FORESTRY COMMISSION
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DENDROCTONUS MICANS, IN NORTH WEST EUROPE

By J. M. B. BROWN, B.Sc., Dip. For.
and D. BEVAN, B.Sc.,
FORESTRY COMMISSION

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FOREWORD

The insect *Dendroctonus micans*, a bark beetle that is found in North West Europe, has for long been held, by forest entomologists, to constitute a potential threat to coniferous plantations in Great Britain, although it is not yet established here. Accordingly, in June 1964, Mr. D. Bevan, the Commission's senior forest entomologist, and Mr. J. M. B. Brown, the Commission's forest ecologist, carried out a tour through Denmark and parts of Germany and Holland, in order to assess the degree of risk.

The purpose of their tour may be expressed in the form of five questions which they had constantly before them:

(A) What is the present status of *Dendroctonus micans* in the regions visited?

(B) What environmental conditions (climatic, edaphic, biotic) are of particular significance in relation to the surge of *Dendroctonus* breeding in Denmark, Holland and Schleswig-Holstein in the last twenty-five years?

(C) Is there a likelihood of *Dendroctonus* gaining a footing in Britain?

(D) Where in Britain would it find suitable habitats, should it ever gain entry?

(E) What precautions can and should be taken to lessen the probability of introduction?

This Bulletin presents the results of their investigations, in which they received generous and willing help from the forest authorities and forest research organisations of Denmark, Holland, and the Federal Republic of Germany.

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25 Savile Row,
LONDON W.1.
June, 1965.

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SUMMARY

During a short tour of Holland, Schleswig-Holstein and Denmark in June, 1964, the authors collected evidence about recent outbreaks of *Dendroctonus micans* Kug. on spruce and about the associated environmental factors. The life cycle of the bark beetle, as recorded in Denmark, is briefly described and the view accepted that a biennial cycle is usual. Attacks have been reported on several species of spruce, or *Picea* (rarely on other conifers), but Sitka spruce (*P. sitchensis*) appears distinctly more susceptible than Norway spruce (*P. abies*); outbreaks have in consequence occurred mostly where Sitka spruce had been widely planted (Jutland, north west Schleswig-Holstein).

Trees under thirty years of age are seldom attacked, and one cause of the very frequent reports of damage between 1940 and 1960 is the attainment of a susceptible age by the plantations of Sitka spruce established early this century. But climatic factors have evidently played an important part, the warm dry summer of 1947 sparking off numerous outbreaks in the region surveyed. Reasons for a decline in *Dendroctonus* activity in recent years are less clear, but weather, the extensive use of insecticides and elimination of the more susceptible stands and trees, may all have played a part.

The apparent connection between the tree's water economy and susceptibility to *Dendroctonus* is further considered with reference to some physiological-ecological studies recently undertaken in Germany on several spruce bark beetles (*Ips typographus* mainly), and a brief comparison is made between the environment of Sitka spruce in its Pacific Coast home and that of the study area in north west Europe. The paper concludes with an assessment of the likelihood of introduction of this insect to Britain and of its prospects of establishment should it ever evade the barriers now against it.

Chapter 1

BIOLOGY OF THE GREAT SPRUCE BARK BEETLE, DENDROCTONUS MICANS

Systematy and Distribution

The genus *Dendroctonus*, with over twenty species, comprises certain bark beetles of the family Scolytidae in the natural order Coleoptera. The name signifies "tree cutter". Most species occur in America, and some are serious pests of pine and spruce in North and Central America (Chrystal, 1949).

Dendroctonus (formerly known as *Hylesinus*) *micans* Kugelann, the only Eurasian species, has a wide distribution, from the island of Sakhalin east of Siberia to northern France. In Europe it is wanting from the Mediterranean lands and from the extreme west and north.

Host Trees

Sporadic attacks occur on Scots pine, *Pinus sylvestris* and several other pines, but the occurrence of the insect is generally linked with that of the spruce genus, *Picea*, and there appear to be no records of serious outbreaks except on spruce. Norway spruce, *Picea abies*, is the principal host in Europe, but breeding is recorded on *P. omorika* in Jugoslavia and *P. jezoensis* in Sakhalin. In western Europe the Sitka spruce has proved a good deal more susceptible than the Norway spruce and there also, in Denmark and the Netherlands, several other introduced spruces (*P. orientalis*, *P. omorika*, *P. pungens*, *P. glauca*, *P. mariana*) have been affected from time to time in recent years. In Denmark, where the insect was first noted in 1861, attack has been recorded on Lodgepole pine, *Pinus contorta*, and Mountain pine, *Pinus mugo*, as well as on Scots pine: in Austria on the native Austrian pine, *Pinus nigra*. There are isolated records of attack on European Silver fir, *Abies alba*, and European larch, *Larix decidua*. No important damage has been caused to trees other than spruces (*Picea*).

Life Cycle

Observations on the life history of *Dendroctonus micans* have been made in several European countries over the past 100 years at least and the evidence is conflicting. Amongst the most thorough field studies were those of Bejer Petersen in Denmark, circa 1950–1955, at a time when the surge of population in several of Jutland's plantations of Sitka and Norway spruce provided plentiful material. In view of this, and of the general climatic resemblance between Jutland and much of Britain, it is appropriate to accept his conclusions provisionally, while recognising that modifications may be imposed by local climatic and topographic factors, or seasonal variations in weather.

Petersen's observations are thus summarised on p. 392 of the joint paper, Gøhrn, Henriksen, Bejer Petersen, 1954:—"Egg-laying begins about June, continuing throughout July and doubtless beyond. The resulting larvae pass their first winter in the second or third stage and during the spring go through the fourth and then into the fifth (final) larval stage. In the course of the summer some of these pupate and attain the imaginal state, while others remain in the fifth stage. The second winter, is, therefore, spent partly as 5th stage larvae, partly as adults: observations indicate that the majority (c. two thirds) are adult. In their second summer these imagines lay eggs: some of the wintering fifth stage larvae may also metamorphose and lay eggs in late summer, but it is not improbable that this is delayed until the third summer."

According to Bejer Petersen, therefore, the life cycle is essentially biennial, with perhaps a triennial cycle for a small proportion of the population. In the German literature (Baudisch, 1903; Bergmiller, 1903; Francke Grosmann, 1952) a more or less speedier generation is assumed (although Eckstein inclines towards a biennial cycle), but the evidence adduced is not altogether convincing. An appreciably shorter life cycle is most likely to occur where, in central and west Germany, spruce is grown at lower altitude and in a milder climate than those of its native home. A relatively slow rate of larval development is admitted by most observers.

Mode of Attack

Dendroctonus micans lays eggs under the bark, after eating out a small, more or less rounded, chamber, about 2 cm in diameter. The scheme (exemplified by the pine bark beetle, *Myelophilus piniperda*) of an elongated mother gallery, with eggs laid singly in niches along the sides, is *not* followed by *Dendroctonus micans*, which lays its eggs in small heaps against the wall of the cavity it has gnawed out. The mother continues feeding and egg-laying through the summer, producing in all a large number of eggs: Petersen records a find of 247 eggs plus 36 newly-hatched larvae (283 altogether), but 100–200 is more usual.He found eggs in small numbers in a few of the brood chambers examined in January: such eggs, presumably laid too late to hatch in the same year, failed entirely to hatch when brought indoors.

The eggs hatch in about a month in the summer and the larvae feed communally at the margin of the brood chamber. As they enlarge it peripherally it becomes filled with their light brown "frass". In severe attacks, two, or even more, brood chambers may coalesce. Pupae are formed singly in the frass and the young adult has its first meal within the brood chamber, but emerges and moves to a fresh position before breeding. From without, attack by *Dendroctonus* is betrayed by a short, horizontal, resinous funnel, incorporating a good deal of excrement, which gives the material a characteristic look, described by Petersen as resembling burnt almonds. Similar funnels, formed of resin only, indicate an unsuccessful, or an incipient, attack.

A distinctive feature, recorded by Bejer Petersen (loc. cit.) Kangas (1939, 1952) and Francke Grosmann (1948) is associated with tentative beetle attack on a spruce not in suitable state for breeding (strong resin flow). The beetle then eats an elongate, arcuate tunnel, partly girdling the stem, but lays no eggs. It stands to reason that the tree is adversely affected in some small degree and it is probable that it will attract normal breeding attack later.

While attacks are normally concentrated near the base of the tree, diminishing sharply in frequency above about 2 metres, a striking feature of the recent outbreaks on plantations of Sitka spruce in Denmark and Schleswig-Holstein is the wide spread of broods in height above the ground. In Gøhrn, Henriksen and Bejer Petersen's (1954) account, 19 affected Sitka spruce trees, in Nystrup Plantage, marked at random, were examined from this point of view. An assessment was made, metre by metre, to a height of 18 metres, and the aggregate numbers of broods for the different levels were:—

Height up tree (m):	0–1	–2	–3	–4	–5	–6	–7	–8	–9	–10	–11
Number of broods:	8	10	13	11	13	13	12	6	5	3	2
Height up tree (m):	–12	–13	–14	–15	–16	–17	–18				
Number of broods:	4	3	3	3	3	0	1				

Of the total number of 113 attacks (average per tree, 6) no fewer than 18 were above a height of 10 m. and 8 trees showed their *lowest* attack above 2 m. These trees were about 60 years old, 22.7 m. (75 ft.) tall and ranged in breast height diameter from 19 to 35 cm. (average quarter girth 8–9 inches). The height of attack is of practical importance where control by spraying Mobe–T from the ground has been undertaken.

NATURAL ENEMIES

Rhizophagus grandis Gyll. (*Nitidulidae*), which appears much the most influential predator, was studied by Bergmiller (1903) in various spruce stands in Württemberg and the Spessart. A close relative of important predators on British bark-beetles, *R. grandis* seems to be restricted to *Dendroctonus micans* broods, in which larvae, pupae, adults and (in the youngest larval stages) frass are devoured. Bejer Petersen (1954) recorded this predator in about 20 per cent of Danish brood chambers he examined? and it was observed frequently in Schleswig-Holstein by Francke Grosmann (1952)? who contributes some useful information about the ecology of this and other natural enemies of *Dendroctonus*. *Rhizophagus* is of special significance in her view, because it is not deterred by the thick bark at the base of the tree where most *Dendroctonus* broods occur: it will also pursue them underground. She found, however, that this predator is relatively much less frequent on Sitka than on Norway spruce, a result which she attributes to the more copious resin flow from Sitka spruce. Only after *Dendroctonus* has been breeding for a couple of years does the reduced resin production allow *Rhizophagus* to move about actively in the brood chamber.

In general, according to Francke Grosmann, the spread of *Dendroctonus* attacks to higher parts of the tree, which is a feature of recent outbreaks in plantations of Sitka spruce in north west Europe, has favoured the natural enemies, particularly the two parasites *Ephialtes* (*Pimpla*) *terebrans* Rabe and *Lonchaea seitneri* Herd. *Ephialtes* is an *Ichneumonid* occurring on many hosts in Britain, which uses a long ovipositor to penetrate relatively thin bark and lay eggs on *Dendroctonus* pupae. *Lonchaea* is one of the *Diptera* and likewise almost restricted to thin bark: unidentified *Dipterous* larvae found by Petersen in large numbers in Nystrup Plantage in 1953 may have belonged to this species.

Brief mention may also be made of the smaller *Rhizophagus dispar*, rarely seen by Bejer Petersen in brood chambers in Nystrup; of the ant beetle *Thanasimus formicarius* L., whose larvae Francke Grosmann found occasionally in brood chambers in Schleswig-Holstein; and of the long-horn beetle, *Tetropium fuscum*, which the same author observed invading (as larvae), and in part destroying, the broods of *Dendroctonus*.

Chapter 2

HISTORY OF RECENT OUTBREAKS OF DENDROCTONUS IN NORTH WEST EUROPE

The distribution and host plants of *Dendroctonus* (*Hylesinus*) *micans* have been briefly considered in the previous section. In western Europe two hosts are important: *Picea abies* and *Picea sitchensis*. *Picea abies* is the normal European host, on which *Dendroctonus micans* was discovered in 1794 (in Brichet et Severin, 1902), but it was not until 1852 that the insect was regarded as destructive. Thereafter there was a gradual westward movement and an increase in numbers of reported outbreaks, particularly among the artificial Norway spruce plantations in western Germany. In 1897 *Dendroctonus* invaded Belgium from the Aachen district, where heavy cuts of damaged spruce were imposed by the beetle in the four years 1897–1900 (Severin, 1902). Accelerated dispersal south-westwards through the Belgian Hertogenwald, which occurred in 1901, was ascribed by this author to the north east winds which then prevailed. In Denmark *Dendroctonus* was recorded in 1861, but the first outbreak not until early in the present century. In 1935 it appeared in Holland, simultaneously in two localities in the Gelderland province.

Rather fuller consideration is given to recent occurrences in Holland, Schleswig-Holstein and Denmark, the three lands included in the authors' tour in 1964.

DENMARK

The first record of *D. micans* in Denmark was by Løvendal (quoted by Bejer Petersen, 1952) in 1861, in Teglstrup Hegn in Nord Sjaelland. This is close to Helsingör on the Øresund, only 3 or 4 miles from the Swedish coast: all further records in the nineteenth century were also in N. Sjaelland, pointing unmistakably to a Swedish source. The first severe attack reported (Boas, 1923) was a good deal later and a good deal farther west, though still in Sjaelland. This was near the Kattegat coast in Jyderup Forest, where from 1907–21 attacks occurred in a 40-years-old stand of Norway spruce and a few Scots pine, both species being affected.

In Jutland, Boas was likewise first in finding the insect, in 1923, in Aabenraa Distrikt in Sønderjylland; several additional records were made in Jutland before the war. After 1940, however, there was evidence of accelerated increase and spread, and by autumn 1947 the situation was grave enough to attract official notice. In 1949 the Zoology Laboratory of Kongelig Landbohøjskolen issued a questionnaire to forest districts, woodland owners and other bodies, with the result that 60 fresh records, mostly in Jutland, came to light. After 1949 there appears to have been some reduction in breeding, which received, however, in some parts at least, a fresh impetus about 1956, since when a decline in population has been observed in most of the affected areas and few new records have been notified.

The sharp rise in *Dendroctonus* numbers about 20 years ago in Jutland is clearly related to the widespread outbreaks on Sitka spruce. Bejer Petersen (loc. cit.) records that only six of the affirmative replies to the questionnaire did not give Sitka spruce as a host tree, whereas twenty gave it as the only tree affected. Norway spruce was also attacked on many sites, but, in relation to the much larger area occupied by it, showed up as distinctly less susceptible. Although not indigenous in Denmark, Norway spruce has been widely planted there for a long time; so the phenomenon may perhaps be likened to that of the native dog tolerating the fleas which plague the immigrant.

There are few old stands of Sitka spruce, but many were created early this century on Jutland's heaths and coastal sands. Only exceptionally (Francke Grosmann, 1954) will *Dendroctonus* attack young trees: therefore, before about 1940, plantations of Sitka spruce at a susceptible age were few and far between. In what measure other factors, either favourable to *Dendroctonus*, or unfavourable to spruce, were influential, will be discussed when further information has been reviewed. The recent decline in populations is specially difficult to interpret in relation to physical and biotic factors of the environment, in view of the application of an insecticide (usually Mobe–T) in many of the affected woods.

SCHLESWIG-HOLSTEIN, WEST GERMANY

The life history of *Dendroctonus micans* and the history of outbreaks have been dealt with in several papers by Francke-Grosmann, (1948–49–52–54), to whom also we are indebted for much information during the tour. *Dendroctonus* does not appear to have attracted attention in Schleswig-Holstein before 1932, though doubtless endemic on Norway spruce (all planted, or sub-spontaneous). In fact the Danish records confirm this, if it be assumed that the beetles discovered by Boas in South Jutland in 1923 had crossed the frontier from Schleswig. From 1938 a progressive increase in beetle populations, mainly in Sitka spruce plantations in northern Schleswig-Holstein, led to intensive studies, in the course of which a general connection was traced between *Dendroctonus* and root rot caused by *Fomes annosus*. However it was recognised that trees might be attacked without previous fungal infection; particularly if damage by animals, or in extraction, or stem forking, provided focal points attractive to the insect. In this region too there has been a decline in population in recent years, due in part to systematic use of insecticides in severely affected stands.

HOLLAND

Unlike their Belgian and Danish colleagues, Dutch foresters have, for obvious reasons, planted but little spruce and so it was not until 1935 that *Dendroctonus micans* was discovered on Oriental and Sitka spruce in an arboretum in Gelderland province. The circumstances attending several subsequent small outbreaks in Holland resemble in three features those of the recent outbreaks in Schleswig-Holstein and Denmark, viz.

(1) There were frequent records between 1943 and 1948.
(2) Sitka spruce proved markedly more susceptible than Norway spruce.
(3) Affected stands were nearly all 40–60 years old.

In Holland also, populations have declined in recent years, but, in a letter sent after our visit, Elton, who reviewed earlier outbreaks (1948), drew attention to a current attack on *Picea mariana* and *P. omorika* in another arboretum.

Chapter 3

ENVIRONMENTAL FACTORS AND OUTBREAKS OF DENDROCTONUS

(1) CLIMATE

Three aspects of the climatic environment must be considered: (a) the general climate of the regions visited, in relation to conditions in Britain; (b) a brief comparison with climatic conditions where spruce is indigenous in Central Europe and the Pacific Coast of North America; (c) special weather phenomena of the past 30 years, which might have a bearing on the increase in bark beetle numbers during that period.

(a) General Climate of the Area of the Tour

For a review of the general climate, reliance has been placed mainly on the statistics for Denmark, in particular Jutland, which were most easily available. It is assumed that northern Schleswig-Holstein differs insignificantly from southern Jutland. Holland enjoys a slightly higher mean temperature, but shares the same dominant maritime influence. A majority of the affected stands visited were in fact in Denmark.

In Appendix 2 (A–H) are set out average values (mostly for about 40 years antedating 1926) of the main climatic properties of representative stations in Denmark. These show:

A. Temperature:
Mean monthly and annual values and (where available) number of days with frost, for 17 stations conveniently situated in relation to the spruce woods visited. Tønder and Løgumkloster in the extreme south of Jutland may represent the spruce sites in North Schleswig-Holstein.

B. Precipitation:
Mean monthly and annual values for the same (with Mejlgaard replacing Hornslet) 17 stations: the lowest total is in bold type, the highest placed in brackets.

C. Absolute minimum temperature (for the period defined) for 20 inland and coastal stations.

D. Sunshine:
Mean monthly and annual values, in total hours of bright sun, for periods of about 15 years for 6 stations, 2 in Jutland, 2 in Sjaelland, 1 each in Fyn and Falster. As in Britain, the instrument was the Campbell-Stokes recorder.

E. Relative Humidity per cent:
Mean monthly and annual values for 5 of the rainfall stations and for Gjerlev.

F. Rain Days:
Number of days each month and yearly total with 0.1 mm, or more, rain for 7 of the rainfall stations.

G. Wind Force:
Percentage frequencies of winds of different force (Beaufort scale), during the 56 years ended 1925, for 7 coastal lighthouse stations, four in Jutland and three in the islands.

H. Wind Direction:
Frequency per cent of winds from the 8 main compass directions, and of calms, for the same 7 stations: most frequent direction in bold type. Data from 2 inland stations in Jutland have been included.

I. Mean Wind Force:
(Beaufort Scale) from each direction: the same 7 coastal lighthouse stations are listed.

In Table 1 below, the spruce sites visited on the tour have been listed in order, with location and date (see Appendix I): against all sites in Denmark and northern Schleswig-Holstein is shown the most appropriate climatological station(s). The following brief review of the climate of the principal region visited is based on information in *Danmark's Klima* (1933), from which the data in Appendix 2 have been extracted. The Gelderland district of Holland and southern Schleswig-Holstein, lying outside that region, may be represented by monthly average values of temperature and precipitation for Utrecht and Hamburg, taken from Kendrew (1953) Table 2, page 8.

TEMPERATURE

South Holland and the Hamburg district are, as would be expected, rather warmer than Denmark, where the values of mean annual temperature mostly lie between 7 and 8 deg. C. These values are matched in many parts of Britain—near sea level in the north of Scotland, at about 1,000 ft. in the south and at intermediate altitudes in the intervening parts. But it is impossible to match the Danish temperature regime with any precision in Britain, because British stations with similar annual means have cooler summers, while those with like summer temperatures are warmer when the year is taken as a whole, and enjoy a slightly longer growing season. Utrecht, Hamburg and the two Falster stations (Nykøbing, Naesgaard) have summer temperatures equivalent to those of the warmest parts of Britain

TABLE 1. LIST OF STANDS EXAMINED IN HOLLAND, SCHLESWIG-HOLSTEIN AND DENMARK

a	b	c	d	e	f	g	h
Ref. No.	*Locality*	*Date June*	*Name of Wood or Forest*	*Tree Composition*	*Age approx*	*Dendroctonus noted*	*Relevant Station for Climatic Data*
	HOLLAND						
1	N.W. Gelderland Nunspeet	2	de Ihorst	Sitka spruce	48	?1948	Utrecht (Table 2)
2	,,		Willemsbos	Spruces: Norway, few Sitka	?60	?1947	,,
3	,,		,,	Sitka spruce	65*	1935–	,,
4	Gelderland (Putten)		Schovenhorst	Mixed spruces, Norway, Oriental, Sitka, Omorika.	?70*	1935–	,,
5	Gelderland	3	Woeste Hoeve	Mixed conifers with plot pure Sitka spruce	64	1943	,,
6	,,		Hoenderlo (group)	Sitka spruce	? *	1947	,,
7	,,		Hoenderlo	Norway spruce	40/45	1962	,,
8	,, (Hoge Veluwe)		In Otterlo National Park	Norway and Sitka spruce, Douglas, Jap. larch, beech.	40	1962 +	,,
	SCHLESWIG-HOLSTEIN						
9	Schleswig-Holstein (South)	8	Trittau, Abt. 40	Sitka spruce, few Norway.	47	(?1955–60)	Hamburg (Table 2)
10	,,		,, 44	Sitka spruce	34	(?1955–60)	,,
11	,,		,, 63	Sitka spruce 70%; Norway 20; birch 10.	27	Nil	,,
12	Schleswig-Holstein (South)	9	Rantzau, Abt. 81	Sitka spruce.	53	?1956 +	,,
13	,,		,, 144	Sitka and Norway spruce.	55	(1955–60)	,,
14	Schleswig-Holstein (North)		Rendsburg Abt. 112	Sitka spruce.	33	1956	Schleswig (Table 5) and Tønder (Appendix 2)
15	,,		Rendsburg 117, a.2.	,,	12	Nil	,,
16	,,		,, 140	Scots pine, N. spruce.	52	?1962	,,
17	,,		,,	Norway spruce	10	Nil	,,
18	,,		,, 62b	,,	57	?1950–60	,,
19	,,		,, 161, d	,,	57	,,	,,
20	Schleswig-Holstein (North)	9	Steinholz (Schleswig Abt. 67)	Sitka spruce	84	Nil	Table 5 Schleswig Tønder (App. 2) Løgum-Kloster
21	Karlum Revier	10	Flensburg Abt. 309a	Norway, Sitka spruce; *Abies alba*, etc.	61	?1955–60 +	,,
22			,, 321b	Sitka spruce; Silver fir.	62	,, +	,,
23	,,		,, 301a	Mixed conifers.	57	? Nil	,,
24	,,		Sprakebull	Sitka spruce	43	?1962 +	,,
25	,,		Wallsbull Abt. 112 113	Sitka, Norway spruce; (Scots pine, Jap. larch)	53	?1947 +	,,

NOTES: In column g brackets denote mild attack. Column f, estimate of years from planting to June, 1964. * indicates complete removal of trees. + Dendroctonus present, June, 1964. A + sign beneath date in column g denotes active breeding.

TABLE 1 (cont.)

a	b	c	d	e	f	g	h
Ref. No.	*Locality*	*Date June*	*Name of Wood or Forest*	*Tree Composition*	*Age approx*	*Dendroctonus noted*	*Relevant Station for Climatic Data*
	DENMARK						
26	Falster	11	Hannenav	Sitka, Norway spruce; Douglas fir.	45	1956	Nykøbing (App. II)
27			,,	Sitka spruce.	37	1956	,,
28	Sjaelland (Sorø Distrikt)	12	Nordskov	Spruces, (Oriental, Norway, Serbian); Douglas fir.	40	1956	Ringsted
29	Sjaelland (North)	14	Gribskov	Norway spruce.	25	Nil	Lyngby
30	Djursland	15	Søstrup Afd. 13	Sitka spruce	45/50	1959	Kolind-sund Hornslet
31	,,		,, 103	,,	45	Nil	Mejlgaard
32	,,		,, 62	,,	15	Nil	,,
33	,,		Mejlgaard Afd. 210	,,	75	(?1960)	,,
34	,,		,, 14	,,	38	Nil	,,
35	,,		,, 85		47	?1956 +	,,
36	Djursland	16	Mols Bjaerge (Hedeselskab)	Norway, Sitka spruce; Douglas fir.	31	1956	Hornslet Kolind-sund
37	,,		,,	Douglas fir; Norway spruce.	31	Nil	,,
38	Djursland		Mols Bjaerge (Hedeselskab)	Black (Corsican) pine Black (Austrian) pine	37 37	Nil Nil	Kolind-sund
40	,,		Skramsø	Sitka spruce	*?	?	,,
41	Jutland (North-East)		Lovnkaer	Sitka spruce	34	1956	Hals Tylstrup
42	,,		,,	Sitka spruce (original 50% Norway deceased).	30	1955	,,
43	,,		,,	Sitka spruce	18	Nil	,,
44	Jutland (Mid)	17	Velling Skov, Afd. 6	Sitka spruce	74	?	Palsgaard or Silkeborg
45	,,		Skaerbaek Afd. 135	Sitka spruce (?originally with Norway).	62	Nil	,,
46	,,		Palsgaard Afd. 70	Sitka spruce	*79	ante 1952	,,
47	,,		,, 71	Sitka spruce Silver fir	70 75	,, +	,,
48	,,		Gludsted Afd. 147	Sitka spruce	75	,,	,,
49	,,		,, 187	Sitka, Norway spruce.	77	?	,,
50	Jutland (South-West)	18	Vrøgum	Sitka spruce	53	?1948 +	Varde
51	,,		,,	Common silver fir	80	Nil	,,
52	,,	19	Vejers	Sitka spruce	55	Nil	,,
53	,,	18	Oksby	Mountain, Austrian pines; Norway spruce etc.	c.110	Nil	,,
54	,,	19	Bordrup	Sitka spruce.	80	Nil	,,
55	,,	18	,,	Scots pine.	85	Nil	,,

NOTES: * next age in column f indicates that stand clear felled.
\+ beneath date in column g denotes active breeding.

TABLE 2. REVIEW OF CLIMATE AT UTRECHT AND HAMBURG

	Altitude meters	*Jan.*	*Feb.*	*March*	*April*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Year*
		Temperature, deg. Centigrade												
Utrecht	2	1·7	2·2	5·0	7·8	12·2	15·0	16·6	16·1	13·9	9·4	5·6	2·8	8·9
Hamburg	20	0·5	1·1	3·3	7·2	12·2	15·5	17·2	16·6	13·3	8·9	3·9	1·1	8·3
		Precipitation, millimetres—												
Utrecht	2	53	45	45	*43*	48	58	70	(82)	65	70	61	65	725
Hamburg	20	53	48	51	*45*	53	68	(86)	82	63	65	53	63	730

along the south coast and in the Thames valley: but Danish summer temperatures in general are closer to those of East Anglia, the south west peninsula and central England and Wales at low altitude.

Though colder than in lowland Britain, winter in Denmark, nowhere far from the sea, is relatively mild. When the land comes within the grip of the Continental or Scandinavian high pressure system, unusually low temperatures are experienced as in Britain. Appendix 2, Table C, shows the minima recorded at a score of inland and coastal stations during the period of 40–60 years preceding 1925. The minima are generally —25 to —20° C for inland stations; but about 5 degrees higher (and equivalent to the minima recorded in Britain early in 1963) near the coast.

PRECIPITATION

In Denmark the range in yearly precipitation is from 750 mm (nearly 30 inches) in the wettest areas of south Jutland and locally on the higher land of the mid-Jutland ridge, to 500 mm (20 inches) near the shores of the Kattegat. The driest area, with just under 500 mm, is in N.W. Sjaelland, but eastern Jutland, especially the Djursland peninsula, is almost as dry. Rainfall in Schleswig-Holstein is like that in South Jutland, as it is also in the Gelderland district of Holland. With few exceptions, February is the driest month in Denmark and August the wettest. In all the regions visited, late winter and spring are relatively dry, as in Britain, and precipitation is substantially more in the second six months than in the first.

Many places in eastern England show a rainfall similar to that of Denmark, though none is quite as dry as the driest places on the shores of the Kattegat. Along the Moray Firth and in some other parts of the east coast of Scotland, in some southern and western coastal districts and in Hereford and adjacent counties (in the "rain-shadow" of the Welsh mountains) similar conditions prevail. The seasonal distribution also is similar in Britain, but with the minimum shifted to March, April, or May and the maximum from August to autumn (usually October). In Denmark the aggregate number of rain days is commonly a little smaller than in British stations with similar total amounts of rain.

RELATIVE HUMIDITY

This too is correlated with precipitation, but generally determined in large measure by the proximity of the sea and the circumstance that the summer rainfall-maximum partly offsets the higher temperature at that season. Thus the Danish values for percentage relative humidity, with annual means for 26 stations ranging from 80 to 87, are high: a large area of central Britain, and two smaller areas, show values below 70 per cent.

WIND

With regard to the water relations of trees and to tree growth generally, the more or less persistent strong winds in Denmark and Schleswig-Holstein are more significant than the high relative humidity. Schimitschek and Wienke (1963), on the evidence of evaporimeter data, suggest that, due to the influence of the wind, evaporation in Schleswig-Holstein is about equal to that on the Hungarian steppe.

