Foliar Water Uptake in the Needles of Pinus Torreyana

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Abstract

In semi-arid climate systems that encounter low clouds or fog, many plants have adapted to capture atmospheric moisture on the foliar surface. The natural habitat of *Pinus torreyana*, the Torrey pine, is restricted to two locales in coastal Southern California that experience substantial fog and low clouds during the dry months of a Mediterranean climate. In this study, droplet contact angles were used to assess surface wettability, and droplet uptake was used to measure the foliar water uptake rate along a needle. We demonstrated that there are only remnants of epicuticular wax on the needle. The results showed that the needle surface of *P. torreyana*, including under the base sheath, is hydrophilic and capable of direct water uptake. There are small spatial gradients in the uptake pattern, but the variability is high and the statistical significance is not strong. However, the decrease in uptake at higher contact angles can be described by an ordinary linear regression ($r^2 = 0.45$, $p = 4 \times 10^{-8}$). On average, the foliar uptake of the adaxial surface of a one-year-old needle is $2.88 \pm 0.60 \times 10^{-2} \text{ mg cm}^{-2}\text{s}^{-1}$. In comparison, the uptake rates by the adaxial surfaces of four local broadleaf plants are between 0.05 and 0.6 of that of *P. torreyana*.

Introduction

The ability to utilize atmospheric moisture from fog or dew to reduce water stress can be an important adaptive feature of plants in semi-arid climates. The inquiry of whether some plants capture dew via aerial structures started close to three centuries ago (Stone 1957a). For pines, Stone and coworkers (Stone et al. 1950; 1956; Stone 1957b) performed some of the earlier studies using potted seedlings. Collectively, their results showed that *Pinus coulteri*, *Pinus ponderosa*, and *Pinus jeffreyi* are capable of surviving a period of drought in soil at the wilting point. Application of mist at night could extend the survival of potted *P. ponderosa* seedlings even longer (Stone 1957b). Similarly, Boucher et al. (1995) found that spraying mist on potted *Pinus strobus* seedlings significantly increased the water potential of the shoots. They attributed the change to foliar water uptake.

Direct foliar uptake as a water subsidy has long been recognized in ecosystems benefitting from fog or mist (Boucher et al. 1995; Breshears et al. 2008; Eller et al. 2013). In exploring the possibility that pines could absorb water directly through foliage, two studies involving *Pinus sylvestris* and *Pinus radiata* provided important insights (Leyton and Juniper 1963; Leyton and Armitage 1968). Leyton and coworkers measured surface wettability in terms of sessile droplet contact angles and water uptake by immersing different sections of the needles in water overnight. Among their findings, it is worth noting that the needles of *P. sylvestris* absorbed water largely near and under the base sheath, while the needles of *P. radiata* exhibited the reverse pattern. Leyton ascribed the difference to the adaptation of *P. radiata* to a climate with summer fog during dry seasons.

Closer to the present, the phenomenon of fog drip is thoroughly studied in California coastal redwood forests (Dawson 1998; Burgess and Dawson 2004; Limm et al. 2009; Goldsmith et al. 2013). Much of the fog intercepted by the leaves of *Sequoia sempervirens* drips onto the ground, and as much as one third of

the annual hydrologic input is attributed to this fog fall. A small quantity of the fog water is absorbed directly into the leaves (Burgess and Dawson 2004). Foliar uptake can increase the leaf water content by 2–11% and helps to reduce water stress during dry seasons (Limm et al. 2009).

The object of the present study is *Pinus torreyana* C. Parry ex Carriere ssp. *torreyana*, a subspecies endemic to a coastal mesa in southern California that includes the confines of Torrey Pines State Natural Reserve (TPSNR). Together with another small population of the subspecies *Pinus torreyana* Parry ex Carrière ssp. *insularis* J. R. Haller on Santa Rosa Island, *Pinus torreyana* is a relic taxon (Haller, 1968) considered critically endangered and the rarest pine in North America (IUCN 2021). Despite its scarcity, there were known disturbance histories (Wells and Getis, 1999). Being in close proximity to an urban setting, *Pinus torreyana* ssp. *torreyana* in particular is jeopardized by modern human activities (Franklin and Santos 2011). A paleoecological study in the TPSNR area revealed that the population of the pine was exceedingly small about 2,100 years ago. A consequence is that the genetic diversity of the pine is very low (Ledig and Conkle 1983; Whittall et al. 2010). Currently, efforts are underway to evaluate the evolutionary potential of the pine for genetic rescue (Hamilton et al. 2017).

