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Variation in budbreak phenology affects the distribution of a leafmining beetle (*Brachys tessellatus*) on turkey oak (*Quercus laevis*)[1]

Charles W. FOX[2], Kim J. WADDELL, Francis R. GROETERS & Timothy A. MOUSSEAU, Department of Biological Sciences, University of South Carolina, Columbia, South Carolina, 29208, U.S.A.

Abstract: Variation in plant phenology may be a major determinant of the distribution of herbivores on their host plants. We describe a field study in which we examined the consequences of budbreak phenology for densities of a leafmining beetle, *Brachys tessellatus*, on turkey oak, *Quercus laevis*. Budbreak phenology varies both within and among populations of *Q. laevis* in South Carolina. This variation appears to reflect mostly environmental variation within and among populations of trees, mediated in part by topography; larger trees and higher elevation trees broke bud earlier than smaller and lower elevation trees. *Q. laevis* that broke bud earlier suffered more leaf area loss to adult herbivory by *B. tessellatus* than trees that broke bud later; early-breaking trees lost as much as 15-20% leaf area to adult *B. tessellatus* feeding, while later-breaking trees generally lost < 5%. The effect of phenology on larval densities was more complicated; early-breaking trees accumulated more eggs than later-breaking trees early in the season. However, this relationship disappeared by mid-summer and there was no relationship between tree phenology and final numbers of mines or miners on trees at the end of the season. Thus, the consequences of variation in tree phenology for *B. tessellatus* abundance and herbivory on *Q. laevis* depend on the life history stage of the insect examined. This variable response to phenology by *B. tessellatus* reflects the patterns reported in other studies; insects primarily attacking young foliage and active early in the season are sensitive to phenological variation among plants, while herbivores primarily attacking mature foliage later in the season are not.

Keywords: budburst, Buprestidae, Fagaceae, herbivory, phenology.

Résumé: Les variations phénologiques chez les plantes constituent un des principaux facteurs expliquant la répartition des herbivores sur leurs plantes-hôtes. Nous décrivons ici une étude de terrain dans laquelle nous avons examiné les conséquences de l'éclosion hâtive ou tardive des bourgeons du chêne *Quercus laevis* sur la densité du coléoptère *Brachys tessellatus*. Cet insecte se nourrit essentiellement de feuilles de *Q. laevis*. En Caroline du Sud, la phénologie de l'éclosion des bourgeons varie entre les populations de *Q. laevis* et au sein même des populations. Cette variabilité semble être le reflet de particularités environnementales distinguant les populations de cette espèce ou distinguant les individus au sein même des populations : les bourgeons des plus gros arbres et des chênes croissant à des altitudes plus élevées éclosent plus hâtivement que ceux des autres arbres. Les chênes dont les bourgeons éclosent de façon hâtive souffrent davantage de pertes de surface foliaire attribuables au broutage des *B. tessellatus* adultes. De tels arbres perdent jusqu'à 15-20 % de leur surface foliaire, alors que les arbres à éclosion tardive ne perdent pas plus de 5 % de leur surface folaire. L'effet de la phénologie sur la densité des larves est plus complexe. Les arbres à éclosion hâtive supportent davantage d'oeufs que les arbres à éclosion tardive au début de la saison de croissance, mais cette tendance disparaît au milieu de l'été. À la fin de l'été, on ne détecte aucune relation entre la phénologie des arbres et le nombre final de coléoptères présents sur les individus. Il semble donc que les conséquences de la variabilité phénologique sur l'abondance de *B. tessellatus* et sur l'importance de la défoliation chez *Q. laevis* varient selon l'étape du cycle de vie de l'insecte que l'on examine. Cette réponse variable à la phénologie chez *B. tessellatus* reflète les tendances détectées dans d'autres études : les insectes qui se nourrissent du feuillage jeune et qui sont actifs dès le début de la saison de croissance sont sensibles aux variations phénologiques des plantes, contrairement aux insectes qui se nourrissent principalement de feuillage mature et qui sont donc actifs plus tard au cours de la saison de croissance.

Mots-clés: éclosion des bourgeons, Buprestidae, Fagaceae, herbivorie, phénologie.

Introduction

In natural populations of animals, individuals are generally distributed non-randomly among resource patches. For insects, this variation is often attributed to genetic variation in plant resistance to herbivory (Service, 1984a; Fritz & Price, 1988; Fritz, 1990; Strauss, 1990), variable rates of attack by natural enemies (Clancy & Price, 1986; Denno, Larsson & Olmstead, 1990; Morris, 1992; Hanks & Denno, 1993), or microclimatic variation among plants (Service, 1984b; Maddox & Cappucino, 1986; Peng, Sutton & Fletcher, 1994). Variation in plant phenology may also be a major determinant of the distribution of herbivores on their host plants (Hunter, 1992; Feder, Hunt & Bush, 1993; Mopper & Simberloff, 1995), and the population dynamics of these herbivores (Hunter, 1990). Variation in the timing of budbreak is generally substantial within and among populations of trees (Holliday, 1977; Faeth, Mopper & Simberloff, 1981; Crawley & Akhteruzzaman, 1988; Floate, Kearsley & Whitham, 1993; Jordano & Gomariz, 1994). However, the consequences of this variation for susceptibility to herbivory, and thus the distribution of herbivores, are poorly understood.

Many insects prefer and perform better on leaves of a specific age-class (Coley, 1980; Thomas, 1987; Raupp,

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[2] Author for correspondence. Present address: The Louis Calder Center, Biological Field Station of Fordham University, 53 Whippoorwill Road, Box K, Armonk, New York, 10504, U.S.A., e-mail: fox@murray.fordham.edu

Werren & Sadof, 1988; Sheppard & Friedman, 1990; Stamp & Bowers, 1990; Walker & Zareh, 1990; Quiring, 1992; Senn, Hanhimaki & Haukioja, 1992; Marino & Cornell, 1993; Jordano & Gomariz, 1994) because leaf quality (chemistry, moisture content, toughness, and pubescence) generally changes as leaves age (Mattson, 1980; Scriber & Slansky, 1981; Raupp & Denno, 1983). Thus, plant tissues are often most suitable for insect development at a specific time in the plant's phenology (Potter & Kimmerer, 1986; Hunter & Lechowicz, 1992; Quiring, 1992; 1994a), and insects using these plant tissues during other phenological stages may suffer reduced success (decreased survivorship or retarded development). Also, differences in budbreak phenology often translate into season-long differences in foliage quality (Kleiner, 1989).

