POPULATION ECOLOGY

White Pine Weevil (Coleoptera: Curculionidae) Attack on White Spruce: Spatial and Temporal Patterns

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ABSTRACT The spatial attack pattern of white pine weevil, *Pissodes strobi* (Peck), on white spruce, *Picea glauca* (Moench) Voss, was studied in a 10-yr-old plantation in the interior of British Columbia. The spatial distribution of the weevil attack changed over time as the outbreak intensified. In the initial stages of the infestation, weevil attack distribution was aggregated, but changed to random when the infestation reached intermediate levels. When the infestation was at peak, attacks followed the pattern of host trees and the distribution was regular over the entire plantation. When attack was aggregated, weevils tended to attack neighboring trees, but not necessarily the 1st nearest neighboring tree. The probability of attack was dependent on the distance from the weevil source (i.e., distance to the trees attacked in the previous year) and on the resistance level of the tree. However, when the attack was at peak, every tree in the plantation was equally accessible to the weevils, and the distance to the attacked tree of the previous year played no role in determining the attack probability and attack was solely dependent on tree resistance level. It is expected that this study will be helpful in formulating a spatially explicit model of white pine weevil attack in British Columbia.

KEY WORDS *Picea* spp., *Pissodes strobi*, attack pattern, modeling, tree resistance

HE WHITE PINE weevil, *Pissodes strobi* (Peck), is ıe most damaging pest of young spruce, *Picea* ɔp., in northwestern North America. In British olumbia its main hosts are Sitka spruce, *Picea* ·chensis (Bongard) Carrière, and white spruce, *cea glauca* (Moench) Voss. Adults emerge in ear- spring from their overwintering sites in the duff, ate, and oviposit on the upper sections of pre- ous year apical growth (leader) of the host trees. ıe larvae mine downward, consuming the phlo- ı which results in girdling and killing of the lead- Weevil attack is successful colonization and de- uction of the tree leader.

Weevil attack can reduce the growth and yield host stands by as much as 40%, depending on estation levels (Alfaro 1982, 1995a). Also leader truction can result in the formation of stem de- ts, such as crooks and forks which reduce lum- quality.

he interaction between *Picea* species and the evil has driven some spruce populations to de- p resistance, a heritable ability of spruce trees epel the attack by the weevil or, if attacked, to "tolerant" and sustain minimal damage (Alfaro Ying 1990, Kiss and Yanchuk 1991). Resistance nsect attack can be attributed to several factors act individually or in synchrony. These include ation in chemical composition of feeding stim- ts and deterrents (Alfaro et al. 1980, 1984), erences in resin canal density (Plank and Ger- 1965, Stroh and Gerhold 1965, Tomlin and Borden 1994, Alfaro 1996), differences in the physical and chemical properties of the resin (Nebeker et al. 1992, Tomlin et al. 1996), and production of traumatic resin (Alfaro 1995b).

Attack probability not only depends on the resistance level of the tree but also on the population characteristics of the pest, such as population level, growth rate, dispersal patterns, and spatial distribution. The spatial distribution of a population is considered an ecological characteristic of a species (Taylor 1984). Species are distributed in aggregated, random, or regular patterns. Weevil attack distribution in a plantation is influenced by the host distribution (i.e., the distribution of weevil food and oviposition sites), environmental factors, and the dispersal behavior of the pest. Spatial patterns of pest, host, and environmental factors are important in pest sampling design and management (Cave et al. 1984, Taylor 1984, Weseloh 1989, Liebhold et al. 1993, Midgarden et al. 1993, Peng and Brewer 1994). Prior knowledge of the distribution of an insect population can facilitate efficient sampling to estimate population parameters. It can also enhance the implementation of pest control methods (Barclay 1992).

In the late 1970s, a large genetic survey of white spruce was conducted in British Columbia, Canada, to identify desirable lumber trees for progeny testing and propagation. The goal was to improve the timber producing qualities of the species for use in reforestation programs. Using seed collected

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Materials and Method

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from selected parent trees, several well-replicated progeny trials were established. Some of these trials were later invaded by *P. strobi*, which provided an opportunity for studying genetic resistance among the genotypes tested. This report evaluates the changes in spatial distribution of the weevil population (as determined by the distribution of attacks) over time, in a progeny trial of 139 white spruce families established in 1984 near Clearwater, BC (51° 42′ N, 120° 03′ W), and determines how the resistance level of the spruce trees affected this spatial distribution.