Among all previous studies on *Pinus torreyana*, there has yet to be a study investigating specific adaptive characteristics of the pine. Both populations of *P. torreyana* are situated in coastal areas encountering moisture from fog and low cloud cover (FLCC), especially during the dry seasons of a Mediterranean climate (Haller 1986; Williams et al. 2008). There is general thinking that the availability of atmospheric moisture is critical to the survival of this pine. Our perspective is that *P. torreyana* is likely capable of capturing atmospheric moisture effectively. For one, it is a diploxylon pine but on average has five needles per fascicle. In addition, the needles are long, usually reaching 200–280 mm and sometimes 300 mm beyond the base sheath, thus producing a large foliage surface area. Considering the local climate regime is similar to northern California coastal forests, where *Sequoia sempervirens* thrives and is known to be capable of direct foliar uptake, we investigated in this study if *Pinus torreyana* can similarly exhibit foliar uptake. We measured droplet contact angles and droplet uptake rates along pine needles. We also explored the relationship between contact angle and the local uptake rate, the droplet absorption flux. We found that the needle surface is predominantly hydrophilic, and the needles are capable of absorbing water directly. We hope this study will foster more detailed studies of this rare pine.

Materials And Methods

Sampling site

Pinus torreyana needles were collected from the campus of the University of California, San Diego on the same mesa as the TPSNP but about 2 km farther south. The sampling location is at the top of a xeriscape ravine with chaparral vegetation. The trees were planted there as saplings in the 1990s. Using the ClimateWNA database and climate model (Wang et al. 2016), the mean annual rainfall at this site over the last decade (2011–2019) was 283 mm, and the computed Hargreaves reference evapotranspiration was 1000 mm. At TPSNP over the same period, the mean rainfall and

evapotranspiration were 271 mm and 952 mm, respectively. Thus, the sampling site had slightly higher precipitation but slightly higher water deficit because of elevated evapotranspiration. Nonetheless, the climate at the sampling site is very similar to TPSNP. The rainfall recorded in this period is slightly higher than the 262.6 mm commonly cited as the historic average over the San Diego region from the National Weather Service (NWS).

Needle fractional moisture

The moisture content of the needles was monitored for 21 months covering wet and dry seasons. Near the end of each month, at least five one-year old fascicles at head level were collected. Within an hour, the beginning 15 mm near the base sheath where the needles are not well separated and the 30-mm uneven tip region were excised to retain a 160-mm minimum uniform segment. The cut ends were capped with a dab of silicone sealant. After the adhesive dried, the fascicles were weighed before being soaked in deionized water overnight in the dark. The saturated weight was taken after the needles were patted dry. To obtain the desiccated weight, the fascicles were heated at 80°C for 5 h. The fractional moisture is calculated as $f_m = (m - m_{dry}) / (m_{sat} - m_{dry})$, where m is the weight of a given sample, and m_{dry} and m_{sat} are the respective desiccated and saturated weights.

Contact angle

The base sheath of freshly collected adjacent fascicles was stripped off. Six needles were removed, and each was mounted horizontally. Three needles were placed with the abaxial surface facing upward and three needles with the adaxial surface facing upward. Droplets of 2 µl deionized water were added to the surface at 2-cm intervals with the distance measured from the marked edge of the base sheath. An additional droplet was applied to the midpoint of where the base sheath was. A side-view 2D image was taken with a digital microscope (Jiusion). The contact angles of the left and right edges of each droplet to the needle surface were measured using the protractor function in the image processing application, GIMP.

