

Gall-Insect Community on Big Sagebrush Varies With Plant Size but not Plant Age

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ABSTRACT There is astounding variation in the abundance and diversity of insect herbivores among plant individuals within plant species in natural systems. One of the most well studied hypotheses for this pattern, the plant architecture hypothesis, suggests that insect community patterns vary with plant structural complexity and plant traits associated with structure. An important limitation to our understanding of the plant architecture hypothesis has been that most studies on the topic confound plant size and plant age. This occurs because, for most plant species, larger individuals are older individuals. This is a limitation because it prevents us from knowing whether insect community patterns are more dependent on traits associated with plant size, like resource quantity or plant apparency, or traits associated with plant age, like ontogenetic changes in phytochemistry. To separate these effects, we characterized galling insect communities on sagebrush (*Artemisia tridentata*)—a shrub in which age and size are not tightly correlated. We identified gall insects and recorded morphological measurements from 60 plants that varied separately in size and age. We found that plant size explained significantly more variation in insect gall abundance and species richness than did plant age. These results suggest that processes supporting the plant architecture hypothesis in this system are driven primarily by plant size and not plant age *per se*. Resource qualities associated with host-plant ontogeny may be less important than resource quantity in the assembly of herbivorous insect communities.

KEY WORDS plant architecture hypothesis, species richness, host-plant use, insect gall, *Artemisia tridentata*

Plants and phytophagous insects together form a major proportion of the global biodiversity, and herbivory may be the most common interspecific interaction on the planet (Strong et al. 1984). Despite the clear importance of the interactions between plants and insect herbivores, we lack a comprehensive understanding of the factors that influence the assembly of communities of insect herbivores on their host plants. Hypotheses that seek to explain insect community patterns on host plants concern all aspects of a plant including physical, chemical, physiological, and spatial characteristics, as well as effects of predators (Lawton and Price 1979, Fritz et al. 1986, Price 1991, Gonzales et al. 2002). One of the most comprehensive and long standing hypotheses is the plant architecture hypothesis (Lawton 1983). It states that insect communities will be more complex with greater richness and abundance on plants with greater structural complexity, both within and between species. This hypothesis is based on the observation that many plant traits important for insect communities vary with structural complexity, including plant apparency, niche diversity, and others. Lawton (1983) described five main components that make up plant architecture: 1) plant size, 2) growth form (e.g., herb

versus shrub), 3) seasonal development (e.g., seasonal change in growth rate and pattern), 4) variety in above-ground organs, and 5) persistence of individual organs. Many studies have supported the plant architecture hypothesis (Cornell 1986, Basset et al. 1992, Araújo et al. 2006, Campos et al. 2006, Espírito-Santo et al. 2007, Costa et al. 2011), whereas others have challenged it (Fernandes and Price 1988, Price et al. 2004).

The simplest component of plant architecture is plant size. One challenge to our understanding of the influence of plant size on variation in herbivore communities among plant individuals within plant species is that plant size is typically confounded with plant age in most species. A popular system for studies of insect communities is trees (Strong and Levin 1979, Neuvonen and Niemelä 1983, Cornell 1986, Fernandes and Price 1988, Basset et al. 1992, Basset 2001, Gonçalves-alvim and Fernandes 2001, Price et al. 2004, Campos et al. 2006, Costa et al. 2011). Unfortunately, tree size almost always correlates positively with tree age—taller or more heavily branched trees are usually older trees. As a result, studies of the plant architecture hypothesis in trees often fail to distinguish whether the differences in insect communities among plants are due to factors associated with age or size. Some studies even use plant height as a proxy for age because of the existence of this correlation (Basset 2001, Costa et al. 2011). Other studies do not clearly address the relationship between the two variables (Cornell 1986, Araújo et al. 2006,

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Sanford and Huntly 2010) or treat the two variables synonymously (Lawton 1983). This common treatment of these two often correlated variables obscures the true mechanism responsible for the observed insect community patterns.

