NON-MORPHOLOGICAL SEPARATION OF A CONOPHTHORUS POPULATION FOUND ON JACK PINE FROM CONOPHTHORUS RESINOSAE HOPKINS, WITH DESCRIPTION OF A NEW SPECIES, CONOPHTHORUS BANKSIANAE (COLEOPTERA: SCOLYTIDAE)

Thesis for the Degree of Ph. D.
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This is to certify that the

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NON-MORPHOLOGICAL SEPARATION OF A CONOPHTHORUS POPULATION FOUND ON JACK PINE FROM CONOPHTHORUS RESINOSAE HOPKINS, WITH DESCRIPTION OF A NEW SPECIES, CONOPHTHORUS BANKSIANAE (COLEOPTERA: SCOLYTIDAE)

presented by

John E. McPherson

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ABSTRACT

NON-MORPHOLOGICAL SEPARATION OF A CONOPHTHORUS POPULATION FOUND ON JACK PINE FROM CONOPHTHORUS RESINOSAE HOPKINS, WITH DESCRIPTION OF A NEW SPECIES, CONOPHTHORUS BANKSIANAE (COLEOPTERA:SCOLYTIDAE)

By

John E. McPherson

Two populations of Conophthorus which are anatomically inseparable occur in Michigan on red and jack pine. The red pine population is known as Conophthorus resinosae Hopkins, the red pine cone beetle. It attacks and reproduces primarily in red pine cones and to a much lesser extent, shoot tips. The jack pine population attacks and reproduces primarily in shoots tips and has been reported to rarely attack cones of jack pine. The problem was to determine if the two populations were different species.

Several studies based on known behavioral differences were designed to further clarify the taxonomic status of the jack pine population. The main studies were of the life cycles of both populations, reciprocal host transfers and resin toxicity tolerances.

The life cycles of the two populations are different. Conophthorus resinosae begins reproduction earlier in the year, and its immature stages are present for a shorter time than the jack pine population. Conophthorus resinosae can attack and reproduce in cones and shoot tips

of jack pine but the jack pine population can not reproduce in cones or tips of vigorous, cone-producing red pine. Conophthorus resinosae can tolerate jack pine resin, but the jack pine population can not tolerate red pine resin.

It is concluded that the jack pine population is a different species and is described as the new species, Conophthorus banksianae.

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INTRODUCTION

The attack of pines by the North American genus *Conophthorus* Hopkins (cone or tip beetles) has been known since about 1884 (Harrington, 1902), and individuals probably were first collected around 1850 (Hopkins, 1915). Harrington found them feeding on red and white pine near Ottawa, Ontario, primarily on the cones but also on the tips, and referred to them as *Dryocoetes affaber* Mannerheim. Hamilton (1893) felt that specimens he had collected from white pine cones at Sparrow Lake, Ontario, might be a new species and possibly a new genus because of differences in the antennal club, tibiae, elytral striation and punctation. Schwarz (1895) thought that similar specimens he had examined from white pine belonged in the genus *Pityophthorus* and had referred to them as *P. coniperda*. Hopkins (1915) concluded that specimens received from Hamilton differed enough from other species to justify the erection of the new genus *Conophthorus*, and he described *Conophthorus resinosae* as a new species from red pine in the same publication.

Pinus resinosa Aiton (red pine), *P. banksiana* Lambert (jack pine), *P. sylvestris* Linnaeus (Scotch pine), *P. strobus* Linnaeus (eastern white pine) and *P. ponderosa* Lawson (ponderosa pine) are attacked by *Conophthorus* in Michigan. When this study was begun there were two species of *Conophthorus* known to occur in Michigan, *C. resinosae* (red pine cone beetle) and *C. coniperda* (white pine cone beetle).

Lyons (1956) determined the life history of *C. resinosae* in central Ontario and found that it primarily attacked second-year cones and current year's shoots of red pine. Herdy and Thomas (1961) studied the life history of a *Conophthorus* population in northwestern Ontario found on jack pine. They stated that this population (hereafter referred to as jack pine tip beetle) relied primarily on jack pine shoots and rarely attacked cones. Both the red pine cone beetle and jack pine tip beetle overwinter on the ground in fallen tips.

Herdy (1963, unpublished) found that the red pine cone beetle could not be reliably separated on the basis of external anatomical features from the jack pine tip beetle. However, he noted that there were differences in their behavior. The most outstanding difference was that the red pine cone beetle attacked cones and shoots, producing broods in both. The jack pine tip beetle primarily attacked tips. Over a two year period, Herdy and Thomas (1961) recorded attacks in only 7 cones; progeny were produced in at least one (Herdy, 1963 unpublished). Consequently, Herdy felt that because of these differences more research should be conducted on the ecological aspects of these two groups to help determine if they were two different species. The purpose of this research was to further clarify the taxonomic status of these two populations through studies on the above noted behavioral differences.

The project consisted of three primary studies: 1) to determine the life cycles of five beetle populations on jack, red, Scotch and ponderosa pines, and on red adjacent to jack pine, 2) to study the behavior and reproductive success of jack and red pine beetle populations forced to remain, with sleeve cages, on reciprocal hosts and

3) to determine the tolerance of jack and red pine beetles to reciprocal resins. The investigation was conducted from 1966 to 1968.

STUDY AREAS

The red pine cone beetle life cycle was studied in a windbreak strip of 20 to 25 year old cone-producing red pine in Wexford County near Cadillac, Michigan (T23N R10W Sec 36).

A red-jack pine plantation in Grand Traverse County near Fife Lake, Michigan (T26N R9W Sec 26) was used for the life cycle studies of the jack pine tip beetle population and the population on red pine adjacent to jack pine. The jack pine was approximately 19 years old and producing cones; the red pine was approximately 14 years old and not producing cones. The red and jack pine were planted in alternating strips, 30 rows per strip.

The life cycle of the population on Scotch pine was studied in a plantation in Wexford County near Cadillac (T22N R9W Sec 17). The Scotch pine was about 12 years old and producing cones.

The life cycle of the population on ponderosa pine was studied in a plantation in Kalkaska County near Fife Lake (T26N R8W Sec 30). These coneless trees were about 12 years old.

In the experiments involving the transfer of beetles to reciprocal hosts (jack and red pine), the jack pine in the plantation near Fife Lake mentioned above, and a red pine plantation in Wexford County near Hoxeyville, Michigan (T21N R12W Sec 36) were used. This red pine plantation consisted of cone-producing trees about 25 years old.

All plantations used for the life history studies are within 25 miles of each other; the majority of the data was collected in 1967. When the Hoxeyville red pines are included, plantations are within 50 miles of each other.

LIFE HISTORY AND HABITS

Methods and Materials

Infested tips and cones were collected at least once a week. They were carefully dissected in the laboratory and if necessary, examined under a microscope. The sex of the adults and the numbers and instars of individuals found per tip or cone were recorded. Notes were taken on the pattern and length of the primary tunnel and any modifications of it (e.g., lateral niches, plugs at entrance hole). The adults and larvae were preserved in 95% ethyl alcohol and the eggs and pupae in 65% ethyl alcohol; these specimens were used for measurements of the life stages.

When few or no specimens were found in the cone or tip samples for any one week, a second trip was made for additional samples. The size of the samples was necessarily small for four of the beetle populations, 10 or less attacked tips or cones per week, because the populations were small. The only exception was the jack pine tip beetle population which was larger and consequently, samples varied between 25 and 40 infested tips collected per week.

Measurements were made with a binocular microscope and a calibrated ocular micrometer. Measurements taken were the widths of the larvae taken across the dorsum of the head capsule and the lengths and widths of the eggs, pupae and adults. The lengths of the pupae and adults were from the anterior dorsal margin of the prothorax to the tip of the elytra; the widths were measured across the dorsum of the prothorax.

General Life History

The life cycles of the populations on ponderosa, Scotch, jack, red, and red growing by jack pine were found to have many similarities. In April-May, the adults emerge and begin to attack tips (red pine cone beetles also attack cones). The early attacks seem to be for feeding purposes since no progeny are found at this time.

The beetle enters the tip within an inch of the bud apex perpendicularly to the longitudinal axis of the shoot and burrows to the center (Figure 1). There it turns toward the bud apex and burrows along the central axis of the shoot up to but not into the bud.

The beetle enters the cone near the base and burrows to the central axis. It then turns toward the tip of the cone and burrows along the axis for a short distance, leaving the apical part of the cone undamaged.

Attacked tips and cones are relatively easy to detect. The beetle, while engaged in burrowing activity, deposits much of the excavated material, mixed with resin, at the entrance hole in the form of a cylindrical pitch tube (Figure 1). When first deposited this material is orange but turns gray in a few hours. After two to three weeks the attacked tips and cones are very noticeable because the tips are brown and stunted, and the cones are smaller than healthy ones, brown, and shriveled (Figure 2).

Figure 1. Entrance hole and pitch tube of jack pine tip beetle in jack pine tip.

Figure 2. Two red pine cones (above) damaged by Conophthorus resinosae and one healthy cone (below) (note pitch tube at base of right attacked cone).

Reproduction begins in new growth in mid-June to early July. It has been stated (Lyons, 1956; Schaefer, 1962) that in some species the female does the excavating of the tip or cone. My own observations support this. During the reproductive period, a short enlargement of the tunnel just inside the entrance hole is found. Copulation may occur here (Lyons, 1956).

In preparing for oviposition, the female burrows along the central cone or tip axis as before, but in addition she constructs lateral niches along the primary tunnel (Figure 3); a maximum of five and six niches was found in tips and cones respectively. In each niche she deposits one egg and covers it with boring material. The eggs are translucent, white and ovoid. Just before leaving the tip or cone, she plugs the tunnel with resinous material just inside the entrance hole.

The larvae, upon hatching, feed in the buds or cones until pupation. The larvae are apodus, C-shaped, white, with a light-brown head capsule. Pupation also occurs in the tips or cones. Young pupae are white, but as they mature they first begin to darken on the eyes, mouthparts and tips of the elytra.

Adult beetles live one year, apparently dying during July and early August. The adults are black, cylindrical, and have the head withdrawn into the thorax. The new adults feed until September when they prepare for overwintering by boring into new tips; even the red pine cone beetles bore into tips after leaving the brood cones.

The overwintering tips are readily distinguishable from those used for reproduction and feeding activities because the buds are completely hollowed out. Because of this damage, the tips weaken, die

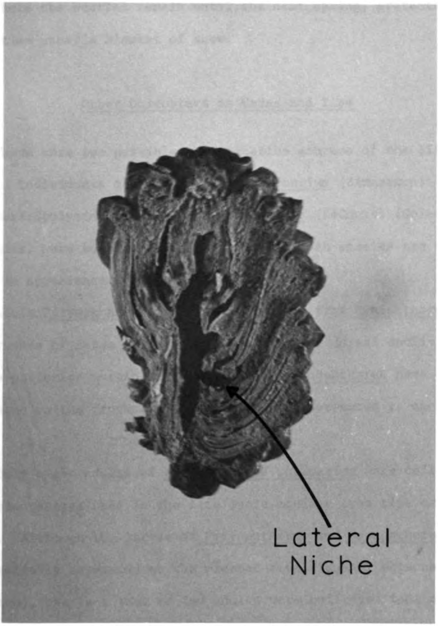

Figure 3. Primary tunnel and lateral niche constructed by red pine cone beetle in red pine cone.

and break off at or just below the base of the bud. They fall to the ground where the beetles remain until the next spring, protected much of this time under a blanket of snow.

Other Coleoptera in Cones and Tips

There were two possible contamination sources of the life cycle results. Individuals of *Pityophthorus pulicarius* (Zimmerman) (Coleoptera:Scolytidae) and *Cimberis elongatus* (LeConte) (Coleoptera: Anthribidae) were both collected. Larvae of both species are very similar in appearance to *Conophthorus* sp.

Adult *Pityophthorus* are distinguishable from *Conophthorus* by the dense brushes of setae on the frons and a slight dorsal declivity toward the posterior margin of the pronotum. *Conophthorus* have much fewer setae on the frons and the dorsum of the pronotum is much more convex.

Only eight adults of *Pityophthorus pulicarius* were collected in all plantations used in the life cycle studies from tips or cones in 1967. Although the larvae of *Pityophthorus* and *Conophthorus* can not be reliably separated at the present time (Thomas, personal communication), the fact that so few adults were collected indicates that this source of contamination was small. In addition, the data from tips or cones with adult *P. pulicarius* in them were not used.

Larvae of *Cimberis elongatus*, which are in buds during part of their development, have a black eyespot, a dark orange-brown head capsule and many setae on the head and body. *Conophthorus* larvae have no eyespot, fewer and more inconspicuous setae on the head and body, and have an amber-colored head capsule (Thomas and Herdy, 1961). Only seven larvae were collected during the study and only from jack pine.

Jack Pine Tip Beetle Life History

The jack pine tip beetle population was studied in a red-jack pine plantation near Fife Lake (p. 4). Measurements of the life stages of this population are given in Table 1. Larval head capsule width frequency shows that there are two instars (Figure 4).

TABLE 1. Measurements of life stages of the jack pine tip beetle population in mm.

