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Summary

Bark beetles with the capacity to kill and colonize living trees are main pests of coniferous forests around the world. The European spruce bark beetle, *Ips typographus,* belongs to a group of bark beetles possessing facultative attack patterns. For long periods *I. typographus* is living in low populations only on seriously weakened hosts. However, following disturbances like storms or drought periods, the amount of suitable breading material increases dramatically and the population size of beetles may rise within a short time to epidemic levels. In the epidemic phase *I. typographus* behaves aggressively, attacking healthy trees and destroying large areas of Norway spruce forest. Bark beetles with this pattern of behaviour are exploiting a different ecological niche than during the endemic, low population phase: in broken or seriously weakened hosts they exploit a relatively poor source of nutrients without dealing with host defences. Instead they have to deal with a higher degree of interspecific competition. On the other hand, a living host provides breeding material, which is rich in nutrients and relatively free from interspecific competition, but there beetles have to fight the defence responses of the host tree. Host defences can be overcome by mass attack of thousands of beetles on the same tree, which is coordinated by aggregation pheromones. The trade-off between evaluating host quality and risk rating host defences is a great challenge for the pioneering beetles, that initiate an attack before any pheromone plumes exist. The host choice mechanism can be divided in several distinct steps:

1. habitat location during flight
2. host location during flight
3. host evaluation after landing, involving detection of host suitability and spacing between species and individuals to avoid inter- or intraspecific competition.
4. risk rating host defences after entrance into host phloem.

The question whether the beetles' attack behaviour is ruled by pheromone attraction alone or is guided by markers for host suitability has been an issue of debate for decades.

The peripheral nervous system of bark beetles possesses olfactory receptor neurons for both pheromones, host volatiles and non-host volatiles. Several studies support the theory that non-host volatiles cues play an important role in habitat location, while host volatiles are involved in host finding and host acceptance, either alone or through modulating pheromone attraction. Host defence responses consist of physical barriers and chemical compounds that may be detrimental to invaders. Conifers maintain a certain level of preformed (constitutive)

defence that can be enhanced during and after the attacks, e.g. by the increased production of defensive metabolites and development of defensive structures. The different metabolites involved in a trees defence responses may be important markers for beetles to evaluate the trees' defensive ability, and guide them in their decision to enter a host.

Because the population density is an important factor influencing the beetles' success in overwhelming a trees defence, it has been hypothesized that it also will modulate beetles behaviour, either directly or through its influence on the beetles' quality.

This introductory paper is written to obtain an overview over the literature dealing with different aspects of host choice in bark beetle species exhibiting so called aggressive host colonisation behaviour. Different hypotheses and aspects of importance for the host choice behaviour are discussed. Finally, I propose a host choice model for the European spruce bark beetle *Ips typographus.*

List of content

Terminology used in this essay

Alleles: variant forms of a gene resulting in different phenotypes.

Allomone: a semiochemical produced and released by an individual of one species that affects the behaviour of an individual of a different species to the benefit of the releaser.

Commensal: a symbiotic relationship between different species favouring one part and leaving the other unaffected.

Constitutive defence: preformed defences involving physical barriers formed by cell structures and availability of for intruders toxic and/or inhibiting chemicals.

Endemic population: local population with low size unable to attack on landscape or regional scale.

Epidemic population: population with exponential growth dispersing on a landscape scale.

Facultative: having the capacity to live under different conditions or to adopt a different mode of life.

Hypersensitive response: mechanism in plants involving rapid cell death and induction of chemical defence pathways in the local region surrounding an infection.

Induced defence: onset of increased defences after infection involving induction of defensive metabolite production and mobilisation of growth of defensive structures.

Kairomone: semiochemical released by a species different from the perceiving species; may be attractive or repellent.

Meristematic: term used for tissues that can divide; growth tissue, either apically (at the top leader or sprouts) or secondary (thickness increase).

Mycangia: structures on the body of an insect adapted to transport fungal spores.

Obligate: limited in a ecological function of a interspecific relationship, e.g. fungi that can not survive without being spread by a bark beetle.

Pheromone: semiochemical used within a species; may be attractive or repellent**.**

Phloemophagous: living on phloem (living inner bark).

Saprophytic: living from dead or decaying organic matter.

Semiochemical: chemical signal; chemical compounds or mixtures carrying a message perceived and recognized by an organism.

Suberized: supplied with suberin, a highly hydrophobic, waxy biopolymer found in cork cells and in endodermal cells in roots.

Xylophagous: living on wood.

1. What are “ aggressive bark beetles”? The ecology of a guild of phloemophagous herbivores.

Bark beetles are beetles (Coleoptera) from the superfamily Curculionoidea that are main decomposers of dead wood. Some species, also called Ambrosia beetles, from the subfamilies Platypodinae and Scolytinae live in symbiosis with different fungi that enable them to break down wooden materials. In the Scolytinae, several species in the genera *Dendroctonus, Ips, Scolytus, Pseudohylesinus* and *Pityogenes* are often termed to be “aggressive” by their capacity to kill and colonize living trees (Wood 1982a and references therein). The use of the term “aggressive” for these genera can be questioned, because of the emotional value imposed on this word. In this literature review, the term “aggressive” will be used for pragmatic reasons to distinguish these genera from bark beetle genera unable to colonize and kill living hosts and to accede to common use in specialist literature. Mass attacks causing the death of living trees within weeks are known only in coniferous forests, mainly belonging to the family Pinaceae (Franceschi et al. 2005). The largest bark beetle outbreak ever recorded (Raffa et al. 2008) is ongoing in British Columbia in western Canada since the late 1990s: *Dendroctonus ponderosa* has caused the death of an estimated 500 million m^2 of lodgepole pine (*Pinus contorta*) (Kärvemo and Schroeder 2010 and references therein). Except for the elm bark beetles *Scolytus multistriatus* and *Scolytus scolytus*, transmitting the vascular wilt *Ophiostoma novo-ulmi* as a vector and devastating European and North American elms, Scolytids are not associated with great economic or ecological impact on angiosperm forests (Ohmart 1989; Wood 1982a).

Hypotheses about the evolution of aggressiveness are difficult to test and remain speculative. Ohmart (1989) propose two possible explanations for the non-aggressiveness of species attacking hardwood: “1) The hypersensitive (induced) response of hardwood phloem to the invasion of fungi introduced by attacking bark beetles has always been too complex and effective for the evolution of beetles which could successfully colonize this phloem; 2) the physiological costs incurred by bark beetles attacking angiosperm phloem are greater than the nutritive benefit gained by the beetles and therefore evolution of successful colonizers of hardwood phloem could not occur.” In spite of the speculative character of these explanations remains the fact, that species exploiting dead or strongly weakened host, like most ambrosia beetles in hardwood, escape the defence system of living trees, while some Scolytids have evolved to combat the strong defence of their conifer hosts. The death of the host is a requirement for a successful beetle establishment and reproduction in a healthy conifer tree, unless the trees' different defence responses will repel either adult beetles or be detrimental for their brood (Raffa and Berryman 1987and references therein).

Aggressive bark beetles possess two mechanisms to overwhelm the defences of a conifer: 1) an efficient pheromone system that allows coordinated mass attacks of thousands of beetles within short time (Berryman et al. 1985), 2) the association with fungi, disseminated during the attack in the wood of the host, and often leading to blockage of the water transport system and finally causing a rapid death of the tree. While the dependence of xylophagous Ambrosia beetles on associated fungi in order to break down cellulose is obligate, the benefit of fungal associates for the tree killing beetles that feed on the living, nutritious inner bark of trees, is much more unclear (Klepzig and Six 2004).

