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Leaf abscission phenology of a scrub oak: consequences for growth and survivorship of a leaf mining beetle

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Abstract *Brachys tessellatus* is a leaf-mining beetle that attacks *Quercus laevis* (turkey oak), a deciduous scrub oak in the fall line Sandhills of the southeastern United States. This oak species varies substantially in leaf abscission phenology. In the fall of 1994 we examined leaf abscission patterns at three sites in central South Carolina and found that leaves containing active miners abscised earlier than leaves without active miners. To quantify the effect of leaf abscission phenology on the survivorship and body size of leaf miners within the abscised leaves, we marked naturally and manually abscised leaves, left leaves on the ground to over-winter, and then collected leaves before beetles emerged the following spring. We found that beetles inside leaves that were abscised early in the season were more likely to be killed by predators, and that they produced smaller pupae than beetles within leaves abscised later in the season. We also evaluated the relationship between adult beetle body size and fecundity; body size of *B. tessellatus* is positively correlated with lifetime fecundity and daily oviposition rate indicating that effects of leaf-abscission phenology on beetle body size likely translate into effects on beetle fitness. We discuss how *B. tessellatus* has adapted to variation of leaf abscission phenology of oaks by evolving developmental plasticity that permits successful completion of larval development over a range of season lengths.

Keywords Early leaf abscission · Leaf mining beetle · Variation · Phenology · Body size

Introduction

Most organisms encounter seasonal environments (Tauber et al. 1986). In the tropics, seasonality is characterized by wet and dry periods, while in the temperate regions seasonality is characterized more by fluctuating temperature (Roff 1983). For many species, only one season is favorable for growth and reproduction and the length of that growing season can influence key life history traits such as development time and body size (Roff 1980; Fairbairn 1984; Nylin and Svärd 1991) both of which are important components of individual fitness (Fairbairn 1984). Variation in development time and body size is often associated with macrogeographic variation in season length, latitude or altitude (Park 1949; Roff 1980; Mousseau and Roff 1989; Nylin and Svärd 1991; Nylin 1992; Ayres and Scriber 1994; Blanckenhorn 1997). Few studies have examined variation in season length at microgeographic scales (Fairbairn 1984; Blanckenhorn 1991).

In many seasonal environments, plants abscise their leaves during or before periods of stress. For leaf-feeding insects, especially those that are unable to move among leaves (e.g., leaf miners, gallers), the time at which leaves are abscised results in an end to the growing season and can affect life history traits such as development time and body size (Connor and Taverner 1997) and alter ecological factors such as exposure to predators and parasitoids (Kahn and Cornell 1983). The date of leaf abscission can be highly variable among individual plants within a population and among leaves within a plant (Williams and Whitham 1986; Stiling et al. 1987; Mopper and Simberloff 1995). This effectively results in season length variation within the population of insects associated with those trees and potentially accounts for much of the phenotypic variation in body size and development time among individual insects within that population.

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Variation in degree of herbivory may be one cause of variation in leaf abscission phenology within plant populations. Leaf-feeding insects often stimulate physiological processes that lead to early leaf abscission (Addicott 1982; Risley and Crossley 1988; Risley 1993). This early leaf abscission then shortens the growing season for the insect herbivores and can increase mortality of insects that are confined to a single leaf (Owen 1978; Faeth et al. 1981). Several field studies have demonstrated that insect populations in which feeding and larval development are interrupted by early leaf abscission suffer correspondingly increased levels of mortality (Williams and Whitham 1986; Simberloff and Stiling 1987; Stiling et al. 1987; Auerbach and Simberloff 1989; Preszler and Price 1993; Connor et al. 1994; Mopper and Simberloff 1995). Conversely, when early leaf abscission does not occur until insects have completed or nearly completed feeding and larval development, it does not increase mortality (Hilemann and Lieto 1981; Pritchard and James 1984; Stiling and Simberloff 1989). Early leaf abscission can also influence herbivore mortality via effects on exposure to predators and parasitoids. When leaves remain on trees for an extended period of time the herbivores inside those leaves may suffer extended exposure to parasitoids and aerial foraging predators (Kahn and Cornell 1983). Conversely, when leaves are dropped early herbivores may experience greater exposure to ground-feeding predators such as ants and carabid beetles.

