchards. (see Chapter 3). Results of many studies support the hypothesis that most pollen falls within 150 metres of its source, Andersson (1955); Lanner (1966); McElwee (1960); Sakai (1971); Sorensen (1972). Furthermore, updraughts and turbulance created at stand interfaces with open areas often form quite effective pollen barriers (McElwee 1970); for this reason the dilution zone should be devoid of all kinds of tall vegetation and trees. Even such an ideal dilution zone is insufficient to prevent some contamination by foreign pollen for the following reasons. Whereas, only a small percentage of pollen from a point source will travel as far as 150 metres, many point sources each contributing a small percentage of its pollen to the total pollen load will yield a high background count of pollen almost anywhere in the vicinity of the species range. If the orchard produced no pollen at all, the background load would give adequate pollination in most cases for normal seed yields (Squillace 1967). Genetic gain from such a seed crop would be about half the gain obtained if orchard pollen were totally effective. However, as the orchard produces more and more pollen with increasing age and crown-size, the percentage contamination by pollen from background sources becomes progressively less (Sorensen 1972).

Short-range pollen movement can be drastically influenced by topography (McElwee 1970). Such a situation was described by Ebel and Schmidt (1964) who cautioned against establishing seed orchards on mountain slope sites located above Douglas-fir stands since studies indicated extensive up-slope transfer of pollen over vertical distances of as much as 900 metres. These physical control measures influence the capacity of the orchard to achieve the goal of increased economic value of the seed crop. When an orchard is established, a major aim must be to control, as far as practically possible, the influence of unknown or undesirable pollen sources; otherwise, maximum genetic gain cannot be realised.

The physical arrangement of clones and families within the seed orchard is an important control over pollen distribution because it has been generally found that the tree itself and its immediate neighbours contribute the majority of pollen which the tree receives (Sorensen 1972). Maximum distance between ramets of the same clone or among siblings will minimise inbreeding between orchard trees but will have no effect on the frequency of selfing within the crown of each tree. Problems of inbreeding are fully discussed in Chapter 11; the more important factors of which are only briefly mentioned here. One factor within the crown of monoecious species is the proximity of male and female flowers; thus selfing will be minimal in a young tree where female flowers usually occur in the upper crown and male flowers only near the bottom. Typical crown development in orchard trees of many species, however, allows the mid-crown to become an area of intimate association of male and female flowers. The result is a tremendous increase in self-pollination in the lower- and mid-crown areas and a corresponding drop in percentage of filled seed, as indicated by results from a single large slash pine in Florida, U.S.A. (Figure 17). (Franklin 1971). Corresponding increases in the frequency of albino seedlings strongly suggests that the increase in empty seeds is the direct result of natural self-fertilisation. Thus where a physical isolation or dilution method fails, the orchard manager may resort to supplemental mass-pollination in order to dilute the effective frequency of self-pollen within the orchard tree crowns. This is a pollen application method to be discussed later.

Physiological Methods

Physiological methods of isolation involve the manipulation of the tree to cause the abortion or

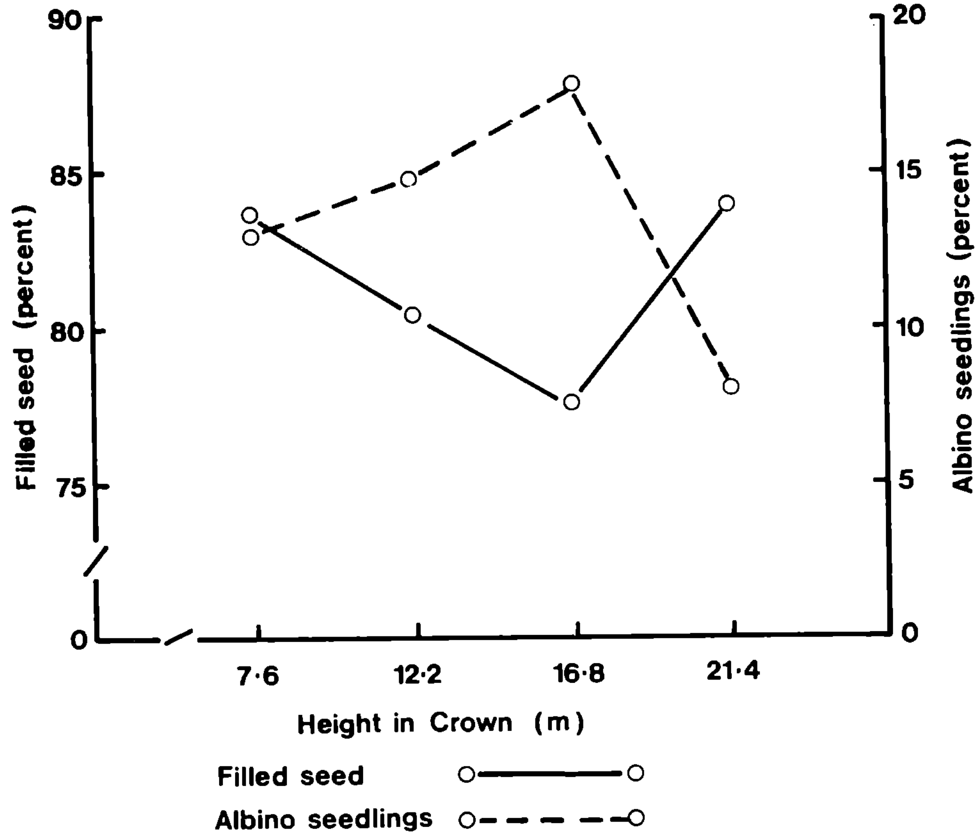

Figure 17. Percentage of filled seed and albino seedlings in seedlots collected from various heights in the crown of a *Pinus elliottii* tree in Alachua County, Florida, U.S.A. (Franklin, 1971).

destruction of the pollen producing structures of the tree and are described more fully in Chapter 7. Methods which have been attempted have generally resulted in varying degrees of pollen dilution rather than isolation. A good example of phenological manipulation was reported by Silen and Keane (1969) who irrigated a Douglas-fir seed orchard with cold water readily available from melting snow. In so doing, they reduced pollen contamination by arresting floral bud development during the period of local pollen release, thus reducing the frequency of foreign pollen grains which amounted to over 13,000 grains per female flower in the control plots, to a level of 100 or even fewer on sprayed plots. Use of organic regulator substances to manipulate the time of pollen anthesis or cause the destruction of the pollen-bearing structures has to-date met with little success; nevertheless, as this technology moves forward, new and more sophisticated methods of physiological control should be available to the seed orchard manager.

Methods for Pollen Application

The simplest form of pollen application is to merely allow trees in the orchard to inter-pollinate in whatever manner results from the design of the orchard in terms of numbers and placement of clones, espacement, the dilution zone, etc. Control-pollination might be considered the most sophisticated type of pollen management. Certainly, it is the most expensive because it uniquely involves complete isolation of flowers prior to introduction of specified pollens. Use of controlled pollination is generally confined to various types of research; however, it has been applied at the Institute of Forest Genetics in Suwon, Korea, to produce several economically important hybrids (Hyun 1969). Because control-pollination has been widely used in research, methods are well documented in the literature (Cumming and Righter 1948; McWilliam 1959; Mergen *et al* 1955). A third method of pollen application, often described as supplemental mass-pollination, can be used where pollen of known high genetic quality is easily obtained in bulk, for example, from most pine species. It includes a wide spectrum of procedures which involve the application of pollen to the tree without the use of a physical isolation barrier.

Supplemental Mass-pollination

Benefits to be derived by supplemental mass-pollination were enumerated by van der Syde (1970); and Denison (1973). Supplemental mass-pollination within seed orchards is receiving particular attention in the southern United States where a Pollen Management Co-operative, representing several private and state and federal organisations has been formed. Needs for, and benefits derived from supplemental mass-pollination are discussed in depth by Franklin (1971); and Woessner and Franklin (1973).

Pollen Quantity and Distribution

In an ideal wind-pollinated seed orchard: (i) the ramets of each select tree are well isolated from surrounding unselected trees; (ii) the ramets are all equally productive of pollen and female flowers; (iii) the pollen flight and female flower receptivity periods coincide; (iv) crosses among clones are equally compatible; (v) natural self-fertilisation occurs at insignificant rates (Woessner and Franklin 1973). In practice the above conditions are seldom realised, and the frequency of self-pollination within the crown of seed orchard trees is often high and leads to substantial reductions in the yields of filled seed (Figure 18) (Franklin 1971). Insufficient quantities of pollen for full seed-set is frequently caused by lack of pollen production, late frosts, or non-synchronous flowering in the orchard.

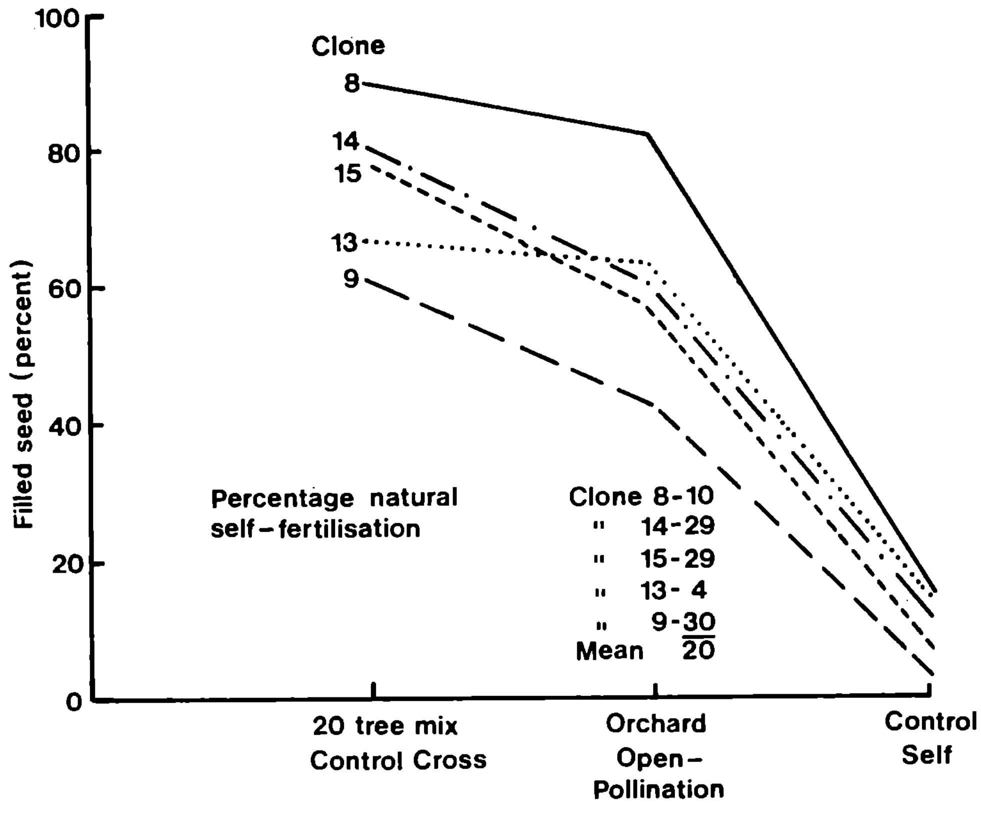

Figure 18. Percentages of filled seed obtained from controlled selfing and crossing and orchard open pollination from 5 clones of *Pinus elliottii* in the Arrowhead Seed Orchard, Wheeler County, Georgia, U.S.A. Percentages of self-fertilisation were estimated by the following relationship:

$$\frac{c - w}{c - s} \times 100,$$

where c, w and s are proportions of filled seed after controlled cross-, orchard open-, and controlled self-pollination respectively (Franklin, 1971).

Benefits

Supplemental mass-pollination can substantially increase the seed yields in many cases. For example, female flowers produced in young orchards before pollen is produced in quantity, can be pollinated and so produce seed of improved genetic quality for commercial afforestation at an early age; the opportunity for background pollen of undesirable types to affect fertilisation can be reduced and seed-set per cone can be increased. Even with abundant pollen production in the orchard, supplemental mass-pollination can more than double the yield of full seeds per cone in comparison with natural pollination (Table 11) (van der Syde 1971) (Denison 1973).

TABLE 11

EFFECT OF SUPPLEMENTAL MASS-POLLINATION ON SEED-SET IN A SOUTH AFRICAN SLASH PINE (PINUS ELLIOTTII) SEED ORCHARD

(van der Syde, 1971)

Percentage full seed per cone

Clone*	Natural pollination	Supplemental pollination
E.1	46	63
E.3	59	85
E.6	59	64
E.7	38	64
E.22	25	79
E.23	11	71
E.25	15	35
E.28	34	63
E.30	23	42
E.33	45	84
E.43	51	71
Average—Sampled clones	36.9	65.5
Average for orchard	15.6	60.1

*At time of pollination, the ramets were 10-years-old.

To a large degree supplemental mass-pollination compensates the imbalance in natural pollination when only a few genotypes produce most of the orchard pollen. In a 10-year-old South African slash pine seed orchard, 20 per cent of the clones contributed over 50 per cent of the pollen (Hagedorn—personal communication from D. R. de Wet Forest Research Station, Sabie, Transvaal), similar observations have been made by Kellison (1971) and van Buijtenen (1971). Bergman (1968) subjectively rated 15 loblolly pine clones for their ability to produce pollen and used a scale of 0 to 5. The poorest clone scored 0.2 and the best clone 5.0. He concluded that 50 per cent of the progeny from one orchard could stem from the two heaviest pollen producing clones. The considerable inter-clonal variation in pollen production certainly invalidates assumptions based on highly sophisticated, statistically designed seed orchards.

Effective supplemental mass-pollination reduces the incidence of selfing in the orchard particularly when female flower receptivity and pollen flight are synchronised in the same tree (Woessner and Franklin 1973). Selfing can be further reduced and the pollen supply extended by collecting and killing the pollen from heavy-pollen-bearing clones and using the dead pollen to dilute the selected pollen mixture.

Supplemental mass-pollination favours an increased selection pressure by using only the best parents as pollen sources and broadens the genetic base by assuring that different male parents are used for fertilisation. Desired pollen can be easily imported from other sources. For instance, parents of high combining-ability for characters, such as high wood-specific-gravity, resistance to fusiform rust or drought tolerance, can be exclusively used on the entire orchard or on specified clones (Woessner and Franklin 1973). In Australia Nikles (per. comm.) is intending to develop techniques for mass producing the hybrid between *Pinus elliottii* and *P. caribaea* var. *hondurensis* using mechanical aids and without isolating the female flowers beforehand. This technique has been used for the production of shortleaf × slash pine hybrids (*P. echinata* × *P. elliottii*) by Wakely *et al* (1966) by dusting large quantities of slash pine pollen onto unbagged shortleaf female flowers using an insecticide duster. Confirmed hybrids accounted for 10.7 per cent of the seedlings in the progeny. Wide variation was found among individual trees in the yield of hybrids which led the authors to conclude that their mass-production method could be substantially improved by selecting shortleaf parents for compatibility with slash pine. The method of mass-dusting with pollen was used by Hyun (1969) in an attempt to produce the pitch pine × loblolly hybrid (*P. rigida* × *P. taeda*). Ten-year-old pitch pines were pollinated four to five times with loblolly pine pollen of high viability which had been diluted with talc in a 1 : 20 ratio. An insecticide duster was also used in this case. On average 88 sound seed per cone were obtained of which 2.5 were hybrid seed compared with 13 hybrid seeds per cone from controlled pollinations. It was concluded in this case that a bigger improvement in the yield of hybrid seed from mass-pollination is needed to make the procedure economical.

Methods

In the Republic of South Africa supplemental pollination of unbagged female flowers has proved to be an effective tool for increasing seed yields and improving genetic quality. The procedure adopted is simple and straightforward. Equal quantities of pollen from selected genotypes are mixed and dusted onto all receptive flowers in the orchard with a simple pollinator, the principle of which was outlined by Mergen *et al* (1955). Approximately 6 grams of pollen were needed to pollinate 1,000 flowers. It is a cheap procedure, since one man can pollinate many hundreds of flowers in a working-day and with increasing age and flower production, the economics of the operation become even more favourable. For certain species, however, unless a cheap and effective means of collecting and applying pollen can be found, supplemental pollination will be a very expensive operation.

One man can pollinate about 5,000 flowers daily on 10-year-old slash pine trees. This figure is based on ramets, the branches of which were staked horizontally to the ground to facilitate pollination and cone collection operations (van der Syde 1970). The branch-bending procedure has now been abandoned. Nevertheless, in "unbent" 6-year-old orchards, supplemental pollination still proved economical and the practice will certainly be continued in older orchards. Tractor-mounted towers, and later-on hydraulically controlled aerial booms, will be needed. Increased flower production per ramet, coupled with greater yields of seed of high genetic potential per cone will certainly outweigh the increased cost of the sophisticated equipment. Current research is aimed at developing pollination equipment which will effectively and efficiently dust pollen over a wide area of the tree crowns. To extend the pollen supply, Callaham and Duffield (1961) showed that pollen can be diluted to produce a mix containing 10–30 per cent of viable pollen without affecting the quantity of sound seed per cone. For dilution purposes unwanted pollen, killed by heat treatment, can be used.

A private company in South Africa, S.A. Forest Investments Ltd, intends to design and establish a second-generation orchard based on single pure rows of different clones. Receptive flowers can then be pollinated artificially with the desired pollen. Emasculation will probably be needed, and the pollen so obtained being used either in the pollen-mix or for dilution purposes. By having the clones in single rows work will be more easily and effectively co-ordinated since the pollination will be more easily synchronised with female flower receptivity.

Pollen Handling

Pollen handling is a term used to cover all aspects of pollen collection, extraction, storage and testing. This important phase of pollen management received considerable attention during the early years of intensive tree improvement, and methods evolved for handling pollen in those days are still largely applicable today. The many aspects of pollination practice in tree improvement, especially with reference to pollen handling, have been well covered by Schreiner (1938); Cumming and Righter (1948); Duffield (1954); Mergen *et al* (1955); Nienstaedt and Kriebel (1955); Orr-Ewing (1956); Rohmeder and Eisenhut (1959); Pawsey (1961); Campbell and Wakeley (1961); Snyder (1961); Barner and Christiansen (1962); Kraus and Hunt (1970); Snyder *et al* (1974). It should be recognised that when dealing with pollen, each species has its own special requirements, and, therefore, the recommendations presented below should be regarded as guidelines only.

Pollen Collection

Pollen must be collected at the right stage of maturity, preferably just prior to shedding. This is particularly important when pollen has to be stored. A test for maturity, as described by Cumming and Righter (1948) is as follows: If aceto-carmine smears of the pollen grains show them to have completed the second division in the development of the gametophyte, (remnants of two prothallial cells will be visible) the male strobili will ripen after picking. According to Snyder (1961), ripeness is indicated when a pasty yellow juice instead of a clear one can be squeezed from the strobili. It may, in certain circumstances, be preferable to hasten the pollen shed and procedures to accomplish this are given by Mergen (1954); Santamour and Nienstaedt (1956); Barner and Christiansen (1958); Worsley (1959); Snyder (1961). Generally, the strobilus-bearing cuttings are best cultivated in a warm atmosphere with the cut ends in water. Results are generally best when the cuttings are taken after the second meiotic division leading to tetrad formation. Chira (1967) has described the effects of tree age and position in the crown on pollen viability for *Pinus sylvestris.*

Pollen Extraction

Germinability of pollen largely depends on the extraction procedure. Although sophisticated pollen extraction equipment has been developed, most organizations still use rather primitive procedures. Ideally, the strobili should be exposed to a warm (30–32°C), dry atmosphere. Temperature and humidity at extraction time can influence the life of the pollen under stored conditions. Dry air conditions during extraction and vacuum drying after extraction normally provide satisfactory pre-storage conditions.

Pollen to be used for controlled-pollination purposes, must be extracted under sterile conditions. It is a good practice to wash freshly collected strobili under running water, afterwards drying the strobili with a sterile, absorbent towel.

Pollen Storage

Various procedures have been advocated for the storage of pollen. Duffield (1954) states that pine pollen, unlike the pollen of most angiosperms, is long-lived and tolerates a wide variety of storage conditions. For storage purposes, the pollen should be sufficiently dry and this is indicated when the pollen flows freely without sticking to the sides of a glass storage container. When in this condition the moisture content of the pollen is around 10 per cent. Snyder (1961) recommends storage over a saturated solution of potassium acetate to maintain an atmospheric humidity of 22 per cent. According to Duffield and Snow (1941); Johnson (1943), pollen can be satisfactorily stored at humidities up to 50 per cent, provided the storage temperature is between 0–4°C. Mergen *et al* (1955) recommend storing pollen at 4°C and at a relative atmospheric humidity of 30 per cent, a humidity which can be achieved by placing an excess of sulphuric acid solution, having a density of 1.45, in the well of a dessicator. Pollen is frequently stored in cotton-stoppered vials in a dessicator containing calcium chloride or silica gel at 2–4°C.

Relative humidity during storage is most important. Duffield and Snow (1941) showed that the germination of *Pinus resinosa* and *Pinus strobus* pollen was reduced practically to zero when stored at relative humidities of 0–10 per cent regardless of temperature, and Fechner and Funsch (1966); Razmologov (1964a, b) found that high relative humidities favoured successful storage of pollen of spruces and various other conifers. On the other hand, Duffield and Callaham (1959) showed that pollen stored at −23°C had about the same germinative capacity as fresh pollen even when used the season following production. Freezer-storage of pollen has been widely adopted for many coniferous species but low moisture contents of around 5 to 10 per cent by weight must be obtained before freezing if the viability is to be preserved (Jensen 1970b). Bingham and Wise (1968) found that *Pinus monticola* pollen stored in a freezer from one to three years gave good seed yields. In an ordinary refrigerator Orr-Ewing (1956) showed that Douglas-fir pollen lost its viability rather quickly. Kraus and Hunt (1970) have showed that seed yields are similar when either fresh or refrigerator-stored pollen of slash and loblolly pines are used for pollination provided the male strobili are collected at the proper stage of pollen maturity.