Materials and Methods

Study Site and Experimental Design. In 1984 a plantation with 8 replicates was established with 3-yr-old seedling offspring of 142 open-pollinated white spruce parents. Each replicate had 142 rows, with each row containing 4 seedlings from the same parent (family), and the families were allocated randomly within each replicate. The layout of the trial included an open space (>10 m) between the replicates and a wide (20 m) open space along the boundary of the plantation. Trees were planted regularly, with a distance between trees ≈2.5 m. Tree mortality occurred in some families; consequently, only 139 families with 4,330 trees were retained for analysis.

The 1st white pine weevil attacks in the plantation occurred in 1986 when the seedlings were 5 yr old. In 1994, we performed a retrospective survey to determine the number of weevil attacks in each year; these measurements were named as ATK86, ATK87, ATK88, ATK89, ATK90, ATK91, ATK92, ATK93, and ATK94. The locations of attacked trees were recorded, which allowed for the determination of the weevil distribution in the plantation. Nine variables, which represented attack intensity (e.g., number of weevil attacks on trees from 1986 to 1994), attack severity (e.g., average length of the internode section), and tree tolerance to *P. strobi* attack (e.g., tree stem form), were measured. Based on these measurements, Alfaro et al. (1996) derived a resistance index for each of the 139 families. This resistance index, scaled into 1 (most resistant) to 100 (most susceptible) units, will be used in this study, along with location variables, to evaluate factors that determine the spatial distribution of weevil attacks on white spruce.

Data Analyses. The spatial analysis was focused on 1 replicate (replicate A). There were 8 replicates in the plantation and we have verified that patterns found on replicate A were similar for other replicates. Replicate A contained 555 trees.

There are several methods available to quantify the distribution of an insect population (Clark and Evans 1954, Taylor 1961, Iwao 1968, Ripley 1981). Among them distance methods are widely used (Skellam 1952, Clark and Evans 1954, Pielou 1959, Donnelly 1978, Sinclair 1985). Clark and Evans (1954) introduced the nearest-neighbor distance statistics to detect a point pattern; however, this method is biased if there is a strong edge effect. Using simulation experiments, Donnelly (1978) modified the statistics to account for edge effect and presented the following equations:

$$r_c = r_e + (0.051 + 0.041/\sqrt{n})\,(L/n) \qquad (1)$$

$$s_r = \sqrt{(0.07A + 0.037L\,\sqrt{A/n})}/n \qquad (2)$$

where r_c is the Donnelly nearest-neighbor distance statistic corrected for edge effect; s_r is the standard error of the Donnelly statistic; r_e is the expected distance to the 1st nearest neighbor without considering edge effect; A is the planar area of the study plot; L is the length of the boundary around the study area; n is the number of points in the plot.

The value of the Donnelly statistic is transformed into a standard normal z deviate, which is amenable to a z-test:

$$z = (r_a - r_c)/s_r, \qquad (3)$$

where r_a is the observed mean distance to the 1st nearest neighbor. Spatial randomness is rejected in favor of clumping or regularity for extreme values in the upper and lower tails, respectively.

To study possible underlying causes of the dispersion pattern of *P. strobi* attacks, we tested whether weevils preferred to attack trees in close proximity to a tree attacked in the previous year, as reported by Alfaro (1995a). For this, we calculated for each tree the distance from the attacked trees to the trees attacked in the following year. In replicate A, there were 16 trees attacked in 1988 and 38 trees attacked in 1989 (Fig. 1 a and b). The following 3 distances were calculated: (1) the 1st nearest-neighbor distance (*d1*) from the 16 trees (attacked in 1988) to the 38 trees (attacked in 1989), (2) the average of the first 10 nearest-neighbor distances (*d10*) from the 16 trees to the 38 trees, and (3) the average of all the distances from the 16 trees to the 38 trees (*d11*). To test if the weevils emerging from the 16 trees attacked in 1988 would selectively attack the nearest trees in 1989 or if the attack was random, the 3 distance measures (*d1*, *d10*, *d11*) were tested by randomization as follows. First, we randomly sampled 38 trees from the total 555 trees in replicate A, then calculated the distance measures (*d1*, *d10*, *d11*) between the 16 attacked trees in 1988 to the randomly selected 38 trees. This procedure was repeated 99 times, thereby generating 99 values for each of the 3 distances. The smallest and largest distances for each of the 3 measures were used as 1% confidence envelope to test whether weevils randomly attacked their neighboring trees or not. If the observed distances fell within the envelope, then we concluded that the weevils emerging in a year randomly attacked the trees in the next year, otherwise, we concluded that the weevil selectively attacked the trees in the replicate.

