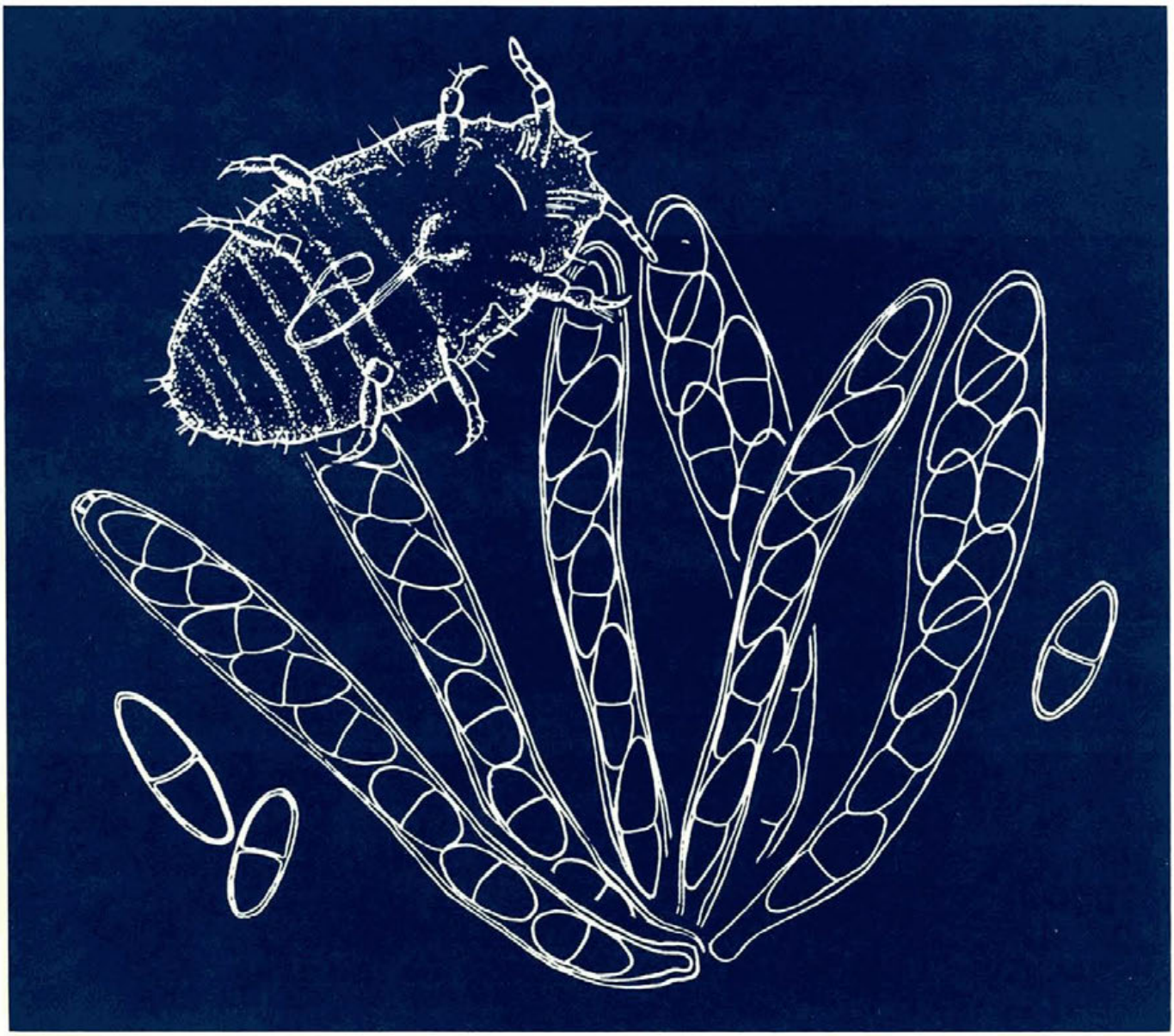
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Hamden, Connecticut
September 26-October 8, 1982





The working party conference followed this route, examining forests affected by beech bark disease. They followed the progress of the beech scale from east to west.

PROCEEDINGS, I.U.F.R.O. BEECH BARK DISEASE

WORKING PARTY CONFERENCE

SPONSORED BY THE

USDA FOREST SERVICE

NORTHEASTERN FOREST EXPERIMENT STATION

HAMDEN, CONNECTICUT

SEPTEMBER 26 - OCTOBER 8, 1982

October 1983

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PREFACE

This conference was the first full meeting of the Working Party since its inception at the Beech Bark Disease Colloquium held in Nancy, France in 1979. The meeting from 27 September to 7 October 1982 took the form of a study tour convened at the College of Forestry, University of Maine,with field trips in the Central New England States and New York and concluding at the U.S.D.A. Northeastern Forest Experiment Station's Center for Biological Control of Northeastern Forest Insects and Diseases, in Hamden, Connecticut. During the tour a series of conference paper sessions was held and field trips were made to sites illustrating various aspects of disease development in the U.S.A.

The meeting brought together many people recently active in beech bark disease research for discussions of current progress on all aspects of the disease. Most contributors were from North America but both the U.K. and Germany were represented and contributions from France appear as published papers.

In introductory sessions at the University of Maine, papers on the status of beech bark disease in both North America and Europe were presented. The college provided a base from which the group visited local 'aftermath' forests. The beech component of these forests was comprised of small trees from root sprouts of trees killed by the disease; larger, highly defective surviving trees; and a few trees unaffected by the disease which passed through Maine during the 1930's and 1940's. In subsequent field trips into New Hampshire, Vermont and New York successive stages in the westward progression of the epidemic were examined.

At the Bartlett Experimental Forest in the White Mountain National Forest in New Hampshire, where the disease caused severe mortality (the "killing front") in the 1950's, discussions and field visits centered on how beech bark disease has affected forest management. Although beech is the lowest value hardwood species, it comprised almost half the trees in the uneven-aged stands at Bartlett. To the west, in the Green Mountain National Forest of Vermont, where the disease was severe in the late 1950's to early 1970's, stands currently developing in the aftermath of the disease were visited. Still further west, at the State University of New York's Adirondack Ecological Center at Newcomb, New York, the group saw trials designed to reduce excessively large amounts of beech by using herbicides in conjunction with shelterwood cutting.

Here, at the Adirondack Ecological Center, the final paper sessions dealing with beech bark disease/forest stand relationships and the ecology of the causal complex, beech scale and Nectria were held.

The closing sessions at the Center for Biological Control, Hamden, CT. focused on where research was still needed to provide guidelines for managing beech bark disease. Recommendations for future research appear at the end of these proceedings.

ACKNOWLEDGMENTS

We wish to thank the College of Forestry, University of Maine at Orono, Maine; Middlebury College, Middlebury, Vermont; and the Adirondack Ecological Center of the State University of New York, School of Forestry and Environmental Sciences at Newcomb, New York, for graciously providing meeting rooms and/or lodging facilities. We appreciate very much the efforts of personnel from the States of Maine, Vermont, and New York, and from the University of Maine, Middlebury College, University of Vermont, the State University of New York, the Connecticut Agricultural Experiment Station, and the Northeastern Forest Experiment Station for their kind assistance during the conference tour. We owe a special thanks to Denis Lachance, Laurentian Forest Research Centre, Canadian Forestry Service, and Klaus Lang, Lehrstuhl für Forstbotanik, for providing the French and German summaries; to David Lonsdale, Forestry Commission Research Station, for help in editing the European contributions; and to Laura Cricco, Northeastern Forest Experiment Station, for her careful attention in handling many of the meeting arrangements and for readying the manuscripts for publication.

-- David R. Houston, Northeastern Forest Experiment Station,

-- David Wainhouse, Forestry Commission Research Station,

Cochairpersons, IUFRO Working Party on Beech Bark Disease.

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BEECH BARK DISEASE IN GREAT BRITAIN[1]

E. John Parker[2]

Abstract.--The status of beech bark disease in Great Britain is summarised with respect both to historical perspectives and to the contemporary situation. Features of the disease which relate particularly to its occurrence in Great Britain are listed. Some tentative findings from recent observations and experimental work are presented.

INTRODUCTION

European beech (Fagus sylvatica L.) is an important constituent of the deciduous broadleaved forests of north-west Europe. About half of the beech in Great Britain is grown in southern England where it is the major hardwood planted on the chalk downlands. It will grow better on these calcareous soils than most other broadleaved trees.

Beech bark disease in its strictest definition is a complex disorder primarily attributed to the effects of a pathogenic species of the ascomycete fungus Nectria Fries, following infestations of the felted beech scale Cryptococcus fagisuga Lind. on the bark of Fagus species. These disease organisms appear to be endemic in stands of F. sylvatica in northwest Europe (Thomsen et al 1949). In Great Britain during the 19th century the death of many European beech was ascribed to the effect of the insect alone. British accounts at that time described it as a most destructive pest. Indeed, eighty years ago the Revd. Wilks (1902), commenting on the situation in southeast England, feared that "..... beech is doomed all over the country, and ..... the next generation will only know by pictures and reports how gloriously beautiful our forest beeches have been". Yet, although serious local outbreaks of the disease can occur, the fears of widespread devastation of beech in Great Britain have never been realised.

Beech bark disease appears to be most prevalent in pole stage beech i.e. with an age range of 20 to 45 years. Extensive plantings of beech in the 1930s fostered the major outbreaks of beech bark disease which built up in the 1960s. The peak of post-war beech plantings occurred in the 1950s, and it is these plantations which will be at their most susceptible during this current decade. Some commentators have suggested that the disease is cyclic in nature, with upsurges every 30 to 40 years. This may be explained in part by the natural tendency for an equilibrium to form in a host/pathogen relationship following an outbreak, particularly where the disease occurs in an endemic situation. However, it is more likely to be a reflection of the peak periods of beech plantings which subsequently give rise to a corresponding series of peaks in disease incidence at the time of maximum host susceptibility.

Variations in symptom expression between diseased beech in different localities can in part be attributed to differences in tree age and local site and climatic factors (Parker 1974a). The occurrence of similar symptoms on older beech trees initiated by adverse environmental conditions (Lonsdale 1979, 1980) also contributes to this variability.

HISTORICAL PERSPECTIVE

Following descriptions of a diseased condition of beech in Europe in the early 19th century, the first report from Britain seems to be that given by McIntosh (1849) who referred to a white rapidly spreading fungus which gave the bark of beech a snow-covered appearance. The latter part of this description would seem to apply to heavy C. fagisuga infestation, although

[1] Paper presented at the I.U.F.R.O. Working Party Conference, Hamden C T., U.S.A. 27 September to 7 October 1982.

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as this usually builds up over a few years, the rapid growth could refer more appropriately to bark surface colonisation by the light coloured mycelium of the fungus Athelia arachnoidea (Berk.) Jül. which commonly appears on healthy beech trunks in years when the summer months are dull and wet. Nevertheless, infestations of C. fagisuga can on occasions appear to change from the imperceptible to the obvious during a two to three year period due simply to the effect of a logarithmic phase of growth that can occur with most plant and animal populations.

Despite much concern about the noticeable infestations of C. fagisuga and associated beech deaths during the latter part of the 19th century, and fears for the general demise of beech in Britain such as those expressed by Wilks (1902), the beech remains one of the leading species of broad-leaved trees grown in Great Britain.

Not all beech trees or beechwoods are seriously affected by the disease. Newstead (1903) referred to the sparse occurrence of C. fagisuga on a stand in the Cotswolds (limestone hills in southwest England). Seventy years later the owner of an estate there claimed that the virtual absence of disease in his beechwoods, which were of excellent form and growth, was the product of continued good management for well over a century (J. Workman, pers. comm.).

Yet the disease problem in the 20th century is a continuing one, and the overall picture now is perhaps not too different from the one seen by our predecessors a century or more ago.

Perhaps the most significant step in our understanding of beech bark disease was the publication of John Ehrlich's monograph in 1934, following his investigations in North America during the early 1930s. It is of interest to note that he subsequently became for a time a Research Fellow at the Commonwealth Mycological Institute, Kew, England, from where he was able to observe for himself the disease in British beech-woods. His initial reaction was that the endemic disease situation amongst British beech differed markedly from the effects of the beech bark disease epidemic occurring in northeast U.S.A. and eastern Canada. A possible explanation for this is that Ehrlich was shown mature beech stands, young plantations being infrequent at that time. Older beech trees are prone to problems somewhat similar to beech bark disease, but the underlying cause and the expression of symptoms differ perceptibly from beech bark disease as it occurs on younger beech. With hindsight Ehrlich's comments seem to be an over-statement of the case. Certainly differences do occur (these are listed in more detail in the next section of this paper) but in essence the beech bark disease complex seems remarkably similar on both sides of the north Atlantic (Houston et al 1979).

Day (1946) brought the subject of beech pathology into discussion once again. His account was followed by Forestry Commission reports of bark dieback and death of beech (Peace 1950-55 inclusive; Peace and Murray 1956 and 1957; Murray 1957). In the course of these studies Peace (1954) commented that some if not all of three factors were associated with the disease: (i) a thin freely-drained soil, (ii) an old crop, often over 100 years of age, and (iii) a history of underthinning, leading probably to great competition among individuals in the stand.

In the 1960s renewed concern was expressed within the Forestry Commission over outbreaks of beech bark disease in young beech plantations. This led to the inception in 1969 of the current research programme, to which Parker (1974a, b) contributed initially, and which was extended in depth from the mid-1970s by the work of D. Lonsdale and D. Wainhouse involving mycological studies, investigations of host tree anatomy and resistance and insect dispersal.

DISTINCTIVE FEATURES ASSOCIATED WITH BEECH BARK DISEASE IN GREAT BRITAIN

Houston et al (1979) noted many of the features of beechwoods and beech bark disease in Great Britain which differed from those observed in North America. In brief, these include:-

1. the different species of host tree and consequent likelihood of differences in bark anatomy;

2. the predominance of young beech plantations often planted closely (1 x 1 m) as a pure first rotation crop in the 1930s and 1940s, but thereafter usually in mixture with a conifer nurse species;

3. the common planting of beech on chalk downland, where there is often a steep scarp slope;

4. the bark flora, including the fungus Ascodichaena rugosa Butin which occupies part of the surface which otherwise could be available to C. fagisuga, and the abundance of the crustose lichen Lecanora conizaeoides Nyl. ex Cromb. which may favour the initial establishment and build-up of the insect;

5. the presence of large old beech trees which

may harbour sources of insect and fungal inocula;

6. the species or variety of Nectria associated with death of beech bark following C. fagisuga infestation - in Great Britain this seems to fit the description of N. coccinea (Pers. ex Fr.) Fries and its imperfect state Cylindrocarpon candidum (Link) Wollenw.;

7. the occurrence of bark pitting associated with the feeding activity of C. fagisuga, which is evident on some but not all, of the young beech trees which become infested by the insect;

8. the secondary organisms associated with the decay of diseased beech stems, in particular the white rot fungus Bjerkandera adusta (Fries) Karsten often linked with the phenomenon of beech "snap".

My previous observations (Parker 1974a, b) suggested that on some sites with good nutrient and moisture supplies producing beech crops of high yield class, the disease became apparent at an early age (15 to 25 years) and subsequently became severe, particularly where a first silvicultural thinning was late (i.e. around 30 years of age). Disease outbreaks were usually first noticed in scattered groups within a plantation. This feature may in part be explained by the localised dispersal of C. fagisuga larvae (Wainhouse 1980), although local soil disturbance may also cause similar expression of some disease symptoms, i.e. chlorosis and/or tarry spots but not of C. fagisuga infestation (Lonsdale et al 1979; Lonsdale and Pratt 1981).

Recent discussion has focused on the methods of beech silviculture (Aldhous 1981; R A G Coxwell, unpublished). Certain observations and results of experimental work suggest that beech bark disease in Great Britain is worse in an overcrowded crop where competition develops between individual trees, and in particular between the developing crowns in the woodland canopy (Parker 1980, R A G Coxwell, unpublished). After a decade or more of observations on the beech bark disease problem in the young beech plantations of southern England it does seem that there is a short phase in the life of a beech plantation during which a "contracted epidemic sequence" of beech bark disease expression occurs. This is centred around a peak of severity at about 30 years of age, i.e. the current scheduled time for the first silvicultural thinning of these crops under Forestry Commission management. Initial incidence starts at about 20 years of age and by 45 years after one or two silvicultural thinnings (which at times may have been partly selective with regard to diseased stems), affected crops appear to be in an aftermath stage. Indeed in some compartments where a decade ago the disease appeared to be at peak severity, the beech crop now looks remarkably healthy, aesthetically pleasing, and with every indication of producing a good final crop of mature trees. An associated factor in the recovery of diseased beechwoods is the ability of the remaining trees to make compensatory growth and to close any gaps in the canopy caused by the death of neighbouring trees within a few years.

What seems to have occurred is a "natural thinning operation" in places where appropriate forest management has been delayed, usually on economic grounds. Only in very exceptional circumstances have affected areas had to be clearfelled and replanted. With regard to market considerations, the death of young pole-stage beech means that the volume available for pulpwood is reduced, but this is an area of uncertain and fluctuating economics. It is indeed difficult to estimate the loss of timber volume or economic return before the basic complexities of beech bark disease and the interaction with silvicultural management are evaluated.

If there were to be an increased movement towards the selection of good crop trees at an early stage, together with heavier and more frequent thinning of the beech crop to produce more high quality timber (Matthews and Newton 1982), then it is possible that beech bark disease may become much less of a problem in the future.

RECENT OBSERVATIONS

In order to gather detailed sequential data on host characteristics, symptom expression, and disease development both on individual trees and on a plot basis, a series of long-term observation plots each containing about 400 beech trees was established early in 1979. In selecting the crops for this experiment consideration was given to ensure representative combinations of age class, site type, and phase of disease. Each of the individually numbered beech trees is assessed annually for a range of host and disease characters. For each such character, descriptions and score classes have been closely defined in order to reduce the degree of error due to subjective assessment. It must be stressed that the data given below (which are mainly concerned with the incidence of C. fagisuga) are on the basis of only three years assessments and must inevitably be preliminary. The experiment in the first instance is scheduled to run for eight years before any major consideration is given to revision of the current procedure.

Initial C. fagisuga establishment on young trees and later the occurrence of stem pitting seems most favoured on the main trunk at a height of about 1 to 3 metres; a fact which relates in part to the pattern of passive dispersal and deposition of the insect larvae and may be partly due to the host bark characteristics on that portion of the young beech stem.

In the early phase of the disease when the crop is about 20 years of age, over half of the trees are still completely free from C. fagisuga infestation (over 75 per cent were "clean" in the 21 year old plot where beech is in mixture with a conifer nurse), the remaining trees usually bearing a trace or very light infestation of the insect. Moderate C. fagisuga infestation was present on less than 3 per cent of these young trees (with virtually no heavy infestation), whereas in the plots which were at about peak disease severity between 12 and 20 per cent of the crop bore moderate or heavy C. fagisuga infestations. In this peak phase of the disease when the trees are about 30 years old, uninfested trees are virtually absent. In many cases the more heavily infested trees are likely to die as beech bark disease takes its course, although in some cases recovery occurs. In the aftermath stage, by about 40 to 45 years of age, few moderately or heavily infested trees can be seen.

There is a marked tendency for the heavier C. fagisuga infestations to occur in trees of the dominant or co-dominant classes, rather than on sub-dominant or suppressed trees. This is perhaps because the bark of these faster growing trees more quickly reaches the stage when it may be anatomically and physiologically suitable for C. fagisuga infestation.

While in general the rate of increase of C. fagisuga infestations on polestage beech is relatively slow, some observations have indicated the possibility of a rapid and heavy build-up on a very small proportion of the crop. Thus, among forty trees under observation in a 35 year old pure beech plantation showing generally low colonisation by C. fagisuga, two initially uninfested trees became heavily infested within seven years (Parker, unpublished data); and one uninfested tree to which C. fagisuga inoculum was artificially introduced developed a heavy infestation after only four years (Houston et al 1979).

CONCLUSIONS

The normal healthy physiology of beech can be disturbed by abnormal external ("stress-inducing") factors of which, in the case of young pole-stage crops, the most important is a heavy infestation of C. fagisuga leading to the subsequent development of beech bark disease. To the owner or manager of a young beech plantation in which the disease can build up to a peak of severity by the time the crop is 30 years of age, the apparent extent of destruction and economic loss induces pessimistic thoughts about the wisdom of growing beech. However, the signs are that even in severely affected young stands the surviving trees will grow on to form a mature beechwood.

There are various characteristics of beech bark disease in Great Britain which differ from those observed in the epidemic which continues to advance westwards and southwards in North America, but the basic theme of the Cryptococcus/ Nectria association is similarly expressed. Current British research into the problem is aimed at elucidating the fundamental mechanisms of disease etiology and epidemiology. Once these basic mechanisms are more fully understood we will be in a better position to advise forest managers on preventative or remedial silvicultural practices aimed at reducing losses due to beech bark disease, and therefore to producing a greater volume and a higher quality of beech timber for use in the 21st century.

ZUSAMMENFASSUNG

Berichte über das Auftreten der Buchen-Rindennekrose in Grossbritannien in der Vergangenheit wurden zusammenfassend dargestellt. Die Befürchtungen, die von den Waldbesitzern und Bewirtschaftern erkrankter Buchenwälder in den 70er Jahren geäussert wurden, sind mit denen aus dem 19. Jahrhundert vergleichbar. Trotz der offensichlich örtlich schweren Krankheitsausbrüche in 20-40 Jahre alten Beständen ist Fagus sylvatica nach wie vor eine der wichtigsten Laubbaumarten in Grossbritannien.

Das Krankheitssyndrom ist in Europa, wo es endemisch, und in Nordamerika, wo es epidemisch auftritt, im Wesentlichen ähnlich ausgeprägt.

Die ökologischen Bedingungen für den Wirt und die spezifischen Mikroorganismen der Rinde bestimmen das Erscheinungsbild der Krankheit in England. In der Regel beginnt der Aufbau der Lauspopulation (Cryptococcus fagisuga) in rund 20jährigen Beständen. Der Höhepunkt der Infektion durch Nectria ist bei etwa 30 Jahre alten Buchen zu beobachten, worauf es zu Ausfällen kommt.

Im Alter von etwa 45 Jahren ist dann eine Phase erreicht, in der die Krankheit nur noch in geringer Intensität vorkommt. In den meisten Fällen weisen die überlebenden Bäume ein vergleichsweise besseres Wachstum auf und die betroffenen Bestände scheinen durchaus zu hiebsreifen Beständen heranwachsen zu können. Es gibt Hinweise dafür, dass die Krankheit bei zu grossem Dichtstand der Bäume verstärkt auftritt, besonders wenn Konkurrenz zwischen den sich entwickelnden Kronen herrscht. Unter Umständen könnten geeignete waldbauliche Massnahmen zu einer Verringerung der Krankheitsintensität und letztendlich zu besserer Holzqualität führen.

RÉSUMÉ

La physiologie normale d'un hêtre sain peut être modifiée par des facteurs externes anormaux ("provocateurs de stress") qui, dans le cas de peuplements de perchis de hêtres sont représentés par les infestations du C. fagisuga conduisant au développement de la maladie de l'écorce du hêtre. Pour le propriétaire ou l'aménagiste d'une jeune plantation de hêtres dans laquelle la maladie peut atteindre une culmination maximum au moment où le peuplement atteint 30 ans, l'importance apparente des dégâts et des pertes économiques conduisent à un pessimisme évident concernant la production du hêtre. Cependant, il semble que même à partir de jeunes peuplements fortement affectés, les arbres survivants puissent croître assez pour former une futaie de hêtres.

Il existe plusieurs particularités de la maladie de l'écorce du hêtre endémique en Grande-Bretagne. Elles diffèrent évidemment de celles de l'épidémie qui continue de s'étendre vers le sud et l'ouest de l'Amérique du Nord, mais la situation fondamentale de l'association Cryptococcus/Nectria s'y retrouve intacte. Actuellement, la recherche britannique dans ce problème essaie d'élucider les mécanismes fondamentaux concernant l'étiologie et l'épidémiologie de la maladie. Une fois ces mécanismes de base bien compris, nous serons dans une meilleure position pour conseiller les aménagistes forestiers sur des pratiques sylviculturales préventives ou correctives pour réduire les pertes dues à la maladie de l'écorce du hêtre, et ainsi à produire un volume plus grand et une meilleure qualité de bois de hêtre pour utilisation dans le 21ème siècle.

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CURRENT STATUS OF BEECH BARK DISEASE IN FRANCE[1]

R. Perrin[2]

Abstract.--The two organisms involved in beech bark disease are endemic everywhere in France. Nevertheless the disease is restricted to the northern part of the beech's range, where it grows on the plains. During the last five years beech bark disease has shown a general decrease in severity but there have been local increases in the north and north-eastern parts of forests where the disease has been present for a long time. Some French foresters feel that beech bark disease is a sanction against the growth of beech in inappropriate ecological conditions.

INTRODUCTION

Beech bark disease is well known to French foresters due to the severe damage it causes and they are thus able to give a good account of the disease situation in France. Thus I was able to prepare this report on the basis of information obtained from the French Forest Service. The current status of beech bark disease can be superimposed on the beech distribution map (Fig 1). Because of its ecological tolerance, beech is present almost everywhere in France especially in the northern part of the country. Nevertheless this map reveals that beech is a plain tree in the northern part of its range whereas it is a mountain tree in the meridional one, (Anon. 1981). Beech grows well in France in a wide range of site conditions.

Cryptococcus fagisuga is endemic everywhere even in high elevation stands of the Alps, Pyrénées and the mountains of the Massif-Central. Heavy infestations of the insect and the consequential dieback of beech after N. coccinea infection are restricted to the northern part of the beech's range particularly in the north-west where the disease has occurred for a long time (Fig 1). From time to time foresters have noticed heavy infestations of C. fagisuga with rare subsequent N. coccinea infections.

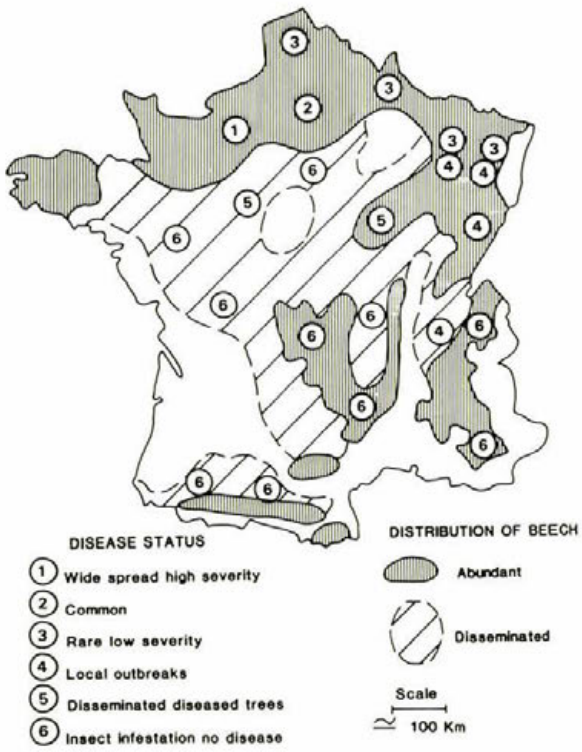


Figure 1.--Status of beech bark disease in France in 1982.

During the last four years, the severity of the disease decreased in most cases after a maximum level of damage during 1977. Recent records indicate a northward or north-eastward trend in the appearance of new out-

[1]Paper presented at the I.U.F.R.O. Working Party Conference, Hamden C T., U.S.A. 27 September to 7 October 1982.

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breaks of the disease. These local outbreaks have been observed following particular circumstances or special events.

Detailed observations are available from the region where the disease first appeared. The harvest of beech bark diseased trees from 1968 can be seen in Fig. 2 for three of the most important forests in Haute-Normandie. Despite some inaccuracy owing to changes in foresters assessment methods from year to year there

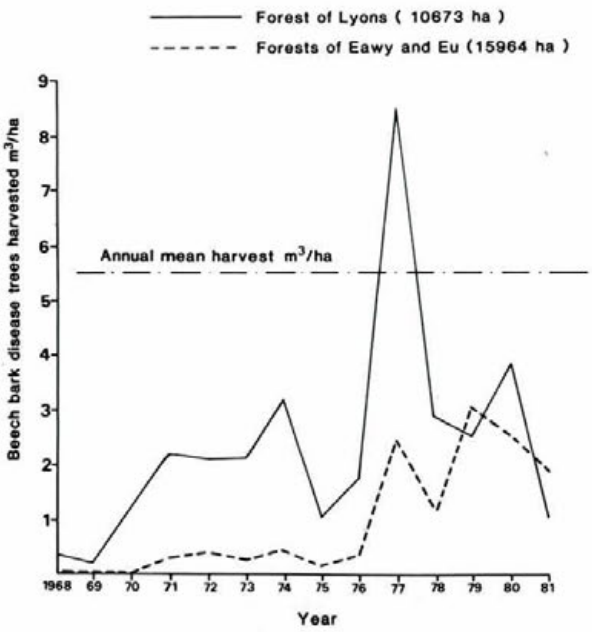


Figure 2.--Annual harvest of trees affected by beech bark disease.

is an obvious decrease in loss of trees to beech bark disease in the forest of Lyons following the peak in 1977. In this forest diseased trees were cut at an early stage but in the forests of Eawy and Eu, trees were removed late in the disease process. These opposite control strategies account not only for the different numbers of trees removed in these forests, but also for the changing rates of loss of trees from the disease (Fig. 2). Foresters from other regions (Alsace, Nord-Pas de Calais) have also noted the benefit of early removal of diseased trees, as recommended in the conclusions of the 1977 colloquium of beech bark disease.

SOME FACTORS INFLUENCING BEECH BARK DISEASE IN FRENCH FORESTS

Foresters agree that the sudden and exceptional increase in mortality in 1977 resulted from the 1976 drought. The influence of climate may also appear as a result of some particular site conditions. Disease development seems most intense in two opposite site conditions; shallow soils above calcareous material where beech may suffer from water stress and clay loamy soils of high yield potential whose physical components are sometimes unfavourable to the beech (pseudogley).

Most of the foresters have noticed that in some areas high density crops and pure stands of beech are the most diseased, whereas the contrary is true in other areas. Thinning which is a necessary silvicultural treatment reduces tree density but does not appear to reduce disease severity. On the contrary the observations of French foresters suggests that there is a renewed outbreak after thinning and efforts to reduce disease development by a stand thinning have proved to be of negative value.

Conflicting opinions are advanced about the most sensitive trees of a stand. Some people maintain that they are the dominant ones, others consider that only suppressed trees are diseased. Old over mature trees are very often sensitive but there is, however, a great variability from one tree to another. Some trees never succumb despite a heavy infestation of C. fagisuga and severe infection of N. coccinea.

CONCLUSIONS

During the last five years beech bark disease has shown a general decrease in severity but has spread northwards or north-eastwards. Nevertheless it is not possible to distinguish a disease front as in the U.S.A.; C. fagisuga and N. coccinea are endemic everywhere in France. The apparent extension of the diseased area is due to local increases in disease severity in the north and north-eastern parts of a region in which forests have been affected for a long time rather than new outbreaks inside a disease free area.

From the observations of French foresters it seems that beech bark disease occurs preferentially or is particularly severe on trees or in stands in adverse ecological conditions: sites near the limit of the ecological range of beech, pure stands, inappropriate silvicultural treatment and the artificial maintenance of beech on the same site for hundreds of years. However, some forests remain healthy for a long time despite high amplitude climatic fluctuations suggesting that beech bark disease appears as a sanction against the growth of beech in inappropriate ecological conditions. Stands or trees having a restricted ecological plasticity are critically exposed to the disease. Will we now learn the lesson of this disease by managing forests on an

ecological basis? Post-disease intervention may not change the course of beech bark disease but we can expect a big influence of preventative management i.e. that which allows beech to have the most ecological resistance.

ZUSAMMENFASSUNG

Die beiden an der Buchen-Rindennekrose beteiligten Organismen sind überall in Frankreich anzutreffen. Nichtsdestoweniger ist die Krankheit auf den nördlichen Teil des Buchenareals begrenzt, wo die Buche in der Ebene wächst. Während der vergangenen fünf Jahre war ein allgemeiner Rückgang der Krankheitsintensität zu beobachten. Örtlich begrenzt kam es jedoch auch zu verstärktem Auftreten der Krankheit in den im Norden und Nordosten gelegenen Wäldern, wo die Buchen-Rindennekrose schon seit langer Zeit vorkommt. Manche Forstleute in Frankreich sind der Ansicht, die Buchen-Rindennekrose sei die Strafe für den Anbau der Buche unter ungeeigneten ökologischen Bedingungen.

RÉSUMÉ

Les deux organismes impliqués dans la maladie de l'écorce du hêtre sont endémiques partout en France. Toutefois, la maladie ne se retrouve que dans la partie nord de l'aire de distribution du hêtre où il croît dans les plaines. En général, la gravité de la maladie de l'écorce du hêtre a diminué au cours des cinq dernières années bien qu'il y ait eu des augmentations locales dans les parties nord et nord-est des forêts où la maladie était présente depuis longtemps. Des forestiers français croient que la maladie de l'écorce du hêtre est une conséquence de la culture du hêtre dans des conditions écologiques inappropriées.

LITERATURE CITED

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PRESENT STATE OF BEECH BARK DISEASE IN GERMANY[1]

Klaus J. Lang[2]

Abstract.-- Beech bark disease can be found at present time in young and old stands (20-150 years old) of Fagus sylvatica. The present state of the disease may be described as "normal" and apart from some cases, it is no threat to the existence of the stands.

In Germany beech bark disease always was the most important disease in beech forests, especially in older ones. Again and again it was the cause of great financial losses because of the very fast decomposition of wood. Moreover the break down of big trees gave rise to silvicultural problems because so called weeds complicated natural regeneration.

In practice foresters therefore try to restrict financial losses by removing trees with heavy scale infestation and necrotic bark or slime flux from the stands. Past experience has shown that people always overlook trees with symptoms of beech bark disease and that in consequence many beeches break down and can be only used for firewood.

Trees which are removed because they show scale infestation or slime flux are put in the same category as others which have to be felled because they are damaged by drought, for example.

The fact that there are different opinions concerning the causes of the symptoms leads to their subjective estimation and makes some information more or less doubtful. Therefore it is rather difficult to get exact data which refer only to damage by beech bark disease in the proper sense. In spite of the factors of uncertainty mentioned above I wish to try to describe the current state of the disease in the Federal Republic of Germany.

Let's begin in the south of our country. In Bavaria, especially in the northern parts where the greatest beech stands are located, in 1979 in 31 forest districts 16000 cubic meters of beech and in 1981 in the same forest districts about 9000 cubic meters had to be felled because the trees were damaged. Unfortunately it is not possible to evaluate clearly to what extent beech bark disease and the drought of 1976 contributed to this 25000 cubic meters of dying or dead trees. Between 1979 and 1981 the damages observed in this region decreased, but this does not necessarily mean that beech bark disease has clearly decreased. On the contrary, many observations and much information led us to the conclusion that the state of the disease development is different in the different parts of the country. This statement is not new because in the past there were also reports on increasing and decreasing disease intensity for different regions at the same time. This may be realized even in places which are not far from each other. Damage is mainly reported from beech stands over 80 years old. Increasingly there are observations in the northern part of Bavaria that Cryptococcus fagisuga also attacks beeches younger than 30 years. In some places many young trees died so that the foresters fear that, from the viewpoint of silviculture, the plots are to give up as lost especially because the best-growing individuals are predominantly attacked. In the past little attention was payed to the scale insect in young stands.

In 1981 in the southwest of the Federal Republic of Germany (Baden-Württemberg and Rheinland-Pfalz) beech bark disease increases in a great number of forest districts were reported. Dr. Bogenschütz,

[1]Paper presented at the I.U.F.R.O. Working Party Conference, Hamden C.T., U.S.A. 27 September to 7 October, 1982.

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from Freiburg, and I visited some of these areas. Beside old damage we found forest districts where actual beech bark disease with insects, slime flux, Nectria, falling bark and so on could be seen.

The disease appears scattered on single trees or concentrated on a rather few beeches which are standing not far from one another. In some cases it seems that the progress of the disease is fast, but the trees are not yet killed and it will perhaps take a lot of time until they break down. (In one case the trees were marked and will not be removed so we shall get further informations on the duration of the disease.)

In the Saar Territory after 1976 Cryptococcus was more often reported than in the years before.
In 1980 in one forest district 5500 cubic meters of beech had to be felled, but again the role of drought cannot be clearly calculated. Since 1980 the disease decreased but there were some exceptions. In most cases single trees in old stands were infected and showed symptoms. From younger stands it is reported that many trees can recover from the attack, a fact which was reported elswhere, too.

It seems that in the southern and southwestern parts of Germany beech bark disease, at the moment, generally plays no great role, and occurs only on limited areas. Damages are significant on these limited areas and do play an important role, however.

In Nordrhein-Westfalen and Niedersachsen no striking increase of beech bark disease was observed in the last years. Of course the disease is not absent but the damage is estimated as "normal" which means that beech bark disease can be found concentrated in small areas and on few individuals scattered in the stands.

During the last years in Hessen a distinct decrease of beech bark disease has been reported. Though at present time there are many stands attacked by the disease, forest officers do not speak of a dramatic situation. In a few cases a very intensive outbreak of the disease is reported on beeches 50-150 years old.

In the northern part of Germany, in Schleswig-Holstein, after 1975 and 1976 damages caused by drought were common. In connection with this, slime flux and wood destroying fungi are part of the appearence of the damaged trees. The damages appeared very rapidly in this region perhaps as a result of the special soil conditions, which are in many cases characterized by shallow upper soil layers where the beeches form root systems which do not penetrate deeply into the ground. These soils are normally well supplied with water.

At the present time Cryptococcus fagisuga occurs in stands which are 20 to 40 years old. Slime flux as a consequence of scale attack and mortality is restricted to small groups of trees and single trees. It is reported that scales seem to be concentrated on understory trees and beeches which are exposed; for example at the periphery of a stand.

The present situation in the Federal Republic of Germany may be summerized as follows. In general it can be stated, that after 1976, when precipitation was poor, damages on beech increased. These damages should not only be attributed to beech bark disease because weather conditions and partly special soil conditions may have also played an important role. With regard to beech bark disease, in the proper sense, the situation is so far unhomogeneous since within our country there are reports of increasing and decreasing disease intensity at the same time. At the moment reports of reduced disease predominate.

In all regions where Fagus sylvatica occurs we can always find trees which are heavily attacked by Cryptococcus fagisuga and which show other typical symptoms. Therefore the present state of the disease in our country may be described as "normal". Certainly it is interesting that the disease has been repeatedly observed in younger stands where in the past it was more or less ignored or overlooked.

SUMMARY

After 1976, a year with very low rainfall, damages on beech trees increased. It seems to be sure that these damages are not the result of beech bark disease alone. The disease can be found today in young and old stands (20-150 years old) but apart from a few cases, it is no threat to the existence of the stands.

Normally beech bark disease occurs in Germany on single trees in all beech stands, especially in

the old ones, or concentrated in rather small areas. This is in general also the present state in our country.

ACKNOWLEDGEMENTS

I thank Mr. J. Arnone and Mr. J.-M. Vincent for their help with preparing the English and French translations.

RESUME

La situation actuelle de la maladie de l'écorce du hêtre en République Fédérale d'Allemagne

Depuis 1976, année exceptionellement sèche, en enrégistre en beaucoup de points de la RFA des dommages et des pertes accrues concernant le hêtre. Toutefois, il semble certain que ces pertes ne soient pas uniquement dues à la maladie de l'écorce du hêtre, mais également en grande partie à la sécheresse, particulièrement en ce qui concerne les peuplements sur sols peu profonds. La maladie sévit actuellement aussi bien dans les peuplements jeunes qu'agés (20-150 ans). A quelques exceptions près, la maladie ne peut toutefois pas être considérée comme menaçant les peuplements infestés.

La maladie de l'écorce du hêtre se rencontre dans pratiquement toutes les hêtraies de manière isolée, en particulier sur des abres agés; ou bien se manifeste en foyers d'infection de dimensions très souvent réduites. La situation actuelle de la maladie en RFA peut être qualifiée de "normale".

ZUSAMMENFASSUNG

Zum gegenwärtigen Stand der Buchen-Rindennekrose in der Bundesrepublik Deutschland

Nach 1976, einem Jahr mit sehr geringen Niederschlagsmengen, wurden in vielen Teilen der Bundesrepublik Deutschland verstärkte Schäden und Ausfälle an Buchen verzeichnet. Es scheint jedoch sicher, daß diese Schäden nicht alleine durch die Buchen-Rindennekrose verursacht wurden, sondern zu einem großen Teil durch Trockenheit. Dies gilt besonders für Buchen auf flachgründigen Standorten. Zur Zeit ist die Krankheit sowohl in jungen als auch in alten Beständen (20-150 Jahre) anzutreffen. Abgesehen von einigen Fällen, stellt sie jedoch keine Bedrohung für den jeweiligen Bestand dar.

Die Buchen-Rindennekrose kommt praktisch in allen Buchenbeständen an einzelnen, besonders an alten Bäumen vor, oder sie tritt gehäuft auf meist kleiner Fläche auf. Der gegenwärtige Stand der Krankheit in der Bundesrepublik Deutschland kann als "normal" bezeichnet werden.

THE STATUS OF BEECH BARK DISEASE IN THE MARITIME PROVINCES OF CANADA IN 1980[1]

L.P. Magasi[2] and W.R. Newell[2]

Abstract.--Beech bark disease first reached North America about a 100 years ago and within a few decades rendered beech an almost useless weed species in the Maritimes. A survey in 1980 to determine the current status of the disease found the scale insect active, though infestations generally light, on over 90% of trees in Nova Scotia and Prince Edward Island but on only about 50% in New Brunswick; *Nectria coccinea* var. *faginata* distributed throughout; some degree of stem cankering on trees; mortality in New Brunswick (3.7%) less than half of that found in Nova Scotia (9.1%) or Prince Edward Island (9.8%). The future of beech as an economical forest species is bleak.

INTRODUCTION

The Maritime Provinces of Canada have been in a vulnerable position with regard to introduction of foreign pests, especially those from Europe. Being the first land upon which most goods were unloaded, particularly in the years when the wounds of separation were still fresh in the memories of both the British Empire and the United States of America, areas around ports of entry such as Halifax, Nova Scotia, were prime targets for escape and establishment of introduced organisms.

One such organism was the beech scale, *Cryptococcus fagi* (Baer.), an insect introduced on imported nursery stock of European beech, *Fagus sylvatica* L., some time prior to 1890 and first found in North America near Halifax, Nova Scotia (Ehrlich 1934, Hawboldt 1944). The scale and the disease were present throughout mainland Nova Scotia by 1925, the same year it was first found established in Prince Edward Island. The first infestation on Cape Breton Island was found in 1926 and in 1927 the first well-established infestation was located in southeastern New Brunswick (Hawboldt 1944). The gradual northwestward spread of beech bark disease in New Brunswick is illustrated in Figure 1. By 1980, beech was affected throughout the Maritime Provinces, but not to the same extent in all areas.

American beech, *Fagus grandifolia* Ehrh., although used mainly for firewood has been also utilized in small amounts in flooring, furniture, veneer, flakeboard, and as corrugated filler in cardboard. The tree was readily attacked by both the beech scale and the fungus *Nectria coccinea* var. *faginata* Lohm. Wats. & Ayers, and by the early 1930's about half of the beech was dead in the older outbreak areas (Ehrlich 1934). In the Fredericton, New Brunswick area where the scale was first found in 1937, 11% of the beech trees died by 1946 (Barter 1947) and by 1952 about 20% of the trees, representing about 40% of beech volume, were dead (Barter 1953).

For a tree species of diminished economic importance, beech bark disease received more than routine attention during assessments by the Forest Insect and Disease Survey. In 1969, a survey was conducted to determine the changes in the status of the disease since the initial wave of tree mortality (Forbes *et al.* 1970). In 1980, partly in preparation for this IUFRO conference, 50 of the original 103 areas from the 1969 survey were re-evaluated to obtain information on the current status of beech bark disease in the Maritime Provinces and to determine changes during the past decade (Magasi 1981).

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[1]Paper presented at the IUFRO Beech Bark Disease Working Party Conference, Hamden, CT. USA, 27 September to 7 October 1982.

[2]Head and Damage Appraisal Technician, respectively. Forest Insect and Disease Survey, Maritimes Forest Research Centre, Canadian Forestry Service, P.O. Box 4000, Fredericton, New Brunswick, Canada E3B 5P7.

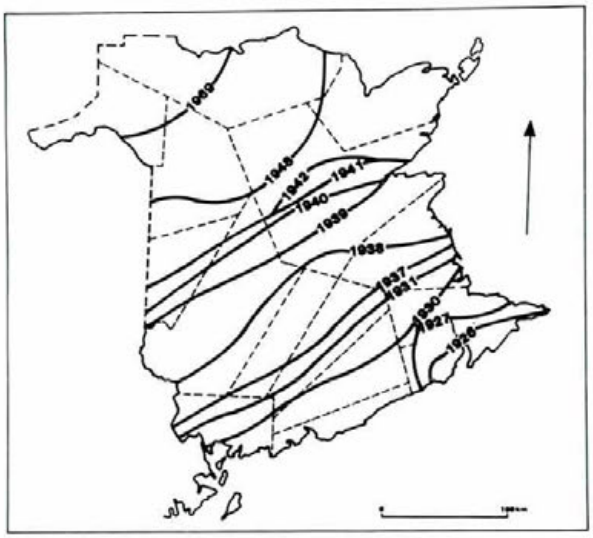


Figure 1.--The spread of beech bark disease in New Brunswick (Based on information from Hawboldt 1944, Forbes *et al.* 1970, and Canadian Forestry Service data).

THE STATUS IN 1980

The host

Beech, once a considerable element in the species composition of hardwoods in the Region, has been decimated by beech bark disease. By 1969 it comprised only 3.5% of the total gross merchantable timber (Forbes *et al.* 1970). Beech now contributes only 1.8%, and 1.7% to the total merchantable inventory of New Brunswick (Anon. 1981) and Nova Scotia (Anon. 1979), representing 1.57 million m^3 and 4.7 million m^3 of wood, respectively.[3]

The size distribution of trees in the 1980 survey was as follows (based on 2505 trees):

diameter	3 - 8 cm	27.5%
	9 - 16 cm	21.1%
	17 - 24 cm	33.8%
	25 + cm	17.6%

The scale insect

Cryptococcus fagi was present at all 21 locations in Nova Scotia and 3 in Prince Edward Island and at 21 of 26 locations in New Brunswick. All five scale-free plots were in the northwestern part of the Province where cankering was also the lowest (Fig. 2). From 2 to 100% of the trees were infested on plots.

[3]The Prince Edward Island forest inventory is in preparation and figures are not yet available.

The amount of wool produced by the insect, expressed as a percentage of surface area covering the lower trunk, varied from low (1-5%) to medium (6-35%) on individual trees. The infestation was generally light and was found moderate only at three locations in New Brunswick and at one location in Nova Scotia. Elsewhere, only occasional trees were moderately infested.

Most trees were infested to some degree in Nova Scotia and Prince Edward Island but only about one-half of the trees in New Brunswick harbored the scale. Trees of all sizes were attacked by the scale in about equal proportions in any given Province (Table 1).

Table 1.--Percentage of scale infested trees by diameter classes in the Maritimes in 1980[a]

Province	Diameter class (cm) 3-8	9-16	17-24	25+	Average infestation
			-percent-		
New Brunswick	44	52	57	47	51
Nova Scotia	96	99	97	96	97
Prince Edward Island	80	97	96	96	90

[a]Based on 963 trees in New Brunswick, 866 in Nova Scotia, and 138 in Prince Edward Island.

The fungus

Nectria coccinea var. *faginata* is the species associated with beech bark disease in the overwhelming majority of mycological collections. Its distribution closely matches that of the disease. *Nectria galligena* Bres. has been collected occasionally from cankered beech.

The canker

Cankering was assessed on the lower 3 m of the trunk of 50 trees at each location and expressed as the percentage of the trunk surface cankered. A severity index was calculated for each plot by multiplying the number of trees in each canker class as follows (Forbes *et al.* 1970):

0 for healthy trees,
1 with 1-20% of lower trunk cankered,
2 with 21-50% of lower trunk cankered,
3 with 51% of lower trunk cankered,
4 dead with cankers.

Beech bark disease was present at all locations in the Maritimes but the incidence

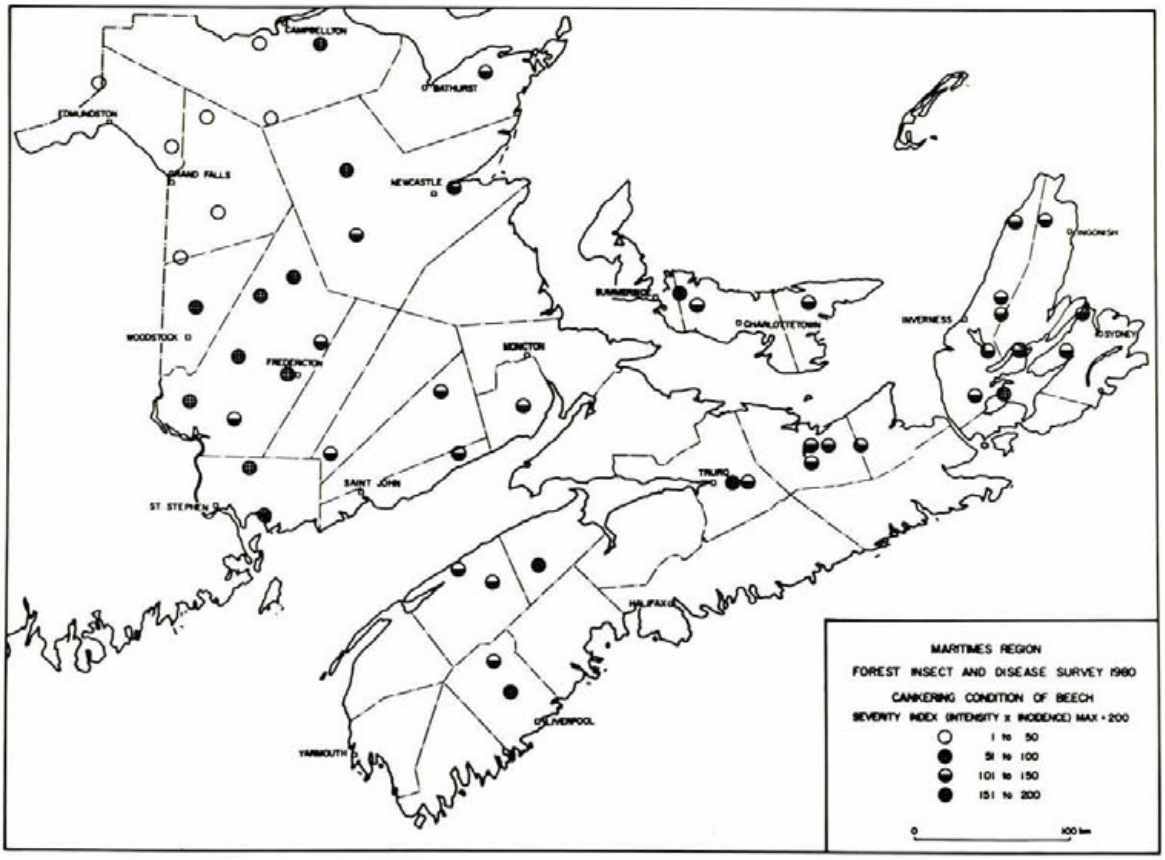


Figure 2.--The degree of stem cankering on beech in the Maritime Provinces of Canada in 1980 (from Magasi 1981).

of severe cankering was lowest in northwestern New Brunswick which has the shortest history of beech bark disease (Fig. 2).

The severity of cankering generally increased with increasing tree size. However, the fact that the percentage of canker-free trees in the smallest size diameter class was not significantly higher than that of larger trees suggests that the prospect of using these trees in the future for anything but firewood is bleak, (Table 2). All but six of the 262 canker-free trees, comprising 10.5% of the sample, were found in New Brunswick, 160 of these (61.0%) on the five northwestern plots (Fig. 2).

The dieback

Crown dieback was assessed in relation to the degree of trunk cankering (Table 3) and to diameter classes (Table 4). The amount of dieback appears to be more dependent on the degree of cankering than on tree size.

Table 2.--Cankering of lower trunk of beech in the Maritimes in 1980[a]

Diam. class (cm)	Living trees: Percent of lower 3 m of trunk cankered				Dead trees	
	Nil	1-20	21-50	51+	with cankers	without cankers
	- - - - - - - - -percent- - - - - - - - -					
3-8	12.3	35.2	29.9	14.8	7.2	0.6
9-16	10.2	23.7	28.4	30.5	7.2	---
17-24	9.9	20.9	18.4	44.5	6.2	0.1
25+	8.2	25.5	19.1	43.0	2.8	1.4
All trees	10.5	27.0	24.9	30.9	6.3	0.4

[a]Based on assessment of 1325 trees.

Table 3.--Crown dieback of beech in relation to severity of lower trunk cankering in the Maritimes in 1980

Severity of trunk cankering (%)	Percentage of crown dieback				
	Nil	1-20	21-50	51-75	76-99
	- - - - - - -percent- - - - - - -				
Nil	8.5	4.5	0.2	0.1	0
1-20	7.5	12.7	1.7	0.4	0.1
21-50	2.8	12.4	6.2	2.1	0.5
51+	0.1	11.0	16.7	8.9	3.6
All trees	18.9	40.6	24.8	11.5	4.2

Table 4.--Crown dieback of beech in relation to diameter classes in the Maritimes in 1980

Diam. class (cm)	Percentage of crown dieback				
	Nil	1-20	21-50	51-75	76-99
	- - - - - - percent - - - - - -				
3-8	35.2	42.6	12.4	6.3	3.5
9-16	16.8	46.1	23.2	10.7	3.2
17-24	10.3	35.3	33.0	15.6	5.8
25+	12.4	41.2	30.5	12.9	3.0
All trees	18.9	40.6	24.8	11.5	4.2

Some degree of dieback was present on 81.1% of the trees and 15.7% of the trees had more than half of their crown dead. The increase of dieback during the past decade was the most significant change in the condition of beech. In 1969 only about 20% of the trees had dieback (Forbes *et al.* 1970).

The mortality

Tree mortality (Table 2) was not excessive and certainly not of the same magnitude reported by Barter (1947, 1953) during the initial wave in the spread of the disease. There was less mortality in New Brunswick, 3.7%, than in Nova Scotia and Prince Edward Island, 9.1% and 9.8%, respectively.

Mortality rate decreased with increasing tree size and was considerably lower in the over 25-cm diameter class, regardless of the location of trees in the Region. The reason for this is unknown but it is plausible that only trees with some degree of resistance to the disease are able to survive long enough to attain that size.