Life stage	No. of specimens	Mean length	Stand. error	Range	Mean width	Stand. error	Range
Adult ♂	18	2.724[a]	.034	2.464-2.940	1.092[b]	.017	.924-1.204
Adult ♀	30	2.867[a]	.028	2.576-3.164	1.142[b]	.017	.924-1.288
Pupa	6	2.904[a]	.143	2.436-3.472	1.050[b]	.045	.840-1.148
Larva II	30				.487[c]	.006	.448-.532
Larva I	25				.342[c]	.003	.308-.364
Egg	12	.795	.022	.616-.896	.560	.022	.420-.700

[a]Anterior dorsal margin of prothorax to tip of elytra.

[b]Across dorsum of prothorax.

[c]Across dorsum of head capsule.

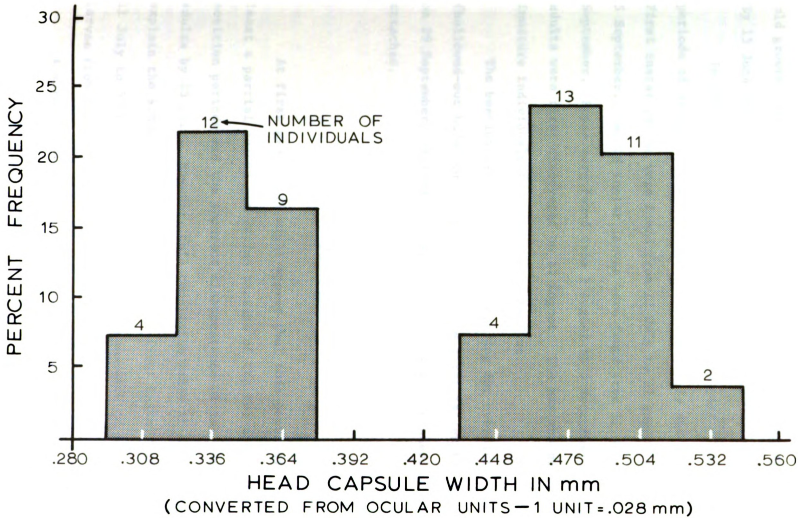

Figure 4. Head width frequency distribution of Conophthorus sp. from jack pine tips showing two larval instars (based on 55 larvae).

Active beetles were first observed on 18 May 1967 (Table 2) in old growth. By 30 May the attacked tips were beginning to turn brown. By 15 June the beetles had begun to attack new growth.

In 1967, reproduction began in the early part of July. Two periods of oviposition were detected, 2 to 11 July and 15 to 22 August. First instar larvae were found from 11 July to 22 August and again on 5 September. Second instar larvae were found from 11 July to 11 September. Pupae were found from 1 August to 5 September and callow adults were first discovered on 15 August. The maximum number of immature individuals found in a tip was five.

The beetles were first noted preparing for overwintering (hollowed-out buds) on 5 September and the first fallen tip was found on 29 September. Fallen tips are brown and with the needles still attached.

Discussion

At first glance, it might appear that this population has at least a partial second generation because of the two apparent oviposition periods and the apparent disappearance of the overwintered adults by 25 July. However, this conclusion makes it difficult to explain the almost constant appearance of first instar larvae from 11 July to 5 September and the constant appearance of second instar larvae from 11 July to 11 September.

A more plausible explanation is that, because of the small sample sizes from 18 July to 8 August, the eggs were missed as well

TABLE 2. Number of individuals of each life stage per sampling date of jack pine tip beetle

Sample dates	Eggs	Larvae I	Larvae II	Pupae	Adults	Total individuals
May 18	-	-	-	-	3	3
May 25	-	-	-	-	7	7
June 2	-	-	-	-	9	9
June 6	-	-	-	-	6	6
June 15	-	-	-	-	9	9
June 23	-	-	-	-	4	4
June 29	-	-	-	-	1	1
July 2	2	-	-	-	2	4
July 11	2	7	1	-	1	11
July 18	-	2	1	-	1	4
July 25	-	4	2	-	-	6
Aug. 1	-	2	4	2	-	8
Aug. 8	-	1	4	2	-	7
Aug. 15	2	3	12	4	1	22
Aug. 22	3	4	4	5	5	21
Aug. 29	-	-	4	2	2	8
Sept. 5	-	1	4	3	5	13
Sept. 11	-	-	3	-	2	5
Sept. 29	-	-	-	-	6	6

as the last of the old generation adults. This would indicate only one generation a year.

The possibility that some of the new adults produced eggs cannot be ruled out, but two complete generations a year is not likely.

Herdy and Thomas (1961) investigated the jack pine tip beetle in northwestern Ontario. They found eggs from 24 May to 16 July. Larvae were first collected in the early part of June and pupae in the early part of July. The young adults were first found on July 8.

There are several similarities between their investigation and the present one. The time between the first and last appearance of eggs was approximately seven weeks in both studies. In addition, they found that the developmental periods of individuals of the two larval instars and the pupae varied greatly. The developmental period for first instar larvae was 4 to 13 days, for second instars 5 to 17 days, and for pupae 6 to 13 days in laboratory-reared individuals. These periods are not unlike those of the present study.

Herdy and Thomas mention that in late June and early July, the parent beetles produce a second brood. This might account for the reappearance of eggs in the present study on 15 August but as mentioned earlier, the possibility that some new adults may have produced some eggs can not be discounted.

The biggest difference between the two studies is the time of appearance of the developmental stages. For example, eggs were first found in northwestern Ontario on 24 May and Fife Lake on 2 July. This difference may be due to seasonal variation. Even in the present study, the first noted appearance of active adults ranged from 27 April to 18 May during the years 1966 to 1968 in the same plantation. Most of the data were collected for this study in 1967, the year in which active beetles were first found on 18 May, a relatively late spring. The average monthly temperature for May that year was 6.4 deg. F below normal in this area according to data from the Weather Bureau of the United States Department of Commerce. Consequently, the date on which the active beetles were first found, as well as the subsequent life stages of the new generation, may have been later than normal.

Red Pine Cone Beetle Life History

The red pine cone beetle population was studied in a plantation near Cadillac (p. 4). Measurements of the life stages of this population are given in Table 3. Larval head capsule width frequency shows that there are two instars (Figure 5).

Active beetles were first observed on 25 May 1967 (Table 4). The first attacks were on cones; attacked shoots were found one week later on old growth. No reproduction was evident until 15 June, and it is assumed that the cones and tips attacked prior to this time were used for feeding. Most of the data were collected from infested cones because the majority of attacks were on them. However, the data from the few available tips (Table 5) corresponded with that from cones (Table 4).

Eggs were found from 15 June until 17 July. Most oviposition occurred in cones but some occurred in new growth tips. First instar larvae were found from 22 June to 17 July, second instar larvae from 22 June to 31 July and pupae from 24 July to 21 August. The greatest number of immature individuals found in a cone was six.

TABLE 3. Measurements of life stages of the red pine cone beetle population from cones in mm.

Life stage	No. of specimens	Mean length	Stand. error	Range	Mean width	Stand. error	Range
Adult ♂	30	3.133[a]	.154	2.492-3.528	1.240[b]	.022	.952-1.400
Adult ♀	30	3.335[a]	.034	2.912-3.612	1.308[b]	.017	1.120-1.512
Pupa	5	3.214[a]	.087	2.912-3.388	1.182[b]	.039	1.036-1.260
Larva II	30				.493[c]	.008	.448-.560
Larva I	30				.361[c]	.006	.252-.392
Egg	30	.865	.017	.672-1.064	.574	.011	.448-.700

[a]Anterior dorsal margin of prothorax to tip of elytra.

[b]Across dorsum of prothorax.

[c]Across dorsum of head capsule.

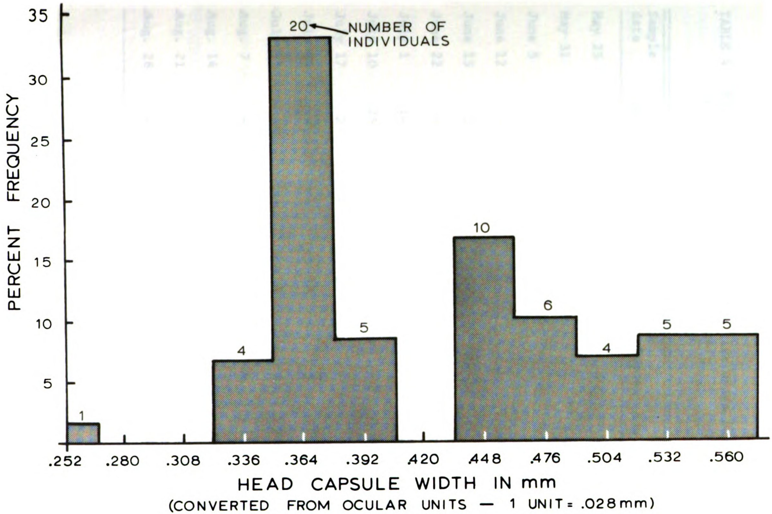

Figure 5. Head width frequency distribution of Conophthorus resinosae from cones showing two larval instars (based on 60 larvae).

TABLE 4. Number of individuals of each life stage per sampling date of red pine cone beetle in cones

Sample date	Eggs	Larvae I	Larvae II	Pupae	Adults	Total individuals
May 25	-	-	-	-	3	3
May 31	-	-	-	-	6	6
June 5	-	-	-	-	6	6
June 12	-	-	-	-	3	3
June 15	5	-	-	-	1	6
June 22	6	6	3	-	-	15
July 1	14	5	2	-	2	23
July 10	26	7	11	-	5	49
July 17	2	4	13	-	-	19
July 24	-	-	18	3	2	23
July 31	-	-	6	2	13	21
Aug. 7	-	-	-	-	17	17
Aug. 14	-	-	-	1	20	21
Aug. 21	-	-	-	1	18	19
Aug. 28	-	-	-	-	4	4

TABLE 5. **Number of individuals of each life stage per sampling date of red pine cone beetle in tips**

Sample dates	Eggs	Larvae I	Larvae II	Pupae	Adults	Total individuals
May 31	-	-	-	-	3	3
June 5	-	-	-	-	3	3
June 12	-	-	-	-	1	1
June 15	-	-	-	-	-	-
June 22	-	3	-	-	-	3
July 1	1	-	-	-	-	1
July 10	-	-	3	-	-	3
July 17	-	-	6	-	-	6

Callow adults were first found on 31 July and the old adults, or at least the majority, had probably died by this time.

Fallen tips were found in the later part of August but did not appear in large numbers until the second week in September. These overwintering tips, including the needles, are about four inches long.

Necessity of Snow Cover to Overwintering Survival

To determine if a blanket of snow was necessary for beetle survival through the winter, two cages, each containing 50 red pine tips collected on the ground, were suspended from red pine branches with wire approximately five feet above the ground. The cages were constructed from window screen wire formed into a cylinder closed at each end with a circular piece of screen. Two sets of 50 red pine tips were placed below these cages on the ground.

The experiment was started on 9 September 1967 in the Hoxeyville red pine plantation and terminated on 9 April 1968. The results are presented in Table 6. Of the 100 caged tips, only 73 contained beetles, all of which were dead. On the other hand, the tips on the ground contained 74 beetles, only three of which were dead.

TABLE 6. Mortality of red pine cone beetles with and without a covering blanket of snow

	Snow cover		No snow cover	
Replication	Alive	Dead	Alive	Dead
I	28	1	0	35
II	43	2	0	38
Total	71	3	0	73

Discussion

It appears from the life cycle data that the red pine cone beetle population is univoltine. It also seems that the beetles require a blanket of snow to successfully overwinter. This is also probably true for all the other beetle populations studied although there were not enough overwintering tips collected from these populations to permit this to be tested.

Lyons (1956) studied the red pine cone beetle in central Ontario. He found that the beetles usually attacked cones for oviposition in late May but this varied from mid-May to mid-June. There was considerable overlapping of the successive immature stages but he estimated the developmental periods of each instar from the peaks of successive stages. The developmental periods were egg, 17 days; first instar larva, 13 days; second instar larva, 22 days; pupa, 19 days. Old adults died by mid-July, about the time the new adults emerged, and the new adults entered overwintering tips by late Summer.

There are some similarities between the investigation in Ontario and the present one. The interval between the peak abundance of first and second instar larvae (10 and 24 July) was 14 days, close to that found by Lyons (13 days). In addition, the old adults appeared to die about the time the new adults emerged and the majority of beetles did enter tips for overwintering purposes in late summer in both studies.

The biggest difference between the two studies is the time of appearance of the developmental stages. Even in the present study, the first noted appearance of active adults ranged from 27 April to 25 May during the years 1966 to 1968 in the same plantation. With this much difference in the date of appearance of active adults in the same plantation in different years, it is not surprising that the dates of various life cycle occurrences were not the same between Michigan and Ontario.

Tip Beetle Life Histories on Other Hosts

Red adjacent to jack pine

In the red-jack pine plantation near Fife Lake (p. 4), both species were attacked, the heaviest attacks on red pine appearing to be on those trees closest to jack. This particular study concerns the beetle population on the red pine adjacent to the jack pine.

Measurements of the life stages are given in Table 7. Larval head capsule width frequency shows that there are two instars (Figure 6).

TABLE 7. Measurements of life stages of population on red pine and adjacent to jack pine in mm.

