ECOLOGICAL FACTORS INFLUENCING DIAPAUSE IN THE SPRUCE BUDWORM CHORISTONEURA FUMIFERANA (CLEM.). (TORTRICIDAE)

Ъу

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م با محمد ری<u>ست</u> می مخت

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ABSTRACT

Investigations were carried out to determine the effect of ecological factors on the induction of diapause in the spruce budworm.

Experimental rearings were conducted at elevations of 2500, 4200 and 4750 feet. The foliage of spruce, Douglas fir and alpine fir were used as hosts. Progeny of Ontario, twoyear and one-year types reared under one-year and two-year life cycle conditions were used as experimental insects.

A trend was observed in emergence from hibernation with the one-year type leading, followed by the two-year and finally the Ontario type.

It was shown that the one-year type larvae may adopt the two-year habit. The main factor influencing this is a prolonged development period for the parents. The larvae reared at the higher elevations showed a greater proportion entering diapause. Food played a

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smaller role with spruce and Douglas fir being more favourable for diapause than alpine fir. The increased percentage of larvae in diapause in 1952 is attributed to a longer development period for their parents and to a sharp drop in temperature occurring about 12 days prior to diapause.

The Ontario material may adopt the two-year habit. The factors contributing to this have not been clearly shown as the rearing results are inconclusive.

There were no definite differences shown in the time for development among the three foods. The insects at the lowest station developed in approximately three weeks less time than at the highest. The difference between the upper stations was slight.

The impracticability of converting a one-year life cycle population to a two-year cycle by forest management is noted. The diapause theories of Wigglesworth and Andrewartha are commented on. A possible course of evolution leading to the establishment of a two-year life cycle population is given

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INTRODUCTION

Diapause is defined by Wigglesworth (1950) as a spontaneous arrest of development which supervenes irrespective of the environmental conditions. Diapause may occur in any stage of the life cycle but the stage at which it occurs in any species is as a rule rigidly fixed. In different insect species it exerts its effect under various circumstances but usually once the individual has entered diapause it has to remain in that state for a certain period, regardless of the conditions of the environment.

Insects in diapause are characterized by a low metabolic rate, greatly diminished activity, practical cessation of development, and an increased ability to survive unfavourable environments. They do not respond immediately to any ordinary amelioration of the external conditions, as do insects whose development has been inhibited by their environment. Development is resumed only after exposure to certain required conditions, such as cold, for a given period.

Diapause plays a major role in the life cycle of the spruce budworm. This species is found in Canada from the Atlantic to the Pacific Ocean and north almost to the limit of timber. It extends down the Appalachian Mountains to Virginia in the Eastern United States and has been reported as far south as New Mexico in the West. In short it is distributed throughout the entire range of its food plants.

Spruce and balsam are the preferred food plants over the greater part of the range of the spruce budworm. In north-western Ontario and the Lake States a form that prefers Scotch pine and jack pine was studied by Graham (1935) and Brown and McKay (1943). In British Columbia

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Douglas fir is one of the main hosts.

In Eastern America, the adults emerge from mid-June to the latter part of July, commencing to lay their eggs within two to five days. The eggs hatch in nine to twelve days. The young larvae find a sheltered niche, spin a cocoon or hibernaculum, molt to the second instar and overwinter in diapause. The following spring the larvae emerge from their hibernacula, coincident with or a few days before the balsam buds open. This is generally in late April or early May. A large percentage of the young larvae form mines in the old needles in spring before attacking the new buds. After passing through five instars the larvae pupate in late May or in June and after a pupal period of about ten days, emerge as adults.

In British Columbia in the Douglas fir regions of the Interior and on the coast the

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life cycle is much the same as that outlined for the eastern insects. The dates vary considerably due to local differences in climate but in general, the period of activity is May, June and July.

On the other hand, in the sprucebalsam forests on the high plateaux of central and southern British Columbia, and extending into the north-western States and in the sprucebalsam forests of the Rocky Mountains, the spruce budworm has a two-year life cycle. This was noted and studied first by Mathers (1932) in the Barkerville district. In this case the larvae emerge from hibernation about the middle of June and develop slowly until the middle or latter part of July when, still in the third instar, they spin hibernacula, molt to the fourth instar and enter diapause and overwinter again. The following spring, feeding is resumed about the middle of June and adulthood reached by the latter

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part of July.

The pupal period is approximately three weeks and the incubation period is about the same length of time.

Because of the synchronization of the development of the population there are small, inconspicuous larvae one year while the next year the larvae are large and feeding voraciously. The two-year life cycle, with heavy feeding only in alternate years, renders the insect much less destructive than it is in a one-year cycle area.

It is apparent that, if by forest management or other means, the one-year cycle could be changed to a two-year cycle the depredations of this insect would be greatly reduced. The crux of the problem lies in the diapause intervening at the close of the third and the beginning of the fourth instar in the two-year cycle. The determination of the factors

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causing this diapause is a necessary preliminary step before any practical measure may be undertaken.

By observation it is known that the one-year type is typically associated with Douglas fir at lower and with spruce and alpine fir at higher elevations. Thus the reasonable factors to investigate are food and altitude.

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DIAPAUSE THEORIES

Published work on diapause in insects is extensive. For comprehensive bibliographies the reader is referred to Uvarov (1931), Prebble (1941), Bonnemaison (1945), Dickson (1949), Wigglesworth (1950) and Andrewartha (1952). The writer will not attempt to review all the work but will summarise the results reported, particularly on the basis of the suggested mechanisms, and the ecological conditions affecting diapause.

Suggested Mechanisms:

A Inception of diapause -

(a) Autointoxication - the theory
of autointoxication was developed by Roubaud (1922),
working with <u>Lucilia sericata Meig.</u>, who
postulated that autointoxication is caused by
the accumulation of metabolic wastes which build

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up faster than they can be eliminated during active growth, so that a period of rest is needed to allow elimination to catch up. This work has been discredited by Cousin (1932), who showed that diapause in <u>Lucilia</u> is caused by environmental factors.

(b) i Diapause factor or hormone -Bodine (1932) studied diapause in the eggs of Melanolplus differentialis (Thos.) and advanced the theory that there is a diapause factor (X factor) present in the diapause type egg of that species at the time the eggs are laid. If these eggs are held at comparatively high temperatures, the amount or potency of the diapause factor increases until it passes a threshold at the "three-weeks" stage and stops embryonic development. The diapause factor is gradually dissipated after this point and eventually allows development to resume. Exposure to low temperature at any time, either before or after the "three-weeks" stage, rapidly destroys the diapause factor, and development

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resumes as soon as the temperature is raised.

This theory was extended by Salt (1947) working with the wheat stem sawfly <u>Cephus cinctus</u> Nort. He speculated that diapause in this species is controlled not only by an X factor as defined by Bodine, but also by a Y factor, which breaks down more slowly than does the X factor but at a constant rate, regardless of temperature. He was able to reinstate diapause by exposure to relatively high temperatures (35°C) at any time before the Y factor was eliminated.

Wigglesworth (1948) believes that diapause is due to the absence of a growthpromoting hormone which controls molting, secreted by the neuro-secretory cells of the brain. He speculates that the raw materials for the hormone in <u>Rhodnius</u> may be vitamins produced by the symbiotic bacterium <u>Actinomyces</u> <u>rhodnii</u> harboured in the gut of the insect.

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Way and Hopkins (1950) consider it probable that diapause in the pupa of <u>Diataraxia</u> <u>oleracea</u> L. is due to the absence of a hormone responsible for adult differentiation rather than the presence of an inhibiting hormone. This conclusion has also been reached by Williams (1946) who found that in <u>Platysamia</u> <u>cecropia</u>, <u>Telea</u> polyphemus and <u>Callosamia</u> <u>promethea</u>, pupal diapause results from an interruption of the normal processes of development by a failure of the brain to supply a non-species-specific factor necessary for adult differentiation.

The causal agent for the inhibition of the hormone secretion has been postulated by Andrewartha (1952) to be an accumulation of an intractable food reserve occurring in the eggyolk or, in post-embryonic stages, in the fat body, which may not be immediately broken down in preparation for the next stage in morphogenesis.

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This intractable food reserve may be due to an unbalance in the metabolism such that the building-up processes go on normally but the breaking-down processes are reduced to a minimum. Whether this unbalance is to be attributed to the accumulation of a different sort of food reserve, or to the absence of a necessary enzyme system or to both, is left to be determined by physiological studies.

B Termination

Recent experiments (Williams 1946, 1947, 1948 and Williams and Sanborn 1948, Pappenheimer and Williams 1952) have shown the brain to be the organ of primary control over diapause in pupae of <u>Platysamia cecropia</u>. It was found, by implantation techniques, that the termination of diapause requires the action of a minimum of two factors, one arising from the brain and the other from the prothoracic glands (Lee 1948). The brain factor is necessary for the activation of the prothoracic glands. Chemical analyses showed that cytochrome c is virtually absent from the diapausing pupa. During the period when development is dependent on the prothoracic glands, the concentration of cytochrome c increases from less than 1 to more than 50 gamma per live weight. Similarly during the period of the brain's secretory activity, the titre of cytochrome oxidase increases from approximately 40 to nearly 700 units. As a result of the combined functions of both the brain and prothoracic glands, the tissues of the dormant pupa, for the first time, come into possession of a complete cytochrome system.

Conditions affecting inception of diapause

A Environment.

The environmental factors commonly

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inducing diapause may be listed as those of temperature, food and water, and photoperiod.

(a) Temperature.

Pupal diapause may be induced in <u>Telea</u> <u>polyphemus</u> (Cramer) by subjecting the last larval stadium to declining temperatures (Dawson 1931). Prebble (1941) found that diapause in emergent stocks of <u>Gilpinia</u> <u>polytoma</u> (Htg.) is determined environmentally, and showed that larval feeding at low temperatures favours entry into diapause as full-fed larvae.

(b) Food and water.

Food and water are closely related in insect dietary as most of the water taken by insects occurs in the food. The condition of the food has been found to influence the induction of diapause. Squire (1940) reported that diapause of the full-fed larvae of the pink bollworm, <u>Pectinophora gossypiella</u> (Sound.), is independent of the season and depends on the moisture content of the seeds in which they feed. Fife (1949) found in the same insect that diapause is most abundant during periods of drought.

(c) Photoperiod.

The effect of photoperiod in inducing diapause in the oriental fruit moth is reported by Dickson (1949) where diapause is controlled by temperature and daily exposure to light during the larval feeding period. Larvae grown in the absence of light do not enter diapause. As the period of light per day is increased to more than three hours, the percentage of diapause increases, reaching 100 per cent with about twelve hours of light. As the photoperiod is increased to more than thirteen hours per day, the percentage of diapause drops suddenly to practically zero.

Way and Hopkins (1950) showed that the induction of diapause in the pupa of

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Diataraxia oleracea L. is influenced by temperature and photoperiod during the larval stage, with low temperatures and short photoperiods tending to induce diapause while high temperatures and long photoperiods tend to prevent diapause.

In mites Miller (1950) and Lees (1950) found that diapause is induced by a shortening day length.

B Heredity

There are many insect species which have but one generation per year, with a considerable part of each year spent in diapause. This behaviour pattern may well be genetically fixed. The diapause occurring in second instar larvae of the spruce budworm falls in this category.

