Robertson, J.L. 1979. Rearing the western spruce budworm. U.S. For. Serv. Washington, D.C. CANUSA pamphlet. 18pp.

Roelofs, W.L., and R.L. Brown. 1982. Pheromones and evolutionary relationships of Tortricidae. Ann. Rev. Ecol. Syst. 13: 395-422.

Roelofs, W.L., and A. Comeau. 1969. Sex pheromone specificity: taxonomic and evolutionary aspects in Lepidoptera. Science 165: 398-400.

Stehr, G. 1954. A laboratory method for rearing the spruce budworm, *Choristoneura fumiferana* (Clem.), (Lepidoptera: Tortricidae). Can. Entomol. 86: 423-428.

Response of *Trichogramma* sp. nr. *sibericum* (Hymenoptera: Trichogrammatidae) to age and density of its natural hosts, the eggs of *Rhopobota naevana* (Lepidoptera: Tortricidae)[1]

LI, S. Y. and D. E. HENDERSON

E. S. CROPCONSULT LIMITED, 2962 WEST 15TH AVENUE, VANCOUVER, B. C. V6T 3A3

CORRESPONDENCE: S. Y. LI, DEPARTMENT OF PLANT SCIENCE, UNIVERSITY OF BRITISH COLUMBIA, VANCOUVER, B. C., CANADA V6T 1Z4, TEL: (604)822-6916

ABSTRACT

Responses of an indigenous *Trichogramma* sp. nr. *sibericum* (Hymenoptera: Trichogrammatidae) to the age and density of eggs of the blackheaded fireworm, *Rhopobota naevana* (Hübner) (Lepidoptera: Tortricidae) were determined in the laboratory. The parasitoid wasp showed a significant ($P < 0.05$) preference for eggs 1-7-day-old over those 21-day-old. No significant differences ($P > 0.05$) in percentages of parasitized eggs, however, were found among groups of eggs below 7-day-old. At host egg densities below 20 per wasp, the number of eggs parasitized significantly ($P < 0.05$) increased with egg density, and tended to stabilize at densities above 30. The rate of parasitism decreased significantly ($P < 0.05$) with increased host egg density. Superparasitization occurred at densities of 5-10 host eggs, but was rarely observed at densities above 20 eggs. The mean number of progeny per wasp significantly ($P < 0.05$) increased with host density, whereas the clutch size (the number of parasitoid offspring per parasitized host) significantly ($P < 0.05$) decreased with an increase in host density.

INTRODUCTION

Although egg parasitic *Trichogramma* (Hymenoptera: Trichogrammatidae) species head the list of beneficial insects as biological control agents (Stinner 1977), no studies have been reported on using *Trichogramma* to control the blackheaded fireworm, *Rhopobota naevana* (Lepidoptera: Tortricidae), a major pest on cranberry in North America. However, the use of *Trichogramma* to control this pest may be realistic and possible because two species of *Trichogramma* have been discovered recently from natural fireworm populations in cranberry fields in British Columbia (Li et al. unpublished data). One of the two indigenous species, *Trichogramma* sp. nr. sibericum, showed a high affinity for fireworm eggs in the laboratory (Li *et al.* unpublished data.). If this fireworm-attacking *Trichogramma* can be successfully mass reared under laboratory conditions, field release for control of the fireworm may be realized.

Host age preference of *Trichogramma* towards a host is fundamental to a release program and is a critical factor in selection of an effective *Trichogramma* as a biological control agent (Marston and Ertle 1969; Schmidt 1970) because timing of a release is one of the most important factors influencing efficacy in the field. Thus, host age preference by *Trichogramma* must be determined before using the wasp in a biological control program. Knowledge of the relationship between host density and parasitism is also critical for both inundative releases in the field and mass rearing in the laboratory. In the present study, we report the effects under laboratory conditions of host age and density on parasitism of fireworm eggs by a field-collected *T.* sp. nr. *sibericum*. Our objectives were: (1) to determine which host egg stages the wasp prefers to parasitize; (2) to determine the relationship between host egg density and parasitization; and (3) to study the effect of host egg density on mean progeny per wasp and on the number of wasp offspring per parasitized host egg (clutch size).

