Forestry Commission

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Beech Bark Disease

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FRONT COVER: A stem heavily infested by the beech scale
insect *Cryptococcus fagisuga*. Patches of bark killed by the
fungus *Nectria coccinea* can be seen as dark areas within
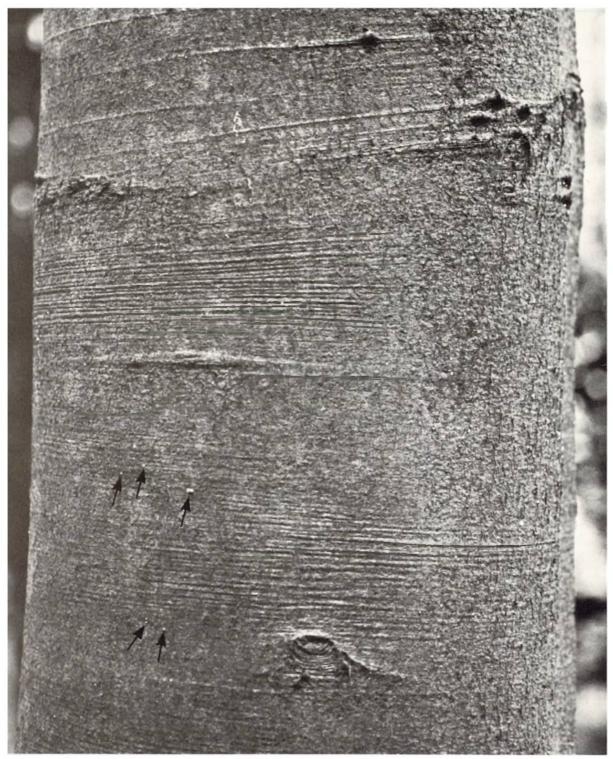the mass of white wax secreted by the insects. *(24663)*.

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Plate 1. A light infestation by the beech scale *Cryptococcus fagisuga.* A few of the small colonies (seen as dots of white wax secretion) are arrowed. *(A10824).*

Beech Bark Disease

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Introduction

The European beech, *Fagus sylvatica* L., is one of our most attractive trees, especially when displaying the pale green of its spring and early summer foliage. Various ornamental varieties, including the well-known copper and purple forms, are common in parks and gardens. Beech is native over a wide zone of central, east-central and western Europe, including southern and eastern Britain, and its range extends into the mountains of southern Europe (Brown, 1953). In Britain, where it has been widely planted, few natural beech woods remain, but semi-natural stands form an apparent climax woodland on the Chilterns and beech is a major component of some ancient woodlands on the more acid soils within the Hampshire and London Basins. In these areas it has considerable ecological importance. Beech can tolerate moderately calcareous soil conditions, and on many chalkland areas it has been planted during the last two centuries or has maintained itself by natural regeneration following earlier plantings.

Beech timber is strong, even textured, and relatively easily worked, and high quality stems are much prized. However, most of the high quality timber used in Britain is imported from the Continent, while much of our own lower grade material is used for pulpwood and firewood.

On trees suffering from beech bark disease, patches or large areas of bark are killed by the fungus *Nectria coccinea* (Pers.) Fr. following heavy infestations by a minute sucking insect, the felted beech coccus or beech scale *(Cryptococcus fagisuga* Lind.) This is considered to be the most serious disease affecting British beech, although its severity varies geographically and temporally.

Early records indicate that the disease was first observed at least 150 years ago, but must certainly have been affecting trees from a much earlier date. The insect and fungus both occur over much of the European range of *Fagus sylvatica* and the disease occurs in many forests within this area. The disease has also occurred since the early years of this century on American beech, *Fagus grandifolia,* in north-eastern USA and south-eastern Canada following the accidental introduction of *C. fagisuga* to Nova Scotia around 1890 and its subsequent

spread to areas further west and south-west (Ehrlich, 1934).

The disease can be most simply described as the result of sequential attack by insect and fungus. It seems appropriate to consider first this model and then to discuss the more complex aspects of disease development.

Development of the Disease and its Symptoms

Beech bark disease is very variable in the nature and severity of the symptoms displayed on individual trees and there are differences between European and American beech in their response to attack. The aetiology was established by work on American beech, and it is impossible to give a complete account of the problem in Europe without reference to this work. We will draw attention to the major differences in the New World and Old World forms of the disease. The North American research provided the first evidence for the straightforward sequence of insect infestation followed by fungal infection (Ehrlich, 1934). In the North American forests the insect, an exotic pest, was advancing into previously unaffected stands and the build-up of its infestations was clearly followed by attack by *Nectria coccinea* var. *faginata* Lohman, Watson and Ayers, a previously undescribed variety of the fungus.

