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Teresa M. Cooper^a

^a Entomology and Nematology Department, University of Florida, Gainesville, FL, USA

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Seasonality and abundance of *Metamasius callizona* (Coleoptera: Dryophthoridae), an invasive insect herbivore, on two species of *Tillandsia* (Bromeliaceae) in Florida

Teresa M. Cooper*

Entomology and Nematology Department, University of Florida, Gainesville, FL, USA

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Seasonality and abundance of an insect herbivore population are regulated by a complex array of forces from the bottom up, from the top down, and from competition and the environment. This paper examines the effect that two host plants have on an insect herbivore in the absence of top-down regulation or competition. *Metamasius callizona* is an invasive bromeliad-eating weevil in south Florida that has escaped its natural parasitoid in its home range. A 4-year field study shows the weevil to be present and active year-round, but to exhibit different patterns of seasonality and abundance on two of its host plants. It is argued that this demographic variability is generated by the differences in leaf type and growth habit that exist between the two host plants.

Keywords: plant–herbivore interactions; demographic variability; *Metamasius callizona*; *Tillandsia fasciculata*; *Tillandsia utriculata*

Introduction

Seasonality and abundance of an insect herbivore population are regulated by a complex array of forces that come from the bottom up (host plant); the top down (predators and parasitoids); and from competition and environmental conditions (Bernays and Graham 1988; Janzen 1988; Wolda 1988; Hunter and Price 1992; Rosenheim et al. 1993). This paper examines the effect of two host plants on the seasonality and abundance of an insect herbivore in the absence of top-down pressures and competition, and under stable environmental conditions.

Metamasius callizona Chevrolat is a bromeliad-eating weevil restricted to eating plants in the family Bromeliaceae; the weevil's natural range is Mexico and Guatemala (Frank and Cave 2005). In 1989, the weevil was detected in Florida, already established on native bromeliad populations (Frank and Thomas 1994). In Florida, there are 16 native species of bromeliads and only one native bromeliad-eating weevil, *M. mosieri* Barber (Frank and Cave 2005). *Metamasius mosieri* is a small, non-aggressive herbivore with a more limited range than *M. callizona* (Cave et al. 2006). In this study, *M. mosieri* was not present. There is no top-down regulator for *M. mosieri* and its population is likely regulated by its host plants and by environmental needs (Frank and Cave 2005). In its native range, it is speculated that *M. callizona* populations are controlled by a specialist parasitoid; in the absence of this, or any other regulator, the *M. callizona* population has grown explosively in Florida and has caused great damage to native bromeliad populations.

*Email: tmcooper@ufl.edu

Of the 16 native species of bromeliads in Florida, 12 are susceptible to weevil attack, and 8 have been found infested in the field (Frank and Cave 2005). These 12 species range in the southern sub-tropical to tropical region of Florida's peninsula (Benzing 1980). These bromeliad species exist in a range of habitats and possess variable life history traits. Variability in host plants may cause variation in an insect herbivore's demographic patterns (McGavin and Brown 1986; Hunter and Price 1992; Novotný 1994; Underwood and Rausher 2000; Nogueira-de-Sá and Vasconcellos-Neto 2003; Rudgers and Whitney 2006).

The weevil is multivoltine and has an estimated mean generation time of 13–17 weeks (Frank and Thomas 1994; Salas and Frank 2001). All life stages of *M. callizona* live on the host bromeliad, which provides a stable microhabitat for the weevil until the plant is killed. The weevil adult consumes leaf tissue and is not fatal to the host plant; the larva, which mines the stem and meristematic tissue, kills the plant (Larson 2000). This sort of damage results in a characteristic death; the stem of the plant falls out, and the inside is a cavity filled with chewed plant tissue, sometimes containing weevil specimens or one to several empty pupal chambers.

Metamasius callizona is limited in host plant selection by the amount of biomass available; there must be enough plant material to rear at least a single weevil larva from egg to pupa (Frank and Thomas 1994; Larson 2000). The four species of native bromeliads in Florida that are not subjected to weevil attack are so because of their small size (they include *Tillandsia usneoides* L., *T. recurvata* L., *T. bartramii* Elliot, and *T. setacea* Swartz). The weevil has shown a preference for medium and large size-class bromeliads such as *T. fasciculata* Swartz and *T. utriculata* L. (Sidoti and Frank 2002; Cooper 2006). Several weevil specimens may be reared on a single, mature large-bodied bromeliad, with all life stages of the weevil coexisting simultaneously. Because bromeliad seedlings and juveniles have exceedingly high mortality compared with mature plants (Benzing 1980), *M. callizona* may prefer these larger bromeliads not just for the greater available biomass, but also because mature plants have greater stability.

