LARVAL DEVELOPMENT AND CONSUMPTION OF SOYBEAN FOLIAGE BY THE VELVETBEAN CATERPILLAR, *Anticarsia gemmatalis* HÜBNER (LEPIDOPTERA:NOCTUIDAE), IN THE LABORATORY

By

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March, 1975

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Co-Chairman: Dr. W. H. Whitcomb
Major Department: Department of Entomology & Nematology

I reared velvetbean caterpillars, Anticarsia gemmatalis Hubner, individually in the laboratory on excised 'Brago' soybean foliage. I determined areas of foliage consumed, development times, and number of larval molts to study the effects of temperature on speed of development and rates of consumption.

The effect of treatments on number of molts was significant. Number of molts was a function of the rate of development through successive stadia, as determined by treatments. It in turn affected final size and final areas consumed.

The effects of temperature on speed of development and rates of consumption were highly significant.

Comparison of larvae reared by the laboratory method and on plants grown in pots gave insufficient evidence that rearing methods affected rates of consumption. Rates of consumption by instars in the laboratory were comparable with rates based on data from Strayer (1973) for field populations.

The study suggests that determination of rates of consumption in the laboratory is useful in understanding the relationship of pest density to economic thresholds; and that precise data from individually reared larvae provides good indications of how development is influenced by treatments when expressed in linear models as a function of time and instar number.

INTRODUCTION

The velvetbean caterpillar, Anticarsia gemmatalis Hübner (Lepidoptera:Noctuidae), feeds as a larva on the foliage of wild and cultivated legumes. The range of A. gemmatalis is restricted to the New World.

A. gemmatalis has been a serious pest of several leguminous crops in the southeastern United States and economic infestations have also been reported from Central and South America. Currently, A. gemmatalis is of major importance on soybeans in parts of South America and the southeastern United States. Distribution records for the United States indicate that A. gemmatalis does not overwinter north of Florida. Adults annually invade susceptible hosts as the growing season progresses, extending populations north and west into the southeastern United States. Increased cultivation of soybeans or alternative legumes in these areas is foreseeable.

Defoliation is the evident point of relationship between A. gemmatalis and soybeans. Economic production will depend partly on incorporation of a body

of knowledge concerning these relationships into pest management policies. Strayer (1973) has recently made studies in North Florida relating loss of yield from A. gemmatalis to population size through measurements of defoliation in the field. Field experiments provide a direct method of examining the impact of infestations on yield but are subject to variables such as mortality and climate which are difficult to control or record. For this reason, the contribution to defoliation per individual in the population and factors affecting rates of defoliation have not been closely examined.

The objectives of the present study were to determine the effects of temperature and foliage maturity on feeding and development of individual velvetbean caterpillars and to estimate defoliation percentages from rates of feeding by larvae in the laboratory.

There were five parts to the study: (1) Feeding and development of individual velvetbean caterpillars were studied under controlled conditions of temperature and foliage maturity in the laboratory; (2) These investigations were extended to find factors related to the number of instars of caterpillars reared because of probable influence of this variable on the interpretation of effects of treatments; (3) Larvae were

reared by the laboratory method and on plants in pots under similar conditions of temperature and foliage maturity to determine if rearing method affected rates of consumption; (4) Crop foliage was measured to relate areas consumed and areas on the crop, estimate weight/unit area, and variation in thickness of foliage; and (5) The results were used to estimate defoliation percentages expected in the field.

LITERATURE REVIEW

The literature on Anticarsia gemmatalis has been assembled by Strayer (1973), who reviewed the areas of systematic history, synonymy, life history, distribution, damage, host plants, and natural enemies; a bibliography of literature on the species has been compiled by Ford et al. (1974). Repetition will be avoided by limiting the present review mainly to those areas and aspects not discussed from a similar standpoint by Strayer.

Description of Stages

The life stages of A. gemmatalis were described by Watson (1915a, 1915b) and briefly by Douglas (1930) and Ellisor (1942). Hinds (1930) and Anon. (1959) presented photographs of the stages.

Egg

Watson (1916b), Douglas (1930), Hinds (1930), Ellisor (1942), and Greene et al. (1973) reported that

the eggs are laid separately on the plant, most commonly on the underside of soybean leaves. Hinds (1930) stated that eggs were laid especially on the leaf stems and midribs where piliosity was heaviest, and Ellisor (1942) noted that eggs were usually attached on the plant hairs. Greene et al. (1973) stated that the egg was usually placed close to the surface between the plant hairs and adhered tightly to the plant.

Watson (1916b) described the color of the egg as changing from white to a delicate pink about a day before hatching. Douglas (1930) also described the egg as white; however, it was described as cryptic green (on soybean foliage) by Greene et al. (1973), and as bluish-green, changing to orange when ready to hatch, by Hinds (1930). Ellisor (1942) stated that the egg was pale green when first laid but that it gradually became darker and reddish-brown before hatching. He also described the egg as almost hemispheric-shaped, 1-1.5 mm across, and sculptured with a series of ridges converging at a very prominent micropyle.

Larva

Watson (1916b) found that there were usually six larval instars and described each of them. He observed individuals with seven larval stadia late in the season. Douglas (1930) and Ellisor (1942) reported six instars.

Watson (1916b) observed that prior to the 3rd stadium, the first 2 of the 4 pairs of prolegs were relatively short and not used in walking. He found that the 1st and 2nd instars could be distinguished by the length of the prolegs on abdominal segments III and IV relative to those on abdominal segment V. Ellisor (1942) noted the value in counting the prolegs to distinguish this species from the green cloverworm and loopers also found on soybeans. He also noted the looping form of progression and the position of the terminal prolegs which are useful in quickly separating A. gemmatalis from Heliothis and armyworm species.

Watson (1916b) described light (green) and dark (blackish) larvae and stressed that specimens could be found exhibiting all color variations between these extremes. He also noted that coloration may change from light to dark during the lifetime of one

individual. Chittenden (1905) and Douglas (1930) apparently described only darker colored specimens. Ellisor (1942) stated that usually larvae turned black only on soybeans that had been heavily defoliated.

Watson (1916b) and Guyton (1940) noted that the larvae turn reddish brown when about to pupate. Watson (1916b) found that larvae reached a maximum size of approximately 48 mm before shortening prior to pupation.

Pupa

Watson (1916b) described the pupa and the earthen cell made prior to pupation. He noted that the caterpillar occasionally omits to make the cell and that the pupa is light green until about a day old, turning brown later.

Adult

A translation of the original description by Hübner (1816, p. 340) has been kindly provided by Dr. W. J. Kloft[1]:

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[1]Dr. W. J. Kloft, Director, Institute Für Angewandte Zoologie, Universität Bonn, Visiting Professor at the University of Florida, 1972.

> The wings are nearly beaked at the end, with a sharp dark line and dark dots on both wings.

Hübner (1818, p. 26) described the moth again from a specimen received from Surinam:

> . . . similar to A. tomyralis but smaller and very much different in design and coloring. The wings are marked above with a bleached kidney dot, a rust brown curved line, several black wavy lines and a depression [?] with several eye-like dots which again have accompanying black waved lines. The illustrations 153, 154 are of females.

Most descriptions have noted the variability between individual moths. Watson (1916b) illustrated adults with various color differences. Watson (1916b) and Ellisor (1942) pointed out that the line from the apex of the forewing to about the centre of the hind margin of the hindwing was the most consistent characteristic. All authors described the coloration of the moth as a combination of browns and greys. Ellisor (1942) stated that darker forms were present later in the season.

Forbes (1954) described sexual characteristics of A. gemmatalis.

Distribution

None of the references consulted during this review suggests that A. gemmatalis occurs outside the Neotropical and Nearctic regions. Strayer (1973) cited literature which indicated that the species has been recorded from the Galapagos Islands (Schaus 1940), Paraguay (Nickel 1958), Brazil (Moschler 1890), widely through the Neotropical region north of the equator (Möschler 1890, Grossbeck 1917, Schaus 1940), and much of North America east of Wisconsin and Texas (Grossbeck 1917, Watson 1915a, 1915b). Watson (1915a, 1915b) reviewed distribution of the species and made inquiries of other entomologists (Watson 1915a) to determine the northern extent of the range. He stated that he found little in the literature but summarised the remaining information as follows:

> No one north of the Gulf states had seen the larvae. The moths have been taken as far north as Ontario; . . . . The moths have not been taken in the New England states and appear to be more common in the Ohio Valley directly north of Florida than at corresponding latitudes on the Atlantic coast or in the prairie states. (p. lvii)

Further distribution records on Anticarsia gemmatalis are available mainly through Cooperative Economic Insect Reports. These provide a more complete indication of the range in the United States and show that adults are not commonly recorded west of Oklahoma and north of Delaware.

Seasonal Distribution

Watson (1915a, 1915b, 1916b) reported that adults were captured at higher latitudes as the growing season progressed and was unable to find moths north of South Florida between December and August.

Watson (1915a, 1915b, 1916b, 1920, 1927) reported that moths and pupae could survive at normal winter temperatures at Gainesville, Florida (latitude 29°40'), but found (Watson 1920) that infestations were lower following winters with several nights of temperatures below freezing. Watson (1927) concluded that absence of suitable food hosts limited the northern range of A. gemmatalis and that the species overwinters in Cuba or South Florida.

Strayer (1973) found that time of arrival of moths at Gainesville corresponded to that reported by Watson (1915a, 1915b, 1916a, 1916b).

Economic History

Chittenden (1905) made the earliest reference to A. gemmatalis as an economic insect. He briefly described adults and larvae collected on velvetbeans in Florida and foresaw the possibility of widespread planting of velvetbeans and ensuing infestations of A. gemmatalis. Scott (1910) reported that A. gemmatalis was the only serious insect attacking velvetbeans and Watson (1921) stated that the velvetbean caterpillar was often the limiting factor in producing velvetbeans. Damage to velvetbeans in Florida ceased to be of major importance as use of the crop decreased (Watson 1930) but continued on soybeans (Watson 1927, 1929, 1930, Lobdell 1931) and to some extent on peanuts (Anon. 1928), snap beans and cowpeas (Lobdell 1931). Nickel (1926) first reported velvetbean caterpillar damage to soybeans. He estimated that 'Otootan' grown in South Carolina sustained losses of over $500,000 and reported that other varieties of soybeans, velvetbeans, and peanuts were also damaged.

Douglas (1930) and Hinds and Osterberger (1931) reported that infestations were widespread in southern Louisiana and southeastern Texas in 1929. Hinds (1930) also referred to this outbreak. Except for local

heavy infestations in 1921, A. gemmatalis had not caused serious injury previously in Louisiana, even though soybean acreage had risen steadily to 500,000 acres over a 10-year period prior to 1929. A. gemmatalis continued to be a yearly pest in Louisiana, attacking soybeans, alfalfa, cowpeas, and peanuts (Ellisor 1942). Specific outbreaks were described by Ellisor and Graham (1937) on alfalfa; by Ellisor, Gayden and Floyd (1938), and Ellisor and Floyd (1939) on soybeans.

In Alabama, A. gemmatalis had been only a minor pest prior to 1939. That year a widespread infestation throughout ten counties caused almost complete defoliation of 85,000 acres of peanuts (Guyton 1940). Further infestations followed almost yearly in Alabama with particularly severe outbreaks in 1944 and 1946 (Arant 1948a). The 1944 outbreak cost an estimated $30 million in losses from peanuts (Purswell 1947). Arant (1948b) indicated that alfalfa and soybeans also suffered infestations.

Ellisor (1942) noted that many inorganic, but not organic (plant derivative), insecticides were highly toxic to A. gemmatalis. Later English (1946) and Arant (1948a, 1948b) found DDT and BHC highly effective in controlling larval populations. Turnipseed et al.

(1974) demonstrated that several chemicals control A. gemmatalis when used at very low rates.

Insecticide treatment costs against the velvetbean caterpillar and other pests for peanut and soybean acreages in Alabama were estimated by Buttram (1962, 1963). Approximately 90,000 acres of peanuts and 80,000 acres of soybeans were treated. Estimated total cost was $170,000. Despite this expenditure, insect damage reduced income by $337,720 and $822,000 respectively for peanut and soybean crops. Turnipseed (1965) estimated that control costs for soybean insects (mainly A. gemmatalis) in South Carolina amounted to $892,800 in 1964. Strayer (1973) has estimated that costs of control of the velvetbean caterpillar in Florida could reach $1.2 million annually. Insecticide applications to prevent only moderate defoliation of soybeans were suggested as being uneconomical following observations on defoliation of determinate soybeans in Arkansas and Mississippi (Anonymous 1960, Laster 1962, Miner 1963). Further studies on defoliation by Begum and Eden (1965), Turnipseed (1972), Todd and Morgan (1972), and Strayer (1973); on sampling (Boyer and Dumas 1963, Pedigo et al. 1972, Strayer 1973); and on biological control agents (Allen et al. 1971) demonstrate

recent interest in examining pest management systems for alternatives to continued high use of insecticides against A. gemmatalis and other pests of soybeans.

Integrated Control

Integrated control is a pest population management system that, in the context of the associated environment, utilises all suitable techniques and methods in as compatible a manner as possible and maintains the pest populations at levels below those causing economic injury (Smith and Reynolds 1966). Smith (1969) stated the two fundamentals basic to this approach: "consider the ecosystem" and "utilise critical injury levels." The second fundamental focuses on the primary importance of a few key pests and of evaluating their role in causing economic damage.