Variation in the phenology of leaf availability can also be critical for insects that have a limited window of time in which to complete development (Quiring, 1994b). Sedentary insects emerging after leaves have matured, and even those using late-produced foliage, may have insufficient time to complete development before leaf abscission (Connor *et al.*, 1994). For these insects, synchrony between budbreak and insect emergence is critical to folivore success, and the attack of early-breaking trees allows a longer window for development.

The above observations suggest that plants breaking bud earlier should be more heavily attacked by herbivores than plants breaking bud later. However, researchers conducting studies examining the effects of budbreak phenology on herbivore density have obtained mixed results. Some studies find that early flushing trees suffer higher herbivore densities than later flushing trees (Holliday, 1977; Collinge & Louda, 1989; Kolb & Teulon, 1991; Hunter, 1992; Floate, Kearsley & Whitham, 1993), while numerous other researchers have failed to find any relationship between budbreak phenology and herbivory (Crawley & Akhteruzzaman, 1988; Watt & McFarlane, 1991; Faeth & Rooney, 1993; Marino & Cornell, 1993; Connor *et al.*, 1994). These latter studies call into question the generality of tree phenology as a major source of variation in the distribution of herbivores on their host plants (Hunter, 1992).

For insects whose distribution among plants is sensitive to plant phenology, environmental factors that alter patterns of phenology can subsequently influence their distribution among plants. For example, shaded plants generally break bud later than neighbor plants in the sun, and these plants suffer lower levels of herbivory (Rausher, 1979; Lincoln & Mooney, 1984; but see Collinge & Louda, 1989). Large trees generally break bud earlier than small trees (Hunter, 1992; Senn, Hanhimaki & Haukioja, 1992), provide higher quality foliage than small trees (Senn, Hanhimaki & Haukioja, 1992), and thus may suffer higher rates of herbivory than small trees. Also, altitude and topography influence temperature and water availability, which in turn influence plant phenology, and thus likely insect abundance (Crawley & Akhteruzzaman, 1988). Therefore, understanding the abiotic factors that influence plant phenology is of central importance to understanding the interaction between environmental variation, plant phenology, and insect distribution and abundance.

We describe a field study in which we examined the consequences of budbreak phenology for herbivore densities on turkey oak, *Quercus laevis* Walter. We find that the consequences of variation in tree phenology for *Brachys tessellatus* (Fabr.) distribution on *Q. laevis* depend on the life history stage of the insect examined. We discuss how this variable response to phenology by *B. tessellatus* reflects the patterns reported in other studies in which insects primarily attacking young foliage and active early in the season are sensitive to phenological variation among plants, while herbivores primarily attacking mature foliage later in the season are not.

Material and methods

STUDY ORGANISMS

Turkey oak (*Quercus laevis*) is a small, scrubby tree, abundantly distributed throughout the coastal plain sandhill communities of the southeastern United States. *B. tessellatus* is a leaf mining beetle abundant on, and largely restricted to, turkey oak (Turnbow & Franklin, 1981; Waddell & Mousseau, 1996). Although numerous herbivores attack *Q. laevis* (*e.g.*, leaf gallers, stem gallers and leaf chewers), *B. tessellatus* is the most conspicuous and abundant herbivore on this oak in South Carolina, resulting in approximately an order of magnitude more tissue loss than all other foliar herbivores combined (Waddell, unpubl. data). Beetles overwinter in the leaf-litter (inside mined leaves) and emerge as adults in March-April, coincident with, or slightly prior to, *Q. laevis* budbreak. Adults feed on expanding leaves through April and begin oviposition on fully expanded leaves in mid to late April. Eggs are laid conspicuously on the upper surface of leaves. Larvae enter leaves (initiate mines) under their eggs approximately 7-10 days after being laid, where they undergo five instars, and finally initiate pupation inside their mines in November-December.

STUDY POPULATIONS

This study was conducted over an approximately 18 month period during 1994-1995, at three sites in South Carolina; two sites in Sesquicentennial State Park in Richland County, South Carolina (high Sesqui site, mean elevation = 125 m; low Sesqui site, mean elevation = 105 m), and on a plot of unmarked county owned property along Clemson Road, *ca* 3 km south of the Clemson University Sandhills Research and Education Center in Richland County, South Carolina (Clemson Road site, mean elevation = 105 m). Both sites are located in the sandhills dominated by longleaf pines (*Pinus palustris* Miller) and turkey oak.

Li-Cor LI-1000 data loggers and associated thermistors were used to estimate ground and air temperature at the center of both Sesqui sites from February to August. Based on hourly averages (5-second sampling intervals), ground temperature at the high Sesqui site averaged 0.47 ± 0.01°C higher than at the low Sesqui site. Similarly, air temperature at 1 m above the surface averaged 0.59 ± 0.06°C higher at the high Sesqui site than at the low Sesqui site.

TREE PHENOLOGY AND SIZE

Budbreak was defined as the first date on which half of the buds on the tree had broken, and was scored by visually estimating the proportion of buds that had broken on each tree. Following budbreak on the earliest tree at the earliest study site (high Sesquicentennial site) in 1994, all trees were examined daily for budbreak in the springs of both 1994 and 1995 (n = 203, 36, and 105 trees in 1994, and 141, 49, and 105 trees in 1995, at the low Sesqui, high Sesqui, and Clemson Road sites, respectively). On some trees, one or a few buds would break very early (usually the highest buds), followed by a long lag before the remaining buds broke. However, the transition from the date on which the first bud broke until 90% of the buds on a tree broke was generally rapid (1 to 3 days).

