Behavioral mechanisms involved in reducing competition in bark beetles

John A. Byers

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Bark beetles feed and reproduce in the phloem/cambium tissue of trees where severe competition between individuals of the same and different species significantly reduces their reproductive success. In this coevolutionary setting, individuals that can avoid competition whenever possible by means of genetically controlled behavioral mechanisms are naturally selected. Avoidance of intraspecific and interspecific competition is accomplished in part even before landing by olfactory perception of specific pheromones and allomones. These olfactory systems may function at least as well after landing. In several species the uniform distribution of attacks on host trees indicates that individuals avoid competition by only attacking if they are at least a minimum distance from other established attacks. Once beetles are under the bark their tunneling patterns indicate that a behavioral mechanism exists to avoid intersecting nearby galleries of competing individuals. Finally, beetles may choose to re-emerge if the expected chances of successful reproduction by continuing their stay become less than the probabilities of finding another host and successfully reproducing.

J. A. Byers, Dept. of Ecology, Univ. of Lund, S-223 62 Lund, Sweden.

Introduction

"Aggressive" bark beetles (Coleoptera: Scolytidae), those that often kill a tree in a "mass attack" in order to reproduce, are especially damaging to coniferous forests. A discussion and review of literature and concepts concerning bark beetle competition for host-tree resources and the effects of interactions of host resistance and beetle virulence/cooperation on such competition may elucidate new approaches to research programs with the ultimate goal of integrated control of pest bark beetles. Two important bark beetle species of California, *Dendroctonus brevicomis* and *Ips paraconfusus*, will be compared with *I. typographus* of Europe concerning the state of our knowledge about the behavioral processes which may operate to reduce competition. Research on closely related species will be discussed to illutrate hypotheses and possible behavioral mechanisms when our knowledge of the above bark beetles is largely lacking.

Host-tree resistance to bark beetles

Bark beetles usually confine their activities to the nutritious, but thin, layers of phloem and cambium which are sandwiched between the outer bark and the often resinous xylem tissue. The combined thickness of these layers is similar to the size of a beetle, and competition can be quite severe for this two-dimensionally limited food resource. Since the adults and their larvae consume the food transporting tissue, this would result in the death of the tree. However, trees generally die first because symbiotic fungi introduced by the beetle paralyze the water transporting system. The loss of turgor pressure reduces resinosis and benefits the beetle (Wood 1982). Trees, therefore, must expend considerable energy to defend themselves against bark beetle attack and colonization.

Besides a tough and thick bark, many trees produce oleoresin as a resistance mechanism. Oleoresin is believed to adversely affect bark beetles through both

chemical and physical means (Smith 1965, Hodges et al. 1979, Wood 1982, Byers et al. 1984). Although there is some question as to the importance of various chemical constituents in the tree for resistance to bark beetles (Byers 1981a, Raffa and Berryman 1983) it is very probable that certain tree terpenoids, tannins and phenolics are repellent and damaging to bark beetles as they are to many phytophagous insects (Rosenthal and Janzen 1979). It is evident that bark beetles must mobilize considerable energy reserves to detoxify these secondary plant substances and this must contribute to the "stress level" and mortality of beetles. It has also been commonly observed that resinous exudations make it more difficult for beetles to excavate tunnels and that crystalization of the resin will entrap adults (Miller and Keen 1960, Byers et al. 1984). Thus, there has been a natural selection for aggressive bark beetles that can partially compensate for the chemical and physical resistance mechanisms of conifers.

On the other side, there is some reason to believe that mechanisms for resistance to insects are selected for in trees. Sturgeon (1979) found correlative evidence that in areas of high western pine beetle "predation" there were relatively more ponderosa pine with higher proportions of a toxic monoterpene (limonene) than in other areas without selection pressure. It was concluded that certain "resistant" high-limonene trees may have been selected for as a result of high bark beetle-induced mortality.

Cooperation among bark beetles

In the coevolutionary "war" between pest bark beetles and their host trees it appears that many species have responded to resinosis by utilizing pheromones which elicit mass aggregations to overpower the tree (Wood 1982). Thus a minimum number or density of beetles is required to cooperate in killing a particular tree and allow reproduction. It is in the interests of each resident adult to advertise the suitability of the food resource in order to obtain help in overcoming the tree's resistance. It is also in the interests of each responding adult to join the attack providing it can determine that successful colonization and brood production will result. The simple presence of pheromone may indicate to arriving adults that the host tree has not been able to resist attack, feeding, and release of pheromone and thus should provide suitable breeding habitat. Several species in the genera *Ips, Dendroctonus,* and *Pityogenes* are known to produce pheromone components only after feeding (Coster and Vité 1972, Byers 1983a, Birgersson et al. 1984, Byers et al. 1988) which is not possible while beetles must struggle against the copius flow of resin from a resistant tree. Once the tree has been killed by the aggregated beetles, each individual must contend or compete with the other beetles in the partitioning of the bark area.

