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PATTERSON, J.E.

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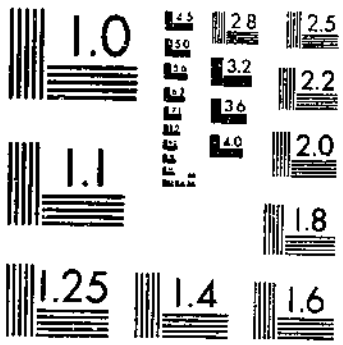

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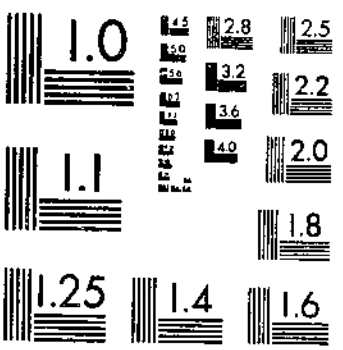

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THE PANDORA MOTH, A PERIODIC PEST OF WESTERN PINE FORESTS

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INTRODUCTION

During the period extending from 1918 to 1925 thousands of acres of merchantable yellow pine on the Klamath Indian Reservation and adjoining timbered tracts in Oregon were severely defoliated by the caterpillars of the pandora moth (*Coloradia pandora* Blake).[1]

This large moth is regularly present in this region, as well as in many other sections of the West, but the history of its past occurrences in destructive numbers reveals the fact that in southern Oregon the insects increase to the proportions of an epidemic at fairly regular intervals of about 20 or 30 years, and continue abundant for from 6 to 8 years.

Indians of the Klamath region report that the caterpillars of the moth recur in large numbers at intervals of about 20 years. An interesting note regarding these large caterpillars is found in a letter to the writer from F. Marion Wilkes, forest topographer of the United States Indian Service, who states that the Klamath and Modoc Indians formerly collected the pupae for food. These they called "bull quanch." Aldrich (*1, 2*)[2] and J. M. Miller (in a letter) state that the Piute Indians in the vicinity of Mono Lake, Calif., collect the mature caterpillars by encircling the infested trees with deep trenches. After descending the trees to pupate, the caterpillars fall into these trenches and are unable to escape. They are then gathered by the Indians, who dry them by burying them in mounds

[1] Order Lepidoptera, family Saturniidae.
[2] Reference is made by italic numbers in parentheses to "Literature cited," p. 19.

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of earth which have been previously heated by fire. The drying process is completed by spreading the caterpillars in the shade. The dried caterpillars, or "peage," are eaten in the form of stew made by boiling them with vegetables. The Klamath Indians were not known to eat the caterpillars, though they considered the chrysalids a delicacy when roasted.

Coloradia pandora has become a forest pest of major importance, at least in the Klamath Reservation and adjoining areas, the repeated defoliations in the years of its abundance having resulted in greatly retarded tree growth, with consequent loss of increment, and, in cases of severe defoliation, in the death of the trees. Even more serious has been the loss from bark-beetle infestations which have developed as a result of the caterpillar's work. Trees which have been weakened by defoliation are very susceptible to the attacks of bark beetles, and an epidemic of these beetles which followed the recent moth outbreak has developed to alarming proportions in these stands during the past few years.

IDENTITY

According to H. G. Dyar, of the United States National Museum, who has identified specimens for the writer, the form of Coloradia occurring in Oregon and California is *Coloradia pandora* Blake. Packard (*9, p. 112*) and Chamberlin (*6*) refer to specimens collected at Fort Klamath, Oreg., as *C. pandora;* and in the publications of Aldrich (*1*) and Essig (*8, p. 670*) on the form of the moth found in California this name is retained. Recently (in 1926) Barnes and Benjamin (*4*) in describing new species of Coloradia have listed specimens from Oregon and California as the new species *C. lindseyi.*

The different forms of Coloradia are not easily separated, and since the insect found in the West is generally known as *C. pandora,* and is thus referred to in economic literature, it seems best to retain this name for the present at least. The species which occurs in southern Oregon and California is therefore referred to in this bulletin as *C. pandora* Blake.

The habits, seasonal history, biology, and economic importance presented in this bulletin apply specifically to the insect in the region of its occurrence in south-central Oregon.

Doctor Dyar in a letter states it as his opinion that there are not more than two species of Coloradia in the United States, of which the larger one, with distinct markings on the hind wings in the male, is *C. pandora* Blake. This is found in different parts of Colorado, and was described from Pike's Peak in that State. Local forms, probably scarcely worthy of separate names, are *C. pandora davisi* Barnes and Benjamin, from the White Mountains, Ariz.; *C. pandora chiricahua* B. and B., from the Chiricahua Mountains, Cochise Co., Ariz.; *C. pandora duffneri* B. and B., from Paradise, Cochise Co., Ariz.; *C. pandora bonnivelli* B. and B., from High Rolls, N. Mex., and *C. pandora lindseyi* B. and B., the form here under consideration. Characters other than locality separating these races are slight, and it is thought best, especially in an economic publication, to ignore these various varietal names.

The other form of Coloradia referred to, namely, *C. doris* Barnes (*3*), is perhaps of specific value. It is from Colorado and Montana,

with a local form, *C. doris luski* B. and B., from the White Mountains of Arizona. This species is not discussed in the present bulletin but is mentioned for the sake of completeness. It is not known, even, that it feeds upon pine.

DESCRIPTION

THE EGG

The eggs of *Coloradia pandora* (fig. 1, C and D) are nearly subspherical or globular in shape, and are slightly compressed on two opposite sides. As incubation progresses the surface has a tendency to shrink, and these flattened sides become strongly depressed. The eggs vary in size, averaging 2.5 mm. in length and 2 mm. in width. The color is pale, semitransparent, bluish green when deposited, later changing to a duller, more opaque, green. They are deposited in clusters of varying size.

THE LARVA

The larvae, when they emerge from the eggs, are approximately 6 mm. long. They are black or brownish and covered with short dark hairs. The head is broad, 2 mm. wide, and shiny black in color. The thoracic segment is nearly as broad as the head, and the rest of the body tapers gradually anteriorly. The full-grown larvae measure from 60 to 70 mm. in length and are yellowish green. (Fig. 2, A, B, and C.)

THE PUPA

The pupae (fig. 2, D), which are dark chocolate brown, range from 13 to 15 mm. in width, and from 25 to 38 mm. in length. The outlines of the folded wings, eyes, antennae, and other characters of the adult are plainly visible on the surface.

THE ADULT

The adults (fig. 1, A and B) are brownish gray. The antennae are biserrate and a little longer than the thorax. The thorax is black, streaked with gray, and is clothed with short, soft hairs. The apex is tufted and extends beyond the wings. The forewings are brownish gray, with an indistinct, wavy, blackish band extending obliquely across them. There is a small, distinct black spot on the discal nervure.