Key Pests

A key pest is one that is a perennial, persistent threat dominating chemical control practices. In the absence of deliberate control by man, its population density often exceeds the economic threshold one or more times during the growing season (Smith and Reynolds 1966).

Strayer (1973) has indicated that the velvetbean caterpillar is perhaps the only key pest on soybeans in North and Central Florida. Extension literature and Cooperative Economic Insect Reports indicate regular use of control measures against A. gemmatalis in Louisiana, South Carolina, Alabama, Georgia, and Florida, and sporadic moderate infestations in Virginia, Mississippi, North Carolina, and Arkansas. Infestations on soybeans, peanuts, and alfalfa are reported most frequently.

Economic Injury Levels

The economic injury level is defined as the lowest population density that will cause economic damage. The economic threshold is the density at which control measures should be determined to prevent an increasing pest population from reaching the economic injury level (Stern et al. 1959). Each term reflects a point on the seasonal population curve and implies a functional relationship between pest abundance and reduction in crop profitability. Stern (1966, 1973) and Smith (1969) have discussed the terms and stressed that economic threshold and injury levels are not fixed. Headley

(1970, 1971) and Smith (1969) emphasised the importance of economists and others in the computations of economic thresholds. The yield/pest density data that the entomologist obtains should be balanced against cost/benefit ratios and fitted to budgetory information on variable costs of control, fixed costs of production and marketing, and the expected income per unit of yield.

Southwood (1966), Stern (1966), and Smith (1969) discussed ecological factors which modify injury levels. Elements of the crop, pest, or environment vary with location and season, producing a range of economic injury levels. Estimates of variation in injury levels with factors such as temperature or condition of the host may predict economic thresholds for several sets of conditions.

Artificial Defoliation

The use of economic injury data in a pest management program requires estimates of insect numbers or an index of plant damage levels.

In the field, the soybean grower usually assesses injury visually, uses information on injury/yield loss ratios, considers the cost/benefit ratios, and applies controls accordingly.

Injury/yield loss relationships have been measured through mechanical removal of pre-set foliage areas from determinate soybeans at various growth stages. The assumption that mechanical removal approximates injury by defoliating insects has been applied by removing foliage either once in the season (Begum and Eden 1965, Turnipseed 1972, and Todd and Morgan 1972), or continually to simulate more closely continuous insect feeding (Turnipseed 1972, Todd and Morgan 1972). Removal performed at or after mid-bloom is of interest in resembling the effects of velvetbean caterpillar infestations. One-time removals of foliage were made on the varieties 'Jackson' and 'Lee' (Begum and Eden 1965); 'Bragg', 'Hampton', 'Hardee', 'Jackson', and 'JEW 46' (Turnipseed 1972) and on 'Bragg' (Todd and Morgan 1972). Defoliation at mid-bloom of 17% resulted in no significant yield loss (Turnipseed 1972); 33% removal failed to reduce yield significantly in all studies excepting one out of three trials by Todd and Morgan (1972). Sixty-seven percent removal at bloom caused significant yield reduction in the majority of studies but not in two trials by Todd and Morgan (1972). One hundred percent defoliation at bloom (Begum and Eden 1965, and Todd and Morgan 1972) resulted

in significant yield reduction except for one trial by Todd and Morgan (1972). Removals after mid-bloom were performed by Begum and Eden (1965) when beans were half-grown and fully grown in the pods, by Turnipseed (1972) at pod-set and pod-fill, and by Todd and Morgan (1972) at 2, 4, 6 and 8 weeks after first bloom. In these trials, 17% defoliation caused no significant yield loss, 33% and 67% removal generally caused significant yield losses. One hundred percent removals made in two studies caused significant yield reductions whenever they were performed.

Continual defoliations by Turnipseed (1972) on 'Jackson' and 'Lee' removed pre-set levels of foliage at bloom and all of the newly-appearing foliage at twice weekly intervals thereafter. Todd and Morgan (1972) using 'Bragg' removed pre-set percentages at specified stages of growth and that percentage of the remaining foliage each week thereafter. Using 'Hampton 226,' they removed 33% of the foliage at a specified growth stage, 33% of the foliage present one week later, and all of the foliage remaining one week after that. Turnipseed (1972) found continual removals caused significant yield losses when performed at the 50% and 67% but not at the 33% levels. Todd and Morgan

(1972) found that 33%, 67% and 100% defoliation levels initiated at any stage of growth significantly reduced yields of 'Bragg.' They found that removing progressively greater percentages of foliage at any stage of growth of 'Hampton 226' also caused significant yield losses. These programs maintaining reduced foliage areas appear to create similar, although more severe, responses in yield loss to programs in which foliage is removed one time only. The data from the three studies indicate that under regimens of cumulative foliage removal expected from insect feeding, damage ratings close to but probably below 33% at mid-bloom will result in significant yield reduction. After mid-bloom, ratings at some point between 17% and 33% and upward will be followed by significant yield losses. The impact is more severe when removal is concentrated within a period including pod-set to beans half-grown in the pods.

Yield/Pest Density Field Studies

Empirical evidence, for example from commercial fields and traditional pesticide evaluations, is often a useful first approximation of threshold levels (Smith 1969). Specially designed experiments can increase

precision in detecting losses and measuring insect abundance (Stern 1973). Statistically significant yield losses will indicate at least the damage threshold under the experimental set of field conditions. The regression of yield upon pest density passes through the damage threshold and when the form of the regression curve is known, prediction of injury levels is possible.

Smith and Bass (1972) placed various levels of artificially reared Heliothis zea (Boddie) on soybean plants in cages. All levels of infestation significantly lowered soybean yields. Yield reduction was correlated to infestation level but differences between yield reductions at two separate sites were large. Attributed to compensation by the plant, they indicate that threshold levels for different environmental conditions (in this case, moisture stress) are necessary for pod feeding by H. zea.

Strayer (1973) maintained infestation levels in cages at 2, 3, 4, and 8 velvetbean caterpillars (3rd instar and larger) per foot of row to remove foliage from soybeans at three stages of growth. Infestation levels were established and maintained over 10 days with field-collected larvae, eliminating the use of

insectary-reared insects and concern over their viability and feeding behaviour in the field. Infestations 4 weeks after bloom; and when averaged across 3 treatments: infestation at bloom, 2 weeks post-bloom, and 4 weeks post-bloom; significantly reduced yields. Mean yields were not significantly different between levels of infestation although defoliation and insect numbers were correlated. Strayer found correlations between larval populations, defoliation, and yield losses in field plots. Summarising injury ratings and larval (3rd instar and larger) counts on 'Hutton' and 'Bragg,' he reported defoliation ranging from 5% for 2 larvae per foot of row to 30% for 14 larvae per foot of row. Mean yields of 'Hutton' differed significantly between 18% and 30% defoliation. Yield data was not obtained for 'Bragg,' but slightly higher densities of larvae were required on this variety to create defoliation equivalent to that on 'Hutton.' Strayer observed differences in height between these varieties in his trials that might be a consideration in economic thresholds. The damage threshold of 18% defoliation suggested by Strayer for 'Hutton' conforms to recommendations arising from mechanical removal studies. Strayer incorporated comprehensive economic information

into his results and concluded that economic thresholds of 12 large larvae per foot of row prior to bloom, or 6 per foot of row later, apply to 'Hutton' soybeans.

Todd, Greene and Strayer are currently using collected and artificially-reared soybean loopers, Pseudoplusia includens (Walker), to obtain soybean defoliation in the field. Their data are expected to relate to simulated defoliation studies and consequently to threshold levels. Although these methods closely approach natural conditions, Greene observed that larval mortality, the presence of other defoliators, and accurate measurement of foliage losses have presented difficulties in field studies (Reid and Greene 1973).

Yield/Pest Density Laboratory Studies

Some aspects of economic threshold determination are performed more easily in the laboratory. Often detection, measurement, or duplication of major uncontrolled variables are impractical in the field. Manipulation of populations of key pests, other defoliators, predators, or parasites may be necessary but difficult. Accessability or survival of individual insects is often poor in the field, but deducing injury levels

from feeding by individuals rather than populations may be less time-consuming or costly.

Stone and Pedigo (1972) measured feeding by green cloverworms, Plathypena scabra (F.), caged singly on excised leaves in the laboratory. They related mean foliage area consumed to defoliation percentages through estimates of foliage area on field crops. Injury thresholds from simulated defoliation of determinate soybeans (Kalton, et al. 1949) and "gain threshold" (management costs/projected yield, Stone and Pedigo 1972) were also incorporated in economic injury levels.

Greene (1971), and Reid and Greene (1973) reared bean leaf rollers, Urbanus proteus (L.), and P. includens respectively, in the laboratory. Mean area of excised foliage consumed by larvae reared in individual containers was calculated. Sufficient feeding for natural populations of U. proteus to effect foliage removal reducing yields of snap beans (Greene and Minnick 1967, Greene 1971) occurred only in the last two stadia. A similar pattern was observed for P. scabra (Stone and Pedigo 1972) and may be usual for defoliating insects (Pond 1961). For soybean loopers on soybean foliage, mean larval consumption was 82 cm^2 of which ca. 70 cm^2 was consumed by the last two instars. Determination of

areas of field crops are required to relate these values to injury levels for the soybean looper.

In nutritional studies of the soybean looper, Kogan and Cope (1974) found that gravimetric and planimetric measurements of foliage consumed were similar ($r = 0.9993$), indicating that either might be acceptable in determining injury levels.

The majority of authors applied laboratory results to field situations. The hypothesis that feeding is similar in the two environments may need to be tested. Shepherd (1972) and Reid and Greene (1973) noted effects among U. proteus and P. includens respectively resulting from different densities in the laboratory. Size of containers may be important for larvae kept individually (Waldbauer 1968). Stone and Pedigo (1972) found the frequency of P. scabra with 7 larval stadia higher in the laboratory. Bonner (1950) pointed out that nutritional status of excised foliage may change over short periods. In the above laboratory studies, additional data were collected on life stages and development. Lack of anomolies in the laboratory data suggest that responses might be similar to those in the field. The two environments may need to be related by a constant obtained only through studies in both,

because failure to detect qualitative differences does not rule out overall quantitative shifts of response curves for consumption.

Yield/Pest Density Computer Simulation

Menke (1973) utilised data on the velvetbean caterpillar from a variety of sources to build stochastic models tracing development and consumption for A. gemmatalis throughout the season. In this way, population characteristics and expected damage levels were generated. Pairs of extreme levels for specific parameters were tested. Menke was able to show, as examples, that the main effects of date of planting and of first adult invasion, although not egg survival or number of invading females, were significant. Menke pointed out the need for selectively obtaining more information about the velvetbean caterpillar to increase the accuracy of models and fully exploit the potential of the systems approach.

Leaf Area Measurements

Measurements of absolute quantities consumed by insects have been discussed by Southwood (1966) and

Waldbauer (1968). In studies emphasising the impact of feeding, measurements of leaf area rather than absolute quantity may be valuable. Thus, Milthorpe (1956) has stressed leaf area in crop productivity; Taylor and Bardner (1968), for Phaedon cochleariea (Coleoptera:Chrysomelidae) defoliating turnips, concluded that while the growth of the insect depended on the dry weight and nutritive value of the food, the growth of the plant is affected by the area rather than the weight of the leaf injured. Papers by Bray (1961), Milthorpe (1956), and Soo Hoo and Fraenkel (1966), illustrate the use of leaf area measurements in ecology, agronomy, and host plant preference respectively. Greene (1971) and Stone and Pedigo (1972) have predicted injury levels on the basis of area without reference to weight or volume consumed. If conversions from leaf area measurements to absolute quantities of foliage are required, they may be obtained from weight per unit area or thickness of foliage used (Kogan and Cope 1974).

Leaf area measurements have been reviewed in Milthorpe (1956) and by Pedigo et al. (1970). Differences in methods hinge on the techniques employed for planimetry and whether measurements are made directly from the leaf or its recorded image.

Techniques

Photometric devices have been modified to assess with reasonable accuracy increases in transmission by discs of foliage or other material after damage: descriptions and reviews have been presented by Soo Hoo (1965); Kogan and Goeden (1969); and Pedigo et al. (1970).

Jones and Thurston (1970) photocopied tobacco leaves and used polar planimetry to measure feeding by groups of tobacco hornworms.

The remaining techniques employ a grid of squares or dots. The leaf is placed "at random" against the grid and the units adjacent to feeding holes are counted. Negisi et al. (1957) compared this method with polar planimetry and gravimetric methods of determining entire leaf areas. Benjamin et al. (1968) evaluated its use in estimation of insect feeding. Negisi et al. (1957) found the dot-grid method rapid: for leaves ca. 80 cm^2 and with the dots spaced .5 cm apart, 40 seconds per leaf were required in contrast to over 4 minutes per leaf for planimetry. Benjamin et al. (1968) found coefficients of variation for 20 measurements of the same replicate were below 5% when more than 30 dots

(2.5 mm apart) per replicate were counted. Negisi et al. (1957) and Benjamin et al. (1968) concluded that precision could be maintained with dot grids when the scale of the grid was chosen according to the areas of damage. Although described as laborious by Soo Hoo (1965) and Pedigo et al. (1970), the dot-grid method was chosen for the present study on the basis of cost, simplicity, mobility, and accuracy.

MATERIALS AND METHODS

Laboratory Reared Larvae

Rearing

Larvae were reared on single excised leaflets by methods similar to those of Greene (1971). Foliage used throughout was from 'Bragg' soybeans grown at Quincy, Florida, according to usual practices but without pesticides. Undamaged leaflets selected from the top third of the crop canopy were kept in closed polythene bags and used within 4 hours of excision. Leaflets were laid flat on moist filter paper in 12 x 12 x 2.7 cm clear plastic dishes.