Competition among bark beetles

At some point the attack density exceeds a certain value based on the characteristics of the particular tree and bark beetle species, above which further increases in density result in increasingly detrimental effects on reproduction due to intraspecific competition between larvae (Berryman 1974). The nature of this competition is probably a combination of interference competition (direct effects such as small larvae being eaten) and exploitative competition (indirect effects such as food starvation). Reports of intraspecific competition in several bark beetle species in the genera *Ips, Dendroctonus, Scolytus,* and *Tomicus* have shown that brood output per female decreases at higher attack densities (Miller and Keen 1960, McMullen and Atkins 1961, Eidmann and Nuorteva 1968, Svihra 1972, Ogibin 1973, Beaver 1974, Berryman 1974, Mayyasi et al. 1976, Wagner et al. 1981, Light et al. 1983, Anderbrant et al. 1985).

Interspecific competition has rarely been studied between scolytid species, but it is hypothesized that resource partitioning (selection of specific host-tree species and/or parts of a host) functions as a means of reducing competition between bark beetle species in northwestern U.S.A. (Schmitz and Rudinsky 1968), California (Miller and Keen 1960, Byers and Wood 1980) and in the southeastern U.S.A. (Paine et al. 1981). The only laboratory study of interspecific competition has involved *I. paraconfusus* and *I. pini* and showed severe effects of competition on reproduction when densities were high (Light et al. 1983). Recent laboratory studies with *I. typographus* and *I. duplicatus* (O. Anderbrant and F. Schlyter unpubl.) and *I. typographus* and *Pityogenes chalcographus* (J. A. Byers unpubl.) also show detrimental interspecific competition.

The adverse effects of competition become apparent even at relatively low densities when beetles colonize wind-thrown trees and broken tops that are less able to resist beetles (Raffa and Berryman 1983). However, the reproductive costs due to increased crowding and competition which may determine whether a beetle decides to continue the attack are probably balanced (in behavioral and evolutionary terms) by the costs of searching elsewhere for suitable breeding areas.

The strong intra- as well as interspecific competition among bark beetles when colonizing a host tree most probably have selected individuals adept at both avoiding and surviving such competition. Behavioral mechanisms for avoiding competition may operate in at least five ways: (1) avoid attraction to and landing in areas with high attack density, (2) leave these areas after landing, (3) avoid initiating an attack near others, (4) avoid tunneling into other gallery systems, and (5) re-emerge if densities under the bark are too high. Interspecific competition can be avoided in addition to the above ways by habitat/host selection (resource parti-
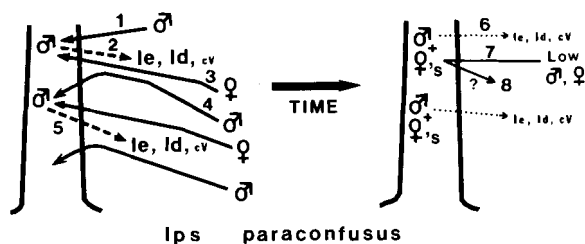
Ips paraconfusus

Fig. 1. Theoretical mechanism for regulation of attack density (intraspecific competition) and termination of aggregation in *Ips paraconfusus* during colonization of a ponderosa pine. The male beetle arrives first (1) and constructs a nuptial chamber in the phloem layer. His release of ipsenol, Ie, ipsdienol, Id, and *cis*-verbenol, cV (2), attracts both sexes (3), but at higher concentrations near the source, males are inhibited in close-range orientation and thus land in adjacent areas of lower male attack density (4). This process is repeated and serves to spread the colonization evenly and regulate attack density (5). After males are joined by several females, their production of the pheromone components, Ie and Id, declines rapidly (6) and the tree becomes unattractive to beetles (7). However, it appears that an additional mechanism (verbenone from microbes in the tree?) is needed to both regulate density and terminate attack initiation during the later stages of colonization (8).

tioning, Paine et al. 1981, Byers and Wood 1980). Olfaction is known to be used in (1) and (2) above while beetles may also use other sensory systems such as auditory/stridulatory, thigmotactic, gustatory, and visual to avoid competition. Various sensory systems may operate in several of the basic ways above but little is known about mechanisms other than olfaction.

Olfactory mechanisms for avoiding intraspecific competition

If a beetle could determine while flying which areas on a tree were densely colonized it would be advantageous because less time and energy would be required compared with walking to gain the same information. Furthermore, flying beetles are relatively immune to predation, especially by bark surface-hunting clerids and other predators. Because of this, apparently, two of the most important pest bark beetles of California on ponderosa pine *Pinus ponderosa* have evolved olfactory systems using pheromones to avoid areas of higher attack densities.

In the California five-spined engraver *I. paraconfusus*, males initiate the attack and release three synergistic components, (−)-ipsenol, (+)-ipsdienol and (−)-(4S)-*cis*-verbenol, which are attractive to both sexes (Silverstein et al. 1966, Wood et al. 1968). During feeding, males hydroxylate the host monoterpenes, myrcene and (−)-α-pinene to the respective pheromone components (Hughes 1974, Renwick et al. 1976, Byers et al. 1979, Hendry et al. 1980, Byers 1983a). At lower concentrations of the attractive pheromone (farther from the source) both sexes are about equally attracted, but as the concentration increases, proportionately more males than females do not fly directly to the

