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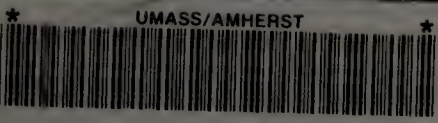
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ADULT ACTIVITY PATTERNS AND OVIPOSITION BEHAVIOR
OF THE CRANBERRY WEEVIL (*Anthonomus musculus* Say)

A Thesis Presented

by

BENJAMIN BRUCE LONG

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
Of the requirements for the degree of

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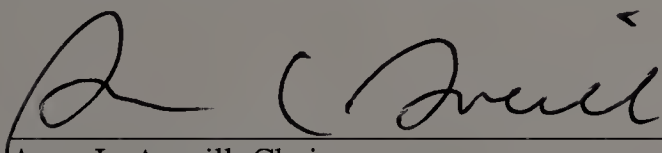
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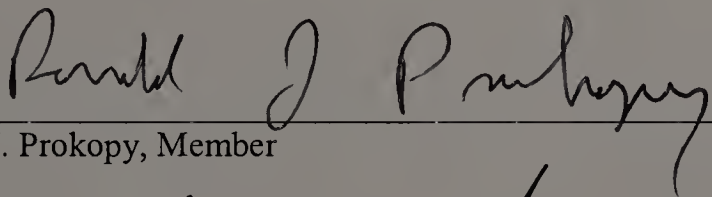
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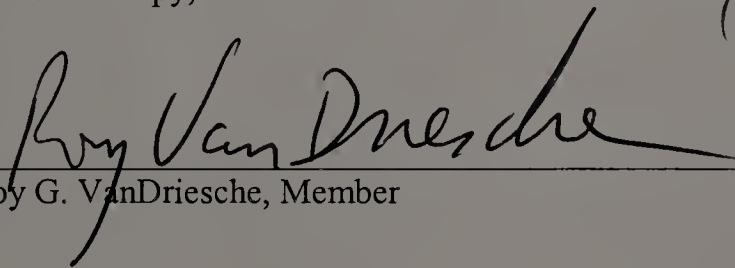
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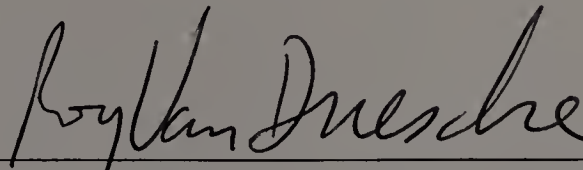
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CHAPTER I

LITERATURE REVIEW

Introduction

Cranberry (*Vaccinium macrocarpon* Aiton) is financially the most important food crop in Massachusetts. With over 14,400 acres of commercial cranberry bogs, Massachusetts accounts for approximately 34% of total cranberry production in 1998, second only to Wisconsin (Farrimond 1999). Other major areas of cranberry production include New Jersey, Washington, Oregon and British Columbia (Sandler, 1997). Although cranberries are grown across the continent and the cranberry weevil (*Anthonomus musculus* Say) range extends from Ontario and New England, west to the Rocky Mountain range and south to Florida, the cranberry weevil (CW) is considered a pest only in Massachusetts (Mechaber 1992). Another common name for *A. musculus* is “blossom weevil” when it is found on cultivated blueberries (Doehlert and Tomlinson 1974; Pritts and Hancock 1992).

Lacroix first described CW as a cranberry pest in 1926. The most successful and cost effective way for controlling CW has been through the use of chemical insecticides. The first such pesticides to be used were Bordeaux mixture (consisting of lime, copper sulphate and water), calcium arsenate and fish-oil soap. In tests conducted by Lacroix (1926), this mixture of insecticides reduced CW populations by 90 to 100%.

Lacroix (1926) also reported on attempts to manipulate cultural practices in order to control CW levels. These practices include flooding and sanding of the bogs. Flooding was done in March in an effort to discourage weevil colonization. Bogs were kept flooded until May 25th. Sanding is another common practice among cranberry growers wherein a layer of sand is spread over a bog surface in order to improve productivity and reduce some pest populations (DeMoranville 1997). However, Lacroix reported that neither of these cultural practices reduced CW populations. In the areas that were sanded, weevil numbers increased. Lacroix speculated that this occurred because sanded areas often support much new growth and would provide conditions preferred by CW.

Present-day control methods for CW have not evolved past using insecticides. The organophosphate chlorpyrifos is currently the only effective material for controlling CW. This chemical can only be applied twice per season and is highly toxic to non-target organisms, including bees, which are essential for pollination and fish that are located in adjacent water supplies.

All insecticide treatments for cranberries are applied via irrigation systems that are connected to large water reservoirs, which also serve as recreational and wildlife areas. Impoundment of water after a pesticide application within a bog system is required to help protect these areas. However, because of human error, occasional failure of irrigation systems to function properly and potential long-term effects of some pesticides on the environment, non-chemical alternatives should be pursued. My hope is that work detailed in this thesis will be one small step among many towards eventually reducing the number of pesticide applications for cranberry production through Integrated Pest Management (IPM).

According to Prokopy (1990), the first stage in Level I IPM is the ability to predict the abundance of pests in order to maximally benefit from a well-timed insecticide application. Being able to effectively time sprays involves a detailed analysis of a pest's biology. Thus, I present a partial interpretation into the world of the cranberry weevil.

Genus *Anthonomus*

Species in the genus *Anthonomus* (Coleoptera: Curculionidae) are often oligophagous and generally feed on plants of one genus or tribe. Of *Anthonomus* species that have been studied, most complete their development in the flowers or fruit of such plants. This strategy has proven to be particularly successful since *Anthonomus* is a relatively large taxon harboring over 330 species (Burke, 1976). Among these 330 species, there are a number of important agricultural pests including the strawberry weevil (*A. signatus* Say) which historically has been mistaken for *A. musculus* and vice versa (Lacroix, 1926). By far the most economically damaging member of this genus is the cotton boll weevil (*A. grandis* Boheman), which has been the subject of much fruitful research over the past century in an effort to calculate its demise.

Physical Description

Lacroix (1926) gives the following descriptions for *A. musculus*. The lemon yellow to white egg is oblong-ovoid measuring 0.4 to 0.5 mm long and 0.29 to 0.32 mm wide. The surface glistens, is viscid and smooth.

A full-grown larva is a cylindrical legless grub that is strongly curved so that the head and anal segments are in close approximation. The length of the grub measures 2.5 to 3 mm. The body is yellowish-white, while the head is pale yellow and the margins of the mandibles support a brown to black color.

The pupae are stout, measuring 2 to 2.5 mm long and 1 to 1.4 mm wide. They are yellowish to white in color with the exception of the eyes, which turn black after a few days. The legs, proboscis and wing pads are all folded tight against the body while several conspicuous spines stick out from the head and abdomen.

The adult is oval in shape with the characteristic long slender snout of curculionids and is 1.5 to 2 mm in length. Older adults have black heads and legs with dark red elytra. Newly emerged individuals are much lighter in color with the head being brown and the elytra golden-brown. Fine white hairs cover much of the body and can be found in dense patches on the elytra to give the appearance of transverse bands.

Sexual Determination

Previously unrecorded sexual dimorphism for CW was discovered to be the same as the cotton boll weevil. Sex can be determined by observing the terminal posterior segments of the abdomen (Agee 1964). This feature has also been found to be helpful in determining the sex of numerous other species of weevils. Males can be identified by a notch in the 8th terga of the abdomen. This notch is found to be lacking in the females of CW.

Although Agee used CO₂ to sedate the weevil to determine sex, we found this unnecessary since weevils often play dead when disturbed. While holding the weevils, under a dissecting scope, between the thumb and index finger so that the weevil was ventral side up and with the opposite hand

carefully inserting a size 0 insect pin between the elytra and abdomen, it is possible to gently pry open the genital opening to reveal the leading edge of the last abdominal segment to be either notched (male) or unnotched (female).

Host Plants

Through both field and laboratory observations Mechaber (1992) recorded 12 species of Ericaceae plants utilized by CW for adult feeding and/or oviposition in Massachusetts and New Jersey (Table 1.1). Host plants are grouped in Table 1.1 according to the relative timing of flower bud availability (early, transitional, mid and late in the season). Through choice feeding tests Mechaber (1992) concluded that CW distribution on potential host plants is determined mostly by the relative abundance of the surrounding vegetation, the weevil being found on whatever host plant was most abundant in the field.

In three plant species, it was observed that a plant was acceptable for feeding by weevils collected from one state and not the other. Massachusetts CW fed on sheep laurel (*Kalmia angustifolia* L.), swamp honeysuckle (*Rhododendron viscosum* L.) and wintergreen (*Gaultheria procumbens* L.) while New Jersey CW did not. With one exception (sheep laurel), where data are available, it was observed that in the late season, plant feeding took place but no oviposition. This is probably because CW does not have time to fully develop from egg to adult on late season plants before the onset of cold weather.

Life History and Biology

CW overwinters as an adult, mostly in uplands adjacent to bogs (Doehlert and Tomlinson 1947 and Brissette, unpublished data) and emerges in late April in Massachusetts at which time it can be found predominately on blueberry plants. Early in the spring, they begin feeding on new blueberry leaves and blossom buds. As the flower buds develop, CW lay eggs in unopened blossoms. As the blueberry buds blossom, a shift in population occurs from blueberries to cranberries.

CWs are first observed on cranberries in mid-May feeding on cranberry leaves and flower buds. In late June and early July, newly emerged weevils (identifiable by their light color) can be

observed on the bogs and populations can increase quickly if pesticides are not applied or are ill timed. During this time, CW feed on smaller berries and new leaves. By early to mid-August weevil population levels on cranberry decline dramatically and is rarely seen.

