

# Assessing the role of bark- and wood-boring insects in the decline of Scots pine (*Pinus sylvestris*) in the Swiss Rhone valley

B. WERMELINGER, A. RIGLING, D. SCHNEIDER MATHIS and M. DOBBERTIN Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

**Abstract.** 1. In several dry inner Alpine valleys higher mortality levels of pine have been observed in recent years. This paper evaluates the role of xylophagous insects in the current pine decline and the influence of climate change on the infestation dynamics.

2. More than 200 trees of different levels of crown transparency (needle loss) were felled between 2001 and 2005 and sections of them incubated in insect emergence traps. Colonisation densities were related to the transparency level of each host tree at the time of attack.

3. Trees with more than 80% needle loss were colonised most frequently, but the breeding density was highest in trees with 65–80% needle loss.

4. The scolytine *Ips acuminatus* and the buprestid *Phaenops cyanea* colonised trees with 30–90% needle loss in high densities. The bark beetle *Tomicus minor* was less aggressive, preferring trees with 60–85% needle loss. The hymenopteran *Sirex noctilio* and the cerambycid *Acanthocinus aedilis* were restricted to greatly weakened trees with 50–85% needle loss. Most species colonised trees that had experienced a decline in vigour, that is an increase in crown transparency shortly before attack.

5. The infestation dynamics of *P. cyanea* covaried with the drought index as well as with temperature.

6. Increased temperatures not only trigger a drought stress rendering the host trees susceptible to insect attack, but also accelerate insect development. As more frequent drought periods are likely as a result of climate change, even trees only slightly or temporarily weakened will be more subject to attack by aggressive species such as *I. acuminatus* and *P. cyanea*.

**Key words.** Bark beetles, climate change, crown transparency, drought, needle loss, pest insects, pine decline.

## Introduction

Since the 1990s, high mortality rates of Scots pine (*Pinus sylvestris* L.) have been observed in central Valais, the dry inner Alpine Rhone valley in South-western Switzerland. In a previous similar incidence in the late 1970s, pine decline could be partly attributed to fluorine air pollution originating from the nearby, upwind aluminium plants (Flühler *et al.*, 1981). The current wave of pine decline obviously has different causes

because filters have been installed in the aluminium plants. Moreover, a similar phenomenon is apparent in other regions in Valais, as well as in other dry valleys in the Central Alps in Austria and Italy (Vertui & Tagliaferro, 1998; Rigling *et al.*, 1999).

A research programme was started in 2001 to elucidate the various aspects of the pine decline in the Valais (Rigling *et al.*, 2006). The projects addressed various issues such as the influence of temperature and drought (Dobbertin *et al.*, 2005; Bigler *et al.*, 2006; Eilmann *et al.*, 2006), genetic variation of the trees (Fournier *et al.*, 2006), tree competition (Weber *et al.*, 2005), silvicultural history (Gimmi & Bürgi, 2007), mistletoe (Dobbertin & Rigling, 2006), fungi, nematodes (Polomski *et al.*,

Correspondence: Beat Wermelinger, Swiss Federal Institute WSL, Zuercherstrasse 111, CH-8903 Birmensdorf, Switzerland. E-mail beat.wermelinger@wsl.ch

2006), and insects (Wermelinger *et al.*, 2006; Dobbertin *et al.*, 2007).

Regarding climate, central Valais experiences an annual precipitation of 500–1000 mm and is the driest region in Switzerland. While no significant change in the rainfall pattern during the past 100 years has been observed in this region (Rebetez & Dobbertin, 2004), temperatures have clearly increased (Begert *et al.*, 2005) with more days with a mean temperature  $>20$  °C during the past 25 years (Rebetez & Dobbertin, 2004). Higher temperatures have been shown to result in an elevated drought stress under these climatic conditions (Zweifel *et al.*, 2007). This reduces the vigour of the trees, increases their susceptibility to insect attack (Mattson & Haack, 1987; Rouault *et al.*, 2006) and enhances the survival of bark living insects (Caldeira *et al.*, 2002). At the same time, higher temperatures induce the insects to develop faster and to reproduce more successfully, which leads to an increase in their infestation pressure (e.g. Wermelinger & Seifert, 1999; Bale *et al.*, 2002; Gan, 2004). Given the pronounced climate change in Switzerland (cf. Fuhrer *et al.*, 2006), the question arises as to the role of insects in the current pine decline observed in many dry Alpine valleys. Reports of insect-related pine mortality in Valais have increased (Dobbertin *et al.*, 2007), but the spatial pattern of pine mortality does not include typical bark beetle infestation spots. Many dying pine trees have apparently experienced no insect attack. Thus, it remains unclear to what extent insects are the cause of the pine decline or whether they are just a consequence of reduced tree vigour.

Forest decline is generally attributed to complex interactions among biotic and abiotic stresses (Erbilgin & Raffa, 2002). One forest decline model, which we refer to as the Manion concept, distinguishes between predisposing, inciting and contributing factors (Manion, 1981). The predisposing factors are usually long-term influences such as climatic stress, while insects may be attributed to the short-term inciting factors or to the long-term contributing factors, depending on the *aggressiveness* of the species involved. While the resistance of trees has been acknowledged for a long time to be a crucial factor for the success or failure of bark beetle attack (Berryman, 1989; Wagner *et al.*, 2002), less is known about the *vigour threshold* below which insects are able to overcome the resistance of a tree. Furthermore, the assessment of the impact of climate change on phloeophagous species has hardly started. The present study therefore aims first to investigate the role of insects developing in the bark and wood of pine trees with various levels of needle loss as a surrogate for tree vigour (cf. Discussion). Second, we relate the infestation dynamics to climatic variables such as temperature and the resulting drought stress.

## Material and methods

Two locations in the Swiss Rhone valley (Canton Valais) were selected for the investigations. One stand was at Stalden (Swiss coordinates 634100/121200), situated along the western slope of a tributary valley of the main Rhone Valley with a 50% incline and an elevation of 900 m a.s.l. This stand consisted mainly of 50- to 170-year-old Scots pines with a yearly mortality rate of

about 1.4% during the past 4 years, mixed with some scattered broadleaves such as birch (*Betula pendula* Roth) and downy oak (*Quercus pubescens* Willd.). Within this forest, an area of roughly 1.2 ha was selected in which some 250 dominant and co-dominant pine trees were marked and numbered. The second stand was located at Salgesch (611000/130200), on the southern slope of the Rhone Valley at 900 m a.s.l. and with a 50% incline. It was composed of 80- to 180-year-old Scots pines, again mixed with some scattered broadleaves, and with fewer dead trees than at Stalden but with higher mortality rates (3.6%) during the 4 years under study. In this forest, an area of roughly 1 ha was selected and again 250 dominant and co-dominant pine trees within this area were marked. The two locations were approx. 25 km apart from each other.

The crown transparency (=needle loss) of the 500 marked trees was first assessed in winter 2001 according to standardised criteria used in the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests) (Eichhorn *et al.*, 2006). The transparency was visually assessed by experts twice a year using standard reference photographs (Müller & Stierlin, 1990), that is in December/January and in April/May, with a precision of 5%. Here, 0% needle loss means a fully foliated tree, 100% means a dead tree without needles. As the project proceeded, increasingly more information became available about the needle loss history of each single tree. The transparency values were assigned to five classes (different from the ICP-classes): healthy (0–20%), slightly weakened (25–40%), moderately weakened (45–60%), greatly weakened (65–80%), and moribund (85–100%). After each assessment, trees from the last four classes were randomly selected for felling.

