

Resistance of Conifers to Bark Beetle Attack: Searching for General Relationships

ERIK CHRISTIANSEN¹, RICHARD H. WARING² and ALAN A. BERRYMAN³

¹*Norwegian Forest Research Institute, N-1432 Ås-NLH (Norway)*

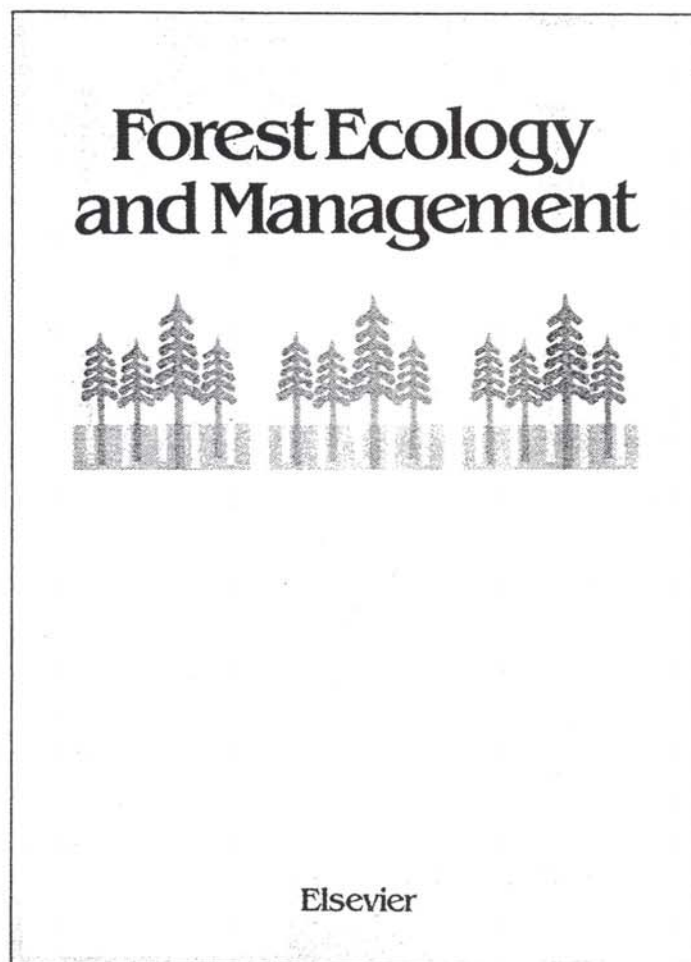
²*Department of Forest Science, Oregon State University, Corvallis, OR 97331 (U.S.A.)*

³*Department of Entomology, Washington State University, Pullman, WA 99164 (U.S.A.)*

(Accepted 14 May 1987)

ABSTRACT

REPRINTED FROM:



ELSEVIER SCIENCE PUBLISHERS, AMSTERDAM

Resistance of Conifers to Bark Beetle Attack: Searching for General Relationships

ERIK CHRISTIANSEN¹, RICHARD H. WARING² and ALAN A. BERRYMAN³

¹Norwegian Forest Research Institute, N-1432 Ås-NLH (Norway)

²Department of Forest Science, Oregon State University, Corvallis, OR 97331 (U.S.A.)

³Department of Entomology, Washington State University, Pullman, WA 99164 (U.S.A.)

(Accepted 14 May 1987)

ABSTRACT

Christiansen, E., Waring, R.H. and Berryman, A.A., 1987. Resistance of conifers to bark beetle attack: searching for general relationships. *For. Ecol. Manage.*, 22: 89–106.

Bark beetles are among the few native insects that can kill large numbers of trees in a single year. The present paper reviews recent work on the relationship between conifer resistance to bark beetle attack and tree vigor, e.g. in terms of wood production per unit of foliage. Experimental studies in the Pacific Northwest and the southeast U.S.A., and in Norway, are drawn upon to show that tree resistance to attack may be closely related to the amount of current and stored photosynthate that is available for defense. An experimental approach is advocated to critically test the relationship between host-tree resistance and the limitations on the transfer of critical resources to the site of attack.

ROLE OF BARK BEETLES IN NATURAL FOREST ECOSYSTEMS

As forests age they become more vulnerable to agents of disturbance such as high winds, fire, fungi, and bark beetles. These disturbing agents gradually cause the old forest to be replaced by new generations of trees. Associated improvements in nutrient cycling help to maintain the long-term productive capacity of the ecosystem (cf. Mattson and Addy, 1975; Romme et al., 1986). The bark beetles thus play an important role in natural ecosystems. The interaction between these beetles and their host trees has been established through some 200 million years of adaptation and counter-adaptation (see, e.g., Raffa and Berryman, 1987).

Bark beetles deposit their eggs in galleries excavated in the phloem, cambium, and outer sapwood of trees, and successful brood production is contingent upon the death of these tissues. Most species of bark beetles can only breed in trees that exhibit severe decline, or are already dead, and so merely promote decomposition and mineralization. A few species, however, are able

to attack and kill living, sometimes quite healthy, trees. Epidemics caused by these 'aggressive' species may dramatically alter the state and function of forest ecosystems over large areas.

Aggressive species have developed three important means of conquering living trees which resist their attack: (1) aggregation pheromones, which are chemicals emitted by pioneer beetles to summon a large number of conspecifics for mass attack (Rudinsky, 1962; Wood, 1982); (2) the ability to tolerate the defensive secretions of their hosts (Raffa and Berryman, 1987), and (3) mutualistic relationships with certain fungi that play an active part in killing the trees (see below).

Berryman (1972) reviewed the current knowledge of bark beetle/conifer interactions and proposed an inclusive hypothesis for conifer resistance to bark beetle/fungus attack. Since then, continuing research has generated new information on conifer interactions with several different bark beetle/fungus complexes. The present review is intended to update our general understanding of conifer defense as related to host-tree vigor.

In the last few centuries the development of forestry has drastically changed natural forest ecosystems. Modern civilization now covets nearly all woody biomass. Tree-killing bark beetles therefore have become a threat to forestry. Foresters are engaged in an endless war against the beetles, losing many a battle, in spite of a large arsenal of weaponry. We believe that the forest can only be successfully defended when we understand the beetles' natural role and take responsibility for preventing large areas of forests from becoming susceptible to attack (cf. Miller and Keen, 1960; Sartwell and Stevens, 1975).

BARK BEETLE EPIDEMICS

Most of the time, even the tree-killing bark beetles exist at low (endemic) population levels, surviving in dying trees, windfalls, or logging debris. Under certain circumstances, however, beetles may increase their breeding rate, and develop large (epidemic) populations which are capable of attacking living trees at sufficiently high densities to kill them.

A theoretical model (Fig. 1) linking the threshold of successful beetle attack to the vigor of individual trees or stands was originally suggested by Thalenhorst (1958) and explicitly formulated by Berryman (1978, 1982). The model assumes that tree vigor determines the number of beetles necessary to overcome its resistance, an assumption that is supported by empirical studies (Waring and Pitman, 1980, 1983; Raffa and Berryman, 1983; Mulock and Christiansen, 1986). Recording the number of attacks on a tree is a simple task; developing an adequate measure for tree vigor, however, is not so straightforward.

