

***POLYSTICHUM MUNITUM* (DRYOPTERIDACEAE) VARIES
 GEOGRAPHICALLY IN ITS CAPACITY TO ABSORB FOG WATER BY
 FOLIAR UPTAKE WITHIN THE REDWOOD FOREST ECOSYSTEM¹**

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- *Premise of the study:* Fog provides a critical water resource to plants around the world. In the redwood forest ecosystem of northern California, plants depend on fog absorbed through foliar uptake to stay hydrated during the rainless summer. In this study, we identified regions within the redwood ecosystem where the fern *Polystichum munitum* canopy most effectively absorbs fog drip that reaches the forest floor.
- *Methods:* We measured the foliar uptake capacity of *P. munitum* fronds at seven sites along 700 km of the redwood forest ecosystem. We quantified the canopy cover of *P. munitum* at each site and estimated how much water the fern canopy can acquire aboveground through fog interception and absorption.
- *Key results:* Throughout the ecosystem, nocturnal foliar uptake increased the leaf water content of *P. munitum* by 7.2%, and we estimated that the *P. munitum* canopy can absorb $5 \pm 3\%$ (mean \pm SE) of intercepted fog precipitation. Strikingly, *P. munitum* had the highest foliar uptake capacity in the center of the ecosystem and may absorb 10% more of the fog its canopy intercepts in this region relative to other regions studied. Conversely, *P. munitum* had no foliar uptake capacity in the southern end of the ecosystem.
- *Conclusions:* This study shows the first evidence that foliar uptake varies within species at the landscape scale. Our findings suggest that the *P. munitum* at the southern tip of the redwood ecosystem may suffer most from low summertime water availability because it had no potential to acquire fog as an aboveground water subsidy.

Key words: California; Dryopteridaceae; herbaceous layer; fog; foliar uptake; *Polystichum munitum*; redwood forest; understory.

Low-altitude fog and clouds provide important terrestrial water subsidies to many ecosystems around the world including neotropical montane cloud forests (Grubb and Whitmore, 1966; Cavelier and Goldstein, 1989; Cavelier et al., 1996; Holder, 2004) and coastal grasslands and forests of the western United States (Azevedo and Morgan, 1974; Ingraham and Matthews, 1995; Corbin et al., 2005; Williams et al., 2008; Fischer et al., 2009; Ewing et al., 2009). In these ecosystems and others, plants gain access to fog and cloud moisture through root uptake of coalesced water that drips to the soil or by direct foliar uptake of water retained by the plant crowns following interception. Foliar uptake occurs when water diffuses through leaf surfaces via the cuticle (Slatyer, 1960; Vaadia and Waisel, 1963; Suárez and Gloser, 1982; Yates and Hutley, 1995; Gouvra and Grammatikopoulos, 2003), absorbent trichomes (Franke,

1967; Benzing et al., 1978), or hydathodes (Martin and von Willert, 2000). Unlike root uptake of water that occurs only when significant fog or cloud inundation causes drip to the soil, foliar uptake allows plants to immediately capture any atmospheric water subsidy that wets foliage but may otherwise never reach the ground (Münne-Bosch, 2009).

Despite the identification of numerous species that exhibit foliar uptake in a variety of ecosystems (e.g., Stone et al., 1950; Rundel, 1982; Boucher et al., 1995; Burgess and Dawson, 2004; Oliveira et al., 2005; Breshears et al., 2008; Limm et al., 2009), it is not yet known if foliar uptake capacity varies significantly within species. If foliar uptake capacity varies significantly across the landscape from either plasticity or genotypic differences among populations, then the magnitude of plant hydration following fog or cloud inundation may vary regionally. Because many species depend on water subsidies of this type during periods of drought when water is otherwise limiting (Cavelier and Goldstein, 1989; Menges, 1994; Yates and Hutley, 1995; Dawson, 1998; Williams et al., 2008), low foliar uptake capacity by plants in a region could greatly limit drought alleviation by fog or clouds and make these plants more vulnerable to drought stress. Across large geographic scales, such variation could also result in atmospheric water subsidies differentially affecting ecosystem water balance if plants in some regions capture water through foliar uptake at higher rates than plants in other regions. By comparing foliar uptake capacities within a species throughout a large ecosystem, we can identify regions where a species will be most able to capture atmospheric water subsidies aboveground, thereby receiving more drought alleviation and ultimately contributing more to the ecosystem water balance.

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The present study evaluates geographic variability in fog-water retention and uptake capacity by fronds of the dominant understory species, *Polystichum munitum* (Kaulf.) C. Presl (western sword fern), which inhabits the coast redwood forest ecosystem in northern California. It is well established that redwood forest plants undergo frequent leaf wetting from fog during the summer months without rain (Byers, 1953; Oberlander, 1956; Azevedo and Morgan, 1974; Ewing et al., 2009; Simonin et al., 2009) and that fog contributes significantly to the annual water budget for many of these species (Dawson, 1998). The majority of dominant redwood forest species become more hydrated when exposed to fog aboveground and 80% exhibit foliar uptake (Limm et al., 2009). However, the fern *P. munitum* absorbs more than twice as much water per leaf area through this pathway than other redwood forest species do (Limm et al., 2009). *Polystichum munitum* is abundant throughout many northwest forested ecosystems of North America, including the entire latitudinal range of the redwood forest ecosystem (Sawyer et al., 2000). In the redwood forest in particular, *P. munitum* forms a dense understory canopy in the herbaceous layer of the forest floor, and it is here where this dominant fern intercepts fog drip that falls from the upper forest canopy in summer.