Between 2001 and 2005, eight samplings of pines were conducted. Each year one sampling was carried out in February and another in May (May only in 2001, February only in 2005), to catch all bark and wood insect species regardless of their life cycle. Every year, 34–46 trees 12–45 cm in diameter at breast height were cut or uprooted (approximately 40% of all marked trees). From each tree, two 75-cm sections from the trunk and two thick sections of branches of the same length were cut and transferred to the laboratory. After measuring their exact length and diameter, all parts of each tree were placed in photo-electors (emergence traps) situated in a greenhouse with ambient temperature. The photo-electors consisted of metal cabinets, with a tube at the bottom and another at the top leading into transparent plastic box traps (elector boxes). The two tubes ensured sufficient air circulation to prevent fungal growth. The traps were filled with water containing a biocidal agent (Dodigen 226, Clariant, Huerth, Germany). Upon emerging in the dark cabinets, the phototactic insects headed for the daylight coming in from the elector boxes and became trapped inside the boxes. The tree parts were kept in the electors until the end of the year and then replaced by logs from the next harvest. In total, 209 tree samples were incubated during the 5 years under study. Their distribution among needle loss classes is indicated in Table 1. Depending on temperatures in the greenhouse, the logs were sprayed with water to prevent too severe desiccation. The elector boxes were emptied at regular intervals. The trapped insects were first sorted according to given taxonomic levels and subsequently identified by specialists to the species level.

**Table 1.** Emergence of the most abundant bark- and wood-feeding insects from trees with four levels of needle loss (as at harvest) at the two locations, Salgesch and Stalden.

Needle loss:	Salgesch				Stalden				Total
	25–40%	45–60%	65–80%	85–100%	25–40%	45–60%	65–80%	85–100%	
Number of sampled trees	34	30	14	26	33	40	11	21	209
Anobiidae	2	2	5	72	48	37	11	18	195
<i>Ernobius mollis</i> (L.)	—	1	5	72	35	11	11	10	145
Buprestidae	—	—	15	155	—	—	—	67	237
<i>Phaenops cyanea</i> F.	—	—	14	153	—	—	—	67	234
Cerambycidae	—	4	35	58	—	2	4	24	127
<i>Acanthocinus aedilis</i> (L.)	—	—	35	25	—	1	4	15	80
Curculionidae	6	12	50	182	7	16	9	52	334
<i>Pissodes piniphilus</i> Hrbst.	—	—	49	130	—	—	1	35	215
Scolytinae (Curcul.)	13	20	2092	1161	144	59	550	490	4529
<i>Ips acuminatus</i> (Gyll.)	2	—	977	86	42	—	—	14	1121
<i>Orthotomicus longicollis</i> (Gyll.)	—	—	100	198	1	—	65	137	501
<i>Tomicus minor</i> (Hartig)	1	16	842	323	34	7	473	226	1922
Siricidae	—	—	37	68	—	—	—	215	320
<i>Sirex noctilio</i> F.	—	—	37	68	—	—	—	215	320
Total insects	21	38	2234	1696	199	114	574	866	5742

In this paper, the taxa with xylophagous feeding behaviour and potential pest status were analysed, that is Anobiidae (anobiid beetles), Buprestidae (jewel beetles), Cerambycidae (longhorned beetles), Curculionidae (weevils), Scolytinae [bark beetles; traditionally the family Scolytidae, now a subfamily of Curculionidae (Marvaldi & Morrone, 2000)], and Siricidae (wood wasps). The most frequent key species making up more than 60% of all individuals within each family were analysed in more detail. The number of emerged individuals was expressed as density, that is the number of individuals per m<sup>2</sup> bark surface of the infested tree parts. For statistical analysis, the insect densities were log-transformed and subjected to an ANOVA with a Scheffé *post hoc* test (DataDesk®).

The host tree condition (expressed as the level of needle loss) preferred by the key species was identified as the crown transparency level at the time of attack. From the literature, the presumed developmental time (from egg to adult emergence) of each species under the climatic conditions in Valais was assessed as: 0.5 year for *Ips acuminatus*, *Orthotomicus longicollis*, and *Tomicus minor*, 1 year for *Ernobius mollis*, *Phaenops cyanea*, *Acanthocinus aedilis*, and *Pissodes piniphilus*, 1 or 2 years for *Sirex noctilio* (cf. Results). *Tomicus minor* is actually a monovoltine species, but it emerges in the summer after oviposition in spring and therefore has a developmental time of 0.5 years. It then performs maturation feeding and overwinters in the shoots or the litter. Subsequently, for each species, the transparency of each tree at the time of attack was defined based on each insect's developmental time and the transparency history of each tree. For trees harvested at the very beginning of the investigation, the previous transparency history was, of course, not available.

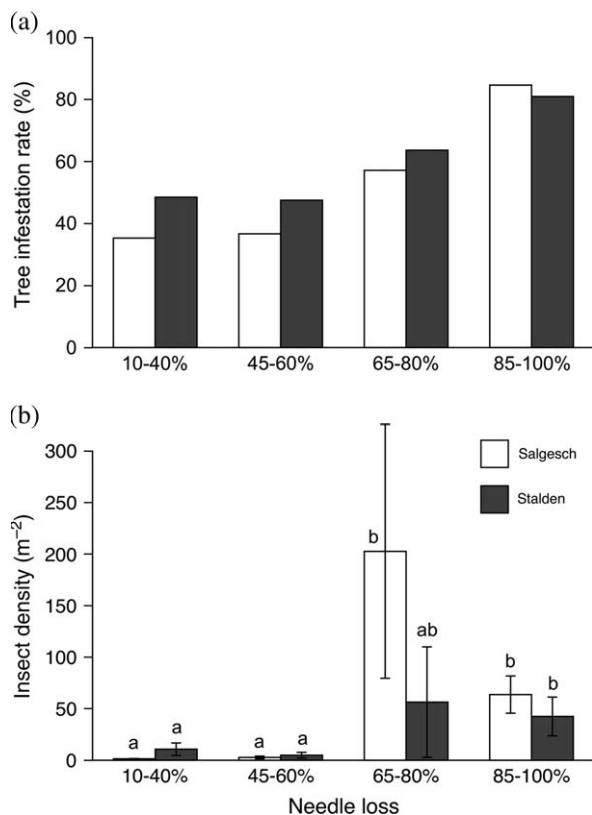
The drought index used in Fig. 7 was computed as the difference between the monthly precipitation and the potential evapotranspiration (Thorntwaite, 1948). The heat sum represents accumulated day-degrees >0 °C (sum of daily temperature means).

## Results

A total of 5742 individuals of the xylophagous families under study (cf. Table 1) emerged from trees of all classes of needle loss. From the 209 trees sampled, 97 trees were uncolonised. There were insect-free pines in all crown transparency classes (Fig. 1a; for the naming of the classes, see Methods), but with a trend for the infestation rates to be higher on trees with elevated needle loss. Even among the moribund trees, almost 20% showed no insect infestation. The two locations revealed no marked or consistent difference.

A much more distinct pattern was, however, observed with insect densities in attacked trees (Fig. 1b). Significantly more insects emerged from greatly weakened and moribund trees than from less affected trees. No significant differences were found between greatly weakened and moribund trees, although at Salgesch infestation clearly peaked in trees with 65–80% needle loss. The large variation in this transparency class was because of two trees with an extremely high infestation by *T. minor* and partly *I. acuminatus*. The insect densities at the two locations did not differ significantly. Exactly the same distribution among classes was obtained when insect density was related to the bark surface of all sampled trees (including uninfested ones) instead of infested trees only (data not shown).

The key species (cf. Methods) in each family were investigated in more detail. In order to assess the preferred range of host tree needle loss of each insect species, that is its aggressiveness, the needle loss of each tree at the time of attack was plotted against resulting insect emergence (offspring production; Fig. 2). The anobiid *E. mollis* appeared to colonise trees with a wide range of needle loss levels except the moribund ones. As this species develops in the outer dead bark layers rather than in the living phloem, the physiological condition of the host seems to be largely irrelevant for colonisation. Infestation of a



**Fig. 1.** (a) Infestation rates of the sampled trees ( $n = 209$ ) by xylophagous insects (Anobiidae, Buprestidae, Cerambycidae, Curculionidae, Scolytinae, Siricidae) at the two locations, Salgesch and Stalden; (b) colonisation density (mean  $\pm$  SE) of the infested trees with four levels of needle loss; columns with different letters differ significantly ( $P < 0.05$ ).

tree with *E. mollis* does not affect tree vigour. The cerambycid *A. aedilis* showed a clearly defined preference: Only greatly weakened hosts with needle losses between 70 and 85% were colonised. An almost identical preference pattern was found for the bark beetle *O. longicollis*, which also attacked greatly weakened trees almost exclusively.