In this paper, we examine the influence of leaf miner herbivory on leaf abscission phenology of a common scrub oak (turkey oak; *Quercus laevis* Walt.), and examine the consequences of this variation in leaf abscission phenology for survivorship and growth of the leaf mining beetle *Brachys tessellatus* (Coleoptera: Buprestidae). Turkey oak is a deciduous species that drops most of its leaves at the end of the growing season, thereby determining the end of the beetle's growing season. However, leaf abscission is spread out across nearly three months, resulting in substantial variation in the length of the beetle's growing season. We thus test the hypotheses that: (1) herbivory by *B. tessellatus* results in early leaf abscission; (2) early leaf abscission increases beetle overwintering mortality and (3) results in smaller beetle size; and (4) *B. tessellatus* body size influences adult fitness traits, including lifespan, total fecundity, and egg-laying rate.

Materials and methods

Study organisms

Brachys tessellatus is one of eleven North American species in this genus of leaf mining beetles. *B. tessellatus* is univoltine (Turnbow and Franklin 1981). Adults emerge in mid-March to mid-April, coinciding with budburst of its primary host, turkey oak (*Quercus laevis*; Fox et al. 1997). Adults initially feed on the early leaves and flowers, often reducing the total leaf area of the tree by more than 15% within the first few weeks following bud-

burst. Adults continue foliar feeding through the spring and summer. Mating and oviposition begin in April when the oak leaves are fully expanded and continue through July into early August. Eggs are deposited singly on the upper surface of the leaves and hatch within 2 weeks of oviposition. Larvae mine into the mesophyll below the egg. They feed and develop through five instars during which they can blotch mine more than 60% of a given leaf. Pupation and over-wintering occur within the leaves after they have senesced and abscised from the tree (pupation starts between October and December). The new adults emerge from the leaf litter the following spring (Waddell and Mousseau 1996) in mid-March to mid-April, coinciding with budburst of turkey oak.

Turkey oak grows as an adventitious hardwood and is one of the dominant species, along with longleaf pine (*Pinus palustris*) and wiregrass (*Aristida stricta*), that defines the open savannah-woodland ecosystem of the southeastern United States (Berg and Hamrick 1993). Turkey oak is a deciduous, wind-pollinated scrub oak that grows in poor, sandy soils. These soils and trees are found throughout the fall-line sandhills that form a 50-km-wide belt that runs from Sanford, North Carolina through Columbia, South Carolina and Macon, Georgia to Montgomery, Alabama (Weaver 1969). As a species, it dominates the more open and xeric ridges and bluffs, but also occurs as an understory species with pines in the more mesic habitats. It exhibits a low tolerance for shade and is found more frequently in open sun (Weaver 1969; Turnbow and Franklin 1981). Like other oak species (Ahlgren 1957; Lechowicz 1984; Crawley and Ahkteruzzaman 1988; Hunter 1992; Connor et al. 1994), individual turkey oak trees vary substantially in their timing of budburst. This variation in budburst phenology affects the distribution of adult *B. tessellatus* before oviposition but does not affect the distribution of eggs (Fox et al. 1997); eggs of *B. tessellatus* are laid on oak leaves throughout the spring and summer, after leaves have fully expanded. Thus, mine initiation and larval development are temporally protracted such that a large portion of the beetle population has not completed development prior to leaf abscission.

Study sites

In September 1994, we selected three forested sites in the fall-line Sandhills of northeast Richland County, South Carolina. Two of the sites were located in Sesquicentennial State Park, a suburban park 16 km northeast of Columbia, South Carolina. Both sites are part of a continuous stand of oaks and sparsely distributed pines (*P. palustris*) on a south-facing slope (2–8% grade). There is no evidence of tree cutting or other disturbances and, as a state park, the forest has been in protected status for over 60 years. The upper site ("Sesqui-high") is approximately 1,000 m north of the lower site ("Sesqui-low") and differs primarily in altitude (20–40 m difference) and in tree phenology, with the upper site breaking bud 10–14 days earlier than the lower site (Fox et al. 1997). The third site ("Clemson") is 6 km east of the Sesqui sites and is located in Clemson University's Sandhill Research and Education Center. This site is relatively flat and the oaks' phenology is similar to that of the Sesqui-low site. Although the site appears to be free of any recent disturbance, it lies adjacent to an abandoned orchard and meadow.

Patterns of leaf abscission for turkey oak

Our first objective was to examine the patterns of leaf abscission of mined and unmined leaves. Within each site a 15×15 m quadrat was established wherein leaf abscission patterns for the oaks were surveyed weekly. Oak densities (of trees >1 m in height) varied among the quadrats. The Sesqui-high quadrat had 52 trees, while the Sesqui-low quadrat had 96 trees, with the majority of trees less than 3 m in height in both quadrats. The Clemson quadrat had 85 trees with the majority of trees less than 3.5 m in height. In all three quadrats, adult trees (taller than 2 m) were randomly spaced, indicating that no substantial burning of the sites had occurred for many years (Berg and Hamrick 1993).