Eggs of CW are usually deposited singularly in flower buds of host plants after the female has drilled a hole into the center of the flower bud. However, Mechaber (1992) reported instances where field-collected buds contained more than one egg. After oviposition, female weevils will often feed on the pedicel of the flower bud sometimes severing the pedicel completely allowing the bud to drop to the ground. A more complete description of egg laying behavior can be found in Chapter III.

Eggs hatch within 3 to 9 days, depending on temperature (Franklin 1948). Larvae feed and pupate, all within the confines of the unopened flower bud. Feeding larvae devour the anther, pistil and stamen of the flower and eventually eat into the center of the immature ovary (Lacroix, 1926). Pupae are generally motionless unless disturbed; at which time they can move by rotating the last few segments of their abdomen in rapid irregular motions. According to Mechaber (1992), at 22 to 25°C both larval and pupal development require between 10 to 15 days.

Table 1.1. Cranberry weevil host plants and food resources in Massachusetts (MA) and New Jersey (NJ)^a.

F = feeding; O = oviposition; NA = not acceptable, or not recognized as food resource; ND = no data. Symbols to the left of the slash (/) represent adult CW feeding responses. Symbols to the right of the slash (/) represent oviposition responses.

Plant Name	MA	NJ
Early Season		
Early low bush blueberry (<i>Vaccinium vacillans</i> Ait.)	F/O	ND/ND
Low sweet blueberry (<i>Vaccinium angustifolium</i> Ait.)	F/O	F/O
High bush blueberry (<i>Vaccinium corymbosum</i> L.)	F/O	F/O
Transitional		
Black huckleberry (<i>Gaylussacia baccata</i> Wang.)	F/O	F/ND
Swamp sweetbells (<i>Leucothoe racemosa</i> L.)	ND/ND	F/O
Staggerbush (<i>Lyonia mariana</i> L.)	F/ND	F/O
Mid-Season		
Dangleberry (<i>Gaylussacia frondosa</i> L.)	F/O	F/ND
Sheep laurel (<i>Kalmia angustifolia</i> L.)	F/NA	NA/NA
Swamp honeysuckle (<i>Rhododendron viscosum</i> L.)	F/ND	NA/NA
Cranberry (<i>Vaccinium macrocarpon</i> Ait.)	F/O	F/O
Late Season		
Wintergreen (<i>Gaultheria procumbens</i> L.)	F/NA	NA/NA
Maleberry (<i>Lyonia ligustrina</i> L.)	F/NA	ND/ND

^aModified from Mechaber and Chew (1991).

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CHAPTER II

DAILY AND SEASONAL ACTIVITY PATTERNS OF CRANBERRY WEEVIL (*Anthonomus musculus* Say)

Introduction

In Massachusetts, there are three key pests that account for most of insecticide use on cranberries (*Vaccinium macrocarpon* Aiton): cranberry fruitworm (*Acrobasis vacinii* Riley), *Sparganothis* fruitworm (*Sparganothis sulfureana* Clemens) and cranberry weevil (*Anthonomus musculus* Say). In 1994, Mahr and Moffitt reported that the average number of insecticide applications (4 to 5) applied to cranberries in Massachusetts over the last 10 years has remained the same, due to the difficulty of managing these key pests. The ability to predict density levels of these pests' populations could help reduce insecticide use and enhance control. Predicting emergence or abundance of insect pests for better timed and more limited applications of insecticides, is one facet of the "first stage" of Level I Integrated Pest Management (Prokopy et al. 1990)

Lacroix first described cranberry weevil (CW) as a pest in 1926. Cranberry weevil most often only causes minor damage but occasionally will devastate large areas of cranberry bogs in Massachusetts (Lacroix 1926). The most effective pesticide to suppress CW populations is the oranophosphate, chlorpyrifos, but its use is limited to two applications per season. Therefore, it is important for growers to have the ability to predict the presence of weevil in order to maximize the effectiveness of each application.

According to Mechaber (1992), over-wintering adults first appear on low bush and high bush blueberry (*Vaccinium angustifolium* Aiton and *Vaccinium corymbosum* L., respectively), often found adjacent to many bogs in southeastern Massachusetts, generally towards the end of April. Beginning in early to mid-May, weevils can be found on cranberry vines. Weevils lay eggs in unopened blueberry and cranberry flower buds and larvae feed and develop inside closed buds and render it useless for fruiting. According to Lacroix (1926), however, the greatest damage from CW is done before egg laying when adults feed on new leaves and tender blossom buds, and again in July when newly

emerged weevils attack the fruit, leaves and terminal buds. When young beetles emerge, they feed on immature cranberries and cause multiple feeding scars.

Studies to predict insect activity, via degree days (Arnold 1960) for closely related species have been conducted for the cotton boll weevil, *Anthonomus grandis* Boheman (Parajulee et al. 1996, 1997) and the strawberry weevil, *Anthonomus signatus* Say (Mailloux and Bostanian 1993, Clarke and Howitt 1975). As with these studies, our goal was to construct a degree day model of adult emergence to predict the abundance of adult cranberry weevils on both blueberries and cranberries. In addition, we made behavioral observations of weevils in the field at different points in the season and throughout the day to elucidate activity patterns on both cranberry and blueberry host plants.

Methods

Daily Activity Patterns. Weevils were collected off of both blueberry plants and cranberry vines in Onset, MA. In late April and early May 1m², white boards were placed under portions of blueberry bushes and the branches shaken vigorously to dislodge the weevils from the host plant and subsequently down on to the board directly below. Weevils were then collected from the board and placed in plastic containers to be later released into the field for behavioral observation studies. In the middle of May and again in early July CWs were collected off of cranberry vines using a 30cm diameter sweep net. Collectors walked over the vines and swept the net across the vines at the same time. Weevils were then taken from the net and again placed in plastic containers. Weevils were kept at 4°C until they were used in observations.

To study their daily activity patterns, 50 to 100 CW were released in the field at 08:00 hours and then observed over a course of a day. The sex ratio of weevils for all releases was approximately 50:50. Hourly observations were made until 18:00h and weevil activities were recorded, including resting, feeding, walking and mating. CW cohorts were released (1) in the spring on blueberry plants, (2) on cranberry vines in early summer and (3) on cranberry vines in late summer.

Observations in the spring were made on low bush blueberry (var. Blue Crop). Only CW collected from blueberry bushes were used in this part of the study. Weevils were released at the base

of a bush and every hour, the bush was checked completely and behaviors were recorded. This procedure was replicated four times between May 7th and May 14th, 1998.

Observations on cranberry vines were made releasing by CWs into the middle of a 62cm² marked area and recording behaviors hourly as described above. This procedure was replicated 4 times between May 20th and June 10th, 1998 and later in the season, between July 20th and August 3rd, 3 times. Only CW collected from cranberry vines were used for this part of the study.

Seasonal Activity Patterns. From 1997 to 1999, approximately one half hectare of State Bog, located in East Wareham, MA at the University of Massachusetts Cranberry Experiment Station, did not receive any treatments for the control of CW. Other pesticides were applied to control fungi, weed and other insect pest populations. Five blueberry bushes (var. Blue Crop) were planted and maintained adjacent to this site in late May of 1997. These blueberry bushes did not receive any pesticide treatments. Both blueberries and cranberries were sampled from early April to late August, on relatively calm, sunny days, for the abundance of CW. Early in the season, sampling was done every day until the first CWs were recorded. After that point, sampling took place 2 to 3 times a week. Blueberry bushes were sampled by placing a 1m² white board under a blueberry bush and shaking it briskly 3 times. Because the blueberry bushes used were relatively small, approximately one meter in height, virtually the entire bush was sampled. Numbers per blueberry bush were recorded. CW on cranberry vines in the bog were sampled by taking 3 sets of sweeps with a 30 cm diameter net. Each sweep set consisted of 25 sweeps, which involved dragging the net over the vines in a 180-degree arc. Sweeping was done continuously while walking in a relatively straight line across the bog. When each sweep set was completed, the CWs were counted.

Daily maximum and minimum air temperature records, at the surface of the bog, were obtained for April 1st to August 25th from weather stations maintained at the research site. Thermal units were calculated by averaging the maximum and minimum temperatures and subtracting the lower threshold temperature (Reissig et al. 1979). Determination of the lower threshold value was

attempted using a traditional method (Johnson et al. 1995; Reissig et al. 1979) of lab-rearing eggs laid in blueberry flower buds at four different temperatures (10°C, 15°C, 20°C and 25°C).

Results and Discussion

Daily Activity Patterns. Resting was the most commonly observed behavior throughout the season (Fig. 2.1). Walking, feeding and mating less commonly observed. Walking and feeding were observed more often earlier in the day as the season progressed (Fig. 2.2) most likely because these activities are temperature dependent. Duan et al. (1996) recorded similar findings for the apple blossom weevil (*Anthonomus pomorum* L.) stating that temperature significantly affected activity patterns such as crawling, feeding and mating. Lacroix (1926) suggested the same link between temperature and oviposition behavior reporting that the greatest activity of egg laying occurred on days in which the temperature was between 34° and 38°C. On these warmest days Lacroix observed three or more eggs deposited, while on cooler days its was only one and on cold days none. This is a relatively low rate of oviposition compared to similar species such as the cotton boll weevil which will lay about one egg per hour throughout the day starting at 08:00h (Mitchell and Cross 1969) and the pepper weevil (*Anthonomus eugenii* Cano) which averages 7.1 eggs oviposited per day (Wilson 1986). Infrequency of CW oviposition, coupled with its short duration (the average time of oviposition being 1.5 minutes [Long, unpublished]) may explain why we did not observe any oviposition in the field.