MATERIALS AND METHODS

Parasitoids

Parasitized fireworm eggs were collected from an abandoned cranberry field in Richmond, near Vancouver, British Columbia. Cranberry leaves bearing the parasitized eggs were incubated on moist filter paper in clear plastic Petri dishes (50 by 9 mm) at 24 ± 2°C, 90±10% RH, and 16L:8D photoperiod in the laboratory. Eclosed females were used in the following experiments.

Host eggs

Field-collected second-generation adult fireworm females were permitted to lay their eggs on cranberry uprights in a cage at 24 ± 2°C, 50±10% RH, and 16L:8D photoperiod in the laboratory. The uprights in the cage were replaced daily. Fireworm eggs obtained from the cage were used as hosts in the following experiments.

General Methods

The experiments were conducted in the open laboratory at 24 ± 2°C and 50±10% RH. The fireworm eggs on cranberry leaves were placed in the Petri dishes (50 by 9 mm) lined with moist filter paper, which was watered daily to prevent the leaves from drying out.

In each of the following experiments, single female parasitoids were transferred into a Petri dish (50 by 9 mm) with fireworm eggs using a fine artist's brush, and were maintained in the Petri dish till their death. Following introduction, the wasps were immediately observed under a dissecting microscope. If the wasps did not examine any of host eggs (*i.e.,* measure the host volume by their antennae) within 5 min following introduction, they were discarded and replaced. Seven days following introduction of the wasps, the host eggs were microscopically examined to determine if they were unparasitized, parasitized or superparasitized. The parasitized eggs turned black when the parasitoids reached the prepupal stage of development, whereas unparasitized eggs remained yellow. Superparasitized eggs are those in which more than one *Trichogramma* offspring has developed from a single host. Superparasitism was determined by counting the wasp offspring through the clear chorion of the parasitized host egg.

Host age preference

In this choice test, four each of 1, 3, 5, 7 and 21-day-old host eggs laid on cranberry leaves, at two equal-aged eggs per leaf, were placed in the center of a Petri dish (50 by 9 mm). Single

Table 1

Effects of host egg density of blackheaded fireworm, *Rhopobota naevana*, on number of progeny and the clutch size of *Trichogramma* sp. nr. *sibericum*[1]

Host density	Progeny±SE	Clutch size±SE
5	7.60±0.31 b	1.52±0.06 a
10	11.80±0.73 ab	1.46±0.06 a
20	11.70±1.53 ab	1.05±0.03 b
30	14.20±1.98 a	1.06±0.03 b
40	14.10±1.55 a	1.10±0.07 b
50	13.90±1.92 a	1.03±0.02 b

1. Mean values followed by the same letters in the same column are not significantly different at the 5% level of Scheffé's F-test.

female parasitoids were introduced in the center of the 10 leaves, which bore a total of 20 variously aged fireworm eggs. Each Petri dish was a replicate, 50 replications were tested.

Host density

Single female wasps were exposed to 1-day-old fireworm eggs at different densities in the Petri dishes (50 by 9 mm). The host egg densities were 5, 10, 20, 30, 40 and 50 eggs divided equally on five cranberry leaves, respectively. Each Petri dish was a replicate and each host density was replicated 10 times. The data recorded were: the percentage of parasitization and superparasitization; the number of progeny per parasitoid; and the clutch size.

Data analyses

Percentage of parasitism was calculated as the numbers of parasitized eggs divided by total eggs exposed in each group in the experiments. Percentage of superparasitism was calculated as the numbers of superparasitized eggs divided by total parasitized eggs. The data were transformed as either arcsin $\sqrt{P}$ or $\sqrt{x+0.5}$ before ANOVA (Zar 1984), where P represents the percentage of parasitization or superparasitization and x is mean progeny per wasp or the clutch size. One-way ANOVA was used to estimate significances ($P < 0.05$). Significant differences were compared among host age groups or among host densities, and were separated by Scheffé's F-test of multiple contrasts at $P = 0.05$ level.