At seven sites spanning over 700 km of the redwood forest ecosystem, we evaluated the capacity of *P. munitum* fronds to retain intercepted water on the leaf surface and then absorb this water via foliar uptake. In addition, we evaluated how leaf size and fern crown density varied geographically throughout the redwood forest ecosystem to estimate fog drip retention and absorption potential by the *P. munitum* canopy along the coastal fog belt of northern California.

MATERIALS AND METHODS

We selected seven old-growth forest locations for this study along the latitudinal gradient of the coast redwood forest range of northern California (Fig. 1). All sites contain an evergreen forest canopy dominated by *Sequoia sempervirens* (D. Don) Endl. and an understory herbaceous layer dominated by *P. munitum*. The most northern sites were Prairie Creek Redwoods State Park (site 1; elevation 59 m a.s.l.) and Humboldt Redwoods State Park (site 2; 86 m a.s.l.) in Humboldt County. The central range sites were the Angelo Coast Range Reserve of the University of California Natural Reserve System in Mendocino County (site 3; 378 m a.s.l.), Henty Woods State Park in Mendocino County (site 4; 79 m a.s.l.), the Grove of Old Trees in Sonoma County (site 5; 347 m a.s.l.), and Roy's Redwoods Open Space Preserve in Marin County (site 6; 148 m a.s.l.). The most southern site was Big Basin State Park in Santa Cruz County (site 7; 304 m a.s.l.). To quantify how annual precipitation varies among the sites, we accessed historical precipitation data from the Western Regional Climate Center stations closest to each forest (Western Regional Climate Center, 2009). From each station, we used the maximum number of years available to calculate the mean total annual precipitation of that region.

At each redwood forest, we selected an understory site of highest fern density dominated by *P. munitum* for all measurements. *Polystichum munitum* samples were collected in midsummer during the peak fog season at sunset (2000 to 2100 hours) to represent a typical time when coastal fog enters the redwood forest and wets foliage (Azevedo and Morgan, 1974; Johnstone and Dawson, 2010). We measured the leaf water potential of 10 randomly selected ferns at each forest site with a Scholander Pressure Chamber (PMS Instruments, Corvallis, Oregon, USA). To assess the water retention capacity of the leaf surface and foliar uptake capacity, we sampled the distal end (approximately 110 cm²) of one frond from the same 10 fern crowns. We wrapped the cut rachis with parafilm to prevent water evaporative loss or absorption through the cut surface and recorded the initial mass of the foliage using a balance accurate to 0.001 g (GemPro-250 Precision, My Weigh, Phoenix, Arizona, USA). We then misted the adaxial side of the frond with deionized water (Green Thumb, TruServ, Chicago, Illinois, USA) until water droplets covered the frond surface (maximum wetness). We tilted the leaf to 45° to allow excess water droplets to

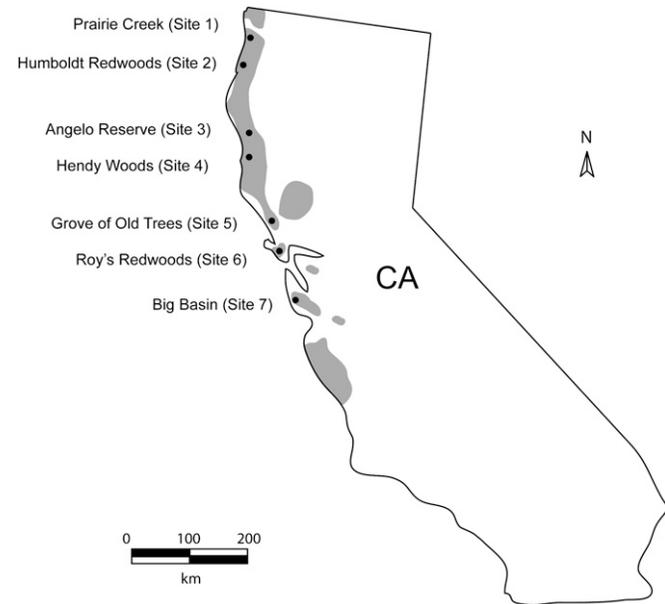


Fig. 1. The locations of *Polystichum munitum* study sites along the redwood forest ecosystem range (gray shading) of coastal northern California.

roll off of the frond and recorded the mass of the wet foliage. We calculated the adaxial leaf surface water retention capacity of each frond (WRC_{surface}) as:

$$WRC_{\text{surface}} = \text{Mass}_2 - \text{Mass}_1, \quad (1)$$

where Mass_2 is the frond mass immediately after wetting and Mass_1 is the initial mass before wetting. We standardized the WRC_{surface} by projected leaf area after measuring foliar uptake capacity on the same fronds (as described below).

