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AN EVALUATION OF THE IMPACT OF THE SARATOGA SPITTLEBUG, APHROPHORA SARATOGENSIS (FITCH), ON THE GROWTH OF RED PINE, PINUS RESINOSA AIT.

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Robert Lewis Heyd

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AN EVALUATION OF THE IMPACT OF THE SARATOGA

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(FITCH), ON THE GROWTH OF RED

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ABSTRACT

AN EVALUATION OF THE IMPACT OF THE SARATOGA SPITTLEBUG, *APHROPHORA SARATOGENSIS* (FITCH), ON THE GROWTH OF RED PINE, *PINUS RESINOSA* AIT.

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The Saratoga spittlebug causes growth loss, deformity and mortality of young red pine in plantations in the Lake States. The biological impact (or damage) of the Saratoga spittlebug was measured to provide basic data to construct an ecological impact model and to more effectively understand the socio-economic aspect of impact.

Several studies were initiated to correlate feeding pressure from spittlebug populations on resulting tree growth and form. When trees were caged and exposed from light to heavy feeding pressure, an upper-whorl concentration of feeding activity occurred. Flagging, too, was concentrated in the upper whorls of the tree.

In another study 16 plots were used representing different ground cover associations, soils, tree heights and ages. From these the following regressions were derived: Reduction of growth = -.558 + .211X; Reduction of photosynthetic potential = -.518 + .221X; and Reduction of branch vigor = -.442 + .136X where X is the log of the insect exposure per branch. These regressions were related to a useable

late-instar nymphal survey and tree-unit evaluation, and the following formula was derived: $Y = -8.140 + 53.897X$ where Y = mean insect exposure per upper-whorl branch and X = nymphs per tree-unit. This formula provided a way to relate feeding pressure from spittlebug populations to growth loss and lost growth potential.

Different degrees of growth loss were related to tree deformity and mortality to develop a predictive model. A value of less than 25 percent growth loss showed only reduced growth of the tree and a small loss of potential growth for the following two-three years. Percentages from 25 to 40, however, showed trees having scattered partial branch flagging and some deformity from light sweep and large lower-bole limbs. Percentages from 40 to 70 provided some trees with top kill, whole branch flagging and serious degrade from sweep, crook, multiple stems and large lower limbs. Growth loss of 70 percent or greater led to numerous trees top killed, heavy degrade and a few to many dead trees.

An analysis of a 45-year-old red pine plantation with a history of spittlebug injury showed that sweep, crook, fork, large and numerous lower bole limbs, wood stain, and growth loss resulted from spittlebug feeding.

An ecological model was developed which incorporated ground cover association, insect population size, tree height and density, tree growth response, form, interior degrade, and susceptability to snow damage, with modifications of the physical environment.

Dedicated to

Sarah Garnet Heyd
David Michael Heyd

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INTRODUCTION

The Saratoga spittlebug, *Aphrophora saratogensis* (Fitch), an insect native to Eastern North America, is a serious pest of pine in the Lake States, especially in northern Wisconsin and Michigan, because it severely deforms and kills young planted pines. Red pine, *Pinus resinosa* Ait., is the preferred host, but jack pine, *Pinus banksiana* Lamb and other pines are also attacked to a lesser degree.

Although easy to suppress, control decisions for the spittlebug are often based on speculation. Ewan (1961) predicted a "severe damage" threshold given the number of insects per unit of tree size and density. This is useful, but knowledge of the effects of populations below severe damage threshold is necessary if the forest manager is to make responsible management decisions. The Saratoga spittlebug causes tree deformities such as limbiness, large knots, crook and sweep, and loss of wood volume from growth loss and/or tree mortality. Thus, control decisions should include criteria for evaluating deformity and growth loss thresholds as well as other multiple use values.

Objective

The objective of this study was to determine mortality, deformity, and growth loss caused by Saratoga spittlebug feeding on young red pine in plantations. This provides the basic data to construct an ecological impact model and to more effectively evaluate socio-economic impact.

Impact Defined

The impact of an insect population can be broadly defined as the cumulative net effects of the insect resulting in modification of management activities for specified forest resource uses and values (USDA 1972). Impact has two components: (1) ecological--the cumulative net effects of the insect on the total forest site and areas offsite; and (2) socio-economic--the value judgments and/or decision criteria established by management objectives (Averill, 1977; USDA 1972). The ecological component of impact deals with the physical changes of the tree and the environment caused by insect activity. This component is as variable as the different types and degrees of insect injury and combinations of trees and environments. The ecological component provides information needed to assess the socio-economic component. The socio-economic component is determined by management objectives as they differentially emphasize multiple use concepts (i.e. timber, wildlife, watershed and recreation). A positive, negative or neutral impact may result from an insect-tree interaction depending upon the management objective of the forest. Suppose timber production is the primary objective. An insect which randomly attacks an area of suppressed trees may kill many trees, but may also release the remaining trees producing an overall positive impact. Pocket-type infestations, however, may result in loss without significant release of trees and excessive limbiness in trees bordering the pockets and this may produce a negative impact. However, if wildlife management is the objective in this situation, a positive impact may result. Pockets create edge and potential forage areas, both of which enhance wildlife values. The interactions are numerous and complex. To evaluate the socio-economic component of impact the specific management objectives and values must be known.

Ecological impact in this dissertation refers to the effects of spittlebug feeding injury upon growth rate, tree form, and mortality as modified by the site. These qualities affect the suitability of the tree as a forest product and a component of multiple use concepts.

BRIEF LIFE HISTORY OF THE SARATOGA SPITTLEBUG

The Saratoga spittlebug overwinters as an egg tucked under the bud scales of the larger buds in the upper whorls of the pine host. The nymphs eclose in early May, drop to the ground and search for and feed upon understory vegetation, primarily within ten feet of the tree. The five nymphal instars feed upon these alternate hosts in spittle-masses for about six weeks. Many herbacious and woody plants serve as suitable nymphal hosts. However, heavy infestations are usually correlated with the density of sweet-fern, Comptonia peregrina (L.) Coult. If 35 percent or more of the ground cover is sweet-fern, or if it is present in certain combinations with other alternate hosts, moderate to heavy damage often results (Wilson, Heaton and Kennedy, 1977).

Adult transformation generally occurs in late June peaking before mid-July. Newly emerged adults move to and feed upon a pine host. The needle bearing internodes of the tree represent the feeding universe (Ewan, 1961). Adults feed two to five times daily depending upon the time of feeding and the temperature. Peak feeding occurs two-three weeks following emergence, and each adult averages 3.5 feeding punctures per day. About 90 percent of the feeding damage is complete by mid-August. In September the few surviving adults feed about 1.5 times each day. The seasonal average is 2.63 feeding punctures per day (Ewan, 1961).

Oviposition starts one or two weeks after adult transformation and peaks in late July or early August. Each female averages 14.6 eggs (Ewan, 1961).

INJURY TO RED PINE

Spittlebugs commonly damage pines two to 15 feet tall. Larger trees may be attacked but a plantation with 6' X 6' spacing generally approaches hosts needed for nymphal survival. Also, as young red pines double in height, the number of branches at least triples (Miller, 1965). Thus larger trees can withstand much more feeding because of the increased total branch area.

The Saratoga spittlebug causes growth loss, chlorosis and necrosis of branches and branchlets (flagging), top kill, tree mortality, and deformity (limbiness, large knots, crook and sweep). When flagging first appears, the tree has already incurred irrepairable growth loss, and if flagging encompasses entire branches or whorls, deformity occurs. Top kill or severe upper-whorl damage causes a lateral branch to become the leader.

Ewan (1961) reported that damage symptoms normally appear the year following feeding unless feeding is extremely heavy. Then, flagging can occur at the end of the same growing season. He also noted the time from first scattered flagging to entire tree mortality was one-two years.

Spittlebug damage generally occurs in pockets corresponding to areas of suitable ground vegetation within the plantation. These pockets can enlarge and coalesce if there are adequate numbers of suitable alternate hosts.

The Feeding Scar

The adult spittlebug damages the tree by sucking sap and leaving a residual feeding scar which serves as a permanent block to xylem and phloem conduction. The first evidence of necrosis occurs within 24 to 48 hours after feeding (Anderson, 1947). This is followed by resin accumulation and spreading of the scar area. A disalignment of trachieds also occurs on the side opposite the transport block (Ewan, 1961). Ewan also found the carbohydrate content of spittlebug injured shoots and roots is lower than that of unattacked trees. This damage is characteristic of moisture stress but differs from girdling which accumulates carbohydrates distal to the girdled area.

Ewan (1961) noted that feeding scars were concentrated on the one-year-old internodes (last year's growth). Older needle-bearing internodes and the current growth had less. He also reported feeding scar densities did not differ between the top and bottom surfaces of branches, but the phloem had 30 percent more feeding scars than the xylem. He found no differences in the distribution of scars between branch whorls within the tree.

Damage Effects on the Tree

In the Lake States, adult Saratoga spittlebug populations peak in mid-July after red pine shoot elongation is nearly complete. Needle elongation has begun at this time and new buds approximately 40 to 50 percent developed (Sucoff, 1971). Thus, feeding injury does not affect current shoot growth, but it can influence needle elongation and bud development.

The developing buds and the current needles are largely responsible for auxin production. Auxin-directed translocation is responsible for the movement of nutrients from storage cells to young growing tissues (Kozlowski, 1964; Kulman, 1965). Water stress, then, induced by withdrawal of liquid from feeding, plus increases in xylem and phloem resistance from the residual feeding scar, inhibits the growth of the terminal meristems and new needle growth. This further decreases auxin production in spittlebug injured branches and reduces translocation to the damaged area, thus reducing needle growth and photosynthesis. Also, greater auxin production by terminal meristems is responsible for inhibition of lateral buds (Kozlowski, 1964; Kozlowski and Winget, 1964). Thus, given less terminal bud development in upper whorls, greater growth of unattacked or less severely attacked lower whorl branches will result. From this, lower whorl branches compete for dominance with a net loss of unidirectional height growth. The following year, the one-year-old needles which are the most important source of food for shoot growth (Gordon and Larson, 1970; Dickmann and Kozlowski, 1968; Kozlowski and Winget, 1964) will be shorter; plus, the expanding bud will have fewer leaf primordia due to the less than optimal conditions for formation in the previous season. Adverse environmental conditions in addition to spittlebug attack would compound the stress. Even if spittlebug populations are controlled the following year, the shorter needles from the previous season and smaller buds will reduce photosynthetic potential for at least three years. Any decrease in photosynthetic potential affects the entire tree--needles, stems and roots.

In addition, the feeding scars persist as a block to water flow in the xylem until stem diameter increases significantly. Aggregates of scars cause necrotic areas which may serve to block phloem and xylem transport for several years.

From another viewpoint, decreased auxin supply and decreased carbohydrate result in decreased tracheid diameters which may increase xylary resistance and decrease wood production (Larson, 1962, 1963).

A change in the growth pattern of spittlebug injured red pine was noted by Ewan (1961). He calculated the ratio of internode lengths within whorls for a given year to the terminal growth for that year, using the lateral/terminal ratio (L/T ratio) developed by Benjamin et al., 1953. They established L/T ratio limits called zones of normalcy within which normal development occurs. A characteristic pattern of longer internodes in upper whorls progressed to shorter internodes in lower whorls. Ewan used the L/T ratio to indicate growth imbalance in attacked trees (i.e. loss of upper whorl dominance and/or asymmetry of crown). He reported that growth imbalance was evident, but the L/T ratio was an indicator only for long-duration light to moderate infestations. The damage of rapidly developing heavy infestations could not be predicted due to the year delay of damage symptoms.

WITHIN TREE DISTRIBUTION OF INJURY

A knowledge of the distribution of spittlebug injury within a red pine is necessary in understanding tree growth response. The objectives of this portion of the study were to determine the distribution of feeding and flagging within the tree, and to relate this to visible signs of tree injury.

Distribution of Spittlebug Feeding

Methods and Materials

In the summer of 1975, six red pines about six feet tall in a 12-year-old plantation (T18N, R12W, Sec. 23, Lake County) (Figure 1) were enclosed in 6.5' X 6.5' X 6.5' cages made of 20 X 20 per inch mesh saran screening. Treatments consisted of 25, 50, 75, 100, 150 and 200 spittlebugs per cage for 21 days (first three weeks of August). Insects were allowed to die normally without replacement. Natural populations seldom exceed 100 insects on trees of this size. Only unattacked trees were selected so the insects would not be influenced by previous spittlebug feeding. At the end of the test live insects were counted in each cage. The trees were then cut at the ground line, and the bark was carefully removed using a blunt knife so as not to damage the scars on the xylem surface. The length of all stem and branch internodes was measured and the number of scars were counted and recorded by location.

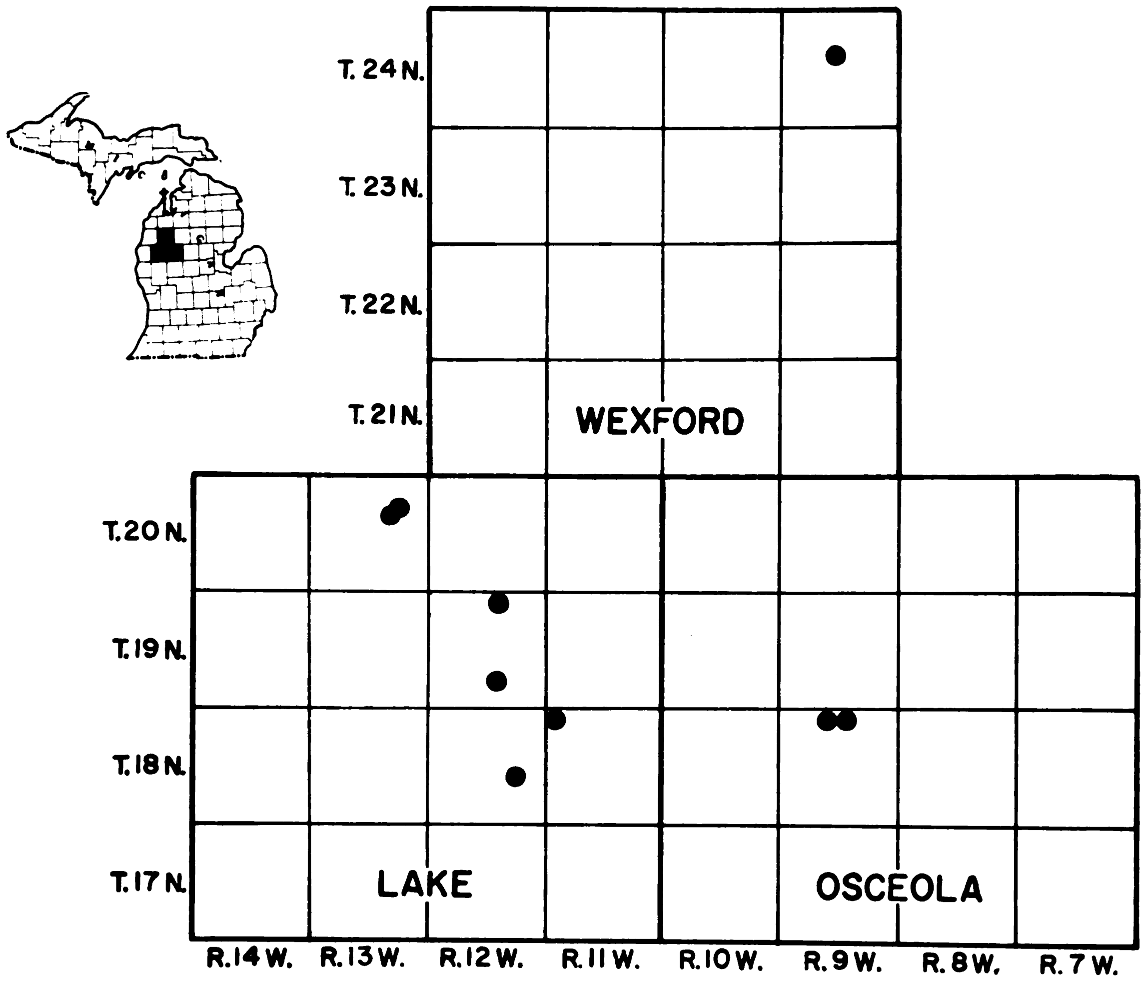


Figure 1.--Location of Saratoga spittlebug research plantations in Michigan.