Of the recorded activities, mating was the least observed activity and was only observed after 12:00h and only in the spring and early summer (Fig. 2.1). Mating was not observed in the late season observations on cranberry. This is consistent with Mechaber's findings of no oviposition on late season hosts in MA (after cranberries have finished flowering) such as Teaberry (*Gaultheria procumbens* L.), Maleberry (*Lyonia ligustrina* L.) and Sweet Pepperbush (*Clethra alnifolia* L.). Summer generation CW may mate in the following spring, as was suggested for the cotton boll weevil (*Anthonomus grandis* Boheman) by Smith and Harris (1994). Direct investigation of insemination levels of CW immediately before and after overwintering will be required to clearly establish mating activity patterns.

Seasonal Activity Patterns. Our original intention to determine the minimum development temperature threshold by the traditional method (Johnson et al. 1995 and Reissig et al. 1979) of rearing out eggs laid in blueberry flower buds in the lab, at four different temperatures (10°C, 15°C, 20°C and 25°C) proved to be a challenge, due to a remarkably low emergence rate at all temperatures. In spite of this, upon dissection of the flower buds, we discovered several unemerged, dead adults at all temperatures except for those held at 10°C. A similar minimum threshold value of 8.3°C was used for the strawberry weevil because of its superiority in predicting development under field conditions. A less reliable threshold value of 3.9°C had been originally calculated via the traditional method described above (Clarke and Howitt 1975). Armed with this knowledge and the fact that the strawberry weevil is a congener found in comparable climatic conditions, I decided to use 10°C as our lower threshold value.

The numbers of CW detected on blueberry and cranberry over the season are shown in Fig. 2.3. Overall, CW increased from 1997 to 1999. This was expected because regular CW insecticide sprays were terminated in 1997. In each year, CW was first observed on blueberry bushes and consistently switched to cranberries within the first 100 DD after April 1st. This is an important finding if growers want to consider using blueberry bushes as a trap crop (Hokkanen 1991).

After the first 100 DD, CW was almost exclusively found on cranberry. However, it should be noted that numbers of CW sampled on blueberry and cranberry are not comparable due to the differences in sampling methods. Levels on cranberry remain relatively low until about 400 DD after April 1st. After 400 DD, CW numbers on cranberry begin to increase. This mid-season increase is due to the emergence of first generation CW adults originating from eggs oviposited earlier in the season on the bog. This assertion is supported by our observation that many of the weevils caught after 400 DD were lighter in color, which is a characteristic of younger weevils as compared to darker, older CW. Therefore, we further assert that oviposition occurs on cranberry between 100 and 400 DD. CW levels stayed relatively high until 700 to 800 DD. After 800 DD, CW were rarely found on the bog.

These results have practical implications. Growers with severe CW problems can consider spraying once during each of three critical periods the season: (1) early in the season (~50 DD) on blueberry; (2) on cranberry at the peak of oviposition by overwintering CW (~200 DD); (3) during peak emergence of the summer generation (between 400 and 600 DD) on cranberry. As with the strawberry weevil (Mailloux and Bostanian 1993) the cranberry weevil field emergence is rapid and peak numbers are present only for a relatively short period of time before the adults move to other habitats (Mechaber and Chew 1991). Thus, it is critical that control measures occur at the peak abundance of CW on both cranberry and surrounding blueberry plants. A similar control plan for the strawberry bud weevil (*Anthonomus signatus* Say) has been implemented and shown to control pest populations and reduce damage on crop plants the following year (Bostanian 1999).

Future studies may further refine the accuracy of these results by discovering the exact overwintering sites of the cranberry weevil. Replacing air temperatures with overwintering habitat temperatures would further the accuracy of predicting spring emergence of CW. Parajulee et al. (1997) reported that the timing of cotton boll weevil emergence was directly related to the different types of habitat boll weevils selected for overwintering. This difference was attributed to the insulating capacity of overwintering habitats. The same may be true for CW if some weevils are overwintering in broadleaf litter as opposed to possibly a grassy field or a habitat dominated by undergrowth.

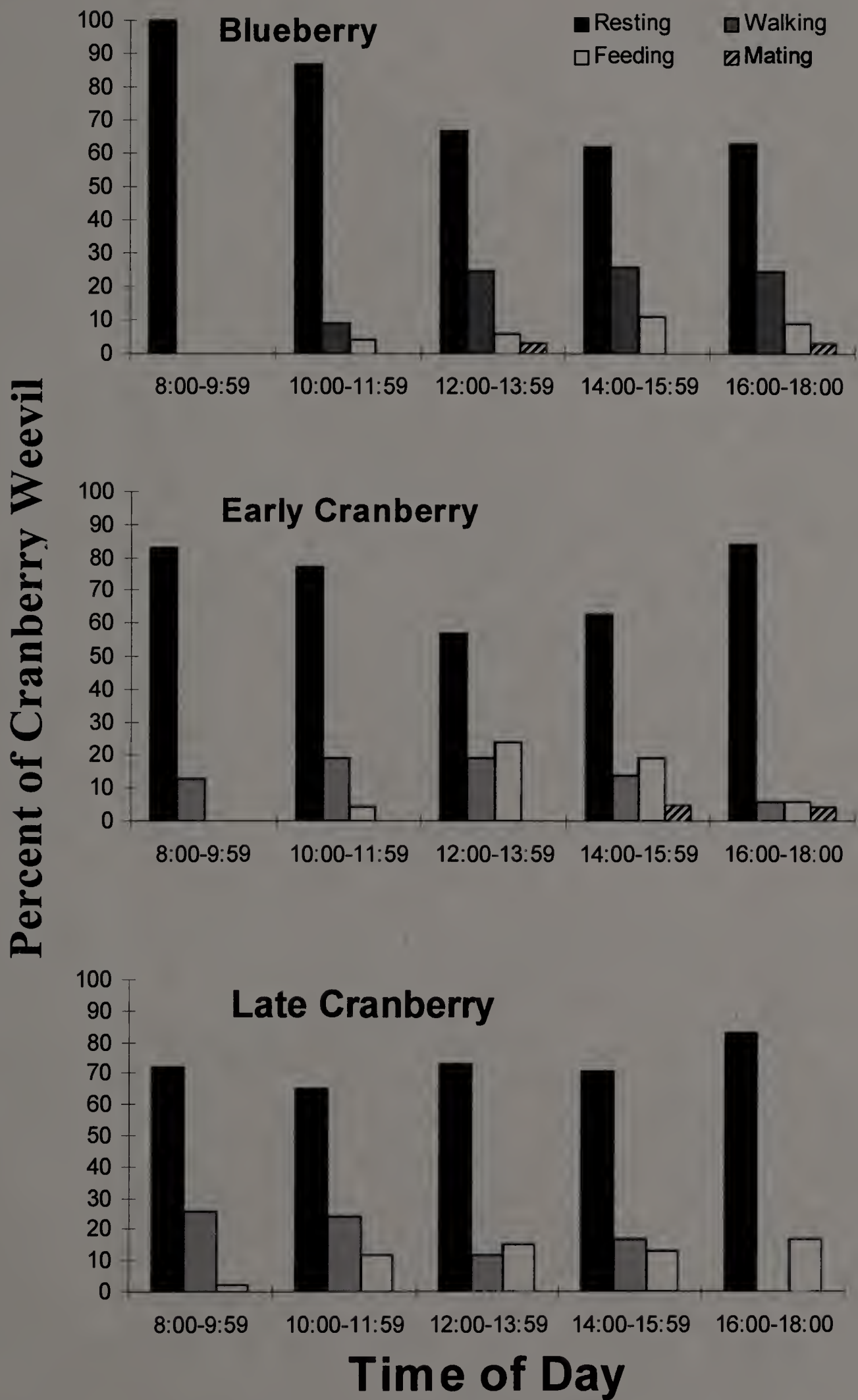


Fig. 2.1. Observed behaviors for cranberry weevil at three different points during the season.

