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Foliar Uptake of Fog in the Coast Redwood Ecosystem: a Novel Drought-Alleviation Strategy Shared by Most Redwood Forest Plants

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Key words: fog, understory, *Polystichum munitum*, leaf wetness, foliar uptake, drought, climate

Introduction

Fog inundates the coast redwood forests of northern California frequently during the summer months (May to September) when rainfall is largely absent (Azevedo and Morgan 1974, Byers 1953, Oberlander 1956). This maritime fog modifies otherwise warm and dry summer climate by increasing humidity, decreasing the air temperature, reducing solar radiation, and contributing water to the ecosystem through leaf wetness and fog drip (Fischer et al. 2008, Grubb and Whitmore 1966, Hutley et al. 1997, Williams et al. 2008). Fog water provides an important water subsidy for redwood forest plants that face high demand for water during the spring growing season and throughout the summer as soil moisture levels decrease (Dawson 1998, Ewing et al. 2009). In this study, we investigated how effectively fog water alleviates redwood forest plant drought stress during the summer and identified foliar uptake as a key mechanism promoting plant hydration following exposure to fog.

Foliar uptake is the absorption of water into plant crowns by leaves and stems (Rundel 1982). It occurs in diverse taxa around the world directly through the leaf cuticle (Gouvra and Gammaikopoulos 2003, Slatyer 1960, Suarez and Gloser 1982, Vaadia and Waidel 1963, Yates and Huxley 1995), specialized water-absorbing trichomes (Benzing et al. 1978, Franke 1967), or hydathode channels in the leaf epidermis (Martin and von Willert 2000). Fog, light rain, and dew may contribute little or no water to the soil profile, but may wet leaves for hours at a time (Boucher et al. 1995, Breshears et al. 2008, Ewing et al. 2009). Plants with foliar uptake capacity can absorb this water whenever their crowns are wet. In this way, foliar uptake provides an efficient mechanism to hydrate photosynthetic tissue when water is available aboveground because the water does not need to be absorbed from the soil first and transported from the roots to the plant crown second (Simonin et al. 2009).

Given the frequent occurrence of fog in the coast redwood forest during the summer and the known contribution of fog to the annual water budget of redwood forest plants (Dawson 1998), we hypothesized that foliar uptake was a common water acquisition strategy alleviating drought in the coast redwood ecosystem. Through a

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combination of glasshouse experiments using artificial fog chambers and field measurements, we studied (1) how many species in the redwood forest absorb fog water directly by foliar uptake, (2) geographical variation in the foliar uptake capacity of the dominant understory fern, *Polystichum munitum*, along the redwood forest range, (3) how foliar uptake influences the water status of *P. munitum*, and (4) how fog influences the seasonal timing and intensity of drought stress for understory plants.

Methods

Foliar uptake

To determine if foliar uptake is a shared mechanism for fog water absorption by redwood forest plants, we measured changes in leaf water content gravimetrically on cut leaves submerged in water for 3 hours to standardize water availability on the leaf surface. Single leaves were sampled from potted plants (n=7 per species) of two ferns species, *P. munitum* and *Polypodium californicum*; two shrub species, *Gaultheria shallon* and *Vaccinium ovatum*; five tree species, *Sequoia sempervirens, Pseudotsuga menziesii, Arbutus menziesii, Notholithocarpus densiflora*, and *Umbellularia californica*; and one herbaceous species, *Oxalis oregano*. Changes in leaf water content (LWC) were calculated as:

Equation 1

$$LWC = 100\% \times [((Mass2-(Mass4-Mass3)-Massdry))/((Mass1-Massdry))-1]$$

Where, Mass1 is the leaf fresh mass before submergence, Mass2 is the towel-dried leaf fresh mass after 3 hours of submergence, Mass3 is the leaf fresh mass after brief air-drying and before a method-control resubmergence, Mass4 is the towel-dried leaf fresh mass after a brief resubmergence, and Massdry is the oven-dried mass of each leaf. We used one-sample t-test to calculate if LWC increased significantly (α=0.05) after leaf wetting. Please see Limm et al. (2009) for further method detail.

