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THE EFFECTS OF WATER STRESS AND INSECT ATTACK ON THE DEVELOPMENT AND BEHAVIOUR OF THE WHITE PINE WEEVIL, *PISSODES STROBI* (PECK) [COLEOPTERA: CURCULIONIDAE] ON WHITE PINE, *PINUS STROBUS* L.

Robert Lavallée

A Thesis
in
the Special Individual Program

Presented in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy at
Concordia University
Montréal, Québec, Canada

February 1994

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ABSTRACT

The effects of water stress and insect attack on the development and behaviour of the white pine weevil, *Pissodes strobi* (Peck) [Coleoptera: Curculionidae] on white pine, *Pinus strobus* L.

Robert Lavallée, Ph. D.
Concordia University, 1993

Three experimental designs were used to study the development of white pine weevil (*Pissodes strobi* [Peck]) in relation to phloem quality as affected by different watering regimes or water availability to the leader of white pine (*Pinus strobus* L.) trees. Initially, white pine leaders currently infested by weevils were harvested in a plantation after the oviposition period, and the larval growing conditions were altered by keeping leaders in water, or under dry greenhouse conditions. In another experimental design, repeated during three years under greenhouse conditions, adults were allowed to oviposit on five and six-year-old plants which were thereafter exposed to three watering regimes (dry, medium, wet). On these plants, insects could complete their development up to emergence from the leader. Finally, during two years, adult weevils were allowed to feed and oviposit on five and six-year-old plants which were then exposed to three watering regimes. At regular intervals, some plants were selected for bark collection and their leaders were also dissected to record insect development. Bark was also harvested from intact plants grown under the same watering regimes. The adult weights and the numbers of emerging insects per leader were used as criteria for insect fitness.

With harvested bark, feeding preference tests were performed to determine whether adults which had emerged in either spring or fall were able to discriminate between bark from water stressed and non stressed plants harvested at different periods during the experiment. Also, tests were done to determine whether insects could discriminate between bark from currently attacked and intact leaders.

On cut leaders weevils performed better on well hydrated leaders. Under greenhouse conditions, the adult weight was not affected by the watering regime. The number of insects per leader was higher in the wet treatment during one year only. No differences in the speed of larval development were observed between the different treatments. Feeding preference tests revealed that adults of both ages could discriminate between bark from water-stressed and non-water-stressed plants, preferring bark from the most hydrated plants. Also, adults preferred bark from infested leaders over bark from intact leaders during the oviposition period, but this preference diminished and, in some instances even reversed later in the growing season.

DEDICATION

À Nicole, Marie-Hélène, Isabelle et Ève-Marie

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INTRODUCTION

A. Project summary

The biology of the white pine weevil (*Pissodes strobi* (Peck)) has been studied for almost 200 years, but this insect is still a major problem of white pine reforestation in eastern North America. Although some host and site characteristics have been associated with population build up, it is still difficult to eliminate insect attack. Characteristics that have been associated with plant susceptibility are young trees growing in open sites with long terminal leaders, thick bark and few resin canals. However, most of these studies measure the incidence by evaluating the number of cumulative attacks per tree or the proportion of attacked trees in a plantation. Some studies have demonstrated that adult weight was related to the host used during larval development. However, no one has determined whether host growing conditions might influence weevil development and feeding behaviour. The objectives of the project reported in this thesis were to determine (1) if white pine weevil development is affected by different levels of water stress when reared on cut leaders; (2) if white pine weevil development is affected by different levels of watering regimes when reared on living white pine; (3) if the feeding preferences of adults are affected by the quality of bark harvested on plants grown under different watering regimes; and (4) if the feeding preferences of the adults are affected by bark quality harvested on intact and on trees currently infested by *P. strobi*. The hypothesis underlying this study is that growing the host under water stress conditions can positively influence insect performance as revealed by biological indicators such as number of insects emerging per leader, insect weight and feeding responses to bark from trees stressed by water shortage or insect damage. Similarly, water stress or prior weevil damage could affect their subsequent feeding responses. A better understanding of the influence of host vigour on insect development and feeding preference will contribute to more biologically sound pest management practices for white pine.

B. The white pine weevil problem

The white pine weevil is a native of North America, and it has long been recognized as an important pest of white pine (*Pinus strobus* L.) (Wallace and Sullivan 1985). Moreover, with the increased tree planting activity in the province of Québec, this insect is more frequently observed on other host species such as Norway spruce (*Picea abies* (L.) Karst.) and white spruce (*Picea glauca* Moench Voss), where it can complete development and cause damage as severe as that which occurs to white pine (Ministère des Forêts 1993; Lavallée *et al.* 1989). In eastern North America, the white pine weevil can also severely damage jack pine (*Pinus banksiana* Lamb.), Scots pine (*Pinus sylvestris* L.), black spruce (*Picea mariana* (Mill.) B. S. P.), red pine (*Pinus resinosa* Ait.) and red spruce (*Picea rubens* Sarg.) (Wallace and Sullivan 1985). On the western coast, Sitka spruce (*Picea sitchensis* (Bong.) Carr.), Engelmann spruce (*P. engelmannii* Parry ex Engelm.) and white spruce (Stevenson 1967) are also affected. Weevil attack causes two major types of loss: a reduction in the recoverable volume of wood caused by destruction of the leader, and also lumber degradation (Marty 1959). For white pine, merchantable volume losses can be as high as 70% and attacked trees become of lower commercial grade (Brace 1971, 1972)

Current knowledge of the white pine weevil gives us a partial understanding of the behaviour of this insect and if damage can be reduced we cannot eliminate the attacks. Knowledge of weevil-host relationships is mainly related to tree age, leader size, planting density, overstory, and site effects. Large trees up to 100 years old can be attacked (Ostrander 1957; Carlson 1966), but it is trees 5 to 30 years old that are most susceptible (Connola and Wixson 1963a; Marty and Mott 1964). Weevil attack may occur on trees as short as on one meter (MacAloney 1943); however, most damage occurs when trees are 12 to 18 years old and damage rarely occurs after 25 and 30 years of age (Belyea and Sullivan 1956). In a plantation, a tree that has been previously attacked seems more likely to be re-attacked compared with a non-attacked tree (Marty and Mott 1964; Lavallée *et al.* 1990). According to Silver (1968), weevils select rapidly growing trees. Trees with thinner bark and smaller leaders are less susceptible (Barnes 1928; Kriebel 1954; Sullivan 1961; Wilkinson 1983b; McMullen *et al.* 1987). Leader length is positively related to the probability of attack (McMullen *et al.* 1987). Also, Wilkinson (1983a) demonstrated that the depth of resin canals in the outer bark dissuades insect attack. Factors like the number of resin canals, resin viscosity and terpene composition of resin have been associated with tree resistance, but they do not confer an absolute protection against weevil attack (Van Buijtenen and Santamour 1972; Overhulser and Gara 1981b; Wilkinson 1983a; Hrutfiord and Gara 1989). Combining some factors associated with weevil resistance, such as bark thickness, limonene concentration, and depth of resin canals, Wilkinson (1983a) explained only 13.1 % of host susceptibility. Some stand characteristics also have been associated with damage levels. Trees planted at higher densities are less severely affected than open grown trees (Graham 1926; Alfaro and Omule 1990). Moreover, pines growing under forest cover are less severely attacked than those growing in open sites (Sullivan 1961; Corriveau and Lamontagne 1977; Stiell and Berry 1985). Finally, damage is more severe when host trees are planted on inadequate sites (Connola and Wixon 1963a; Xydias and Leaf 1964; Connola and Birminghan 1978; Lavallée 1992; Archambault *et al.* 1993).

Chemical control techniques against the weevil, although demonstrably efficient, (De Groot 1985), presently are not environmentally acceptable. Mechanical control, recommended only when plantations are young (Lavallée and Morissette 1989), becomes expensive in large plantations. Finally, research results on resistance to white pine weevil are contradictory, some work indicates that there is no resistance to insect attack (Garrett 1972; Mitchell *et al.* 1974; Fogal *et al.* 1982; Wilkinson 1983c), while other research claims resistance between trees or provenances (Holst 1955; Wilkinson 1983a; Coleman *et al.* 1987; Alfaro and Ying 1990). Long term breeding programs for resistance against the weevil which were considered as unlikely according to Brooks *et al.* (1987) are now in progress in British Columbia (Alfaro, personal communication).

As mentioned earlier by Kulman and Harman (1965), weevil damage is not a direct indication of the weevil's biological performance. A better knowledge of the influence of host growing conditions on weevil development could help to reduce the impact of this insect by lowering its biological performance. This thesis will consider the impact of the host watering regime on the weevil's fitness.

C. Literature review

Life cycle

The adult white pine weevil overwinters in the uppermost litter beneath the host (Dixon *et al.* 1979). In early spring, generally toward the end of April, adults leave the litter and move toward one-year-old leaders to feed, copulate and subsequently disperse to nearby trees (Graham 1926; Harman and Kulman 1969). A positive phototropism and the vertical silhouette of leaders are cues which guide the insects to the leader (VanderSar and Borden 1977a,b,c). However, Gara *et al.* (1971) found that feeding and oviposition can also occur on leaders arranged horizontally. Pheromonal communication is also suspected (Booth *et al.* 1983). Oviposition lasts about six weeks, and each female will deposit approximately one hundred eggs (Taylor 1929; Maughan 1930). As many as 350 eggs can be found per leader (MacAloney 1943). Initially, eggs are laid in the uppermost part of the leader Sullivan (1961).

Eggs hatch after two weeks, and the young larvae bore downward under the bark, feeding on the phloem. Larvae frequently are observed in the two-year-old section of the stems (Belyea and Sullivan 1956) and rarely in lateral branches (Taylor 1929). When they are numerous, girdling occurs and the current growth plus the two-year-old section die. Larval development proceeds through four instars over 5 to 6 weeks. The final instar will then pupate in the pith or the outer xylem, according to the weevils position in the leader. The pupal stage lasts two weeks and the new adult may remain in the leader for two more weeks before emerging. By the end of July to as late as early September, adults will emerge from leaders. Thus a period of 2.5 to 3 months was necessary for insect development (MacAloney 1943). The new adult generation will then be found in the buds and the current year's shoots (Dixon *et al.* 1979) and will pass the winter in the litter.

Phloem insect - host relationships

Host-insect relationships are complex, and they can be modified by stressful environmental factors (Rhoades 1983). One of these elements, the plant water regime, may affect plant physiology and, in turn, influence insect development by modifying host defense and/or food quality.

The nutritional quality of plants has been implicated as a major factor in the dynamics of herbivore insect populations (House 1961; Dixon 1970; McClure 1980). According to White (1978), survival of animal species, principally young individuals, depends on their access to quality food. Proteinous nitrogen is considered an important element in the nutrition of phytophagous insects (White 1978). Generally, the efficiency of food assimilation and insect growth are favoured by augmenting the plant nitrogen content (McNeill and Southwood 1978; Mattson 1980). However, in some circumstances nitrogen fertilization can also lead to poor insect performance (Stark 1965; Smirnoff and Bernier 1973; Xydias and Leaf 1964). This illustrates the diversity of insect responses and indicates that the available form of nitrogen and other factors, such as the water content, must be considered (Strong *et al.* 1984).

The role of water is important in food ingestion, assimilation and possibly insect reproduction. With chewing insects food water content affects growth rate and conversion efficiency of nitrogen and plant tissues into animal tissue (Connor 1988). For rice weevil species, higher levels of water in rice plants was associated with faster insect development and, more importantly, fecundity (House 1961). Mordue (1967) demonstrated that the female of *Tenebrio molitor* L., deprived of water during a short period, had reduced oocyte production. Females of the white pine weevil prefer to oviposit on shoot sections having a high water content (O'Dell 1972). Wilkinson (1975) artificially modified the shoot water content of natural white pine trees by a silicone spraying and observed an increase in weevil attacks on these trees.

The nutritional quality of a plant can be modified substantially by environmental stress. According to White (1978), theoretically, outbreaks of phytophagous insects may be caused by plant stress that leads to increased amino acids essential to insect fecundity and survival. Concentrations of soluble metabolites having nutritional potential such as proline, sugars, glycerol, malate and shikimate increase in plant tissues following stress (Rhoades 1983). Levels of free amino acids rise after a stress, while proteic amino acids tend to be reduced slightly (Brodbeck and Strong 1987). Sugar levels may rise after moderate water stress, but under severe water stress they are reduced (Kramer 1983).

Larval development of the white pine weevil occurs under the bark of the leader. According to Broadbeck and Strong (1987), this specific site should be advantageous for insect development. Even if the nitrogen concentration in the phloem is relatively low compared with that of foliage, the net flux into the phloem may be very high, approaching 100 % of the plant nitrogen concentration (Broadbeck and Strong 1987). All the organic carbon and most of the organic nitrogen implicated in plant growth passes through the phloem (Raven 1983). Moreover, phloem nitrogen is incorporated into small molecules, free amino acids and amides, more easily assimiled by insects compared with larger proteic molecules. Phloem also does not contain the variety or concentration of toxic phytochemical substances found in the foliar tissue (Broadbeck and Strong 1987). It is also an abundant source of water (Scriber and Slansky 1981). It seems reasonable to speculate that weevil development is affected by these nutritional characteristics.

Besides food quality, insects have to cope with plant defense mechanisms. These may be classified into three groups: physical, nutritional and allelochemical (Strong *et al.* 1984). An easily observed first line of plant defense is conferred by thick sclerophyllous foliage or abundant pubescence. Plant phenology is also considered as a defense mechanism. Maintaining a high level of nitrogen in tissues for a short time also constitutes a type of plant defense (McNeill and Southwood 1978; Mattson 1980). Less evident are the chemical substances already present in plant tissue or those induced by herbivore damage, that confer a defense against some insect species. Some chemical substances can reduce plant digestibility for insects (tannins, resins, silica) or be toxic (alkaloids, cyanogenic glucosides) (Feeny 1976, 1980; Rhoades and Cates 1976; Cates and Rhoades 1977; Rhoades 1979). However, according to the insect species, these substances can be phagostimulants, they may be cues used to find their host or these substances may be assimilated by the insect and provide a form of protection against predators (Chapman and Blaney 1979; Bernays 1981).

With conifers, the defense system resides partly in resin. This material may be present already or induced after physical damage. Resistance of some conifers to bark beetle attack depends on the characteristics of oleoresin. Bark beetle attack may fail as a result of an elevated oleoresin exudation pressure (OEP) (Reid *et al.* 1967; Wood 1962; Vité and Wood 1961). Oleoresin pressure and flow are affected by a number of environmental factors, most particularly, by those affecting the internal water balance (Boudreau and Schopmeyer 1958; Vité 1961; Lorio and Hodges 1968a,b). Hence, well hydrated trees have a higher OEP than water stressed trees and should resist insect attack (Vité 1961; Lorio and Hodges 1968a,b). For the white pine weevil, resin is an important factor affecting mortality (Johnson 1965; Silver 1968). If a resin canal does not close rapidly after being pierced by an adult weevil, then egg survival is compromised (Overhulser and Gara 1981b). Thus, water stress should act on resin quality and quantity and, in turn, affect weevil development and survival. Also, some weevil resistance is associated with the terpene composition of bark (Harris *et al.* 1983). According to their concentration, some terpenoid products may be stimulatory or repulsive to the white pine weevil. High levels of α-pinene, and low levels of limonene are associated with resistant trees (Wilkinson 1980). Alfaro *et al.* (1980) found that α-pinene, β-pinene and β-myrcene are feeding stimulants while higher concentrations of (+)-camphor and limonene are inhibitors. According to Carlson (1971), increased limonene in spring, when adults disperse, indicates that this substance might be a signal for host recognition. Thus, some host substances like resins and terpenes may act as defensive or attractive substances according to their concentration. However, Wilkinson (1985) showed that the terpene profiles of western white pines resistant to the weevil were similar to those observed for susceptible eastern white pines.

Most studies concerning the effect of water stress on plants and on insect development involved foliage feeding insects (see Mattson and Haack 1987b), and it may be difficult to extrapolate to a coniferous phloem feeding species. Phloem insects, even if protected from weather, will be sensitive to variation in food quality (White *et al.* 1970, White *et al.* 1972, Chararas 1979). Environmental events acting on bark chemistry may influence phloem insects (White *et al.* 1972). However, the role of the phloem is physiologically different from that of the foliage (Kozlowski *et al.* 1991). Therefore, chemical modifications occurring in the phloem as a result of plant stress may be different from those observed in foliage, and insect response might also be different. Water availability and damage caused by phytophagous insects are two important stress factors that can influence the plant's physiology. Considering that the water regime is an important variable for white pine growth (Cauboue and Malenfant 1988), we pose the hypothesis that the white pine weevil development can be positively affected when its developpement occur on a water stressed host.

D. Goals and objectives

The goal of this study was to determine whether development of a phloem feeding insect can also be affected by the growing conditions of its host, as has been demonstrated for a number of folivorous insects. We assumed that an important perturbation factor such as soil water availability may modify the plant's physiology and, consequently, act on white pine weevil development. We studied the influence of white pine watering regime on weevil performance, expressed as the number of adults emerging per leader, their mean weight and their feeding preference. The first objective was to determine if weevil development was affected by physiological perturbations caused by rearing on cut leaders provided with or deprived of a water source. The second objective was to determine if development of weevils reared on plants was affected by the host's watering regime. The third and fourth objectives were to determine whether adult weevils could discriminate between bark from plants grown under different watering regimes and also to determine if previous weevil damage affects feeding preference. Though not a specific objective, we also developped a simple and rapid technique to sex white pine weevil adults.

CHAPTER 1

Development of the White Pine Weevil, *Pissodes strobi* (Peck) (Coleoptera: Curculionidae), on Cut Leaders of White Pine, *Pinus strobus* L.

A. Abstract

In 1989 and 1990, after the egg-laying period, leaders of young white pine, *Pinus strobus* L. infested by *P. strobi* (Peck) were harvested. To test the influence of moisture regime on weevil development, leaders were set directly in water or kept dry. The number of insects emerging from each leader and the mean weight of the adult weevils were measured for leaders exposed to both treatments. During the second year, data were also collected on weevil development in the field. White pine weevil completed development on cut leaders. However, the dry treatment significantly reduced the weight and the number of weevils when compared with the wet treatment. The adult weight was a better indicator of larvae growing conditions than was the number of insect emerging per leader.

B. Introduction

The white pine weevil, *Pissodes strobi* (Peck), is a major pest of white pine, *Pinus strobus* L., and Norway spruce, *Picea abies* (L.) Karst., but it also attacks several other pine and spruce species (Graham 1926; Jaynes and MacAloney 1958; Wallace and Sullivan 1985; Lavallée and Benoit 1989). In Québec, it is one of the most common pests of pine and spruce plantations (Ministère des Forêts 1991). Damage is more serious when the host is planted on open (Graham 1918; MacAloney 1930; Alfaro and Omule 1990) or unsuitable (Maughan 1930; Connola and Wixson 1963a,b; Connola and Birmingham 1978) sites. After overwintering in the litter beneath the host trees, adults resume their activity in early spring (Dirks 1964). Males and females are attracted to the previous years' leaders and, after mating, the females oviposit in feeding cavities made in the bark. Larvae bore downward and feed on the phloem (i.e., inner bark [Jensen *et al.* 1963]). Pupation takes place in the xylem or the pith, and a new adult generation emerges in late summer (Jaynes and MacAloney 1958; Sullivan 1961; Wallace and Sullivan 1985). The annual attack destroys at least two years growth, reduce height growth (Marty and Mott 1964) and jeopardize seriously the commercial value of this lumber without killing the tree (Brace 1971).

Insect-host relationships are only partly documented for the white pine weevil. Several studies have shown that different host species produce different numbers of insects per leader (Dirks 1964; Overhulser and Gara 1981a; Phillips and Lanier 1983; Alfaro 1988). In addition, Alfaro (1988) showed that adult weight is affected by the host species. The white pine weevil is also affected by morphological characteristics of its feeding site. Sullivan (1960) reported a positive effect of bark thickness on feeding and oviposition. McMullen *et al.* (1987) presented a positive relation between leader length and the number of adults emerging per leader. However, it has never been established whether white pine weevil development can be affected by different growing conditions that affect phloem quality.

Host quality is known to influence the reproductive performance and development rate of many phloem-feeding Coleoptera (Haack *et al.* 1984a,b; Haack and Slansky 1987; Haack *et al.* 1987b; Popp *et al.* 1989). Moreover, the final body size of a number of phloem-feeding Coleoptera is directly related to host quality (Andersen and Nilssen 1983; Amman and Pasek 1986; Slansky and Haack 1986; Haack and Slansky 1987; Haack *et al.* 1987a). The effect of phloem quality on white pine weevil development is only partly documented. Most of these studies are concerned only with phloem thickness, not the intrinsic quality of the host as revealed by indicators such as the water content or the water potential of the plant. The water potential of a plant reflects its water stress (Hsiao 1973), and water stress can cause chemical changes in the bark (Schulze 1991). Plant stresses have been associated with increased nutritional quality of the host for phytophagous insects (Cates *et al.* 1983; Brodbeck and Strong 1987; Mattson and Haack 1987a,b; Louda and Collinge 1992). Outbreaks of phloem insects such as bark beetles have been also associated with moisture stress (Blackman 1924; Lorio 1968; Ferrell 1978; Waring and Pitman 1983; Paine *et al.* 1989).

The hypothesis underlying this study is that, under hydric stress, modifications in phloem quality can affect the development of the white pine weevil.

C. Materials and methods

In 1989 and 1990, infested white pine leaders of similar size were harvested in a 13-year-old plantation located at Saint-Luc-de-Champlain (46° 30' N; 72° 30' W), 25 km east of Trois-Rivières (Québec). In 1989, 47 leaders were collected on 6 June, about 1 month after the initial egg-laying period. In 1990, 41 leaders were collected on 17 May, during the oviposition period. After harvest, all leaders were placed in the Laurentian Forestry Centre greenhouse and exposed to either a wet or a dry treatment. For the wet treatment, shoots were set vertically in plastic containers (38 by 12 by 45 cm) filled with water, and for the dry treatment the basal part of each shoot was protected from water with a plastic bag (10 cm by 15 cm). Both treatments were mixed in alternate rows.

In 1990, to monitor the field performance of weevils in the same plantation, 20 infested leaders were protected against weevil predators with a nylon-mesh tissue that was tied at the top and bottom of the leader. The mesh was installed on 17 May and leaders were harvested on 26 July at the end of larval development and before adult emergence.

Before adult emergence, all leaders were individually caged in plastic tubes (5 cm by 80 cm) closed at one end with a nylon-mesh tissue and a plastic bottle (Pharma No. 16, MHAC, Pointe-Claire, Québec) at the other end, kept in the laboratory at 20°C, and observed daily. Insect performance was measured as mean number of weevils emerging per leader and mean adult weight. Sex was determined using the techniques described in Chapter 5. In 1989, leaders were caged from 14 July to 21 August. In 1990, the caging period was from 9 July to 9 September. At the end of that period, leaders without emerging adults were dissected to determine the presence of larval feeding scars under the bark. Only leaders with larval feeding were used in data analysis.

Bark water content and xylem water potential were measured on cut leaders. Before leaders were caged in 1990, a bark sample was taken from each. Bark water content (BWC %) was recorded on a dry-weight basis (BWC = 100 (fresh weight minus dry weight)/dry weight), after a drying period of 24 h at 70°C. Five infested leaders in the plantation were cut on 7 July and their bark water content determined. The same design was used in 1991 to regularly evaluate the xylem water potential of cut leaders. At each sampling date, three needle fascicles harvested in the uppermost living part of each leader were used to measure the midday water potential using a Scholander pressure chamber (Scholander *et al.* 1965) (Model 1000, PMS Instrument, Corvallis, OR) according to the technique of Johnson and Nielsen (1969). The length of needle fascicle protruding from the top of the chamber was maintained at <0.5 cm, and the pressure was raised slowly (Joly 1985). Observations were made with a binocular microscope at 30x magnification, and the true endpoint was recognized when water appeared on the needle-fascicle cross section. The terminal leaders were harvested on 13 June, kept in a greenhouse and observed weekly until 26 July.