The only non-coleopteran species relevant in this context is the hymenopteran wood wasp *S. noctilio*. According to the literature, this species has a generation time of 1–3 years. Because in our situation generation time is most likely 2 years or at best 1 year (Eichhorn, 1982), the offspring density is presented for both cases (Fig. 2). Possibly both generation times occur at the same time, depending on the host quality. *S. noctilio* also attacks trees with little more than 50% needle loss, but preferably colonises heavily defoliated trees.

The weevil *P. piniphilus* tunnels in the phloem and pupates in the wood surface (Day *et al.*, 2004). It was found to infest only moderately and greatly weakened hosts, reaching its highest reproduction rate at 70–80% needle loss. An even wider range of host crown transparency was found for the bark beetle *T. minor*. While most of the attacked trees suffered from a needle loss of 50% and more, one tree with only 30% showed a fair amount of

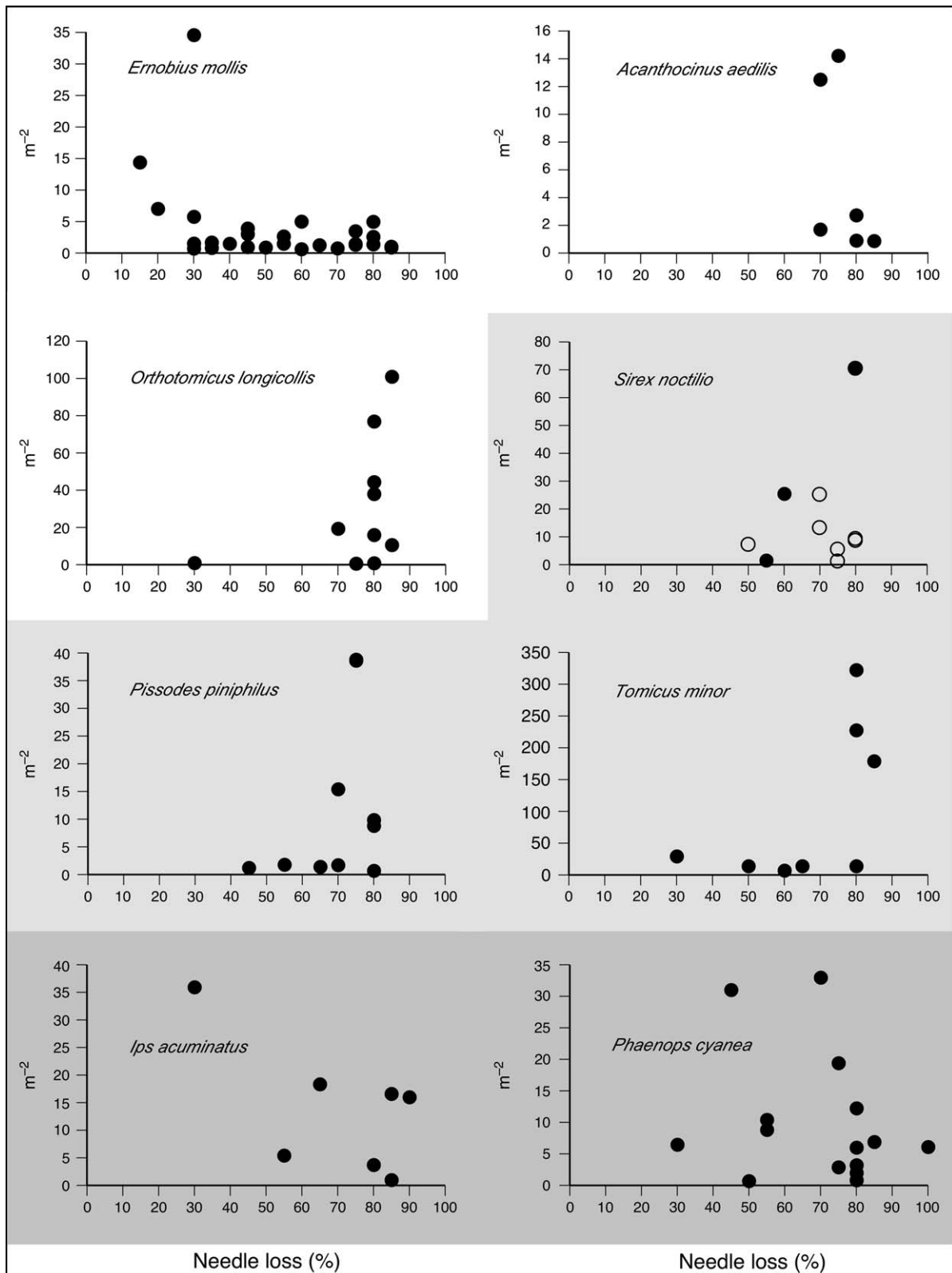
*Tomiscus* emergence. On the other hand, peak emergence was found in greatly weakened trees where offspring production was extremely high. The congener *Tomiscus piniperda*, with a very similar biology, was 10 times less abundant than *T. minor*.

The bark beetle *I. acuminatus* appeared to have the same infestation range as *T. minor*, although it produced its maximum offspring in one tree with only 30% needle loss. Likewise, the buprestid *P. cyanea* started colonising only moderately weakened trees with needle losses well below 50%. At the same time, this buprestid was able to breed in an extremely wide range of tree conditions with needle losses between 30 and 100%.

In an attempt to rank the species according to their aggressiveness, that is their ability to successfully attack trees of different susceptibility levels, they were grouped in three categories (shading in Fig. 2). Three species were assigned a *non-aggressive* behaviour: *E. mollis*, which feeds in the dead bark and therefore does not affect tree vigour, and the cerambycid *A. aedilis* and the bark beetle *O. longicollis*, which feed only on greatly weakened or moribund trees. The wood wasp *S. noctilio*, the weevil *P. piniphilus*, and the bark beetle *T. minor*, which generally attack hosts with 50% or more needle loss, were classified as *moderately aggressive*. The most *aggressive* species were the bark beetle *I. acuminatus* and the buprestid *P. cyanea*. Both species also infested trees with less than 50% needle loss.

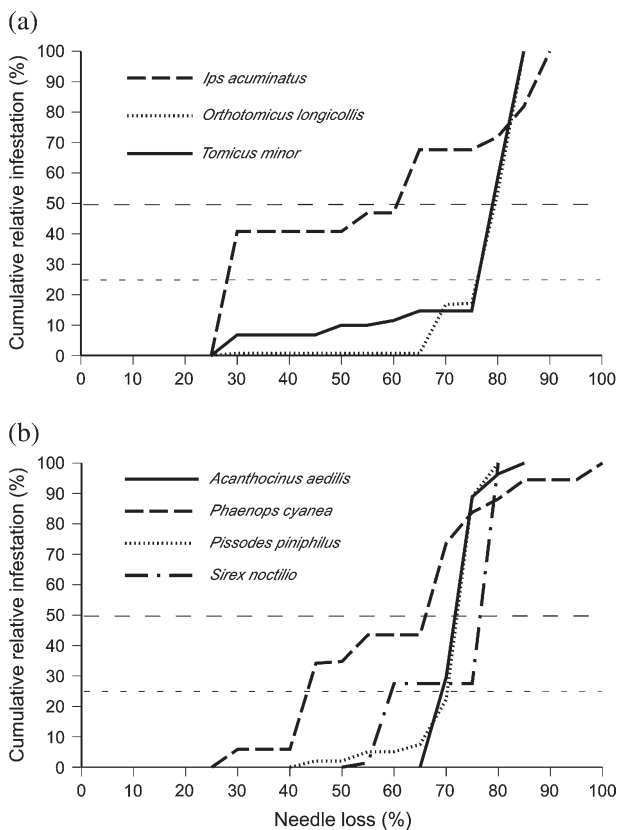
The theoretical colonisation sequence of a model tree is depicted in Fig. 3. It shows insect colonisation as the declining tree suffers from increasing loss of needles. As *E. mollis* did not exhibit a distinct preference for crown transparencies (Fig. 3), it is not included. The curves represent the proportions of total offspring production that accumulated up until the death of the tree (100% needle loss). To compare the aggressiveness of the different species, it is convenient to consider given infestation thresholds, for example 25 and 50% (horizontal dashed lines). For example, the intercept of the 50% threshold with the colonisation curves indicates the degree of needle loss at which 50% of the final colonisation is reached. In agreement with the previous findings, *I. acuminatus* was the first bark beetle to reach this threshold (Fig. 3a) and *P. cyanea* the first other insect species (Fig. 3b). This characteristic was even more pronounced at the 25% infestation threshold. *Ips acuminatus* reached it already in trees with less than 30% needle loss, which is a much lower level of needle loss than that of the other bark beetles (Fig. 3a). The second species to reach this threshold was *P. cyanea* (Fig. 3b), again confirming the earlier assessment of this species (Fig. 2).