Tree size was estimated for all trees as the circumference of the trunk at 20 cm aboveground level. In a sample of 47 trees at the low Sesqui site, circumference at 20 cm positively correlated with the log of the total number of leaves on the tree ($r^2 = 0.59$, $p < 0.001$, $n = 47$; data from 1994). Neither tree height nor tree circumference at 1 m correlated better with the total number of leaves ($r^2 = 0.59$ and $r^2 = 0.45$, respectively).

ASSESSMENT OF ADULT FEEDING DAMAGE

Early in the season (late March to late April) adult *B. tessellatus* congregate and feed on expanding *Q. laevis* foliage. Because leaves are attacked while still expanding, adult feeding has a large effect on the resulting size of these leaves (reducing total leaf area by as much as 20%; Waddell & Fox, unpubl. data). On 1-2 May 1994 (after leaves had fully expanded), 13 August 1994 (after most adults had died) and 20 September 1995 (prior to widespread leaf senescence and leaf abscission; Sesqui sites only), we estimated the amount of leaf area lost by each tree to adult *B. tessellatus* feeding (n = 134, 36, and 92 trees at the low Sesqui, high Sesqui, and Clemson Road sites in 1994, and n = 133 and 91 trees at the low and high Sesqui sites in 1995). Leaf area loss was estimated independently by two observers, one of whom was blind to the objective of the experiment. Each tree was subjectively classified as having approximately < 5, 5, 10, 15, or > 15% leaf area loss. While these estimates are subjective, they are relatively precise; both observers classified almost all trees identically (Pearson moment correlations > 0.945 at each site).

ASSESSMENT OF EGG AND LARVAL DENSITIES

The number of eggs laid on leaves was estimated first in late April (26-27 April 1994, low Sesqui site only, n = 30) and again in late May (26-31 May 1994, n = 36). Eggs are attached flat against leaves (Waddell & Mousseau, 1996), and remain attached for a month or more unless removed by predators. Egg densities were estimated by haphazardly selecting 20 leaves from each tree (10 leaves from the west side of the tree, and 10 from the east). The number of eggs and number of newly initiated mines were recorded for each leaf.

At the end of the season, just prior to leaf abscission (9-13 September, 1994), 100 leaves were haphazardly selected on each tree and censused without removing them from the tree (all three sites; n = 143, 68, and 36 trees at the low Sesqui, high Sesqui, and Clemson Road sites, respectively). The number of small (< 1 cm^2), medium (1 to 5 cm^2), large (> 5 cm^2), and successful mines was recorded for each leaf. Successful mines were defined as any mine with a living larva in it on the date of census. All other classes of mines lacked living larvae. In a previous experiment, > 90% of these larvae successfully become pupae (Waddell, unpubl. data). Because ants remove eggs from leaves during the summer (Waddell & Fox, pers. observ.), egg densities were not counted again at the end of the season.

Results

To be concise, we emphasize the results from our low Sesqui site because more trees were studied at this site than either of the other sites (high Sesqui and Clemson Road). Except where noted, results at all three sites are consistent.

VARIATION IN BUDBREAK PHENOLOGY

Both within and among our three study sites budbreak phenology of *Q. laevis* varied substantially. In both years, high Sesqui trees broke bud earlier, on average, than either low Sesqui or Clemson Road trees (Figure 1; Mann-Whitney U-tests, $p < 0.001$ for each comparison). For example, in 1994 trees began to break bud on 15 March at the high Sesqui site, while budbreak did not begin until March 22 at the low Sesqui site and 23 March at the Clemson Road site (Figure 1). Also, budbreak continued well into April at the low Sesqui (11 April) and Clemson road (8 April) sites, but most trees at the high Sesqui site had broken by early April (last tree broke 1st April).

Within sites, large trees broke bud earlier than small trees (Figure 2), although tree size explained only a small proportion of the variation in budbreak phenology (r^2 = 0.09 to 0.10, $p < 0.05$ for each site). Tree size did not explain the difference in phenology among sites; there was no difference among sites in the size of marked oak trees (Mann-Whitney U-tests, $p > 0.05$ for each comparison).

Tree elevation explained more of the variation in date of budbreak; trees at higher elevation broke bud earlier than trees at lower elevation. This was evident both among sites (Figure 1) and within the low Sesqui site (Figure 3). Trees at the high Sesqui site (mean elevation = 125 m) broke substantially earlier than trees at either the low Sesqui or Clemson Road sites (mean elevation = 105 m each; Figure 1). Within the low Sesqui site, tree elevation explained 25% of the variance in budbreak phenology ($r^2 = 0.25$, $p < 0.001$, $n = 202$), while tree size and tree phenology combined explained 31% of the variance ($r^2 = 0.31$, $p < 0.001$, $n = 202$). Because the variation in elevation at both the high Sesqui and Clemson Road sites was complicated by sun-shade relationships (lower elevation trees are more shaded than higher elevation trees), the effect of elevation on phenology was not analyzed at these sites.

