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Humera S. Mirza
*California State Polytechnic University, Pomona*

Lauren M. Tucker
*California State Polytechnic University, Pomona*

Rodrigo Méndez-Alonzo
*California State Polytechnic University, Pomona*

Edward G. Bobich
*California State Polytechnic University, Pomona*

Frank W. Ewers
*California State Polytechnic University, Pomona*

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COMPARATIVE LEAF WATER ABSORPTION BETWEEN CHAPARRAL ISLAND AND MAINLAND TAXA: A COMMON GARDEN EXPERIMENT

Humera S. Mirza1,2, Lauren M. Tucker1,3, Rodrigo Mendez-Alonzo4, Edward G. Bobich1, and Frank W. Ewers1,5

1Department of Biological Sciences, California State Polytechnic University, 3801 W. Temple Ave, Pomona, California 91768; 2Present address: Department of Botany and Plant Sciences, University of California, Riverside, California 92521; 3Present address: Department of Biological Sciences, Idaho State University, Pocatello, Idaho 83209; 4Departamento de Biología de la Conservación, CICESE, C.P. 22860 Ensenada, Baja California, Mexico; 5Corresponding author (fwewers@cpp.edu)

ABSTRACT

In California and other Mediterranean-type ecosystems, island species are typically exposed to more fog but less rain than mainland species. Because adaptations to absorb water from fog may conflict with those to minimize water loss, we hypothesized that island species should have greater fog absorption than their mainland congeners due to foliar uptake but at the cost of modifying other leaf structural and functional traits. To determine whether foliar water absorption is an adaptation to insularity, we compared seven physiological and anatomical leaf traits between congeneric island and mainland species of two genera, Ceanothus and Arctostaphylos, in a common garden in Claremont, California. We quantified leaf water potentials, maximum leaf water absorption rates, leaf hydrophobicity, leaf mass per area [LMA], succulence, stomatal density, and wax morphology. All taxa exhibited water permeability through their leaf surfaces, but only one of the three island taxa showed greater water absorption than their mainland counterparts. The island and mainland varieties of C. megacarpus were similar in water absorption and hydrophobicity, but the mainland variety had greater LMA, greater succulence, and thicker epicuticular wax. In Arctostaphylos, insularity promoted species-specific responses: A. catalinae had greater foliar absorption compared to the mainland species, whereas A. insularis displayed mesophytic traits such as hypostomatal morphology, horizontally oriented leaves and low LMA. Relative surface hydrophobicity was not linked to absorption rates, but the mainland species A. glauca had the most hydrophobic leaf surfaces in the study, achieved by their ornate epicuticular wax. Overall, island taxa displayed more mesophytic leaf traits than their mainland congeners. The results may have implications for biogeography in Mediterranean-type ecosystems that may be losing seasonal coastal fog with global change.

Key words: Arctostaphylos, Ceanothus, foliar water absorption, island and mainland plants, LMA, leaf contact angle, leaf hydrophobicity, leaf succulence, scanning electron microscopy.

INTRODUCTION

In addition to groundwater, plants may absorb fog water directly into the leaves (foliar absorption: Burgess and Dawson 2004; Limm et al. 2009; Guzmán-Delgado et al. 2018). Under some circumstances, for example, when fog envelops trees, the atmosphere around the leaves has a higher water potential, due to extremely low vapor deficit values, than the leaves themselves, which could allow foliar uptake (Eller et al. 2013, 2016). Foliar uptake occurs when atmospheric water droplets coalesce on plant shoots and move along a water potential gradient (Rundel 1982). This kind of water absorption immediately increases foliar hydration and plant water potential (Grammatikopoulos and Manetas 1994). Wetting of leaves with fog, mist, and dew may provide a significant water subsidy in many ecosystems and thereby positively affect plant water balance without noticeably increasing soil wetness (Kerfoot 1968; Leyton and Armitage 1968; Kerr and Beardsell 1975; Boucher et al. 1995; Yates and Hutley 1995; Ebner et al. 2011). Fog may change the system energy balance by reducing solar heating and increasing relative humidity above and within a plant canopy, thus reducing evapotranspiration during photosynthetic gas exchange (Dawson 1998; Weathers 1999).