Beginning on 24 September 1994, all abscised leaves found inside the quadrats were collected, counted, and marked. All leaves that contained a living larva were labeled at the petioles with color-coded tape that indicated the week of abscission. For simplicity, we refer to leaves that contained a living larva at the time of sampling as "successfully mined" leaves. Other leaves may have been partially mined, but larvae either did not survive until leaf abscission or died quickly after abscission (between the day of abscission and the day on which they were counted, a period of <7 days). For simplicity, we refer to these as "other" leaves. All other leaves were marked (hole-punched) with hand held paper punches so that they would not be counted in subsequent surveys. Once marked, all leaves were returned to the ground. We surveyed plots for new leaves once every week for 11 weeks (Sesqui sites) or 10 weeks (Clemson). The leaves remaining on the trees were then counted and treated as having abscised on week 11+ (Sesqui) or 10+ (Clemson), and we terminated our weekly surveys. By the end of the census period more than 90% of all successfully mined leaves had been abscised (90.1% at Clemson, 92.8% at Sesqui-high, and 95.2% at Sesqui-low) and more than 50% of all leaves (successfully mined + other) had been abscised. In total, we marked 150,175 leaves on the ground inside the three quadrats (excluding the leaves counted on the trees), 5,447 (3.6%) of which were successfully mined.

Consequences of leaf abscission phenology for *B. tessellatus* survivorship and growth

After larvae had pupated, but before they emerged from their mines, the labeled leaves were collected from the field and brought into the laboratory (collections were made throughout February 1995). Of the 5,447 successfully mined (and labeled) leaves that had naturally abscised and the 2,300 successfully mined leaves that were manually abscised, 92% were recovered. Leaves were dissected and examined for the presence and condition of the pupae. Leaves that were torn open and/or the beetle was missing; leaves that showed evidence of parasitoid attack, i.e., mines with emergence holes, pupal exuviae of parasitoids, or larvae or pupae with "characteristic imploded morphology of host feeding" by parasitoids (Connor 1991), were categorized as preyed upon. Leaves where the larvae or pupae were killed by an undetermined factor were categorized as dead from other causes, which could include early leaf abscission-mediated death, hypersensitive responses of host plant, parasitoid stinging without oviposition, and winter/climate mediated death (Connor et al. 1994). Surviving pupae from the collected leaves were removed from leaves and individually weighed (in late February; we measured wet mass). Mean pupal mass was calculated for each of the weekly cohorts at all three sites.

Our survey of natural abscission patterns was expected to reveal a correlation between abscission phenology and parameters of beetle success such as survivorship and pupal mass. To test for a causal relationship between leaf abscission and parameters of beetle success we manually removed leaves containing living larvae from randomly selected trees adjacent to each quadrat. At both of the Sesqui sites (outside the quadrats) 100 leaves were "manually abscised" each week and labeled with color-coded tape. Due to the low mine densities at the Clemson site, only 50 leaves were manually abscised per week. All leaves were dropped to the ground within a couple hours of being abscised. This was repeated weekly until leaves on the trees had senesced to the point where the beetles were no longer feeding inside their mines (week 7 at the Sesqui-high site, week 8 for the Sesqui-low and Clemson sites). In total, 2,300 leaves were manually abscised.

Relationship of body mass to fecundity in *B. tessellatus*

In the spring of 1995, shortly after adult emergence and before any observation of mating or oviposition, 250 female beetles were collected from the three sites, weighed, and then paired with males. One hundred pairs were set up in a laboratory-based census of

lifetime fecundity. Each pair was placed into a plastic cage with one excised turkey oak leaf (with its stem inserted in a cotton-stoppered water bottle) as an oviposition substrate. Cages were placed in environmental chambers in our laboratory at USC and maintained at 32°C, 14 h light and 28°C, 10 h dark per day. Leaves were removed and replaced every 48 h. Because adult *B. tessellatus* are foliar feeders on turkey oak, leaves were occasionally replaced sooner if feeding damage exceeded levels observed in the field at that time. Removed leaves were examined for eggs.