Testing for Pollen Viability

The pollen viability should be tested before storage and use. Several viability testing procedures have been described in the literature and include those by Duffield (1954); Righter (1939); Orr-Ewing (1956); Manzhos (1958). A simple procedure for pine species is described by Dillon and Zobel (1957), the basic requirements for which are distilled water, a small vial, a slide and a simple microscope to observe the development of the pollen grains which germinate in a room temperature of between 22–28°C. Honey (.01 per cent solution) may be added to the distilled water.

The importance of temperature on germinating pollen is indicated by McWilliam (1959). For *Pinus nigra* the optimum incubation temperature was determined to be 30–32°C. Pollen cell development and tube growth were adversely affected above 40°C and temperatures above 46°C were lethal.

Germination data is needed to determine whether or not a given lot of pollen is sterile or very weak. The germination tests themselves, however, do not provide a reliable index of fertilising-ability; they only show that a certain percentage of grains is able to cross a certain functional threshold (Duffield 1954). Viability testing of *Larix* and *Pseudotsuga* pollen presents special problems since a pollen tube is not formed and special media are required for optimal germination (Christiansen (1972); Ho and Rouse (1970); Ho and Sziklai (1972)). An excellent, recent review of literature on pollen testing and other aspects of pollen handling has been made by Jensen (1970a and b).

Costs

There are no published data on the costs of supplemental pollination at present. Undoubtedly the costs are high because of the high labour content and need for special equipment.

Summary

Pollen management is essential to all tree improvement programmes and is basic to even the least sophisticated system of seed orchard management. In its simplest form, pollen management aims at reducing or preventing pollen contamination from sources of unknown or undesirable quality. In seed orchards, this is accomplished through the establishment of dilution zones, control of the positioning of orchard clones, plant espacement, etc. Further refinements of pollen management include controlled crosses where the pedigree of the cross is required. Supplemental mass-pollination, the application of pollen to unbagged orchard flowers for commercial seed production, is a practice which has been developed in the Republic of South Africa where it

offers many benefits to the tree improvement programmes. Not only does it increase the early seed yields from orchards but it also reduces the occurrence of selfing and pollination from unwanted background pollen. In addition, selection of desirable pollen parents can considerably upgrade the genetic potential of the seed produced. It is expected that, for those species which provide fairly copious amounts of pollen readily, supplemental mass-pollination will soon become an integral part of many seed orchard management systems.

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CHAPTER 10

CONE AND SEED HARVESTING FROM SEED ORCHARDS

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Introduction

Problems associated with the collection of seed from forest trees have prevailed from pre-historic times when early man relied upon fruit and seed as a staple part of his diet. Access to the fruit and seed was by climbing, by training animals to collect the crop, and by felling trees with whatever simple tools were available.

Collection methods have not changed greatly with the advent of forest plantation programmes. Using ladders instead of grass ropes and chain-saws instead of stone axes, we still climb or fell trees to collect seed. We have still not entirely abandoned the time-honoured method of robbing squirrels caches for the collection of Douglas-fir (*Pseudotsuga menziesii*) and Lodgepole pine (*Pinus contorta*) cones, for example, and we still skim the backwaters of ponds and streams for the seed of *Betula, Acer Salix* and *Populus* species. Clearly, the harvesting of forest-tree seed has been a neglected subject in an age of technological advances.

Most forest-tree seed orchards for the commercial production of genetically improved seed have been planted since the late 1940's. Concerned initially with methods of establishment, design, espacement and isolation, and later with genetic evaluation of the parent trees and seed production, the orchardist gave little thought to the logistics of harvesting the crop. Even when some of the early-established orchards began producing crops on a commercial scale no particular problems were envisaged because the trees were relatively small and single stemmed, allowing easy collection from the ground or from within the crown, or from make-shift platforms outside the crown. The need to mechanize the operation became apparent with the massive expansion of seed orchards and with the large crowns of those trees which develop as a result of special management practices. The objectives of this Chapter are to summarise the progress made in effecting cone and seed collection from orchards and to identify areas where additional research and development are needed.

Setting Priorities

At present harvesting seed orchard crops is a local rather than a universal concern. The orchardist with a limited labour supply and a species that produces a heavy seed crop which ripens over a short period will be more concerned about mechanizing the harvesting operation than his counterpart with an unlimited labour supply and dealing with a species which produces light annual crops of serotinous cones. Also, the establishment of most orchards is so recent that the orchardists in various parts of the world have not yet encountered the logistics of seed harvesting on a commercial scale. With time the problems will become of much more general concern and are, therefore, treated accordingly in this chapter.

The development of special seed harvesting methods will probably be unnecessary for those species which bear heavy crops when young, as commonly found within the subsection Contortae of the genus *Pinus* and for those species which commonly bear serotinus cones, some of which are common to the sub-section Oocarpae also of the genus *Pinus*. Clones of these species can be easily propagated vegetatively, allowing part of the orchard to be felled for seed in good seed years followed by replacement of the felled trees with new propagules. Likewise, certain angiosperms, for example, some *Eucalyptus* species, will present few seed harvesting problems because the grafted trees generally bear good crops at young ages. In such cases seed can be collected from within a few metres of the ground, or, for those species which coppice, the orchard can be worked on a coppice rotation (see Chapter 13, Part C). However, such species will constitute a relatively small proportion of the total orchard area and their presence will not lessen the need for developing suitable special seed harvesting equipment.

Bridging the Gap

Some orchardists, recognising the difficulties of harvesting seed crops from fully-grown orchard trees, have tried to control crown-shape by pruning, disbudding and branch bending (see Chapters 5 and 7) to circumvent the problem. With the exception of some success in keeping Douglas-fir tree crowns small and productive by pruning (Copes 1973) most of these efforts have failed. Also, in contrast to the successes achieved for some horticultural fruit crops, attempts to control tree and crown size, shape and fruit production of forest trees by grafting onto dwarfing rootstocks or on to rootstocks of other species (van den Driessche, 1973) or by the application of growth-retardants (Jett and Finger, 1973) have so far been largely unsuccessful.

There is an extensive literature on suitable climbing equipment for the collection of cones and seed from natural- and plantation-grown standing trees; cf. Allan (1960); Seal *et al* (1965). Such equipment is rarely suitable for orchard cone and seed collections because the tree crowns often extend almost to ground-level thus obviating the need for Swedish ladders, Swiss tree-bicycles, pole-spurs and pole-steps for climbing; the trees are too valuable to risk possible attack by insects and diseases into wounds caused by the use of some types of tree-climbing equipment. Further, collecting the crop from within the crown by a man who has gained position by climbing or by mechanical placement, is ineffective for many species because the cones or fruit are borne near the end of long branches and cannot be safely reached without damaging the tree. Faced with failure to effectively control crown size and shape and with the limitations of existing equipment, the orchardists began to develop and modify equipment to meet specific needs.

Cones or Seeds as the Unit of Collection

The earliest equipment used for harvesting the crop in relatively young orchards consisted of step-ladders, manually-operated extension ladders (Johansen and Arline, 1958) and both stationary and vehicle-mounted scaffolds (Plates 5 and 11, central inset). For larger trees, these items were, of necessity, superseded by vehicle-mounted scissor scaffolds, extension ladders (Plate 6) and elevating platforms. Even aerial platforms supported by balloons received more than passing interest.

For trees less than eight metres tall, make-shift scaffolds (Plate 11) and self-propelled elevating platforms (F.A.O., 1959) have been particularly useful for both seed harvesting and tree-crown maintenance work. For taller trees, where high scaffolds are too unstable, knuckle-boom hydraulically raised platforms (Plate 5, left) have proved to be more functional than electrically- or hydraulically-powered ladders because of their greater versatility.

Knuckle-boom elevating platforms (Plate 5, left) are of various designs and can raise a person to heights ranging from 8 metres to 20 metres above the ground (F.A.O., 1955). Mounted, either on a flat-bedded truck or a self-powered vehicle of special design, these devices can, provided the terrain is reasonably level and the vehicle stabilisers are in position, operate within a circle of any range within the limits of the full extended boom. Valuable features of the elevating platforms include controls which can be operated either from the ground or the bucket, and a safety device which permits gradual descent of the platform in the event of a mechanical malfunction. Most models are designed to accommodate one operator although two-man platforms are available. Some models are also equipped with hydraulic or electricity outlets to which special pruning and cone-harvesting loppers can be attached. In 1974 the approximate cost of a mounted unit, complete with a vehicle of commensurate size ranged from U.S. $16 000 for a 13 metre model to $26 500 for a 20 metre model. Because of their versatility and in spite of the large initial investment these machines are now widely used in American seed orchards. The machines can be put to alternative out-of-season uses, especially around industrial complexes, thus reducing the objection to investing in special equipment for which the need is highly seasonal. Some organizations rent the platforms from municipalities and public-utility companies, an alternative which is well worth exploring when the justification for purchase is questionable.

Concurrent with the development of scaffolds, ladders and elevated platforms, various hooks and cutters (Plate 5, right), usually attached to light-weight rods for greater working-range, have been devised for separating cones or fruits from the tree (King 1959). Although effective for harvesting the crop, these instruments can cause damage to the tree when used by unskilled and careless operators. The damage may pre-dispose the tree to attack by insects and diseases and may also reduce future seed crops through the loss of potential flowering shoots. These concerns are largely responsible for the widespread use of secateurs and electrically-or hydraulically-powered pruners or loppers for harvesting sessile cones of certain pines.

For many forest tree species, seed maturation may precede natural ripening of the cone- or seed-bearing structure by up to six weeks (Bonner 1970; Mátyás 1972). This phenomenon can often be used to extend the harvesting-season if measures are taken to ripen the immature cones and seed-bearing structures after collection. Methods of ripening include: indoor storage under warm, dry conditions for sweetgum (*Liquidambar styraciflua*), yellow-poplar (*Liriodendron tulipifera*) and American sycamore (*Platanus occidentalis*); outdoor storage in full sunlight for Virginia pine (*P. virginiana*); and, outdoor storage in a moist, shaded area for loblolly (*P. taeda*), shortleaf (*P. echinata*), and slash (*P. elliottii*) pines (North Carolina State University, 1968). To prevent both heat damage and trapping the pine seeds inside the cones by case-hardening during maturation, it is important to keep cones in layers no deeper than three times their diameter.

Trees as Units of Collection

All equipment designed to put collectors either within or outside a tree crown and within easy reach of the crop eliminate the arduous and often dangerous task of climbing the tree itself and result in lower harvesting costs. Such equipment does not, however, eliminate the need to harvest each cone or fruit separately.

The first step in harvesting crops on an individual tree basis was to mechanically shake the cones, fruits or seeds, to the ground for easier collection. Mechanical shakers, designed and made for orchard-grown table-fruits and nut crops (Kelly, 1967) were evaluated for a wide variety of forest tree species (F.A.O., 1968; Faulkner and Oakley, 1971; Kmecza, 1970). Although of many sizes and designs the available shakers are of three basic types: a self-contained unit supported and powered by a truck of 1½ tonne or greater capacity (Plate 7); a detachable unit which can be mounted on the 3-point linkage of a wheeled-tractor, of at least 35 horse power capacity, and powered from the tractor power take-off; and a self-powered unit attached to the chassis of a light-weight truck, trailing-frame or dolly. All units are operated by a hydraulic system.

The first two types (referred to here as shock-wave shakers) are similar in design and operation. They consist of a pivoted shaker-head, capable of being firmly clamped to tree boles up to 900 millimetres in diameter, which is fixed to the end of a boom (Plates 7 and 8). The shakerheads which weigh up to 320 kilograms are designed to prevent bark and cambial damage, and can be adjusted to grip a tree bole at any height up to four metres above ground-level. An omnidirectional shaking action is achieved by two unbalanced weights counter-rotating around two parallel axes (U.S.D.A. Forest Service, 1972). The intensity of vibration can be varied by using weights of different mass. Although the performance of the two machines is similar, the 3-point hitch unit is gaining wider acceptance mainly because the initial cost is less than one-third of the cost of the truck-shaker unit combination. Furthermore, it can be used with existing tractor equipment and can be quickly detached; the shaker-truck combination is highly specialised and has very limited value for other purposes.

The self-contained vehicle-mounted unit is equpped with a rigid shaker-head. This restricts the clamping position to the plane of the boom, thereby increasing the chance of cambial damage. Oscillation of the shaker-head is induced by a hydraulically propelled slider-crank (U.S.D.A. Forest Service, 1972). Although capable of shaking trees up to 550 millimetres in diameter at breast-height this piece of equipment is really better suited to harvesting certain nut-crops or cones from individual branches of large trees where clamping can be effected with minimal damage to the tree.

The shock-wave shakers can be used effectively on most nut-crop species and for those conifer species which form an abscission layer across the base of the cone peduncle (see Table 12 for a restricted list of species on which shakers have been evaluated). Variable results have been obtained, particularly for conifer species where a positive correlation exists between the ease of collection and stem form-factor, and ease of cone collection and cone position in the crown (Faulkner and Oakley, 1971). Cones from the lower one-third of the crown of open-grown trees are particularly resistant to the shaker, and it is often necessary to harvest those cones by hand if total collection is required. Stage-of-cone-maturity resulting from differences among and within clones also affects the effectiveness of the shaker; for Sitka spruce (*Picea sitchensis*) a decrease from 61 to 24 per cent of the total crop was encountered over a one-month period, indicating that the effectiveness of the shaker decreased in proportion to a decrease in cone dry-weight caused by cone ripening (Faulkner and Oakley, 1971). For species with an abscission layer at the base of the cone peduncle, best harvesting results are obtained when the cones are fully mature.

Although the release of winged-seed from *Acer* and *Fraxinus* species, for example, can be encouraged by shakers, the operation is impractical on all but small trees because of the impossibility of directing the seed to fall on a localised area. For conifers which do not form an abscission layer at the base of the cone, shakers have been partially or completely unsuccessful, much depending on the rigidity of the branches and the mass of the cones. In contrast to advances made in artificially inducing drop of some stone and pit fruits (Kelly, 1967), chemical abscissants have been ineffective for inducing cone-drop in loblolly and slash pines (McLemore, 1973).

For those species suited for cone or seed harvesting by mechanical shakers, best results are obtained with engine speeds of between 400 and 1,100 revolutions per minute; the duration-of-shake should not exceed 10 seconds if severe damage to the tree crown is to be avoided. With these time restrictions and on dry flat ground, 60 to 120 orchard trees can be serviced by one operator per hour, thus creating a situation in which releasing the cones or seed is secondary to that of collecting the fallen material from the ground and processing.

Despite fears to the contrary, tree health, vigour and reproductive potential are not adversely affected by tree shakers if reasonable care is practised by the operator (McLemore and Chappell, 1973).

TABLE 12

EFFECTIVENESS OF MECHANICAL SHAKERS FOR CONE AND SEED HARVESTING FROM FOREST TREE SPECIES

Species	Estimated percentage of cone crop removed	Where Tested
Douglas-fir (*Pseudotsuga menziesii*)	50	U.S.A.
,, ,, ,, ,,	22	Britain
Grand fir (*Abies grandis*)	95	U.S.A.
Noble fir (*Abies procera*)	0	Britain
Western hemlock (*Tsuga heterophylla*)	0	Britain
Engelmann spruce (*Picea engelmanni*)	67	U.S.A.
Sitka spruce (*Picea sitchensis*)	50	Britain
Loblolly pine (*Pinus taeda*)	10	U.S.A.
Longleaf pine (*Pinus palustris*)	80	U.S.A.
Ponderosa pine (*Pinus ponderosa*)	50	U.S.A.
Shortleaf pine (*Pinus echinata*)	5	U.S.A.
Scots pine (*Pinus sylvestris*)	0	Britain
Slash pine (*Pinus elliottii*)	75	U.S.A.
European beech (*Fagus sylvatica*)	95	Britain
Oak (*Quercus* species)	95	U.S.A.
American sycamore (*Platanus occidentalis*)	0	U.S.A.
Sweetgum (*Liquidambar styraciflua*)	0	U.S.A.
Yellow-poplar (*Liriodendron tulipifera*)	75	U.S.A.

Precautions include:

Clamping the machine to the bole at a height normally two metres above ground level. With an increase in bole diameter, a better shaking action is obtained by clamping at proportionally greater height.

Exercising great care when clamping and unclamping the machine.

Clamping the shaker-head at right-angles to the bole.

Positioning the vehicle to avoid rolling after positioning the shaker-head, thereby avoiding bark-wrenching.

Limiting the shake-time to 10 seconds or less at an engine speed previously determined as best for the species under the prevailing conditions.

Cone Collections from the Ground

The logistics of collecting cones from the ground by hand has resulted in attempts to mechanise the operation. Special cone-catching frames used in conjunction with tree-shakers for collecting slash pine cones in the U.S.A. were too cumbersome for general use. Similarly, hydraulically-operated pull-out collection sheets, made of ribbed canvas or heavy gauge polyethylene, which extend beneath the tree crown from a harvest processing machine have limited potential because of their slow pace, and because the shaker remains idle until the processor has been repositioned under the next tree.

The chief limitation of any type of catchment-frame or roll-out sheet is the area of ground to be covered. For slash pine trees averaging 11 metres in height and 6 metres in crown diameter, the radial dispersion of cones, harvested by a shock-wave shaker, ranged from 9 metres for 100 per cent recovery to 4.5 metres for 90 per cent recovery (Tietz, 1971). To keep any catchment-covers or -frames to a size suitable for easy manoeuverability it would be necessary to sacrifice the collection of some cones, or to collect by hand those which fall beyond the frames.

The most practical method of collection for large-scale operations is to sweep the cones into rows, using machines similar in action to street sweepers or side-delivery hay rakes, after which they are uplifted and placed in transportable containers by a second machine resembling a potato harvester. Successful trials of such a two-stage system have been conducted in slash pine seed orchards in the U.S.A. (Tietz, 1973).

Conifer Seed Collection from the Ground

In 1966, when faced with the enormous problem of collecting cones and/or seed from about 1 000 hectares of southern pine orchards in the U.S.A., mostly of loblolly pine which has very firmly attached cones which disperse their seed when mature, the North Carolina State Tree Improvement Cooperative concluded that, for the species of concern, the only logical method would be to collect seed after dispersal from cones ripened on the tree. As a consequence the following methods were tested:

1. Covering the orchard floor with fine-mesh polyethylene or synthetic fibre netting.
2. Erecting frames under the crowns of the orchard trees at heights below which normal orchard operations could be conducted. The frames were covered with tobacco shade-cloth to intercept the falling seeds.
3. Completely bagging the crowns with tobacco shade-cloth.
4. Constructing catchment frames which resembled Japanese hand-fans and which were positioned on the ground under the tree crowns or, were mounted to the frame of a wheeled-vehicle onto which a rubber bumper, for shaking the tree, and a hopper for collecting the seed, were attached.

For one or more of the following reasons, all systems gave less than satisfactory results:

1. Much of the seed was lost after falling on to the ground covers; probably blown away by the wind or eaten by birds and rodents.
2. The tobacco cloth on both the elevated frames and the bagged trees was severely damaged by wind and rain and seed was lost.
3. Seed dispersal from cones ripened on the tree is sporadic and occurs over a four to five-month period under natural conditions; it took even longer from cones developing within the bagged crowns.
4. Shaking or bumping a tree when the cones were fully opened resulted in good seed-fall but the winged-seed dispersed beyond the catchment frames devised for their collection.

These abortive attempts resulted in the decision to develop a suitable method of collecting fallen seed from the ground after natural or forced dispersion of the seeds from the cones. Tree-shakers, operating at engine speeds of 100 revolutions per minute or less and for durations of 5–10 seconds per tree, effectively dislodged 87 per cent of the sound seed from the loblolly seed orchard trees (Malac and Zoerb, 1971).

Methods evaluated for collecting the seed from the orchard floor following forced dispersal included:

1. Ground-covers of synthetic fibres from which the seed is manually or mechanically collected.
2. The modification of commercially available nut, grain and leaf harvesters, which operate on the principle of mechanical or vacuum pick-up.
3. The development of a vacuum-harvester especially designed for sucking up thin-coated pine seeds without causing damage to them.

After rejecting the first two systems the last alternative is now being vigorously pursued by the North Carolina State Cooperative (Plate 9). Also other organisations are continuing developments on other methods of collecting cone-dispersed seed. For example, the Georgia Forestry Commission (U.S.A.) has had a measure of success in recovering loblolly pine seeds from sheets of synthetic fibre covering the orchard floor (Plate 10).

By 1973, trials conducted with a vacuum-harvester have indicated that near-perfect recovery of the seed can be achieved providing the ground is relatively free of depressions deeper than 100 millimetres; is covered with a good mat of grass, preferably of a single-stemmed variety, and is pre-cleaned of needles and twigs before the operation begins. After seed dispersal has begun, the trees are shaken at approximately weekly intervals over a four-week period and the orchard is "vacuumed" immediately after each shake. To save time and effort the sweeper travels along the rows after the first and third shaking operations and across the rows after the second and fourth operations. This results in an effective coverage of about 85 per cent of the orchard with each sweep. Because some seeds are lost, due to incomplete coverage and pick-up due to depressions and other causes, the developmental engineers were asked to design a "sweeper" capable of recovering 80 per cent of the sound seed on the orchard floor in an undamaged condition. The self-powered sweeper is also being designed to harvest a net area of 0.8 hectare per hour.

To date, the chief limitation of the harvester has been its inability to separate seed from debris. In trials with a prototype sweeper in a pre-cleaned orchard, the ratio by weight of debris to seed was 98.5 : 1.5. Modifications have recently been made to obtain better separation of seed and debris but even then complete separation is not expected, nor is it a point of great concern. If the seed can be harvested to the set standards, separation of seed from debris can be attained in other ways, notably by winnowing, water flotation, and by clipper mills.

Development of the sweeper is now nearing completion; it will be field-tested in autumn 1974 and if successful, production models will be available in 1975. The cost of the production machines is expected to range between U.S. $12 000 to $14 000. To this amount must be added the cost of the shaker.

Based on trials with one of the prototype sweepers it was determined that, for pine species having tenaceous cones, seed orchards over 20 hectares in area could be most economically harvested by the shaker-sweeper combination. Elevating platforms are reckoned to be the best economic alternative for harvesting orchards between 4 and 20 hectares in area. No special harvesting equipment can be justified for orchards under four hectares in area (Malac and Zoerb, 1971). These recommendations do not necessarily hold true for orchards of other species in other parts of the world, but they do, perhaps, provide guidelines.

