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Foliar Water Uptake and Resurrection: Mechanisms of Drought Tolerance in Eight Species of Ferns in the Santa Monica Mountains

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Abstract

In a region where drought is severe, ecological surveys provide insight into the adaptations of organisms living on the edge of survival. In this study, the mechanisms of drought tolerance for eight species of ferns in the Santa Monica Mountains were assessed with a focus on foliar water uptake and resurrection strategies. We find that species are significantly different (P < 0.001) in their ability to absorb water through leaves (assessed gravimetrically) and correlate this to minimum seasonal water potential and hydrophobicity of leaf surfaces. Secondly, we irrigated *Pentagramma triangularis* in the field and tracked chloroplast recovery. We found possible evidence of embolism reversal. Taken together, this study explored the methods of survival of the most ancient family of vascular plants.

Introduction

Water scarcity is at an all time high in the Santa Monica Mountains of California. Of the world's five mediterranean-climate ecosystems, mean annual rainfall is lowest in California, where the drought is most consistent and the dry season lasts at least six months (Cowling et al. 2005). Chaparral is the dominant vegetation type in these ecosystems, exhibiting numerous mechanisms of withstanding drought stress. Best assessed by overall plant survival, drought tolerance refers to the extent with which a species can withstand long periods without precipitation. All fern species in the Santa Monica Mountains must have some method of drought tolerance in order to persist. The four methods of drought tolerance applicable to this study are: water stress tolerance, water stress avoidance, desiccation tolerance, and drought escape.

Interestingly, a survey of eight species of ferns in the Santa Monica Mountains reveals at least one fern species that fits in each of these categories. Water stress tolerance is defined as the tolerance to tissue dehydration (i.e. low water potentials and/or cavitation resistance) and is seen in *Dryopteris arguta*, an evergreen specie. Water stress avoidance is defined as species that occupy microsites where water is found, a mechanism seen in *Woodwardia fimbriata* and *Adiantum capillus-veneris*. Desiccation tolerance refers to the ability of an organism to dry to equilibrium with the air and then regain normal functioning upon rehydration (Alpert 2006), and we believe this rare phenomenon is occurring in *Pentagramma triangularis* and *Pellaea andromedifolia*. Plant species can also be characterized with regard to their life history type. For instance, deciduous species such as *Pteridium aquilinum*, *Adiantum jordanii*, and *Polypodium californicum*, which we consider as drought escapers, lose photosynthetically active tissue in the winter months whereas evergreen species preserve their leaves throughout the year. Drought deciduous species escape water stress of tissues by going dormant during periods of drought: evergreen species endure tissue water stress by structural and physiological mechanisms.

Parallels can be drawn between these fern species and corresponding chaparral species, which may help explain how ferns co-occurring within chaparral shrub communities. Most importantly, the ability of ferns to persist under severe drought, as predicted for climate change in California, is not well documented and challenges previous assumptions that ferns fail to withstand very negative water potentials (severe water stress of their tissues).

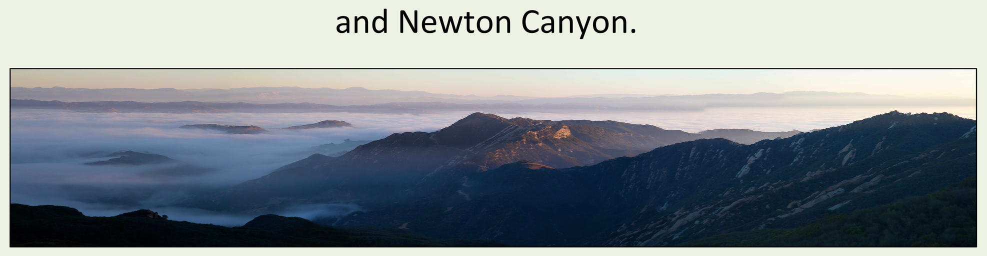
Foliar uptake is the process by which water is absorbed by stems and leaves (Rundel 1982). Ferns differ from angiosperms and gymnosperms in that xylem transport is a poor predictor of water relations in ferns (Pittermann et al. 2013). Unlike higher plants, which depend primarily on fenced xylem tissue for water transport and support from tension, previous studies suggest that ferns primarily depend on stored water (capacitance) and foliar uptake for water (Limm et al. 2009; Limm and Dawson 2010). Xylem transport is thought to play a secondary role (Pitterman et al. 2013). Evolutionarily, if xylem transport is relatively recent, how are ferns tolerant of drought induced water stress?