The number of weevils per leader and their mean weight were compared between treatments for each year. A General Linear Models (GLM) procedure was used to detect treatment differences, and the means were separated using orthogonal contrast (Statistical Analysis System (SAS) Institute 1989). Numbers of weevils per leader were transformed to their square root to achieve variance homogeneity and normality of the residuals. Bark water contents were compared using Tukey's (Honestly Significant Difference) test (SAS Institute 1989).

D. Results

Hydric status of leaders. Average water contents of white pine bark for all treatments were significantly different (Table 1.1). Bark from the wet treatment had a higher water content than bark from the field but was not significantly different. However, both of them were significantly higher than the water content of bark from the dry treatment.

Average midday xylem water potentials of needle fascicles from leaders exposed to dry and wet treatments are presented in Table 1.2. Water potential dropped below -4.0 MPa soon after the dry treatment was established (12 days). The wet treatment maintained an average value of -1.6 MPa, reaching -2.8 MPa at the end of the experiment.

Number of adults. In 1989, the leaders were observed for 35 days and in 1990 they were observed during 44 days. The total number of adults that emerged in the different treatments were, respectively, 610 and 588 for dry and wet treatments in 1989; and 88, 628, and 580 in 1990 for dry, wet, and field treatments. In the 1990 dry treatment, adults emerged from only 5 of the 18 leaders. There was no significant difference between the numbers of adults emerging from the dry and wet treatments in 1989 ($P = 0.92$) (Tables 1.3 and 1.4). In 1990 when we compared the dry treatment with the two other treatments we found highly significant differences ($P < 0.01$) (Table 1.3). More adults per leader emerged from the leaders subjected to the wet treatment compared with those from the dry treatment.

Table 1.1. Final phloem water content (dry weight basis) of white pine leaders (Lsmean ± S.E.M.) from dry, wet, and field treatments.

Treatment	Water content (%)	Sample size
Dry	53.7 ± 16.55a	7
Wet	245.0 ± 17.89b	6
Field	187.4 ± 19.58b	5

Means followed by the same letter are not significantly different (Tukey's [HSD] test; *F* = 54.35, *P* < 0.01, df = 2, 15 [SAS Institute 1989]).

Table 1.2. Average xylem water potential (-MPa) of white pine needle fascicles by treatment at different observation dates in 1991.

	Date				
Treatment	14 June[a]	25 June	2 July	16 July	26 July
Dry	1.7 ± 0.2 (10)[b]	<4.0 (3)	<4.0 (3)	<4.0 (3)	<4.0 (3)
Wet	0.8 ± 0.5 (10)	1.0 ± 0.6 (5)	1.8 ± 0.3 (7)	1.8 ± 0.2 (7)	2.8 ± 0.2 (3)

[a] For the first date, analysis of variance revealed significant difference between treatments ($F = 23.74$; df = 1,18, $P < 0.01$).

[b] Mean ± standard deviation; number of replicates in parentheses.

Table 1.3. Analysis of variance of numbers of adult *P. strobi* emerging per white pine leader for each treatment and each year.

Source of variation	Degrees of freedom	Mean square	*P* value
Year	1	16.1425	0.0267
Treatment * year	3	81.1899	0.0001
1989: dry vs wet	(1)	0.0359	0.9157
1990: dry vs wet and field	(1)	243.2796	0.0001
1990: wet vs field	(1)	0.51009	0.6902
Error	100	3.1917	

Table 1.4. Mean number of adult *P. strobi* emerging per white pine leaders for each treatment and each year.

Year	Treatment		
	Dry	Wet	Field
1989	23.2 ± 0.14 (23)[a]	23.7 ± 0.14 (23)	*
1990	1.3 ± 0.18 (18)	31.7 ± 0.16 (20)	29.2 ± 0.15 (21)

[a] Back-transformed least squares means and standard error of transformed data; number of replicates in parentheses.

* Not evaluated.

In 1990, a comparison of wet and field treatments indicated no significant difference. The significant treatment * year interaction ($P < 0.01$) (Table 1.3) is related to a lower number of insects per leader in the dry treatment in 1990 than in 1989 and a higher number in the wet treatment in 1990 than in 1989 (Table 1.4). Consequently, the treatments' effects were not the same during both years.

Mean weight of adults. The male and female weights were affected by treatments in both years (Table 1.5). Females and males emerging from the dry treatment in 1989 were, respectively, 11 and 9% smaller than those from the wet treatment (Table 1.6), and these differences were significant (Table 1.5). The dry treatment in 1990 produced smaller adults of both sexes than in the two other treatments. The difference between the mean adult weight of insects reared on wet cut leaders and those in the field was not significant ($P = 0.08$ for females and $P = 0.07$ for males) (Table 1.5).

The weight of insects grown on cut leaders in 1990 was less than in 1989 ($P = 0.02$, Table 1.5), and females were heavier than males ($P < 0.0001$). The absence of interaction between treatment and sex indicates that both sexes reacted to treatments in the same way ($P = 0.90$).

Table 1.5. Analysis of variance of weight of adult *P. strobi* for each treatment and each year.

Source of variation	Sex	Degrees of freedom	Mean square	*P* value
Year		1	0.000059	0.0190
Treatment (year)		3	0.000071	0.0005
Leader (treatment * year)		87	0.000025	0.0001
Sex		1	0.000051	0.0001
Year * sex		1	7.04×10^{-8}	0.8604
Treatment * sex (year)		3	4.56×10^{-7}	0.8961
1989: dry vs wet	♀♀	(1)	0.000081	0.0042
	♂♂	(1)	0.000074	0.0071
1990: dry vs wet and field	♀♀	(1)	0.000026	0.0190
	♂♂	(1)	0.000045	0.0042
1990: wet vs field	♀♀	(1)	0.000032	0.0825
	♂♂	(1)	0.000035	0.0666
Error		2397	0.000002	

Table 1.6. Mean[a] weight (g) of adult *P. strobi* for each treatment and each year.

Year	Sex	Treatment		
		Dry	Wet	Field
1989	♀♀	0.0081[b](303)[c]	0.0091 (288)	*
1989	♂♂	0.0078 (307)	0.0086 (300)	*
1990	♀♀	0.0078[d] (42)	0.0089 (309)	0.0095 (310)
1990	♂♂	0.0072[d] (46)	0.0086 (319)	0.0092 (270)

[a] Least squares means.

[b] Each mean standard error is 0.0001 except for means identified with[d].

[c] Number of insects in parentheses.

[d] Mean standard error is 0.0004.

* Not evaluated.

E. Discussion

The white pine weevil can complete its development on cut leaders as reported by Graham (1926) and Maughan (1930), but the number of adults per leader and the adult mean weight were affected by the treatments. In 1990, for both sexes, the leaders from the field and those placed in water produced significantly heavier adults than those without water. Although not significant, the field leaders produced heavier adults than leaders that were cut and kept wet. In 1989, the wet treatment also gave heavier adults. The adult weights obtained on wet and field leaders were comparable with other weights reported for white pine weevil emerging from preferred host species (VanderSar *et al.* 1977, Alfaro 1988). When adults emerge from a less-preferred host species (Alfaro 1988), their weights are smaller than those we obtained in 1990 in the dry treatment. In 1990, the number of adults per leader was higher in wet and field leaders than in dry leaders. However, there was no significant difference between these treatments, or those in 1989.

Lack of a significant difference in the number of emerging adults between treatments in 1989 may be due to the stress intensity and its duration. Both types of stress were imposed after the oviposition period when larvae had completed part of their development. Therefore, in the 1989 dry treatment, the larvae were exposed to extreme water stress only for a short period. Conversely, in 1990, the insects were mostly in the egg stage at the start of the treatments. Consequently, larvae were exposed to water stress during a longer period. Keeping cut leaders in water did not reduced the number of insects emerging per leader, and these numbers were similar to those observed in the field.

The larger number of insects emerging from leaders in the wet treatment in 1990 compared with 1989 is probably more related to a different population level present in the plantation in 1990 than to a treatment effect. The annual survey made by the Forest Insect and Disease rangers of Quebec in the area of our plantation indicated an increase in damage by the weevil in 1990 from 1989 (Ministère des Forêts 1991).

Our results suggest that the number of adults per leader and adult mean weight are not equivalent indicators of larval growing conditions; adult mean weight may be a more sensitive biological indicator. In 1989, the number of insects emerging per leader did not differ significantly between treatments although the mean weights did. Similar results were found in 1990 when there was no significant difference in the average number of insects per leader, but the difference in weight between wet and field treatments was nearly significant for both sexes. Alfaro (1988) did not find any difference in the number of insects per leader but found significant differences in the weight of emerging adults when comparing insect performance on cut leaders of various western host species. This variability in adult weight may illustrate the high degree of plasticity in the critical larval body size required to molt or pupate, as mentioned by Slansky and Scriber (1985) and demonstrated with a phloem-feeding scolytid, *Ips calligraphus* (Germar) (Haack *et al.* 1987b).

According to Haack *et al.* (1984b), chemical variations in bark can affect insect development. Although not evaluated, cutting the leaders surely modified the chemical composition of the bark and influenced the insect's development. As expected, the water content of bark was lower in leaders of the dry treatment compared to wet treatment (Table 1). Xylem water potential, which is used here as an indicator of internal plant water balance, reflects the rapidity of desiccation of the larval habitat (Table 2). However, no studies have yet demonstrated a relationship between the plant water potential and white pine weevil development. The lower water content of bark in the dry treatment can partly explain the insect's performance. It has been shown that higher water content in food of foliage-chewing and phloem-feeding insects is associated with better development (Reid 1962; Scriber 1977; Reese and Beck 1978; Scriber and Feeny 1979; Feeny 1980; Mattson 1980; Scriber and Slansky 1981; Clancy 1991). The slight difference between mean weights in wet and field treatments suggests that essential elements may be lacking for insects living on hydrated cut leaders. Most translocation of organic compounds occurs through the phloem (Jensen *et al.* 1963; Kozlowski *et al.* 1991). Consequently, when living on cut wet-treatment leaders, the larvae do not have access to an array of elaborated products of photosynthesis, and this may be associated with their smaller mean weight.

Alfaro (1988) mentioned that cut leaders may have lost some resistance factor to white pine weevil development. Our results contradict this statement because it is on intact leaders that the insects show the best performance. This suggests that white pine weevil performance is probably more related to the nutritional status of bark than to plant defense mechanisms. Although a number of insect species can perform normally on low vigour, dying, or dead trees (Finnegan 1958, 1962; Knight and Heikkenen 1980; Corneil and Wilson 1984; Coulson and Witter 1984; Barbosa and Wagner 1988), the white pine weevil performed better on a living host with well-hydrated bark. It may be hypothesized that conditions that influence plant growth and development, and modify phloem chemistry play an important role in white pine weevil population dynamics. Xydias and Leaf (1964) reported more damage by the white pine weevil after fertilization in a white pine plantation. Also Wilkinson (1975) observed more attacks on trees with higher bark water content. In plantations where phloem quality allows white pine weevil to perform better, the population build up can be accelerated. A positive correlation between female weight and the number of eggs laid has been observed (R. L., unpublished data). A similar phenomenon has also been reported for another phloem-feeding insect, *Dendroctonus ponderosae* Hopkins (Reid 1962). Heavier adults emerging from leaders enhance population build up in a plantation.

In summary, adult weight and number of adults emerging per leader are affected by phloem quality, and weevil performance is negatively affected by extreme water stress. It is on intact and well hydrated leaders that the best performance is obtained, and adult weight is a better indicator of the insect's fitness than the number of adults per leader.

CHAPTER 2

Development of White Pine Weevil, *Pissodes strobi* (Peck), (Coleoptera: Curculionidae) on White Pine Grown Under Different Watering Regimes

A. Abstract

During the summers of 1989, 1990 and 1991, 5 and 6 years old white pine (*Pinus strobus* L.) under greenhouse conditions, were subjected to white pine weevil (*Pissodes strobi* [Peck]) feeding and oviposition and, thereafter, grown under dry, medium and wet watering regimes. The objective of this study was to test the effect of the watering regime on the weevil development. Larval development was followed and emerging adults were captured to determine if the number per leader or their weights were affected by treatments. No differences were observed in the rate of development of larvae and in the adult mean weights between the water regimes. The number of insects emerging per leader was affected by treatment in one year, and more adults emerged from the wet treatment. Plant water potential and bark content in water were lower under the dry watering regime. Phosphorus and potassium contents were higher in bark from the dry watering regime, however, the nitrogen content was unaffected. Year to year variation was observed in the treatment effects on insect weights.

B. Introduction

Host plants play an important role in the population dynamics of phytophagous insects, and a number of studies have demonstrated the effect of biotic and abiotic stresses on plant insect interactions (Painters 1936, White 1976, Barbosa and Wagner 1988). Drought, one of the most studied factors, can modify tree physiology and increase or decrease the nutritional quality of foliage, and thus possibly promote insect performance and lead to outbreaks (White 1978, 1984; Mattson 1980; Mattson and Haack 1987a,b; Louda and Coliinge 1992). Drought may also weaken the chemical defenses of trees and increase susceptibility to insect outbreaks (Mattson and Addy 1975; Rhoades 1983, 1985; Mattson and Haack 1987 a,b; Louda and Collinge 1992). However, evidence for the stress theory is largely circumstantial and there is little direct experimental data on the responses of insects to plant water stress (Mattson and Haack 1987b; Louda and Collinge 1992; Waring and Cobb 1992).

The effects of plant stress on insects have been studied mainly with folivorous (White 1976; Beckwith 1976; Wagner 1986; Watt 1986; McCullough and Wagner 1987; Ellsworth *et al.* 1989; Tisdale and Wagner 1991) and sap feeding species (White 1969; Connor 1988; Oloumi-Sadeghi *et al.* 1988; English-Loeb 1989). Except for bark beetles (Hodges and Lorio 1975; Raffa and Berryman 1982; Larsson *et al.* 1983; Waring and Pitman 1985; Mulock and Christiansen 1986), there are few plant stress studies of other phloem feeding insects. Outbreaks of bark beetles associated with moisture stress may partly be explained by a lowering of plant defense mechanisms (Blackman 1924; Lorio 1968; Ferrell 1978; Waring and Pitman 1983; Paine *et al.* 1989), but the quality of the phloem could also play an important role. The reproductive performance and development rates of other phloem feeding Coleoptera is affected by phloem quality (Andersen and Nillsen 1983; Haack *et al.* 1984a,b; Amman and Pasek 1986; Slansky and Haack 1986; Haack and Slansky 1987; Haack *et al.* 1987a,b; Popp *et al.* 1989).

Among the phloem feeding insects, weevils have received little attention, even though some species have been specifically associated with host growing conditions or vigour (Warren 1956; Finnegan 1958, 1959, 1962; Giblin-Davis and Howard 1989). The white pine weevil (*P. strobi* (Peck)), an important pest to pine and spruce reforestation, attacks mostly young and vigourous plantations rather than older ones, and it prefers trees with the longest terminal shoots and larger leader diameters (Graham 1926; Plummer and Pillsbury 1929; MacAloney 1930; Prebble *et al.* 1951; Kriebel 1954; Holst 1955; Connola 1965; Wilkinson 1983a; Alfaro 1989; Lavallée *et al.* 1990). Recently, Lavallée *et al.* (1993) demonstrated that the adult weight of this insect was affected by bark quality of its host and reported better insect performance on vigourous well hydrated white pine leaders. Also, site characteristics have been associated with weevil damage (Maugham 1930; Connola and Wixson 1963a,b; Dirks 1964; Connola and Birmingham 1978; Warkentin *et al.* 1992; Archambault *et al.* 1993). However, these studies were concerned with the level of damage in plantations and do not give any information on the biological performance of the weevil.

White pine trees can grow in a variety of soil types (Sims *et al.* 1990) and are particulary adapted to tolerate drought conditions (Lopushinsky 1969). However, no studies have examined the influence of hydric stress on white pine and white pine weevil development. Hence, the objective of this research was to compare the development of weevils reared on plants exposed to different watering regimes extending from well watered to dry or near the permanent wilting point of the plant. The hypothesis is that white pine weevil development can be better on water stressed white pines.

C. Materials and methods

Biology of the white pine weevil. The white pine weevil is the most important pest in artificial reforestation in Québec (Bonneau et Guérin 1990). This insect is a major pest of white pine (*Pinus strobus* L.) and Norway spruce (*Picea abies* (L.) Karst.), but it also can be found on several pine and spruce species (Graham 1926; Jaynes and MacAloney 1958; Wallace and Sullivan 1985; Lavallée and Benoit 1989). On white pine, attack by the weevil begins when trees are 1 m high and 5 to 6 years old (MacAloney 1930). Without killing the tree, this phloem insect destroys only the uppermost part of its host, the leader. After overwintering in the litter, adults resume their activity in early spring (Dirks 1964). Males and females are attracted to the uppermost part of the previous years' leaders where they feed on phloem and mate. Thereafter, the females oviposit in feeding cavities and close these cavities with their frass. After 2 weeks, the eggs hatch and larvae bore downward eating the phloem. Pupation takes place in the xylem or in the pith and a new generation of adults emerges in late summer (Jaynes and MacAloney 1958; Wallace and Sullivan 1985).

Tree collections. In 1989 and 1990, white pine plants (5 and 6 years old, respectively) were obtained from the Canadian Forest Service nursery located near

Valcartier (47°57'N, 72°30'W) and in 1991 (6 years old plants) from a plantation located near L'Islet (47°35'N, 70°00'W). Plants were removed from soil and planted in 6 L perforated plastic pots before the resumption of growth in early spring (May 17, 1989; May 19, 1990; May 7, 1991). Soil mixtures were a sandy loam in 1989 and sand in 1990 and 1991. The soil was water saturated and the plants stored in a cold room at 5°C until used in the greenhouse experiments.

Insect collections and rearing. Adult insects were collected from white pine leaders in two plantations (Saint-Luc de Champlain (46°30'N, 72°30'W) and Sainte-Beatrix (46°13'N, 73°38'W)). during the first week of May prior to oviposition. Adults were sexed according to techniques described by Lavallée *et al.* (1993) and kept at 2°C on fresh material until future use.

Tree treatments and water monitoring. In one experiment, white pine plants were subjected to insect feeding and oviposition and, thereafter, to three watering regimes. Plants were placed in the greenhouse by the end of May and watered every day during 2 weeks. An automatic drip watering system provided approximately 200 ml twice a day to each seedling to maintain soil moisture until the beginning of treatments. The plants were arranged in 25 blocks (37 blocks in 1991), with one tree per treatment per block. Treatments were randomized in each block. On each tree, two male and two female weevils were introduced into a screened plastic bag placed over the leaders of the previous year to allow feeding, mating and oviposition. In 1989, insects were allowed to feed, copulate and lay eggs from June 1 through June 14, and in 1990 insects were left in caged plants from May 31 through June 18. In 1991 insects were left on plants from June 11 through June 28. To induce treatment effects on young larvae, five days before removal of the adult insects, the plants were watered according to their respective treatment.

In a second experiment, white pine plants were subjected the same three watering regimes. Half of each watering treatment was subjected to insect attack, and half were left as controls. In 1989 and 1990, plants were placed in the greenhouse on May 29 and watered until June 10 (1989) and June 15 (1990). Each year, 96 trees were arranged in 4 randomized blocks, with or without insect attack, 3 watering regimes, and 4 sampling dates. On 4 randomly selected plants per block and per watering regime, two male and two female weevils were introduced into a screened plastic bag arranged over the leaders of the previous year to allow feeding, mating and oviposition. In 1989 and 1990, insects were allowed to feed, copulate and lay eggs during the periods mentioned previously. About five days before removal of the insects, the plants were watered according to their respective treatment.

In 1989, 33 gypsum blocks (Hoskin Scientific., Montréal) were distributed evenly between treatments and were used to estimate the general water status of soil under each water regime. Each block was read with a portable soil moisture meter (Model 5910-A, Soil Moisture Equip., CA, USA). The mean soil moisture value for each treatment was used to determine the amount of water to be added to all the plants for a given treatment. In 1990 and 1991, all potted plants received a gypsum block and these were monitored daily with a soil moisture apparatus built by the Arts and Science Faculty Technical Center at Concordia University. Direct meter readings were transformed into soil water tension values according to the following equation provided by the manufacturer: Soil Tension (-MPa) = [(54.8566*(1/Meter Reading)) + ((-0.25594)*(0.1))]. In the dry treatment, we tried to maintain soils around -0.15 MPa; in the medium treatment around -0.08 MPa; and in the wet treatment less than -0.03 MPa. Plants in the dry and medium treatments received 100 or 200 mL of water as necessary to raise their soil water status. Plants in the wet treatment received 300 mL or more of water daily.

Water potential and bark collection from greenhouse plants. In the second experiment, every two weeks, 24 white pine trees were removed from the greenhouse for bark collection and measurements of plant moisture stress (PMS). Total shoot water potential was measured with a pressure chamber in the manner described by Scholander *et al.* (1965) and Cleary and Zaerr (1980). The first measurements were done on June 15, 1989 and June 20, 1990 (Julian dates 166 and 171 respectively). To measure larger differences in water potential between irrigation treatments, the xylem water potential was taken at noon (Ruiz-Sanchez *et al.*. 1988). At each sampling date, plants were brought into the laboratory and three twigs per tree were cut with a razor blade and potential was determined using a pressure chamber (Model 1000, PMS Instrument Co., Corvallis, OR, USA). Near the cut surface, a 1.5 cm length of bark was removed from the branch, and the shoot placed into the pressure chamber. The length of stem protruding from the top of the chamber was maintained at less than 0.5 cm. As suggested by Joly (1985) the pressure was raised slowly. To eliminate observation difficulties caused by resin extrusion, the true endpoint was recognized when water appeared on a filter paper placed on the cut end and observed with a binocular microscope at 30x magnification. To reduce water loss from the sample, the inside of the chamber was moistened with a piece of wet filter paper. In 1991, in the first experiment, plant water potential was also measured regularly on ten reference plants per treatment. Xylem water pressure of each tree was estimated with 3 needle fascicles (Johnson and Nielsen 1969).

In 1989 and 1990, bark water content (BWC) was recorded on a dry weight basis [BWC = 100*((Fresh wt - Dry wt)/Dry wt)] after a drying period of 48h at 70°C. The bark was then ground in a Wiley Mill at 20 mesh and kept at -20°C for chemical analyses. Each year, one and two-year-old sections of the main stem were treated and evaluated separately. Chemical analyses (nitrogen, phosphorus and potassium) were performed on bark from the 1989 greenhouse experiments. Bark from the 1990 experiment was gathered according to their respective treatment and consequently analysed.

Insect observations. For the first experiment, leaders were removed before adult emergence and individually caged in plastic tubes (5x80 cm) closed at one end with a nylon mesh tissue and at the other end with a plastic bottle (Pharma #16, MHAC Inc, Pointe-Claire, Québec), kept in the laboratory at 20°C and observed daily. Insect performance was measured as the mean number of adults that emerged per leader, and adult mean weight. Sex was determined using the techniques described by Lavallée *et al.* (1993). In 1989, 1990 and 1991 leaders were caged on July 26, July 20 and July 29, respectively, and observed until the end of emergence in September. At this time, leaders that did not produce adults were dissected to determine the presence of larval feeding scars under the bark. Only leaders with larval damage were used in data analysis.

In the second experiment, harvested leaders were dissected under a binocular microscope and the number of insects was determined according to their developmental stage. Instars were evaluated according to Harman (1970). A developmental index which represented the mean instar was calculated for the insect population found under the bark of each leader.

Statistical analysis. The effects of treatments on soil water tensions, plant water potential, adult number and mean weight were compared using the GLM or MIXED procedures (SAS Institute 1990), after using the appropriate transformation to achieve variance homogeneity and normality of the residuals. If significant differences were found between treatments, the Waller-Duncan (WALLER/SAS Institute 1990) test or probability values (PDIFF/SAS Institute 1990) were calculated to determine where those differences occurred. Bark water and chemical content were analysed with the PROC MIXED procedure from SAS software and orthogonal contrasts were used to determine the shape of the regression curves and estimate their coefficients.