The first sign of insect attack is the appearance of specks of wool-like white wax secreted by the minute yellow larvae and adults (Plate 1). With the build-up of the insect infestation over several years, the wax cover may increase to a complete covering of much of the main stem often referred to as 'whitewashing' (Plate 2). The wax frequently persists on the bark for some years following its secretion and may become blackened by the growth of saprotrophic fungi. On many trees the infestation does not reach extreme densities, and in addition the timing of initial attack and the subsequent rate of build-up may vary. Thus it is rare, at least in Europe, to see more than a small percentage of trees very

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heavily infested at any one time, although there is often a peak of infestation within a stand where such trees may be very conspicuous. In North American forests, where *Fagus grandifolia* is exposed to the insect for the first time, heavy infestation is more frequently observed.

The feeding activities of the insect induce alterations in the bark and cambium which eventually give rise to externally visible abnormalities. Sites of intensive feeding are often marked by pits or 'dimples' on the stem (Thomsen *et al.*, 1949) (Plate 3) which are formed due to abnormal and greatly reduced development of xylem beneath the colony (Lonsdale, 1983a). A more general reduction in annual increment occurs when the overall infestation is high. Despite these obvious effects on the stem, the cambium is rarely killed by the insect alone except perhaps on very thin-barked trees (D. Lonsdale, unpublished). However, localised death of the cork cambium (phellogen) and cortex may give rise to fissuring of the infested bark surface (Plate 4). Wound phellogens then form within the cortex, isolating the outer dead tissues and forming a rough, dead outer bark (a rhytidome) which is typical of many tree species but usually absent in beech. Formation of such a rhytidome results in the decline of the insect population, restricting colonisation to the fissures which form protected settling sites where living cells are near enough to the surface for insect feeding to take place. Even before this stage is reached, there may be some loss of feeding sites due to the induced lignification of parenchyma cells (Malphettes, 1981).

The first sign of *Nectria coccinea* infection on European beech is usually the exudation of liquid from one or more points on the trunk around which algae, lichens and colonies of *C. fagisuga* tend to die out (Plate 5). Here, *Nectria* is killing bark tissue, including the phloem and cambium, and also staining the outermost xylem. The liquid exudes from these tissues most copiously in spring and autumn and appears to be derived both from sap and the necrotic breakdown of the tissues, aided by secondary saprotrophs ('saprophytes'). Darkening and congealing of this 'slime-flux' gives rise to a tarry appearance, and to the descriptive term 'tarry spot'. The bark tissues, when exposed by a knife cut, are characteristically orange-brown but may be dark brown or black in old lesions.

The severity of *Nectria* attack may vary from the development of one or two small lesions which soon become surrounded by callus to the rapid girdling of the tree by the coalescence of many lesions or a few fast-developing ones. In large, thicker-barked beech, *Nectria* lesions sometimes do not penetrate to the cambium and thus can be delimited entirely within the bark by wound periderm. This is perhaps more typical of American beech infected by *N. coccinea* var. *faginata*

(Ehrlich, 1934) in which the lesions are often restricted to a few centimetres in width and are frequently circular, rather than elliptical or irregular. Fruiting of *N. coccinea* (Plate 6) often occurs on bark overlying older lesions and can give the stem a reddish appearance where lesions are extensive. A dead stem of European beech covered by fruit bodies of *N. coccinea* does not, however, always indicate beech bark disease, since the fungus often fruits on trees killed by suppression, etc.

A number of gross external symptoms may be associated with attacked trees but their exact cause is the subject of some debate. In Britain premature seasonal yellowing of the foliage often occurs on heavily insect-infested and *Nectria*-girdled trees. However, it is not uncommon for them to sustain quite severe attacks of the disease without showing foliar symptoms if growing in good conditions. In lethal attacks there may be several seasons during which leaves are under-sized and sparsely produced. The yellowing condition is accentuated by lime-induced chlorosis on some calcareous soils and this is alone responsible for much of the yellowing of beech and other species on the chalklands of southern England.

Trees killed by *Nectria* may be secondarily invaded by various saprotrophic fungi, the fruiting structures of which may be seen on the bark surface. These include *Diatrype disciformis* (Hoffm.) Fr. and *Hypoxylon fragiforme* (Skop.) Kickx (Parker, 1974a). Like *N. coccinea* itself, such fungi may also occur on trees which have died from causes other than beech bark disease.

Attack by decay fungi is common on trees bearing *Nectria* lesions. Ambrosia beetles, especially *Trypodendron domesticum* L., bore deeply into the xylem underlying diseased bark and these galleries often seem to be infection courts for *Bjerkandera adusta* (Willd. ex Fr.) P. Karsten, a white-rot fungus which may cause the bole to snap, sometimes whilst the tree is still alive, at a height of about 3 to 5 metres (Plate 7). In some parts of continental Europe the typical cause of this 'beech snap' is *Fomes fomentarius* (L. ex Fr.) Fr.

