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B658: Susceptibility and Vulnerability of Forests to the Pine Leaf Aphid Pineus Pinilolile (Fitch) (Adelgidae)

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SUSCEPTIBILITY AND VULNERABILITY OF FORESTS TO THE PINE LEAF APHID, *PINEUS PINIFOLIAE* (FITCH) (ADELGIDAE)[1]

John B. Dimond[2] and Robert H. Bishop[3]

INTRODUCTION

Maine, and surrounding regions, recently experienced an outbreak of the pine leaf aphid (or adelgid). The population progression began about 1955, as indicated by tree growth reductions (2), a peak was reached about 1961, and populations have been in a gradual regression through the present (3). As a result of the outbreak, there was considerable growth reduction of white pine in some regions and scattered tree mortality.

Among the many observations on the insect made during the outbreak were (a) the aphid was abundant in only certain portions of Maine and remained uncommon in the remainder of the state, and (b) in those regions where the insect was abundant, some stands of pine suffered relatively severe damage while others were largely unaffected. This study sought to provide explanations for these differences and to allow characterizations of those stands which did and those which did not sustain damage.

Information gained in a study of this sort is useful in explaining the distribution and abundance of the insect and in suggesting silvicultural procedures designed to increase resistance of stands to insect damage.

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Biology of the insect

The life history of the pine leaf aphid has been described in some detail (1); only those aspects pertinent to this study are presented below.

Many of the aphids and adelgids have complex life cycles involving alternation of host plants and a progression through alate and apterous,

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and sexual and parthenogenetic forms. This is also true of the pine leaf aphid. Red spruce, *Picea rubens* Sarg., and black spruce, *P. mariana* (Miller) B.S.P., are the primary hosts of the insect, with the former species apparently preferred and much more heavily infested (7). Cone-like galls are produced on spruce within which developed a generation of winged forms which migrate to the secondary host, eastern white pine, *Pinus strobus* L. The offspring of the migrants feed on the current shoots of pine, and where abundant, cause needle stunting or shoot killing. Subsequently, another generation of winged forms is produced, carrying the population back to the primary hosts. Significant damage does not result on spruce from the aphid infestation.

The entire cycle requires a minimum of two years and four generations: gallicola migrans, sexupara, sexualis, and fundatrix. Under some conditions, a fifth generation, the exsule, has been seen, and where present, causes the cycle to be lengthened beyond two years. Through the recent outbreak in Maine, the population has been synchronized so that most of the gall formation and migration to pine occur in odd-numbered years.

Concepts of susceptibility and vulnerability

The concepts of susceptibility and vulnerability have recently been redefined by Mott (8). It became necessary to distinguish between the two related ideas since it is recognized that the forest has an influence on the insect, an influence involved with susceptibility, and also that the insect has an influence on the forest, involved with vulnerability. With susceptibility we are dealing with the degree to which a forest provides conditions sufficiently favorable to the reproduction and survival of an insect that it is likely to increase to damaging numbers. Thus, the probability of abundance of an insect increases as the susceptibility of the forest increases. The term vulnerability can be restricted to susceptible forests and is concerned with the probability that a stand will sustain damage in the presence of abundant numbers of the insects. A stand of low vulnerability will be little damaged in the midst of an insect outbreak.

The pine leaf aphid is an insect requiring two hosts, spruce and white pine, and the regular migrations between the two probably contribute to dispersal of the insect over large distances. With insects of such high dispersive tendency, susceptibility is determined by the forest and not by the stand. Large insect numbers in one locality may be the result of high production of the insect several miles away. Thus, observations on susceptibility must encompass large areas. With insects of this nature, outbreaks develop over extensive areas, although extensive outbreaks may not necessarily be restricted to insects with high dispersive powers.

Insofar as the concept of vulnerability is concerned it is appropriate to consider smaller segments of the forest, e.g. stands or perhaps individual trees.

The same factors may contribute to both susceptibility and vulnerability of a forest to insect attack, but this is not always the case. Where appropriate, the two phenomena are discussed separately.