Life stage	No. of specimens	Mean length	Stand. error	Range	Mean width	Stand. error	Range
Adult ♂	1	2.856[a]	---	---	.980[b]	---	---
Adult ♀	4	2.892[a]	.118	2.576-3.136	1.114[b]	.042	1.008-1.176
Pupa	6	2.834[a]	.087	2.436-3.052	1.106[b]	.076	.980-1.204
Larva II	30				.482[c]	.006	.448-.532
Larva I	27				.364[c]	.003	.336-.392
Egg	10	.860	.017	.728-.896	.585	.011	.532 .644

[a]Anterior dorsal margin of prothorax to tip of elytra.

[b]Across dorsum of prothorax.

[c]Across dorsum of head capsule.

Attacks were found only on the current year's growth and overwintered adults were not found until 2 July 1967 (Table 8). Eggs were found concurrently and later on 11 July. A second period of oviposition occurred from 15 to 22 August. First instar larvae were present from 18 July to 29 August. Second instar larvae were present from 18 July to 11 September. Pupae were present from 8 August to 5 September but on 29 September only adults were found. Callow adults first appeared on 15 August and adults preparing for overwintering

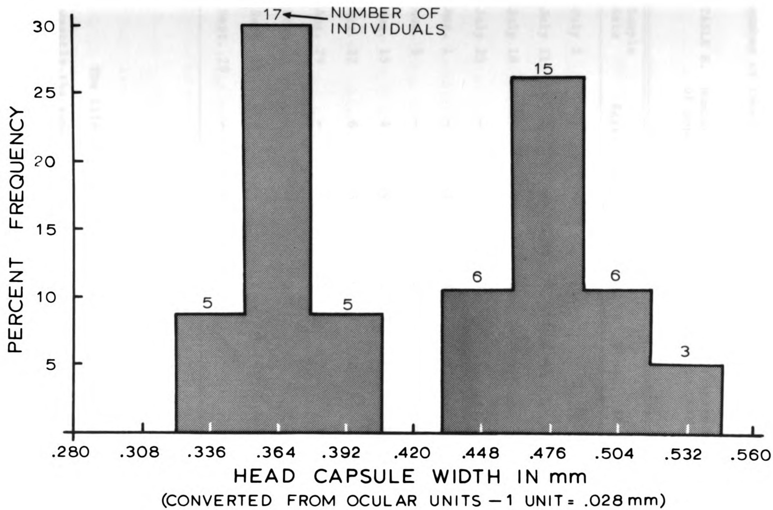

Figure 6. Head width frequency distribution of Conophthorus sp. from red pine tips adjacent to jack pine showing two larval instars (based on 57 larvae).

(hollowed-out buds) were first seen on 11 September. The greatest number of immature individuals found in a single tip was three.

TABLE 8. Number of individuals of each life stage per sampling date of population on red pine adjacent to jack pine

Sample date	Eggs	Larvae I	Larvae II	Pupae	Adults	Total individuals
July 2	1	-	-	-	2	3
July 11	2	-	-	-	1	3
July 18	-	4	5	-	-	9
July 25	-	5	5	-	-	10
Aug. 1	-	3	3	-	-	6
Aug. 8	-	1	6	3	-	10
Aug. 15	4	4	6	1	1	16
Aug. 22	6	5	6	2	2	21
Aug. 29	-	3	10	3	1	17
Sept. 5	-	-	5	5	2	12
Sept. 11	-	-	2	-	4	6
Sept. 29	-	-	-	-	5	5

Discussion

The life cycle for this population can be interpreted in exactly the same way as that of the jack pine tip beetle (p. 15) in terms of the number of generations a year. The constant appearance of first instar larvae from 18 July to 29 August and the second instar larvae from 18 July to 11 September makes it difficult to interpret the data as showing two generations a year. The absence of eggs from 18 July to 8 August could have easily been due to the extremely small sample sizes.

It should be noted that after reproduction began, this life cycle and that of the jack pine tip beetle (Table 2) were practically identical.

Scotch pine

Attacks of a *Conophthorus* population on Scotch pine were originally reported by Thomas and Lindquist (1956) from several areas in Ontario. However, they stated that the complete life history of this population was unknown. Therefore, determination of a similar population was undertaken in Michigan.

This population was studied in a plantation near Cadillac (p. 4). Measurements of the life stages are given in Table 9. Larval head capsule width frequency shows that there are two larval instars (Figure 7).

Adults were first observed on 17 May 1967 (Table 10). Eggs were found from 1 to 31 July and from 14 to 21 August. First instar larvae were present from 1 July to 7 August and again on 21 August. Second instar larvae were found from 10 July to 4 September and pupae from 7 August to 11 September. Callow adults were present on 31 July before any pupae were found (Table 10). This was probably because only small weekly samples could be taken and consequently, the first pupae were missed. The greatest number of immature individuals found in a tip was five.

TABLE 9. Measurements of life stages of population on Scotch pine in mm.

Life stage	No. of specimens	Mean length	Stand. error	Range	Mean width	Stand. error	Range
Adult ♂	30	2.755[a]	.039	2.268-3.220	1.092[b]	.017	.924-1.288
Adult ♀	30	2.839[a]	.036	2.268-3.220	1.114[b]	.014	.952-1.288
Pupa	14	3.021[a]	.059	2.688-3.500	1.173[b]	.020	.980-1.288
Larva II	30				.493[c]	.006	.448-.532
Larva I	23				.358[c]	.006	.308-.392
Egg	22	.826	.011	.756-.952	.552	.014	.392-.700

[a]Anterior dorsal margin of prothorax to tip of elytra.

[b]Across dorsum of prothorax.

[c]Across dorsum of head capsule.

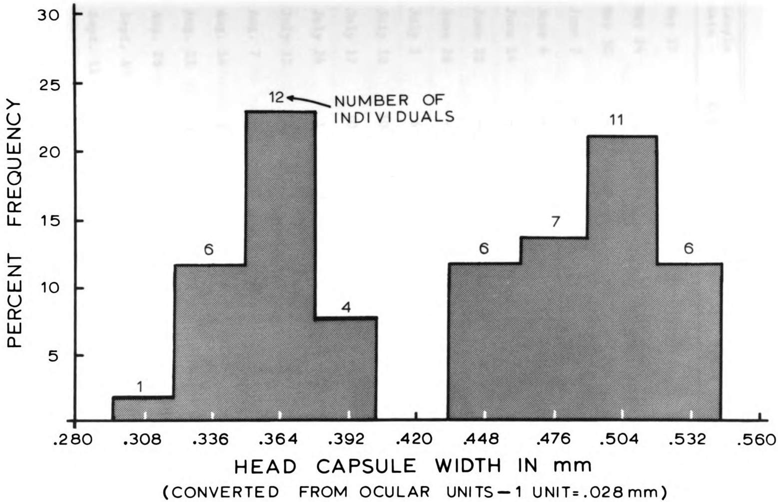

Figure 7. Head width frequency distribution of Conophthorus sp. from Scotch pine tips showing two larval instars (based on 53 larvae).

TABLE 10. Number of individuals of each life stage per sampling date of population on Scotch pine

Sample date	Eggs	Larvae I	Larvae II	Pupae	Adults	Total Individuals
May 17	-	-	-	-	3	3
May 24	-	-	-	-	4	4
May 30	-	-	-	-	7	7
June 2	-	-	-	-	4	4
June 6	-	-	-	-	5	5
June 14	-	-	-	-	7	7
June 22	-	-	-	-	8	8
June 28	-	-	-	-	2	2
July 1	6	3	-	-	13	22
July 10	10	3	1	-	6	20
July 17	10	3	2	-	-	15
July 24	1	7	5	-	-	13
July 31	3	4	7	-	2	16
Aug. 7	-	1	8	2	-	11
Aug. 14	2	-	4	5	4	15
Aug. 21	3	2	12	4	2	23
Aug. 28	-	-	4	9	22	35
Sept. 4	-	-	2	7	20	29
Sept. 11	-	-	-	5	13	18
Sept. 29	-	-	-	-	6	6

Overwintering preparation (hollowed-out buds) was first found on 4 September. The buds drop to the ground during the fall; no needles are attached. Only the adults overwinter.

Discussion

There is only one generation a year in this population. Four points support this conclusion: 1) eggs were present almost constantly in samples from 1 July to 21 August, 2) first instar larvae were present almost constantly in samples from 1 July to 21 August, 3) second instar larvae were present from 10 July until 4 September and 4) pupae were present from 7 August until 11 September. The possibility that eggs were produced by new adults from 14 to 21 August can not be discounted.

This life cycle more closely resembles that of the jack pine tip beetle than that of the red pine cone beetle.

Ponderosa pine

The population on ponderosa pine was studied in a plantation near Cadillac (p. 4). Measurements of the life stages of this population are given in Table 11. Larval head capsule width frequency shows that there are two instars (Figure 8).

This population was later in appearance relative to the beetle populations on jack (Table 2) and Scotch pine (Table 10). The first appearance of adults was noted on 30 May 1967 (Table 12). Two periods of egg production were detected, 2 to 25 July and 15 to 22 August. First instar larvae were found continuously from 2 July until 29 August and second instar larvae from 11 July until 11 September. Pupae were

TABLE 11. Measurements of life stages of population on ponderosa pine in mm.

Life stage	No. of specimens	Mean length	Stand. error	Range	Mean width	Stand. error	Range
Adult ♂	9	2.638[a]	.078	2.184-2.856	1.070[b]	.034	.868-1.176
Adult ♀	24	2.878[a]	.039	2.436-3.360	1.162[b]	.014	1.008-1.316
Pupa	12	2.887[a]	.081	2.380-3.416	1.058[b]	.031	.840-1.260
Larva II	30				.479[c]	.006	.420-.532
Larva I	30				.350[c]	.003	.308-.364
Egg	18	.851	.014	.728-.980	.605	.011	.560-.700

[a]Anterior dorsal margin of prothorax to tip of elytra.

[b]Across dorsum of prothorax.

[c]Across dorsum of head capsule.

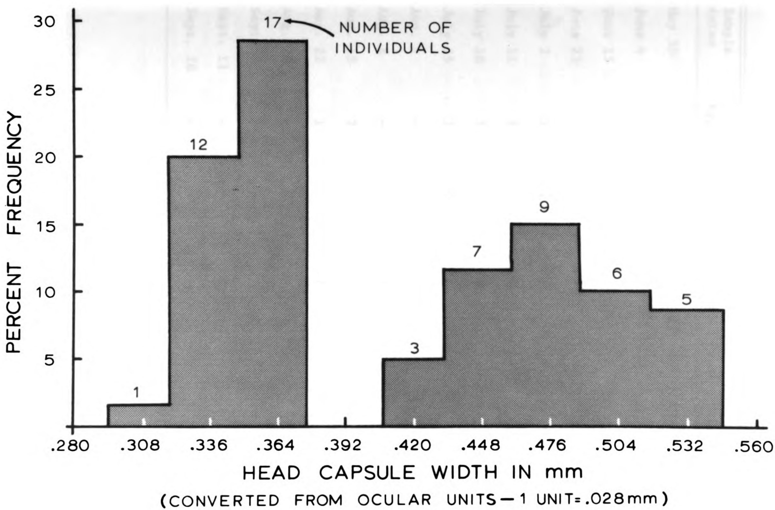

Figure 8. Head width frequency distribution of Conophthorus sp. from ponderosa pine tips showing two larval instars (based on 60 larvae).

TABLE 12. **Number of individuals of each life stage per sampling date of population on ponderosa pine**

Sample dates	Eggs	Larvae I	Larvae II	Pupae	Adults	Total individuals
May 30	-	-	-	-	1	1
June 6	-	-	-	-	1	1
June 15	-	-	-	-	9	9
June 23	-	-	-	-	2	2
July 2	7	1	-	-	9	17
July 11	7	7	1	-	5	20
July 18	5	1	5	-	2	13
July 25	2	2	4	2	3	13
Aug. 1	-	4	6	6	3	19
Aug. 8	-	1	6	1	3	11
Aug. 15	2	7	5	6	2	22
Aug. 22	1	1	8	8	1	19
Aug. 29	-	2	1	5	6	14
Sept. 5	-	-	4	6	4	14
Sept. 11	-	-	1	6	10	17
Sept. 28	-	-	-	1	4	5

present from 25 July until 28 September at which time collections were ended. The greatest number of progeny in a single tip was four.

Callow adults were first discovered on 1 August and the first evidence of overwintering preparations (hollowed-out buds) was noted on 5 September. Fallen tips have few to no needles attached to the bud.

Although pupae were found in the last collection in the fall (28 September), it can be assumed that at least the majority complete development to adults during the fall. This is based on the fact that on 9 April of the following spring, before the beetles had emerged from overwintering tips, an additional collection yielded only adults.

Discussion

This population appears to have only one generation a year. Facts supporting this conclusion are: 1) eggs were almost constantly present from 2 July until 22 August, 2) first instar larvae were present from 2 July until 29 August, 3) second instar larvae were present from 11 July until 11 September and 4) pupae were present from 25 July until 28 September. The possibility that some new adults produced eggs from 15 to 22 August can not be discounted.

This life cycle closely resembles that of the population on Scotch pine and more closely resembles that of the jack pine tip beetle than that of the red pine cone beetle.

It should be mentioned that another species of *Conophthorus* (*C. ponderosae* Hopkins) attacks ponderosa pine on the Pacific Coast; this species attacks only cones (Miller 1914, 1915).