Aggressiveness can be regarded as a gradation continuum among different bark beetle species: the most 'aggressive' species are able to attack healthy trees whereas less aggressive species only overcome weakened or completely nonvigorous host trees (Wood 1982a). Weakened hosts may be spatially and temporally rare and migratory losses during dispersal to suitable hosts can be high. Moreover, while the weakened breeding material is easy to invade, it may also be nutritionally less valuable and in some cases also attractive to interspecific saprophytic competitors (Raffa 2001). Raffa (1987) examined two different 'aggressive' scolytid beetles and their hosts: the fir engraver (*Scolytus ventralis*) infesting grand fir (*Abies grandis*) and the mountain pine beetle (*Dentroctonus ponderosae*) infesting lodgepole pine (*Pinus contorta* var. *latifolia*). The fir engraver is attacking only trees that are severely weakened, while the mountain pine beetle usually attacks healthy lodgepole pines and to some extent also other pine species. Raffa (1987) concluded that evolution may have favoured the development of aggressiveness and a high tolerance against monoterpenes in the mountain pine beetle due to a generally high level of preformed (constitutive) defence (resin and monoterpene content) in pine bark and sapwood and relatively low induced defence reactions after attack. In contrast, grand fir maintains a lower level of preformed defences, but is capable to raise highly variable and strong induced responses after attack; inoculation of the beetles symbiotic fungus induced a multiple increase in resin production and a dramatic change in monoterpene composition with big differences between single trees. Thus, fir engravers encounter an unpredictable, diverse environment upon host choice, making a cooperative, aggressive behaviour less adaptive.

The European spruce bark beetle *Ips typographus* (L.) belongs to a group of bark beetles possessing facultative attack patterns. For long periods *I. typographus* is living in small populations on sporadically occurring weakened hosts. However, following windstorms, drought periods or other environmental disturbances the availability of suitable breeding material may increase abruptly and the population size can rise to epidemic levels. In the epidemic phase *I. typographus* behaves aggressively, attacking healthy trees and destroying large areas of Norway spruce forest . Bark beetles with this pattern of behaviour are exploiting two different ecological niches: the sudden increase of population size opens up a new ecological niche, rich in nutrients and relatively free from interspecific competition, that can be exploited allthough there are no more trees with poor defences (Berryman et al. 1989; Raffa et al. 2005; Wallin and Raffa 2004). If the epidemic population would have been reduced to only exploit weakened hosts, these would have been quickly exhausted resulting in equally sudden crashes of the population. Healthy trees seem to be preferred during an epidemic phase as newly wind thrown trees can be seen unattacked while groups of standing trees are been attacked (personal observations). Boone et al. (2011) measured the constitutive resin flow of lodgepole pine and found that eruptive populations of *D. ponderosae* preferred trees with higher resin flow rate than beetles from endemic densities. The ability to modify host preferences according to group size is similar to the behaviour of packhunting predators. It requires some degree of pre-adapted communal behaviour and that the benefits of a group attack exceeds the costs of sharing the host for an individual bark beetle (Berryman et al. 1985; Schlyter and Birgersson 1999; Wertheim et al. 2005).

Epidemics can suddenly collapse when different factors individually or in synergy depress the epidemic population under the critical level that allows beetles to overwhelm the defence of available trees. There are several major factors affecting the development of an ongoing epidemic: temperature during summer and autumn, precipitation (affecting both host tree condition and dispersal possibilities), the phase of the ongoing epidemic and the build-up of predator population size, intraspecific competition (affecting size, number and health of offspring) and finally the availability of suitable host trees (trees with a relative defence ability being below the attacking power of the beetle population) on a landscape level. The different factors are involved in feedback processes that may amplify themselves and increase or decrease the threshold for an epidemic to arise or collapse (Hedgren and Schroeder 2004; Långström et al. 2009; Raffa et al. 2008; Wermelinger 2004).

2. What is a suitable victim for an ‘aggressive’ herbivore?

At times of low population size, also ‘aggressive’ bark beetle species are entirely dependent of finding rare, severely weakened hosts. The bark of wind broken trees will dry out during one summer, but can still offer a good food resource for the reproduction of one beetle generation depending on bark thickness, temperatures and precipitation. Wind fallen trees with some root contact left will last for a longer time, but are severely stressed and will not be able to mobilize strong defence reactions. A common attack pattern observed in an incipient outbreak is, that new attack spots on standing trees are concentrated to places affected by stress, like e.g. drought, increased sun exposure on new forest borders or tree decline (Moeck et al. 1981 and references therein; Wermelinger 2004). At very high population levels even apparently healthy trees are going to be attacked. In attacked areas, where almost all trees have been killed, single unattacked trees can be found, either with unsuccessful attacks or without any visible signs of attack. Successful tree defence often results in copious resin flow flooding out beetles from their entrance holes, but even dry entrance holes without beetles have been observed (personal observations). Thus, the suitability does not seem to be an immutable property of a tree, but depends on an intricate balance between the physiological state of trees, population dynamics of the beetles and environmental factors, such as weather (Raffa et al. 2005).

3. About Conifer defence.

The lifetime of a conifer tree spans over many decades, during which it encounters various stresses: abiotic like drought, storms, high levels of ground water, different nutrient shortages or biotic like root pathogens, fungi and herbivores affecting cones and needles, unsuccessful bark beetle attacks or mechanic injury caused by mammals or accidentally by forest management. Conifers have evolved effective defence strategies that made them to successful colonizers of a wide range of different climatic zones in more than 100 million years (Franceschi et al. 2005; Prager et al. 1976). Preformed defence systems are referred to as ‘constitutive’ while reactive defence upon a challenge is referred to as ‘induced defence’ mechanisms. Various induction events due to stress during the long lifespan of a tree, however, may alter the status quo of the constitutive defence systems (Christiansen et al. 1999). There is usually marked phenotypic plasticity in conifer defences and it is generally difficult to discern it from the genotypic variation (Huber et al. 2004).

Constitutive defence of conifers

The different conifer families and genera have evolved a great diversity of structures within the non functional part of the phloem (without intact sieve tubes) that work as physical and chemical barriers to intruders. The outer bark (periderm) provides a physical barrier, that protects the vital assimilate transport within the nutrient and energy rich phloem, and the thin and weak meristematic cambium layer (Fig 1.). The periderm consists of several tight layers of mostly dead cork cells with lignified and suberized walls (Fig. 2). Calcium oxalate crystals, that can be found as intracellular deposits in the phloem and as extracellular layers in the periderm may function as sharp hinders against boring and chewing (Hudgins et al. 2003). Lignified stone cells (sclereids) can build up clusters containing mostly lignin, but even soluble phenolics (Franceschi et al. 2005; Li et al. 2007). They have been shown to affect the reproduction of *Dendroctonus micans* in *P. abies* (Wainhouse et al. 1990). Different phenolic compounds in the bark can have antifungal and antifeedant properties (Brignolas et al. 1998; Evensen et al. 2000; Faccoli and Schlyter 2007). The periderm can contain large amounts of solid phenolic material and the secondary phloem phenolics are deposited in the vacuoles of so called polyphenolic parenchyma cells (PP-cells). The PP-cells can form annual tangential rings separated by sieve cell layers outward from the cambial zone into the secondary phloem. They can be discerned like the annual rings in the xylem for decades (Franceschi et al. 2005; Krekling et al. 2000) (Fig. 4). The large amount of phenolic compounds in the bark and the continuous production of PP-cells underpins the importance of these compounds and structures in the constitutive defence system of conifers. Nevertheless their functions and effects in the defence of conifers against bark beetles are up to now poorly understood.

Upon wounding, trees exude resin, which is the most obvious defence in the Pinaceae. Intensive research efforts have been made to characterize the resin producing and storing structures, the chemical composition and effect of resin, and the biosynthetic pathways of resinosis (Borg Karlson et al. 1993; Cox et al. 2007; Huber et al. 2004; Keeling and Bohlmann 2006a; Keeling and Bohlmann 2006b; Lewinsohn et al. 1993; Lombardero et al. 2000; Persson et al. 1993; Rosner and Hannrup 2004; Wainhouse et al. 1997) and others. While the resin producing cells form sac-like structures, called blisters in the genera *Abies*, *Cedrus*, *Tsuga*, *Pseudolarix*, they form tube-like ducts in both xylem and phloem in *Picea*, *Pinus*, *Larix*, and *Pseudotsuga* (Fig. 3). The resin is synthesized in the epithelial cells lining the cavities within these structures and extruded and stored there under pressure (Nagy et al. 2000). The resin is formed by volatile monoterpenes (10 carbon), semi-volatile sesquiterpenes

(15 carbon) and the 20 carbon diterpenoid compounds. After volatilization of the mono- and sesquiterpenes the crystallized diterpenes build up a mechanical barrier against antagonists. The constitutive defense ability is thus dependent on the amount of stored oleoresin, but also on it's chemical composition and on the effect to any antagonist (Huber et al. 2004). Both ray cells and resin ducts are involved in the translocation of resources between phloem, sapwood and heartwood (Berryman 1972), and therefore the resin produced in the xylem is able to extrude into the phloem. Ray cells have been speculated to be involved also in the production of soluble phenolics and they may provide a way for signal sensing and spreading in the systemic induction of defense reactions (Franceschi et al. 1998; Franceschi et al. 2000; Hudgins et al. 2004; Hudgins and Franceschi 2004).