source (Byers 1983b). In the laboratory bioassay it was shown that at the higher release rates of pheromone components $(2.2 \times 10^{-7}$ and 2.2×10^{-6} g min^{-1}), the attraction response of walking males was inhibited or reduced compared with lower rates, while female response increased proportional to the dosage (Byers 1983b). During the attack of a felled ponderosa pine by *I. paraconfusus*, relatively more males than females were found landing adjacent to the origin of attack (baited with an infested log at the tree-top) while more females than males were attracted to the origin. This pattern of males preceding females as colonization proceeded down the trunk was evident for a few days until attacks were occurring throughout the bole (Byers 1983b). Then at the peak of female aggregation relatively fewer males landed on the tree and instead may have decided to search for less densely colonized hosts. Thus it appears that these differences in behavior are ultimately due to differences in sexual strategy. The polygynous *Ips* male establishes a gallery system under an area of bark (resource defense). Newly arriving males can avoid competition by avoiding high concentrations of pheromone and search for the less densely colonized areas on the "weakened tree". On the other hand, females apparently rely on the male's "judgement" concerning the likelihood of competition and resource desirability and simply want to join the harem (the more males per area, the easier to find one; or more simply, females continue orienting up to pheromone gradient to find the male source).

Based on these and other data (Byers 1981b), a semiochemical description of aggregation and colonization is presented in Fig. 1. However, the mechanism of sex-specific responses to pheromone will not explain how the process of aggregation terminates in *I. paraconfusus*. For instance, as the release of pheromone from the original males declines when joined by females after a few days or so (Byers 1981b), in theory new unmated males should continue to be attracted and then replenish the release of pheromone, resulting in a perpetuating attack and overcrowding – but this does not occur. It is not known what inhibits attacks later in the colonization. More likely, however, an attack-spacing mechanism (minimum allowed distance between attacks) may operate throughout the attack sequence as was indicated for *I. typographus* (Byers 1984).

In the spruce bark beetle of Europe, *Ips typographus*, males also initiate the attack in Norway spruce *Picea abies*, and are less attracted than females to higher concentrations of their aggregation pheromone (Schlyter et al. 1987a, b). Males and females are about equally attracted at lower release rates of the attractive components, methylbutenol and (−)-(4S)-*cis*-verbenol, produced by males in the greatest amounts during the initial phases of aggregation (Bakke et al. 1977, Birgersson et al. 1984). (−)-α-pinene, this time from Norway spruce, is used as the precursor to (−)-*cis*-verbenol (Klimetzek and Francke 1980). By comparing a range of
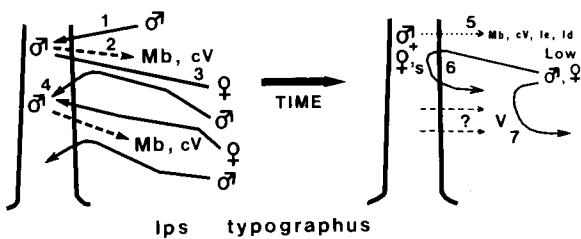
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Ips typographus

Fig. 2. Theoretical mechanism for regulation of attack density and termination of aggregation in *Ips typographus* during colonization of a Norway spruce. The male arrives first (1) and releases 2-methyl-3-buten-2-ol, Mb, and *cis*-verbenol, cV, (2) which attracts both sexes from a distance (3), but as males approach high concentrations of pheromone they become less precise than females in close-range orientation and so land in adjacent areas (4). These sex-specific behaviors function to spread the attack and limit attack density in a way similar to *I. paraconfusus*. Males of *I. typographus* also reduce their release of pheromone components after "mating" (5) but in addition they release small quantities of ipsenol, Ie, and ipsdienol, Id, which inhibit response of both sexes probably only at close range (6). These compounds could function to both regulate attack density and terminate aggregation (along with a decline in attractants). However, verbenone, V, from microorganisms in the decaying tree (7) could be the more general inhibitor responsible for termination of aggregation.

attractive pheromone concentrations and as well by placing passive traps at a distance from attractive sources, it was possible to show that males were less likely than females to reach the source, especially at the higher dosages released (Schlyter et al. 1987a, b).

Thus, *I. typographus* males in Europe act in a similar way to males of *I. paraconfusus* in California in regard to avoiding competition by landing in areas adjacent to the highest pheromone release, which indicates a fully-colonized zone. This behavioral similarity is not surprising since both species have similar polygynous mating systems and ecological requirements. However, our understanding of the semiochemical systems of *I. typographus* seems more complete than that of the Californian counterpart. This is because males of *I. typographus* (unlike *I. paraconfusus*) have ipsenol and ipsdienol in small amounts in their guts during the later phases of aggregation (Vité et al. 1972, Birgersson et al. 1984) which, at least in higher doses, inhibits attraction (Schlyter et al. 1987a). These inhibitors could signal at close range to walking beetles that areas are occupied. Another compound, verbenone, has been shown to inhibit attraction of both *I. paraconfusus* (Byers and Wood 1980, 1981) and *I. typographus* (Bakke 1981) and verbenone is produced by some yeasts found in association with *I. typographus* (Leufvén et al. 1984). Verbenone amounts were also found to increase with time in the male nuptial chamber walls (Leufvén and Birgersson 1987). Brand et al. (1976) found that verbenone was released by fungal metabolism in southern pine beetle galleries in loblolly pine. Possibly verbenone indicates to *I. paraconfusus, Dendroctonus brevicomis*

(Byers et al. 1984), and *I. typographus* that a host is decadent and has become unsuitable for colonization. Based on the above findings, a semiochemical model of aggregation and colonization for *I. typographus* is shown in Fig. 2.

