Some effects of photoperiod on the development of *Neodiprion swainei* Midd.

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Received December 20, 1971


Interrupted development of *Neodiprion swainei* Midd. occurs if feeding larvae are reared under 16.5- to 19-h photophases. Experimental evidence indicates that the limitations placed on *N. swainei* by its host specificity, diapause requirements, and developmental rates effectively rule out more than one generation per year. Because of the photoperiodic control of diapause, it is unlikely that the insect can develop under natural conditions without a prepupal diapause.


Des photopériodes de 16.5 à 19 h permettent aux larves de *Neodiprion swainei* Midd. de se développer de façon ininterrompue. Les résultats d’expériences indiquent que certains facteurs, soient la spécificité d’hôte, les conditions exigées par la diapause et les rythmes de croissance, empêchent *N. swainei* de produire plus d’une génération par année. L’importance de la photopériode dans le contrôle de la diapause porte à croire que l’insecte est incapable, dans des conditions naturelles, de se développer sans entreprendre une diapause pré-nymphale.

Introduction

This paper reports the results of experiments on the effects of daylength on the development of *Neodiprion swainei* Midd. Similar studies on *Neodiprion sertifer* (Geoff.) have been underway for several years and it became evident that the responses of this egg-overwintering species should be compared with those of a cocoon-overwintering species. *Neodiprion swainei* was chosen as the latter test insect because earlier work provided us with a basis for experimentation.

The seasonal history and habits of *N. swainei* have been described in detail by Schedl (1937), Atwood and Peck (1943), Becker and Benjamin (1964), and Tripp (1965); and much additional published information is available. *Neodiprion swainei* is univoltine and overwinters as a cocooned, prepupal larva in the duff or mineral soil. Pupation takes place in late spring and early summer following by adult emergence from June through late July. Mating and oviposition occur shortly thereafter; the females lay their eggs singly near the fascicle sheaths of elongating needles of jack pine, *Pinus banksiana* Lamb. Embryological development ranges from 3 to 6 weeks and feeding larvae may be observed from early July into October, depending on site and year. Upon completion of feeding, the larvae molt to prepupae which leave the tree, spin cocoons, and enter a diapause that delays morphogenesis until the following spring. Laboratory studies (Wallace and Sullivan, unpublished) showed that the diapause is fulfilled in 40 to 80 days at 6 to 8°C. A variable proportion of prepupal larvae remain in diapause for longer periods.

Autumn emergence of adults in rearings in an office having uncontrolled temperature and natural plus supplemental fluorescent lighting, as recorded by Maxwell (1958), led to a pilot experiment on the role of daylength in diapause induction. This test, done in 1958–1959, suggested that *N. swainei* is a long-day insect. The
foregoing early work took on new significance when we studied the effect of temperature and photoperiod on diapause in *N. sertifer*, and photoperiod experiments were conducted on *N. swainei* in 1963 and 1964.

**Methods and Results**

The experimental equipment and design used to determine the effect of photoperiod on diapause induction have been described elsewhere (Sullivan and Wallace 1965). Branches of jack pine bearing clusters of *N. swainei* eggs in late stages of embryogenesis were collected in Ontario west of Lake Temiskaming (Lat. 47° N; Long. 80° W) on July 16, 1963, and transported to the laboratory with the cut ends in water. On July 17, four to six egg clusters were placed in each of seven chambers providing 0, 4, 8, 12, 16, 20, and 24 h of light per day, respectively, at 22 ± 1°C and 60 to 75% relative humidity (R.H.). Hatch was synchronous within a cluster but differed between clusters by as much as 10 days because of the natural variation in date of oviposition. The mean hatch date was July 22.

The first-instar larvae were allowed to feed on the egg-bearing branch. At about the third instar, the larvae were placed in 2-quart Mason jars with gauze tops and fed 1-year-old jack pine foliage. After the feeding period, cocoons were removed daily, marked for identification of photophase and date of spinning, and held in darkness at 21 ± 1°C. About 84% of the larvae survived to produce 1187 cocoons.