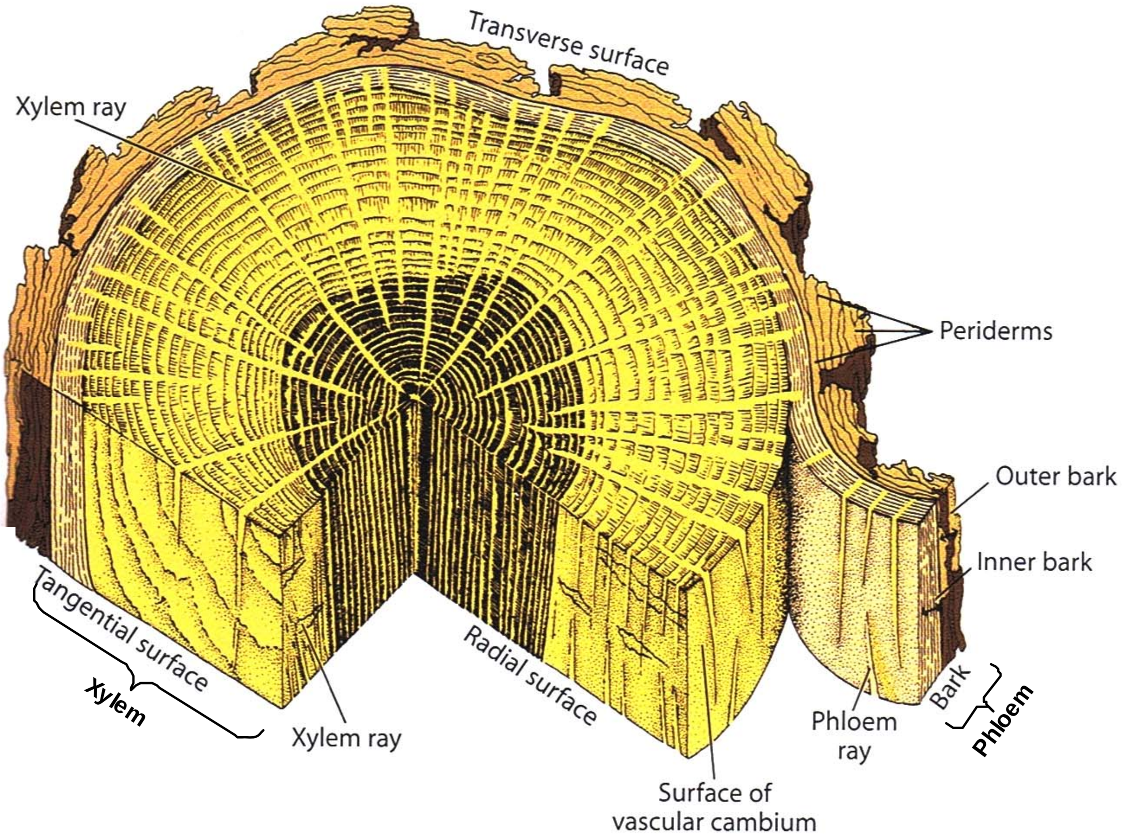

Figure 1:

Block diagram of red oak (*Quercus robur*) stem, showing the transverse, tangential, and radial surfaces. In between the inner bark (phloem) and the outer bark (periderm) a meristematic cell layer (cork cambium) produces protective tissue (cork) to the outside and living parenchyma tissue (phelloderm) to the inside. The phloem consists of the functional phloem with sieve tubes surrounded by various forms of parenchymatous tissues and old non-functional phloem with collapsed sieve tube elements. The arrangement of the functional elements in the bark does not differ essentially between angio- and gymnosperms, while the wood of conifers is distinguished from that of angiosperms by lacking vessels. Instead, long tapering tracheids constitute the dominant cell type in the wood. In *Picea*, *Pinus*, *Larix*, and *Pseudotsuga* rays often contain large intercellular lumens, so called resin ducts (see Fig. 3).

From Raven, Evert and Eichhorn, *Biology of plants,* 5th edition, Worth Publishers, 1992, New York

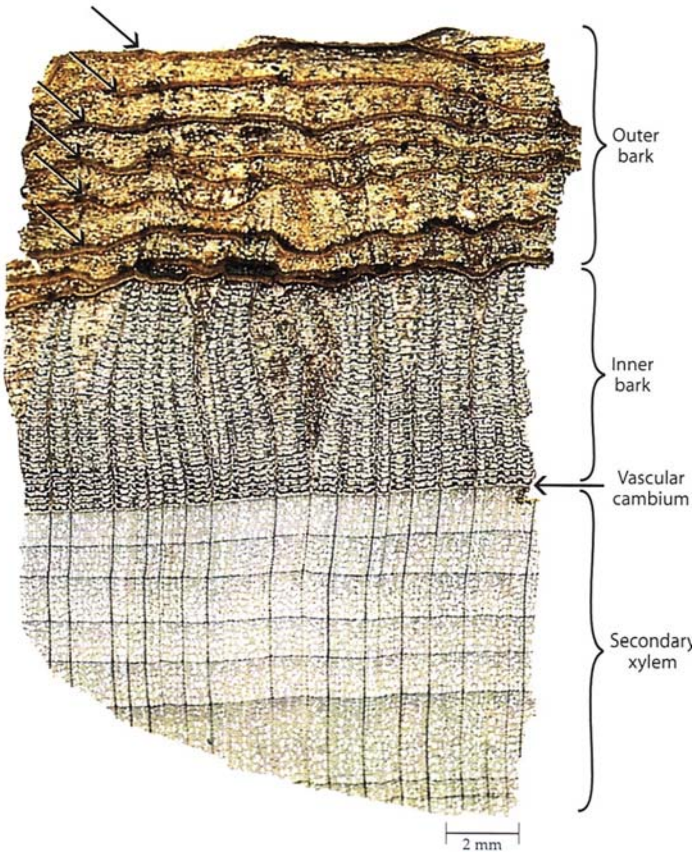

Figure 2: Transverse section of the bark and some secondary xylem from the old stem of basswood (*Tilia americana*). Several layers of periderm (arrows) can be seen in the outer bark. From Raven, Evert and Eichhorn, *Biology of plants,* 5th edition, Worth Publishers, 1992, New York

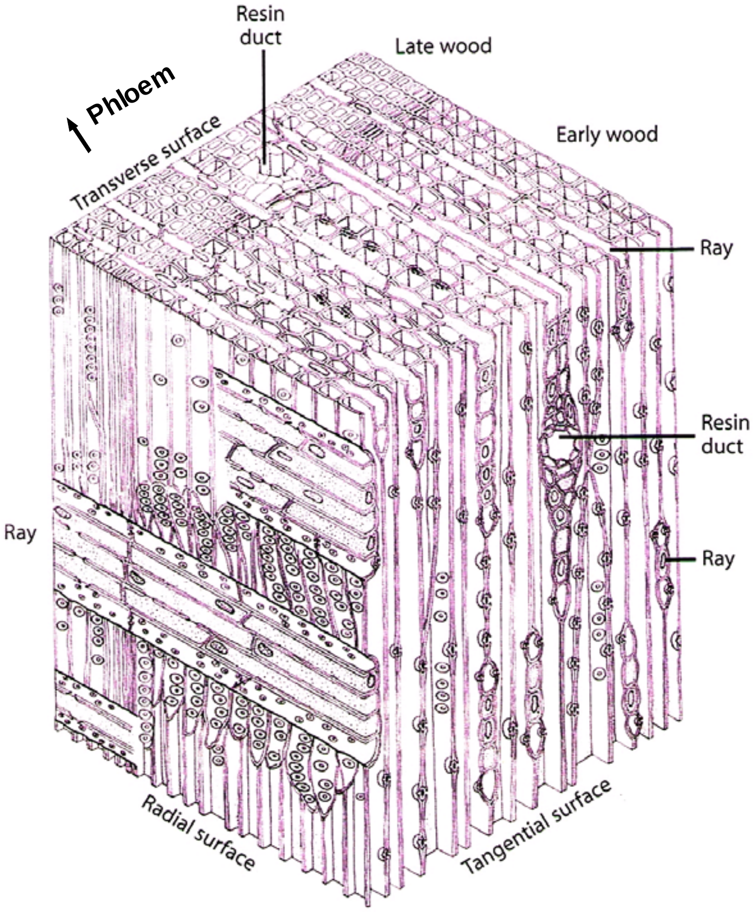

Figure 3: Block diagram of secondary xylem of white pine (*Pinus strobus*), showing the transverse, tangential, and radial surfaces. Rays consist of ray tracheids and ray parenchyma cells. Those containing resin ducts are lined with epithelial cells to the inner lumen.
From Raven, Evert and Eichhorn, *Biology of plants,* 5th edition, Worth Publishers, 1992, New York

