



Ecology and management of the spruce bark beetle *Ips typographus*—a review of recent research

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Received 14 July 2003; received in revised form 16 April 2004; accepted 8 June 2004

Abstract

The outbreaks of *Ips typographus* (L.) in Central Europe after severe storms in the 1990s triggered extensive research. Molecular techniques were used to analyze the relations and origins of European *Ips* species. The biological characteristics of *I. typographus* such as the influence of temperature on life history parameters and flight behavior have been analyzed in detail. The spruce bark beetle was found to disperse well beyond 500 m. However, new attacks mostly occurred in the vicinity of old ones.

Many studies refer to invertebrate natural enemies of *I. typographus* such as predatory beetles and flies as well as various parasitoids. While the species assemblages of antagonists have been extensively investigated their dynamics and impact on *I. typographus* populations are controversial.

The susceptibility and defense mechanisms of host trees are crucial for a successful attack by bark beetles. Newly attacked trees respond with preformed resin, local wound reactions and eventually with systemic changes in their physiology. Risk assessments have been performed at both tree and stand level. Risk of attack seems to be mainly related to the exposition, age, and nutrient and water supply of the trees. The dynamics of outbreaks largely depends on insect abundance, tree susceptibility, weather conditions, and human measures. This renders predictions difficult. Various control techniques are reviewed and the need for more sophisticated risk assessment tools is stressed.

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Keywords: Forest protection; Bark beetles; Damage; Biology; Pheromones; Management

1. Introduction

With regard to forest protection, the last decade of the 20th century in Central Europe was marked by the storms ‘Vivian/Wiebke’ in February/March 1990 and ‘Lothar’ in December 1999. Both events were disastrous and gave rise to an enormous propagation of the

European spruce bark beetle (*Ips typographus* [L.]) in the affected spruce forests (Engesser et al., 2002; Flot et al., 2002; Schröter et al., 2002). The extent of bark beetle damage was huge and a large amount of public money was invested in clearing windthrow areas and subsequent sanitation fellings. Consequently, questions concerning the feasibility, efficiency and purpose of traditional phytosanitary measures were raised, triggering intensive research on ecological, economical and phytosanitary aspects of *I. typographus*. There were

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still considerable gaps in our knowledge of its basic development, biology and behavior. In addition, many questions arose concerning the complex interactions between the population dynamics and natural regulation of *I. typographus*, tree susceptibility, and management.

The wealth of new findings on *I. typographus* published in Europe in the 1990s means it is worthwhile to compile and critically review these results, thus replenishing earlier reviews and compilations on scolytids in general (Rudinsky, 1962; Christiansen and Bakke, 1988; Stenseth and Kirkendall, 1989). The synopsis here discusses the literature published on *I. typographus* and its natural enemies between 1990 and 2002. The focus is mainly on European studies since *I. typographus* is native only to Europe and Siberia, and on scientific investigations and analyses rather than on descriptive reports. Some key findings are summarized in Table 1. In the conclusion, some needs for future research from a central European perspective are pointed out.

2. Phylogenetics

Stauffer et al. (1992, 1999) analyzed the genetic composition of the European populations of *I. typographus* by means of molecular techniques. In Central Europe they found various haplotypes while in Scandinavia only one of these types was present. In Russia and Lithuania a separate type has evolved. They suggest that during the last ice age the populations, along with their host tree *Picea abies* (L.) Karst., moved to refugial areas in the south (Apennine, Dinaric and Carpathian Alps) and north of Moscow. With post-glacial warming the spruce bark beetle remigrated from the Apennine and Dinaric Alps into the former areas, while the spruce moved in also from the east. *I. typographus* is closely related to *I. amitinus*, *I. cembrae*, and *I. acuminatus* and to a lesser degree, to *I. sexdentatus* (Stauffer et al., 1997).

3. Life history

Most aspects of the immature development, adult reproduction and behavior of the European spruce bark beetle have been known for a long time (for a

review see, e.g. Christiansen and Bakke, 1988; Stenseth and Kirkendall, 1989). However, the influence of temperature on its development has, for example, only recently been analyzed in detail (Coeln et al., 1996; Wermelinger and Seifert, 1998). Using a linear relationship between the developmental rates and temperature, the lower developmental threshold (i.e. the minimally required temperature for development) was computed to be 8.3 °C. With a nonlinear model the threshold was around 6 °C. The heat sum for total development ranged from 334 degree-days (Wermelinger and Seifert, 1998) to 365 degree-days (converted from data from Abgrall and Juvy, 1993).

The reproduction of *I. typographus* has similarly been investigated (Wermelinger and Seifert, 1999). Egg production was also found to depend on temperature, with a lower temperature threshold of 11.4 °C (linear model). With nonlinear models an optimum temperature of 30.4 °C for the juvenile development and 28.9 °C for reproduction were calculated (Wermelinger and Seifert, 1998, 1999). Such data are prerequisites for building simulation models of bark beetle population dynamics.