The present vacuum-sweeper has been developed especially for the collection of loblolly pine seed. Since seeds of other conifer and broadleaved species have different properties to those of loblolly pine, modifications of the sweeper will be necessary if the system is to have wide application. Therefore, it is strongly recommended that seed orchard programmes, in other parts of the world where the need for special cone and seed harvesting equipment is anticipated, should start the development of similar equipment before the need becomes critical. A loss of even a relatively small part of one year's seed crop, due to an inability to harvest the crop, can easily be far greater than the investment in harvesting equipment to prevent that loss. A well-planned seed or fruit harvesting programme should be an integral part of all tree improvement programmes.

Safety Precautions

Crippling and even fatal accidents occur all too often during tree seed harvesting operations and every effort should be made to guard against them. Detailed papers by Snyder and Rossoll, 1958; Seal *et al*, 1965, describe the maintenance and use of tree climbing equipment and all concerned with tree climbing should familiarise themselves with the appropriate techniques and precautions for each type of equipment. Many governments have passed safety acts, such as the U.S.A. Occupational Safety and Health Act, and these often detail the types of equipment and maintenance required for seed harvesting work. Thus it is only prudent that operators be familiar with the law and be well trained in the use of approved equipment at their disposal.

Summary

Large areas of forest-tree seed orchards have been established in various parts of the world with little thought given to methods of cone or seed harvesting. This has created logistics problems where maturation of the fruit is highly seasonal and where labour is scarce and costly.

Attempts to control the shape and size of the tree and its crown, in order to ease cone and seed collection, by controlling apical dominance or by grafting onto dwarfing rootstock have been largely unsuccessful. Also, limited attempts to induce cone-drop by applications of chemical abscissants have not been promising.

Until recently, harvesting equipment has been modified or developed for collecting the individual seeds or cones. Step-ladders, extension ladders, scaffolds, and raised and self-elevating platforms are the commonest types of equipment. Knuckle-boom elevating platforms are now being used more widely because of their versatility in orchards with trees over eight metres tall.

Ever-increasing seed crops are now resulting from the expansion of seed orchard programmes and from the larger and older trees within the orchards. In some countries the concept of seed collection has now progressed from the individual seed or cone upon a tree, to the whole tree within the orchard, or even to a whole orchard basis. On the individual tree basis, tree-shakers have proved their value for harvesting crops from most nut-species and from those conifers which develop an abscission layer at the base of the cone peduncle. Repeated use of shakers does not adversely affect health, vigour or reproductive potential of trees, providing reasonable precautions are exercised during the shaking operations.

In orchards of those species which respond to shaking and where the terrain is reasonably smooth, up to 120 trees per hour can be serviced by one shaker. Collection of fallen cones or fruit from the ground becomes the biggest problem. A two-stage system based on a sweeper for windrowing, and a mechanical collector, shows good promise for collecting slash pine cones harvested by a shaker.

For those conifers which have tenaceous cones and which disperse their seed over a relatively short period of time when mature, good progress is being made on developing equipment which is designed to harvest the seed directly from the orchard floor. The two-stage system, consists of a tree-shaker to disperse the seed, and a vacuum harvester to collect it.

It is strongly recommended that seed orchard programmes in other parts of the world include the development of seed harvesting equipment before the need becomes critical.

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PROBABILITY OF INBREEDING IN SEED ORCHARDS

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Introduction

Forest-tree seed orchards are designed and managed with the principal objective of providing a source of seed of high genetic quality for a relatively long period of time. Cross-fertilisation, as a result of wind or insect pollination, is the normal breeding system for trees and orchards are designed to promote the best opportunities for out-crossing (see Chapter 3). With few exceptions self-pollination, when it occurs, often results in inbreeding depression which is usually characterised by high seedling mortality at an early-stage, chlorophyll deficient seedlings and plants of below average vigour. Therefore it is most important to assess the degree of cross-pollination and inbreeding as soon as an orchard begins to flower regularly and abundantly.

An awareness of the reduction in tree vigour and related loss of wood production associated with inbred material prompted this study in which special attention has been directed to the extent and effects of self-pollination in seed orchards. The importance of the study is heightened when it is recognised that intensive and efficient nursery practices are designed to produce the maximum number of "usable" seedlings from each kilogram of seed. Thus many more inherently weak seedlings and transplants, derived from self-pollinations, can nowadays be fairly easily grown to sizes acceptable for planting. Such plants will be out-planted along with "normal" plants with quite obvious harmful long-term effects. Because many forestry schemes are now based on a wide initial espacement of trees and intentions of only conducting one or two or even no thinnings during a rotation, it is obviously essential that all trees established should be of the highest genetic as well as physical quality.

In spite of using large numbers of clones and sophisticated planting designs, which theoretically ensure that plants of the same clone or related families are planted as far apart as possible in a seed orchard, the risk of self-pollination can only be reduced but not eliminated. Also there is always a very high probability that spontaneous fertilisation will occur within the same tree. The occurrence and effects of inbreeding depression on several important tree characters has been verified and Franklin (1970) has presented the results of a detailed survey of investigations into many species of the Pinaceae. The effects of inbreeding depression on stem volume in a 61-year-old *Picea abies* experimental plantation in Sweden, in which four self and four open-pollinated progenies were compared (Eriksson, Schelander and Åkebrand, 1973) is illustrated in Figure 19.

This paper focuses attention on the extent of self-pollination, the most serious degree of inbreeding, in an orchard after open-pollination. It also aims to estimate, on the basis of available information on the mechanism of pollination in the special environment of the seed orchard, to what extent inbred seed is produced after open-pollination. The probability both of self-pollination, resulting from the transfer of pollen from a male strobilus to a female strobilus on the same tree or of the same clone, and of self-fertilisation resulting from the union of male and female gametes of the same genotype, is quite obvious.

The paper is concerned only with trees of the family Pinaceae.

Genetic Principles of Self-fertilisation

Many cross-breeding plant species have self-incompatibility mechanisms which prevent self-fertilisation even when self-pollination has taken place and when both the pollen grains and the gynoecia are active. A serologic reaction retards the growth of the pollen tube so that syngamy cannot take place. Such a mechanism does not operate when conifers are self-pollinated although incompatibility reactions have been observed in the case of some inter-specific pollinations in *Pinus* and *Picea* (Mergen, Burley and Furnival, 1965; Hagman and Mikkola, 1963; Mikkola, 1969).

From reported cytological examinations of material derived from controlled self-pollinations, both pollen-tube growth and syngamy was normal. Thus it can be concluded that inbreeding after self-fertilisation is a common occurrence. In the case of repeated selfings performed on various conifer species, the yields of healthy seed have usually been very low in comparison with those derived from open- or controlled cross-pollinations.

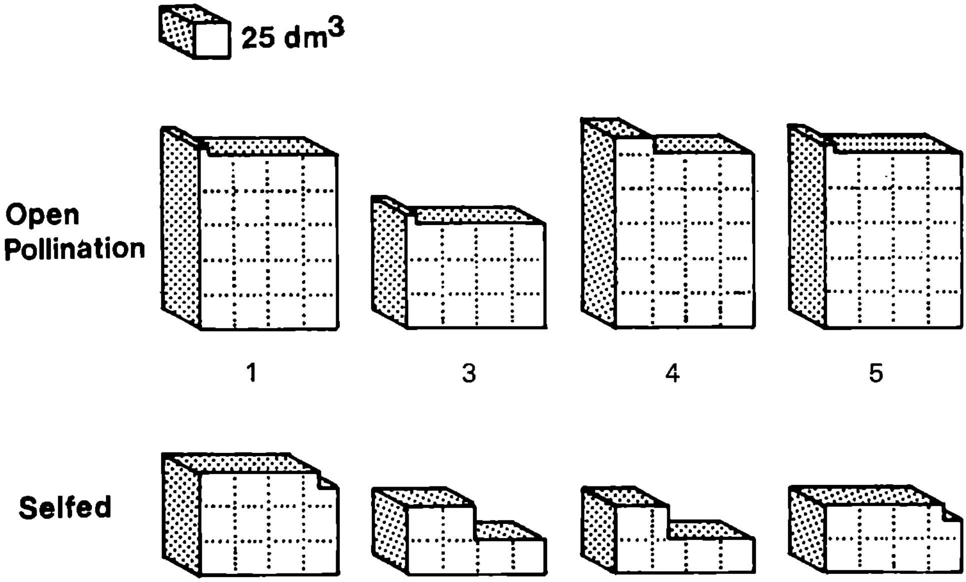

Figure 19. Norway spruce, *Picea abies*. Average stem volume of four selfed and four open-pollinated progenies at the age of 61 years. (The selfed progeny from mother tree No. 5 consists of only one tree.) From Eriksson *et al* (1973).

Cytological and anatomical studies have shown that an embryo originating from self-fertilisation is often unviable and according to Orr-Ewing (1957), this unviability is due to homozygosity of recessive lethal genes. Sarvas (1972), on the basis of open-pollinated material, discusses the nature of the "lethal load" in conifers and the analogy between the "lethal load" of conifers and the self-incompatability of angiosperms.

The frequency of embryo abortions following self-fertilisation is usually about 90 per cent. A genetic model based on the homozygosity of recessive genes at a single locus cannot explain this phenomenon and therefore there is good reason to assume that several independent loci may simultaneously carry lethal alleles in a heterozygous combination. Fowler (1965) published the earliest results from calculations concerning the cumulative effects of multiple lethal genes and polyembryony in five *Pinus resinosa* trees. Sorensen (1969, 1971) examined 35 individuals of *Pseudotsuga menziesii*, and Franklin (1972) 116 individuals of *Pinus taeda*. Koski (1973) has published results from studies concerning *Pinus sylvestris* and *P. peuce* as well as *Picea abies* and *P. omorica*. In all species studied, the number of lethal genes, which were estimated from the percentage empty seed produced from controlled self-pollinations, were surprisingly high in each genotype. It may be concluded therefore, that zygotes originating from self-fertilisation in conjunction with open-pollination, will be unviable in most cases. Inbreeding in conifers is prevented only after syngamy has occurred and by a system which is almost as efficient as the self-incompatibility mechanism of angiosperms.

Abnormal seedlings, such as albinos, low seed viability and weak plant growth are also characteristic of selfed material. All these phenomena reflect the existence of a concealed genetic load. In the case of open-pollinated plantings, in which selfed seedlings occur among the more vigorous material produced through out-crossing, selection works against the selfed material. The elimination of selfed zygotes carrying deleterious genes which manifest themselves only after germination is obviously relatively unimportant. The frequency of such genes is low in comparison with that of embryonic lethals and homozygosity in them is, therefore, a much rarer phenomenon.

Recessive lethal and sub-vital genes can readily be detected by means of controlled self-pollinations. For the study of embryonic lethals the average numbers of fertilisations per ovule is determined from microscopic examination and the percentage of empty seeds by X-ray photography. On the basis of these two numerical values, the number of embryonic lethals can be estimated from the table presented by Bramlett and Popham (1971) or from the graphs prepared by Koski (1971)—both of which are based on identical formulae.

Significant differences have been observed to occur both within and between a few species of the Pinaceae. Results which have been published so far are:

Species	*Number of trees*	*Average number of embryonic lethals*	*Range*	*Author*
Pseudotsuga menziesii	35	8.7	3–27	Sorensen, 1971
Pinus sylvestris	127	8.9	2–20	Koski, 1973
P. taeda	116	8.5	2–26	Franklin, 1972
P. peuce	7	3.1	2–9	Koski, 1973
P. resinosa	5	5.4	2–8	Fowler, 1965
Picea abies	87	9.6	2–20	Koski, 1973
P. omorica	12	4.7	2–12	Koski, 1973

Figure 20 shows the probability of embryo abortion after self-fertilisation when the parent tree has a certain number of embryonic lethals. The graph indicates that, even individuals representative of the highest degree of self-fertilisation in all the species studied, more than 50 per cent of the embryos originating from self-fertilisation are viable. On average, the proportion of abortions in selfed embryos is about 90 per cent in *Pseudotsuga menziesii, Picea abies, Pinus sylvestris* and *P.taeda.* The result obtained for *Picea omorica, Pinus resinosa* and *P. peuce* suggests that there may be considerable differences between various tree species. The embryonic lethals can only be regarded as hypothetical at present, and their estimated numbers only rough approximations. Despite any criticism of the model, it is now established that controlled self-pollinations yield an average of 90 per cent empty seeds and that considerable differences exist between individual genotypes. If the embryonic lethals have their counterparts in the genomes of conifers, they will also be expressed in sibling matings; full sibs will have one-half of the lethals of their parents in common, one-quarter for half-sibs, etc. Such common lethals will of course eliminate a part of the offspring.

The genetic basis of inbreeding depression cannot be explained by means of a simple model. Partly because it is due to the homozygosity of deleterious recessive genes, and partly to the more narrow reaction norms of homozygous loci. Some of the consequences of inbreeding become visible in a favourable environment, for example, low seed

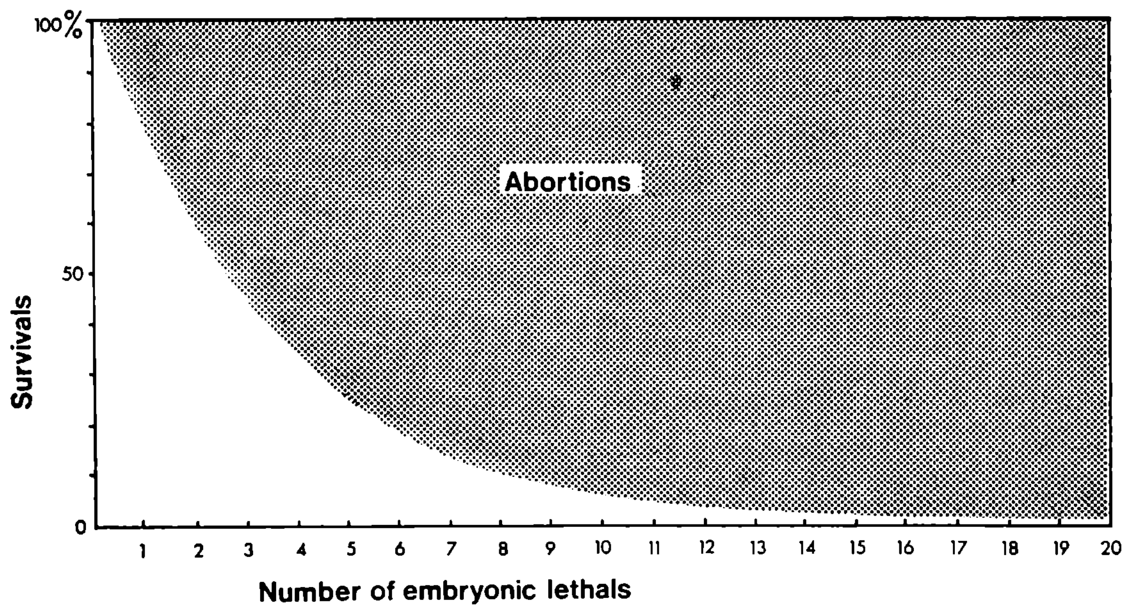

Figure 20. Average probability of survival or abortion of embryos originating from self-fertilisation in trees with 1, 2, . . . , 20 embryonic lethals. From Koski (1973).

viability, albino seedlings, colour deviants, and malformations, amongst others, but the differences in rate-of-growth are far more pronounced under field conditions (Eriksson, 1972).

Estimating the Degree of Self-fertilisation

Self-pollination, and subsequently self-fertilisation, in orchards always takes place to some extent. The degree of self-fertilisation, however, cannot simply be calculated on the basis of the orchard design or the number of clones and their espacement since it is predominantly controlled by variations in the biological behaviour of the component genotypes. This leads to differences in the quantities of pollen and the times of flowering. In order to obtain factual information about self-fertilisation, empirical measurements must be made. Methods which can be used are similar to those practised in ordinary stands when studying self-fertilisation. Three different direct methods have been employed, namely, marked pollen; genetic markers; and iso-enzyme analysis. Some indirect methods have also been used.

Labelling the pollen of individual trees makes it possible to trace the distribution of pollen grains after they have been shed from the pollen sacs. Only *in vivo* labelling is meaningful when this technique is practised to determine the efficiency of mating designs. Furthermore, only elements which can be identified because of their emission of radiation can be used for labelling pollen grains. Both radioactive isotopes and stable isotopes in combination with activation analysis have been used. Radioactive phosphorus P^{32}, which is a β particle emitter with a half-life of some 14 days, is probably the most suitable element for pollen dispersal studies. In activation analyses a large number of different elements have been tested, and studies have been performed using manganese and gold. The methods are not described here but reference is made to McElwee (1970) and Koski (1970) for the use of P^{32}, and to McElwee (1970) and Schmidt (1970) for activation analysis with manganese and gold.

The radioactive-tracer techniques have several disadvantages. These are:

1. In the same orchard only one or very few individuals can be studied simultaneously. If several adjacent trees are labelled, it is impossible to distinguish between the different pollen sources.

2. The labelling substance is unevenly distributed throughout the crown of the marked trees and every pollen grain cannot be detected.

3. The use of radioactive elements carries with it a certain degree of danger, and experiments have to be conducted in remote areas.

4. During activation analyses many other elements also become radioactive and these may create identification problems.

5. The method is expensive and time-consuming.

6. The proportion of own pollen occurring in female flowers or ovules cannot be assessed because all tissues of the labelled tree contain the tracer element. When pollen samplers are used only the proportional share of self-pollination can be estimated.

Genetic markers provide a natural tool for studies of the proportion of self-fertilisation. Different foliage colour deviants are readily found in seedlings of both selfed and open-pollinated progenies. In many cases the marker trait can be explained by means of the homozygosity of only one recessive gene. In such cases the segregation ratio of the marker trait should be 1:3 after controlled selfing. This is not always the case, however, but the proportional number of deviants is smaller. This deviation can be explained in several ways (see, for example, Sorensen, 1967).

In estimating the degree of self-fertilisation in a seed orchard only clones which have an identifying genetic marker can be used. Open-pollinated progenies of such genotypes are raised separately, and the number of deviant types can be accurately counted at the seedling stage immediately after germination. The total number of seedlings is determined by counting at the end of the germination period, and the proportion of marker individuals in the total seedling number is calculated. If the segregation ratio is known or assumed to be 1:3, the proportional number of deviants multiplied by four gives the proportion of self-fertilization. If the segregation ratio is not 1:3 then the coefficient must be calculated. In ordinary forest stands this method has indicated 5–10 per cent as the average degree of self-fertilisation for many tree species (Squillace and Kraus, 1963; Bannister, 1965; Fowler, 1965; Franklin, 1971; Eiche, 1955; Koski, 1973): none of these determinations were from seed orchard data.

The use of isoenzyme studies for investigations of primary gene products and genotype analysis is new among the techniques used in genetic studies. Although isoenzyme methods are still in the developmental stage they do seem very promising. Tree geneticists are still very far removed from the compilation of chromosome maps or pedigrees of certain alleles, but they can already assess whether individuals are homozygous or heterozygous at several loci. The occurrence of haploid endosperm in the gymnosperms provides a sound basis for further investigations into progenies and Bergmann (1971) and Tigerstedt (1973) have examined haploid

TABLE 13

FREQUENCY OF EMPTY SEEDS AFTER SELF-POLLINATION, CROSS-POLLINATION AND OPEN-POLLINATION IN A SEED ORCHARD OF SCOTS PINE (PINUS SYLVESTRIS)

From Johnsson (1972)

Clone	Percentage of empty seeds			Difference open-pollination cross-pollination
	Self-pollination	Cross-pollination (1)	Open-pollination in the seed orchard (2)	
E2	—	15.8	11.3	− 4.5
E20	85.9	14.3	18.8	+ 4.5
E66	61.1	13.8	15.4	+ 1.6
F17	78.2	16.2	19.4	+ 3.2
F20	99.2	46.6	44.3	− 2.3
F43	90.5	17.3	28.6	+ 11.3
F53	98.6	19.8	21.3	+ 1.5
G7	—	20.7	27.3	+ 6.6
G21	—	16.5	20.0	+ 3.5
G23	89.3	21.4	22.3	+ 0.9
G31	—	11.8	10.4	− 1.4
G51	—	10.5	10.3	− 0.2
H2	86.4	17.5	20.1	+ 2.6
H11	97.2	16.3	19.6	+ 3.3
H14	—	19.8	17.9	− 1.9
H16	83.5	25.9	26.5	+ 0.6
H30	85.0	14.5	15.6	+ 1.1
H31	97.1	13.2	16.1	+ 2.9
H32	95.5	21.4	32.7	+ 11.3
H43	86.0	16.7	27.3	+ 10.6
H555	—	36.9	36.2	− 0.7
H58	74.3	24.7	23.1	− 1.6
H76	97.3	11.9	24.3	+ 12.4
H78	—	—	17.9	—
H98	84.4	7.0	7.9	+ 0.9
H100	91.5	11.0	14.8	+ 3.8
H101	92.5	13.1	20.1	+ 7.0
H109	58.0	17.3	18.3	+ 1.0
H122	—	15.6	18.3	+ 2.7
H125	87.9	31.1	31.9	+ 0.8
Average	86.6	18.6	21.4	+ 2.8

(1) Average of 4 common testers

(2) Average of 6 years 1966–1971

endosperm tissues of *Picea abies*. Allele frequencies and combinations can also be studied in diploid tissues, (see Bergmann, 1973; Rudin, Eriksson, Ekberg and Rasmuson, 1973). Although isoenzyme analysis cannot solve all the problems associated with measuring self-fertilisation it can provide a valuable tool for this work. One of its greatest benefits is that it enables many genotypes to be studied, not just the rare exception.

The proportional share of self-pollination and self-fertilisation has also been studied by means of certain indirect methods. Sarvas (1962) compared the proportions of unpollinated ovules in emasculated pine trees with those of similar ovules in untreated control trees. Johnsson (1972) compared the percentages of empty seeds deirved from controlled self- and controlled cross-pollination as well as open-pollination in seed orchards (Table 13). Both of these methods are extremely laborious and reliable results can be obtained only by examining large numbers of cones and seeds. Furthermore, it seems that pollination also involves certain chance factors which may lead to errors irrespective of whether the pollination is natural or controlled. Certainly reliable results can only be obtained from a series of experiments covering several years and for these reasons the writer (Koski) considers that both of the indirect methods are unsuitable for long-term routine studies. The easiest and still sufficiently accurate method to use when feasible, is that based on genetic markers.