CONCLUSION

Beech bark disease has rendered beech an unimportant hardwood species in the forests of the Maritimes. The disease is present throughout the Region and has transformed a tree with a clear, straight trunk of high-quality wood into a poorly-formed, low-grade weed species. The exception, to date, is in a small corner of northwestern New Brunswick. Until a way is found to produce disease-free beech, its significance to the forest economy in the Region is a liability by occupying valuable space needed to grow some 6.3 million m^3 of a better-quality hardwood species.

RÉSUMÉ

La maladie de l'écorce du hêtre fit son apparition en Amérique du Nord il y a une centaine d'années, mais il ne lui fallut que quelques décennies pour réduire le hêtre au niveau d'une essence sans valeur dans les Maritimes. En 1980, un relevé effectúe pour mettre à jour la situation de cette maladie, révéla la présence active de la cochenille, bien qu'en infestations généralement légères sur plus de 90% des arbres en Nouvelle-Ecosse et à l'Ile-du-Prince-Edouard, mais sur seulement 50% au Nouveau-Brunswick: le Nectria coccinea var. faginata était présent partout; on notait une certaine quantité de chancres aux arbres; au Nouveau-Brunswick, le taux de mortalité (3.7%) était moins de la moitié de celui observé en Nouvelle-Ecosse (9.1%) ou à l'Ile-du-Prince-Edouard (9.8%). L'avenir du hêtre comme essence forestière commerciale n'est pas prometteur.

ZUSAMMENFASSUNG

Die Buchen-Rindennekrose trat in Nordamerika vor rund 100 Jahren erstmals auf. Innerhalb weniger Jahrzehnte ließ sie die Buche in den Provinzen an der Ostküste zu einer fast wertlosen Baumart werden. Eine Bestandsaufnahme der Krankheit im Jahre 1980 ergab, daß Cryptococcus fagisuga vorhanden, der Befallsgrad der Bäume in der Regel aber gering ist. In Neuschottland und auf der Prinz-Edward-Insel sind mehr als 90% der Buchen befallen, in Neubraunschweig nur rund 50%. Nectria coccinea var. faginata war im ganzen untersuchten Bereich anzutreffen, ebenso ein gewisses Maß an Stammkrebsen. Die Sterberate der Buche lag in Neubraunschweig mit 3,7% deutlich unter der in Neuschottland (9,1%) und der Prinz-Edward-Insel (9,8%). Die Zukunft der Buche als einer forstlich und wirtschaftlich bedeutenden Baumart muß als düster angesehen werden.

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STATUS OF BEECH BARK DISEASE IN THE PROVINCE OF QUEBEC[1]

Denis Lachance[2]

Abstract.--The distribution of beech bark disease has not changed significantly in recent years in Quebec. It has remained as scattered infected stands located within relatively old beech-scale-infested areas. This scale covers the southeastern half of the beech natural range in the province and it is spreading slowly westward.

INTRODUCTION

The natural range of american beech (*Fagus grandifolia* Ehrh.) in Quebec follows rather closely the location of most private lands in the province. On these private lands, the gross standing volume of beech is estimated at 12 million cubic meters (Barrette & Langevin, 1979). This represents 3% of the total standing wood volume which is composed of 57% hardwoods and 43% softwoods.

Beech occurs in southern Quebec, mainly at elevations lower than 300 m, from Outaouais river to La Malbaie on the north shore of the St.Lawrence River, and to Rimouski and in the Matapedia Valley on the south shore. Although not a commercially preferred species, beech wood is used in flooring, tool handles, household articles and increasingly as firewood.

THE BEECH BARK DISEASE IN QUEBEC, 1965-1975

In 1976, Lavallée compiled the history of the spread of the disease in Quebec from 1965 to 1975. The causal fungus (*Nectria coccinea* var. *faginata* Lohm. Wats. & Ayres) along with the beech scale (*Cryptococcus fagisuga* Lind.) were found for the first time at Les Etroits, Temiscouata County in 1965. The following year, the disease complex was found in another beech stand located 6 km east of the first sighting. These were the only known infested areas in Quebec until 1969, despite annual surveys in beech stands located in adjacent counties. In 1969, the scale-fungus complex was found west of Quebec City, about 200 km west of the previously known sites. In 1970, 71 and 72, several new infected stands were discovered in southern Quebec (Lavallée, 1976). Lavallée estimated that 10 000 km^2 of forest were affected by the disease in 1972. Three years later, this increased to 19 000 km^2.

In 1975 then, the beech scale occurred south-east of Sherbrooke to Quebec City and Rimouski, and in few infected stands located near Matapedia, Bonaventure County and around Quebec City. The fungus had been found in 22 beech stands appearing as eleven relatively small infected spots scattered throughout these areas.

PRESENT STATUS OF THE DISEASE AND THE SCALE

The most recent intensive survey on this insect-disease complex was done in 1980. We feel the results of this survey are still very up-to-date in 1982, as our field technicians who make regular and numerous survey visits in the forest stands of their respective territories, have not noted appreciable changes in the levels of insect populations or disease incidence, nor have they encounted previously unreported infected stands.

In the 1980 survey, 50 beech stands where the scale, and sometimes the disease

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[1]Paper presented at the IUFRO Beech Bark Disease Working Party Conference, Hamden, CT. USA, 27 Sep to 7 Oct 1982.

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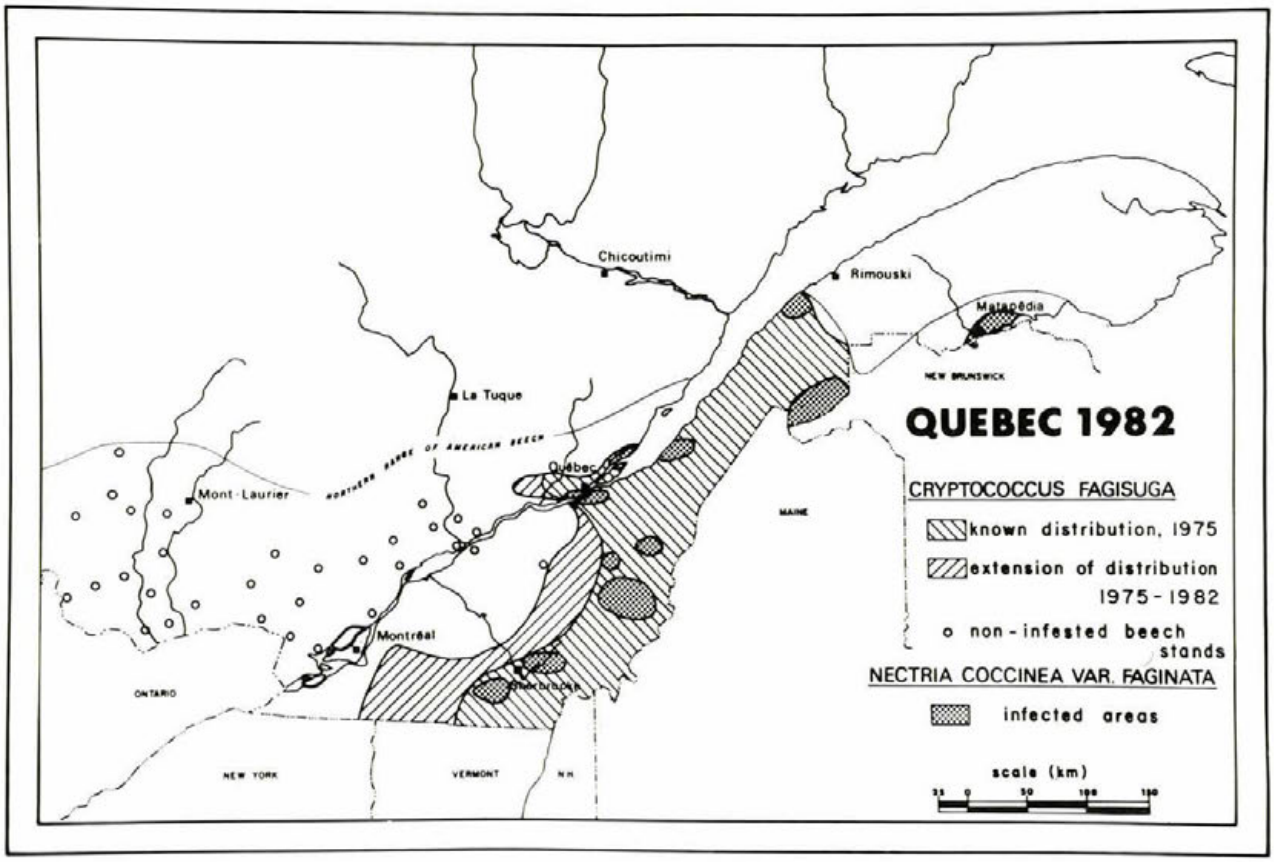


Figure 1.--Distribution of the beech scale and of the beech bark disease in the Province of Quebec in 1982.

had previously been reported were visited. In addition, another 50 beech stands, mostly outside the known range of distribution of the beech scale, were also surveyed. In each stand 5 sample plots of 10 trees each were studied. When present, the scale or the fungus or both were rated on each tree, according to the proportion of stem bark that was affected. Detailed results of this survey were reported in our Annual Forest Insect and Disease Survey Report, 1980 (Lachance et al. 1981).

In five years, the insect has spread about 80 km west of its previous known range (see Fig. 1). Its distribution on the south shore of the St.Lawrence River goes eastward south of Montreal, then arches away from the St.Lawrence between that city and Quebec City, and covers all the area to Rimouski. The insect is still present around Matapedia and on the north shore of the St.Lawrence River where it extends as a relatively narrow strip to about 60 km east and west of Quebec City. Generally, the insect populations surveyed were found to have decreased slightly in the stands where the scale had been reported previously.

The 1980 survey has shown also that areas infected with the beech bark disease have not changed since 1975. They remain as relatively small scattered spots within the 1965-1975 known range of the beech scale. The severity of the disease has declined; there were even places where the fungus could not be detected where it had been found previously. In other cases, we noted that better forest management and cutting of infected and healthy beech trees for firewood reduced dramatically the amount of visible damage by this disease in forest stands.

SUMMARY

The beech scale is present in most of the southern and eastern half of the natural growing range of beech in the Province of

Quebec and it is spreading slowly westward. It now occurs on the south shore of the St. Lawrence River, from Montreal to Rimouski, and at two locations elsewhere, near Matapedia and around Quebec City. Recently the insect populations have remained relatively low.

The beech bark disease on the other hand has not spread in recent years and it remains as scattered infected stands within relatively old scale-infested areas. Better forest management practices and a recent increasing demand for beech as firewood has reduced significantly the visible damage caused by the fungus in the forest.

RESUME

Situation de la maladie corticale du hêtre au Québec

La distribution de la maladie corticale du hêtre a très peu changé ces dernières années au Québec. La maladie ne se retrouve que dans certains peuplements groupés en onze unités dispersées sur le territoire infesté depuis longtemps par la cochenille du hêtre. Cette cochenille se retrouve présentement dans la moitié sud-est de l'aire de distribution naturelle du hêtre et elle avance lentement vers l'ouest.

ZUSAMMENFASSUNG

Zustand der Buchenrinde-nekrose in Québec

Das von der Buchenrinde-nekrose befallene Gebiet in Québec hat sich kaum verändert während der letzten Jahre. Das Vorkommen der Krankheit beschränkt sich auf elf zerstreute Örtlichkeiten im Gebiet wo die Wollschildlaus schon seil langer Zeit Schaden anrichtet. Diese Schildlaus befindet sich nun in der süd-östlichen Hälfte des natürlichen Buchengebiets und dehnt sich allmählich nach Westen aus.

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CURRENT STATUS OF BEECH BARK DISEASE IN NEW ENGLAND AND NEW YORK[1]

Margaret Miller-Weeks[2]

Abstract.-- The advancing front of beech bark disease in the northeast is now located in western New York and Pennsylvania. The disease is killing trees as far west as central New York. Cryptococcus fagisuga scale was found on nearly every tree examined during a northern New England disease survey. From that survey and Resource Evaluation plot data, beech mortality is estimated as high as 50 percent in Maine and about 30 percent in New Hampshire and Vermont.

INTRODUCTION

Beech bark disease has been spreading westward throughout New England into New York and Pennsylvania since the early 1930's when the disease was first discovered in Maine (Houston et al. 1979). Its spread throughout the northeastern states follows three stages: the advancing front, the killing front, and the aftermath zone (Shigo 1972). The advancing front, characterized by scattered Cryptococcus fagisuga Lind. scale pupulations, is presently located in western New York and north-central Pennsylvania. The killing front is found in central New York and northeastern Pennsylvania. Here heavy Nectria infection is causing mortality at a high rate. The aftermath zone is in Maine and New Hampshire, where the disease has been present the longest. In these areas scale and Nectria populations are endemic, beech sprout thickets are abundant, and many trees are defective (Houston 1975).

MATERIALS AND METHODS

From 1975 to 1977, the Forest Pest Management group of the USDA Forest Service, Northeastern Area, State & Private Forestry, conducted a survey to determine the relative prevalence of the causal organisms of beech bark disease, including C. fagisuga, Nectria coccinea var. faginata Lohman, Watson, and Ayers, and Xylococcus betulae (Perg.) Morrison. Northeastern Forest Experiment Station Resource Evaluation permanent survey plots in Maine, New Hampshire, Vermont, and New York were used to obtain a well-distributed sample. Few Resource Evaluation plots in southern New England contained beech, therefore Massachusetts, Connecticut, and Rhode Island were not included in the survey. Recently, Resource Evaluation crews were asked to continue the surveys in Maine and New York. Since these surveys have only just concluded, few data are available from those states. However, Forest Pest Management has compiled preliminary results for New Hampshire, Vermont, and several counties in Maine.

RESULTS AND DISCUSSION

Overall, populations of C. fagisuga scale were low throughout the three states surveyed. However, scale was present on every plot examined. Of the nearly 1000 trees examined, only 12 trees less than 8 inches in diameter and 2 trees greater than 8 inches in diameter were found uninfested. Various amounts of Nectria fruiting and X. betulae were noted throughout the survey area. Figure 1 illustrates the advancing front in western New York, where only scale is present on the majority of the plots, and the killing front throughout the central portions of the state where Nectria is abundant.

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[1] Paper presented at the IUFRO Beech Bark Disease Working Party Conference, Hamden, CT. USA, 27 Sep to 7 Oct 1982.

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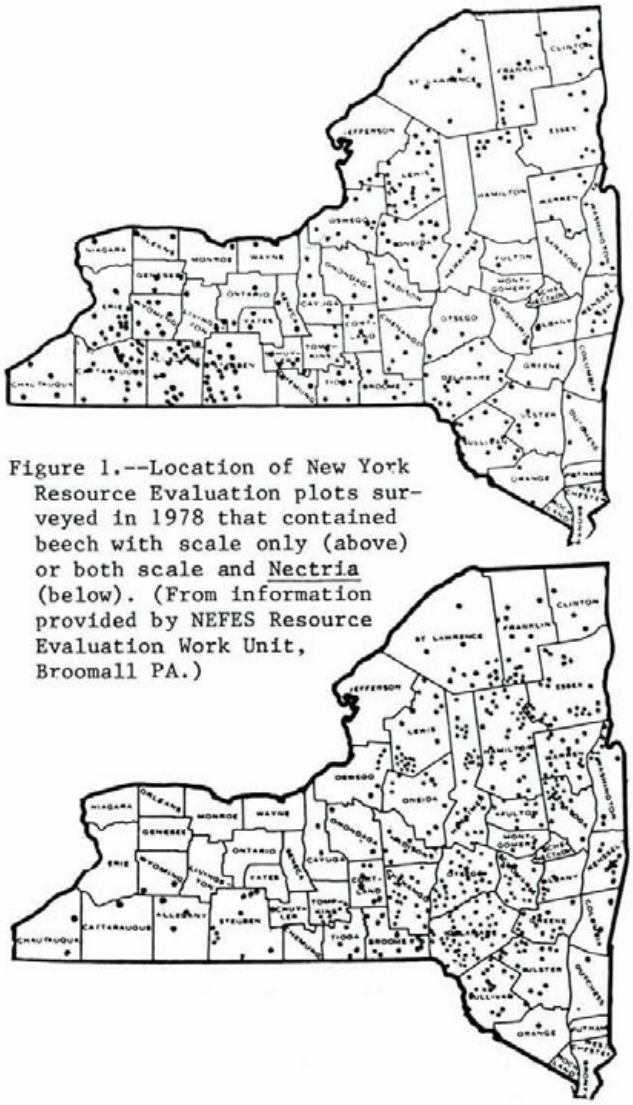


Figure 1.--Location of New York Resource Evaluation plots surveyed in 1978 that contained beech with scale only (above) or both scale and Nectria (below). (From information provided by NEFES Resource Evaluation Work Unit, Broomall PA.)

Mortality differed from plot to plot, but was found on about half of the plots examined. (The number of beech trees per plot ranged from 1 to 20, the smallest average number being in New Hampshire.) Overall, a higher percentage of the larger diameter trees have died from the disease (Fig. 2).

Table 1 shows the beech mortality on the Forest Survey plots from the early 1940's to 1970 and from 1970 to 1977. For trees greater than 8 inches in diameter at breast height, losses range from 24 percent in New Hampshire to 50 percent in Maine.

Comparing percent mortality in the aftermath zone in Maine with the killing front in Vermont suggests that a higher percentage of smaller trees are now being killed by the disease in the aftermath zone (Table 2). In Hancock County, Maine, where the disease has been active for more than 40 years, more than 50 percent of the trees in the 5- to 11-inch diameter classes are now dead; less than 20 percent of these smaller trees are dead in Vermont.

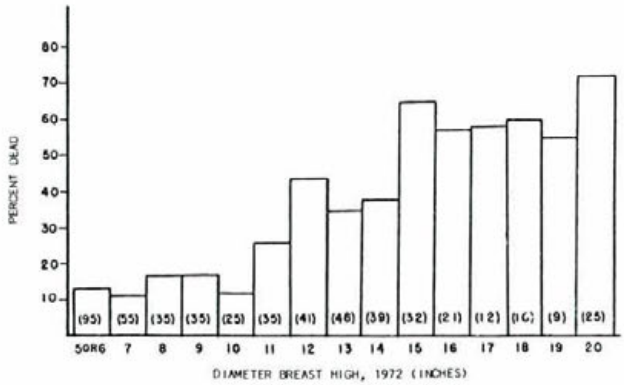


Figure 2.--Distribution of beech mortality in northern New England by diameter class. (Number of trees in each class in parentheses.)

From mortality, damage, and tree volume estimates, the merchantable timber volume loss to beech bark disease in Vermont was estimated at nearly 300 million board feet. This includes the volume of trees killed (135 million bd. ft.), the volume of dying trees (62 million bd. ft.), and the volume of live trees rendered cull by the disease (95 million bd. ft.). Merchantable timber losses have not yet been calculated for the other states in the survey.

Table 1.--Cumulative beech mortality on forest survey plots in New Hampshire, Vermont and Maine up to 1970 and 1970 to 1977.[a]

State	Percent mortality			
	≥8" DBH[b]		<8" DBH	
	1970	1977	1970	1977
New Hampshire				
State & private lands	20	24	8	12
National forest land	19	30	7	19
Vermont				
State & private lands	29	37	18	18
National forest land	29	32	35	35
Maine				
Hancock County	29	50	23	54
Franklin and Oxford Counties	23	29	44	44

[a]Based on USDA Forest Service Resource Evaluation plot data and Pest Management disease survey data.

[b]Tree diameter at breast height in 1971 for New Hampshire, 1972 for Vermont, and 1968 for Maine.

Table 2.--Cumulative beech mortality (in percent) by diameter class on forest survey plots in Vermont and Hancock County, Maine from the time of initial infection until 1977. (Number of trees examined in parentheses)

State	Diameter class (inches)				
	5-7	8-11	12-15	16-19	20-22
Hancock County, Maine[a]	58(24)	50(16)	40(10)	100(1)	100(1)
Vermont[b]	12(150)	18(130)	44(158)	58(52)	72(25)

[a]Infection present 40+ years.

[b]Infection present 20+ years.

RÉSUMÉ

La maladie de l'écorce du hêtre s'est étendue vers l'ouest depuis sa découverte dans le Maine au début des années trente. Des populations de la cochenille Cryptococcus fagisuga se retrouvent maintenant dans l'ouest de l'état de New-York et le centre de la Pennsylvanie. L'avance meurtrière, caractérisée par un taux élevé de mortalité des arbres causée par des infections graves de Nectria se situe dans le centre de New-York et le nord-est de la Pennsylvanie. La zone ravagée inclut le Maine et le New-Hampshire.

De 1975 à 1977, des équipes du groupe Forest Pest Management ont visité les parcelles de l'Unité Forest Resource Evaluation situées dans le New-Hampshire, le Vermont et plusieurs comtés du Maine, pour déterminer la présence du C. fagisuga, du Nectria coccinea var. faginata, et du Xylococculus betulae. La cochenille C. fagisuga fut retrouvée sur presque chaque arbre examiné. On estime que jusqu à 50% des hêtres dans le Maine et environ 30% dans le New-Hampshire et le Vermont sont morts à cause de la maladie. En général, une plus grande proportion d'arbres à fort diamètre sont morts. Dans la forêt ravagée du Maine, plus de 50% des arbres de petit diamètre (5-11 pouces au d.h.p.) sont morts, comparativement à moins de 20% au Vermont. Dans cet état, près de 300 millions de pieds mesure de bois furent perdus à cause de la maladie.

ZUSAMMENFASSUNG

Seit die Buchen-Rindennekrose um 1930 in Maine entdeckt wurde, hat sich die Krankheit stetig nach Westen ausgebreitet. Die Buchenwollschildlaus (Cryptococcus fagisuga) ist derzeit im westlichen New York und im mittleren Pennsylvanien anzutreffen. Die "killing front", die als Folge starken Nectria-Befalls durch hohe Sterberaten der Buchen gekennzeichnet ist, verläuft im mittleren New York und dem nordöstlichen Pennsylvanien. Die "aftermath zone", also das Gebiet, über das die Krankheit bereits hinweggegangen ist, umfaßt Maine und New Hampshire.

Von 1975 bis 1977 wurden auf Beobachtungsparzellen in New Hampshire, Vermont und Maine Bestandsaufnahmen durchgeführt und das Auftreten von C. fagisuga, Nectria coccinea var. faginata und Xylococculus betulae registriert. C. fagisuga wurde dabei an fast jeder untersuchten Buche (Fagus grandifolia) festgestellt. Nach Schätzungen sind in Maine fast 50% und in New Hampshire rund 30% der Buchen als Folge der Krankheit abgestorben. Dabei ist der Anteil der Bäume mit größerem Stammdurchmesser noch höher. Im "aftermath forest" in Maine sind über 50% der dünneren Buchen (12,5 - 27,5 cm BHD) abgestorben, im Vergleich dazu in Vermont weniger als 20%. In Vermont gingen durch die Krankheit fast 8 Mio. fm Buchenholz verloren.

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STATUS OF BEECH BARK DISEASE IN PENNSYLVANIA[1]

Barry Towers[2]

Abstract.--Results of periodical surveys for beech bark disease in Pennsylvania from 1958 to 1982 reveal that the disease is slowly spreading in a south- and westward direction. Although the disease complex is still confined to the northern and eastern portions of the state, beech mortality is occurring in the areas infested longest.

The beech scale, *Cryptococcus fagisuga* Lindinger, was first found in Pennsylvania at Promised Land State Park in Pike County in 1958 (Drooz 1959). It was not until 1969 that *Nectria coccinea* var. *faginata* was found in association with the scale on one tree near Gouldsboro, Pennsylvania, about 15 miles west of the original scale location (Nichols and Towers 1969). A survey of northeastern Pennsylvania in the summer of 1970 showed evidence of the ingress of the scale into northeastern Pennsylvania in a southwestward movement from New York State. *Cryptococcus fagisuga* infestation became less severe as one moved southwestward from Zone 1 to Zone 3 (Fig. 1). There was no significant difference in either total basal area of all tree species or beech basal area between zones. Therefore, the difference in scale severity was due to its movement in a southwestward direction. Overall, 62 percent of the beech basal area was infested to some degree with scale, and of the 1,285 trees examined, 64, or 5 percent, displayed *Nectria*-like symptoms (Towers 1971).



Figure 1.--County map of Pennsylvania showing counties included in beech zones surveyed in 1970.

A resurvey of northeastern Pennsylvania in 1973 revealed that the scale had spread westward 18 miles from the 1970 survey boundaries while *Nectria* was found 80 miles farther west and 20 miles farther south than in the 1970 survey (Fig. 2). Approximately 40 percent of the beech trees in the woodlot in which *Nectria* was first discovered now had obvious fruiting or typical *Nectria* cankers (Towers et al. 1974).

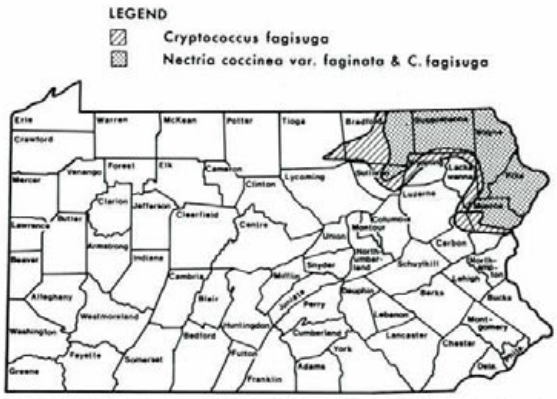


Figure 2.--Known distribution of beech bark disease in Pennsylvania in 1973.

Resurveys in 1977 and 1978 revealed that the scale had moved about 40 miles farther west and about 50 miles southward along the eastern border (Fig. 3) (Nichols 1978), while

[1]Paper presented at the IUFRO Beech Bark Disease Working Party Conference, Hamden, CT 06514, USA, September 27 to October 7, 1982.

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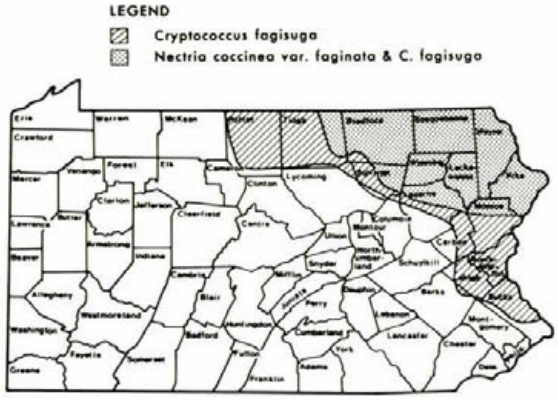


Figure 3.--Known distribution of beech bark disease in Pennsylvania in 1978.

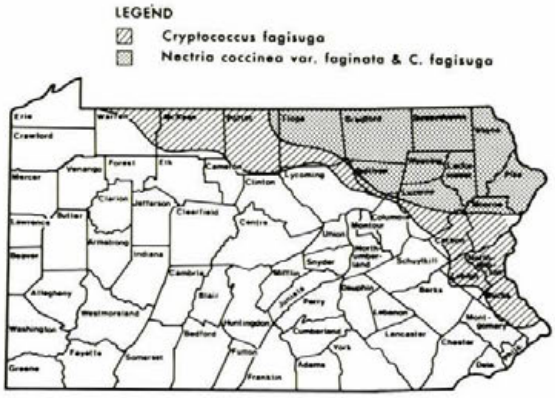


Figure 4.--Known distribution of beech bark disease in Pennsylvania in 1982.

the distribution of *Nectria* remained essentially the same.

It was at this time that populations of *C. fagisuga* decreased drastically throughout Pennsylvania, and only very light infestations of scale could be found on trees throughout the known range of scale.

Mortality and typical "beech snap" began to occur about 1979 in the *Nectria*-infested areas, but to date no surveys designed to determine losses have been conducted. Conservatively, mortality could now be estimated at 5 percent of the beech basal area in the *Nectria*-infested area in northeastern Pennsylvania.

In 1981 the presence of a mealybug, *Phenacoccus serratus* (Ferris), led personnel to incorrectly diagnose the presence of beech scale throughout the eastern one-third of the Commonwealth. In areas where the beech scale is at very low levels, individual *P. serratus* may be mistaken for isolated colonies of *C. fagisuga* unless a hand lens is used for positive identification.

A survey conducted in the late summer of 1982 revealed that both scale and *Nectria* had spread westward of their previous locations in northcentral Pennsylvania (Fig. 4). Future disease development will be monitored through periodic surveys and 12 long-term observation plots scattered throughout Pennsylvania.

SUMMARY

Periodical surveys from 1958 to 1982 for beech bark disease along the advancing zone in Pennsylvania reveal that the disease complex is slowly spreading in a south- and westward direction. The scale was first observed in 1958 and the *Nectria* component in 1969 when tree mortality began to be reported. The future development of the disease will be monitored through periodic surveys and 12 long-term observation plots scattered throughout Pennsylvania.

RÉSUMÉ

Les résultats de relevés périodiques sur la maladie de l'écorce du hêtre en Pennsylvanie de 1958 à 1982 révèlent que la maladie s'étend lentement en directions sud et ouest. Bien que ce complexe pathologique soit encore confiné aux parties nord et est de l'Etat, la mortalité du hêtre survient dans les aires infestées depuis le plus longtemps.

ZUSAMMENFASSUNG

Die Ergebnisse regelmäßiger Überwachungen der Buchen-Rindennekrose von 1958 bis 1982 zeigen, daß die Krankheit sich langsam nach Süden und Westen ausbreitet. Noch ist sie auf die nördlichen und östlichen Teile des Landes beschränkt. Ein Absterben der Buchen ist in den Gebieten zu beobachten, in denen die Krankheit am längsten vorkommt.

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BEECH BARK DISEASE IN WEST VIRGINIA: STATUS AND IMPACT ON THE MONONGAHELA NATIONAL FOREST[1]

Manfred E. Mielke and David R. Houston[2]

Abstract.--Cryptococcus fagisuga has infested over 70,000 acres (28,000 ha) of forest in West Virginia. Beech bark disease is causing heavy mortality in two areas of the Monongahela National Forest and additional scattered mortality. In the areas most affected, per-acre losses total 1,369 board feet of sawtimber and 2.67 cords, with a potential loss of 5,697 board feet and 9.29 cords. Nectria galligena appears to be the only species of Nectria involved in the disease complex.

INTRODUCTION

Beech scale (Cryptococcus fagisuga Lind.) was first discovered in August 1981 infesting American beech (Fagus grandifolia Ehrh.) in West Virginia at the Gaudineer Scenic Area on the Greenbrier Ranger District of the Monongahela National Forest (Mielke et al. 1982). A survey conducted in October 1981 established the presence of C. fagisuga scattered over approximately 70,000 acres (28,000 ha) of primarily national forest land and some adjacent private lands. Nectria galligena Bres. was found in association with C. fagisuga in the Gaudineer Scenic Area and at two additional survey points on Shavers Mountain within 3 miles of the Scenic Area (Mielke et al. 1982), in the southcentral portion of the area infested by C. fagisuga (see fig. 1). Scale populations were heavy (based on density of wax secretions) in scattered areas throughout the generally infested area. Based on our observations of scale populations and tree mortality, we estimate the infestation to be older than 20 years at the Gaudineer Scenic Area. The previous known range of C. fagisuga was only as far south as northeast Pennsylvania, a distance of over 300 air miles (480 km), over an area characterized physiographically by the Allegheny Mountains and the Ridge and Valley system.

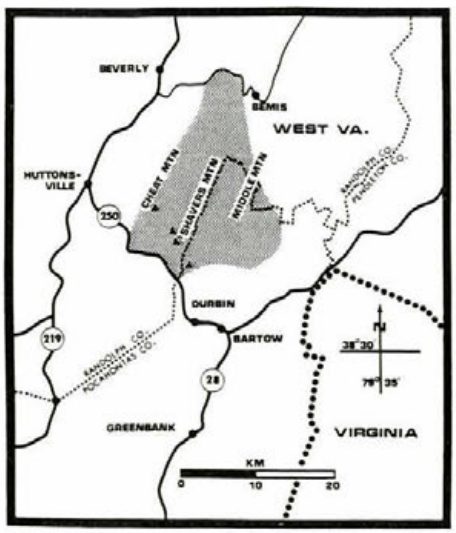


Figure 1.--Infestation by beech scale (shaded area) in West Virginia. Solid triangles indicate the presence of Nectria galligena. County lines are indicated by small dots and State lines by large dots.

Nectria coccinea var. faginata Lohm. et al., the fungus commonly implicated in the disease complex in the northeast United States, was not found. N. galligena, a common canker-causing fungus of hardwoods in West Virginia (Ashcroft 1934), is the only species of Nectria associated with beech bark disease in samples from more than 10

[1] Paper presented at the IUFRO Beech Bark Disease Working Party Conference, Hamden, Connecticut, USA, September 27 to October 7, 1982.

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affected trees within the infested area. The species was determined from ascospore size (Cotter and Blanchard 1981) and cultural characteristics (Booth 1959, 1966).

Subsequent observations have established the presence of beech bark disease on Cheat Mountain, 5 miles (8 km) due west of Shavers Mountain, with considerable mortality in both areas.

Beech is a major component of the northern hardwood forest on the unglaciated Allegheny Plateau region of the Monongahela National Forest. More than 11 percent of the total sawtimber volume on the entire forest is beech (USDA 1978). In the areas where beech occurs, the percentage is even higher. A survey to assess the damage caused by beech bark disease was conducted in July 1982.

MATERIALS AND METHODS

The Gaudineer Scenic Area (140 acres or 56.65 ha) was selected for an impact survey because there was beech bark disease and resultant mortality there. Twenty-eight, 20-basal-area-factor prism plots were systematically located on a 132-ft. (40.2 m) grid. Data taken for all trees were tree species, diameter at breast height (4.5 ft. or 1.37 m), crown class, and crown condition. Additional data taken on beech included an average score of C. fagisuga populations (Houston 1981), the presence of N. galligena (perithecia and sporodochia), tarry spots, the mycoparasite Gonatorrhodiella highlei A. L. Smith and, as appropriate, an estimate of how many years a tree had been dead.

RESULTS AND DISCUSSION

The stand is virgin red spruce (Picea rubens Sarg.) together with associated hardwoods. Stand composition and diameter data are summarized in Table 1.

Thirty-six percent of the total basal area is beech. Of this, 29 percent or 15 square feet of basal area per acre has died. In terms of sawtimber (12 inches and greater dbh to a 9-inch merchantable top), 5,697 board feet per acre is beech of which 1,369 or 24 percent has died. On those plots where beech is present, there are 6,613 board feet per acre of which 1,562 has died. The error rate is 15.6 percent at the 68 percent level of confidence, range 5,581 to 7,645 board feet per acre. In addition to

Table 1.--Stand composition and diameters

Species	Average basal area[a]		Average dbh	
	(Ft^2/Acre)	(M^2/Ha)	(Inches)	(Cm)
Red spruce	68.57	15.74	18.87	47.93
American beech	55.71	11.79	13.74	34.90
Yellow birch (Betula alleghaniensis Britton)	28.57	6.56	17.98	45.67
Red maple (Acer rubrum L.)	12.14	2.79	14.32	36.37
Black cherry (Prunus serotina Ehrh.)	3.0	.69	24.16	61.37
Other	2.0	.46	8.7	22.10
Total	169.99	39.03	16.68	46.36

[a]Only stems greater than 5.5 inches (13.97 cm) dbh were tallied.

sawtimber volume, there are 9.29 cords per acre (6-11 inches dbh to a 4-inch minimum top) of which 2.67 or 29 percent has died. Volume data are summarized in Table 2.

Table 2.--Volume of beech per acre

Plots	Board feet of sawtimber[a]		Cordwood[b]	
	Total	Dead	Total	Dead
All plots	5,697[c]	1,369	9.29[d]	2.67
Plots with beech	6,613	1,562	10.84	3.11

[a]In metric equivalents, sawtimber size classes are 27.94 cm dbh and greater to a 22.86 cm minimum top diameter.

[b]Cordwood size classes are 15.24 up to 27.94 cm dbh to a 10.16 cm minimum top diameter.

[c]Metric equivalents of sawtimber from left to right, respectively, 33.22, 7.98, 38.56 and 9.11 m^3 per ha.

[d]Metric equivalents of cordwood from left to right, respectively, 52.0, 14.95, 60.68 and 17.41 m^3 per ha.

In all, 78 beech trees were examined. Fifty-six live beech had an average dbh of 13.64 inches, and 22 dead beech, 13.26 inches. Fifty-two of 56, or 92 percent, of live beech had C. fagisuga ranging from a trace to very heavy. The average infestation score was moderate. Of the 56 live beech infested, 52 (46.4 percent) had tarry spots, 12 (21.4 percent) had N. galligena perithecia, and 8 (14.3 percent) had G. highlei. Only one infested tree had G. highlei and no N. galligena perithecia.

Of the 22 dead beech examined, 14 had signs of infection by Nectria spp., either perithecia, G. highlei or both. Six of the eight remaining trees were estimated to have been dead for at least 4 years and had lost most of their bark. Only two trees estimated to have been dead less than 2 years bore no evidence of infection.

The present value of beech sawtimber and cordwood in West Virginia is $40 per mbf, and $12 per cord. Using these figures, the value of timber lost at the Gaudineer Scenic Area is $87 per acre ($215 per ha). The total beech component is worth $252 per acre ($623 per ha). If beech bark disease continues to kill trees as our observations suggest it will, this also represents the total potential loss.

There are three major considerations when one looks at the status of beech bark disease in West Virginia: 1) Cryptococcus fagisuga is a relatively new insect in the state and has not yet spread throughout the entire range of beech, 2) beech bark disease mortality has just started over the past few years and will continue to increase, and 3) the apparent relationship between C. fagisuga and N. galligena may be unique to West Virginia. The fact that N. galligena, a common pathogen of many hardwood hosts, can rapidly invade and kill beech trees infected with C. fagisuga is one that researchers and foresters in other beech bark disease areas should be aware of.

RÉSUMÉ

Le Cryptococcus fagisuga fut trouvé sur le hêtre à grandes feuilles dans la Virginie de l'Ouest en août 1981. Un relevé exécuté en octobre 1981 a révélé la présence éparse de l'insecte sur approximativement 28 000 ha. Le Nectria galligena fut trouvé associe au C. fagisuga dans la portion centre-sud de l'aire infestée. Le N. galligena semble être la seule espèce de Nectria impliquée dans cette situation. La distribution connue à ce jour du C. fagisuga ne s'approchait qu'à environ 500 km de cet endroit et en était séparée par un territoire surtout montagneux.

Un relevé subséquent a révélé la présence du N. galligena avec le C. fagisuga à 8 km à l'ouest du premier endroit, avec beaucoup de mortalité survenant aux deux endroits. Les pertes dans le peuplement le plus affecté de la maladie de l'écorce du hêtre dépassait 22 m^3 à l'hectare. Le volume total du hêtre dépasse les 85 m^3 à l'hectare, ce qui représente la perte totale potentielle.

ZUSAMMENFASSUNG

Im August 1981 wurde Cryptococcus fagisuga erstmals auf Buchen (Fagus grandifolia) in West Virginia festgestellt. Eine Überprüfung im Oktober 1981 bestätigte, daß das Insekt zerstreut auf rund 28000ha vorkommt. Nectria galligena wurde in Verbindung mit C. fagisuga im südlichen Teil des zentralen Befallsgebietes angetroffen. N. galligena

scheint die einzige Nectria-Art zu sein, die hier am Krankheitskomplex beteiligt ist. Die Grenze des bisher bekannten Verbreitungsgebietes von C. fagisuga ist rund 500 km entfernt und durch vorwiegend bergiges Gelände vom Gebiet des derzeitigen Vorkommens in West Virginia getrennt.

Eine weitere Überprüfung ergab das Auftreten von *N. galligena zusammen mit C. fagisuga* 8 km westlich des ersten Gebietes sowie beträchtliche Ausfälle in beiden Gebieten. Die Holzverluste in den von der Buchen-Rindennekrose am meisten betroffenen Beständen übersteigen 22 fm/ha. Das Gesamtvolumen an Buche beträgt über 85 fm/ha, was mit dem möglichen Gesamtverlust pro Hektar gleichzusetzen ist.

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INTERACTION BETWEEN BEECH AND BEECH SCALE[1]

D. Wainhouse[2]

Abstract.--Trees heavily infested with beech scale are commonly observed either singly or in small groups within infested forests. This appears to be due partly to the presence of resistant trees and also, in the U.K. at least, to the existence of sub-populations of scale insects, some of which appear to be adapted to individual host trees. It is suggested that the greater susceptibility of American beech to attack by beech scale may be due in part to the absence of co-evolved defence mechanisms.

In Europe, beech scale (*Cryptococcus fagisuga* Lind.) is indigenous and some scale insects are present in most stands over about 20 years old. Recent observations have indicated that many trees within the forest remain either uninfested or only lightly infested for several years (E.J. Parker, D. Lonsdale, D. Wainhouse unpublished data) even when artificially inoculated (Houston *et al.* 1979). This suggests that some trees are resistant at least for part of their life. It is a common observation that trees heavily infested with scale occur singly or in small groups throughout infested stands and that heavily infested and uninfested trees frequently occur together (Boodle and Dallimore 1911, Thomson *et al.* 1949, Kuthe and Krämer 1961). This further indicates heterogeneity in susceptibility of trees to attack. Work in the U.K. suggests that there is a genetic basis to this resistance (Wainhouse and Deeble 1980, Wainhouse and Howell this volume).

Recent experiments in England in which trees were artificially infested with beech scale show that there is intraspecific variation within scale populations in their ability to attack individual trees (Wainhouse and Howell 1983). This variation was shown by differences in survival of larvae from different individual infested trees when they were inoculated onto a single susceptible tree. Some populations appear to be adapted to individual trees and their survival when they are experimentally re-inoculated onto their own host tree is higher than that of larvae derived from other infested trees. Although some unattacked trees in the forest may be more or less completely resistant (Wainhouse and Howell 1983, D.R. Houston pers. comm.) the level of resistance exhibited by other trees may depend on the origin of larvae used to infest them. This suggests that resistance in some trees may only be partial and must be defined in the context of the particular attacking sub-population of scales (Edmunds and Alstad 1978). The rate of development of scale populations within forests therefore may depend on a complex interaction between host resistance and variation in the scale insect's ability to survive on individual trees.

In North America some trees resistant to beech scale appear to be present in the mixed hardwood forests (D.R. Houston pers. comm.), however, the majority of trees are affected by the disease. In previously uninfested forests 90% of trees may be infected with *Nectria* which occurs on trees previously infested with beech scale (Ehrlich 1934). The rate of spread of beech scale into uninfested areas also appears to be quite rapid, averaging 6-8 km/year (Wainhouse, 1980, Houston *et al.* 1979). The apparently greater susceptibility of *Fagus grandifolia* may be partly due to the absence of the kind of interactions we have described between European beech and beech scale. The interaction between tree defences and scale populations would tend to reduce the rate of spread of beech scale through forests. The absence of beech scale from the U.S.A. until about 1900 (Ehrlich 1934) reinforces the view

[1] Paper presented at the I.U.F.R.O. Working Party Conference, Hamden, C T., U.S.A. 27 September to 7 October, 1982.

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that intraspecific diversity of defences to beech scale may be absent in American beech.

Clearly more information is needed on the nature of resistance of trees to beech scale attack, its stability when the trees are growing on different sites (see Wainhouse and Howell, this volume) and its relationship to tree age. The relative role of tree resistance and scale insect sub-populations in determining the dynamics of scale populations and ultimately beech bark disease would repay further study.

ZUSSAMMENFASSUNG

Stark von der Buchenwollaus befallene Bäume sind gewöhnlich entweder einzeln oder in kleinen Gruppen in den befallenen Bestanden anzutreffen. Dies scheint zum Teil mit der Resistenz der Buchen zusammenzuhängen und, zumindest in England, mit dem Verkommen von Teilpopulationen der Buchenwollaus, die teilweise an ihre Wirtsbäume speziell angepasst zu sein scheinen. Es ist gut denkbar, dass die höhere Anfälligkeit von Fagus grandifolia gegenüber der Buchenwollaus zum Teil darauf beruht, dass Resistenzmechanismen wegen des Fehlens einer gemeinsamen Evolution von Wirt und Pathogen bei der amerikanischen Buche nicht entwickelt werden konnten.

RÉSUMÉ

Les arbres gravement infestés par la cochenille du hêtre s'observent communément soit isolés, soit en petits groupes à l'intérieur des forêts infestées. Ceci semble être dû en partie à la présence d'arbres résistants et aussi, du moins dans le Royaume-Uni, à l'existence de sous-populations de cochenilles, certaines semblant s'être adaptées à des arbres hôtes donnés. Il semblerait donc que la grande susceptibilité du hêtre à grandes feuilles aux attaques de la cochenille soit due en partie à l'absence de mécanismes de défense co-évolutionnaires.

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DISTRIBUTION OF ATTACK BY BEECH SCALE *Cryptococcus fagisuga* IN BEECH PROGENY TRIALS[1]

D. Wainhouse,[2] R. S. Howell[3]

Abstract.--Surveys of beech scale infestation among progeny of single beech trees demonstrated significant variation in susceptibility between the progenies. Relative differences in susceptibility of some progeny were maintained on three different sites in southern England.

INTRODUCTION

At a previous beech bark disease symposium it was shown (Wainhouse and Deeble, 1980) that there were clonal differences in susceptibility of beech to beech scale (*Cryptococcus fagisuga* Lind.). The present paper is an extension of this investigation in which we were able to examine the progeny of single trees to determine their relative resistance to infestation by beech scale.

GENERAL METHODS

The progeny of trees of exceptionally good silvicultural characteristics ('plus' trees) had been established by the Genetics Department of the Forestry Commission in a series of trials to assess their survival, growth rate and form. When the trees had reached pole-stage, natural infestations of beech scale had developed in all the progeny trials and this provided an opportunity to determine their relative susceptibility to attack.

To establish the progeny trials, seed was collected from parent 'plus' trees or from their grafts or rooted cuttings. The trees were open pollinated with or without a pollen mixture supplement.

The data collected on the abundance of the scale or other beech bark disease symptoms from two trials (Arundel and Wendover) were analysed in detail. Data from a third, unreplicated trial were used in a between-trial comparison of the susceptibility of progeny to attack by beech scale.

The parent 'plus' trees were growing on various estates in the UK and the estate name and original Forestry Commission reference numbers were retained to simplify data handling.

Arundel Progeny Trial

This trial was situated in Arundel forest, Sussex. There were six replicates of each of ten progeny planted in 1964 in a randomised block design (Fig 2) with three surrounding guard rows. Each plot, originally contained 36 trees planted 1.5 x 1.5 m apart. The plots were unthinned with about 12% of trees missing through natural mortality.

Many trees within the plots had beech scale colonies on them but there were few other symptoms of beech bark disease present. In October/November 1980, the total number of colonies (discrete areas of wax) in a 3 cm x 3 cm quadrat placed at 0.8 m and 1.7 m above ground on the east and west side of each non-forked tree was determined. Counts were made by three different observers, each allocated two blocks at random. The total count for the four quadrats was used as an index of scale population on each tree. The girth of each living, non-forked tree at breast height (1.3 m) was measured in May 1981.

Results.--An analysis of variance of the girth of trees showed that there were significant

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[1] Paper presented at the IUFRO Beech bark disease Working Party Conference, U.S.A., September-October, 1982.

[2] Entomologist, and

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differences (P<0.001) between the progeny. Furthermore mean counts of beech scale for the ten progeny and mean girth are significantly (P<0.01) positively correlated (Fig 1).

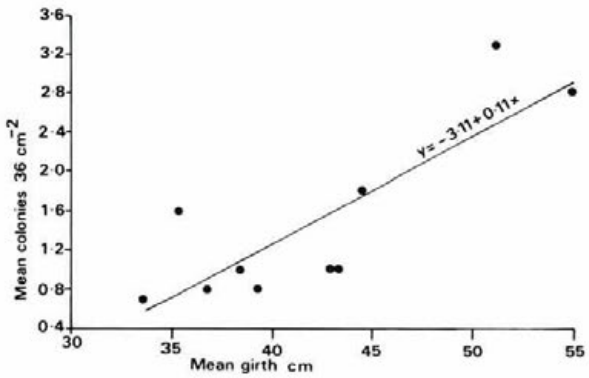


Figure 1.--Relationship between mean number of colonies 36 cm^{-2} and mean girth for progeny at Arundel.

Consequently in the analysis of variance of counts of beech scale (transformed to ln (count +1)), tree size was included as a covariate. Basal area calculated from the estimated mean girth of plots was used as an estimate of tree size. The analysis of variance results are shown in Table 1. The apparent difference between observers in the

Table 1 Covariance analysis Table for number of beech scale colonies on progeny at Arundel

Source of Variation	D.F.	S.S.	M.S.	V.R.	Probability (P)
Between observers					
Covariate	1	0.923	0.923	2.934	
Residual	1	0.315	0.315	4.266	P<0.05
Total	2	1.238			
Between blocks within observers					
Covariate	1	0.572	0.572	1.970	
Residual	2	0.581	0.291	3.940	P<0.05
Total	3	1.154			
Between plots					
Progeny	9	2.242	0.249	3.378	P<0.01
Covariate	1	0.445	0.445	6.030	P<0.05
Residual	44	3.246	0.074		
Total	54	5.933			
Grand Total	59	8.324			

estimation of abundance of beech scale appears to be due to the significant (P<0.05) difference between blocks. Results show that there are highly significant (P<0.01) differences between the progeny in attack by beech scale, (Table 2) independently of the effects of tree size.

Table 2 Mean number of colonies of beech scale 36 cm^{-2} on progeny at Arundel.

Parental 'plus' tree origin	Reference No.	Mean No. of scale colonies 36 cm^{-2} adjusted for covariate
West Dean	51	2.7
West Dean	52	2.0
Slindon	63	1.9
Slindon	65	1.7
Amberley	107	1.1
Pennwood	81	1.0
Pennwood	84	1.0
Brecon	100	1.0
Slindon	60	0.9
Maiden Bradley	90	0.9

The residual variation of counts of *C. fagisuga* after removal of the effects of progeny, girth and observers are plotted in Figure 2.

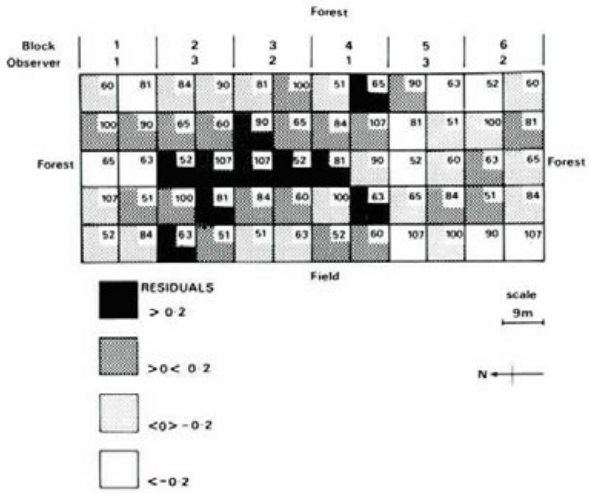


Figure 2.--Distribution of residual beech scale infestation (see text) among plots of progeny at Arundel.

Negative residuals indicate less and positive ones more beech scale infestation than the mean expectation. The results clearly illustrate the significant block effect in the analysis and show that the area in the centre of the trial has more, and the two ends less, beech scale infestation than the average.

Wendover progeny trial

This plot was situated in Wendover forest, Hertfordshire. There were three replicates of each of ten progeny in a randomised block design and one unreplicated block of a further twelve progeny. Each plot originally contained 25 trees, 1.2 m x 0.9 m apart planted in 1953. At the time of assessment, the plots were unthinned but about 50% of trees had died from either suppression or beech bark disease. In August 1979, the trees were assessed for severity of beech scale attack. It was not possible to use a quadrat counting method because of the high density of insects on some trees. Instead, a visual scoring (Table 3) of the insects' wax secretion was used. Two other disease symptoms, dimpling and tarry spots (Houston et. al. 1979) were also noted. Dimpling of the bark surface caused by beech scale feeding was assessed as light, moderate or extensive and tarry spots noted as present or absent. In addition to these disease symptoms the proportion of the basal circumference of trees damaged by the bark stripping activities of squirrels was assessed. Unlike the trial at Arundel, these plots were affected by fairly extensive bark stripping. In April 1980, the girth of trees at 1.3 m above the ground was measured.

Table 3 Visual assessment scores for beech scale infestation at Wendover.

Score	Description, applying to at least ¼ of main trunk
1	Up to 5 small colonies visible.
2	Some small colonies scattered over surface of bark. Few large colonies.
3	Moderate numbers of small colonies and large colonies present.
4	Many large and small colonies present.
5	Very many colonies, with large colonies coalescing.

Results.--Only data from the replicated plots were analysed. Analysis of variance of tree girth and squirrel damage showed that they did not differ significantly among the progeny. These two variables were used as covariates in the analysis of the three disease symptoms, beech scale wax cover, dimpling and tarry spots. The analysis of variance results for mean wax cover are shown in Table 4. As well as significant variation in beech scale infestation between blocks, there were highly significant differences between progeny (Table 5) supporting the results obtained from Arundel. However, no progeny differences were detected either for dimpling or for tarry spots.

Table 4 Covariance analysis Table for beech scale wax cover on progeny at Wendover

Source of variation	D.F.	S.S.	M.S.	V.R.	Probability (P)
Blocks	2	0.945	0.472	5.154	$P<0.05$
Progeny	9	2.419	0.269	2.932	$P<0.01$
Covariates	2	0.385	0.192	2.099	
Residual	16	1.467	0.092		
Total	27	4.271			
Grand Total	29	5.217			

Table 5 Mean infestation score of beech scale on progeny at Wendover

Parental 'plus' tree origin	Reference No.	Mean score adjusted for covariates
Goodwood	42	3.2
West Dean	51	3.1
Cirencester	30	3.1
Cowdray	71	3.0
Kingscote	3	2.9
West Dean	52	2.7
Kingscote	5	2.6
Slindon	61	2.6
Pennwood	83	2.3
Brecon	100	2.3

Comparisons between progeny trials

In addition to the progeny trials at Arundel and Wendover, one further trial was examined. This was an unreplicated trial at Alice Holt forest, Surrey planted in 1953. This had been visually assessed for beech scale infestation by E.J. Parker (unpublished 1975) using a scoring system similar to that described in Table 3.

The plot had been thinned in 1963 and 1968 and at the time of assessment in 1975 thinning and mortality had accounted for 80% of the trees which were originally planted at a spacing of 1.2 m x 0.9 m in plots of 25 trees.

