Predation and overwintering mortality of the white pine weevil, *Pissodes strobi*, in planted and seeded jack pine

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Predation by birds and insects and overwintering mortality of the white pine weevil, *Pissodes strobi* Peck, were examined in planted and seeded stands of jack pine (*Pinus banksiana* Lamb.) in northern Ontario to develop recommendations for management. No significant difference was found in weevil damage to the stand and in mortality of weevils due to natural enemies between planted and seeded stands. On average, 7.3 ± 0.3 (mean ± 1 SE) weevils emerged as adults from dead terminals. Birds consumed up to 6.4% of late-larval and pupal weevils in planted stands and up to 8.9% in seeded stands. More weevils emerged from screened than from unscreened leaders, indicating a significant mortality of larvae and pupae, presumably owing to insect predators and parasitoids and high density of pupae. Overwintering mortality of adult weevils was 92% in the planted and 76% in the seeded stand. Mammalian predation significantly reduced survival of overwintering weevils. Factors related to other silvicultural treatments, such as the presence of weeds, may be affecting the survival of *Pissodes strobi* and the susceptibility of *Pinus banksiana* stands to *Pissodes strobi* infestation. The manipulation of both mammalian predation and overwintering sites should be emphasized in the management of *P. strobi* in *Pinus banksiana* plantations.

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La prédation par les oiseaux et les insectes de même que la mortalité hivernale du charançon du pin blanc, *Pissodes strobi* Peck, ont été étudiées dans une plantation et un peuplement ensemencé de pin gris, *Pinus banksiana* Lamb., du nord de l'Ontario dans le but d'élaborer des recommandations d'aménagement. Aucune différence significative n'a pu être détectée entre la plantation et le peuplement ensemencé au niveau de l'impact des ennemis naturels et des dégâts causés par le charançon. En moyenne, $7,3 \pm 0,3$ (moyenne $\pm$ erreur standard) adultes ont émergé des flèches terminales mortes. L'impact des oiseaux sur les larves en fin de développement et les pupes était de 6,4 et 8,9% dans la plantation et le peuplement ensemencé respectivement. Le nombre de charançons ayant émergé de flèches terminales ensachées était supérieur à celui des flèches terminales non ensachées. Ceci laisse présumer que les prédateurs, les parasitoïdes et les fortes densités de pupes ont un impact significatif sur la mortalité des larves et des pupes. La mortalité hivernale des charançons adultes était de 92 et 76% dans la plantation et le peuplement ensemencé respectivement. La prédation par les petits mammifères diminua significativement la survie hivernale des charançons adultes. Certains facteurs reliés à d'autres activités sylvicoles telle que la présence d'herbacées pourraient influencer la survie des charançons et la susceptibilité des peuplements de *Pinus banksiana* aux infestations de *Pissodes strobi*. Les manipulations reliées à la prédation par les petits mammifères et aux sites de dormance hivernale devraient être accentuées lors de l'élaboration de programmes de gestion intégrée du *Pissodes strobi* dans les peuplements de *Pinus banksiana*.

[Traduit par la rédaction]

Introduction

Jack pine (*Pinus banksiana* Lamb.) is a common species in the Canadian boreal forest and one of the most important in lumber and pulp production. *Pissodes strobi* Peck (the white pine weevil) attacks several species of pine and spruce throughout North America, causing terminal shoot destruction and thus reducing timber value. Most studies, however, have focused on eastern white pine (*Pinus strobus* L.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.). *Pinus banksiana* was originally cited as an occasional host of *Pissodes strobi* (Taylor 1929), but recent reports show attack rates over 30% (Canadian Forest Service 1987) and a reduction of 13% in the commercial value of mature stands in northern Ontario (Davidson 1991).

Stand conditions greatly influence attack and development of *Pissodes strobi* (Sullivan 1961). Silvicultural treatments create different environmental conditions for weevil development and its natural enemies. Reforestation technique (hand planting or aerially seeding) may result in differences in density and spatial pattern of host trees. It can also contribute to differences in microhabitat conditions between exposed and shaded stands or patches, with consequent differences in temperature and humidity that affect all stages of weevil development. In addition, the management of stands may also affect the abundance and diversity of weevil predators. Treatment of slash, for instance, may result in an increase in the abundance of some species of small mammals (e.g., Larson et al. 1986).

The biology, behaviour, and life tables of *Pissodes strobi* are well documented for *Pinus strobus* (Wallace and Sullivan 1985), although essentially no information is available on similar patterns in *Pinus banksiana*. Studies on the biology and behaviour of *Pissodes strobi* emphasize the effects of weather and physical attributes of host trees (Sullivan 1959, 1960, 1961; Wallace and Sullivan 1985). Life tables show that the main mortality factors include intraspecific competition of larvae, natural enemies, pitch drowning of larvae and pupae, and abiotic elements acting against overwintering adults (Dixon and Houseweart 1982).