The remaining 150 pairs of beetles were caged on leaves in the field (at the Clemson field site). Each pair of beetles was placed in a fine mesh bag and attached to small clusters of oak leaves (one or two clusters of four to six leaves) on haphazardly selected oaks. Beetles were rotated among the trees every 48 h, and leaves were examined for eggs. Beetle pairs were used continuously until the female died. Males were replaced if they died before the female. In the data analysis, three variables were examined for their relationship with body mass: lifespan, total number of eggs deposited, and the rate of eggs deposited per day. A regression analysis was used to examine the effect of body mass on lifespan, lifetime fecundity, and daily oviposition rate for both laboratory and field populations.

Statistical analysis

A contingency table analysis was used to test whether the timing of leaf abscission was independent of their condition (successfully mined or not). Because data for over-winter survival of the beetles were binomially distributed we used a non-parametric analysis of variance to test for variation among abscission dates. However, a non-parametric analysis of variance only tests for variation among classes and not directionality of an effect. To quantify effect direction we used a linear regression to examine the relationship between leaf abscission date and mean beetle over-winter survival. This analysis provides an estimate of r , but we did not use the analysis for statistical hypothesis testing. To test for effects of leaf abscission phenology on pupal mass, we used an analysis of covariance with date of leaf abscission as a covariate (using SAS Proc GLM; SAS 1996).

Results

Patterns of leaf abscission for turkey oak

At all three sites, successfully mined leaves (those containing a living larva) abscised earlier than leaves that were not successfully mined (Fig. 1; Clemson: $\chi^2=1268$, $df=9$, $P<0.0001$; Sesqui-low: $\chi^2=1327$, $df=9$, $P<0.0001$; Sesqui-high: $\chi^2=2936$, $df=9$, $P<0.0001$). At the two Sesqui sites (Fig. 1A,B), abscission of successfully mined leaves peaked in week 7, 3 weeks earlier than the peak for other leaves at these sites. The abscission of successfully mined leaves peaked in week 6 at the Clemson site (Fig. 1C), 4 weeks earlier than the annual peak for abscission of other leaves at that site.

Consequences of leaf abscission phenology for *B. tessellatus* survivorship and growth

Over-winter survivorship averaged (across study sites) 37% for beetles in naturally abscised leaves and 45% for beetles in manually abscised leaves (not significantly different between the two types of abscission). Over-

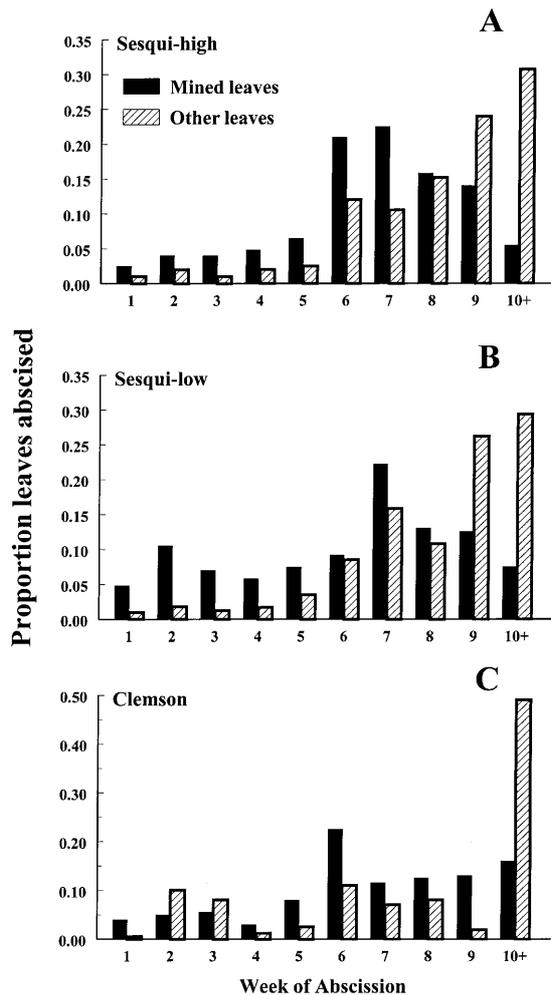


Fig. 1 The phenology of leaf abscission for turkey oak (*Quercus laevis*) leaves that contain living *Brachys tessellatus* larvae (successfully mined) versus those not containing living larvae (other leaves) over 10 weeks at three sites in South Carolina