The hind wings are rufous gray, with an indistinct, cloudy band tapering from the interior to the exterior margin. There is a distinct brownish spot on the disk. The base of the wing and interior margin are clothed with pinkish hairs which in the male shade to wine color. Length of body of female 40 mm., of male 28 mm., wing expanse of female 96 mm., of male 85 mm.

HOSTS AND DISTRIBUTION

Coloradia pandora attacks only pines. Western yellow pine (*Pinus ponderosa*) is the preferred host throughout the greater part of the insect's range in the Pacific States. Jeffrey pine (*P. jeffreyi*) and lodgepole pine (*P. murrayana*) are sometimes infested by this moth. The attacks on lodgpole pine appear to be purely incidental, as this species suffers only when it occurs in stands of yellow pine.

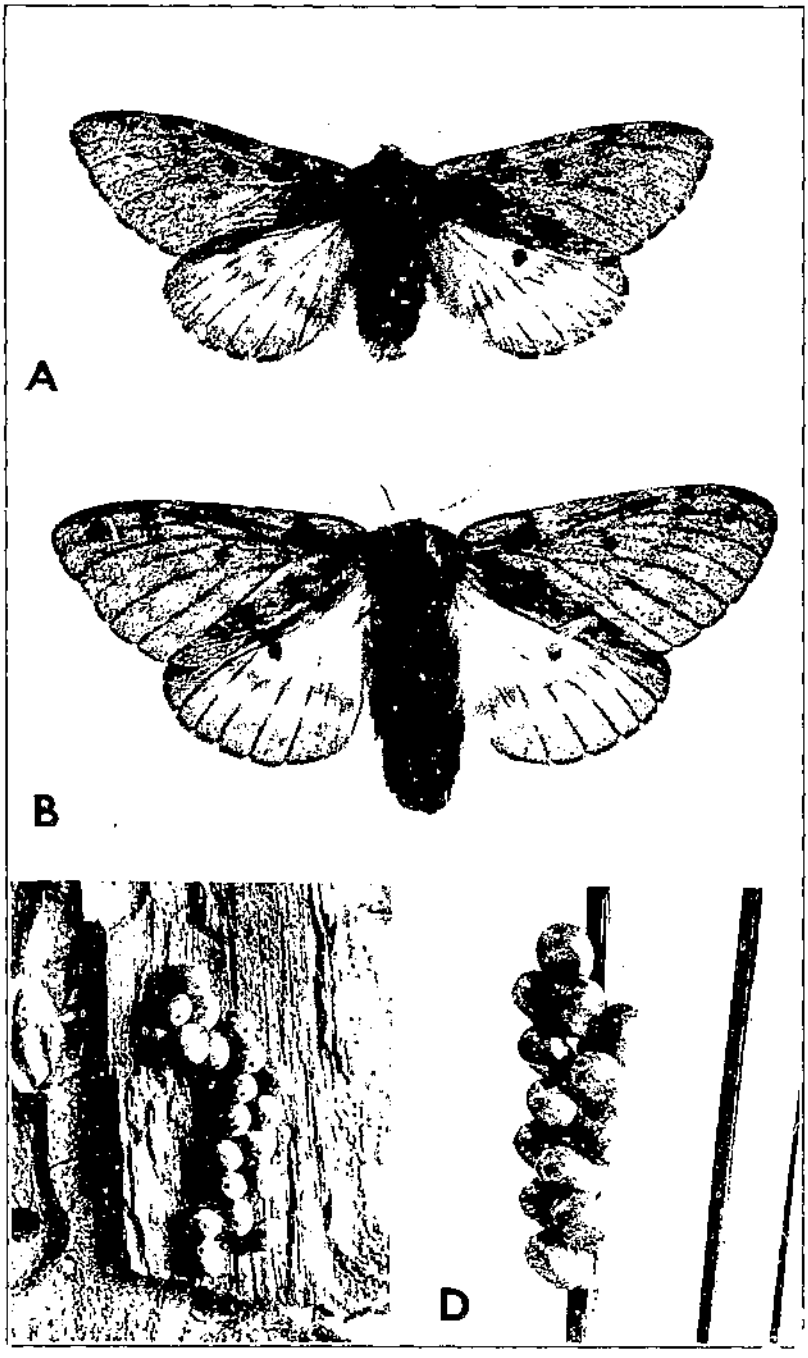

FIGURE 1.—*Coloradia pandora*: A, Male moth, natural size; B, female moth, natural size; C, cluster of eggs on yellow pine bark, ×2; D, eggs attached to yellow pine needle