The biotic mortality factors are mainly insect predators and parasitoids (Alfaro and Borden 1980; Dixon and Houseweart 1982; Hulme 1990), although Taylor (1930) has shown that bird predation may also play an important role in decreasing weevil numbers. Birds forage mainly on late

larvae and pupae, thus do not prevent damage in leaders already infested, but help to decrease the subsequent adult population (Szuba and Pinto 1991). Small mammals are expected to forage mainly on overwintering adult weevils in the duff layer, and probably contribute to the already high overwintering mortality of weevils. This could be important to decrease the adult population and the resulting damage to plantations.

In our study, we (*i*) examine selected mortality factors of *Pissodes strobi* in *Pinus banksiana*, such as predation by birds and insects and overwintering mortality; (*ii*) compare mortality of *Pissodes strobi* in hand planted and aerially seeded stands; and (*iii*) survey birds and small mammals in weevil-infested *Pinus banksiana* stands to identify potential predator species and estimate their abundance.

Materials and methods

Study area, stand characteristics, and weevil damage

The study was conducted in young *Pinus banksiana* plantations in the southern boreal forest, approximately 30 km south of Gogama (47°31′N; 81°40′W), Ont., between June 1991 and September 1992. Ten weevil-infested stands were used in the study, five hand planted and five aerially seeded. Stands 1.5–3.0 m in height were selected because they were expected to have the greatest incidence of weevil damage in the Gogama District (Parton 1988).

Stands were described in terms of spatial pattern, density, and height of trees, and percent weevil damage. Length (from the tip to the end of the previous year's growth) and diameter (at the end of the previous year's growth) of weevil-killed leaders were measured after clipping. The spatial pattern and density of *Pinus banksiana* were estimated for each stand using *T*-square sampling on 50 points randomly selected along a transect. This method provided a relatively unbiased estimate of stand density when the trees were clumped (Krebs 1989). Using the *T*-square method, we tested the hypothesis of a random spatial pattern of *Pinus banksiana* and estimated density and its confidence limits. The height of the trees and length and diameter of killed terminals were measured for the 10 stands. Two-level nested ANOVA was conducted on log-transformed data to test for differences in these variables between planted and seeded stands and within stands of the same type of reforestation. A *t*-test was conducted on arc sine transformed data to test for differences in percentage of trees damaged by weevils between planted and seeded stands.

Mortality of weevils caused by birds and insects

To examine mortality of weevils caused by bird predation, 572 terminals killed by weevils were randomly collected in five planted (278 leaders) and five seeded (294 leaders) stands after emergence was complete in the fall of 1991. The number of emergence holes and pupal chambers were counted for each leader. The number of emergence holes was considered to represent the number of weevils that successfully complete development and emerged as adults. Pupal chambers excavated by birds (the bark was torn in a manner characteristic of birds; Taylor 1929) were recorded as weevils eaten by birds, while those without emergence holes or signs of disturbance by birds were considered as pupae killed by mortality factors other than bird predation. Thus, the number of pupal cells excavated by birds included both healthy and dead or parasitized weevils, as these could not be differentiated after the cells had been opened. The percentage of killed leaders showing signs of bird predation on the bark was calculated for each stand and the percentage of pupae eaten by birds was calculated relative to the total number of pupal chambers.

To examine mortality caused by invertebrates, 10 exclusion cages (small mesh screen that excluded insects) were placed over infested leaders selected randomly in three planted stands (total 30 cages) in early June 1991. In June 1992, a similar procedure was followed in a dense and an open patch of three seeded stands; in this case, 15 exclusion cages were placed in each patch (total of 90 cages). Dense and open patches were considered in seeded stands because the density of trees was thought to create different conditions of shade that would affect weevil development (Graham 1918; Sullivan 1961). Cages were removed in late September and the leaders were clipped for examination. Control leaders (unscreened) were also collected in the same stands and patches, and the number of emergence holes were counted for both the control and screened leaders. Those leaders that showed bird predation were not considered as controls for this analysis because the cages also excluded birds. Dixon and Houseweart (1982) showed that mortality of weevil eggs, larvae and pupae caused by a number of factors was similar in screened and unscreened leaders, with the exception of natural enemies. These authors showed, however, that the density of weevil pupae (crowding) appeared as a new mortality factor in screened leaders. Therefore, the difference between the number of emergence holes in screened and unscreened leaders in our study, would reflect mortality due to both insect predators and parasitoids and crowding of pupae.

