



Original article

Oak-insect herbivore interactions along a temperature and precipitation gradient

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ABSTRACT

The interactions between herbivorous insects and their host plants are expected to be influenced by changing climates. Modern oaks provide an excellent system to examine this assumption because their interactions with herbivores occur over broad climatic and spatial scales, they vary in their defensive and nutritional investment in leaves by being deciduous or evergreen, and their insect herbivores range from generalists to highly specialized feeders. In this study, we surveyed leaf-litter samples of four oak species along an elevation gradient, from coastal northern California, USA, to the upper montane woodlands of the Sierra Nevada, to examine the relationship between climatic factors (mean annual temperature and precipitation) and oak herbivory levels at multiple scales; across all oak species pooled, between evergreen and deciduous species and within species.

Overall, temperature and precipitation did not appear to have a significant effect on most measures of total herbivore damage (percent leaves damaged per tree, percent leaf area removed and average number of feeding damage marks per leaf) and the strongest predictor of herbivore damage overall was the identity of the host species. However, increases in precipitation were correlated with an increase in the actual leaf area removed, and specialized insects, such as those that make leaf mines and galls, were the most sensitive to differences in precipitation levels. This suggests that the effects of changing climate on some plant–insect interactions is less likely to result in broad scale increases in damage with increasing temperatures or changing precipitation levels, but is rather more likely to be dependent on the type of herbivore (specialist vs. generalist) and the scale (species vs. community) over which the effect is examined.

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1. Introduction

Terrestrial ecosystems function through a complex web of interactions between members of different trophic levels, and the strength of these interactions is often modified by abiotic factors (Ayres, 1993; Lawton, 1995; Bale et al., 2002; Lewinsohn et al., 2005; Danks, 2007; DeLucia et al., 2012). At the base of these interacting webs lie two diverse and dominate groups, plants and their insect herbivores, whose interactions can be strongly influenced by the prevailing climate of the region, as well as by seasonal changes in temperature and precipitation (Coley, 1998; Adams et al., 2010;

Zvereva and Kozlov, 2010; Garibaldi et al., 2011; Pearse and Hipp, 2012). With regard to plants, temperature may affect their developmental rates (Went, 1953; Kramer et al., 2000; Körner and Basler, 2010; Hänninen and Tanino, 2011), leaf phenology, nutritional quality and defensive compounds in leaves (Reich and Oleksyn, 2004; Reich et al., 2007; Veteli et al., 2007; Asner et al., 2009; Janecke and Smit, 2011). These changes may then directly or indirectly influence the susceptibility of plants to herbivores (Aizen and Patterson, 1995; Dury et al., 1998; Menzel et al., 2008; Wu et al., 2011). In turn, variation in temperature may influence the diversity of insect herbivores in an area, their population sizes, overwintering survival rates, and thermal budgets for growth and reproduction (Sanderson, 1910; Headlee, 1914; Golightly and Lloyd, 1939; Headlee, 1941; Davidson, 1944; Wagner et al., 1985; Gilbert and Raworth, 1996; Régnière et al., 2012); all these are factors that influence the potential impact of insect herbivores on their hosts (Bale et al., 2002; Laws and Belovsky, 2010; Leimu et al., 2012).

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While the effects of temperature on plant–insect interactions have received much attention, the effects of precipitation on levels and types of herbivory experienced by plants are less understood (Bale et al., 2002; Ellwood et al., 2012). Many workers investigating the role of precipitation on herbivore–plant interactions have focused on examining the effects of temporary stressors such as drought (Huberty and Denno, 2004; Mazía et al., 2004; Guarín and Taylor, 2005) rather than comparing herbivory levels associated with areas that have differing levels of annual rainfall (but see Sinclair and Hughes, 2008; Mazía et al., 2012). However, both types of studies have shown that drought stress and naturally occurring precipitation regimes can affect the abundance, development and distribution of plants and insects, while also affecting the nutritional quality and defenses of plants (Ordoñez et al., 2009; Gutbrodt et al., 2012; Mazía et al., 2012). Precipitation-associated changes in plants and insects may also influence the type and strength of interactions that occur between these two groups. It has been further demonstrated that internal-feeding insects, such as those making galls or leaf mines, are particularly sensitive to variation in precipitation levels. Drier climates tend to have higher survivorship for gall-inducing insects (Fernandes and Price, 1992; Price et al., 1998), and decreased survivorship for leaf mining insects (Fernandes et al., 2004; Yarnes and Boecklen, 2005).

The response of plants to changes in climatic factors, and thus their susceptibility to insect herbivores, may be further modified by whether they employ a deciduous or evergreen strategy of leaf permanence (Dirzo et al., 2008; Pringle et al., 2011). Leaf permanence plays a role in plant–insect interactions because the timing of leaf development, the investment in leaf defenses and differences in the nutritional quality of leaves play a critical role in influencing a plant's susceptibility to insect herbivores (Field and Mooney, 1983; Barone, 2000; Karban, 2007; van Asch et al., 2007; Karban, 2008; Pearse and Karban, 2013). In short, deciduous leaves are relatively short-lived and are associated with a relatively high photosynthetic potential but may be more vulnerable to herbivores because fewer resources are invested in their defenses, both physically and chemically (Coley, 1988). The leaves of evergreen trees, on the other hand, have higher leaf permanence, which requires a larger allocation of resources to defense (both physically and chemically), leading to an associated reduction in nutritious quality and a lowering of a leaf's photosynthetic potential (Mooney and Gulmon, 1982; Field and Mooney, 1983; Coley and Barone, 1996; Borchard et al., 2011).