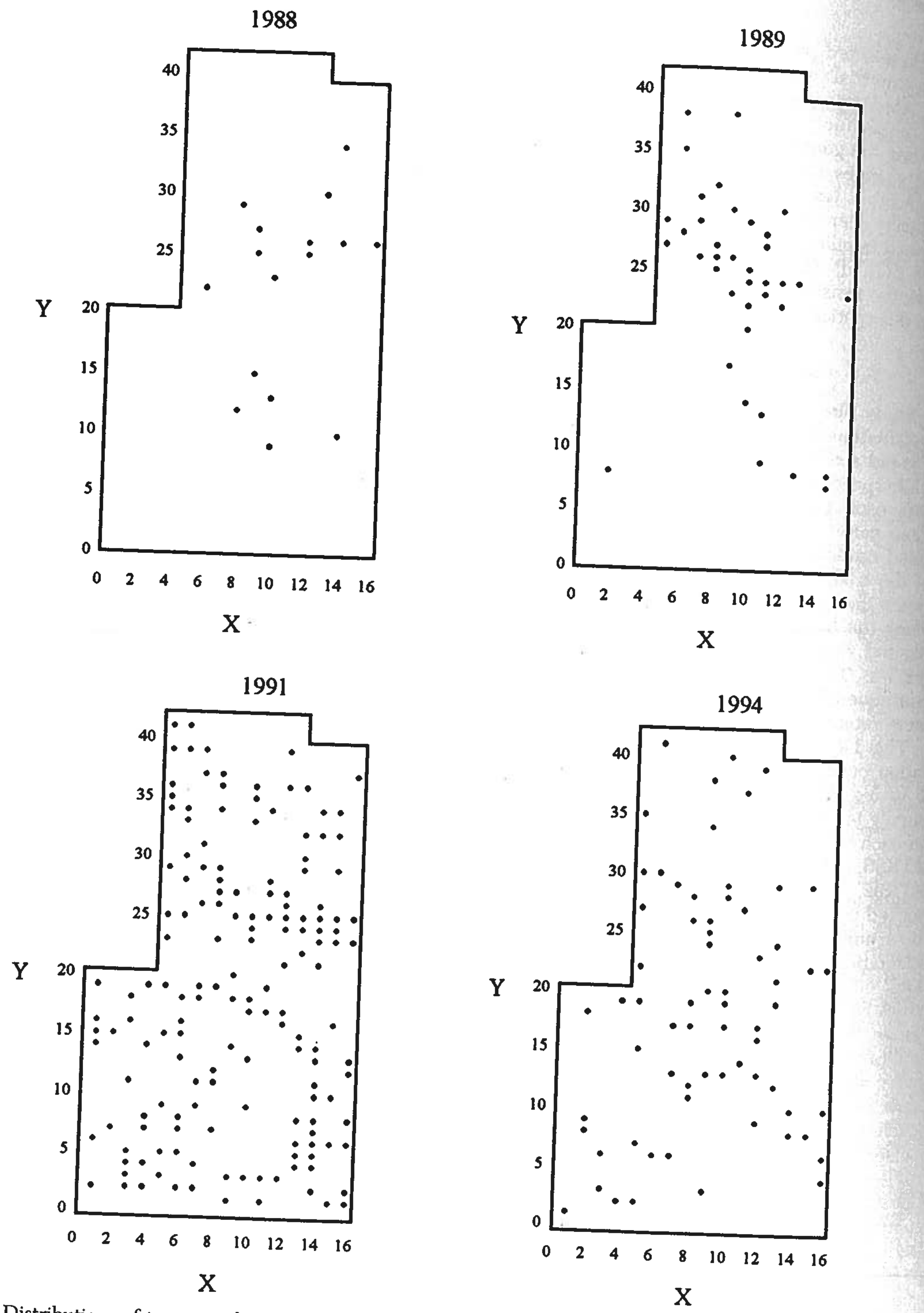

Fig. 1. Distributions of trees attacked by the white pine weevil in selected years (1988, 1989, 1991, and 1994) in replicate A of a white spruce family trial, near Clearwater, BC. X and Y refer to the number of rows and columns of trees, the distance between rows (columns) is 2.5 m.