Changes in units and standards of measurement, and the sparse and irregular distribution of stations, make comparison between Danish and British wind statistics difficult and potentially misleading. Danish data (Appendix 2, G.H.I.) are mostly for coastal lighthouse stations, but two inland stations in Jutland are included in 2 H. The Beaufort scale of wind force was used, but there appears at the time of these observations to have been a slight divergence of interpretation between British and Danish observers, so that, at the low end of the scale, each value denotes a slightly stronger wind in Denmark, while at the high end of the scale a rather less violent wind is denoted. In the middle range (forces 5–7) there is no such discrepancy: accordingly, for comparison with some representative British values (Bilham, 1938) the Danish data for percentage frequencies of winds of different force (2 G) have been grouped, so that a reliable comparison may be made between these 7 Danish coastal stations and 8 British coastal stations, in respect of the percentage frequency of strong winds (force 6 and over)—See Table 3.

TABLE 3. WINDS IN DENMARK AND IN THE BRITISH ISLES

DENMARK			BRITISH ISLES		
Station	*Location*	*Frequency % Winds of Force 6 and above*	*Station*	*Location*	*Frequency % Winds of Force 6 and above*
Bovbjaerg	West Jutland	19·8	Kirkwall	Orkney	12·6
Hanstholm	N.W. Jutland	10·3	Aberdeen	E. Scotland	3·1
Skagen	N. tip of Jutland	11·1	Spurn Head	N.E. England	12·6
Fornaes	East Jutland	11·2	Gorleston	East Anglia	6·1
Nakkehoved	North Sjaelland	7·1	Dover	S.E. England	7·2
Gjels Nor	South Langeland	16·4	Holyhead	Anglesey	17·0
(Fakkebjerg)			Scilly	Off S.W. England	19·0
Gjedser	S.E. Falster	21·1	Dun Laoghaire	E. Ireland	12·6

The much higher values quoted by Bilham for Butt of Lewis (29%) and Lerwick, Shetland (25%) have been omitted as unrepresentative of any parts of mainland Britain. Beaufort force 6 and over represents a wind velocity of 24 miles per hour (*c.* 11 metres per second) and over.

At inland stations winds are less strong: no places in Denmark are as far from the coast as is much of central England; on the other hand the increasing velocity of winds with increase in altitude, so important in highland Britain, is not much in evidence in Denmark, where the highest parts (on the central Jutland ridge) are only 120–150 metres (400–500 feet) above sea level.

SUNSHINE

As in Britain, the data are still scanty, but reliable values from 6 widely distributed Danish stations (Appendix 2 C) enable a comparison to be made with British values. Four of the Danish stations, with annual values of 1,750 hours and over, are like stations in the sunniest part of Britain near the Sussex coast and on the Isle of Wight. It will be observed that one of these (Tylstrup) is in north Jutland. The other two stations, one on the west Jutland coast, the other on the island of Fyn, 16 km from the coast, receive much less sunshine: and they are comparable with the east of Scotland, or central England at moderate altitude; but receive more than in the north west of Britain, in the industrial areas and in the mountains; and less than in the southern counties and along the coasts of England and Wales.

(b) Comparisons Between Climates Where Spruces Are Native and the Denmark-Schleswig Region.

It remains to make a brief and necessarily very tentative comparison between the climate of Denmark and Schleswig on the one hand and, on the other, see (1) and (2) following:

(1) the climate of the natural range of *Picea abies*.

(1) Merker (1952/3) in an important study of the outbreaks of *Ips typographus* in southern Germany 10–15 years ago, gives temperature and precipitation figures for several stations in the Black Forest and the region of Lake Constance, where his investigations were conducted. Inasmuch as the Bodensee stands are nearly, if not quite, outside the natural range of spruce, it is well to use only the Schwarzwald stations (Table 4).

TABLE 4. CLIMATIC COMPARISONS BETWEEN SOUTH GERMANY AND DENMARK

Station	*Height above sea (metres)*	*Mean Temperature deg. C*		*Precipitation (mm)*	
		Year	*April–Oct.*	*Year*	*April–Oct.*
1 St. Blasien	785	5·9	10·8	1402	794
2 Bonndorf	850		11·1	949	587
3 Lenzkirch	810		10·7		651
4 Neustadt	807		10·3		682
5 Todtnau	648		12·3		844
Mean, Schwarzwald ..			**11·0**		**712**
6 Hanstholm Fyr	46	7·1	11·0	628	385
7 Nykøbing	9	8·1	12·6	603	377
8 Tystofte	13	7·8	12·3	522	343
9 Tønder	4	7·6	11·8	750	489
Mean, Denmark		7·35	**11·65**	**647**	**406**

TABLE 5. CLIMATIC DATA FOR WESTERN NORTH AMERICA AND NORTH-WEST EUROPE

No.	Name of Station	Altitude (M)	Latitude	Frost-free period, days	Days with 10° C & over	Monthly Mean Temperature, deg. C. Jan.	Aug.	Range	Absolute min. temp.	Mean Temperature Apr.–Sept.	May–Sept.	Year	Precipitation (mm.) Apr.–Sept.	May–Sept.	Year
1	Juneau, Alaska	24	58,18′	163	112	−2·9	12·8	15·7	−26·1	10·5	11·6	5·6	934	807	2019
2	Port Simpson, British Columbia	8	54,34′	169	123	1·1	14·0	12·9	−23·3	10·8	11·9	7·2	871	741	2303
2A	Terrace ,, ,,	70	54,33′			−4·5	16·7	21·2		13·0	14·2	6·7	323	272	1140
3	Masset, Q. Charlotte Is.	9	53,58′	169	128	2·2	14·4	12·2	−18·9	11·1	12·2	7·7	530	415	1410
4	Quatsino, Vancouver Is.	20	50,32′	209	148	2·7	15·0	12·3	−16·7	12·0	13·0	8·5	643	470	2433
5	Darrington, W. Washington	171	48,15′	137	162	0·1	16·8	16·7	−23·9	13·6	14·6	8·7	400	276	1862
6	Quinault ,,	91	47,26′	199	180	3·3	17·7	14·4	−11·6	14·2	15·2	10·2	740	537	3105
7	Aberdeen ,,	32	47,00′	187	176	3·9	15·8	11·9	−14·4	13·1	14·0	9·8	484	334	2072
8	Astoria, W. Oregon	7	46,11′	272	194	4·5	16·3	11·8	−12·2	13·8	14·6	10·6	455	320	1931
9	Port Orford, W. Oregon	30	42,44′	285	207	7·7	15·1	7·4	− 6·7	13·0	13·6	11·1	378	241	1711
10	Eureka, N.W. California	19	40,46′	276	224	8·3	13·5	5·2	− 6·7	12·3	12·7	10·9	177	91	991
	Schleswig	35	54,31′	193	145	0·3	15·1	14·8	−21·9	12·5	13·8	7·7	422	372	812
	Denmark Average of 17 Stations	26	57,12′ / 54,45′		140	−0·14 (Feb.)	15·94 (July)	16·1	−18 / −26	11·65	12·3	7·35	338	297	647

The four Danish stations listed for comparison comprise the coolest and warmest, the driest and wettest, but the means are based on all 17 included in Appendix 2.

As a whole the Danish sites show a higher summer temperature, but they are mainly distinguished from the native spruce sites of the Black Forest by the higher annual means (i.e. milder winters) and lower rainfall.

(2) the climate of the natural range of *P. sitchensis*.

(2) The climatic features of the native Sitka spruce forests, which span a great latitudinal range, may be illustrated by data from a series of stations ranging from Alaska in the north to northern California in the south. The data in Table 5 are mostly due to Schober (1962), who provides also the figures for Schleswig, which, with average values of the 17 Danish stations listed in Appendix 2. are included in the table, for comparison with those from the Pacific coast of North America. Apart from the expected differences in temperature regimes, in relation to latitude and distance from the coast, the main feature of the North American statistics is that, although all stations show a precipitation maximum in the winter, the summer rainfall is usually greater—in northern coastal stations considerably greater—than in Denmark, North West Germany, or eastern Britain. The two southern stations provide an exception to this rule; but this is of little consequence, as it is unlikely that seed for north west Europe has been obtained from so far south. Terrace, 220 km inland on Skeena River and experiencing a less oceanic climate than the other stations, also shows a rather lower summer rainfall. The conditions in this locality were examined by Day (1957), presumably because, in contrast with his other main study area on Graham Island (vide data for station 3, Masset, in Table 5), it is a little outside the Sitka spruce optimum. Characteristic of this optimum is the high humidity and rather persistent mist or cloud, which, though not evident in the statistics cited, are commented on by all observers: Day finds additional evidence of humidity in the rich moss cover on tree trunks and branches in Graham Island.

(c) Recent Weather Phenomena in North West Europe

Several accounts of outbreaks of *Dendroctonus* in the countries visited made reference to the drought of 1947 as a contributory cause (Francke Grosmann 1952, Bejer Petersen, 1952). But there were outbreaks before 1947 and others so long after as to rule out that warm dry summer as an immediate cause; so it was considered desirable to obtain evidence about comparable summers (in Denmark particularly: it was assumed that events in Holland would closely resemble events in south east England) during the past 30 years. Through the courtesy of the Director of the Danske Meteorologisk Institut in Copenhagen, monthly statistics for summer temperature, rainfall and sunshine, relating to three stations with long records, were obtained for 11 individual years (including all years with fine summers in England).

Table 6 presents the essence of these statistics, with the monthly values summed (rainfall, sunshine), or averaged (temperature), and conspicuously high values of sunshine and temperature and low values

TABLE 6. CLIMATIC DATA FOR THREE DANISH STATIONS

Station	*Tylstrup*			*Askov*			*Tystofte*		
Location	*North Jutland*			*South Jutland*			*South-west Sjaelland*		
	April to September			*April to September*			*April to September*		
	Mean temp. °C	*Total Sunshine hours*	*Total Rainfall mm*	*Mean temp. °C*	*Total Sunshine hours*	*Total Rainfall mm*	*Mean temp. °C*	*Total Sunshine hours*	*Total Rainfall mm*
Normal (1931–1960)	12·6	1401	344	12·6	1322	419	13·4	1377	301
1921	12·8	**1688**	**235**	12·4	*Caret*	**230**	13·45	**1580**	262
1933	13·0	**1556**	326	12·95	1412	326	13·7	1493	**182**
1934	12·9	**1560**	450	13·1	1394	308	**14·2**	**1518**	302
1939	12·9	1436	369	13·35	**1472**	357	13·9	**1618**	249
1940	12·1	1513	**206**	12·1	1411	383	12·65	1399	285
1947	**14·2**	**1654**	**201**	**14·1**	**1640**	**250**	**14·65**	**1638**	**187**
1949	13·3	1319	304	13·05	1222	357	13·8	1304	335
1950	12·9	1384	551	13.2	1277	643	13·8	1362	375
1953	12·9	1317	535	13·0	1308	527	13·9	1408	330
1955	12·8	1398	327	12·6	1306	343	13·2	1445	324
1959	**13·7**	**1697**	**211**	**13·8**	**1562**	**230**	**14·7**	**1612**	**153**

of rainfall in bold type. There results a clear picture of 1947 and 1959 as the outstandingly good summers, scoring at all three stations on all three counts. 1921, which one author vaguely remembers in Dublin, though sunny and dry, was not especially warm: between them, 1933 and 1934 contribute some unusual values, but no other year appears to call for comment as a potential drought year.

Some further consideration is now given to these statistics in chronological sequence.

1921

It need cause no surprise that the notorious drought of this year, which affected all western Europe from Britain to the Mediterranean and from early spring until October, is not associated with reports of outbreaks of *Dendroctonus* on spruce in the countries visited. At that time very few stands of the more susceptible host (Sitka spruce) had reached the susceptible age of *circa* 40 years: but it may perhaps be significant that the first record of the insect in Jutland was in 1923.

1933/34

In southern, central and eastern England, 1933 was very dry and sunny throughout the growing season, and drought conditions persisted through part of the 1934 summer: many wells ran dry in eastern England. If it may be supposed that such unusual weather affected Holland also, the two outbreaks of *Dendroctonus* in 1935 may be connected with the occurrence. For Denmark the data in Table 6 show nothing very remarkable about these two years, nor in fact are there many reports of *Dendroctonus* outbreaks until several years later. But a scrutiny of the monthly records of precipitation for the three stations shows peculiar features which may account for the slump in diameter increment of Sitka spruce reported by Henriksen (1958) in one or other (usually both) of those years. At Tylstrup the seemingly abundant rainfall of the 1934 summer was due to the very wet months of August and September: rainfall was below normal from April through July. This was in fact the rule for both years at all three localities: only Tylstrup shows a small excess in 1933.

		Tylstrup	*Askov*	*Tystofte*	*Aggregate*
Percentage of normal rainfall 1.4 to 31.7	1933	111	92	66	76%
	1934	78·5	56·5	50·5	

With an appreciable surplus of warmth and sunshine, 1933 and 1934 are thus shown as critical years for Sitka spruce on the freely-draining, sandy soils of the Jutland heaths and dunes. Holmsgaard (1955) has shown that in Sitka, as in Norway spruce, ring width in Denmark is determined mainly by (a) growth conditions in the preceding year; (b) rainfall during the period May-July.

1938 is not included in the table, but is of some interest in respect of the very dry spring (including an exceptionally warm March), which initiated serious erosion of the sands of West Jutland. Premature growth of Douglas fir, spruce and larch, due to the warm sunny days of March, resulted in severe frost damage in many plantations in April (Ladefoged, 1938; Bornebusch and Ladefoged, 1943). It may be that these occurrences affected the resistance of Sitka spruce to *Dendroctonus*, but the only evidence of this is from Karlum Forest in Schleswig-Holstein (Francke Grosmann, 1952).

1947

Increment data for Sitka spruce recorded in Henriksen's monograph (1958) provide no circumstantial evidence of serious water deficiency between 1935 and 1947. Although Bejer Petersen refers to local outbreaks of *Dendroctonus* in 1943 (North West Sjaelland) and 1945 (Jutland), it was not until 1947, and the years immediately after, that frequent reports arrived from all parts of Denmark, in particular Jutland. In Schleswig-Holstein also, Francke-Grosmann (1952) refers to a stand of Sitka spruce at Süderlügum, near the Danish frontier, growing on a sandy soil with ground water at 90 cm and free from *Dendroctonus* and *Fomes* until the drought of 1947, after which severe invasion by both organisms led to the disappearance of the stand in a few years.

1949–1954

It is evident that Denmark did not share the dry sunny summer which England enjoyed in 1949. 1953 was a dry, though somewhat cool summer in England, but in Denmark rainfall was above normal at all three stations. 1954 was generally cool and wet in north west Europe and the decline in increment recorded in several Jutland stands of Sitka spruce is ascribed by Henriksen to the effect of *Dendroctonus* attack.

1955

Evidence of fresh attacks by *Dendroctonus*, reported first in 1956 in some of the stands visited (Hannenov, Nordskov, Mols Bjaerge, Lovnkaer), recalled to mind the unusually good summer which Britain enjoyed in 1955, and the climatic data from Denmark were awaited with interest. There is certainly nothing remarkable in the six-monthly values given in Table 6; but, as happens frequently, a scrutiny of the monthly values disclosed some unusual features which were totally obscured by the period averages and totals.

These extended data present a clear and consistent pattern of a large excess of warmth and deficiency of rainfall in July and August, a large excess of

TABLE 7. 1955 SUMMER WEATHER AT THREE DANISH STATIONS

Station	April	May	June	July	Aug.	Sept.	Mean Temp.	Total Rainfall mm Sunshine hrs.
TYLSTRUP								
Mean temperature	4·5	8·5	13·3	18·8	17·9	13·6	12·8	
Excess (+) or deficiency (−)	−1·2	−2·1	−0·9	+2·4	+2·0	+1·0	+0·2	
Sunshine (hours)	166	209	264	345	246	168		1398
Excess or deficiency	−24	−55	−10	+77	+ 7	+ 2		−3
Rainfall	18	77	16	26	77	113		327
Excess or deficiency	−20	+43	−35	−50	+ 5	+40		−17
ASKOV								
Mean temperature	5·1	8·5	12·5	17·7	17·9	13·7	12·6	
	−1·0	−2·5	−1·6	+1·7	+2·1	+0·9	Nil	
Sunshine	160	201	210	345	244	146		1306
	−15	−53	−46	+99	+16	−17		−16
Rainfall	41	94	46	22	52	88		343
	− 5	+51	− 4	−77	−50	− 1		−76
TYSTOFTE								
Mean temperature	5·4	9·1	13·1	18·3	18·6	14·9	13·2	
	−1·0	−2·2	−1·8	+1·3	+1·7	+1·1	−0·2	
Sunshine	183	222	242	345	278	175		1445
	+ 1	−39	−18	+97	+20	Nil		+68
Rainfall	32	82	52	48	31	79		324
	− 1	+43	+11	−18	−35	+23		+23

sunshine in July, a cold sunless spring and a markedly cold, wet, sunless May: whereas the seasonal values show only a small excess of sunshine at Tystofte and a moderate deficiency of rainfall at Askov.

Oksbjerg (1956) provides some further information for a site in mid Jutland (intermediate between Tylstrup and Askov) where similar conditions prevailed. Here the July rainfall was almost all in the first few days, the August rain almost all in the last few days: in between were 7 weeks of very warm, sunny weather with scarcely any rain. The cold cloudy spring (three night frosts were recorded in June), following a cold winter, caused vegetation growth to be exceptionally late and Oksbjerg records some interesting observations on the response of plots of early—and late—flushing spruce, planted side by side in Saltendal. Early trees, having completed their extension, were unharmed by the July drought, which caught the late-flushing trees at the peak of their height growth, causing widespread dieback of tips.

It is uncertain what effect the weather of 1955 had on older Sitka spruce in Denmark: it can scarcely be doubted that the warmth and sunshine of July and August, coinciding with the main period of breeding, had a stimulating influence on *Dendroctonus*. In Hannenov Skov, Falster, Bejer Petersen made the interesting suggestion that the gale of January 21, 1956, which blew down much of the adjacent stand to south, damaged the fine roots, and thus increased the susceptibility, of the Sitka and Norway spruce where *Dendroctonus* was found breeding in the summer of 1956. On the other hand, West Nielsen was inclined to ascribe the contemporaneous outbreak in the Mols Bjaerge plantations seen on 16th June to the drought of 1955. The data discussed above make out a plausible case for this.

1957

Britain's phenomenally mild winter was matched, in some degree, in Denmark and Schleswig-Holstein, where a great increase in the population of *Elatobium* (*Neomyzaphis*) *abietina* was observed (Ohnesorge, 1959; Petersen, 1962). While this impaired the vigour of Sitka spruce stands, there appears to be no evidence that it was followed by increased *Dendroctonus* attack.

1959

There is evidence of local increase (or halted decrease) in *Dendroctonus* populations (Schober, 1962, p. 47), but it is clear that this warm, dry, sunny year was not followed by a widespread surge of populations such as characterised the comparable summer of 1947. Three possible explanations can be tentatively advanced, but until closer investigation has been made, the question must remain open.

a. Nearly all susceptible stands had already been invaded and susceptible trees destroyed, leaving only the most resistant trees in susceptible stands; together with stands which, because of age, or favourable site factors, were not readily attacked by *Dendroctonus*.
b. The interval of 12 years since the first increase had allowed parasites and predators to increase enough to check *Dendroctonus* breeding.
c. Man's intervention, involving early removal of affected trees and the use of chemical sprays against the beetles, nipped further outbreaks in the bud.

A fourth possible explanation is that summer weather is not a major factor in *Dendroctonus* outbreaks and that the association between the outbreaks of 1947–49 and the magnificent summer of 1947 was fortuitous. The authors hold to the view that the weight of evidence is against such an explanation.

Recent Years

Until 1964, with its warm sunny spring and early summer, weather since 1959 has not favoured *Dendroctonus*. The 1962 summer was cold and dull and the ensuing winter exceptionally severe. Whether this latter occurrence affected the beetles adversely is uncertain: they occur in the spruce forests of Finland, Karelia and Sweden and are thus unlikely to be harmed in a severe winter in Denmark, or countries farther west. Furthermore the severe 1947 winter was followed by widespread increase of populations.

(2) SOIL

There are two distinct considerations bearing on the relation between soil factors and insect outbreaks, namely their effect on the survival and breeding of the insect and their influence on the host tree (or other plant)—on its general health, its resistance to attack and its capacity for recovery after attack. The many insects which spend an important part of the life cycle in the soil are greatly affected by its temperature, aeration and moisture supply. *Dendroctonus micans* is not strictly one of these, though breeding does occur below ground level and there is some evidence (Merker and Klein Krautheim, 1940) that where the insect has long been endemic on old trees, the underground activity may be more general and important. The probability is that it occurs more widely than is realized. In stands where a little root disease forms the only stain on an otherwise clean record of health, the ability to attack the roots may be a condition of the beetle's maintenance of its numbers.

As far as the stands seen on this tour are concerned, there is little ground for supposing that *Dendroctonus* breeding can have been directly hindered by adverse soil properties, though a few sites subject to winter wetness form a possible exception to this statement. For the most part the soils seen were sandy, freely drained, well aerated and likely to warm up early in summer: in short they were well suited to soil-dwelling insects.

Accordingly it is on their effect on host susceptibility that the interest in soil properties is focussed: nor can it be seriously disputed that the property of over-riding significance is the water-supplying potential. The data in Table 5 show that (with unimportant exceptions) summer precipitation is less in these European sites than in native Sitka spruce sites; very much less than in coastal sites of British Columbia, whence (although the literature studied gives little guidance) it may be supposed that some of the seed came. It is logical to assume, therefore, that throughout the areas visited, and specially in the dry areas of East Jutland, a condition of the maintenance of healthy vigorous growth of Sitka spruce is a satisfactory capacity in the soil for water retention without serious waterlogging. Broadly the same argument applies to Norway spruce, which is also sensitive to moisture stress and adapted to a somewhat more plentiful summer rainfall (and perhaps lower temperatures): but its inherently more rapid rate of increment may render Sitka spruce more sensitive to shortage than the European species.

The significance of soil properties for the growth and health of spruce has been studied by many authors, among them Day (1953, 1955, 1957), Henriksen (1958), Løfting (1937), Merker (1952/3, 1955, 1956), Müller (1939), Schimitschek (1964), Schober (1951, 1962), Wittich (1943), Wood (1955). In the context of planted spruce (particularly Sitka spruce) in north west Europe, the most important discussions are by Day (*passim*), Henriksen (1958), Schober (1962). To attempt a summary review of the relevant literature is beyond the scope of this report and it is proposed to concentrate on those conditions which appear to bear on outbreaks of *Dendroctonus*: other important considerations, affecting increment, stability in face of storms, timber properties, resistance to other diseases, must be left out of account, except insofar as there is substantial evidence that they have an indirect bearing on susceptibility to *Dendroctonus micans*.

Schober (loc. cit. p. 26) summarising Day's description of the soils on which Sitka spruce shows its optimum development in British Columbia, writes of: "deep soils, plentifully supplied with moisture, but free from drainage impedance; with open structure, permitting a uniformly good development of fibrous roots, if possible in proximity to ground water". Incidentally, who, reading this sentence out of context, could be sure that it did not refer to G. Manil's studies of the Ardennes beechwood soils, E.-F. Debazac's study of the Corsican pine forest soils, or one of W. R. Day's own studies of some other tree? Almost all our trees, native and alien, relish the kind of soil on which most of the exotics were planted when first introduced. It would be easier for the Government of this country to provide (without currency inflation) an income of at least £5,000 a year for all its citizens, than for us to offer only soils as good as these to even one of our main species. We must make the most of the soils available to us, assessing their main shortcomings with reference to alternative, otherwise suitable, species; trying to remedy them where we can and, short of that, ensuring that other environmental factors (climate, topography) are not far from optimum.

Among the more important recurrent defects of the soils cursorily examined on this tour are:

a. Deficient water supply, due to rapid drainage, a remote water table and a not very plentiful summer rainfall.
b. Restrictions on root development, caused either by a high water table, or by a compacted, structureless, fine sand of rather homogeneous particle size. B. horizons of strong podzols were the most conspicuous examples of these; but weakly podzolised soils sometimes showed compaction and structural poverty.
c. Acute mineral deficiency of the dune and outwash sands.

Brief notes on the soils of most of the stands will be found in Appendix I. There are many ways in which these and the other soils of the region might be grouped: by genetic type; by parent material; by texture, hydrological condition, or mineral constitution; or by former land use. The complexity of the interactions of these—and doubtless other—factors precludes any attempt at systematic arrangement and it must suffice to draw attention to one of the most influential land—and soil—forming influences in Denmark and Schleswig-Holstein, namely the great Scandinavian end-moraine, which runs nearly North to South through the middle of the peninsula, then (continuing roughly parallel with the Baltic coastline) swinging towards the east a little north of Hamburg. To the east of this ridge, marking the ultimate extent of the last, or Weichsel, glaciation, is boulder till, usually with a rather sandy matrix, yielding the relatively fertile soils of east Jutland and the Baltic fringe; to west are fluvioglacial outwash sands, partly derived from the maximum (Saale) glaciation. These much older sands (one might term them the "washed-out" sands) provide the extensive heaths of west Jutland and Schleswig: near the western edge of the moraine they are overlain by slightly less impoverished Weichsel sand. Southern Holland was unaffected by this last glaciation and the heath soils encountered there are developed from outwash material.

To complete this very broad physiographic sketch, it is of course necessary to refer to the widespread blown sand, covering, to a variable depth, more especially near the west coasts, much of the water- and ice-borne drift. In fact the majority of the stands seen were influenced by blown sand, at least in the surface.

Evidence has been presented connecting outbreaks of *Dendroctonus* with summer drought: it is important to enquire how far this connection is influenced by soil factors. Unless warm, dry, sunny summers act only by promoting *Dendroctonus* breeding, it may be supposed that soil factors, particularly soil water relationships, would have an influence. This problem is illuminated by some observations of Henriksen's (1958) in the experimental thinning plots on the Nystrup coastal sand plantations in north west Jutland. The figure overleaf, from p. 296 of his bulletin, shows the results of a contour survey of the main southern group of plots, where there were interesting differences in *Dendroctonus* attack, in storm damage and in growth of Sitka spruce.

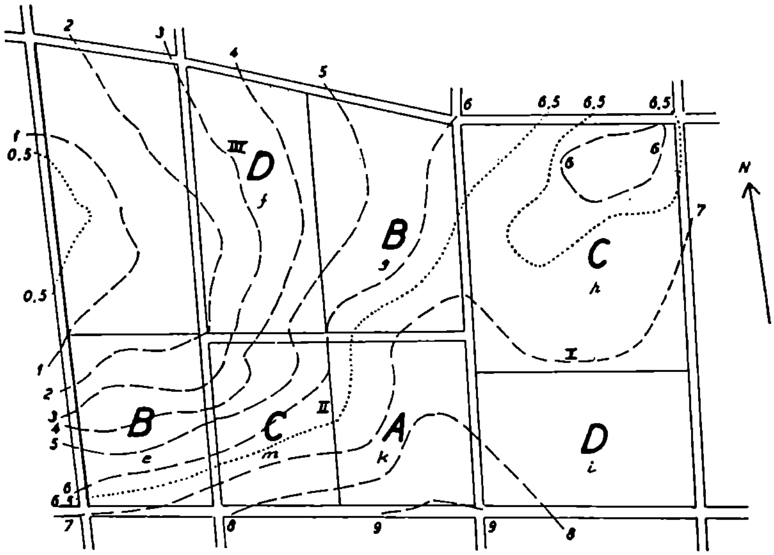
Points from Table 8:

Dendroctonus Attack

In the B grade, more than twice as many trees were attacked in *e* as in *g*: in the C grade, twice as many in *m* as in *h*: in the D grade, more than twice as many in *f* as in *i*. In brief the attack was considerably more severe in the plots on sloping ground, than in the plots on the slightly higher flat ground to the east. The generally more severe attack in the heavily thinned plots, referred to again below, will be noted. At the time of the final assessment in June 1955, the rapid general increase of attack had blurred some of the inter-plot differences, but they were still present.

Growth of Spruce

More severe *Dendroctonus* attack on the slope was not associated with poorer growth: on the contrary, height and basal area, identical through the B grade,



(*Courtesy of H. A. Henriksen*)

FIG. 1. Contouring of soil surface of southern part of plot MB (autumn 1956). Scale 1 : 3,000.

I, II, III: positions of three soil pits. Contours in meters. A–D: thinning grades. *e, f, g, h, i, m:* plot reference letters.

TABLE 8. SOME DATA FROM SITKA SPRUCE THINNING PLOTS IN NYSTRUP DUNE PLANTATIONS (AFTER HENRIKSEN, 1958)

Thinning grade	*Plot*	*% dead or dying trees June,* 1955	*Dendroctonus attack % fall,* 1952	*Measurements fall,* 1951		*Storm damage in or before* 1956	
				Height, m.	*Basal area sq. m.*	*Overthrown*	*Snapped*
A	k	17	2				
B	e	42	26	21·4	2·42	2	9
B	g	20	11	21·5	2·40	2	3
C	h	31	23	21·4	2·61	14	1
C	m	30	47	22·1	2·72	2	7
D	f	69	74	22·0	2·86	3	3
D	i	43	30	21·0	2·48	14	2

are slightly better in plots *m* and *f* on sloping ground than in plots *h* and *i* on the flat.

STORM DAMAGE AND ROOT DEVELOPMENT

On the slope, where examinations showed good deep root development, most of the damaged trees were snapped off: on the flat most were overthrown, showing superficial root development.

Examination of the soil in September, 1956, showed a variable thickness of blown sand over a retentive loamy layer. In pit I, on the flat, water stood at a depth of 65 cm: in pits II and III, with loam appearing at 150 cm and 30 cm respectively, there was no standing water. Accordingly the superior growth in the plots on the slope may be associated, here as elsewhere, with satisfactory site drainage and the absence of any tendency to winter waterlogging. Provided the normal summer rainfall is received, the trees on sloping ground can make good their water loss and maintain their vigour. But they are living only just within their income and, in a drought year such as 1947 (when the trouble started at Nystrup), vigour is impaired and, as it seems, resistance to *Dendroctonus* is lowered. On the flat ground, where growth is more or less restricted by shallow root development due to winter wetness, a summer drought has not such serious consequences, because more of the winter rainfall is retained.