Results

The number of scars on each whorl generally paralleled branch size as measured by total centimeters of internode (Figure 2). This suggests a somewhat even distribution of feeding throughout the tree. Analysis of scar density (Figure 3), however, revealed more scars per branch length in upper whorls than in lower whorls in all treatments except the 25-insect exposure. In the latter, the low feeding pressure did not result in any areas of high scar density.

The highest scar densities were found on the one and two-year-old main branch stems followed by all the needle bearing internodes except the current growth (Figure 3). There was a proportionately greater amount of one and two-year-old main branch stem available relative to less preferred sites in upper-whorl branches. This may account for the upper-whorl feeding preference. However, scar density on the little preferred non-needle-bearing internodes was also greater in upper whorls. In the 200-insect treatment, the bare internode scar density of the fourth and fifth whorls actually exceeded that of the total branch in lower whorls. This may be due to the greater moisture and nutrient content of upper-whorl branches (Mamaev, 1956; Clausen and Kozlowski, 1967; Szymanski and Szczerbinski, 1962). The spittlebug may not actively select upper whorls to land on an indicated by the general parallel between number of scars and branch size; however, upon landing in an upper whorl, the high nutrient and moisture conditions may cause prolonged and/or repeated feeding.

The 50, 100 and 150 insect treatments showed more scars than expected per branch length on the one and two-year-old main branch stems

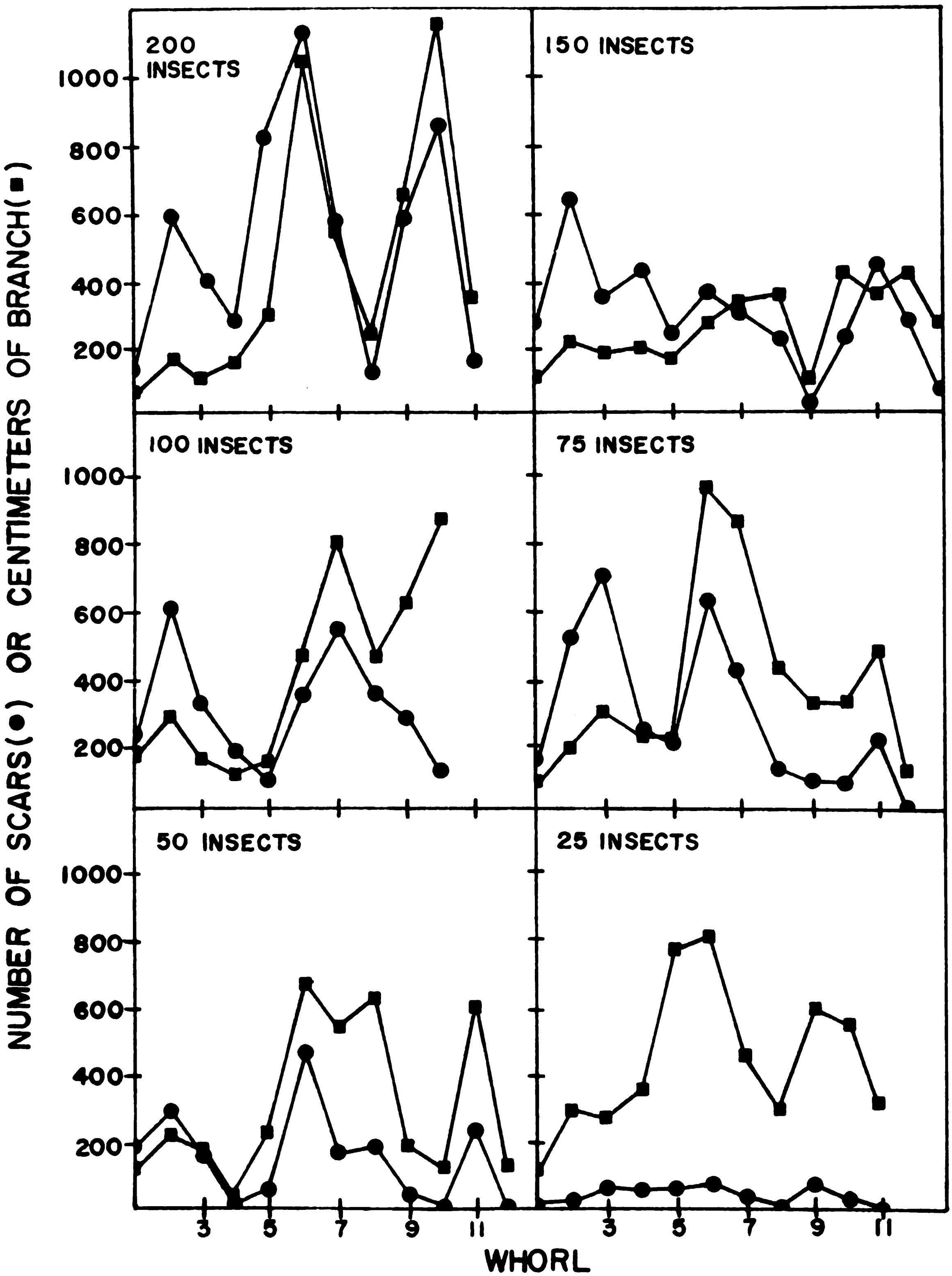


Figure 2.--Distribution of scars and centimeters of branch per whorl from the feeding distribution study.

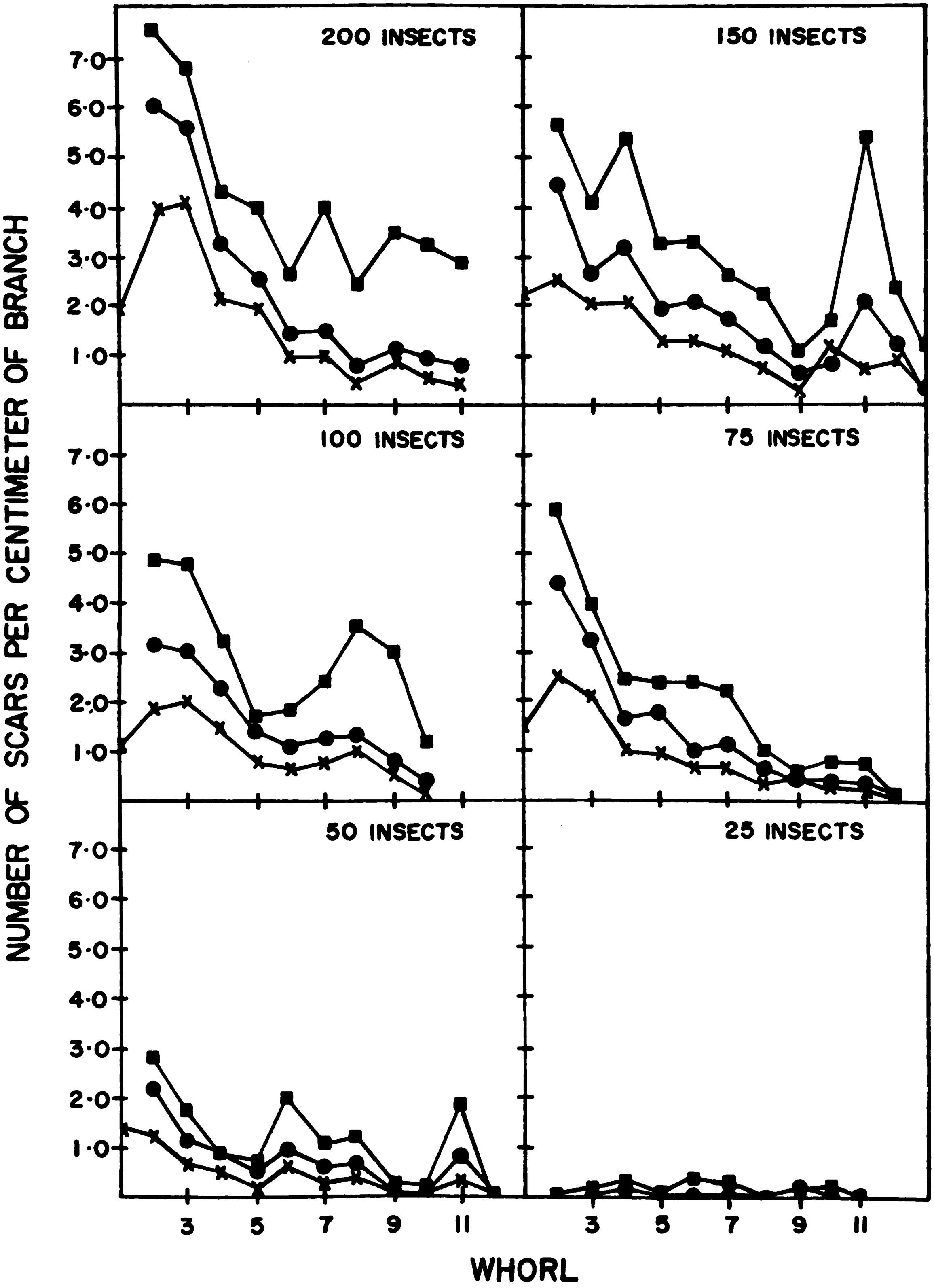


Figure 3.--Scar density on (X) total branch area, (●) needle-bearing internodes less current growth, and (■) one and two year old main stem from the feeding distribution study.

in lower-whorl branches (Figure 3). The branches were larger in these whorls compared to surrounding whorls, and probably received more than their share of insects. The needle bearing internodes did not show higher scar densities in lower whorls. This may be due to the lower proportion of one and two-year-old main branch stems in the needle bearing internodes of lower-whorl branches.

The Distribution of Flagging

Methods and Materials

Seven plots within five red pine plantations with spittlebug flagged branches were examined in August, 1976. The locations of the plantations (Figure 1) and plots in Michigan were:

Plot Number	Location	County
1	T18N,R11W, Sec. 6, SW¼	Lake
2	T24N,R9W, Sec. 16, NE¼	Wexford
3	T18N,R9W, Sec. 4, NE¼	Osceola
4	T18N,R9W, Sec. 4, NE¼	Osceola
5	T19N,R12W, Sec. 3, NW¼	Lake
6	T19N,R12W, Sec. 3, NW¼	Lake
7	T18N,R9W, Sec. 3, NW¼	Osceola

The trees ranged from 4.5 to 14.0 feet tall, and contained light to severe injury. A one tenth-acre plot was established in each plantation, and the distribution of flagged branches and the proportion of flagging were recorded for each whorl of each tree.

Results

Analysis of the first six plots showed flagging was highest in the upper whorls and diminished with declining whorl position (Figure 4).

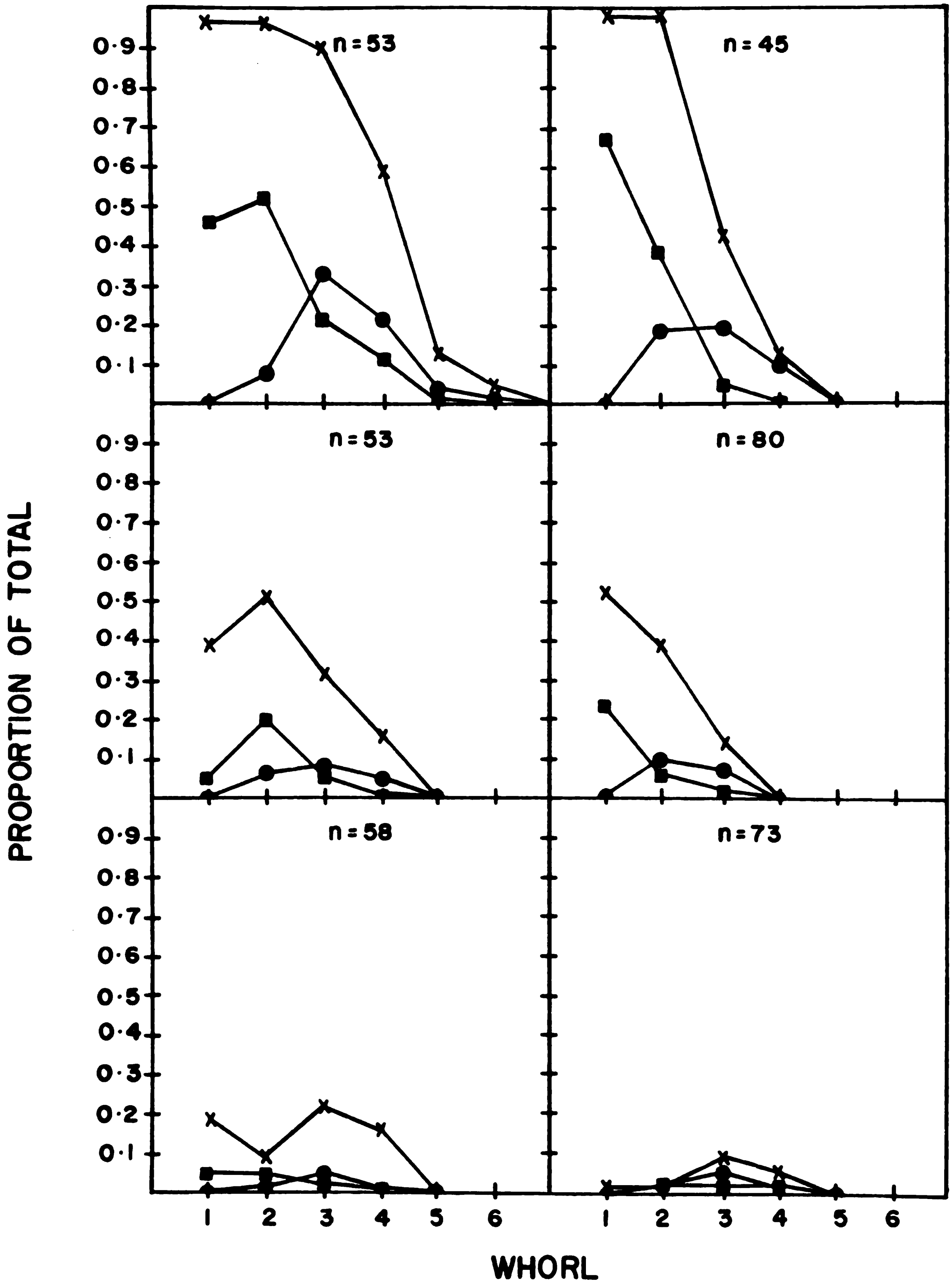


Figure 4.--Distribution of spittlebug flagging by whorls in six study areas showing heavy to light injury: (X) trees flagged; (■) entire branch flagged; (●) partial branch flagged.

The frequency of branches displaying partial flagging was greatest in the third whorl because second whorl branches primarily exhibit whole branch flagging. Second whorl branches were composed of only one internode of preferred feeding sites and a whorl of current growth. Generally, the one-year-old internode received a lethal scar density first, causing the entire branch to flag. Also, the mortality of the current whorl was due mainly to girdling of the one and two-year-old bole and not from feeding directly on the whorl.

The seventh plot was more heavily flagged than the others because of two consecutive years of heavy feeding. All of the trees had some degree of flagging, and, only in this plot, the flagging extended lower than the fifth whorl. The first year of heavy feeding killed the top three or four whorls in most trees. The buds remained intact, however, allowing the adults to successfully overwinter. In the spring the lush ground cover with abundant sweet-fern supported a high population of spittlebugs, and resulted in heavy flagging of the remaining whorls. As in the other six plots, flagging severity diminished with lower whorl position, showing that the remaining higher whorls were still preferred even following top kill.