Because the number of emergence holes did not follow a normal distribution, a *G*-test was conducted to test for independence between the frequency of emergence holes (and pupal chambers) and the type of reforestation. Replicated tests of goodness of fit were used to test the number of emergence holes in control and screened leaders against a 1:1 hypothesis. A *t*-test was conducted on arc sine transformed data to test for differences in the percentage weevils eaten by birds on weevil-killed terminals, and in the percentage of weevil-killed leaders showing bird predation between seeded and planted stands.

Overwintering mortality

To quantify overwintering mortality of *Pissodes strobi*, 15 exclusion cages for small mammals were set in a line (15 m apart) in one planted and one seeded stand in late October 1991. An exclusion cage consisted of an aluminum ring (20 cm diameter, 12 cm deep) covered on top with a screen (7 × 7 mm mesh) and inserted flush with the ground. Control cages (similar rings without screen) were set under the same tree approximately 0.5 m apart from the exclusion cages. Cages were placed at less than 20 cm from tree boles, in the area where weevils naturally overwinter (Dixon et al. 1979).

Eight adult weevils were placed in each cage, and an aluminum screen (1 × 1 mm mesh) was placed on top of both the control and exclusion cages to keep the weevils inside the cages until the weather was consistently cool enough for them to find their own natural overwintering sites in the duff. A small branch of fresh *Pinus banksiana* foliage was placed inside each cage to provide food until the weevils had gone into the duff. The fine mesh screen was removed from all cages in late November, and the cages were left with natural snow cover and environmental conditions until the following spring. In March, 3–4 weeks before emergence, a black funnel (30 cm diameter) was inverted over the top of each cage to collect emerging weevils. Funnels were checked every 1–3 days to ensure that they remained in the right position so that weevils could not escape. During this period, funnels were periodically removed for short periods of time (10–15 min, on cold days, and with an observer controlling) to allow ventilation. The overwintering weevils walked up the sides of the funnel into a clear plastic cup where the total number of emergent weevils per cage was recorded.

Because the frequency of surviving weevils was not normally distributed, *G*-tests with Williams' correction were conducted to test for independence between the number of surviving weevils in the control and screened cages.

Abundance of birds and small mammals

To identify potential predacious birds, surveys were conducted in three planted and three seeded stands. Birds were counted by the same observer, along four parallel transects (150 m long and

TABLE 1. The height of trees (mean ±1 SE), length and diameter of weevil-killed leaders, density and spatial pattern of *Pinus banksiana*, and percent damage by *Pissodes strobi* in five planted and five seeded stands of *Pinus banksiana* in northern Ontario during 1992

Type of reforestation	Stand	Height (cm)	Length (cm)	Diameter (mm)	Density (trees/ha)[a]	Spatial pattern[b]	% damage
Planted	1	173±5	58.5±1.0	15.8±0.2	3660 (2646–5935)	Aggregated[†]	23.9
	2	225±6	63.1±1.2	17.4±0.2	2325 (1771–3383)	Aggregated[‡]	7.8
	3	231±7	62.6±0.9	15.9±0.2	2547 (2066–3321)	Aggregated*	9.9
	4	244±6	60.9±1.0	15.5±0.2	1735 (1552–1967)	Regular[‡]	7.8
	5	217±7	63.1±1.3	15.9±0.2	2821 (2298–3652)	Random	10.5
Seeded	1	189±9	61.0±1.3	16.3±0.2	4760 (3232–9025)	Aggregated[‡]	12.3
	2	167±6	61.1±0.9	15.7±0.2	4370 (2888–8976)	Aggregated[‡]	12.3
	3	251±7	57.8±0.9	15.6±0.2	4649 (3491–6958)	Aggregated[‡]	16.9
	4	266±8	59.5±1.0	15.6±0.2	3273 (2444–4954)	Aggregated[‡]	16.1
	5	219±8	60.6±0.8	15.0±0.1	2899 (2098–4692)	Aggregated[‡]	12.6

[a]The values in parentheses are 95% confidence limits.

*, $P < 0.05$, [†], $P < 0.025$, [‡], $P < 0.005$.