To determine if the dominant redwood forest understory fern *P. munitum* exhibits intraspecific variation in foliar uptake capacity along the redwood forest range, in mid-summer we randomly sampled fronds from ten *P. munitum* crowns in Prairie Creek Redwoods State Park, Humboldt Redwoods State Park, the Angelo Coast Range Reserve, Hendy Woods State Park, the Grove of Old Trees, Roy's Redwood Preserve, and Big Basin State Park. Foliar uptake capacity was measured on the frond samples by calculating the change in LWC gravimetrically after the fronds were exposed to water misted on the adaxial leaf surface for ten hours overnight. LWC was calculated using equation 1, where the leaves were misted with water droplets instead of submerged. We used a linear regression to determine the relationship between LWC increase and foliar uptake among sampled redwood forest sites. Please see Limm and Dawson (2010) for further method detail.

Fog effects on plant water status

To determine if nocturnal fog exposure provides enough hydration to eliminate plant water deficit even when soil moisture availability is low, we exposed potted plants of *P. munitum* to four consecutive nights of artificial fog in glasshouse fog chambers and measured changes in plant water status. To isolate the effect of leaf wetting, we constrained fog exposure to the fern crowns by preventing fog drip into the soil and measured soil moisture volumetrically using sensors transecting 20 cm of the rooting zone. Over the course of the experiment, we did not add any water to the soil to allow the soil moisture to decline. We evaluated maximum plant water status at predawn after the fogging treatments ended by measuring the leaf water potential using a Scholander Pressure Chamber (PMS Instruments, Corvallis, OR) and compared fog-exposed fern hydration to control (no-fog exposure) fern hydration levels. We used non-linear regression to evaluate the relationship between leaf water potential and soil volumetric water content. Please see Limm (2009) for further method detail.

To determine if and when fog alleviates redwood forest plant drought stress, we measured seasonal trends in water status for three dominant understory species at the Grove of Old Trees, a central forest in the coast redwood ecosystem range. From 2007 to 2009, we measured the predawn leaf water potential of randomly selected plants of *S. sempervirens, U. californica*, and *P. munitum* distributed throughout the forest (n=15 per species). At each forest location where we measured plant water status, we quantified fog drip to the forest floor using throughfall collectors as described by Ewing et al. (2009). Please see Limm (2009) for further method detail.

Results

Foliar uptake

We found that 80 percent of the redwood forest species we studied exhibit capacity for foliar uptake. Only *U. californica* (a broadleaf tree) and *O. oregano* (a herbaceous understory plant) exhibited no measurable capacity for foliar uptake. We observed that LWC increased most (11 percent) in the dominant understory fern*, P. munitum* (*fig. 1*). Throughout the redwood forest ecosystem, the magnitude of *P. munitum* LWC increase following overnight leaf wetting varied significantly (*fig. 2*) among sites. While an 11 percent LWC increase for *P. munitum* was observed in one site (the Grove of Old Trees), *P. munitum* from most sites averaged LWC increases of approximately 5 percent. *Polystichum munitum* from one of the seven sites (Big Basin State Park) exhibited no measureable foliar uptake capacity.