Discussion

The Saratoga spittlebug feeds primarily on the needle bearing internodes of red pine and preferably on the one and two-year-old main branch stem. Although feeding activity is distributed throughout the tree, greater scar density occurs in the upper whorls. Flagging also appears first in upper whorls. Thus, both studies support using upper whorls to determine the influence of feeding injury upon tree growth.

This information helps explain the increased number and size of limbs, fork, crook and sweep associated with spittlebug injured trees. By damaging upper whorls, the spittlebug causes tree deformity as well as growth loss and mortality. The upper whorls suppress the growth of lower whorls, maintaining the desirable conical shape of the tree (Pharis, 1976; Forward and Nolan, 1962). Thus, feeding imposed on the upper whorls causes lower whorls to compete for dominance, with a net loss of unidirectional height growth and an increase in girth. This may result in limbiness and large knots in the lower bole, fork and/or crook if upper whorls are stressed enough to allow lower-whorl branches to assume dominance.

EVALUATION OF TREE GROWTH RESPONSES

An evaluation of growth loss of red pine from Saratoga spittlebug attack is an essential step in assessing impact. The observed parameters should reflect the growth responses of the tree accurately and meaningfully.

It is well known that the length of a bud in red pine is directly related and highly correlated to the length of the resulting shoot (Kozlowski, et al., 1972; Hanover, 1963; Szymanski and Szczerbinski, 1962). There is also a high correlation between bud length and the number of needle primordia which determine the number of fascicles on the next year's shoot (Kozlowski, et al., 1972; Marion, et al., 1968; Duff and Nolan, 1953). Thus, bud length reflects potential shoot length and photosynthetic potential, and therefore shoot vigor. The most vigorous buds (largest) are located in the upper whorls and they more accurately reflect the vigor of the tree. Also, bud length is a better indicator of potential shoot length for upper-whorl branches than for lower whorl branches or the terminal leader (Szymanski and Szczerbinski, 1962).

These relationships between bud length and resulting shoot length and number of needle primordia suggest a method of evaluating the effects of different levels of feeding intensity upon growth. By measuring bud lengths on treated and control branches in upper whorls of red pine and then measuring and comparing the resulting shoot lengths and needle dry weights the following year, growth response can be evaluated. Also, a ratio of bud length to the resulting shoot bud length will reflect changing shoot vigor.

Methods and Materials

The effect of feeding injury upon tree growth was examined by placing adult spittlebugs on red pine branches in sleeve cages. The effects of different intensities of feeding injury were monitored by examining the following parameters: (1) the ratio of bud length and resulting shoot length as a measure of expressed growth potential, (2) the ratio of needle dry weight to bud length as a measure of expressed photosynthetic potential, and (3) the difference between bud length and the resulting shoot bud length as a measure of changing shoot vigor. Needle chlorosis and flagging were used as indicators of branch stress and mortality.

Plot Selection

Sixteen plots were selected in Lake County, Michigan, to represent a variety of ground covers, tree heights and other conditions which characterized Saratoga spittlebug infested plantations throughout the Lake States (Table 1). Individual plot sites, however, were chosen to display uniformity of ground cover, little slope, and no sign of insect injury or presence of potentially damaging insect populations.

Each plot was selected by delimiting an area in a stand with about 30 trees. Five trees were picked randomly in the plot for

Table 1.--Tree heights and ground cover for all spittlebug plots in Lake County, Michigan, 1974-1976.

Plot Number	Average Tree Height (feet)			Ground Cover (percent)[a]							
	1974	1975	1976	Grass	Bare Ground & Moss	Rubus	Core-opsis	Cento-urea	Berga-mont	Solida-ago	All Others
1	9.0	10.7	11.9	80	2	8	--	--	--	--	10
2	8.2	9.6	11.0	94	--	--	--	--	--	--	6
3	5.1	6.7	7.7	20	27	30	7	7	3	2	4
4	6.9	8.5	9.6	32	27	16	18	3	2	2	--
5	10.5	12.8	14.1	2	86	2	1	--	--	--	9
6	11.2	13.3	14.8	82	10	6	--	--	--	--	2
7	8.4	10.0	11.3	56	38	--	--	--	--	--	6
8	--	8.6	9.9	80	--	--	--	5	8	3	4
9	--	7.0	8.5	84	--	--	--	8	6	--	2
10	--	7.0	8.2	74	2	--	--	10	6	2	6
11	--	8.1	9.3	73	--	--	--	7	6	3	11
12	--	8.4	9.7	85	--	10	--	--	--	--	5
13	--	7.8	9.2	78	17	2	--	--	--	1	2
14	--	9.4	10.5	93	5	--	--	--	--	--	2
15	--	9.8	11.7	56	--	--	--	9	--	23	12
16	--	8.2	9.9	15	5	--	--	45	--	14	21

[a]Ground cover surrounding each test tree (n=5) and of the entire plot was averaged to derive these values.

experimentation. On each tree, two or three similar branches from the same whorl were used for testing. One branch was exposed to different insect feeding pressures. The other branches were controls. Upper whorl (third and fourth node) branches were used. The one-year-old branch whorl (second node) was not suitable because of the small area of preferred feeding site. Upper whorls were selected because spittlebugs prefer upper-whorls, because upper-whorl branches flag first, and because buds are larger and better represent shoot growth and vigor.

Plot Treatments

Sixteen plots were established in 1974 or 1975, and used for one, two, or three consecutive years. Sleeve cages were used to contain spittlebugs on the host branches for all feeding tests. Each cylindrical sleeve cage was 3' long by 1' in diameter. The body of the cage was plastic window screen and the ends were muslin cloth. One end was tied around the branch base, the other end was tied shut beyond the branch tip and supported with a string to the branch above. When used, one of the control branches on each tree was also caged but was without insects. The other control branch was left uncaged. Cages were removed at the end of each year and placed on the tree again the next season if the procedure was repeated.

Plot 1 contained 20 spittlebugs per test cage for 72 hours to evaluate within plot variation, and plot 2 included no spittlebugs to determine the effect of the cage alone on shoot development (Table 2). Plots 3 to 7 received 5, 10, 20, 40 and 80 spittlebugs per cage on

Table 2.--Red pine plot locations in Lake County, Michigan, and spittlebug sleeve cage treatments for 1974-1976.

Plot Number	Location			Years Treated	Spittlebugs per test cage no.:					Spittlebug Exposure Time
	T.	R.	S.		1	2	3	4	5	
1	20N	13W	11	1974,1975,1976	20	20	20	20	20	72 hrs.
2	20N	13W	11	1974,1975,1976	0	0	0	0	0	72 hrs.[a]
3	19N	12W	3	1974	5	10	20	40	80	72 hrs.
4	19N	12W	3	1974	5	10	20	40	80	72 hrs.
5	20N	13W	11	1974,1975,1976	5	10	20	40	80	72 hrs.
6	20N	13W	11	1974,1975,1976	5	10	20	40	80	72 hrs.
7	20N	13W	11	1974,1975,1976	5	10	20	40	80	72 hrs.
8	19N	12W	27	1975	10	20	30	40	60	72 hrs.
9	19N	12W	27	1975	10	20	30	40	60	72 hrs.
10	19N	12W	27	1975-1976	10	20	30	40	60	72 hrs.
11	19N	12W	27	1975-1976	10	20	30	40	60	72 hrs.
12	18N	12W	23	1975-1976	10	20	30	40	60	72 hrs.
13	18N	12W	23	1975-1976	10	20	30	40	60	72 hrs.
14	20N	13W	11	1975-1976	5	10	15	20	25	30 days
15	19N	12W	27	1975-1976	5	10	15	20	25	30 days
16	19N	12W	27	1975	5	10	15	20	25	30 days

[a]Empty cages placed on tree for this period.

fourth whorl branches for 72 hours. These numbers were selected to represent a wide range of attacks. After the first year (1974) new treatments (plots 8 to 13) were made with 10, 20, 30, 40 and 60 spittlebugs per cage on third whorl branches because the range was too broad in the 1974 tests and the feeding distribution study indicated an upper whorl feeding preference. Also, the new tests gave data that filled in the intermediate ranges of insect feeding exposures. Plots 14 to 16 included 5, 10, 15, 20 and 25 spittlebugs respectively per cage for a 30 day period to simulate effects of long term, low intensity (chronic) feeding (Table 2). The 30-day exposure closely corresponded to peak feeding activity of the insect. Three test branches per whorl were used in plots 14 to 16 instead of two as in the other plots. One branch had a test cage with insects, another one had only a test cage, and the third was uncaged. This permitted assessment of the effects of the cage on growth response. The sleeve cages used here were modified slightly. The outer end was covered with a screen cone instead of a muslin sleeve. This allowed greater light penetration and better air circulation. The long exposure (30 days) necessitated checking the insect-occupied cages for dead insects twice weekly. Dead insects were removed and replaced with live ones caught in nearby plantations. Cages on branches without insects were also opened at the same intervals to equalize the test conditions.

Most tests were repeated for one or two years on the same branches to simulate repeated infestations. Three plots (8, 9, 16) were tested for only one year to determine branch recovery following a simulated population decline or control program.

Feeding Frequency Determination

Living insects were counted at the end of each test and multiplied by the number of days the test was run. When insects died they were considered dead for one-half the test period. In the 30-day exposures this was calculated from one recharge (i.e. twice a week replacement of dead insects) to the next and accumulated. This provided an index of insect-days (ID). That is, ID = i x d where i is the number of insects alive for each day of the test and d is the number of days of the test.

At the end of the tests scars were counted on all branches after removing the bark. The number of scars per branch was divided by the insect-days to determine the mean number of scars per insect-day or the feeding frequency (F). That is, $F = \Sigma S/ID$ where ΣS is the sum of scars.

Branch size, or the amount of branch available to the exposed insects, was estimated to adjust insect-days to an equal volume of feeding material. A branch-unit index (BUI) was derived using the sum of all the bud lengths on the test branches. That is, $BUI = b_1 + b_2 \ldots b_n$ where $b_1 \ldots b_n$ are bud lengths in millimeters. The number and size of buds were representative of branch size and vigor, and after treatment, equal shoot lengths were not equal in vigor due to different treatment. Insect-days per branch-unit was determined by ID/BUI.

Shoot, Needle, and Bud Measurements

A growth factor based on the ratio of shoot length to bud length was used to determine growth loss following spittlebug feeding. On each branch, terminal and terminal-lateral bud lengths of the leader shoot and terminals of all lateral shoots were measured. Lengths of the shoots resulting from these buds were measured in September when fully developed. The mean bud and shoot lengths per branch were used to calculate growth factors.

The difference in growth between treated and control branches was determined by subtracting the growth factor of the treated branch (GF_t) from the growth factor of the control branch (GF_c) and dividing by the growth factor of the control. That is, the growth difference (GD) was: $GD = (GF_c - GF_t)/GF_c$. The control branch growth factor represented the normal or expected growth factor.

Similarly, the effects of insect exposures upon the ratio of needle dry weight to bud length was used to determine the reduction of photosynthetic potential. All needles were collected after tests were terminated in September, 1976. The needles, separated by year, were carefully removed and placed in small paper bags. They were dried at 75 C for three days (until loss of weight reached an equilibrium) and weighed to the nearest 0.01 gram. Needle dry weights were then divided by the total length of buds which produced the needles. (Bud length is highly correlated to the number of needle primordia.) The difference in needle dry weight per unit bud length (NDW) was determined as follows: $NDW = (NDW_c - NDW_t)/NDW_c$, where NDW_c = control branch value, and NDW_t = treated branch value.

The effects of the insect exposures upon the change in average bud length per branch each year was also observed to quantify changes in branch vigor. On each branch, terminal and terminal-lateral bud lengths of the leader shoot and terminals of all lateral shoots were measured. The mean bud lengths per branch were used for the comparisons.

Bud lengths were measured before placement of the sleeve cages in the first season of treatment and remeasured each year thereafter in

September and early April before bud swell to test for differences between these periods.

The difference in bud length (BLD) between the control and experimental branch was calculated by subtracting the treated branch difference in average bud length (BLD_t) from one measurement period to the next from the control branch difference in average bud length (BLD_c) and dividing by the control branch average difference as an estimate of the normal or expected difference. That is, $BLD = (BLD_c - BLD_t)/BLD_c$.

Tree Vigor Evaluation

A means of determining plot differences in tree vigor was needed to help understand possible differences in treatment response. The resulting measure of vigor must take into account that branches were treated, not the entire tree. The size, or vigor, of a branch within a whorl differs between trees. Thus, a measure of tree vigor and branch vigor was combined to produce a tree vigor index. The mean height of the trees within a plot was divided by the tree age (number of whorls) to give a relative measure of site quality (or tree vigor). This quantity was then multiplied by the mean total bud length per branch per plot as a measure of branch vigor. This gave an overall vigor index for each plot (Table 3).

Statistical Analyses

Data from similarly treated plots were combined into groups for statistical analysis (Table 4). The results were treated using an

Table 3.--Tree heights, ages, and vigor for all plots, 1975.

Plot Number	Mean Tree Height (feet)	Tree Age (years)[a]	Mean Total Bud Length/Branch ±SE(mm)[b]	Vigor Index[c]
1	10.7	12	89 ± 8	79
2	9.6	12	102 ± 8	81
3	6.7	12	84 ± 8	47
4	8.5	12	93 ± 9	66
5	12.8	13	98 ± 7	97
6	13.3	13	85 ± 7	87
7	10.0	13	73 ± 7	58
8	8.6	9	170 ± 17	162
9	7.0	9	105 ± 8	81
10	7.0	9	96 ± 9	74
11	8.1	9	138 ± 10	124
12	8.4	11	122 ± 9	93
13	7.8	11	115 ± 5	81
14	9.4	12	140 ± 14	109
15	9.8	9	116 ± 14	126
16	8.2	9	101 ± 11	92

[a]Age = no. of whorls

[b]Standard error (n = 10)

[c]Vigor index = (tree height/age)(total bud length/branch)

analysis of covariance with dummy variables. Insect-days per branch-unit and insect-days per branch each were regressed on proportionate differences in growth, bud length, and needle dry weights as determined by the treatment vs. control branch paired comparisons. Insect-days per branch were regressed to test the significance of the treatment-

Table 4.--Plot groups formed by combining similarly treated plots, and number and duration of spittlebug treatments.

Plot Group	Plots Combined	Number of Consecutive Treatments	Duration of Treatment (days)
PG1	1,3,4,5,6,7	1	3
PG2	1,5,6,7[a]	2	3
PG3	1,5,6,7	3	3
PG4	8,9,10,11,12,13	1	3
PG5	10,11,12,13	2	3
PG6	8,9	1	3
PG7	14,15,16	1	30
PG8	14,15	2	30
PG9	16	1	30

[a]Plots 3 and 4 discontinued after first year due to flare-up of endemic spittlebug population.

response correlations without considering the amount of branch area exposed or the branch vigor. The analysis of covariance determined if a significant relationship existed between insect exposure per branch and the observed parameters, and if there were between plot differences in treatment response.

Results

To more effectively interpret the results of these studies, the influence of the acute and chronic sleeve cage environments upon the observed growth responses was evaluated. A paired t-test was used to examine differences in response between the caged and uncaged control branches of the chronic plots (plots 14,15,16) and of the control plot

(plot 1). No significant differences were found; thus, treatment response was not influenced by either sleeve cage environment.

Also, tree vigor may significantly affect the response of red pine to Saratoga spittlebug attack. Thus, to help broaden our understanding of factors influencing tree vigor, the soil and ground cover from each site was analyzed and correlated with tree vigor measured as mean tree height/plot age. The percent area occupied by each plant species and bare ground on the floor of each plot was determined (see Table 1), and a soil pit was dug in each plot to determine the depth, thickness, texture (Bouyoucos hydrometer method) and particle sizes of the sand fraction for each horizon and color band. No significant correlations were found between any of the soil measurements and mean tree height/plot age, or between percent abundance of any plant species or bare ground and tree height per plot age, or any combination thereof. Thus, soil and ground cover analysis was not needed to interpret the effects of site on tree vigor, and subsequently on growth responses.