In general it can be stated that the practical importance of self-fertilisation is negligible if the seedlings grown from orchard seed contain such a low proportion of albinos and other deviants that they can be disregarded in normal nursery practice.

Factors Affecting the Proportion of Selfed Seeds after Open-pollination

Most of the available information on the proportion of natural self-pollination and self-fertilisation in species of the Pinaceae has been obtained from investigations in ordinary stands; only limited studies have been made in seed orchards. An orchard being defined as "a plantation of selected clones or progenies which is isolated or managed to avoid or reduce pollination from outside sources, managed to produce frequent, abundant and easily harvested crops of seed" (O.E.C.D. Scheme for the Control of Forest Reproductive Material, 1973). The factors discussed below mainly relate to clonal orchards, although in several respects they are also relevant to seedling orchards.

Both hereditary and non-hereditary factors govern the extent to which selfed seeds are produced after open-pollination in orchards. The most important one among all the hereditary factors is probably the load of recessive lethal genes carried in each clone. In most of the species studied (see page 110) the average number of embryonic lethals is high, which results in a high frequency of empty seeds and an increase in the degree of natural self-fertilisation. It should also be noted that there is also a large between-tree variation in the number of embryonic lethals.

The species and clonal composition of an orchard will, therefore, influence the amount of selfed seed in the total seed yield. This conclusion, of course, is only valid in those cases where both self-pollination and self-fertilisation actually occurs in conjunction with open-pollination. This has been partly confirmed by the results from a study carried out in a *Pinus sylvestris* orchard (Hadders, 1971).

This study was based on cone and seed samples collected from 14-year-old grafts growing at a spacing of 5 × 5 metres. Separate samples were collected from the upper and lower parts of the crowns of each graft. In 1969 the cone samples were collected from a total of 36 representative grafts of 15 clones, and in 1970, from 43 grafts of the same clone, seventy of the 79 grafts had higher percentages of empty seeds in the lower crown. In 1969 the percentage of empty seeds was 15.1 in the upper crown and 33.7 in the lower crown (Figure 21). In 1970 the corresponding figures were 10.3 per cent and 20.8 per cent respectively. Another important result of this study was that the percentage of empty seeds in the lower crown increased with increased amounts of male flower (Figure 22).

More recently, 500 individuals grown from seeds representing each of the two crown positions were examined for isoenzyme separation. The examinations suggested that the number of cross-pollinations was 11.2 per cent less in the material from the lower crown in comparison with material from the upper parts; indicating that inbreeding is more frequent in the lower crown (Rudin, 1973).

Other studies have also been made in stands of *Pinus sylvestris* and other conifers which indicate that natural self-pollination and self-fertilisation takes place to greater or smaller extents (Sarvas, 1962; Fowler, 1963, 1965; Franklin, 1971).

Of decisive importance in whether a spontaneous crossing will result in self- or cross-fertilisation is the origin of the pollen which first reaches the receptive female strobilus. The extent to which self-fertilisation takes place must be mainly dependent upon the proportion of own pollen in the general orchard pollen cloud at the time, together with the frequency of pollen from other nearby seed orchards and other outside sources. The background pollen is usually

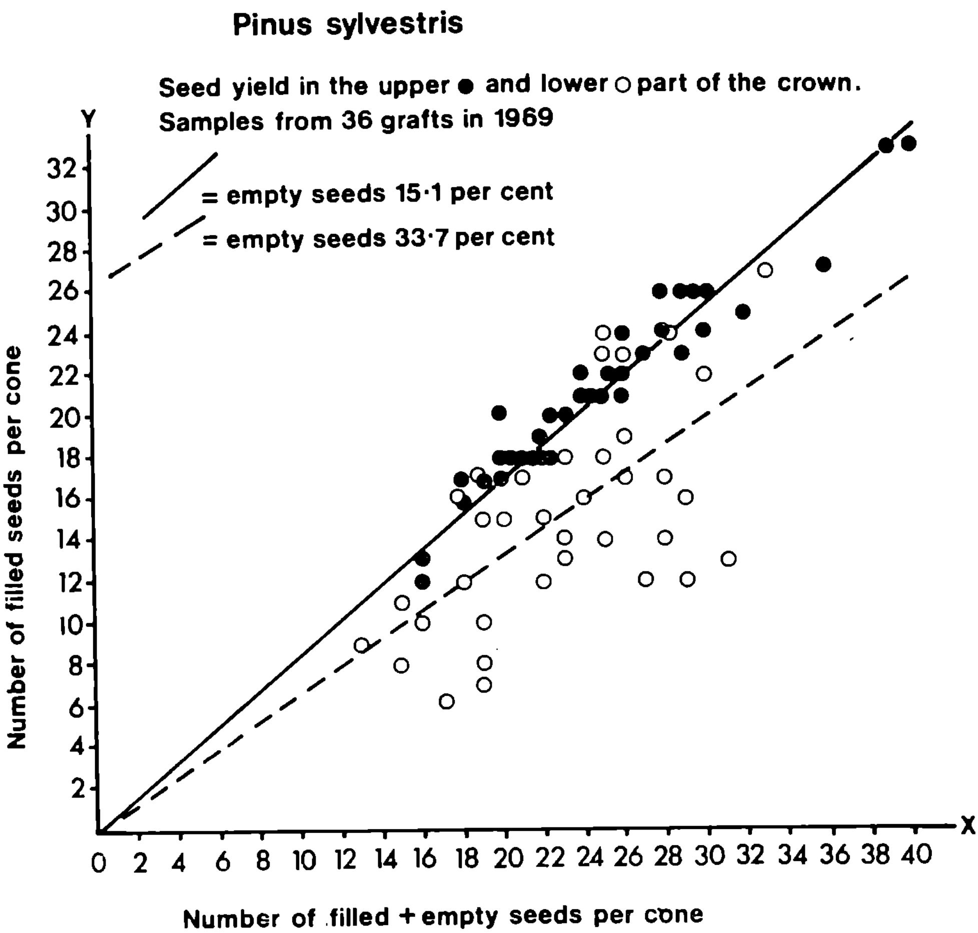

Figure 21. Scots pine, *Pinus sylvestris*. Seed yield in the upper and lower part of the crown. From Hadders (1971).

more important in young seed orchards (Koski, 1970; Hadders, 1972), and as such is of real importance in this respect.

Johnsson (1972), in an unpublished preliminary report, provides an example of a low frequency of self-fertilisation in the case of a well isolated 30-clone Scots pine seed orchard which was established in 1955. On the basis of the percentage of empty seeds after cross-, self- and open-pollinations, it was estimated that 95.9 per cent of the ovules had been cross-fertilised and 4.1 per cent self-fertilised (Table 13). It was also estimated that less than one per cent of the seeds originating from this orchard result from self-fertilisation.

The degree of self-pollination in a natural pollination situation will vary between seed orchards and largely depends on various external factors which may or may not interact with each other. Among these are such factors as: the size and age of the orchard; the number of clones and design; the intensity and distribution of male and female flowers in the tree crown; the synchronisation of flowers of different sex both within and between clones; the isolation of the seed orchard; and the wind conditions during the pollination period.

As previously mentioned controlled self-pollinations have indicated that there are differences both between species and between individuals of the same species with regard to selfing. In orchards of species with a relatively high degree of self-fertility, external pollination conditions are of much greater importance in reducing the frequency of selfed seeds than orchards composed of species of lower self-fertility. Similarly, and irrespective of the species concerned, pollination conditions are of greater importance in influencing the yields of selfed seeds in orchards in which many of the clones are highly self-fertile.

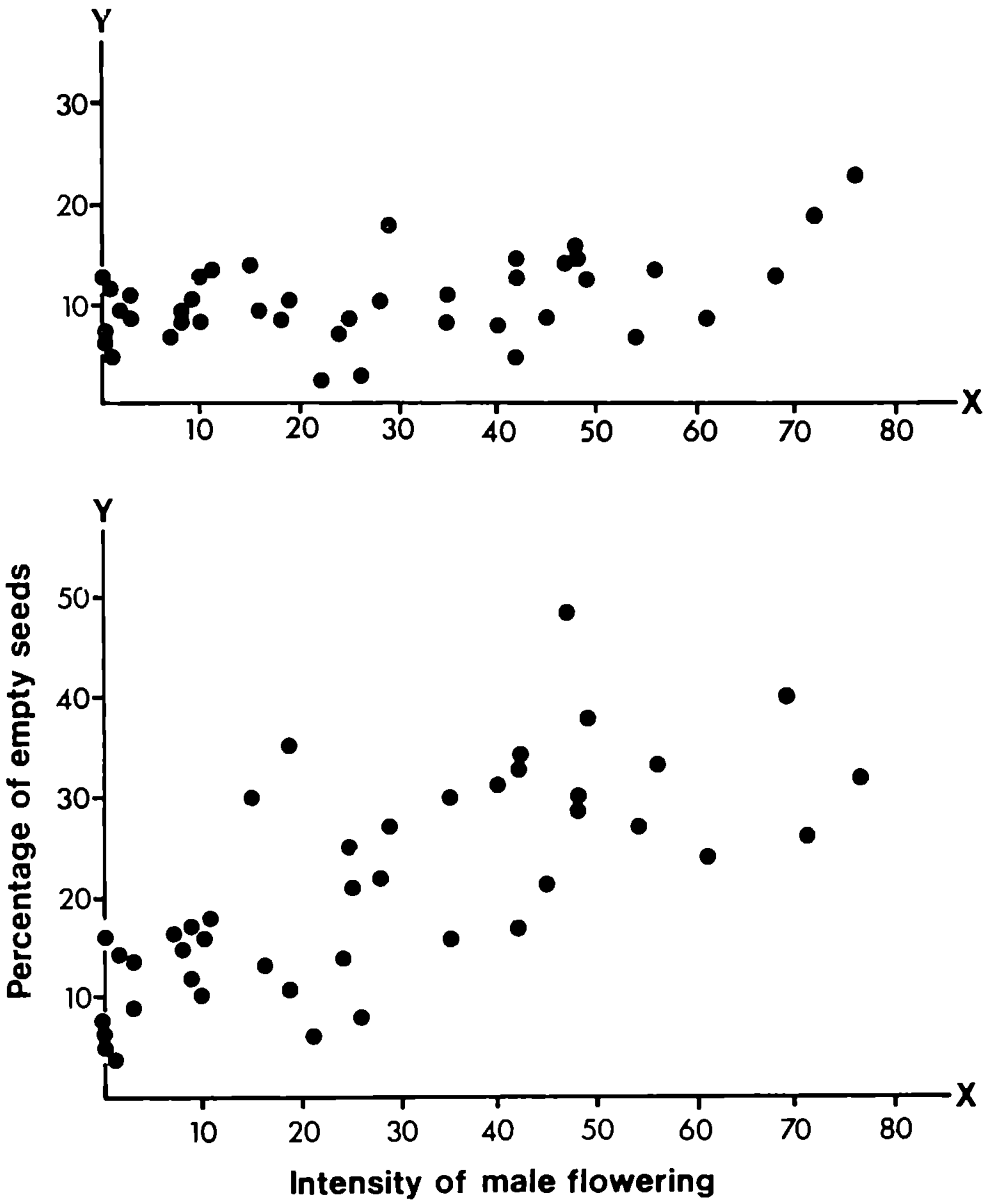

Figure 22. Scots pine, *Pinus sylvestris*. Relationships between the intensity of male flowering and the percentage empty seeds in the upper part of the crown (top diagram) and in the lower part of the crown (bottom diagram). Samples from 43 grafts in 1970. From Hadders (1971).

Summary

Both for first- and second-generation seed orchards it is essential to recognise the importance of cross-pollination and how it is effected in orchards. This Chapter deals with problems concerned with the extent to which selfed seeds are produced in orchards after open-pollination. Among the factors affecting the degree of inbreeding two are dominant, namely, the load of recessive lethal genes of each clone and the synchronisation of anthesis and gynesis in different clones.

In most of the species of the Pinaceae already studied, the average number of embryonic lethals has been found to be so high that it may be reasonably expected that the amounts of viable selfed seeds resulting from open-pollination in seed orchards will be very small.

Nevertheless, it must be stressed that there are obvious differences between clones with regard to their self-fertility. Thus it is necessary to test each seed orchard clone for this property.

The timing of male and female flowering of each clone is also discussed.

As natural self-pollination and self-fertilisation will always occur to some extent, it is important to take this aspect of cross-pollination into account when planning second-generation orchards.

In those orchards in which the number of clones in first-generation orchards has to be reduced for some reason, then the degree of self-sterility of the clones has also to be taken into account. Similarly external conditions for promoting cross-pollination must also be improved by improved mixing of the clones and encouraging conditions for promoting wind turbulence etc.

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CHAPTER 12

ADVANCED-GENERATION SEED ORCHARDS

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Introduction

The entire rationale justifying a genetic improvement programme is keyed to intensive forest management on an extensive scale. Genetically better trees must be used in conjunction with proper site preparation, fertilizer application as needed, and best silvicultural methods. Without the proper balance of the inter-related components of an intensive management system, the optimum benefit from genetically improved planting—stock would not be realised. It is on this underlying concept of intensive forest management that the following discussion on advanced-generation *production* seed orchards is based.

In an applied forest tree improvement programme, even small genetic gains can be of enormous economic benefit when distributed over the thousands of hectares of plantations established annually. The ultimate objective is to get the greatest gain per unit of time. To achieve maximum gain for a given character, a long period of selection is required; however, it is possible to obtain and utilise portions of the total gain at an earlier time. Obtaining gains quickly will optimise total improvement per unit time on a given land area. For this reason it is essential that improved material obtained through recurrent selection be introduced into production orchards as soon as possible.

While many techniques of improvement in advanced-generation orchards are similar to those of the first generation, new and improved technology must be utilised with advanced-generation applied improvement cycles if the greatest gain per unit of time is to be achieved. The second-generation orchard breeding programme now under way by members of the North Carolina State University Cooperative provides examples of how theories are put into practice. Alternatives, which may be applied to species other than the southern American pines having different patterns of variation, base-population characteristics, environmental conditions or management objectives, are also discussed.

Development of an Advanced-generation Programme

A strategy for developing and testing suitable material for future generations must be developed very early during the first-generation breeding programme if the long-term programme is to avoid the consequences of a restricted genetic base and particularly the risk of inbreeding. If improvements are to be realised the intensive selection of orchard parents will necessarily restrict the gene-base for certain desired characters, but at the same time the gene-base for adaptability must be increased. To successfully improve (restrict the base) economically important characters, such as stem straightness, wood qualities, and growth and still retain the necessary adaptability, it is vitally important to maintain and increase genetic variation within the breeding population, if significant genetic gains are to be efficiently obtained in future cycles of improvement. To simultaneously accomplish, what appear to be the contradictory objectives of maximum production of the best seed as soon as possible and to develop a continually expanding genetic base, it is necessary to segregate the immediate seed production function from the long-term goal of developing broad-based genetic populations by continuous breeding. The North Carolina State Cooperative Tree Improvement plan for the short-term production and the long-term gene-base enrichment provides an example of such a scheme in which the two objectives run in parallel. It is illustrated in Figure 23. Other strategies for the complete development of long-term genetic improvement programmes are discussed by Libby (1973) and Burdon and Shelbourne (1973). Although the techniques differ all three programmes have the same common objective.

Since the main function of production orchards is to supply the most improved seed as quickly as possible for current forestry needs, it is obvious that the seed they produce is a dead-end as far as a main source of genetic material on which to develop advanced-generations is concerned. Production orchards will always be constructed from the very best genetic material developed in the breeding population for a given generation. For this to be effective, the breeding population from which selections are made must be enriched by other material derived from controlled crossings and carefully planned breeding. Each breeding population can then effectively provide a base on which to develop successively better production orchards.

To obtain continued improvement, the breeding population must cycle through a selection phase before each successive regeneration stage. Rigour

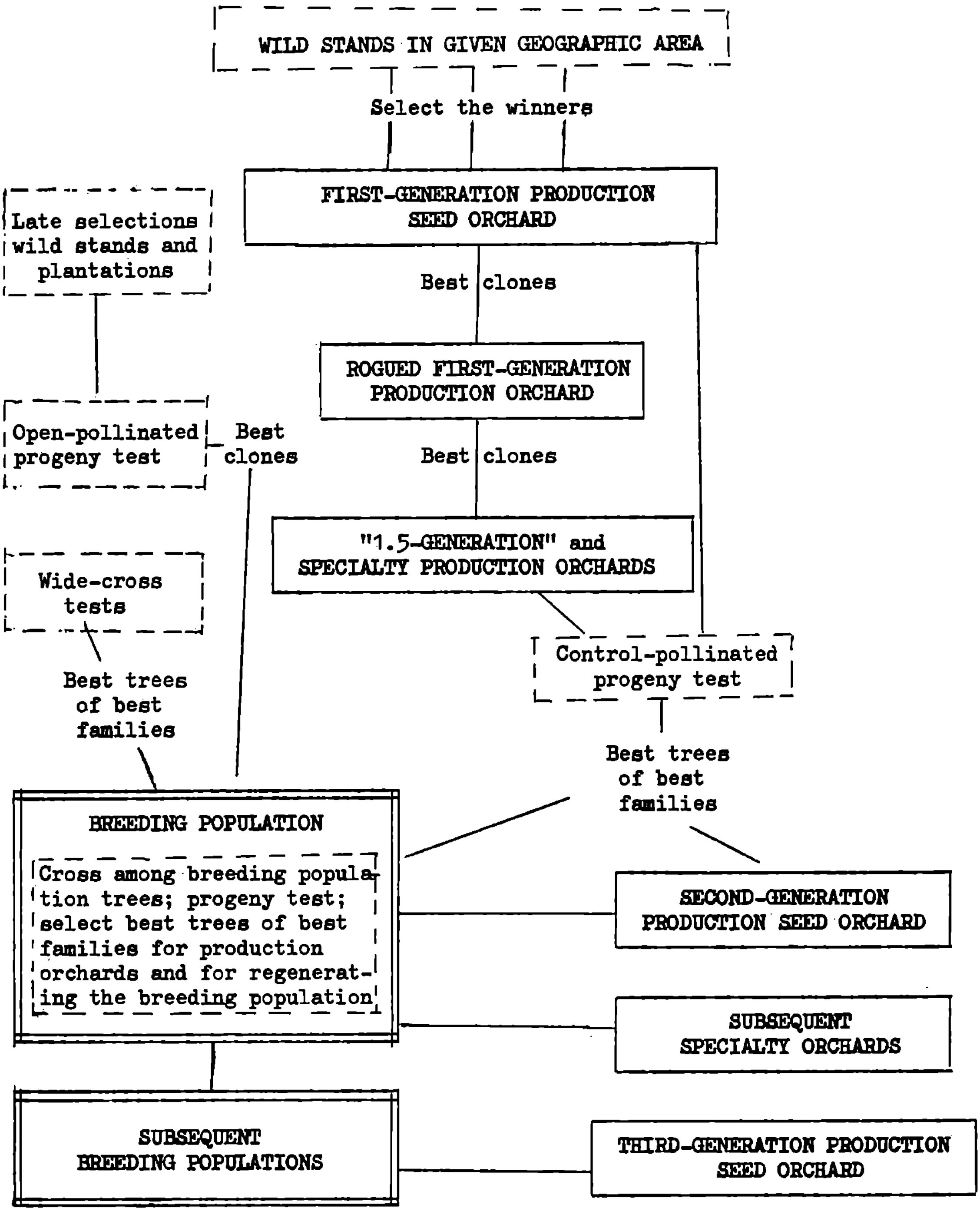

Figure 23. Schematic representation of the North Carolina State Cooperative tree improvement plan for short-term production and long-term gene-base enrichment ("1.5-Generation" orchards imply greatly improved first-generation orchards constructed with the best general-combiners from a number of orchards).

of selection applied to the base breeding-population, while less stringent than that used for the development of production orchards, will continually restrict variability if a worthwhile improvement of important characters is to be achieved. Great care must be taken, therefore, to avoid restricting variability after several generations to a few outstanding genotypes.

A breeding programme must provide for a continual infusion of new genetic material into the population to avoid inbreeding. This can be accomplished by: new selection from wild stands; selections from other regions or foreign countries; special crossing of selections among trees of different geographic areas. All new genotypes introduced into the main breeding population from an outside source must first be evaluated for performance and only the very best should be retained and used in new production orchards.

Strategy for Developing a Breeding Population

Many different breeding schemes can be used to develop a base for advanced-generation selections, but unless extreme care is taken the work-load and expense can soon become overwhelming. It is especially difficult to choose an efficient mating pattern when there is a dual objective of testing to determine the clones of greatest value in the production seed orchard, and the development of a sufficiently broad genetic base to minimise the risk of inbreeding in advanced generations. Each objective could most simply be achieved by using a separate mating design, but the cost in time, effort and money would be prohibitive. For efficiency and practicability a mating system is required, therefore, which will: provide a reasonable assessment of the breeding value of the parents; and produce a sufficient number of unrelated families to form an adequate selection base for advanced-generation orchards. Pedigree information increases with each successive generation of breeding and, in the course of time, the emphasis in the mating designs will be towards developing populations from which selections can be made, rather than evaluating the genetic worth of those parents already established in orchards (van Buijtenen and Saitta, 1972).

The use of controlled crosses with complete pedigrees is mandatory if the greatest gains are to be achieved and harmful inbreeding effects are to be avoided. Each Cooperative orchard has produced one to several clones (5 to 20 per cent of the clones tested) which are outstandingly good general-combiners (Weir and Zobel, 1972; Zobel *et al*, 1972). In this general situation, mass selection of the best individual trees with no regard to family performance will result in progenies from the good general-combiner clones being chosen in a disproportionately high frequency. This is illustrated by the second-generation selections from loblolly pine (*Pinus taeda*) progeny tests of the International Paper Company, Georgetown, South Carolina (Figure 24). If selection for a second-generation orchard were made from open-pollinated, top-cross, or pollen-mix matings, it is certain that many selections would have *one* common, outstanding male parent. If selections were made from commercial plantations derived from orchard seed, many of the trees selected would have *both* parents in common. The use of such related parents in production orchards would result in a possible disastrous reduction of genetic gains caused by inbreeding depression. Although the needed definitive tests have yet to be made, an early study shows that a volume growth-depression of 20 per cent can result from matings among half-sibs (Gansel, 1971). Common-sense dictates that related matings should be avoided until experimental proof indicates otherwise; unrelatedness can only be assured with a complete knowledge of the pedigree of the parents used in second- and subsequent-generation orchards.