Tillandsia fasciculata and *T. utriculata* are widespread, large-bodied bromeliads that have suffered high mortality caused by *M. callizona* (Frank and Cave 2005). Both are perennial evergreen monocots with an epiphytic habit (Benzing 1980; Isley 1987). The mature plants can hold water in the axils of their leaves; this, coupled with their large biomass, makes the plants resistant to changes in temperature and rainfall in a subtropical region (Benzing 1980). Aside from these similarities, *T. fasciculata* and *T. utriculata* are very different in their growth habits and, consequently, in their size, leaf type, and architecture (Isley 1987). *Tillandsia fasciculata* (Figure 1) is polycarpic, has tough leathery leaves, and when mature, is a giant clump of multiple vegetative offsets and is much larger than a mature *T. utriculata*. *Tillandsia utriculata* (Figure 2) is monocarpic (in Florida) (Isley 1987), has soft pliant leaves, and when mature, has a classic tank bromeliad shape that holds much more water than *T. fasciculata*. From seed, both species may take 10–20 years to put out their first inflorescence, which equals the life span of a mature *T. utriculata*; however, *T. fasciculata*'s polycarpic habit allows it to persist for several decades after its initial seed release (Benzing 1980).

Host plant seasonality is often a dominant force in determining insect herbivore seasonality (Wolda 1978; Denlinger 1980); the food source must be present in order for the herbivore to be present and active. In south Florida, as in many tropical

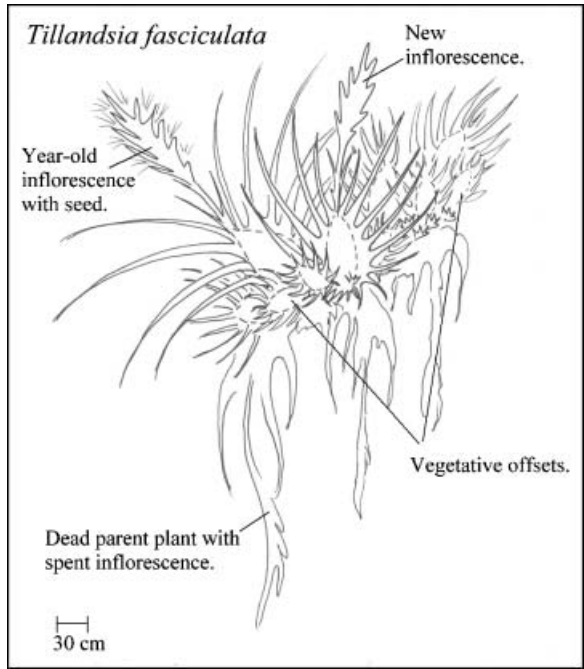


Figure 1. *Tillandsia fasciculata* is a polycarpic bromeliad with tough leaves.

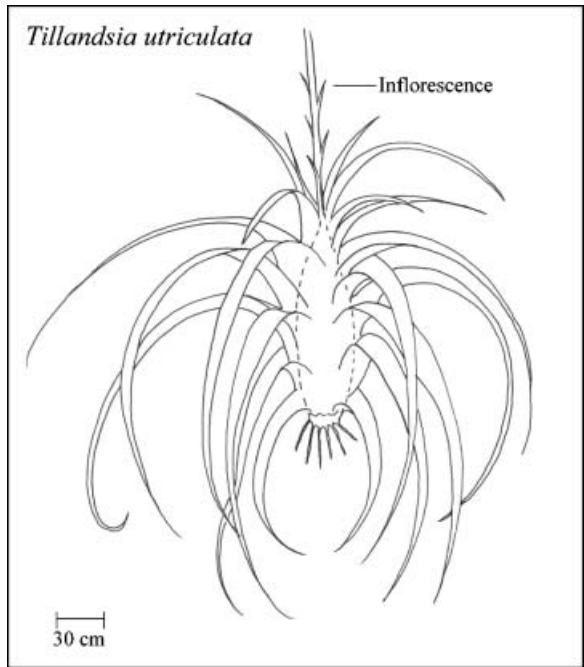


Figure 2. *Tillandsia utriculata* is a monocarpic, tank bromeliad with soft, pliant leaves.

regions, the seasons are defined by rainfall; the winters are cool and dry, the summers are hot and wet (Myers and Ewel 1990). The compact structure of mature *T. fasciculata* and *T. utriculata* plants, as well as their water-holding capacity, helps buffer them against variation in temperature and rainfall (Benzing 1980). However, the more defined tank architecture and greater water-holding capacity of *T. utriculata* may make it more resistant than *T. fasciculata* to environmental variation. One of the questions asked in approaching this study was, does *T. utriculata*, with its more defined tank architecture and greater water-holding capacity, resist environmental change more than *T. fasciculata*; and if so, does this translate to differences in seasonal patterns exhibited by *M. callizona*?

The available nutrition, presence and absence of secondary chemicals, and the degree of leaf toughness, affect the growth rate and, therefore, abundance of insect herbivore populations (Feeny 1970; Potter and Kimmerer 1986; Brunt et al. 2006). *Tillandsia fasciculata* is adapted to more exposed habitat than *T. utriculata*, and persists longer due to its vegetative growth habit. These differences in habitat and reproductive strategy are associated with different leaf types; exposed and persistent leaves are tougher than shaded, less persistent leaves (Coley and Barone 1996; McGavin and Brown 1986). *Tillandsia fasciculata*'s leaves are tough; *T. utriculata* has soft leaves. Tough leaves are associated with low nutrition and low digestibility and result in slower growth rates for insect herbivores (Feeny 1970; Rausher 1981; Potter and Kimmerer 1986; Damman 1987). Another question asked was: do the varying leaf qualities of these two host bromeliads translate to varying patterns of abundance in the *M. callizona* population?