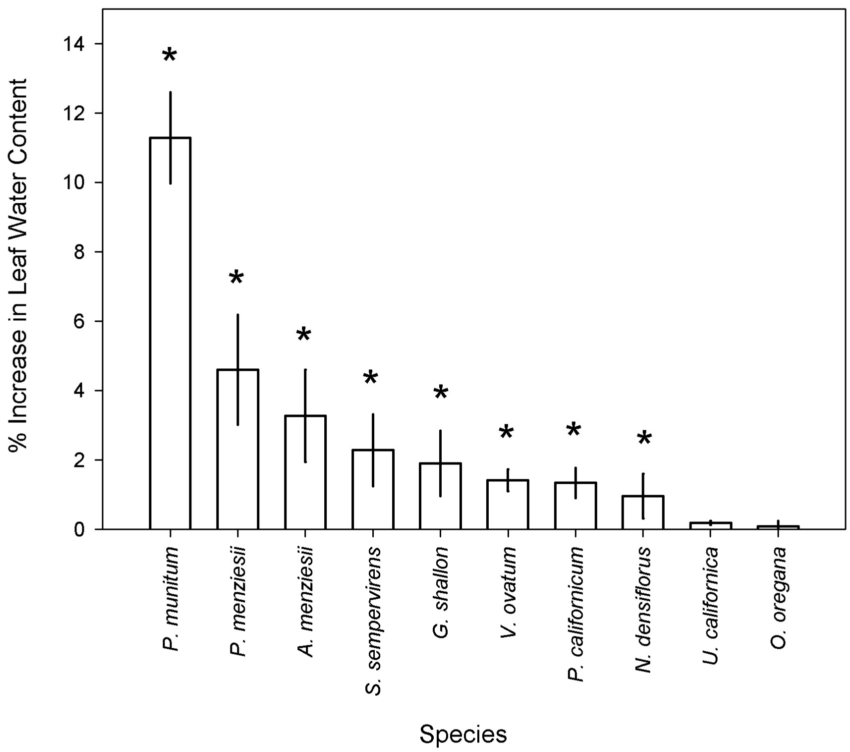

Figure 1—Foliar uptake significantly increased (*) mean (±SE) leaf water content (LWC) in the leaves of eight of the ten species studied following three hours of foliar submergence in water. This figure is modified from Limm et al. (2009).

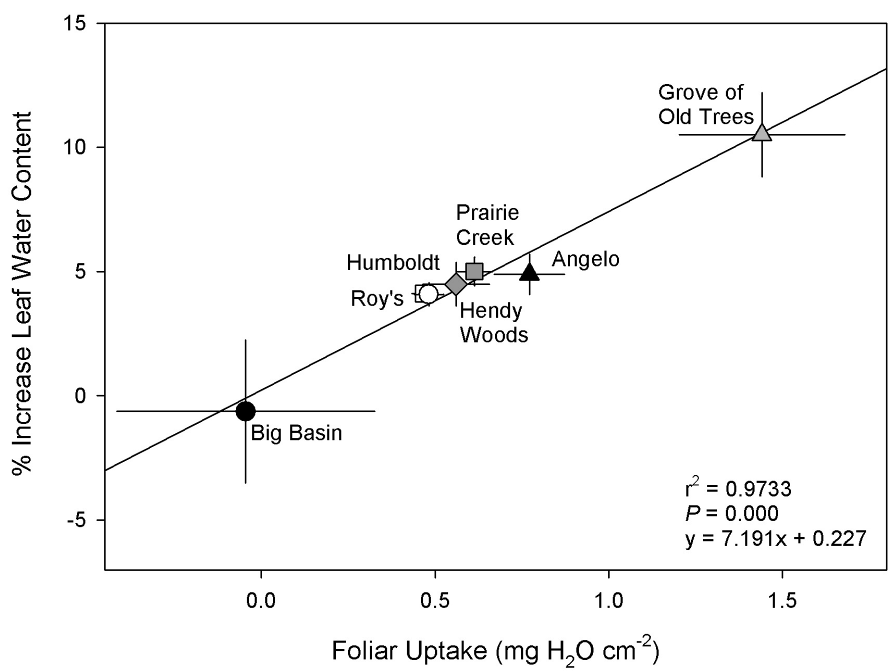

Figure 2—Among redwood forest sites, the mean (±SE) leaf water content (LWC) of *Polystichum munitum* increased with overnight foliar uptake of water misted on the frond adaxial surface. This figure is modified from Limm and Dawson (2010).

Fog effects on plant water status

In the glasshouse, both fog-exposed and control *P. munitum* plants maintained high predawn water potential (greater than -0.75 MPa) when the soil volumetric water content (VWC) was above 5 percent (*fig. 3*). The water potential of ferns exposed to four consecutive nights of leaf-wetting by artificial fog remained high even when their soil VWC dropped below 5 percent. In contrast, the water status of ferns that received no leaf wetting and only ambient, control conditions for four consecutive nights decreased sharply as the soil dried out. Without fog exposure, soil VWC below 5 percent resulted in *P. munitum* predawn water potentials decreasing to less than -2 MPa.