winter survivorship of beetles varied among study plots for both the natural and manual leaf abscission treatments (non-parametric analysis of variance, $P < 0.001$ for both) but the pattern was inconsistent between the two treatments; Sesqui-low had the lowest mean over-winter survivorship ($0.31 \pm \text{SEM } 0.01$) and Sesqui-high the highest (0.41 ± 0.01) for beetles in naturally abscised leaves, while Sesqui-high had the lowest mean over-winter survivorship (0.36 ± 0.02) and Clemson the highest (0.53 ± 0.03) for beetles in manually abscised leaves. The timing of natural leaf abscission (week of abscission) had a significant effect on beetle over-winter survivorship at both Sesqui sites (non-parametric analysis of variance, $P < 0.002$ for both Sesqui sites); beetles in leaves that abscised later were more likely to survive over-winter ($r = 0.53$ and 0.33 for Sesqui-high and low, respectively; Fig. 2A,B). There was no detectable effect of leaf abscission phenology on beetle survivorship at the Clemson site ($r < 0.01$; non-parametric analysis of

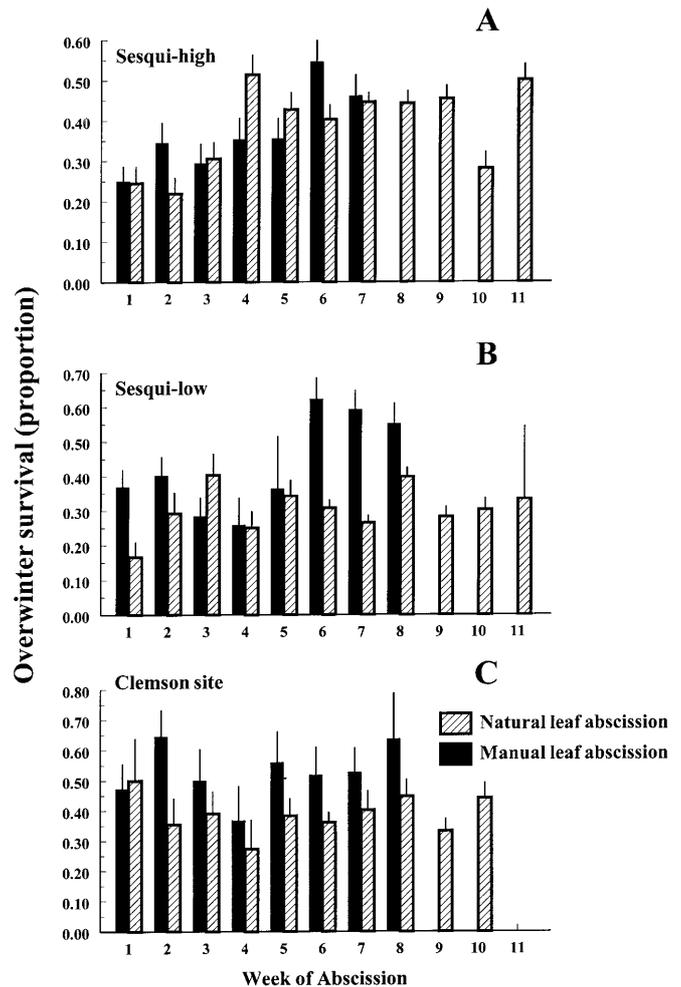


Fig. 2 The relationship between week of turkey oak (*Quercus laevis*) leaf abscission and over-winter survival of *Brachys tessellatus* inside the leaves. The manual leaf abscission experiment was only conducted through week 7 at the Sesqui-high site and week 8 for the Sesqui-low and Clemson sites

variance, $P > 0.7$) (Fig. 2C). The patterns observed for the manual leaf abscission experiment were similar; beetles survived better when in leaves that abscised later at both Sesqui sites ($r = 0.84$ and 0.69 for Sesqui-high and low, respectively; non-parametric analysis of variance, $P < 0.0005$ for both sites) but not at the Clemson site ($r = 0.26$; non-parametric analysis of variance, $P > 0.6$).

Most of the over-winter mortality of beetles was due to natural enemies (Fig. 3). *n* average, $42 \pm 3\%$ (natural abscission) or $46 \pm 8\%$ (manual abscission) of all over-wintering beetles were killed by a predator or parasitoid. Predation was higher at the two Sesqui sites (40% and 47% for the manual abscission treatment at the Sesqui-low and Sesqui-high sites, respectively; 58% and 48% for the natural abscission treatments) than at the Clemson site (39% and 32% for manual and natural abscission treatments, respectively), even though fire ants (*Solenopsis invicta*) are much more abundant at the Clemson site (Waddell, Fox, and Mousseau; personal observations).