The general experience that *Dendroctonus micans* attacks spruce plantations which are apparently in full vigour of growth on well-drained soils was in accordance with what we saw on this tour. There were a few examples of outbreaks on sites affected by winter wetness—No. 12, Rantzau; No. 35, Mejlgaard; No. 54, Bordrup. In two of these stands honey fungus and wind had contributed a good deal to the losses and *Dendroctonus* attack was not devastating. Schober (loc. cit. pp. 47–55) discusses a serious outbreak of *Dendroctonus* and *Fomes* on 50 years Sitka spruce in the Solling (Holzminden/Schiesshaus), in which a root-restricting gley soil is seen as predisposing cause. Otherwise there is little evidence connecting outbreaks with retarded growth due to extreme soil poverty, or restricted root systems. On the contrary the indications are that attacks are most likely where satisfactory growth, promoted by free root development in a well-drained soil, is linked with a summer rainfall maximum. Where the summer rain falls far short of normal, while excess warmth augments transpiration, the trees cannot maintain their rapid growth, loss of turgor results and bark beetles have an opportunity of penetrating the defences.

(3) STAND CONDITIONS

(a) Specific Composition

The host plants of *Dendroctonus micans* in Europe were discussed in Chapter 1, where it was stressed that Sitka spruce is less resistant than Norway spruce. Valid comparisons with other *Picea* species are not possible, but attacks have been reported on *P. orientalis* and *P. omorika* and on several exotics from western North America.

Significant attacks on Norway spruce are less frequent in pure stands than in mixed stands including susceptible species like Sitka or Oriental spruce. Attacks on pines appear to be rare and of no practical importance.

(b) Age

It is said that in the indigenous forests of *Picea abies*, old trees are the usual habitat of *Dendroctonus micans*. Kangas (1952) (whose detailed studies of *D. micans* attacks in Finnish spruce forests in relation to the condition of the bark and the attacks of other organisms will be referred to again) gives the age range of the trees where his analyses were made as 80–127 years. But he mentions that he has found *Dendroctonus* elsewhere in much younger trees and stresses that it is characteristic of the species to affect trees which are almost, if not quite, in full vigour. From this it appears that if *Dendroctonus* in northern Europe occurs most frequently on old trees, this is not because they are senescent, even moribund: if it fails to attack young trees this may be because they are too small, or the bark is too thin. Some direct chemical stimulus may well be involved.

Obviously Sitka spruce in Denmark, Schleswig and Holland will grow much faster than Norway spruce in Finland and in fact, for the great majority of affected stands examined, the range in age at the time of the first outbreak was not great. Reference may be made to Table I, where the age given in column *f* is the actual age in 1964: a 60-year-old stand first attacked in 1947 would have been about 44 years then. Nearly all stands were aged between 30 and 50 when first attacked, but Gøhrn, Henriksen and Petersen (1954) describe an outbreak in 20 years old Sitka spruce in Vilsbøl dune plantation and Francke-Grosmann (1954 a) also records attacks on relatively small trees down to 6 cm DBH.

(c) Thinning

The *Dendroctonus micans* outbreak, which developed after 1947 in the Nystrup experimental thinning plots in north west Jutland, provided an opportunity of obtaining precise information about the relation between stand density and susceptibility to *Dendroctonus*. Some of this information has been given in Table 8: mean values (in percentages of trees affected) for all the thinning plots were, in autumn, 1952 (data from Henriksen, 1958):

Thinning treatment	A	B	C	D
Number of plots	2	4	4	4
Mean percentage of trees attacked	5·1	34·5	56·9	65·9

The clear evidence of more severe attack in plots heavily thinned prompted the comprehensive series of temperature measurements which Haarlov and Bejer Petersen (1952) carried out in the Nystrup plots in July, 1951. These showed large differences in bark and wood temperatures, both in relation to density of canopy and, under the more open canopies particularly, between north and south aspects of the same tree. The precise bearing of these observations on *Dendroctonus* breeding is not so clear. Several observers have denied that southerly aspects of stems are more prone to attack than northerly aspects and we can confirm this from our own limited experience. Survival of broods may be better, or the life cycle may be slightly shortened, in the warmer summer climate of the more open stand: but until these points have been illuminated by ad hoc investigations, speculation is unprofitable.

Among several other possible reasons for the apparently greater susceptibility of heavily-thinned stands may be mentioned:—

(i) *Number and Size of Trees. Dendroctonus* showed a slight preference for the larger trees (at least within the diameter range of 15–35 cm in the Nystrup plots). Large trees are more frequent under heavy thinning and, as the trees are fewer, the chances of attack would in any case be greater, if an even spatial distribution of the insects be assumed.

(ii) It is a known fact (Rishbeth, 1951) that, other things being equal, *Fomes annosus* attacks are more severe in heavily-thinned, than in unthinned, or lightly-thinned stands. If, as many observers believe, *Dendroctonus* attack tends to follow *Fomes* infection, the beetle would presumably find relatively more trees suitable for breeding in stands heavily thinned. This argument appears to have little force in the Nystrup environment, where *Fomes* attack was light, with no good evidence of correlation between *Fomes* and *Dendroctonus*.

(iii) The more open canopy under heavy thinning must affect the stand climate in ways beyond the important modification of the temperature regime in and beneath the bark discussed by Haarlov and Bejer Petersen. There is, temporarily at least, less intense root competition and thus a possibility of improved supply of water and plant foods to the individual tree. On the other hand it may be argued that the freer penetration of the stand by wind, in a stormy coastal situation such as that of the Nystrup plantations, would entirely offset any greater water intake from the soil. Other influences, above and below ground, of heavy thinning, will not be considered, as they seem unlikely to affect the susceptibility of spruce to *Dendroctonus*.

(iv) One aspect of the effect of thinning on stand temperatures which does not seem to have been considered in Denmark and adjacent lands is the possible effect on chemical stimuli to which *Dendroctonus* is sensitive. There is evidence that many bark beetles are drawn by chemical stimuli emanating from trees in certain conditions of health. If *Dendroctonus* reacts in this way, the higher air temperature at swarming time, and especially the higher bark temperature of heavily thinned woods, must cause a greater production of the vapour and draw a preponderance of the beetles into such woods. This aspect of the susceptibility of spruce to bark beetle attacks has been examined particularly by Krämer (1953) and Merker (1956).

(d) BRASHING, PRUNING, ETC.

There are many references to *Dendroctonus* attacks initiated at, or close to, brashing or pruning wounds, logging scars, or wounds caused by deer: plate 7 shows a very coarsely-branched, 33 years old stand of Sitka spruce in Rendsburg Forest, where brashing and pruning wounds may have contributed to the attack by *Dendroctonus*. It does not appear that evidence has been collected bearing on the question whether wounds and abrasions merely serve to canalise breeding attempts which would have been made in any case: and, if so, whether the proportion of abortive attacks is smaller on such coarse or bruised trees. In this, too, the factor of chemical stimuli may be important.

(4) STATE OF HEALTH OF TREES

All who have given much attention to *Dendroctonus micans* outbreaks in Europe have considered the problem of host susceptibility.

Important contributions on this subject have come from Kangas (1939, 1949, 1950, 1952), from Schimitschek and Wienke (1963), and from Krämer (1953), who have approached the problem from very different standpoints which may be loosely called entomological, ecological and physiological. A subsequent publication by Schimitschek (1964) is also relevant.

Kangas made a great many detailed examinations of trees in Finnish spruce forests where *Dendroctonus* occurred, recording the positions of attacks by this and other insects over a period of years, if possible until the tree's death. Its state of health at the outset of observations was evaluated partly by visual symptoms of the crown, partly by reference to the other organisms—if any—detected anywhere on the stem or roots. He shows that *Dendroctonus micans* has a high attacking potential (Angriffsvermögen) and very often attacks seemingly wholly sound spruces, even though the percentage of failures (usually signified by a long horizontal tunnel, perhaps with an adult engulfed in resin) is then relatively high (43% in Kangas' material). This author suggests that, because such attacks on seemingly sound bark are not, as it were, forced on the insect by want of unsound breeding material, sound trees may provide the best conditions for the broods; and that, although initial failures are then relatively frequent, the species profits by the attempt, more than if it waited on definite weakening of the tree.

Although some observers do not accept Kangas' view that *Dendroctonus* can attack wholly sound trees, it is undeniable that the trees affected are often in apparently good condition and show no reduction in increment. It may be suggested that this aggressive behaviour of *Dendroctonus* is linked with the manner of breeding and the length of life cycle. Ailing spruce trees are a magnet for many insects (*Ips typographus*, *Pityogenes chalcographus*, *Ernobius explanatus*, *Polygraphus poligraphus*, *Pissodes hercyniae*, *Tetropium* spp, *Monochamus*) and fungi (*Armillaria mellea*, *Fomes annosus*, *Nectria cucurbitula*, *Dasyscypha resinaria*); some of the insects larger, or with more rapid growth, than *Dendroctonus*, whose slowly developing broods might risk being jostled out of place, were the mother not adapted to stealing a march on many of these potential competitors. In fact, as Francke Grosmann attests (1954 a), *Tetropium*, especially *T. fuscum*, larvae may invade and damage broods of *Dendroctonus*.

A point stressed by Kangas is that the grading of whole trees from the fitness point of view is only a rough general appraisal. The condition of the bark may differ from place to place round the circumference and from top to ground (and below): *Dendroctonus* attacks may still be repulsed in one part, where the bark is sound, some years after attacks have been successfully made elsewhere on the same tree. This is shown by the appreciable percentage (16·5) of abortive attacks on his "class 4" trees, already losing their general attraction. Thus Kangas regards *Dendroctonus* as insistently probing the defences of the spruce, often defeated, and sometimes destroyed, at the first attempt; but then perhaps successful at the second or third attempt. In much the same way Merker and Klein-Krautheim (1940), investigating an outbreak on 50-year-old Sitka spruce (with some old Scots pines) near Giessen, regard the encounter as a struggle between the insect and the resin flow, which both symbolises and effects the tree's resistance. Provided the resin is no more than can be absorbed by the bast debris resulting from the beetle's feeding, a brood can develop. After a time resin production at that place diminishes and the last frass produced by the older larvae a year later is free from resin and can be used by them for moulding the pupal cells.

Whereas the investigations of Kangas—and other entomologists—have shown that some examples of attack by *Dendroctonus micans* can be linked with perceptible local abnormalities (infection by *Armillaria* or *Fomes*, stem cankers, or wounds causing resin exudation, etc)., he found that attacks (some of them abortive) often occur on trees which are entirely sound and healthy as far as outward appearance tells. Schimitschek and Wienke have taken the enquiry a stage further, adducing evidence that there is some degree of anatomical abnormality and physiological weakening in the seemingly healthy spruce trees affected by *Dendroctonus*. They were mainly concerned with Sitka spruce in Schleswig-Holstein, but comparative data were obtained for Norway spruce there, and in an indigenous spruce forest in Austria. Apart from examinations in cross sections of the anatomy of bark and cambium of trees in healthy and affected stands, physiological and ecological investigations were undertaken, viz:

1. Studies of the water economy of the tree by:—
   a. Measurement of the speed of the transpiration (sap) stream.
   b. Measurement of the quantity of water transpired.
   c. Evaporimeter data.
2. Measurement of osmotic pressure of fluid expressed from the needles.
3. Measurement of the electrical resistance of the bark.

A translation of Schimitschek and Wienke's summary forms Appendix 3 to the present report, but it is hoped that all concerned with our own Sitka spruce troubles will read the full paper. Although Schimitschek was concerned with different pathological symptoms in a different environment, his general approach and some of the methods of investigation appear relevant to retarded growth, "bent top" and related phenomena on Sitka spruce in Britain.

A few points from the authors' evidence which have a close bearing on the present discussion will be mentioned briefly.

(a) Physiological weakening (physiologischer Schwächung; *Dendroctonus*-Disposition.) It is not clear from the context whether these attributes are based on subjective estimates, backed of course by a great deal of field experience; or whether they describe trees which did in the event become attacked by *Dendroctonus*.

(b) Prominent among the anatomical abnormalities in trees liable to attack, or already attacked, are the traumatic resin ducts. Local resources of resin are mobilised in face of attack. The depletion of the *parenchyma* cells is perhaps linked with the lowered osmotic pressure recorded by Krämer.

(c) Measurements of the speed of the sap stream and of the transpiration of young Sitka spruce stands in Schleswig-Holstein gave values equivalent (or a little superior) to those of native Austrian spruce stands: but the values dropped in older stands—rapidly from the age of 40 years. Trees showing debility and those affected by *Dendroctonus*, *Neomyzaphis*, *Armillaria*, *Fomes*, or canker showed lower values.

(d) Osmotic pressure measurements pointed to an abnormal fall in physiologically weakened stands and a rise after attack by fungi or insects. Zwölfer (1957) had previously provided evidence that a lowering of the osmotic pressure of the bark cell sap is a symptom of trees prone to attack by bark-dwelling insects.

(e) Earlier evaporimeter data collected by Dr. G. Repp in Schleswig-Holstein (1954) and in Hungary (1941) had indicated that the effect of the wind in Süderlügum was such as to increase evaporation to values typical of the hot dry plains of Central Europe. In the more recent comparisons in 1956/57, spruce sites in Schleswig-Holstein showed values of evaporation generally more than ten times as great as those of the Austrian site of the indigenous spruce at Lunz-am-See.

(f) Trees affected by *Fomes annosus* showed abnormalities in some respects different from those of trees attacked by *Dendroctonus:* this appears to confirm field evidence that *Dendroctonus* attack may be (and usually is) independent of attack by *Fomes*.

Krämer (1953), who, in a previous study of silver fir, had traced a correlation between the osmotic pressure of the bark sap and susceptibility to attack by bark beetles, undertook a similar investigation in several Bavarian spruce stands, where four bark beetles were more or less common:

(1) *Ips typographus*
(2) *Pityogenes chalcographus*
(3) *Polygraphus poligraphus*
(4) *Dendroctonus micans*

Ips typographus, the most important of the four, received the fullest treatment: there was very good agreement among the many samples from trees naturally exposed to attack in the field and those artificially infected with beetles. Trees attacked showed a reduction in osmotic pressure below the normal value of about 10 atmospheres: in all series of tests there was a critical value of 6·5/7 atm., below which *typographus* attack was almost invariably present and above which it was very rare. A somewhat similar, but less clear cut, result was obtained for *Pityogenes chalcographus*, which, although also clearly secondary, proved able to attack at a rather higher osmotic pressure of the bark sap (critical value 7·5/8 atm.). There has never been any doubt that *Polygraphus poligraphus* attacks ailing, if not actually dying, spruce; osmotic pressure measurements showed a critical value of about 6 atm., but a peak of susceptibility to this insect when the value had sunk to the almost fatally low value of 4/5 atm.

Dendroctonus micans, alone among the insects tested, showed an ability to attack spruce trees showing values of osmotic pressure not significantly below the normal, but the zone of intensive attack corresponded to values between 6 and 8, approximately the same as the critical value for attack by *Ips typographus*. Accordingly Krämer's evidence, based on a technique developed by Walter and Thren in 1934 and applied by Zwölfer (1956) to this kind of problem, is in good agreement with the field evidence of Kangas and others that *Dendroctonus micans* has a high attacking potential and may breed (particularly where the population is high) in trees that are very nearly in full vigour.

The bearing of Krämer's investigations on the fundamental influence of the tree's water economy calls for some elucidation, because the comprehensive study by Merker (1956) of osmotic pressures of bark cell sap of Norway spruce, in relation to locality factors and attack by *Ips typographus*, shows fairly consistently a correlation between *enhanced* values (15 atm. and over) of osmotic pressure and susceptibility. This is indeed the result one would expect, if the predisposing cause is reduced moisture supply from dry soil, or increased transpiration in a dry sunny windy atmosphere: less water must mean a higher concentration of the cell sap. But if the water deficiency is severe, or long continued, the stomata will close, the sap stream will be slowed up as the pull of the leaves weakens, and the intake of carbon dioxide will be drastically reduced. Before long the interruption in the supply of the products of photosynthesis will result in a lowering of the osmotic pressure of the cell sap, which depends partly on the sugar content.

This eventuality is in fact recognised by Merker, who reports some instances where increased susceptibility to *Dendroctonus* was associated with subnormal values of the osmotic pressure of the bark sap. He draws attention also to differences in osmotic pressure in different parts of the trunk and to the effect of important seasonal influences: a rise in osmotic pressure on the approach of winter results in greater winter hardiness: a fall in spring signalises the movement of assimilates to the growing parts.

Merker's work is of particular importance in showing the influence of local factors of topography and soil on the supply of water to the tree in dry periods and thus indirectly on its susceptibility to bark beetles.

SUMMARY OF CHAPTER III

There is convincing evidence that recent outbreaks of *Dendroctonus micans* in north west Europe were connected with the summer weather—beneficial to the insect, unfavourable to spruce—of certain years, particularly 1947, when numerous stands of Sitka spruce had reached a susceptible age. This receives some confirmation in a paper seen since this section was drafted, by Kollar (1858), who relates an outbreak in Laxenburg Park near Vienna to the very warm dry summers of 1856 and 1857. The effects of reduced summer rainfall and accelerated loss by transpiration are governed by the local soil conditions, but most of the woods seen were on freely drained sandy soils, where the maintenance of healthy growth is dependent on the summer rainfall. A very few stands (e.g. Mejlgaard) on favourable sites with ground water withstood the droughts well: on soils showing impeded drainage, or a sharply fluctuating water table, spruce growth had been slower and, perhaps for this reason, the effects of drought may have been less sharply felt.

Sitka spruce has proved considerably more susceptible than Norway spruce and practically all the serious outbreaks have occurred where it forms a large proportion of the stand. Evidence is wanting about the reason for this difference in susceptibility—whether it resides in the specific properties of the bark, in differing water needs, or in varying powers of adaptation to an environment which is far from optimal for either species. Such evidence as there is indicates that Sitka spruce does not fall behind its congener in root exploitation of the sandy soils.

Stand conditions have an important influence in ways not fully understood: but the increased severity of attack in heavily thinned stands may be a result both of improved conditions for the insect (higher summer temperature, perhaps freer release of attractants) and worse conditions for the tree, in particular free access of wind and sun in circumstances where the conservation of a cool, humid stand climate is vital. Field studies and laboratory tests are in fairly good agreement about the relation between *Dendroctonus* attack and the physiological condition of the trees in which it breeds. Relative to other bark beetles, *Dendroctonus* (like most of its American allies) is aggressive: nevertheless the apparently sound trees which are frequently affected can generally be shown to be suffering from some disturbance of their water economy. The high percentage of unsuccessful attacks on outwardly sound trees is additional evidence in support of this interpretation.

Chapter 4

DISCUSSION AND CONCLUSIONS

It was considered superfluous, indeed presumptuous, to allot a section of this paper to a general review of the performance of Sitka spruce in the environment of Denmark, Holland and Schleswig-Holstein, as it appeared on the tour. Day (1955) who spent not 2 weeks, but 2 months, in roughly the same territories, has presented his impressions in some detail: for Denmark particularly, a fuller treatment is given in Henriksen's monograph (1958), while Schleswig is dealt with by Emeis (1923, etc.) and Schober (1962). These authors are agreed on two things, viz. (a) the widespread instability of the Sitka spruce stands in north west Europe (the word stable being used here in the sense of general ecological fit, not in the limited sense of "wind-firm"); (b) the importance of good water supply. Whereas Day sees the main difficulty in the restriction on free healthy root growth imposed by unfavourable soil conditions, Henriksen is inclined to regard the overall environment as falling short of the optimum, but he stresses the factor of wind. Where *Fomes*-infected trees drop out (commonly with the intervention of gales acting on impaired root hold) wind is admitted and the stand climate disturbed. A similar effect is produced by heavy thinning, which, as has been shown, may be associated with more severe *Dendroctonus* attack. In fact Henriksen adduces some evidence that, quite independently of attack by fungi or insects, increased exposure to the wind (resulting perhaps from initial storm damage) may have a deleterious influence. But this will of course happen only if other factors, rainfall, humidity, soil physical conditions, are in some degree unfavourable (as indeed they are on many of the sites seen).

Such strong evidence of a relationship between the tree's water balance and its general vigour is even more convincing when the special question of susceptibility to *Dendroctonus micans* is approached. The chronological connection outlined in Chapter 3 between recent outbreaks and warm dry summer weather; the increased susceptibility when the larger size of the trees augments their demands on the soil; the distribution of affected stands in relation to critical factors of the environment; and the physiological-ecological studies (admittedly more concerned with *Ips typographus* attacks on *Picea abies*) all point to water stress as the predisposing cause, even if the insect's own response to weather, its population status and the influence of its predators determine whether an incipient outbreak becomes a disaster or quickly subsides.

It is relevant now to consider in what circumstances water stress, of the kind postulated as rather frequent in Denmark and Schleswig-Holstein, may occur on Sitka spruce sites in Britain, where the rainfall is generally more plentiful and the soils are so different. British Sitka spruce sites obviously differ enormously among themselves, in these two, as well as other, factors. For the present discussion therefore, it is well to restrict consideration to a few of the sites where increment fall off, or other symptoms of unsatisfactory growing conditions, have shown up in recent years. Among these are Blairadam (4), Forest of Deer (1, 2) Hallyburton (3), Lennox (5), Chopwell (6), Rothbury (7, 6), Alnwick Castle Estate (7) and Allerston (9, 8). The numbers in brackets refer to the weather stations, for which average values of summer rainfall (April to September inclusive) are given in Table 9.

Comparison with 9 representative Danish stations shows that the average summer rainfall there (336 mm) is *c.* 18 per cent less than the average (409 mm) at the "marginal" Sitka spruce sites in Britain, but this difference may be largely offset by greater evaporation, due to stronger winds, at the

TABLE 9. SUMMER RAINFALL AT SOME BRITISH AND DANISH STATIONS

No.		1	2	3	4	5	6	7	8	9
Name of Station		*Fyvie Castle*	*Craib-stone*	*Glamis Castle*	*Loch Leven Sluice*	*Paisley*	*Morpeth Cockle Park*	*Ilderton Lilburn*	*Kirkby Moorside*	*Guis-borough*
Annual Rainfall	in.	34·63	33·90	33·79	37·09	44·22	28·73	31·00	29·37	34·12
	mm.	882	864	860	845	1114	730	790	746	868
Summer Rainfall	in.	16·26	16·29	15·79	17·67	18·54	14·25	14·69	13·95	16·81
	mm.	416	417	402	451	473	364	374	356	432
Summer Rainfall Denmark	mm.	339 Thisted	380 Varde	306 Hals	305 Mejl-gaard	369 Pals-gaard	290 Tystofte	323 Ring-sted	313 Nykøbing	403 Tønder

upland British stations. In fact the observed decline in growth (sometimes associated with "bent top") at these probably results from a combination of not-over-plentiful precipitation, strong evaporation in a windy climate and a restrictive soil. Sometimes one factor, sometimes another, is preponderant: at Lennox, for instance, the precipitation seems more than adequate, but the soil is conspicuously ill-drained and hostile to good root development, and winds are strong. On the east, soil physical conditions are often better, but rainfall is appreciably less and, except near the coast, humidity lower. Some of the stands appear to lend support to Henriksen's thesis that heavy thinning (whether due to conscious intervention, or resulting from *Fomes* and wind) may cause some retardation, even stagnation, of growth and increase susceptibility to disease. None of the affected stands enjoys two advantages common to native Sitka spruce stands in the optimum zone:—

(a) High humidity and low evaporation in the fog belt.

(b) The influence of an understory of hemlock and red cedar, which slows down the wind, increases humidity and buffers temperature changes.

It is accordingly in conditions such as these—repeated, though usually on a small extent, in many forests in the south—that trouble might be expected from *Dendroctonus*, should it ever gain entry and become established in Britain. No-one can predict whether this misfortune will occur: the authors' own feeling is that accidental introduction is likely sooner or later, but that the chances of broods being established in Britain are exceedingly small. There are two circumstances which appear to increase the difficulties of ensuring the exclusion of *Dendroctonus* from unbarked export timber. One is the occasional (locally frequent) occurrence of broods high on the stem, where—at least in standing timber—they are not very evident from the ground. The other is the long life cycle (if Bejer Petersen's evidence is accepted): this provides the possibility of live larvae, pupae, or adults arriving here even after many months' delay in transport from forest to port and in storage. But the practical restriction of the insect to spruces, and among them to trees of susceptible age and special physiological condition, together with the distance of most spruce forests from seaports, must place great obstacles to breeding in the way of any beetles which might casually gain admission.

There is, however, no justification for complacency. Apart from the imposition of further restrictions on the import of unpeeled spruce, forest scientists in Britain can arm themselves against this threat (slight as it now seems) by finding out more about *Dendroctonus* ecology, by making themselves familiar with the emergency use of chemicals and above all by learning more about Sitka spruce, so that practical foresters may become more discriminating and skilful in its use and treatment. It is hoped that this report, despite the tentative nature of much of the evidence, may provide a few pointers in all these directions.

ACKNOWLEDGMENTS

A wide-ranging tour such as this could not have been undertaken without the ready co-operation of the entomologists directly concerned with *Dendroctonus micans* outbreaks in the countries visited, and in particular Dr. E. T. G. Elton, of the Instituut voor Toegepast Biologisch Oenderzoek in de Natuur, Arnhem, Holland; Dr. H. Francke-Grosmann, Bundesforschungsanstalt für Forst und Holzwirtschaft, Reinbek, near Hamburg, West Germany; Dr. B. Bejer Petersen, Den Kongelig Veterinaer- og Landbohøjskole, Copenhagen, Denmark. All gave generously of their time and their wealth of information. We are much indebted to them for this and for their introductions to forest officers, woodland owners and agents (too numerous for individual mention), who took trouble to show us the woods in their charge and went out of their way to make the tour fruitful and enjoyable. In Denmark Sitka spruce is one of the species used for afforesting the coastal sands of W. Jutland, where information and guidance were most kindly provided by Klitdirektor (Director of Dune Forests) P. Thaarup and Herr Skarregaard.

In Göttingen and Hannoversch-Münden, Professor F. Schwerdtfeger and Professor E. Schimitschek and their colleagues provided much information about outbreaks of *Dendroctonus* and other forest insects, while Dr. Voûte was another valued contact at Arnhem (ITBON). Without the information courteously supplied by the Dansk Meteorologisk Institut, it would not have been possible to correlate recent outbreaks of *Dendroctonus* with fluctuations in summer weather. Finally grateful acknowledgment should be made to the travel organizers at Forestry Commission Headquarters, who booked all the rail, sea and air journeys; to the photographers at Alice Holt, who produced good prints from some not very promising negatives; and to our library staff for much help in sifting voluminous and sometimes rather inaccessible literature.

REFERENCES TO LITERATURE

ANDERSEN, M. 1951. Balancen i blandings bevoksninger af rødgran og sitkagran. *Dansk Skouforenings Tidsskrift*, 1–44.

BAUDISCH, F. 1903. Dendroctonus micans Kug. *Zentralbl. ges. Forstw.*, 29; 151–152.

BERGMILLER, F. 1903. Dendroctonus micans und Rhizophagus grandis. *Ibid.* 252–256.

BILHAM, E. G. 1938. *The Climate of the British Isles.* Macmillan, London.

BRICHET, O. ET SEVERIN, G. 1902. Le Dendroctonus micans Kugelann en Belgique. *Bull. Soc. Cent. For. Belg.*, 9; 72–81.

BORNEBUSCH, C. H. og LADEFOGED, K. 1943. Hvidgranens og Sitka-granens dødelighed i hede-og klitplantager i 1938 og 1939. *Forstl. Forsøgsv. i Danmark*, XV, 209–232.

CHRYSTAL, R. N. 1949. The bark-beetle problem in Europe and North America. *Forestry Abstracts*, 11, 1; 3–12.

DAY, W. R. 1953. The growth of Sitka spruce on shallow soils in relation to root disease and wind throw. *Forestry* 26, 81–95.

—. 1955. The failure of Sitka spruce in north west Europe. Unpublished report to Forestry Commission, London.

—. 1957. *Sitka Spruce in British Columbia.* Forestry Commission Bulletin 28, pp 110; London, H.M.S.O.

DET DANSKE METEOROLOGISKE INSTITUT. 1933. *Danmark's Klima.* København.

ECKSTEIN, K. 1904. Der Riesenbastkäfer, Hylesinus (Dendroctonus) micans Kug. *Z.f. Forst-u Jagdw.* 36 : 243–249.

EIDMANN, F. E. 1953. Zur Entwicklungsdynamik westamerikanischer Waldgesellschaften. *Forstarchiv*, XXIV; 59–64.

ELTON, E. T. G. 1950. Dendroctonus micans Kug., a pest of Sitka spruce in the Netherlands. *Proc. VIII Internat. Entomological Congress, Stockholm*, 1948.

EMEIS, W. 1923. Erfahrungen mit ausländischen Holzarten in der Provinz Schleswig-Holstein. *Mitt. d. deutschen dendrologischen Gesellschaft* 35; 133–156.

—. 1933. Wahrnehmungen au ausländischen Nadelhölzem in Schleswig-Holstein. *Mitt. d. DDG.* 45; 116–120.

—. 1939. Schlechtes Wachstum der Sitkafichte. *Mitt. d. deutschen dendrologischen Gesellschaft.* p. 170.

FRANCKE-GROSMANN, H. 1948. Rotfäule und Riesenbastkäfer. *Forst und Holz* 3 (23); 232–235.

—. 1949. Über Kopulation, Eiablage und Gelbkörperbildung beim Riesenbastkäfer, Dendroctonus micans Kug. *Verh. d. deutschen Gesellschaft f. angew. Entomologie;* 142–153 (München).

—. 1950. Über ein Massenvorkommen von Gilletteella Gallen an Sitkafichte. *Anzeiger F. Schädlingskunde*, 4.

—. 1952. Populationsdynamische Faktoren bei der Massenvermehrung des Dendroctonus micans Kug. an der Sitkafichte in Schleswig-Holstein. 12 *Verhandlungsber. d. deutschen Gesellschaft f. angew. Entomologie*, Berlin.

—. 1954 (a). Feinde und Krankheiten der Sitkafichte in Schleswig-Holstein auf norddeutschen Standorten. *Der Forst und Holzwirt*, 9: 117–119.