D. Results

Greenhouse environment. The mean daily temperatures in the greenhouse and total daily sunshine hours prevailing during the three years of the study are presented in Figure 2.1. During the egg-laying periods, the mean daily temperatures were 18.9, 21.0 and 23.4°C and during the post-oviposition periods, they were 21.7, 19.6 and 22.9°C in

1989, 1990 and 1991, respectively. If we compare the temperatures during the three year's tests, they were all significantly different during the oviposition ($P < 0.01$) and the post-oviposition period ($P < 0.01$) (Figure 2.2).

Humidities in the greenhouse during the egg-laying periods were 76.2, 79.0 and 75.0% in 1989, 1990 and 1991, respectively. During the post-oviposition periods, humidity was 75.8 (1989), 79.6 (1990) and 78.0% (1991). For both periods, humidity was not significantly different between years ($P_{\text{Ovipo.}} = 0.51$; $P_{\text{Post-ovipo}} = 0.11$) (Figure 2.3).

During oviposition, the mean daily hours of sunshine were 6.9, 5.7 and 9.3 and during the post-oviposition periods, 9.8, 7.6 and 9.2 for 1989, 1990 and 1991, respectively for 1989, 1990 and 1991. The mean daily hours of insolation during the oviposition and post-oviposition periods was not significantly different during the three years ($P_{\text{Ovipo.}} = 0.056$; $P_{\text{Post-ovipo.}} = 0.12$) (Figure 2.4).

Soil water potential. During the 1989 and 1990 egg-laying periods, no significant differences were observed between soil water tensions for the different treatments ($P_{1989} = 0.36$; $P_{1990} = 0.67$) (Table 2.1). However, in 1991, soil tension was lower in the dry treatment than in the two other treatments ($P_{1991} < 0.01$). For each year, during the larval development periods, all soil tensions were significantly different ($P_{1989} < 0.01$; $P_{1990} < 0.01$; $P_{1991} < 0.01$).

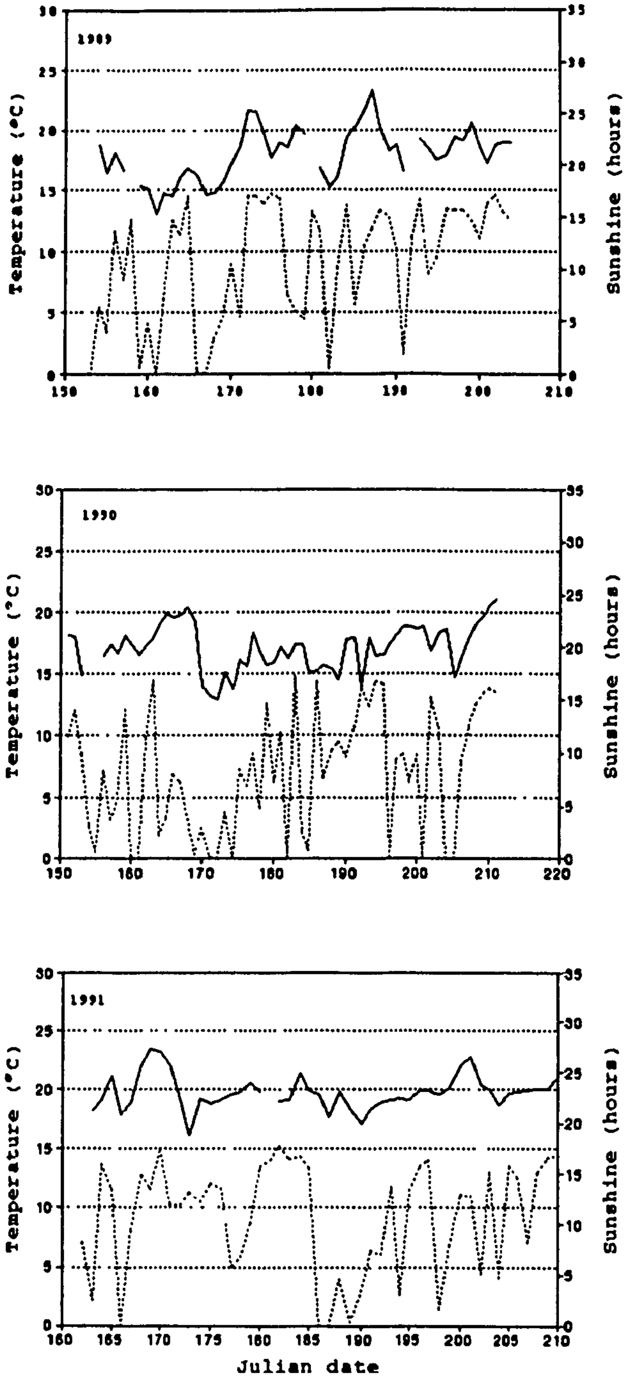

Figure 2.1. Mean daily temperatures (°C) in the greenhouse (-------) and total daily sunshine hours (..........) in 1989, 1990 and 1991.

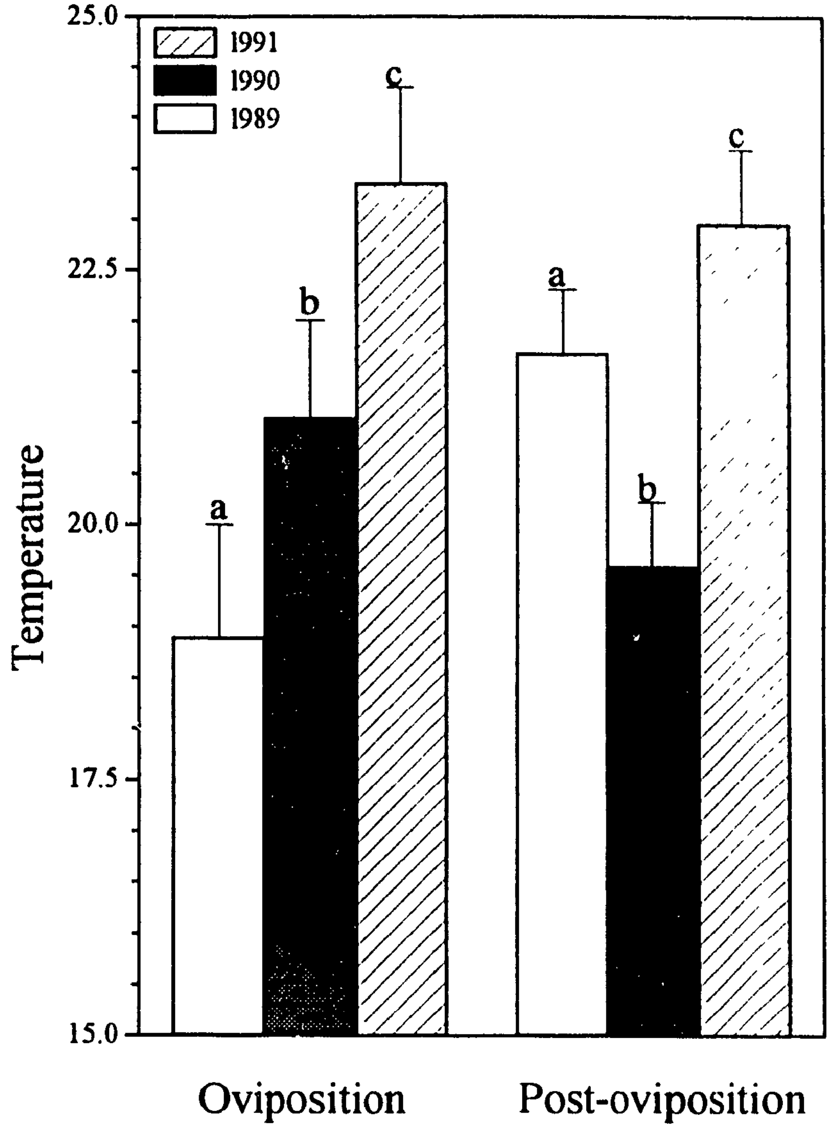

Figure 2.2. Mean (+95% C.I.) daily temperatures (°C) in the greenhouse during the oviposition and post-oviposition periods of the three years of tests. Adjacent columns followed by different letters are significantly different ($P<0.05$).

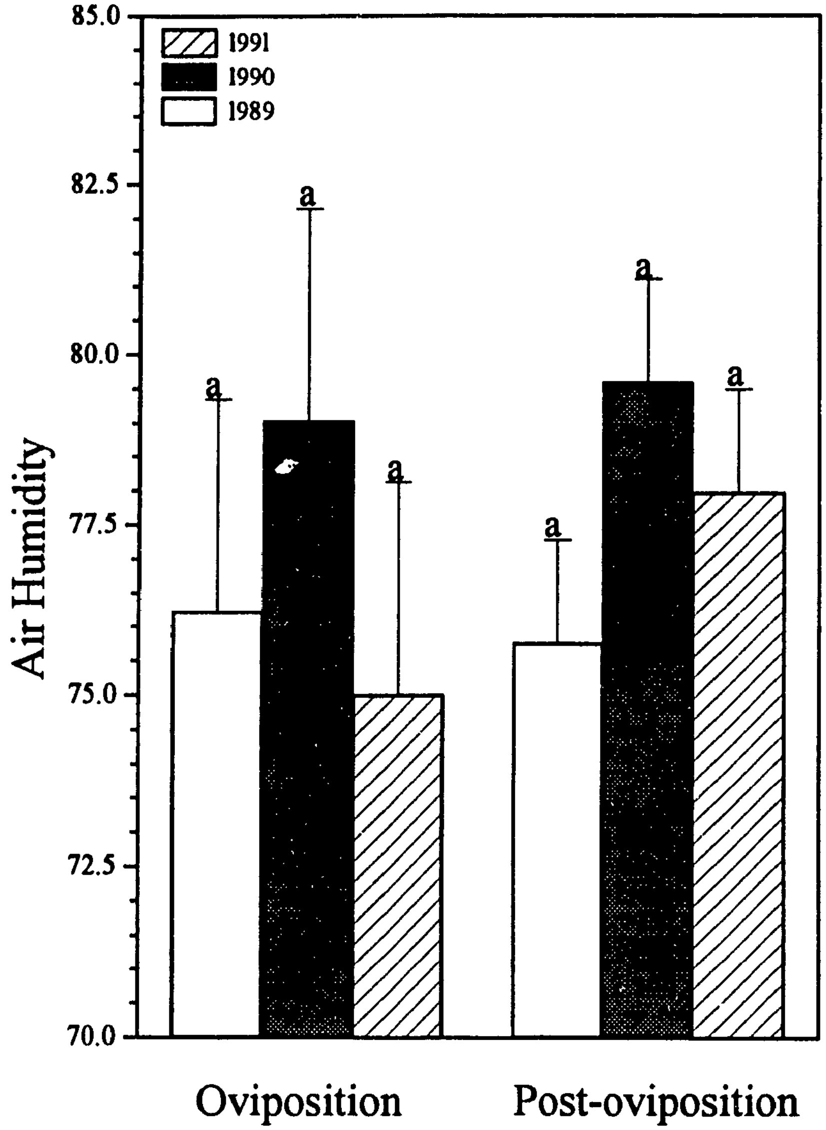

Figure 2.3. Mean (+95% C.I.) daily relative humidity (%) of air in the greenhouse during the oviposition and post-oviposition periods of the three years of tests. Adjacent columns followed by different letters are significantly different ($P < 0.05$).

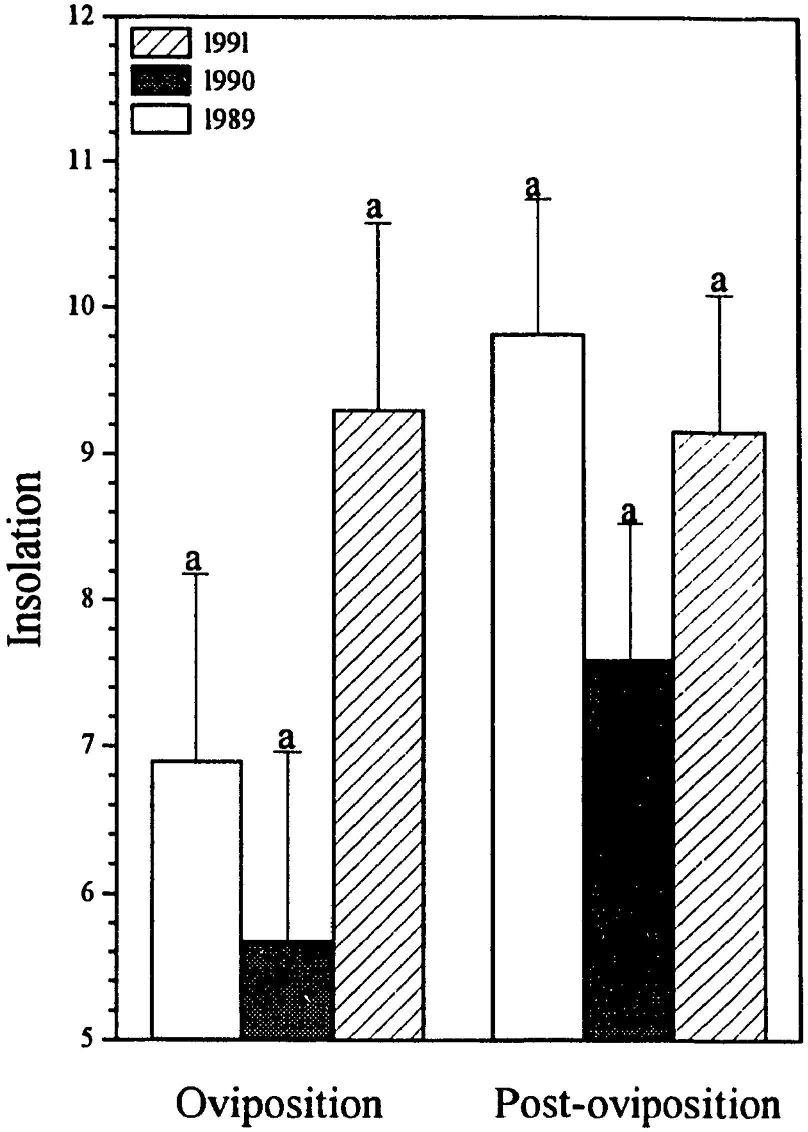

Figure 2.4. Mean (+95% C.I.) daily total insolation (hours) in the greenhouse during the oviposition and post-oviposition periods of the three years of tests. Adjacent columns followed by different letters are significantly different ($P<0.05$).

Table 2.1. Soil water potential (-MPa) during the egg laying and larval development of the white pine weevil in 1989, 1990 and 1991.

YEAR	PERIOD	TREATMENTS		
		DRY	MEDIUM	WET
1989	Oviposition	0.041a*	0.035a	0.037a
1989	Post-oviposition	0.172a	0.117b	0.036c
1990	Oviposition	0.035a	0.036a	0.035a
1990	Post-oviposition	0.094a	0.058b	0.035c
1991	Oviposition	0.043a	0.035b	0.035b
1991	Post-oviposition	0.114a	0.077b	0.035c

*Means within the same row followed by the same letter do not differ significantly according to Waller-Duncan test at $P < 0.05$

Plant water potential. In 1989, for each sampling date, values between treatments were significantly different for all the sampling days except on day 166 when medium and wet treatments did not differ (Table 2.2). In 1990, for each sampling date, the treatments were significantly different, but dry and medium treatments differed only at the last sampling period. However, dry and wet treatments were always significantly different. In 1991, xylem water potentials were significantly different between treatments for all the sampling dates. However, on Julian date 193, medium and wet treatments were not different statistically. During the 1989 and 1990 tests, we observed that plant water potential was not affected by the presence of current insect damage ($P_{1989}= 0.86$; $P_{1990}= 0.41$). For both years, the interaction of treatment with insect presence was not significant ($P_{1989}= 0.73$; $P_{1990}= 0.48$).

Comparisons of year to year variations indicate that xylem water potentials of plants exposed to a similar treatment were not the same (Figure 2.5). In the dry treatment, no difference was found between the 1989 and 1990 values but in 1991 the dry treatment was more severe ($P < 0.01$). In the medium treatment more severe stress was obtained in 1990 ($P < 0.01$). In the wet treatment, the 1991 value was significantly higher than in the two other years which were not different one from the other ($P < 0.01$).

These values for xylem water potential may be close to the real values of leaf water potential. Kaufmann (1968) showed that xylem pressure potentials in white pines were as much as 0.5 MPa lower than leaf water potentials when these were between -1.0 and -2.0 MPa, while at higher water potentials the values were similar.

Table 2.2. Mid-day water potential (-MPa) of white pine during the sampling periods in 1989, 1990 and 1991.

YEAR	DATE	TREATMENTS			*P>F*
		DRY	MEDIUM	WET	
1989	166	1.31a*	1.05b	0.99 b	0.0032
	178	2.11a	1.37b	0.85c	0.0001
	192	2.92a	1.92b	0.72c	0.0001
	206	2.95a	2.25b	0.78c	0.0001
1990	171	1.26a	1.30a	0.94b	0.0332
	185	2.22a	2.15a	0.87b	0.0001
	199	2.59a	2.59a	0.67b	0.0001
	211	2.60a	2.19b	0.90c	0.0020
1991	186	2.27a	1.67b	1.20c	0.0001
	193	2.52a	1.76b	1.50b	0.0232
	203	2.58a	1.85b	1.24c	0.0003
	207	2.76a	1.95b	1.31c	0.0003
	221	3.00a	2.01b	1.31c	0.0001

*Means within the same row followed by the same letter do not differ significantly according to Waller-Duncan test at $P < 0.05$

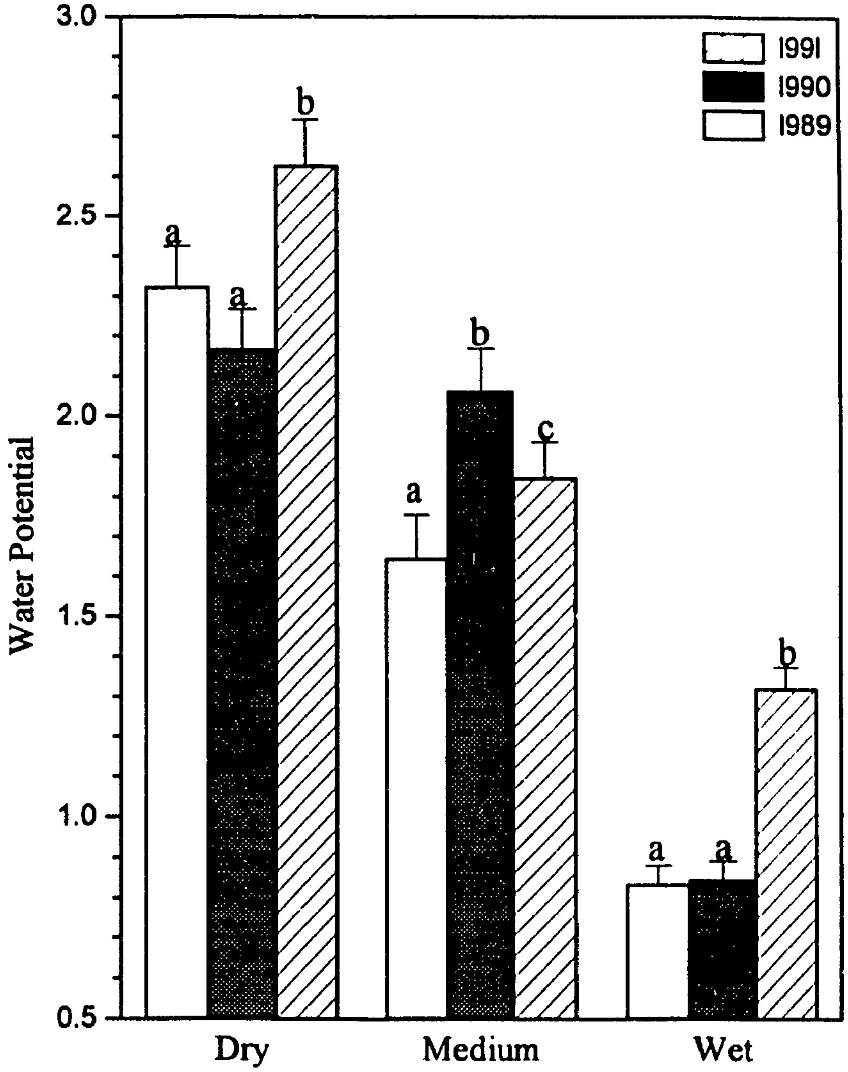

Figure 2.5. Mean (+95% C.I.) mid-day xylem water potential (-MPa) of white pine grown under different regimes and during the three years of observation. Adjacent columns followed by different letters are significantly different ($P < 0.05$).

Bark water content. In 1989, values between treatments were significantly different for each sampling date (Table 2.3, Figure 2.6). Bark from the wet treatment had the highest water content and was relatively steady except in two-years-old leader where insects were present. The water contents of bark from plants under medium and dry treatments were similar and both decreased during the season. In the medium and dry treatments, more water was present in the one-year-old growth with insects damage than in the equivalent section without insect damage. The water contents of the dry and medium treatments were not significantly different ($P = 0.36$), but in the wet treatment was always higher than in the two other ($P < 0.01$) (Table 2.4). More water was associated with the two-year-old leader section ($P = 0.02$). The effect of insect damage on bark water content was not significant in 1990 ($P = 0.69$).

Year to year comparisons of the bark water contents for similar treatments indicate that the bark water content was higher in the 1990 test when compared to the 1989 test ($P < 0.01$) (Figure 2.7).

Chemical content. The nitrogen content was higher in bark from water stressed plants, but the differences were not significant ($P = 0.07$) (Table 2.5, 2.8). There was significant interaction between the effect related to insect presence and leader section ($P < 0.01$) and more nitrogen was associated with the one-year-old sections ($P < 0.01$) (Table 2.9). However, the difference was more important in infested plants.

The phosphorus content was higher in bark from water stressed plants ($P = 0.02$) (Table 2.6) than in bark from the wet watering regime (Table 2.8).

Table 2.3. Variance analysis of the mean water content (% dry weight) of bark from white pine grown in the greenhouse during the sampling periods in 1989.