Shoot Growth Response

When growth differences were regressed on the log of insect-days per branch and per branch-unit for plot groups 1, 2, 4 and 7 (Table 5), the branch-unit values gave higher correlations (r-values). Plot group 4 gave the lowest correlation because it had the largest branches and the narrowest range of insect exposures. This diluted insect exposures consequently increasing response variability.

Plot groups 1 and 4 each had a deviant plot which was eliminated in the regressions (i.e. plots 3 and 8 were significantly different from

Table 5.--Plot group correlation statistics between log of insect-days per branch and per branch-unit and reduction of growth.[a]

Plot Group	Insect-days per Branch	Insect-days per Branch-unit	Plot Group Combination	Insect-days per Branch	Insect-days per Branch-unit
PG1	.89[b] .14[c] n=30	.93 .12 n=30	PG1, PG2	.86 .15 n=43 (N.S.)[d]	.90 .13 n=43 (N.S.)[d]
PG2	.82 .17 n=18	.88 .14 n=18	PG4, PG7	.80 .17 n=40 (N.S.)	.88 .13 n=40 (N.S.)
PG4	.69 .10 n=30	.75 .09 n=30	PG1,PG4,PG7	.77 .18 n=65 (.84)	.86 .14 n=65 (.89)
PG7	.76 .20 n=15	.88 .14 n=15	PG1, PG2 PG4, PG7	.78 .18 n=83 (.84)	.86 .14 n=83 (.89)

[a]Combinations exclude deviant plots.

[b]Correlation coefficient (all significant at the 1 percent level of probability).

[c]Standard error of the estimate.

[d]If plot groups are significantly different, the correlation coefficient taking this difference into consideration is given to show improvement in correlation if plot group differences could be accounted for quantitatively; if not given, N.S. = not significant.

their respective plot groups). Plot 3 in PG1 was the least vigorous of all plots (see Table 3) and displayed 23 percent greater growth loss; however, a portion of this loss may have been due to unrecorded feeding from an endemic spittlebug population. Plot 8 in PG4 was by far the most vigorous of all plots and displayed 12 percent less growth reduction. Thus, growth loss may be over- or under-estimated by the given percentages with trees of very low or very high vigor.

Plot groups were further combined to test differences between plot groups (Table 5). That is, comparisons were made between years, consecutive treatments (accumulated), whorls, chronic and acute exposures, and plot locations.

No significant difference was found between PG1 and PG2 (Table 5). This supports accumulating insect exposures for two years and indicates no significant difference in response between years (Table 6). Thus, the feeding pressure of the previous year should be added to that of the current year when assessing growth loss.

No significant difference was found between PG4 and PG7, indicating the acute and chronic treatments and the different locations of the two plot groups elicited similar responses. Thus, the regression applies to growth loss incurred by different types of feeding pressure at different locations.

The plot group combinations 1, 4 and 7, and 1, 2, 4, and 7 included significant differences which may be due to differences in whorl position, location of plot, tree vigor (Table 6) or some combination of these and others. However, without considering group differences the correlations by themselves were significant at the 1 percent level (Table 5).

Reasonable correlations occurred when all plot groups (excluding plots 3 and 8) were used. Both insect exposure per branch and insect

Table 6.--Between plot group similarities and differences within plot group combinations.

Plot Group Combinations	Similarities	Differences
PG1, PG2	Same branches Same treatments	Years of treatment PG2--two years of treatment
PG4, PG7	Whorl treated Year of treatment	Acute vs. chronic exposures Plot locations and conditions
PG1,PG4,PG7	First year of treatment	Year of treatment Acute vs. chronic exposures Whorl treated Plot locations and conditions
PG2,PG4,PG7[a]	Year of treatment	PG2--two years of treatment Acute vs. chronic exposures Whorl treated Plot locations and conditions
PG2,PG5,PG8[b]	Second year of treatment	Acute vs. chronic exposures Whorl treated Year of treatment Plot locations and conditions
PG1,PG2 PG4,PG7	-----	PG2--two years of treatment Year of treatment Acute vs. chronic exposures Whorl treated Plot locations and conditions
PG1,PG2,PG5 PG8,PG9[b]	-----	PG2 and PG8--two years of treatment PG9--one year of treatment, then one year without Year of treatment Acute vs. chronic exposures Whorl treated Plot locations and conditions

[a]Used in study of photosynthetic potential.

[b]Used in study of branch vigor.

exposure per branch-unit related directly to proportionate growth reduction (Figures 5 and 6). Thus, a prediction of growth loss given insect-days per branch or per branch-unit without considering the between plot group differences is a good, broad-based predictive tool. However, growth loss may be over- or underestimated with trees of very low or very high vigor.

Photosynthetic Potential

When differences in needle dry weight (NDW) were regressed on insect-days per branch and per branch-unit for plot groups 1, 2, 4 and 7 (Table 7), the branch-unit values gave stronger correlations than the branch values alone. Plot group 4 displayed the weakest correlations as in the growth response study.

Plot groups 1 and 4 each had a deviant plot which was eliminated in the regressions (i.e. plots 1 and 8 were significantly different from their respective plot groups). Plot 1 in PG1 consisted of five equal low-intensity insect exposures, and displayed significantly less NDW reduction. The regression line in plot 1 was not representative of a range of exposures, and, therefore, a comparison with other plots was invalid. It was included in the regression to provide additional measurement of low-intensity treatment-response variability.

Plot 8 in PG4 was the most vigorous of all plots in all plot groups and displayed less reduction of NDW in the insect-days per branch analysis only. Unlike the growth response study, the branch-unit modification accounted for the greater vigor of plot 8. Thus, unless

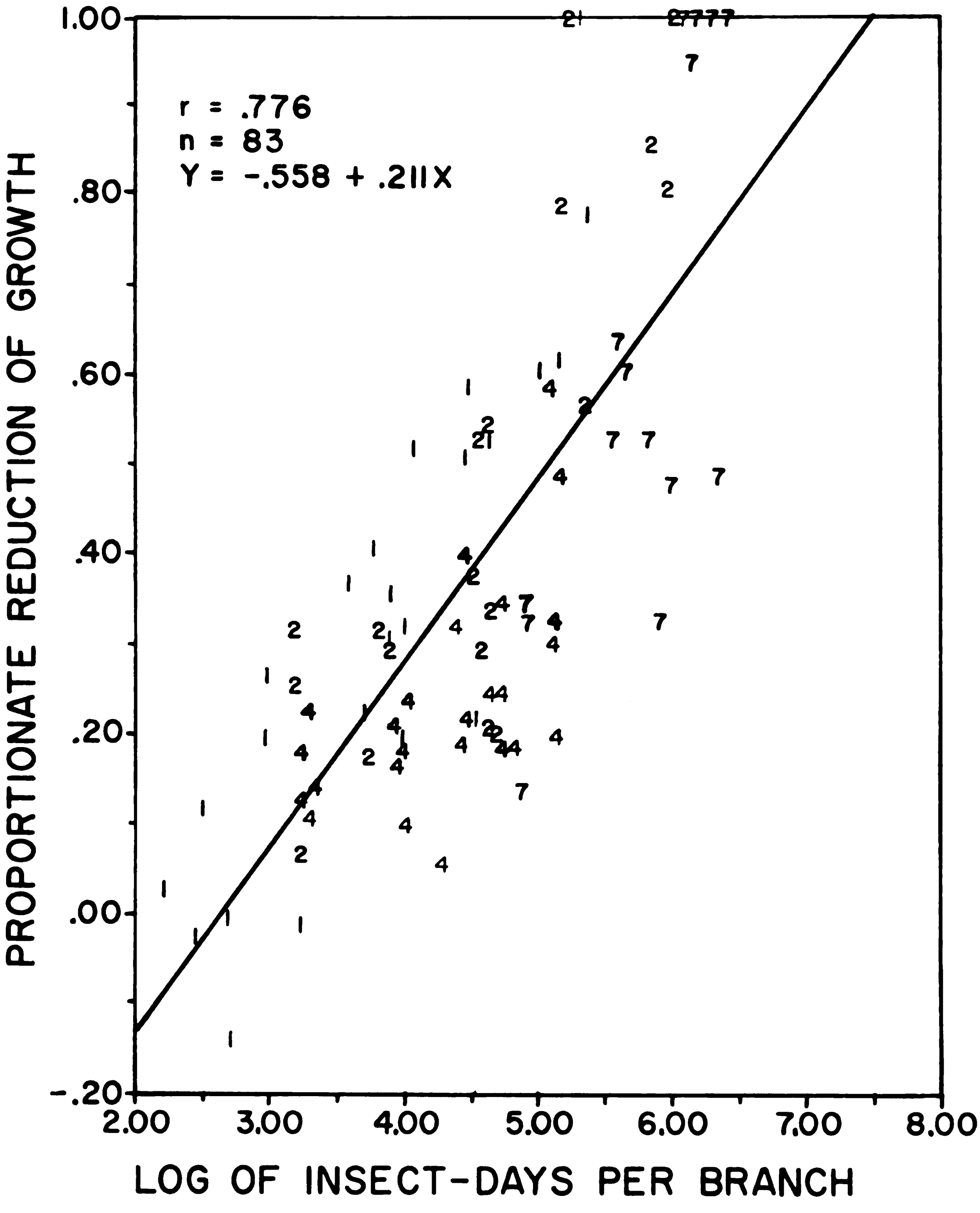


Figure 5.--Log of insect-days per branch regressed on proportionate reduction of growth for the plot group combination PG1, PG2, PG4 and PG7.

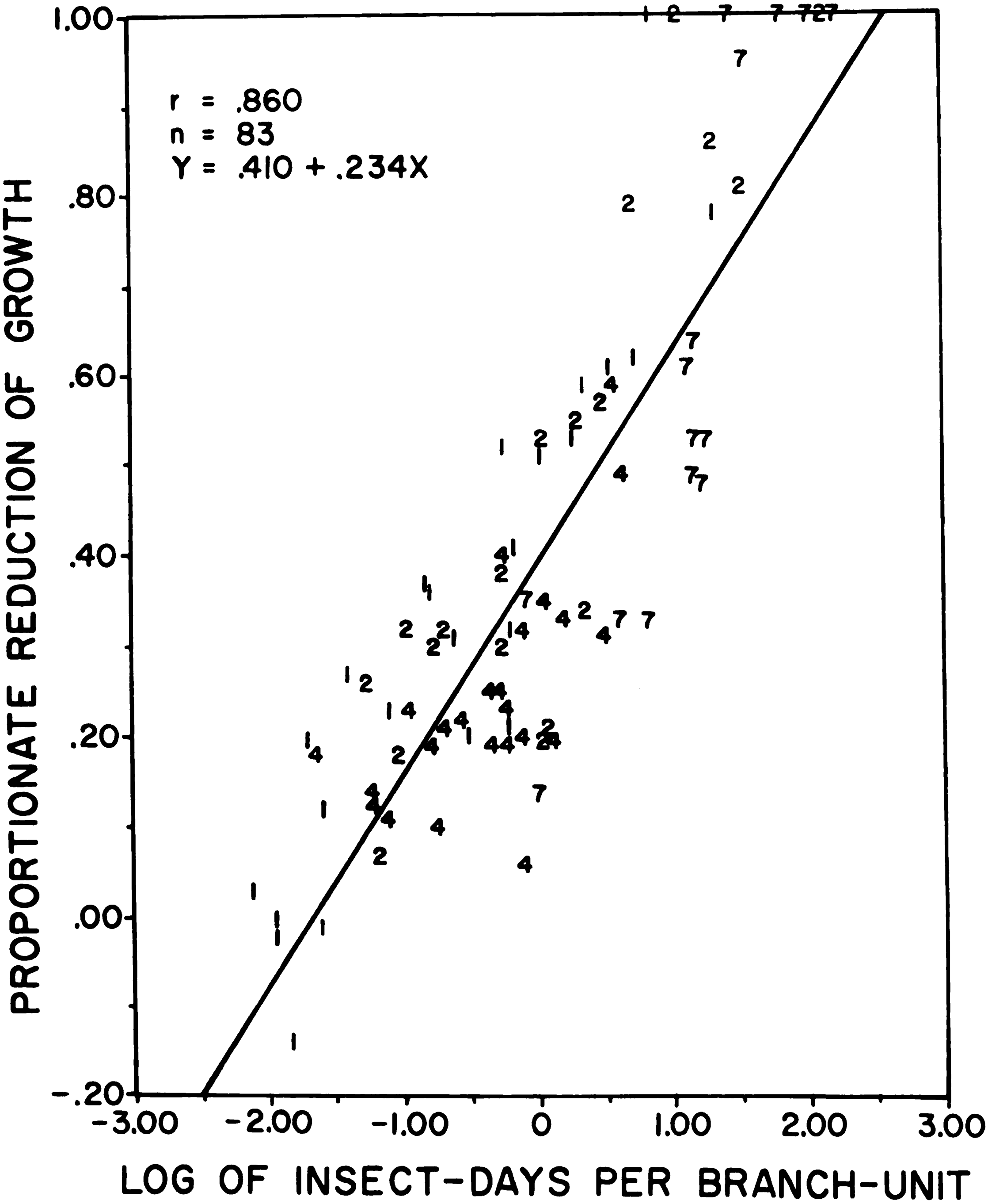


Figure 6.--Log of insect-days per branch-unit regressed on proportionate reduction of growth for the plot group combination PG1, PG2, PG4 and PG7.

Table 7.--Plot group correlation statistics between log of insect-days per branch and per branch-unit and reduction of needle dry weight.[a]

Plot Group	Insect-days per Branch	Insect-days Per Branch-unit	Plot Group Combination	Insect-days per Branch	Insect-days per Branch-unit
PG1	.82[b] .14[c] n=20[d]	.85 .12 n=20	PG1, PG2	.71 .22 n=33 (.79)[e]	.74 .22 n=33 (.85)
PG2	.80 .17 n=18	.85 .17 n=18	PG4, PG7	.85 .15 n=40 (.87)	.90 .12 n=40 (N.S.)
PG4	.65 .14 n=30	.67 .14 n=30	PG1,PG4,PG7	.78 .18 n=55 (.84)	.84 .16 n=60 (.88)
PG7	.82 .12 n=15	.88 .10 n=15	PG2,PG4,PG7	.84 .16 n=53 (N.S.)	.88 .14 n=58 (N.S.)
			PG1,PG2 PG4,PG7	.78 .19 n=73 (.83)	.83 .17 n=78 (.88)

[a]Combinations exclude deviant plots.

[b]Correlation coefficient (all significant at the 1 percent level of probability).

[c]Standard error of the estimate.

[d]Plots 3 and 4 were discontinued after the first year due to a flare-up of an endemic spittlebug population.

[e]If plot groups are significantly different (5 percent level of probability), the correlation coefficient taking this difference into consideration is given to show improvement in correlation if plot group differences could be accounted for quantitatively; if not given, N.S. = not significant.

host vigor is evaluated, the reduction of photosynthetic potential (NDW) will be over-estimated with trees of very high vigor.

Several plots in plot groups 1, 2 and 4 approached a significant difference at the 10 percent level of probability, which may be because bud length is highly correlated to number of needle primordia and not needle dry weight directly. Environmental factors influencing the growth of the needle primordia influence the expression of potential NDW and, therefore, increases response variability between locations and from one year to the next.

Plot groups were combined to test between plot group differences in treatment response (Table 7). Plot groups 1 and 2 are significantly different indicating that one year and two consecutive years accumulated exposures do not relate and/or response is different between years of treatment. This is contrary to the findings of the growth study which showed no significant difference between PG1 and PG2.

A significant difference was found between PG4 and PG7 in the insect-days per branch regression only. Perhaps the branch-unit analysis found no significant difference because branch size and vigor was considered, thereby decreasing response variability. This indicated no actual difference between PG4 and PG7. Thus, the acute and chronic treatments, and the different locations elicited similar responses as in the growth response study. This was supported by the lack of a significant difference when combining PG2, PG4 and PG7. This also indicated no difference between response of the different whorls, and that the two years accumulated exposures of PG2 relate to one year's exposure of PG4 and PG7. Thus, the difference between PG1 and PG2 was primarily due to the different years of treatment, and the primary difference between PG1, PG2, PG4 and PG7 was the difference in response between years.