In contrast to the *Ips* species, the western pine beetle of California, *D. brevicomis*, does not appear to exhibit sex-specific responses to high concentrations of their attractive components (Byers and Wood 1981, Byers et al. 1984). *Exo*-brevicomin, produced by the attack-initiating females, and frontalin, produced by males, are synergistically attractive to both sexes (Silverstein et al. 1968, Kinzer et al. 1969). Several host monoterpenes, such as myrcene, will increase the attraction slightly (Bedard et al. 1980). Verbenone was shown to inhibit the attraction of *D. brevicomis* to its aggregation pheromone and was suggested to be produced by males later in order to terminate aggregation (Renwick and Vité 1970). However, it was later found that verbenone is contained in males in the largest quantities at the time of landing and its content in the guts declines more rapidly during colonization than any of the other components in either males or females (Byers and Wood 1980, Byers 1983c, Byers et al. 1984). Thus, verbenone from males probably is used as a close-range signal to indicate that the immediate area or gallery is occupied by a pair.

(−)-*trans*-verbenol is produced in both sexes of *D. brevicomis* equally from the host monoterpene (−)-α-pinene, but in nature females typically contain significantly more than males (Byers 1983c, Byers et al. 1984). Both sexes contain major amounts of *trans*-ver-
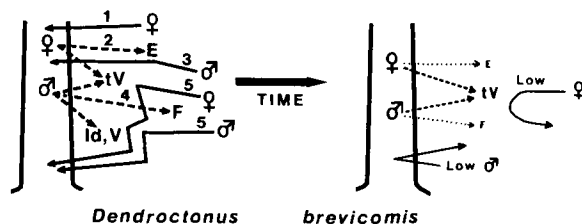

Dendroctonus brevicomis

Fig. 3. Theoretical mechanism for regulation of attack density (intraspecific competition) and termination of aggregation in *Dendroctonus brevicomis* during colonization of a ponderosa pine. The female beetle arrives first (1) and bores into the trunk and after feeding produces *exo*-brevicomin, E (2), which primarily attracts males (3). Males, upon locating a female gallery, soon release frontalin, F (4), which synergizes with E to elicit a mass aggregation (5). However, at the same time females and males produce *trans*-verbenol (tV) and males produce verbenone (V) and (+)-ipsdienol (Id). At close range these compounds apparently inhibit the attraction of beetles to E and F (tV appears to primarily affect females while Id and V affect both sexes), which would regulate the attack density. After several days the production and release of E and F diminishes to unattractive leves (at long range). The few females attracted during this latter period may be inhibited from attacking by the still significant, although reduced levels of tV. The few males would not find any unpaired females and so would continue searching elsewhere.
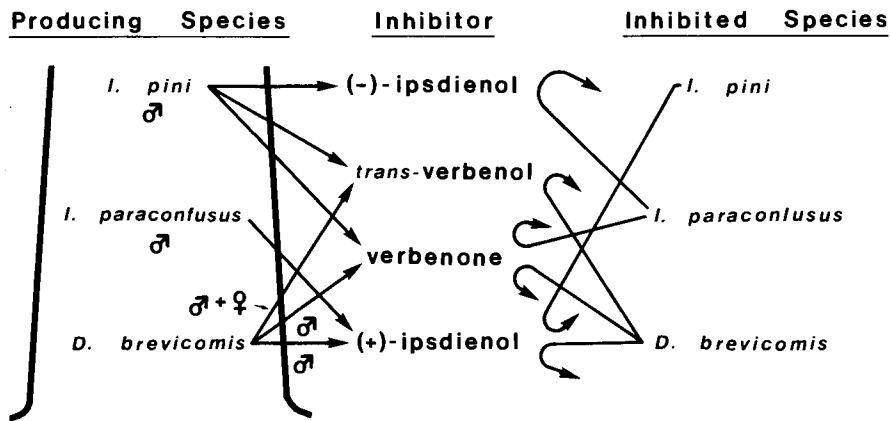
Fig. 4. Inhibition of the attraction response to conspecific pheromone by pheromones/kairo-allomones produced by three sympatric bark beetles, *Dendroctonus brevicomis*, *Ips paraconfusus*, and *I. pini* which may function to reduce interspecific competition for their host ponderosa pine in California. Response inhibition by *trans*-verbenol, verbenone, and (+)-ipsdienol may also reduce intraspecific competition in *D. brevicomis*.

benol (comparable to peak amounts of the attractants) for the entire aggregation period and for some time thereafter (Byers et al. 1984). *Trans*-verbenol was shown to inhibit only the female's close-range orientation and entering of beetle-sized holes into a trap with attractants. The inhibitor did not reduce the longer-range attraction at the dosages used (Byers 1983c). Because of these results, Byers et al. (1984) hypothesized that females utilize *trans*-verbenol, primarily produced by colonizing females, to avoid areas heavily infested with conspecifics. Furthermore, while amounts of the attractants in the hindguts of females declined to subliminal levels after a week or more of colonization, the content of *trans*-verbenol was still relatively high. This would explain the termination of aggregation. However, the picture is probably more complex than this as males produce ipsdienol from myrcene in the tree in quantities which probably have a short-range inhibitory effect on both sexes (Byers et al. 1984). Finally, as discussed above, verbenone release from microbial degradation of host tissue surrounding the galleries could also indicate to host-seeking beetles that this area is unsuitable. In Fig. 3, a diagramatic view of the olfactory mechanisms which function in reducing competition and termination of aggregation is shown.