To assess foliar uptake capacity, we placed the wet fronds on a 10-mm nylon mesh platform inside a sealed box to prevent evaporation and left them overnight in darkness for 10 h. In the morning, the foliage was towel-dried thoroughly to remove excess water, and the mass of the leaves was again recorded. We quantified any error associated with the towel-drying method by measuring residual water on the frond surface after towel-drying and calculated the quantity of water absorbed via foliar uptake as:

$$\text{Uptake} = (\text{Mass}_3 - \text{Mass}_1) - (\text{Mass}_5 - \text{Mass}_4), \quad (2)$$

where Mass_1 is the initial leaf mass before wetting, Mass_3 is the mass of the towel-dried leaf after 10 h of wetness, Mass_4 is the leaf mass after 15 min of air-drying following the measurement of Mass_3 and before rewetting, and Mass_5 is the towel-dried mass after a 1-s rewetting event that quantifies any residual water persisting on the frond surface after drying (Limm et al., 2009). To standardize the uptake quantity per unit leaf area, we determined the projected frond area digitally using the software program ImageJ (U. S. National Institutes of Health, Bethesda, Maryland, USA). To determine how the leaf water content increased from frond wetting, we calculated the percentage increase in leaf water content (% LWC) for each frond as:

$$\% \text{LWC} = \left[\frac{(\text{Mass}_3 - (\text{Mass}_5 - \text{Mass}_4) - \text{Mass}_6)}{(\text{Mass}_1 - \text{Mass}_6)} - 1 \right] \times 100, \quad (3)$$

where Mass_6 is the dry mass of the leaf measured after drying at 60°C for 72 h. Linear relationships across all sites between foliar uptake capacity and leaf water content, leaf surface water holding capacity, and leaf water potential were determined by least-squares lines fit to nontransformed data using the program SigmaPlot 10.0 (SYSTAT Software, San Jose, California, USA).

We sampled an additional 20 mature and herbivory-free fronds of *P. munitum* that represented the full range in leaf size in each population to determine

the allometric relationship between frond length and area. We measured the length of each frond rachis (stipe excluded) and determined digitally the combined projected leaf area of the pinnae and rachis using the program ImageJ as above. After measuring the individual frond dimensions throughout the ecosystem range, we fit a least-squares line to the combined log-transformed frond length and area data from all sites to determine regression parameters using SigmaPlot as:

$$\log y = a \cdot \log x + b, \tag{4}$$

where y is the total frond area, x is the rachis length, a is the slope of the line (1.782), and b is the y -intercept (−0.484). We used this relationship to estimate the leaf area of *P. munitum* fronds from rachis length measurements at each redwood forest site (described next).

We randomly selected ten 4-m² plots within a 250-m² area at each site and estimated the total *P. munitum* leaf area within each plot. To do so, we first counted the total number of fronds in each fern crown within the plot. If the plot edge bisected a fern crown, we only counted a frond if at least half the total rachis length occurred within the plot. Then we measured the frond lengths (rachis base to frond tip) of five representative fronds from each fern crown or fewer if the crown had fewer than five fronds and calculated the mean length of these subsampled fronds. This approach demonstrated high accuracy; across 10 randomly selected fern crowns, this value differed from the actual whole-crown mean frond length by only $-1 \text{ cm} \pm 0.8$ (SE). We determined frond area from the measured frond lengths using the allometric relationship described by Eq. 4 and calculated the mean (\pm SE) frond area for the five fronds. We calculated the total leaf area (c_{area}) of each whole or partial fern crown as:

$$c_{\text{area}} = \bar{a}_{\text{frond}} \cdot n_{\text{frond}}, \tag{5}$$

where, \bar{a}_{frond} is the mean frond area of measured fronds from the fern crown and n_{frond} is total number of fronds in the fern crown. Crown areas were summed together to determine the total leaf area of *P. munitum* within each plot, and we calculated the mean (\pm SE) canopy cover of *P. munitum* in the herbaceous layer at each forest site as the average leaf area of all 10 plots. We defined the linear relationship between the fern canopy cover and annual precipitation using a least-squares line fit to site means using SigmaPlot. In addition, we used a one-way random factor ANOVA followed by Tukey’s honestly significant difference (HSD) test in the program JMP 8 (SAS Institute, Cary, North Carolina, USA) to test whether the size and abundance of *P. munitum* crowns and fronds differed significantly among sites.

Estimates of the fog-drip canopy-retention capacity for each site were calculated as the maximum quantity of water the fern canopy could hold on the adaxial leaf surfaces of *P. munitum* as:

$$r_{\text{site}} = \bar{s} \cdot \bar{w}, \tag{6}$$

where r_{site} is the total quantity of water retained on the leaf surfaces of *P. munitum* if all plant crowns were wet to capacity (units: g water·m⁻² ground), \bar{s} is the mean *P. munitum* leaf area at the site, and \bar{w} is the mean water retention capacity (WRC_{surface}) of *P. munitum* fronds at the site. To estimate the fog drip absorption capacity at each site, we calculated the quantity of water the *P. munitum* canopy could absorb through foliar uptake from a single leaf-wetting event at each site as:

$$a_{\text{site}} = \bar{s} \cdot \bar{u}, \tag{7}$$

where a_{site} is the quantity of water absorbed by the fern canopy (units: g water·m⁻² ground), and \bar{u} is the mean foliar uptake capacity of *P. munitum* fronds at the site.