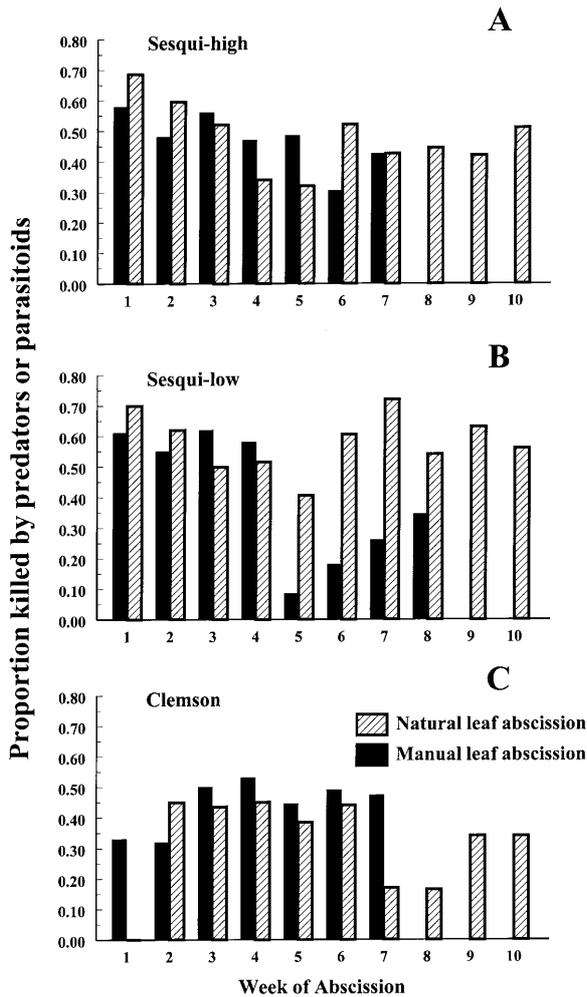


Fig. 3 The proportion of total over-winter mortality of *Brachys tessellatus* due to predators and parasitoids. Leaves that were torn open and/or the beetle was missing and leaves that showed evidence of parasitoid attack, including mines with emergence holes, pupal exuviae of parasitoids, or larvae or pupae with “characteristic imploded morphology of host feeding” by parasitoids (Connor 1991), were categorized as preyed upon. The manual leaf abscission experiment was only conducted through week 7 at the Sesqui-high site and week 8 for the Sesqui-low and Clemson sites

At both Sesqui sites, beetles in leaves that abscised earlier were more likely to be killed by predators than were beetles in leaves that abscised later (Fig. 3; Sesqui-high, $r=0.45$ and 0.75 for natural and manual abscission, respectively, $P<0.05$ for each; Sesqui-low, $r=0.03$ and 0.70 , $P<0.05$ for manual abscission only). The relationship between abscission phenology and predation was unclear at the Clemson site (Fig. 3C). The only evidence that the remaining unexplained mortality (our “other” class) was related to leaf abscission phenology was for the manual abscission treatment at the Sesqui-high site (“other” mortality decreased with increasing week of abscission, $r=-0.72$, $P<0.01$). In the remaining manual abscission analyses and all natural abscission analyses, correlations ranged between $r=-0.24$ and 0.31 with no interpretable pattern ($P>0.05$ for each).