The waxy cuticle is crucial for retaining water in land plants, but the structure and function of cuticle is variable (Sevanto 2019), and its effects on water relations have been explored for plants ranging from trees (e.g., Schreel and Steppe 2020) to epiphytes (Pan et al. 2021). Understanding the features that help plants absorb and retain water for survival, including foliar water uptake, should improve our basic understanding of plant hydraulics, which will improve predictive models of vegetation distributions in the event of global change.

One suitable model to test the prevalence of foliar water absorption is island species, which may take advantage of the fog water more than the mainland plant species. In the Channel Islands of California, sea-level fluctuations have promoted allopatric speciation of plant species of the chaparral vegetation since the Miocene period (Axelrod 1958); therefore, species from this archipelago should evidence adaptations related to exposure to a fog-prone environment. In the present study, we examined leaf features of island and mainland congeners...
of both _Ceanothus_ and _Arctostaphylos_, two well-represented genera of the chaparral in the California Floristic Province.

Island and coastal species are often exposed to more fog, but often less rain, than mainland species in the Mediterranean regions of the world (Dawson 1998; Holmlund et al. 2016). At the foliar level, adaptations to absorb water from fog or mist may conflict with adaptations to minimize water loss, which might result in dew evaporating into the atmosphere. Plants living where frequent fog or dew events occur may have significant tissue hydration (Limm et al. 2009). There are other physiological advantages of foliar water absorption that include higher survival rates (Vaadia and Waisel 1963), increased plant growth (Boucher et al. 1995; Holmlund et al. 2016), and enhanced gas exchange after surfaces of leaves dry (Simonin et al. 2009; Holmlund et al. 2016). In the present study we tested whether insularity promotes adaptations to enhance water balance due to atmospheric water utilization. We hypothesized that, due to natural selection, island species would have a greater capacity for foliar absorption of fog and mist compared to closely related mainland species. If selection has indeed produced adaptations to promote leaf water absorption in insular species, the island species should have leaf anatomical and physiological features allowing for increased absorption or retention of water derived from fog or mist. We investigated this hypothesis by comparing island to mainland taxa in a common garden (California Botanic Garden, Claremont, California). We compared leaf water absorption, leaf water potentials, leaf hydrophobicity, stomatal density, succulence, leaf dry mass, and performed scanning electron microscopy (SEM) of the leaf cuticle on six taxa of the two genera, three taxa with an insular provenance (Channel Islands, California), and three from mainland chaparral.

**MATERIALS AND METHODS**

**Study Site and Species**

All plant material was collected within the confines of the 0.348 km² California Botanic Garden located about 56 km East of Los Angeles. The plants were all growing within 500 m of one another in full sun, on relatively flat terrain. Plants were all irrigated periodically. The Garden was an ideal location to investigate the hypotheses because it includes live specimens of both island and mainland taxa of the same genus. The plant material used in this study all had detailed records of accession. The garden also has an active research department including an anatomy lab with scanning electron microscopy (SEM).

The taxa that were investigated are listed in Table 1. _Ceanothus_ is a genus of 50-60 dicotyledonous shrubs and small trees of the Rhamnaceae (Dale 2000; Baldwin et al. 2012). Two taxa of _Ceanothus_ served as study subjects: the mainland taxon _C. megacarpus var. megacarpus_ and the island taxon _C. megacarpus var. insularis_ (Table 1). Both varieties occur on rocky slopes and canyons with chaparral vegetation and differ by the island form having slightly larger leaves (< 4 cm vs. < 2.6 cm) than the mainland form, and opposite leaves (vs. alternate) (Baldwin et al. 2012).

_Arctostaphylos_ is a genus in the Ericaceae comprised of about 60 species of shrubs and small trees (Baldwin et al. 2012). Four taxa of _Arctostaphylos_ served as study subjects (Table 1), all residing in subgenus _Arctostaphylos_ that contains three sections: _Arctostaphylos_, _Foliobracteata_, and _Picobracteata_. _Arctostaphylos glauca_ Lindl., _A. pungens_ Kunth (both mainland species), and _A. insularis_ Greene ex Parry (island species) belong to section _Arctostaphylos_, and _A. catalinae_ (island sp.) belongs to section _Foliobracteata_. Nomenclature is based on Baldwin et al. (2012) and Simpson (2019).

