Bionomics of *Pissodes nemorensis* Germar (Coleoptera: Curculionidae) in Northern Florida

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ABSTRACT   Brood development and adult activity of *Pissodes nemorensis* Germar were studied in slash pine (*Pinus elliottii* Engelm. var. *elliottii*) plantations in northern Florida in 1977–78. The insect is basically univoltine in this area, but immatures are present in infested hosts for almost 9 mo during the cooler part of the year. Eggs were present in the field from late August until mid March; most oviposition occurred from October through February. Development from egg to adult within hosts required 7–25 wk depending on date of oviposition. Most adults emerged from late March to mid May. Some adults emerged before December from eggs laid in late summer, but it is not known whether these reproduced during the same season. Adults were caught in sticky traps next to trap trees, in window traps, and in pheromone traps from August until early April, with a major peak in October or November and a smaller peak in March. Most adults trapped were apparently mature (i.e., had developed in the previous season), for trap catches declined as new adults emerged. Adults were not observed in the summer months and were not caught in traps. *P. nemorensis* has five instars. At constant temperatures of 15, 20, and 25°C, egg-to-adult development required ca. 180, 70, and 58 d, respectively. Principal causes of mortality to weevil brood were the parasite *Coeloides pissodis* (Ashmead) (Hymenoptera: Braconidae) and woodpeckers. Disease and competition, principally with *Ips* spp., also appeared to be important.

KEY WORDS   Insecta, slash pine, *Pinus*, development

Pissodes nemorensis Germar is a minor pest of native pines and exotic cedars (*Cedrus* spp.) in eastern and boreal North America (Phillips et al. 1987). Adults feed on the phloem of branches and trunks of host trees and larval development occurs in the phloem of terminals, branches, trunks, and roots of weakened or recently dead trees (Baker 1972). Adult feeding on seedlings may cause mortality (Beal 1952) and on larger trees may result in "scorched" foliage and needle drop (Ollieu 1971). Also, the weevil may vector the fungus *Fusarium moniliforme* var. *subglutinans* Wr. and Reink, the causal agent of pitch canker in southern pines (Blakeslee et al. 1981). Recent studies have focused on aggregation pheromones (Fontaine & Foltz 1982, Phillips et al. 1984, Phillips & Lanier 1986), reproductive anatomy and seasonal development (Fontaine et al. 1983), fecundity and oviposition (Fontaine & Foltz 1985), and biosystematics (Phillips et al. 1987). Our objectives were to determine the seasonal patterns of adult activity and immature development in northern Florida, to identify mortality factors acting on *P. nemorensis* within host trees, and to make limited studies on immature development time at constant temperatures in the laboratory.

Materials and Methods

Study Areas. Activity and development of *P. nemorensis* were studied in three slash pine (*Pinus elliottii* Engelm. var. *elliottii*) plantations in Flagler and Volusia counties, northeastern Florida. The 19-yr-old Barberville plantation was the older of the two commercial plantations and had 1,250 trees/ha averaging 13.4 m in height and 16 cm diameter at breast height (dbh). The B-216 plantation was 16 yr old and had 925 trees/ha averaging 9.8 m tall and 13 cm dbh. The Enclosure plot, located within a former experimental area, had a higher stocking (2,300 trees/ha) than is normal in commercial plantations; the 9-yr-old trees were 7.1 m tall and 11 cm dbh. Saw palmetto (*Serenoa repens* Bartr.), gallberry (*Ilex glabra* (L.) Gray), and wax myrtle (*Myrica cerifera* L.) were common in the understory in all areas. The canopy of the B-216 plot was relatively open and the understory was dense. The Enclosure and Barberville plots, especially the former, were densely shaded, and the understory was light and discontinuous. Weekly temperature extremes were recorded in the B-216 and Enclosure plots throughout the study with maximum-minimum thermometers hung at 1.5 m on the north sides of trees.