Surveys in south Florida from 1989 to 2001 were made to monitor the expansion of *M. callizona*'s range and to collect weevil specimens for laboratory use (Frank and Thomas 1994; Frank 1996). Observations made during these surveys showed the weevil to be present in all life stages throughout the year. Weevils were also observed at higher numbers on *T. utriculata* compared with *T. fasciculata*, and *T. utriculata* populations often suffered near to total destruction, while *T. fasciculata* populations appeared to be more resistant. Based on these observations, as well as the life history of the host bromeliads, the differences in size, leaf type, and architecture of the two host bromeliads, and the cryptic nature of the weevil, the following predictions were made:

- (1) Mature *T. fasciculata* is more responsive to changes in temperature and rainfall than *T. utriculata*.
- (2) *Metamasius callizona* is aseasonal on both host species.
- (3) *Metamasius callizona* occurs at greater abundance on *T. utriculata* than on *T. fasciculata*.

These predictions were tested in Myakka River State Park (Sarasota County, Florida) from June 2001 to June 2005 on a population of weevil-infested bromeliads. Myakka River State Park (MRSP) is a natural area dominated by the Upper and Lower Myakka Lakes, which are connected by the Myakka River. The habitat includes hardwood hammock and swamp forest along the banks of the lakes and river, spanning out to wet prairie. The park floods once or twice per summer and has a pronounced dry season in the winter. Prairie sloughs support hardwood hammocks. The bromeliad population consisted of 72% *T. fasciculata* and 27% *T. utriculata*. Only large size-classes of these two species were considered in this study,

because the weevil has a preference for the larger size-class host plants; because these two species of host plants deviate most at maturity (they are more similar as juveniles); and because the mature plants could be easily and accurately identified from the ground when looking up in the canopy.

Materials and methods

A multi-tiered method was used to monitor bromeliad and weevil populations in Myakka River State Park, Sarasota County, Florida, beginning in June 2001 and ending in June 2005. Data were collected from demarcated Sections that were defined by bromeliad habitat and Bromeliad host density. Bromeliad hosts are the substrates upon which the bromeliads grow; usually a host was a tree, but some were vines or stumps, and a few of the bromeliads grew terrestrially. The tiers, by decreasing size, were called Natural area, Region, Area, Section and Bromeliad host. Table 1 lists and defines these tiers. For greater detail on mapping and monitoring see Cooper (2006).

Forty-eight Sections were mapped in hardwood forests, hammocks and mixed hardwood/palm forests using basic surveying equipment and skills. Total land area monitored in MRSP was 2.98 hectares. Data were collected from the weevil population (from fallen dead or near-dead bromeliads containing such specimens) and from the bromeliad population in MRSP that was susceptible to weevil attack. The bromeliad population was primarily composed of *T. fasciculata* (72%) and *T. utriculata* (27%); and, rarely, *T. balbisiana* Schultes (1%).

Table 1. Description and parameters for the five tiers used to define demarcated Sections and Bromeliad hosts.

Tier	Definition and parameters
I Natural areas	State and federal parks and refuges. Bromeliad-supporting habitat present.
II Region	Bromeliad-supporting habitat in the Natural areas. At least 10 Bromeliad hosts; no upper limit.
III Area	Regions were divided into Areas based on Bromeliad host density and local landmarks that defined the Area. Region must have one or more Areas; upper limit was defined by the habitat, or by limitations in resources and time.
IV Section	10–100 Bromeliad hosts per Area must be present at the initial mapping. 3–10 Bromeliad hosts per Section must be present at the initial mapping. Of these Sections, half (or half of the Sections +0.5, if there was an odd number of Sections) were randomly selected for monitoring for weevil specimens.
V Bromeliad host	Each Section contained 3–10 Bromeliad hosts; of these Bromeliad hosts, half (or half of the Bromeliad hosts +0.5, if there was an odd number of Sections) were randomly selected for monitoring. Bromeliad hosts were sketched from a particular direction and the bromeliads growing on the host were indicated on the sketch; these are the bromeliads that were monitored monthly. Updates to replace lost or dead bromeliads were made every 6 months.

From the bromeliad population: bromeliad health ratings

A portion of the bromeliad population was selected from each Section for monitoring. In order to maintain a constant population, bromeliads that were lost or that had died were replaced every 6 months, except for the final year in which no replacements were made. Each selected bromeliad was given a unique identification number and classified according to size based on longest leaf length: Small, ≤ 15 cm; medium, 15–60 cm; and large, >60 cm for *T. fasciculata* and *T. utriculata*; for *T. balbisiana*, small, ≤ 5 cm; medium, 5–15 cm; and large, >15 cm.