No sawfly adults emerged in the fall of 1963 and on October 17, after about 65 days at 21°C, the cocoons were placed in cold storage at 7°C. It seemed possible that the range of daylengths inducing non-diapause development is so narrow that it was completely straddled by the photophases spaced at 4-h intervals in our test. Consequently, an experiment was conducted in 1964 employing photophases of 15, 16, 17, 18, 19, and 20 h at 22 ± 1°C and 60 to 75% R.H. The egg clusters were obtained by introducing 150 pairs of adults, emerging from the 1963 experimental stock following normal diapause, into a cage placed over a young jack pine growing under natural conditions near Sault Ste. Marie. The adults were placed in the cage from June 23 to 25 and the egg-bearing twigs were removed to the laboratory rearing chambers on July 13. Seven clusters were placed at each photophase.

Hatch occurred July 17 to 19, with the mean hatch date on July 18. The greater reliability of the mean hatch date in 1964, compared with 1963, shows the advantage of limiting the oviposition period even when oviposition takes place under quasi-natural conditions. This procedure is unnecessary with egg-overwintering species such as *N. sertifer* because larval eclosion under equivalent conditions is naturally synchronized, even though oviposition takes place over a long span of time in the fall preceding hatch.

Ninety-two percent, or 3415, of the hatching larvae spun cocoons. A high proportion of the prepupae from larvae fed under 17- and 18-h photophases metamorphosed without a diapause and emerged in about 3 weeks. Figure 1A shows the relationship between the induction of non-diapause development is striking and places *N. swainei* among those insects having the intermediate type of photoperiodic reaction described by Danilevskii (1965), or the long day–short day response (Type IV) described by Beck (1968). The cocoons remaining after adult emergence in the fall of 1964 were transferred to 7°C on October 8, about 55 days after spinning.

Figures 1B and 1C show the relationship between photophase and the mean larval developmental times obtained in the 1963 and 1964 experiments with *N. swainei*. Males apparently require less time for development than females and the range of larval developmental times across the whole span of photophases studied is greater for females than males. In addition, there is an indication that photophases within and just outside the daylength range producing non-diapause affect the length of larval development.

Although we did not observe the number of feeding instars, our results on developmental times may reflect differences in the number of these larval stages. For example, the shorter times for male than female larvae probably relate to the presence of one or more fewer instars among males as reported by Becker and Benjamin (1964) and Tripp (1965). These authors found that the number of feeding instars, particularly among females, varied from five to seven and Tripp (1965) suggests that "the number of instars depends in part on factors acting
through relatively small differences in seasonal history.” In *N. sertifer*, on the other hand, there is general agreement (Lyons 1964) on the number of feeding instars and we could not detect that photoperiod affected the length of the larval feeding period (Sullivan and Wallace 1965). In *N. swainei*, however, where the number of feeding instars varies, our results indicate that photoperiod does affect the length of larval development. This circumstantial evidence suggests that small changes in daylength may regulate the number of feeding instars in *N. swainei*.

In 1963 and 1964, cocoons containing diapauing prepupae were placed in cold storage for the winter and incubated the following spring at 21°C in darkness, to determine some of the characteristics of diapause. Tables 1 and 2 give the percentages of prepupae that followed non-diapause, normal diapause, and prolonged diapause courses of development. In both experiments, mortality of individuals showing no development remained low throughout incubation and cold storage. In the 1963 material (Table 1), there were large differences in the incidence of normal diapause associated with photophase during larval rearing. Mortality of individuals metamorphosing following this normal diapause was low. However, after emergence

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![Graphs](image-url)