RESULTS

The age of the host egg had a significant effect ($F = 7.0$; $df = 4, 245$; $P = 0.0001$) on parasitism of fireworm eggs by the wasps (Fig. 1). The percentage of parasitization was significantly lower ($P < 0.05$) for 21-day-old eggs than 1-7-day-old eggs, suggesting that T. sp. nr. *sibericum* prefers to parasitize young fireworm eggs. Although parasitism varied from 61% to 72.5% among eggs

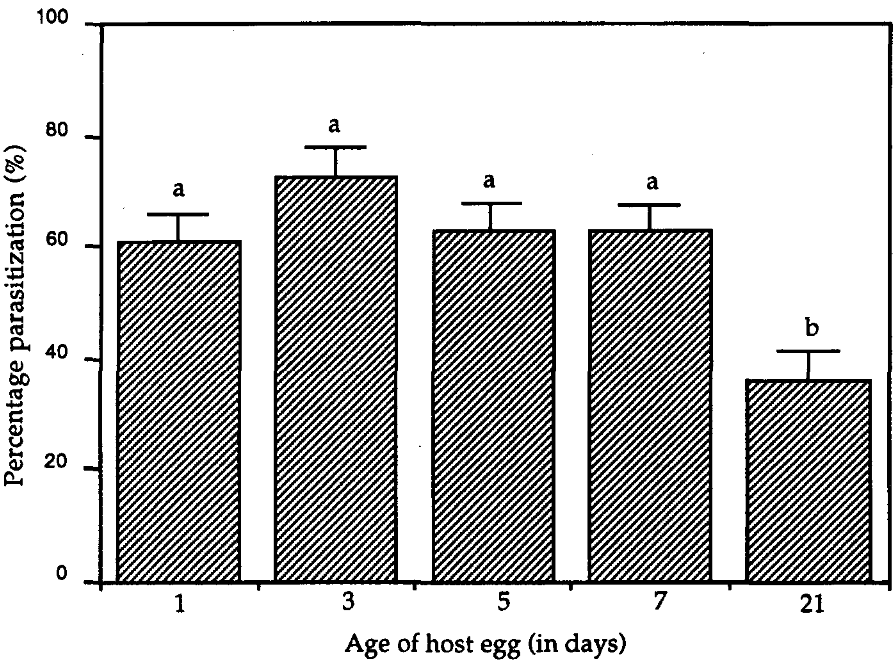

Figure 1. Effects of host age on parasitization of *Rhopobota naevana* eggs by an indigenous *Trichogramma* sp. nr. *sibericum*. Vertical bars indicate standard errors of mean parasitism. Bars with the same letters indicate that mean parasitism is not significantly different ($P > 0.05$; Scheffé's F-test) (Zar 1984).

aged from 1-7 days, no significant (P > 0.05) differences were found within this age group.

The number of parasitized fireworm eggs increased significantly (F = 6.0; df = 4, 54; P = 0.0002) with host egg density, and tended to stabilize at host densities higher than 30 eggs (Fig. 2: A). The maximum number of parasitized eggs was about 13, suggesting that females of the wasp had a limited supply of eggs. The percentage of parasitism significantly (F = 42.1; df = 4, 54; P = 0.0001) decreased with increased host egg density (Fig. 2: B). At a parasitoid/host ratio of 1/5, 100% of the host eggs were parasitized. However, only 30% of the eggs were parasitized at a ratio of 1/50. Superparasitization also significantly (F = 22.5; df = 4, 54; P = 0.0001) decreased as host density increased beyond 10 host eggs per wasp (Fig. 2: C). At high parasitoid/host ratios (1/5 - 1/10), 40-50% of the parasitized eggs were superparasitized, which was significantly higher (P < 0.05) than at low ratios (1/20 - 1/50).