TABLE 2. The number of weevil emergence holes (mean ±1 SE) and pupal chambers per weevil-killed leader, the percentage mortality of pupae and percentage pupae eaten by birds in weevil-killed leaders in five planted and five seeded stands of *Pinus banksiana* in northern Ontario during 1991

Type of reforestation	Stand	No. of leaders analyzed	No. of emergence holes per leader	No. of pupal chambers per leader	Mortality of pupae (%)	Pupae eaten by birds (%)
Planted	1	69	7.3±1.0	17.1±1.7	54.3	7.0
	2	58	7.8±0.8	20.5±1.5	61.2	11.9
	3	46	6.0±0.8	15.9±1.5	61.9	13.2
	4	52	6.6±0.7	15.4±1.6	52.5	0.1
	5	53	11.0±1.5	20.4±2.1	47.9	0.1
Mean		278	7.8±0.5	17.9±0.8	55.4	6.4
Seeded	1	66	9.4±1.0	23.0±2.0	55.9	9.1
	2	64	8.2±1.1	17.4±1.8	48.3	1.3
	3	55	5.6±0.6	16.5±1.4	65.6	20.2
	4	52	3.6±0.4	12.1±1.4	63.6	7.6
	5	57	6.9±1.0	15.6±1.5	55.9	7.9
Mean		294	6.9±0.4	17.2±0.8	56.9	8.9
Average		572	7.3±0.3	17.5±0.6	56.1	7.7

50 m apart) in each stand, between 1 and 8 August 1991, from 07:00 to 09:30. Observations were only made on sunny days when cloud cover was <75%. Each transect was walked once by the observer with three stops (50 m apart) of 10 min. At each station, birds were identified according to sight and song. The relative abundance was estimated as the number of birds recorded per unit of distance

The relative abundance of small mammals was estimated in the same stands between 31 July and 11 August 1991. Small mammals were captured using Victor snap traps because these are more likely to capture most of the small mammal species in young *Pinus banksiana* plantations than either live or pitfall traps (Innes and Bendell 1988). Four parallel trap lines, 50 m apart, were set in each stand. Trap lines consisted of 10 stations with 15 m between stations and two traps per station; this number was considered sufficient according to Innes and Bendell (1988). The traps operated for five nights to produce a sampling effort of 400 trap nights in each stand (total effort = 2400 trap nights). The traps were baited with peanut butter (rebaited as required) and checked daily. Captured animals were frozen for later identification and their relative abundance was estimated as the number captured per 100 trap nights.

A Wilcoxon–Mann–Whitney test was conducted to test for differences in the abundance of birds and small mammals between planted and seeded stands.

Results

Stand characteristics and weevil damage

Seeded stands were denser than planted stands ($t = 2.78$, $P < 0.05$, df = 8). The spatial pattern of *Pinus banksiana* was strongly clumped in all seeded stands whereas it varied in planted stands (Table 1).

The mean length of weevil-killed leaders was not significantly different between planted and seeded stands ($F = 0.84$, $P > 0.25$) or within stands with the same type of reforestation ($F = 0.66$, $P > 0.25$) (Table 1). The height of the trees and the diameter of weevil-killed terminals were similar between planted and seeded stands ($F = 0.07$, $P > 0.5$ and $F = 1.34$, $P > 0.25$, respectively), but they were significantly different within *Pinus banksiana* stands of the same type of reforestation ($F = 21.12$ and $F = 3.51$, $P < 0.001$, respectively). In summer 1992, the percentage of trees damaged by weevils was similar between planted and seeded stands ($t = 1.76$, $P > 0.1$) (Table 1).

Successfully emerged weevils

The number of weevils emerging from each killed terminal ranged from 0 to 45 in the planted stands and from 0 to 49 in the seeded stands. The frequency of emergence
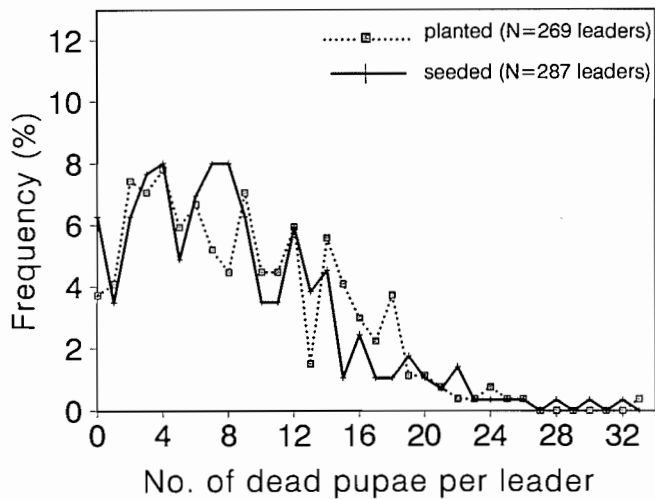
FIG. 1. Percent frequency of weevil emergence holes per weevil-killed leader of *Pinus banksiana* in northern Ontario.
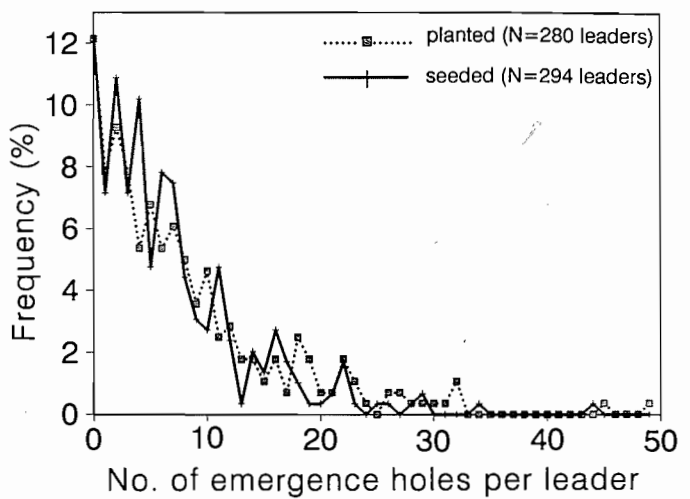