Of the large number of progeny planted in these trials, only five were present at all three sites. At each site these five progeny were ranked for mean infestation level and this forms the basis of the comparison in Table 6. The degree of association among the rankings was tested by the Kendall coefficient of concordance (W) (Siegel 1956). The result was non-significant indicating that the ranks did not agree closely at all three sites. However, the estimated value of W = 0.6 indicates some agreement between the rankings. Some progeny such as 51 and 52 were consistently the most heavily attacked whereas others such as 100 were apparently less susceptible.

Table 6 Ranks of mean scores of beech scale infestation on progeny at three sites in southern England

Parental 'plus' tree origin	Reference No.	Site		
		Arundel	Alice Holt	Wendover
West Dean	51	1	3	1
West Dean	52	2	1	3
* Slindon	60	3	2	4
* Maiden Bradley	90	4	5	2
Brecon	100	5	4	5

Kendall coefficient of concordance (W) = 0.6 (S = 54)

* Unreplicated at Wendover

DISCUSSION

At Arundel, the larger trees harboured greater populations of beech scale, supporting previous observations of this effect (Ehrlich 1934; Barter 1947; Wainhouse and Deeble 1980; E.J. Parker, D. Lonsdale and D. Wainhouse unpublished observations). The trees within each progeny trial were even-aged so the differences in tree girth are due to different rates of growth of the individual trees. The present observations therefore clearly separate the effect of tree size/growth rate from their age on the population development of beech scale. The differences in infestation between progeny at Arundel are nevertheless independent of variations in the size of trees.

The present results showing significant differences in beech scale infestation between progeny on at least two sites extend the previous results of Wainhouse and Deeble (1980). The trees are not grafted and are therefore free of possible rootstock effects on susceptibility so they are expressing presumed maternal variation in susceptibility to attack. A large amount of genetic variation is likely to exist between the trees within these open pollinated progeny. Nevertheless there is good evidence that relative susceptibility to infestation is consistently expressed independently of the site on which the trees are growing. That site may have some effect on host-plant susceptibility to this insect is suggested by the non-random distribution of residual variation in infestation level at Arundel and by the significant effect of blocks on infestation at Wendover.

The assessments were made at the three sites when the trees were 16 (Arundel), 22 (Alice Holt) and 26 (Wendover) years old, showing that differences between progeny are present at an early age and persist at least into the period when trees are considered maximally susceptible (Parker 1974). However, our results do not exclude the possibility that changes in relative susceptibility may occur during subsequent growth and development of the trees.

ACKNOWLEDGEMENTS

Our thanks to Angela Revett and Martin Jukes for assistance with fieldwork. David Lonsdale and Clive Carter made valuable criticism of the manuscript.

RÉSUMÉ

Les descendants d'arbres de caractéristiques sylvicoles exceptionnellement bonnes avaient été plantés dans le cadre d'une série d'essais sylvicoles, permettant ainsi de constater le degré d'invasion des descendants par la cochenille du hêtre et de déterminer leur sensibilité à l'attaque.

Nous avons pu démontrer des variations significatives de la sensibilité des descendants à l'invasion par la cochenille du hêtre. Il y avait aussi des indications que les mêmes différences relatives de sensibilité de certains descendants se retrouvaient a trois emplacements différents dans le sud de l'Angleterre.

ZUSAMMENFASSUNG

In einer Reihe von Versuchsanbauten mit Nachkommen von Bäumen mit außergewöhlich guten Eigenschaften bot sich die Gelegenheit, die Ausmaße eines Buchenwollschildlausbefalls aufzunehmen und die relative Anfälligkeit der Nachkommen festzustellen.
Wir konnten zeigen, daß bei den Nachkommen wesentliche Unterschiede in der Anfälligkeit gegenüber der Buchenwollschildlaus bestehen. Es zeigte sich auch, daß relative Unterschiede in der Anfälligkeit bei einigen der Nachkommen an drei verschiedenen Anbauorten in Südengland beibehalten wurden.

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AMERICAN BEECH RESISTANCE TO *CRYPTOCOCCUS FAGISUGA*[1]

David R. Houston[2]

Abstract.--American beech trees that were free of beech bark disease in forests long-affected by beech bark disease were challenged with C. fagisuga using the 'foam' technique. Trees were resistant: no insects reached maturity. In Nova Scotia, 12-15 disease-free trees per hectare occurred in the stands examined. Many of these trees occurred in groups.

INTRODUCTION

In forests of Canada and New England, beech trees are often highly defective (Shigo 1972; Houston 1975). The defect is the consequence of accumulated attacks by the now endemic causal agents of beech bark disease, Cryptococcus fagisuga (Lindinger) and Nectria spp., on young trees emerging in the aftermath of disease-caused mortality or salvage.

The extreme defect has significantly reduced the value of beech. For example, in the Maritime Provinces of New Brunswick and Nova Scotia, and in many stands in Maine, beech has little value other than that for firewood. As developing stands become more and more defective, some trees remain disease free. It has been suggested that such trees are resistant to beech bark disease, but no trials have been conducted expressly to determine this, or to ascertain if disease-free trees occur in sufficient numbers or are distributed in ways that could be exploited in forest management.

This paper presents the results of tests to determine (1) if disease-free trees are resistant to C. fagisuga and (2) the abundance and patterns of distribution of disease-free trees in selected forests of Nova Scotia.

Study 1. Resistance of disease-free trees to C. fagisuga.

Methods and materials.--Seventeen disease-free trees in Maine and New Hampshire were challenged with C. fagisuga in August of 1980, 1981, and 1982 (Table 1). The "foam technique" (Houston 1982) was used to introduce the insect to candidate trees located by systematically searching the forests being studied. Disks of bark supporting heavy infestations of C. fagisuga were removed from trees in July with a 1.12-inch-diameter (2.8-cm) arch punch and kept in covered plastic cups over ice until used. One or two disks with abundant eggs were placed against the tree beneath 10- by 10- by 5-cm polyurethane foam squares, bark side inward, covered with a 10- by 10- by 0.6-cm square of tempered Masonite[3] and held in place with rope. Usually four blocks, and at least two on opposite sides of the bole, were used for each tree.

Eight susceptible (infested) neighboring trees were used as controls. Existing scale populations were removed from control trees by scrubbing bark surfaces with a stiff-bristle brush before challenging. Scale populations beneath the foam covers were assessed in August, one year after challenging. If no C. fagisuga

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[3] The use of trade, firm, or corporation names is for the information and convenience of thr reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture or the Forest Service of any product or service to the exclusion of others that may be suitable.

Tree	Location	Challenged 8/80	Results 8/81 Average no. of healthy scale insects[a]	Rechallenged or challenged 8/81	Results 8/82 Average no. of healthy scale insects[a]	Rechallenged 8/82
P1-R	Bradley, ME	*	0	*	0[b]	*
P1-C	"	*	++	*	++++	*
					+++	
F1-R	Franklin, ME	*	0[c]	*	0	*
F1-C	"	*	+++	--	++++	*
F2-R	"			*	0[d]	--
F2-C	"			*	++++	*
F3-R	"			*	0[e]	*
B1-R	Bartlett, NH			*	0	*
B2-C	"			*	++++	*
B3-R	"			*	0	*
B4-R	"			*	0	*
B5-R	"			*	0	*
B6-R	"			*	0	*
B7-R	"			*	0	*
B8-R	"			*	0	*
B9-C	"			*	+++	*
B10-C	"			*	++++	*
HB1-R	W.Thornton, NH			*	0	--
HB2-R	"			*	0	*
HB3-C	"			*	++	*
HB4-R	"			*	0	*
HB5-R	"			*	0	*
HB6-R	"			*	0	*
HB7-C	"			*	+	*
HB8-R	"			*	0	*

Table 1.--Schedule and results of challenge with beech scale on selected disease-free (R) and susceptible (C) beech trees.

* Indicates challenge or rechallenge.

[a] Average number healthy scale insects: + = 10-50, ++ = 51-100, +++ = 101-200, ++++ = 200+

[b] 50 colonies beneath 1 cover, all tiny, moribund, poor wax, no eggs.

[c] 100+ tiny immature colonies, poor wax, no eggs.

[d] 25-50 tiny, immature colonies beneath 3 covers, no eggs.

[e] 10-200 tiny colonies, all immature with no eggs.

colonies were present, new disks bearing fresh eggs were placed beneath the same foam covers. When colonies were present, the foam was replaced; and the infestation technique was repeated beneath new covers at different locations on the tree.

Results.--The results indicate clearly that the disease-free trees growing in the generally defective aftermath forests are resistant to C. fagisuga (Table 1). On susceptible trees, C. fagisuga succeeded in completing its life cycle. One year after eggs were introduced, abundant, healthy mature females had become established and had produced copious numbers of eggs. By contrast, C. fagisuga failed to become established on most resistant trees. If insects became established and overwintered, they failed to resume development the following spring. None became adults, no eggs were laid, and all were dead or moribund after 1 year. This relationship held for the second year in the four trees challenged first in 1980. All trees will be rechallenged and monitored for at least 5 years.

The associated scale, Xylococculus betulae (Perg.) Morrison, introduced via the bark disks along with C. fagisuga, was able to successfully establish itself and mature on the disease-free trees. On some trees, numerous colonies developed beneath some of the bark covers.

Study 2. Abundance and patterns of distribution of disease-free trees in selected forests of Nova Scotia.

Methods and materials.--Two stands in Nova Scotia were examined in 1982 for the presence of beech trees free of beech bark disease.[4] In one stand growing on flat terrain, near Riversdale, a 5.4-ha block (385 x 140 m) was searched systematically. Each disease-free tree was numbered, its diameter at 1.4 m and crown class were

[4] The stands were selected by personnel of the Canadian Forestry Service, who had noted previously the occurrence of a disease-free tree in each.

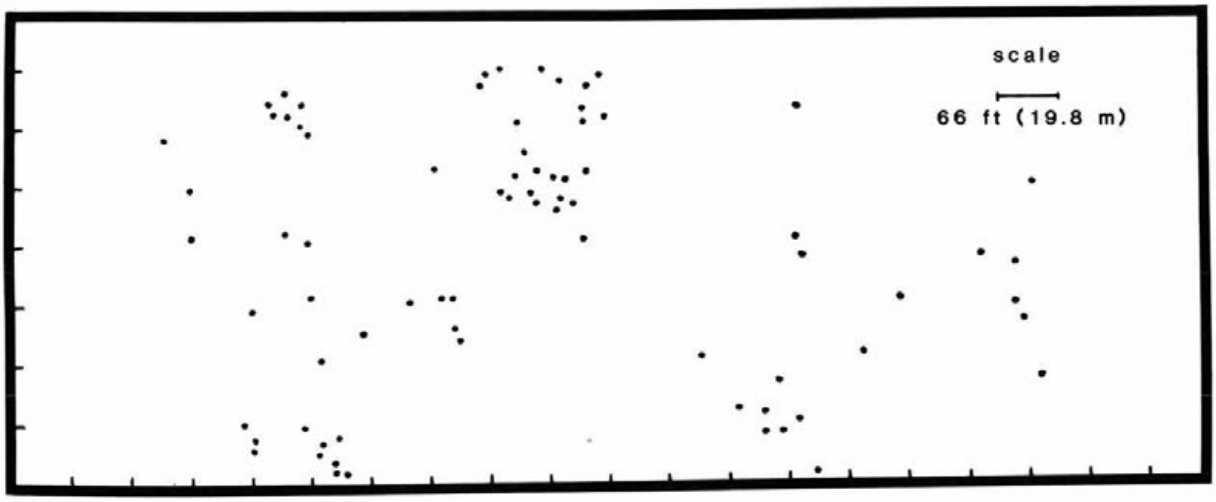


Figure 1.--Distribution pattern of 75 disease-free beech trees in a 5.4-ha block of forest near Riversdale, Nova Scotia. The distributions of the approximately 370 diseased beech trees per hectare are not shown.

determined, and its location was mapped (Fig. 1). The second stand in Brookside was a more diverse forest growing on a steep east-southeast facing slope. A 2.4-ha swath (60 x 400 m along the upper slope was searched for disease-free trees, which were measured and mapped as previously described.

Both stands were sampled to obtain information on species composition and density. At 10 points located 40 m apart along a midstand transect, trees were selected with a 10 ft^2 (approximately 2 m^2) basal-area-factor prism. For each tree, the species, diameter, crown class, condition, and, for beech, a general defect level were noted.

Results.--In the stand at Riversdale, considerably more disease-free trees were found than were anticipated (Fig. 1). While some of these trees were scattered at random throughout the stand, most were concentrated in groups. In the 2.4-ha Brookside stand, all but two of the disease-free trees were located in one .04-ha area.

The distributions by size classes for disease-free trees are shown in Figures 2 and 3. Relatively more disease-free trees than diseased trees occurred in the largest (21-40 cm) and smallest diameter classes (1-10 cm) in the Riversdale stand (Fig. 2); while at Brookside, most of the disease-free trees were less than 15 cm in diameter (Fig. 3).

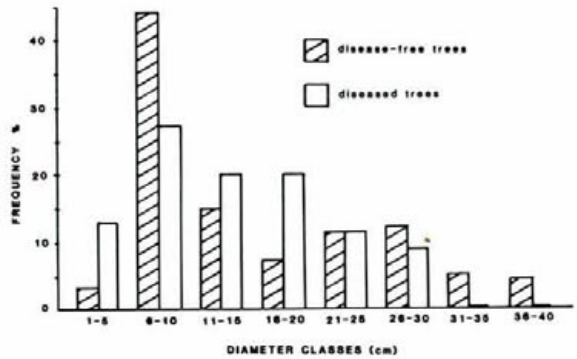


Figure 2.--Frequency distribution, by diameter classes (at 1.4 m) for 75 disease-free and 45 diseased beech trees, Riversdale, Nova Scotia.

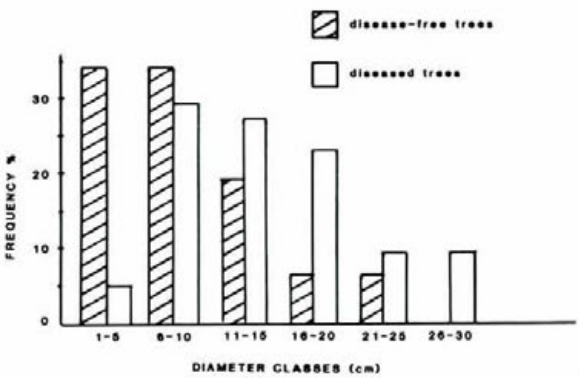


Figure 3.--Frequency distribution, by diameter classes (at 1.4 m) for 32 disease-free and 64 diseased beech trees, Brookside, Nova Scotia.

The Riversdale stand was predominately beech and sugar maple (Table 2). Although the basal area of the two species was nearly the same, beech far outweighed sugar maple in stems per hectare. There were many small overtopped defective beech trees. The greater diversity of the Brookside stand (Table 3) reflects its more diverse physiography, past disturbance, and its probable greater age. Beech predominated here also. In both stands, approximately 12-15 disease-free trees occurred per hectare, though their distributions were highly aggregated.

Table 2.--Composition of beech stand--Riversdale, N.S. (75 disease-free trees in 5.4 ha = 15 trees/hectare)

Species	No. stems/hectare (3-40 cm diameter)	Basal area (m^2/hectare)
Fagus grandifolia	2129	10.00
Acer saccharum	766	10.45
Picea rubens	37	1.56
Betula alleghaniensis	2	.67
Abies balsamea	2	.22
Total	2936	22.9

Table 3.--Composition of beech stand--Brookside, N.S. (32 disease-free trees in 2.4 ha = 12 trees/hectare)

Species	No. stems/hectare (3-40 cm diameter)	Basal area (m^2)/hectare
Fagus grandifolia	1872	14.22
Acer saccharum	143	2.89
Acer rubrum	314	2.67
Populus grandidentata	39	2.67
Amelanchier arborea	121	1.56
Betula alleghaniensis	161	1.11
Betula papyrifera	54	.89
Abies balsamea	30	.67
Total	2734	26.68

DISCUSSION

Results from Study 1 confirm earlier opinions that the disease-free trees encountered occasionally in highly defective aftermath forests are indeed resistant to beech bark disease. They repeatedly resisted challenge with C. fagisuga under conditions highly favorable to the insect, and this suggests that the mechanism(s) involved is extremely effective. And, resistance to C. fagisuga offers promise that the expressed resistance may be enduring. Even though C. fagisuga, which reproduces parthenogenetically, is capable of expressing genetic diversity (see Wainhouse 1983, these proceedings), the opportunity for overcoming host resistance is undoubtedly less than that which would be expected through sexual processes.

The preliminary study in Nova Scotia revealed that a higher level of disease-free trees occurred in the highly defective forests than that recognized previously. Although the two stands examined differed in species composition, topography, and possibly age, both contained about 12-15 disease-free trees per hectare. In both stands, the majority of disease-free trees were in groups. It was not clear, however, whether this aggregation resulted from trees arising from root sprouts or from localized seed fall. This question, now under investigation, is important because understanding the mode of propagation will help determine forest management practices to enhance the spread and development of resistant trees.

The nature of the observed resistance to C. fagisuga is not yet known. The inability of overwintered insects to reach maturity on trees completely free of disease suggests either the presence of a toxin, or the absence of some required chemical substance. In addition, the lack of any development on many trees (Table 1) or the consistent development of low numbers of insects on others (Houston 1982; Wainhouse, these proceedings) suggests the presence of a complete or partial anatomical barrier. Management trials to favor resistant trees would be enhanced if such trees could be recognized before or during the early phases of disease development.

SUMMARY

American beech trees that are free of beech bark disease in forests long affected by the disease in New England were challenged with C. fagisuga, the initiator of the disease complex. Results indicate that these trees are resistant to the insect. The inability of insects to establish themselves on some trees, or to mature on others, suggests that both anatomical and chemical bases for resistance may exist.

Levels of resistance in two Nova Scotia forests were higher than previously believed; 12-15 trees/hectare. Many resistant trees occurred in groups that could have arisen either vegetatively from root sprouts or from local seed fall.

RÉSUMÉ

Des hêtres à grandes feuilles, exempts de la maladie de l'écorce du hêtre, et croissant dans des forêts de la Nouvelle-Angleterre affectées depuis longtemps par la maladie, furent exposés au C. fagisuga, l'initiateur de ce complexe pathologique. Les résultats indiquent que ces arbres sont résistants à l'insecte. L'inhabilité de l'insecte à s'établir sur certains arbres ou de compléter son cycle évolutif sur d'autres, suggère l'existence d'une résistance ayant des bases anatomiques et chimiques.

Les niveaux de résistance dans deux forêts de la Nouvelle-Ecosse étaient plus élevés que prévus; de 12 à 15 arbres à l'hectare. Plusieurs arbres résistants se trouvaient en groupes à partir de rejets de racines, ou de semences locales.

ZUSAMMENFASSUNG

In Wäldern Neuenglands, in denen seit langer Zeit Buchen-Rindennekrose auftritt, wurde versucht, Cryptococcus fagisuga, den Auslöser des Krankheitskomplexes, auf gesund gebliebenen Buchen anzusiedeln. Die Ergebnisse dieser Versuche weisen darauf hin, daß diese Bäume gegen die Buchenwollaus resistent sind. Daß das Insekt einerseits, auf manchen Bäumen, nicht in der Lage ist, überhaupt Fuß zu fassen oder, auf anderen Buchen, sich nicht zu ausgewachsenen Tieren zu entwickeln vermag, legt die Annahme nahe, daß sowohl anatomische als auch chemische Resistenzursachen im Spiele sind.

Die Anzahl der gegenüber der Laus resistenten Buchen in zwei Waldgebieten Neuschottlands ist mit 12-15 Bäumen/ha größer als ursprünglich angenommen. Viele resistente Bäume treten in Gruppen auf, die entweder vegetativ durch Wurzelbrut oder durch örtlich begrenzten Samenfall zustande gekommen sein können.

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WOOD AND BARK ANATOMY OF YOUNG BEECH IN RELATION TO *CRYPTOCOCCUS* ATTACK[1]

David Lonsdale [2]

Abstract.--Within a sample of European beech, partial resistance to attack by the beech scale, *Cryptococcus fagisuga*, was associated with a smooth bark which had a regular, vertical pattern in its surface 'growth lines'. Such bark contained relatively little lignified outer parenchyma, and the main stone cell layer was strongly developed. The 'dimpling' symptom of infested stems was brought about by locally reduced and abnormal xylem development.

INTRODUCTION

The bark structure of beech, *Fagus* spp. is of a type unusual among temperate hardwoods, since even in old trees live parenchyma tissue is present just beneath the outer surface. It is this tissue from which the beech scale, *Cryptococcus fagisuga* Lind. obtains its food supply. The relationship between the anatomy of the host and feeding by the insect is of relevance to beech bark disease (BBD) for two reasons. First, if there are any anatomical factors which can influence the availability of nutritive parenchyma tissues, they may determine whether or not infestation can become severe enough for the fungal phase of BBD to develop (Lonsdale 1980a). Second, it is known that abnormalities of the host tissues can develop in response to feeding by the insect, and it is possible that these abnormalities may contribute to the pathological processes involved in BBD.

The effects, if any, of host anatomy on susceptibility to scale feeding have received little attention, but it appears from the work of Kunkel (1968) and Braun (1976/77) that infestation itself can affect bark structure to the extent that feeding may be enhanced or inhibited by different phases of the histological response to attacks. Enhancement seems to occur at least for a short time due to the formation of gall-like structures within the outer bark parenchyma, while inhibition occurs when the cells in and around this structure become necrotic (Kunkel *op. cit.*). The formation of a wound phellogen at some depth beneath the primary phellogen occurs in response to feeding damage (Braun 1976b) and may serve further to isolate the outer parenchyma, thus causing extension of necrosis. A type of gall formation in young trees and also necrosis were described over a hundred years ago by Hartig (1878, 1880).

Little information is available on the possibly variable influence on insect feeding of the anatomy of trees which have never been previously infested, although it has been observed by Ehrlich (1934) and by Kunkel (1968) that the stone cells in outer bark can act as a barrier to stylar penetration. It has also been observed by S. Fink (pers. comm.) that trees with rhytidome formation, exceptional in beech, are more or less resistant to attack. This applies particularly to the 'male' or rough-barked beech (Feucht 1910, Münch 1914). The findings of Wainhouse and Deeble (1980) indicated that different genetic strains of beech may vary in their susceptibility to attack, and it is also a common observation that very young trees seldom become heavily infested. It may be that these differences are at least in part related to anatomical factors. The external smoothness and apparent hardness of the bark have been regarded as factors in susceptibility to attack (Eckstein 1920, Bertelsmann 1913, Reichling 1920), and attention has been drawn in particular to the role of fissures in providing suitable sites for settling of the insects (Thomsen, Buchwald and Hauberg 1949, Anon 1956). Surface growth of lichens (Ehrlich 1934) or of algae (Houston, Parker and Lonsdale 1979) may also enhance the build-up of colonies, while the fungus *Ascodichaena rugosa* Butin can act as a physical barrier to feeding (Houston 1976, Houston *et al. op. cit.*).

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[1] Paper presented at IUFRO Beech Bark Disease Working Party Conference, Hamden, CT. USA, 27 September to 7 October 1982.

[2] Forest Pathologist, Forestry Commission Research Station, Alice Holt Lodge, Farnham, Surrey, England.

As far as the health of the tree is concerned, there is uncertainty over the importance of the structural changes in the bark as reported by Kunkel (1968 and Braun 1977). Both these authors considered that the deep necrosis of the type typical of BBD could occur from scale feeding alone, and Braun (*op. cit.*) suggested that *N. coccinea*, though often present, was not essential in the etiology of BBD. However, no evidence for this has been obtained in the absence of micro-organisms and so they cannot be ruled out as a factor in the development of deep bark necrosis.

Another type of abnormal anatomy of infested stems is 'dimpling' or 'pitting'. In this condition the surface of the stem bears depressions approximately one centimetre in diameter and several millimetres deep. The first report which seems to describe the symptom in its current recognised form came from Thomsen *et al.* (*op. cit.*) in Denmark. The nature of dimpling has received little attention, although Parker (1974) suggested that it is the result of callusing around the margins of sites where small bark necroses associated with scale feeding have extended as deeply as the vascular cambium.

The objects of the present studies were to compare the bark structure of trees with apparently different degress of susceptibility, and to describe some of the anatomical abnormalities caused by scale feeding.

MATERIALS AND METHODS

The bark surface was examined *in situ* before and after removal of algae and lichens. The characteristics noted were as follows: general smoothness, shape and disposition of lenticels and abundance, size and orientation of vertical 'growth'lines. ('Growth' lines appeared to be associated with tangential expansion of the phellem.)

The bark anatomy was examined by cutting 15µm-thick sections on a freezing microtome after an embedding procedure involving six hours' immersion in a 5% agar solution at 45°C Phloroglucinal/HCl and Sudan Black were used to stain lignified and suberised tissues respectively. Other stains used were acid fuchsin and safranin/light green. The characters recorded were the thicknesses of the different tissue layers and the extent and continuity of stone cell layers. For examination of 'dimples' the wood and/or bark in the affected zones were transversely sectioned at 8-12 µm after a softening procedure in a mixture of equal parts glycerol and ethanol (Jane 1956). Longitudinal sections were cut at 2 µm using glass 'Ralph' knives (Lindner and Richards 1978). The frequencies and sizes of different xylem cell types were measured within the dimpled zone.

RESULTS

The bark surface in relation to susceptibility.

This study was carried out on eight clones comprising the four most resistant and the four most susceptible clones present in a seed orchard experiment (D. Wainhouse pers. comm.). The trees were located at Hemsted Forest in Kent (23 years old) and Alice Holt Forest in Hampshire (20 years old). In order to minimise the presence of alterations induced by insect feeding, bark samples were taken from zones of stem beyond the limits of any heavy infestation. The replicate trees, numbering from four to ten per clone, showed much less variation within clones than between clones. In view of the subjective nature of the assessments and the small number of clones available, the apparent differences between clones in bark surface morphology are expressed here in the form of the following observational summary. The general bark surface (i.e. excluding lenticels and 'growth lines') varied considerably in smoothness, and trees in all the 'susceptible' clones were rough, while the trees in three of the four 'resistant' clones were smooth. One clone with almost total absence of infestation was exceptionally smooth. Variations in lenticel shape, size and abundance showed little association with resistance. The most consistent difference between resistant and susceptible clones was in the pattern of 'growth lines'. These lines were present on all trees except on some replicate trees in two of the resistant clones. On the resistant clones the vertical linearity of these lines was considerably more regular than on the susceptible clones.

Several trees in the above study showed a linear pattern of *C. fagisuga* colonies and this was associated with fissures in the epiphytic covering of algae and lichens. In these cases the epiphytic covering was apparently so thick and dense that the fissures, apparently produced by expansion of the stem, were more favoured as feeding sites than the general surface.

Internal bark structure in relation to susceptibility

The data were obtained from three series of trees: the eight clonal trees mentioned above,

ten 'resistant' and 'susceptible' trees in a progeny trial whose genetic origin was different but unspecified, and fifteen plantation trees which had been heavily infested by *C. fagisuga*.

There was considerable variation in the relative thicknesses of the alternating layers of stone cells and unlignified parenchyma. As with the bark surface features, replicated clonal trees showed much less variation in bark anatomy between individual trees than between clones. In particular, the shape and extent of the sclerenchyma surrounding the heads of the sclerotic phloem rays was characteristic for a given clone. Among both the clonal trees and the genetically unreplicated progeny trial trees, there was a relationship between apparent susceptibility and the structure of the outermost layers of parenchyma and stone cells. In most trees there were two or three tangentially oriented layers of lignified cells. The outermost of these usually appeared poorly defined and discontinuous in transverse section, while the next layer was usually more strongly defined and in some trees was continuous over many millimetres of stem circumference. In trees classed as 'resistant', the depth of unlignified parenchyma outside the well defined stone cell layer was either small compared with 'susceptible' trees, or the outermost lignified layer was strongly developed. A few susceptible trees were atypical in that they had a very limited depth of external parenchyma, but the 'strong' stone cell layer was less continuous and less well defined than in the more resistant trees. Examples of bark from a resistant and a susceptible tree are shown in Figure 1.

An index was devised which incorporated the measurements of parenchyma and stone cell layers as follows:

$$\frac{100\ (a + b)^2}{\%L1\ .\ \%L2\ (a + b + c)}$$

where, as shown in Figure 1, a+b and c are the mean depths in μm occupied by the unlignified and lignified cells respectively in the tissue external to the 'strong' stone cell layer, and %L1 and %L2 are percentage values representing the degree of lignification within the layers designated.

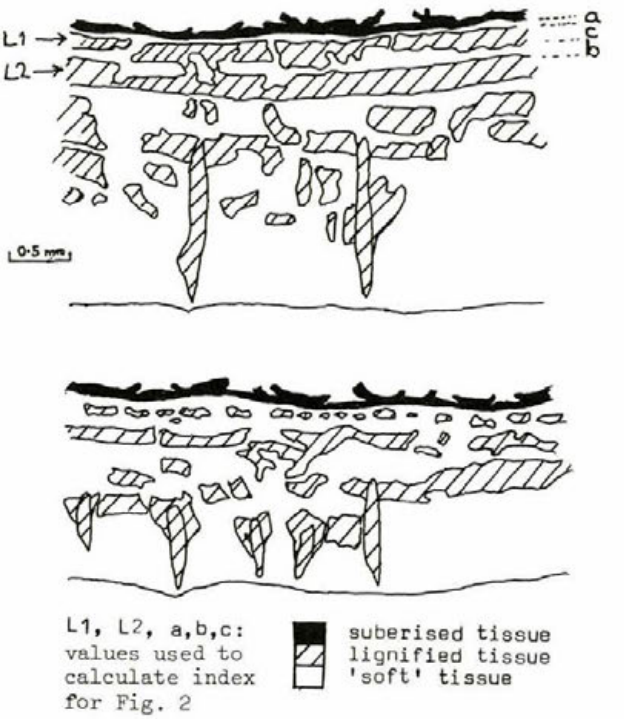


Figure 1.--Drawings of transverse sections of bark from trees with apparently high (above) and low (below) resistance to attack.

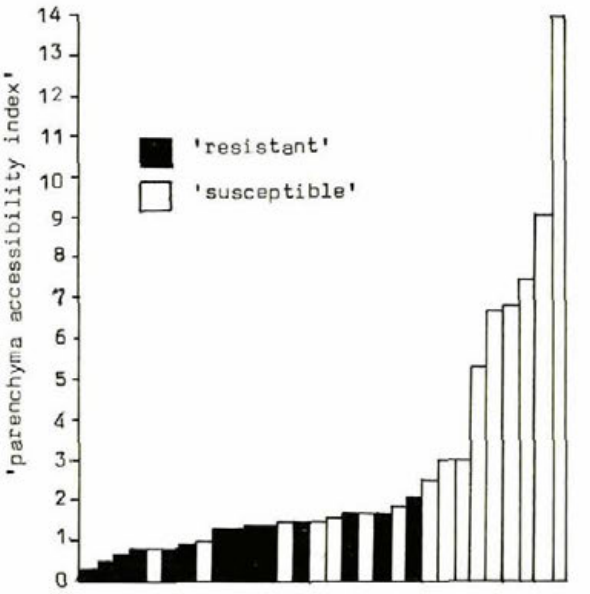


Figure 2.--Index values of the depth and accessibility of outer parenchyma in trees with apparent high and low resistance to *C. fagisuga* attack.

The evaluation of the index was carried out for bark samples from thirty trees and the results are shown in Figure 2. Replication of samples within trees was limited to between three and five 1 cm diameter bark discs, since it was established that variation within individual trees was small. The susceptible trees gave higher indices than the resistant trees. The most obvious exceptions to this were samples in which the tangential boundaries of the 'strong' stone cell layer were uneven; a score for unevenness was recorded for all samples but was not incorporated into the index.

Anatomical changes in bark due to *C. fagisuga* attack

Infested bark sections frequently showed gall formation and/or necrosis in the outer parenchyma and sometimes also in the parenchyma deeper than the 'strong' stone cell layer, the galls were 200-500 µm in diameter in the transverse plane. In addition to discrete galls, there was usually an abnormally thick phellem, suggesting stimulation of meristematic activity in the phellogen. Wound phellogens were frequently formed within the bark parenchyma. The gall tissues were often the sites of initial 'spot' necrosis, while old infestations were often associated with necrosis in much of the outer parenchyma. This necrosis affected the normal range of feeding depths for *C. fagisuga* so that heavy infestation could not have been maintained. Such bark was usually fissured however, and along the fissures, live parenchyma was present near the surface and hence accessible to *C. fagisuga*. These feeding sites were often the only areas of continuing infestation.

The nature of 'dimpling' or 'pitting'

Sections incorporating both bark and wood often showed that a necrotic spot was present in the bark parenchyma overlying a dimple. Such spots very rarely extended into the phloem and vascular cambium. Thus dimpling did not usually involve cambial necrosis. The wood showed a great reduction in annual ring width in the centre of a dimple, and most of this reduction was confined to one or two rings. The number of vessels in the intensely affected zone was very low, and often they were absent. The cells in general appeared undifferentiated and parenchyma-like. They tended to form chains of ray-like appearance. The number of cells across the ring width was also greatly reduced. Table 1 shows the results of a survey of intense dimples, and Plate 1 shows a transverse section of wood in which a dimple had formed nine to ten years before the sample was taken and where abnormal wood formation had continued and later re-intensified.

Table 1.--Dimpling : xylem cell size and number and ring width[a]

	Percentage of normal	
	Mean values for 26 dimples	Values for the most intense dimple
Total cell no.	36.3	7.8
Vessel no.	3.6	0.0[b]
Mean cell diameter	60.0	40.0
Ring width	24.9	3.3

[a] data relate to the most affected annual ring in each dimple, compared with values in the healthy zone of the same ring.

[b] of the 26 dimples, 22 had no vessels in the most affected zone.



Plate 1.--Transverse section of a 'dimple', showing abnormal and reduced xylem production.

DISCUSSION

The apparent relationships between bark structure, external and internal, and susceptibility to *C. fagisuga* attack seem relevant to recent studies on genetically determined resistance

(Wainhouse & Deeble 1980, Wainhouse, these Proc.). If these relationships are valid for a wider range of beech populations it may be possible to use them in developing selection procedures, both in the forest and in future planting programmes. Observations of six-year-old stems suggest that differences may appear at an early stage of growth (D. Lonsdale, unpublished data). If resistant trees can be anatomically characterised in this way, it may be possible to develop a workable method for the simple detection of the desired characters.

The time factor is extremely important in beech bark disease, not least with respect to the onset of susceptibility in *Cryptococcus* attack. Perhaps some of these temporal effects could be explained anatomically, and it is essential to take the time factor into account in any research which depends upon concepts of resistance and susceptibility.

The gall-like structures in the bark parenchyma were somewhat larger than the 'cell complexes' which Kunkel (1968) observed near the apices of individual insect stylets. They are, on the other hand, considerably smaller than the externally protuberant galls described by Hartig (1880). It seems likely, in any event, that they may enhance insect feeding, and, as such, are of interest in the population dynamics of *C. fagisuga*. Of similar interest is the necrotic breakdown of the feeding zones, noted previously by Kunkel (*op. cit.*) and by Braun (1977). It does not seem to have been noted previously that the fissures characteristic of superficially necrotic bark provide sites for residual *C. fagisuga* colonisation after much of the general bark surface has become resistant to attack by virtue of the necrotic layers. This must be set against previous statements (e.g. Anon 1956) that bark fissures are sites of initial, rather than residual, colonisation. This may be nearer the truth in the case of the 'fissures' in dense and deep epiphytic growth observed during the present studies. In either situation, the colonisation shows a 'line' pattern.

The nature of 'dimpling' or 'pitting' is of interest in relation to the observation that parenchyma feeders such as some adelgids and coccids produce plant hormone-like compounds (Balch, Clark and Bonga 1964). This has been suggested in the case of *C. fagisuga* (Fink and Braun 1980) and is a likely explanation for gall formation in the bark. However, the abnormal differentiation of vascular cambium occurs at some depth below the feeding zone, and the possibility must be considered that the effect may be an indirect one. In particular, the abnormalities are of a type often observed in cambial tissues exposed to ethylene, a gas which is produced by senescing tissue such as occurs in the necrotic feeding sites present in the bark overlying dimples. Similar defects have been artificially induced in beech wood by implanting the ethylene precursor 2, chloro-ethyl phosphonic acid into the bark (Lonsdale and Parker 1981).

Dimpling is known to occur on other tree species infested by scales, such as alder, sallow and ash (C. Carter, C.W.T. Young, D. Lonsdale, unpublished data), but detailed studies of xylem abnormalities seem to have been confined to conifers, such as *Abies* spp. attacked by Adelgids (Bryant 1974) and *Pinus pinaster* attacked by *Matsucoccus feytaudi* (Carle, Carde and Boulay 1970). The abnormalities in these conifers are different to those observed on beech in the present study but it is of interest that the abnormal production of short tracheids with narrow lumens seriously affects water movement in the xylem of *Abies* spp. (Bryant *op. cit.*). A beech tree with several years' heavy dimple formation might perhaps suffer loss of water conductivity, and this could contribute to the stress which seems prerequisite for *Nectria* attack (Houston 1973, Lonsdale 1980b). It is of interest in this connection that necrotic spots in the bark, associated with dimples, may harbour *N. coccinea* (Lonsdale and Sherriff, these proceedings).

The histological relationships between *C. fagisuga* and its host are relevant to stress and to latent infection by *Nectria* as well as to resistance mechanisms both preformed and elicited by insect attack. Perhaps studies of this type may help to explain the precise etiology of beech bark disease which remains uncertain.

ACKNOWLEDGEMENTS

I thank Dr D. Wainhouse for supplying data concerning the clonal trees and for helpful discussion. Awards from the Stanley Smith Horticultural Trust and from the Thoms Phillips Price Trust are gratefully acknowledged.

RÉSUMÉ

L'anatomie et la morphologie extérieure de l'écorce du hêtre furent étudiées en fonction des variations de sensibilité de différents clones d'arbres à l'infestation par la cochenille du hêtre, Cryptococcus fagisuga.

Extérieurement, l'ecorce des clones les plus résistants avait tendance à être plus lisse et montrait des 'lignes de croissance' soit peu nombreuses, soit ayant une forme régulière et verticale. A l'intérieur, les clones plus résistants différaient des clones sensibles par une épaisseur moindre et/ou une quantité plus grande de cellules lignifiées dans le parenchyme tendre situé à l'extérieur de la principale barrière de cellules scléreuses. C'est dans cette strate que l'insecte semblait s'alimenter et on propose l'hypothèse que l'alimentation n'a pas lieu facilement si la strate n'est pas arrivée à une certaine profondeur. Des observations analogues ont été faites sur des arbres dont l'origine génétique n'était pas connue.

L'anatomie du bois fut étudiée afin de déterminer la nature des lésions présentes sur les arbres envahis par le C. fagisuga. Les zones centrales des lésions contenaient un ou deux anneaux annuels dans lesquels le nombre de cellules de xylème était réduit considérablement et dont des vaisseaux étaient absents. Les cellules ressemblaient au parenchyme et, en coupe transversale, formaient des chaînes rayonnantes traversant plusieurs anneaux annuels successifs. Il se produisait généralement une certaine quantité de bois anormal durant plusieurs années et parfois les symptômes intenses se produisaient de nouveau sur l'emplacement d'une lésion plus ancienne.

ZUSAMMENFASSUNG

Anatomie und äußeres Erscheinungsbild der Buchenrinde wurden im Hinblick auf die unterschiedliche Anfälligkeit verschiedener Klone gegenüber der Buchenwollschildlaus untersucht. Äußerlich neigten die resistenteren Klone zu glatterer Rinde und wiesen weniger oder regelmäßig senkrecht verlaufende "Wachstumslinien" auf. Im Inneren unterschieden sich die resistenteren Klone von den anfälligen durch eine dünnere und/oder an verholzten Zellen reichere Parenchymschicht außerhalb der Hauptsteinzellschicht. Für die Ernährung der Läuse scheint diese Parenchymschicht von Bedeutung zu sein und es wird angenommen, daß die Ernährung erst dann ohne Schwierigkeiten erfolgen kann, wenn das Parenchym eine bestimmte Dicke erreicht hat. Ähnliche Beobachtungen wurden auch an unverklonten Bäumen gemacht.

Die Anatomie des Holzes wurde untersucht, um die anatomischen Ursachen für das "dimpling"-Symptom, Eindellungen am Stamm von lausbefallenen Buchen, zu klären. Unter den zentralen Bereichen der Vertiefungen zeigten ein oder zwei Jahresringe keine Gefäße und eine stark verringerte Zahl an Xylemzellen. Die Zellen in diesem Bereich ähneln Parenchymzellen und bilden im Querschnitt markstrahlähnliche Ketten über die Jahresringgrenzen hinweg. Bis zu einem gewissen Grade erfolgt anormale Holzbildung mehrere Jahre lang und in manchen Fällen sind über älteren Eindellungen starke frische Symptome zu beobachten.

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SPECIFICITY OF CRYPTOCOCCUS FAGISUGA AND NECTRIA COCCINEA ASSOCIATION IN BEECH BARK DISEASE IN EUROPE[1]

R. Perrin[2]

Abstract.--The specificity of the Cryptococcus fagisuga and N. coccinea association is studied by artificial inoculation of 4 species of Nectria: N. coccinea, N. ditissima, N. galligena and N. cinnabarina on bark infested with beech scale. N. coccinea appears to be the most efficient species for producing necrosis at the cambial level. The composition of the bark, in relation to induced pectinase activity gives a good explanation of the specificity recorded here.

INTRODUCTION

During the last 10 years European beech trees have been seriously affected by two diseases both involving Nectria species. Dense young stands arising from natural beech regeneration are affected by a canker disease caused by Nectria ditissima Tul. Nectria coccinea is associated with Cryptococcus fagisuga Lind. in the beech bark disease (Parker 1974, Perrin 1974). Other Nectria species are known only as saprophytes on beech (Perrin 1976), Nectria cinnabarina (Tode ex Fr.) Fries being undoubtedly the most widespread among them. This latter species is sometimes recorded as a pathogen on other trees e.g. elm. The well known agent of European canker of apple also belongs to the genus Nectria: N. galligena Bres has been implicated in beech bark disease in North America (Cotter 1977) and by mistake in Danish forests (Thomsen et. al. 1949). Despite the great number of Nectria species associated with beech trees from the most specific one N. ditissima, to the most common saprophyte N. cinnabarina, N. coccinea is the only fungus which has been isolated with any obvious consistency from necroses on trees carrying heavy infestations of the beech scale. These observations suggest a close specificity of the association C. fagisuga/N. coccinea. Very frequently both N. ditissima forming cankers on twigs and N. coccinea causing necrosis on the trunk can be observed on the same tree in French forests but N. ditissima has never been found following Cryptococcus fagisuga attack. Nevertheless some bark necroses may be produced by N. coccinea alone without previous infestation of the scale insect (Leibundgut and Frick 1943) or perennate after disappearance of the insect ('T disease', 'cankered necrosis' (Perrin 1979) drought damage (Lonsdale 1980)). It seems that the specificity of the association is the result of a special advantage given to N. coccinea after physiological alteration of the bark by C. fagisuga.

The purpose of this investigation was to study the specificity of the association C. fagisuga/N. coccinea, a key feature of the disease process, by artificial inoculations.

MATERIALS AND METHODS

Ten beech trees, heavily infested by beech scale, between 50-80 years old were selected at four different sites in the forest of Amance (north-east France). The degree of infestation by C. fagisuga was recorded using the scoring system of Parker (1974). Infestation varied between 3 and 5 at the site of inoculation (Table 1). These sites were randomly distributed along the most infested side of each tree. Wound inoculations were made according to the method previously described (Perrin 1980) with four different species of Nectria; N. coccinea, N. ditissima, N. cinnabarina and N. galligena and a control

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Table 1.--Bark necrosis incited by four different species of Nectria eleven months after artificial inoculations. N. coccinea = N.C., N. galligena = N.G., N. ditissima = N.D., N. cinnabarina = $N.C._i$

Tree	Size of the necrosis mm^2								External appearance
	Phelloderm level				Cambium level				
	N.C.	N.G.	N.D.	$N.C._i$	N.C.	N.G.	N.D.	$N.C._i$	
1	375.0 b (4)	110.1 (4)	104.3 (5)	44.0 (3/4)	15.2	0	86.2	0	N.C. dark depressed spot
2	85.5 (5)	8.7 (4/5)	71.7 (5)	10.9 (5)	16.7	6.5	0	0	-
3	25.4 (5)	39.1 (5)	12.3 (5)	0 (5)	0	28.3	0	0	N.G. dark depressed spot
4	31.9 (5)	30.4 (4/5)	27.5 (4/5)	8.7 (5)	4.3	0	0	0	-
5	66.7 (4/5)	30.4 (4)	45.6 (4/5)	15.2 (5)	12.3	6.5	0	2.9	-
6	10.9 (4)	13.8 (4)	2.0 (4)	0 (4)	0	13.8	0	0	-
7	287.0 (5)	70.3 (5)	60.9 (5)	10.1 (4)	37.7	40.6	0	0	N.C./N.G. dark depressed spots and slime fluxes
8	- (5)	- (5)	- (5)	- (5)	-	-	-	-	Numerous slime fluxes natural necrosis
9	39.1 (3)	39.1 (3)	30.4 (3)	4.3 (3)	42.7	5.1	3.0	0	N.C./N.G. dark depressed spots and slime fluxes
10	28.3 (4)	26.7 (4)	32.6 (4)	3.1 (4)	29.1	2.3	16.2	0	-
Mean	105.5^a_1	40.9_1	43.0_1	10.7_2	32.7_1	11.5_2	11.7_2	0.3_3	

a Means followed by the same number are not significantly different according to the Mann-Whitney 'u' test (P = 0.05)

b Numbers in brackets are degree of C. fagisuga infestation

treatment (without any fungus) on each tree. The first three were mycelial strains freshly isolated from beech material in the forest of Amance, the last one was isolated from an active canker on an apple tree. Inoculation was done on 13th November, 1979 and protection devices were removed approximately one month later.

Monthly observations were made until October 1980. At the end of October the necrotic area was assessed at the phelloderm level after removing the suberized layer and at the cambium level giving an idea of the depth extension of the necrosis. The size of the necrosis was recorded by tracing off the discoloured zone around the wound. Identification of the organism causing necrosis was made by placing a piece of aseptically sampled bark on malt agar.

RESULTS

No change in the external appearance of the bark occurs during the dormant period. Frost which was especially severe because of the artificial wet conditions under protective devices appeared to induce a large decrease in the density of beech scale.

Reddish black depressed spots appeared externally around some inoculation wounds (Table 1) during the last fortnight of April and slime fluxes occurred early in May at the time of flushing. The occurrence and size of the necrotic patches (Plate 1) are gathered in Table 1.

For all of the control treatments no necrosis developed either at the phelloderm or cambium level. Healing over of the wound was always effective. The same result was obtained for two inoculations with N. cinnabarina.

The size of the necrosis shows a great variability from one tree to another for each fungal species and also between species on the same tree. Data collected on tree 8 cannot be taken into consideration because of natural infection occurring in the vicinity of inoculation sites. The ranking of trees according to the size of the necrosis at the phelloderm level did not differ greatly from one Nectria species to another. Tree 1 allowed the greatest and tree 6 the least extension of the necrosis whichever fungus was inoculated. Some trees seemed to be very sensitive, others more resistant to attack by any species of Nectria. No relationship was found between the sensitivity of a tree and degree of C. fagisuga infestation (Table 1) but this may be due to the limited range of scale insect infestation levels on the trees. Despite an extension of N. coccinea induced necrosis of more than twice those of N. ditissima and N. galligena this was not significant (Mann and Whitney 'u' test, Siegel 1956). On the other hand the necrosis caused by N. cinnabarina was significantly smaller than those caused by the other fungi.

At the cambial level the frequency and size of the necrosis allows a better distinction between the species. Only one inoculation with N. cinnabarina led to a cambial necrosis, restricted to a point, from which the fungus could not be re-isolated.

N. ditissima produced a cambial necrosis on only three trees and there was great variation in the size of the necroses. There were seven successful inoculations for both N. coccinea and N. galligena. The necroses generated by N. coccinea were on average 3 times larger than those resulting from N. ditissima or N. galligena inoculation. Since necroses cannot be induced on uninfested bark (Perrin 1979, 1980), the significant differences indicated by the 'u' test express the specific advantage to N. coccinea of changes in C. fagisuga infested bark.

DISCUSSION AND CONCLUSIONS

A phelloderm lesion can be easily overcome by the tree, whereas a cambial necrosis indicates that the organism causing the necrosis has overcome host defence mechanisms and will have a long term effect on tree health. The specificity of the association between N. coccinea and C. fagisuga observed in natural conditions could be explained by the advantage which it showed over other Nectria species in the present inoculation experiments on infested bark.

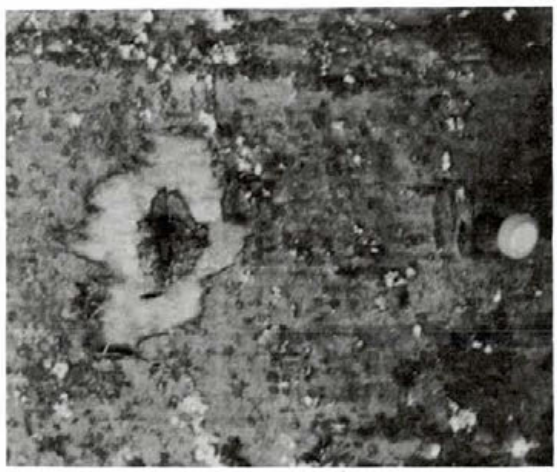


Plate 1--Nectria coccinea necrosis at the phelloderm level.

Flack and Swinburne (1977) did cross-inoculation experiments with N. galligena, N. ditissima and N. coccinea on various hosts. They reported that the wide host-range of N. galligena which included beech was in contrast to the close specificity shown by N. ditissima and N. coccinea which are restricted to beech. From our results and observations N. galligena and N. ditissima are able to destroy trunk bark of scale infested beech but not as efficiently as N. coccinea. In addition penetration courts may not have the same receptivity for all pathogens. By comparison of the pathogenicity of N. coccinea and N. ditissima we can distinguish another level of specialisation. Nectria ditissima seems to be well adapted for parasitising juvenile bark whereas N. coccinea has a greater ability to destroy the old trunk bark. Many authors have described the composition of the bark of beech. All of them revealed substantial differences between the trunk and the twigs. The most

important variation concerned the proportion of calcium present. Kreutzer (1976) indicated 0.9% Ca^{2+} for the trunk and 0.19% for the twigs. Pathogenicity of N. ditissima decreases rapidly when the proportion of Ca^{2+} increases in the bark (Perrin unpublished data). In addition some pectinase activity of N. coccinea like endopolygalacturonase, essential for pathogenicity are specially and strongly stimulated in vitro when the fungus uses the bark of the trunk as a carbon source (Perrin this volume). The pectinase pool of N. coccinea differs from those of N. ditissima by an intense endopolymethyltranseliminase activity (R. Perrin, In Prep.).

In conclusion differences in the composition of the bark in relation to variation in the potential pectinase arsenal of the pathogens induced by the bark give a good explanation of parasitic specialisation and subsequent specific localisation or association of the pathogens.

ZUSSAMMENFASSUNG

Das charakteristische gemeinsame Auftreten von Cryptococcus fagisuga und Nectria coccinea wurde mit Hilfe von Infektionsversuchen untersucht. Von der Buchenwollaus befallene Rinde wurde mit Nectria coccinea, N. ditissima, N. galligena und N. cinnabarina infiziert. Von den 4 Pilzen scheint N. coccinea für die Entstehung von Nekrosen im Kambiumbereich am wichtigsten zu sein. Die Besonderheit des Laus-Pilz-Komplexes lässt sich an Hand der Zusammensetzung der Rinde im Hinblick auf die Pectinaseaktivität erklären.

RÉSUMÉ

La spécificité de l'association Cryptococcus fagisuga et Nectria coccinea est étudiée à l'aide d'inoculations artificielles de 4 espèces de Nectria: N. coccinea, N. ditissima, N. galligena et N. cinnabarina, sur de l'écorce infestée par la cochenille du hêtre. N. coccinea semble être l'espèce la plus efficace à produire une nécrose au niveau du cambium. La composition de l'écorce en relation avec l'activité pectinolytique résultante donne une bonne explication de la spécificité exprimée ici.

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PECTINASE ACTIVITY OF NECTRIA COCCINEA (PERS ex FRIES) FRIES IN RELATION TO BEECH BARK DISEASE[1]

R. Perrin[2]

Abstract.--The pectinase activity of Nectria coccinea was studied in vitro and in vivo in relation to the pectinases of Cryptococcus fagisuga and the nature of the bark. Any pectinases necessary for degradation of pectic material were secreted by the fungus in vitro. Some pectinases produced by the insect are of great significance in the predisposition of the bark to alteration by the fungus. The assistance given by the scale insect and the pectinase pool of N. coccinea which is well adapted to the trunk bark, is a possible explanation of the specificity of the association C. fagisuga/N. coccinea.

INTRODUCTION

Recent outbreaks of beech bark disease especially in Europe have been of great economic importance and have promoted a renewal of interest and research on the disease complex. Recent investigations have brought some clarification of the aetiology of various bark necroses. Ehrlich's (1934) interpretation of disease development is widely accepted and demonstrated, and N. coccinea following Cryptococcus fagisuga attack is the main cause of the dieback of beech in Europe (Parker 1974; Perrin 1974, 1977, 1979). The insect provides more than just a means of entry for Nectria (Perrin 1979, 1980; Lonsdale 1980; Kunkel 1968). Predisposing factors are an important part of the disease. Nectria coccinea has been involved with beech bark necrosis without previous infestation by Cryptococcus fagisuga (Leibundgut and Frick 1943; Perrin 1977). Various factors like nutritional deficiency and abiotic stresses lead to predisposition of the tree, favourable to Nectria induced necrosis (Lonsdale 1980). The ability of N. coccinea to destroy the bark of beech has been frequently demonstrated but has always been related to previous predisposing factors, the most common of them being Cryptococcus fagisuga. This breakdown of bark tissue must depend not only on the presence of predisposing factors but also on the ability of N. coccinea to degrade cell wall materials.

Despite our imperfect knowledge of the nature of plant cell walls, pectic substances are regarded as of primary importance because of their abundance and above all as the principal constituent of the matrix of the cell wall. Alteration of pectic substances leads to a loss of tissue coherence. With respect to beech bark degradation, pectic enzymes may be prominent among the complex of factors involved in pathogenesis. Pectic enzymes produced by various pathogens have been the subject of numerous investigations but surprisingly very few of them have been related to bark necrosis fungi.

The aim of this study was to investigate the pectinase "weapons" of N. coccinea and their involvement in the beech bark disease process particularly in relation to C. fagisuga.