Immature Development and Mortality. Trap trees were cut monthly over a 13-mo period in all
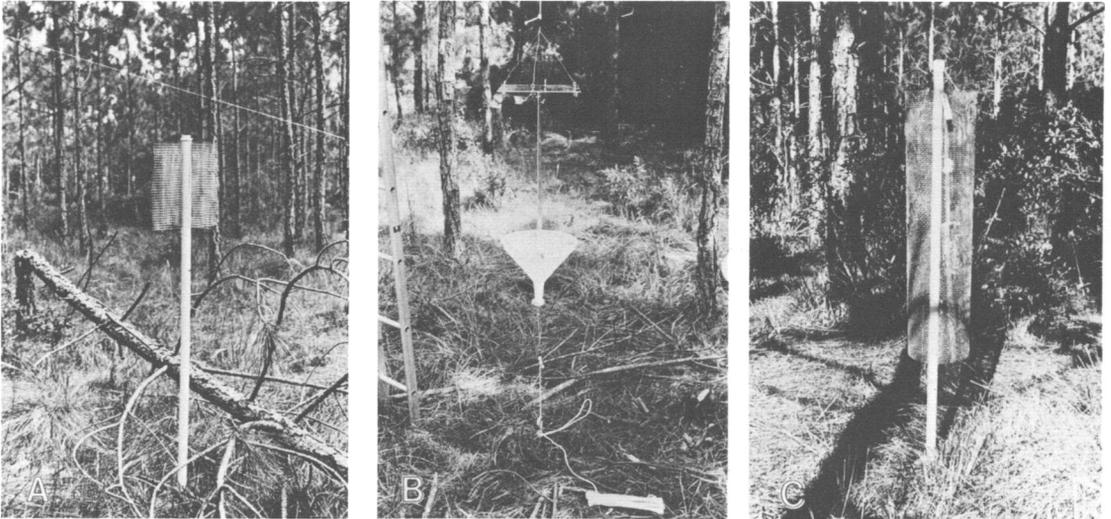
Fig. 1. Traps used to monitor adult activity of *Pissodes nemorensis*. (A) Four-vaned sticky trap adjacent to slash pine trap tree. (B) Four-vaned Plexiglas window trap (collecting jar not shown). (C) Sticky pheromone trap.

areas to provide breeding material for *P. nemorensis*. The material was prepared by partially severing slash pines at a height of approximately 0.5 m and tipping the trees over (Fig. 1A), which severely weakened them but did not kill them outright. Four trees were felled monthly in the B-216 plot from 22 June 1977 to 22 June 1978 (52 trees); two per month in the Barberville plot from 4 August 1977 to 3 August 1978 (26 trees); and three to five per month in the Enclosure plot from 28 September 1977 to 21 September 1978 (55 trees). Trees cut on a given date were felled in different parts of the stands to minimize interactions.

Each felled tree was examined biweekly for activity and breeding of *P. nemorensis* and other phloem-breeding insects, particularly Scolytidae, Buprestidae, and Cerambycidae. At each examination, approximately 200 cm^2 of the bark was removed from the sides or bottom surface of the lower, middle, and upper bole, and the phloem was examined for presence of immature stages and a subjective measure of relative abundance. Observations on a given tree were continued until weevils began emerging or until all phloem had been consumed or degraded. In either case, all remaining bark was stripped from the main stem and large branches to count and observe the remaining weevils.

Paired 30-cm-long sections were cut at monthly intervals for 4 mo from the bases of five trees cut in September and five cut in November 1977 in the Enclosure plot (total of 20 paired samples for each series). One of the two sections was dissected in the laboratory to record the numbers and stages of *P. nemorensis* and other insects. Head capsules of all weevil larvae were measured. The second section was placed in a screened cage held at ambient temperature in a shade house next to the laboratory in Gainesville, Fla. Cages were checked every other day for emerging weevils and associates.