Larvae were progeny of moths caught at black-light traps. On each date that treatments were initiated, the adult colony contained 5 - 10 females in 1971 and 20 - 50 females in 1972. Eggs laid on soybean foliage were maintained at approximately 24°C. One larva was transferred to each leaflet within 3 hours of eclosion. Relative humidity in the closed dishes was maintained

at above 80%. Unless otherwise stated, dishes were randomly positioned on trays in controlled constant temperature ± 1.5°C chambers and kept under a 14-hour photophase with interruptions in the scotophase whenever dishes were inspected at night. Chambers were three converted refrigerators with temperatures set at 15.6°C, 18.3°C, and 23.9°C respectively, and a rearing room (ca. 28 m^3) with temperature set at 29.4°C.

Dishes were inspected at 6- to 9-hour intervals during the end of each stadium to move larvae in the premolt stage or when more food was needed. In this way, each larva was transferred to a fresh leaflet in a clean dish before feeding resumed in the next stadium. Last instar larvae were transferred into a clear dish containing unmoistened filter paper before they spun a web. Time of inspection at which the old head capsule was last seen on the larva at ecdysis was recorded as the end of the stadium. Age of larvae at ecdysis was estimated to ± 12 hours.

Foliage areas were measured using the dot-grid method (Benjamin et al. 1968). The grid was marked on clear plastic with 1 dot = .1024 cm^2. Small areas of foliage consumed during larval stadia I and II were estimated by the mean of 4 grid measurements. After

stadium II, larvae began feeding on the margin of the leaflet so its original area was retained by tracing the leaf outline on the filter paper. Cumulative and total areas consumed were obtained through addition of areas recorded for each previous stadium.

Head capsule widths of larvae in the laboratory were measured to .025 mm by eyepiece micrometer for the instars and within treatments shown in Fig. 4. Capsules were measured while still on the larvae. Individuals measured and number of larvae measured frequently differed for each stadium. A frequency distribution of head capsule widths of velvetbean caterpillars from the field was compared with widths in the laboratory to determine the number of stadia in the field. Larvae from 'Hampton' and 'Bragg' soybeans not treated with insecticides were collected[1] during September and October, 1972, by D-vac^{R} and stored in 70% isopropyl alcohol. Distance across the widest part of the head capsule was measured by stage micrometer to .005 mm for 406 individuals.

Number of molts was recorded for all individuals reared.

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[1]Specimens provided by T. M. Neal, Graduate Research Assistant, University of Florida, Gainesville, Florida.

Pupae were weighed 24 ± 12 hours after pupation, and weight and duration of the pupal period was recorded for the number of individuals and within treatments shown in Table 4.

Individuals which emerged as adults were sexed by the method of Forbes (1954).

A few individuals were observed for brief periods to determine their activity at selected stages of development.

Separate experiments were conducted to study the effect of temperature, foliage maturity, and rearing method. The effects of treatments on number of molts was studied first so that the influence of number of stadia on the interpretation of treatment effects could be understood. Treatments, date of initiation of treatments, and number of larvae reared are indicated in Fig. 1.

Number of Larval Stadia

The number of molts larvae underwent in the laboratory varied in each experiment. Depending on whether they passed through 5, 6, or 7 larval stadia, larvae will be referred to here as 5-, 6-, or 7-stadia type larvae.

Initially, the frequency distribution of larvae into the classes 5-, 6-, or 7-stadia type was computed for each sex and differences between the distributions from each sex tested by chi-square.

To test whether the frequency with which each stadia type occurred was different between repeats (repeats are denoted by the dates on which they were initiated, see Fig. 1) of the same treatment, stadia type frequency distributions for each date were compared by chi-square. Comparisons were made within the mature foliage treatment of 1971, mature foliage and young foliage treatments of 1972, and the temperature experiment of 1972.

To test whether treatments affected the number of molts, stadia type frequency distributions were again computed, this time for treatments, and differences between them tested by chi-square. Distributions were compared between the 3 'Bragg' foliage maturity treatments, between the 4 constant temperatures, and between dishes and plants in pots (Trial I and II).

To determine whether changes in number of stadia might be peculiar to the rearing regimens used, 4 further treatments (shown in Fig. 1) were initiated.

In each treatment except Trial III, larvae were reared in dishes by methods described above.

(1) Larvae were reared on mature leaflets in the weather shelter. The shelter was positioned ca. 10 cm above the ground in the field. Temperature in the shelter calculated from measurements every 2 hours averaged 27.4 ± 2°C and ranged between 19-33°C during the treatment.

(2) Larvae were reared on intermediate-aged leaflets in the winter temperature treatments. Temperature within the chamber was controlled to range smoothly between 4.5-28°C on a daily cycle with a mean of 14.5 ± 1.5°C.

(3) Larvae were reared at 29.4 ± 1.5°C on intermediate-aged kudzu leaflets in 1971 and 1972.

(4) In Trial III, intermediate-aged leaves were excised with 5-10 cm of the petiole attached. Leaves with the freshly cut petiole in 10 ± 2 cm water-filled vials were maintained on a screen porch and received similar temperature and photoperiodic regimens as in Trial II. Larvae were reared one per leaf and were not confined throughout the treatment. Number of molts and duration of the larval and pupal stages were recorded in each of the above 4 treatments.

To determine their relationship to number of larval stadia, dependent variables were summarised by stadia type within treatments (ignoring dates of initiation). Mean areas consumed within 2nd and later stadia and in the entire larval stage and pupal weights were compared by analysis of variance within treatments. Mean age for each stadia type at the end of successive stadia was plotted on log scale and differences between stadia types compared only visually since they were small compared to the error in recording time of each molt. Mean cumulative area consumed by each stadia type was plotted on log scale and the relation log $\bar{Y}$[1] = a + bX (X = stadium number) was fitted by regression for each stadia type within treatments.

For head capsule widths, overall differences between treatments in means and ranges for each stadia type appeared sufficiently small (see Fig. 4) to permit summary by stadia type ignoring treatments and computation of the regression log $\hat{Y}$ = a + bX (X = stadium number) as a way of overcoming the problem of missing or few values for instars in some treatments.

To measure effects of treatments on the number of molts, the total number of molts in each treatment was divided by the number of larvae in the treatment,

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[1] Log denotes logarithm to the base 10 throughout.

to obtain on a per larva basis the response to treatments of the variable(s) governing the number of stadia individuals passed through. This value can also be obtained by summarising the stadia type frequency distributions as shown by the equation:

$$\frac{\text{mean number of stadia}}{\text{larva}} = \sum_{i=5}^{7} \text{stadia type}_i (\text{frequency}_i).$$

Association of the response with feeding and growth was examined by testing Spearman's coefficient of correlation between the ranks of: rate of increase with successive stadia in cumulative area consumed, rate of increase with successive stadia in head capsule width, 5th instar capsule width, final instar capsule width, and mean number of stadia per larva; each summarised by treatment. Rate of increase of cumulative area consumed was antilog b from the curve $\log \hat{Y} = a + bX$ (X = stadium number) fitted for each treatment, ignoring stadia type (using mean number of stadia per larva and total area consumed in the larval stage as the 5th values of X and Y respectively). Head capsules of each stadia type were not recorded in the proportions that each stadia type occurred in the treatment so the mean rate of increase which would

have been obtained by measuring every head capsule in the treatment was estimated: average rate of increase per molt in mean capsule width ($\bar{Y}_n/\bar{Y}_{n-1}$, Y = width) for each stadia type was multiplied by the frequency of that stadia type and the values for both stadia types were then averaged. Fifth and final instar widths were similarly adjusted.

Constant Temperature Experiment

Larvae were reared on intermediate foliage at constant temperatures ± 1.5°C: 15.6°C, 18.3°C, 23.9°C, and 29.4°C. Larvae and foliage were randomised among 4 temperatures on each of 3 dates that treatments were initiated. Data were not obtained for 2 adjacent stadia of 21 individuals which molted and began feeding before they were transferred to a new dish.

Foliage Maturity Experiment

Larvae were reared at 29.4°C ± 1.5°C on soybean foliage visually selected for uniformity in 1 of 3 age classes: young--newly unrolled, pale green leaflets; mature--fully expanded, dark green leaflets,

hardening off; intermediate--growing leaflets not yet hardening off.

Mature foliage treatments were initiated on 4 dates in 1971 and 2 dates in 1972. Young foliage treatments were initiated on 2 dates in 1972. Data for larvae reared on intermediate foliage were taken from the 29.4°C treatment of the temperature experiment. Data were not obtained for 2 adjacent stadia of 35 individuals which molted undetected.

In the constant temperature and foliage maturity experiments, age was plotted as a function of molt number and cumulative areas consumed plotted as a function of age for each treatment, ignoring dates of initiation. Curves were examined visually and data fitted to the approximately linear relationship $\log \hat{Y} = a + b \log X$ by the least squares regression method. Homogeneity of regressions was tested by F. Final instars were excluded from the regressions relating age to molt number because they included a non-feeding period which possibly did not follow the same relationship as the previous larval period. The non-feeding period was included in the relationship of cumulative area consumed to age since it had little effect on predictions the relationship produced.

Effect of Rearing Method

Two trials were conducted to detect differences in consumption and development periods between larvae reared on growing plants and larvae reared on excised foliage in dishes.

In each trial, soybeans in bloom were transplanted from the field into 13 cm diam. plastic plant pots. After about 7 days the plants were growing well and excess plants, damaged leaves, and all arthropods were removed from each pot. One to 4 plants remaining in each pot were used to feed a pair of larvae. To insure that each received similar food, both larvae were kept on leaflets from the same leaf. This was accomplished by cutting one leaflet from an intermediate-aged leaf and placing one larva on this in the dish. The other larva was placed on one of the two leaflets remaining on the petiole. Plants and dishes were inspected three times per day.

Larvae on the plants were able to move freely. Larvae found feeding on another leaflet were returned to an intermediate-aged leaflet and the larva in the dish transferred to a leaflet excised from this leaf. Both larvae were moved to leaflets of a new leaf once

per day and whenever either entered the premolt stage. Each leaflet was removed for measuring as soon as the larva was moved off it. Two to 3 pots were used to rear each pair of larvae, each pot being replaced when no intermediate-aged leaves were left.

In Trial I, plants and dishes were kept in a growth chamber at 23.9 ± 2°C and 14-hour photophase. Relative humidities in the chamber were ca. 60% and 80% respectively. Light was provided by Growlux^{R} bulbs. Under these, excised leaflets, unlike the laboratory or the second trial, dried out within 8 hours, presumably because they continued to photosynthesise and lost water by transpiration. To prevent this, a second piece of filter paper was placed in each dish to fit loosely over the leaflet. With this modification, RH in the dishes was above 80%.

In Trial II on a screen porch, dishes and plants received daylight but not direct sunlight. Temperatures fluctuated between 21-32°C ± 2°C, the average calculated from 2-hourly measurements through the trial was 25.3°C. Relative humidities ranged from 50-100% with the mode close to 100%. Differences between each trial and between pots and dishes in the regressions $\log \hat{Y} = a + b \log X$ (X = age) were tested by F.

Crop Foliage Measurements

Area

In 1972, areas of centre leaflets on each of approximately 10 plants were measured to estimate leaf areas of plants in a 16 hectare crop at Quincy, Florida, on each of 5 sampling dates. A centre leaflet area: leaf area ratio of 1:2.93 calculated from 20 plants sampled over a similar period in 1971, was used to compute total leaf areas from centre leaflet areas. Plant foliage areas were used to calculate crop foliage area based on an estimated plant stand of 5/foot of row (= 180,000/ha). Plant stand was estimated from the number of plants at bloom per foot in 5 10-foot lengths of row.

Width and length were determined for a subsample of 44 leaflets in 1972 to determine the regression of leaflet area on leaflet dimensions.

Thickness

Variation in thickness of 'Bragg' leaflets was determined for sections cut from young, intermediate-aged, and mature leaflets removed from a crop at Gainesville, Florida, on a single date in 1973 at pod-set.

Two safety razor blades clamped side by side cut the leaflets, freeing sections which were measured on a stage micrometer with divisions of .001 mm. Five leaflets from separate plants were measured for each age of foliage. Sections were cut from 4 regions of each leaflet shown in Table 8. Four sections were measured at each region. Differences in thickness between regions, maturity levels and leaves of the same maturity was examined by analysis of variance. Correlations between regions of the leaf were calculated.

Weight

Fresh and dry weights and dry weight percentages were estimated for foliage removed from the crop at Quincy during the second week in August, 1972.

Weight of each age class of foliage was estimated from one sample each of intermediate, mature, and young foliage collected on two dates, and one sample each of intermediate and mature foliage collected on 4 additional dates. All samples were collected at 3:30-4:00 p.m. Weights were obtained for newly excised leaflets which were then maintained in larval containers at 29.4°C and 80% RH to determine by t test whether dry weight percentages of foliage changed over 24 hours.

An additional sample of intermediate foliage was excised at 10:00-10:30 p.m. on each of 4 dates to determine by t test if foliage excised at night differed from that excised in the day in dry weight percentage.

A cork borer was used to cut 50 21-mm diam. discs, one per leaflet, from each sample. Each replicate of 50 discs was weighed immediately after cutting, dried at 60°C for 24-48 hours, and reweighed.