The mean number of progeny produced per parasitoid at a host density of 5 eggs was significantly (P< 0.05) lower than at densities of 30 - 50 eggs (Table 1). At a host density of 30 eggs, the number of progeny reached its maximum of 14.2. Then the number tended to stabilize even though host density continued to increase. The clutch sizes at host densities of 5 - 10 eggs were significantly higher (F = 22.3; df = 4, 54; P = 0.0001) than those at higher densities of 20 - 50 eggs (Table 1).

DISCUSSION

Much research has been previously conducted on host-age selection by *Trichogramma* spp. (e.g., Marston and Ertle 1969; Pak et al. 1986). The relationships between a given *Trichogramma* and its host species may be different. Pak (1986) summarized six types of relationships between host age and parasitism by different combinations of *Trichogramma* species and their hosts. The observed effect of host age on parasitism of fireworm eggs in this study appeared to be Pak's type II-a: *i.e.*, reduced parasitism of the oldest host eggs. Female parasitoids may use physical (e.g., size, shape, texture, movement), physiological and/or chemical cues (e.g., kairomones) to recognize and parasitize their hosts (Arthur 1981; Pak *et al.* 1986). Hosts used in the present study were second-generation fireworm eggs. Because more than 80% of these eggs are in diapause (Fitzpatrick and Troubridge 1993), there may not be significant differences in physical and physiological between young and old eggs. Therefore, the wasp's preference for young eggs may be based on chemical cues. Vinson (1975) found a chemical factor present in *Heliothis virescens* F. (Lepidoptera: Noctuidae) eggs to be important in host acceptance by an egg-larval parasitoid, *Chelonus texanus* Cresson (Hymenoptera: Braconidae). A few studies have demonstrated that kairomones on moth scales play an important role in host-finding by *Trichogramma* (Lewis *et al.* 1971, 1975; Thomson and Stinner 1990). Whether fireworm eggs or scales of the adult moth contain such kairomones is unknown.

The parasitism of fireworm eggs by *T.* sp. nr. *sibericum* is host density dependent, i.e., an increase in host egg density leads to a reduction in the percentage of parasitized eggs as has been found by Hirose *et al.* (1976) and Morrison *et al.* (1978) with other species. Figure 2 C shows that the rate of superparasitism here decreases with an increase in host density. This is a common phenomena described by many researchers (e.g., Waage 1986, 1988). Wajnberg *et al.* (1989) showed that the control of superparasitism of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) by *Trichogramma maidis* Pintureau and Voegelé seems to be genetically determined. In this study, however, superparasitism at a host density of 5 eggs was 50%, whereas at a host density of 50 eggs it was 2.8%. Superparasitism of fireworm eggs by *T.* sp. nr. *sibericum* may be an example of adaptive reproductive strategy proposed by Strand (1988) and Waage (1988). Superparasitism is often viewed as a maladaptive mistake (Van Lenteren 1981). As long as a parasitoid egg deposited in a host still has a finite probability of survival in competition with a previously laid clutch, however, superparasitism may be advantageous (Bakker *et al.* 1985; Strand 1988; Waage 1988). In the present study, two adult *Trichogramma* often were eclosed successfully from single fireworm eggs. It would therefore be of prime interest to conduct experiments to determine the relationship between fitness per host and the clutch size of the parasitoid.