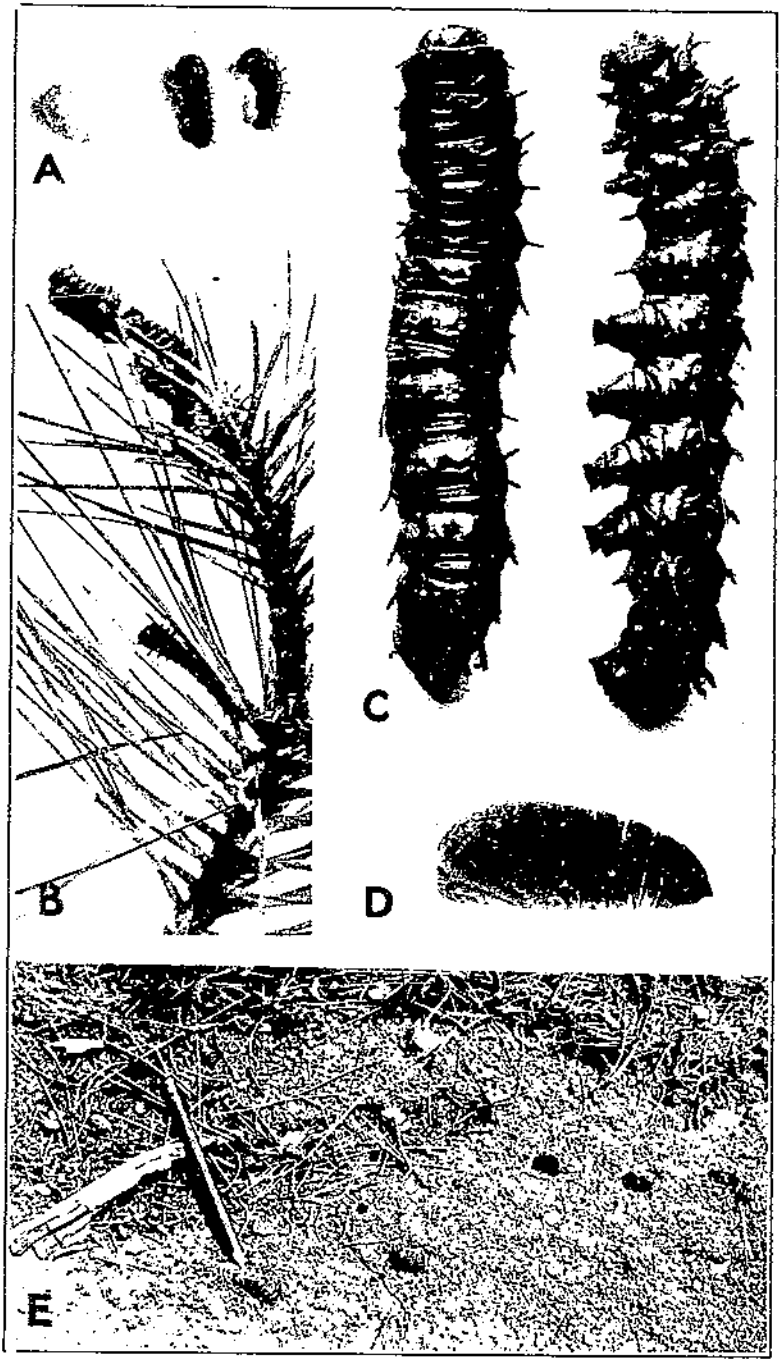

FIGURE 2.—*Coloradia pandora:* A, Newly hatched caterpillars and empty egg-shell, ×3; B, caterpillars in first spring feeding stage, eating yellow pine needles, ×⅝; C, full-grown caterpillars ready to pupate, ×1⅛; D, pupa, natural size; E, pupae in natural position in surface of soil (the debris on the ground and the top of soil have been removed to expose the pupae)

Coloradia pandora has been recorded from various sections in all the Pacific States[3] (*1, 2, 5, 9, 10*). Its range is probably coincident with that of the western yellow pine, its principal host. The writer has collected the insect throughout the pine belt from the Sierra National Forest in south-central California to as far north as Bend in central Oregon. Though the species is thus shown to be of rather wide distribution, severe infestations of this pine defoliator have been recorded from only two localities, south-central Oregon and the Inyo National Forest in east-central California. In the latter section occurrence of the species has not been epidemic in the true sense of the term, but has had more of the character of a high endemic infestation. There are definite records of the species occurring in highly epidemic form in the former region only. Packard (*9, p. 113*) states that the insects were common at Fort Klamath for a few years prior to 1893. The recent epidemic developed on the Klamath Indian Reservation, Oreg., in 1918 and continued unabated until 1925, when there was a noticeable decline in the number of caterpillars and pupae, and the defoliated trees began to show recovery. In 1926 the number of adults was negligible as compared with the number of those of the previous flight years, and it was apparent that the recent epidemic had about run its course.

It is possible that the decline of the epidemics and the comparative exemption from moths in the intervening years are due to the activity of the moth's natural enemies, which under normal conditions may be capable of holding the infestation in check.

Pupation takes place in the ground, and it seems that a loose, pumice soil in which the caterpillars can easily bury themselves is necessary to the most successful development of the moth. It is significant that epidemics of *Coloradia pandora* have occurred only where this type of soil is found.

NATURE AND EXTENT OF INJURY

The following discussion of the damage done by *Coloradia pandora* is not exhaustive. Unfortunately it was not possible to study from its beginning the recent epidemic of this insect on the Klamath Indian Reservation. There is need for a more detailed and comprehensive study of this injury than has been possible in the past.

It must be borne in mind that under normal conditions infestations of this pine defoliator are of no economic consequence, because defoliations are not then severe enough to have any appreciable effect on a tree's growth or vitality. It is only during epidemics of the insect that damage results. This damage naturally divides itself into two phases: The primary injury to the tree, or that resulting directly from its loss of needles, and the secondary injury, brought about by the weakened condition of the tree, rendering it more susceptible to bark-beetle attacks.

PRIMARY INJURY

Although *Coloradia pandora* may at some periods cause practically complete defoliation of the trees which it attacks, it is not always of

[3] SNYDER, T. E. FOREST INSECT INVESTIGATIONS. U. S. Dept. Agr., Bur. Ent. Mo. Letter 108: 4-5. 1923. [Mimeographed.]
——— FOREST INSECT INVESTIGATIONS. U. S. Dept. Agr., Bur. Ent. Mo. Letter 112: 2-3. 1923. [Mimeographed.]

itself fatal to its host.[4] The amount of defoliation which a tree may suffer and yet live is suprising, and the amount of defoliation which accompanies normal infestations of *C. pandora* does not affect the trees in the least degree. That even seemingly complete defoliation does not always cause the death of trees is due to two facts: (1) The terminal buds are not eaten by the caterpillars, and the tree thus retains the power to put forth new needles; and (2) the tree has a breathing spell every second year, even during epidemics, because the insect has a 2-year life cycle, and the period of heavy feeding occurs only in alternate years.

The greatest economic loss for which *Coloradia pandora* is directly responsible comes about through the suppression of the tree's growth, particularly during years of severe defoliation.[5] The width of the annual rings may be as much as 80 per cent less than normal, and in some cases the trees fail to put on any new wood on one or more sides of the trunk. It is evident that a great loss of increment occurs during the period of an epidemic, and this loss, when sustained over large areas of merchantable timber, amounts to many hundred thousands of board feet. Although this loss is known to exist, many complicated factors make it difficult to estimate, even roughly, the total loss occasioned by the recent epidemic. The greatest difficulty is encountered in the fact that there is very wide variation in the degree of defoliation of individual trees. This is one of the most striking features of these epidemics. Frequently a completely defoliated tree or group of trees will be found standing side by side with trees only slightly defoliated. (Fig. 3, A.) The amount of increment loss is entirely dependent upon the degree of defoliation, and the variableness of this latter factor makes an accurate estimate of the loss over large areas almost impossible.

Some idea of the loss was obtained by making a study of individual trees in areas where the epidemic had occurred and comparing their rate of growth with that of trees under normal conditions outside of defoliated areas. As before stated, however, the study does not date from the beginning of the epidemic, and it was not always possible to determine accurately in what year the trees selected for comparison were first attacked. Despite these difficulties, the writer believes it well within conservative limits to place the loss thus far sustained during the recent epidemic in the Klamath region at not less than several hundred thousand dollars. Although the epidemic infestation has declined, it will be a number of years before the trees which have suffered severe defoliation regain their

[4] Recent investigations in the epidemic areas on the Klamath Reservation have revealed the fact that many severely defoliated trees have died as a direct result of the defoliation. Though these trees died two years after the last severe defoliation, this must have been the direct cause of death, since there was no damage present due to insects or other causes. As this result of severe defoliation is now known to occur, it is very probable that the death of many of the defoliated trees, formerly attributed to the bark beetles, was due primarily to defoliation.