The separate effects of plant size and age are an important distinction because they can have different effects on plant quality and different consequences for insect communities. A major effect of greater plant size is the greater quantity of resources available. Most fundamentally, larger plants may have greater species richness because of a sampling effect as well as greater environmental heterogeneity as more species are sampled over space (Scheiner 2003). Therefore, one would expect greater richness of insects associated with a larger plant, but there is little empirical evidence showing natural relationships between insect species richness and plant size independent of age. Additionally, greater size offers more microclimates and microhabitats both vertically and horizontally, resulting in a variety of environmental conditions on the plant along axes including temperature, shading, and foliage density (Lawton 1983, Gonçalves-alvim and Fernandes 2001). Also, a larger plant may be more apparent to an insect, so one may expect more insects on a larger plant (Feeny 1976, Espírito-Santo et al 2007). Plants taller than their neighbors may have leaves that are relatively more nutritious—or, alternatively, have higher concentration of defensive secondary compounds—because they have better access to sunlight (Mattson 1980). More foliage results in more layering of leaves, and shaded leaves tend to be thinner, larger, and have more chlorophyll *a* than nonshaded leaves (Thomas 2004). Varying degrees of shading can diversify resources to support different insect types, such as leafcutter ants that only use the sun-exposed leaves of *Inga oerstediana* (Nichols-Orians 1991). Finally, larger plants may be larger because they are more vigorous, a trait shown to be important in some systems (Price 1991).

Plant age, on the other hand, is often associated with qualitative ontogenetic changes that, though often correlated with plant size, can be different from the effects of plant size on the quantity or diversity of resources. Older trees often have tougher leaves than saplings, and this may prove important for insects that can only feed on a certain texture of leaves (Basset 2001). Leaves of mature trees, such as *Pourouma bicolor*, also exude more latex when damaged than the leaves of saplings, and this may alter palatability (Basset 2001). Some insects may prefer leaves or other above-ground parts of a certain age on a plant. For example, chewers only consume young foliage of *Pourouma bicolor* (Basset 2001) and ants that consume *Copaifera langsdorffi* depend on younger leaves because they have more extrafloral nectarines (Costa et al. 2011). If insect species specialize on plant parts of specific ages, then richness should be highest on older plants that have both old and young organs simultaneously. The leaf concentration of tannins can vary with age positively (Fritz et al. 2001), negatively (Bowers and Stamp 1993), or not vary at all (Costa et al. 2011) depending on the species of plant under study. Additionally, if plant traits

associated with ontogeny led to differential resistance and susceptibility to different herbivore species, then insect community composition may change as a plant ages (Mattson 1980, Lawton 1983, Kearsley and Whitham 1989, Basset 2001, Carmona et al. 2011).

We used the community of gall-forming insects on mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana*) to examine the separate effects of plant age and size on assembly of herbivore communities on host plant individuals. Sagebrush individuals can have a variety of growth rates. Because of their brittle stems, they are typically pruned to varying degrees by small disturbances including snow and wind, resulting in old plants of a variety of sizes (Bilbrough and Richards 1991). This growth form reduces the correlation between size and age, and allowed us to tease apart their effects on herbivore communities. Galling insects are an abundant guild of herbivorous insects on sagebrush (Sanford and Huntly 2010). We asked whether sagebrush age or size is a better predictor of 1) galling insect diversity, 2) galling insect abundance, and 3) galling insect community composition.

Materials and Methods

Study System. The research was conducted at the University of California's Valentine Eastern Sierra Reserve (37° 37'30" N; 118° 59'30" W) located in Mammoth Lakes, California, USA. This reserve sits at an elevation of ~2,400 m with an average annual precipitation of 51 to 64 cm and an average daytime temperature of 25°C in the summer and -10°C in the winter. The habitat is montane sagebrush steppe, of which sagebrush is the dominant woody plant.

Sagebrush is an evergreen shrub that is distributed throughout the intermountain west. It produces sclerophyllous leaves, is wind-pollinated, branches near to the ground, has a woody stem and branches, and is aromatic (Monsen and Shaw 2000). The shrub often dies back due to wind, snow, and ungulate movement among other factors, resulting in a reduction of foliage area, which does not return (Bilbrough and Richards 1991). Therefore, there is a high variation in size that allows for the existence similarly aged individuals with canopies that range from greater than 2 m to less than 20 cm in diameter.