Although *T.* sp. nr. *sibericum* prefers to parasitize young eggs (Fig. 1), they still parasitized

21-day-old eggs at the rate of 36%. In order to obtain maximum efficacy as a control in the field, *Trichogramma* should be released within one week of egg deposition. The results, however, also suggest that releasing *Trichogramma* three weeks following egg deposition may still have a positive effect on the reduction of fireworm populations. The total fecundity per female *T.* sp. nr. *sibericum* observed in this study was lower than those reported previously with other species (Yu *et al.* 1984; Smith and Hubbes 1986; Hohmann *et al.* 1988). The low fecundity of the wasp reported here may be due to unfed adults with honey. Yu *et al.* (1984) found that fed *Trichogramma minutum* Riley with honey produced 6 times of eggs as much as unfed wasps. The

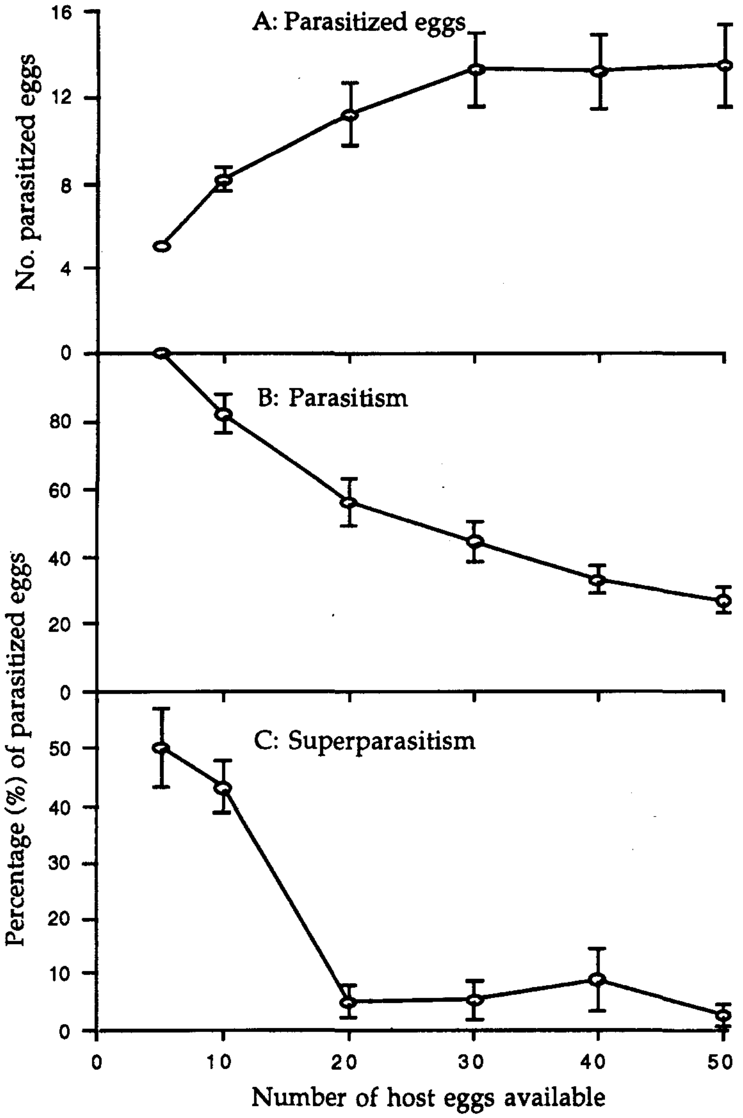

Figure 2. Effects of host egg density on the number of parasitized eggs (A), percentage parasitism (B), and percentage superparasitism (C) of *Rhopobota naevana* eggs by an indigenous *Trichogramma* sp. nr. *sibericum*. Vertical bars indicate standard errors of means.

findings that single female *T.* sp. nr. *sibericum* can parasitize about 13 fireworm eggs (Fig. 2: A) and that a negative relationship between host density and parasitism exists (Fig. 2: B), should be taken into account in both mass rearing this species in the laboratory and commercial release in the field.

ACKNOWLEDGMENTS

We are most grateful to J.H. Myers (University of British Columbia, Vancouver, B. C.) for allowing us to use her laboratory facilities for this study. We thank three anonymous reviewers for their helpful comments on the manuscript and R. Feng for field and laboratory assistance. Financial support was received from the Science Council of British Columbia in the form of an Industrial Postdoctoral Fellowship to the senior author, the National Research Council of Canada, British Columbia Cranberry Growers Association, and Ocean Spray Cranberries Incorporation.