Olfactory mechanisms and resource partitioning for avoiding interspecific competition

Many of the inhibitory pheromones and attractive pheromone components that are reliable indicators of higher intraspecific competition on areas of a pine tree appear also to be useful as interspecific messages (allomones) for reducing competition between cohabiting species. In the southern half of the Sierra of California, *D. brevicomis* and *I. paraconfusus* are sympatric and compete for the phloem tissue of ponderosa pine. They compete with a third beetle, *I. pini*, in the northern half of the Sierra (mountains) and through the Cascade

range into Oregon. In Oregon and Idaho, *D. brevicomis* and *I. pini* are predominant. The situation is complicated by a fourth major competitor, *D. ponderosae*, which in northern California, Oregon, Idaho, and Montana competes with these species on ponderosa or with *I. pini* in lodgepole pine *P. contorta*. There is some niche separation between these species as the *Dendroctonus* species when found alone attack the lower two-thirds or more of the tree while the *Ips* species when alone usually attack the upper half or more (Miller and Keen 1960, Strubble and Hall 1955). However, on larger logging debris, smaller wind-thrown trees, and in a broad overlap area on standing trees there are habitats eminently suitable for all the species. In spite of this, each species maintains a surprising degree of conspecific "purity" (often 100%, J. A. Byers unpubl.) in mutually colonized trees, and gradations from one species to another along the tree trunk are described as abrupt (Miller and Keen 1960, Birch and Wood 1975, Byers and Wood 1980).

Verbenone released by male *D. brevicomis*, in addition to its intraspecific effects, appears to inhibit the response of its competitor, *I. paraconfusus*, to its pheromone (Byers and Wood 1980, 1981). Verbenone was also found in *I. pini* males from Idaho that had fed in red pine logs *P. resinosa*, but Lanier et al. (1980) could not ascribe any "biological activity" to the compound. However, in view of these reports, it seems that the observed inhibition of attraction of *I. paraconfusus* to its pheromone by infested logs of *I. pini* (Birch and Wood 1975) is due in part to verbenone, a major component in *I. pini* (Vité et al. 1972, Lanier et al. 1980). Earlier it was believed that (−)-ipsdienol from *I. pini* was solely responsible for inhibition of *I. paraconfusus* (Light and Birch 1979). Thus, the behavioral effect of verbenone on *I. paraconfusus* may have resulted from selection pressures to reduce interspecific competition from both *D. brevicomis* and *I. pini* (Fig. 4). Furthermore, the inhibitory effects of verbenone on *D. brevicomis* could be the result of selection pressures from
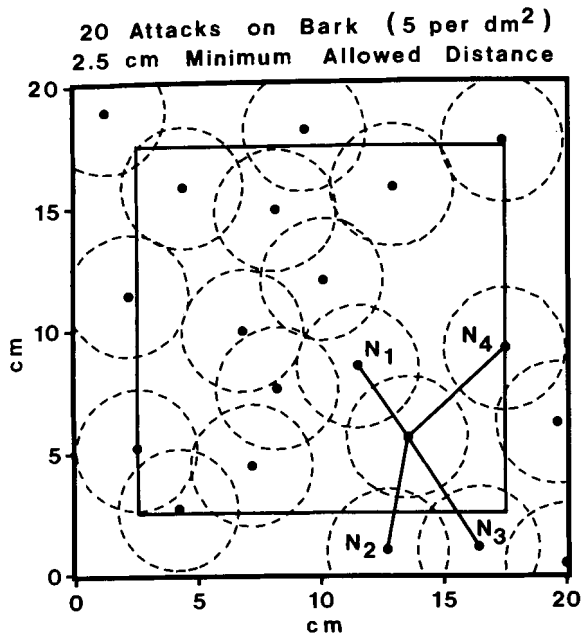
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20 Attacks on Bark (5 per dm^2)
2.5 cm Minimum Allowed Distance

Fig. 5. Computer simulation of bark beetle attacks on bark surface (5 dm^{-2}). The attacks of 20 beetles in a 20×20 cm area are represented such that all attacks are separated by at least 2.5 cm (the calculated minimum allowed distance for *Ips typographus*, Byers 1984). Attacks occurring outside a perimeter border of 2.5 cm (inner square) were not considered except as neighbors in determining the average distances (cm) to the four nearest neighboring attacks (N = 11): $n_1 = 3.33$, $n_2 = 3.96$, $n_3 = 4.74$ and $n_4 = 5.41$. The average expected distances to the four nearest neighboring attacks, if the distribution was random, are 2.36, 3.40, 4.43 and 5.74 for n_1 to n_4, respectively (Byers 1984).