FIG. 2. Percentage frequency of weevil pupal chambers per weevil-killed leader of *Pinus banksiana* in northern Ontario.

holes was independent of the type of reforestation ($G = 17.77$, $P > 0.25$). The pooled data showed an average of 7.3 ± 0.3 (mean ± 1 SE) emergence holes per weevil-killed terminal (Table 2). Of the killed leaders, 12% had no emergence holes and 69% had less than eight holes per leader (Fig. 1).

The number of pupal chambers ranged from 0 to 54 per weevil-killed leader in the planted stands and from 0 to 62 in the seeded stands (Table 2). On average, 56% of the pupae population did not emerge (55% in planted and 57% in seeded stands). The number of pupae killed by mortality factors other than bird predation ranged from 0 to 33 per weevil-killed leader in planted stands and from 0 to 32 in seeded stands. Over half of the leaders killed by weevils (52%) contained two to nine pupae which had failed to emerge (Fig. 2). The frequency of unemerged pupae was independent of the type of reforestation ($G = 17.15$, $P > 0.25$). In 3% of the leaders, no pupal chambers were observed suggesting that these weevils died as larvae after killing the leaders.

Mortality of weevils caused by birds, insects, and crowding

Birds apparently ate up to 8% of the weevil pupae available in weevil-killed terminals of a stand, ranging between 0.1 and 13.2% in the planted and between 1.3 and 20.2% in the seeded stands (Table 2). Although the percentage of pupal cells stripped by birds was higher in the seeded than in the planted stands, it was not significant ($t = 0.84$, $P > 0.5$). In the planted stands, 1.9–43.5% of the weevil-killed leaders showed signs of bird predation on the bark while 9.4–34.8% of the leaders showed bird predation in the seeded stands. The percentage of killed leaders showing signs of bird predation was similar between stands with different types of reforestation ($t = 0.64$, $P > 0.2$). Birds removed 27% of the pupae available on explored leaders. The percentage of pupae eaten by birds in a stand may be predicted from the percentage of leaders in the stand showing signs of bird predation ($R^2 = 0.689$, $N = 10$) (Fig. 3).

More weevils emerged from screened than from open leaders, indicating a significant mortality of weevils, presumably owing to insect predators or parasitoids and crowding of pupa weevils (Table 3). In both the planted and seeded stands, the number of emergence holes in screened and open leaders was different from a 1:1 hypothesis (planted: $G = 8.79$, $P < 0.05$; seeded dense patches:
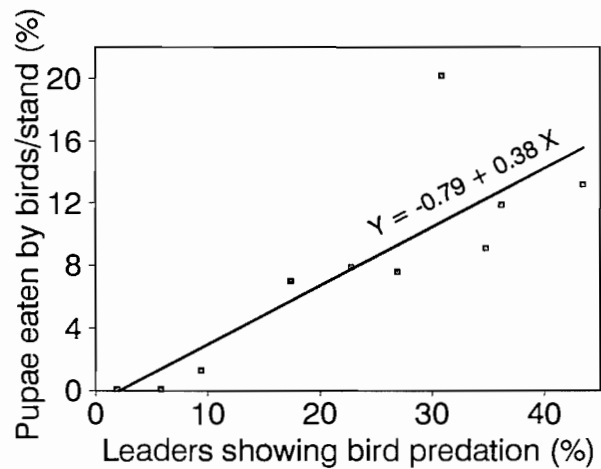

FIG. 3. Percentage pupae eaten by birds in weevil-killed leaders as a function of the percentage of weevil-killed leaders stripped by birds in 10 *Pinus banksiana* plantations in northern Ontario.

$G = 22.58$, $P < 0.001$; seeded open patches: $G = 26.63$, $P < 0.001$).