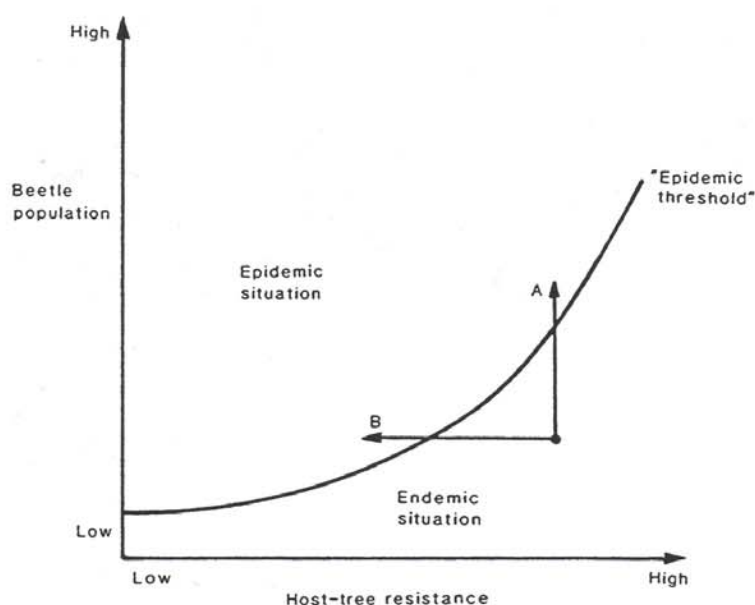


Fig. 1. A theoretical model for the relationship between host-tree resistance and threshold of successful bark beetle attack (After Berryman, 1978, 1982).

WHAT MAKES THE FOREST SUSCEPTIBLE TO BARK BEETLE ATTACK?

Numerous empirical studies relate susceptibility to bark beetles to a wide variety of environmental factors, and to structural characteristics of trees and stands. In several cases, outbreaks are associated with drought (e.g. Hopping and Mathers, 1945; Miller and Keen, 1960; Worrell, 1983a). Particular drought-prone sites can be identified by evaluating local hydrological factors. Conifers vary greatly in their capability to cope with drought, but species adapted to widely different water regimes are predisposed to bark beetle attack by extreme and persistent water deficits, viz. ponderosa pine and Norway spruce (Miller and Keen, 1960; Worrell, 1983a). Excessive moisture may also lead to increased susceptibility (Lorio and Hodges, 1968; Kalkstein, 1976).

Wind-felling frequently triggers epidemics. Many bark beetle species can take advantage of abundant breeding material which becomes available on such occasions (Schwerdtfeger, 1955; Furniss, 1962; Worrell, 1983a). Furthermore, it is generally assumed, although not yet experimentally proved, that many trees which escape wind-falling have their roots injured by swaying and hence become easy prey for bark beetles. Recent thinning could also produce this effect, by increasing air turbulence within the stand.

Other stochastic events have also been connected with bark beetle outbreaks. For example, lightning strikes may produce weak trees that serve as starting points for outbreaks (Coulson et al., 1983); large fire scars may weaken trees (Miller and Keen, 1960; Geiszler et al., 1980); and severe defoliation can render forests vulnerable to beetle infestation (Wright et al., 1979, 1984).

On the other hand, forest stands may *gradually* become susceptible to bark beetles. Studies connect beetle outbreaks to tree senescence (e.g. Miller and Keen, 1960) and to various indicators of severe competition, such as slow diameter growth (Person, 1928; Thatcher et al., 1980; Hard, 1985), high standing volume, basal area, or crown competition (Sartwell and Stevens, 1975; Schenk et al., 1980; Stevens et al., 1980; Thatcher et al., 1980; McCambridge and Stevens, 1982; Worrell, 1983b). Infection by root pathogens, which is often characteristic of ageing trees, may also predispose trees to bark beetle attack (e.g., Geiszler et al., 1980, and references therein).

Because phloem is a major food source of bark beetles, its quantity and quality have a bearing on the development of an epidemic. Stands with a preponderance of thin-phloemed trees cannot generate a large population of beetles (Amman, 1969; Berryman, 1976).

To put it briefly, experience shows that an array of events and developments may render forests susceptible to bark beetle epidemics. At first glance, these different disturbances and stand developmental changes may seem to have different causes. We believe, however, that it is possible to find a common denominator for the impact on host tree resistance by most of these factors — a general principle that will validate predictions of susceptibility of trees and stands. We believe that the key lies in the tree's carbon balance, carbon being the source of energy for defensive reactions and, hence, resistance to attack. The present paper elaborates on this hypothesis.

HOST TREE DEFENSES AGAINST BARK BEETLE ATTACK

During their long co-evolution with bark beetles, coniferous trees have developed two major defense mechanisms to counteract attacks by these insects (Berryman, 1972). Several genera such as *Pinus*, *Picea* and *Larix* possess a system of resin ducts in the phloem and xylem. If copious amounts of stored resin are exuded from these ducts, intruding beetles may be repelled, or 'pitched out' (e.g. Schwerdtfeger, 1955; Miller and Keen, 1960; Vité and Wood, 1961).

The exudation of constitutive resin depends on the storage capacity of the duct system and the viscosity of the oleoresin, whereas exudation pressure appears less important (Hodges and Lorio, 1971; but see Vité and Wood, 1961). The density of resin ducts may reflect various events in a tree's life, but does not appear directly related to radial growth (Reid and Watson, 1966, and references therein).

The amount of resin available also varies with season (Schwerdtfeger, 1955), new ducts being formed in the outer (latewood) part of the annual ring (Reid and Watson, 1966). Time of duct formation is assumed to be critically important to trees that are attacked year-round by consecutive generations of beetles, e.g. pines of the southeastern U.S.A. (Lorio, 1986). This first line of defense

seems highly developed in some of these pines which are able to mobilize large quantities of oleoresin and to pitch out large numbers of attacking beetles.

In other species, this first-line defense appears to be unreliable: Norway spruce, for example, often exudes very little resin upon initial attack (Christiansen and Horntvedt, 1983; Christiansen, 1985b) and the quantity tapers off rapidly as the number of attacks increases (Schwerdtfeger, 1955). In lodgepole pines, Raffa and Berryman (1982a) found no differences in exudation flow between trees that resisted or died from mountain pine-beetle attack.

Despite the erratic influence of external events on resin duct formation, oleoresin exudation flow still seems related to tree vigor: thinned, vigorously growing loblolly pines produced more pitch than unthinned ones, and had also accumulated higher starch reserves in spring (Matson et al., 1987, this volume).

Other trees such as true firs (*Abies*) do not have well-developed resin ducts in the xylem but possess resin-filled blisters in the cortex. These blisters, however, are usually avoided by attacking bark beetles (Ferrell, 1983).

If the flow from resin-containing structures fails to stop the beetles, they infect the host tissues with propagules of a variety of microorganisms, among which are usually woodstaining fungi. Inoculation experiments (Fig. 2) have shown that fungi of the genus *Ceratocystis* can kill healthy trees by penetrating their sapwood and blocking the transpiration stream (Nelson and Beal, 1929; Wright, 1935; Mathre, 1964; Basham, 1970; Horntvedt et al., 1983). In other cases, the role of the fungi seems more questionable viz. the southern pine beetle (Bridges et al., 1985).

When infected by microorganisms, be they fungi, bacteria, or viruses, most plants respond with a hypersensitive reaction (Klement and Goodman, 1967). A necrotic area is formed around the point of infection, depriving the invader of living tissues for food (Wong and Berryman, 1977).