Although a significant difference was not found between PG2, PG4 and PG7, a significant difference was found between PG1, PG4 and PG7. Again, this indicates that the between year of treatment difference was the primary factor in the plot group response differences of PG1, PG2, PG4 and PG7.

By combining all plot groups (i.e. PG1, PG2, PG4 and PG7) a regression equation, which accounts for all plot variation, was derived to predict reduction of photosynthetic potential (i.e. needle dry weight) from insect-days per upper-whorl branch (Figures 7 and 8). The resulting correlation serves as a broad-based predictive tool. However, by using it, a reduction of photosynthetic potential may be overestimated if trees are highly vigorous as observed in plot 8.

Branch Vigor

Plot groups 1, 4 and 7 are summer (pretreatment) to spring bud length comparisons after one treatment. Plot group 2 is a spring to spring comparison after two treatments and plot groups 5, 6, 8 and 9 are spring to fall comparisons after two treatments. Plot group 3 is a spring to fall comparison after three consecutive years of treatment. No significant difference was found between the fall and the following spring's average bud lengths. Thus, a treatment response is reflected equally at both times.

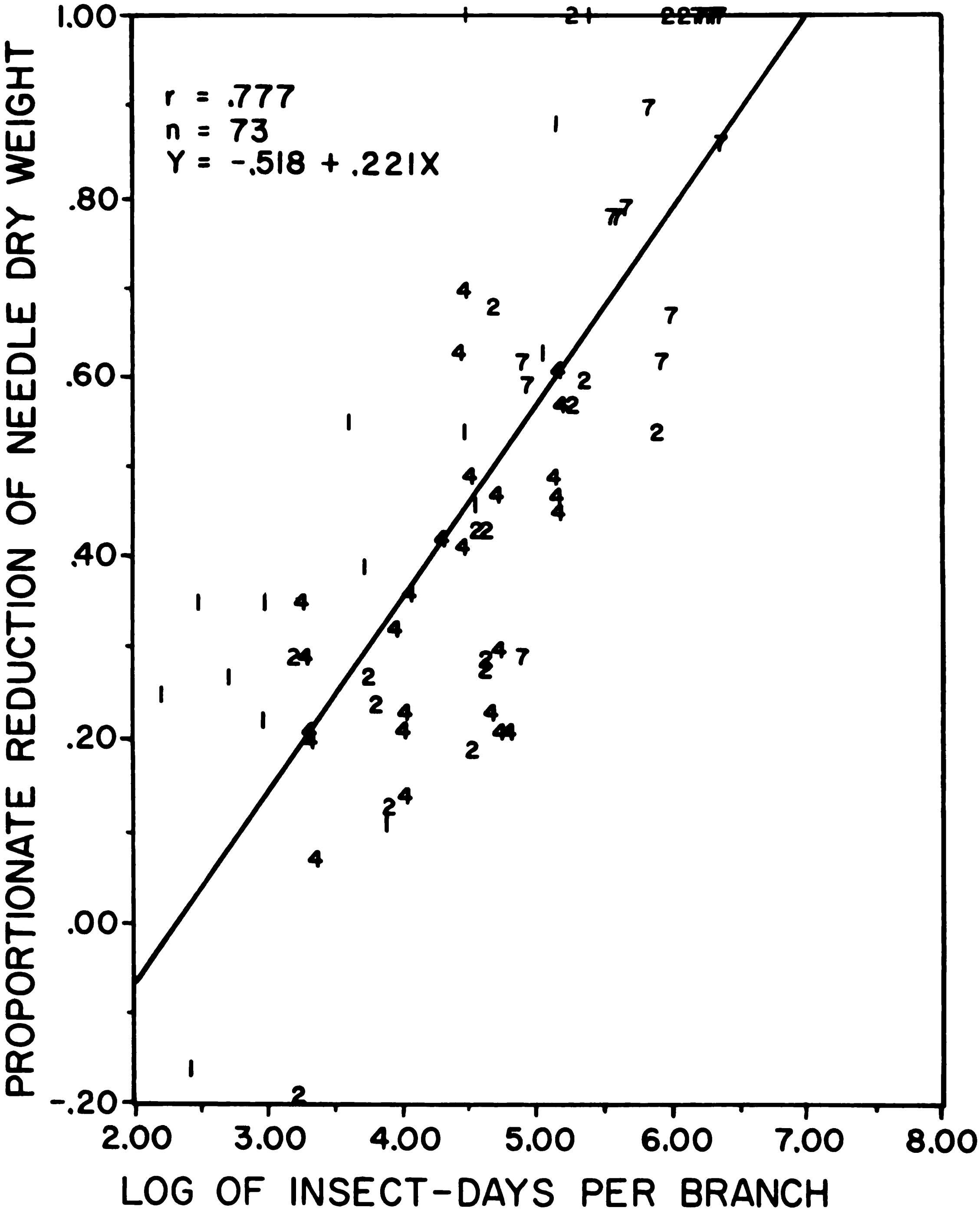


Figure 7.--Log of insect-days per branch regressed on proportionate reduction of needle dry weight for the plot group combination PG1, PG2, PG4 and PG7.

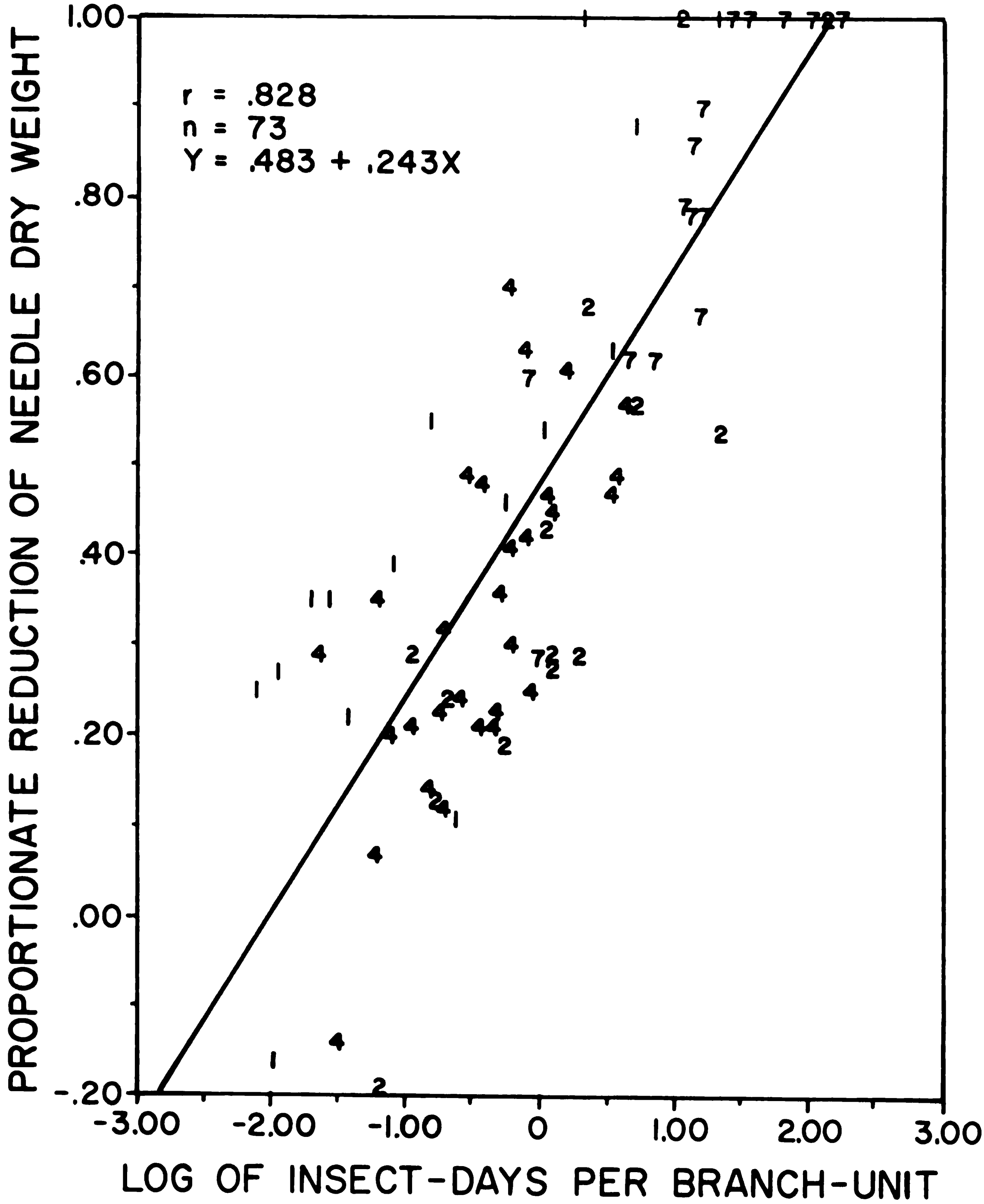


Figure 8.--Log of insect-days per branch-unit regressed on proportionate reduction of needle dry weight for the plot group combination PG1, PG2, PG4 and PG7.

Differences in bud length were regressed on the log of insect-days per branch and per branch-unit for all plot groups (Table 8). The branch-unit values gave higher correlations than the branch values alone as in both the growth response and photosynthetic potential studies.

The bud length correlations were generally weaker than the growth and photosynthetic potential analyses (Tables 6, 7 and 8), and as in the latter study several plots in PG1, PG2 and PG4 approach significant difference at the 10 percent level of probability. This may be due in part to small differences in bud length (millimeters) being compared with a measurement error of approximately 0.5 millimeter and/or to the year to year sequence of environmental influences unique to each location which change the progression of bud lengths independently of treatment effects.

No significant correlations were found in PG4 and PG6. These plots displayed the weakest correlations in both the growth response and photosynthetic studies because of their high vigor and low to moderate treatments which produced greater response variability. This along with the small differences in bud lengths and measurement error may explain the non-significant correlations. Plot group 6 consisted of two plots from PG4 which were not treated the second year; thus, a significant relationship would not be expected. However, PG5 displayed a significant correlation in response to two consecutive seasons of treatment. Apparently, the accumulated exposures elicited large enough responses to overcome measurement error and response variability. Plot

Table 8.--Plot group correlation statistics between log of insect-days per branch and per branch-unit and reduction of bud length.

Plot Group	Insect-days per Branch	Insect-days per Branch unit	Plot Group	Insect-days per Branch	Insect-days per Branch unit
PG1	.68[a] .10[b] n=30	.71 .10 n=30	PG6	N.S.	N.S.
PG2	.77 .20 n=18	.86 .16 n=18	PG7	.47[d] .11 n=15	.69 .09 n=15
PG3	.73 .16 n=17	.78 .14 n=17	PG8	.78 .12 n=10	.86 .10 n=10
PG4	N.S.[c]	N.S.	PG9	.93 .12 n=5	.96 .09 n=5
PG5	.75 .05 n=20	.81 .04 n=20			

[a]Correlation coefficient (all significant at the 1 percent level of probability).

[b]Standard error of the estimate.

[c]Correlation not significant.

[d]Significant at the 7.7 percent level of probability--listed for comparative purposes.

10 in PG5 displayed a greater reduction of branch vigor in response to treatment. This may be due to the low relative vigor of this plot in PG5. This plot, however, was included when combining PG5 with the other less vigorous plot groups.

Plot group 7 demonstrated a significant correlation between insect-days per branch-unit only. Again, this indicated the advantage of considering branch size and vigor. The weaker correlations of PG7 in comparison to PG8 and PG9 were probably due to our inability to interpret bud mortality in the spring and, therefore, including measurements of dead buds. Heavy flagging and branch mortality was found the following summer, but the chlorosis which developed in the spring was not interpreted as mortality. So, the buds were recorded as 20 to 40 percent bud length reductions instead of 100 percent loss. By the following summer, the results of PG8 and PG9 could be interpreted in view of the obvious flagging. Repetition of these severe treatments in PG8 was less influencial because the already greatly stressed branches could lose little more. Thus, although PG9 represented a year of treatment followed by a year of release, the correlation was strongest because of the severity of the treatments and little recovery.

Plot groups were combined to test differences between locations, acute vs. chronic treatments, whorl position and years of treatment (Table 9). Significant differences were found with all combinations of plot groups. This may be due to the greater response variability of this study already explained. Also, unlike the growth response and photosynthetic potential analyses the average bud length per branch from one measurement period to the next has no relationship other than larger buds will produce longer shoots with larger buds on them and smaller buds will produce smaller shoots with smaller buds.

The good correlation achieved when combining PG1 and PG2 (Table 9) lends support for accumulating insect exposures for two years.

Table 9.--Combined plot group correlation statistics between the log of insect-days per branch and per branch-unit and reduction of bud length.[a]

Plot Groups	Insect-days per Branch	Insect-days per Branch unit	Plot Groups	Insect-days per Branch	Insect-days per Branch unit
PG1,PG2	.73[b]	.76	PG1,PG7	.45	.55
	.17[c]	.16		.11	.11
	n=48	n=48		n=45	n=45
PG1,PG2	.60	.69	PG2,PG5	.59	.70
PG3	.20	.18	PG8	.19	.17
	n=60	n=60		n=48	n=48
PG8,PG9	.80	.84	PG1,PG2	.69	.75
	.13	.12	PG5,PG8	.17	.15
	n=30	n=30	PG9	n=78	n=78
PG7,PG8	.70	.76			
PG9	.16	.15			
	n=30	n=30			

[a]Combinations exclude deviant plots; all combinations include significant differences.

[b]Correlation coefficient (all significant at the 1 percent level of probability).

[c]Standard error of the estimate.

However, the addition of PG3 greatly weakened the correlation indicating a shortcoming in combining three consecutive accumulated treatments. This may be due to a small effect of two-year-old scars on branch vigor. Or perhaps, small losses of already stressed branches are hidden in measurement error and/or difference in response between years. Thus, two years of exposures may be the limit in correlating treatment with reduction of branch vigor.

Further examinations of the data suggested that PG1, PG2, PG5, PG8 and PG9 could be combined to formulate the best prediction equations (Figures 9 and 10). These equations can be used to predict the effect of one or two years accumulated insect exposures on the reduction of branch vigor. Again, the branch-unit analysis produced a better correlation.

Discussion

Strong correlations were found between the insect exposures and reductions of shoot growth, photosynthetic potential and branch vigor. The branch-unit analyses consistently strengthened these correlations because they included host size and vigor.

The relationships obtained can be used to assess growth responses of plantation red pine to Saratoga spittlebug attack. Shoot growth correlations can be used to evaluate growth loss directly, and the photosynthetic potential and branch vigor correlations can be used to measure lost growth potential. Reduced photosynthetic potential means less carbohydrate production and, therefore, reduced fiber production. Reducing photosynthetic potential for one year affects growth potential for at least three years--until these needles are shed. A reduction of branch vigor as indicated by reduced bud lengths means fewer needle primordia and less potential for shoot growth the following year. Thus, the following year's photosynthetic potential is directly reduced in addition to the effects of less photosynthetic area from the current year. So, tree growth is actually influenced for at least four years.