MATERIALS AND METHODS

The names of pectic enzymes conform to the classification proposed by Bateman and Millar (1966). Three isolates of N. coccinea were used. All of them are mycelial strains freshly isolated from typical beech bark diseased trees in three different regions of France: strain A, Forest of Lyons (west), strain I, Forest of Amance (east), strain W, Forest of Climbach (Alsace).

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A preliminary test of most of the media traditionally used by various authors has led to a choice of the best appropriate medium composed as follows:-

KH_2PO_4 0.1%, NH_4NO_3 0.1%, $MgSO_4$ 0.05% in distilled water, pectin (1%), pectic or polygalacturonic acids (0.25%), powdered bark (2%) or glucose (0.5%) for control, were used as carbohydrate sources.

The bark used in this study was of three different types collected on the same tree: bark of the trunk infested with C. fagisuga (score 5 Parker scoring system), bark of the trunk not infested with the beech scale (score 0) and bark of the twigs, corresponding to the juvenile state of the bark. Bark was stored as dry powder at 0°C for growth substrate use, or as water extracts by freezing (-24°C) for a study of the influence of bark contents on pectinase activity of N. coccinea. Twenty ml of medium were dispensed per 125 ml flask, autoclaved, then seeded with an 8 mm disk from an actively growing malt agar colony. Cultures were incubated without shaking at 23°C. After a few days, the liquid from the 5 replicate flasks was pooled and filtered on paper. Enzyme preparations were assayed immediately.

Table 1.--Enzyme assay methods

Enzyme Substrate	Assay Method	
	Buffer	
	Sodium citrate 0.02 M pH 4.5	Tris HCl 0.05 M pH 8.5
1% Pectin sodium salt	Polymethylgalacturonase.PMG endo-PMG: viscosimetry (a)	Polymethyltranseliminase.PMTE endo-PMTE: viscosimetry (a)
	exo-PMG: D.N.S. test (optical density 575 mμ)	exo-PMTE: T.B.A. test (optical density 547 mμ)
1.2% Sodium polypectate	Polygalacturonase.PG endo-PG: viscosimetry (b)	Polygalacturonatetranseliminase.PGTE endo-PGTE: viscosimetry (b)
0.25% Poly-galacturonic acid	exo-PG: D.N.S. test (optical density 575 mμ) T.B.A. test (optical density 515 mμ)	exo-PGTE: T.B.A. test (optical density 547 mμ)

Viscosimetry with Feuske-Oswald viscosimeter for liquid viscosity.

(a) viscosity between 63-100 centipoises (b) viscosity between 16-25 centipoises

Enzyme assay methods are summarised in Table 1. Quantitative enzymatic data are expressed by the number of units of enzymatic activity per ml culture filtrate or water extract. Three assay methods were used:
1. Viscosimetric method for endo-polymethylgalacturonase (endo-PMG), endopolymethyltranseliminase (endo-PMTE), endopolygalacturonase (endo-PG) and endo-polygalacturonatetranseliminase (endo-PGTE). Units of enzymatic activity were defined by the quantity necessary for a 50% decrease of reaction mixture viscosity in 100 mins.
2. Dinitrosalicylic acid test (DNS) (Bompeix 1972) for exopolymethylgalacturonase (exo-PMG) and exopolygalacturonase (exo-PG). Units of enzymatic activity were the quantity of enzyme necessary for liberation of 1 micro-mole of galacturonic acid per minute and per ml of culture filtrate. 3. Thiobarbituric acid test (TBA) (Bugbee 1975) for exopolymethyl-transeliminase (exo-PMTE) and exopolygalact-uronatetranseliminase (exo-PGTE). Units of enzymatic activity were equal to the quantity of enzyme arbitrarily corresponding to 0.1 optical density variation for 30 minutes.

Preparation of bark extracts for in vivo measurements

In vivo assay of pectinase activity was made for different types of bark, and from liquid produced by homogenising many insects. Bark was collected during spring and autumn from:- trunk heavily infested by C. fagisuga, trunk with typical beech bark disease syndrome, young trees artificially inoculated with strain A of N. coccinea alone and from a "healthy" trunk. The tissue was homogenised in a Waring blender and extracted with water (1/1 volume) with or without added NaCl (0.5 M). After centrifugation (2000 g) the supernatant was dialysed against distilled water at +5°C for 24 hours. If not assayed immediately enzyme preparations were stored at -5°C and tested within 2 days.

RESULTS

1. In vitro expression of pectinase activities

The results are presented in Tables 2-10 and Figs 1-2. In vitro results reveal that all strains of N. coccinea can be induced to secrete any pectinases necessary for degradation of

Tables 2 to 5.--Pectinase activity of the three strains of N. coccinea. Cultures on various substrates were 14 days old (one hour incubation). For method of assessment and units of enzymatic activity see text.

Table 2 endo-PG / Table 3 exo-PG

Strains	A	I	W	A	I	W
Culture substrate						
Twig bark	2.43	1.99	0.80	3.05	3.39	2.66
Trunk bark	2.66	2.33	2.36	2.90	2.72	2.98
C. fagisuga infested trunk bark	2.93	2.30	2.36	2.99	3.13	3.11
Pectic acids	0.47	0.63	0.37	1.05	1.54	0.09
Control (glucose)	0.02	0.00	0.00	0.00	0.03	0.01

Table 4 endo-PMG / Table 5 endo-PMTE

Twig bark	1.53	1.86	1.23	2.00	1.93	1.37
Trunk bark	2.63	1.27	2.57	2.80	1.70	2.67
C. fagisuga infested trunk bark	2.43	2.16	2.43	2.60	2.70	2.67
Pectin	0.87	1.90	0.40	2.90	1.60	1.00
Control (glucose)	0.07	0.01	0.03	0.04	0.02	0.00

pectic substances. Extensive investigations of the last 15 years have demonstrated that many

fungal pathogens when growing saprophytically have these abilities.

The nature of the substrate is one of the many factors affecting the level of pectinase activity in culture filtrates. For these isolates of N. coccinea, the inducing power for hydrolase activity of natural substrates e.g. bark powder was many times greater than those of artificial substrates (Tables 2-4). This is especially true for the W strain hydrolase activity which was very low on artificial substrates and became equivalent to those of other strains on trunk bark only. Bark of the trunk enhances endohydrolase activity while the bark of the branch allows the greater exo-PG activity of some strains.

Table 6.--exo-PMTE and exo-PMG activities of the three strains of Nectria coccinea. Cultures were 14 days old on pectin as substrate. For method of assessment and units of enzymatic activity see text.

Strains	A	I	W	A	I	W
Enzyme	exo-PMTE			exo-PMG		
Substrate						
Pectin	2.47	1.25	0.10	4.99	7.14	1.06
Control (glucose)	0.01	0.00	0.00	0.00	0.00	0.00

Transeliminase activities were not affected to the same extent by the nature of the substrate (Tables 5 and 7). The natural substrate elicited a greater transeliminase activity than did artificial substrates only in the case of strain W alone (Tables 5 and 7). Exo-PGTE activity was greatest when N. coccinea grew on bark from an infested trunk and the twig bark as substrate reduced endo-PMTE activity (Table 5).

Table 7.--exo-PGTE activities of three strains of Nectria coccinea. Cultures were 14 days old on various substrates. For method of assessment and units of enzymatic activity see text.

Strains	A	I	W
Substrates			
Twig bark	0.942	0.754	0.825
Trunk bark	0.554	0.292	0.308
Infested trunk bark	1.375	1.125	1.133
Pectic acids	1.300	1.470	0.000
Na Polypectate	0.070	0.090	0.040
Control (glucose)	0.010	0.030	0.000

2. In vivo evidence of pectinase activities

The results are shown in Table 8. In vivo evidence of transeliminase activity except endo-PMTE was lacking whatever the type of bark and the sampling season. Endo-PMTE activity could be revealed as well as hydrolase activity other than exo-PMG in the bark at various stages of disease development but only at spring time.

Table 8.--In vivo evidence of pectinase activities in beech bark, or in C. fagisuga larvae at spring time. For method of assessment and units of enzymatic activity see text.

Enzyme activity	endo-PG	exo-PG	endo-PMG	endo-PMTE
Extract				
Diseased bark	0.033	trace	trace	0.024
Bark with N. coccinea necrosis	0.089	0.280	0.070	0.124
C. fagisuga infested bark	0.057	0.200	0.052	0.045
C. fagisuga larvae	0.067	0.000	0.047	0.042
"Healthy" bark	0.000	0.020	0.000	0.000
Control (Healthy bark autoclaved)	0.000	0.000	0.000	0.000

Cryptococcus fagisuga showed clear endohydrolase and endo-PMTE activities at spring time.

3. Influence of bark additives on pectinase activities of N. coccinea

One ml of healthy bark or C. fagisuga infested bark of beech was added to the enzyme substrate reaction mixture at the beginning of the reaction. The results are summarised in Table 9. The different exoenzyme activities were slightly reduced by C. fagisuga infested bark. Endo-PMG was the only endoenzyme influenced by bark extracts. C. fagisuga infested bark induced an increase of that activity.

Table 9.--Influence of bark additives on some pectinase activities of N. coccinea culture filtrates. Cultures were 14 days old on bark substrates. For method of assessment and units of enzymatic activity see test.

Strains	A			I		
Additive	Water	Healthy bark	Infested bark	Water	Healthy bark	Infested bark
Enzyme activity						
exo-PMTE	2.467	2.208	1.921	1.250	1.196	0.987
exo-PGTE	1.300	1.563	1.396	1.470	1.671	1.533
endo-PMG	0.800	0.870	1.470	1.600	1.660	2.100

4. Sequential occurrence of pectinases

These investigations were conducted with the most efficient strain A. Data are presented in Table 10 and Fig. 2.

The development of endoenzyme activities with culture age followed the same rate except for endo-PGTE which was delayed. In 8 day old

Table 10.--Development of exo-PG and exo-PGTE activity in culture filtrates of strain A of N. coccinea growing on healthy bark of C. fagisuga infested bark. For methods of assessment and units of enzymatic activity see text. Figures underlined for emphasis.

Age of culture (days)	2		4		6		8		14	
Pectinase activity	exo-PG	exo-PGTE	exo-PG	exo-PGTE	exo-PG	exo-PGTE	exo-PG	exo-PGTE	exo-PG	exo-PGTE
Substrate										
Healthy bark	0.005	0.003	0.024	0.000	0.389	0.133	0.330	0.170	2.900	0.550
C. fagisuga infested bark	0.000	0.000	0.250	0.000	1.514	0.092	1.380	0.210	3.000	1.380

culture filtrates endo-PG activity was slightly greater than that of endo-PMG and endo-PMTE.

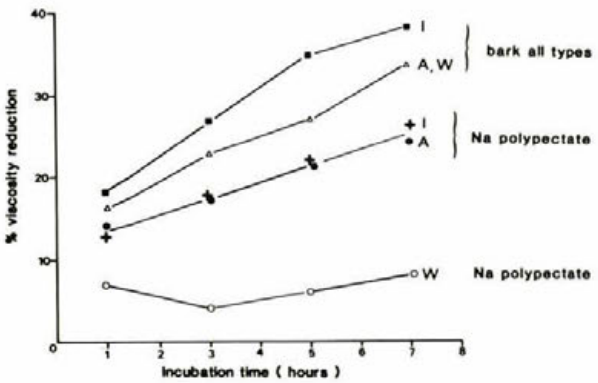


Figure 1.--endo-PGTE activity of three different strains of Nectria coccinea. Cultures were 14 days old on various substrates.

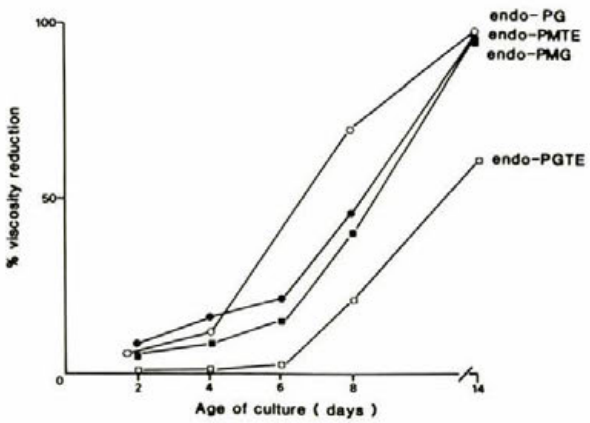


Figure 2.--Sequential appearance of endopectinases in culture filtrates of strain A of Nectria coccinea.

Exo-PG activity appeared very early in culture filtrates. The level of exo-PGTE activity was very low even after 8 days of growth of the fungus. C. fagisuga infested bark allowed a better exo-PG activity in culture as young as 6 days of age and led to a greater level of exo-PGTE activity.

DISCUSSION AND CONCLUSIONS

In vitro, it was possible to induce N. coccinea to secrete any pectinase necessary for degradation of pectic material in the cell wall. In vivo evidence of some pectinase, hydrolase and endo-PMTE activities gave a satisfactory proof of their implication in the process of necrosis. With respect to these considerations production of endohydrolase and endo-PMTE by the insect may be of great significance in the predisposition of the bark to alteration by the fungus. The beech scale seems to be capable of initiating the first steps of the degradation of pectic substances. In addition the presence of C. fagisuga and its influence on bark contents enhance some pectinase activities of the fungus. In vitro studies indicated that N. coccinea secretes first polygalacturonases, while pH is in the acid range (4.3-4.5). These activities were strongly increased when N. coccinea grew on infested bark as the substrate. Transeliminase activity appeared a few days later in culture filtrate, when the pH had reached 5-5.5. Moreover C. fagisuga infested bark induced an increase of exo-PGTE activity of N. coccinea. Bark pH measured in nature changes from 4.5 in healthy bark to 6.5-7.5 in typical beech bark disease necrosis (R. Perrin, unpublished data). The pH of C. fagisuga infested bark is 0.5 units greater than that of healthy bark.

According to Skou (1979) calcium strongly inhibited polygalacturonase activity, whereas this cation weakly stimulated transeliminase activity. The calcium concentration of trunk bark is almost 5 times greater than that of the twig (Kreutzer 1976). It seems that pectinase weapons of N. coccinea and the help given by pectinase of the insect are well adapted to the bark environment of the beech trunk, a possible cause of the specificity of this association.

No relation can be found between the potential enzymatic pool and the virulence of these different strains of N. coccinea (unpublished data). Pectic enzymes are only one of the weapons of the pathogen, acting in concert, to destroy plant tissues and the results reported here indicate a complete pectinase potential of the organisms involved in beech bark disease which seems not to be a limiting factor in pathogenesis.

ZUSSAMENFASSUNG

Die Pektinaseaktivität von Nectria coccinea wurde in vitro und in vivo in Abhängigkeit von den Pektinasen von Cryptococcus fagisuga und der Art der Rinde untersucht.

In vitro wurden von dem Pilz alle Pektinasen gebildet, die für den Abbau entsprechenden Materials benötigt werden. Einige von der Buchenwollaus gebildete Pektinasen sind im Zusammenhang mit der Prädisposition der Rinde für Veränderungen durch den Pilz von grosser Bedeutung. Das gut auf die Stammrinde abgestimmte Pektinasebesteck von N. coccinea und die Unterstützung durch Cryptococcus fagisuga sind eine mögliche Erklärung für das Besondere dieses Laus-Pilz-Komplexes.

RÉSUMÉ

L'activité pectinolytique du Nectria coccinea fut étudiée in vitro et in vivo en relation avec les pectinases du Cryptococcus fagisuga et la nature de l'écorce. Toutes les pectinases nécessaires à la dégradation du matériel pectique étaient sécrétées par le champignon in vitro. Certaines pectinases produites par l'insecte sont très importantes dans la prédisposition de l'écorce à l'altération par le champignon. La situation d'une production de pectinases bien adaptées à l'écorce du tronc de N. coccinea et de l'assistance donnée par la cochenille peut expliquer l'association spécifique C. fagisuga/N. coccinea.

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SOME ASPECTS OF THE ECOLOGY OF *NECTRIA* ON BEECH[1]

David Lonsdale[2] and Christine Sherriff[3]

Abstract. --Observations of the mycoflora of beech bark infested with *Cryptococcus fagisuga* suggested that *Nectria coccinea* can colonise sites on and in the outer tissues, and that invasion of inner bark could later develop. Although these sites harboured fungi antagonistic to *N. coccinea*, experiments suggested that it is well adapted under some circumstances to escape serious competition.

INTRODUCTION

Despite the prominence of canker diseases in forest pathology research, little attention has been paid to the pre-infection ecology of the organisms involved. In most cases, our knowledge corresponds to an idealised cycle whose most significant stages are the initiation of the infection and the production of infective propagules. This simple concept is valid only where these propagules can alight on a site where susceptible host tissues are available for infection during the life of these propagules, and there are clearly many cases where these conditions are not fulfilled. Their fulfilment may be obstructed by several possible barriers and, in *Nectria* diseases of beech, at least three such barriers can be recognised.

Before defining these barriers it is important to bear in mind the relative parasitic strengths of *Nectria* species, as well as their relative fitnesses to exist outside the parasitic niche. For example, *N. ditissima* seems able to invade unstressed beech bark more aggressively than *N. coccinea* (Parker 1974), while *N. cinnabarina* apparently includes strains ranging from those which can cause perennating cankers on hardwoods to others which are purely saprophytic.

The most obvious barrier to infection is the intact outer bark of the stem. For the more parasitic *Nectria* species, leaf scars may be a point of weakness in the barrier through which infection may occur. This certainly applies to twig canker of apple caused by *N. galligena* (Wiltshire 1921) and may apply in the case of *N. ditissima* on the twigs of beech. No evidence exists for this mode of entry for the less specialised parasites, *N. coccinea* and *N. cinnabarina*, suggesting that some form of injury is necessary for the barrier to be breached. For *N. coccinea*, this is apparently achieved by the wounds caused by the beech scale, *Cryptococcus fagisuga* (Ehrlich 1934).

Once in direct contact with the inner bark tissue, the fungus encounters additional barriers formed by the living cells in response to attack. For *N. ditissima* and possibly for some strains of *N. cinnabarina*, this resistance can probably be overcome, at least at certain times of the year. For *N. coccinea*, however, it seems that invasion of the tissues is soon delimited by host response (Parker 1974, Perrin 1979) unless the tree is infested to the point of stress by *C. fagisuga* (Houston 1973, Lonsdale 1980a, Perrin 1980) or is otherwise stressed (Lonsdale *op cit.*).

Thus, the relative parasitic weakness of *N. coccinea* imposes on it a dependence on agents which can not only break down the tree's pre-existing barriers but can also impair its ability to form barriers in response to attack. In these respects, *C. fagisuga* seems to be a dual agent. Heavy infestations of *C. fagisuga*, however, generate a third possible kind of barrier: an ecological barrier, or more precisely an ecosystem which must be negotiated by *N. coccinea*. The commonly observed discoloration of the insects' waxy secretion attests to the presence of a dense microflora and microfauna, an ecosystem which will be encountered by the propagules of any canker fungus alighting on the bark. In other words, it seems unlikely that

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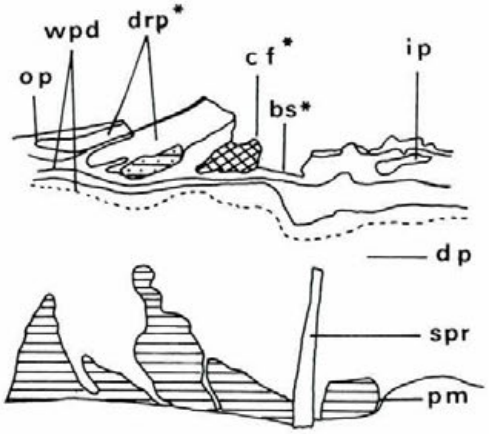
beech bark disease is consequent upon the simple process of *Nectria* spores alighting on the bark surface and immediately giving rise to invasion of the tissues. The corollary is that this disease involves some form of persistence, saprophytic or otherwise, on or near the bark surface.

These arguments prompt the questions: 'Where is *N. coccinea* before it invades the bark tissues; how does it survive out of the parasitic environment, and why is it the characteristic invader of beech bark rather than other weak parasites? It is to these questions that the present work was directed.

EXPERIMENTAL

Characterisation of the bark mycoflora

Preliminary observation of beech bark, heavily infested by *Cryptococcus*, suggested that three main possible niches of latent colonisation by *N. coccinea* could be characterised. They were: a) colonies of the insect itself (i.e. insects plus wax) b) the bark surface around the colonies and c) superficial necroses produced within the bark as a result of mass feeding by the insects. These sites are illustrated in Figure 1.



op: original phellem, wpd : wound periderm, drp: disrupted necrotic parenchyma, cf: C. fagisuga wax, bs: bark surface near wax, ip: 'island' of parenchyma, dp: deep tissue of cortex & phloem, pm: phloem, spr: sclerotic phloem ray

Figure 1.--Illustration of possible sites of latent colonisation by *N. coccinea* on beech bark undergoing prolonged and severe *Cryptococcus*-attack (drawn from a t.s).

Small fragments of insect colony material, of the bark surface layers and of necrotic phelloderm tissue were plated out on 2% malt extract agar (MA) and on tap water agar containing 250 µM vinclozolin, a fungicide which can to some extent select for *Nectria* (D. Lonsdale & M. Turton unpublished[1]). The samples were collected from thirty to forty-five-year-old beech plantations in Alice Holt and Queen Elizabeth Forests in Hampshire, southern England. Care was taken to avoid sampling any material which might have come from typical *Nectria* lesions of the inner bark. Fungi growing on the isolation plates were identified at least to genus wherever possible, and a full list will be published elsewhere.

In order to examine the fungus flora more sensitively, individuals of *C. fagisuga* from trees with various intensities of infestation were plated on 0.01% yeast extract agar (YEA). The insects were either removed from colony debris using a wet sieving technique (D. Wainhouse personal communication) or individually picked from the trees using a tripod-mounted dissecting microscope. The agar plating of bark and insect material was felt to be a limited method of gaining insight into the nature of the beech bark microflora, and so direct observations of fungal development on infested bark were made. The bark was taken in July 1982 from trees at Queen Elizabeth and Marden Forests in southern England, representing a range of infestation catagories, and 25 mm discs were incubated on moist tissue paper at room temperature (19 - 27^{0}C for three weeks. During this period the dominant fungi developing from the insect colonies were examined using the high power of a dissecting microscope. The individual insect plating and the bark disc incubation are reported in more detail elsewhere (Lonsdale, these Proc.). An additional survey of dominant species of the mycoflora was carried out by microscopic examination of fungal fruiting masses which had developed under natural conditions on infested bark at Alice Holt, Queen Elizabeth and Marden Forests.

For present purposes, the direct observations and the isolation data are summarised in a descriptive form (Table 1). This excludes the many genera of hyphomycetes which seemed to occur only occasionally, and it also excludes yeasts and bacteria. It must also be emphasised that the role of the bark microfauna seemed to be very important in relation to grazing of the fungal colonies and dissemination of propagules, but no quantitative data could be gathered concerning these effects.

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[1] University of Bath undergraduate industrial placement report.

Among the fungi listed in Table 1, *Cladosporium cladosporioides* (Fres.) de Vries was usually the most frequent and abundant of the dematiaceous species which caused blackening of the insect wax, although *Ramichloridium subulatum* de Hoog was dominant on some trees. It may be noted here that blackened wax was more wettable than fresh wax, a characteristic which could influence the micro-environment of the bark. *Verticillium lecanii* Viegas, a known entomophagous species (Petch 1948) was also a very dominant component of the mycoflora but was dependent on the presence of massed insect colonies (Lonsdale, these Proc.). *Nectria viridescens* Booth was also noteworthy for its frequency. *Nectria coccinea*, however, was infrequent, yet it was one of only three species found in all the three niches: insect colony material, the bark surface and necrotic flecks in the phelloderm. The other species were *C. cladosporioides* and *V. lecanii*. It was also found in preliminary work that *N. coccinea* artificially introduced on to infested bark readily grew and formed micro-conidia (Plate 1).

Table 1.--Summary of the apparent ecological status of the more frequent fungi of *Cryptococcus*-infested beech bark

Cryptococcus colonies	Bark surface	Phelloderm necroses
Ecological Status		
Cladosporium cladosporioides		
Dominant on old colonies and present on live insect bodies, especially those in young colonies.	Largely confined to sites under or near insect colonies.	Occasionally present.
Pyrenochaeta sp.		
Occasionally present.	Not detected.	Frequent.
Ramichloridium subulatum de Hoog		
Frequently present, and occasionally more dominant than *Cladosporium*.	Confined to sites near insect colonies.	Not detected.
Verticillium lecanii Viegas		
Very frequent on live insect bodies and dominant on colonies, but only where the colonies are large.	Much of the bark surface around colonies may be colonised.	Occasionally present.
Nectria viridescens Booth		
Frequent on live insect bodies and on colonies at all stages of development.	Often growing extensively around insect colonies.	Not detected.
Mucor spp.		
Sometimes dominant colonists of single or very small massed colonies.	Rarely present beyond margins of insect colonies.	Not detected.
Acremonium spp.		
Occasionally present on live insect bodies and may overgrow colonies.	Common on general surface.	Not detected.
Penicillium spp		
Never dominant but frequently present.	Rarely dominant, but frequently present.	Occasionally present but sp. not same as insect associate.
Fusarium lateritium Nees		
As *Penicillium* spp.	Not detected, though isolated from uninfested bark.	Frequently present.
Nectria coccinea		
Infrequently detected.	Infrequently detected	Infrequently detected.

Many other fungi which were observed occurred with too low a frequency or abundance to be associated with a particular niche. Most common among these were *Trichoderma viride*, *Trichothecium* sp., *Fusarium avenaceum*, *Alternaria alternata*, *Stemphylium botryosum*, *Pyrenochaeta* sp., (an un-named species), *Coniothyrium* sp., *Epicoccum* sp., and several yeasts and yeast-like fungi including *Aureobasidium pullulans*. Bacteria were frequently isolated, but were visually inconspicuous on the natural substrates.

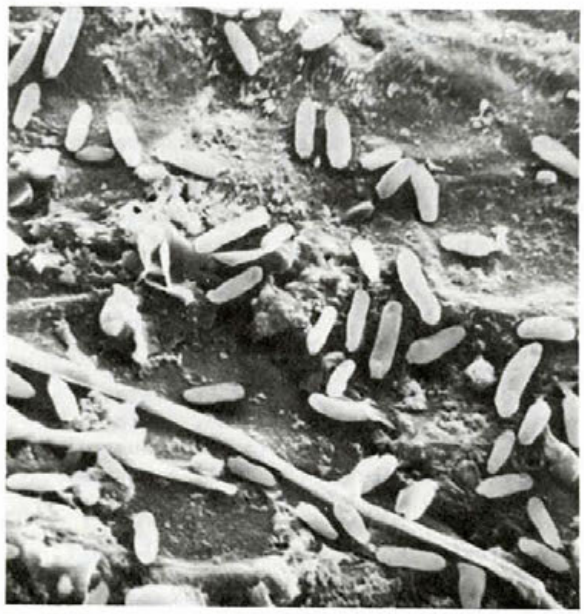


Plate 1. --*N. coccinea* growing and forming micro-conidia on *Cryptococcus*-infested beech bark, following artificial inoculation (scanning electron micrograph, X 2 250) (copyright: Long Ashton Research Station)

In vitro interactions of some beech bark fungi

The recognition of those fungi which seemed to be dominant colonisers of scale-infested bark suggested two lines of enquiry into possible fungal interactions. These were: a) interactions between *N. coccinea* and dominant or frequent bark fungi and b) between *C. cladosporioides* (apparently the most dominant fungus) and other bark fungi. These other fungi were to include *N. coccinea* and several of the commoner species in the mycoflora.

The *in vitro* interactions were observed on agar challenge plates, with the opposing inocula on 6mm diameter blocks cut from young cultures on 2% MA placed 4cm apart on 15cm^3 85mm diameter plates. The initial medium used

was 2% MA, but other media were used to represent a wider range of nutrient concentrations, perhaps bearing some relationship to the variations in nutritional status occurring on the bark surface. These media contained a mineral/amino-acid/thiamine base (Elliott 1972) with the addition of 0.2, 0.4, 0.6, 0.8 and 1.0% sucrose of 1% tyndallised citrus pectin (Sigma Chemical Co. Inc., St Louis, MO, U.S.A.) as carbon source. Pectin was felt to be of some interest in relation to colonisation of internal niches in the bark tissues.

The results of these challenge tests are summarised in Table 2. The strong inhibition of *N. coccinea* by *F. lateritium* on malt and sucrose agars was noteworthy, as was the total compatibility of *N. coccinea* with *C. cladosporioides*. It was also of interest that *V. lecanii*, a dominant fungus on mass *C. fagisuga* colonies, was able to cause lysis of *N. coccinea*, and that the degree of lysis was dependent upon the concentration of sucrose in the basal agar medium. To examine the effect further, a series of similar challenges was set up between these two fungi using sucrose concentrations of 0, 0.5, 1.0, 1.5, and 2.0%. Five replicates were set up for each concentration and incubated at 20^0C.

Three different effects were evident after the opposing mycelia met. Most striking of these was virtually total lysis of the *Nectria* colony (Plate 2a). Individual hyphae of *V. lecanii* grew alongside those of *N. coccinea* and the latter became devoid of contents (Plate 2b). This extreme lysis only occurred on the 0.5% sucrose medium as shown in Table 3. Secondly a partial lysis occurred at 0 and 1.0% sucrose and on one replicate at 2.0%. The third effect was a surface overgrowth of *N. coccinea* by *V. lecanii*, this occurring at all sucrose concentrations, even where lysis was only partial or absent.

Table 3.--Lysis of *N. coccinea* by *V. lecanii* on agar challenge plates

	Sucrose concentration in basal medium				
	0.0	0.5	1.0	1.5	2.0 %
Mean radius of lytic zone 25 days after meeting of colonies (mm)	0.0	20.0	0.0	0.0	0.0

The above data refer only to the intense form of lysis

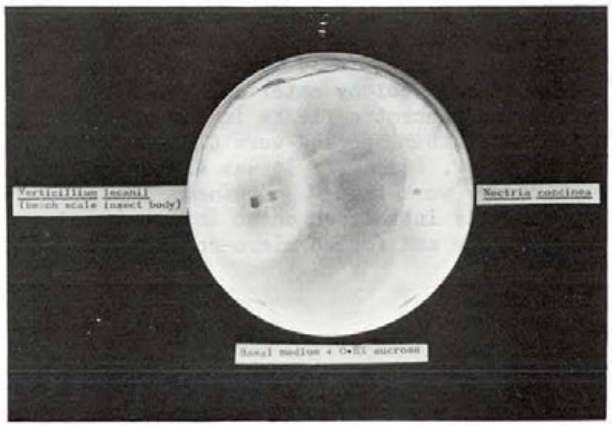


Plate 2a.--Lysis of a culture of *N. coccinea* by *V. lecanii*

Table 2.--Summary of agar challenge tests between *N. coccinea* and other fungi

Test fungus	Degree of inhibition of *N. coccinea*							Interaction in contact zone between colonies
	Malt	Basal medium plus sucrose					Pectin	
	0.2%	0.2%	0.4%	0.6%	0.8%	1.0%	1.0%	
N. coccinea	0	-	-	-	-	-	-	free intergrowth
Acremonium sp.	+	+	+	+	+	+	+	slight intergrowth
F. lateritium	+++	+	++	+	+	+	0	no intergrowth
Pyrenochaeta sp.	+	+	+	+	+	+	+	no intergrowth (sucrose)
V. lecanii	NT	+	++	++	++	+++	++	*Nectria* lysed and overgrown on sucrose
C. cladosporioides	0	0	0	0	0	0	0	free intergrowth



Plate 2b.--Hyphal interaction between *N. coccinea* (wider hyphae) and *V. lecanii* showing loss of content from the hyphae of *N. coccinea* (x 3250)

Comparative compatibility of *N. coccinea* and other bark fungi with *C. cladosporioides*

The challenge tests and much preliminary work had shown that *N. coccinea* and *C. cladosporioides* could intergrow freely on a range of agar media, including the basal medium supplemented with several sucrose concentrations. The dominance of *Cladosporium* on *Cryptococcus*-infested beech bark and its presumably intense competition for nutrients may favour the growth of fungi which are compatible with it at the expense of their potential antagonists. In order to compare the success of *N. coccinea* with that of other bark fungi in the presence of *C. cladosporioides* at low nutrient concentrations, two series of challenge inoculations were set up. The first series involved 'colony opposition' challenges on 0.1 and 0.01% yeast extract (Difco Laboratories, Detroit, U.S.A.) agar (YEA), 5mm diameter inoculum discs being placed 4cm apart on the plates, before incubation at 20°C. The second series involved the inoculation of the test fungi on to 'lawn' cultures of *C. cladosporioides* on 0.01% YEA and on 0.2% *Cryptococcus* colony agar which contained a suspension of insect bodies plus wax. The 'lawn' cultures were inoculated after three different establishment periods.

The results of the 'colony opposition' challenges are summarised in Table 4 and show that, of the test fungi chosen *N. coccinea* was the only one which was completely uninhibited and which freely intergrew with *C. cladosporioides* at both nutrient levels.

In the 'pre-establishment' challenges on 0.01 YEA and on 0.2% CfA the growth of the test fungi was measured by microscopic inspection of the plates at intervals of 16, 25 and 30 days. Four different *Nectria* species were included in this experiment. The results are shown in Table 5 and represent the reduction of growth rate of each test fungus, as compared with its growth in axenic culture. The growth rate of *F. lateritium* was reduced significantly more than the rates of all three British *Nectria* sp. This was of particular interest in view of the potentially antagonistic effect of *F. lateritium* upon *N. coccinea*. *Verticillium lecanii* was also of interest in this respect, and it was more strongly inhibited than *N. coccinea*, at least on the six-day-old lawns. Its growth in axenic culture was in any case much slower than that of *N. coccinea*. The growth of the N. American isolate of *N. coccinea* var. *faginata* was reduced more than that of the British *Nectria* spp. with most combinations of lawn age and nutrient medium. Over the entire range of combinations, the only fungus which tolerated the presence of *Cladosporium* nearly as well as the British *Nectria* isolates was the *Ceratocystis* sp.

Table 4.--Inhibition of the growth of fungi challenged against C. cladosporioides in low nutrient conditions

Test fungus	% YEA	Inhibition score (0,+,++,+++)	Presence of colony contact (+/-)	Presence of intergrowth (+/-)
N. coccinea ACR	0.01	0	+	+
	0.1	0	+	+
F. lateritium S2	0.01	+	+	-
	0.1	+	-	-
F. lateritium ED	0.01	+	+	-
	0.1	+	+	-
F. lateritium EL	0.01	+	-	-
	0.1	+	-	-
V. lecanii F3	0.01	+	-	+
	0.1	+	+	-
Pyrenochaeta F3A	0.01	0	+	+
	0.1	+	+	-
Acremonium A	0.01	+	+	+
	0.1	0	+	-

Table 5.--Growth of some beech bark fungi through *Cladosporium* lawn cultures in low nutrient conditions

Age of lawn (days) at introduction of test fungus	Growth rate: reduction (percent) of axenic rate						Axenic growth rate (mm day^{-1})	
	0.01% YEA+			0.2% CfA†				
	6	13	20	6	13	20	YEA+	CfA†
Test fungus								
N. coccinea ACR	20c	33ab	51bc	9a	39bcd	14a	4.5	3.4
N. viridescens F3	19b	24a	43bc	13b	9a	9a	2.1	1.9
N. ditissima EJP	15a	28a	43a	27cd	33b	7a	3.9	3.5
N. coccinea var. *faginata* 33A	45e	75d	56cd	62e	65de	76c	3.2	2.7
F. lateritium EL	81g	86e	86d	79f	84e	82c	6.5	5.7
Pyrenochaeta F3A	48f	63cd	74cd	51e	46bcd	50bc	1.9	1.7
V. lecanii CF1	44e	56bcd	52bcd	38d	37bcd	51c	2.5	2.3
Ceratocystis PCM	36d	38abc	32b	20bc	24ab	27ab	6.3	4.8

+ 0.01% yeast extract agar † *Cryptococcus* agar

Analysis of variance, following angular transformation of the data for each lawn age, showed overall significant differences between test species ($p < 0.005$) within each lawn age, values followed by the same letter did not differ at the 5% level in Duncan's New Multiple Range Test (Steel & Torrie 1960).

Comparative roles of different *Nectria* spp.

The above data suggested that *N. coccinea* may be ecologically favoured on bark dominated by *C. cladosporioides*, and the more limited data for *N. viridescens* and for *N. ditissima* provided similar evidence for these species. The log inoculations, described below, indicated that *N. viridescens* has no ability to parasitise beech bark and that its presence in natural lesions is probably due to secondary colonisation. *Nectria ditissima*, however, is a more aggressive parasite in unstressed bark than is *N. coccinea* (Parker 1974) and if it is ecologically favoured on *Cryptococcus*-infested beech bark, it should be expected to occur as a major cause of beech bark disease.

In order to study further the interactions between *N. ditissima* and *C. cladosporioides* a series of challenge plates was set up on the basal medium agar amended with 1% autoclaved pectin or sucrose at 0.2, 0.6 and 1.0%. In all these challenge tests *N. ditissima* suppressed the growth of *C. cladosporioides* and, on the pectin agar, it overgrew the latter. These findings indicated that *N. ditissima* and *N. coccinea* differ in their interaction with *C. cladosporioides*, but they gave no reason to assume that *N. ditissima* might thus be at a relative disadvantage.

Fungal interactions in the phytoparasitic environment

The typically dominant status of *N. coccinea* in beech bark lesions indicated that this fungus is well adapted to the parasitic invasion of stressed host tissues. A number of other fungi have, however, also been isolated from the bark lesions, some of them frequently, and three of these were selected for a series of bark inoculations designed to test a) their abilities to invade stressed tissue in their own right and b) their interactions with *N. coccinea* in lesions. At the same time a number of isolates of *N. coccinea* from niches in or on the outer bark were tested for their ability to form lesions. In order to standardise the plant material, detached logs were used in preference to standing *C. fagisuga*-infested trees.

The logs, one metre in length, were obtained from a forty-nine year-old beech plantation. In order to minimise difference in rates of drying-out and tissue senesence, they were selected for similarity of diameter and their cut ends were sealed with a latex emulsion.

Inoculation was performed using a bolt wound and cling-film wrapping technique as described by Lonsdale (1980b), using in each case approx. 0.1 g of an inoculum consisting of a 3% maizemeal/sand culture (Butler 1953) of the test fungus. The cultures had been grown at 20^0C in $250cm^3$ Ehrlenmeyer flasks over a period of two to four weeks, depending on the growth rate of the fungus.

Each log received inoculations at four points around its circumference at each of either two or three positions along its length, and each treatment was replicated between six logs and between all longitudinal inoculation positions. Incubation took place out-of-doors during the winter and spring of 1980/81, with the logs held in a near-vertical position and supported above a concrete surface by nails driven into one of the cut ends.

The treatments and the fungi used were as follows:-

a) *N. coccinea* pathogenicity tests with four 'outer bark' isolates of the fungus, and a mixture of isolates obtained from inner bark lesions:

   BC1 from the bark surface of a *C. fagisuga*-infested beech.

   CW2 from a colony of *C. fagisuga*.

   F2 from a necrotic fleck in the phelloderm of an infested beech.

   F3 as F2, from another beech tree.

   LM4/2/1 lesion mixture containing three isolates.

b) Mixed inoculations (i.e. at one wound site):

   N. coccinea LM4/2/1, mixture of three bark lesion isolates in combination with each of the following fungi -

   N. viridescens L1, a lesion isolate of this frequently occurring bark surface fungus.

   Fusarium lateritium C, a bark lesion isolate of this ubiquitous beech bark fungus and known antagonist of *N. coccinea*.

   Pyrenochaeta sp. F3, an isolate from a necrotic fleck of the type possibly utilised by *N. coccinea* during latent infections.

c) 'challenge' inoculations between *N. coccinea* LM/4/2/1 and each of the fungi named in (b), with the inoculation points 4cm longitudinally apart.

('Controls' were set up using a sterilised maizemeal/sand mixture).

The assessment of each log took place when at least one lesion could be detected by preliminary probing, a stage reached by all the logs within a four-week period in May-June 1981. The measurements of lesion lengths and breadths (Table 6) showed that all the *N. coccinea* isolates, whether obtained from bark lesions, necrotic flecks, the bark surface or from *C. fagisuga* colonies, were able to invade stressed beech bark tissue. None of the other fungi had this ability.

Table 6.--Lesion development following single-species inoculations on beech logs

Inoculant fungus	Lesion length (mm)	Lesion width (mm)
N. coccinea LM4/2/1	61.7 ± 29.5	19.9 ± 12.7
N. coccinea BC1	60.8 ± 25.6	16.5 ± 8.1
N. coccinea CW2	70.8 ± 46.7	12.6 ± 5.6
N. coccinea F2	70.4 ± 34.6	18.2 ± 10.1
N. coccinea F3	56.4 ± 27.7	12.9 ± 3.9
N. viridescens L1	9.2 ± 2.6	5.1 ± 1.6
F. lateritium C	9.0 ± 6.3	6.5 ± 2.9
Pyrenochaeta sp F3	9.3 ± 4.4	6.3 ± 3.4
control	8.0 ± 2.7	5.0 ± 2.7

mean values are followed by 95% confidence intervals.

At the time when the lesions were measured, a series of bark plugs was removed from all zones of each lesion and plated out on 2% MA for isolation of micro-organisms. The re-isolation frequencies of the inoculant fungi in the mixed species and 'challenge' inoculations are shown in Figures 2a and 2b together with mean lesion dimensions. These date show that despite the inability of *F. lateritium*, *N. viridescens* and *Pyrenochaeta* sp. to colonise the bark tissues as primary invaders, they were able to colonise tissue freshly invaded by *N. coccinea*. They did not reduce the invasive ability of *N. coccinea* but they did reduce the frequency with which it was re-isolated from colonised tissue. Thus, in the lesions arising from mixed inoculations of *N. coccinea* and *F. lateritium*, only 17% of attempted re-isolations from the central zones yielded *N. coccinea*, compared with 42% for *F. lateritium*. It could not be judged whether this reduced recovery of *N. coccinea* was partly the result of competition on the isolation plates.

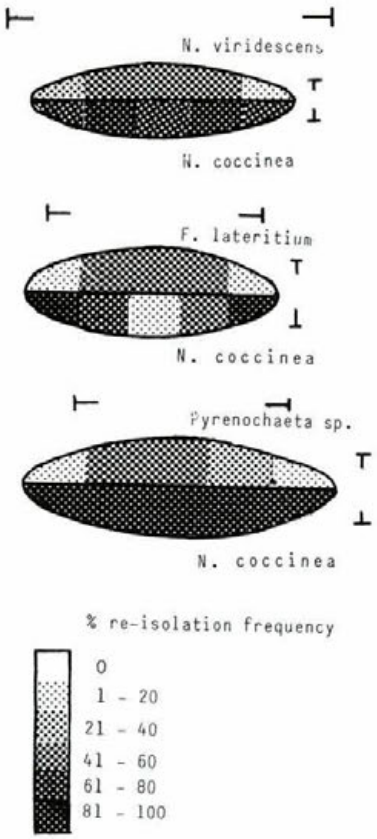


Figure 2a.-- Lesion size and re-isolation of inoculant fungi in mixed inoculations on beech logs. The diagrams show mean lesion lengths and breadths (less 10mm for the inoculation holes; bars indicate 95% confidence limits). Each diagram is split to show re-isolation frequencies for N. coccinea (below) and for the other inoculant fungus (above) as indicated by labels.

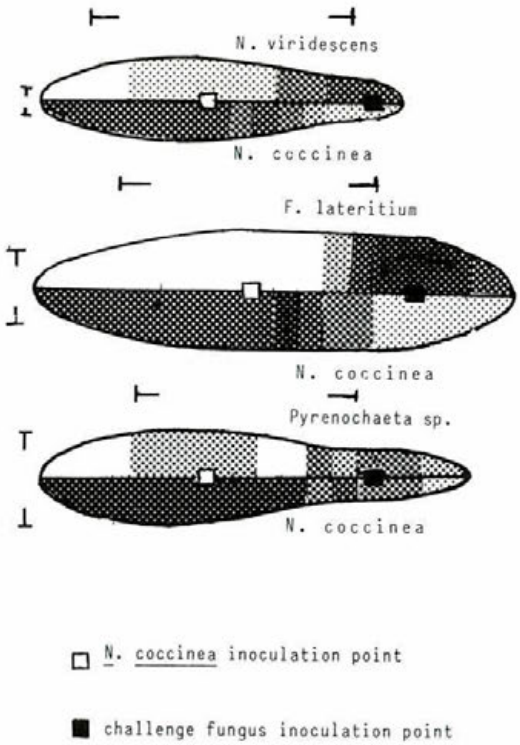


Figure 2b.-- Lesion dimensions and re-isolation of inoculant fungi in challenge inoculations on beech logs. Data are presented as for Figure 2a with the addition of markers for the two inoculation sites. Confidence intervals for lesion breadth refer only to the 'N. coccinea' ends of the lesions.

DISCUSSION

The detection of *Nectria coccinea* on the surface of scale-infested beech bark in the small necrotic flecks within such bark supports the idea that latent colonisation is involved in beech bark disease. The fact that isolates taken from these outer bark sites were pathogenic on logs also supports this view. It seems unlikely, however, from the sampling and observational data, that *N. coccinea* is a major component of the cauloplane microflora, and further work will be necessary to determine whether a link exists between its colonisation of the outer bark and its invasion of deeper tissues. In particular, the development of better selective isolation methods would show whether the apparent infrequency of occurrence of *N. coccinea* is due in part to competition on the culture medium from *Fusarium lateritium* or other antagonists. Cotter (1977) found that a *Fusarium* sp. was much more readily isolated

from perithecia of *N. coccinea* var. *faginata* on *Fagus grandifolia* than was *Nectria* itself. The present work represents a preliminary characterisation of the ecosystem which *N. coccinea* must negotiate in order to gain access to inner bark tissue. It is interesting that the fungus, at least *in vitro*, seems to grow much better than its most obvious competitors in the presence of *Cladosporium cladosporioides*, a very dominant member of this ecosystem. It remains unclear to what extent these 'most obvious competitors', the antagonistic *F. lateritium* and the mycoparasitic *Verticillium lecanii*, may suppress *N. coccinea* on the bark. The effects of sugar concentration on the mycoparasitic ability of *V. lecanii* were of particular interest, and helped to emphasise the need to understand the temporal and spatial nutrient gradients that occur on the bark.

The log inoculations drew a distinction between those fungi which can invade stressed host tissues and those which are secondary colonists of lesions. Although some secondary colonists may have a powerful inhibitory effect on the growth of other fungi, as is the case with *F. lateritium*, there seems little doubt that the ability of *N. coccinea* to act as a pioneer invader must often enable it to escape such inhibition. This can also be concluded from the findings of Gotwols, Blanchard & Shortle (1980). Whether secondary colonisation of lesions could reduce the ability of *N. coccinea* to persist to the fruiting stage is not clear but it has often been isolated from old lesions.

The present findings are consistent with the idea that *N. coccinea* occurs on the bark, that it is ecologically favoured in this environment and that it can readily exploit the inner bark when stress in the tree becomes sufficiently severe. The rarity of *N. ditissima* and of the more pathogenic strains of *N. cinnabarina* or of other canker fungi in the necrotic bark of scale-infested beech is not, however, explained by these data. The explanation might be simple; for example, the reluctance of *N. ditissima* to form micro-conidia in culture may suggest also a lack of ability to achieve adequate dispersal on the bark in conditions where it cannot produce sporodochia or perithecia. It is worth noting that infection of apple leaf scars by the similar twig canker fungus *N. galligena* can be inhibited by saprophytes in the outer scar tissue (Swinburne 1973), an effect which can be used in biocontrol procedures (Corke & Hunter 1979). These outstanding questions clearly demand more detailed observational and experimental work and they highlight the importance of understanding not only the processes of pathogenesis but also the ecological interactions upon which pathogenesis may often depend.

ACKNOWLEDGEMENTS

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RÉSUMÉ

Une étude de mise en culture de l'écorce du hêtre envahie par la cochenille Cryptococcus fagisuga a révélé la présence du Nectria coccinea dans les trois niches suivantes: (1) les colonies du Cryptococcus, (2) la surface de l'écorce à proximité de ces colonies, et (3) des points nécrotiques dans l'écorce extérieure des arbres envahis depuis longtemps. Ceci indique la possibilité que les maladies de l'écorce du hêtre comportent un élément d'infection latente, bien que le N. coccinea n'ait pas souvent été isolé pendant cette étude.

Parmi les nombreux autres champignons présents sur ou dans l'écorce, seules les deux espèces suivantes étaient présentes dans toutes les susdites niches: Cladosporium cladosporioides, dominant dans de vieilles colonies de Cryptococcus, et Verticillium lecanii, abondant parmi les fortes infestations d'insectes. D'autres champignons souvent isolés sont: Ramichloridium subulatum, Pyrenochaeta sp., Nectria viridescens, Mucor spp., Acremonium spp., Penicillium spp. et Fusarium lateritium.

Des essais de provocation in vitro et à différentes concentrations de sucre, entre N. coccinea et des champignons ordinaires de l'écorce démontrent que deux espèces, V. lecanii et F. lateritium, sont antagonistes à N. coccinea; la première serait fortement mycoparasitaire. Un essai de taux de croissance sous conditions de faible nutrition démontre que la croissance de trois espèces britanniques de Nectria obtenues de l'écorce du hêtre, à travers les cultures "en pelouse" de C. cladosporioides est moins inhibée que celles de F. lateritium et de V. lecanii. La variété nord-américaine, N. coccinea var. faginata est plus fortement inhibée que les isolats britanniques.

L'inoculation de bûches de hêtre démontre que les isolats de N. coccinea obtenus des susdites niches dans l'écorce extérieure sont capables de provoquer la nécrose de l'écorce, contrairement à F.

lateritium, N. viridescens et Pyrenochaeta sp. Toutefois, ces autres champignons sont capables de coloniser les tissus envahis par N. coccinea et de réduire la fréquence avec laquelle cette espèce est ré-isolée.

ZUSAMMENFASSUNG

Isolierungen von Buchenrinde, die von der Buchenwollschildlaus (Cryptococcus fagisuga) befallen waren, ergaben, daß Nectria coccinea in den folgenden Nischen anzutreffen war: 1. Lauskolonien, 2. Rindenoberfläche in der Umgebung von Lauskolonien, 3. Nekrosen in der äußeren Rinde von länger befallenen Bäumen. Dies deutet darauf hin, daß, obwohl N. coccinea während der Untersuchung nicht häufig isoliert werden konnte, der Pilz latent vorhanden und Teil des Krankheitskomplexes ist.
Von den vielen in und auf der Rinde vorhandenen Pilzen waren nur die folgenden zwei Arten in allen drei Nischen anzutreffen: Cladosporium cladosporioides, ein Pilz der hauptsächlich von alten Lauskolonien isoliert wurde, und Verticillium lecanii, der in großem Umfang in Bereichen mit intensiver Verlausung anzutreffen war. Andere häufig isolierte, aber nicht in allen drei Nischen vertretenen Pilze sind: Ramichloridium subulatum, Pyrenochaeta sp., Nectria viridescens, Mucor spp., Acremonium spp., Penicillium spp. und Fusarium lateritium.
In Dualkulturen zwischen N. coccinea und häufig vorkommenden Rindenpilzen auf Nährböden mit unterschiedlichem Zuckergehalt ergab sich, daß sich V. lecanii und F. lateritium antagonistisch zu N. coccinea verhielten. V. lecanii wirkt offenbar als starker Mykoparasit. Wachstumsversuche bei niedrigem Nährstoffgehalt zeigten, daß drei englische Nectria spp. von Buchenrinde beim Durchwachsen von C. cladosporioides-Kulturen weniger gehemmt wurden als F. lateritium und V. lecanii. Nectria coccinea var. faginata aus Nordamerika wurde stärker gehemmt als die Isolate aus Großbritannien.
Inokulationsversuche an Stammabschnitten zeigten, daß N. coccinea-Isolate aus den obenerwähnten Nekrosen in der äußeren Rinde im Gegensatz zu F. lateritium, N. viridescens und Pyrenochaeta sp. Rindennekrosen hervorrufen konnten. Allerdings waren die letztgenannten Pilze in der Lage, von Nectria coccinea befallenes Gewebe zu besiedeln. Die Reisolierbarkeit von N. coccinea ging dadurch zurück.

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CHARACTERISTICS AND DEVELOPMENT OF NECROPHYLACTIC PERIDERMS IN MATURE BARK OF AMERICAN BEECH[1,2]

William D. Ostrofsky and Robert O. Blanchard[3]

Abstract.--Investigations were made of necrophylactic periderms which were found to delimit natural and experimentally induced cankers in American beech. Anatomical evidence is presented which supports the hypothesis that the necrophylactic periderm is generated from recent derivatives of the vascular cambium as well as from living cells of the bark tissues present at the time of wounding or infection.

INTRODUCTION

Woody plant periderms which arise as the result of mechanical injuries, insect, or pathogen attack have been referred to as wound periderms (Bramble 1936, Tainter 1970) or necrophylactic periderms (Mullick 1977, Soo 1977). As a general rule, such a periderm provides a barrier which effectively limits the spread of pathogenic fungi through the bark tissues and prevents them from reaching the vascular cambium. As a result of periderm development in response to bark injuries, a certain degree of resistance to pathogen invasion is imparted to the plant (Horsfall and Cowling 1980).

Necrophylactic periderms have been shown or implicated to play a role in tree diseases such as chestnut blight (Bramble 1936), white pine blister rust (Struckmeyer and Riker 1951), Nectria canker of hardwoods (Grant and Spaulding 1939), yellow-laminated root rot of Douglas-fir (Mullick 1977) and the beech bark disease of European beech (Bazzigher 1957, Braun 1976, Braun 1977, Fink and Braun 1980). Braun (1976) and Fink and Braun (1980) have suggested that the bark damage in European beech resulting from the feeding activity of the scale insect *Cryptococcus fagisuga* Lind. allows the bark to dry and crack along the sclerified phloem rays to the vascular cambium. The presence of the rays themselves may also prevent the wound periderm from forming an uninterrupted barrier to the subsequent invasion of the beech bark by *Nectria coccinea* (Pers. ex Fr.) Fries.