Discs were cut approximately equidistant from the margin and the main vein and opposite the midpoint of the main vein. Most discs included some portion of one side vein.

Defoliation Percentages

Regressions relating cumulative area of intermediate foliage consumed to age and age to instar number in the laboratory evaluated at 27.4°C were differentiated to find rates of feeding expected in the field during the infestation period.

RESULTS AND DISCUSSION

Development and Activity in the Laboratory

Egg

Eggs on soybean foliage were blue-green when first laid, gradually turning green and then grey. Eggs hatched in 2-3 days when maintained at 24 ± 2°C.

Feeding

Newly eclosed larvae most often ate 50-100% of all but the base of the eggshell. One larva at 29.4°C was observed to consume the eggshell within 5 minutes of eclosion and began feeding on soybean foliage approximately 2.5 hours later.

Larvae at 29.4°C began feeding on foliage 1-4 hours after being transferred to dishes. As they consumed foliage, larvae changed from grey to green in general appearance.

First and 2nd instar larvae almost always ate from the underside of the leaf. Larvae on young foliage

sometimes fed on the upper epidermis of young leaflets before the first molt, but larvae on older foliage did not eat completely through the leaf until late in the 2nd, or in the 3rd stadium.

Some larvae began to consume side veins during the 3rd stadium, and larger larvae sometimes ate the apical portion of the main vein before they consumed all of the leaf blade.

The majority of all instars held onto the underside of the leaf or its margin when in dishes. Older individuals were more often found on the upper side of the leaf and sometimes stood on the filter paper while feeding.

Larvae in Trials I, II, and III which were not reared in dishes seldom moved from the leaf on which they were placed until the end of the stadium. Four larvae in Trial I, and 1 larva in Trial II, were lost because they left the plant.

Foliage was removed from all regions of the leaf blade by every instar. Undisturbed larvae usually removed a single area of damage, and frass on the filter paper indicated that there was little change in the position of the hind end of the abdomen while the larva fed.

Foliage was consumed at all hours of the day during every stadium.

Molt

Larvae usually moved from the damaged area to another portion of the leaf or to the surface of the container prior to molting. All instars placed silk upon the surface and remained with the prolegs on the silk. Young larvae in the premolt stage were most easily recognised by their paler color after the alimentary canal was emptied. The premolt stage in many individuals was noticeable by the setae of the new cuticle pressed between the body and the old cuticula, and in others by the glabrous appearance of the new head capsule immediately behind the old one. Larvae ate the exuvium but not the head capsule after ecdysis. Larvae at 29.4°C occasionally took less than 6 hours from the first signs of ecdysis to the resumption of feeding on foliage, but usually the non-feeding period lasted from 12-18 hours. Larvae at 15.6°C discontinued feeding for 48-60 hours during the molting process.

Coloration

Larvae reared individually in the laboratory at temperatures higher than 18.6°C were variable in color but all conformed to the description of lighter individuals given by Watson (1916b).

Larvae reared individually at temperatures below 18.6°C were dark colored during the last one or two stadia, however, many of these larvae and some larvae at 18.6°C darkened to a reddish or brown rather than black color.

Prepupal Stadium

Last instar larvae which had finished feeding began to move around the dish and develop pinkish coloration described by Watson (1916b) prior to establishing the pupation site. Larvae were transferred to dry dishes at this time. Pupation took place within a silken web between the filter paper and the dish. Most larvae removed small portions of filter paper which were later seen attached to the web close to the perimeter. Larvae removed from silk during the early part of the spinning process built a second web. Ecdysis to pupa occurred

between 18-30 hours after feeding stopped at 29.4°C and 4 or more days after feeding stopped at 15.6°C.

Last instar larvae on plants in pots at 25.3°C were observed during the prepupal period. Each of 6 larvae observed developed pink coloration and became slightly stout while still on the plant; 2 of the 6 underwent these changes 7 or more hours after moving from the leaf to the stem.

Two larvae crawled to the ground down the plant stem. Both entered the soil near the base of the plant within 30-40 minutes of leaving the foliage. Three larvae dropped from the plant to the ground. One fell from the leaf unobserved, and 2 were seen dropping from the plant stem. The first of these crawled without stopping from the leaf to a height of 20-30 cm on the stem and then remained motionless with the prothoracic legs in the air. After 2 minutes, the front end of the larva moved rapidly to the side so that the head touched, or nearly touched, the abdomen at segment III or IV. As the head returned, the larva dropped and landed approximately 6 cm from the base of the plant. The second larva was observed crawling 10 cm down the stem. It stopped crawling and remained still with the prothoracic legs raised off the plant for periods of

6 and 8 minutes before reaching a point 41 cm above the ground. After 10-20 seconds, the larva then made a rapid movement and fell to the ground approximately 12 cm from the base of the plant.

Mortality

Less than 10% of any group of larvae at temperatures other than 15.6°C failed to pupate.

At 15.6°C approximately 40% of the larvae died. At least 5 larvae, 3rd instar and younger, drowned in droplets of condensation; 2 larvae were unable to shed the head capsule; and the cause of 12 remaining deaths was undetermined. The larvae which died may have been mainly 7-stadia type so that the effect of the 15.6°C treatment may not be fully reflected in these data.

Adults

Adults emerged in all treatments. Of these, 51.2% had tufts on the metathoracic legs, indicating they were males.

Number of Larval Stadia

Chi-square tests comparing stadia type frequency distributions showed no significant difference in the proportion of larvae of each stadia type between males and females or between larvae reared in dishes and those on plants in pots (in Trial I and Trial II).

Stadia type frequency distributions for each date of initiation of treatments, listed as 3 values within each area, are shown in Fig. 1. They were highly significantly different between the 4 dates in the mature foliage treatment of 1971 (chi-square = 46.6, 3 df), and not significantly different between dates in the constant temperature experiment or in the young or mature foliage treatments of 1972. This suggests poor experimental control from date to date or non-randomness of response by larval samples from each date in the first year. Experimental control was not knowingly improved in the second year, the only noticeable change being increase in the size of the adult colony. Therefore, proportions of larvae of each stadia type in 1971 may reflect biological variation with regard to stadia type which was present at the time larvae entered the treatment (≤3 hours

Figure 1.

Areas indicating relative size of groups of velvetbean caterpillars reared and frequencies of each stadia type at the end of treatments initiated on indicated dates in 1971 and 1972. Boxes are equal in area to the number of larvae reared and are divided into areas proportional to the number of larvae from each date and/or treatment. Frequencies for 5-, 6-, and 7-stadia type larvae respectively are listed vertically within each area.

Intermediate

	7/22	7/28	8/14
15.6°C	0 0 1	0 .625 .375	0 .857 .147
18.3°C	0 1 0	0 1 0	0 1 0
23.9°C	.800 .200 0	.916 .084 0	.928 .072 0
29.4°C	0 1 0	.417 .583	.100 .900

Dish vs. Plant

Trial I — 23.9°C

8/8	
.474	.579
.526	.421
0	0

Trial II — 25.3°C

8/14	
.714	.947
.286	.053
0	0

Young — 29.4°C

7/17	8/16
.545	.467
.455	.533
0	0

Winter Temp. — 14.4°C

7/30	8/15
0	0
.300	1
.700	0

Trial III — 25.3°C

8/14
.917
.083
0

Mature 1972 — 29.4°C

7/16	7/17
.400	.609
.600	.391
0	0

Kudzu 1972 — 29.4°C

7/17	8/14
0	0
1	.929
0	.071

Mature 1971 — 29.4°C

7/11	7/13	7/15	7/17
1	.250	.273	.667
0	.750	.727	.333
0	0	0	0

Weather Shelter 1971 — 27.5°C

8/5
.692
.308
0

Kudzu 1971 — 29.4°C

8/5
0
.500
.500

□ = 1 larva

after eclosion), this variation being lower among larvae eclosing on a single date than among those from separate dates as a result of samples on each date being too small or from too few adults to be random in 1971. Stadia type frequency distributions in each treatment (except 18.3°C) (Fig. 1) show variation between dates on which treatments were repeated which may be associated with uncontrolled differences in temperature, foliage consumed, time of inspection of treatments with regard to the photoperiodic cycle, and distrubance of larvae in the premolt stage, as each repeat progressed.

Stadia type frequency distributions for treatments are listed in Table 1. Temperature had a highly significant (chi-square = 35.8, 3 df) effect on stadia type frequency distributions in the constant temperature experiment. The proportion of larvae with fewer molts increased with temperature up to 23.9°C but was lower at 29.4°C than at 23.9°C. This suggests a curvilinear relationship of number of molts to temperature and that a temperature between 29.4°C and 23.9°C is optimum for completing development in the minimum number of stadia. Stadia type frequencies in Trial III (mean 25.3°C), the weather shelter (mean 27.4°C), and

Table 1. Number of velvetbean caterpillars reared, stadia type frequencies, and mean number of stadia per individual for treatments in 1971 and 1972, ranked by response of stadia type frequencies.

Rank	Treatment	N	Frequency for indicated stadia types			Mean number of stadia per larva
			5	6	7	
1	Trial III	12	.917	.083	0	5.08
2	Inter. 23.9°C	55	.891	.109	0	5.11
3	Trial II	38	.825	.175	0	5.18
4	Weather shelter	13	.692	.308	0	5.31
5	Mature 1971	45	.533	.467	0	5.47
6	Mature 1972	38	.526	.474	0	5.47
7	Trial I	38	.526	.474	0	5.47
8	Young	26	.500	.500	0	5.50
9	Inter. 29.4°C	40	.175	.825	0	5.83
10	Inter. 18.3°C	29	0	1.000	0	6.00
11	Kudzu 1972	22	0	.955	.045	6.05
12	Winter temp.	23	0	.739	.261	6.26
13	Inter. 15.6°C	36	0	.638	.362	6.34
14	Kudzu 1971	12	0	.500	.500	6.50

winter temperature experiment (mean 15.4°C) are most like those in the 23.9°C, mature foliage and 15.6°C treatments respectively (Table 1), showing little effect of fluctuations in temperature on the number of molts. All temperatures except 18.3°C produced two types of larvae: larvae reared at temperatures higher than 18.3°C were either 5- or 6-stadia type and all larvae reared at lower temperatures were 6- or 7-stadia type (Table 1).

Maturity of 'Bragg' foliage had a highly significant (chi-square = 11.7, 2 df) effect on stadia type frequency distributions, and frequency distributions for kudzu are clearly different from those for 'Bragg' (Table 1), showing a large effect of foliage consumed on the number of molts. The proportion of larvae with fewer molts was highest on mature and young foliage, lower on intermediate foliage, and much lower on kudzu.

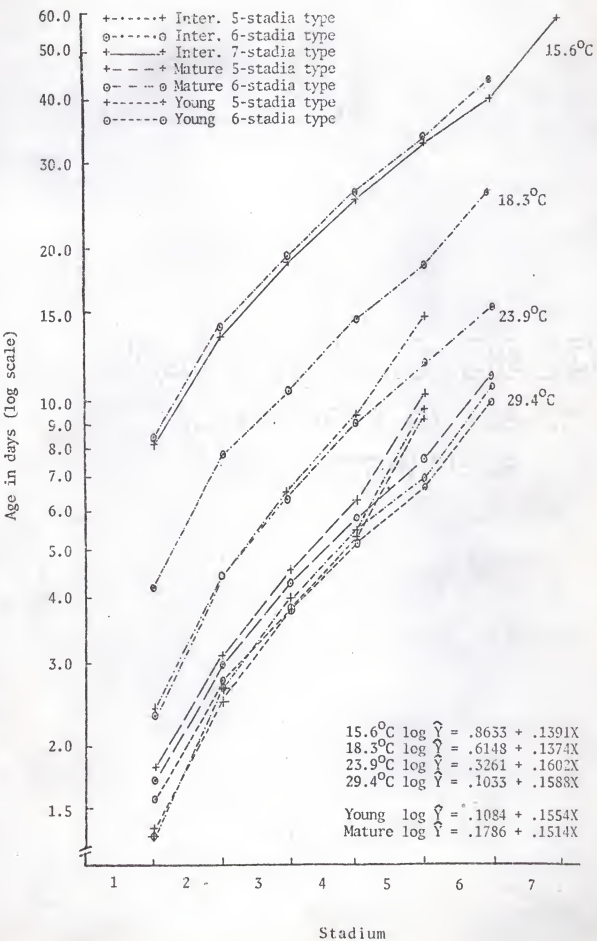
Ranking of treatments by mean number of stadia per larva (Table 1) shows a change in stadia type frequencies over their range which strongly suggests they reflect a continuous quantitative response to treatments of the factor(s) determining the number of molts in individuals. The dependent variables: speed of development, area consumed, and head capsule width,

were examined for factors which showed a similar response to treatments and could be found to have had an effect on the number of molts. An initial analysis of these data instar by instar revealed no single event which determined the number of molts passed through but revealed an embarrassment of significant differences and correlations among the variables, indicating that it would be more valuable to study them as functions of instar number or age over several stadia.

Age at ecdysis for instars of each stadia type in the temperature experiment and on young and mature foliage is shown in Fig. 2. Differences in mean age between stadia types within treatments at the end of equivalent stadia were small relative to the accuracy with which age was measured--less than 30 hours at 15.6°C and less than 9 hours at other temperatures, when last instars were ignored. Larvae passing through an extra molt entered their penultimate stadium at approximately the same age that other larvae in the treatment entered their final stadium, showing little difference in the rates at which each stadia type passed through successive stadia up to this point. Larvae then passing through only one more stadium did so more slowly than expected from examination of the

Figure 2.

