

A BIOLOGICAL STUDY OF THE
WHITE PINE WEEVIL, Pissodes strobi PECK, WITH
SPECIAL REFERENCE TO THE EFFECT OF PHYSICAL
FACTORS ON ITS ACTIVITY AND BEHAVIOUR

A THESIS
Submitted to the Faculty of Graduate
Studies and Research of
McGill University

by
Calvin R. Sullivan

In Partial Fulfilment of the Requirements
For the Degree of
Doctor of Philosophy
May, 1957

TABLE OF CONTENTS

	Page
I. ACKNOWLEDGEMENTS.....	v
II. INTRODUCTION.....	1
III. LITERATURE REVIEW.....	3
A. TAXONOMIC POSITION.....	4
B. DISTRIBUTION.....	4
C. SEASONAL LIFE HISTORY AND HABITS.....	5
D. INJURY.....	12
E. CONTROL.....	16
F. HOST TREES.....	24
IV. EXPERIMENTAL STUDIES.....	28
A. LOCATION AND STAND HISTORY.....	28
B. LABORATORY INVESTIGATIONS.....	31
1. LIGHT REACTIONS.....	31
a. Experimental Material.....	31
b. Methods of Experimentation.....	32
c. Results.....	34
(1) Reactions to a point source	34
(2) Reactions to diffuse light.	41
d. Discussion.....	51
C. FIELD INVESTIGATIONS.....	57
1. LIFE HISTORY.....	57
2. EFFECT OF WEEVIL INJURY ON TREE GROWTH.....	60
3. SURVIVAL.....	73

	Page
4. EFFECT OF ENVIRONMENTAL FACTORS	
ON ACTIVITY AND BEHAVIOUR.....	92
a. Materials And Methods.....	92
(1) Meteorological obser-	
vations.....	92
(2) Biological Observations..	95
b. Results.....	97
(1) Spring population of	
adults.....	97
(a) Emergence from hiber-	
nation.....	97
(b) Habitat temperature	
and its effect on weevil	
behaviour.....	101
(c) Effect of weather on	
feeding, copulation, and	
oviposition.....	107
(2) Larval population.....	124
(a) Effect of temperature	
on larval movement.....	128
(3) Autumn population of	
adults.....	133
(a) Emergence from	
infested leaders and	
subsequent behaviour.....	133

	Page
(b) Effect of weather on feeding activity.....	137
(c) Hibernation.....	141
(4) Dispersal and flight habits.....	147
5. THE EFFECT OF SHADE ON THE HABITAT OF THE WEEVIL.....	157
V. DISCUSSION.....	179
VI. CONCLUSIONS.....	191
VII. CLAIM OF CONTRIBUTION TO KNOWLEDGE.....	198
VIII. REFERENCES.....	199

1. ACKNOWLEDGEMENTS

This investigation was carried out for the Division of Forest Biology, Canada Department of Agriculture, and this organization granted permission to use the results for thesis purposes. I wish to thank Dr. M.L. Prebble, Chief, Division of Forest Biology, for his invaluable help in the initial planning and organization of the field work.

The investigations were carried out with the help of assistants employed by the Department of Agriculture, including the following: J. M. Anderson, H. Matulis, E. Vuorimaki, I.D. West, D.W. Fleming, and L.W.P. Legault. Photographic work was carried out by D.C. Anderson.

I wish to acknowledge the invaluable help of Dr. W. G. Wellington, Head, Bioclimatology Section, Forest Biology Laboratory, Victoria, B.C. His assistance, comments and criticisms during the investigation are greatly appreciated.

Thanks are also due to members of the Forest Insect Laboratory, Sault Ste. Marie, Ontario, who gave advice and assistance, and in particular, Dr. R. M. Belyea, Officer-in-Charge, and G. W. Green who offered many helpful suggestions during the field work, analysis of the data, and preparation of the manuscript.

It is a special pleasure to acknowledge the advice

and criticisms of Dr. E. M. DuPorte, Professor and
Chairman, Department of Entomology, Macdonald College,
which were both helpful and encouraging.

II INTRODUCTION

The white pine weevil, Pissodes strobi Peck has been the object of numerous investigations since the early nineteenth century, from which an extensive literature has developed. Despite these efforts, the weevil continues to be a serious pest and one of the most important factors limiting successful reforestation with white pine, Pinus strobus L. It has, therefore, become increasingly apparent that detailed studies of the physical and biological requirements of the weevil are necessary before further efforts can be made to protect white pine stands, both natural and planted, from attack by this insect.

Silvicultural control of any insect must result in a satisfactory balance between the insect and its host, where the insect is held at acceptable levels, and the host develops rapidly enough that profitable yields may be realized. To achieve such a balance between the white pine weevil and its hosts, it is necessary to understand the physical and biological requirements of the weevil in terms of measurable factors of the environment. At the present time, it is well known that the weevil has a decided preference for vigorous, open-growing young pine trees rather than similiar trees growing in mixture with either hardwoods or softwoods. The decrease in susceptibility of attack of the shaded trees might be the result of the relationship between the insect and its physical environment or between the insect and the growth and vigour of its host,

or a combination of both. Once the relation between the insect and its physical environment is fully understood, and once we know the exact physical requirements for satisfactory growth of white pine, successful silvicultural control of the weevil may be possible. The present work is the first of a series of investigations to be undertaken in an attempt to establish these relationships.

In 1817, when Professor Peck described the weevil, (Peck, 1817) he stated that the insect was generally "diffused" over the entire pine country and he clearly recognized its importance to the succession of the pine forests in the east. Since that time, however, the many publications that have appeared have not been concerned with detailed studies of the micrometeorological aspects of the insect's habitats or of the limitations imposed on the behaviour and development of the weevil by extremes in the microclimate to which it is exposed. The investigations herein reported were carried out in both the laboratory and the field. Field studies were first limited to open-grown stands of white pine where the insect occurred abundantly. More recently, exploratory studies have been conducted in young pine stands shaded by hardwood canopies in an attempt to establish the relation between the climate and tree vigour and the general lack of weevil attack in the understory pine. It is hoped that this study will form a sound basis for the successful management of white pine in eastern North America.

III LITERATURE REVIEW

Peck's original description of P. strobil is of interest historically because it is one of the first records of an injurious native insect in North America. Although he did not completely understand the insect's life history, he recognized that it was found wherever white pine grew, and noted its probable importance in the development of pine forests in the east unless some means of checking it were developed. This became especially evident between 1850 and 1900 when, with the abandonment of cleared farms, much of the land reverted naturally to white pine while in other areas plantations were established. The latter practice, which continued throughout the early part of the present century, furnished additional food growing under ideal conditions for the weevil, and the percentage of infested pine increased greatly.

From 1817 until the beginning of the twentieth century much general information on the life history and habits of the weevil was presented by such workers as Harris (1862), Fitch (1858), Saunders (1884), Packard (1881,1890), and others. Since the work of Hopkins (1906,1907) many observers have recorded certain erroneous inferences made by the earlier authors, some occurring as a result of confusion between closely related species. During this period much information has been published on the life history, habits, injury, dispersal, and natural, silvicultural and chemical control. In addition, investigations along anatomical and

physiological lines have also been carried out. Perhaps the most informative publications are those of Hopkins (1906,1907), Blackman and Ellis (1916), Blackman (1919), Graham (1918,1926), Peirson (1922), MacAloney (1926,1930, 1930a,1932), Barnes (1928,1929), Plummer and Pillsbury (1929), Taylor (1929,1930), Potts et al (1942), Crosby (1950), Shenefelt (1951) and Connola et al (1955). It is intended in the following pages to bring this information together as a review of current knowledge of the white pine weevil. A brief report of this type has recently been published by Belyea and Sullivan (1956).

A. TAXONOMIC POSITION

The first reference to the white pine weevil was made in 1817 by Peck when he described the weevil as Rhynchaenus strobi. In 1824, Germar (reported by Hopkins, 1911) proposed and described the genus Pissodes. In 1831, Thomas Say first referred to the white pine weevil as Pissodes strobi. Peck and Champion (1902) described and catalogued P. strobi, giving as synonyms Rhynchaenus strobi Peck and Pissodes nemorensis Germar.

B. DISTRIBUTION

The range of P. strobi has generally been considered to be more or less coincident with the range of white pine. The following is a list of the Canadian provinces and

American states in which this insect has been recorded.

Canada: Alberta, Saskatchewan, Manitoba, Ontario, Quebec,
New Brunswick, Nova Scotia.

United States: Minnesota, Iowa, Wisconsin, Illinois,
Michigan, Indiana, Ohio, Kentucky, Tennessee,
North Carolina, Virginia, Maryland, Pennsylvania,
New York, Connecticut, Massachusetts, Vermont,
New Hampshire, Maine.

The insect is, however, only occasionally found in Alberta, Saskatchewan, Manitoba, Iowa, Illinois, Indiana and Ohio. Taylor (1928) states that it also has been found in scattered states westward to the Rocky Mountains. Although this information is not well documented, it does suggest a range exceeding that of the primary host tree.

It is of interest to note that the weevil has also been reported outside North America. Taylor (1928) reported its presence on white pine trees shipped from the United States and established in Japan during the 1920's.

C. SEASONAL LIFE HISTORY AND HABITS

The first description of the life history and habits of the white pine weevil was by Peck (1817) and the substance of his remarks is given in the following quotation from his paper.

"The insect is so small that it is impossible to detect it in the act of depositing its eggs, which are probably placed under the thin skin or epidermis of the shoot. I suspect that the larva remains in

the wood more than one year, and that the shoot dies the second year after the eggs are placed in it.

When the feeding state is passed, and before the pupa state comes on, it prepares an exit for itself by opening a passage outward, but leaves the exterior skin of the bark untouched, so that it is perfectly secured from any injury by rain. The pupa remains quiet for a time, and the perfect insect has only to cut away the epidermis to escape.

The perfect insect begins to come out early in September, and continues to leave the wood through that month and a part of October; the shoot at that time is pierced on all sides with small round holes, sometimes thirty or forty may be counted in one shoot."

To this may be added an observation by Harris (1862) which, together with Peck's observation, indicates the general opinion on the life history and habits of the white pine weevil during the nineteenth century.

".....the beetles are found in great numbers, in April and May, on fences, buildings, and pine-trees; that they probably secrete themselves during the winter in the crevices of the bark, or about the roots of the trees, and deposit their eggs in the spring; or they may not usually leave the trees before spring."

During the early part of the twentieth century, Hopkins (1907) recognized that earlier publications contained numerous inaccuracies. He was the first to establish definitely that the weevil completes one generation each year, the greatest part of which, including hibernation, is spent in the adult stage. He observed that the insect overwinters in the ground litter and this observation was later corroborated by Graham (1918) and MacAloney (1930).

A search of the literature reveals the futility in attempting to establish a calendar date associated with the time of emergence from hibernation. This is due, primarily,

to seasonal variations at different latitudes and altitudes. MacAloney (1930) stated that emergence from hibernation is associated with site and weather conditions. In the southern range of white pine, emergence occurs during late March and early April, but in the northern range of the tree, activity may not be resumed until late April or early May. Graham (1926) observed that the insect resumes activity in the spring upon exposure to heat. In terms of air temperature, Barnes (1928) showed that weevils leave the pine litter under the trees in the spring when the mean temperature rises to between 40° to 60°F. An example of weevil dependence on the weather has also been recorded by MacAloney (1930,a). In 1927, at the Harvard Forest, Petersham, Massachusetts, he observed early bud swelling and weevil activity following a warm period during late March and early April. This was followed by a drop in temperature to a minimum of 16°F which lasted for several days and was associated with a general disappearance of all weevils into the ground litter and a temporary cessation of height growth of the trees. The resumption of weevil activity and tree growth coincided with the occurrence of a second warm period.

Graham (1926) observed that weevil emergence from hibernation coincides with first swelling of the pine buds, onset of leaf production in cherries, the beginning of fruit formation in American elm, and the full blooming of aspens.

Upon resumption of activity the adults move to the terminal shoots and begin feeding on the apical buds and upper portion of the leaders produced the previous year. Copulation occurs in the same general area. MacAloney (1930) observed that as the season progresses weevils are more numerous on leaders attacked earlier the same season, and he suggested that this was due to the increased odour emanating from them.

About one week after the resumption of activity oviposition begins and may extend over a period of six to eight weeks, occurring first on the upper part of the leaders of the previous year (MacAloney, 1930). The method of oviposition has been reported by numerous authors, including Blackman (1919), Graham (1926), Plummer and Pillsbury (1929) and MacAloney (1930). Using her beak, the female weevil makes a hole in the bark resembling a normal feeding puncture, but a chamber is excavated at the inner end which is distinctly larger than the outer tube. When this is completed, she reverses her position, inserts her ovipositor and deposits one or occasionally two or three eggs in the chamber.

The number of eggs deposited per female varies. Graham (1926) reported a single female laying 115 eggs, Barnes (1928), 150 eggs and MacAloney (1930) found that females deposit from 50 to 150 eggs. Plummer and Pillsbury (1929) after elaborate studies found the number varied from 25 to 201 with the average at 129 per female. Females may deposit

eggs in more than one leader and two or more may be observed ovipositing in a single leader at the same time.

MacAloney (1930) reported that the length of the incubation period of the eggs and the time required for larval development is dependent on the weather. Normally larvae emerge from the eggs in from 6 to 14 days, but Plummer and Pillsbury (1929) showed a decrease in the incubation period as the season progressed. They found larvae emerging from eggs from 6 to 20 days after oviposition with the average length of time being about 9 days. Upon emergence, the young larvae feed on the cambium and innermost bark but, as they mature, they consume the entire cortex with the exception of the outer bark. Newly hatched larvae show no tendency to feed downwards but this is strongly developed at an early age, at which time they form a concentric ring around the leader and feed in a downward direction. When mature, the larvae leave the ring surrounding the terminal and construct a pupal cell in the parenchymous tissue or the pith.

The average pupation period lasts from 10 to 15 days in addition to a prepupal resting period of about 10 to 14 days (Plummer and Pillsbury, 1929). The new adults may remain within the pupal cells from one to three weeks before emerging. They leave the leader by making a near-perfect circular exit hole from the chamber through the intact outer bark.

Upon emergence from the infested leaders, the young adults generally become dispersed throughout the pine stand, feeding on new and old growth and on lateral growth as well

as the leader. Graham (1926) reported the possibility of successful copulation of newly emerged adults and MacAloney (1930) observed copulation which was not, however, followed by oviposition. Barnes (1928) and Plummer and Pillsbury (1929) carried out histological studies of the weevil ovaries before and during hibernation and concluded that the immature state of the ovaries precluded the possibility of oviposition until the following spring.

With the onset of unfavourable weather during late autumn the insects enter the ground cover and hibernate until the following spring.

Peirson (1922) stated that adult weevils reach the terminal shoots of pine by flying over the stand and lighting on the upper part of the stem. This observation has been questioned by later writers. Graham (1926) reported weevils in flight on only one occasion during a four-year period of investigation. On this occasion flight occurred during early spring and the weevils were strong flyers. This prompted Graham to suggest the possibility of a short period of flight during early spring, whereby they seldom if ever take wing. By banding 40 white pine trees with tanglefoot and liberating 200 insects in a plot Graham attributed the lack of attack on the leaders to the inability of the insects to cross the tanglefoot barrier and concluded that weevils usually travel to the terminal shoots by crawling up the mainstem. Plummer and Pillsbury (1929) reached a similar conclusion, adding that dispersion by flight does not occur

during the autumn.

Barnes (1928, 1929 - reported by MacAloney, 1930) showed that on the basis of his experimentation Graham's conclusions concerning the infrequency of weevil flight was not acceptable. He found powerful flight muscles occupying a large part of the metathorax, the dorsal longitudinal and sterno-tergal flight muscles being especially prominent. Weevils flew readily during May and June and also in August and September when permitted to attain a vantage point on the end of a needle or branch of a tree from which to commence flight. When landing, the insect normally alights on the mid-portion of young trees and in the crown canopy of older, sub-mature trees. In either case, it invariably lands on individual needles or fascicles of needles, crawls to the mainstem and up to the leader.

MacAloney (1930,1932) carried out an investigation to determine if weevils attained the leading shoots by means other than movement up the tree from the ground cover. To determine the importance of flight in this respect, he marked off a series of one-tenth acre plots and banded the trees with tanglefoot at various levels from the base to a position just above the level of the lateral growth of the previous year. After examination to determine the incidence of weevilling in the plots his conclusions corroborated those of Barnes, i.e., weevils may reach a leader by direct flight or by flight to the lower portions of the tree followed by movement up the mainstem, the latter method

being the more common.

Barnes and MacAloney also showed that temperature is an important factor controlling flight activity. Barnes found the minimum temperature associated with flight to be about 70°F, with the optimum 80°F or above, and MacAloney found flight commencing at temperatures between 70° and 75°F with the optimum between 75° and 80°F. At temperatures above 85°F the insects moved to shaded sites.

From the foregoing review it is apparent that there is considerable overlapping of specific activities and developmental stages during the weevil season. Plummer and Pillsbury (1929) have shown that the development of adults from eggs laid early in the season takes longer than from eggs laid during the latter part of the season. Under insectary conditions the number of days from egg to adults ranged from 44 to 69 days, with an average of 56 days.

D. INJURY

The first evidence of injury to the tree following adult emergence from hibernation is the presence of feeding punctures on the leading shoots of the pine. Injury caused by adult feeding is usually negligible although Plummer and Pillsbury (1929) and MacAloney (1932) reported that damage to the buds resulting from adult feeding may, on occasion, be serious.

The greatest damage occurs as a result of larval feeding, which results in the loss of the growth of the

previous year and the potential growth of the current year. Larval damage is easily detected by the wilted, drooping appearance of the new growth. The larvae may cause greater damage by girdling stems beyond the level of the first node and on occasion three or four years' growth may be killed. MacAloney (1930) stated that the number of years' growth killed depends on two conditions: the vigour of the tree and, specifically, the height growth of the preceding year; and the relation of the diameter and length of the leader to the number of eggs deposited in it. Leaders thus destroyed are normally replaced by one or more of the lateral shoots. When a single lateral assumes the leadership the tree frequently succeeds in straightening, but Spurr and Friend (1941) found such trees to be poor saw-logs owing to the presence of cross-grains, large knots, and relatively brittle compression wood. Two laterals competing equally for leadership result in the formation of a forked stem, and repeated attacks over a number of years result in multiple top shrubs generally rendered useless for timber production (Watson, 1935).

Weevil infestations sufficient to kill the leader always result in a loss of height growth equal to the excess of the leader length over that of the lateral which assumes leadership. Graham (1918) showed graphically that this difference increases as the length of the leader increases, and MacAloney (1930) showed that additional height loss occurs during ensuing seasons until the new

leader is firmly established.

MacAloney (1930) has shown that weevil injury may also affect radial growth. Certain parts of the trees show definite decreases in diameter growth while other parts show abnormal increases. He suggested that this may be caused by excessive use of the food supply and reserve food supply (the amount of which is lowered by the death of the leader) of the tree in its attempt to overcome the effects of the injury. The total loss in diameter growth varies in relation to the number of year's growth killed and the amount of growth which has taken place before the terminal is girdled. These factors have a bearing on the amount of materials stored in the lower portion of the stem. When considered in terms of average growth of attacked trees there is a decrease in diameter growth at the base, at breast height and at the internode below the dead leader. This decrease may continue for several years after the year of weevilling. On the other hand, while the leader shows a decrease corresponding to the lower parts during the year of attack, its radial growth is often accentuated in subsequent years.

Weevil attack seldom occurs on young pine trees below two to three feet in height but increases steadily as the height of the trees increases up to about 18 to 20 feet. At about 30 feet, weevil damage is negligible, and Peirson (1922) suggested that the occurrence of excessive injury in a given stand is directly associated with tree height. On

the other hand, Graham (1926) has shown that the weevil prefers the most rapidly growing trees, irrespective of their height, until they reach a height of about 20 feet, and he suggested the general lack of weevilling at levels approaching 30 feet is a result of changes in the ecological conditions which occur as the trees develop.

Injury to white pine which closely resembles that of weevilling may be caused by animals other than P. strobi or by purely mechanical factors. These include aphid feeding, squirrel feeding, deer browsing, frost damage and tree whipping. MacAloney (1930) reported that the black aphid, Dilachnis strobi Fitch attacks the terminal shoot of white pine and that when severely injured the shoot dies. Hosely (1928) stated that squirrels feeding on the apical buds of pine may cause more damage than the weevil in certain localities, and West (1947) reports as much as 90 per cent of the terminal buds destroyed by squirrels during the autumn. Abnormally low temperatures during late winter and spring occasionally result in bud freezing (Belyea and MacAloney, 1926), and whipping by overstory broad-leaved trees during high winds may result in injury to the terminal shoots of understory pine. The death of the leaders and terminal buds may easily be confused with weevil damage upon superficial examination or during later years, but normally a search for emergence holes of the young adults, if the shoots are present, will determine whether death may be attributed to P. strobi. If the shoots are lacking, it is

impossible to determine the agent causing the injury.

E. CONTROL

Observations by Blackman (1919) indicated that during the previous 50 years the incidence of weevilling of pine had greatly increased. Consequently, during the first 35 years of the present century, considerable interest was shown in the white pine weevil problem and, as a consequence, an extensive literature developed on control by biological agents and by chemical and silvicultural means.

The weevil is an organism well adjusted to its environment and therefore has numerous biological control agents. Taylor (1928, 1929, 1930) carried out intensive and extensive investigation on this phase of the weevil problem. During his studies he was able to draw on the published and unpublished data of MacAloney, Barnes and Plummer, in addition to published observations by Packard (1885), Hopkins (1907), Felt (1913), Forbush (1913), Steiner (1930) and others. Taylor estimated that, in the eastern United States, birds were responsible for about 18 per cent of the mortality of a weevil population during development, insect parasites accounted for an additional 16 per cent and predation by other insect species amounted to about three per cent. The importance of small mammals as control agents has not been investigated closely but they undoubtedly take their toll of weevil adults during the spring and

autumn. Disease has never been considered an important factor in natural control. Taylor concluded that the control of the weevil by biological means, particularly by the selection of native parasites for applied biological control, did not appear promising.

The possibilities of developing specific strains of white pine and norway spruce resistant to weevil attack are presently being investigated by Holst (1955) and by Heimbürger (personal communication). Attempts by Holst to breed the resistance of white spruce into norway spruce by direct crossings have been unsuccessful as the two species seldom, if ever, hybridize. He is presently attempting to breed the desired qualities of white spruce into norway spruce through Sitka spruce. Since white pine with slender leaders often escapes serious injury, Heimbürger has been investigating the possibility of producing thin leaders on grafts from scions of unweevilled mature trees. In addition, Heimbürger has indicated that it may be possible to produce a vigorous leader strain of white pine which contains a sufficiently heavy concentration of resin to drown out weevil larvae attempting to develop therein. By this latter means, Miller (1950) succeeded in obtaining a Jeffrey pine hybrid highly resistant to the pine reproduction weevil, Cylindrocapturus eatoni Buchanan. At the present time the work of Heimbürger and Holst has not progressed to the stage where suspected resistant types have been tested under field conditions. This work will, of

necessity, be of a very long term nature, but the possibilities which it offers are great.

Less than a quarter of a century ago, direct control measures to reduce weevil populations included (1) the use of banding materials, (2) hand picking of the beetles, (3) jarring the insects into a net, (4) pruning of infested leaders before the new generation adults emerge and (5) the use of sprays and repellents. To-day these methods are still considered as practical control measures for individual shade and ornamental trees but, with the possible exception of pruning and chemical means, they are of no value in stands established for commercial purposes. In 1817, Peck recommended the removal and destruction of infested leaders and later Hopkins (1907), Blackman and Ellis (1916), and Blackman (1919) recommended that leaders be removed but placed in cages constructed of fine wire mesh that would permit the escape of insect parasites but not the weevil adults. Maughan (1930) obtained effective control by initiating a programme of removing infested leaders in the Eli Whitney Forest in Connecticut, starting as soon as weevilling was first detected and continuing each year until the stand closed. According to Maughan, permanent damage to attacked trees was minimized, since removal of infested leaders tended to stimulate the lateral which succeeded as the leader to straighten up more rapidly, but the more recent work of Spurr and Friend (1941) showed that they make poor saw-logs. Maughan also states that subsequent

thinnings to remove badly weeviled trees while maintaining suitable age-class densities gave 200 to 400 unweevilled or slightly weevilled butt logs per acre. In some areas in New York, South Carolina, Ontario, and Quebec, vigorous programmes of pruning leaders resulted in holding weevil populations to a level below that necessary to cause economic damage (MacAloney, 1930). Pruning of infested leaders is, however, an expensive operation, particularly in larger trees, and must be thoroughly carried out for a number of years to obtain satisfactory results. Also, the practice is only recommended for stands growing on good sites where vigorous growth is assured. On poor sites, even with this treatment, not enough acceptable stems are secured to recommend the method.

Cline and MacAloney (1931, 1933, 1935) successfully reclaimed white pine stands which had suffered extensive weevilling. They selected the better co-dominant and intermediate trees and favoured them as the final crop trees by girdling or removing the badly damaged trees.

The protection of plantations through the application of chemical sprays was attempted in the early days by numerous workers (Britton and Walden, 1912; Walden, 1915, 1916; Britton, 1920; Graham, 1916; and MacAloney, 1930), but the results varied considerably. Satisfactory control was not definitely established until recently (Potts et al, 1942; Crosby, 1950; Shenefelt, 1951). During the last fifteen years, many spray formulations have been tested

from the air and from the ground, and to date lead arsenate and DDT have produced the best results. It is almost certain, however, that no spray programme will eliminate the weevil from plantations, but populations may be reduced and maintained at levels that will ensure adequate crop trees.

In ground application, the insecticide is applied only to the leaders in the early spring, after the adults emerge from hibernation but before the onset of oviposition. Lead arsenate has been favoured because it leaves a visible deposit, adheres well to the leader, and has no contact action on weevil parasites and other insects that might encounter it. Sprays applied by means of pack-sack hand sprayers are recommended with the object of protecting the young pine during the period of maximum susceptibility to weevil attack, but usually not after one clear butt log is assured. Excellent control is afforded even in areas of heavy weevil populations; reinfestation is reported to be slow, with a single application protecting stands for as long as four years. Best results have been obtained when spraying operations have been undertaken in young stands as soon as the first indications of weevilling are observed. More than one treatment is required however, and Crosby (1950) states that about three treatments, timed to correspond with reinfestations of about five per cent of the leaders, should afford sufficient protection to the tree so that at least one clear butt log will be produced.

After World War II, the aerial application of insect-

icides and sprays became common, and experiments in the control of the white pine weevil by aerial spraying were begun in New York State (Connola et al., 1955). These observers found that DDT formulations applied during early spring from fixed-wing aircraft and helicopters resulted in successful control of the weevil for two or three years.

Investigations carried out in both natural and planted stands early in the century uncovered certain facts regarding the habits of the weevil which have formed the basis for concepts regarding the susceptibility of trees to attack and the possibilities of silvicultural control even to the present day. Thus, it was early recognized that the weevil feeds and oviposits more readily in pure, open-grown stands of pine where soil, climate, and other conditions are most favourable to rapid and vigorous leader growth. Graham (1918) and Peirson (1922) recognized that in open stands where the crowns are all free, the trees were subjected to heavy attack, whereas in denser stands attack was lighter, and in very dense stands injury was practically absent. Since, trees in dense stands must compete for light and space (which stimulates them to straight growth), it was concluded that close planting of about 1200 to 1500 trees per acre was the most effective method of controlling the weevil in forest plantations if it was maintained during the early growth period and was followed by maintenance of a fully stocked stand.

Colville (1923) and Taylor (1929) observed that the

effectiveness of close planting varied greatly with locality. Thus, in areas where weevil injury is severe, heavy damage may occur in stands irrespective of spacing. MacAloney (1930) found that dense planting was not satisfactory in areas where the yearly infestation of the stands exceeded about 50 per cent. He showed, however, that the incidence of a tree being weevilled more than once was directly related to tree spacing, but he found that trees of the intermediate or suppressed classes were unable to recover even after a single year of weevil injury. He concluded that unless dense stands were produced naturally, it was financially impractical to space trees closer than 6'x6', a spacing associated with severe injury.

Blackman and Ellis (1916) observed that if no weevil damage occurred for several miles around a certain area, white pine might be grown with little chance of injury, provided it was systematically inspected and thorough measures were taken when any evidence of weevilling was found. Additional observations by these authors showed, however, that white pine could be successfully grown in mixture with other tree species without such rigid restrictions. The results of investigations by later workers (Fisher and Terry, 1920; Belyea, 1923; Graham, 1918, 1926; Belyea and MacAloney, 1926; Fisher, 1928; and MacAloney, 1930) seemed to substantiate this, and it became generally accepted that some system of silviculture should be used to provide shade to young pines during their susceptible period,

that is until they reach 15-20 years of age or between 20 and 30 feet in height. Since white pine is an intolerant species, Graham (1926) warned that the density of shade it would tolerate would vary with site and, hence, must be determined for each site, and must not be such that the growth of the pines would be unduly retarded.

It was found that several mixtures of both hardwoods and conifers with white pine gave satisfactory protection from weevil damage and that, in such mixtures, the white pine cleaned its bole relatively early so that clear lumber could be obtained from crop trees.

In addition, it was pointed out (MacAloney, 1930) that the white pine should be planted in mixture with a species that would be of value in the final crop and that early and successive thinnings, particularly in mixture with hardwoods, would be necessary so that the pines would not be crowded out. MacAloney recognized that the accompanying species must be faster growing than the pine in the early years if both species were the same age or, if slower growing, it must be considerably older so that it would be taller during the period of weevil attack and hence shade the pines. MacAloney also stated that the maximum amount of good lumber will be found where there is a groupwise mixture of white pine with the better hardwoods. In a stem-wise mixture, there is danger of whipping which may be almost as injurious to the leading shoots as the white pine weevil.

During the past 35 or 40 years, the many attempts to grow pine satisfactorily free from weevil damage in various kinds of mixtures have been either not successful or only moderately so because there was no clear understanding of why shaded conditions were a deterrent to weevil activity and abundance or of what degree of shading was actually required under varying conditions of soil, exposure, tree species in the mixture, etc. The results of recent studies of weevil attack in open-growing natural white pine regeneration and in white pine understories (Prebble, 1951) show clearly that the observation that white pine under hardwood and other shade is less susceptible to attack requires careful study to determine whether the relation is direct between the weevil and the physical environment, indirect involving growth and vigor of the understory trees, or a combination of both. It is concluded that such relations can only be understood when the physical and biological requirements of the weevil are carefully defined in measurable factors of the environment.

F. HOST TREES

In Table 1 host plants of the white pine weevil are listed under two species classes, native or not native to the region in which the insect is known to occur. In addition, they are roughly classified according to their susceptibility. The primary host plant of P. strobi is eastern white pine, Pinus strobus L. However, Norway

TABLE 1

Host plants of P. strobil, native and not
native to the range of the insect.

Species Class	Species	Damage Class	Reported by:	Date
Native	Eastern white pine, <u>Pinus strobus</u> L.	severe	Peck	1817
	Jack pine, <u>Pinus banksiana</u> Lamb.	common	Hopkins	1911
	Pitch pine, <u>Pinus rigida</u> Mill.	common	Hopkins	1911
	Red pine, <u>Pinus resinosa</u> Ait.	rare	Hopkins	1911
	White spruce, <u>Picea glauca</u> (Moench) Voss.	rare	Walker	1912
	Red spruce, <u>Picea rubra</u> Link	rare	Hopkins	1911
	Black spruce, <u>Picea mariana</u> (Mill.) B.S.P.	rare	MacAloney	1930
Not native	Norway spruce, <u>Picea abies</u> (L.) Karst.	severe	Blackman and Ellis	1916
	Scotch pine, <u>Pinus sylvestris</u> L.	common	Graham	1926
	Western white pine, <u>Pinus monticola</u> Dougl.	common	MacAloney	1930
	Limber pine, <u>Pinus flexilis</u> James	common	MacAloney	1930
	Foxtail pine, <u>Pinus balfouriana</u> Murray	common	MacAloney	1930
	Japanese red pine, <u>Pinus densiflora</u> Sieb. & Zucc.	common	Peirson	1922
	Western yellow pine, <u>Pinus ponderosa</u> Dougl.	common	MacAloney	1930
	Douglas fir, <u>Pseudotsuga taxifolia</u> (LaMark) Britton	rare	MacAloney	1930
	Mugho pine, <u>Pinus montana mughus</u> (Scop.) Willk.	rare	MacAloney	1930

spruce, Picea abies (L), Scots pine, Pinus sylvestris L., and jack pine, Pinus banksiana Lamb., the latter particularly in areas of the United States bordering the Great Lakes, also are heavily attacked, and may at times be as severely injured as white pine.