In discussing the effect of inheritance on diapause, Dickson (1949) reviews two notable

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cases as follows: "A few insect species are known in which there are both single-generation strains (univoltine) and multiplegeneration strains (multivoltine). One of these is the silkworm Bombyx mori L., in which the diapause occurs in the egg. The univoltine strains of the silkworm have but one generation annually, and the diapause occurs in every generation. Multivoltine strains have two to several generations annually; eggs laid in the summer hatch in a short time; those laid in the fall enter diapause. The inheritance of voltinism in the silkworm is somewhat complex, there being some evidence for somatic inheritance from the mother. It is reported by Uyema (1926) that if the ovaries from an individual of one race are transplanted to an individual of another race during the larval stage the eggs produced show the voltinism of the moth in which they are grown rather than that of their true ancestors.

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The likelihood that a given batch of eggs will enter diapause is also influenced by the temperature at which the eggs and larvae of the preceding generation were held."

Dickson (1949) continues: "In the case of Pyrausta nubilalis (Hbn.), a species which enters diapause as full-fed larvae, it is well known that some areas are occupied bv one-generation strains and others by two-Babcock (1924) reported generation strains. that when specimens of the one-generation strain were transferred to an area occupied by the two-generation strain, and vice versa, they persisted in retaining the same seasonal histories that they had shown in their original environments. Arbuthnot (1944) found that in Connecticut the population is homozygous for multiple generations, while in Ohio it is mixed, containing factors for both single and multiple generations. He was able to

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isolate a homozygous single-generation strain from the Ohio population, and found that the genetic factors responsible for the single generation are recessive. O'Kane and Lowry (1927), working with this insect in New Hampshire, showed that although the population was homozygous for multiple generations, only a part of them actually went through two generations per year, the rest having but one. All the larvae from the first eggs of the season pupated that same summer and produced a second generation, while larvae from eggs that hatched after a certain date, usually about July 20 to 25, entered diapause and so had only one annual generation. Apparently, environmental factors are involved in the induction of diapause in this species, at least in the multiple-generation strain."

Prebble (1941) found that in the European spruce sawfly, <u>Gilpinia polytoma</u> (Hartig)

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there are different strains within the species, with respect to the inherent tendency towards diapause or continued development. The population in the southern areas has two or more annual generations while the population in northern areas is composed of a strain having one annual generation, diapause intervening after a single generation even under favourable environmental conditions.

PROCEDURE

The present investigation was primarily designed to determine the effects of environmental conditions and food on diapause and secondarily to ascertain the effects of these factors on development of the budworm.

Preliminary work on this project was started at Lillooet, B. C., in 1949. The basic plan was to introduce two-year type larvae into a one-year area with rearings made at different elevations. From this it was hoped to determine the approximate conditions under which diapause occurred. As there were no laboratory-reared insects available, reliance was placed on fieldcollected larvae. Due to delays the local oneyear larvae were well advanced before rearing could be begun. Larvae of the two-year form were collected at Bolean Lake, near Falkland, B. C., by Mr. W. G. Mathers, and at Castle Mountain, Alberta, by Dr. K. Graham on June 21 and sent to

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Lillooet. These larvae entered diapause between June 28 and July 5 although very hot weather prevailed at that time. This indicated that the factors producing the diapause were operative early in the larval stage, if not in the preceding generation.

In 1950, studies were carried out from a camp at Bolean Lake, situated at an elevation of 4750 feet in the alpine fir-Engelmann spruce forest type. There is a high endemic population of two-year spruce budworm in this locality.

Three rearing stations were used, located as follows:

Station I (2500 feet) in a typical Douglas fir-yellow pine forest type.

Station II (4200 feet) in a transition zone with a mixture of Douglas fir, Engelmann spruce and alpine fir.

Station III (4750 feet) in a typical Engelmann spruce-alpine fir forest type.

One-year stock, progeny of adults mated at Lillooet, two-year material which had

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entered diapause at Lillooet, and Ontario stock air-expressed from Port Arthur were confined in sleeve cages on Douglas fir at Station I, spruce and alpine fir at Station III and on all three hosts at Station II, and in vials on the same foods at Station III. From these studies it was found that food is not a major factor in the initiation of diapause. Some individuals of the one-year type entered diapause in the vials. Also on the basis of one specimen it was seen that Ontario one-year material may be induced to take two years to develop.

Following the findings of Uyema (1926) and the indications given at Lillooet in 1949 it was suspected that the treatment of the parents might have some effect on the diapause of the progeny. It was arranged in 1950 to have matings made of one-year adults at the Trinity Valley Field Station (2100 feet elevation). The

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moths were from Forest Insect Survey collections made in the Lillooet district. This series provided larvae whose parents had matured under one-year conditions.

Matings were also made at Bolean Lake (4750 feet elevation), of two-year, Ontario and one-year stock from the material reared there. This series provided larvae whose parents had matured under two-year conditions.

The resulting larvae, from both breading series, were overwintered in vials at Trinity Valley. Thus in 1951, the following types of larvae were on hand. Each type was given a code letter for convenience in recordkeeping.

Two-year life cycle from B. C. (S) progeny of budworm reared at Bolean Lake.

One-year life cycle from B. C. (D) progeny of budworm reared at Bolean Lake.

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One-year life cycle from B. C. (F) progeny of field-collected larvae reared at Trinity Valley.

One-year life cycle from Ontario (B) progeny of budworm reared at Bolean Lake.

Vials containing the overwintering larvae were distributed among the three stations on May 18, so that at each station there was a supply of each type of larva. As the larvae became active they were transferred to sixounce jelly jars, with taped-on tops. Ten larvae, in the majority of cases, were placed in each jar with sufficient foliage to support the feeding of that number. A series of four or five jars of each type of larva was reared on each of the three hosts, spruce (Picea Engelmanni Parry.), Douglas fir (Pseudotsuga taxifolia (Poir.) Britton), and alpine fir (Abies lasiocarpa (Hook.) Nutt). As a means of reducing possible variation due to food source foliage was taken from Station II to feed the insects at Stations I and III.

feed the insects at Stations I and III.

Breeding was carried out again as the insects reached maturity in 1951. Difficulty was experienced in obtaining hibernating larvae of the Ontario type at Stations II and III so that none was available for rearing in 1952. The one-year type failed to hatch satisfactorily at Station III but sufficient numbers were obtained from Station II. The second instar larvae from the breeding program, and those larvae in the fourth instar diapause were overwintered at Trinity Valley. Thus, the experimental larvae on hand for the 1952 season consisted of the following, coded as indicated.

Two-year cycle from B. C. (S) progeny of budworm reared at Bolean Lake (4750 feet) in 1950, overwintering in the fourth instar from 1951.

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One-year cycle from B. C. (D) progeny of budworm reared at Bolean Lake (4750 feet) in 1950 and overwintering in the fourth instar from 1951.

One-year cycle from B. C. (F) progeny of fieldcollected larvae reared at Trinity Valley (2150 feet) in 1950 and overwintering in the fourth instar from 1951.

- One-year cycle from B. C. (F1) progeny of F material reared and bred at Station I (2500 feet) in 1951.
- One-year cycle from B. C. (F₁₁₁) progeny of F material reared at Station II (4200 feet) in 1951.
- One-year cycle from Ont. (B) progeny of budworm reared at Bolean Lake (4750 feet) in 1950 and overwintering in the fourth instar from 1951.
- One-year cycle from Ont. (B₁) progeny of B material reared and bred at Station I (2500 feet) in 1951.

As the analysis of the 1951 results showed that Station II was almost a duplicate of Station III, it was decided to eliminate Station II from the 1952 program. The original designations for Stations I and III were retained. The second year larvae from Station II were placed at Station III to complete their development. The rearing technique used was the same as in 1951 except that when the larvae were available six jars were used for each series.

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RESULTS

Emergence.

The overwintering larvae were placed in the field on May 18 in 1951 and on May 19 in 1952. The following tables (I and II) give the dates for the first emergence for each type at each station for the two years. The date for the first emergence is used as the great majority of the one-year larvae emerged on that day. The emergence of the second instar twoyear type was extended over approximately five days. In Table I in two instances two dates are given and explained below. The coding is as given above.

TABLE I

Dates for beginning of emergence from hibernation 1951.

| Station | 1 yr.B.C. reared at TV. | | l yr rear Sta. | ed at III | 2 yr rear Sta | ed at | l yr.Ont. reared at Sta. III B | | |
|---------|-------------------------------|------------|----------------------|-----------|---------------------|-------|---|---------|---|
| |] | 3 | D | | | S | | | |
| I | May | 20 | May | 20 | May | 22 | May | 22 | |
| II | May | 22 | May | 22 | May | 26 | June | 4 | |
| III | May | 22 & 26 | May | 26 | May | 31 | May June | 22 4 | & |

TABLE II

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Dates for beginning of emergence from hibernation 1952.

| | Second instar | | | | | : Fourth instar | | | | | | |
|---------|----------------|----|---------|----|-----|-----------------|------|----|-----------|----|------------------|-----------|
| Station | F ₁ | | F 11 | L | В | | F | | D | | В | S |
| I | May | 20 | May | 21 | May | 24 | :May | 26 | May | 26 | | May 22 |
| III | May | 22 | May | 22 | May | 30 | :May | 29 | May 28 | ľ | Iay 29 | May 26 |

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In Table I it is seen that the one-year cycle larvae came out together at the three stations. The two-year larvae were later in each case, appearing at the same date as the Ontario-Bolean material at Station I. At Station II the Ontario-Bolean material was later than the two-year larvae. At Station III a few Ontario-Bolean larvae came out on May 22, but the onset of a period of cold weather delayed the main emergence until June 4. The same thing happened to the one-year Trinity Valley type, but in this case emergence was resumed on May 26.

In 1952 (Table II) there was very little difference between the dates for Stations I and III. This was due probably to the insects being on the verge of emergence when they were removed from storage. The Ontario type larvae,

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as in 1951, were the last to emerge of the second instar larvae at both stations. The fourth instar one-year type larvae were appreciably later than the second instar at both stations. The S, or two-year type, however, emerged prior to the other types.

These data show a trend in the beginning of activity with the one-year material leading, followed by two-year and finally the Ontario stock.

Feeding.

The larvae readily accepted the three foods offered. Atwood (1944), in Ontario, reported the mining of needles by second instar larvae. This habit has been noted also by officers of the Vernon Forest Biology Laboratory; in one-year type larvae on Douglas fir at Lillooet in 1949, by W.G. Mathers, and in two-year type larvae on the same host at Heart Lake in 1951 by

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J. Grant. In this experiment, individuals of all stocks mined needles of the three hosts at all stations in 1951 and 1952.

Development.

The results of the rearing are summarised and tabulated by Stations and year (Tables III, IV, V, VI for 1951; Tables VII, VIII for 1952). In these tables the first column gives the type and food. The code for types is as given on pages 23 to 24 and 25 to 26 while the foods are coded as follows: spruce -- s, Douglas fir -- df, alpine fir -- a.

The second column "emerged" shows the number of larvae originally placed in the jar. "Established" gives the number of larvae which began to feed successfully. "Unestablished" are those that failed to feed successfully and died. The "died" column gives the number of

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larvae that died after establishment. "Killed" gives those that were accidentally killed while the food was being changed in the jar. "Unaccounted" includes those larvae that disappeared: many of these were in the early instars and probably represented dead larvae whose cadavers could not be found but in a few instances cannibalism may have taken place. Under "diapause" the number of larvae entering diapause is given. Under the heading "pupae" the number that died as pupae, the number of specimens of each sex, and the mean number of days from the time of emergence to pupation are found. Under "adults" the number of each sex and the mean number of days from pupation to adulthood are given.