PROCEDURES

Regions susceptible to an outbreak of an insect can be delineated by population surveys during the course of the outbreak. Susceptible regions will correspond to areas of high population density. The common appearance of damage to the host also identifies susceptible areas, however, a lack of damage cannot be used to locate areas of low susceptibility since they may represent areas of low vulnerability within high-susceptibility regions. The areas of Maine susceptible to pine leaf aphid attack were located by a combination of intensive population surveys in the southeastern quarter of the state (7), and by reference to published reports of damage (4, 10, 11), Maine Forest Insect Survey reports (Forest Insect Notes Series, issued periodically by the Maine Forest Service, Entomology Division), and by extensive but cursory personal surveys of the remainder.

Contrasts between the high-and low-susceptibility portions of the state were made with regard to a number of biotic, edaphic, and climatic factors which seemed potentially significant for determining aphid abundance. For the state-wide data needed for extensive comparisons, reference was made to existing literature, e.g., for forest composition, "The Timber Resources of Maine" (5) and for soils composition, "The Soils of Maine" (9). Much of this part of the study was analyzed cartographically.

Intensive comparisons also were made from data collected on 98 circular, quarter-acre field plots located in Washington, Hancock, and southern Penobscot counties. The plots were about equally distributed in areas of high and of low susceptibility to the pine leaf aphid.

Each plot was measured for the following variables:

X_1. *Plot density*—measured in terms of total basal area of stems on the plot using the sums of the squared diameters-at-breast-height (d.b.h.) as an index. Only stems of two inch d.b.h. and over were considered.

X_2. *Density ratio of red spruce and black spruce to white pine*—computed as the ratio of the sum of squared d.b.h. values for all red and black spruce stems over two inches to the corresponding value for white pine. This variable was selected because of the suspected importance of the relative quantities of host plants of the aphid in influencing its abundance. Low values of the ratio indicated relatively more pine; high values, more spruce.

X_3. *Density ratio of red spruce to total of red spruce and black spruce* —indicating the percent red spruce of the total red spruce and black spruce present on a plot. This variable was selected because of the noted preference of the aphid for red spruce (7).

X_4. *Average basal area per tree*—determined by dividing the total plot density (X_1) by the total number of stems over two inches at d.b.h. This provides an index to basal area rather than a true estimate.

X_5. *Average basal area per white pine*—determined by dividing total white pine density by the number of pine stems.

X_6. *Average basal area per spruce*—calculated as for white pine.

X_7. *Height-growth index for white pine*—calculated for each plot by measuring the height of five dominant or codominant pines and dividing the height by the age as estimated from increment cores extracted at breast height from the same trees. The average value of the five trees was used, except in the instances where less than five pines occurred on a plot.

X_8. *Average age of pine*—estimated from the increment cores extracted at breast height from the five dominant or codominant pines studied intensively on each plot.

X_9. *Average d.b.h. of pine*—average for all pines on the plot.

X_{10}. *Density of pine*—determined in the same manner as for total stand density, but for white pine only.

X_{11}. *Density of spruce*—computed for red spruce and black spruce in the same manner as for pine.

X_{12}. *The ratio: density of conifers to total plot density*—as an indicator of forest type, i.e. largely softwoods, hardwoods, or mixed.

X_{13}. *The ratio: density of pine and spruce to total plot density*—indicating the proportion of the plot volume composed of the aphid's host trees.

Field plots were purposely selected to meet certain prerequisites and to facilitate collection of data. Plots had to contain some white pine stems over two inches d.b.h. Because of the larger number of plots needed, accessibility was important thus limiting selection to roadsides. Plot locations were selected at uniform intervals along roads to assure a more or less even distribution over the sampling universe and to reduce bias. The data necessary to compute values for the 13 variables listed above were obtained by tallying every living tree, two inches d.b.h. and over on each plot by species and in one inch diameter classes. In addition, the total height and age at d.b.h. of five white pine trees selected from among the dominant and codominant crown classes on each plot were determined.

For comparisons, means of the 13 variables described above were computed for 48 plots in areas of high susceptibility and for 40 plots in areas of low susceptibility. Significant differences between means were determined by application of Student's "t" test.