Induced defence

Most trees in a sufficiently good physiological condition are able to enhance the preformed defence mechanisms. This can involve activation of already existing pathways to increase and modulate the production of defensive metabolites, e.g. resin production and the production of phenolic compounds. In addition, the production of pathogenesis-related proteins, like lytic enzymes and chitanases, affecting and degrading fungal cell walls has been reported during induction (Bonello et al. 2006). The induction of these defences may be rapid and specific and elicited by the antagonist organisms themselves. The activation of protein-based defences may also result in the formation of new structures that increase the production of defence compounds in a long term, and also may result in new physical barriers. If the tree defences are activated to a higher level as a consequence of a challenge or weak attack, the responses provide the tree with an increased defence for future challenges, a process often referred to as acquired resistance or priming (Bonello et al. 2006; Franceschi et al. 2005).

The most explicit defence reaction resulting in both structural and chemical changes is the hypersensitive response. It implies the rapid death of individual cells occurring locally at the site of attack or infection and results in lesions of dead tissue that encapsulates pathogens and in the release of defensive metabolites in the surrounding tissues (Nagy et al. 2000). Lesions are cut off from the intact parts of living tissue by callus formation, subsequently lignified, suberized, impregnated by phenolics and finally forming wound periderms and replacing damaged structures (Franceschi et al. 2005).

After one to three weeks following wounding or infection, changes in the cambium near the site of challenge leads to the formation of traumatic resin ducts (TD) (fig. 3 B,D). They differentiate axially imbedded in the new xylem and are interconnected with the radial resin ducts to the phloem. TD increase the area of resin producing epithelial cells; the resin produced in the new structures can be different from the composition of constitutive resin and may be more toxic to invaders (Martin et al. 2002). The proliferation and swelling of polyphenolic parenchyma cells (PP-cells) (fig. 3A-D) is an other visible sign for an induced defence reaction. Together with the formation of TD, the PP-cells have been shown to be associated with increased resistance to pathogenic fungi (Krokene et al. 2003).

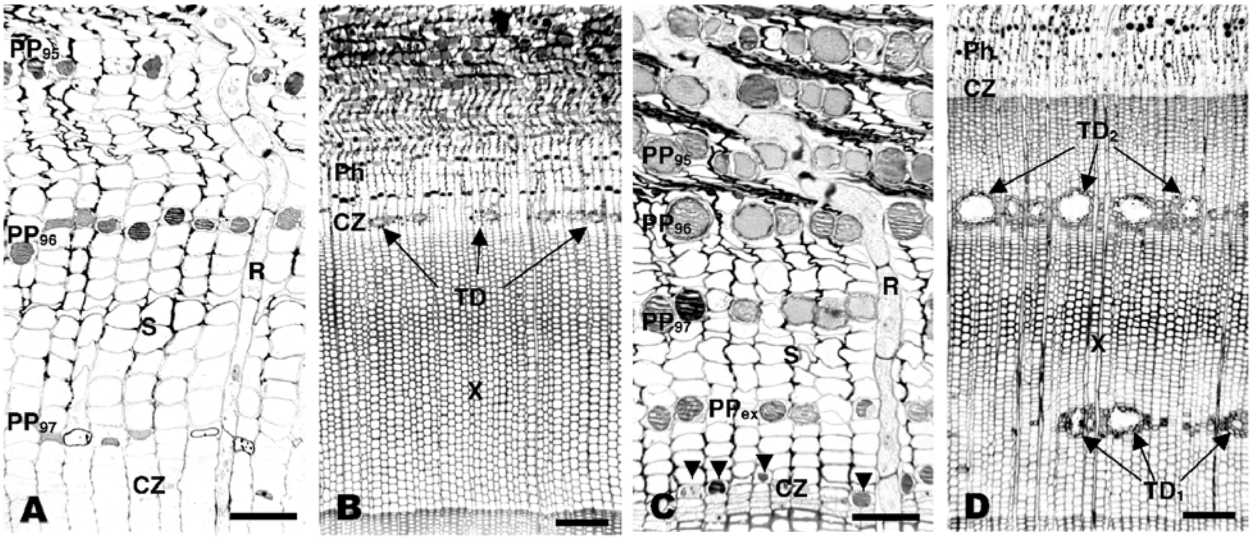

Figure 3

Induced anatomical responses in sapwood and phloem of Norway spruce after pretreatment inoculation and mass inoculation with the "blue-stain fungi" *Ceratocystis polonica*. All figures are cross sections.

(A) Fresh bark at the time of pretreatment (June 24) showing anatomy typical of untreated samples. Sieve cells (S) and the three most current annual layers of PP cells (PP97-95) can be seen above the cambial zone (CZ). R = radial ray.

(B) Sample taken 3 weeks after pretreatment inoculation, with a layer of large traumatic resin ducts (TD) at the interface of the xylem (X) and cambial zone.

(C) Bark sample taken above the mass inoculated section 15 weeks after mass inoculation, showing swelling of PP cells, crushing of the older sieve cell layers, and abundant extra PP cells between the cambial zone and PP97 (PPex) and adjacent to the cambium (arrowheads).

(D) Sample taken 15 weeks after mass inoculation from a tree that was pretreated 24 weeks earlier. Two distinct layers of large TDs can be seen; the layer close to the cambium (TD2) was probably induced by the mass inoculation, whereas the layer deeper within the xylem (TD1) was probably induced by the pretreatment 9 weeks earlier.

Bars = 50 µm (A and C) and 200 µm (B and D).

from (Krokene et al. 2003)

3. The adaption of bark beetles to their host

The ‘aggressive’ behaviour of bark beetles in conifers is tightly interconnected with the defensive capacity of their host trees. The aggregating behaviour, however, is a multifaceted phenomenon for these beetles. Under endemic conditions and when suitable breeding material with low defensive capacity is scarce, a single individual will hardly benefit from sharing a limited resource. Males that only respond to pheromones released during an ongoing attack and not to kairomones evaluating host quality, may find a limited resource exhausted by the time they arrive. However, during the epidemic phase the aggregation is necessary for the survival of the pioneers. When sharing an attack on vigorous trees during epidemics, those beetles responding to pheromone signals will cheat from the risks of a primary attack and shorten dispersal time. Thus, the question is: what then, are the driving forces in the evolution of an aggregating behaviour? There seem to be as many drawbacks as advantages associated with aggregation: costs for the emitters of aggregating signals (producing pheromone and experience competition); costs for the responders (competition and exhausted breeding material); benefits for the emitters (avoiding to fight alone against the defence system of the host); benefits for the responders (to avoid the risks being pioneers, shorter dispersal before host finding, avoid costs to detoxify poisonous host compounds and produce pheromones) (Raffa and Berryman 1987). The advantages have to outweigh the costs for the trait to become adaptive and to evolve; both emitters and responders have to benefit, otherwise the system would have been lost during evolution by natural selection. The origin of the aggregation behaviour in an ancestral non-killing bark beetle species may simply have been a sex-pheromone, exploited by other males to increase the change of finding mates. The behaviour of tree killing by a mass attack cannot have been the driving force for the original evolution of aggregation pheromones, because they are the prerequisite for this behaviour (Schlyter and Birgersson 1989; Wertheim et al. 2005). The successful detoxification of toxic levels of host compounds in weakened, but still fresh, living bark may stepwise have adapted bark beetles to a new, more valuable resource, making the outcome of this process (oxygenated derivates of host compounds) to a part in the aggregation pheromones (Alcock 1982; Birgersson and Bergström 1989; Vanderwel 1994). Thus, the trees defence has been turned into a weakness by it’s assassinator. However, during an endemic phase the few beetles present will not be able to defeat a healthy trees defence. Only a few species belonging to the genus *Dendroctonus,* such as the European *D. micans,* possess the ability to survive in phloem of a living tree without killing them, literally swimming in the resin flow of defending hosts (Storer and Speight 1996).