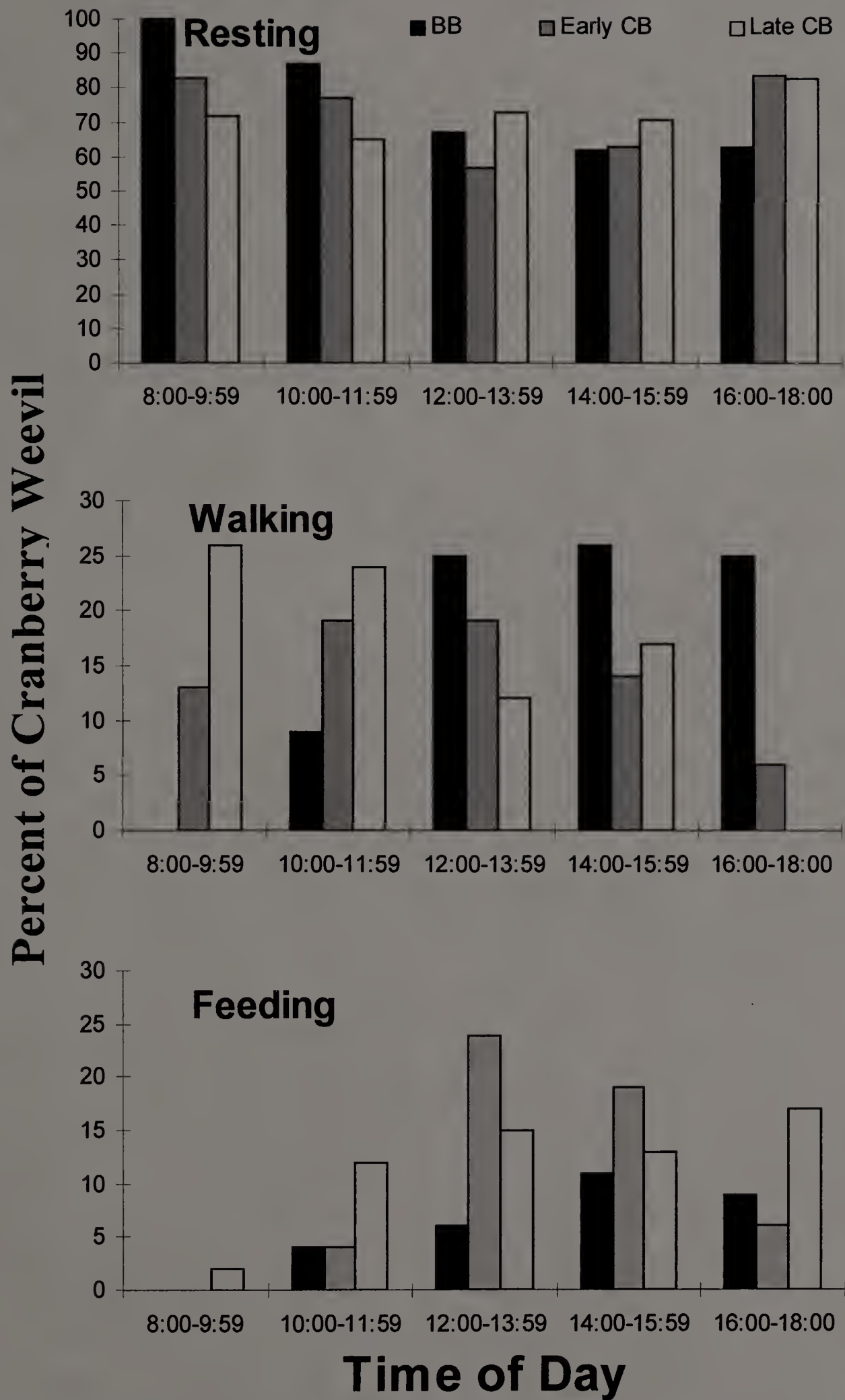


Fig. 2.2. Distribution of behaviors through out the day for cranberry weevil at three different points in the season.

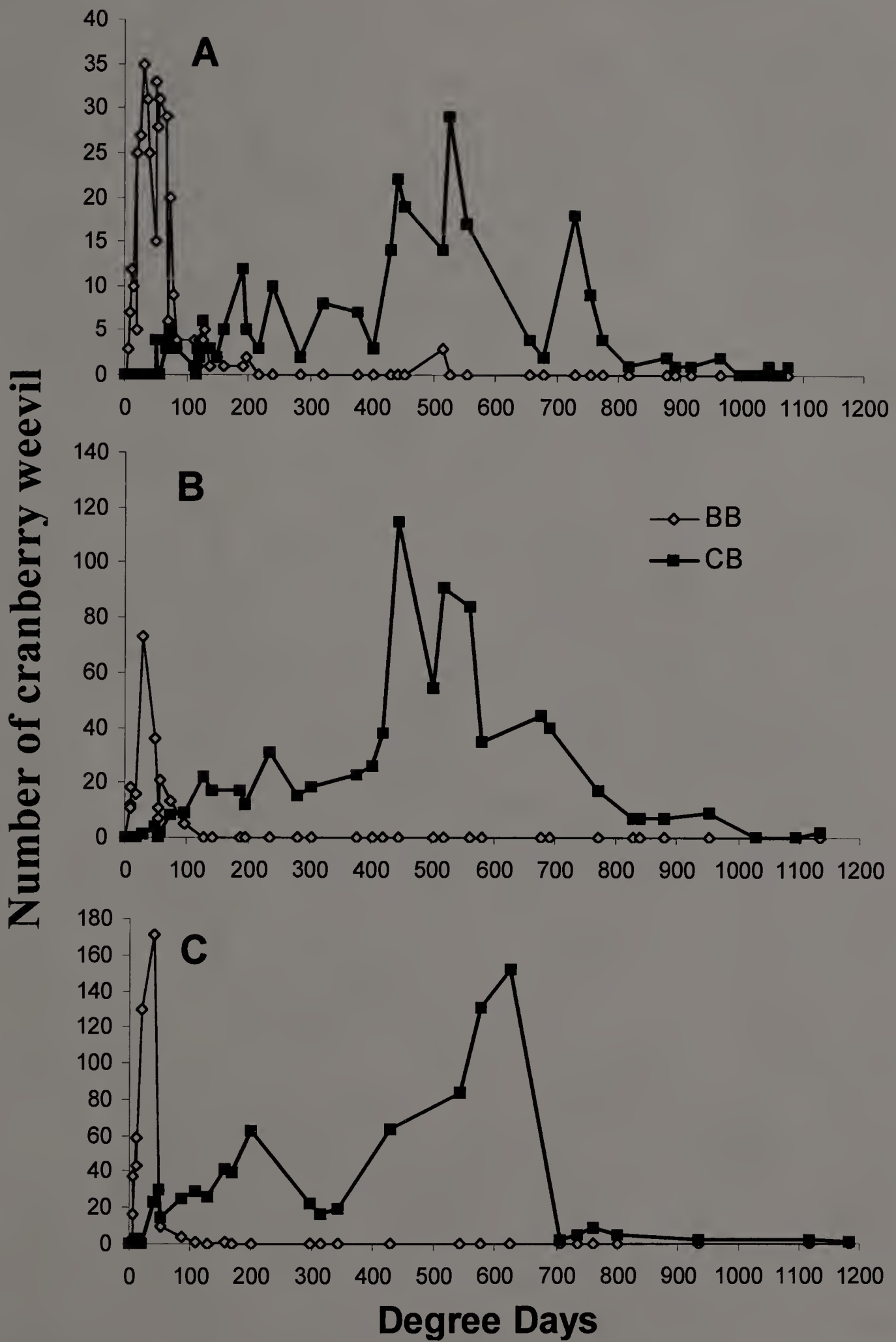


Fig 2.3. Number of cranberry weevil on blueberry bushes (BB) and cranberry vines (CB) in relation to degree days at state bog for A) 1997, B) 1998 and C) 1999.

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CHAPTER III

OVIPOSITION BEHAVIOR OF THE CRANBERRY WEEVIL (*Anthonomus musculus* Say)

Introduction

The cranberry weevil (*Anthonomus musculus* Say) oviposits in the flower buds of both low and high bush blueberry (*Vaccinium angustifolium* Aiton and *Vaccinium corymbosum* L.), as well as cranberry (*Vaccinium macrocarpon* Aiton). Seasonal transition between these host plants was detailed in Chapter II. In southeastern Massachusetts, weevils were observed on blueberry bushes beginning in late April. As the season progresses, the number of blueberry flower buds decreases and the number of cranberry flower buds increase and there is a corresponding increase in cranberry weevil (CW) numbers on cranberry. At the same time, there is a corresponding decrease of CW found on blueberry.

CW is especially damaging to host crops because eggs are deposited inside the flower buds and the bud is destroyed as the developing larva feeds on the internal flower parts. Even partial destruction of a flower can result in the loss of potential fruit. After egg deposition, CW will sometimes girdle the pedicel of the flower bud. This girdling results in the flower being partially or completely clipped from the host plant

Usually, CW lays only a single egg per flower bud and during these studies no more than one larva completed development per bud (Long unpublished). Dispersion of populations is common among insects that have limited food resources (Prokopy 1981), particularly those insects that feed on small or ephemeral plant parts (Thompson 1983). Since CW larvae do not have the ability to move to locate additional food resources, females that can discriminate against buds that already contain an egg have a distinct adaptive advantage. Therefore, it seems logical that CW would exhibit a discriminatory behavior similar to that of other curculionids that exploit buds or buds, such as the cotton boll weevil (*Anthonomus grandis* Boheman) (Stansly and Cate 1984, McGovern et al. 1987), pepper weevil, (*Anthonomus eugenii* Cano) (Wilson 1986), and cabbage seed weevil, (*Ceutorhynchus assimilis* Payk.) (Kozlowski et al. 1983).

This chapter reports results of detailed studies of the oviposition behavior of the cranberry weevil, including an examination of how bud size is related to pedicel clipping by the female following egg laying. Also, the ability of females to discriminate against infested and damaged host buds was evaluated. Lastly, it is determined whether or not the addition of a second egg to an occupied bud affected larval survival.

Methods

Insects. Weevils observed on blueberry were collected in Chatsworth, New Jersey and Onset, Massachusetts. In mid-April, blueberry branches were shaken vigorously over a 1m² board placed under the bush. Dislodged weevils were then collected into plastic containers and transported to the lab in chilled coolers. Weevils from cranberry were collected in cranberry bogs in Sandwich, Massachusetts through out the season as needed, using a 30cm diameter sweep net. Males and females were held in a container with food but without oviposition sites for at least 24 hours. This was done to ensure the presence of gravid females. Weevils were then separated into containers by sex and kept at 4°C until they were used in the study.