Source of variation	df	*F* value	*P* value
Watering (W)	2	45.86	0.0001
Insect (I)	1	2.01	0.1613
W * I	2	0.08	0.9273
Harvest period (H)	3	5.85	0.0013
W * H	6	4.93	0.0003
I * H	3	0.74	0.5294
W * I * H	6	1.61	0.1573
Leader section (L)	1	10.87	0.0019
W * L	2	2.61	0.0849
I * L	1	22.06	0.0001
W * I * L	2	0.29	0.7493
H * L	3	1.91	0.1409
W * H * L	6	1.23	0.3075
I * H * L	3	3.96	0.0138
W * I * H * L	5	0.81	0.5864

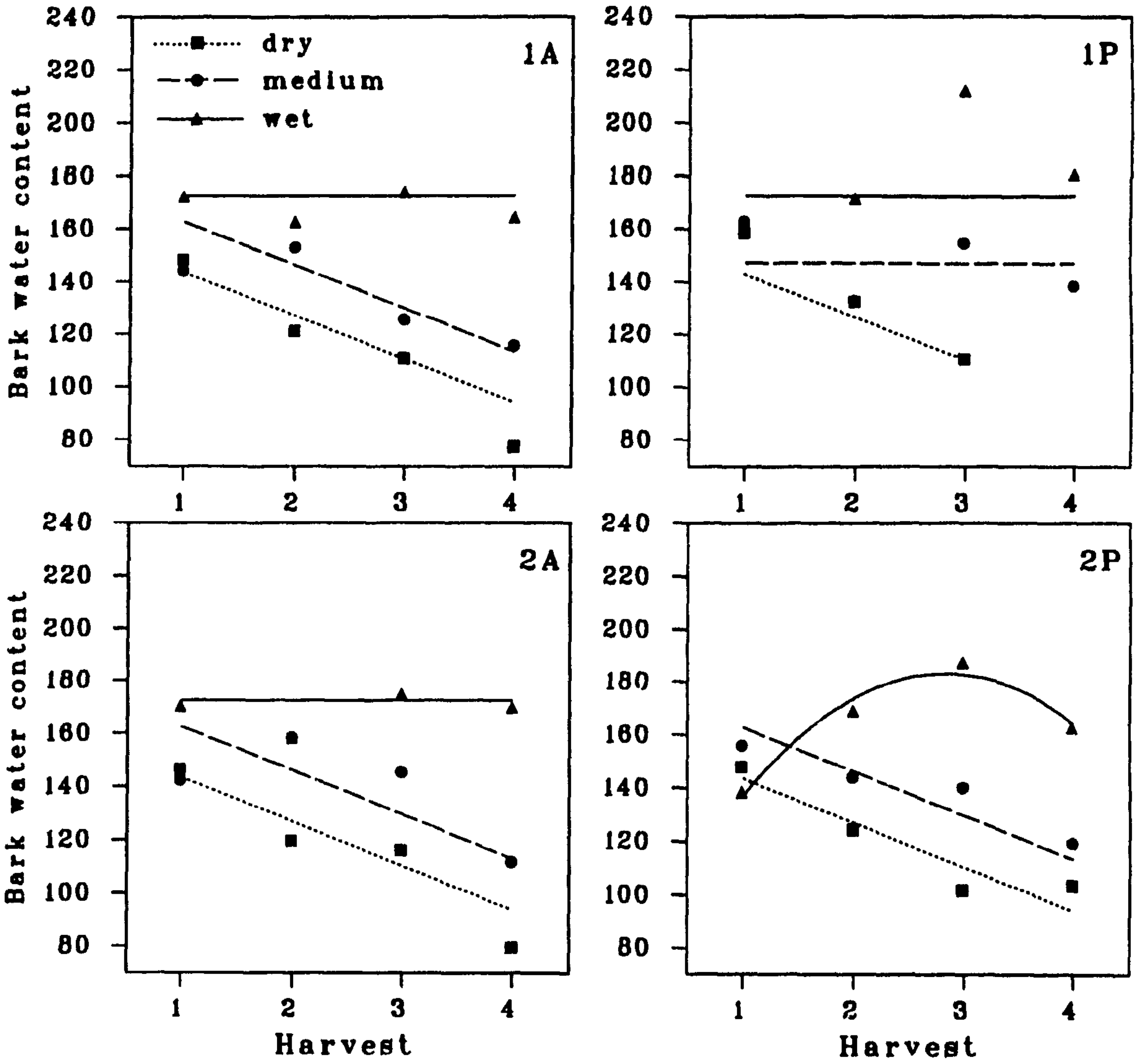

Figure 2.6 Bark water content (%) from plants of the 1989 greenhouse test according to the leader section, presence or absence of insect attack and the watering regime during the four harvest periods; 1:one-year-old leader section, 2:two-year-old leader section, A: insect absent, P:insect present.

Table 2.4. Variance analysis of the mean water content (% dry weight) of bark from white pine grown in the greenhouse during the sampling periods in 1990.

Source of variation	df	*F* value	*P* value
Watering (W)	2	17.75	0.0001
Insect (I)	1	0.00	0.9797
W * I	2	0.37	0.6943
Harvest period (H)	3	15.61	0.0001
W * H	6	1.29	0.2782
I * H	3	0.76	0.5225
W * I * H	6	1.72	0.1472
Leader section (L)	1	5.94	0.0199
W * L	2	0.18	0.8327
I * L	1	0.38	0.5378
W * I * L	2	0.04	0.9659
H * L	3	0.65	0.5880
W * H * L	6	1.36	0.2592
I * H * L	3	0.37	0.7722

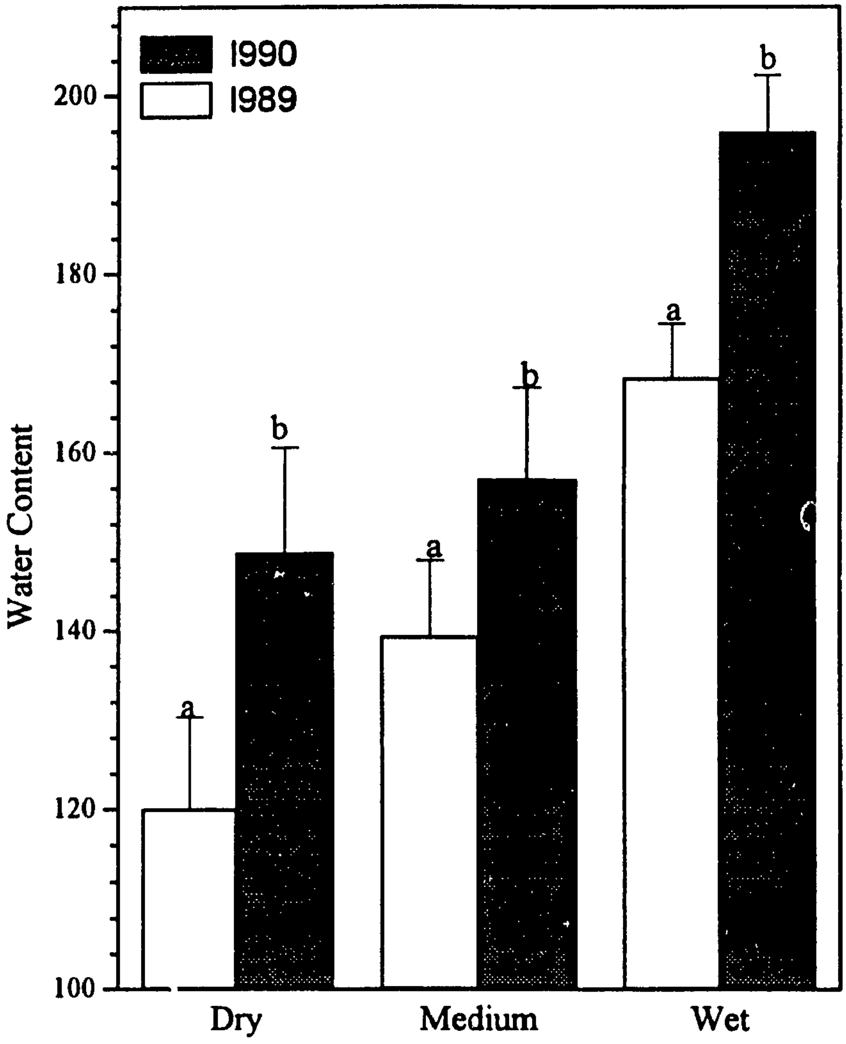

Figure 2.7. Mean (+95% C.I.) bark water content (% dry weight) of white pines grown under different regimes and during the first two years of observation. Adjacent columns followed by different letters are significantly different ($P<0.05$).

Table 2.5. Variance analysis of the mean nitrogen content (%) of bark from white pine grown in the greenhouse during the sampling periods in 1989.

Source of variation	df	*F* value	*P* value
Watering (W)	2	2.71	0.0740
Insect (I)	1	3.11	0.0825
W * I	2	0.04	0.9567
Harvest period (H)	3	4.33	0.0076
W * H	6	1.92	0.0915
I * H	3	1.05	0.3775
W * I * H	6	1.69	0.1370
Leader section (L)	1	71.58	0.0000
W * L	2	0.38	0.6850
I * L	1	9.66	0.0032
W * I * L	2	1.26	0.2942
H * L	3	1.40	0.2561
W * H * L	6	2.19	0.0609
I * H * L	3	1.14	0.3428
W * I * H * L	5	0.84	0.5255

Table 2.6. Variance analysis of the mean phosphorus content (mg/g) of bark from white pine grown in the greenhouse during the sampling periods in 1989.

Source of variation	df	*F* value	*P* value
Watering (W)	2	4.08	0.0214
Insect (I)	1	2.31	0.1332
W * I	2	0.56	0.5767
Harvest period (H)	3	4.21	0.0088
W * H	6	0.77	0.6001
I * H	3	1.28	0.2901
W * I * H	6	1.45	0.2084
Leader section (L)	1	114.71	0.0000
W * L	2	0.04	0.9628
I * L	1	5.93	0.0189
W * I * L	2	2.90	0.0649
H * L	3	0.41	0.7444
W * H * L	6	1.18	0.3349
I * H * L	3	1.09	0.3643
W * I * H * L	5	0.85	0.5221

Table 2.7. Variance analysis of the mean potassium content (mg/g) of bark from white pine grown in the greenhouse during the sampling periods in 1989.

Source of variation	df	*F* value	*P* value
Watering (W)	2	5.58	0.0058
Insect (I)	1	7.13	0.0096
W * I	2	2.93	0.0605
Harvest period (H)	3	8.37	0.0001
W * H	6	1.34	0.2516
I * H	3	3.00	0.0369
W * I * H	6	3.16	0.0087
Leader section (L)	1	44.2	0.0000
W * L	2	0.83	0.4414
I * L	1	1.58	0.2156
W * I * L	2	2.81	0.0704
H * L	3	0.81	0.4935
W * H * L	6	0.82	0.5636
I * H * L	3	2.51	0.0708
W * I * H * L	5	0.57	0.7195

Table 2.8. Mean nitrogen and phosphorus content according to watering regimes.

	Watering	Mean (SEM)	$P > F$
Nitrogen (%)	Dry	0.94 (0.03)	0.07
	Medium	0.90 (0.03)	
	Wet	0.86 (0.03)	
Phosphorus (mg/g)	Dry	1.40 (0.05) a	0.02
	Medium	1.32 (0.04) ab	
	Wet	1.19 (0.04) b	

Table 2.9. Mean nitrogen and phosphorus content according to leader section and insect presence on plants, all other factors confounded.

		Insect		$P > F$
	Leader section	Absent	Present	
Nitrogen	1	0.90	1.03	0.01
	2	0.81	0.83	0.58
	$P > F$	0.0001	0.0001	
Phosphorus	1	1.35	1.50	0.02
	2	1.14	1.17	0.67
	$P > F$	0.0001	0.0001	

Also, there was a significant interaction between the effect related to insect presence and leader section ($P < 0.02$). More phosphorus was associated with the one-year-old sections ($P < 0.01$) (Table 2.9). However, the difference was greater in infested plants.

With potassium, there was a significant interaction between watering regime, insect presence and harvest period ($P < 0.01$) (Table 2.7). Potassium content was affected by watering regime and by insect damage (Figure 2.8). With bark from the 1990 test, the nitrogen and phosphorus contents were significantly higher in the dry treatment than in the wet treatment for plants without insect attack ($P_N < 0.01$, $P_P < 0.01$). However, it was the opposite on infested plants ($P_N < 0.01$, $P_P < 0.01$). The potassium content was significantly higher in bark from the dry watering regime for intact and infested plants ($P_{\text{Intact}} < 0.01$, $P_{\text{Infested}} < 0.01$). Also, on two-year-old leader sections, nitrogen and phosphorus content were significantly higher on infested plants ($P_N = 0.01$, $P_P = 0.01$, $P_K = 0.13$). On one-year-old leader sections, nitrogen was significantly higher on infested plants ($P_N = 0.02$, $P_P = 0.46$, $P_K = 0.29$).

Insect development. In 1989 and 1991, no-significant differences were found between treatments for the number of insects per leader ($P_{1989} = 0.12$; $P_{1990} = 0.03$; $P_{1991} = 0.30$) although in 1990 more insects per leader were associated with the wet and medium treatments than the dry treatment (Figure 2.9). No significant variations were observed between years for the mean number of insects per leader ($P = 0.74$) for each treatment. However, there was a significant year * treatment interaction ($P = 0.04$).

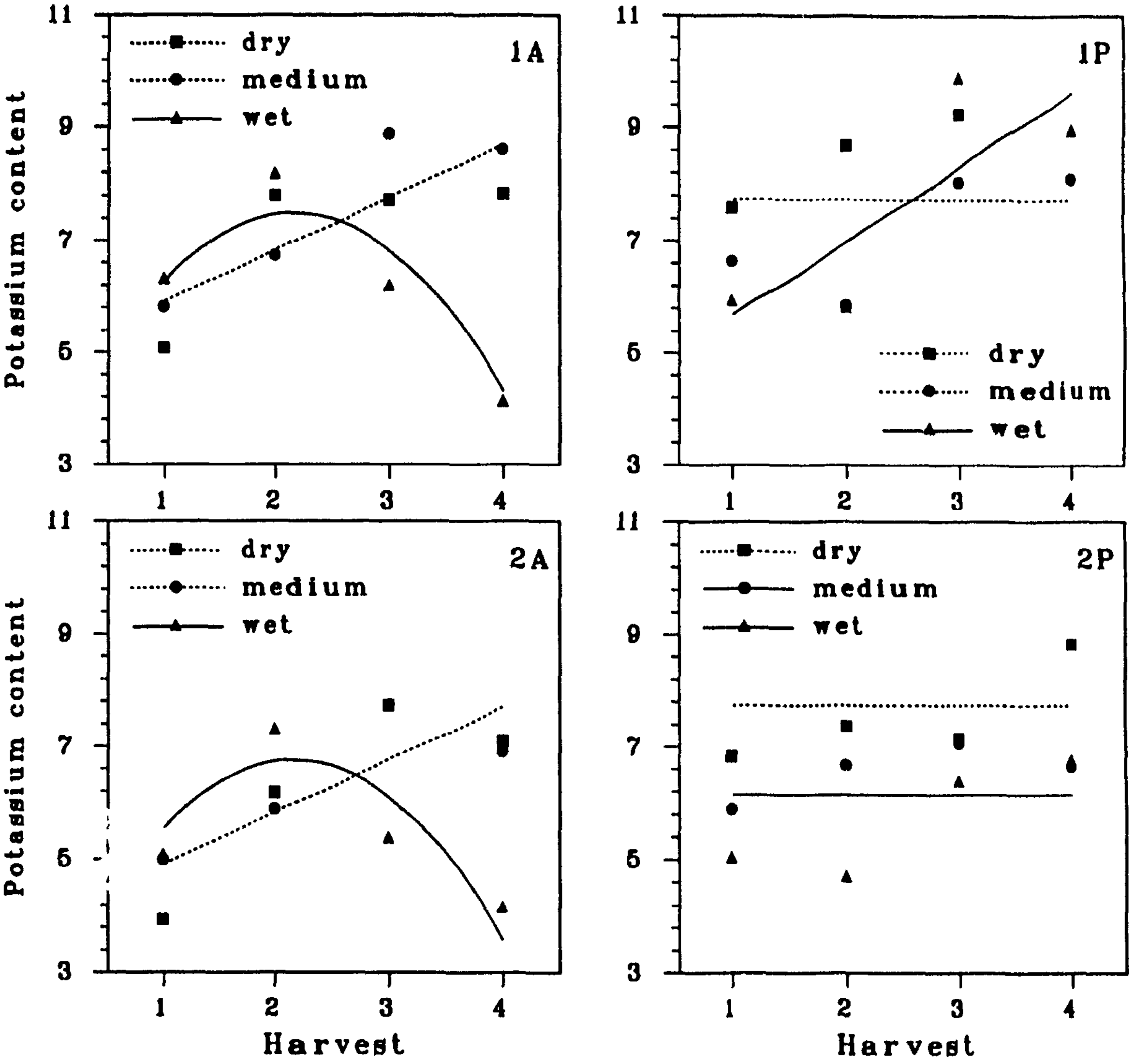

Figure 2.8. Potassium content (mg/g) from plants of the 1989 greenhouse test according to leader section, presence or absence of insect attack and watering regime during the four harvest periods; 1: one-year-old leader section, 2: two-year-old leader section, A: insect absent, P: insect present.

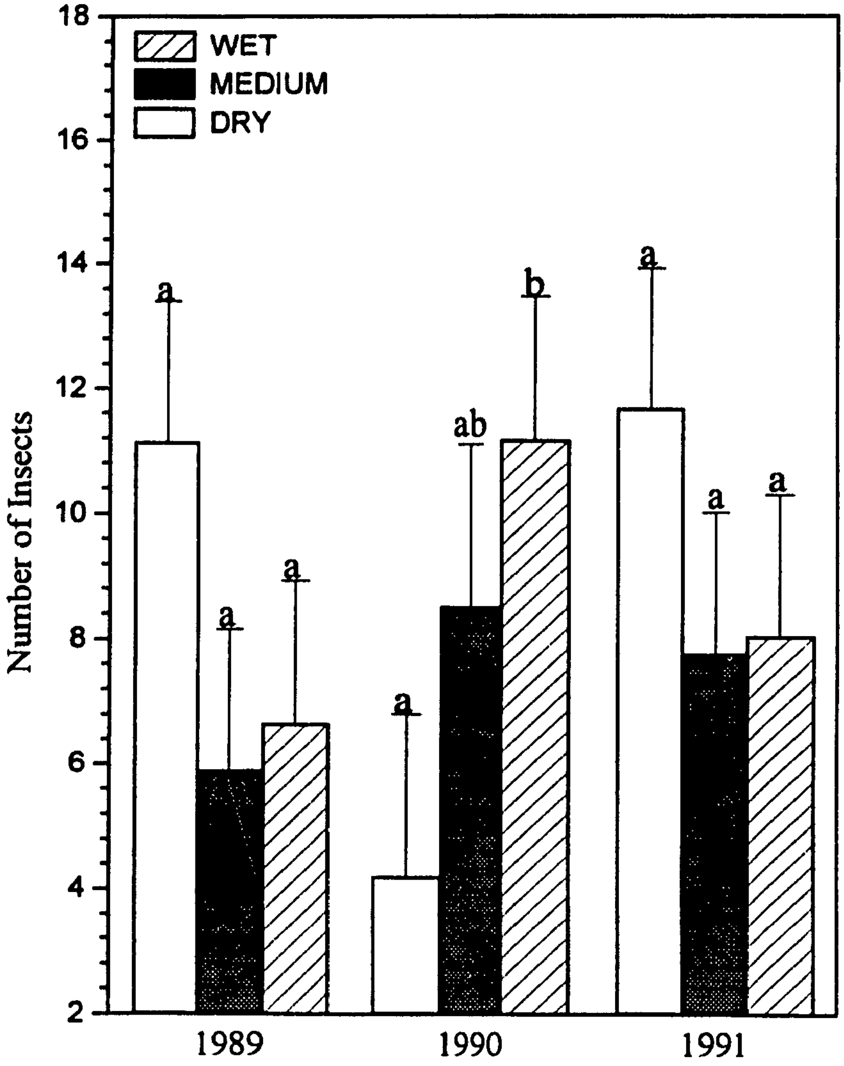

Figure 2.9. Mean (+95% C.I.) numbers of adult white pine weevils emerging per leader according to the different watering regimes during the three years of observation. Adjacent columns followed by different letters are significantly different ($P<0.05$).

During the three years of this experiment, adult mean weights were not affected by treatments ($P_{1989} = 0.41$, $P_{1990} = 0.92$, $P_{1991} = 0.71$) (Figure 2.10). Female weight was higher than male weight in 1990 and 1991 ($P_{1989} = 0.12$, $P_{1990} = 0.04$, $P_{1991} < 0.01$). During the three years, the block * treatment interaction was significant ($P < 0.01$). Adult mean weight was higher in 1991 compared with the two other years ($P = 0.01$), but there was no significant year * treatment effect ($P = 0.61$).

The adult mean weight per leader is partly related to the number of insects per leader and can be expressed by the equation : Adult Weight = 0.0082 + [Number of Emerging Insects per Leader * (0.0003)] ($r = 0.32$, $P < 0.01$).

Finally, larval development showed no effect of treatment in 1989 ($P = 0.60$), or 1990 ($P = 0.55$).

E. Discussion

During three years, the development of the white pine weevil was relatively unaffected when the watering regime of its host tree ranged from hydrically stressed to well watered. The only difference observed was a higher number of insects per leader in the wet treatment in 1990. No differences were observed in the speed of larval development. Treatments did not affect the female to male ratio, which was similar to that reported by Dixon and Houseweart (1982).

Although the plants in the dry and medium treatments (and to a lesser extent the wet treatment) were subjected to water stress, the adult weights we obtained were similar

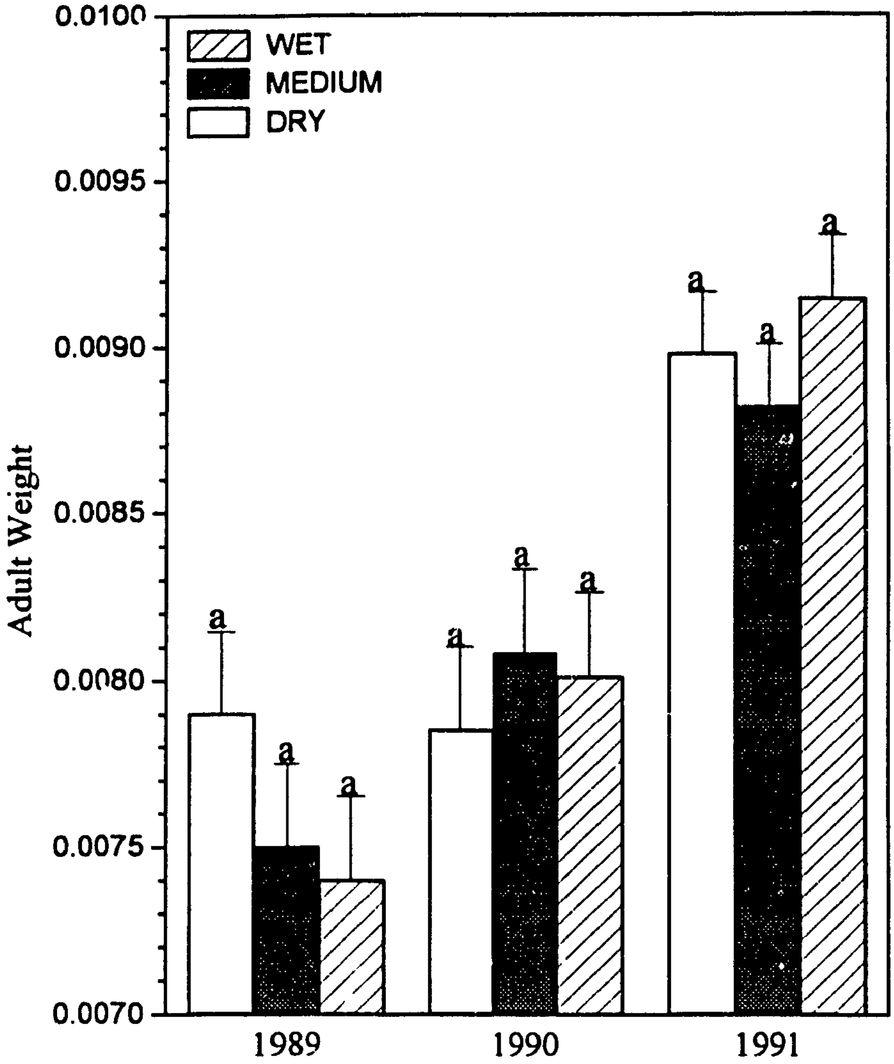

Figure 2.10. White pine weevil adult mean (+95% C.I.) weight (g) according to the different watering regimes during three years of observation. Adjacent columns followed by different letters are significantly different ($P<0.05$).

to those of insects emerging from older host trees (Alfaro 1988, Lavallée *et al.* 1993). Consequently, under this range of water stress conditions, insect weight was unaffected.

White pine trees are adapted to dry sites (Sims *et al.* 1990, Lopushinsky 1969), thus the levels of water stress used in our experiment may not have been enough to influence weevil larval development. Wagner (1986) mentioned that water stress greater than -2.0 MPa in *Pinus ponderosa* Dougl. Ex. Laws might be necessary before affecting the pine sawfly, *Neodiprion autumnalis* Smith. In a previous test, Lavallée *et al.* (1993) demonstrated better weevil development on well watered leaders than on severely water stressed ones (-4.0 MPa), which was much lower water potentials than in this experiment.