Intraspecific competition at high breeding densities affects behavior. High densities result in shorter maternal galleries and thus in reduced oviposition (Anderbrant, 1990; Weslien, 1994). The optimal density is at roughly 500 maternal galleries per square meter (Schopf and Köhler, 1995). Each male mates with two or three females, who together construct a gallery system. Thereby, the females deposit up to 80 eggs (likewise in sister broods, Heidger, 1994) preferably on the side of the maternal gallery that least interferes with other maternal galleries (Schlyter and Zhang, 1996). The sex ratio of the progeny depends on the phase of gradation. This was demonstrated during an outbreak of *I. typographus* in southern Bavaria between 1990 and 1995 (Lobinger, 1996). At the beginning of the outbreak (i.e. progradation phase) the proportion of females increased far beyond 50% and re-approached the 50% level towards the end of the outbreak (retrogradation). This pattern also affected the harem size: in vital broods the gallery system of each male mostly consisted of three maternal galleries. Females at higher elevations produced fewer sister broods than those at low elevations (Netherer et al., 2001).

Table 1
Selected data from research on *Ips typographus* published between 1990 and 2002

Feature	Data	Section
Biology		
Minimum temperature for development	6–8.3 °C	3
Minimum temperature for oviposition	11.4 °C	3
Optimum temperature for development and oviposition	29–30 °C	3
Fecundity	Up to 80 eggs/female	3
Sex ratio (% females)	50% (retrogradation) ≫50% (progradation)	3
Overwintering mortality	~50%	3
Optimum breeding density	~500 maternal galleries m ⁻²	3
Optimum harem size	Three females	3
Minimum temperature for flight (threshold)	16.5 °C	4
Optimum flight temperature	22–26 °C	4
Main flight time	Noon, early afternoon	4
Minimally required number of days with temperatures > flight threshold for successful attack on living trees	3–4 days in a row	4
Active flight distance	>500 m	6
Natural enemies		
Most important insect groups	Clerid beetles, dolichopodid flies, pteromalid wasps, braconid wasps	7
Prey consumption		7
Clerid larvae	Approximately 50 scolytid larvae	
Clerid adults	Approximately 100 scolytids	
Dolichopodid larvae	5–10 scolytid larvae	
Mode of host/prey finding		7
Parasitoids	Volatiles	
Clerids	Bark beetle pheromones	
Host susceptibility		
Host defense mechanisms	Stored resin, toxins, deteriorated food quality, wound reaction	8.1
Trees at high risk	South, west exposition, sunlit, >70–100 years old, trees with heart rot	8.2
Radius of higher risk of attack around infestation	100 m	6
Outbreaks		
Causes of outbreaks/prolongation of outbreaks	Windthrow, drought, high temperatures, snow/ice break	9
Peak abundance of <i>I. typographus</i> in windthrow areas	2nd to 3rd summer after storm	9
Management		
Optimum period for salvage harvesting of windthrown logs	Between infestation and emergence of first generation	10.1
Estimated catch rates of pheromone traps	3–10% of population	10.2
Optimum exposition of pheromone traps	South	10.2
Catch efficiency of baited trap trees relative to pheromone traps	Up to 30×	10.2
Size of phytosanitary buffer zone around reserves	500 m (100–1500 m)	10.4
Bark beetle mortality with machined debarking	93%	10.1

Section numbers refer to the text. For references see text.

Mortality experienced during winter can be attributed to both biotic and abiotic factors. A mortality rate of roughly 50% for *I. typographus* beetles overwintering in fallen trees was attributed to air temperatures down to –10 °C (Faccoli, 2002). Immature stages were more affected than adult

beetles. The emergence and migration of beetles of monovoltine generations were found to depend on the geographical latitude: northern populations emerged later and migrated less frequently before overwintering than those of southern origin (Forsse, 1991).

4. Flight activity

Diurnal flight activity is from approximately 9 a.m. to 9 p.m., with maximum at noontime and in the early afternoon (Funke and Petershagen, 1991). Obviously, this depends on the temperature—minimum air temperature for flight was 16.5 °C, and optimum temperature between 22 °C and 26 °C (Funke and Petershagen, 1994; Lobinger, 1994). This may be important for optimizing water use in sprinkled log storage systems. Swarming depended greatly on sunshine. Even with short sunbursts, more *I. typographus* beetles took flight than during periods without sunshine (Lobinger and Skatulla, 1996). Flight activity had an upper threshold of 30 °C (Lobinger, 1994). Males emerged earlier than females (Zuber and Benz, 1992). This makes sense since pioneer males have to find and colonize susceptible trees and excavate the nuptial chambers before females can reproduce.

Studies in the Bavarian Forest have confirmed that, for a successful attack on living trees in spring, at least three to four warm days in a row are needed with temperatures well above the swarming threshold (Weissbacher, 1999). Otherwise the frittered flight lowers the chance of successfully overcoming the defense mechanisms of a living tree (see Section 8.1).

5. Pheromone biology

It is known that the aggregation pheromones of *I. typographus* consist of terpenoids that are biosynthesized from tree resin components. These intraspecific semiochemicals are much more attractive than the volatiles (kairomones) emitted by the spruce trees. Conspecific bark beetles are attracted by aggregation pheromones when a suitable breeding substrate is available. However, there is also evidence that *I. typographus* produces repellent pheromones where the substrate is unsuitable for breeding (Francke et al., 1995). Traps baited with both the commercial lure Pheroprax[®] and the anti-aggregation pheromone verbenone or the tree volatile (+)-alpha-pinene caught only 2–30% of the number of beetles caught in traps baited exclusively with Pheroprax[®] (Niemeyer et al., 1995b; Reddemann and Schopf, 1996; Zhang et al., 1999). While the pinene component also prevented trees from being attacked, verbenone did not. The

attractiveness of a vital spruce tree, which is low per se, was distinctly higher when a pheromone dispenser was attached (Franklin and Gregoire, 1999).