In Tables VII and VIII the total mean days for development from emergence to maturity is given. These figures are given in Table VI

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for the 1951 results. This mean development period is for the individuals which matured and thus of course does not include the larval periods of those that died as pupae.

2

| Be Bdf Ba | a df S S S S S S S S S S S S S S S S S S S | Ds Ddf Da | Far Far | Type and Food | ı |
|----------------------|---|----------------------|---------------------------|------------------|-------|
| 51 40 40 | 60 71 | 52 50 50 | 51 50 49 | Emerged | |
| ນ ຜູ້ນ ດ ບີ ນ | 417 66 61 | 38 40 45 | 37 49 45 | Established | |
| 29 5 14 | 13 10 10 | 14 5 | 4 1 4 | Unéstablished | LAR |
| 0 N N | 4 | ന ന ന ന | N G N | Died | VAI |
| 00 KO 00 | 20 | 3 H 8 | H N N | Killed | |
| 8 4 K | | 4 00 | 41 10 10 | Unaccounted | |
| ÷ | 43 63 59 | រិនខ | ч | Diapause | |
| សស | | 041 | ល 4 ល | Died | |
| 12 14 | · | 10 12 | 12 -13 22 | No. Male | |
| 50.2 46.0 44.1 | | 49.2 50.8 | 48.4 48.5 49.0 | Mean No. Days | PUPA |
| 5 4 A | ಸ | 13 11 11 | 16 26 17 | No. Female | F |
| 49.6 45.8 | 45.5 | 51.4 52.6 | ମ ମ ମ ଓ ଓ ଓ ୦ ଓ ଡ଼ି | Mean No. Days | |
| 12 13 | | 10 16 12 | 12 13 21 | No. Male | |
| 10.5 10.5 | | 11.1 10.8 10.5 | 12.1 11.6 11.8 | Mean No. Days | A D U |
| 344 | N | 11 12 | 11 22 15 | No. Female | LTS |
| 000 37 8 | 10.0 | 9.7 10.2 10.0 | 11.4 10.3 10.6 | Mean No. Days | |

TABLE III Summary of Rearing Results, Station I 1951

- 2,500 feet.

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| Bdf | S C C C C C C C C C C C C C C C C C C C | Ds Ddf Da | Fe Fdf Fa | Type and Food | |
|-----------------------|---|----------------------|---|------------------|-------|
| 36 | 50 50 | 90 00 00 | 39 50 50 | Emerged | |
| 18 | 45 45 | 47 77 44 | 41 39 33 | Established | |
| 18 | 5 5 | 13 13 | 9 6 | Unestablished | LAR |
| ч | 6 13 | 13 6 16 | 8 7 8 | Died | VAH |
| ц | чч | о Т | دی | Killed | |
| 4 | ი U -J | 13 8 | 17 7 1 | Unaccounted | |
| ບາ | 10 17 31 | 18 19 4 | л н ———————————————————————————————————— | Diapause | |
| ц | | 4 10 10 | <u>н</u> ю | Died | |
| 3 | | 124 11 | 6 16 1 | No. Male | ЪЧ |
| 62.0 | | 63.5 64.2 64.0 | 64.0 65.9 64.2 | Mean No. Days | JPAE |
| 4 | ب | 2 14 10 | 14 21 | No. Female | |
| ອ ອ ອ ອ ອ | ,57 . 0 | 67.5 67.9 66.4 | 66 • 63 • 66 • 0 | Mean No. Days | |
| N | | 9 22 22 28 28 | 15 9 | No. Male | |
| 22.5 | | 18.5 18.1 17.7 | 20:2 21.1 | Mean No. Days | A D |
| 4 | . ــــــــــــــــــــــــــــــــــــ | 11 7 | 2 P/ | No. Female | U L T |
| 21.7 | 14.0 | 18.8 18.4 | 21.0 33.8 | Mean No. Days | Ω |

Summary of Rearing Results, Station II - 4,200 feet. 1951 TABLE IV

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| | | | |] _ ` | |
|----------------------|----------------------|----------------------|-----------------------|--------------------------|----------------|
| a a a | Ca f | Da df | a a f a f | Type and Food | |
| 28 49 40 | 51 60 42 | 35 39 | 50 64 61 | Emergence | |
| 16 31 | 40 25 | 23 23 23 | 37 50 49 | Established | |
| 12 18 4 | r 28 28 | 6 11 | 13 14 12 | Unestablished | н |
| 1-12 | щ | ъго | 15 4 | Died | ARV |
| N | ын | ч | ц 4 | Killed | A E |
| 0 o N | <u>ы</u> 22 | 4004 | 040 | Unaccounted | |
| 7 17 20 | 33 22 22 09 02 22 | 5 ¹¹³ | ЧЧ | Diapause | |
| τυ | | ち上4 | 0 7 G | Died | |
| ω Η ΓΟ | | ᆸᅭᇬ | 14 25 | No. Male | г о |
| 48.3 65.0 51.0 | · · | 67.4 67.0 61.1 | 71.6 67.8 64.8 | Mean No. Days | JPAE |
| 01 4 00 | | 12 4 2 | 12 16 | No. Female | |
| 50.5 68.5 53.1 | | 65.2 67.5 63.0 | 67.5 70.4 69.1 | Mean No. Days | - |
| , 3 | | 11 3 | 8 10 10 | No. Male | |
| 12.3 16.0 14.0 | • • | 25.3 17.0 | 27.0 21.3 20.0 | Mean N o. Days | À D |
| 03 4 W | | 440 | 122 | No. Female | ULT |
| 17.5 22.5 17.5 | | 26.5 26.5 | 20.0 21.5 21.6 | Mean N o. Days | ß |

TABLE V

Summary of the Rearing Results, Station III - 4,750 feet. 1951

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TABLE VI

Mean Days of Development from Emergence from Hibernation to Adulthood 1951

| | | | | | | ~ | | | | <u> </u> | | | | | <u>-</u> | | | |
|-------------|---------------------------|----------------|----------------------|----------------|----------------------|-----------------|----------------------|---------------|----------------------|---------------|----------------------|--------------|----------------------|------|----------|------|--------|--|
| | | | 5 | PR | U C E | В | UDW | ORI | M T | YP. | E A | ND | OR | IG | IN | | | |
| | | (ne-ye | ear Trin | ity V | alley | One-year Bolean | | | Ontario-Bolean | | | ean | Two-year Bolean | | | lean | | |
| | | M | Male Female | | | М | ale | Fe | male | M | ale | Fe | male | Male | | Fe | Female | |
| <u> </u> | Food | No. | Days | No. | Days | No. | Days | No. | Days | No. | Days | No. | Days | No. | Days | No. | Days | |
| Station I | Spruce D. fir Abies | 12 13 21 | 60.6 60.1 60.5 | 11 22 15 | 62.4 63.2 62.8 | 10 16 12 | 60.3 61.7 61.1 | 12 9 10 | 61.1 64.4 62.9 | 2 12 13 | 60.5 56.5 54.7 | 4 11 3 | 62.2 59.3 55.6 | | - | 2 | 55.5 | |
| Station II | Spruce D. fir Abies | 15 9 | 85.1 85.6 | 4 12 | 87.5 86.4 | 2 21 9 | 82.0 82.1 80.7 | 12 7 | 85.1 85.4 | 2 | 82.0 | 4 | 78.2 | | | 1 | 71.0 | |
| Station III | Spruce D. fir Abies | 8 18 10 | 97.6 89.5 84.9 | 3 13 13 | 87.5 91.8 90.3 | 3 11 | 92.6 78.2 | 4 4 8 | 91.5 94.0 82.5 | 3 1 3 | 60.6 81.0 66.0 | 2 4 8 | 68.0 90.7 72.8 | | | - | | |

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| B1 DF | F111S F111DF F111A F111A | F1S F1DF | Type and Food | , | |
|----------------|-----------------------------------|----------------------|--------------------------------|-------------|-------|
| 70 | 60 60 | - 60 60 | Emerged | | |
| 46 | 54 55 | 5 4 6 2 6 0 | Established | - - - | |
| 24 | 5 5 5 5 0 10 | α 14 8 | Unestablishe | ed | н |
| · و، | 27 7 16 | 31 21 21 | Died | | ARI |
| د ی | N | てもて | Killed | | 7 À 1 |
| 11 | 11 6 91 | ი ი თ | Unaccounted | | |
| н | 404 | ч ч | Male | 4 | |
| 4 | 20 7 | н, н | Female | Diapa | |
| | ччч | $r \infty \infty$ | ? | ause | |
| | <u>н</u> 0 | 8 ¹¹ 4 | Died | | |
| ЦЗ | 15 15 | 12 14 14 | No. Male | | ਾਰ |
| 53 • 5 | 58.8 50.5 | 51.2 58.7 51.9 | Days | | UPA |
| ບາ | 0 J 10 | 4 17 00 | No. Female | | E |
| 55.0 | 54.0 58.4 53.5 | 64:2 61.8 56.1 | Days | | |
| 12 | 15 12 | ഗരഗ | No. Male | | |
| 13.1 | 15.0 14.0 | 14.3 14.6 16.8 | Days | | A D U |
| ບາ | ๛งง | 60 4 FC | No. Female | | L J |
| 11.4 | 15.0 12.8 14.3 | 11.0 11.7 14.2 | Days | | Ω. |
| 67.1 | 0 70.2 64.7 | 72.3 72.1 67.1 | Total Mean Days <u>MALE</u> | | |
| 66.4 | 69.0 71.2 67.8 | 73.6 75.4 70.4 | Total Mean Days FEMALE | | |

TABLE VII Station I - Tabulation of one-year and Ontario results. 1952

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| BIDE | F111S F111DF F111A | F1S F1DF F1A | Type and Food | |
|------|--------------------------|--|----------------------------------|--------|
| 58 | 35 40 40 | 888 | Emerged | |
| 45 | 15 22 27 | 41 52 52 | Established | |
| 13 | 20 18 13 | 81 88 81 | Unestablished | LA |
| თ | 4 4 | 8 12 8 | Died | RV |
| | ЧЧ | ∾ ⊢ | Killed | E A |
| 12 | 50 CH | 737 | Unaccounted | _ |
| | 3 10 | 0 H 4 | Male 5 | |
| | ະ | Ю 4 | Female p | |
| ß | 14 6 | ちゃよ | ? • | |
| ω | | បាសផ | Died | |
| 0T | . ପ <u>ା</u> | 14 12 14 | No. Male | ਿ |
| 64.8 | | 75.0 81.0 71.7 | Days | UPA |
| 14 | 4 | 0 N S S S S S S S S S S S S S S S S S S | No. Female | B |
| 70.4 | 68.0 | 79.5 73.1 | Days | |
| 10 | <u>ମ</u> | 13 | No. Male | |
| 22.5 | 17.6 | 20.1 | Days | ADU |
| თ | 4 | ດຮວ | No. Female | н Н |
| 26.6 | 16.7 | 27.4 30.5 21.3 | Days | |
| 90.3 | හ ඉ •. ප | 0 92.1 | Total Mean Days <u>MALE</u> | |
| 98.5 | 88 20 20 | 104.4 110.0 94.2 | Total Mean Days <u>FEMALE</u> | |

TABLE VIII

Station III - Tabulation of one-year and Cntario results 1952

-07-

Ontario-Bolean Larvae (B).