**Water Absorption Measurements**

The capacity of leaves to absorb water was measured by submerging the leaf samples directly into water. First, the youngest, fully expanded leaves were cut from all five plants for each species. The exposed surface of the petiole was then sealed with super glue (Locotite Brand, Henkel Corporation, Ohio) to avoid any error in weighing before and after water submergence and to prevent evaporation or water absorption from the exposed petiole surface during measurement. The initial mass of the leaf was measured using an electronic balance. The leaf was then submerged in deionized water for five seconds, removed quickly, pat-dried using a paper towel and the leaf mass was recorded again to measure the possible artifact of residual water remaining after patting the leaves with a paper towel. The leaf was submerged again in deionized water and kept in dark for three hours to allow water absorption by the leaf. After removing the leaf from the water container and patting it with a paper towel, leaf mass was recorded again to determine water absorption by the leaf. The amount of water absorbed for each leaf was calculated by evaluating the change in leaf mass after submergence (% increase) using the following equation:

\[
\text{Uptake} = \left[ \frac{(\text{Mass2} - \text{Mass1})}{\text{Mass1}} \right] \times 100\%
\]

**Table 1. Sources of material for the common garden study.**

<table>
<thead>
<tr>
<th>Family</th>
<th>Taxon</th>
<th>Distribution</th>
<th>Locality</th>
<th>County</th>
<th>Propagation material</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhamnaceae</td>
<td><em>Ceanothus megacarpus var. megacarpus</em> Nutt.</td>
<td>Mainland</td>
<td>Santa Ynez Mountains</td>
<td>Santa Barbara</td>
<td>Seed</td>
</tr>
<tr>
<td>Rhamnaceae</td>
<td><em>Ceanothus megacarpus var. insularis</em> Munz</td>
<td>Island</td>
<td>Santa Catalina Island</td>
<td>Los Angeles</td>
<td>Seed</td>
</tr>
<tr>
<td>Ericaceae</td>
<td><em>Arctostaphylos pungens</em> Kunth</td>
<td>Mainland</td>
<td>Oy Mountains</td>
<td>San Diego</td>
<td>Cutting</td>
</tr>
<tr>
<td>Ericaceae</td>
<td><em>Arctostaphylos glauca</em> Lindl</td>
<td>Mainland</td>
<td>Santa Ana Mountains</td>
<td>Orange</td>
<td>Seed</td>
</tr>
<tr>
<td>Ericaceae</td>
<td><em>Arctostaphylos catalinae</em> P.V. Wells</td>
<td>Island</td>
<td>Santa Catalina Island</td>
<td>Los Angeles</td>
<td>Seed</td>
</tr>
<tr>
<td>Ericaceae</td>
<td><em>Arctostaphylos insularis</em> Greene ex Perry</td>
<td>Island</td>
<td>Santa Cruz Island</td>
<td>Santa Barbara</td>
<td>Cutting</td>
</tr>
</tbody>
</table>
where Mass1 is the beginning mass of leaf after five seconds of submergence and Mass2 is the mass of leaf after submergence for 180 minutes (Limm et al. 2009).

Leaves were all collected in midmorning and leaf water potential was measured on three leaf samples per plant of five individual plants of each species, both before and after the water absorption experiment, using a pressure chamber (Scolander et al. 1965). To avoid possible artifacts caused by the pressure chamber treatment, we ran duplicate leaves in the water absorption measurements. Water potential was sampled again after submergence using the pressure chamber to evaluate the increase in water content in the symplast. To remove the super glue before measurement of water potential, ca. 1 mm of tissue was cut off the petiole from each sample.

To determine whether initial water potential impacted absorbance, one set of leaf samples was kept in plastic bags and processed the same day they were collected. The values were representative of the winter (wet season) water potentials found in field conditions for these species. Another set of leaves was left on the bench overnight in open plastic bags to air dry and the water absorption experiment was repeated the next day. This bench dry treatment resulted in water potentials typical for the summer dry season for these taxa and was used to determine if dehydration reflected in lower leaf water potential values impacted the amount of foliar absorption.