Earlier work has already shown that the energy reserves of *I. typographus* beetles need to be depleted before the beetles will respond to pheromones (Gries, 1985). Likewise, Nemeč et al. (1993) found that beetles not responding to pheromone had a higher body weight than those attracted to the lure. The beetles attracted to the pheromone traps differed in glycogen (representing reserves) and protein (representing flight muscles) levels, 30% of them had high glycogen and low protein levels and were hypothesized to originate from local populations and 70% were assumed to be migrants (high protein levels).

Other primary scolytids have been found to produce aggregation pheromones only until the moment when the host resistance threshold was reached (expressed in attacks per unit area), i.e. as long as the host's resin system remained active (Paine et al., 1997).

6. Dispersal

Dispersal is tightly connected to the response of the beetles to pheromones. Several authors have performed mark-recapture experiments to estimate the dispersal and flying distance of bark beetles after emergence. This involves marking the beetles, releasing them and recapturing them in traps. Usually, only a small proportion of the released beetles are recaptured. In Sweden, Weslien and Lindelöw (1990) caught 8% of the released beetles in pheromone traps at a distance of 100 m, and 2% at 1200–1600 m. They employed pipe traps with Ipslure[®], while in Central Europe slot traps with Pheroprax[®] are commonly used. Similar recapture rates at the above distances from the release point were reported by Zumr (1992) and Duelli et al. (1997). Re-emerged parental beetles (seeking facilities to produce sister broods) seem to travel less far (Zolubas and Byers, 1995). From the recapture data several authors have calculated diffusion curves in the form of power or exponential functions. Using such equations and based on an attraction radius of a pheromone trap of 17–34 m (Schlyter, 1992), a trap at 25 m distance from an infested tree would catch from 20% (Weslien and Lindelöw, 1990) to 54% (Duelli et al., 1997) of the local population. However,

these percentages relate to the total number of recaptured beetles. If the catches reported by Duelli et al. (1997) are related to the total number of released beetles (both recaptured and non-recaptured) only 26% of the beetles are caught at this distance. In traps at 5 m from the release point, 35% of the marked beetles were trapped (Duelli et al., 1997). Therefore, it seems that at most a third of the local population may react to pheromones immediately after emergence, while the remainder travels farther. More than 50% are thought to fly further than 500 m. Further evidence of this is the fact that thousands of unmarked *I. typographus* were caught in a pine forest 6 km away from the nearest spruce stand. In a bivoltine situation, the overwintering generation was found to disperse more extensively than the summer generation (Furuta et al., 1996).

It needs to be stressed that the risk of a spruce tree being attacked is not only related to its proximity to an existing infestation spot. The risk also depends on, e.g. the density of the beetles, and, most importantly, on the susceptibility of the trees. However, under epidemic conditions, 90% of new infestations were found to occur within 100 m of an old attack (Wichmann and Ravn, 2001). When susceptible trees are more than 100 m apart, dispersion losses among the beetles could restrict the spread of an infestation (Becker and Schröter, 2000).

The flight paths of *I. typographus* beetles, their dispersal, and their reaction to pheromone traps have been modeled in computer simulations by Byers (1993, 1996, 1999, 2000).

7. Natural enemies

Until recently natural enemies of bark beetles have been assigned only a minor role in controlling bark beetle populations. In the past decade research has reevaluated the regulatory capacity of these antagonists. Extensive work has been carried out on the assemblages of antagonists associated with bark beetles. Among insects some of the most abundant natural enemies of *I. typographus* are predatory beetles (Cleridae) and flies (Dolichopodidae), as well as parasitic wasps (Pteromalidae, Braconidae) (Eck, 1990a,b; Schopf and Köhler, 1995; Weslien and Schroeder, 1999; Wermelinger, 2002). The biology of most of

these species is fairly well documented (recent papers: Eck, 1990a,b; Weslien and Regnander, 1992). The species assemblage of natural enemies depends on the host tree species and within the same tree species, on the bark texture (Lawson et al., 1996). Parasitic pteromalid wasps, for example, preferred a smooth bark surface. Within the same tree, individual pteromalids are more abundant in the upper part of the stem where the bark is thinner (Wermelinger, 2002).

In general, parasitoids find their hosts by optical, tactile, vibrational, thermal or olfactory stimuli. Investigations on some important braconid and pteromalid wasps showed that host finding most likely occurs by volatiles (Mills et al., 1991). These cues (e.g. oxygenated monoterpenes) are produced by the interaction of the host or introduced microorganisms with the surrounding bark tissue (Pettersson, 2000, 2001; Sullivan et al., 2000). Clerid beetles respond to the same pheromones as their prey (Bakke and Kvamme, 1981; Aukema et al., 2000; Zhou et al., 2001). Antagonists colonize the trees later than their prey (Weslien and Regnander, 1992) and they leave the trees later as well (Fig. 1).