The "single-pair" mating scheme has been proposed by Libby (1968) for developing a selection base with a maximum number of unrelated individuals; this mating scheme was integrated into an improvement programme by Burdon and Shelbourne in 1973. Each clone is mated to only one other clone and, therefore, all resulting crosses are unrelated, thus achieving one of the main objectives. However, since a given genotype is never mated to more than one genotype, there is a danger that a useful parent may be lost or a poor one maintained because of chance involvement in a poor or good specific combination; the same parent combined with a third one might be quite valuable or worthless in its contribution to subsequent generations. The pair-matings system provides unrelated progeny but does not provide the needed selection differential to take full advantage of the gene-pool. In addition, with the single-pair matings the effects of the desired general-combining-ability are completely confounded with specific-combining-ability. Because combining-ability effects are confounded the utility of this scheme, for producing a base for future selection, is limited because intended selection for high general-combining-ability may be biased by strong dominance or specific-combining-ability effects, which are difficult to utilise in operational orchard programmes.

Tester designs, such as the North Carolina State Design II, are useful for control-pollinated progeny test purposes but are of primary value only where the main emphasis is on parental breeding-evaluation. Also where the breeding populations of several programmes are used for selections which

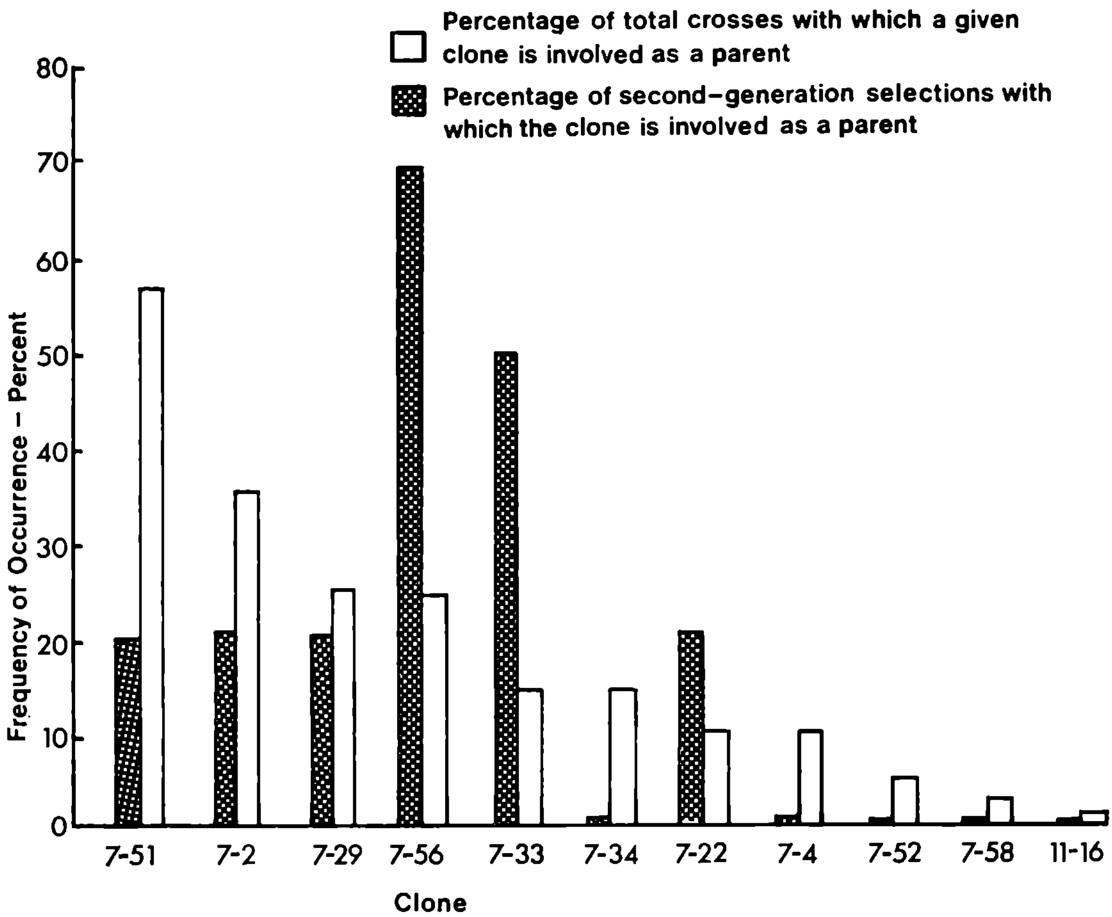

Figure 24. Relative frequencies with which clones from International Paper Company were used as a parent in crosses within a seed orchard and the second-generation selections made in progeny tests of that orchard. *Note:* Parental percentages total 200% since the number of crosses (or selections) serve as a base and each cross has two parents.

are combined to provide a sufficient number of unrelated selections for continued programme development into advanced generations. The tester design uses from four to six clones designated as testers, generally pollen parents, which are mated to all other trees in the population. The tester design provides a satisfactory estimate of parental breeding-value, but, the progeny population, generated for use as a base for selection in the next generation is restricted by having only a few unrelated crosses. The number of unrelated crosses can never exceed the four to six testers which were used, no matter how great the number of clones included in the breeding population. When an organisation relies solely on limited gene resources, that is, those having a relatively closed breeding system, the tester method is inadequate. This is especially true in areas dependent on exotic species, for example, many tree improvement programmes for exotic conifers in South America. With a restricted genetic base, and with restricted opportunities for exchanging unrelated material, the tester system is unsuitable.

The ideal mating design is the diallel or half-diallel which provides good estimates of the breeding-value of parental clones and the general- and specific-combining-abilities of the parent trees, along with the maximum number of unrelated crosses from which selections for advanced generations can be made. The diallel is rarely used and the assumption is made that reciprocals react similarly under test. The primary limitation of both the diallel and half-diallel is that they require a large outlay of resources to make the necessary crosses; for example, when

30 clones are tested, 435 crosses are needed to complete a half-diallel compared to 150 for a five-tester system.

A partial diallel mating design is often used to obtain most of the advantages of a half-diallel but at less cost. Such a design provides a reasonable estimate of the general-combining-abilities of the parental clones and at the same time creates the maximum number of unrelated half-sib families suitable for advanced-generation selection. The number of crosses, and thus the cost of crossing and testing, is much reduced in comparison with the half-diallel in that each clone is only mated with six to ten others (a fixed number is chosen at the start). If designed correctly, the number of unrelated half-sib families equals one-half of the number of clones under test and is identical to the number generated by the paired-mating system or the half-diallel. The additional combinations over that of a single-pair mating scheme make possible a substantial increase in the selection differential for advanced-generation orchards, allowing greater genetic gains to be achieved. A traditional partial-diallel design in the form suggested by Zobel *et al* (1972) is very satisfactory for developing a base for advanced-generation breeding. There are many variations of partial diallels; the efficiencies of several alternatives have been described by van Buijtenen (1972). One especially desirable feature of partial diallels is the flexibility of application, characterised by the disconnected type advocated by Franklin and Squillace (1973).

Effective advanced-generation breeding programmes must use some form of partial diallel if the maximum number of unrelated crosses is to be obtained together with a reasonable estimate of the breeding-value of the parental clones. The exact form of the partial diallel used will depend on the genetic base, the availability of breeding stock, and the skills and desires of the plant breeder.

Selection Methods

When developing plans for advanced-generation selections it is most important to determine at what age the progeny should be chosen. Early selection will allow a rapid turnover of generations but might result in more selection errors as a result of low juvenile-mature correlations (La Farge, 1972; Sluder, 1972; Wakeley, 1971). Individual genotypes have quite different growth rates over time; some are "sprinters" which initially grow very rapidly but slow down at a rather young age. Others start more slowly but increase their growth-rate in later years; some genotypes appear to grow at nearly constant rates throughout the rotation. Selection for volume at one-half rotation age is a general rule adhered to by a number of researchers in an attempt to minimise selection errors. More recent studies of juvenile-mature relationships have recommended selection at surprisingly early ages; for example, six or seven years was felt to be optimum for slash pine (*P. elliottii*) (Squillace and Gansel, 1972). It is apparent that compromises will be needed to optimise the total cumulative improvement as measured over a considerable period of time. The greatest long-term genetic improvement would be achieved by effecting a rapid turnover of generations, rather than unduly delaying selection to ensure that the transition from one generation to the next is made with only fully proven "winner" genotypes. Recognition of the influence of time on the progress of long-term genetic improvement, coupled with constant pressure to provide more high quality seed for current planting programmes, has forced the North Carolina State Cooperative Program and many other breeders to begin advanced generation selection in relatively young families, recognising that some errors of judgment are probable.

Advanced-generation selection, whether for production orchards or for the general breeding population, involves evaluating and culling on the basis of phenotypic value of individual trees together with family merit. Individual or mass selection consists of choosing trees solely on the basis of apparent phenotypic superiority in growth, form, wood quality, disease resistance or other desirable characters. Such mass selection for advanced-generations is similar to wild (natural) stand selection in the initial improvement cycle, except that a greater response to selection is anticipated as a result of greater control over site uniformity, spacing, competition and tree age. When first-generation selection is from a plantation, improvement in rate-of-growth from the second cycle of mass selection may not be significantly larger than the first; and environmental control may not be significantly improved. Individual tree selection is the simplest to apply and will provide a great deal of genetic improvement for those characters having a high heritability.

Several hundred second-generation trees have now been individually selected for the North Carolina State Cooperative. Selections were made by initially screening data from four- or five-year-old progenies; final acceptance or rejection being based on a field assessment. Three or four ramets of each selected tree are grafted and established in a breeding or research clone bank for insurance, and for evaluating the suitability of each for grafting, graft survival, flower production and phenological characters. As the early selections continue to develop in the test, they are re-assessed after eight growing-seasons and again when approximately

12 years of age. A feature of selections based on individual tree performance alone has been the too-frequent choice of outstanding trees from families of average or below average performance. This is to be expected where narrow-sense heritabilities are low (below 0.30), and which are a common feature of a number of forest tree characters. To overcome this inadequacy it is most important to use additional information from family values.

Controlled cross-pollinations of specific parents provide full-sib family information, and, with the exception of the single-pair mating scheme, half-sib family information is also obtainable. Discrimination for or against parents based only on a full-sib family should be made with caution. Instead of selection for high-general-combining-ability, outstanding positive dominance deviations or specific-combining-ability may be favoured; the use of specific-combining-ability has only limited usefulness with production orchard methodology. For maximum efficiency it is more satisfactory to base selections on both full- and half-sib family information.

Family data can be used most simply by an approach which employs an independent culling level. This requires that the selected individual trees demonstrate outstanding merit and that they are all chosen from full- and half-sib families within an arbitrarily chosen upper percentile of the population. Such an independent culling system produces a marked improvement in the quality of the chosen individuals when compared with mass selection alone. It is a striking fact that most of the chosen trees are from progenies of the better first-generation general-combiners. For characters with low heritabilities, incorporation of family performance into the selection scheme results in more efficient selections and greater gain in advanced-generation orchards.

The ultimate refinement of advanced-generation selection is the development of indices which optimise the relative weighting of half-sib, full-sib, and individual tree performance. To use index selection, however, it is essential to have precise variance estimates of heritability values to decide the appropriate weighting of each character. Precise variance estimates are seldom obtainable from forest tree progeny tests since most are designed to evaluate breeding-values or clonal performance rather than variance estimates. The use of published heritability or variance estimates introduces the danger of extrapolating from data applicable to only one population in a single environment or set of environments. Any results using combined index selection are no better than the data used to construct the index; quite often the available data are of limited value for the purpose. Thus there is a real need to obtain useful variance estimates.

The job of selection does not end with the initial identification of outstanding trees from the best families. Although early selections from young tests can be used at the earliest practical time for advanced-generation production orchards and in breeding populations, maximum efficiency is obtained by the continuous reappraisal of the breeding-value of each selected tree as it approaches rotation age. Should a select individual fail to maintain superiority, it must be removed from the breeding and production orchards. Conversely, trees which are passed over during the first assessment may later become outstanding. Such late-developers can then be incorporated into the breeding population and sometimes used in sections of production orchards provided for expansion purposes. It is apparent that a breeding population for advanced generations will be quite dynamic since it is continually supplemented with new and better selections and purged of trees which fail to maintain the required measure of excellence.

Orchard Establishment

Most second-generation select trees will be obtained from matings among the best and the strongest general-combiners of the first generation breeding population (see Table 14). However, a dilemma arises when establishing advanced-generation production orchards. The geneticist is inevitably confronted with the choice of whether to use the several most outstanding but related (full- and half-sib) selections, or, whether to restrict the degree of relatedness among parent trees and thus be forced into using slightly inferior clones. The use of some related selections is permissible providing the orchard design and spacing within the orchard ensures that the related trees are kept sufficiently apart. However, the extent to which a high proportion of superior but related clones will be beneficial greatly depends upon the likely degree of inbreeding depression and the probability of it negating genetic gain. It is perhaps worth noting that in a case-study reported by Squillace (1973) the predicted genetic gain from the best 25 selections, chosen without regard to relatedness, exceeded the predicted gain from a set of the best 25 unrelated selections.

With most improvement programmes it is best to establish second-generation orchards on a deliberate step-wise time-scale in which part of the total orchard is established in each of several successive years. This approach is necessary when progeny tests, which are used as the selection base, span a period of years; it is the usual situation.

In an applied breeding programme progeny testing need not be delayed until all the required pollinations are completed, otherwise valuable time

TABLE 14

CLONES FROM NINE LOBLOLLY PINE SEED ORCHARDS, ILLUSTRATING HOW PROGENY FROM OUTSTANDING GENERAL-COMBINERS WERE SELECTED A GREATER NUMBER OF TIMES THAN WOULD BE EXPECTED FROM THEIR FREQUENCY IN THE PROGENY TEST AND THE RELATIONSHIP EXPRESSED AS A DISPROPORTIONALITY RATIO

Clone	A—Percent of Second-Generation Selections with Clone as One Parent	B—Percent of Crosses in the Progeny Test with Clone as One Parent	Disproportionality Ratio (A/B) (*1*)
7–33 (*T*)	50.0	14.3	3.50
7–56*	70.0	23.2	3.02
4–18	41.3	17.9	2.30
1–66	29.4	12.9	2.28
10–39	38.5	20.3	1.90
11–2	34.2	20.0	1.71
6–20 (*T*)	45.0	26.3	1.71
4–4	31.0	18.8	1.64
10–14	38.5	23.4	1.64
7–56(*)	31.5	20.0	1.58
12–12	37.7	25.0	1.51
5–33 (*T*)	53.5	36.2	1.48
1–60	23.5	16.1	1.46
14–10 (*T*)	50.0	35.2	1.42
4–6	34.4	26.4	1.30

Notes:

(*T*) Clone used as a tester. Many of the testers demonstrate outstanding general-combining ability (G.C.A.).

(*) Clone 7–56 occurs in the seed orchards of several companies, including those of Westvaco Corporation and International Paper Company, for which test data have been summarised. In all orchards in which it occurs, it shows outstanding G.C.A. just as for the two summarised in the above table.

(*1*) A disproportionality ratio of 1.0 would indicate progeny selection at exactly the same frequency with which the clone occurs as a parent.

will be lost between generations. Testing should begin as soon as enough seeds are available and should continue throughout the period necessary for its completion. The spread of progeny tests over time and their subsequent assessment allows some balancing of the work load. Since progeny tests, from which selections will be made, are established over a period of years it is recommended that only a few hectares of the total orchard area be established in each of the early years. This deliberate approach allows an annual reassessment of available second-generation selections and provides an opportunity to establish the best available genotypes each year, including new selections obtained from the annual selection programme.

To obtain the greatest and earliest gain it is necessary to start developing advanced generation production orchards with very young selections. Because a certain amount of selection error and inefficiency is inevitable when selecting young trees, it is essential that the orchards are established at closer-than-normal spacing so that trees which fail to produce suitable progenies can be rogued; thus more trees are established per unit of area than are necessary when the orchards are mature. In the later years of a step-wise orchard establishment programme, many of the selections will be based on selections from older tests which provide more reliable data; because of higher juvenile mature correlations with age, the numbers of trees established per unit of area of orchard can be safely reduced.

To allow flexibility in roguing it is necessary to have a broad genetic base, derived from a large number of clones, and as many trees per unit of area as practicable. However, *only* the best genotypes should be used, thus ensuring that intense selection is practised in order to achieve substantial genetic gains even prior to roguing.

The dilemma of numbers *versus* quality must always be confronted, and the final choice of individuals must be a compromise largely determined by the strength of the juvenile-mature correlation among actual and potential superior second-generation parent trees. There is, however, a lower limit to the number of clones to be included in an orchard if the desired minimum 30 metres spacing between ramets of the same clone is to be maintained to minimise the risk of selfing (McElwee, 1970). The lower limit depends upon the spacing of ramets. Currently, the North Carolina State Cooperative uses a 5 metres square spacing with every second space in every second row left void. Under these conditions, 23 unrelated clones are needed to maintain a 30 metres interval between ramets. If related selections are used in an orchard they are treated as if they were ramets of the same clone and must also be spaced 30 metres apart.

Previous experience with young southern pine grafts has shown that female flowering begins 3 to 5 years after grafting and that pollen production normally starts after a further three years. In an attempt to provide an interim but good pollen source the North Carolina State Cooperative now introduces grafts of the very best general-combiners from the first-generation orchards to provide "pollen parents" within the second-generation orchards. This creates difficulties when the most outstanding first-generation parents are also the parents of the best second-generation selections; this is often the case. Thus a compromise has to be made as to the choice of clones to be used as pollen parents. The *best available unrelated* first-generation clones for pollen production are used by the North Carolina State Cooperative to provide an acceptable useful interim pollen source. Since these clones will be rogued as soon as the second-generation clones themselves produce pollen, they do not provide a long-term dilution of genetic gain in the advanced-generation orchard.

In first-generation orchards, a 125 metres to 150 metres isolation or dilution zone is maintained which is kept clear of trees which will cross-pollinate the orchard species. This distance appears to be satisfactory for increasing the ratio of improved to contaminating pollen (McElwee, 1970)—see also Chapters 5 and 8. Dilution zones are more critical for second-generation orchards since the contaminating pollen from wild stands becomes, in relative terms, increasingly inferior to that from the orchard trees, and particularly when pollen production during the formative years of an orchard is inadequate.

Although of less importance, second-generation orchards should also be isolated from first-generation orchards. If this cannot be fully accomplished, the adjacent portions of the first-generation orchards must be very heavily rogued before the onset of commercial seed production in the newer advanced-generation orchards. In particular, all parents with progeny in the second-generation orchard must be removed to prevent inbreeding.

Genetic Improvement

The primary objective of an applied forest tree improvement programme is the production of enough improved seed to meet regeneration requirements. It is essential to maximise the genetic quality of such seed at all times. Realised genetic gains of first-generation improvement programmes for the southern pines in the south-eastern United States have averaged 10 to 20 per cent for growth and quality characters for progenies from rogued seed orchards. Mass selection for fusiform rust (*Cronartium fusiforme*) resistance has resulted in less improvement than for growth and form because some selections are escapes from natural infection in certain stands and because of the nature of the inheritance of the disease resistance. However, when combined with progeny testing, subsequent orchard roguing, or the establishment of improved special disease-resistant first-generation orchards, the percentage of diseased trees can be reduced by as much as 20 per cent (Blair and Zobel, 1971). First-generation orchards have indeed paid good economic dividends for pest resistance, growth, form and wood qualities.

Genetic gains from advanced generations are presently restricted to predictions of improvement; the estimates of expected improvement are most encouraging. With the best available data from the extensive heritability study of loblolly pine, conducted cooperatively by the International Paper Company and the North Carolina State University, the application of a selection intensity of one in a hundred results in a predicted improvement, through mass selection, in the order of 25 per cent for volume and 26 per cent for dry weight production (Table 15). Results from this large advanced study also show that by simple mass selection, excellent improvement of quality traits such as disease resistance, specific gravity and form can be achieved.

Applied tree improvement programmes usually aim at the simultaneous improvement of a complex of several traits. Surprisingly, data from a Weyerhaeuser progeny test (see Table 15) show gains for several traits selected under a multiple-trait index procedure compared with a single-trait selection in the heritability study. The two methods should not be compared when applied to different populations with different variation patterns; yet each gives cause for optimism and approximate estimates of the potential which can be exploited in advanced generations.

TABLE 15

PREDICTED GENETIC GAINS FROM MASS SELECTION OF THE BEST ONE IN ONE HUNDRED PHENOTYPES: IMPROVEMENT EXPRESSED AS PERCENT OF THE MEAN

Character	Multiple Trait Index Selection (*1*)		Single Trait Selection	
	South Coastal progeny test	North Coastal progeny test	Heritability Study (*2*)	New Zealand progeny test (*3*)
Diameter	9.2	6.6	18 (*4*)	8.7
Height	7.2	3.6	14	—
Volume	23.4	7.9	25	—
Crown form	4.2	2.2	4	—
Straightenss	4.6	5.6	7	37.7
Cronartium fusiforme score	26.4	23.3	42	—
Specific gravity	—	—	10	—
Dry weight	—	—	26	—

Notes:

(*1*) Data from 8-year assessment of control-pollinated *P. taeda* progeny of Weyerhaeuser Company grown in North Carolina, U.S.A. (Matziris, 1974).

(*2*) Data from 5-year assessment of open-pollinated *P. taeda* heritability study of International Paper Company grown in south-west Georgia, U.S.A. (Stonecypher *et al*, 1973).

(*3*) Data from 14-year assessment of open-pollinated *P. radiata* progeny of New Zealand Forest Service grown in Nelson, New Zealand (Shelbourne, 1969).

(*4*) Basal area rather than diameter.