[5] This type of damage is characteristic of many forest-tree defoliators, especially of the spruce budworm (*Harmologa fumiferana* Clem.), occurring in the northeastern part of North America. F. C. Craighead, in his studies on this insect (7), found that it was possible to trace previous epidemics and to date the years of feeding by the characteristic suppression of the annual rings.

normal growth rate, and thus a further loss in increment will be sustained. This will depend upon the rapidity of their recovery, which at this time is merely a matter of conjecture.

FIGURE 3.—Yellow pine and lodgepole pine on the Klamath Indian Reservation, Oreg., defoliated by *Coloradia pandora*: A, Clump illustrating different degrees of defoliation in yellow pine. The large tree with the figure at the base has been severely defoliated. The large tree immediately behind it shows only about 50 per cent defoliation. B, A lodgepole pine in an open situation that has been completely defoliated. The men in the foreground are searching in the soil for pupae. July, 1921

Transverse sections from defoliated trees are illustrated in Figures 4, 5, and 6. The reduction in annual growth during the years of defoliation, compared with the normal growth during the years preceding heavy loss of needles, is clearly shown. In Figure 5, A and B, are cross-section disks from the top portion of the stems

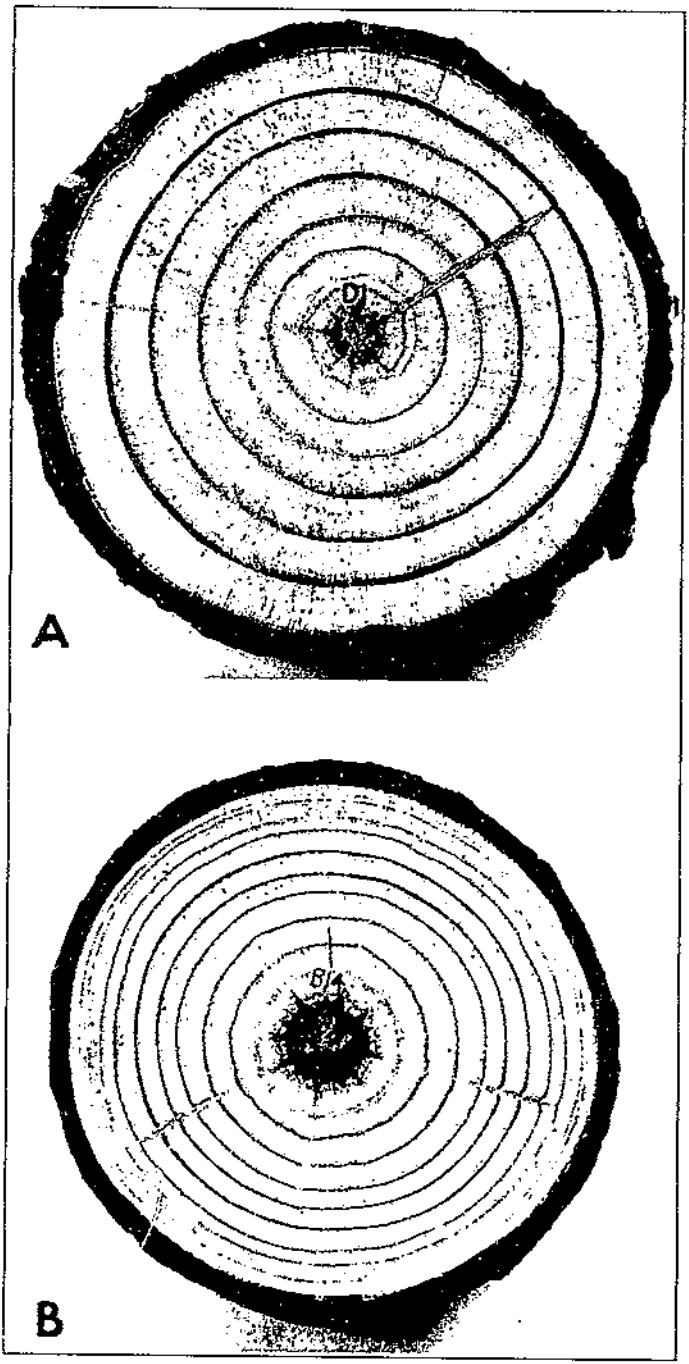

FIGURE 4.—Transverse sections of normal and defoliated yellow pine: A, Apical portion of the stem of a fast-growing tree which has not been defoliated, natural size; B, apical portion of the stem of a tree from Calimus Butte which had been defoliated biennially since 1918 by *Coloradia pandora*. The last feeding was in 1925; note the partial suppression of the outer rings, owing to defoliation. August, 1926

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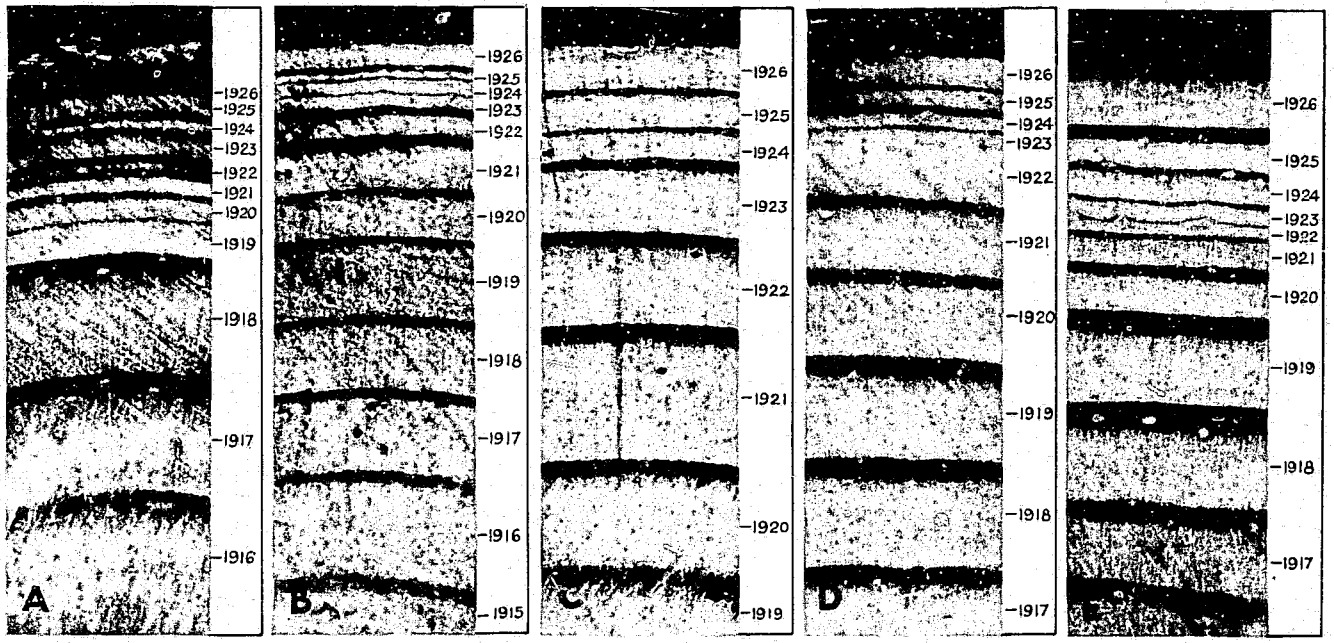