Outbreaks of *I. typographus* trigger an increase in their natural enemies. In a Swedish outbreak region, the ratio of the clerid beetle *Thanasimus formicarius* (L.) to *I. typographus* was ten times the ratio in a non-outbreak region (Weslien, 1994). Likewise, unmanaged spruce stands undergoing *I. typographus* attack harbored two to three times more predators than managed forests without bark beetle attack, although bark beetle levels were comparable (Weslien and Schroeder, 1999). The occurrence and efficiency of natural enemies is also affected by silvicultural practices. There is evidence that predators may be more sensitive to certain forest management practices than their prey (Weslien and Schroeder, 1999). However, this does not imply that predators (specifically *T. formicarius*) are generally more abundant in unmanaged forests (Schlyter and Lundgren, 1993). Pathogens, such as viruses and microsporidia, were reported to be more frequent in late emerging *I. typographus* than in early ones (Wegensteiner and Weiser, 1996).

The impact of antagonists on bark beetles depends, among other factors, on their density and voracity. The clerid beetle *T. formicarius* is a conspicuous and well-investigated predator. Each larva consumes roughly 50

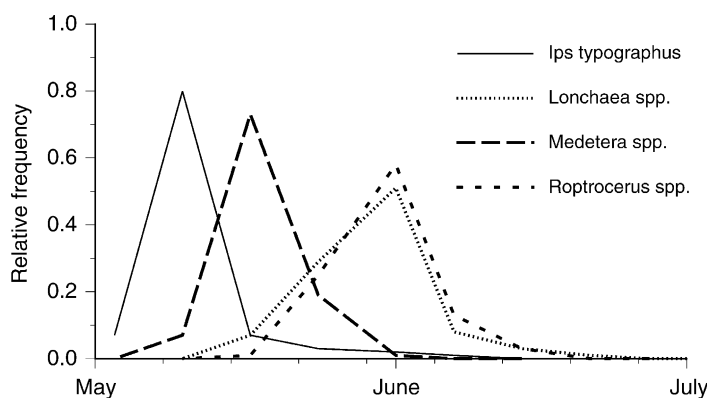


Fig. 1. Emergence dynamics of bark beetles and associated natural enemies from logs of bark-beetle-infested spruce trees: *Ips typographus* (Scolytidae), *Lonchaea* spp. (Lonchaeidae), *Medetera* spp. (Dolichopodidae; both predatory Diptera), and *Roptrocercus* spp. (Pteromalidae, parasitic Hymenoptera). Methods in Wermelinger (2002).

bark beetle larvae during its development (Heidger, 1994; Hérard and Mercadier, 1996; Dippel et al., 1997). In addition, the adult beetle devours some 100 *I. typographus* during its life span (Heidger, 1994). At high densities of *T. formicarius* cannibalism or emigration may occur (Weslien, 1994). Among the most important mortality factors acting on the spruce bark beetle larvae seem to be predatory *Medetera* flies (Schopf and Köhler, 1995; Lawson et al., 1996; Wermelinger, 2002), although their larval consumption is only 5–10 scolytid larvae (e.g. Dippel et al., 1997). Their low voracity can be compensated for by their high abundance.

Relatively high mortality rates of the European spruce bark beetle due to natural enemies have been documented in short term investigations. Eck (1990b) recorded local parasitism rates of up to 30%. In exclusion experiment the offspring production of *I. typographus* in caged logs without predation and parasitism was found to be 1.3–5 times higher than that in uncaged logs (Weslien and Schroeder, 1999).

In a biennial study, mortality imposed by predators and parasitoids increased from 55% to 82% during two years of an ongoing infestation (Wermelinger, 2002). While the predators were the main cause of mortality in the first year, higher bark beetle mortality was caused by parasitoids in the second year of the study. However, a 3 year study in the National Park Bavarian Forest revealed no consistent pattern in the development of antagonistic species (Schopf and Köh-

ler, 1995). Cold temperatures during wintertime seem to be equally detrimental to parasitoids and to bark beetles (Faccoli, 2002).

A density-dependent response of natural enemies to bark beetle outbreaks was documented by Lawson et al. (1996). On the other hand, local bark beetle populations in existing infestation spots may be replenished by immigrating *I. typographus* but not by, e.g. *T. formicarius* beetles (Weslien and Schroeder, 1999), even though they are also good flyers (Heidger, 1994). The spruce bark beetle has high dispersal abilities and can thus escape the local mortality agents. At new potential infestation spots the local density of antagonists may be still low, which allows the bark beetles to build up new populations successfully.

Antagonists depend on food not only during their development, but also as adults. While adult predators, such as clerid beetles, have food sources similar to those of their larvae, parasitic wasps depend on energy sources such as pollen, nectar or honeydew. It has been shown that, even in spruce plantations, several plant species are able to provide these resources (Hougardy and Grégoire, 2000).