both intraspecific competition and interspecific competition exerted by *I. pini*. This could also be true of the inhibitory effects of *trans*-verbenol on *D. brevicomis* (Fig. 4) which is produced in significant amounts by *D. brevicomis* (Byers 1983c), by *I. pini* (Vité et al. 1972, Lanier et al. 1980) and by *D. ponderosae* (Pitman et al. 1968). Again, the (+)-ipsdienol produced by male *I. paraconfusus* (Silverstein et al. 1966) and by male *D. brevicomis* in the early stages of colonization may function both to reduce intraspecific competition in both species (Beyers 1982, Beyers 1983b) and to reduce interspecific competition from *I. pini* in both species, Fig. 4 (Birch et al. 1980, Byers 1982).

Therefore, the above discussion argues for olfactory systems to evolve as a result of the relative benefits of multiple functions (intra- and interspecific). Because of evolutionary constraints on sensory complexity and for reasons of energy efficiency, the coevolution of various olfactory systems of these species would favor the sharing of certain behavioral chemicals. Once a specific chemical was established and recognized for a particular function in one species, such as avoidance of intraspecific competition, then individuals of other species might

be selected that use this compound to avoid interspecific competition and then intraspecific competition as well. Concurrently, there would be a selection of individuals with biosynthetic pathways that produce the appropriate behavioral chemicals, and energy considerations should favor a ready source of precursor, the host monoterpenes. In this mutually reinforcing type of selection, (+)-ipsdienol may have become inhibiting to several bark beetle species of California. Similarly, verbenone may have become inhibiting to many species spread world-wide. However, it is increasingly apparent that verbenone may have been produced "first" during evolution by degrading microorganisms that indicated to beetles the presence of unsuitable host material, and then subsequently used additionally by them as pheromones and allomones that indicated competition.

Selection of attack sites to avoid competition

A beetle should be able to make a more precise determination of the likelihood of competition after landing, and as pointed out above, some of the olfactory mechanisms appear to operate while walking (Byers 1983b, c). It would certainly be advantageous for a beetle to avoid initiating an attack too close to other established attacks. An early observation that beetles may space their attacks was made by Miller and Keen (1960) who summarized reports of natural attack densities of *D. brevicomis* and found them to vary from 0.59 to 2.32 dm^{-2} but "always within certain limits". They further stated that "beetles seem instinctively to distribute their attacks so that overcrowding does not occur in any particular bark area". Later, the attack patterns of *D. ponderosae*, *D. frontalis*, *D. pseudotsugae*, *Tomicus piniperda*, and *I. typographus* were analyzed and found to be more uniformly, regularly spaced than would be expected if the patterns were random (Shepard 1965, Safranyik and Vithayasai 1971, Mayyasi et al. 1976, Hedden and Gara 1976, Nilssen 1978, Byers 1984).

Recently, the attack patterns of *I. typographus* at three different densities were compared with a computer model which randomly simulated the same densities, but at several degrees of uniform spacing, such that the nearest neighbor distances overlapped those of the natural patterns (Byers 1984). By this method and regression analysis, a certain distance of spacing between attacks was found (2.5 cm) which could explain the nearest neighbor average distances between attacks for all three natural densities (Fig. 5). Since the estimated minimum allowed distance of 2.5 cm did not differ appreciably at the three densities, this may indicate that it is behaviorally controlled and inherently fixed. There would be, as expected, individual genetic variation. Thus, the "minimum allowed distance" may be a population or species parameter and allow comparisons with other species. In each species there may be a specific upper density which can never be exceeded because of the particular spacing requirements. There-
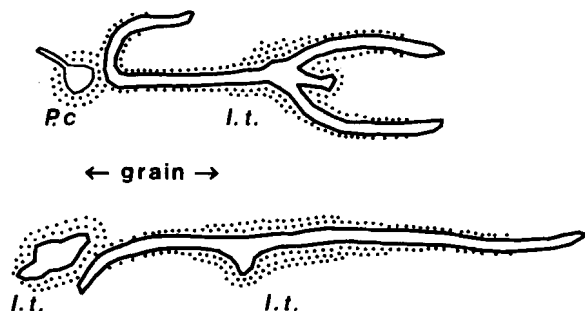
← grain →

Fig. 6. Avoidance of parent galleries and nuptial chambers of conspecific or heterospecific individuals, *Ips typographus* (I.t.) and *Pityogenes chalcographus* (P.c.) in Norway spruce, Grib skov, northern Sjaelland, Denmark (May 1984). Sketched from bark-stripped galleries, stipled areas represent oxidative discoloration of phloem tissue.

fore, at an upper density a spacing mechanism would prevent new attacks from occurring, and then termination of the aggregation would result since it has been shown that production of pheromones declines after mating in several species (Hughes 1973, Coster and Vité 1972, Gore et al. 1977, Byers 1981b, Byers et al. 1984, Birgersson et al. 1984).