FIGURE 5.—Comparison of annual radial increment of yellow pine trees defoliated by *Coloradia pandora:* A to D, Upper portion of stems; E, base of tree shown in parts of transverse sections, ×7.5; A, tree from Wocus Bay showing partial recovery. First heavy feeding in 1919, last heavy feeding in 1925. Note reduction in width of growth layers since year of first feeding and increased width of next to the last ring, indicating recovery. B, Tree from Black Hills successively defoliated since 1921. Note narrowness of outer five rings, showing suppression of increment owing to defoliation. C, Tree from Pot Holes defoliated during only three years, 1923, 1924, and 1925. Note suppression in rings of 1924 and 1925, and narrow width of the fall wood of these rings. D, Tree from Calimus Butte defoliated annually since 1919. Note suppression, due to defoliations, in the growth of the 1923, 1924, and 1925 wood. Apparent recovery in 1926 is indicated by the greater width of this ring. No fall wood had formed in the 1926 ring because the section was cut in the late summer. E, Section from base of the same tree as shown in D. Note comparative narrowness of the annual rings from 1919 to 1925, showing the suppressed increment at the base of a defoliated tree

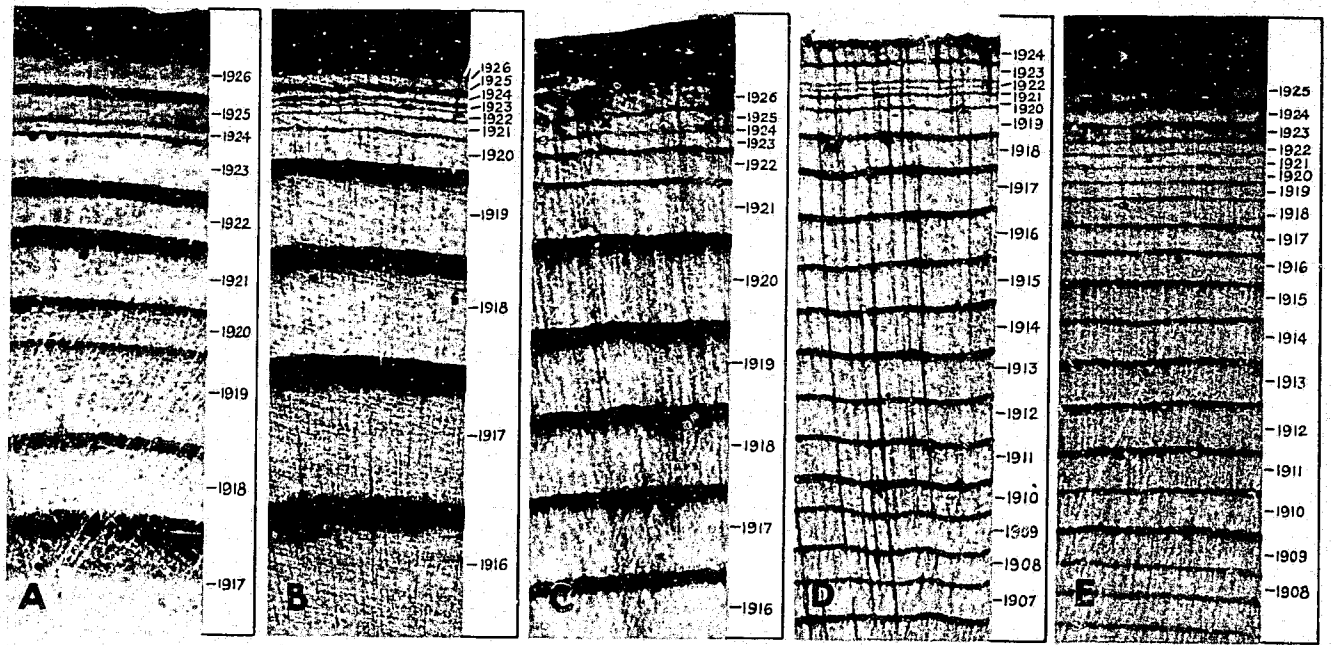

FIGURE 6.—Transverse sections of pine stems showing increment rings of years of normal growth and of years of defoliation by *Coloradia pandora*, all shown ×7.5: A, Apical portion of lodgepole pine from River Beds, Oreg., in a stand defoliated since 1919. Note narrowness of the ring for 1924, the year which marked the peak of the epidemic. The comparative absence of fall wood is also a conspicuous feature of this ring. The last two rings represent the growth of 1925 and 1926. Their widths indicate that the tree was rapidly recovering. B, Middle portion of stem of yellow pine, from Wocus Bay, Oreg., defoliated since 1918. Note narrowness of last seven rings and the entire absence of the next to the last ring beyond the point marked X. C, Section from top of a yellow pine from Long Bell, Oreg., defoliated since 1918. Note that at X one annual ring fades into the previous ring, showing the loss of the earlier ring on one side of the tree. D, Section from top of yellow pine from the Klamath Indian Reservation, Oreg., defoliated since 1918. This tree was attacked and killed by *Dendroctonus brevicomis* late in the summer of 1924. Note retardation of growth for four years previous to attack by the bark beetle. E, Section from yellow pine from Long Bell, defoliated since 1918 and attacked and killed by *D. brevicomis* late in the summer of 1925. Note the series of narrow annual rings preceding the attack by the bark beetle

of two yellow pines, selected to show the contrast between the rate of growth of defoliated and that of nondefoliated trees.

The transverse sections in Figure 5, A to E, and Figure 6, A, illustrate the loss in increment of trees selected from various sections of the defoliated stands. The variation in the ring growth in these pictured sections is due to the variation in the degree of defoliation suffered by the trees in these separate localities.

Sections B and C, of Figure 6, which are transverse sections from trees defoliated since 1918, show the omission of part of an annual ring on one side of the stem. Figure 6, B, is a transverse section from the middle portion of the stem. It will be seen that the next to the last ring is missing at the point marked X. Figure 6, C, is a transverse section from the top portion of the stem and shows the partial loss of the third ring from the cambium. It fades into the previous ring at the point marked X.

