IPS TYPOGRAPHUS AND OPHIOSTOMA POLONICUM VERSUS NORWAY SPRUCE: JOINT ATTACK AND HOST DEFENSE

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INTRODUCTION

During the years 1971 to 1982, major epidemics of the spruce bark beetle, *Ips typographus* L., occurred in southeastern Norway and adjoining parts of Sweden. The outbreaks were triggered by large-scale wind-fellings and long-lasting drought (Worrell 1983). This "epidemic of the century," hitting our important timber tree, Norway spruce, *Picea abies* (L.), stimulated research in Norway and other countries of the region on the relationship between the beetle, its fungal symbionts, and the host tree.

It is assumed that the outcome of a bark beetle attack generally depends on 1) the local density of beetles that can respond to aggregation pheromones and 2) the resistance of host trees to attack (Berryman 1978, 1982). Field experiments lend support to this hypothesis (Waring and Pitman 1980, 1983, Raffa and Berryman 1983, Mulock and Christiansen 1986).

In this paper, I describe the relationship between the spruce bark beetle and its fungal symbionts and discuss how the symbiosis enables the beetle to successfully attack living trees. I also outline the method by which the trees defend themselves against the joint beetle/fungus attacks and discuss the important factors in that defense.

THE BEETLE-FUNGUS ASSOCIATION

In the 1970s we discussed with colleagues in the Section of Forest Pathology of the Norwegian Forest Research Institute the role that fungi might play in the colonization of trees attacked by *I. typographus*. Looking into the literature, we found that there existed a good deal of interesting information.

Discoloration of wood in connection with insect damage had already been noted by Hartig (1878), and early in this century bark beetles were directly associated with blue-staining fungi (Münch 1907, 1908). In 1928 the American forest entomologist F.C. Craighead demonstrated that blue-stain fungi play a primary role in the rapid death of pines infested with *Dendroctonus* beetles. He argued that mere girdling by the insects would not kill a tree within a few weeks, since artificially girdled trees often live on for months and years. Instead, he suggested, the fungi interrupt the tree's transpiration stream, thus causing its desiccation and death.

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Following Craighead's suggestion, a number of researchers conducted experiments with American pines. Several staining fungi of the family Ophiostomataceae were inoculated into the trees, and in some cases caused their wilting and death (Horntvedt et al. 1983). Over the years several Ophiostomataceae have been isolated from blue-stained sapwood of Norway spruce (Horntvedt et al. 1983, Solheim 1986). An early attempt to establish some of these fungi in spruce trees through artificial inoculation proved futile (Münch 1907, 1908).

In 1980 our pathologist, Richard Horntvedt, decided to try an inoculation experiment using two *Ophiostoma* (= *Ceratocystis*) species that had frequently been mentioned as associates of the spruce bark beetle, *Ophiostoma piceae* H. and P. Syd. and *O. penicillatum* Siem. Three cambium-deep girdles were cut around the stem of each tree. Cotton ropes soaked in agar and thoroughly infected with the fungi were placed in the girdle and covered by tape. The experiment failed as Münch's had done; no fungal infection of the xylem could be observed.

At this time a mycologist, Halvor Solheim, had just joined our group to study the succession of microorganisms in beetle-killed spruce trees. He soon made a very significant discovery: the species *Ophiostoma polonicum* Siem., to which no one had hitherto paid much attention, was always found at the advancing front of blue stain in the sapwood of beetle-attacked trees. In 1981 we inoculated both *O. polonicum* and *O. penicillatum* under the bark of young and old spruce trees, using the cork-borer technique (Wright 1935) and infected wood-chips inserted under the bark (Reid et al. 1967). The inocula were placed 2 cm apart along rings encircling the stem. We discovered that *O. polonicum*, but not *O. penicillatum*, was able to kill trees of normal health. It penetrated sapwood of normal water contents, and in doing so caused a blockage of the transpiration stream through the stem (Horntvedt et al. 1983).

Repeated experiments have verified that *O. polonicum* will kill healthy spruce trees provided an adequate load of inoculum is given (Christiansen and Horntvedt 1983, Christiansen 1985a, 1985b, Christiansen and Ericsson 1986, Horntvedt 1988, Solheim 1988). On the other hand, further studies confirmed that our isolates of *O. penicillatum* and *O. bicolor* are unable to kill trees of normal health (Solheim 1988). The differences in pathogenicity between the fungal species can probably be explained by their differential abilities to colonize wet sapwood. *O. polonicum* seems to tolerate low oxygen conditions better than the other species mentioned here and consequently also tolerates a wetter growth substrate (H. Solheim, pers. comm.).