When combined family together with within-family selection is used, improvement can be even greater. Second-generation clonal seed orchards were shown to provide the possibility of 27 per cent improvement for diameter of *P. radiata*, a trait with low heritability. A highly heritable trait such as stem straightness had total predicted gains as high as 87 per cent through the second generation cycle (Shelbourne, 1969). Experience with stem straightness in the south-east states of the U.S.A. has shown additional gains to be feasible in advanced generations but, because of the excellent response to initial selection, merely maintaining the level of improvement already realised will be satisfactory. This strategy recognises that additional improvement in form would be obtained at the expense of additional gains in volume production or disease resistance.

It is apparent that possible genetic gains from properly executed advanced-generation seed orchard programmes are well in excess of improvements experienced to date. Based on our experience, and the selection differential and heritability, we estimate that second-generation orchards will produce volume improvements of 35 per cent or more above the unimproved planting stock currently being used. Second and subsequent improvement cycles are expected to have an increasing impact on intensive forest management practices throughout the world.

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CHAPTER 13

BROADLEAVED SEED ORCHARDS

Part A.—Notes on Temperate Broadleaved Species Including Intensive Methods for Small-Seeded Species

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Introduction

Broadleaved tree species are generally much less important than conifers for forestry purposes in the temperate climatic regions of the world. In consequence little attention has been paid to seed procurement and the establishment of orchards of broadleaved species despite the fact that beech was mentioned in the early tree breeding papers of Opperman (1908) and Larsen (1934). Published lists of seed orchards show that in most countries only small areas (at the most 2–3 hectares) have been established. For many broadleaved species this is understandable since the annual planting programmes are generally small and this is reflected by the area of the orchards needed to meet part of the requirements. The establishment, management and protection, particularly by fencing, costs of small orchards are high per unit area. Only a limited number of genotypes can be included in a small orchard and this is usually an undesirable feature. Furthermore, the satisfactory pollination of anemophilous species, for example, *Betula*, *Alnus*, *Quercus* species, is seldom attained in orchards of limited area. Because of the numerous reservations associated with small orchards other alternative sources of seed supply should be given serious consideration before embarking on a programme of orchards. Seed collections from selected trees or stands will normally produce sufficient planting material and at a very much lower total cost than from a seed orchard. Vegetatively propagated planting material may, in some species, for example poplars and willows, be the safest and most economic method. However, no substantial genetic gain can be achieved by this method of plant production. If a genetic gain of 20–30 per cent can be achieved for any economically valuable character then it is worth considering more intensive methods of seed production than those used in normal seed orchards. Particularly rewarding from the technical point of view are small-seeded species which yield very large quantities of seeds from a relatively small area.

Broadleaved forest tree species are represented by many families and genera and are much more heterogeneous than conifers. There are great differences in the biology of flowering and both entomophilous and anemophilous species occur. Also the seed of most broadleaved species matures in a short time since the duration of the growing-season is seldom a limiting factor in the seed maturation process.

Traditional Seed Orchards

At present there is little to record on individual temperate broadleaved tree species regarding normal seed orchards based on field-planted grafts or seedlings. The few seed orchards which have been planted have developed fairly slowly and orchards of several broadleaved species, established with grafted material on the northern boundary of their area of distribution in Finland, have taken approximately 15 years to flower regularly on a significant scale. The extreme scarcity of published data on broadleaved seed orchards and their flowering behaviour and seed yields suggests that they are still relatively unimportant. In recent years, however, there has been a growing interest particularly in North America in the development of orchards for *Liriodendron tulipfera*, *Liquidambar styraciflua* and *Juglans* species, some reference to which is made in the Annual Reports of the North Carolina State University Cooperative Tree Improvement and Research Programmes. Breeding temperate broadleaved tree species has been very much overshadowed by the breeding of the economically more valuable conifers. From some aspects this is perhaps surprising because most broadleaved species, from an evolutionary point of view, have a much broader and genetically plastic base in relation to conifers which became stabilised long ago. Because of this the approach to breeding some broadleaved species may best be done by other methods, some of which may be more intensive and aimed at more profound genetic changes.

Intensive Methods for Small-seeded Broadleaved Tree Species

Since 1967 the Finnish Foundation for Forest Tree Breeding has raised certain tree species in plastic-houses with the object of inducing both seedling and grafted plants to flower and produce seed at an early age. Broadleaved species included in the work are European silver birch, *Betula pendula*, syn. *B. verrucosa*, grey alder, *Alnus incana*, aspen, *Populus* *tremula*, and North American aspen, *Populus tremuloides*. The rooting medium is garden peat fortified with artificial fertilizers. The plastic-houses are unheated, but due to solar heat and the "greenhouse-effect" the vegetative period begins two months earlier than out-of-doors. Excessively high temperatures during the summer are avoided by irrigation sprays and forced ventilation. The carbon dioxide (CO_2) content of the internal atmosphere is increased during the vegetative period by burning pure propane, since experience has shown that increasing the CO_2 content by about 1 000 ppm during the morning and before artificial ventilation is needed gives the best results. Natural sunlight filtered through the transparent plastic cover of the house is the only form of lighting.

Birch (see Plate 12, central inset) and alder raised in this environment grow quickly and attain heights of 6–7.5 metres during the third or fourth growing-season; aspens reach similar heights in the second summer and it is necessary to remove or bend over the tree tops. The method successfully induces seedlings of European silver birch (*Betula pendula*, syn. *B. verrucosa*), but not alder or aspen, to produce abundant flowers and seed (Plate 13) when the plants are only a few years old.

The initial experimental results were so encouraging that in 1970 a complete experimental seed orchard was established under plastic cover. Individual, fast-growing, 1–3 year-old progenies of phenotypically superior selected plus trees were chosen as parent seed producers. The seedlings had already been raised in a "banana climate" from the outset and they produced a certain amount of seed in the first summer. Data on the 1970–1973 seed crops is given in Table 16 and Figure 25.

From Table 16 and Figure 25 it can be seen that European silver birch seedlings grown in a plastic-house "orchard" can be very successfully induced to produce abundant seed crops five years after sowing.

The climate inside a plastic-house "orchard" is vastly different from that immediately outside and in southern Finland the vegetative growth inside the plastic-house begins approximately two months earlier. Consequently the physiological processes which occur during the active period also begin two months earlier than normal. Thus European birches in plastic-houses flower during April when trees out in the open are still dormant, and their flowers therefore are totally isolated against contaminant pollen from local natural birch stands. Since there is insufficient air movement to ensure adequate

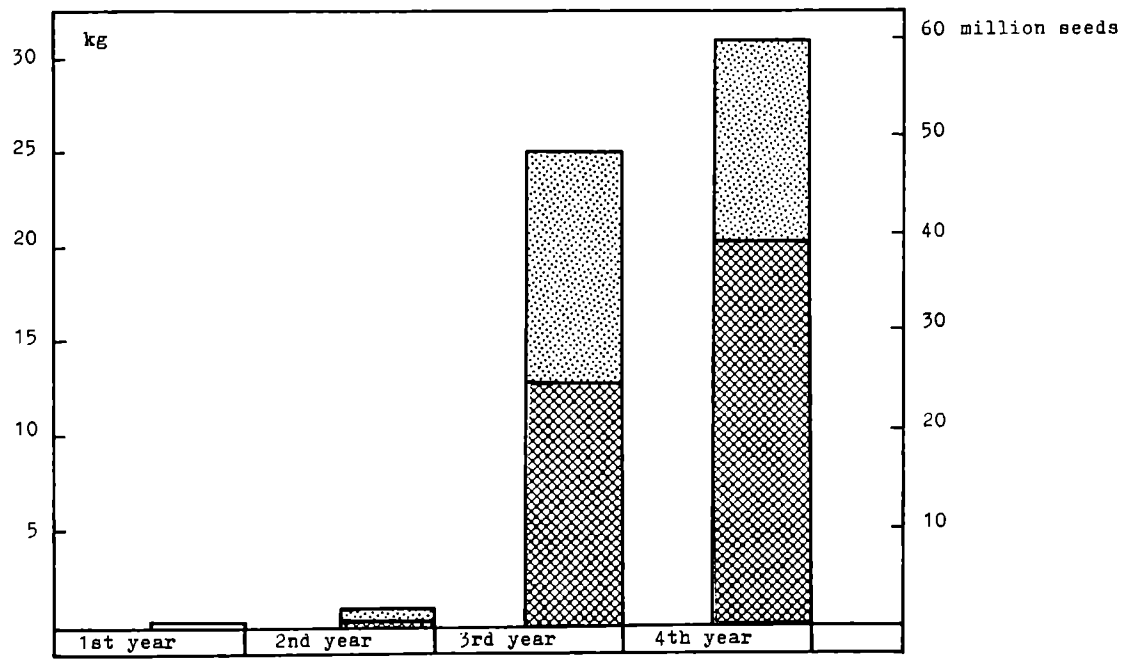

Fig. 25. *Betula pendula* (*verrucosa*). Seed crop per 1 000 square metres in an experimental seed orchard under plastic cover. Based on 62 seedling parents planted when 1, 2 or 3-years old in 1970. The whole column represents total seeds, the shaded part germinated seeds.

TABLE 16

BIRCH (BETULA PENDULA): 1970–1973 SEED YIELDS FROM A 900 SQUARE METRE EXPERIMENTAL SEED ORCHARD GROWN UNDER PLASTIC COVER

Year	Seed crop		Germinability
	kilograms	Approximate number of seeds	
1970	0.25	0.7×10^6	Not determined
1971	1.5	4.5×10^6	21
1972	23.0	47.0×10^6	51
1973	29.0	54.5×10^6	65

pollination inside the closed space of the plastic-house, turbulent air conditions must be artificially provided. Different methods can be used, the simplest of which is to circulate the internal air by means of powerful fans and at the same time lightly shaking the trees to free pollen from the stamina. Ventilation equipment must be switched off during the operation to prevent pollen from being drawn-out of the "house". Alternatively fresh pollen can be collected either from the orchard itself, or, during the previous summer from naturally growing trees or other sources. This artificially collected pollen can be applied to female flowers inside the "house" with a pollen sprayer or fan—a household vacuum-cleaner can be satisfactorily used as the fan.

Very short-lived rather primitive types of "seed orchards", in which the seed is produced on detached branches which are kept alive by placing the cut branch-ends in water, under greenhouse conditions might also be considered. The technique is well known and widely used particularly for species of *Populus* and *Salix* which flower in very early spring and when outside temperatures are well below the summer levels. In "orchards" of this kind it has been often noticed that female catkins often absciss before the maturation of the seeds—probably due to excessively high temperatures during early growth.

Faster hybrid *seed* development might be achieved by raising the "house" temperatures to perhaps 25–30°C, and temporarily perhaps even higher, to shorten the maturation processes although some observations indicate that a greater number of female catkins mature but over a prolonged period when the temperature is kept below + 15 or + 20°C. There may be other reasons for the shedding of female catkins, such as a lack of suitable nutrients in the branches, or, lack of water resulting from bacterial growths which block the water conducting vessels. Lepidopterous larvae can also cause flower abscission unless controlled by insecticides. Because of these risks and practical difficulties methods similar to those successfully developed for European silver birch are now being explored for *Populus* and *Salix* species.

To conclude it can be stated that results obtained from birch seed orchards under plastic covered houses show that it is possible to manipulate seed production for some small-seeded broadleaved tree species by unconventional tree breeding methods. Similar results should be obtainable with certain other tree species. Shortening the time interval from seed to flowering by the use of intensive cultural techniques permits the application of breeding methods based on several successive generations. Furthermore the production of seed of new varieties on a practical scale can be speedily achieved in a relatively short period of time.

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Part B.—Notes on Tropical and Semi-tropical Species other than Eucalyptus Species and Teak

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Introduction

The exploitation of natural forest in many tropical and semi-tropical countries is becoming increasingly expensive and as a consequence large-scale afforestation schemes have been started to provide cheaper sources of wood. Exotic species are often used for the purpose and amongst the broadleaved species Teak (*Tectona grandis*) and some species of *Eucalyptus* are by far the most popular. However, several other species can be successfully raised in plantations and these are becoming increasingly important.

The wattles, and *Acacia mearnsii* in particular, have been extensively planted in eastern and southern Africa, and for many years *Cassia* species were favoured in several other African countries. Currently *Gmelina arborea* is one of the most popular exotic species in West Africa which, together with local species such as *Aucoumea klaineana*, *Entandrophragma utile*, *Nauclea diderrichii*, *Terminalia ivorensis*, *T. superba* and *Triplochiton scleroxylon*, are widely planted in both West and Central Africa. Lamb (1968) suggested that another exotic, *Cedrela odorata*, could also be important in these countries because of its excellent wood qualities and resistance to a shoot-boring insect which attacks other mahoganies. In some parts of tropical Asia, Central America and in the Caribbean area species of *Acrocarpus*, *Anthocephalus*, *Chlorophora* and *Khaya*, are being planted (see Streets, 1962). However, most afforestation developments are still in their infancy and the main need in many countries is for a systematic programme of species, provenance and management experiments.

Present-day Sources of Fruit or Seed

At present seed crops are collected from both natural stands and plantations which may have been culled to form seed stands. Known groups of trees and individual trees in gardens, streets and arboreta are also frequently used as sources of seed despite the fact that collection costs are often high and the genetic and physical qualities are frequently poor.

The drier tropical and semi-tropical countries have the longest history of tree plantation establishment, particularly for species of *Cassia*, *Acacia*, and more recently *Azadirachta indica*. Fruits or seeds for the annual planting programmes of such species are either harvested from old established plantations or alternatively they are imported.

In the naturally wet or moist evergreen or deciduous forests there are very few old plantations with the exception of some experimental plots or plantations developed by the national forestry departments over the years, often in isolated areas. Such areas usually form major seed sources.

Seed of some species are still collected from the open forest and the number of trees from which such collections are made depends upon several variables including the density of stocking and pattern of distribution in particular. Some tropical forests, for instance, are composed of relatively few and sometimes closely related species, for example, the Dipterocarp forests of south-eastern Asia. More frequently, however, the tropical forest is heterogeneous and often contains relatively large numbers of species growing together in close mixture. In extreme cases there may be only two isolated trees of a given species per hectare, for example, the important species *Chlorophora excelsa*, *Khaya ivorensis*, and *Terminalia ivorensis*. Other species may occur in groups or clusters even at the limit of their range.

Reliable phenological data for both tropical and semi-tropical broadleaved species are rarely obtainable although Taylor (1960) produced a useful table covering many Ghanaian species and Medway (1972) reported nine years of observations on 45 species of Dipterocarps in West Malaysia. This lack of information is understandable since flowering is often localised and the conditions for fruit development are variable. Similarly a knowledge of the best time for seed collecting is needed, particularly if collections are made from isolated trees or clusters because of the expense in relation to the size of the crop.

Additionally little is known about the fruit or seed development of tropical trees. Quality often varies

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from year to year, possibly due to the climatic conditions during development and the tendency to harvest at the same time each year, and also because seed processing methods are usually primitive. Insects and pathogens attack developing fruits and Roberts (1969) listed a large number of flower- and fruit-borers which attack Nigerian tree species. In Ghana, Kudler has made some interesting observations on insects attacking *Terminalia ivorensis*, *Triplochiton scleroxylon* and *Guarea cedreta* (Jones and Kudler, 1971a, 1971b; Kudler, 1970). There are few fungal pests recorded but a smut on *T. scleroxylon*, described by Zambettakis and Foko (1971), could be very important.

The Case for Seed Orchards

Because of the difficulties of regularly collecting seed from widely scattered indigenous high forest trees, the difficulties of collecting basic information on flowering and breeding systems, and the frequent use of inferior seed sources around settlements, it should be well worthwhile developing seedling and clonal seed orchards on a small scale at this stage. These would provide facilities for collecting basic information and testing the feasibility of seed orchards for the different species. Obviously it is essential that satisfactory propagation methods be developed for each species and that the plants be satisfactorily grown to a flowering stage under orchard conditions; this is now happening in some cases.

Seed Orchards

Although the need for clonal and seedling orchards has been recognised for some time very few have been established, mainly because few countries have made any real effort to survey systematically the forests and plantations for superior phenotypes, a task which is very difficult in the natural tropical forest. Furthermore, for some species, there have been great difficulties in developing satisfactory vegetative propagation techniques for clonal orchards; some of these are still to be overcome.

Replies to a questionnaire from respondents in nineteen African, Asian, Australasian and American countries revealed that in 1973, for broadleaved tropical species other than teak and *Eucalyptus* species, clonal orchards are established for only six species. These are listed in Table 17. Many of these orchards are small and often poorly designed, managed and protected, largely because there is locally a lack of conviction in their value. Many are based on "seed trees" selected in plantations which are considered to be good on the basis of an assessment of stem quality.

Details of other orchards for wattle in South Africa are given in Table 18. Many of these orchards have not yet flowered or produced seed.

Cedrela odorata in Ghana

A four acre clonal seed orchard was established in the South Formangsu Forest Reserve in 1971; this contains three, 144-plant blocks each based on 12

TABLE 17

LIST OF CLONAL SEED ORCHARDS OF TROPICAL AND SUB-TROPICAL BROADLEAVED SPECIES, OTHER THAN TEAK, EUCALYPTUS AND ACACIA SPECIES IN 1973

(Based on replies from 19 countries to a widely circulated questionnaire; only clonal orchards have been established).

Species	Area (hectares)	Number of clones	Age	Method of propagation	Location of orchard			
					Country	Latitude	Longitude	Altitude metres
Maesopsis eminii	About 0.28	11	3	Grafting	Uganda	0° 33′ N	33° 12½′ E	1200
Cedrela odorata	4.0	23	2	Budding	Ghana	6° 30′ N	1° 00′ W	300
Terminalia ivorensis	4.0+	20	1	Budding	Ghana	6° 30′ N	1° 00′ W	300
Triplochiton scleroxylon	4.0+	20	1	Budding	Ghana	6° 30′ N	1° 00′ W	300
Melia azaderach	?	8	?	Roots & Grafts	Argentina	27° 30′ S	55° 20′ W	300

ramets of 12 clones; the plants are spaced six metres apart (Anon., 1971). Budded transplants, which were raised in beds, provided most of the planting stock although some pot-raised grafts and air-layered plants were also used. Post-planting losses were negligible. A second seed orchard containing 23 clones was also established in 1971.

Acacia mearnsii in South Africa

Improvement of wattle (*Acacia* species) for tannin yield has been in progress at the Wattle Research Institute, Pietermaritzburg, for many years. Details of both clonal and seedling orchards, which date back to 1965, are given in Table 18.

Vegetative Propagation

A tree improvement programme for Nigeria was launched in 1962 with the help of the Danish Technical Assistance Programme (Keiding *et al*, 1964). Keiding demonstrated the various techniques of budding and grafting, the most successful of which was "vorkert" budding as used for *Hevea brasiliensis*. Species successfully budded onto potted rootstock were *Azadirachta indica*, *Gmelina arborea*, *Nauclea diderrichii*, *Terminalia ivorensis*, *T. superba*, and *Triplochiton scleroxylon*. *G. arborea* has also been successfully budded on to one-year-old field-planted rootstock one year after establishment. A similar programme began in Ghana during 1965 (Jones, 1969) in which *Afrormosia elata*, *Cedrela odorata*, *Terminalia ivorensis* and *Triplochiton scleroxylon* are included; of the four species only *A. elata* has proved difficult to bud-graft. Air-layering has also been used for propagating *C. odorata* in Ghana. Rooting cuttings and grafting were successful methods for propagating eight clones of *Melia azederach* in Argentina. Budding and air-layering have been used to produce plant

TABLE 18

DETAILS OF ACACIA MEARNSII SEED ORCHARDS IN SOUTH AFRICA IN 1973

Located at Latitude 29° 30′ S, Longitude 30° 29′ E, at an altitude of 900 metres

Type	Area (hectares)	Basis	Age years	Age of first flowering	Yield of seed kilograms/hectare in average year	Propagation method of clonal orchards
Seedling	0.8	11, Open-pollinated progenies	8	2 years 7 months	Approx. 150	—
Seedling	0.8	18, F_1 progenies	5	2 years 7 months	Approx. 150	—
Seedling	1.3	18, Open-pollinated generation from above orchard	½	—	—	—
Seedling	1.0	10, F_1 progenies	2	2 years 7 montys	—	—
Seedling	2.6 } 1.6 }	29, Open-pollinated or F_1 progenies	1	—	—	—
Clonal	0.5	22, Mainly F_1 selections	1 to 2	2 years	—	Budding
Clonal	0.4	17, Selections in S_1 or S_2 inbred lines	1	1 year 7 months	—	Air

material for two small orchards of *Acacia mearnsii* in South Africa. *Maesopsis eminii* has been successfully grafted in Uganda where there is now a small orchard of this species.

Conclusion

With the exception of the South African orchards, seed orchards play an insignificant role in the provision of seed for most tropical broadleaved species. There are several reasons for this, the most important of which are: firstly a lack of appreciation of the value of tree improvement through soundly based selection and breeding techniques; secondly, the frequent lack of a national plan for a tree improvement programme within which seed orchards can play a prominent role; thirdly, techniques and facilities for vegetative propagation are frequently unknown or unavailable for large-scale operations; fourthly, information on phenology, breeding systems, and seed developmental processes are often lacking.

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Part C.—Eucalyptus Species

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Introduction

Since the late 1960's eucalypt seed orchards have been established in many parts of the world to provide seed for short-rotation crops, mainly for pulpwood. In contrast to the situation for many conifers only a few eucalypt orchards have been established to furnish material for the sawn timber markets.

Although eucalypts occupy perhaps one fifth of the world's man-made forests (Logan, 1967) only a very small part of the world's tree breeding effort has been devoted to the genus. This is puzzling since, in comparison with conifers, the prospects of quicker financial returns on a breeding investment are much higher, due to the earlier and abundant production of seed and shorter plantation rotations. The main reason is, perhaps, that foresters recognised the need to first solve the basic problems of correct choice of species and provenance before starting a breeding programme. In many countries these problems are now much nearer solution and there is an increasing interest in the production of genetically improved eucalypt seed.

The three main stages in the genetic improvement of a forest tree species are: identifying the best provenance; selecting some of the best individuals within that provenance; and "packaging" (Libby, 1973) the selected genes, by means of seed orchards, to produce commercial quantities of seed for establishing improved forests.