— and RÜHM, W. 1954 (b). Die bekämpfung des Riesenbastkäfers. *Zeitschr. f. Weltforstwirtschaft*, 17, 2 : 48–52.

GERHARD, H. 1954. Zur Anzucht von Sitkafichten. *Der Forst und Holzwirt* : 97.

—. 1955. Carl Emeis und die Schleswig-holsteinische Probleme. *Allg. Forst u. Jagdztg.*, 126, 1 : 29–30.

GØHRN, V., HENRIKSEN, H. A., PETERSEN, B. BEJER. 1954. Jagttagelser over Hylesinus (Dendroctonus) micans. *Forstl. Forsøgsv. i Danmark* (Nr 180), XXI : 383–433.

HAARLOV, N. og PETERSEN, B. BEJER. 1952. Temperaturmaalinger i bark og ved af Sitkagran. *Forstl. Forsøgsv. i Danmark* (Nr. 170), XXI : 43–91.

HENRIKSEN, H. A. 1951. Et Udhugningsforsøk i Sitkagran. *Forstl. Forsøgsv. i Danmark* (nr. 168), XX : 403–418.

— and JØRGENSEN, E. 1952. Rodfordaerverangreb i relation till Udhugningsgrad. *Ibid* (nr. 173), XXI : 215–252.

HENRIKSEN, H. A. 1955. Undersøgelser over Sitkagranens vaekst, sundhed og stabilitet i Vilsbol og Nystrup Plantager. *Dansk Skovforenings Tidsskrift*, 40. 33–40.

—. 1957. Forsøgsvaesenets prøveflader i Abiesarter *Forstl. Forsøgsv. i Danmark* (nr. 188), XXII : 281–343.

—. 1958. Sitkagranens vaekst og sundhedstilstand i Danmark. *Ibid.* (nr. 191), XXIV : 1–371.

HOLMSGAARD, E. 1955. Aaringsanalyser af danske Skovtraer. *Ibid.* (nr. 183), XXII : 1–246.

HUSSON, R. et STAUDER, F. 1954. A propos du *Dendroctonus micans* Kug. *Revue forestière française*, 6 : 355–359.

I.U.F.R.O. 1962. *Conference and study tour on Fomes annosus; Scotland, June* 1960. 151 pp. Firenze.

JENSEN, C. F. 1952. Orkanen den 11 Februar, 1952. *Dansk Skovforenings Tidsskr.* 37 : 290–298.

KANGAS, E. 1939. Über die Widerstandsfähigkeit der Fichte gegen Angriffe von Dendroctonus micans. *VII. Internationaler Kongress für Entomologie*, 1990–2004. Berlin, 1938.

—. 1949. Über die Vertrocknung der Fichtenbestände als Waldkrankheit-und Waldbaufrage. *Acta Forestalia Fennica* 52, 5, 1–166 (German summary, 167–192).

—. 1950. Die Primarität und Sekundarität als Eigenschaften der Schädlinge. *VIII Internationaler Kongress f. Entomologie, Stockholm*, 1948 (pp. 7).

—. 1952. Über die Brutstättenwahl von Dendroctonus micans Kug. (Col. Scolytidae) auf Fichten. *Annales Entomologici Fennici*, 18, 4 : 154–170.

—. 1952. Maannousemasienen (Polyporus annosus Fr) esüntymisestä, tartunnasta ja tuhoista suomessa. (Über Auftreten, Infektion, und Schäden des Wurzelschwamms, Polyporus annosus Fr., in Finnland). *Communicationes Instituti Forestalis Fenniae*, 40, 33 : 34 pp.

—. 1954. On the possibility of pests being conveyed in export timber: Survey of biological requirements. *Acta Forestalia Fennica*, 61 : 11 pp.

KENDREW, W. G. 1953. *The climates of the continents*, Oxford.

KINDT, S. 1956. En prøveflade i Sitkagran afsluttet. *Dansk Skovforenings Tidsskr.*, 41 : 147–149.

KOLLAR, V. 1858. Beiträge zur Naturgeschichte des grossen Fichtenbastkäfers, Hylesinus (Dendroctonus) micans Kug. *Verh. d. k.-k. zool-bot. Gesellschaft in Wien* : 23–28.

KRÄMER, G. D. 1953. Die kritischen Grenzen der Brutbaumdisposition für Borkenkäferbefall an Fichte. *Zeitschr. f. angew. Entomologie*, 34 : 463–.

LADEFOGED, K. 1938. Frostringsdannelser i vaarveddet hos unge douglasgraner, sitkagraner og laerketraeer *Forstl. Forsøgsv. i Danmark* (nr. 102), XV: 97–112.

LAING, E. V. 1947. Preliminary note on a disease of Sitka spruce in Cairnhill Plantation. *Forestry*, 21 : 217–220.

LOOS, K. 1925. Dendroctonus micans Kug. an Kiefer. Sudetend. *Forst.-u. Jagdzeitung*, 25 : 53.

LØFTING, E. C. L. 1937. Rodfordaerverangrebenes Betydning for Sitkagranens Anvendelighed i Klitter og Heder. *Forstl. Forsøgsv. i Danmark* (nr. 119), XIV : 133–160.

MCMAHON, F. 1945. Sitka spruce in Irish forestry. *Irish Forestry* 2, : 66–71.

MERKER, E. and KLEIN-KRAUTHEIM, F. 1940. Der Riesenbastkäfer an Sitkafichte. *Allg. Forst-u. Jagdztg.* 116 (10) : 255–261.

MERKER, E. 1952/3. Das Wetter der Jahre 1939 bis 1950 und sein Einfluss auf die Massenvermehrung des grossen Fichtenborkenkäfers in Südbaden. *Ibid.* 123 (8) : 213–233 : 124 (1) : 1–22.

—. 1956. Der Widerstand der Fichten gegen Borkenkäferfrass. *Ibid.* 127 (7) : 129–145; 127 (8/9) : 157–187.

—. 1955. Der Massenwechsel des grossen Fichtenborkenkäfers und seine Abhängigkeit vom Standort. *Beiträge zur Entomologie*, Bd 5 (3/4) : 245–.

—. 1965. Die Schädlinge und ihre Nährpflanzen. *Allg. Forst- u. Jagdztg.*, 136 (1) : 10–22.

MULLER, H. 1939. Zur Frage des Zuwachses der Sitkafichte in Schleswig. *Zeitschr. f. Forst- u. Jagdwesen*, 71 : 404–411.

MURRAY, J. S. 1954. Two diseases of spruce under investigation in Great Britain. *Forestry*, 27 : 54–62.

OHNESORGE, B. 1959. Die Massenvermehrung der Sitkalaus in Nordwestdeutschland. *Forstarchiv.*, 30 : 73–.

OKSBJERG, E. 1956. Sommervejret 1955 paa en midtjydsk lokalitet og tørkens virkning paa parceller med tidligt- og sentudspringende rødgraner. *Dansk Skovforenings Tidsskr.*, 41 : 273–302.

OUDEMANNS, TH. C. 1935. Het voorkomen van Dendroctonus micans Kugel. op Schovenhorst. *Ned. Boschbouw. Tijdschrift.*, 8 : 444–446.

PEACE, T. R. 1962. *Pathology of trees and shrubs*. Oxford.

PETERSEN, B. BEJER. 1952. Hylesinus micans, artens utbredelse og en oversigt over dens optraeden i Danmark. *Dansk Skovforenings Tidsskr.* 37 : 299–322.

—. 1962. Peak years and regulation of numbers in the aphid, *Neomyzaphis abietina* Walker. *Oikos* 13(1); 1962: 155–168.

RISHBETH, J. 1951. Observations on the biology of Fomes annosus. *Annals of Botany*, NS : XIV (55), 365–383; XV (57), 1–21; XV (58), 241–246.

RÜHM, W. 1954. Der Riesenbastkäfer und seine Bekämpfung. *Merck-Bl. Beiträge zur Schädlingsbekämpfung.* Folge 2.

—. 1956. Die Auswirkungen der Bekämpfung des Dendroctonus micans durch Mobe T. *Ibid*, Folge 1.

SCHIMITSCHEK, E. und WIENKE, E. 1963. Untersuchungen über die Befallsbereitschaft von Baumarten für Sekundärschädlinge. *Z. f. angew. Entomologie*, 51 : 219–257.

SCHIMITSCHEK, E. 1964. Grundsätzliche Betrachtungen zur Frage der ökologischen Regelung. *Z. f. angew. Entomologie*, 54 (1/2) : 22–48.

SCHOBER, R. 1951. Zum Einfluss der letzten Dürrejahre auf den Dickenzuwachs. *Forstwiss. Centralbl.*, 70 : 204–228.

—. 1955. Die Ertragsleistung der Nadelhölzer in Grossbrittanien und in Deutschland. *Forstwiss. Centralbl.*, 74 (1/2) : 36–59.

—. 1962. Die Sitkafichte. *Mitt. d. Niedersächs. forstl. Versuchsanstalt*, 24/25 : 230 pp.

SCHWAPPACH, A. 1915. Das Verhalten der Picea sitchensis und Picea excelsa in Schleswig-Holstein. *Zeitschr f. Forst-u. Jagdw.*, 47 : 423–426.

SCHWEROTFEGER, F. 1957. *Die Waldkrankheiten*. Paul Parey, Berlin.

SEVERIN, G. 1902. L'invasion de l'hylésine geánte. *Bull. Soc. For. Belg.*, 9; 145–152.

SIEBENBAUM. 1957. Die Sturmwürfe vom 21/22 Januar, 1956. *Bauernblatt v. 2 u.* 30.

STOCKER, O. 1947. Probleme der pflanzlichen Dürreresistenz. *Die Naturwissenschaften*, 34. Berlin u. Göttingen.

—. 1951. Kälte und dürrefeste Pflanzen. *Die Umschau in Wissenschaft und Technik*, 20/22; p. 679.

THAARUP, P. 1953. *Klitplantagerne 100 aar efter plantnings begyndelse*. København.

THALENHORST, W. 1953. Die Borkenhäferkatastrophe in Deutschland. *Zeitschr. f. Pflzkr., Pflzpath. u. Pflzschutz* 60 (1) : 15–19.

THOMSEN, M. 1943. Angreb af Tomicus chalcographus paa unge sitkagraner, rødgraner og Douglas graner. *Forstl. Forsøgsv. i Danmark* XV, 199–208.

WITTICH, W. 1943. *Die heutigen Grundlagen der Holzartenwahl*. M. und H. Schaper, Hannover.

WOOD, R. F. 1955. *Studies of north west American forests in relation to Silviculture in Great Britain.* Forestry Commission Bulletin 25 : pp. 42. H.M.S.O. London.

ZWÖLFER, W. 1957. Ein Jahrzehnt forstentomologischer Forschung, 1946–1956. *Zeitschr. f. angew. Entomologie*, 40 : 422–430.

Plate 1. DENDROCTONUS MICANS. Entrance tunnels of the Great Spruce bark-beetle, *Dendroctonus micans*, at base of 60-year-old Sitka spruce in a mixed stand on podzolized outwash sands, said to have been formerly cultivated. Such unadulterated resin indicates that breeding has not begun, or has failed.

Karlum Revier, Abteilung (Compartment) 309. N.W. Schleswig-Holstein, Germany.

Plate 2. DENDROCTONUS MICANS. Brood chamber of the Great Spruce bark-beetle, *Dendroctonus micans*, near base of 60-year-old Sitka spruce in mixed stand on podzolized outwash sands. These well-grown larvae—some of which have slipped down during examination—are presumably derived from eggs laid in summer, 1963.

Karlum Revier, Abteilung 309. N.W. Schleswig-Holstein, Germany.

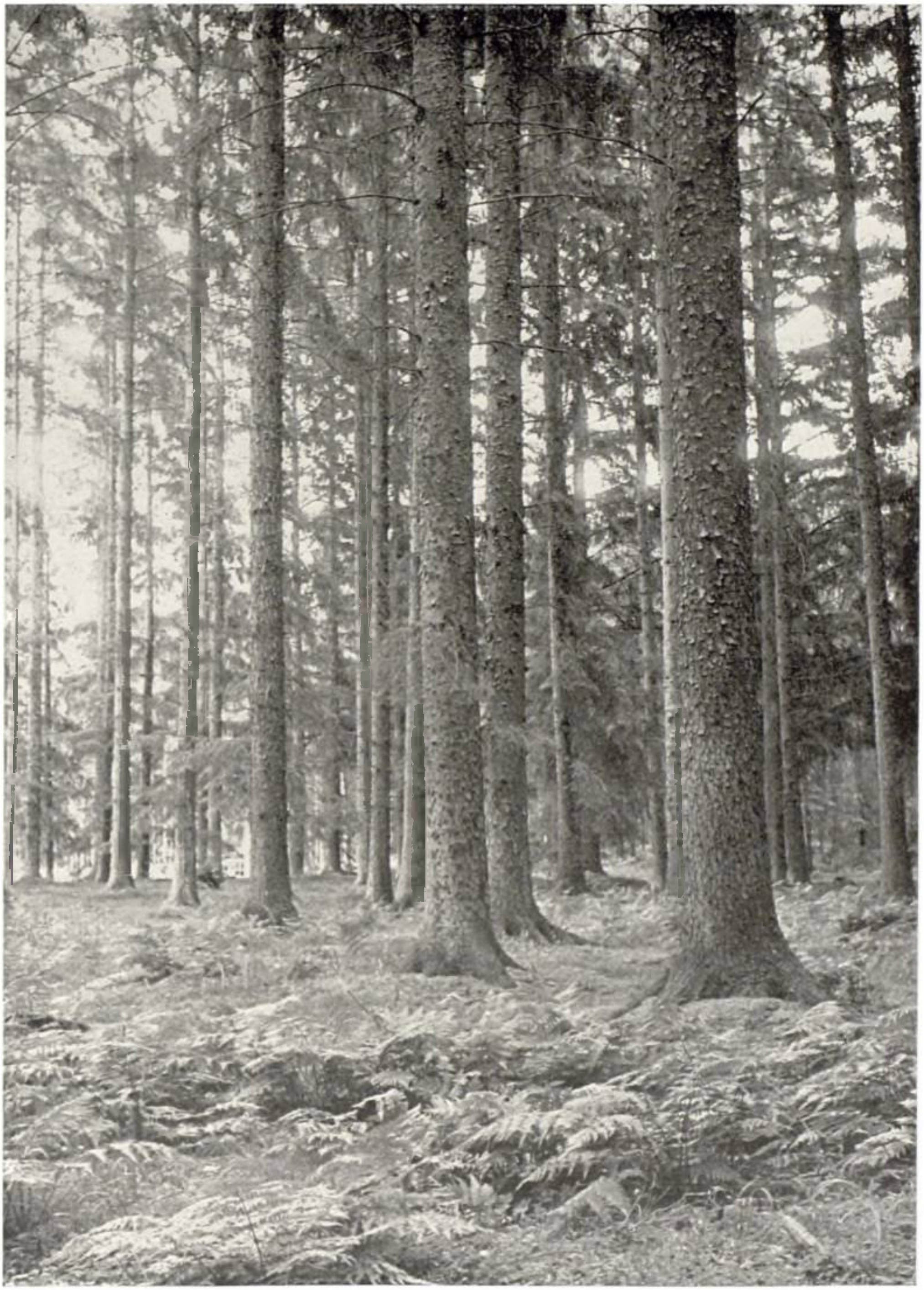


Plate 3. SITKA SPRUCE IN JUTLAND. The finest mature stand of Sitka spruce in Denmark and one of the best in Europe, growing on *ca* 40 cm fen peat over sand near the E. Jutland coast. In 1952, at age 62, the mean height was 32 m (105 feet), volume 619 m^3/ha (6,950 hoppus feet per acre) (locally more), current annual increment 17 m^3/ha (191 hoppus feet per acre). Slight attack by *Dendroctonus micans* followed other injuries a few years ago.

Mejlgaard, Afdeling (Compartment) 210, Djursland. East Jutland, Denmark

Plate 4. DENDROCTONUS MICANS ETC., ON SITKA SPRUCE. 53-year-old Sitka spruce with occasional oak on ill-drained flat: *ca* 1 m sand over retentive silty clay, with fluctuating water table. Sporadic attack some years ago by the Great Spruce bark-beetle, *Dendroctonus micans*, was followed by storm damage, February 1962: honey fungus also prevalent. The ground has just been replanted. Forstamt Rantzau, Abteilung 81. S. Schleswig-Holstein, Germany.

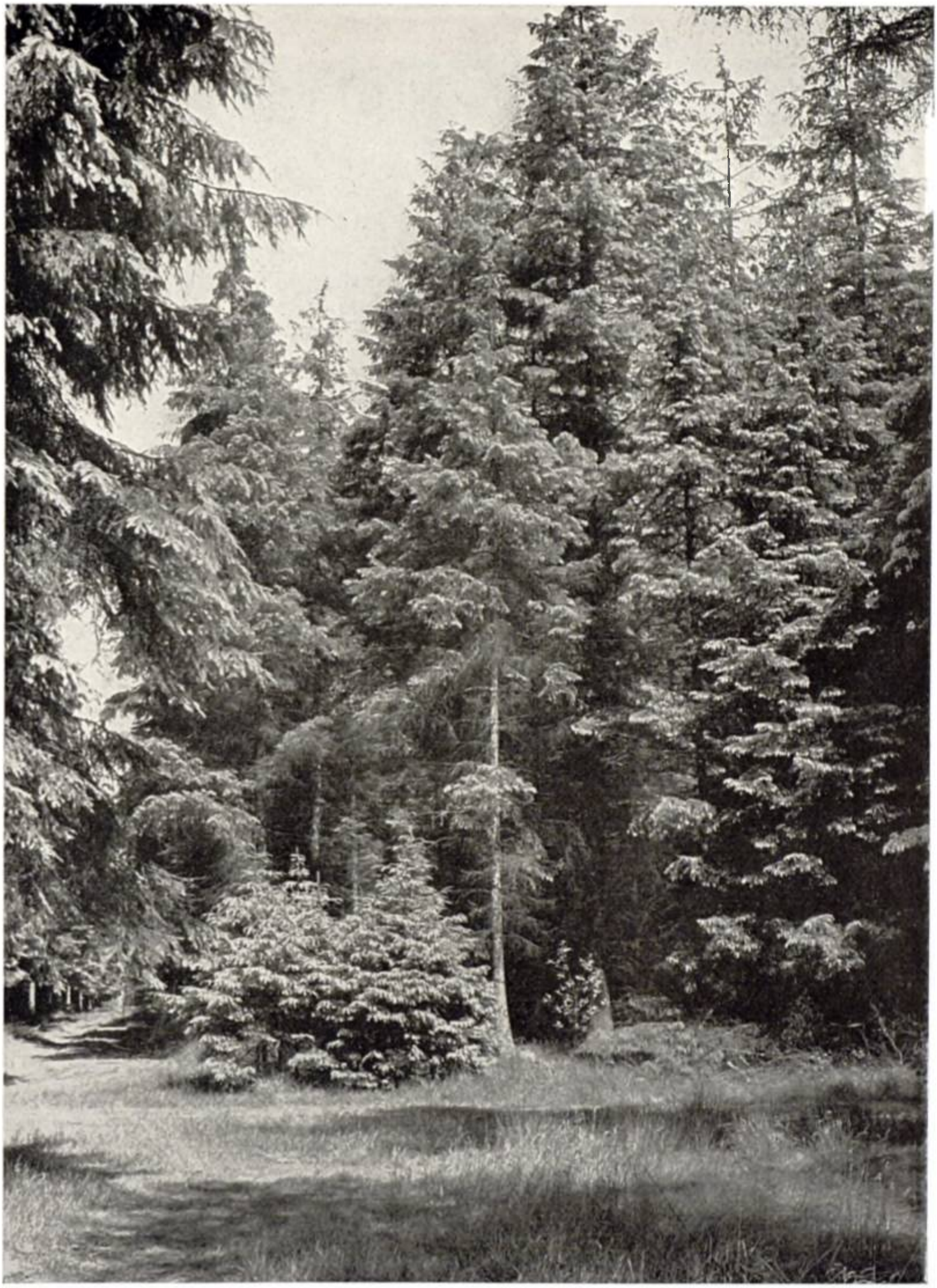


Plate 5. DENDROCTONUS MICANS ON SPRUCE. On right a mixed stand of Norway and Sitka spruce, 55 years old, on fluvio-glacial outwash sand. The Great Spruce bark-beetle, *Dendroctonus micans*, affected this stand several years ago, mainly in 1959; outbreaks in southern Schleswig-Holstein were much less serious than in the north.

Forstamt Rantzau, Abteilung 144. S. Schleswig-Holstein, Germany.

Plate 6. Break-up of 50/60 Years Sitka Spruce. Dead Sitka spruce with honey fungus, *Armillaria mellea*, near margin of 53-year-old stand affected also by sporadic attacks of Great Spruce bark-beetle, *Dendroctonus micans*, and severe storm damage in February 1962. Site an ill-drained flat with *ca* 1 m sand over retentive material, giving a sharply fluctuating water table.

Forstamt Rantzau, Abteilung 81. S. Schleswig-Holstein, Germany.

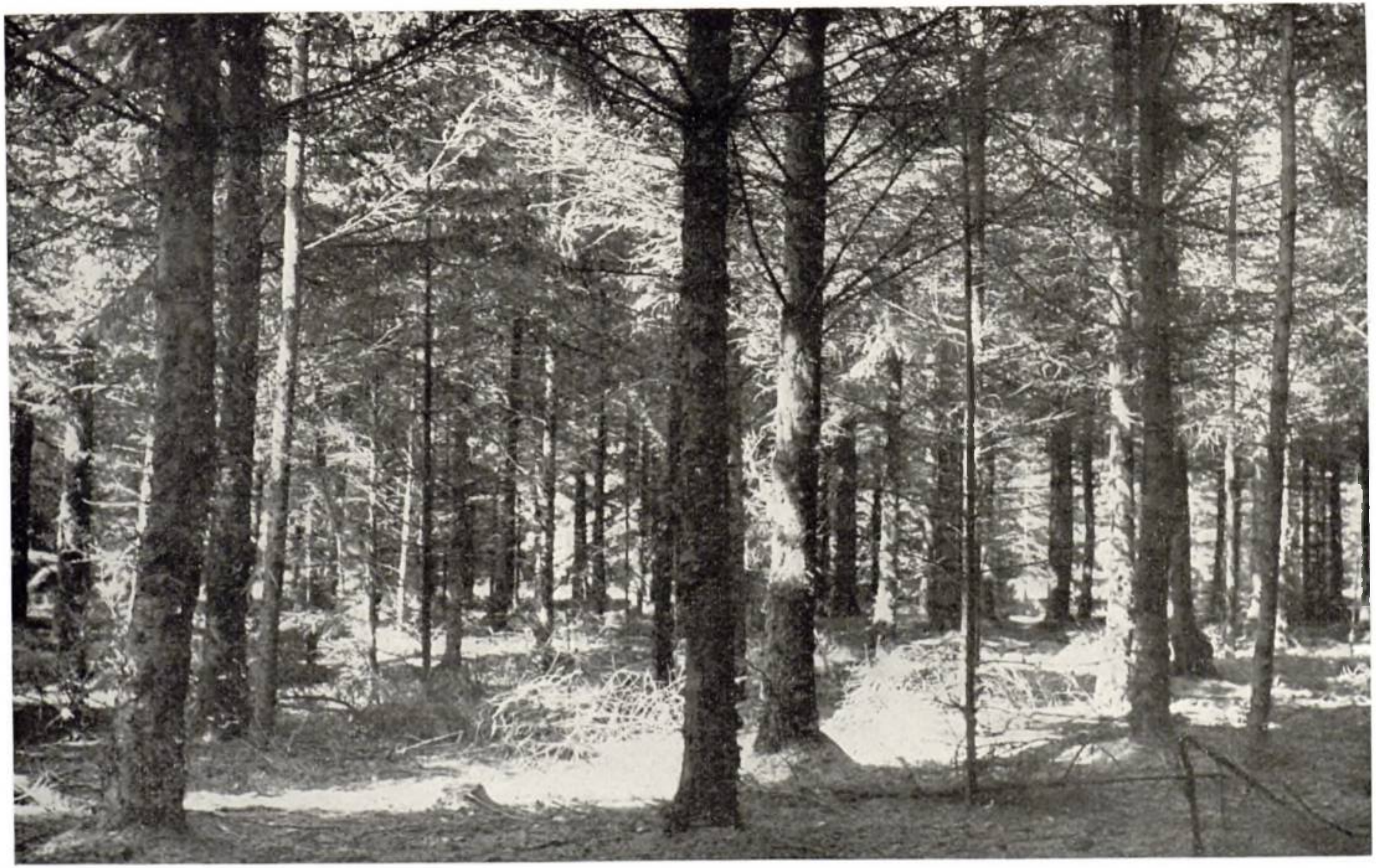


Plate 7. DENDROCTONUS MICANS ON SITKA SPRUCE. 33-year-old Sitka spruce, on poor glacial outwash sand, affected in 1956 by Great Spruce bark-beetle, *Dendroctonus micans*, and by Elatobium in 1957. Note the coarse branching: among other things, pruning and brashing wounds are said to attract this beetle.

Kropp Revier, Forstamt Rendsburg, Schleswig-Holstein, Germany.

Plate 8. Natural Regeneration of Spruce. Norway spruce and Scots pine, with abundant natural regeneration of spruce, near Heidbunge Forsthaus, growing on poor glacial outwash sands formerly cultivated.

Kropp Revier, Forstamt Rendsburg, Schleswig-Holstein, Germany.

Plate 9. SPRUCE NATURAL REGENERATION. Natural regeneration of Norway spruce, *Picea abies*, in an opening in a 70-year-old mixed stand with Scots pine on poor glacial outwash sand. *Fomes annosus* and storm damage have drastically thinned the stand in recent years. Kropp Revier, Forstamt Rendsburg, Schleswig-Holstein, Germany.

Plate 10. AFFORESTATION IN SCHLESWIG HOLSTEIN. Remnants of a first generation, 70-year-old, stand of Norway spruce and Scots pine on glacial outwash, formerly cultivated. *Fomes annosus* and storm damage have greatly reduced the stand, but there are some clumps of spruce regeneration.

Kropp Revier, Forstamt Rendsburg. Schleswig-Holstein, Germany.

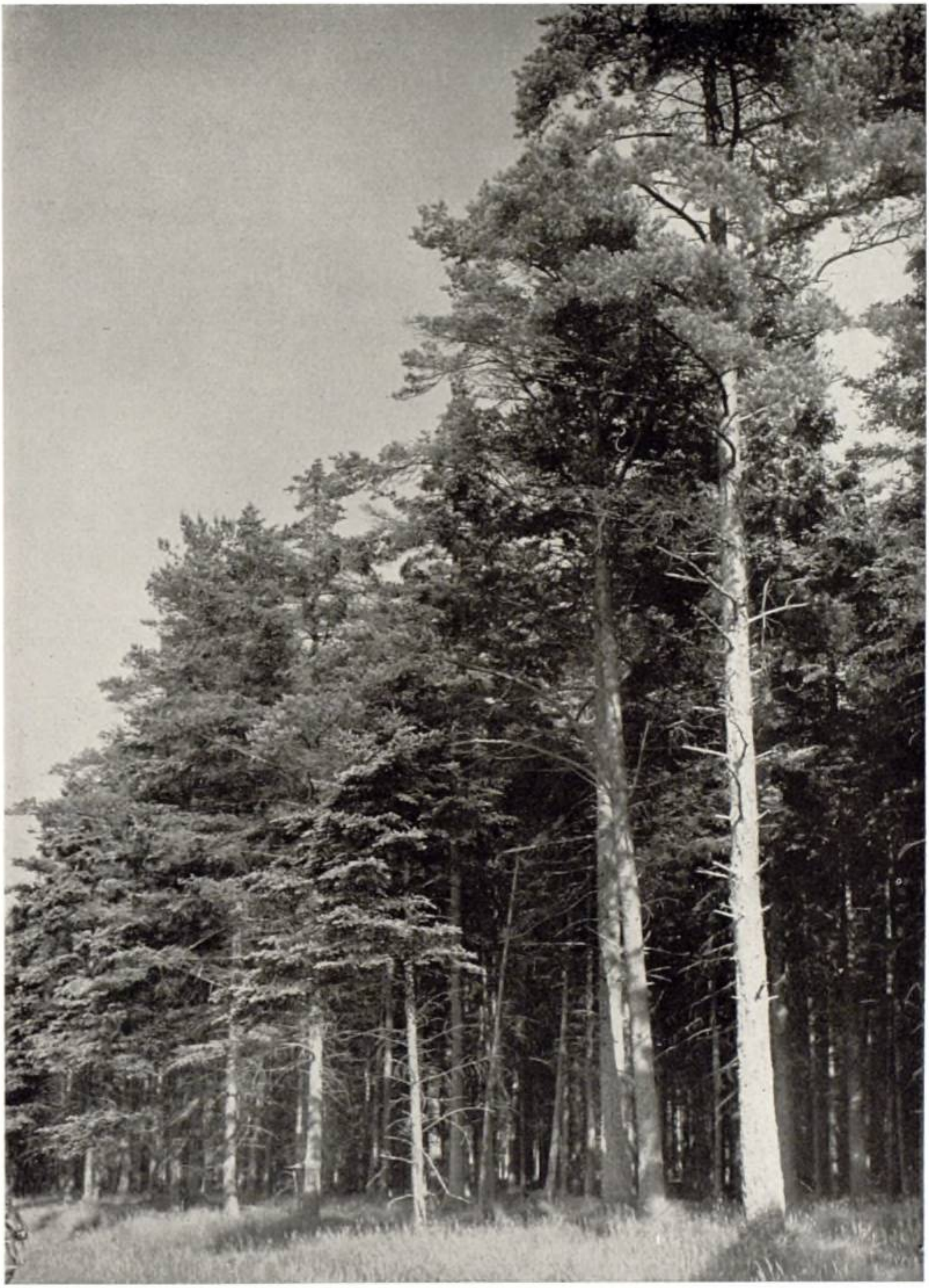


Plate 11. Dendroctonus micans on Spruce. Mixed stand of 57-year-old Scots pine and Norway spruce on extremely poor glacial outwash sands. Sporadic attacks by *Dendroctonus micans* occurred a few years before, on spruce only.