The relationship between *I. typographus* and its fungal symbiont is an example of true mutualism, since both parts benefit from it. The pathogenic fungus helps the beetles kill trees, thus making them available for beetle reproduction. The benefit for the fungus is transportation to new hosts and effective inoculation under the bark. Since the mutualists have joined forces in such a deadly way, there must be a means by which the trees defend themselves against attack, thereby securing their own future existence as well as that of the parasites.

DEFENSE MECHANISMS OF THE TREES

Coniferous trees have coevolved with insects and parasitic microorganisms, including fungi, for over 200 million years. To survive they have developed effective systems of defense. Whereas a tree can lose large parts of its crown and root biomass and still survive, loss of the cambium around the stem constitutes a mortal threat. In several important conifers, the defense of stem tissues is based upon secretion of resinous materials.

"Resin" in its broadest sense has long been regarded as important for the defense against bark beetles in Norway spruce (Gmelin 1787) and other conifers. The pioneering work of Reid et al. (1967) on lodgepole pine, *Pinus contorta*, in Canada added a new dimension to the concept. It became clear that the resin observed in the case of beetle/fungus attack has two different origins: on the one

hand, there is the preformed (or "constitutive") resin in ducts in the bark and sapwood, and on the other hand, there is the resin produced by an induced reaction to wounding and infection. The two types of resin are termed "primary" and "secondary," referring to the order of their appearance in the tree.

Preformed Resin: The "Standing Forces"

Preformed resin originates from an interconnected system of ducts in the phloem and xylem. This system comprises the "standing forces" of the tree, which become operative once a resin duct is severed, e.g. by a mining beetle. After the resin has been flowing for a short period of time, its surface will crystallize to form a hard, protective surface over the wound. A system of resin ducts exists in some coniferous genera (e.g. *Larix*, *Picea*, *Pinus*, and *Pseudotsuga*), but is absent in others (e.g. *Cedrus*, *Sequoia*, and *Thuja*). *Abies* species have resin blisters in the bark, but these can in some cases be avoided by bark beetles (Ferrell 1983).

The preformed resin has been subjected to extensive studies in pines, partly in connection with its commercial use. Investigations related to bark beetle attack on ponderosa pine have emphasized the importance of oleoresin exudation pressure (OEP) because OEP would influence the quantity of resin that an attacking beetle would have to cope with (Vité 1961, Vité and Wood 1961). Because OEP is often correlated with the turgor pressure of the epithelial cells surrounding the resin ducts, droughty conditions could lower OEP and possibly facilitate beetle attack.

Studies of pines in the southern U.S.A. have, however, indicated that the exudation flow (OEF) largely depends on the storage capacity of the resin duct system and the viscosity of the resin, whereas OEP seems to be less important (Hodges and Lorio 1971). It seems logical to assume that OEF and total quantity exuded are the critical factors for an attacking beetle. The formation of resin ducts seems likely to be influenced by the growth-differentiation balance of the tree (Lorio 1986).

Induced Resinosis: The "Mobilization Defense"

Preformed resin may repel, flush out, and even drown attacking beetles. If these "standing forces" of the tree are inadequate for arresting the beetles, however, the phloem, cambium, and outer sapwood become infected with propagules of microorganisms. Most important of these are the spores of blue-stain fungi, which are specially adapted for transportation by insects by being covered with an adhesive, mucilaginous sheath. After these spores germinate, the fungus may soon spread into the surrounding tissues. It has been pointed out that since the preformed resin does not permeate the host tissues in advance of fungal growth, it is unlikely that it can prevent the spread (Berryman 1972).

When infected by microorganisms, whether fungi, bacteria, or vira, most plants have a hypersensitive reaction (Klement and Goodman 1967). A necrotic area forms around the point of infection so that the invading organism is deprived of food. Such necrotic reaction zones forming in the cambial region of conifers may also become impregnated with resinous and phenolic compounds, which creates an environment very unfavorable to beetles and fungi (Reid et al. 1967, Berryman 1969, Shrimpton 1973, Wong and Berryman 1977). The wound resin is produced by living parenchyma cells of the phloem and sapwood, including new-formed callus parenchyma. It is synthesized from carbohydrates stored in parenchyma cells of the phloem and xylem (Reid et al. 1967, Shrimpton 1978, Cheniclet et al. 1988, Lieutier and Berryman 1988), the reaction being elicited by substances produced by the fungus (Lieutier and Berryman 1988).