Necrophylactic periderm development has been generally accepted as a major defense mechanism in woody plants (Horsfall and Cowling 1980, Mullick 1977), but few studies have been made of the ontogeny of the process. Temperature (Marks and Minko 1970), light conditions (Borger and Kozlowski 1972a), growth regulating substances (Borger and Kozlowski 1972b), plant water relations (Butin 1952, Puritch and Mullick 1975), and season of wounding (Grant and Spaulding 1939, Mullick and Jensen 1976) influence necrophylactic periderm development. Differences in these environmental conditions may often account for the success or failure of the plant to defend itself against pathogen ingress. With the exception of a study conducted by Ehrlich (1934), the role of the first exophylactic periderm in canker development, and the development of necrophylactic periderms in American beech (*Fagus grandifolia* Ehrh.) have not been reported.

The objectives of the present investigation were to (i) describe canker formation on American beech resulting from mechanical injury and inoculation with *Nectria coccinea* var. *faginata* Loh., Wats. & Ayers during each of the four

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[2]Scientific Contribution Number 1188 from the New Hampshire Agricultural Experiment Station.

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seasons, (ii) compare necrophylactic periderm development in trees which are susceptible with that in trees apparently resistant[4] to the beech bark disease, and (iii) describe two canker types of the beech bark disease resulting from natural infections on American beech.

MATERIALS AND METHODS

Seasonal inoculation study

Twenty-four American beech, each 5 to 10 cm in diameter, were selected at the Kingman Research Farm in Madbury, New Hampshire. One of four groups of six trees each was selected for treatment in each season. Treatments were initiated in the summer (8/23/79), fall (10/23/79), winter (1/16/80), and spring (4/1/80). Trees for each treatment were harvested for anatomical study two years from the time of treatment initiation.

Five whorls of 12 mm diameter wounds were inflicted on each of five trees in each group. Each whorl consisted of two wounds inoculated with a three week old malt agar culture of a single-ascospore isolate of *Nectria coccinea* var. *faginata*, a wound left uninoculated, and an area of the bark inoculated but left unwounded. The wounds were inflicted by the removal of a 12 mm diameter disc of periderm tissue. Wounds were approximately 0.5 mm in depth. All wounds were inflicated the same day in a given season. Wounds to be inoculated were so treated from the top whorl to the bottom whorl after 0, 2 days, 1, 2, and 4 weeks had passed, respectively, since the time of injury. These five trees were designated as the treatment trees.

The remaining tree in each group served as a control for time of inoculation. This tree was wounded, by whorl, at the corresponding treatment time intervals. All wounds were inoculated immediately after being inflicted. This tree was designated as the control tree.

Trees were inspected regularly for canker development over a period of two years, after which time they were harvested. Representative samples of uninoculated wounds, inoculated wounds, and healthy bark were sectioned to a thickness of 10 to 20 µm on a cryostat set at approximately -25 C. Sections were either stained with Toluidine Blue O or left unstained, and mounted in glycerol on standard glass microscope slides. Small samples (1 X 1 X 2 mm) of bark tissues were also fixed, dehydrated, infiltrated, and embedded in Spurr's epoxy resin (Kosakai 1973). Epoxy embedded tissues were sectioned at 3 to 5 µm with an ultramicrotome equipped with a glass knife. Sections were stained with Toluidine Blue O or left unstained, and examined microscopically.

Development of Necrophylactic periderm in American beech either susceptible or apparently resistant to the beech bark disease

Four pairs of American beech, each pair consisting of one tree susceptible and one tree apparently resistant to the beech bark disease, were selected for study. Two pairs were located at the Hubbard Brook Experimental Forest near West Thornton, New Hampshire, and two were located at the Bartlett Experimental Forest near Bartlett, New Hampshire.

Trees selected as pairs were a maximum of 2 m apart. Susceptible trees had obvious delimited cankers on which evidence of fruiting by *Nectria coccinea* var. *faginata* could be found. The scale insect *Cryptococcus fagisuga* was present in moderate to low populations. Apparently resistant trees had no evidence of cankering or fruiting by *N. coccinea* var. *faginata*. An occasional individual scale insect was found on some of the apparently resistant trees. All trees were between 19.6 and 30.0 cm in diameter (dbh).

Four whorls of eight injuries per whorl were made between 0.5 and 2 m above ground on the bole of each tree. Wounds were made by removing a 10 mm diameter disc of tissue approximately 0.5 mm in thickness from the bark. Susceptible trees were wounded where the bark was free of both primary causal agents of the beech bark disease. Wounds were inflicted on 18 and 20 September, 1981.

Wounds of the top two whorls of each tree were left uninoculated; wounds of the bottom two whorls were inoculated with a 10 mm diameter malt extract agar disc from a three-week old single-ascospore isolate of *N. coccinea* var. *faginata*. Inoculations were made the same day as wounds were inflicted. Bark samples of wounds of both treatments from all trees were collected at approximately bimonthly intervals and analyzed for anatomical changes. The cryostat was used to prepare fresh tissue sections, and the ultramicrotome was used to

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[4] In this study "apparently resistant" is used to describe healthy beech trees occurring in forest stands which have been heavily damaged by the beech bark disease. The term should not be taken to imply actual resistance or tolerance.

prepare epoxy-embedded tissues, as described previously.

Two canker types of the beech bark disease on American beech

A large number of American beech growing in natural forest stands at the Hubbard Brook and Bartlett Experimental Forests were inspected over a three-year period. Both research areas are classified as aftermath zones (Shigo 1970) with respect to the beech bark disease. The disease has been present in both areas for approximately thirty years.

Bark samples were collected from healthy trees and from trees exhibiting various degrees of cankering by *N. coccinea* var. *faginata*. Sections of bark samples were prepared for microscopic examination as described previously, and anatomical characteristics were related to general canker appearance.

RESULTS

Seasonal inoculation study

Nectria coccinea var. *faginata* was able to incite cankers on American beech stems when applied to bark tissues from which only the first exophylactic periderm had been removed (Fig. 1). Although many cankers developed, none grew larger than 3.5 cm in length or 2.2 cm in width. The slowest cankers to develop reached a maximum size within 12 months after initiation.



Figure 1.--Canker development around wounds 18 months after being inoculated. Arrow indicates erumpent sporodochia of the fungus. Scale bar represents 5 mm.[5]

Frequency of canker development was influenced by the season in which the trees were wounded and inoculated (Table 1). Twenty-two of the fifty wounds inflicted and inoculated in the fall resulted in cankers, compared with 0, 1, and 4 of those inoculated in winter, spring, or summer, respectively.

Table 1.--Effect of season of wounding and inoculation with *Nectria coccinea* var. *faginata* on canker development on American beech. Wounds were areas of the bark from which only the first exophylactic periderm had been removed.

Season of wounding and inoculation	Number of inoculated wounds forming cankers	
	Treatment trees[a]	Control trees[b]
Spring	1	0
Summer	4	1
Fall	22	7
Winter	0	0

[a]Each value represents the number of wounds forming cankers from a total of 50 inoculated wounds. Wounds were inflicted the same day in a given season but inoculated after various time intervals of up to four weeks.

[b]Each value represents the number of wounds forming cankers from a total of 10 inoculated wounds. Wounds were inflicted at various time intervals but inoculated immediately after being inflicted.

The time interval between wounding and inoculation influenced canker development (Table 2). The longer the time interval between wounding and inoculation, the fewer cankers developed. No wounds left uninoculated resulted in cankers, nor were any cankers formed when inoculum was applied to nonwounded bark.

Canker development on trees used as controls for the time intervals was also affected by season of inoculation. Again, most cankers occurred on wounds inflicted in the fall. However, canker development became less frequent as the fall season progressed, even when wounds were inoculated immediately after being inflicted. Of the seven fall wounds resulting in cankers, only one of four wounded and inoculated after 15 November resulted in canker formation, compared with six of six wounds inflicted and inoculated prior to 2 November. No cankers developed from wounds inflicted and inoculated during the winter season.

[5]For all Figures: FEP = First exophylactic periderm, NP = Necrophylactic periderm, NZ = Necrotic zone, P = Phloem, PH = Phellem, S = Sclerified parenchyma, SPR = Sclerified phloem ray.

Table 2.--Effect of various time intervals between wounding and inoculation of *Nectria cocoinea* var. *faginata* on canker development of American beech. Wounds were areas of the bark from which only the first exophylactic periderm had been removed.

Days between wounding and inoculation	Number of inoculated wounds forming cankers	
	Treatment trees[a]	Control trees[b]
0	10	3
2	7	2
7	3	2
14	4	1
28	3	0

[a]Each value represents the number of wounds forming cankers from a total of 40 inoculated wounds. A total of 10 wounds were inflicted in a given season and inoculated after each given time interval.

[b]Each value represents the number of wounds forming cankers from a total of 8 inoculated wounds. Two wounds were inflicted in a given season and inoculated after each given time interval.

Examination of tissue sections cut from two-year-old wounds which had resulted in cankers revealed that a well-developed necrophylactic periderm had formed. This periderm consisted of a phellem from twenty to twenty-five cell layers in thickness (Fig. 2). A phelloderm could not be distinguished. The necrophylactic periderm was never observed to be interrupted by the sclerified phloem rays. Rather, it always formed a continuous barrier between healthy and necrotic tissue, with the sclerified phloem rays separated completely from healthy tissues (Fig. 2). Large groups of sclerified parenchyma were commonly observed as short bands centripetal to the sclerified phloem rays which had been separated from healthy tissue by the necrophylactic periderm.

Healthy bark tissue was composed of long files of phloem cells (Fig. 3). The cells were uniform in size and shape. Bands of sclerified parenchyma were a common characteristic of this bark tissue.

Development of necrophylactic periderm in susceptible and apparently resistant American beech

The general appearance of one pair of American beech selected for study is shown in Figure 4. On close examination, many small delimited cankers were apparent on the susceptible tree. The bark of some cankers shows deep splits indicating infestation by the scale insect *Xylococculus betulae* (Perg.). Even though the trees are touching at the base, one tree of the pair has no cankers and is considered to be apparently resistant to the beech bark disease.

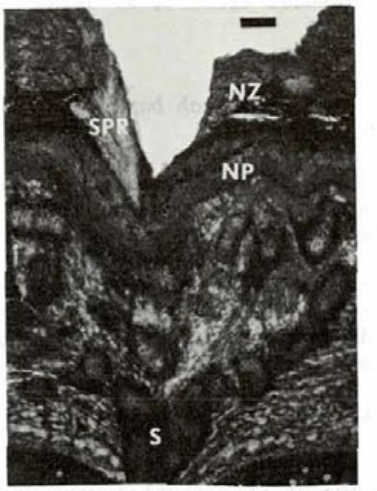


Figure 2.--Necrophylactic periderm delimiting the canker shown in Figure 1. The wound was inflicted in the fall and inoculated one week later. Note the shape of the sclerified phloem ray which has been delimited to the necrotic zone. Scale bar represents 40 µm; transverse section.

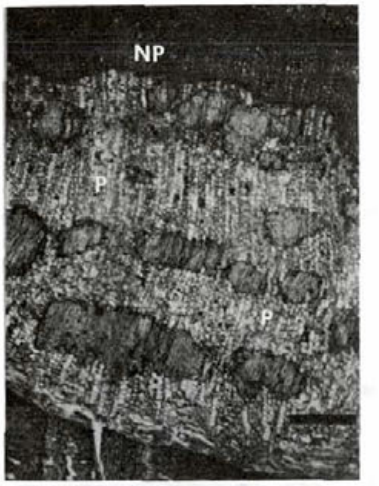


Figure 3.--Appearance of phloem centripetal to the necrophylactic periderm. Note the long, even radial files of vascular cambium derivatives. Scale bar represents 20 µm; transverse section.

Bark tissues behind wounds of both susceptible and apparently resistant trees eight weeks after injury appeared slightly discolored. Healthy bark tissues appeared light brown or tan, while tissues abutting the wound surface were dark red-brown. Tissues of wounds which had been inoculated appeared even darker, and the extent of the discolored tissues was larger than of wounds left uninoculated. No

differences in wounds between susceptible and apparently resistant trees were evident.



Figure 4.--Susceptible (right) and apparently resistant (left) American beech at the Hubbard Brook Experimental Forest. Scale bar represents 15 cm.

The bark surface around wounds 20 weeks after wounds had been inflicted was smooth, with no evidence of cankering (Fig. 5). Fruiting structures of *N. coccinea* var. *faginata* were not observed when inoculated wounds were examined. Microscopic examination of wounded tissues revealed that the extent of the discolored zone had increased only slightly from that of the eight week old wounds. No anatomical changes were apparent in bark tissues at this time.

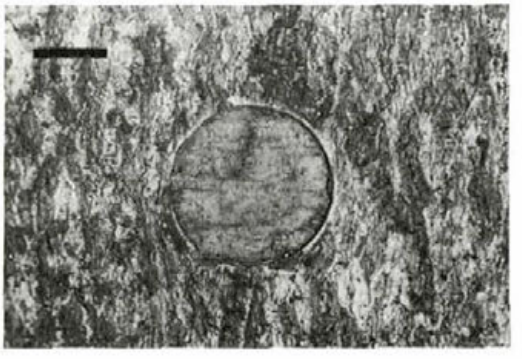


Figure 5.--The appearance of a wound twenty weeks after being inflicted on the bark of a susceptible tree and inoculated with *Nectria coccinea* var. *faginata*. No cankering is yet apparent. Scale bar represents 5 mm.

Significant changes in canker appearance and bark anatomy had occurred in tissues collected and examined 38 weeks after injuries had been inflicted. Abundant sporodochia of *N. coccinea* var. *faginata* were observed (Fig. 6). Anatomical changes in bark tissues behind both inoculated and uninoculated wounds were also evident (Fig. 7). A necrophylactic periderm was confluent with the first exophylactic periderm, and formed a continuous barrier between healthy and necrotic tissues. Neither sclerified phloem rays nor large groups of sclerified parenchyma interrupted the necrophylactic periderm (Fig. 8).



Figure 6.--Canker appearance 38 weeks after a wound was inflicted and inoculated with *Nectria coccinea* var. *faginata*. Sporodochia of the fungus are present (arrows). Scale bar represents 5 mm.

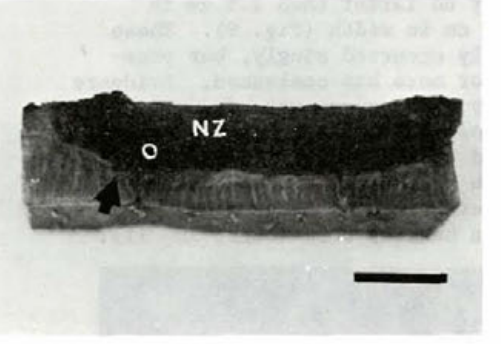


Figure 7.--Bark sectioned through a wound to show canker extent. The necrotic zone which has developed is delimited from the healthy tissue by a necrophylactic periderm, seen here as a narrow band (arrow). Scale bar represents 5 mm; transverse section.

Two canker types of beech bark disease on American beech

Two distinct types of bark cankers were evident on infected trees. Cankers restricted in size and defined in cross section by a distinct necrophylactic periderm were designated as delimited cankers. Cankers not defined in cross section by a necrophylactic

periderm were designated as diffuse cankers. Diffuse cankers were not restricted in size, and usually resulted in large necrotic areas. Populations of *C. fagisuga* were low on trees exhibiting either canker type. This does not necessarily reflect past scale populations on those trees.

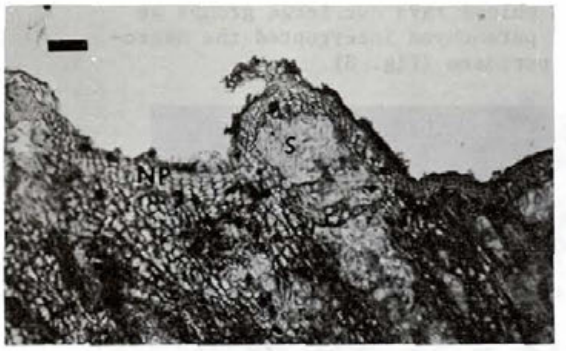


Figure 8.--Section of tissue from the canker shown in Figure 7. Note that the groups of sclerified cells do not interrupt the continuity of the necrophylactic periderm. Scale bar represents 100 µm; transverse section.

Characteristics of delimited cankers, the most common type encountered, are shown in Figures 9 through 14. Delimited cankers were small, usually no larger than 1.5 cm in length by 2.5 cm in width (Fig. 9). These cankers usually occurred singly, but occasionally two or more had coalesced. Evidence of fruiting by *N. coccinea* var. *faginata* was observed on most delimited cankers. Cankers were delimited by a distinct necrophylactic periderm which apparently always formed a continuous protective sheath between the necrotic tissue and the healthy bark (Figs. 10, 11).



Figure 9.--Appearance of typical delimited cankers. Scale bar represents 15 mm.

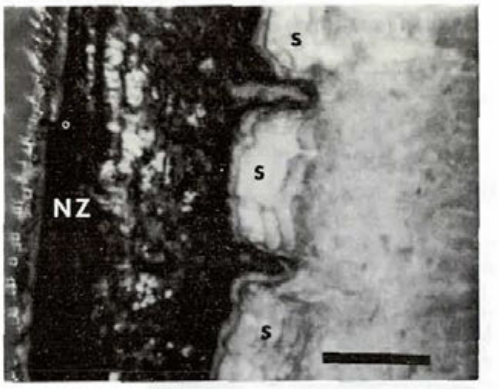


Figure 10.--Well defined necrophylactic periderm delimiting necrotic tissue from healthy bark. Note the bands of sclerenchyma developing behind this periderm. Scale bar represents 1 mm; transverse section.

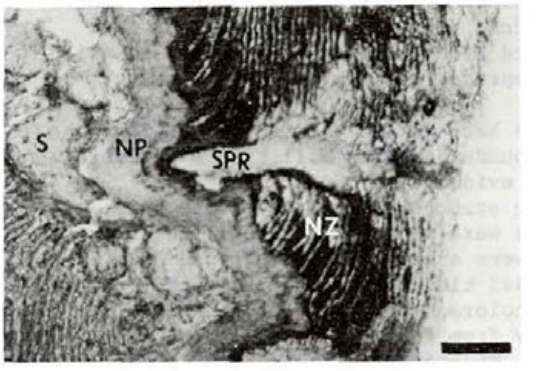


Figure 11.--Exclusion of the sclerified phloem rays from the healthy bark tissues by the necrophylactic periderm. Scale bar represents 300 µm; transverse section.

Evidence that the necrophylactic periderm of delimited cankers was continuous was demonstrated by autoclaving bark samples containing cankers for ten minutes. After autoclaving, the entire canker, consisting of the necrotic bark tissue and the phellem of the necrophylactic periderm, could be easily separated as a single piece from the healthy bark tissue (Fig. 12). The necrophylactic periderm was not interrupted either by large groups of sclerenchyma or by the sclerified phloem rays. This periderm included a well-developed phellem twenty-five to thirty-five cell layers in thickness, and a single phellogen layer (Fig. 13). A phelloderm was apparently lacking.

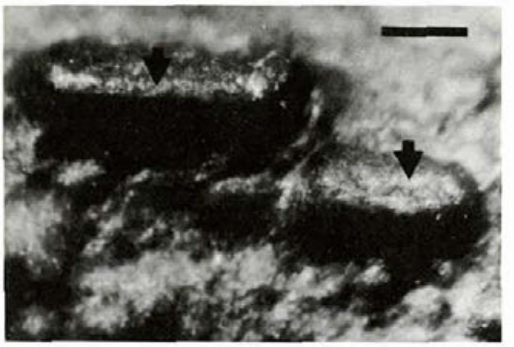


Figure 12.--Appearance of the necrophylactic periderm entirely ensheathing the necrotic zone, or canker. Arrows indicate where the necrophylactic periderm formed centripetal to the sclerified phloem rays. Scale bar represents 0.5 mm.

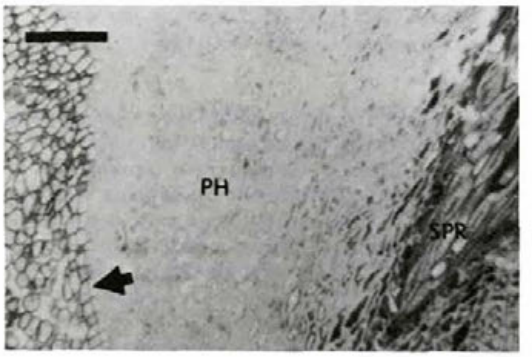


Figure 13.--Necrophylactic periderm showing sclerified phloem ray excluded from healthy tissue, a well developed phellem, and the phellogen (arrow). Scale bar represents 50 µm; transverse section.

Bark tissues centripetal to the necrophylactic periderm appeared similar to those of other healthy bark tissues, with the exception of the arrangement of sclerenchyma. Often, bands of sclerified parenchyma were arranged so that they formed one to several sheets of tissue immediately centripetal to the necrophylactic periderm (Figs. 10, 11). Other large groups of sclerenchyma were located in alignment with the sclerified phloem rays which had been excluded from the living bark by the necrophylactic periderm (Fig. 14).

Diffuse cankers were observed on only a few trees. This canker type is more common in the killing front zone of the disease which is now located in New York and Pennsylvania.

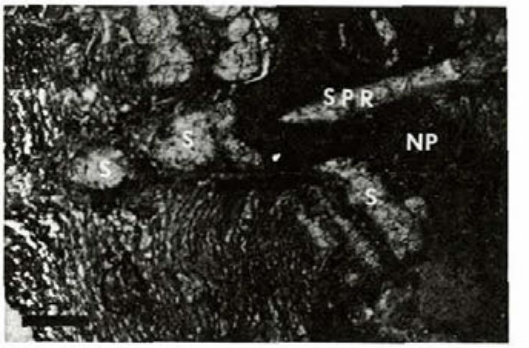


Figure 14.--Appearance of sclerenchyma centripetal to the necrophylactic periderm, and the sclerified phloem rays. Compare the general shape of the sclerified phloem ray to that shown in Figure 2. Scale bar represents 300 µm; transverse section.

Active diffuse cankers may be recognized by the relatively large numbers of perithecia of *N. coccinea* var. *faginata* on extensive areas of the bark, although the bark is not disrupted. Two tree boles were completely covered with perithecia, and the canker presumably involved the entire tree stem. In both instances, tree mortality had occurred within a few months after the initial observation.

A necrophylactic periderm had not developed in diffuse cankers (Figs. 15, 16). The bark area between healthy and necrotic tissues was often discolored in a random pattern, with no distinct demarcation between these tissues. The exophylactic periderm, parenchyma, and phloem cells were killed before an anatomical response to the advancing pathogen had occurred (Fig. 16).



Figure 15.--General appearance of bark at the canker margin. Perithecia of *Nectria coccinea* var. *faginata* (arrow) are present. Scale bar represents 1 mm; transverse section.

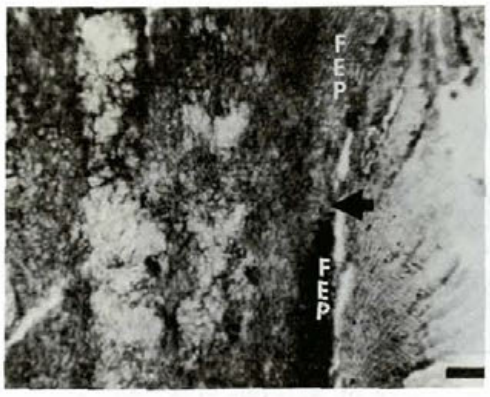


Figure 16.--Extent of necrosis in the first exophylactic periderm (arrow). Note that no apparent anatomical barriers occur in the region between the discolored and healthy areas. Scale bar represents 200 µm; transverse section.

DISCUSSION

The seasonal inoculation study demonstrated that the fungus *N. coccinea* var. *faginata* can grow through healthy bark tissues and induce cankers, thereby acting as a parasite, but the fungus cannot directly penetrate the phellem. The fungus was most successful when wounds were inflicted and inoculated in the early fall. This agrees with the findings of Grant and Spaulding (1939), who studied the effects of season of wounding on canker development resulting from inoculation with another species of *Nectria* on various species of hardwoods. Injuries made by the feeding activity of *C. fagisuga* may be more receptive to infection in the early fall, after the eggs have been laid and the adults have died. Ascospore and conidia discharge by *N. coccinea* var. *faginata* is also likely to occur during the fall, when moist climatic conditions are prevalent.

For these reasons, it appears likely that early fall is critical in terms of beech bark disease development. Wounds have been made by the insect, the fungus is disseminating spores, and necrophylactic periderm is slow to develop in response to injury (Mullick and Jensen 1976). Cankers developed as a result of inoculating wounds, but they had become delimited within two growing seasons by a well-developed necrophylactic periderm. Perrin (1979) and Lonsdale (1980) studied canker development on European beech resulting from inoculation of *N. coccinea* on trees stressed by high populations of *C fagisuga*, and reported less severe cankering when the insect was not present or was removed. Perrin (1979) suggested that it was the continued presence of relatively high populations of *C. fagisuga* that ultimately resulted in the inability of the tree to limit canker size. European beech is apparently capable of limiting damage caused by *N. coccinea* alone (Bazzigher 1957). The present study supports this concept. Inoculated trees were free of *C. fagisuga*, and were not under the influence of any apparent stress factor. Damage resulting from infection by *N. coccinea* var. *faginata* was limited and localized.

A necrophylactic periderm was initiated between 30 and 38 weeks after fall wounding and inoculation. This provided a long period of time for the pathogen to become well established in bark tissues. However, it is unlikely that the fungus was active during this entire period, since cankers failed to develop from wounds inoculated in the late fall or winter.

No apparent difference was observed in rate of necrophylactic periderm development between susceptible and apparently resistant trees. Necrophylactic periderm development is influenced by genetic processes, but it was not possible to relate genetic differences to susceptibility to the beech bark disease in this study.

There was a substantial difference in canker characteristics between inoculated and uninoculated wounds. A clearly discernable canker developed around inoculated wounds, and the necrotic region of these cankers were approximately 1.5 times the diameter of those resulting from uninoculated wounds. Also, sporodochia of *N. coccinea* var. *faginata* developed in abundance around inoculated wounds. No differences in characteristics between the necrophylactic periderms of inoculated and uninoculated wounds were apparent.

The characteristics of the naturally induced delimited cankers were similar to those of cankers induced by mechanical wounding and inoculation. Sheets of sclerified parenchyma were arranged in layers centripetal to the necrophylactic periderm, and large groups of sclerenchyma developed in alignment with sclerified phloem rays now included with the necrotic tissue. The necrophylactic periderm had developed as a continuous protective sheath, and was not interrupted by sclerified phloem rays. This observation is not consistent with those of Braun (1976), but perhaps the European beech responds differently with respect to necrophylactic periderm formation. Specific comparative studies are needed.

These investigations have led to the hypotheses that the necrophylactic periderms produced in response to mechanical injury or natural infections in American beech are generated from recent derivatives of the vascular cambium as well as from living cells of the bark already present at the time of wounding. This hypothesis is supported by two key anatomical observations. First, the sclerified phloem rays

present in the necrotic zone centrifugal to the necrophylactic periderm were shaped as those in healthy bark (Figs. 11, 13). That is, the ray end closest to the vascular cambium was sharply pointed or tapered. Sclerified phloem rays were generally uniform in width except in this region. Secondly, the radial files of cells centripetal to bark cankers likely resulted from a rapid and uniform development of the vascular cambium. Stimulation of the vascular cambium to produce substantially different xylem cells in response to injury has been well explored (Mulhern, Shortle and Shigo 1979, Shigo and Marx 1977, Tippett and Shigo 1981). A different response, one involving the phloem, is also apparently stimulated by certain specific conditions resulting from bark injury.

The development of a necrophylactic periderm from existing cells in the bark tissue is also evident from Mullick's investigations (Mullick 1977, Mullick and Jensen 1973) and the present study (Figs. 7 and 9), but the development of an uninterrupted necrophylactic periderm in American beech may still depend on the ability of the vascular cambium to produce phloem derivatives capable of differentiating into a new phellogen. However, these events may only occur in those localized areas where sclerified phloem rays are found within a few cells of the vascular cambium (Fig. 7).

In light of the work by Perrin (1979) and Lonsdale (1980), it may be rewarding to investigate the influence of high populations of *C. fagisuga* on the vascular cambium. The insect may be capable of preventing the vascular cambium from producing phloem derivatives which are in turn capable of differentiating into a necrophylactic periderm. Bark invasion by *N. coccinea* var. *faginata* may then be anatomically unopposed by the host. Once the fungus reaches and kills the vascular cambium, its further progress in the bark tissue is usually not interrupted.

SUMMARY

Necrophylactic periderms provide a barrier which can effectively limit the spread of pathogenic fungi through bark tissues of woody plants. Knowledge of the characteristics and development of necrophylactic periderms in American beech (Fagus grandifolia) would provide insight into the etiology of the beech bark disease, and may help to explain reported differences in susceptibility of American beech to this disease. The objectives of this study were to (i) describe canker formation on American beech resulting from mechanical wounds followed by inoculations with Nectria coccinea var. faginata during each of the four seasons, (ii) compare necrophylactic periderm development in trees which are susceptible with that in trees apparently resistant to the beech bark disease, and (iii) describe two canker types of the beech bark disease resulting from natural infections. Nectria coccinea var. faginata was able to incite cankers on American beech stems when applied to bark tissues from which only the first exophylactic periderm had been removed. Most cankers developed from wounds inflicted and inoculated in the fall. Two years after wounds had been inflicted, the necrophylactic periderm which had developed consisted of a phellem twenty to twenty-five cell layers in thickness and a single layer of phellogen. A phelloderm could not be distinguished. The necrophylactic periderm was never observed to be interrupted by sclerified phloem rays. Anatomical changes in bark tissues in response to wounds inflicted in the fall on susceptible or apparently resistant trees did not occur until after thirty weeks. No difference in time of initiation of the necrophylactic periderm was observed between susceptible and apparently resistant trees, or between inoculated and uninoculated wounds. Two distinct types of natural bark cankers were evident on infected trees. The majority of trees examined had numerous small (2 cm diam.) cankers which had become effectively delimited by a necrophylactic periderm. A few trees had large, diffuse cankers which were not delimited by a necrophylactic periderm. The characteristics of the naturally induced delimited cankers were similar to those of cankers induced by mechanical wounding and inoculation. Sheets of sclerified parenchyma were arranged in layers centripetal to the necrophylactic periderm. The necrophylactic periderm developed as a continuous sheath and was not interrupted by sclerified phloem rays. These observations have led to the hypothesis that the necrophylactic periderms produced in response to mechanical injury or natural infections are generated from recent derivations of the vascular cambium as well as from living cells of the bark already present at the time of wounding.

RÉSUMÉ

Les péridermes nécrophylactiques sont une barrière efficace pour limiter le développement des champignons pathogènes dans les tissus de l'écorce des plantes ligneuses. La connaissance des propriétés et du développement des péridermes nécrophylactiques chez le hêtre à grandes feuilles (Fagus grandifolia) nous aiderait à comprendre l'étiologie de la maladie de l'écorce du hêtre, et peut aider à comprendre les differences connues dans la susceptibilité du hêtre à cette maladie. Les objectifs de la présente étude sont: 1) de décrire la formation de chancres sur le hêtre par suite

d'une blessure mécanique suivie d'inoculations avec le Nectria coccinea var. faginata, à chacune des quatre saisons, 2) de comparer le développement de péridermes nécrophylactiques chez les arbres qui sont susceptibles aveccelui chez les arbres apparamment résistants à la maladie, et 3) de décrire deux types de chancres de la maladie de l'écorce du hêtre issus d'infections naturelles. Le Nectria coccinea var. faginata produisait des chancres sur les troncs de hêtres seulement lorsqu'appliqué sur de l'écorce dont le premier périderme exophylactique avait été enlevé. La majorité des chancres se développaient de blessures infligées et inoculées à l'automne. Deux ans après le moment de la blessure, le périderme nécrophylactique qui s'était développé consistait en une assise de tissus subéreux de 20 à 25 cellules d'épaisseur et d'une seule couche de phellogène. On n'a pu distinguer de phelloderme. On n'a noté aucune interruption du préiderme nécrophylactique par des rayons de phloème à cellules épaissies. Aucun changement anatomique dans les tissus de l'écorce ne sont apparus durant les trois semaines suivant l'apparition d'une blessure faite à l'automne sur les arbres susceptibles ou apparamment résistants. Aucune différence ne fut observée dans le moment de l'initiation du périderme nécrophylactique entre les arbres susceptibles ou apparamment résistants, ou entre les blessures inoculées ou non. Deux types distincts de chancres de l'écorce d'origine naturelle étaient évidents chez les arbres infectés. La majorité des arbres examinés avaient de nombreux petits chancres (2 cm diamètre) qui étaient effectivement délimités par un périderme nécrophylactique. Quelques arbres montraient de gros chancres diffus qui n'étaient pas délimités par un tel périderme. Les caractères des chancres délimités et d'origine naturelle étaient similaires à ceux des chancres par blessure mécanique et inoculation. Des assises de parenchyme à cellules épaisses étaient disposées en couches centripètes par rapport au périderme nécrophylactique. Celui-ci se développait en une assise continue et n'était pas interrompue par des rayons de phloème à cellules épaisses. Ces observations nous amènent à l'hypothèse de la formation de péridermes nécrophylactiques en réponse à une blessure mécanique ou à des infections naturelles et à son développement à partir de formations récentes du cambium vasculaire ainsi que de cellules vivantes dans l'écorce, déjà présentes au moment de la blessure.

ZUSAMMENFASSUNG

Wundperidermien können die Ausbreitung pathogener Pilze im Rindengewebe von Holzpflanzen wirkungsvoll begrenzen. Die Kenntnis der Eigenschaften und der Entwicklung von Wundperidermien bei Fagus grandifolia könnte mithelfen, die Ätiologie der Buchen-Rindennekrose zu verstehen und gleichzeitig Resistenzunterschiede gegenüber dieser Krankheit zu erklären. Die Ziele der vorliegenden Untersuchung waren: 1. Die Beschreibung der Krebsentwicklung bei Fagus grandifolia nach künstlicher Verwundung und nachfolgender Inokulation mit Nectria coccinea var. faginata zu allen vier Jahreszeiten, 2. ein Vergleich der Wundperidermentwicklung bei anfälligen und offensichtlich gegen die Krankheit resistenten Buchen und 3. die Beschreibung von zwei Krebstypen im Zusammenhang mit der Buchen-Rindennekrose und natürlichen Infektionen. Nectria coccinea var. faginata verursachte Krebse an Buchen, bei denen nur das äußerste Rindenperiderm entfernt worden war. Die meisten Krebse entwickelten sich nach Verwundung und Inokulation im Herbst. Zwei Jahre nach der künstlichen Verwundung war ein Wundperiderm aus einem Phellogen und 20 bis 25 Phellemzellschichten entstanden. Ein Phelloderm war nicht zu beobachten. Das Wundperiderm war in keinem Falle von sklerotischen Baststrahlen unterbrochen. Anatomische Veränderungen im Rindengewebe anfälliger und offenbar resistenter Buchen als Folge der Verwundungen im Herbst traten erst nach 30 Wochen auf. Hinsichtlich des zeitlichen Beginns der Wundperidermbildung waren zwischen anfälligen und offenbar resistenten Buchen keine Unterschiede festzustellen. Auch beim Vergleich infizierter und nicht infizierter Wunden waren keine Unterschiede zu beobachten. An natürlich infizierten Bäumen traten zwei deutlich verschiedene Krebstypen auf. Die Mehrzahl der untersuchten Bäume wies viele kleine (2cm Ø) Krebse auf, die jeweils von einem Wundperiderm wirksam abgegrenzt waren. Wenige Bäume zeigten große ausufernde Krebse, die nicht von Wundperidermien begrenzt waren. Das Aussehen der natürlichen abgegrenzten Krebse ähnelte dem der Krebse, die nach künstlicher Verwundung und Inokulation entstanden waren. Sklerenchymatische Zellschichten traten zentripetal zum Wundperiderm auf. Wundperiderm entwickelte sich in einer geschlossenen, nicht von sklerotischen Baststrahlen unterbrochenen Schicht. Die Beobachtungen führten zu der Hyothese, daß Wundperidermien als Folge mechanischer Verletzungen oder natürlicher Infektionen aus jungen Abkömmlingen des Kambiums wie aus lebenden Rindenzellen hervorgehen können, die zum Zeitpunkt der Verwundung schon vorhanden sind.

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ARMILLARIA MELLEA AND MORTALITY OF BEECH AFFECTED BY BEECH BARK DISEASE[1]

Philip M. Wargo[2]

Abstract.--The role of Armillaria mellea in the mortality of beech trees affected by beech bark disease was determined by excavating root systems of beech trees infested by beech scale, Cryptococcus fagisuga, or also infected by the bark fungus, Nectria coccinea var. faginata. Only trees infected by Nectria showed any effect on the root system. They had fewer 4th-order nonwoody branch roots and less starch than trees only infested by scale. A. mellea colonized roots only on Nectria-infected trees and was consistently found on roots associated circumferentially with areas of stem bark necrosis caused by Nectria. Complete colonization by A. mellea of the root system of dying trees occurred infrequently. The majority of trees were partially colonized and colonization occurred after stem necrosis. A. mellea did not accelerate mortality in those stands affected by beech bark disease.

INTRODUCTION

In studies on beech bark disease, aerial photos and ground examination showed that many diseased American beech, Fagus grandifolia Ehrh., persisted for several years, although a few trees died within 1 year (Houston 1974). Excavation of these trees at the root collar showed that Armillaria mellea (Vahl ex Fr.) Kummer (Armillariella mellea (Vahl. ex Fr.) Karst.) had girdled the root collar region of the trees that died within 1 year. It was absent from the root collars of the diseased trees that had symptoms but persisted (personal communication, D.R. Houston). This suggested that beech bark disease predisposed some trees to infection by A. mellea and that the fungus affected the rate of tree death in beech stands affected by beech bark disease.

Attack of trees by A. mellea has been consistently associated with stress factors that apparently predispose them to attack by this fungus (Wargo 1980a). Stress, such as defoliation, can cause changes in the root tissues of the chemical constituents that can stimulate growth of A. mellea (Wargo 1972) and increase susceptibility of roots to infection by this fungus (Wargo and Houston 1974).

Beech bark disease could be effecting similar changes in the root system. Trees stressed by the scale, Cryptococcus fagisuga Lindinger (C. fagi Bar.), and bark fungus, Nectria coccinea var. faginata Lohman, Watson and Ayers, could also be attacked by A. mellea, killing the tree faster than if it were affected by beech bark disease alone. If A. mellea affected the rate of mortality it would also affect the rate of subsequent deterioration of the trees, and the root fungus would have to be considered in formulating plans to manage stands affected by beech bark disease.

This study was done to determine the status of A. mellea in the roots of beech and assess its role in stands where beech bark disease was killing trees.

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MATERIALS AND METHODS

Stands of beech, infested with beech scale and currently infected by N. coccinea var. faginata, were located in the "killing front" (Shigo 1972) in northeastern and north-central New York on the eastern and western edges of the Adirondack Preserve, and in the "advancing front" in north-central Pennsylvania in the Tioga State Forest. Two stands in north-central New York were observed in July 1980 and two stands in northeastern New York and Pennsylvania were observed in June 1981.

Intensive root observations

In one stand in north-central New York, where high mortality was just occurring, 15 trees were selected for intensive observations on the root system. Five trees had zero to trace populations of beech scale (control trees) and five trees had heavy to very heavy scale, judged by the density of their white waxy excretion (Lonsdale 1980). None of these trees were infected by N. coccinea var. faginata. The remaining five trees were infected by N. coccinea var. faginata and had a range of scale infestations. Necrotic lesions in the bark with evidence of old or new perithecia and tarry spots verified infection.

On all 15 trees, three second-order woody branch roots (laterals) on each of four first-order woody lateral roots (buttress) were excavated until three first-order nonwoody roots having intact fibrous branches (<1 mm diam) were uncovered (terminology after Lyford 1975). This distance was usually 2 to 3 meters from the root-stem base. The living and dead 4th-order branches were counted on the three nonwoody roots from each lateral root. If the stele was cream colored or white when the bark was peeled it was counted as living, if it was brown it was counted as dead. Nonwoody branch roots on the next 60 cm of root on all the lateral roots were also counted.

The density of rhizomorphs of Armillaria mellea on the bark of the woody roots was estimated as absent, low, moderate or high. The bark tissue was then stripped to the wood on all excavated roots to locate necrotic lesions, mycelial patches of A. mellea, or decaying tissues.

A root sample was taken from each of three healthy woody roots from each of the 15 trees and their starch content was determined by the histochemical iodine technique (Wargo 1975). Starch content was used to judge the physiological condition (vigor) of each tree and relate it to scale and Nectria status.

Extensive root observations

In all six stands, beech trees that were dying or had recently died and were infected by N. coccinea var. faginata were selected for extensive observations on the root system. Trees were considered to have died recently if bits of leaves, twigs, and buds were present in the crown and the entire circumference of stem bark was necrotic but intact at the root-stem base. Dying trees had brown or green wilted and chlorotic foliage in the crown and only streaks of necrotic stem bark down to the root-stem base. In one stand in each area a site was chosen where at least five trees of each category could be observed on the same site. The status and pattern of A. mellea colonization observed on these trees was then verified by arbitrarily selecting trees in each category throughout that stand and a nearby stand. Evidence of Nectria infection, i.e. tarry spots, necrotic lesions, necrotic patches, and old or new perithecia; the extent of bark necrosis on the stem and its distance above the root-stem base; and the presence of decay were recorded. In addition, the chronology of crown death was reconstructed. The size of twigs and branches, remnants of leaves, tightness of the bark, and evidence of decay in the crown were used to judge whether the tree had died slowly in stages over several years or whether the whole crown had died rapidly during one year.

In one stand in New York, five trees that were infected by N. coccinea var. faginata and had dead portions of the crown but otherwise healthy foliage were also examined for colonization by A. mellea. Similar trees in each of the other stands were arbitrarily selected and examined to verify the initial observations.

On each tree, all the buttress roots were excavated to .50 to .75 meters from the tree. The density of rhizomorphs on their surfaces was estimated and the bark was peeled to locate areas colonized by A. mellea. If no colonization by A. mellea was observed, two roots on opposite sides of the tree were excavated to at least 2 meters. The bark was also stripped from these roots and all their branches in the excavated zone to see if they were colonized by A. mellea.

RESULTS

Intensive Root Observations

Nonwoody roots.--There were no significant differences in mean number of first-order nonwoody roots among trees scarcely or heavily infested with scale or infected by N. coccinea var. faginata. All trees averaged 26±2 first-order nonwoody roots per 60 cm of length. However, trees infected with Nectria had substantially ($P=.05$) fewer 4th-order nonwoody roots (Table 1). Two of the five trees infected by Nectria also had a substantially higher than average percentage of dead 4th-order roots, 18 percent versus 5 to 8 percent.

Table 1.--Mean number of living and dead and percent dead 4th-order nonwoody roots on scale-infested and Nectria-infected beech trees.

Tree category	Living	Dead	% Dead
Scale-infested trees			
Zero to trace (control)	599±57[a]	29±5	5±1
Heavy to very heavy	674±35	45±8	7±1
Nectria-infected trees	364±34[b]	32±17	8±4

[a]Mean of five trees for total number of 4th-order roots on 36 nonwoody roots per tree (3 nonwoody roots per 3 lateral roots per 4 buttress roots) ± standard error.

[b]Significantly lower than other two averages for living roots ($P=0.05$).

Armillaria mellea colonization.--No evidence of colonization by A. mellea was found on roots of trees with zero to trace or heavy scale. The lack of colonization was not because the fungus was absent or scarce; most of their woody roots had moderate to high densities of rhizomorphs on their surfaces. Occasionally a rhizomorph was found on a nonwoody branch.

A. mellea occurred on roots of two of the five trees infected by N. coccinea var. faginata. On one tree a buttress root and all but one of the branch roots were colonized by the fungus. On the other tree, lateral branch roots on three of the four buttress roots were colonized by the fungus. These two trees had been extensively colonized by Nectria and had dead bark on greater than 50 percent of their circumferences from midcrown down to within 2 meters of the root-stem base. Conks of the decay fungi Phellinus ignarius (Fr.) Quel. and Fomes fomentarious (L. ex Fr.) Kickx. were growing on the bark. Fifty percent of the trees' crowns were dead.

The three trees whose roots were not colonized by A. mellea also had necrotic stem bark. However, the necrotic streaks extended only to midbole, were less than 50 percent of the circumference of the bole, and appeared to be more recent necrosis. No symptoms or signs of decay were visible.

Root starch.--Seven of the 10 trees infested with either trace or heavy scale had high starch content in the roots and three trees had moderate root starch. The level of scale infestation had no effect (Table 2). In contrast, one of the five trees infected by N. coccinea var. faginata had moderate starch; the others had less or were starch-depleted. The two trees with roots that were colonized by A. mellea had low starch.

Table 2.--Numbers of trees with various root starch levels in relation to scale infestation and Nectria infection.

Tree category	Starch level[a]			
	High	Moderate	Low	Depleted
Scale: zero to trace	3	2	0	0
Scale: heavy	4	1	0	0
Nectria-infected	0	1	2[b]	2

[a]Estimated by histochemical technique (Wargo 1975).

[b]Both trees had roots colonized by A. mellea.

Extensive root observations

In all areas A. mellea had colonized roots on 50 of 78 trees examined, 18 of the 23 trees that had died recently and 32 of the 55 trees that were dying (Table 3). However, the fungus had totally colonized the root system on only four trees, two dead and two dying (Table 3). On these four trees the whole crown appeared to have died at once. Freshly wilted foliage or remnants of necrotic leaves were present on all branches and there was no evidence of previous upper-crown dieback.

Not all trees that appeared to have died suddenly and totally were colonized by A. mellea. In New York there was one such tree in each area. In Pennsylvania there were nine trees that were not colonized by A. mellea (Table 3). These trees, which were heavily colonized by beech scale, had apparently leafed out in the spring and then

wilted. Bark necrosis occurred on the complete circumference of the trees down to within 0.5 meters of the root-stem base. No perithecia of N. coccinea var. faginata were visible on the bark of these trees but there were many tarry spots that indicated Nectria infection. The ratio of colonized to uncolonized trees in the Pennsylvania area was 0.6, much lower than the 3.1 and 5.0 for the two New York areas. This area in Pennsylvania had abnormally low precipitation that spring and summer (1981) and these trees were probably also stressed by drought.

Table 3.--Numbers of beech trees with crowns that died slowly over several seasons or rapidly within one season and with roots that were or were not colonized by Armillaria mellea.

Area	Crown death	Numbers of recently dead or dying beech trees: Colonized by A. mellea: dead	dying	total	Not colonized by A. mellea: dead	dying	total
Northeastern New York	slow	4	14	18	1	2	3
	rapid	2[a]	0	2	0	1	1
	Total	6	14	20	1	3	4
North-central New York	slow	10	7	17	0	5	5
	rapid	0	2[a]	2	0	1	1
	Total	10	9	19	0	6	6
Pennsylvania	slow	2	9	11	0	9	9
	rapid	0	0	0	4	5	9
	Total	2	9	11	4	14	18
All Areas	slow	16	30	46	1	16	17
	rapid	2	2	4	4	7	11
	Total	18	32	50	5	23	28

[a]Couplete root system colonized by A. mellea.

The crowns of most trees that were colonized by A. mellea appeared to have died progressively from the top down. Upper crown branches had no leaves, twigs, or small branches on them, the bark was sloughing off branches and portions of the main stem, and on some trees fruiting bodies of the decay fungi F. fomentarius and P. ignarius were present on the main stem. The lower crowns had either chlorotic living or recently dead foliage and buds on the branches. On these trees A. mellea was always confined to roots associated with the oldest bark necrosis that resulted from colonization of the stem bark by N. coccinea var. faginata.

On some trees where necrosis of the stem bark was recent (bark dead but hard, tight, and intact), A. mellea was not present on roots associated with the dead streak. On other trees with recent stem necrosis, the fungus was just beginning to colonize the roots associated with the dead streak. Patches of mycelial fans occurred in the inner bark or cambial zone. On other trees with recent stem necrosis, some roots associated with the dead streak were entirely colonized by A. mellea. On some trees A. mellea was decaying roots associated with the oldest stem necrosis (bark soft, not intact, wood decaying); it had colonized the cambial zone tissues of roots associated with more recent stem necrosis, and was just invading the cambial zone tissues of roots associated with the most recent stem necrosis. This pattern was typical of the trees that had died recently. The fungus appeared to colonize these new root tissues from both rhizomorphs on the newly affected roots and mycelium from the previously colonized tissues. A. mellea had not colonized roots that were not associated with necrotic stem bark. These patterns were similar in New York and Pennsylvania.

A. mellea had also colonized roots associated with dead sections of the stems on the trees that had dead portions in the upper crowns and apparently healthy lower crowns. However, on these trees callus tissue had developed along the edges of root tissues colonized by A. mellea and no additional tissues were invaded. Colonization of the stem bark by N. coccinea var. faginata had also stabilized. Scale populations were scarce to light. In three of the five trees both roots and stem were in the advanced stages of decay.

DISCUSSION

Armillaria mellea was not a very aggressive colonizer of beech trees that were infested by beech scale, C. fagisuga and infected by N. coccinea var. faginata in four stands in New York in the "killing front" and in two stands in Pennsylvania in the "advancing front". Although A. mellea had colonized roots of dead and dying trees that were infected by Nectria, on most trees the root fungus had colonized less than 50 percent of the buttress roots and was restricted to roots associated with stem necrosis caused by Nectria colonization. The fungus was not observed colonizing adjacent roots in advance of the circumferential margins of stem necrosis. Most trees died because they were first girdled above ground by N. coccinea var. faginata, killing the stem bark, not because A. mellea colonized and killed the roots.

The sequence and timing of stem necrosis caused by N. coccinea var. faginata and colonization of roots by A. mellea seems to be as follows: scale insects infest and N. coccinea var. faginata colonizes and kills stem bark (Fig. 1a); the area of bark necrosis (and therefore the portion of the root system affected) is determined by the scale population density and area of infestation (Perrin 1980); a portion of the root system is affected and the roots may be colonized by A. mellea (Fig. 1b); if no additional stem bark necrosis occurs, the tree compartmentalizes the necrotic areas and the affected tissues decay (Fig. 1c); if additional stem bark necrosis occurs (Fig. 1d), additional roots are affected and may be subsequently colonized by A. mellea (Fig. 1e). Stem and root necrosis could develop quite rapidly if scale infestation were heavy for extended periods and large areas of stem bark were infected by Nectria.

The limited colonization of the root systems by A. mellea in beech stands stressed by beech bark disease is in contrast to colonization of northern hardwoods and oaks stressed by defoliation where the fungus aggressively attacks whole root systems and kills trees (Houston and Kuntz 1964, Wargo and Houston 1974, Wargo 1977). Observations on the fine roots and starch content of the roots in this study suggest that this difference occurs because the beech scale itself has a minimal effect on root growth and the effects of Nectria's killing the stem bark are confined to those roots associated with that portion of the tree. Defoliation, however, has a general debilitating effect on the whole root system.

The combination of defoliation by insects such as the saddled prominent, Heterocampa guttivita, and beech bark disease could be disastrous. Beech trees infected by Nectria could be "preinoculated" with A. mellea and therefore predisposed to rapid colonization by the root fungus when defoliation occurs. In this situation A. mellea could cause significant rapid mortality. In studies of A. mellea on oak, mortality after heavy defoliation was higher in areas that had a history of defoliation (Wargo 1981a). Excavation of surviving trees that were defoliated revealed that A. mellea was established in the roots and these trees were predisposed to subsequent colonization by A. mellea when the next defoliation occurred (Wargo 1977).

The lack of aggressiveness by A. mellea could also be due to the strain of the root fungus. Several clones and biological species of A. mellea have been identified (Anderson and Ulrich 1978) and they may differ in their ability to infect trees (Shaw 1978). Isolates from northern hardwoods are different from isolates from oak in their ability to metabolize tannins and related phenols (Wargo 1980b, 1981b). Beech is related to oak and may be chemically similar and therefore less susceptible to isolates that evolved in predominantly birch-maple stands.

Houston (1974) reported that some trees affected by beech bark disease were colonized by A. mellea and these trees died rapidly. My study shows that the majority of trees affected by beech bark disease are colonized to some extent by A. mellea but only a few are colonized enough that the fungus can be considered a major factor in the trees' death. The fungus colonizes the roots of most trees after the stem tissues have died and begun deteriorating, late in the decline of the tree when the tree is already beyond salvage. Houston (1974 and personal communication) compared rapidly killed trees with living trees that had symptoms of beech bark disease and excavated only the root collar area. He may have looked at trees before their colonization by the root fungus or perhaps missed the fungus by not looking farther out on the roots.

A. mellea does not seem to accelerate mortality in stands affected by beech bark disease except in a few trees. Most trees attacked by N. coccinea var. faginata and by A. mellea do not appear to die faster than those attacked by Nectria alone. It seems that A. mellea will not contribute significantly to the management problem associated with rapid tree deterioration in stands where beech bark disease is occurring.