SECONDARY INJURY

That there is close interrelation between the work of this pine defoliator and subsequent attacks by the bark beetle is shown by the abnormal increase of beetle infestations in the stands of defoliated pine. Beetle infestations became highly epidemic in the stands which had been severely defoliated, while at the same time they showed but slight increase in stands outside these areas.

The data on beetle infestations in the defoliated areas were obtained by surveys of an area of 2,000 acres made annually since 1921, and by observations made throughout the infested region.

The damage caused by bark beetles has been far greater in its effect than the primary damage of the defoliator, which results in retarded growth but not always in the death of the trees. Attack by the two species of bark beetles *Dendroctonus brevicomis* Lec. and *D. monticolae* Hopk., infesting these stands, always results in the death of the tree.

Sections from defoliated trees, later killed by bark beetles, are shown in Figure 6, D and E. These are typical in that the annual growth for a few years previous to the attack of the beetles had been greatly retarded.

Previous to 1923 the defoliated stands were remarkably free from infestations by the bark beetle, and had been so for a long period. In 1923, however, five years after the pine-moth epidemic began, the defoliated stands were invaded by these beetles, and within two years an outbreak of them developed which seriously menaced the entire area. The progress of the outbreak on the 2,000-acre area mentioned was as follows: In 1923 the area contained 50 trees infested by beetles, which may be considered a normal infestation in these stands. In 1924 this infestation included in all 391 trees, an increase of 682 per cent. Five hundred and six trees had become infested in 1925, an increase for the year of 29 per cent, and in 1926 a total of 744 trees had been killed, an increase of 47 per cent in the third year. These figures show that in three years the bark-beetle epidemic, which was a secondary result of the defoliations, had increased 1,388 per cent. This is a very abnormal increase in infestations by these beetles.

That a similar increase in infestations by the beetles during the same years occurred throughout all the defoliated stands was shown by observations made in widely separated sections.

The loss by bark beetles in merchantable trees throughout the defoliated stands from the beginning of the epidemic in 1923 to and including the year 1926 was tremendous. In 1926 this loss amounted to nearly 100,000,000 board feet of pine on the Klamath Indian Reservation. However, it is not probable that this enormous loss will continue after the trees have recovered from the effects of the defoliation. It is now believed that a return to normal growth will very probably be followed by a sharp decline in the losses due to the beetles. The rapidity of recovery of these stands will depend upon a number of factors, chief of which are the disappearance of the defoliator, the physiological condition of the severely defoliated trees, soil conditions, and precipitation.

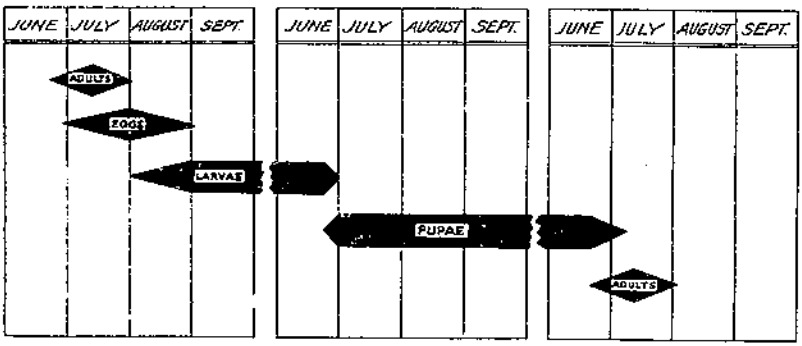

FIGURE 7.—Chart showing the stages of *Coloradia pandora* as related to its 2-year life cycle. The two intervals, each extending from September to June, are omitted, one being occupied by the larval period and the other by the pupal

BIOLOGY

The generations of *Coloradia pandora* are biennial, the life cycle of the species covering a period of exactly two years, as shown in Figure 7. The adults emerge between June 20 and July 20 of alternate years. On the area studied by the writer, flights of the adults have occurred in the even years—1920, 1922, 1924, and 1926, although it was found that a few stragglers departed from the cycle of the main broods and emerged in the odd years. However, these stragglers have the same life span as the others, and two years are required to complete their development.

After emerging from the pupal cases near the surface of the soil, the new adults crawl through the litter on the ground to the trunks of trees or to bushes, which they ascend. On these they remain at rest for from 20 minutes to an hour while their wings are unfolding, and the scales and hairs on the body and wings become dry. The adults are strong fliers, and are strictly diurnal. In the writer's studies individuals could never be found active at night, nor could they be attracted to lights displayed in the forest after dark or before daylight. The males take to flight as soon as their wings have hardened,

and fly erratically about through the forest, searching for mates. The females, while equal to the males in their ability for sustained flight, usually do not fly until after mating.

The males appear two or three days before the females and die soon after mating. The females die shortly after they have finished depositing their eggs. The writer observed that in a lot of 20 individuals, 12 males and 8 females, confined in a wire-screen cage in the open woods, all the males died first, and within the day of mating. The females lived from 5 to 7 days longer, but all died within from 1 to 3 days after oviposition.

Females have been observed in the act of oviposition in the field as well as in captivity, and under both conditions the procedure is the same. The moth does not make a preliminary search for a suitable location in which to place her eggs, but deposits them indiscriminately on the bark of tree trunks, in the foliage, on brush and undergrowth, and even on the litter covering the ground. A moth does not always lay all her eggs in one cluster or in one location; a second or even a third cluster may be deposited. It is quite usual, for instance, for a moth to deposit her first cluster of eggs upon the trunk of a tree, and then crawl or fly to the foliage, where the rest of her eggs are laid. The eggs are but loosely attached to the support upon which they are deposited, although they adhere to one another very firmly.

The eggs are deposited in clusters containing from 3 to 70 eggs each. (Fig. 1, C and D.) In one instance a total of 258 eggs were laid by 5 females caged separately, or an average of 51.6 eggs each. The greatest number laid by 1 female was 68 and the smallest, 42. A period of 6 days was covered in the deposition of these eggs, 2 laying all their eggs in 1 day, the other 3 taking 2 days each for the egg laying.

The maximum period of oviposition extends from July 10 to July 20. The incubation period is rather prolonged, lasting approximately 40 days. Eggs deposited by moths in captivity on July 16, 1924, hatched on August 25. Changes in the external appearance of these eggs during incubation were not noticeable until August 2, or 17 days after they were laid. At this time the color had changed to a deep olive, the sides were deeply depressed, and the embryo had taken form. From August 11 to 14 the well-incubated young caterpillars became visible through the egg walls. On August 25 all the fertile eggs hatched. It has been found that incubation in the field follows the same course and is of the same duration.

