Role of genetic resistance in managing ecosystems susceptible to white pine weevil¹

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This paper describes the conditions that make stands of spruce (*Picea* spp.) susceptible to attack by the white pine weevil, *Pissodes strobi* Peck, in British Columbia and discusses how host genetic resistance could be utilized to complement silvicultural tactics in the management of this pest.

Key words: *Pissodes strobi*, pest management, *Picea* spp., silviculture

Cet article décrit les conditions qui rendent les peuplements d'épinettes (*Picea* spp.) susceptibles d'être attaqués par le charançon du pin blanc, *Pissodes strobi* Peck, en Colombie-Britannique et élabore comment la résistance génétique de l'hôte pourrait être utilisée pour compléter les tactiques sylvicoles utilisées dans la gestion des ce ravageur.

Mots clés: *Pissodes strobi*, gestion des ravageurs, *Picea* spp., sylviculture

Introduction

The white pine weevil, *Pissodes strobi* Peck, is an indigenous insect of North America, and can be found in most regions of Canada (Humble *et al.* 1994) and the United States. In British Columbia (BC) this insect has become a serious pest of reforestation, causing severe damage to young stands of Sitka spruce, *Picea sitchensis* (Bong) Carr., Engelmann spruce, *Picea engelmannii* Parry, white spruce, *Picea glauca* (Moench) Voss, and their hybrids, and occasionally to lodgepole pine, *Pinus contorta* Dougl. The hosts attacked in eastern North America include eastern white pine, *Pinus strobus* L., Jack pine, *Pinus banksiana* Lamb., Norway spruce, *Picea abies* (L.) Karst, Scots pine, *Pinus sylvestris* L., white spruce, and red spruce, *Picea rubens* Sarg.

Adult *P. strobi* overwinter in duff, usually near the tree from which they emerged in the previous fall. Early in the spring the weevils become active and can be seen feeding on the bark of branches and stem. Later, adults move to undamaged leaders of host trees where they mate and lay eggs below the apical bud, in feeding punctures which are then covered with a fecal plug. After hatching, the larvae orient downwards and consume the phloem. As their galleries merge, the larvae form the characteristic "feeding ring", in which they move downwards in synchrony, consuming all phloem, girdling and destroying the leader. Pupation takes place in chambers excavated in the xylem which are covered with wood fibers. New adults emerge from late July to September, feed for a while, and when temperatures drop and photoperiod shortens, move to the duff to hibernate (Silver 1968).

After a successful attack, a tree may take from one to several years to recover. In this process, branches from the uppermost whorl below the damaged terminal compete for dominance, and the tree remains for one or more years with multiple lead-

ers. Depending on the number of internodes destroyed and the growth characteristics of the tree, a permanent stem defect could form at the point of injury (Alfaro 1989; Alfaro and Omule 1990). Losses in severely infested stands, due to reduced growth and defect can be as high as 40% of the stand volume (Alfaro 1992, 1994).

Understanding how weevil populations are held in check under natural conditions, and why outbreaks develop in plantations, is important for the development of silvicultural systems that are successful in reducing outbreak risk. This review examines the causes of outbreaks in natural stands and plantations, and discusses how host genetic resistance could be used along with silvicultural manipulation, to reduce stand susceptibility to weevil outbreaks.

Weevil populations are regulated by several factors (Alfaro 1994), with the most important being availability of oviposition sites (upright healthy leaders), larval food supply (leaders with thick phloem), climate (McMullen 1976) and vertebrate and invertebrate natural enemies (Alfaro *et al.* 1985). Although the weevil feeds throughout the main stem and branches, the niche for oviposition is exclusively the upright, year-old leader. Once a leader has been destroyed, the tree is usually not available for re-attack unless a new leader has formed. Re-attack of a leaderless tree has been reported (Cozens 1987), but it is uncommon. Therefore, the availability of oviposition sites is a major population regulation factor.

The Need for Ecosystem Restoration and Management

The widespread planting of single-species spruce stands in the 1960s and 1970s created optimal conditions for weevil development. Large plantations with vigorous regeneration provided an enormous supply of oviposition sites and food for the weevil. Also, in these open plantations, heat accumulation (McMullen 1976) was more than appropriate for weevil development. Under these conditions, population explosions or outbreaks developed. Outbreaks on monocultured Sitka spruce (Alfaro and Omule 1990) begin when plantations are about five years old. First, a few trees are attacked, then the population grows rapidly to rates of 30–50% trees attacked per year (Fig.