Mean age in days (log scale) at each molt for velvet-bean caterpillars of each stadia type reared on intermediate foliage at 4 constant temperatures and at 29.4°C on young and mature foliage. Regression formulae of log mean age, ignoring stadia type, on molt number between stadia 2 and 5 in each treatment.


+------+ Inter. 5-stadia type
⊙------⊙ Inter. 6-stadia type
+——————+ Inter. 7-stadia type
+- - - -+ Mature 5-stadia type
⊙- - - -⊙ Mature 6-stadia type
+------+ Young 5-stadia type
⊙------⊙ Young 6-stadia type
15.6°C
18.3°C
23.9°C
29.4°C
15.6°C log Ŷ = .8633 + .1391X
18.3°C log Ŷ = .6148 + .1374X
23.9°C log Ŷ = .3261 + .1602X
29.4°C log Ŷ = .1033 + .1588X
Young log Ŷ = .1084 + .1554X
Mature log Ŷ = .1786 + .1514X
Age in days (log scale)
60.0
50.0
40.0
30.0
20.0
15.0
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.5
1
2
3
4
5
6
7
Stadium

curves connecting values for previous stadia (Fig. 2), while other larvae passing through 2 more stadia went through the penultimate stadium at approximately the expected rate and continued through the final stadium at a similar or lower rate (Fig. 2). The delay in the final stadium can most likely be attributed to the non-feeding period prior to pupation, which may not depend on age or stadia type. Differences in development times over the feeding period appear to be the result of an additional feeding period following failure to pupate at the previous molt and thus are an effect rather than a cause of differences in stadia type.

Foliage areas consumed by instars of each stadia type were highly variable. Coefficients of variability for area consumed ranged from 50-173% for 1st instars and from 25-60% for later instars, whereas coefficients of variability for head capsule width and duration in each stadium were only approximately 10% and 20% respectively. Variation in areas consumed may be attributed partly to variation in thickness between leaflets and between regions of leaflets consumed because coefficients of variability in the data for leaf thickness of similar foliage (Table 8) were also high (ca. 25%) for each age of leaf. Also, larger

variation of areas consumed in early stadia can be attributed partly to low precision in estimating small areas of feeding by dot-grid because coefficients of variability for 10 estimates (each the mean of 4 measurements) made of the same damaged area were high (49% for feeding by a 1st instar and 13% for feeding by a 2nd instar). High variation limits the value of statistics based on small areas of foliage so that comparisons of areas consumed by 1st instars and correlations using areas consumed by individuals were not undertaken.

Cumulative areas consumed at the end of successive stadia are summarised in Table 2 and Figure 3. Table 2 lists regression formulae of the form $\log \hat{Y} = a + bX$ (X = stadium number) for stadia types within treatments and for treatments ignoring stadia type. Figure 3 shows (on log scale) observed values for each stadia type within each treatment and regression lines for each stadia type at 15.6°C, 23.9°C, and 29.4°C (other regression lines fell between these and are excluded for clarity). Slopes of regressions are significantly different between stadia types within each treatment (Table 2 and Fig. 3) showing higher rates of increase with successive stadia in cumulative areas consumed

Table 2. Regression formulae ($\log \hat{Y} = a + bX$, X = stadium number) of cumulative area consumed on stadium number for each stadia type and treatment of the temperature and foliage maturity experiments.

	Regression formulae[a]		
	other stadia type[b]	6-stadia type	Treatments[c] (ignoring stadia type)
Inter. 15.6°C		$\log \hat{Y} = .5496 + .5658X$	$\log \hat{Y} = .5747 + .5486X$
Inter. 18.3°C		$\log \hat{Y} = .3850 + .6031X$	$\log \hat{Y} = .3640 + .5137X$
75° Inter. 23.9°C	$\log \hat{Y} = .3603 + .7289X$	$\log \hat{Y} = .5036 + .5593X$	$\log \hat{Y} = .3720 + .7166X$
85° = Inter. 29.4°C	$\log \hat{Y} = .3952 + .6721X$	$\log \hat{Y} = .6005 + .5597X$	$\log \hat{Y} = .5608 + .5863X$
Young	$\log \hat{Y} = .3498 + .7154X$	$\log \hat{Y} = .5231 + .5863X$	$\log \hat{Y} = .4438 + .6491X$
Mature	$\log \hat{Y} = .3614 + .7157X$	$\log \hat{Y} = .6125 + .5652X$	$\log \hat{Y} = .4993 + .6410X$

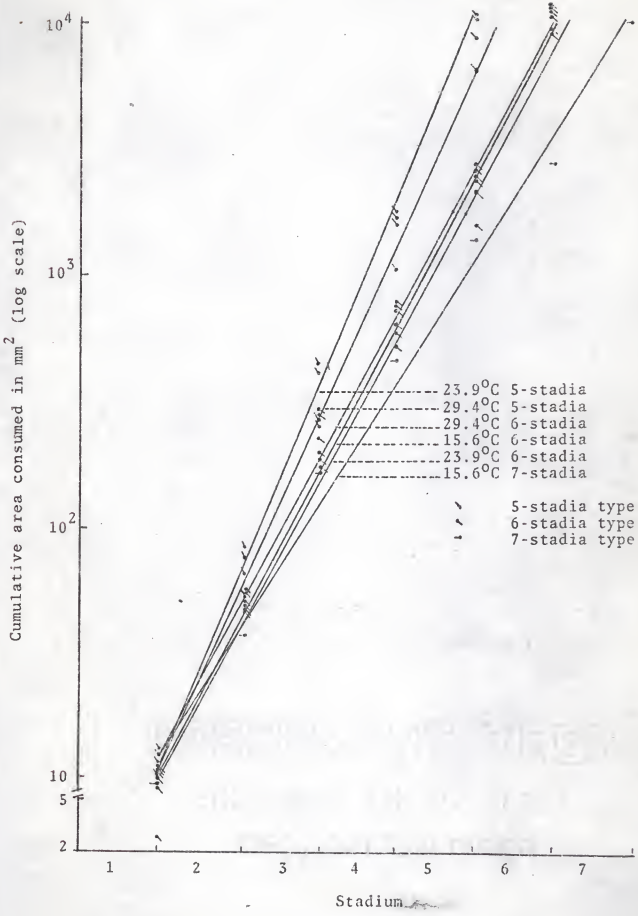
[a] Slopes of regressions in rows significantly different at .05 level between stadia types.

[b] Seven-stadia type at 15.6°C, 5-stadia type in remaining treatments.

[c] Slopes of regressions in final column significantly different at .05 level between treatments (ignoring stadia type).

Figure 3.

Observed values of cumulative area consumed (log scale) for velvetbean caterpillars of each stadia type in the 6 treatments of the constant temperature and foliage maturity experiments, and regression lines ($\log \hat{Y} = a + bX$) relating cumulative area consumed to molt number for each stadia type in indicated treatments. Regression formulae are listed in Table 3.


Cumulative area consumed in mm² (log scale)
10⁴
10³
10²
10
5
2
1
2
3
4
5
6
7
Stadium
23.9°C 5-stadia
29.4°C 5-stadia
29.4°C 6-stadia
15.6°C 6-stadia
23.9°C 6-stadia
15.6°C 7-stadia
5-stadia type
6-stadia type
7-stadia type

among larvae which molted fewer times. Slopes (Table 2) are also significantly different between treatments, ignoring stadia type, showing that treatments produced changes in rates of increase; but they are not significantly different between treatments among larvae of the same stadia type, suggesting that changes in rates of increase then affected the number of molts passed through.

Head capsule widths show a response among the treatments and stadia types similar to that of cumulative areas consumed. Means and positions of ranges (Fig. 4) show little difference in size of head capsules between treatments among instars of the same stadia type, and slopes of the regressions $\log \hat{Y} = a + bX$, X = stadium number (Fig. 5), are significantly higher for larvae passing through fewer stadia (antilog b is 1.66, 1.55 and 1.43 for 5-, 6-, and 7-stadia type respectively).

The data show that larvae passed through additional stadia following low rates of feeding and growth per instar. The effect of treatments on these variables are demonstrated in Table 3. Significant correlations (Table 3) indicate that treatments in which increases with successive stadia in area consumed were lower

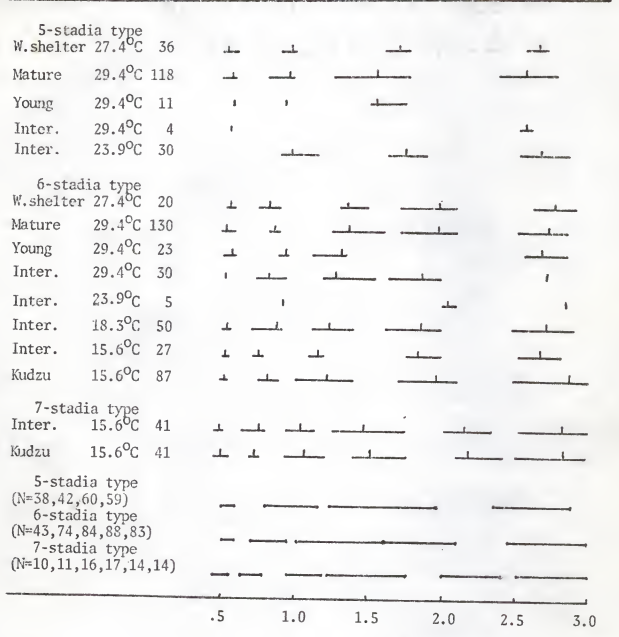


Figure 4. Range (horizontal line) and mean (perpendicular line) of head capsule width of 2nd and later instar velvetbean caterpillars measured in indicated treatments. N = number of head capsules measured.

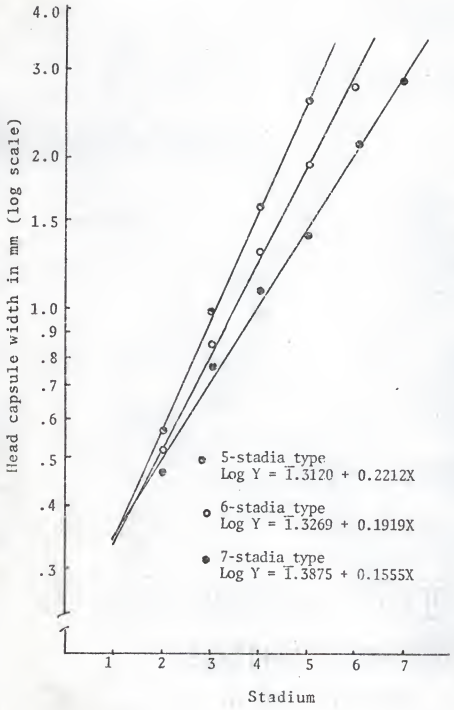


Figure 5. Regression lines, regression formulae, and observed values of log mean head capsule width on stadium number for each stadia type among 2nd and later instars in treatments of 1971 and 1972.

Table 3. Values of each variable and comparison by Spearman's rank correlation coefficient (r_s) of ranks of: mean number of stadia per larva, increase with stadium in mean cumulative area consumed, adjusted rate of increase with stadium in mean head capsule width, adjusted mean 5th instar head capsule width, and adjusted mean final instar head capsule width.

Treatment	Stadia per larva		Cumulative consumption		Head capsule width[a]					
					Rate of increase		5th instar		Last instar	
	$\bar{X}$	Rank	Antilog b	Rank	$\bar{Y}_{n+1}/\bar{Y}_n$	Rank	Width (mm)	Rank	Width (mm)	Rank
Inter. 15.6°C	6.34	8	3.537	1	1.49	1	1.70	1	2.73	6
Inter. 18.3°C	6.00	6	4.102	3	1.51	3	1.88	3	2.72	5
Inter. 23.9°C	5.11	1	5.205	6	1.62	7	2.60	7	2.67	2.5
Inter. 29.3°C	5.83	5	3.888	2	1.53	4	2.00	4	2.68	4
Young	5.50	4	4.445	5	1.59	6	NR		NR	
Mature	5.47	3	4.375	4	1.58	5	2.23	5	2.60	1
W. shelter	5.31	2			1.64	8	2.42	6	2.67	2.5
Kudzu	6.21	7			1.50	2	1.86	2	2.87	7
				r_s values						
Stadia/larva		-		-.886*		-.952*		-1.000*		+.848*
Antilog b				-		+.943*		+ .900		-.800
$\bar{Y}_{n+1}/\bar{Y}_n$						-		+ .964*		-.830*
5th instar width								-		-.830*
Final instar width										-

[a]Adjusted for stadia type frequencies
*Significant at .05 level
NR = none recorded

produced smaller increases in size at ecdysis and, therefore, smaller 5th instars, and also suggest that as a result, some larvae had to feed for one or two additional stadia before reaching a minimum size necessary for pupation. Ranges for head capsule width (Fig. 4) show that all larvae pupated from head capsules 2.3 mm or wider, and examination of individual measurements in the region of 2.3 mm indicated that all larvae except one (on mature foliage, head capsule 2.3 mm wide) having capsules 2.4 mm or narrower continued as larvae after the next molt. Thus, the number of molts apparently is determined by the effect of treatments on growth per stadium because only those larvae attaining a head capsule width of ca. 2.4 mm or more are able to pupate at the next molt.