We define the fog drip acquisition potential as the percentage of leaf-surface water absorbed through foliar uptake by the *P. munitum* canopy when retaining maximum water on all frond surfaces and calculate this potential as:

$$p_{\text{site}} = \frac{a_{\text{site}}}{r_{\text{site}}} \times 100, \tag{8}$$

where p_{site} is the percentage of water absorbed from the total water available on the leaf surfaces of the *P. munitum* canopy. We used error propagation to calcu-

late the uncertainty associated with estimates of crown, plot, and forest site leaf area in addition to the estimates of fog drip retention and absorption at all sites (see Appendix 1 for equations).

RESULTS

Polystichum munitum fronds from six of the seven sites absorbed water by foliar uptake after misting of the adaxial leaf surfaces (no absorption measured in fronds from site 7, the southernmost site sampled). Leaf water content was positively correlated ($F = 182.31$, $df = 1$, $P = 0.000$, $r^2 = 0.9733$) with the mass of water absorbed per unit leaf area (Fig. 2A) via foliar uptake through the frond surface. Misting increased leaf water content by 4–5% at a majority of sites (1–4 and 6) and by 11% at site 5. Fronds from site 7 did not take up water, and consequently the leaf water content of these fronds did not increase after leaf wetting. There was no significant correlation ($F = 0.008$, $df = 1$, $P = 0.933$, $r^2 = 0.002$) between the leaf water potential of *P. munitum* when foliar uptake capacity was measured at each site and the resultant quantity of water absorbed (Ψ_{leaf} values ranged between -0.35 to -0.7 MPa among sites). The maximum quantity of water retained by the adaxial leaf surface of *P. munitum* fronds after wetting varied among sites,

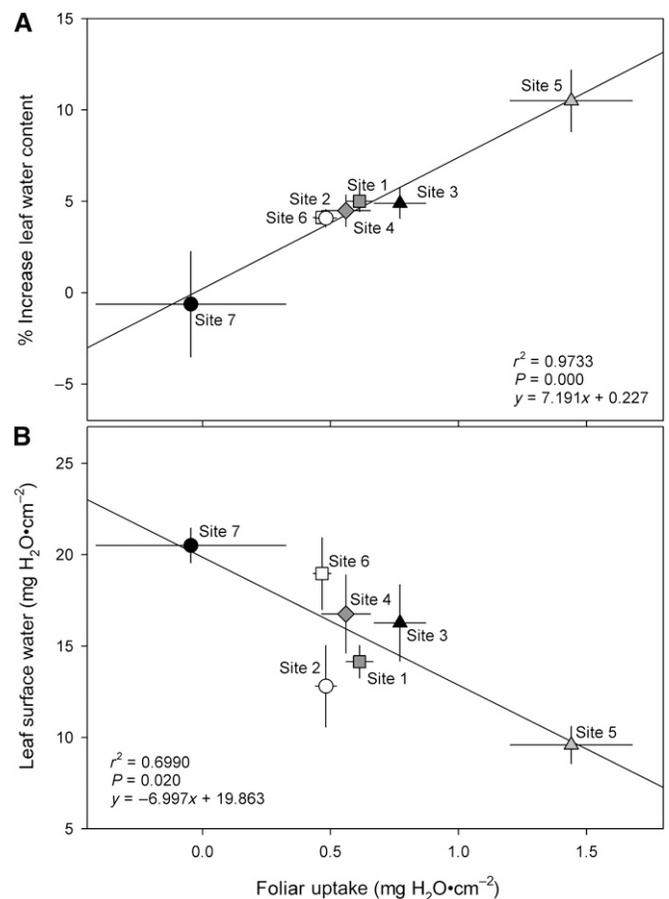


Fig. 2. The linear relationships between the foliar uptake capacity and (A) the percentage increase in leaf water content and (B) maximum water retained by the leaf surfaces after leaf wetting of *P. munitum* fronds at seven redwood forest sites in California. See site name descriptions in the methods section.

with the water retention capacity of fronds ranging from $9.6 \pm 1.0 \text{ mg H}_2\text{O}^{-1}\cdot\text{cm}^{-2}$ (mean \pm SE) at site 5 up to $20.5 \pm 1.0 \text{ mg H}_2\text{O}^{-1}\cdot\text{cm}^{-2}$ (mean \pm SE) at site 7. This leaf surface water retention capacity was negatively correlated ($F = 11.45$, $df = 1$, $P = 0.020$, $r^2 = 0.6990$) with foliar uptake capacity (Fig. 2B).

Fronch rachis length scaled linearly ($F = 5083.77$, $df = 1$, $P = 0.000$, $r^2 = 0.9724$) with frond area for log-transformed data combined from all seven sites (Fig. 3).