Oaks (*Quercus* spp.), members of the beech family (Fagaceae), are distributed across a wide range of Mediterranean semi-desert and temperate to subtropical forests throughout North and Central America, Europe and Asia (Nixon, 2006). Because of their widespread distributions and, at times, dominance within forests, oaks play a significant ecological role within a variety of communities and are often considered keystone species (Leach and Givnish, 1999; Grivet et al., 2008). In this study, we use four oak species distributed along an elevational gradient spanning coastal to inland California, to explore how climatic factors and leaf permanence strategies (deciduous vs. evergreen) influence the relationship between oaks and their insect herbivores, both generalist, external feeding insects and internal feeding insects which are often more specialized (Gaston et al., 1992). Consistent with the literature on plant–insect herbivore interactions in general and within oaks specifically, we test the predictions that 1) herbivory will be greatest where temperature and precipitation are highest (Bale et al., 2002; Huberty and Denno, 2004; Adams et al., 2010; Garibaldi et al., 2011), 2) that deciduous oak species will have higher levels of herbivory than evergreen species (Pearse, 2011; Pringle et al., 2011), and 3) that specialized, internal feeding types may be particularly sensitive to changes in climatic conditions, with

a higher frequency of galls in more xeric conditions (Fernandes and Price, 1992; Price et al., 1998) and a higher frequency of leaf mines corresponding to areas with higher annual rainfall (Fernandes et al., 2004; Yarnes and Boecklen, 2005; but see Nakamura et al., 2008). Finally, we also measured the leaf sizes associated with each oak species along the elevational gradient to explore whether climate along the gradients may influence leaf size and to determine whether such a change could influence our measures of herbivore damage (Ackerly et al., 2002; Qi et al., 2009).

2. Materials and methods

To examine the role that climate and leaf development strategies (deciduous vs. evergreen) play in determining insect herbivory in oaks, we examined insect herbivore damage levels associated with four oak species native to California. Of the four species, two were evergreens, *Quercus agrifolia* (Coast Live Oak) and *Quercus chrysolepis* (Canyon Live Oak), and two were deciduous, *Quercus kelloggii* (California Black Oak) and *Quercus douglasii* (Blue Oak). The gradient encompassed an elevation gain of 1804 m (from 137 to 1941 m), which was associated with a 6.1 °C range in mean annual temperature (9.7–15.8 °C) and a 57 cm range in annual precipitation (28.9–86.3 cm). The sites along this gradient were surveyed in July 2007 and included coastal to inland areas located within Landels-Hill Big Creek (0–1220 m elevation; 36°4' N, 121°34' W) and Hastings Natural History Reserves (467–953 m elevation; 36°12.5' N, 121°33.5' W), within the University of California Natural Reserve System, and Sequoia National Forest (305–3658 m elevation; 35°56' N, 118°29' W), which is located in the southern Sierra Nevada. While none of the oak species were found at all sites, each species was found at several elevations within at least two sites (Fig. 1). *Quercus agrifolia* was found at Landels-Hill and Hastings; *Q. chrysolepis* was found at Landels-Hill, Hastings and Sequoia National Forest; *Q. kelloggii* was found at Landels-Hill, Hastings and Sequoia National Forest; and *Q. douglasii* was found at Hastings and Sequoia National Forest. Each species was sampled over a portion of its elevational range at this latitude: *Quercus agrifolia* (range from below 1,000 m), *Q. chrysolepis* (from 200 to 2600 m), *Q. kelloggii* (from 300 to 2,500 m), and *Q. douglasii* (below 1200 m; elevation data from Knops and Koenig, 1997).

2.1. Herbivory levels and specialized feeding types

The herbivory levels and specialized, internal feeding types associated with ten trees of each species (for a total of 40 sampled trees) along the elevational gradient were examined from leaf litter samples. A focal tree, representative of the trees in its elevational zone, was selected. Below each focal tree, 20 leaves were sampled from three locations directly beneath the canopy by placing a 1 m² quadrat haphazardly at distances of one-third and two-thirds from the trunk of the tree to the canopy edge and at the canopy edge (60 leaves/tree × 10 trees/species = 600 leaves/species). Leaves were collected in July 2007 from the upper leaf litter layer to avoid the inclusion of leaves that could be damaged as the result of physical processes or by detritivores (*sensu* Smith and Nufio, 2004). Leaf litter sampling was used in order to sample leaves from the whole tree, as herbivory is not evenly distributed throughout a tree's canopy (Reynolds and Crossley, 1997; Cornelissen and Stiling, 2005), and because higher canopy leaves are difficult to access. In addition, leaf litter samples allow for greater standardization of samples between trees (Adams and Zhang, 2009). It was assumed that the sampled leaves beneath the deciduous trees were shed during the previous fall and winter and that the leaves beneath the evergreens were part of the regular, periodic process of leaf shedding by these species.

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