In coniferous trees, the necrotic area is also impregnated with resinous and phenolic compounds (Fig. 3) that prevent beetle gallery construction and fungal proliferation (Reid et al., 1967; Berryman, 1969; Richmond et al., 1970; Shrimpton, 1973). This wound resin is highly toxic to bark-beetle eggs and larvae, and inhibits fungal growth (Cobb et al., 1968; Shrimpton and Whitney, 1968; Reid and Gates, 1970; Raffa et al., 1985). In grand fir, which lacks a resin-duct system, the wound reaction alone defends against the attack (Raffa and Berryman, 1982b). It also appears to be the most important defense in lodgepole pine (Raffa and Berryman, 1982a), and also in Norway spruce where the primary pitch-out capacity is very variable and generally low (Christiansen and Horntvedt, 1983).

The wound response is localized to areas immediately surrounding the infection and does not exceed a size necessary to contain both beetle and fungus (Wong and Berryman, 1977; Raffa and Berryman, 1982a; but see Stephen et al., 1983). This adaptation has two major advantages: (1) it conserves carbohydrates; and (2) it reduces the amount of cambium that must be replaced.

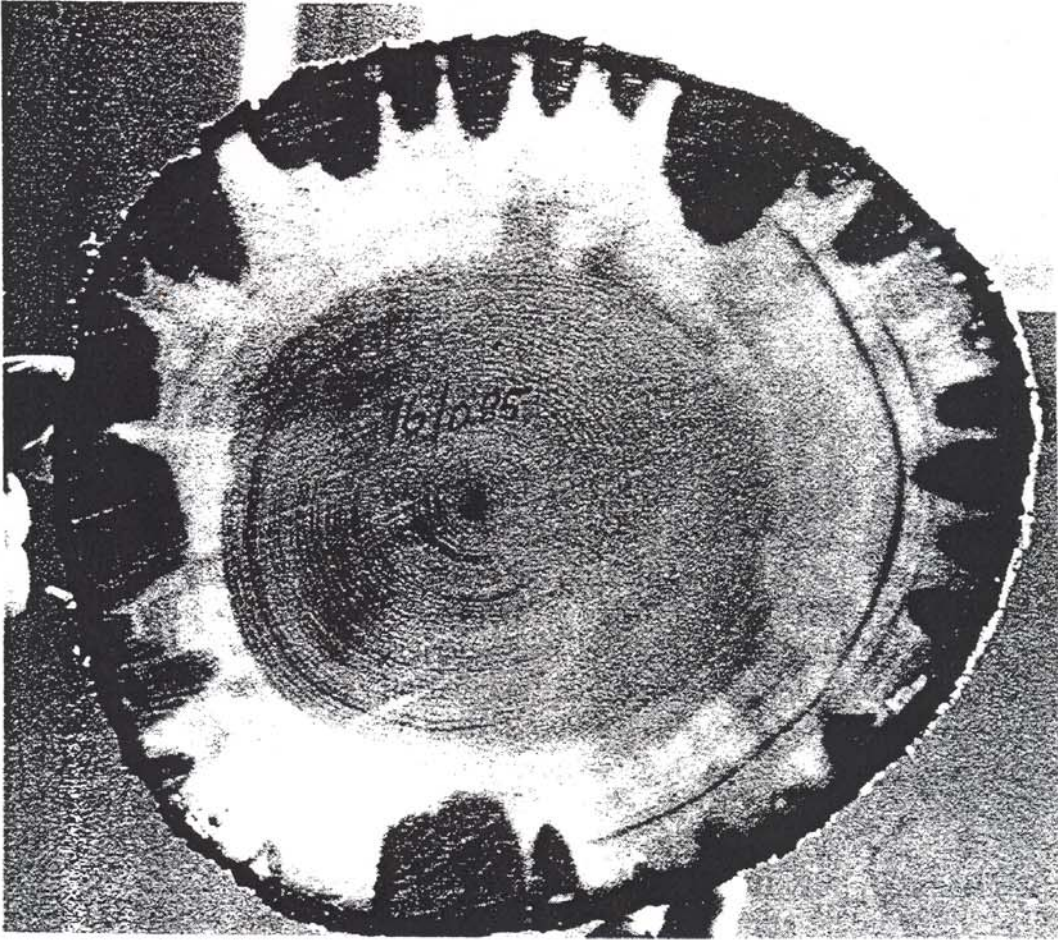


Fig. 2. In a Norway spruce tree inoculated with the fungus *Ceratocystis polonica* part of the sapwood has been invaded by the fungal hyphae. The infected sapwood appears opaque on a thin disc held against the light, due to low moisture content and discoloration by the blue-staining fungus.

Dosage-response experiments with fungal inoculations demonstrate that the concentration of defensive chemicals within the zone is crucial (Raffa and Berryman, 1983; Christiansen, 1985a). Such intensive, but conservative, reactions are observed in resistant grand fir and lodgepole pine (Raffa and Berryman, 1982a, b), and Norway spruce (Fig. 3).

If adequate resin is not secreted in time, the fungus may 'break out' of the wound reaction zone (Fig. 4). In such cases, the tree may then produce one or more additional zones outside the first one, until either the tree or the fungus wins the race.

Because an effective accumulation of resinous material is crucial for the containment of the fungus, an increasing number of attacks on a tree can exhaust the defense. This assumption has been experimentally confirmed in *Pinus* and *Picea*: when the number of attacks increases above a certain threshold level, the resin concentration of the individual reaction zones decreases (Raffa and