**Hydrophobicity**

To determine hydrophobicity of leaf surfaces, the contact angle that forms between drops of water and the adaxial and abaxial leaf surfaces was measured with an automatic contact angle meter (Attension Theta Lite optical tensiometer, Biolin Scientific, Gothenburg, Sweden). Contact angle is an indicator of the relative hydrophobicity of any surface. The degree of hydrophobicity depends on the chemical and physical properties of the surface, where a contact angle above 90° indicates water repellency (hydrophobic), and below 90° indicates leaf wettability (hydrophilic) (Koch and Barthlott 2009; Papierowska et al. 2018).

Leaves and shoots were collected from California Botanic Garden and damped dry with a paper towel, then left overnight in open plastic bags, which were sealed the next morning to assure the leaves had dry surfaces and fairly low water potentials, but were within the normal range for these plants.

The samples were transported the next day to the Center for Scientific Research and Higher Education (CICESE), Ensenada, Mexico, for hydrophobicity measurements. Slides were prepared by attaching a 3 mm x 4 mm piece of leaf sample onto a slide with double-sided tape. The samples were from the median part of the leaf adjacent the midrib.

For each leaf, adaxial and abaxial slides were prepared and contact angles were measured. A drop of ultrapure water was placed on the leaf surface and the contact angles were automatically measured by taking photographs every 20th of a second over a 3-second period using a 2048 frames per second camera (i.e., ca. 60 photographs per sample). Photographs were automatically analyzed using OneAttension software (Biolin Scientific, Gothenburg, Sweden). Left and right contact angles in each picture were recorded and the mean contact angle for each set of pictures per sample was calculated.

**Leaf Area and Succulence**

To measure leaf area and succulence, three leaves per plant for five plants per species were sampled. An LI-3100C Leaf Area Meter (LI-COR Biosciences, Nebraska) was used to measure leaf area in cm². The fresh leaf mass (in g) was recorded by using an electronic balance. Leaves were then dried in an oven at ca. 70°C to constant mass, which occurred after two days. The difference in the fresh and dry mass of leaves demonstrated the water content (Mantovani 1999). Succulence of each leaf was calculated in g of water per cm² by using the following equation:

\[
\text{Succulence} = \frac{(\text{Fresh Leaf Mass} - \text{Dry Leaf Mass})}{\text{Leaf Area}}
\]

where Fresh Leaf Mass is the leaf mass measured before drying and Dry Leaf Mass is the leaf mass measured after drying the leaf sample (Mantovani 1999).

**Scanning Electron Microscopy**

Scanning electron microscopy (SEM) was performed at California Botanic Garden using a Hitachi SU3500 SEM (Hitachi High-Technologies, Tokyo, Japan) on leaf samples from each taxon to obtain the surface anatomy and composition. Tissue was cut in the lab from the middle portion of the blade half-way between the midrib and the leaf margin, fixed in FAA (formaldehyde-ethanol-glacial acetic acid), and dehydrated in ethanol. Specimens were processed with critical point drying and sputter-coated with gold. The SEM images were used to measure stomatal density and to investigate whether anatomical features may play any role in water absorption or retention in the leaf. Stomatal density was calculated as the number of stomata per mm² based upon relatively low magnification (50×) so that a fairly large area of leaf (4.8 mm²) could be sampled. In this process, five leaves, one per plant, were sampled per species.

The SEM images were also used to make measurements of stomatal frequency. Stomatal density was not measured in *Ceanothus*, since both *Ceanothus* taxa lacked adaxial stomata, and the abaxial surface was completely covered with trichomes such that the stomata were not visible in SEM.

**Statistical Analyses**

Leaf water potential, succulence, leaf dry mass per area, water absorption, stomatal density and contact angle measurements were analyzed among species and between categories (insular vs. mainland species). One-way analysis of variance (ANOVA) was used for leaf water absorption measurements (species as the categorical factor), and two-way ANOVA was performed for leaf water potential, succulence, leaf dry mass per area, stomatal density, and contact angle measurements (species × insularity as categorical factors). If significant differences were found, these procedures were followed by a Tukey’s HSD (Honest significant difference) post-hoc comparison between all species of both genera.