The Insect and its Ecology

Cryptococcus fagisuga Lindinger (= *Cryptococcus fagi* Baer.) is a minute scale insect, classified in the order Homoptera, family Eriococcidae, which feeds only on beech trees (*Fagus* spp.). Like a number of similar scale insects, it is parthenogenetic, populations consisting only of females. The lemon yellow adults reach up to 1 mm in length and are immobile with only vestigial legs and antennae, being attached to the bark by their sucking mouthparts. They are present throughout the summer

usually from May/June to September, increasing in size and becoming distended with eggs as they reach maturity. They may occur singly or more usually in colonies, some of which may contain hundreds of individuals and coalesce with others, secreting an extensive cover of protective white wax. The eggs, which are large in relation to the adult, are laid from June to September and are protected by 'ovisacs' formed from the wax. They take on average 25 days to hatch into the first instar which is the active dispersal stage and is found from July to November. It is the only instar which possesses functional legs – hence the name 'crawler'.

Crawlers are active during the day and the number of active individuals, as well as their rate of movement, increases with temperature. The largest numbers of highly active crawlers can usually be seen on warm days during September. Some of those that wander over the bark surface fall off and are carried away by the wind, a proportion being deposited on new hosts. Present estimates suggest only a short range of dispersal, 10 metres or so, from 'source' trees. However, about 1 per cent of dispersing crawlers are carried up above the canopy by turbulent air and may then be dispersed over much greater distances both within and between stands. The distance over which long range dispersal occurs depends only on the wind speed and the ability of the crawlers to survive in the prevailing conditions (Wainhouse, 1980). Most crawlers, however, do not disperse from the parent tree but settle under old colonies or wander over the trunk, seeking new feeding sites.

After the crawlers begin to feed, they gradually become so distended that they are unable to walk. At this stage the dispersal period is over and they overwinter in their settled positions, moulting to the pre-adult or second instar during April to June. Both the juvenile and adult stages secrete the white wax which increases in quantity during the spring and summer. This can give the false impression that the population of scales has increased dramatically on trees that appeared relatively uninfested earlier in the year. Conversely, persistence of several years' wax production may make the population seem denser than it is.

Within infested stands, many trees, even a majority, carry only low density insect infestations, and thus contrast with the few trees which are very heavily infested. These 'whitewashed' trees usually occur singly or in small groups distributed throughout the stand. Studies with sibling and clonal trees have provided strong evidence for a genetic component in the resistance of trees to attack by *C. fagisuga* (Wainhouse and Deeble, 1980; Wainhouse and Howell, 1983a). There is also evidence that this natural variation between trees is complemented by considerable variation within

populations of scales. Experiments involving the transfer of insects between trees show that their survival is usually higher on their original host (Wainhouse and Howell, 1983b), suggesting that they have become adapted to these individual hosts, thus forming 'sub-populations' within the forest. Such adaptation would be encouraged by the isolation resulting from the relatively limited dispersal powers of the insects and the absence of outcrossing in parthenogenetic reproduction. The relatively poor survival of dispersing insects on trees to which they are not adapted partly explains why heavily infested and almost uninfested trees often occur side by side.

The Fungus and its Ecology

Nectria coccinea (Pers.) Fr., an ascomycete fungus of the order Hypocreales, is the species usually associated with the disease in Europe, while *N. coccinea* var. *faginata* Lohman, Watson and Ayres predominates in North America. The origin of the American fungus is obscure, since it is not known from forests uninfested by *C. fagisuga*. The European and American 'varieties' of the fungus have separate specific names in their imperfect stages; *Cylindrocarpon candidum* (Link) Wollenw. and *C. faginatum* Booth respectively. Another species, *N. galligena* Bres., is the sole fungal pathogen in a geographically isolated disease outbreak in West Virginia (Mielke *et al.*, 1982) and has also been named in connection with the disease in Denmark (Thomsen *et al.*, 1949). European beech is also attacked by *Nectria ditissima* Tul. & C. Tul., which causes a canker initiated on young twigs. The name '*N. ditissima*' formerly also included the beech bark disease fungus *N. coccinea*.

Three types of spore are produced by *N. coccinea* (Booth, 1959). Their respective ecological and genetic roles have not been studied in detail but it seems likely that they are involved at different stages, before, during and after the development of the bark lesions. The unicellular microconidia are perhaps involved in pre-infection development of the fungus on the infested bark surface since, unlike the other two spore types, they can be formed during saprotrophic growth on the surface of bark infested by the insect, at least under laboratory conditions (Lonsdale and Sherriff, 1983). They can be spread in water films and perhaps also by micro-arthropod vectors.