Overwintering mortality

More weevils survived the winter in screened than in open cages ($G = 7.75$, $P < 0.01$) and in the seeded than in the planted ($G = 12.92$, $P < 0.001$) stand. A total of 102 weevils (21%, $N = 480$) survived the winter in the cages, 35 (15%, $N = 240$) in the planted and 67 (28%, $N = 240$) in the seeded stand. In the planted area, 10 weevils (8%, $N = 120$) survived in open cages while 25 (21%, $N = 120$) survived in screened cages. In the seeded stand, 27 (22.5%, $N = 120$) weevils survived in open and 40 (33%, $N = 120$) in screened cages. Total overwintering mortality (open cages) was 92% in the planted and 78% in the seeded stand. Based on results obtained from the exclusion cages, 13% and 11% of the total mortality was caused by small mammal predation.

Abundance of birds and small mammals

A total of 31 species of birds was recorded (21 in the planted and 23 in the seeded stands), of which five were potential predators of late-larval and pupal weevils because they could remove the bark to forage for insects (Table 4). During the study, 363 birds were counted, 182 (5% were potential preda-

TABLE 3. Number of emergence holes per weevil-killed leader in control and screened terminals, calculated dead weevils per leader, and percentage mortality caused mainly by insect predators and parasitoids and crowding of pupae in planted stands and in open and dense patches of seeded *Pinus banksiana* in northern Ontario

Type of reforestation	Stand	Patch	No. of emergence holes/leader		Dead weevils per leader	% mortality
			Screened	Control		
Planted	1	—	12.2	7.7	4.5	22.6
	2	—	21.7	7.9	13.8	46.6
	3	—	12.0	6.7	5.3	28.3
Seeded	1	Dense	30.6	3.8	26.8	77.9
		Open	12.4	3.4	9.0	57.0
	2	Dense	10.7	8.7	2.0	10.3
		Open	20.3	11.8	8.5	26.5
	3	Dense	17.8	2.7	15.1	73.7
		Open	29.3	1.0	28.3	93.4

TABLE 4. Main food, foraging technique, and abundance of bird species surveyed in planted and seeded stands of *Pinus banksiana* in northern Ontario

Species	Main food[a]	Foraging technique[b]	No. of birds/1800 m	
			Planted	Seeded
Tyrannus tyrannus (eastern kingbird)	In	Ae	6	0
Vireo olivaceus (red-eyed vireo)	In	Fo	14	15
Zonotrichia albicollis (white-throated sparrow)	In	Gr	66	62
Corvus corax (northern raven)	Om	Gr	6	10
Empidonax minimus (least flycatcher)	In	Ho	7	7
Empidonax alnorum (alder flycatcher)	In	Ae	7	0
Perisoreus canadensis (grey jay)	Om	Gr	1	2
Bombycilla sp. (unidentified waxwing)	In–Be	Fo	9	5
Cyanocitta cristata (blue jay)	Om	Gr	1	7
Colaptes auratus (common flicker)	In	Gr–Ba	4	11
Catharus guttatus (hermit thrush)	In	Gr	3	3
Turdus migratorius (American robin)	In	Gr	1	0
Carduelis tristis (American goldfinch)	Se	Fo	0	1
Parus stricapillus (black-capped chickadee)	In	Fo	10	0
Sitta sp. (unidentified nuthatch)	In	Ba	1	2
Falco sparverius (American kestrel)	Bi	Ae	3	0
Chordeiles minor (common nighthawk)	In	Ae	0	3
Archilochus colubris (ruby-throated hummingbird)	Ne	Ho	3	0
Dendroica pinus (pine warbler)	In	Ba	1	2
Vermivora celata (orange-crowned warbler)	In	Fo	0	1
Junco hyemalis (slate-colored junco)	Se	Gr	0	6
Dendroica coronata (yellow-rumpled warbler)	In	Fo	0	3
Mniotilta varia (black-and-white warbler)	In	Ba	0	1
Dendroica pensylvanica (chestnut-sided warbler)	In	Fo	2	2
Passerculus sandwichensis (savannah sparrow)	In	Gr	9	0
Nuttallornis borealis (olive-sided flycatcher)	In	Ae	0	6
Melospiza lincolnii (Lincoln's sparrow)	In	Gr	0	5
Geothlypis trichas (common yellowthroat)	In	Fo	2	4
Picoides villosus (hairy woodpecker)	In	Ba	1	0
Wilsonia canadensis (Canada warbler)	In	Ne	0	1
Vermivora peregrina (Tennessee warbler)	In	Fo	0	1
Unidentified woodpeckers	In	Ba	2	2
Unidentified warblers	In	Fo–Ba	14	12
Unidentified birds			8	11

NOTE: Information is derived from Ehrlich (1988).
[a]In, insects; Om, omnivore; Se, seeds; Be, berries; Ne, nectar; Bi, birds.
[b]Fo, foliage; Gr, ground; Ho, hover; Ae, aerial; Ba, bark.