The observed variation in budbreak phenology was highly repeatable among years. At all three sites, 1995 budbreak began within 2 days of the date that budbreak began in 1994 (Figures 1 and 4). Also, the variation within sites was highly repeatable ($r^2 > 0.77$, $p < 0.001$ for each site). This high repeatability was due only in part to elevation and size effects on phenology; when the effects of tree elevation (low Sesqui site only) and size (all sites) are removed using multiple regression, the correlation between years is still

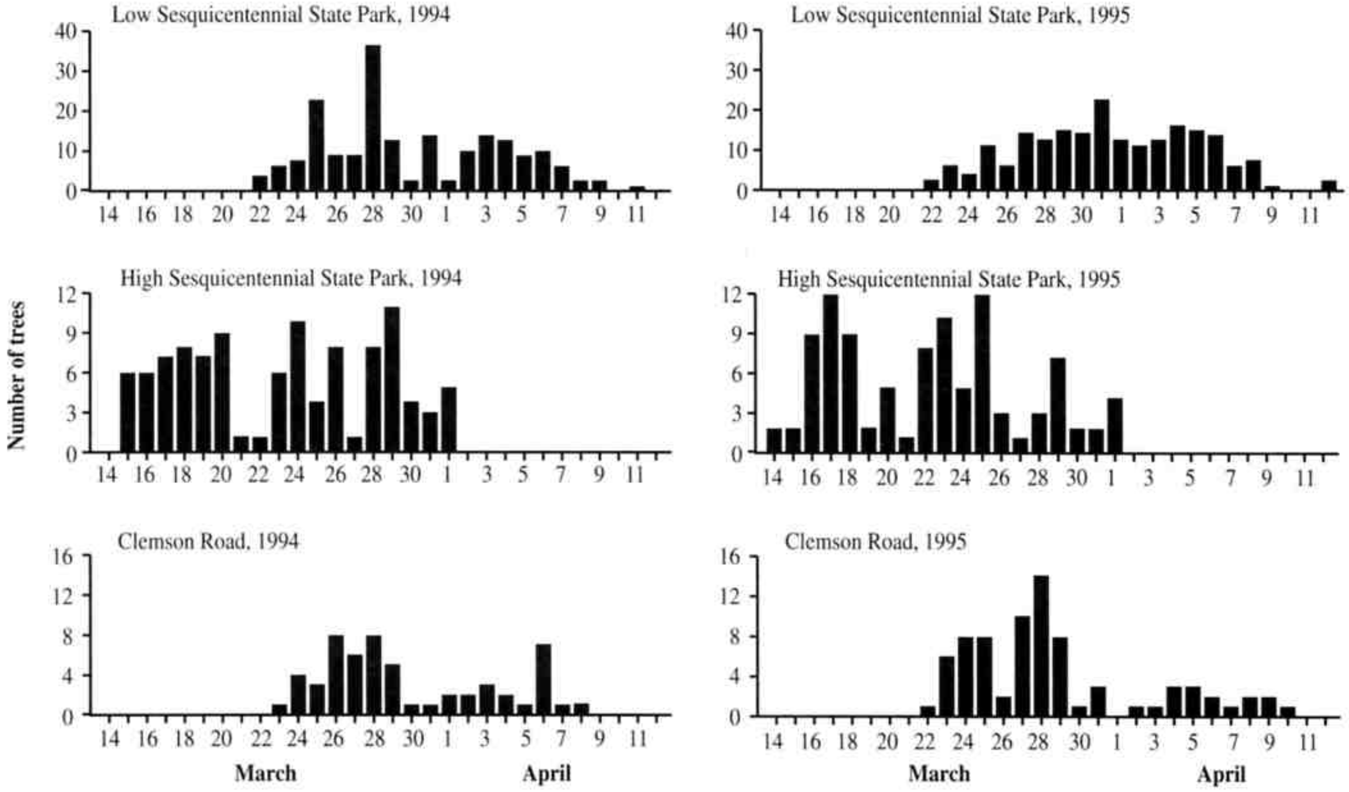

FIGURE 1. Distributions of tree budbreak phenology at the low Sesqui, high Sesqui, and Clemson Road sites in 1994 and 1995.

high ($r^2 > 0.64$, $p < 0.001$ for each).

BUDBREAK PHENOLOGY AFFECTS DAMAGE BY HERBIVORES

At all three study sites in 1994, early-breaking *Q. laevis* were more heavily attacked by leaf-chewing adult *B. tessellatus* than late-breaking trees (Figure 5a; low Sesqui, Spearman rank correlation, $r = -0.43$, $p < 0.001$, $n = 134$; Clemson Road, $r = -0.53$, $p < 0.01$, $n = 31$; censused at high Sesqui site late in the season only). The earliest breaking trees at each site lost as much as 20% of their leaf area to adult *B. tessellatus* feeding, while late trees rarely lost more than 5% (on many late trees we could detect no evidence of adult feeding). This relationship between phenology and adult damage lasted throughout the entire summer (Figure 5b) indicating that adult feeding by *B. tessellatus* after early May had little effect on tree leaf area.

In 1995, beetle emergence was asynchronous with tree budbreak for the first time in the 5 years we have worked at these sites. Beetles began emerging from the leaf-litter approximately one week after budbreak began (after leaves

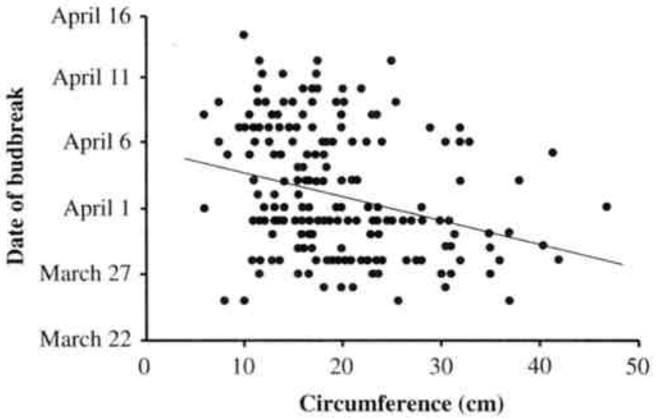

FIGURE 2. The relationship between tree size and date of budbreak in 1994 at the low Sesqui site ($r^2 = 0.09$, $p < 0.01$, $n = 202$). The patterns are similar for the high Sesqui and Clemson Road sites ($r^2 > 0.09$, $p < 0.05$ for each, $n = 103$ and 56, respectively).