Behavioral Observations. This study was done between 1000h and 1600h under a dissecting scope at room temperature on fresh cuttings of blueberry with the leaves removed and the flower buds left intact. The same cuttings were used by one observer throughout the day. Thus, two to three CWs were presented with host material that contained both infested and uninfested buds. Test females were allowed to crawl onto the cuttings, at which point a stopwatch was started and observations begun. Females were replaced after seven minutes if they crawled off the plant cutting and showed no initial signs of oviposition. They were also replaced after 30 minutes if they remained on the cutting but, showed no initial signs of oviposition, such as inspection of the bud or feeding, but then did not lay an egg. If a weevil laid one egg, it was allowed to continue to lay eggs until it abandon the cutting or 30 minutes elapsed since its last egg laying.

During the observation weevil activity was reported. Every behavior was recorded but this study only reports the behaviors of the weevils that eventually did oviposit. These behaviors were

ultimately broken down into four repeatable and recognizable categories including bud inspection, egg cavity formation, egg deposition and feeding on pedicel (clipping). The duration of each of these behaviors were recorded in seconds.

Clipping as a Function of Bud Size. Two or three female weevils were held in containers holding 15 to 20 flower buds that ranged in length from 2 - 12mm. Flower buds were on cut uprights, which were placed into water pics. After 48 hours, the weevils were removed and flower buds were checked for eggs. Records were made of bud length, presence of eggs, and whether the pedicel of the bud had been clipped. Instances where the pedicel had been fed upon but was not completely severed were recorded, as “clipped” if the feeding cut was more than halfway through the pedicel. Weevils originating from Massachusetts were observed on both blueberry and cranberry flower buds while New Jersey weevils were only tested on blueberry flower buds. Observations of Massachusetts weevils on cranberries were done one year before the other observations.

Because the tests were not run simultaneously, each bioassay group (Massachusetts weevil on blueberry, New Jersey weevil on blueberry, and Massachusetts weevil on cranberry) was evaluated separately. Within each bioassay group, relationship of clipping behavior to bud length was assessed by means of a G-test.

Discrimination Tests. A series of two-choice tests were run wherein single females were provided both an uninfested bud and a damaged or infested bud. On blueberry, the following 7 treatments were bioassayed: (1) newly infested with oviposition plug exposed, (2) infested 24 h prior to bioassay with oviposition plug exposed, (3) infested with oviposition plug not exposed, (4) infested with oviposition plug removed, (5) feeding cavity created by a female (6) feeding cavity created by a male, or (7) simulated feeding damage (a cavity created by piercing the bud with a number zero insect pin). On cranberry, only treatments 1, 3, 4 and 7 were tested. In the bioassay, flower buds were removed from the plants and placed in covered 30ml cups with an individual female. The buds were checked every half-hour and the number of eggs recorded. If no oviposition occurred after six hours,

the test was discarded. Buds were used in trials only once. Discrimination in bioassays was assessed by means of a χ^2 test.

Double Oviposition Survival Study. A total of one hundred and fifty blueberry buds were presented to 50 potentially gravid females in the following configuration: three buds and a female were placed into a capped 30ml cup. These cups were monitored daily for eggs. After 72 hours, 30 different weevils had infested 53 buds with one egg and 47 buds with two eggs. Flower buds with one or two eggs were put into individual 30ml containers with a 1cm long piece of damp dental wick. After two months at room temperature, if no adult CW had emerged, the flower buds were cut open to observe the extent of development of immature weevils.

The relationship between survivorship and initial egg number per bud was assessed by means of a G-test.

Results

Behavioral Observations. Forty-two ovipositions by 23 different females were observed. CW oviposition behavior can be broken down into the following activities: inspection of the flower bud, egg cavity formation, egg deposition, plugging of the egg cavity, and feeding on pedicel. These are described below.

Bud Inspection. Just before oviposition, females inspect flower buds by repeated antennation of the bud surface, using a tapping motion. Females moved up and down the flower bud two to three times, apparently exploring the whole surface of the bud. Inspection resulted in either acceptance or rejection of the bud for oviposition. When acceptance occurred, time of inspection ranged between 30 and 420 sec. The average inspection time was $98 \text{ sec} \pm 67$.

Seven bud rejections were observed. Rejections were only scored if the weevil went on to lay an egg in a different bud. Inspection times before rejection ranged from 14 to 88 sec. The average time for rejection of a flower bud was $50 \text{ sec.} \pm 30$. In five out of the seven rejections, the flower bud that was rejected contained an egg. In only one instance was an egg laid in a flower bud where another egg had already been deposited.

Egg Cavity Formation. After inspecting and accepting a flower bud, the female weevil would generally choose a site one third of the way down from the basal end of the bud and commence feeding. The time spent feeding to create the egg cavity was highly variable, even among cavity formations by the same weevil, and ranged from 30 to 1650 sec. The average time was 616 sec. \pm 401. Females always fed to the point where their entire rostrum was inserted into the cavity.

Egg Deposition and Plugging of Egg Cavity. After forming the egg cavity, females turned 180 degrees, and inserted their ovipositor into the hole. One egg was deposited and subsequently, the egg cavity hole was filled with a very viscous fluid that dried, forming an oviposition plug. Since positioning of a weevil often made it difficult to determine the exact occurrence of these two events, they were grouped together and will be referred to collectively as oviposition. Normal oviposition took between 30 and 120 sec. The average oviposition time was 86 sec. \pm 69. In three instances, oviposition took longer than 180 sec due to the awkward positioning of the egg cavity underneath the overhanging lip of the calyx.

Feeding on Pedicel. Following 29 of the 42 (69%) observed ovipositions, female weevils fed on the pedicel of the flower bud that had been used as an oviposition site. When feeding occurred on the pedicel, times ranged from 120 sec to 24 minutes, with an average feeding time of 466 sec. \pm 320. Results of feeding on the pedicel ranged from feeding on only a very limited site to complete separation of the flower bud from the rest of the plant. A further description and discussion of this clipping behavior is given below.

Clipping as a Function of Bud Size. A clear pattern of clipping as a function of bud size was observed. The majority of females clipped larger buds after oviposition but not smaller buds (Table 3.2, 3.3 and 3.4). On various length blueberry buds presented to New Jersey females (Table 3.2), no 3 or 4 mm buds were clipped whereas the majority (59-96%) of buds that were 6 mm or longer were clipped. At intermediate bud lengths, females demonstrated a fairly precise response to even 1mm differences in bud length. Significantly more ($G=4.49$, $P<0.05$) females clipped 5mm buds compared to 4mm buds (0% vs. 23%, respectively); likewise, significantly more ($G = 7.38$, $P<0.01$)

females clipped 6 mm buds compared to 5mm buds (23% vs. 59%, respectively). A similar pattern was observed for Massachusetts females on blueberry buds (Table 3.3), with several exceptions. Here, 6% of the smallest buds (4mm) were clipped and the majority of females (69-85%) clipped buds that were 7 mm or longer. At the intermediate clipping levels, 5 and 6mm buds were clipped with equal frequency (22% and 33%, respectively; $G=0.98$, ns), but 7mm buds were clipped significantly more often than 6mm buds (69% vs. 33%; $G=11.77$, $P<0.001$). Finally, a very similar pattern of response, but again with differences in detail, was shown for Massachusetts origin females presented with cranberry buds (Table 3.4). Here, 6-7% of buds that were 6mm or smaller were not clipped but the majority of buds that were 8mm or longer were clipped (62-91%).

Discrimination Tests. The results of the choice tests in which uninfested and either infested or damaged buds were offered are summarized in Tables 3.5 and 3.6. On the blueberry bud (Table 3.5), females preferred uninfested buds over all infested or damaged buds with one exception. When given a choice of an uninfested or an infested blueberry bud with the oviposition plug unexposed, such that the plug should not have been detectable by the female, no discrimination was exhibited (Table 3.2). When oviposition plugs were fully exposed, females preferred uninfested flower buds significantly more often for oviposition, irrespective of whether the egg and plug were newly deposited ($\chi^2 = 10.93$, $df = 33$, $P < 0.001$) or had been deposited 24 h prior to the bioassay ($\chi^2 = 19.16$, $df = 23$, $P < 0.001$). Uninfested buds were also preferred more often than infested buds, even following removal of the oviposition plug ($\chi^2 = 11.57$, $df = 28$, $P < 0.001$). Uninfested buds were also preferred over buds that were damaged with a feeding cavity made by either a female ($\chi^2 = 6.55$, $df = 22$, $P < 0.01$), a male ($\chi^2 = 4.17$, $df = 24$, $P < 0.05$), or simulated with an insect pin ($\chi^2 = 5.00$, $df = 20$, $P < 0.05$).

Treatments done with cranberry buds are shown in Table 3.6. Similar to the blueberry bud bioassays, females rejected infested buds significantly more often than uninfested ones ($\chi^2 = 20.00$, $df = 20$, $P < 0.001$) and continued to do so if the oviposition plug was removed ($\chi^2 = 13.24$, $df = 17$, $P < 0.001$). They also rejected uninfested buds that had been damaged with a pin more often than intact buds ($\chi^2 = 7.12$, $df = 17$, $P < 0.01$). Numerically, females accepted uninfested buds more often than

infested buds when the oviposition plug was unexposed, but this difference was not significant ($\chi^2 = 2.67$, $df = 24$, $P > 0.05$).

Double Oviposition Survival Study. Survivorship was significantly higher ($G = 57.92$, $P < 0.001$) for eggs developing singly in buds as compared to those in buds with two eggs. Upon dissection of 53 flower buds with one egg, the following were tallied: 0 eggs, 10 larvae, and 43 adults. In very few instances did an adult complete development and emerge from a flower bud (Table 3.7). The pupal stage was never observed upon inspection of all 104 buds. Dissections of flower buds initially containing 2 eggs yielded 3 eggs, 28 larvae and 20 adults. For the buds with two eggs, in only 4 instances did we observe the presence of more than one CW/bud. In three cases, we saw an adult weevil and an egg together in the same bud and in the remaining case, we saw an adult weevil together with a larva. There were no instances of two adults together in the same bud.