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Fig. 1. Schematic representation of white pine weevil outbreaks on monocultures of Sitka spruce in stands located in high, moderate and low weevil hazard zones of British Columbia

1). The rapid infestation increase in this initial stage is due to the large proportion of trees available for attack, and to the fact that many attacks result in multiple leaders, increasing the number of oviposition sites and the supply of food for the larvae. After this initial period of invasion, the percentage of trees attacked each year stabilizes with annual fluctuations due to the variable effects of weather, natural enemies, larval crowding, and other mortality factors. This stability phase may last 10 to 20 years and is caused by a dynamic equilibrium between the weevil population and the supply of oviposition sites and larval food. The stability level is higher on good, warm sites, where vigorous growth ensures a rapid development of new leaders, than on poor, cool sites (Fig. 1). Gradually, this equilibrium gives way to a population decline phase, in which the rate of attack drops to less than 5% of the trees yr^{-1} by plantation age 30–40 years. The reasons for the decline are probably multiple. By this age, the plantation has passed the stage of most vigorous growth and leader size declines, which results in a gradual reduction in larvae food supply and breeding substrate. Also, with the onset of canopy closure, there are changes in the stand microclimate (see below) which have a negative impact on weevil oviposition and survival.

Lessons from Natural Stands

Pissodes strobi is rare in natural, undisturbed stands. Here the weevil is found mostly in exposed regeneration occurring at stand edges or in openings, such as those created by the fall of older trees. Outbreaks develop where catastrophic events such as fire or wind storms create large patches of open-grown spruce regeneration. Studies on older stands located near Williams Lake indicate that weevil attacks in fire-regenerated white spruce were frequent between tree heights of 3 to 17 m (Fig. 2).

Natural stands have several characteristics which prevent outbreaks from occurring:

(a) Shaded, Cool Habitats

Climate and microclimate play a major regulatory role in the population dynamics of the white pine weevil. McMullen (1976) calculated that a minimum heat accumulation of 888 degree-days above 7.2 °C was necessary for completion of weevil development in coastal Sitka spruce (785 degree-days for white spruce). Natural spruce stands (coast and interior) are shadier and

cooler than plantations and have a microclimate less favourable for weevil development. Ongoing work by Taylor *et al.* (1996) on white spruce demonstrated that weevil damage decreases under canopies with increasing crown closure (shading) (Fig. 3). McLean (1989, 1994) found a similar reduction of weevil damage in Sitka spruce grown under red alder, *Alnus rubra* Bong. in BC. In eastern Canada, Wallace and Sullivan (1985) concluded that dense, shaded eastern white pine stands have conditions of temperature and humidity which are unfavourable for weevil feeding, oviposition and development.

(b) Low Food Supply and Sub-optimal Oviposition Sites

Spruce regeneration under shade grows slowly, producing thinner leaders which contain less food for the weevil larvae. Often these natural stands contain mixed species and a low host density ha^{-1} , which further decreases availability of oviposition sites and larval food. In addition, observations in eastern white pine (Sullivan 1961) indicated that egg deposition on shaded leaders tended to occur in a diffused pattern rather than be concentrated in the upper sections of the leader as is more frequent on open grown trees. Concentrated egg deposition (mass attack) seems to be a requirement for successful leader colonization as the larvae need to aggregate and move downwards in synchrony, forming the feeding ring, in order to quickly overcome the tree defenses (Alfaro *et al.* 1996a). Solitary larva are more susceptible to pitch drowning.

(c) Complex Trophic Webs

A number of parasitoids (Alfaro *et al.* 1985) as well as vertebrate and invertebrate predators consume the various stages of *P. strobi*. However, this natural enemy complex is not effective in reducing weevil populations once they reach outbreak levels. Although untested, probably the parasitoid and predator complexes (e.g. ground carabid predators) are more diverse or more effective in natural stands than in plantations. Effectiveness of natural enemies could be higher in natural stands because the overall ecosystem complexity is much higher than in single-species plantations, and because the weevil populations are lower. Not only are the plant communities more diverse, but their structural complexity is much higher, as they form multilayered stands. Due to their sensitivity to habitat destruction (LaSalle and Gauld 1993), parasitic

Fig. 2. Number of *P. strobi* attacks visible on stems of white spruce in a 60-year-old stand, tabulated by height above ground. The stand regenerated naturally after fire. Figure based on dissection of 41 trees.