In an account of seed orchard work in South Africa, Hodgson (1974) presents general notes on vegetative propagation, lay-out, management, flowering and seed production, and gives special attention to orchard lay-out under the breeding system and potential inbreeding problems.

This paper examines four types of eucalypt seed orchards and provides some information on existing orchards for illustration. Nomenclature follows Johnston and Marryatt (1965).

Types of Orchards

Outline plans of operation for four types of orchard are described against a time-scale in years. The time-scales are based on orchards in South Africa and Zambia, and progeny-tests in Australia and Florida, U.S.A. For tropical and sub-tropical species the period before the first abundant seed crops is four and six years for grafts and seedlings respectively. Eucalypts of the temperate zone produce seed at least two years later. Comparative genetic gains from each type of orchard, based on the same heritability assumptions, are summarised after the descriptions.

1. Orchards Based on Open-pollinated Seedlings

Years 1 and 2	In even-aged stands of a suitable provenance select 200 or more plus trees at an intensity of approximately one per two hectares. Collect seed and raise plants.
Year 2	Establish the orchard in an environment similar to the planting area and in a way which ensures that progeny identities are retained.
Years 4 and 5	Cull heavily both among and within families.
Year 8	Collect the first abundant seed crop.

The attractions of this type of orchard are cheapness and simplicity, since grafting or other complex techniques are not required. Genetic gain is not expected to be as high as with other methods. Although this method is suitable for all *Eucalyptus* species difficulties can arise with *Eucalyptus regnans* and *E. grandis*; some plus trees of these two species have been rejected for lack of seed.

The first open-pollinated eucalypt seed orchard was of *E. maculata* and was established in Brazil in 1952 (Castro, 1962). The Brazilian orchards were initially intended to minimise hybridisation and to purify species derived from mixed and hybrid plantations.

A programme for the genetic improvement of *E. robusta* in southern Florida, U.S.A. (Franklin and Meskimen, 1973) provides a good example of the use of open-pollinated seedlings. The largest trees were selected in a six-year-old provenance test of nine origins; lower selection intensities were used in the better provenances. All unselected trees were removed from the test before the 1966 flowering season and, of the 118 trees which remained, 57 yielded sufficient seed in 1967 to raise 100 seedlings from each. In 1967 seedlings were planted in a randomised block design and in 1972 the best one to three trees per family were selected; all the other trees were removed from the test. The remaining trees constituted an open-pollinated seedling seed orchard.

Seed from plus trees in natural forests were used to establish a 9 hectare orchard of *E. regnans* between 1970 and 1973 near Morwell, Australia (Richmond, 1971; Eldridge, 1971). The off-spring of 160 plus trees were planted as clusters of five seedlings of each family and were repeated many times in a randomised-block design. A space of 6.6 metres separated the clusters. The less successful individuals and families are being removed at intervals after assessing growth in the orchard and in separate progeny tests.

A similar orchard started in 1972 with *E. grandis* at Coffs Harbour, Australia, is based on 170 trees selected for outstanding straightness, natural good branch-shedding and occlusion of knots (Burgess, 1973). In two other similar projects more than 150 plus trees have been selected in natural forests of *E. diversicolor* in south-east Western Australia and of *E. deglupta* on the island of New Britain, Papua New Guinea.

Genetic gain from a seedling seed orchard depends largely on effective selection within the orchard. For characters of low heritability (little additive variance) worthwhile genetic gain can only be obtained by selecting the best families. For characters of high heritability, selecting the best individuals within families can be so effective that selection of the best families is unnecessary. Heritability values are still largely uncertain for most characters and therefore it is prudent to assume that they will be low. Thus provision should be made for selections both among and within seedling seed orchard families.

2. Orchards Based on Grafted Material from Mature Trees

Years 1 and 2	Select more than 50 plus trees and produce grafts of each.
Year 2	Establish grafts to form an orchard.
Year 6	Collect the first abundant seed crop.

Grafted orchards of several eucalypts have been made in numerous countries. The degree of success of these orchards has been largely dependent upon scion/rootstock compatibility which varies enormously between and within species (see Chapter 4).

Between 1958 and 1965 three grafted orchards of *E. camaldulensis* and one each of *E. tereticornis* and *E. gomphocephala* were established at Marmora, Morocco (A. Zaki pers. comm.). Four of these orchards contained only a single clone and the other, five clones. The disadvantages of such a limited genetic base have been acknowledged and an orchard of 24 clones of a selected provenance of *E. camaldulensis* was established at Marmora in 1973.

Boden (1968) advocated grafted eucalypt orchards and described a successful pilot-scale orchard of *E. melliodora* planted in 1963 in Canberra, Australia.

Grafted orchards of *E. grandis* and *E. saligna* were established in 1964 at Zomerkomst, South Africa. A high risk of graft-incompatibility necessitated planting three grafts per planting position, and even re-planting those positions where all three plants failed. Even so the *E. grandis* orchards have been highly successful in producing seed. Individual trees have yielded 1 kilogram of seed in a single year and the production from only a few hectares of orchard was 190 kilograms seven years after planting (South Africa, 1972). The number of clones in the South African *E. grandis* orchards was increased from nine in 1964 to 28 by 1972. Similar orchards of *E. cloeziana* and *E. diversicolor* have also been established in South Africa.

Grafted orchards of *E. grandis* are also widely used in Zambia where, as in South Africa, persistence in replacing failed grafts has often been rewarded by a high yield of seed (Christensen, 1973). An experimental 3.6 hectare orchard, based on a limited number of clones was planted in 1965. This orchard produced enough seed in 1972 to provide plants for 450 hectares of plantation. The need for a wider genetic base than originally used in 1965 has been well recognised and by 1972, 59 clones had been chosen for future orchards. In 1973 Zambia had grafted orchards of *E. grandis*, *E. tereticornis*, *E. grandis* × *E. tereticornis*, *E. resinifera* and *E. cloeziana*, totalling 25 hectares.

An extreme case of graft-incompatibility was reported by Burgess (1973) for *E. grandis* at Coff's Harbour, Australia. Although initial grafting was 80 per cent successful most of the grafts died within two years. C. Pires (pers. comm.) reported similar experiences in Brazil. As a consequence the use of grafted plants has been abandoned at both these places for this species.

In Portugal a private cellulose-pulp company embarked on the genetic improvement of *E. globulus* in 1966 (Dillner *et al*, 1971; Luhr, 1973). A progeny test planted in 1966 has since shown that rate-of-growth and wood density in this species are strongly inherited whereas cellulose content is not. Since 1970 two grafted orchards have been established using bottle-grafting techniques. Twenty-five clones, from about 260 selected trees, have been selected for high wood-density and other characters. These young orchards yielded 4 kilogram of seed three years after planting.

Other countries also use grafted plants for their eucalypt seed orchard programmes and an F.A.O. project in the Mediterranean region for the genetic improvement of *E. camaldulensis* has been reported by Lacaze (1972) and by E. Giordano (pers. comm.). Grafts have been made of 18 plus trees selected in the best provenance in several provenance trials. Grafted orchards are to be established in Italy, Tunisia and Morocco. Martin (1971) has reported on the early stages of work on 15 and 30 clone orchards of *E. tereticornis* in the Republic of Zaire.

Two-clone orchards, based on clones with high specific-combining-ability, could be made for the mass-production of seed of valuable intra- or interspecific crosses, provided that excessive selfing is not a problem.

One basic defect in the design of several untested grafted eucalypt orchards is that relatively small numbers, 15 to 30, of clones have been used. It is expected that subsequent orchards will be based on at least 50 clones so that effective culling, based on progeny performance and flowering data, can be made and still leave an acceptably broad genetic base.

3. Orchards Based on Rooted Cuttings from Young Trees or Coppice

Years 1 and 2	Select a large number of plus trees and collect seed.
Year 2	Establish tests of open-pollinated families.
Years 5 and 7	Select the best families and the best individuals within families when three to five years of age.
Year 7	Vegetatively propagate the selected trees by rooting cuttings taken from basal shoots which arise from stumps after felling (Pryor, 1973; Christensen, 1973).
Year 11	Collect the first abundant crop of seed.

Several years can be saved by selecting parent trees within existing seedling orchards and progeny tests, or in plantations of a suitable age and origin.

Pryor (1973) described the use of cuttings as a means of circumventing graft-incompatibility problems associated with *E. grandis*. "*E. grandis* does not ordinarily strike from cuttings but by inducing coppice shoots from the basal 15 centimetres of three-year-old plantation trees it is found that about 50 per cent strike under mist spray quite readily and can be potted on and planted out in the field where they develop normal orthotropic growth. Clones are found to reproduce vigour, stem and branching habit quite precisely." It is expected that seed will be harvested by cutting down the trees repeatedly on a coppice rotation of about four years. The first orchard of this type was planted near Coff's Harbour, Australia, in 1973.

It is planned to use this method in Zambia where Christensen (1973) claims that cutting propagation in mist beds is a much more efficient and faster method of propagation than grafting which is to be discontinued.

The method should be well worth attempting with any eucalypt which coppices freely, although most of the fast-growing eucalypts of cooler climates do not respond to coppicing treatments (Jacobs, 1955). Coppice shoots do occasionally occur on the stumps of young saplings of *E. regnans* and other "non-coppicing" eucalypts, and it may be possible to develop new techniques which would increase responses to coppicing.

4. Orchards Based on Control-pollinated Seedlings

Years 1 and 2	Select plus trees and make a few grafts of each.
Years 3 to 6	Conduct artificially controlled-pollinations on the grafts.
Year 7	Establish seedling progenies to form an orchard in an environment similar to the planting area.
Years 9 and 10	Cull heavily among and within families.
Year 13	Collect the first abundant crop of seeds.

Initially the mating design would be based on random single-pair (bi-parental) matings. The time needed for completing the crossing programme could be reduced by using established flowering-grafts of a proportion of the plus trees and by developing techniques for grafting scions bearing flower-buds. Pollen could be collected directly from the plus trees.

No eucalypt orchards based on control-pollinated seedlings have yet been reported. Quite obviously the method proposed would be technically difficult for those species with graft-incompatibility problems, or, with flowers too small for easy emasculation.

MANAGEMENT FOR SEED PRODUCTION

By 1974 there was no reliable body of experience on eucalypt seed orchards on which to base sound management plans. It is expected, however, that management methods will, in most cases, follow those outlined in Chapter 5. However, special methods will have to be developed for harvesting seed because climbing eucalypts, to pluck the small seed-bearing capsules from the extremities of long thin branches, is quite impractical. In the early years, therefore, seed will be harvested from fruit-picking, tripod ladders. Later on the most likely methods will be to either pollard the tree crowns and to collect the capsules from the fallen branches, or, for those species which coppice, to fell the whole tree for easy seed collection and to manage the orchard on a coppice rotation. Orchards of non-coppicing species may have to be felled for their seed crop and be completely replanted with new trees afterwards, a practice which would facilitate the widely recommended progressive replacement of seed orchards with genetic material of higher quality.

Prospects for Genetic Gain

Estimates of genetic gain, derived from theoretical calculations made and described by Shelbourne (1969a, 1969b), are given for comparative purposes in Table 19. The table is based on assumed selection intensities, for example, "1,000" indicates the selection of the best tree per thousand trees for one character. Genetic gain is expressed as a percentage of the base-population mean, per generation and per year. The estimates of gain were calculated for an assumed case of high heritability (0.60) in which all the genetic variance was additive, and a case of assumed low heritability (0.19) in which half the genetic variance was additive and half due to dominance (Shelbourne, 1969a).

Discussion and Conclusions

Although this account of eucalypt orchards does not discuss the effect of seed origin on performance it must be emphasised that, in most cases, large genetic gains are still to be obtained through finding and using the best provenances; any orchards should be based on parent trees selected from among the best provenances.

When deciding which type of orchard to use for the improvement of a selected eucalypt provenance

TABLE 19

CALCULATED GENETIC GAINS FROM DIFFERENT TYPES OF SEED ORCHARD—USING ASSUMED SELECTION INTENSITIES AND HERITABILITY VALUES

After Shelbourne, 1969a

Type of orchard	Selection intensity at each stage			Genetic gain per generation per cent		Time per genera-	Genetic gain per year per cent	
	Phenotypic	Family	Within family	h^2 0.60	h^2 0.19	(years)	h^2 0.60	h^2 0.19
1. Open-pollinated seedlings	1000	4	5	47	13	8	5.9	1.6
2. Clones as grafts or cuttings	1000	—	—	48	11	6	8.0	1.8
3. Clones, culled after progeny test	1000	5	—	63	20	8	7.9	2.5
4. Cuttings from open pollinated progeny test	1000	10	100	64	18	11	5.8	1.6
5. Control-pollinated seedlings	1000	4	5	71	18	13	5.4	1.4
						9	8.7	2.0

it must be recognised that costs, realisable genetic gain, seed yield, and economic returns are unknown for the species of this genus. Any decision will involve some risk of being wrong and, therefore, it may be wise to spread the risk by attempting more than one type of orchard.

A seed production area, made by heavy, early-thinning in a suitable provenance should provide some genetic gain at little cost in money or technical skills, and should be included in the overall tree improvement programme as a security against the failure of more elaborate plans.

Grafted clonal seed orchards are obviously the best choice if the technical skills are available for grafting, providing the risk of incompatibility is low or can be accepted. If there are difficulties with grafting, an open-pollinated seedling seed orchard is the next best choice.

Rooted cuttings from the stumps of selected young trees may provide a satisfactory alternative to grafting for those species which coppice and especially for large orchard programmes.

Although orchards based on seedlings derived from controlled-pollinations need more technical skills than the other methods, they do offer the prospect of much higher genetic gains per generation. Orchards of this type should be attempted, at least on an experimental scale, if only to develop satisfactory techniques aimed at reducing the time and costs per generation.

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Part D.—Teak

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Introduction

This section reports the experiences gained on the establishment and the management of teak (*Tectona grandis*) seed orchards over a ten-year period since the establishment of the first seed orchard in New Guinea in 1963, and with particular reference to experience in Thailand. Since 1963 the establishment of further orchards has been accomplished at varying speeds in several parts of the tropics and notably in Thailand from 1966 onwards. Many technical problems have been tackled, some of which, such as vegetative propagation, have been solved; others still await further investigation. Although the final outcome of the seed orchard programmes is still to some extent speculative, sufficient evidence has been accumulated to suggest that they will form a very important means of providing seed sources for the future planting and improvement of teak.

Teak is widely planted in several countries and there are extensive annual planting programmes of, for example, 20 000 and 15 000 hectares per year in India and Thailand respectively. These programmes are dependent on large amounts of seed of both high genetic and physical qualities. The ease of vegetative propagation and good seed production from grafted plants makes the clonal seed orchard a particularly suitable method for the mass production of improved material (Keiding, 1973). It is, therefore, of considerable interest to review the experiences from Thailand, a country in which the establishment of teak seed orchards has been most active. The following account of various aspects of seed orchard establishment and management is mainly confined to practices developed in connection with the Thai/Danish Teak Improvement Centre (T.I.C.). Seed orchards have been, or are being, established in India, New Guinea, and Nigeria.

All first generation orchards are composed of selected clones primarily chosen for their superior phenotypic qualities and which have not yet been rogued on the basis of any genetic evaluation in progeny or clonal tests.

Flowering Behaviour and Natural Pollination

Individual flowers occur in large panicles in the outer, unshaded part of the tree crown. Each flower is perfect, regular, and normally has six petals in the ring. The pistil is composed of an ovary with four ovules and a style with a forked stigma. Both the style and stamens are about 6 millimetres long; the diameter of the corolla is 6–8 millimetres (Bryndum and Hedegart, 1969). The flowering period for individual inflorescences last from two to four weeks and during this period approximately 3,000 (1,200–3,700) flowers may appear, with up to 100–300 new flowers opening each day. The flowers of the day open a few hours after sunrise, but the optimum fertilisation period is limited to 1130 to 1300 hours. (Hedegart, 1973). In northern Thailand flowering starts in mid-July and continues throughout the rainy season until November; it varies considerably between individuals.

Teak is mainly a cross-pollinating species and self-incompatibility is high and ranges from 96–100 per cent. It is pollinated by insects and at the T.I.C. two Apidae species (*Heriades parvula* and *Ceratina hieroglyphica*) are important pollinators. Fertilisation following natural pollination is frequently low and during the period 1967–72 varied between 0.4 and 5.1 per cent with an average of 1.3 per cent. The low percentage of flowers which develop into fruits has been ascribed to an insufficient number of pollinating insects in the locality (Hedegart, 1973).

In Thailand flowering normally starts at the age of 8–10 years but with considerable variation between individuals. At the T.I.C. nursery trees have been observed to flower at the age of three months. while a few plus trees selected at the age of 27 years have not yet flowered.

Clonal tests have suggested that the age of first-flowering is under genetic control (Larsen, 1966) and the onset of flowering in teak is of major interest, since the first inflorescence usually appears from the terminal bud and causes stem forking.

Orchard Site Selection

Considerations of the accessibility and social and economic factors are similar to those outlined in Chapter 5 and have been fully discussed by Watt (1973). Only those ecological factors which are specific to teak are presented here.

Teak will survive and grow under a wide range of climatic conditions but the effect of climate on flowering and fruit production is still unknown. Preliminary observations in Thailand have indicated that orchards planted within the natural range of the species are unhealthy under dry conditions, and under moist conditions outside the range. It is recommended, therefore, that any large-scale orchards should, for the present, be restricted to within the natural range, avoiding the drier regions. Preliminary investigations in both plantations and natural stands have shown that seed germination is not related to site quality but an average increase of about nine per cent in fruit yields and 0.18 millimetres in fruit diameter has been observed for each five metre increase in dominant-tree height. However, a significant regression was not established due to the large amount of variation associated with the stand density, the proportion of trees flowering, previous management and amount of undergrowth. Thus conditions favouring tree growth are also likely to promote seed production.

The first orchards in Thailand were considered completely isolated with a surrounding teak-free zone of about 1 kilometre but for the want of suitable sites the isolation distance has now been reduced to approximately 200 metres. Attempts to establish the distances over which insects carry teak pollen have so far been unsuccessful and if contamination is considered to be likely, seed collections from orchard edge trees will be omitted.

Design

A spacing of 3 metres × 3 metres was used in the first orchard but since this orchard required three thinnings, during the first five years after completion in order to obtain reasonable flowering, orchards are now established with an initial spacing of 12 metres × 12 metres between ramets. It is expected that all ramets in new orchards will flower freely 10–15 years after establishment.

Since the species is insect-pollinated "complete randomisation" of the ramets is necessary. Some minor adjustments are usually made to the randomisation so that ramets of the same clone not do occupy adjacent positions either before or after thinning.

The number of clones incorporated into the orchard designs has largely been a reflection of the amount of available bud-wood in the multiplication gardens (scion banks). The first orchards were based on 16 clones and more recent ones on 25 clones. It is likely that future orchards will be based on 50 clones but much will depend upon the breeding value and seed production of the selected component clones.

To facilitate the administration, control of layout and record keeping, the orchards are divided into blocks of a convenient size; each block is demarcated by posts which are colour coded so that plant positions can be easily located and identified.

Establishment

The first orchards were established by bud-grafting on stocks which had been planted 1–3 years earlier on the orchard site. The success varied from 20–80 per cent and was strongly influenced by climatic conditions. Subsequently and to shorten the establishment period, two stocks were planted and eventually budded in each position.

A more recent and promising technique is the production of pre-budded potted-planting stock. One- or two-year-old stumped seedlings (stumps) which are 15–30 millimetres in diameter at the root collar are lifted from nursery beds during March, April or May. After budding, the budded stumps are transplanted into 200 millimetres × 400 millimetres pots and placed in a glass-house for 5–12 days when sprouting takes place. In 1973 the average success for 1,250 buddings using this method was 98 per cent. The budded plants are hardened-off by gradually exposing them to normal nursery conditions before planting in the orchards. Survival three months after planting on the orchard site was 80 per cent; however, survival after the first dry-season has still to be determined.

Experiments have clearly demonstrated the benefits to be obtained from complete weed control around each plant. A 2.8 metres × 2.8 metres square around each plant kept constantly free of weeds increased the plant height growth by more than 100 per cent in comparison with ordinary slashing of undergrowth and grass treatments. In consequence the complete weeding of a 2.5–3.0 metres patch around each plant, coupled with cutting inter-row weeds either once or twice per year, is now recommended for seed orchard establishment. Experience has proved that fire-lines are incapable of protecting the orchards and this weeding scheme is now followed by a controlled burn during the first month of the dry-season.

Various cover- and catch-crops such as *Centrocima* species, *Mimosa* species, and "Green Beans" have been unsuccessfully tried. The main problems have been difficulties associated with their establishment and susceptibility to fire. The cultivation of agricultural crops can be practised between the weeded patches at each plant position.

Management

The effects of crown pruning has not been fully investigated since it is doubtful that it will significantly increase the amount of flowering in comparison with well thinned, unpruned orchard trees; furthermore, tree height has no influence on seed collection costs since fruits are collected from the ground.

Where the initial spacing is 12 metres × 12 metres two systematic thinnings are planned to provide a final spacing of 24 metres × 24 metres. It seems probable that the thinnings will be undertaken during the 10–12 and 15–20 year periods. Evidence from progeny tests will be used as the basis for roguing the orchards and these may result in a modification to the systematic thinning scheme. However, a reduction in the initial spacing is not advisable since teak is very sensitive to shading and a reduction of spacing will inevitably result in decreased fruit production.

The effect of fertilizers on flowering and fruit production is under investigation; data are not yet available. Fertilisation percentages obtained from hand-pollinations have been considerably higher than those observed from open-pollinations i.e. 6 to 60 per cent (average 20 per cent) from the former compared with 0.4 to 5.1 per cent (average 1.3 per cent) from the latter (Hedegart, 1973). This suggests that large-scale hand-pollinations should be considered. However, this would necessitate the erection of extensive scaffolds the cost of which might not be justified on economic grounds. A more realistic approach will, therefore, be to intensify research into pollinating insects in order to determine measures which will favour the more desirable ones. Suitable insects could then be introduced into seed orchard areas when required.

