

# Proceedings

## Integrating Cultural Tactics into the Management of Bark Beetle and Reforestation Pests<sup>1</sup>

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## PREFACE

This proceedings results from a conference held at the Monastery of Vallombrosa, near Florence, Italy, on September 1st - 3rd 1996. The meeting, held under the guidelines of the International Union of Forestry Research Organizations, gathered three IUFRO Working Parties: S7.03.03 (Insects Affecting Reforestation), S7.03.05 (Integrated Control of Scolytid Bark Beetles) and S7.03.07 (Population Dynamics of Forest Insects). Forty-nine participants, from 15 countries, presented 33 papers and 8 posters. These figures understate the contributors' input; considerable sharing of expertise and enthusiasm also occurred between the sessions, and links for present or future co-operation were renewed or established.

The organizers wish to express their gratitude to the Italian colleagues who helped to organize locally the meeting: Prof. Riziero Tiberi and Dr. Franco Cerchiarini (Istituto di Patologia e Zoologia Forestale e Agraria, Universita degli Studi, Firenze), Dr. Andrea Battisti and Mr. Massimo Faccoli (Istituto di Entomologia Agraria, Universita' degli Studi, Padova).

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# The natural role of spruce beetle and root pathogens in a sub-boreal spruce forest in central British Columbia: A retrospective study

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**ABSTRACT** The spruce beetle, *Dendroctonus rufipennis* (Kirby), is the most significant insect pest of spruce forests in North America. This bark beetle is responsible for intermittent, large scale outbreaks in mature stands, sometimes causing up to 90 % mortality. For that reason, spruce beetle outbreaks, along with stand replacing fires, have been considered driving forces in landscape level dynamics of these forests. In sub-boreal spruce stands in central British Columbia, we found that these stand replacement events are infrequent, and stand change generally gradual, largely due to root diseases and stem decays. Spruce beetle outbreaks act as species specific "high-grading" agents, removing mostly large, over-mature stems. Affected stands remain dominated by spruce, apparently due to this species' lower susceptibility or higher tolerance to stem and root decay than subalpine fir, *Abies lasiocarpa*.

**KEY WORDS** Spruce beetle, *Dendroctonus rufipennis*, root disease, decay, gap dynamics, *Picea*, *Abies lasiocarpa*, dendrochronology

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THE SPRUCE BEETLE, *Dendroctonus rufipennis* Kirby (Coleoptera: Scolytidae) is the most significant insect pest of North American spruce forests. During the last century, extensive mortality of spruce due to sporadic spruce beetle outbreaks has occurred in eastern Canada and the New England states (U.S. Dept. Agric. 1991) and throughout western North America (Furniss and Carolin 1977). In three outbreaks between 1962 and 1982, spruce beetles killed an estimated 18 million m<sup>3</sup> of spruce in the Prince George Forest Region in northeastern British Columbia alone (Humphreys and Safranyik 1993). During such outbreaks up to 90 % of the spruce can be killed, sometimes over large areas. In British Columbia, spruce beetle mortality may account for as much as 10 % of the total volume of spruce harvested in any one year (Humphreys and Safranyik 1993).

Traditional methods of control include sanitation clear cutting, and the use of conventional trap trees, i.e., live trees felled into the shade (Humphreys and Safranyik 1993). The Bowron Valley clear cut in central British Columbia, a huge area stretching from the Bowron Lakes Provincial Park in the south to Purden Lake Provincial Park in the north, and subject to considerable controversy, was the result of sanitation and salvage logging in the wake of a devastating outbreak (Humphreys and Safranyik 1993). Other methods frequently used for spruce beetle management in northern B.C. include lethal trap trees and pheromone baiting.

Increased domestic and international public opinion against clear cutting as a generally acceptable forest harvesting method has led to forest management legislation in British Columbia restricting clear cut size. Partially in response to a public perception that traditional harvesting methods are unnatural, there is an increasing trend toward ecosystem management, central to which is the concept that we must learn from natural processes in order to effectively manage forest ecosystems in a sustainable fashion (Harvey 1994).

Schmid and Hinds (1974) made the first attempt at conceptualizing the successional dynamics of spruce-subalpine fir ecosystems in response to spruce beetle and other disturbances. They speculated that spruce and subalpine fir dominance in these ecosystems shift back and forth as the result of the influence by the spruce beetle and the western balsam bark beetle, *Dryocoetes confusus* Swaine. Because of its higher shade tolerance, subalpine fir dominates the understory, but spruce maintains overstorey dominance due to a much lower mortality rate (Schmid and Frye 1977, Veblen 1986).

Using dendrochronological techniques and age structure analysis (Veblen et al. 1990), Veblen et al. (1991) found that the predominant effect by spruce beetle outbreaks in Engelmann spruce-subalpine fir stands in Colorado was the sustained growth release of previously suppressed understory trees. This growth was sustained for more than 40 years, and was similar in magnitude for both spruce and subalpine fir. Both species continued to co-dominate stands following outbreaks. Veblen et al. (1994) calculated a mean return interval of spruce beetle outbreaks of 116.5 years, and a mean turnover time of 259 years. The return interval is the time between outbreaks in a particular stand, and the turnover time is the time interval during which all the stands in an area are affected by epidemics. Close to 39 % of the stands had been affected by spruce beetle epidemics, while 59 % had been affected by fire. Fire return interval in the same study was 202 years and turnover time 521 years (Veblen et al. 1994). Veblen et al. (1991) concluded that spruce beetle outbreaks may be as important as fire as a disturbance agent in some Colorado subalpine forests.

This study is a component of the research conducted within the context of the McGregor Model Forest. In response to increased national and international pressure, Canada implemented "Canada's Green Plan for a Healthy Environment" in December 1990. A component of the Green Plan was the "Partners in Sustainable Development of Forests" program, an element of which is the Model Forest Network (Oberle 1992). The Model Forest Network focuses on facilitating the implementation of sustainable forest management by developing innovative techniques, and by testing and demonstrating the best sustainable forestry practices available (Brand et al. 1996). The objective of our study is to assess historical natural impact of spruce beetle and other forest health agents on stand- and landscape-level ecological processes. The information will be integrated with other research and operational data, and used in the development of forest management strategies and tactics in spruce-subalpine fir ecosystems in central British Columbia. This paper presents some preliminary findings from this study.

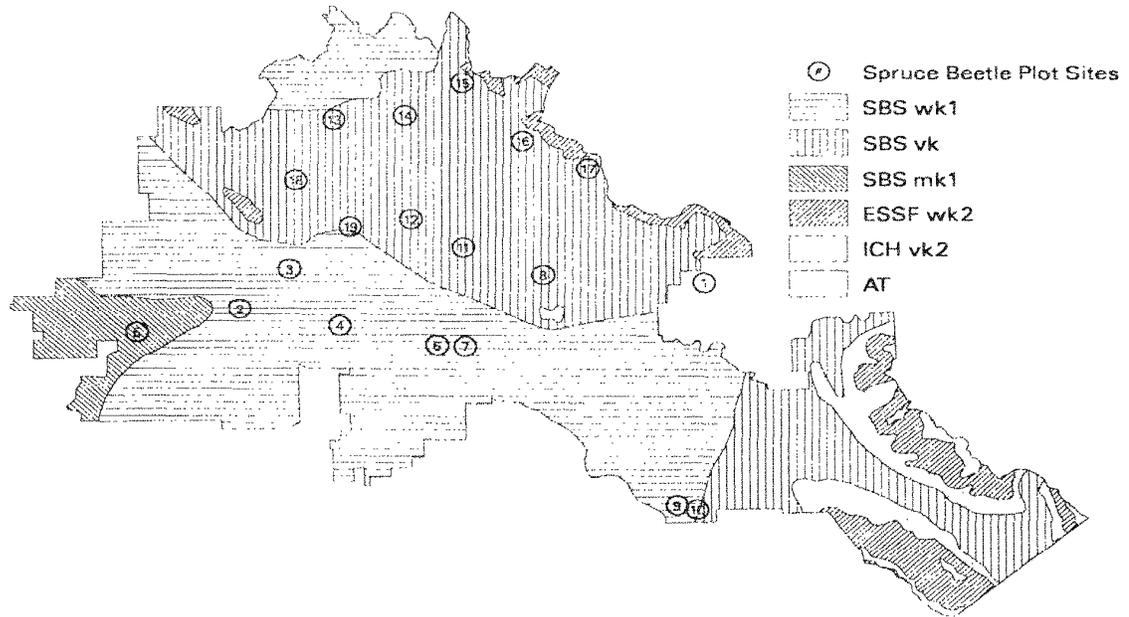
## Materials and Methods

The McGregor Model Forest consists of Northwood Pulp and Timber's Tree Farm License 30 (TFL 30), situated northeast of Prince George in the central interior of British Columbia. Its forests are dominated by white x Engelmann hybrid spruce and subalpine fir, with some lodgepole pine in the drier western areas, Douglas-fir mainly on well-drained ridges, and western hemlock and western red cedar in the wetter eastern part of the Model Forest. The majority of the Model Forest falls within the Sub-Boreal Spruce biogeoclimatic zone, (Pojar et al. 1987) which is characterized by a relatively cool and wet climate. The area has a history of harvesting, including selective harvesting of spruce conducted up until the 1950's, and clearcutting over the past 30-40 years. Spruce beetle infestations have had considerable impact on forestry activities in this area, and large areas of mature spruce forest have been clear cut in an attempt to control outbreaks.

Age class 8 and older (>140 years) spruce-leading stands were identified from Northwood Pulp and Timber inventory data. Eighteen stands were selected within TFL 30, and one stand outside the TFL. The stands were distributed across the central and western parts of the TFL to provide a reasonable coverage of the two major biogeoclimatic subzones within the sub-boreal spruce zone. In order to determine the kind of response resulting from overstorey removal in the study area, two sample stands were selected in areas where harvesting occurred in the 1940's and 1950's. One plot at site 10 was inadvertently placed outside the harvested area, and was not used for this assessment.

Increment cores were collected between September 11 and October 30, 1996. In each stand, cores were collected at 1.0-1.1 m from five or more dominant trees (mainly spruce, with some subalpine fir or Douglas-fir) in each of two plots. Thus, a minimum of 10 trees were cored in each of the stands. The diameter at breast height (dbh) and species were recorded. The cores were stored in a freezer until analyzed. Each core was mounted and sanded and ring width measurements were made using a WinDENDRO system at the Pacific Forestry Centre, Victoria, B.C. Ring widths were standardized using a horizontal line method, since this preserves early life growth characteristics, and provides better resolution for detecting growth releases (Veblen et al. 1990). Indices of all samples in each plot were averaged, to determine if there were consistent growth trends within and between plots, as well as within and between stands. The graphed data were visually assessed to detect long periods (30-40 years) of significantly increased growth occurring over a larger area. Such growth increases may signify a large scale disturbance, such as a spruce beetle outbreak (Veblen et al. 1990).

Preliminary data on butt decay were collected from a clearcut near site 3. A 6 m wide line transect survey was conducted on July 12, 1996. Each stump along the line was visually examined for evidence of butt rot. The species of the stump was determined and its diameter measured. The incidence of butt rot was then calculated by tree species and 10 cm diameter class.

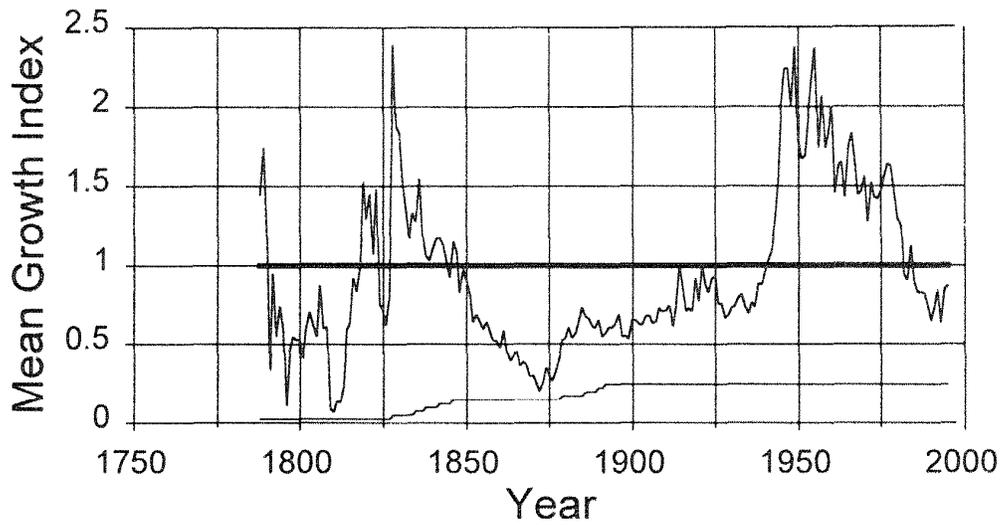


**Figure 1.** Map of Tree Farm Licence 30, northeast of Prince George, B.C., showing sample locations and biogeoclimatic zones and subzones. SBS = Sub-boreal spruce, wk = wet-cool, vk = very cool, mk = moist cool, ESSF = Engelmann spruce - Subalpine fir, ICH = Interior Cedar-Hemlock, AT = Alpine Tundra. See Pojar et al. 1987 for an explanation of the classification system.

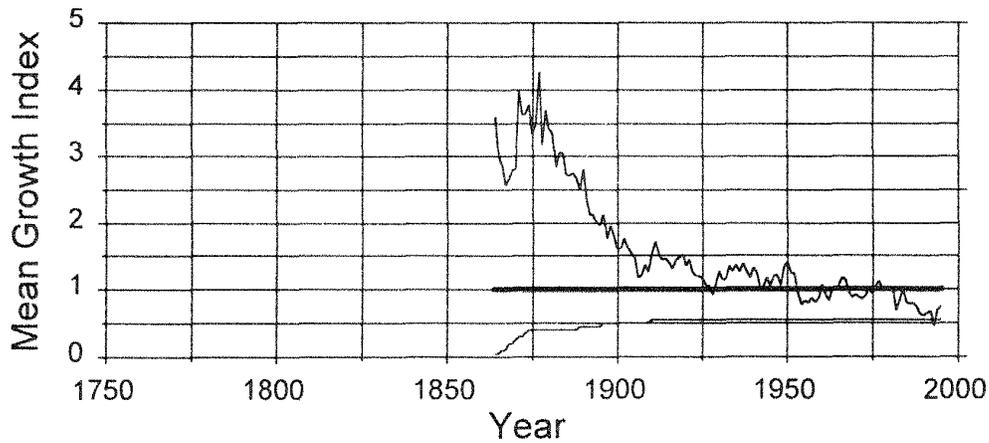
### Results and Discussion

Figure 1 shows the location of the sample sites in the TFL. Sites 9 and 10 were selected in areas which had experienced overstorey removal by selective harvesting in the 1940's and 1950's. At site 9, a significant release of tree growth is evident starting in the early 1940's and extending to the 1980's, after which growth rates are reduced (Fig. 2). Veblen et al. (1990) used a 250 % increase in growth to define a release. They argued that smaller increases could be due to widespread wind throw, or other events that affected surviving trees to a lesser extent than a widespread spruce beetle outbreak. The growth increase visible in site 9 is consistent with a release as defined by Veblen et al. (1990).

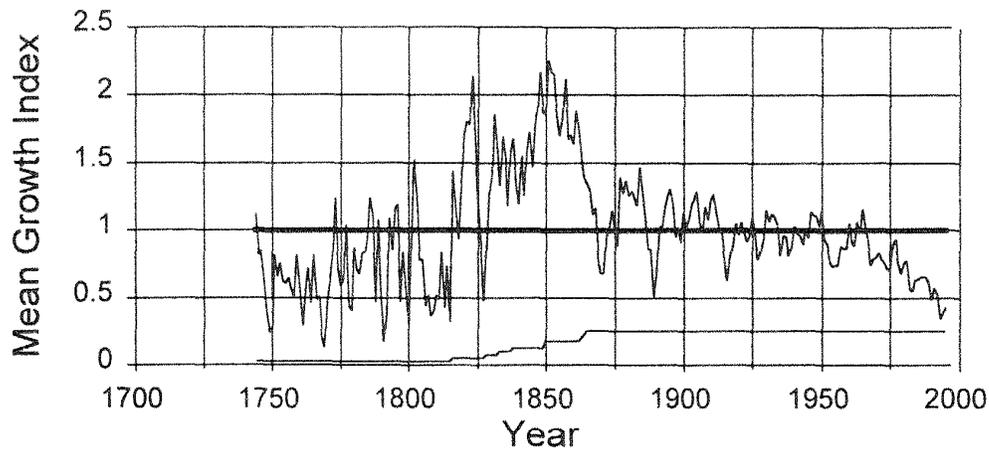
Stands in the eastern part of the TFL (sites 2, 3, and 5, and possibly 4) exhibited rapid initial growth in the mid- to late 1800's (Fig. 3). This indicates that the sample trees were established under open conditions, as would be the case following a stand replacing fire, or some other stand replacing disturbance event (Veblen et al. 1990). The oldest trees in these areas were about 130 - 140 years old.



**Fig. 2.** Mean growth index of 10 trees at site 9, showing strong growth release following overstorey removal due to partial cutting in the 1940's. Note the increased growth in the early 1800's. The line at the bottom of the graph denotes sample size 1-10.



**Fig. 3.** Mean growth index of 10 trees at site 3, showing rapid initial growth indicating that the trees were established during open conditions. The line at the bottom of the graph denotes sample size 1-10.



**Figure 4. Mean growth index of 10 trees at site 11, showing increased growth from about 1820 to 1870, possibly indicating that this stand experienced a major disturbance, e.g., spruce beetle outbreak, at the beginning of this period. The line at the bottom of the graph denotes sample size 1-10.**

In the rest of the TFL, the oldest trees sampled were 200 - 330 years old. In most of these stands there is a clear increase in growth rates starting in the early 1820's, and extending into the 1860's (Fig. 4).

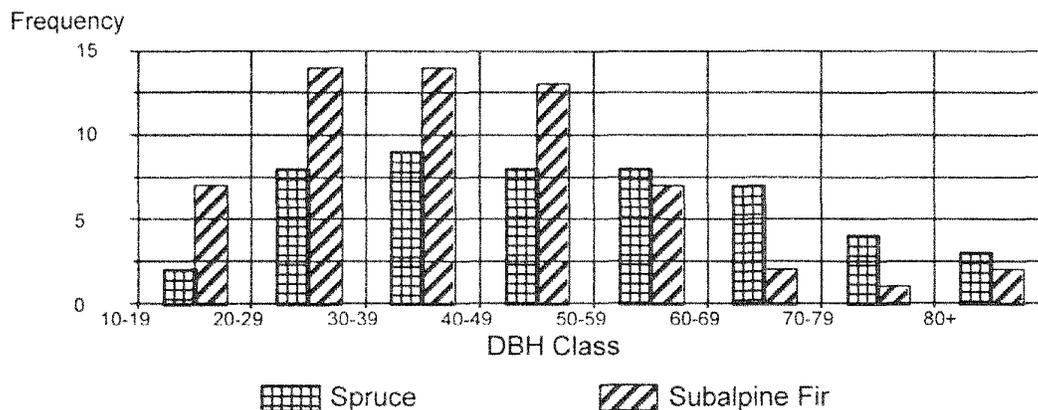
The data prior to this period is highly variable, because only a low number of trees were found that were significantly older than 220 years. The level of increased growth is generally lower than defined by Veblen et al. (1990) as constituting a release, indicating that it could be the result of some influence other than spruce beetle. The increased growth occurs during a period which has been interpreted as cooler than normal, and it precedes a general warming trend which started around 1840, based on a climate reconstruction from tree ring indices of *Picea glauca* in Alaska and the Yukon (Jacoby et al. 1985). Climate reconstructed from *Pinus flexilis* in southwestern Alberta indicates a decrease in tree ring widths lasting from 1840 - about 1875 (Case and MacDonald 1995). Thus, it appears unlikely that climate is responsible for the observed increase in growth.