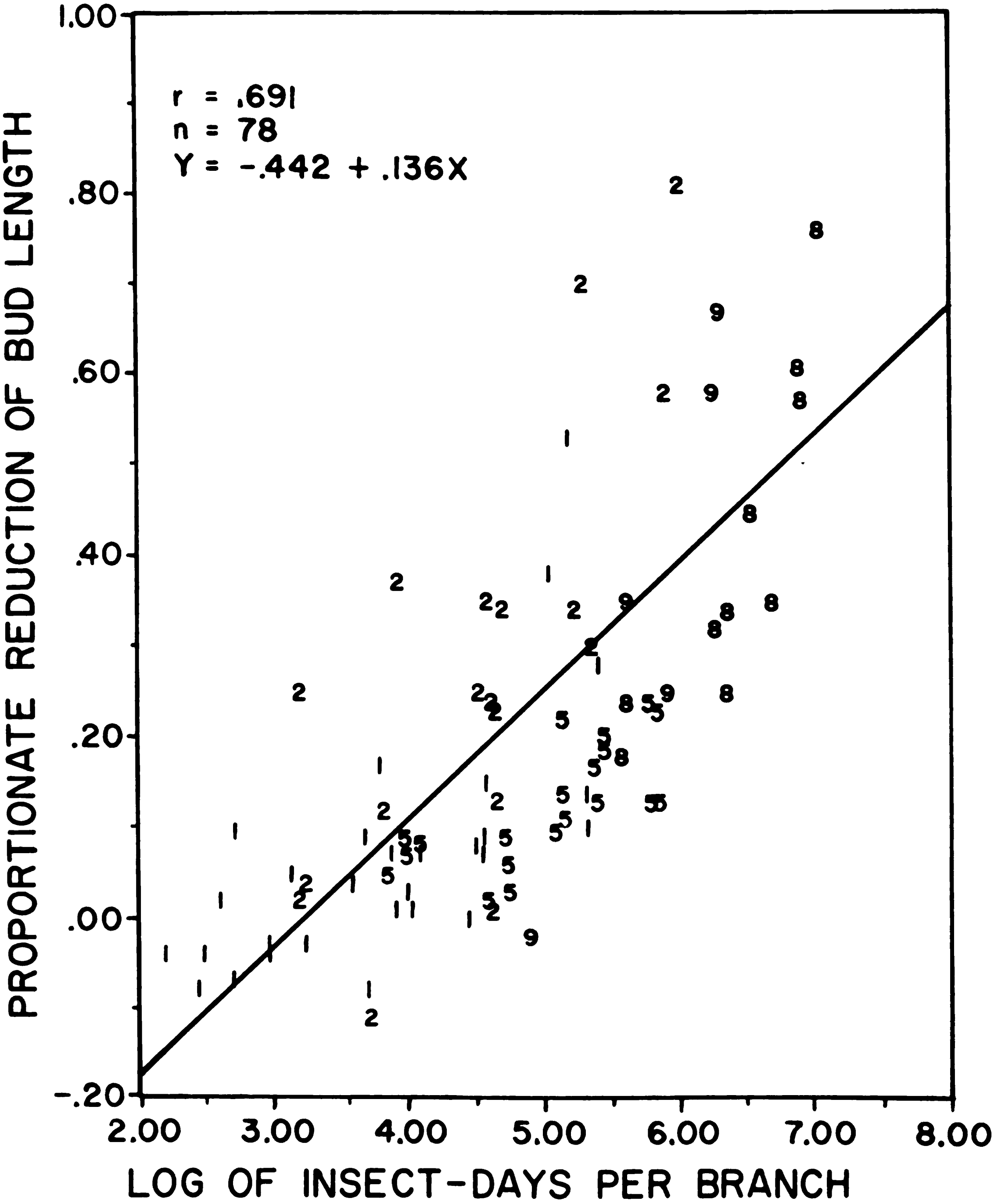


Figure 9.--Log of insect-days per branch regressed on proportionate reduction of bud length for plot group combination PG1, PG2, PG5, PG8 and PG9.

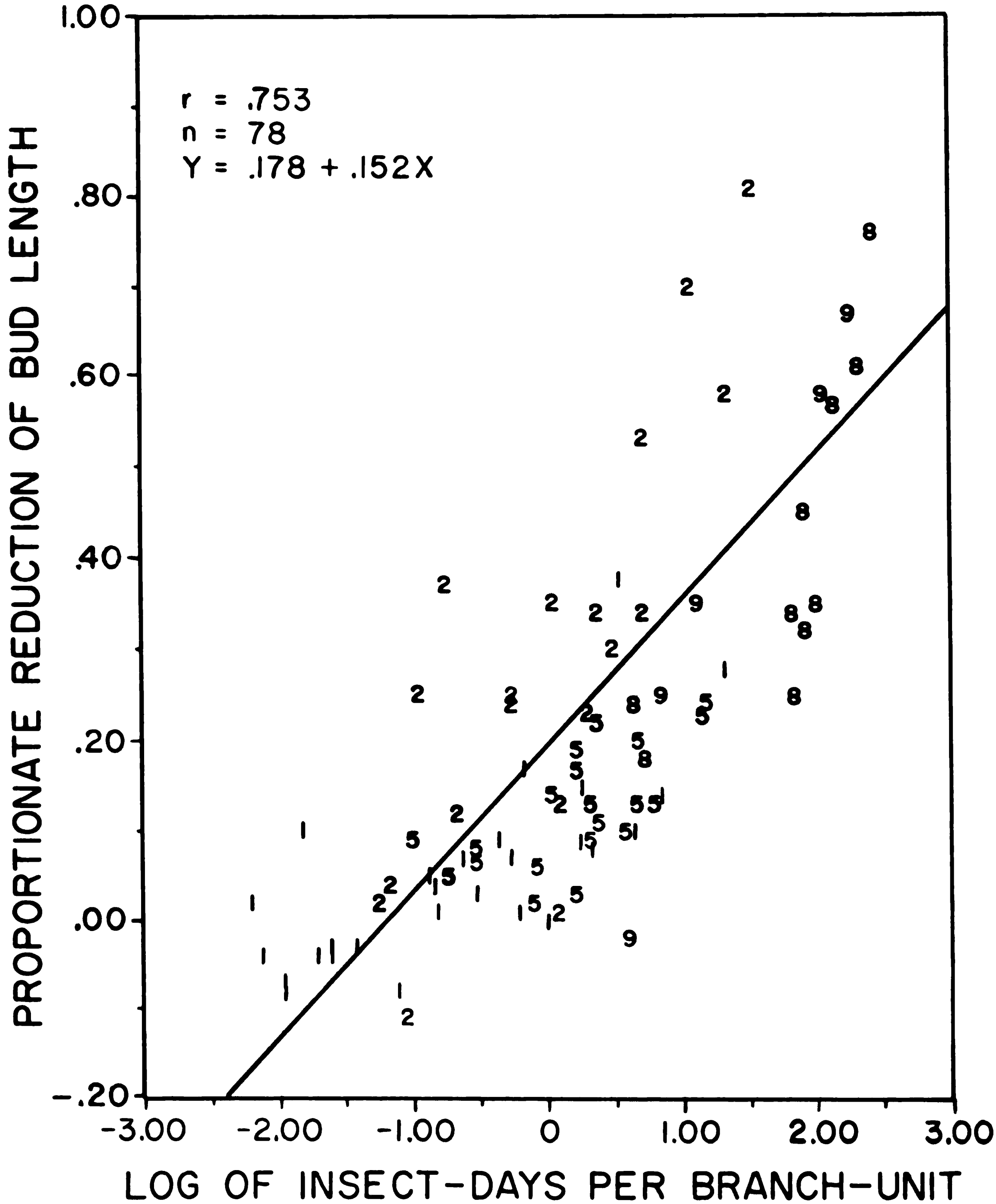


Figure 10.--Log of insect-days per branch-unit regressed on proportionate reduction of bud length for the plot group combination PG1, PG2, PG5, PG8 and PG9.

Growth loss and lost growth potential can be calculated by determining the insect exposure (i.e. insect-days) per branch resulting from a population of spittlebugs. The next sections explain how insect exposures were derived, and how these studies related to evaluations of whole tree growth response.

PREDICTION OF INSECT EXPOSURES PER BRANCH

The objective of this study was to examine the relationship between insect exposure per upper-whorl branch of the growth response studies and exposures of trees to spittlebug populations.

A formula developed by Ewan (1961) relates the population of late instar spittlebug nymphs to the number of feeding scars per ten linear centimeters of two-year-old branch internode. By relating this formula to the insect exposures per branch of the growth response studies, a nymphal survey can be derived which links populations of spittlebugs to tree growth responses.

According to Ewan (1961) if one is given an estimate of the population of nymphs (A) and the tree-units (B) in an infested population, the number of feeding scars per ten linear centimeters of two-year-old branch internode (X) can be calculated. That is, $X = K(A/B)$ where $K = 31.3$ (constant).

Methods and Results

To relate Ewan's formula to the insect exposures of the growth response studies (insect-days per upper-whorl branch), insect-days per branch was calculated for all third to sixth whorl branches ($n = 91$) of all six trees of the feeding distribution study. This was done by dividing total scars per branch by the seasonal average of 2.63 feeding scars per day (Ewan, 1961). When the mean insect-days per branch per tree was regressed on the mean number of scars per ten centimeters of two-year-old internode per tree, a correlation of .96 ($p < 0.01$)(S.E. = 8.86) resulted.

In order to corroborate these findings, four plots were established in red pine plantations in the summer of 1977 in areas with low to moderate spittlebug infestations. Unfortunately, severe infestations could not be found due to a widespread decrease of spittlebug populations. Four branches from the upper whorls of two trees in each plot were collected in late August after 90-95 percent of the feeding injury had occurred. These branches were peeled and scar counts made. By regressing the mean insect-days per branch per tree (calculated as before) on the mean feeding scar density on the two-year-old internodes per tree, a correlation of .88 ($p < 0.01$) (significant at the 1 percent level of probability)(S.E. = 1.87; n = 8 trees) resulted. Combining the two studies gave a correlation of .97 (S.E. = 6.89; n = 14 trees) (Figure 11). Therefore, by equating this combined regression with the initial formula, average insect-days per upper-whorl branch can be estimated. That is, $Y = -8.14 + 66.54X$ where Y = mean insect-days per upper-whorl branch and X = nymphs per tree-unit. However, a closer look at the relationship between an entire season's branch exposure compared to the branch exposures of the growth responses studies is needed. The growth response data gave an average of 3.28 feeding punctures per day instead of the seasonal average of 2.63. Treatments in this study, however, were conducted in the first part of the season when the number of feeding

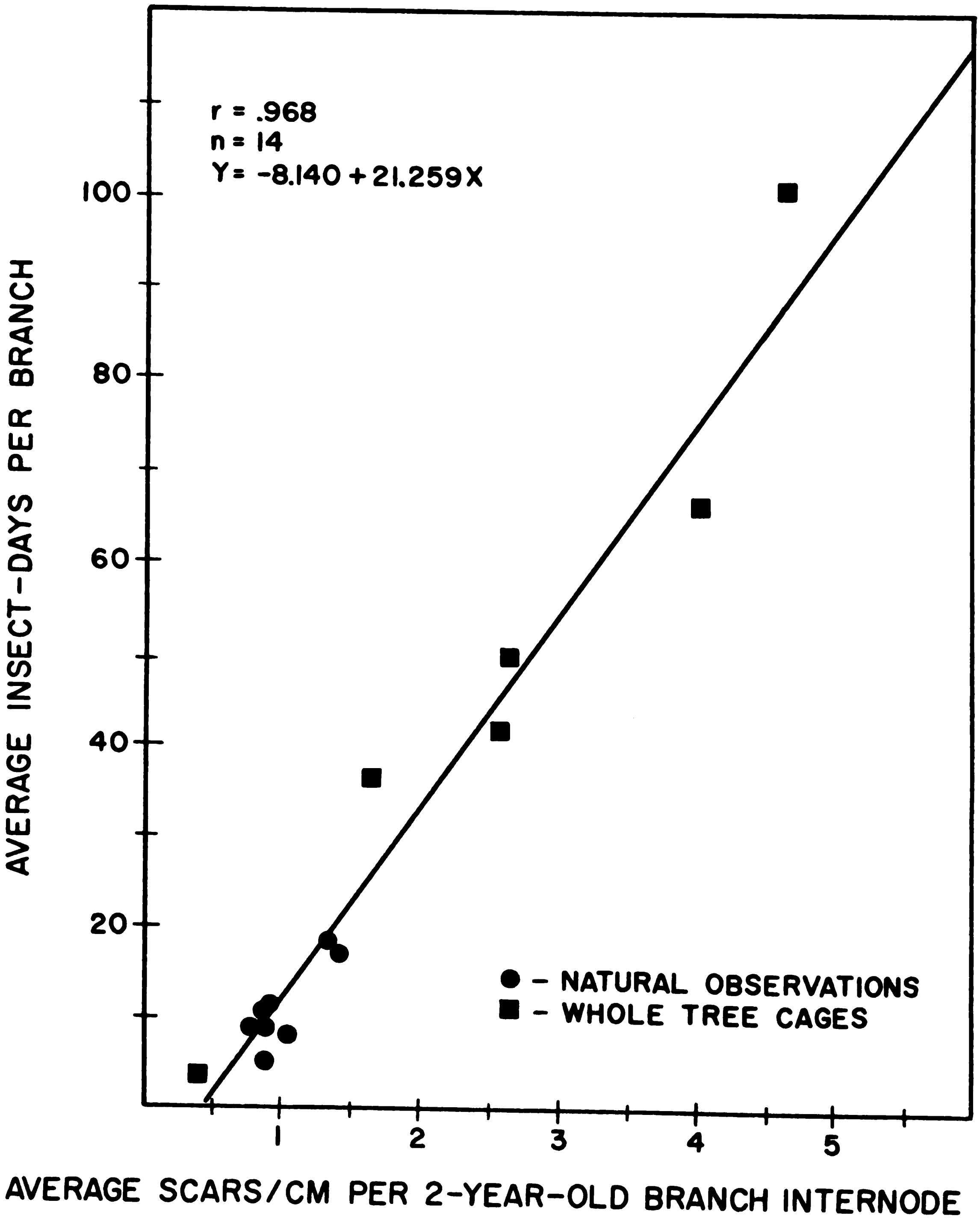


Figure 11.--Average scars per centimeter of two-year-old branch internode per tree regressed on average insect-days per branch per tree.

punctures per adult per day is higher (Ewan, 1961). Therefore, the ratio of 2.63 to 3.28 or .81 should be used as a multiplier to relate insect-days predicted by this formula to the growth response insect exposures. Considering this, the modified formula is Y = -8.14 + 53.90X.

Discussion

Thus, it appears a survey of late-instar spittlebug nymphs and tree-units can be directly related to insect-days per branch of the growth response studies to predict reduction of growth, photosynthetic potential, and branch vigor.

By considering branch size and vigor in the insect exposures of the growth response studies (i.e. branch-unit analysis) consistently stronger correlations resulted. This was determined by the time-consuming measurement of many buds and would be considered practical only on a very small scale. However, the tree-unit evaluation, used in the formula to estimate insect exposure per branch, correlates directly with host size and density (i.e. total length of needle-bearing internodes). Thus, by considering host size and density, some of the variability accounted for by the branch-unit analysis may be accounted for by the tree-unit analysis--producing better correlations than indicated in the insect-days per branch analyses.

PREDICTION OF TREE DEFORMITY AND MORTALITY

The objective of this study was to relate the insect exposures of upper-whorl branches of the growth response study to tree deformity and mortality.

The relationship between growth loss, deformity, and mortality is not well defined. Tree deformity results from loss of apical dominance causing loss of unilateral height growth (Pharis, 1976; Kozlowski, 1964; Kozlowski and Ward, 1957). Spittlebugs stress upper-whorl branches the most. When the stress is sufficient to cause lower-whorl branch dominance or codominance, fork, sweep and/or crook result. Even if the leader maintains dominance, lower-bole limbs grow large. This means more and larger knots. Also, undesirable compression wood formed in large vigorous branches may extend into the bole (Pharis, 1976). Any of these deformities mean degrade or loss for most wood products.