Kropp Revier, Forstamt Rendsburg, Schleswig-Holstein, Germany.

Plate 12. TETROPIUM FLAVUS. Galleries of Spruce long horn beetle, *Tetropium flavus*, about breast height (1–2 m) on trunk of 60-year-old Norway spruce. *Tetropium* spp. often follow attacks of *Dendroctonus micans*, which affects trees which are only slightly, if at all, diseased.

Karlum Revier, Abteilung 309. N.W. Schleswig-Holstein, Germany.

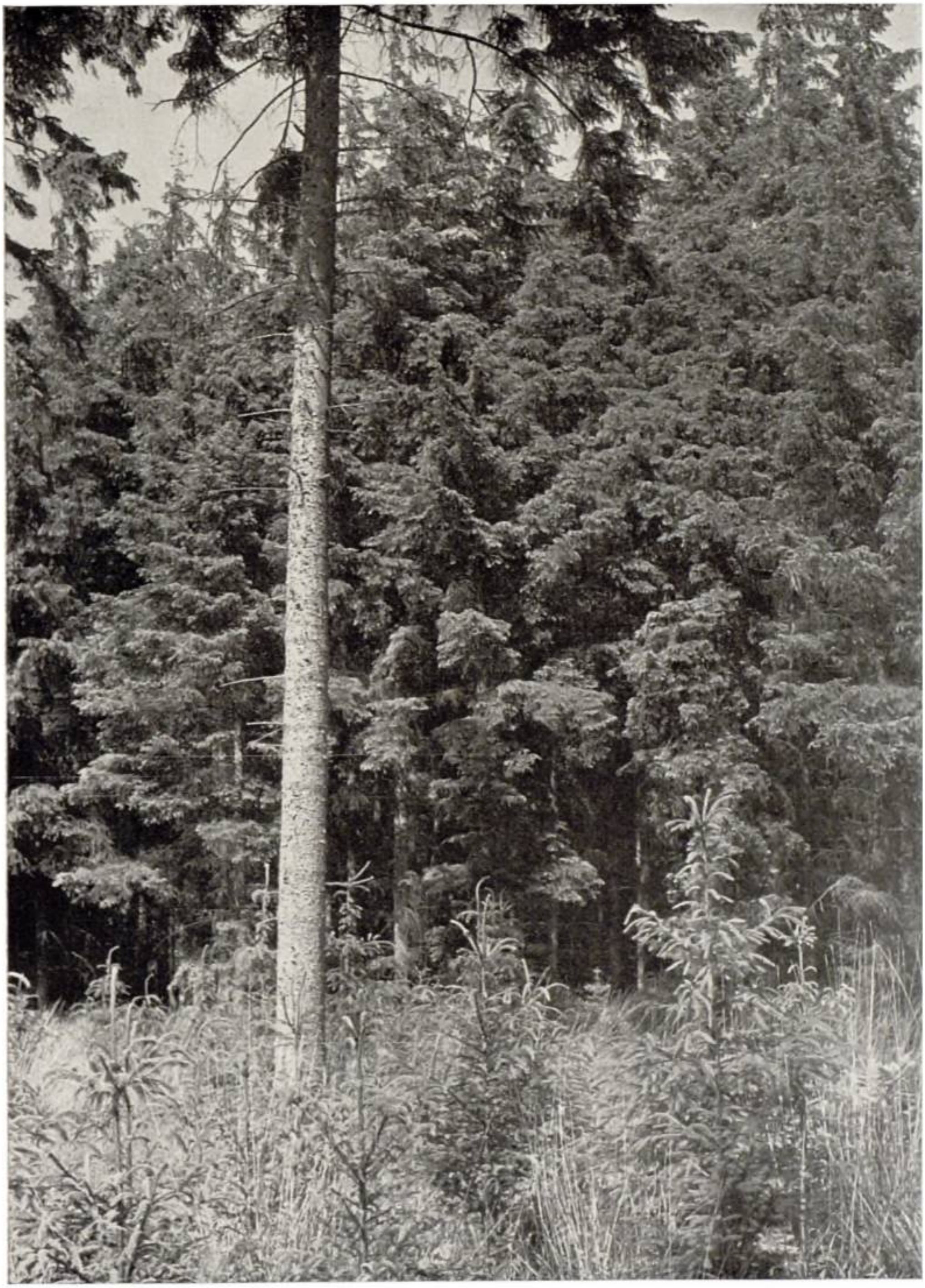


Plate 13. SITKA SPRUCE IN DENMARK. West edge of good stand of 45-year-old Sitka spruce on sandy podzol near the coast. *Dendroctonus micans* did not attack this stand when several other Sitka spruce woods in the locality were affected a few years ago.

Søstrup, Afdeling 103, Djursland, East Jutland, Denmark.

Plates 14 and 15. Sun Scorch on Sitka Spruce in Denmark. Death of 40/45 year Sitka spruce, following severe sun scorch at south margin, abruptly exposed after storm damage in adjoining stand. An outbreak of *Dendroctonus micans*, dating from 1956, has subsided and the wood (Norway and Sitka spruce, with some Douglas fir), with thinnings suspended, is fully stocked.

Hannenav Skov, Falster, Denmark.

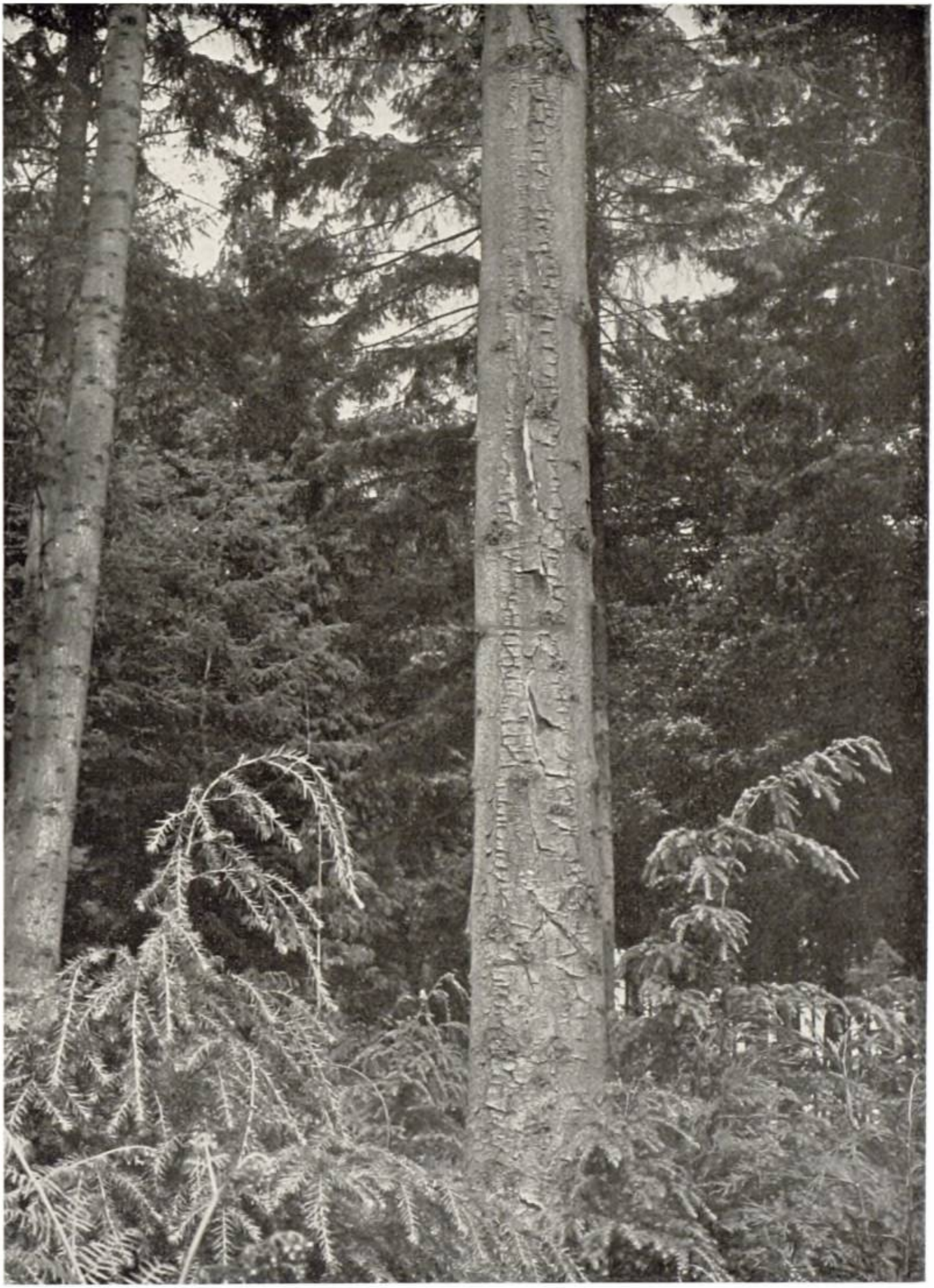
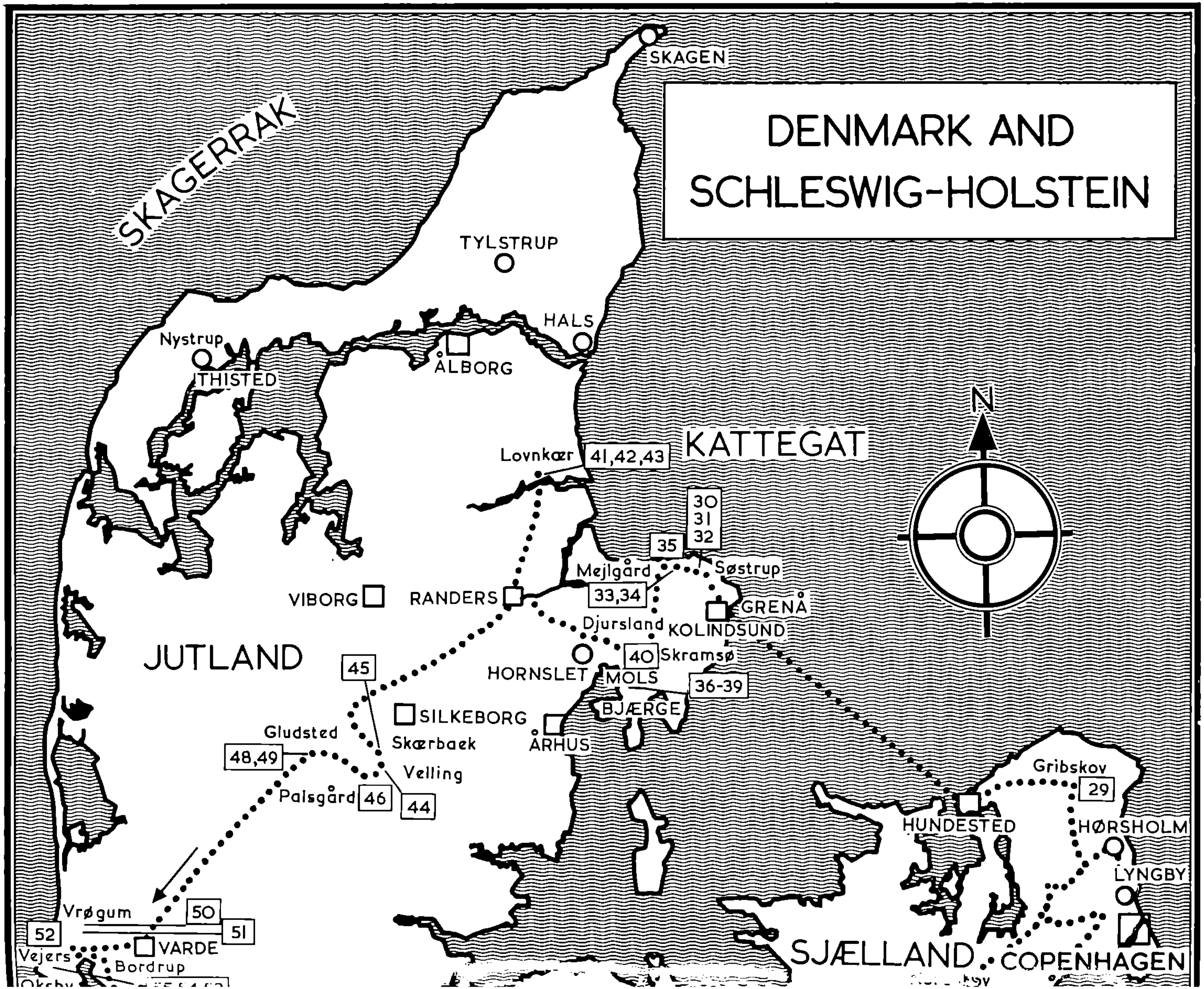


Plate 15. See plate 14 opposite.


DENMARK AND
SCHLESWIG-HOLSTEIN
SKAGEN
SKAGERRAK
TYLSTRUP
HALS
Nystrup
ÅLBORG
THISTED
N
KATTEGAT
Lovnkær
41,42,43
30
31
32
35
Mejlgård
Søstrup
33,34
GRENÅ
VIBORG
RANDERS
Djursland
KOLINDSUND
JUTLAND
40
Skramsø
45
HORNSLET
MOLS
36-39
BJÆRGE
SILKEBORG
ÅRHUS
Gludsted
Skærbaek
48,49
Velling
Gribskov
29
Palsgård
46
44
HUNDESTED
HØRSHOLM
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COPENHAGEN

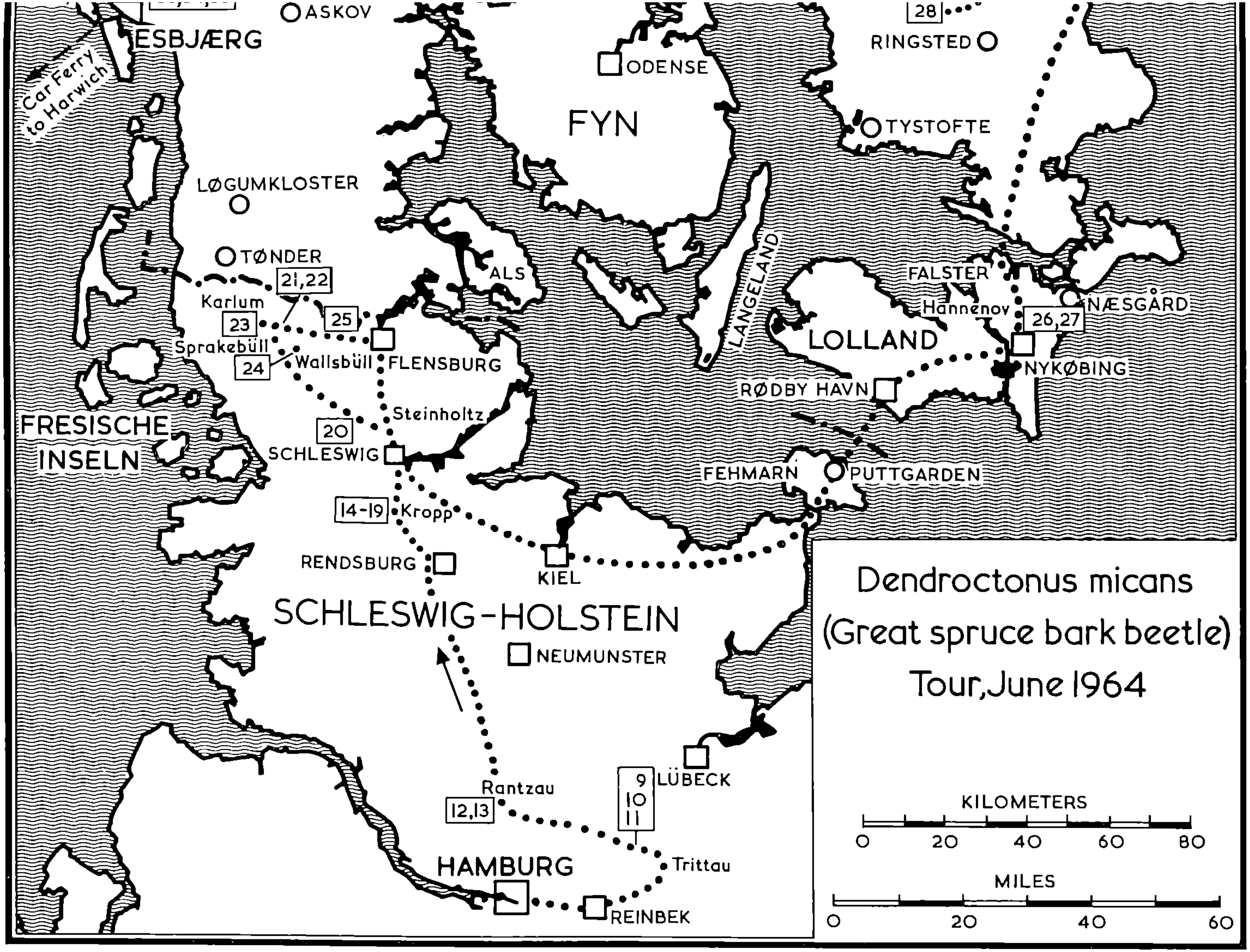


Plate 16. Map of Tour to study Dendroctonus Micans, June, 1954.

Plate 17. PODZOL PROFILE, NORTH SCHLESWIG-HOLSTEIN. The profile shows an old heath podzol overlain by blown sand, *ca* 30 cm (12 ins.) thick. The partly eroded, humose A1 layer of the old podzol can be discerned as a slightly oblique dark line, right centre: below lie 25/30 cm (10 to 12 ins.) leached fine sand (A2); then a very compact, dark, humus-iron B1, over ferruginous compact coarse sand dating from the Saale glaciation. 62-year-old Silver fir (*Abies alba*) and Sitka spruce (*Picea sitchensis*) are growing on this site.
Karlum Revier: Flensburg Distrikt, Schleswig-Holstein, Germany.

Plate 18. DENDROCTONUS MICANS ON SITKA SPRUCE. South edge of 40/45-year-old mixed stand of Norway and Sitka spruce exposed by storm damage, 1956, and consequent clearance. An outbreak of *Dendroctonus micans*, dating from 1956, later subsided and there is no present activity. Several marginal Sitka spruce are badly affected by sun scorch.

Hannenav Skov, Falster, Denmark.

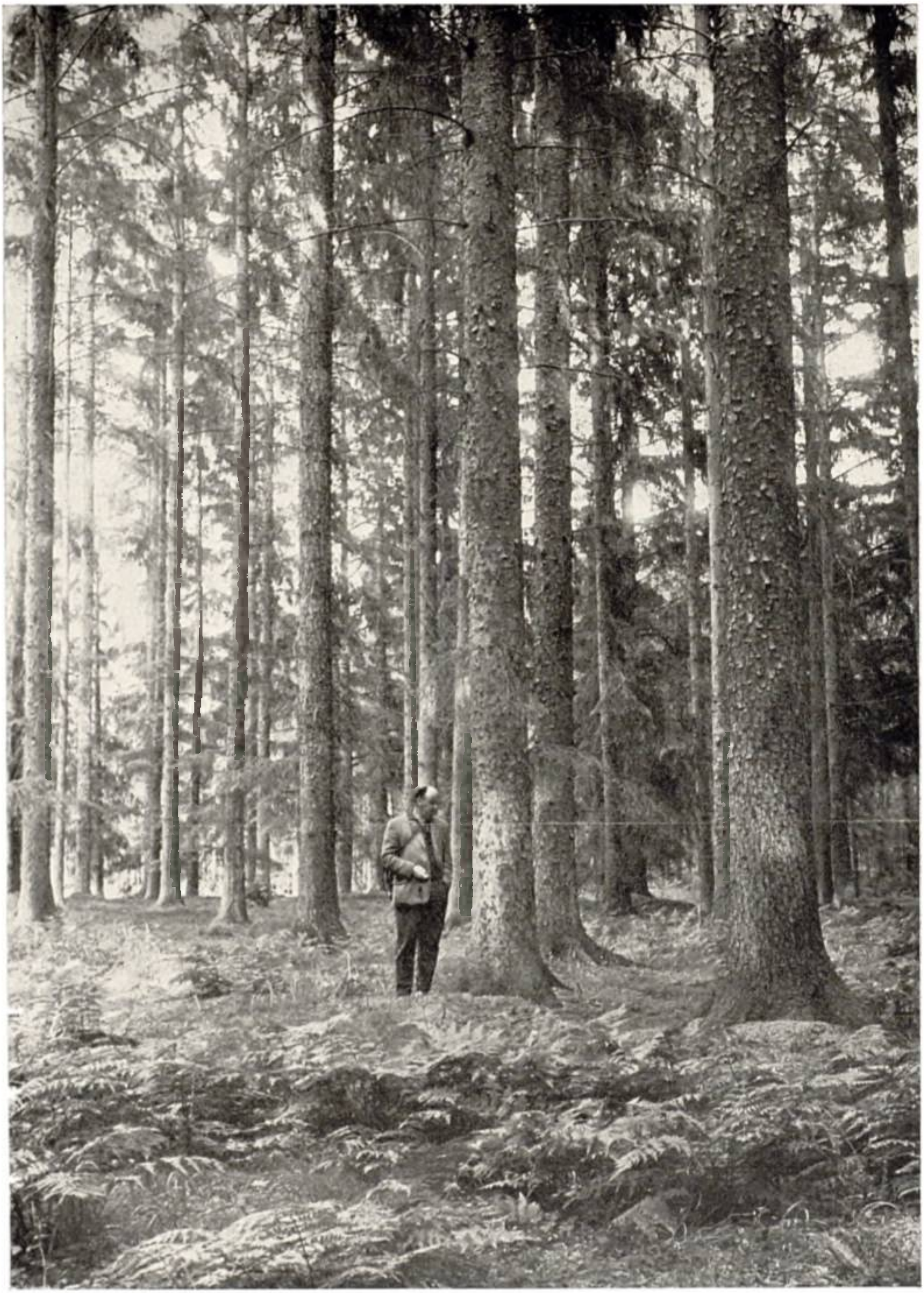


Plate 19. SITKA SPRUCE IN JUTLAND. The finest mature stand of Sitka spruce in Denmark and one of the best in Europe, growing on *ca* 40 cm (16 ins.) fen peat over sand near the East Jutland coast. In 1952, at age 62, the mean height was 32 m (105 feet), volume 619 m³/ha (6,950 hoppus feet per acre) (locally more), current annual increment 17 m³/ha (191 hoppus feet per acre). Slight attack by *Dendroctonus micans* followed other injuries a few years ago.

Mejlgaard, Afdeling 210, Djursland, East Jutland.

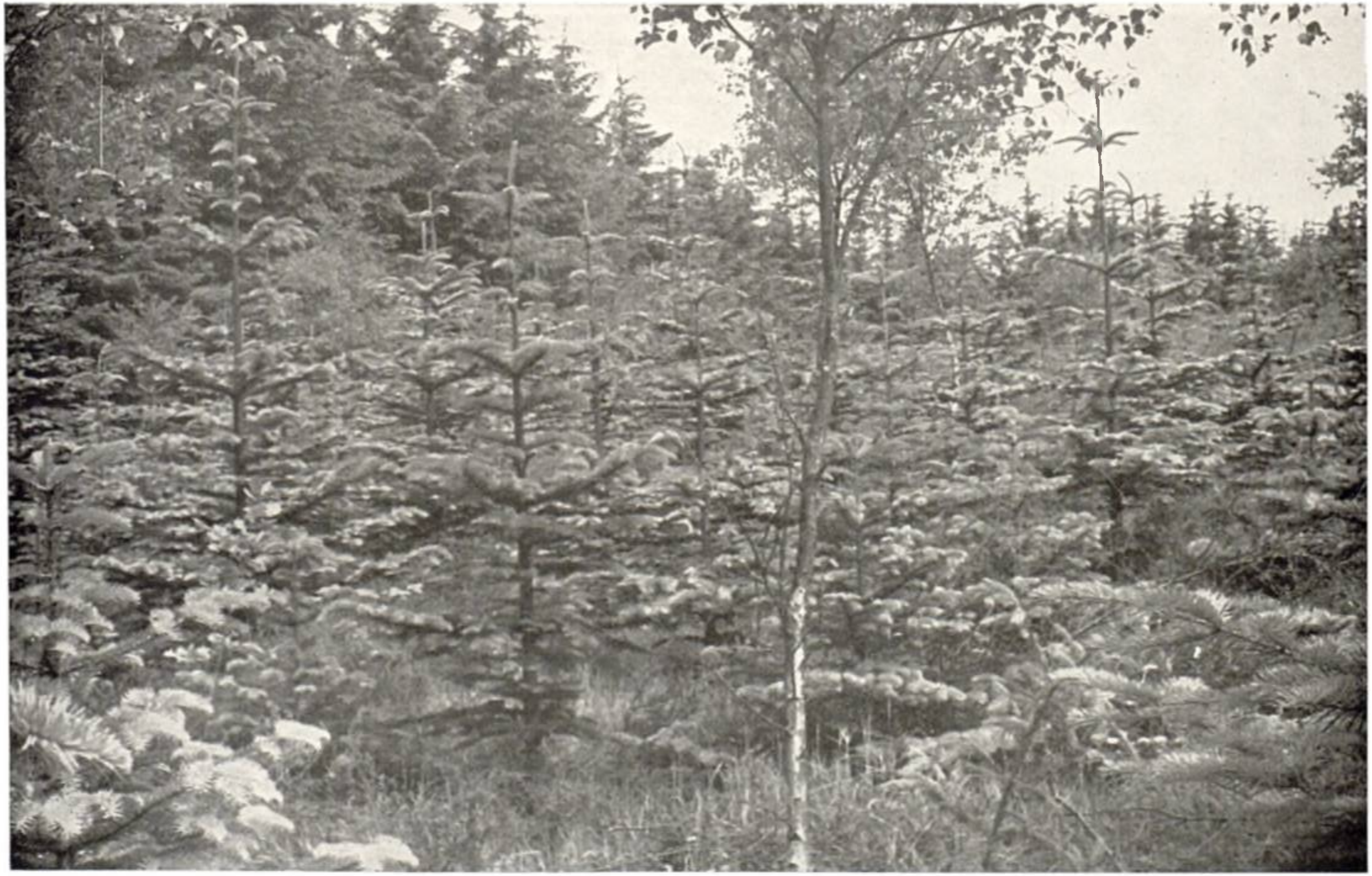


Plate 20. SILVER FIRS IN JUTLAND. Nine-year-old plantation of Nordmann and Noble firs (*Abies nordmanniana*, *A. procera*), a first planting on land previously carrying open birch and oak scrub. The young stand is surrounded by older stands of spruces, pine, Douglas fir and it was partly the damage by fungi (*Fomes annosus*) and insects (*Dendroctonus micans*) in these which prompted the trial of *Abies* spp.

Mols Bjaerge, Djursland, East Jutland, Denmark.

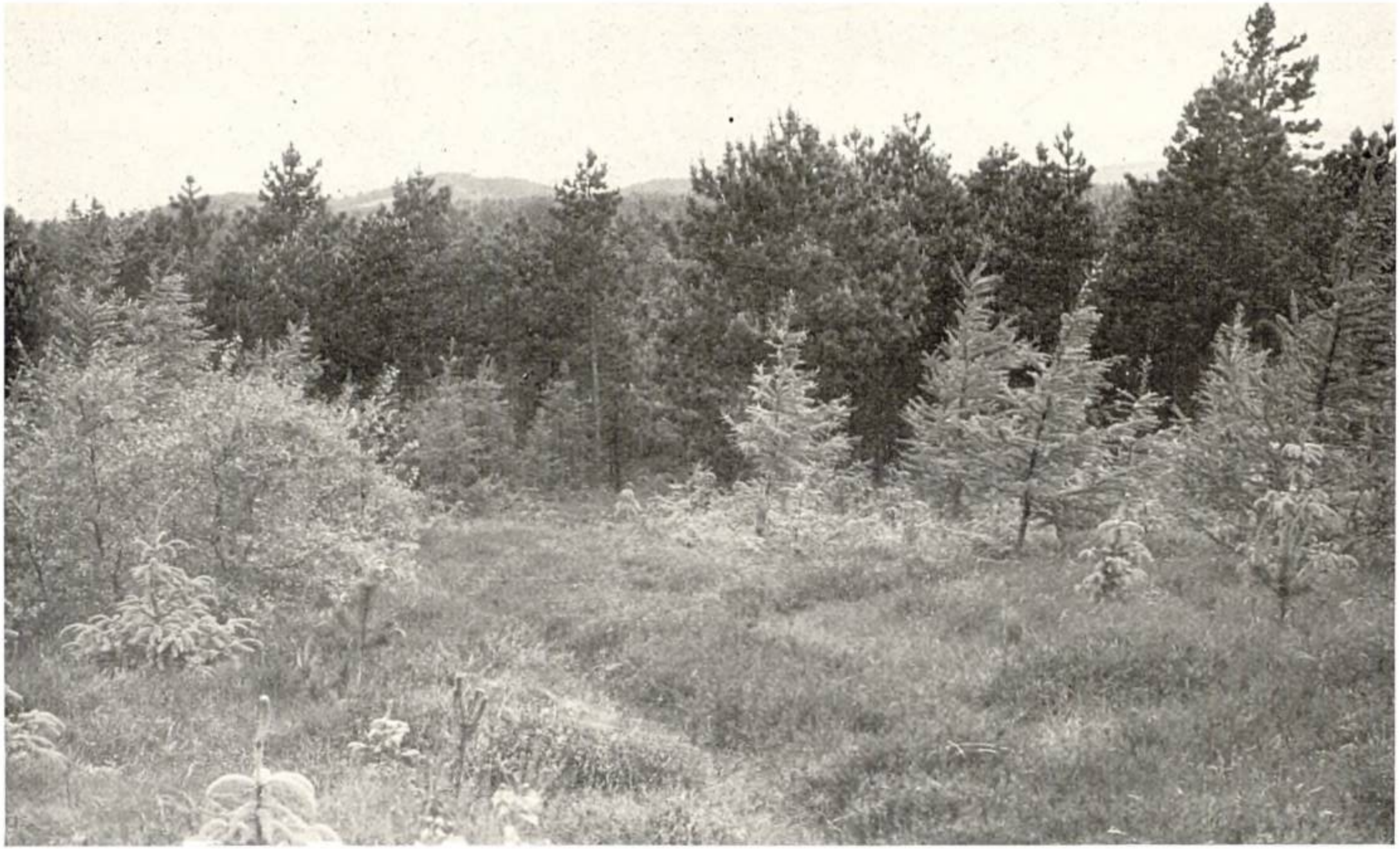


Plate 21. Black (Austrian) Pine in Jutland. 36-year-old *Pinus nigra* var. *austriaca* on sandy moraine near the coast on the Djursland peninsula of East Jutland. In the foreground the large gap on the north slope of the ridge was caused by frost—perhaps associated with *Brunchorstia pinea*—about 10 years ago. On the south slope no deaths occurred. The gap was replanted with Japanese larch 8 years ago.