The most compelling support for the hypothesis that at least some of the growth increase is a result of spruce beetle-caused mortality comes from a fur trader by the name of John McLean. Describing the beautiful scenery of New Caledonia, as the area around Prince George was called, he noted in his diary in 1836 that "...unfortunately, however, the woods are decaying rapidly, particularly several varieties of fir, which are being destroyed by an insect that preys on the bark: when the country is denuded of this ornament, and its ridges have become bald, it will present a desolate appearance (McLean 1849). The "fir" he refers to would have been spruce. Thus, it is probable that significant mortality occurred some time before the mid 1830's, and that large scale spruce beetle outbreaks may in fact have occurred in the area as early as the 1820's.

Nevertheless, there are several potential explanations for the low rate of increased

growth relative to Veblen et al.'s (1990) definition of a release. Firstly, the phenomenon may be due to widespread windthrow, as suggested by Veblen et al. (1990), and secondly, growing conditions may have become more favourable. However, John McLean's account (McLean 1849) indicates that significant bark beetle-caused mortality of spruce did occur in the area during this time. Thus, it is reasonable to assume that the growth increase is due at least in part to mortality of overstorey trees. The lower than expected response could then be explained by stand structure, at least if today's conditions are representative of what the stands looked like 180 years ago. The spruce stands in TFL 30 are relatively open to begin with, exhibiting many gaps and a very uneven canopy. Thus, moderate overstorey removal may not have affected stands as drastically as may be the case in Colorado. The growth release observed following partial cutting (Fig. 3) may be more similar to the release observed in Colorado since it is a sudden, very complete opening, while bark beetles kill the overstorey gradually, the killed trees remain standing for some time, and the distribution of mortality is frequently patchy.

Veblen et al. (1990) found that chronologies could be extended significantly by coring dead trees in areas with relatively recent mortality. Spruce trees killed by spruce beetle sometimes remain standing for up to 40 years in Colorado. In central British Columbia, however, dead trees appear to be rapidly colonized by decay fungi, and in most cases they become unsuitable for coring well within 10 years.

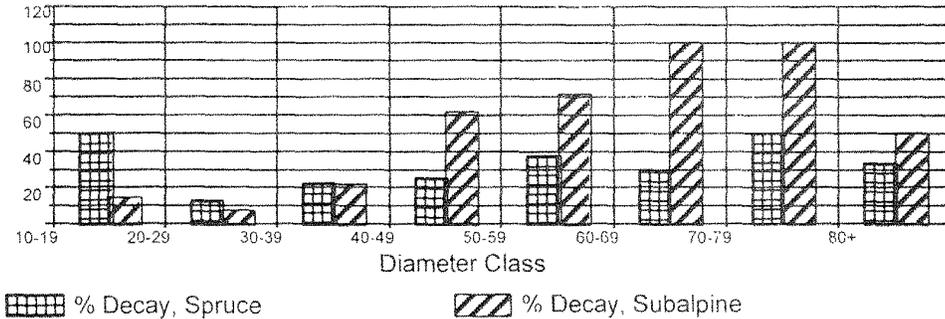


**Figure 5. Diameter class distributions of spruce and subalpine fir, respectively, based on a stump survey of a clearcut near Site 11.**

The preliminary survey of stumps revealed that small diameter classes were dominated by subalpine fir, i.e., subalpine fir dominated the understorey, whereas large diameter classes were dominated by spruce (Figure 5). If spruce beetle outbreaks periodically removed overstorey spruce, one should see a shift in stand composition to subalpine spruce, which obviously has higher recruitment rates in these mature stands. This is expected, since subalpine fir regenerates more readily than spruce under the canopy. However, similar to what Veblen (1986) observed in the Colorado front range, spruce continues to dominate the canopy trees in TFL 30. Veblen (1986) concluded that this was due to differential mortality

of understory trees. Our survey of stumps indicated that a similar phenomenon occurs in TFL 30, and that the mortality agents are pathogenic and decay fungi (Figure 6). In fact, it was extremely difficult to find large diameter subalpine firs for coring in these stands, since virtually all of these were more or less severely affected by butt rot. These trees would eventually die and fall, providing gaps and nurse logs, which act to increase recruitment of spruce in the stand.

% Stumps with Rot



**Figure 6. Percent of stumps with visible evidence of butt decay in a clear cut near Site 11.**

## CONCLUSION

Stand replacement fires in the area are very rare (B. Hawkes pers. comm.). For example, there is no evidence of fire in a stand of 350-400 year-old Douglas-fir even though the spruce component in the stand is only 200 - 250 years old. Based on this, and our preliminary data, we hypothesize that pathogenic and decay fungi are the primary agents of renewal in these ecosystems. These organisms accentuate the uneven stand structure by causing small gaps. They cause particularly high levels of mortality in subalpine fir, ensuring that stands remain spruce dominated even if spruce beetle outbreaks do occur.

The increased growth during the early part of the 19th Century could possibly be interpreted to be the result of a spruce beetle outbreak in TFL 30. However, the dendrochronological indication of this is unclear, possibly due to the open and uneven stand structure in the study area. The best support for the spruce beetle outbreak hypothesis is gained from the 1836 diary notation of a Hudson's Bay Company fur trader (McLean 1849), but his testimony does not reveal the exact geographical location of the bark beetle-caused mortality he observed. Thus, more extensive sampling is required to clarify how these stands have developed over the last centuries.

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# *Tomicus destruens* (Wollaston): biology and behaviour in Central Italy

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**ABSTRACT** The symptoms of decline that increase in Italian coastal pinewoods are caused by abiotic and biotic factors with the scolytid *Tomicus destruens* playing a leading role. Frequent and repeated physiological stresses, such as drought, climatic and ground water anomalies, phytophagous infestations (by sucking and defoliating insects) and fungal infections, have promoted the demographic increase of this endemic bark beetle. Like those of the others *Tomicina*, *T. destruens* infestations are very detrimental to the host because adults have to feed on the shoots of vigorous plants to enable their gonads to mature. Shoot death causes physiological anomalies and makes the plants vulnerable to subsequent attacks. In Central and Northern Italy, *T. destruens* develops two overlapping generations a year. The overlap in generations also occurs during hibernation, when adults, pupae, larvae and sometimes eggs have been observed at the same time. No significant difference has been observed concerning the biology of *T. destruens* in Central and Northern Italy, except that in the Northern Adriatic area mostly adults overwinter, in the shoots or in the stumps. These *T. destruens* biological characteristics greatly complicate pest management, which is already difficult in natural areas.

**KEY WORDS** *Tomicus destruens*, biology, behaviour, control

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*TOMICUS DESTRUENS* (WOLLASTON), Coleoptera Scolytidae, which some authors still regard as a *Tomicus piniperda* L. termophile entity (Santini and Prestininzi 1991), is spread throughout the Mediterranean coastal area, and like the other *Tomicina* that are present in Italy, its preferred host are of the genus *Pinus*, especially, *P. halepensis* and *P. pinea*.

During the last few years, the coastal pinewoods of Central and Northern Italy have endured intense infestations from *T. destruens*. The high susceptibility of these biocoenoses to infestation appears to be connected with climatic and ground water unbalances that have caused physiological stress to the trees and have led to intense and repeated attacks by phytophagous insects and pathogenic agents (above all fungi) (Moriando *et al.* 1995).

The purpose of the research was to study the role of *T. destruens* in the phenomena leading to the decline of pine stands and to define more precisely some aspects of their biology. The overall objective is to develop a programme for a rational and effective control.

## Materials And Methods

The research was initiated in 1992, at two sites: in pine stands situated on the Tirrenic coast of Central Italy (Alberese, situated in Uccellina Park, and Feniglia on the Argentario

promontory); and in pine stands of the North Adriatic coast (Cervia and Classe, both situated in Po Delta Park).

The forests under examination consist of unevenaged *P. pinea*, with isolated plants or sporadic groups of *P. pinaster*, and broad-leaved trees. In the Tirrenic pine forests, the broad-leaved trees are present within relatively small groups of evergreen species, while in the Adriatic pine forests they are more frequent, represented by species such as *Quercus robur*, *Q. pubescens*, *Fraxinus* spp., *Populus* spp., *Salix* spp., *Alnus glutinosa*, *Carpinus orientalis*.

Biological and behavioural research of *T. destruens* has taken place previously in areas where its density was high, through systematic surveys in the field. Moreover, the life-cycle of this insect has been observed in detail on samples of infested trunks taken from different heights of the trees and reared in the laboratory.

Periodical monitoring has also been carried out throughout the entire pine forests in order to verify the extent and intensity of infestations.

### Results

The data gathered in the Tirrenic and Adriatic pine stands did not show any significant differences between the two areas with regard to the development of the two generations that *T. destruens* completes each year, except that in the Northern Adriatic area primarily adults hibernate, and they do so in the shoots or in the stumps of the trees. In Tirrenic pinewoods pupae, larvae, adults and occasionally eggs can be observed at the same time. Adults remain in shoots or under bark from autumn to spring, and in some cases they were also observed reproducing.

In Central Italy, therefore, hibernation during different growth phases results in the oviposition of the first generation potentially spread over a long period of time (from February to May). However, most hibernating adults start their reproductive activity in April and May, attacking branches and boughs of vigorous plants which do not appear to be stressed. On pines broken off and on those that have just been cut down during normal silvicultural practices, we observed about 50 attacks for every metre of length on the entire trunk. In Northern Adriatic pinewoods, where adults hibernate, the oviposition of the first generation occurs over a much shorter period (between March and April). In spite of these differences, the adults of the first generation emerge at both sites at the beginning of the summer. This is indicated by the characteristic resin cones which appear on the shoots of vigorous plants. The resin cones demonstrate that adults have entered the shoots in order to attain reproductive maturity. This can be observed as early as July. In August, the infested shoots become reddish, an indication of both the presence and the intensity of the attack upon the crown of the plant by the adults of the first generation.

In August, the oviposition of the second generation also takes place. In the Adriatic pine stands oviposition is concluded before winter, while in the Tirrenic pinewoods it follows an irregular course. This is because the adults of the first generation remain in the shoots longer in order to reach sexual maturity. This delay is probably due to the high temperatures and the long drought periods which occur during the summer in Central Italy, and which influence the vegetative growth of the trees, thus slowing scolytid maturation.

In Adriatic pinewoods, *T. destruens* is more common in back dune areas, where ground water level is high and salt water enters. This weakens the plants, enabling primary attack by fungi, such as *Heterobasidion annosum* (Fr.) Bref. and *Phellinus (Fomes) pini* (Bref. ex Fr.) A. Ames (Nanni pers. obs., 1995). Similarly, the areas most attacked in Tirrenic pine stands are those where salt water infiltration occurs as a result of the lowering of the water-table, due to the intense drawing of fresh water which take place during the summer.

### Discussion

The results that were obtained from the research have helped clarify several aspects of scolytid biology and the behaviour in Central and Northern Italian pinewoods.

This information is very important for pest management in these biocoenosis, the stability of which is very low from a silvicultural point of view (Tiberi 1995).

Generally, for the purpose of forest protection, it is impossible to use all the technical means available, not only in order to avoid undesirable collateral effects in the biocoenosis, but also because there is no economic imperative in the short term.

Moreover, many forests, which were planted for a range of different reasons now fulfill mainly environmental, protective and recreational roles. In pest management, therefore, it is necessary to consider the potential benefits from action, which depends on the use and the ecological importance of the forests concerned, the constraints of forestry politics, and the expectation of the public. To draw up a rational intervention programme it is necessary to have considerable knowledge of the interactions between the various ecosystem components as well as of the nature of the problem itself. This would guarantee a wide range of choice amongst the various defences that could be undertaken (Covassi 1989, Tiberi 1996). However, that choice is difficult when the forest concerned has been severely destabilized and subject to xylophagous attack, as is the case with the pine stands which have been the object of this research. In these situations, there are many obstacles in the way of creating an adequate control of *T. destruens*, primarily because of the behaviour of this insect. The long periods spent under the bark or within the shoots make it vulnerable to control methods for only a short period of time. Therefore, control efforts must rely upon preventive measures, such as the quick elimination and removal of stressed trees, which are more susceptible to scolytid infestation. Another course of preventive action, is to prepare several pieces of bait-trunk to attract the reproducing adults. Obviously, this practice is effective only if it is repeated over a period of many years.

### Conclusions

During the last few years the Adriatic and Tirrenic coastal pine stands have been subject to various forms of stress as a result of a variety of interacting factors. The most important among these have been drought, ground water fluctuations, the attacks of primary pest-insects (sucking and defoliating insects) and fungal infection.

This phenomenon of extreme disturbance of the ecological balance of the forest stand has increased the activity of biotic factors, referred to as "weakness agents", and amongst

these, *T. destruens* is the most prevalent. Attacks of *T. destruens* is, therefore, a symptom of a greater problem.

In the areas under investigation *T. destruens* is endemic and has undergone dangerous and sometimes catastrophic increases. Intense attacks have taken place in limited but nevertheless wide areas, such as in the Alberese pine stands where, since 1988, some 200 mature trees have been felled each year, in addition to those young infested trees which are felled during the usual thinnings that are part of the standard working plan.

With regards to the coastal pinewoods of Central Italy, this investigation has confirmed that *T. destruens* develops two generations a year, with a considerable overlapping taking place of the different growth phases. This phenomenon also occurs during hibernation, when adults, pupae, larvae and sometimes eggs have all been observed at the same time. Clearly, this overlapping of different growth phases greatly complicates pest management.

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# Integrating Pheromone and Silvicultural Methods for Managing the Douglas-fir Beetle

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**ABSTRACT** Historically, approaches to reducing losses caused by the Douglas-fir beetle have focused on protecting the timber resource. Past recommendations included harvesting mature stands, treatment or removal of large diameter slash, prompt salvage of dead and dying trees, preventing tree stress and injury, thinning of young stands, and treatment or processing of infested material to destroy developing brood. Although some of these recommendations are still appropriate, there are limitations to implementing them in the context of ecosystem management. Recently, several new methods of using aggregation and antiaggregation pheromones of the Douglas-fir beetle have been shown to be effective for manipulating the distribution and possibly amount of tree mortality during outbreaks. These new methods along with existing silvicultural and pheromone-based treatments provide new opportunities to develop integrated programs for managing this important forest pest. The potency of these pheromone technologies suggest the potential for regulating beetle activity over wide areas, thus raising the need for field-testing at landscape scales.

**KEYWORDS** Scolytidae. *Dendroctonus pseudotsugae*, pheromones, 3-methylcyclohex-2-en-1-one, MCH, mass trapping

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THE DOUGLAS-FIR beetle, *Dendroctonus pseudotsugae* Hopkins, is found throughout the range of Douglas-fir, *Pseudotsugae menziesii* (Mirb.) Franco, in western North America (Furniss and Carolin 1977). This beetle usually breeds in portions of tree boles that are greater than about 20 cm in diameter. At low population densities, most infestations occur in trees that have recently died or live trees with limited defenses resulting from stress or injury (McMullen and Atkins 1962, Furniss 1965, Rudinsky 1966, Furniss et al. 1981, Wright et al. 1984). When populations reach high densities, large numbers of healthy trees may be successfully attacked and killed (Johnson and Belluschi 1969, Furniss et al. 1979). Epidemics often develop following natural or human-caused disturbances that create abundant breeding sites. Tree mortality during epidemics can alter the structure, composition, and ecological processes of forests in ways that may conflict with resource management objectives (Cornelius 1955, Furniss and Orr 1978, Hadley and Veblen 1993).

The Douglas-fir beetle is similar to other aggressive bark beetle species in the genus *Dendroctonus*. This species has only one generation per year, although sister broods may be produced when the weather is favorable. Adults fly from early spring through mid-summer (Ross and Daterman 1996). Broods overwinter within the phloem in the adult, pupal, or late larval stages. The pheromone system of the Douglas-fir beetle has been well studied. Among the many compounds that have been found to be attractive to the Douglas-fir beetle, combinations of frontalin with seudenol, ethanol, and/or MCOL elicit the strongest responses (Pitman and Vité 1970, Vité et al. 1972, Rudinsky et al. 1974, Pitman et al. 1975, Libbey et al. 1983, Lindgren et al. 1992, Ross and Daterman 1995a). The antiaggregation pheromone, 3-methylcyclohex-2-en-1-one (MCH), significantly reduces beetle response to attractant

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Pages 135-145 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997.

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odors (Kinzer et al. 1971, Furniss et al. 1972, Rudinsky et al. 1972, Furniss et al. 1974, McGregor et al. 1984, Lindgren et al. 1988).

### **History of Management Practices**

Until recently, management of Douglas-fir in the U.S. was primarily directed toward timber production. Consequently, the earliest recommendations to prevent losses caused by the Douglas-fir beetle were developed to protect the timber resource. These recommendations emphasized silvicultural activities that either reduced the availability of breeding sites or directly reduced the beetle population (Bedard 1950, Furniss 1959, Lejeune et al. 1961, Williamson and Price 1971, Furniss and Orr 1978, Furniss et al. 1979). Recommendations for limiting potential breeding sites included harvesting mature stands, treatment or disposal of slash greater than 20 cm in diameter, prompt salvage of windthrown, fire-damaged, and otherwise dead and dying trees, fire prevention, and thinning of young stands. Harvesting or treatment of infested material to destroy developing broods was also encouraged to reduce beetle populations. During outbreaks, the use of felled trap-trees was recommended to concentrate beetle activity in accessible areas where the brood could be destroyed (Lejeune et al. 1961). The effectiveness of these practices was often limited because of an inability to treat the entire infested area in a timely manner.

New possibilities for managing the Douglas-fir beetle arose following the identification of its aggregation and antiaggregation pheromones. Because outbreaks often occur following disturbances, particularly windstorms, a considerable effort was devoted to developing ways to use MCH to prevent the infestation of windthrown trees. Although an effective treatment was developed and shown to be operationally feasible (McGregor et al. 1984), it has never been implemented because of continuing delays in the registration process. Aggregation pheromones have been used to bait trap-trees making them more competitive with natural sources of attraction (Knopf and Pitman 1972, Pitman 1973, Ringold et al. 1975, Thier and Weatherby 1991). Since this application of pheromones does not require registration in the U.S., baited trap-trees have been used in operational programs (Patterson 1992). However, the efficacy of baited trap-trees has never been fully evaluated.