In addition to the above list, Packard (1881) reported that eastern hemlock, Tsuga canadensis (L.) Carr., and balsam fir, Abies balsamea (L.) Mill., are subject to attack by the white pine weevil, although this record has never been verified by later workers. MacAloney (1930) stated that the weevil was earlier reported as far south as Texas on shortleaf pine, Pinus echinata Mill., and loblolly pine, Pinus taeda L., but he suggested that the weevil causing the damage was probably Pissodes nemorensis Germ., which is the only species generally found in the area. Currie (1905) reported the weevil attacking Himalayan cedar, Cedrus deodara (Roxb.) Loud., but Hopkins (1911) described the insect as P. deodarae Hopk. Later, Dietrich (1931) showed that the latter species is a synonym of P. nemorensis, which moves from its normal habitat (the lower trunk region of its host) to attack the cedar in much the same manner as the white pine weevil attacks white pine. It is probable that Currie and Hopkins were confusing P. nemorensis with P. strobi.

When there is doubt as to the species associated with a particular host tree and the general anatomical characters are not sufficient to separate species, general knowledge of the habits of the insect will sometimes permit positive identification. P. strobi is the only known species of weevil within its range that is associated with the terminal shoots of its host trees. Outside this range however, Pissodes sitchensis Hopk. and P. engelmanni Hopk. also infest the terminal shoots of saplings and small Picea sitchensis (Bong.) Carr. and Picea engelmanni Parry, respectively (Hopkins, 1911). Hopping (1920) described a new

weevil species, P. terminalis Hopp., attacking the terminal shoots of lodgepole pine, Pinus contorta Dougl., in California.

IV EXPERIMENTAL STUDIES

A. LOCATION AND STAND HISTORY

The investigations reported herein were carried out at the Petawawa Forest Experiment Station, located in the Ottawa Valley, about four miles southeast^a of Chalk River, Ontario. The area lies within the Middle Ottawa Section of the Great Lakes-St. Lawrence Forest Region (Halliday, 1937), and is characterized by an abundance of white pine, Pinus strobus L. and red pine, P. resinosa Ait.

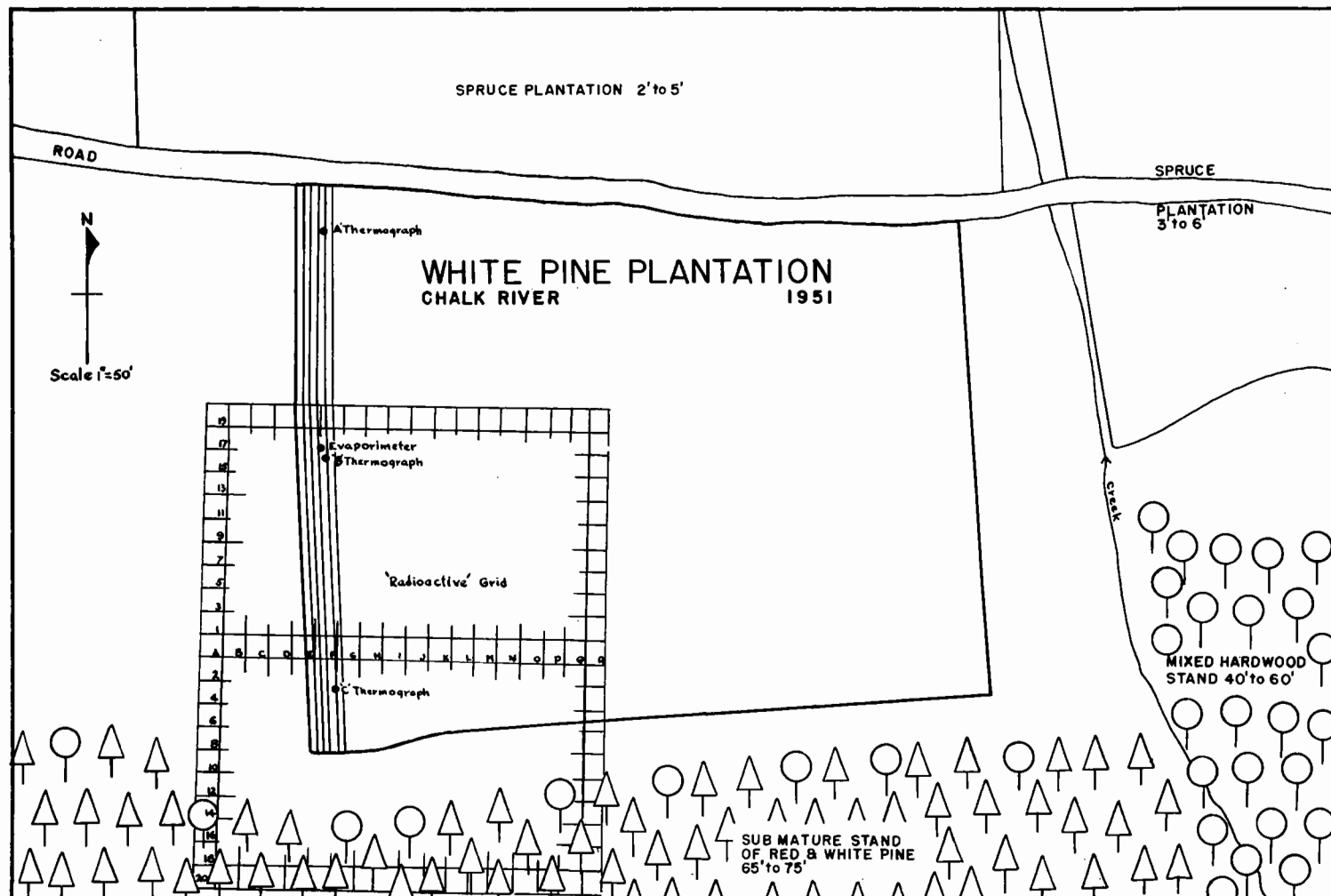
The station climate is continental sub-humid, with consequent extremes of temperature. The following data were derived from station weather records taken between 1936 and 1950 (Anonymous, 1952). The mean annual temperature is 39.4°F, and the lowest and highest temperatures on record are -38.2°F and 98.1°F. The warmest month is July, with a mean of 67.2°, and the coldest, January with a mean of 8.8°. The latest freezing temperature on record occurred on June 1, and the earliest on September 9, giving a minimum frost-free period of 100 days, although this is unusual. The average growing season is 136 days. The average annual precipitation is 29.7 inches; of this, the equivalent of 7.5 inches falls in the form of snow, which usually covers the ground from the beginning of November until April.

The prevailing wind for all months of the year is northwest, with a mean velocity of 6.2 miles per hour. Winds violent enough to cause damage to trees in the forest are rare.

The site selected for the investigations of the white pine weevil was a 2.5 acre nursery plantation of white pine set out with 2.5 by 3 foot spacings in 1942 as three-year transplants (Fig. 1). This stand contained at least two broad exposure conditions, the trees at the southern end of the plantation being shaded for about five hours around mid-day by a stand of sub-mature red and white pine and mixed hardwoods, and the remainder of the stand being fully exposed. Detailed studies on the activity and behaviour of P. strobi were conducted chiefly in trees of the first six rows on the west side.

The plantation was originally subdivided into 21 plots, each containing seed trees from either New York, New Hampshire, Massachusetts, Quebec, or Ontario. Preliminary surveys in 1951 on the incidence of weevil damage before this date showed that the amount of damage attributable to P. strobi would at best be empirical since it was impossible to take into account the damage to the pine terminals due to other agents such as deer browsing, etc. However, by the presence of dead, weevilled stems still attached to trees it was determined that weevilling occurred as early as 1947. Additional surveys made during 1951 and 1953 showed that the incidence of weevil attack and terminal mortality increased during the period of the present investigation. During 1951, weevil attack was found to be 27.7 per cent, and during 1953, it was 43.5 per cent. Terminal mortality during these two years amounted to 7.3 and 15.9 per cent, respectively. The

Fig. 1. Map of white pine nursery plantation where most of the investigations of the white pine weevil were carried out.



b. Methods Of Experimentation

The responses of adult weevils to point sources of light were observed on a light board originally designed by A. W. Ghent (unpublished data). This apparatus differed from other types in that the insect platform was constructed from glass which was marked off into a series of radiating lines extending at 30° angles from the light source with cross-lines spaced equidistant from the bulb. This grid was then transposed on a viewing mirror placed below the platform. By covering the mirror with cello paper the movements of an adult placed on the platform could be observed and easily traced with a wax pencil. The light source consisted of a 2.4 volt flashlight bulb. The insects were placed approximately one foot from this source.

In experiments dealing with the response of adult weevils to diffuse light, a dark-light alternative chamber described by Wellington (1948) was used during the initial tests. Although this chamber proved satisfactory for determining the light reactions of the spruce budworm (Wellington, 1948) and colonial larvae (Sullivan and Wellington, 1953), it was not satisfactory for testing the reactions of adult weevils. The insects were sensitive to a slight shadow pattern formed along the light-dark boundary, so that there was some difficulty in distinguishing photopositive and photonegative responses. This difficulty was overcome in subsequent tests with a modified type of chamber designed by Green (1954) for testing the effect of temperature on the light reactions of

sawfly larvae and later used by Wellington et al., (1954) with the spotless fall webworm. In addition to eliminating the presence of shadow patterns along the edge of the dark-light boundary the new design presented a much longer boundary.

A single 200-watt bulb served as the light source and the heating unit. The heat from the light served to warm a water supply below the reaction platform at a rate of about 1°C per minute. Heating the water raised the chamber temperature and kept the enclosed air saturated, thus eliminating any possible effects of increased evaporation rate with increasing temperature on the reaction of the insects. Chamber temperatures were measured with a Rubicon portable potentiometer and a No. 24 copper-constantan thermocouple with its junction placed in contact with the silk platform in a central position in the chamber. Each time an insect moved out of the lighted portion of the chamber the temperature was recorded.

Preliminary tests showed that only small numbers of insects could be observed efficiently at any one time in the chamber. Large numbers lowered the accuracy of the observation because, on occasion, one or more insects which had moved across the boundary would return to the lighted portion. Thus, ten insects were used in each test.

Before testing, adults of the autumn and spring populations were conditioned for a period of 12 hours to the temperatures shown below:

		No. tested	Acclimation	Temperatures, C°.	
Autumn adults	Fed	100	20±2	12±2	0±1
	Starved	100	20±2	12±2	0±1
Spring adults	Fed	100	20±2	12±2	0±1
	Starved	50	20±2	12±2	0±1

The results were analysed to obtain the mean reversal temperature or the temperature at which the insects moved from the lighted to the dark portion of the chamber. Analysis of variance tests showed that there was no significant difference between the temperatures at which members of each replicate became photonegative. Consequently, the mean reversal temperature obtained by group analysis was accepted as the true mean and further analysis simply involved calculating its standard error.

c. Results

(1) Reactions to a point source

During experiments on the light board it was found that light conditioning did not affect the response of fed or starved individuals of either the autumn or spring populations. In these tests three types of light conditioning were used. Insects were held for 24 hours under constant light, under constant darkness, or under normal daily light rhythms. Examples of typical paths made by fed adults are shown in Fig. 2, which shows the position of the insects at 10-second intervals during the reaction. All insects exhibited a photopositive response with little difference in the rate of movement of individuals depending on the type of pre-

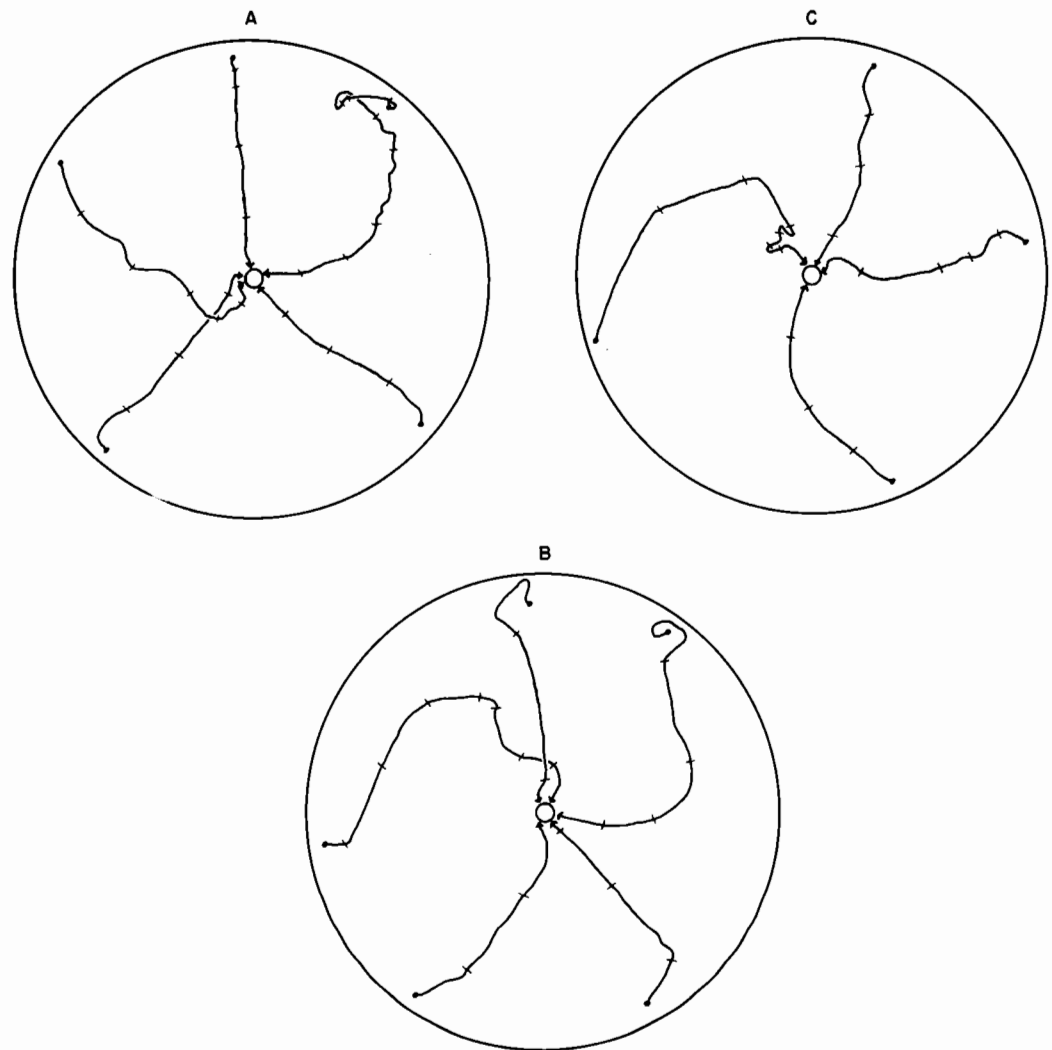


Fig. 2. Representative paths taken by P. strobi adults in response to a 2.4-volt flashlight lamp. Insects conditioned for 24 hours on food at room temperature in: A, constant light; B, normal daily light rhythms; C, constant darkness. Time marks represent 10-second intervals.

vious light conditioning. Also, in consecutively run tests no appreciable difference could be detected in the time required to reach the light between groups conditioned in total darkness and the other groups. Thus, the possibility of light adaptation of insects placed on the light board could be eliminated.

However, differences did occur between members of a single group. The chief variation was in the time required by individuals of a group to complete the reaction and appeared to be due to the extent the paths were convoluted. Since fed insects almost consistently shifted their direction one or more times before reaching the light, the time spent in travel in the new direction determined the time required to complete the reaction. Raising the temperature of the light board resulted in an increase in the speed of movement but the paths taken appeared to be equally irregular.

After 24 hours starvation, adult weevils continued to show a strong photopositive reaction. Examples of typical paths of members of the two populations are shown in Fig. 3A and A1. Starved individuals reacted in much the same manner as their fed counterparts but with a greater tendency to more direct paths. Consecutive trials showed no consistent change in the type of response. Additional starvation to two days before death resulted in a slower rate of movement along somewhat more irregular paths (Fig. 3B and B1), but the reaction was still strongly photopositive.

Differences in the response of individual insects be-

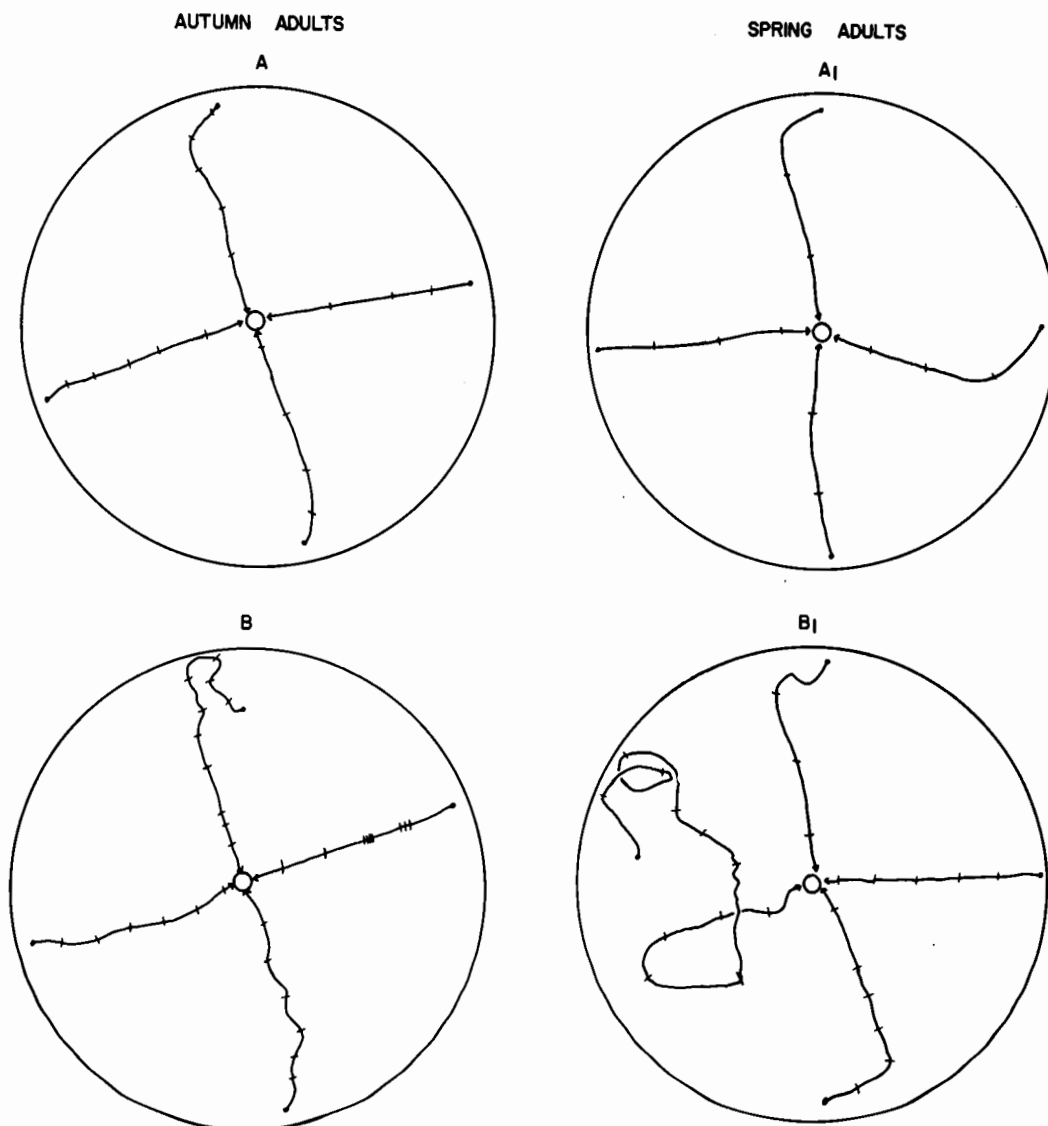


Fig. 3. Representative paths taken by adults of the autumn and spring populations of P. strobi in response to a 2.4 volt flashlight lamp. Tracks in A and A₁ made by insects starved for 24 hours and tracks in B and B₁ made by insects starved up to 48 hours before death. Time marks represent 10-second intervals.

came apparent after starvation up to a period of 24 hours before death, but no consistent single pattern of behaviour was demonstrated (Fig. 4). This was particularly true among members of the autumn population which took at least four different paths. First, individuals which reacted strongly positive, such as those of tracks 2 and 3 of diagram A (Fig. 4), generally maintained these headings during subsequent trials. Secondly, during its initial trial, an adult would fail to reach the light (track 1, diagram A) during an observation period of ten minutes, but in its second trial it would move almost directly to the light (track 1, diagram A₁), while in its third trial it would revert to a prolonged period of indifference before moving to the light (track 1, diagram A₂). Track 6 of diagrams A, A₁, A₂, show the third type of reaction observed. In this case the insect reacted photopositively but the path taken to the light was quite indirect. During subsequent trials however, the insect reacted strongly photonegatively and maintained this heading during the period of observation. As indicated by the time marks shown in the figure, the insect was quiet throughout most of the observation period and prodding with a brush failed to result in additional movement. The fourth and most commonly observed response took the form shown in trials 4 and 5 of diagram A, A₁, and A₂. The insects exhibited a long period of indifference during the initial trial but during subsequent trials this was progressively reduced until they moved almost directly to the light in the

Fig. 4. Representative paths taken by adults of the autumn and spring populations of P. strobi in response to a 2.4 volt flashlight lamp. Tracks in A, A₁, A₂ and B, B₁, B₂ respectively, represent consecutive trials^u with brief time lags between each. Insects starved up to 24 hours before death at room temperature. Time marks represent 10-second intervals except where shown.

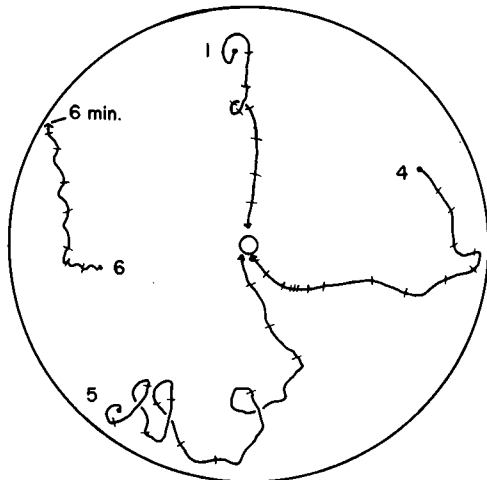
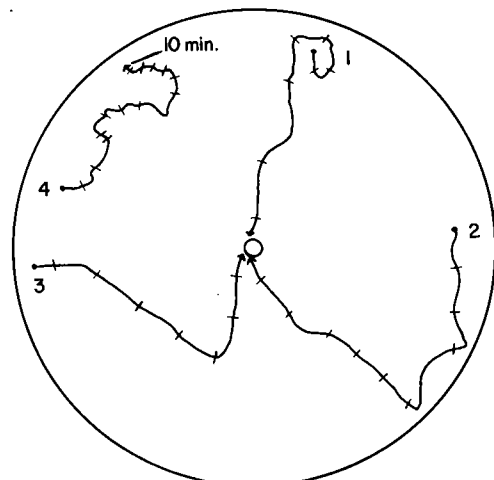
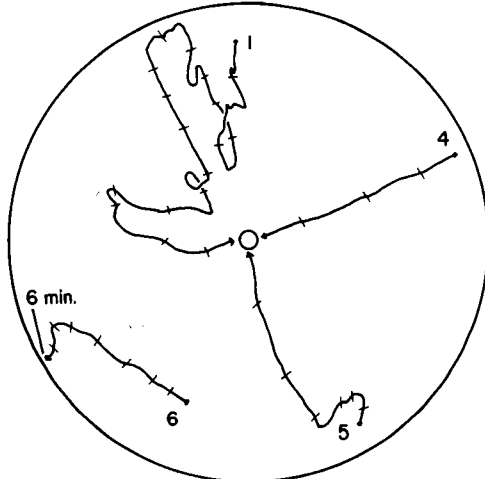
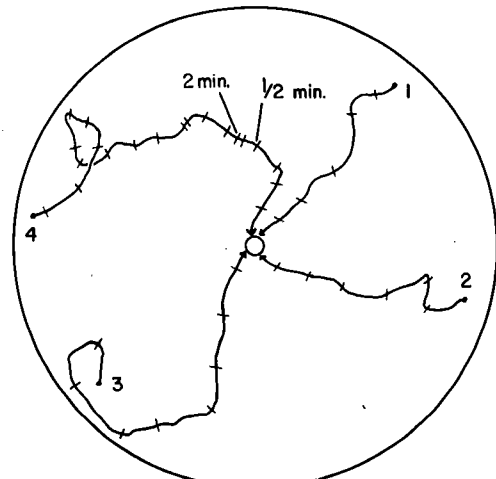
AUTUMN ADULTS

A



SPRING ADULTS

B

A₁B₁A₂B₂

third trial.

After starvation to 24 hours before death, individuals of the spring population showed a much greater consistency in their response to the light source (Fig. 4B, B₁, B₂) than did the members of the autumn population. During initial trials (tracks 1, 2 and 3) the insects showed a more intense photopositive reaction and this response was maintained during subsequent trials. On occasion, an insect would react photonegatively during its first and second trials (track 4, Fig. 4B, B₁) but, during the third trial it would respond photopositively (track 4, Fig. 4B₂).

It will be seen that most of the responses of the starved adults function to take the insects to the light. The chief differences that occur are in the length of time and the number of trials required before definite photopositive behaviour is expressed. The most common type of initial reaction, that which includes extended periods of indifference, may be expressed as a reaction to particular light intensities. Since this behaviour tends to break down during subsequent trials, it is somewhat overshadowed by the stronger, more direct tendency to move directly to the light. When compared with the trials of insects either fed or starved for shorter periods of time (Figs. 2 and 3, respectively) it is found that the insects normally require a longer period of time and additional trials before the reactions become similar.

The initial responses of members of the spring popula-

tion approximately one day before starvation death are much more direct than those of the autumn adults. In addition, the path taken during subsequent trials does not change appreciably. Common to both age groups is the tendency of the occasional individual to react in a photonegative manner.

When the tests with starved adults were continued during the final 24 hours before death, the irregularity and indirectness of the paths was simply intensified until four or five hours before death. At this time, the adults became strongly photonegative. Examples are shown in Fig. 5, which also show that the rate of movement and amount of travel was sharply reduced.

(2) Reactions to diffuse light

During the initial tests the chamber used was divided so that one-half was dark and the other half light. The light source was overhead. Adult weevils placed in the lighted portion of the chamber remained quiet in this section until the chamber was heated. With an increase in temperature the insects moved about the lighted portion often taking up positions near the light-dark border where they remained through a wide range of rising temperature. At temperatures between 34 and 40°C many moved to the dark and by the time the chamber was heated to near 45°C, all adults had shifted from the light to the dark half of the chamber. It is doubtful if the tendency of the adults to remain along the border of the dark-light boundary would have been observed in the absence of the secondary shadow pattern in

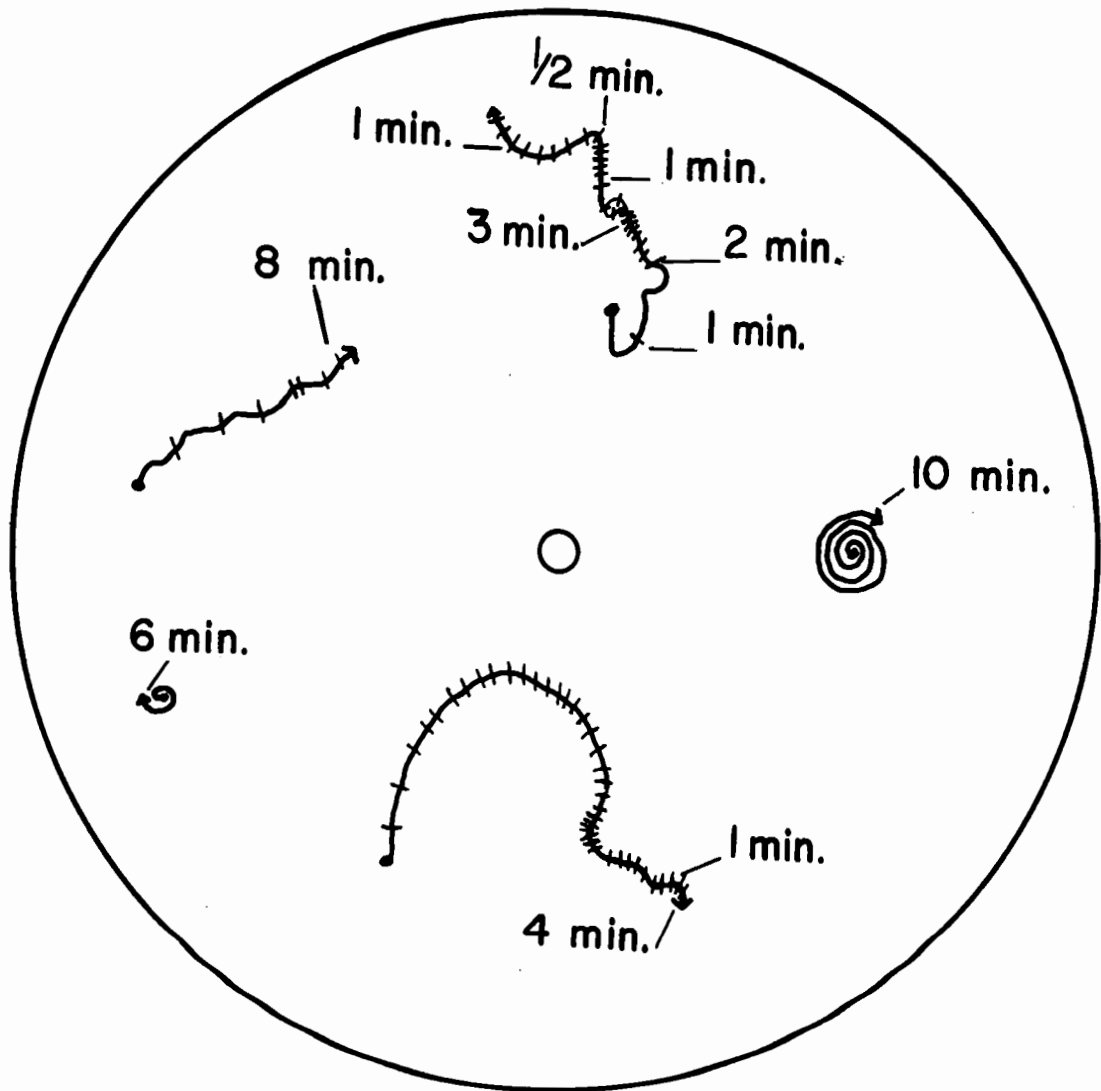


Fig. 5. Representative paths taken by *P. Strobi* adults in response to a 2.4 volt flashlight lamp after starvation up to 5 hours before death at room temperature.

the area and the results had to be verified by further tests in the modified type of chamber referred to earlier.

The chief difference in the behaviour of adults in the two chambers was in the temperature at which they became photonegative. The range continued to be quite large, but with the increased sharpness between the light and dark sections, the insects failed to exhibit the border reaction mentioned above and consequently became photonegative at lower temperatures.

Since the light source in the modified chamber also served as the heating unit, it was necessary to use an overhead lamp when testing the reaction of adults at moderate temperatures. After they were conditioned at approximately 20°C and 60 to 80 per cent relative humidity for 12 hours or longer and then given a choice between the light or dark portions of the chamber, fed adults remained relatively quiet in the lighted section. On occasion an individual would move across the border temporarily. Normally the insects perceived the border line and failed to continue movement into the dark section, so that their movements were restricted to the lighted portion of the chamber. Insects acclimated to 12 and 0°C normally remained quiet in the light until warmed to room conditions, at which time they reverted to the typical behaviour described above. On occasion however, an individual moved into the dark and remained in this section. Adults starved during acclimation at all three temperature levels reacted in much the same way when

placed in the chamber. These behaviour patterns were more fully understood when the adult responses to light with rising temperatures were determined.

As the reversal temperature was approached, individuals of both populations showed indications of impending movement by increased antennal movement, brushing of the head and mouthparts with the fore-legs, and short jerky movements. This behaviour was generally followed by rapid movement to the dark. Occasionally an adult would return to the light but when this occurred it either reversed its direction of travel and returned to the dark or it continued rapidly in the original direction of travel, recrossing the dark-light boundary at another point on its circumference.

Reversal temperatures of fed and starved adults of the two populations are shown in Figs. 6 and 7 respectively, which illustrate the frequency distributions obtained when adults, acclimated to 20, 12, and 0°C for 12 hours were tested in the alternative chamber. Although broad temperature ranges were obtained, the results show a marked difference in the temperature levels at which starved and fed weevils become photonegative to diffuse light except where acclimated to 0⁺10°C.