Mols Bjaerge, Djursland. (Danish Heath Society).

Plate 22. BLACK (AUSTRIAN) PINE IN JUTLAND. Discussing the choice of species for the afforestation of Jutland's heaths and coastal sands in a large gap caused by dieback of *Pinus nigra* nearly 10 years ago. B. BEJER PETERSEN (left—Kgl. Veterinaer og Landbohojskole, Denmark); WEST NIELSEN (Danske Hedeselskabet); and D. BEVAN (right—Forestry Commission).

Mols Bjaerge, Djursland. (Danish Heath Society property).

Plate 23. Jutland Forest House. The old Palsgaard Forest District, whose District Officer (or Skovrider) lives in the house, now includes, besides Velling and Palsgaard Forests, largely on the morainic soils of the Central Jutland Ridge, the new Gludsted heath plantations on the podzolised outwash sands west of the ridge.

Palsgaard Skovridergaard. Mid Jutland, Denmark.

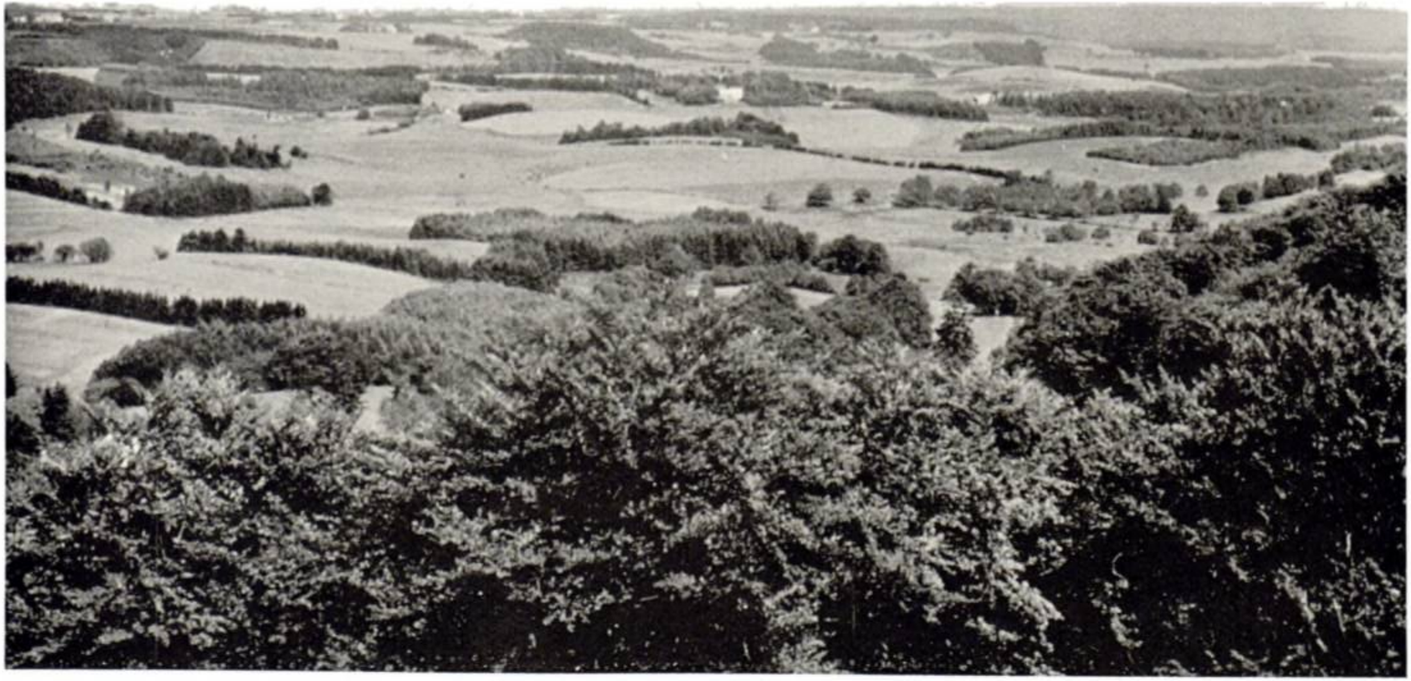


Plate 24. VIEW FROM MID-JUTLAND RIDGE. The North-South mid Jutland ridge, forming part of the great Scandinavian end moraine, separates the more fertile land of East Jutland from the poor outwash sands of the west. This view towards the west shows, first, the remnants of old indigenous beech, then some fairly good farm land (with morainic enrichment) and, beyond, the coniferous plantations on Hjølund and Gludsted heaths.

Velling-Paisgaard Skovdistrikt, Denmark.

Plate 25. DENDROCTONUS MICANS ON SITKA SPRUCE. Sitka spruce, 70 years, probably attacked by *Dendroctonus micans* high up on the stem (an unusual occurrence, but relatively frequent in recent outbreaks in Denmark). *Fomes annosus* is prevalent too in this stand, which includes some healthy, 75-year-old, silver fir (*Abies alba*). The site is near the west edge of the moraine and the soil is sandy and moderately stony.

Palsgaard Skov, Mid Jutland, Denmark.

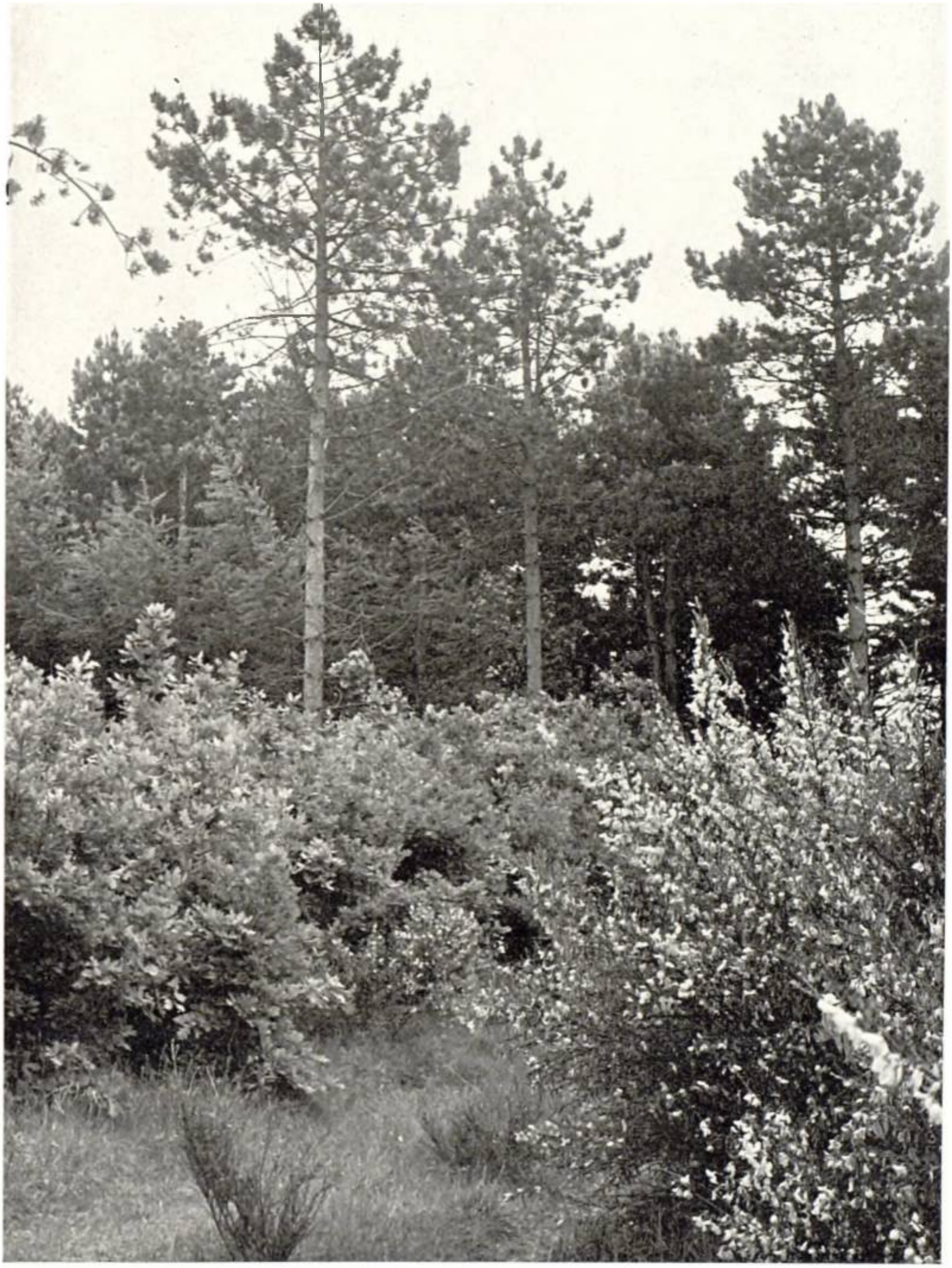


Plate 26. BLACK PINE (PINUS NIGRA) IN JUTLAND. Black (probably Austrian) pines surviving well in an open sunny position on sandy soil about 4 miles from the coast on the Djursland peninsula, East Jutland. The adjacent spruce stand, seriously affected by *Dendroctonus micans* and *Fomes annosus*, was cleared a few years before.

Skramsø, Djursland, East Jutland, Denmark.

Plates 27 and 28. SILVER FIR AND SPRUCE IN JUTLAND. This mixed stand of 70–75-year-old Silver fir (*Abies alba*) and Sitka spruce (*Picea sitchensis*) was established on glacial moraine near the west edge of the mid-Jutland ridge as a first afforestation on poor cultivated land. The spruce has suffered from moderate *Dendroctonus micans* and severe *Fomes annosus* attacks, contrasting with the healthy silver fir.

Palsgaard Skov, Mid Jutland, Denmark.

Plate 28. See plate 27 opposite.

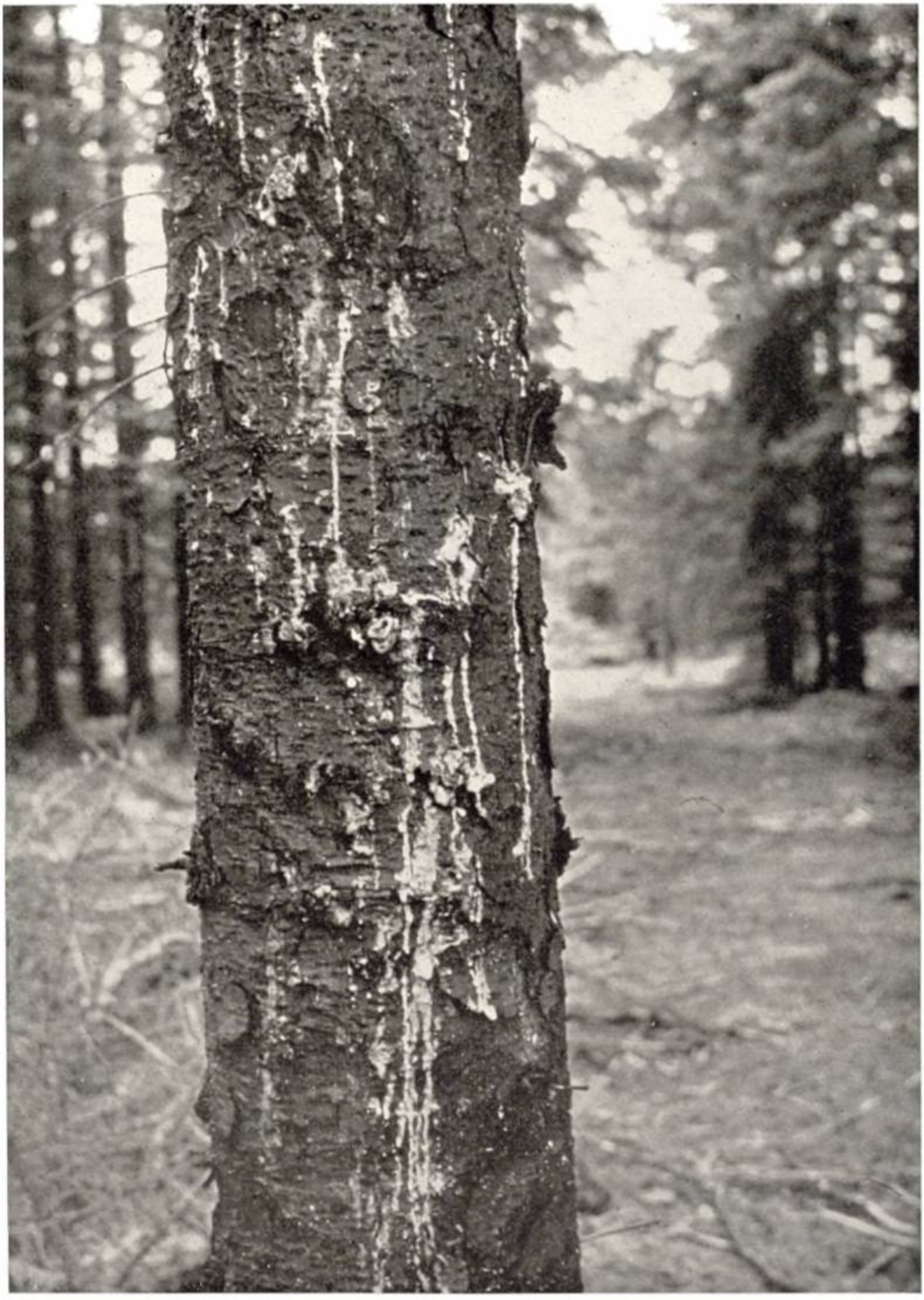


Plate 29. DENDROCTONUS MICANS ON SITKA SPRUCE. Attacks (some repulsed) by *Dendroctonus micans* on 50/55 year-old Sitka spruce on coastal sand about 4 miles from the sea. Attacks originated after the warm dry summer of 1947; a few years ago serious storm damage, resulting from the removal of dead trees, led to a clear cut of the western half of the stand.

Vrøgum Plantage, West Jutland, Denmark.

Plate 30. DENDROCTONUS MICANS ON SITKA SPRUCE. West edge of 50/55-year-old Sitka spruce (*Picea sitchensis*) exposed in 1962, after clear fall in part severely damaged by *Dendroctonus micans* and storm. *Dendroctonus* is still breeding on a modest scale in the residual stand, some trees showing much resin flow. This site is about 4 miles from the west coast and the soil is blown sand over more retentive material.

Vrøgum Plantage, West Jutland, Denmark.

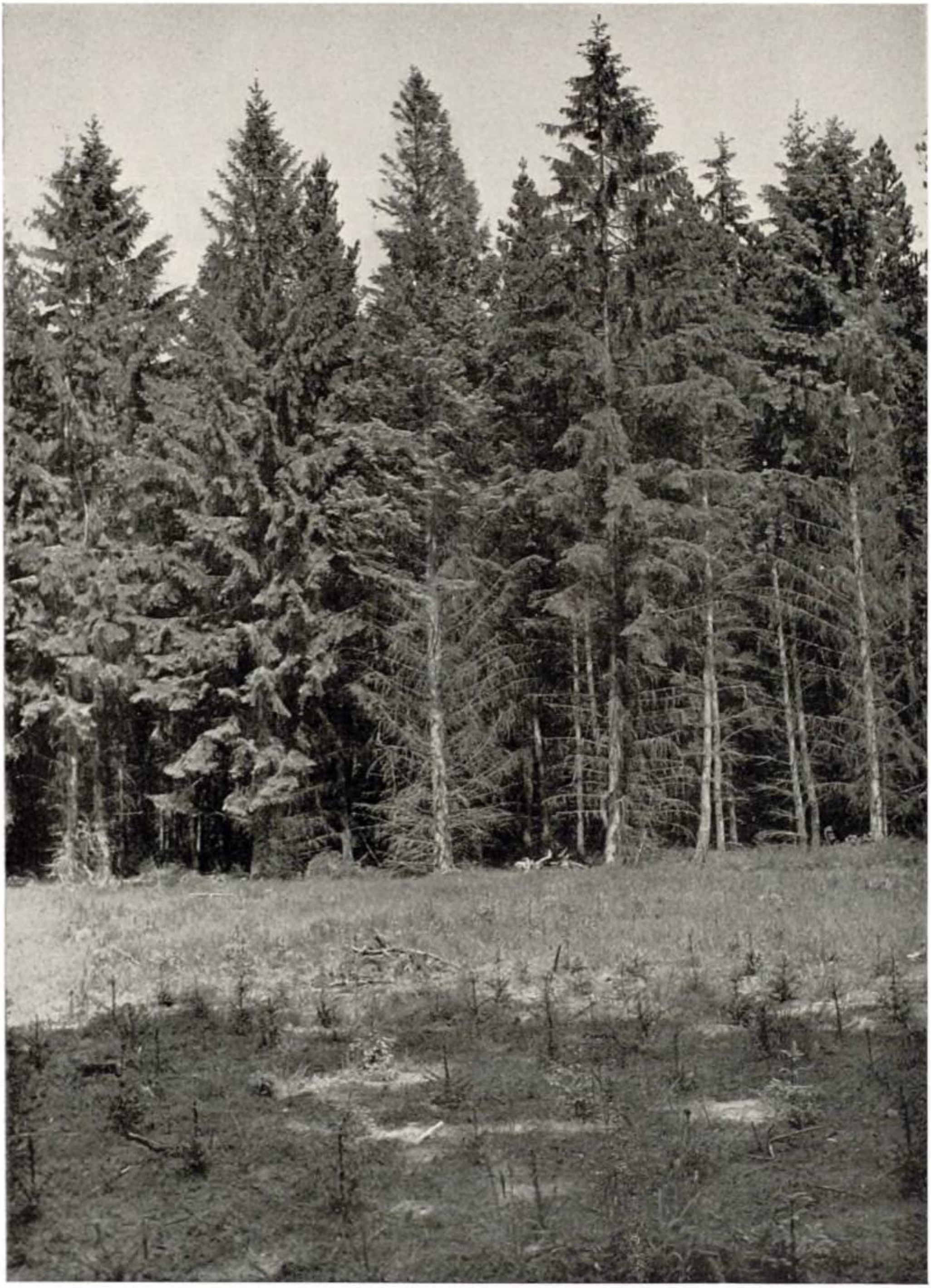


Plate 31. DENDROCTONUS MICANS ON SITKA SPRUCE IN DENMARK. Sitka spruce, 45 years old, viewed from large clearing resulting from attack by *Dendroctonus micans* in 1959 and subsequent storm damage. Soil is a weakly podzolised sand.

Søstrup, Afdeling 13, Djursland, East Jutland, Denmark.

Appendix 1

NOTES ON SITES

A: GELDERLAND PROVINCE OF HOLLAND

The numbers used here agree with those in Table 1, where the sites are listed with only the briefest of notes; also, where appropriate, with the numbers on the map, plate 16.

Tuesday, 2nd June

1. NUNSPEET : de Ihorst. A small stand of c. 48 years Sitka spruce, which, apart from a few trees at the S.W. end, was recently acquired by the State Forest Service from Dr. H. van Vloten, who had previously parted with most of the rest of his woodlands: probably planted to protect adjoining cultivated land from wind and wind erosion of the fine sandy soil, the Zuider Zee being 4 km distant to W.N.W. The soil is a weak podzol and root exploitation by spruce seemed good: *Deschampsia flexuosa* is dominant in the ground flora.

   Spruce growth had not been remarkably good and slight bending of tips was seen here and there. *Dendroctonus* attacked soon after the war, perhaps following the 1947 drought, but the date was not recorded. *Armillaria mellea* and *Fomes annosus* were concerned in the deaths of recent years: active *Armillaria* was detected on June 2nd, but not *Dendroctonus*. The stand was being cleared, except those trees on private land.

2. WILLEMSBOS : An avenue of mixed spruces (mostly Norway), about 50 years old, standing 2 km E.S.E. of 1. The soil showed a "double-deck" profile, with 15 cm recently blown sand over a well-formed, though shallow, heath podzol, with compact Bl(h).

   One Norway spruce showed unsuccessful attacks, with resin flow and frass at 10, 50, 240 cm above ground level: first attack also post war, but date uncertain.

3. WILLEMSBOS : Only c. 1 km. S.W. of 2 is the site of one of the two original (1935) attacks by *Dendroctonus micans* in Holland. The soil showed a strong podzol and, according to the late Dr. van Vloten (whose land it once was) the heath was deeply and thoroughly cultivated by hand and treated with phosphate before the planting of Sitka spruce about 1900. The *Dendroctonus* attack proved severe and many trees died, so that the stand was eventually cleared and replanted with Scots pine and larch (Danish seed), now 17 years old.

4. SCHOVENHORST : It was in Professor Th. C. Oudemanns' private arboretum that the very first Dutch find of *Dendroctonus* was made by a local schoolmaster in 1935. This was on *Picea orientalis*, but *P. abies*, *P. sitchensis*, *P. omorika* in the wood were affected too. The soil is derived from pre-glacial sand and examination showed a brown soil with mull, evidently of fairly good fertility. Affected trees were all cut down some years ago.

Wednesday, 3rd June

5. WOESTE HOEVE : The four sites examined today are farther from the sea, lying about 15 km N. or N.W. of Arnhem and roughly 25–30 km from the Zuider Zee. The Woeste Hoeve ('wild farm') site carried mixed conifers (Norway and Sitka spruce, Douglas fir, Scots pine, larch) planted about 1900, with a belt of pure Sitka spruce at the north west. *Dendroctonus* appeared on spruce in 1943 and the Sitka spruces were almost all removed, Norway spruce being relatively little affected. Douglas fir, now 20 years old and growing well, has replaced the pure Sitka stand on a good, deep, freely-drained sandy soil. No evidence was obtained of current *Dendroctonus* breeding.

6. HOENDERLO : Near the public entrance to Hoenderlo State Forest, attack by *D. micans* was recorded on a group of Sitka spruce (all later removed) in 1947.

7. HOENDERLO : About 500 m. N.W. of 6, a slow-growing stand of c. 40 years old Norway spruce showed attack by *Dendroctonus* in 1962, but no brood succeeded and no tree was killed. Many of the trees showed copious resin exudation (usually from nodes) which Elton considered a normal result of pruning wounds.

This Hoenderlo soil is an impoverished humus podzol, with thick A2 layer: the humus B1 at about 60 cm showed several medium thick horizontal roots in and just above it.

8. OTTERLO : A mixed 40-year-old plantation of beech and conifers (Sitka and Norway spruce, Japanese larch, Douglas fir) on the site of a former forest nursery. Tree growth has been good on this deep, reddish brown, stoneless, medium sand, formerly cultivated.

Many spruces of both species show resin flow and incipient tunnels of *Dendroctonus*, which were seen first in 1962. In 1963 a live imago was found and today, on a Sitka spruce at the north edge, fresh work and several live imagines were observed at a height of 1·5 to 2 m. The main roots of this tree on the same side showed much resin flow, but root samples brought back to Farnham failed to yield *Fomes annosus* on culture.

B : SCHLESWIG-HOLSTEIN

Monday, 8th June

9. TRITTAU : Forstamt Trittau, including sites 9, 10, 11, is situated in the south east of the province, a little north of Reinbek and only 25 km E.N.E. of Hamburg. Ecologically it is widely different from the forests in the north west visited on Tuesday afternoon and Wednesday. In the first place it stands on the end moraine of the last, or Weichsel, glaciation, not on outwash or dune sands, typical of western Schleswig-Holstein. Secondly, the climate is drier, with less pronounced maritime influence. Thirdly (and due to these physical factors) Sitka spruce has been planted very sparingly and, therefore, *Dendroctonus* attacks have been sporadic and light, the insect being first detected in 1957, after severe *Neomyzaphis* defoliation on a group of trees near the Forstamt.

The stand first visited, in Cpt. 40, is on hummocky, morainic land, with a deep sandy soil, moderately podzolised: it was said that the land had always been under forest—formerly pine, spruce and beech. This was a 47-year-old mixture of Sitka and Norway spruce of good height growth and forms, but thin in the crown, due in large measure to soil dryness, *Neomyzaphis* and neglect of thinning before 1951.

Fomes annosus is present, but not severe, affecting Norway more than Sitka spruce. *Dendroctonus* on the other hand, which appeared several years ago (?1959), was practically confined to Sitka spruce; there is no current breeding.

10. TRITTAU CPT. 44 : A younger (34 years) stand of pure Sitka spruce on a low-lying, somewhat swampy site with peaty soil. Ground preparation before planting consisted of ridging by spade at intervals of 1·5 to 2 m, the spruce being set on top of the ridge. It was presumed that the site had formerly grown alder/birch wood. There was trifling *Dendroctonus* attack a few years ago.

The trees are of poor form, with rather coarse low branching, which Oberforstmeister Meyer ascribed to provenance rather than to site factors. He believed that provenance differences in Sitka spruce were often reflected in stem form and coarseness of branching and that more discrimination was needed in the procurement of seed.

11. TRITTAU, Cpt. 63. 27-year-old Sitka spruce (with occasional birch) on another moist site, but less peaty than the last. This stand is still rather too young for *Dendroctonus* and none had been recorded. In thinning, the best birch stems have been kept, to form about 10 per cent of the stand.

The low level of *Fomes* infection in Trittau Forest is no doubt partly due to the prevalence of beech in former times. There are still large areas of beech, forming a difficult management problem, due to declining demand for the timber, unprofitable thinnings, deer damage and regeneration troubles. It is now a usual practice to convert the older stands (often of good quality and stem form) to spruce/beech/oak in the proportion of 40/40/20. As elsewhere, *Orchestes fagi* is abundant this year and beech bark disease has been prevalent since the dry summers of 1947 and 1949. Paradoxically, Meyer finds this worse in the best stands on more retentive soils: conceivably these foster a smaller root system than on the hungry sands, so that when rainfall is seriously deficient the good stands suffer more.

Tuesday, 9th June

12. RANTZAU, Cpt. 81 (Plates 4, 6). Rantzau is a scattered forest district about 30 km N.W. of Hamburg and stands of Sitka or mixed spruce are few and far between. Attacks by *Dendroctonus* were said to date from 1954–56, affecting (albeit slightly) Sitka, *omorika*, white and common spruce. The 53-year-old stand of Sitka spruce examined in Cpt. 81 was the most affected in the locality, and there is now only a remnant recently underplanted. But it was the storm of February, 1962, aided by the previous cutting out of *Dendroctonus*-affected stems, and by honey fungus, which precipitated the break-up of the stand.

    This stand is on a wet flat surrounded by broad leaf forest on three sides: the soil is derived from about 1 metre of drift sand over less pervious material and the water table is high, with sharp seasonal fluctuations: water seepage occurred at 40 cm on 9 June. A rather open stand of birch, alder and sallow is presumed to have occupied the site in the past.

13. RANTZAU, Cpt. 144 (Plate 5). A mixture of Norway and Sitka spruce, aged about 55, on a rather dry, sandy soil, with ground water at 6–9 metres. Superficial examination of the soil showed a rather thin layer of humose fine sand over a gritty fluvioglacial sand, with fairly frequent rounded granite and other stones.

    Dendroctonus was active between 1955 and 1960, mainly 1959, but this stand was much less severely affected than the preceding, nor was it ravaged by storm.

14. RENDSBURG, Cpt. 112 (Plate 7). Forstamt Rendsburg is a considerable distance north of Rantzau and the main part is close to the village of Kropp, midway between Rendsburg and Schleswig and about 35 km from the North Sea. Annual rainfall is about 760 mm (30 in.), the topography is flat, the land lying 20 m above the sea, and the sandy soils, often cultivated in former times, are more or less leached.

    The 33-year-old Sitka spruce in Cpt. 112 was affected by *D. micans* in 1956 and *Neomyzaphis* in 1957: Mobe-T was applied from 1957. A few current attacks were noted.

15. RENDSBURG, Cpt. 117 a 2. A 12-year-old Sitka spruce plantation 2–2·5 m. in height, following clearance of first generation spruce/pine: a dressing of NPK was given this year. Several dead trees were recorded and bad planting, followed by *Hylastes* attacks, perhaps aggravated by prolonged warm dry weather in May–June, 1964, was the suspected cause. Professor Francke Grosmann collected some material, which yielded *Ascochyta piniperda* Lindau (a pathogen affecting leaves and twigs of young spruce) and an unidentified fungus.

    The adjoining 70-year-old pine and spruce is greatly thinned by *Fomes annosus* and storm damage, but there are some good groups of spruce natural regeneration (Plates 9, 10).

16. RENDSBURG, Cpt. 140 (Plate 11). 52-year-old Scots pine and Norway spruce: the *Dendroctonus* attack on spruce (top height about 60 ft.) 3 years ago has died out.

17. RENDSBURG. A ten-year-old plantation of Norway spruce spaced 100 × 80 cm with evidence (in a warm and dry period) of needle browning and incipient dieback. It was agreed that the excessive density (normal spacing is 130 × 130 cm) had intensified root competition on a dry sandy soil, thus lowering the trees' resistance in a critical dry period.

18. RENDSBURG, Cpt. 62b.

19. ,, ,, 161d.

    Two sections of a large block of 57-year-old Norway spruce in the north west of the forest, representing the first plantation on heath or derelict farm land. The few signs of *Dendroctonus* were old or abortive attacks.

20. FORSTAMT SCHLESWIG, Cpt. 67. Sometimes referred to as STEINHOLZ, this 80-year-old Sitka spruce stand, established by Schwappach in 1886, is at Bollingstedt, 10 km N.W. of Schleswig, about 30 km from the North Sea, rather more from the Baltic. It was planted following the clearance of sessile oak, with some birch; the quality of the oak was such as to attract many distant buyers.