### **Emerging Pheromone-Based Methods**

Since 1992 we have been studying new pheromone-based management strategies for the Douglas-fir beetle. We have focused primarily on two treatments. First, using pheromones to protect live trees in relatively small, high-risk, high-value stands during outbreaks. And second, using pheromone-baited traps to affect the amount and distribution of beetle-caused tree mortality at the landscape scale during outbreaks.

### **Antiaggregation Pheromone, MCH**

A study conducted in northeastern Oregon in 1992 demonstrated the feasibility of using pheromones to protect live trees in small, high-value stands (Ross and Daterman 1994). A combination of pheromone-baited traps and MCH application significantly reduced the percentage of host trees that were infested compared with an untreated control (Fig. 1). Although this treatment was successful in reducing the infestation within the area designated

for protection, there were some problems associated with using traps for this purpose including "spill-over" attacks on nearby trees. Consequently, a follow-up study was conducted in the same general area in 1993 to test the efficacy of MCH alone (Ross and Daterman 1995b). The results indicated that MCH alone was at least equal to and perhaps more effective than the combination of baited traps and MCH that was tested the previous year (Fig. 1). In both of these studies, MCH was applied as bubble capsules at a rate of 150 capsules per hectare (60 g/ha).

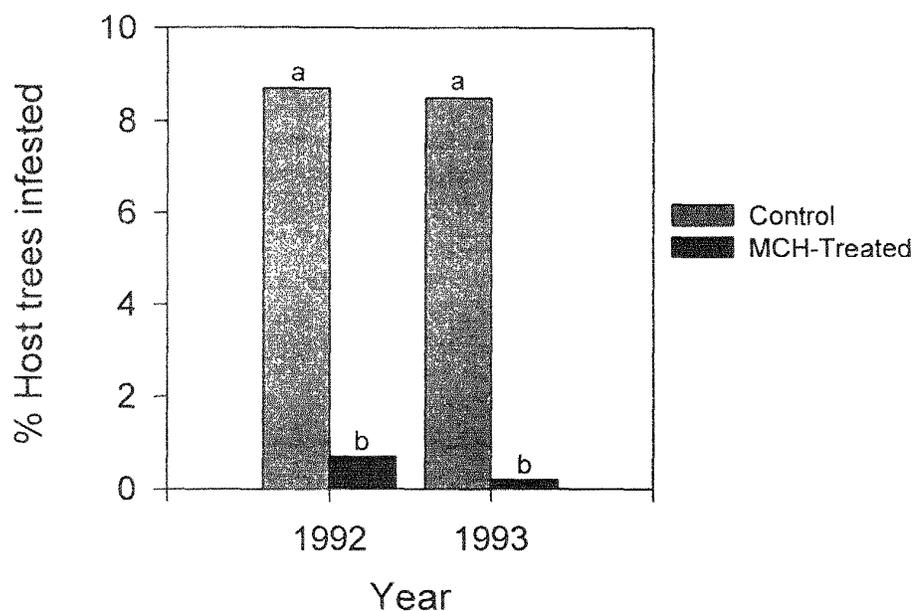


Fig. 1. Percentage of host trees infested on MCH-treated (60 g/ha) and control plots during studies conducted in northeastern Oregon in 1992 and 1993. In 1992, the treatment was a combination of MCH and pheromone-baited traps. In 1993, the treatment was MCH alone. Both years, differences between treated and control plots were significant ( $P < 0.05$ ).

Further studies were conducted in 1994 and 1995 to determine the lowest effective dose of MCH for protecting live trees (Ross et al. 1996). Each year, the tests were replicated in high-risk stands in Oregon, Idaho, Montana, and Utah. In 1994 and 1995, MCH was applied at rates of 0, 20, 40, and 60 g/ha and 0, 6, 12, and 20 g/ha, respectively. In 1994, all three doses of MCH were equally effective in reducing infestations compared to the untreated control (Fig. 2). In 1995, there were no significant differences in the percentage of host trees that were infested among the treatments, although the infestation rate at the highest dose was less than half that following any other treatment (Fig. 3). These results

demonstrated that MCH applied at rates as low as 20 g/ha can reduce the probability that high-risk trees will become infested. However, for practical purposes slightly higher doses should be used to ensure treatment efficacy.

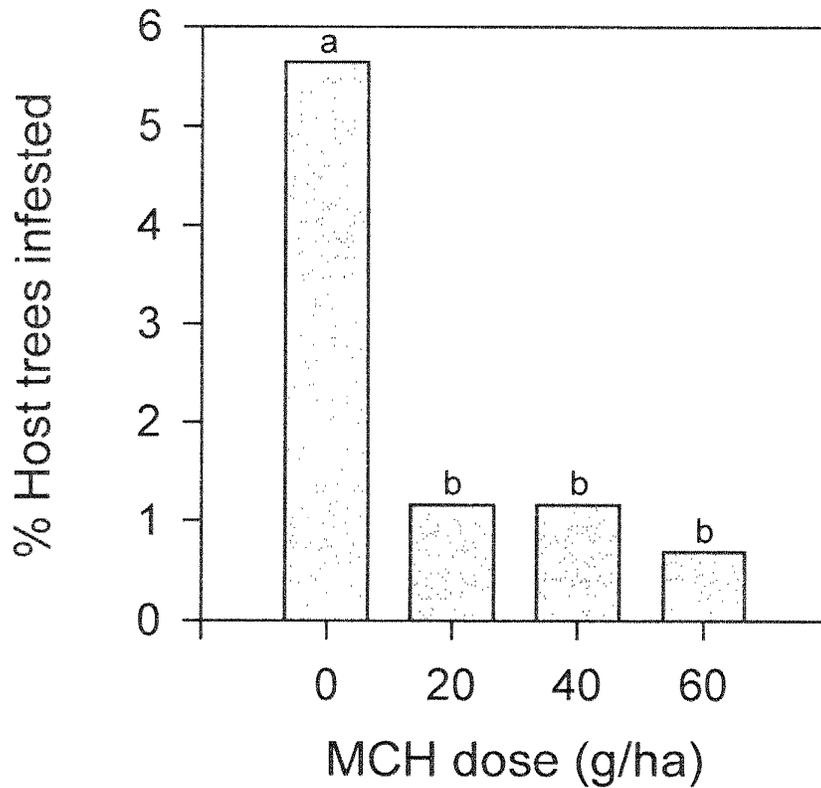
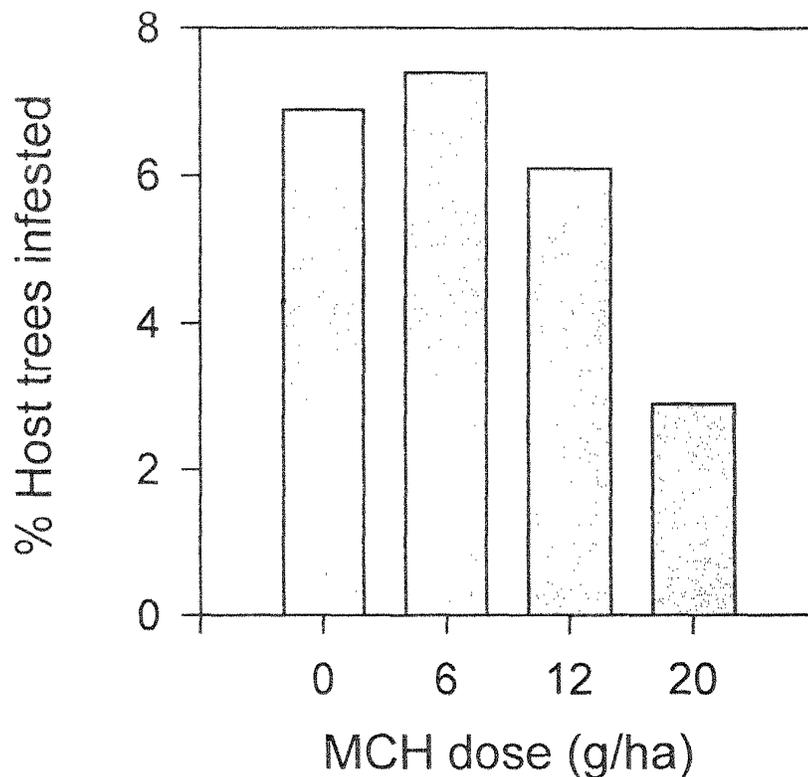


Fig. 2. Percentage of host trees infested following application of MCH at various doses on plots throughout the western U.S. in 1994. Letters indicate significant differences ( $P < 0.05$ ).



**Fig. 3.** Percentage of host trees infested following application of MCH at various doses on plots throughout the western U.S. in 1995. There were no significant differences among treatments ( $P > 0.05$ ).

In all four studies conducted between 1992 and 1995, pheromone-baited traps were placed at the center of MCH-treated and control plots to evaluate treatment effects. In every case, traps on MCH-treated plots caught significantly fewer Douglas-fir beetles compared with traps on untreated controls. In contrast, there were much smaller or, in most cases, no differences in catches of predators among MCH-treated and control plots (Fig. 4). Furthermore, there were no significant differences in abundance of natural enemies or brood production from the lower 7 m of mass-attacked trees on MCH-treated and control plots in 1995 (Table 1, unpublished data). This limited evidence suggests that MCH treatments have no negative impacts on natural enemies.

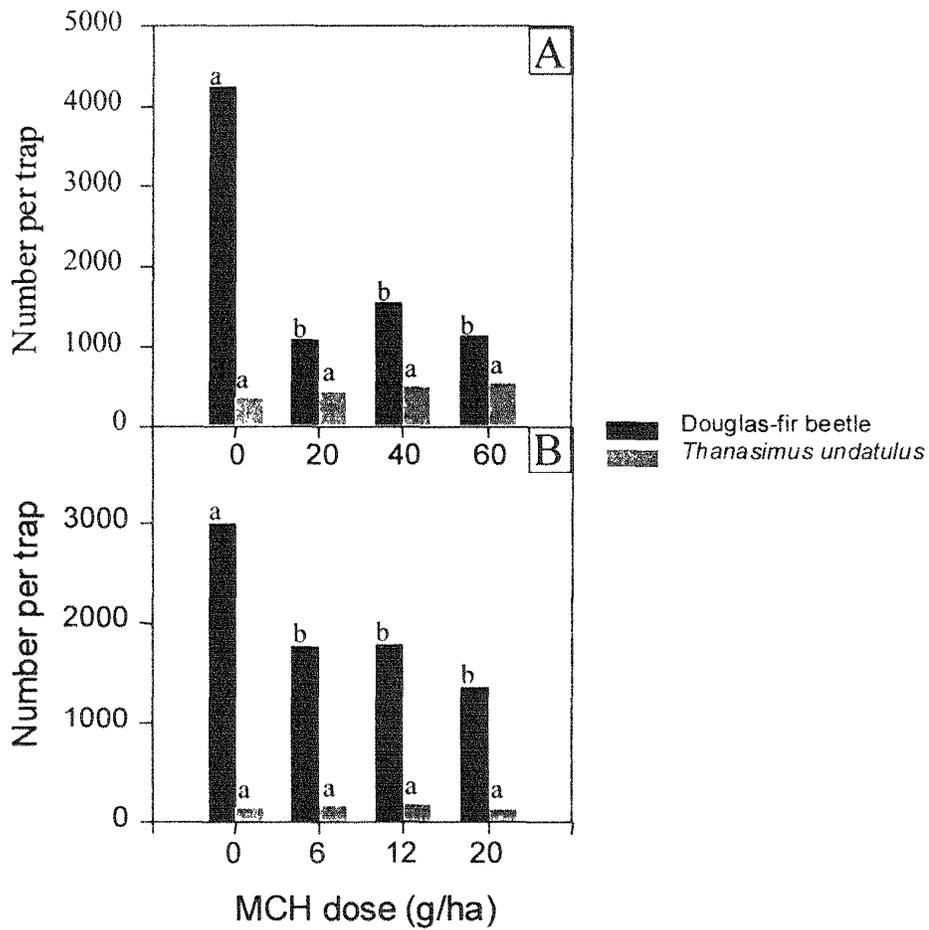


Fig. 4. Mean numbers of Douglas-fir beetles and *Thanosimus undatulus* collected in pheromone-baited traps at plot centers following application of MCH at various doses in (A) 1994 and (B) 1995. For each year and insect species, letters indicate significant differences ( $P < 0.05$ ).

**Table 1. Brood production and brood adult and natural enemy densities (#/m<sup>2</sup>) in bark samples collected at 7 m height from Douglas-fir beetle infested trees on MCH-treated and control plots in northeastern Oregon, 1995.**

	Control	MCH-treated
Brood production (brood adults/2(attacks))	0.58	0.59
Brood adults	138.2	162.3
Hymenopteran cocoons	129.2	144.9
<i>Thanasimus undatulus</i>	0	3.3
<i>Enoclerus sphegeus</i>	5.8	3.3

Data from four 120 cm<sup>2</sup> samples collected from 7 trees in each treatment. There were no significant differences between treatments ( $P > 0.05$ ).

At the present time, the use of MCH to protect live trees in high-value stands is an operational treatment. The only obstacle to full implementation of this technology in the U.S. is registration of MCH by the Environmental Protection Agency.

#### Aggregation Pheromones

Aggregation pheromones have been used in the trap-tree harvest method to concentrate Douglas-fir beetles. In this approach, pheromone-baited trees are harvested after they become infested to destroy the developing brood. Replacing the baited tree with an artificial trap could potentially increase the efficiency of a trapping program in a number of ways. Possible advantages of traps over trees include more flexibility in placement, unlimited trapping capacity, no reemergence, and less impact on some natural enemies.

A study conducted in northeastern Oregon in 1992 and 1993 demonstrated the potential for using pheromone-baited traps to manage the Douglas-fir beetle (Ross and Daterman 1997). Large numbers of beetles were collected in the traps and infested trees were concentrated near the trap sites. Although this study did not demonstrate conclusively that trapping reduced tree mortality in the outbreak area, it did show that mass-attacked trees were concentrated in the vicinity of traps even though traps were placed in openings 50-150 m from host trees. In British Columbia, pheromone-baited traps had a similar effect (Paulson 1995). Another potential problem with traps is the large numbers of predators that are collected. In the Oregon study, *Thanasimus undatulus* represented over 97% of the predators that were trapped and the ratio of Douglas-fir beetles to *T. undatulus* was about seven to one (Ross and Daterman 1996). The significance of catching such large numbers of *T. undatulus* is unknown. Under laboratory conditions, *T. undatulus* prefers smaller scolytids that are sometimes associated with the Douglas-fir beetle (Schmitz 1978). Additionally, over the last two years we have found approximately equal numbers of *T. undatulus* and *Enoclerus sphegeus* in bark samples from the lower 8 m of Douglas-fir beetle infested trees (unpublished data). The number of predators collected in multiple-funnel traps can be reduced by physical modifications that selectively exclude them or provide for their escape (unpublished data). Lure composition and pheromone release rates can affect trap selectivity

also. There are still many questions that remain to be answered regarding the most efficient design of an operational trapping program. Other possible uses of Douglas-fir beetle pheromones include creating snags and canopy gaps to increase structural diversity in managed stands, monitoring population trends, and enhancing effectiveness of natural enemies.

### **Meeting Ecosystem Management Objectives Through IPM**

Forest management in the U.S. has been undergoing dramatic changes in recent years, particularly on public lands. The emphasis on timber production that prevailed through the mid 1980's has been replaced by the concept of ecosystem management. Maintaining the ecological integrity and sustainability of forests while producing desired resources is the cornerstone of ecosystem management. Forestry has become much more complex as a result of this shift in policy. Forest managers are currently struggling to find the appropriate balance in producing a diverse array of resources and values.

Pest management has also become more complicated in the context of ecosystem management. There are now more constraints to implementing silvicultural controls for the Douglas-fir beetle than there were just a few years ago. However, silvicultural treatments remain the first line of defense for preventing undesirable tree mortality. Silvicultural strategies should be used wherever they are compatible with resource management objectives, especially on private lands managed primarily for timber. On most public lands, there are limited opportunities to prevent Douglas-fir beetle outbreaks through silviculture. For example, virtually all existing mature or old-growth stands on public lands are now reserved as habitat for species that depend upon late successional stage forests. The goal of management is to protect existing old-growth stands and facilitate successional processes in younger stands to increase the area of forests with similar characteristics. The short supply of old-growth forests makes them highly valued, but also places them at high risk to infestation by the Douglas-fir beetle which prefers to breed in large, old trees (Furniss et al. 1979).

A number of recent changes in silvicultural practices on public lands could potentially create favorable habitat for the Douglas-fir beetle. Rather than removing or treating large diameter slash following harvest operations as was common in the past, the current trend is to leave more of this material on the site. In some cases, trees are purposely topped or felled and left on the site to create standing and down woody debris for added structural diversity, wildlife habitat, and forage. There is also increasing opposition to removal of dead and dying trees such as those damaged by windstorms and wildfires. Much of this material is now being left in the forest for its ecological value rather than being removed for economic, pest management, or wildfire prevention considerations. There has been increasing interest in allowing wildfires to burn if they do not threaten life or property. If this trend continues, it may result in more fire-damaged trees some of which will not be salvaged. Although there is interest in thinning the abundance of overstocked stands on public lands, many areas will remain untreated to provide thermal and hiding cover for wildlife, to protect soil and water resources, and for other reasons. The combined effect of these changes in management practices will be to create more breeding sites for the Douglas-fir beetle.

Pheromone applications could help to prevent or alleviate some of the potential Douglas-fir beetle problems associated with changing silvicultural practices. MCH could be applied to high-value stands such as recreational, cultural, and administrative sites, highway

corridors, old-growth reserves, and riparian areas to reduce the probability of tree mortality occurring in these locations during beetle outbreaks. At the same time, pheromone-baited traps could be located in general forest areas where tree mortality is less disruptive to management objectives. Sanitation or salvage logging might be prescribed in the vicinity of trap sites if it is consistent with management objectives. Where large volumes of fresh woody debris from natural or human-caused disturbances must be left in the forest, MCH could be applied to prevent the buildup of beetle populations that could threaten resource values. Other pheromone-based strategies that are yet to be developed could further compliment existing pheromone and silvicultural treatments. We plan to begin testing the application of pheromones at the landscape scale beginning in 1997.

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# The attractiveness of pine branches infected with selected wood-colonising fungi to the Large Pine Weevil (*Hylobius abietis*)

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**ABSTRACT** This paper describes laboratory experiments designed to evaluate the attractiveness of pine branches overgrown by fungi to Large Pine Weevil (*Hylobius abietis*) females. These experiments attempt to explain differences observed in the field where *H. abietis* females have been shown to exhibit different colonisation rates of Scots Pine stumps infected with *Phlebia gigantea* (Fr.: Fr.) Donk and *Trichoderma harzianum* Rifai.