The mean reversal temperatures of fed weevils collected during autumn are shown in Table II. Successive pairs of these means were subjected to t-tests. The results indicated that adults acclimated to 20°C became photonegative at a significantly higher temperature than adults acclimated

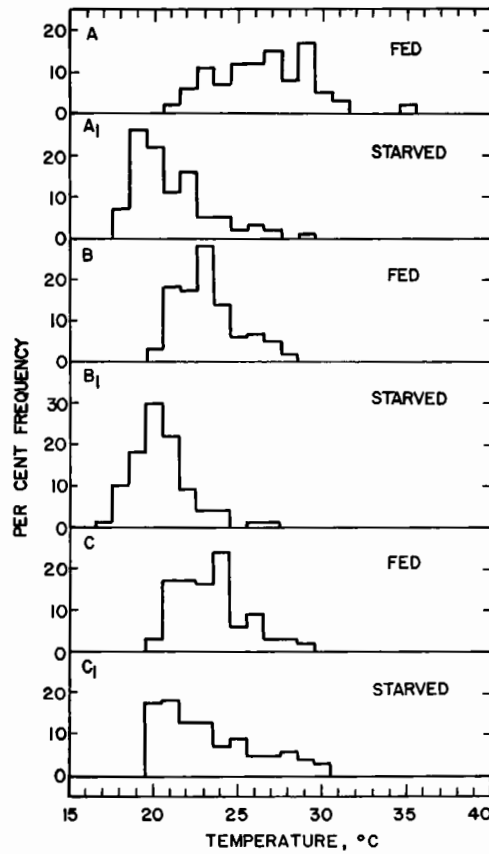


Fig. 6. Comparison of the ranges of temperature at which fed and starved adults of the autumn population of *P. strobi* became photonegative to diffuse light after acclimation to, A - A₁, 20 ± 20 ; B - B₁, $12 \pm 2^\circ$; C - C₁, $0 \pm 1^\circ$ C.

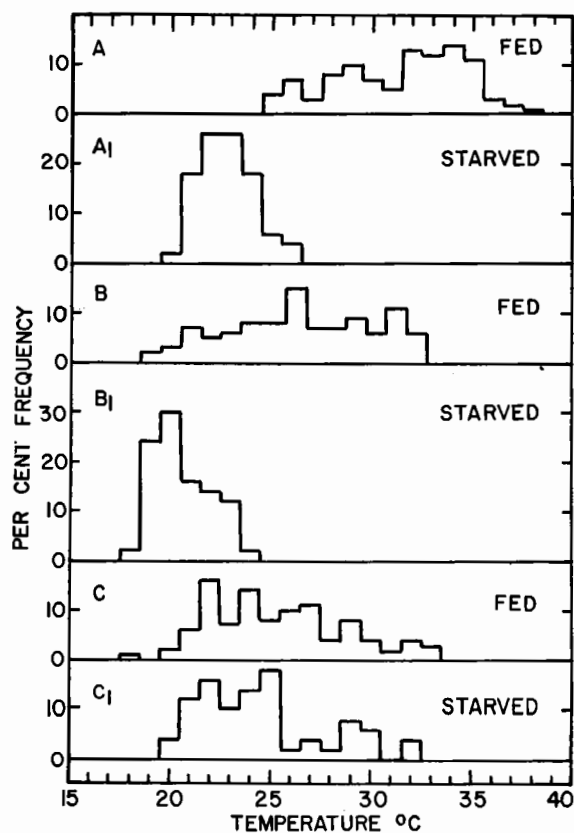


Fig. 7. Comparison of the ranges of temperature at which fed and starved adults of the spring population of *P. strobi* became photonegative to diffuse light after acclimation to, A - A₁, $20 \pm 2^\circ$; B - B₁, $12 \pm 2^\circ$; C - C₁, $0 \pm 1^\circ$.

to 12° and 0°C ($P < 0.01$), but no significant difference was indicated between the means of the latter two groups ($P > 0.40$). When the insects were starved, however, there was no significant difference between the reversal temperatures of adults acclimated to 20° and 12°C ($P > 0.05$), but both groups became photonegative at significantly lower temperatures ($P < 0.01$) than the adults acclimated to 0°C (Table III).

TABLE II

Comparison of the mean temperatures at which fed adults of the autumn population of *P. strobi* became photonegative in saturated air after acclimation to three temperature levels for 12 hours.

Accl. level	20°C	12°C	0°C
n	100	100	100
$\bar{x}$	26.4	23.2	23.4
$S\bar{x}$	.281	.187	.205

n, sample size; $\bar{x}$, mean reversal temp.; $S\bar{x}$, standard error of the mean.

TABLE III

Comparison of the mean temperatures at which starved adults of the autumn population of P. strobi became photonegative in saturated air after acclimation to three temperature levels for 12 hours.

Accl. level	20°C	12°C	0°C
n	100	100	100
$\bar{x}$	20.9	20.4	23.4
$S\bar{x}$	.227	.172	.290

n, sample size; $\bar{x}$, mean reversal temp.; $S\bar{x}$, standard error of the mean.

Comparison of the mean reversal temperatures in Tables II and III indicates the effect of starvation on the response of weevils to diffuse light. Fed weevil adults acclimated to 20° and 12°C became photonegative at significantly higher temperatures than starved weevils acclimated to similar temperatures ($P < 0.01$). When acclimated to 0°C however, the presence or absence of food during acclimation was not associated with corresponding changes in reversal temperatures.

Fed and starved adults of P. strobi collected during the spring activity season were also tested in the dark-light chamber. The mean reversal temperatures of fed weevils are shown in Table IV. When successive pairs of these means were subjected to t-tests the results indicated that adults acclimated to 20°C became photonegative at a significantly higher temperature than adults acclimated to

12° or 0°C ($P < 0.01$), but no significant difference was indicated between the mean reversal temperatures of insects acclimated to the latter two levels ($P > 0.05$).

TABLE IV

Comparison of the mean reversal temperatures at which fed adults of the spring population of *P. strobi* became photonegative in saturated air after acclimation at three temperature levels for 12 hours.

Accl. level	20°C	12°C	0°C
n	100	100	100
$\bar{x}$	31.4	26.3	25.4
$S\bar{x}$	.323	.355	.339

n, sample size; $\bar{x}$, mean reversal temp.; $S\bar{x}$, standard error of the mean.

When starved spring adults were tested in the dark-light chamber the mean temperatures obtained were all significantly different ($P < 0.01$). The means are shown in Table V. Comparison of these means with the means observed for fed weevils (Table IV) indicated that fed adults acclimated to 20° and 12°C became photonegative at significantly higher temperatures than starved adults acclimated to similar temperatures ($P < 0.01$). These tests also indicated no significant difference between the reversal temperatures of fed and starved weevils acclimated at 0°C ($P > 0.10$).

TABLE V

Comparison of the mean reversal temperatures at which starved adults of the spring population became photonegative in saturated air after acclimation at three temperature levels for 12 hours.

Accl. level	20°C	12°C	0°C
n	50	50	50
$\bar{x}$	22.7	20.6	24.6
$S\bar{x}$	.184	.206	.447

n, sample size; $\bar{x}$, mean reversal temp.; $S\bar{x}$, standard error of the mean.

By inspection of the reversal temperatures of weevil adults tested during the autumn and spring it will be seen that some striking differences occurred, particularly among the fed insects (Tables II and IV). The means obtained at each of the acclimation temperatures were compared. These tests indicated that fed adults during the spring season became photonegative at significantly higher temperatures than fed adults tested during the autumn ($P < 0.01$). Similarly, at the 20° acclimation level (Tables III and V) starved adults of the spring population became photonegative at a significantly higher temperature than starved adults tested during the autumn ($P < 0.01$). The same relationship held between fed and starved adults acclimated to 0° ($P < 0.05$). The mean reversal temperatures obtained at the 12° acclimation level were, however, practically identical and no significant difference was indicated ($P > 0.05$).

d. Discussion

There are several aspects of the light reactions of adults of the autumn and spring populations of P. strobil which require some discussion. First, however, it should be mentioned that any differences in behaviour observed between the two groups are occurring within the same generation, but at different periods in the life of the adults. They are referred to as the autumn and spring populations to simplify reference to age groups.

Adults of the spring and autumn populations of the white pine weevil are basically photopositive to discrete sources of light and this response is maintained to a greater or lesser degree until a few hours before death due to starvation. At this time they become strongly photonegative. Such changes in photic orientation are not common and, in fact, may be much more striking among other insects than the weevil. For example, Wellington (1948) found males of Choristoneura fumiferana (Clem.) consistently photopositive, whereas the females were just as consistently photonegative. Menusan (1935) reported that young adults of the bean weevil were photonegative, but old adults and spent females became photopositive. More recently, Richards (1951) reported that adult weevils of Calandra granaria (L.) were mostly photonegative but that a small percentage of them always moved towards a light. In this example however, Richards showed by selective matings of photopositive and photonegative adults for two generations

that the difference was genetic. He obtained two populations, one totally photonegative and the other more or less indifferent to light. With reference to P. strobi adults, the fact that the initial photopositive response is reversed only as a result of prolonged starvation up to a few hours before death is of interest chiefly in respect to the observed behaviour of the insects in the field.

Any differences observed in the behaviour of the adults before the photonegative response occurs seems to be in the intensity of the response between individuals, all of which eventually move towards a light. Adults tested after emergence from infested leaders or from hibernation sites are strongly positive while fed adults of either age group almost consistently shift their direction of travel one or more times before reaching a light. After a short term of starvation their paths become more direct and regular. It has recently been suggested by Dethier (1956) that failure of insects which have been taken from their food to react strongly photopositively is due to a short period of excitation resulting from the abrupt removal from the food. The fact that weevil adults taken directly from their food and placed on the light board, consistently shift their direction of travel, whereas adults starved from a short period of time take more direct paths supports Dethier's hypothesis.

Prolonged starvation results in differences between the spring and autumn adults. Young adults of the autumn

population commonly exhibit an extended period of indifference before moving towards a light, but older adults in the spring exhibit much more directed movements which do not vary much from those of adults starved for shorter periods of time. It is possible that these changes in intensity of response occur as a result of changes in the visual response mechanism of the adults after periods of prolonged starvation.

It should be emphasized that the variations between the response of starved adults about one day before death and those starved to two or more days before death are not related to the actual number of days the insects have been starved but to the length of time before death. During the tests which required a conditioning period of starvation it was observed that adults of the spring population could survive approximately one day longer than adults of the autumn population (roughly, death occurred on the fifth and sixth day, respectively). This agrees well with recent results of experiments dealing with the effect of x-radiation on longevity of adult weevils (Sullivan and Simpson, 1957). This difference in life-span together with the normal variation in death rate of starved weevils about the mean tended to confuse the results until it was realized that an orderly set of responses occurred in relation to the length of time before death. It is a point worthy of consideration during investigations dealing with the behaviour of starved insects, particularly when conditioning includes prolonged

periods of starvation. Recently, Green (1954), during experiments on the light reactions of diseased larvae of Neodiprion lecontei (Fitch), showed that as the disease progressed the insects became more and more indifferent to a light source. At the same time as the disease progressed, however, the insects failed to feed, so that the increase in their indifference to the light may have occurred as a result of prolonged starvation for periods approaching the time of death as well as from the disease characteristics. It would be of interest to re-open the problem with healthy larvae since Green did not test the reactions of healthy larvae starved beyond 72 hours.

Reversal of the photic orientation of insects exposed to high temperatures is common. This has been demonstrated with lepidopterous larvae by Wellington (1948) and Wellington et al., (1951, 1954), with hymenopterous larvae by Green (1954), and with dipterous adults by Jack and Williams (1937) and Dolley and White (1951), to mention only a few examples. In most cases, the observed changes in orientation to light at specific temperatures have helped the investigators to explain changes in the behaviour of the insects in the field which normally have a definite survival value. So far as adult weevils are concerned, the results of this study indicate that the insects are capable of adapting to temperature conditions which may be interpreted in terms of survival and therefore are of practical significance.

The results have shown that autumn and spring adults reverse their photic orientation from positive to negative at correspondingly higher temperatures as the temperature of acclimation is raised from 12 to 20°C. The only apparent difference which occurred between these groups was that adults acclimated to the lower temperatures were less active and fed less than those kept at 20°C during the period of acclimation. This does not mean that the insects held at the lower temperature were starved because, at the lower temperatures, a decrease in their metabolic rate would be directly reflected in their feeding frequency. Hence, the insects may have been reacting entirely in accordance with their previous temperature conditioning. On the other hand, it is possible that the insects kept at the lower temperatures may have been reacting as partially fed individuals and, as such, might be expected to reverse at a temperature level below that of fully fed individuals. The results of tests with starved insects partially support this suggestion. It was observed that starved insects did not always show the same pattern of reversal with respect to temperature as those of fed groups. Starved insects of the spring group acclimated to 12° and 20°C appeared to react in accordance with their acclimation temperature but insects of the autumn group reacted at virtually identical temperatures irrespective of their previous temperature conditioning. It is apparent that partial starvation, as well as temperature acclimation, may function to limit the reversal temperature

of the insects previously classified as fed. The effect of starvation in tests with insects which are kept without food during the period of acclimation is clearly indicated in the general drop in the reversal temperature of groups of both the autumn and spring populations, particularly among those acclimated to 12° and 20°C. To understand clearly the relationships involved however, further investigation is required on the effect of temperature acclimation and starvation on the behaviour of the insects. In addition, some criteria should be established for defining fully fed and starved insects in relation to the level of temperature acclimation but irrespective of the presence or absence of food. This was not investigated further because the results obtained were sufficient to explain particular behaviour of adults in the field without the sharp distinction between the individual effects of starvation and acclimation on the responses of the insects to light at specific temperatures.

So far, this discussion has been limited to fed and starved insects acclimated to 12°C or above. This is due to the fact that these temperatures occur within the recognized temperature-activity range of the insect. At 0°C, which is well below the lower range of temperature associated with weevil activity, no difference was observed in the reversal temperatures of insects during the spring, irrespective of the presence or absence of food. Similar results were recorded during the autumn. When the mean rever-

sal temperatures of the autumn group were compared with those of the spring group however, they did vary significantly. These observations are in line with the results observed between the groups kept at warmer temperatures, indicating that young adults of P. strobi which are active during autumn are unable to withstand temperatures as high as older adults which are active during spring without reacting photonegatively. These differences have a definite bearing on the behaviour of the insects in the field. This aspect is treated in some detail in conjunction with the field studies (Section V).

C. FIELD INVESTIGATIONS

The field investigations were concerned chiefly with studies of the physical requirements of the white pine weevil. In addition, investigations of a limited nature were carried out on the life history of the weevil, its survival, and the injury caused by it, in order to obtain information pertinent to the assessment of the factors limiting successful weevil development.

1. LIFE HISTORY

Despite numerous publications dealing with the seasonal life history of the white pine weevil, no accurate account for areas within the northern limits of the insect's range exists in the literature. Since such knowledge is of

prime importance to future control measures, investigations of the life history of the white pine weevil in the Chalk River area were carried out as an integral part of the present study. Since there seems to be little value in establishing the limits of each phase of the development cycle in terms of calendar dates only, because of seasonal variations, development has been related to the general condition of arboreal vegetation, particularly leader growth in white pine. The following description applies to the life history of the weevil in fully exposed white pine stands only.

Emergence from hibernation in the spring occurs at about the time the terminal buds of white pine begin to swell. Additional observations indicated that weevils are active from one to two weeks in advance of the appearance of any foliage on white birch, aspen, or red oak.

Fig. 8 illustrates the seasonal history of the white pine weevil at Chalk River in relation to the growth of the terminal shoot of white pine. Weevil oviposition does not begin until several days after the adults have emerged from hibernation, and once begun it continues throughout the remainder of the period that the adults are found attacking the leaders of the pine. This period extends through the initial portion of the accelerated growth of the terminal shoot. Larval hatching begins about one month after the resumption of activity of the adults and larval development continues well beyond the period of accelerated growth of

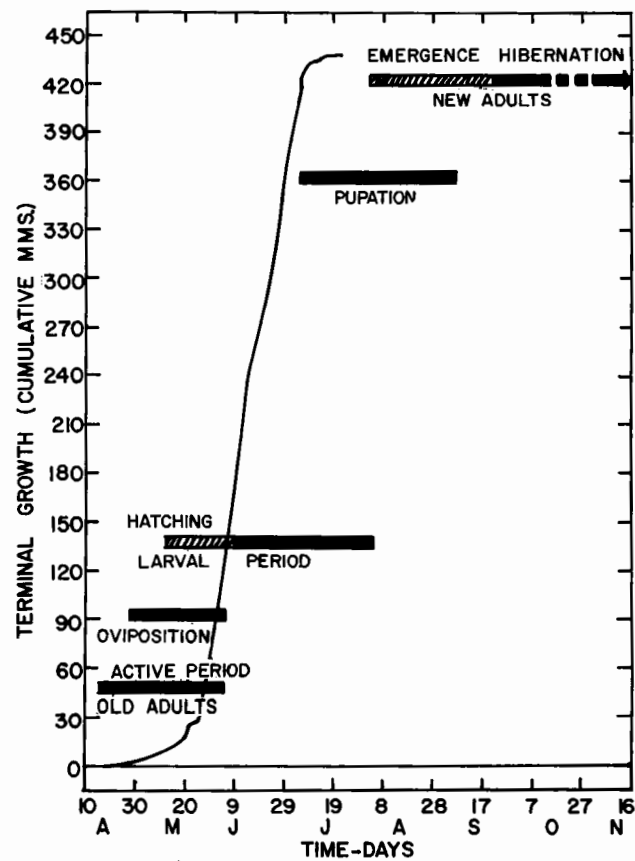


Fig. 8. Life history chart of *P. strobi*, superimposed over growth curve of current years terminal shoot of white pine.

the terminal shoot. Larval hatching begins about one month after the resumption of activity of the adults and larval development continues well beyond the period of accelerated growth of the leading shoot of the pine. First pupation corresponds rather closely with the end of the growing season of the leader and continues over a period of about two months. About one month after the beginning of pupation, or approximately two weeks after the end of the growing season of the leader, the new generation adults begin emerging from the infested shoots. Although the insects remain as pupae for about two weeks only, the young adults remain within the infested shoot for from two to three weeks before emerging.

When these results are compared with those of MacAloney (1930), it is found that there is a marked difference in the timing of the various phases in the seasonal history of the white pine weevil at the northern and the southern limits of its range. The insect emerges from hibernation and resumes activity much earlier in the warmer southern climates and its seasonal period of feeding, copulation, and oviposition extends beyond the active season of the weevil in the north.

2. EFFECT OF WEEVIL INJURY ON TREE GROWTH

Damage to white pine resulting from the activity of the weevils during autumn is negligible and of no consequence to the growth or shape of the trees. Damage of a very ser-

ious nature, however, occurs as a result of the activity of this insect during spring and early summer. The occurrence of small resin droplets marking adult feeding punctures on the upper two or three inches of the previous year's growth (Fig. 9) marks the resumption of weevil feeding activity in spring. Such damage seldom seriously affects the leader; occasionally, however, adult feeding on the apical buds may result in the death of one or more of the buds. An example of the death of the terminal bud and one lateral bud is shown in Fig. 9.

Leader mortality is caused by the larvae feeding on the inner bark while leaving the outer bark intact. Death of the leader may easily be detected by the characteristic drooping and discoloration of the new terminal growth later in the season (Fig. 10). Normally, the new growth withers and the tip bends over and turns brown, but occasionally the shoot is killed before much new growth is added. When this occurs, all that remains is a short brown stub.

During 1952, growth records were taken on the new shoots on 73 weeviled leaders that eventually died. In 15 of these, no drooping occurred and the maximum amount of new growth added did not exceed 3.5 inches. In the remaining 58 the drooping characteristic was recorded in conjunction with the time of season and amount of new growth added. The results indicated that drooping occurred between 34-52 days after emergence of first-instar larvae, or approximately from mid-June through the first week in July.



Fig. 9. A weevilled tip showing feeding punctures, resin droplets and a dead terminal and one lateral bud.



Fig. 10. A weevilled white pine leader.

The characteristic browning of the new shoots occurred during the month of July. Before drooping and subsequent death, a wide range in the amount of new growth added was observed. This varied from about one to thirteen inches with a mean of about six inches. Drooping normally did not occur until the maximum amount of growth of the infested shoots was added.

Mortality of the leading shoots as a result of larval feeding affects the shape of the trees in one of two ways. A single lateral may assume the leadership resulting in a permanent crook in the mainstem (Fig. 11), or two or more of the laterals may compete for the leadership, the subsequent forking rendering the tree commercially useless (Fig. 12). Weevil damage often results in the development of "staghorn" or multiple-top "cabbage" trees of no value (Fig. 13A,B).

Attempts to estimate the effect of weevil damage in white pine has proven a difficult task. Graham (1926) and MacAloney (1930) have shown that a loss in axial and radial growth occurs on trees recovering from a single attack. Normally only two years growth on the mainstem is destroyed, and the loss in height growth is equal to the difference between the maximum amount of growth on non-infested stems and the growth added by the laterals which assume leadership on infested stems. Thus, in measuring the total loss, consideration must be given to the difference between the growth of the terminal shoot and of the lateral shoot of

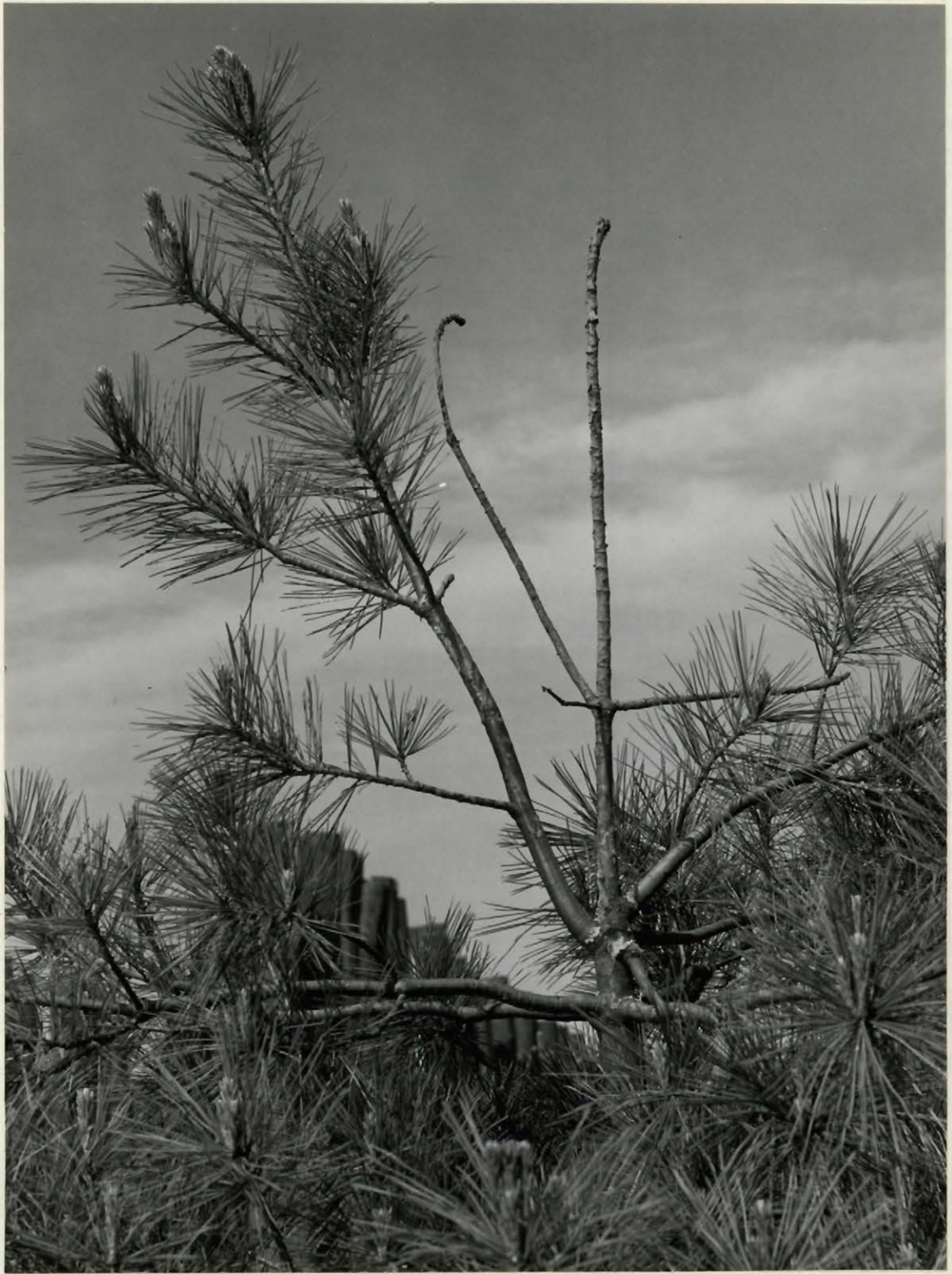


Fig. 11. Lateral shoot assuming the leadership after the death of the leader.

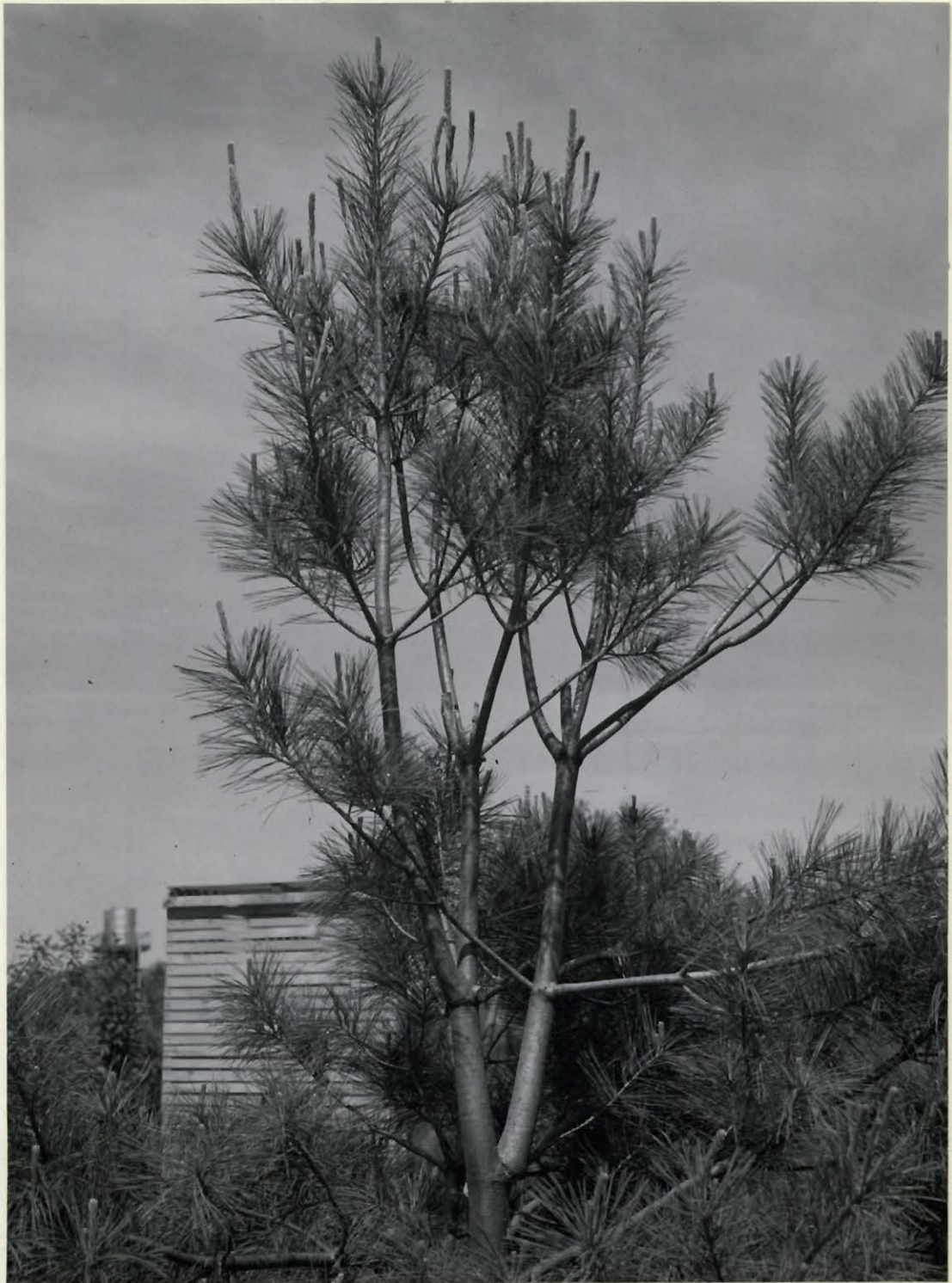
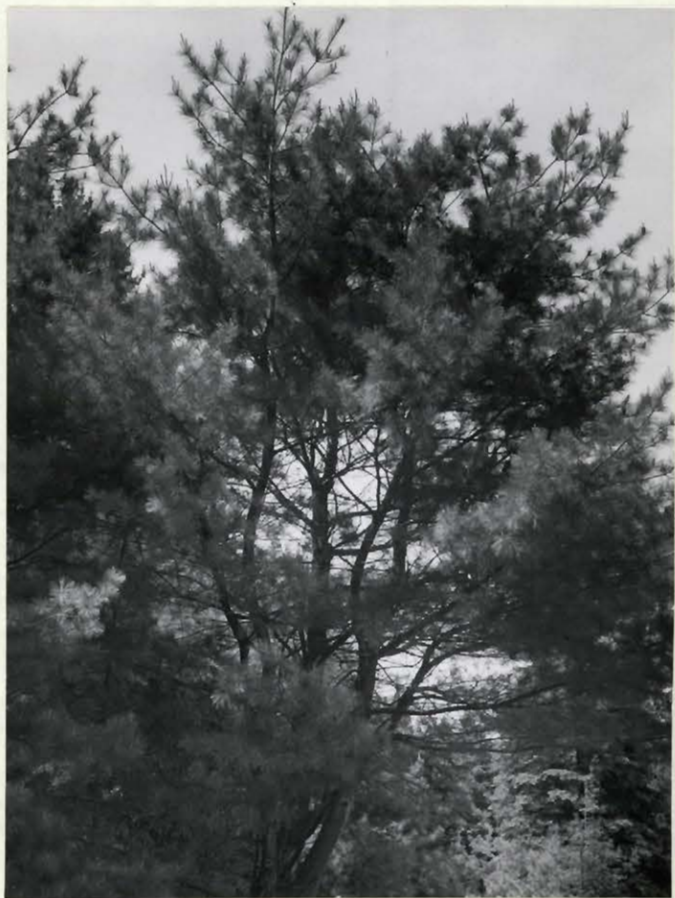


Fig. 12. Growth pattern of white pine when two or more laterals compete for the leadership.

Fig. 13. A. Staghorn pine resulting from several weevil attacks.

Fig. 13. B. A typical cabbage pine.



the previous year. MacAloney (1930) followed the growth pattern of 60 non-infested and 60 infested trees for five years and showed the approximate loss in height growth of trees killed back two years at each attack by the weevil. Because it is characteristic of the weevil to attack the previous year's growth, MacAloney's measurements began one year before the year of attack. By interpreting his curves an estimate of the percentage loss in height growth of infested trees may be obtained. The results are shown in Table VI.

TABLE VI

Loss in height growth of white pine trees killed back two years by the white pine weevil each time a leader is infested. Data taken from MacAloney (1930)

Year	Non-infested trees: average growth of leader (inches)	Infested trees: Per cent loss ave. growth of lateral assum- ing leadership weevilling (inches)	in growth as result of
one year before attack	17	11	35.3
year of attack	20	14	30.0
one year after attack	22	20	9.1
two years after attack	24	23	4.2
three years after attack	25	25	0.0
four years after attack	23	24	0.0

It is apparent that most of the annual height loss occurs as a result of the growth of the new leaders the year before and the year of the death of the original leaders. In subsequent years, the differences in growth between the non-infested and infested trees are small.

The results discussed above have dealt only with infested leaders which succumb to weevil attack. There is, however, a high percentage of survival of the attacked leaders each year. Surveys of leader attack and survival during 1951 and 1953 at Chalk River indicated that between 65 and 75 per cent of the attacked leaders recover. Leader survival is directly related to the amount of larval damage occurring; thus, many leaders that are only lightly attacked resist the attack and maintain supremacy over the laterals and a straight bole is formed. If few in number, the larvae are normally pitch-drowned before serious damage to the leader occurs, and the presence of larvae is indicated by individual trails seldom exceeding 4-6 inches in length. Occasionally, individual trails may extend 9-10 inches down from the top of the leader without killing it, but the damage as measured by retardation of the terminal growth may be severe. Some leaders, although not completely destroyed, are retarded to such an extent that one of the laterals assumes substitute leadership.

To determine the relationships that exist between leader survival and intensity of attack, measurements were made of the number of leaders surviving and of mean annual height

growth in a sample of 401 white pine subjected to various levels of larval attack. The annual height growth of a control sample of 96 non-infested trees was also measured (Table VII).

TABLE VII

Per cent survival of white pine leaders infested with P. strobi larvae and comparison of the mean annual height growth on non-infested and surviving infested leaders at various levels of larval attack. Standard error of mean in brackets.