Discussion

Oviposition by CW consisted of bud inspection, egg cavity formation, egg and plug deposition, and clipping of the pedicel. While the first three behaviors were observed without exception, the final behavior, pedicel clipping, was variable in both occurrence and duration. Clipping ranged from creation of a small chewed area on the pedicel to complete severing of the flower bud from the plant. Clipping behavior was significantly related to bud size. In all three experiments run where females provided buds of various sizes for oviposition, the majority of females clipped buds that were 8 mm or larger and did not clip buds that were 5mm or smaller. Because buds are still capable of blooming following feeding cavity creation (Mechaber 1992), CW clipping of large buds following egg deposition may insure that larval establishment can occur before bloom. LaCroix (1926) noted that the unopened bud provides a protective cell in which the larva can complete its development. As the larva feeds, the lobes of the corolla remain tightly closed and become dry and rigid. These studies indicate that there is no chance that small, undeveloped buds will bloom prior to larval establishment and thus, these buds were not clipped. Continued growth of small, unclipped buds may provide greater resources for larval development. The association of pedicel clipping with oviposition is

exhibited by two congeneric species, the strawberry blossom weevil, *Anthonomus rubi* Herbst (Cross and Burgess 1998) and the strawberry bud weevil, *Anthonomus signatus* Say (Khanizadeh et al. 1992, Clarke and Howitt 1975, Mailloux and Bostanian 1993).

The ability of a female to adjust her behavior (clipping of pedicel) based on bud size has not been reported in other *Anthonomus* species. However, assessment of host size has been reported a number of times for species whose larvae feed enclosed within spatially restricted hosts and where larval competition may be likely. For example, *Callosobruchus maculatus* (F.) females inspecting oviposition sites are able to select the largest beans from an array (Mitchell 1975) and *Trichogramma* spp. are known to adjust the number of eggs laid based on host size (Schmidt and Smith 1987). Schmidt and Smith (1987) studied the mechanisms underlying size discrimination in *Trichogramma minutum* Riley. They asserted that the parasitoid uses the absolute length of its initial examination walk, measured as the duration of the walk, over the surface of the egg to assess the egg's volume. This is a likely mechanism for *A. musculus* females as well. Prior to oviposition, they consistently moved up and down the flower bud during inspection.

These studies demonstrate that when more than a single egg is deposited within a host bud, competition was severe. In all instances where buds contained two eggs, only a single larva completed development. Avoidance of egg-occupied buds by CW females should be favored, and in fact, our results clearly showed that CW females assessed flower buds before oviposition. Weevils discriminated against buds that contained eggs, feeding cavities or holes made with an insect pin. These findings parallel those of McGovern et al. (1987) who reported supporting evidence indicating that *A. grandis* is able to discriminate against damaged oviposition sites. There was no evidence that the frass plug (deposited after egg laying) served as a host-marker that deterred additional oviposition. This finding is in contrast to McGovern et al.'s (1987) study that suggested that *A. grandis* used both physical and chemical signals to discriminate between acceptable and non-acceptable oviposition sites. However, they were unable to identify a specific female deterrent in the oviposition plug.

Unlike many other phytophagous insects, these studies provided no evidence that a host-marking pheromone is deposited over the bud surface following egg laying (Roitberg and Prokopy 1987). However, the results were not consistent owing to inadequacies of the experimental design. When infested blueberry buds were placed plug side down so that the site of egg deposition was not exposed, these buds were accepted as often as uninfested buds. Although not significant, infested cranberry buds handled in like fashion were rejected more often than uninfested buds. This may have occurred because cranberry flower buds did not always lie as flat on the bottom of the cup as did the blueberry flower buds, leaving the plug on the cranberry slightly exposed despite being face down. Further, the substantially smaller cranberry flower could have been manipulated by inspecting females resulting in the plug being detected.

As with most experiments we have uncovered more questions than we have answered. Why the cranberry, strawberry blossom and strawberry bud weevils exhibit clipping behavior still remains unknown. What is the adaptive significance for a cranberry weevil to clip larger flower buds while leaving smaller ones intact? How does a female CW measure a flower bud? Future investigators may wish to pursue these questions.

Table 3.1. Average duration (\pm SD) of activities involved in oviposition by cranberry weevil.

Behavior	Mean time (sec) \pm SD	Range (sec)
Bud inspection and acceptance	98 \pm 67	30-420
Bud inspection and rejection	50 \pm 30	14-88
Egg cavity formation	616 \pm 401	30-1650
Egg deposition	86 \pm 69	30-120
Clipping	466 \pm 320	120-1440

Table 3.2. On blueberry, percentages of different-size flower buds that were severed from the plant (clipped) following oviposition. Females originated from New Jersey blueberry.

Bud length (mm)	Percentage clipped	Total no. buds
3	0a	13
4	0a	11
5	23b	22
6	59c	32
7	69cd	48
8	85de	46
9	86de	44
10	84de	38
>11	96e	24

Values followed by a different letter are significantly different at $P < 0.05$ based on a G-test.

Table 3.3. On blueberry, percentage of different-size blossom buds that were severed from plant (clipped) following oviposition. Females originated from Massachusetts cranberry.

Bud length (mm)	Percentage clipped	Total no. buds
3	0a	11
4	6a	16
5	22b	27
6	33b	39
7	69c	52
8	75c	60
9	66c	41
10	84c	45
11	81c	53
12	85c	26

Values followed by a different letter are significantly different at $P < 0.05$ based on a G-test.

Table 3.4. On cranberry, percentage of different-size blossom buds that were severed from the plant (clipped) following oviposition. Females originated from Massachusetts cranberry.

Bud length (mm)	Percentage clipped	Total no. buds
<5	6a	16
6	7a	14
7	35b	26
8	62c	45
9	81d	52
10	84d	69
>11	91d	33

Values followed by a different letter are significantly different at $P < 0.05$ based on a G-test.

Table 3.5. Number of eggs laid by individual cranberry weevils in choice tests that contained uninfested blueberry flower buds and buds that were either infested or damage

Bud treatment	Number of eggs	χ^2	P-value
Uninfested Egg + oviposition plug (newly deposited)	26 7	10.93	P<0.001
Uninfested Egg + oviposition plug (24h after deposition)	22 1	19.16	P<0.001
Uninfested Egg + oviposition plug unexposed ^a	11 11	0.00	n.s.
Uninfested Egg + oviposition plug removed	23 5	11.57	P<0.001
Uninfested Feeding cavity made by female	17 5	6.55	P<0.01
Uninfested Feeding cavity made by male	17 5	4.17	P<0.05
Uninfested Punctured with pin	15 5	5.00	P<0.05

^aoviposition plug unexposed = excised bud placed on surface with plug facing down

Table 3.6. Number of eggs laid by individual cranberry weevils in choice tests that contained uninfested cranberry flower buds and buds that were either infested or damaged.

Bud treatment	Number of eggs	χ^2	P-value
Uninfested Egg + oviposition plug	20 0	20.00	P<0.001
Uninfested Egg + oviposition plug unexposed ^a	16 8	2.67	n.s
Uninfested Egg + oviposition plug removed	16 1	13.24	P<0.001
Uninfested Punctured with pin	14 3	7.12	P<0.01

^aoviposition plug unexposed = excised bud placed on surface with egg cavity and plug facing down

Table 3.7. Stage of development after 2 months in cranberry blossom buds that contained either one or two eggs.

Treatment (Number of buds)	Egg	Larva	Adult	Percent survivorship of eggs initially deposited ^a
	Number observed (%) ^b			
1 egg/bud (53)	0 (0)	10 (19)	43 (53)	100a
2 eggs/bud (47)	3 (3)	28 (30)	20 (21)	54b

^aValues followed by a different letter are significantly different at P < 0.001 based on a G-test.

^bFor buds with two eggs, there were three instances of an adult weevil and an egg recovered from the same bud, and in one instance, an adult and a larva recovered from the same bud.

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CHAPTER IV

COMPENSATORY RESPONSE OF CRANBERRY TO SIMULATED CRANBERRY WEEVIL (*Anthonomus musculus* Say) OVIPOSITION DAMAGE

Introduction

Herbivores that feed on flower buds, flowers, or fruit clearly could have a negative effect upon a plant's fitness. However, many species produce mature fruit from only a portion of their female flowers and regularly abort both flowers and immature fruits (Stephenson 1981). This occurs as a result of competition among flowers and fruit for limited resources on the plant.

Among several possibilities, one advantage of "surplus" flowers and fruit could be that partial destruction by herbivores could be tolerated, allowing the plant to recover from early season damage. While it is clear that a plant's compensatory response to herbivore damage varies, based on factors such as the timing, intensity, and frequency of injury (Trumble et al. 1993, Crawley 1997), some plants consistently compensate for damage, particularly in response to floral damage (McNaughton 1983, English-Loeb 1999, Hendrix 1979). Indeed, there has been discussion as to whether overcompensation in response to injury is an adaptation of plants (see Belsky 1986, Crawley 1997).

In this study, I simulated the damage of *Anthonomus musculus* (Say), commonly known as the cranberry weevil (CW) and looked at the compensatory responses of cranberry. Of the herbivores on cranberry (*Vaccinium macrocarpon* Aiton), *A. musculus* is a key insect attacking cranberry buds. Females deposit eggs inside the flower buds and, protected within the unopened bud, a single larva completes development. Following oviposition, the female typically completely severs the pedicel of the flower bud if the bud is large (>7 mm) but does not do so if the bud is small (< 7 mm) (see Chapter III). In the latter case, infested buds drop from the upright as the larva develops.