**Fig. 1.** A, relationship between photophase and percent non-diapause for *Neodiprion swainei* prepupal larvae held in darkness at 21°C after larval development at various photoperiods during 1963–1964. B and C, relationship between larval developmental time and photophase for *N. swainei* reared on jack pine at 22°C and various photoperiods in 1963 and 1964, respectively.
in 1965 after 1 year of prolonged diapause, no living prepupae remained and the number of adults obtained was much lower than the number of prepupae showing some development. The principal mortality occurred among late pro-
ymphs, pupae, and adults. In the 1964 experi-
ment (Table 2) in which the range of photophases 
was from 15 to 20 h, the percentage of the sam-
ple developing with normal diapause was high 
and fairly uniform except for the material from 
17- and 18-h photophases. The low values for 
normal diapause in these latter samples is mainly 
the result of depletion of the initial sample by 
individuals developing without diapause. The 
prepupae alive when the experiment was com-
pleted in the fall of 1965 were considered to be 
in prolonged diapause. The lower incidence of 
prolonged diapause in 1964 than in 1963 may 
reflect population differences in the two lots of 
material since the parents of the 1964 test insects 
did not represent the total 1963 population and 
were, in fact, those without prolonged diapause. 

Table 3 gives the developmental times (duration 
of prepupal metamorphosis, pupal, and 
pharate adult development within the cocoon) at 
21°C and darkness for sawflies emerging without 
an intervening diapause, after a normal diapause, 
and after prolonged diapause 1 year longer than 
the normal. The most striking feature of these 
data is the similarity of the values for all photophases and developmental sequences. In the 
majority of sets, the females required longer than 
the males, but in the large non-diapause samples 
from 17- and 18-h photophases, the females took 
slightly less time to develop and emerge. The 
1963 and 1964 data both indicate that there are

**TABLE 1**

Summary of development and mortality of *Neodiprion swainei* within the cocoon following larval rearing under several photophases in 1963

<table>
<thead>
<tr>
<th>Photophase, h</th>
<th>Developing in 1963, % (no diapause)</th>
<th>Developing in 1964, % (normal diapause)*</th>
<th>Developing in 1965, % (prolonged diapause)*</th>
<th>Mortality, % (no development)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>93.7</td>
<td>73.0</td>
<td>9.9</td>
</tr>
<tr>
<td>4</td>
<td>0</td>
<td>17.1</td>
<td>59.7</td>
<td>4.8</td>
</tr>
<tr>
<td>8</td>
<td>0</td>
<td>35.5</td>
<td>55.1</td>
<td>4.0</td>
</tr>
<tr>
<td>12</td>
<td>0</td>
<td>40.9</td>
<td>57.6</td>
<td>4.3</td>
</tr>
<tr>
<td>16</td>
<td>0</td>
<td>38.1</td>
<td>41.4</td>
<td>0</td>
</tr>
<tr>
<td>20</td>
<td>0</td>
<td>58.6</td>
<td>44.9</td>
<td>0</td>
</tr>
</tbody>
</table>

*Cold treatment first "winter:" 139 days at 7°C and 84 days at 1°C. Total incubation at 21°C in darkness, second "summer:" 134 days.

**TABLE 2**

Summary of development and mortality of *Neodiprion swainei* within the cocoon following larval rearing under several photophases in 1964

<table>
<thead>
<tr>
<th>Photophase, h</th>
<th>Developing in 1964, % (no diapause)</th>
<th>Developing in 1965, % (normal diapause)*</th>
<th>Living at end of exp., % (prolonged diapause)*</th>
<th>Mortality, % (no morphogenesis by end of normal emergence period)</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>0</td>
<td>73.3</td>
<td>26.1</td>
<td>0.5</td>
</tr>
<tr>
<td>16</td>
<td>1.4</td>
<td>73.7</td>
<td>24.0</td>
<td>0.9</td>
</tr>
<tr>
<td>17</td>
<td>7.6</td>
<td>5.5</td>
<td>12.9</td>
<td>2.0</td>
</tr>
<tr>
<td>18</td>
<td>7.8</td>
<td>16.1</td>
<td>9.9</td>
<td>1.2</td>
</tr>
<tr>
<td>19</td>
<td>14.2</td>
<td>68.7</td>
<td>15.4</td>
<td>1.7</td>
</tr>
<tr>
<td>20</td>
<td>0</td>
<td>61.6</td>
<td>37.6</td>
<td>0.8</td>
</tr>
</tbody>
</table>

*Cold treatment, first "winter:" 242 days at 7°C. Incubation at 21°C and darkness, second "summer:" 100 days.