In the analysis, *P. munitum* frond lengths (rachis only) across sites ranged from 3.7 to 131.4 cm and frond surface area (one-sided rachis and pinnae area) ranged from 3.0 to 1257.2 cm^2 .

The size and abundance of *P. munitum* fronds and crowns in plots differed between redwood forest sites (Table 1). We defined crown size as the total number of fronds per *P. munitum* crown. Site significantly affected crown size ($F_{6, 256} = 4.80$, $P = 0.0001$), but this effect was largely driven by the small mean crown size of site 7 ferns because the other sites had similar mean frond number per crown. The total number of fern crowns in the plots also varied with site ($F_{6, 63} = 5.40$, $P = 0.0001$), with the lowest crown abundance per plot at site 7 and the highest at site 1. Site significantly affected frond abundance per plot ($F_{6, 63} = 7.75$, $P < 0.0001$), but only site 7 had significantly lower frond abundance than the other forests. Sites differed most in mean frond length ($F_{6, 1922} = 164.80$, $P < 0.0001$). The mean frond length was lowest at sites 6 and 7 and highest at site 1.

The estimated total canopy cover of *P. munitum* differed between sites (Fig. 4) and correlated significantly with mean annual precipitation ($F = 11.34$, $df = 1$, $P = 0.020$, $r^2 = 0.6940$). Total annual rainfall increased along the northward latitudinal gradient represented by the seven redwood forest sites. As *P. munitum* canopy cover increased with latitude, the estimated capacity for the *P. munitum* canopy to retain intercepted fog water dripped to understory herbaceous layer increased (Fig. 5) from $63 \pm 21 \text{ g H}_2\text{O}^{-1}\cdot\text{m}^{-2}$ ground (mean \pm SE) at site 7 to $416 \pm 117 \text{ g H}_2\text{O}^{-1}\cdot\text{m}^{-2}$ ground (mean \pm SE) at site 1. Along the same latitudinal gradient, the absorption capacity also increased from negligible foliar uptake at site 7 of $0 \pm 1 \text{ g H}_2\text{O}^{-1}\cdot\text{m}^{-2}$ ground (mean \pm SE) to $18 \pm 3 \text{ g H}_2\text{O}^{-1}\cdot\text{m}^{-2}$ ground (mean \pm SE) at site 1. The fog drip acquisition potential describes the proportional quantity of water absorbed by the canopy given maxi-

mum fog drip retention. Site 5 (a central site) had the highest acquisition potential, and we estimate that the *P. munitum* canopy at this site may absorb $15 \pm 5\%$ (mean \pm SE) of fog drip retained by fronds. Only site 7 had a negligible acquisition potential of $0 \pm 2\%$ (mean \pm SE), and across all sites along the redwood forest ecosystem, the fog drip acquisition potential was $5 \pm 3\%$ (mean \pm SE).

DISCUSSION

Foliar uptake by fern fronds—*Polystichum munitum* in the redwood forest ecosystem varied significantly in its foliar uptake capacity during midsummer when leaf wetting from fog drip frequently occurs. This variation renders *P. munitum* differentially able to acquire fog-water subsidies throughout the ecosystem, and the mechanism behind this variation operates at the leaf surface.

The difference in water potential across the leaf surface forms the driving gradient for foliar uptake (Rundel, 1982). Interestingly, the variation in foliar uptake by *P. munitum* between sites is not correlated with initial leaf water status (before leaf wetting). In addition, foliar uptake capacity does not result from water limitation on the leaf surface because *P. munitum* fronds with high capacity to retain leaf-surface water (more water available) absorbed less water than fronds with low water-retention capacity (less water available). In fact, the mean water uptake quantity absorbed by site 7 fronds was slightly negative due to the significant retention of water on the leaf surface during the measurements and subsequent large residual water correction during the calculation of foliar uptake capacity (Eq. 2). In other species, high water retention on leaf surfaces without trichomes is attributed to leaf surface roughness and the composition and arrangement of epicuticular waxes (Neinhuis and Barthlott, 1997; Brewer and Nuñez, 2007). *Polystichum munitum* leaf surface roughness may vary significantly within the redwood forest ecosystem and could explain the regional differences we observed in the capacity for leaf-surface water retention.

We cannot attribute the variation in foliar uptake between sites to differences in the driving gradient for water absorption or to water availability on the leaf surface. Therefore, variation in absorption must result from differences in the specific pathway for water entry into the fronds throughout the ecosystem. We assume that water enters *P. munitum* fronds by diffusing through the cuticle as observed in other species (Slatyer, 1960; Vaadia and Waisel, 1963; Suárez and Gloser, 1982; Yates and Hutley, 1995; Gouvra and Grammatikopoulos, 2003) without absorbent trichomes or hydathodes. Variation in cuticular composition, architecture, or environmental damage will greatly affect leaf surface permeability and could result from genotypic differences between populations or anatomical plasticity driven by environmental conditions in the ecosystem (Berlyn et al., 1992; Kerstiens, 1996; Riederer and Schreiber, 2001; Shepherd and Griffiths, 2006). It is not yet understood whether leaf cuticular properties are plastic in *P. munitum* or if distinct *P. munitum* ecotypes occur within the redwood forest ecosystem. However, environmental exposure is highly variable throughout this ecosystem and likely explains some of the variation in foliar uptake capacity we observed. Specifically, both wind and precipitation abrade the cuticle (Baker and Hunt, 1986; Pitcairn et al., 1986; Hoard et al., 1992) and may facilitate increased foliar