Summary Discussion of Life History Data

The populations on jack, Scotch, ponderosa and red adjacent to jack pine have similar life cycles. With the exception of the first instar larvae, the various life stages were found within two weeks of each other. In fact, eggs were found within two days of each other.

The duration of the various immature stages was also similar with the exception of the pupae. Had not the one pupa been found on 28 September in ponderosa pine, this stage would have also been similar in duration for the above populations. The small sample sizes could have easily accounted for the variation in the appearance and subsequent disappearance of these stages.

The data for these four populations were combined with the above justifications in mind (Table 13). When this is done, the sample sizes for the various dates of collection become more consistent. The combined life cycle appears more clearly to be univoltine.

The combined life cycle was compared to that of the red pine cone beetle (Figure 9). Larger sample sizes were obtained in the red pine cone beetle study than in each of the other populations and consequently, the results are more reliable.

The two life cycles are different. The dates of appearance of the various *immature* life stages are much earlier, other than that of

TABLE 13. Total number of individuals of each life stage per sampling date of combined beetle populations on jack, red adjacent to jack, Scotch and ponderosa pine

Sample dates	Eggs	Larvae I	Larvae II	Pupae	Adults	Total individuals
May 15	-	-	-	-	3	3
May 18	-	-	-	-	3	3
May 24-25	-	-	-	-	11	11
May 30	-	-	-	-	8	8
June 2	-	-	-	-	13	13
June 6	-	-	-	-	12	12
June 14-15	-	-	-	-	25	25
June 22-23	-	-	-	-	14	14
June 28-29	-	-	-	-	3	3
July 1-2	16	4	-	-	26	46
July 10-11	21	17	3	-	13	54
July 17-18	15	10	13	-	3	41
July 24-25	3	18	16	2	3	42
July 31-Aug. 1	3	13	20	8	5	49
Aug. 7-8	-	4	24	8	3	39
Aug. 14-15	10	14	27	16	8	75
Aug. 21-22	13	12	30	19	10	84
Aug. 28-29	-	5	19	19	31	74
Sept. 4-5	-	1	15	21	31	68
Sept. 11	-	-	6	11	29	46
Sept. 28-29	-	-	-	1	16	17

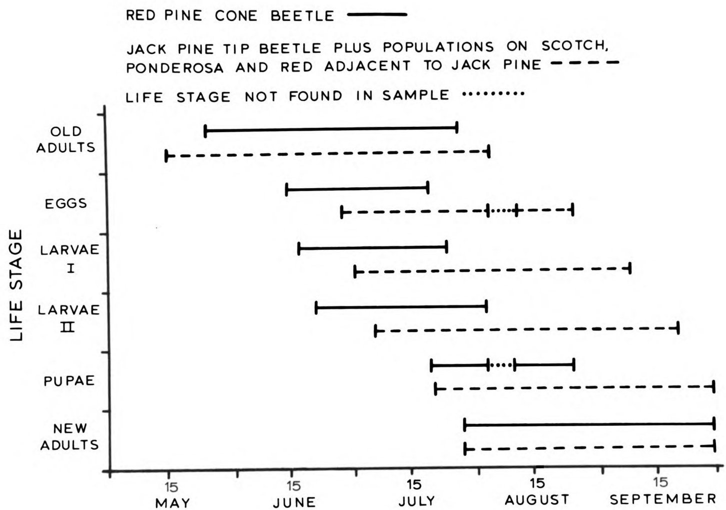

Figure 9. Comparison of life cycle of red pine cone beetle with the combined life cycles of jack pine tip beetle plus populations on Scotch, ponderosa and red adjacent to jack pine.

the pupal stage, for the red pine cone beetle. In addition, each immature life stage of the red pine cone beetle was present in samples for a much shorter length of time than in samples of the combined life cycle.

It should be noted that the same conclusion of different life cycles can be reached if the life cycles of the populations on jack, Scotch, ponderosa and red adjacent to jack pine are compared separately to that of the red pine cone beetle.

Comparison With Other Conophthorus Species

The majority of species in this genus appear to attack only pine cones. Those mentioned in the literature are C. ponderosae (Miller 1914, 1915) on P. ponderosa (ponderosa pine), C. contortae Hopkins (Ruckes, 1963) on P. contorta Douglas (lodgepole pine), C. radiatae Hopkins (Ruckes, 1958; Schaefer 1962) on P. radiata D. Don (monterey pine) and C. monophyllae Hopkins (Ruckes, 1963) on P. monophylla Torrey and Fremont (singleleaf pinyon or piñon pine). Those which attack cones, but also occasionally attack shoots are C. lambertianae Hopkins (Miller 1914, 1915; Ruckes, 1957) on P. lambertiana Douglas (sugar pine) and C. coniperda on P. strobus (white pine).

Though the other species in this genus discussed here attack cones, they damage them in different ways. If the cone is attached by a stem, the beetle enters the stem in most cases; if the cone is sessile, it enters at the base.

Depending on the species, the form of the gallery is either a straight tunnel along the central axis, a similar tunnel with a spiral twist proximally or, in one species (*C. radiatae*), a tunnel which begins with a spiral twist, then extends distally on one side, turns, and continues proximally on the other.

With the exception of *C. contortae* which overwinters as a pupa, all of these species overwinter as adults. In addition, all have one generation a year except *C. monophyllae* which appears to have two (Ruckes, 1963).

Of the five populations investigated in this study, only the red pine cone beetle has habits similar to other described *Conophthorus* species. The remaining four populations form a distinct group, principally because they are found only in tips, as a rule. It should be noted, however, that had cones been available to the beetle populations on ponderosa pine and red adjacent to jack pine, they might have attacked them.

Comparisons of Adult Measurements

The life cycles of the jack pine tip beetle and the beetles on Scotch, ponderosa and red adjacent to jack pine were more similar to each other than to that of the red pine cone beetle. To determine if the adult measurements followed this same pattern, the following procedure was used. A one-way analysis of variance was used to test the significance of the difference between the populations with similar life cycles; the assumption of variance homogeneity was met in all these tests. The population on red pine adjacent to jack was not included because of the small sample size. Tables 14-15 give the results of the tests; there was no significant difference between these populations at the 5% level.

TABLE 14. Comparisons of adult females of the jack pine tip beetle and adult females on Scotch and ponderosa pine using a one-way analysis of variance

Source	Deg. of freedom	Sum of squares	Mean sum of squares	F value	Prob.
			width		
Among treatment	2	1.20	0.60	2.73	> .05
Within error	81	17.66	0.22		
Total	83	18.86			
			length		
Among treatment	2	0.90	0.45	0.39	> .05
Within error	81	93.62	1.16		
Total	83	94.52			

TABLE 15. Comparisons of adult males of the jack pine tip beetle and adult males on Scotch and ponderosa pine using a one-way analysis of variance

Source	Deg. of freedom	Sum of squares	Mean sum of squares	F value	Prob.
			width		
Among treatment	2	0.13	0.07	0.26	> .05
Within error	54	14.44	0.27		
Total	56	14.57			
			length		
Among treatment	2	3.39	1.70	1.19	> .05
Within error	54	77.08	1.43		
Total	56	80.47			

Since the primary purpose of this project was to investigate the red pine cone beetle and jack pine tip beetle, these populations were compared next. The Student t was used to compare the females but because the assumption of variance homogeneity could not be met with the males, they were compared with the non-parametric z-test (Tables 16-17). T values of 7.47 and 10.84 were obtained for the female width and length respectively and z values of 12.5 and 14.8 were obtained for the male width and length respectively; all showed a highly significant difference between the adults of the two populations at the 1% level.

TABLE 16. Comparison of adult females of the red pine cone beetle and the jack pine tip beetle using a t-test analysis

Dimension	Deg. of freedom	t value	Probability
Width	58	7.47	< .005
Length	58	10.84	< .005

TABLE 17. Comparison of adult males of the red pine cone beetle and the jack pine tip beetle using a z-test analysis

Dimension	z value	Probability
Width	12.5	< .00003
Length	14.8	< .00003

Discussion

These tests show that the adult measurements of the jack, Scotch and ponderosa pine beetle populations are very similar to each other and that the jack pine tip beetle is significantly smaller than the red pine cone beetle. It appears on this basis, therefore, that the red pine cone beetle is a taxon different from the other beetles considered here.

Although there was a significant difference between the red and jack pine beetles, the dimensions (length and width) can not be reliably used to separate the two groups because there is a large overlap in their ranges. Herdy (1963, unpublished) also found that the adults of the red pine cone beetle were larger than the adults of the jack pine tip beetle in Ontario and that the ranges overlapped.

JACK PINE TIP BEETLE OVERFLOW STUDY

Relationship of Red Pine Tip Attack and Distance from Jack Pine

As discussed earlier, the beetle population on red pine adjacent to jack had a life cycle more similar to the jack pine tip beetle than the red pine cone beetle. If this population was indeed jack pine tip beetle, then it was likely that the number of red pine tips attacked was highest nearest the jack pine. Consequently, a study was conducted to determine this.

Methods and Materials

The number of tips attacked was counted in six transects across rows of red pine perpendicular to the jack pine. Each transect consisted of 10 trees six feet apart. Transects were made at 60 foot intervals (every tenth row).

Results

The results are shown in Table 18. It can be seen that the greatest number of tips attacked was in the first two rows and rapidly decreased thereafter. Rows 5 to 10 were found to be non-significantly different from each other at the 5% level with the New Multiple Range Test. The inclusion of row four did not change this conclusion but was much closer to significance at the 5% level. Therefore, it was decided to analyze only rows one to four. It should be mentioned that one tree in the second row had 19 tips attacked; this high number can not be readily explained.

TABLE 18. The distribution of red pine tip attacks as related to distance from jack pine

		Row 1	2	3	4	5	6	7	8	9	10
		Red pine									
Jack pine Transect	I	0	7	0	0	0	0	0	0	0	0
	II	5	0	0	0	0	0	0	0	0	0
	III	3	1	6	1	0	0	0	0	0	0
	IV	1	19	2	2	0	0	0	0	0	0
	V	8	2	0	0	0	0	0	0	0	0
	VI	8	3	2	0	1	0	0	0	0	0
	mean	4.2	6.2	.8	.3	.2	0	0	0	0	0
Distance (ft) from jack		6	12	18	24	30	36	42	48	54	60

Using a linear regression analysis with replication, it was found that rows one to four were significantly different from each other at the 5% level and that they were linearly related (Table 19 and Figure 10).

This was not an edge effect since the number of tips attacked on jack pine did not decrease moving deeper into the jack perpendicular to the red pine (Table 20).

TABLE 19. Comparison of number of red pine tips attacked per tree and distance from jack pine using a linear regression analysis with replication

Source	Deg. of freedom	Sum of squares	Mean sum of squares	F value	Prob.
Treatment	3	138.46	46.15	3.10	< .05
regression	1	85.14	85.14	5.71	< .05
lack of fit	2	53.32	26.66	1.79	> .05
Error	20	298.16	14.91		
Total	23	436.62			

TABLE 20. The distribution of jack pine tip attacks as related to distance from red pine

	Tree number 10	9	8	7	6	5	4	3	2	1	
	Jack pine										Red pine
Transect I	166	96	53	211	65	139	142	151	81	170	
Distance (ft) from red	60	54	48	42	36	30	24	18	12	6	

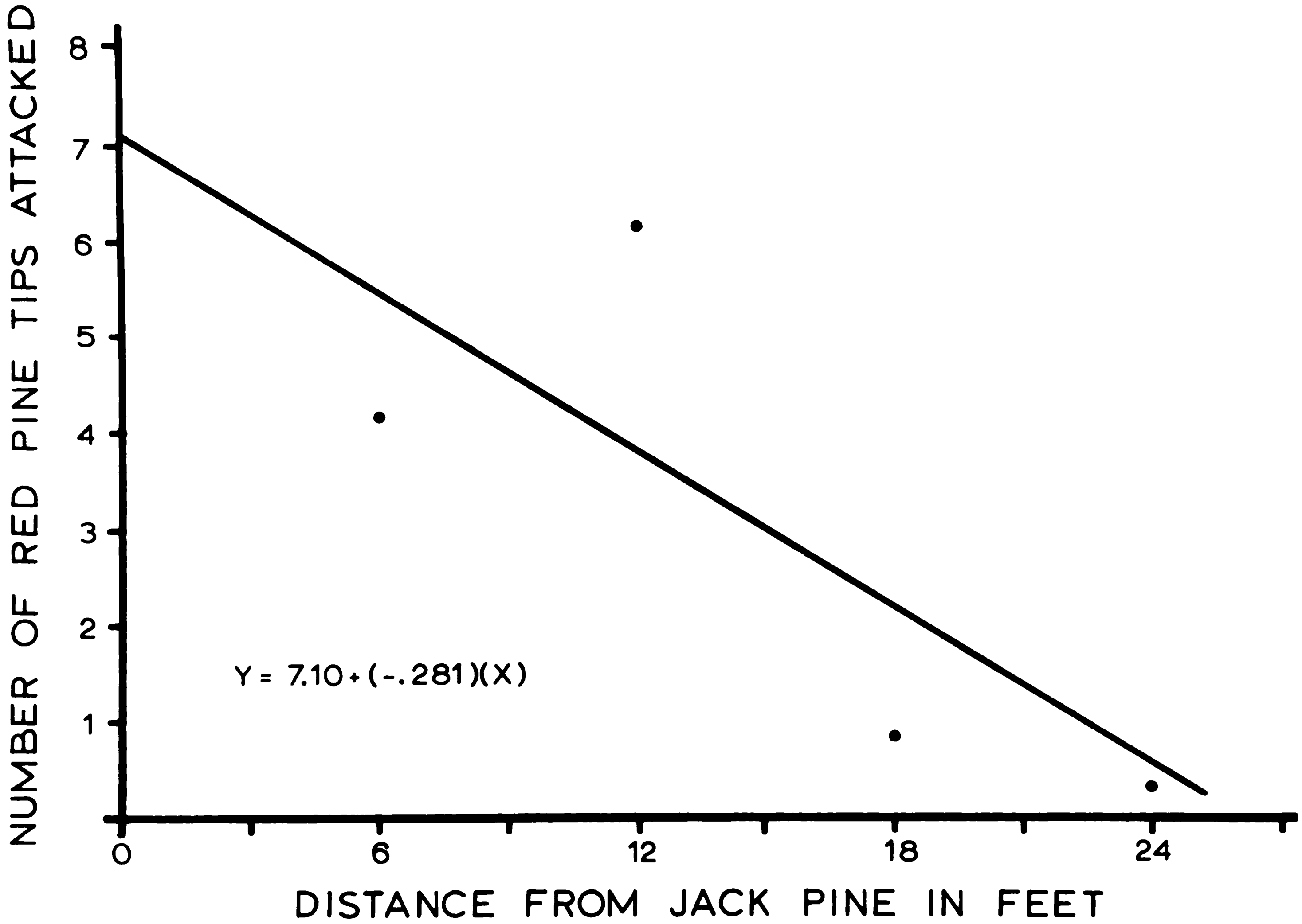

Figure 10. Relationship of number of red pine tips attacked to distance from jack pine.

