GENETIC VARIATION IN RESISTANCE OF SCOTCH PINE TO THE EASTERN PINESHOOT BORER

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ABSTRACT

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By

Kim C. Steiner

Larvae of the *Eucosma gloriola* moth kill young twigs on Scotch pine, causing unsightly damage. To determine if some varieties of this tree are genetically resistant to *Eucosma*, attack was measured on 110 seedlots of Scotch pine belonging to 19 varieties. The trees were planted at three locations in southern Michigan: Allegan County (70 seedlots), Shiawassee County (76 seedlots), and Kalamazoo County (106 seedlots). Each plantation was measured in either one or two different years. Most results were consistent from plantation to plantation and year to year.

There were highly significant differences in attack among seedlots in all plantations and years, indicating that there are genetic differences in resistance. Most of the variation was due to differences among varieties. At the most heavily-attacked plantation, the short northern varieties had from 1 to 4 attacks per tree, the tall central

European varieties had from 2 to 6 attacks per tree, and the medium-height southern and western varieties had from 6 to 10 attacks per tree.

Some variation was due to differences among seedlots within varieties, but no seedlots were significantly better or worse than their varietal means at every plantation.

Of the characters studied in searching for a possible mechanism of resistance, winter foliage color was most highly correlated with resistance. Yellow varieties were least-attacked and green varieties were most-attacked. Height, mineral nutrients, and resistance patterns to other insects were not related with susceptibility to attack. There was a very limited correlation between two cortical monoterpenes and resistance to eucosma.

The varieties which are most preferred for Christmas tree planting are also most susceptible to eucosma, but variety *aquitana* was the least-attacked member of this group.

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Kim Carlyle Steiner

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INTRODUCTION

In Michigan and other northeastern states, Scotch pine is one of the most common ornamental and Christmas trees. Its short, blue-green foliage and its excellent adaptability are two of the many features of this tree species which make it popular. Unfortunately, however, it is afflicted with several damaging insect pests. One of these insects is the eastern pineshoot borer (*Eucosma gloriola* Heinrich).

Although a plant species may be characterized as being susceptible to an insect pest, it is sometimes possible to find individuals of that species which are inherently resistant. These resistant individuals can be bred, if desired, to produce a strain that is not subject to damage by the insect. However, if the plants that are resistant come from a certain part of the species range, one need only collect seed there to get plants which are less susceptible to insect damage. This study was intended to explore the possiblity that some of the Scotch pine varieties are inherently resistant to *Eucosma*. Known examples of genetic differences within plant species in resistance to insects are common in crop plants, but they are relatively rare in forest trees.

A BRIEF HISTORY

The study of insect resistance in plants is quite old. As early as 1831 one apple variety was known to be more resistant than other varieties to the woolly apple aphid, *Eriosoma lanigerum* (Hausm.). Later in the 19th century several varieties of winter wheat were found to be resistant to the Hessian fly, *Mayetiola destructor* (Say). But not until the early part of this century were concentrated efforts begun in breeding for resistance. These studies were mainly on economically important food plants and their more destructive pests. In his classic book, Painter (1951) reviewed these early studies and described the theory and application of breeding for insect resistance in crop plants.

Although research in agriculture preceded that in forestry, several possible cases of genetic insect resistance in forest tree species have been reported. Unfortunately, most of these studies do not present conclusive evidence because they suffered from a lack of replication.

Some of the research was fairly early. Hall (1942) reported that he thought several races of black locust (*Robinia pseudoacacia*) were resistant to the locust borer (*Megacyllene robiniae*). Austin et al. (1945) felt that they had found possible resistance to the resin midge (*Retinodiplosis* sp.) in ponderosa pine (*Pinus ponderosa*). Those trees with glaucous or glabrous shoots were less attacked than those with viscid shoots. Miller (1950) reported that the backcross hybrid {*Pinus jeffreyi* x (*P. jeffreyi* x *P. coulteri*)} was resistant to the pine reproduction weevil (*Cylindrocopturus eatoni*). This insect is a serious pest on Jeffrey pine, and a large-scale breeding program based on his results has been initiated (Libby, 1958).

Good evidence of insect resistance in forest trees was shown in a replicated test by Schreiner (1949). He found differences among full-sib clones of poplar (*Populus* sp.) seedlings in resistance to the Japanese beetle (*Popillia japonica*). Among the second-generation hybrid progeny of the same two species, some clones suffered no attack and others 100% attack. His paper is the earliest statistically adequate proof of genetic variability in insect resistance in forest trees.

Two recent studies in forestry show good statistical evidence of intraspecific differences in genetic resistance. Batzer (1962) demonstrated in a well-replicated experiment in Minnesota that some origins of jack pine (*Pinus banksiana*) were more susceptible than others to white pine weevil (*Pissodes strobi*). Wright et al. (1966 and 1967) studied European pine sawfly (*Neodiprion sertifer*) on Scotch pine at four replicated plantations in Michigan. In general, the resistance of a variety was correlated with its growth rate; the tallest varieties were attacked most. However, variety *uralensis* was much more resistant than expected for its height. They found that larval development was slower on that variety than on others. They also found possible differences in resistance to three other insects: white pine weevil, jack pine budworm, and pine webworm. For a more complete review of the literature on insect resistance in forest trees, see Gerhold et al. (1966).

THE TREE

Scotch pine (*Pinus sylvestris* L.) is the most widely distributed conifer in the world. It is also one of the most genetically variable forest trees. In northern Europe, where it is native, Scotch pine is the most important commercial timber species. In the United States, where it has been introduced, it is our most important plantation Christmas tree.

Its importance and variability have led to considerable study of insect resistance in Scotch pine. Much of the research has been in comparing this and other species in relative resistance to certain insects. Information on such differences is valuable in determining which species to plant on a site. Other research has been in investigating the possibilities of intraspecific differences in resistance to insects.

Scotch pine has been compared to other pines in relative susceptibility to European pine shoot moth (*Rhyacionia buoliana*) by Neugebauer (1952), Miller and Heikkenen (1959), Harris (1960), Haynes and Butcher (1962), Holst (1963), and Schönborn (1966). Bennett (1954) demonstrated that Scotch pine is more resistant to *Exoteleia pinifoliella* than lodgepole pine (*Pinus contorta*) or jack pine, possibly due to its larger number of resin canals. In an early study involving *Rhyacionia frustrana*, Graham and Baumhofer (1930) reported Scotch pine to be one of the most resistant of the five pines studied. These authors were ahead of their time in characterizing resistance as genetic variation in two factors -- preference for oviposition and ability to recover after attack.

Several possible examples of intraspecific differences in resistance have been cited for Scotch pine. In one of the earliest studies, MacAloney and Johnston (1933) reported that the "Riga strain" appeared to be most resistant to the white pine weevil; however, their report has not been substantiated by later studies. Rudolf and Patton (1966) also reported apparent genetic differences in resistance of Scotch pine to this insect.

Voûte (1940) observed that adults of *Pissodes piniphilus* seemed to prefer certain individual trees for oviposition. These trees were not diseased or weakened, and no other reason could be found for this preference. Skuhravý and Hochmut (1969) reported that certain geographic origins of Scotch pine were attacked more than others by *Thecodiplosis brachyntera*.

In the only replicated experiment to date, Wright et al. (1966 and 1967) found that resistance to European pine sawfly differed significantly among varieties of Scotch pine at four plantations. In smaller experiments they also found significant differences among varieties in attack by three other insects.

THE INSECT

The eastern pineshoot borer (*Eucosma gloriola* Heinrich, Lepidoptera, Olethreutidae), commonly called eucosma, is a pest of Scotch pine. This insect occurs east of the Rocky Mountains in Canada and the northern United States. In addition to Scotch pine, it has been reported to attack eastern white pine (*Pinus strobus*), red pine (*P. resinosa*), Austrian pine (*P. nigra*), pitch pine (*P. rigida*), jack pine, mugho pine (*P. mugho*), Norway spruce (*Picea abies*) and Douglas-fir (*Pseudotsuga menziesii*). However, its favorite hosts are eastern white pine and Scotch pine (Drooz, 1960).

Adults of eucosma are coppery-red moths with wing spans of about one-half inch. In late April or early May the females deposit their eggs on the needle sheaths of the trees' new growth. After a period of two to four weeks the larvae hatch and bore directly into the twigs. Usually only one larva per brood will survive to reach the pith of the twig. Once inside it mines up and down the pith from just above the node to near the tip.