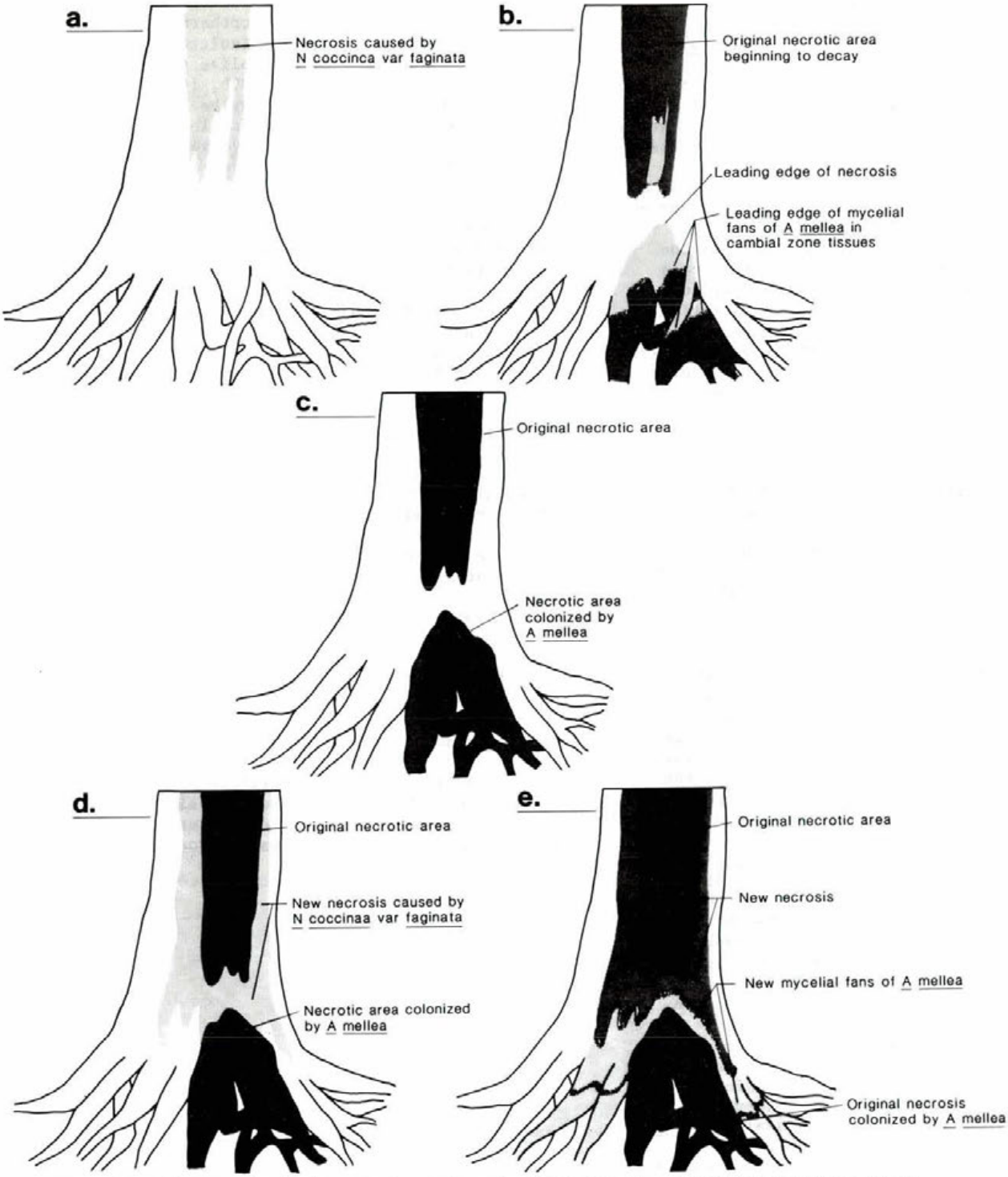


Figure 1.--Diagram of the lower stem and root-stem base of a beech tree illustrating the timing and pattern of stem colonization and subsequent necrosis caused by Nectria coccinea var. faginata and corresponding colonization of the roots by Armillaria mellea. *a*. Initial stem necrosis caused by N. coccinea var. faginata. *b*. Necrotic area of stem tissue beginning to decay; corresponding section of the root system colonized and killed by A. mellea. *c*. Necrotic area on stem in advanced stages of decay; necrotic area in roots completely colonized by A. mellea and beginning to decay. *d*. New stem necrosis caused by N. coccinea var. faginata adjacent to original necrosis. *e*. Invasion by A. mellea of roots corresponding to area of new stem necrosis.

SUMMARY

Excavation of beech trees in stands affected by beech bark disease in New York in the "killing front" and in Pennsylvania in the "advancing front" revealed that infestation by the scale had little effect on the root system. Only trees infected by Nectria coccinea var. faginata showed any effect on the root system. They had fewer 4th order nonwoody branch roots and less starch than trees only infested by the beech scale, Cryptococcus fagisuga. Trees infected by Nectria were also the only ones with roots that were colonized by Armillaria mellea. The fungus was found on the majority of trees and was consistently found on roots associated circumferentially with areas of stem bark necrosis caused by Nectria. Complete colonization of the root system by A. mellea on dying trees occurred infrequently and occurred on trees that appeared to have died during a single growing season. The majority of trees were partially colonized, or colonized in stages associated with episodes of stem bark necrosis and crown death. The crowns of these trees appeared to have died in stages over several growing seasons. The roots were colonized by A. mellea after stem bark necrosis. A. mellea did not seem to accelerate mortality in these stands affected by beech bark disease.

RÉSUMÉ

L'excavation de hêtres dans des peuplements situés dans la "zone d'avance meurtrière" de la maladie dans l'Etat de New-York et dans la "zone d'avance primaire" en Pennsylvanie, a révélé que l'infestation par la cochenille avait peu d'effet sur le système radiculaire. Seuls les arbres infectés par le *N. coccinea* var. *faginata* montraient quelques effets sur le système radiculaire. Ils avaient moins de radicelles du 4ème ordre de ramification et non lignifiés, et moins d'amidon que les arbres infestés seulement par la cochenille du hêtre, le *Cryptococcus fagisuga*. Les arbres infectés par le *Nectria* étaient les seuls possédant des racines colonisées par l'*Armillaria mellea*. Le champignon se retrouvait sur la majorité des arbres et était constamment présent sur les racines associées (circonférentiellement) avec des parties nécrosées de l'écorce du tronc causées par le *Nectria*. La colonisation complète du système radiculaire par *A. mellea* chez les arbres mourants était peu fréquente et survenait sur les arbres qui semblaient être morts à l'intérieur d'une saison de croissance seulement. La majorité des arbres étaient partiellement colonisés ou colonisés à différents stades selon les étapes de la nécrose de l'écorce du tronc et de la mortalité de la cime. Les cimes de ces arbres semblaient être mortes par étapes à l'intérieur de plusieurs saisons de croissance. La colonisation des racines par le *A. mellea* survenait après une nécrose de l'écorce du tronc. Le *A. mellea* n'a pas semblé accélérer la mortalité et de là la détérioration dans ces peuplements affectés par la maladie de l'écorce du hêtre.

ZUSAMMENFASSUNG

Ausgrabungen des Wurzelwerks von Buchen in Beständen, die von der Buchen-Rindennekrose befallen sind, ergaben, daß der Lausbefall sowohl im Bereich der "killing front" (New York) als auch im Bereich der "advancing front" (Pennsylvanien) nur geringe Auswirkungen auf das Wurzelsystem hat. Nur Bäume, die von Nectria coccinea var. faginata befallen waren, zeigten Wirkungen im Wurzelbereich. Sie wiesen weniger unverholzte Seitenwurzeln 4. Ordnung und einen geringeren Stärkegehalt auf als Buchen, die nur von Cryptococcus fagisuga befallen waren. Auch wiesen nur von Nectria befallene Bäume Wurzeln auf, die von Hallimasch besiedelt waren. Der Pilz war an den meisten Bäumen zu finden und zwar regelmäßig an den Wurzeln auf der Stammseite, wo auch Teile der Rinde von Nectria befallen waren. Eine völlige Besiedlung des Wurzelsystems absterbender Buchen kam nicht häufig vor und dann nur bei Bäumen, die offenbar innerhalb einer Vegetationsperiode abgestorben waren. Die meisten Bäume waren nur teilweise oder in Relation zu Rindennekrose und Absterben der Krone vom Hallimasch befallen. Die Kronen dieser Bäume schienen schrittweise, im Laufe mehrerer Vegetationsperioden, abgestorben zu sein. Die Besiedlung der Wurzeln durch A. mellea fand nach der Rindennekrose statt. Der Hallimasch scheint demnach das Absterben der Buchen und damit die Verschlechterung des Gesamtzustandes der von der Buchen-Rindennekrose betroffenen Bestände nicht zu beschleunigen.

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CHILOCORUS STIGMA (COLEOPTERA:COCCINELLIDAE) AND OTHER PREDATORS OF BEECH SCALE IN CENTRAL NEW YORK[1]

Mark Mayer[2] and Douglas C. Allen[3]

Abstract.--The twice-stabbed lady beetle Chilocorus stigma (Say), was studied in two infestations of beech scale, Cryptococcus fagisuga Lind., to elucidate predator biology and to determine the predator's effect on scale populations. C. stigma is univoltine in north-central regions of New York and its seasonal occurrence is well synchronized with that of C. fagisuga. The predator was most abundant in dense scale populations and exhibited a numerical response at high scale densities. The effectiveness of C. stigma was limited by the propensity of adults to disperse following eclosion, its apparent failure to feed on all life stages of the scale, mortality during the beetle's pupal stage and high rate of host reproduction. Four species of mites were also noted as predators of C. fagisuga.

INTRODUCTION

Beecn bark disease first appeared in North America during the 1890's when the beech scale, Cryptococcus fagisuga Lind., was introduced from Europe on a species of ornamental beech, Fagus sylvatica L. The disease results when C. fagisuga initially infests the stems of American beech, Fagus grandifolia Ehrh. and a fungus, Nectria coccinea var. faginata Lohman, Watson and Ayers then penetrates the bark through feeding wounds. Scale populations alone evidently have little impact on the health of the tree, but in conjunction with Nectria, moderate to heavy scale populations may kill trees within 3-5 years. Presently, extensive areas of dead beech pervade northern hardwood forests in the northeastern United States.

This disease has generated more concern in recent years because modern kiln drying methods have enhanced the value of beech, whose wood is used for flooring, plywood, dowels, shuttles, containers and furniture. Beech is also an important pulpwood species and makes excellent fuelwood. Spread of the disease south and west from its initial point of entry in Nova Scotia has encouraged research on the ecology (Houston 1975; Houston et al. 1979) and management of infested stands (Filip 1978). However, relatively little information about the twice-stabbed lady beetle, Chilocorus stigma (Say), a native coccinellid predator of the beech scale, is available, and other natural enemies of C. fagisuga have received only cursory attention.

C. stigma was first associated with populations of C. fagisuga by Ehrlich (1934) who noted the presence of C. stigma (identified as C. bivulnerus Muls.) in beech scale-infested sample plots in Nova Scotia. Ehrlich reviewed the European literature and reported several vague references to other insects and arachnids that were thought to be predators of beech scale. Brown (1934) suggested that C. stigma was the only predator in New England that had potential to control populations of beech scale.

The general biology of C. stigma was first investigated by Girault (1907), who determined that the beetle oviposited in bark cracks, crevices, and under loosened bark on scale-infested apple trees. Marlatt (1902) and DeBoo and Weidhaas (1976), on the other hand, reported that the beetle oviposited beneath scale secretions and predominantly fed

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on immature scales. Muma (1955) indicated that oviposition occurred on the leaves, trunk, fruit and twigs of Florida citrus trees. He found that adults and all four instars voraciously fed on adult scales. C. stigma has been recorded as a predator of 18 species of scales, 7 species of aphids, and one species of coccinellid (Thompson and Simmonds 1965).

DeBoo and Weidhaas (1976) examined C. stigma in central New York as a predator of pine needle scale, Phenacaspis pinifoliae (Fitch). The coccinellid colonized moderately and severely infested Scotch pine (Pinus sylvestris L.) in naturally regenerated stands, but was absent on sparsely infested trees. Lady beetles aggregated on trees that harbored the greatest number of scales, but only in stands that had a large number of infested trees. In areas with small isolated infestations, the beetles did not remain (or reproduce) on scale-infested trees and did not significantly reduce scale density. DeBoo and Weidhaas hypothesized that alternate prey on nearby plants prevented C. stigma from congregating on trees infested with pine needle scale. Monocultures (plantations) of Scotch pine resulted in high numbers of pine needle scale, which subsequently supported abundant natural enemies that eventually controlled this host.

The objectives of the present study were to (1) determine the biology of C. stigma, (2) to evaluate the effect of C. stigma on populations of C. fagisuga, and (3) to identify other predators of C. fagisuga.

MATERIALS AND METHODS

The study sites at Wanakena, New York (St. Lawrence County) and Tully, New York (Cortland County) consisted of mature beech, eastern hemlock, Tsuga canadensis (L.) Carr, sugar maple, Acer saccharum Marsh, red maple, Acer rubrum L., and yellow birch, Betula alleghaniensis Britton. To determine the response of C. stigma to different densities of C. fagisuga at Wanakena, as well as to facilitate observations, 12 beech trees 10-20 m tall that represented a range of C. fagisuga densities were selected for population measurements. The four most heavily infested trees were sampled weekly from June through October, 1979 (n = 17-19 obs./tree) and the remainder were examined biweekly (n = 8-9 obs./tree).

Sample trees were divided into 1 m vertical segments and each meter was subsectioned into 10 cm x 10 cm squares. This was accomplished by marking every 10 cm around the circumference of the tree at each meter height. Two strings, one meter long and subdivided into 10 cm units, were vertically attached to the 10 cm marks around the circumference of the tree. A ladder and tree trimmer's apparatus were used to climb each tree and sample 360° around the bole.

The number and position of Chilocorus were determined within each 10 cm sq. Populations of C. fagisuga in each sq were arbitrarily classified as light, medium, and heavy (DeBoo and Weidhaas 1976), based on five subsamples that were obtained by placing the mouth of a vial (2 cm dia.) on an ink pad and then pressing the ink-coated rim onto the tree. Counts were made of the number of adult scales within the circle. The sample unit was 3.14 sq. cm of bark, and an average of 1-10 scales, 11-25 scales and 25+ scales per sample were regarded as light, medium and heavy populations, respectively.

Adults and pupae of C. stigma were easy to recognize. The last three instars were distinguished by size; color was used to identify first instars. The dorsal midline of the thoracic and abdominal regions and much of the dorsum of the first abdominal segment of instars II-IV are light cream to white (Muma 1955). First instars are uniformly dark gray and approximately 1 mm long. Second instars are 2.5 to 3.5 mm long, the third instar is 4.0 to 5.0 mm long, and fourth instars are 6.0 mm or longer. Whenever identification of instars was questionable, setaceous dorsal and lateral processes, the senti (sic Gage 1920), were examined.

RESULTS AND DISCUSSION

Periodic examination of beech boles made it possible to (1) determine temporal changes in populations of C. stigma; (2) estimate population density by mapping the scale infestation; (3) examine the relationship between changes in the scale and predator populations and; (4) observe the effect of physical variables on the scale and beetle populations. Also, this approach enhanced the probability of finding other predators and/or parasites of C. fagisuga, because a large total area of tree bole was systematically examined throughout several 24 hr periods.

Effect of C. fagisuga density on populations of C. stigma

There was a significant positive correlation between the density of C. stigma and that of its prey. While the correlation ($r = 0.75$, $p = .05$) between scale density and predator density is encouraging from a natural control standpoint, it is important to examine

the within-tree distribution of the predator population at different host densities. In other words, predator abundance should be viewed in terms of the proportion of total bark surface area occupied by an infestation level (i.e., light, medium or heavy) (Fig. 1). Initially, as the proportion of bole area occupied by each infestation level increased, the proportion of predators found in that area also increased. However, the data indicate that beetles do not readily establish themselves on trees that are lightly infested. This may account, in part, for the fact that sparse scale colonies are capable of rapid numerical increases over a relatively short period. Apparently, the predator concentrates on trees, or portions of trees, where the host is easily found (i.e., dense populations). The decrease in predator density when 15% of the infested area contained a medium scale density, and the increase in predator density where 30% of the bark area was lightly infested (Fig. 1) probably are a result of sampling error. Also, there could be a limit to the number of predators that will occur on an infested area of bark at a given time. This limit may have little to do with the carrying capacity of the food base, but rather with Chilocorus itself. Predator density may be determined by other mechanisms, irrespective of the fact that more than enough prey are available.

The relationship between the density of C. stigma and total bark area occupied by C. fagisuga infestation categories (Figs. 2-5) further support the hypothesis that high beetle density is associated with high host density. The figures indicate that heavy infestations (H) were usually associated with

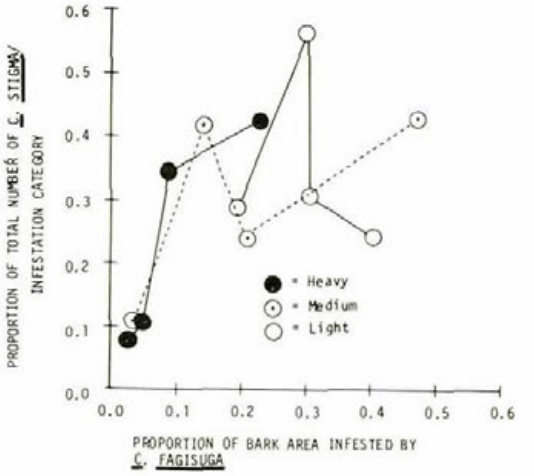


Fig. 1. Distribution of total C. stigma population in relation to proportion of scale-infested bark in 3 infestation categories (n = 4 trees).

a higher predator density than the medium infestations (M), which in turn supported more predators than did the light infestation (L). This relationship is typical of a predator with well developed searching behavior and host finding capabilities. C. stigma was able to locate prey colonies even when a small proportion of the bole was infested. The data indicate that the density and distribution of C. stigma on beech boles was influenced by the density and distribution of C. fagisuga. Even though a light infestation occupied a relatively large total bark area, the beetle density in that category was usually lower than that in the next highest infestation category.

Life history of C. stigma

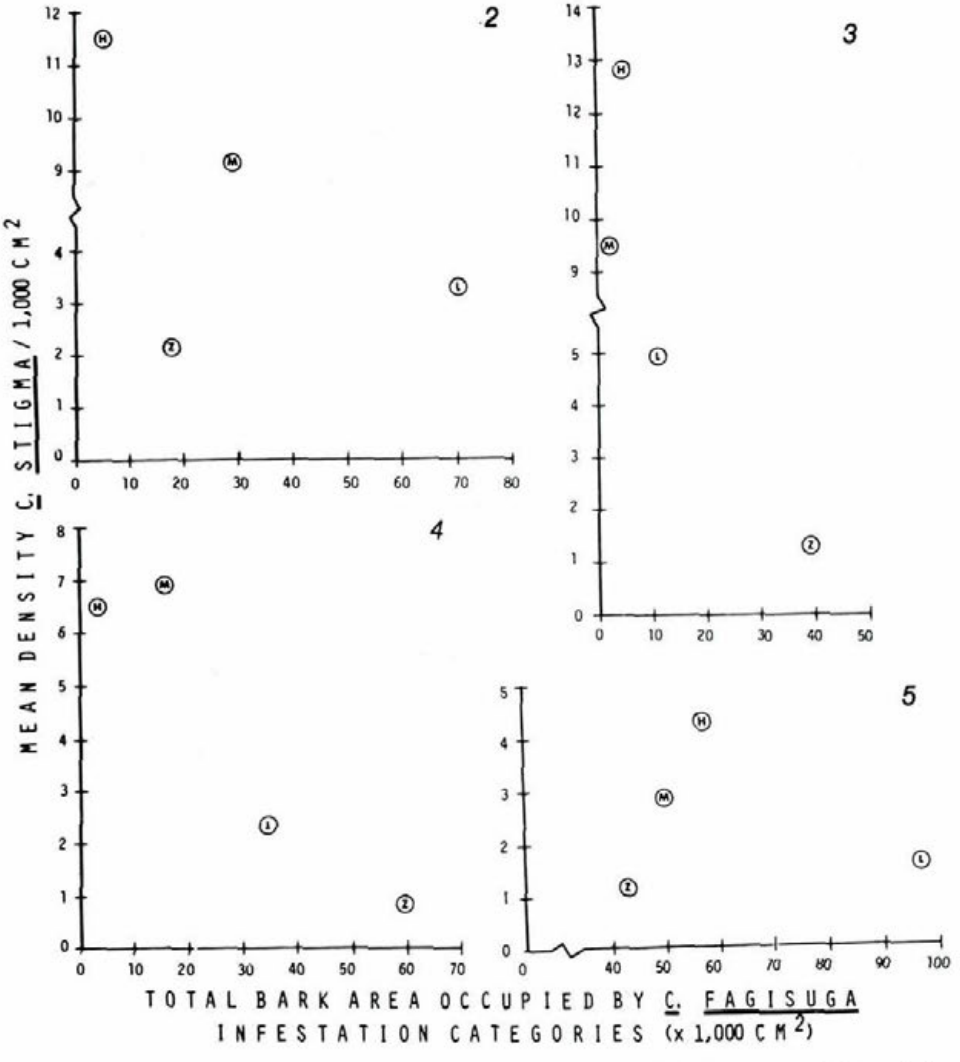
C. stigma overwintered as an adult in the duff. Adults at Tully, New York were first observed feeding on beech scale on a warm day (max. 13°C) in early March. For example, during one day of observation they remained on the lower bole until the temperature increased (max. 13-14°C) at which time they moved up the tree several meters. In late afternoon adults descended and eventually dropped into the duff. Adults often congregated on the lower boles of trees, and mated during mid-April and early May at Tully and Wanakena, respectively.

Oviposition by C. stigma was first observed at Tully in late April. The scale oviposited in bark fissures, some of which were caused by another scale, Xylococculus betulae Pergande. The last first instar was observed on 15 August (first instars were difficult to see because they were camouflaged on the gray beech boles) and second instars were observed four weeks later. The last second instar was noted on 13 October. Most third- and fourth-instars disappeared the first week in October, and larvae that did not pupate by October did not survive. Adults were most numerous on 20 June and 9 August. During this period only 8 of 21 median weekly temperatures were above 16.7 C. At median temperatures below this, C. stigma larvae require 12 weeks or longer to complete one generation (Muma 1955).

Evidence for one generation a year was strengthened by the temporal distribution of C. stigma life stages in the more northerly Wanakena (Fig. 6), indicating only one peak abundance for each stage. If there were two generations a year at Wanakena, there should be two peaks. Admittedly, the data do not cover early spring, but pupae would have been present prior to July if there were two generations a year. DeBoo and Weidhaas (1976), who also worked in central New York,

recorded two distinct populations for all life stages. The first generation occurred from late July through August. No pupae were observed at Wanakena until July and large numbers of them did not appear until August. Climatological records from Oswego, NY, the weather station closest to where DeBoo and Weidhaas did their study, indicated that 16 of 24 median weekly temperatures approximated 16.7°C. This lends further support to the hypothesis that their population of C. stigma was bivoltine.

Interestingly, the hosts in Muma's study, Florida red scale, Chrysomphalus aonidum (L.) (=ficus Ashmead), and purple scale, Lepidosaphes beckii (Newman) have three generations a year, as did the local population of C. stigma. On the other hand, in New York, P. pinifoliae and C. stigma each had two generations a year (DeBoo and Weidhaas 1976). Hemlock scale, Fiorinia externa (Ferris), in Connecticut is univoltine, as is the local population of C. stigma (McClure 1979). This association between the voltinism of predator and prey is most likely related to temperature, rather than to the number of prey generations. However, it is highly probable that C. stigma is able to synchronize its development with that of the most suitable (=abundant) host. Coccinellids display close synchrony with their prey, especially on sedentary hosts (Hagen 1962). The coccinellids reproduce when populations of their prey are increasing and hibernate when the prey is dormant.



Figs. 2-5. Mean density of C. stigma in relation to total bark area infested by C. fagisuga. Each Fig. represents a single tree (H = >25 scales; M = 11-25 scales and L = 1-10 scales/sample unit.

Biology and behavior of C. stigma

Adult Chilocorus (Fig. 7C) moved from tree to tree in search of prey which apparently were located tactilely or visually. Some coccinellids locate their prey by means of prey odor (Hodek 1967), but this has never been established for the Chilocorini; other species apparently rely on visual cues (Allen et al. 1970; Stubbs 1980). Approximately half of the beetles' time was spent apparently resting (and possibly digesting prey) and the remaining time was spent searching for prey and feeding. Adults rested for a few minutes to hours, probably in response to temperature and hunger level. As long as the maxillary palpi remained in contact with the prey, the beetles fed until the prey was consumed or the beetle was sated. Hourly observations of marked beetles for a 24 hr. period indicated that adults were dirunal and relatively quiescent at night.

First instars searched for food soon after eclosion. Searching appeared random and feeding occurred only when the prey were contacted with the maxillary palpi. Thereafter, the larvae slowed down and conducted a more thorough search of the surrounding area by moving in a circular pattern and frequently changing direction. The small size of first instars allowed them to search bark fissures that were inaccessible to later instars. Beech scales within the fissures were utilized with little competition from later instars. Larvae in bark openings

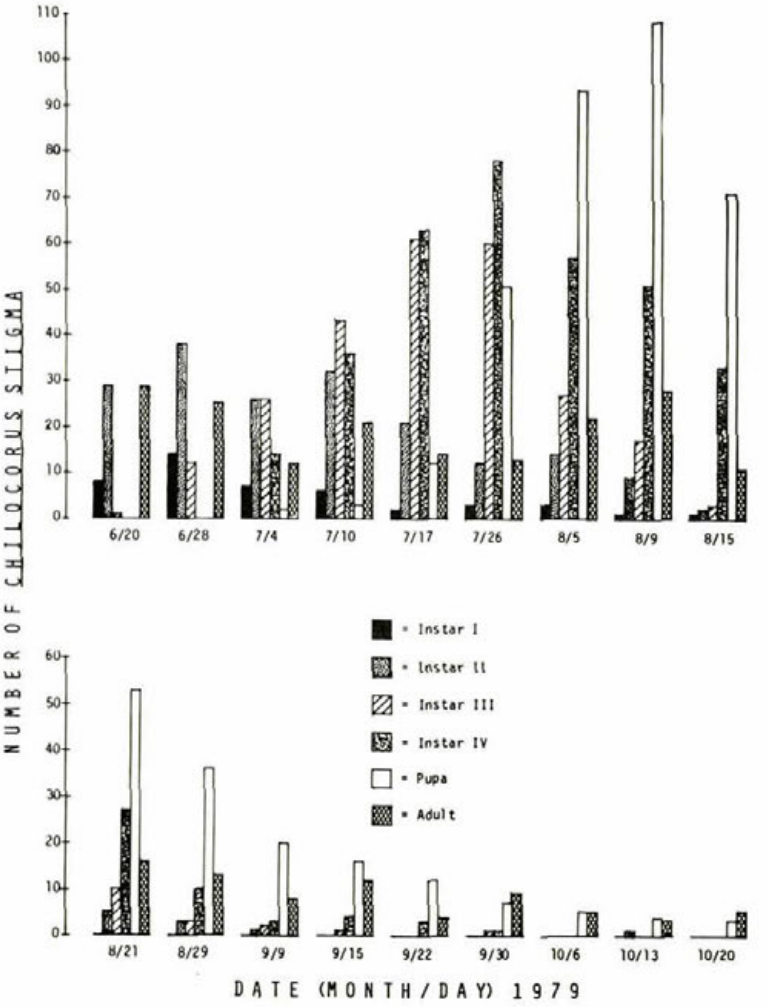


Fig. 6. Temporal distribution of C. stigma life stages, Wanakena, New York.

were difficult to detect and are probably better protected from the weather and predators than are older larvae. Larvae spent more time moving and feeding than the adults and rested 10-25% of the time. It took longer for a first instar to consume prey than it did other instars, because prey size was large relative to the predator. The first instars fed by working their way through the waxy secretion of the scale. When contacted, a scale was pierced by the predator's mandibles and the scale's body fluids were withdrawn. Once first instars located an area with abundant prey, they rarely left.

Second instars behaved much like first instars except the former were more mobile when not feeding.

Because of their larger size, third instars covered more area as they searched for prey. During this stage, prey seeking was more involved: larvae moved 10-20 cm over the tree bole in a limited zigzag pattern. If no prey were encountered within this distance the larvae turned around and sometimes retraced their original trail. Why larvae stopped going in one direction and proceeded in another is not known. They did this on all bark types, oftentimes walking over scale colonies in the process. Feeding did not commence until the maxillary palpi contacted a scale, at which time larvae masticated prey with the mandibles and did not use their mouthparts in a piercing-sucking manner. The eggs of C. fagisuga were occasionally eaten. Sometimes only part of a scale was consumed before another one was attacked. The larvae were not observed feeding on the scale crawlers and seemed to prefer more sedentary hosts.

Behavior of fourth instars (Fig. 7A) conformed to that of the third except the former were more mobile and searched a larger area. As fourth instars approached pupation, their zigzag search pattern became disorganized. Once an appropriate spot was found the larvae became quiescent for one to three days before pupation.

The gregarious pupae of C. stigma (Fig. 7B) were found on the main bole, under branches, and in other sheltered areas. The reason why larvae selected particular areas for pupation was not revealed until trees were climbed during a rainstorm. Pupae beneath tree limbs and other protected areas on the main bole were not exposed to stem flow. Rain, especially a heavy downpour, is usually intercepted by the tree crown and then flows down the main branches; thence down the bole. In almost all cases, pupae were found in island-like refugia that were protected from runoff.

Population fluctuations and prey consumption

Although larval populations were not readily estimated, abundance of sedentary pupae was easily determined. The number of new pupae and the dead or missing pupae on four sample trees were tallied weekly. The greatest number of new pupae were found on 5 August, 9 August and 15 August (Fig. 6). Pupal mortality (number dead or missing pupae ÷ total number of pupae) ranged from 18% to 29%. The average for the combined samples is 24.1%. Cause of mortality was attributed to two factors: (1) the nymph of a predaceous bug, Podisus sp. and (2) the fact that some pupae, even though sheltered, were still exposed to the elements and enough pressure may have been placed on the sucking disc to detach the insect.

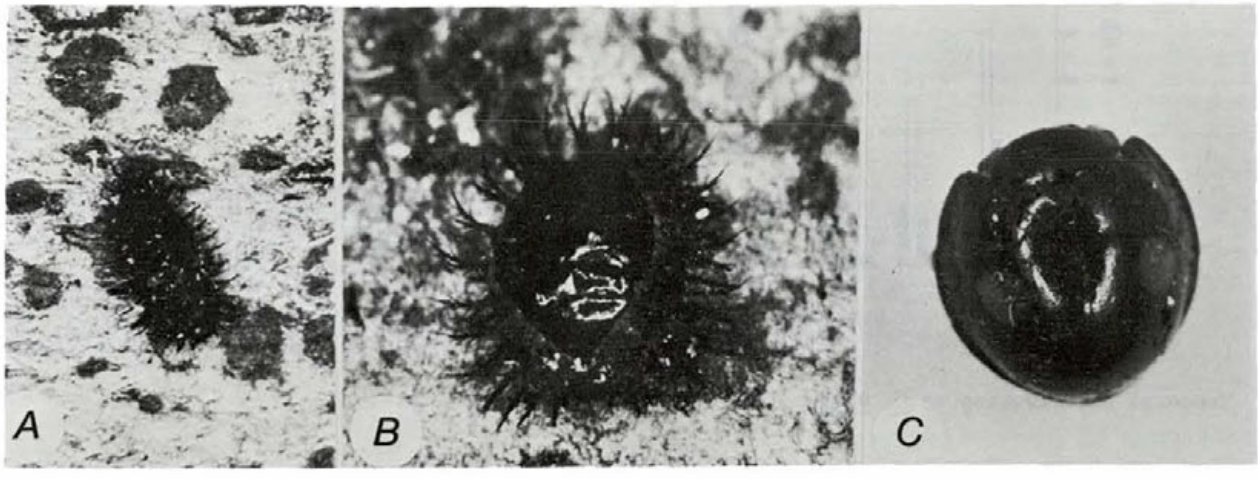


Fig. 7. Life stages of C. stigma: A, fourth instar; B, pupa; C, adult.

Feeding studies were undertaken with C. stigma to determine how many C. fagisuga each life stage of the predator consumed per day and over a period of 72 hr (Table 1). The feeding capacity of each stage was significantly ($p = .05$) greater than that of the preceeding stage, except for adults, which consumed the same number of prey as fourth instars. All stages, except adults, consumed less on the first day than they did on succeeding days. Possibly the larvae required an adjustment period before they settled down to feed, and adults probably located the host more quickly than did larvae.

Table 1.--Beech scale consumption by Chilocorus stigma.

Life Stage	N	Average No. Prey Eaten (± SD) 0-24 hrs	24-72 hrs
Instar I	13	6.5 ± 4.8	21.3 ± 10.4
Instar II	19	13.9 ± 5.9	33.9 ± 7.5
Instar III	20	23.8 ± 8.8	52.6 ± 21.7
Instar IV	19	30.4 ± 16.1	64.2 ± 18.3
Adult	20	30.8 ± 16.0	54.7 ± 17.3

Adults tended to disperse after eclosion and this behavior may prevent a buildup of C. stigma in areas where there are few prey. DeBoo and Weidhaas (1976) observed natural control by C. stigma in populations of pine needle scale in a monoculture of Scotch pine. When C. stigma dispersed under these conditions, the probability of finding alternative prey was low. Therefore, the beetle had a significant impact on scale populations in the monoculture due to lack of alternative prey and low dispersal losses. The northern hardwood forest is a relatively diverse community, however, and it probably offers a variety of prey, which may dilute the influence of C. stigma on beech scale populations. Even though C. stigma exhibited good host-predator synchronization and displayed an apparent numerical response to high prey density, the hosts' parthenogenetic mode of reproduction, apparent failure of the predator to feed on all host life stages, the tendency for adult C. stigma to disperse after eclosion and mortality during the pupal stage suggest that (1) this predator is an opportunist and (2) it has little potential for controlling populations of C. fagisuga.

Another coccinellid, Calvia (=Anisocalvia) quatuordecimguttata var. similis Randall, purportedly feeds on C. fagisuga in New York and Pennsylvania, but we did not observe it on our study trees. C. stigma and C. quatuordecimguttata closely resemble each other; both are black with a red spot on each elytra. The spots on C. stigma, however, are round and smaller than the squarish spots characteristic of C. quatourdecimguttata.

Acarine predators

Mites were the only other organisms that were observed feeding on beech scale. The most frequently encountered mite, Anystis sp. nr. kochi Oudemans (Fig. 8A) was very mobile and preyed on all stages of the scale, especially eggs and crawlers. Baker (1965) characterized Anystis spp. as general predators with non-specific prey preference, and he observed a species of Anystis preying upon another mite, Tydeus; we observed the latter preying on C. fagisuga eggs. Several Anystis molting chambers, craters in the bark covered with white papery silk, were examined and usually one large Anystis was found with several smaller protonymphs. Anystis appeared in late June and was present until the end of August. The silken chambers, which can be easily mistaken for beech scales, were first observed in early July. This species may be bivoltine because the mites were not noticed until June, and this would allow time for an earlier generation.

A second acarine predator, Tydeus sp., was difficult to observe because it was usually colorless, except after it fed when the gut turned gray. Tydeids were first observed on a section of infested bark that was placed under a dissecting microscope to look for scale parasites. Several tydeids were observed feeding on the eggs of C. fagisuga, but not on crawlers or adults.

Two erythraeid mites were encountered, Abrolophus sp. (Fig. 8B) and Leptus sp. (Fig. 8C). A few instances of scale predation were noted when attempts were made to study what were thought to be anystids, but were Abrolophus sp. instead. Erythraeids are predators in the adult, trito-, deuto- and protonymphal stages, and feed on a wide variety of prey. However, their larval stages are ectoparasitic. The larva of Leptus sp. was noted as an ectoparasite on Anystis sp. Of 37 anystids collected, 9 were parasitized by Leptus. No adult Leptus or nymphal Abrolophus were encountered.

One bdellid mite (Fig. 8D) was observed preying on C. fagisuga crawlers, but it could not be identified to genus because the palps were accidentally removed during mounting.

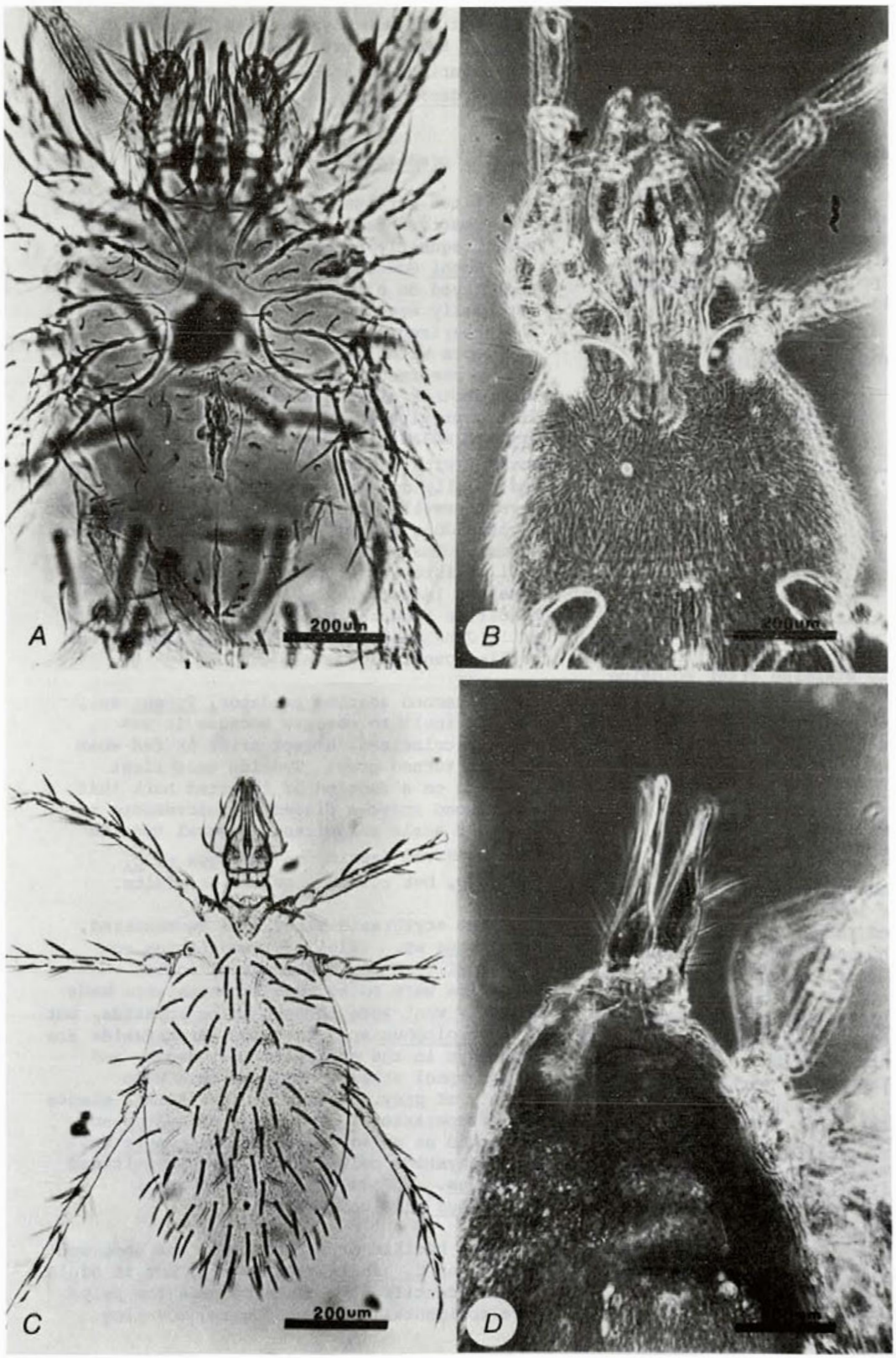


Fig. 8. Mite predators of C. fagisuga: A, Anystis sp.; B, Abrolophus sp.; C, Leptus sp.; D, a bdellid.

CONCLUSIONS

The occurrence of extensive beech mortality and flourishing populations of beech scale in North America are cogent evidence of the fact that indigenous natural enemies are not able to control this exotic pest. C. stigma was the most abundant, and usually the only, insect predator of beech scale that we observed in two forest stands in central New York. Parasitic and predaceous mites were frequently associated with immature scales, but apparently are not able to hold scale populations below damaging levels.

ACKNOWLEDGEMENTS

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RÉSUMÉ

La coccinelle stigma, Chilocorus stigma (Say), fut étudiée durant deux infestations de la cochenille du hêtre, Cryptococcus fagisuga Lind., pour en élucider sa biologie et déterminer son effet sur les populations de la cochenille. Dans la région centre-nord de New York, le C. stigma est univoltin et sa présence saisonnière est bien synchronisée avec celle du C. fagisuga. Le prédateur était le plus abondant dans les populations élevées de cochenilles et montrait une corrélation numérique positive aux hautes densités de celles-ci. L'efficacité du C. stigma était limitée par la progression des adultes à se disperser après l'éclosion, son attitude apparente à ne pas se nourrir de tous les stades de la cochenille, la mortalité observée durant le stade nymphal de la coccinelle et le taux élevé de reproduction de l'hôte. Quatre espèces d'acariens furent aussi notées comme prédateurs du C. fagisuga.

ZUSAMMENFASSUNG

Marienkäfer (Chilocorus stigma (Say.)) wurden in zwei Vorkommen der Buchenwollschildlaus (Cryptococcus fagisuga Lind.) hinsichtlich ihres Beuteverhaltens und der Auswirkung auf die Lauspopulationen untersucht. Chilocorus stigma bildet in den nördlichen Teilen Zentral-New Yorks eine Generation im Jahr. Sein jahreszeitliches Auftreten ist gut auf C. fagisuga abgestimmt. Die Marienkäfer treten in dichten Lauspopulationen - als zahlenmäßige Reaktion auf hohe Lausdichten - am zahlreichsten auf. Die Wirksamkeit von C. stigma gegenüber C. fagisuga ist begrenzt, da die Tiere offenbar nicht alle Entwicklungsstadien der Laus fressen, wegen der Mortalität der Käfer im Puppenstadium und wegen der hohen Reproduktionsrate der Läuse. Fünf verschiedene Milbenarten wurden ebenfalls als Fraßfeinde von C. fagisuga festgestellt.

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FUNGAL ASSOCIATIONS IN THE BUILD-UP AND DECLINE OF *CRYPTOCOCCUS FAGISUGA* POPULATIONS[1]

David Lonsdale[2]

Abstract.--The fungal flora of *Cryptococcus fagisuga* colonies on *Fagus sylvatica* bark included the entomogenous species *Verticillium lecanii* wherever infestation was or had been very heavy. This fungus seemed to accelerate insect mortality *in vitro*. *Cladosporium cladosporioides* was present at all stages of insect colony development and, with other fungi, caused blackening of the wax secretion.

INTRODUCTION

The great economic importance of many species of scale insect has long made them a major object of man's efforts in biological control. Their colonial, sessile habit and predictable occurrence in space and time favours the use of predators and parasites. As the primary agent in the beech bark disease complex (Ehrlich 1934, Parker 1974) *Cryptococcus fagisuga* Lind. seems a worthwhile target for biocontrol, and yet it has been studied very little to this end.

Several predators of *C. fagisuga* are known. These include the coccinellids *Exochomus* and *Chilocorus* spp., the cecidomyid fly *Lestodiplosis* sp. and various chrysopids and hemerobiids, but their importance in regulating populations of the insect is thought to be limited (D. Wainhouse pers. comm.). No insect parasites of *C. fagisuga* are known.

As far as microbial control agents are concerned, only one fungus has been reported to exert some influence over *C. fagisuga*. This is *Ascodichaena rugosa* which forms a tough, black stroma at the bark surface, thus deterring the insertion of the insect's stylets (Houston 1976; Houston, Parker and Lonsdale 1979). No association between *C. fagisuga* and any entomogenous fungus has been reported, although it seems clear that a microflora is associated with the insect colonies, as evidenced by the commonly observed blackening of the white wax secretion. This blackening has been recognised as an indication that the colonies contain many dead insects and are probably declining. It appears that blackening is also related to the degree of wetting from rain, in relation both to water runnels on stems and to varying weather conditions.

The microflora of infested bark merits study not only for the possible detection of entomogenous fungi but also for elucidating the pre-infection ecology of bark-invading species of *Nectria*. It is of particular interest that *C. fagisuga* is consistently associated with *Nectria coccinea* Fries. or with *N. coccinea* var. *faginata* Lohman, Watson & Ayers in the beech bark disease complex. Some *Nectria* spp. are known as parasites of scale insects (Petch 1921) and although this does not necessarily imply that the relationship between *C. fagisuga* and *N. coccinea* involves parasitism, it does seem likely that *N. coccinea* is ecologically favoured within the microflora of *Cryptococcus*-infested beech bark (Lonsdale and Sherriff, these Proc.).

The objectives of the present work were to investigate the fungal flora associated with different phases in the growth and decline of *C. fagisuga* populations and to examine the possibility that the insect is susceptible to attack by entomogenous fungi.

EXPERIMENTAL

Detection of fungi associated with *C. fagisuga*

Throughout this work several types of *C. fagisuga* colony development were defined so as to represent different phases of build-up and decline. In defining these types, the colonies were classified by size and by the extent to

1 Paper presented at the IUFRO Beech Bark Disease Working Party Conference, Hamden, CT. USA, 27 Sep to 7 Oct 1982.

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which dead insect bodies and blackened wax had accumulated. In this way, colonies are described as small or large and new or old. Where appropriate, a score class for the overall insect density on the stems was used in combination with the classification of colony type.

Preliminary observations indicated that the most frequently occurring fungi on *C. fagisuga*-infested bark were present at all forest sites studied, and that all heavily infested trees carried populations of these fungi. Three fungi commonly isolated were *Verticillium lecanii* Viegas which is an entomogenous species (Petch 1948), a synnematous *Acremonium* (the imperfect stage of *Nectria viridescens* Booth) and *Cladosporium cladosporioides* (Fres.) de Vries which seemed primarily responsible for blackening of the wax secretion.

On the basis of these observations, a series of platings of individual live second instars was set up on 0.01% YEA. These insects were obtained from trees at Alice Holt Forest, Hampshire and were removed by dissection of colonies *in situ*. Five different types of insect infestation were recognised in this survey as shown in Table 1, which includes all fungi which were isolated from 10% or more of insects in at least one of the infestation types. These data show that *V. lecanii* was abundantly present on insects where the infestation either was or had been in the form of extensive cover on the bark. *Nectria viridescens* and *C. cladosporioides* were present on insects from all infestation types. *Fusarium lateritium* Nees. seemed to be associated with old, declined infestations, while *Mucor* sp. was largely confined to small, recently established colonies. The fungi which occurred on fewer than 10% of the insects in

Table 1.--Fungi frequently isolated from live *C. fagisuga* adults and larvae plated on 0.01% YEA[b] (see text for other species)

Fungus	Percentage of insects yielding each fungus				
	A[a] (discrete)	B (discrete)	C (residual)	D (whitewashed)	E (residual) ('BBD tree')
Verticillium lecanii	0	0	56	69	74
Nectria viridescens	31	21	8	3	14
Cladosporium spp.[c]	25	36	16	3	6
Fusarium lateritium	0	0	16	0	9
Mucor sp.	38	0	4	0	0
Penicillium sp.	6	0	4	19	3

a: fuller descriptions of infestation types are: A, small isolated (≤2mm mean diameter), well separated colonies with little or no black wax; B, large (>5mm mean diameter), well separated colonies; C, low current infestation on trees with previously heavy infestation; D, stem continuously colonised over large areas; E, infestation pattern as for 'C' but bark with inactive, callused *Nectria* lesions.

b: yeast extract agar.

c: almost entirely *C. cladosporioides*.

any infestation type included the following hyphomycetes: *Trichoderma viride*, *Trichothecium* sp., *Fusarium avenaceum*, *Ramichloridium subulatum*, *Alternaria alternata*, *Stemphylium botryosum*, *Catinula* sp., *Diplodina* sp., *Pyrenochaeta* sp. (an un-named species), *Epicoccum* sp. *Monilia* sp. *Stachylidium* sp. *Dactyella* sp. and at least three non-sporulating fungi. Yeasts, especially *Aureobasidium* sp., were frequently present on insects from all colony types other than 'whitewashed', and bacteria were present throughout the samples. *Nectria coccinea* was not detected on individual insects, but was isolated from mass platings of insects together with their wax.

Of the fungi detected, *V. lecanii* was the only species known to include entomogenous strains, and a further study was carried out to gain further information on the extent to which this fungus was dependent on insect density. This study involved the counting of insect colonies from which *V. lecanii* grew during the incubation of 25mm discs of *C. fagisuga*-infested bark. The fungus was readily detectable after three or four days' incubation under humid conditions at room temperature. Only *V. lecanii* was scored in this way, although some of the fungi named above were also observed by this method, together with several *Acremonium* spp. and a *Sporothrix* sp. The discs were taken from trees with different overall infestation densities at Queen Elizabeth and Marden Forests in Hampshire and West Sussex respectively. The data, which are shown in Table 2, are based on infestation classes (scores 0 to 5) of the type used by Houston, Parker and Lonsdale (1979), classes 0 and 1 being excluded from the present study. Within each of these classes variation occurred in the apparent age of the colonies, and a classification of old and new infestation was used. 'Old' infestations were recognised by the presence of substantial blackening and erosion of the wax.

These bark disc incubations provided confirmation that *V. lecanii* was dependent on insect density and they also showed an effect of age of infestation. On new infestations, only class 5 yielded a substantial score for *V. lecanii*. However, in older infestations

Table 2.--Outgrowth of *V. lecanii* from incubated bark discs in July 1982

Infestation class		Mean percentage of individual wax masses yielding *V. lecanii*			
		2(light)	3(moderate)	4(heavy)	5(very heavy)
Colony type					
'New'	small[a] colonies	6	1	2	50
infestation	large[b] colonies	Abs.	0	0	100
'Old'	small[a] colonies	0	40	16	76
infestation	large[b] colonies	Abs.	29	73	94

a <3mm mean diameter b ⩾3mm mean diameter.

Abs. indicates large colonies absent in class 2 infestation.

For clarity, the above data are pooled for the two forest sites and expressed as percentages. Due to heterogeneity between sites, statistical significance, based on χ^2 tests of the actual counts was estimated separately for each site and for old and new infestation with the omission of poorly replicated classes. The effect of infestation class was highly significant ($p < 0.01$ to $p < 0.001$) except for small colonies on new infestations at Marden Forest ($0.10 < p > 0.05$).

the fungus was substantially present on colonies with a score class of three to four. This occurred whether or not most of the old colony material had been washed away by rain.



Plate 1.-- Conidiophores of *V. lecanii* growing from *C. fagisuga* colonies (x 100)

Fungal inoculations of *C. fagisuga in vitro*

In all the inoculation studies, individual live first instars were placed on sterilised filter paper in humidity chambers (95% R.H.) at 20°C. The inocula were applied as spore suspensions of equal concentration for each fungus, these being pipetted on to each insect (or in one trial, applied to the filter paper). The fungi were divided into two groups: species found on *Cryptococcus*-infested beech bark, and species of known entomogenous character which had been isolated in separate studies from beech wood but not from bark.

A satisfactory *in vitro* culture technique for the insects was not available and, for this reason, substantial mortality occurred in distilled water controls. The effects of the inoculations were assessed by comparison with these controls. After seven days' incubation, an excess of mortality compared with the controls seemed to occur with some of the inoculations, especially those involving *V. lecanii* isolates NDl and CFl (Table 3), but the differences were not significant. The natural fungal inocula carried by the insects included *V. lecanii* and *N. viridescens*, a factor which would have reduced any effect of artificial inoculation with these species.

In view of the difficulties in assessing the effects of inoculations on mortality, assessments for the beech wood fungi were carried out simply by scoring the production of external growth of the fungi on the insect bodies after death (Table 4). These date show that *Paecilomyces farinosus* was by far the most effective colonist of the insects.

Table 3.--Inoculations of *C. fagisuga* with bark fungi

Inoculant fungus	Insect mortality (excess % over control) 4 days	7 days	% isolation of fungus on 0.1% YEA Inoculated	Uninoculated
V. lecanii F3	0	+ 3	93	19
V. lecanii NDl	0	+17	70	19
V. lecanii CFl	0	+17	97	19
C. cladosporioides CFW	-6	-14	67	0
Nectria coccinea ACR	+4	+ 7	23	0
N. coccinea v. *faginata* 33A	0	+10	7	0
N. viridescens	-2	- 7	17	20
N. ditissima	NT	NT	0	0

NT signifies not tested. χ^2 tests, carried out on the counts of insects observed dead and alive, showed no significant effects of fungal inoculations at the 5% level.

Table 4.--Inoculation of C. fagisuga with potential entomogenous fungi obtained from beech wood

Inoculant fungus	% of insects giving rise to external growth of test fungi after death Inoculated	Uninoculated	No. in sample
Paecilomyces farinosus	80	0	20
Beauveria bassiana	0	0	20
Nodulisporium sp.	17	0	35
Isaria umbrina	0	0	22

Observations of individual insects inoculated with *N. coccinea* suggested that it failed to colonise them in the presence of a natural inoculum of *V. lecanii*. In view of the apparent mycoparasitic ability of *V. lecanii* (Lonsdale and Sherriff, these Proc.), a series of mixed inoculations was set up, with three different ratios of conidial concentration of the two fungi. The results showed a very high incidence (80%) of natural infection with *V. lecanii*, and this prevented a quantitative assessment of any competition between the fungi. However, it was found that *N. coccinea* was recoverable from insects inoculated with both fungi, even at a *Verticillium:Nectria* ratio of 3:1.

DISCUSSION

The main finding in the present work was that *Cryptococcus fagisuga* colonies carry a microflora which includes at least one fungus of an entomogenous type: *Verticillium lecanii*. This fungus showed a dependence on high insect density, or more precisely on the presence of substantial coalescence between insect colonies. Its absence in small isolated colonies of apparently recent establishment and its presence in older colonies of only moderate density, suggests a possible sequence of events in its colonisation. This sequence may begin with the spread of the fungus through the colonies when they reach an advanced stage of coalescence. Later, as the infestation declines, the fungus may persist, even though the population of the insect has perhaps become quite low. Such a relationship would be consistent with the apparent absence of aerially dispersed spores in this fungus and with its tendency to produce long conidiophores which trail over the insect colonies. Initial infection of young colonies could be effected through vector activity by micro-arthropods, a process observed during the present work.

It is not clear to what extent if any the decline of the insect population is due to infection by *V. lecanii*, and this uncertainty stems partly from difficulties of obtaining reliable results from inoculation experiments with *C. fagisuga*. However, the frequently recorded role of the fungus as a weak parasite of insects together with observations of rapid death of *C. fagisuga* crawlers in contact with heavy inocula, suggest that further studies are worthwhile.

None of the other fungi observed on *C. fagisuga* is of known insect-parasitic ability, but they are clearly of considerable interest in the ecology of *N. coccinea* (Lonsdale and Sherriff, these Proc.). It is interesting that *N. viridescens*, a frequently occurring member of the insect colony microflora, has a synnematous imperfect stage, since this sporing habit is common to many entomogenous fungi. Preliminary observations suggest that this and some other fungi may develop on dead insect bodies subsequent to the outgrowth of *V. lecanii*. It was not evident that *N. coccinea* develops in this way; indeed the apparent absence of this fungus on individual insects seems to confirm the findings of Stone (1967) who attempted to isolate *N. coccinea* var. *faginata* from *C. fagisuga*.

The dominance of *Cladosporium cladosporioides* on old insect colonies exemplifies the well known relationship between dematiaceous hyphomycetes and scale insects and aphids, although in most such cases the fungi are thought to utilise honeydew, an excretion which seems not to be produced by *C. fagisuga*. There is no reason to suppose that *C. cladosporioides* can parasitise the insect, but by dominating the microflora it could perhaps influence the development of entomogenous species. This may operate through competition for nutrients or through a reduction in the water-repellent properties of the wax secretion.

It remains unclear as to whether biocontrol of the insect is feasible. If it can be reliably shown that *V. lecanii* is capable of causing substantial mortality, it may be possible to introduce it at an earlier stage of insect build-up than seems naturally to occur. The fungus has been successfully used against aphids such as *Macrosiphonella sanborni* (Hall 1975) and scale insects such as *Coccus hesperidum* (Samšiňáková and Kálalová 1975). The apparent dual role of *V. lecanii* as a control agent for insect pests and fungal pathogens is an interesting possibility, first suggested by Hall (1980).