Discussion

From the results of this study, it seems that the number of red pine tips attacked is directly related to the distance from the jack pine. However, there was another possible cause of the attack distribution, namely the height of the trees involved. This is discussed below.

Relationship of Height of Red Pine to Distance from Jack Pine

The red pine was five years younger than the jack and it appeared, from observations, that those red pines nearest the jack were suppressed by it (Figure 11). In fact, some of the red pines in the row six feet from the jack were actually shaded by jack pine branches.

If the red pine nearest the jack averaged shorter than those farther away, this, instead of distance from jack, might be responsible for the greater number of attacks on red pine being concentrated close to the jack. Their suppressed growth might produce conditions making them more susceptible to attack. Jack pine tip beetle can not survive on large cone-producing red pine (to be discussed later).

Methods and Materials

Concurrently with the collection of data on tip attack on red pine discussed in the previous study, the height of these same trees was recorded. The data are presented in Table 21.

Figure 11. The suppressing effect of jack pine on the first row of red pine (beneath the sleeve cage) and the next row to the right.

TABLE 21. Height of red pine related to distance from jack pine (ft)

		Row 1	2	3	4	5	6	7	8	9	10
		Red pine									
Jack pine Transect	I	4.5	12.0	12.5	11.0	11.0	11.5	11.5	14.0	14.0	14.5
	II	11.0	11.0	13.5	11.0	12.5	11.5	11.0	13.0	14.5	12.5
	III	9.0	10.0	9.0	13.5	11.5	13.5	11.0	13.0	14.5	15.5
	IV	7.0	9.5	10.5	11.0	14.5	15.0	14.0	11.0	13.5	12.0
	V	9.0	11.5	13.5	15.0	13.5	18.0	14.5	11.5	13.0	12.0
	VI	8.0	10.5	11.5	13.0	13.5	13.0	12.0	10.5	14.5	15.0
	Mean	8.1	10.8	11.8	12.4	12.4	13.8	12.3	12.1	14.0	13.3
Distance (ft) from jack		6	12	18	24	30	36	42	48	54	60

Results

The New Multiple Range Test showed that rows 5 to 10 were non-significantly different from each other but that the inclusion of row four made this conclusion closer to significant at the 5% level. Consequently, rows one to four were further analyzed with a linear regression analysis with replication. It was found that these rows were significantly different from each other at the 5% level and that they exhibited a linear relationship (Table 22 and Figure 12).

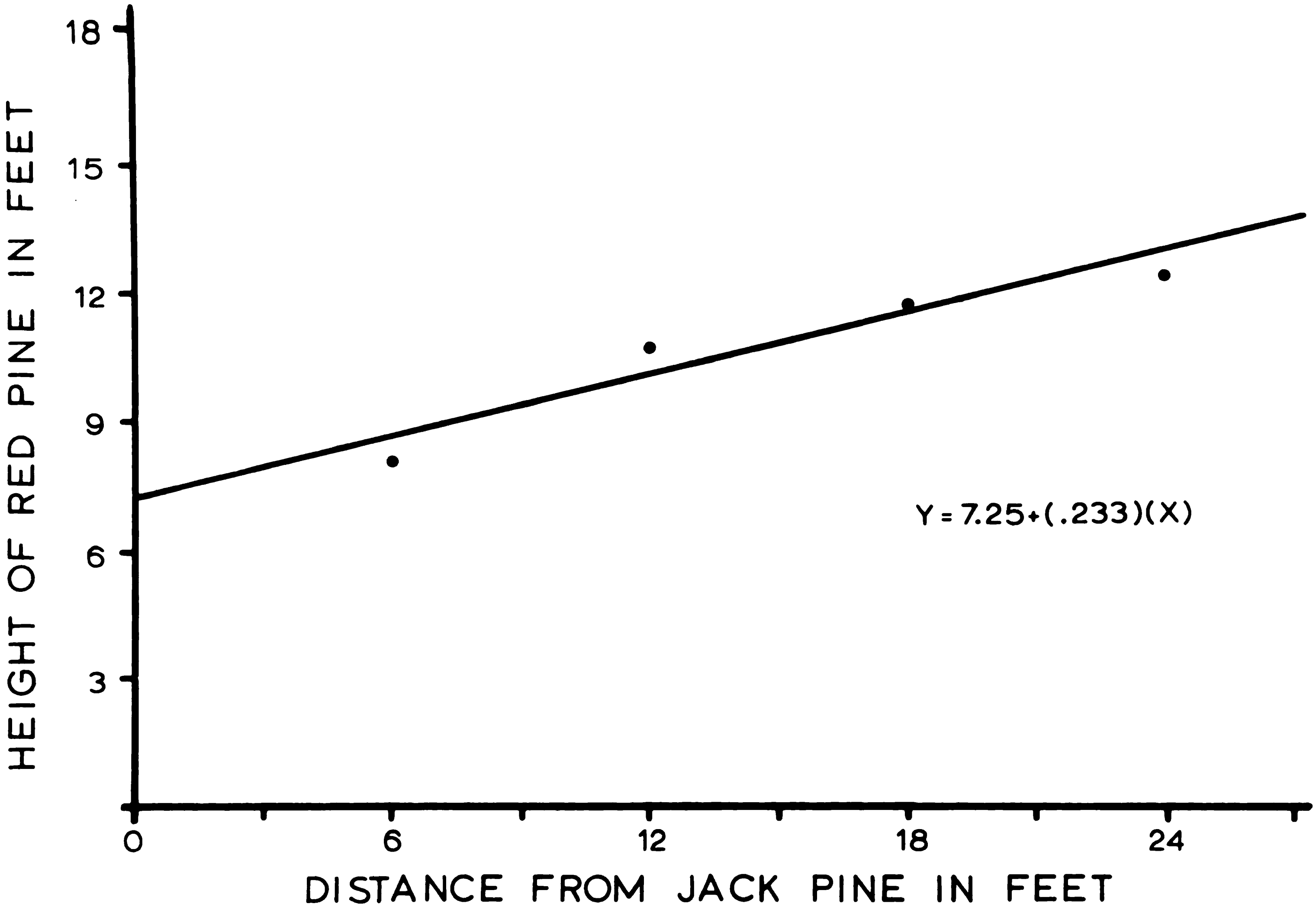

Figure 12. Relationship of height of red pine and distance from jack pine.

TABLE 22. Comparison of height (ft) of red pine and distance from jack pine using a linear regression analysis with replication

Source	Deg. of freedom	Sum of squares	Mean sum of squares	F value	Prob.
Treatment	3	65.34	21.78	7.43	< .005
regression	1	58.72	58.72	20.04	< .005
lack of fit	2	6.62	3.31	1.13	> .05
Error	20	58.66	2.93		
Total	23	124.00			

Discussion

These data suggest that those red pine growing nearest the jack pine are being suppressed by it and as a result, are shorter in height and probably less vigorous than the other red pine.

Correlation of Number of Tips Attacked and Height of Red Pine

From the two previous studies, it was impossible to determine if distance from the jack pine or height of the red pine was the important determining factor in the number of tips attacked per red pine tree. Therefore, it was necessary to eliminate distance from jack pine as a factor and test for the significance of the red pine height alone.

Methods and Materials

A row of red pine consisting of 24 trees parallel to the jack pine was chosen for this study. Because some of the trees in the row six feet from the jack pine were overgrown by jack pine branches, the row 12 feet away was used. The height and number of tips attacked was recorded for each tree. The height of these trees ranged from 6 to 12 feet. These data were tested for correlation between tree height and number of attacks.

Results

A correlation coefficient (r) of 0.16 was obtained which gave a non-significant F value of .58 at the 5% level.

Discussion

The results indicate that height of the red pine trees, up to at least 12 feet in this plantation, has no effect on the number of tips attacked. Consequently, the conclusion must be drawn that the number of red pine tip attacks is related to the distance from jack pine, and supports the idea that this population is coming from the jack pine and is the jack pine tip beetle.

Some Additional Attack Patterns from other Plantations

Two mixed red and jack pine plantations were found which furnished some additional information about attacks on red pine near jack.

Both plantations were in Wexford County, Michigan. The first plantation (T22N R9W Sec 8), near Cadillac, consisted of 17 to 22 foot red and 16 to 21 foot jack pine approximately 16 years old; only the jack pine was producing cones. There was no discernable pattern to the planting but it consisted of rows of red interspersed by rows of jack. Dirt roads had been constructed through this area. Walking along them, averaging one step per second, an average of 72 attacked tips per minute was seen on the jack pine. No attacked tips were seen on the red pine during an equal amount of counting time. These results suggest that jack pine tip beetles do not attack tall red pine to any great extent.

The second plantation (T24N R9W Sec 29), near Manton, also was not planted in any distinct pattern. However, the part which was interesting in terms of tip attack consisted of 18 rows of 12 to 14 year old red pine (5-10 feet in height) followed by one row of 15 to 20 year old red pine (13-21 feet in height) and then, three rows of 15 to 20 year old jack pine (14-20 feet in height). Again, only the jack pine was producing cones. Using the same counting procedure as above, an average of 54 attacked tips per minute was counted on the jack pine. Absolutely no attacked tips were found on any of the red pine and it appeared that the row of large red pine between the infested jack pine and the small red pine was acting as a barrier to the beetle.

Summary of Tip Beetle Overflow Results

From the studies of the jack pine tip beetle overflow onto red pine and the information from the two additional plantations, it appears that the jack pine tip beetle can exist on suppressed red pine and that its distribution on these trees is inversely related to the distance from the jack pine. However, once this red pine reaches an undetermined threshold in height, the beetle is no longer able to attack it successfully, even if the red pine is immediately adjacent to heavily infested jack pine.

RESPONSES OF RED PINE CONE BEETLE AND JACK PINE TIP BEETLE CAGED ON RECIPROCAL HOSTS IN THE FIELD

This experiment was set up to determine the behavior of the two beetle populations (red and jack) when exposed to reciprocal hosts and what effect branches with cones removed, with shoots removed or with both cones and shoots present would have.

Methods and Materials

Sleeve cages (Figures 11, 13) were used in this study. The frames were approximately 22 inches in diameter and 36 inches long. Each frame consisted of three gas welding rods spaced evenly around and enclosing four galvanized steel wire hoops; the four hoops were spaced nine inches apart and welded to the rods. Each of the three proximal hoops had a radially-positioned wire which extended just past the center of the hoop; the ends of these three wires were wrapped around the enclosed branch, thus securing the frame to the branch.

The six-foot-long sleeve cage was made of 32 x 32 mesh Lumite® Saran. The sleeve was cylindrical and open on one end where the branch was inserted. To help close the open end of the cage tightly around the branch, a piece of folded cloth was wrapped around the

Figure 13. Sleeve cage used in reciprocal host study.

branch and the sleeve tied at this point with 2 pieces of nylon cord.

Each sleeve cage had a laterally-placed 2 foot-long zipper. In addition, to help prevent the weight of the cage from breaking the enclosed branch, a wire running through an eye sewn to the top of each cage was tied to a convenient trunk or branch nearby.

Trees with cones and ones without were chosen for this experiment. In the jack pine plantation enough trees with cones were present to position all cages facing the same direction (west); only the outermost trees were used.

In the red pine plantation, there were not enough trees producing cones along the outermost row to allow all cages to be placed facing the same direction (southwest). Therefore, an additional row from an adjacent plantation was used which was at right angles to the first. The cages in this second plantation faced northwest. This introduced possible sources of variation, namely that the two plantations might differ in some way (e.g., physiologically, genetically). This was partially resolved in the following way. The first year the jack pine tip beetles were placed in one plantation and the red pine cone beetles in the other. The next year, the beetle populations were reversed.