	Larval attack class (inches)	Number of leaders		Per cent survival	Mean growth of survivors (inches)
		living	dead		
Non-infested trees	-	96	-	100	17.90 (± 4.80)
Infested trees	1	48	1	98.0	16.00 (± 6.00)
	3	44	2	95.6	13.00 (± 7.30)
	5	33	5	86.8	10.75 (± 8.21)
	7	16	25	39.0	10.40 (± 7.79)
	9	6	34	15.0	8.40 (± 9.55)
	11-21	0	187	0.0	-----

The table shows that survival decreases sharply among leaders in which larval damage never exceeded about 5 inches in length and that loss in height growth in trees surviving larval attack increases as the amount of larval damage increases up to a point where the survivors only add about one-half the growth of non-infested terminals. It is appar-

ent that the loss in height growth serves to lower the average growth of the stand as a whole, therefore maintaining it within the height class most susceptible to weevil attack for a longer period. Comparison of the mean annual height growth of infested and non-infested trees shows that at each larval attack class the amount of growth retardation is highly significant ($P \leq .02$).

From the above data a measure of the loss in annual height growth of surviving trees subjected to various amounts of larval attack may be demonstrated graphically. Fig. 14A, expresses the percentage survival of leaders that may be expected at various levels of larval attack, and 14B, shows the loss in height growth expected in survivors at similar levels of larval attack, expressed as a percentage of the growth of non-infested trees.

Thus, the ability of attacked white pine leaders to overcome weevil attack is directly related to the amount of larval damage to which they are subjected. In leaders only lightly attacked the larvae may feed individually rather than with a common feeding ring, and move down the leaders as much as 9-10 inches before being pitch-drowned. Although such leaders may survive, the effect of larval feeding is reflected in the amount of new growth added by the current year's terminal shoot. This loss varies from about 10 per cent of the maximum growth of the season at the one-inch level of larval attack to 100 per cent at the ten-inch level of attack, and its severity in terms of loss in height over

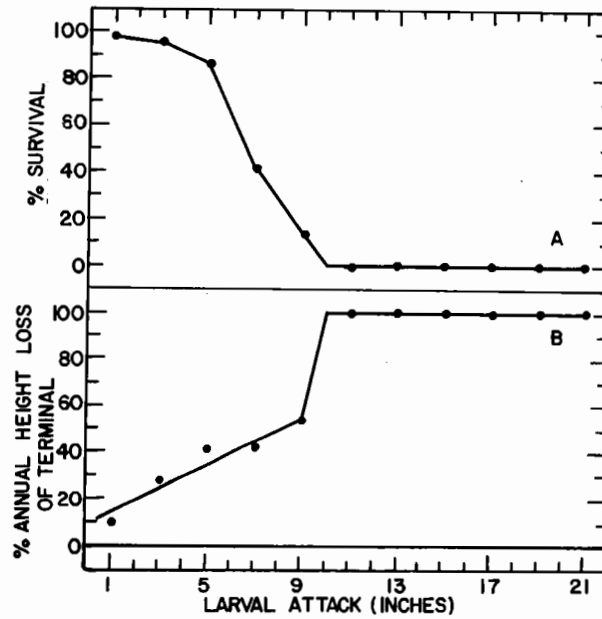


Fig. 14. Relation between level of P. strobi larval attack and: A, percentage survival of infested leaders and B, percentage loss in annual height growth of the current year's terminal.

an entire stand is of course dependent on the extent of weevil damage occurring within the stand. However, the loss is not as severe unless the leaders are killed because the trees do not suffer any deformity.

3. SURVIVAL

When young exposed stands of white pine reach a size susceptible to weevil attack, the initial attack in the stand is relatively low. During subsequent years, and barring the occurrence of unusual environmental conditions associated with an abnormal death rate of the insect, the incidence of attack increases steadily until the trees either outgrow the height range associated with high leader mortality or are reduced to multiple-top "cabbage" pine shrubs. Since the increase in leader mortality is associated with an increase in the abundance of the weevil in the stand, one phase of these investigations has been concerned with determining the factors associated with the general increase in the weevil population.

Increase in population may occur by three different means, (1) flight from more heavily infested stands, (2) multiplication of the existing population and (3) survival of the adults for two or more years. Here we will be concerned chiefly with the second point. The work was initiated with the intention of estimating the mortality under field conditions during the egg, larval, pupal, and adult stages of development. It was also apparent that these data

might be very useful in determining the suitability of existing habitat conditions for weevil development. The developmental characteristics peculiar to the white pine weevil impose limitations on the conclusions that may be drawn from such a study. For example, a single mass of eggs could not be selected and followed through each successive stage of development; rather, separate samples had to be taken at intervals through the developmental period to establish the relationships used in estimating percentage survival from eggs to mature adults.

Additional limitations on the usefulness of such information, which also apply to similar studies on any organism, include those environmental conditions under which the insect developed. The results discussed below refer only to weevil populations occurring in fully exposed stands of white pine within the northern range of the insect.

Because of the extended period of oviposition and the variation in the time of emergence of the young larvae, a measure of the success of hatching was particularly difficult to obtain. However, since it is characteristic of the adult females to deposit eggs in the upper part of the leaders first and in the lower parts of the leaders as the season progresses, it was assumed that eggs laid during late season had an equally good chance of survival because they would not be seriously affected by the drying out of the bark and xylem tissue following the feeding activity of larvae hatching from eggs deposited earlier in the season.

First hatching occurred about two weeks after the beginning of oviposition and, as the season progressed, the percent hatch increased ^{steadily} ~~still~~ to the end of the period of activity of the adults. The number of eggs and larvae, their distribution in the leader, and the percentage hatch at four-day intervals extending from the beginning of the hatching period until the end of the oviposition season, are shown in Table VIII. About 25 per cent of the eggs failed to hatch by the end of the oviposition season. Many of these were found at the lower levels of attack on the leaders, as indicated in the distribution of the eggs and larvae. Attempts to determine the percentage hatch of the remaining eggs were not satisfactory because by this time the leaders had been too badly damaged by larvae hatching earlier. Thus, an estimate of the hatch was obtained by taking a partial sample within the first four inches of attack on the leaders. The eggs laid here were deposited early in the season and had exceeded the period of incubation (6 to 20 days) by about one week. The percentage hatch ranged from 92.0 to 95.8 per cent with an average of 93.9 per cent (Table IX).

TABLE VIII

Per cent hatch of P. strobi eggs at four day intervals from the beginning of the hatching period until the end of the oviposition season.

Date	No. of leaders	Eggs		Larvae		Per cent hatch
		Number	Distribution	Number	Distribution‡	
13/5/55	5	345	1-7	9	1-2	2.6
17/5/55	5	486	1-8	22	1-2	4.5
21/5/55	5	763	1-11	232	1-6	30.4
25/5/55	5	689	1-12	298	1-7	43.3
29/5/55	5	1113	1-14	755	1-10	67.8
2/6/55	3	847	1-18	640	1-14	75.6

‡Refers to the distance from tip of leader, in inches, where the eggs and larvae were found during the counts.

TABLE IX

Percentage hatch of P. strobi eggs deposited within the upper four inches of three white pine leaders.

Adult attack class - (inches)	Number of eggs	Number of larvae	Per cent hatch
1	131	124	94.7
2	95	91	95.8
3	100	92	92.0
4	71	66	93.0
1-4	397	373	93.9

Comparison of the numbers of adults emerging from infested leaders with the numbers of eggs deposited within the leaders indicated that a high level of mortality occurred during the period of development from the egg to the adult. Hopkins (1907) estimated that not more than 3 to 5

per cent of the hatched larvae reach maturity and emerge as adults, but he did not show how these figures were obtained. Taylor (1929) estimated that the percentage of eggs of one year represented by mating forms the following spring ranged from 2.5 to 5 per cent, based on an assumed average of 100 to 125 eggs laid per leader. From actual larval counts he estimated that only 10 to 20 per cent of these were represented by mature larvae. Only one-half of the mature larvae, or five to ten per cent of the eggs laid, emerged as adults. Taylor then assumed that only one-half of the adults survived through the autumn activity season and winter hibernation to appear as mating forms the following spring. His figures are almost identical with those of Hopkins. One of the chief weaknesses in Taylor's studies appears in the estimation of the number of eggs laid per leader. The number of eggs laid in individual leaders varies with the extent of adult attack, and the relationship is linear. During the present study, 81 leaders subjected to various levels of adult attack were dissected and the eggs in them were counted. The regression of the average number of eggs deposited on the extent of adult attack is shown in Fig. 15. It is apparent that as the attack by the adults increases, the number of eggs increases proportionately.

Because of the necessity of dissecting the leaders to obtain figures on the numbers of eggs deposited in individual leaders it was impossible to observe the same sample throughout the season and obtain absolute values of the

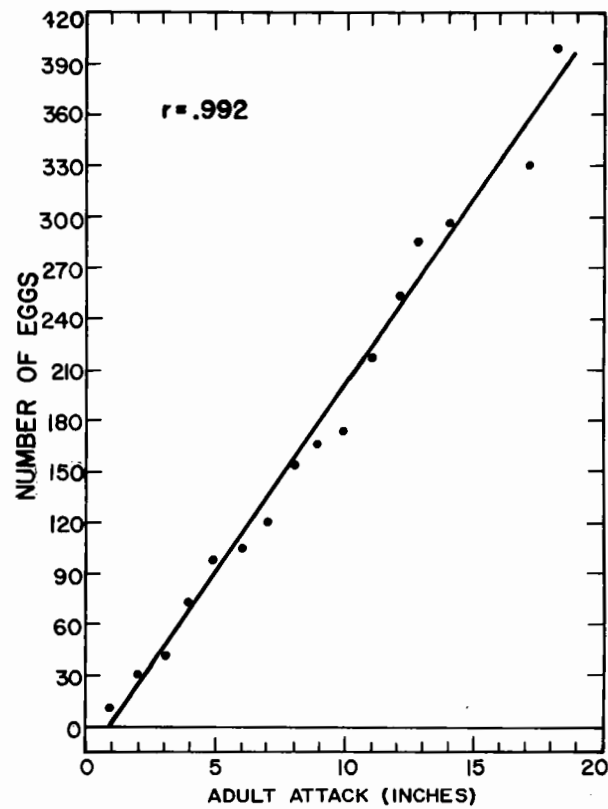


Fig. 15. The relation between the mean number of eggs deposited and attack by P. strobi adults.

survival of P. strobi from egg to adult. Consequently, separate samples were taken to demonstrate the relations leading to an estimation of percentage survival from egg to adult. This necessitated the comparison of average values obtained by interpolation of the relationships between two or more different samples, each with a common variable. With a significant relationship between adult attack and number of eggs laid, the problem seemed to be one of measuring the amount of adult attack at the end of the adult activity season on a sample of standing trees and estimating the number of eggs laid from Fig. 15. An additional survey at the end of the period of emergence of the new adults would produce figures on the number of adults arising from the eggs deposited. However, it was not possible to obtain an accurate count of the number of adults emerging from leaders when these were left standing in the field because of the high incidence of bird damage and leader breakage during the period of larval development. It was possible, however, to estimate the amount of larval damage in relation to the amount of adult damage in the field, since larval predation by birds was considered one of the natural factors of the environment affecting the survival rate.

The steps involved in determining the amount of larval damage based on the number of eggs laid included calculating the relation between the amount of larval attack and the amount of adult attack. This is shown in Fig. 16 and is based on measurements of 401 leaders which were subjected to

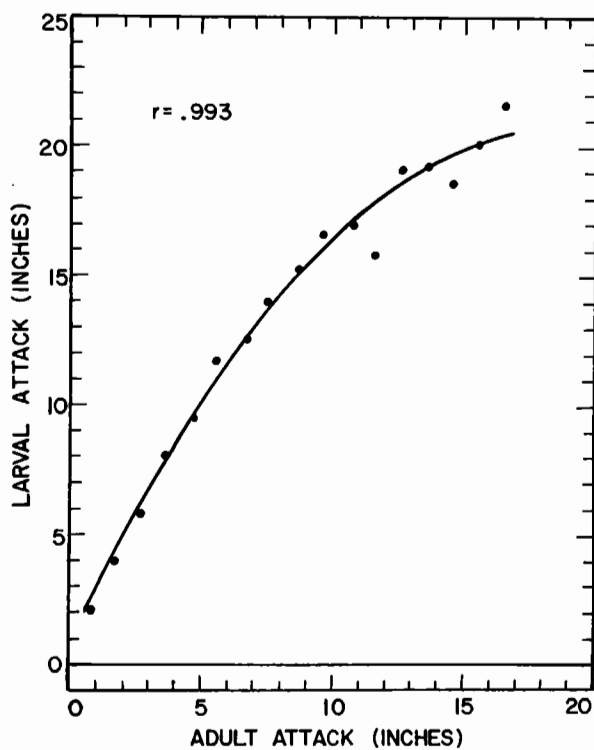


Fig. 16. The relation between mean larval attack and attack by P. strobi adults.

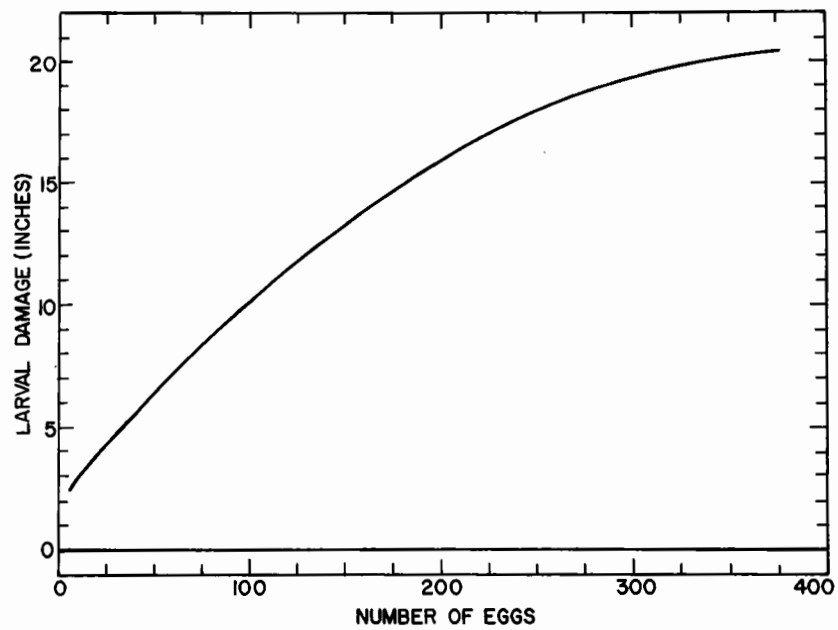


Fig. 17. Estimated relation between the number of eggs deposited and the amount of larval damage.

various levels of adult attack. It will be observed that at the higher levels of adult attack, the curve of larval damage tends to level out into a plateau. This might be expected since leaders heavily attacked contain upwards of 300 to 400 eggs, and with about 94 per cent hatch, the competition between larvae would be exceptionally high. A greater number of larvae would die, leaving only those capable of obtaining sufficient food to complete development.

As the factor of adult attack is the independent variable common to both Figs. 15 and 16, interpolation of the two permits one to express the relation between the number of eggs laid and the amount of larval damage occurring (Fig. 17). As expected, the resultant curve is similar in shape to that of Fig. 16, with the amount of larval damage in the leaders showing a decrease in intensity as egg numbers increase, particularly at the upper end of the curve.

Counts on the number of adults emerging from infested leaders were obtained by collecting leaders in the field during the pupal period and trapping the adults as they emerged. By this method it was possible to eliminate inaccuracies in counts made in the field which involved counting the number of emergence holes in the leaders. Leaders collected in the field and taken to the laboratory are no longer accessible to birds and other predators but by this time of the season their value as natural control factors is reduced to near zero because pupation and adult development take place almost wholly within the pith. The

control exerted by parasites within the leaders would not be affected by removing the leaders from the field.

The number of adults emerging from the leaders was compared with the amount of larval damage. Fig. 18, which is based on counts of adults trapped from 418 leaders originally infested with larvae over a range of from 1 to 23 inches of attack, shows that there is a very low incidence of adult emergence from leaders suffering from 1 to 7 inches of larval attack, but that the number emerging increases sharply from this level up to about 19 inches of attack and then levels out into a plateau at about the 21-inch level of attack, which is associated with an average of about 8.2 adults per leader.

Following the system of working with averages, the relation between the number of eggs deposited per leader and the number of adults emerging from the leaders was determined by interpolations of Figs. 17 and 18. The results are illustrated in Fig. 19A, which shows that more than about 260 eggs per leader does not add greatly to the number of adults emerging. This is undoubtedly because of the more intense competition between larvae. Fig. 19B shows the percentage of the eggs laid per leader which ultimately become adults. The highest percentage of eggs giving rise to adults occurs in leaders containing between about 145 and 220 eggs; within this range, from 3.0 to 3.1 per cent of the eggs are represented by adults emerging from the shoots. Of the entire egg population, about 2.6 per cent become adults.

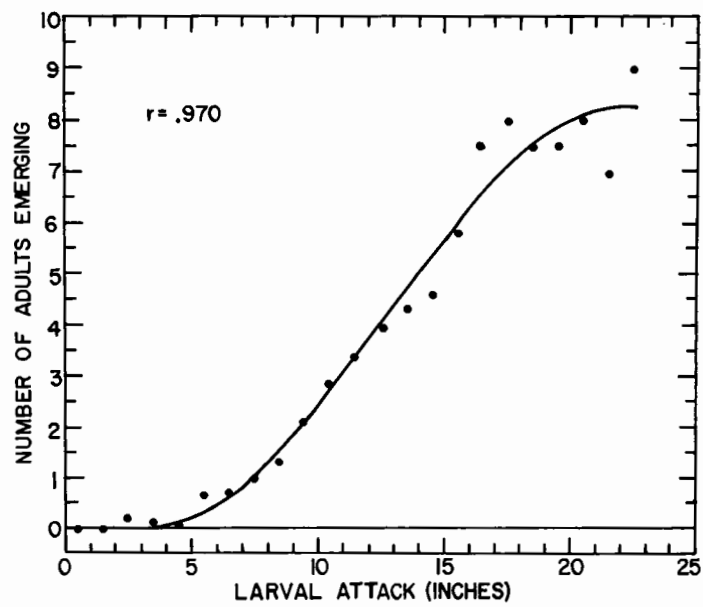


Fig. 18. Relation between the mean number of P. strobi adults emerging from infested leaders and larval attack.

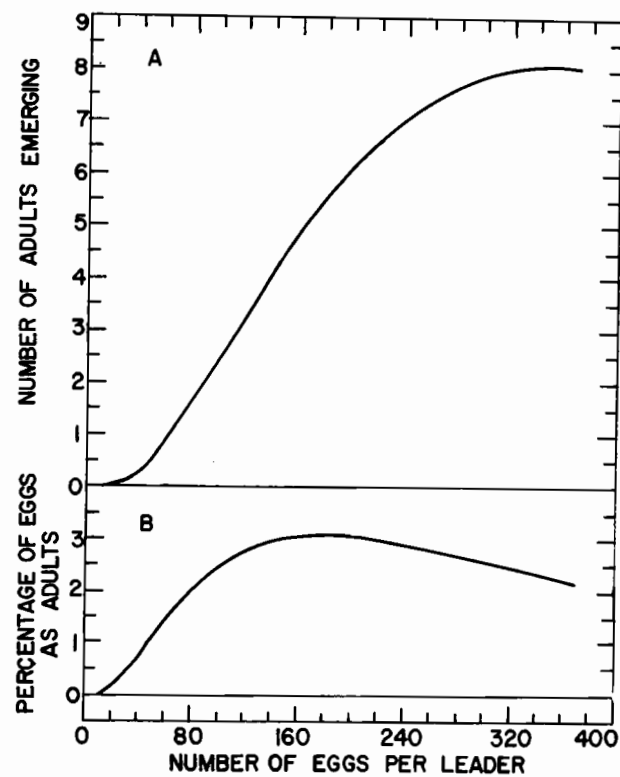


Fig. 19. Relation between the average number of eggs deposited per leader by P. strobi adults and: A, average number of adults emerging per leader; B, percentage of eggs represented by adults emerging per leader.

The results described above indicate that high mortality occurs during the period of development from egg to adult. As shown earlier, however, the percentage hatch of the egg is about 94 per cent. Thus a high level of mortality must occur during the period extending from the time of hatching of the eggs to the time of emergence of adults from the leaders. Therefore, studies were undertaken to determine the percentage of larvae and pupae reaching maturity, and the survival of adults before emergence from the leaders.

Table X shows the percentage of larvae maturing in a sample of 37 leaders with larval damage ranging from 6 to 20 inches that were collected and dissected after the completion of larval development. The Table shows that 87 to 92 per cent of the larvae die before maturing with the average at 90 per cent. In this Table, the number of eggs laid has been calculated on the basis of the extent of larval damage as shown in Fig. 17, and assuming a hatch of 94 per cent as indicated in Table IX.

TABLE X

Percentage survival of P. strobi larvae. The number of eggs hatching determined by estimating the number of eggs laid on the basis of the extent of larval damage as shown in Fig. 17 and assuming a hatch of 94 per cent.

Larval damage (inches)	No. of leaders	No. of eggs	No. of eggs hatching	No. of mature larvae	Per cent larval mortality
6-10	10	800	751	72	90
11-15	15	2230	2094	276	87
16-20	12	3043	2857	230	92
6-20	37	6073	5703	578	90

Following the period of adult emergence, 69 leaders from which a known number of adults had emerged were dissected and the numbers of dead pupae and adults were recorded. The results showed that of a total of 288 insects recorded, 275 or 95.5 per cent completed pupal development and 263 or 95.6 per cent of the mature pupae emerged from the leaders as adults.

The information presented in the previous pages dealing with the survival of the white pine weevil during its development may be grouped into a table showing the survival and mortality of each successive stage of development from the time the eggs are deposited in the spring until the adults emerge from the infested leaders during the autumn (Table XI). In this table, the percentage mortality and survival during the prepupal period represents the difference between the number of mature larvae observed and the total number of pupae and adults.

The table shows that mortality of the weevil is particularly high during larval development and during the prepupal period.

TABLE XI

Survival and mortality during the various stages in the development of P. strobi from egg to adult.

Stage of Development	Per Cent Survival Range	Average	Average Per Cent Mortality
Egg	92 - 96	94	6
Larva	8 - 13	10	90
Prepupation		32	68
Pupa		95	5
Adult (before emergence)		96	4

Cumulative mortality may be obtained by determining the mortality of the larvae, pupae and adults on the basis of the estimated number of eggs deposited in each sample of leaders collected during these studies. In all leaders used the extent of larval damage was recorded, and with this information the average number of eggs deposited was read directly from Fig. 17. Thus, it was found that on the basis of the number of eggs deposited in the leaders dissected during the mature larval count, mortality amounted to 91 per cent. Mortality during prepupation amounted to an additional 6 per cent, and pupal and adult mortality within the leaders amounted to 0.3 per cent. The total of these values, when subtracted from 100 indicate the percentage of the eggs which are represented by adults emerging from the infested leaders. The difference is 2.7 per cent, which is quite

close to the 2.6 per cent based on the egg population shown in Fig. 19B.

When considered in terms of hibernating insects, these values will be reduced by 16.7 per cent which represents the amount of mortality during the autumn season before hibernation. An additional 16.6 per cent die during hibernation. Thus, when 2.6 per cent is used as the base it can be calculated that the percentage of the eggs represented by adults emerging from hibernation the following spring is 1.8. Since each weevil female deposits an average of about 125 eggs, the percentage quoted above may be multiplied by 1.25 to give an accurate indication of the population increase. The resulting value is approximately 2.25. On the basis of this figure, it appears that we have the requisite conditions for a growing population of P. strobi within the limited range of habitat conditions mentioned earlier. With a ratio of at least one female to one male weevil in the population (J. M. Anderson, personal communication) the above value indicates a population increase of 13 per cent per year. This percentage is undoubtedly higher than that which actually occurs in the field because the mortality of the adult weevils during the period extending from the time of emergence from hibernation until the full complement of eggs have been deposited has not been taken into consideration.

There is some evidence indicating that weevil adults are capable of surviving two years and depositing as many eggs the second year as the first (Hopkins, 1907; Taylor,

1929). Survival studies carried out under insectary conditions at the Petawawa Forest Experiment Station indicated that only about 14 per cent survived for two years. Thus, it appears that the general increase in weevil populations throughout the susceptible period of white pine results from the normal productivity of the existing population. Although flight from near-by stands is undoubtedly an important factor in the initial infestation of the stand, the increase in the weevil population associated with an increase in white pine leader damage depends more on local increase than upon weevil migration.

It is of interest to speculate on the causes of mortality during the larval period. In lightly attacked leaders the young larvae are generally pitch-drowned shortly after hatching. In heavily attacked leaders it is suspected that many of the larvae hatching from eggs laid very late in the season meet the same fate since such larvae, found at the lower level of the attack range, are fewer in number and are therefore unable to form a concentrated ring about the leader. In addition, large numbers of larvae undoubtedly die from starvation, since as they mature the number that can encircle the leader drops greatly and those failing to maintain position within the feeding ring are unable to obtain sufficient food.

The presence of parasites also accounts for a part of the high mortality observed during the period of larval development. While dissecting leaders it was noticed that

groups of the eggs of the parasite, Lonchaea corticis Taylor, became more frequent during the latter part of the oviposition season of P. strobil. Clusters of the up-ended eggs were first observed about three weeks after the beginning of weevil oviposition. Very rarely were they observed in punctures containing weevil eggs. When hatched, the maggots usually follow the weevil larvae down the leader, consuming many in the process (Taylor, 1928a). This parasite has a wide distribution, extending over the entire range of the white pine weevil.

Taylor (1929) estimated that mortality of larvae as a result of parasitism by other insects and bird and insect predation accounts for about 30 per cent of the larval population. Therefore, it is suggested that excessive competition for food in leaders containing high larval populations and pitch-drowning of low larval populations accounts for the additional mortality that occurs. It should be pointed out that pitch-drowning may result from too slow movement, which in turn results from too low temperatures. Hence, although pitch-drowning is the immediate cause of death, it appears that the influence of bark temperature on the rate of movement of the larvae is the real reason for the high mortality. With the possible exception of prepupa mortality, mortality at all other stages of development is negligible when compared with that during the period of larval development. It is suggested that the high percentage mortality of the prepupae may be the result of

excessive heat within the dead leaders.

It is recognized that the use of average values calculated from separate samples is not the most satisfactory method for predicting the survival of insects and demonstrating that a population is either increasing or decreasing, but the necessity of using such methods in studies on certain insects is often inherent in the developmental characteristics peculiar to the insect. Although they are of limited predictive value, the results of this study indicate that natural reproduction of the white pine weevil and survival of the adults for more than one year are factors largely responsible for the general increase in weevil populations in susceptible, fully exposed white pine stands.

It should also be mentioned that preliminary observations in shaded white pine stands indicate that the yearly attack by the weevil is almost wholly dependent upon the flight of weevils from open-grown stands. Inspection of mixed stands of white pine and aspen and white pine and red oak where leader mortality was in the order of 10 per cent or less of that occurring in adjacent open stands showed that an average of less than one adult emerged per leader. The foregoing results indicate that this number is not sufficient to maintain a population.

4. EFFECT OF ENVIRONMENTAL FACTORS ON ACTIVITY AND BEHAVIOUR

a. Materials and Methods

(1) Meteorological observations

Meteorological observations were made with standard Stevenson screen equipment. Additional thermographs, a sling psychrometer, a portable potentiometer with thermocouples, and a General Electric pocket radiation meter formed part of the equipment used in the field. An Eppley pyrliometer installed at the laboratory was used to calibrate the pocket radiation meter and to accumulate seasonal records of total radiation.

The pocket meter was used to measure solar radiation under different kinds of cover. The portable potentiometer and thermocouples were used to take temperature readings at sites pertinent to weevil behaviour. For example, they were set up to record temperatures of the bark, ambient air, and the air among white pine bud clusters, in conjunction with the biological observations. The bark temperatures measured represent the surface temperature of the bark. As pointed out by Wellington (1950), thermocouples cannot be expected to give a true surface temperature of the bark since the thermocouple is affected by the bark temperature itself and the thin layer of air surrounding it so that the measurements obtained give only an approximation of the temperature of the bark. However, they describe most accurately the measurable temperatures directly pertinent to insect activity.

Air temperatures recorded by means of thermocouples were made by shielding a junction from direct radiation with small squares of aluminum foil attached to the wires

← one to two inches back of, and mounted above, the junction (Wellington, 1950). The accuracy of all junctions was checked in the laboratory before being used in the field. Those which varied by more than 0.5°C of the temperature of a water bath were discarded.

Temperature measurements were made with No. 24 and No. 30 glass-insulated, copper-constantan thermocouples. In the early stages of these studies, temperature measurements were made with a portable potentiometer measuring in millivolts so that it required a reference junction. In the field, the reference temperature was obtained by mounting a thermometer within the potentiometer housing. At each observation, the millivolt and thermometer readings were recorded consecutively. Actual temperatures of pertinent sites were obtained by means of an alignment chart. Throughout most of the field studies, however, a portable potentiometer calibrated to read directly in degrees centigrade was used for measuring temperatures with the thermocouples. A ten-foot copper-constantan lead which could be readily connected to each of a series of thermocouples in turn was attached to this instrument.

Additional hygrographs and thermographs were set up in selected sites to supplement the Stevenson screen records. One black-bimetal thermograph was set up in the observation area to obtain a measure of insolation. In conjunction with the above records hourly records were kept on cloud types and amounts, wind speed and direction, and types and duration

of rainfall for the daily period, 0800 to 2000 hrs. Also available for examination were records of the hours of sunshine, temperature, relative humidity and rainfall maintained by the Petawawa Forest Experiment Station.

(2) Biological observations

Biological observations were made in conjunction with the meteorological observations discussed above. These included records on the emergence of weevil adults from hibernation during the spring and their initial activity. Following emergence, a programme of observations of their behaviour and activity was initiated and continued throughout the season. Four major types of activity of the adults during the spring were noted and classified as feeding, copulation, oviposition and inactivity. Spot readings on an hourly basis were taken on a number of trees. During preliminary observations, entire trees were examined, but this proved to be very time consuming. Since the records indicated that spring weevil activity was confined chiefly to the terminal shoot of the previous year, the observations thereafter were limited to an examination of this portion of the trees. On occasion, however, whole trees were critically examined, particularly when differences in the daily behaviour pattern of the insects became evident.

Field records were also obtained to show the influence of physical factors of the environment, particularly temper-

ature, on larval developmental rate. The larvae spend their entire developmental period within a leader and cannot be directly observed. However, they normally form a concentric ring about the leader soon after hatching and move down it by feeding on the inner bark. The position of the feeding ring of larvae is readily detected by the discoloration and texture of the outer bark, which is left intact. Thus, the observations consisted of recording the amount of movement within individual leaders by marking the consecutive positions of the feeding ring with pins and measuring the distance between marks. These measurements were taken at two-day intervals throughout the larval period.

During the autumn young adult weevils emerging from infested leaders are active for an extended period of time before hibernating, and field studies were continued during this period. These studies included observations on emergence, activity, and hibernation. Activity during this season is limited chiefly to feeding on lateral as well as terminal shoots and on both new and old growth. Consequently, it was necessary to examine the trees critically to locate the insects and observe whether they were feeding or inactive. As mentioned earlier, this process is time consuming, so that additional records were obtained by inspection of caged trees containing a known number of insects.

Preliminary investigations in the field indicated that there are certain periods in the development of the weevil during which behaviour cannot be accurately studied by

ordinary observation. This is particularly true of the period during which adults are active before hibernation. Therefore, such adults were tagged externally with radioactive cobalt, liberated in selected areas, and their movements were traced with suitable detecting instruments (Sullivan, 1953).

The dispersal and flight habits of the weevil were observed in conjunction with the meteorological observations. In these studies, Co^{60} -labelled adults were used in an attempt to determine the dispersal and mortality of insects liberated in shaded and exposed sites.

All times quoted are Eastern Standard and all temperatures quoted are in Centigrade degrees.

b. Results

(1) Spring population of adults

(a) Emergence from hibernation

As pointed out earlier, first emergence of the white pine weevil from hibernation corresponds closely to the time the terminal buds of white pine begin to swell. The time and rate of emergence, however, also varies in relation to temperature and to the exposure of the hibernation site. Fig. 20 shows the cumulative percentage emergence of 723 weevils from three hibernation sites of different exposure in relation to the maximum daily air temperature. Minimal conditions for emergence occurred on days when the maximum

air temperature reached about 9°C . On such days the amount of emergence was maintained at a very low level. Optimum conditions for emergence occurred on days when the maximum air temperature exceeded about 16°C .