The same field plot data were used to study vulnerability of stands within the susceptible area. The method of analysis selected involved a search for functional relationships between variables described above and the amount of aphid damage to pine observed on the plot. This last variable, called Y, was measured from the increment cores taken at d.b.h. from the pines on each plot. It was assumed that the reduction in radial growth attributable to aphid attack provided a useful index of damage as a measure of vulnerability. Reduction in growth due to aphid attack was identified by the particular configuration of annual rings (2), showing a sharp decline in growth starting about 1955 and continuing for a period of nine years. Thus, the index of damage, Y, was computed as the percent difference between the actual basal area growth from 1955 to 1964, years of aphid attack, and the expected basal area growth had there been no aphid attack during the period. This latter value was believed to be similar to and was estimated from the nine years of growth immediately prior to the aphid outbreak, 1945 to 1954.

Stepwise multiple regression analyses were used to determine the independent variables significantly related to the index of damage. The independent variables were entered as measured and also as squares and reciprocals in a search for both linear and curvilinear relationships. These statistical computations were made through arrangement with the University of Maine Computing Service.

RESULTS—SUSCEPTIBILITY

Areas of high susceptibility to the pine leaf aphid, as determined by population and damage surveys during the recent outbreak, are illustrated in figure 1. The major regions are Washington and Hancock counties in eastern Maine, and portions of Oxford and Franklin counties in western Maine. Additional localized areas occurred in the immediate vicinity of Mt. Katahdin, and along the Penobscot, Piscataquis, Kennebec, Pleasant (Piscataquis County) rivers and Carrabassett Stream.