The nature of the supposed behavioral spacing mechanism in *I. typographus*, and in other beetles, is virtually unknown. One possibility is the avoidance of higher concentrations of male pheromone attractants emanating from an attack site, as discussed above for *I. paraconfusus* and *I. typographus*. Another possibility is that ipsenol/ipsdienol and verbenone (Bakke 1981, Schlyter et al. 1987a) inhibit beetles from attacking too close to others, but these compounds may be produced too late in the attack sequence (Birgersson et al. 1984) to be of much use in spacing and avoiding competition. Stridulation by beetles has been suggested to play a role in spacing of attacks usually by the induction of pheromone inhibitor release (Rudinski and Michael 1973, Rudinsky et al. 1976, Hedden and Gara 1976). *I. typographus* is supposedly able to stridulate (Rudinsky 1979), but stridulatory organs typical of other *Ips* (Barr 1969) are not apparent nor can stridulatory sounds by the beetle be heard (while male *D. brevicomis* and *T. piniperda* and female *I. paraconfusus* are easily heard). Other possible mechanisms are avoidance of frass piles of beetles by olfaction or simply by visual inspection. Finally, it may be that beetles prefer to attack bark surface structures that are uniformly distributed, as suggested by Shepard (1965) for *D. ponderosae* on lodgepole pine.

Safranyik and Vithayasai (1971) concluded that the regular attack pattern of *D. ponderosae* in nature is due to the regular pattern of bark niches. They drilled holes in a 2.5-cm hexagonal pattern in logs and found that beetles only chose the holes to initiate galleries and that the proximity of previously established attacks did not affect the choice of a hole. However, unoccupied drilled holes are not normally encountered by beetles in nature and once entered may arrest the beetle and short-cut the natural behavioral sequence (Borden 1974). Thus, any behavioral spacing mechanisms for boring holes that is dependent on the presence of other beetles might have been obviated under these conditions. Furthermore, in most cases bark niches seem much more dense than the attacks of beetles. Obviously, much further work is needed to narrow the range of possibilities.

Gallery construction and re-emergence to avoid competition

Assuming a beetle has tried to locate areas of lower attack density during its flight, then has avoided attacking near sites of others, but still finds crowded conditions under the bark, it has a few options left. For instance, the galleries of various bark beetle species are commonly observed to circumscribe other galleries of their own or other species (Schmitz and Rudinsky 1968, Wagner et al. 1981). For example, of 27 *I. typographus* male attacks that I inspected on Norway spruce trees in Denmark (two examples shown in Fig. 6), six female galleries "bent away from" (>30°) another conspecific gallery when about 3 mm distant, while eight turned similarly before reaching nuptial chambers of *P. chalcographus*, and the remaining 48, which did not encounter other galleries, were not so bent (P < 0.01, χ^2-test). The distribution of female galleries of 1, 2, 3, or 4 per male was 3, 14, 9, and 1, respectively. It seems that chemicals in the oxidative discoloration zone surrounding larval and adult galleries and nuptial chambers, as well as saprophytic fungi, may be responsible for the avoidance of tunneling adults. It seems quite possible that larvae use a similar mechanism to avoid other larval mines (which also appear to avoid each other). The mechanism could be either gustatory or olfactory or both, but next to nothing is known about the specifics. Schmitz and Rudinsky (1968) and DeJong and Saarenmaa (1985) also suggest that larvae, and perhaps adults, may avoid each other under the bark by means of vibrations (sounds) from the movement and feeding of adjacent larvae (and adults), although no acoustical and behavioral evidence has been found to date. Wagner et al. (1981) concluded that since the slope of the decay curve of gallery length with increasing female *D. frontalis* density was more gradual than the egg/density curve, this indicated females avoided other galleries as they proceeded in order to lay eggs. However, these mathematical functions do not provide direct evidence that females can disperse their galleries evenly to reduce competition.

Bark beetles will re-emerge earlier at high attack densities than at lower densities (McMullen and Atkins 1961, Ogibin 1973, Coulson et al. 1978, Anderbrant et al. 1985). Perhaps the adult beetle decides to re-emerge after repeatedly tunneling into areas unsuitable
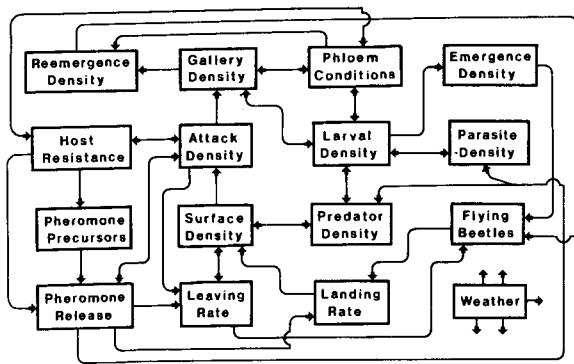
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Fig. 7. Schematic presentation of theoretical interactions between ecological components which may influence the intra- and interspecific competition of bark beetles in host trees. Weather affects all components to some extent.

for larval development (due to ageing, fermentation, and drying of host tissue as well as deterioration from feeding/defecation). Wagner et al. (1982) provide evidence that later attacking *D. frontalis* pairs were likely to stay for shorter periods and lay fewer eggs in small bark slabs than initially attacking pairs. The effect of host age and density could not be separated, however, and pair site positioning was not randomized so that the last pairs always had the log-end areas.