Adult Activity. Three types of traps were used to monitor adult activity. Four-vaned sticky traps (Fig. 1A) were placed next to each trap tree in the B-216 and Barberville plots. These were checked weekly from the time of cutting until *P. nemorensis* and other insects had consumed most of the phloem. The traps consisted of two 30-cm squares of hardware cloth cut halfway through the center and joined along the cuts. Plastic PVC pipes, with the ends cut to receive the screens, supported traps at a height of 1 m. Screens were sprayed with aerosol Tanglefoot, a nondrying, sticky compound. Traps were monitored from July 1977 until September 1978 at the B-216 plot and from August 1977 until March 1978 at the Barberville plot.

Omnidirectional Plexiglas window traps were built as designed by Wilkening et al. (1981), but without the upper collecting chamber (Fig. 1B). In the B-216 plot, four arrays of three traps each were checked weekly from 16 September 1977 to 22 November 1978. Traps in each array were hung at ground level (center of trap at 1 m), center of clear bole (3 m) and midcrown (5 m). Four arrays of two traps each (at 1.5 and 3.5 m) were checked weekly in the Enclosure plot from 22 November 1977 to 28 November 1978. Ethanol was the collecting fluid in the window traps.

After preliminary tests indicated the pheromone compounds isolated from *Pissodes approximatus* Hopkins (Booth et al. 1983) were attractive to *P. nemorensis* (Atkinson 1979), pheromone traps were placed in all plots (four traps in B-216 and Enclosure plots, two in Barberville plot) from 22 November 1977 until 18 April 1978 and again from 19 July to 22 November 1978. Traps consisted of cylinders (90 by 29 cm diameter) of hardware cloth sprayed with Tanglefoot and suspended from plas-
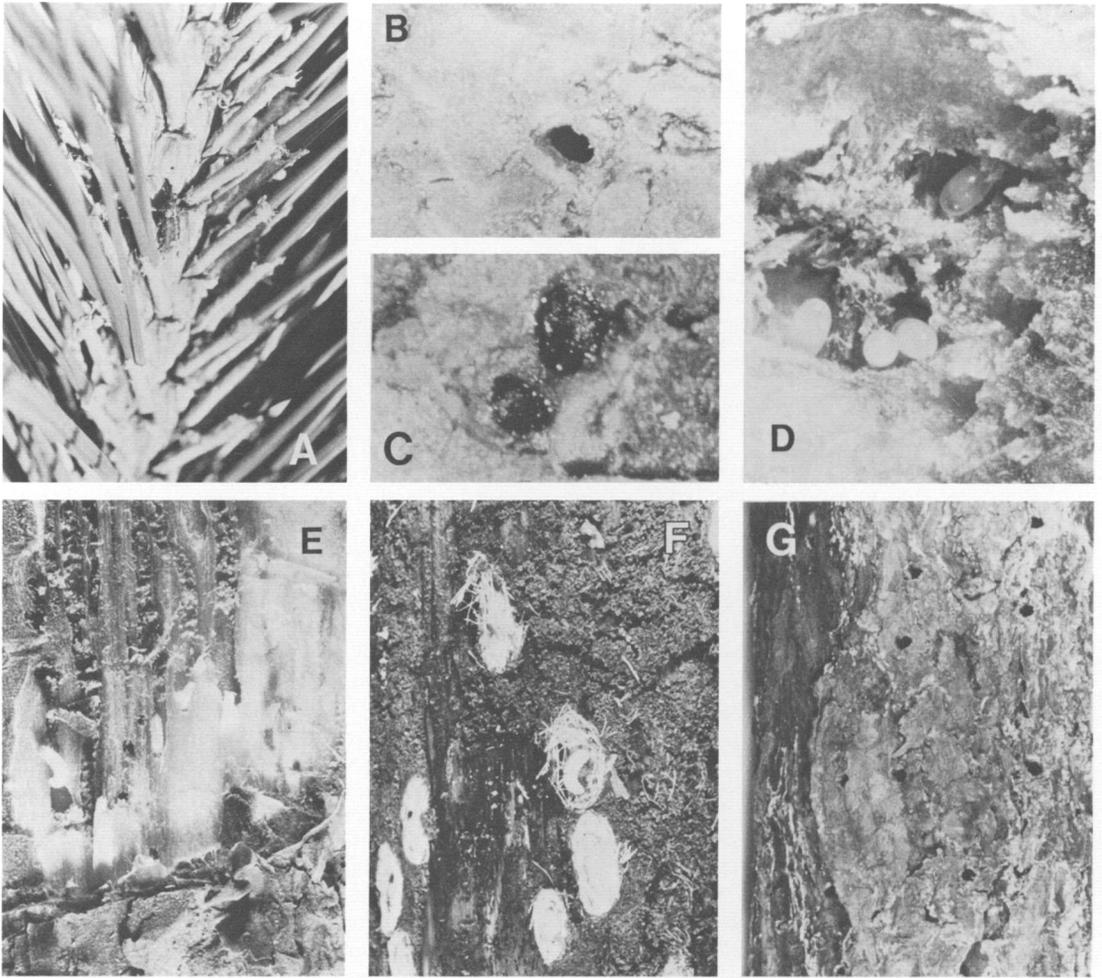
Fig. 2. Life cycle of *Pissodes nemorensis*. (A) Adult feeding on slash pine branch (adult length 7 mm). (B) Adult feeding puncture (0.45 mm diameter). (C) Plugged oviposition puncture (0.65 mm diameter). (D) Eggs (0.40 by 0.80 mm). (E) Actively feeding larvae. (F) Prepupal larvae in chip cocoons (exposed larva 10 mm long). (G) Emergence holes in bark (3–4 mm diameter).