Monitoring was conducted monthly and consisted of assigning a “health rating” to the individual bromeliads. The health rating was based on assessment of outwardly observable physical characteristics, such as the colour and fullness of the leaves and physical injuries or signs of disease or infestation. Health ratings ranged from 3.0 (thriving and well; no injuries, discolouration, or dehydrated leaves) to 1.0 (completely dead; no green left remaining on the plant). The 3.0–1.0 range was divided into four quarters: 3.0–2.5 (healthy); 2.4–2.0 (moderately stressed); 1.9–1.5 (heavily stressed); and 1.4–1.0 (seriously stressed; almost always ending in death). Table 2 categorizes the health ratings.

Seven hundred and thirty-nine bromeliads were selected for monitoring. Two data sets from the large size-class sub-population (21% of the total population) were examined and are detailed in this paper: large *T. fasciculata* ($n=109$) and large *T. utriculata* ($n=41$).

Average health ratings were calculated for each month of the year for *T. fasciculata* and *T. utriculata* and plotted over the course of one year. Upper and

Table 2. Health rating chart describing the four quarters of the scale.

Quarter	Description
3.0–2.5 First quarter (healthy)	At 3.0, the bromeliad has good, strong green colour and no discolouration; no obvious injuries; and turgid leaves. As the health rating falls to 2.5, there may be a few injuries or minor discolouration, but nothing serious.
2.4–2.0 Second quarter (moderately stressed)	Outward stresses are more apparent; leaves chewed, moderate discolouration; slight desiccation or freeze trauma. If the stresses were removed, the plant would likely recover.
1.9–1.5 Third quarter (heavily stressed)	Heavy injury, major discolouration or browning of leaves covering up to half of the plant’s biomass; core leaves falling out; severe frost or drought damage. If the stress or injuries were removed, the plant might recover, but would suffer long-term consequences from the experience.
1.4–1.0 Fourth quarter (seriously stressed)	Very poor health; heavy injury and/or loss of leaves affecting more than half of the plant’s biomass; core missing; severe discolouration. Plant is likely to die. Death=1.0=no green tissue on plant.

lower boundaries (\pm two standard errors) were included for the calculated health ratings. The plots were examined for seasonal patterns. This same analysis was used to examine seasonal patterns in the average monthly rainfall (cm) and the average lowest temperature ($^{\circ}\text{C}$) for the Bradenton/Sarasota area during the same time period as the research (June 2001 to June 2005; collected by the National Weather Service 2005).

Cross-correlations were made for the bromeliad data sets with the average monthly rainfall and with the average lowest temperature. The number of lags was set at ± 17 using the calculation shown in Equation (1):

$$(\sqrt{n}) + 10$$

where n =length of the time series (49 months). The cross-correlation factor (CCF) was determined for each lag time. The hypothesis that the CCF for a given lag time is equal to zero (there is no correlation) was tested at $\alpha=0.05$ using the test statistic shown in Equation (2):

$$TS = 2 \div \sqrt{(n - |k|)}$$

where n =length of the time series and $|k|$ =the absolute value for each lag time. The null hypothesis was rejected for a given lag time if the CCF for that lag time was greater than its associated test statistic. For each analysis, the CCF with the greatest significant difference was tabulated with its corresponding lag time and test statistic.

From the weevil population: seasonal variation in weevil activity

Dead or near-dead bromeliads that had fallen within the demarcated Sections (fallout) were collected monthly and examined for cause of death. Fallout plants were deemed to be small, medium or large size-class based on longest leaf length (small, ≤ 15 cm; medium, 15–60 cm; and large, >60 cm); bulk of the fallen mass; and visible remains of the plant base in the canopy. Large size-class fallout were identified as *T. fasciculata* or *T. utriculata*. If weevil specimens or pupal chambers were present in fallout, the specimens were collected and itemized as adult, pupa, or larva, and as alive or dead. Larvae and pupae were reared to adulthood to confirm species identification.

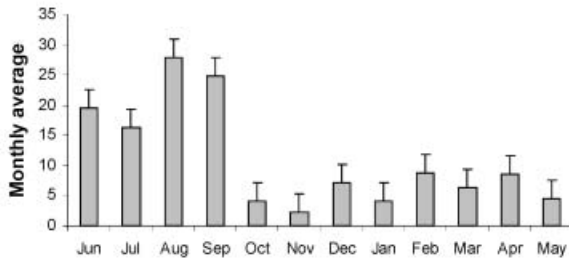
The average weevil count per fallout per month (\pm two standard errors) was calculated for large size-class *T. fasciculata* and *T. utriculata* fallout and plotted on a graph. The plots were examined for peaks indicating seasonal fluctuation in weevil abundance; and to compare average weevil abundance on *T. fasciculata* to *T. utriculata*. The weevil count included living weevil adults and living or dead weevil larvae or pupae.