The food supply required by the beetles in each sleeve cage was difficult to estimate. Shoots were never a problem, 20 or more being more than enough because they were never all attacked. Cones were much more scarce. However, 5 or more appeared to be enough for the number of beetles used because all cones were attacked in only one cage.

The experimental beetles were collected in different ways. In 1966, overwintering buds containing red pine cone beetles were collected (4-19 May) from the leaf litter and placed in a cage in the field. During the winter, the buds may separate from the fallen tip needles but usually remain in close proximity to them. Because the majority of needles of these tips are still green in the spring and on a brown background of leaf litter, the task of finding the nearby buds is not difficult. The beetles were brought into the laboratory on 30 May and sexed.

It was not possible to collect overwintering buds of jack pine tip beetles in sufficient numbers to complete the experiment; the small, brown tips are extremely difficult to locate on a brown background of leaf litter. Consequently, they were collected from newly attacked tips on 31 May and sexed on 1 June. The beetles (red and jack populations) were placed in sleeve cages in the jack pine plantation on 2 June and in the red pine plantation on 3 June. Three pairs of beetles were placed in each cage. Each cage contained one of the following sets of branches: 1) with cones and shoots, 2) with only shoots and 3) with only cones (the shoots had been snipped off). Each set was replicated eight times in each plantation (48 cages for the total experiment). Half of each set was used for each beetle population.

In 1967, the process was changed slightly. The infested jack pine tips were collected in the same way on 18 June and the beetles sexed the next day. However, the red pine buds (containing beetles) were taken from overwintering sites at the beginning of May and placed in cold storage (4.4 ± 1.1 C) until 20 June at which time they were sexed. The procedure was changed for the red pine cone beetles because of unseasonably warm weather during late April and early May and it was feared the beetles might emerge too early and escape. However, temperatures subsequently dropped and the average temperature during May proved to be lower than normal.

Beetles are sexed in the following way. The beetle is placed on its back and held gently by the thorax with a pair of forceps; the abdomen is then pushed upward until it forms approximately a 45 degree angle with the horizontal axis, the head remaining flush with the substrate. In this position, the beetle begins to curl its abdomen and exposes the tip from beneath the elytra. The caudal margin of the seventh abdominal tergum is squarely cut-off in the male, but forms an acute semi-circle in the female; the eighth tergum is visible only in the male (Herdy 1959, 1963 unpublished). Thus the sex of the beetle is easily determined when it curls its abdomen.

The beetles were placed in cages in the jack pine plantation on 21 June and in the red pine plantation on 22 June. The 1967 experiment was started approximately three weeks later than in 1966 because it had been discovered from life cycle studies the previous year that the beetles only oviposited in new growth. Therefore, by delaying an additional three weeks, there would be more new growth present and hence, more of a chance for oviposition.

The beetles were divided among the cages in 1967 the same way as in 1966 with the following modifications: 1) each experiment was replicated three rather than four times because it was felt that more beetles per cage might result in more reproduction and 2) five pairs of beetles were used in the cages containing cones and shoots and four pairs were used in the other two sets.

After the experiments were terminated at the end of the summer (1966 and 1967), the tips and cones were opened and the progeny (both numbers and stages) recorded.

The non-parametric Mann-Whitney U test was used to analyze the data which consisted of the total number of attacks (entrance holes) observed on the enclosed shoots and cones.

Results

Differences were most evident between the two populations in the red pine plantation (Table 23). The only test which was definitely non-significant at the 5% level was with the shoots of 1966, but even in this test, the results still showed a trend toward red pine cone beetles attacking a greater number of tips than jack pine tip beetles; only the red pine cone beetles attacked cones.

In the jack pine plantation, no significant differences were found in any of the tests at the 5% level (Table 24). However, closer examination of the results reveals an interesting point. In 1967, the experiment with cones and shoots gave a P value of .275. However, if the attack of cones in this set is analyzed separately, a P value of .150 is obtained (Table 24). In the 1966 experiment using branches with only cones, a P value of .171 was obtained. It should be mentioned that in all tests using cones (cones or cones and shoots) in this jack pine plantation in 1966 and 1967, the red pine cone beetles attacked 12 cones and the jack pine tip beetles attacked none. Though

TABLE 23. Comparisons of attacks on red pine by red pine cone beetle and jack pine tip beetle using a Mann-Whitney U analysis

Test	Replication	No. of attacks by: Red pine beetle	No. of attacks by: Jack pine beetle	U	Prob.
Cones, 1966	I	0	0	2	.057
	II	1	0		
	III	1	0		
	IV	6	0		
Cones, 1967	I	2	0	0	.050
	II	2	0		
	III	8	0		
Shoots, 1966	I	1	0	3	.171
	II	2	0		
	III	2	1		
	IV	2	2		
Shoots, 1967	I	1	0	0	.050
	II	1	0		
	III	3	0		
Cones & shoots, 1966	I	0	0	2	.057
	II	2	0		
	III	6	0		
	IV	12	0		
Cones & shoots, 1967	I	2	0	0	.050
	II	2	1		
	III	5	1		

TABLE 24. Comparisons of attacks on jack pine by red pine cone beetle and jack pine tip beetle using a Mann-Whitney U analysis

		No. of attacks by			
Test	Replication	Red pine beetle	Jack pine beetle	U	Prob.
Cones, 1966	I	0	0	4	.171
	II	0	0		
	III	1	0		
	IV	3	0		
Cones, 1967	I	0	0	3	.350
	II	0	0		
	III	3	0		
Shoots, 1966	I	3	0	5.5	.293
	II	3	2		
	III	6	6		
	IV	11	7		
Shoots, 1967	I	1	2	4	.500
	II	3	2		
	III	9	6		
Cones & shoots, 1966	I	2	1	5	.243
	II	3	3		
	III	5	3		
	IV	8	4		
Cones & shoots, 1967	I	0	0	2.5	.275
	II	3	1		
	III	5	2		
Cones & shoots, 1967 (cones analyzed separately)	I	0	0	1.5	.150
	II	2	0		
	III	2	0		

these results are not conclusive, they all show a trend; there was a tendency for the red pine cone beetles to transfer their cone attacking behavior from red pine to jack pine.

Discussion

From these feeding experiments on reciprocal hosts, it appears there is a definite difference between the two populations in their feeding behavior. On red pine, the red pine cone beetle showed a distinct preference for cones over shoots as it does in the natural situation. In the cages containing both cones and shoots, 16 of 20 attacks in 1966 and six of nine attacks in 1967 were on cones. The red pine cone beetle was also successful in attacking tips, and to a lesser extent cones, on jack pine.

The jack pine tip beetle showed a marked difference from the red pine cone beetle in feeding behavior. It did not attack cones on either jack or red pine, even when this was the only source of food available to it. In some cases where only jack pine cones were available, the beetles burrowed into the stem from which the tip had been removed, sometimes as much as a couple of inches below the cut end, rather than attack the cones. They did attack tips of jack pine, and in a few exceptional cases (six attacks out of 102 beetles) made partial penetrations into red pine tips. In some of these attacks on red pine the beetles died shortly after beginning penetration and were found protruding from the entrance hole.

Reproductive success in these experiments yielded different results for the two populations. For the two years of this study, only three individuals of jack pine tip beetle were recovered (two pupae and one second instar larva) from jack pine tips and none were recovered from red pine. For the same two years, the red pine cone beetle produced 10 individuals (two adults, two pupae and six second instar larvae) in jack pine tips and cones and 26 individuals (23 adults and three pupae) in red pine cones and tips. It should be noted that half the 10 individuals of red pine cone beetle in jack pine were taken from one tip. Had this tip not been present, the numbers produced by both beetle populations on jack pine would have been much more similar.

The number of progeny found in the jack pine plantation was extremely small for both beetle populations and this was undoubtedly due, at least partly, to a species of aphid (Cinara sp.) which was protected from predators and parasites in many of the cages during both years and which, because of its honeydew production and the subsequent appearance of sooty mold, caused the complete blackening of several branches. This must have had an effect on the number of attacks and subsequent reproduction by the beetles.

Cross-fertilization of jack pine tip beetles and red pine cone beetles

In the summer of 1967 an attempt was made to cross the jack pine tip beetle and red pine cone beetle populations on jack pine using sleeve cages. Three cages were used and these contained branches with only shoots. Four males of red pine cone beetle were placed in each of two cages with four females of jack pine tip beetle. Four males of jack pine tip beetle and four females of red pine cone beetle were placed in the third cage.

No evidence of reproduction was found although tips were attacked in two of the three cages; the only exception was one of the cages containing red pine males and jack pine females. However, as with the previous experiment, Cinara sp. was present in all the cages and the resultant honeydew production may have also affected attack and consequently, reproduction by the beetles in this study.

Summary of Reciprocal Host Study

From these experiments, it was found that the red pine cone beetle can attack and reproduce in tips and cones of jack and red pine. The jack pine tip beetle, however, can only survive attack of jack pine tips. Reproduction occurred only in jack pine tips but because the number of progeny produced was so small, the possibility that reproduction could occur in jack pine cones or on red pine can not be discounted. However, of the two pine species studied, reproduction would be more likely to occur on jack pine since the jack pine tip beetle was not even able to survive on cone-producing red pine.

From the little data available, it appears that the two populations may not be able to interbreed on jack pine.

BEHAVIOR OF RED PINE CONE BEETLE AND JACK PINE TIP BEETLE GIVEN A CHOICE BETWEEN JACK AND RED PINE TIPS

Methods and Materials

To determine the behavior of beetles of both populations when exposed to red and jack pine simultaneously, the following experiment was conducted. The stems of six cut shoots (three red and three jack pine) were inserted through corks into water-containing vials and cotton was wrapped around the cut ends; the cotton prevented water from leaking out of the vial between the inserted stem and the surrounding cork. The shoots of both pine species were placed horizontally in a ring (six inch inside diameter) with the tips facing inward in an alternating fashion (e.g., red, jack, red).

Thirty five jack pine tip beetles and 30 red pine cone beetles were used in two runs, one per population. Both populations had been stored at 4.4 ± 1.1 C for approximately 30 days after being collected on 30-31 May 1966. They were released in the center of the ring and the results were recorded 12 hours later. The test was run in the dark at room temperature (22.2 C).

Results

The red pine cone beetles were evenly divided between the two pine species and in addition, one entered a red pine tip (Table 25). The jack pine tip beetles showed a distinct preference for jack pine tips, with five times as many on and in them as red pine. In addition, they did not enter red pine tips.

TABLE 25. Preference of red pine cone beetle and jack pine tip beetle when exposed to jack and red pine tips

	Jack pine shoots		Red pine shoots	
	No. on tips	No. in tips	No. on tips	No. in tips
Red pine cone beetle	15	0	14	1
Jack pine tip beetle	22	7	6	0

Discussion

These results correlate well with those found in the reciprocal host field experiments. The red pine cone beetles appear capable of using both pine species as a food source while the jack pine tip beetles appear to be limited to jack pine.

OLFACTORY RESPONSES OF RED PINE CONE BEETLE AND JACK PINE TIP BEETLE

Methods and Materials

To determine if red pine cone beetle and jack pine tip beetle were attracted to their hosts through odor, an olfactory experiment was conducted. The olfactometer was similar to the type originally designed by McIndoo (1925); a brief summary of the literature is presented by Wilson and Bean (1959). It consisted of a central chamber with five air-inlet arms (Figure 14). Associated with this apparatus was a 500 ml flat-bottomed flask with glass inlet and outlet extensions in a rubber stopper. The inlet was connected to an air source by a tygon plastic tube. The outlet was connected with plastic tubes to flowmeters through which air could be regulated to insure an equal flow between the two. The air-exits from the flowmeters were connected with plastic tubes to the arms of the olfactometer.

A preliminary test was conducted to determine if the beetles would show a position effect in the testing chamber (e.g., if the beetles would tend to move to one side of the chamber or the other whether or not tips were present in the olfactometer). The beetles used had been stored at 4.4 ± 1.1 C for approximately 30 days after being collected on 30-31 May 1966. In this test, air was passed only

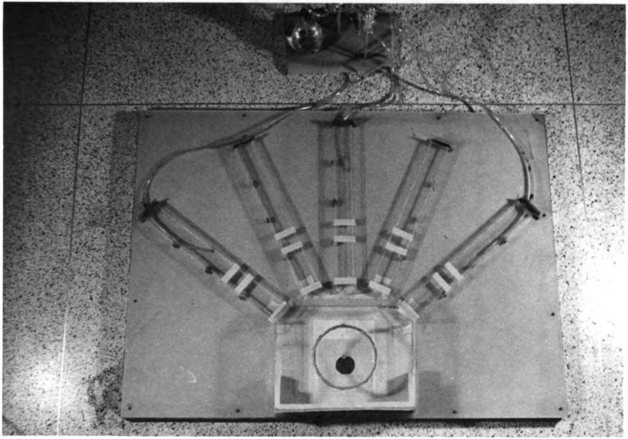

Figure 14. Olfactometer consisting of central chamber and five air-inlet arms. Connected with this is air-regulating apparatus consisting of flat-bottomed flask connected to two flowmeters which are in turn, connected to arms of olfactometer by plastic tubes.

through the first, third and fifth air channels (arms); the second and fourth were blocked off. Ten males and 10 females were used from one of the two populations in each run. The runs were conducted in the dark at room temperature (22.2 C). No position effect was found.