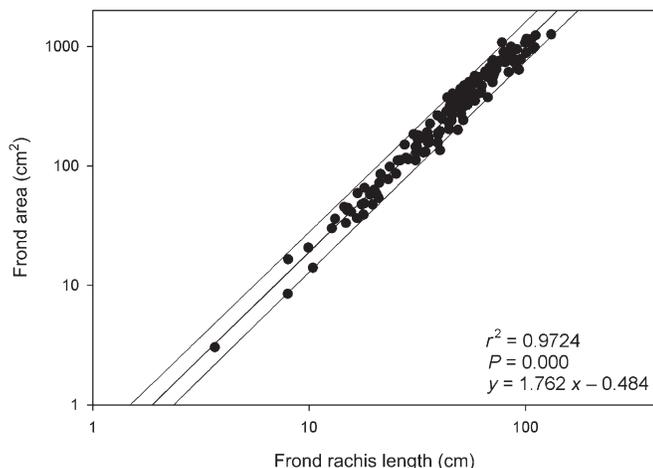


Fig. 3. The allometric relationship between the frond rachis length and total frond area for *Polystichum munitum* sampled at seven sites along the redwood forest range of northern California. Data are presented on log axes with a least-squares line and 95% prediction intervals.

TABLE 1. The mean (\pm SD) size and abundance of *Polystichum munitum* crowns and fronds measured inside plots at each redwood forest site in California.

Site name	Site number	Crown count	Crown size (cm)	Frond count	Frond length (cm)
Prairie Creek	1	5.4 \pm 1.3 a,b	22.8 \pm 20.6 a	123.0 \pm 42.8 a	86.6 \pm 19.7 a
Humboldt Redwoods	2	6.5 \pm 3.0 a	14.5 \pm 11.4 b,c	94.2 \pm 27.0 a	74.3 \pm 21.1 b
Angelo Reserve	3	6.1 \pm 1.9 a	18.9 \pm 13.7 a,b	115.3 \pm 44.8 a	60.2 \pm 11.9 c,d
Hendy Woods	4	7.8 \pm 2.6 a	13.9 \pm 9.3 b,c	108.1 \pm 27.0 a	62.1 \pm 12.9 c
Grove of Old Trees	5	6.8 \pm 1.5 a	15.2 \pm 12.6 b,c	103.2 \pm 26.0 a	56.7 \pm 15.0 d
Roy's Redwoods	6	5.5 \pm 2.0 a,b	16.2 \pm 10.8 b,c	88.9 \pm 32.5 a	51.4 \pm 16.9 e
Big Basin	7	2.9 \pm 1.9 b	11.5 \pm 8.8 c	33.5 \pm 29.7 b	48.1 \pm 15.7 e

Notes: Crown size is the number of fronds per crown for ferns completely within the plot boundary. Crown count is the number of fern individuals contributing leaf area to the plot (including crowns bisected by the plot edge). Frond count is the number of fronds within the plot. Frond length is the rachis length (excluding the stipe) of fronds within the plot. For each *P. munitum* variable, site means sharing the same letter are not significantly different ($P < 0.05$, Tukey's HSD post hoc test for significant differences among means).

uptake in fronds at sites with high wind exposure and frequent leaf wetting. *Polystichum munitum* fronds at site 5 exhibit the highest foliar uptake capacity, and this site receives more frequent onshore winds and fog exposure as a ridge-top forest when compared to the other sites, including site 7, which is in a valley and more sheltered from both wind and fog. If environmental abrasion does decrease leaf cuticular integrity in *P. munitum*, ferns with affected cuticles may have increased foliar uptake, but may also lose more water through cuticular transpiration when the leaf surfaces are dry (Leyton and Armitage, 1968). More research into the foliar uptake pathway in this species would improve our understanding of the mechanism behind variation in *P. munitum* foliar uptake capacity throughout the redwood forest ecosystem.

Fog acquisition by the fern canopy—Scaling frond foliar uptake and capacity to retain leaf-surface water to the whole fern canopy revealed that *P. munitum* in the redwood forest ecosystem may absorb up to 15% of fog drip retained by its crowns when wet to capacity. This uniform leaf wetting may not occur during brief or low-intensity fog events when little fog drip falls from the upper forest canopy. However, we do routinely observe complete canopy wetness during typical fog events when the weight of the fog drip on foliage decreases the frond angle of *P. munitum* and creates more horizontal leaf surfaces for drip interception and retention. If prolonged wetting allows fronds to absorb more water than needed to fully hydrate leaf tissues, the fern canopy capacity for absorption may in fact be higher than we calculated since excess water can move through the fern crowns along a water potential gradient from fronds to the rhizome, roots, and leak to the soil (Limm, 2009). Such movement of absorbed water from foliage through stems is observed as reverse sap flow in woody species with foliar uptake (Burgess and Dawson, 2004; Oliveira et al., 2005) and was observed in *P. munitum* after nocturnal exposure to artificial fog in the glasshouse (Limm, 2009). If internal redistribution of water occurs in *P. munitum* throughout the redwood forest range, this would increase the fog drip absorption capacity at each site and therefore increase the proportion of water absorbed from the leaf surfaces when the canopy is wet for extended periods of time.