The cranberry plant produces recumbent woody runners that send out short vertical stems called uprights. Typically, each flowering upright produces 3-6 flowers from which 1-3 fruits mature (Bergman 1950, Filmer 1955). The sequence of flowering occurs from the basal to the terminal positions on an upright. Typically, the earliest flowers in the lowermost positions on the upright are pollinated first. The resulting fruit at the base of the upright become the main sinks for nutrients and suppress fruit development in the upper positions (Baumann and Eaton 1986).

Current threshold values utilized in CW management assume no compensatory response of the cranberry plant to CW oviposition damage (Brodel 1982). However, no work supports this assumption for the principal cultivars in Massachusetts, which are 'Early Blacks' and 'Howes.' In Wisconsin studies, utilizing the cultivar 'Searles,' experiments showed that when the lowest two flowers were removed, thus removing the most competitive sinks for an upright's resources, fruit set of flowers in the upper positions on the upright increased (Birrenkott and Stang 1990). However, for these same uprights, yield reductions were observed, suggesting that an incomplete level of compensation occurred under the experimental conditions. To gain a better understanding of the relationship between CW damage and yield, and ultimately to develop updated economic thresholds, I evaluated the level and pattern of weevil damage among uprights on two bogs that supported moderate to high levels of weevil activity. I simulated weevil oviposition damage in the field by clipping flower buds from some uprights and compared the resulting yield to uprights where no clipping was done. Two key factors that could influence compensatory response were studied: timing of clipping and intensity of clipping.

Methods

General. All work was carried out on commercial bogs in Wareham, MA. Clipping damage was simulated by cutting off buds with sharp scissors. In both experiments, I selected uprights with a standard number of buds/upright to control for variability in "vigor" among uprights (Filmer 1955, Patten and Wang 1994, Bergman 1950). Only lowermost buds were clipped. This pattern of damage mimics CW damage, based on a study carried out in our laboratory in which it was found that most of buds chosen for oviposition by CW are in the lowermost positions on the upright. Once uprights were collected for evaluation at harvest, they were stored at 4°C.

Pattern of Clipping Damage/Upright. In order to establish a baseline gauge of CW clipping intensity in the field, in 1999 and 2000, uprights were collected from a portion of an 'Early Black' bog that supported a relatively high infestation of adult CW, twice the level given as the current action threshold (Averill and Sylvia 1998). Ten random uprights were collected from each of 25 plots equally spaced in a 5 m x 5 m grid. Uprights from each plot were individually bagged. For each upright, the number of pedicels with berries (including aborted berries) and without berries (empty pedicels) was recorded. Percentage of pedicels with and without berries was calculated. Uprights were placed in the

category “heavy clipping” if the number of empty pedicels exceeded 33% of the upright’s total pedicels, and into “light clipping” if the percentage of clipped pedicels was less than 33%.

Timing of Clipping. To evaluate the impact of clipping at two points in the development of the upright, four transects were set up on four commercial bogs (sites A, B, C and D) of the cranberry cultivar ‘Howes.’ In each transect, each of 150 uprights bearing four developing flower buds was marked with tape and subjected to one of three treatments (1) the lowest two flower buds were clipped immediately following formation of all four flower buds on the upright (early clipping) (2) the lowest two flower buds were clipped ca. 10 days later, just before bloom (late clipping), or (3) no flowers buds were clipped (control). Treated uprights were collected at harvest and evaluated as to the number of berries per upright and the weight of each berry. Data were subjected to ANOVA followed by Duncan’s Multiple range test (SAS Institute, 1993).

Intensity of Clipping. In the above timing and intensity studies, to evaluate the effect of variation in the intensity of clipping per upright on yield, an approach similar to the one described above was used, with the following exceptions. Transects were set up on four different commercial bogs (sites E, F, G, and H) of the cultivar ‘Early Black’ and uprights that supported six flower buds were selected. Just prior to bloom, the following treatments were applied (1) the lowest two flower buds were clipped (light clipping) (2) the lowest four flower buds were clipped (severe clipping) or (3) no buds were clipped (control). At harvest, treated uprights were evaluated and data analyzed as above.

Fruit Set Response to Clipping. To evaluate how the clipping treatment of the lower buds affected fruit set for remaining flowers, the number of fruit/upright was divided by the total number of unclipped flower buds/upright.

Results

Pattern of Damage. Of the uprights sampled from a CW-infested bog in 1999, 25% bore at least a single clipped pedicel, with the remainder undamaged. Of the damaged uprights, 36% were lightly clipped (<33% of total pedicels/upright were clipped) and 64% were severely clipped (>33% of total pedicels/upright were clipped). In 2000, 62% bore at least a single clipped pedicel, and of these damaged uprights, 54% were lightly clipped and 46% were severely clipped.

Timing of Clipping. When data from all four sites were combined, there was a significant effect of clipping on both the number of fruit ($F=61.74$; $df=2$, 519; $P=0.0001$) and weight of berries ($F=49.63$; $df=2$, 519; $P=0.0001$) per upright. There were significant differences among sites for both the number of fruit ($F=15.81$; $df=3$, 519; $P=0.0001$) and weight of berries ($F=19.16$; $df=3$, 519; $P=0.0001$) per upright. There was a significant treatment effect on number of fruit per upright at site A ($F=5.19$; $df=2$, 116; $P=0.0070$), site B ($F=63.55$; $df=2$, 142; $P=0.0001$), site C ($F=5.58$; $df=2$, 129; $P=0.0047$), and site D ($F=18.26$, $df=2$, 132; $P=0.0001$). Weight of berries per upright differed within site A ($F=3.64$; $df=2$, 116; $P=0.0293$), site B ($F=47.05$; $df=2$, 142; $P=0.0001$), site C ($F=5.85$, $df=2$, 129; $P=0.0037$) and site D ($F=12.60$; $df=2$, 132; $P=0.0001$).

At sites A-C, there was no effect of timing when the two clipping treatments were compared: the number and total weight of berries per upright were not significantly different for the early clipping and late clipping treatments (Table 4.1). At site D, weight of fruit per upright was significantly different among all three treatments. Fruit weight was greatest for control uprights and the lowest for the early clipped uprights.

In general, clipping of 2 of the 4 buds from an upright, regardless of timing, resulted in a decrease in both number and weight of berries/upright. At all sites except A, berry weight per upright was significantly lower for the two clipping treatments when compared to the control uprights. For site A, mean weight of berries/upright in the early clipping treatment was the same as the control.

Intensity of Clipping. When data from all four sites were combined, there was a significant effect of intensity of clipping on both the number of fruit ($F=25.75$; $df=3$, 470; $P=0.0001$) and the weight of the berries ($F=22.13$; $df=3$, 470; $P=0.0001$) per upright. Also for combined data, light clipping and the control both differed significantly from severe clipping. Light clipping and the control were the same for both the number of fruit and weight of berries per upright.

There were significant differences among sites for both the number of fruit ($F=5.90$; $df=3$, 470; $P=0.0006$) and weight of berries ($F=3.61$; $df=3$, 470; $P=0.0134$) per upright. For individual sites, number of fruit per upright differed within site E ($F=7.27$; $df=2$, 97; $P=0.0012$), site F ($F=6.55$; $df=2$, 133; $P=0.0020$), site G ($F=13.07$; $df=2$, 106; $P=0.0001$), and site H ($F=4.11$, $df=2$, 134; $P=0.0186$).

Weight of berries per upright differed within site E ($F=7.41$; $df=2, 97$; $P=0.0010$), site F ($F=4.82$; $df=2, 133$; $P=0.0096$), site G ($F=10.40$, $df=2, 106$; $P=0.0001$) and site H ($F=4.58$; $df=2, 134$; $P=0.0119$).

For sites F, G and H, there was no significant effect of the light clipping treatment when compared to the control for both the number of fruit and weight of berries per upright. For these same three sites, the severe clipping treatment resulted in significantly fewer (18-48%) fruit and lower (26-45%) weight of berries per upright when compared to both of the other treatments. In contrast, at site E, there was no significant difference between the two clipping treatments. Both light and heavy clipping resulted in significantly fewer fruit and lower fruit weight per upright when compared to the control.

Fruit Set Response to Clipping. For 'Howes' uprights with four buds, when no clipping was done, the percentage of fruit set from total flowers/upright was an average of 55.1%; for uprights where the two lowermost buds were clipped, ca. 74.2% of the remaining flowers set fruit. For 'Early Black' uprights, when no clipping was done, 33.4% of the total flowers set fruit. Clipping of the two lowermost flowers resulted in 48.8% of the remaining flowers developing fruit and clipping of the four lowermost flowers resulted in 67.4% of the remaining flowers setting fruit.

Discussion

Crawley (1983) concluded that when plants are resource limited, there is great scope for compensation following the removal of sinks by herbivores. Further, he pointed out that the ability of the plant to compensate for herbivore damage to buds or fruits is often a function of the intensity of the attack as well as the timing of the attack.

Regarding cranberry recovery following attack of varying intensity, at 3 of the 4 'Early Black' sites, I observed complete compensation when 2 of 6 buds were clipped from uprights. However, when 4 of 6 buds were clipped, over all sites, there was an average decline of 33% (2.2 berries to 1.5 berries) in the number of fruits/upright. Similarly, in the timing study, on 'Howes' uprights originally bearing 4 buds, there was a decline of 35% (2.0 berries to 1.3 berries) in the number of berries/upright when 2 buds were clipped. The common observation for both cultivars was that on uprights where only the top two buds remain, typically only one flower set to produce a berry. In contrast, undamaged uprights, irrespective of original flower number, typically set two flowers and produce 2 berries in the basal

positions with a much smaller number of uprights bearing 0, 1 or 3 berries. (An exception to this trend occurred at Site F where the majority of uprights bore 3 fruits).