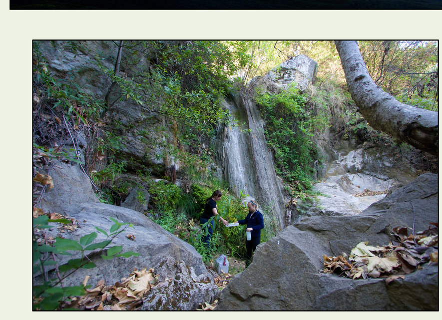
Hypotheses:

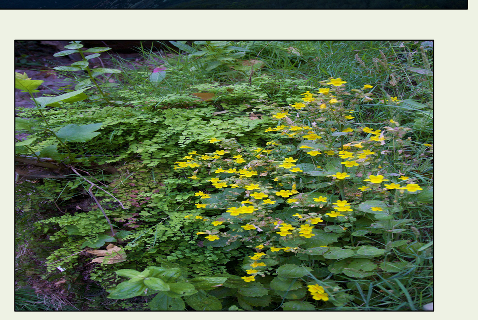
1. We hypothesize that drought tolerant ferns will have higher foliar water uptake than drought escaping ferns.
2. *Pentagramma triangularis* will desiccate completely, but will resurrect in response to irrigation in situ.

Study Sites

All fern species were collected from three sites in the **Santa Monica Mountains**.
These sites include the Piuma Road Backbone Trail, Cold Creek Canyon and Newton Canyon.







Abbreviations for Species Studied

Aj – *Adiantum jordanii*
Ac – *Adiantum capillus-veneris*
Da – *Dryopteris arguta*
Pn – *Pellaea andromedifolia*
Pq – *Pteridium aquilinum*
Pc – *Polypodium californicum*
Pt – *Pentagramma triangularis spp. triangularis*
Wf – *Woodwardia fimbriata*

Materials and Methods

H1

Figure 1. Foliar water uptake samples were collected pre-dawn and excised under water. Samples were immediately returned to the lab in a dark cooler to maintain dark adaption.

Figure 3. Foliar water uptake was determined gravimetrically using a 4 digit analytical balance. A stopwatch was used to monitor rate of mass loss. At achievement of constant rate it was assumed all standing liquid water on leaf surfaces had evaporated.

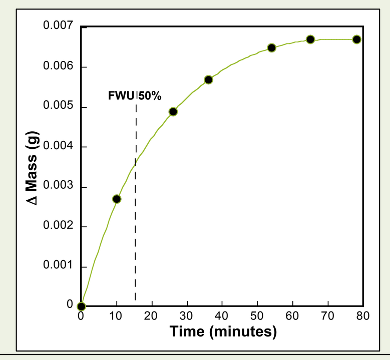


Figure 4. The rate at which foliar water uptake occurred was determined by removing the frond from water every 10 min, drying, then massing. The treatment time was determined by calculating the 50% point of water uptake. Shown is an example for Aj.