The induced response constitutes the "mobilization forces" of the defense, which come into action more slowly, but can stay active for an extended period of time. In lodgepole pine, where this reaction has been studied most intensively, it is considered the main defense against bark beetle attack,

the preformed resin merely delaying the beetles and allowing more time for the secondary response (Raffa and Berryman 1982). The induced response is concentrated in a small area surrounding the infection, thereby keeping the loss of cambium to a minimum (Raffa and Berryman 1982). The process is highly energy-demanding (Wright et al. 1979) and probably related to the overall vigor of the host tree (Raffa and Berryman 1982).

STUDIES OF THE DEFENSE IN NORWAY SPRUCE

In 1983 we carried out a field experiment to establish the number of *I. typographus* attacks necessary to kill a Norway spruce tree (Christiansen 1985b). Pheromone dispensers were attached to a number of trees, and shortly after the main flight of the beetles, the number of attacks was recorded.

In several trees, the attack appeared to be successful, only dry frass being expelled from the entrance holes. However, about 1 month after attack, we observed that liquid resin was now seeping from formerly dry holes. Removing the outer cork bark, we found resin-impregnated reaction zones surrounding egg galleries of different lengths (Fig. 1). Obviously, the preformed resin had been inadequate to prevent the beetles from excavating their nuptial chambers and initial egg galleries. Later, however, secondary resinosis had put an end to the breeding. This was one of the reasons why we wanted to take a closer look at the relative importance of the two defense systems in Norway spruce.

The Preformed Defense

Schwerdtfeger (1955) studied the efficiency of the resin duct system under different conditions by making cambium-deep cuts of a standard size in the bark and measuring resin exudation within a maximal period of 3 days. One of his conclusions was that the quantity of resin exuded by a standard wound in the phloem-cambium region will rapidly taper off when the number of wounds increases. He also established a clear seasonality in resinosis, the quantity of exudate showing a strong positive correlation to ambient temperature. The amount of preformed resin exuding from a mechanical wound varies greatly from tree to tree, and even between places on a given tree (Christiansen and Horntvedt 1983). Within a stand, there is a trend toward a higher yield of duct resin per wound among the larger trees (Fig. 2), also suggested by Schwerdtfeger (1955). Likewise, older trees seem to exude at least as much resin as younger (Schwerdtfeger 1955, Christiansen and Horntvedt 1983).

There are several sources of seasonal and annual variation in amounts of duct resin. Newly formed resin ducts of the sapwood may not become connected with phloem ducts until most of the year-ring has been laid down, as observed in pines (P.L. Lorio, Jr., pers. comm. 1986). Also, different year-rings of Norway spruce may hold highly variable numbers of resin ducts, which can be formed in response to external stresses, i.e. frost, drought, or attack by insects and fungi. During extremely dry years of the mid-1970s, unusually high numbers of ducts were formed in connection with drought rings in the spruce trees we examined. Due to this variability, pioneer beetles may encounter "standing forces" of variable strength depending on where and when they attack.

An experiment we conducted in Norway in 1985 sheds some light on the relative importance of the two defense systems. It was just after the recent large epidemic and very few trees were spontaneously killed by *I. typographus* that year. In the experiment, pheromone dispensers were attached to 77 spruce trees of variable vigor. All 77 came under attack, but only 20 of them died. Shortly after the main flight of the spruce bark beetle, we counted the number of attacks on each tree. In doing so, we distinguished between entrance holes where liquid resin or moist frass occurred and holes where only dry frass was expelled. Very few attacks occurred after this major inspection.

Figure 1. The spruce bark beetle has been able to enter the phloem and initiate its galleries without being stopped by the preformed resin of the tree. Later, however, the induced defense has produced abundant resin that permeates the phloem locally around the galleries. The eggs have been killed, and the fungus is contained inside the resin-soaked areas.