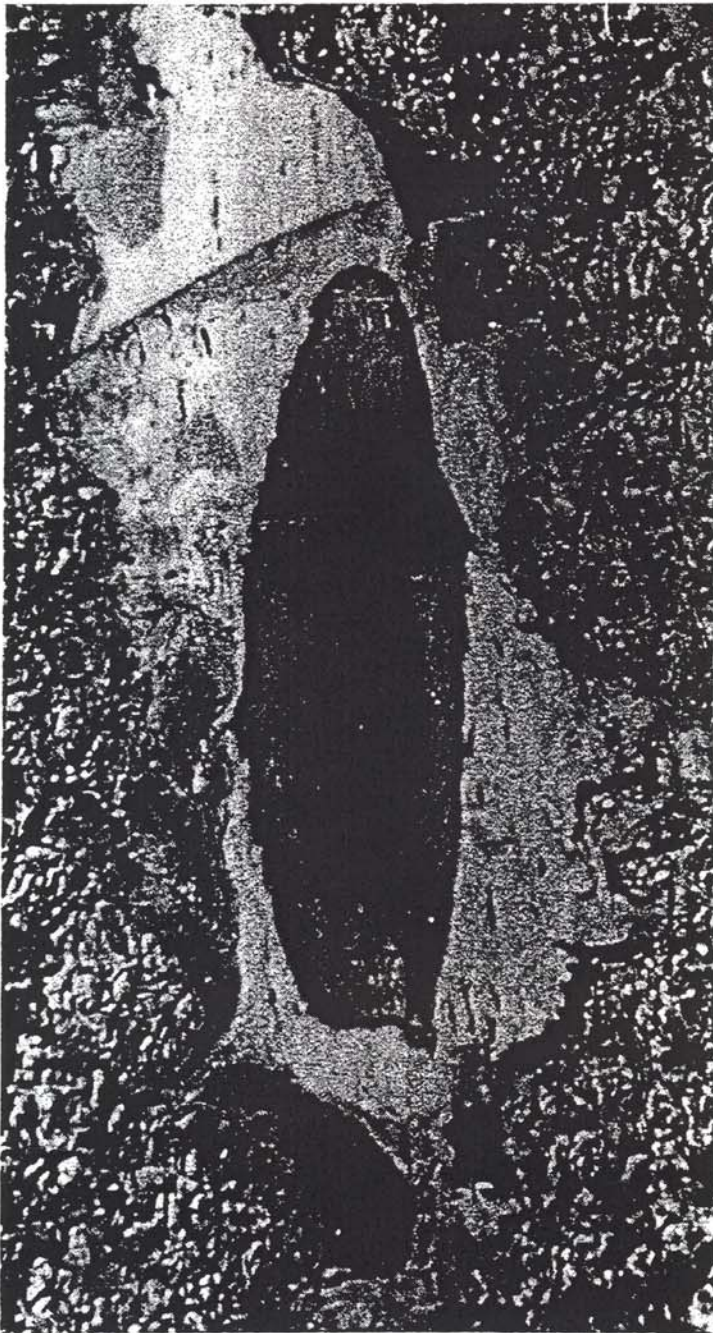


Fig. 3. A *Ceratocystis polonica* infection in Norway spruce has produced a characteristic wound reaction zone in the phloem. The inner, dark-colored area is penetrated with fungal hyphae; in the outer, lighter zone the fungal growth has been arrested by the resinous reaction. Along the outer border of the reaction zone a new periderm is being formed, and the resin-impregnated necrotic body is eventually sloughed off with the bark. The length of the reaction zone shown is about 50 mm.

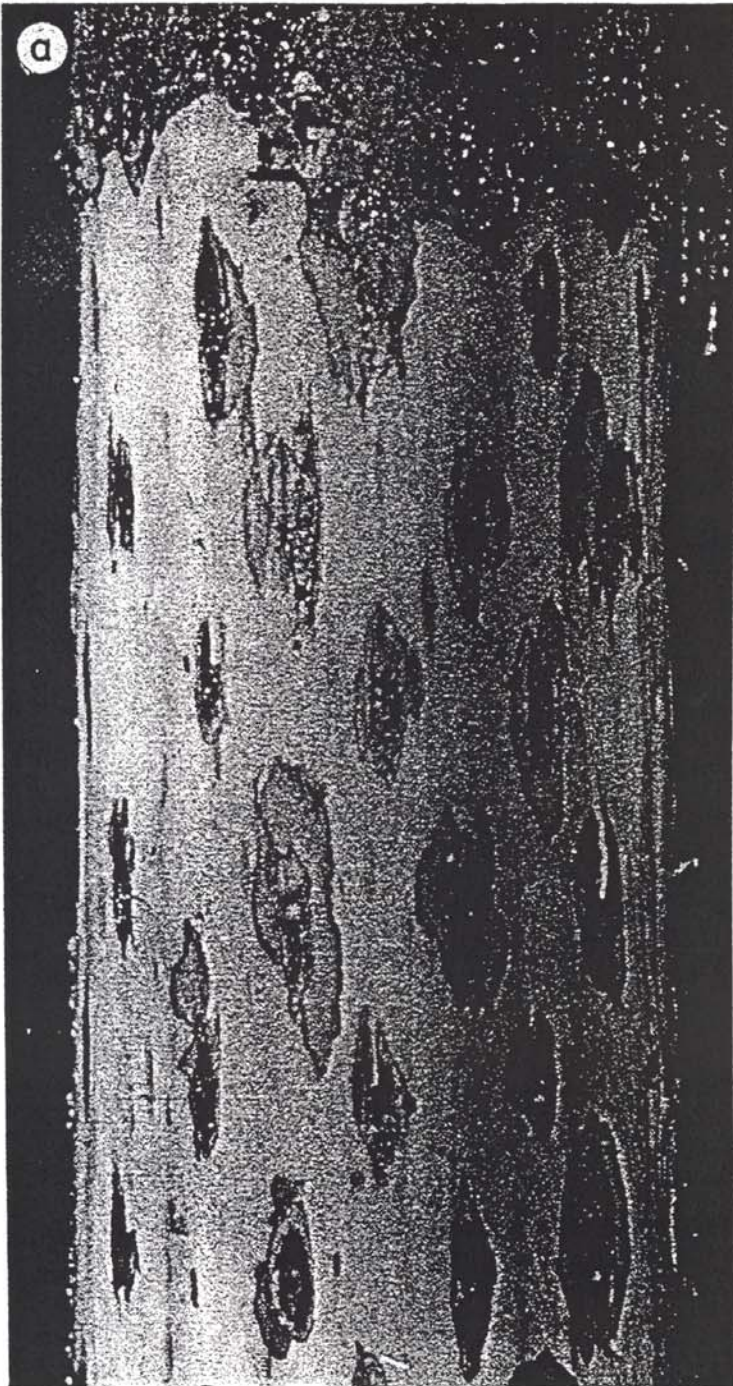


Fig. 4. (a) After mass inoculation with *C. polonica* in Norway spruce, wound reaction zones are formed around the points of infection. However, since the inoculations are too numerous to permit maximal resin accumulation, the fungus has been able to break out of many zones. In response to these outbreaks, the tree has erected new barriers outside the original ones.

Berryman, 1983; Christiansen, 1985a). This reduced resin concentration is accompanied by an increasing ability of fungi to invade the sapwood (Christiansen, 1985a).

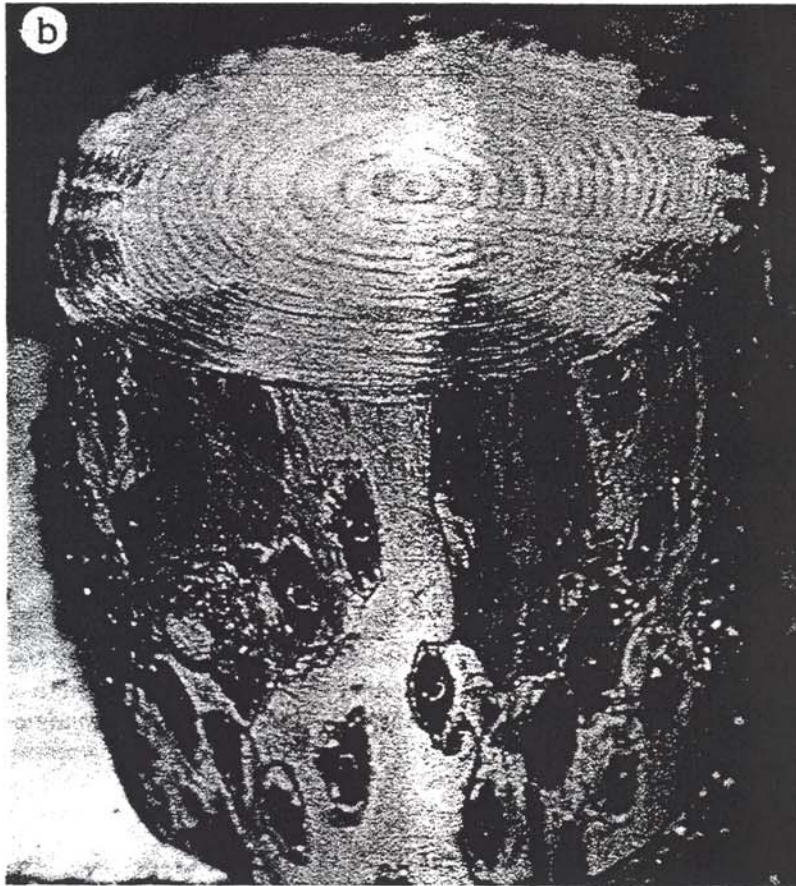


Fig. 4. (b) When the infections exceed a certain number, wound reactions can no longer contain the *C. polonica* infection and the fungus spreads out into the phloem and the underlying sapwood. (From an experiment by Christiansen, 1985a.)

