



Original article

Compensatory responses in plant-herbivore interactions: Impacts of insects on leaf water relations

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ABSTRACT

Herbivore damage to leaves has been typically evaluated in terms of fractions of area removed; however morpho-physiological changes in the remaining tissues can occur in response to removal. We assessed the effects of partial removal of the leaf mesophyll by *Caliroa cerasi* (Hymenoptera) on leaf hydraulic conductance (K_{leaf}), vascular architecture, water relations and leaf size of three *Prunus avium* cultivars. The insect feeds on the leaf mesophyll leaving the vein network intact (skeletonization). Within each cultivar there were trees without infestations and trees chronically infested, at least over the last three years. Leaf size of intact leaves tended to be similar during leaf expansion before herbivore attack occurs across infested and non-infested trees. However, after herbivore attack and when the leaves were fully expanded, damaged leaves were smaller than leaves from non-infested trees. Damaged area varied between 21 and 31% depending on cultivar. The non-disruption of the vascular system together with either vein density or capacitance increased in damaged leaves resulted in similar K_{leaf} and stomatal conductance in infested and non-infested trees. Non-stomatal water loss from repeated leaf damage led to lower leaf water potentials in two of the infested cultivars. Lower leaf osmotic potentials and vulnerability to loss of K_{leaf} were observed in infested plants. Our results show that skeletonization resulted in compensatory changes in terms of water relations and hydraulics traits and in cultivar-specific physiological changes in phylogenetic related *P. avium*. Our findings indicate that detrimental effects of herbivory on the photosynthetic surface are counterbalanced by changes providing higher drought resistance, which has adaptive significance in ecosystems where water availability is low and furthermore where global climate changes would decrease soil water availability in the future even further.

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1. Introduction

Leaf injury by insects (either miners or mass consumers) can induce a wide range of metabolic and physical changes in host-plants (Oleksyn et al., 1998). Plant responses to insect injury are highly dependent on leaf phenological state, intensity of damage, type of plant tissue attacked, type of injury (that is, the feeding guild of the herbivore), species and environmental conditions (Welter, 1989; Peterson and Higley, 2001). Research on biotic stress

traditionally has focused on the biological agents causing the infestation, rather than on the physiological responses of plants to tissue removal (but see McNaughton, 1983; Raimondo et al., 2003; Aldea et al., 2005; Kerchev et al., 2012). In particular the influence of herbivory on plant water relations and hydraulic traits is less understood (Raimondo et al., 2003; Aldea et al., 2005; Nardini et al., 2010; Pittermann et al., 2014).

The removal of leaf tissue by herbivores can result in a reduction of the total photosynthetic surface; while the remaining leaf tissue can experience changes in liquid phase water movement and stomatal conductance, which could affect whole leaf functioning (Delaney and Higley, 2006; Turnbull et al., 2007). When the leaf vasculature is damaged, in particular the main veins, leaf hydraulic conductance drastically decreases, and this effect persists even

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after the damage has healed. Nevertheless, redundancy in the venation can buffer leaf water transport against the damage by providing alternative pathways for water transport to the mesophyll (Sack et al., 2008). Mechanical damage to inter-veinal tissue (skeletonization) produces substantial water loss from cut edges and surfaces (Ostlie and Pedigo, 1984; Aldea et al., 2005) affecting the leaf extra-vascular water transport. This higher water loss may result in leaf water potentials decline and eventually in total leaf dehydration. Some of the few studies that have examined the effects of defoliation on whole-plant water relations, however, have shown improved plant water status in response to increased water supply per unit leaf area (Hart et al., 2000; <http://jxb.oxfordjournals.org/content/64/6/1625.full> Quentin et al., 2011).

Leaf size can be genetically determined or can be regulated by consumption (e.g. herbivores), mechanical damage (e.g. wind) or physiological processes (e.g. water deficits). High levels of herbivore pressure apparently favor the evolution of small leaf size (Brown et al., 1991; Moles and Westoby, 2000). The loss of part of the leaves during leaf expansion by herbivores, not only implies a loss of structural components but also of proteins and lipids associated with photosynthesis and leaf growth (Kursar and Coley, 1992). Simultaneously, the excessive loss of water from edges after defoliation may have a negative effect on both leaf expansion rates and final leaf size (Mazzoleni and Dickmann, 1988; Metcalfe et al., 1990).

The objective of this study was to investigate the effects of leaf infestation by *Caliroa cerasi* L. (cherry slugworm) on three sweet cherry (*Prunus avium* L.) cultivars. This insect is one the most important pests in sweet cherries crops in the Argentinean Patagonia and their larvae produce skeletonization of the leaves leaving relatively intact the vein network of the eaten leaves. We asked whether: i) the herbivory by *C. cerasi* during the leaf expansion phase of *P. avium* impacts on the leaf size, ii) leaf damage affects leaf water potential components, and iii) responses to herbivory can counter/offset the effects of herbivore attack, in particular anatomical and physiological changes related to leaf hydraulics. To respond those questions we used intact leaves of non-infested trees as control and damaged leaves from chronically infested trees occurring at least during the last three years before this study was done.