An increasing body of research is revealing the genetic background for conifers constitutive and induced defences. The terpene products are synthesized by terpene synthases (TPSs) with high functional plasticity, most of them forming multiple products (Keeling et al. 2008; Phillips and Croteau 1999). The high number of genes coding for TPSs are believed to be the result of multiple gene duplications. It has been shown, that only a few mutations have to occur to completely change the products derived by two di-TPSs (Keeling et al. 2008). In the arms race to defend and overcome defence, the high plasticity may be important for conifer trees, to cope with the bark beetles, which comprise hundreds of generations during the life time of one tree.

The evolution of the bark beetles' pheromone production by making use of and detoxifying defence compounds could be counteracted by the trees in a reduced production of monoterpenes that are precursors of the pheromones. Trees with this trait could be resistant by the inability of attacking beetles to call for conspecifics to join the attack. In the case of *Ips typographus* one component of the aggregation pheromone (2-methyl-3-buten-2-ol) (Fig. 4) is produced *de novo* (Lanne et al. 1989), while the other component 4S-(–)-*cis*-verbenol (Fig. 4) (Bakke et al. 1977) is derived by oxygenation of the host monoterpene (–)-α-pinene (Fig. 4). Beetles attacking trees that produce more of the (+)- enantiomer produced the *trans*-verbenol (Fig. 4), which is not functional as pheromone, in a corresponding proportion (Lindström et al. 1989). The proportion of the (–)-enantiomer of α-pinene varied between 28% to 78% (C. Schiebe, unpublished results), corresponding with 32% to 98% found by Lindström et al (1989). The production of *cis*-verbenol in male *I. typographus* correlate to a high extent with the amount of (–)-α-pinene in individual trees (Birgersson 1989). The other pheromone component methyl butenol, which is produced *de novo* by males did not correlate with any specific monoterpene hydrocarbon, but was inversely related to a trees defence reaction and the total monoterpene content (Birgersson and Leufven 1988; Zhao et al. 2011). It can be hypothesized, that the pheromone production may be reduced, when beetles allocate resources to detoxify detrimental levels of defensive compounds.

The large individual variation in the enantiomeric proportion of α-pinene is commonly found in all terpenes in the oleoresin (Persson et al. 1993; Persson et al. 1996) and also for phenolics produced in Norway spruce bark (Lieutier et al., 2003 , C. Schiebe, unpublished results). It seems unlikely that an adaptation by bark beetles to use highly variable host compounds as kairomones would occur; only individual compounds that are specifically up-or downregulated during stress responses could be thought of becoming kairomones signalling either suitable (weakened) or resistant hosts.

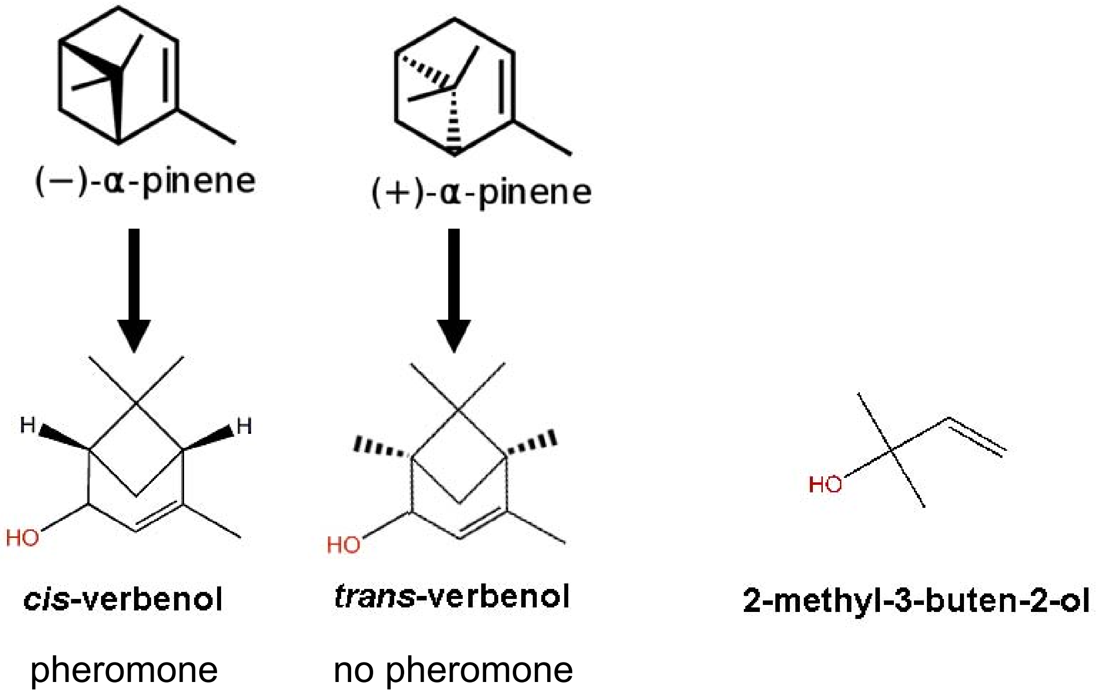

Figure 4:

Ips typographus pheromone components and host monoterpene precursors.

4. Beetles recognition of host state: acceptance or resistance

Orienting towards an host by flying bark beetles is mostly facilitated by olfactory cues (Wood 1982b) although visual cues may be involved (Niemeyer 1985; Strom et al. 1999). In non-aggressive species of bark beetles the attraction to host kairomones is well established (Schlyter and Birgersson 1999; Schroeder and Lindelow 1989). For the aggressive behaviour of bark beetle species the existence of a strong pheromone system is a necessary prerequisite. The pheromone attraction in tree killing species is generally designated secondary attraction, while the primary attraction accounts for the attraction to host semiochemicals by so called pioneer beetles (Person 1931). The host choice of pioneers may involve a long-range habitat recognition during flight and a close range post-landing decision whether to enter a host or to leave it again if found unsuitable. After landing even tactile and gustatory sensations may affect host acceptance behaviour (Raffa and Berryman 1982). The example of empty entrance holes and tunnels, mentioned above, indicates even a third step of host acceptance: beetles may encounter tree defence or recognize an unsuitable bark quality after the first tunnelling attempts in the phloem.

Only volatile compounds are conceivable as long-range attractants to hosts. The most volatile compounds are monoterpene hydrocarbons and their alcohol-, ketone- or other derivates and to some degree at high temperatures even sesquiterpenes. Neither diterpenes, phenolics, alkaloids nor other compounds associated with host defence emit high amounts of volatiles at natural conditions. Beetles may possibly encounter detectable concentrations at really close range, when they walk on or enter the bark.

A primary long-range kairomone attraction has been difficult to show for aggressive species, which has led to a considerable debate, whether these species select suitable hosts in the attack initiation process by volatile host compounds or only by random landing (Byers 1996; Gries et al. 1989; Moeck et al. 1981; Pureswaran and Borden 2003b; Saint-Germain et al. 2007). But McCarty (1980) showed a significant and dose-dependant response to α-pinene in *D. frontalis* in a laboratory walking bioassay. While *D. ponderosae* was significantly attracted in field to traps baited with γ-terpinene alone (Miller and Borden 2003), there was no primary attraction found to different mixtures of monoterpenoids in the same species (Pureswaran and Borden 2005). *Ips pini* was weakly attracted to β-phellandrene alone in a behavioural field assay (Miller and Borden 1990). Baier et al. (1999) found some correlation of different release rates of the pinenes and limonenes from felled trees to attack of either *I. typographus* or *Pityogenes chalcographus* and *Polygraphus polygraphus*. Other studies were able to show the enhancement of pheromone attraction when pheromones were used in combination with different monoterpenes or host tree turpentine. Very high release rates of host compounds either increased or decreased the attraction to pheromones (Seybold et al. 2006 and references therein). In *Ips typographus* the attraction to it's aggregation pheromone was increased by the combination of (–)-α-pinene and (+)-limonene, but was reduced by β-myrcene and (+)-α-pinene in a study by (Reddemann and Schopf 1996). Later Erbilgin et al. (2007) could confirm the attraction to a high dose of (–)-α-pinene and a low dose of pheromone.