The rate of emergence also varies in relation to exposure of the hibernation site (Fig. 20). Emergence from fully exposed sites may be as much as 30 per cent higher than emergence from shaded sites, particularly during the early part of the season. Additional observations showed that emergence occurred only when the soil at the hibernation sites was warmed to about 6°C or above. Hence, the differences in rate and time of emergence were dependent chiefly upon the temperature difference between exposed and shaded hibernation sites. Examples of the trend in the temperatures of these sites and the air temperature at four feet above ground level during the early and latter portion of the emergence period are shown in Fig. 21. This figure clearly shows the effect of radiant heating on the temperatures of the two sites. Early in the season, exposed sites are warmed well above the temperature threshold for emergence while the shaded sites are maintained near or well below the temperature threshold. By late season, the temperature of shaded sites has increased to a level comparable to that occurring in exposed sites during the early part of the season. Thus, the length of the emergence season is dependent upon the penetration of insolation to the soil surface in shaded sites and the rate of warming of

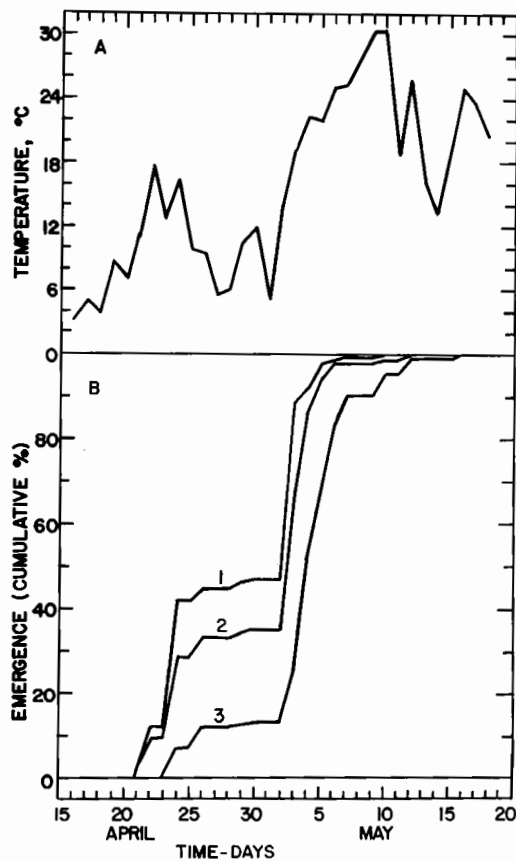


Fig. 20. Relation between emergence of Pissodes strobi from hibernation and maximum daily temperature. A, temperature, °C; B, emergence from hibernation from: 1, fully exposed site; 2, southern exposed site, and 3, shaded site receiving only flecked lighting.

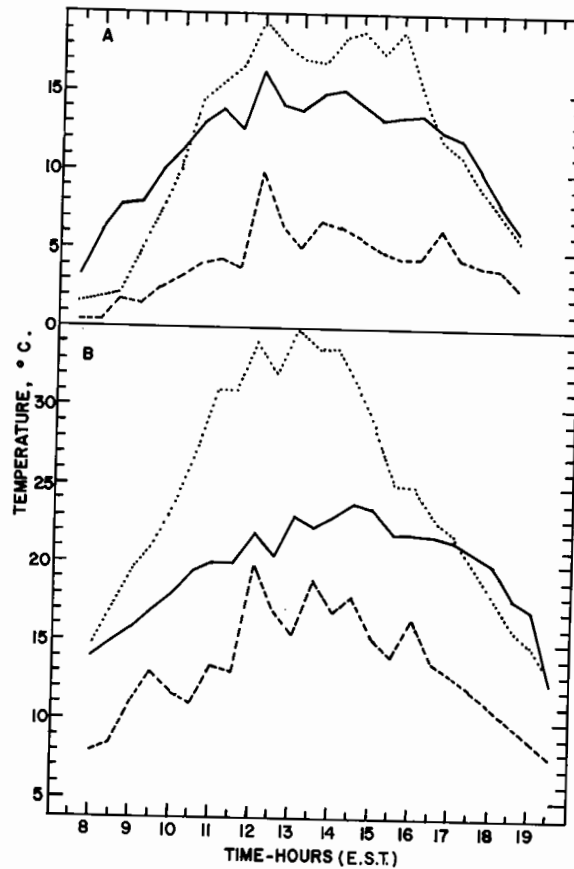


Fig. 21. Comparison of temperatures at hibernation sites of P. strobi adults during: A, early portion of period of emergence; B, latter portion of period of emergence. Solid line - air temp. at 4 feet above ground level; dotted line - temp. of surface of mineral soil at exposed hibernation site; broken line - temp. of surface of mineral soil at shaded hibernation site.

the soil. In terms of maximum daily temperature, a period of about 5 to 6 days of relatively clear warm weather during which the temperature rises from about 16° to 25°C is required for most rapid emergence of the weevil from shaded hibernation sites. Low temperatures such as occurred between April 25 and May 2 (Fig. 20) tend to prolong the period of emergence considerably.

(b) Habitat temperature and its effect on weevil behaviour

When they become active after emergence from hibernation, adult weevils may travel through a wide range of temperature within the limits of a single habitat. However, the level and variation in the diurnal temperatures of the habitat and, consequently, the amount of weevil activity, depend on the time of day and season, and on exposure. During the early part of the season, relatively cool weather prevails, whereas the latter part of the season has relatively warm weather. These conditions are reflected in the temperatures of weevil habitats. Tables XII and XIII show habitat temperatures pertinent to weevil behaviour on relatively clear days during the early and latter parts of the season of activity of the adults. These tables, in addition to showing that a general rise in habitat temperatures occurs as the season progresses, show that, at exposed points of the habitat (e.g., the bark surface of exposed leaders in an open grown stand) the temperature is maintained at a level equal to or higher than the temperature of the surrounding air throughout most of the daylight hours. On the

other hand, at shaded points of the habitat such as the base of the trees, the temperatures are normally maintained below the air temperature.

TABLE XII

Temperature and temperature differences at various points within an exposed habitat of P. strobil adults on a clear day during the latter part of April.

Time	1	2	3	4	5
0900	15.6	0.5	-0.2	-8.8	-9.3
1000	16.4	2.0	1.1	-6.9	-6.5
1100	17.6	3.0	2.2	-4.0	-3.6
1300	18.5	4.4	3.7	-4.6	-1.7
1400	18.8	3.0	1.8	-0.5	-1.6
1500	20.5	2.3	0.6	-1.7	-2.7
1600	21.1	1.9	-1.5	-4.9	-4.5
1700	18.9	0.6	1.2	-4.3	-4.2
1900	13.1	0.8	0.0	-5.4	-5.7

Code: 1. Air temp. at 4 feet above ground level.
 2. Bark t. one inch from top of leader minus No. 1.
 3. Air t. among terminal buds minus No. 1.
 4. Bark t. at base of tree minus No. 1.
 5. Surface t. of ground cover at base of tree minus No. 1.

The weevils move to the warmest points of the habitat and this travel serves to place them on the upper part of the leader and terminal buds. They feed on both the leader and the terminal buds and deposit eggs in the bark of the leader. The intensity of these activities is directly de-

pendent upon the temperature of these sites, particularly the bark of the leader. Consequently, during early season, the daily temperatures permit only an abbreviated period of feeding and oviposition activity which is kept at a relatively low level. As the season progresses, higher temperatures at the activity sites result in a high level of weevil activity which persists throughout most of the daylight hours. It should be mentioned that, during the latter part of the season, the terminal buds of white pine have expanded into new shoots, so that they no longer enclose a pocket of air warmer than that of the surrounding air.

TABLE XIII

Temperature and temperature differences at various points within an exposed habitat of P. strobi adults on a relatively clear day during the latter part of May.

Time	1	2	3	4
0745	15.0	3.2	-0.5	2.1
0815	18.1	2.5	-2.2	1.8
0845	19.8	3.2	-1.0	4.6
0915	20.1	5.3	-2.9	4.9
0945	21.1	5.4	-3.1	0.9
1015	22.5	4.0	-4.0	0.0
1045	24.9	3.7	-6.1	-2.8
1115	26.0	1.7	-7.1	-3.5
1145	26.3	1.4	-7.3	-4.0
1215	27.0	1.0	-8.0	-5.0
1245	27.7	1.3	-7.9	-4.1
1315	26.1	0.9	-7.1	-4.6
1345	27.8	2.7	-7.4	-1.9
1415	26.0	3.0	-6.0	-3.8
1445	27.1	3.2	-5.2	-1.0
1515	26.6	5.5	-5.6	-0.7
1545	25.5	3.5	-5.6	-1.9
1615	25.0	5.3	-5.5	-1.4
1645	26.8	6.2	-6.4	-2.8
1715	26.2	3.8	-6.4	-2.9
1745	26.1	3.0	-7.0	-4.2
1815	24.1	2.9	-5.2	-3.0
1845	20.9	3.0	-3.1	-2.0
1915	16.7	1.2	-0.8	-1.0

Code: 1. Air temp. at 4 feet above ground level.
 2. Bark t. one inch from top of leader minus No. 1.
 3. Bark t. at base of tree minus No. 1.
 4. Surface t. of ground cover at base of tree minus No. 1.

Terminal bark temperature level is a product of ambient air temperatures and insolation. During the early period of weevil activity, ambient air temperatures are often below levels associated with weevil activity but leader bark temperature during periods of maximum insolation (about solar noon at this time of year) may be raised to limits permitting a low amount of activity. The actual level of the leader bark temperature is regulated by ambient air temperatures, which are generally low enough at this time of year so that the highest bark temperatures reach a level associated with a relatively low intensity of weevil activity.

However, later in the year, ambient air temperatures are more often within the range associated with a relatively high level of weevil activity. At this time of the season the greater elevation of the sun early in the morning and late in the afternoon provides more radiant energy and so maintains leader bark temperatures at levels associated with high weevil activity. At mid-day, even though the angle of incidence of the sun's rays is less than at mid-day during the early season, higher ambient air temperatures keep leader bark temperatures within the range associated with high weevil activity. Hence, as the season of weevil activity progresses, the daily period of high weevil activity is progressively extended, starting earlier in the morning and ending later in the afternoon and evening.

Introduction of clouds produces a general drop in the

range of temperature differences observed. Thin cirriform and broken cumulus clouds allow sufficient passage of insolation to maintain the bark temperature of an exposed white pine leader from about 0° to 5.5° above air temperatures ranging between 15 and 28°C . This represents a reduction of about $1\text{--}2^{\circ}\text{C}$ in the range of temperature differences occurring on clear days. Under a heavy overcast of cumuliform or stratiform cloud, the bark temperature of a leader does not exceed the air temperature by more than 2.2°C . During rain, the bark temperature of a leader varies slightly above and below the air temperature but the differences are negligible. In conjunction with the general drop in the bark temperature of the leader there is a general drop in the amount of weevil feeding and oviposition.

When the bark temperature of the leader does not rise above 25°C the insects exhibit a more or less orderly trend of diurnal behaviour. During early morning the insects rest at the base of the trees and among the bases of the terminal buds. As they are warmed and activated they move to the most exposed sector of the leader which is on the east side early in the day. As the day progresses, they move around the leader, keeping within the more exposed sectors until late evening when they finally take up positions in the west and north sectors. Bark temperatures in exposed sectors may range as high as 4°C above shaded sectors and the insects by maintaining exposed

positions remain within temperature zones permitting greater activity. During periods when the bark temperature ranges between 25° and 32°C, observations on groups of adults indicate random movements which can only be interpreted with a knowledge of their reactions to light and temperature. Thus, a single observation on a group of weevils on a leader may show insects feeding and ovipositing on exposed and shaded sectors, others moving up and down exposed and shaded sectors, and still others moving out to the ends of needles in preparation for flight. This variation in behaviour is the result of the previous temperature conditioning of the insects. For example, some of the insects may be moving from shaded, cooler temperature zones and hence have not become overheated, whereas others which have been exposed and overheated are beginning to shift to shaded, cooler sectors of the habitat. At temperatures above about 32°C those insects which have not left the leader begin congregating in the shaded sectors. Many leave the leader entirely. At bark temperatures near 38°C all insects have left the leader. It should be mentioned that at the higher temperatures the insects are very sensitive to touch and drop readily after slight prodding.

(c) Effect of weather on feeding, copulation, and oviposition

It has been mentioned that feeding and oviposition activities of weevil adults during the spring are confined

to the leader. These activities occur in a definite pattern, beginning first on the uppermost portion of the leader just below the buds and occasionally on the buds themselves. Consequently, early in the season a high percentage of the punctures are within the upper two to three inches of the leaders. As the season progresses, punctures are found progressively farther down the shoots. This pattern of attack may occur as a result of the upper regions of the leaders approaching a puncture threshold. Thus, by the end of the season, the general pattern of puncture distribution becomes relatively even throughout much of the area of the leader containing feeding and oviposition sites.

Several adults may feed and oviposit in a single leader. On the other hand, a single female may feed and deposit eggs in several leaders. Once leaders are attacked it is suspected that the odour from them serves to attract other adults to the same leaders. Tests on the reactions of adults when exposed to alternative choices of white pine odour and odourless air within an olfactometer at approximately 24°C and 55-60 per cent relative humidity gave a range of index of reaction of 53 ± 9.0 . The index of the olfactory response may be calculated from the formula $100(D-W)/N$, where D is the sum of the positions occupied by the insects in the odour choice, W the sum of the positions in the odourless, and N the total number of positions per choice (Bentley, 1944). This result, based on two tests involving 200 observations, indicates a strong response of

the insects to white pine odour, so that they might be expected to return to leaders previously subjected to attack.

It was possible to determine the number of punctures accurately but impossible to separate these into feeding and oviposition punctures. Consequently, a number of infested leaders were collected for dissection in the laboratory. The leaders were first marked off into one-inch intervals beginning at the tip, and the number of empty punctures and punctures containing eggs were recorded for each interval. Twenty-eight leaders were collected and dissected: ten during early season, April 27 to May 1; ten during mid-season, May 13 to May 17; and eight during the latter part of the season, May 29 to June 2. Fig. 22 shows the percentage frequency of feeding and oviposition punctures per leader in relation to distance from the top of the leader during the three periods. During early season, the attack is limited to the upper three to four inches of the leader with about 50 per cent or better of the punctures occurring within the first inch (Fig. 22A, A1). Most of the punctures present during this period are the result of feeding activity and only 11-12 per cent of those observed contain eggs. Nevertheless, as Fig. 22A1 shows, about 55 per cent of the eggs present are found within the first inch of attack. By mid-season the percentage of punctures containing eggs has risen to 35-36 per cent but the general pattern of their distribution followed closely that of the feeding punctures (Fig. 22B, B1). The attack

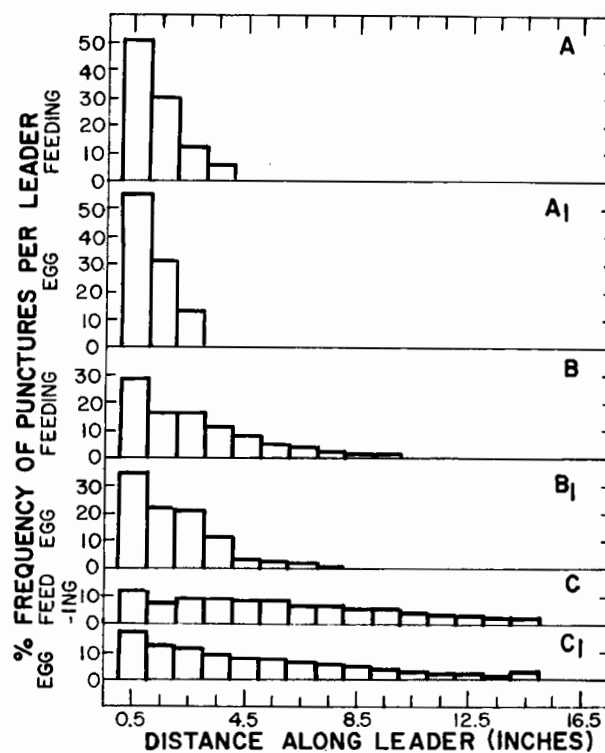


Fig. 22. Percentage frequency of feeding and ovipositing punctures of *P. strobi* adults per leader in relation to the distance along the leader from the base of the terminal buds.
A, A₁ - early season; B, B₁, - mid-season; C, C₁ - late season.

has, however, extended further down the leader, presumably the result of a puncture threshold being reached at the upper levels. Parts C and C1 of Fig. 22 show the pattern of puncture distribution near the end of the season when 51-52 per cent contained eggs. In contrast to parts A and A1 of this figure, where the punctures were confined to the upper few inches of the leader, the distribution near the end of the season shows a relatively constant percentage of punctures at each interval over the entire leader.

It is indicated in Fig. 22C-C1 that the percentage of punctures containing eggs and those free of eggs at each interval along the leader fit a ratio of approximately 1:1. Leaders were collected at the end of the oviposition season to determine if this ratio varied significantly from the suspected 1:1. The results of chi-square analysis of data recorded from seven leaders is shown in Table XLV. The results for heterogeneity indicate no differential effect of the position on the leaders on the ratio of one egg puncture to one feeding puncture. The greater portion of the total chi-square is due to the failure of the number of eggs and feeding punctures at the 1.5- and 9.5 inch intervals to fit under the 1:1 hypothesis. For the other class intervals the fit of 1:1 is reasonably good.

TABLE XLV

Numbers of oviposition and feeding punctures of P. strobil adults at inch intervals along seven white pine terminals with numbers expected under the 1:1 hypothesis and values of Chi-square.

Class interval	Oviposition punctures		Feeding punctures		Total	Chi-square
	Obs.	Exp.	Obs.	Exp.		
0.5	200	190	180	190	380	1.152
1.5	167	144	121	144	288	7.346
2.5	156	149.5	143	149.5	299	.566
3.5	123	120.5	118	120.5	241	.104
4.5	107	103.5	100	103.5	207	.236
5.5	103	103	103	103	206	.000
6.5	102	95.5	89	95.5	191	.884
7.5	101	109.5	118	109.5	219	1.320
8.5	86	89.5	93	89.5	179	.274
9.5	71	86	101	86	172	5.232
10.5	41	45.5	50	45.5	91	.890
11.5	51	49	47	49	98	.163
12.5	40	43	46	43	86	.419
13.5	19	22	25	22	44	.818
14.5	27	21.5	16	21.5	43	2.814
15.5	14	15.5	17	15.5	31	.290
16.5	13	12.5	12	12.5	25	.040
17.5	6	9	12	9	18	2.000
Totals	1427		1391		2818	24.548
						DF
Total chi-square					24.548	18
Pooled chi-square					.460	1
Heterogeneity					24.088	17
P-- .10 - .20						

During the observations it was observed that punctures containing eggs were very frequently covered with a cap which appeared to be composed of a mixture of wood chips and a cementing material. On occasion, small piles of bark chips were found lying beside the feeding punctures, but the open-

ings were seldom plugged. Records were taken to determine the consistency of the presence or absence of caps closing off the openings of the feeding and oviposition punctures. When the data were set up as a 2x2 contingency table, the relationships were so striking that there was no need to complete the calculation of the chi-square values. The results, shown in Table XV indicate the regularity with which the punctures containing eggs are capped while those without eggs are left exposed.

TABLE XV

Comparison of capped and uncapped punctures in relation to the presence or absence of eggs therein.

	Capped	Not capped	Total
with eggs	2334 (1268.2)	217 (1281.8)	2551
without eggs	174 (1239.8)	2320 (1254.2)	2494
total	2508	2537	5045

The amount of weevil feeding, copulation, and oviposition observed during a given period is a function of the existing climate. Within reasonable limits, factors such as wind seem to have little effect on the amount of insect activity. Heavy rain halts all activity although a small percentage of the insects remain active during periods

of light rain. The most important element affecting the classified types of weevil activity is the bark temperature of the leader, although solar radiation and relative humidity can not be ignored. Solar radiation affects the body temperature of the insects, but it affects the bark temperature in much the same way. The two temperatures are maintained within 2°C . of one another with the body temperature of the insects being higher. Therefore, solar radiation has not been treated in as much detail as the bark temperature and relative humidity.

The data were first analyzed to determine the independent influence of each factor on the percentage activity of the insects. Each percentage was calculated on the number of insects observed at definite levels of each weather factor. Regression analysis was carried out and in all cases the classified type of activity was used as the dependent variable. The observations were repeated during consecutive years (1951-52) and the results were tested for significance to determine whether the insects of different generations reacted similarly to temperature and humidity. The calculated "b" values and mean square of error values of regression analysis were compared and the results are shown in Table XVI. During 1951, the amount of oviposition observed was not sufficient to warrant treatment in this manner, hence the two years' data could not be compared. Table XVI shows that none of the "b" values were significantly different. In only one of the mean square of error

comparisons did the "F" value indicate borderline significance. This occurred in the regression of percentage copulation on relative humidity and appeared to result from an insufficient number of observations during 1951.

TABLE XVI

Comparison of "b" values and mean square of error values calculated from regression analysis of the classified types of weevil activity on air temperature, leader bark temperature and relative humidity for the years 1951 and 1952. "b" values compared by t-test and mean squares by F-test.

Weather factor	Activity type (%)	b value		t	P	Mean square		F	P
		1951	1952			1951	1952		
Air t.	total activity	3.704 (n=18)	2.834 (n=23)	.897	>.05	87.26	136.03	1.56	>.05
Bark t.	feeding	2.419 (n=15)	1.187 (n=25)	1.229	>.05	160.75	92.16	1.74	>.05
	copulation	1.457 (n=21)	1.306 (n=24)	.331	>.05	30.82	15.93	1.93	>.05
	inactivity	-2.763 (n=21)	-2.392 (n=25)	.426	>.05	176.30	125.04	1.41	>.05
Rel. hum.	feeding	-0.440 (n=12)	-0.468 (n=17)	.121	>.05	47.97	49.54	1.03	>.05
	copulation	-0.318 (n=13)	-0.298 (n=16)	.138	>.05	18.97	6.26	3.03	.05
	inactivity	-0.810 (n=12)	-0.749 (n=17)	.168	>.05	66.50	64.88	1.03	>.05

Orthogonal polynomial curves (Snedecor, 1950) based on 7592 observations of individual weevil activities are used to show the relationships between insect activity and physical factors. In Fig. 23, which shows the regression of the percentage of the total combined weevil activity on air temperature, the correlation between the expected and the actual values is highly significant ($r=.941$). The curve shows that weevil activity increases as the air temperature increases to an optimum of 28°C . The lower limit of air temperature associated with weevil activity occurs between 5° and 6°C .

The percentage activity of the weevil population on the leaders is most closely related to the bark temperature of the leader. This might be expected since the bark temperature represents the temperature of the surface with which the insects are in contact and, therefore, is close to their actual body temperature. Fig. 24 shows the general increase in weevil activity as the bark temperature increases from about 8° to 32°C and the rapid decrease from maximum to zero activity between 32° and 35°C . Thus, the insects are active within a bark temperature range which is higher by 2 to 4°C than the comparable air temperature range.

The insects are sensitive to changes in solar radiation (Fig. 25) but as pointed out earlier, solar radiation is directly reflected in the bark temperature at the activity site so that its effect may be observed in the bark temperature-percentage activity relationship shown in Fig. 24.

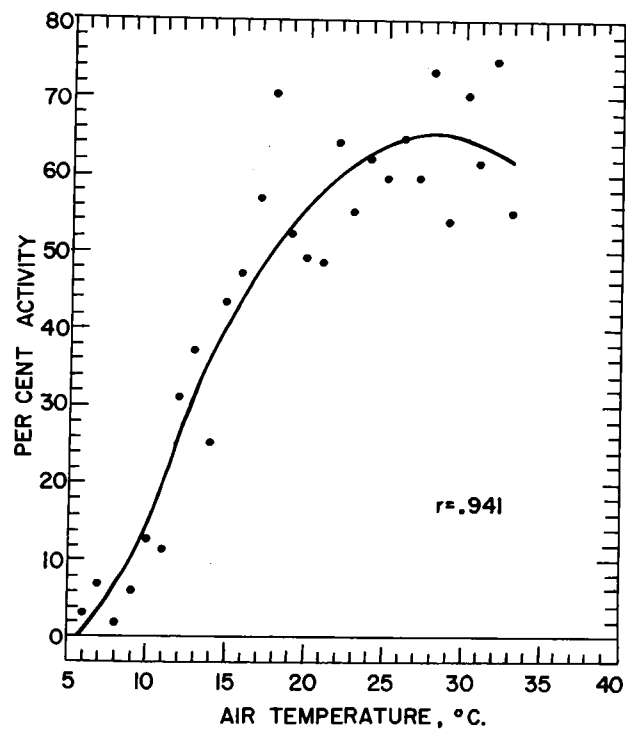


Fig. 23. Regression of percentage activity on air temperature.

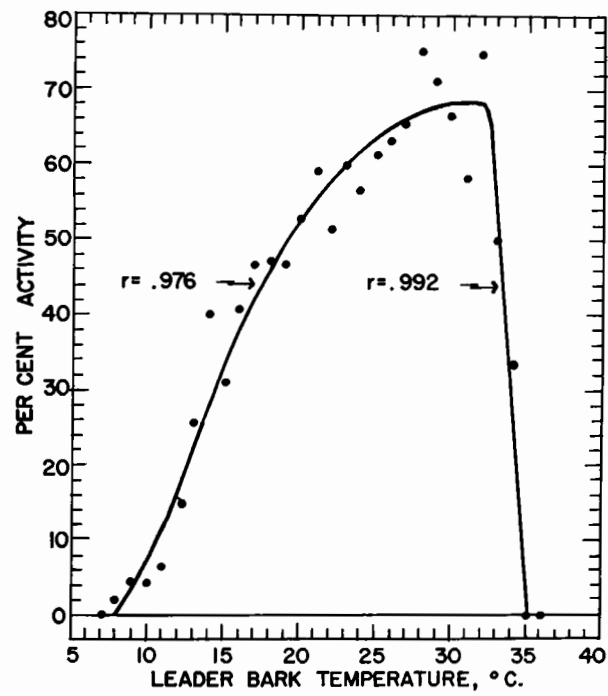


Fig. 24. Regression of percentage activity on leader bark temperature.

Further analysis of the temperature-activity relations involved determining the influence of bark temperature on the individual classified types of weevil activity. The regression of percentage feeding, copulation, and oviposition on the bark temperature of the leader is shown in Figs. 26, 27 and 28, respectively. Fig. 26 shows a marked increase in per cent feeding occurring at bark temperatures between 8° and 29°C . Below 8°C no feeding occurs and between 29° and 35°C feeding activity decreases rapidly. The rapid increase in percentage feeding at the lower end of the temperature scale indicates that a large percentage of the insects may engage in this activity over a wide range of bark temperature. The increase in percentage copulation (Fig. 27) occurs at a relatively steady rate between 8° and 33°C but it drops rapidly between 33 and 35°C . On the other hand, percentage oviposition (Fig. 28) increases slowly between bark temperatures of 10° and 20°C , accelerating rapidly at temperatures between 20 and 29°C . Between 29 and 35°C , the intensity of oviposition decreases rapidly. The results show that oviposition activity is sharply limited by the bark temperature of the leader - a significant fact for interpreting population differences in different types of stands.

During the spring the adults also appear sensitive to changes in atmospheric moisture. Fig. 29 shows the regression of per cent activity on relative humidities between 20

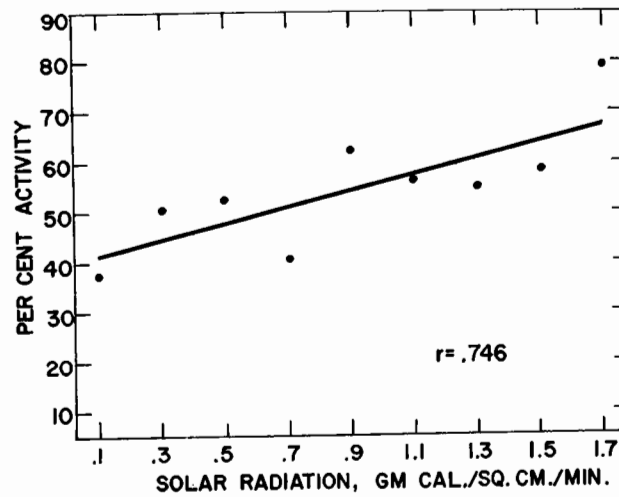


Fig. 25. Regression of percentage activity on solar radiation.

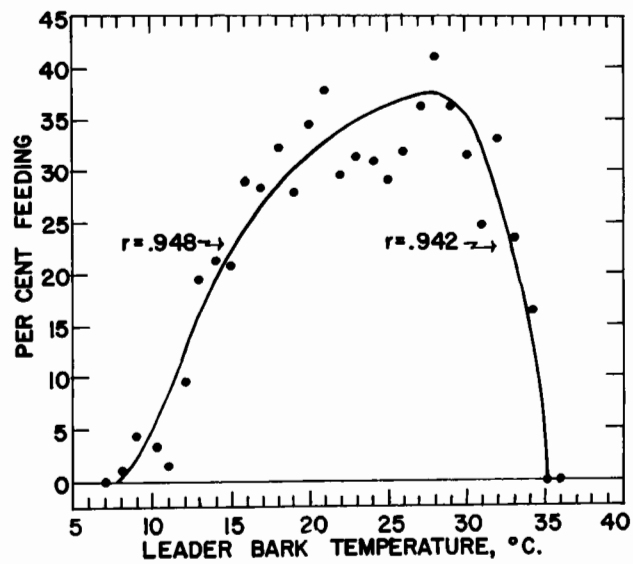


Fig. 26. Regression of percentage feeding on leader bark temperature.

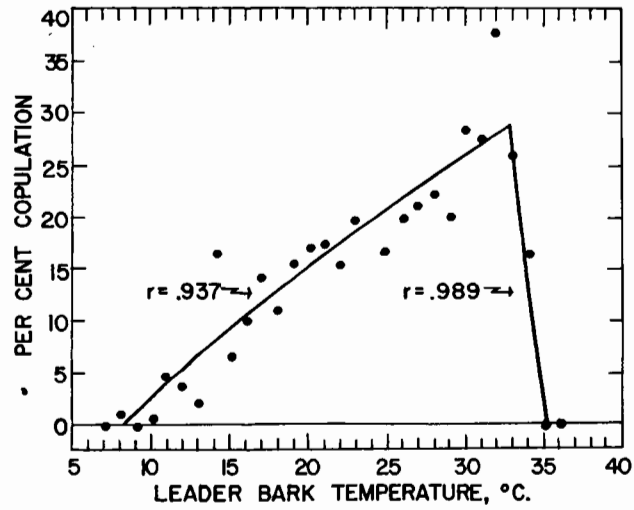


Fig. 27. Regression of percentage copulation on leader bark temperature.

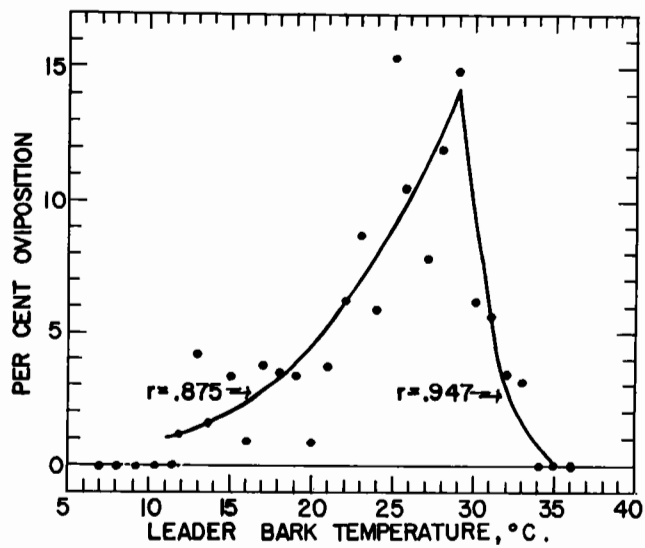


Fig. 28. Regression of percentage oviposition on leader bark temperature.

and 100 per cent. As the humidity rises the percentages of weevils engaged in feeding, copulation, and oviposition decrease until only about 7 per cent of the insects are active at 100 per cent relative humidity. Further analysis indicated that this relation is at least partially reflected in the temperature-activity relations. To show this, the relation between relative humidity and air temperature has been calculated and the results, based on weighted averages of the relative humidity records taken in conjunction with observations on insect activity, are shown in Fig. 30. It is apparent that, on occasion, unusual combinations of temperature and humidity occur so that their influence on weevil activity cannot be demonstrated by correlations between the response of the insects to individual factors of the environment. Therefore, three-dimensional graphs have been used to represent by isopleths the variations in percentage activity with bark temperature of the leader and with relative humidity.