2. Materials and methods

2.1. Location and study species

The study was conducted in El Porvenir Ranch located in Los Antiguos town in northwest Santa Cruz, Argentina at the foot hills of the Andes (46° 19' S, 71° 62' W, altitude 220 m), one of the main areas for commercial cherry growth in southern Patagonia. The climate can be characterized as temperate or cold-temperate. Mean monthly temperatures range from 2.5 to 14.9 °C and the chilling requirements of cherries are easily satisfied. This area is dominated by Pacific air masses and strong westerly winds. The Andes mountain range presents an orographic barrier for these humid masses of air coming from the Pacific Ocean which precipitate on the western side of the Andes, resulting in a very low annual precipitation in the eastward of Andes. The mean annual precipitation in the study site is 192 mm falling mostly in the fall and winter (April–September). The cherry slugworm, *C. cerasi* (Hymenoptera: Tenthredinidae), is conspicuous in many South America countries and it is one of the most important pests in sweet cherries. The larvae feed in such a way that the leaf veins remain intact. They rarely remove the abaxial leaf surface determining the characteristic skeletonized appearance. *Prunus* is an important host genus (Carl, 1972; Naumann et al., 2002). *P. avium* is a deciduous woody

species that flowers before new leaves are produced. Three cultivars of sweet cherry trees (*P. avium*) were selected for the study: Lapins, Bing and Van. These cultivars are the most commonly used in Southern Patagonia (Cittadini and San Martino, 2007). In the study area and in the three cultivars new leaves expand from November to January and they are fully developed in February. The study was carried out before tree infestation by *C. cerasi*, (November 2009) and during the month of most intense defoliation by the insect (February 2010). Three to six infested (at least during the three previous years before this analysis) and non-infested individuals in each cultivar were randomly chosen resulting in a total of 18–36 trees across all three cultivars depending on the variable measured. These grouping (infested and non-infested trees) used to classify trees were determined by the presence or absence of herbivory during three years before this study began. The infested trees had more than 50% of damaged leaves (eaten to some degree), while non-infested trees (control group) had less than 1% of damaged leaves. All the trees were seven years old with similar total leaf surface area and height, planted as free standing trees (280 trees ha⁻¹) and irrigated by gravity (Muñoz, 2004). All trees from the three cultivars were grown under similar environmental conditions. Leaves within each group were sampled on the same calendar date and were of similar age. In this study we will use hereafter “damaged leaves” and “intact leaves” to refer to leaves with substantial tissue removal by the insect from infested trees and intact leaves from non-infested trees, respectively.

2.2. Leaf area, leaf dry mass per unit area and venation architecture

To determine the effects of herbivory on leaf size, twenty full expanded damaged leaves and twenty full expanded intact leaves were collected both in February (end of the leaf expansion phase) from six trees per cultivar and condition. A similar number of leaves (n = 20) from five infested and non-infested trees were collected in November (prior to infestation and when leaves were expanding). Fresh leaves images were acquired using a scanner and the images analyze for leaf size was performed with the ImageJ 1.47k software. The total non-damaged area and the area removed by the insects were also determined in each leaf. The leaves collected in February were oven-dried at 70 °C until constant weight, and dry mass was used for leaf dry mass per area (LMA) determination.

To evaluate the effects of infestation on leaf vasculature several intact leaves recently expanded from infested trees were marked. The next day those leaves infested by *C. cerasi* were identified. At least five damaged leaves after five days of infestation and five intact and recently expanded leaves from non-infested trees in each cultivar were cut off under distilled and filtered water. Then their petioles were placed in contact with filtered aqueous Phloxine B for 30 min to check whether the veins in damaged leaves were still intact as revealed by their light red staining. Leaves were then cross-sectioned using fresh razor blades and major and minor veins were observed under a microscope for their structural and functional integrity (Raimondo et al., 2003). Leaves of infested and non-infested trees per cultivar were cleared for studying venation traits. Leaf major vein density and vein diameter were determined from not damaged sections cut centrally on the right-hand side of each leaf. The major vein density was determined as the sum of 1°, 2°, and 3° vein densities (Scoffoni et al., 2011). Images of approximately 0.5 mm² per section were obtained with a color microscope camera (TCA-3C Tucsen, China) mounted on a light microscope (Axioplan ZEISS, Germany). The images were then obtained with TSVIEW v 6.1.3.9 Software and the veins were measured and counted using the ImageJ 1.47k software.

Twenty four to fifty three sections of the middle part of the leaf midrib from infested and non-infested trees were obtained using a

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