The larvae become 1/2 to 1 inch in length. They feed until July when they bore exit holes, drop to the ground, and pupate. The damage to the trees occurs when the larvae girdle the stems from the inside shortly before exiting. This is considered to be an adaptive mechanism that prevents the insects from becoming entrapped in pitch as they leave the shoots. The attacked shoots die by late summer. For a more complete description of the insect and its damage, see Drooz (1960) and Newman (1968).

Damage caused by *E. gloriola* is similar to that of *Rhyacionia frustrana*, the Nantucket pine tip moth. Drooz (1960) stated that the importance of *E. gloriola* has gone unrecognized because of its confusion in the past with this other, better-known species.

Another similar species is *Eucosma sonomana* Kearfott. The life history of this insect is the same as that of *E. gloriola*. In fact, Heinrich, (1931) in his original description of *E. gloriola*, stated that it may be a race of *E. sonomana*. The hosts of these two species are similar; however, the latter has also been reported on ponderosa pine and Engelmann spruce (*Picea engelmannii*). DeBoo (1967) examined specimens referred to as *E. sonomana* on jack pine in Minnesota and concluded that the insect was actually *E. gloriola* and that *E. sonomana* is restricted to the western states where ponderosa pine grows. According to Butcher and Hodson (1949), damage from *E. sonomana* has also been often attributed to *Rhyacionia frustrana*.

Damage from *Eucosma* sp. is sometimes important. Drooz (1960) reported that high incidence of leader attack by *E. gloriola* on Scotch pine is a serious problem to Christmas tree growers. Butcher and Hodson (1949) and Shenefelt and Benjamin (1955) observed, respectively, up to 70% and 90% of the leaders on jack pine to be destroyed by *E. sonomana* (or *E. gloriola*). Repeated attacks reduced growth and resulted in a bushy appearance characterized by the absence of a dominant leader.

Genetic studies on resistance to either *E. gloriola* or *E. sonomana* are inconclusive and have been performed only on jack pine. In a study of eight geographic origins in a 9-year old plantation of this tree species, Butcher and Hodson (1949) reported possible differences in susceptibility to *E. sonomana* (or *E. gloriola*). However, they were cautious in attaching significance to the results since diversity with respect to site and age had not been considered in the analysis. These results were contradicted by those of Schantz-Hansen and Jensen (1952) from a study done on jack pine in the same area (in Minnesota). They found no relation between source of seed and the amount of infestation. In their analysis, they included 32 origins, from New Brunswick and Maine to Alberta and Minnesota.

More recently, King (1971) reported a study of *E. gloriola* attack on 11 replicated plantations of jack pine in Minnesota, Wisconsin, and Michigan. The plantations included 26 geographic origins from these three states. None of the 8 plantations which were attacked five years after planting showed significant differences among seed sources in amount of attack. However, three of the four plantations which were heavily attacked 10 years after planting showed significant differences among seed sources. Seed source x plantation interaction was also significant. Most of the variation was explained by a negative correlation between attack incidence and 10-year height.

OBJECTIVES

The principal objective of the present study was to determine if there are genetic differences among varieties and among seedlots (seed sources) within varieties of Scotch pine in resistance to attack by *Eucosma gloriola*. A secondary objective was to determine the possible mechanism of resistance by attempting to correlate attack with other genetically-controlled and variable characteristics of this tree species.

MATERIAL AND METHODS

THE PLANTATIONS

In 1961, Michigan Agricultural Experiment Station, in cooperation with other states, established several plantations of Scotch pine as part of the NC-51 range-wide provenance test of this species. These plantations were established with 2-0 seedlings grown from seed obtained in 110 native stands of Scotch pine, although every stand is not necessarily represented in each plantation. In the present study the offspring of a single stand are referred to as a seedlot. These 110 seedlots represent the entire range of this species in Europe and Asia.

The plantations are arranged in a randomized complete block design, with an 8 x 8 foot spacing between trees. Each seedlot is represented once in each block by a 4-tree plot. Further details of the history and design of these plantations can be found in Wright and Bull (1963).

This experiment has been the basis of many studies on Scotch pine. Wright and Bull (1963) studied geographic variation on the basis of seedling performance. Steinbeck (1965) examined trees in some of the plantations for differences among the seedlots in foliar mineral accumulation. Wright et al. (1966) analyzed variation in mortality, growth rate, winter color, needle length, winter injury, flower production, and susceptibility to four insects at 31 plantations in eight north-central states. Ruby (1964) used the material for part of his work on the taxonomy of Scotch pine. He recognized 21 varieties of this species. Wright et al. (1967) detected differences among the varieties in resistance to European pine sawfly. Tobolski (1968) used the plantations for part of his study on the variation in monoterpene composition among varieties and half-sib families of Scotch pine.

The location and size of the three plantations used in my study are given in the following tabulation. Further descriptions are contained in the succeeding paragraphs.

Plantation	County	North Lat.	West Long.	No. of Seedlots	No. of Blocks
		o	o		
Allegan	Allegan	42.5	86.0	70	10
Rose Lake	Shiawassee	42.8	84.3	76	7
Kellogg	Kalamazoo	42.3	85.3	106	6

Allegan Recreation Area is located near the town of Allegan, Michigan. The Scotch pine plantation here was nearly perfect for this study. The trees were well-formed, mortality had been negligible, and damage from winter injury and other insects was very slight. The plantation occupies a level site and is well-separated from other tall trees. Average height was the lowest of any plantation, probably due to the sandy, infertile soil. The canopy was still open at the time of this study. Eucosma infestation was heavy in 1970.

Rose Lake Wildlife Experiment Station is located 10 miles northeast of Michigan State University, East Lansing, Michigan. The Scotch pine plantation, located on a gentle slope, is bordered by a gravel road, a small grassy field, a hedge of multiflora rose, and a tall Scotch pine windbreak. Some trees were more than 20 feet tall at the time of this study, and the canopy was beginning to close. Eucosma infestation was heavy in 1970.

W. K. Kellogg Experimental Forest is located 15 miles from Battle Creek, Michigan. The site is rolling, and the Scotch pine plantation occupies the middle and both sides of a large draw. In places the slope is as much as 30%. This plantation is surrounded by other plantations, but it is separated from them by fire lanes. Many trees exceeded 20 feet in height at the time of this study, and the canopy was beginning to close. Some slower-growing seedlots were less than knee height, but this was true at all plantations. Eucosma infestation was light at this plantation in 1970.

MEASUREMENT OF ATTACK

As early as 1968, *Eucosma gloriola* began to invade these plantations. In the autumn of that year, George Howe and Warren Nance, graduate students at Michigan State University, counted the number of trees attacked in each plot at Allegan. In the autumn of 1969, Fred Hain, another graduate student, counted the number of trees attacked by this insect at Rose Lake.

This was the situation when, at the suggestion of Dr. J. W. Wright, I elected to look for possible variation in resistance to this insect. In the autumn of 1970, I counted the number of trees attacked at the Kellogg plantation and made new counts at the Allegan and Rose Lake plantations. Measurements were also made of the total number of attacks in each plot (4 trees).

The measurements to be statistically analyzed comprised eight sets of data: the number of attacks per plot at Allegan (1970), Rose Lake (1970), and Kellogg (1970); and the number of trees attacked per plot at Allegan (1968), Allegan (1970), Rose Lake (1969), Rose Lake (1970), and Kellogg (1970).

STATISTICAL ANALYSIS

Analysis of Variance

An analysis of variance was performed on each of the 8 sets of data using the plot totals as items. When there were one or two trees dead on a plot, the plot totals were adjusted to a 4-tree basis. If there were more than two trees dead on a plot, that plot was not considered in the analysis. For missing plots I substituted the seedlot mean, and subtracted an appropriate number of degrees of freedom from the error term.

The total variation in attack for each set of data was separated into the variances due to blocks, error, and seedlots. The seedlot variance was then separated into that due to variety differences (using varieties recognized by Ruby, 1964) and that due to seedlot-within-variety differences. In order to determine the levels of significance, the seedlot-within-variety variance term was tested against the error variance of seedlots within varieties.