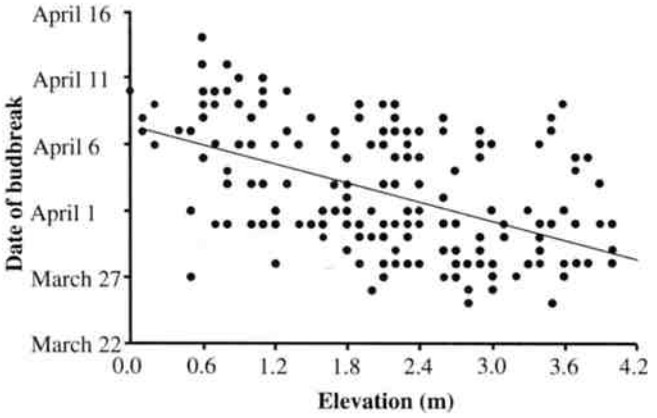

FIGURE 3. The relationship between tree elevation and date of budbreak in 1994 at the low Sesqui site ($r^2 = 0.25$, $p < 0.001$, $n = 202$). Tree elevation is expressed as the height above the lowest marked tree at the site (in m). The relationship between elevation and phenology was not examined at the other sites.

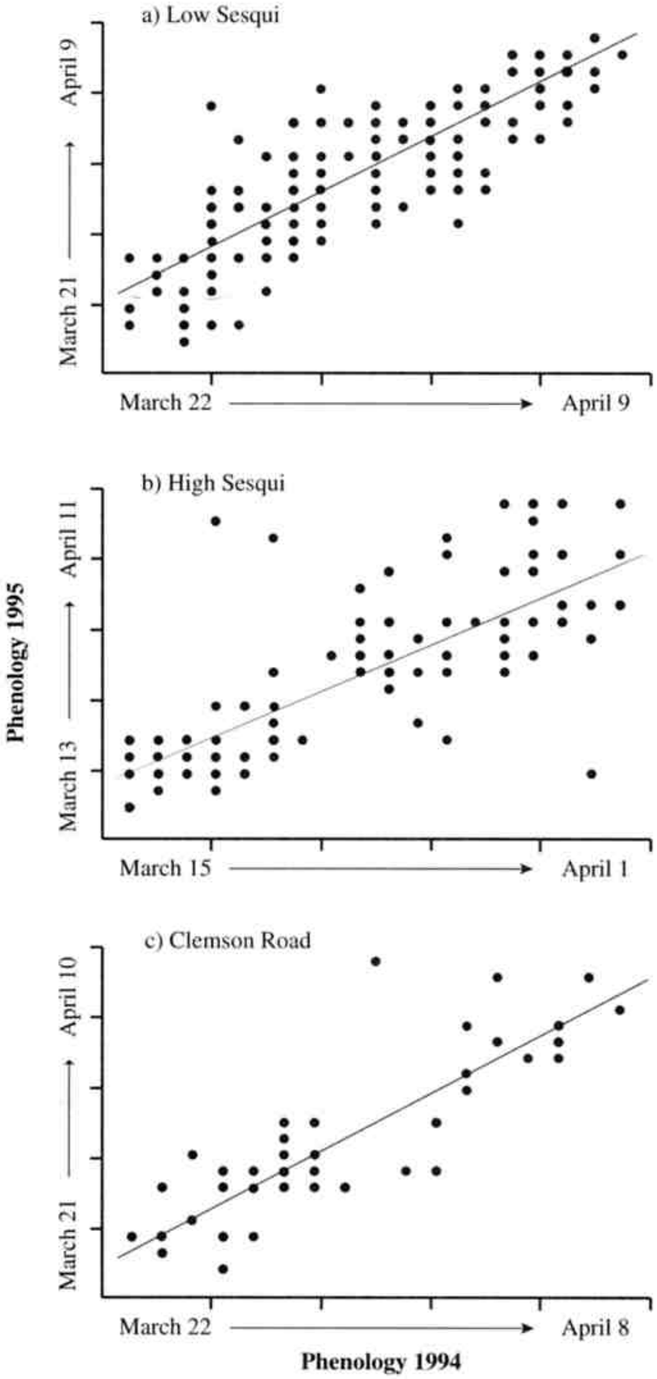

FIGURE 4. The repeatability of budbreak phenology; a) low Sesqui site ($r^2 = 0.85$, $p < 0.001$, $n = 133$), b) high Sesqui site ($r^2 = 0.77$, $p < 0.001$, $n = 103$), and c) Clemson Road site ($r^2 = 0.88$, $p < 0.001$, $n = 35$). When the effects of tree elevation and size are removed using multiple regression (low Sesqui site only), the correlation is still high ($r^2 > 0.64$, $p < 0.001$).