Manipulation of the bark surface environment may encourage development of *V. lecanii* from natural inocula; in particular the application of wetting agents to infested bark is a possible treatment suggested by the microbial overgrowth and decline of insect colonies in naturally wet conditions (D. Lonsdale unpublished data). The use of other fungi such as *Paecilomyces farinosus*, which readily colonised *C. fagisuga* bodies in the present work, also deserves further attention.

It remains unclear whether the microflora associated with *C. fagisuga* exerts an important control on populations of the insect. It seems likely, however, that the composition of the microflora may be an indicator of the state of insect build-up and decline on individual trees and within entire stands.

ACKNOWLEDGEMENTS

The author thanks Christine Sherriff for technical assistance, Dr P.C. Mercer for supplying fungal cultures and the Commonwealth Mycological Institute for help in the identifications of fungi. Drs D. Wainhouse and J.N.Gibbs are also thanked for helpful discussions. Awards from the Stanley Smith Horticultural Trust and the Thomas Phillips Price Trust are gratefully acknowledged.

RÉSUMÉ

La flore fongique associée aux colonies de C. fagisuga a été étudiée par mises en cultures et par observations directes. Les champignons Dématiacées, surtout Cladosporium cladosporioides, étaient présents à tous moments de la gradation de l'insecte et étaient responsables du noircissement de la sécrétion de cire des insectes.

Lorsque les colonies étaient devenues très grandes ou coalescentes, un champignon entomophyte connu, Verticillium lecanii, était généralement présent. Il était également présent dans les populations en déclin, même quand la densité des insectes était beaucoup réduite. Par contre, une espèce de Mucor était principalement limitée à de petites colonies isolées, tandis que le Nectria viridescens était présent pendant toutes les phases de développement des colonies. Le Fusarium lateritium était principalement associé aux populations en post-déclin.

L'inoculation in vitro de C. fagisuga avec plusieurs champignons a démontré que les corps des insectes sont facilement envahis par V. lecanii, N. viridescens, N. coccinea, C. cladosporioides et Paecilomyces farinosus. Il n'a pas été possible de déterminer de manière fiable l'effet des inoculations sur la mortalité des insectes, mais une augmentation non significative de la mortalité a été associée à V. lecanii.

ZUSAMMENFASSUNG

Die Pilzflora in Kolonien von C. fagisuga wurde anhand von Isolierungen und direkten Beobachtungen untersucht. Hyphomyceten mit dunklem Myzel, in erster Linie Cladosporium cladosporioides, waren in allen Entwicklungsstadien der Lauskolonien bis zu deren Zusammenbruch festzustellen und sind für die dunkle Verfärung der Wachswolle verantwortlich.
In sehr großen oder flächig ausgebildeten Kolonien war gewöhnlich Verticillium lecanii, ein von Insekten bekannter Pilz, anzutreffen. Dieser war auch in absterbenden und weitgehend abgestorbenen Kolonien vorhanden. Im Gegensatz dazu war eine Mucor-Art hauptsächlich auf kleine, isolierte Lauskolonien beschränkt. Nectria viridescens war hingegen in Kolonien aller Entwicklungsstadien zu finden. Fusarium lateritium trat hauptsächlich nach dem Zusammenbruch der Populationen auf.

Inokulationen von C. fagisuga mit mehreren Pilzen in vitro zeigten, daß die Insekten leicht von V. lecanii, N. viridescens, N. coccinea, C. cladosporioides und Paecilomyces farinosus besiedelt werden können. Die Wirkung der Pilze auf die Sterblichkeit der Insekten war nicht zuverlässig zu ermitteln, aber im Zusammenhang mit V. lecanii war ein, wenn auch nicht signifikanter Anstieg der Sterberate zu beobachten.

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INFLUENCE OF LICHEN SPECIES ON COLONIZATION OF *FAGUS GRANDIFOLIA* BY *CRYPTOCOCCUS FAGISUGA*: PRELIMINARY OBSERVATIONS FROM CERTAIN NOVA SCOTIAN FORESTS[1]

David R. Houston[2]

Abstract.--Some crustose lichens that colonize the stems of beech trees favor infestation by *C. fagisuga*, while others do not favor infestation. A predominance of species unsuited for infestation appears to be a reason why trees growing on some sites in Nova Scotia are remarkably free of beech bark disease.

INTRODUCTION

Bark epiphytes, especially mosses and foliose lichens, are known to provide habitats that favor the establishment of *Cryptococcus fagisuga* in North America (Ehrlich 1934). Houston et al. (1979) suggested that young European beech trees in southern England may be rendered prematurely susceptible by dense coatings of the common crustose lichen, *Lecanora coniziodes*. In 1981, we observed that beech trees growing on several steep south-facing slopes in Nova Scotia were nearly free of both *C. fagisuga* and the severe stem defects associated with beech bark disease usually abundant in that region. Bark surfaces of these trees were heavily colonized by a number of light-colored, densely compacted crustose lichens. In 1982, a study was conducted to determine if the absence or presence of *C. fagisuga* was influenced by specific lichens.

METHODS AND MATERIALS

Bolts cut from lichen-colonized trees, growing on steep slopes near Marble Mountain, Cape Breton Island, and on North Mountain near Bridgetown, Nova Scotia,[3] were used for lichen identification. A field key was developed for the species present.[4]

In August 1982, 49 scale-infested trees growing on a steep, south-facing slope near Bridgetown, N.S., were sampled. The bark of each tree was examined from ground line to a height of 1.8 m. Whenever *C. fagisuga* was detected, the following information was recorded: associated lichen species, thallus size (LxW), height aboveground, aspect of the lichen thallus, and the number of *C. fagisuga* colonies present in the lichen thallus.

RESULTS

Trees growing on the study site were very heavily colonized by lichens. Often, no uncolonized bark could be found on the stem sections surveyed (Figs. 1 and 2). The lichens formed intricate mosaics of individual colonies separated by dark lines. Of the nine species most often encountered on these trees, only two were never infested by *C. fagisuga* (Table 1). But great differences existed in the degree to which the other species were infested.

Trypethelium virens infested by *C. fagisuga* occurred on 80% of the trees, yet this dominant lichen was only lightly

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[1]Paper presented at the IUFRO Beech Bark Disease Working Party Conference, Hamden, CT. USA. 27 Sep to 7 Oct 1982.

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[3]Samples were obtained by personnel of the Canadian Forestry Service, Truro, N.S.

[4]Lichens were identified and a key was developed by Dr. Mason Hale, Smithsonian Institute, Washington, D.C.

infested (5.2 insects/thallus, and .05 insects/cm^2 of lichen area). T. virens seemed to be infested only when the centers of old colonies fractured and provided refuges for the insect. By contrast, infested colonies of Buellia stillingiana occurred on about half as many trees (43%) but were much more heavily colonized (2.9 insects/thallus and 0.9 insects/cm^2 of lichen surface). Bacidia spp. were next in dominance, and differences occurred between the two Bacidia species. The granular-surface species of small size was much more favorable for infestation than the smooth-surface species both in numbers of trees with infested colonies and in numbers of insects/cm^2. An as yet unidentified foliose species rarely encountered in this survey also harbored C. fagisuga.

One colony each of Pyrenula laevigata and Graphis scripta was found with C. fagisuga. P. laevigata was encountered rarely, but G. scripta was present on every tree and was especially dominant near the base of the tree. The one infested thallus of G. scripta was on a roughened area of a buttress root.

Table 1.--Association of Cryptococcus fagisuga and lichen species, on the lower 1.8 m of 49 beech trees, Bridgetown, N.S. 1982.

Species	Trees with scale-infested lichen colonies	Lichen colonies	Average lichen colony size	Av. scales per lichen colony	Av. scales per cm^2 lichen colony
	Percent	No.	cm^2	No.	No.
Trypethelium virens	80	161	110.4	5.2	0.05
Buellia stillingiana	43	39	3.1	2.9	.93
Bacidia spp. (granular surface)	31	40	5.5	4.2	.76
Bacidia spp. (smooth surface)	14	8	852.6	10.6	.01
Foliose sp.a/	8	11	10.3	5.5	.54
Pyrenula laevigata	2	1	825.0	5.0	.01
Graphis scripta	2	1	24.0	5.0	.21
Ochrolechia pallescens	0	0	0	0	0
Lecanora subfusca	0	0	0	0	0

a/ Unidentified.

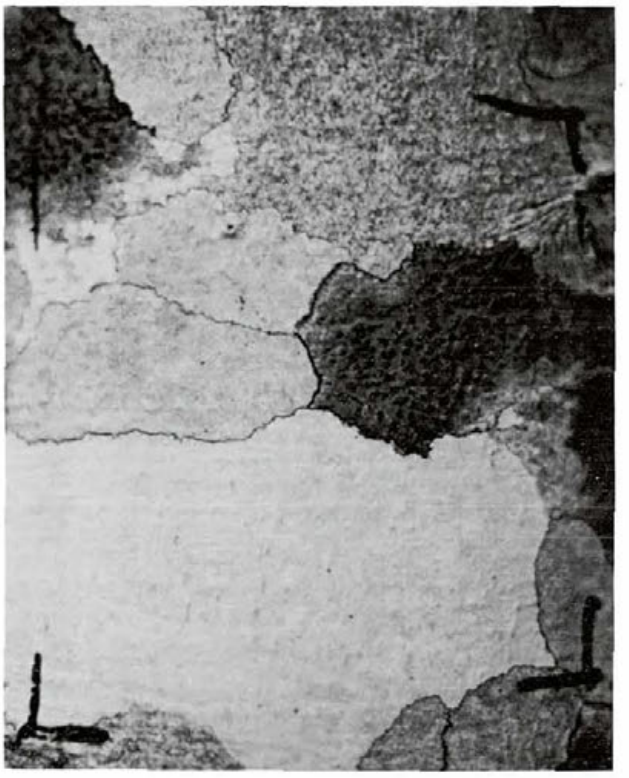


Figure 1.--Photo of a 10 cm x 10 cm area of beech bark colonized by lichens.

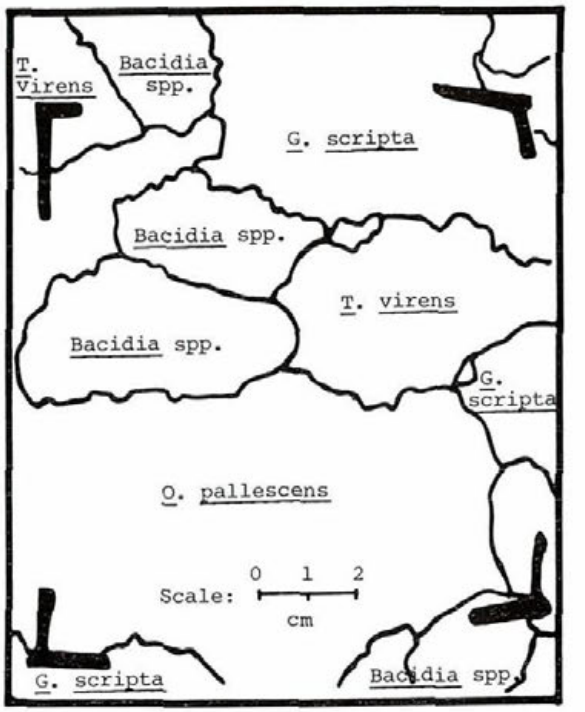


Figure 2.--Diagram of the area photographed in Figure 1 with lichen species identified.

Ochrolechia pallescens and Lecanora subfusca were never infested even though they were very common on these trees.

The 261 infested lichen colonies on the lower 1.8 m of 49 trees from Bridgetown, N.S., were distributed nearly equally from 20 cm to 140 cm aboveground:

Height aboveground (cm)								
1-20	21-40	41-60	61-80	81-100	101-120	121-140	141-160	161-180
Percent								
0.4	12.9	16.0	14.9	14.5	14.5	14.9	6.5	5.3

Above and below these heights, however, populations were lower. The virtual absence of insects from ground line to 20 cm (one infested colony) can be explained by the nearly total colonization of this region by lichens that are unfavorable for infestation, especially G. scripta.

Aspect also influenced the distribution of lichen species, and therefore of scale infestation (Fig. 3). Infested colonies of both B. stillingiana and Bacidia spp. occurred more frequently on the north sides of the trees, while slightly fewer infested colonies of T. virens occurred there.

DISCUSSION

Beech trees growing on certain sites in the aftermath forests of Nova Scotia differ markedly from those in nearby stands in that they support low populations of C. fagisuga and are nearly free of defect attributable to beech bark disease.

The nearly scale-free trees on these sites are remarkably well colonized by crustose lichen species, most of which are not readily infested by C. fagisuga. Conversely, lichen species that are readily infested by the insect occur in low numbers on trees on these sites. It may be that environmental conditions peculiar to these steep, south-facing slopes preferentially favor the early establishment and continued development of the less-hospitable lichens. The nearly complete colonization of lower stem and buttress root bark by less-hospitable lichens, especially G. scripta, may reflect the early establishment of these species on young trees. Future studies may reveal the site/environmental factors that enhance the spread and development of less-hospitable lichens. Such information would enable forest managers to predict where and under what conditions beech could be grown protected from beech bark disease by coatings of lichens.

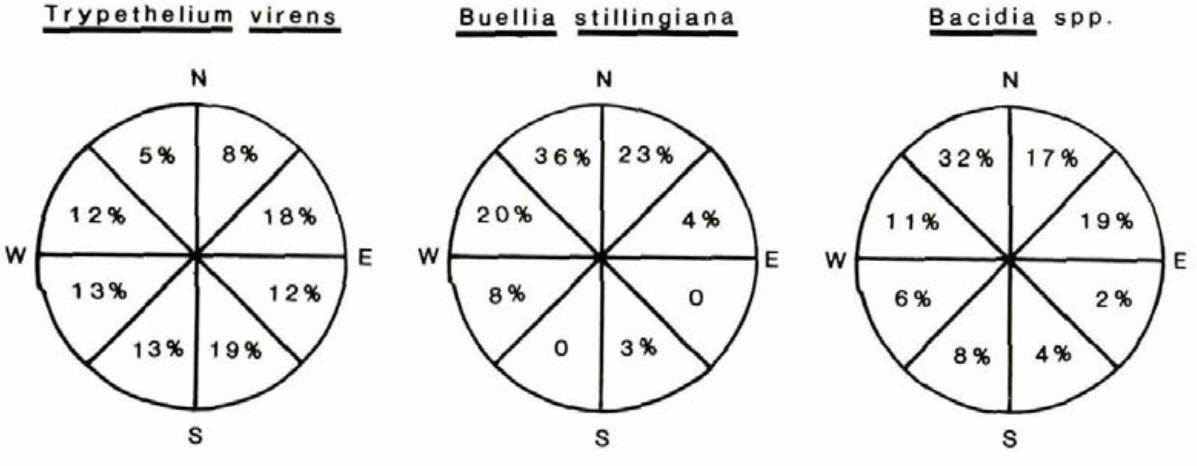


Figure 3.--Aspect distribution of the major lichens associated positively with beech scale (248 colonies) on the lower 1.8 m of 49 beech trees, Bridgetown, N.S., 1982.

Although it is not yet clear why some lichens are favorable and others unfavorable for infestation by C. fagisuga, it is probable that colony surface topography, thallus thickness, the relationship of the thallus to the bark substrate, and lichen chemistry, singly or in combination, are involved. Thalli of species that are unfavorable for infestation are thick, smooth surfaced and densely compacted and are epigenous (elevated above the bark surface). By contrast, thalli of species that are favorable for infestation tend to be thin, loosely compacted and rough or granular surfaced and are usually hypogenous--growing partly beneath the outer bark layers. Such surfaces would provide insects more protection from wash-off by stem flow, and would permit insects to settle nearer to the bark tissues they must probe.

SUMMARY

In the aftermath forests of Nova Scotia, certain mixed hardwood stands include beech trees remarkably free of C. fagisuga and defect. These trees are heavily colonized with crustose lichens, most of which are not infested by C. fagisuga. Uninfested species included O. pallescens, L. subfusca, P. laevigata, and G. scripta. Trypethelium virens, uninfested when young, became infested as it roughened and fractured with age. Bacidia spp. were infested often, and Buellia stillingiana, although occurring only as small colonies, was most frequently and heavily infested. A predominance of lichens unsuited for infestation by C. fagisuga may explain why trees on these sites are disease free.

RÉSUMÉ

Dans les forêts ravagées de la Nouvelle-Ecosse, certains peuplements feuillus mélangés incluent des hêtres complètement exempts de C. fagisuga et de défauts. Ces arbres sont abondamment colonisés par des lichens crustacés, dont la plupart ne sont pas infestés par le C. fagisuga. Les espèces non infestées incluent O. pallescens, L. subfusca, P. laevigata, et G. scripta. Le Trypethelium virens, non infesté lorsque jeune, devient infesté lorsque devenant rugueux et fissuré en vieillissant. Les Bacidia app. étaient souvent infestés et le Buellia stillingiana, bien que recontré en petites colonies seulement, était le plus fréquemment et le plus sévèrement infesté. Une prédominance de lichens inappropriés aux infestations du C. fagisuga peut expliquer pourquoi les arbres sur ces sites sont exampts de la maladie.

ZUSAMMENFASSUNG

In den Wäldern Neuschottlands, in denen die Buchen-Rindennekrose aufgetreten war ("aftermath forests") fallen in manchen Laubholz-Mischbeständen Buchen auf, die bemerkenswerterweise keinen Lausbefall aufweisen und frei von Schäden sind. Diese Bäume sind stark von Krustenflechten besiedelt, von denen die meisten keinen Besatz mit C. fagisuga aufweisen. Zu diesen gehören O. pallescens, L. subfusca, P. laevigata und G. scripta. Trypethelium virens war in der Jugend frei von Läusen, wurde aber im Alter, wenn sie rauher und rissiger wird, besiedelt. Bacidia spp. war oft mit Läusen besetzt und Buellia stillingiana war, obwohl sie nur in kleinen Kolonien vorkommt, am häufigsten und am stärksten besiedelt. Das Vorherrschen von Flechten, die für die Besiedlung durch C. fagisuga nicht geeignet sind, könnte erklären, daß diese Bäume von der Krankheit verschont blieben.

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EFFECTS OF PARASITISM BY NEMATOGONUM FERRUGINEUM (GONATORRHODIELLA HIGHLEI) ON PATHOGENICITY OF NECTRIA COCCINEA VAR. FAGINATA AND NECTRIA GALLIGENA[1]

David R. Houston[2]

Abstract.--The mycoparasite Nematogonum ferrugineum (Gonatorrhodiella highlei) was associated commonly with Nectria galligena cankers on Betula lenta in New Hampshire and Connecticut, and was isolated from N. galligena cankers on Juglans nigra from Virginia. In inoculation trials, parasitized isolates of N. coccinea var. faginata and N. galligena spread more slowly than non-parasitized isolates in bark and cambial tissues; parasitized N. coccinea var. faginata produced fewer perithecia.

Nematogonum ferrugineum (Pers.) Hughes (Gonatorrhodiella highlei A.L. Smith), is a biotrophic contact mycoparasite (Barnett and Binder, 1973), that gets its nutrients from living cells of the host it parasitizes. This is accomplished through the contact of host hyphae with specialized short hyphae or hook cells (Blythe 1949a, Walker and Minter 1981). The ability of a contact biotrophic mycoparasite to successfully attack a potential host (a fungus that produces an essential nutrient termed 'mycotrophein') depends on its ability to penetrate the host's cell walls. Whaley and Barnett (1963) postulated that the mechanism entailed enzymatic breakdown or alteration of the host's cell-wall permeability. Hoch (1977a, 1977b, 1978) showed that in some contact mycoparasites the cytoplasm of parasite and host were intimately connected by plasmodesmata, or by a large pore at the point of contact. Many fungi produce mycotrophein, but N. ferrugineum has the ability to "extract" it from only a few (Ayers 1941, Blyth 1949a, Gain and Barnett 1970, Houston 1976). Six mycoparasites of this type are known. All are Fungi Imperfecti, and their hosts are either Ascomycetes or Fungi Imperfecti (Barnett and Binder, 1973).

Ayers (1941), Blyth (1949a), and Ehrlich (1942) recognized that N. ferrugineum parasitizes Nectria coccinea and N. coccinea var. faginata. Although N. ferrugineum was first recorded from England, on bulbs of Allium (Smith and Carlton 1908), and later in Scotland, associated with N. coccinea on poplar logs and with N. cinnabarina on beech logs (Blyth 1949a, 1949b), its first association with beech bark disease was in North America (Ayers 1941). N. ferrugineum was found recently parasitizing N. coccinea on trees with beech bark disease in England (Houston 1976) and in France (Perrin 1977).

In nature, N. ferrugineum (as Gonatorrhodiella highlei) has been reported in North America only as a parasite of N. coccinea var. faginata. Yet, in culture it parasitized Tritirachium sp., Cladosporium sp., Verticillium albo-atrum, Graphium sp., and Chaetomella raphigera (Gain and Barnett 1970) and it grew well in the presence of N. galligena, a fungus commonly associated with perennial canker diseases of many hardwood species including beech (Ayers 1941). Cotter (1977) reported a few cases where beech trees, infested with beech scale, were infected with N. galligena in a manner similar to N. coccinea var. faginata but no mention was made of N. galligena being parasitized by N. ferrugineum.

Although growth in culture is little affected (Blyth 1949a, Gain and Barnett 1970) parasitism of Nectria species by N. ferrugineum reduces pigment formation and greatly reduces production of conidial and perithecial initials (Shigo 1964).

[1]Paper presented at the IUFRO Beech Bark Disease Working Party Conference, Hamden, CT. USA, 27 Sep to 7 Oct 1982.

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The effects of parasitism of N. coccinea var. faginata by N. ferrugineum in nature are not known. In most instances, high populations of N. ferrugineum occur only following severe outbreaks of beech bark disease. Houston (1976) successfully inoculated Nectria-infected European beech trees with axenic cultures of N. ferrugineum.

The objectives of the studies reported here were to determine 1) if N. ferrugineum parasitizes N. galligena in nature, and 2) if parasitism by N. ferrugineum affects pathogenesis of N. coccinea var. faginata and N. galligena in artificial inoculation trials.

Study 1. Association of Nematogonum ferrugineum and Nectria galligena in nature.

Methods and materials.--In March of 1981, we observed fruiting of N. ferrugineum on several N. galligena cankers on Betula lenta that had been collected the previous November in south-central Connecticut.[3] To our knowledge, this was the first record of an association in nature of these two organisms and prompted a brief survey to determine the frequency of the association.

Cankers, collected from a number of trees from several areas, were placed separately in black polyethylene bags and incubated at 4°C for periods of up to 1 month. In most cases several cankers were collected from each tree. Cankers were carefully examined with a hand lens before, during, and after incubation for the presence of N. ferrugineum sporophores. N. galligena was confirmed in each case by the measurement of mature ascospores from perithecia (Cotter and Blanchard 1981) and cultural morphology (Booth 1959).

Results.--N. ferrugineum was associated commonly with N. galligena on black birch cankers in the four Connecticut and the two New Hampshire locations sampled.[4] Frequencies ranged from one of five trees (1 of 25 cankers) to five of five trees and 22 of 30 cankers (Table 1). Usually more than 50% of the trees and 40% of the cankers bore N. galligena parasitized by N. ferrugineum. In all but one case N. ferrugineum was not apparent before incubation in the dark at 4°C. The schedule of collection and results of incubation are presented in Table 1.

In addition, N. ferrugineum was isolated from several N. galligena cankers on Juglans nigra collected near Blacksburg, Va.[5] and from N. galligena associated with the beech bark disease outbreak on the Monongahela National Forest in West Virginia first reported in 1981 (Mielke et al. 1982). Subsequent examinations there showed that the mycoparasite was very common on diseased beech trees--often fruiting prolifically on bark surfaces killed by N. galligena (see Mielke and Houston, these proceedings).

Study 2. Effects of parasitism by N. ferrugineum on pathogenicity of N. coccinea var. faginata and N. galligena.

Methods and materials.--Trees growing in Madison and North Branford, CT. were prepared for use in these trials by infesting them with C. fagisuga. In August 1979, eggs of C. fagisuga were placed against the bark beneath 10- x 10- x 5-cm polyurethane foam blocks (Houston 1982). Paired adjacent covers without eggs were installed as controls. In May of 1980, insects that had become established beneath each block 'cover' were counted and the foam replaced. In June or October 1981 the bark beneath selected covers, with and without C. fagisuga, was inoculated with N. coccinea var. faginata and N. galligena free or parasitized by N. ferrugineum.

Inoculum consisted of N. coccinea var. faginata isolated from beech trees affected by beech bark disease. Two isolates were used, one for the June inoculations and the other for those in October. N. galligena mass isolates were obtained from perithecia on the black birch cankers described in Study 1. N. ferrugineum was obtained from N. coccinea var. faginata-infected beeches from a number of locations in New York and Vermont. Axenic cultures of N. ferrugineum, grown on Blyth's medium (Blyth 1949a), were used to inoculate 1-week-old cultures of the candidate Nectria isolates growing on 2% malt agar. Challenged cultures (and unchallenged cultures) were grown in the dark at room temperature for 3 weeks before use.

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[3] Observations on the cankers, stored at 4°C in the dark for 4 months, were made by Nancy Smith, Hamden, CT.

[4] New Hampshire cankers collected by K. Dudzik, Durham, NH.

[5] Cankers collected by G.J. Griffin, Blacksburg, VA.

Date Collected	Location	Tree no.	No. cankers	No. cankers parasitized	Percentages	
4/81	Haddam, CT	1	4	1	25%	
5/81	Area 1	2	17	15	88%	3 of 4 trees = 75%
		3	4	2	50%	22 of 30 cankers = 73%
		4	3	0	0%	
		5	6	5	83%	
10/81	Haddam, CT	6	5	3	60%	
	Area 2	7	5	3	60%	5 of 5 trees = 100%
		8	5	5	100%	16 of 25 cankers = 64%
		9	5	3	60%	
		10	5	2	40%	
12/81	Woodbridge, CT	11	5	0	0%	
	Area 1	12	5	2	40%	4 of 5 trees = 80%
		13	5	4	80%	10 of 25 cankers = 40%
		14	5	1	20%	
		15	5	3	60%	
12/81	Woodbridge, CT	16	5	0	0%	
	Area 2	17	5	0	0%	1 of 5 trees = 20%
		18	5	1	20%	1 of 25 cankers = 4%
		19	5	0	0%	
		20	5	0	0%	
3/82	Durham, NH	21	1	1	100%	
	Area 1	22	1	0	0%	3 of 6 trees = 50%
		23	1	1	100%	3 of 6 cankers = 50%
		24	1	1	100%	
		25	1	0	0%	
		26	1	0	0%	
5/82	Durham, N.H.	27	3	3	100%	
	Area 2	28	3	0	0%	3 of 5 trees = 60%
		29	3	2	67%	6 of 15 cankers = 40%
		30	3	0	0%	
		31	3	1	33%	

Total = 59 of 130 cankers with N. ferrugineum or 45% and 20 of 31 trees with parasitized cankers = 65%.

Table 1.--Association of Nematogonum ferrugineum with Nectria galligena-incited cankers on Betula lenta.

Inoculations were made by removing the foam covers and inserting the inoculum into 0.5 cm diameter drill holes made to the cambium. When possible, parasitized and unparasitized isolates were inoculated into separate holes beneath each cover. Any C. fagisuga colonies present beneath the "noninfested" covers were removed before inoculation by scrubbing with a stiff-bristled brush. After inoculation, the covers were replaced. Assessments were made 8 months or 1 year later.

Eight months after inoculation, the bark around each wound was examined carefully with a hand lens for bark necrosis, and fruiting structures of Nectria spp. or N. ferrugineum. After 1 year, the bark was removed and the cambial necrosis was measured.

Results.--Parasitism by N. ferrugineum reduced markedly the number and the area of the bark cankers produced, the number of cankers with Nectria perithecia (Table 2), and the extent of cambial necrosis (Tables 3 and 4). The presence of scale also appeared to increase the ability of both fungi to spread in the tissues (Tables 2, 4), although this was variable, and was confounded to some degree by the presence or absence of N. ferrugineum. The mycoparasite also appeared to reduce the frequency to which the associated Nectria spp. could be reisolated after 1 year (Table 3).

Scheme			No. external bark cankers/no. inoculations	Av. size (LxW, cm)	No. cankers with perithecia	No. inoculation points with N.f. fruiting
	N.f.	*C.f.*				
N. coccinea var. *faginata*	(-)	(+)	3/6	2.29	2	0
	(-)	(-)	4/6	2.43	1	0
Inoc. 9/81 Meas. 6/82 Madison, CT	(+)	(+)	0/6	-	0	4/6
	(+)	(-)	0/6	-	0	4/6
N. coccinea var. *faginata*	(-)	(+)	8/8	8.07	4	0
	(-)	(-)	3/4	3.82	2	0
Inoc. 10/81 Meas. 6/82 N. Branford, CT	(+)	(+)	3/8	3.91[a/] (0 54)	1	3/8
	(+)	(-)	1/4	0.27	0	1/4
N. galligena	(-)	(+)	7/10	3.99	0	0
	(-)	(-)	4/4	5.49	0	0
Inoc. 10/81 Meas. 6/82 N. Branford, CT	(+)	(+)	1/9	0.33	0	0
	(+)	(-)	0/4	-	0	1/4

Table 2.--Numbers and sizes of bark cankers resulting from fall inoculation of bark, infested or uninfested with *C. fagisuga* (C.f.), with *N. coccinea* var. *faginata* and *N. galligena*, parasitized or not parasitized by *Nematogonum ferrugineum* (N.f.).

[a/] One large canker developed. The value in parentheses shows the average canker size when this canker is omitted.

Table 3.--Cambial necrosis resulting from spring inoculations with *Nectria coccinea* var. *faginata* (n.c.f.) and *N. galligena* (N.g.) parasitized (P) and not parasitized (NP) by *Nematogonum ferrugineum*. *Cryptococcus fagisuga* absent.

Madison, CT Inoc. 6/15/81 Measured 6/9/82	No. cankers	Av. cambial necrosis (LxW, cm)	No. cankers with perithecia	No. cankers w/Nectria reisolated
N.c.f. (NP)	8	1.90	1	6/6
N.c.f. (P)	9	1.09	0	1/3
N.g. (NP)	14	4.39	0	3/5
N.g. (P)	14	1.40	0	0/4

Table 4.--Cambial necrosis resulting from spring inoculations of bark infested and uninfested with *C. fagisuga*, with *N. coccinea* var. *faginata* and *N. galligena* parasitized or not parasitized by *Nematogonum ferrugineum*.

Scheme North Branford, CT Inoc. 6/14/81 Meas. 6/10/82	No. cankers	Av. cambial necrosis (LxW, cm)
N. coccinea var. *faginata*		
(-) *N. ferrugineum* (+) *C. fagisuga*	3	4.03
(+) *N. ferrugineum* (+) *C. fagisuga*	3	2.84
N. galligena		
(-) *N. ferrugineum* (+) *C. fagisuga*	2	6.34
(-) *N. ferrugineum* (-) *C. fagisuga*	4	2.92
(+) *N. ferrugineum* (+) *C. fagisuga*	2	2.10
(+) *N. ferrugineum* (-) *C. fagisuga*	4	1.69

DISCUSSION

The ready isolation of *N. ferrugineum* from *N. galligena* cankers, not only from stands in New Hampshire, where beech bark disease was severe in the past, but also from areas of southern Connecticut where the disease has yet to occur and from Virginia far beyond the current range of the disease, is significant from several aspects. First, it reveals that the mycoparasite occurs commonly on a host not previously recorded in nature and is much more widespread than was previously recognized. Second, it is without question native to North America and was not, as Ayers speculated (1941), introduced on *N. coccinea* var. *faginata*. (Indeed, it is not at all certain that *N. coccinea* var. *faginata* was introduced.)

That N. ferrugineum had not previously been recorded on N. galligena in nature is surprising in light of its high frequency of association with N. galligena as shown in this study, and the numerous past studies of N. galligena. This is perhaps attributable to the paucity of fruiting by N. ferrugineum until after prolonged incubation in the dark at 4°C. The one canker found with sporophores of N. ferrugineum before incubation was well covered with bark and was collected in early May.

The abundant fruiting of N. ferrugineum on trees with beech bark disease in West Virginia (where until now only N. galligena is known) compared to the limited fruiting on black birch cankers may be a consequence of the relative amounts of fungus host tissues present in each case. The probable sources of N. ferrugineum on diseased beeches in West Virginia are the abundant N. galligena cankers on Betula alleghaniensis and other hardwoods present in the areas.

Under the conditions of the trials reported here, N. coccinea var. faginata and N. galligena parasitized by N. ferrugineum were markedly reduced, compared to unparasitized isolates, in their abilities to 1) spread in bark and cambial tissues, 2) persist in invaded bark tissues, and 3) (at least for N. coccinea var. faginata) produce perithecia. Because it is unlikely that the inoculation conditions are met in nature (i.e., pre-parasitized mycelium introduced to wounds extending to the cambium) the results must be interpreted with caution. Nevertheless, it is apparent that parasitism reduces host fitness in measurable ways. Trials are underway to determine how the interactions of different forms of inocula, types of wounds, and times and sequences of infection affect host pathogenicity.

SUMMARY

The contact biotrophic mycoparasite, Nematogonum ferrugineum (Gonatorrhodiella highlei) was found commonly associated with Nectria galligena cankers on Betula lenta in New England and on Juglans nigra in Virginia. It was also present on N. galligena associated with the isolated outbreak of beech bark disease in West Virginia. This suggests strongly that N. ferrugineum is native to this continent, and that N. galligena cankers probably serve as "reservoirs" of the parasite.

Parasitized isolates of N. coccinea var. faginata and N. galligena, inoculated into bark wounds made to the cambium, were markedly less pathogenic than to unparasitized isolates. Parasitized isolates produced fewer and smaller cankers and persisted for shorter times in bark tissues. And parasitized N. coccinea var. faginata isolates produced fewer perithecia.

RÉSUMÉ

Le mycoparasite biotrophique de contact, Nematogonum ferrugineum (Gonatorrhodiella highlei) fut trouvé communément associé aux chancres Nectria galligena sur le Betula lenta en Nouvelle-Angleterre et sur le Juglans nigra en Virginie. Il était aussi présent sur le N. galligena associé à l'apparition locale de la maladie de l'écorce du hêtre en Virginie de l'Ouest. Ceci suggère fortement que le N. ferrugineum est indigène à ce continent, et que les chancres N. galligena servent probablement de "réservoirs" du parasite.

Des isolats parasités du N. coccinea var. faginata et du N. galligena, inoculés dans des blessures de l'écorce jusqu'au niveau du cambium, étaient distinctement moins pathogéniques que des isolats non parasités. Les isolats parasités produisirent moins et de plus petits chancres et persistèrent moins longtemps dans les tissus de l'écorce. De plus, les isolats parasités du N. coccinea var. faginata produisirent moins de périthèces.

ZUSAMMENFASSUNG

Der Mykoparasit Nematogonum ferrugineum (Gonatorrhodiella highlei) war regelmäßig in Verbindung mit Nectria galligena-Krebsen an Betula lenta in Neuengland und an Juglans nigra in Virginia anzutreffen. Er war an Nectria galligena vorhanden, der in West Virginia in Verbindung mit einem isolierten Auftreten der Buchen-Rindennekrose beobachtet wurde. Es ist demnach sehr wahrscheinlich, daß N. ferrugineum auf dem nordamerikanischen Kontinent heimisch ist und daß N. galligena-Krebse als "Reservoir" des Mykoparasiten anzusehen sind.

Von N. ferrugineum parasitierte Isolate von N. coccinea var. faginata und N. galligena waren nach Inokulation in bis zum Kambium reichende Rindenwunden deutlich weniger pathogen als parasitenfreie Isolate. Parasitierte Isolate verursachten weniger und kleinere Krebse und überdauerten kürzere Zeit im Rindengewebe. Darüber hinaus bildeten parasitierte N. coccinea var. faginata-Isolate weniger Perithezien.

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MANAGEMENT OF BEECH STANDS INFECTED BY CRYPTOCOCCUS FAGISUGA IN WEST GERMANY[1]

Hermann Bogenschutz[2]

Abstract.--Beech trees in an experimental plot in the Odenwald (southwest Germany), with different intensities of attack by Cryptococcus fagisuga Lind. since at least 1970, were observed from 1972 until 1982 in order to ascertain the role of scale insects in beech bark disease and to facilitate decisions for the management of infested stands. At the beginning of the research 13% of the dominant trees were infested by C. fagisuga. Until 1979 the attack decreased continuously, only in the dry years 1975 and 1976 did the number of trees with moderate attack increase. Since 1980 new infestations on previously uninfested trees have been observed. Eighteen per cent of the trees, which had been moderately or heavily attacked in 1972, died during the following years. The recovered trees exhibited pathological bark induced by the sucking activity of the scale insects. According to these results, practising foresters are recommended not to do a sanitation felling, if locally not more than 6% of the beech trees reach the attack class moderate or heavy.

INTRODUCTION

Practising foresters in Germany are advised by the forest protection authorities to fell beech trees suffering heavily from beech bark disease immediately in order to avoid losses in timber value and to eliminate sources of infection. However, the logging should be done carefully in order to keep changes in the stand structure as small as possible since it is known that even heavily attacked beech can regain health. If there are many trees with bark necrosis, the forester has to consider, whether timber loss or changes in the stand structure is of higher ecological or economic importance. Therefore he urgently needs advice for decision making. In order to gather information on the course of the disease, the Department of Forest Protection of the Forest Research Institute in 1970 established a sample area within a stand heavily infested by the beech scale, Cryptococcus fagisuga Lind. The trees selected and marked for observation have been checked at annual intervals since 1972. The following results are a supplement to those obtained by Rhumbler (1931) in north Germany in the first quarter of this century.

Experimental stand and methods

The experimental plot covers an area of 3.3 ha in the Odenwald in southwest Germany. It is situated on a northeast slope about 350 m above sea level. The stand consisting of 80% beech (Fagus sylvatica L.) was initiated in the seed year 1888. It was thinned for the first time after about 40 years; the last selective logging was in 1978.

Beginning in 1972 every autumn I determined the degree and extent of the white woolly wax secretions on the lower 4 m of the trunk of 96 marked beeches using three classes of infestation: light (1), moderate (2) and heavy (3). I registered the position (height and direction) of the densest cover, from which I took a bark sample in order to determine the vitality of the scale insects by means of a microscope. Furthermore I described the structure of and the injuries to the bark, and finally I noted whether

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there were slime flux spots or fruit bodies of Nectria coccinea and white-rot fungi.

RESULTS AND DISCUSSION

At the beginning of the investigation 7% of the trees in the experimental plot were attacked lightly, 5% moderately and 1% heavily by C. fagisuga. The infestation of 96 marked sample trees reached the highest level in 1972, and declined continuously until 1979. Only in the dry years 1975 and 1976 and in 1982 did the number of beech trees with moderate attack (class 2) increase clearly (Fig. 1). However, changes in density of C. fagisuga could not be correlated with annual weather conditions, as has been done by Schindler (1962) in north Germany.

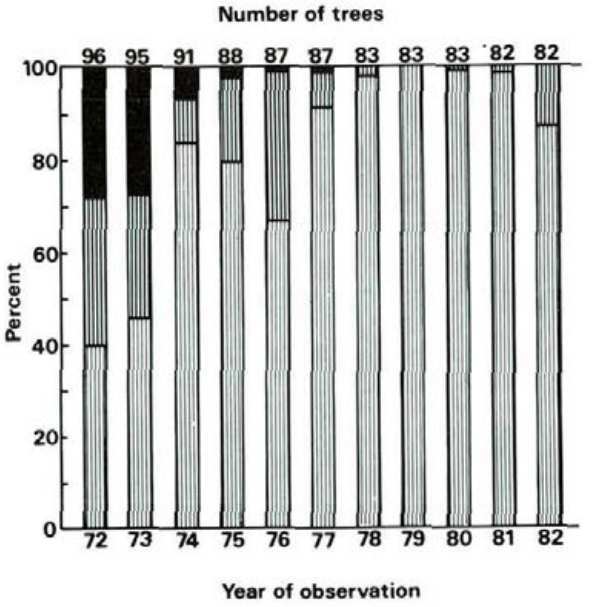


Figure 1.--Percentage of the sample trees attacked lightly (light line), moderately (heavy line) or heavily (black) by Cryptococcus fagisuga in the years from 1972 till 1982.

Slime fluxing was observed on 10 trunks. The first spots on the bark of one tree appeared in 1975. The occurrence of new spots culminated in 1976 with six trees affected. Two followed in 1977 and one in 1978. It appears that slime fluxing was induced by warm and dry weather. The level of the beech scale density appeared to have had no influence on the production of slime flux spots, because they were found on trees having had heavy, moderate and light infestations. Trees without any scale attack never showed slime fluxing. Only one of the trunks with tarry spots snapped during the observation period; this was two years after the appearance of the exudations. The other trees recovered.

During the whole observation period (1972-1982) I never found fruit bodies of Nectria or white-rot fungi on trees not yet broken, except for one beech with fruit bodies of Inonotus nodulosus (Fr.) one year before snapping of the trunk.

Of 96 sample trees 13 died or were missing of which 10 belonged to the dominant stand components and three were suppressed (Table 1).

Table 1.--History of sample trees dying between 1972 and 1982

Tree No	Crown class	Attack class in the year 1972	1973	1974	1975	1976	1977	1978	1979	1980	1981
1	suppressed	1	1	1	1	dry[a]					
2		2	2	1	1	1	1	1	1	1	dry[a]
3		3	2	1	1	1	1	dry[a]			
4	dominant	2	2	1	1	1	1	snap			
5		3	3	1	decaying			snap			
6		3	3	dry[b]							
7		3	3	snap							
8		3	snap								
9		3	snap								
10		3	snap								
11		1[c]	1	missing							
12		3	3	1	1	2	0	missing			
13		3	3	2	missing						

Dry = Standing tree with no leafing

a Suppression
b Beech bark disease
c Heavy attack above 4 m

The suppressed trees died without snapping and the scale attack only accelerated the natural die-back. Five of the dominant trees (tree numbers 6-10) snapped or died in the second or third year after the heaviest attack, two suffered a long decline promoted by the dry period in 1975/76 (tree numbers 4 and 5). The remaining three trees disappeared for unknown reasons. Because of the heavy attack in 1971-72 I classified them as having died from the beech bark disease. With one exception (tree number 4) every decaying tree of the dominant stand level has been heavily attacked by the beech scale before.

Rhumbler (1931) called trees with moderate or heavy attack "scale-insect-beeches" (Lausbuchen). After the C. fagisuga outbreak in the Odenwald, 10 of 56 scale-insect-beeches (18%) and 9 of 17 trees (53%) belonging to attack class 3 died. Since only 5% of all (dominant) beech trees were moderately attacked and only 1% were heavily infested, the losses remain small relative to the whole stand.

In Lower Saxony, 17% of scale-insect-beeches



Plate 1.--Dead bark of a beech formerly infested by Cryptococcus fagisuga partly removed (right picture) to show the formation of wound callus.

died during an outbreak in the first quarter of this century. This value agrees well with that of Baden-Württemberg (18%).

The fact that slime fluxing was observed on 47% of scale-insect-beeches in Lower Saxony compared to only 7% in Baden-Württemberg makes it necessary to contradict the general opinion of foresters that appearance of slime flux spots can be used as a measure of the severity of the disease.

It was pointed out by Rhumbler (1931) that one can expect 80% of scale-insect-beeches to recover. However, the disease does not disappear without leaving a trace. The bark surface shows distinct marks originating from attacks in previous years. If bark dies on a larger area, there remain wounds which slowly occlude Plate 1). If a rhytidome can be built up, the bark cracks later on and fissures appear, because sclerotic phloem rays prevent the formation of a normal interior periderm (Braun 1976, 1977) (Plate 2).

CONCLUSIONS FOR FOREST MANAGEMENT

Quantitative studies on the influence of beech bark disease on individual trees in the timber stage in north and south Germany in different years have shown that less than 20% of beech trees moderately or heavily infested by C. fagisuga died. It is not possible to recognise these trees in advance. Therefore it is recommended not to do an extra logging, if no more than 6% of the dominant stand components are infested. According to our experiences the financial loss remains small, whereas extra logging is expensive, and moreover, it often interferes with silvicultural concepts. Diseased or dead trees remaining in the stand do not increase the risk to healthy trees. Of course, removing trees heavily infested by the beech scale reduces the number of crawlers invading neighbouring trees. But there are enough larvae, coming from lightly attacked trees, to infect those disposed to the disease (Wainhouse, 1980). The same holds true for fungi. Mülder and Zycha (1980) pointed to the fact, that spores are present everywhere. Certainly, scale-insect-beeches should be watched carefully, when routine quality thinning is done. Trees with bark showing marks of former attacks should also be favoured for felling because each necrosis reaching the cambium induces timber damage and discoloration, resulting in quality loss (Wujciak 1976).

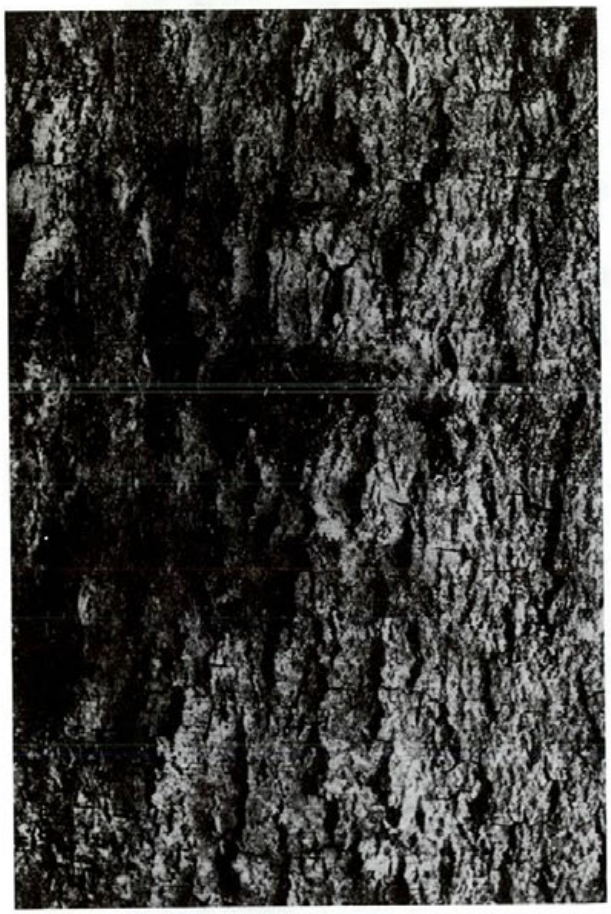


Plate 2.--Abnormal (cracked) bark of a beech induced by Cryptococcus fagisuga.

ZUSAMMENFASSUNG

Im Jahre 1970 unterschiedlich stark von Cryptococcus fagisuga Lind. befallene Buchen auf einer Versuchsfläche im Odenwald (Südwestdeutschland) wurden bis 1982 beobachtet, um den Einfluss der Läuse auf den weiteren Verlauf der Buchenrindennekrose zu ermitteln und um der forstlichen Praxis Entscheidungshilfen bei der Behandlung von verlausten Beständen zu geben.

Zu Beginn der Untersuchung waren 13% der herrschenden Bäume von C. fagisuga befallen. Bis 1979 nahm der Befall kontinuierlich ab, lediglich in den Trockenjahren 1975 and 1976 stieg die Anzahl der Bäume mit mittlerem Befall an, Seit 1980 ist wieder eine schwache Zunahme der Verlausung festzustellen.

Von den Buchen, die 1972 mittleren oder starken Befall aufwiesen, sind in der Folge 18% gestorben. Die wieder gesunden Bäume besitzen heute pathologische Rinden, deren Entstehung durch die Saugaktivität der Läuse ausgelöst wurde.

Aufgrund der vorliegenden Ergebnisse wird der Forstpraxis empfohlen, auf sanitäre Hiebe zu verzichten, wenn lokal nicht mehr als 6% der Buchen verlaust sind (d.h. der Befallsklasse mittel oder stark angehören).

RÉSUMÉ

Dans le but de préciser le rôle de la cochenille dans la maladie de l'écorce du hêtre et pour faciliter les décisions des aménagistes de peuplements infestés, on a observé annuellement de 1972 à 1982, des hêtres montrant différentes intensités d'attaques par le Cryptococcus fagisuga Lind. depuis au moins 1970. Ces arbres étaient situés sur des parcelles expérimentales situées dans le Odenwald (sud-ouest de l'Allemagne). Au début de nos observations, 13% des arbres dominants étaient infestés par le C. fagisuga. L'infestation a diminué constamment jusqu'en 1979, sauf dans les années sèches de 1975 et 1976 où le nombre d'arbres avec infestation modérée a augmenté. Depuis 1980, des infestations ont été observées sur des arbres antérieurement non touchés. Dix-huit pour cent des arbres modérément ou sévèrement attaqués en 1972 moururent dans les années subséquentes. Les arbres survivants montraient des malformations pathologiques de l'écorce causées par l'activité de la cochenille. Selon ces données, nous conseillons aux forestiers de ne pas faire de coupe d'hygiène si moins de 6% des hêtres sont dans les classes d'attaques modérées et sévères.

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DEVELOPMENT OF BEECH BARK DISEASE DURING A SEVEN YEAR PERIOD ON TWO PLOTS IN NORTHERN BAVARIA [1]

Klaus J. Lang [2]

Abstract.-- Since 1976 on two observation plots in northern Bavaria 600 trees have been regularly observed. Preliminary results of disease development on 96 trees, formerly moderately or heavily infested by Cryptococcus fagisuga, are reported.

INTRODUCTION

As we know, beech bark disease in Europe is repeatedly the cause of great financial losses and sometimes of silvicultural problems. Especially between forest-officers there is no unique opinion on causes and etiology of the disease. Moreover, the reports of foresters concerning the duration of the disease from the first symptoms to the death of a tree are contradictory and one question asked very often is that of the chance of survival of trees which have been attacked.

That is why two observation plots were established in 1976 in the northern part of Bavaria where beech bark disease was common during this time.

The first plot at the forest district of Rohrbrunn is situated within an area where many trees suffered from the disease. Many beeches were already killed at that time in the neigborhood of and within the plot and many fruitingbodies of wood deteriorating fungi, especially Fomes fomentarius were found on dead trees. The second plot is located at the forest district of Rothenbuch, a few kilometers away from the first one. In the vicinity of this plot there was rather little damage and comparatively very few fruitingbodies.

At Rohrbrunn on an area of 1 ha, 200 trees were marked and numbered in a pure beech stand (with only a few Norway spruces). At Rothenbuch we marked 400 beeches on 1.6 ha in a stand mixed with old oaks (Quercus petraea). On both plots the oldest trees were about 120 years old. At Rohrbrunn the stand was very uniform but at Rothenbuch there were also younger trees present.

Since 1976 the 600 trees were observed three times a year; once in the spring when the foliage was developing, once during summer and once in fall when the leaves were being shed. We recorded the intensity of scale infestation with a simplified method on the basis of Rhumbler's scheme (with a scale from 0 - 5) the condition of the crown, tarry spots (slime flux), fructifications of Nectria and Cylindrocarpon, fruitingbodies of wood decomposers, dead bark, and so on. Investigations about the spore discharge of Fomes fomentarius and Fomitopsis pinicola have already been reported at the meeting in Nancy (Lang 1980). In 1977, 1978 and 1980 the two plots were photographed from the air with Kodak Aerochrome IR on a scale of 1 : 5000.

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These pictures should yield information about the earliest stage of the disease, which can be seen using this method, and the possibility of predicting the death of the trees utilizing variations in crown density from the aerial photographs.

RESULTS

The observation period began at about the time the disease was culminating. Therefore, we have no dates from our plots that could tell us how much time was needed to reach this state. In 1976 on the plot at Rohrbrunn 73 trees (= 36,5%) were infested with scale insects, 23 of these trees were moderately or heavily attacked. Up to 1982 moderate or heavy scale infestation was observed on 36 trees (= 18%). Tarry spots occured during the years on 32 trees (= 16%). To date, of the 36 trees, 14 are dead (= 39%). On the larger plot at Rothenbuch the relationships are comparable. Of the 130 trees (= 32%) that were infested with scale insects in 1976, 60 showed medium or heavy infestation, slime flux was observed in 55 cases (= 14%) and 25 out of 95 trees (= 26%) have died (Table 1).

Table 1. -- Scale infestation intensity, slime flux, and tree mortality on two observation plots in northern Bavaria during a 7-year observation period.

	Rohrbrunn	Rothenbuch
area of the plots	1 ha	1.6 ha
number of trees	200	400
stand type	beech	beech and oak
scale infestation 1-5 (1976)	73 (36,5%)	130 (32,5%)
3-5 (1976)	23 (11,5%)	60 (15,0%)
3-5 (1976-1982)	36 (18,0%)	95 (23,75%)
slime flux	32 (16,0%)	55 (13,75%)
trees killed by BBD	14 (7,0%)	25 (6,25%)*

*) six trees that were heavily attacked and removed before they were killed can be added here.

Figure 1 shows the development of the disease on 36 (Rohrbrunn) and 60 (Rothenbuch) attacked trees, respectively, during the observation period.