Although fire can be fatal during the first-three-year period of establishment, it appears to have little effect during later stages. Thus, provided tall weeds, such as bamboos and shrubs, do not appear, and provided soil erosion risks are not serious, a light burning of dry ground-cover can be applied to advantage before fruit collection. The potentially harmful effects of burning on pollinating insects should not, however, be ignored.

Occasionally teak is severely defoliated by three insect species, namely, *Hyblaea puera*, *Aularches miliaris* and *Hapalia machaeralis;* their effects on defoliation on flowering and fruit production are unknown. The larvae of *Pagida salvaris* (Pyralidae) have, in certain years, been observed to cause serious damage to the flowers. The larvae of this insect feed on developing flower buds which then fail to develop into fruits. Attempts to find suitable selective insecticides, which avoid killing the pollinating insects also, have so far proved unsuccessful (Hedegart, 1973).

Harvesting

Teak fruits grow to full size approximately fifty days after pollination and are ripe after a further 70–150 days. At this time (January–February) the fruit may be hand-picked from the trees (Hedegart, 1973). However, large-scale fruit collections from the tree crowns are not practicable and collections are usually made from the ground after the fruits are shed. Investigations indicate that the most viable fruits are the last ones to be shed (Hedegart, 1973). To facilitate fruit collection from the ground, a light burning of the surface vegetation in January–February may be considered.

Fruits are normally produced every year in varying quantities. In two T.I.C. seed source areas situated in 20–25 year old plantations the amount of fruits collected in 1973 varied from 15 kilograms to 150 kilograms per hectare.

One T.I.C. seed orchard came into production five years after completion. At this age 28 per cent of the ramets flowered and 46.4 kilograms of fruit were collected per hectare. This amount is equivalent to an average of 0.61 kilograms per flowering ramet; the highest yielding ramets produced up to 3 kilograms each. Based on this evidence a conservative estimate of seed yields for an orchard in full production is 200 kilograms per hectare.

The number of fruit per kilogram varies, but in Thailand it is approximately 1,800 fruits. This is lower than the overall average (2,062 fruits per kilogram) found in an international teak provenance experiment in 1971–72 in which the number of fruits per kilogram varied from 1,070 to 3,500.

Observations are being made on the annual variation in fruit production and will be continued until general equilibrium is achieved. Early data shows that there is considerable variation between clones, a feature which is common to seed orchards of all species, and which may be of importance when deciding thinning treatments and the composition of future orchards.

The Thai government plans to establish 15,000 hectares of teak plantations annually during the period 1975–85 (Kittinanda, 1973). Taking into account the technical and financial resources available, the expected genetic gain from the seed orchard material, and the variety of conditions under which teak should be planted, a seed orchard programme aimed at supplying seed for one-third, or 5,000 hectares, of the annual programme seems to be a realistic target. It is known that the number of usable one-year-old seedlings derived from each kilogram of fruit is often as low as six per cent of the fruits sown after one season in the seed beds. Experimentally it has been shown that with better nursery cultural practices and the inclusion of seedlings derived from delayed second-year germination a plant per cent of 18 or more can be produced. Thus, if it is assumed that 10 per cent is a realistic seedling production figure, then 250 hectares of seed orchards should meet the needs of the country. Quite clearly it can be argued that improved nursery techniques, which ensure better utilisation of orchard-produced seeds, should form part of all tree-improvement programmes; this is particularly relevant to teak.

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SEED CERTIFICATION

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Introduction

The English-language version of the Terminology of Forest Science, Technology, Practice, and Products defines the adjective *certified*: "(1) Of seed and plants, derived from e.g. tree seed orchards and seed stands whose genetic superiority has been proved by progeny testing to meet standards defined by a designated authority. *Note*: Proven interspecific hybrids may be included in this category of seed and plants." "(2) Of seed covered by seed certification" (Ford-Robertson, 1971).

Matthews (1964) has defined certification in this manner: "The object of certification of tree seed and plants is to maintain and make available to the practicing forester sources of seed, plants, and other propagating materials of superior provenances and cultivars so grown and distributed as to ensure the genetic identity and high quality of the seeds and plants." Over the years, the term *certification* has had many connotations and has been defined in several fashions according to the desires of the user. In the seed trade "certified seed" is now generally accepted as reproductive material of proven genetic constitution, superior in one or more economically important traits.

Early discussions of the subject dealt with certificates of origin where the main concern was the correct identification of seed source (Baldwin, 1954; Anonymous, 1941; Anonymous, 1951). Over the last two decades, developments in the certification of forest reproductive materials have brought the concepts and definitions into closer agreement with those of the agronomist and the seed trade.

Laws governing the collection, distribution, and use of forest tree seed have been established and enforced for nearly half a century in Europe. These laws, which can be regarded as labelling laws, provided certain minimum requirements for the identification of source, quality of seed, and handling and distribution practices. Examples are the British Seed Act of 1920 (Matthews, 1959), the West German Seed Law of 25 September 1957 (Rossmässler, 1957; Langner, 1963), and the Austrian Federal Law of 18 May 1960 (Bayer, 1960). Since 1939 about one-third of the 50 States in the U.S.A. have developed labelling laws that are interpreted to cover tree seeds.

Certification Standards

The first certification standards for forest tree seed developed specifically to include genetically improved material were adopted by the Georgia Crop Improvement Association, U.S.A., on 8 February 1958 (Barber and Darby, 1959). Immediately following this, the Association of Official Seed Certifying Agencies, A.O.S.C.A. (until 1968 known as the International Crop Improvement Association, I.C.I.A.), adopted a set of minimum certification standards for use by its member agencies in the United States and Canada.

Many foresters thought that the A.O.S.C.A. (I.C.I.A.) standards were too restrictive to meet the needs of various regions. In response, the Society of American Foresters distributed a questionnaire to determine the need for certification in the U.S.A. The replies were strongly affirmative (Society of American Foresters, 1961). A committee of the Society was therefore appointed and worked with the A.O.S.C.A. (I.C.I.A.) to develop the Certification Standards which were adopted in 1962 and modified in 1967 (Rudolf, 1974).

Simultaneously, activity was developing in Europe. In 1963 the World Consultation of Forest Genetics and Tree Improvement recommended "... that Member Nations of F.A.O. and O.E.C.D. (Organisation for Economic Cooperation and Development) should take steps to promote fully effective schemes for the certification of tree seeds and plants moving within their borders, thus paving the way for the certification of tree seed and plants moving in international trade". The Consultation also noted the initiative of O.E.C.D. in forming an expert group to study and promote certification of such seeds and plants, and recommended that all member states of F.A.O. adopt the scheme being developed by O.E.C.D. (F.A.O., 1970)[1].

The Second World Consultation on Forest Tree Breeding gave further support: "The Consultation recommended that the seed certification scheme of the O.E.C.D. be extended to all countries as a means of providing a uniform system for the identification and control of genetic identity of all forest reproductive material" (Callaham, 1970).

The development of the O.E.C.D. Scheme is described by Rudolf (1966) and Barner (1972a). A committee of experts first met in September 1963, and after several drafts the O.E.C.D. Scheme for the Control of Forest Reproductive Material Moving in International Trade was adopted in 1970 (O.E.C.D., 1971). The Scheme and the A.O.S.C.A. Standards are in close agreement, thus posing little difficulty in moving seed between North America and O.E.C.D. countries on other continents. The Scheme has achieved broad acceptance from many countries and provides a model for the control of forest reproductive materials.

A parallel development was taking place in the European Economic Community (E.E.C.) The E.E.C. Directives of 14 June 1966 deal with trade in forest reproductive material among Common Market countries. These E.E.C. Directives were in general agreement with the O.E.C.D. Scheme, but different on some significant points. Meetings of the E.E.C. group and the O.E.C.D. Committee in 1972 and 1973 attempted to remove remaining differences. The O.E.C.D. Scheme was amended significantly in 1974[1] to provide an additional category which will enable O.E.C.D. seed from untested seed orchards to be traded within the E.E.C. The O.E.C.D. Scheme now has four categories of seed: source-identified reproductive material, selected reproductive material, reproductive material, from untested seed orchards, and tested reproductive material.

These various schemes and standards are much broader than the "seed orchard" in concept and coverage; they include all reproductive material. Orchard seed will be classed in only one or two categories within each scheme. It is assumed that orchards will be established only from material that is selected with the high expectation of genetic superiority in one or more traits, *or* from material that has been proven superior through progeny testing. Under the A.O.S.C.A. scheme, seed from untested orchards falls within the category "selected reproductive material", and seed from progeny-tested parentage is classed as "certified reproductive material". The revised O.E.C.D. Scheme identifies the first category as "reproductive material from untested seed orchards". This new category distinguishes orchard seed from reproductive material originating from selected stands and cultivars, or in tested orchards. Seed from tested orchards is "tested reproductive material".

Some difficulty has been encountered with the term *certified*. In many situations and languages it simply means the provision of a certificate for any specific reason, not necessarily associated with the genetic constitution of the material. One suggestion is to substitute the term *tested*, but even this word does not imply genetic superiority (Jones and Burley, 1973). It is desirable to agree on a single term. *Certified* is preferred by many because in much of the world seed trade it is defined to assure genetic quality and superiority of performance and, as noted at the beginning of this chapter, it is so defined in the Ford-Robertson Terminology (1971). However, current E.E.C. and O.E.C.D. discussions indicate a desire to abandon *certified* and substitute the less well defined term *tested*.

[1] Organization for Economic Co-operation and Development. Decision of the Council establishing an O.E.C.D. Scheme for the control of forest reproductive material moving in international trade. Adopted 5 March, 1974. Paris.

Basis for Certification

To have an adequate basis for certification, certain information is needed about the seed parents and the origin of each clone or the parentage of each tree in the orchard must be known. In addition, the criteria for selecting the individuals in the orchard, must be described and the scoring of each tree made a matter of permanent record available for verification. Each parent should have been proven to be superior for the one or more traits proposed for certification. In addition it should have been evaluated for other important traits to ensure that the balance of the genotype is acceptable. The orchard must be isolated to minimise contamination from undesirable pollen. Phenology of the individual clones or trees must be known to ensure that pollen from other genotypes is in sufficient quantity to minimise the risk of selfing. This is especially important in pine orchards.

A distinction should be recognised between performance estimates based on a bulk sample of orchard seed and those derived by testing each orchard component separately. Either method will be invalid if the material tested is not representative, an especially important factor when orchards are young and flowering is at a low level. Where bulk seed is collected, all parents must be adequately represented in the sample and in a proportion similar to the expected orchard yields. If individual parents are tested, the "average" performance will have to be constructed for the orchard; knowledge of phenology and of the yields of individual parents is important. Tests based on individual parents have a major advantage in that they may provide information for roguing orchards to increase average performance.

In summary, the basis for certification is a high level of probability that the average progeny of the orchard will be genetically superior to the material normally available and used by a prudent forester.

Certifying Agency

The certifying agency may be an independent organisation, a government body, or a quasi-government agency with vested legal authority. The independent agencies, such as A.O.S.C.A. in the United States, must be protected by law to prevent false claims of certification by unauthorised persons. In any case, the agency must be independent, exercise its control authority, and make unbiased evaluations of seed producers, their orchards, and progeny tests.

The certifying agency's primary responsibility is to provide control. Among its many functions are:

1. Formulation of minimum standards for clonal and/or seedling material established in orchards.
2. Establishment of minimum standards for orchard design and isolation.
3. Establishment of minimum standards for progeny testing.
4. Evaluation of test results and establishment of the genetic quality of seed to be certified.
5. Provision of an inspection authority.
6. Supervision of a permanent record system.
7. Inspection and control of seed collection, processing, storage, and movement.
8. Provision for the transfer of the "certificate" from seed to subsequently produced seedling.
9. Provision of information describing each lot of material certified.

A fundamental principle of any certification scheme is a recognition that the basis of certification will vary according to species, according to country, and according to the proposed use of the seed. The same species may be certified for a wide range of uses requiring gentic superiorities in quite different traits. For example, traits of highest value for shelter-belt purposes (broad, dense crowns and retention of branches) would be in contrast to desirable characteristics for timber production (small branches, narrow crown, and early natural pruning). Or, in a species such as Scots pine (*Pinus sylvestris*) material desirable for Christmas tree production would have traits different from material intended for timber production.

Responsibilities

Each country must provide its own certification authority and in so doing develop progeny-testing standards specific to its needs. It is hoped that certification schemes and progeny testing standards developed by individual countries or associations of countries will be in close agreement with the broadly recommended scheme of O.E.C.D. and the recommendations of the I.U.F.R.O. Working Parties on Seed Orchards and Progeny Testing. Such compatibility will ensure the free interchange of material among nations.

The exchange of information about the selection of plant material, its establishment in orchards, and the subsequent progeny tests must be free and open between the producer, the certifying agency, and the buyer. The certifying agency has the responsibility for assuring the buyer that the genetic superiority certified is meaningful and, where known, for pointing out the environmental limits to which the certification is applicable. It must be able to make available to the buyer or user the records and analyses that show the superiority attained and the limitations of the test results. The agency also has the responsibility of aiding the producer to establish valid progeny tests.

The producer, in turn, must be able to present complete information about the material being certified and must stand behind his claims. A good seed producer must have integrity and should assist the buyer or user to choose the best seed and plants for the site to be planted.

The buyer must know where and how he plans to use the seed, and he should have some basis for determining which seed will be best suited to his needs. The final decision to purchase or to use particular seed or plants must be the responsibility of the buyer.

Progeny Testing

Ultimately all orchard seed should be produced from progeny-tested clones or trees. The validity of the tests is fundamental to progress in tree improvement. Appendices to the O.E.C.D. Scheme (1974) deal with minimum requirements for the approval of basic material and minimum requirements for progeny tests. Though more than a decade old, the "Minimum Standards for Progeny-testing Southern Forest Trees for Seed-Certification Purposes", formulated by the Committee on Southern Forest Tree Improvement (U.S.A.), provides an excellent outline of the factors that should be taken into consideration during the establishment and conduct of orchard tests. The guidelines, for the most part quoted directly from the Committee's publication (1960), are as follows:

1. Each progeny test must be designed to evaluate differences in a specified character or characters; similarly, test results must be expressed in terms of such characters.
2. All measurements and observations made in the course of a progeny test, whether of characters it was planned from the start to evaluate, or of characters subsequently included, must be

preserved in readily understandable form, together with clear, verified summaries. Any statistical analyses that have been made must be similarly preserved.

3. The utmost care must be exercised to insure that the seed subjected to test truly represents that subsequently to be submitted for certification. If the methods of pollination and seed collection differ in any way from the methods to be used for production purposes, or if the seed used for the test is not a random sample of the seed produced by these methods, the progeny tester must show that such departures do not bias the test results.

4. The lack of a check (syn. *standard* or *control*) in a progeny test will, as a rule, disqualify the test as a basis for certification. (In the unusual case of a check being dispensable, as in certain tests of hybrids, the burden of proof that it is not needed will rest upon the progeny tester.)

5. With occasional exceptions (as in some progeny tests of racial entities), the checks incorporated in progeny tests for seed certification purposes must consist of seed which, at the time the tests were set up, was accepted as "local" (and hence adapted) to the planting sites under consideration, or of a provenance demonstrated to be, and generally accepted as, well adapted to the planting sites. Exceptions will occur, however, and must be considered on their merits by the certifying agency when it evaluates the results of the progeny tests.

6. There must be at least clear presumptive evidence that the check represents seed that would have been acceptable to a prudent, well-informed purchaser had the "improved" seed not been produced. Such evidence must be included in the plan for and records of the progeny test. Seed ordinarily unacceptable for checks will include: (1) That of ill-adapted provenances; (2) That collected from conspicuously "high-graded" stands, that is those from which the better trees have been harvested one or more times. It is a dysgenic practice. (3) That collected exclusively from the poorer components of any stand, for example, from trees removed in an improvement cut; and (4) Seed a larger-than-usual fraction of which may have originated from self-pollination and hence be subject to inbreeding depression.

7. Improvement can be certified only in terms of the particular environment or environments in which it has been tested.

8. The record of each test must describe the test site or sites (including location, climate, soil, past use, and site preparation), any cultural treatments applied after planting, and the occurrence or non-occurrence, throughout the course of the test, of frosts, droughts, infections, infestations, and the like. The certifying agency has the responsibility of deciding whether any cultural treatments that have been applied may have influenced the results to the advantage of the progeny being tested for certification.

9. Improvement revealed by a progeny test can be certified as characteristic only up to and including the most advanced age at which it has been observed in the test.

10. Progeny tests for seed certification purposes must embody REPLICATION AND RANDOMISATION, both of which are essential to the calculation of error terms. Without some estimate of error applicable to the evaluation of progeny differences, test results are unacceptable for seed-certification purposes. Randomisation may be either complete, or restricted as specified in conventional balanced block, Latin-square, or various lattice designs.

11. The actual design of the established test must be recorded in detail, to guide not only the tester's analyses of the test data, but also the certifying agency's evaluation of the results submitted in applying for seed certification.

12. Nursery stock must be grown on nursery sites, and must be planted on planting sites, which are as uniform as it is reasonably possible to obtain.

13. Seedlings to be planted for progeny tests must be grown together on soil as uniform as can possibly be obtained, or, if they are grown on different soils, must be so distributed that similar proportions of all progenies are produced on each distinct soil class. Production of all of one progeny in one nursery and of another progeny (for example, the check) in a distinctly different part of the same nursery, or in a different nursery, automatically disqualifies the test from consideration for seed-certification purposes.

14. The assignment of progenies, including the check or checks, to individual plots within the nursery area or areas, must be at random, and this must be attested.

15. Seedlings to be used in progeny tests must be from seed sown at approximately the same time and within a very few days of each other at the most. They must be grown as nearly as possible under identical conditions of soil, on sites with a similar cropping history, soil preparation, fumigation, fertilization and soil amendment,

watering, cultivation, late-season fertilization, and density. The records of nursery production must attest explicitly to establishment and maintenance of uniformity in these respects.

16. The lifting, packing, storage, transportation, and planting of all the progenies in the test must be the same. The record of establishment must attest explicitly to the practical identity of these processes throughout, and particularly to their application to all the progenies as nearly simultaneously as possible.

17. If stock is graded rather than selected at random from the whole nursery population of each progeny, the fact must be recorded, and the utmost care must be taken that the grading process itself does not bias results for or against any given progeny. When grading is done, the percentages plantable and for culling must be recorded separately by progenies, as large disparities in these percentages from progeny to progeny would indicate probable bias. The burden of proving that grading may not have affected the results will rest upon the progeny tester.

18. In nursery sowing, in stock lifting, storage, and transportation, in planting, and in labelling and documentation in the nursery and the plantation, every precaution must be taken against mixing, or losing the identity of, any of the several progenies included in the test. (This applies also to any replicate sowings or plantings of each progeny, except as compositing of nursery replications may be specifically provided for in certain test designs.) Any evidence in plantation labelling and documentation, or any internal evidence in nursery or plantation records, that strongly indicates that such mixing or loss of identity has occurred, will disqualify the test from consideration for certification purposes.

19. The report on the progeny test must, as a minimum: (1) Identify and describe (usually in terms of provenance, parentage, and mode of selection and breeding) the variety, strain, or other genetic entity for which certification is sought; (2) Show that the seed subjected to progeny test is representative of the seed to be certified; (3) Specify the conditions (nursery, plantation location, planting site, cultural treatment, climatic, and other) under which the progeny test was made; (4) Detail the design and size of the test; (5) State the date of establishment of the test; (6) Itemise the characters measured and the age or ages at which the measurements were made; and (7) Specify and describe the check or checks with which the progeny to be certified was compared.

20. The report must further make quantitative comparisons between the candidate progeny and the check, in terms of each character measured and for each measurement date. This must be done regardless of whether the differences revealed are statistically significant or non-significant, or whether they are favourable or unfavourable to the candidate progeny. If the test includes two or more checks, the candidate progeny must be compared with each individually. If other progenies beside the candidate progeny and the check or checks are included in the test design, all must be included in the analyses and each must be distinguished in the comparisons presented.

21. Differences between the candidate progeny and the check or checks and between these and any other progenies included in the test, must be expressed both in the units of measurement (survival per cent, height, in feet and the like) and in terms of level of significance. For any character evaluated, the mean of the candidate progeny shall be shown, together with its standard error. The difference between the mean of the candidate progeny and the mean of each check shall be shown, together with the standard error of the difference. Finally, details concerning significances (including their levels) of reported differences shall be shown.

Stern (1970) has presented minimum standards recommended by the Working Group on Quantitative Genetics, I.U.F.R.O. Section 22, as a basis for certifying genetic superiority in one or more characters of economic importance. These standards are in agreement with those of the Committee on Southern Forest Tree Improvement, but were not developed in such detail. In addition to these two sets of general standards for progeny testing, the Georgia Crop Improvement Association (1967) and South Carolina Crop Improvement Association (1969) have provided specific standards for progeny testing southern pines for certification. Georgia and South Carolina standards place considerable emphasis on the check or control lots used as the basis for determining genetic superiority.

It is readily evident that there is a fundamental need for standards to ensure the validity of progeny tests as a sound basis for certifying genetic superiority. Because progeny evaluation usually takes many years, it is likely that new methods of design or analysis will be developed during the lifetime of a single test. (For example, see Proceedings of a Meeting of the Working Party on Progeny Testing—Kraus, 1972). Therefore, a progeny test for seed certification purposes must be established in co-operation with the certifying agency. This co-operation will ensure that the test is adequate, on the basis of current knowledge, for the evaluation of chosen traits. Even though the test method may be outmoded before completion, the results will be acceptable to the certifying agency.

Conclusions

Fundamentally, the certification of orchard seeds provides a mechanism for the control of genetic identity and quality. It further ensures through testing that the material is, in fact, superior to existing standards. Whether the certification is handled through a law providing mandatory control, or, whether it is accomplished through voluntary associations, the most important aspect is that the standards be met. We must, in good faith, encourage the use of certified seed and ensure the demise of the practice of using unidentified seed or seed of less than the best genetic constitution available.

The certification and control of forest reproductive material has been discussed also in recent years by numerous authors not previously cited (Barber, 1965, 1969; Society of American Foresters 1963a,, 1963b; Barner, 1972b, 1973; Larsen, 1961; Rudolf, 1963; Rohmeder, 1962; Isaac, 1962).

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