tic poles (Fig. 1C). Baits consisted of a 15-cm-long slash pine bolt with 14 mg grandisol (*cis*-2-isopropenyl-1-methylcyclobutaneethanol) and 5 mg grandisal (*cis*-2-isopropenyl-1-methylcyclobutane-ethanal) placed inside a hollow polyethylene vial stopper (rates suggested by D. C. Booth, personal communication). Traps were baited biweekly and checked after 1 wk.

Immature Development at Constant Temperatures. In the fall of 1978, adult weevils were collected in the field near Gainesville, Fla. Groups of 40–50 unsexed adults were caged on 23-cm-long slash pine bolts for 24 h per bolt on 47 bolts. The bark was smoothed to prevent weevils from hiding in bark crevices, and the ends were waxed to reduce moisture loss. After exposure to ovipositing adults, bolts were held at constant temperatures of 15, 20, and 25°C with a 12:12 (L:D) photoperiod. At regular intervals (1–2 d at 25°C, 2–3 d at 20°C, 3–5 d at 15°C) one-fourth to one-half the bark was re-

moved from one of the bolts at each temperature, and the stages of all individuals were recorded. Head capsules of all larvae were measured. Prepupal larvae and pupae were placed in gelatin capsules and held inside humidors at 70% RH in the temperature cabinets. These individuals were examined daily and their development noted. When most individuals encountered were prepupae and pupae in a given temperature regime, some of the bolts were placed in 3.78-liter jars and checked daily for emergence. The percentage occurrence of each developmental stage was calculated for each sample. Median durations for each stage were calculated by interpolation of the plotted points. Median emergence time was taken directly from the emergence data.

Results

Immature Development. Eggs are laid in the phloem of susceptible hosts in punctures made by
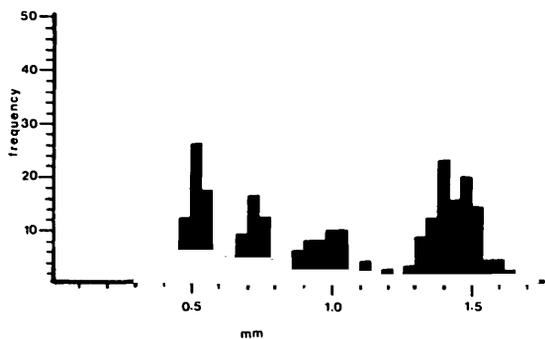
Fig. 3. Frequency distribution of head capsule widths of 382 larvae of *Pissodes nemorensis* reared in the laboratory in slash pine logs.