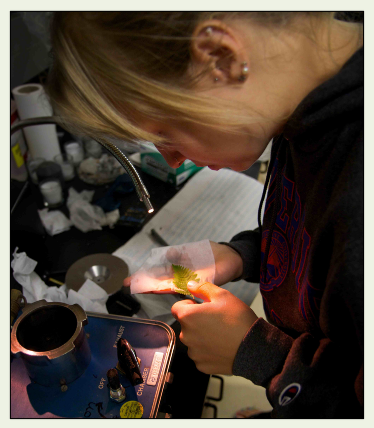


Figure 2. Foliar water uptake samples were dried with Kimwipes, then placed in a Scholander-Hammel pressure chamber and driven to -1.5 MPa. This ensured that all water potentials were even in samples. The stipe (stem) was then sealed with paraffin wax.

Figure 5. Samples were submerged horizontally in DI water. An ultrasonic fogger was used to keep RH ≥ 95%. A LI-COR area meter was used to normalize data to per unit leaf area.

H2

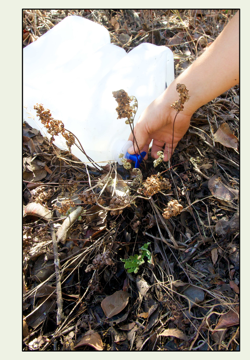


Figure 6. Thirteen microsites with Pt were irrigated *in situ* with 9.5 L of water. Irrigation was done a total of 5 times.

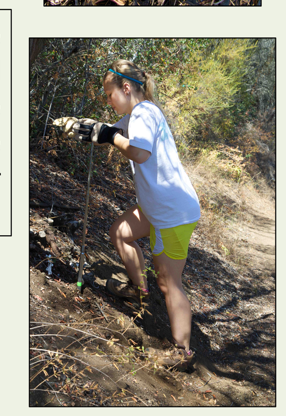


Figure 7 & 8. Soil samples were taken at 0.1 m before irrigation and after 5 times of irrigation. Soil moisture (MPa) was determined using a WP4C dewpoint potentiometer.

Figure 9. A pulse-modulated fluorometer was used to take Fv/Fm measurements. Diameter was measured using a vernier caliper.