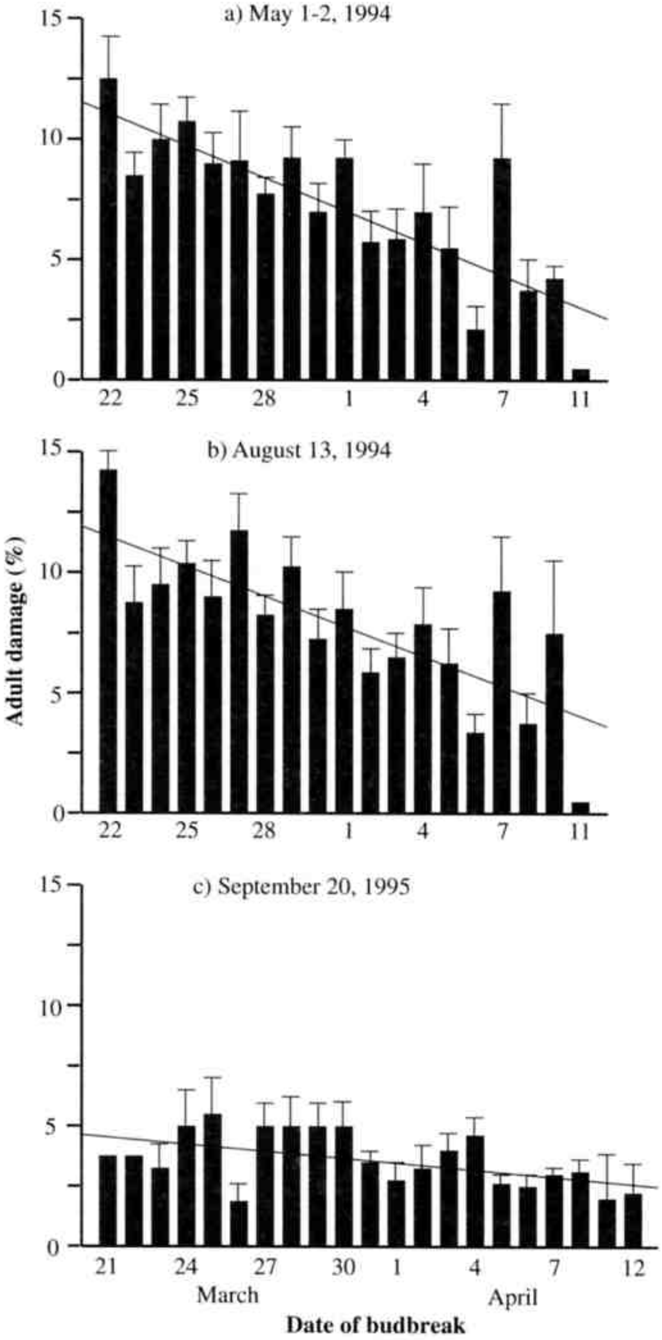

FIGURE 5. The effect of budbreak phenology on levels of adult damage at the low Sesqui site. The histogram presents the average damage for all trees that broke on each subsequent date. The line represents the linear regression through the original data points, before means were calculated; y = amount of damage, x = date of budbreak. a) Damage estimates from May 1-2, 1994; Spearman rank correlation, $r = -0.43$, $p < 0.001$, $n = 134$; b) Damage estimates from August 13, 1994; $r = -0.39$, $p < 0.001$, $n = 133$; c) Damage estimates from September 20, 1995, $r = 0 - 0.22$, $p < 0.01$, $n = 128$. Patterns are similar at both other sites. No censused trees broke bud on March 30, 1994 , April 10, 1994, or April 10-11, 1995.

on early trees were largely expanded), rather than emerging prior to budbreak as they had in 1994 and previous years. We predicted that, because more trees were available to beetles at the time of emergence, and because leaves on early-breaking trees had largely expanded by the time adult *B. tessellatus* initiated feeding, damage to trees would be more dispersed than in 1994, and would represent less leaf area loss (because leaves had largely expanded before suffering damage from adult beetles). In part, this prediction was supported; early trees suffered substantially less damage in 1995 than they had suffered in 1994 (Figure 5c). However, as in 1994, early trees still suffered more damage than late-breaking trees (low Sesqui, Spearman rank $r = -0.22, p < 0.01, n$ 128; high Sesqui, $r = -0.327, p < 0.001, n = 105$; not examined at Clemson Road in 1995). The amount of leaf area lost to *B. tessellatus* in 1995 was also highly correlated with the amount lost in 1994, even after the effects of tree phenology were removed using a linear regression analysis (low Sesqui, partial $r^2 = 0.45, p < 0.001, n = 133$; high Sesqui, partial $r^2 = 0.33, p < 0.001, n = 105$), indicating that some factor other than tree phenology is also affecting damage by *B. tessellatus.*

Early in the season (before April 26-27), *B. tessellatus* laid more eggs on early-breaking trees than on late-breaking trees (Figure 6a). However, this relationship soon disappeared; by mid-summer (late May) *B. tessellatus* egg load (eggs/leaf) was unaffected by date of budbreak (Figure 6b; low Sesqui, $r^2 = 0.30, p = 0.002, n = 29$; Clemson Road, $r^2 = 0.04, p = 0.21, n = 43$).

At the end of summer, there was no relationship between the date of tree budbreak at any site and either the total number of mines initiated per leaf, the number of small (< 1 cm^2), medium (1 to 5 cm^2), or large (> 5 cm^2) mines per leaf, or the number of successful mines per leaf (*i.e.*, those producing a successful larva) (Figure 7). Thus, we conclude that, although date of budbreak affected the amount of leaf area lost to adult *B. tessellatus* foliar feeding, it did not affect the amount of leaf area lost to larval *B. tessellatus* mining.

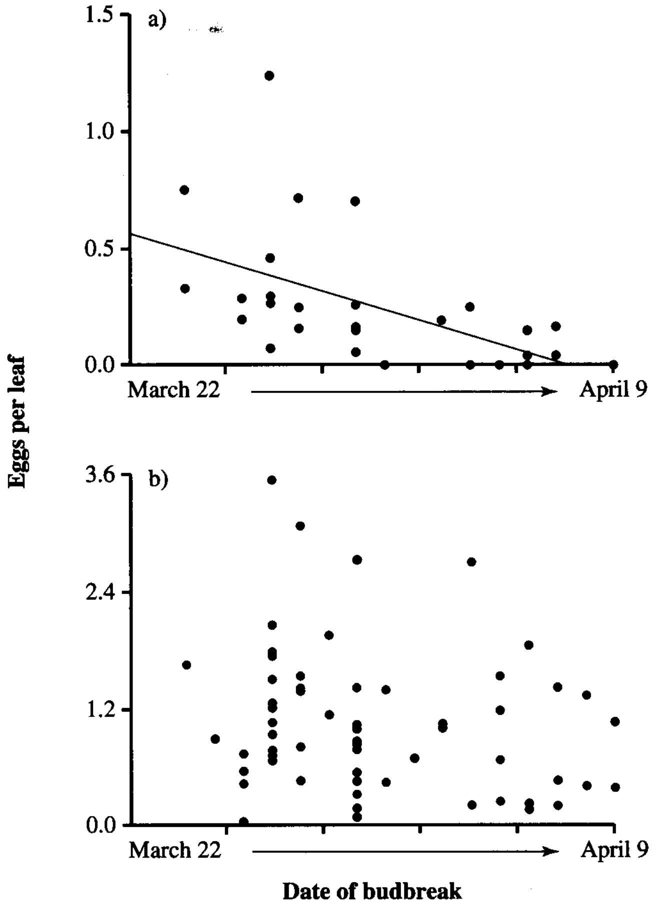

FIGURE 6. The effect of budbreak phenology on the number of eggs per leaf at the low Sesqui site. a) Early summer, estimated on 26-27 April 1994 ($r^2 = 0.30, p = 0.002, n = 29$). b) Mid-summer, estimated in late May, 1994 ($r^2 = 0.04, p = 0.12, n = 61$). Egg numbers were not examined at the high Sesqui site.