The geographic variation in fog drip retention and absorption capacities within the redwood forest ecosystem reflects site differences in *P. munitum* canopy leaf area in addition to frond wettability and absorption properties. Higher total leaf area occurs as the size and abundance of *P. munitum* fronds increase along the northern latitudinal and precipitation gradient. Fronds

are longer in more northern sites, yet maintain geometric proportionality as leaf size increases. This leaf-size scaling characteristic was observed in the Hawaiian arborescent fern *Cibotium glaucum* (Arcand et al., 2008). In addition, the trend of increased frond abundance with higher water availability was observed by Ticktin et al. (2007) in the Hawaiian ferns *Sphenomeris chinensis* and *Microlepia strigosa*, for which frond density in the forest understory fluctuated interannually with precipitation. Interestingly, the summertime water subsidy potentially obtained through fog drip acquisition appears 10% higher in the center of the redwood forest range than in the north where total canopy area for fog drip interception is higher or in the south where water is more limiting and demand for fog may be greater. Foliar uptake can support plant growth and reproduction (Boucher et al., 1995; Díaz and Granadillo, 2005), and therefore the ferns in central redwood forest ecosystem may benefit most from leaf wetting by fog.

Fog drip acquisition by *P. munitum* canopies may impact the hydrology of the redwood forest understory in addition to directly supplementing the water budget of *P. munitum*. As reported in Ewing et al. (2009), the forest understory at site 5 receives 18.6 \pm 1.5 mm total fog drip as throughfall (mean \pm SD) during the 4-mo fog season (June–September). This small quantity of water reflects the accumulation of multiple fog events that typically deliver less than 1 mm to the forest under-

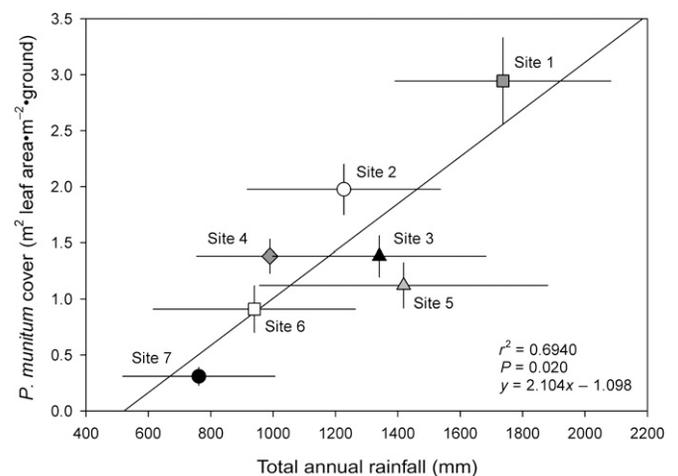


Fig. 4. The positive linear relationship between the calculated leaf area cover of *Polystichum munitum* (mean \pm SE) and the total annual rain input (mean \pm SD) into each region of the redwood forest ecosystem.

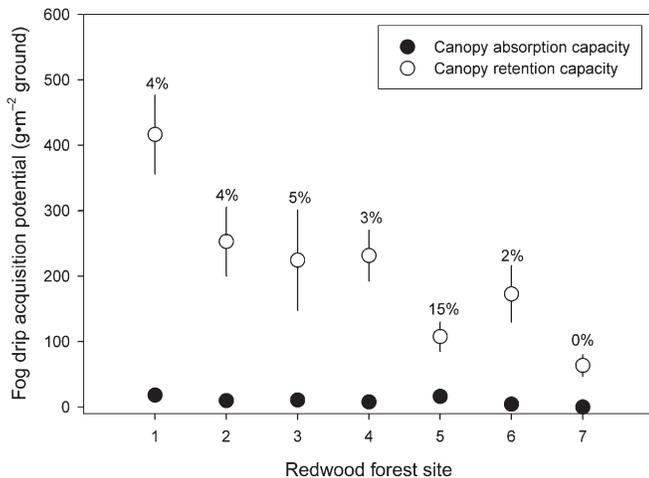


Fig. 5. The estimated potential for *Polystichum munitum* canopy cover in the forest herbaceous layer to intercept, retain, and absorb fog drip by foliar uptake. As forest latitude decreases (from site 1 to 7), the canopy water retention capacity (mean \pm SE) decreased disproportionately more than the canopy absorption capacity (mean \pm SE). Each percentage represents the proportion of retained water potentially absorbed through foliar uptake by the *P. munitum* canopy when wet at the site.