The same three arms were used for the olfactory experiment. A jack pine tip was placed in one of the outer arms and a red pine tip in the other. Air was passed through them with the middle one acting as a control.

The tips used had been collected within the hour and were prepared for use in the same manner as in the laboratory feeding preference experiment.

Ten male and 10 female red pine cone beetles were released in the central chamber and exposed to air moving over the two pine species for three hours. This was later repeated with the same number of jack pine tip beetles. The experiments were again conducted in the dark at room temperature.

Results

No response by either species was detected. In fact, some individuals of both populations were observed to walk up to a tip and subsequently turn around and walk away. Varying the strength of the air flow did not alter the results.

Discussion

There appears to be no olfactory response of the beetles to their hosts using the apparatus described above. However, it may be that the response is very weak and the olfactometer was not sensitive enough.

RESIN TOXICITY

As shown earlier, jack pine tip beetles could not survive on cone-producing red pine. It is possible that this was due to red pine resin toxicity. Red pine beetles were not adversely affected by either red or jack pine.

Santamour (1965) concluded from his studies of the resistance of pines to bark beetle attacks that resin might be an important factor. Smith (1961a, b) developed various methods by which he could subject bark beetles to resin vapors from different pine species in the laboratory, and account for differences in the resulting mortality. His objective was to find if resin could play a significant role in the success or failure of bark beetle attack on pine trees. He found that *Dendroctonus brevicomis* LeConte which attacks *Pinus ponderosa* and *P. coulteri* D. Don survived when exposed to vapors of *P. ponderosa*, but could not when exposed to vapors of *P. jeffreyi* Greville & Balfour. On the other hand, *Dendroctonus jeffreyi* Hopkins survived when exposed to vapors of its own host but died when exposed to vapors of *P. ponderosa*. He thus showed that resin could be a determining factor in attack success. It seemed that this might be an additional way to help determine if the jack pine tip beetles and the red pine cone beetles were different taxa.

Methods and Materials

Of the various techniques developed by Smith (1961a) for his experiments, he felt that his fumigation chamber was the most reliable. Consequently this chamber was used in the present experiment.

The fumigation chamber consisted of a 4-ounce jar closed by a screw-cap (Figure 15). The cap was sealed with a teflon gasket. One-fourth dram vials were tied in groups of four with nylon thread, and two groups were stacked within the jar; each vial held an individual beetle, and each was closed with a plug of lumite (32 x 32 mesh). The bottom half of a 2-dram shell vial (approximately one and one-fourth inches high) was used to hold the resin, and was placed beside the stack of vials in the fumigation chamber.

Two additional points should be mentioned about this fumigation chamber. First, each material used (e.g., teflon, nylon, lumite, glass) was found by Smith not to absorb resin vapor. Second, it was found in the present study that a more effective seal could be made by using a ring of silastic® (Dow Corning) around the inside diameter of the cap in addition to the teflon gasket.

The collection of resin was done differently than by Smith (1961a). Since the experiment involved both cone and tip beetles and since both populations attacked tips, it was felt that the resin should be collected from tips. However, it was not possible to collect enough resin from this source for the experiments. Therefore, a sample of a few tips from each of 10 trees in the red and jack pine plantations used in the life cycle studies was used for gas

Figure 15. Equipment used in resin toxicity experiment, from left to right: fumigation chamber, resin vial and vials for holding beetles.

chromatograph analysis of the resin components with the goal of synthesizing average red pine and jack pine resins. The tips were cut in half and the exuded drops of resin drawn into a capillary tube with a rubber tube. Resin from each tree was kept separate. The samples were collected on 4 and 5 September and analyzed on 10 September. During this interval, they were stored at 4.4 ± 1.1 C. There is no difference qualitatively in resin produced in the spring and fall and very little difference quantitatively (Hanover, personal communication).

A polyparapylene glycol column was used in the gas chromatograph. A standard containing the monoterpenes found in general pine resin was first analyzed and the retention time recorded for each component. Only monoterpenes were used because they are the most volatile major components in resin and it was felt that they would be most likely to show toxic effects if any were present.

Next, the samples were analyzed. The peaks on the charts were identified by comparison with the standard and from these peaks, the percent of each component in the samples was determined.

Only four of the 10 samples of red pine resin were analyzed and used in the determination of an average resin because the percent of each resin component in red pine is very consistent from tree to tree (Hanover, personal communication).

The percent of each resin component in the jack pine resin samples was more variable. Several of the charts had one or two very small peaks which were difficult to identify and rather than introducing doubt into their identification, and because they represented such a small percent of the total resin, these charts were not used. Consequently, the charts of four samples which had peaks which could be most confidently identified were used in the determination of an average resin.

Each of the two average resins was synthesized from sources of the pure monoterpenes. The percent of each monoterpene in the synthesized resin of the two pine species is given in Table 26.

TABLE 26. Percent of each resin component in the synthesized resin of jack and red pine

Component	Jack pine	Red pine
α-pinene	26.31	60.87
camphene	4.79	2.67
β-pinene	22.69	29.12
myrcene	21.80	2.10
3-carene	13.61	3.86
α-terpinene	1.53	.11
limonene	7.14	.95
terpinolene	2.13	.32

In agreement with Smith (1961a), it was felt that the beetles should be exposed to as constant an atmosphere within the chamber as was possible. The simplest to obtain was a saturated atmosphere; most likely this is what the beetles are exposed to in tips and cones in the field. The test was conducted in an incubator held at 21.1 ± .3 C in the dark. One ml samples of the synthesized resins were weighed and placed in the resin vials in the fumigation chambers, and then placed in the incubator. At 6, 18, 24, 30, 48 and 54 hours some of the chambers were removed from the incubator and the resins reweighed.

The point at which no further loss occurred was considered to be the atmospheric saturation point. The results are shown in Figure 16. It can be seen that saturation was reached in 48 hours for both resins. Therefore, before the experiment with the beetles could be started, 48 hours had to elapse after the resin was introduced into the chambers.

Three males and five females of jack pine tip beetle were introduced into fumigation chambers containing jack pine resin (three replications), red pine resin (three replications) or a control containing no resin (one replication); this was duplicated with the red pine cone beetle.

Results

The results and the analyses (non-parametric Mann-Whitney U) are given in Tables 27 and 28. At the end of 72 hours after introduction of the beetles, there was no significant difference at the 5% level between the two populations when exposed to jack pine resin. However, there was a significant difference when they were exposed to red pine resin; the jack pine tip beetle was much more susceptible to red pine resin. There was no mortality in the control for either population. The beetles were considered dead if they were on their back and motionless.

At the end of 120 hours, the experiment was terminated and the dead beetles were sexed. They were examined under a binocular microscope to determine mortality. If the sex of the beetles is ignored, the results are exactly the same as the 72 hour results (Table 28). With respect to sex, there was no significant difference in mortality

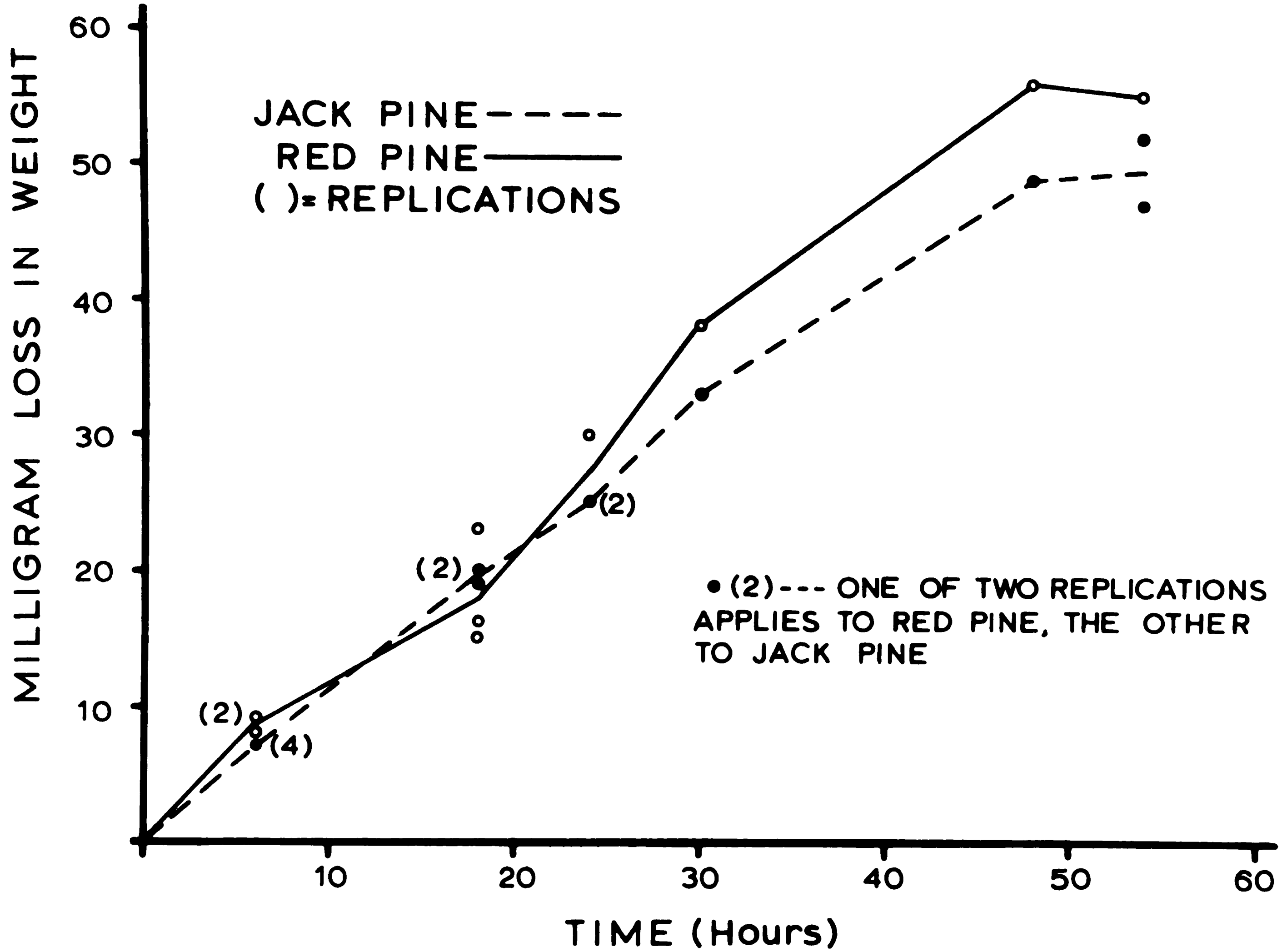

Figure 16. Weight loss of jack pine and red pine resin in fumigation chamber (21.1 ± .3 C).

TABLE 27. Comparisons of mortality of red pine cone beetle and jack pine tip beetle exposed to red and jack pine resin for 72 hours using a Mann-Whitney "U" analysis

		No. of dead individuals of			
Test	Replication	Jack pine beetle	Red pine beetle	U	Prob.
Jack pine resin	I	0	0	4	.500
	II	0	0		
	III	3	1		
Red pine resin	I	2	0	0	.050
	II	4	0		
	III	5	1		

TABLE 28. Comparisons of mortality of red pine cone beetle and jack pine tip beetle exposed to red and jack pine resin for 120 hours using a Mann-Whitney "U" analysis

Test	Replication	No. of dead individuals of: Jack pine beetle	Red pine beetle	U	Prob.
		(females)			
Jack pine resin	I	0	1	5.5	.650
	II	2	1		
	III	4	2		
		(males)			
Jack pine resin	I	0	0	4.5	.500
	II	1	1		
	III	1	1		
		(females)			
Red pine resin	I	2	0	0	.050
	II	2	0		
	III	3	1		
		(males)			
Red pine resin	I	1	0	2	.200
	II	1	1		
	III	3	1		
		(males plus females)			
Jack pine resin	I	0	1	3.5	>.350
	II	3	2		
	III	5	3		
		(males plus females)			
Red pine resin	I	3	0	0	.050
	II	3	1		
	III	6	2		

between females and between males in jack pine resin for either population. There was also no significant difference between the males of the two populations in red pine resin. However, there was between the females in red pine resin; more jack pine tip beetle females died. Again, no mortality occurred in the controls after 120 hours exposure.

Discussion

As stated earlier, monoterpenes were used because they are the most volatile of the major components of resin. The results have to be viewed with the small sample size of the experimental beetles in mind. Because the samples were so small in the replications, the difference in resin toxicity between the two populations may have been due to chance alone (e.g., these particular beetles may have been in a weakened condition). Consequently, it can only be stated that the resin toxicity effects on the two populations observed in the laboratory does not prove that these effects can occur in the natural environment but only that they may. The artificial resin may also have had an unnatural effect on the beetles.

With these qualifications in mind, the following statements can be made. The fact that red pine cone beetles can tolerate resins of both species while jack pine tip beetles can only tolerate jack pine resin may explain the ability of the red pine cone beetle to attack both species and the inability of the jack pine tip beetle to attack cone-producing red pine.

There was no difference in the mortality between the males of the two populations on red pine but had the sample sizes been larger, a difference might have become evident.