TABLE 5. The abundance of birds and small mammals in three planted and three seeded stands of weevil-infested *Pinus banksiana* in northern Ontario in summer 1991

Type of reforestation	Stand	No. of birds/ 150 m	No. of small mammals/ 100 trap nights
Planted	1	12.75	2.75
	2	19.75	8.25
	3	12.75	2.25
Seeded	1	21.50	3.75
	2	14.00	2.25
	3	10.75	2.00

TABLE 6. Number of small mammals captured per 100 trap nights in planted and seeded stands of weevil-infested *Pinus banksiana* in northern Ontario

Species	Planted	Seeded
Sorex cinereus (masked shrew)	1.58	0.42
Blarina brevicauda (short-tailed shrew)	0.08	0
Peromyscus maniculatus (deer mouse)	1.17	1.50
Zapus hudsonian (meadow jumping mouse)	0.17	0.17
Napaeozapus insignis (woodland jumping mouse)	0	0.08
Phenacomys intermedius (heather vole)	0.25	0.25
Microtus pennsylvanicus (meadow vole)	0.42	0
Clethrionomys gapperi (Gapper's red-backed vole)	0.67	0
Eutamias minimus (least chipmunk)	0.08	0.25

tors of weevils) in the planted and 185 (10% were potential predators) in the seeded areas (Table 5). The abundance of birds was similar between planted and seeded stands (Wilcoxon–Mann–Whitney, $P > 0.5$).

Nine species of small mammals were caught during the trapping period, eight in the planted and six in the seeded stands (Table 6). Of these species, three (*Sorex cinereus* Kerr, *Blarina brevicauda* (Say), and *Peromyscus maniculatus* (Wagner)) are expected to feed on adult weevils during the winter. A total of 85 individuals was captured during the study, 53 in the planted and 32 in the seeded stands (Table 5). Total abundance of small mammals was similar between the planted and seeded stands (Wilcoxon–Mann–Whitney, $P > 0.2$); however, more shrews were captured in the planted than in the seeded stands (Wilcoxon–Mann–Whitney, $P = 0.05$). A total of 29% of the traps were placed beside logs, and 51% of the small mammals were captured in those traps.

Discussion

Most of the terminals killed by weevils had few emergence holes, which suggests that the weevils died as larvae and pupae. The number of emergence holes per leader estimated in this study was lower than that reported by Dixon and Houseweart (1982) in *Pinus strobus* (12 weevils/leader), and approached those observed by Davidson (1991) in planted (7.0, 7.8, and 14.1 weevils/leader) and seeded (8.5 and 9.3 weevils/leader) *Pinus banksiana* stands. This suggests that *Pinus banksiana* leaders are smaller than *Pinus strobus* and can support fewer weevils.

Exclosures are widely used to examine predation in mammal–insect (e.g., Churchfield et al. 1991), bird–insect (e.g., Sanders 1985), insect–weevil (e.g., Dixon and Houseweart 1982; Hulme 1990), and mammal–weevil (e.g., Andersen and Folk 1993) interactions. According to Dixon and Houseweart (1982), differences in mortality between screened and unscreened leaders are mainly due to natural enemies of larvae and pupae or high density of pupae. These two factors were not separated in our study because the focus was on comparing mortality between stands, not on developing detailed life tables for *Pissodes strobi*.

We assumed that the number of weevil eggs was similar in both control and screened leaders when leaders were caged. In early June 1991–1992, when cages were placed, more than 78% of the *Pinus banksiana* showed oviposition punctures with a mean of 25 oviposition punctures per leader (maximum mean reached 27), and a mean of 29 eggs per puncture (maximum reached 32) (Applejohn 1993). Cages had to be placed on the leaders after the weevils had oviposited

and natural enemies emerged (for those that overwinter in the leaders) but before the natural enemies had oviposited. For example, *Lonchaea corticis* Taylor, a primary insect predator of *Pissodes strobi*, overwinters in the leader and its emergence peak closely corresponds with peak oviposition by *Pissodes strobi* (Taylor 1929). Because leaders were caged at peak oviposition by the weevils, and *L. corticis* oviposition occurs when larvae are consolidating the feeding ring (Alfaro and Borden 1980), we expect most of the insect predators and parasitoids were successfully excluded.