The other two spore types, macroconidia and ascospores, are formed in moist weather after bark death. Macroconidia occur in short-lived pustules (sporodochia) 1-2 mm across, which burst through the paper-thin outer bark, while ascospores occur in red,

pinhead-sized, more persistent perithecia, clusters of which succeed the sporodochia. Both spore types can be either water or wind-dispersed and can thus provide inoculum for re-infection and for the infection of new hosts. The ascospores are discharged whenever the weather has been wet (Parker, 1974b).

Relative Roles of Insect, Fungus and Environmental Factors

There has been much controversy over the relative importance of the insect, the fungus and abiotic factors in disease development. The most widely held view is that bark invasion by *N. coccinea* follows the development of dense populations of scales. Under normal conditions, the fungus has only a limited ability to invade healthy beech bark and the development of extensive lesions requires both physical and chemical alterations to the bark; alterations which are induced by the feeding activities of dense scale populations.

Hartig (1880, 1900), one of the first writers to describe the disease, considered the insect alone to be capable of causing serious damage but he later noted that the invasive ability of '*N. ditissima*' (which then encompassed our *N. coccinea*) was enhanced in the presence of heavy infestations of *Chermes fagi* (= *C. fagisuga*). On the other hand, Ehrlich (1934) found that *N. coccinea* var. *faginata* could invade wound-inoculated *F. grandifolia* bark, even when *C. fagisuga* was absent, leading him to suggest that the role of the insect was merely the breaching of the intact bark, principally by inducing fissuring of the surface, and thus facilitating fungal infection. Lyr (1967) also favoured a primary role for the fungus but suggested that the water deficit in the bark was a predisposing factor. On the other hand, Braun (1976, 1977) regarded the insect as the primary cause of all stages of disease development. Although climatic factors may have some role in disease development as suggested, for example by Zycha (1951), they are not generally considered to be a primary cause. These conflicting views are perhaps reconciled by recent work which has shown that massive *N. coccinea* lesions can be formed on stems either heavily infested by the insects or stressed by other factors such as drought, nutrient imbalance and root disease (Lonsdale, 1980a). This work suggests that a range of interactions between insect, fungus and environment is possible, a fact not fully appreciated in earlier accounts of the disease.

As an example of the influence of stress, most cases of 'beech bark disease' affecting trees 80 or more years old

in southern England occur in the absence of significant *C. fagisuga* infestation, and are apparently caused by the rapid invasion of trees by *N. coccinea* following stress associated with dry conditions (Lonsdale, 1980b). Other disorders, such as strip cankers associated with normally 'saprotrophic' *Hypoxylon* spp., are also common on such trees (Lonsdale, 1983c). There are thus a number of possible pathways whereby beech trees may be made susceptible to extensive invasion by *N. coccinea*, although heavy infestation by *C. fagisuga* is by far the most common. Whether all such conditions should be termed 'beech bark disease' is a matter of semantics, but they can all be clearly distinguished from death of bark caused by extreme environmental conditions such as sun scorch.

The ways in which *C. fagisuga* predisposes tissues to fungal invasion are not fully understood, but there is evidence that the fungus may benefit both by insect-produced pectolytic enzymes and from enhanced fungal pectolytic activity induced by an increase of pH in insect-infested bark (Perrin, 1983a). The lesions produced by *N. coccinea* on heavily infested trees may be very large, but the enhanced invasive ability of this weak parasite seems to persist only during and immediately after the heavy infestation. Decline in the insect population (Lonsdale, 1980b) or its artificial removal (Perrin, 1980) seems to be followed by some restoration of the tree's defences against invasion by *N. coccinea*.

The insect may also assist the establishment of *N. coccinea* on the tree before the onset of stress allows extensive fungal invasion, since the fungus can form part of the microflora which develops on the wax-covered bark and in the necrotic spots in the cortex (Lonsdale and Sherriff, 1983).

The damage caused by the insect alone can be serious, as evidenced by the severe reduction and disruption of xylem formation (Lonsdale, 1983a). Preliminary data from long term observation plots indicate that the lethal suppression of smaller trees is hastened by infestation, but that dominant and subdominant trees do not usually die without the obvious intervention of *Nectria*. The importance of the fungus is clearly shown in North America, where trees in the 'invasion front' survive heavy insect infestations until *N. coccinea* var. *faginata* makes its appearance (Ehrlich, 1934). The separate effects of insect and fungus on the host are difficult to study in Britain and continental Europe, since both organisms are usually present simultaneously. The suggestion that beech bark disease is primarily caused by the disruption and ineffective repair of the phellogen following insect infestation (Braun, 1976, 1977) cannot be regarded as tenable until experiments involving the exclusion of fungal pathogens can be devised.