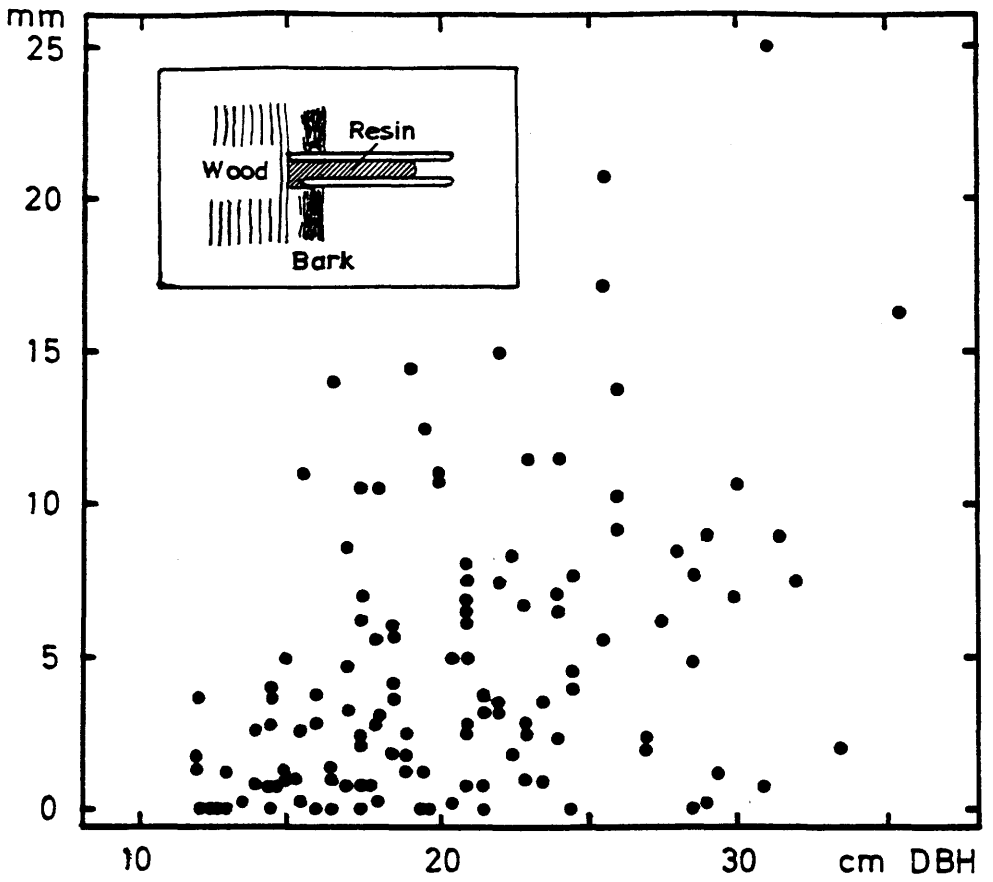

Figure 2. The inserted drawing shows measurement of the yield of constitutive resin: plastic tubes are cut at an angle and fitted into holes cut to the cambium with a cork borer. After 24 hr the length of the resin column is measured. The main figure gives mean values of 10 measurements per tree for 128 spruce trees growing in a small stand.

There was great variation in total number of attacks per tree (Fig. 3). Surviving trees showed a maximum of about 500 entrance holes, whereas killed trees had no less than 200 to nearly 1,200. In the killed trees only a small percentage of the boring holes had resin exudation; the proportion was almost zero in some trees. Surviving trees had fewer attacks in general and a higher, but extremely variable proportion of holes with primary resin. On one of these trees, over 300 boring holes were recorded, all of which were oozing resin, whereas in others only a small share of the entrance holes exuded resin.

Although the results mentioned here are only fragmentary, I think it is safe to conclude that the "standing forces" of the resin duct system are inadequate as a sole defense against a mass attack of *I. typographus*. It should be pointed out that in other trees, such as certain pines, this first line of defense may be much more important (Christiansen et al. 1987).