Fig. 4. Relative abundance of *Pissodes nemorensis* life stages in northern Florida based on examination of 133 trap trees and adult traps at three sites. Thickness of line represents subjective abundance for each stage.

females with their rostra, or "beaks." Oviposition punctures can be distinguished from feeding punctures because the former are often slightly larger and are plugged with macerated phloem (Fig. 2 A–C). Eggs are deposited singly or in groups of up to five in a single puncture (Fig. 2D). Larvae make individual tunnels longitudinally oriented in the phloem (Fig. 2E) but generally avoid areas containing other insects, microorganisms, or resin-soaking. Mature larvae gouge pupal chambers in the sapwood and construct "chip cocoons" lined with excelsiorlike strips of wood (Fig. 2F). After eclosion, adults chew individual emergence holes through the bark (Fig. 2G). Most breeding occurs in trunks and larger branches, although successful development was observed in twigs and roots. Larvae feed entirely in the phloem in thick-barked breeding material, but larvae (especially later instars) often score the sapwood in hosts of smaller diameter. *P. nemorensis* has five instars (Fig. 3) in Florida.

Pissodes nemorensis is basically univoltine in northern Florida (Fig. 4), although oviposition occurs over an extended period, and immatures may be present for 8–9 mo, depending on the site.[2] This conclusion is consistent with the observations of Dietrich (1931), Jones (1965), Overgaard & Nachod (1971), and Ollieu (1971), except that the period of reproductive activity was longer than they indicate, continuing into the winter and early spring. Initiation of oviposition in our study was related to the degree of canopy closure. Oviposition was observed as early as late July in the Enclosure plot (most densely shaded) but not until October in the B-216 plot (the most open). Weevils oviposited in all parts of trees and on all sides of the trunk during the late fall and early winter. During late summer, early fall, and late winter, oviposition and
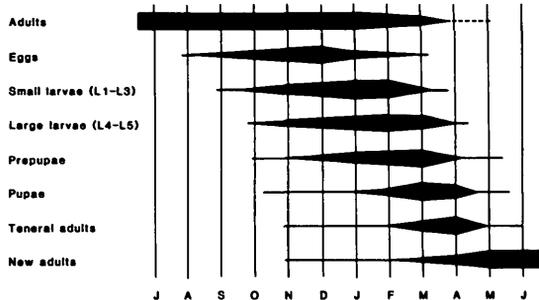
immatures were restricted to the crown and the lower sides of trunks. Fontaine et al. (1983) found that *P. nemorensis* adults were more active during the cooler parts of the day during the summer months and did not mature sexually until late summer. Presumably, weevils in shadier and cooler stands become reproductively active earlier in the year. Most oviposition occurred from October until February, but some eggs were observed as late as the first week of April.

Oviposition in trap trees began 2–5 wk after felling, with longer intervals during colder weather. Most trees cut in the spring and summer were not attacked. Total immature development time in the field varied from 22 to 25 wk for eggs laid during mid to late October, to 7 to 8 wk for eggs laid during the late summer. Although most oviposition occurred during a 5-mo period in the fall and winter, most adults emerged during a 2-mo period from late March to mid May. Total development time decreased with later date of oviposition from October to March, probably because of the effects of low temperatures in January and February on development. Some weevils developing from eggs laid in late summer emerged in late November and early December before the onset of cold weather, but the number was very small compared with the main peak of emergence during the spring. It is not known whether these reproduced in the same season, but results of limited laboratory tests at constant temperatures (Atkinson 1979) indicate this would have been unlikely.