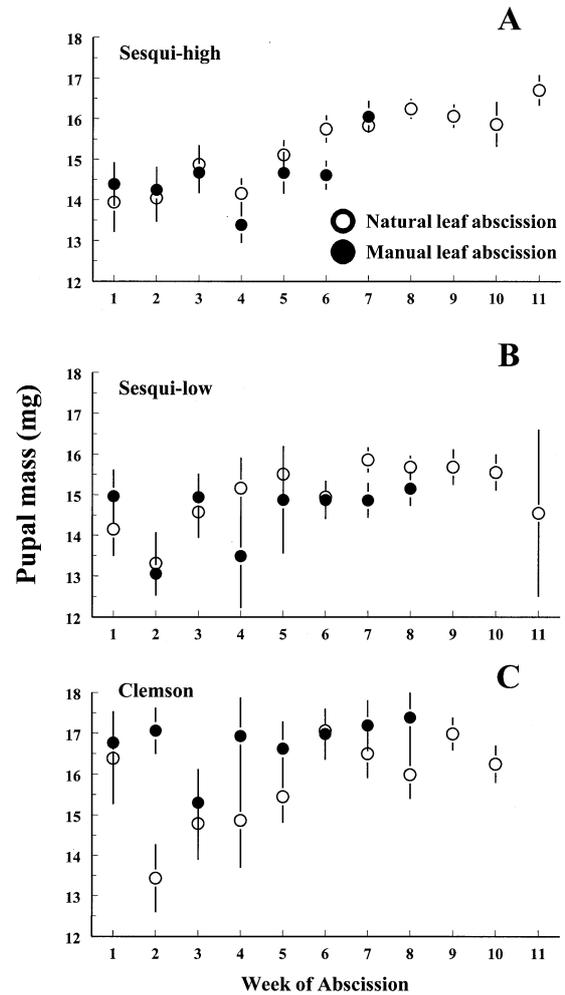


Fig. 4 The relationship between leaf abscission date and mean pupal mass of cohorts of *Brachys tessellatus* that over-wintered in the abscised leaves. The manual leaf abscission experiment was only conducted through week 7 at the Sesqui-high site and week 8 for the Sesqui-low and Clemson sites

Week of abscission had a large effect on pupal mass (Fig. 4); beetles emerging from late-abscised leaves were on average larger than beetles that emerged from early abscised leaves. In the full-model analysis of variance, week of abscission (a covariate) had the largest influence on beetle adult body mass ($F=30.68$, $P<0.001$) with a positive linear coefficient of 0.023 . Body mass also varied among study sites ($F=8.46$, $P=0.002$), but not between the natural and manual leaf abscission treatments ($F=1.63$, $P=0.20$). None of the two or three way interactions were significant ($P>0.19$ for each).

Beetle adult body mass and fecundity relationship

Brachys tessellatus adults can vary more than 3-fold in body mass, from 60 mg to more than 200 mg. We found no significant correlation between beetle mass and lifespan (lifespan after mating) in either the laboratory or

field populations. We found a positive but weak correlation between body mass and lifetime fecundity (total number of eggs deposited) in the laboratory population ($r=0.24$, $n=91$, $P<0.019$), but not in the field population ($r=0.14$, $n=151$, $P>0.1$). We also examined the daily oviposition rate as a time-independent measure of reproduction. Body mass and daily oviposition rate were found to be positively correlated in both laboratory and field populations (laboratory: $r=0.32$, $n=91$, $P<0.002$; field: $r=0.36$, $n=151$, $P<0.001$).

Discussion

Turkey oak leaves that contained living *Brachys tessellatus* larvae abscised from trees sooner than leaves that did not contain living larvae. This is consistent with results for other leaf miners (Hilemann and Lieto 1981; Preszler and Price 1993; Riskey 1993), non-mining folivorous insects (Smitley and Peterson 1996; Gharadjedaghi 1997) and other parasites (e.g., Whiting et al. 1997). Similar patterns are also generally observed for other plant tissues; for example, flowers and fruits that are damaged by herbivores are generally abscised earlier than undamaged flowers or fruits (e.g., Philips and Walker 1997; Wilson and Addicott 1998). The acceleration of leaf abscission phenology by *Brachys* is probably due to changes in leaf hormone concentrations caused by larval feeding, as observed for some other systems (e.g., Philips and Walker 1997). Our data do not allow us to test whether early abscission of mined leaves is advantageous to the plant.

This project did, however, address the fitness consequences of early leaf abscission for the leaf mining beetle. We expected a priori that beetle over-winter survivorship would be lower for beetles in leaves that abscised early because these larvae would both be smaller at abscission and be exposed to ground-feeding predators (such as carabids and fire ants) for an extended period of time. Our results for both Sesqui sites are generally consistent with this prediction, although the effects were small. We also expected a priori that average mortality of beetles would be substantially higher at the Clemson site because imported fire ants (*Solenopsis invicta*) are particularly abundant at this site and relatively rare in our Sesqui plots. *S. invicta* is a common and opportunistic invasive ant in the southeastern US (Wilson and Oliver 1969; Lofgren et al. 1975) and has been observed on several occasions removing beetle larvae from mined leaves on the ground (K. J. Waddell, personal observation). We found that average mortality due to predation was actually lower at the Clemson site and that leaf abscission phenology did not explain beetle mortality at this site, inconsistent with our prediction. However, our experimental design did not identify the various sources of predation and other predators, such as spiders and carabid beetles, may be more abundant at the Sesqui sites than at the Clemson site. Fire ants have been shown to reduce densities of other ground-foraging predators (e.g., Howard and Oliver 1978; Cherry and Nuessly 1992),

and thus may actually improve beetle over-winter performance.