Results

H1

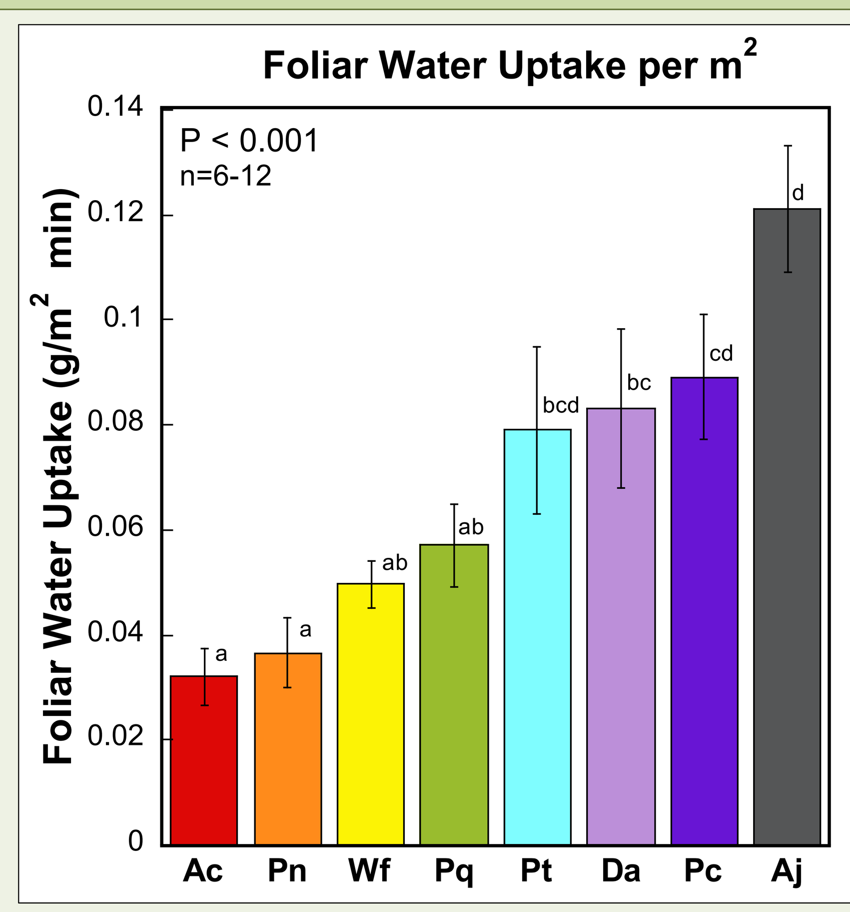


Fig. 10: Foliar water uptake (g/m² min) compared for 8 species of the Santa Monica Mountains by one-way ANOVA, followed by log-transformed Fisher's LSD test. Letters denote significance; P < 0.001. Bars represent ± 1 S.E. n = 6-12

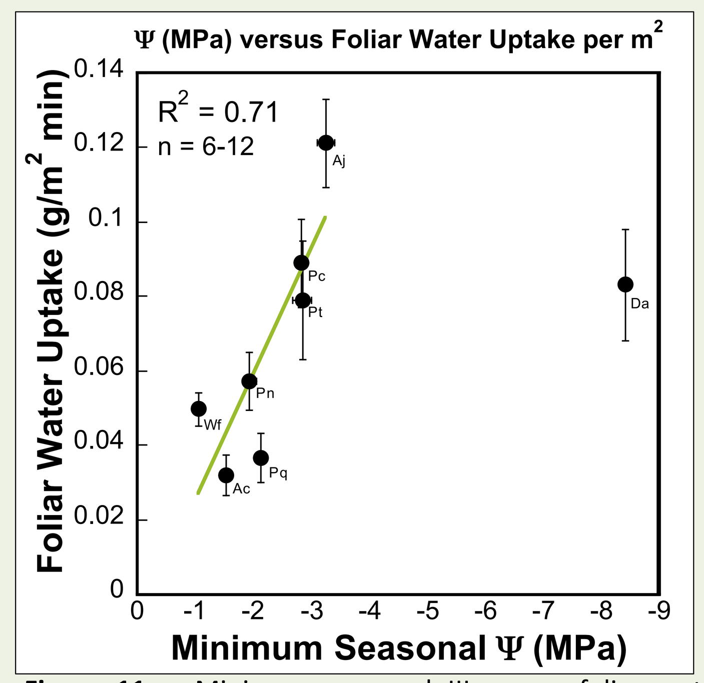


Figure 11: Minimum seasonal Ψ versus foliar water uptake (MPa, g/m² min). Da not included in regression to better represent normal ecological trend. Linear regression $R^2 = 0.71$. Bars represent ± 1 S.E. n = 6-12.

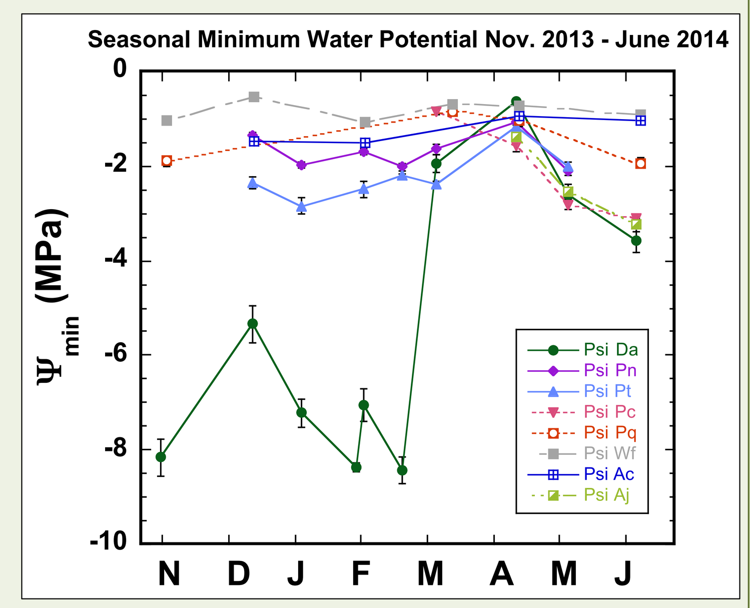


Figure 12: Seasonal midday water potential (MPa) from November 2013 – June 2014. Bars represent ± 1 S.E. n = 6.