For xylophagous insects, the rate (velocity) of deterioration of the physiological status of a host tree, rather than the absolute levels of needle loss, might be crucial. For this reason, offspring production was plotted against the difference between the crown transparency level of a given tree at the time of attack and that half a year previously (Fig. 4). This means that, if this difference is a positive number, transparency increased during the half year before attack. It is negative if transparency decreased, that is, if tree needle production increased before attack (recovery). The response of the most important insect species to transparency change is depicted in Fig. 4. All of them preferred trees that recently lost needles or showed no change at all. As an exception,



**Fig. 2.** Offspring production per m<sup>2</sup> bark surface of the key insect species in trees with different levels of needle loss at the time of attack. *Sirex*: assumed generation time = 1 year (open circles) or 2 years (black dots). The background shading identifies different levels of insect aggressiveness in tree colonisation: white = non-aggressive, light grey = moderately aggressive, dark grey = aggressive.



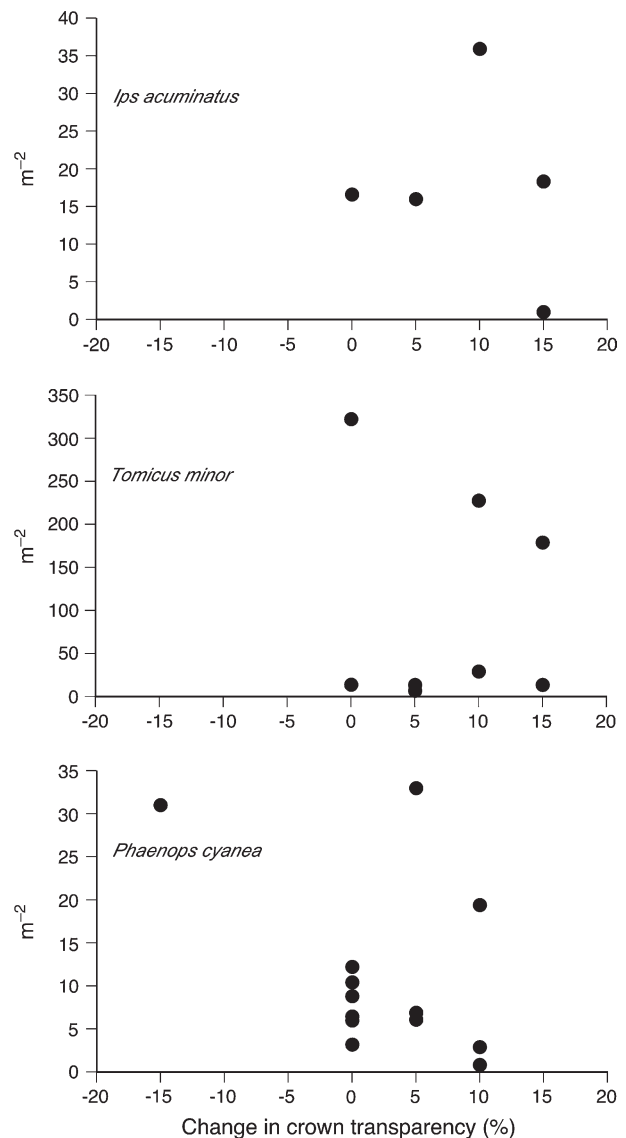


**Fig. 3.** Infestation dynamics (cumulative proportions of insect densities) during the gradual decline of a model tree. (a) bark beetles, (b) other insects.

one tree suffering from a very high *P. cyanea* infestation had improved its needle density by 15% before colonisation. An increase in needle density (decrease in crown transparency) may be attributed to two possible causes: either (i) an assessment error of at least 10% in one of the two assessments that occurred (Dobbertin *et al.*, 1997), or (ii) the increase in needle density is the result of the formation of a significant number of new needles. As the assessment experts have frequent training courses and their measurements are regularly calibrated, an increase in needle density of this order of magnitude is more likely to be the result of an improvement in the tree condition than of measurement error.

The other insect species showed heterogeneous patterns (data not shown). The beetles *A. aedilis*, *E. mollis*, and *P. piniphilus* were present in trees irrespective of their change in transparency, while *O. longicollis* preferably attacked trees that had deteriorated. For the wasp *S. noctilio* only two data points were available. An extremely high offspring production was found in one tree that had increased needle loss from 45 to 80% during the half year before the attack. The majority of all the trees investigated did not change in transparency 1 year before they were cut.

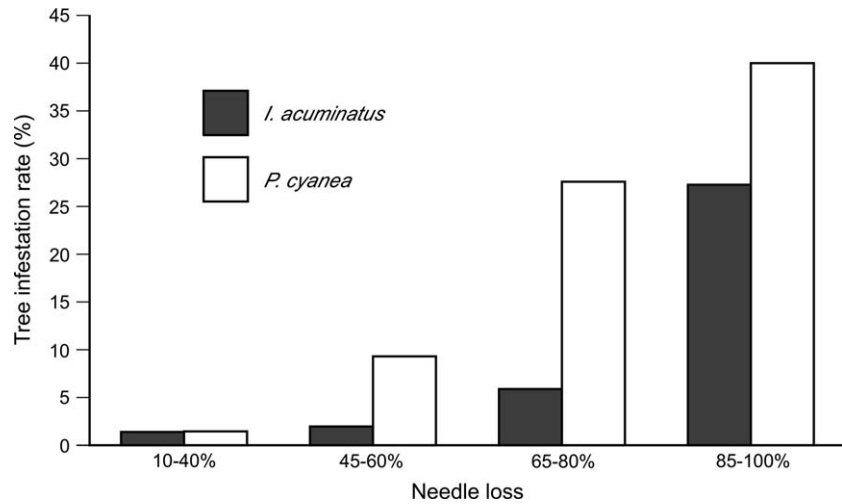
Although the two species *I. acuminatus* and *P. cyanea* turned out to be the most aggressive insects, they did not attack all of the weakened trees (Fig. 5). The colonisation rate strongly



**Fig. 4.** Emergence of the bark beetles *I. acuminatus* and *T. minor*, as well as of the buprestid *P. cyanea*, from host trees with different changes in crown transparency (needle loss) half a year before attack. Positive x-values indicate an increase in transparency, negative values a decrease in transparency, that is an increase in needle density.

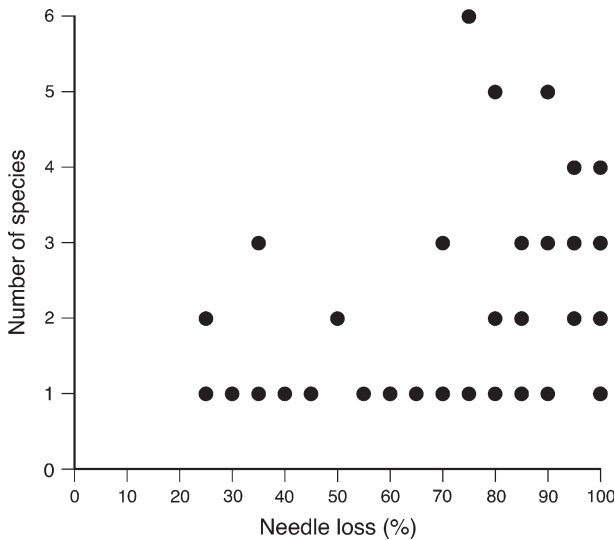
depended on the level of needle loss, and in moribund trees they were found in at most 40% (*Phaenops*) and 27% (*Ips*) of all pines. Only one single tree was attacked by both species. About 15–20% of the trees of the highest transparency class were not colonised by either species under study (cf. Fig. 1a).