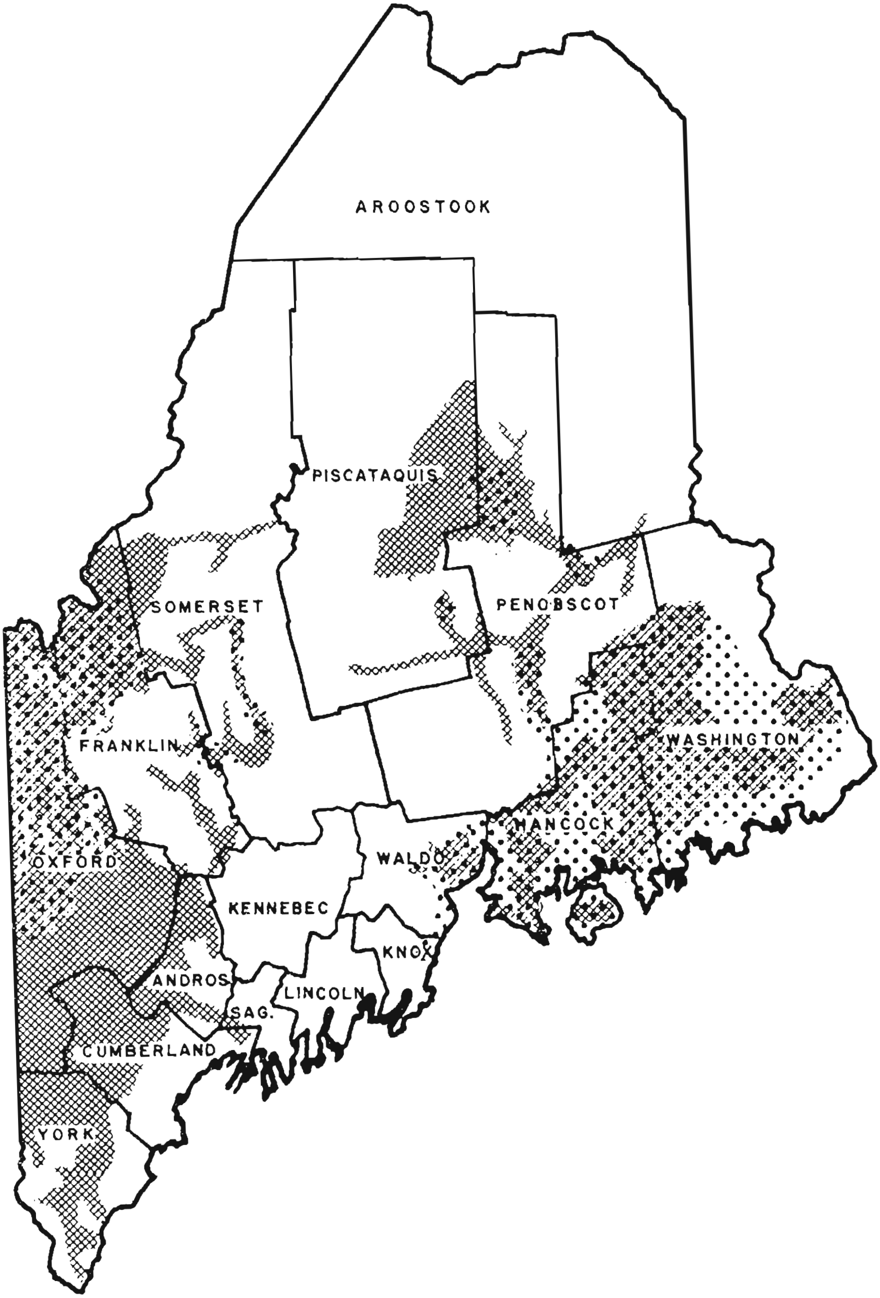

Figure 1. County map of Maine illustrating areas susceptible to pine leaf aphid during the 1955-65 outbreak (stippled) and the distribution of sandy and gravelly soils (crosshatched).

Intuitively, it seems most reasonable to attempt to explain this distribution of high and low susceptibility on the basis of forest composition since a significant representation of the host plants of the aphid would seem an essential requisite for its abundance. One can first examine the results of the intensive survey made of quarter-acre field plots in eastern Maine. Table 1 presents the mean value of each of the variables studied for plots in areas of high susceptibility and for those in areas of low susceptibility.

Probably the most important differences seen in table 1 are those dealing with the relative quantities of white pine and red and black spruce (X_2, X_{10}, X_{11}). Plots in areas of high susceptibility contained more spruce and less pine than those in areas of low susceptibility. Presumably, one important characteristic of a highly susceptible area is that both hosts are well represented.

There is no indication that the significant difference noted in total plot densities (X_1) is an important determinant of susceptibility. Rather the lower density characteristic of areas of high susceptibility is probably related to soil differences which are discussed later in more detail. The very light soils found in highly susceptible areas contribute to open forest stands which may facilitate aphid migration, however.

Table 1. Mean values of field plot variables compared for areas of high and low susceptibility to pine leaf aphid, and results of comparisons of the pairs of means using Student's t test.

Variable	Mean High susceptibility plots	Mean Low susceptibility plots	Result: t test*
X_1 Plot density[1]	5640	7074	.01
X_2 Spruce: pine[2]	1.94	0.43	.01
X_3 Red spruce: total red and black spruce[2]	0.82	0.73	ns
X_4 Average basal area (Aba) per tree[3]	39	50	.05
X_5 Aba per pine	103	148	.05
X_6 Aba per spruce	33	32	ns
X_7 Height-growth index[4]	0.98	1.18	.01
X_8 Average age of pine	60	53	ns
X_9 Average d.b.h. of pine	10.9	12.2	.05
X_{10} Density of pine[1]	2119	4342	.01
X_{11} Density of spruce[1]	1610	650	.01
X_{12} Softwoods: density[2]	0.83	0.85	ns
X_{13} Pine and spruce: density[2]	0.63	0.61	ns

*Numbers listed are probabilities of means being different; ns indicates no significant difference.
[1] Square inches of basal area
[2] Density ratio
[3] Square inches
[4] Height to age ratio

The significant difference shown in height-growth index (X_7) is probably also related to differences in soils and is probably not a direct determinant of susceptibility. We would expect, however, that the site might be related to vulnerability with the less vigorous trees on poorer sites sustaining greater damage.

The remaining significant variables (X_4, X_5, X_9) are primarily concerned with size of pines. Although the ages of pines (X_8) were not significantly different in the two areas, their sizes were, with smaller diameters in areas of high susceptibility. This is, partly at least, a result of high susceptibility to aphid attack rather than a determinant of it.

It is perhaps appropriate to warn of certain limitations to the use of the data in table 1 due to the plots being established in a non-random fashion. One might be tempted, for example, to conclude from an examination of variable X_{12} in table 1 that the coniferous component of forests was the same in both types of areas studied. Such a conclusion would have no basis, however, since only certain types of stands, i.e. those with one or more pines, were sampled. Mean differences illustrated in table 1 probably apply only to pine stands within the areas studied.