Data for final instars suggest that larvae passing through additional stadia consume more foliage (Table 4), reach a larger final size (Table 3), and so develop into heavier pupae (Table 4) because their gain in size on passing into the final stadium is larger than differences in size between them (when in their penultimate stadium) and larvae pupating one molt sooner (Fig. 4). It should be noted that, when individuals of more than one stadia type are included,

Table 4. Area of 'Bragg' foliage consumed in entire larval stage and pupal weight at 24 ± 12 hours for velvetbean caterpillars of each stadia type in the constant temperature and foliage maturity treatments.

Treatment	Area consumed (cm^2)				Pupal weight (mg)					
	other stadia type[a]		6-stadia type		5-stadia type			6-stadia type		
	$\bar{X}$	S.D.	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.
Inter. 15.6°C	105.7	17.5	95.1	16.7						
Inter. 18.3°C			103.8	14.4				3	221.1	15.8
Inter. 23.9°C	99.6	19.9	104	51.6	6	225.4	33.8	1	243.2	
Inter. 29.4°C	67.9	12.0	90.7	17.5	4	190.5	16.3	13	209.4	27.7
Young 29.4°C	114.6	32.9	111.7	17.0	9	220.0	38.7	6	232.9	57.4
Mature	89.3	16.1	99.3	16.9	39	195.9	25.6	36	214.9	22.7

[a]Seven-stadia type at 15.6°C, 5-stadia type in remaining treatments.

data for the total larval stage, pupae, and adults reflect 2 responses to treatments: a direct response to treatments and an opposite response to stadia type, which is an effect of treatments, and so are poor indicators of the effect of treatments on growth and development.

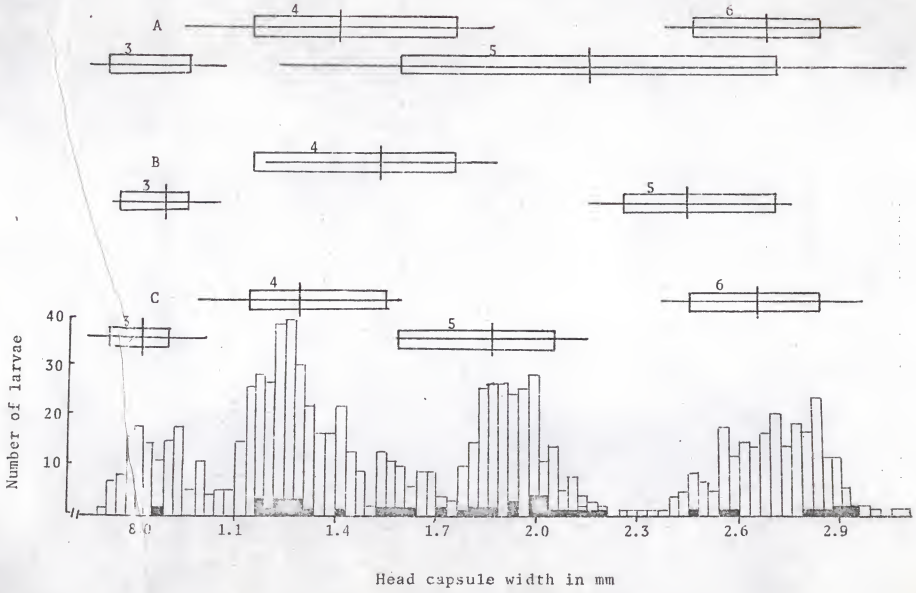
Larvae from the field had head capsule width frequency distributions which, compared with data for larvae in the laboratory, suggest that, at least on 'Hampton,' they were all 6-stadia type (Fig. 6). Mean temperatures in field were approximately 27.4°C and larvae feeding on 'Bragg' were most usually found on intermediate foliage so that populations were expected to have a percentage of 5-stadia types somewhat similar to that at 29.4°C on intermediate foliage, i.e. ca. 17.5% (Table 1). Reasons for the data indicating a higher number of stadia in the field were not determined, but the apparent difference cautions against assuming that larval performance in the laboratory directly indicates their performance in the field.

Relationship of Head Capsule Width to Other Variables

Because the data were collected primarily to provide estimates of rates of consumption rather than

Figure 6.

Head capsule widths of velvetbean caterpillars. Mean (vertical bar), ± 3 standard deviations (length of horizontal bar), and range (length of rectangle) for larvae reared on mature and intermediate aged 'Bragg' foliage at 29.4°C in the laboratory. A, combined data for 5- and 6-stadia type larvae; B, 5-stadia type larvae; C, 6-stadia type larvae. Frequency distribution of head capsule widths of 59 larvae from 'Bragg' (darkened areas) and 347 larvae from 'Hampton' collected by D-vac September 3 - October 10, 1972, at Quincy, Florida.


A
3
4
5
6
B
3
4
5
C
3
4
5
6
Number of larvae
40
30
20
10
8.0
1.1
1.4
1.7
2.0
2.3
2.6
2.9
Head capsule width in mm

estimates of parameters associated with larval development, specific values relating larval growth to speed of development and areas consumed were not computed. Treatments could have been considered in terms of the increase in size of larvae per unit of foliage consumed in order to measure the nutritional value and utilisation of foliage area consumed had I exercised more control over foliage consumed, measurement of foliage volume, and head capsule widths. That each larva was identified and maintained individually throughout the treatments aided greatly in ascribing causes to stadia type changes. The data obtained here give the impression that much information could have been obtained by measuring the variables with higher precision and correlating them on a per individual basis.

The form of the relationship between head capsule width and other variables can be understood by considering the curves which the observed data appear to fit and the functional relationships these curves imply.

There is a good fit of the data for head capsule width to the relationship $Y = 10^{a}(10^{b})^{X}$ indicating that an initial width ($10^{a}10^{b}$) increases at a fairly constant rate (antilog b) with each molt (X), as

Dyar's rule states. The regressions in Fig. 5 predict that the first term is approximately .33 mm and Table 3 shows that the average rate of increase is about 1.5 per stadium and varies depending on treatment (this rate determining the number of larval stadia, as previously discussed).

Successive stadia generally increased in duration (Fig. 2) so that the relationship of head capsule width to larval age is not well represented by $Y = 10^a(10^b)^X$, where X = age, but rather by the relationship $Y = 10^a X^b$, X = age, in which X as well as Y is expressed logarithmatically, this diminishing larger values of X and so maintaining a linear relationship when age is substituted for stadium number in the relationship. Similarly, there appears to be a reasonable fit of data for cumulative area consumed to the relationships $Y = 10^a(10^b)^X$, where X = stadium number (Fig. 3), and $Y = 10^a(X)^b$, where X = age (Fig. 7). Average increase per stadium in cumulative area consumed varied about 3.54 - 5.20, depending on treatment (Table 3). These results indicate that head capsule width and cumulative area consumed increase as products of effects 10^a, which are constant, and effects X^b, which are cumulative, as the treatments

proceed. On the basis of Fig. 3, it appears reasonable to use either $Y = 10^a(10^b)^X$ or $Y = 10^a X^b$ (where X = molt number) to express the relationship of age to molt number.

Temperature and Foliage Treatments

Speed of Development

Age at ecdysis in the temperature and foliage maturity treatments is estimated by means for each stadia type in Fig. 2. They show that stadium I was longer than stadium 2, stadia 2 and 3 were of similar duration, and successive stadia increased in duration thereafter in each treatment.

Increase in age over stadia 2, 3, and 4 (Fig. 2) was close to geometric. Regression formulae $\log \hat{Y} = a + bX_1$ X_1 =molt number, (Fig. 2) for these instars give predictions of age at the end of 2nd and later stadia in these treatments which might be used with reasonable accuracy to forecast time elapsing between two points in the development of a population with a known age structure. However, the regression

$\log \hat{Y} = a + b \log X_1$, X_1 = molt number, gives a better fit to the data for age at the first four molts in each treatment and reasonable predictions of age at the end of later stadia when the non-feeding period of the final stadium is excluded. The intercepts (a) decrease as the effect of the factors contributing to speed of development towards ecdysis increases and the steepness of the slopes (b) decreases as the effectiveness of the factors in hastening development shifts from later instars to earlier instars.

Temperature

The regressions ($\log \hat{Y} = a + b \log X_1$) at each of the four constant temperatures are:

15.6°C, $\log \hat{Y} = .9051 + .8144 \log X_1$;

18.3°C, $\log \hat{Y} = .6243 + .8802 \log X_1$;

23.9°C, $\log \hat{Y} = .3671 + .9634 \log X_1$;

29.4°C, $\log \hat{Y} = .1207 + 1.0051 \log X_1$,

where Y = age in days and X_1 = molt number. They show that development towards ecdysis was more rapid at higher temperatures, and particularly so in earlier rather than later stadia. Possibly the response to temperature was larger among younger larvae because they had more physical difficulty feeding in colder

treatments, or because all eggs were maintained at 24°C, necessitating a period of acclimation following entry into treatments at other temperatures.

The relationship of age to temperature at each of the first four molts is close to linear when plotted as $\log \hat{Y} = a + b \log X_2$, X_2 = temperature. Combining data from the four temperatures gives this linear model relating age to molt number and temperature: $\log \hat{Y} = 4.1613 - .0034 \log X_1 - 2.7491 \log X_2 + .6934 \log X_1 \log X_2$. From this, the relationship of age to molt number at 27.4°C (mean temperature during the infestation period) is: $\log \hat{Y} = .2088 + .9936 \log X_1$, which predicts that 5- and 6-stadia type larvae are respectively 8.0 and 9.6 days old when they finish feeding at the end of their final stadium. Since both stadia types were produced at 23.9°C and 29.4°C, it may be expected that, on average, larvae in the field finish feeding when about 9 days old.

Duration of the larval and pupal stages (Table 5) was largely influenced by temperature. Where recorded, age at adult emergence was 1.59-1.77 times that at pupation, smaller ratios indicating treatments with slow larval development relative to pupal development. Using 1.7 times age at pupation to find missing values,

Table 5. Mean duration of larval and pupal stages in treatments of 1971 and 1972.

Treatment	Temperature	X (days) Larva	X (days) Pupa[a]
Intermediate	15.6	53.0	NR
Intermediate	18.3	26.8	19.4
Intermediate	23.9	13.7	NR
Intermediate	29.4	10.7	7.7
Young	29.4	9.5	7.3
Mature	29.4	10.7	7.6
Intermediate	(15.4)[b]	35.5	26.3
Trial I and II	(24.6)	13.8	8.5
Weather shelter	(27.4)	14.3	9.5
Kudzu	29.4	13.5	8.0

[a]Adjusted for frequencies of each stadia type.

[b]Temperatures in parenthesis were not constant.

NR = None recorded.

age at adult emergence is estimated as 18, 23, 46, and 90 days at 29.4°C, 23.9°C, 18.3°C, and 15.6°C respectively in the constant temperature experiment. These data indicate that temperature has a particularly large effect on the period which can elapse before adults emerge during the colder part of the year. Host plant availability at this point limits population increase (Watson 1927), so that warm winters producing a shorter life cycle could hasten population decline where host plants are scarce. Development in the winter temperature (15.4°C) treatment (Table 5) indicates that adults emerge about 9 weeks after eclosion in the 2-3 coldest months in North to Central Florida. Development periods at 23.9°C and 29.4°C (Table 5) show that small differences in mean temperature during the infestation period have little effect on development and that adults emerge 19-20 days after eclosion at this time. I was unable to determine why development was slower at temperatures fluctuating about 27.4°C in the weather shelter than at 23.9°C and at 24.6°C (Table 5).

Foliage maturity

The regression ($\log \hat{Y} = a + b \log X_1$) relating age and molt number is $\log \hat{Y} = .1491 + .9317 \log X_1$ for

larvae on young foliage and log Y = .2315 + .8853 log X_1 for larvae on mature foliage, they show no significant effect of foliage maturity on the rate at which larvae passed through successive stadia, but indicate a delay in reaching each molt on mature foliage which is attributable to a significantly longer period in stadium 1 on mature (1.75 ± .35 days) than on young (1.44 ± .20 days) and intermediate foliage (1.33 ± .11 days). I did not notice at what points the delay in stadium 1 occurred.

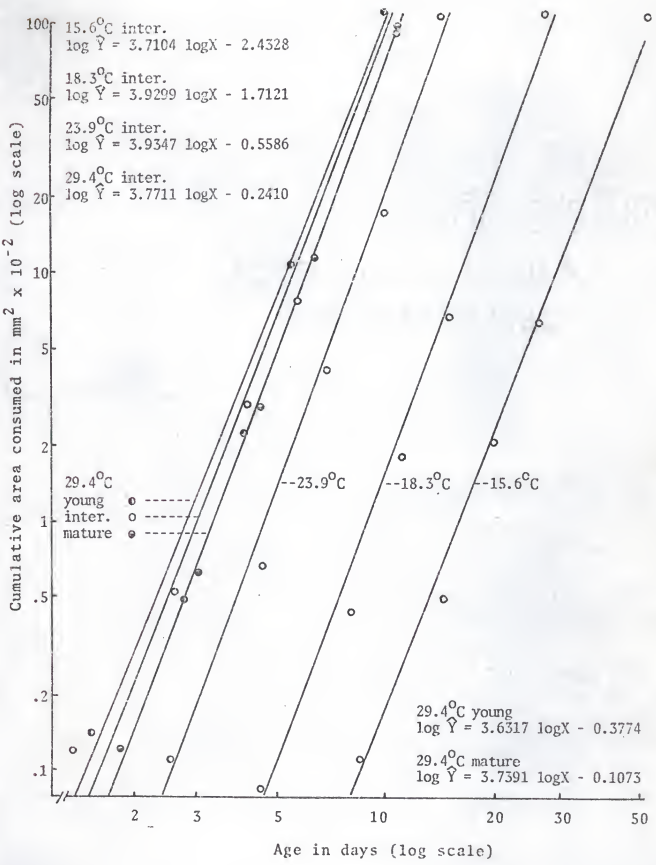
Maturity of 'Bragg' foliage appears to have little effect on age at adult emergence, but development of larvae took an average of 67 hours longer on kudzu than on intermediate 'Bragg' foliage, showing an effect of host plant species on speed of development (Table 5).