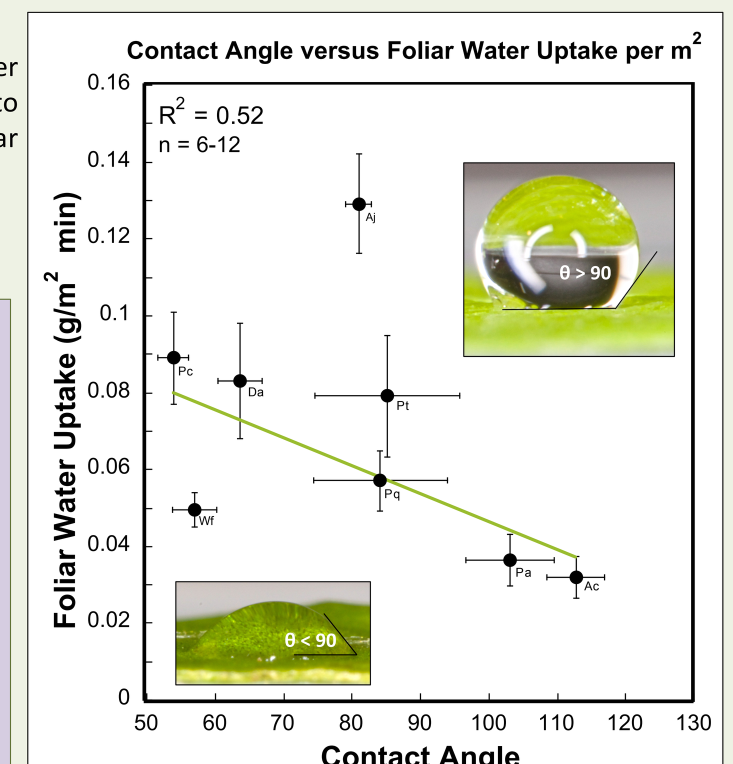


Figure 13: Contact angle, in degrees, (measure of hydrophobicity of leaf) versus FWU (g/m² min). Aj not included in linear regression to better represent normal ecological trend. Linear regression $R^2 = 0.52$. Bars represent ± 1 S.E. n = 6-12. Photo shown demonstrates finding the contact angle for Ac.

H2

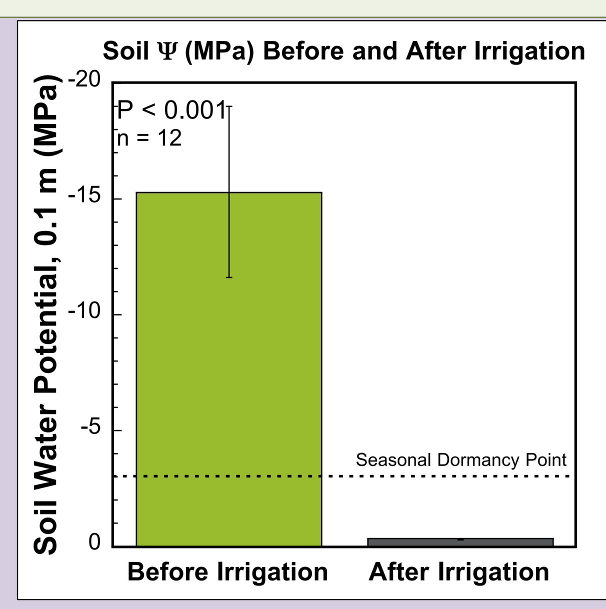


Figure 14: Soil water potential at 0.1 m before and after irrigation (MPa). One-way ANOVA P < 0.001. Bars represent ± 1 S.E. n = 12. Seasonal dormancy point marked.