story during a single leaf-wetting event. At site 5, we estimate that the *P. munitum* canopy can intercept 0.11 ± 0.04 mm of fog drip at a given time and therefore may retain all of the fog drip that reaches the fern canopy and significantly reduce fog inputs directly below *P. munitum* crowns. Negishi and colleagues (2006) found the dense canopy of the pioneer fern *Dicranopteris curranii* in Malaysia intercepts 1.2 ± 0.1 mm rainfall (mean \pm SE), thereby reducing rainfall to the ground by as much as the upper forest canopy in this ecosystem. While fern canopy interception of throughfall can prevent this water from reaching the soil in other ecosystems, *P. munitum* may actually facilitate throughfall availability in the soil by directly redistributing the water belowground (Limm, 2009). By intercepting throughfall with fern fronds and then leaking water to the soil in the rooting zone, aboveground water subsidies bypass the absorbent litter layer on the forest floor that limits the percolation and diffusion of water down into the soil.

Given that winter precipitation input to California ecosystems will likely change in the coming decades (Hayhoe et al., 2004; Loarie et al., 2008, 2009), understanding the fog drip acquisition potential of fern populations may aid predicting how *P. munitum* abundance will be affected by climate change. If rainfall decreases, *P. munitum* may rely more on fog water during the summer months to sustain the current frond size, crown density, and total canopy cover. If foliar uptake is a plastic trait, fog drip absorption efficiency may increase in response to higher demand for fog if rainfall decreases. However, if *P. munitum* differs genotypically in foliar uptake capacity in the ecosystem today, climatic changes may drive local extinctions of populations unable to efficiently absorb fog water as demand for water increases.

Although the results from our present study show that a majority of the *P. munitum* canopies throughout the redwood forest range can acquire this subsidy today, we still poorly understand how available fog is as water subsidy throughout the ecosystem. Satellite imaging and ground-based cloud height detection may provide reasonable quantification of when fog

cover is present over the redwood ecosystem, but future research is needed to quantify the duration of leaf wetness during fog events so we can better understand how often the plant canopy actually has access to fog and can absorb this water subsidy aboveground. While we do not yet understand how much fog exposure and leaf wetting occurs throughout the redwood forest ecosystem, we do know that fog frequency along the coast of California is generally decreasing (Johnstone, 2008; Williams et al., 2008; Johnstone and Dawson, 2010). Because *P. munitum* depends on fog-water subsidies to maintain optimal summertime water status in many areas, the future canopy cover and distribution of *P. munitum* in the redwood forest ecosystem may change with further fog loss, affecting the understory ecosystem it helps define.

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APPENDIX 1. Error propagation equations for fern crown estimates.

We estimated the uncertainty associated with calculating the total leaf area at the plot level using error propagation as:

$$s_p = \sqrt{(a \cdot s_x)^2 + (b \cdot s_y)^2 + (c \cdot s_z)^2 + \dots}, \quad (\text{A1})$$

where s_p is the standard error associated with the summed crown leaf area of all *P. munitum* individuals in each plot, each constant (a , b , c , etc.) is the number of fronds in each crown, and each crown standard error (s_x , s_y , s_z , etc.) represents the uncertainty of the mean leaf area for each crown as calculated from the five measured fronds.

We averaged the plot leaf area means to determine site-specific total fern cover and estimated the associated uncertainty for each site as:

$$s_s = \sqrt{(s_p)^2 + (s_q)^2 + (s_r)^2 + \dots}, \quad (\text{A2})$$

where s_s is the standard error of the mean *P. munitum* leaf area cover for each forest site and each plot standard error (s_p , s_q , s_r , etc.) represents the uncertainty of the leaf area cover in each plot as calculated above (Eq. A1).

We estimated the maximum fog drip interception capacity of each site and calculated the associated uncertainty as:

$$s_t = \bar{t} \cdot \sqrt{\left(\frac{s_s}{\bar{s}}\right)^2 + \left(\frac{s_w}{\bar{w}}\right)^2}, \quad (\text{A3})$$

where s_t is the standard error of the mean fog interception capacity for the forest site (\bar{t}), s_s is the standard error (as calculated in Eq. A2) of the mean *P. munitum* leaf area cover at the site (\bar{s}), and s_w is the standard error of the mean leaf surface water-holding capacity (\bar{w}).

We estimated the fog drip absorption capacity for each site and calculated the associated uncertainty as:

$$s_a = \bar{a} \cdot \sqrt{\left(\frac{s_s}{\bar{s}}\right)^2 + \left(\frac{s_u}{\bar{u}}\right)^2}, \quad (\text{A4})$$

where s_a is the standard error of the mean foliar uptake capacity for the forest site (\bar{a}), s_s is the standard error (as calculated in Eq. A2) of the mean *P. munitum* leaf area cover at the site (\bar{s}), and s_u is the mean foliar uptake capacity (\bar{u}).

We estimated the fog drip acquisition potential as the proportion of fog drip absorption given maximum interception and calculated the associated uncertainty as:

$$s_p = \bar{p} \cdot \sqrt{\left(\frac{s_a}{\bar{a}}\right)^2 + \left(\frac{s_t}{\bar{t}}\right)^2}, \quad (\text{A5})$$

where s_p is the standard error of the mean fog drip acquisition potential for the site (\bar{p}).