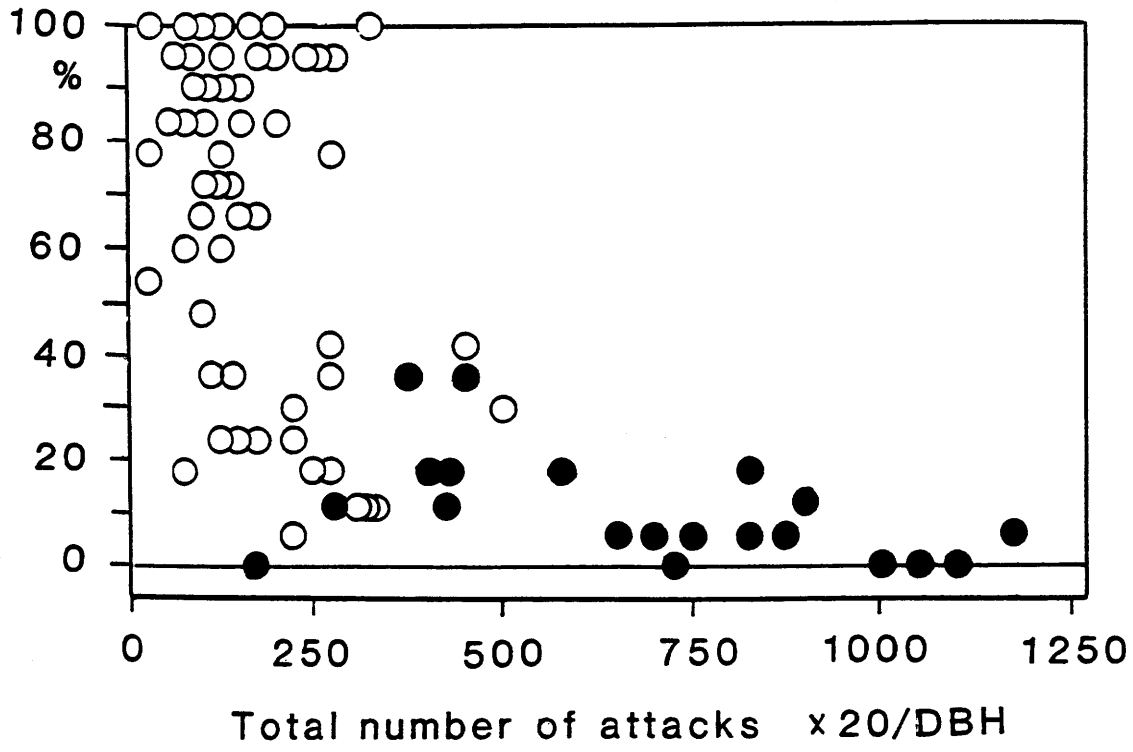

Figure 3. Performance of the constitutive defense in Norway spruce: percent of beetle entrance holes with liquid resin or resinous frass in relation to total number of attacks per tree. Black circles = trees killed by the attack; white circles = trees surviving.

The Induced Defense

The induced defense reaction in Norway spruce has been studied using artificial inoculations with *O. polonicum*. It turns out that other *Ophiostoma* species will produce reactions of a similar type (Horntvedt et al. 1983, Solheim 1988), but we have concentrated on *O. polonicum*, which is able to penetrate the sapwood and kill experimental trees.

Artificial inoculation offers an interesting opportunity for experimental study of the relative resistance of individual trees. By using this technique, we can administer exact numbers of infections to a given tree. Theoretically, this can also be achieved by subjecting the tree to a controlled number of beetle attacks. In practice, however, it is very difficult and laborious because the experimental beetles inevitably attract "wild" conspecifics to the tree. Thus the part of the bole which is suitable for *I. typographus* would have to be screened in order to prevent unwanted attacks.

It is possible that the reaction of a tree to one single inoculation could be used as a predictor of its resistance to mass inoculation, as demonstrated for lodgepole pine (Raffa and Berryman 1983). This might possibly be used to assess resistance to beetle attack as well. In our experiments, however, we have studied only the tree's reaction to mass inoculation. Our technique has been to mark out a belt on the stem, 60 or 80 cm high, around breast height. Within this belt, the trees are inoculated at

different densities, ranging from one to eight inoculations per square decimeter. A template is used to ensure even spacing of the points of inoculation. Alternatively, the inocula are placed along rings encircling the stem, virtually covering the same area as the inoculation belts. The cork borer technique has been used as a standard. Placing the inoculations so densely within a limited area, instead of spreading them out over a larger section of the bole, is considered a "worst case" for the defense. However, a pilot study in which an equal number of inoculations was given over 60, 120, or 240 cm of the stem did not reveal any dramatic differences in fungal success (unpubl. data).