Mortality Factors of Immatures. Methods used to study immature mortality did not permit precise identification and estimation of all mortality factors. *Coeloides pissodis* (Ashmead) (Braconidae) was the only parasitoid observed in samples reared in the laboratory. *C. pissodis* killed 22.1% of sampled larvae in trees cut in September 1977 but only 1.55% in trees cut in November 1977 in the same area (parasitism determined by presence of ectoparasitic larva or silken cocoon in larval tunnel) (Table 1). The parasitoid may be unable to parasitize weevil broods during the colder months of the year. Disease was also more important in the

[2] This summary is based on a synthesis of subjective observations of presence and abundance for all trees in all sites. Groups of trees were cut at regular intervals, but weevil breeding was irregular in terms of initiation and density of oviposition, number of trees attacked, and parts of trees utilized. Quantitative indices of breeding activity are difficult to apply here. Greater detail is given by Atkinson (1979).

Table 1. Summary of mortality and survival of *P. nemorensis* in slash pine trap trees; enclosure plot, Flagler Co., Fla.; trees cut 28 October 1977 and 16 November 1977

	September series		November series	
	Density[a]	%[b]	Density	%
Mortality factor				
Coeloides pissodis	1.061	22.10	0.047	1.55
Disease	0.544	11.33	0.127	4.18
Woodpeckers	0.787	16.40	0	0
Chip cocoon mortality	0.235	4.90	0.546	17.97
Unknown	1.467	30.56	1.652	54.36
Total mortality	4.094	85.29	2.372	78.05
Surviving *P. nemorensis*	0.706	14.71	0.667	21.95
Maximum *P. nemorensis*[c]	4.800	100.00	3.039	100.00
Emerged *Ips calligraphus*[d]	1.078	—	5.062	—
Emerged *I. grandicollis*[d]	0.095	—	1.931	—

[a] Numbers/100 cm².

[b] Percentage of maximum density of *P. nemorensis*.

[c] Maximum is maximum observed in any period plus all previous mortality.

[d] Maximum emerged in any sample period.

September series (11.3%) than in the November series (4.18%) (dead, discolored immatures with no evidence of parasitism, predation, or desiccation were considered to have died from disease). Woodpeckers killed an appreciable number of large larvae and prepupae (16.4%) in the September trees but none in the November series (based on number of empty chip cocoons and larval galleries in area exposed by foraging, corrected to include estimated mortality from other causes). Woodpecker feeding was observed at irregular intervals in trap trees in all plots throughout the year. An appreciable number of weevils died inside chip cocoons (chip cocoon mortality, Table 1). In most cases, the condition of the remains did not permit a more precise identification of the causes of mortality, but disease seems most likely. The intact condition of most cocoons suggests that parasitism or predation was not the cause of death.