Almost half of all trees were colonised by just one of the eight key species. In 25% of the trees only *E. mollis* was present. At the other end of the scale, only 6 out of the 64 trees infested by key species were colonised by as many as five or six species (data not shown). The number of species colonising trees with different crown transparency levels confirms the general infestation pattern: moderately and greatly weakened trees



**Fig. 5.** Proportion of pine trees infested by *Ips acuminatus* and *Phaenops cyanea* with different levels of needle loss.

(25–70% needle loss) supported one to three insect species, whereas in trees with more than 75% needle loss up to six species were found (Fig. 6). An analysis of the species involved in trees colonised by  $n = 1 \dots 6$  concurrent species did not reveal obvious patterns (data not shown). The most conspicuous species was *E. mollis*, which was present in many trees with only one or two insect species but was missing in most trees with four to six species. It therefore did not appear to be very competitive. Similarly, *P. cyanea* colonised trees mostly as single species or concurrently with only one or two other species. This pattern, however, is brought about by the fact that this buprestid is a pioneer in attacking weakened trees. In high densities, however, it mostly kills them quickly, thus eliminating them as hosts for other species that favour severely weakened trees.



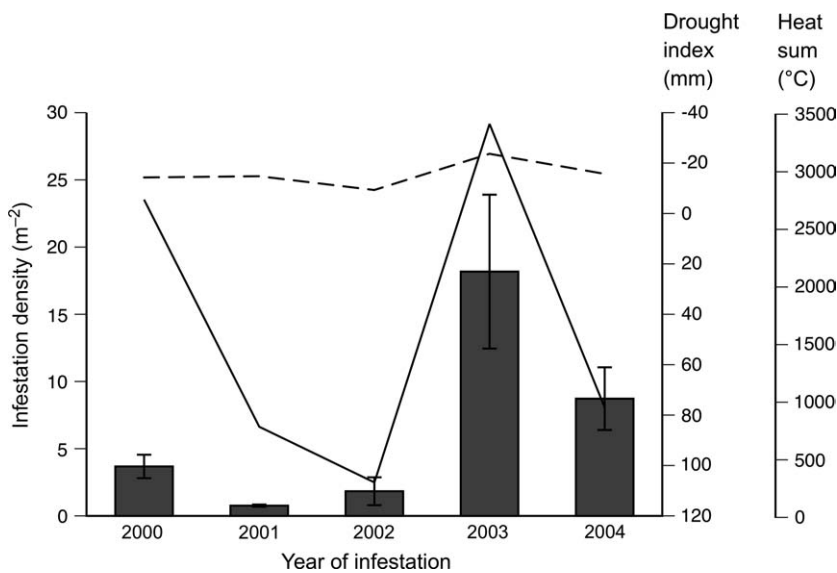
**Fig. 6.** Number of colonising species (from a total of eight key species) in pine trees with different levels of needle loss.

The key insect species showed different patterns in their temporal infestation dynamics. The buprestid *P. cyanea* is one of the most important insects and showed a marked increase in the last 2 years of the investigation. Especially in the year 2003, the infestation density was significantly ( $P < 0.05$ ) higher than in the previous years. This can be attributed to the exceptional weather conditions in this year. The two curves superimposed on the densities in Fig. 7 represent drought and temperature. The drought index (water deficit, solid line) is a measure of the drought stress experienced by the tree. There was an elevated drought stress in 2000 and 2003. In 2003 this clearly coincided with a high infestation density. The infestation in 2000 was relatively low despite the high drought index, probably because: (i) the initial populations of *P. cyanea* were low, and (ii) their density may have been underestimated because the first tree harvest during this study was in May 2000, at a phenological time when most *Phaenops* had already left the trees. In the subsequent years, they emerged primarily from trees cut in February rather than from those cut in May. This signifies that most adults emerge and oviposit before May under the local conditions in the Valais region.

While the drought index is an important qualifier of tree susceptibility to insect attack, the temperature is positively correlated with successful insect development and reproduction (Wermelinger & Seifert, 1999). In Fig. 7, the dashed line represents the heat sum accumulated during adult oviposition and larval development, that is from May to October. The heat sum peaked in 2003 coinciding with the highest *P. cyanea* densities.

**Discussion**

Insects rely on host plants with different levels of vigour and nutritional states for oviposition and development. While the nutritional condition can be defined and quantified quite easily, *vigour* is more difficult to assess. Needle loss (crown transparency) is widely used as a surrogate estimator in assessing tree health (Dobbertin, 2005). The level of transparency has previously been



**Fig. 7.** Yearly density (mean  $\pm$  SE) of *P. cyanea* infestations of Scots pines (columns). The drought index (solid line) was calculated from January to May and the heat sum (in day-degrees  $>0$  °C, dashed line) from May to October.

found to correlate directly with tree mortality (Dobbertin & Brang, 2001; Dobbertin & Rigling, 2006). It has also been related to tree growth (Dobbertin, 2005), which in turn correlates with tree mortality (Bigler *et al.*, 2006). Assuming that mortality depends on tree vigour, these findings suggest that needle loss is a valid measure of a tree's vigour.

The quality of this measure is additionally supported by the colonisation behaviour of some of the subcortical insects under study. For example, *Acanthocinus* or *Orthotomicus* colonised trees within a very narrow range of needle loss. This indicates that these trees clearly shared some common physiological properties that differed from those of other trees. These properties most probably represent a certain host condition, that is susceptibility or vigour. The attack by *Tomicus* species could reportedly not be correlated with most other tree vigour estimators, such as morphological characteristics (tree and growth parameters, vigour index; Waring & Pitman, 1980; Långström & Hellqvist, 1993) or biochemical compounds (resin, hydrocarbons, phenolics; Annala *et al.*, 1999). In our study, however, crown transparency showed a relatively distinct maximum of successful *Tomicus* colonization at around 80% needle loss.

An open question is how effective the defence capabilities of trees with different degrees of needle loss are against attacking insects. It is well known that trees possess preformed (constitutive) as well as induced defence mechanisms (e.g. Mattson *et al.*, 1988; Larsson, 2002; Lieutier, 2002). Conifers can deter insect attack by releasing resin from preformed resin ducts, which is then followed by *de novo* resin formation induced by the attack (Lieutier, 2002). While a mild stress may increase a plant's resistance (Lorio, 1988; Dunn & Lorio, 1993), trees with more than 50% needle loss obviously suffer from a severe stress. Severely defoliated pines were shown to have reduced resin flow (Annala *et al.*, 1999), but how various levels of needle loss affect in detail the constitutive and induced defence mechanisms of a tree is largely unknown (Lieutier, 2004).

Among the species investigated, *P. cyanea* and *I. acuminatus* seem to have the most aggressive role in pine decline. Both are known to increase their populations after heat and drought periods (Markalas, 1992; Kailidis & Markalas, 2005). The bark beetle *I. acuminatus* is reported to be economically relevant (Grégoire & Evans, 2004), but in our study most trees infested by this species were found to be moderately to greatly weakened (60–80% needle loss). Moreover, the emergence densities of up to 35 individuals per m<sup>2</sup> were well below the attack densities of 850 m<sup>-2</sup> reported to be lethal for Scots pine (Guérard *et al.*, 2000). This bark beetle species apparently does not react to tree volatiles (Brattli *et al.*, 1998), but conspecifics respond to pheromone emission by successfully established pioneer beetles (Bakke, 1978).