Results

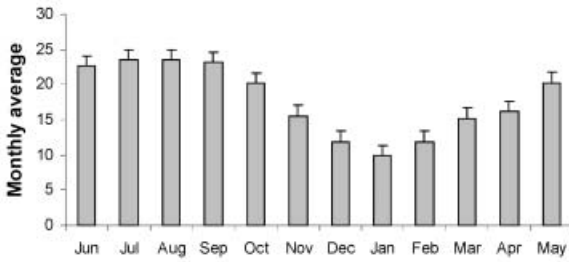
Rainfall and temperature

The average monthly rainfall (Figure 3A) had two distinct seasons: from June to September when rainfall was high; and October to May, when rainfall was low. Rainfall ranged from 0 to 45 cm and had an average of 12 cm and a median of 9 cm.

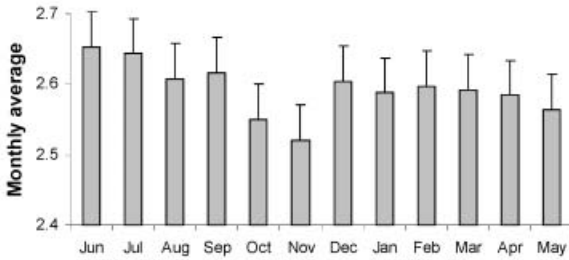
A Rainfall, cm



B Lowest temperature, C



C Health ratings, *T. fasciculata*



D Health ratings, *T. utriculata*

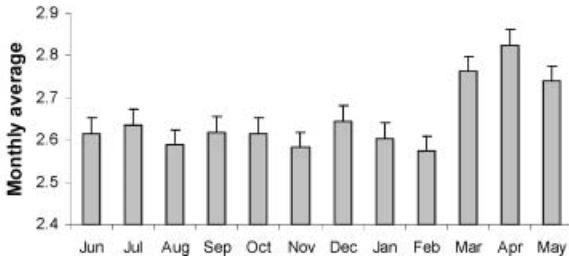


Figure 3. Average monthly values (\pm two standard errors) for: (A) rainfall (cm); (B) lowest temperature ($^{\circ}$ C); (C) health ratings for *Tillandsia fasciculata*; and (D) health ratings for *Tillandsia utriculata*.

The average lowest temperature (Figure 3B) fluctuated from high (June to September) to low (December to February) temperatures, and transited smoothly from one season to the next (October and November in the autumn and March, April and May in the spring). The range of temperatures was 6.7–24°C with an average of 18°C and a median of 19.5°C.

Bromeliad seasonality

Tillandsia fasciculata had a range of health ratings from 2.2 to 2.9; the average was 2.6 and the median 2.7. The average monthly health ratings showed a mild dip in October and November. The remaining months had similar health ratings (Figure 3C). Highest CCFs for *T. fasciculata* were higher than their associated test statistics (Table 3); therefore, the null hypothesis that the cross-correlation for the lag time is equal to zero was rejected (i.e. there is correlation). *Tillandsia fasciculata* has much higher CCFs for temperature than for rainfall. Lag times for rainfall and temperature are –1, indicating a response time that changes rapidly with the changes in temperature and rainfall.

Tillandsia utriculata had a range of health ratings from 2.4 to 2.9; the average was 2.6 and the median 2.7. The average monthly health ratings showed a relatively stable seasonal pattern from June to February and a peak in health ratings in March, April, and May (Figure 3D). *Tillandsia utriculata* showed little cross-correlation with rainfall or temperature; CCFs were only slightly higher than the associated test statistics and the lag times (–8 for rain and 3 for temperature) were unreasonable.

Large *T. utriculata* weevil infestations progressed rapidly and the first signs of infestation were usually dramatic, such as the centre falling out of the plant. Health ratings commonly dropped from healthy (3.0–2.5) to seriously stressed (1.4–1.0) from one monitoring trip to the next and an infested plant was usually dead within a few months. Large *T. fasciculata* clumps could support a weevil infestation for several years, during which the health ratings would gradually decline. Other insects, pathogens and diseases did not influence the health ratings. The decline in health ratings experienced by *T. fasciculata* in the winter months corresponded to signs of

Table 3. Cross-correlations for comparing the bromeliad data sets large size-class *T. fasciculata* and large size-class *T. utriculata* with the average monthly rainfall and the average lowest temperature.

	Average rainfall (cm)	Average lowest temperature (°C)
<i>T. fasciculata</i>		
Lag time	–1	–1
CCF	0.418	0.614
Test statistic (alpha=0.05)	0.289	0.289
<i>T. utriculata</i>		
Lag time	–8	3
CCF	0.374	0.332
Test statistic (alpha=0.05)	0.312	0.295

Note: CCF, cross-correlation factor.

temperature and drought stress. The increase in health ratings for *T. utriculata* in the spring months were associated with new leaf growth and increased size.

Weevil seasonality

In total, 652 fallen, dead or near-dead bromeliads were collected in the demarcated Sections; of these, 78% had been killed by the weevil and 22% had been killed by other causes (primarily falling from the canopy and rotting). Of the 78% fallout killed by the weevil, 36% ($n=179$) contained weevil specimens (living adult and living or dead pupa and larva; no eggs).