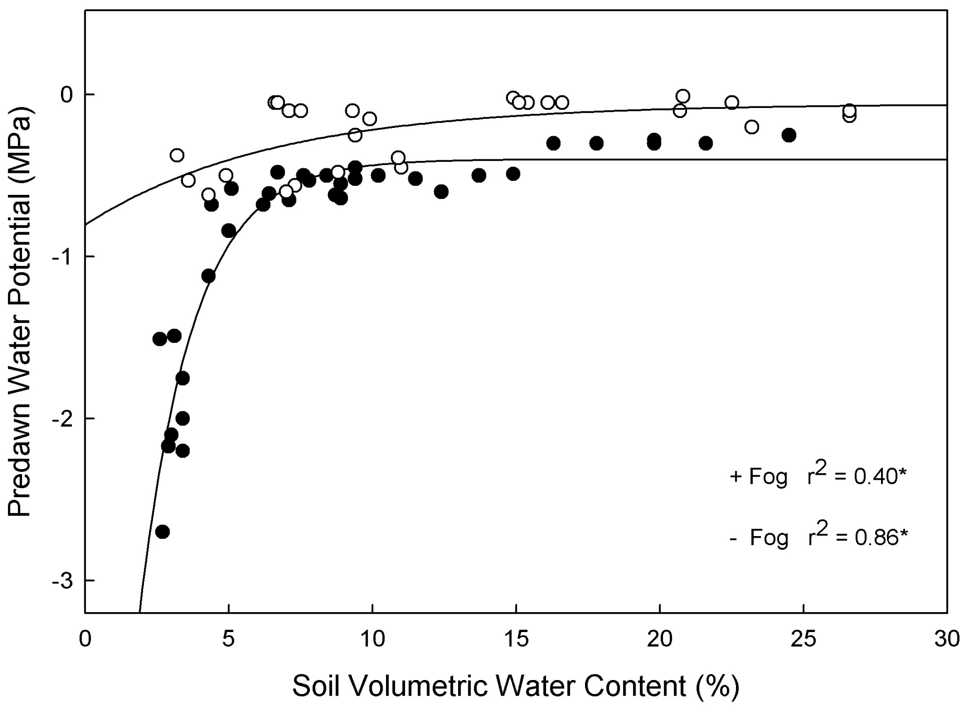

Figure 3—Predawn water potential decreased markedly in control ferns (- Fog; closed circles) that received no fog exposure during the experiment when the soil volumetric water content (VWC) dropped below 5 percent. In contrast, the predawn water potential stayed high in the fogged ferns (+ Fog; open circles) that received overnight fog exposure regardless of declining soil VWC.

At the Grove of Old Trees, the predawn water potential of all three species studied varied significantly, both seasonally and between years (*fig. 4*). In general, *S. sempervirens* maintained the highest water status in comparison to *U. californica* and *P. munitum* unless the measurements occurred during a fog event. When foggy, *P. munitum* hydration increased significantly, resulting in higher predawn water potentials than observed in either tree species. When not foggy, *P. munitum* predawn water potential was lowest. We measured significantly more water input to the forest floor as measured by the throughfall collectors during the rainy season (October to April) than during the fog season (May to September). In each year, the hydration levels of all three species increased at least once during the summer fog season when no rain fell. For all three species, the positive hydration response to fog occurred despite the disproportionately low volume of water delivered by fog drip.