Actual total forest composition of areas of high and low susceptibility can be derived, however, from existing literature and applied to the entire state. The reported composition of forests of Washington-Hancock counties and of Oxford-Franklin counties, which are largely categorized as highly susceptible in figure 1, are compared with the remaining county groups, mostly of low susceptibility, in table 2. These data are derived from table 26 of Ferguson and Longwood (5).

Table 2 provides much the same picture as that derived from the data taken from small plots. Areas susceptible to the pine leaf aphid have significant quantities of both pine and spruce. Those regions to the south contain considerably greater volumes of pine and less spruce;

Table 2. Volumes in millions of board-feet of white pine and spruce on commercial forest land in county groups, and percent that these species comprise of the total forest composition.

County group	Volume pine	Volume spruce	Percent pine	Percent spruce
Washington-Hancock	686	1,184	19	33
Oxford-Franklin	952	654	27	19
Somerset	505	974	13	25
York-Cumberland-Androscoggin	1,029	137	51	7
Sagadahoc-Kennebec-Lincoln-Knox-Waldo	848	161	44	8
Piscataquis	279	1,245	6	28
Penobscot	237	1,058	6	28
Aroostook	464	2,069	6	28

those to the north have similar volumes of spruce but much less pine. The values for spruce in table 2 include white spruce, not a host of the pine leaf aphid, as well as red spruce and black spruce.

High susceptibility to the pine leaf aphid, implying abundant populations of the insect and often damage to the secondary host, pine, occur where both primary and secondary hosts are important components of the forest. The factors which have produced susceptible forests are both edaphic and climatic. The shaded area of figure 1 depicts the areas of Maine which have either sandy soils derived from granitic till or soils derived from gravel deposits, chiefly of the Colton and Canaan-Hermon-Waumbek associations. Delineation of soil associations was derived from a soils map prepared by Rourke and Hardesty (9). North of the highly susceptible regions are found mostly heavier loam soils such as Thorndike and related associations (9), which favor genera other than *Pinus.* Soils suitable for pine exist south of the susceptible regions in southern Oxford and parts of York, Cumberland, and Androscoggin counties, however, the warmer climate favors extensive stands of pine and restricts spruce to local microhabitats.

Table 2 indicates that Somerset County contains significant quantities of both spruce and pine, and yet forests in this county have a low susceptibility to pine leaf aphid except in restricted locations, primarily the upper Kennebec River valley (fig. 1). Field observations indicate, however, that a considerable proportion of the listed spruce component of that county is white spruce on the heavier loam soils that predominate (9). Thus, the volume of host spruces in Somerset County is considerably lower than listed in table 2. White spruce is a minor component on the sandy podzols that characterize the susceptible area (6). Substracting the volume of white spruce from the total volume of spruces in Washington-Hancock and Oxford-Franklin counties would cause little reduction in total volume. Thus, the low susceptibility of Somerset County forests to pine leaf aphid can probably be explained on the basis of relatively low volumes of both pine and of the host spruces, and a considerable dilution with various non-host species.

RESULTS—VULNERABILITY

Multiple regression analyses of data from 59 plots located within the area regarded as susceptible to pine leaf aphid indicate 3 of the 13 measured independent variables as significantly related to the index of damage. The significant variables are listed in table 3 together with the associated statistics.

Only one variable, spruce to pine ratio (X_2), accounted for a sizable block of the variance in the damage index. This relationship is

Table 3. The identity and associated statistics of independent plot variables significantly related to a pine leaf aphid damage index.

Variable	Form entered in the regression	Coefficient	Error of coefficient	Accumulated r^2	f
X_2 Spruce/pine	$1/X_2 + 0.1$	0.2982	0.0768	.28	21.72
X_7 Height-growth index	$(X_7)^2$	0.1087	0.0487	.33	4.31
X_5 Av. basal area, pine	$(X_5)^2$	-0.2135×10^{-5}	0.1389×10^{-5}	.35	2.36

illustrated in figure 2. The figure shows a negative curvilinear relationship between the damage index, Y, and the reciprocal of the spruce to pine ratio, (X_2). As proportion of spruce in the plots increased, pine growth decreased, presumably because of increased pine leaf aphid damage.