Methods and Results

Ewan (1961) predicted that if trees are exposed to approximately one nymph per tree-unit there would be enough adults for branch mortality and growth deterioration to occur within one to two seasons. An estimate of the corresponding growth reduction from the growth response study was derived by converting one nymph per tree-unit to average insect-days per upper-whorl branch, and using the equation Y = -.558 +

.211 (log X) from the growth response study where Y = reduction of growth and X = insect-days per upper-whorl branch. One nymph per tree-unit resulted in 45.8 insect days per branch. This means about 25 percent growth reduction of upper-whorl branches. Two consecutive years of this insect exposure resulted in about 40 percent growth reduction. By comparing these observations with insect exposures from the growth response study which resulted in partial and total branch flagging, deformity and mortality thresholds were derived. The smallest insect exposure which caused partial branch flagging produced a 20 percent growth reduction. The smallest insect exposure which caused total flagging produced a 40 percent growth reduction, and no branch survived a 70 percent growth reduction. Mortality was somewhat more variable than growth reduction. Some branches displayed partial flagging only after a 40 percent growth reduction, and some did not totally flag until growth reduction approached 70 percent. This may be due to the feeding behavior of the spittlebug. That is, if scars are clustered so as to girdle a portion of the branch or branchlet, partial or total branch flagging will result sooner than if the scars are spread more evenly over the entire branch.

With the above relationships, deformity and mortality thresholds were estimated. Since no branch survived a 70 percent growth reduction, top-kill and serious deformity occurred at 70 percent or greater growth reduction. Serious degrade, whole branch flagging, and some top kill occurred when there was 40 percent or more growth reduction. This latter value corresponded to a two-year exposure of one numph per tree-unit and to the minimum insect exposure required to elicit whole branch flagging. Degrade from limbiness, large knots, and some degree of sweep or crook may result with growth reductions higher than 25 percent. This value corresponded to a one year exposure of one nymph per tree-unit, and represented a value 5 percent greater than the minimum insect exposure required to produce partial branch flagging. Growth reduction below 25 percent primarily related directly to loss of wood volume only. One should note that variability of insect exposures per branch increased with lower spittlebug populations (Ewan, 1961). This means growth reduction and flagging is less predictable in light infestations.

EXAMINATION OF THE GROWTH AND FORM OF TREES WITH HISTORIES OF SPITTLEBUG ATTACK

The effects of Saratoga spittlebug feeding injury on the product suitability of red pine is an important aspect of its impact. The influence upon growth responses of red pine has been evaluated, and the influence of various levels of growth loss upon tree deformity and mortality have been suggested. To complete this picture, an examination of a plantation well beyond the normal Saratoga spittlebug susceptable height range was made to observe the growth and form of trees with a history of Saratoga spittlebug injury.

Methods

A 45-year-old red pine plantation that had previously been attacked by the Saratoga spittlebug was located near Big Rapids, Michigan. Tree form and tree height were observed within the previously attacked area and compared with the surrounding unattacked areas of the plantation. A portion of the stand was still being attacked by spittlebugs.

The heights of five trees were measured in each of five randomly selected locations within and outside the area of damage giving a 25 tree estimate of height in each area.

Ten trees of different heights and degrees of deformity were cut at the ground line and topped at 15 feet--a section representing the portion of the bole most heavily influenced by feeding. These sections of the main stem were then halved and quartered with a band-saw to observe residual scarring, and to understand the relationship between feeding damage and tree deformity.

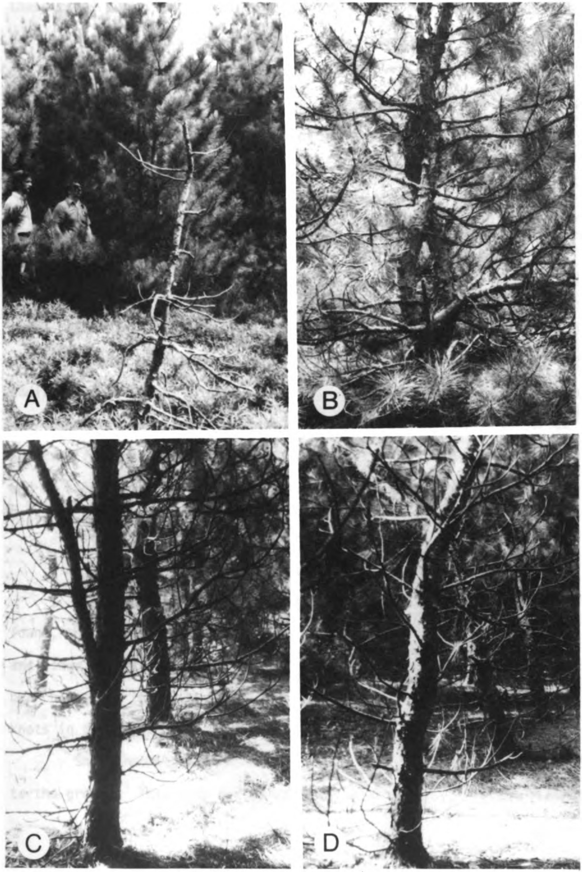
Results

The area of obvious spittlebug damage encompassed approximately 7.5 acres with about 3/4 of an acre in a narrow, heavily vegetated sweet-fern pocket. The few trees remaining within the pocket were stunted and still sustained heavy injury (Figure 12 A,B). Trees at the pocket perimeter were taller and were attacked to a lesser degree.

A mean tree height of 22.7 feet with a range of 17 to 27 feet (S.E. = .94; n = 25) was found within the damaged area. This measurement excluded trees within the pocket, but included some perimeter trees. A mean tree height of 34.5 feet with a range of 32 to 39 feet (S.E. = .77; n = 25) was found for trees in the surrounding uninjured area of the plantation. Thus, an overall difference of approximately 12 feet, or a 30 percent reduction in height was found. The perimeter trees were about four feet shorter than this, and the variation in height was greater.

The trees within the damaged area showed sweep, crook, forks and large and excessive lower limbs (Figure 12 B,C,D). Most of these trees greatly exceeded tolerances for utility poles, lumber, and other products which limit the size and number of limbs, knots and the amount of sweep or crook (Campbell, 1962; Guilkey, 1958; Jackson, 1962). Nearly all deformities were in the lower 15 to 20 feet of the bole. Harvesting

Figure 12.--Forty-five year old plantation with current spittlebug injury: (A) sweet-fern pocket showing current mortality; (B) extreme sweep and multiple stems of a pocket tree; (C) large lower limb characteristic of spittlebug injured trees; and (D) sweep from spittlebug injury and snow damage.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these trees for pulpwood would be difficult because of the loading and hauling problems associated with sweep and crook (whole tree chippers are not used in these areas at present).

In contrast, the trees of the unattacked, or at least much less attacked surrounding area were free of deformities, and were suitable for lumber, utility poles, etc.

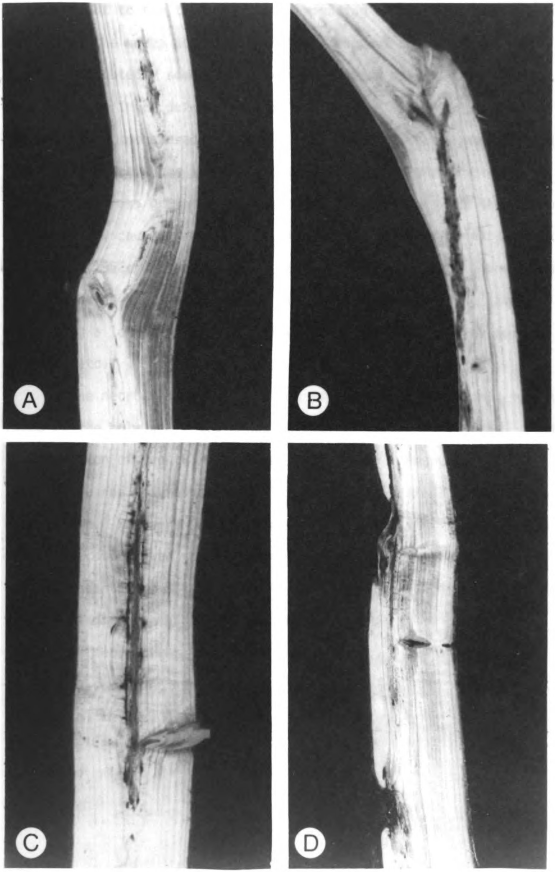
Examination of the interior bole showed that crook and sweep from Saratoga spittlebug feeding resulted from stem necrosis and lower-whorl branch dominance (Figure 13 A,B,D). Necrosis of one side of the bole caused compensatory growth on the opposite side and resulted in sweep. Sweep often occurred in more than one plane in the same stem due to necrosis on different sides of a tree at different points. In addition, lower-whorl branches became dominant or competed for dominance due to upper-whorl stress or mortality, and were responsible for crook and tree fork. Also, scarring on the inner four or five growth rings and on knots extending through the bole caused necrotic, stained and resin soaked areas (Figure 13 B,C,D).

Discussion

Although relatively little open area and tree mortality was found, the 7.5 acres of spittlebug injured trees were useless for lumber and other quality products due to spittlebug-caused sweep, crook, fork, branchiness in the lower bole, scarring of the inner growth rings, and knots in the bole.

Snow probably caused some stem crookedness where trees were bent to the ground. This snow damage occurred only to the spittlebug injured

Figure 13.--Logitudinal sections of red pine trees from a 45-year-old plantation showing residual spittlebug feeding injury: (A and B) crook due to lateral branch dominance after spittlebug injury; (C) necrosis and stain of inner growth rings and a knot; and (D) extreme necrosis extending from inner growth rings to outer surface of bole showing compensatory growth on the opposite side of the bole.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trees and not to the trees of the surrounding area. This snow damage compounded the sweep and increased the amount of compression wood.

Undoubtedly some of the crook and sweep may be corrected in time, but the inner defects will still remain. The lower 15 feet of the boles had uncentered, wandering cores meaning that lumber from these trees will contain the low-grade core wood. Sweep and crook produce lumber with cross grain and compression wood which weakens the lumber structurally, causes warp, and creates surfacing and machining problems (Campbell, 1962; Jackson, 1962). The large and excessive limbs leave numerous large knots which result in lumber degrade. Large limbs persisting a long time make the trees unsuitable for utility poles, pilings, etc.

The necrosis and stain caused by scarring on the inner growth rings of the bole and knots cause structural weakness which could lead to separation of growth rings, and cause a finish degrade.

The reduced height growth also reflects a significant loss of wood volume. However, the portion directly attributable to spittlebug injury as compared to ground cover (sweet-fern) competition and perhaps soil is uncertain. Continued spittlebug injury, ground cover competition, soil differences and/or limbiness reduced the height of the pocket perimeter trees 30 percent more than the other trees in the spittlebug damaged area. The infestation in the pocket areas was still detrimental to tree growth and form after 45 years.

DISCUSSION

The adult Saratoga spittlebug is a sapsucking insect that feeds primarily in the upper whorls of its hosts. The insect saliva and feeding punctures together form necrotic areas in the woody tissues which causes a moisture stress in the tree. The tree responds with reduced and irregular growth. Flagging occurs as deformity thresholds are reached, and whole tree mortality results if the feeding is heavy or if the feeding is moderate to heavy and repititious.

Basic damage data were obtained in the study in order to derive an ecological model of spittlebug impact, and to relate these aspects of impact to socio-economic considerations.

Ecological Model

An ecological model of Saratoga spittlebug shows diagramatically the influence of the physical environment on the discrete interactions between the insect, the tree, and alternate hosts (Figure 14).

The numbers and kinds of ground cover plants present in any spittlebug susceptable stand are critical to ecosystem because these plants affect both insect and tree development. Alternate hosts are obligatory for the insect and some, especially sweet-fern, are necessary for high nymphal survival and population buildup. Thus, the more favorable the alternate hosts present, the greater the change for tree

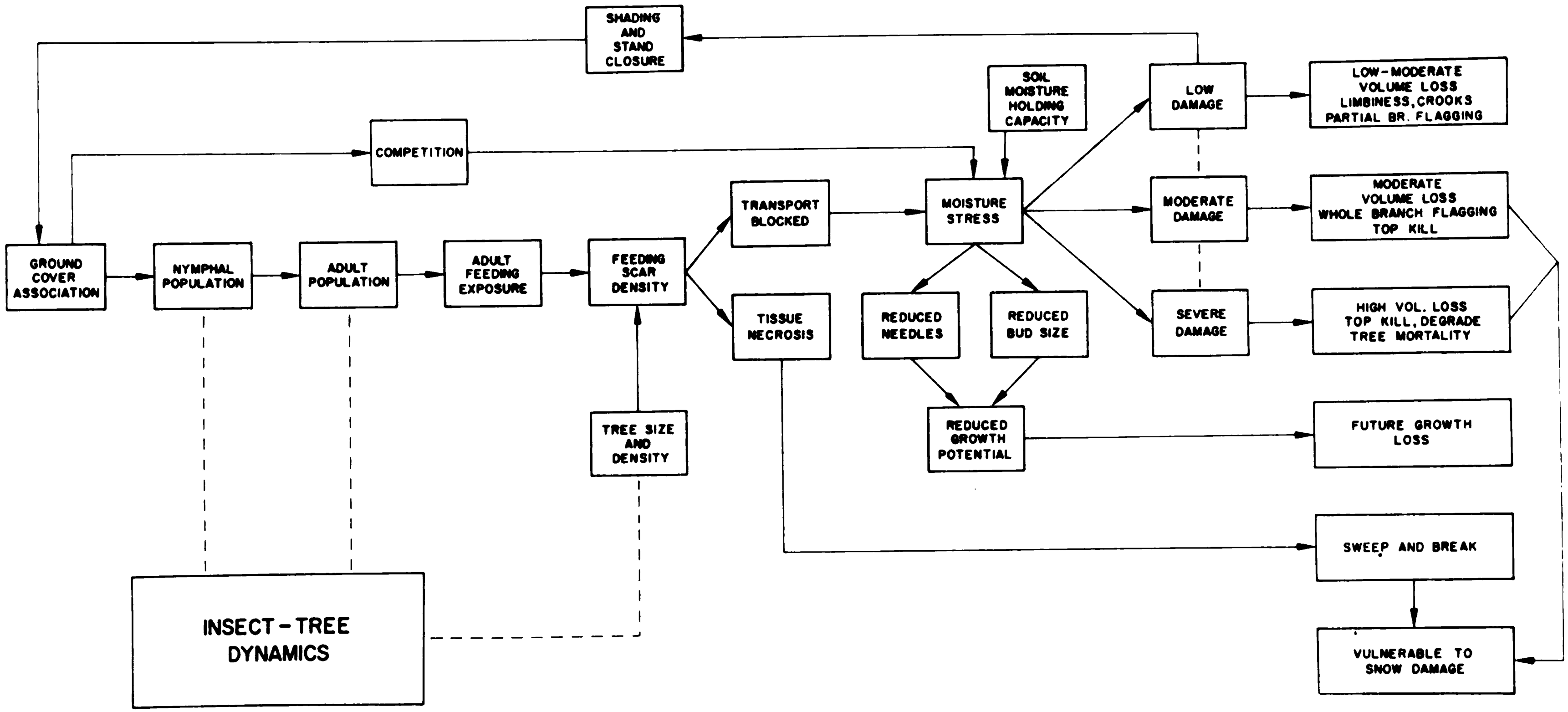

Figure 14.--Ecological model of the Saratoga spittlebug.

injury. A greater density of nymphal hosts not only means a greater population potential, but also greater competition for soil moisture. This, in turn, reduces tree growth--particularly on the moisture poor spodosols of northern lower Michigan. This means there will be smaller trees which are more susceptible to injury, and a longer time to crown closure which shades out the nymphal hosts. So, both the insect and the ground cover reduce tree growth and, thereby, increase the probability of tree injury.

The population of late-instar nymphs relates directly to the population of adults (Figure 14). Further, the adult population can be estimated with a high probability from the nymphal population because there is little late-instar nymphal mortality. The adult population determines the feeding exposure to the tree and this in turn determines the density of feeding scars--relative to tree size and density. The scars make resin filled pockets which block water transport, and cause a moisture stress within and distal to the damaged areas. Scars occur all over the tree but predominate on the upper whorls where adult feeding concentrates. Stress reduces shoot and needle growth as well as future growth potential. Evidence of the latter appears as shorter needles and smaller buds. Shorter needles reduce photosynthetic potential, and smaller bud size means less needle primordia for needles the next year. These together mean less capability to produce carbohydrates and, therefore, wood fiber due to decrease in the amount of needle area for at least three years--the period the tree retains its needles. The immediate reduced growth means less wood volume in the current year, and if reduced sufficiently it can cause tree deformity and mortality. As the upper-whorl growth decreases, resulting deformities increase. Deformity progresses from limbiness and large knots, to sweep, fork, and crook from lower-whorl branch dominance and bole necrosis to tree mortality. Also, as crook and sweep increases, the susceptibility to snow damage also increases. That is, trees bend excessively under snow load from the sweep and crook.