*Experiment terminated during fall, 1965.*
TABLE 3
Developmental times (duration of prepupal metamorphosis, pupal, and pharate adult development within the cocoon) in days for *N. swainei* at 21 ± 1°C in darkness following various photoperiod and temperature treatments that resulted in three developmental sequences related to diapause

<table>
<thead>
<tr>
<th>Developmental sequence and exp. year</th>
<th>Sex</th>
<th>0</th>
<th>4</th>
<th>8</th>
<th>12</th>
<th>15</th>
<th>16</th>
<th>17</th>
<th>18</th>
<th>19</th>
<th>20</th>
<th>24</th>
</tr>
</thead>
<tbody>
<tr>
<td>No diapause 1964</td>
<td>♀♂</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>24.3</td>
<td>24.6</td>
<td>23.8</td>
<td>22.0</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>3</td>
<td>98</td>
<td>84</td>
<td>1</td>
<td>0.882</td>
<td>0.130</td>
<td>0.132</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Normal diapause 1963</td>
<td>♀♂</td>
<td>27.2</td>
<td>29.5</td>
<td>27.1</td>
<td>27.5</td>
<td>---</td>
<td>34.2</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>28.4</td>
<td>28.4</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>64</td>
<td>12</td>
<td>18</td>
<td>16</td>
<td>5</td>
<td>3.626</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>1.071</td>
<td>0.779</td>
</tr>
<tr>
<td></td>
<td>♂♀</td>
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<td>40.6</td>
<td>30.7</td>
<td>29.7</td>
<td>---</td>
<td>28.7</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>28.7</td>
<td>28.6</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>98</td>
<td>5</td>
<td>30</td>
<td>35</td>
<td>41</td>
<td>0.483</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>0.431</td>
<td>0.546</td>
</tr>
<tr>
<td>Normal diapause 1964</td>
<td>♀♂</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>22.1</td>
<td>22.4</td>
<td>22.4</td>
<td>22.8</td>
<td>21.3</td>
<td>21.0</td>
<td>---</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>---</td>
<td>101</td>
<td>136</td>
<td>12</td>
<td>48</td>
<td>169</td>
<td>118</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td></td>
<td>♂♀</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>22.5</td>
<td>23.2</td>
<td>25.4</td>
<td>25.6</td>
<td>21.7</td>
<td>21.3</td>
<td>---</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>291</td>
<td>276</td>
<td>11</td>
<td>18</td>
<td>295</td>
<td>233</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Prolonged diapause 1963</td>
<td>♀♂</td>
<td>24.0</td>
<td>---</td>
<td>26.0</td>
<td>---</td>
<td>22.8</td>
<td>---</td>
<td>---</td>
<td>---</td>
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<td>---</td>
<td>---</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>0.707</td>
<td>---</td>
<td>0.742</td>
<td>---</td>
<td>1.368</td>
<td>1.354</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td></td>
<td>♂♀</td>
<td>27.0</td>
<td>28.2</td>
<td>1</td>
<td>29.2</td>
<td>---</td>
<td>27.3</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>27.2</td>
<td>20.1</td>
</tr>
<tr>
<td></td>
<td>n</td>
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<td>0.975</td>
<td>2.540</td>
<td>2.070</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>1.146</td>
<td>0.431</td>
</tr>
</tbody>
</table>

<sup>*Dashes indicate no data.  
Note: *x̄* = standard error of the mean.</sup>
sex-related differences in the regulation of development with normal and prolonged diapause. Our experiments, however, do not provide evidence for interpreting these differences satisfactorily.