The data for the development period of the Ontario-Bolean type are inadequate for definite analysis, notably at Stations II and III in 1951, and due to the low number available for rearing in 1952. However, Table VI shows that at Station I the food apparently had some effect on the time for development with alpine fir being the most favourable, followed by Douglas fir, with spruce the least favourable. On spruce the number of days taken was approximately the same as that for the one-year stock. On Douglas fir and alpine fir the time was roughly five days less. In 1952 the time for the Ontario-Bolean type on Douglas fir was much the same as that taken for the one-year type on alpine fir. Comparing the time in 1951 for the two female adults recovered from the two-year larvae, with the Ontario material on alpine fir and Douglas fir, shows that these are somewhat similar.

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One-year larvae

Again, Table VI shows that at Station I the differences in days for development between foods and between types were slight. An analysis of variance of the mean days for development for the two types was made, based on five rearing jars on each of three foods for both sexes of the two types. The mean for four jars was used as a fifth in the case of the male Trinity Valley type on spruce, and for a female on Douglas fir in the Bolean type. The mean for three jars was substituted for the missing two in the Bolean type on alpine fir.

The analysis showed that the differences between the means for food and types were not significant at the 5 per cent level. The difference for sex was significant at 1 per cent. A further analysis was done of the days for development of the two types at the three stations on alpine fir. This host was chosen as having

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the best distribution of adults, necessitating substitution of means in only three cases. The analysis showed that the differences due to sex were highly significant and those due to station were significant at the 5 per cent level. The interactions of type and station were significant at the 5 per cent level. The differences due to type were not significant.

The results for the other foods are erratic and somewhat contradictory. This may be due to the small numbers of individuals in some cases and to the fact that the larvae were being reared in an environment differing from their natural one.

The data for 1952 are not adequate for analysis but inspection of the days for development as given in Tables VII and VIII suggest that the F_{111} type developed more quickly than the F_1 . It is suggested that a diet of alpine fir favoured more rapid development.

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Two-year larvae.

Because of the very few adults recovered from this type, no conclusions regarding the period of development can be drawn. The significant fact is established that some individuals of the two-year life cycle type can develop in one year.

The two-year larvae completed their life cycle in 1952 and were bred. No noteworthy data were obtained on their development as it proved impossible to trace the development of individuals as emergence was spread over several days in the spring. The main object in rearing this type in 1952 was to obtain progeny for use in 1953.

Comparison of Stations.

In comparing the entire results from the three stations, it is evident that development was markedly faster at Station I than at

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Stations II and III but the latter two showed very little difference. In an attempt to evaluate these differences the means for the sexes at each station were calculated, combining the data for the four stations. The following means were obtained:

| | | - | M | ale | Fena | ale | |
|------|---------|-----|--------------|------|------|------|--|
| | Station | I | 59.5 | days | 60.9 | days | |
| 1951 | | II | 82 .9 | days | 84.5 | days | |
| | | III | 81.3 | days | 85.4 | days | |
| 3050 | Station | I | 68.9 | days | 70.5 | days | |
| TAPS | | III | 90.2 | days | 99.0 | days | |
| | | | | | | | |

Thus development at Station I was faster by about 23 days in 1951 and 25 days in 1952 than at Station III. Stations II and III were practically the same in 1951.

'n

Diapause

The number of larvae surviving in diapause or to pupation and the number and percentage of these entering diapause is given by type, food, and station in Table IX for 1951 and in Table X for 1952. Table XI presents the data given in Tables III, IV and V and Table XII presents the data in Tables VII and VIII in condensed form showing the total number of larvae reared and their fate expressed in percentages. TABLE IX

Total number in diapause or surviving to pupation and the percentage in diapause in 1951.

| | | | Picea Engelman | ni | · P | seudotsuga taxifolia | a | | Abies lasiocarpa | | | |
|-------------|------------------|----------------------|--------------------|----------------------------|----------------------|-------------------------|-------------------------------|----------------------|---------------------|----------------------------|--|--|
| | Type | No. of Survivèrs | No. in Diapause | ∦ in Diapause | No. of Survivors | No. in Diapause | % in Diapause | No. of Survivors | No. in Diapause | % in Diapause | | |
| Station I | F D S B | 29 26 43 6 | 1 6 43 0 | 3.4 23.1 100.0 0 | 39 32 65 26 | 0 3 63 0 | 0 9.3 96.9 0 | 39 36 59 19 | 0 13 59 0 | 0 36.1 100.0 0 | | |
| Station II | F D S B | 3 24 10 | 1 18 10 | 33.3 75.0 100.0 | 25 57 17 12 | 5 19 17 5 | 20:0 33.3 100.0 41.6 | 21 25 32 | 0 4 31 | 0 8.0 96.8 | | |
| Station III | F D S B | 16 23 22 12 | 0 13 22 7 | 0 56.5 100.0 58.3 | 37 16 20 22 | 1 11 20 17 | 2.7 68.7 100.0 77.2 | 32 28 39 33 | 0 5 39 20 | 0 17.8 100.0 60.6 | | |

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TABLE X

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Total number in diapause or surviving to pupation and the percentage in diapause for one-year and Ontario types in 1952.

| | Picea Engelmanni | | | a anni | P | seudots taxifol | uga ia | Abies lasiocarpa | | |
|-------------|---------------------|---------------------|--------------------|------------------|---------------------|--------------------|---------------------|---------------------|----------------------------|------------------|
| | Type | No. of Survivors | No. in Diapause | % in Diapause | No. of Survivors | No. in Diapause | % in Diapause | No. of Survivors | N o. in Diapause | % in Diapause |
| Station I | F1 F111 B1 | 20 7 | 4 2 | 20.0 28.5 | 23 38 23 | 2 16 5 | 8.7 42.1 21.7 | 25 26 | 3 7 | 12.0 26.9 |
| Station III | Fl Flll Bl | 20 8 | 12 8 | 60 100 | 12 14 27 | 8 14 3 | 66.6 100 11.1 | 35 25 | 9 16 | 25.7 64.0 |

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TABLE XI

Rearing Results Condensed and Expressed as Percentage 1951

| | | | | | | | Fate of Larvae | | | | | | | |
|-------------|--------------------|-------------|------|---------|------------|----------|----------------|---------------------|------------|---------------------------------------|-------------|--|--|--|
| | • | | | | | | | Establis | hed | | | | | |
| | | | | | Die | d | | | | | | | | |
| , | | | Fail | ed to | Afte | r Es- | | | | | | | | |
| | | | Esta | blish | tabl | ished | | Diapause | d | Pupa | ated | | | |
| | Rearing | | | | | | | | As % Of | | | | | |
| Rearing | History of | Total | | | · | | | As % Of | Larvae | | % Of | | | |
| Environment | Parents | No. | NO. | % | No. | % | No. | Total | Establ. | No. | Total | | | |
| | l yr. B.C. Stock | 150 | 10 | 10.05 | - | | | 9.0 | D C | 100 | 50 5 | | | |
| | Reared at T.V. | 120 | Ta | TS • 65 | 24 | 18.3 | ـــ ر | •55 | .76 | 106 | 70.7 | | | |
| Station I | l yr. B.C. Stock | 161 | 3 | | | 0000 | 20 | 7.4.6 | | | 10.0 | | | |
| | Reared at Sta. III | 191 . | 28 | 18.55 | 26 | 20.8 | 22 | 14:6 | 17.6 | 75 | 49.0 | | | |
| 2,500' | 2 yr. B.C. & Alta. | 007 | 77 | 15 0 | 7 | | 1.05 | n o n | | | 0.0 | | | |
| | Reared at Sta. III | 207 | 55 | T2. A | 7 | 4.0 | T 60 | 79.7 | 95.0 | ະ | .96 | | | |
| · · · | l yr. Ont. Reared | 177 | 40 | | 70 | 70 F | , | 0 | • | - 1 | 70 0 | | | |
| | at Sta. III | 131 | 48 | 36.6 | 32 | 38.5 | 0 | U | 0 | 51 | 39.0 | | | |
| | l yr. B.C. Reared | | | | C 4 | - | | 1.0 | E 7 | 4.77 | 70.4 | | | |
| | at T.V. | 141 | 28 | 19.9 | 64 | 56.5 | 6 | 4.2 | 5.3 | 43 | 50.4 | | | |
| Station II | 1 yr. B.C. Reared | 00 (| 7 n | 10.0 | C F | 77 0 | 47 | 10.0 | | | 71 E | | | |
| | at Sta. III | 206 | 37 | 18.0 | 63 | 37.2 | 41 | 19.9 | 24.3 | 60 | 51.5 | | | |
| | 2 yr. B.C. Reared | 150 | 477 | A | A A. | 40 7 | 50 | - 70 C | | , , , , , , , , , , , , , , , , , , , | FT | | | |
| 4,200' | at Sta. III | 120 | 47 | 51.4 | 44 | 42.7 | 58 | 38.6 | 50.5 | 1 | . 30 | | | |
| • | l yr. Ont. Reared | n .c | 10 | F0 0 | C | 7777 | _ | 17.0 | 07 7 | | 10.4 | | | |
| | at Sta. III | 30 | 10 | 50.0 | 0 | 55.5 | G. | 19.8 | 21.1 | 7 | 19.4 | | | |
| | l yr. B.C. Reared | 175 | 70 | | 50 | RCE | 0 | | | 0= | 40 5 | | | |
| | at T.V. | 175 | 39 | 22.0 | - 50 | 30.0 | 2 | | 1.40 | 60 | 48.5 | | | |
| Station III | l yr. B.C. Reared | 194 | 70 | 05 0 | 05 | 07.0 | | 10.0 | | 70 | RO C | | | |
| | at Sta. III | 164 | 52 | 20.0 | ະ ເລ | -21.2 | 29 | 12.0 | 31.5 | 58 | 30.6 | | | |
| | 2 yr. B.C. Reared | 100 | | 17 0 | 0 | | | 50.0 | 07.1 | | | | | |
| 4,750' | at Sta. III | 103 | 66 | 43.0 | 6 | 6.9 | 81 | 52.2 | 93.1 | <u> </u> | 0 | | | |
| | 1 yr. Ont. Reared | 117 | 34 | 20 0 | 16 | זי מר | ΔΔ | 37 6 | 53.0 | 93 | 10 6 | | | |
| | at Sta. III | TT (| U± | 63.0 | 10 | 12.0 | · ±·± , | 57.0 | 0.0 | au | 15.0 | | | |

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TABLE XII

Rearing Results, Condensed and Expressed as Percentages - 1952

| | |] | Fate of Larvae | | | | | | | | |
|---------------------------------------|-------------------|-------|----------------|-------------|-------|------|------|-----------|---------|-----|-------|
| | | | | Established | | | | | | | |
| | | | | | Died | 1 | | | | | |
| | | | Fail | ed to | After | Es- | | | | | |
| | | | Esta | blish | tabli | shed | | Diapaused | | Pup | ated |
| | Rearing | | | | | | | | As % Of | | |
| Rearing | History of | Total | | | | | | As % Of | Larvae | | % Of |
| Environment | Parents | No. | NO. | % | No. | % | No. | Total | Establ. | No. | Total |
| · · · · · · · · · · · · · · · · · · · | l yr. B.C. Reared | | | | | | | | | | |
| | at Sta. I | 190 | 32 | 16.8 | 91 | 57.6 | 9 | 4.7 | 5.6 | 59 | 21.0 |
| Station I | 1 yr. B.C. Reared | | | | | | | · · · · | | | |
| | at Sta. III | 180 | 21 | 11.3 | 88 | 55:3 | 25 | 13.8 | 27.1 | 46 | 25.5 |
| | 1 yr. Ont. Reared | | | | | | | _ | | | |
| | at Sta. I | 70 | 24 | 34.2 | · 23 | 50.0 | 5 | 7.1 | · 10.8 | 6 | 8.5 |
| | 1 yr. B.C. Reared | 100 | | | | | | | | | |
| | at Sta. I | T80 | 60 | 33.3 | 53 | 44.L | 29 | 16.1 | 24.1 | 38 | 21.1 |
| | l yr. B.C. Reared | | | | | | | | | | |
| Station III | at Sta. III | 115 | 51 | 44.3 | 17 | 26.5 | - 38 | 33.0 | 59.3 | 9 | 7.8 |
| | l yr. Ont. Reared | 50 | | | | | | | | | |
| | at Sta. I | 58 | 13 | 22.4 | 18 | 40.0 | 3 | 5.1 | 6.6 | 24 | 41.7 |

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Ontario-Bolean type (B and B1).