Little research has been carried out in recent years on the impact of woodpeckers on *I. typographus*. Although they generally prefer larger prey than scolytids (Nuorteva and Saari, 1980), the three-toed woodpecker (*Picoides tridactylus* [L.]) in particular is considered an important forager on conifer and broadleaf bark beetles. In a faeces analysis of this

species the scolytid *I. typographus* amounted to 89% of the total prey (Pechacek, 1994). The effects of insectivorous birds have been discussed in an earlier paper by Otvos (1979).

A more extensive review on natural enemies of Scolytidae in general is provided by Kenis et al. (2004).

8. Susceptibility of trees

8.1. Tree level

Bark anatomy and the physiological condition of a potential host tree are crucial for the success of a bark beetle attack. Vital trees possess defense mechanisms at several levels to prevent attacking bark beetles from successfully establishing broods. These mechanisms have been studied in detail under field and laboratory conditions (Baier, 1996a,b; Rohde et al., 1996; Lieutier et al., 1997). The first level of defense is when stored resin is released upon attempted penetrations of the bark. This is referred to as primary, preformed or constitutional resistance (Paine et al., 1997). Spruces with thick bark and dense resin ducts seem to be more efficient in repelling boring attempts than thin-barked, low resin trees (Nihoul and Nef, 1992; Baier, 1996b). Trees in mixed stands had a higher primary resin flow than those in pure spruce stands (Baier et al., 2002). When the preformed resistance is exhausted, it is superseded by induced resistance mechanisms. This second level of a tree's defenses involves a change in the local metabolism around the entrance hole. Defensive chemicals such as procyanidine are produced, which impair the food quality and hence the establishment of a brood (Rohde et al., 1996). The third defense level is a systemic change in the whole tree metabolism. This leads to the production of fewer carbohydrates but more proteins, which are needed for defense. This deterioration in nutrition quality interferes with the establishment of other beetle broods. In the last defense phase, when attack densities are high, a wound reaction sets in where periderm tissue and resin ducts are newly formed. Successful bark beetle establishment is therefore considered to occur in two successive steps, i.e. first the tree's defenses are exhausted by pioneer beetles and second, final colonization of the tree occurs (Lieutier, 2002).

Trees with a medium relative sapwood growth allow more successful broods than trees with high or low growth (Baier, 1996a). Similarly, beetles breeding in trees with intermediate crown density appear to produce more progeny than beetles in trees with other crown densities (Mattanovich et al., 2001). In the latter study, breeding success could be related to several plant compounds such as sulfates, proteins and C/N ratio. Brignolas et al. (1998) found the phenolic composition of the phloem could be used as a measure of tree resistance. The cortical terpene pattern did not change between felling and colonization by *I. typographus* (Führer et al., 1992).

8.2. Stand level

It is generally agreed that pioneer bark beetles are attracted to susceptible trees by tree volatiles (primary attraction, Lindelöw et al., 1992; Tunset et al., 1993). However, on the basis of computer simulations, Byers (1996) suggested that the encounter rates between searching bark beetles and susceptible host trees are sufficiently high when beetles just travel at random, without necessarily being attracted by kairomones. Nevertheless, the exposition and age of spruce stands do seem to be related to their susceptibility to bark beetle attack. South-exposed and sunlit trees were preferably attacked, especially after abrupt increases in solar radiation levels (Lobinger and Skatulla, 1996; Jakus, 1998b). Higher proportions of spruce trees in a stand were found to enhance bark beetle attack as were trees older than 70 years, with trees over 100 years being most susceptible (Becker and Schröter, 2000).

Several risk analyses have been performed in order to assess the factors affecting the susceptibility of stands. Multiple regression analyses indicate that altitude and soil nutrients, such as nitrogen, phosphorus, and magnesium, have a significant influence on *I. typographus* attack rates (Nef, 1994; Dutilleul et al., 2000). Lexer (1995, 1997) found attack probability to depend mainly on the water supply, the proportion of stand borders exposed to south and west, the proportion of trees with heart rot, the age of stand, the trend in radial growth and the proportion of spruce. No statistical relation could be found between forest decline ('Waldsterben') symptoms and bark beetle attack (Prien et al., 1996).

8.3. What causes the tree to die?

The dieback of an infested tree is not only the result of *I. typographus* feeding but also of beetle-associated blue-stain fungi such as the *Ophiostoma* and *Ceratocystis* species (Paine et al., 1997; Lieutier, 2002). They are mainly vectored on the beetle's pronotum and elytra (Furniss et al., 1990). A number of fungal species have been found to be associated with *I. typographus* (e.g. Furniss et al., 1990; Solheim, 1993; Krokene and Solheim, 1996; Kirschner, 1998). Among different bark beetle species, *I. typographus* was found to carry more pathogenic fungi than other species (Krokene and Solheim, 1996). Attacked trees die faster than would be expected by solely phloem girdling due to larval feeding. The fungi may dry the tissue and induce tracheid aspiration or vascular plugging (Paine et al., 1997).

Recently, the mechanisms of conifer resistance, the corresponding colonization strategies of different bark beetle species, and the process of tree death have been extensively summarized by Lieutier (2002).