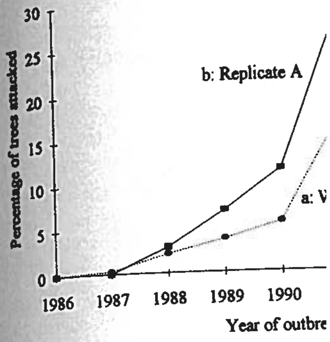

Fig. 2. Yearly percentage of
white pine weevil in a white sp
Clearwater, BC. Weevil attack sta
trees were 5 yr old. (a) Outbreak
plantation. (b) Outbreak in replica

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Result

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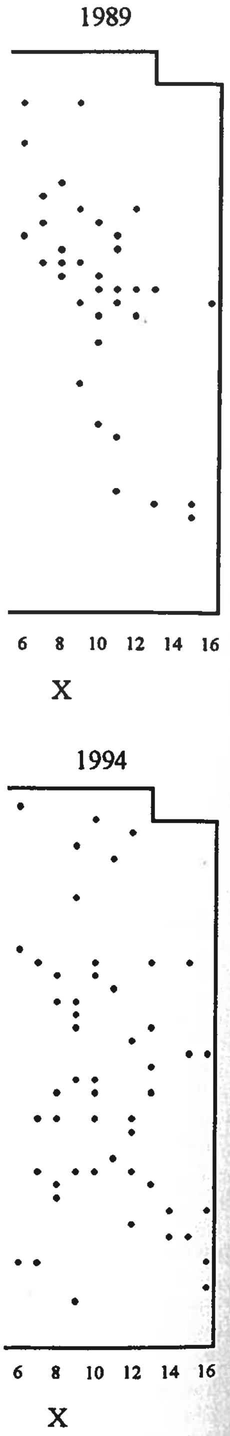

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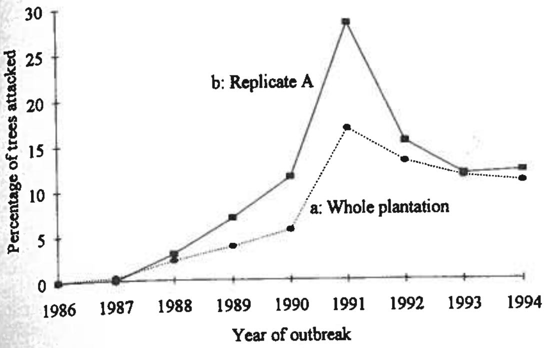

Fig. 2. Yearly percentage of trees attacked by the white pine weevil in a white spruce family trial near Clearwater, BC. Weevil attack started in 1986 when the trees were 5 yr old. (a) Outbreak pattern in the whole plantation. (b) Outbreak in replicate A.

We hypothesized that the condition of being attacked or not attacked in a tree (1 and 0) in a given year is dependent not only on the distance from the attacked trees of the previous year, but also on the resistance level of the tree. Logistic regression was used to model the relationship of attack probability of spruce trees with respect to these 2 explanatory variables. An odds ratio is defined as the ratio of the probability of obtaining a 1, divided by the probability of obtaining a 0: $P/(1\text{-}P)$, where p is the probability of attack. The logarithmic transformation of the odds ratio, or logit, is a continuous and unbounded variable. The logit can then be modeled as a linear function of the explanatory variables, resistance index (*ri*) and distance (*d10*), to produce a logistic regression:

$$\log\frac{P}{1-P} = b_0 + b_1 \times ri + b_2 \times d10, \qquad (4)$$

where log is the natural logarithm; b_0, b_1, and b_2 are regression coefficients.

The fitting of the logistic regression was performed using the method of maximum likelihood (Helsel and Hirsch 1992). The inverse of the logit transformation

$$P = \frac{1}{1 + \exp(-b_o - b_1 \times ri - b_2 \times d10)} \qquad (5)$$

was used to predict values of the response variable to original units (i.e., the estimated probability of attack).

Results

Weevil Epidemiology. In this plantation, the yearly infestation rate was relatively low between 1987 to 1990, however, in 1991 the infestation increased to 17% of the total 4,330 attacked (Fig. 2). Since 1991, weevil infestation has decreased steadily. Weevil infestations can last >30 yr in a stand, hence it is still not clear whether the attack rate will continue to decrease hereafter in this plantation. Some trees were subjected to as many as 8 attacks during the 10-yr period. By 1994, 42% of the trees in the plantation had been attacked at least once.