Water uptake rate

Two methods were used. We first measured water absorption in different sections of the needle following the works of Leyton and coworkers. The excised end of a fascicle, including the base sheath, was sealed with Parafilm. Afterward, the fascicle was immersed, with the tip end down, in deionized water to a designated depth. The weight gain was measured at different times. Five fascicles were used for each immersion depth. In the second method, we took microdroplet uptake measurements. In step with the contact angle procedure, after the 2-µl droplets were applied to the surface, the times for their disappearance were recorded. Concurrently, several 2-µl droplets were applied to a Parafilm surface to measure the evaporation rate. The rate of water absorption into the needle is the net of the total loss rate minus the evaporation rate, $r_{uptake} = r_{tot} - r_{evap}$. The rate is divided by the footprint area of the water droplet to obtain the local absorption flux. To expand the range of probable contact angles, a dozen

young shoots under 4 months old and varying between 11 to 96 mm were used to measure the droplet uptake rates.

Electron microscopy

We examined the surface of *P. torreyana* needles using environmental scanning electron microscopy (Quanta 200, FEI). Fresh needle samples were lightly sputter coated with iridium to enhance conductivity before being placed on a sample mount.

Comparison with selected plants

The leaves of *Eriodictyon crassifolium*, *Malosma laurina*, *Heteromeles arbutifolia*, and *Rhus integrifolia* were tested. Three samples of each plant were taken, and on each, five 2- μ l droplets of deionized water were applied widely spaced on the adaxial surface. As with the procedures on the needles, images of the droplets were taken to measure the contact angles, and droplet disappearance times were recorded. Droplets on Parafilm were used as the evaporation control. To measure the evaporative drying of detached leaves, 5 leaves from each plant and 5 pine fascicles were used. Images of the leaves were taken, and their areas were calculated from a pixel count calibration using GIMP. The needle area was calculated using ruler and micrometer measurements. All leaves were left to dry in open air under ambient conditions. The weights were taken daily, and the weight loss, taken to be that of water, was normalized by the respective total area of each leaf.

Statistical analysis

Sample comparisons used the t-test, and for comparison among groups, Tukey's post hoc test was used. Linear regression used ordinary least squares and weighted least squares with internally studentized residues. All analyses used a significance level of 0.05 and were carried out with R running under RStudio.

Results

Needle moisture saturation

The fractional moisture of the needles varies within a relatively narrow range. For the survey period beginning in October 2019, the value on average hovered above 0.8 (Fig. 1a). October is generally taken as the beginning of the local rainy season, which lasts until April. There was no precipitation in October 2019 (Fig. 1b), but over a year from October 2019 to September 2020, the cumulative rainfall was 345 mm, which was 32% above the historic average of 262.6 mm. The rainfall in Fig. 1b is based on the NWS record rather than ClimateWNA, which as of this study has not posted data beyond 2019. The rainfall pattern during that year was episodic. After several large rainstorms in November and December of 2019, the fractional moisture was as high as 0.92. The weather was unusually warm and dry at the beginning of 2020. The total precipitation of April 2020 was reasonable, but it all came at the beginning of the

month. Based on NWS records, a hot spell of several days went up to 32 °C, and the fractional moisture dropped to 0.76 near the end of April 2020.

The onset of onshore stratus clouds and ground level fog in the marine boundary layer arrived in early May 2020. Despite the lack of rainfall and warmer temperatures, the fractional moisture crept up through the summer. Fluctuations to an extent are tied to hot spells. For example, in June 2020, the temperature went as high as 34 °C in the middle of the month. The dashed line represents the average fractional moisture of 0.85 from October 2019 through September 2020. After the unusual wet year, the rainy season beginning in October 2020 was extremely dry, and the rainfall was well below average. Nonetheless, the fractional moisture remained within the neighborhood of 0.8. April 2021 was a dry month, but it already received periodic FLCC, which became consistent and heavy in May 2021. The temperature did not go above 24 °C in May and June of 2021. This condition is reflected in the measurements. The fractional moisture dropped to only 0.81 in April 2021 through June 2021. The values were better than the corresponding months in 2020.