The diapause reaction of the Ontario-Bolean type in 1951 was different from both the one-year Bolean and the two-year type. At Station III the majority of these insects entered diapause. As can be seen in Table IX food appeared to be an influence, Douglas fir being more favourable to diapause than alpine fir or spruce. Unfortunately, the data for Station II are incomplete but from those available it is seen that approximately 41 per cent went into diapause. At Station I none of the larvae entered diapause.

Because of the paucity of material it was not feasible to use three foods in 1952. The behaviour of the insects reared was contradictory to that of 1951 in that a higher percentage (Table XII) entered diapause at Station I than at Station III. No explanation of this anomaly is offered other than to stress the small number of larvae involved. The result was unexpected as it was thought that being the progeny of parents reared under oneyear conditions very few of the larvae would enter diapause.

One-year types.

Trinity Valley type (F and F₁) Of the individually-reared larvae at Station III in 1950, five of the one-year larvae went into diapause. In 1951, at the three stations, a total of eight one-year Trinity Valley larvae entered diapause. In 1952 a total of 44 larvae entered diapause, 15 at Station I and 29 at Station III. The results for Station III (Table X), indicate that alpine fir tended to reduce the percentage entering diapause. This was not apparent at Station I. The effect of the higher elevation in increasing diapause is demonstrated.

Bolean type (D and F_{111})

As will be seen from Table IX individuals of the one-year Bolean type entered diapause at all stations and on all foods in 1951. An analysis of variance was made to determine the effect of foods and stations and their interactions. The means of five jars were used. At Station II, with six jars available on spruce and alpine fir, one was discarded from each. In both cases these were of the same value as another jar used in the calculation. There were nine jars available for Douglas fir. In this case the odd numbered ones were used. The calculations were based on the percentage of larvae <u>not</u> going into diapause. This device was used to reduce the number of zeroes.

It was shown that the differences between the means for Stations were significant at the 5 per cent level, and those for Foods at the 1 per cent level. The mean percentages <u>not</u> entering diapause for stations and food are given below. The mean difference required for significance was calculated and is shown below.

-53-

| I | 80.08% |
|-------------------------------------|---|
| II | 61.24% |
| III | 51.22% |
| alpine fir Douglas fir spruce | 76.50% 63.23% 46.81% |
| at 5 per cent | 18.75% |
| at 1 per cent | 25.30% |
| | I II III alpine fir Douglas fir spruce at 5 per cent at 1 per cent |

Thus in the case of stations the difference between I and II is significant at 5 per cent, but the difference between II and III is not significant. The difference between I and III is significant at 1 per cent.

It was shown that alpine fir and spruce differed significantly at 1 per cent but alpine fir and Douglas fir did not differ significantly neither did Douglas fir and spruce. The fact that alpine fir markedly reduced the

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percentage of diapausing larvae is somewhat anomalous, as it is one of the foods on which the two-year cycle larvae normally feed. Douglas fir, the host commonly supporting a one-year cycle population showed a higher percentage of diapausing larvae than did spruce, but the difference was not significant.

Due to the uneven survival in the rearing jars in 1952, statistical analyses of the data have not been undertaken. Inspection of Table X, however, shows that the results obtained in 1951 are verified with a higher percentage of larvae entering diapause at the higher elevation and a diet of alpine fir reducing the number in diapause at both stations.

Comparison of the one-year types

Referring to Tables IX and X it is apparent that the larvae (D and F_{111}) whose

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parents had been reared at Station III in 1950 and Station II in 1951 went into diapause in considerably greater numbers than did those (F and F₁) whose parents had been reared at Trinity Valley in 1950 or Station I in 1951.

In each case the two stocks were overwintered under the same conditions. In the rearing experiments they were treated identically. The only dissimilarity lies in the treatment of the parents.

The matings of the Trinity Valley (F) type were made from July 13 to 26, 1950, while those for the Bolean (D) type were made from August 31 to September 5, 1950. These latter averaged 75.1 days for males and 76.2 days for females for development from emergence to adulthood. The one-year type reared in cages at Station I in 1950 took 52.5 and 52.8 days for development for males and females: these matured from July 12 to 21. Thus the dates of eclosion for the Trinity Valley (F) type and those reared at Station I are roughly comparable. It is assumed that the days for development are similarly comparable. Then the development period for the parents of the Bolean (D) type was 23 and 24 days longer than for the Trinity Valley (F) type.

The parents of the F_1 type averaged 60.4 days for males and 62.8 days for females at Station I in 1951. The parents of the F_{111} type averaged 85.3 days for males and 86.8 days for females at Station II. Thus the development period for the F_{111} parents was 24 and 25 days longer than that of the F_1 parents.

This shows that prolonging the development period of the parents by about 24 days has a profound effect on the ability of the larvae to enter diapause.

Comparison of 1951 and 1952 results of oneyear types.

The percentage of larvae entering diapause in 1952 was higher than that found in 1951. One factor contributing to this difference may be the

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longer development period of the parents of the 1952 larvae than of the 1951 material. This difference is about 8 days, the period being approximately 52 days in 1950 and 60 days in 1951 at Trinity Valley and Station I respectively, and 75 days in 1950 and 84 days in 1951 at Stations III and II respectively. There was a further increase in 1952 with a mean for Station I of 70 days and for Station III of 95 days.

Another factor may be the weather conditions occurring prior to the larvae entering diapause. An examination of the daily mean temperatures (Appendix B) shows that at Station I in 1952, the mean daily temperature fell from 59.6°F on June 9 to 41.8°F on June 12. There was no similar change in 1951 (Appendix A) during this period. The larvae at Station I entered diapause from June 24 to July 14 approximately. Thus there was a drop, within three days of 18° F in the mean temperature roughly 12 days before the appearance of diapause. A second depression, from July 3 to 5 from 61.6°F to 45.3° F, in 1952, corresponds to one in 1951 of 10° F difference between 66.1° F for July 3 and 56.8° F for July 4.

At Station III in 1952 from July 3 to 5, the mean fell from 55.8° F to 38.0°F, or 17.8° F in two days. The similar decline in 1951 was from 57.5° F for July 3 to 45.1° F on July 7, or a drop of 12° F over a period of 5 days. The larvae at Station III entered diapause from approximately July 16 to August 1. Thus there was, in 1952, a drop of 17.8° F in two days roughly 13 days before diapause was observed.

The fact that at both stations there was a decrease in the daily mean temperature of 18° F, about 12 days before diapause was noted, could be a factor in causing some larvae to enter diapause that would have developed in one year in the absence of this stimulus.

DISCUSSION

One objective of this project was to determine the possibility of converting a population from the potentially highly destructive one-year cycle to the less destructive twoyear cycle by changing the forest composition. The results, showing that food is a minor factor, that Douglas fir and spruce are equally favourable foods, and that alpine fir tends to reduce diapause inception, indicate that it would not be possible to effect this change.

Some interesting observations may be made regarding diapause and the theories put forth to explain its inception on the basis of the life cycle of the budworm. One theory, postulated by V. B. Wigglesworth (1948), is that diapause is due to the absence of a growthpromoting hormone, which controls molting, secreted by neuro-secretory cells in the brain.

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This theory is substantiated by the observation that diapause occurs at the close of a larval instar or in the pupa, never interrupting a stage of active growth, and the completion of diapause is followed by a larval molt or the beginning of the next stage in metamorphosis.

The budworm shows contradictions to this theory in its habit of molting, from first to second, and third to fourth instar. While it is difficult to determine exactly when a larva is in diapause, the cessation of feeding, the search for a sheltered niche, and the construction of a hibernaculum are behaviour patterns definitely associated with diapause. The molt in the hibernaculum, following this bahaviour pattern strongly suggests that diapause can not be due to the absence of the hormone that controls molting.

If we ignore the associated behaviour pattern and assume that diapause begins after the

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molt, then it might be due to the absence of the hormone and this is due in turn to complete utilization of the hormone in the molting process. However, if this were true, then it would be logical to expect diapause after each molt in the life of the larva due to depletion of the hormone.

Andrewartha (1952) has postulated that diapause is caused by the accumulation of a reserve of intractable food in the fat-body or egg yolk. That the food supply is not available for metabolism may be due to the quality of the food reserve, to the absence of a necessary enzyme system, or to both, is left open for physiological determination.

The intractable food supply, it is suggested, fails to stimulate the neuro-secretory cells to produce the molting hormone, whose absence in turn causes diapause. The writer has no information on the quality or quantity of the food reserves of the budworm larva. These

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reserves could play a part in the diapause reaction but it may well be a secondary one as this experiment has shown that the maternal physiology has an important effect on the incidence of diapause in the progeny which must be due to some substance carried in the cytoplasm of the egg. This substance may be of the nature of an enzyme system which acts directly to cause diapause, or as a stimulus to a tissue which in turn secretes a hormone which causes diapause. It is simpler to think of the intractable food supply as part of the diapause reaction rather than as a causal link in the chain of events leading to diapause.

The two-year life cycle, occurring in regions with a relatively short frost-free season and low daily mean temperatures, permits the budworm to regularly complete its life cycle. The development of the larvae is arrested prior to the advent of cold weather by the intervention

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of diapause and thus the danger of frostkilling is greatly reduced. The following spring the larvae are small enough to find the developing buds of the host trees a satisfactory food source, yet are able to complete their development in time for the new generation of larvae to enter diapause before being endangered by frost. The evolutionary process leading to the establishment of two types of population of the insect, each adapted to its environment, invites speculation.

If it is assumed that the one-year cycle is primitive, the following explanation may be given:

Consider a mountain slope with Douglas fir growing at the lower elevations, and the upper slope leveling off into a plateau with spruce and alpine fir. The budworm population on the Douglas fir has a one-year cycle. As this population reaches the limit of its range at the

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upper elevations, the retarded development of one generation will cause some of the next to adopt a two-year cycle. This cycle permits the migration of the insect onto the plateau where the conditions are such that only the two-year cycle can survive due to the late spring and early autumn frosts. A cold, wet summer may now intervene and eliminate the one-year type from the transition zone. Thus the two-year type is isolated on the higher regions. The individuals adopting the two-year cycle in an area favourable to the one-year will be eliminated probably by a combination of desiccation and predation, as they will be in their hibernacula from mid-July onwards and will thus have to withstand some of the hottest weather of the season, and also will be available to the still active predators for at least two and possibly three months. As the populations remain separate, selection will favour those individuals whose genetic constitution predisposes them to the appropriate life cycle.