A relatively high percentage of the eggs are infertile. Out of a lot of 200 eggs taken in the field and put into glass vials, 1 egg in each vial, 40 eggs, or 20 per cent, proved to be infertile, while in 58 eggs, or 29 per cent, the embryos partially developed, but died.

The young larvae begin to emerge about August 20 and continue emerging until September 15. The maximum emergence occurs between August 25 and September 5. The larvae leave the eggs by way of holes gnawed in the ends of the shells (fig. 2, A) and immediately crawl to the tips of the branches and begin feeding on the needles of the current year's growth. They develop rapidly, and by September 20 reach a length of 14 mm. They are gregarious

during the first feeding stage; from 4 to 20 may be found together on the needles at the terminals of the twigs. They attain a length of 23 mm. by the end of the first feeding season.

When winter conditions set in, which at the altitudes where the species occurs is normally about October 20, the caterpillars go into hibernation, in clusters of from 4 to 30 individuals, at the base of the needles on the ends of the pine branches, and are more or less dormant during the winter. They have not been observed to feed during hibernation and do not increase in size. With the cessation of winter conditions, usually at about April 1, the caterpillars again become active. The hibernating masses break up and the individuals disperse to some extent and resume feeding.

During the spring feeding period, which lasts until June 20, the caterpillars consume an enormous quantity of needles and grow rapidly. The following record made of caterpillars which were confined in a wire-screen cage at the Klamath Falls laboratory illustrates the development of the larvae during this second feeding period:

Date (1923)	Average length	Color	Date (1923)	Average length	Color
	(*Mm.*)			(*Mm.*)	
Apr. 1	28	Olive green.	May 12	55	Greenish.
Apr. 14	28	Do.	June 6	60	Light green.
May 5	33	Do.	June 16	70	Yellowish green.

On June 18 all had pupated.

Feeding is not confined during the spring period to the needles at the tips of the branches, but the caterpillars work back along the stem and consume all needles of whatever previous years' growth. (Fig. 2, B.) From about May 1 to the time of pupation they also eat the new needles which unfold from the buds, and make their greatest growth during this period. The terminal buds, however, are not eaten, although the new needles are nearly all devoured. (Fig. 8, A.) Owing to the 2-year life cycle of the insect this wholesale destruction of the new needles at the critical period of the tree's growth occurs only on alternate years, the corresponding time of the intervening years being passed by the moth in the pupal stage.

The prepupal caterpillars are excessive feeders and consume an enormous quantity of needles. A lot of 34 nearly full-grown caterpillars were kept in a cage from June 1 to June 16. During this time they ate an average of 700 yellow pine needles each 24 hours, or an average per caterpillar of 21 needles a day.

The great quantity of food taken by these caterpillars is attested in the field by the masses of droppings found under infested trees. These droppings closely resemble the dried and fallen male pine catkins, and under large trees completely cover the surface of the ground from the base of the tree outward as far as the branches extend.

When full-grown the caterpillars crawl down the trunks of the trees on which they have been feeding and enter the surface of the soil to pupate. They have never been observed to lower themselves from trees by silken threads.

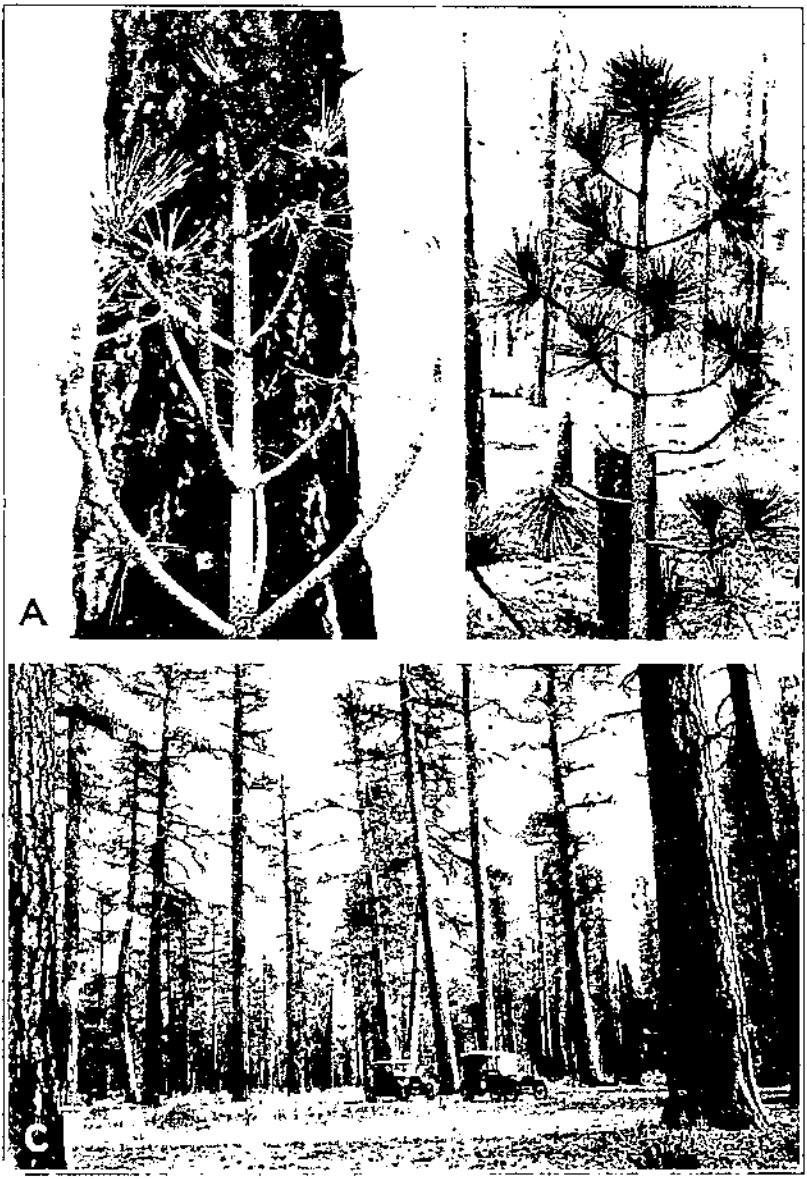

FIGURE 8.—Effects of feeding of *Calocalpia pendora*: A, Top of yellow pine, showing almost complete defoliation resulting from successive biennial feeding of the caterpillars; note that the terminal buds are not injured; B, top of yellow pine which has been repeatedly defoliated up to the last two years; note recent recovery and contrast with A; C, a stand of mature yellow pine at Worms Bay, Klamath Indian Reservation, Oreg., severely defoliated, July, 1921

Pupation occurs in the upper layer of the soil (fig. 2, E), from 1 to 5 inches below the surface, both directly beneath the defoliated trees and at some distance from them. The caterpillars, after entering the soil to the desired depth, usually sufficient to prevent des-

sication, revolve in their tunnels, making elliptical cells in which they transform to pupae. Some of these cells are sparsely lined with a silky material, but the greater number are entirely unlined. The pupa rests within the cell, head up, and inclined about 60° from the vertical. Pupae begin to form June 20, and pupation is over by July 5. This stage lasts one full year, the insects passing the second winter of their life as pupae in the ground.