Analysis of Seedlot X Year Interaction

Seedlot x year interaction is an estimate of the differences between years in the relative incidence of attack among seedlots in the same plantation. I calculated the 1968 versus 1970 interaction for Allegan and the 1969 versus 1970 interaction for Rose Lake, using data on percentage of trees attacked. The interaction variance term for each plantation was tested over its pooled error variance to determine significance.

There was one important problem associated with testing the seedlot x year interaction terms. At each plantation the error variances for the two years were unequal. Cochran and Cox (1957) give a conservative procedure to follow in such cases. I applied both their procedure and the normal procedure to the analyses and obtained the same significance levels.

Evaluation of Varietal Differences

Number of attacks per tree. To determine the significance of individual varietal differences for these data, I used the Student-Newman-Keuls least significant range procedure (Sokal and Rohlf, 1969), which is one of the more conservative multiple range tests. I applied the test separately to the data for each plantation. In this method the significance of the difference between two varieties is based upon their distance apart in rank, their sample sizes, and the error variance. Because the varieties often had unequal sample sizes, it was necessary to employ weighted averages.

Number of trees attacked per plot. To analyze these data, I chose to use one of the tests for proportions which approximate the Chi-Square distribution. For this purpose the data were converted into percentage of trees attacked in each variety.

A preliminary test using the "chi-square" test of differences showed that Allegan (1970) and Rose Lake (1970) were so highly attacked that very few differences could be found. For this reason these plantations were ignored for those years, and the results for the remaining plantations and years were combined to obtain an overall percentage of attack for each variety.

These proportions were analyzed by the G-statistic of Sokal and Rohlf (1969). Each variety was compared to every other variety. A significant difference in this test is based upon the magnitude of difference between the observed proportion of trees attacked and the expected proportion. The expected proportion is calculated on the assumption that there exists no real difference between the varieties.

GENETIC DIFFERENCES IN RESISTANCE

DIFFERENCES WITHIN AND AMONG VARIETIES

There were highly significant differences in attack among seedlots, indicating that there are genetic differences in resistance. This was true at all plantations and in all years (Tables 1 to 4). Most of the variation among seedlots was due to differences among varieties rather than differences among seedlots within varieties -- as indicated by the smaller F-values of the latter. This tends to support Ruby's (1964) method of grouping the seedlots into varieties.

Consequently, the differences within varieties were less consistent. At Rose Lake (1970) this variance term was significant for both number of attacks per tree and percentage of trees attacked, and at Allegan (1970) it was significant for number of attacks per tree (Tables 2 and 4). But all other plantations and years did not show significant differences among seedlots within varieties. No particular seedlots departed significantly from the varietal averages in all plantations or in all years.

Wright et al. (1966) stated that the within-variety variation in the traits they measured was best considered to be geographically at random. This seems to be true for

Table 1.--Varietal differences in number of eucosma attacks per tree at each of three plantations in 1970. Varieties not sharing the same letter are significantly different at the 5% level.

Variety of Scotch pine	Attacks per tree			Rank 1=fewest attacks 19=most attacks			Significance of differences		
	Allegan	Rose Lake	Kellogg	Allegan	Rose Lake	Kellogg	Allegan	Rose Lake	Kellogg
			Scandinavian and Siberian Varieties						
lapponica	1.0	1.4	.1	2	2	1	a	ab	a
mongolica	.3	.5	.2	1	1	2	a	a	ab
altaica	2.7	2.0	.3	3	3	4	b	ab	ab
septentrionalis	4.0	3.1	.3	8	9	5	cd	ab	ab
rigensis	4.1	3.9	.4	9	11	6	cd	ab	ab
uralensis	4.7	2.5	.2	13	5	3	d	ab	ab
			Central European Varieties						
polonica	3.0	2.0	1.1	5	4	17	bc	ab	bcd
borussica	3.2	2.7	.6	6	7	9	bc	ab	abc
hercynica	3.6	3.7	.7	7	10	11	bcd	ab	abc
haguenensis	2.8	2.6	.6	4	6	8	b	ab	abc
'East Anglia'	- -	3.1	.5	-	8	7	---	ab	abc
pannonica	5.0	5.5	.8	14	13	12	de	abc	abcd
illyrica	4.5	4.7	1.0	11	12	15	cd	abc	bcd
			West and South European Varieties						
'North Italy'	- -	9.1	1.0	-	17	16	---	d	bcd
scotica	- -	10.1	.6	-	19	10	---	d	abc
iberica	4.4	9.3	1.3	10	18	19	cd	d	d
aquitana	4.7	7.4	1.0	12	15	13	d	cd	bcd
rhodopaea	5.9	5.6	1.2	15	14	18	e	bc	cd
armena	6.0	7.8	1.0	16	16	14	e	cd	bcd

Table 2.--Analyses of variance for number of eucosma attacks per tree at each of three plantations in 1970.

Plantation and year	Block	Variety	Seedlot within variety	Error
		Degrees of Freedom		
Allegan (1970)	9	16	53	603
Rose Lake (1970)	6	19	56	419
Kellogg (1970)	5	19	86	508
		Mean Squares		
Allegan (1970)	229.5522[a]	820.2825	122.7362	35.0977
Rose Lake (1970)	1551.1550	2581.9478	226.6273	167.3841
Kellogg (1970)	13.8080	54.9373	6.2298	5.8371
		F - Values		
Allegan (1970)	6.54***	6.68***	3.50***	- -
Rose Lake (1970)	9.27***	11.39***	1.35*	- -
Kellogg (1970)	2.37*	8.82***	1.07	- -

a) Analyses were computed using 4-tree plot totals. Divide mean squares by 16 to convert to a per-tree basis.

*, ***) Indicates significance at the 5 and 0.1% levels, respectively.

Table 3.--Percentage of trees attacked by eucosma in each variety in all plantations and years.

Variety of Scotch pine	Percent of trees attacked at					Weighted average
	Allegan		Rose Lake		Kellogg	
	1968	1970	1969	1970	1970	
Scandinavian and Siberian Varieties						
lapponica	2	49	25	79	5	24
mongolica	--	18	0	32	15	16
altaica	11	88	30	75	18	48
septentrionalis	15	94	25	80	22	50
rigensis	25	98	38	81	33	59
uralensis	14	98	24	73	15	48
Central European Varieties						
polonica	27	96	29	79	58	61
borussica	32	98	38	73	33	59
hercynica	37	95	42	82	47	63
haguenensis	40	94	37	76	38	59
'East Anglia'	--	--	32	75	38	46
pannonica	36	100	54	89	46	69
illyrica	25	100	46	86	63	67
West and South European Varieties						
'North Italy'	--	--	58	92	54	69
scotica	--	--	36	100	43	52
iberica	52	98	61	94	59	75
aquitana	45	99	49	94	50	68
rhodopaea	52	99	49	95	56	72
armena	42	99	60	95	49	68
Plantation mean	32	93	40	83	39	59

Table 4.--Analyses of variance for percentage of trees attacked by eucosma at each of three plantations in different years.

Plantation and year	Block	Variety	Seedlot within variety	Error
		Degrees of Freedom		
Allegan (1968)	6	15	53	393
Allegan (1970)	9	16	53	605
Rose Lake (1969)	6	19	56	431
Rose Lake (1970)	6	19	56	419
Kellogg (1970)	5	19	86	508
		Mean Squares		
Allegan (1968)	6.2750[a]	9.7500	1.4989	1.2143
Allegan (1970)	.3911	10.6043	.3384	.2479
Rose Lake (1969)	34.7183	7.2179	1.2291	.9477
Rose Lake (1970)	8.5450	4.0463	1.1084	.6986
Kellogg (1970)	2.7220	12.0742	1.1331	1.1257
		F - Values		
Allegan (1968)	5.17***	6.50***	1.23	- -
Allegan (1970)	1.58	31.34***	1.36	- -
Rose Lake (1969)	36.63***	5.87***	1.30	- -
Rose Lake (1970)	12.23***	3.65***	1.59**	- -
Kellogg (1970)	2.42*	10.66***	1.01	- -

a) Analyses were computed using numbers of trees attacked per plot.

*, **, ***) Indicates significance at the 5, 1, and 0.1% levels, respectively.

resistance to eucosma attack, also. In any particular variety, northern seedlots performed the same, on the average, as southern seedlots. However, considering the means of all varieties, there was a noticeable north to south trend in number of attacks per tree (Table 1). Northern varieties were attacked least and southern varieties were attacked most. This is in agreement with the results of studies on other genetically variable traits in Scotch pine. Most characters which vary do so in a north to south manner (Wright and Bull, 1963).