SEM

A scanning electron micrograph of one-year-old *P. torreyana* needle surfaces indicates that there are only remnants of epicuticular wax, exposing the underlying epidermis. On both the abaxial or curved (Fig. 2a) and adaxial or flat (Fig. 2b) surfaces, one can identify ridge lines with spines spaced sparsely apart and more distinctly, stomata with Florin rings of epicuticular wax, especially on the adaxial surface. The spacing in between stomatal lines is not uniform. The quantity of vestigial epicuticular wax is uneven; there are more residues on the adaxial surface, where there is epicuticular wax between stomata and between some stomatal lines. The uneven surface leads to variability of droplet measurements.

Foliar uptake by fractional immersion

Following the works of Leyton and coworkers (1963, 1968), we made an attempt to measure foliar uptake by immersing various lengths of needles, beginning from the distal end. The time varied from 18 min to 24 h. The short 18 min was chosen to be so brief that the uptake would be well under the absorption capacity of the needle based on droplet measurements, thus limiting the extent of probable vascular transport. This possibility is clearly exhibited by needles immersed to one-fourth of its length (Fig. 3). Within 18 min, the uptake quantity was hardly measurable. However, by 1 h immersion, it would appear that this section near the tip could uptake water much more quickly, as compared with the one-half immersion to full-length submersion cases. This apparent uptake is accentuated when the quantity is normalized by the immersion length as in Fig. 3. It is apparent that after water is absorbed near the distal end, it can be transported to the proximal part of the needle. This vascular transport becomes less important as more of the needle is immersed, as with the half and three-quarter immersion cases. When the entire needle is submerged, the 24 h weight gain corresponds to a saturated needle. The uptake within 18 min appeared high, but it could be an unusually low measurement at 1 h. It is evident that fractional immersion is not a good method to measure spatial variations.

Foliar uptake by droplet absorption

Droplet measurements provide a better characterization of probable spatial distributions of wettability and foliar uptake. As hinted in Fig. 2, there is large variability because of the heterogeneity of the uneven surfaces. All droplets have different contact angles at the two edges of a 2D image, but unlike the advancing and receding angles on an inclined plane, the present differences are not as drastic. Within this study, the maximum difference of the two droplet contact angles on the abaxial surface was 7.3° with a mean of 0.9° and on the adaxial surface, a maximum of 8.1° with a mean of 1° . In the analyses, the average of the two edge readings was taken as the contact angle of a given droplet. Droplet placement was guided by a scale. On the abaxial surface, the maximum placement error in absolute value was 2.9 mm with a mean error of 0.07 mm, and on the adaxial surface, the maximum error was 2.1 mm with a mean of 0.06 mm. Hence, in the regressions of contact angle and uptake rate versus location, the x -axis location error was taken to be negligible. Standard error bars are not based on repeated sampling as the needle properties cannot be ensured to remain identical after each use. Instead, needles from adjacent fascicles were used, and hence the error bars are an indication of the variability of similar needles. The results in Fig. 4 revealed that while there are variations in contact angles and water uptake rates, the spatial gradients are relatively small, especially that of the uptake flux.

The needle samples in Fig. 4 were from the same branch. The one-year and two-year samples were about 10 and 22 months old respectively. Figs. 4a and b show adaxial measurements, while Figs. 4c and d are from the abaxial surface. The scattered plots are accompanied by their respective ordinary least square regression lines and 95% confidence bands. Comparing the contact angles, which are all under 65° , both surfaces of the two-year old needles have lower values. However, the spatial gradients have slight differences. From an ordinary least squares, both slopes of the abaxial surface are statistically significant ($p < 0.05$, Table 1), even though the coefficients of determination, r^2 , are quite low (0.44 and 0.72, respectively), implying other physical factors may also play a role in the spatial gradient.

The droplet absorption fluxes in Figs. 4b & d, with the exception of the year-2 adaxial surface, are lower toward the needle tip, where the contact angles are larger. In Fig. 4b, the two-year old needles also have a noticeably higher absorption flux. It is logical to associate a more wettable surface with a lower contact angle and a correspondingly higher water uptake rate. Nonetheless, this pattern is not definitive; the functional dependence is not precise on these uneven surfaces. With an ordinary least squares calculation, only the regression of the year-1 adaxial uptake flux is statistically significant ($p = 0.034$, Table 1) and has a relatively low r^2 . The year-2 adaxial uptake clearly demonstrated no spatial dependence ($p = 0.91$). In Fig. 4d, the abaxial uptake fluxes of both the one-year and two-year old needles appear to be the same, but because of the variability of the data, the statistical significance is not strong (two-tailed t -test of the slopes, $p = 0.05$). Clearly, the spatial variation of the uptake flux does not strictly follow that of the contact angle.