Fig. 31 shows that the influence of relative humidity on weevil activity is increased as the bark temperature of the leader is raised. This effect is clearly shown in Fig. 32 which shows the decrease in per cent activity at different levels of relative humidity when the bark temperature of the leader is held constant. Thus, at a constant temperature of 31°C a maximum of 80 per cent activity may occur over a relative humidity range of 25 to 65 per cent, but at humidities above about 65 per cent the amount of activity

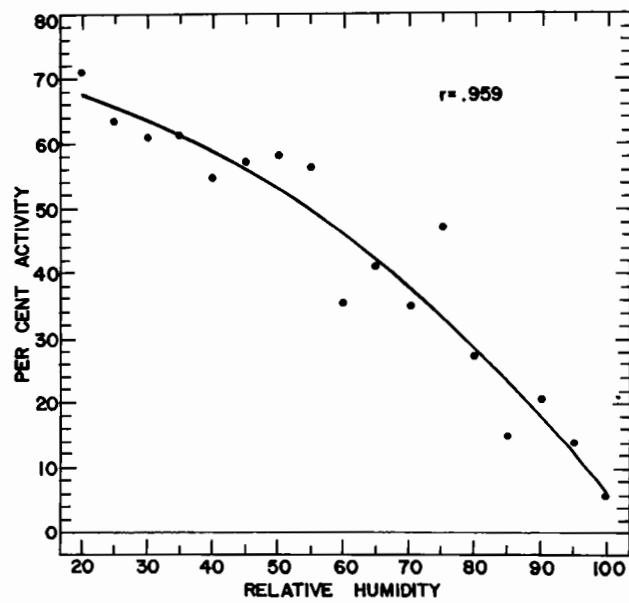


Fig. 29. Regression of percentage activity on relative humidity.

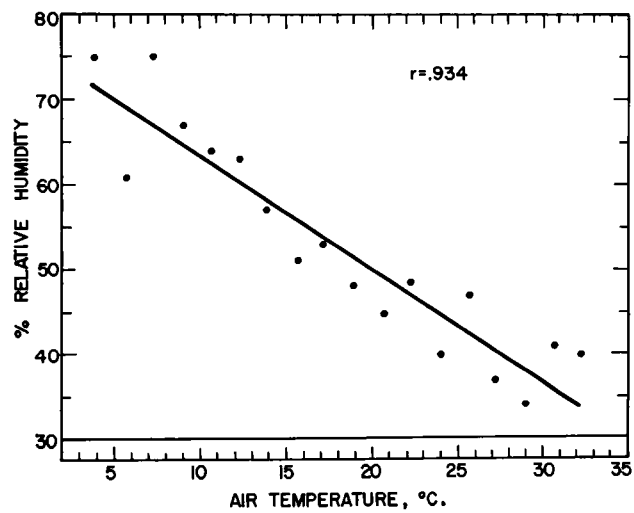


Fig. 30. The relation between humidity and air temperature.
(Based on weighted averages of relative humidity recorded
in conjunction with observations on insect activity.)

drops progressively until at 31°C and about 87 per cent relative humidity no weevil activity occurs. At a constant temperature of 20°C (Fig. 32) the amount of activity does not exceed 50 per cent, but this intensity of activity may continue over a relative humidity range from 20 to 86 per cent.

The conditions under which adults are able to oviposit are of prime importance. Consequently, isopleths indicating the variation in percentage oviposition with bark temperature and relative humidity are shown in Fig. 33. This figure shows that oviposition most commonly occurs at temperatures between 25 and 29°C when this range is associated with relative humidities from 20 to 55 per cent - a comparatively narrow range of conditions.

(2) Larval population

White pine weevil larvae form a concentric ring about the leader and move down the shoot by feeding on the entire cortex, with the exception of the outer layer of bark. Their entire developmental period is spent within the leader and, therefore, they are not directly exposed to the surrounding elements. Weather factors such as relative humidity and wind had little effect on the amount of movement of the larvae. Solar radiation could be correlated with the amount of movement but, as shown earlier its affect is reflected in the bark temperature of the leader. Temperature proved to

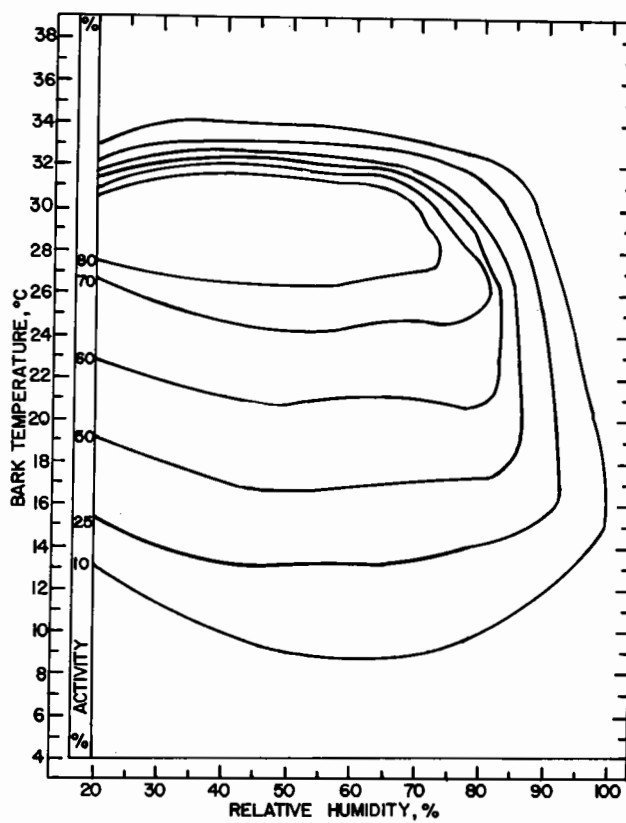


Fig. 31. Three - dimensional graph of the variation in percentage weevil activity with bark temperature of the leader and with relative humidity.

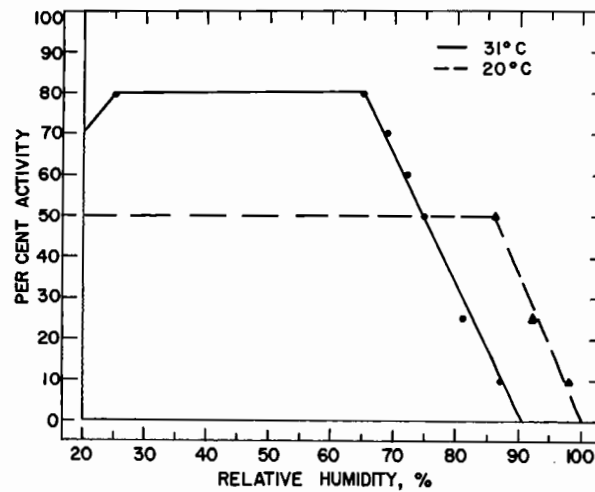


Fig. 32. The effect of relative humidity on the activity of white pine weevil adults when leader bark temperature is held constant. (Data abstracted from Fig. 31).

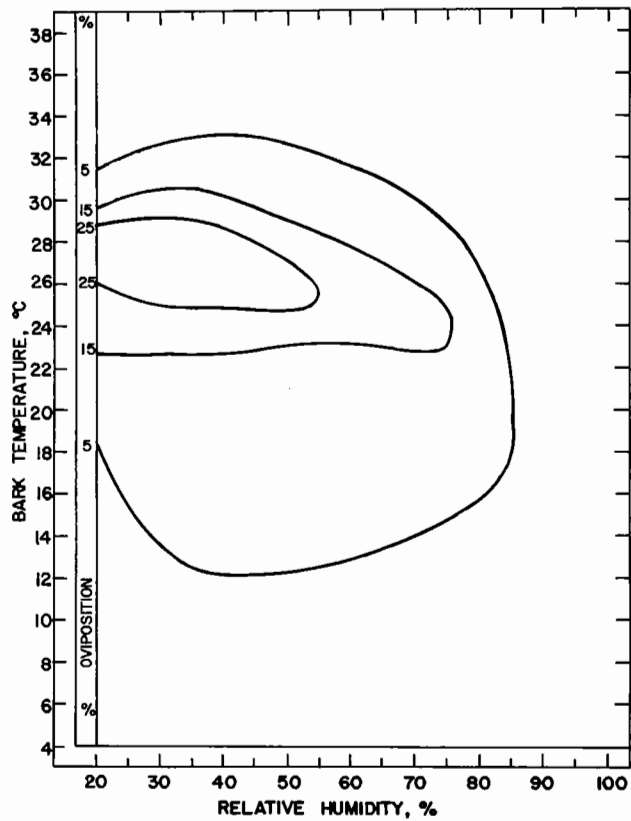


Fig. 33. Three dimensional graph of the variation in percentage weevil oviposition with bark temperature of the leader and with relative humidity.

be the most important of the physical factors affecting the rate of movement of the larvae.

(a) Effect of temperature on larval movement

During the field studies, a number of attacked leaders were inspected at 48-hour intervals and the amount of movement of the larvae was recorded. The total movement of all the leaders was indexed in an attempt to eliminate, at least partially, the effect of variability resulting from mortality, parasitism, and maturity of the larvae. The method used to bring the two-day totals to a comparable basis is shown in the following formula,

$$\text{Movement index} = \frac{(\text{total movement})}{\text{number of trees showing movement}} \frac{(\text{total number of trees observed})}{\text{number of trees showing movement}}$$

The change in movement index was then determined. This represented the positive or negative difference between two consecutive readings recorded at two-day intervals and brought to a comparable basis using the above formula. Regression analyses were calculated between the change in movement index and the positive or negative change in two-day mean temperature. Preliminary observations showed that no detectable movement of the larvae occurred at night. Therefore, mean temperatures for correlation with larval movement were calculated from temperatures recorded every two hours between 0800 and 2000 hrs.

These studies were repeated a second year and, as shown in Table XVII, the rate of movement of the larvae of

TABLE XVII

Comparison of "b" values and mean square of error values calculated from regression analysis of larval movement index on air and bark temperature for years 1951 and 1952.

Weather factor	b-values		t	P	Mean square		F	P
	1951	1952			1951	1952		
Air temp.	7.788 (n=12)	8.603 (n=19)	0.317	>.50	1226.87	1259.20	1.03	>.05
Bark temp.	4.703 (n=12)	8.920 (n=19)	1.180	>.20	1104.20	1108.90	1.00	>.05

different generations is influenced similarly by temperature. The results are based on observations of 69 infested leaders in 1951 and 99 infested leaders in 1952. When the data were combined, regression analysis of movement index on mean air temperature change gave a highly significant b-value of 8.336. Over the range of mean two-day air temperatures, 17.1° to 29.7°C , for each change of 1°C , the average change in the movement index during a two-day period was 8.336 ± 1.52 cms. Similarly, regression analysis of movement index change on mean bark temperature change gave a highly significant b-value of 6.547. For each 1°C change in mean bark temperature, the average change in the movement index was 6.547 ± 1.19 cms. (over a range of two-day mean bark temperatures of 18.5° to 31.8°C).

The foregoing results show that the rate of larval movement is influenced by temperature. In addition, variations in the temperature-movement relations of the larvae exist which are directly related to the age of the individual populations in each leader. The percentage movement in each leader was determined for each of the two-day periods based on the total amount of movement which occurred during the season. By selecting those leaders in which the complete developmental period of the larvae was recorded, the influence of temperature on the mean percentage movement of larval populations of known age could be obtained. Fig. 34A1 and A11 express the influence of the bark temperature of the leader on the amount of movement of larval populations

during their 3rd and 4th days and, 24th and 25th days of development, respectively. These lines represent the outer limits of the observed differences in amount of movement which occurs during the developmental period of the larvae. It is apparent that the amount of movement and, therefore, feeding of young and old larval populations increase as the temperature of the bark increases. In addition, the lines show that young larval populations move a greater distance than older larval populations within similar temperature ranges.

When all the data are combined irrespective of age of the larval populations, the rate of movement continues to be directly related to the bark temperature (Fig. 34B). It will be seen that this line falls between lines 1 and 11 of Fig. 34A and that it lies closer to the latter. It should be mentioned that the calculated line in Fig. 34B extends over a bark temperature range of 22 to 31°C only. The points at the 19 and 20°C intervals were not used, as these temperatures did not occur during the latter portion of the developmental season of the larvae.

The differences in amount of movement of young and old larval populations (Fig. 34A) may be due to differences in the number of larvae present in the leaders at the two periods of the season. Although there is about a 94 per cent hatch, mortality of the larvae during their development amounts to about 90 per cent. Thus, a much larger number of larvae are present during the early season. It is suggested

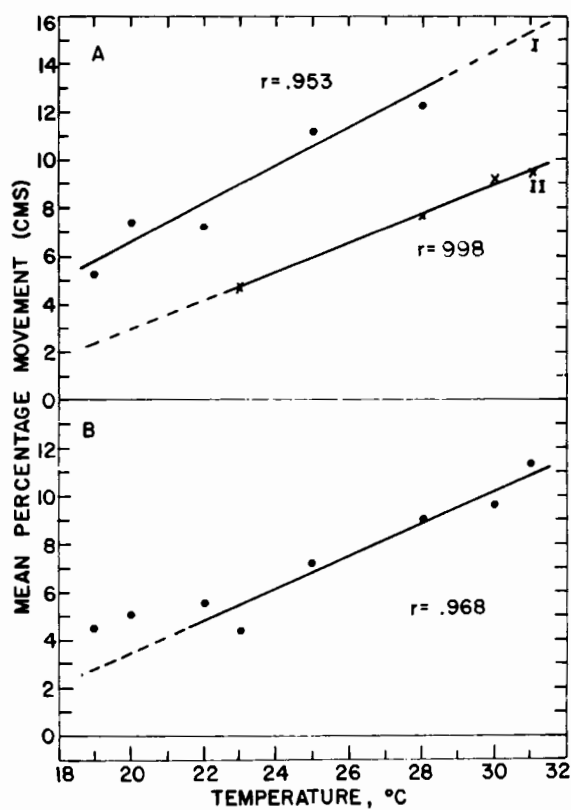


Fig. 34. Relationship between the amount of movement of white pine weevil larvae and the mean bark temperature of a white pine leader. AI, amount of movement during the 3rd and 4th day of development; AII, during the 24th and 25th day of development; B, mean 2-day movement.

that these larvae, although consuming less food per individual, move a greater distance as a result of their greater number. In addition, the fact that the regression line of mean percentage movement on bark temperature (Fig. 34B) lies closer to line 11 of Fig. 34A indicates that a high percentage of larval mortality probably occurs during the early stages of development, the period of maximum competition and of relatively lower temperatures that might slow movement enough to permit pitch-drowning.

(3) Autumn population of adults

(a) Emergence from infested leaders and subsequent behaviour

Emergence of the new generation adults normally begins during late July or early August and continues until about mid-September. Upon completion of the transformation from pupa to adult, the insect remains within the pupal chamber for about two weeks before emerging. Complete emergence is closely correlated with temperature. The insects commonly cut their emergence holes to the inner surface of the outer intact bark layer and, after making a small hole through this layer of bark, they remain relatively quiet until temperatures favour completion of the outlet and final emergence.

Twenty-five infested leaders were placed in a cage shaded from direct sunlight and the number of adults emerging were recorded at hourly intervals in conjunction with the air temperature. The number of adults emerging was

checked by counts on the number of emergence holes in each of the leaders. The results are shown in Fig. 35. This figure shows that emergence occurs at temperatures between 10 and 35°C with an optimum at approximately 29°C. Percentage emergence increases rapidly with air temperature between 10 and 30°C and decreases suddenly at temperatures above 30°C. Normally the insects emerge during periods of rising temperature. At temperatures between about 10° and 20°C, they move to the upper portion of the dead leader after emergence but, as this region is warmed they react in much the same manner as adults emerging at temperatures above about 20°C; they drop to the ground or to a lower portion of the tree, crawl down the mainstem, or begin flight. In any event, their behaviour removes them from the dead leader.

Individuals observed moving up a tree with a dead leader commonly continued to the demarkation line at the junction of the healthy and attacked wood but usually would not move over the boundary onto the attacked wood. After repeated attempts to move over the dead portion of the leader the insects would return down the leader or out onto one of the lateral shoots. This behaviour seemed to be regulated by the bark temperature of the leader because it occurred only on relatively clear days when the bark was warmed to 27°C or above. On such days the bark temperature of a dead leader ranged as much as 2.5 to 6.5°C above the ambient air temperature when this ranged between 15 and 30°C

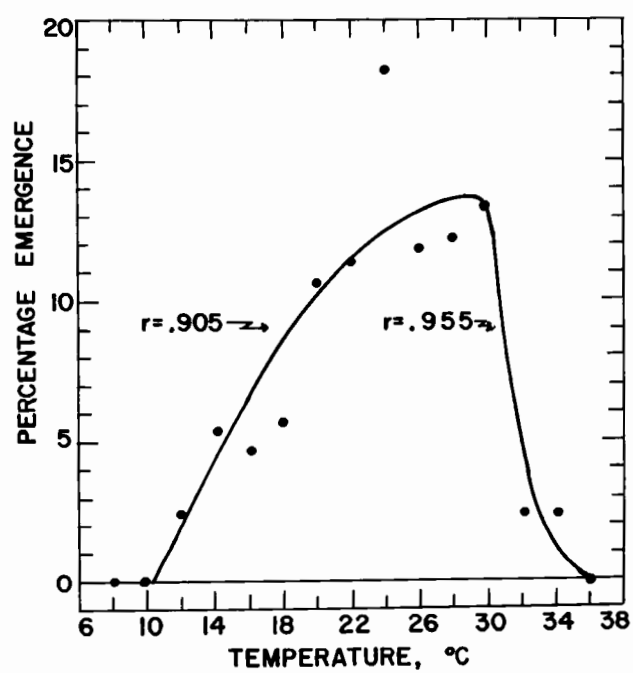


Fig. 35. Regression of mean percentage emergence of weevil adults from infested leaders on air temperature.

and from 0.5 to 3.5°C above the bark temperature of a living leader. Hence, the difference in the temperature of the dead and healthy bark was frequently sufficient to limit weevil travel to the living portion of the leaders.

The behaviour of young adults during the autumn is similar to that described for the old adults during the spring. They show a strong preference for the most exposed parts of the habitat and when these sites are overheated they move to shaded areas. When forced to move to the shaded sites, however, they may continue to feed. Spot observations indicated that at bark temperatures exceeding about 27°C the insects leave the exposed sites and move to shaded sites on the leaders and laterals and continue feeding. At bark temperatures above about 31°C the adults are seldom found on the leaders, but a search of the lower foliage reveals many feeding in shaded areas at bark temperatures below 27°C. The temperature differences between the exposed and shaded sites indicated the effect of solar radiation on the habitat. Once in the shaded sites, the cooled insects do not show as strong a tendency as spring adults to move back to the exposed sites. It is suggested that this results from the ability of the insects to feed on older growth. Thus, as fed insects, they do not exhibit such strong photopositive responses. However, during late afternoon and evening when the intensity of solar radiation has decreased the insects move back to the more exposed, but not overheated sites.

(b) Effect of weather on feeding activity

Activity of young adults during the autumn is limited to feeding which continues until they hibernate. Feeding activity is not, however, confined to the leader as it is during the spring. Records kept on the incidence of feeding indicate that about 25 to 30 per cent occurs on the new and previous years' terminal growth of the main stem. The remaining 70 to 75 per cent occurs on the lateral shoots, where preference is shown for the last three whorls, particularly the new growth and the growth of the previous year. These locations are normally the most exposed and their selection as feeding sites is in accordance with the positive response of the insects to light. It is not uncommon, however, to observe adults feeding on older growth produced as much as three years before, and rarely they have been observed feeding on lateral growth laid down five years previously.

During this study, extensive rearings of young adults under insectary conditions were carried out in conjunction with the observations in the field. At no time were the young adults observed copulating or ovipositing. Examination throughout the season of food pieces containing 1134 punctures failed to reveal any eggs.

During field studies, 3959 individual observations on the activity of the insects were made in conjunction with observations on the existing weather conditions. It was

found that autumn weather influences the feeding activity of the insects in much the same manner as it does during the spring, with two notable exceptions. First, the insects are less sensitive to changes in atmospheric moisture (Fig. 36). No major change occurs in the response of the insects at relative humidities between 30 and 80 per cent. Between 80 and 95 per cent the percentage of the population engaged in feeding decreases slowly, but when the air becomes saturated the percentage feeding drops sharply to about three per cent. Secondly, no significant relation could be obtained between solar radiation and percentage feeding. This might be expected, since considerable feeding occurred in shaded sites.

The bark temperature of the leader is again the most important factor influencing weevil feeding. Fig. 37 shows the regression of percentage feeding on the bark temperature of the leader. Feeding activity occurred over a range from 7° to 37°C with the optimum temperature between 28 and 29°C. This temperature range exceeded that of the air temperature by from 1 to 4°C. The slow decrease in feeding intensity between bark temperatures of 29 to 34°C resulted from the ability of the insects to feed in shaded areas which were considerably cooler than the bark of the leader. Since the temperature at all the various feeding sites could not be taken during each observation period, the bark temperature of the leader was selected as the standard temperature for comparison.

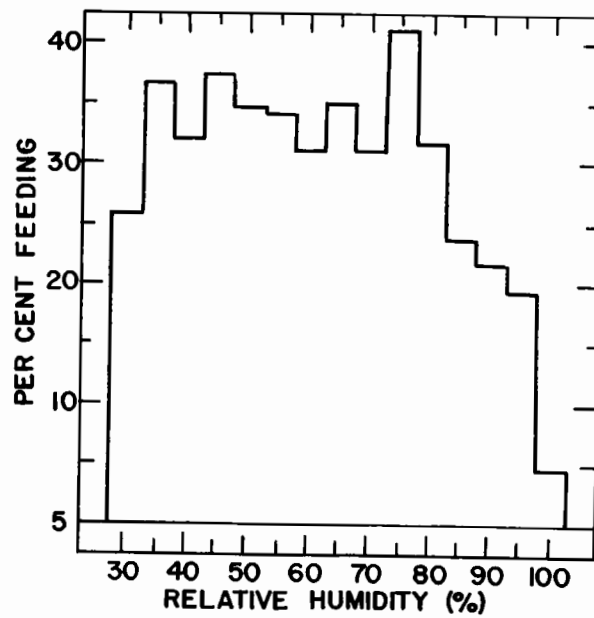


Fig. 36. Percentage frequency of feeding of P. strobi adults of the autumn population in relation to the relative humidity of the air.

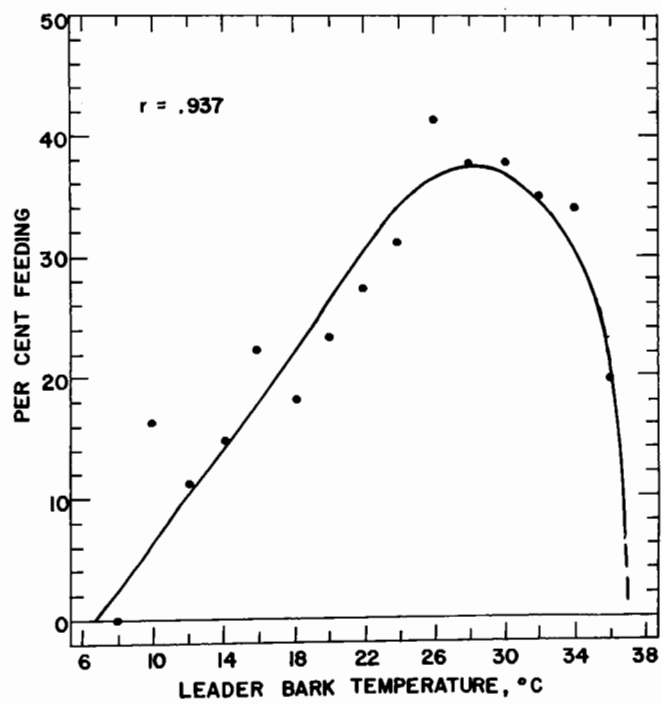


Fig. 37. Regression of percentage feeding on leader bark temperature during autumn.

(c) Hibernation

Weevil adults normally hibernate during the latter part of October, but this may vary, depending on the temperatures ~~conditions~~ occurring at this time of the season. Observations on adults labelled with the radioactive isotope Co^{60} during 1951 and 1952 showed that all insects had hibernated after a prolonged period of mean daily temperatures below 5°C (Fig. 38). This figure shows that the insects had hibernated by October 30, 1951 and October 21, 1952, and that in both cases completion was associated with a period of six to seven days when the mean daily temperature remained below 5°C .

The insects hibernate at the surface of the mineral soil below the ground cover. Final hibernation sites are limited to two general areas, (1) in shaded sites within a radius of about one foot from the base of the tree and (2) in more exposed locations at greater distances from the base of the tree. During 1952, about two weeks before hibernation was complete, 24 Co^{60} -labelled adults were liberated individually on trees within the section of the pine plantation enclosed by the "radioactive grid" (Fig. 1). Periodic checks were made with suitable detecting instruments and the positions and amounts of movement of the insects were recorded. The following notes are presented to show the general distribution of the adults shortly before, during, and after hibernation.

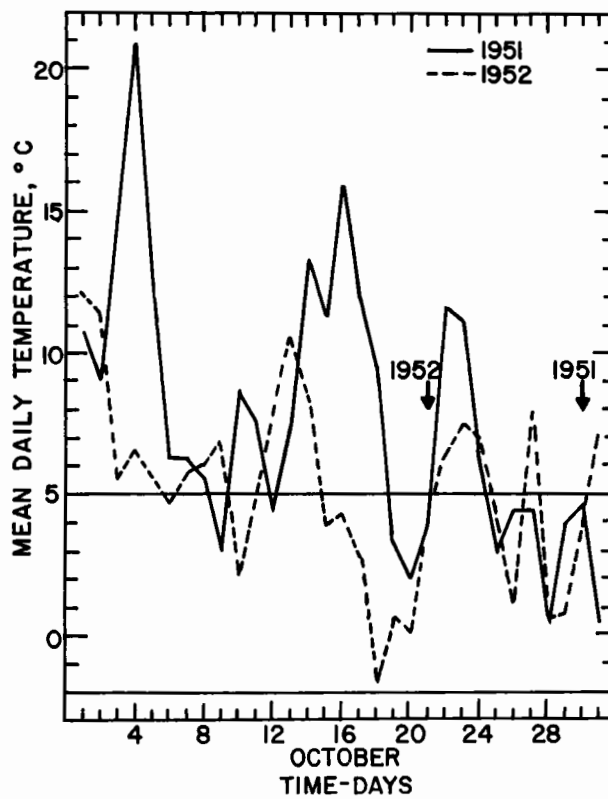


Fig. 38. Mean daily temperatures during October, 1951 and 1952, at nursery plantation. Arrows denote day of final hibernation of the white pine weevil.

- Oct. 7/1952: 24 weevils tagged with Co⁶⁰ placed on individual trees.
- Oct. 14/1952: One insect has moved three feet to an adjoining tree and the remainder are still on or at the base of the trees on which they were originally placed. Five of the insects are in tree locations. Of the 19 insects on the ground, 14 are in shaded sites within 6 inches of their respective trees and 5 have moved out to exposed ground positions.
- Oct. 16/1952: All but one of the insects are in the duff at or near the bases of the trees on which they were originally placed. Of the 19 insects on ground on October 14, 15 have moved, the maximum distance being about one foot. Maximum distance of any insect from tree base is about five feet.
- Oct. 21/1952: All insects are in the duff at or near the base of the tree on which they were originally placed. Twelve insects have moved from previous locations recorded on October 16. Eighteen insects are now within a one-foot radius of their respective trees and 6 are within a radius of five feet. Of the 24 locations, seven are in exposed or partially exposed sites and the remainder are

in heavily shaded sites.

Oct. 25/1952: No change from the observations on October 21.

The above notes indicate that the insects do not move far from the trees on which they are located at the time of the drop in mean daily temperature. The insects are, however, sensitive to temperature changes during this period and during the period just before the general drop in temperature. On days before the general drop in temperature the insects may be warmed sufficiently to permit movement up the trees to feeding sites where they may remain for a few hours around mid-day and early afternoon. During the evening of such days, there is a sharp drop in the temperature of the exposed sites when insolation is reduced to near zero. The insects then move to the warmest locations available, which at this time of the season are at the base of the trees (Table XVIII). On subsequent days, if the mean temperature remains below 5°C very little movement occurs. The longer these conditions persist, the more insects hibernate. On the other hand, if subsequent days are warmer, many of the insects move back up the trees while others move out from their bases. The direction of travel is dependent on the temperature of the ground and the bark at the base of the trees, particularly during the morning. Table XVIII shows that steep vertical and horizontal temperature gradients occur from the shaded to the exposed sites on the trees and on the ground, but the direction of movement of the insects is dependent on the level of the temperature at the lower ends

of the ranges. Thus, movement over the horizontal gradient may be possible at a time when the bark temperature at the base of the tree does not favour upward movement. Consequently, the number of insects found in shaded and exposed sites is a function of the temperature which occurs prior to hibernation. Brief warm periods permit movement but prolonged cool periods inhibit movement and more insects hibernate near the bases of the trees.

TABLE XVIII

Comparison of temperatures pertinent to weevil activity at various points in a typical weevil habitat and the air temperature at four feet above ground level. October 10, 1952.

Time	1	2	3	4	5
0900	6.7	4.8	-3.8	-1.9	3.3
1000	7.9	3.0	-3.9	-0.7	6.0
1100	10.2	5.9	-3.8	-2.4	6.0
1200	10.5	2.7	-4.7	1.3	3.8
1300	11.1	3.8	0.2	0.2	9.0
1400	12.8	1.2	-2.1	-1.0	8.0
1500	11.8	6.2	4.7	3.0	6.9
1600	9.3	2.8	0.9	0.5	0.2
1730	-1.0	1.7	3.1	2.4	8.6

Code: 1. Air temperature at four feet above ground level.
 2. Bark t. of white pine leader minus No. 1.
 3. Bark t. at base of tree minus No. 1.
 4. Temp. of hibernation site at base of tree minus No.1.
 5. Temp. of exposed hibernation site minus No. 1.

After the completion of hibernation, the temperatures of pertinent sites within the confines of a single habitat still vary in relation to the degree of exposure, but they are for the most part reduced to levels below that associated with weevil activity even on relatively clear days (Table XIX). This table shows that there is very little difference between the temperatures of the exposed and shaded sites. The exposed hibernation sites may vary as much as 1.5°C above the shaded sites during the hours of incident solar radiation but during early morning and late afternoon they are cooler than the shaded locations. At these times, back radiation from the exposed sites is stronger than in the shaded sites, so that they are cooled to lower levels.

TABLE XIX

Temperatures of *P. strobil* activity and hibernation sites on a relatively clear day approximately five days after the completion of hibernation. October 26, 1952.

Time	1	2	3	4
1000	4.9	-0.5	-3.4	-4.1
1100	7.5	-0.4	-4.9	-3.9
1300	9.5	1.0	-6.4	-6.4
1400	7.5	0.7	-1.2	-0.5
1500	7.8	0.5	-3.9	-2.4
1600	8.5	-0.1	-4.0	-3.4
1700	3.9	1.7	-1.0	-2.0

Code: 1. Air temperature at four feet above ground level.
 2. Bark t. of white pine leader minus No. 1.
 3. Temp. of shaded hibernation site at base of tree minus No. 1.
 4. Temp. of exposed hibernation site three feet from base of tree minus No. 1.

(4) Dispersal ^{and} ~~flight~~ habits

The white pine weevil may disperse by crawling or by flight. In exposed stands, both methods account for the dispersal which occurs within the limits of the stand. Field observations gave no indication of a definite flight period during the spring or autumn. Flight is most commonly observed during ~~of~~ wind speeds of less than 8 miles per hour and occasionally during gusts up to 10 to 12 miles per hour. The direction of flight was noted in relation to the direction of the wind and the position of the sun's disc but sufficient data were not obtained to correlate these factors with flight. Temperature proved to be the most important factor influencing flight. During the field observations a total of 150 weevil adults were observed landing or taking off and at no time was flight observed at air temperatures below 15°C (Fig. 39A.). The optimum temperature was 26°C. In terms of bark temperature of the leader, flight occurred most commonly at 25°C and above but was observed occasionally at bark temperatures as low as 16°C (Fig. 39B).