NOTE

1. Paper presented at the 91th Annual Meeting of the Entomological Society of British Columbia. October 23, 1992, Simon Fraser University, Burnaby, B. C.

REFERENCES

Arthur, A. P. 1981. Host acceptance by parasitoids. pp. 97-120. In: D. A. Nordlund, R. L. Jones and W. J. Lewis (eds.). Semiochemicals, their role in pest control. Wiley, New York.

Bakker, K., J. J. M. Van Alphen, F. H. D. Van Batenburg, N. Van der Hoeven, H. W. Nell, W. T. F. H. Van Strien-Van Liempt and T. C. Turlings. 1985. The function of discrimination and superparasitization in parasitoids. Oecologia. 67: 572-576.

Fitzpatrick, S. M. and J. T. Troubridge. 1993. Fecundity, number of diapause eggs and egg size of successive generations of the blackheaded fireworm (Lepidoptera: Tortricidae) on cranberries. Environ. Entomol. 22: in press.

Hirose, Y., H. Kimoto and K. Hiehata. 1976. The effect of host aggregation on parasitism by *Trichogramma papilionis* (Hymenoptera: Trichogrammatidae), an egg parasitoid of *Papilio xuthus* (Lepidoptera: Papilionidae). Appl. Entomol. Zool. 11: 116-125.

Hohmann, C. L., R. F. Luck and E. R. Oatman. 1988. A comparison of longevity and fecundity of adult *Trichogramma platneri* (Hymenoptera: Trichogrammatidae) reared from eggs of the cabbage looper and the angoumois grain moth, with and without access to honey. J. Econ. Entomol. 81: 1307-1312.

Lenteren, J. C. Van. 1981. Host discrimination by parasitoids. pp. 153-179. In: D. A. Nordlund, R. L. Jones and W. J. Lewis (eds.). Semiochemicals, their role in pest control. Wiley, New York.

Lewis, W. J., A. N. Sparks and L. M. Redlinger. 1971. Moth odor: a method of host-finding by *Trichogramma evanescens*. J. Econ. Entomol. 64: 557-558.

Lewis, W. J., R. L. Jones, D. A. Nordlund and H. R. Gross. 1975. Kairomones and their use for management of entomophagous species: II. Mechanisms causing increase in rate of parasitization by *Trichogramma* spp. J. Chem. Ecol. 1: 349-360.

Marston, N. and L. R. Ertle, 1969. Host age and parasitism by *Trichogramma minutum* (Hymenoptera: Trichogrammatidae). Ann. Entomol. Soc. Am. 62: 1476-1481.

Morrison, R. K., S. L. Jones and J. D. Lopez. 1978. An unified system for the production and preparation of *Trichogramma pretiosum* for field release. Southw. Entomol. 3: 62-68.

Pak, G. A. 1986. Behavioral variations among strains of *Trichogramma* spp.: A review of the literature on host-age selection. J. Appl. Entomol. 101: 55-64.

Pak, G. A., H. C. E. M. Buis, I. C. C. Heck and M. L. G. Hermans. 1986. Behavioral variations among strains of *Trichogramma* spp.: Host-age selection. Entomol. exp. appl. 40: 247-258.

Schmidt, G. T. 1970. The effect of host development on parasitism and mortality of two pests attacked by *Trichogramma evanescens* (Hymenoptera: Trichogrammatidae). Ann. Entomol. Soc. Am. 63: 1319-1322.

Smith, S. M., and M. Hubbes. 1986. Isoenzyme patterns and biology of *Trichogramma minutum* as influenced by rearing temperature and host. Entomol. experi. & appli. 42: 249-258.

Stinner, R.E. 1977. Efficacy of inundative releases. Ann. Rev. Entomol. 22: 515-531.