Plate 2. A very heavy infestation by the beech scale.

Plate 3. A tree showing severe 'dimpling' and moderate beech scale infestation. *(37561)*.

Plate 4. Bark fissuring, induced by heavy and prolonged beech scale infestation. The fissures are themselves sites where conditions are favourable for persistence of the infestation after it has declined over most of the bark surface. *(37558)*.

Plate 5. 'Tarry spots', caused by the exudation of fluid from patches of bark killed by the fungus *Nectria coccinea*. *(37560)*.

Plate 6. A close-up view of the clusters of minute fruiting bodies (perithecia) formed by *Nectria coccinea* after it has killed an area of bark. *(37559)*.
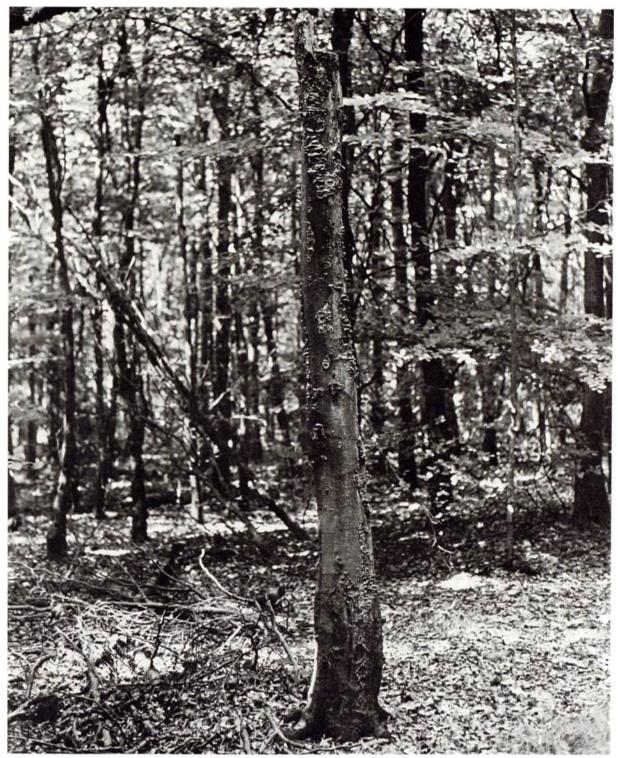
Plate 7. 'Beech snap' caused by a wood decay fungus, in this case *Bjerkandera adusta*, which has invaded a tree following attack by *Nectria coccinea*.
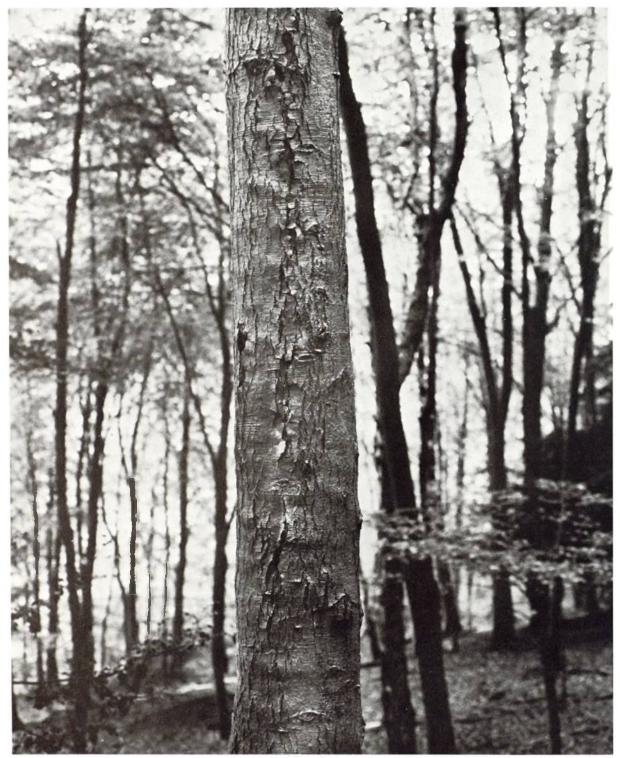
Plate 8. A highly defective stem, affected by long term *Nectria coccinea* cankering. Some longitudinal fissuring, induced by previous beech scale infestation, is also present in association with the cankers. *(A10826)*.