    A soil pit showed a well-developed humus—iron podzol, in appearance not unlike the Lower Greensand podzols near Farnham. The humus pan lay about 50 cm down, the iron pan ("Ortstein") 10 cm deeper. Some laboratory tests on the soil were done by Müller (1939), who ascribed the very good growth to the high content of alkali felspars and associated good supply of plant foods, especially potash. It is difficult to reconcile the present profile with the antecedent oak-birch, but changes may have been considerable in 80 years.

    Schwappach began recording growth of a sample plot in 1908, and the latest assessment was due to Schober (1962), when mean height was 34·3 m and mean yearly increment since planting 17 cubic metres. Noteworthy was the steady decline in current annual increment from 25·6 cu. m in 1925 to 20·4 in 1954 and only

10·7 in 1963. The large size of the best boles is impressive: so too is the rather sparse, thriftless look of the crowns.

Dendroctonus has not been seen in this wood, although younger neighbouring stands have been affected. A photograph forms the frontispiece to Schober's monograph: it was nearly dusk when the stand was seen on 9 June and too late for photography.

Wednesday, 10th June

21. FLENSBURG, KARLUM REVIER, Cpt. 309 a. Karlum is but 6 km from the Danish border, 20 km from the North Sea Coast. In the maritime environment ("Atlantic climatic wedge") Sitka spruce has been planted more widely, but always in mixture with other species. The soils are sandy podzols, with thin organic layer and soft pan (h, Fe) often with a veneer of recent blown sand: they were formerly heath or poor farm land.

    The first stand seen in Cpt. 309 was a 61-year-old mixture of Sitka spruce and Norway spruce and silver fir, established with 60% "Schutzholz" (mountain pine, alder, willow, et al). Mean heights at 59 years were: S.S. 24 m, N.S. 21 m, S.F. 21·5 m, standing volume 190 cu. m/ha. The stand is thinly and irregularly stocked, due to *Fomes* (mainly) storm damage and *Dendroctonus*, of which some trees with current breeding yielded specimens and photographs (Plates 1, 2, 12).

22. KARLUM, Cpt. 321 b (Plate 17). Silver fir (*Abies alba*), now 62 years, following removal in 1939 of the associated Sitka spruce, which was severely attacked by *Fomes:* some *Dendroctonus* was recorded more recently. Gaps have been filled by group planting of Douglas fir, larches (mostly Japanese) and Sitka spruce, now 22 years old. The silver fir benefited in early years from the faster growth of the spruce, removed at age 37: Forstmeister Loetz maintains that cover must be maintained for about 30 years if *Abies* is to make healthy growth.

23. KARLUM, Cpt. 301 a. Planted 57 years ago on heath, the original stand was a mixture of Douglas fir, Japanese larch, Norway spruce, Austrian pine and European silver fir. *Fomes annosus*, deer and some neglect have produced a very uneven canopy: but the gaps are becoming filled by natural *Abies* seedlings and by larch and red oak, planted in deer-proof enclosures, the object being an uneven aged mixed stand ("Blenderwald").

24. SPRAKEBÜLL. A private wood of c. 45-year-old Sitka spruce, 20 km from the coast. Formerly a sandy, moist, *Molinia*-covered flat, the site is now thinly covered with recent blown sand and *Deschampsia flexuosa* shares dominance with *Molinia*. There is a little current, as well as former, *Dendroctonus* activity, an imago with eggs being taken from a small new frass chamber. Spruce seedlings are common.

25. FLENSBURG: WALLSBÜLL. Cpts. 112, 113. These 52-year-old plantations are 12 km. west of Flensburg and 30 km from the west coast. The soil, which shows a compacted iron accumulation zone at 40/45 cm depth, is derived from outwash sands of the last (Weichsel) glaciation, of which the end moraine is some 15 km E.N.E.: ground water occurs at 1·5 to 2 metres.

    The stand was a mixture of Sitka and Norway spruce with 10% Scots pine and Japanese larch edgings, the present heights in metres being respectively 19·5, 16·5, 14, 18. It began to decline about 15 years ago (? following 1947 drought) with *Fomes* decay and *Dendroctonus*. It is now breaking up and plans for rebuilding are well forward: plots 60 × 40 metres have been marked out for:

    (a) Sitka spruce natural regeneration, or
    (b) planting of Douglas fir, or
    (c) „ „ European silver fir.

    Plots (b) and (c) will be planted as and when the light becomes sufficient: (a) will also be planted, if regeneration fails. Subsequently the whole area will be underplanted (after *n* years) with silver fir, the aim being an uneven-aged *Abies alba* stand, with some large Douglas fir and larch.

    Dendroctonus was present on several trees, one Sitka spruce showing fresh frass 20 cm above the base, on the south side, with a compact cluster of about 50 eggs in a chamber of 1·5 cm diameter. Mobe-T had been used with good effect.

C. DENMARK

Thursday, 11th June

26. FALSTER: HANNENAV SKOV. Hannenav is a State Forest on the island of Falster, in which a proportion of the broad-leaved woodland (mainly beech) has been replaced by conifers. It is c. 10 km from the sea in all directions, low lying, with no topographical shelter.

    The stand first seen, c. 45-year-old mixed conifers (Norway and Sitka spruce and Douglas fir), or in part pure Norway spruce (Plates. 14, 15, 18), adjoins on the south a large clearing where severe gale damage was caused on 11th February, 1956. *Dendroctonus micans* was recorded in the summer of that year, causing serious damage in the following few years and it was suggested that rocking by the wind had damaged the fine roots and so increased susceptibility. On the other hand there is circumstantial evidence connecting the outbreak with drought in the summer of 1955. The expected spread of attack and virtual elimination of spruce (at least the Sitka spruce) have not taken place and no current *Dendroctonus* activity was observed. Application of Mobe-T since 1957 has contributed to this result.

The frequent occurrence of *Asperula, Anemone, Melica uniflora, Milium* and other beechwood plants indicated a first generation of conifers; and the soil pit showed a somewhat enigmatic, weakly podzolized sand, with discontinuous iron accumulation zone at 40 cm. Beneath this a very compact pale sand, with rusty mottle, suggested a relic of permafrost in glacial times.

27. HANNENAV. Pure Sitka spruce, 500 m south of 26, about 35 years old and markedly affected by *Dendroctonus* in and after 1956. Again no current activity was found, but the trees are thin in the crown and appear in very poor condition. This is a small stand open all round as a result of recent fellings and it may be suggested that the stand climate is such as to promote transpiration in dry windy conditions: the unretentive sandy soil is also an unfavourable factor in the water economy of the trees.

Friday, 12th June

28. SJAELLAND: NORDSKOV (Sorø Distrikt). A c. 40-year-old stand of mixed conifers (Douglas fir, Norway, Serbian and Oriental spruce) in the centre of a wood of beech and oak, 14 km N.W. of Ringsted in mid Sjaelland. The soil, derived from glacial till, contains many boulders, but is fertile and freely drained, though of no great depth. *Dendroctonus* attacked in 1956, following storm damage in February, first on *P. orientalis*, but the other two spruces were later attacked, some stems being affected high up. It may be of interest that the oriental spruce group, where the first attacks occurred, stands on a dry knoll. The outbreak died out between 1959 and 1962, partly, perhaps, because of the elimination of the more susceptible trees, and only one very small family of 2nd stage larvae was found on a Serbian spruce.

Sunday, 14th June

29. GRIBSKOV. 25-year-old common spruce, growing on one of the poorest soils seen on the tour—a rather coarse, strongly podzolized, glacial sand, very deficient in plant foods, under a thick mor layer. The exceedingly poor adjacent beechwood on the same soil provides an interesting contrast in current increment. There is no evidence of *Dendroctonus*, the trees being probably rather too small.

Monday, 15th June (Plate 31).

30. SØSTRUP, Afd. 13. (Plate 31). Søstrup is a private estate on the north coast of Djursland, a rather dry peninsula joined with east Jutland. The rainfall is 550–600 mm annually and the soils are weakly podzolized sands, with rather compact B horizons, which seem to discourage deep root penetration.

The first halt was in 45/50-year-old Sitka spruce, which followed a stand of Norway spruce overthrown by wind. There was a full canopy until 1959, when *Dendroctonus* attacked, killing several trees: clearance of these and of trees later overthrown by wind has left a large opening. Only slight current attack was observed.

The same wood includes stands of Norway spruce and European silver fir of about the same age. Mean heights in metres and breast high diameters in cms recorded by Henriksen (1958) in 1952 were:

Sitka spruce: 22·0 m, 28·8 cm at 37 years.
Norway ,, : 19·4 m, 22·5 cm at 37 years.
Silver fir : 16·9 m, 22·7 cm at 41 years.

31. SØSTRUP, Afd. 103 (Plate 13). A high quality 45-year-old stand of Sitka spruce, height 30 m, basal area 50 sq. m, volume 600 cu. m/ha. Like the surviving part of the preceding stand this is being kept close, because timber size spruce is not at present attracting the price it should: the last thinning was in 1950. The site was said to have been formerly under broadleaf forest for 200 years at least; nevertheless a well developed finely sandy podzol, with very compact B1 (h, Fe) at 35–40 cm was found under 4 cm granular mor.

No *Dendroctonus* attack had been recorded in this stand.

32. SØSTRUP, Afd. 62. Two small areas of younger (15 and 11 years) Sitka spruce on a fertile low-lying peaty site, artificially drained. This land had previously been in arable cultivation, but the natural plant association was probably *Alnus/Salix*. The soil is fertile, with plenty of moisture, and growth of spruce was good,

the older stand having recently received its first thinning: poplar, or ash, would probably have grown well too.

33. MEJLGAARD, Afd. 210. (Plates 3, 19). Mejlgaard estate lies only a few km west of Søstrup and, like it, is close to the north Djursland coast of E. Jutland. The owner, Hr. Jule, is a keen and active forest manager and accompanied us to three stands of Sitka spruce. The present, c. 75-year-old, stand was the finest seen on the tour and perhaps the best in Denmark, but the origin of the seed is not recorded. Assessments have been made locally since an age of 22 years: at the last assessment in 1952, when the records were taken over by the Research Station, the mean height was 32 m (presently up to 37 m) volume 619 m^3 per hectare (locally more), current annual increment 16–19 m^3/ha.

The terrain is very gently undulating and the soil is formed of peat over sand. The peat layer is of variable thickness, mostly 40–45 cm, well decomposed below and thoroughly exploited by roots. Below it lies a thin layer of bleached fine sand, then a rather compact sandy B1 down to 60 cm (including peat): underneath is yellow brown sand, slightly compacted and faintly mottled, with frequent spruce roots. Ground water is not distant, though below 140 cm. The previous land use is not recorded, but there is little doubt that mixed woods, of ash, alder, birch, mainly, formerly occupied the ground.

There was a slight attack by *Dendroctonus*, following other injuries, a few years ago: the old lesion was seen at a height of about 12 m on one tree. There has been no trouble from *Fomes*.

34. MEJLGAARD, Afd. 14. This stand of c. 38-year-old spruce was derived from seed collected in the stand just described and it shows the same vigour and good forms. It is in the same wood as the parent stand and the soil, though much less peaty, is somewhat similar, having formerly borne a mixed broad-leaf wood of ash, alder and some beech. Henriksen (1958, p. 180–181) describes a weakly podzolized marine sand, humose and leached in the upper 25 cm and from 85 cm down greyish blue in colour (from ferrous iron), with a few clayey pockets and some mussel shells. In autumn 1952 the water level was at 120 cm, roots reaching a little short of it. He made bore holes in this stand in March, 1956, taking periodic measurements of water level from 13/3 until 23/12: the minimum depth of water was 50 cm on 13/3, the maximum 125 cm on 22/11. These measurements were compared with those taken in the same year, on a similar soil, in Tranum Plantage, where the growth of Sitka spruce was much inferior. These data, and the reasons for the difference in spruce performance, are considered on pages 186–190 (Henriksen 1958).

The height of the spruce is now about 25 m; pruning was done over 2·8 hectares in 1959. The ground vegetation of *Mercurialis perennis, Athyrium, Dryopteris filix-mas, Rubus caesius* indicates a fertile soil, derived from somewhat calcareous sea sand.

35. MEJLGAARD, Afd. 85. Sitka spruce, about 48 years old, in another wood (Nederskov) rather nearer the sea. This stand was also derived from the older high-quality stand in Graeskaerholm and the height growth and stem form are good, but not so the health. *Armillaria mellea* attack was recorded in one place and *Dendroctonus* is prevalent, both successful and abortive attacks being observed. Attention was drawn by beetle attacks high on the stems of some trees, of which the tops were dead or dying above a relatively sound lower live crown. When Henriksen recorded this stand in autumn 1952, it was in good health, with mean height of 21 m: the present height is c. 27 m.

The site is flat and low-lying, only about 4 m above sea level, and therefore, difficult to drain. Examined at the S.W. end the soil showed 20–25 cm peat, then c. 5 cm of bleached sand: a wavy humus accumulation zone from 5–10/15 cm was followed by ochreous fine sand, moist, with rust and some humus mottling. Roots of spruce, in contrast with those seen in 34 and 35, extended only about 30 cm into the mineral earth. The soil is rather more peaty at the east end and evidently bore alder before the spruce was planted in furrows. The surrounding slightly higher ground bears beech of extremely poor height and stem form.

Tuesday, 16th June

36. MOLS BJAERGE. The plantations seen this morning on Mols Bjaerge (itself a small peninsula at the southern end of the Djursland peninsula) are all managed, on behalf of the landowners, by the Danish Heath Society (Dansk Hedeselskabet). The terrain is very hummocky, with sandy morainic soils—locally with blown sand cover—and the rainfall is only 500–550 mm yearly. In the hollows, where moisture supply is better, frost may be important.

The mixed Norway and Sitka spruce, with a little Douglas fir, seen first is 30 years old; due to spring frosts in early years, Norway spruce preponderates. The soil, examined high on the slope, showed 20–25 cm of moderately leached, very stony, gritty sand, followed by 20 cm yellow sand, with stones of flint and granite, both layers with abundant roots. From 40/45 to 77+ cm there was a medium coarse sand, very porous and friable, rather dry, with few stones and frequent Sitka spruce roots.

This deep thorough exploitation of the sandy soil by Sitka spruce roots is relevant to our guide's (Hr. West Nielsen's) remark that this species does not need plentiful soil moisture, if it has free root run and high atmospheric humidity. He thinks Norway spruce more tied to moist soil. This poor soil received, before planting, a phosphatic dressing, cultivated in to 50 cm depth: superficial application is considered less effective and liable to encourage shallow roots, or even to injure roots. Superphosphate or Thomas meal is used.

37. MOLS BJAERGE. Douglas fir and Norway spruce, 30 years old, with Douglas overtopping spruce except in the frost-ridden bottom (NB. these plantations must have suffered in the widespread April frosts, following an extraordinarily warm March, in 1938: cf. Ladefoged, 1938, Bornebusch and Ladefoged, 1943). Representative pure stands of the three main species show current annual increments of 26 (Douglas), 23 (Sitka), 17 (Norway spruce) cubic metres.

Both *Fomes annosus* and *Dendroctonus micans* have affected the spruce here fairly seriously and Douglas too has suffered from *Fomes*, to which it seems very susceptible until about 30 years old, with little trouble in later life. *Dendroctonus* attacks evidently dated from the dry summer of 1955: Mobe-T was used with good effect.

A limited trial of alternative species was exemplified in a small plantation of 9-year-old *Abies procera* and *A. nordmanniana* in a deer-proof enclosure near the ridge crest. Surrounded by old conifers, this first planting was made on land occupied by broad-leaf scrub, some of which was left for shelter (Plate 20).

38. MOLS BJAERGE. *Pinus nigra*, 36 years, on a hill near Trehøjes. This small stand of Corsican pine was said to have grown wholly free from disease, or die-back, by West Nielsen, who took charge in 1946. There are small gaps on the east slope and some indications of early disease, but deaths and dieback were probably negligible. Favourable conditions for the species are provided by a sunny position, good ventilation and a freely-drained sandy soil. Current annual increment about 12 cu. m per hectare.

39. MOLS BJAERGE. 36 years old *Pinus nigra austriaca* (Plates 21, 22), planted in the same year as 38, on an east-west ridge. Whereas the pines on the south slope have remained healthy and grown moderately well, dieback disease and deaths affected the upper part of the north slope, so that a substantial area was cleared and replanted with Japanese larch about 8 years ago. Though needle discolouration (*Lophodermium*) is prevalent, production slightly surpasses that of adjoining Norway spruce.

40. SKRAMSØ. The stand of Sitka spruce, which had been under observation for several years, became so severely affected by *Dendroctonus* and *Fomes annosus* that it was cleared and, after ploughing, replanted mostly with Japanese larch and silver firs. The soil is a yellow brown sand, with only faint signs of podzolisation and noticeably dry today.

Tuesday, 16th June, afternoon

41. LOVNKAER. This property lies on the north shore of Mariager Fjord, near the east Jutland coast, and provided the most northerly point of the tour. The terrain is flat and only c. 4 m above sea level, so that site drainage is difficult: but the surface soil is sandy and, given such artificial drainage as circumstances allow, Sitka spruce thrives, at least for several decades. Professor Carl Mar Møller very kindly showed us over his diverse woods.

The first Lovnkaer stand examined was a 34-year-old pure plantation of Sitka spruce, with a mean height of 22 m and annual increment of 20 cu. metres per hectare. The soil is sandy and the water table high. *Dendroctonus* was reported in 1956, after which half the stand was sprayed yearly for 3 or 4 years with Mobe-T, the southern half being left as control. Most of this half was overthrown in an abnormal S.E. gale in 1960, but not until after the insecticide had proved its efficacy. *Dendroctonus* is now generally rare and a stack of recent thinnings showed only one old attack 12 m from the ground.

42. LOVNKAER. This 30-year-old plantation originated as a row-about mixture of Sitka and Norway spruce at an approximate spacing of 2 × 1·4 m. Norway spruce sickened and died within a few years leaving Sitka widely spaced and somewhat heavily branched. Sporadic attacks by *Dendroctonus* have occurred since 1955.

43. LOVNKAER. Sitka spruce 18 years old, in which an unreplicated thinning experiment was initi-

ated 6 years ago. The treatments, with approximate money yields to date, are:—

(a) No thinning, Nil

(b) Light, low thinning, 2,000 kroner per hectare

(c) Heavy low thinning (alternate years), 4,000 kroner per hectare

(d) Heavy crown thinning (yearly), 6,000 kroner per hectare

(1,000 kr/ha. is equivalent to nearly £20 per acre).

Treatment (c), following normal present Danish practice, is marked by Prof. Møller and his forester: (d) by Hr. Juncker, a forestry consultant and landowner, who removes large trees systematically as soon as they reach readily saleable size, leaving rather smaller, often straighter, stems to exploit the generous allowance of light and root space. Apart from enhanced value yield, he claims improved humus decomposition and surface soil conditions from the extra warmth and light reaching the ground and thus, indirectly, improved growth. On the other hand the more open stand may predispose to *Dendroctonus* attack and offer too much freedom for penetration by wind.

Wednesday, 17th June

44. VELLING. The plantations seen today are further from the sea (east coast 30–40 km, west coast 60 km or more) than those seen elsewhere in Denmark. Velling is an old forest on the mid-Jutland ridge (part of the Scandinavian end moraine) with relict 250-year-old beech, as well as plantations of conifers. The 74-year-old Sitka spruce stand visited is on a favourable N.E. or E.N.E. slope and had grown well: in 1952 (age 62) there were 224 trees per hectare with mean height 34·3 m, diameter 41 cm, volume 530 and C.A.I. 21 cubic metres per hectare. The stand had been affected by wind, *Fomes* and *Dendroctonus*, but in no way seriously.

45. SKAERBAEK. Afd. 135. 62 years Sitka spruce of fairly good growth on a poor podzolic sand of morainic origin. Planted as a mixture of Norway and Sitka spruce, this became in time a pure stand by competition. *Fomes* is prevalent and the stand, in Hr. Elmquist's view, is beginning to break up. He places more reliance on Norway spruce and common silver fir, seen in mixture in the adjacent compartment.

46. PALSGAARD, Afd. 70. 74 years Sitka spruce, cleared in 1959 and replanted with silver fir and Japanese larch. This stand was examined in 1952 by Henriksen (1958) who reported the prevalence of *Fomes* (more general and severe in 1954) and sporadic *Dendroctonus micans* attack. In 1952 assessment here, and in an adjoining Norway spruce stand of the same age, provided these figures:—

		Mean		*Per Hectare*			
	Age	*Height metres*	*Diameter cm.*	*No. of trees*	*Basal area sq. m.*	*Volume cu. m.*	*Current increment cu. m.*
Picea sitchensis	68	28·8	38·5	310	36·3	520·6	29·8
,, *abies*	68	24·0	28·0	610	37·6	474·3	17·5

47. PALSGAARD, Afd. 71 (Plates 25, 27, 28). Sitka spruce, 70 years, with European silver fir, 75 years, occupying the northern part of the compartment. In this stand, adjoining 46 on the north, there had been much *Fomes*, some *Dendroctonus* and a little storm damage to spruce: thin tops are widespread, with some dead or dying, while swollen butts may indicate *Fomes* infection. A contrast is provided by the healthy look of the silver fir.

These two plantations were made on poor cultivated land. The soils are weakly podzolised loamy sands, with a surface layer, 30-35 cm thick, of somewhat leached, stony sand overlying a yellow brown slightly loamy sand with frequent fragments of granite, etc. Root exploitation is intense in the upper 40–50 cm, with occasional roots in the more compact, less stony, sand below.

48. GLUDSTED, Afd. 147. This interesting stand of Sitka spruce, of which the early growth was described by Oppermann (*det Forstl. Forsogsv. i, Danmark*, 1922) was planted in 1891 and cleared, in view of its unhealthy condition, in 1955. The heath, on a sandy podzol, was ploughed and the spruce planted in mixture with mountain pine. Repeated frosts, with the other difficulties of the site, caused a very slow start; but subsequently, after eventual closure of canopy, growth improved, with the result that, between ages 31 and 69, the quality (Danish rating) improved from 5·3 to 2·7.

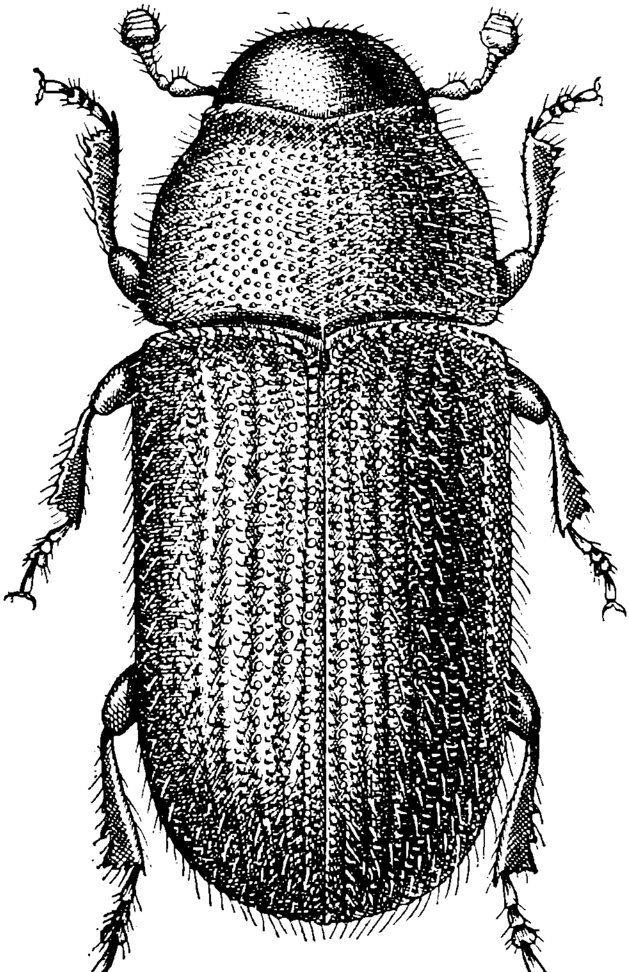


Plate 32. Adult Dendroctonus micans. × 15.

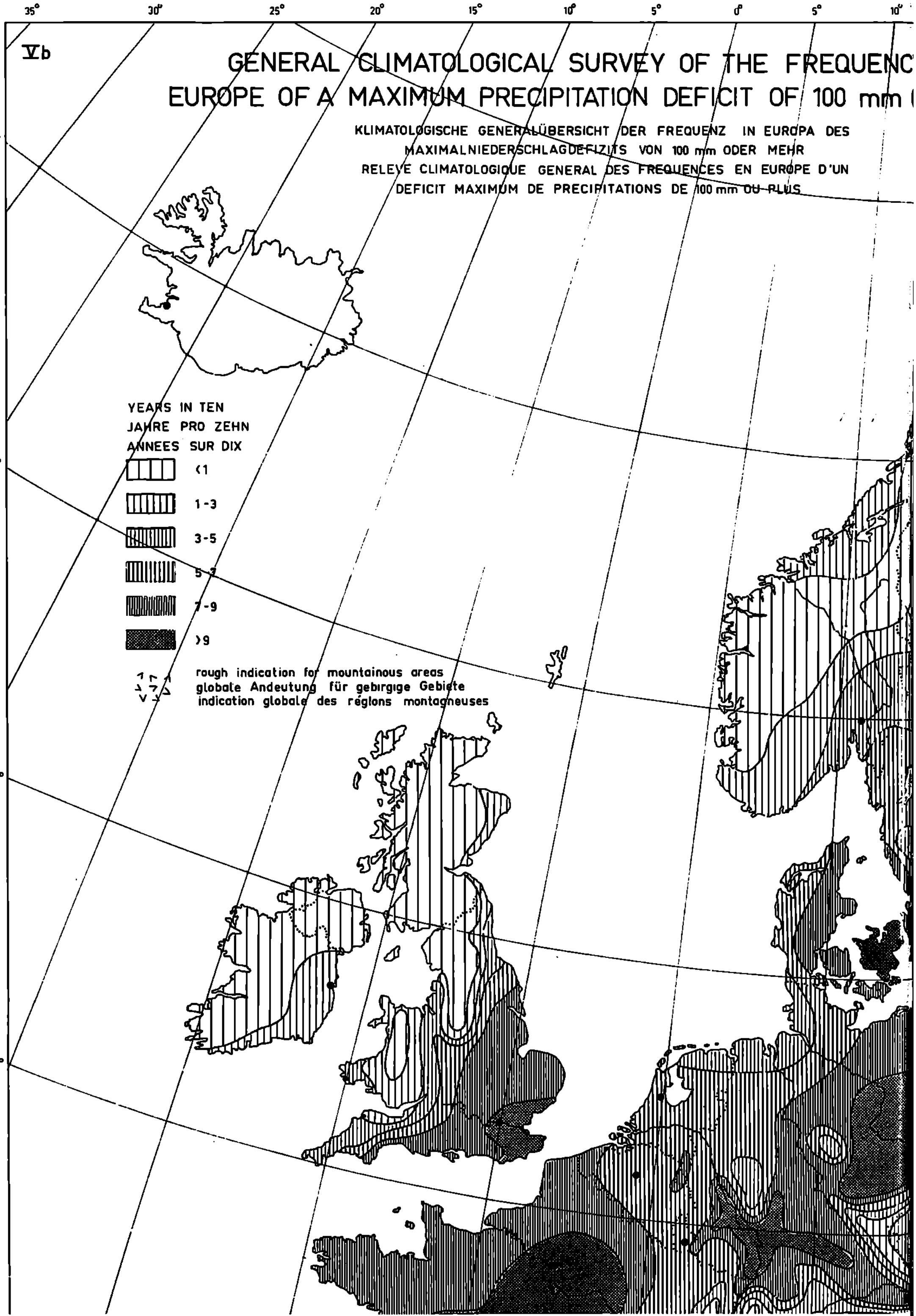
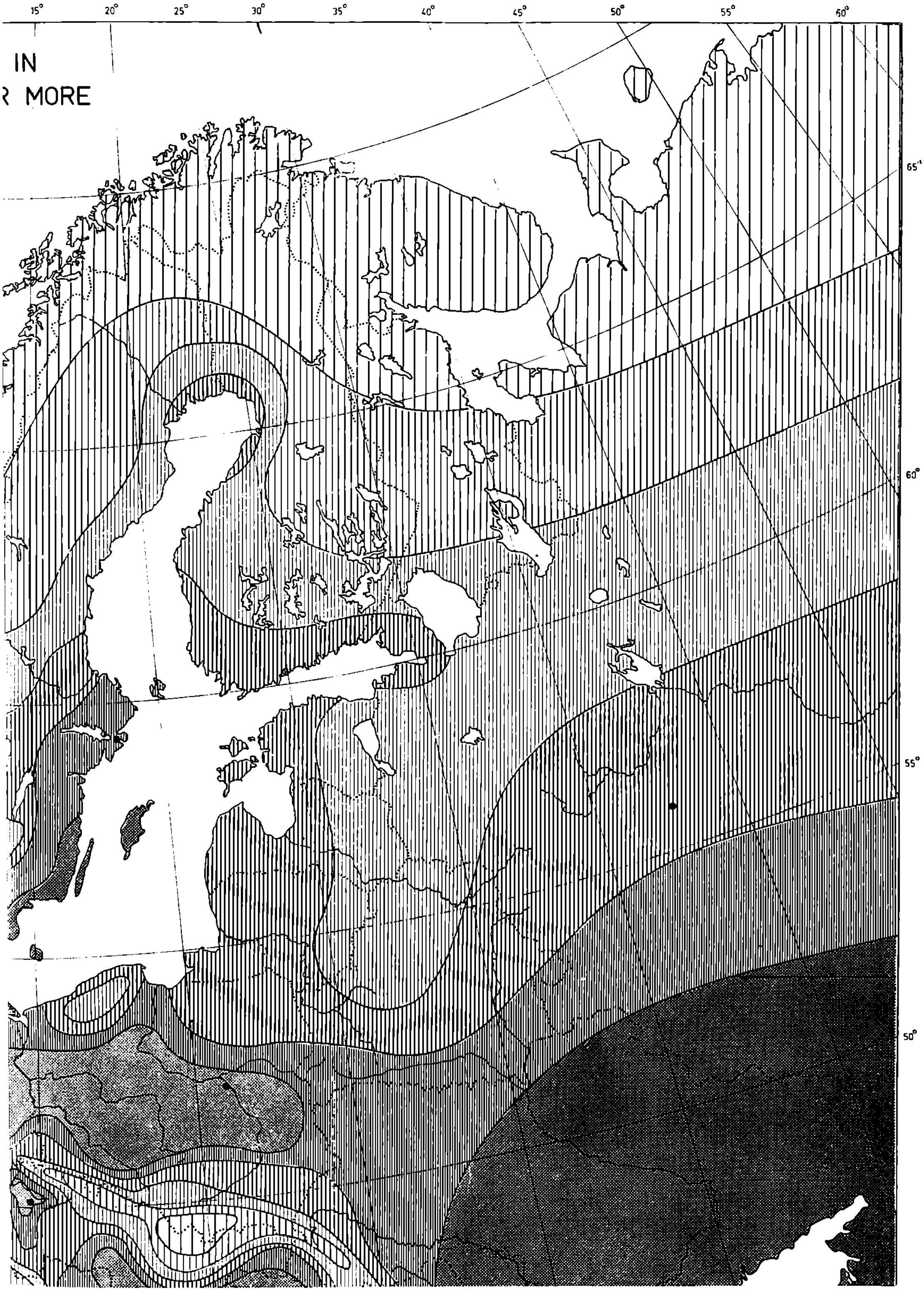