Large expenditures of energy are required to synthesize terpenes and phenolic compounds in wound reactions (Croteau et al., 1972; Croteau and Loomis, 1975), and this depletes the carbohydrate reserves in the region surrounding the wound (Reid et al., 1967; Richmond et al., 1970; Christiansen and Ericsson, 1986; Miller and Berryman, 1986). Apparently, stored carbohydrates in adjacent tissues cannot be mobilized fast enough during beetle mass attack, and translocation of sugars from the tree crown is therefore necessary (Christiansen and Ericsson, 1986; Miller and Berryman, 1986).

STRUCTURAL INDICES OF TREE VIGOR

Resistance of the forest to attack by bark beetles is found to be related to several indices of tree vigor, which are generally based on some expression of relative stem growth (see review by Berryman, 1986). The validity of such

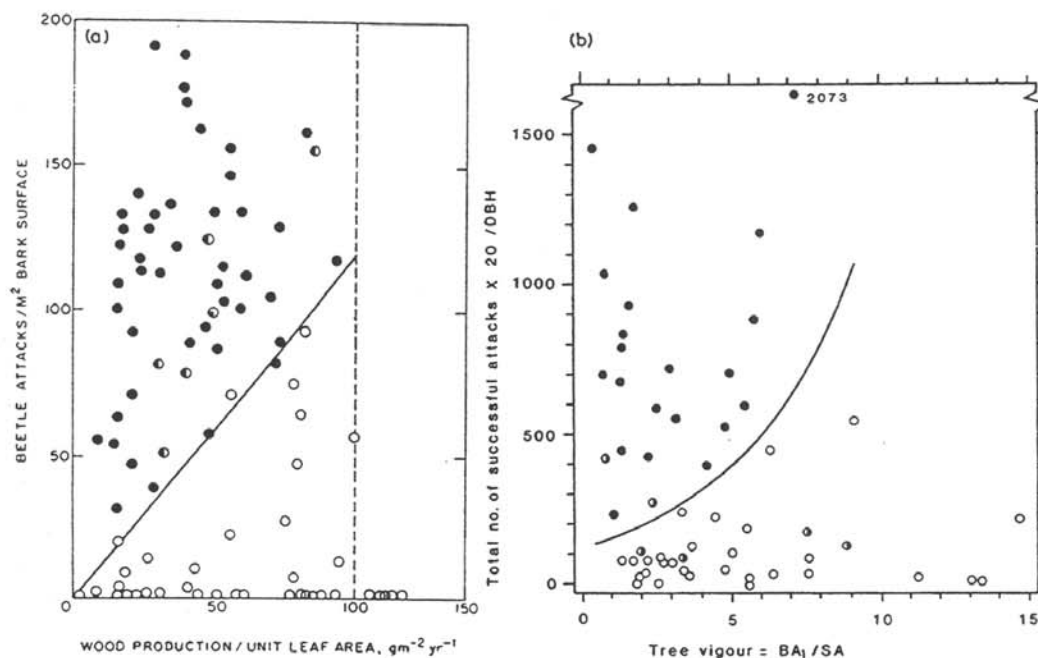


Fig. 5. Experimental demonstration of threshold of attack by bark beetles as influenced by tree vigor: filled circles, killed trees; open circles, surviving trees; partly filled circles, strip-killed trees (i.e., part of the stem tissues killed). Left: In lodgepole pine attacked by *Dendroctonus ponderosae*. (After Waring and Pitman, 1983.) Right: In Norway spruce attacked by *Ips typographus*. (After Mulock and Christiansen, 1986.)

indices has been evaluated through field observations and experiments with different parasitic organisms.

Resistance to bark beetle attack is related to the periodic growth rate of pine and spruce trees (Mahoney, 1978; Raffa and Berryman, 1982a; Christiansen, 1985a). In lodgepole pine, Waring and Pitman (1980, 1983) demonstrated that the threshold of successful attack (cf. Fig. 1) by mountain pine beetles increases with increasing relative sapwood growth, or wood production per unit of foliage (Fig. 5). An experiment with spruce bark beetles in Norway spruce gave similar results (Mulock and Christiansen, 1986).

Experimental mass inoculations with blue-stain fungi, simulating bark beetle attacks, have also indicated that host tree susceptibility is related to periodic growth (Christiansen, 1985a) and relative sapwood growth (Christiansen and Ericsson, 1986).

Tree growth efficiency, as measured by stemwood production per unit of foliage area, has been suggested as a 'universal' tree vigor index (Waring, 1983). This vigor index views the actual production of wood in relation to the production apparatus of the tree. Since stemwood production is of low priority compared with the production of other tissues (buds, fine roots, shoots), it is assumed to be a sensitive index of the relative ability of trees to mobilize carbohydrates. The index is usually calculated on an annual basis, but in situa-

tions where conditions vary rapidly, it could be measured at more-frequent intervals (cf. Blanche et al., 1985).

In a study in lodgepole pine stands, Mitchell et al. (1983) showed that trees with a growth efficiency exceeding ca. 100 g wood produced per m² of foliage were highly resistant to attack by mountain pine beetles. Ponderosa pines growing at a similar efficiency proved equally resistant to these beetles (Larson et al., 1983). In another study, however, Amman (1985) could not ascertain differences in resistance among lodgepole pine stands by measuring their growth efficiency. These stands, however, generally had vigor ratings lower than 100 g per m², and attack densities were not quantified.

It has been pointed out that vigor indices based on annual stem increment are unreliable predictors when trees are exposed to beetle attack throughout the year. In such cases, more sensitive measures of tree vigor may be needed (Lorio, 1986).

Growth efficiency has also proved to be important in assessing the resistance of conifers to root-rotting fungi (Matson and Waring, 1984; Entry et al., 1986; Waring et al., 1987).

ALTERNATIVE DEFENSE STRATEGIES

Matson and Hain (1985) hypothesized that different pine species may have evolved different defensive strategies. They point out that pines of the southeastern U.S.A. are exposed to asynchronous attacks by several multivoltine bark beetle species, in contrast to species of the western states which usually experience fewer annual attack periods. Due to the omnipresent threat of attack, it may be more energy-efficient for southern pines to adopt a constitutive defense (i.e. resin-duct system), whereas western species may be energetically better off with an induced defense (i.e. hypersensitive wound reaction). This interesting dichotomy may be extended: spruces and firs, which grow in cooler and more-humid climates than pines, are even less exposed to bark beetles. This could explain why Norway spruce has a resin-duct system that is highly unreliable for defense, and firs no such system. On the other hand, defenses of conifers may be related to their life history strategies, with long-lived 'climax' species relying more on complex and variable chemical formulations (Raffa and Berryman, 1987).

In the case of the constitutive defense, the energy has already been invested at the time of attack. By contrast, the wound response only draws energy after attack occurs, and only to the extent necessary to overcome the actual number of invaders. Regardless of the system that has evolved, considerable energy expenditure is required for an effective defense (cf. Wright et al., 1979; Matson and Hain, 1985). Both defense systems thus draw heavily on the carbon budget of the tree.

CONNECTION BETWEEN HOST TREE VIGOR AND RESISTANCE TO BARK
BEETLE-FUNGUS ATTACK*Explanatory power of a hypothesis linking defense to energy availability*

In summary, the threshold for successful attack by bark beetles and their accompanying wood-staining fungi (Fig. 1) is determined by the total defensive capacity of the tree. This capacity is contingent on: (1) the amount of constitutive resin available at the time of attack; and (2) the tree's capability to mobilize defensive chemicals in the distinctive reaction zones surrounding the points of attack.