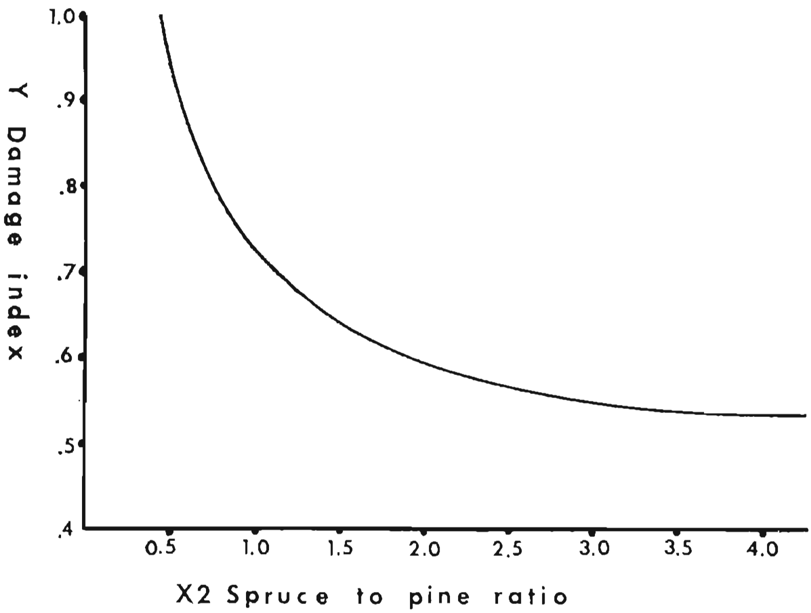

Figure 2. Relationship of the ratio of spruce to pine volumes of forest stands to a pine leaf aphid damage index. The curve follows the equation $Y = .3766 + .2983\ (1/X_2 + 0.1) + .1087\ (X_7)^2 - .214 \times 10^{-5}\ (X_5)^2$ where X_7 and X_5 are held at their mean value.

The relationships of height-growth index and average size of pine, both entered as squares, to the damage index were also curvilinear with damage greater on poorer sites and with damage greater on the larger trees. These relationships are not illustrated because of the small contribution they make to explaining variance in the damage index. In addition, the relationship with height-growth index may be questioned in that the reduced height to age ratio found on the heavily damaged plots could be due to aphid damage and therefore a result of high vulnerability rather than a determinant of it. DeBoo *et al.* (2) found radial growth to be quite sensitive to varying degrees of pine leaf aphid attack while height growth remained unaffected except under conditions of extreme damage. A possible reduction in height growth in the most heavily damaged plots may have been sufficient to produce the regression relationship seen in table 3, however.

One can estimate from the regression line in figure 2 the ratio of spruce to pine that may constitute a hazard to the pines in terms of the past or a future outbreak. The average damage index for plots in non-susceptible areas was 0.95 (s.e. $= \pm$ .06). This value approaches 1.0 which indicates equal volume of growth in the nine years preceding the outbreak and in the nine years of the outbreak. Lower values of the damage index, characteristic of the susceptible area, represent poorer growth or increasing damage during the outbreak. The tolerability of greater degrees (i.e. lower index values) of damage is a subjective evaluation varying with the nature of the stand and the proposed utilization of the forest products thereon. For many purposes, one may consider the critical level to be reached when the degree of damage is such that some codominant trees are killed. Among 15 plots in the susceptible area containing codominant trees apparently killed by the aphid, the average damage index was 0.56 $\pm$ .03. Figure 2 indicates that indices of this level are a possibility where the spruce to pine ratio reaches 2.90 or higher. Considerable growth reductions unaccompanied by mortality can be expected when the spruce to pine ratio equals or exceeds 1.0.

The use of the regression line in figure 2 to assess damage hazard in a stand is subject to great error as indicated by the low r^2 value of the regression equation. A great deal of the variance in damage index has not been accounted for with the variables measured. Attempts have not been made to increase the predictive value of the equation for the following reason. It is felt that the principal unmeasured variable in the system is the composition of the forest immediately surrounding each plot. An alternate way of stating this is that plot size was too small to adequately describe the several variables studied. The aphid is influenced by the stand factors encompassed within its effective dispersal range. Since the effective range of the insect is presently unknown, it is impossible to select the most biologically meaningful plot size, and the selection of the one-quarter acre plots in this study was made for convenience in data gathering, there being no other criteria available. Presumably, r^2 could be increased by measuring larger plots, e.g. one acre, however, one might find the degree of increase in precision to not be worth the effort. There seems to be little hope of improving the predictability of the equation until studies of aphid migration provides a firm basis for plot size selection. In the meanwhile, the present regression equation may serve as a rough guide.