The results indicated, that in contrast to *T. harzianum*, the *Ph. gigantea* fungus inhibited the attractiveness of pine branches to this insect. The *Ph. gigantea* mycelium as well as the *T. harzianum* mycelium decreased the attractiveness of pine branches as food to the weevil.

**KEY WORDS** *Hylobius abietis*, *Phlebia gigantea*, *Trichoderma harzianum*, pine branches, pine stumps

WEEVILS OF THE genus *Hylobius* (Coleoptera: Curculionidae) are pests of young conifer plantations. The large pine weevil (*Hylobius abietis* L.) is perhaps the most important species commercially and is widely distributed throughout temperate parts of Europe and Asia. *H. abietis* is at its most damaging where reafforestation is attempted in clearfelled areas that previously supported a conifer crop. The beetles of *H. abietis* are attracted by the volatiles emanating from the resin of fresh conifer stumps left during clearfelling. These fresh conifer stumps then act as breeding material for the large pine weevil's development from egg to larvae and then pupae. Adults then emerge from the stumps causing serious economic seedling losses by feeding on the bark of these seedlings (mainly pine, spruce and larch). Heavy infestations caused by this pest may result in the widespread loss of young trees for several years after planting. *Hylobius pinastri* Gyll. is also a well known species, but of minor economic importance.

To estimate or to control the population density of those two species, pine billets or artificial traps with food attractant are commonly used in Poland (Kolk 1994). The most common method of protecting reforested areas against both species (Glowacka 1991) is to dip the seedlings in contact insecticides before planting and/or by spraying them with these chemicals after planting.

To protect forest plantations without the use of labour-consuming traps or insecticides, which may have a negative impact on the forest environment, experiments using a biological control agent were carried out in Poland. The main aim of these studies was to reduce pine weevil abundance within restocked areas, by disturbing the development of the *H. abietis* larvae in conifer stumps. The research estimated the impact of *Phlebia gigantea*

(Fr.: Fr.) Donk and *Trichoderma harzianum* Rifai fungi on the colonisation of Scots pine (*Pinus sylvestris* L.) stumps by the large pine weevil (Skrzecz 1996). *Ph. gigantea* as a competitor of *Heterobasidion annosum* (Fr.) Bref develops in pine stumps and their roots and causes a rapid decay of wood (Sierota 1981). The *Trichoderma* species are also wood-colonising fungi, which cause the suppression of the *H. annosum* mycelium (Sierota 1979).

The results of the field trials showed, that the infection of stumps with *Ph. gigantea* mycelium reduced their colonisation by *H. abietis* (Skrzecz 1996). Stumps infected with *T. harzianum* mycelium were colonised by the pest to the same degree as uninfected ones.

To find the causes of the differences between large pine weevil colonisation of stumps uninfected and infected with fungi, the laboratory tests were set up to evaluate the attractiveness of pine branches treated with the *Ph. gigantea* and *T. harzianum* mycelia. These experiments were carried out while the principal author was on research attachment at the Forestry Commission Research Division's, Northern Research Station in Scotland.

### Materials and Methods

Beetles of *H. abietis* were collected in 1994 from a 1yr old clear-cut area felled in March 1993, in Tentsmuir forest on the eastern coast of Scotland. In the laboratory, the sex of the insects was determined with the use of a microscope and females were used in tests. Before the experiment, females were stored in plastic boxes without any food for 24 hours.

Fresh Scots pine branches were cut into fragments 10 cm in length and 2.5-3.0 cm in thickness. The fragments were divided into three groups. The first group consisted of fragments infected with *Ph. gigantea* mycelium, the second of fragments infected with *T. harzianum* mycelium, the third group were uninfected control fragments. The branch fragments were infected by placing an inoculated fungal disc of 0.5 cm diameter on each end of the stem section. These discs had been previously dissected from a maltose-agar medium overgrown for 8-days by pure strains of the fungi under study. Each group of fragments were placed in separate plastic containers with water-soaked filter paper in the bottom. All branch fragments were incubated for 4 weeks at a temperature of 20°C. In the tests, the fragments of pine branches overgrown by a 4-week mycelium of *Ph. gigantea* or *T. harzianum* were used. After 4 weeks of branch incubation, about 50% of the surface area of each fragment infected with *Ph. gigantea* was covered by the mycelium, while the mycelium of *T. harzianum* overgrew about 30-40% of the surface area of each infected fragment. No mycelium were found on the control branch fragments.

The attractiveness of pine branches to large pine weevil females was tested using both a Time Lapse Video Arena and a 4-arm olfactometer.

The Time-Lapse Arena consisted of a glass box filled with dry forest litter. A video camera mounted over the arena was used to observe the beetles' behaviour over a long time period. Six fragments of pine branches were placed on the forest litter inside the glass box, these consisted of 2 replicate stem sections of uninfected material, 2 replicates of stem infected with *Ph. gigantea* and a further 2 infected with *T. harzianum*. The final position of branch fragments had the shape of a star, because the fragments infected with the same fungus and control ones were placed opposite to each other. Females of *H. abietis* were placed in the centre of this "star". To prevent beetles escaping from the Time Lapse Arena, the inner top border of the glass box was coated with fluon.

In a six-day experiment, 5 females marked with white paint were tested every day. Each test was started at 3 p.m. and the video camera placed above the glass box, recorded the insects' behaviour for 18 hours a day during the females most active feeding period. Prior to each test, the insects and fragments of pine branch were replaced.

After the tests, the video films were analysed and the attractiveness of pine branches to the insects was estimated on the basis of the number and duration of beetle visits to individual pine branches.

The statistical software programme STATGRAPHICS 5.0 was used for statistical analysis. The data related to the duration of insects visits to pine branches were analysed by one-way analysis of variance after applying Bartlett's transformation and Tukey's test.

The reaction of *H. abietis* females to the volatiles emanating from pine branches uninfected and infected with the fungi under study was determined using a 4-arm olfactometer. The main part of the olfactometer consisted of a flat square chamber joined in the corners with four glass containers, in which pine branches were placed. The air mixed with volatiles from branch fragments was driven to the main chamber, where individual beetles could choose to move towards an attractant odour or control. Each test was recorded by the video camera placed above the main chamber.

The fragments of pine branches infected with *Ph. gigantea* or *T. harzianum* and uninfected ones were placed separately in the 3-glass containers of the olfactometer while the fourth one was empty to test the responses of the beetles to the air without volatiles. Every two hours the pine branches were replaced.

One hundred females of the large pine weevil were studied and each insect was tested only once in the arena. The response of a beetle in this test was regarded as positive, when the insect went from the main chamber into the selected glass container and stayed there for at least 1 minute. The speed of the air flown from the containers with pine branches to the main chamber was 0.4 l/min. The experiments were conducted after 3 p.m. during the period of greatest weevil activity.

## Results

The results obtained for the experiments in the Time Lapse Arena indicated that the beetles visited pine fragments infected with *Ph. gigantea* for the shortest time. The females remained slightly longer on the pine branches overgrown by *T. harzianum* but the longest visits were to control fragments. The average duration of each visit by *H. abietis* to pine branches are shown in Fig. 1.

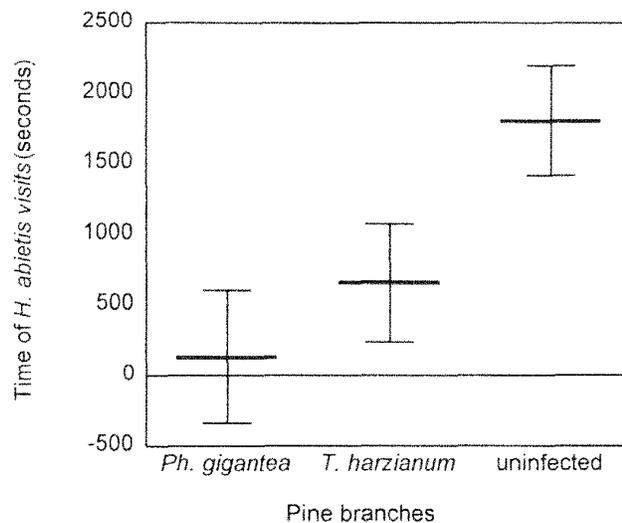
The results of the one-way analysis of variance showed significant differences between the time of beetle visits on the pine fragments (Table 1).

**Table 1. The duration of *H. abietis* visits to pine branches uninfected and infected with fungi *Ph. gigantea* or *T. harzianum*. One-way analysis of variance.**

Source of variation	Sum of squares	d. f.	Mean square	F-ratio	Significance level
Between groups	2.469414	2	1.2347068	70.112	0.001
Within groups	15.215406	864	0.0176104		
Total	17.684820	866			

The Tukey's test revealed two homogenous groups (Fig. 1):

1. The time of beetles' visits to the pine branches infected with *Ph. gigantea* or *T. harzianum*.
2. The time of beetles' visits to the uninfected pine branches.



**Fig. 1. The duration of *H. abietis* visits on pine branches uninfected and infected with the fungi *Ph. gigantea* or *T. harzianum*. The results of Tukey's test**

Analysis of the frequency of pine weevil visits showed that a lower number of visits were made to the branches overgrown with *Ph. gigantea* mycelium (Table 2). A greater number of visits were made to branches infected with *T. harzianum* than *Ph. gigantea*, but uninfected branches were visited most frequently.

No evidence of beetle feeding was found on pine branches infected with these fungi but feeding was observed on uninfected pine branches.

**Table 2. The number of *H. abietis* visits to pine branches uninfected and infected with the fungi *Ph. gigantea* or *T. harzianum*.**

Pine branches	The number of visits
<i>Ph. gigantea</i> infected	233
<i>T. harzianum</i> infected	296
uninfected	338

The results of the olfactometer study indicated that the time to test each individual female of the large pine weevil was different and ranged from 5 to 45 min. Some of the beetles selected the attractant in a short time, while the others first chose one of the attractants and then they selected a different one.

It was found that pine branches overgrown by the *Ph. gigantea* mycelium attracted the lowest number of females (Table 3). Pine branches infected with the *T. harzianum* mycelium and volatile-free air attracted similar number of beetles, but the highest number of females was attracted by uninfected branches.

**Table 3. Percentage of *H. abietis* females attracted by pine branches uninfected and infected with *Ph. gigantea* and *T. harzianum*.**

Pine branches	Percentage of females
<i>Ph. gigantea</i> infected	6
<i>T. harzianum</i> infected	30
uninfected	37
air	27

### Discussion

The beetles of the large pine weevil are attracted to clearfelled areas by the odours emanating from cut timber, stumps and slash. Experiments carried out in the 1970s in Finland (Selander 1979) and in the 1980s in Sweden (Tilles et al. 1986 a,b) indicated that monoterpenes such as alpha-pinene and 3-carene and the bio-degradation product ethanol were the most important attractants for the migrating pine weevils. As pine stumps treated with *Ph. gigantea* are not colonised by *H. abietis*, it raises the question of whether *Ph. gigantea* mycelium can inhibit the attractiveness of pine stumps to the pest. To answer this question laboratory tests of the attractiveness of fungi-infected and uninfected pine branches to *H. abietis* were performed.

In contrast to the more prevalent natural conditions, pine stem sections were used in the experiments rather than roots or stumps. This was because the experiments were

logistically much easier to perform and also because pine branches and stems are also known to be used for weevil feeding and oviposition (Christiansen 1971, Skrzecz 1996).

The results revealed that *Ph. gigantea* mycelia inhibited the attractiveness of pine branches to *H. abietis* females. The lowest frequency, the shortest visits as well as the lowest number of female beetles were attracted to pine branches infected with *Ph. gigantea*. *T. harzianum*-infected branches showed intermediate attractiveness while the frequency and duration of beetle visits to control branches was found to be greatest for uninfected pine branches. These therefore appeared to be most attractive to *H. abietis* females.

Both fungi inhibited the attractiveness of branches as a food and probably would also decrease the value of stumps as an oviposition site for these insects.

The results obtained from early field tests and laboratory experiments suggest that *Ph. gigantea* grows rapidly in infected stumps, changes their wood structure and the quantity or composition of the volatiles emanated from the pine and that the infected stumps become less attractive to the *H. abietis* females.

### Acknowledgements

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# Spatial and Temporal Attack Dynamics of the Mountain Pine Beetle: Implications for Management

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**ABSTRACT** Colonization of a host tree by the mountain pine beetle, MPB (*Dendroctonus ponderosae* Hopkins, Coleoptera: Scolytidae), involves a complex, synergistic interaction between host-produced chemicals and beetle-produced pheromones. This system of chemical communication enables a massive aggregation of beetles on a single resource, thereby ensuring host death and subsequent beetle population survival. Because a single host tree is a limited food and breeding resource, MPB populations have evolved mechanism(s) for termination of colonization on a tree at optimal beetle densities, with a concomitant shift of attacks to nearby trees. Several hypothesis attempt to explain this pheromone-mediated phenomena. In an effort to more fully understand the entire colonization process, including the switch of attacks among trees, we observed the daily spatial and temporal attack process of MPB (non-epidemic) attacking lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann). Our results from this preliminary study suggest that beetles switch attacks to a new host tree before the original focus tree is fully colonized, and that verbenone, an anti-aggregating pheromone, may be acting within a tree rather than between trees. Results from this and additional on-going studies are being used for parameterization of a spatially explicit model of MPB dispersal. Alternative hypotheses for MPB colonization and management implications are discussed.

**KEY WORDS** mountain pine beetle, verbenone, switching, spatial, lodgepole pine

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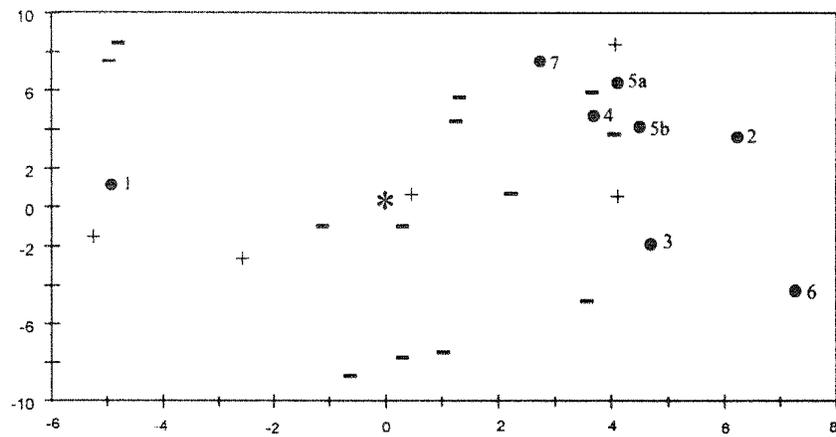
MANY SPECIES OF bark beetles in the genus *Dendroctonus* (Coleoptera: Scolytidae) use kairomones and pheromones in the processes of host selection, attack, and colonization (Borden 1982, Wood 1972). Female *D. ponderosae* Hopkins (MPB), which in this species are usually responsible for initiating a new attack, bore into the bark and through a chemically mediated synergistic reaction with host chemicals, release *trans*-verbenol. *Trans*-verbenol is an aggregative pheromone attracting both sexes (Pitman et al. 1968, Hughes 1973, Pitman 1971). At higher concentrations of *trans*-verbenol, higher proportions of males are attracted (Renwick and Vite 1970). Males produce *exo*-brevicommin which at low concentrations primarily attracts females (Conn et al. 1983). Both inhibition (Borden et al. 1987, Rudinsky et al. 1974) and attraction (Shore et al. 1992) of beetles at higher concentrations of *exo*-brevicommin have been observed. This system of chemical communication enables a massive aggregation of individuals on a single "focus" tree which, for species such as MPB, is selectively advantageous in overcoming host defensive mechanisms. As with most herbivores, however, there is an optimal density range of individuals on an exhaustible food resource (Berryman et al. 1985). If beetle densities on a single tree are too high, mortality can result from within-tree competition for limited

breeding and feeding space.

Several hypothesis attempt to explain the termination of colonization on a single tree at optimal beetle densities. The first assumes that anti-aggregative or inhibitory pheromones such as verbenone and *exo*-brevicomine deter incoming beetles, thereby terminating additional attacks and ensuring that beetle attack density does not exceed the threshold for optimum brood survival (Borden et al. 1987). Verbenone is a semiochemical produced by MPB (Rudinsky et al. 1974), through autoxidation of host terpenes, and by enzymatic conversion by yeasts (Hunt and Borden 1989). Based on this hypothesis, as verbenone is released, the majority of beetles are dispersed at some distance, switching attacks from the focus tree to adjacent recipient trees (Gieszler et al. 1980).

A second hypothesis emphasizes the role of host resistance, citing cessation of resin exudation as the primary cause for termination of colonization on a particular tree (Renwick and Vite 1970, Raffa and Berryman 1983). As with the first hypothesis, attacks switch to adjacent trees once the focus tree becomes fully utilized--the difference lying in the roles of inhibitory pheromones and host-tree resins. In the second hypothesis, inhibitory pheromones are one component of a series of territorial behaviors which, in conjunction with a decrease in resin exudation, enable individual colonizers to maximize reproductive potential (Raffa and Berryman 1982, 1983). From this perspective, inhibitory pheromones are perceived and function at the local scale, while attacks switch to neighboring trees because the focus tree has become fully colonized and resin exudation ceases. A third hypothesis, labeled the "threshold model", assumes that as a tree is mass attacked, the high concentration of *trans*-verbenol being emitted in the local area causes incoming beetles to attack neighboring trees which are enveloped in the pheromone cloud (Coster and Gara 1968, Gara and Coster 1968, see Geisler et al. 1980). A threshold level of *trans*-verbenol is necessary to cause landing and attack on adjacent trees.

The presence of inhibitory pheromones in the genus *Dendroctonus* is known (Hunt et al. 1989, Libbey et al. 1985, Pitman et al. 1969, Ryker and Yandell 1983, Rudinsky et al. 1974). However, our lack of knowledge about the explicit function of these pheromones in MPB community ecology is exhibited by confounding results in past research endeavors (see Amman and Lindgren 1995 for a review). It is unclear whether inhibitory pheromones such as verbenone have a shielding effect around the tree under attack and are the main cause of switching, or if their function is to regulate attacks once beetles are on or very near the tree surface, playing a more localized role in the switching process. If indeed verbenone has a shielding effect, unknown parameters include the size of the shielding plume, and timing of its influence. The main objective of this study was to collect information on the spatial and temporal sequence of the MPB switching process. Original motivation for the study was to obtain quantitative information for parameterization of a mathematical model of MPB dispersal which includes chemical ecology and spatial interaction between beetles and host trees (Powell et al. 1996). Data at the fine spatial and temporal resolution necessary for deriving model parameters was unavailable in published literature. In this study we did not measure pheromone emission, but rather the effect of these pheromones on beetle behavior.