Both defense systems depend on energy in the form of carbohydrates. In the former case this energy is already invested at the time of beetle attack, whereas the wound reaction demands energy only at the time of attack.

From the above discussion, we hypothesize that *defense against bark beetles and their associated fungi is directly related to the tree's carbon balance.*

This hypothesis helps us to understand why so many different factors have been empirically linked to resistance. We will elaborate this in the following section.

Drought is known to affect trees in many ways. Acute (short-term) water stress has often been thought of as a factor that increases host-tree susceptibility by affecting the exudation flow of constitutive resin. However, acute drought is mostly restricted to late summer and fall, *after* the time that most bark-beetle attacks occur.

The carbon balance of trees is affected by drought in several ways (e.g. Brix, 1962; Hsiao, 1973). Mild drought that does not completely halt photosynthesis may actually increase carbohydrate reserves and levels of defensive compounds because demands for shoot growth are immediately reduced (Hodges and Lorio, 1969; Sharpe and Wu, 1985; Lorio, 1986). While some studies showed an increase in amino nitrogen, neither drought nor flooding changed the concentration of phloem amino N in loblolly pines (Hodges and Lorio, 1969). Hence, the building blocks for critical enzymes such as amylase should not be adversely affected. But translocation of sugars from the crown, which may be critical for defense against a mass attack, could be seriously compromised (Christiansen and Ericsson, 1986; Miller and Berryman, 1986).

Extended drought, however, halts photosynthesis, depletes carbon reserves and defensive compounds, and eventually reduces the size of the canopy (Bradford and Hsiao, 1982; Landsberg and Wylie, 1983; Pook, 1985). Thus, following droughty periods, less carbon is available for defense. This would explain why extended large-scale bark-beetle outbreaks are often preceded by drought.

Wind-swaying with disturbance of fine roots can lead to a higher carbon demand to replace the torn roots. If a large proportion of the roots is damaged,

assimilation may be hampered by reduced water and nutrient uptake. Carbon stores may be depleted, leaving less available for defense.

Defoliation is known to reduce carbon stores of trees (Wright et al., 1979), while damage due to *lightning* and *fire* may also draw considerable amounts of carbon for repair. Attacks by *rot fungi* will draw on resources for defense and tissue repair, and may eventually reduce the photosynthetic capacity of the tree.

Some of the factors mentioned above, however, may lead to the formation of more resin ducts, and may over time strengthen the first line of defense at the expense of the wound reaction potential.

The energy stores of the trees may also gradually decrease as a result of natural stand development. As trees age, an increasing fraction of their photosynthate is needed for maintenance of living tissues, which increase at a faster rate than their photosynthetic capacity (approximately as a cubic function of the stem diameter vs. a square). In a sample of Norway spruce trees aged 20–106 years, the phloem concentration of hot-water-soluble carbohydrates decreased by one-third in the older trees (Christiansen and Horntvedt, 1983).

Competition clearly affects the carbon stores of trees (e.g. Waring et al., 1987). When a given stand approaches its maximum leaf area, even dominant trees experience a gradual shading of their foliage, resulting in decreased assimilation, as seen from their decreasing annual ring widths. Although the carbon production of suppressed trees is small, so also are their maintenance demands, and such trees may therefore not necessarily be very susceptible to attack.

Many agents of natural disturbance that reduce the amount of leaves or standing biomass of other respiring tissues lead to an eventual increase in forest productivity. This conclusion follows from reports on long-term effects of defoliating insects (Mattson and Addy, 1975), bark beetles (Waring and Pitman, 1985), pathogens (Oren et al., 1985) and wind (Harcombe, 1986).

In conclusion, we hypothesize that *the ability of trees to withstand attacks by bark beetles and their associated fungi is linked to the amount of carbohydrates that can be utilized directly for defensive wound reactions. Therefore, any environmental factor that restricts the size of the canopy or its photosynthetic efficiency can weaken a tree's resistance.* Although growth indices and stores of energy are general indicators of resistance, the actual flux of carbohydrates for synthesis of protective chemicals appears to be the critical variable determining the defensive capacity of conifers.

Establishing a firm link between the carbon balance of trees and their resistance to beetle/fungus invasion would greatly improve our understanding of this important herbivore/host-plant interaction. We therefore recommend that more experimentation be carried out to elucidate how defense in coniferous trees is related to their carbon balance. Because the wound reaction to fungal

infection can easily be studied through artificial inoculation, and apparently relates directly to the carbon flux in the tree, the study of this reaction seems a particularly interesting approach.

REFERENCES

- Amman, G.D., 1969. Mountain pine beetle emergence in relation to depth of lodgepole pine bark. USDA For. Serv. Res. Note INT-96, 7 pp.
- Amman, G.D., 1985. A test of lodgepole pine hazard rating methods for mountain pine beetle infestation in southeastern Idaho. In: L. Safranyik (Editor), The Role of the Host in the Population Dynamics of Forest Insects. Proc. IUFRO Conf., Banff, Alta., 4-7 September 1983. Pacific Forest Research Centre, Victoria, B.C., pp. 186-200.
- Basham, H.G., 1970. Wilt of loblolly pine inoculated with blue-stain fungi of the genus *Ceratocystis*. Phytopathology, 60: 750-754.
- Berryman, A.A., 1969. Response of *Abies grandis* to attack by *Scolytus ventralis* (Coleoptera: Scolytidae). Can. Entomol., 101: 1033-1041.
- Berryman, A.A., 1972. Resistance of conifers to invasion by bark beetle-fungi associations. BioScience, 22: 598-602.
- Berryman, A.A., 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. Environ. Entomol., 5: 1225-1233.
- Berryman, A.A., 1978. A synoptic model of the lodgepole pine/mountain pine beetle interaction and its potential application in forest management. In: A.A. Berryman, G.D. Amman, R.W. Stark and D.L. Kibbee (Editors), Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests. College of Forest Resources, University of Idaho, Moscow, pp. 98-105.
- Berryman, A.A., 1982. Biological control, thresholds, and pest outbreaks. Environ. Entomol., 11: 544-549.
- Berryman, A.A., 1986. Forest Insects. Principles and Practice of Population Management. Plenum Press, New York/London, 279 pp.
- Blanche, C.A., Hodges, J.D. and Nebeker, T.E., 1985. A leaf area-sapwood area ratio developed to rate loblolly pine tree vigor. Can. J. For. Res., 15: 1181-1184.
- Bradford, K.J. and Hsiao, T.C., 1982. Physiological responses to moderate water stress. In: O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler (Editors), Physiological Plant Ecology. II. Water relations and carbon assimilation. Springer, Berlin, pp. 264-324.
- Bridges, J.R., Nettleton, W.A. and Connor, M.D., 1985. Southern pine beetle (Coleoptera: Scolytidae) infestations without the bluestain fungus, *Ceratocystis minor*. J. Econ. Entomol., 78: 325-327.
- Brix, H., 1962. The effect of water stress on the rates of photosynthesis and respiration in tomato plants and loblolly pine seedlings. Physiol. Plant., 15: 10-20.
- Christiansen, E., 1985a. *Ceratocystis polonica* inoculated in Norway spruce: Blue-staining in relation to inoculum density, resinosis and tree growth. Eur. J. For. Pathol., 15: 160-167.
- Christiansen, E., 1985b. *Ips/Ceratocystis*-infection of Norway spruce: what is a deadly dosage? Z. Angew. Entomol., 99: 6-11.
- Christiansen, E. and Ericsson, A., 1986. Starch reserves in *Picea abies* in relation to defence reaction against a bark beetle transmitted blue-stain fungus, *Ceratocystis polonica*. Can. J. For. Res., 16: 78-83.
- Christiansen, E. and Horntvedt, R., 1983. Combined *Ips/Ceratocystis* attack on Norway spruce, and defensive mechanisms of the trees. Z. Angew. Entomol., 96: 110-118.
- Cobb, F.W., Jr., Krstic, M., Zavarin, E. and Barber, H.W., Jr., 1968. Inhibitory effects of volatile