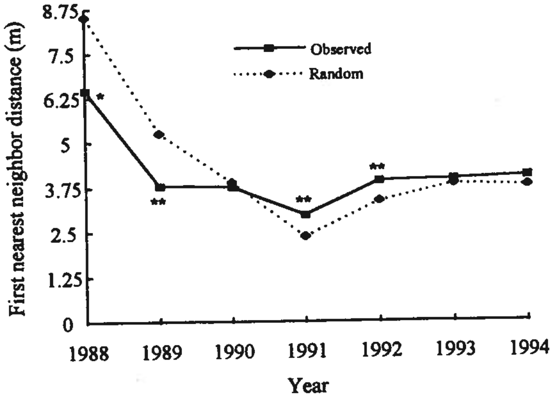

Fig. 3. Comparison between the observed 1st nearest-neighbor distance of white spruce trees attacked by the white pine weevil from 1988 to 1994 (——) and that of random points in replicate A of the Clearwater trial (·····). *, $P < 0.1$; **, $P < 0.05$.

The weevil attack pattern in replicate A was similar to that for the whole plantation, albeit more intense (Fig. 2). Among the 555 trees in this replicate, from 1988 to 1994 there were 16, 38, 63, 157, 85, 65, and 67 trees attacked each year, respectively.

Spatial Distribution of the Weevil Attack Over Time. The 1st nearest-neighbor distance of attacked trees in each year from 1988 to 1994, is compared with that of a random distribution pattern in Fig. 3. The z-test demonstrated that the distribution of attacked trees varied from 1988 to 1994. At the initial stages of the weevil outbreak (1988 and 1989), the attack distribution was significantly aggregated, probably because of the aggregation of weevils themselves; when weevil populations peaked (1991 and 1992), attacks occurred in a more regular pattern, following the distribution of the host trees; when weevil infestation level was intermediate, the attack pattern was at random (1990, 1993, and 1994). Fig. 1 typifies the spatial distribution of attacks from 1988 to 1994.

Distance of Attack. The 1st nearest-neighbor distance (*d1*), the average of the first 10 nearest-neighbor distances (*d10*), and the average of all distances (*d11*) from the attacked trees in a year to those attacked in the next year and their 1% confidence envelopes, are shown in Fig. 4 a–c, respectively. All of the 1st nearest-neighbor distances between adjacent years, from 1988 to 1994, are within the 1% confidence region (Fig. 4a). This suggests that weevils emerging from an attacked tree in a year did not necessarily prefer to attack the 1st nearest-neighbor tree in the next year, regardless of the distribution pattern of the weevil attack and the population level. The distances *d10*