According to Stevenson (1981), it is typical for the proportion of pollinated flowers that set fruit to decrease as the numbers of pollinated flowers increase. When buds or newly opened flowers are artificially thinned from many orchard species, the percentage of pollinated flowers that initiate fruit increases in proportion to the intensity of the thinning (Stephenson 1981). In the intensity of damage study, given that 33% of buds set fruit on intact uprights bearing 6 buds, if the increase in proportion was congruent, then 50% should have set following light clipping and 100% following heavy clipping. In fact, the actual values were 33% (2/6), 50% (2/4) and 67% (1.3/2).

The above data suggest that uppermost buds on an upright are less likely to set fruit. Measurements done show a strong relationship between position on the upright and bud size: the higher a bud appears on an upright, the smaller it is (Averill, unpublished). On uprights bearing 6 buds, the most terminal bud was, on average, 50% smaller in length than the most basal buds and 25% smaller than mid-position buds. Perhaps this difference in size results in the uppermost flowers to be visited by pollinators less often, and thus, being less likely to set fruit in equal number or size compared with the lower flowers. This hypothesis is not supported by a study done by Birrenkott and Stang (1990) in which they removed the bottom two flower buds from uprights during the pre-blossom stage. They controlled for poor insect pollination by hand-pollinating both clipped and unclipped uprights. They still observed fewer fruits on the clipped upright and a significantly lower (20%) yield. Given that most of the uprights in their study initially bore >4 buds, if all flowers were equal in capacity to set fruit, then the clipped and unclipped uprights should have produced an equivalent yield.

A more likely explanation of low fruit set in the uppermost positions is that the smaller buds remaining in the terminal positions on clipped uprights probably are pollinated but produce a below average number of developing seeds. This is true for some other plants, for example, the black currant, *Ribes nigrum* (Stephenson 1981) where studies have shown that the lower seed number in terminal flowers results in an overall inability of the seeds to attract resources. This leads to ovule degeneration prior to fertilization, and ultimately abscission.

The cranberry weevil's pattern of oviposition damage typically results in a serious impact on the potential yield of an upright. First, within a bog, CW populations are exceedingly patchy. Adults are typically most abundant near wooded areas where they overwinter. This leads to more intense injury per upright in these concentrated areas of weevil, as evidenced in the pattern of damage study where I found that it was common for damaged uprights to have more than 33% of pedicels clipped. Further, within a single upright, there is a marked tendency of female CW to select the lowermost flower buds for egg laying (Averill, unpublished). If, on the other hand, CW oviposition damage was randomly distributed throughout a cranberry bed and females strongly preferred the "surplus" uppermost buds, a much higher population of weevils could be supported before any impact on yield was observed.

Such a case of "surplus" bud attack occurs in strawberry plants, where primary (largest) through quarternary (smallest) buds are produced. Here, the strawberry clipper (*Anthonomus signatus* Say) rarely clips primary buds in any given year (Kovach et al. 1999), instead preferring secondary or tertiary buds. English-Loeb et al. (1999) and Cross and Burgess (1998) showed that compensatory mechanisms following bud removal involved increase in fruit weight of remaining buds and increase in the number of higher order buds matured. In fact, damage to a limited number of tertiary and quarternary fruits in strawberry may be advantageous because the secondary and primary fruits will grow larger and more marketable. On the other hand, many tertiary and quarternary buds produce fruits that are unmarketable owing to their small size so their removal may actually be desirable (Pritts et al. 1999). Regarding variation among cultivars, most, but not all, showed some level of compensation to flower bud removal (Khanizadeh et al. 1992, Pritts et al. 1999, Cross and Burgess 1998).

Cultivar response may also vary among sites. Levels of compensation that will occur in any given system may be affected by interactions among available nutrients, water stress, and plant competition (Trumble et al. 1993). I observed variation among the 'Early Black' sites where uprights fully compensated for light clipping at three sites. However, at the fourth site, the number of fruit was significantly (24% less) lower than the control. In sum, for any plant system, care must be taken if one hopes to advance generalizations about compensatory responses.

Along with intensity of damage, another factor known to influence a plant's ability to compensate is timing of damage. In the case of *A. musculus* on cranberry, the sink attacked is always unopened buds and open flowers are not accepted for oviposition (Lacroix 1926). Thus, the timing of floral damage is always early in upright development. I showed that when the timing of bud clipping during the pre-blossom stage was varied, representing the interval of greatest CW activity in the field, there was no significant difference in berry production between the early clipping vs. late clipping treatment. Clipping was done as far apart temporally as possible, but in order to insure that each upright bore four flower buds, clipping treatments could only be done 10-11 days apart. However, based on work of Birrenkott and Stang (1990) using the 'Searles' cranberry cultivar, even if a greater interval had separated my clipping treatments, there may have been no differences observed. They clipped the two lowermost flowers not only at pre-blossom, but also even later in plant development (at late bloom) and saw no difference in yield between the two clipping treatments. On the other hand, among the clipping treatments, there was an effect if removal was delayed until the early fruit development stage. Here, the fruit production of uprights in the two earlier treatments (pre-blossom and late bloom) was significantly higher than for uprights where fruit had begun development. Thus, while there appears to be no difference in upright response to clipping in the pre-blossom and even into the bloom stage, once young fruit have set and these are clipped, the upright seems to have inadequate time to respond, perhaps being unable to remobilize carbohydrate.

Mechanical removal of plant parts may not adequately simulate herbivore damage, and thus normal compensatory reactions might not occur (Hendrix 1979, Hoffman et al. 2000). In my study, it is unknown if the female's saliva that is deposited during clipping of the pedicel may affect the cranberry plant's response, as has been shown in other plant systems for some insects as well as other animals (Belsky 1986). However, when reporting on simulated feeding damage on cucurbits, Hoffman et al. (2000) pointed out that simulated injury allows for accurate quantification of injury and thus, is a first step in characterizing yield loss.

An understanding of the link between yield loss and CW oviposition damage is key in any effort to update management recommendations. In strawberry, after a number of years of study, Pritts et al. (1999) suggested substantial elevation of strawberry clipper thresholds. They recommended

adjustments based on a given cultivar's rating for compensatory ability and counts of the total number and class (primary through quaternary) of buds/plant. On cranberry, a more substantial data base will be required to form such generalized recommendations. An important factor will be counts of the number of buds per upright, since averages on an 'Early Black' or 'Howes' bed could range from 3 to 6 bud/upright (DeMoranville, personal communication). The among-bed variation in compensation that I observed at 'Early Black' sites is problematic and suggests that our overall ability to predict the levels of compensation will be poor until the mechanisms responsible for such variation are elucidated.

Table 4.1. Yield of cranberry uprights (cultivar Howes), which originally bore 4 flower buds, where buds were not clipped, the 2 lowermost buds were clipped early in pre-blossom stage (early clipping), or the 2 lowermost buds were clipped late in pre-blossom stage (late clipping).

	<u>Treatment</u>	<u>Site A</u>	<u>Site B</u>	<u>Site C</u>	<u>Site D</u>
Number of fruit/upright	No clipping	1.84 \pm 0.78a	2.90 \pm 0.78a	1.85 \pm 1.13a	2.22 \pm 0.80a
	Early clipping	1.53 \pm 0.60b	1.71 \pm 0.46b	1.32 \pm 0.69b	1.36 \pm 0.69b
	Late clipping	1.34 \pm 0.65b	1.61 \pm 0.57b	1.30 \pm 0.76b	1.63 \pm 0.58b
Weight of berries(g)/upright	No clipping	1.91 \pm 0.82a	3.18 \pm 1.04a	1.95 \pm 1.32a	2.04 \pm 0.80a
	Early clipping	1.65 \pm 0.69ab	1.85 \pm 0.64b	1.36 \pm 0.84b	1.28 \pm 0.74b
	Late clipping	1.42 \pm 0.83b	1.71 \pm 0.71b	1.27 \pm 0.76b	1.59 \pm 0.61c

Within a measured parameter (number of berries or weight of berries), values followed by a different letter are significantly different based on Duncan's Multiple Range test at $p < 0.05$.

Table 4.2. Yield of cranberry uprights (cultivar 'Early Blacks'), which originally bore 6 buds, where buds were not clipped, 2 buds/upright were clipped (light clipping) or 4 buds/upright were clipped (severe clipping).

	<u>Treatment</u>	<u>Site E</u>	<u>Site F</u>	<u>Site G</u>	<u>Site H</u>
Number of fruit/upright	No clipping	2.34±1.39a	2.17±1.02a	2.02±1.01a	1.60±0.72a
	Light clipping	1.77±1.14b	2.17±0.82a	2.00±0.74a	1.74±0.79a
	Severe clipping	1.27±0.53b	1.60±0.59b	1.04±0.69b	1.31±0.64b
Weight of berries(g)/upright	No clipping	2.15±1.27a	1.85±0.91a	1.69±0.97a	1.51±0.71a
	Light clipping	1.51±1.04b	1.69±0.69a	1.88±0.60a	1.49±0.72a
	Severe clipping	1.18±0.54b	1.35±0.63b	0.98±0.69b	1.12±0.69b

Within a measured parameter (number of berries or weight of berries), values followed by a different letter are significantly different based on Duncan's Multiple Range test at $p < 0.05$.

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