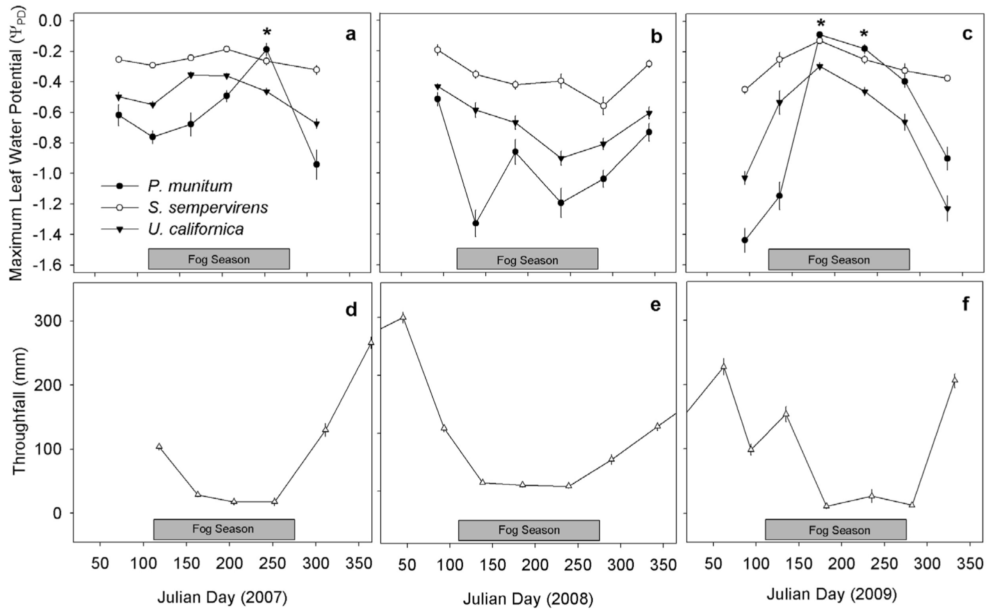

Figure 4—The predawn maximum water potentials of *S. sempervirens*, *U. californica,* and *P. munitum* changed throughout the summer fog season in (a) 2007, (b) 2008, and (c) 2009 at the Grove of Old Trees in Sonoma County. The understory received less water input during the rainless summer fog season relative to the winter rainy season in (d) 2007, (e) 2008, and (f) 2009. On foggy mornings (*), the hydration status of *P. munitum* was higher than the other species.

Discussion

Foliar uptake is a water acquisition strategy shared by most plants of the coast redwood forest (Burgess and Dawson 2004, Limm et al. 2009). While a common phenomenon among this taxonomically and morphologically diverse plant assemblage, the magnitude of potential hydration by foliar uptake varies significantly both between species and even within species. The species with foliar uptake capacity possess a wide range of leaf types, from evergreen broadleaves to fern fronds to coniferous needles and no one leaf form appears more adapted for foliar uptake than another. *Polystichum munitum* demonstrated double the capacity to increase its leaf water content following leaf wetting relative to all other species studied, but even this plant exhibits a range of foliar uptake capacity in the field. The mechanistic pathway for foliar uptake is unknown in *P. munitum* and the other redwood forest species, but we hypothesize that the leaf cuticle is the most likely pathway for water absorption as in most other species known to do foliar uptake (Limm and Dawson 2010). If the cuticle does facilitate water absorption in redwood forest plants, variation in chemical composition and architecture of the cuticle between species and populations in the ecosystem may explain the range of foliar uptake capacities we observed (Kersteins 1996, Riederer and Schreiber 2001, Shepherd and Griffiths 2006). Specifically for *P. munitum*, the greatest foliar uptake capacity was observed at the Grove of Old Trees, the windiest and foggiest site studied. Both wind and fog abrade the cuticle (Baker and Hunt 1986, Hoad et al. 1992, Pitcairn et al. 1986) and may have resulted in greater capacity of *P. munitum* to absorb water directly through its fronds in this forest.

Foliar uptake is physiologically important for coast redwood forest plants because it provides opportunities for hydration after the rainy season ends and soil water availability declines. Many fog events contribute little or no fog drip into the soil profile where plant roots access water (Ewing et al. 2009), but leaf wetting associated with short-duration or low-intensity fog events provides a subsidy that foliage can access. In the glasshouse, we observed that overnight fog exposure maintains a high *P. munitum* hydration status despite extremely low soil moisture. Simonin et al. (2009) also observed that water absorption by *S. sempervirens* crowns can decouple plants from soil water deficit. When foliar uptake readily occurs as observed in *P. munitum* and *S. sempervirens*, the potential for soil water deficit to cause plant drought stress diminishes significantly. If plants stay hydrated throughout the summer because of fog water subsidies as we observed at the Grove of Old Trees, plants can maintain higher photosynthetic rates and extend the length of their growing season.

Seasonal water deficit may increase in the coast redwood region as climate changes over the next decades (Hayhoe et al. 2004, Loarie et al. 2008). This will increase plant demand for water and dependence on fog water subsidies. Fog frequency is declining along the coast of California (Johnstone and Dawson 2010), reducing the number of days when redwood forest plants receive drought alleviation by fog exposure. The future availability of fog remains uncertain, but continued fog presence in the coast redwood forest would likely lessen the redwood forest drought stress imposed by climate change.

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