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SUMMARY

Investigations were carried out to determine the effect of ecological factors on the induction of diapause and development in the spruce budworm.

Experimental rearings were conducted at elevations of 2500, 4200 and 4750 feet in 1951 and at 2500 and 4750 feet in 1952. The foliage of spruce, Douglas fir and alpine fir was used as food. Progeny of Ontario, twoyear and one-year types reared under one-year and two-year conditions, was used.

Conclusions are drawn as to the effects of the treatment of the parents, food, altitude and weather on diapause in the budworm larvae and the effects of food and altitude on development.

The growth-promoting hormone theory of diapause by Wigglesworth and the intractable food supply theory by Andrewartha are commented on. The impracticability of converting a one-year cycle population of budworm to a two-year cycle is shown. Speculation is made as to the probable cause of evolution leading to the establishment of a two-year cycle population.

CONCLUSIONS

A trend was noted in emergence from hibernation with the one-year material leading, followed by the two-year and finally the Ontario stock.

The three types of larvae can adopt the habit of mining needles in the second instar.

There was no significant difference in the time for development of the one-year types on the three foods at Station I in 1951. However, it is suggested by the data for 1951 and 1952 that alpine fir favoured more rapid development in the one-year and Ontario types than did spruce or Douglas fir.

Females took significantly longer than males to develop.

The difference in time for development between Station II and III in 1951 was not marked but these two differed from Station I.

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Development at Station I was faster by 23 days in 1951 and by 25 days in 1952 than at Station III.

On the basis of three individuals it is seen that the two-year type can develop in one year. It was shown in 1951 and amply verified in 1952 that the one-year British Columbia and the Ontario type mayadopt the twoyear habit.

The elevation of the rearing site is a factor in promoting diapause in the one-year type.

A diet of spruce or Douglas fir is more favourable to diapause than one of alpine fir for the one-year types.

The impracticability of changing a oneyear cycle population to a two-year cycle by forest management is indicated.

Prolonged development of the parents is a major factor in causing the one-year type to adopt the two-year habit.

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The higher percentage of larvae entering diapause in 1952 may be attributed to a longer development period of the parents of the 1952 larvae or to a drop of 18° F in the mean daily temperature about 12 days prior to the appearance of diapause, or to a combination of these two factors.

The growth-promoting hormone theory of diapause, as postulated by Wigglesworth, is untenable for the budworm. It is suggested that an enzyme, carried over in the cytoplasm of the egg, is more probable as a causal agent than is the intractable food supply suggested by Andrewartha.

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APPENDIX A

Weather Records

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STATION I

Tabulated mean daily temperatures and relative humidities

1951

| DATE | | MEAN DAILY TEMP. | MEAN DAILY R.H. | DATE | | MEAN DAILY TEMP. | MEAN DAILY R.H. |
|--------|-----|------------------------|-----------------------|--------|------------|------------------------|-----------------------|
| Mav | 8 | 56.0* | 54.6* | June | 6 | 43:8 | 75.1 |
| July 3 | 9 | 55.1 | 55.0 | oune | 7 | 51.6 | 65.1 |
| | าด้ | 57.5 | 46.5 | | 8 | 56.1 | 48.8 |
| | 11 | 54.8 | 52.3 | | ğ | 56.3 | 47.3 |
| | 12 | 42.5 | 83.0 | | 10 | 56.3 | 52.8 |
| | 13 | 47.1 | 63.0 | | īī | 57.1 | 54.1 |
| | 14 | 54.3 | 52.6 | | 12 | 58.5 | 55.0 |
| | 15 | 55.3 | 53.0 | | 13 | 58.3 | 55.6 |
| | 16 | 58.0 | 47.0 | | 14 | 62.5 | 50.1 |
| | 17 | 50.5 | 55.6 | | 15 | 58.0 | 34.8 |
| · · | 18 | 47.6 | 56.6 | | 16 | 53.8 | 45.3 |
| | 19 | 49.1 | 48.8 | | 17 | 55.3 | 53.3 |
| | 20 | 54.8 | 44.3 | | 18 | 50.0 | 77.1 |
| 1 | 21 | 57.0 | 46.0 | | 19 | 53.0 | 49.3 |
| | 22 | 62.8 | 39.5 | | 20 | 48.8 | 65.3 |
| 1 | 23 | 56.3 | 46.5 | | 21 | 50.1 | 63.5 |
| 1 | 24 | 46.8 | 47.1 | | 22 | 55.1 | 62.3 |
| · | 25 | 50.3 | 35.0 | | 23 | 53.0 | 71.6 |
| 2 | 26 | 51.6 | 44.1 | | 24 | 55.3 | 52 .3 |
| 2 | 27 | 52.3 | 35.3 | | 25 | 57.3 | 48.3 |
| 2 | 28 | 41.3 | 6 6.1 | | 2 6 | 59.5 | 31.3 |
| 1 | 29 | 41.0 | 66.6 | | 27 | 54.5 | 40.1 |
| | 30 | 41.5 | 53.8 | | 28 | 59.0 | 39.8 |
| | 31 | 47.6 | 44.6 | | 29 | 61.6 | 36.1 |
| June | 1 | 48.6 | 41.6 | - - | 30 | 61.6 | 62.3 |
| | 2 | 52.3 | 54.1 | July | 1 | 57.8 | 75.0 |
| | 3 | 47.6 | 80.0 | | 2 | 62.6 | 53.0 |
| | 4 | 50.8 | 64.8 | | 3 | 66.1 | 43.0 |
| | 5 | 47.8 | 64.8 | | 4 | 56.8 | 64.3 |
| | | | • | | 5 | 56.0 | 61.1 |

t Incomplete records

| | | MĘAN DATIV | MEAN DATIV | | MEAN | MEAN |
|------|----|---------------|---------------|---------|-----------------|-----------------|
| DATE | | TEMP. | R.H. | DATE | TEMP. | B.H. |
| | | | | | 2. 3.3 (14.4. U | |
| July | 6 | 52.0 | 66.6 | Aug.16 | 62.8 | 63.1 |
| | 7 | 51.1 | 63.3 | Ŭ 17 | 62.3 | 60.0 |
| | 8 | 54.6 | 67.6 | 18 | 62.1 | 38.0 |
| | 9 | 59.0 | 54.6 | 19 | 63.3 | 38.0 |
| | 10 | 58.1 | 36.0 | 20 | 63.0 | 37.0 |
| | 11 | 62.6 | 41.6 | 21 | 68.5 | 35.0* |
| | 12 | 69.6 | 33.0 | 22 | 58.3 | |
| | 13 | 68.6 | 45.0 | 23 | 53.1 | |
| | 14 | 65.1 | 50.1 | 24 | 55.0 | 29.54 |
| | 15 | 68 .3 | 43.8 | 25 | 61.0 | 35.5 |
| | 16 | 69.5 | 42.1 | 26 | 59.6 | 41.3 |
| | 17 | 69.6 | 44.0 | 27 | 52.6 | 48.5 |
| | 18 | 69.1 | 38.5 | 28 | 41.1 | 85.1 |
| | 19 | 60.1 | 49.6 | 29 | 47.5 | 81.0 |
| | 20 | 55.8 | 61.6 | 80 | 51.3 | 78.8 |
| | 21 | 61.5 | 52.3 | 31 | 54.6 | 68.6 |
| | 22 | 66.3 | 49.3 | Sept. 1 | 55.3 | 64.3 |
| | 23 | 70.5 | 32.6 | 2 | 55.8 | 67.0x |
| | 24 | 67.5 | 43.6 | 3 | 55.3 | 74.21 |
| | 25 | 69.6 | 43.5 | 4 | 56.8 | 30.31 |
| | 26 | 66. 6 | 43.6 | 5 | 57.8 | 50.8 |
| | 27 | 69.3 | 27.3 | 6 | 59.8 | 47.8 |
| | 28 | 70.1 | 30.8 | 7 | 60.0 | 55.1 |
| | 29 | 6 8.8 | 41.6 | 8 | 59.8 | 47.5 |
| | 30 | 67.1 | 30.1 | 9 | 57.5 | 52.5 |
| | 31 | 66.1 | 40.3 | 10 | 52.0 | 46.8 |
| Aug. | 1 | 66.1 | 43.5 | 11 | 37.6 ± | 78.1 x |
| | 2 | 71.0 | 37.6 | 12 | | |
| | 3 | 70.5 | 33.8 | 13 | | |
| | 4 | 68.5 | 41.0 | 14 | | |
| | 5 | 60.0 | 42.3 | 15 | بيو هو شر مه | فتقر غي عدر مأد |
| | 6 | 61.0 | 43.0 | 16 | | |
| | 7 | 60.3 | 44.8 | 17 | 73. 31 | |
| | 8 | 64.1 | 46.6 | 18 | 62.0 | 25 .3 x |
| | 9 | 64.6 | 47.5 | 19 | 54.5 | 39.8 |
| | 10 | 67.0 | 49.3 | 20 | 52.1 | 48.3 |
| | 11 | 61.1 | 63.0 | 21 | 56.5 | 44.0 |
| | 12 | 57.0 | 66.5 | 22 | 56.8 | 46.3 |
| | 13 | 57.6 | 58.5 | 23 | 48.1 | 68.5 |
| | 14 | 51.0 1 | 72.1 | 24 | 46.6 | 87.1 |
| | 15 | 71.1± | 63.7 | 25 | 43.0 x | 85. 3 1 |

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STATION II

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| Tabulated | mean | daily | temperatures | and | relative |
|-----------|------|-------|--------------|-----|----------|
| | | humi | ldities | | |