Though adult weight was unaffected the numbers of insects emerging per leader were about 50 % less than those reported for older white pine under natural conditions (Dixon and Houseweart 1982; Phillips and Lanier 1983). This difference may be associated with the terminal leader length, which was relatively short (around 25 cm) compared to those of more mature trees. McMullen *et al.* (1987) proposed a positive relationship between Sitka spruce leader length and the number of emerging adults.

However, the different watering regimes used in these tests affected the physiology of white pine as revealed by the xylem water potential and the content of water, phosphorus and potassium in bark. Though the effect of water stress on precise physiological processes was not evaluated, a major impact on the plant is suspected. High water potential levels ensure vigorous trees and at levels above -1.0 MPa water potential does not limit photosynthesis (Cleary and Zaerr 1980). For ponderosa pine seedlings, photosynthesis was slowed or stopped at water potentials between -1.0 and -2.0 MPa, at values between -2.0 and -5.0 MPa seedling vigour declined and at levels below -5.0 MPa seedlings die (Cleary and Zaerr 1980).

Phosphorus and potassium content were significantly affected by the watering regime. A rise in their concentration was associated with plant stress. However, on *Picea abies* (L.) Karst., the nitrogen and potassium content of xylem sap were reduced by 33% and 50%, respectively, with an increase of the leaf water potential from -0.2 MPa to -1.2 MPa (Osonubi *et al.* 1988). Wagner (1986) also observed a slight decrease in nitrogen in the foliage of water stressed ponderosa pines. Under stress, resource allocation can be different according to the plant part considered. The phloem transports hydrolysed protein (Mattson and Haack 1987a), therefore nitrogen may decrease in older tissues but not in phloem.

Our results showed an increase in the water content of the bark of infested plants. Webb and Franklin (1978) also reported an increase of water content in bark of trees attacked by *Dendroctonus frontalis* Zimmerman. The increase in water content may be advantageous for the larvae. Food conversion efficiency is indirectly affected by water content (Reese and Schmidt 1986). Moreover, the increase in nitrogen, phosphorus and potassium in infested plants indicates an effect of the insects presence on the plant's physiology, which may also be advantageous to insect development. A similar type of induction was reported by Lewis (1979). Herbivores are frequently responsive to subtle biochemical changes in host quality (Mattson and Addy 1975), and these modifications of bark quality may be advantageous for weevil development.

The higher concentration of the major elements in the leader compared to the two-year-old section may explain the weevil's preference for the terminal part of the tree at spring time. Madgwick and Mead (1990) also observed that nitrogen, phosphorus and potassium in branches (bark and wood) of *Pinus radiata* decreases with branch age. Larvae may, therefore, obtain a nutritional advantage for completiting development on the leader rather than using the two-year-old section. Consequently, trees with short leaders may be unfavourable for insect growth.

Other factors more important than the watering regime may have played major roles in weevil development as revealed by the significant block * treatments interaction during the tests. These factors can be related to the quality of seedlings and/or of the ovipositing females.

An important year to year variability was observed in the adult weights. Different factors, not evaluated in this study, may explain this variability. The period when water stress was imposed on the young larvae was difficult to control. For a number of insects, the quality of the nutrition is more important during the first instars than the late instars (Scriber and Slansky 1981, Montgomery 1982, Lavallée and Hardy 1988). According to White (1978), it is a shortage of nitrogenous compounds for juvenile larvae that limits insect abundance. During our three years of tests, water stress may not have affected the young larvae at the same time. Lavallée *et al.* (1993) observed that when weevil larvae had accomplished part of their development, they were less sensitive to subsequent imposed stress. Another factor which may explain the variability between years is that the plants we used cannot be considered physiologically similar from year to year, having experienced different weather and soil conditions before their use in the greenhouse. Finally, the real impact of the higher air temperature in 1991 on weevil oviposition and larval development was not evaluated.

Our results and other data available on the white pine weevil, suggest that the population dynamics of this insect may be more related to the plant vigour hypothesis, as has been shown for a number of other insect species (Price 1991) than with the stress hypothesis (White 1969, 1984, Mattson and Haack 1987a, Larsson 1989). Lavallée *et al.* (1993) did not find significant differences in the weights of adult weevils emerging from intact field leaders or previously cut leaders kept in water. In this context, the weevil may look for vigorous trees which are suitable in terms of physical setting, and the relation with the host may be based primarily on food availability and to a lesser extent on bark nutritional quality. Better insect performance on non-stressed trees has been demonstrated for a number of insect species (Wagner 1986, Price 1989, Ellsworth *et al.* 1989, Wagner and Frantz 1990). Consequently, females of the white pine weevil may select for vigourously growing trees with large terminal leaders to assure an abundant food supply to their brood, as is observed foı gall-forming insects (Price and Clancy 1986, Craig *et al.* 1989, Price 1989). As will be shown in Chapter 3, females prefer to feed on bark from vigorous trees rather than on bark from stressed trees. Also, induced chemical modifications of the bark, resulting from insect attack and larval development, may stimulate more feeding and oviposition on these plants. Alfaro and Ying (1990) indicate that weevils prefer to attack trees that have been previously attacked. In a natural stand, Wilkinson (1975) observed higher levels of weevil attack on white pine trees treated with an antitranspirant and having more water in their bark. O'Dell (1972) also reported more eggs on branch sections having higher water content. Also, trees fertilized with potassium seem more palatable to adult white pine weevil (Xydias and Leaf 1964).

Finally, the similar performance of insects under the different watering regimes indicates that the role of plant defenses other than resin exudation and resin canal system may be minimal against the weevil. Rhoades (1985) hypothesized that herbivore with low and relatively invariant, population levels may display adaptations to minimize damage and defensive responses of their host. In this context, Mattson and Haack (1987a) considered the capacity of an attacked tree to produce a new leader to be a high tolerance reaction to the white pine weevil. At spring time, during oviposition and larval development, resource allocation of the tree is toward the production of new foliage and not for producing defense substances and in meristematic cells, the limited expression of secondary metabolism is apparently a fundamental constraint (Herms and Mattson 1992).

Therefore, we suggest that white pine phloem should constitute a steady state environment for weevil development, even when the host is growing under stressful conditions. However, the chemical quality of the phloem can be affected by adult feeding and larval development.

CHAPTER 3

Influence of White Pine Watering Regimes on Feeding Preferences of Spring and Fall Adults of the White Pine Weevil, *Pissodes strobi* (Peck)

A. Abstract

Spring and fall adults of the white pine weevil, *Pissodes strobi* (Peck), were exposed in no-choice and two-choice tests to bark from water-stressed and non-water-stressed white pine (*Pinus strobus* L.) which also had been exposed or not exposed to previous weevil attack. This experiment demonstrated that the weevils could discriminate between bark from water-stressed white pine preferring bark from the non-stressed plants. The weevils also preferred bark from non-stressed plants which were previously exposed to weevil damage. Spring and fall adults displayed the same feeding preferences. No sex differences were found in feeding preferences. Less nitrogen, phosphorus and potassium were found in bark from the non-stressed, non-infested plants and these elements were generally higher in damaged plants. We expect that the fitness of the weevil will be better in vigorous growing plants rather than in stressed plants.

B. Introduction

In a natural environment, plants are subjected to a number of biotic and abiotic stresses which can influence their growth and development (Heinrichs 1988; Waring 1991). Plant stress resulting from drought or poor growing conditions can have positive effects on insect development (White 1969; Goyer and Benjamin 1972; Hodges and Lorio

1975; Munster-Swendsen 1984; Mattson and Haack 1987a,b). It has been proposed that plant stress resulting from water deficit or nutrient imbalances can lead to improvement of the nutritional quality of the plant, and/or to a decrease in individual plant resistance that results in enhanced insect performance (White 1974, 1984; Rhoades 1979, 1983; Cates *et al.* 1983; Larsson *et al.* 1983; Waring and Pitman 1985; Mulock and Christiansen 1986; Mattson and Haack 1987a,b). However, insect responses to plants growing under stressful environmental conditions are poorly documented (Louda and Collinge 1992). Moreover, as indicated by Mattson and Haack (1987a), the stress theory is largely based on circumstantial evidence. The review made by Waring and Cobb (1992), illustrates the diversity of insect responses to water stress. However, for some insect species it has been demonstrated that a non-stressed or vigorous plant constitutes a more adequate host (Miles *et al.* 1982; Myers 1985; Wagner 1986; Waring and Price 1988; Price 1989; Wagner and Frantz 1990).

The white pine weevil (*Pissodes strobi* [Peck]) is a native insect which attacks the terminal leader of several pine and spruce species, although white pine (*Pinus strobus* L.) and Norway spruce (*Picea abies* (L.) Karst) are preferred in eastern North America (Belyea and Sullivan 1956). Most of the studies and field observations on the white pine weevil show a positive relationship between vigorous pine growth and weevil attack. The insects of this species attack young plantations more frequently than old ones, and prefer plants with long terminal shoots and large leader diameters (MacAloney 1930; Prebble *et al.* 1951; Kriebel 1954; Holst 1955; Connola 1965; Wilkinson 1983a). Lavallée *et al.* (1993) demonstrated that weevil development, expressed as the weight of emerging summer adults, can be affected by bark quality, as adult weight is heavier on well-hydrated white pine leaders than on severely water-stressed ones. Some investigators have reported that damage can be more pronounced when white pines are growing in nutrient deficient or poorly drained soils (Maughan 1930; Connola and Wixson 1963b; Dirks 1964; Xydias and Leaf 1964; Connola and Birmingham 1978). On Sitka spruce (*Picea sitchensis* (Bong.) Carr.), a common host of the white pine weevil in western North America, Warkentin *et al.* (1992) have shown that more serious damage occurs in plantations located in geographic areas where trees are subjected to high midday air moisture stress. To understand these apparent contradictions in the white pine weevil host relationship, it is important to examine the sensitivity of the adult weevil to the growing conditions of its host, as assessed by its feeding preferences.

The objectives of this study were to determine 1) if the white pine weevils could discriminate between bark from white pine plants grown under different water regimes, 2) if weevils could discriminate between bark from previously infested and intact hosts and 3) if the age or sex of the adults influenced feeding preferences.

C. Materials and methods

Insect collection and rearing. Adult insects were collected on white pine terminal leaders during the first week of May in 1991 in two white pine plantations (Saint-Luc-de-Champlain (46°30' N, 72°30' W) and Sainte-Béatrix (46°13' N, 73°38' W). The insects were sexed according to techniques described by Lavallée *et al.* (1993) and kept at 5°C on an artificial diet (see below). These adults are referred to here as spring adults. In

July 1991, white pine leaders infested during the spring were harvested at the Saint-Luc plantation and stored in cages at room temperature (20°C). The insects that emerged from these leaders were then placed on an artificial diet and kept at 5°C. These insects are subsequently referred to as fall adults.

To facilitate insect rearing and to avoid the possible effects of chemical variations of natural diet on feeding preferences, weevils were kept on an artificial diet (Trudel *et al.* in press) to which was added 2% (w/v) oven dry white pine bark collected in the spring. The diet was dispensed into Petri dishes (100 x 15 mm) and the diet surface was covered with a piece of Whatman #1 filter paper while still hot. The diet was replaced bi-monthly to avoid contamination.

Plant treatments and monitoring of soil water moisture. Barks used in the present experiment came from a larger experimental design presented in Chapter 2, of which a brief description follows. Five- and six-year-old white pine were used in 1989 and 1990 respectively. Trees were planted in a sandy loam and subjected to three watering regimes, with and without insect attack. In 1989 and 1990, the experiments were conducted in a greenhouse in which the plants were placed on 29 May for both years and watered daily until 10 June (1989) and 15 June (1990). Each year, 96 white pines were arranged in four randomized blocks, with or without insects, three watering regimes, and four sampling dates. Four plants in each block per watering regime were selected randomly; two male and two female weevils were introduced into a screened plastic bag placed over the terminal leaders of the previous year to allow feeding, mating and oviposition. In 1989, insects were allowed to feed, copulate and lay eggs from 1

June through 14 June, and in 1990 insects were left on plants from 31 May through 18 June. Gypsum blocks (Hoskin Scientific, Montréal) were used to measure soil water potentials. In the dry treatment, soil water potentials were maintained close to -0.15 MPa; in the medium treatment, around -0.08 MPa; whereas for the wet treatment, soils were kept above -0.03 MPa. In the dry and medium treatments, plants received between 100 to 200 ml of water to raise the soil water potential when necessary. Plants in the wet treatment received at least 300 ml of water on a daily basis. Soil water potential values between treatments were compared using an *F* test in the general linear model procedure (GLM) (SAS Institute 1989).

Bark collection and measurements on greenhouse plants. Every two weeks over an 8-week period, 24 plants were removed from the greenhouse for bark collection and measurements of seedling water potential, starting on 15 June and 20 June, respectively, in 1989 and 1990. To measure differences in the water potential related to the different watering regimes, the midday xylem water potential was taken (Ruiz-Sanchez *et al.* 1988). The midday stress may reflect more accurately the living conditions of insects on the plants given environmental conditions prevailing at that time of the year. Moreover, Sucoff (1972) demonstrated with red pine that midday stress shows less variation during hours on high evaporation days. Then, at each sampling date, plants were brought to the laboratory around noon; three twigs per plant were cut with a razor blade to measure the xylem water potential using a Scholander pressure chamber (model 1000, PMS Instruments, Corvallis, OR). Bark water content (BWC) was recorded on a dry weight basis [BWC = 100*((Fresh weight - Dry weight)/Dry weight)] after a drying period of 48 h at 70°C. The bark was then ground in a Wiley Mill (20 mesh) and kept at -20°C for feeding preference tests and chemical analyses.

The chemical analyses (nitrogen, phosphorus and potassium) were performed on bark from two-year-old leader sections of each seedling from the 1989 greenhouse test according to the techniques of Kalra and Maynard (1991). The bark mixtures from the 1990 greenhouse test that were used in the feeding preference tests were also analyzed for chemical content. Differences in chemical content among treatments were compared by analysis of variance using the GLM procedure (SAS Institute 1989).

Feeding preference tests. The feeding preference tests were run with bark from two-year-old leader section of the 1990 greenhouse test. Feeding tests were completed using a design modified from that of Alfaro *et al.* (1979). A 3.7 mm thick lining of white styrofoam with four equidistant wells of 1 cm in diameter was placed in a 50 mm by 9 mm Petri dish. A few drops of 2% (w/v) neutral agar (USP, 100 mesh, Bioserv) were dispensed into each well to seal the bottom. Two types of feeding tests were performed. In the two-choice tests, bark from each treatment was added to the agar at 1% per volume (Alfaro *et al.* 1979) and dripped into diagonally opposed wells. In no-choice feeding tests, bark was added at 1% (w/v) and dispensed into the four wells. A filter paper (1.1 cm diameter, Reeves Angel #202, Whatman) was placed on each well while the agar was still hot. Holes 1 mm dia. were drilled in the Petri cover to prevent condensation.

Before beginning a feeding preference test, insects were starved for 24 h at 25°C under a 16 h photoperiod. For each test, two females or two males were placed per Petri dish during 24 h under the same light and temperature conditions. The number of feeding punctures made by the insects, which has been shown to be a good indicator of food preference (Alfaro *et al.* 1979; Piskornik *et al.* 1989), was used to compare insect response to bark from the different treatments.

Preference for bark from water-stressed and non-water-stressed plants. In a series of two-choice tests, spring or fall adults of both sexes were exposed to barks from water-stressed and non-water-stressed plants. We used bark from plants with or without insects from the first (20 June) or last (30 July) harvest. Each test was done with 15 Petri dishes and repeated twice, for a total of 240 observations per test. Numbers of feeding punctures were transformed to their square root to achieve variance homogeneity and normality of the residuals. All analyses were performed using the GLM procedure (SAS Institute 1989).

In a second type of two-choice test, we simultaneously tested preference for bark from water-stressed and non-water-stressed plants with spring or fall adults of each sex, and with bark from the four sampling dates (Julian dates 171, 185, 199, 211). A schedule of nine replications gave a total number of 576 observations. Statistical analyses were performed with the GLM procedure (SAS Institute 1989).

In no-choice tests, we evaluated the absolute feeding on bark from stressed or unstressed plants with spring or fall adults of each sex, and with bark from the four sampling dates. A schedule of four replications gave a total of 512 observations. Statistical analyses were performed using the GLM procedure (SAS Institute 1989).

D. Results

Soil and xylem water potential. Soil water potential and xylem water potential were affected by the different watering regimes. Measurements of soil water tension in 1989 and 1990 are presented in Table 3.1. During the 1989 and 1990 egg-laying periods, no significant differences were observed between soil water tensions for the different treatments (P_{1989}= 0.27; P_{1990}= 0.59). For each year, during the larval development periods, all soil tensions were significantly different (P_{1989}< 0.01; P_{1990}< 0.01). In the dry treatment, the water potential of plants (-MPa) increased gradually during this period suggesting a rising level of stress (Table 3.2).

Water, nitrogen, phosphorus, and potassium content. Bark water content decreased from one sampling date to another in the dry treatment but remained unchanged in the wet treatment in 1989 and decreased only slightly in 1990 (Table 3.3). For both years, at the first harvest, the bark water content was not significantly different between treatments but became different thereafter. In 1989, the bark from water-stressed plants had the highest nitrogen, phosphorus and potassium contents (Table 3.4). The mean values for the three elements were slightly higher in the bark from infested plants. However, the nitrogen and phosphorus content of bark from damaged plants was not statistically different from that of intact plants (P_N = 0.93, P_P = 0.78, P_K = 0.05). If we consider the chemical content according to insect presence or absence, plants with insects had the highest content of each element and only the difference for potassium was non-significant (P_N = 0.02, P_P = 0.04, P_K = 0.50).

Table 3.1. Soil water potential (-MPa) during the egg laying and larval development periods of the white pine weevil in 1989, and 1990.

		Treatment		
Year	Period	Dry	Wet	*P* > *F*
1989	Oviposition	0.041	0.037	0.2732
1989	Post-oviposition	0.172	0.036	0.0001
1990	Oviposition	0.035	0.035	0.5884
1990	Post-oviposition	0.094	0.035	0.0001

Table 3.2. Midday xylem water potential (-MPa) from needles of white pines subjected to wet and dry soil moisture treatments for the different sampling periods in 1989 and 1990.

		Treatment		
Year	Date[a]	Dry	Wet	*P* > *F*
1989	166	1.31 (0.05)[b]	0.99 (0.04)	0.0001
	178	2.11 (0.08)	0.85 (0.06)	0.0001
	192	2.92 (0.18)	0.72 (0.04)	0.0001
	206	2.95 (0.14)	0.78 (0.02)	0.0001
1990	171	1.26 (0.07)	0.94 (0.03)	0.0001
	185	2.22 (0.03)	0.87 (0.02)	0.0001
	199	2.59 (0.11)	0.67 (0.02)	0.0001
	211	2.60 (0.19)	0.90 (0.01)	0.0001

[a] Julian date: 1989:166, 178, 192, 206=15,27 June, 11, 25 July.
1990: 171,185,199,211= 20 June, 4, 18, 30 July.

[b] Means (S.E.M.).

Table 3.3. Bark water content (% dry weight) of the white pines subjected to wet and dry soil moisture treatments for different sampling periods in 1989 and 1990.

		Treatment		
Year	Date[a]	Dry	Wet	$P > F$
1989	166	147.2 (6.0)[b]	154.4 (6.0)	0.4171
	178	122.1 (4.8)	163.8 (4.8)	0.0002
	192	109.1 (12.4)	182.2 (13.7)	0.0041
	206	89.4 (9.1)	164.1 (9.1)	0.0015
1990	171	197.7 (9.2)	225.8 (9.2)	0.0581
	185	139.0 (4.2)	203.5 (4.2)	0.0001
	199	108.9 (4.1)	193.7 (3.7)	0.0001
	211	109.7 (6.2)	169.3 (4.4)	0.0160

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[a] Julian date: 1989:166, 178, 192, 206=15,27 June, 11, 25 July.
1990: 171,185,199,211= 20 June, 4, 18, 30 July.

[c] Means (S.E.M.).

Table 3.4. Nitrogen (%), phosphorus (mg/g) and potassium (mg/g) content [mean values (S.E.M.)] of bark harvested in 1989 and 1990 from white pines grown under dry and wet treatments.

		Watering regime		
Element	Year	Dry	Wet	*P* > *F*
Nitrogen	1989	0.92 (0.03)	0.78 (0.03)	0.019
	1990	0.98 (0.02)	0.87 (0.02)	0.012
Phosphorus	1989	1.25 (0.03)	1.05 (0.03)	0.001
	1990	1.39 (0.03)	1.20 (0.03)	0.027
Potassium	1989	6.88 (0.25)	5.61 (0.25)	0.006
	1990	7.43 (0.35)	6.06 (0.35)	0.070

Feeding preference tests. If we consider only bark from plants that were not subjected to previous insect attack and larval feeding, the feeding response of adult weevils was affected by the watering regime and also by the period when bark was harvested (Figure 3.1). With the first bark harvested (date 171) from plants without insect damage, spring adults did not differentiate between bark from wet and dry treatments ($P = 0.87$) (Figure 3.1a). There was no sex difference in the number of feeding punctures ($P = 0.75$) and there was no interaction between sex and treatment ($P = 0.73$). However, fall weevils preferred bark from non-water-stressed plants over bark from water-stressed plants but the difference is non-significant ($P = 0.07$) (Figure 3.1a). Again, there was no difference between sexes in their preferences ($P = 0.24$) and there was no significant sex*treatment interaction ($P = 0.33$).

With the bark last harvested (Julian date 211) from plants without insect damage, spring and fall weevils of both sexes showed a significant preference for bark from wet treatments (Figure 3.1b). The spring and fall weevils made, respectively, 38% and 43% more feeding punctures on bark from the wet treatment than on bark from the dry treatment ($P_{spring} = 0.01$; $P_{fall} = 0.01$) (Figure 3.1b). For both ages, there was no difference between sexes in the number of feeding punctures ($P_{spring} = 0.33$; $P_{fall} = 0.33$) and the sex*treatment interaction was also not significant ($P_{spring} = 0.55$; $P_{fall} = 0.76$).