A large part of the mortality was unexplained (unknown, Table 1). Unknown mortality was calculated by subtracting densities of surviving weevils and mortality from known causes from the maximum observed densities of immature *P. nemorensis* in the samples. The two most likely causes of mortality were predation and competition. Adults and larvae of *Temnochila virescens* (F.) (Coleoptera: Trogositidae) were frequently observed on and in trap trees in all plots, but none was encountered in the sample dissected for estimation of mortality. This species is a predator of a variety of subcortical insects (Baker 1972) including *P. nemorensis* (Overgaard & Nachod 1971). Larvae of *Lonchaea* sp. (Diptera: Lonchaeidae) and *Medetera* sp. (Diptera: Dolichopodidae) were abundant in both series. Species of both genera have been considered predators of subcortical insects including *Pissodes* spp., but studies by Harman & Wallace (1971) and Kishi (1969, 1972) suggest that they
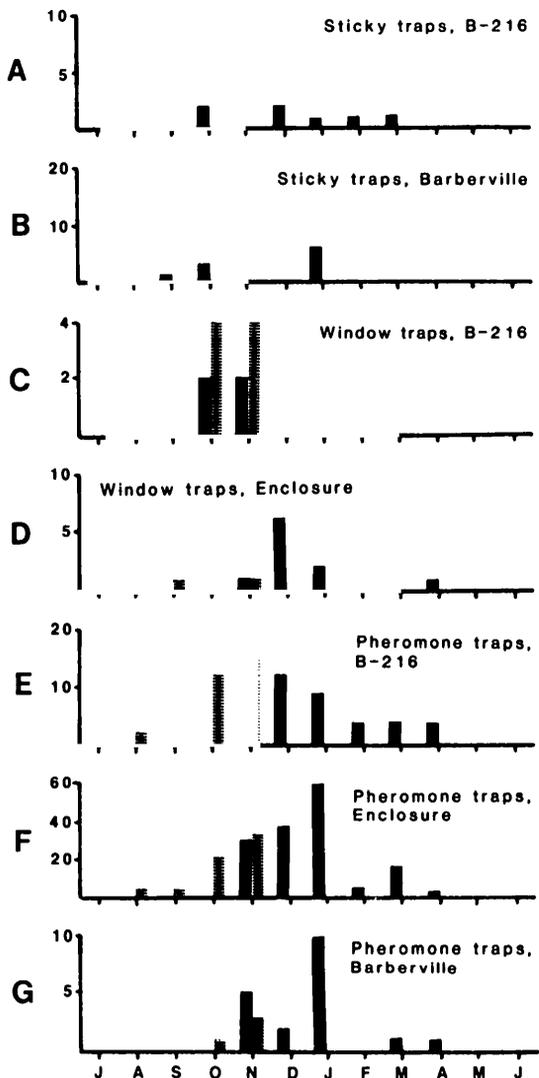
Fig. 5. Adjusted monthly totals of *Pissodes nemorensis* adults in different traps and plots. Solid lines, 1977–78; dashed lines, 1978–79. (A) Sticky traps, B-216 plot (July 1977–November 1978). (B) Sticky traps, Barberville plot (August 1977–March 1978). (C) Window traps, B-216 plot (September 1977–November 1978). (D) Window traps, enclosure plot (November 1977–November 1978). (E) Pheromone traps, B-216 plot (November 1977–November 1978). (F) Pheromone traps, Enclosure plot (November 1977–November 1978). (G) Pheromone traps, Barberville plot (November 1977–November 1978).

are probably scavengers. Alfaro & Borden (1980) showed that *L. corticis* larvae may be scavengers or predators on *P. strobi,* depending on the size and condition of immatures. When these larvae were found feeding on immatures of *P. nemorensis,* the true cause of death could not be determined. Large numbers of *Ips calligraphus* (Germar) and *I. grandicollis* (Eichhoff) (Scolytidae) emerged from the November samples (Table 2). Competition from these bark beetles may have ac-

counted for much of the unexplained mortality (54.36%) in these samples. Although they were relatively uncommon in the sample dissected for estimating mortality, the cerambycids *Rhagium inquisitor* (L.), *Neacanthocinus obsoletus* (Olivier), and *Monochamus* spp., all of which feed on phloem during all or part of their development, were commonly observed in trap trees and probably caused significant mortality of weevil broods.

Adult Activity. Trends in catches of adult weevils in all trap types and areas were similar (Fig. 5). Weevils were trapped from August or September until March or April with a major peak in October or November, or both. Some traps in some plots showed a second, smaller peak in March. The winter drop in trap catches was probably because of reduced activity associated with very low temperatures in January and February. Apparently, newly emerged adults were not caught in any of the traps in appreciable numbers, because trap catches had declined or dropped to zero before most new adults had emerged.

Window traps were not associated with any known attractant and presumably reflected general flight activity of weevils in stands (ethanol used in the collecting jars is attractive to some subcortical insects, but its attractiveness to *P. nemorensis* is not known). In the Enclosure plot, weevils were caught in similar numbers in traps at both 1.5 and 3.5 m. In the B-216 plot, most weevils were trapped at 1 m or 5 m and fewest were caught at 3 m (χ^2 = 5.38, df = 1, $P \leq 0.02$). Weevils responding to pheromones or searching for breeding material may fly near the ground, whereas those moving short distances may fly between crowns of adjacent trees. Fontaine et al. (1983) showed that during the summer, *P. nemorensis* adults feed during the cooler parts of the day in northern Florida and that they are relatively inactive and reproductively immature. Weevils may disperse only during the breeding season.