9. Dynamics of infestations

There are only few reports on the natural development of *I. typographus* outbreaks without control measures. The most striking example is the situation in the German National Park 'Bavarian Forest' (Weissbacher, 1999; Nüsslein and Faisst, 2000; Nüsslein et al., 2000; Heurich et al., 2001). From 1992 to 2000 spruce trees on 3700 ha were killed. This long-lasting gradation is thought to have been triggered by a combination of insufficient water supply, windthrows, and above-average temperatures. It was subsequently nurtured by further windthrows, snow breaks and heavy cone production (Nüsslein et al., 2000; Heurich et al., 2001). The outbreak declined after 2000 (Rall and Martin, 2002). Likewise, in other unmanaged spruce forests large bark beetle outbreaks occurred after the storms in 1990 (Niemeyer et al., 1995a; Becker, 1999). They stopped after a shorter time without human interventions, but still killed a considerable proportion of the spruce trees. Interestingly, four years after the onset of the outbreak in the German National Park 'Harz' maternal galleries were shorter and fewer overwintering beetles survived in

the areas without control measurements than in the areas with integrated control (Niemeyer et al., 1995a). Most of the regions with bark beetle outbreaks corresponded with those affected by the storm.

In windthrown timber, the peak of abundance of *I. typographus* depends on the desiccation process of the bark. At low elevations or in windthrows with broken trees, the peak was usually reached in the second summer after the storm. In mountain forests or with uprooted trees where the roots still had contact with the soil, the peak was rather in the third summer (Forster, 1993; Wermelinger et al., 1999; Becker and Schröter, 2000; Göthlin et al., 2000). Colonization occurs more often in broken and windthrown trees than in the remaining stumps (Feiger et al., 1996; Göthlin et al., 2000). Large trunks are infested more frequently than thin ones. The time of maximum abundance of *I. typographus* beetles in the windthrows is independent of whether the fallen wood is cleared or left (Wermelinger et al., 1999). However, the beetles are obviously much more abundant in uncleared areas.

The dynamics of an outbreak largely depends on weather, drought periods, further storms or other stressors, as well as the availability and susceptibility of host plants. The dynamics is also driven by negative feedback mechanisms such as intraspecific competition. It has been demonstrated that the number of larvae decreases with increasing density of maternal galleries (Anderbrant, 1990; Schopf and Köhler, 1995). Another negative feedback may be the lethal impact of natural enemies, which seems to increase with time (Wermelinger, 2002).

The spatial development of outbreaks is difficult to predict and findings are controversial. New attacks have been reported both as independent of old infestations (Schröter, 1999) or infested windthrows (Peltonen, 1999), as well as more frequent in the vicinity of old spots (Wichmann and Ravn, 2001; see Section 6). In this context the current level of susceptibility of potential host trees plays a major role.

10. Management of *I. typographus*

The aim of managing bark beetles is to minimize attacks on living trees. The measures most commonly applied for this purpose are clearing windthrows,

sanitation felling of infested trees, and the installation of trapping devices.

10.1. Salvage

Salvage in this context involves the harvesting of windthrown timber, i.e. the preventive removal of breeding substrates, as well as the sanitation felling of infested standing trees. Timely removal of windthrown timber is an important factor in the integrated management of *I. typographus*. Spruce logs should, if possible, be removed from the windthrows before following midsummer after the windthrow (Göthlin et al., 2000). A Danish study (Wichmann and Ravn, 2001) showed that the density of attacks of standing trees around a windthrow area was least when the timber was harvested between the infestation of the logs after the spring flight and the emergence of the new generation. The logs acted then as trap trees, and the resulting bark beetle progeny were killed. However, this is often too short a time span for a complete clearing of large windthrows. On-site debarking, which is a potential alternative, is hardly less time-consuming and elaborate.

Sanitation felling of infested trees is the most widespread measure to defeat *I. typographus*. This procedure is effective provided that (a) the trees are cut before the adult beetles emerge; (b) the logs are debarked before storing in or near the forest or alternatively removed from the forest; and (c) the brood is disposed of in some appropriate way if there are teneral beetles present in the bark. This can be done by burning or chipping. With debarking machines, the mortality of beetles was found to be 93%. At high densities, this is considered to be still too low (Dubbel, 1993).

10.2. Trapping

Pheromone traps are used as surrogates for trap trees. A key component of the pheromone lures is cis-verbenol (e.g. Jakus and Blazenec, 2002). The number of bark beetles caught in pheromone traps very much depends on environmental and local conditions, such as temperature, exposition, sun exposure, and competition from nearby woody debris, slash, log stacks, windthrows, and susceptible trees (Lobinger, 1995). Traps exposed to the south,

for example, were found to catch four times more *I. typographus* than those exposed to the north (Lobinger and Skatulla, 1996). Yearly catches could be correlated with the previous year's temperatures in May and June (Bakke, 1992). Most authors question the efficiency of pheromone traps as a measure for reducing bark beetle populations (Dimitri et al., 1992; Lobinger and Skatulla, 1996; Wichmann and Ravn, 2001). It has been calculated that only up to 10% of a population are caught with high trap densities (Weslien and Lindelöw, 1990; Lobinger and Skatulla, 1996). In one study 24 traps per hectare caught only an estimated 3% of the population (Lobinger and Skatulla, 1996). A total of 270,000 traps were used during an outbreak in a Swedish province, but the breakdown of *I. typographus* in the early 80's was not attributed to this measure (Weslien, 1992a). Wichmann and Ravn (2001) found no correlation between trap catches and the density of tree attack around the traps, in contrast to earlier findings by Weslien et al. (1989). High trap catches did not necessarily correlate with high infestations, but low catches usually meant that little damage would occur (Weslien, 1992b; Lindelöw and Schroeder, 2001).