The experiments have demonstrated a clear threshold of successful infection (Christiansen 1985a, 1985b). When the number of infections in a tree increases, there is a point where the resin concentration of the phloem reaction zone drops (Fig. 4). At this critical point, the fungus is able to break out of the enclosure and spread out into the phloem. This is parallelled by increasing success of the fungus in penetrating the sapwood.

There also appears to be a difference in defensive capacity between spruces of different vigor. Suppressed, slow-growing trees appear to tolerate fewer infections than dominant and vital ones (Christiansen 1985a). This accords with a study of host resistance to *I. typographus* attacks by Mulock and Christiansen (1986).

Role of Carbohydrates in the Induced Defense

From the threshold response described above, it may be inferred that defensive capability is influenced by the availability of some limited resource. Since it is known that carbohydrates (C) are both raw material and energy source for the wound response, availability of C in the infected area would seem one likely candidate for a critical factor. I have tested this assumption experimentally (Christiansen and Ericsson 1986). Our first hypothesis was that if substantial amounts of sugar are mobilized for the induced defense, then C (starch) reserves of the surroundings should be depleted. Second, we assumed that trees with low reserves should be more vulnerable to fungal attack than trees with high starch concentrations.

We inoculated spruce trees in belts as described above, and measured the starch concentrations at different distances above the belt. Our first hypothesis was supported in that starch concentrations were significantly reduced as far as 1.5 m above the inoculated belt. But the experiment failed to support our second hypothesis. Trees ranging from 12 to 20.7 percent in starch concentration showed no differences in defensive capacity. Similar results were found in a later investigation (Horntvedt 1988).

In a second experiment (Christiansen and Ericsson 1986), we girdled some of the trees above the inoculation belt to manipulate their starch reserves. A cambium-deep girdle at 2 m above ground shut off the assimilate flux from the crown. One group of trees was girdled in April, before the spring build-up of C reserves. In these trees the starch concentration reached only half the normal (Fig. 5). Another group was girdled at the time of inoculation (i.e. mid-May) and consequently had normal starch reserves. In this experiment we had carefully chosen our inoculation dose so that inoculated, ungirdled trees withstood the infection quite well; only a small fraction of their sapwood became blue stained (Fig. 5). Low-starch (i.e. early-girdled) trees were much more stained, but so were trees girdled at the time of inoculation. We therefore concluded that it may not be the size of the C reserves (starch) per se, but rather the efficacy of C (sugar) translocation that is critical for the mobilization defense. Our conclusions are corroborated by a study of lodgepole pine in the U.S.A. (Miller and Berryman 1986) performed simultaneously, but independently.