Temporal Patterns in Outbreaks of the Disease

Variations in the rate and severity of the attack on individual trees make it hard to assess the overall impact of the disease on an entire stand. At any one time the disease is absent from many trees in a stand, whilst on others it is building up, reaching a peak (perhaps with mortality) or declining. Thus, disease development follows a complex and dynamic pattern. Nevertheless, in the even-aged plantations of southern England, it is possible to recognise a period when the number of severely affected trees reaches a maximum and then declines. In consequence, outbreaks can often be divided into 'early', 'peak' and 'aftermath' phases at about 15-25, 20-35 and 30-40 or more years of age respectively. It is not clear whether all plantations go through this sequence or whether some remain relatively unaffected with no obvious peak of insect population density or disease occurrence. In other situations such as the naturally regenerated stands of continental Europe, or the previously unattacked stands of N. America, other temporal patterns of disease development may occur (e.g. see Houston, 1975).

Although limited mortality may continue to occur through the 'aftermath' phase in British plantations, there seems in general to be no threat to the production of a final crop. Mortality and reduction in growth may be significant during the 'peak' phase but the losses are unlikely to exceed substantially the volume of pulpwood or firewood which are, in any case, products of relatively low pecuniary value.

Factors Influencing Disease Severity

Host resistance to the insect

A major factor in the survival of individual trees is their susceptibility to infestation by the insect. As discussed above, European beech stands contain a proportion of relatively resistant individuals, but the degree of resistance is related to the genetic make-up of the scale populations. This variation of host and insect usually helps to ensure the survival of sufficient trees in a stand to meet most silvicultural requirements. The American beech, however, has been exposed to attacks by beech scale only during this century, and its obviously greater susceptibility may be due to the general absence of the resistance factors which have evolved in European beech trees. Clearly, the impact of beech bark disease has been much greater in North America than in Europe. In some North American forests, however, occasional clumps of resistant stems do occur (Houston, 1983a.)

Relationship of host resistance and age
Tree age may influence susceptibility to *C. fagisuga* infestation. In general, very young stems (under *c.*15 years old) of *F. sylvatica* and *F. grandifolia* rarely carry more than a light infestation, perhaps because of the relative lack of accumulated parenchyma tissue in the phelloderm. While there is no upper age limit for heavy infestation, an accumulated thickness of outer corky bark on older trees may deter insect feeding. Heavy infestations are rare on old trees in Britain, but common in newly infested North American stands and in some parts of continental Europe (Perrin, 1977). The eventual decline of long-established scale populations is partly due to the response of the bark to *C. fagisuga* attack. This response involves the formation of layers of dead and sclerified cells which cannot support further feeding by the insects.

Mechanisms of host resistance to the insect
Little work has been done on the genetically determined mechanisms of resistance to *C. fagisuga,* but it may be presumed that biochemical factors are involved. There is, however, some evidence that stone cell layers in the cortex form a physical barrier to feeding. The effectiveness of these layers appears to be determined by their depth and continuity which varies between trees and may have a genetic basis (Lonsdale, 1983a). This variation can be recognised microscopically even in stems as young as 6 years old. In addition, prolonged feeding by the insect may induce lignification of bark parenchyma and rhytidome formation, as mentioned above.

Modification of host resistance by bark flora
Bark surface lichens are sometimes important in affecting colonisation by the insect. It may be encouraged to settle by some kinds of foliose lichen or the crustose lichen *Lecanora conizaeoides* (Ehrlich, 1934; Houston *et al.,* 1979). Areas of bare smooth bark alongside areas encrusted with *L. conizaeoides* and the alga *Desmococcus vulgaris* often carry much lighter *C. fagisuga* populations than the encrusted areas. Recent extension of the range and abundance of *L. conizaeoides* (Seaward and Hitch, 1982), due to its tolerance of atmospheric pollution, may have increased endemic levels of this insect. On the other hand, some crustose lichens and the fungus *Ascodichaena rugosa* Butin which grows in the phellem and forms a tough black stroma on the bark surface, can strongly inhibit establishment (Houston, 1976, 1983a; Houston *et al.,* 1979). Where such inhibitory lichens form a continuous covering,

much of the bark surface may be protected from the insect.

Host resistance to the fungus

Nectria coccinea is an opportunistic parasite which is unable to attack *F. sylvatica* in normal health. However, variation in fungal pathogenicity has been observed (Lonsdale, 1980a) and there is some variation in host resistance, as shown in experiments on seedlings (Perrin, 1984). Such variations may determine whether lesions will develop at a given scale infestation density. Such variation is perhaps of questionable significance, given the over-riding importance of the insect in the epidemiology of this disease.