Traps are more often used to prevent attacks on living trees than to diminish *I. typographus* populations. This approach is often regarded a reasonable protection measure (Niemeyer et al., 1990; Dubbel et al., 1995; Jakus, 2001), although it involves considerable effort (Dimitri et al., 1992; Jakus, 1998a). Jakus (1998a) reported that an infestation front came to a standstill after one year when a two-row barrier of pheromone traps was used. Unfortunately, there was no simultaneous control treatment in this study. Trap trees, which were used more often before pheromones became commercially available, proved to be up to 14 times more efficient in trapping beetles than artificial traps (Drumont et al., 1992). In Belgium living trap trees baited with pheromones and treated with insecticides are still common. This kind of trap tree caught up to 30 times more beetles than the widespread Theyson[®] trap (Raty et al., 1995), especially when the bait was protected from the sun. Extensive application of trap trees has also been reported to protect windfalls, with the number of trap trees being dependent on the previous year's number of attacked trees (Grégoire et al., 1997).

10.3. Further techniques

Conventional chemical insecticides are mostly used to protect stored timber. Their application varies according to the legislation in different countries. Systemic chemicals have been reported to protect single susceptible trees (Dedek and Pape, 1990; Bombosch et al., 1992; Bombosch and Dedek, 1994).

Biological agents, which are partly established in agriculture, have not yet been commercially applied against the spruce bark beetle. Among pathogens the fungus *Beauveria bassiana* (Bals.) Vuill. has been tested for biological control (Vaupel and Zimmermann, 1996; Kreutz, 2001). The offspring production of females contaminated with fungal spores in modified pheromone traps was up to 53% of the control. However, the fungus was not passed on to the progeny (Vaupel and Zimmermann, 1996). There are technical and ecological limitations to the application of spores to timber or to the forest litter containing overwintering *I. typographus*.

10.4. Managed forests and forest reserves

Unmanaged spruce forests do not necessarily have higher populations of *I. typographus*. In a Swedish study (Schlyter and Lundgren, 1993), bark beetle densities were similar or even lower than in surrounding managed forests. However, after disturbances, such as storms or fire, the populations in unmanaged forests are very likely to rise to epidemic levels (Schlyter and Lundgren, 1993).

Large infestation spots are said to pose a threat to adjacent stands up to approximately 500 m away (Schröter, 1999; Wichmann and Ravn, 2001). Intensely managed forests that are adjacent to forest reserves are supposed to have a higher risk of bark beetle infestation (Becker, 1999). However, this is presumably not exclusively the result of emigration of beetles from the reserves. When a storm triggers an outbreak in a reserve, it most probably also weakens the adjacent stands. Thus, these stands are more susceptible to attack and have probably fostered their own local *I. typographus* populations as well.

In some cases (e.g. in the German National Parks 'Bavarian Forest' and 'Harz') phytosanitary protection zones have been established around reserves with *I. typographus* gradations. The control of the beetles in

these buffer zones has proven difficult and labor-intensive because of the size of the area to be monitored and the continuing supply of beetles from the reserve. In practice, buffer zones between 100 m (Niemeyer et al., 1995a) and 1500 m (Heurich et al., 2001) have proven efficient and prevented significant attacks in adjacent managed forests.

A sustainable strategy to reduce the risk of *I. typographus* attack in managed spruce forests in the long term is to reduce the proportion of spruce and to form heterogeneous stands. Multi-tree species forests are often less susceptible to bark beetle attack. This may be the result of there being fewer and less susceptible host trees, of natural enemy effects, or of volatiles of non-host trees interfering with bark beetle pheromone communication (Byers et al., 1998; Zhang et al., 1999).

10.5. Risk assessment

From the forest manager's point of view it is crucial to assess the risk of a stand being attacked by *I. typographus*. For this purpose different approaches have been used including GIS and regression analyses (Lexer, 1995; Dutilleul et al., 2000; Wichmann and Ravn, 2001). Stands at most risk were those neighboring windthrows harvested after the first beetle generation and those within 500 m of an old attack (Wichmann and Ravn, 2001). Pheromone traps are not a reliable means of evaluating the risk (cf. Section 10.2). However, several site and silvicultural characteristics seem to be related to attack probability (mainly water availability and slope, Lexer, 1995). Physiological predictors at the single tree level (water status, nutrients, phenolics, resin; cf. Section 8.1) seem to be less suited for the risk assessment of complete stands.

11. Discussion

The spruce bark beetle *I. typographus* is an essential component of every spruce forest ecosystem. As a pioneer it colonizes dying and newly dead trees and thus starts the decomposition of bark and wood. As a typical r-strategist, it is able to exploit short-lived resources and to rapidly multiply, e.g. after windthrows, to extremely high numbers. When the fallen

logs are too dry for breeding, the large populations are forced to infest living, apparently vital spruce trees. In such epidemic situations *I. typographus* can pose a serious threat to forests rich in spruce, especially to planted stands outside their optimum area range.