It is very difficult to estimate the concentrations of volatile host compounds in odour plumes that flying beetles may perceive. From measurements of emissions from felled spruce trees and standing trees under attack we can estimate the release of the most abundant monoterpene α-pinene from a single tree to approximately 10 – 20 mg / hour (C. Schiebe, unpublished results). However, the upper parts of the stem, where the bark is thinner, usually release a multiple of these values during sun exposure. Flying insects do not experience mean concentrations or a continuous odour plume, but rather package like concentration fluctuations in a meandering odour plume. Insects are able to respond to concentration fluctuations experienced during parts of seconds, and host finding behaviour may reflect response to momentaneous high concentrations of host volatiles (Strand et al. 2009 and references therein). Moreover, it has been shown that bark beetles readily recognize non-host volatiles (Poland et al. 1998; Pureswaran et al. 2004; Zhang and Schlyter 2004). Thus, habitat finding may involve both host and non-host cues. Little is known about how the perception of for bark beetles relevant compounds is affected by the background odours in a landscape, i.e.. with noise or conflicting signals, e.g. host volatiles versus non-host volatiles. In the 'semiochemical diversity hypotheses' Zhang and Schlyter (2003) propose, that host location by specialist herbivores may be influenced of such "semiochemical diversity" in a diverse landscape.

Final host choice, manifested by attack and colonization does not seem to be directly connected with host finding, as landing does not reflect the susceptibility of the tree. Beetles can land on trees in great numbers without attacking them and have been caught even on non-hosts with passive landing traps (personal observations). In an extensive study comparing landing rates on artificially weakened or naturally diseased trees, that were thus predisposed to bark beetle attack, Moeck et al. (1981) found that beetles landed on weakened and subsequently colonized trees as often as on healthy trees. Thus, they found no evidence for primary attraction and concluded that final host choice must occur after landing. However, this study did not allow for testing a possible importance of host odours in a habitat scale, i.e. the finding of host patches in mixed habitats or discriminating groups of host trees with high emission rates (e.g. stressed trees exposed to high sun irradiation or drought stressed) from trees with relatively low emission rates. After habitat location mediated by semiochemicals the landing on single trees still may occur randomly.

Host acceptance during a mass attack is known to be modulated by anti-aggregation pheromones, changes in rates and composition of aggregation pheromones or oxygenated host compounds indicating an already colonized and possibly overexploited host (Alcock 1982; Schlyter and Anderbrant 1989; Schlyter et al. 1989). The repellent signals help avoiding intraspecific competition and are involved in the switch over of an attack to a neighbouring tree. Verbenone, for example, is produced by autoxidation and by microorganisms from α-pinene in the galleries of bark beetles and has a repellent influence on several genera like *Dendroctonus* and *Ips* (Miller et al. 1995; Rudinsky et al. 1974; Schlyter et al. 1989).

Semiochemicals affecting host acceptance or rejection after landing are likely to contain also less volatile compounds like phenolics, diterpenoids and alkaloids. Various laboratory assays on beetle response to media amended with host monoterpenes indicate that the concentration rather than type of monoterpenes may be a critical factor for postlanding acceptance. Depending on the physiological condition of beetles (see more in part 8), low and medium concentrations tend to increase acceptance to artificial media, while high concentrations always prevent tunnelling (Raffa and Smalley 1995; Wallin and Raffa 2000; Wallin and Raffa 2002; Wallin and Raffa 2004). Phenolic compounds are a part in the defence system of conifers (see above) but to what extent these compounds are effective in the constitutive defence and confer resistance against bark beetles is still poorly understood. As mentioned above, most of the aggressive species are more or less closely associated with symbiotic fungi. If these fungi are affected by defensive metabolites from the host, this may in turn affect bark beetle colonisation and survival (Franceschi et al. 2000). The antifungal effect of several phenolics against bark beetle associated fungi has been shown in some studies (Brignolas et al. 1995; Brignolas et al. 1998; Evensen et al. 2000; Lieutier et al. 1997), but the connection of this effect to the host choice of bark beetles remains unclear. A feeding assay with *I. typographus*, however, showed a direct antifeedant dose-response effect for three phenolics, particularly on pioneering males (Faccoli and Schlyter 2007). In addition to phenolics, also the potential role of diterpene acids and other diterpenoids has so far not been studied comprehensively. Kopper et al.(2005) found a strong antifungal effect for abietic and isopimaric acid, but no effect on host acceptance or larvae survival of *I. pini*. Alkaloids can be found in pines and other conifers in very variable concentrations, but these are generally present in much lower concentrations than either phenolics or terpenoids (Gerson and Kelsey 2002; Gerson and Kelsey 2004). In spite of their toxicity, the role of alkaloids as anti-feedants against bark beetles is still unknown.

5. Beetle - fungi association – a key factor for host acceptance?

General consensus has not been reached in the debate if the association between fungi and tree killing bark beetles is obligate for the beetles or not (Lieutier et al. 2009). While the association is obligate for the fungi, as these are transported by the beetles and in many cases seem to be disseminated solely by them, there are arguments for both points of view regarding the dependency of the beetles on their fellow-travellers (Klepzig and Six 2004). In addition, there is a lack of knowledge about the interactions of various symbiotic, commensal or antagonistic fungi that can be found in trees colonized by bark beetles. An example of an antagonistic interaction between bark beetles and fungi is the endophytic fungus *Phomopsis oblonga* in Elm trees (*Ulmus ssp.*), that prevent the successful breeding of the vector of Dutch elm disease *Scolytus spp.* (Webber and Gibbs 1984). In a study in southern Poland 65 different taxa of fungi were obtained from phloem infested by *I. typographus*, 14 of which belonged to the ophiostomatoid blue stain fungi (Jankowiak 2005) containing the genera usually establishing first and being most virulent (Solheim 1992; Solheim et al. 2001). There is a large variation in the fungal flora present and vectored by bark beetles depending on region, time or hibernation site (Jankowiak 2005; Klepzig and Six 2004; Persson et al. 2009; Solheim 1992). The establishment of bark beetles in a tree is associated with a fungal complex more than single fungal species. The intricate interaction between a trees defensive capacity and the establishment of different antagonistic fungi with different virulence may be important for the outcome of beetle colonisation (Klepzig and Six 2004; Lieutier et al. 2009). Furthermore new data indicate that the establishment of fungi can be promoted by symbiotic bacteria carried by beetles or inhibited by bacteria found on host trees (Adams et al. 2009). Considering this tightly interconnected web of adapted organisms it would be surprising if bark beetles did not have evolved any means to sense the successful establishment of symbiotic organisms as an indicator for a favourable environment for colonization. Such a mechanism might require a fast reaction of tree defence on pathogens, recognized by the beetles or a direct (presumably enzymatic) influence of bacteria and/or fungi on the contact surface between tree and beetle.