Fig. 3. Percentage of interior spruce trees attacked by the white pine weevil when growing under increasing conditions of overstory crown cover. Class 1 = open-grown tree; Class 8 = 100% overstory crown cover. Redrawn from Taylor *et al.* 1996.

hymenoptera may be affected negatively in single-species plantations. In agroecosystems, natural enemy diversity is enhanced by crop diversity, abundance of ground cover, weeds and native vegetation adjacent to crops (Altieri 1994). Companion vegetation satisfies other needs of the parasitoid (shelter, food, water, pollen, alternate hosts). Interactions in the complex trophic web of natural stands probably suppress weevil populations, reducing the likelihood of weevil epidemics.

Management of the White Pine Weevil

An Integrated Pest Management System (IPM) has been proposed for *P. strobi* (Alfaro *et al.* 1995). This system relies on restoring ecosystem balance by reducing the conditions that lead to outbreak development. The system recommends tactics that diminish heat accumulation in the stand by encouraging growth of suitable non-host conifers as well as an overstory of deciduous species such as aspen or alder. These conditions render the stand cooler and shadier, reduce oviposition sites and food supply because trees produce short, thin leaders, and may create conditions which enhance natural enemy populations. Reduction of stem defects by sanitation thinning and by planting at close spacing is also recommended.

Central to IPM is the continuous monitoring of weevil populations and forecasting of weevil impacts on forest productivity. This can be accomplished through a computerized decision support system, which helps to evaluate the need for, and the possible benefits of a given tactic.

Adding Host Genetic Resistance to Ecosystems Susceptible to Weevil Infestations

A salient feature of the IPM system for *P. strobi* is the combination of tactics involving silviculture and host genetic resistance. The tactics depend on a preliminary weevil hazard rating of the area based on a determination of the potential degree-day accumulation for a site (Spittlehouse *et al.* 1994). In low hazard areas, silviculture-driven tactics such as mixed-species planting and increased planting density may be sufficient to produce a successful spruce crop. In high hazard areas, the silvicultural prescription could include the use of resistant stock if available.

The existence of Sitka spruce genotypes with resistance to weevil damage was first noted in British Columbia in the early 1930s (Alfaro 1982; Alfaro *et al.*, 1995), and recently, host resistance was demonstrated in replicated trials in Sitka spruce

Fig. 4. Whether a tree is successfully colonized by the white pine weevil depends on a delicate balance between tree defenses and the strategies used by the weevil to overcome them. Silvicultural manipulations can be used to tip the balance in favour of the tree.

Fig. 5. The resin canals present in the bark of spruce help in its defense against the weevil. The graph shows the percentage of white spruce trees with resistance to white pine weevil among trees tabulated by density of resin canals in the bark of the uppermost lateral branches.

(Alfaro and Ying 1992; Ying 1991) and in white spruce (Alfaro *et al.* 1996b; Kiss and Yanchuk 1991; Kiss *et al.* 1994). In eastern North America, resistance of eastern white pine, *Pinus strobus* L., to *P. strobi* damage, was demonstrated by Wright and Gabriel (1959), Plank and Gerhold (1965), Connola (1996), and others.

Successful utilization of host resistance requires an understanding of the mechanisms used by spruce to defend against *P. strobi*, and of the strategies used by the weevil to overcome these defenses, and how these are effected by site conditions and silviculture. Optimal silvicultural systems will enhance tree defenses and reduce the possibility of weevil success. The wee-

Fig. 6. One of the strategies used by *P. strobi* to overcome the tree defenses is to deactivate the bark resin canal system. This cross-section of a spruce leader shows a first instar white pine weevil larval gallery (center, filled with frass) between two collapsed bark resin canals. *P. strobi* adults and larvae avoid puncturing bark resin canals during initial feeding. Consumption of the canal's supportive tissue causes resin canal collapse and de-activation, allowing subsequent mass colonization of the leader.