Most of the biological characteristics of *I. typographus* are well known, apart from topics such as overwintering behavior or various aspects of sister brood production. Despite this knowledge, the population dynamics of *I. typographus* is far from fully understood and even farther from being predictable. To a large extent, this is due to the uncertainty of the weather and of other decisive events, such as storms or drought. In addition, the recovery process of weakened spruce trees, e.g. after strong winds, is difficult to assess and depends on the weather as well. Furthermore, human control measures affect the survival of bark beetles and their antagonists, as well as host availability and susceptibility. In practice, the efficacy of control measures varies greatly, depending on whether they are carried out in time and thoroughly enough.

Outbreaks are usually caused by disturbances or extreme weather conditions. Extensive windthrows in spruce forests almost inevitably give rise to subsequent outbreaks of *I. typographus*. The populations first develop in the fallen timber and then the beetles attack living trees along adjacent stand borders and elsewhere in the forest nearby. Strong winds creating large windthrow areas also cause scattered windthrows in the vicinity and presumably also constitute a significant stress to the remaining standing trees. *I. typographus* populations can build up not only in large windthrows but also locally within the stand. The higher the pressure of *I. typographus* on the trees, the less susceptible the trees need to be for an attack to be successful. The further course of the outbreak depends on the regulatory influence of natural enemies and sanitation measures and in particular, on the susceptibility of the remaining trees. This in turn depends to a large extent on the weather since drought or wind are additional stresses on the trees recovering from the storm. Given 'normal' conditions an outbreak usually lasts between three and six years. For a better understanding of this dynamics, existing risk analysis models from the viewpoint of the host trees should be combined with models of bark-beetle population dynamics. On a regional scale, the spatial develop-

ment of infestations can be analyzed by GIS and multiple regression techniques, to explore potential correlations between climatic, stand specific, and phytosanitary factors and the infestation dynamics. These techniques provide valuable tools for risk assessments by pinpointing the most significant driving variables behind outbreaks. It might be possible to control some of these by forest management.

There are various strategies for minimizing the loss of spruce due to *I. typographus*. Pheromones and other semiochemicals are considered as just one among several components in integrated control. Pheromone traps can be useful for protecting susceptible stand borders and for monitoring. However, trap catches are not only a measure of the abundance of *I. typographus* but also of the traps' attractiveness relative to nearby natural pheromone and kairomone sources. Anti-aggregation pheromones or mating disruption techniques are still in the early stage of development. However, it is questionable whether such techniques would be applicable and efficient on a large scale, and their impact on the ecosystem still has to be evaluated.

Salvage or 'clean management' is the oldest and at present still most efficient strategy. However, the success of windthrow clearing and sanitation felling largely depends on their timely and thorough accomplishment. In many cases, this in turn depends on the financial and human resources available and on timber prices. The economic situation, changes in forest functions, and ecological considerations, such as promoting dead wood, generating a more natural stand composition, and enhancing biodiversity, have prompted various private and public forest owners to refrain from taking control measures in specific situations. Methods to identify the least spatial unit that allows efficient control measures and minimum measures required to ensure particular forest functions are fulfilled still need to be developed.

Natural enemies probably play an important role in endemic situations and towards the end of an outbreak. Like *I. typographus*, they also greatly depend on the weather. We need to find out more about the efficiency of antagonists in various forest compositions, and their temporal population dynamics relative to that of *I. typographus*. It is unlikely that these natural enemies will ever be employed in the sense of classical biological control. Rather, understanding the interactions between bark beetles, antagonists, host plant and

control measures will guide silvicultural practices to sustain and increase the regulatory capacities of natural enemies.

In the long run, the most reliable and ecologically sound strategy to confine outbreaks of *I. typographus* will involve habitat management, i.e. silvicultural adaptations. The key question is how to reduce the susceptibility of forests and spruce trees. One way to reduce the susceptibility of a forest is to transform uniform spruce stands into more diverse ecosystems. Forests with highly diverse tree composition, age structure, and ground vegetation have a different tree physiology and are more resistant to windthrow and bark beetle attack (cf. Jactel et al., in press). Where pure spruce forests are to be maintained for economic reasons, factors affecting tree and stand susceptibility will have to be considered. The physiological state of potential host trees and of course, the weather is crucial for a successful attack by *I. typographus* and for the dynamics of an outbreak. Many of the key factors are difficult or even impossible to manage, e.g. altitude, soil nutrients, tree growth characteristics, and resin production. Others, such as stand age, fungal infection risk, or tree provenances, are more readily manageable through silvicultural practices. However, non-autochthonous spruce stands will always be prone to bark beetle infestations, even more so as global change is very likely to alter the tree/bark beetle system. How changes in temperature, precipitation and wind regimes will affect the individual host tree, the stand, the spruce bark beetles and their natural enemies is open to speculation. It would be worthwhile to model in an explorative way various scenarios of this complex system, so as to be better prepared for managing bark beetle outbreaks in the future.

Acknowledgments

I thank J. Bucher, B. Forster, R. Gall, and two anonymous reviewers for valuable comments on earlier versions of the manuscript. Silvia Dingwall kindly checked the English writing.

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