Development at Constant Temperatures. Egg to emerged adult development required 58, 70, and 180 d at 25, 20, and 15°C, respectively (Fig. 6). These times are similar to those reported for *P. strobi* (Peck) (McMullen 1976). Although too few temperatures were tested for linear regression analysis, an eye-fitted line of reciprocal development times plotted against temperature indicates a developmental threshold in the vicinity of 9°C, in close agreement with values calculated for *P. strobi* (McMullen 1976).

Discussion

The seasonal life history of *P. nemorensis* in northern Florida is unusual compared with the same and other species of *Pissodes* in America. *Pissodes strobi* (Taylor 1929), *P. terminalis* Hopping (Stark & Wood 1964), *P. affinis* Randall (Martin 1964), *P. fasciatus* LeConte (Deyrup 1978), and *P. schwarzi* Hopkins (Stevens 1966) all breed in the
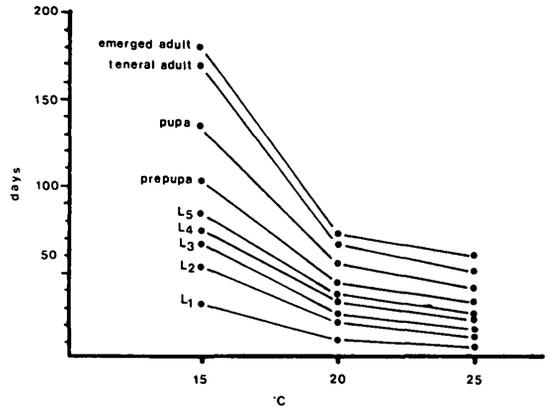
Fig. 6. Median development times for immature stages of *Pissodes nemorensis* at constant temperatures in slash pine bolts.

late spring or early summer. Some of these species may require 2 yr to complete development in the northern parts of their ranges. The only other *Pissodes* known to breed in the fall and winter is *P. obscurus* Roelofs, a Japanese species (Yoshikawa 1977).

Pissodes nemorensis (sensu Phillips et al. 1987) shows considerable variation in seasonality of breeding in different parts of its range. In Ontario (Finnegan 1958) and Pennsylvania (Bliss & Kearby 1970, as *P. approximatus* in both cases), most oviposition occurs in the summer and early fall; most brood matures and emerges before winter, but immatures developing from late oviposition overwinter as larvae or pupae and complete their development the following spring. In Arkansas (Jones 1965) and Louisiana (Overgaard & Nachod 1971), fall breeding has been reported. In general, the species "shifts" its breeding period to the cooler periods of the year in the more southerly parts of its range where summers are "too hot." In northern Florida, where winters are mild, breeding activity continues throughout the winter. In both the northern and southern parts of its range, *P. nemorensis* appears to oviposit and breed over a long period, probably as long as temperatures are suitable, and has overlapping generations.

Phillips et al. (1987) synonymized *P. nemorensis* and *P. approximatus* on the basis of morphological, cytological, behavioral, and chemical evidence. They found that adults responded to pheromones in summer in the northern parts of its range and in the fall in the southern parts, with some intermediate populations responding in both periods. We found that *P. nemorensis* responded throughout the fall and winter breeding season in northern Florida. Changes in seasonality of breeding in different parts of the insect's range are consistent with their results on adult response to pheromones. Except for differences in seasonality and local hosts, the bionomics of *P. nemorensis* as reported here do not differ in any significant aspect from studies

on "*approximatus*" in Ontario (Finnegan 1958) and Pennsylvania (Bliss & Kearby 1970).

Acknowledgment

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