The buprestid *P. cyanea* is ranked among the most aggressive and economically most important xylophagous insects affecting pine in Western Europe (Evans *et al.*, 2004; Grégoire & Evans, 2004). Our results show that it colonises trees with a very broad range of crown transparency levels including trees that are only slightly weakened. This species has not been considered detrimental in the forests in the study region until recently, but it seems to have increased its population levels in the past few years (cf. Fig. 7; Dobbertin *et al.*, 2007). The two species have different colonisation characteristics. While *P. cyanea* can colonise slightly weakened trees in low densities without necessarily killing them (Dengler & Wilhelm, 2002), bark beetles such as *I. acuminatus* need high numbers for colonisation and its success depends very much on the susceptibility of the tree and on the size of population (e.g. Paine *et al.*, 1984; Guérard *et al.*, 2000).

In our study, *I. acuminatus* mostly colonised trees with a recent deterioration in needle density (Fig. 4). In contrast, *P. cyanea* also attacked many pines with no recent change in needle loss. From this point of view, this species may be even more significant than *I. acuminatus*. In any case, neither species qualifies as a *primary* pest in the strict sense, as the term is usually used to describe attacks on vigorous trees (Edmonds *et al.*, 2000).



The cerambycid *A. aedilis* and the bark beetle *O. longicollis* colonised trees with a conspicuously narrow transparency range >70%, that is greatly weakened or moribund trees. The preferred substrate of *A. aedilis* is known to be the phloem of physiologically weakened trees (Postner, 1974) or that of trees that have recently died (Bense, 1995; Schroeder, 1997). The species colonises dead trees that were killed by some abrupt impact such as a storm, lightning or cutting, and therefore still have a nutritious phloem. In our study, this species was not found in dead trees (100% needle loss) because the phloem quality gradually deteriorates in a slowly declining tree. Thus, when the tree finally dies, it is no longer attractive to many pioneer species. Conversely, pine trees rapidly defoliated up to 90% by sawfly attacks were reported to be not attacked by *Tomicus* species, because the trees' reserves were not sufficiently exhausted (Annala *et al.*, 1999). Therefore, the susceptibility of a defoliated or newly dead tree greatly depends on the history of its defoliation. A pine killed by a storm or momentarily defoliated by some phyllophagous insect attracts an assemblage of xylophagous insects different from that attracted by a dying tree that has been declining for years.

The species assessed as moderately aggressive were *P. piniphilus*, *T. minor*, and *S. noctilio*. The weevil *P. piniphilus*, the most aggressive species of the *Pissodes*-genus (Kudela, 1974), is known to usually prefer weakened, air-pollution affected or freshly killed trees, and is therefore considered a secondary pest (Day *et al.*, 2004). In our study it colonised greatly weakened pines most frequently, but did not exploit moribund trees. The bark beetle *T. minor* is considered less aggressive than its congener *T. piniperda*, which was found only in very low numbers in our study, and it generally does not have significant economic impact (Grégoire & Evans, 2004). In our study, this species preferably colonised trees with around 80% needle loss. In this it is similar to *T. piniperda*, which prefers greatly weakened pine trees with high needle loss (Schroeder, 1987). *T. minor* is also reported to require extremely high attack densities to successfully colonise even weakened trees, so that it very much depends on newly dead or moribund trees (Långström & Hellqvist, 1993).

In Europe, the Eurasian wood wasp *S. noctilio* is of minor importance. It has rarely been found to colonise living trees, and it usually does not kill them (Spradbery & Kirk, 1978). The larvae do not develop in the phloem, but rather tunnel themselves through the sapwood. Thus, this wood wasp has some significance only in terms of technical wood impairment. On the other hand, it is very detrimental in regions where it has been accidentally introduced, such as New Zealand, Australia, South America, South Africa, and more recently the US, where it mainly affects *Pinus radiata* D. Don plantations (Madden, 1988; Långström *et al.*, 2004; www.aphis.usda.gov). Along with oviposition, the female inserts toxic mucus and a fungus into the wood (Madden, 1988), which further reduces the tree's vigour. In vital trees, a high proportion of ovipositor drills are made without oviposition, but with insertion of mucus and fungus. More eggs are then deposited as the tree becomes less vigorous (Madden, 1988). This pattern is well supported by our data (Fig. 2). Trees suffering from just little more than 50% needle loss yielded a lower wood wasp density than trees with higher needle loss at the time of attack.

Once the aggressiveness of the species involved has been assessed, the question arises as to their role in the observed pine decline in the Valais region. Many bark beetle species require a minimum number of attacking individuals to overcome a tree's defence. The more aggressive a species is (Raffa, 1988; Guérard *et al.*, 2000; Lieutier, 2002, 2004), the less the stress needs to be to allow a successful colonisation, and the higher the risk of a tree being attacked before it can recover and reach normal resistance. In our investigation, even the most aggressive species preferentially colonised pines with more than 50% needle loss, that is pines with clearly reduced vigour. Nevertheless, insects that colonise trees with less than roughly 60% needle loss may be considered harmful, because such trees could possibly recover under better conditions and without insect attack.

With the pine decline in Valais and referring to the Manion (Manion, 1981) concept, insects such as *P. cyanea* and *I. acuminatus* may be inciting factors, while most others merely contribute to the decline. There must be other inciting factors, such as drought or pathogens, because for example *P. cyanea* infested at most 40% of the trees even in the category with highest crown transparency (Fig. 5). From the more than 200 trees investigated, only 12% showed *P. cyanea* infestation, and just 18% of the trees with at least 45% needle loss were actually infested with this species.

The infestation dynamics were closely related to the climatic conditions. The warm and dry year in 2003 was well reflected by the infestation peak of, for example, *P. cyanea* (Fig. 7), and was reported to be favourable for other insect species as well (Rouault *et al.*, 2006). The extraordinary conditions prevailing in 2003 were more than just moderate changes in environmental stress (Långström & Hellqvist, 1993) and seem to have triggered the instant attacks of this buprestid. Climate change scenarios for Europe, and in particular for Switzerland, predict an increase in temperature, drought periods, and heat waves (Führer *et al.*, 2006). This suggests that infestations will become more prevalent in future and lead to more tree mortality as a result of *P. cyanea* and possibly other aggressive species.

In conclusion, it seems that beetles such as *P. cyanea* and *I. acuminatus* can be quite important inciting factors in a pine decline like that observed in the Swiss Rhone valley. This may possibly also play a role in other central Alpine valleys experiencing this phenomenon. Most other insect species are merely contributing or even irrelevant factors. It is very probable that the pine stands are suffering directly and indirectly from the effects of the ongoing global warming. Not only do higher temperatures (Rebetez & Dobbertin, 2004) and an unfavourable change in the precipitation regime (Bigler *et al.*, 2006) result in drought stress, which increases the susceptibility of the pine host tree to insect attack (Mattson & Haack, 1987), but they also lead to a more rapid population development of the associated insects (Wermelinger & Seifert, 1999; Bale *et al.*, 2002). Thus, the observed decline of *P. sylvestris* and subsequent replacement by the more drought-adapted *Quercus pubescens* (Weber *et al.*, 2005; Rigling *et al.*, 2006; Zweifel *et al.*, 2006) seems to be the result of both a change in the abiotic environment and of the impact of biotic agents. These agents may include the semi-parasitic mistletoe (Dobbertin & Rigling, 2006), nematodes (Polomski *et al.*, 2006) and insects.

## Acknowledgements

The assistance in the fieldwork by Beat Fecker, Roger Koechli, Isabella Sedivy, and Martin von Arx is gratefully acknowledged. We thank Magdalena Furrer, Miloš Knížek and Petr Zahradník for their support in beetle identification. MeteoSwiss provided the meteorological data and Silvia Dingwall kindly checked the English language. This project was financially supported by the Federal Office for the Environment BAFU and the Canton Valais.