- oleoresin components on *Fomes annosus* and four *Ceratocystis* species. *Phytopathology*, 58: 1327-1335.
- Coulson, R.N., Hennier, P.B., Flamm, R.O., Rykiel, E.H., Hu, L.C. and Payne, T.L., 1983. The role of lightning in the epidemiology of the southern pine beetle. *Z. Angew. Entomol.*, 96: 182-193.
- Croteau, R. and Loomis, W.D., 1975. Biosynthesis and metabolism of monoterpenes. *Int. Flavours Food Addit.*, 6: 292-296.
- Croteau, R., Burbott, A.J. and Loomis, W.D., 1972. Apparent energy deficiency in mono- and sesqui-terpene biosynthesis in peppermint. *Phytochemistry*, 11: 2937-2948.
- Entry, J.A., Martin, N.E. and Cromack, K., Jr., 1986. Light and nutrient limitation in *Pinus monticola*: seedling susceptibility to *Armillaria* infection. *For. Ecol. Manage.*, 17: 189-198.
- Ferrell, G.T., 1983. Host resistance to the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae): frequencies of attacks contacting resin blisters and canals of *Abies concolor*. *Can. Entomol.*, 115: 1421-1428.
- Furniss, M.M., 1962. Infestation patterns of Douglas-fir beetle in standing and windthrown trees in southern Idaho. *J. Econ. Entomol.*, 55: 486-491.
- Geiszler, D.R., Gara, R.I., Driver, C.H., Gallucci, V.F. and Martin, R.E., 1980. Fire, fungi, and beetle influences on a lodgepole pine ecosystem in South-Central Oregon. *Oecologia Berlin*, 46: 239-243.
- Harcombe, P.A., 1986. Stand development in a 130-year-old spruce-hemlock forest based on age structure and 50 years of mortality data. *For. Ecol. Manage.*, 14: 41-58.
- Hard, J., 1985. Spruce beetles attack slowly growing spruce. *For. Sci.*, 31: 839-850.
- Hodges, J.D. and Lorio, P.L., Jr., 1969. Carbohydrate and nitrogen fractions of the inner bark of loblolly pine under moisture stress. *Can. J. Bot.*, 47: 1651-1657.
- Hodges, J.D. and Lorio, P.L., Jr., 1971. Comparison of field techniques for measuring moisture stress in large loblolly pines. *For. Sci.*, 17: 220-223.
- Hopping, G.R. and Mathers, W.G., 1945. Observations on outbreaks and control of the mountain pine beetle in the lodgepole pine stands of Western Canada. *For. Chron.*, 21: 98-108.
- Hornthvedt, R., Christiansen, E., Solheim, H. and Wang, S., 1983. Artificial inoculation with *Ips typographus*-associated blue-stain fungi can kill healthy Norway spruce trees. *Medd. Nor. Inst. Skogforsoeksesves.*, 38(4): 20 pp.
- Hsiao, T.C., 1973. Plant responses to water stress. *Annu. Rev. Plant. Physiol.*, 24: 519-570.
- Kalkstein, L.S., 1976. Effects of climatic stress upon outbreaks of the southern pine beetle. *Environ. Entomol.*, 5: 653-658.
- Klement, Z. and Goodman, R.N., 1967. The hypersensitive reaction to infection by bacterial plant pathogens. *Annu. Rev. Phytopathol.*, 5: 17-44.
- Landsberg, J. and Wylie, F.R., 1983. Water stress, leaf nutrients and defoliation: a model of die-back of rural eucalypts. *Aust. J. Ecol.*, 8: 27-41.
- Larsson, S., Oren, R., Waring, R.H. and Barrett, J.W., 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. *For. Sci.*, 29: 395-402.
- Lorio, P.L., Jr., 1986. Growth-differentiation balance: a basis for understanding southern pine beetle-tree interactions. *For. Ecol. Manage.*, 14: 259-273.
- Lorio, P.L., Jr. and Hodges, J.D., 1968. Oleoresin exudation pressure and relative water content of inner bark as indicators of moisture stress in loblolly pine. *For. Sci.*, 14: 392-398.
- Mahoney, R.L., 1978. Lodgepole pine/mountain pine beetle risk classification methods and their application. In: A.A. Berryman, G.D. Amman, R.W. Stark and D.L. Kibbee (Editors), *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*. College of Forest Resources, University of Idaho, Moscow, pp. 106-113.
- Mathre, D.E., 1964. Pathogenicity of *Ceratocystis ips* and *Ceratocystis minor* to *Pinus ponderosa*. *Contrib. Boyce Thompson Inst.*, 22: 363-388.
- Matson, P.A. and Hain, F.P., 1985. Host conifer defense strategies: a hypothesis. In: L. Safranyik

- (Editor), The Role of the Host in the Population Dynamics of Forest Insects. Proc. IUFRO Conf., Banff, Alta., 4-7 September 1983. Pacific Forest Research Centre, Victoria, B.C., pp. 33-42.
- Matson, P.A. and Waring, R.H., 1984. Effects of nutrient and light limitation on mountain hemlock: susceptibility to laminated root rot. *Ecology*, 65: 1517-1524.
- Matson, P.A., Hain, F.P. and Mawby, W., 1987. Indices of tree susceptibility to bark beetles vary with silvicultural treatment in a loblolly pine plantation. *For. Ecol. Manage.*, 22: 107-119.
- Mattson, W.J. and Addy, N.D., 1975. Phytophagous insects as regulators of forest primary production. *Science*, 190: 515-522.
- McCambridge, W.F. and Stevens, R.E., 1982. Effectiveness of thinning ponderosa pine stands in reducing mountain pine beetle-caused losses in the Black Hills — preliminary observations. USDA For. Serv. Res. Note RM-414, 3 pp.
- Miller, J.M. and Keen, F.P., 1960. Biology and Control of the Western Pine Beetle. USDA, Washington, DC, 381 pp.
- Miller, R.H. and Berryman, A.A., 1986. Nutrient allocation and mountain pine beetle attack in girdled lodgepole pines. *Can. J. For. Res.*, 16: 1036-1040.
- Mitchell, R.G., Waring, R.H. and Pitman, G.B., 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *For. Sci.*, 29: 204-211.
- Mulock, P. and Christiansen, E., 1986. The threshold of successful attack by *Ips typographus* on *Picea abies*: a field experiment. *For. Ecol. Manage.*, 14: 125-132.
- Nelson, R.M. and Beal, J.A., 1929. Experiments with bluestain fungi in southern pines. *Phytopathology*, 19: 1101-1106.
- Oren, R., Thies, W.G. and Waring, R.H., 1985. Tree vigor and stand growth of Douglas-fir as influenced by laminated root rot. *Can. J. For. Res.*, 15: 985-988.
- Person, H.L., 1928. Tree selection by the western pine beetle. *J. For.*, 26: 564-578.
- Pook, E.W., 1985. Canopy dynamics of *Eucalyptus maculata* Hook. III. Effects of drought. *Aust. J. Bot.*, 33: 65-79.
- Raffa, K.F. and Berryman, A.A., 1982a. Physiological differences between lodgepole pines resistant and susceptible to the mountain pine beetle and associated microorganisms. *Environ. Entomol.*, 11: 486-492.
- Raffa, K.F. and Berryman, A.A., 1982b. Accumulation of monoterpenes and associated volatiles following inoculation of grand fir with a fungus transmitted by the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae). *Can. Entomol.*, 114: 797-810.
- Raffa, K.F. and Berryman, A.A., 1983. Physiological aspects of lodgepole pine wound responses to a fungal symbiont of the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Can. Entomol.*, 115: 723-734.
- Raffa, K.F. and Berryman, A.A., 1987. Interacting selective pressure in conifer-bark beetle systems: a basis for reciprocal adaptations? *Am. Nat.*, 129: 234-262.
- Raffa, K.F., Berryman, A.A., Simasko, J., Teal, W. and Wong, B.L., 1985. Effects of grand fir monoterpenes on the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae), and its symbiotic fungus. *Environ. Entomol.*, 14: 552-556.
- Reid, R.W. and Gates, H., 1970. Effect of temperature and resin on hatch of eggs of the mountain pine beetle (*Dendroctonus ponderosae*). *Can. Entomol.*, 102: 617-622.
- Reid, R.W. and Watson, J.A., 1966. Sizes, distributions, and numbers of vertical resin ducts in lodgepole pine. *Can. J. Bot.*, 44: 519-525.
- Reid, R.W., Whitney, H.S. and Watson, J.A., 1967. Reactions of lodgepole pine to attack by *Dendroctonus ponderosae* Hopkins and blue stain fungi. *Can. J. Bot.*, 45: 1115-1126.
- Richmond, J.A., Mills, C. and Clark, E.W., 1970. Chemical changes in loblolly pine, *Pinus taeda* L., inner bark caused by blue stain fungus, *Ceratocystis minor* (Hedg.) Hunt. *J. Elisha Mitchell Sci. Soc.*, 86: 171.