Because of the large data scatter, a weighted least square calculation was also applied to reduce the weights of outliers (Table 1). The regressions of the contact angle become significant except for the year-

2 adaxial surface ($p = 0.051$), while the values of r^2 remain relatively low. With the uptake flux, three of the slopes are significant with the exception of the year-2 adaxial surface ($p = 0.33$). These three slopes have a reasonable coefficient of determination, but considering the small gradient, $O(10^{-4})$ mg cm⁻² s⁻¹ per cm change, the physical functional dependence of the spatial variation along the needle is not large.

A Tukey test, which does a comparison disregarding spatial distribution, was also applied to the data set. In terms of the contact angles, the surfaces are different ($p < 0.05$), except for the pairing between year-2 adaxial and year-1 abaxial. These 2 surfaces also turned out to have similar slopes of linear regression in Table 1. With respect to the uptake flux, the year-2 adaxial surface differs from the other surfaces, which among themselves are similar. Considering the variability of the data and the varying spatial gradients of the contact angle within the data set, it is probable that there are no fundamental differences in the needle surface. Observations, including the year-2 adaxial measurements, were results of uneven weathering of the needle surfaces.

Correlation of the local absorption flux with contact angle

To explore the functional dependence of the local absorption flux versus contact angle, all the data in Fig. 4 with additional data from young shoots is plotted in Fig. 5. Overall, the decrease in uptake flux at higher contact angles can be described by a linear regression. The slope is -4.3×10^{-4} mg cm⁻² s⁻¹ per degree change using ordinary least squares ($r^2 = 0.45$, $p = 4 \times 10^{-8}$), and with a weighted least squares to discount outliers, the adjusted slope is -4.5×10^{-4} mg cm⁻² s⁻¹ per degree change ($r^2 = 0.94$, $p = 2 \times 10^{-16}$).

The contact angles of the droplets on matured needles are predominately below 65°. At the low end (< 45°) and the high end (~ 60°), there is some consistency in that a lower contact angle corresponds with a higher absorption flux. However, in the range roughly from 50° to 55°, the variability of the absorption flux is extremely high. This aspect is what leads to the variability of the spatial gradients in Fig. 4. The contact angles of droplets on young shoots are higher, between 60° and 80°, but there are exceptions, as shown by the hydrophobic droplet.

Comparison with other plants

To address how the adaptation of the Torrey pine may compare with other species, several plants with large, broad, evergreen foliage were chosen. They are *Heteromeles arbutifolia* (toyon), *Malosma laurina* (laurel sumac), and *Rhus integrifolia* (lemonadeberry) from maritime chaparral and *Eriodictyon crassifolium* (thick-leaf yerba santa) from coastal sage scrub. They are common where *P. torrey* inhabits.

Detached leaf samples were left drying on a benchtop under ambient conditions. The drying is taken as evaporative. The initial fractional moisture of the leaf samples were not the same (Table 2). Nonetheless, the values show that all these plants, including the pine, have moisture content within a comparable range. How well the leaves of each plant withhold water is shown in Fig. 6. The leaves lose moisture via evaporation relatively quickly in the beginning, but moisture loss levels off when the moisture content drops to ambient relative humidity. *E. crassifolium* loses moisture most rapidly, with a precipitous drop in

weight within a few days (Fig. 6a), which corresponds with a high evaporative flux (Fig. 6b). *M. laurina* also loses moisture relatively quickly, while *H. arbutifolia* has a more steady drop. *R. integrifolia* retains its moisture almost as well as *P. torreyana* for the first five days, after which it starts to lose moisture more quickly in an unsteady pattern. In contrast, *P. torreyana* never exhibits a steep drop in weight or sharp rise in evaporative flux. From the beginning, the needles hold a steady evaporative flux and lose moisture very gradually.