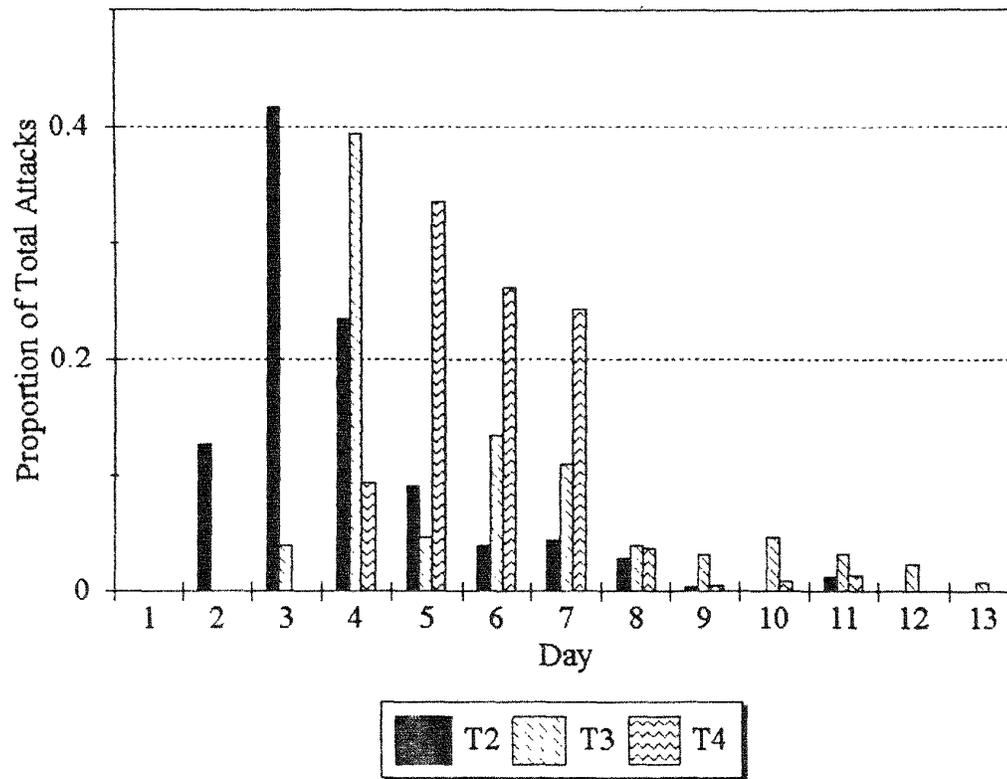
**Figure 1.** Spatial map (in meters) of all trees in Plot 1. ☆ is the baited tree at plot center, ① are successfully attacked trees, with the number representing the day in the attack sequence, ⊕ are strip-attacked trees, and ⊙ are live trees at the end of the attack period. Size of circle indicates relative dbh of each tree.

### Methods

Three plots in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) stands in the Gold Creek drainage of the Sawtooth National Recreation Area were selected. Species composition in the drainage is approximately 80% lodgepole pine and 20% Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.). Currently there is a sub-epidemic MPB population which has been slowly building during the last 4-5 years. All plots were at an elevation of approximately 2073 meters, and at least 100 meters apart. On August 6, 1995, an MPB pheromone tree bait<sup>1</sup> was placed on the north side of a single tree in each plot. Based on emergence data from a nearby experiment (Bentz unpublished data), beetle flight in the area had just begun. The bait was left on each focus tree for 24 hours, then removed. All trees within a radial distance of 10 meters (20 meter diameter) from the focus tree were monitored for beetle attacks until August 18 at

which time colonization of trees within the plots had, for the most part, stopped. Attacks were tallied twice per day (approximately 8:00 am and 5:00 pm), by height on the bole (0-1.2 meters, 1.2-1.8 meters, and 1.8-2.4 meters) and aspect of the bole (N, E, S, W) where the attack was located. An attack was counted once the nesting hole was initiated and resin or frass was noticed, and consequently landing rates were not included.

Each entry was marked with a colored push pin, and later tallied. Because our intent was to monitor the 'natural' attack process of MPB on lodgepole pine, those trees attacked while the bait was on the focus tree were removed from data analysis. A stem map was developed for each plot including diameter of each tree at 1.5 meters above the ground (dbh) (Fig. 1). Only results for plot 1 are included here.

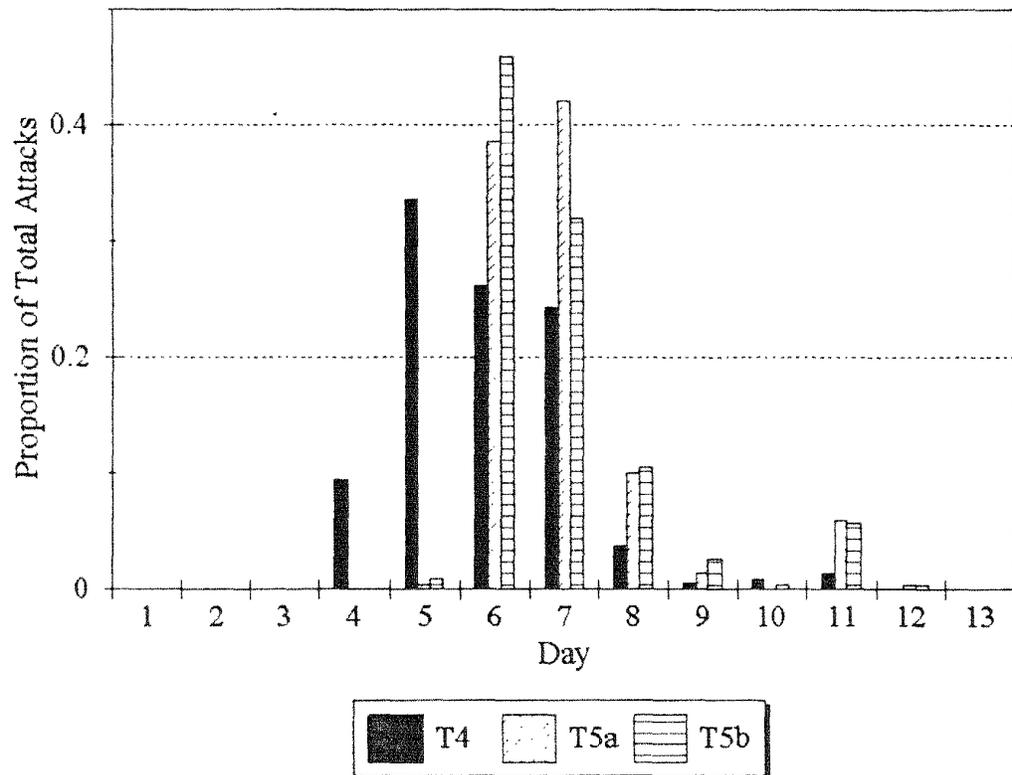


**Figure 2.** Proportion of total attacks on lower 2.4 meters of bole of 3 successfully attacked trees, by day of attack. Day 1 is August 6, 1995.

### Results and Discussion

The first hypothesis for switching suggests that the production of inhibitory pheromones during the latter stages of colonization deter incoming beetles and therefore cause a switch to adjacent trees. If this is true, then inhibitory pheromones would be

perceived prior to beetles landing on the focus tree, with a switch of attacks to adjacent trees once the original focus tree was fully colonized. At the point of full optimization of the focus tree, inhibitory pheromones would produce a shield, resulting in no additional attacks on that tree. Our results do not support this hypothesis. On the day of peak attack density on Tree 2, new attacks occurred on Tree 3. The following day, at peak attack density of Tree 3, Tree 4 was initially attacked (Fig. 2). The next day, at peak attack density on T4, T5a and T5b were attacked (Fig. 3). In all cases, on the day when attacks switched to another tree, the proportion of attacks on the current focus tree was less than 45% (Figs. 2, 3). These results suggest that attacks are redirected to a new tree prior to full utilization of the current tree under attack. McCambridge (1967) also observed that trees adjacent to the focus tree came under attack by MPB before the initial focus tree had been fully mass attacked. Anderbrandt et al. (1988) observed a similar pattern with *Ips typographus* Linnaeus. Others (Geiszler et al 1980), however, reported that the switch to a new tree occurred after the original focus tree had been fully mass attacked.



**Figure 3.** Proportion of total attacks on lower 2.4 meters of bole of 3 successfully attacked trees, by day of attack. Day 1 is August 6, 1995.

The basis of the second hypothesis is that resin exudation would cease when the original focus tree was fully colonized. At this time, attraction to that tree would be terminated due to an absence of the tree-produced precursor,  $\alpha$ -pinene, necessary for beetle production of *trans*-verbenol. Without production of the aggregating pheromone *trans*-verbenol, additional attacks would not occur on the focus tree once the switch to adjacent trees begins. Again, our results do not support this hypothesis for switching of attacks. Beetles continued to attack the original focus tree after adjacent trees came under attack (Figs. 2, 3).

The basis for the third hypothesis is that given a threshold number of attacking beetles on a focus tree, the level of *trans*-verbenol being produced would be great enough to envelope surrounding trees in the aggregating plume. All trees within the aggregation pheromone plume would be attractive and experience attacks. Therefore, additional landing and attacks could occur on the focus tree even after attacks were initiated on adjacent trees. The larger the focus tree the greater number of attacks, and hence the larger the size of the aggregating pheromone plume. Data from our preliminary study support this hypothesis for switching of attacks. We observed that attacks on nearby trees were initiated while the focus tree was also still being attacked.

We use the term "switch" to represent a shift in attacks on consecutive days between a focus tree and surrounding trees. In our study, switch in attacks from a focus tree to nearby trees typically occurred the second day of attack, and at time of peak daily attack density on the focus tree (Figs. 2, 3). This coincides with the time of maximum production of *trans*-verbenol which peaks for individual beetles at about 24 hours of feeding (Pitman and Vite 1969). However, female MPB which had fed in lodgepole pine bolts for 24 hours also contained significant amounts of verbenone (Hunt and Borden 1989). Therefore, the large concentrations of both aggregation and inhibitory pheromones in the first few days of attack on a tree may cause MPB to be attracted to the focus tree, and both space out on the bole and participate in the tree-switching mechanism (Bedard et al 1980, Birgersson and Bergstrom 1988). The function of inhibitory pheromones such as verbenone in this tree-switching mechanism is unclear, however.

Based on results in our study, shift in attacks to a new host occurred before the focus tree was fully colonized, although each tree continued to be attacked at a decreasing daily rate for 5-6 days. If beetles were responding to verbenone before landing on a tree as suggested by Bertram and Paine (1994), the range of perception in our study plot was smaller than the distance between the two closest trees attacked within a day (< 1 meter). If verbenone was providing an inhibitory plume around a tree, most attacks on that focus tree would cease, signaling a fully utilized resource, although additional attacks may occur due to variability in the response threshold of individual beetles. However, because attacks shifted to a new tree while less than 50% of total attacks had occurred on the focus tree, verbenone (and other inhibitory pheromones) could be functioning at a more local scale, perhaps around a particular entrance hole as was suggested previously (Raffa and Berryman 1983, Renwick and Vite 1970). While large amounts of aggregating pheromones are still being produced, verbenone may provide a means to reduce competition within a tree, while some other component of the pheromone system is the primary cause of attack switch to a new tree. Our results indicate that a shift in attacks to a new tree occurred on the day of greatest attack rate

on a nearby tree. If we assume that time of greatest attack rate on a particular tree coincides with peak *trans*-verbenol emission from that tree, switch in attacks to a new tree could be explained by a spill-over effect. This would occur when the concentration of aggregation pheromone was large enough to envelope surrounding trees, resulting in random attacks on trees enveloped by the plume, setting up a new focus tree. The new focus tree then has an increase in number of attacks, while attacks on the old focus tree declines due to a reduction in attacks and concomitant *trans*-verbenol production (Pitman and Vite 1969). These results were seen in our data, whereby number of attacks on recipient trees the first day of switching was always less than number of attacks on the focus tree that same day, although the following day, attacks on recipient tree were greater than previous focus tree (Figs. 2, 3). Although we do not know the size of aggregation pheromone plumes, our data does suggest that the inhibitory, or anti-aggregation plume being released is smaller than the distance between two consecutively attacked trees spaced less than 1 meter apart.

### Implications for Management

Techniques for identifying bark beetle semiochemicals were first developed in the 1960's (Silverstein et al. 1967). A plethora of field and laboratory trials for measuring the response of beetles to these semiochemicals have occurred since that time. Because opportunities for exploitation of beetle pheromones for forest management purposes are numerous, the temptation for researchers in this field to hastily launch into applied programs has been great. However, if the immense natural complexity of these semiochemicals is not fully understood, effectiveness of field applications may be inconsistent and often times unsuccessful (Borden 1995). This has been the case with attempts at applying synthetically produced verbenone for protecting stands of trees from attack by the mountain pine beetle (Amman et al. 1989, Amman et al. 1991, Amman and Lindgren 1995, Bentz et al. 1989, Gibson et al 1991, Lindgren and Borden 1993, Lindgren et al. 1989, Lister et al. 1990, Shore et al. 1992). The inconsistent results from year to year and between host types and geographic regions could be due to a number of reasons (Borden 1995) including: 1) technical problems with deployment of the pheromone, 2) effects of microclimate, 3) changes in behavior and/or genetic makeup with changes in the insect population phase (Amman 1993) and 4) inadequate knowledge of the functional role of inhibitory pheromones in MPB population dynamics.

Because verbenone is used by so many species of aggressive bark beetles, and a large portion is produced by microorganisms in decaying wood, it may be a signal to beetles that the immediate substrate, either an entire tree or a localized space on a tree, is no longer suitable for colonization (Borden et al. 1987, Leufven and Birgersson 1987). The question remains whether MPB are responding to verbenone prior to or after landing on the tree. Our results suggest that verbenone may be acting within a tree rather than between trees, and that it does not provide a very large inhibitory shield around the tree under attack. This is a different functional role for verbenone in MPB chemical ecology than the role researchers previously had in mind when applying synthetic capsules in field trials. To this date, synthetic verbenone has been applied either aerially or by stapling single capsules on trees spaced throughout an MPB infested stand. These experiments were aimed at deploying a certain dose of verbenone per hectare. Conversely, if the functional role of verbenone is to

space beetles on a tree rather than between trees, alternative verbenone applications will need to be field tested.

Researchers have been tantalized by the hope that synthetically produced pheromones might be the answer to management of epidemic phase MPB populations. However, we need to step back and conduct additional research at the behavioral level to more fully understand the sequence of the colonization process, and the spatial and temporal influence of inhibitory pheromone(s) in MPB population dynamics. Inconsistent results in attempts to apply inhibitory pheromones in a management scenario attest to a current deficiency in our knowledge of their role in MPB chemical ecology.

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# Does drought really enhance *Ips typographus* epidemics? -A Scandinavian perspective

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**ABSTRACT** Availability of defenceless or weakly defended breeding material, e.g. trees felled or damaged by major wind storms, is a necessary requirement for an outbreak of the spruce bark beetle, *Ips typographus*. Water stress is also hypothesised to be an important predisposing factor, although this idea is mostly based on circumstantial observation of a coincidence between dry weather and beetle outbreaks. Whereas a causal relationship may well exist for certain scolytid beetles, experimental evidence is often scarce and in some cases contradictory. We examine information pertaining to population dynamics of the spruce bark beetle *Ips typographus* in Norway. This includes (1) experiments to assess effect of drought stress on host tree susceptibility to the beetle's pathogenic fungal associate, *Ceratocystis polonica*, and (2) results from a population monitoring program which has been in operation since 1980. Because drought often coincides with hot weather, one can confuse a direct effect on beetle propagation by hot weather with an indirect effect on insect dynamics through predisposition of the host trees. We conclude that apart from extremely rare cases of severe droughts lasting for a long period of time, direct effects of spring weather on beetle propagation are more likely to affect *I. typographus* dynamics than are indirect physiological effects working through the host trees.

**KEY WORDS** Bark beetles, Scolytidae, *Ips typographus*, water stress, weather, population dynamics

BARK BEETLE OUTBREAKS are often associated with water stress on the host trees. This connection is largely based on circumstantial observation of a temporal coincidence between dry weather and beetle outbreaks, but very few experiments have been carried out to test this assumption.

Here we review some recent evidence pertaining to the spruce bark beetle, *Ips typographus* L., and stress conditions of its host Norway spruce, *Picea abies* (L.) Karst. Recurring outbreaks of this insect in Eurasia may encompass thousands of square kilometres and lead to the killing of millions of spruce trees (Christiansen & Bakke 1988, Führer 1996).

For an *I. typographus* epidemic to erupt, local populations must reach a certain density to exceed the "Threshold of Successful Attack" on living spruce trees (Thalenhorst 1958). Windstorms undoubtedly act as precursors by providing defenceless breeding substrate in the form of fallen trees. Moreover, trees left standing after a gale with part of their root system torn are probably an easier prey than are intact trees.

Epidemics often also coincide in time with extended periods of hot and dry weather (for discussion, see Christiansen & Bakke 1988). This weather situation could boost beetle populations in two different ways: (1) indirectly - by drought influencing the physiological state of the trees rendering them susceptible to attack, and (2) directly - by high temperatures promoting extensive flight and search for host trees and accelerating brood development.

## Two Important Traits Of *Ips Typographus* Biology

A summary of our knowledge on the beetle's biology has been presented before (Christiansen & Bakke 1988), and we will only mention a few points that are relevant to our discussion here.

Very few of the world's ca 6000 bark beetle species are indeed "aggressive" or "primary" in the sense that they kill healthy trees. There is considerable evidence to support a general hypothesis that aggressive species have two crucial "assault weapons" in their arsenal: (1) effective aggregation pheromones, and (2) mutualistic fungi that help them in overcoming the tree's defences (Berryman 1972, Krokene 1996).

*I. typographus* possesses a highly efficient system of aggregation pheromones (Bakke et al. 1977, Schlyter 1985), the two main components being *cis*-verbenol and 2-methyl-3-buten-2-ol. *Cis*-verbenol is produced by oxidising  $\alpha$ -pinene from host resin (Vité et al. 1972) and methylbutenol is synthesised *de novo* (Lanne et al. 1989, Ivarsson 1995).

*I. typographus* also vectors several blue-stain fungi, spores of which are carried both externally and internally (Furniss & al. 1990). The role of these fungi in tree-killing has been debated for a long time. Experimentally, the question could be addressed in two different ways; by inducing attacks of axenic beetles, or by artificially inoculating the fungi into trees. The first alternative is experimentally difficult and has not yet been tested, but in 1980 we took the other approach, and have since then carried out a series of inoculation experiments. An important result of these studies is that one particular species of blue-stain fungus, *Ceratocystis polonica* (Siem.) C. Moreau, (= *Ophiostoma polonicum* Siem.) is constantly at the advancing front of micro-organisms spreading into *I. typographus*-attacked trees (Solheim 1992). The experiments have also established that *C. polonica* is pathogenic enough to kill trees of various spruce species when artificially inoculated under the bark in adequate doses (e.g., Horntvedt & al. 1983, Christiansen 1985a). Douglas-fir may also get killed by artificial inoculation of this fungus (Christiansen & Solheim 1990).