Foliage Consumption

Figure 7 shows cumulative area consumed at the end of the first 4 stadia and the larval stage in the constant temperature and foliage maturity treatments. Height of the observed values show little difference between treatments in areas consumed, except that instars 2, 3, and 4 ate significantly more at 23.9°C

Figure 7.

Observed means and regression lines and formulae of log mean area consumed on log age for velvetbean caterpillars, reared on intermediate foliage at 4 constant temperatures and at 29.4°C on young and mature foliage. Values recorded at molts 1 through 4 and at pupation.


15.6°C inter.
log Ŷ = 3.7104 logX - 2.4328
18.3°C inter.
log Ŷ = 3.9299 logX - 1.7121
23.9°C inter.
log Ŷ = 3.9347 logX - 0.5586
29.4°C inter.
log Ŷ = 3.7711 logX - 0.2410
29.4°C
young
inter.
mature
--23.9°C
--18.3°C
--15.6°C
29.4°C young
log Ŷ = 3.6317 logX - 0.3774
29.4°C mature
log Ŷ = 3.7391 logX - 0.1073
Cumulative area consumed in mm² x 10⁻² (log scale)
Age in days (log scale)
100
50
20
10
5
2
1
.5
.2
.1
2
3
5
10
20
30
50

than in other treatments. Total areas consumed were similar (approximately 100 cm^2) in each treatment. There appears to be a reasonable fit of the data for each treatment to regressions of the form $\log \hat{Y} = a + b \log X$, relating cumulative area consumed, Y, to age, X.

The regressions include the non-feeding period in the final stadium so that age at pupation is approximated when 10,000 mm^2 is substituted for $\hat{Y}$ in the regression. The regressions have slightly lowered slopes because of the inclusion of the non-feeding period of the final stadium, but comparison of the predicted and observed values (Fig. 7) shows this not to be serious.

Temperature

There is no significant difference in slopes of the regressions ($\log \hat{Y} = a + b \log X_3$, Y = cumulative area consumed in mm^2, X_3 = age in days; Fig. 7) between the 4 constant temperatures so that an average value of $b_3 = 3.8366$ in the regressions at each temperature gives a reasonable estimate of cumulative area consumed. Cumulative area consumed increased with temperature (X_2)

and age in an approximately linear fashion according to the regression: $\log \hat{Y} = -14.5677 + 10.0582 \log X_2 + 3.8366 \log X_3$. Differentiation with respect to time of this relationship gives rate of consumption from the derivative $dY/dX_3 = 10^a b X_3^{b-1}$. Thus, the relationship of rate of consumption to age and temperature is given by: $\log [d\hat{Y}/dX_3] = -13.9839 + 10.0582 \log X_2 + 2.8366 \log X_3$. Substituting in the two previous equations for X_3, the right-hand side of the equation relating age to molt number and temperature, gives the relationship to molt number and temperature of cumulative area consumed as: $\log \hat{Y} = 1.3975 - .0130 \log X_1 - .4890 \log X_2 + 2.6603 \log X_1 \log X_2$, and the relationship to molt number and temperature of rate of consumption of foliage area as: $\log [d\hat{Y}/dX_3] = -2.1799 - .0096 \log X_1 + 2.2691 \log X_2 + 1.9669 \log X_1 \log X_2$. These 2 regressions assume a logarithmic increase in rate of consumption whereas the rate at which larvae eat is fairly constant within stadia. Therefore it is necessary to derive the rate of consumption at the geometric midpoint, $(\log \bar{X}_{ln} + \log \bar{X}_{ln+1})/2$, of the stadium to estimate average rate of consumption for the instar of interest. Rates of consumption calculated by the more usual method of dividing consumption by duration

for each stadium and plotted against the geometric midpoints of their respective stadia increase with molt number and temperature according to the regression: $\log [\bar{Y}_{n+1} - \bar{Y}_n/\bar{X}_{3n+1} - \bar{X}_{3n}] = -1.9929 + .06815 \log X_1 + 2.1245 \log X_2 + 1.9836 \log X_1 \log X_2$. Agreement between the last 2 regressions is good except in the second term which contributes no significant amount to either regression. In the third term, they show an effect on rate of consumption of temperature which is constant for all instars, and in the last term, an increase in the rate with successive molts which is larger as temperature increases. Respectively, the last two terms may be regarded as the effect of temperature directly on feeding activity and indirectly on the amount removed as a function of size of the larva. The third term fails to express a smaller gain in size per instar at 29.4°C than at 23.9°C suggested by the data for head capsule width, cumulative area consumed, and mean number of stadia per larva (Table 3); and by the slope of the regressions shown in Fig. 7. These data indicating a slightly curvilinear relationship to temperature of utilisation of feeding periods in terms of development, with an optimum utilisation at 23.9°C or thereabouts. Error in the prediction as a result is small. The effect

temperature is divided over factors, indicated by the first term, characteristic of 'Bragg' foliage consumed under these conditions, important among which are thickness and nutritional value per unit volume.

Substituting 27.4°C for X_2 in the preceding regressions gives predicted values of use during the infestation period. The relationship of rate of consumption to molt number at 27.4°C in the laboratory is: $\log [d\hat{Y}/dX_3] = 1.0696 + 2.8279 \log X_1$, from which the average rate for each instar is:

instar 2	.31 cm^2/day
instar 3	1.47 cm^2/day
instar 4	3.94 cm^2/day
instar 5	8.11 cm^2/day
instar 6	14.39 cm^2/day

Foliage maturity

Positions of the regressions indicate little difference with foliage maturity in areas consumed (Fig. 7), but show that larvae were slightly older at each molt because of delay in reaching the first molt on mature foliage. The areas may indicate volumes consumed since thickness of foliage did not differ between the

3 maturity levels among leaflets from a similar crop (Table 8); however, differences with maturity in weights per unit area (Table 9) of foliage from the crop used to feed larvae appear to be too large for there not to have been some difference in thickness between each maturity level consumed. Therefore, little reliance was placed on areas consumed as a means of comparing absolute quantity consumed between maturity levels. Weights per unit area (Table 9) indicated that larvae consumed more dry weight and fresh weight as foliage maturity increased, presumably because older foliage had less nutritious value per unit fresh weight even though it had higher dry weight percentages.

Infestations on the crop at Quincy were present when senescence was exceeding new growth so that average foliage maturity was increasing from intermediate to mature. Larvae were observed feeding on foliage of each maturity level but larger individuals were most common on intermediate leaves. Therefore, differences in maturity of foliage consumed in the field and in areas of each maturity level consumed in the laboratory were too small to show that this factor has an effect on defoliation.

In summary, results of the temperature and foliage maturity treatments indicate that defoliation may be largely unaffected by crop foliage maturity or selection of foliage of a particular maturity, but that injury levels are approached more rapidly because of fast development at warmer temperatures. Total areas removed are not widely different between treatments so that area removed per generation does not vary greatly and defoliation increases mainly according to the speed of development of individuals and the effect of this on increase in population density.

Effect of Rearing Method

Soybeans removed from the field grew leaves which were thinner than those on the crop so that foliage areas consumed from transplanted soybeans were not comparable to areas consumed in other treatments. Data for larvae in Trial I and II are summarised in Table 6. Effects of the trials or rearing method on slopes of the regressions: $\log \hat{Y} = a + b \log X_3$ (X_3 = age) and $\log \hat{Y} = a + bX_1$ (X_1 = stadium number) were not significant. Intercepts of the regressions (Table 6) indicate that foliage areas removed by larvae of the same age were

Table 6. Regression formulae relating cumulative area consumed to molt number ($\log \hat{Y} = a + bX_1$) and to age ($\log \hat{Y} = a + b \log X_3$) for velvetbean caterpillars feeding on 'Bragg' foliage on plants and in dishes in Trials I and II.

Treatment	Regressions	
	$\log \hat{Y} = a + bX_1$	$\log \hat{Y} = a + b \log X_3$
Trial I plants	$\log \hat{Y} = .715 + .616\ X_1$	$\log \hat{Y} = 3.770 \log X_3 - .298$
Trial I dishes	$\log \hat{Y} = .782 + .611\ X_1$	$\log \hat{Y} = 3.921 \log X_3 - .216$
Trial II plants	$\log \hat{Y} = .760 + .640\ X_1$	$\log \hat{Y} = 3.808 \log X_3 - .290$
Trial II dishes	$\log \hat{Y} = .866 + .622\ X_1$	$\log \hat{Y} = 3.932 \log X_3 - .318$
Trials I and II plants		$\log \hat{Y} = 3.884 \log X_3 - .384$
Trials I and II dishes		$\log \hat{Y} = 3.915 \log X_3 - .257$

larger in dishes than on plants in Trial I, slightly larger on plants than in dishes in Trial II, and approximately 1.3 times larger in dishes when data were summarised from both trials. Testing the significance of this difference appears unjustified in the light of variation in foliage consumed and time of each molt. The effect of rearing method on stadia type (Fig. 1) and duration of the larval stage was not significant. The data of Trials I and II probably fail to give sufficient evidence that rates of consumption in the laboratory need to be corrected for rearing method before applying them to the field.

Crop Foliage Measurements

Area

Measurements of foliage area for the crop are summarised in Fig. 8. Foliage area per plant (Fig. 8C) was greatest during the end of bloom and then rapidly declined. Similar trends in amounts of foliage were reported by Henderson and Kamprath (1970) for determinate 'Lee' soybeans and by Hanway and Weber (1972) for indeterminate 'Hawkeye' soybeans. Decline in foliage area of 'Bragg' resulted from senescence (Fig. 8A)

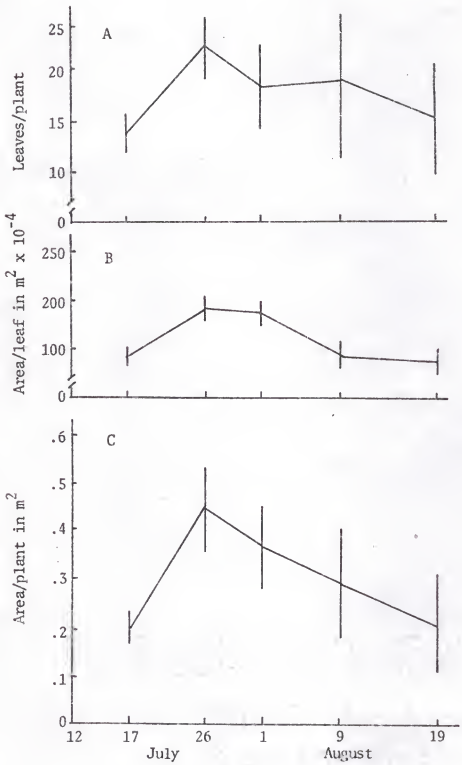


Figure 8. Foliage of 'Bragg' soybean crop planted 5/15/72. Means + 1 S.D. for: A, leaves/plant; B, area/leaf; and C, area/plant, for each of 5 sampling dates. First bloom approximately 12-15 July, full bloom approximately July 22.

and small size (Fig. 3B) of the later foliage. Senescence began before mid-bloom: the majority of plants had lost 2 leaves by July 27 and about 7 lower leaves plus up to 15 other leaves by August 9. Production of new foliage ceased about August 25 so that foliage area continued to decline after the final sampling date. Foliage area of the crop was measured only up to the early part of the infestation period but shows a decline which may be expected to continue until harvest, so that defoliation percentages can increase more rapidly as the season progresses even if the infesting population does not. For decline in foliage continuing at the same rate byond the sampling period, predicted area of foliage plus damaged area remaining on the crop is: $\hat{A} = 8.7377 - .1608\ X_3$. The right side of the equation is the linear regression of foliage area over the last 4 sampling dates; A is measured in m^2/meter of row, and X_3 = days from the date of maximum foliage area (July 26). Predicted crop foliage area was approximately 8.74 m^2/meter of row on July 26 and 0 after September 19, 55 days later.

Regression equations of leaflet dimensions on leaflet area are shown in Table 7. The high r^2 values indicate that dimensions, in particular the area of

Table 7. Formulae and r^2 values for linear regression of area on dimensions for 44 'Bragg' soybean leaflets at pod-set in 1972.

Dimension	Regression formula	r^2
Width	$\hat{Y} = -272.180 + 11.880X$	.938
Length	$\hat{Y} = -384.744 + 7.389X$	.884
Area of ellipse	$\hat{Y} = 9.560 + 0.076X$	.977

an ellipse, could be measured to rapidly estimate area of leaflets by regression with acceptable loss in precision.

Thickness

Thickness in 'Bragg' leaflets from a crop at Gainesville, Florida, are shown in Table 8. Foliage maturity had no significant effect on thickness of these leaflets. Differences in thickness between leaflets and between the regions of each leaflet shown are significant, suggesting that similar variation contributed to large variation in areas consumed at Quincy.

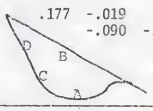
Correlations between regions of the leaflets measured were not high, suggesting that thickness must be known at the region of the leaflet consumed before area can give a very good estimate of absolute quantities consumed.