NATURAL ENEMIES

Coloradia pandora has many natural enemies. During the prepupal stage, and while the caterpillars are descending the trees to pupate, a large percentage of them are attacked by a wilt disease, in general appearance quite similar to the gipsy-moth polyhedral wilt. Caterpillars infected with this disease become limp, turn black, and shrivel to about one-third the normal size. Great numbers of the caterpillars are destroyed by this disease during epidemics of *C. pandora* and it is doubtless a major factor in the decline of severe infestations.

Ground squirrels (several species of Callospermophilus) and a chipmunk (a species of Eutamias) dig up and eat large numbers of the pupae. These rodents were observed on many occasions uncovering the pupae; some pupae were eaten at the time they were removed, though many were stored for future food. A chipmunk was seen carrying pupae to a rotten log, and when the cache was examined 54 were found in a hollow in the interior.

Birds have been observed to feed sparingly on the caterpillars. Steller jays and vireos are known to eat the caterpillars, although the stiff bristles and hairs on the backs and sides of the larvae are a great protection from birds. Creepers and nuthatches feed on the eggs of the moth and no doubt destroy large numbers of them.

The following insects are parasitic on *Coloradia pandora*.[6]

No. 1. *Blepharipeza adusta* Loew. This dipteron is a larval parasite. The maggots emerge from the prepupal caterpillars after the latter have entered the ground to pupate, and form naked puparia in the soil near the remains of the host. The percentage of parasitism was not determined, though as many as 41 puparia were taken from an area of ground 5 feet square where 76 pupae of *C. pandora* were found.

No. 2. A species of Tetrastichus. This is a hymenopterous parasite of eggs of *C. pandora*. Of 100 isolated eggs of the moth 17 were parasitized by this species and from them a total of 128 individuals emerged. The smallest number emerging from one egg was 3 and the largest 11, the average being $7\frac{1}{2}$.

No. 3. *Trichogramma minutum* Riley. This small species is a cosmopolitan parasite; it breeds in the eggs of *C. pandora* as well as having many other hosts. Of 100 isolated eggs of *C. pandora*, 5 were parasitized by this species, and a total of 147 individuals emerged from them. The smallest number emerging from one egg was 20 and the largest 37, the average being $29\frac{1}{2}$.

[6] Determination by specialists of the Bureau of Entomology has been as follows: No. 1 by C. T. Greene; Nos. 2 and 3 by A. B. Gahan; No. 4 by R. A. Cushman.

No. 4. *Hemiteles tenellus* Say. Only one individual of this rather large braconid was reared by the writer from a larva of *C. pandora*. This species is a larval parasite, and its papery cocoons are attached to the body of the caterpillar. It emerges late in May. The percentage of parasitism by this species is not known.

METHODS OF CONTROL

It seems probable that this pine defoliator might be held in check during the incipient stages of an epidemic by spraying infested trees with arsenicals. The caterpillars could easily be poisoned by spraying the foliage during the spring period of maximum feeding. The spraying of large forested areas, however, if delayed until after an epidemic had developed, would be impracticable because of the excessive cost of such operations. Airplane dusting might be done at a reasonable expense, and would probably be effective.

SUMMARY

The Pandora moth (*Coloradia pandora* Blake) is an important enemy of pine forests in certain areas of the West. During the years from 1918 to 1925, inclusive, a serious epidemic of this moth occurred in the yellow-pine forests of the Klamath Indian Reservation in southern Oregon.

This insect attacks only pines, its principal hosts being western yellow pine (*Pinus ponderosa*) and Jeffrey pine (*P. jeffreyi*). Lodgepole pine (*P. murrayana*) is sometimes attacked. Infestations by this moth have also occurred in the Inyo National Forest of east-central California. Its range is known to cover the Pacific States, and specimens have been collected in Colorado and Montana.

Under normal conditions infestations of this moth are of no economic consequence because no appreciable injury is done to the tree. Epidemic infestations by this moth are, however, a serious menace to pine stands. The damage resulting from such infestations divides itself into two phases: The primary injury to the tree, which results directly from the loss of needles, and the secondary injury through the impaired vitality of the tree, which renders it susceptible to bark-beetle attack.

Although *Coloradia pandora* at some periods may cause practically complete defoliation of the trees which it attacks, it is not always of itself fatal to its host. This is due to the fact that the terminal buds are not eaten by the larvae and that the trees have a rest every other year. Thus the more vigorous specimens survive the defoliations. Economic loss results, however, even though the trees attacked are not killed, because their growth is greatly suppressed during years of heavy defoliation, as shown by comparison of the width of the annual rings. Losses on the Klamath Indian Reservation from this suppression of growth during the last epidemic have been conservatively estimated at several hundred thousands of dollars.

The damage caused by bark-beetle attacks in stands of pine defoliated by the Pandora moth has been far greater than the primary damage of the defoliator. Infestations of *Dendroctonus brevicomis* and of *D. monticolae* have shown an abnormal increase

in the defoliated areas studied. These infestations were of far greater intensity than were contemporary infestations in stands adjoining the defoliated areas, and beetle attacks upon defoliated trees were always fatal.

The life cycle of this moth covers a period of two years. The adults are brownish gray with a wing expanse of approximately 3 inches. They are diurnal, and in epidemic infestations countless numbers are seen on the wing. The eggs are deposited on the bark and foliage of trees and bushes, and sometimes on ground litter. The incubation period is approximately 40 days. The young larvae feed in colonies upon the needles of the terminal shoots during the first summer and, when winter sets in, hibernate in clusters at the base of the needles. Feeding is resumed the following spring, and during this second feeding period large quantities of needles are consumed, and the greatest damage is suffered by the host. Pupation begins in June of the second year and takes place in the ground from 1 to 5 inches below the surface. The pupal stage covers one full year, the species passing the second winter as pupae in the ground.

The caterpillars are subject to a wilt disease similar in general manifestations to the gipsy-moth wilt. Ground squirrels eat large numbers of the pupae, and birds prey upon the caterpillars. The insect enemies of *Coloradia pandora* are three hymenopterous parasites and one dipteron.

No direct efforts have been made to control this moth. It seems probable that it might be held in check during incipient stages of its attack by spraying with arsenicals or by airplane dusting.

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