Strand, M. R. 1988. Adaptive patterns of progeny and sex allocation by parasitic Hymenoptera. pp. 293-312. In: V. K. Gupta (ed.), Advances in parasitic Hymenoptera research. E. J. Brill, Amsterdam.

Thomson, M. S. and R. E. Stinner. 1990. The scale response of *Trichogramma* (Hymenoptera: Trichogrammatidae): variation among species in host specificity and the effect of conditioning. Entomophaga. 35: 7-21.

Vinson, S. B. 1975. Source of material in the tobacco budworm which initiates host searching by the egg-larval parasitoid, *Chelonus texanus*. Ann. Entomol. Soc. Am. 68: 381-384.

Waage, J. K., 1986. Family planning in parasitoids: adaptive patterns of progeny and sex allocation. pp 63-95. In: Waage, J.K. & D.J. Greathead (eds.), Insect parasitoids. Academic Press, London.

Waage, J.K., 1988. Understanding progeny and sex allocation in egg parasitoids. pp 283-294. In: Voegelé, J., J. K. Waage & J. C. Van Lenteren (eds.), *Trichogramma* and other egg parasites. INRA, Paris.

Wajnberg, E., J. Pizzol and M. Babault, 1989. Genetic variation in progeny allocation in *Trichogramma maidis*. Entomol. exp. appl. 53: 177-187.

Yu, D. S. K., E. A. C. Hagley and J. E. Laing. 1984. Biology of *Trichogramma minutum* Riley collected from apples in southern Ontario. Environ. Entomol. 13: 1324-1329.

Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N. J.

Variation in attack by Sitka spruce weevil, *Pissodes strobi* (Peck), within a resistant provenance of Sitka spruce

RENÉ I. ALFARO and M. HULME

FORESTRY CANADA, PACIFIC FORESTRY CENTRE, 506 WEST BURNSIDE ROAD, VICTORIA, BC, CANADA V8Z 1M5

C. YING

BRITISH COLUMBIA MINISTRY OF FORESTS, RESEARCH BRANCH, BASTION SQUARE, VICTORIA, BC, CANADA V8W 3E7

ABSTRACT

Variation in tree height and numbers of attacks by the Sitka spruce weevil (= white pine weevil), *Pissodes strobi* (Peck), were studied among families of a resistant provenance of *Picea sitchensis* (Bong.) Carr. at two Vancouver Island sites. At Sayward, after 14 years, the number of trees attacked varied by family from 0 to 80%. A significant association was found between the percentage of trees attacked in a family and the mean height of the family. Tall families were generally attacked more. At Fair Harbour (a clonal test), only 12% of the trees from the resistant provenance have been attacked after seven years, with all but one of the attacks concentrated on one of the two families tested. A multigenic or multicomponent basis for resistance is proposed and discussed.

INTRODUCTION

The Sitka spruce weevil (=white pine weevil), *Pissodes strobi* (Peck), is a major cause of failure in reforestation programs with Sitka spruce, *Picea sitchensis* (Bong.) Carr., in coastal British Columbia (B.C.), Washington, and Oregon (Furniss and Carolin 1977). The adults emerge from overwintering in early spring, and move to the 1-year old terminal shoot (leader) where the females lay eggs under the bark near the tip. If the weevil larvae become established, they move downwards, mining and consuming the phloem and eventually killing the leader (Silver 1968). In the literature, the successful colonization and destruction of the tree leader by *P. strobi* is generally called a weevil attack; this terminology is also used here. Repeated leader destruction causes height-growth loss and stem deformities which reduce the tree's value (Alfaro 1989a, 1992). Although the tree survives the attack, stunted trees are often suppressed by competing vegetation (Alfaro 1982). Other important tree species damaged by this insect are eastern white pine, *Pinus strobus* L., in eastern North America (MacAloney 1930), Engelmann spruce, *Picea engelmannii* Parry, and white spruce, *Picea glauca* (Moench) Voss., in central British Columbia and the prairie provinces (Stevenson 1967).

Analysis of several trials in British Columbia provided strong evidence of genetic variation