Weight

Table 9 summarises measurements of foliage cut from freshly excised leaflets. Measurement of a second set of discs cut from the same leaflets indicated

Table 8. Thickness of leaflets of field-grown 'Bragg' soybeans at pod-set. Mean and 1 standard deviation of sections cut from 4 regions of each leaflet and correlation of thickness between regions. Data combined for equal number of measurements from mature, young, and intermediate aged leaflets.

Region[a] of leaflet	Thickness (mm)		Correlation coefficients			
	$\bar{X}$	S.D.	A	B	C	D
A	.710	.179		.177	-.019	.052
B	.641	.157			-.090	-.213
C	.601	.171				.269[b]
D	.630	.136				
grand mean	.646	±.159(n=240)				



[a]Each region about .25 total leaflet area, labelled alphabetically as shown.

[b]Significant at .05 level.

Table 9. Weights of foliage and dry weight per cent for field-grown 'Bragg' soybeans at pod-set.

Age of foliage	Number of replicates[a]	Weight g /m^2		Dry weight % at indicated time (hrs)	
		Fresh	Dry	1	24
Young	2	80.95	17.29	21.4%	21.3%
Inter.	6	121.35	35.88	31.1%	28.1%
Mature	6	130.02	44.31	35.1%	33.1%

[a]One replicate equals 50 discs, each 3.465 cm^2; weights were similar between replicates within each age of foliage.

no significant change in weight after 24 hours on moist filter paper in dishes. Fresh weights, dry weights, and dry weight percentages (Table 9) for foliage of each age show that foliage weighed more per unit area and had higher percentages of dry weight as age increased.

Mean dry weight percentage of intermediate-aged leaflets excised at 10 p.m. was not significantly different to that of leaflets excised at 4 p.m., showing that time of excision probably had no effect on the moisture content of foliage consumed.

Defoliation Percentages

Defoliation percentages are typically determined by visual rating. At the time of inspection, the grower looks at representative foliage and estimates the ratio:

> [sum of areas of leaves were they undamaged - visible foliage area]/[sum of areas of leaves were they undamaged]= defoliation percentage/100.

The numerator (designated here as C) is an estimate of cumulative area consumed when no significant changes

in damaged area result from changes in foliage area. Leaves which reach senescence and fall after the start of infestation lose a small percentage of their foliage to feeding, but the area missing from fallen leaves on average cannot exceed the critical injury level before this level is reached and is actually much less than this, therefore, areas actually consumed in the field are only slightly different from areas of visible damage until near harvest. Damaged areas on plants grown in pots and in the field were not examined closely to determine if growth of leaves changed the size of damaged areas, but this factor is not considered significant because most larvae are found on nearly full-grown leaves. The denominator (designated as A) is an estimate of foliage area which would have been present in the absence of the pest, given that changes in foliage area resulting from growth or senescence are not significantly affected by presence of the pest.

To use the ratio for timing control activities, the grower needs: (1) the size of the ratio at the economic threshold, (2) the date at which the economic threshold will be reached. Strayer (1973) suggested that size of the ratio should not exceed .20. The time

required to reach the economic threshold can be estimated when the rate of change in [C/A] as a function of time and [C/A] at some point prior to the economic threshold are known. The grower is particularly interested in the ratio at the action threshold, since this is the point at which controls must be initiated to prevent the ratio reaching .20. The grower commonly estimates the entity [C/A], rather than the components C and A, and expects that it will increase at the same average rate as in previous infestations, thus assuming that for every infestation, both sides are the same in the equation:

$$[C/A]_e - [C/A]_a = .20 - \int_a^e \frac{d[C/A]dt}{dt}, \quad (t = \text{time})$$

where [C/A] is a function of time, and d[C/A]/dt is the rate of change in the ratio between the action threshold (a) and the economic threshold (e). Obviously this is so only to the extent that C and A are the same between infestations.

If C and A are measured independently, the difference in the ratio between the action threshold and the economic threshold is:

$$\frac{Ce - Ca}{Ae - Aa} = .20 - \int_a^e \frac{dC}{dT}\frac{1}{A}\,dt \quad \int_a^e \frac{dA}{dt}\frac{C}{A^2}\,dt$$

where C and A are independent functions of time, it can be shown that when A is large relative to C and remains fairly constant over the period of interest, the last equation can be reduced and the increase in the ratio between the action and economic thresholds is approximately:

$$.20 - \frac{Ca}{Aa} \doteq .20 - \frac{1}{Aa} \int_a^e \frac{dC}{ct}\, dt.$$

The notation in these equations can be expressed more simply when the difference between ratings at only 2 points in time is being considered, but they are expressed in Leibnitz notation here to stress that possibly accurate functions of C and A can be obtained only by 3 or more measurements during the infestation period, as shown by the curves for pest abundance (Strayer 1973) and foliage area (Fig. 8).

The curves may be expected to vary between infestations with differences in dates of planting and first invasion of adults, as Menke (1973) has shown, and differences in subsequent rates of development of the crop and pest population. The quantity dC/dt depends on feeding rate per individual and number of individuals present so that unless one of these variables is constant,

multiple integration is necessary to fully represent the relationship of defoliation percentage to foliage and pest density. Where an average feeding rate per individual is supplied, the relationship of defoliation percentage, [C/A]100, to larval density is given by:

$$[C/A]100 = \frac{100}{A}\left[\frac{dY}{dX_3}\right]\int\frac{dL}{dt}\,dt,$$

where L is the number of larvae as a function of time, and $[dY/dX_3]$ is the rate of feeding. From this equation, values expressing on a per unit basis the relationship of defoliation percentage to larval density can be found. For example, using the rate of consumption for each instar at 27.4°C predicted by the laboratory data, gives the percent defoliation caused to 1 m^2 of foliage by 1 larva feeding for 1 day, and inversely, the number of larvae which will cause 1% defoliation to 1 m^2 of foliage in 1 day, shown in Table 10.

Strayer (1973) measured the contribution to defoliation per 3rd and later instar larvae assuming that each contributes equally to defoliation. The contribution per 3rd and later instar larva is the average of rates of feeding of the last 4 instars if 6 instars are normal in the field and the larvae

Table 10. Per cent defoliation caused to 1 m^2 of foliage by 1 larva of the indicated instar feeding for 1 day and number of larvae to cause 1% defoliation to 1 m^2 foliage in 1 day, based on rates of feeding by each instar in the laboratory predicted at 27.4°C.

Instar	% defoliation/m^2/larva/day	larva/m^2/% defoliation/day
2	.0031	323
3	.0147	68
4	.0394	25
5	.0811	12
6	.1440	7

counted are equally distributed among the 4 stadia. From Table 10, this average is 6.98×10^{-4} m^2 at 27.4°C. Strayer (1973; Fig. 14) presented a seasonal occurrence curve of the infestation on the crop from which I collected foliage area samples at Quincy in 1972. It shows that the crop had 3.7 - 3.8 larvae (3rd and later instars only) present per foot of row for each day from the start of the sampling period (when defoliation was negligible) up until approximately 35 days later (August 30) at the economic threshold of 18-20%. The linear regression for foliage area, $\hat{A} = 8.7377 - .1608\ X_3$, predicts that the sampled crop had approximately .95 m^2 of foliage area per foot of row on August 30. In lieu of any better limits for the estimate of A, a maximum error of 50% was arbitrarily placed on it because of variation between those parts of the field which Strayer (1973) and I sampled, and the very small number of foliage area samples I obtained. With these values, rates of feeding by the larvae counted were estimated as being in the range:

$$\frac{20}{100} \times \frac{.95 \times .5}{3.8 \times 35} = 7.1 \times 10^{-4}\ m^2/\text{day minimum, to}$$

$$\frac{20}{100} \times \frac{.95 \times 1.5}{3.7 \times 35} = 22.0 \times 10^{-4}\ m^2/\text{day maximum.}$$

The laboratory results predict that larvae do not consume foliage at 7.1×10^{-4} m^2/day until just after the 4th molt, so that the range suggests that the laboratory data underestimate rates of feeding in the field. Considering the difference in the way the rates from the laboratory and field data were calculated and the possible sources of variation in the comparison, the differences between them are small.

An example of the use of values in Table 10 is that they can be used with a single inspection of the field if the area of foliage, A, (possibly using numbers of leaves or leaflet dimensions as an index), numbers of each instar, and defoliation percentage are determined. Summing the contribution to defoliation of the instars and multiplying this by the length of time until a date of interest and dividing by the area of foliage, A, gives the additional percent defoliation which will be suffered if the age structure and density of the populations and foliage area of the crop remain stable. Because these 3 factors are dynamic, further investigations in the field would be valuable in improving the usefulness of the laboratory values.

SUMMARY AND CONCLUSIONS

Velvetbean caterpillars reared in dishes consumed foliage at rates which depended on their age and on temperature but not on foliage maturity. Areas consumed and head capsule widths were more similar at pupation than in equivalent stadia regardless of treatment, the data indicating that larvae continued to pass through stadia until they became an instar ready to pupate. The final instar was characterised by a head capsule ca. 2.4 mm or larger and had on average consumed about 100 cm^2 of foliage at the time that it pupated. Therefore, differences in the increase in size per stadium as a result of treatments was reflected in differences in the number of stadia passed through. This complicated interpretation of treatment effects from data of individual stadia and their application to field situations. Computation of regressions by the least squares method avoided this problem and provided linear models summarising effects throughout the larval stage and identifying sources of variation.

Cumulative area consumed increased logarithmically with larval age, areas consumed differed more with effects of treatments on size of larvae than with other factors, indicating the importance of size grouping of individuals in the field. From this study and 3 recent studies reporting areas consumed (Stone and Pedigo 1972, Reid and Greene 1973, and Kogan and Cope 1974), it is reasonable to assume that a range of noctuid defoliators remove foliage under actual field conditions at rates which are as closely related to their size (regardless of species) as to any rates which have been determined under artificial conditions. A comparison of 2 rearing methods was probably inconclusive in showing that the artificial conditions provided a close approximation of feeding in the field. More attention to evaluating feeding in the field would have been valuable in the present study.

Consideration of the way in which control decisions are arrived at show that the grower is assuming that the rate of change in defoliation percentage will be similar to that in infestations on which recommendations are based unless he measures independently foliage area removed and areas remaining. If he measures only the density of the pest population as an index, he is

failing to include area of the crop and thus pest impact and making gross averages of the rates of consumption per individual in the field. Rates of consumption may be a useful way of demonstrating factors which affect defoliation but possibly the only good methods which would allow the use of rates of consumption continuously in a scouting program would be to group larvae falling on the shake cloth precisely by instar (or possibly by biomass gravimetrically) and determine the rate of feeding of the sample, or to count larvae in the final, most important instar and calculate from the average length of that instar what proportion are pupating and have therefore removed approximately 100 cm^2 of the foliage. Whether the grower uses values of [C/A] or individual values of C and A, he must extrapolate the defoliation over a future period from the rate at which it has progressed in that season or in previous infestations. By combining a knowledge of the rate of change in defoliation percentage and using C and A as checks to compare his crop with other infestations, he may improve the timing of his controls. Menke (1973) has shown the origins of the curves will be affected by first planting date and time of invasion so the effect of factors such

as latitude and variety on the relative positions of the origins may be as important as effects of temperature and foliage condition on slopes of the curves later in the season.

The failure to predict crop foliage area in the present study was mainly attributable to the work involved in measuring individual leaflets. An approximation of foliage area from regressions of leaflet dimensions or simply from the number of leaves might have been made more frequently and over a longer period to provide an equal amount of information at the same cost.

Variation in weight and thickness of foliage areas consumed and concentration of the study on this variable precluded extensive correlations being made between size, age, and other parameters which would have been of value in analysing further the relationship between stadia type frequencies, larval development, and treatments.

The study emphasises that further attention should be given to trying to delay the rate of increase in cumulative areas removed in the field by limiting invasion or subsequently the size that individuals or populations attain on average, and to insuring that the

crop has sufficient foliage area so that a reduction in materials translocated to the pod, or in leaf area index, can be kept at insignificant levels. The population curve given by Strayer (1973) suggests that if this can be done up to the end of the first (conspicuous) generation, a valuable delay in the need to apply controls may result.

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BIOGRAPHICAL SKETCH

Jonathan Carter Reid was born January 14, 1945, in Lancashire, England. His preparatory and grammar school education took place in Lancashire.

He worked on farms in Yorkshire and Lancashire between 1961 to 1963 and 1964 to 1966. He graduated from Lancashire College of Agriculture with a National Certificate of Agriculture in 1964 and a National Diploma of Agriculture in 1968. In 1970 he concluded 18 months of study at Wolverhampton Polytechnic Staffordshire, and 6 months supervised research at the Entomology Research Laboratory, Ministry of Agriculture, Fisheries and Food, Reading, Berkshire; leading to Membership of the Institute of Biology (London) by Examination in Entomology.

In September 1970 he traveled to the United States through a Fulbright-Hays travel grant and commenced graduate studies in the Department of Entomology, Purdue University, West Lafayette, Indiana. In April 1971, he transferred to the graduate school of the University of Florida.

He is a member of the Institute of Biology, London, the Entomological Society of America, the Florida Entomological Society, and the British Herpetological Society.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

G. L. Greene, Chairman
Associate Professor of Entomology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

W. H. Whitcomb, Co-Chairman
Professor of Entomology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

J. E. Lloyd
Professor of Entomology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

March, 1975

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