Most of the fallout containing weevil specimens consisted of large size-class bromeliads (115 out of 179; 64%); 102 were *T. fasciculata* and 13 were *T. utriculata*. Figure 4 shows the average weevil count per fallout per month (\pm two standard

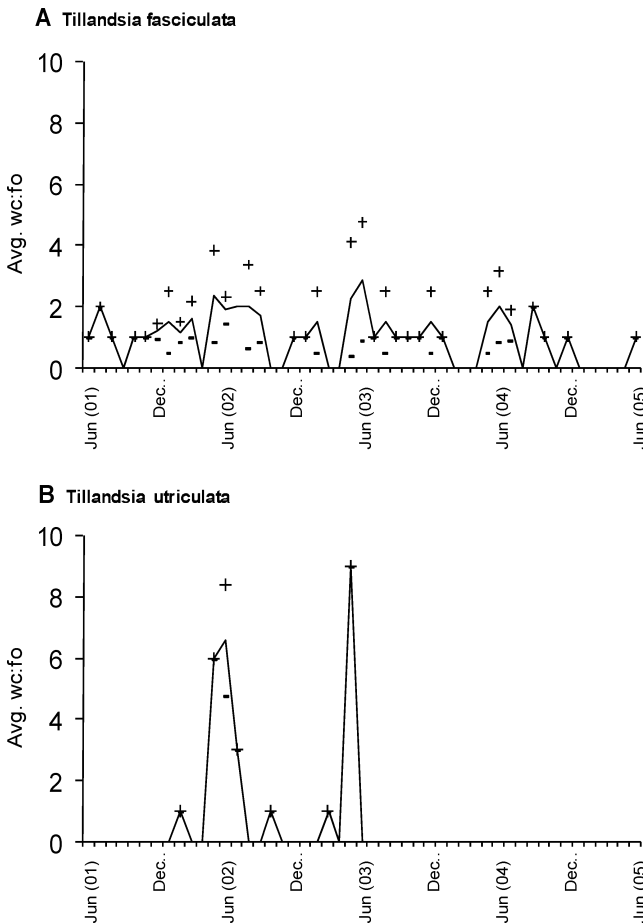


Figure 4. The average weevil count per fallout (wc:fo) per month (\pm two standard errors) for: (A) *T. fasciculata*; and (B) *T. utriculata* from June 2001 to June 2005. Note: The weevil count was the number of living weevil adults and living or dead weevil larvae and pupae found in fallout.

errors) for: (A) large size-class *T. fasciculata*; and (B) large size-class *T. utriculata* fallout.

Tillandsia fasciculata had consistent fallout and weevil specimens collected throughout the year. A total weevil count of 164 was recorded; the overall average weevil count per fallout was 1.6 (with two standard errors ranging from 1.8 to 1.4). The monthly average weevil counts per fallout had no outstanding peaks.

Weevil specimens from *T. utriculata* fallout were all collected in the first 2 years. A total weevil count of 69 was recorded; 67 of these were recorded in the months of May, June, and July. The average weevil count per fallout was 5.3 (with two standard errors ranging from 7.0 to 3.6). Monthly average weevil counts per fallout peaked in the months of May, June and July.

Discussion

In the absence of top-down regulation and competition, the forces that govern seasonality and abundance for the *M. callizona* population in south Florida arise from the bottom up and/or from the environment. Because the weevil lives in the protective microhabitat of its host bromeliads, its environmental conditions are dependent on the conditions created by the host plant. It was predicted that while *T. utriculata* would show less response to variations in temperature and rainfall than would *T. fasciculata*, both species would remain green and healthy throughout the year and therefore available as habitat and as a potential food source for the weevil year-round. This prediction was supported by the data (Figure 3 and Table 3).

The presence of the host plant, however, does not guarantee the availability of edible food for a herbivore (Wolda 1978). It was predicted that the weevil would be aseasonal on both host bromeliads, but the data show a spring peak of the weevil on *T. utriculata* (Figure 4). During this spring activity, *T. utriculata* supported a higher average number of weevils per host plant than did *T. fasciculata*. *Tillandsia fasciculata* supported low numbers of weevils consistently throughout the year, indicating an overall leaf quality with consistently low nutrition.

The seasonal variation exhibited by the weevil on *T. utriculata* likely reflects a change in the nutritional quality of the plant. The spring peak in the apparent health of the *T. utriculata* population did not correlate with changes in temperature and rainfall (Table 3); it did, however, coincide with the timing for reproductive activity. Cues that signal reproductive activity may also be used to cue new leaf growth. Why would *T. utriculata* have a growth spurt that begins 3 months before the onset of the rainy season? Water held by bromeliads not only provides buffering capacity against the environment, but also provides nutrition generated by ecosystems supported in the water (Butler 1974; Frank 1983; Frank et al. 2004). Richardson (1999) showed a positive correlation in the amount of organic matter, species richness and abundance with the plant size of a tank bromeliad. New growth would increase available area for impounding water; growth at the base of the leaves may strengthen and tighten the fit of the existing tank leaves. By initiating this growth before the rainy season, *T. utriculata* would maximize its ability to collect water.