There was one striking departure from the latitudinal trend. This occurred at Allegan. The northern Asian variety *uralensis* had significantly more attacks per tree than some of the central European varieties. This was also true to a lesser extent for the northern European varieties *septentrionalis* and *rigensis*.

Table 1 shows which varieties differed from one another in average number of attacks per tree. At Rose Lake all northern and central European varieties were not significantly different. The western European variety *scotica* was most highly attacked and tended to group with the southern European varieties. Of the southern varieties, *rhodopaea*, with the fewest attacks in this group, was most unlike the others. At Kellogg all varieties except for three were not significantly different. This was because of the overall low degree of infestation. Variety *lapponica* had significantly fewer attacks per tree than varieties *rhodopaea* and *iberica*, but the latter were not significantly different from one another.

Among the varieties which performed most consistently, *mongolica* and *lapponica* warrant special comment. At all plantations (Tables 1 and 3) these varieties were least attacked. This was probably because they are by far the shortest of all the varieties and offer only small targets for attack. This was especially true at Allegan, where occasional individuals in these varieties were less than one foot tall at age 11.

CONSISTENCY IN THE RESULTS

In Tables 1 and 3 I list the number of attacks per tree and the percentage of trees attacked in each variety for all plantations and years. These tables show good consistency in the results from different plantations and years. Nevertheless, there were a few apparent variety x plantation interactions. Some can be explained as probable artifacts. For example, in Table 1 the unusually high (relative to other plantations) number of attacks on variety *uralensis* at Allegan is largely due to two exceptional plots. The other 18 plots in that variety were much less attacked.

Several inconsistencies, however, cannot be explained in this manner. In Table 1, variety *scotica* had relatively many more attacks per tree at Rose Lake than at Kellogg; and variety *iberica* had relatively fewer attacks per tree at Allegan than at Rose Lake and Kellogg. In Table 3, variety *polonica* had a relatively larger percentage of trees attacked at Kellogg than at Allegan (1968) and Rose Lake (1969); and variety *illyrica* had a relatively smaller percentage of trees attacked at Allegan (1968) than at Rose Lake (1969), and a relatively larger percentage of trees attacked at Kellogg than at Rose Lake (1969).

The data offer no clues to the reasons for these apparent interactions. However, interaction of insect resistance with site is not unusual. According to Painter (1951) edaphic factors can influence insect resistance in a plant. Thus, differences in the responses of varieties to an edaphic factor can indirectly affect their relative insect resistance.

Two plantations were statistically analyzed for consistency in the results from different years (Table 5). Seedlot x year interaction was highly significant at Allegan (1968 and 1970), but not significant at Rose Lake (1969 and 1970). Inspection of Table 3 reveals the source of the inconsistency in results between years at Allegan. The interaction may be considered an artifact due to differences in insect population levels in different years rather than differences in the relative resistance of some varieties. Many varieties which were significantly different in 1968 were virtually the same in 1970, causing the interaction term in Table 5 to be significant.

The fact that differences among varieties in percentage of trees attacked decreased under high levels of insect population does not necessarily mean there are no genetic differences in resistance. Insect resistance in plants usually exhibits continuous variation. It is rarely an absolute, all or none, character. Under high population levels the chances become proportionately smaller of a tree escaping attack entirely.

Table 5.--Analyses of variance for percentage of trees attacked by eucosma combined over two years at each of two plantations. Seedlot variation is principally due to varietal differences.

Plantation and year	Year	Seedlot	Seedlot x year	Pooled error
		Degrees of Freedom		
Allegan (1968 and 1970)	1	69	69	998
Rose Lake (1969 and 1970)	1	75	75	850
		Mean Squares		
Allegan (1968 and 1970)	1779.48[a]	4.2499	1.8662	.6458
Rose Lake (1969 and 1970)	783.43	3.6385	.9604	.8232
		F - Values		
Allegan (1968 and 1970)	953.63***	2.16**	2.89***	- -
Rose Lake (1969 and 1970)	816.07***	3.79***	1.17	- -

a) Analyses were computed using numbers of trees attacked per plot.

, *) Indicates significance at the 1 and 0.1% levels, respectively.

Although high population levels can increase the absolute number of attacks per tree, the relative number of attacks per tree should not be affected if differences are due to genetic resistance. So it is that Allegan (1970) showed few differences in percentage of trees attacked (Table 3) but many in number of attacks per tree (Table 1). For example, *haguenensis* and *septentrionalis* both had 94% of their trees attacked at Allegan in 1970, but the former averaged 2.8 attacks per tree and the latter averaged 4.0 attacks per tree, a difference which is significant. The conclusion that there are genetic differences in resistance to eucosma is not weakened by the lack of differences in percentage of trees attacked at Allegan (1970).

It is interesting to note that although the attack level was high at Allegan in 1970, there were a few individual trees that escaped attack entirely, even in the varieties which had many attacks per tree. This was emphasized in the field where I occasionally observed a single unattacked tree in an otherwise highly-attacked 4-tree plot.

Almost all trees were attacked in years of heavy infestation. Therefore, to look at differences among varieties in percentage of trees attacked, I used only the data from years of moderate infestation: Allegan (1968), Rose Lake (1969), and Kellogg (1970). Table 6

Table 6.--Varietal differences in percentage of trees attacked by eucosma averaged for three plantations in years of moderate infestation[1], with 1971 relative height averaged for four plantations[2]. Varieties not sharing the same letter are significantly different at the 5% level.

Variety of Scotch pine	Trees attacked (% of total)	Significance of differences	Relative height (% of mean)[3]
Scandinavian and Siberian Varieties			
lapponica	7	a	55
mongolica	9	ab	93
altaica	18	abc	76
septentrionalis	21	bcde	82
rigensis	31	cdef	96
uralensis	19	abcd	92
Central European Varieties			
polonica	37	fgh	112
borussica	34	defg	112
hercynica	42	fghij	119
haguenensis	38	fgh	124
'East Anglia'	36	efgh	111
pannonica	47	fghijk	114
illyrica	44	fghijk	110
West and South European Varieties			
'North Italy'	56	jk	101
scotica	41	fghi	99
iberica	58	k	86
aquitana	49	ghijk	106
rhodopaea	53	ijk	104
armena	51	hijk	94

[1]) Allegan (1968), Rose Lake (1969), and Kellogg (1970).

[2]) Kellogg and three similar plantations in Cass, Newaygo, and Crawford counties in southern Michigan.

[3]) Mean height of the four plantations was 12.1 feet.

shows specifically which varieties differed significantly from one another at these combined plantations using the G-statistic of Sokal and Rohlf (1969).

This made it possible to look at consistency in results between number of attacks per tree and percentage of trees attacked. In general the results presented in Table 6 agree well with those presented in Table 1. To be more certain of this consistency, I regressed mean number of attacks per plot (a function of mean number of attacks per tree) for those seedlots common to all plantations on the percentages of trees attacked in those seedlots at Allegan (1968), Rose Lake (1969), and Kellogg (1970):