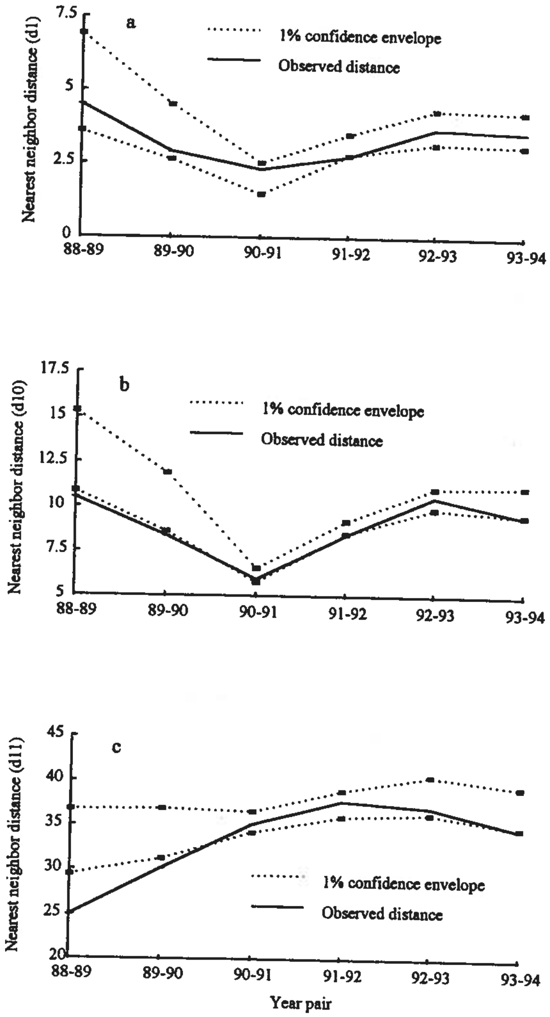

Fig. 4. Neighbor distances (*d1*, *d10*, *d11*) between the white spruce trees attacked by the white pine weevil in 1 yr to those attacked in the next year, from 1988 to 1994. (a) First nearest-neighbor distance (*d1*). (b) Average of the first 10 nearest-neighbors (*d10*). (c) Average of all the distances (*d11*).

and *d11* are out of the 1% envelope in the years from 1988 to 1989 and from 1989 to 1990 (Fig. 4 b and c). This indicates that at the initial stages of the infestation, weevils emerging in a year preferred to attack trees close to the tree from which they emerged, resulting in an aggregated distribution. However, later on, because of a random distribution of the pest over the entire replicate, emerging weevils did not preferably attack their neighboring trees.

Attack Probability, Resistance Level, and Distance of Attack. Using logistic regression, attack probability of a white spruce tree in a year was related to the resistance index of the spruce tree family (Alfaro et al. 1996) and to the distance to the attacked trees in the previous year. Because we demonstrated in the last section that the weevil did not necessarily prefer to attack its 1st nearest-neighbor trees, we used the distance *d10* instead of *d1* as an explanatory variable in logistic regression.

The probability of attack of a tree in 1989 was directly related to the resistance index for the tree family (higher index, more susceptible), and inversely to the distance to the trees attacked in 1988. The same trend was observed in the other years except for 1991–1993 when distance was not significant. As expected, the resistance level of a family always played a significant role to reduce probability of attack, whereas the role of distance to previous attack varied (Fig. 5). At the initial stages of the outbreak (in attack years 1989 and 1990) or when the weevil population was low (in attack year 1994), distance significantly affected the attack probability: the farther from a tree attacked in the previous year, the lower the chance of being attacked (Table 1; Fig. 5 a, b, and d). When the weevil population was at peak or the weevil was distributed randomly over the plantation, distance lost its role in affecting the attack probability, and only tree resistance determined the chance of attack (Table 1; Fig. 5c).

Discussion

Weevil distribution on white spruce varied in space and time in the Clearwater progeny trial. Our results showed that the weevil had an aggregated distribution in the initial stages of infestation development, but with the increase in the weevil population, the distribution changed to random or regular. Many studies have demonstrated aggregated distribution of pest species in nature (Taylor 1984, Weseloh 1989); however, our results indicate that the distribution could change over time. The distribution of a pest can be affected by several factors, such as its biological behavior (reproduction or dispersion), the availability and distribution of host, the heterogeneity of environment. In the Clearwater plantation, all the families of white spruce were mixed randomly and regularly planted, hence, the weevil had the same distance to fly from one tree to another. Because the white pine weevil is not a very mobile insect, in the 1st few years of the infestation (1988 and 1989) they preferably attacked proximate trees, which resulted in aggregated attacks. Because the host distribution was regular, if every tree had the same resistance level, the weevil distribution should have shifted toward a regular distribution with the gradual increase of the weevil population. However, attack probability was different among the families because of differences in heritable resistance. Because of the random location of the resistant families in the plantation, the distribution of the weevil was random instead of regular in the years of intermediate population level (1990, 1993, and 1994; Fig. 3). When the weevil infestation peaked (1991 and 1992), virtually every tree except the extremely

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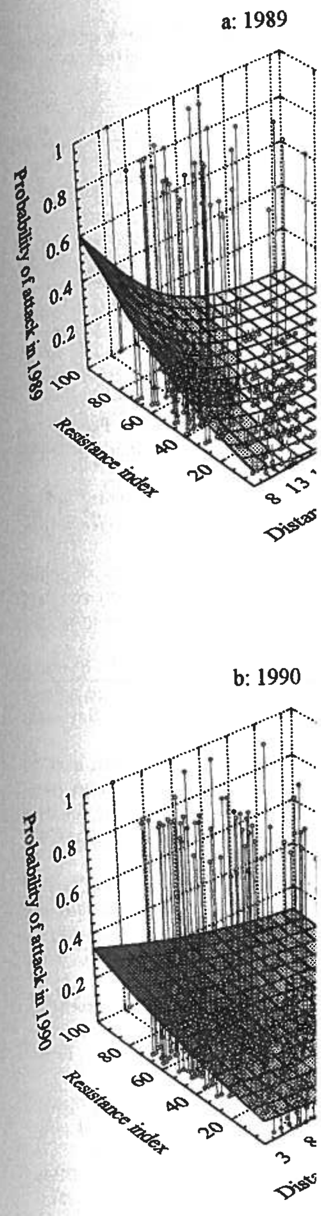