6. Olfactory detection in *Ips typographus* and other ‘aggressive’ bark beetles.

In spite of the difficulties to show a clear behavioural role of host compounds in host choice, the response to host compounds through single olfactory receptor neurons has clearly been shown on *I. typographus* and *I. pini* antenna (Mustaparta et al. 1979; Tømmeras and Mustaparta 1987) and lately in a comprehensive assessment for *I. typographus* by Andersson et al. (2009). Andersson and co-workers (2009) found a large proportion of narrowly tuned, highly specific olfactory receptor neurons (ORNs), that responded to host compounds. In addition, a considerable proportion (≈ 25%) of responding neurons where found to be tuned to non-host volatiles, emphasizing the importance of non-host cues in orientation by this bark beetle. In contrast to other insects, where ORNs related to pheromones can be found on specific sensillum types, spatially separated from other ORNs, there was a poor segregation between pheromone responding ORNs and those responding to plant odours in *I. typographus* (Andersson et al 2009). This distribution may be an indication for the integrated system of pheromone- and plant odour detection for host selection. ORNs for the specific detection of the host-compound, 1,8-cineole, are even co-localized on the same sensillum with the ORNs for a pheromone component *cis*-verbenol (Andersson et al. 2009). Interestingly, high doses of 1,8-cineole were found to inhibit the response to *cis*-verbenol, underlining the potential of this host compound as a key marker for host suitability (Andersson et al. 2010). The response to host compounds on the peripheral nervous system detected by GC-EAD (coupled gas-chromatograph – electroantennographic detection) has also been reported for other aggressive bark beetle species (*Dendroctonus pseudotsugae, D. ponderosae, D. rufipennis* and *Dryocoetes confuses*) (Pureswaran et al. 2004) and detected through SSR (single-sensillum recordings) on *D. pseudotsugae* (Dickens et al. 1984). The detection of oxygenated monoterpenes in the host by bark beetles is still rarely identified, but the strong responses to (–)-verbenone, 1,8-cineole and other oxygenated monoterpenes involved in the semiochemical systems of bark beetles are well-known (Andersson et al. 2009; Tømmeras et al. 1984). Recent work show strong responses in *I. typographus* to small amounts of several oxygenated compounds in volatiles from felled *P. abies* (Schiebe unpublished). The proportion of oxygenated monoterpenes rises after bark beetle attack in the bark surrounding beetle galleries (Leufven and Birgersson 1987) and after induction of defence responses elicited by treatment with methyl jasmonate in volatiles from foliage in Norway spruce (Martin et al. 2003), as it did in spruce logs with ageing (Schiebe unpublished). The proportion of oxygenated compounds in the volatiles of a host as indicators for stress and degradation may be an important cue for the evaluation of it's suitability.

It should be kept in mind that the ability to detect host volatiles still does not tell us anything about the behavioral function of these responses. They could facilitate e.g. a general host habitat selection on a landscape scale, discrimination between non-host odours and distinct host patches with high release rates of host odours, indication of stressed or damaged hosts (true primary attraction), or detection of competition in already colonized hosts. The detection of single compounds by the peripheral nervous system is still not completely explored, neither is the integration of the signals reaching the central nervous system understood. The behavioural function of the detection of single compounds may mainly be integrated in whole semiochemical blends, modulated by compositional shifts in these blends.

7. The interface of individual host choice and population dynamics

So little we know about host selection by means of kairomones and allomones, so much more apparent and dominant is the importance of a strong aggregation pheromone system for the behaviour of ‘aggressive’ bark beetles. These pheromones have in most species a triple function: to attract mates as a sex pheromone; to attract conspecifics of both genders, but by changed rates of release or composition they may also shut of the attraction of conspecifics in order to avoid overcrowding (Raffa 2001; Schlyter and Anderbrant 1989; Schlyter et al. 1987). As discussed in a previous chapter, there are not only advantages of an aggregation behaviour. Rather, the importance of aggregation can depend on the actual state of the population. In cases of very limited supply of breeding material it would be more adaptive for the host selecting gender to locate suitable breeding material by perceiving host odours. Beetles that are able to recognize and find suitable breeding material with the best available quality would have the best fitness. A less prevailing influence of pheromone attraction can be suspected in situations of excess of breeding material during endemic population conditions e.g. after a storm with huge amounts of downed trees. It has been observed that the colonization of wind fallen trees occurs in many logs rather than is concentrated on few logs when the population is low (Komonen et al. 2011; pers. observations; G. Birgersson pers. comm.). In an outbreak situation, however, the benefit of aggregation behaviour seems clear. In a study testing the fitness consequences of different arrival time during an attack sequence in *D. frontalis*, the first arriving beetles seemed to have higher costs by pheromone production and suffered from higher risks by the tree’s defence, whereas beetles that arrived in the middle of an attack sequence had highest fitness (Pureswaran et al. 2006). As a consequence, beetles during the epidemic phase could be considered to have a higher fitness by quickly responding to pheromone signals, rather than evaluating host quality by means of kairomones. The beetles responding to host signals are taking higher risks during dispersal and by evaluating host suitability or fighting host defences. It has been speculated that these two different situations in population dynamics could result in different behavioural patterns (phenotypic plasticity) or even heritable traits (alternating selection on traits favouring actual population size) (Wallin and Raffa 2004; Wallin et al. 2002). In an extensive comparative study between *D. rufipennis* from 29 eruptive versus endemic sites, Wallin and Raffa (2004) found pronounced between-population differences regarding acceptance of host monoterpene amended artificial media, but also high variation within populations. Differences between endemic and epidemic populations persisted following three generations rearing in a common environment. The heritability of host acceptance behaviour has even been tested on *I. pini* in a laboratory bioassay by both positive and negative selection of the trait. Acceptance of a medium amended with α-pinene increased by positive selection from 59 ± 7 % (mean ± SD) to 90 ± 11 % in the third generation and dropped by negative selection from 50 ± 6 % to 9% in the third generation (Wallin et al. 2002). In the study of Wallin and Raffa two other interesting factors influenced beetle acceptance of host media: total lipid body content was positively correlated with acceptance of terpene concentrations regardless population; beetles from eruptive sites had lower mean fat content; the lower acceptance to higher concentrations in epidemic beetles was unexpected by the authors. An other factor, however, compensated for the lower acceptance in these populations: adding higher number of beetles in the assay arena increased the acceptance in the epidemic, but not in the endemic populations. The beetles seem to perceive the presence of each other. Because the risk of being killed by a trees defence is dependent on the number of attacking beetles, this reaction would be ecologically relevant. In an other study Wallin and Raffa (2002) tested the host acceptance and gallery construction in *I. pini* in a series of assays with medium containing different concentrations of α-pinene and limonene. They found that both entrance and gallery construction behaviour was affected by the number of beetles present on the surface of the medium or boring galleries. Gallery construction but not entrance was influenced by the presence of aggregation pheromone. Hence, both visual, auditory (Rudinsky et al. 1973; Rudinsky et al. 1976) or tactile sensing may be involved to evoke a shift in behaviour towards a higher tolerance of toxic host compounds. Sallé et al. (2005) found significant body size differences related to attack densities between endemic and epidemic populations of *I. typographus*. High densities in outbreak conditions rendered a reduced body size and was hypothesized to influence male pheromone emission and dispersal capacities (see also Anderbrant et al. 1985). Potentially even the perception of beetles could be influenced by reduced size and fat content, as the fat content of 3000 tested beetles correlated with both dispersal length and response to pheromones and trap trees (Gries 1985). *Trypodendron lineatum* became responsive to host odours first after several hours of flight exercise (Graham 1959).

To summit, there are several possible explanations for the shift of attack patterns that can be observed in aggressive species during an outbreak situation and back to periods of latent aggressiveness:

1. **Genetic variability:** There is a large variation in acceptance behaviour (Wallin et al. 2002) and in pheromone production (Birgersson et al. 1988; Pureswaran et al. 2008). It can be presumed that a great part of this variation is of genetic

origin. The aggregation behaviour with common strong pheromone plumes and associated attack behaviour may allow extreme phenotypes and a large variability to persist. As aggregation pheromones coordinate the attacks, only few individuals need to be able to perceive kairomones to start an attack on weakened hosts and the individual contribution to the pheromone plume in a mass attack will have a limited potential as a driving force in natural selection (Pureswaran et al. 2008). In the same time, this large variability also could provide the necessary diversity in a population to quickly adapt to fast shifts in a changeable environment.