Site factors

There have been many statements relating disease severity to site factors such as steepness of slope (see Parker, 1974a). In most of these statements the effects of site on the insect and fungal phases of the disease are poorly distinguished, so that the significance of the observations is not clear. Individual aspects of disease severity were, however, studied by Houston *et al.* (1979), who found that beech on the wooded slopes of a West Sussex chalkland valley supported higher populations of the insect than did trees in the valley bottom. They also found that the incidence of *Nectria* lesions was higher on trees in the mid-slope areas. It was not clear whether these patterns of disease development were related to the site topography or to soil variations across the chalkland valley profile. Subsequent studies in the same forest have, however, enabled some effects of soil variation within plantations to be assessed independently of topographic effects, by virtue of the presence of sharp, linear demarcations between a 'chalky' and a 'non-chalky' soil type (Lonsdale and Pratt, 1981). Both soil types were underlain by chalky drift, but the 'non-chalky' type included an upper horizon which was free from finely-divided chalk. At age 29, the trees on both soil types carried very similar *C. fagisuga* densities, but those on the chalky soil bore significantly more *Nectria* lesions, and such lesions were present on trees which had suffered only a moderate infestation by the insect.

The apparent effect of soil type on host resistance to *Nectria* infection may help to explain the occurrence on some sites of an atypical form of attack in which the stem undergoes non-lethal cankering over many years (Perrin, 1979). The stem lesions often reach only a few centimetres in length before being surrounded by callus, but fresh extension of the lesions occurs long after the insect population has declined to a light infestation. Such

cankering which, on steeply sloping sites, is often restricted to one side of the tree stem, can give rise to highly defective stems (Plate 8). In Britain the condition is found most frequently on very chalky soils and appears similar to that attributed by Day (1946) to the chalkiness of the soil *per se*. The mechanism for this apparently increased susceptibility to *Nectria* infection is not known but, bearing in mind the involvement of calcareous soil conditions in many cases, it is interesting to note that the calcium content of the bark may influence the pectolytic activity of *N. coccinea* (Perrin, 1983b) and therefore its ability to invade host bark.

Silvicultural factors

The effects of silvicultural practices on the rate of disease development are poorly understood, but various anecdotal accounts suggest that thinning practices and the use of species mixtures can be important. Winter shading of beech stems in the mixed North American forests by hemlock *(Tsuga canadensis)* may perhaps favour the build-up of *C. fagisuga* by protecting the insect against repeated freezing and thawing (Twery and Patterson, 1983). In Britain the presence of a conifer nurse is widely believed to reduce disease incidence, but no studies of this have been made in adequate detail. In pure stands, a thinning experiment initiated during the early phase of insect infestation to compare four stocking densities, showed no significant differences in insect population increase over 8 years although mortality was somewhat greater in the denser stands in which there was more competition between trees (Parker, 1980).

Factors directly affecting the insect and the fungus

Climate
Temperature extremes, and perhaps other climatic factors, can affect the survival of the insect. D.R. Houston (unpublished) observed widespread high mortality in the USA as a result of extreme winter cold (*c.* $-40°C$) and also following an exceptionally hot spell (*c.* 32°C) in April when the unshaded stems received direct sunlight. Rainfall seems also to affect the insect, since bark exposed to heavy rain-wash is often relatively free from infestation. However, detailed measurements on a few trees over a season indicated that less than 1 per cent of crawlers were washed off by rainfall during the crawler dispersal period (I.M. Gate, unpublished observation). Climate may affect the endemic insect population density which underlies the patterns of build-up and decline that occur within stands. The temperature and moisture tolerances of *N. coccinea* and *N. coccinea* var. *faginata* (Parker, 1974b; Ehrlich, 1934)

seem unlikely to be limiting factors in any of the regions currently affected by beech bark disease.

Natural enemies of insect and fungus
No insect parasites have ever been recorded from *C. fagisuga* but the predatory coccinellid beetles *Chilocorus* and *Exochomus* spp., larvae of the cecidomyid fly *Lestodiplosis* spp., together with some other insects and mites, will feed on it. Although substantial predation has occasionally been noted, generally predators seem unable to hold the infestations below damaging levels (Mayer and Allen, 1983). The entomogenous fungus *Verticillium lecanii* Viegas is frequently present in scale colonies (Lonsdale, 1983b) but, like the predatory arthropods, is only abundant in populations which are at least locally dense on the tree. Interestingly, *V. lecanii* is also parasitic on *N. coccinea* (Lonsdale and Sherriff, 1983) but any value which it may have as a natural control agent may be restricted by its limited ability to grow out from its insect foodbase and survive competition from other members of the bark microflora. This microflora is typically dominated, on scale-infested trees, by *Cladosporium cladosporioides* (Fresen.) de Vries which is mainly responsible for the characteristic blackening of the insect wax. In culture, *C. cladosporioides* inhibited the growth of *V. lecanii* and other antagonists of *N. coccinea* such as *Fusarium lateritium* Nees., while allowing unimpeded growth of *N. coccinea*.