## References

- Annala, E., Långström, B., Varama, M., Hiukka, R. & Niemelä, P. (1999) Susceptibility of defoliated Scots pine to spontaneous and induced attack by *Tomicus piniperda* and *Tomicus minor*. *Silva Fennica*, **33**, 93–106.
- Bakke, A. (1978) Aggregation pheromone components of the bark beetle *Ips acuminatus*. *Oikos*, **31**, 184–188.
- Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K. et al. (2002) Herbivory in a global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **88**, 1–16.
- Begert, M., Schlegel, T. & Kirchhofer, W. (2005) Homogeneous temperature and precipitation series of Switzerland from 1864 to 2000. *International Journal of Climatology*, **25**, 65–80.
- Bense, U. (1995) *Longhorn Beetles – Illustrated Key to the Cerambycidae and Vesperidae of Europe*. Margraf Verlag, Weikersheim.
- Berryman, A.A. (1989) *Forest Insects – Principles and Practice of Population Management*. Plenum Press, New York.
- Bigler, C., Bräker, O.U., Bugmann, H., Dobbertin, M. & Rigling, A. (2006) Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. *Ecosystems*, **9**, 330–343.
- Brattli, J.G., Andersen, J. & Nilssen, A.C. (1998) Primary attraction and host tree selection in deciduous and conifer living Coleoptera: Scolytidae, Curculionidae, Cerambycidae and Lymexylidae. *Journal of Applied Entomology*, **122**, 345–352.
- Caldeira, M.C., Fernández, V., Tomé, J. & Pereira, J.S. (2002) Positive effect of drought on longicorn borer larval survival and growth on eucalyptus trunks. *Annals of Forest Science*, **59**, 99–106.
- Day, K.R., Nordlander, G., Kenis, M. & Halldorson, G. (2004) General biology and life cycles of bark weevils. *Bark and Wood Boring Insects in Living Trees in Europe – A Synthesis* (ed. by F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire and H. F. Evans), pp. 331–349. Kluwer Academic Publishers, Dordrecht.
- Dengler, K. & Wilhelm, G.J. (2002) Der Blaue Kiefernprachtkäfer und das Kiefernsterben. *Allgemeine Forstzeitschrift/Der Wald*, **57**, 1266–1269.
- Dobbertin, M. (2005) Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. *European Journal of Forest Research*, **124**, 319–333.
- Dobbertin, M. & Brang, P. (2001) Crown defoliation improves tree mortality models. *Forest Ecology and Management*, **141**, 273–286.
- Dobbertin, M. & Rigling, A. (2006) Pine mistletoe (*Viscum album* ssp. *austriacum*) contributes to Scots pine (*Pinus sylvestris*) mortality in the Rhone valley of Switzerland. *Forest Pathology*, **36**, 309–322.
- Dobbertin, M., Landmann, G., Pierrat, J.C. & Müller-Edzards, C. (1997) Quality of crown condition data. *Ten Years of Monitoring Forest Condition in Europe. Studies on Temporal Development, Spatial Distribution and Impacts of Natural and Anthropogenic Stress Factors* (ed. by C. Müller-Edzards, W. De Vries and J. W. Erisman), pp. 7–22. *United Nations Economic Commission for Europe/ European Commission*, Geneva and Brussels.
- Dobbertin, M., Mayer, P., Wohlgenuth, T., Feldmeyer-Christe, E., Graf, U., Zimmermann, N.E. et al. (2005) The decline of *Pinus sylvestris* L. forests in the Swiss Rhone valley – a result of drought stress? *Phyton*, **45**, 153–156.
- Dobbertin, M., Wermelinger, B., Bigler, C., Bürgi, M., Carron, M., Forster, B. et al. (2007) Linking increasing drought stress to Scots pine mortality and bark beetle infestations. *The Scientific World Journal*, **7**, 231–239.
- Dunn, J.P. & Lorio, P.L. (1993) Modified water regimes affect photosynthesis, xylem water potential, cambial growth, and resistance of juvenile *Pinus taeda* L. to *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Physiological and Chemical Ecology*, **22**, 948–957.
- Edmonds, R.L., Agee, J.K. & Gara, R.I. (2000) *Forest Health and Protection*. McGraw-Hill, Boston.
- Eichhorn, J., Szepesi, A., Ferretti, M., Roskams, P. & Durrant, D. (2006) Visual assessment of crown condition. *Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests* (ed. by P. C. Centre), pp. 1–69. Federal Research Centre for Forestry and Forest Products, Hamburg.
- Eichhorn, O. (1982) Siricoidea. *Die Forstschädlinge Europas, Vol. 4: Hautflügler und Zweiflügler* (ed. by W. Schwenke), pp. 196–231. Paul Parey, Hamburg.
- Eilmann, B., Weber, P., Rigling, A. & Eckstein, D. (2006) The influence of drought on the wood structure of *Pinus sylvestris* L. and *Quercus pubescens* Willd. in Valais, Switzerland. *Dendrochronologia*, **23**, 121–132.
- Erbilgin, N. & Raffa, K.F. (2002) Association of declining red pine stands with reduced populations of bark beetle predators, seasonal increases in root colonizing insects, and incidence of root pathogens. *Forest Ecology and Management*, **164**, 221–236.
- Evans, H.F., Moraal, L.G. & Pajares, J.A. (2004) Biology, ecology and economic importance of Buprestidae and Cerambycidae. *Bark and Wood Boring Insects in Living Trees in Europe – A Synthesis* (ed. by F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire and H. F. Evans), pp. 447–474. Kluwer Academic Publishers, Dordrecht.
- Flühler, H., Keller, T. & Schwager, H. (1981) Die Immissionsbelastung der Föhrenwälder im Walliser Rhonetal. *Mitteilungen der Schweizerischen Anstalt für das forstliche Versuchswesen*, **57**, 399–414.
- Fournier, N., Rigling, A., Dobbertin, M. & Gugerli, F. (2006) Faible différenciation génétique, à partir d'amplification aléatoire d'ADN polymorphique (RAPD), entre les types de pin sylvestre (*Pinus sylvestris* L.) d'altitude et de plaine dans les Alpes à climat continental. *Annals of Forest Science*, **63**, 431–439.
- Fuhrer, J., Beniston, M., Fischlin, A., Frei, C., Goyette, S., Jasper, K. et al. (2006) Climate risks and their impact on agriculture and forests in Switzerland. *Climatic Change*, **79**, 79–102.
- Gan, J.B. (2004) Risk and damage of southern pine beetle outbreaks under global climate change. *Forest Ecology and Management*, **191**, 61–71.
- Gimmi, U. & Bürgi, M. (2007) Using oral history and forest management plans to reconstruct traditional non-timber forest uses in the Swiss Rhone Valley (Valais). *Environment and History*, **13**, 211–246.
- Grégoire, J.-C. & Evans, H.F. (2004) Damage and control of BAWBILT organisms – an overview. *Bark and Wood Boring Insects in Living Trees in Europe – A Synthesis* (ed. by F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire and H. F. Evans), pp. 19–37. Kluwer Academic Publishers, Dordrecht.
- Guérard, N., Dreyer, E. & Lieutier, F. (2000) Interactions between Scots pine, *Ips acuminatus* (Gyll.) and *Ophiostoma brunneo-ciliatum* (Math.): estimation of the critical thresholds of attack and inoculation densities and effects on hydraulic properties in the stem. *Annals of Forest Science*, **57**, 681–690.