Spring and fall weevils made 26% and 60% more feeding punctures, respectively, on bark from the wet treatment ($P_{spring} < 0.01$; $P_{fall} < 0.01$) (Figure 3.2a). Female spring adults ate more than males ($P < 0.01$) but there was no sex*treatment interaction ($P = 0.22$). With fall adults, males and females performed similarly ($P = 0.11$) and

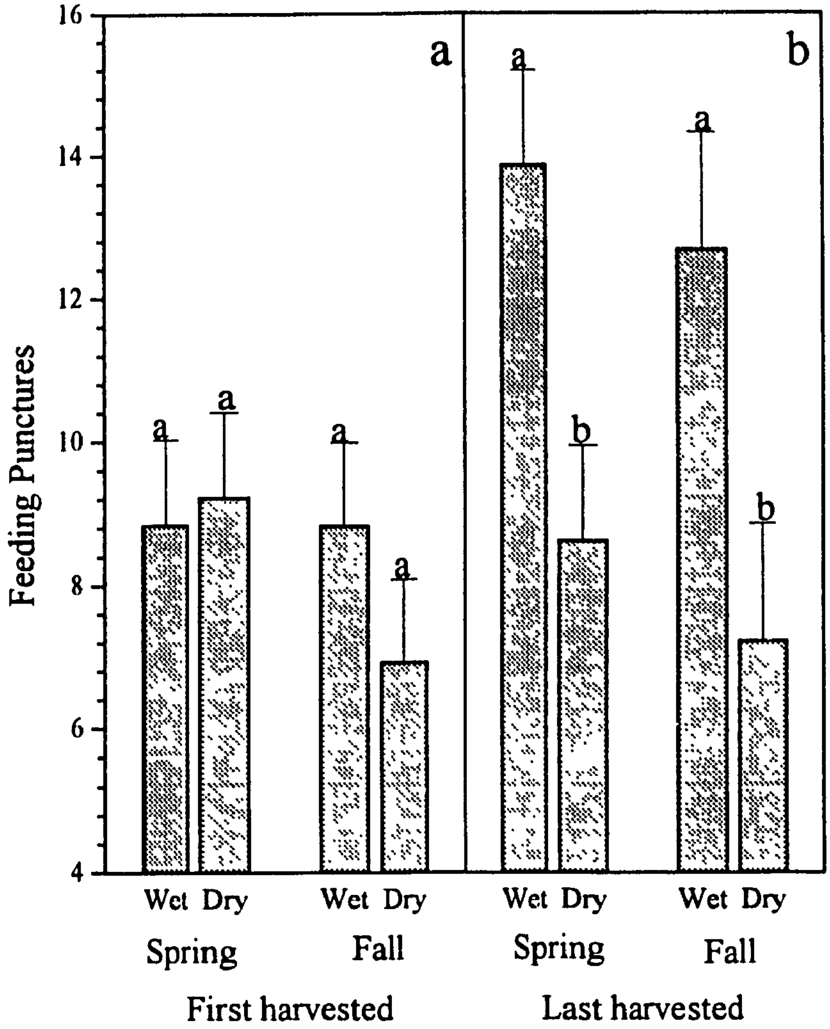

Figure 3.1. Mean (+95% C.I.) number of feeding punctures on bark of non-water-stressed (Wet) and water-stressed (Dry) plants made by spring and fall white pine weevil adults on first harvested (Julian date 171) (a) and last harvested (Julian date 211) (b) bark from greenhouse-grown white pines that were not previously infested by insects; for each pair, values followed by different letters are significantly different ($P < 0.05$).

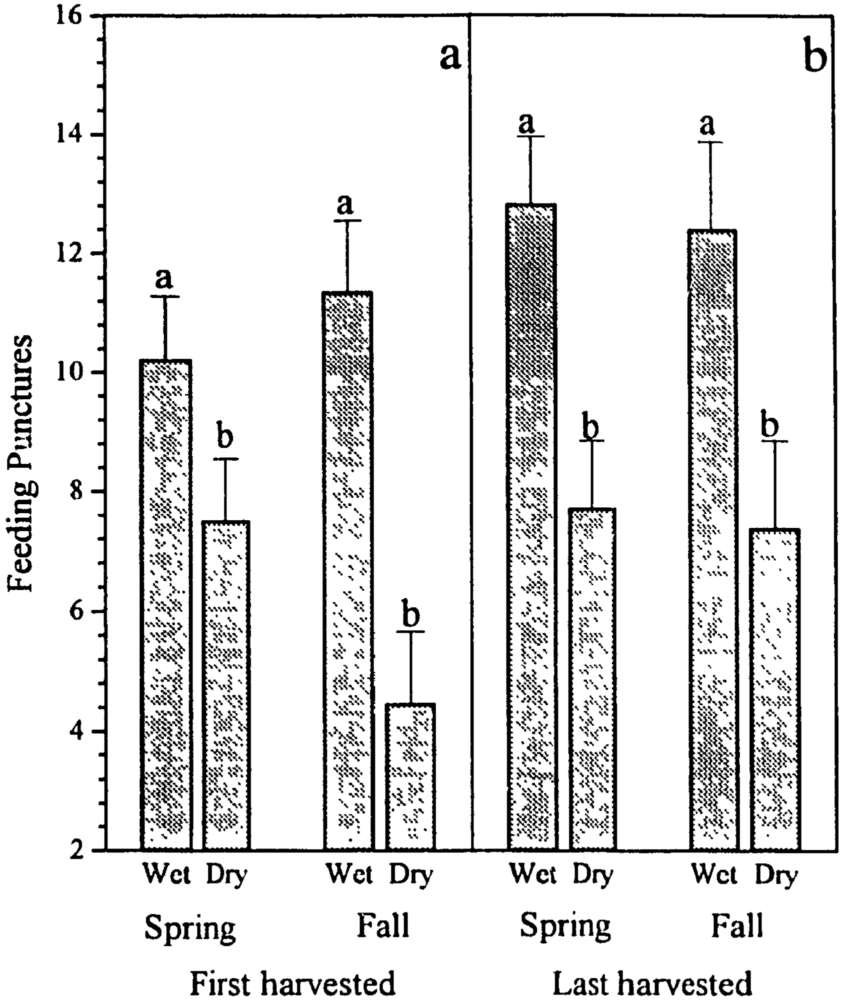

Figure 3.2. Mean (+95% C.I.) number of feeding punctures on bark from non-water-stressed (Wet) and water-stressed (Dry) plants made by spring and fall white pine weevil adults on first harvested (Julian date 171) (a) and last harvested (Julian date 211) (b) bark from greenhouse-grown white pines that were previously infested by insects; for each pair, values followed by the different letters are significantly different ($P < 0.05$).

there was no significant sex*treatment interaction ($P = 0.69$). Also, if we consider the bark first harvested, using plants infested by weevils, the preference for bark from the wet treatment was more pronounced (Figure 3.2a) than for bark from plants without insect damage (Figure 3.1a). With bark from the fourth harvest, spring and fall adults preferred bark from the wet treatment over the dry treatment ($P_{spring} < 0.01$; $P_{fall} < 0.01$) (Figure 3.2b). There was no significant difference in the number of feeding punctures between sexes of both ages ($P_{spring} = 0.96$, $P_{fall} = 0.89$). There was no sex*treatment interaction ($P_{spring} = 0.16$, $P_{fall} = 0.47$).

In a two-choice test, in which the four harvest periods, sex and age were considered, wet bark was preferred over dry bark ($P = 0.01$) (Figure 3.3). Fall weevils made more feeding punctures than spring weevils ($P = 0.01$) (Figure 3.3). Females ate more than males ($P < 0.01$) and there was no age*treatment ($P = 0.30$). The effect of harvest date was not significant ($P = 0.72$).

In a no-choice test, when we considered simultaneously age, sex and the four harvest dates, there was no significant difference in the preference for wet and dry bark ($P = 0.71$). The mean number of feeding holes were 17.6 (S.E.M. = 0.87) and 17.2 (S.E.M. = 0.87) for bark from wet and dry treatments, respectively. This indicates that, when forced to feed, the weevils will consume equal amounts of both types of bark. The effect of the harvest periods was not significant ($P = 0.62$). There was no significant interaction between bark and insect age ($P = 0.39$) and fall weevils did not eat more than spring weevils ($P = 0.07$). However, females consumed more than males ($P < 0.01$), but there was no sex*treatment interaction ($P = 0.53$).

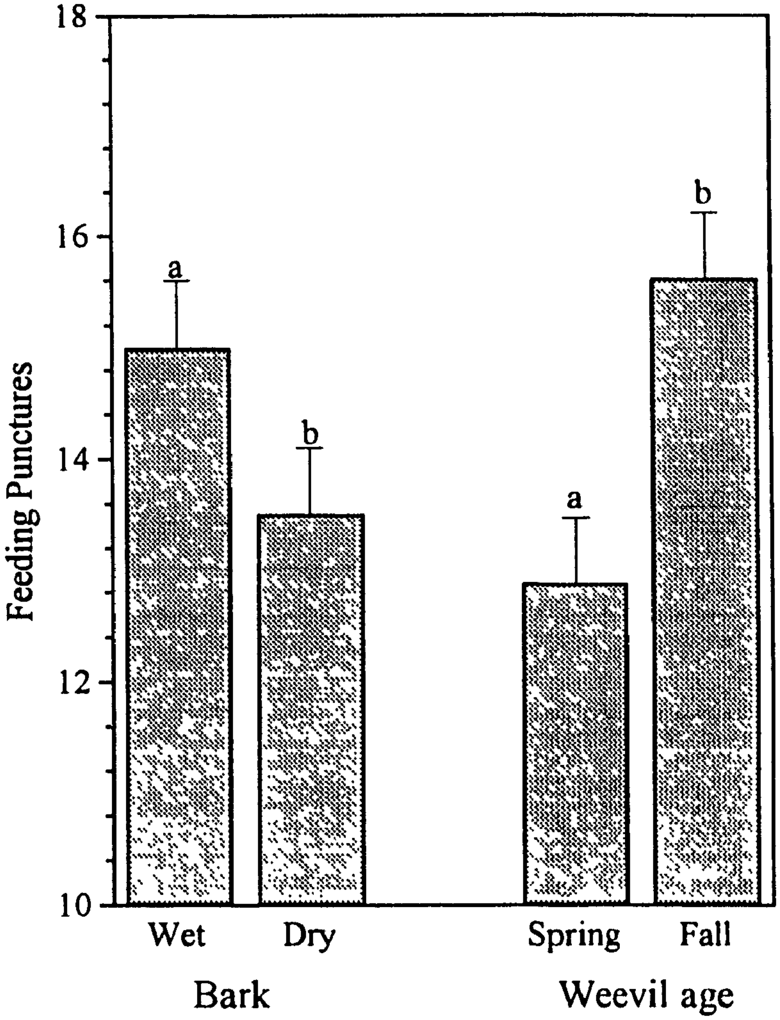

Figure 3.3. Mean (+95% C.I.) number of feeding punctures made by spring and fall adult white pine weevils on bark from non-water-stressed (Wet) and water-stressed (Dry) white pines; for each pair, values followed by the different letters arc significantly different ($P < 0.05$).

E. Discussion

The different watering regimes used in these tests affected the physiology of white pines as indicated by the xylem water potential. Though the effect of the water stress on precise physiological processes was not evaluated, a major impact on the plant may be suspected. Water stress can decrease growth directly by reducing turgor, photosynthesis and translocation (Kaufmann 1968). Plants under the wet watering regime had a higher water potential ($>$ -1.0 MPa on all sampling dates) and, therefore, can be considered vigorous (Cleary and Zaerr 1980). For ponderosa pine seedlings, photosynthesis was slowed or stopped at water potentials between -1.0 and -2.0 MPa and at values between -2.0 and -5.0 MPa seedling vigor declined and at levels below -5.0 MPa seedlings died (Cleary and Zaerr 1980). Kaufmann and Thor (1982), working on lodgepole pine, considered a midday xylem water potential of -2.3 MPa as a severe water stress. Running (1976) reported xylem water potentials ranging from -0.6 (predawn) to -1.5 MPa (midday) for Douglas fir and -0.7 (predawn) to -2.0 MPa (midday) for ponderosa pine.

These experiments demonstrate that the white pine weevil can discriminate between bark from water-stressed and non-water-stressed white pine plants, with a preference for the latter at a certain period of the year. This is in agreement with a number of field observations which suggest that the most vigorous trees are preferred by the weevil (Graham 1926; Plummer and Pillsbury 1929; Kriebel 1954; Hoslt 1955; VanderSar and Borden 1977a). The possibility that some herbivores could attack the most vigorous hosts was suggested by Price *et al.* (1987a,b) and Price (1989) for several gall-forming sawfly species and their willow host plants. The bud-galling sawfly, *Euura mucronata* (Hartig) Man. (Churchil), attacks the longer shoots of its willow host, where establishment and survival are better (Price *et al.* 1987b). Other studies on herbivores have also shown that more vigorous growing plants can have positive effects on insect performances or susceptibility to insect attack (Miles *et al.* 1982; Craig *et al.* 1986; Wagner 1986; Watt 1986; Bultman and Faeth 1987, McCullough and Wagner 1987; Price *et al.* 1987a,b; Craig *et al.* 1989; Kimberling *et al.* 1990; Craig *et al.* 1991). If we consider the limited resources available for larvae under the bark of the terminal leader, a careful selection by the ovipositing female appears biologically sound. Craig *et al.* (1989) mentioned that when the offspring of an insect complete all their subsequent development at the oviposition site, the females are under strong selective pressure to optimize oviposition site selection. Females of the white pine weevil can also select for vigorous growing trees with larger terminal leaders to assure abundant food resources to their brood, as is observed with gall-forming insects (Price and Clancy 1986; Craig *et al.* 1989; Price 1989).

The lack of significant feeding response with early season bark from non-infested plants may reflect the physiological condition of plants which are still similar considering that the watering treatments are just starting. However, with the white pine weevil in Sitka spruce, Alfaro *et al.* (1979) demonstrated a concentration-dependent feeding response. Thus, using higher concentrations of bark to compare the preference of the weevil in a two- choice test may enhance the differences between the two types of bark.

Results of the no-choice tests indicate that when forced to feed on only one type of bark, weevils ate equally bark from water-stressed and non-water-stressed plants. This can explain why in inadequate stands, where trees are less vigorous, the weevils are still able to feed on these hosts. However, field observations related to more pronounced weevil damage on inadequate sites for white pine growth (Maughan 1930; Connola and Wixson 1963b; Dirks 1964; Connola 1965; Connola and Birmingham 1978) are difficult to explain without biological data on the insect. More damage does not necessarily indicate more significant feeding and oviposition on trees growing under stressful conditions. Because the female can lay her eggs on one or more leaders (Plummer and Pillsbury 1929; MacAloney 1930), it is possible that on sites where tree growth is reduced, the smaller size of the previous year's leader could cause females to oviposit on more trees and, in so doing, contribute to an increase in the number of trees attacked yearly. Also, it is possible that because the tree is stressed, the same amount of feeding may result in more damage.

The preference for bark was accentuated on plants with previous (Figure 3.2a) relative to plants not-previously-infested (Figure 3.1a) with the first harvested bark. We can hypothesize that weevil attack will modify bark chemistry and could lead to an increase in feeding activity by other attacking weevils. Lewis (1979) mentions that *Melanoplus differentialis* (Thomas) nymphs frequently feed on portions of leaves affected by previous insect feeding. For another weevil species, Ericsson *et al.* (1988) also observed that *Hylobius abietis* (L.) prefers to attack wounded Scots pine seedlings. For the white pine weevil, if sufficient oviposition is done by a number of females, the formation of a feeding ring under the bark will efficiently kill the leader (Wallace and Sullivan 1985). The biological advantages of this situation could be a reduction in the oleoresin exudation pressure on larvae consequent to death of the leader or simply to be more numerous to cope with resin extruding from canals.

The almost identical feeding preference of both ages of weevils is surprising. Considering that it is spring adults that lay eggs, we expected better discrimination with this age group compared with fall weevils. Because host selection and oviposition occur early in the spring (Dixon and Houseweart 1983), it can be advantageous for the weevil to also select its host tree during the summer and fall periods when weather is still favorable, and thus allow adult dispersion. The new adult generation is active during a period of two months before individuals enter into quiescence (Sullivan 1959). MacAloney (1930) observed that feeding may take place even after heavy snow has fallen, if the weather warms up again. Consequently, we can expect the active participation of fall weevils in host selection.

Our results demonstrate that feeding preference tests can be done with adults of both sexes without significant interaction. Both sexes react similarly to bark type, with both prefer bark from non-water-stressed plants. VanderSar and Borden (1977a) and Alfaro *et al.* (1979) reported similar feeding preferences for both sexes although they speculated that male weevils could be less sensitive in selecting hosts. The only difference we occasionally saw between males and females was that females ate more than males. This was also observed by Alfaro *et al.* (1979).

Specific chemical compounds playing an important role in feeding stimulation of the white pine weevil still have not been identified. Alfaro *et al.* (1980) demonstrated that feeding is stimulated by nonvolatile substances, and that volatile chemicals could act as synergists, but he did not identify any of nonvolatile substances involved. We observed that sucrose (5 μM) had a stimulating effect when added to white pine bark (R.L., unpublished data). In the present experiment, chemical analyses were performed to obtain general information on bark chemistry following the watering regimes. Precise relations between bark chemistry and weevil preferences are difficult to establish. However, there was less nitrogen, phosphorus and potassium in bark from non-water-stressed plants in 1989 and 1990. Goyer and Benjamin (1972) also observed in weevil-infested plantations that roots from jack pine had significantly less total nitrogen than did the roots of trees in adjacent non-infected stands. Enhancement of the feeding response on damaged bark is also associated with a higher potassium content in this bark. Xydias and Leaf (1964) observed more attacks on white pine trees fertilized with potash. Also, the insect's preference for bark with a low content in nitrogen, phosphorus and potassium may indicate that these elements are too general as indicators of food quality, and that specific products which play an important role in insect feeding preferences have to be identified. Some phenols, amino acids and carbohydrates are known to act as phagostimulants for other weevil species (Blanc 1972; Thomas and White 1971; Hsiao 1969; Doss 1983), but this remains to be demonstrated for the white pine weevil.

Larsson (1989) mentioned that it is unlikely that a range of insect species with different feeding habits will respond consistently to stress-induced changes in plant tissues. Price (1989) considered that a dichotomy could help to explain that some herbivore species are keyed to stressed plants, while other species develop a specialization for the most vigorous plants or plant parts. The white pine weevil's preference for non-stressed plants may also explain the typical damage caused by this insect. On a vigorous tree, the leader will allow maximal oviposition by one female and support brood development. In conclusion, the white pine weevil, like a number of other insect species, prefers to feed on non-stressed plants and, therefore, we would expect its fitness to be favored by vigorous growing plants rather than by stressed plants.

CHAPTER 4

Feeding Preferences of the White Pine Weevil, *Pissodes strobi* (Peck), on Intact and Currently Infested White Pine Leaders

A. Abstract

Adults of the white pine weevil, *Pissodes strobi* (Peck), were fed in two choice tests on bark originating from previously infested or intact white pine leaders and also on bark from one- and two-year-old leader sections. Leaders came from trees selected in a white pine plantation and from greenhouse grown plants. With field collected bark early during the season, the weevils preferred bark from previously infested trees. With bark harvested later, they did not discriminate between the two types of bark. With bark from greenhouse plants, no preferences were observed with the bark harvested at the end of the oviposition period but when bark was harvested at the end of larval development, weevils showed a feeding preference for bark from non-infested leaders. Chemical analysis demonstrated that, generally, bark from infested trees had higher nitrogen, phosphorus and potassium content. These results suggest that insect attack modifies bark chemistry and the resulting feeding preference. The bark from the two-year-old leader section was preferred over that of the one-year-old leader section.

B. Introduction

The white pine weevil (*Pissodes strobi* (Peck)), is an important pest of white pine (*Pinus strobus* L.) and Norway spruce (*Picea abies* (L.) Karst.) plantations. This insect attacks and kills the leader and the terminal growth of the preceding 1-2 years. Although it has been studied for more than 100 years, current knowledge does not allow a complete prevention of its attacks. It is mainly physical factors such as tree age and height, leader length, diameter, and the presence of numerous resin canals that have been associated with tree susceptibility (Barnes 1928; Kriebel 1954; Sullivan 1961; Connola and Wixson 1963a; Marty and Mott 1964; McMullen *et al.* 1987). Factors that lead the insect to the uppermost part of the trees are the verticality of the shoot (VanderSar and Borden 1977c) and positive phototropism and negative geotaxis (VanderSar and Borden 1977b). However, though the uppermost part of the leader is the most frequent site of oviposition (Sullivan 1961) sections from the previous year's growth of the leader can also be used for oviposition (Gara *et al.* 1971; VanderSar *et al.* 1977).

A few studies show that chemical factors are probably very important in the process of tree attack. Some terpenoid products, according to their concentration, can be stimulatory or inhibitory to the white pine weevil (Carlson 1971; Wilkinson 1980; Alfaro *et al.* 1980). Studies on the feeding behavior of white pine weevils demonstrated that they are sensitive to different chemical substances, such as sucrose (Alfaro 1980) and also to wax and resin acids present in the cuticle of the leader (Alfaro and Borden 1985).

However, other factors can affect insect feeding preference. In Chapter 3, where a preference for bark from non-water-stressed over water-stressed white pine plants was observed, the feeding response was enhanced on bark from plants that had previously suffered weevil damage. Plank and Gerhold (1965) observed in an experiment that white pine weevils tend to group on some leaders. Also, Dixon and Houseweart (1983), reported that some tree leaders had more weevil feeding punctures than others, indicating a preferential attraction to certain trees during the oviposition period. Enhancement of the feeding response on infested plants has been observed for other insect species, including weevils (Lewis 1979, Ericsson *et al.* 1993).

The objective of the present study was to determine whether the feeding preference of adult *P. strobi* is affected by previous weevil damage and if adults can discriminate between bark from different leader sections. Adult weevils were exposed in choice tests to bark from previously infested or intact field collected leaders and greenhouse plants subjected to and free from insect attack. Also, the preference for bark from one and 2-year-old leader sections was studied. The number of feeding punctures was used as an indicator of weevil preference .

C. Materials and methods

Biology of the white pine weevil. The phloem feeding white pine weevil (*Pissodes strobi* Peck) is an important pest of white pine (*Pinus strobus* L.) and Norway spruce (*Picea abies* (L.) Karst.) plantations in Québec (Ministère des Forêts 1993). By the end of April, males and females are attracted to the terminal leader of their host, where they feed and mate. The females oviposit in feeding cavities and, after hatching, the first instar larvae bore downards in the leader, eating the phloem (i.e. inner bark [Jensen *et al.* 1963]). Pupation takes place in the outer xylem or in the pith and a new adult generation emerges during July and August. The damage caused by this weevil is characteristic, killing only the terminal leader, current growth and occasionally the two-year-old leader. The reaction of the plant to insect damage is easily observed by the resulting crooked or forked stem caused by the competition of the lateral shoots for apical dominance (Lavallée and Benoit 1989).

Insect collection and rearing. Overwintering spring adults were collected on white pine leaders during the first week of May in 1991 in two white pine plantations [Saint-Luc de Champlain (46°30' N, 72°30' W) and Sainte-Béatrix (46°13' N, 73°38' W)]. Weevils were sexed according to techniques described by Lavallée *et al.* (1993) and kept at 5°C on an artificial diet (Trudel *et al.* in press). White pine leaders infested during the spring were harvested in July, 1991, at the Saint-Luc plantation and stored in cages at room temperature (20°C). Adults that emerged from these leaders, were then placed on an artificial diet and kept at 5°C.

Bark collection and manipulation. In 1990, 30 infested and 30 intact white pines were selected at the Saint-Luc plantation on May 4. From these, 25 infested and 25 intact leaders were protected with nylon mesh tissue to prevent additionnal weevil attack. Weekly, from May 4 to July 11, 5 infested and 5 intact leaders were harvested for bark analysis and subsequent use in feeding tests. Temporally, this corresponds to the periods of egg laying and larval development. For each tree, the one- and two-year-old leader sections, the 1989 and 1988 sections, respectively, were harvested and wrapped with a plastic bag to prevent excessive evapotranspiration their basal part was placed in water. After less than 2 hours, the bark was removed and the fresh weight measured. Bark water content (BWC) was recorded on a dry weight basis [BWC =

100*((Fresh weight - Dry weight)/Dry weight)] after a drying period of 48h at 70°C. The bark was ground in a Wiley Mill (20 mesh) and kept at -20°C for feeding preference tests and chemical analyses. The bark of the trees corresponding to a similar treatment were combined for their use in feeding tests.

Bark from greenhouse plants which were well watered daily also was used. These plants came from a larger experimental design presented in Chapter 2 and for which a brief description follows. Five- and six-year-old white pine were used in 1989 and 1990, respectively. Trees were planted in a sandy loam and subjected to three watering regimes, with and without insect attack. In 1989 and 1990, the plants were placed in a greenhouse on May 29 and watered daily until June 10 (1989) and June 15 (1990). Each year, 96 white pine were arranged in four randomized blocks, with or without insects, three watering regimes, and four sampling dates. Four plants in each block per watering regime were selected randomly; two male and two female weevils were introduced into a screened plastic bag placed over the terminals of the previous year to allow feeding, mating and oviposition. In 1989, insects were allowed to feed, copulate and lay eggs from June 1 through June 14, and in 1990 insects were left on plants from May 31 through June 18. Gypsum blocks (Hoskin Scientific, Montréal) were used to measure soil water potentials. In the dry treatment, soil water potentials were maintained to -0.15 MPa; in the medium treatment to -0.08 MPa; whereas for the wet treatment, soils were kept above -0.03 MPa. In the dry and medium treatment, plants received between 100 to 200 ml of water to raise the soil water potential. Plants in the wet treatment received at least 300 ml of water on a daily basis to maintain the soil fresh.