Big sagebrush supports a community of herbivorous insects. Galls are growths on plants induced by insects for their own habitat and nutrition (Abrahamson and Weis 1997). Members of the gall community include at least 15 species of Cecidomyiidae midges from the genus *Rhopalomyia* (Hufbauer 2004, Sanford and Huntly 2010) and the Tephritidae fruit fly *Eutreta diana* (Goeden 1990). *Rhopalomyia* species make galls on the leaf, bud, or stem of the plant depending on the species while *Eutreta diana* only forms stem galls (Graham et al. 2001). Most species of gall-forming insects on big sagebrush have one generation per year (Gagné 1989) that generally involve laying eggs in the spring or fall that result in the development of the gall, overwintering, and then emergence the next year (Graham et al. 2001).

Field Sampling. We haphazardly chose 20 young and small, 20 old and large, and 20 old and small sagebrush individuals (Supp Fig 1 [online only]). Large plants had $>40,000\text{ cm}^3$ of foliage, while small plants had $\leq 6,000\text{ cm}^3$. For plant size we used mean canopy radius, which we calculated by measuring three orthogonal diameters of the plant canopy, assuming the canopy was an ellipsoid, multiplying the ellipsoid volume by the visually estimated proportion of the canopy that was occupied by foliage, and taking the cube root to convert back to a unit of length. We estimated plant age by measuring the total cross-sectional area of stems coming out of the ground because older individuals have larger woody stems than younger individuals, similar to the rings on a tree trunk. Counting growth rings of mountain sagebrush is both difficult and unnecessary when there is a significant correlation (average $R^2 = 0.62$) present in the subspecies (Perryman and Olson 2000). Young plants had stem areas $<10\text{ cm}^2$ while older plants had stem areas $>30\text{ cm}^2$. Young individuals with a large amount of foliage were not sampled because it is impossible for young sagebrush plants to have a large amount of foliage at that stage of development due to their small size.

Finally, we counted all current-year galls on each plant. We grouped galls into a total of 10 morphotypes based on morphological differences in shape, color, location on the plant, tissue texture, and size. All but three gall morphotypes were identified to species (using Gagné 1989 and Russo 2007). The three unknown species were labeled as *Rhopalomyia* sp1, *R.* sp2, and *R.* sp3. The seven identified species were *Rhopalomyia pomum*, *R. ampullaria*, *R. hirtibulla*, *R. anthoides*, *R. calvipomum*, *R. lignea*, and *Eutreta diana*. Individual plants had 0 to 5,695 galls and 0 to 8 species of galls. We subsampled abundances when there were >500 galls of a species on a plant by counting the number of galls on a smaller portion of the canopy and then multiplying the gall count by the estimated amount of times that the volume of the smaller portion of the canopy would fit in the volume of the entire canopy.

Statistical Methods. We used linear regressions to address our first and second questions about insect diversity and abundance. First, we employed linear regressions on plant size (mean canopy radius) and log-transformed total gall abundance, plant size and species richness, plant age and log-transformed total gall abundance, and plant age and species richness. Additionally, we log-transformed total gall abundance to achieve normality. We then performed a linear regression on log-transformed species richness and log-transformed plant size as well as on log-transformed total gall abundance and log-transformed plant size to analyze the linearity of the species–area relationship. Further, we employed a linear regression on the rarefied richness, or Hurlbert's Probability of Interspecific Encounters (PIE), with plant age and plant size. PIE is a metric of richness that is independent of sample size (Gotelli and Colwell 2001; Okansen et al. 2013).