Fig. 5. Observed (circle) ar
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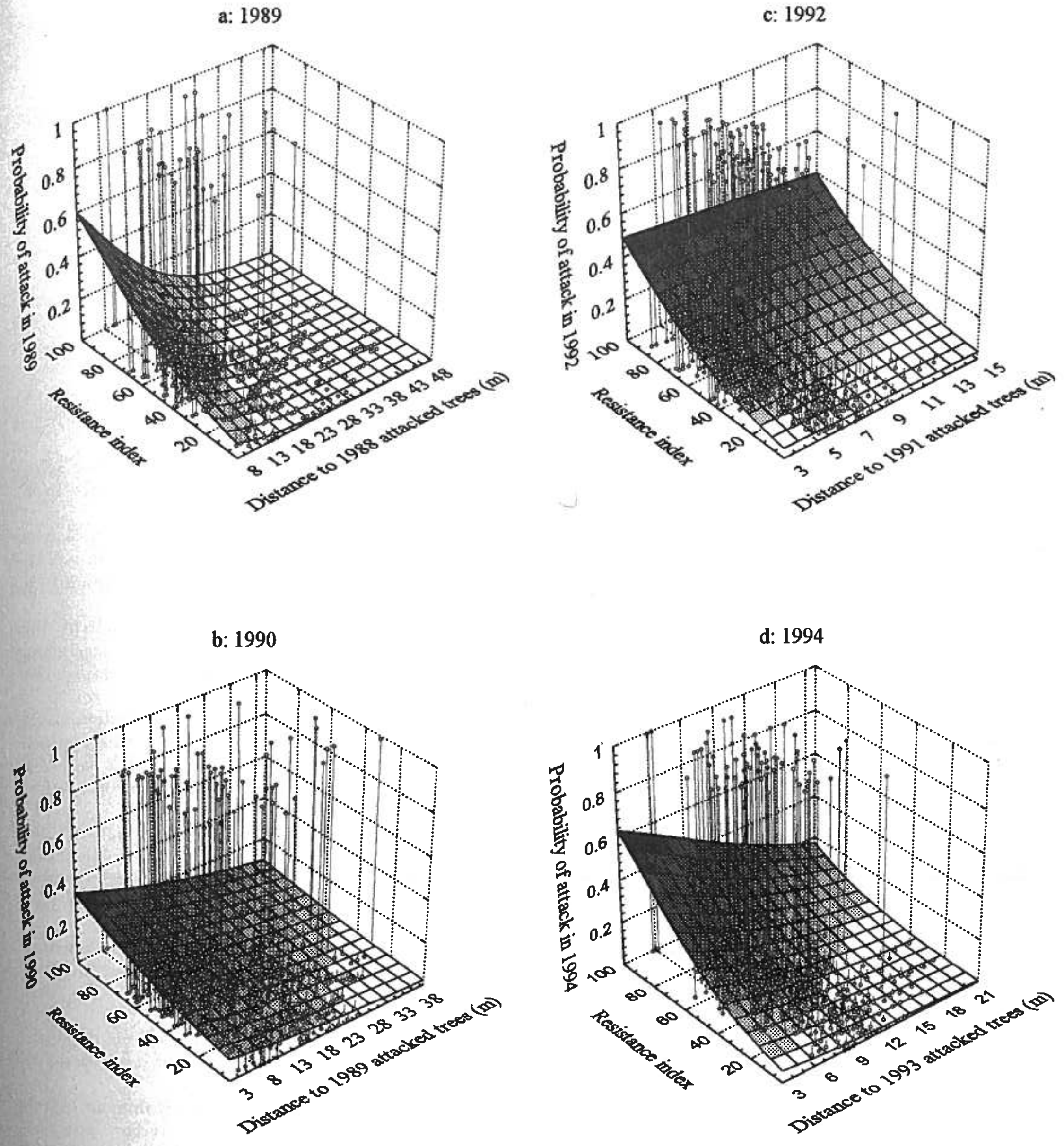

Fig. 5. Observed (circle) and predicted (surface) probabilities of attack in selected years in replicate A of a white spruce family trial, near Clearwater, BC (a) 1989, (b) 1990, (c) 1992, and (d) 1994. The logit function was regressed to resistance index of white spruce families and the distance (d10) to the attacked trees of previous year. The increasing numbers in resistance index indicate increasing susceptibility. The predicted surface of other years was similar to the one for 1992 (c).

resistant ones could be attacked; consequently, the attack patterns followed the regular host distribution.