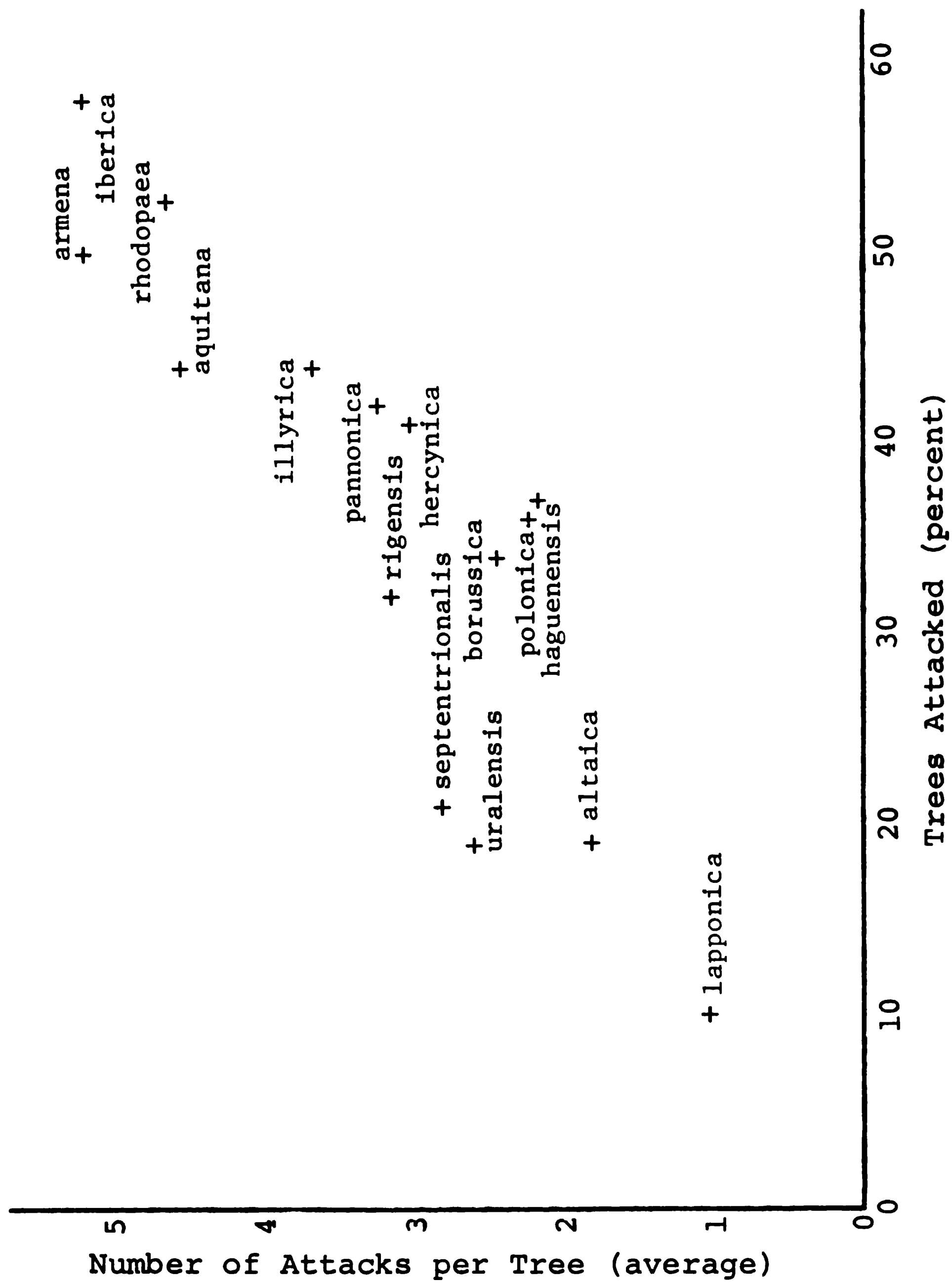
Source	df	Mean Squares	F
Regression	1	584.11	47.72***
Residual	56	12.24	
Total	57		

***) Indicates significance at the 0.1% level.

The significance of the regression shows that the two measurements agreed well in their results (r = .68).

In Figure 1, I have plotted mean number of attacks per tree and percentage of trees attacked for each variety. Most varieties fall close to the regression, with the exceptions that varieties *polonica* and *haguenensis* had

Figure 1.--Relation between percentage of trees attacked by eucosma and number of attacks per plot. (Averaged over three plantations using only seedlots common to those plantations.)



armena
iberica
rhodopaea
aquitana
illyrica
pannonica
hercynica
rigensis
borussica
septentrionalis
polonica
haguenensis
uralensis
altaica
lapponica
0
10
20
30
40
50
60
Trees Attacked (percent)
0
1
2
3
4
5
Number of Attacks per Tree (average)

FIGURE 1.

more trees attacked than varieties *uralensis* and *septentrionalis*, but the former varieties sustained fewer attacks per tree than the latter. However, only *haguenensis* was significantly (α = 1%) off the regression line and this may have occurred by chance.

However, if these incongruities are real and not due to error, then they may mean that the two measurements reflect different resistance mechanisms in those varieties, or that interactions in the insect-host relationship are occurring in those varieties. For example, if the presence of one insect influenced the presence of others, the two counts would be affected differently. Nevertheless, there is not sufficient reason at present to conclude that the two measurements are not equivalent at low and moderate levels of attack.

Table 6 shows even more clearly than Table 1 a latitudinal trend in amount of attack. Northern varieties had the fewest trees attacked, southern varieties the most. It is noteworthy that the western European variety *scotica* is more similar to the central European varieties in percentage of trees attacked but to the southern European varieties in number of attacks per tree. This variety is usually grouped with the southern European varieties in other traits: growth rate, color, needle length, and resistance to European pine sawfly (Wright et al., 1966).

The general consistency in results between the two measurements reinforces the conclusion that there are genetic differences in resistance to eucosma in Scotch pine. The next problem to be considered is what causes resistance.

POSSIBLE MECHANISMS OF RESISTANCE

GENERAL MECHANISMS

Painter (1951) listed three major mechanisms of resistance. They are as follow.

(1) Nonpreference is the tendency of a plant to be unattractive or repulsive to an insect. Plants are nonpreferred if they do not present stimuli to which the insect has a positive response, or if they do present stimuli to which the insect has a negative response. These stimuli may be visual, tactile, or by taste or smell. Lack of a color attractant normally present would be an example of nonpreference resistance.

(2) Antibiosis is the adverse effect of a plant on the biology of an insect. This resistance mechanism in plants is usually chemical. For example, a monoterpene may be present which is toxic to insects of a certain species. Some plants may be preferred for oviposition by the adults and yet have antibiotic effects on the larvae.

(3) Tolerance is the ability of the plant to recover after an insect attack, or the ability to incur attack without detrimental effects. If an attacked plant were able to quickly form wound tissue, its resistance would be

classed as tolerance.

The present evidence is insufficient to definitely eliminate any of these three general mechanisms from consideration. However, it seems improbable that the young Scotch pine twigs can exhibit tolerance to invasion by the large eucosma larvae. Some adverse effects on the tree undoubtedly result from any successful attack. Therefore, the two most likely manners in which resistance to eucosma may operate are (1) nonpreference by the adult for oviposition and (2) antibiotic effects on the larvae. Resistance could be due to one or both of these general mechanisms.

DISTINCTIVE FEATURES OF RESISTANT AND SUSCEPTIBLE VARIETIES

There was a general latitudinal trend in resistance -- southern varieties were attacked much more than northern ones. Therefore, I examined other traits which varied with latitude in a search for a possible mechanism of resistance. The among-variety differences in amount of attack were much greater than the within-variety differences, so I devoted most of my attention to varietal means.

Height

Height or growth rate is sometimes suggested as being a factor in insect resistance. For example, Wright et al. (1967) found that susceptibility to European pine sawfly generally increased with increasing height of Scotch pine, and King (1971) reported that incidence of attack by eucosma on jack pine generally decreased with increasing height.

Height measurements made in 1971 were available for the Kellogg and three other southern Michigan plantations. They are summarized in Table 6. It is apparent from this table that eucosma attack was not related to height. For example, varieties *rigensis* and *armena* were virtually the same height but had significantly different amounts of attack. The heavily attacked southern varieties were only of medium height and the fastest-growing variety, *haguenensis*, suffered only moderate attack (Tables 1 and 6).