**RESULTS**

**Leaf Water Potential**

Leaf water potential was measured before and after the leaf absorption experiment. The absorption treatments resulted in
only small increases in leaf water potential; in most cases the increases were less than 1 MPa and were not statistically significant (Fig. 1). In Arctostaphylos, the bench dry treatment resulted in water potentials that were about 2–3 MPa lower (more negative) than for fresh samples. Following the bench dry water absorption experiments, two Arctostaphylos species, A. glauca and A. pungens, had significant increases (P = 0.016 and 0.017, respectively) of 1 MPa or more in their initial versus final leaf water potentials (Fig. 1B).

Stomatal Density.—In Arctostaphylos, the adaxial versus abaxial surfaces of A. pungens, A. glauca, and A. catalinae were very similar in stomatal density. However, the adaxial versus abaxial surfaces were significantly different for A. insularis because the adaxial surface had no stomata whereas the abaxial surface had very high stomatal density, that is, it had hypostomatous morphology (Fig. 2). The abaxial stomatal density for A. insularis was almost double compared to the other three species of Arctostaphylos (Fig. 2). As noted in the methods section, the stomata of Ceanothus were not visible with SEM due to the abundance of abaxial trichomes which obscured the stomatal crypts.

Leaf Mass per Area and Succulence

The leaf mass per area (LMA) was lower for C. megacarpus var. insularis than for C. megacarpus var. megacarpus (P = 0.04; Fig. 3A). Similarly, LMA of Arctostaphylos insularis tended to be lower compared to mainland species of Arctostaphylos (P < 0.10). LMA for mainland species A. pungens and A. glauca did not differ from each other (P = 0.37; Fig. 3A). Succulence, the amount of water present per leaf area, measured in g/m², was greater in C. megacarpus var. megacarpus compared to C. megacarpus var. insularis (P = 0.07; Fig. 3B). For Arctostaphylos, leaves of A. pungens were significantly more succulent than those of the island species A. catalinae and insularis. However, succulence for A. glauca was similar to the other three species of Arctostaphylos (Fig. 3B).

Water Absorption Measurements

All six studied species demonstrated the capacity for leaf water absorption when submerged for 180 minutes. Ceanothus megacarpus var. megacarpus and C. megacarpus var. insularis had similar values for water absorption. They both showed
an increase in leaf mass of about 5% over 180 minutes, with similar results before and after the bench dry treatment (P = 0.37 and 0.25; Fig. 4A).

For freshly collected samples of Arctostaphylos species, the absorption ranged from medians of about 0.8% to 6% after 180 min of submergence. The island species A. catalinae had significantly higher absorption rates than all the other species followed in order by A. pungens, A. glauca and A. insularis, which did not differ from each other (Fig. 4A). After bench drying the samples overnight, the absorption rates were greater, ranging from medians of about 2% in A. glauca to 10% in A. catalinae. However, following the bench dry treatment, there was much more variance in results, such that the ANOVA test showed no significant difference between Arctostaphylos species in absorption. (Fig. 4A).

Contact Angle Measurements

For both C. megacarpus var. megacarpus and C. megacarpus var. insularis the contact angle on the adaxial surfaces was less than 90°, which was significantly more hydrophilic than for the abaxial surfaces (P < 0.10; Fig. 4B). However, the contact angle measurements were not significantly different between these taxa for either leaf surface (P = 0.33).
Arctostaphylos glauca had the most hydrophobic leaf surfaces of all the species examined; both the adaxial and abaxial surfaces demonstrated significantly greater contact angles with values over 120°. However, none of the other Arctostaphylos species differed from each other (Fig. 4B) in contact angle for the adaxial or abaxial surfaces. For all species of Arctostaphylos, the adaxial surface of the leaf had a similar contact angle value to that of the abaxial surface.

Scanning Electron Microscopy

The adaxial versus abaxial surfaces differed for C. megacarpus var. megacarpus (Fig. 5a, b). The adaxial surface lacked stomata and had a thick layer of wax uniformly distributed all over the surface (Fig. 5a), whereas the abaxial surface was found to be covered entirely with a dense layer of entwined trichomes (Fig. 5b). No stomata were visible with SEM as they were obscured by the trichomes. Each trichome had very distinct snowflake-like wax structures resting on it (Fig. 5b inset). Ceanothus megacarpus var. insularis (Fig. 5c, d) leaf surfaces were similar to those of var. megacarpus, but the adaxial surface of var. insularis had a thicker layer of wax (Fig. 5c) than that of var. megacarpus (Fig. 5a). The abaxial trichomes of var. insularis were speckled with thin flakes of wax throughout their length (Fig. 5d), but they lacked the snowflake-like structures of the other variety.