To address our third question about insect community composition, we examined differences in

multivariate mean community composition using a permutational multivariate analysis of variance on $\log(x+1)$ transformed count data using Euclidean distances (Okansen et al. 2013). We examined differences in beta-diversity, variance in community composition among plants within groups, by testing for homogeneity of multivariate dispersion among old-small plants, young-small plants, and old-large plants (Anderson et al. 2006, 2011). Finally, we used Tukey's honest significant difference test to test as a post hoc test of differences in dispersion among the groups. All statistical analysis was done using the R statistical program (R Core Team 2013) and the R package vegan (Okansen et al. 2013).

Results

Insect gall species richness and total abundance increased with plant size and had no relationship with plant age. The linear regression of species richness with canopy size (Fig. 1a) displayed a strong positive linear relationship ($F_{1,58} = 135.9$; $P < 0.001$; $R^2 = 0.696$). These results were not changed when we considered richness and canopy size on log scales ($F_{1,58} = 125.9$; $P < 0.001$; $R^2 = 0.679$). On the other hand, there was not a significant relationship between rarefied species richness (Hurlbert's PIE) and plant size ($F_{1,33} = 2.844$; $P > 0.1$; $R^2 = 0.0515$). The relationship between total gall abundance and canopy size (Fig. 1b) was strongly positive ($F_{1,58} = 137.9$; $P < 0.001$; $R^2 = 0.699$), even on the log scale ($F_{1,58} = 128.7$; $P < 0.001$; $R^2 = 0.684$).

On the other hand, stem total cross-sectional area—a proxy for age—was not a significant predictor of gall insect species richness (Fig. 2a; $F_{1,58} = 3.587$; $P = 0.063$; $R^2 = 0.042$). Similarly, the linear regression of rarefied species richness and stem area had a weak relationship ($F_{1,33} = 2.381$; $P > 0.1$; $R^2 = 0.0390$). The linear regression of stem area and total gall abundance (Fig. 2b) also did not display a strong relationship ($F_{1,58} = 2.476$; $P > 0.1$; $R^2 = 0.024$). Additionally, plant size had only a weak correlation with stem area, our proxy for age ($r = 0.214$).

Mean multivariate community composition varied significantly with plant size ($F_{1,57} = 43.8$; $P < 0.001$; $R^2 = 0.43$) but not with plant age ($F_{1,57} = 0.34$; $P = 0.82$; $R^2 < 0.01$). In non-metric multidimensional scaling (NMDS) ordination space, gall communities on large-old plants had clear separation from those on young- and old-small plants (Fig. 3). In addition, there were significant differences in beta-diversity (multivariate dispersion) among the three groups of plants ($F_{2,57} = 29.8$; $P < 0.001$). Old-small and young-small plants had significantly lower beta-diversity than old-large plants (Tukey's HSD: $P < 0.001$), but old-small and young-small did not have significantly different beta-diversity ($P > 0.05$).

Discussion

Our results showed a positive relationship between the abundance and richness of the gall community on