1951

| DATE | MFAN DAILY TEMP. | MEAN DAILY R.H. | DATE | MEAN DAILY TEMP. | MEAN DAILY R.H. |
|--|---|--|---|---|--|
| May 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 June 1 23 4 5 6 7 8 9 10 11 | $\begin{array}{c} 46.3 \\ 50.3 \\ 50.3 \\ 55.1 \\ 57.0 \\ 35.8 \\ 40.6 \\ 47.3 \\ 50.5 \\ 51.5 \\ 46.0 \\ 41.1 \\ 45.1 \\ 49.6 \\ 55.1 \\ 60.0 \\ 51.0 \\ 40.6 \\ 42.8 \\ 45.6 \\ 45.6 \\ 45.3 \\ 34.8 \\ 38.3 \\ 44.1 \\ 47.8 \\ 48.6 \\ 42.6 \\ 45.3 \\ 34.3 \\ 44.3 \\ 49.3 \\ 50.6 \\ 53.1 \\ 53.0 \\ 53$ | $79.0 \pm$ 69.1 60.5 64.5 89.3 81.8 72.5 63.6 66.6 64.1 65.1 60.1 56.8 52.0 64.5 68.0 61.6 62.5 55.0 63.8 80.0 62.5 55.0 63.8 86.1 76.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 82.0 63.8 85.1 76.0 63.8 82.0 64.5 64.5 82.0 82.0 83.6 70.3 66.8 70.6 70.6 70 | June 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 July 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 July 1 21 25 26 27 28 29 30 July 1 21 25 26 27 28 29 30 July 1 21 25 26 27 28 29 30 July 1 21 25 26 27 28 29 30 July 1 21 25 26 27 28 29 30 July 1 21 25 26 27 28 29 30 July 1 22 31 24 25 26 27 28 29 30 10 11 21 25 26 27 28 29 30 10 11 21 25 26 27 28 29 30 10 11 12 13 14 15 16 17 17 18 19 20 20 21 28 29 30 10 11 12 13 14 15 16 17 | 52.3 56.6 51.6 55.4 47.8 63.5 1.5 54.7 46.3 54.3 54.3 55.5 55.5 61.6 53.8 63.5 1.3 51.6 55.5 55.6 55.5 55.6 55.5 55.6 55.5 555 | $\begin{array}{c} 75.8\\69.0\\56.3\\59.6\\68.8\\80.8\\68.6\\71.6\\70.3\\74.8\\82.5\\66.0\\65.1\\38.0\\53.3\\55.6\\75.5\\78.0\\68.1\\63.0\\79.6\\75.3\\81.1\\82.8\\81.1\\82.8\\55.8\\1.5\\63.0\\79.6\\75.3\\81.1\\82.8\\81.1\\82.8\\55.8\\1.5\\6.5\\63.0\\68.1\\56.5\\63.6\\1.0\end{array}$ |
| 12 | 52.0 | 74.6 | | | |

it Incomplete records

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| | MRAN | MEA N | | MEAN | MEAN |
|--|----------------|----------------------|--------------|---------------------------------------|--------------|
| | DAILY | DAILY | | DAILY | DAILY |
| DATE | TEMP. | R.H. | DATE | TEMP. | R.H. |
| ······································ | | | | · · · · · · · · · · · · · · · · · · · | |
| July 18 | 60.5 | 61.8 | Aug.22 | 51.6 | 72.8 |
| 19 | 53.0 | 67.3 | 23 | 47.3 | 75.8 |
| 20 | 49.5 | 74.8 | 24 | 52.6 | 65.5 |
| 21 | 54.6 | 69.1 | 25 | 56.3 | 61.3 |
| 22 | 61.5 | 62.6 | 26 | 54.8 | 62.3 |
| 23 | 64.3 | 50.8 | 27 | 47.3 | 72.3 |
| . 24 | 63.0 | 62.0 | 28 | 43 .3 | 86.3 |
| 25 | 62.6 | 66.5 | 29 | 46.0 | 85.0 |
| 26 | 60.8 | 63.8 | - 3 0 | 46.3 | 82.8 |
| 27 | 62.1 | 48.5 | 31 | 50 .6 | 81.5 |
| 28 | 63.1 | 54.0 | Sept. 1 | 50.6 | 79. 0 |
| 29 | 60.8 | 65.0 | 2 | 50.6 | 69.6 |
| 30 | 61.1 | 64.8 | 3 | 50.8 | 66.1 |
| 31 | 61.0 | 59.6 | 4 | 55.1 | 62.8 |
| Aug. 1 | 62.6 | 5 8 .6 | 5 | 56.6 | 62.3 |
| - 2 | 66.0 | 54.1 | 6 | 61.1 | 59.6 |
| 3 | 63.6 | 57.5 | 7 | 54.8 | 68.6 |
| 4 | 61.0 | 63.0 | 8 | 52.3 | 74.3 |
| 5 | 52.5 | 70.5 | 9 | 53.8 | 65.3 |
| 6 | 54.1 | 67.5 | 10 | 45.0 | 72.6 |
| 7 | 56.5 | 67.0 | 11 | 44.3 | 70.0 |
| 8 | 59.0 | 69.6 | 12 | 49.6 | 70.8 |
| 9 | 5 8.6 | 70.8 | 13 | 52.1 | 63.8 |
| 10 | 62.0 | 70 .0 | 14 | 53.1 | 64.3 |
| 11 | 5 8.0 | 76.5 | 15 | 58.6 | 62.0 |
| 12 | 52.3 | 78.0 | 16 | 60.3 | 63.6 |
| 13 | 51.6 | 79.3 | 17 | 61.1 | 59.1 |
| 14 | 50 .5 # | 77.1 | 18 | 61.1 | 55.1 |
| 15 | 54 .6 x | 70.5 | 19 | 48.0 | 62.3 |
| 16 | 64 .01 | 62.8 | 20 🕤 | 46.6 | 68.8 |
| 17 | 57.4 | 60 . 5 | 21 | 52.5 | 61.1 |
| 18 | 57.6 | 58.5 | 22 | 52.5 | 72.0 |
| 19 | 59.0 | 59.6 | - 23 | 45.5 | 77.0 |
| 20 | 60 .5 | 55.3 | 24 | 43.8 | 88.1 |
| 21 | 66.5 | 51.6 | . 25 | 41.0 | 82.6 |
| | | | | | |

1 Incomplete records

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STATION III

Tabulated mean daily temperatures and relative humidities

19**51**

| | MEAN | MEAN | | MEAN | MEAN |
|------------|---------------|-------------|-----------------|--------------|--------------|
| | DAILY | DAILY | | DAILY | DAILY |
| DATE | TEMP. | R.H. | DATE | TEMP. | R.H. |
| | | | | ···· | |
| May 15 | 51.0 ± | | Ju ne 18 | 44.6 | 84.5 |
| 16 | 44.5 | 64.6 | 19 | 45.8 | 59.1 |
| 17 | 40.5 | 55.6 | 20 | 43.5 | 69.0 |
| 18 | 40.6 | 62.0 | 21 | 45.8 | 65.6 |
| 19 | 47.0 | 58.3 | 22 | 48.5 | 68.0 |
| 20 | 42.5 | 56.8 | 23 | 46.5 | 77.5 |
| 21 | 46.0 | 52.0 | 24 | 48.8 | 50.6 |
| 2 2 | 49.6 | 50.6 | 25 | 51.0 | 57.1 |
| 23 | 43.8 | 46.5 | 26 | 49.5 | 46.6 |
| 24 | 37.1 | 52.0 | 27 | 48.3 | 45.8 |
| 25 | 39.3 | 48.1 | 28 | 51.0 | 48.1 |
| 2 6 | 41.3 | 46.1 | 29 | 53.6 | 45.3 |
| 27 | 42.3 | 42.6 | 30 | 53.0 | 76.5 |
| 2 8 | 32.8 | 56.6 | July 1 | 51.0 | 82.3 |
| 29 | 32.8 | 70.1 | 2 | 55.0 | 68.6 |
| 3 0 | 35.8 | 56.0 | 3 | 57.5 | 59.8 |
| 31 | 39.1 | 47.0 | 4 | 51.1 | 76.1 |
| June 1 | 41.6 | 45.5 | 5 | 51.5 | 74.1 |
| 2 | 43.0 | 53.8 | . 6 | 45.8 | 80.3 |
| 3 | 40.3 | 66.0 | 7 | 45.1 | 76.8 |
| 4 | 42.3 | 61.5 | 8 | 49.3 | 79.6 |
| 5 | 40.3 | 52.6 | 9 | 51.5 | 66.3 |
| 6 | 37.0 | 55.0 | 10 | 52.1 | 47.1 |
| 7 | 42.1 | 63.1 | 11 | 57.5 | 48.3 |
| 8 | 46. 5 | 56.6 | 12 | 61.6 | 52.0 |
| 9 | 46.1 | 45.5 | 13 | 61.6 | 53.6 |
| 10 | 41.3 | 45.1 | 14 | 57.5 | 64 .3 |
| 11 | 46.8 | 46.1 | 15 | 59.1 | 61.1 |
| 12 | 50.1 | 50.3 | 16 | 5 8.8 | 61.0 |
| 13 | 49.5 | 56.5 | 17 | 62.1 | 55.8 |
| 14 | 53.3 | 51.1 | 18 | 58.8 | 53.0 |
| 15 | 49.6 | 36.1 | 19 | 53.0 | 67.3 |
| 16 | 47.8 | 40.1 | 20 | 47.3 | 71.8 |
| 17 | 48.1 | 64.8 | 21 | 51.0 | 69.1 |

x Incomplete records

-80-

| DATE | | MEAN DAILY TEMP. | MEAN DAILY R.H. | DATE | MEAN DAILY TEMP. | MEAN DAILY R.H. |
|------|-------------------|------------------------|-----------------------|---------------------------------------|------------------------|-----------------------|
| | | | | | | |
| July | 22 | 58.0 | 61.6 | Aug.24 | 47.3 | 60.6 |
| | 20 | 62.0 | 45.2X | 25 | 51.6 | 60.6 |
| | 24 | 50.1 | 60 .I | 20 97 | 51.6 47 6 | 00.1 |
| | 20 | 09.0 57 5 | 0U.0 57 7 | 27 | 40.0 | 74.0 |
| | 20 97 | 07.0 50 % | 07.0 70 7 | 20 | 46.0 | 81.8 86 0 |
| | <i>ୟ ।</i> ରୁବ | 09.0 60 3 | 30.0 | 27 | 40.1 | 00.0 |
| | 20 20 | 591 | 44.U | 20 | 44.0 AV 7 | 00.1 |
| | 27 | 59.1 | 46 0 | Sant 1 | 41.0 | 97.0 |
| | 31 | 50.0 | 40.0 59 A | Dehe T | 41.0 | 75 3 |
| Anc | 1 | 58 3 | 60 0 | 2 2 | 40.0 | 70.0 |
| Hug. | 2 | 61.3 | 50.6 | L L L L L L L L L L L L L L L L L L L | 47.6 | 69.0 |
| | 3 | 59.8 | 48.6 | 5 | 49.0 | 66.0 |
| | A | 57.6 | 58.3 | 6 | 50.5 | 64.6 |
| | 5 | 48.8 | 69.8 | 7 | 50.6 | 70.3 |
| | 6 | 50.6 | 63.6 | 8 | 47:6 | 77.6 |
| | 7 | 52.3 | 63.6 | 9 | 47.1 | 69.5 |
| | 8 | 54.8 | 66.0 | 10 | 41.6 | 76.2 |
| | 9 | 54.3 | 64.0 | 11 | 39.6 | 71.1 |
| | 10 | 56.3 | 68.3 | 12 | 46.1 | 70.3 |
| | īī | 54.3 | 79.0 | 13 | 45.3 | 68.3 |
| | 12 | 49.0 | 80.0 | 14 | 46.0 | 68.3 |
| | 13 | 49.1 | 89.7 | 15 | 49.6 | 63.6 |
| | 14 | 50.5 | 81.2 | 16 | 52.3 | 65.0 |
| | 15 | 51.5 | 68.0 | 17 | 53.5 | 64.0 |
| | 16 | 53.1 | 57.5 | 18 | 54.0 | 60.0 |
| | 17 | 50.8 | 58.6 | 19 | 46.8 | 49.0 |
| | 18 | 52.3 | 61.3 | 20 | 41.8 | 68.0 |
| | 19 | 53.6 | 56.0 | 21 | 46.5 | 63.3 |
| | 20 | 53.6 | 59.0 | 22 | 45.8 | 69.8 |
| | 21 | 59.0 | 50.3 | 23 | 41.0 | 86.1 |
| | 22 | 49.1 | 75.3 | 24 | 41.3 | 92.5 |
| | 23 | 44.6 | 80.8 | 25 | 37.2 1 | 90 .01 |
| | | | | · · · · · | | |