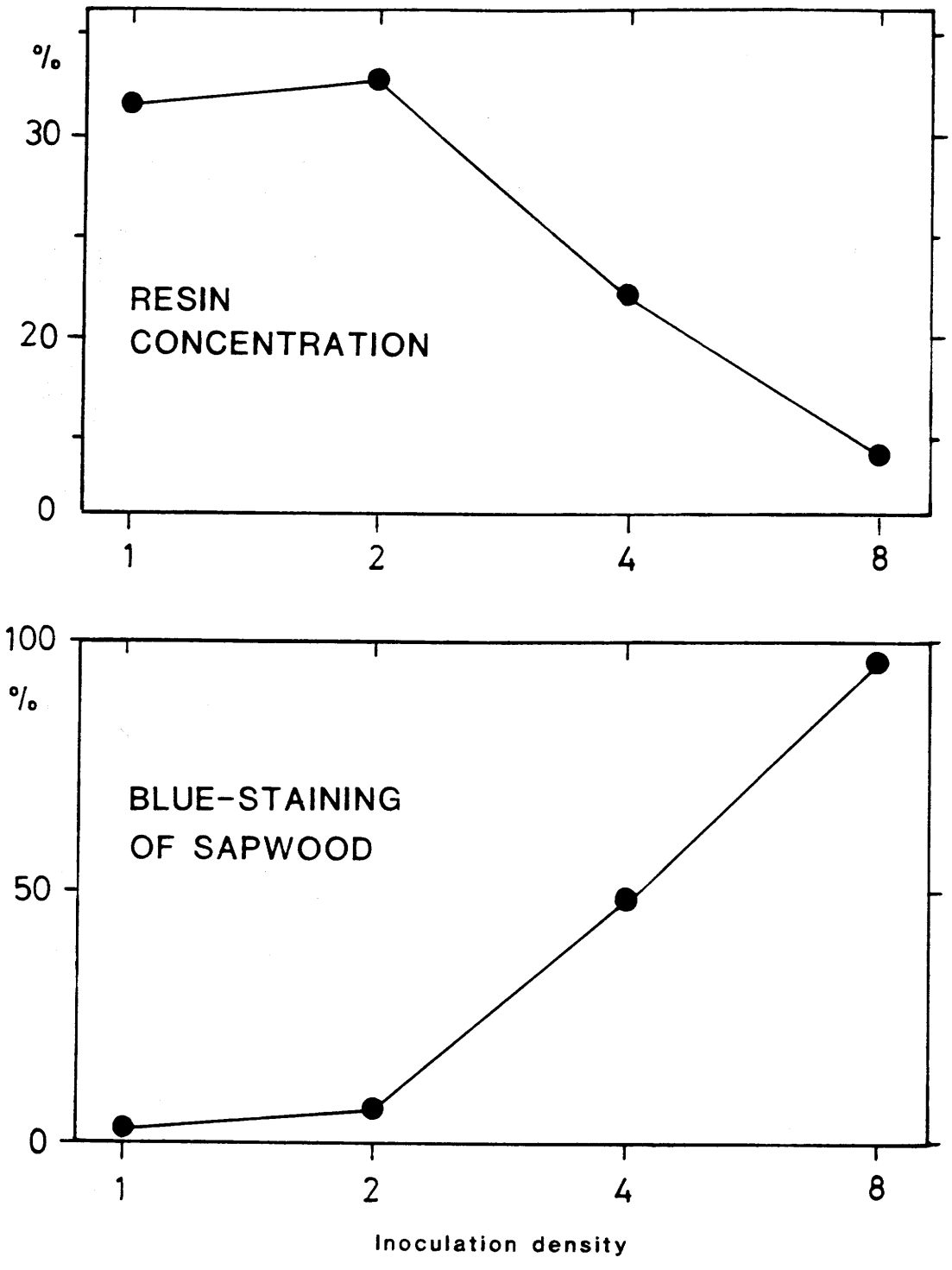

Figure 4. Performance of the induced defense in Norway spruce: resin concentration in phloem reaction zones and fungal success in relation to inoculation density. Data from Christiansen 1985a.