2. **Allelic shift:** During endemic phases, beetles that are able to perceive volatile host compounds indicating a weak host, would be strongly favoured by selection because of the high dispersal losses (Raffa et al. 2005). The level of alleles favouring host finding behaviour may rise quickly (as shown in Wallin et al. 2002) and provide the population with a higher general host sensitivity, which in the initial phase of an outbreak promotes localization of weak hosts when the amount of weakened trees suddenly has risen.
3. **Nutritional state:** Larger beetles with higher lipid reserves can be observed in endemic sites (Furuta 1989; Wallin and Raffa 2004) and in low density offspring (Botterweg 1983). Physiological differences alone or in concert with allelic shifts may explain the observed differences in attack pattern. Beetles with high lipid content have been found to show higher acceptance to host compounds (Wallin and Raffa 2004), and large beetles produced more anti-aggregation pheromones (Pureswaran and Borden 2003a) or more aggregation pheromones (Anderbrant et al. 1985), all of which provides these beetles with better abilities to pioneer an attack under risky circumstances. The lipid content and nutritional state of bark beetles seems also to influence the timing when beetles respond to host signals or pheromones. Dispersing beetles do not land on trap trees or are caught in pheromone traps until lipid reserves are used up during flight or hibernation (Gries 1985; Hagen and Atkins 1975; Krauße-Opatz et al. 1995; Nemec et al. 1993). Even brood density resulting in beetles with different nutritional state, hence may influence the response to kairomones or pheromones differently (Botterweg 1983).
4. **Population size** may influence the attack behaviour *per se* due to beetles' increased acceptance to higher levels of toxic host compounds when they

experience that they are many (Wallin and Raffa 2002; Wallin and Raffa 2004). The ground for such semi-social behaviour presumably exceeds pure olfactory communication and needs to be explored further.

8. A suggested host choice model in *Ips typographus*:

First – second year:

Endemic populations are reduced to find single downed trees, which may be of relatively low quality depending on freshness, but may release relatively high plumes of host volatiles. Survival rates in endemic populations are suggested to be low due to large dispersal losses (predator losses and exhaustion during extended searching for suitable hosts reduces population size). Healthy host trees release low amounts of volatiles and possess strong defences. Successful host finding is facilitated by host odours released by stressed trees or by pheromones released by pioneering beetles. Offspring quality depends on host quality and intra/interspecific competition. A low population size can be maintained during many years, as long as conditions remain the same. The poor supply of suitable breeding material favours beetles with good host detection ability, reducing their dispersal losses and giving them a head-start in reproduction.

Third year:

A storm or other environmental disturbances may result in large amounts of suitable high quality breeding material. This altered condition allows more beetles to find a suitable host, resulting in higher survival and high reproduction and offspring quality due to low intraspecific condition and high host quality. Host finding is facilitated by high host volatile release rates, but pheromone plumes will remain relatively small due to low beetle densities. Depending on the weather conditions even a second generation may be able to reproduce and the population increases epidemically. There are several circumstances that may shift the attack behaviour towards standing trees, e.g. fallen trees lying near by standing trees attract many beetles by host volatile and pheromone release. When the colonisation density in the fallen trees exceeds the available space, new beetles will try to attack near by standing trees and eventually succeed when the population size is big enough to overcome host defences. In addition, single standing trees that release larger host volatile plumes compared to surrounding trees may attract beetles initiating an attack. The release of host volatiles from standing trees increases in high temperatures especially when they are damaged or stressed.

The release of pheromones from beetles attacking high quality trees (healthy trees with higher nutritious value) is higher than from poor trees. Beetles that attack standing trees attract large number of beetles from the growing population pool. The attack will switch over to neighbouring trees and continue until no more beetles join the attack. The attack is maintained solely by pheromone attraction. As long as the balance between trees' defensive ability and beetles' population size supports the continued 'aggressive' behaviour of beetles, no favour is given to beetles with a good host detection ability and the genetic variation of perception is maintained. However, trees with extraordinary defence reactions may survive even under extreme attack conditions. When weather and other environmental factors favours the defence ability of the trees and prevents the dispersal activity of the beetles, the epidemic population may suffer by overpopulation depression and the population size may fall under the critical threshold that allows beetles to overwhelm the defence of living trees. This reduces the population to an endemic level until new events increase the amount of available breeding material.

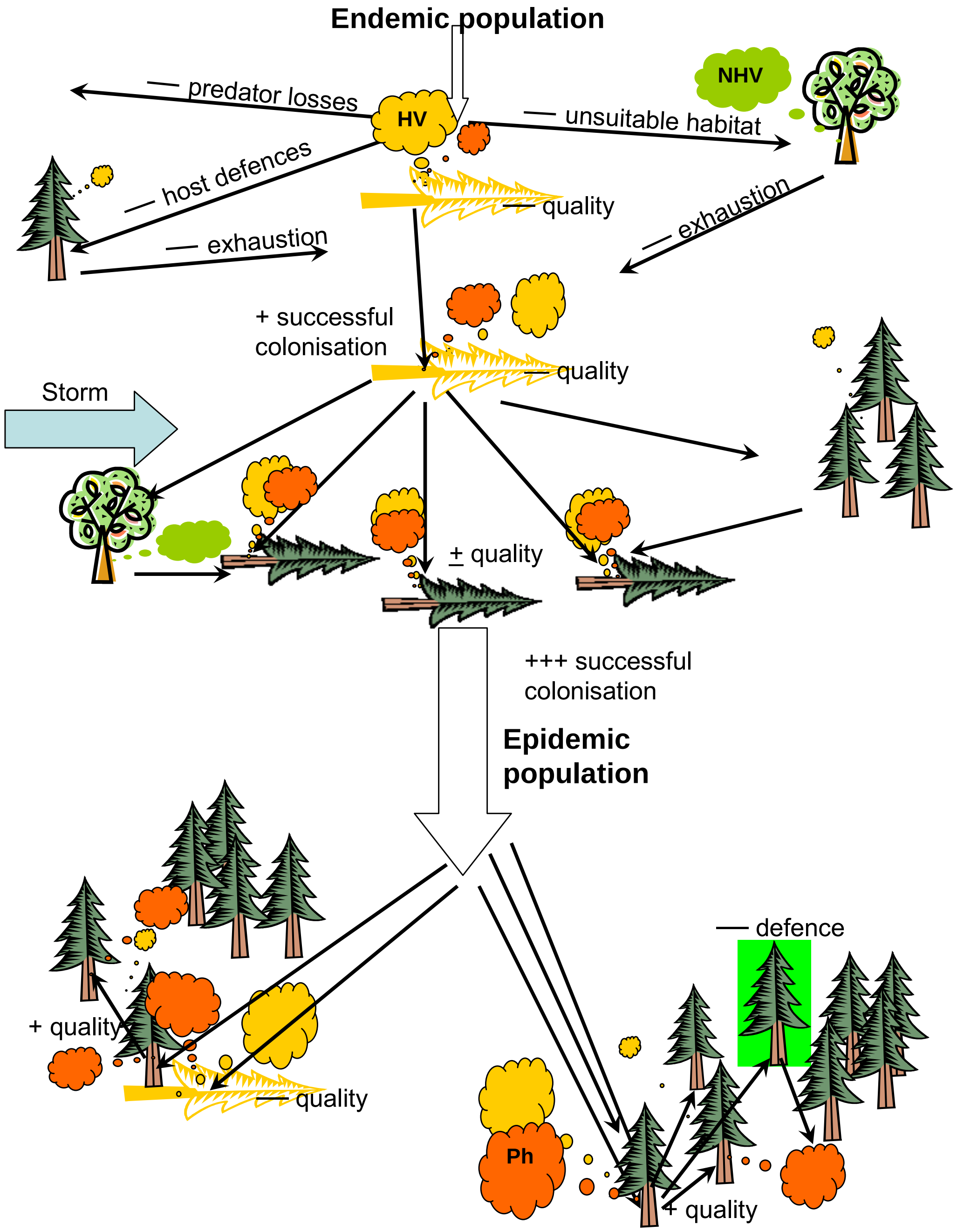

Figure 5:

Factors influencing survival and colonisation success in endemic beetle populations and factors leading to a bark beetle outbreak.

9. Gaps of knowledge: issues for further research in the ecology of *Ips typographus*

On basis of the review of recent literature, the following crucial gaps in our current knowledge on ecology of *Ips typographus* can be identified and should be topics of future research:

1. What are the behavioural functions of known host odour responses of the peripheral nervous system?
2. Can we find responses to other compounds indicating host quality and influencing host choice, e.g. oxygenated host compounds?
3. What is the importance of gustatory cues (taste) in host choice?
4. What is the importance of host defensive capacity for pheromone production and thus for the resistance of host trees?
5. To what extent do symbiotic and antagonistic fungi influence host acceptance by aggressive bark beetles?
6. Does the nutritional state and quality of beetles influence the olfactory system?
7. Is attack density influencing the host choice behaviour of *I. typographus*. Can beetles perceive that they are many and what are the mechanisms for such ‘semi-social’ behaviour?

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