1 Incomplete records

APPENDIX B

Weather Records

STATION I

Tabulated mean daily temperatures and relative humidities

1952

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| DATE | MEAN DA ILY TEMP. | MEAN DAILY R.H. | DATE | | MEAN DAILY TEMP. | MEAN DAILY R.H. |
|---|--|--|------|--|--|--|
| May 7 8 9 10 11 12 13 14 15 | 46.5 49.5 53.8 55.0 52.5 52.3 46.3 46.3 52.1 | 41.0 36.6 48.8 52.0 68.6 54.8 81.1 70.5 60.6 | Jane | 8 9 10 11 12 13 14 15 | 55.3 59.6 51.0 45.6 41.8 46.3 50.6 52.5 45.8 | 42.6 43.5 68.0 70.6 84.3 52.8 49.1 40.5 74.5 |
| 16 17 18 19 20 21 22 23 | 45.6x 56.3x 48.5x 51.3 51.6 52.1 | 77.0x 62.32 72.4x 54.8 48.6 46.8 | | 17 18 19 20 21 22 23 24 | 48.3 53.5 59.3 56.3 49.3 45.6 51.0 | 66.5 60.0 39.8 54.6 59.1 81.0 68.6 59.6 |
| 24 25 26 27 28 29 30 | 56.3 57.8 55.6 56.0 50.6 45.6 46.5 | 47.8 40.0 38.5 61.1 62.1 50.6 50.5 | July | 25 26 27 28 29 30 | 59.3 56.3 58.0 56.0 53.3 52.5 53.1 54.5 | 64.3 70.6 71.8 81.3 74.3 70;5 55.8 |
| June 1 2 3 4 5 6 7 | 51.0 54.5 53.3 54.5 56.1 59.8 53.3 | 67.0 45.3 50.6 66.5 47.6 38.0 36.0 | | 23456789 | 61.6 60.6 45.3 49.6 58.6 65.5 69.1 | 53.6 50.8 70.6 60.3 49.8 48.8 44.3 |

± Incomplete records

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| | MEAN | MEAN DATLY | | MEAN DATLY | MEAN DATLY |
|---------------|---------------|---------------|------------------|---------------|----------------------|
| DATE | TEMP. | R.H. | DATE | TEMP. | R.H. |
| July 10 11 | 69.0 67.3 | 35.6 41.6 | Aug. 20 21 | 61.1 60.3 | 48.6 48.1 79.3 |
| 12 | 66.6 | 44. 6 | 23 | 56.8 | 42.3 |
| 14 | 72.3 | 48.24 | 24 | 50.1 | 64.8 |
| 15 | 69.6 | 28.7年 | 25 | 49.0 | 79.5 |
| 10 | 60.8 69 1 | 49.8 | 20 27 | 51.0 | 55.0 |
| 18 | 57.5 | 66.5 | 28 | 52.3 | 55.8 |
| 19 | 60.5 | 55.0 | 29 | 50.3 | 55.8 |
| 20 | 55.1 | 56.6 | 30 | 49.8 | 55.1 |
| 21 | 51.8 | 65.0 | 31 | 54.0 | 53.6 |
| 22 | 50.8 | 67.1 | Sept. 1 | 57.1 | 44.1 |
| 23 | 61.6 | 85.5 | 2 7 | 60.1 47 7 | 50.1 33 P |
| 24 | 50 3 | 79.9 56 3 | О Д | 52.5 | 42.5 |
| 26 | 63.6 | 60.3 | 5 | 54.1 | 43.0 |
| 27 | 67.6 | 37.0 | 6 | 58.6 | 42.6 |
| 2 8 | 65.1 | 47.6 | 7 | 49.5 | 42.6 |
| 29 | 68.6 | 44.8 | 8 | 50.8 | 45. 8 |
| 30 | 69.6 | 36.3 | · · 9 | 50.3 | 62.8 |
| 31 | 71.3 | 30.6 | 10 11 | 51.1 50] | 56 1 |
| Aug. 1 | 66.8 | 0010 37.1 | 12 | 48.0 | 66.6 |
| 3 | 68.5 | 44.1 | 13 | 47.3 | 50.5 |
| 4 | 70.5 | 43.3 | 14 | 49.3 | 49.8 |
| 5 | 73.3 | 22.34 | 15 | 55.5 | 45.8 |
| 6 | 69.1 | 43.8 | 16 | 53.3 | 50.1 |
| 7 | 65.0 | 59.1 | 17 | 60.3 50 0 | 49.0 61 1 |
| 8 | 6 9 .5 | 0.0C | 19 | 57.3 | 52.6 |
| 10 | 71.8 | 42.3 | 20 | 53.1 | 52.6 |
| 11 | 68.0 | 46.5 | 21 | 57.6 | 51.8 |
| 12 | 69.5 | 41.5 | 22 | 59.0 | 50.6 |
| 13 | 78. 6 | 39.5 | 23 | 60.0 | 47.5 |
| 14 | 68.5 | 41.5 | 24 | 60.6 | 38.0 |
| 15 | 61.6 | 50.5 | 25 | 60.0 61 0 | 00.0 10 9 |
| 16 17 | 57.5 E0 4 | 55.5 | 20 9 7 | 55.1 | 47.6 |
| 12 12 | 62.0 | 39.5 | 28 | 52.3 | 64.3 |
| 19 | 58.5 | 52.3 | 29 | 57.0 | 51.6 |
| - | · · · | | | | |

★ Incomplete records

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| DATE | MEAN£ DAILY TEMP. | MEAN DAILY R.H. | DATE | | MEAN DAILY TEMP. | MEAN DAILY R.H. |
|---------|-------------------------|-----------------------|--------------|----|------------------------|-----------------------|
| Sept.30 | 58.3 | 44.6 | 0 ct. | 7 | 51.8 | 45.1 |
| Oct. 1 | 51.5 | 58.3 | | 8 | 53.5 | 43.6 |
| 2 | 51.6 | 57.3 | | 9 | 52.8 | 49.5 |
| 3 | 50.3 | 35.1 | | 10 | 49.0 | 58.0 |
| 4 | 45.6 | 42.0 | | 11 | 52.3 | 51.8 |
| 5 | 47.6 | 48.5 | | 12 | 51.3 | 59.3 |

APPENDIX B

Weather Records

STATION III

Tabulated mean daily temperatures and relative humidities

1952

| | MEAN | MEAN | | MEAN | MEAN |
|------------|--------------|--------------|---------|--------------|--------------|
| | DAILY | DAILY | | DAILY | DAILY |
| DATE | TEMP. | R.H. | DATE | TEMP. | R.H. |
| | | | | | |
| May 21 | 40.6 | 84.3 | June 22 | 38.8 | 89.1 |
| 22 | 41.3 | 75.8 | 23 | 43.0 | 86.3 |
| 23 | 39. 8 | 73.1 | 24 | 49.6 | 76.5 |
| 24 | 46.5 | 71.5 | 25 | 51.5 | 81.3 |
| 25 | 47.1 | 64.3 | 26 | 49.5 | 85.0 |
| 26 | 48.0 | 57.0 | 27 | 52.6 | 81.8 |
| 27 | 49.5 | 65.3 | 28 | 50.6 | 88.5 |
| 2 8 | 46.1 | 80.5 | 29 | 47.1 | 85.8 |
| 29 | 37.5 | 81.8 | 30 | 4 4.3 | 84.1 |
| 3 0 | 41.5 | 72.0 | July 1 | 45.0 | 78.8 |
| 31 | 43.1 | 81.8 | 2 | 46.5 | 75.6 |
| June 1 | 44.5 | 75.8 | 3 | 55.8 | 71.8 |
| 2 | 49.1 | 69.5 | 4 | 52.6 | 73.0 |
| 3 | 49.0 | 67.6 | 5 | 38.0 | 83.8 |
| 4 | 46.1 | 85.5 | 6 | 43.0 | 75.3 |
| 5 | 48.0 | 69.6 | 7 | 52.0 | 67.8 |
| 6 | 50.5 | 63.5 | 8 | 60.8 | 65.5 |
| 7 | 45.3 | 61.5 | 9 | 63.1 | 60.8 |
| 8 | 49.3 | 61.0 | 10 | 62.5 | 52.5 |
| 9 | 54.3 | 58.8 | 11 | 58.3 | 62.3 |
| 10 | 43.5 | 80.0 | 12 | 56.5 | 63.1 |
| 11 | 40.8 | 79.6 | 13 | 60.0 | 61.6 |
| 12 | 35.3 | 90 .0 | 14 | 63.6 | 60 .5 |
| 13 | 38.1 | 79.3 | 15 | 60.6 | 53.1 |
| 14 | 44.8 | 69.5 | 16 | 52.5 | 70.6 |
| 15 | 44.6 | 69.0 | 17 | 48.6 | 80.6 |
| 16 | 37.1 | 88.1 | 18 | 50.6 | 78.0 |
| 17 | 40.6 | 79.6 | 19 | 52.6 | 73.3 |
| 18 | 45.8 | 69.5 | 20 | 45.5 | 80.3 |
| 19 | 51.5 | 61.3 | 21 | 43.3 | 83.3 |
| 20 | 48.3 | 74.3 | 22 | 44.8 | 84.9 |
| 21 | 41.6 | 79.5 | 23 | 46.3 | 88.8 |

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| DATE | | MEAN DAILY TEMP. | MEAN DAILY R.H. | DATE | MEAN DAILY TEMP. | MEAN DAILY R.H. |
|--------------------------|---|--|--|--|--|--|
| July 2 July 2 Aug. | 24 25 27 28 29 30 12 34 56 7 89 01 12 34 56 7 89 01 12 34 56 7 89 01 12 34 56 7 89 01 12 34 56 7 89 01 12 34 56 7 89 01 12 34 56 7 89 00 12 23 4 56 7 89 00 12 23 4 56 7 89 00 12 23 4 56 7 89 00 12 23 4 56 7 89 00 12 23 4 56 7 89 00 12 23 4 56 7 89 00 12 23 4 56 7 89 00 12 23 4 56 7 89 00 12 23 23 23 23 23 23 23 23 23 23 23 23 23 | 44.8 50.0 55.8 54.6 56.8 61.1 63.1 60.0 58.6 60.0 62.8 63.6 59.1 55.1 56.3 60.6 59.3 60.6 59.3 60.6 59.5 60.6 59.5 60.6 59.3 60.6 59.5 50.6 | 87.3 73.5 61.0 69.1 70.6 63.3 60.8 65.0 61.0 62.0 66.3 58.6 63.3 58.6 68.6 77.5 80.1 70.0 69.5 68.5 64.3 63.0 68.5 63.0 68.5 63.0 68.5 74.5 79.0 72.1 66.0 74.6 69.6 71.6 85.1 71.3 86.0 | Aug. 25 26 27 28 29 30 31 Sept. 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 | 41.6 43.6 44.5 46.3 40.8 43.6 45.0 48.5 51.5 53.6 42.0 45.5 47.5 38.5 40.5 43.1 41.3 42.0 39.3 38.6 42.1 46.5 48.6 51.8 46.6 49.3 50.5 53.3 52.8 57.5 | 87.3 83.0 79.3 74.3 83.3 78.6 77.5 74.3 73.5 62.6 71.6 66.0 73.3 72.1 78.0 80.5 81.8 81.1 80.0 75.1 69.0 73.8 73.6 73.8 73.6 58.5 73.6 73.5 66.3 58.5 |
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