## Experiments To Assess Resistance Of Norway Spruce

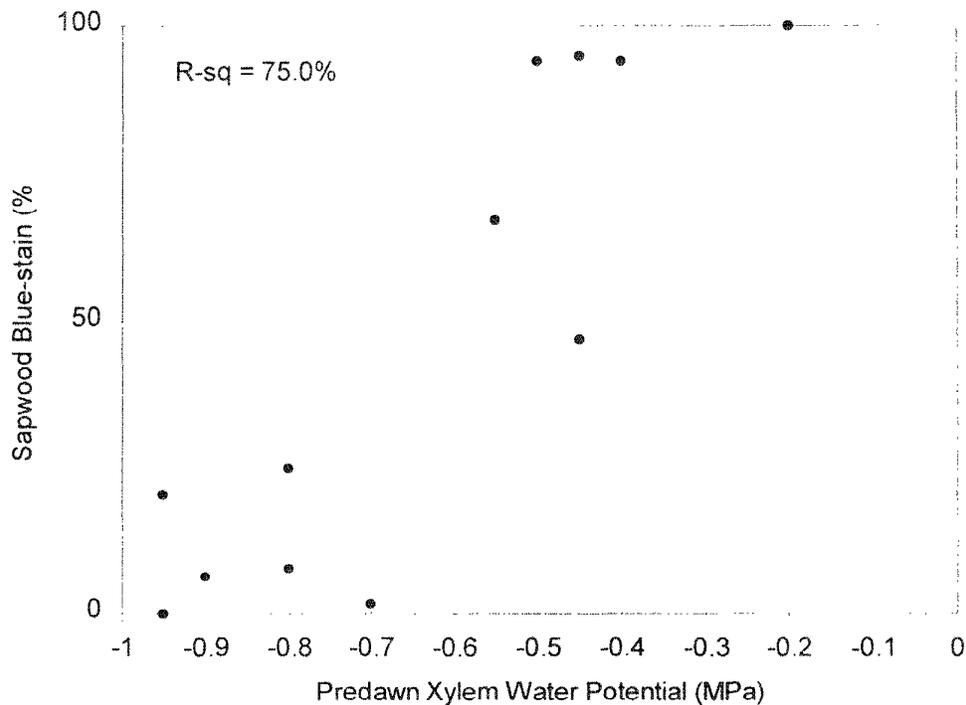
Despite the assumed links between host tree condition and beetle attack, few experiments have been carried out to test this idea. A main reason is probably the logistic problems involved in such experimentation; both in manipulating water relations of large trees and in administering a controllable number of beetle attacks. Ideally, trees of the right size and age should be experimentally treated to alter their physiology and then exposed to a prescribed number of beetle attacks. However, a fixed "attack force" of beetles would, by means of their aggregation pheromones, summon an uncontrollable number of "wild" beetles from the surroundings and thus upset an experiment, unless it be carried out in a beetle-free area. One way to overcome this problem is to screen the trees with a fine mesh netting to deny access to newcomers. This can be done with beetles that mainly utilise the branch-free part of the stem (Raffa and Berryman 1983), but *I. typographus* attacks normally extend well into the green crown, making this approach impractical.

We have tried an indirect approach to the problem by substituting bark beetle attacks with artificial mass-inoculation of agar holding *C. polonica* mycelium. By administering a specific number of infections to a tree we can define its "Threshold of Successful Infection"

above which the tree will succumb (Christiansen 1985a, b). This is parallel to Thalenhorst's (1958) "Threshold of Successful Attack", and although infection with mycelium is different from spore introduction by beetles, the number of *C. polonica* inoculations required to kill a given spruce tree appears to be roughly equivalent to the critical number of *I. typographus* attacks (Christiansen 1985b). Artificial mass-inoculation has also been used to estimate the relative resistance of Norway spruce trees subjected to various kinds of stress, such as drought and defoliation (Christiansen & Ericsson 1986, Christiansen 1992, Christiansen & Fjone 1993, Christiansen and Glosli 1996).

One experiment tested after-effects of water deficiencies (Christiansen 1992). Experimental trees (4-5 m tall) were deprived of precipitation for 3 consecutive growth seasons, during which they developed a significant but not extreme water stress, their pre-dawn xylem water potentials averaging ca -1.0 MPa (extremes down to -1.85), as compared to mean  $\Psi$  values of ca -0.5 MPa in unstressed controls. The experimental trees showed macro-nutrient deficiencies and lost a third of their foliage. In the fourth season they were not drought stressed but together with the controls they were mass-inoculated with a prescribed dose of *C. polonica*, high enough to cause fungal invasion of xylem and phloem. The hypothesis that stress would enhance the susceptibility to infection was refuted: on an average more cambium and phloem tissue was killed in control trees than in stressed ones (59% vs. 48%). This difference was, however, not statistically significant because of a high degree of variation between individual trees. Sapwood blue-staining did not differ between the two groups.

A later field experiment addressed the effect of current drought at the time of *C. polonica* infection (Christiansen & Glosli 1996). Clonal Norway spruce trees were used in this case, which significantly reduced the individual variation in host resistance. In autumn 1992 the ground below six ramets of each of two clones (#194 and #582) was covered with plastic tarpaulins to prevent winter precipitation from percolating into the ground, while six other ramets served as untreated controls. Next spring the tarpaulins were lifted from the ground and placed under the canopy of the (10-12 m tall) trees to lead precipitation away. By late June the experimental trees of clone #194 were significantly more stressed than controls, while clone #582 showed only slight differences. All trees were then mass inoculated with a standardised dose of *C. polonica*. When sapwood blue-staining was measured in autumn 1993 the stressed ramets of clone #194 proved to be much more resistant than the controls (Fig. 1). In clone #582 differences were small. Thus in clone #194 drought must have triggered some defence mechanism which enhanced the resistance to infection.



**Figure 1. Percent of sapwood cross-sectional area discoloured in individual Norway spruce trees by 14 September after mass-inoculation with the blue-stain fungus *Ceratocystis polonica* on 25 June; in relation to pre-dawn xylem water potentials measured on 23 June. Clone #194.**

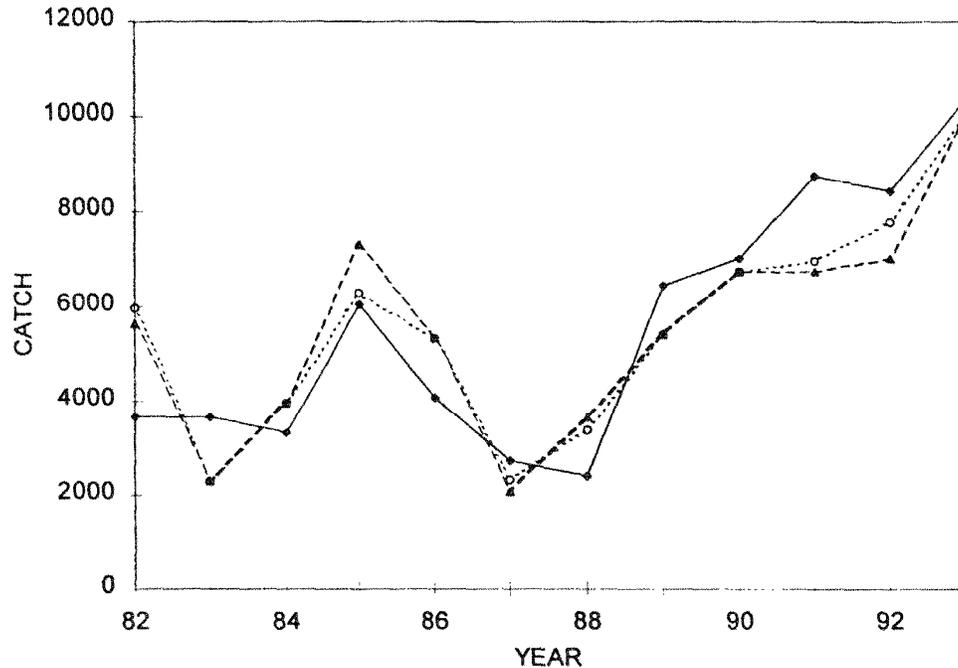
The studies may shed some light on the drought - susceptibility issue. They provide no direct evidence since artificial inoculation of *C. polonica* was used instead of real bark beetle attacks, but, as stated earlier fatal threshold numbers for *I. typographus* attacks and *C. polonica* inoculations seem to be of the same magnitude (Christiansen 1985b). Another criticism of the results is that the trees used (particularly in the first experiment) were smaller than those normally attacked by *I. typographus*. Despite these problems, it seems fair to conclude that the experiments do not support the idea that drought promotes bark beetle outbreaks by rendering spruce trees more susceptible.

### Population Dynamics And Weather

If drought does not promote *I. typographus* epidemics in South Norway by rendering trees more susceptible, we should consider the possibility that weather conditions act directly upon bark beetle propagation.

Since 1980 *I. typographus* populations in South Norway have been monitored annually with pheromone traps (Bakke & al. 1983). The captures, which show distinct

annual fluctuations (Fig. 2), are analysed in relation to weather factors and a model is developed which applies for areas where *I. typographus* is univoltine (Bakke 1992, Bakke & al. 1995). According to this analysis the catch in a given summer is positively correlated to the mean monthly maximum temperature of the previous May ( $R^2 = 0.40$ ). If the same temperature expression for the current May is included the correlation is improved ( $R^2 = 0.64$ ). Autocorrelation with catches of the previous summer improves the fit slightly.



**Figure 2.** Catches of *Ips typographus* in drain-pipe pheromone traps (solid line) compared to predictions from a model based on mean maximum temperature for May of the previous and current year, without (dashed line) and with (stippled line) autocorrelation of the previous year's population.

The results are interpreted thus: May is normally the main flight period of *I. typographus*, which has a temperature threshold for flight at ca 20 °C. When warm weather prevails in May, beetles emerge and fly within a short period of time; this results in concentrated and successful attacks on living trees. Consequently a large new generation ensues and a high number of beetles is caught the following summer; more so if warm spring weather increases attraction to the traps. Several consecutive warm days in May can, however, be rare in some years; these warm spells are often interspersed by periods of cool weather. This precludes mass flight and concentrated, successful attacks. Consequently, propagation is hampered and next year's flying population correspondingly smaller.

### Discussion: Do We Confuse “Dry Summers” And “Hot Summers”?

As stated initially, bark beetle epidemics often coincide with hot and dry weather, and a causal relationship could be that drought stress reduces host tree resistance.

In South Norway severe drought on larger trees is probably a rather unusual condition at the time of *I. typographus*' main flight, i.e., only 1-2 months after snow melt and thawing of the ground. However, in extremely rare cases a drought may prevail for an extended period of time: during the years 1968-76 a water deficit developed corresponding to one whole year's precipitation and water tables dropped by several meters in deep gravel deposits of south-eastern Norway. From 1968 through 1973 a significant part of this deficit was recorded as a lack of autumn and winter precipitation; this was followed by three unusually dry summers and this sequence may have aggravated the bark beetle epidemics of the 1970s (Worrell 1983). A prolonged drought of the same magnitude also occurred during the 1840s, prior to an outbreak around 1850. This was the last major epidemic in South Norway before the 1970s; no comparable dry period is recorded over the 130 years that elapsed between the two events (see Worrell 1983 for discussion). Under such extreme conditions, and when summer droughts also coincide with snow-poor winters, spruce trees could conceivably suffer from drought even in spring and early summer.

Some work related to a major pest in the USA, the southern pine beetle *Dendroctonus frontalis* Zimm., may shed light on our problem. *D. frontalis* is multivoltine and its infestation levels exhibit a clear annual variation which appears to be related to water availability. However, beetle attacks are most severe in spring and early summer when water is abundant and trees are in good growth. According to the principles of plant growth-differentiation balance (see Lorio 1986), a physiological model has been suggested (Reeve & al. 1995). According to this idea moderate water stress (limiting growth but not photosynthesis) increases the production of carbon-based secondary metabolites (i.e. resin), thus reducing the suitability for the beetles. A more severe drought (limiting both growth and photosynthesis) reduces resin yield, and host susceptibility increases. Field experiments corroborate this idea (Dunn and Lorio 1993, Reeve & al. 1995).

The model is derived from a more generalised growth-differentiation balance model for plant defence (e.g., Herms and Mattson 1992, Lerdau et al. 1994), and also seems to be in accordance with the C/N balance - host suitability hypothesis (Bryant et al. 1983). It would also explain the results of the *P. abies* - *C. polonica* experiment described above, where resistance increased under mild water stress.

Coniferous trees also have other chemicals that play a part in the defence against invasion of their tissues, and it appears that phenolic and tannic substances play a role in the defence of Norway spruce against *C. polonica* infection (Brignolas et al. 1995). Tannins may, however, be differently affected by changes in the growth-differentiation balance than are terpenes (Lerdau et al. 1994).

In conclusion it appears that apart from extremely rare cases of severe droughts lasting for a long period of time, direct effects of spring weather on beetle propagation are more likely to affect *I. typographus* dynamics than are indirect physiological effects working through the host trees.

This conclusion applies for areas with univoltine *I. typographus* populations (viz. the Scandinavian peninsula), and may not at all hold true for southern areas where a second

generation of beetles may encounter spruce trees suffering from much more severe late-season drought. Moreover, this reasoning may have no bearing on other bark beetle species, some of which seem adapted to exploiting their host trees during dry periods in late summer, e.g. *Polygraphus poligraphus* L. (Lekander 1959).

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# Observations on the Transmission of *Ophiostoma ulmi* by the Smaller Elm Bark Beetles (*Scolytus spp.*)

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**ABSTRACT** The spreading of the Dutch elm disease caused by the fungus *Ophiostoma ulmi* by the smaller elm bark beetles belonging to the genus *Scolytus* has been studied in Northern Italy. The percentage of beetles (*Scolytus multistriatus* and *S. pygmaeus*) carrying spores of *O. ulmi* at emergence from infested logs is higher in the spring (May-June: 58%) than in the summer emergence (August: 10%). No significant differences between beetle species have been found. The effectiveness in the transmission of the fungus during the adult maturation feeding has been evaluated for the two most abundant species (*S. multistriatus* and *S. pygmaeus*) on different species/hybrids of *Ulmus spp.* A variable infection rate (3.3 - 22 %) has been recorded, using insects artificially loaded with different strains of *O. ulmi*. The results show that the smaller elm bark beetles can successfully transmit the fungus, and this may cause additional work in the usual sanitation programs.

**KEY WORDS** vector, bark beetles, fungus, transmission

THE TRANSMISSION OF *Ophiostoma ulmi* by the elm bark beetles via maturation feeding has always raised a great interest, in order to be able to intervene in a decisive way in the apparently perfect symbiosis existing between the insects and the fungus (Brasier 1990). The bark beetles of the genus *Scolytus* Geoffroy are known to act as vectors of the fungus since the 30's, immediately after the first description of the disease (Fransen 1931, in Webber and Brasier 1984). However, precise information on the relationships between the life cycle of both the fungus and the insects has been given rather recently (Webber and Brasier 1984). In another paper Webber (1990) compares the spore load of 3 species (*S. scolytus* (Fabricius), *S. multistriatus* (Marshall), and *S. kirschii* Skalitzky) emerging from infested logs collected in August-September in Spain. *S. scolytus*, characterized by the biggest size, is supposed to be the only species able to successfully transmit the fungus, and this fact is related to the pupation behavior. In fact, the pupal chambers of this species are located in the moist inner bark, whereas the smaller species pupate in the outer bark. Such material tends to dry out quickly during summer, and this may hinder the development of the fungus and then the contamination of the smaller species of bark beetles. Information on the real effectiveness in the successful transmission of the fungus to the trees by beetles is not given, neither it is available from other literature sources. However, there is evidence that a minimum of 10<sup>5</sup> spores/beetle are required for a successful transmission.

The research presented in this paper has been based on two smaller species of bark beetles, *S. multistriatus* and *S. pygmaeus* (Fabricius), a species vicariant of *S. kirschii* in Northern Italy. Bark beetles of larger size (*S. scolytus*, *S. sulcifrons* Rey) were not available because of the lack of big elms for breeding (Zanta and Battisti 1989). The work has been focused on 2 main aspects: 1. estimation of the percentage of beetles (*S. multistriatus* and *S. pygmaeus*) carrying spores of *O. ulmi* at both first (May-June) and second (August)

emergence. 2. evaluation of the effectiveness in the transmission of the fungus to the tree by adults of *S. multistriatus* and *S. pygmaeus* artificially loaded with spores of *O. ulmi*. Some preliminary results have been already published (Basset et al. 1992, Favaro and Battisti 1993).

### Materials and Methods

**Beetles carrying spores at emergence.** Logs of *Ulmus minor* apparently infested by both the fungus and larvae of elm bark beetles were collected in various sites of North-Eastern Italy in the period 1991-1994. The logs were kept outdoor in boxes and adult emergence was recorded twice a day. Each beetle was put individually in sterile tubes, then identified, sexed, and inoculated in selective plates for *O. ulmi* (Gibbs and Brasier 1973) within 24 hours from the emergence. The plates were kept in the darkness at 20° C (Brasier, 1981) and the presence of *O. ulmi* mycelium was detected after one week.

**Fungus transmission by bark beetles.** Adults of *S. multistriatus* and *S. pygmaeus* coming from fungus-free logs were artificially loaded with spores of *O. ulmi* (aggressive strains North American (NAN 182), Eurasian (EAN H328 and H351)) by immersion and shaking for 60 seconds in a spore suspension (10<sup>6</sup> spores/ml). The final load of spores was determined with the dilution method (Webber and Brasier 1984). Adults were then forced to feed on 2 to 3-year-old branches of elm trees (*U. minor* x *U. pumila* and *U. glabra*). Bark beetles were introduced individually in dark plastic tubes with holes ensuring a correct air change. The tubes were then fastened to the branches with Parafilm. After 48 hours the bark beetles were removed and each tunnel was labelled. After one month the branches were collected and wood samples were taken at the tunnel level (0 cm), at 3 and 6 cm below. The wood samples were inoculated in selective plates for *O. ulmi*, kept in the darkness at 20° C and checked for the presence of the fungus after one week.

### Results and Discussion

**Beetles carrying spores at emergence.** The proportion of *S. multistriatus* and *S. pygmaeus* carrying spores of *O. ulmi* at spring emergence from the logs is on the average 58% (Table 1). The infection was found on the 88% of the elm logs used for rearing beetles. A considerable amount of the beetles (65%) carried also other fungi, mostly belonging to the genus *Penicillium*. The sex-ratio of the adults was 0.94. No significant differences emerged between species and sexes (X<sup>2</sup> test).

The tests performed on beetles of summer emergence gave significantly inferior values in the percentage of insects carrying the fungus, around 8% on the average (X<sup>2</sup> test)(Tab. 1). The sex-ratio (0.55) is remarkably female-biased, suggesting the possible presence of re-emergence of adult females after the first egg-laying. No significant differences emerged between species and sexes (X<sup>2</sup> test).