The adaxial surface contact angles and water uptake of the four leaves are compared with the pine in Table 2. The properties of *E. crassifolium* stand out. With its tomentose surface, a droplet placed carefully on its surface demonstrates a Cassie-Baxter state with hydrophobic contact angles (Dorrer and Rhe 2007). The droplet uptake flux is not absolute zero because as the droplet becomes small enough via evaporation, it may slip through the hairs and impale the surface, transitioning to the Wenzel state. The *E. crassifolium* leaf is extremely absorbent if water is in direct contact with its surface, consistent with how it loses moisture the fastest in Fig. 6a.

It is rather unexpected that the leaf surfaces of the three chaparral plants are hydrophilic and capable of foliar uptake, especially *R. integrifolia*, which is thick and leathery. The difference is small, but *H. arbutifolia*, which has a larger contact angle, also has a lower water uptake flux. Even though these leaves are capable of foliar uptake, their uptake fluxes are lower than the matured needles of *P. torreyana*. Specifically, the uptake flux by the adaxial surfaces of *E. crassifolium*, *M. laurina*, *H. arbutifolia*, and *R. integrifolia* are only, respectively, 0.05, 0.38, 0.48, and 0.6 of the rate of the year-1 adaxial surface of *P. torreyana*. The average contact angle of the young shoots is higher (Table 2) and similar to that of *M. laurina*, but the young shoots have a higher uptake flux, which is about half of the matured needle. The surface under the base sheath tends to have a slightly higher contact angle than the exposed needle surface, with a corresponding smaller decrease in the uptake flux.

Discussion

Although cutin, a biopolyester, is a major component in cuticles, a cuticle is a complex composite material, and its properties are not governed strictly by cutin. Depending on the composition and physico-chemical properties, many leaf surfaces are wettable and provide pathways for foliar uptake of water and solutes (Fernndez et al. 2017). Although the uptake mechanisms are not fully understood, it is essential that the epicuticular wax coverage is not intact. This layer is not only hydrophobic, but with the right nanostructure, may impart superhydrophobicity. The degradation of epicuticular wax by weathering or air pollution has been observed in pine needles. Cape (1983) observed that the contact angles of a young *Pinus sylvestris* needle decreased from above 100 to under 90 in four months. Two-year old needles had contact angles as low as 75. The decrease was ascribed to the degradation of epicuticular wax. Other studies have also observed similar changes in older needles (Leyton and Armitage 1968; Lin et al. 2001).

The needle fractional moisture during the spring underscores the importance of FLCC and provides complementary information to tree ring studies. In a study of *P. torreyana* ssp. *insularis*, Williams et al. (2008) refined the work of Biondi et al. (1997) on *P. torreyana* ssp. *torreyana* and showed that while precipitation in winter and spring is important and affects soil moisture, there is a significant correlation of tree-ring widths to summertime cloud frequency. While needle moisture is not a growth indicator, the measurements from April to June provide useful insights. The regions with the heaviest FLCC migrate northward from southern California from May to September. Dense FLCC, especially when low clouds prevail until mid-day, reduces solar radiation. Thus, FLCC moderates the maximum daytime temperature, reduces evapotranspiration, and narrows the water deficit. Plants capable of direct water uptake further improve the water balance. (Clemesha et al. 2016; Torregrosa et al. 2016; Williams et al. 2008). These possibilities are reflected in the spring needle moisture measurements. With consistent FLCC, what locally is referred to as May Gray and June Gloom weather patterns, the needle moisture began to recover in May. With heavier cloud covers in May 2021, the fractional moisture recovered even more. Similarly, despite an unusual heat wave that hit the western states during June 2021, the fractional moisture stayed close to 0.83. It is apparent that the needles are capable of compensating for water deficit with the presence of FLCC. During this study, the needles of *P. torreyana* were capable of maintaining its fractional moisture around 0.8.