Every two weeks over an 8-week period, 24 plants were removed from the greenhouse for bark collection. Bark water content (BWC) was recorded on a dry weight basis [BWC = 100*((Fresh weight - Dry weight)/Dry weight)] after a drying period of 48 h at 70°C. The bark was then ground in a Wiley Mill (20 mesh) and kept at -20°C for feeding preference tests and chemical analyses.

The chemical analyses (nitrogen, phosphorus and potassium) were performed on bark of each seedling from the 1989 greenhouse test according to the techniques of Kalra and Maynard (1991). The bark mixtures from the 1990 greenhouse test that were used in the feeding preference tests were also analyzed for chemical content. Differences in chemical content among treatments were compared by analysis of variance using the GLM procedure (SAS Institute 1989).

Feeding preference tests. Feeding preference tests were performed as described in Chapter 3. Before each test, insects were starved for 24 h at 25 °C under a 16 h photoperiod. For each test, two females or two males were placed in each Petri dish for 24 h under the same light and temperature conditions. The number of feeding punctures, which is a good indicator of the food preference (Alfaro *et al.* 1979; Piskornik *et al.* 1989), was used to compare insect response to bark from the different treatments.

Preference for bark from infested and intact field leaders. Adults of each sex were exposed to bark from the terminal leader of either infested and intact trees. Tests were performed with bark from the first or last harvest (May 4 and July 11). Each test was done with 16 Petri dishes and repeated twice, for a total number of 256 observations. After the appropriate transformation, to achieve variance homogeneity and normality of the residuals, the number of feeding punctures was analysed using the GLM procedure (SAS Institute 1990).

Preference for infested and intact bark from greenhouse plants. Adults of both sexes were exposed to bark from the two-year-old leader section (1988 section) of infested and intact well watered plants. The tests were performed with bark from the first (20 June) or last (30 July) harvest. Each test was done with 15 Petri dishes and repeated twice, for a total number of 240 observations per test. Data were analysed as described above.

Preference for bark from one and two-year-old leaders from field trees. Adults of each sex were exposed to bark from the 2-year-old leader section (1988) and from the one-year-old section (1989). Bark from infested or intact trees from the first (May 4) or last harvest (July 11) was used. Each test was done with 15 Petri dishes and repeated twice, for a total of 240 observations per test. Data were analysed as described above.

Preference for bark from one and two-year-old leaders from greenhouse plants. Spring or fall adults of both sexes were exposed to bark from one- and two-year-old leader sections and from seedlings which had not been infested from the first or last harvest. A six replicate design gave a total of 192 observations. Data were analysed as described above.

D. Results

Water, nitrogen, phosphorus, and potassium content. The water content of bark from field leaders with insect damage was not significantly higher ($P = 0.09$) than bark without insect damage (Figure 4.1a). The water content of bark was not affected by leader age ($P = 0.15$). Significantly more water was associated with the infested one-year-old sections in 1989 ($P < 0.01$) (Figure 4.1b). In the 1990 greenhouse tests, the water content of bark was similar in infested and non-infested leaders ($P_{1990} = 0.66$). However, the water content was affected by the leader section ($P = 0.03$) (Figure 4.1c).

The nitrogen content of bark with insects was generally higher than in bark without insects (Figure 4.2). However, a significant interaction between insect presence and leader section was observed with both field and greenhouse data ($P_{1990\text{-}F} < 0.01$; $\mathrm{P}_{1989\text{-}G} < 0.01$, $P_{1990\text{-}G} < 0.01$) (Figure 4.2a,b,c). A higher nitrogen content was found in infested one-year-old leader compared to infested two-year-old section ($P_{1990\text{-}F} < 0.01$; $\mathrm{P}_{1989\text{-}G} < 0.01$, $P_{1990\text{-}G} < 0.01$).

The phosphorus content of bark with insects was generally higher than in bark without insects (Figure 4.3). However, a significant interaction between leader section and insect damage was observed for field trees and in the 1989 greenhouse test ($P_{1990\text{-}F} < 0.01$ $\mathrm{P}_{1989\text{-}G} < 0.01$, $P_{1990\text{-}G} = 0.67$). The difference between intact and infested leaders was significant only with field leaders (Figure 4.3a). Higher phosphorus levels occured in infested one-year-old leader sections rather than 2 year-old leader sections, significant differences were found with field trees and in the plants from the 1989 test ($P_{1990\text{-}F}\,P < 0.01$, $\mathrm{P}_{1989\text{-}G} < 0.01$, $P_{1990\text{-}G} = 0.14$).

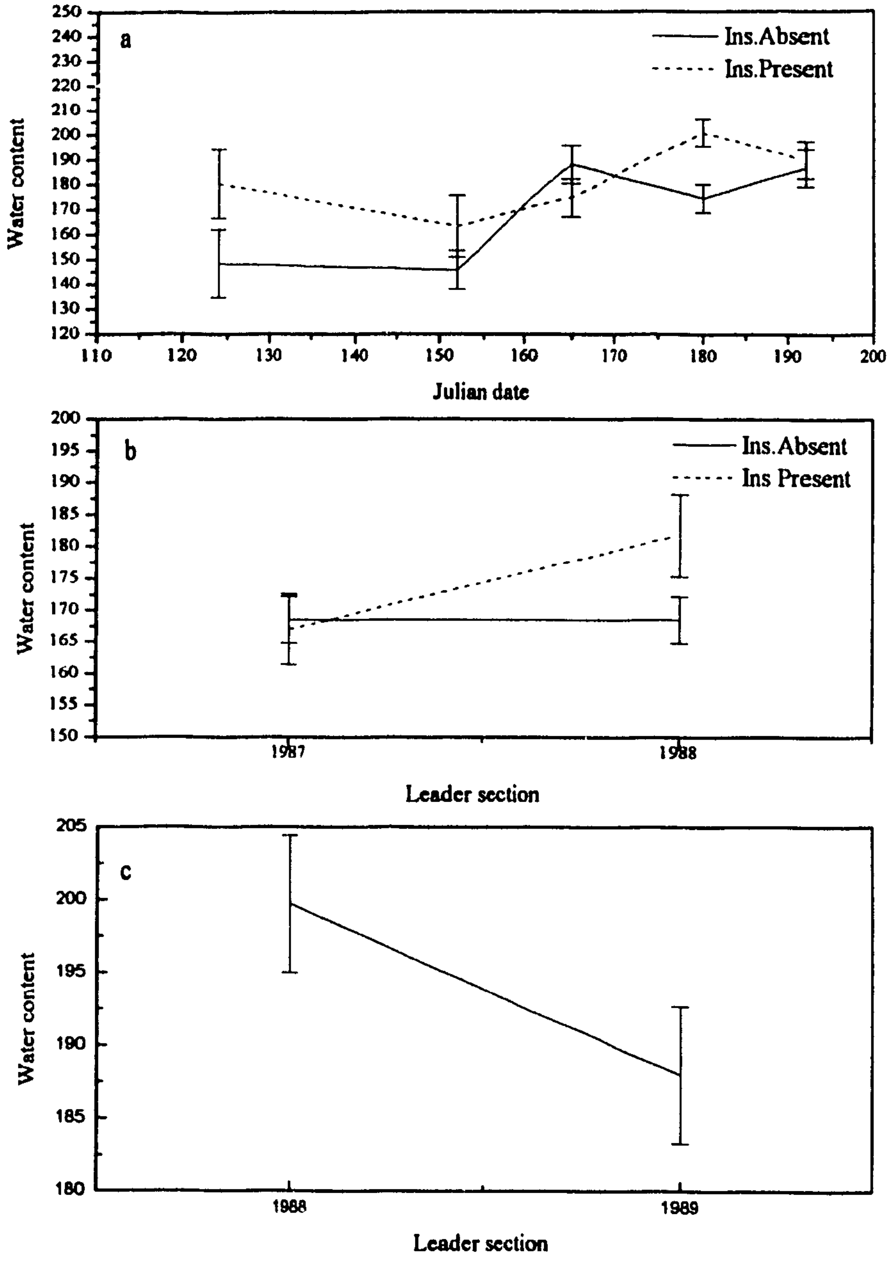

Figure 4.1. Water content (% ± S.E.M.) of bark from (a) leader of field white pine infested or not by the white pine weevil; (b) greenhouse plants in 1989 test according to leader section and weevil damage (% ± 95% C.I.); (c) greenhouse plants in 1990 test according to leader section (% ± 95% C.I.) insect presence and absence confounded.

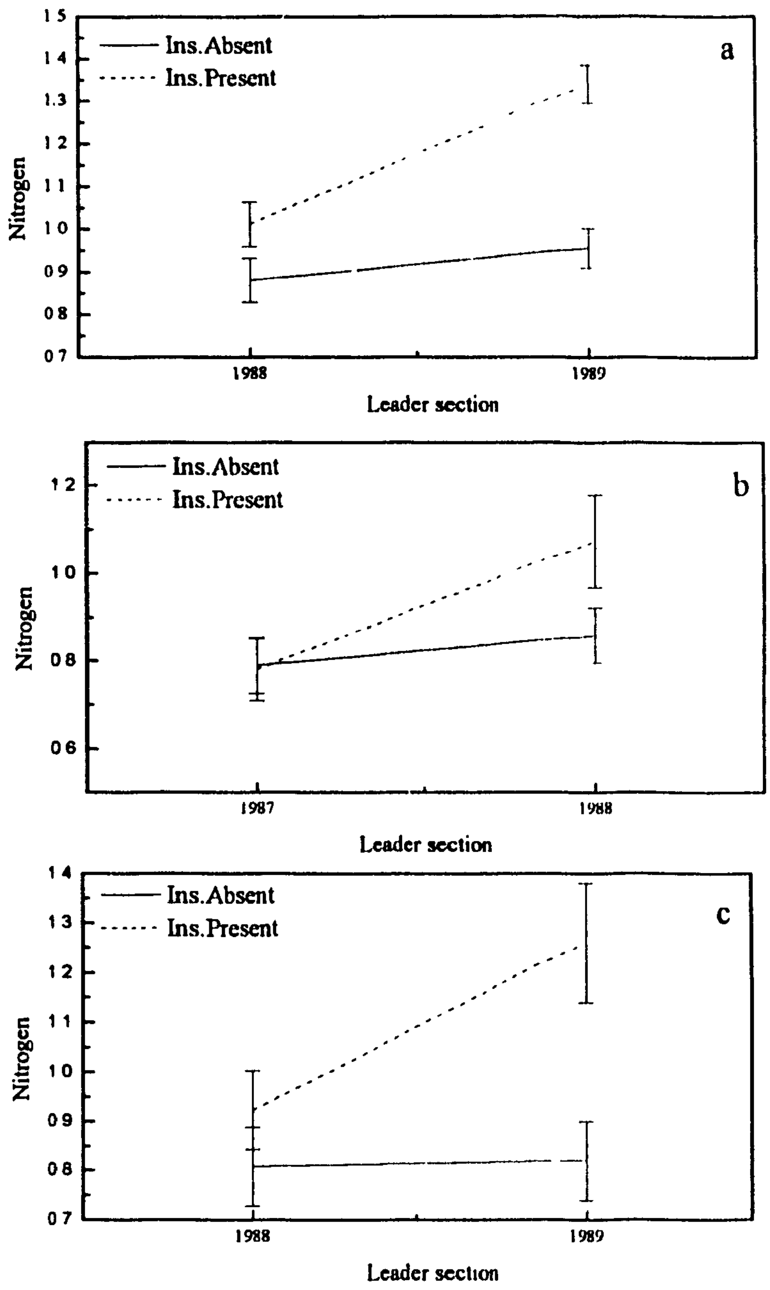

Figure 4.2. Nitrogen content (% ± 95% C.I.) of bark from different leader sections from (a) intact and infested plants from field white pine; (b) greenhouse plants in the 1989 test; (c) greenhouse plants in the 1990 test.

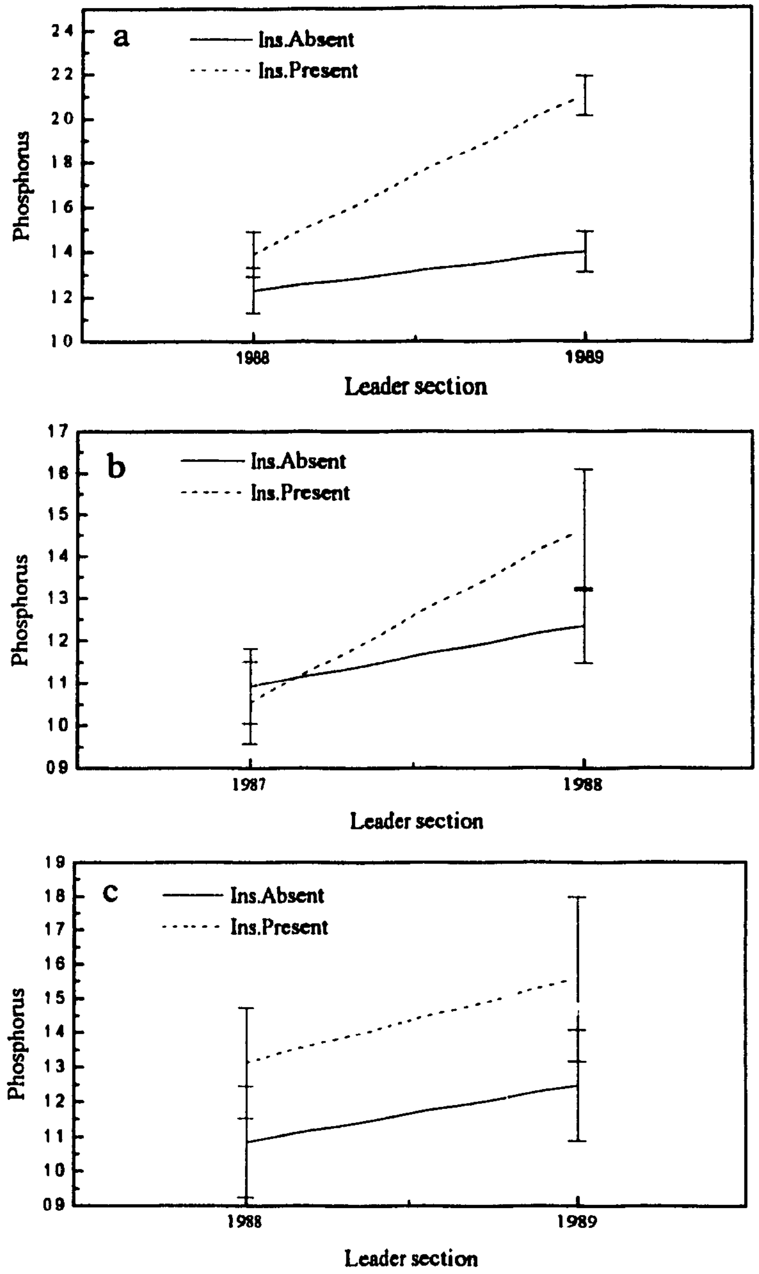

Figure 4.3. Phosphorus content (mg/g ± 95% C.I.) of bark from different leader sections from (a) intact and infested plants from field white pine; (b) greenhouse plants in the 1989 test; (c) greenhouse plants in the 1990 test.

The potassium content of bark also was affected by the leader age and presence of insect damage (Figure 4.4). With bark from field leaders and greenhouse plants, a significant interaction between leader section and insect attack was observed ($P_{1990\text{-}F} < 0.01$, $P_{1989\text{-}G} = 0.04$, $P_{1990\text{-}G} = 0.68$). The potassium content of bark that contained insects was higher than in bark without insects on the one-year-old sections from field trees and in 1989 greenhouse plants ($P_{1990\text{-}F} < 0.01$, $P_{1989\text{-}G} = 0.01$, $P_{1990\text{-}G} = 0.79$ (Figures 4.4a,b,c).

Preference for bark from infested or intact field leaders. Using bark collected on 4 May, the preference of adults for infested bark was 40% higher compared to intact bark ($P < 0.01$, Figure 4.5). There was no difference in the number of feeding punctures made by males and females ($P = 0.16$). When exposed to bark from the last harvest (July 11), the number of feeding punctures made by adults on infested bark was only 17% higher than on intact bark ($P = 0.05$). Females ate more than males ($P = 0.01$) and there was no significant sex*treatment interactions ($P = 0.73$).

Preference for bark from infested or intact greenhouse plants. Current insect attack and development under the bark of greenhouse plants affected weevil feeding preference (Figure 4.6). With infested bark from the first harvest (June 20), weevils of both sexes made more feeding punctures on previously infested bark but the difference was non-significant ($P_{spring} = 0.37$). The number of feeding punctures made by both sexes was similarly ($P_{spring} = 0.31$) and there was no sex*treatment interaction ($P_{spring} = 0.54$). When bark from the last harvest (July 30) was offered to insects, weevils

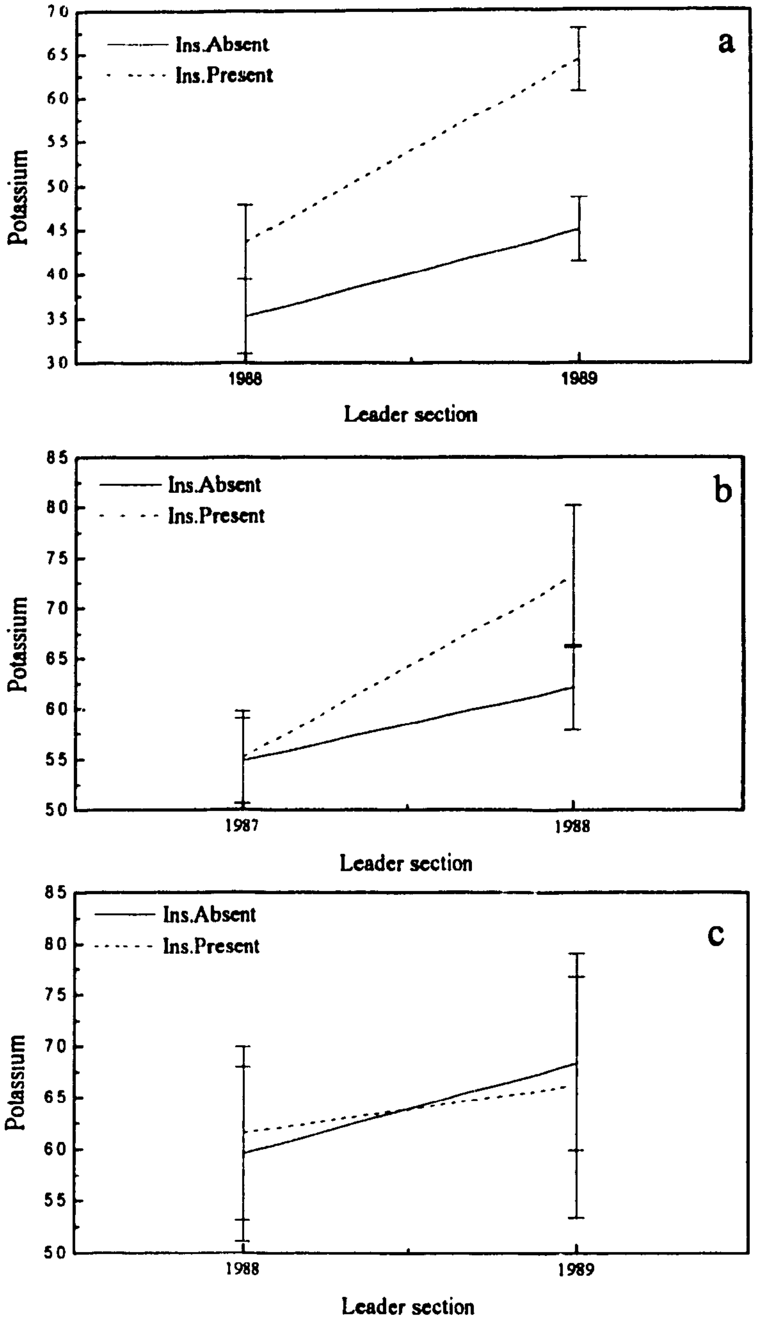

Figure 4.4. Potassium content (mg/g ± 95% C.I.) of bark from different leader sections from (a) intact and infested plants from field white pine; (b) greenhouse plants in the 1989 test; (c) greenhouse plants in the 1990 test.

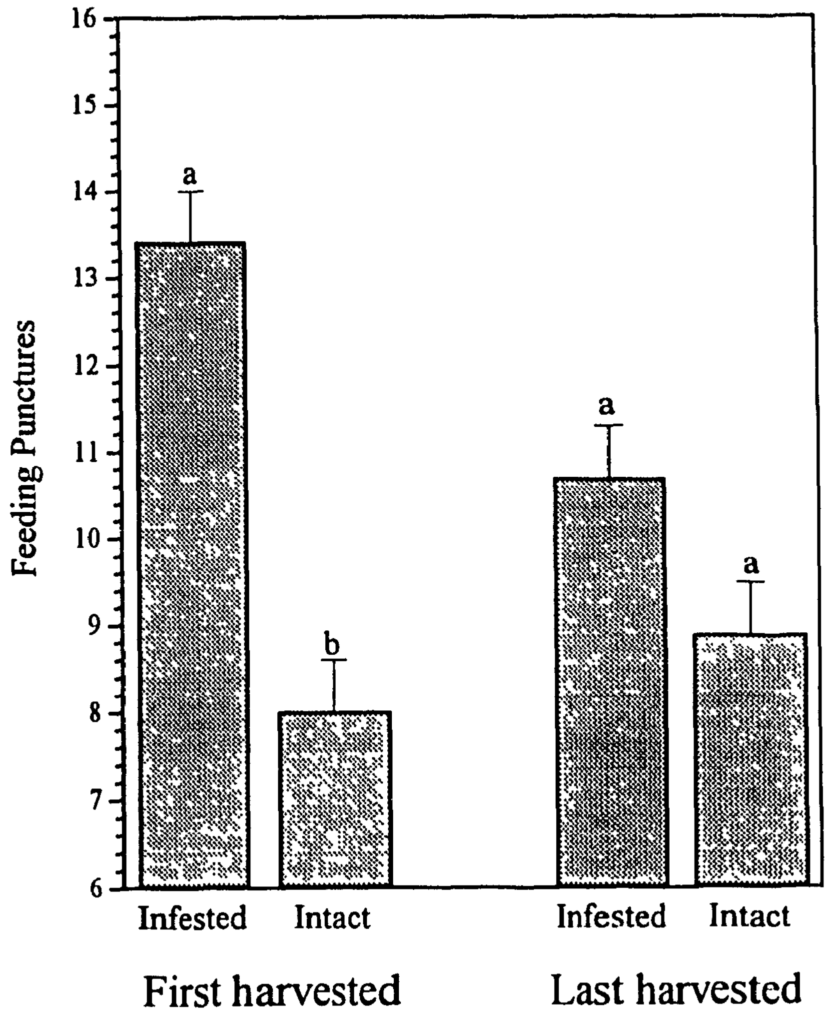

Figure 4.5. Mean (+95% C.I.) number of feeding punctures made by weevils on bark harvested on two dates (First= 4 May; Last= 11 July) from field trees infested or not by weevils; for each pair, values followed by the different letters are significantly different ($P<0.05$).

preferred intact bark ($P_{spring} < 0.01$). The number of feeding punctures made by both sexes was similarly ($P_{spring} = 0.70$) and there was no sex*bark interaction ($P_{spring} = 0.31$).

Preference for one- and two-year-old bark from field trees. In a two choice test with bark harvested on 4 May from non-infested leaders, adults of both sexes preferred bark from two-year-old (1988) leaders over one-year-old (1989) leaders ($P < 0.01$, Figure 4.7a). There was no sex*treatment interaction ($P = 0.15$). Exposed to bark harvested later (July 11), the weevil's preference for intact bark from the 1988 section was more pronounced ($P < 0.01$). Females ate more than males ($P = 0.04$) and there was no sex*treatment interaction ($P = 0.10$).