The weevil, taking advantage of this new growth, peaks on this host plant in the spring, similar to the winter moth population peaking on new oak leaves in the spring (Feeny 1970). Unlike the winter moth, however, the weevil is multivoltine and, unfortunately, the mature *T. utriculata* population in MRSP was small ($n=41$; of which

only 13 contained weevil specimens), and was practically destroyed by the end of the second year (only four plants remained). Therefore, questions persist, such as what level of weevil infestation does *T. utriculata* support from August to May, the time outside of the observed growth period? Or, how significant is the seasonal peak of the weevil on *T. utriculata*? Research is continuing in a larger, weevil-infested population of *T. utriculata* in Brevard County, Florida in order to answer these questions.

Demographic patterns of insect herbivores may feed back and affect the host plant population (Brown et al. 1991; Hunter and Price 1992; Rudgers and Whitney 2006). The monocarpic habit of *T. utriculata* faced with the rapid growth rate of the weevils on its soft leaves result in rapid death of the individual plants as well as plant populations. The polycarpic habit of *T. fasciculata* and the slow growth rate of the weevil on this plant result in a slow infestation that requires 1 to a few years for the death of a large *T. fasciculata* clump. Many factors will determine host bromeliad response to the weevil attack in south Florida; one of them is the host bromeliad response to the weevil's herbivory patterns, as described by seasonality and abundance.

A potential biological control agent, a tachinid fly from Honduras, *Lixadmontia franki* Wood and Cave, was found on a related bromeliad-eating weevil, *M. quadrilineatus* Champion (Cave 1997; Frank and Cave 2005; Wood and Cave 2006). After several years of research and testing, the fly was recently released in four locations in south Florida. Successful establishment of the fly will re-establish the tri-trophic system of bromeliad–weevil–fly in this new range. As an agent of mortality, the fly will function as a force that influences the weevil's abundance, and potentially other demographics. However, this top-down force will act in coexistence with the bottom-up forces from the host bromeliads. Host plants are known to affect indirectly mortality and distribution of an herbivore by directly interacting with the parasitoid or predator (Hunter and Price 1992; Clark and Messina 1998; Rudgers and Whitney 2006); it is likely that the weevil population will suffer variable mortality rates depending on which host bromeliad it inhabits.

Traits adaptive to the harsh canopy environment (tank architecture and compact structure) make *T. fasciculata* and *T. utriculata* resistant to environmental changes; as such, *T. fasciculata* and *T. utriculata* provide *M. callizona* with a protected, year-round micro-habitat. The weevil is active year-round, but exhibits different patterns of seasonality and abundance on these two host plants. This demographic variability is generated by the differences in leaf type and growth habit that exist between the two host plants. The weevil's herbivorous activity affects the fitness of the host bromeliads by its preference for larger size-class plants, which results in increased mortality for the bromeliad reproductive class. In the absence of top-down regulation, the weevil has become invasive, thus magnifying the effect of the weevil's herbivory. Future studies will examine host bromeliad survivability in the presence of the weevil and changes in demographic patterns pending the establishment of the fly in the field.