Insects are the main source of food for most bird species recorded in young *Pinus banksiana* (Table 4). Some of these species forage on the ground or foliage and, therefore, could potentially feed on adult weevils during the spring and fall. Others remove the bark of trees to feed on insects underneath, and they would have a more significant impact on weevils during the larval and pupal stage in the summer months. The mean percentage of weevil-killed leaders excavated by birds in our study (23%) was lower than the 38% reported by Taylor (1929) in *Pinus strobus*. On the other hand, the regression of the percentage of leaders excavated by birds versus the percentage of pupae eaten by birds calculated in our study is similar to that obtained from data provided by Taylor (1929, p. 196) ($Y = -1.827 + 0.478X$, $R^2 = 0.683$, $N = 19$). According to our equation, birds must exploit at least 35% of the weevil-killed leaders in a stand to kill 10% of the weevil pupae. Taylor (1929) considered birds to be one of the chief biological factors in the natural control of *Pissodes* and reported an average of 17.6% of late larvae and pupae killed by birds in *Pinus strobus* at different localities. In contrast, we found only 7.7% of pupal cells disturbed by birds in *Pinus banksiana*, suggesting possible differences in the composition of the bird community or in the abundance of some bird species. Specifically, we recorded relatively few woodpeckers and nuthatches (Table 4). Predation by birds was variable among stands which might be linked to the type of habitat surrounding the young stands. Appropriate management to increase the abundance of some species of insectivorous birds may increase the levels of predation on *Pissodes strobi*. Leaving old stands around young plantations, for instance, may encourage cavity nesters such as woodpeckers.

Winter mortality of *Pissodes strobi* was higher than that reported in previous studies in *Pinus strobus* (Taylor 1930; Sullivan 1961; Dixon and Houseweart 1982). Funnels that

collected emergent weevils from cages were placed very early in the spring and checked often; thus, it is unlikely that our technique missed weevils emerging during the spring. It is possible, however, that some weevils could eventually have escaped and that the total overwintering mortality could have been overestimated. The number of weevils placed in the cages does not seem to be high enough to add any new density-dependent mortality factors. In nature, overwintering weevils are generally separated from each other by more than 1 cm (Dixon et al. 1979); and in the cages, there was a surface of 39 cm^2 per weevil available.

Because the overwintering mortality of adult weevils is crucial to subsequent infestations, the manipulation of both overwintering sites and mammalian predation should be emphasized in the management of this pest. *Pissodes strobi* overwinters in the needle duff at the interface between the wet and dry litter (Wallace and Sullivan 1985). Winter mortality of insects by inoculation of ice crystals has been related to high moisture content of overwintering sites (Danks 1978). The needle duff in *Pinus banksiana* is shallower than that in *Pinus strobus*, and this may result in duff with a high moisture level that could facilitate ice crystallization. It would seem that the depth of the duff may be an important factor influencing overwintering survival of weevils, and that a shallower duff may increase overwintering mortality. Removing pine litter from under host trees, for instance, might increase mortality of weevils by altering the overwintering sites, as suggested by Dixon et al. (1979). Taylor (1929) did not consider mammalian predation on overwintering weevils as a factor of much importance, arguing that weevils hibernate in the dense needle duff in *Pinus strobus* stands and would be less accessible to small mammals than other larvae and pupae found in the soil. We found that mammalian predation significantly increased mortality of adult *Pissodes strobi* in *Pinus banksiana* during winter. Studies on acorn weevils also showed that the presence of small mammals (especially *Blarina brevicauda* and *Peromyscus maniculatus*) reduced survival of overwintering adult weevils, having a positive effect on oak populations (Andersen and Folk 1993). Leaving fallen logs in the stands during site preparation, for instance, might increase the abundance of mammalian predators and predation impact on weevils.

The number of emergence holes and the number of pupae per leader were similar between planted and seeded stands, suggesting that intraspecific competition, predation, and other mortality factors of larvae and pupae acted equally in both types of stands. Although planted stands were expected to have a more regular spatial pattern of trees, results showed a varied pattern apparently due to natural regeneration. Previous studies have reported that trees in shaded stands tend to have lower attack rates by weevils than those in open stands, e.g., in *Pinus strobus* (Graham 1918) and *Picea sitchensis* (Alfaro and Omule 1990) plantations. Davidson (1991), however, reported a higher population of *Pissodes strobi* in seeded than in planted *Pinus banksiana* in northern Ontario. In our study, there is no evidence that the reforestation technique itself (and the resulting difference in density of host trees) itself affected the extent of damage caused by *Pissodes strobi* to young *Pinus banksiana* plantations. Factors related to other silvicultural treatments such as presence of weeds, stand structure, and humidity may be affecting the survival of *Pissodes strobi* and the susceptibility of *Pinus banksiana* stands to weevil infestation.

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