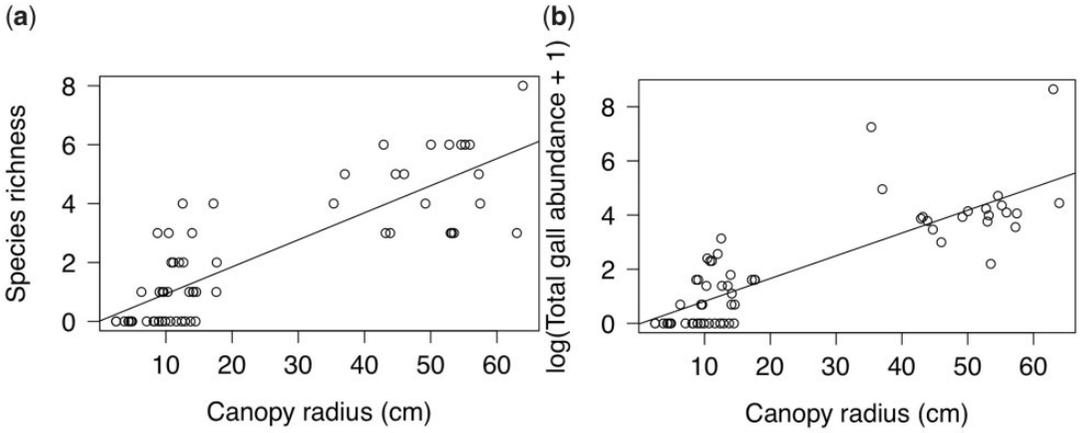


Fig. 1. (a) Gall insect species richness increased with plant size (canopy radius). The plotted line is the prediction from a linear regression ($F_{1,58} = 135.9$; $P < 0.001$; $R^2 = 0.696$). (b) Log gall abundance increased with plant size ($F_{1,58} = 137.9$; $P < 0.001$; $R^2 = 0.699$).

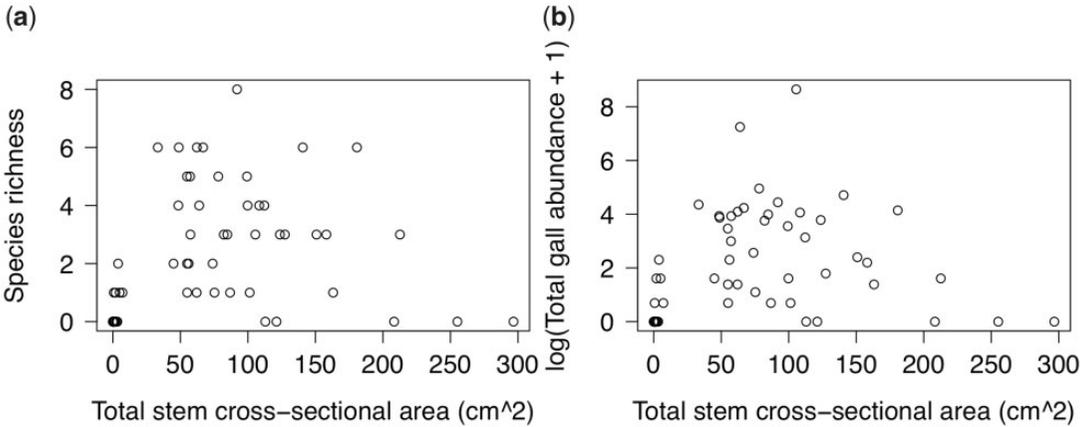


Fig. 2. (a) Gall insect species richness did not vary significantly with plant stem cross-sectional area ($F_{1,58} = 3.587$; $P = 0.063$; $R^2 = 0.042$). Stem area is strongly related with plant age. (b) Log gall abundances did not vary with plant stem cross-sectional area ($F_{1,58} = 2.476$; $P > 0.1$; $R^2 = 0.024$).

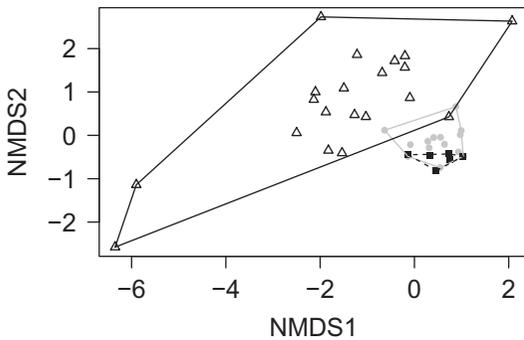


Fig. 3. NMDS ordination of gall insect community composition on sagebrush individuals. Young-small plants are black squares outlined by the broken black line. Old-small plants are gray circles outlined by the solid gray line. Old-large plants are white triangles outlined by the solid black line.

individual sagebrush plants and their sizes, but no relationship with plant age (Figs. 1–2). In addition, the mean multivariate composition of the gall community on sagebrush was similar on small plants regardless of size, but different on large plants (Fig. 3). These results ultimately support the plant size component of the plant architecture hypothesis defined by Lawton (1983) and reveal that insect herbivore community patterns in our system likely depend on plant traits related to plant size, not plant age.