Arctostaphylos pungens was amphistomatous with stomata on both sides of the leaf. It also contained patches of wax resting on a thick compressed layer of epicuticular wax on the adaxial and abaxial surfaces (Fig. 6a, b). The adaxial surface had few trichomes (Fig. 6a) whereas the abaxial surface had many trichomes (Fig. 6b). Magnification revealed the stomatal structure covered in a waxy ledge as well as curved trichomes and identifiable guard cells (Fig. 6b inset). The trichomes appeared to be entwined in a rope-like fashion.

Arctostaphylos glauca was amphistomatous and appeared to have very similar adaxial and abaxial surfaces (Fig. 6c, d). Both of the surfaces were covered with very ornate wax, showing a layer of barrel-shaped epidermal cells (Fig. 6c, d). At 1200× magnification, clusters of stomata and epidermal cells in a floral pattern were apparent (Fig. 6c and 6d insets). There was a very prominent layer of wax with an ornate, net-like appearance covering both regular epidermal cells and guard cells (Fig. 6c and 6d insets).

Arctostaphylos catalinae was amphistomatous but had very different adaxial and abaxial surfaces (Fig. 6e, f). The adaxial

Fig. 5. Ceanothus megacarpus var. megacarpus (5a, b) and C. megacarpus var. insularis (5c, d). Scanning electron micrographs (SEM) of the adaxial (5a, c) and abaxial (5b, d) leaf surfaces. The adaxial surface had a rough appearance at low (5a, c) and high (5a and c insets) magnification and lacked stomata. On the abaxial surface a dense mass of trichomes was apparent at low (5b, d) and high (5b and d insets) magnification, obscuring stomatal crypts. The trichomes were covered with particles of unknown nature (5b and d insets).
Fig. 6. *Arctostaphylos*: Scanning electron micrographs (SEM) of the adaxial (6a, c, e, g) and abaxial (6b, d, f, h) leaf surfaces. Inserts show high magnification views. For *Arctostaphylos pungens* (6a, b), the two surfaces had a similar frequency of stomata. There were some trichomes on the abaxial surface. In *Arctostaphylos glauca* (6c, d), both surfaces had a similar frequency of stomata. Both surfaces had very ornate epicuticular wax. In *Arctostaphylos catalinae* (6e, f), the two surfaces had a similar frequency of stomata. There were some trichomes on the abaxial surface. In *Arctostaphylos insularis* (6g, h), stomata occurred only on the abaxial surface. Both surfaces lacked trichomes.
surfaces were glabrous, that is, completely devoid of trichomes prominent and protruded above the surface (Fig. 6). The stomata were more noticeable in an elevated ledge resulting in a cavity between the guard cells and the ledge openings (Fig. 6 inset). The abaxial surface had stomata and plates of epicuticular wax on the regenerative face relate to absorptive capacity (Sevanto 2019; Bueno et al. 2020). The dense layer of wax may instead be an adaptation to mitigate drought by reducing the incidence of radiation on the leaf surface, thus diminishing evapotranspiration and photoinhibition (Ehleringer et al. 1976; Ehleringer and Björkman 1978). Conversely, thinner wax on the island species would be considered a mesophytic characteristic, although we did not effectively quantify this trait with our SEM technique.

Within Arctostaphylos, A. catalinae, an island species, exhibited the greatest water absorption of all taxa in this study. Whereas A. catalinae responded as predicted in terms of its ability to absorb water, the other island species in the study did not. While A. catalinae may have adapted to the island climatic regime by enhancing foliar water absorption, A. insularis leaves are more classically mesophytic with low LMA and glabrous, horizontally oriented hypostomatus leaves (Table 2). Those leaf traits should enhance maximum photosynthetic rates under well hydrated conditions. The two island species of Arctostaphylos are both part of the chaparral vegetation on the islands, but A. catalinae is more characteristic of extreme xeric sites, such as volcanic outcrops and ridges, whereas A. insularis is characteristic of both chaparral and woodland sites (Baldwin et al. 2012). Perhaps heavy fog combined with extremely poor soil hydration favors the possibly more extreme foliar hydration strategy of A. insularis. Differences between the two island species of Arctostaphylos could also be related to distinct phylogenetic backgrounds. Arctostaphylos insularis shares section Arctostaphylos with the mainland species A. glauca and A. pungens of this study. In contrast, A. catalinae is in section Foliofracteata (Baldwin et al. 2012) and most likely had a separate evolution of mesic island traits.