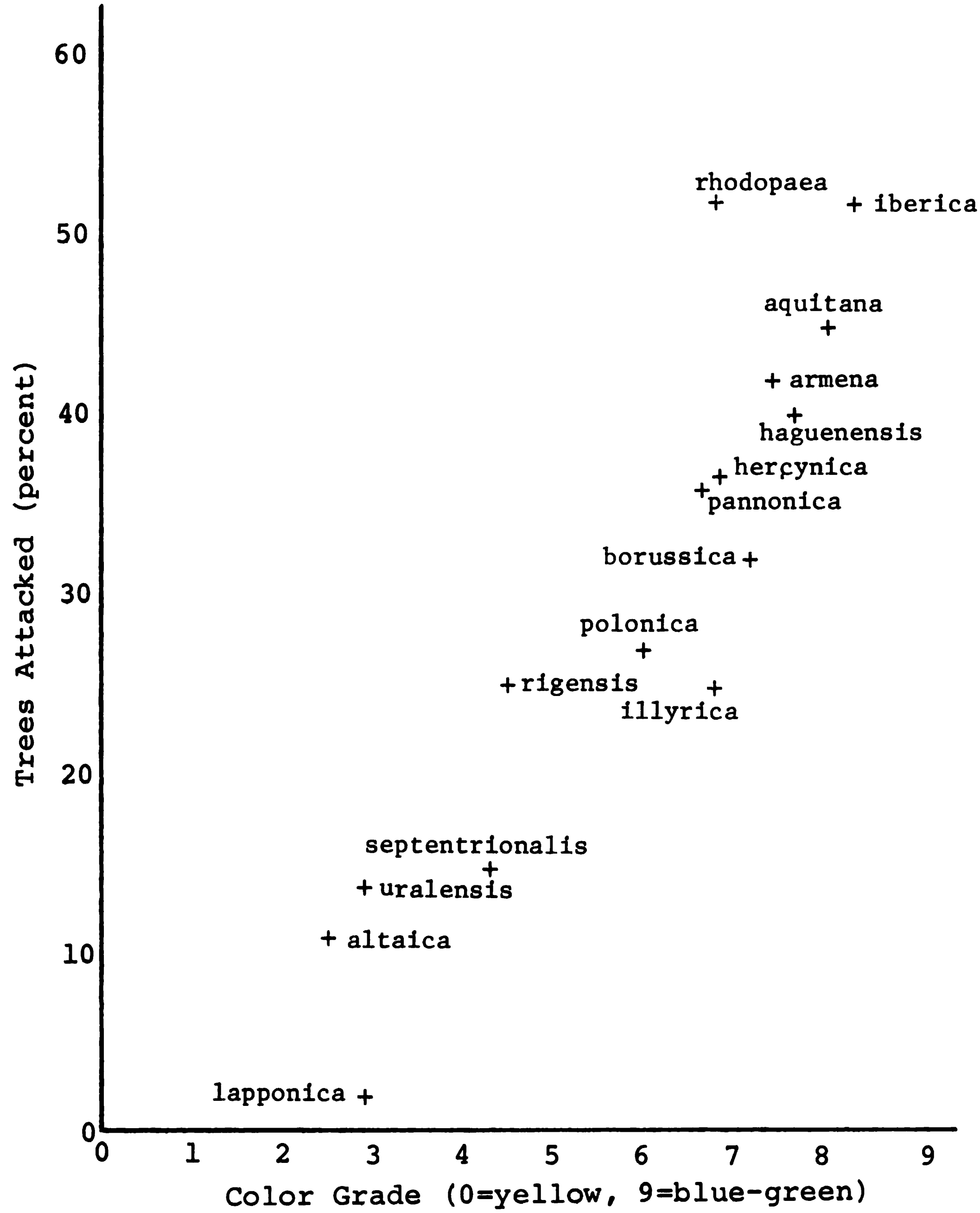
Color

The character which varies most consistently with latitude and eucosma resistance is winter foliage color. The southern-most varieties remain blue-green throughout the year. But in the autumn, trees from progressively more northern localities retain less green in the needles and develop a conspicuous yellow foliage color. In the spring, the color change reverses and the trees become green. This happens when there are three successive days above 60° F (White and Wright, 1967). In Michigan, this usually occurs in April. Eucosma oviposit in late April or early May.

In the winter of 1970-71, I measured color at the Allegan plantation, using color grades of 0 = yellow to 9 = green, as used previously by Wright et al. (1966). The results I obtained were very similar to those and other previous measurements. My color data were compared with the percentages of trees attacked at the same plantation in 1968 (Figure 2). There was a strong correlation between amount of attack and winter color. The varieties which remained greenest during the winter were attacked most heavily.

I calculated the regression of number of trees attacked per plot on color, using seedlot means. The results are as follow:

Figure 2.--Relation between percentage of trees attacked by eucosma and winter foliage color. (Measured at Allegan in 1968 and 1970, respectively.)



Trees Attacked (percent)
0
10
20
30
40
50
60
rhodopaea
iberica
aquitana
armena
haguenensis
hercynica
pannonica
borussica
polonica
rigensis
illyrica
septentrionalis
uralensis
altaica
lapponica
0
1
2
3
4
5
6
7
8
9
Color Grade (0=yellow, 9=blue-green)

FIGURE 2.

Source	df	Mean Squares	F
Regression	1	10,879.9	91.74***
Residual	67	118.6	
Total	68		

***) Indicates significance at the 0.1% level.

This regression accounted for 58% of the variation in attack (r = .76; number of trees attacked per plot = -10.1 + {6.9}{color grade}).

If color is a factor in resistance, it may operate on female eucosma moths as they select trees for oviposition. Painter (1951) quoted a study by Weiss on the response of 50 species of insects in several orders to different wavelengths of light. Weiss found that ultraviolet and blue-blue-green light were most attractive to the insects and that red and yellow light were least attractive. Thus, it is possible that eucosma can differentiate foliage color and be attracted most to the trees which are greenest at the time of oviposition.

Mineral Nutrients

Steinbeck's (1965) foliar mineral nutrient accumulation data were re-examined. None of the 12 elements studied by him were correlated with resistance to eucosma.

Monoterpenes

Amount of eucosma attack was also compared to Tobolski's (1968) data on percent composition of 11 cortical monoterpenes. A relationship of some of these with resistance would be reasonable since eucosma bores through the cortex on its way to the pith. Terpenes have been suggested as factors in insect resistance by previous investigators (Smith, 1965; Gilbert and Norris, 1968).

However, upon comparing the varietal means for his data with those for my data there appeared no trends between resistance and any of the 11 monoterpenes, with two obscure exceptions. Among the southern and western varieties, *scotica* had the smallest percentage of attacked trees, the least α-pinene, and the most 3-carene; and *iberica* had the greatest percentage of attacked trees, the most α-pinene, and the least 3-carene. However, this relationship did not hold for all the varieties.

COMPARISON WITH RESISTANCE PATTERNS TO OTHER INSECTS

Wright et al. (1966) and Wright and Wilson (1971) found five other insects (European pine sawfly, white pine weevil, jack pine budworm, pine webworm, and pine root collar weevil) whose attack differed significantly among varieties of Scotch pine (Table 7). These studies were performed on the same seedlots and some of the same plantations as the present study. Comparison of Tables 1 and 6 with Table 7 indicates no common trends in resistance. Scotch pine resistance to eucosma is apparently unrelated to its resistance to these other five insects.

Table 7.--Varietal differences in susceptibility to attack by five insect pests, as reported by Wright et al. (1966) and Wright and Wilson (1971).

Variety of Scotch pine	Percent of trees attacked by				
	European pine sawfly	White pine weevil	Jack pine budworm	Pine webworm	Pine root collar weevil
Scandinavian and Siberian Varieties					
lapponica	0.2	12	39	- -	14
mongolica	1.1	20	52	0.0	53
altaica	.9	45	21	- -	30
septentrionalis	2.4	57	43	.0	37
rigensis	6.1	76	46	1.2	45
uralensis	3.2	86	34	.0	40
Central European Varieties					
polonica	19.1	77	80	.0	67
borussica	20.6	41	55	.0	68
hercynica	19.5	80	54	1.9	43
haguenensis	25.7	65	42	1.1	70
'East Anglia'	26.5	--	--	- -	39
pannonica	20.1	97	25	10.0	52
illyrica	18.7	68	54	10.0	10
West and South European Varieties					
'North Italy'	11.6	--	--	3.8	10
scotica	6.5	--	--	7.5	18
iberica	10.6	15	22	7.0	17
aquitana	9.6	72	23	2.0	12
rhodopaea	9.3	72	38	10.0	18
armena	6.7	46	35	10.0	12
Significance, variety	**	**	**	**	**
Significance, within variety	ns	*	*	ns	ns

*, **) Indicates significance at the 5 and 1% levels, respectively.

PRACTICAL APPLICATION

Differences among varieties were much greater than differences within varieties. So the most gain in resistance can be made by selecting among the varieties. Variety *uralensis*, which is intermediate in growth rate, averaged fairly low in amount of attack. Variety *haguenensis*, the fastest-growing variety, was intermediate in percentage of trees attacked and below average in number of attacks per tree. However, neither of these varieties are preferred for Christmas tree planting. The southern and western varieties are most commonly planted for this purpose. These varieties were least resistant to eucosma. Of the varieties suitable for Christmas-tree use, variety *aquitana* had by a small margin the fewest attacks per tree. It also has good color, short needles, modest growth rate, high resistance to pine root collar weevil, and moderate resistance to European pine sawfly.