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References

- Benzing DH. 1980. The biology of the bromeliads. Eureka (CA): Mad River Press. 305 p.
- Bernays E, Graham M. 1988. On the evolution of host specificity in phytophagous arthropods. *Ecology* 69(4):886–892.
- Brown VK, Lawton JH, Grubb PJ. 1991. Herbivory and the evolution of leaf size and shape (and discussion). *Philos Trans R Soc Lon.* 333(1267):265–272.
- Brunt C, Read J, Sanson GD. 2006. Changes in resource concentration and defence during leaf development in a tough-leaved (*Nothofagus moorei*) and soft-leaved (*Toona ciliata*) species. *Oecologia* 148(4):583–592.
- Butler J. 1974. Pineapples of the treetops. *Fla Nat.* 47:13–17.
- Cave RD. 1997. *Admontia* sp., a potential biological control agent of *Metamasius callizona*. *J Bromeliad Soc.* 47:244–249.
- Cave RD, Duetting PS, Creel OR, Branch CL. 2006. Biology of *Metamasius mosieri* (Coleoptera: Dryophthoridae) with a description of larval and pupal stages. *Ann Entomol Soc Am.* 99(6):1146–1153.
- Clark TL, Messina F. 1998. Plant architecture and the foraging success of ladybird beetles attacking the Russian wheat aphid. *Entomol Exp Appl.* 86(2):153–161.
- Coley PD, Barone JA. 1996. Herbivory and plant defenses in tropical forests. *Annu Rev Ecol Syst.* 27:305–335.
- Cooper TM. 2006. Ecological and demographic trends and patterns of *Metamasius callizona* (Chevrolat), an invasive bromeliad-eating weevil, and Florida's native bromeliads [Master's thesis]. [Gainesville (FL)]: University of Florida. 69 p.
- Damman H. 1987. Leaf quality and enemy avoidance by the larvae of a pyralid moth. *Ecology* 68(1):88–97.
- Denlinger DL. 1980. Seasonal and annual variation of insect abundance in the Nairobi National Park, Kenya. *Biotropica* 12(2):100–106.
- Feeny P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51(4):565–581.
- Frank JH. 1983. Bromeliad phytotelmata and their biota, especially mosquitoes. In: Frank JH, Lounibos LP, editors. *Phytotelmata: terrestrial plants as hosts for aquatic insect communities*. Medford (NJ): Plexus. p. 101–128.
- Frank JH. 1996. Bromeliad biota: biology of the weevil *Metamasius callizona* [online]. Gainesville (FL): University of Florida [cited 2007 Sep 1]. Available from: <http://BromeliadBiota.ifas.ufl.edu/wvbrom5.htm>.
- Frank JH, Cave RD. 2005. *Metamasius callizona* is destroying Florida's native bromeliads. In: Hoddle MS, editor. *USDA Forest Service publication FHTET-2005-08. Vol 1. Second International Symposium on Biological Control of Arthropods; 2005 Sep 12–16; Davos, Switzerland*. Washington D.C.: USDA Forest Service. p. 91–101.
- Frank JH, Sreenivasan S, Benschoff PJ, Deyrup MA, Edwards GB, Halbert SE, Hamon AB, Lowman MD, Mockford EL, Scheffrahn RH, et al. 2004. Invertebrate animals extracted from native *Tillandsia* (Bromeliales: Bromeliaceae) in Sarasota County, Florida. *Fla Entomol.* 87(2):176–185.
- Frank JH, Thomas MC. 1994. *Metamasius callizona* (Chevrolat) (Coleoptera: Curculionidae), an immigrant pest, destroys bromeliads in Florida. *Can Entomol.* 126(1):673–682.
- Hunter MD, Price PW. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73(3):724–732.
- Isley PT. 1987. *Tillandsia*, the world's most unusual air plants. Gardena (CA): Botanical Press. 256 p.
- Janzen DH. 1988. On the broadening of insect-plant research. *Ecology* 69(4):905.
- Larson BC. 2000. Save Florida's native bromeliads: damage caused by the Mexican bromeliad weevil [online] [cited 2007 Sep 1]. Gainesville (FL): University of Florida. Available from: <http://savebromeliads.ifas.ufl.edu/damage.htm>.

- McGavin GC, Brown VK. 1986. Variation in populations of mine- and gall-forming Diptera and the growth form of their host plant, bracken (*Pteridium aquilinum* (L.) Kuhn). *J Nat Hist.* 20(4):799–816.
- Myers RL, Ewel JJ. 1990. *Ecosystems of Florida*. Orlando (FL): University Press of Florida. 765 p.
- National Weather Service. 2005. National Weather Service, southern region headquarters: climate – past weather [online] [cited 2006 June 1]. Fort Worth (TX): National Weather Service. Available from: <http://www.srh.noaa.gov/tbw/html/tbw/climate/climatemain.htm>.
- Nogueira-de-Sá F, Vasconcellos-Neto J. 2003. Host plant utilization and population abundance of three tropical species of Cassidinae (Coleoptera: Chrysomelidae). *J Nat Hist.* 37(6):681–696.
- Novotný V. 1994. Association of polyphagy in leafhoppers (Auchenorrhyncha, Hemiptera) with unpredictable environments. *Oikos* 70(2):223–232.
- Potter DA, Kimmerer TW. 1986. Seasonal allocation of defense investment in *Ilex opaca* Aiton and constraints on a specialist leafminer. *Oecologia* 69(2):217–224.
- Rausher MD. 1981. Host plant selection by *Battus philenor* butterflies: the roles of predation, nutrition, and plant chemistry. *Ecological Monographs* 51(1):1–20.
- Richardson BA. 1999. The bromeliad microcosm and the assessment of faunal diversity in a neotropical forest. *Biotropica* 31(2):321–336.
- Rosenheim JA, Wilhoit LR, Armer CA. 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* 96(3):439–449.
- Rudgers JA, Whitney KD. 2006. Interactions between herbivores and a plant architectural dimorphism. *J Ecol.* 94(6):1249–1260.
- Salas J, Frank JH. 2001. Development of *Metamasius callizona* (Coleoptera: Curculionidae) on pineapple stems. *Fla Entomol.* 84(1):123–126.
- Sidoti BJ, Frank JH. 2002. The effect of size of host plant (*Tillandsia utriculata*: Bromeliaceae) on development of *Metamasius callizona* (Dryophthoridae). *Selbyana* 23(2):220–223.
- Underwood N, Rausher MD. 2000. The effects of host-plant genotype on herbivore population dynamics. *Ecology* 81(6):1565–1576.
- Wolda H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. *J Anim Ecol.* 47(2):369–381.
- Wolda H. 1988. Insect seasonality: why? *Annu Rev Ecol Syst.* 19:1–18.
- Wood DM, Cave RD. 2006. Description of a new genus and species of weevil parasitoid from Honduras (Diptera: Tachinidae). *Fla Entomol.* 89(2):239–244.