The contact angle measurements were very similar for all species of Arctostaphylos with the exception of A. glauca which was quite hydrophobic. This is consistent with the SEM results, which revealed that only A. glauca has a thick layer of ornate wax on both leaf surfaces. There was no difference in the adaxial versus abaxial hydrophobicity level within any of the four species of Arctostaphylos in this study. The water absorption measured in this study occurred in the winter, even though the plants were well hydrated due to rain.

### Table 2. Summary of mesophytic versus xerophytic leaf traits in the island and mainland taxa of Ceanothus and Arctostaphylos. Island taxa and mesophytic traits are in bold. Abbreviations: ns = not significantly different from related taxa, hypo = hypostomatous, HSC = hairy stomatal crypts, Amp = amphistomatous, OEW = ornate epicuticular wax, glab = glabrous.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Leaf mass per area</th>
<th>Succulence</th>
<th>Foliar absorption</th>
<th>Contact angle Adaxial</th>
<th>Contact angle Abaxial</th>
<th>Epidermal features</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. megacarpus var. megacarpus</td>
<td>high</td>
<td>high</td>
<td>ns</td>
<td>ns</td>
<td>high</td>
<td>hypo-HSC</td>
</tr>
<tr>
<td>C. megacarpus var. insularis</td>
<td>low</td>
<td>low</td>
<td>ns</td>
<td>ns</td>
<td>high</td>
<td>hypo-HSC</td>
</tr>
<tr>
<td>A. pungens</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>high</td>
<td>high</td>
<td>amp-OEW</td>
</tr>
<tr>
<td>A. glauca</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>hypo-glab</td>
</tr>
<tr>
<td>A. catalinae</td>
<td>low</td>
<td>ns</td>
<td>high</td>
<td>ns</td>
<td>ns</td>
<td>amp</td>
</tr>
<tr>
<td>A. insularis</td>
<td>low</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>amp</td>
</tr>
</tbody>
</table>
High foliar uptake occurs in adequately hydrated plants even when the water potential driving gradient across the leaf surface is relatively small (Limm et al. 2009). In the current study, drying the leaves by two or three MPa only incrementally increased the rates of water absorption by leaves. In most cases the increases in water potential due to the water absorption treatment were not statistically significant in this study, but even a small increase in water potential can have a large impact on plant processes such as cellular expansion, increased solute transport, and photosynthesis (Burgess and Dawson 2004; Limm et al. 2009; Simonin et al. 2009).

For both genera, increased sample sizes might have led to more significant differences between species, but we were limited by the number of individuals cultivated at the garden. Also, for both genera, the results might have been different if the plants were collected from their place of origin instead of a common garden since the common garden did not account for possible plastic responses to the environment.

Foliar absorption can be an important trait when analyzing adaptations of plant species to island environments. Arctostaphylos catalinae had an extremely high foliar absorption capacity, which may be a key adaptation for this island species (Table 2). However, traditional matrices such as LMA and succulence (Poorter et al. 2009) are also relevant and may evolve independently from foliar absorption. Arctostaphylos insularis was also different from the other Arctostaphylos species in having horizontally oriented, glabrous hypostomatous leaves, which are generally considered to be mesophytic traits (Table 2).

With potential global climate change and concomitant loss of coastal fog, some mesophytic island traits may become mal-adaptive. The cell- and leaf-level adaptations would then have implications for species distributions and community structure in drying habitats of Mediterranean-type ecosystems. In addition to foliar absorption there are likely several functional traits by which leaves may become more xerophytic in the future, including increased succulence, increased LMA, and amphistomatous morphology. However, as a functional trait enhanced foliar water absorption may be independent from increased LMA and increased succulence and it may be singularly adaptive in those extreme xeric habitats with very high amounts of fog.

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