Discussion

SOURCES OF VARIATION IN BUDBREAK PHENOLOGY

Budbreak phenology varies within and among populations of *Quercus laevis*, partially explainable by variation in tree size and elevation. That higher elevation *Q. laevis* broke bud earlier than low elevation trees is counter to the expected result; at a macrogeographic scale, higher elevation trees generally break bud later than lower elevation trees, due in part to lower temperatures that delay budbreak (Kramer, 1995). Our results likely reflect localized variation in environmental variables, such as soil water retention, solar exposure, and cold air drainage. For example, the high Sesqui site is more exposed to the sun than either the low Sesqui or Clemson Road sites, and is thus warmer and drier in the spring than either of the other sites. Thus, elevational differences in phenology in our study are not comparable to larger scale altitudinal effects observed in other studies, but instead, likely reflect local microgeographic environmental variation.

Patterns of budbreak phenology of *Q. laevis* within sites were highly repeatable between years, as observed in other studies of oak trees (Crawley & Akhteruzzaman, 1988). This repeatability may reflect genetic differences among trees within populations (McGee, 1973; Billington & Pelham, 1991) or consistent micro-environmental variation. Preliminary analyses comparing clones and unrelated trees indicate genetic variation in budbreak phenology, but genetic effects explain only a small amount of the variation (Waddell & Mousseau, unpubl. data). Consistent micro-environmental variation likely explains the remaining correlation between years.

CONSEQUENCES OF BUDBREAK PHENOLOGY

Numerous studies have found that herbivores prefer and perform better on younger foliage (Hough & Pimental, 1978; Schroeder, 1986; Thomas, 1987; Sheppard & Friedman, 1990; Stamp & Bowers, 1990; Walker & Zareh, 1990; Quiring, 1992; Senn, Hanhimaki & Haukioja, 1992; Marino & Cornell, 1993; Jordano & Gomariz, 1994; but see Fowler & Lawton, 1984), likely reflecting variation in foliage quality associated with leaf age (Coley, 1980; Raup & Denno, 1983). Younger leaves generally have higher nitrogen (Potter & Kimmerer, 1986; Stamp & Bowers, 1990; Hunter & Lechowicz, 1992; Quiring, 1992; Jordano & Gomariz, 1994), potassium (Quiring, 1992), phosphorous (Quiring, 1992), and water (Potter & Kimmerer, 1986; Stamp & Bowers, 1990; Hunter & Lechowicz, 1992; Quiring, 1992; Jordano & Gomariz, 1994) content, lower tannin content (Feeny, 1970; Faeth, 1985), and are less tough (Potter & Kimmerer, 1986; Stamp & Bowers, 1990; Hunter & Lechowicz, 1992; Jordano & Gomariz, 1994). Similar patterns of declining leaf quality with leaf age have been documented for oaks (Feeny, 1970; Lawson *et al.*, 1984; Mauffette & Oechel, 1989). Although we have not examined the preferences of adult beetles for young foliage, nor their performance on young *versus* old foliage, we