vil/spruce relationship is the product of millions of years of co-evolution, in which a number of defences and counter-defences have developed (Fig. 4). These are gradually becoming apparent. Alfaro (1994) and Lewis (1995) outlined possible sources of resistance to weevil attack in spruce trees. Blockage of successful host colonization could occur at a number of places in the complex host/weevil interaction leading to a successful brood. Olfactometer and feeding bioassay studies (Alfaro and Borden 1985; Tomlin 1995; Alfaro 1996) demonstrated that odours from certain host genotypes are repellent to the weevil; thus, in some cases, blockage of host selection could occur before the weevil arrives to the leader. The resin canal system present in the bark of spruce plays a major role in the resistance to weevil attack (Santamour and Zinkel 1977; van Buijtenen and Santamour 1972). Berryman (1972, 1988) termed this system "constitutive resistance", describing the resistance which exists in the tree prior to infestation, such as resin ducts and other plant structures. Sitka and white spruce resistant to the white pine weevil have denser resin canals in the cortex than susceptible trees (Tomlin and Borden 1994) (Fig. 5). *P. strobi* avoids puncturing resin canals during adult feeding and egg-laying (Stroh and Gerhold 1965), as well as during initial larval feeding (Alfaro 1995). In addition to this constitutive resistance, spruce can turn on an inducible resistance mechanism. In response to weevil feeding and oviposition, traumatic resin canals develop from the cambium and produce resin which kills eggs and larvae (Alfaro 1995). Traumatic resin has higher ratios of monoterpenes to resin

acids, hence it is more fluid than resin produced in the bark resin canals (Connor 1996). Low viscosity resin is probably more toxic to weevils than viscous resin. Sahota *et al.* (1994) are investigating the existence of chemicals in the bark of resistant spruce which may have negative effects on the weevil reproductive physiology.

The weevils utilize several strategies for overcoming the tree defenses. Hulme (1995) found that even the most resistant Sitka spruce clones could be successfully colonized if the attack occurred early in the season. Thus, it appears that the physiological processes that underlie the tree defenses may not be active the entire year, but they may be gradually activated in the spring. Therefore, when planting spruce, (either resistant or not) it would be advisable to utilize a mixture of genotypes from sources with different phenology. This would make more difficult the formation of weevil races with optimal host synchrony. Stock from sources with different altitude or latitude should differ in phenology.

Another weevil strategy for overcoming the tree defenses is the de-activation of the bark resin canal system. Feeding on the tissues that surround the bark resin canals prior to oviposition deprives the canals from support and nourishment and causes their collapse (Fig. 6). Mass-attack, i.e., deposition of many eggs in a short period over a given leader surface area, ensures collapse of the resin canal system over significant portions of the leader and ensures that at least some larvae will survive to adult. Working with interior spruce, Alfaro *et al.* (1996a)

found that little emergence occurred if the weevil excavated fewer than 60 egg punctures (deposition of about 100 eggs) and the brood was overcome by bark and traumatic resin. Gregarious larval feeding, evident in the formation of the "feeding ring", in which the larvae move below the bark consuming the phloem in synchrony, is an effective adaptation to overcome the tree defenses. Gregoire (1985) discusses the advantages of gregarious feeding in bark beetles. We are currently working to test if, as suggested by Wallace and Sullivan (1985), the cooler conditions prevalent in shaded stands, slow down the process of egg deposition making more difficult mass-attack and feeding ring formation.

An important consideration when utilizing resistant genotypes in reforestation programs is its deployment in mixtures with susceptible stock. Using cage experiments, Alfaro (1996) found that, when confined to resistant trees, gravid females oviposited lower in the stem, below the leader, where resin canal density was reduced by the increase in stem diameter (a dilution effect). Therefore, there is a risk that, if large plantations of purely resistant genotypes are created, the weevil could adapt to attack older internodes, where resin canal density is lower. There is no difficulty in rearing this insect, under greenhouse conditions, on bolts of Sitka spruce.

Different degrees of resistance could be added to ecosystems at risk of weevil infestations. Ecosystems located in low weevil hazard zones could contain a high proportion of susceptible spruce (higher than 50%) mixed with non-host species and still yield a reasonable amount of good quality timber. Seeds collected from naturally-resistant provenances, e.g., Big Qualicum wild seed collections for Sitka spruce (Ying 1991), would produce stock with an increased, but variable, level of resistance over that of wild seed. This variable resistance may be adequate, particularly in a silvicultural system which combines tactics that increase tree and stand resistance and reduce the likelihood of the weevil overcoming these defenses: increased plantation density, mixed species planting and shade conservation. Intensive silviculture (pruning, sanitation thinning) should be practiced to remove defective trees and concentrate growth on good-form trees. In the future, increased levels of resistance will be available from vegetative propagation of resistant trees, and from seed-orchard seed. However, the deployment of these genotypes should, at all times, take into consideration the need for avoiding the risk of insect selection leading to biotypes capable of overcoming the resistance mechanisms. Judicious use of genetic resistance, along with other measures for restoring ecosystem balance and maintenance of biodiversity, will secure continued production of spruce timber in BC.

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