- Kailidis, D. & Markalas, S. (2005) Dürreperioden in Zusammenhang mit sekundärem Absterben und Massenvermehrungen rindenbrütender Insekten in den Wäldern Griechenlands. *Anzeiger für Schädlingskunde/Journal of Pest Science*, **61**, 25–30.
- Kudela, M. (1974) Pissodes. *Die Forstschädlinge Europas, Vol. 2: Käfer* (ed. by W. Schwenke), pp. 299–310. Paul Parey, Hamburg.
- Långstöm, B., Heliövaara, K., Moraal, L.G., Turčáni, M., Viitasaari, M. & Ylioja, T. (2004) *Non-coleopteran insects. Bark and Wood Boring Insects in Living Trees in Europe – A Synthesis* (ed. by F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire and H. F. Evans), pp. 501–538. Kluwer Academic Publishers, Dordrecht.
- Långström, B. & Hellqvist, C. (1993) Induced and spontaneous attacks by pine shoot beetles on young Scots pine trees: tree mortality and beetle performance. *Journal of Applied Entomology*, **115**, 25–36.
- Larsson, S. (2002) Resistance in trees to insects – an overview of mechanisms and interactions. *Mechanisms and Deployment of Resistance in Trees to Insects* (ed. by M. R. Wagner, K. M. Clancy, F. Lieutier and T. D. Paine), pp. 1–29. Kluwer Academic Publishers, Dordrecht.
- Lieutier, F. (2002) Mechanisms of resistance in conifers and bark beetle attack strategies. *Mechanisms and Deployment of Resistance in Trees to Insects* (ed. by M. R. Wagner, K. M. Clancy, F. Lieutier and T. D. Paine), pp. 31–77. Kluwer Academic Publishers, Dordrecht.
- Lieutier, F. (2004) Host resistance to bark beetles and its variations. *Bark and Wood Boring Insects in Living Trees in Europe – A Synthesis* (ed. by F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire and H. F. Evans), pp. 135–180. Kluwer Academic Publishers, Dordrecht.
- Lorio, L.L.J. (1988) Growth differentiation-balance relationships in pines affect their resistance to bark beetles (Coleoptera: Scolytidae). *Mechanisms of Woody Plant Defenses against Insects – Search for Pattern* (ed. by W. J. Mattson, J. Levieux and C. Bernard-Dagan), pp. 73–92. Springer-Verlag, New York.
- Madden, J.L. (1988) *Sirex* in Australasia. *Dynamics of Forest Insect Populations* (ed. by A. A. Berryman), pp. 407–429. Plenum Press, New York.
- Manion, P.D. (1981) *Tree Disease Concepts*. Prentice-Hall, Englewood Cliffs.
- Markalas, S. (1992) Site and stand factors related to mortality rate in a fir forest after a combined incidence of drought and insect attack. *Forest Ecology and Management*, **47**, 367–374.
- Marvaldi, A.E. & Morrone, J.J. (2000) Phylogenetic systematics of weevils (Coleoptera: Curculionoidea): a reappraisal based on larval and adult morphology. *Insect Systematics & Evolution*, **31**, 43–58.
- Mattson, W.J. & Haack, R.A. (1987) The role of drought in outbreaks of plant-eating insects. *BioScience*, **37**, 110–118.
- Mattson, W.J., Levieux, J. & Bernard-Dagan, C. (ed.) (1988) *Mechanisms of Woody Plant Defenses against Insects – Search for Pattern*, p. 416. Springer-Verlag, New York.
- Müller, E. & Stierlin, H.R. (1990) *Sanasilva Kronenbilder*. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, Birmensdorf.
- Paine, T.D., Stephen, F.M. & Taha, H.A. (1984) Conceptual model of infestation probability based on bark beetle abundance and host tree susceptibility. *Environmental Entomology*, **13**, 619–624.
- Polonski, J., Schönfeld, U., Braasch, H., Dobbertin, M., Burgermeister, W. & Rigling, D. (2006) Occurrence of *Bursaphelenchus* species in declining *Pinus sylvestris* in a dry Alpine valley in Switzerland. *Forest Pathology*, **36**, 110–118.
- Postner, M. (1974) Scolytidae (= Ipsidae), Borkenkäfer. *Die Forstschädlinge Europas, Vol. 2: Käfer* (ed. by W. Schwenke), pp. 334–482. Paul Parey, Hamburg.
- Raffa, K.F. (1988) The mountain pine beetle in western North America. *Dynamics of Forest Insect Populations* (ed. by A. A. Berryman), pp. 505–530. Plenum Press, New York.
- Rebetez, M. & Dobbertin, M. (2004) Climate change may already threaten Scots pine stands in the Swiss Alps. *Theoretical and Applied Climatology*, **79**, 1–9.
- Rigling, A., Dobbertin, M., Bürgi, M., Feldmeier-Christe, E., Gimmi, U., Ginzler, C. et al. (2006) Baumartenwechsel in den Walliser Waldföhrenwäldern. *Wald und Klimawandel, Forum für Wissen 2006* (ed. by T. Wohlgenuth), pp. 23–33. Eidg. Forschungsanstalt WSL, Birmensdorf.
- Rigling, A., Dobbertin, M., Bürgi, M., Gimmi, U., Graf Pannatier, E., Guggerli, F. et al. (2006) Verdrängen Flaumeichen die Walliser Waldföhren? *Merkblatt für die Praxis, Eidg. Forschungsanstalt WSL*, **41**, 16.
- Rigling, A., Forster, B., Wermelinger, B. & Cherubini, P. (1999) Grossflächige Veränderung des Landschaftsbildes im Kanton Wallis: Waldföhrenbestände im Umbruch. *Wald und Holz*, **80**, 8–12.
- Rouault, G., Candau, J.N., Lieutier, F., Nageleisen, L.M., Martin, J.C. & Warzee, N. (2006) Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. *Annals of Forest Science*, **63**, 613–624.
- Schroeder, L.M. (1987) Attraction of the bark beetle *Tomicus piniperda* to Scots pine trees in relation to tree vigor and attack density. *Entomologia Experimentalis et Applicata*, **44**, 53–58.
- Schroeder, L.M. (1997) Oviposition behavior and reproductive success of the cerambycid *Acanthocinus aedilis* in the presence and absence of the bark beetle *Tomicus piniperda*. *Entomologia Experimentalis et Applicata*, **82**, 9–17.
- Spradbery, J.P. & Kirk, A.A. (1978) Aspects of the ecology of siricid woodwasps (Hymenoptera: Siricidae) in Europe, North Africa and Turkey with special reference to the biological control of *Sirex noctilio* F. in Australia. *Bulletin of Entomological Research*, **68**, 341–359.
- Thorntwaite, C.W. (1948) An approach toward a rational classification of climate. *Geographical Review*, **38**, 55–94.
- Vertui, F. & Tagliaferro, F. (1998) Scots pine (*Pinus sylvestris* L.) dieback by unknown causes in the Aosta Valley, Italy. *Chemosphere*, **36**, 1061–1065.
- Wagner, M.R., Clancy, K.M., Lieutier, F. & Paine, T.D. (ed.) (2002) *Mechanisms and Deployment of Resistance in Trees to Insects*. Kluwer Academic Publishers, Dordrecht.
- Waring, R.H. & Pitman, G.B. (1980) *A Simple Model of Host Resistance to Bark Beetles*. Oregon State University, School of Forestry, Corvallis.
- Weber, P., Bugmann, H. & Rigling, A. (2005) Differences in drought response of *Pinus sylvestris* L. and *Quercus pubescens* Willd. in the Swiss Rhône valley. *TRACE, Tree Rings in Archaeology, Climatology and Ecology, Proceedings of the Dendrosymposium 2004* (ed. by H. Gärtner, J. Esper and G. H. Schleser), Schriftenreihe des Forschungszentrums Jülich, Reihe Umwelt/Environment, **53**, 48–52.
- Wermelinger, B. & Seifert, M. (1999) Temperature-dependent reproduction of the spruce bark beetle *Ips typographus*, and analysis of the potential population growth. *Ecological Entomology*, **24**, 103–110.
- Wermelinger, B., Polonski, J., Heiniger, U., Rigling, D. & Rigling, A. (2006) Föhrensterben im Wallis: Welche Rolle spielen Schädlinge und Krankheiten? *Wald und Holz*, **87**, 58–61.
- Zweifel, R., Steppe, K. & Sterck, F.J. (2007) Stomatal regulation by microclimate and tree water relations: interpreting ecophysiological field data with a hydraulic plant model. *Journal of Experimental Botany*, **58**, 2113–2131.
- Zweifel, R., Zimmermann, L., Zeugin, F. & Newbery, D.M. (2006) Intra-annual radial growth and water relations of trees – implications towards a growth mechanism. *Journal of Experimental Botany*, **57**, 1445–1459.

Accepted 24 September 2007

First published online 1 February 2008