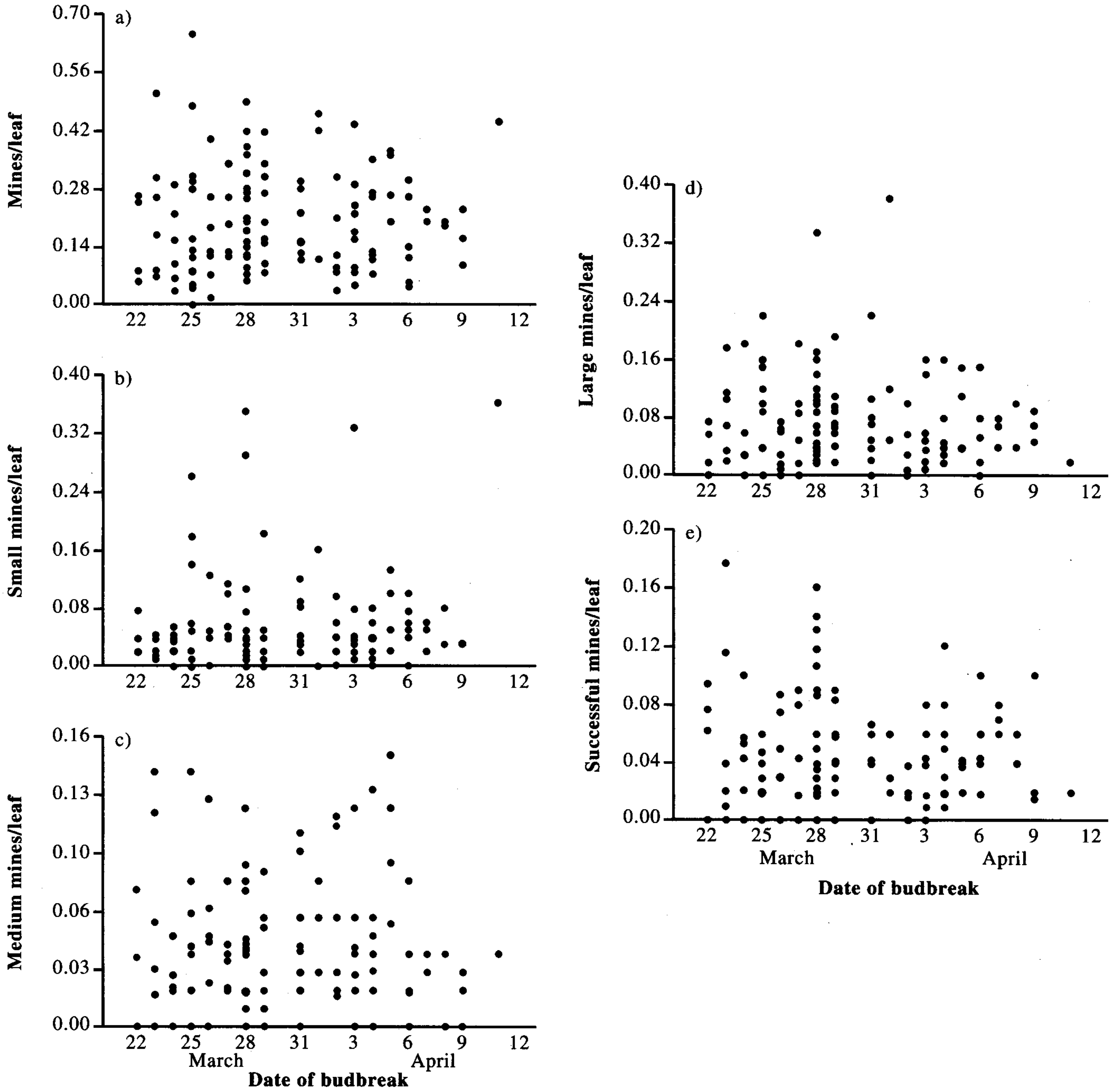

FIGURE 7. The relationships between budbreak phenology and the number of mines per leaf at the low Sesqui site. Patterns are similar for the other two sites. a) total mines: $r^2 = 0.00$, $p > 0.05$, $n = 136$; b) small unsuccessful mines (< 1 cm^2): $r^2 = 0.01$, $p > 0.05$, $n = 136$; c) medium unsuccessful mines (1 to 5 cm^2): $r^2 = 0.00$, $p > 0.05$, $n = 136$; d) large unsuccessful mines (> 5 cm^2): $r^2 = 0.00$, $p > 0.05$, $n = 136$; e) successful mines: $r^2 = 0.01$, $p > 0.05$, $n = 136$. Likewise, there were no significant relationships at either the Clemson road or high Sesqui sites.

suspect that variation in leaf quality is not the primary explanation for the increased leaf area lost to adult herbivory by *Q. laevis* that broke bud earlier. Instead, the damage patterns likely result from the approximately coincident emergence of adult beetles from the leaf litter (their overwintering site) and budbreak of *Q. laevis*. Adult beetles emerge approximately one week prior to budbreak and form large aggregations on the earliest flushing trees because foliage of later-breaking trees is unavailable. As the later-breaking trees flush, more trees become available for adult feeding. Thus, beetles become dispersed among more trees such that each tree supports a smaller number of adults and damage is more dispersed.

The effect of tree phenology on larval densities was more complicated. Early trees accumulated more eggs than later-breaking trees early in the season, likely because early-breaking trees provided the only suitable oviposition sites. However, this relationship disappeared by mid-summer.

Similar results were found for leaf chewing insects on Gambel oak (*Quercus gambelii*) (Faeth & Rooney, 1993); trees with artificially advanced budbreak suffered increased herbivore densities early in the season, but these differences disappeared later in the season, due at least in part to a preference for undamaged leaves by leaf-chewing insects. Female *B. tessellatus* defer egg laying until leaves complete expansion, with the earliest laying females ovipositing on the first expanded leaves, resulting in a relationship between egg number and phenology early in the season. However, by the time all females have initiated egg-laying, most leaves have fully expanded and thus the small effect of phenology detected early in the season is swamped by the large number of eggs laid after all leaves have expanded (females lay eggs until late July, but all leaves have fully expanded by late April).

Our results demonstrate that the effects of tree phenology on herbivore abundance can depend on the type of herbivore examined, or the stage of the insect life history examined. That early-breaking trees suffer increased herbivory by adult *B. tessellatus* illustrates that the limited availability of a critical resource (turkey oak foliage) alters the distribution of a mobile herbivore population; adults congregate on the few trees available early in the season (the early budbreak trees). Critical resources can also be temporally constrained because foliage quality rapidly deteriorates soon after budbreak (Quiring, 1992), or because the chemical or structural aspects of a plant limit its availability as a host later in the season (Potter & Kimmerer, 1986). These examples demonstrate intense selection on the herbivore for phenological synchronicity with its host. For *B. tessellatus* larvae, on the other hand, rapid changes in leaf abundance and quality observed early in the season do not coincide with larval development because eggs are laid on mature leaves. Thus, as observed for many herbivores that feed primarily on mature foliage (Karban & Ricklefs, 1984; Mauffette & Oechel, 1989; Matsuki & MacLean, 1994) plant phenology has no effect on the distribution of *B. tessellatus* larvae.

That *Q. laevis* budbreak phenology explained only *ca* 9% of the variation among trees in the amount of leaf area lost to adult herbivory suggests that factors other than tree phenology are likely better predictors of the distribution among trees of adult *B. tessellatus*. For example, plant genotype often affects the distribution of herbivores among trees (Moran, 1981; Service, 1984a; Fritz & Price, 1988; Mopper *et al.*, 1991), mediating herbivore distribution through genetic differences in either acceptability or suitability of leaves for the herbivore. Preliminary evidence suggests that plant genotype may affect the distribution of *B. tessellatus* herbivory on *Q. laevis* (Waddell & Mousseau, unpubl. data). Also, localized variation in environmental variables, such as solar exposure, water availability, and soil nutrient content likely affect attractiveness and suitability of leaves for *B. tessellatus*. Disentangling these different sources of variation of trees and their effects on herbivore distribution requires further investigation.

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