Stiling and Simberloff (1989) reviewed systems where plant leaf abscission and subsequent insect larval mortality had been quantified. When plant species abscise their leaves after pupation and/or emergence of the herbivores, the herbivores generally suffer low levels of post-abscission mortality in leaves. In contrast, when plant species abscise their leaves before herbivore pupation and/or completion of larval development, herbivores generally suffer greater mortality in leaves. These results suggest that leaf abscission before completion of larval development is itself a source of beetle mortality separate from mortality caused by exposure to ground-foraging predators. In our study, total mortality was split into two categories, either predation or "other" mortality. This "other" mortality accounted for 20.9% of the total mortality of *B. tessellatus* (summed from the three sites and two treatments), but did not correlate with leaf abscission phenology except at the Sesqui-high site. This suggests that early leaf abscission had little effect on non-predator-mediated mortality. These results contrast with those for two other "blotch" leaf miners and oak host plants; 32% of total mortality of *Brachys ovatus* (a congener of *B. tessellatus*) on *Q. virginiana* and 34.7% of total mortality of a moth species, *Tischeria citrinipennella*, on the same host was attributed to early leaf abscission (Faeth et al. 1981). However, the increased importance of early leaf abscission-mediated mortality on *Q. virginiana* is possibly due to the contrast in abscission patterns between evergreen (*Q. virginiana*) and deciduous (*Q. laevis*) oaks; evergreen trees abscise more leaves earlier in the growing season when the herbivores are more vulnerable to leaf abscission-mediated mortality (Bultman and Faeth 1986). Also, for bivoltine species leaf miner mortality due to early leaf abscission may vary between seasonal generations (Connor et al. 1994). However, at this time too few data are available to generalize.

B. tessellatus larvae in leaves that abscised early pupated at a smaller size than did larvae in leaves abscised later. Because we weighed beetles in late February (and thus weighed only those that survived over winter) this result might reflect an interaction between leaf abscission phenology and survivorship of small versus large beetles. If large beetles have a survival advantage when abscised late, or if small beetles have a survival advantage when abscised early, we would generate the observed relationship between abscission phenology and pupal mass after winter (after mortality has occurred). However, this pattern is also consistent with the general observation that an increased growing season allows insects to attain a larger body size before over-wintering (e.g., Roff 1980; Fairbairn 1984) and thus have higher fecundity in the spring. In *B. tessellatus* early leaf abscission likely terminates the growing season of a larva (no green islands are created within leaves), requiring it to stop feeding and pupate at a smaller size than if it could continue feeding. That we were unable to detect an in-

crease in non-predator-mediated over-winter mortality of larvae, and yet we observed covariation between body size and leaf abscission phenology at the end of the experiment, suggests a level of developmental plasticity that permits successful completion of larval development over a range of season lengths (Bradford and Roff 1993; Abrams et al. 1996). Similar forms of developmental plasticity occur in insects where several individuals may compete for a limited resource and often run out of resource prior to achieving their targeted body size; e.g., in a single leaf for the native holly leaf miner (Potter 1985) or in a seed for seed beetles (Bruchidae; Fox and Savalli 1998). Previous authors (e.g., Fox 1997; Fox et al. 1999) have suggested that this developmental plasticity is likely an adaptive response to larval competition. Development plasticity in *B. tessellatus* might likewise be an adaptive response to variation in season length caused by variation in leaf abscission phenology.

Our data thus demonstrate that variation in the timing of leaf abscission affects *B. tessellatus* survivorship and growth. Most studies of the adaptive timing of insect life cycles to seasonal events (Roff 1983; Tauber et al. 1986; Danks 1987; Gilbert 1990) are scaled at the macrogeographic level to discern patterns of geographic variation. Although a few studies examine variation at a microgeographic scale (Fairbairn 1984; Blanckenhorn 1991; Dingle and Mousseau 1994), these studies explore adaptations among populations that exhibit limited gene flow, due either to geographic barriers or behavioral/physiological constraints of mobility in the insects. Our study is more localized in scale, yet variation in leaf abscission phenology is analogous to how macrogeographic seasonal patterns may affect life cycles in a widely distributed species. In this context, variation in leaf abscission phenology makes the period of growth and development for *B. tessellatus* temporally indeterminate. This study provides evidence that variation in abscission phenology has fitness consequences for larvae developing inside leaves, and that *B. tessellatus* has adapted to variation in leaf abscission phenology by evolving the ability to complete development over a range of season lengths within a microgeographic scale.

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