Bark temperatures of 25°C or above commonly occur during the active season of the adults, particularly at the feeding and oviposition sites. If overheated at these sites the insects move down the trees to cooler temperature zones. Although this movement usually takes them to zones of lower temperature, the reverse situation occurs

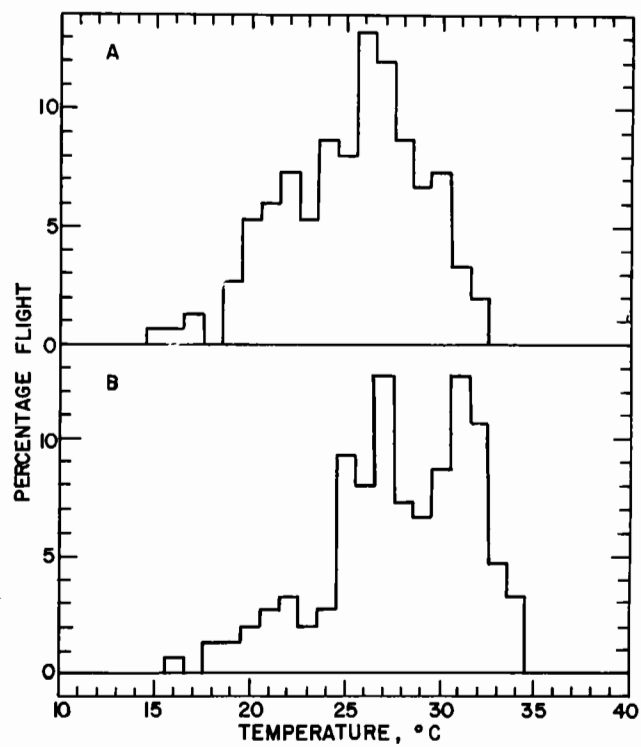


Fig. 39. Percentage frequency of weevil adults observed in flight in relation to: A, air temperature; B, bark temperature of the leader.

on occasion. On exposed trees such as those on the fringe of a plantation or roadside, movement down the tree may bring the insects into contact with higher temperature zones (Table XX). At such times when they are trapped between two high temperature zones, the insects take flight. Before taking flight, a weevil moves up on some projecting point such as the tip of a needle, moves about the tip excitedly with frequent antennal movements, and then flies off. When landing, the insects usually settle on the needle fascicles of lateral branches or of the leader. Subsequent movement normally takes the form of attempts to move to the upper portion of the leaders.

Single flights exceeding eight to ten feet are rarely observed. The insects normally fly only to the surrounding trees. On one occasion, however, a weevil was observed leaving a tree on the west side of the plantation and flying into a light west wind at about 15 feet above the ground, and was followed for approximately 200 feet before it landed in a small clump of white pine. Similar observations have been made by Barnes (1928). It appears that the weevil is capable of relatively long flights.

TABLE XX

Bark temperatures at different points along the mainstem of an exposed white pine tree located on the fringe of a plantation minus the air temperature.

Time	1	2	3	4
0800	21.3	1.2	2.0	-4.8
0900	23.4	3.0	6.4	-2.9
1000	25.6	2.6	4.6	-4.6
1100	26.4	1.3	8.3	-5.0
1200	25.9	2.3	5.0	-2.5
1300	25.7	1.8	4.5	-3.4
1400	27.5	1.5	4.2	-1.6
1500	27.6	1.7	7.4	-2.9
1600	25.6	2.4	2.6	-1.8

Code: 1. Air temperature at 4 feet above the ground.
 2. Bark t. of a white pine leader minus No. 1.
 3. Bark t. one-half way down the mainstem minus No. 1.
 4. Bark t. at base of tree minus No. 1.

During the field studies a number of experiments were carried out to obtain some information on the dispersal of adults of the spring and autumn populations of the weevil in exposed and shaded stands. Co⁶⁰-labelled insects were liberated in selected areas. The recovery program included periodic checks with suitable detecting instruments (Sullivan, 1953). In the first experiment during the autumn of 1951, 56 weevils were liberated within the "radio-active grid" (Fig. 1). Forty-two insects were liberated

in section K, seven in section D, and seven in section Kl6. Between September 1st and November 1st, nine weevils or about 16 per cent of the tagged insects could not be located. Loss of these insects may have been due to bird and small mammal predation or to flight outside the limits of the check area. In one instance, a small mammal fecal dropping was detected that gave a high radioactive count. The results indicated that only a small percentage of the population actually left the area.

In section K, the insects moved chiefly in a northerly direction (Fig. 40). This release area was selected mainly because it was shaded for a few hours around mid-day by a sub-mature stand of red and white pine (Fig. 1). The results of the recovery programme showed that the insects moved to sites which were considerably more exposed. This indicated that the insects have a preference for exposed areas when they are placed in sites which are shaded for a portion of each day.

In section D, movement of the insects in a NNE and SW direction occurred but in no case did the recovered insects move more than about 10 feet. In section Kl6, the insects were released within a clump of young white pine situated about 15 feet inside the stand of sub-mature red and white pine so that they were shaded throughout the entire daylight hours. They were released on September 1st and, by late afternoon of September 2nd, three of the insects had left the area. In addition, there was evidence

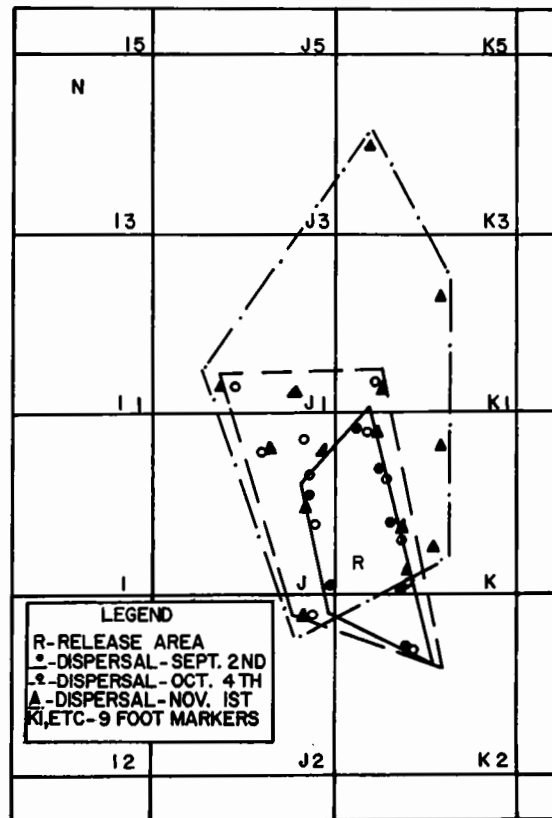


Fig. 40. Dispersal limits of recovered Co^{60} -labelled weevil adults released in a white pine plantation on Aug. 31 and Sept 1, 1951.

that the remaining insects had fed. By September 8th, they were all on ground locations within a radius of five feet from the release area and, when recovered, were found to be dead. Movement which had occurred was in a northerly and northwesterly direction towards the exposed stand, an area of greater light intensity.

The second experiment was carried out during the autumn of 1952. On August 17, 26 Co⁶⁰-labelled insects were liberated in a young stand of Norway and white spruce at a point about 30 feet from the edge of the white pine plantation (Fig. 1). Four insects died and were removed. The recovery of the remaining insects is shown in Table XXI.

Table XXI shows that 13 of the original 22 insects or about 59 per cent could not be located. This represents an increase of 43 per cent over that which occurred among the insects released in the white pine plantation the previous autumn. It is suggested that this increase may be partly the result of the food preference of the weevil. Since Norway spruce stands may, on occasion, be heavily attacked by the weevil, the insects were given a choice of white pine and Norway spruce odours in an olfactometer held at approximately 28°C and 60 per cent relative humidity. Tests involving 200 observations gave an index of reaction of 22 ± 8.0 in favour of the white pine odour. When given a choice of Norway spruce odour and odourless air, the results gave an index of reaction of 3 ± 1.0 in favour of the spruce odour. The definite preference of the in-

sect for the white pine odour indicates that the high percentage loss of the tagged insects from the spruce stand occurred as a result of a preference for the adjacent white pine stand. This is substantiated by the movement of the recovered insects. The maximum distance moved by these insects was about 15 feet and this was in the direction of the adjacent white pine stand.

TABLE XXI

Recovery of 22 weevil adults tagged with Co^{60} and liberated on Norway and white spruce trees about 30 feet from an exposed white pine stand.

Date	No. recovered	No. lost
August 17/52	22	0
August 20/52	18	4
September 10/52	17	5
September 30/52	13	9
October 21/52	9	13
October 25/52	9	13

A third experiment was carried out during June, 1954. Seventeen Co^{60} -labelled insects were liberated in a small group of exposed white pine situated near the northwest end of the white pine plantation about 25 feet west of the main body of the stand (Fig. 1). In addition, 60 Co^{60} -labelled adults were liberated in an unweevilled stand of white pine averaging about five feet in height and shaded by an overstory

of red oak 25 to 30 feet in height. The results of the recovery program in the two sites are shown in Tables XXII and XXIII, respectively.

TABLE XXII

Recovery of 17 Co⁶⁰-labelled adults of the white pine weevil liberated in an exposed group of white pine during June, 1954

Date	No. Recovered		No. Lost
	Living	Dead	
1954			
June 15	17	0	0
June 18	13	0	4
June 21	11	0	6
June 24	10	1	6

TABLE XXIII

Recovery of 60 Co⁶⁰-labelled adults of the white pine weevil liberated in a young stand of white pine shaded by a red oak overstory during June, 1954.

Date	No. Recovered		No. Lost
	Living	Dead	
1954			
June 15	60	0	0
June 17	54	0	6
June 21	37	6	17
June 24	21	12	27

It should be mentioned that the recovery program in the shaded stand was terminated rather abruptly by the occurrence of a hail storm about 12 days after the insects were liberated. As a result, most of the foliage canopy was removed and many of the white pine leaders and laterals were broken. Only one insect was found on the trees. Thus, the results in Tables XXII and XXIII show weevil recovery only to the last observation before the storm.

On June 21st, two of the recovered insects in Table XXII were found about 40 feet east of the release area feeding on trees within the main body of the white pine plantation. The remaining insects did not move appreciable distances from the release point. No evidence of predation was observed. It should be pointed out that during the period of observation, the daily temperatures were within the range associated with flight of the weevil.

There was no evidence that any of the 12 dead insects recorded in Table XXIII died as a result of predation. It is assumed that most of the 27 lost insects left the stand of their own volition.

Some marked differences occurred in the rate of loss of the insects through mortality and non-recovery between the exposed and shaded stands during the nine days of observation. The results of these comparisons are shown in Table **XXIV**.

TABLE XXIV

Comparison of percentage mortality and loss of Co⁶⁰-labelled weevils liberated on exposed and shaded white pine trees on June 15th and inspected on June 24, 1954.

Exposure	Number Liberated	Per cent lost	Per cent Mortality
Exposed	17	35.3	5.9
Shaded	60	45.0	20.0

Table XXIV shows that a higher percentage of the insects placed in the shaded stand are lost and a greater percentage die. This is another indication that the environmental conditions within the shaded stands are not as suitable for weevil activity and survival as they are in adjacent exposed white pine stands.

5. THE EFFECT OF SHADE ON THE HABITAT OF THE WEEVIL

It is well known that shaded stands of white pine are less severely attacked by the white pine weevil than open-grown stands, but the reason for the difference in weevil preference has never been investigated fully. Therefore, the present studies included observations on this aspect of the problem. Although these studies are still in progress and are of a relatively long-term nature, marked differences pertinent to weevil behaviour and activity have been obtained between exposed and shaded habitats, particularly during the period of feeding and oviposition of the spring population. The results of these preliminary studies are presented below.

The investigation was begun during the summer of 1956. Observations were confinedⁿ to a study of the differences in habitat climate and tree growth in white pine stands of varying exposure and weevil attack. These included: (1) a heavily weevilled, open-growth plantation of pine; (2) a lightly weevilled stand of natural regeneration pine under a light red oak, Quercus texana Buckley, overstory where leader mortality of the pine has never exceeded about 10 per cent of that which occurs in the open; and (3) an unweevilled stand of natural regeneration pine under a medium red oak overstory. The red oak ranged from 25-40 feet in height. Included in the mixed stands were a few scattered, mature white pine seed trees.

The young pine in the study areas ranged from 15 to 19 years of age. Because of abnormally cool weather during April and early May of 1956, shoot and foliage growth on all trees and first weevil activity were delayed about three weeks. The white pine buds began swelling between May 9-13 in the exposed stand and between May 13-17 in the shaded stands. The amount of height and diameter growth was reduced in proportion to the density of the overstory. Thus, the open-grown trees added the most growth and the pine under the more heavily shaded stand added the least growth (Table XXV).

TABLE XXV

Mean growth of 15-19 year old open-grown and shaded white pine at Chalk River, 1956.

Exposure	No. Trees	1955 Leader Diameter (mms.)★		Leader Length (inches)		
				1955		1954
Open	99	7.33	±.173	12.2	±.398	16.5 ±.418
Light oak overstory	103	4.90	±.102	7.7	±.260	9.9 ±.337
Medium oak overstory	104	3.66	±.123	5.5	±.195	6.2 ±.192

★ Diameter measured one inch from top of leader.

The effectiveness of the overstories as barriers against the penetration of light to the undergrowth pine varied throughout the spring season of weevil feeding and oviposition. The amount of light penetration was obtained by recording the intensity in foot-candles at fixed distances along a line strung through the stands at leader height for a distance of one to two chains. The observations were taken at hourly intervals throughout most of the daylight hours on clear days and have been interpreted in terms of percentages of the maximum available light recorded in the open. Figs. 41A and B show the percentage of maximum available light penetrating to the white pine leaders under the light and medium oak overstories before (May 8), during (June 6), and at the com-

pletion (June 18) of the growth of the foliage canopy. In addition to the large differences in light penetration at different periods of the season there is also a large variation in the amount of light reaching the pine during any one day. The greatest penetration occurs during a period of a few hours around midday, corresponding with the time the sun is near its maximum elevation.

The effectiveness of the different densities of shade in reducing light penetration may be seen by a comparison of parts A and B of Fig. 41. Before the growth of the oak foliage began (May 8th) a maximum of 85 and 75 per cent of the total light available to open-grown pine reached the pine under the light and medium oak overstories, respectively. In addition, the effectiveness of the mature pine seed trees in reducing the amount of light penetration at this time of the season is shown, particularly during early morning (Fig. 41A) and late afternoon (Fig. 41B).

The difference in light penetration through the two oak stands increases progressively with the development of the hardwood foliage. This results from the difference in density of the foliage. Thus, by June 18th, when foliage growth was complete, a maximum of about 55 per cent of the available light penetrated the foliage canopy of the light oak stand whereas a maximum of only about 20 per cent penetrated the dense foliage canopy of the medium oak stand.

Corresponding with the reductions in light penetration in the stands there are also marked changes in the temper-

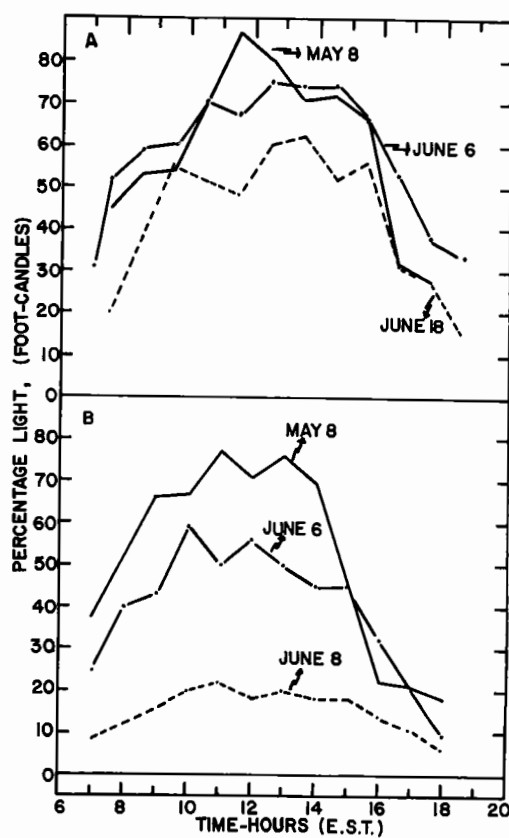


Fig. 41. Percentage of maximum light reaching white pine leaders on three clear days during May and June. White pine growing under: A, light oak overstory; B, medium oak overstory.

atures of weevil feeding and oviposition sites throughout the part of the season that the insects are engaged in these activities. To show these differences, it was first necessary to obtain comparable temperature records on a single selected day (Wellington, 1957). Therefore, a number of black bimetal thermographs were set out at leader height, three in each of the shaded stands and one in the exposed stand. Black bimetal temperatures were chosen because they approximated the daily trend of bark temperature at the feeding and oviposition sites of the weevil more closely than did the ambient air temperature. The relation between the diurnal trend of black bimetal temperature and the actual temperature of the bark, as measured with thermocouples, was determined during cloudless days in each of the stands under observation. The results, as shown in Fig. 42, 43 and 44 were used for correcting black bimetal temperatures to the level of the bark temperature of the leaders. Hence, the diurnal cycles of bark temperature in the three stands could be compared on selected days.

Fig. 45 shows the percentage growth curve of red oak foliage superimposed over the seasonal trend of the mean bark temperature of shaded white pine leaders minus the mean bark temperature of exposed leaders on relatively clear days during a period extending from late April until mid-July. The mean bark temperatures were obtained by averaging the temperatures recorded at 0900, 1300 and 1700 hrs. of clear days. This figure shows the rapid rise in

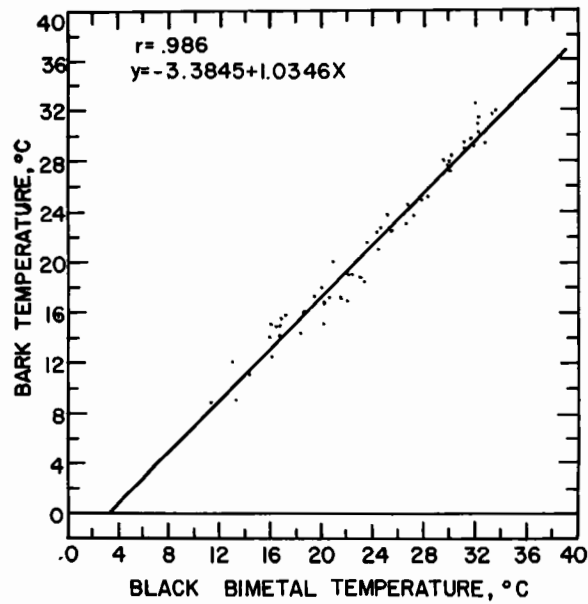


Fig. 42. Clear day relation between bark temperature of the leader and black bimetal temperature under full exposure.

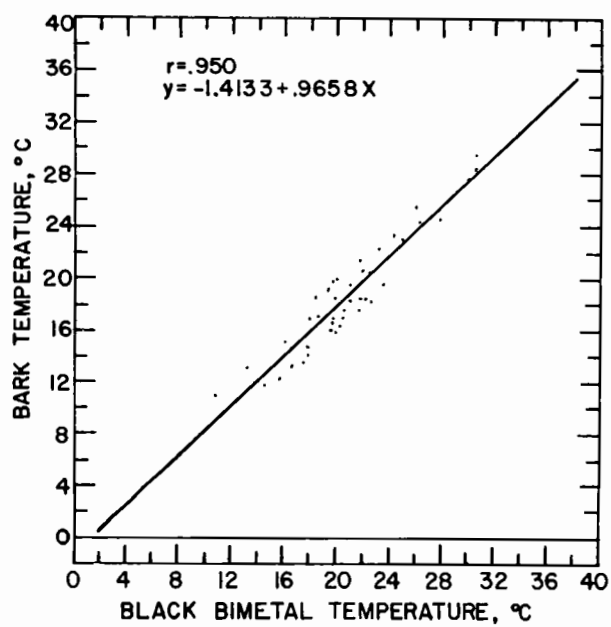


Fig. 43. Clear day relation between bark temperature of leader and black bimetal temperatures under a light red oak canopy.

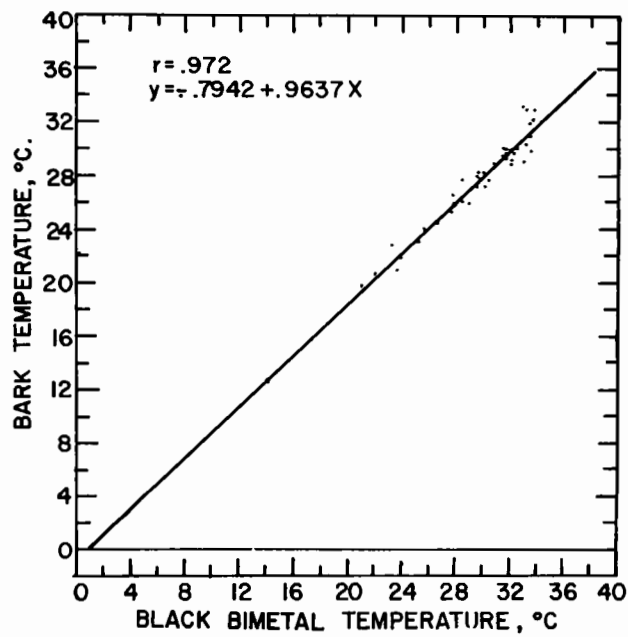


Fig. 44. Clear day relation between bark temperature of leader and black bimetal temperature under a medium red oak canopy.

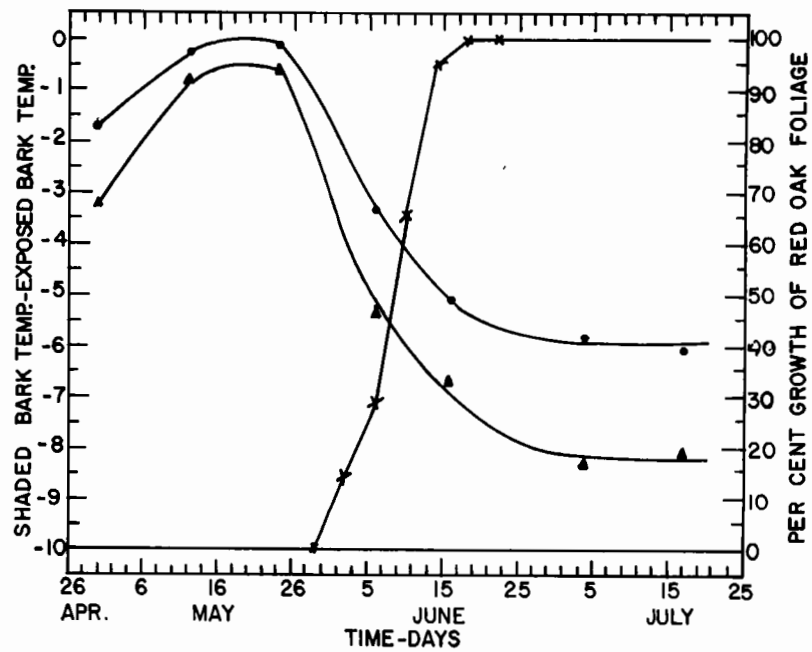


Fig. 45. Growth curve of the foliage of red oak superimposed over the seasonal trend of the mean bark temperature of shaded white pine leaders minus the mean bark temperature of exposed white pine leaders. Triangles: Pw leaders under medium oak canopy; dots: Pw leaders under light oak canopy; crosses: percentage growth of oak foliage.

bark temperature differences associated with the development of the canopy. In addition, there is decrease in the temperature differences occurring up to the period of minimum differences. This may be explained partly on the basis of the sun's elevation at this time of the year and partly on the thawing of the ground under forest conditions. At this time of year, thawing permits increasing back radiation from the ground.

Corresponding with the variation in the daily trend of light penetration through the overstories, there is a daily variation of bark temperature between the exposed and shaded leaders. Minimum differences in both light penetration and bark temperature occur around mid-day, the period of maximum insolation. Thus, prior to oak foliage growth, there is a brief period each clear day when the temperatures of the feeding and oviposition sites are almost equal to that occurring in open-grown stands. However, these temperatures in the shaded habitats persist for only a brief period around mid-day. During early morning and late afternoon the reduction in light penetration (Fig. 41) increases greatly and this corresponds with a decrease in the bark temperature of the shaded leaders (Table XXVI). At no time during the latter part of the season when the hardwood foliage nears complete development are the bark temperatures of exposed and shaded leaders equal (Table XXVI). The daily cycle of the bark temperature of the shaded leaders which occurs is, however, within a range associated with a reduced level of weevil

activity.

The insects emerge from hibernation during the period of minimum temperature differences between the exposed and shaded sites. First emergence corresponds with the initiation of growth of the terminal buds of the pine and the insects normally feed and copulate for about one week before depositing any eggs. Thus, first oviposition of insects coincides with the beginning of the increase in bark temperature differences between the exposed and shaded sites, or near the time of the beginning of hardwood foliage development. This indicates that the most critical period from the standpoint of oviposition attack in the shaded stands occurs during the initial stages of the development of the foliage canopy.

TABLE XXVI

Differences observed between the bark temperature of shaded and exposed white pine leaders about two weeks before the development of the foliage canopy and immediately following the development of the foliage canopy. Temperatures and temperature differences in Centigrade.

Time	No Foliage Canopy			Foliage Canopy Complete		
	1	2	3	1	2	3
0800-1000	16.9	-3.9	-4.6	23.8	-6.5	-6.7
1200-1400	21.2	0.1	-1.7	26.6	-3.1	-4.7
1500-1700	20.0	-2.1	-2.8	27.8	-3.4	-6.7

- Code: 1. Mean bark temp. of fully exposed leader.
 2. Mean bark t. of leader under light oak canopy minus No. 1.
 3. Mean bark t. of leader under average oak canopy minus No. 1.

An increase in atmospheric moisture is associated with the reduction in light and temperature in shaded weevil habitats. Hygrograph records show that during the period of weevil emergence from hibernation, but before the development of the hardwood foliage, the relative humidity in the exposed stands on relatively clear days is only about 5 per cent lower than in the shaded sites. With the development of the foliage canopy the difference in humidity increases to about 15 and 30 per cent in the light and medium oak stands, respectively.

The above results show clearly that the shaded stands are cooler and more moist than exposed stands. The effect that these conditions have on reducing the amount of weevil activity may be shown by interpreting the climatic differences occurring between the exposed and shaded stands in terms of probable weevil feeding, copulation, and oviposition. The equal activity curves shown in Figs. 32 and 34 have been used as the basis for comparison. Two relatively clear days were selected to show these comparisons, one during the early part of the active season of the weevil before the development of the hardwood foliage and one during the latter part of the active season of the weevil at about the time the foliage is fully developed. The results are shown in Table XXVII.

Table XXVII shows that, on the basis of the climate of shaded habitats, the maximum percentage of total ac-

tivity, mainly feeding, and the maximum percentage of oviposition is considerably lower than that occurring in adjacent exposed stands. Minimum differences occur during the early part of the season. The percentage reduction in activity, particularly oviposition, is increased greatly during the season of foliage development. Thus, it appears that white pine stands are not attacked by the weevil when shaded sufficiently to reduce the habitat climate to levels associated with a reduction of 40 to 75 per cent of the oviposition experienced in exposed stands during ideal weather conditions. On the other hand, white pine stands may experience light weevil attack if the habitat climate is reduced to levels limiting oviposition only by 35 to 55 per cent of that experienced by exposed trees during ideal weather conditions.

TABLE XXVII

Estimated reduction in percentage total weevil activity and oviposition at various combinations of leader bark temperature and relative humidity on clear days in shaded white pine stands based on the observed relationships in exposed stands.

Exposure	Reduction in Activity (%)			
	Without Foliage Canopy		With Foliage Canopy	
	Ovi-			
	Total Activity	position	Total Activity	Oviposition
Light oak overstory	25	35	35	55
Medium oak overstory	30	40	35	75

Additional studies were carried out with caged weevils to determine the accuracy of these results. In each of the shaded stands, the upper four or five years' growth of five selected trees were enclosed within a screen cage at the beginning of the season. Five males and five females were liberated in each cage. Control samples of thirty weevils on three similarly caged stems were set up in the exposed stand. At the end of the season these stems were inspected and the amount of damage recorded. The results are shown in Table XXVIII.

Table XXVIII shows that all leaders of the control sample experienced heavy weevil damage and died, whereas the intensity of damage in the shaded stands was greatly reduced. Only one of the leaders situated under the light oak overstory received sufficient attack to succumb. In no case did this occur in the more heavily shaded pine stand. The weevils in the shaded stands were unable to survive the normal life-span of weevils in the exposed stand.

TABLE XXVIII

Weevil damage occurring on white pine at three different levels of exposure during 1956.

Exposure And Tree Number	Leader Diameter (Top-mms)	Leader Length (inches)	Remarks
Exposed			
1	6.0	15.00	Heavy feeding and oviposition on leader. Larval damage, - 13.5 inches. New growth dead.
2	5.5	11.50	As above except that larval damage amounted to 12.0 inches
3	5.4	9.50	As above except that larval damage amounted to 8.0 inches
Light oak shade			
1	6.7	19.50	Heavy feeding and moderate oviposition on leader. Larval damage, - 4.5 inches plus single trails extending 2 inches lower. New growth dead.
2	5.0	14.00	Moderate feeding and light oviposition on leader. Larval damage as a single trail 2.75 inches long. New growth healthy.
3	6.3	16.00	As on No. 2 except that larval damage covered one-half the circumference of the leader for a distance of 2 inches.

TABLE XXVIII(Cont'd)

Weevil damage occurring on white pine at three different levels of exposure during 1956.

Exposure And Tree Number	Leader Diameter (Top-mms)	Leader Length (inches)	Remarks
Light oak shade			
4	3.9	14.75	Light feeding extending over entire length of leader. Moderate feeding and light oviposition at top of 1954 mainstem growth. Larval damage as a single trail 2 inches long. New growth healthy.
5	3.8	10.50	Light feeding and very light oviposition on leader and 1954 mainstem growth. Larval damage as two spots about one-quarter inch long. New growth healthy
Medium oak shade			
1	2.8	7.00	Light scattered feeding on leader and 1954 and 1953 mainstem growth. Oviposition very light and only on the 1953 growth. Larval damage as two spots about one-quarter inch long. New growth healthy.
2	3.9	10.00	Light scattered feeding on leader and 1954 mainstem growth. Very light oviposition on 1954 growth. Larval damage as three spots, one-

TABLE XXVIII (Cont'd)

Weevil damage occurring on white pine at three different levels of exposure during 1956.

Exposure And Tree Number	Leader Diameter (Top-mm)	Leader Length (inches)	Remarks
Medium oak shade			quarter inch long. New growth healthy.
3	3.4	7.00	As on number two except that very little feeding occurred on the leader.
4	2.9	6.25	Very light feeding on leader and 1954 growth. No evidence of oviposition or larval damage. New growth healthy.
5	3.2	11.00	As on tree No. 2.

The above results indicate that weevils may feed and oviposit in stands normally unweevilled, although the amount of damage occurring is greatly reduced. On many of the shaded trees, particularly those of small leader diameter, an abnormal pattern of attack occurred. As indicated by the distribution of the punctures on these stems all oviposition and larval damage which occurred was confined to the 1953 and 1954 mainstem growth. It is suggested that this abnormal pattern of behaviour occurs because the thin leaders present a mechanical barrier to oviposition. It appears therefore, that some other factor is functioning in combination with the habitat climate to render the shaded stands less favourable to weevil survival and development.

In addition to the foregoing studies, experiments were carried out to determine whether the weevil showed any preference for leaders of different lengths and diameters. These tests were conducted under insectary conditions in screened cages designed to hold eight white pine leaders in a vertical position and spaced four inches apart. The stems were cut so that a five-inch stub of older growth protruded below the floors of the cages into water troughs. In this way they could be left undisturbed for one week without excessive drying. The top of each cage was hinged to facilitate leader change and the introduction of the insects. The leaders were changed every seven days and the number of punctures contained in each was used as the criterion of preference. All means were compared by t-test.

In the first experiment, attempts were made to determine weevil preference for long or short leaders of similar diameter. The test was repeated three times, and on each occasion the insects were given a choice of four long and four short leaders alternately spaced in the cage. The results shown in Table XXIX indicate clearly that the weevil shows no preference when given a choice of long thick vs short thick leaders. The high standard errors of the mean number of punctures per leader are due partly to the leaders being removed before some of them were extensively attacked and partly to an unavoidable variation in the number of adults contained in the cage during the tests.

The tests in the second cage were run concurrently with those described above. In this cage, attempts were made to determine the preference of the weevil for leaders of various lengths and diameters. The experiment was repeated four times and on each occasion two each of long thin, long thick, short thin, and short thick leaders were placed alternately in the cage. In addition, during each test, leaders characteristic of each of these types were placed in a different position in the cage. The results shown in Tables XXX and XXXI show the preference of the weevil for short thick vs short thin leaders and short thick vs long thin leaders, respectively. They indicate that the weevil has a decided preference for thick leaders irrespective of their length.

TABLE XXIX
Preference of *P. strobi* adults for short thick vs long
thick white pine leaders.

	Length (inches)		Diameter-Top (mms)		No. of Punctures	
	Short	Long	Short	Long	Short	Long
n	12	12	12	12	12	12
$\bar{x}$	6.96	13.46	6.33	6.39	63.9	65.8
$S_{\bar{x}}$	.465	.560	.185	.235	9.576	12.210
P	<.01		>.50		>.50	

n, number of leaders; $\bar{x}$, mean; $S_{\bar{x}}$, standard error of mean; P, probability

TABLE XXX

Preference of *P. strobi* adults for short thick vs short
thin white pine leaders.