- Romme, W.H., Knight, D.H. and Yavitt, J.B., 1986. Mountain pine beetle outbreaks in the Rocky Mountains: Regulators of primary productivity? *Am. Nat.*, 127: 484-494.
- Rudinsky, J.A., 1962. Ecology of Scolytidae. *Annu. Rev. Entomol.*, 7: 327-348.
- Sartwell, C. and Stevens, R.E., 1975. Mountain pine beetle in ponderosa pine, prospects for silvicultural control in second-growth stands. *J. For.*, 73: 136-140.
- Schenk, J.A., Mahoney, R.L., Moore, J.A. and Adams, D.L., 1980. A model for hazard rating lodgepole pine stands for mortality by mountain pine beetle. *For. Ecol. Manage.*, 3: 57-68.
- Schwerdtfeger, F., 1955. Pathogenese der Borkenkäfer-Epidemie 1946-1950 in Nordwestdeutschland. *Schriftenr. Forstl. Fak. Univ. Göttingen* 13/14, 135 pp.
- Sharpe, P.J.H. and Wu, H., 1985. A preliminary model of host susceptibility to bark beetle attack. In: L. Safranyik (Editor), *The Role of the Host in the Population Dynamics of Forest Insects*. Proc. IUFRO Conf., Banff, Alta., 4-7 September 1983. Pacific Forest Research Centre, Victoria, B.C., pp. 108-127.
- Shrimpton, D.M., 1973. Extractives associated with the wound response of lodgepole pine attacked by the mountain pine beetle and associated microorganisms. *Can. J. Bot.*, 51: 527-534.
- Shrimpton, D.M. and Whitney, H.S., 1968. Inhibition of growth of blue stain fungi by wood extractives. *Can. J. Bot.*, 46: 757-761.
- Stephen, F.M., Paine, T.D. and Lih, M.P., 1983. Understanding bark beetle/host interactions: a means for improving decision strategies. *Z. Angew. Entomol.*, 96: 257-265.
- Stevens, R.E., McCambridge, W.F. and Edminster, O.B., 1980. Risk rating guide for mountain pine beetle in Black Hills ponderosa pine. USDA For. Serv. Res. Note RM-385, 2 pp.
- Thalenhorst, W., 1958. Grundzüge der Populationsdynamik des grossen Fichtenborkenkäfers *Ips typographus* L. *Schriftenr. Forstl. Fak. Univ. Göttingen* 21, 126 pp.
- Thatcher, R.C., Searcy, J.L., Coster, J.E. and Hertel, G.D. (Editors), 1980. *The Southern Pine Beetle*. USDA For. Serv. Tech. Bull. 1931, 266 pp.
- Vité, J.P. and Wood, D.L., 1961. A study on the applicability of the measurement of oleoresin exudation pressure in determining susceptibility of second growth ponderosa pine to bark beetle infestation. *Contrib. Boyce Thompson Inst.*, 21: 67-78.
- Waring, R.H., 1983. Estimating forest growth and efficiency in relation to canopy leaf area. *Adv. Ecol. Res.*, 13: 327-354.
- Waring, R.H. and Pitman, G.B., 1980. A simple model of host resistance to bark beetles. *Oreg. State Univ. For. Res. Lab. Res. Note* 65, 2 pp.
- Waring, R.H. and Pitman, G.B., 1983. Physiological stress in lodgepole pine as a precursor for mountain pine beetle attack. *Z. Angew. Entomol.*, 96: 265-270.
- Waring, R.H. and Pitman, G.B., 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology*, 66: 889-897.
- Waring, R.H., Cromack, K., Jr., Matson, P.A., Boone, R.D. and Stafford, S.G., 1987. Responses to pathogen-induced disturbance: decomposition, nutrient availability, and tree vigor. *Forestry*, 50 (in press).
- Wong, B.L. and Berryman, A.A., 1977. Host resistance to the fir engraver beetle. 3. Lesion development and containment of infection by resistant *Abies grandis* inoculated with *Trichosporium symbioticum*. *Can. J. Bot.*, 55: 2358-2365.
- Wood, D.L., 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. *Annu. Rev. Entomol.*, 27: 411-446.
- Worrell, R., 1983a. Damage by the spruce bark beetle in South Norway 1970-80: A survey, and factors affecting its occurrence. *Medd. Nor. Inst. Skogforsøksves.*, 38(6): 34 pp.
- Worrell, R., 1983b. Skoglige bestandsfaktorer som påvirker omfanget av granbarkbilleskade i Sør-Norge. (Eng. summary: Stand factors affecting the occurrence of damage by *Ips typographus* in South Norway). *Rapp. Nor. Inst. Skogforsøksves.*, 18/83, 9 pp.
- Wright, E., 1935. *Trichosporium symbioticum*, N.Sp., a wood-staining fungus associated with *Scolytus ventralis*. *J. Agric. Res.*, 50: 525-538.

- Wright, L.C., Berryman, A.A. and Gurusiddaiah, S., 1979. Host resistance to the fir engraver beetle, *Scolytus ventralis* (Coleoptera: Scolytidae). 4. Effect of defoliation on wound monoterpene and inner bark carbohydrate concentrations. Can. Entomol., 111: 1255-1262.
- Wright, L.C., Berryman, A.A. and Wickman, B.E., 1984. Abundance of the fir engraver, *Scolytus ventralis*, and the Douglas-fir beetle, *Dendroctonus pseudotsugae*, following tree defoliation by the Douglas-fir tussock moth, *Orgyia pseudotsugata*. Can. Entomol., 116: 293-305.