Once *Nectria* has begun to invade the bark, it seems unlikely that antagonistic fungi can reduce the rate and extent of lesion development, although some species can replace the pathogen in older parts of the lesions (Cotter, 1977; Gotwols *et al.*, 1980; Lonsdale and Sherriff, 1983). Survival and fruiting of *N. coccinea* in older lesions may, in this way, be reduced, as has been shown in the case of parasitism by the fungus *Nematogonum ferrugineum* (Shigo, 1964). Interestingly, the pathogenicity of *N. coccinea* var. *faginata* in artificially established bark lesions is reduced by pre-inoculation infection of the culture with *N. ferrugineum* (Houston, 1983b).

Control Measures

Infestations of *C. fagisuga* can easily be removed by scrubbing the trunk with a mild detergent. Tar oil winter washes applied at high volume as recommended for fruit trees are also highly effective and should be applied after leaf fall while the buds are dormant. The organophosphorus insecticides Diazinon and Malathion can be used when the tree is in leaf but, unlike tar oil wash, are not effective against the egg stage and should, therefore, be applied when eggs are absent; in winter or

spring. In general, the use of these chemicals is not regarded as desirable and the cost of any treatments, physical or chemical, can only be justified for trees of particular value.

Control of the insect, as well as reducing direct damage, can help to re-establish the tree's natural defences against invasion by the fungus. Excision of *Nectria* lesions followed by fungicidal treatments (Collis, 1979) has not been clearly shown to have more effect than the natural defences of the tree in arresting lesion development. This treatment may, however, offer some protection against wood decay fungi which are often introduced by ambrosia beetles entering the stem via areas of dead bark.

Biological control of the insect or the fungus is unlikely to be developed. The most significant natural control seems to be the resistance of the trees to attack by *C. fagisuga,* but there will be little incentive to select resistant genotypes as long as natural resistance and escape from disease ensure the survival of the majority of trees within existing beech populations.

The economic constraints on artificial disease control leave the management of stands as the main potential means of limiting losses in British forests. Hitherto, affected stands have been managed by removal of diseased stems to salvage them or to attempt to reduce the spread of the insect and fungus by sanitation. Thinning has also been carried out in the hope that it would modify stand conditions in a way unfavourable for the build-up of the insect or the fungus. There is, however, no good evidence that any of these treatments reduces the rate of disease development.

Salvage of severely affected stems may be economically worthwhile in some cases. Heavily infested stems have a very small annual increment (Lonsdale, 1980a) and should be selectively removed whenever a thinning is carried out. Moderately and lightly infested stems should not be selectively removed, since they may well survive.

Sanitation, as opposed to salvage, thinning is not likely to be of value where the causal organisms of the disease are present throughout the stand or will inevitably become so. Trees heavily infested by *C. fagisuga* may be a locally intense source of infestation for neighbouring stems, but the studies on dispersal and rates of population development on individual stems described here suggest that these local sources are of little importance for the stand as a whole.

Some attempts have been made to evaluate the effect of thinnings on the subsequent build-up of scale populations, but the findings have been inconclusive, perhaps because the procedures used did not take account of the complexity and variability of disease development. The recognition, in even-aged stands, of

the 'early', 'peak' and 'aftermath' phases may help to avoid confusion in the future.

In general, stands in which disease has occurred may be replanted with beech if soil conditions are suitable. Although beech grows well on soils over chalk, it should not be planted on sites where finely divided chalk is present to the surface. Such soils are easily recognised because the soil particles, as well as visible chalk fragments, will effervesce when treated with dilute hydrochloric acid. Few other species will grow well on highly calcareous soils, but Norway maple, ash, sycamore, Small-leaved lime or Italian alder may be planted instead of beech if the soil is deep and fertile (Wood and Nimmo, 1962). Norway maple is perhaps the best choice if the soil is shallow (Evans, 1984). The use of a conifer nurse in a beech plantation may retard or reduce the disease development (Parker, 1974c; Coxwell, 1983) and may also increase the total productivity of the site (Coxwell, *op. cit.*).

The prospects for diseased stands in Britain seem generally quite good, judging by the performance of the trees in 'aftermath' areas. Despite some gaps in the crop, the stocking density and volume are compatible with theoretical yield expectations (R.A.G. Coxwell, unpublished). These older stands can be managed on a normal silvicultural basis, provided that defective stems with perennial cankering are selectively removed during thinnings. Continuing mortality, if significant at this stage, may be related to unsuitable site conditions, especially where severe lime-induced chlorosis is apparent.

The progression of disease is being monitored in a number of stands in a continuing research programme. Latest information is available from the Forestry Commission Research Station, Alice Holt Lodge, Wrecclesham, Farnham, Surrey GU10 4LH.

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