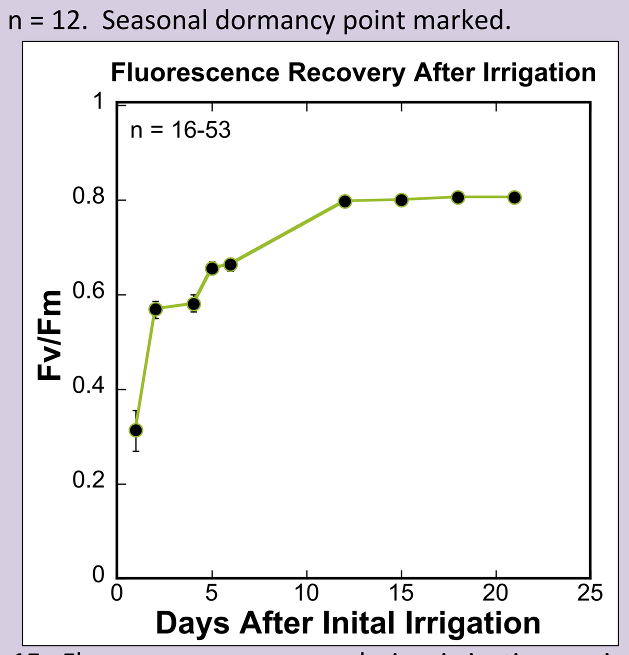
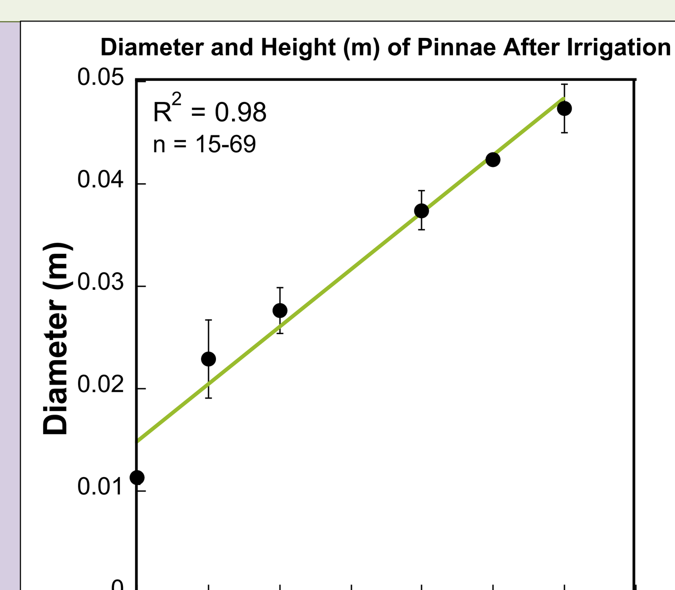


Figure 15. Fluorescence recovery during irrigation period. Optimal Fv/Fm functioning occurs ~ 0.8. n = 16-53.