A comparison of the numbers of dead individuals in Table 27 and the lower part of 28 (males plus females) reveals an interesting point. There was no mortality at the end of 120 hours in the controls. However, there were more dead individuals in the groups from each population exposed to their own host's resin at the end of 120 hours than at the end of 72 hours. This suggests that the beetles can not tolerate their own host's resin for an indefinite period of time.

HOST DAMAGE

A tip attacked by a beetle is brown within two to three weeks, but what effect does this have on growth the following year? The object of this study was two-fold: 1) to find if the tree responds differently the next year to old tips killed in the spring before the current year's growth begins than it does to new tips killed during and just after the growing season and 2) to find if this response differs in red and jack pine.

Methods and Materials

Sixty seven old growth jack pine tips attacked before, and 86 new tips attacked during and just after the current year's growth were marked with pieces of string in May and July, 1966, respectively. Twenty five old red pine tips attacked before and 41 new tips attacked during and just after the current year's growth were marked in a similar manner at the same time. All groups of tips were rechecked in July of the following year after the subsequent growth had ceased.

Results

Jack pine showed a significant difference between the subsequent growth of tips attacked before and tips attacked during and just after the current year's growth at the 1% level (Table 29). It appears that if tips are attacked before they have begun to elongate (e.g., May 1966), their growth the following year (1967) is impaired; they fail to produce adventitious buds. However, very little effect is found on subsequent growth (1967) when tips are attacked during and just after the current year's growth has ended (July, 1966).

TABLE 29. Chi-square analysis of the effects of attacks on growth of jack pine

Test	Growth	No growth	Total	Chi-square	Prob.
Before current year's growth (May)	14	53	67	44.87	> .001
During and just after current year's growth (July)	66	20	86		
Total	80	73	153		

If growth continues the next year at the site of the old attacked tip, several new shoots (1-5) are produced. These tips grow at various angles and none grow in the same direction as the original tip.

The results from red pine showed that the time of attack did not affect subsequent growth differently (Table 30). In addition, even though the new tips came off at various angles, one of them was always able to curve forward around the dead tip and continue growing in nearly the same direction as the original one.

TABLE 30. Fisher exact probability analysis of effects of attacks on growth of red pine

Test	Growth	No growth	Total	Probability
Before current year's growth (May)	25	0	25	.382
During and just after current year's growth (July)	39	2	41	
Total	64	2	66	

Discussion

Beetle attack of red pine tips seems to have very little effect on the growth and shape of the tree. However, jack pine tip damage is more serious, and if it were severe and extensive enough, probably would result in a bushy tree.

The fact that time of tip attack has an effect on subsequent jack pine growth (Table 29) and no effect on subsequent red pine growth (Table 30) is probably due to a difference in the hormone balance between the two species, leading to the formation of adventitious buds in red pine no matter when it is attacked but considerably reducing the formation of adventitious buds in jack pine attacked before new growth begins (Hanover, personal communication). The importance of auxin in the regulation of terminal and lateral shoot growth in *Ginkgo biloba* L. has been reported by Gunckel and Thimann (1949).

DISCUSSION

Based on all available data, it appears that the beetle populations found on jack, Scotch, ponderosa and young red adjacent to jack pine are the same species and appear to be biologically different from the red pine cone beetle, Conophthorus resinosae.

Although the jack pine tip beetle cannot be reliably separated by any known structural characters from the red pine cone beetle at the present time, both adult males and females are statistically shorter and narrower than adult red pine cone beetles; however, the ranges of these dimensions for the two populations do overlap.

Although the jack pine tip beetle is able to reproduce in red pine in certain situations, it is not able to reproduce in cone-producing red pine. On jack pine, it was found to only attack and reproduce in tips. It has been reported to rarely attack jack pine cones (Herdy and Thomas, 1961), but it is possible that these attacks could have been made by Conophthorus resinosae since the red pine cone beetle was able to attack and reproduce in jack pine cones under caged conditions in this study.

The red pine cone beetle normally reproduces in red pine cones and to a lesser extent, in tips. Since it has been shown to be capable of reproducing in jack pine cones and tips in this study, it conceivably could attack Scotch and ponderosa pine, too.

The inability of the jack pine tip beetle to reproduce in cone-producing red pine appears to be due to its intolerance of resin from vigorous red pine. More precisely, it appears to be susceptible to the monoterpenes of the resin. The red pine cone beetle is better able to tolerate jack pine resin. However, both beetle populations show increased mortality when exposed to an array of monoterpenes, similar to levels in their own host's resin, for an indefinite period of time. In the laboratory, both populations of beetles began to succumb to their own host's resin in less than a week.

Both beetle populations are univoltine. However, jack pine tip beetle begins reproduction later in the year than the red pine cone beetle, and all of its immature life stages are present in the field for longer periods of time.

These data all point to the fact that the jack pine and red pine beetle populations are different. However there are certain problems which should be kept in mind. First, there was the underlying problem of a lack of large numbers of beetles throughout these experiments. Consequently, in most experiments smaller numbers of beetles had to be used than were desired and as a result, some data are not beyond question.

In the reciprocal host cage studies, small numbers were used out of necessity. It was mentioned earlier that the red pine cone beetles showed a trend toward attacking jack pine cones when confined to these trees. Had numbers been larger, possibly this trend would have become statistically significant. Correlated with this is the possibility that if more jack pine tip beetles had been available, some might have attacked jack pine cones.

The fact that jack pine tip beetles were, out of necessity, collected differently than red pine cone beetles may have affected the results. Possibly the fact that jack pine tip beetles had been feeding on jack just prior to their collection may have affected their subsequent behavior.

These possible sources of error weighed against the results from the various experiments seem to be rather remote possibilities. I conclude that the jack pine tip beetle is a different species than *C. resinosae*.

FUTURE RESEARCH POSSIBILITIES

Thirty-seven species of pine occur in the United States and Canada, and 20 additional species only in Mexico (Critchfield and Little, 1966). Only 17 species, including two from Mexico, have been reported to be attacked by *Conophthorus* species (Table 31); *C. scopulorum* was originally described from *Pinus scopulorum* (Hopkins, 1915) which has since been combined with *P. ponderosa*. Of the 17 *Conophthorus* species described from pines, the biology of only 7 has been studied. These are *C. coniperda* on *P. strobus* (Godwin 1958, 1959), *C. lambertianae* on *P. lambertiana* (Miller 1914, 1915; Ruckes, 1957), *C. monophyllae* on *P. monophylla* (Ruckes, 1963), *C. resinosae* on *P. resinosa* (Lyons, 1956), *C. ponderosae* on *P. ponderosa* (Miller 1914, 1915), *C. contortae* on *P. contorta* (Ruckes, 1963) and *C. radiatae* on *P. radiata* (Ruckes, 1958; Schaefer, 1962).

With so little reliable information available on the biology of these beetles, it is impossible to determine whether a correlation exists between the taxonomic groupings of the pine species and the different kinds of life cycles of the *Conophthorus* species attacking them. At present, however, there would seem to be no relationship between whether the host is a hard or soft pine and the life cycle pattern of the attacking *Conophthorus*.

Two main studies should be conducted to help clarify the relationships of the *Conophthorus* species and their relationships with

TABLE 31. A list of the pine species from the United States and Canada[1] with remarks on the biology of the Conophthorus species known to attack them

Pinus sp.	Conophthorus sp.	Biology
Subgen. Strobus		
Sect. Strobus		
Subsect. Cembrae		
P. albicaulis		
Subsect. Strobi		
P. strobus	C. coniperda	attacks cones, overwinters in cones[2,3]
P. monticola	C. monticolae	attacks cones[4]
P. lambertiana	C. lambertianae	attacks cones, overwinters in cones and tips[5,6,7]
P. flexilis	C. flexilis	attacks cones[4]
P. strobiformis		
Sect. Parrya		
Subsect. Cembroides		
P. cembroides		
P. edulis	C. edulis	attacks cones[8]
P. quadrifolia		
P. monophylla	C. monophyllae	attacks cones, overwinters in cones[9]
Subsect. Balfourianae		
P. balfouriana		
P. aristata		
Subgen. Pinus		
Sect. Ternatae		
Subsect. Leiophyllae		
P. leiophylla		
Sect. Pinus		
Subsect. Sylvestres		
P. resinosa	C. resinosae	attacks cones and tips, overwinters in tips[10]
Subsect. Australes		
P. palustris		
P. taeda	C. taedae	probably attacks cones[4]
P. echinata		
P. glabra		
P. rigida		
P. serotina		
P. pungens		
P. elliottii		
P. occidentalis		

TABLE 31 Cont'd.

Pinus sp.	Conophthorus sp.	Biology
Subgen. Pinus (Cont.)		
Sect. Pinus (Cont.)		
Subsect. Ponderosae		
P. ponderosa	C. ponderosae	attacks cones, overwinters in cones[5,6]
	C. scopulorum	attacks cones[4]
P. washoensis		
P. jeffreyi		
P. engelmannii	C. apachecae	attacks cones[4]
Subsect. Sabinianae		
P. sabiniana		
P. coulteri		
P. torreyana		
Subsect. Contortae		
P. banksiana	C. banksianae n.sp.	attacks tips; overwinters in tips[11]
P. contorta	C. contortae	attacks cones[9]
P. virginiana	C. virginianae	attacks cones[4]
P. clausa		
Subsect. Oocarpae		
P. radiata	C. radiatae	attacks cones, overwinters in cones[12,13]
P. attenuata		
P. muricata		
No host given	C. clunicus[4]	

[1]Classification according to Critchfield and Little, 1966.

[2]Godwin, 1958.

[3]Godwin, 1959.

[4]Hopkins, 1915.

[5]Miller, 1914.

[6]Miller, 1915.

[7]Ruckes, 1957.

[8]Little, 1943

TABLE 31 Cont'd.

[9]Ruckes, 1963.

[10]Lyons, 1956.

[11]Herdy and Thomas, 1961.

[12]Schaefer, 1962.

[13]Ruckes, 1958.

the pines. First, a survey must be taken of those species of pines from which no Conophthorus have been reported. This survey should help determine the number and distribution of existing Conophthorus species. Second, investigation of the biology of those species of Conophthorus for which only an anatomical description has been given to date, and of those species which may be described from additional pine species, must be conducted. Interpretation of these results may eventually provide a fuller knowledge of the evolution, present distribution and interrelationship of the species in this genus.

The beetles are possibly of more recent origin than the pines and may be more likely to have evolutionary links remaining between them. Consequently this survey might eventually lead to a better understanding of the interrelationships of the pines.

The results from this thesis suggest that different Conophthorus species are not equally tolerant of different pine resins. This suggests another means to help determine the interrelationships of these beetles. It may also be a possible means of control through selective tree breeding.

To further support the findings of this thesis, and to possibly provide a means of morphological identification, search for possible differences between the internal morphology of the jack pine tip beetle and the red pine cone beetle should be conducted. The preliminary cross-fertilization attempt between the two beetle populations reported above should be expanded. In addition, other techniques such as the antibody-antigen reactions, blood protein analysis or genetical techniques such as chromosome studies should be considered.

Conophthorus banksianae, n. sp.

This species is nearly identical to C. resinosae Hopkins but differs in size, behavior and preferred host.

Male holotype.--Length from anterior dorsal margin of pronotum to tip of elytra 2.604 mm. (paratypes 2.576-2.716); width of pronotum 1.008 (paratypes 1.064-1.120); body color very dark brown to black.

Frons slightly convex; feeble median carina at anterior margin; surface almost smooth, sparsely punctate. Antennal club 1.1 times as long as wide.

Pronotum about equal in length and width; summit about midway between anterior and posterior margins; broadly rounded basally, slightly constricted anteriorly; anterior 2/3 roughened, posterior 1/3 punctate with medial area free of punctures; posterior margin with two rows of small setae and punctures.

Elytra approximately twice as long as wide; sides very slightly arcuate, apex rounded distally; surface smooth, shining; strial and interstrial punctures uniform in size and density on dorsal and lateral areas. Declivity moderately steep, bisulcate; stria 1, 2, 3 present; 1 weakly impressed, 2, 3 approximate; interstria 2 smooth, impunctate and strongly impressed; interstriae 1 and 3 punctate and with setae. Vestiture of moderately long setae, more abundant laterally.

Abdomen with seventh and eighth tergites separate and distinct.

Allotype.--Length 2.744 mm. (paratypes 2.548-2.968); width 1.120 (paratypes 1.092-1.204); abdomen with seventh and eighth tergites appearing as single plate, otherwise similar to male in external appearance.

Food plants.--jack, Scotch, ponderosa and non-vigorous, non-cone-producing red pine.

Biology and behavior.--univoltine species. Overwinters in fallen tips; emerges in spring; feeds on old and new growth; oviposits in new growth; most progeny complete development by end of September. Attacks tips primarily, reported to rarely attack cones.

Diagnosis.--C. banksianae attacks and reproduces in tips of jack, Scotch, ponderosa and non-vigorous, non-cone-producing red pine. C. resinosae attacks and reproduces in cones, and to a much lesser extent tips, of red pine. The immature life stages of C. banksianae are present in the field for a much longer time than those of C. resinosae. The male and female adults average shorter and narrower than the adults of C. resinosae; however, the ranges of these measurements do overlap with resinosae.

Type locality.--Fife Lake, Michigan (T26N R9W Sec 26).

Type material.--The male holotype, allotype, three male and eight female paratypes were collected at the type locality from May-June, 1967. All types are temporarily deposited in the Michigan State University Entomology Museum.

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