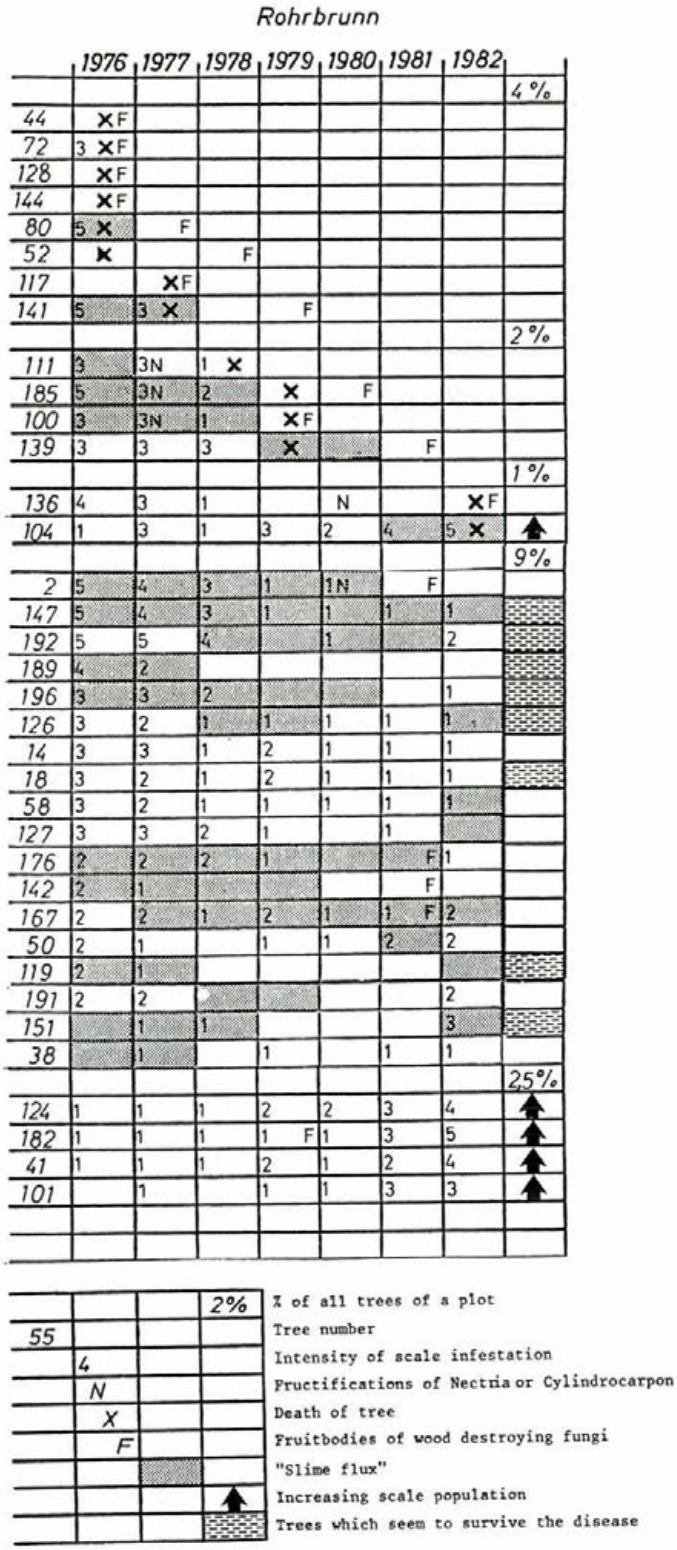
The figure shows that infestation of the trees by the scale insect decreases after a culmination point or remains rather unchanged for a long time. During the first 5 years no drastic increase in the scale population was observed. Normally, slime flux appears during or after the stage of most intensive infestation. Although they were heavily infested, some trees showed no slime flux. Perithecia of Nectria and sporodochia of Cylindrocarpon also occured during or after heavy attack. On the trees which are still alive it is apparent that rather few fructifications occur. This does not mean, however, that the fungus is absolutely absent, since the Nectria fungus isolations made from the non-fruitingbody material present on the margin of tarry spots were normally successful.

Sporodochia of Cylindrocarpon also appeared after the inoculation with spore suspension after the wounding of bark of healthy beeches outside the plots. The sporodochia appeared two years after inoculation. Today, after five years, all 25 wounds have healed.

After 1976, which was characterized by drought, no clear increase of the scale population was noticed, but on both plots there were some trees with increasing scale infestation. This development apparently took place gradually or rapidly within two years. The number of observations is not yet great enough to present exact data. Some trees with very different infestation intensity showed signs of recovery in the sense of healing-up old or relatively fresh necroses. There were scars and longitudinally running rolls on the trunk but bark necrosis was not evident to any great extent. These individuals showed either moderate scale infestation throughout the 7 year period or were heavily infested 7 years ago.

On some of the trees the scale insects were concentrated on one side of the trunk. This could not have been the only explanation for their recovery, however, because most of the trees which were still alive showed heavy infestation all around the stem. Eventually differences in the vitality, whatever this means, play a role in limiting bark necroses by a periderm. Another possibility could be the absence of Nectria but there was no evidence for this.

The duration of the disease, as it looks at the moment, seems to reach about 10 years from the installation of a strong scale population until the death of the tree. Here the time needed for the build-up of the scale population must be added. Fruitingbodies of wood deteriorating fungi are formed at different times on the



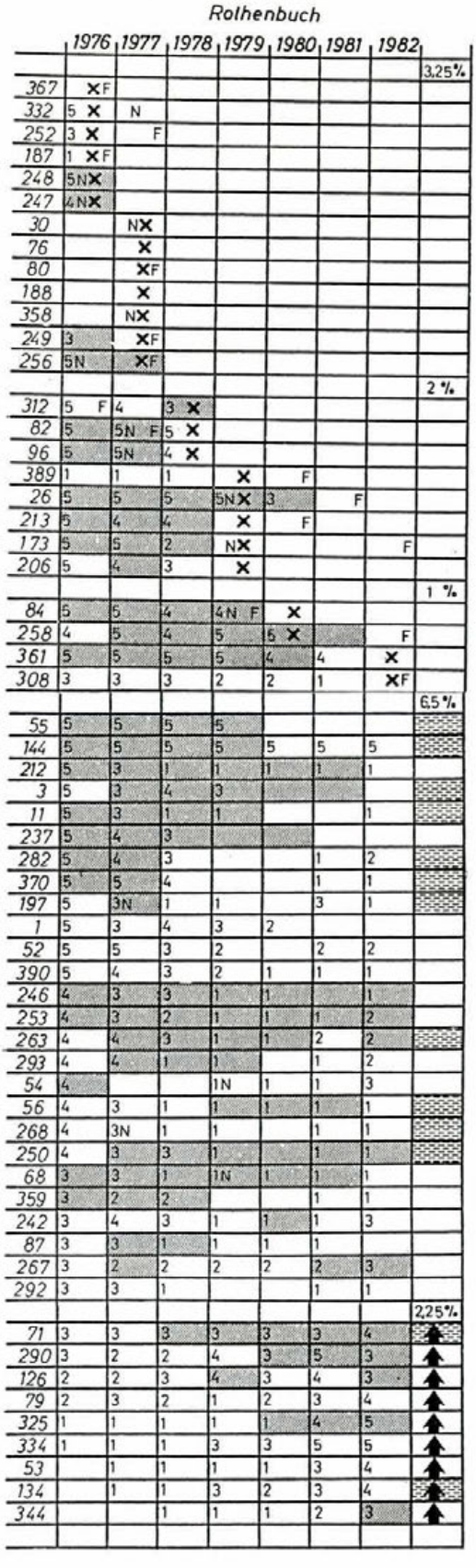


Figure 1.-- Development of beech bark disease on two plots during a seven year period.

heavily attacked trees. We can find them in the year of the death of the tree, 1 to 3 years before, or 1-3 years later. Because the fructification time is to be considered, infection by those fungi may take place very early, perhaps at the time when tarry spots appear. In 1982 the following fungi could be detected on dead or still-living trees (Table 2).

Table 2. -- Wood decomposing fungi on dead and still-living trees.

	Rohrbrunn	Rothenbuch
dead trees with fruitingbodies	12/14 (85,7%)	15/25 (60%)
living trees with fruitingbodies	5/22 (22,7%)	0/35 (0%)
Fomes fomentarius	17	4
Fomitopsis pinicola	3	1
Stereum spp.	2	2
Bjerkandera adusta	-	2
Inonotus nodulosus	-	1
Trametes gibbosa	1	2
Ganoderma applanatum	-	2
Armillaria sp.	+	+

It is conspicuous that Fomes fomentarius occurs four times more frequently at Rohrbrunn than at Rothenbuch and also that 5 living trees were attacked by this fungus at Rohrbrunn. The first plot is located in a forest with many dead trees which were not removed and were crowded with fruitingbodies, especially of Fomes fomentarius. Thus, this fungus was dominant in this region. Near the second plot there were only few dead trees and Fomes fomentarius did not yet play (1976) a dominant role. This fact had clear consequences for the infection of beeches on the different plots and also for the infection of living trees which took place probably under high infection pressure.

Fomes fomentarius and Fomitopsis pinicola produce many fruitingbodies and it seems that normally, a tree is invaded only by one species at first. If both fungi occur on the same tree their fruitingbodies appear far from one another.

Trametes gibbosa and Ganoderma applanatum appear much later (after some years). Then we can find them on broken stems and near the soil surface on the base of broken trees. Many dead trees are also attacked by Armillaria.

Since 1976 the foliage of all 600 trees was observed in spring, summer, and fall. Although heavily damaged, some trees show no significant symptoms in the crown, but most of the trees which died during the last years previously had poor foliage during the summer, late flushing, and early defoliation.

On the aerial photographs we took in 1977, 1978, and 1980 the regions of heavy attack were clearly seen. Although the scale of the pictures (1 : 5000) was rather small, many single trees could be identified when compared with an exact map of the plots. Therefore it was possible to pursue the development of the disease, to some extent, on aerial photographs.

It is true that many trees which show clear alteration in the foliage will be dead in a few years. This is interesting in as far as forestry practices are concerned, since small areas with heavily attacked trees can be detected before the trees are dead and useless. The completely exact prediction of the future of an attacked tree and also the detection of slightor moderately attacked trees seem not to be possible by this method. This is probably a reason why we get no significant correlation between scale infestation and foliation if we include trees with a few scale insects on the bark (Figure 2).

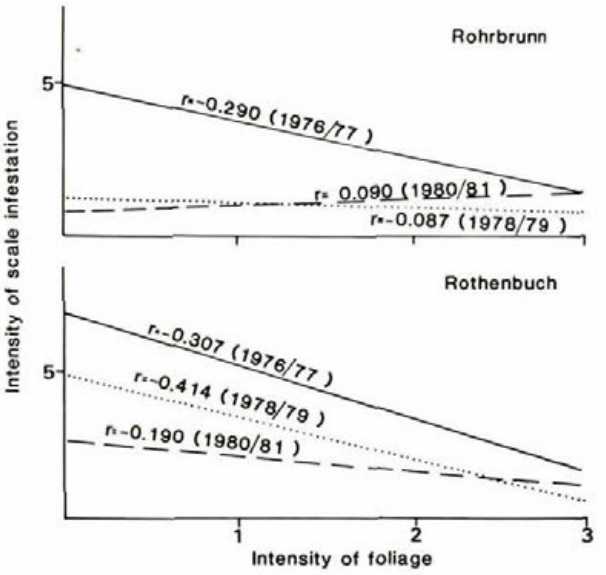


Figure 2. -- "Correlations" between the intensity of scale infestation and the alteration of foliage.

These observations will be partly finished in 1982 but we wish to also continue the observation of single trees in the future. We hope to complete the picture, that we have obtained to present under our conditions in the northern part of Bavaria.

DISCUSSION

Because the observations are not yet finished and the data are not completely evaluated, the preliminary results shall only be briefly discussed.

On the two observation plots 7% and 6.25% respectively of all beeches died between 1976 and 1982 after heavy attack by beech bark disease. This is much more than reported by Rhumbler (1931) who found 2% of the trees to be dead. Also the proportion of trees with heavy scale infestation and tarry spots was clearly higher and explains the higher mortality. Sporodochia of Cylindrocarpon could be found for a short time after the inoculation of healthy bark but the fungus could not spread into the unwounded tissue. That means that heavy scale infestation enables the fungus to grow within the tissue which is perhaps weakened and predisposed by the scales (Lonsdale 1980).

It seems to be possible that climatic conditions also play a role in predisposing trees (Parker 1974, Lonsdale 1980), for example the fungus cannot be restricted by the formation of a periderm and the disease development could be accelerated. The fact that many heavily attacked trees are still alive could be explained by the favorable climatic conditions in the last several years which effectively increased their vitality or by a different degree of resistance against fungal attack. We have to wait and to see if the development of healing and recovery will take place as Ehrlich (1934), Rhumbler (1931), and Piraux (1980) observed or if the process of dying is only delayed. Rhumbler (1931) observed that trees may die about 15 years after the outbreak of the disease.

The drought of 1976 seemed not to have an influence on the scale population on our plots. An increase of the scale population of some trees started much later. On the other hand such a connection is often proposed by foresters (Lang 1982).

Different degrees of resistance against Cryptococcus fagisuga (Wainhouse 1980) could also explain the great differences in scale infestation. Schimitschek (1980) found that there is some relationship between the number and size of sclereids in the bark and the intensity of scale infestation.

The fact that heavily attacked beeches can be detected on aerial photographs is well known (Parker 1977, Perrin 1977, Heeschen 1977). A prognosis of the further development of single attacked individuals is still doubtful. Therefore the recommendation to the foresters remains the same as it has been for 100 years, namely to remove heavily attacked trees from the stand because wood deteriorating fungi invade the trees very early, especially where the infection pressure from the surroundings is high, and also because after a healing process, which may take place, there remain damages in the wood which devaluate the quality of the stem (Wujciak 1975).

ACKNOWLEDGEMENTS

I thank Mr. J. Arnone and Mr. J.-M. Vincent for their help with preparing the English and French translations.

SUMMARY

Since 1976 the development of beech bark disease was observed on two plots in northern Bavaria. Of 600 trees marked for our experiment about 200 have been infested by Cryptococcus fagisuga. Between 1976 and 1982 about 125 of them had, at least for some time, moderate or heavy infestation. Tarry spots were observed on 87 trees during this time, and 39 beeches (= 6,5%) are dead now. Slime flux nearly always appeared in connexion with heavy scale infestation. Fructifications of Nectria and Cylindrocarpon were found on many of these trees. The fungus could also frequently be isolated from the margins of bark necroses. On the other hand fructifications were rare on trees which are still alive.

Fruitingbodies of wood deteriorating fungi occured on the two plots to different degrees. On the plot at Rohrbrunn Fomes fomentarius dominated, on the plot at Rothenbuch the distribution of Fomes fomentarius, Fomitopsis pinicola, Stereum spp., Bjerkandera adusta and Inonotus nodulosus was rather uniform.

The high infection pressure at Rohrbrunn also seemed to be responsible for the invasion of Fomes fomentarius on the relatively great number of dead and still-living trees.

With the aid of aerial photographs at a scale of 1 : 5000 areas with beech bark disease were

easily detected. In some cases alterations of the crown of single trees could be persued for some years until the death of the tree. It seems, however, that only heavily attacked trees could be located with sufficient certainty.

On both plots the duration of the disease from the installation of a strong scale population to the break down of the tree took about 10 years. The development of the scale population required two years in some cases but longer in other cases.
On the bark of some beeches there were signs of recovery and healing from the disease.

RESUME

L'évolution de la maladie de l'écorce du hêtre sur deux parcelles expérimentales en Bavière du nord. Résultats préliminaires.

Le développement de la maladie de l'écorce du hêtre est observé depuis 1976 sur deux parcelles expérimentales en Bavière du nord. Sur 600 arbres marqués, environ 200 sont attaqués par Cryptococcus fagisuga. A peu près 125 d'entre-eux présentaient entre 1976 et 1980, en partie de manière discontinue, de fortes ou moyennes pullulations de l'insecte. Dans le même intervalle, on constata un suintement sur 87 arbres dont 39 (= 6,5%) sont morts depuis lors.

Dans presque tous les cas, une forte pullulation était liée à un suintement, souvent pendant une assez longue période. Un grand nombre de ces arbres portait des périthèces de Nectria et des coussinets conidiens de Cylindrocarpon. Nectria spp. fut également régulièrement isolé à partir de la zone periphérique de nécroses corticales. D'un autre côté, on ne put qu'assez rarement relever des carpophores de ce champignon sur les arbres encore vivants.

L'observation des carpophores de champignons lignivores sur les deux parcelles donna des résultats nettement divergents. Sur la parcelle de Rohrbrunn, on releva principalement Fomes fomentarius , tandis qu'à Rothenbuch Fomes fomentarius, Fomitopsis pinicola, Stereum sp. et Bjerkandera adusta étaient présents dans des porportions presque identiques. Sur la parcelle de Rohrbrunn, également en raison de conditions plus favorables à une infection, un nombre relativement plus élevé d'arbres morts, au même encore vivants, portait des carpophores.

L'observation de photographies aériennes à l'échelle 1/5000 permet de reconnaître aisément les peuplements atteints de la maladie de l'écorce du hêtre. Dans de nombreux cas, on put également suivre pendant plusieurs années l'évolution du houppier d'arbres bien délimités. Il semble toutefois que seul des dommages importants puissent ainsi être décelés d'une manière sûre.

La durée de la maladie, à compter de l'apparition d'une forte population de cochenilles jusqu'à la mort de l'arbre, devrait se situer sur les deux parcelles aux alentours de 10 années à peine.

Les populations de cochenilles se développent dans certains cas très rapidement, en l'espace de deux années; mais cette évolution peut demander également beaucoup plus de temps.
L'écorce de plusieurs hêtres presentent des indices qu'une cicatrisation et guérison des plaies est en cours.

ZUSAMMENFASSUNG

Entwicklung der Buchen-Rindennekrose auf zwei Beobachtungsflächen in Nordbayern im Verlauf von 7 Jahren.

Auf zwei Beobachtungsflächen in Nordbayern wird seit 1976 die Entwicklung der Buchen-Rindennekrose beobachtet. Von den 600 markierten Bäumen sind rund 200 von Cryptococcus fagisuga befallen. Zwischen 1976 und 1982 wiesen etwa 125 von ihnen zumindest zeitweise mittleren oder starken Lausbefall auf. Schleimfluß war im gleichen Zeitraum an 87 Bäumen festzustellen, 39 Bäume (= 6,5%) sind inzwischen abgestorben.

Im Zusammenhang mit starkem Lausbefall wurde fast regelmäßig und oft über einen längeren Zeitraum Schleimfluß beobachtet. Fruchtformen von Nectria und Cylindrocarpon waren an vielen dieser Bäume zu finden. Auch aus dem Randbereich nekrotischer Rindenpartien konnte Nectria spp. fast regelmäßig isoliert werden. Andererseits hat dieser Pilz an den noch lebenden Buchen relativ selten Fruchtkörper gebildet.

Fruchtkörper holzzerstörender Pilze kommen auf den beiden Beobachtungsflächen in deutlich unterschiedlichem Maße vor. Während in Rohrbrunn überwiegend Fomes fomentarius vorkommt, sind in Rothenbuch Fomes fomentarius, Fomitopsis pinicola, Stereum spp., Bjerkandera adusta und Inonotus nodulosus fast in gleichem Maße vertreten. Der starke Infektionsdruck auf der Fläche in Rohrbrunn ist auch dafür verantwortlich zu machen, daß hier verhältnismäßig mehr abgestorbene und sogar noch lebende Bäume Fruchtkörper tragen.

Auf Luftbildern im Maßstab 1 : 5000 lassen sich Gebiete, in denen die Buchen-Rindennekrose

auftritt, deutlich erkennen. In einer Reihe von Fällen lassen sich auch die Veränderungen an der Krone einzelner Bäume über mehrere Jahre verfolgen. Es scheint jedoch, daß nur starke Schäden mit ausreichender Sicherheit nachgewiesen werden können.

Auf den beiden Beobachtungsflächen ist mit einer Krankheitsdauer der einzelnen Bäume, von der Entwicklung einer starken Lauspopulation bis zum Absterben, von schätzungsweise knapp 10 Jahren zu rechnen. Die Entwicklung der Lauspopulation verläuft in einzelnen Fällen sehr rasch innerhalb von zwei Jahren, kann jedoch auch erheblich länger dauern. An der Rinde einer Reihe von Buchen sind Anzeichen von Überwallung und Ausheilung der Schäden erkennbar.

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EFFECTS OF SPECIES COMPOSITION AND SITE FACTORS ON THE SEVERITY OF BEECH BARK DISEASE IN WESTERN MASSACHUSETTS AND THE WHITE MOUNTAINS OF NEW HAMPSHIRE: A PRELIMINARY REPORT[1]

Mark J. Twery and W. A. Patterson III[2]

Abstract.--The extent of beech bark disease was examined on permanent inventory plots in western Massachusetts and on Bartlett Experimental Forest in New Hampshire. The amount of disease-caused defect was correlated with a reduction in the proportion of beech in a stand. Sites on lower slopes and with greater abundance of hemlock contained more defective beech.

INTRODUCTION

Beech (Fagus grandifolia) is a major component of the northern hardwood forests of New England. Although it is of less commercial importance than its companion species, sugar maple (Acer saccharum) and yellow birch (Betula alleghaniensis), beech is a valuable timber tree used for furniture parts, turning stock, fuelwood, and pulp. Beech mast is of great value to wildlife in the northern hardwood forests. The beech bark disease (BBD) has caused widespread destruction of mature beech stands resulting in lost value of standing timber and forest production. The true extent of this loss is unknown. Different species mixtures and environmental factors have been suggested as important potential sources of variation in the disease (Houston 1980). Conversely, the disease is a potential major influence on future species composition and stand structure (Filip 1978). This paper is a preliminary report on a study designed to examine both of these problems and to determine some of the specific causes and effects of variations in BBD.

BBD in North America is generally accepted to be a complex of the scale insect Cryptococcus fagisuga Lindinger, and the fungus Nectria coccinea var. faginata, as described by Ehrlich (1934). The insect was first noted in the western hemisphere in Halifax, Nova Scotia in 1890. The first disease outbreak in the United States occurred in Maine about 1930. The disease has since spread throughout New England, parts of eastern Canada, New York, and into Pennsylvania (Houston et al. 1979). Shigo (1972) described the progress of the disease as consisting of three stages: the advancing front, the killing front, and the aftermath zone. Most of New England is now in the aftermath zone, and BBD is endemic throughout (Houston 1975).

Diseases have been shown previously to be causes of considerable changes in forest composition. Davis (1981) has postulated that a disease of yet undetermined origin destroyed widespread hemlock stands about 4800 B.P. and caused changes in forest species composition (as determined by pollen analysis) that lasted for several hundred years. More recently, the destruction of chestnut (Castanea dentata) in the early 20th century substantially altered species composition of oak hardwood stands of the northeastern United States (Aughanbaugh 1935 e.g.). During the past two to three decades, Dutch elm disease (Ceratocystis ulmi) has also changed stand make-up (Eyre 1980). Similar effects might be expected from BBD. Beech, however, because of its ability to reproduce vegetatively by root suckers, has in some areas increased in basal area and density after destruction of overstory individuals by BBD (Houston 1975).

Few studies have examined the factors affecting the intensity of BBD within a stand. Mize and Lea (1974) found the highest

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[1] Paper presented at the IUFRO Beech Bark Disease Working Party Conference, Hamden, CT. USA, 27 Sep to 7 Oct 1982.

[2] Master's candidate and Assistant Professor, respectively, Department of Forestry and Wildlife Management, University of Massachusetts, Amherst, MA 01003, USA.

probability of beech mortality among trees of large diameter and low vigor. Parker (1980) found that competition within a stand lowers host resistance and increases risk of mortality for European beech (F. sylvatica). Lonsdale (1980) found that drought was an agent of stress which contributed to more severe disease symptoms. Parker (1974) and Lonsdale et al. (1979) also detected a correlation between depth of soil over chalk and amount of chalk incorporated into soils and the incidence of BBD in England. Topographical influences have also been found important in previous studies. Those trees likely to be first affected were found by Houston et al. (1979 and 1979a) and Parker (1974) to be ones on midslope or ones downwind of large, old, infested trees. Site conditions and soils are also recognized as significant influences on the ability of beech to compete with other species (Leak 1978, 1980) and may influence the impact of BBD on a stand.

STUDY AREAS

Because part of this study is an attempt to document changes in forest compositions attributable to beech bark disease, we needed stands with available data regarding the composition prior to infection. The most readily accessible data are from the Massachusetts Continuous Forest Inventory (CFI), for which permanent plots have been sampled periodically since the early 1960's. Because BBD mortality did not occur in substantial amounts in Massachusetts until the late 1960's, these records were considered acceptable. In order to examine differences over a wider geographical area and to include areas where BBD has been present longer, we also studied permanent inventory plots in the Bartlett Experimental Forest in NH. The plots in Bartlett were established initially in the 1930's and the BBD killing front passed through the area in the 1950's (Filip 1978).

Initially, we selected all plots on which beech made up at least 20% of the stems with a diameter at breast height (DBH) $\geq$ 5 inches (13 cm). Those plots with recent cutting were subsequently omitted.

The CFI plots sampled in Massachusetts are well distributed over state forest lands in four western counties. They vary in elevation from 600 to 2900 ft (180 m to 900 m). We sampled 41 plots during the summers of 1981 and 1982 from 94 which met the initial criteria. CFI plots are circular and cover an area of 0.20 acre (0.08 ha).

Bartlett Experimental Forest is in the eastern part of the White Mountains National Forest in New Hampshire. It occupies 2600 acres (1053 ha) on a generally northeast facing slope. Elevation varies from 700 ft to 3000 ft (210 m to 930 m). The plots sampled were from both the lower, gentler slopes and the upper, steeper slopes ranging from 800 to 2000 ft (240 m to 610 m) elevation. The inventory plots on Bartlett are 0.25 acre (0.10 ha) squares. A total of 25 plots were sampled for this study out of 47 which met the initial criteria. Time constraints and accessibility (< 1 mi from a road) limited the number of plots we could sample. Selection was subjective, with an attempt to distribute samples over a wide range of elevation, physiography, and geographical location (Figure 1).

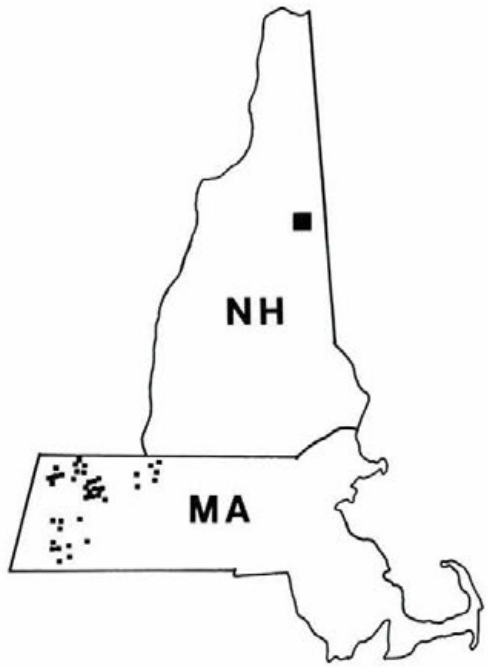


Figure 1.--Locations of sample plots in Massachusetts and New Hampshire.

PROCEDURES

On each plot, all woody stems $\geq$ 2 inches (5 cm) dbh were recorded by species, diameter class (to the nearest inch), crown class (dominant, codominant, intermediate, or suppressed), and condition (good, fair, poor, or dead). On beech $\geq$ 2 in dbh, variables relating to the incidence of BBD were also recorded according to the systems developed cooperatively by the USDA Forest Service and the British Forestry Commission (Houston et

al. 1979a; Houston personal communication). These include the amount of wax present (as an indicator of scale population) by height zones and aspect, presence of Ascodichaena rugosa, abundance and aspect of algae and lichens, and the amount of fruiting of N. coccinea var. faginata present by height zones. Because current fruiting was considered insufficient to describe the amount of Nectria attack over a prolonged period, we added an index of visible defect due to old infections, using the same scale as for fruiting (0 to 4 for none to very heavy, respectively) of Nectria. Each tree was divided into three height zones: 0 to 2 m, 2 to 4 m, and over 4 m. We also recorded the number of tarry spots present, the number of Xylococculus betulae present, and the presence or absence of callusing. Site data recorded for each plot included 11 variables: aspect, percent slope, slope position (1=ridge and upper slope, 2=midslope, 3=lower slope, 4=bottom), elevation, canopy closure, canopy height, and percent cover of hardwood litter, softwood litter, bare soil, exposed rock, and fallen wood.

All analyses described in this paper were performed only on 1981 data, on 10 plots each from Massachusetts and New Hampshire. Results and the hypotheses generated will be tested against the 1982 data when they are available.

RESULTS

The first question to be addressed was whether the data recorded provided a meaningful index of the severity of the disease on any given plot. The amount of current fruiting of Nectria was deemed inappropriate, for much of the damage had occurred up to 25 years ago and often little fruiting was present in obviously damaged stands. The appropriate index appeared to be evidence of both past and present Nectria activity provided by the defect variable, which was recorded on each beech by intensity in each of three height zones. A total defect index for each tree was arrived at by summing the scores for each zone (possible scores 0-12 for live trees). A tree apparently killed by BBD was given a score of 13. The mean defect score for trees $\geq$ 5 in dbh on each plot was used as an index of BBD severity on that plot.

The six most important species found were beech, sugar maple, red maple (Acer rubrum), yellow birch, black birch (Betula lenta), and hemlock (Tsuga canadensis). These six species accounted for at least 80% of stocking on almost all plots. Total density and basal area in trees $\geq$ 5 in dbh were computed, as were the relative proportions of each of the six species. These figures were then used in analysis of composition of the plots. Important variables are summarized in Table 1.

Table 1.--Defect, stand, and site parameters on plots in Massachusetts (all digits) and New Hampshire (lettered plots).

Plot	Average Defect	Net Change Beech BA	Percent Hemlock BA	Slope Position
R-28	9.25	-26.0	51.4	4
M-28	7.96	-0.7	22.8	3
T-28	7.89	-28.4	24.0	4
V-11	7.80	-5.2	15.4	2
1026	7.67	-12.6	2.9	3
1057	7.65	-8.4	10.8	2
O-28	7.09	-31.0	62.9	3
V-13	6.22	-18.3	27.7	2
1087	6.00	10.3	0.8	1
83	5.88	-4.9	32.3	1
1037	5.88	20.1	41.4	2
Y-34	5.79	-9.4	17.7	3
1018	5.67	-7.6	32.4	2
X-12	5.39	-16.6	10.7	2
89	5.15	-8.3	0	1
1022	5.15	5.2	6.9	2
Z-32	5.00	25.9	0.8	2
915	4.53	0.4	0	2
V-28	3.94	18.1	0	4
1045	1.46	7.5	0	1

The total defect of each tree was compared to its diameter and crown class to determine whether this produced results similar to those described elsewhere (Mize and Lea 1979, Ehrlich 1934, Shigo 1972). Diameters were grouped into four classes: saplings (2 to 4 inches; 5 to 12 cm), poles (5 to 9 in; 12 to 23 cm), small sawlogs (10 to 14 in; 25 to 36 cm), and large sawlogs (over 14in; 36 cm). Saplings had significantly less defect than the poles, which had significantly less defect than the sawlogs (Table 2). The two sawlog classes, however, were not significantly different.

Crown class also had a significant effect on defect (Table 3). All crown classes were significantly different from each other, with dominant having the most defect, codominant next, then intermediate, and suppressed trees showing the least defect.

Severity of BBD varied significantly among the plots (Table 1). That variation was along a continuum and separation of plots into meaningful discrete groups by amount of defect alone was not possible. Average defect was significantly negatively correlated with the change in the percentage of total basal area in beech (Figure 2).

Table 2.--Average Nectria defect by diameter class, live trees only.

Diameter Class	Number of trees	Mean Defect
Saplings	248	2.02
Poles	203	3.84
Small sawlogs	91	5.73a
Large sawlogs	38	6.24a
Total	580	3.52

[a]Values followed by the same letter are not significantly different at p = 0.05.

Table 3.--Average Nectria defect by crown class, live trees only.

Crown Class	Number of trees	Mean Defect
Dominant	20	6.75
Codominant	169	5.33
Intermediate	105	3.46
Suppressed	286	2.24
Total	580	3.52

The current beech density was significantly negatively correlated with average defect by plot (Table 4). Average defect was not significantly correlated with either total density or total basal area. However, average defect was significantly correlated with the proportion of basal area in hemlock (Figure 3). Average fruiting was very highly correlated to average defect. Average defect was significantly correlated with slope position. Analysis of variance showed no overall difference by slope position, but an a priori contrast of the two upper positions vs. the two lower ones did indicate significantly more defect on the lower slopes.

None of the other site variables were significantly correlated with the severity of BBD. An additional variable, solar radiation index (SRI), was derived from a combination of aspect and slope (Frank and Lee 1966), but it was correlated only with total density, and had no relation to the disease. Abundance of the scale was almost totally independent of defect (R=0.01). Elevation was the only plot variable which showed a significant correlation with the scale.

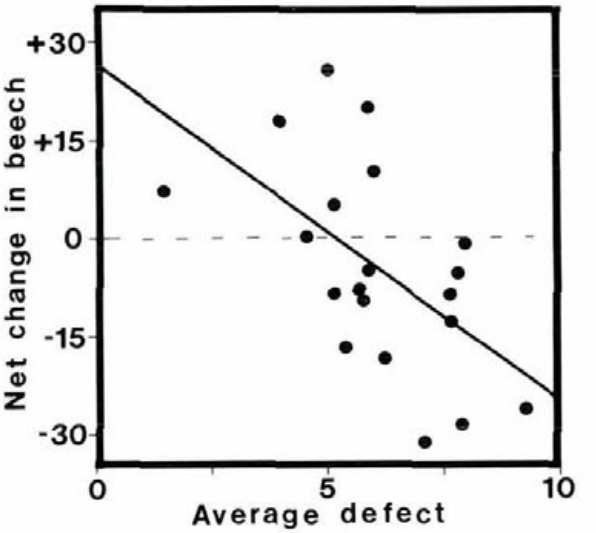


Figure 2.--Regression plot of change in percent basal area beech vs. average defect.

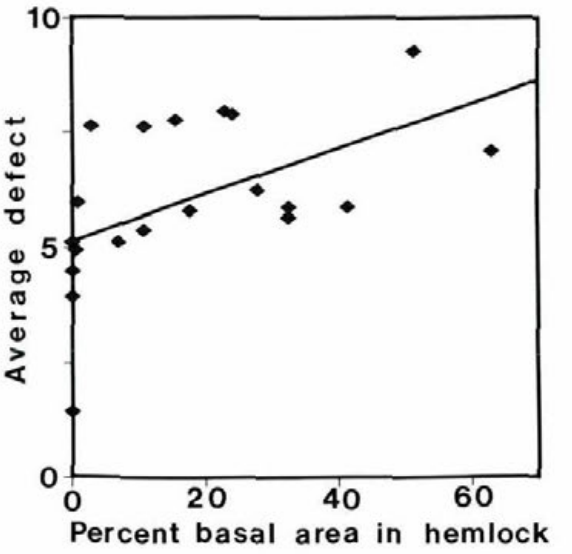


Figure 3.--Regression plot of average defect vs. percent basal area in hemlock.

Table 4.--Correlations of average defect with various site characteristics.

Variable	Correlation Coefficient(R)	Significance Level
Current Hemlock Density(%)	.5521	.006
Current Hemlock Basal Area(%)	.5195	.009
Average Fruiting Index	.8913	.001
Slope Position	.4858	.015
Net Change in Beech Basal area(%)	-.5688	.004
Net Change in Beech Basal Area(absolute)	-.4564	.022
Current Beech Density(%)	-.4199	.033
Net Change in Beech Density(%)	-.3836	.048

Stepwise multiple regression techniques produced the following equation:

$$Y=1.187(X_1)-0.698(X_2)+0.656(X_3)+0.590(X_4)$$

$$R=.816 \quad R^2=.665 \quad p=.002$$

where Y = predicted average defect

X_1 = current proportion of basal area in beech

X_2 = current proportion of stems in beech

X_3 = current proportion of basal area in hemlock

X_4 = slope position

and all coefficients are standardized. Figure 4 illustrates the goodness-of-fit of this prediction equation. The standardization of the coefficients allows comparison of their magnitudes despite differences in scale of the original variables.

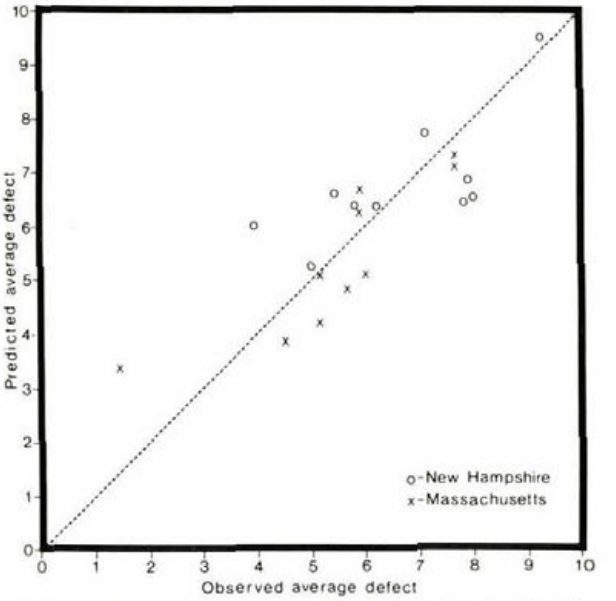


Figure 4.--Plot of predicted vs. observed values from the multiple regression equation. A perfect prediction would lie on the diagonal.

DISCUSSION

Beech bark disease has had a major impact on the composition of some northern hardwood stands in this study. An undisturbed stand of northern hardwoods in New England tends to increase its proportion of beech (Forcier 1975). Those stands where intensity of BBD is high, however, have experienced a reduction in beech generally in proportion to the intensity. This net loss of beech either through mortality or growth loss is important to the forest manager, who must decide how to deal with the effects of the disease.

The multiple regression equation is a remarkably good predictor of defect based on so few cases. If the final results of this study confirm these findings, it should prove useful and practical for management use because it involves only four easily measured variables.

In the part of New England where this study was conducted the most virulent attacks appear to be over. Those stands which have been only lightly attacked are less susceptible, due in part to composition or site characteristics. In those areas such as Pennsylvania or West Virginia, where the killing front has not yet passed, a classification of risk by composition and site could be very useful in deciding which stands to cut in advance of BBD attack. The

fact that BBD attacks in a similar manner in this study area and in other previously mentioned areas suggests that our results may be applicable elsewhere.

Variation in the severity of BBD and its impact on a stand can be due to a number of factors. The lesser severity of BBD on plots with many small trees, as evidenced by the negative correlation of defect with beech density, implies that younger stands may not have catastrophic dying-off of beech. Ingrowth of small trees may account for increases found in beech stocking despite heavy disease of the larger trees, as on plot 1087. Other unrelated stand dynamics, such as the deaths of overmature paper birch (Betula papyrifera) may also lessen the noticeable impact of BBD on percent composition, as on plot M-28. The high correlation between fruiting and defect implies that the activity of Nectria has persisted on those sites where it has established itself. The scale is present in some numbers on all plots. The lack of correlation between defect and scale population may be due to the lag time involved between infestation and infection or to the cumulative nature of the defect index. The population dynamics of the scale in the aftermath zone appear to be based on some factors other than those measured in this study.

Those factors which had the most influence on the severity of BBD , aside from the presence of large beech, were the amount of hemlock and the slope position. Both of these factors appear to be explicable as increasing the protection which the site affords to the disease agents. Protected sites such as these would be subject to less extreme fluctuations of temperature and would maintain higher humidities. The presence of hemlock would serve to shade the trunks of the beech all winter, when alternate freezing and thawing might otherwise have a detrimental effect on the scale population.

CONCLUSIONS

This study found greater average defect in the presence of greater proportions of hemlock and on lower slopes. Other variations in species composition were not significant. Other site factors such as soil texture and drainage have not yet been examined. Nor has the additional data from the second field season been analyzed to determine whether it might confirm these hypotheses.

One outgrowth of the effect of increased hemlock on the severity of BBD is that where beech and hemlock are mixed presently, the hemlock appears to be taking a large share of the stocking and may eventually reduce beech to a minor species on these sites. On those upper slopes where hemlock is not present, BBD appears much less severe and beech is maintaining its proportion in the stand.

If these observations are confirmed by further study, they should prove useful as quick indicators to the forest manager of whether beech should be discriminated against because of high risk of BBD.

ACKNOWLEDGEMENTS

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RÉSUMÉ

L'importance de la maladie de l'écorce du hêtre (Fagus grandifolia) a été examinée sur les parcelles d'inventaire permanent dans l'ouest du Massachusetts et dans la forêt experimental de Bartlett au New Hampshire. La quantité de défaut causé par la maladie a été corelée à la reduction de la proportion de hêtre dans un peuplement. Les endroits situés au bas des pentes et avec une plus grande abondance de Tsuga canadensis sont couverts de hêtre plus susceptible à être attaqués par cette maladie.

ZUSAMMENFASSUNG

Das Ausmass der Buchen-Rindennekrose wurde auf Dauerbeobachtungsflächen im westlichen Massachusetts und im Bartlett Experimental Forest in New Hampshire untersucht. Es zeigte sich, dass eine Beziehung zwischen dem Ausmass der Schäden und dem Rückgang des Buchenanteils in den Beständen besteht. Flächen im unteren Teil von Hängen und solche mit höherem Anteil an Tsuga canadensis enthielten mehr geschädigte Buchen.

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AN APPROACH TO MODELING THE CONSEQUENCES OF BEECH MORTALITY FROM BEECH BARK DISEASE[1]

Harry T. Valentine[2]

Abstract.--Changes to an extant model of forest growth and transition that allow an evaluation of the consequences of beech bark disease are outlined. Required are a function to scale beech growth for the effects of beech bark disease, a function to predict beech mortality from beech bark disease, and a function that predicts root-sprout regeneration of beech.

The introduction of Cryptococcus fagisuga to North America and the ensuing occurrence of beech bark disease has caused noticeable, but largely unquantified, changes in the relative species composition and productivity of northern hardwood forests. One way to quantify the effects of beech bark disease is to use a model of forest growth and transition that can project changes in a stand over time with, and then without, the influence of beech bark disease. No model that is currently available can do this with any degree of validity, but a model has been developed that yields quantitative descriptions of northern hardwood growth, transition, and nitrogen dynamics in the absence of beech bark disease. This is the FORTNITE model as documented by Aber and Melillo (1982). This model has as its underpinnings the JABOWA model, which was first documented by Botkin, Janak, and Wallis (1970). This paper discusses modifications to JABOWA or FORTNITE that would be needed to simulate the effects of beech bark disease on forest growth and transition.

Both JABOWA and FORTNITE project the growth of individual trees on 10- by 10-m plots on a yearly time-step. The fundamental tree growth function as the form:

$$\frac{d[D^2H]}{dt} = R \cdot LA \cdot (1 - DH/D_{max}\, H_{max}) \qquad (1)$$

where

R is a growth rate parameter,

LA is the estimated leaf area of the tree,

D is tree diameter measured at breast height (137 cm),

H is tree height, and

D^2H is proportional to tree volume.

The value of R depends on intertree crowding, yearly evapotranspiration, and growing degree days. The crowding factors vary among trees on a plot; the environmental effects vary among species. In FORTNITE, R also is scaled for available nitrogen, which is a dynamic variable. To simulate beech bark disease, an additional scaling factor is needed to slow the growth of diseased beeches. Mize and Lea (1979) reported that the 10-year diameter growth of beech during a disease episode in the central Adirondacks of New York was 74% of the predisease rate. How much of this diameter-growth reduction was due to beech bark disease is unknown as diameter growth may decrease over time in the absence of disease.

To scale diameter growth, we note that

$$d[D^2H]/dt = (d[D^2H]/dD)\,dD/dt \qquad (2)$$

[1]Paper presented at the IUFRO Beech Bark Disease Working Party Conference, Hamden, CT. USA. 27 Sep to 7 Oct 1982.

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so that

$$dD/dt = R \cdot LA \cdot (1-DH/D_{max} H_{max})/(2DH+D^2 dH/dD) \quad (3)$$

In JABOWA and FORTNITE, H and dH/dD are removed from the right hand side of (3) using the assumed relation

$$H = 137+b_1 D-b_2 D^2 \quad (4)$$

for which

$$dH/dD = b_1-2b_2 D \quad (5)$$

The values of b_1 and b_2 are constrained to yield $H=H_{max}$ and $D=D_{max}$ when $dH/dD=0$, i.e., $b_1=2(H_{max}-137)/D_{max}$; $b_2=(H_{max}-137)/D_{max}$, where 137 is breast height (cm). Thus, the parametrization is based on H_{max} and D_{max}, i.e., the heights and diameters of record trees for each species.

Stout and Shumway (1982) have shown that the H vs D relation in hardwoods varies with site quality, and have proposed the relation

$$dH/dD = b(S-H) \quad (6)$$

S is site dependent, and b varies among species, but is constant within species. This function can be solved in closed-form to yield

$$H = 137+S(1-\exp(-bD)) \quad (7)$$

where 137 (cm) is a correction for D measured at breast height. Utilization of (6) and (7) would require a function that predicts S with the environmental variables in JABOWA or FORTNITE. Whether (4) and (5) or (6) and (7) are used on the right-hand side of (3), a scaling function is needed to account for the effects of beech bark disease. Undoubtedly, the growth reduction will vary in time and place.

Perhaps the greatest impact of beech bark disease is the mortality of beech in regions that are newly infested by beech bark disease. In JABOWA and FORTNITE, tree death is a random event. Each species (i) is assumed to have a maximum age ($AGEMX_i$) to which it can live. Each tree of the i^{th} species has a yearly probability of death equal to $4.0/AGEMX_i$. In addition, if dD/dt is less than a minimum increment, a tree's probability of death is increased by .368.

To determine whether a tree should be removed, a uniform random deviate from $\underline{U}(0,1)$ is generated. If the random number is less than the probability of mortality, the tree is removed. Although we can scale dD/dt to account for beech bark disease and may thereby increase the probability of death, this will not cause enough trees to die to simulate a disease episode.

One way to proceed is to use the logistic function to predict the probability (P) that a tree will die within a year as:

$$P = 1/[1+EXP(b_o+b_1X_1+b_2X_2+\cdots+b_nX_n)] \quad (8)$$

where

X_i are variables describing the tree and its disease, if any

b_i are coefficients estimated by logistic discrimination

The probability of tree death will change as one or more of the X_i change.

An obvious disease variable is disease presence (1) or absence (0) in the location of interest. Figure 1 shows the estimated beech mortality rate at the generally infested Huntington Wildlife Forest, Newcomb, NY, between 1976 and 1981, by diameter class. Mortality rate was extreme in the largest diameter classes, but quite low in the smallest classes. On the basis of this relation we can speculate that after the initial onslaught of the disease has removed the largest trees, overall rate of mortality due to beech bark disease should decrease because growth is slowed and trees remain longer in the lower diameter classes. This appears to be the case in the so-called aftermath zone. Also included in Figure 1 for comparative purposes are the estimated 5-year mortality rates for sugar maple and yellow birch by diameter class. In the absence of beech bark disease we should expect beech mortality to be similar.

Another major component of forest transition models is a procedure to simulate ingrowth. In FORTNITE, the number of trees of each species that is added to a plot each year depends on available light, soil moisture, nitrogen, and degree-day variables. The diameter at breast height (1.37 m) of a new stem ranges between 0.5 and 0.7 cm according to a uniform random deviate. The procedure makes no distinction between new stems of seed or sprout origin and may

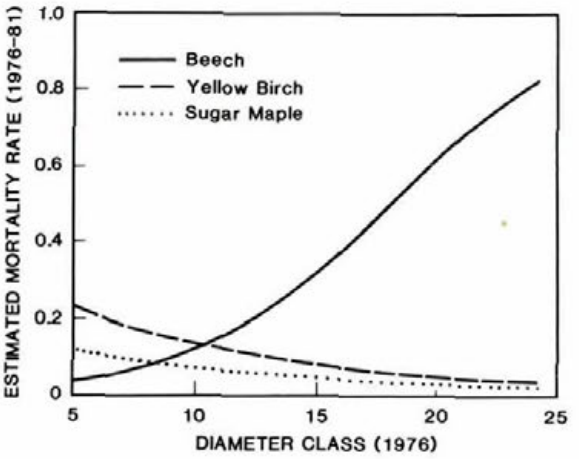


Figure 1.--Estimated five-year mortality rates for beech, yellow birch, and sugar maple at the Huntington Wildlife Forest, Newcomb, New York, by diameter class.

underestimate the ingrowth of small beeches of root-sprout origin which are released when the parent stems die from beech bark disease. This deficiency can be overcome by adding to FORTNITE a sprout regeneration procedure patterned after the one described by Shugart and West (1976).

Before a model is used to draw conclusions about the consequences of beech bark disease, trials should be undertaken to see if solutions of the model bear some correspondence to reality. With such assurance obtained, ameliorative silvicultural treatments can be simulated and their respective expected marginal benefits computed and ranked. It is then wise to determine whether the best (most profitable or least costly) treatment changes when small changes in the values of the parameters and initial values of the state variables are imposed. If the suggested silvicultural alternative is sensitive to a small change in the model, it may be necessary to obtain a more precise estimate of a parameter or an initial value. There is also the possibility that two or more treatments will yield virtually equivalent returns, but this should be obvious before the sensitivity analysis is undertaken.

SUMMARY

The FORTNITE model (Aber, Melillo, and Federer, 1982) simulates the growth, transition, and nitrogen dynamics of the northern hardwood forest type in eastern North America. A major species of this forest is beech, which recently has become infected by beech bark disease. As structured presently, the model does not simulate the influence of beech bark disease. This paper outlines the changes and additions to FORTNITE that are needed before such simulations are possible. Required are a function to scale beech growth for the effects of beech bark disease, a function to predict beech mortality from beech bark disease, and a function that predicts root-sprout regeneration of beech. After these changes are incorporated into FORTNITE it should be possible to do simulations with and without the influence of beech bark disease in order to assess some of its ecological consequences.

RÉSUMÉ

Le modèle FORTNITE (Aber, Melillo et Federer, 1982) simule la croissance, la transition et la dynamique de l'azote dans le type forestier de la forêt feuillue du nord-est américain. Une essence très importante de ce type forestier est le hêtre à grandes feuilles, qui est récemment devenu infecté par la maladie de l'écorce du hêtre. Tel qu'organisé présentement, le modèle ne simule pas l'influence de cette maladie. Le présent article donne un aperçu des changements et additions nécessaires à FORTNITE afin de rendre ces simulations possibles. Les paramètres requis sont: une fonction qui estime la croissance du hêtre pour connaître les effets de la maladie de l'écorce du hêtre; une fonction pour prédire la mortalité due à la maladie; et une fonction qui prédit la régénération par rejets de racines chez le hêtre. Après l'insertion de ces changements dans FORTNITE, il devrait être possible de faire des simulations, avec ou sans influence de la maladie de l'écorce du hêtre, afin d'en évaluer quelques-unes de ses conséquences écologiques.

ZUSAMMENFASSUNG

Das FORTNITE-Modell (Aber et al. 1982) simuliert Wachstum, Entwicklung und Stickstoffverhältnisse des nördlichen Laubwaldtyps im Osten Nordamerikas. Eine Hauptbaumart dieser Wälder ist die Buche, die derzeit unter der Buchen-Rindennekrose leidet. Das bisherige Modell berücksichtigt diese Krankheit nicht. Die vorliegende Arbeit befaßt sich mit den Änderungen und Ergänzungen des FORTNITE-Modells, die nötig sind, um diesem veränderten Sachverhalt Rechnung zu tragen und eine Simulierung zu ermöglichen. Dazu werden benötigt: eine Funktion für die Lausentwicklung im Zusammenhang mit der Buchen-Rindennekrose, eine Funktion für die Ausfallrate der Buche durch die Krankheit und eine Funktion, die die Wurzelbrutentwicklung der Buche erfaßt. Nach einer entsprechenden Erweiterung des FORTNITE-Modells sollte es möglich sein, die Bestandesentwicklung mit und ohne den Einfluß der Buchen-Rindennekrose zu simulieren und so einige ökologische Folgen der Krankheit abzuschätzen.

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THE LOOK AHEAD

The members of the IUFRO Beech Bark Disease Working Party agree that beech bark disease research ultimately should aim toward developing tactics for forest managers to minimize the adverse effects of the disease. Discerning what tactics are appropriate will require intensive studies of both Cryptococcus and Nectria and particularly their interaction with the host tree. Long-term observation of the natural disease situation will be necessary to determine the course of the disease under a particular set of ecological conditions and to estimate probable loss of yield.

Causal Organism Relationships

Cryptococcus fagisuga.--The utilization of resistance of trees to C. fagisuga is potentially one of the most promising aspects of disease management. We feel that characterization of resistance of trees to beech scale should be an important part of future work on the ecology of this insect. In particular we need to determine whether the observed resistance in the field is genetically determined and the relative importance of physical and biochemical factors which both seem to be involved in resistance. An assessment of how both site factors and bark epiphytes influence environmental resistance would also contribute greatly to our overall understanding of the ecology of host-tree resistance.

Current work on the population ecology of C. fagisuga should continue with some emphasis on the role of abiotic factors and possible role of entomogenous fungi in reducing populations. Genetic variation between sub-populations of C. fagisuga on different trees may contribute to the observed variation in the rate of build-up of populations within the forest. The consequences of this for subsequent disease development need to be assessed.

Some work on the biochemical mechanisms by which insects render host tissue susceptible to Nectria seems essential to an understanding of the nature of resistance and of the host's response to injury both from Cryptococcus and from Nectria.

Nectria fungi.--The inability of Nectria spp. to invade beech bark extensively in the absence of C. fagisuga infestation or other stress factors has recently emphasized the importance of the insect as the initiator of disease development. However, until populations of C. fagisuga can be reduced by appropriate management, we consider it essential to work towards limiting the impact of Nectria in infested stands.

The ability of Nectria spp. to exploit C. fagisuga-infested bark appears to have a biochemical basis and further study of this is essential in understanding the aetiology of beech bark disease. This exploitive ability seems to vary between the species of Nectria which are associated with the disease and measurement of variation could be important for developing epidemiological models in relation to the pathological potential of the Nectria population in any given region.

The response of the bark itself to Nectria attacks appears to be an important factor in the post-infection survival of trees and further work is needed to determine the nature and extent of this response among attacked trees. The ability of some trees at least in Fagus grandifolia to delimit lesions through the formation of necrophylatic periderm is of particular interest.

Further study of the pre-infection ecology of Nectria may be useful, especially as it suggests the possibility of reducing inoculum potential at a stage before serious damage to the tree has occurred. Biocontrol may be possible even at the stage of lesion extension, and this too may repay further work.

Forest stand relationships

Results from both Europe and North America suggest that the course of beech bark disease may differ both between trees and between forests. One manifestation of this in the aftermath beech forests of North America is that while most trees are highly defective, some trees and some stands appear to be little affected. In the forest emphasis should be placed on characterizing apparent resistance so that it can be enhanced or manipulated through appropriate forest management.

The root sprouting habit of F. grandifolia is an important consideration in the management of beech stands. Studies are needed to learn what factors influence the formation of root sprouts so that it may be enhanced in resistant trees and reduced in susceptible ones.

The beech plantation forests of Europe offer a unique opportunity to determine how disease development is affected by age, stand density, site factors and provenance. Data acquired from long-term disease observation plots are essential for understanding interactions between host, insect and fungus; environment and forest stand development. Such understanding is necessary before sound management practices can be prescribed.

The data from more intensive investigations could be incorporated in simulation studies of the ecological and economic consequences of the disease in both managed and unmanaged forests in order to determine possible management options. This approach seems deserving of emphasis given our improving knowledge of disease dynamics, the complexity of forests and the existence of new forest growth models.

NOTE

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