The works of Leyton and coworkers demonstrated that *P. sylvestris* and *P. radiata* have different needle properties and water uptake patterns. Extensive epicuticular wax with tube-like morphology was observed with *P. sylvestris* needles, while epicuticular outgrowths covered only a portion of the *P. radiata* needles. Despite the epicuticular wax, the needles of *P. sylvestris* have a slightly hydrophilic surface with contact angles of 85.7° and 77.3° on the adaxial and abaxial surfaces, respectively. In contrast, *P. radiata* needles have lower contact angles, with average values of 57.6° and 72.6°, respectively for the adaxial and abaxial surfaces. The exposed needle surface is capable of water uptake, unlike *P. sylvestris*, which absorbs water predominantly under the base sheath (Leyton and Juniper 1963; Leyton and Armitage 1968). In contrast, *P. torreyana* has very little epicuticular wax, and there are no considerable differences between the two surfaces. The spatial gradients, especially the uptake flux, are small. Furthermore, the surface underneath the base sheath, as shown in Table 2, is hydrophilic, albeit having lower wettability. The sheath material is fibrous and absorbs water like a sponge. Many fascicles in the upper branches are spreading-ascending in orientation. It is conceivable that condensed droplets may roll downward and be absorbed in the base sheath. Nonetheless, the length of the base sheath of matured fascicles is usually under 20 mm and hence is a small supplemental contribution to the long, exposed needle surface.

Even though we can measure the local water absorption flux, we cannot project the probable plant uptake, which is a much more complex and difficult problem, as demonstrated by the studies of Dawson and coworkers on *Sequoia sempervirens* (Burgess and Dawson 2004; Limm et al. 2009). The confounding factor is that absorbed foliar water can be distributed to other parts of the plant. Under heavy fog, the sap flow in *S. sempervirens* can be reversed, albeit slightly at 5–7% of the maximum transpiration rate. Stone (1956, 1957b) demonstrated reverse flow in experiments with potted ponderosa

seedlings. The redistribution of foliar water toward the root system was also demonstrated with *Drimys brasiliensis* in the cloud forest (Eller et al. 2013).

The local water absorption flux measured in *P. torreyana* needles is quite high. By submerging *S. sempervirens* leaves, Burgess and Dawson (2004) measured an average flux of approximately $0.89 \text{ mmol m}^{-2} \text{ s}^{-1}$, which is equivalent to $1.6 \times 10^{-3} \text{ mg cm}^{-2} \text{ s}^{-1}$, about 6 times lower than $0.01 \text{ mg cm}^{-2} \text{ s}^{-1}$, which is the order of magnitude of the *P. torreyana* needle uptake flux. The foliar uptake of *S. sempervirens* is relatively small, and the main role of fog is to suppress transpiration and generate fog drip to provide for its shallow root system. While the present measurement of *P. torreyana* needle is high, the uptake is expected to represent the upper bound of realistic *in situ* conditions, and the rate should slow down as the needles approach saturation, and the uptake begins to be governed by redistribution.

Without epicuticular wax, there arises the question of the trade-off between higher cuticular transpiration versus adaptation to moist atmospheric conditions (Leyton and Armitage 1968; Kerstiens 1996; Williams et al. 2008). Otherwise, *P. torreyana* would be growing among other pines in inland habitats. Leyton and Armitage (1968) considered that *P. radiata* might not be very tolerant of drought. They suggested that the capability of this pine to uptake moisture from its foliage could help maintain water balance and would have considerable survival value.

The comparative tests in this study demonstrated that *P. torreyana* is highly competitive with maritime chaparral broadleaf plants. The detached needles do not lose water as quickly, and it has the highest foliar uptake rate. Unexpectedly, the leaves of the chosen chaparral shrubs have wettable surfaces and are capable of foliar water uptake. Other species in the coastal redwood forest also have this capability (Limm et al. 2009). One may hypothesize that *P. torreyana* has evolved to acquire some features of maritime chaparral shrubs and exceeded the capabilities of these shrubs.

In this respect, *P. torreyana* is better equipped to capture atmospheric moisture than *P. radiata*. Leyton and coworkers suggested that *P. radiata* is adapted to the California coastal “fog belt” region. However, with three-needle fascicles that vary between 90–150 mm in length, *P. radiata* has a much smaller foliage surface than *P. torreyana*. Furthermore, the abaxial surface of *P. radiata* on average has a higher contact angle, implying a lower water uptake rate. In contrast, the entire length of the long *P. torreyana* needles and its small sheath base are all capable of foliar water uptake.