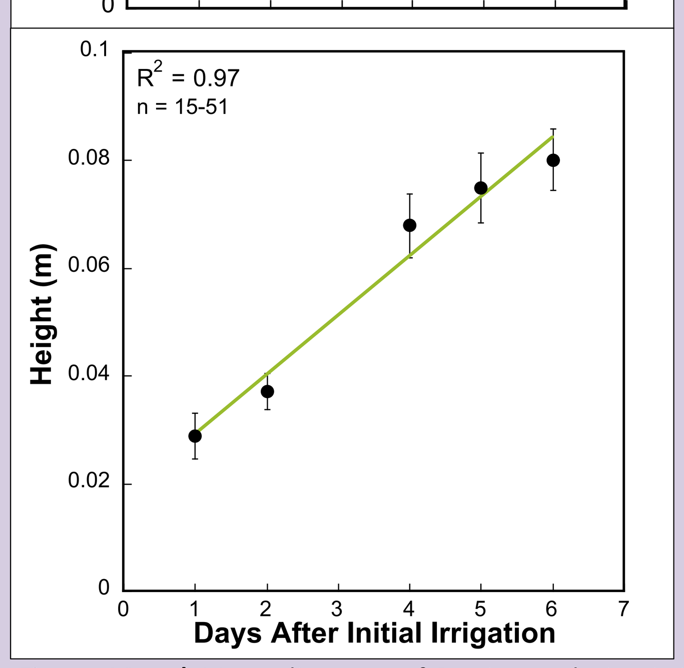


Figure 16. a) Mean diameter of Pt pinnae during irrigation period (m). Linear regression $R^2 = 0.98$. Bars represent ± 1 S.E. n = 15-69. **b)** Height of uncurled fronds during irrigation period (m). Linear regression $R^2 = 0.97$. Bars represent ± 1 S.E. n = 15-51.

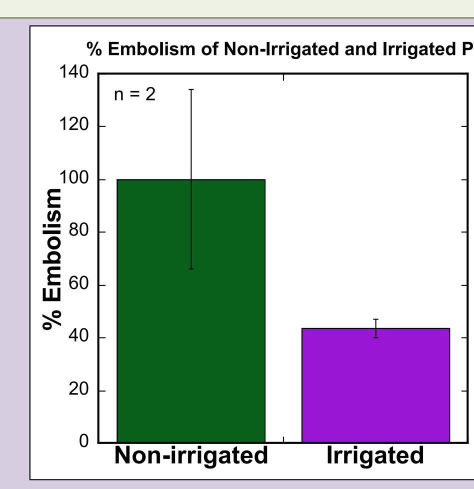


Figure 17. Preliminary data for % embolism of non-irrigated and irrigated Pt. Bars represent ± 1 S.E. n = 2; hint of embolism reversal.

Discussion & Conclusions

H1: This comparison of foliar water uptake for eight species of ferns in the Santa Monica Mountains shows wide variation in the capacity for uptake among species. For example, Aj was four-fold higher than Ac which is of interest considering these species are in the same genus (figure 10). When comparing foliar water uptake to minimum seasonal water potential and contact angle, a correlation exists for seven of the eight species (figures 11 & 13). Seasonal water potential data shows that Da is unlike the other seven species (figure 12). Importantly, a previous study done in the Californian redwood forest suggests that water status of the fern does not impact absorption; however our results suggest otherwise, perhaps due to drought (Limm and Dawson 2010). Additionally, Aj has higher foliar absorption than the other species but contact angle is not a good predictor of foliar water uptake in this situation showing other factors than hydrophobicity impact foliar uptake.

H2: Rehydration of Pt in the field reveals a multi-day "waking up" period where the chloroplasts are regaining function (figure 15). It is possible that this is a protection mechanism in that a lag time from irrigation allows the plant to increase root pressure until the fronds can finally uncurl. Data suggests that the shortest and smallest fronds uncurl first, perhaps as a function of embolism reversal (figure 16 & 17).

- Species found in water, such as Wf and Ac, exhibit low capacity for foliar water uptake, whereas ferns that grow on dry hillsides, such as Aj and Pc, exhibit the highest capacity for foliar water uptake.
- Contact angle is a measure of leaf surface hydrophobicity that negatively correlates with foliar water uptake.
- Pt exists by utilizing a resurrection strategy, perhaps facilitated by positive root pressure that could reverse embolism.

This study demonstrates the importance of ecological niches in fern survival. In the Santa Monica Mountains, where drought is a key limiting factor, the exploitation of different survival mechanisms allows for continuing success even in dry conditions. Evolutionarily, the patterns observed in ferns "living on the edge" sheds light into the continued success of these ancient vascular plants.

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