The lack of a significant relationship between rarefied species richness (Hurlbert's PIE), a diversity metric that removes the effect of community size, further highlights the importance of plant size for insect community patterns. When rarefied richness is equivalent between two communities, it suggests that they would have the same richness if they were the same size. This result suggests that the strong increase in total richness with plant size may be driven by a biological sampling

effect: larger plants sample a greater proportion of the regional pool of gall insect species. This means that plant size *per se* is an important determinant of community patterns of insects on plants.

Plant size can have diverse effects on whether herbivore individuals and populations will use a particular plant as a resource. For instance, a large plant can offer more microclimates and microhabitats due to variations in the combinations of foliage layering, sun exposure, temperature, moisture, and light intensity on a single plant (Strong and Levin 1979, Lawton 1983, Gonçalves-alvim and Fernandes 2001). Additionally, the different microclimates can impact the diversity in physical appearance and composition of leaves, a resource utilized by many galling insects (Strong and Levin 1979). For instance, shaded leaves tend to be larger, thicker, and have more chlorophyll *a*, so varying sun exposures can result in a large amount of leaf types with some herbivores preferring shaded leaves over more sun-exposed leaves (Nichols-Orians 1991, Thomas 2004). Simply, insects are more likely to find larger plants, thus a larger plant will be found and likely used by more individuals and species (Feeny 1976, Espírito-Santo et al 2007). Another explanation is that insect survival varies with plant size. For example, structurally complex *Baccharis pseudomyriocephala* plants had greater gall insect survival, possibly due to large plants having fewer plant defenses or the complexity increasing the chances of a successful oviposition (Araújo et al. 2006). Additionally, the rate of successful gall initiation for at least one sagebrush gall species (*Eutreta Diana*) declines with increasing gall insect density, and such competition may be stronger on smaller plants (Wetzel 2014). On the other hand, it appears that qualities commonly associated with plant age, such as leaf toughness and the concentrations of secondary compounds, may not be important for patterns of gall-insect abundance on big sagebrush, perhaps because gall insects feed internally and modify the quality of the plant tissues on which they feed (Mattson 1980, Bowers and Stamp 1993, Basset 2001, Fritz et al. 2001, Costa et al. 2011).

The NMDS ordination (Fig. 3) suggests that old-small and young-small plants had similar gall communities with relatively little variation in community composition. Large plants, however, had significantly more variation in gall community composition. Communities on some large plants were similar to those on young- and old-small plants, but more often the communities were very different. The similarity between communities on young- and old- small plants and the differences between small and large plants suggest that plant size has a greater influence on gall community composition than plant age. This is also suggested by the multivariate dispersion (Fig. 3), whereby the old-large plants have a greater mean distance from the centroid than either of the two categories of plants. This means that the larger older plants have a higher beta diversity (mean multivariate dispersion) than the young- or old-small plants. Again, this suggests that plant size is more important for community patterns than plant age.

Plant-herbivore ecologists often focus on the effects that the quality of a plant, such as the nitrogen content

or concentration of chemical defenses, has on herbivore communities, rather than plant quantity (Awmack and Leather 2002). Our study indicates that the quantity of a resource—the size of a plant—can also play an important role in influencing herbivore community patterns and deserves more attention from ecologists.

The plant architecture hypothesis states that plants with greater size, more complex growth form, certain seasonal developments, a larger variety of above-ground parts, and a greater persistence of these components will support more herbivorous insects due to greater resource size, diversity, and apparency (Lawton 1983). Past studies on other host-plant systems have often used plant size and age synonymously due to its usual correlation, making it unclear as to which variable is mechanistically responsible for the observed pattern (Lawton 1983, Cornell 1986, Basset 2001, Araújo et al. 2006, Sanford and Huntly 2010, Costa et al. 2011). It is important to note that plant age and size can have very different effects on the insect community in the big sagebrush system. Because size and age are not correlated in sagebrush, we were able to show that plant size has a larger effect on insect community patterns in this system. This finding may hold true for other systems where the correlation is present and where the correlation would make it more difficult to separate and determine which variable is affecting the community.

Supplementary Data

Supplementary data are available at Environmental Entomology online.

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