Plate 33. An expression of frequency of precipitation deficits in North West Europe. From: *Water deficiencies in European Agriculture: A Climatological Survey* by J. C. J. Mohrmann and J. Kessler, International Institute for Land Reclamation and Improvement, Wageningen, Holland.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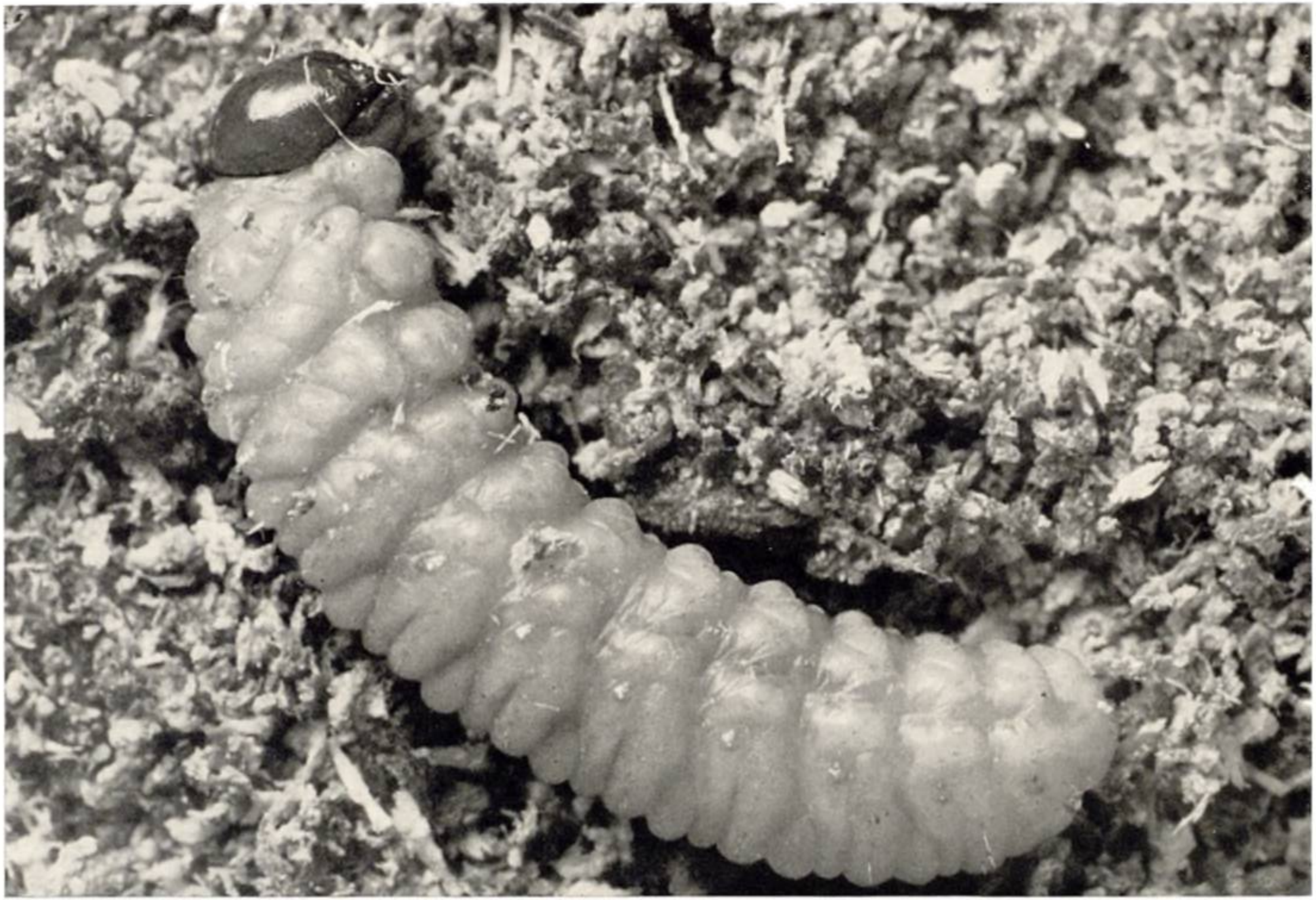

Plate 34. Larva of Dendroctonus micans. × 15.

Increment slumped abruptly in 1954/55 and, after felling, Henriksen (1958, p. 336) made an assessment of the condition of the trees and the incidence of attack by *Dendroctonus* amd *Fomes*. The proportion of trees affected by the bark beetle was too small to have influenced health very much: on the other hand 68 per cent of the trees were infected by *Fomes annosus*, without any evidence of association between the two organisms. Henriksen considered, nevertheless, that *Fomes* was rather a symptom of ill health than its fundamental cause.

Henriksen also examined the sandy soil to a depth of about 3 m, to find if possible a reason for the good growth of Sitka spruce, surpassing that of other stands in Gludsted. His excavation disclosed two loamy bands or veins, at 180 and 225 cm, both exploited by deep Sitka spruce roots.

49. GLUDSTED, Afd. 187. Norway and Sitka spruce aged 77 years, illustrating the much greater production of Sitka spruce, which is ascribed in part to better exploitation of the soil by roots.

Thursday, 18th June

50. VRØGUM. Stands 50–55 are all in the coastal sand plantations close to the west Jutland coast north of Esbjaerg.

The present stand of 55-year-old Sitka spruce (plates 29, 30) was attacked by *Dendroctonus micans*, probably after the 1947 drought. The removal of dead and dying trees admitted the wind, much of the western half of the stand was overthrown in 1962, and the ground was cleared and replanted with Japanese larch.

The residual stand, of which the mean height is 21 m, shows a small resident population of *Dendroctonus*. Several trees show a copious resin flow resulting from beetle attacks, some of them abortive. Growth and health are unsatisfactory, but the site is considered more suitable for spruce than those on the deep aeolian sands. Under 3 cm mor there is an ashy grey leached sand, 25 cm thick, then a compact humose B (25–40 cm) followed by mottled silty fine sand, compact, moist (40–60 cm). The strongly gleyed silty fine sand below this (examined to 125 cm) was practically free from roots. A distance of 5–9 km separates the various parts of Vrøgum Plantation from the shore.

51. VRØGUM. European silver fir, 65 years, on a deep leached sand.

The threat to Sitka spruce on the dunes arising from *Fomes annosus* and *Dendroctonus micans* has recently prompted the trial of silver firs (mostly *Abies alba*, but including some *A. nordmanniana* and possibly other species). They are always planted under cover—usually of thinned white spruce—without which the young trees are crippled or destroyed by frost, drought, or wind.

This 65-year-old stand recalls some earlier trials of *Abies alba* towards the end of last century. They were soon given up because of *Adelges*, but this plantation made good and the health, as well as the height and diameter growth, are very encouraging. In the maritime environment of Schleswig-Holstein 30 years was considered not too long for the maintenance of cover over *Abies* spp.: this may apply also to W. Jutland.

Under *Deschampsia flexuosa* mor, the soil showed 30/45 cm ashy grey leached sand with occasional roots, then an ill-defined humus-iron B, 5/10 cm thick. From 40–60 cm a reddish-brown medium sand, with occasional stones, was richly exploited by roots: under this, from 60–110 cm lay a similar sand, with few stones, sparsely rooted for the most part, but with dense more or less horizontal roots filling the rather dry zone at 100–110 cm. Below this the paler compact sand was rather dry, with few roots.

Eggs and young larvae of *Dendroctonus* were found in the neighbouring, 30-year-old, 18 m tall, stand of Sitka spruce which succeeded unsatisfactory white spruce.

Friday, 19th June

52. VEJERS. 55 years old Sitka spruce on a sandy flat, formerly under heath, about 2 km from the sea. The soil, under *Deschampsia flexuosa*, moss and litter, showed 5 cm mor, then 10 cm humose fine sand with very abundant roots, followed by a transitional layer, also well exploited by roots. From 20–53 cm the pale buff sand has few roots: it was succeeded by a buried A1 layer, a very humose sand extending from 53–70 cm with occasional roots. The dull grey medium sand which underlay this had a greenish tinge, with water seepage at 93 cm.

In correspondence with the close proximity to the sea and the nutrient poverty and fluctuating water level in the soil, Sitka spruce had grown poorly, the mean height at 55 years being 13 m (42½ ft.). The stand was opened out, then ploughed and underplanted in 1959: with the young Sitka spruce plants there is a good deal of natural regeneration.

Near this stand, on ground cleared of Sitka spruce because of *Dendroctonus* attack, is a very young plantation, originating from Sitka spruce seed collected in a locality where the summer rainfall is appreciably lower than in the seed source areas generally drawn on hitherto. The intention is to raise a stand potentially more resistant to drought, to *Dendroctonus* and perhaps to *Fomes*.

53. OKSBY. The plantation seen at Oksby, situated 5–6 km from the shore in two directions (west and south) represents the earliest coastal sand planting in west Jutland. It is accordingly 110 years old, but there is not much left of the three trees originally planted—Norway spruce, Austrian pine and mountain pine. The spruce was ill-adapted to the extreme maritime conditions and dry sandy soil, surviving only in sheltered hollows; Austrian pine, after starting well, was nearly eliminated by disease when 15–20 years old, but the scattered survivors stand out with their abundant dark green foliage. Much more dwarf mountain pine has persisted, but the production is extremely small and exposed parts of the plantation show much blast by salt wind.

54. BORDRUP. 80-year-old Sitka spruce on a moist sandy flat about 6 km from the sea. The first stand of Sitka spruce on the Jutland dunes, this was planted in strips in 1885 in an unthrifty mountain pine plantation where, with some shelter from the pines and on a moist flat, it developed surprisingly well, prompting further trial of the species in similar situations. The stand is now rather open, following some damage by storm and *Fomes* and the height growth is mediocre—average 21·3 (70 ft.); but production surpasses that of most dune plantations of similar age.

The soil was examined on 18/6, when water stood at just 1 metre: during the night heavy rain amounted to about 25 mm and the water level rose to 55 cm. Under thick peaty mor, a 5 cm thick humose A1 bore abundant spruce roots; the succeeding layer (5–53 cm.) of leached, whitish, medium sand was very sparsely exploited by roots. At 53–55 cm a thin, sharply defined dark brown band was taken to be an illuvial layer. From 55–120+cm the medium sand was dull pale grey with a greenish tinge and free from roots. Winter wetness evidently restricted root development.

The ground was generally covered by heath plants (*Deschampsia, Molinia, Galium, Calluna*) with locally abundant spruce seedlings. *Dendroctonus* had not been recorded.

55. BORDRUP. 85-year-old Scots pine on an aeolian sand. Under a little recent blown sand there was a 4 cm thick humose layer, then medium fine sand, only slightly leached, down to 65/70 cm, where the very humose layer was clearly the original A1 horizon thickly covered by blown sand. Below 75/80 cm rusty mottle and compaction were prominent and pine roots, frequent above this, were very rare: this presumably represented the usual winter water level. The pit was dug on 18/6 before the rain, and water occurred rather unusually far down at 150 cm. 20/25 years old Sitka spruce occurs in the adjacent compartment.

Appendix 2
SUMMARISED CLIMATIC DATA FROM DANMARKS KLIMA, 1933

Table A—Mean Monthly Temperature for 17 Representative Danish Stations, 1886–1925

	Altitude (metres)	Year	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Apr.–Sept.	Apr.–Oct.	May–Sept.	No. of days with Frost
Hanstholm Fyr	46	7·1	0·7	0·0	1·3	4·8	9·3	12·9	14·9	14·7	12·3	8·4	4·5	1·9	11·5	11·0	13·2	84
Thisted	12	7·3	0·5	0·0	1·7	5·4	10·3	13·8	15·5	14·9	12·1	8·0	4·2	1·7	12·0	11·4	13·3	
Varde	12	7·3	0·4	0·2	1·9	5·6	10·6	13·6	15·3	14·7	11·9	8·0	4·0	1·6	12·0	11·4	13·2	92
Askov	65	7·2	0·0	−0·1	1·7	5·6	10·8	14·0	15·6	14·8	12·0	7·8	3·6	1·2	12·1	11·5	13·4	101
Hals	3	7·2	0·0	−0·3	1·3	5·3	10·3	14·2	16·1	15·1	12·0	7·8	3·8	1·2	12·2	11·5	13·5	105
Tylstrup	12	6·9	−0·3	−0·5	1·1	5·2	10·3	13·9	15·7	14·7	11·7	7·4	3·2	0·8	11·9	11·3	13·3	121
Hornslet	30	7·3	0·1	−0·2	1·6	5·5	11·0	14·2	15·9	15·0	11·9	7·8	3·6	1·3	12·3	11·6	13·6	
Kolindsund	3	7·3	0·1	−0·3	1·4	5·4	10·8	14·4	16·2	15·1	11·9	7·7	3·7	1·3	12·3	11·6	13·7	111
Silkeborg	30	7·4	0·0	−0·2	1·7	5·7	11·2	14·7	16·1	15·1	11·8	7·6	3·5	1·1	12·4	11·7	13·8	
Palsgaard	91	6·8	−0·4	−0·6	1·2	5·1	10·4	13·7	15·3	14·4	11·5	7·2	3·1	0·8	11·7	11·1	13·1	123
Lyngby	34	7·3	−0·5	−0·7	1·3	5·5	10·9	14·5	16·3	15·4	12·3	7·9	3·6	1·0	12·5	11·8	13·9	108
Tystofte	13	7·8	0·0	−0·1	1·8	5·9	11·2	14·8	16·7	15·9	12·8	8·5	4·2	1·6	12·9	12·3	14·3	86
Ringsted	55	7·3	−0·7	−0·6	1·4	5·4	11·0	14·8	16·5	15·4	12·4	7·8	3·4	0·7	12·6	11·9	14·0	
Nykøbing	9	(8·1)	0·1	0·3	2·3	6·3	11·4	15·2	17·1	16·4	13·2	8·7	4·3	1·7	13·3	12·6	14·7	88
Naesgaard	10	7·6	0·1	0·0	1·9	5·6	10·4	14·2	16·3	15·8	13·0	8·6	4·3	1·7	12·6	12·0	13·9	
Tønder	4	7·6	0·6	0·4	2·1	5·6	10·9	14·0	15·8	15·4	12·4	8·2	4·1	1·6	12·4	11·8	13·7	82
Løgumkloster	14	7·4	0·4	0·3	2·0	5·7	10·6	13·7	15·4	15·0	12·1	8·2	4·0	1·7	12·1	11·5	13·4	

Table B—Mean Monthly Precipitation in Millimeters for 17 Representative Danish Stations, 1886–1925

	Altitude (metres)	Year	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Apr.–Sept.	Apr.–Oct.	May–Sept.
Hanstholm Fyr	46	628	44	36	37	36	40	38	47	88	58	78	67	61	307	385	271
Thisted	12	716	58	45	47	42	45	40	61	86	65	83	71	74	339	422	297
Varde	12	(755)	56	43	47	43	41	53	68	94	81	87	68	74	380	459	337
Askov	65	733	54	38	47	43	45	55	72	96	73	79	63	69	384	463	341
Hals	3	556	38	26	33	38	43	42	56	77	50	57	47	49	306	363	268
Tylstrup	12	618	40	31	34	40	46	48	65	89	50	67	54	56	338	405	298
Mejlgaard	12	589	40	28	36	43	38	41	64	77	52	61	53	56	305	366	262
Kolindsund	3	593	43	35	38	41	40	43	59	76	52	63	51	55	311	374	270
Silkeborg	30	672	50	38	45	44	43	50	66	85	57	68	61	65	345	413	301
Palsgaard	91	725	54	43	49	45	45	50	70	95	64	74	66	69	369	433	324
Lyngby	34	592	39	30	37	42	39	52	63	82	53	56	47	53	331	387	289
Tystofte	13	522	33	26	33	35	36	44	63	66	46	53	42	45	290	343	255
Ringsted	55	622	46	37	45	44	38	46	68	75	52	61	52	61	323	384	279
Nykøbing	9	603	47	32	42	38	41	48	68	66	52	64	49	55	313	377	275
Naesgaard	10	586	44	32	40	37	43	44	70	67	49	60	47	55	310	370	273
Tønder	4	750	48	41	52	44	51	47	81	108	72	86	59	68	403	489	359
Løgumkloster	14	736	52	41	47	41	46	50	72	100	75	84	63	65	384	468	343

Table C—Absolute Minimum Temperature

Station	*Locality*	*Record period*	*Minimum*	*Year/Month*
Skagen	N. Tip of Jutland	1876–1925 (50)	−16·8	1893/Jan.
Vestervig	N.W. ,,	1876–1925 (50)	−19·9	1893/Jan.
Herning	W. ,,	1874–1920 (45)	−25·9	1895/Feb.
Birkebaek	W. ,,	1882–1925 (44)	−23·3	1895/Feb.
Fanø	S.W. ,,	1876–1925 (50)	−18·0	1895/Feb.
Askov	S. ,,	1886–1925 (40)	−20·5	1893/Jan. 1922/Feb.
Viborg	C. ,,	1875–1925 (51)	−24·1	1897/Feb.
Hals	E. Coast ,,	1881–1925 (45)	−25·3	1893/Jan.
Randers	E. ,,	1864–1925 (60)	−26·4	1895/Feb.
Tvingstrup	,, (Aarhus)	1881–1925 (45)	−21·8	1893/Jan.
Stenderup	S.E. ,,	1885–1925 (41)	−21·3	1893/Jan.
Anholt	Kattegat (Island)	1886–1925 (40)	−17·1	1893/Jan.
Samsø (Tranebjerg)	,, (Island)	1873–1925 (53)	−18·2	1881/Jan.
Assens	Fyn	1883–1925 (43)	−18·4	1893/Jan.
Hofmannsgave	Fyn	1877–1925 (49)	−19·5	1893/Jan.
Frihedslund	N. Sjaelland	1878–1925 (48)	−23·4	1893/Jan.
Lille Dyrehavegd	N. Sjaelland	1879–1925 (47)	−22·1	1893/Jan.
Landbohøjskole	København	1861–1925 (65)	−25·0	*1871/Feb.
Bogø	S. Sjaelland	1873–1925 (53)	−23·0	1893/Jan.
Hammershus	Bornholm	1873–1925 (53)	−14·3	†1881/Mar.

* −23·2 in 1893/Jan.
† −12·3 in 1893/Jan.

Table H—Wind Directional Frequency per cent

	Years of Records	*N.*	*N.E.*	*E.*	*S.E.*	*S.*	*S.W.*	*W.*	*N.W.*	*Calm*
1 Hanstholm		4·4	9·3	12·0	14·0	10·3	14·7	**19.5**	13·8	2·1
2 Bovbjaerg		5·8	7·9	10·5	14·0	10·4	16·2	14·6	**18·4**	2·1
3 Skagen		7·5	10·0	10·5	9·5	11·3	14·7	**20·4**	12·3	3·9
4 Fornaes		7·0	7·6	9·8	11·9	12·2	18·8	**20·2**	9·2	3·4
5 Nakkehoved		8·3	6·3	7·7	14·8	12·2	**20·1**	13·5	11·2	5·9
6 Fakkebjerg		6·6	7·7	11·1	12·0	8·4	17·2	**19·3**	14·4	3·2
7 Gjedser		8·2	4·3	15·4	12·0	9·1	14·0	**18·3**	16·0	2·7
Inland Løgumkloster	10	6·0	9·0	6·6	17·2	9·0	15·6	10·3	**20·2**	6·1
Herning	45	5·0	6·4	7·5	10·1	10·2	16·8	13·2	12·1	18·6

Table I—Mean Wind Strength (Beaufort Scale) from Each Direction

	Years of Records	*N.*	*N.E.*	*E.*	*S.E.*	*S.*	*S.W.*	*W.*	*N.W.*	*Calm*
1 Hanstholm		2·6	2·9	3·1	2·6	2·4	3·1	3·6	4·0	
2 Bovbjaerg		3·2	3·3	3·2	3·2	3·4	4·0	4·3	4·6	
3 Skagen		2·8	3·0	3·1	3·0	3·2	3·2	3·6	3·6	
4 Fornaes		3·0	3·7	3·8	3·6	3·0	3·0	3·1	3·2	
5 Nakkehoved		3·3	3·2	2·8	2·4	2·2	2·5	3·3	3·5	
6 Kjels Nor (Fakkebjerg)		2·9	3·1	3·7	3·7	3·3	3·8	4·0	3·9	
7 Gjedser		2·7	3·3	4·0	3·5	3·3	4·1	4·5	4·2	

Table D—Sunshine Duration: Mean Monthly Total Hours

Station	*Altitude (Metres)*	*Year*	*Jan.*	*Feb.*	*Mar.*	*April*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Duration of Records (Years)*
Tylstrup	12	1818	41	70	115	182	287	286	268	220	165	105	56	23	11
Bovbjaerg	41	1345	29	49	90	154	210	206	196	155	129	73	39	15	24
Søllinge	67	1354	28	42	81	156	202	222	217	153	136	65	37	14	15
Tystofte	13	1818	44	74	120	184	288	272	248	216	167	114	61	30	12
Lyngby	34	1750	41	62	113	184	276	270	255	202	165	105	50	26	14
Naesgaard	10	1771	35	68	109	183	287	273	247	214	170	108	53	24	12

Table E—Relative Humidity per cent (Range for 26 stations 80/87%)

Station	*Altitude (Metres)*	*Year*	*Jan.*	*Feb.*	*Mar.*	*April*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*
Thisted	12	84	91	91	87	80	75	76	79	82	80	87	89	91
Tylstrup	12	83	92	89	87	81	73	73	75	81	83	87	89	92
Tystofte	13	84	92	92	87	78	75	74	78	79	82	86	90	87
Lyngby	34	86	94	91	87	77	78	78	78	81	86	90	92	92
Gjerlev	34	80	90	88	82	74	69	60	72	77	81	87	90	91
Tønder	4	86	92	91	90	85	79	78	78	81	84	88	90	92

Table F—Number of Days Each Month with Rain > 0·1 mm. (Range for all stations recording 194/118)

Station	*Altitude (Metres)*	*Year*	*Jan.*	*Feb.*	*Mar.*	*April*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Total Annual Precipitation*
Thisted	12	154	15	11	13	10	10	9	10	15	13	16	15	17	716
Varde	12	157	14	11	12	11	10	11	12	16	14	15	15	16	755
Askov	65	155	13	11	12	12	11	11	13	16	13	15	14	15	733
Hals	3	125	10	8	9	9	10	9	10	14	11	12	11	12	556
Tylstrup	12	138	12	9	10	10	10	10	11	15	11	12	14	14	618
Kolindsund	3	165	14	11	14	13	12	11	12	16	15	16	15	16	593
Lyngby	34	163	14	12	13	13	11	11	13	16	14	15	14	17	592

Table G.—Wind Direction and Force at some Coast Stations. Percentage Frequency of Winds of Different Force (Beaufort Scale)

	Years of Records	0	1	2	3	4	5	6	7	8	9	10	11	12	*SUMMARY Approx. miles/Hour* <4 0,1.	5–12 2,3.	13–24 4,5.	>24 6–12
1 Hanstholm Fyr, N.W. Jutland	50	2·1	17·4	22·3	26·1	14·4	7·4	5·2	2·1	1·4	0·3	1·1	0·03	0·001	19·5	48·4	21·8	10·3
2 Bovbjaerg, West Jutland ..	47	2·1	10·5	18·4	23·7	16·6	8·9	9·1	4·0	3·9	0·9	1·7	0·2	0·04	12·6	42·1	25·5	19·8
3 Skagen, North Tip of Jutland	50	3·9	16·8	20·2	22·5	15·7	9·7	6·0	3·2	1·2	0·3	0·4	0·02	0·004	20·7	42·7	25·4	11·1
4 Fornaes, East Jutland ..	47	3·4	11·9	26·2	29·3	11·6	6·4	4·1	2·8	1·7	1·1	1·5	0·01	0·002	15·3	55·5	18·0	11·2
5 Nakkehoved, North Sjaelland	50	5·9	23·8	23·3	19·5	12·7	7·6	4·0	1·7	1·0	0·1	0·3	0·02	—	29·7	42·8	20·3	7·1
6 Fakkebjerg, South Langeland	50	3·2	9·6	16·3	26·0	17·8	10·6	8·6	3·5	2·7	0·9	0·7	0·05	—	12·8	42·3	28·4	16·4
7 Gjedser, South-east Falster ..	50	2·6	10·8	16·2	21·3	14·7	13·3	11·0	5·4	2·9	1·0	0·8	0·04	—	13·5	37·5	28·0	21·1

Appendix 3

STUDIES OF THE SUSCEPTIBILITY OF TREES TO ATTACK BY SECONDARY INSECT PESTS

Paper by Erwin Schimitschek and Elisabeth Wienke (1963)
Translation by J. M. B. Brown

AUTHORS' SUMMARY

The object of these studies is the recognition of the symptoms which distinguish trees susceptible to attack by secondary pests: information is sought also about the causal complex. The work was focussed on Sitka spruce, which, in Schleswig-Holstein, shows, at a relatively early age, physiological disturbances, a marked susceptibility and, in effect, more or less severe attack by *Dendroctonus micans*. Investigations were, however, made not only with Sitka spruce, but with Norway spruce (*Picea abies*) also, for comparison.

Examinations of bark anatomy showed well-defined annual rings in healthy Sitka spruce, with a row of parenchyma cells amid the sieve tube bands in the bast first laid down. From the second year the sieve tubes, sometimes under pressure from layers of stone-cells in the outer bark, begin to collapse. The medullary rays are sinuous, with an oblique course, and may contain resin canals.

With incipient physiological disturbance of Sitka spruce, the parenchyma cells begin to lose their contents and the medullary rays likewise (early stage of susceptibility to attack). There is still no evidence of cambial injury.

With protracted disturbance ("*Dendroctonus*-prone stage") large traumatic resin ducts appear in the wood and the cambium degenerates. There is some increase in parenchyma formation, while the cells of parenchyma and medullary rays are partly depleted. With advancing *Dendroctonus* attack these symptoms become more prominent and the nuclei in the medullary rays disintegrate: further intensification of the symptoms presages death.

Sitka spruce infected by fungi shows normally-filled cambial cells, no fusion of sieve plates, and medullary rays which are not bent. Parenchyma cells are numerous, with something of a chess-board pattern, and well filled. Characteristic are the many traumatic resin ducts and stone cell plates.

Investigations of the water economy showed, in the natural range of the European spruce in Lunz-am-See (Lower Austria) that the youngest, 10-year-old trees have the greatest speed of sap stream and highest transpiration: both rates decline gradually with increasing age. In artificial stands of European spruce in Schleswig-Holstein, the values for both transpiration and for sap stream speed are appreciably lower than in the optimum zone of indigenous spruce. For young Sitka spruce the values are a little higher than for indigenous spruce in Austria: but with advancing years the values decline—rapidly from the age of 40.

Physiological disturbance of Sitka spruce results in a fall in speed of sap stream and in transpiration, in proportion to the degree of disturbance; a like effect is caused in Sitka spruce attacked by *D. micans*, *Neomyzaphis*, *Fomes*, honey fungus, or canker. Broadly the degree of disturbance in the water economy is proportional to the extent of the disease.

Evaporation in Schleswig-Holstein is 10, occasionally up to 20, times as great as in Lunz, due to the powerful evaporative strength of the wind.

Cryoscopic examination of needles of healthy Sitka spruce indicated a fall in osmotic pressure of the sap with increasing age. Physiological disturbance appeared to result in a lowering of osmotic pressure, age for age, as compared with healthy trees; the same was found in dying trees. But when the tree became attacked by insect or fungus, there was evidence of a rise in osmotic pressure, subject to the proviso that the wide scatter of values made any inference uncertain.

Measurements of electrical resistance of the living bark showed a very high resistance for young spruce

at Lunz-am-See, with a fall in older trees. Measurements on healthy, 30-year-old Sitka spruce trees in Gahrenberg Forest showed (with spruce of diverse provenances) a fall in resistance with increase in diameter.

In Schleswig-Holstein resistance values on young Sitka spruce were relatively low and declined with increasing age or diameter: 10-year-old European spruce gave appreciably higher values, but yet not equal to those at Lunz.

First measurements of electrical resistance of the bark of Sitka spruce (a) in health, (b) in a physiologically disturbed state, and (c) attacked by *Dendroctonus micans*, showed for all age classes, higher values for (b) and lower values for (c), as compared with (a). Honey fungus and canker seemed to cause higher resistance: in trees affected by *Fomes* the values were widely dispersed and difficult to interpret.

It was demonstrated that the high susceptibility of Sitka spruce in Schleswig-Holstein is connected with certain environmental factors bringing about serious disturbance of the water economy. The lessons to be learnt about the use of forest trees outside their natural range are discussed.

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