**Table 1. Proportion of smaller elm bark beetles carrying spores of *O. ulmi* at emergence.**

Species	<i>O. ulmi</i> at spring emergence			<i>O. ulmi</i> at summer emergence		
	presence	absence	% of beetles	presence	absence	% of beetles
<i>S. multistriatus</i>	158	126	55.6	87	793	9.8
<i>S. pygmaeus</i>	28	19	59.6	23	363	5.9

The dramatic reduction in the percentage of beetles carrying *O. ulmi* in summer is likely due to the high temperature and to the consequent drying out of the outer bark where the beetles pupate, as it was observed by Webber (1990) in Spain. However, the same species are largely contaminated with spores in spring, when the conditions are more favourable to the development of the fungus and to a successful transmission of the spores in the large vessels of the early wood. In conclusion, *S. multistriatus*, *S. pygmaeus* and possibly its vicariant *S. kirschii* cannot be disregarded as potential vectors of *O. ulmi*, as suggested by Webber (1990). An indirect demonstration of this fact is given by the continuous spreading of the disease in Northern Italy, where the large species of bark beetles have been almost disappeared in the last decades.

**Fungus transmission by bark beetles.** The results concerning the transmission effectiveness are presented in Table 2. The artificial load of beetles as estimated with the dilution method was  $130.1 \pm 14.7$  colonies/beetle. It must be considered that one colony may be originated by more than one spore. In any experiment the transmission was successful, but with a rather low rate (min 3.3 - max 22.5 % at 3 cm from the feeding tunnel) considering that all the beetles were artificially loaded with the fungus.

The decrease in the transmission of the fungus at 3 cm from the feeding tunnel is statistically significant (ANOVA) in all the cases with the exception of *Ulmus glabra*. This proves that the spreading of the fungus into the tree is related to the diameter of the vessels. They are in fact much larger in *U. glabra* than in *U. pumila x minor*, the latter being selected also for this feature (Mittempergher 1985). No significant differences in the spreading of the fungus have been observed between *S. multistriatus* and *S. pygmaeus* in 1991. The significant differences observed in 1994 between the fungus strains H328 and 182 seem to be probably linked to a different aggressiveness of the strains.

**Table 2. Effectiveness in the transmission of *O. ulmi* by smaller elm bark beetles artificially loaded with spores.**

Year	Species	Strain of <i>O. ulmi</i>	Tested trees (n)	Beetles/ tree	Transmission rate (%) at distance of cm		
					0	3	6
1991	<i>S. multistriatus</i>	H351	50	34	\	11.9	11.9
1991	<i>S. pygmaeus</i>	H351	50	22	\	9.1	9.1
1993	<i>S. multistriatus</i>	H328	20	40	20	12.5	\
1993	<i>S. multistriatus</i>	H328	20	40	22.5	22.5	\
1994	<i>S. multistriatus</i>	H328	15	20	20	6.7	\
1994	<i>S. multistriatus</i>	182	15	10	10	3.3	\

In conclusion, it seems evident that the fungus may be successfully transmitted by the smaller species of bark beetles also when the spore load is not as high as it could be expected (minimum of  $10^3$  spores/beetle according to Webber 1990). As a consequence, sanitation felling must include all parts of the tree because these species may breed in very thin twigs, and this may represent an additional problem in the control of the Dutch elm disease.

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# Intensive silvicultural practices increase the risk of infestation by *Dioryctria sylvestrella* Ratz (Lepidoptera: Pyralidae), the Maritime pine stem borer.

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**ABSTRACT** The infestation dynamics of *Dioryctria sylvestrella* was studied in relation to fertilisation and pruning of the Maritime pine. The percentage of infested trees was recorded by comparing three levels of fertilisation doses and four levels of pruning severity. Fertilised trees exhibited significantly greater tree growth and higher infestation rates than controls. The removal of live branches resulted in an increase in *D. sylvestrella* infestation, demonstrating a significant positive correlation with the number of pruning wounds. A model of infestation behaviour was hypothesised which involved primary attraction mediated by oleoresin components exuding from the pruning wounds. Gas chromatographic analysis of volatile terpenes of the wood resin of Maritime pines showed that infested trees contained a significantly higher percentage of terpinolene. The rate of infestation of ten full-sib families showed a significant positive correlation with the mean percentage of terpinolene. In a cross-table analysis of the interaction between tree diameter and terpinolene richness, the distribution of infested trees frequencies indicated that both tree pruning, which creates bark wounds, and tree vigour, which increases bark cracking, could simultaneously increase wood resin flow, thus enhancing tree attractiveness. Modifications of forestry practices are proposed to reduce stem borer damage.

**KEY WORDS** *Dioryctria sylvestrella*, Maritime pine, fertilisation, pruning, tree selection, resin, terpene

THE MARITIME PINE, *Pinus pinaster* Ait, is the primary coniferous species in France (Merzeau, 1995) in terms of surface area (1.4 million ha) and harvest volume (5 millions m<sup>3</sup> per year). It is also one of the most intensively managed species: draining, fertilising, planting, thinning, and pruning are all commonly performed in Maritime pine stands. This intensive culture has yielded dramatic increases in profitability, by shortening rotations to 40 years, increasing annual productivity from 5 m<sup>3</sup>/ha/year in the 1960s to 9 m<sup>3</sup>/ha/year in the 1980s and increasing the proportion of clear lumber in the logs (Guyon, 1996).

In addition, there is a widespread belief among foresters that vigorous forest crops undergo outbreaks of insect pests more rarely than forests under stress. By improving the growth and the vigour of the trees, intensive management could increase overall "resistance" to forest pests. The evidence to support this theory are mainly provided by bark and shoot borer dynamics (Speight, 1986) since numerous bark beetles severely damage conifers during periods of water stress (Waring and Pitman, 1983; Worrell, 1983; Lieutier, 1990). A negative effect of fertilisation on chewing insects has also been reported (Smirnoff and Bernier, 1973). However, fertilisation of pine trees can increase forest pest populations, such as sap feeders (Heliovaara *et al.*, 1983), tip moths (Folz and Blakeslee, 1989; Ross and Berisford, 1990) and pine weevils (Selander and Immonen, 1991). In addition, vigorous coniferous trees are more

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prone to attack by some bark beetles, such as *Dendroctonus micans* (Vouland, 1991) and *Dendroctonus ponderosae* (Cole and Amman, 1980). The same relationship has been observed for *Dioryctria sylvestrella*, one of the major Maritime pine pests. Female moths attack fast growing pine trees more frequently (Guinaudeau, 1969) and fertilised or highly productive stands experience more severe damage (Ménassieu and Lévieux, 1990, Carisey *et al.*, 1994). This variability in the response of insect infestation to tree vigour may result from the complexity of tree physiology. Tree growth improvement could increase the amount of photosynthate available for defense reactions and thus improve resistance to insect pests (Christiansen *et al.*, 1987). However, it could also increase the nutritive value of tree tissues and shift the process of carbohydrate allocation from the synthesis of secondary defensive chemicals to the development of organs and energy storage so that overall susceptibility to insect attack might increase (Speight and Wainhouse, 1989).

Recent studies have demonstrated that tree pruning also increases the level of *D. sylvestrella* attack (Jactel *et al.*, 1994 and 1996a). Tree pruning, i.e. the removal of live branches, is used to reduce the occurrence of knots and increase the proportion of clear lumber in the log. It was hypothesized that primary attraction, mediated by oleoresin terpenes exuding from bark wounds, might attract insects to host trees. The dynamics of the European stem borer, *D. sylvestrella*, could be closely related to the intensity of Maritime pine stand management. The aim of this study was to investigate the pattern of pine tree susceptibility as related to the intensity of growth and pruning. The information presented should help foresters to adjust their cultural tactics to reduce the risk of *D. sylvestrella* damage.

### Materials and Methods

**Effects of pruning on Maritime pine infestation by *D. sylvestrella*.** The study was conducted in a pure stand of Maritime pine (13 ha), grown on mesophilous humid heaths in the Station de Recherches Forestières, Gazinet, France. Trees were 10 years old, with an average normal diameter of 10.3 cm. The experiment was a completely randomised block design with ten replications of four pruning treatments: removal of dead branches only (all live whorls retained), or removal of all branches except the four, three, or two upper whorls. Each replicate contained 32 trees, and every fourth tree was pruned in 1991 (8 pruned trees and 24 control trees). In 1991, all trees from all plots (1358 pine trees) were sampled for diameter at breast height and *D. sylvestrella* attack. For each pruned tree, the number of fresh wounds, resulting from the removal of live branches, was recorded as it varied according to the number of branches per pruned whorls and to tree polycyclism. For each attacked tree, the location of the attack on the trunk was recorded along with the age of the attacked stem internode.

**Effects of fertilisation on Maritime pine infestation by *D. sylvestrella*.** The study was conducted in two Maritime pine plantations, grown on a mesophilous humid heath at the Station de Recherches Forestières, Gazinet, France. Trees were 20 years old with an average normal diameter of 20.5 cm and 20.1 cm respectively. The experiment was a randomised block design with four replications of three fertilisation treatments: control, 63 and 126 kg.ha<sup>-1</sup> P<sub>2</sub>O<sub>5</sub> (natural phosphate). The fertiliser was mechanically broadcast over the rows. Each plot consisted of five rows of 4 to 60 trees separated by 4 m between the rows and 2 m between the plants in the row. The plots were separated by one row with no fertilisation

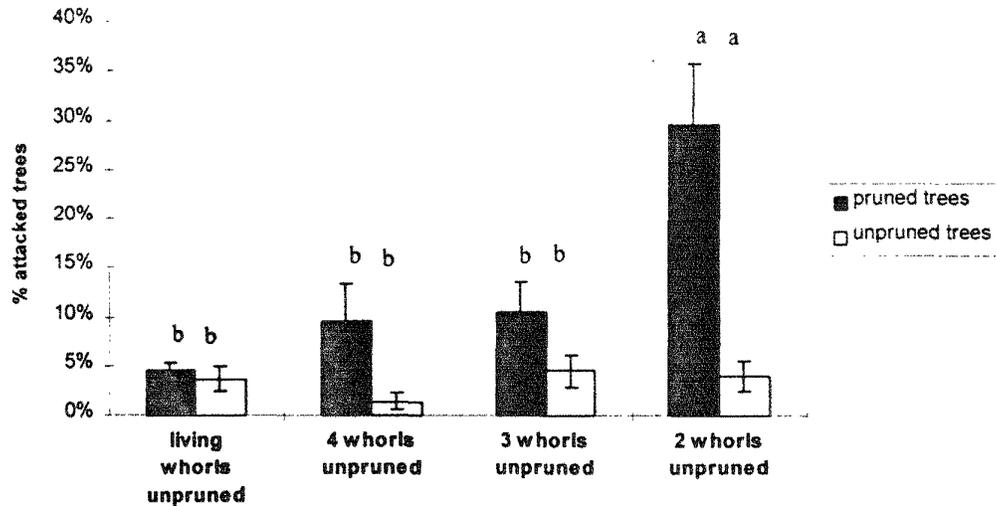
treatment. In 1985 and 1995, all trees from all plots (2031 pine trees) were sampled for diameter at breast height. In 1995, all trees from the first plantation (793 trees) and the second plantation (1238) were sampled for *D. sylvestrella* attack.

**Effects of terpene composition of wood resin on Maritime pine infestation by *D. sylvestrella*.** The study was conducted in a Maritime pine clonal test comprising full-sib families, from a local provenance grown on a mesophilous humid heath at the Station de Recherches Forestières, Gazinet, France. Three to four trees per family were cloned 3 to 5 times by grafting. Trees were 10 years old with an average normal diameter of 14.7 cm. In 1995, 143 clones, of 10 families, were sampled for diameter at breast height, *D. sylvestrella* attack and wood resin composition. Constitutive oleoresin was collected at 2 m above the ground level and stored according to the method described by Jactel *et al.* (1996). For chromatographic analysis, 1 ml of oleoresin was solubilized in 1.5 ml of pentane and purified by column chromatography on SDS silica 70-230 mesh (10 ml). The terpenes were eluted by a pentane-ether solution (30ml; 98:2). The extract was concentrated by evaporation under moderate vacuum and analysed by FID-GC (Hewlett Packard® 5890; temperature program. 60°C to 90°C at 6°C.mn<sup>-1</sup>, 90°C to 102°C at 3°C.mn<sup>-1</sup>, 102°C to 280°C at 6°C.mn<sup>-1</sup>; splitless (injector 270°C, detector 290°C)) on a 30 -m x 0.25-mm-ID HP1 column (He 15 psi, 0.5 µl sample). The relative percentages of mono- and sesquiterpenes were calculated from the total of all recorded terpene peaks. Only 10 terpenes, with relative proportions higher than 0.1%, were used throughout the study. In order of increasing retention time, 6 monoterpenes ( $\alpha$ -pinene, camphene,  $\beta$ -pinene, myrcene, limonene, terpinolene) and 4 sesquiterpenes (longipinene, longifolene,  $\beta$ -caryophyllene,  $\alpha$ -humulene) were found.

**Statistical analyses.** All statistical analyses were performed using SAS Software (SAS Institute Inc., 1990). Analyses of variance (GLM, *t* test) of percentage variables were computed using the arcsin $\sqrt{x}$  transformation (Dagnelie, 1973). A non-parametric analyses of variance (NPAR1WAY, Wilcoxon test) was used for oleoresin composition data which are proportions of *p* terpenes with the constraint  $\sum_i p_i = 1$ .

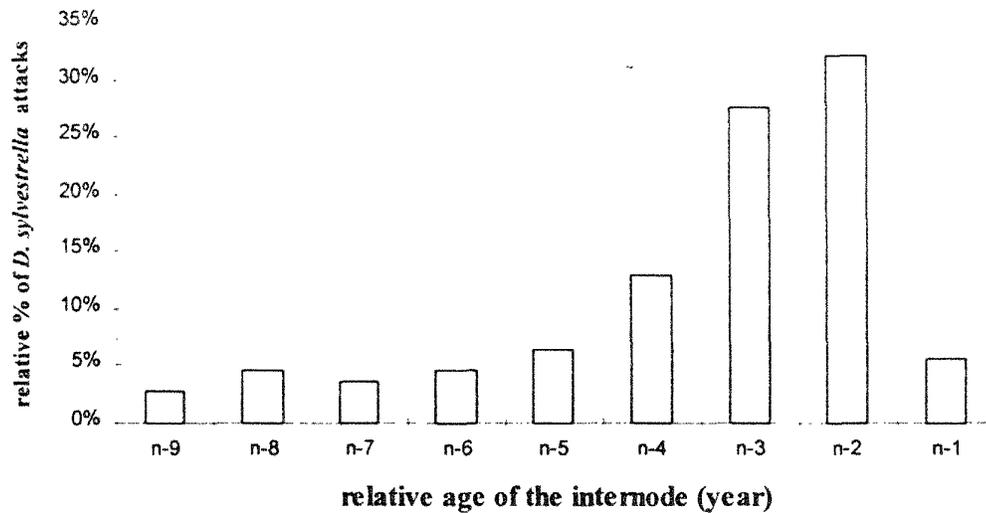
## Results

**Tree pruning.** The percentage of attacked pruned trees increased significantly with the severity of pruning ( $F = 14.2$ ,  $P < 0.001$ ,  $N = 40$ ) and the control trees were similarly damaged in the four pruning treatments ( $F = 2.3$ ,  $P > 0.05$ ,  $N = 40$ , Fig. 1).



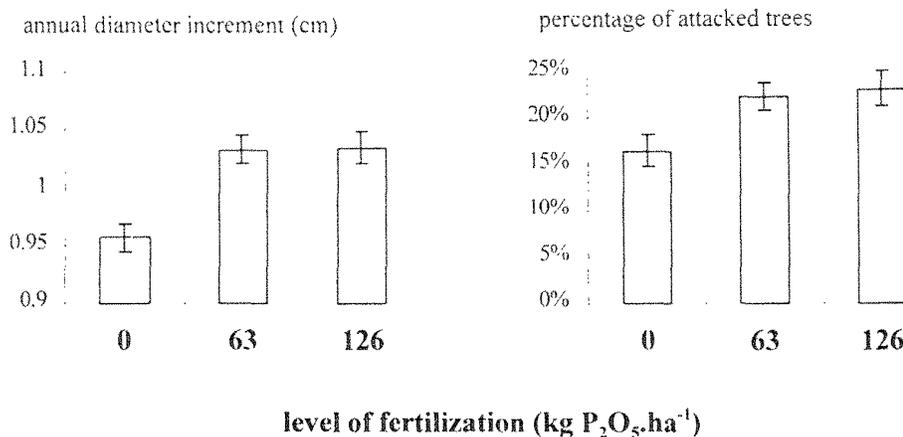
**Fig. 1.** Mean percentage of Maritime pine trees attacked by *D. sylvestrella* in relation to pruning severity. Means indicated by different lowercase letters are significantly different ( $P < 0.05$ ) according to Duncan's multiple range test. Standard errors are indicated by vertical bars.

Attacked pruned trees exhibited significantly more fresh wounds than unattacked pruned trees ( $t$  test,  $P < 0.05$ ) but did not differ significantly for normal diameter or for height of pruning ( $t$  test,  $P > 0.05$ ). In contrast, attacked unpruned (control) trees had a significantly greater diameter than unattacked unpruned trees. The mean number of attacks per attacked tree did not differ significantly between pruned and control trees and averaged  $1.4 \pm 0.1$ . The mean height of *D. sylvestrella* attack did not differ significantly between pruned and control trees, or between pruning treatments. A Wilcoxon test demonstrated that the distribution of attacks among the internodes for pruned and control trees was similar ( $Prob > Z = 0.56$ ). Their mode was observed for 2- to 3-year-old internodes (Fig. 2.). Ninety-five percent of the observed attacks were located less than 10 cm from the insertion point of the branch, left in place or removed by pruning.



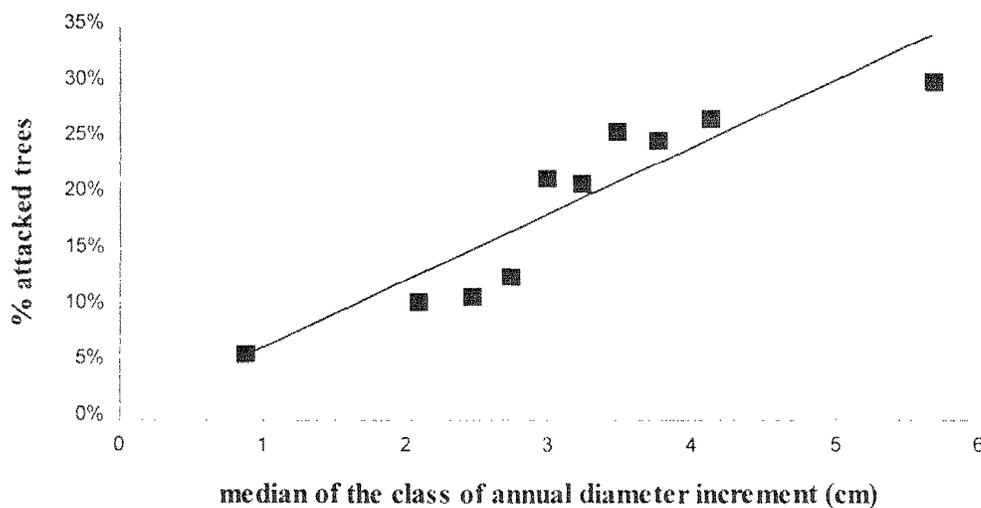
**Fig. 2.** Distribution of *D. sylvestrella* attacks among the internodes of 10-year-old pruned Maritime pine trees, expressed as the percentage of the total number observed. Internodes are identified by their relative age with respect to the year of study.