Differences among seedlots within varieties were significant at two plantations, but no particular seedlots were exceptional in resistance at both. The within-variety variation seemed to be at random geographically. Growers who wish to procure quality seed of a particular variety can only expect seed of average quality for that variety, regardless of what part of the range it comes from.

I was not able to determine the cause of resistance, but it is not necessary to know this for breeding purposes. Color was highly correlated with resistance, but probably not enough to warrant selection on the basis of color, especially if there is a moderate level of insect attack with which to distinguish resistant trees.

SUMMARY

Larvae of the *Eucosma gloriola* moth kill young twigs on Scotch pine, causing unsightly damage. To determine if some varieties of this tree are genetically resistant to eucosma, attack was measured on 110 seedlots of Scotch pine belonging to 19 varieties. The trees were planted at three locations in southern Michigan: Allegan County (70 seedlots), Shiawassee County (76 seedlots), and Kalamazoo County (106 seedlots). Each plantation was measured in either one or two different years. Most results were consistent from plantation to plantation and year to year.

There were highly significant differences in attack among seedlots in all plantations and years, indicating that there are genetic differences in resistance. Most of the variation was due to differences among varieties. At the most heavily-attacked plantation, the short northern varieties had from 1 to 4 attacks per tree, the tall central European varieties had from 2 to 6 attacks per tree, and the medium-height southern and western varieties had from 6 to 10 attacks per tree.

Some variation was due to differences among seedlots

within varieties, but no seedlots were significantly better or worse than their varietal means at every plantation.

Of the characters studied in searching for a possible mechanism of resistance, winter foliage color was most highly correlated with resistance. Yellow varieties were least-attacked and green varieties were most-attacked. Height, mineral nutrients, and resistance patterns to other insects were not related with susceptibility to attack. There was a very limited correlation between two cortical monoterpenes and resistance to eucosma.

The varieties which are most preferred for Christmas tree planting are also most susceptible to eucosma, but variety *aquitana* was the least-attacked member of this group.

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APPENDIX

Table A1.--Varietal differences in percentage of trees attacked by eucosma at Allegan and Rose Lake in 1970, a year of heavy infestation at those plantations. The data were analyzed by the "chi-square" test of proportions. Varieties not sharing the same letter are significantly different at the 5% level.

Variety of Scotch pine	Trees attacked (% of total)		Significance of differences	
	Allegan	Rose Lake	Allegan	Rose Lake
	Scandinavian and Siberian Varieties			
lapponica	49	79	b	b
mongolica	18	32	a	a
altaica	88	75	c	b
septentrionalis	94	80	c	b
rigensis	98	81	c	b
uralensis	98	73	c	b
	Central European Varieties			
polonica	96	79	c	b
borussica	98	73	c	b
hercynica	95	82	c	b
haguenensis	94	76	c	b
'East Anglia'	--	75	c	b
pannonica	100	89	c	b
illyrica	100	86	c	b
	West and South European Varieties			
'North Italy'	--	92	c	b
scotica	--	100	c	b
iberica	98	94	c	b
aquitana	99	94	c	b
rhodopaea	99	95	c	b
armena	99	95	c	b

Table A2.--Number of attacks by eucosma in each seedlot at all plantations in 1970, and average color grade of each seedlot at Allegan in 1970.

Variety, MSFG seedlot number, and country of origin[1]	Plantation name and number and number of trees per seedlot (plots x 4)					
	Alle-gan 11-61 40	Rose Lake 12-61 28	Kell-ogg 2-61 24	All plantations 92	Per tree	Alle-gan 11-61 Per tree
	Number of Attacks					Average Color Grade[2]
lapponica						
229 FIN	30	--	1	--	---	2.3
546 SWE	54	39	1	94	1.0	3.5
547 SWE	--	--	2	--	---	---
548 SWE	--	--	0	--	---	---
549 SWE	--	--	2	--	---	---
mongolica						
234 SIB	--	--	11	--	---	---
254 SIB	13	13	0	26	0.3	1.5
altaica						
227 SIB	122	--	7	--	---	3.1
255 SIB	131	56	10	197	2.1	2.5
256 SIB	76	55	2	133	1.4	2.0
septentrionalis						
201 NOR	230	169	8	407	4.4	5.3
222 SWE	155	101	7	263	2.9	4.2
228 FIN	--	--	2	--	---	---
230 FIN	154	93	12	259	2.8	3.2
232 FIN	--	--	5	--	---	---
233 FIN	--	--	6	--	---	---
273 NOR	139	110	5	254	2.8	5.0
274 NOR	172	79	4	255	2.8	4.0
521 SWE	135	105	18	258	2.8	4.7
522 SWE	194	86	4	284	3.1	4.0
523 SWE	115	53	5	173	1.9	3.9
524 SWE	149	63	12	224	2.4	4.2
543 SWE	180	47	8	235	2.6	4.6
544 SWE	154	78	9	241	2.6	4.2
545 SWE	129	72	7	208	2.3	3.9

Table A2 (cont'd.).

rigensis						
223 LAT	168	155	13	336	3.7	4.0
224 LAT	173	116	7	296	3.2	5.0
541 SWE	167	79	19	265	2.9	4.9
542 SWE	149	87	5	241	2.6	3.1
550 SWE	175	--	11	--	---	5.3
uralensis						
257 URA	--	84	10	--	---	---
258 URA	152	79	6	237	2.6	2.6
259 URA	227	61	--	--	---	3.2
260 URA	--	56	1	--	---	---
polonica						
211 POL	134	65	23	222	2.4	5.8
317 POL	106	48	28	182	2.0	6.2
borussica						
202 GER	155	113	18	286	3.1	7.4
210 GER	100	40	12	152	1.7	7.0
hercynica						
203 GER	208	115	13	336	3.7	7.3
204 GER	145	--	17	--	---	6.3
207 GER	97	74	14	185	2.0	7.7
208 GER	125	123	25	273	3.0	7.4
209 GER	--	--	14	--	---	---
248 GER	--	73	--	--	---	---
305 CZE	168	108	16	292	3.2	7.1
306 CZE	170	115	13	298	3.2	6.8
307 CZE	116	--	12	--	--	6.9
308 CZE	137	116	16	269	2.9	6.7
309 CZE	180	170	23	373	4.1	6.6
310 CZE	125	108	19	252	2.7	7.0
311 CZE	168	107	16	291	3.2	7.1
312 CZE	114	47	19	180	2.0	6.7
313 CZE	--	--	19	--	---	---
314 CZE	--	--	13	--	---	---
315 CZE	--	--	11	--	---	---
319 AUS	114	71	--	--	---	7.0
525 GER	152	82	16	250	2.7	6.7
526 GER	--	--	28	--	---	---
527 GER	147	138	20	305	3.3	6.7
528 GER	117	--	13	--	---	6.6
529 GER	--	--	20	--	---	---

Table A2 (cont'd.).

Variety, MSFG seedlot number, and country of origin[1]	Plantation name and number and number of trees per seedlot (plots x 4): Allegan 11-61 40	Rose Lake 12-61 28	Kellogg 2-61 24	All plantations 92	All plantations Per tree	Allegan 11-61 Per tree
	Number of Attacks					Average Color Grade[2]
haguenensis						
206 GER	122	51	10	183	2.0	7.5
250 GER	--	68	17	--	---	---
251 GER	93	87	17	197	2.1	8.1
252 GER	113	99	20	232	2.5	7.4
253 GER	112	91	11	214	2.3	7.5
236 FRA	--	--	16	--	---	---
237 FRA	--	--	9	--	---	---
241 FRA	132	80	12	224	2.4	7.9
318 BEL	108	44	10	162	1.8	7.6
530 BEL	97	54	17	168	1.8	7.6
'East Anglia'						
269 ENG	--	86	11	--	---	---
270 ENG	--	--	14	--	---	---
pannonica						
552 HUN	--	230	--	--	---	---
553 HUN	200	76	18	294	3.2	6.7
illyrica						
242 YUG	179	131	24	334	3.6	6.8
'North Italy'						
554 ITA	--	270	--	--	---	---
555 ITA	--	--	27	--	---	---
556 ITA	--	258	20	--	---	---
557 ITA	--	232	26	--	---	---
scotica						
265 SCO	--	--	17	--	---	---
266 SCO	--	--	12	--	---	---
267 SCO	--	283	13	--	---	---
268 SCO	--	--	17	--	---	---