In this study, we did not consider migration of weevils from or to other replicates, and we assumed that most attacks originated within a replicate. Though we did not rule out the possibility that some trees may be attacked by invading weevils, it seemed that migration was not an important factor in weevil population demography in this plantation and most attacks appeared to originate within each replicates. Therefore, in this study, the factor of migration was not considered.

One of the goals stemming from studies of the spatial distribution of insects is to develop efficient sampling methods to assess pest population levels to determine the need for control methods. Past studies have developed sampling programs based on data from only 1 or 2 yr of observation. Because the distribution of a pest species changes over

Table 1. Coefficients of the logistic regression equations used to determine the relationship between probability of attack on a white spruce tree and tree resistance (b_1) and distance to the nearest 10 neighbors attacked in the previous year (b_2) (equations 4 and 5)

Attack year	*n*	$b_0 \pm$ SE (intercept)	$b_1 \pm$ SE (resistance)	$b_2 \pm$ SE (distance)	λ^2 (*P* value)
1989	38	−1.653 ± 0.713*	0.031 ± 0.009**	−0.126 ± 0.0286**	45.17 (0.0001)
1990	63	−2.073 ± 0.468**	0.015 ± 0.006	−0.042 ± 0.019*	12.96 (0.0015)
1991	157	−2.314 ± 0.414**	0.030 ± 0.005**	0.002 ± 0.026	42.68 (0.0001)
1992	85	−2.964 ± 0.680**	0.030 ± 0.006**	−0.029 ± 0.085	29.73 (0.0001)
1993	65	−3.367 ± 0.885**	0.029 ± 0.007**	−0.006 ± 0.085	21.89 (0.0001)
1994	67	−2.556 ± 0.685**	0.034 ± 0.007**	−0.110 ± 0.053	38.05 (0.0001)

n, Number of attacked trees among total of 555 samples (coded as 1, otherwise as 0). *, $P = 0.05$; **, $P = 0.001$. Last column is the λ^2 statistics and associated *P* value (df = 2) for the model in equation 5, based on maximum likelihood method.

time, parameters estimated from such sampling should be used with caution. Whenever possible, sampling is better done on a long-term basis.

Theoretically, the 1st nearest-neighbor tree of a weevil attacked tree should have the greatest chance of being attacked, because the white pine weevil is not very mobile and because the cost of dispersion increases with distance. This would be true if all the trees had the same resistance or susceptibility level and if the environment was homogeneous. In this study we showed that this is not the case. Alfaro et al. (1996) have shown that there were statistically significant differences in resistance among the families tested in the Clearwater trial. Even within the same family, trees may have differences in resistance that could be sensed by the weevil. Also, seemingly homogeneous environments may vary, for example, wind direction and other microclimate effects may influence attack patterns.

Past pest control schemes have been developed mainly on the basis of time, ignoring spatial effects (i.e., recommending control actions based on mean population levels measured at given time intervals). Recent studies have shown that space is one of the important aspects of a pest management program (Barclay 1992, Liebhold et al. 1993). The results in this study will be used in an integrated pest management simulation model to estimate weevil population level, to assess individual tree attack probability, and to evaluate damage on spruce plantations in British Columbia. We expect that this study on the spatial patterns of the white pine weevil in the Clearwater trial will not only help in understanding the spatial behavior of the weevil infestation but also increase the accuracy of the outputs of our simulation model.

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E (distance)	λ^2 (*P* value)
± 0.0286**	45.17 (0.0001)
± 0.019*	12.96 (0.0015)
± 0.026	42.68 (0.0001)
± 0.085	29.73 (0.0001)
± 0.085	21.89 (0.0001)
± 0.053	38.05 (0.0001)

= 0.05; **, *P* = 0.001. Last column is
um likelihood method.

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