On bark from infested leaders, the preference for the 1988 section was less pronounced (Figure 4.7b). In a two choice test with first harvested field bark from infested leaders, adults of both sexes still preferred bark from two-year-old leaders over one-year-old bark ($P < 0.01$). The numbers of feeding punctures made by females and males were similar ($P = 0.64$). Exposed to seasonally older infested bark, adults still preferred the two year old bark, but the difference was non significant ($P = 0.14$). The feeding preferences of both sexes were similar ($P = 0.59$) and there was no sex*treatments interaction ($P = 0.86$).

Preference for one- and two-year-old bark from greenhouse plants. There was no significant difference in the number of feeding punctures made by both spring and fall adults ($P = 0.64$) and there was no age*bark interaction ($P = 0.42$). Therefore, the data were combined. When offered bark from the first or last harvest from greenhouse plants without insects, weevils fed more on bark from two-year-old sections ($P = 0.02$,

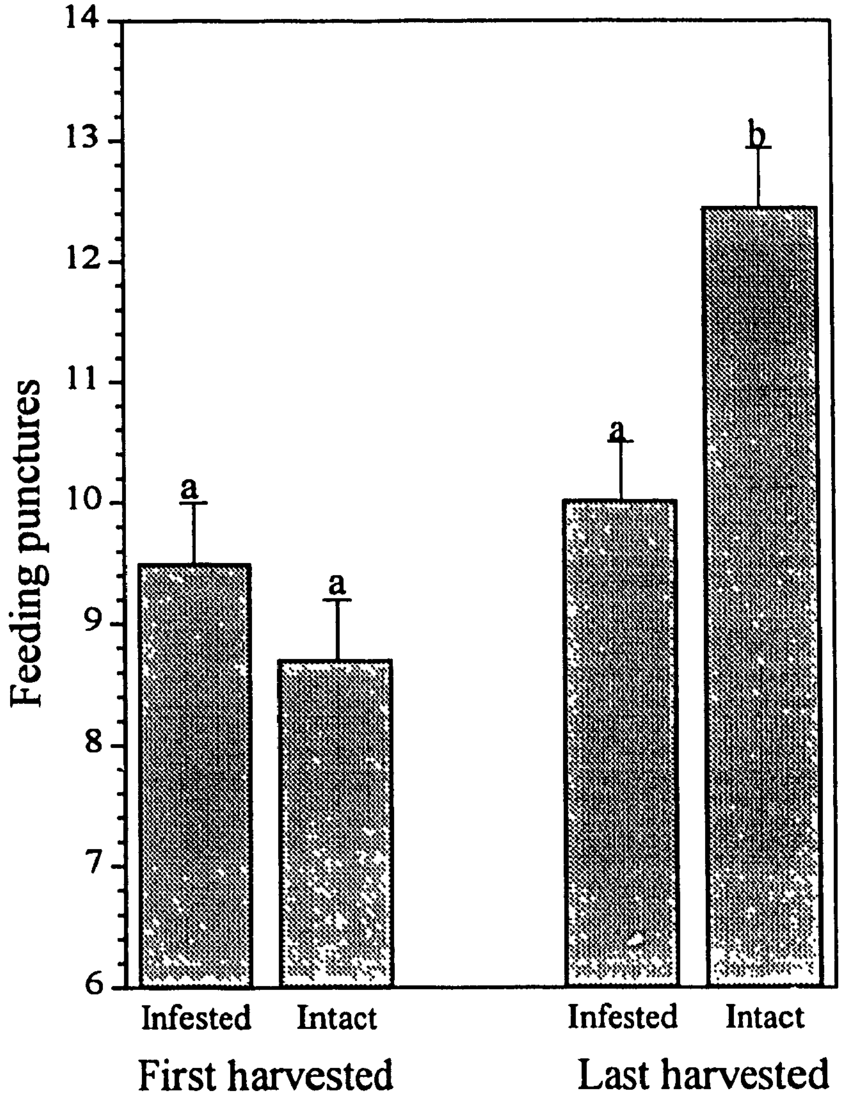

Figure 4.6. Mean (+95% C.I.) number of feeding punctures made by weevils on bark harvested on two dates (First= 20 June; Last=30 July) from greenhouse plants infested or not by weevils; for each pair, values followed by different letters are significantly different (*P* < 0.05).

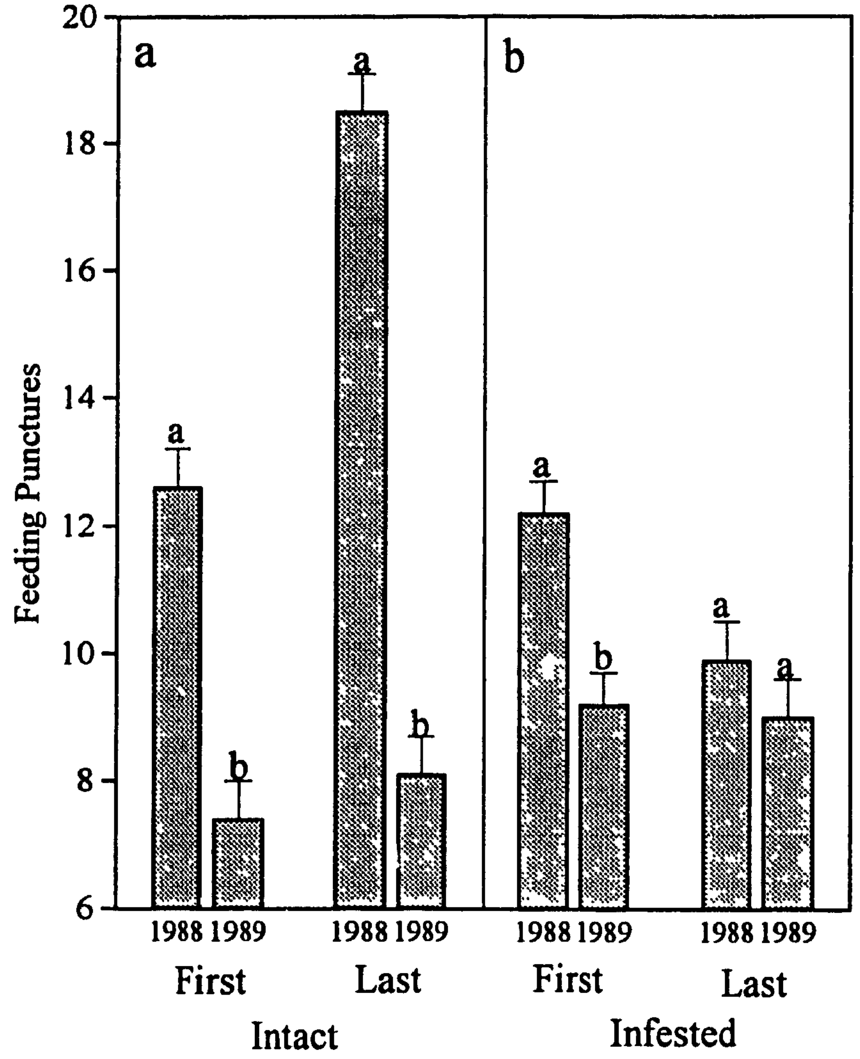

Figure 4.7. Mean (+95% C.I.) number of feeding punctures made by weevils on bark from the 2-year-old leader section (1988) and the one-year-old section (1989) harvested on two dates (First= 4 May; Last= 11 July) from field trees infested or not by weevils; for each pair, values followed by different letters are significantly different ($P<0.05$).

Figure 4.8). The bark*harvest interaction was non-significant (*P* = 0.96) and both sexes did the same number of punctures (*P* = 0.20).

E. Discussion

These experiments demonstrate that adults of the white pine weevil were able to discriminate between bark from wild field trees whether subjected to insect attack and larval development or not. With field collected bark harvested at the beginning of the oviposition period (May 4), we observed that weevils preferred bark from infested trees. With greenhouse bark harvested after the oviposition period (June 20), a similar preference for bark from infested leaders was also observed, although this preference was not statistically significant.

Plants are subjected to multiple stresses which directly influence their development and growth (Heinrichs 1988). Because insects feed on plants, they are a source of stress and may modify the physiology of the plant. Induced responses in plants following physical damage or stress may deteriorate (Edwards and Wratten 1983; Raupp and Denno 1984; Baldwin 1988; Tallamy and Raupp 1991) or improve (Williams and Myers 1984; Wagner and Evans 1985; Roland and Myers 1987; Haukioja 1990) plant quality for insects. Most of the studies listed above dealt with foliage feeders and induced modifications are related to the quality of foliage.

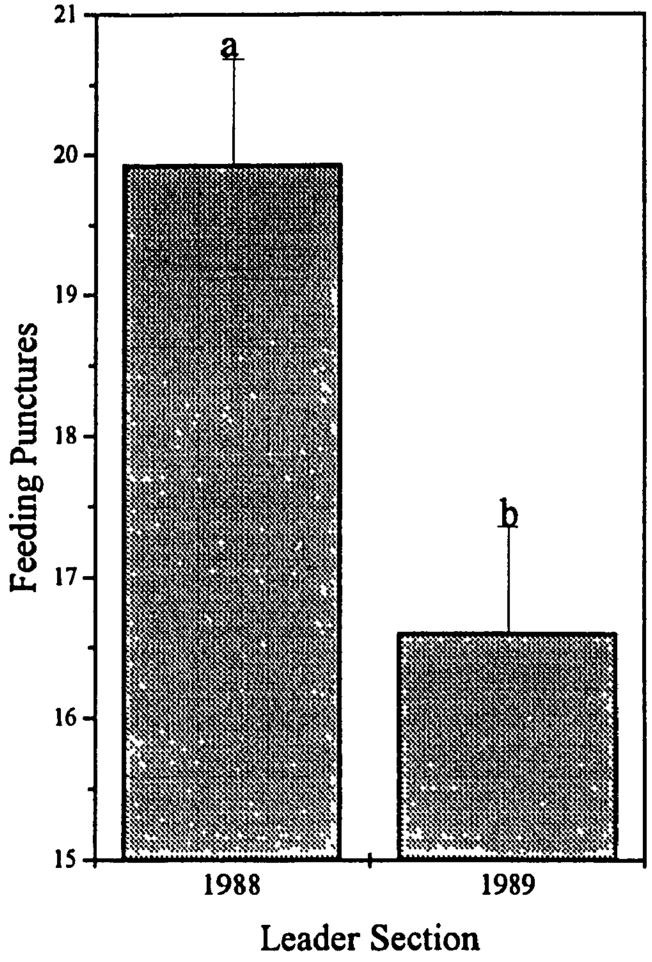

Figure 4.8. Mean (+95% C.I.) number of feeding punctures made by weevils on bark from 2-year-old leader section and one-year-old leader section from greenhouse plants without insect damage; for each pair, values followed by different letters are significantly different ($P < 0.05$).

From the feeding response observed with the white pine weevil in these tests, we can hypothesize that weevil attack will modify bark chemistry, leading to increased feeding activity by other attacking weevils. With another weevil species, *Hylobius abietis* (L.), Ericsson *et al.* (1988) also observed a preference for attack-wounded Scots pine seedlings. They suggested that increased emission of host volatiles from wounded hosts may be an attractive cue for adult *H. abietis*, although this was not clearly demonstrated. In our tests, host volatiles may not explain weevil preference for damaged plants since in our protocol we used oven-dry bark.

The chemical analyses provided evidences of a consistent tendency under greenhouse and field conditions for chemical modification of phloem from the infested leaders. Although the quantities of some chemical elements were, in some years, not statistically different between infested and intact leaders, there was a consistent pattern toward an increase in the measured chemical in the phloem of the infested leaders. A similar positive response was reported by Lewis (1979) with *Melanoplus differentialis*. Even if relatively small, these modifications of bark quality may be advantageous for progeny development. Herbivores frequently are responsive to subtle biochemical changes in host quality (Mattson and Addy 1975). According to Haukioja (1990), under certain conditions insects may create positive feedback loops via the quality of their host tree. This may positively affect the developing weevil larvae, because they will feed on a better quality material. Considering the important role of terminal buds in phytohormonal translocation, it has been proposed that insects feeding on apical parts of shoots, especially on buds, are the most likely to elicit a positive effect (Haukioja 1990).

The discrimination between bark from intact and infested leaders varied during the season. With field collected bark harvested at the end of the larval period (July 11) the preference for infested trees was less marked than with bark harvested earlier (May 4). This indicates that feeding stimulation in response to damaged bark is reduced during the growing season. On bark from greenhouse plants harvested when adults were close to emerging from the leaders (July 30), the feeding preferences were reversed, the insects preferring bark from intact leaders. In natural circumstances the behaviour of the white pine weevil is somewhat similar to that seen in these experiments. Dixon and Houseweart (1983) reported from field observations that, initially, the spring weevils are located mainly on the leader and in terminal buds and that some leaders have more insect feeding punctures than others but, by the end of June, spring adults are found on lateral intact branches. The adults of the new generation (fall weevils) are not localised in the leader but rather they are dispersed in the current-year growth of the lateral branches in the upper crown of attacked trees (Dixon *et al.* 1979). Piskornik (1989) also reported that the hazelnut weevil (*Curculio nucum* L.) feeds less later in the season, on nuts that were initially preferred, suggesting the capacity of the adult for recognizing the nuts occupied by larvae.

The preference for the two-year-old leader section was surprising considering the natural behaviour of the weevil in spring to attack one-year-old section. A similar phenomenon is observed in feeding tests reported by Bauce and Hamel (1991) with Norway spruce bark. Chemical analysis of the leader sections indicate a trend toward lower concentrations of the measured elements in the preferred two-year-old growth.

Also, the insect's preference for bark with a low content of nitrogen, phosphorus and potassium suggests that these elements are too general as indicators of food quality. Specific products which play an important role in insect feeding preferences have to be identified. Some phenols, amino acids and carbohydrates act as phagostimulants for other weevil species (Blanc 1972; Thomas and White 1971; Hsiao 1969; Doss 1983), but this remains to be demonstrated for the white pine weevil. Also, the present results indicate that the preference for two-year-old sections was accentuated on non-infested field leaders when compared with infested field leaders. This suggests that modification of plant chemistry resulting from insect damage affects the one-year-old section and then the 2-year-old leader section. Later in the season, no difference is observed between the leader sections.

Finally, as mentioned by Karban and Myers (1984), the effects we observed are highly artificial and may be different from effects experienced by herbivores dealing with living plants where other chemical stimuli may be important. Consequently, we should extend the bioassay to living trees and determine if damage stimulates feeding and enhances larval development. Induced responses should not be assumed to be defensive (Karban and Myers 1984).

CHAPTER 5

Techniques for Sexing Live Adults of the White Pine Weevil, *Pissodes strobi* (Peck) (Coleoptera: Curculionidae)

A. Abstract

Two techniques for sexing adults of the white pine weevil *Pissodes strobi* Peck are described. Both techniques are based on the external anatomy of the terminal segments of the abdomen as viewed with a dissecting microscope.

B. Introduction

Males and females of the white pine weevil (*Pissodes strobi* Peck) are almost identical externally, and there are no evident dimorphisms which can be used to rapidly determine sex. Morphological differences in the sizes of different insect parts presented by MacAloney (1930) are not reliable for precise sex determination. Observations by Hopkins (1911) showed that females had seven visible tergites, and males had eight. To determine the sex of the live adult of the white pine weevil, MacAloney (1930) proposed observing the dorsal part of the abdomen to determine the number of visible tergites. This technique requires opening the elytra, which can often lead to injury. In 1966, Harman and Kulman proposed a technique based on the anatomy of the anogenital vestibule. Although precise, this technique requires some dexterity and can also lead to internal injury to the insect when opening the posterior end of the abdomen.

During our study on the biology of the white pine weevil, we saw that other methods of sexing live adults could be used advantageously. We propose two methods for sexing the weevils, both requiring only observation of the external anatomy of the abdomen using a binocular microscope. Scanning electron micrographs were used to confirm our observations mode with the light microscope.

C. Materials and Methods

Weevil specimens were collected from white pine terminal leaders in plantations located near Saint-Luc-de-Champlain (46°30'N, 72°30'W), 25 km east of Trois-Rivières (Quebec), and near Sainte-Beatrix (46°13'N, 73°38'W), 25 km north of Joliette (Quebec). These were kept at 2°C on fresh branch sections in the laboratory.

For scanning electron microscopy, specimens were cleaned, dehydrated in an acetone series, critical point dried, mounted on stubs and sputter-coated with about 100Å of gold (Kapoor 1989). The specimens were examined and photographed using a Hitachi-520 scanning electron microscope.

D. Results

Technique A: Presence of membranous lobes. As mentioned by Hopkins (1911), males have eight visible dorsal tergites and the females have only seven. On tergites 6 and 7 of both sexes, pairs of membranous lobes are evident (Figures 5.1, 5.3, 5.5 and 5.6). By observing these lobes under a dissecting microscope, the sex of the animal can easily be determined. The weevil is held ventrally on the thumb and held in place with the index finger. The observation is done at low (X30) magnification. With an entomological pin, sternite 7 (last) is pulled out from the elytra so that the dorsal part of the abdomen becomes visible. In the male, no membranous lobes are visible on the last (eighth) tergite (Figures. 1 and 5). The first pair of membranous lobes on tergite 7 are not visible unless pressure is applied to the abdomen. In the female, the pair of membranous lobes are readily apparent on tergite 7; thus, two pairs are visible, one each on tergites 6 and 7 (Figures 3 and 6).

Technique B: Distal shape of the last sternite. This technique is based on morphological differences between the distal part of sternite 7 on both the male and female. As in the preceding technique, sternite 7 is pulled away slightly from the elytra. In the male, the edge of sternite 7 is thick and elevated in its medial portion (Figure 5.2). In the female, the sternite is thin, curved, and without any deformation in its medial portion (Figure 5.4).

We found these same characteristics in preserved adults of *Pissodes approximatus* Hopk. and *P. terminalis* Hopping, and believe that these techniques will be useful in sexing live adults of these species as well. In biological studies of the white pine weevil, it is often necessary to know the sex of the adult. Our observations, added to the other sexual differences shown by Hopkins (1911) and Harman and Kulman (1966), should provide rapid and accurate methods for sexing live adults of the white pine weevil.

Figures. 5.1-5.4. Light micrographs. 5.1, dorsal view of male abdomen - note the membranous lobes on tergites 6 and 7 at arrowheads (X30); 5.2, distal portion of sternite 7 of male abdomen - note the thickened and elevated medial portion at arrow (X60); 5.3, dorsal view of female abdomen - note the membranous lobes at arrowheads (X30); 5.4, distal portion of sternite 7 of the female abdomen (X60). Figures. 5.5-5.6. Scanning electron micrographs. 5.5, dorsal view of the male abdomen (X50); 5.6, dorsal view of the female abdomen (X50). Membranous lobes are indicated by arrowheads in both figures.

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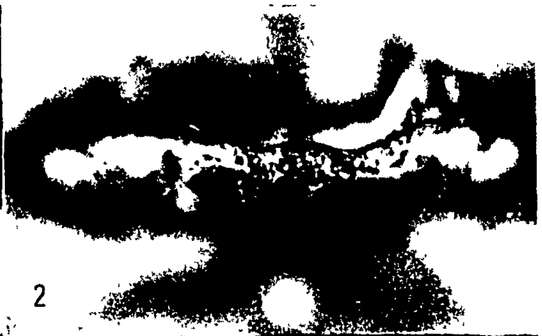

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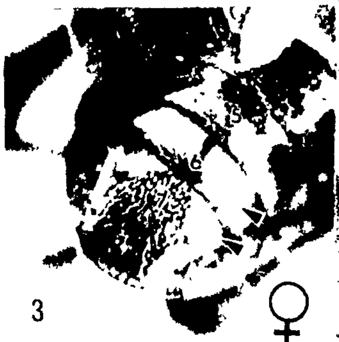

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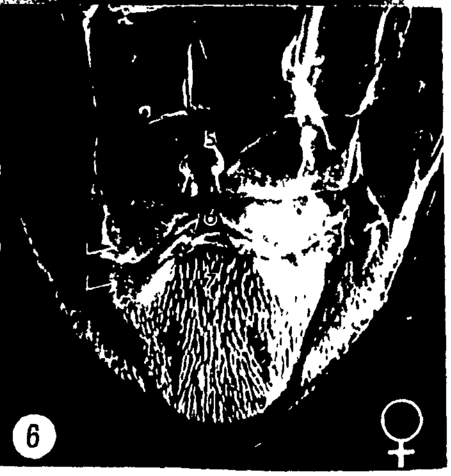

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CONCLUSION

The object of this study was to determine whether the white pine weevil fitness was affected by the quality of the bark of its host growing under different conditions. Field observations frequently reported that the host vigour was related to the tree's susceptibility weevil attacked.

Experiments demonstrated that white pine weevil development was affected by severe water stress imposed on larval development in cut leaders kept in dry conditions. Adult weight and the number of insects per leader were relatively unaffected when larval development occurred on living plants exposed to different watering regimes. However, the adult's feeding behaviour was affected by modifications of bark quality induced by different watering regimes and by previous insect attack.

As opposed to a number of subcortical insects, hydric stress does not improve weevil performance as measured by the number of insects per leader or adult mean weight. These results coincide with previous field observations indicating a preference of the white pine weevil for vigorous growing trees rather than those that are stressed and dying. Recent studies (R. L. unpublished data) have demonstrated that weevils emerging from vigorous trees had higher adult weights when compared with weevils from stressed trees growing under poor drainage conditions. The biological significance of this observation could be that, once the females have deposited their eggs under the bark of a host leader, the young larvae have to survive with a limited resource of a specific quality. Thus, the preference for living on vigourous trees could be partly related to the abundance of food for the development of the brood. Piskornik *et al.*

(1989) also observed that the hazelnut weevil, *Curculio nucum* L., prefers to feed on the largest nuts.

After visual stimuli attract weevils to a terminal leader (VanderSar and Borden (1977b,c), the chemical composition of the bark seems to play a major role in insect feeding performance. Our results with bark demonstrate that the adults are sensitive to chemical modifications induced by the growing conditions of plants, preferring to feed on bark from well hydrated plants over bark from a hydrically stressed one. This indicates that both sexes can also select vigorous plants based on chemical cues. Chemical analyses of major elements such as nitrogen, phosphorus and potassium did not explain the relationship between insect preference and tree treatments. However, unidentified chemical substances may play important roles in food discrimination. Adults were able to discriminate between bark from infested and intact leaders, indicating that insect attack may also modified bark chemistry. The biological significance of this behaviour could be to initially select trees where attack is starting, and later to avoid leaders where insects are present in large numbers under the bark. A similar phenomenon is reported by Piskornik (1989) with the hazelnut weevil, where beetles avoid feeding in nuts where previous feeding has occurred. Alfaro and Ying (1990) also indicate that weevils prefer to attack trees that have been previously attacked.

The feeding preference of adult weevils for two-year-old leader sections over the normally preferred one-year-old leaders is difficult to explain. Considering that the harvested bark was submitted to heat desiccation before use in feeding tests, it is possible that chemical substances normally present in the leader were destroyed, leaving other substances that influenced feeding behaviour.

Sound silviculture practices lead to plant trees on appropriate site to optimize tree growth. However, it appears that the white pine weevil is also selecting for these vigorous growing trees. Then, to reduce the impact of the weevil in plantations, only an integrated approach could help to reduce the impact of this pest. One avenue should be the possibility of planting trees expressing some resistance to the weevil. Plant breeders often select trees according to their growth capacity, but the resistance or tolerance to a pest is rarely considered. If phototropism and geotropism play a role in the attraction of the weevil to the uppermost part of the terminal leader, particular chemical substances inducing feeding and oviposition but also affecting larval development must be identified to increase our knowledge on the weevil-host relationship.

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