Table A2 (cont'd.).

iberica							
218	SPA	203	198	30	431	4.7	8.8
219	SPA	172	199	28	399	4.3	8.7
245	SPA	141	325	14	480	5.2	8.6
246	SPA	200	318	52	570	6.2	7.5
247	SPA	165	261	32	458	5.0	8.3
aquitana							
212	FRA	--	--	14	--	---	---
238	FRA	219	261	15	495	5.4	8.4
239	FRA	191	275	17	483	5.3	8.4
240	FRA	--	--	40	--	---	---
316	FRA	--	--	26	--	---	---
320	FRA	--	219	24	--	---	---
249	AUS	--	183	--	--	---	---
235	FRA	151	96	20	267	2.9	7.6
rhodopaea							
243	GRE	248	174	32	454	4.9	6.6
244	GRE	195	178	16	389	4.2	7.1
271	GRE	156	--	39	--	---	7.2
272	GRE	--	118	13	--	---	---
551	GRE	344	--	38	--	---	6.5
armena							
213	TUR	282	251	13	546	5.9	7.4
214	TUR	--	--	19	--	---	---
220	TUR	171	179	33	383	4.2	7.8
221	TUR	271	198	21	490	5.3	7.2
261	GEO	--	248	22	--	---	---
262	GEO	--	--	29	--	---	---
263	GEO	--	--	22	--	---	---
264	GEO	--	--	19	--	---	---
other[3]							
205	AUS	--	--	27	--	---	---
225	N.Y.	147	107	23	277	3.0	8.1
Overall average		153.3	126.0	15.8	286.0	3.1	6.4

[1]) AUStria, BELgium, CZEchoslovakia, ENGland, FINland, FRAnce, GEOrgian SSR, GERmany, GREece, HUNgary, ITAly, LATvian SSR, NORway, POLand, SCOtland, SIBeria, SPAin, SWEden, YUGoslavia, URAl Mountains.

[2]) Trees were graded for color on the basis of 0 = yellow to 9 = blue-green.

[3]) These two seedlots were not considered in the results because of their questionable origin.

Table A3.--Number of trees attacked by eucosma in each seedlot at all plantations and in all years.

Variety, MSFG seedlot number, and country of origin[1]	Plantation name and number, year of count, and number of trees per seedlot (plots x 4)				
	Allegan 11-61 1968 28	Rose Lake 12-61 1969 28	Kellogg 2-61 1970 24	Allegan 11-61 1970 40	Rose Lake 12-61 1970 28
	Number of Attacked Trees				
lapponica					
229 FIN	1	--	1	17	--
546 SWE	0	7	1	22	22
547 SWE	--	--	2	--	--
548 SWE	--	--	0	--	--
549 SWE	--	--	2	--	--
mongolica					
234 SIB	--	--	7	--	--
254 SIB	--	0	0	7	9
altaica					
227 SIB	4	--	5	40	--
255 SIB	5	8	6	35	22
256 SIB	0	9	2	31	20
septentrionalis					
201 NOR	11	16	4	40	28
222 SWE	6	7	6	40	23
228 FIN	--	--	2	--	--
230 FIN	1	3	10	38	23
232 FIN	--	--	5	--	--
233 FIN	--	--	6	--	--
273 NOR	3	11	4	34	24
274 NOR	3	6	2	38	23
521 SWE	8	9	11	37	26
522 SWE	1	8	2	40	21
523 SWE	0	2	3	37	18
524 SWE	3	8	7	37	20
543 SWE	4	6	7	38	14
544 SWE	8	6	6	37	25
545 SWE	2	3	4	34	23

Table A3 (cont'd.).

rigensis					
223 LAT	6	13	10	39	24
224 LAT	12	10	6	39	22
541 SWE	3	10	12	38	23
542 SWE	6	9	4	40	22
550 SWE	8	--	8	39	--
uralensis					
257 URA	--	5	6	--	21
258 URA	4	7	4	39	22
259 URA	4	5	--	39	20
260 URA	--	10	1	--	19
polonica					
211 POL	6	7	12	38	25
317 POL	9	9	16	39	19
borussica					
202 GER	11	14	8	40	22
210 GER	7	7	8	38	19
hercynica					
203 GER	10	10	9	40	26
204 GER	14	--	12	38	--
207 GER	5	15	8	35	18
208 GER	8	9	13	38	22
209 GER	--	--	8	--	--
248 GER	--	10	--	--	20
305 CZE	7	10	11	39	27
306 CZE	10	13	10	40	24
307 CZE	13	--	8	37	--
308 CZE	11	10	10	37	25
309 CZE	11	12	15	40	27
310 CZE	17	14	13	36	24
311 CZE	10	16	9	40	23
312 CZE	9	8	13	39	19
313 CZE	--	--	14	--	--
314 CZE	--	--	9	--	--
315 CZE	--	--	10	--	--
319 AUS	11	14	--	34	22
525 GER	10	12	11	39	21
526 GER	--	--	17	--	--
527 GER	8	11	12	40	22
528 GER	10	--	9	38	--
529 GER	--	--	14	--	--

Table A3 (cont'd.).

Variety, MSFG seedlot number, and country of origin[1]	Plantation name and number, year of count, and number of trees per seedlot (plots x 4)				
	Allegan 11-61 1968 28	Rose Lake 12-61 1969 28	Kellogg 2-61 1970 24	Allegan 11-61 1970 40	Rose Lake 12-61 1970 28
	Number of Attacked Trees				
haguenensis					
206 GER	12	10	6	39	15
250 GER	--	13	11	--	26
251 GER	15	9	13	35	24
252 GER	15	15	13	39	24
253 GER	10	11	10	38	23
236 FRA	--	--	11	--	--
237 FRA	--	--	8	--	--
241 FRA	10	6	6	37	24
318 BEL	6	9	7	36	19
530 BEL	10	10	6	39	15
'East Anglia'					
269 ENG	--	9	8	--	21
270 ENG	--	--	10	--	--
pannonica					
552 HUN	--	17	--	--	26
553 HUN	10	13	11	40	24
illyrica					
242 YUG	7	13	15	40	24
'North Italy'					
554 ITA	--	17	--	--	25
555 ITA	--	--	14	--	--
556 ITA	--	16	12	--	27
557 ITA	--	16	13	--	25
scotica					
265 SCO	--	--	10	--	--
266 SCO	--	--	8	--	--
267 SCO	--	10	11	--	28
268 SCO	--	--	12	--	--

Table A3 (cont'd.).

iberica					
218 SPA	12	12	12	40	26
219 SPA	21	16	14	40	27
245 SPA	9	18	11	39	26
246 SPA	16	20	17	39	27
247 SPA	15	20	17	38	26
aquitana					
212 FRA	--	--	11	--	--
238 FRA	13	14	11	40	26
239 FRA	11	13	10	39	25
240 FRA	--	--	16	--	--
316 FRA	--	--	10	--	--
320 FRA	--	19	15	--	27
249 AUS	--	14	--	--	26
235 FRA	14	9	11	40	27
rhodopaea					
243 GRE	15	14	14	40	26
244 GRE	14	17	11	40	28
271 GRE	9	--	16	40	--
272 GRE	--	10	8	--	26
551 GRE	20	--	18	38	--
armena					
213 TUR	14	18	9	39	27
214 TUR	--	--	9	--	--
220 TUR	7	17	16	40	27
221 TUR	14	14	11	40	25
261 GEO	--	18	13	--	27
262 GEO	--	--	11	--	--
263 GEO	--	--	13	--	--
264 GEO	--	--	12	--	--
other[2]					
205 AUS	--	--	15	--	--
225 N.Y.	13	15	14	40	26
Overall average	8.9	11.2	9.4	37.4	23.2

[1]) AUStria, BELgium, CZEchoslovakia, ENGland, FINland, FRAnce, GEOrgian SSR, GERmany, GREece, HUNgary, ITAly, LATvian SSR, NORway, POLand, SCOtland, SIBeria, SPAin, SWEden, YUGoslavia, URAl Mountains.

[2]) These two seedlots were not considered in the results because of their questionable origin.