**Tree vigour.** The variance of the mean annual diameter increments, which characterised tree vigour, were analysed according to site (2 plantations,  $df = 1$ ), fertilisation level (3 doses of phosphorus,  $df = 2$ ) and their interaction ( $N = 2031$ ). Tree growth, recorded between the tenth and the twentieth years, differed significantly between sites ( $F = 36.1$ ,  $P < 0.0001$ ) and significantly increased with fertilisation level ( $F = 12.9$ ,  $P < 0.0001$ , Fig. 3); however these two factors interaction did not induce any significant differences ( $F = 2.2$ ,  $P > 0.05$ ). The variance of the infestation rate by *D. sylvestrella*, calculated as the percentage of attacked trees per row, was similarly analysed according to site, fertilisation level and their interaction ( $N = 24$ ). The site and the two factors' interaction did not exhibit any significant differences (respectively,  $F = 1.33$  and  $F = 0.07$ ,  $P > 0.05$ ). The level of attack was significantly higher in fertilised rows than in controls ( $F = 4.02$ ,  $P < 0.03$ , Fig. 3).



**Fig. 3.** Effects of fertilisation on Maritime pine radial growth and susceptibility to *D. sylvestrella*. Means indicated by different lowercase letters are significantly different ( $P < 0.05$ ) according to SNK multiple range test. Standard errors are indicated by vertical bars.

The regression between the percentage of attacked trees per class of diameter increment and the median value of the class was significant (Fig. 4).

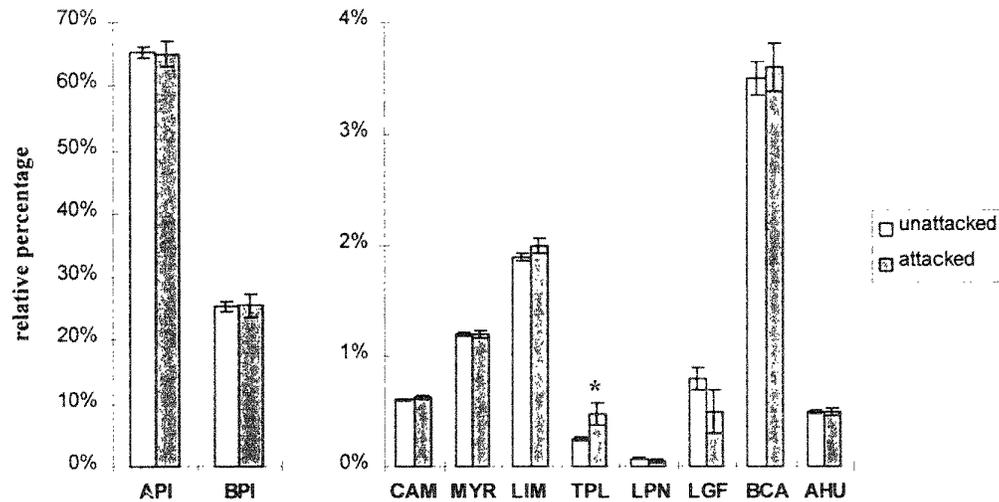


**Fig. 4.** Relationship between the class of tree growth and susceptibility to *D. sylvestrella*. Susceptibility to the moth is expressed as the percentage of attacked trees per class of annual diameter increment ( $r^2 = 0.84$ ,  $P < 0.001$ ,  $n = 10$ ).

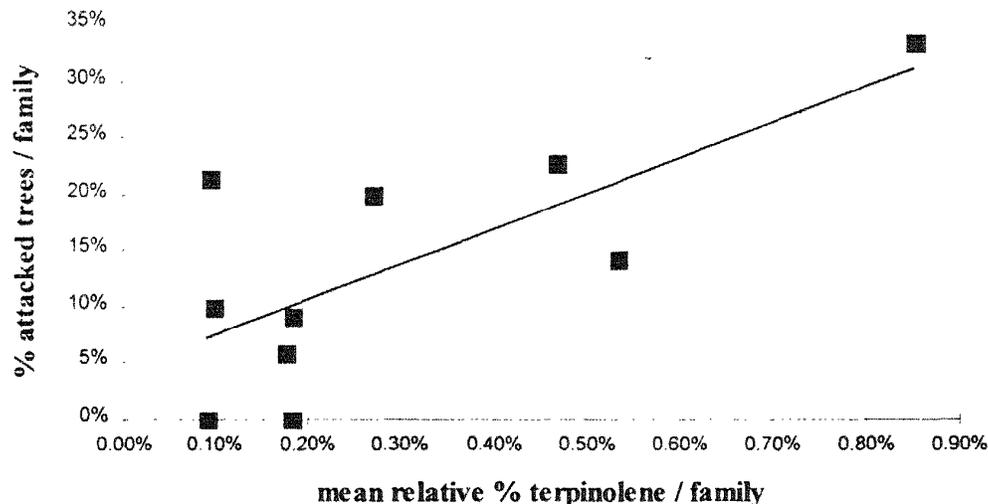
**Terpene composition of the wood resin.** Wood resin did not differ qualitatively between attacked (13.3 %) and unattacked trees, since both types of trees produced the same typical

chromatogram of the same 10 terpenes. However, attacked trees exhibited significantly more terpinolene (Wilcoxon test,  $Prob > Z = 0.046$ , Fig. 5) and the regression between the percentage of attacked trees and the mean proportion of terpinolene per full-sib families ( $N = 10$ ) was significant (Fig. 6).

In the same sample of 143 pine trees, the normal diameter was significantly higher for attacked trees than unattacked trees (respectively 14.8 cm and 13.7 cm,  $t$  test,  $P < 0.05$ ).



**Fig. 5.** Comparison of mean terpene profiles of wood resin in attacked and unattacked Maritime pine trees. Standard errors are indicated by vertical bars. One star above a pair of bars indicates a significant difference ( $P > 0.05$ ). API:  $\alpha$ -pinene, BPI:  $\beta$ -pinene, CAM: camphene, MYR: myrcene, LIM: limonene, TER: terpinolene, LPN: longipinene, LGF: longifolene, BCA:  $\beta$ -caryophyllene and AHU,  $\alpha$ -humulene.



**Fig.6. Relationship between the percentage of attacked trees and the mean relative percent of terpinolene in the wood resin per full sib family of Maritime pine. ( $r^2 = 0.53$ ,  $P < 0.05$ ,  $n = 10$ ).**

The interaction between vigour and oleoresin composition of the trees in relation to the risk of infestation by *D. sylvestrella* was investigated using two models of conditional probabilities. In the first model, it was assumed that attacked trees would exhibit both a large diameter *and* a high percentage of terpinolene in the oleoresin. Because the terpene composition of the resin was not correlated to tree vigour ( $P > 0.05$ ), the theoretical frequencies of attacked trees in a cross table testing the interaction between those two factors could be calculated (Table 1, in italics) and compared with observed frequencies (in bold). The  $\chi^2$  test proved the observed and theoretical distribution frequencies to be different ( $df = 4$ ,  $\chi^2 = 123.9$ ). In the second model, it was assumed that attacked trees would exhibit either a large diameter *or* a high percentage of terpinolene in the oleoresin. The  $\chi^2$  test proved the observed and theoretical distribution frequencies (Table 1, in underlined characters) to be equal ( $df = 4$ ,  $\alpha = 0.01$ ,  $\chi^2 = 11.2$ ).

**Table 1. Observed and calculated\* frequencies of Maritime pine trees attacked by *D. sylvestrella* in a cross table analysis of the interaction between the relative percentage of terpinolene in the wood resin and tree class diameter.**

		class of terpinolene proportion (%)		
		1 [0.07 ; 0.1] n = 35	2 ]0.1 ; 0.22] n = 63	3 ]0.22 ; 1.6] n = 45
class of tree diameter (cm)				
1	[9.5 ; 13.4] n = 60	<b>0 (0 %)</b> <u>2.4</u> <i>0.1</i>	<b>2 (7.4 %)</b> <u>4.8</u> <i>0.2</i>	<b>3 (15.8 %)</b> <u>5.8</u> <i>0.4</i>
2	]13.4 ; 15.3] n = 50	<b>2 (14.3 %)</b> <u>2.9</u> <i>0.1</i>	<b>1 (5 %)</b> <u>4.3</u> <i>0.2</i>	<b>3 (18.8 %)</b> <u>5.5</u> <i>0.4</i>
3	]15.3 ; 18.8] n = 33	<b>1 (14.3 %)</b> <u>2.3</u> <i>0.2</i>	<b>3 (18.8 %)</b> <u>5.4</u> <i>0.4</i>	<b>4 (40.0 %)</b> <u>4.7</u> <i>0.5</i>

\* The events are labelled as follows: A (attacked tree), A/D (attacked tree with known its diameter), A/T (attacked tree with known its terpinolene proportion).

**in bold:** observed frequencies and related percentage of attacked trees

underlined: theoretical frequencies calculated under the hypothesis that tree infestation depends on diameter *or* proportion of terpinolene in the wood resin

Proba (A) = Proba (A/(D or T)) = Proba (A/D) + Proba (A/T)

*in italics:* theoretical frequencies calculated under the hypothesis that tree infestation depends on diameter *and* proportion of terpinolene in the wood resin

Proba (A) = Proba (A/(D and T)) = Proba (A/D) x Proba (A/T)

### Discussion

**Effect of pruning on Maritime pine susceptibility to *D. sylvestrella*.** Pruned Maritime pine trees were significantly more prone to attack by *D. sylvestrella* than control trees (Fig. 1.). It has already been shown that stem borers such as *Dioryctria zimmermani* Grote (Wright *et al.*, 1975) and *D. sylvestrella* (Jactel *et al.*, 1996) preferentially damage pruned trees, but this study demonstrated a significant positive correlation between the risk of *D. sylvestrella* infestation and the severity of pruning (number of live branches or whorls removed). Forestry policies recommend pruning Maritime pine up to 5.5 m above ground level to produce clear lumber in the two timber bolts. It can therefore be predicted that intensive silviculture practices which increase the number of live branches in the lower part of young trees, such as fertilising and low density planting, may in turn increase stem borer damage after pruning.

The increase in infestation rate with pruning severity could result either from the increase in a survival brood or from the improvement of tree selection. There is a little information concerning the effect of pruning on forest pest insect abundance. Hard (1992) records that pruning live branches of spruce trees reduces successful *Dendroctonus rufinervis* Kby attacks. The effect of pruning was related with micro-climatic changes near pruned boles, which reduced the survival rate of scolytids. But this hypothesis is unlikely to apply to *D. sylvestrella* infestation as it would assume that a significant correlation exists between the number of attacked trees and the volume freed by removal of branches, i.e. pruning height. It could also be assumed that removing live branches might induce physiological stress which would in turn modify the quantity or the quality of available food. However, if this were the case, the number of successful attacks per suitable tree and their location on the trunk, would also be changed. Moreover, due to the low number of attacks per tree (one or two), any food deficiency is unlikely to prevent the development of *D. sylvestrella* larvae. In contrast, only the removal of live branches appears to result in a higher infestation rate. Baer (1906) and Olmi *et al.* (1977) observed that injuries to the stem bark resulted in *D. sylvestrella* attacks. It is thus possible that pruning wounds release volatiles which act as a primary attractant for mature female moths. Since the removal of live branches created a resin flow outside the wounded bark area, one may assume that primary attractants are components of Maritime pine wood resin. Primary attraction to host odours has been suggested as a mechanism of host tree selection by numerous bark beetles (Raffa and Berryman, 1983; Vité *et al.*, 1986) and often involves monoterpenes, a family of volatile compounds naturally occurring in conifer resin. Hanula *et al.* (1985) have shown that a combination of  $\alpha$ -pinene, myrcene and limonene is attractive to *Dioryctria amatella* (Hulst) and stimulates oviposition. The significant correlation between wound number and infestation level may also support the theory of a quantitative effect of this primary attraction. Olmi *et al.* (1977) link the susceptibility to *D. sylvestrella* of *Pinus excelsa* x *Pinus strobus* hybrids to the amount of resin exudate.

**Effect of fertilising on Maritime pine susceptibility to *D. sylvestrella*.** Fertilised trees, even at low doses, were more frequently attacked by *D. sylvestrella* than controls (Fig. 3.). While no nutrient analyses were made in the bark, the effects of fertilisation were studied in relation to tree growth. Fertilised trees exhibited significantly greater annual growth increments and were more heavily infested by *D. sylvestrella* (Fig. 4.). This result is consistent with data obtained in a previous study (Jactel *et al.*, 1996) as well as in numerous studies that investigated the relationship between tree vigour and sensitivity to the stem borer (Ménassieu et Léveux, 1990; Carisey *et al.*, 1994). Wright *et al.* (1975) found that fast growing varieties of Scots pine are more susceptible to *D. zymmermani*. It is possible that vigorous trees present thicker phloem and thus improve the survival of *D. sylvestrella* brood by providing larger amounts of food to the larvae. However, due to the low number of attacks per tree, any variation in food availability is unlikely to affect the development of *D. sylvestrella* larvae. In contrast, Maugé (1987) observed that bark cracks were more common in fast growing pine trees. Therefore, Maritime pine trees with large annual diameter increments might release more attractive resin exudates. This hypothesis is consistent with the phenological concordance between the period of maximum radial growth in Maritime pine (Lemoine,

1975), which occurs from April to June, and period of female moth flight (Ménassieu *et al.*, 1989) which begins in June.

**Effect of terpene composition of the resin on Maritime pine susceptibility to *D. sylvestrella*.** In this study, the Maritime pine sensitivity to *D. sylvestrella* was significantly correlated with a high level of terpinolene proportion in the wood resin (Fig. 5.). In a previous study (Jactel *et al.*, 1996b), attacked and unattacked trees were discriminated by the relative proportion of six monoterpenes, including terpinolene, in the resin wood. Wright *et al.* (1975) also related the resistance of southern Scots pine varieties to *D. zimmermani* to low levels of terpinolene. Moreover, in an electroantennography test, terpinolene was the terpene which yielded the highest response in *D. sylvestrella* females (Jactel *et al.*, 1996b). Therefore, terpinolene could be a possible candidate for an effective host attractant. The action of terpinolene is also compatible with the quantitative effect of pruning wound attraction as the level of family infestation was significantly related to their mean terpinolene proportion (Fig. 6). Rappaport *et al.* (1995) consistently correlated the attack rate of *Megastigmus spermotrophus* Wachtl with the terpinolene levels in *Pseudotsuga menziesii* Mirb. cones.

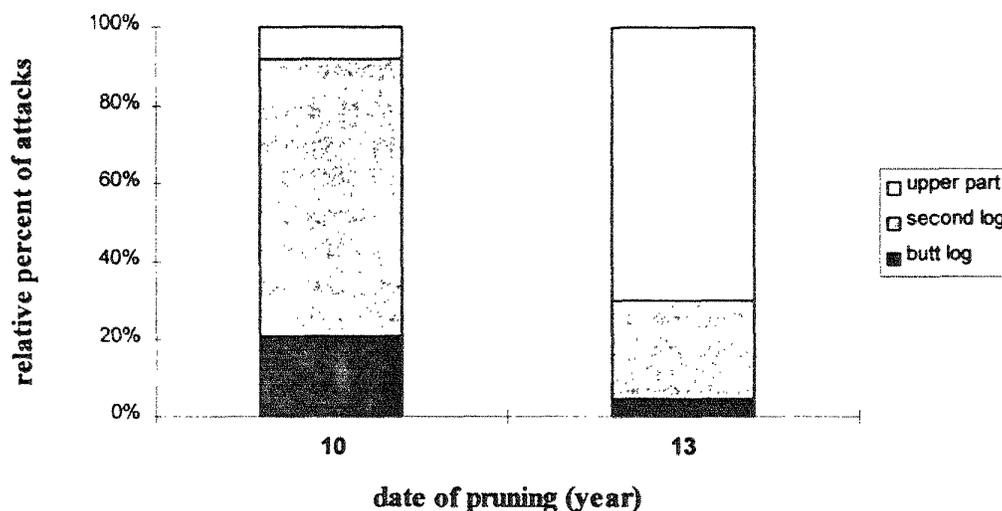
If tree selection depended only on the presence of large amounts of attractants and tree colonisation depended only on the bark thickness, successful infestations should be recorded more frequently in trees with both a large diameter *and* a high percentage of terpinolene in the oleoresin. If this infestation process were correct, the frequencies of attacked trees which combine diameter and terpinolene proportion classes would have been significantly lower than those found (Table 1). In contrast, it appears that brood survival is slightly related to tree vigour and that female moth attraction requires the emission of a sufficient amount of terpinolene. Here, attacked trees should exhibit either a large diameter, *i.e.* a cracked bark from which large amounts of resin can flow, *or* a high percentage of terpinolene in the wood resin. In the sample of 143 trees, this model fitted the observed data (Table 1). Similarly Jactel *et al.* (1996 a) showed that both tree vigour, due to increased bark cracking, and tree pruning, due to bark wounding, effected tree attractiveness, and helped increase oleoresin flow.

### Conclusions

In light of these results and data collected in our previous experiments, a model of host-infestation by *D. sylvestrella* can be proposed. Susceptible trees develop a primary attraction to the stem borer, mediated by some volatile attractants originating from the constitutive oleoresin. One of these compounds could be terpinolene. The attraction would not be effective unless the terpinolene, or a mixture of volatile attractants, is released in a sufficient concentration into the surrounding atmosphere. Factors that increase resin exudation may then be expected to increase tree attractiveness. It can be assumed, therefore, that forestry practices that favour tree wounding, such as pruning, or tree vigour (*i.e.* bark cracking), such as fertilising, intensive thinning and low density planting, may in turn increase stem borer damage.

In practice, foresters should be advised to reduce the severity of pruning or to delay its application to focus the attacks above the butt and second log, which is the stem region with the greatest timber value (Fig. 7).

Reduction of tree growth can hardly be recommended as a goal for wood production. Nevertheless, two strategies could be developed to reduce tree attractiveness, which have been proven to be the key step in tree infestation. Terpinolene proportion in the wood resin, provided that its heritability can be demonstrated, could be a suitable biochemical marker for selecting genetic resistance to *D. sylvestrella* (Jactel *et al.*, 1996b). Since bark thickness and cracking exhibit high infraspecific variability in *Pinus pinaster* (Shvester and Ughetto, 1986), the genetic improvement of bark permeability to resin exudates is also conceivable.



**Fig. 7.** Distribution of *D. sylvestrella* attacks in the butt log (0-3 m), the second log (3-5.5 m) and the upper part of the tree, as a percentage of the total number observed in 10-year-old trees and as a percentage of the total number calculated for 13-year-old trees according to the internode distribution model (Fig. 4.).

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