Kirkendall (1983) formulated three reasons why bark beetles may re-emerge: (1) *the bankruptcy hypothesis,* beetles can not lay more eggs unless they pause to restore energy reserves by feeding as they re-emerge; (2) *the greener pastures hypothesis,* after laying a minimal brood it is better to spread the risks by establishing a second brood in another distant area; and (3) *the overcrowding hypothesis,* beetles keep laying eggs unless the habitat becomes crowded such that new progeny would be adversely affected. Hypothesis (1) does not seem to explain re-emergence since adults could restore reserves without re-emerging, although it appears they could replenish energy supplies by feeding during re-emergence. Hypotheses (2) and (3) are probably both operating and of different relative importance based on the environmental conditions. The decision to re-emerge, according to theory, must balance the risks of the increasingly unfavourable conditions under the bark with the risks of a second host-seeking flight and brood establishment. The "decision threshold" is probably genetically variable and averaged through time by natural selection during periods of epidemic and endemic population levels.

Interacting components regulating competition

Competition in bark beetles is affected by several ecological factors as shown in Fig. 7. Initially, host tree properties such as monoterpene quality and quantity affect the pheromone precursor availability and the physiological processes within the beetle such as phero-

mone biosynthesis and general toxicity. These influence the release of attractive and inhibitory pheromones that affect leaving and landing rates of the beetle, in order to avoid competition, as well as attraction of predators and parasites. The density of bark beetles on the tree is affected by the flying population of beetles (and leaving and landing rates) as well as predator populations. The attack density, which is dependent on the surface density of beetles, host resistance, and pheromone release, affects gallery density which in turn can affect re-emergence, phloem conditions, and larval density. Larval density and emergence density, the reproductive outcome, are primarily affected by gallery density, phloem conditions, and predators and parasites. An understanding of these interactions, and the mechanisms affected, will help focus our questions of how beetles avoid competition.

Practical or applied considerations

While the foregoing interactions among beetles and host will provide interesting hypotheses and background for future basic research, are there any prospects for applying this knowledge to protect trees? The intraspecific attractive pheromones have been used to trap-out large numbers of *D. brevicomis* and *I. typographus* in attempts to reduce tree mortality (Wood et al. 1985, Lie and Bakke 1981). McLean and Borden (1979) used pheromone baits to catch an estimated 65.1% of the total population of *Gnathotricus sulcatus,* an ambrosia beetle, in a suppression program at a sawmill. Other programs have used attractive baits to keep emerging brood adults within an active infestation which otherwise would have mass attacked trees in nearby areas (*D. pseudotsugae* – Pitman 1973, *D. frontalis* – Richerson et al. 1980). Intraspecific inhibitory pheromones (for reducing competition) have been used to protect trees so that beetles apparently perceive them as already colonized or decadent and thus do not respond or are repelled. MCH (3-methyl-2-cyclohexene-1-one) has been used in this way to protect Douglas-fir trees from attack by *D. pseudotsugae* (Furniss et al. 1974, St. Clair et al. 1977, Furniss et al. 1977, Hedden and Pitman 1978) and Sitka spruce from *D. rufipennis* (Rudinsky et al. 1974). Larger test plots of windthrown Douglas-fir were treated with granular controlled-release formulations of MCH which significantly reduced *D. pseudotsugae* infestation of windthrown trees and adjacent stands compared with nearby check areas (McGregor et al. 1985, Furniss et al. 1982). They found that beetle populations were reduced by up to 96.4% and protection of trees was indicated for up to two years following the MCH treatment. *Endo-* and *exo-*brevicomin have significantly reduced landing of southern pine beetle on host pines (Payne et al. 1977). Possibly one could combine repulsion from host trees by inhibitory pheromones or allomones with attraction to traps by pheromones in a very effective control system.

Another way may be to attract beetles to a tree with pheromones and then confuse or disrupt the attack spacing mechanism to create a perpetual attack in which overcolonization destroys the adults and brood (a super trap-tree). Since we understand little about attack-spacing mechanisms, one can not be more specific about the methods. Furthermore, we need to determine the mechanisms by which aggregation is terminated (Byers et al. 1984) or whether "old" trees are perceived as unsuitable. A better understanding of the attractant and inhibitory properties of pheromone blends will also help in the design of monitoring and population-reducing traps. For example, the synthetic pheromone bait used to reduce populations of *I. typographus* in Europe consists of a three-component blend, *cis*-verbenol, methylbutenol, and ipsdienol (Bakke et al. 1983). However, ipsdienol is not produced in the male during colonization except after females have joined them, and then only in trace nanogram quantities (Bakke 1976, Birgersson et al. 1984). Ipsdienol has probably no observable behavioral effect on flying beetles at this level, and at commercial bait levels may reduce response (Schlyter et al. 1987a). This could be because *I. duplicatus* produces large amounts of ipsdienol (Bakke 1975, G. Birgerson unpubl.) which may act interspecifically to inhibit *I. typographus*. Aside from the extra cost of including ipsdienol, it also attracts the bark beetle predator *Thanasimus formicarius* to traps. Thus, a binary blend (without ipsdienol) for *I. typographus* may be more attractive, economical, and biologically advantageous.

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