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Tables

Table 1 Summary of linear regression of contact angle and local water uptake flux Contact angle. Slope is degree per cm change

	Ordinary least squares			Weighted least squares		
Age	Slope	r^2	p	Slope	r^2	p
Adaxial						
Year-1	0.3 ± 0.2	0.21	0.16	0.25 ± 0.07	0.58	6.6×10^{-3}
Year-2	0.17 ± 0.11	0.23	0.14	0.14 ± 0.06	0.36	0.051
Abaxial						
Year-1	0.17 ± 0.06	0.44	0.025	0.17 ± 0.06	0.44	0.025
Year-2	0.35 ± 0.07	0.72	0.001	0.35 ± 0.07	0.72	9.5×10^{-4}

Local absorption flux. Slope is $\text{mg cm}^{-2} \text{s}^{-1}$ per cm change

	Ordinary least squares			Weighted least squares		
Age	Slope	r^2	p	Slope	r^2	p
Adaxial						
Year-1	$-3.5 \pm 1.4 \times 10^{-4}$	0.41	0.034	$-3.9 \pm 0.6 \times 10^{-4}$	0.84	6.4×10^{-5}
Year-2	$-0.2 \pm 1.7 \times 10^{-4}$	0.0015	0.91	$-0.7 \pm 0.7 \times 10^{-4}$	0.11	0.33
Abaxial						
Year-1	$-1.9 \pm 1.3 \times 10^{-4}$	0.2	0.16	$-2.2 \pm 0.4 \times 10^{-4}$	0.77	3.6×10^{-4}
Year-2	$-2.4 \pm 1.3 \times 10^{-4}$	0.26	0.11	$-2.1 \pm 0.4 \times 10^{-4}$	0.75	6.1×10^{-4}

Table 2 Comparison of average contact angle and droplet uptake flux with sample standard errors

Plant	Contact angle (°)	Uptake flux (mg cm ⁻² s ⁻¹)	Uptake ratio	f_m
<i>E. crassifolium</i>	112.9 ± 9.0	0.15 ± 0.18 x 10 ⁻²	0.05	0.75
<i>M. laurina</i>	70.7 ± 10.6	1.09 ± 0.10 x 10 ⁻²	0.38	0.88
<i>H. arbutifolia</i>	46.9 ± 5.9	1.39 ± 0.16 x 10 ⁻²	0.48	0.88
<i>R. integrifolia</i>	49.5 ± 6.5	1.72 ± 0.20 x 10 ⁻²	0.60	0.91
<i>P. torreyana</i>				
Matured needles*	53.4 ± 5.6	2.88 ± 0.60 x 10 ⁻²	1	0.85
Matured, under sheath	66.1 ± 5.0	1.32 ± 0.14 x 10 ⁻²	0.46	
Young shoots	70.6 ± 4.2	1.47 ± 0.01 x 10 ⁻²	0.51	0.82
Young, under sheath	74.5 ± 2.9	1.22 ± 0.01 x 10 ⁻²	0.42	

* The values for *P. torreyana* were taken from the year-1 abaxial surface

Figures

Figure 1

Records of (a) needle fractional moisture and (b) rainfall from October 2019 to June 2021. The dashed line represents the average fractional moisture from October 2019 to September 2020

Figure 2

Scanning electron micrographs of one-year old needles, showing how there is little epicuticular wax coverage: (a) abaxial surface, 130x; (b) adaxial surface, 120x. Scale bars represent 400 μm

Figure 3

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Relative weight gain of needles from various fractional lengths immersed in water for different durations

Figure 4

Contact angle and local water absorption flux along one-year old and two-year old needles; (a) and (b) adaxial surfaces; (c) and (d) abaxial surfaces. The results of ordinary least squares are shown as solid lines and 95% confidence bands

Figure 5

Correlation of local water absorption flux with contact angle, with ordinary least squares and 95% confidence band

Figure 6

Comparison of moisture evaporative loss with broadleaf plants