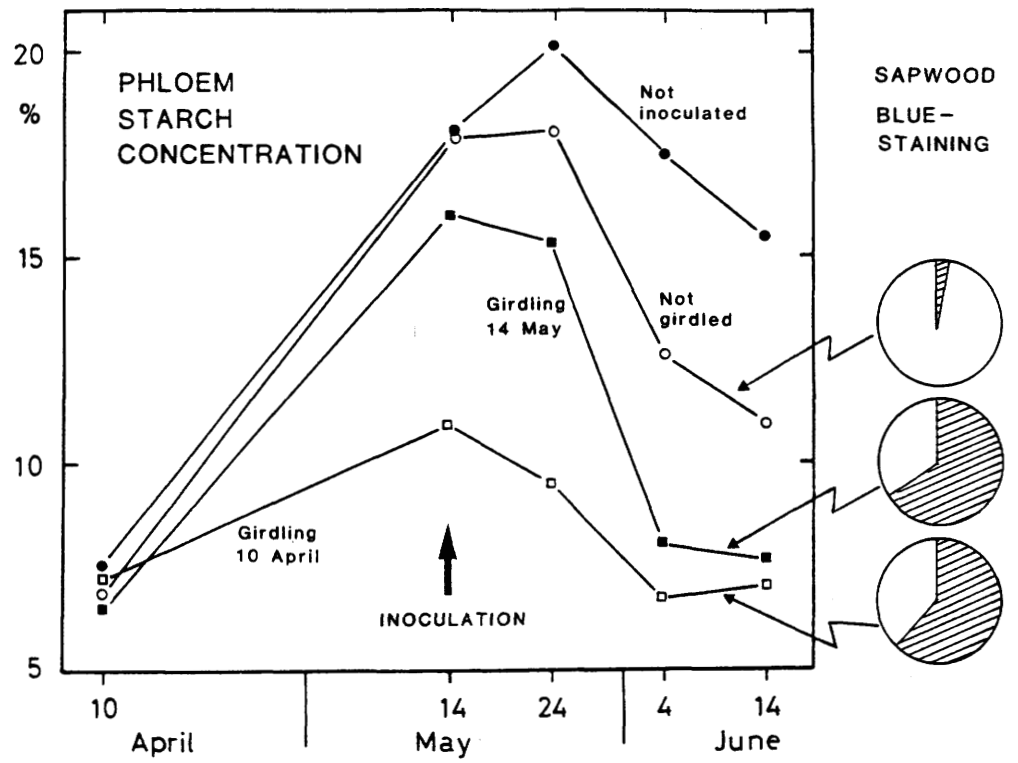

Figure 5. Starch dynamics of Norway spruce in relation to fungal inoculation and girdling of the stem and fungal success in invading the sapwood. Data from Christiansen and Ericsson 1986. See text for further explanations.

During the growth season, many sinks compete for the available C in a tree. Priorities for C allocation seem to exist. In a defoliation experiment with Scots pine, Ericsson et al. (1980) found the following order of allocation (moving from high to low priority): 1) bud formation, 2) needle biomass, 3) shoot length, and 4) year-ring width. Allocation for defense may not be the highest priority (Waring and Pitman 1985), but a high drain on C by numerous induced defense reactions considerably affects year-ring growth in Norway spruce (Christiansen 1985a).

Since carbohydrate availability varies during the growing season (e.g. Ericsson et al. 1980), this is likely to affect the defensive capacity of the trees. An experiment with monthly inoculations of Norway spruce showed considerable variation in defensive efficacy over the season (Horntvedt 1988). The success of *O. polonicum* in infecting the sapwood was very low in May, moderate in June, and high in July, then declined through August and September. The lack of fungal success in spring could not be explained by lower temperatures only; the trees were evidently more resistant in the early season.

Because *I. typographus* has its main flight in spring (mid-May in South Norway), the beetles appear to encounter host trees in a highly resistant state. Nevertheless, they are able to overcome the resistance of the host given an adequate number of attackers. On the other hand, during an epidemic, when the parent beetles produce one or more sister broods, increasing susceptibility late in the season may reduce the number of beetles necessary to kill a tree. This may have a bearing on population dynamics, as pointed out by Horntvedt (1988).

It has been suggested that tree resistance in general may be closely related to the amount of photosynthate that is immediately available for defense (Christiansen et al. 1987). A wide variety of

factors is known to predispose trees to bark beetle attack, among them drought, flooding, wind-swaying, defoliation, lightning strike, fire, rot fungi, competition, and old age. These seemingly unrelated factors may have a common denominator: they all reduce the C availability. It would thus be interesting to test the relationship between limitations on the transfer of C to the sites of attack and host tree resistance.

At present, we are testing this hypothesis in experiments with Norway spruce. We are trying to reduce C stores--and hence, presumably, availability--by two techniques: 1) by exposing the trees to prolonged drought and 2) by reducing the crown biomass considerably through branch pruning. Later the trees will be inoculated with *O. polonicum* to test their resistance.

EPILOGUE

Together, the two defense systems will define the "threshold of successful attack" for a given tree. Both defenses become exhausted when the number of attacks reaches the critical level. Given the high population densities of an epidemic, any tree can be killed in a mass attack. When the trees are rapidly overwhelmed by a large number of beetles, no constitutive defense will suffice and no evidence of the induced defense can be observed, as there is no time for the reaction to take place.

Even though the described defense mechanisms are no safeguard during an epidemic, they do protect the spruce trees in a normal situation. They prevent the tree from being conquered by a handful of attackers, and they contribute to reduction of the beetle population. Since at least the induced defense reaction seems related to the vigor of the host tree, the forest manager can probably reduce the possibility of beetle outbreaks by maintaining a vigorous forest.

SUMMARY

This paper describes the relationship between the bark beetle *Ips typographus* and its fungal symbionts, in particular *Ophiostoma polonicum*, attacking Norway spruce, *Picea abies*. Against a joint beetle-fungus attack, coniferous trees defend themselves by means of 1) their preformed (constitutive) duct resin and 2) an induced reaction producing highly resinous zones around the points of infection in bark and outer sapwood. The performance of the two defense systems is discussed, with particular reference to Norway spruce. The importance of carbohydrate availability for the induced defense reaction is discussed.

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