An additional effect of the feeding occurs when the bole is partially girdled by necrosis from a high density of feeding punctures. Compensatory growth occurs on the opposite sides of the stem producing a sweep in the bole and structurally weakened wood. Trees often break at this point, and lower-whorl take-over results in multiple stems, crook, and/or more sweep.

Several factors interact to bring about a spittlebug outbreak that results in severe host damage. Some of these factors can be manipulated so that spittlebug populations will be arrested before intolerable damage occurs. These can be examined through an insect-tree population dynamics model (Figure 15) which interlinks with the ecological model (Figure 14).

It is evident that if the ground cover could be regulated, spittlebug control would follow. However, to date this approach has met with little success. Sweet-fern, which is the most important nymphal host, propagates from a rhizome-like stem. Defoliation studies indicate that due to subsequent sprouting, the crop actually increases in density the year after control. Herbicidal applications are usually unsuccessful

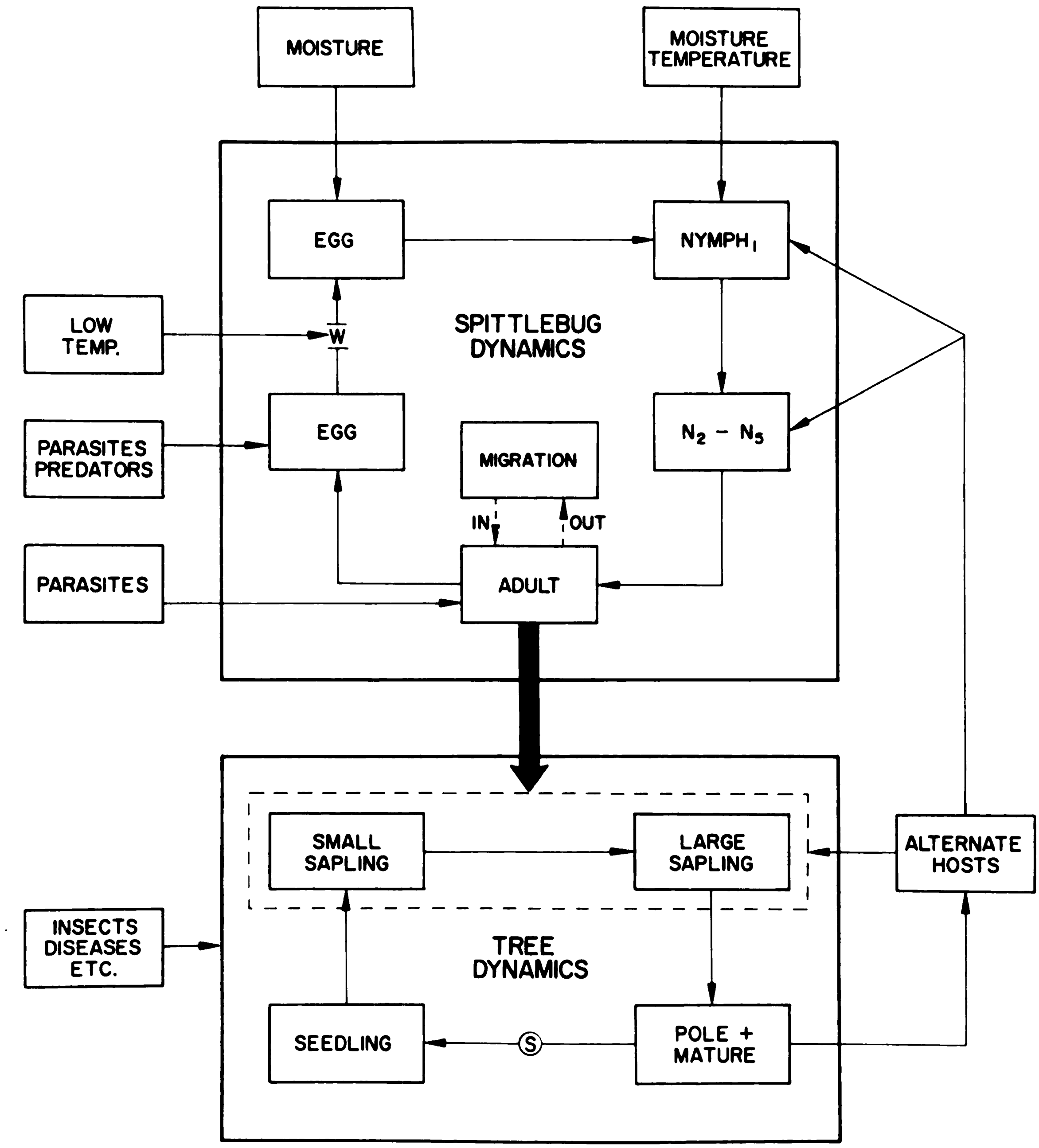

Figure 15.--Population dynamics model of the Saratoga spittlebug--red pine ecosystem.

because adequate dosage to kill the sweet-fern is expensive and harmful to the tree. A biological agent (defoliator, etc.) has not been found to control sweet-fern.

The soil influences both tree vigor and species of ground cover and their abundance. Poor soils produce poor tree growth and generally sparse ground cover. Although planting on poorer sites might reduce ground cover abundance and therefore spittlebug risk, tree growth would probably be reduced more. More logically, better sites allow trees to attain crown closure at an earlier age and/or allow trees to surpass the spittlebug susceptable height (15 feet) sooner. Even though better sites potentially foster higher risk ground cover associations, fewer controls would be necessary to get plantations past the spittlebug susceptible stage. Close spacing insures early stand closure. However, the current tendency is to plant 8' X 10' or 10' X 10' spacing, so closure time will be lengthened in future plantations.

Besides the alternate host, there are several other factors which limit the spittlebug in its various life stages. Parasites, predators, migration, and weather are but a few. Some of these can be manipulated, and will be, after extensive population dynamics studies are made and key factors useful for management are isolated.

Predictive Model

Quantification of certain parameters derived from this study permits construction of a predictive model of spittlebug damage (Figure 16). Potential damage can be predicted for any susceptible red pine stand and for land proposed for planting red pine (Figure 16). To do

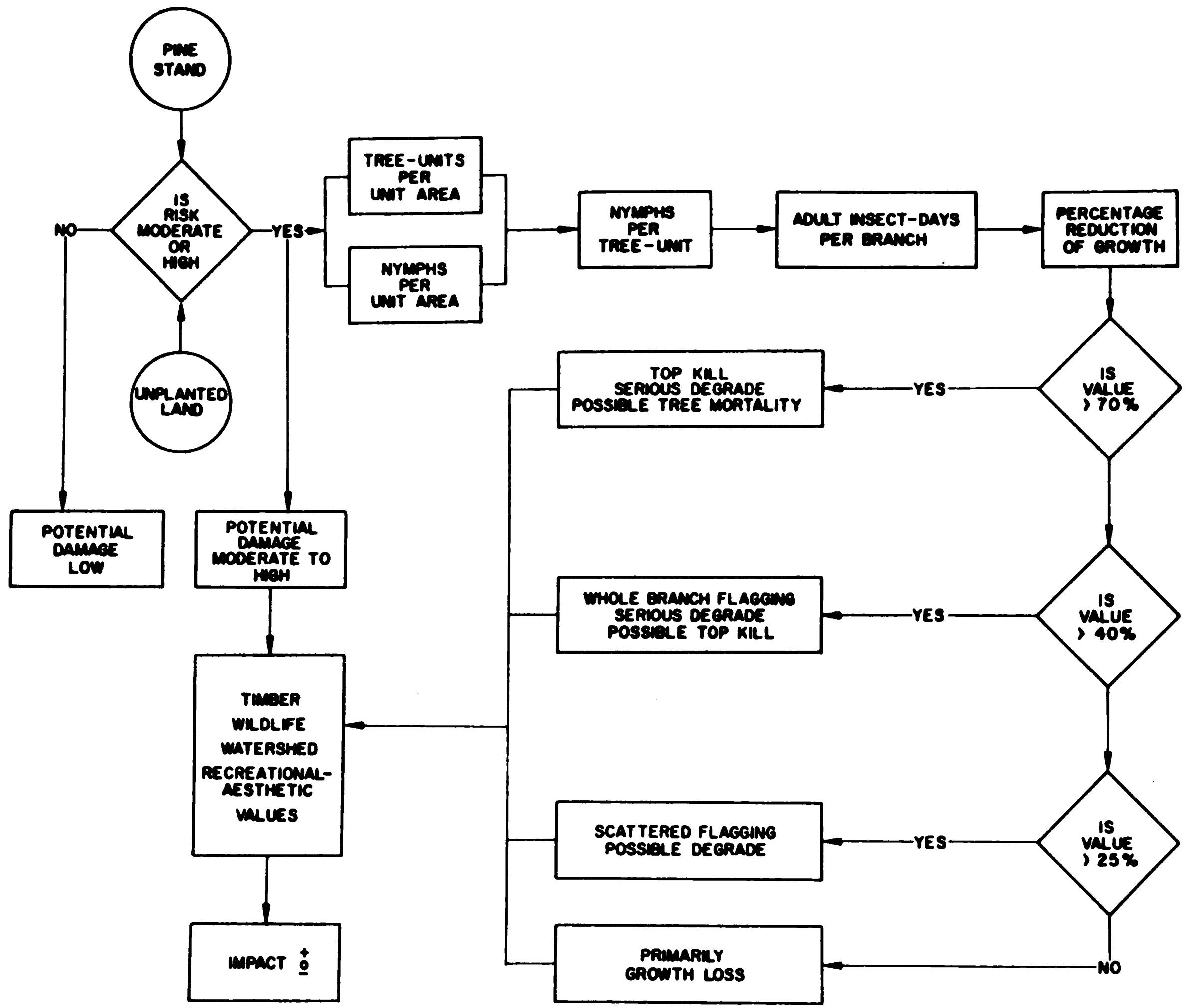

Figure 16.--Predictive model for Saratoga spittlebug attack.

this the area of concern should be delimited and then risk rated. Wilson et al. (1977) have shown that the alternate host association is useful for estimating the risk of spittlebug damage. Damage is thus based on the sum of the percentage of ground cover occupied by sweet-fern and other alternate hosts. Low risk means low damage potential and the stand is safe from the insect or fallow land is safe to plant to red pine. Should the area be rated moderate or high risk, then potentially there will be moderate to high potential damage. Unplanted land, then, should not be planted to red pine unless alternate host and/or insect control is considered in the management plans. Established plantations should be examined further in order to predict the degree of damage. This can be done by surveying the late-instar nymphal population and determining the tree-units. Together these give nymphs per tree-unit which then can be related to the mean number of adult insect-days per upper-whorl branch by using the equation $Y = -8.140 + 53.897X$ where Y = mean insect-days per upper-whorl branch and X = nymphs per tree-unit. Insect-days can further be related to growth loss by the equation: Proportionate reduction of growth = $-.558 + .211X$ where X is the log of the insect-days per upper-whorl branch for one or two consecutive years accumulated feeding exposures. Yearly surveys provide more accurate means of accumulating insect exposures; however, this degree of accuracy may be unnecessary. As an alternative, the current insect exposure can be used alone as a conservative estimate of potential growth loss. Spittlebug populations in areas of moderate to heavy damage can build up rapidly, making the previous insect exposure a relatively small proportion of the total exposure. On the other hand, the added influence of the previous feeding could be used as a subjective modifier if near-threshold values are derived from the current insect exposure. In both instances it is assumed that the population is being monitored as the population increases--before a critical damage threshold has been exceeded.

The degree of growth loss directly predicts tree damage. A value of less than 25 percent growth loss shows only reduced growth of the tree and a small loss of potential growth for the following two-three years. Percentages from 25 to 40, however, show trees having scattered partial branch flagging and some deformity from light sweep and large lower-bole limbs. Percentages from 40 to 70 provide some trees with top kill, whole branch flagging and serious degrade from sweep, crook, multiple stems and large lower limbs. Growth loss of 70 percent or greater leads to numerous trees top killed, heavy degrade, and a few to many dead trees.

These predictive values and actual results have certain socio-economic considerations which must be considered by the land manager before he can ascertain insect impact.

Socio-Economic Considerations

Forest lands are managed for a multiple of uses, though only one may dominate at a particular time or location. Multiple use concepts then should be considered for established and planned red pine plantations. The Saratoga spittlebug can modify the tree and the environment in a stand, and, therefore, can change or modify management goals.

The socio-economic reaction from such changes determines the impact from the insect in terms of timber, wildlife, recreation and watershed values.

The quantity and quality of timber produced is a category of impact of considerable interest to the forest manager. Plantations are managed to produce an end product such as lumber, utility poles, pilings, pulp, posts, or some combination thereof. The spittlebug reduces the growth of trees, and deforms, degrades and kills them--all detriments to timber management goals. Saratoga spittlebug damage often reduces sawlog and utility pole quality by $100-$200 per acre, and may completely degrade a stand of trees for these uses.[1]

Once damage thresholds are surpassed the resulting degrade may render the trees unfit for many other forest products, depending upon the size of the tree and the severity of the injury. Small trees may recover if the spittlebug population is kept under control, and the residual scars and deformities could be confined to the lower half log of the bole. However, severe injury which causes lower-whorl branch dominance and codominance leading to multiple stems, sweep, and crook could render the trees useless for utility poles, pilings, and portions of the lower log for lumber. Tree mortality, especially of small trees, could also result. Corrective pruning could help recovery of tree form, but this is costly and the benefits may not out-weigh the costs. Also, the interior scars (necrosis and stain) would still degrade the bole for lumber. Pulpwood could be considerably degraded as well. There

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[1]Personal communication from William Stump, State and Private Forestry, U.S. Forest Service, St. Paul, Minnesota.

are extra loading and hauling costs in transporting crooked pulp sticks. Because whole tree chippers are not widely used, crooked pulp sticks could be culled. If the end product of many years' growth cannot be economically utilized, then there is a waste of time, energy and space. Also, growth loss from spittlebug attack results in increased rotations and decreased wood volume. In general, the spittlebug causes a sizeable negative impact on the forest from the timber production standpoint.

The watershed component of spittlebug impact seems minimal in the Lake States and probably should be considered of neutral value. Generally, the spodosols underlying a majority of these red pine plantations allow little run-off due to rapid penetration and infiltration of water. Also, the nymphal stage of the spittlebug requires surrounding ground vegetation for survival. Consequently, the spittlebug's damage potential is dependent upon a sufficient density of suitable ground vegetation; thus, abundant ground cover relative to initial site conditions remains after tree mortality to protect the soil surface from rain-drop compaction, wind erosion and aids soil stabilization.

Areas with moderate to heavy damage or damage potential could be left as natural habitat for the enhancement of wildlife values or recreational-aesthetic values. The influence upon wildlife values is uncertain as yet, but an overall positive impact may result from such areas. Spittlebug mortality occurs as a pocket infestation. These pockets correspond to areas of suitable ground vegetation for nymphal survival and population build-up. The pockets are generally well vegetated and tree mortality creates "edge" within the plantation--both of which are amenable to wildlife.

Recreational-aesthetic values may be enhanced by providing increased variety of scenery, but are probably little affected depending upon public notice. Leaving large pockets unplanted provides less substrate for spittlebug build-up because nymphs establish primarily within ten feet of the tree (Ewan, 1961). Therefore, the decision to leave large areas natural may have a positive impact upon timber values too. Of course, increased branchiness of perimeter trees and loss of pocket area for wood production would have to be weighed against possible savings of control costs and impact upon all multiple use values.

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