**Discussion**

The seasonal sequence of developmental stages of *N. swainei* does not vary under natural conditions. Although Smirnoff and McLeod (1966) found evidence that a large proportion of the individuals in a field population of *N. swainei* in Roberval County, Quebec, had begun morphogenesis in the fall of 1963, adult emergence, mating, and oviposition during the fall have not been observed in many years of intensive research by a number of investigators since 1930. There is only one published record (Schedl 1937) of a single egg cluster in mature needles, a condition required for proof of fall oviposition. The geographic range of *N. swainei* and its developmental rate are such that if eggs are laid in the fall, they would have to survive low winter temperatures approximating those that *N. sertifer* can survive (Sullivan 1965). In addition, if *N. swainei* eggs have sufficient cold hardiness to prevent mortality by freezing, it is still not known if they could survive a protracted exposure to low temperature above the level causing direct mortality without dormancy as in *N. sertifer* (Brygider 1952). The control mechanisms of egg dormancy (embryonic) in *N. sertifer* and other egg-overwintering species have not been clearly defined.

If morphogenesis begins in the fall, but cannot be completed because of the onset of low temperatures, and if the partly developed individuals survive, pupation, adult emergence, and oviposition would be expected earlier than usual the following summer. However, Smirnoff and McLeod (1966) reported that although many larvae resumed morphogenesis in the fall of 1963 at Roberval, and temperatures in the spring of 1964 were high, adults did not emerge earlier than usual. This suggests that in *N. swainei*, as in *N. sertifer* (Sullivan and Wallace 1967), an exposure of potentially non-diapause individuals to a period of low temperature increases the time they subsequently require to complete development. If adult emergence did take place unusually early, the developing current year’s needles would not be available to the females for oviposition, and because females rarely oviposit in mature needles, an out-of-phase population could not become established.

On the basis of our results on the photoperiodic control of diapause at 21°C, it cannot be seen how *N. swainei* can develop under natural conditions without the prepupal diapause. At 47° N Lat., the approximate origin of our samples, the time (hours and minutes) from sunrise to sunset and durations of civil twilight (U.S. Naval Observatory 1945) are as follows:

<table>
<thead>
<tr>
<th>Date</th>
<th>Sunrise to sunset</th>
<th>Civil twilight</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 15</td>
<td>15:53</td>
<td>1:20</td>
<td>17:13</td>
</tr>
<tr>
<td>July 15</td>
<td>15:52</td>
<td>1:16</td>
<td>17:08</td>
</tr>
<tr>
<td>August 15</td>
<td>14:14</td>
<td>1:06</td>
<td>15:20</td>
</tr>
<tr>
<td>September 15</td>
<td>12:36</td>
<td>1:02</td>
<td>13:38</td>
</tr>
</tbody>
</table>

In our experiments, continuous development took place in the range 16.5 to 19 h of light per day when the insects were exposed from 4 to 6 days before hatch to the end of the larval feeding period. The natural photophases appear too short to permit avoidance of diapause except possibly early in the season when the sawfly may be present as eggs or young larvae during July. We do not know the stage or stages of development sensitive to photoperiod, the light intensity threshold and, therefore, the effective natural photophase, or the manner in which daily and seasonal temperature regimes during the photoperiod exposure affect the response. The effect of the natural progression of daylength may also be important, as well as geographic variation if work is done on material from different populations, particularly if they originate from different latitudes.

**Neodiprion swainei**, as expected of a valid biological species, appears to have several mechanisms maintaining its seasonal developmental sequence and breeding synchrony. The conclusion of Maxwell (1958) that diapause and life history pattern are not stable isolating factors is unwarranted. Experimental evidence is far from complete, but the limitations placed upon *N. swainei* by its host specificity, diapause requirements, and developmental rates effectively rule out more than one generation a year.

Our knowledge of diapause and its controlling mechanisms in *Neodiprion* sawflies is elementary. Both *N. swainei* and *N. sertifer* have only one
generation a year, although *N. sertifer* in some alpine habitats is regularly hemivoltine (Pschorn-Walcher 1970). *Neodiprion rugifrons* Middleton, according to King and Benjamin (1965), has a second generation some years on certain sites in response to photoperiod and temperature. No species such as *Neodiprion lecontei* (Fitch) which has one generation a year in Canada but more than three per year in the Gulf States (Benjamin 1955) has been investigated. We are currently studying the role of photoperiod in diapause regulation in a number of *Neodiprion* species native to Ontario. We believe that such studies will provide valuable leads to understanding some of the isolating mechanisms among these sawflies.