	Length (inches)		Diameter-Top (mms)		No. of Punctures	
	Thick	Thin	Thick	Thin	Thick	Thin
n	8	8	8	8	8	8
$\bar{x}$	6.41	6.72	6.21	2.96	100.25	38.25
$S_{\bar{x}}$	.402	.418	.260	.165	12.104	10.267
P	>.50		<.01		<.01	

n, number of leaders; $\bar{x}$, mean; $S_{\bar{x}}$, standard error of mean;
P, probability

TABLE XXXI

Preference of P. strobil adults for short thick vs long thin white pine leaders.

Length (inches)		Diameter-Top (mms)		No. of Punctures	
Short	Long	Short	Long	Short	Long
n	8	8	8	8	8
$\bar{x}$	6.41	13.34	6.21	3.86	100.25
$S_{\bar{x}}$	.402	.788	.260	.121	12.104
<.01		<.01		<.02	

n, number of leaders; $\bar{x}$, mean; $S_{\bar{x}}$, standard error of mean; P, probability.

It should be pointed out that the pattern of attack on the thin and thick leaders varied in much the same way as it did between the thin and thick leaders in the shaded and exposed stands (Table XXVIII). Thus, many of the punctures on the thin leaders occurred at their base, which was of greater diameter. Hence, the differences in number of punctures per leader shown in Tables XXX and XXXI are masked to a certain extent by changes in the pattern of feeding damage of the weevils. Nevertheless, the results obtained indicate clearly a definite preference of the weevil for the thick more vigorous leaders such as those in open-grown stands rather than the thin, slower growing leaders found in shaded stands.

V DISCUSSION

It is clear from the foregoing results that weather exerts considerable influence on the behaviour, activity, and survival of the white pine weevil. The insect is, however, well adjusted to the environment of its natural habitat and hence does not experience the large fluctuations in numbers common to populations of many other forest insects. Indeed, the very nature of the habitat serves to modify the climate so that the insect is seldom required to contend with extreme fluctuations such as occur in xeric habitats (Green, 1955). Adverse weather conditions ranging above and below the upper and lower limits tolerated by the weevil occasionally occur, but behaviouristic peculiarities pertinent to survival carry the insects in exposed stands to sites of modified climate. As might be expected, adverse weather conditions prolong weevil development and, if they persist for long periods of time, may result in excessive mortality. However, the adult weevil is capable of remaining active over a relatively large range of climatic conditions so that prolonged periods of adverse weather which result in the insect remaining inactive for a sufficient length of time to result in death due to starvation seldom occur. On the other hand, the effects of stand climate on the rate of larval development may result in a high level of larval mortality.

Emergence of adults from infested leaders during late summer occurs over a wide range of temperature extending from 10°C to 36°C with the optimum at about 30°C. Emergence occurs almost always at periods of rising temperature. Adults emerging during the cooler temperatures move up to the top of the dead terminal and remain there until the temperature rises to levels associated with their reversal to photonegative behaviour. At this time they either take flight or move down the tree to cooler areas. This photonegative behaviour which removes the insects from a temperature regime which may prove harmful is in response to a token stimulus (Fraenkel and Gunn, 1940).

A large part of the life of the weevil is spent on or in the tissues of white pine. At moderate temperatures during autumn the photopositive response of starved or fed weevils takes them to the outer more exposed regions of the upper shoots. When these sites are warmed above the reversal temperature of the weevil their subsequent photonegative response takes them down the leader or in towards the mainstem to cooler sites where they may continue feeding. On the other hand, both the feeding and the oviposition of the spring population is restricted to the terminal shoot, and their higher reversal temperatures permit them to remain at this site for a longer period each day. If exposed to moderate

temperatures, they remain on the exposed portion of the leader. When overheated, they respond by movement to shaded, cooler areas of the leader.

It has been shown in this study that weevil adults may move through a temperature range of as much as 13°C from the upper exposed sites to the lower, shaded sites of the habitat. This represents a broad temperature gradient which, from the standpoint of survival, is used to advantage by the weevils when their feeding and oviposition sites become overheated. When overheated at these sites the insects move to shaded, cooler zones of the habitat but, since members of the spring population do not feed and oviposit at the lower regions, their subsequent photopositive behaviour upon cooling consists of attempts to move back to the feeding or oviposition sites. This response is very strong and accounts for the difference which occurs in the direction of movements of groups of adults at any one time.

The wide range in temperatures at which weevil adults reverse their light reactions explains the variation in behaviour sometimes shown by different directions of movement by individuals. Some may be moving to shaded sites while at the same time others are moving to exposed sites. On the basis of the laboratory results, it appears that these adults are reacting in accordance with

weather previously experienced. When they are subjected to lower temperatures, such as occur at night or during cool days, the insects become acclimated to these levels and hence are unable to withstand high temperatures unless these occur gradually. Changing temperature conditions generally are gradual during the season the insects are active (except during frontal movements) and acclimation appears to parallel these changes. Nevertheless, after a change from one extreme of temperature to the other, mixed directions of movement are commonly observed.

The behaviour of the adults during the period when they are moving to the hibernation sites requires some discussion. The initial reaction, that of movement down the trees appears to be a response to temperature gradient alone since the insects are photopositive at all times below their reversal temperature. Thus, movement to the base of the trees during late afternoon serves to place the photopositive insects in the warmest region of their habitat. Upon resumption of activity the following morning, the insects attempt to move back up the tree in accordance with their strong photopositive response at low temperatures and in response to their strong negatively geotactic reaction. However, at this time of the season, the early morning temperature of the ground surface may be as much as 3°C above the temperature of the bark surface at the base of the tree. Consequently, the photopositive re-

sponse of the insects plus their reaction to temperature gradients may serve to take them out from the base of the tree to more exposed ground locations. Thus, the distribution of the insects prior to hibernation during any one season is dependent on the normal response of the insects to light together with their response to temperature. It is suggested that the occurrence of continuous cool weather conditions during the time the insects are reacting in this manner represents a conditioning period during which the insects are prepared for hibernation.

It has been shown that emergence of the weevil from hibernation is closely related to the maximum daily temperature, though the time of the season the insects emerge varies with the exposure of the hibernation site. In the average white pine stand, the location of the hibernation site is dependent upon the weather experienced during the period in which the insects enter hibernation the preceding autumn. It is apparent that this would have to be taken into consideration before accurate predictions could be made of the percentage of a population which have emerged by a given time during the spring.

Recently, Godwin and Bean (1956) observed emergence by means of trapping weevils moving up the stems of selected trees. These data were correlated with daily cumulative degrees above 40°F (4.44°C) between 0600 and 1800 hrs., as measured on a thermograph placed one foot

above the ground. They concluded that at approximately 730 cumulative degrees above 40°F, 50 ± 12 (odds, 19:1) per cent of the weevil population will have emerged from hibernation. From the standpoint of chemical control, this is a very practical approach, but their results, do not really refer to insects emerging from hibernation but only to those moving up the trees. It is suggested that the percentage emergence from hibernation may be considerably higher, depending upon the distribution of the hibernation sites. Exposed sites may be warmed to the level associated with emergence well in advance of shaded sites but the insects which have emerged may be unable to move through the temperature zone occurring at the base of the tree. Hence, they may wander for several days before moving up the trees.

The most critical period in the development of P. strobi occurs during the spring. From the study of the two-dimensional graphs relating the classified types of weevil activity with the various components of the weather, it is apparent that bark temperature of the leader, solar radiation, and relative humidity all influence the amount of activity at any one time. The effect of radiant heating is reflected in the bark temperature-percentage activity curves. Of the remaining two factors, it would be erroneous to assume that accurate predictions of the intensity of activity could be made on the basis of either

factor independent of the other. This has been shown by the studies of the three-dimensional graphs relating temperature and relative humidity with percentage total activity of the weevil and with percentage oviposition. It is immediately apparent that feeding and copulation may commonly occur during weather conditions which are not conducive to oviposition.

Pierce (1916), working with the cotton-boll weevil Anthrenus grandis Boh., was one of the first to show conclusively that definite changes in responses occur outside particular combinations of temperature and humidity. Similar results have been obtained by Shelford (1927) on the codling moth, Carpocapsa pomonella Linne, by Parker (1930) on the grasshoppers, Melanoplus mexicanus mexicanus Saussure and Camnula pellucida Scudder and, more recently, by Edmunds (1952) on black flies. In the present work, it has been shown that relative humidity influences the amount of weevil feeding and oviposition, particularly at or near the optimal temperatures for these activities. It is suggested that the rate of water loss at optimal temperature is of primary importance to the insect and its ability to remain at feeding and oviposition sites.

By reducing the penetration of light to young pine, the shade afforded by a hardwood canopy changes the climate of weevil habitats as well as lowering the growth

rate of the understory pine. It is apparent that the changes in habitat conditions which occur must be viewed in relation to the level of light penetration. As mentioned earlier, the most critical period in the development of the weevil occurs during the spring and early summer. At this time, habitat conditions must be suitable for emergence, feeding, copulation, oviposition, and larval development. These conditions are met in exposed habitats except during very cold, cloudy years, but in many shaded habitats they never favour weevil development and multiplication even in warm sunny years. The reasons for this are discussed in some detail below.

It has been shown that on clear days during the spring, the climate in unweevilled stands of shaded pine limits the amount of oviposition which would occur if the weevils were introduced into the stands. Thus, in stands where the penetration of maximum available light varies from 75 to 20 per cent, the maximum amount of oviposition possible varies from 60 to 25 per cent of that which may occur in open stands. When overstory hardwoods are leafless some oviposition may occur on the pines beneath them, but it is considered negligible since at this time of the season oviposition is slight in even the most favourable sites. Later, when there is more oviposition generally, the shaded stands are less favourable for it. Moreover, they are not suitable for rapid feeding by young larvae,

and so promote pitch-drowning.

In exposed stands a broad temperature regime exists within the habitat that is maintained, particularly during diurnal periods of maximum weevil activity, throughout the season. In shaded stands the temperature variation between the upper and lower levels of the habitat is not broad and is not consistently directional (Sullivan, unpublished data). The shaded habitats appear to receive the least amount of their heat by radiation and the major portion from the surrounding air by conduction and convection.

Another point worthy of mention is the effect of early morning temperatures on weevil activity. Nocturnal resting often occurs at the top of the previous year's leader. Thus, in exposed stands the insects are warmed early by radiant heating and the daily period of activity not only occurs under more favourable conditions, but is increased considerably. In mixed stands, even before the development of the foliage of the overstory, the lack of radiant heating prevents the development of high morning temperatures. In fact, bark temperatures favourable for relatively high weevil activity occur in shaded stands on clear days, only for a brief period about solar noon. This condition is especially pronounced in the more heavily shaded stands where no weevilling occurs.

When weevils are forced to remain in heavily shaded stands, their behaviour is abnormal, with the result that

the damage occurring is negligible. There is a general decrease in feeding activity and oviposition. Much of this reduction may be attributed to unfavourable climate conditions, but the direct affect of leader diameter of the white pine is also important.

Under a stand of more widely spaced oak where the penetration of light on clear days varies from 85 down to 45 per cent of the available maximum throughout the season of weevil activity, the differences in climate and leader diameter are intermediate between the open and heavily shaded stands. These conditions permit greater weevil activity which more closely approaches open-stand levels. Although some of the leaders may be destroyed, the amount of damage is kept to a tolerable level. The damage occurring in such stands appears to depend entirely upon the influx of insects each year from adjacent open stands.

The high percentage of lost Co⁶⁰-labelled insects placed in shaded stands indicates that many leave such stands of their own volition. In addition, there appears to be a considerable amount of travel between shaded and open stands, particularly on relatively clear and warm days that are conducive to high weevil activity. When overheated, the insects may fly into the shaded areas but, they return to the exposed sites when cooled. Consequently, it is suggested that the population in the shaded stands is not large enough nor sufficiently static, nor is its be-

haviour sufficiently normal to result in damage beyond tolerable limits.

If silvicultural control is to work, many points must be considered in addition to providing minimal shading conditions which afford protection from weevil attack. The trees must be allowed to grow rapidly enough to warrant their maintenance in particular areas. Certainly this will depend on such factors as soil type and root competition. However, on the better Petawawa sites where the required condition of shading results in no weevil damage, the trees are sufficiently vigorous to maintain average leader diameters of 3.66 ± 1.26 mms. On similar sites where the shade is somewhat reduced, weevil damage may occur within tolerable limits and the trees are sufficiently vigorous to maintain leader diameters of 4.90 ± 1.04 mms. Thus, in terms of diameter growth, the pine grows at a slower rate but is maintained at a level about 50 to 70 per cent of that occurring in open stands on comparable sites.

It is recognized that the type and density of the overstory is of prime importance in studies of this nature. To date these factors have not been treated in detail. So far, studies have been concerned chiefly with determining the biological requirements of the weevil and comparing them with the physical conditions which occur in unweevilled or lightly weevilled stands of white pine. Thus, it has been shown that weevil development is governed by the cli-

mate and it seems highly probable that the criterion for the establishment of weevil-free stands of pine may be found in the limitations that weather imposes on weevil behaviour and survival. While light penetration appears to be a suitable criterion for establishing the limits of shade required to produce white pine undamaged by the weevil, the results must be interpreted in terms of type and density of overstory for specific sites.

*

VI CONCLUSIONS

1. At room temperature, adults of the spring and autumn populations of P. strobi are photopositive to discrete sources of light. Starvation simply intensifies the reaction until about 48 hours before death. At this time the insects still respond photopositively, but their paths to the light are more irregular and the time they require to reach the light is increased considerably. At 24 hours before death, starved insects of the autumn population do not show a consistent pattern of behaviour. Most of the adults of this population exhibit an extended period of indifference during initial trials, but during subsequent trials they become more strongly photopositive. On the other hand, old adults during the spring are more strongly photopositive during initial trials and maintain this response during subsequent trials. After starvation up to five hours before death, both young and old adults become photonegative.

2. At room temperature, fed young and old adults are positive to diffuse light but become negative when overheated, and this reversal also appears in their field behaviour. The temperature at which they reverse varies with their previous temperature conditioning. The main difference between young and old adults is that the former become negative at lower temperatures.

3. When starved and conditioned to temperatures within

their normal activity range, adults of both the spring and autumn populations become negative at lower temperatures than when they are fed. When conditioned to temperatures below their normal activity range, there is no change in the temperature at which they become negative. Starved adults of the autumn population acclimated at 20 and 0°C become negative at lower temperatures than starved adults of the spring population acclimated to similar temperatures. When conditioned to 12°, there is no difference in the temperature at which either young or old adults become negative.

4. In the field, the occasional absence of an orderly pattern of movement of weevil adults can be explained on the basis of the response of the insects to light and temperature. Thus, the observed reaction of individuals to light and temperature is simply a function of their previous temperature conditioning and amount of feeding.

5. The lower reversal temperatures of the autumn population of weevils does not present a hazard to survival. When overheated at exposed points of the habitat the insects move to shaded cooler points where they may continue to feed. Feeding and oviposition of the spring population is, however, limited to the leader and their higher reversal temperatures permit them to remain at this exposed site for a longer period each day.

6. The yearly increase in leader mortality in young open-

grown white pine stands is more dependent on local increase in population than upon weevil migration, whereas in shaded stands of white pine where leader damage is only 10 per cent of that occurring in the open, the extent of leader mortality is entirely dependent upon annual migrations from the open stands.

7. The ability of white pine leaders to overcome weevil attack is directly related to the amount of larval damage to which they are subjected. Unless the larval population is large enough to encircle the leader, the insects die and the leader survives. The effect of partial damage is reflected in the amount of new growth added by the current year's terminal shoot.

8. The rate of development of the larvae is related to the temperature of the bark. At higher temperatures the insects consume more food and hence move down the stems more rapidly.

9. The greatest portion of the mortality occurring during the development of the white pine weevil occurs during the larval stage. In lightly or weakly attacked leaders the young larvae are generally pitch-drowned shortly after hatching. In heavily attacked leaders, excessive competition between larvae results in excessive mortality but the survivors complete their development if they can feed rapidly enough to avoid drowning.

10. Emergence of the new generation adults from infested leaders is influenced by temperature. Emergence may occur

over an air temperature range of 10 to 36°C, with the optimum temperature at 30°C.

11. During the autumn, no well-defined pattern of feeding occurs, but the adults prefer the leader and exposed parts of the laterals of the upper three whorls of the trees when the weather permits feeding there. The amount of feeding of the adults is influenced chiefly by temperature and the insects are less affected by changes in atmospheric moisture and solar radiation. This is due to the fact that they may continue feeding in shaded points of the habitat where the temperatures are not extreme.

12. The autumn population begins winter hibernation during a period of six to seven consecutive days in which the mean daily temperature does not exceed 5°C. The amount of movement before hibernation and the final selection of exposed or shaded hibernation sites is governed by the reaction of the insects to light and temperature.

13. First emergence of the white pine weevil from hibernation corresponds closely to the time the terminal buds of the white pine begin to swell. The percentage of adults emerging at any one time and the length of the emergence season is dependent upon the exposure and temperature of the hibernation sites.

14. Feeding and oviposition on leaders during the spring follow a very definite pattern which is conducive to successful larval development and a high degree of ter-

minal mortality. These activities first occur on the upper part of the leader and extend downward as the season progresses. More feeding occurs during the early part of the season but, by the end of the spring season of activity, the ratio of oviposition punctures to feeding punctures at all levels along the leader is 1:1. In addition, punctures containing eggs are capped while those without eggs are left exposed.

15. During the spring, maximum weevil activity occurs on relatively clear, warm days which are characterized by bark temperatures of 26 to 31.5°C and relative humidities of 20 to 72 per cent. At lower temperatures, the amount of activity decreases but remains relatively constant over the greater part of the normal range of relative humidity. At bark temperatures above the optimum level, the amount of activity drops rapidly and is zero at bark temperatures of 35°C and above.

16. Of the classified types of activity, oviposition occurs within much narrower limits of temperature and relative humidity. Maximum oviposition occurs at leader bark temperatures of 25 to 29°C in conjunction with relative humidities of 20 to 55 per cent. At lower temperatures and higher humidities the amount of oviposition is reduced much more sharply than are feeding and copulation. Consequently, considerable feeding may occur during weather not conducive to oviposition.

17. There is no definite flight period. Flight may occur at any time during the spring and autumn when bark temperatures of the leaders exceed about 16°C. Optimum conditions for flight occur on relatively clear warm days when the bark temperature exceeds about 25°C. At higher temperatures, the insects normally fly to cooler sites. This flight may simply take them to near-by trees or they may fly into adjacent shaded stands of pine. When cooled, however, they return to the more exposed sites.

18. When placed in unweevilled shaded stands of pine a greater number of the insects are lost and it is concluded that at least a portion of them move out to exposed stands. When placed in stands which are partly shaded for only a portion of each day, the insects move to the fully exposed sectors of the stand.

19. White pine in mixture with red oak is not subjected to weevil attack when the penetration of light near solar noon on clear days is reduced from about 75 to 20 per cent of the maximum light occurring in the open. Stands shaded by less dense red oak overstories may be lightly weevilled when the overstory density serves only to reduce the penetration of available light near solar noon on clear days from 85 to 45 per cent. The amount of weevilling which occurs is, however, within tolerable limits.

20. There are at least two reasons for the reduction in weevil attack and abundance in shaded stands.

(A) The climate of the shaded habitat is greatly reduced so that even during ideal conditions in the open, the climate of comparable shaded habitats permits only minimal adult and larval activity.

(B) Added to this is the effect of the reduction in leader vigour of the shaded trees which results in an abnormal pattern of weevil oviposition that is not conducive to successful development of the larvae.

21. The change in habitat climate and the change in behaviour associated with the reduction in leader vigour result in conditions which cause greater mortality among the existing population of adults and greatly reduce the chances of survival of any larvae which may be produced.

VII CLAIM OF CONTRIBUTION TO KNOWLEDGE

Evidence has been presented indicating that weather influences the activity, behaviour, and survival of the white pine weevil, Pissodes strobi Peck. By applying quantitative methods in the field, the influence of climate on the weevil has been shown as a series of curves which can be used to predict the extent of activity during specified weather.

The results of preliminary studies have shown that the criterion for the establishment and growth of white pine stands free of weevil attack may be found in the limitations that weather and the attributes of the pine trees impose on weevil behaviour and survival.

It has been shown by studies of the light reactions of weevil adults that their observed behaviour in the field which enables them to avoid extremes in climate is a response to light and temperature.

VIII REFERENCES

Anonymous

1952. The petewawa Forest Experiment Station. Can. Dept. Resources and Development, For. Res. Div. Misc. Publ. 3: 3 - 27.

Barnes, T. C.

1928. Enquiry concerning the natural history of the white pine weevil (Pissodes strobi). IV Int. Cong. Ent. 2: 412 - 413.

Belyea, H. C.

1923. Control of the white pine weevil (Pissodes strobi) by mixed planting. J. For. 21: 284 - 390.

Belyea, H. C. and MacAloney, H. J.

1926. Weather injury to terminal buds of Scotch pine and other conifers. J. For. 4: 685 - 691.

Belyea, R. M. and Sullivan, C.R.

1956. The white pine weevil: a review of current knowledge. For Chron. 32: 58 - 67.

Bentley, E. W.

1944. The biology and behaviour of Ptinus tectus Boie (Coleoptera, Ptinidae), a pest of stored products. J. Exp. Biol. 20: 152 - 158.

Blackman, M. W.

1919. Report on the white pine weevil. Maine For. Dept. pp. 3 - 12.

Blackman, M. W. and Ellis, W. O.

1916. Some insect enemies of shade trees and ornamental shrubs. Bull. N. Y. State Coll. For. 26: 1 - 123.

Britton, W. E.

1920. The white pine weevil.
Conn. Agr. Exp. Sta. Bull. 218: 144 - 155.

Britton, W. E. and Walden, B. H.

1912. Record of preliminary tests to prevent damage by the white pine weevil.
Conn. Agr. Exp. Sta. Ann. Rept. 35: 307 - 309.

Champion, G.C.

1902. Biologia Centrali-Americana, Insecta. Coleoptera.
Vol. 4: 119 - 120.

Cline, A.C. and MacAloney, H.J.

1931. A method of reclaiming severely weeviled white pine plantations.
Mass. For. Assoc. Bull. 152: 3 - 11.

1933. Additional notes on the improvement of weeviled white pine plantations.
Con. Forest and Park Assoc. Pub. 24: 1 - 11.

1935. Progress report of the reclamation of severely weeviled white pine Plantations.
J. For. 33: (11).

Connola, D.P., McIntyre, T. and C.J. Yops.

1955. White pine weevil control by aircraft spraying.
J. For. 53: 889 - 891.

Colville, P.

1923. A few hypotheses on white pine losses from weevil damage.
Amer. Forester 11: 72 - 80.

Crosby, D.

1950. Concentrated lead arsenate spray for control of white pine weevil.
J. For. 48: 334 - 336.

Currie, R.P.

1905. The white-pine weevil.
U.S.D.A. Bur. Ent. Bull. 53: 91.

Dethier, V.G.

1956. A physiological basis for communicative dancing by insects.
Paper presented at Xth. Int. Cong. Ent. Montreal, Canada, Aug. 17-25.

Dietrich, H.

1931. Synonymy and notes on the Pissodes weevil attacking Cedrus deodara.
J. Econ. Ent. 24: 872 - 874.

Dolley, W.L. and White, J.D.

1951. The effect of illuminance on the reversal temperature in the drone fly, Eristalis tenax.
Biol. Bull. 100: 84 - 89.

Edmunds, A.G.

1952. The relation between black fly activity and meteorological conditions. (Simuliidae, Diptera).
M.A. Thesis. University of Toronto.

Felt, E.P.

1913. White pine weevil.
29th. Rept. N.Y. State Entomol. pp. 30 - 33.

Fisher, R.T.

1928. Soil changes and silviculture on the Harvard Forest.
Ecology 9: 6 - 11.

Fisher, R.T. and Terry, E.I.

1920. The management of second growth white pine in central New England.
J. For. 18: 358 - 366.

Fitch, A.

1858. Fourth report of the noxious and other insects of the state of New York. pp. 732 - 738.

Forbush, E.H.

1913. Useful birds and their protection. Mass. State Bd., Agr., Boston. pp. 168, 254 - 256.

Fraenkel, G. and Gunn, D.L.

1940. The orientation of animals: kineses, taxes, and compass reactions. Oxford University Press, London.

Godwin, P.A. and Bean, J.L.

1956. Predicting emergence of the white-pine weevil from hibernation. For. Sci. 1: 187 - 189.

Graham, S.A.

1916. Notes on the control of the white pine weevil. J. Econ. Ent. 9 : 549 - 551.

1918. The white-pine weevil and its relation to second growth white pine. J. For. 16: 192 - 202.

1926. Biology and control of the white pine weevil, Pissodes strobi Peck. Cornell Univ. Agric. Exp. Sta. Bull. 449: 1 - 32.

Green, G.W.

1954. Some laboratory investigations of the light reactions of larvae of Neodiprion americanus banksianae Roh. and N. lecontei (Fitch) (Hymenoptera: Diprionidae). Canad. Entomol. 86: 207 - 222.

Green, G.W.

1955. Temperature relations of ant-lion larvae.
(Neuroptera: Myrmeleontidae).
Canad. Entomol. 87: 441 - 459.

Halliday, W.E.D.

1937. A forest classification for Canada.
Canada, Dept. Mines and Resources, For. Ser.
Bull. 89. (Revised, 1949).

Harris, T.W.

1862. A treatise on some of the insects injurious
to vegetation.
William White, Boston. pp. 1 - 640.

Holst, M.J.

1955. Breeding for weevil resistance in Norway spruce.
Zeitschrift fur Forstgenetik und
Forstpflanzenzuchtung 4: 33 - 37.

Hopkins, A.D.

1906. Insect enemies of forest reproduction.
U.S.D.A. Yearbook, 1905: 249 - 256.

-
1907. The white pine weevil.
U.S.D.A. Bur. Ent. Circ. 90: 1 - 8.

-
1911. Contributions towards a monograph of the
bark-beetles of the genus Pissodes.
U.S.D.A. Bur. Ent., Tech. Ser. 20: 1 - 68.

Hopping, R.

1920. A new species of the genus Pissodes.
Canad. Entomol. 52: 132 - 134.

Hosley, N.W.

1928. Red Squirrel damage to coniferous plantations
and its relation to changing food habits.
Ecology 9: 43 - 49.

Jack, R.W. and Williams, W.L.

1937. The effect of temperature on the reaction of Glossina marsitans Westw., to light.
Bull. Ent. Res. 28: 499 - 503.

MacAloney, H.J.

1926. The white pine weevil problem in the New England States.
For. Prot. Conf., N.Y. State Coll. For. pp. 31 - 43.

1930. The white-pine weevil (Pissodes strobi Peck.)
Its biology and control.
N.Y. State Coll. For. Bull. 3: 5 - 87.

- 1930a. Weather conditions a factor in white pine weevil injury.
For. Worker 6: 18.

1932. The white pine weevil.
U.S.D.A. Circ. 221: 1 - 30.

Maughan, W.

1930. Control of the white pine weevil on the Eli Whitney forest.
Yale Univ., School For. Bull. 29: 1 - 37.

Menusan, H.

1935. Effect of constant light, temperature and humidity on the rate and total amount of oviposition of the bean weevil, Bruchus obtectus Say.
J. Econ. Ent. 28: 448 - 453.

Miller, J.M.

1950. Resistance of pine hybrids to the pine reproduction weevil.
U.S.D.A., Calif. For. Range Exp. Sta., For. Res. Notes 68: 1 - 17.

Packard, A.S.

1881. Insects injurious to forest and shade trees.
U.S. Ent. Comm. Bull. 7, pp. 185-188, 236
241.

1885. The white pine weevil and its injury to shade
and forest trees.
Rept. Comm. Agric. pp. 322 - 325.

1890. The white pine weevil.
U.S. Ent. Comm. Rept. No. 5. pp. 734-741,
829-830, 861, 872.

Parker, J.R.

1930. Some effects of temperature and moisture up-
on Melanoplus mexicanus mexicanus Saussure,
and Camnula pellucida Scudder (Orthoptera).
Montana Agr. Exp. Sta. Bull. 223: 1 - 132.

Peck, W.D.

1817. On the insects which destroy the young
branches of the pear tree, and the leading
shoot of the weymouth-pine.
Mass. Agr. Jour. 4: 205 - 211.

Peirson, H.B.

1922. Control of the white pine weevil by forest
management.
Harvard For. Bull. 5: 1 - 42.

Pierce, W.D.

1916. A new interpretation of the relationships
of temperature and humidity to insect devel-
opment.
J. Agr. Res. 5: 1183 - 1191.

Plummer, C.C. and Pillsbury, A.E.

1929. The white pine weevil in New Hampshire.
N.H. Exp. Sta. Bull. 247: 3-31.

Potts, S.F., Cline, A.C. and H.L. McIntyre

1942. The white pine weevil and its control by the application of concentrated sprays.
J. For. 40: 405 - 410.

Prebble, M.L.

1951. Unpublished Report, Forest Insect Laboratory, Sault Ste. Marie, Ontario.

Richards, O.W.

1951. The reaction to light and its inheritance in grain weevils, Calandra granaria (L.) (Coleoptera: Curculionidae).
Proc. Zool. Soc. London 121: 311 - 314.

Saunders, W.

1884. Insects injurious to white pine (Pinus strobus).
14th Rept. Ent. Soc. Ont. p. 55.

Shelford, V.E.

1927. An experimental investigation of the relations of the codling moth to weather and climate.
Bull. Ill. Nat. Hist. Survey 16: 397 - 440.

Shenefelt, R.D.

1951. A further note on the control of the white pine weevil.
J. For. 49: 575 - 576.

Snedecor, G.W.

1950. Statistical methods.
Iowa State Coll. Press. 4th ed.

Spurr, S.H. and Friend, R.B.

1941. Compression wood in weeviled northern white pine.
J. For. 39: 1005 - 1006.

Steiner, G.

1930. Neodiplogaster pinicola, N.sp., a nema associated with the white pine weevil in

terminal shoots of the white pine.
J. Agr. Res. 41: 125 - 130.

Sullivan, C.R.

1953. Use of radioactive cobalt in tracing the movements of the white-pine weevil, Pissodes strobi Peck.
(Coleoptera: Curculioidae).
Canad. Entomol. 85: 273 - 276.

Sullivan, C.R. and Simpson, S.D.

1957. Longevity of the white pine weevil, Pissodes strobi Peck, tagged with radioactive cobalt.
(In preparation).

Sullivan, C.R. and Wellington, W.G.

1953. The light reactions of larvae of the tent caterpillars, Malacosoma disstria Hbn., M. americanum (Fab.) and M. pluviale (Dyar).
(Lepidoptera: Lasiocampidae)
Canad. Entomol. 85: 297 - 310.

Taylor, R.L.

1928. The Arthropod fauna of coniferous leaders weeviled by Pissodes strobi (Peck).
Psyche 35: 217 - 225.

- 1928a. A new species of Lonchaea Fallen (Lonchaeidae: Diptera).
Bull. Bklyn. Ent. Soc. 23: 191 - 194.

1929. The biology of the white pine weevil, Pissodes strobi (Peck), and a study of its insect parasites from an economic viewpoint.
Ent. Amer. 9: 167 - 246.

Taylor, R.L.

1930. The biology of the white pine weevil, Pissodes strobi (Peck), and a study of its insect parasites from an economic viewpoint. Ent. Amer. 10: 1 - 86.

Walden, B.H.

1915. Experiments in controlling the white pine weevil.
Conn. Agr. Exp. Sta. Ann. Rept. 38: 173 - 176.

1916. Experiments in controlling the white pine weevil in 1915.
Conn. Agr. Exp. Sta. Ann. Rept. 39: 134 - 136.

Walker, E.M.

1912. Some injurious insects of De Grassi Point, Lake Simcoe.
Rept. to Ent. Soc. Ont. p 58.

Watson, E.B.

1935. Preliminary notes on the white pine weevil situation in the Petawawa Forest Reserve, Ontario.
66th Rept. Ent. Soc. Ont. pp. 7 - 8.

Wellington, W.G.

1948. The light reactions of the spruce budworm, Choristoneura fumiferana Clemens. (Lepidoptera: Tortricidae).
Canad. Entomol. 80: 56 - 82A.

1950. Effects of radiation on the temperatures of insectan habitats.
Sci. Agr. 30: 209 - 234.

1957. The synoptic approach to studies of insects and climate.
Ann. Rev. Ent. 2: 143 - 162.

Wellington, W.G., Sullivan, C.R. and G.W. Green

1951. Polarized light and body temperature level as orientation factors in the light reactions of some hymenopterous and lepidopterous larvae. *Canad. J. Zool.* 29: 339 - 351.

Wellington, W.G., Sullivan, C.R. and W.R. Henson

1954. The light reactions of larvae of the spotless fall webworm, Hyphantria textor Harr. (Lepidoptera: Arctiidae). *Canad. Entomol.* 86: 529 - 542.

West, A. S.

1947. The effect of the white pine weevil on plantations on the University of New Brunswick forest. *For. Chron.* 23: 291 - 296.