Several additional observations can be made regarding vulnerability of stands or trees based, not on data collected in the study described here, but upon observations made over several years of work with the pine leaf aphid. Pines measured in the present study were all codominant or dominant trees in stands of sapling age or older. This tells us little about vulnerability of smaller pines and the more suppressed crown classes.

Among advanced reproduction, suppressed trees are much more vulnerable to pine leaf aphid damage, as might be expected. Many two-storied stands have been observed where the understory pines have been heavily damaged, sometimes approaching total mortality, while overstory trees have been only lightly affected. This effect is a combination, apparently, of poor tolerance to attack in the understory trees as well as heavier attack. Unpublished aphid population data show much lighter populations on dominant pines when the upper forest canopy is incomplete, as in a cutting. Apparently where crowns of larger trees are exposed to winds, migration of aphids is hindered and the bulk of the population is restricted to the more protected understory. Attack on larger trees equals that on smaller trees when the upper canopy is more or less continuous, however.

Aphid migration through dense, pure stands of pine, e.g. in plantations, is not particularly effective and the bulk of the aphid population and the damage will occur on the peripheral trees. In more open, pure stands, as in some natural reproduction, aphids may penetrate deep into the stand in damaging numbers.

Pines on the edges of roads, streams and forest openings often sustain heaviest damage. Any feature of the landscape that serves as a wind corridor will direct the migrating aphids, which have feeble capacity for directed flight, to the most exposed trees. In the several cases that have been seen where pines that are remote from spruce sustain damage, natural wind channels can be identified that serve to direct the aphid migration and concentrate it in a small area.

DISCUSSION

Both susceptibility and vulnerability of forests to pine leaf aphid attack are apparently determined largely by the same factor, the relative quantities of the host plants present. For high susceptibility, both primary and secondary host species must be well represented, and presumably both above a certain threshold level. If one or the other host species is less abundant, aphid population losses during migration apparently become sufficiently large that the insect becomes rare. Within a susceptible area, vulnerability of the pine is largely dependent on the quantity of spruce in the vicinity. If there is a considerably greater volume of pine than spruce, the aphid population migrating to pine will be sufficiently diluted that little damage will result to individual trees.

The data suggest that pine vulnerability may be lowered by reducing the spruce component of the stand. The safe level, according to our present experience, seems to lie where the spruce volume is equal to or less than that of the pine. In much of the susceptible forest of Maine, however, management is primarily directed towards pulpwood production in which spruce is a desired species. It seems unlikely that managers of these lands will become interested in undertaking a program of spruce reduction to protect pine. Such a program might be considered as part of management of certain smaller land holdings where pine production is stressed. Because the pine leaf aphid is migratory in its behavior, such management would need to be applied to moderately large acreages to be effective. Until data on migration range of the aphid is available it will be difficult to specify the required size of a management unit.

CONCLUSIONS AND SUMMARY

Forests susceptible to pine leaf aphid attack contain significant quantities of red spruce or black spruce and white pine, the required hosts of the insect. Maine counties that are largely susceptible have forests composed of about 50% spruce and pine and with roughly equal representation of these two genera. Susceptible forests are restricted to gravel and sandy soils, which favor pine and where the climate is sufficiently cool and humid that spruce is of common occurrence. The heavier soils of northern Maine support forests in which pine is rare; in southwestern Maine, although soils are suitable, the warmer climate restricts spruce to local microhabitats. These areas are of low susceptibility to pine leaf aphid apparently because of scarcity of one of the required host species.

Within the susceptible forests, vulnerability of pine to aphid damage is a function of the relative quantity of spruce in the stand. Experience in the recent pine leaf aphid outbreak indicates that stands in which the volume of host spruce equals or exceeds that of pine can be expected to suffer significant growth loss and mortality in extreme cases among the codominant trees. The vulnerability of pine stands can be decreased by reducing the spruce component, however, present management in much of the susceptible forest favors spruce. Therefore, reduction of the volume of spruce as a means of controlling pine leaf aphid damage can probably be of value only in limited situations.

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