FOLIAR ABSORPTION OF INTERCEPTED RAINFALL IMPROVES WOODY PLANT WATER STATUS MOST DURING DROUGHT

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Abstract. A large proportion of rainfall in dryland ecosystems is intercepted by plant foliage and is generally assumed to evaporate to the atmosphere or drip onto the soil surface without being absorbed. We demonstrate foliar absorption of intercepted rainfall in a widely distributed, continental dryland, woody-plant genus: *Juniperus*. We observed substantial improvement in plant water status, exceeding 1.0 MPa water potential for drought-stressed plants, following precipitation on an experimental plot that excluded soil water infiltration. Experiments that wetted shoots with unlabeled and with isotopically labeled water confirmed that water potential responded substantially to foliar wetting, that these responses were not attributable to re-equilibration with other portions of the xylem, and that magnitude of response increased with water stress. Foliar absorption is not included in most ecological, hydrological, and atmospheric models; has implications for interpreting plant isotopic signatures; and not only supplements water acquisition associated with increases in soil moisture that follow large or repeated precipitation events, but also enables plants to bypass soil water uptake and benefit from the majority of precipitation events, which wet foliage but do not increase soil moisture substantially. Foliar absorption of intercepted water could be more important than previously appreciated, especially during drought when water stress is greatest.

Key words: climate change impacts; Juniperus monosperma; *plant physiological ecology; plant water potential; vegetation dynamics.*

INTRODUCTION

Acquisition of water is critical to the growth and survival of plants, with conditions of water status being of particular importance in dryland environments (Kramer 1983, Ehleringer 1993, Gutschick and Bassiri-Rad 2003). The amount of water available to plants is not determined by precipitation alone but rather is dependent on several components of a water budget, including interception, runoff and soil water storage, and soil evaporation (Loik et al. 2004). At a given location on the land surface, the water budget generally is dominated by evapotranspiration, which accounts for >95% of the precipitation input via water flux to the atmosphere in most continental dryland ecosystems (Wilcox et al. 2003*b*). Included under the umbrella of "evapotranspiration" are plant transpiration, evaporation from the soil, and evaporation of water intercepted by the plant canopy (Wilcox et al. 2003*b*). A large proportion of annual precipitation is intercepted by

plant foliage and is generally assumed to evaporate back into the atmosphere or drip to the soil without being directly absorbed, an assumption held in ecology (Waring and Running 1998), hydrology (Brooks et al. 1991), and atmospheric science (Bonan 2002). However, absorption of water through foliage has been demonstrated previously in studies that focused primarily on dew or fog condensate (Stone 1963, Louw and Seely 1982, Kramer 1983, Nobel 1983, Yates and Hutley 1995, Hutley et al. 1997, Munné-Bosch et al. 1999, Burgess and Dawson 2004) or melted snow (Katz et al. 1989, Sparks et al. 2001) rather than rainfall (see also Oliveira et al. 2005). Foliar absorption of intercepted rainfall could be particularly important in dryland ecosystems because plants commonly undergo periods of water stress, which under extreme conditions can be severe enough to trigger widespread tree mortality (Allen and Breshears 1998, Breshears et al. 2005). Essentially all precipitation events are at least partially intercepted by foliage, but only a few larger precipitation events substantially increase soil water content (Loik et al. 2004, Owens et al. 2006). Precipitation in many arid and semiarid environments most frequently occurs as medium to small events (Loik et al. 2004), with few if any

large events occurring during drier periods (Sala et al. 1992). Therefore, if substantial foliar absorption occurred, it could be more important than previously appreciated because it might not only supplement water uptake following increases in soil moisture associated with large or repeated precipitation events, but could also enable plants to bypass soil water uptake and benefit from the majority of precipitation events, which wet foliage but do not increase soil moisture substantially.

Our overall goal was to evaluate plant water dynamics of *Juniperus monosperma* [Englem.] Sarg., a widely distributed, dryland, woody species in continental North America, in a suite of experiments that included manipulation of water inputs at the plot scale for whole plants and at the shoot scale for twigs that were either still attached to the tree or removed prior to treatment. We discuss our findings, which demonstrate that foliar absorption of intercepted rainfall does occur in *Juniperus*, in the context of how foliar absorption allows water-stressed dryland plants to bypass and/or supplement soil water uptake, especially during drought, when water stress is greatest. We also discuss how our results contrast with a widely-held assumption in ecological, hydrological, and atmospheric sciences; may alter interpretation of plant isotopic signatures of climate; and, perhaps more importantly, highlight a mechanism that can improve plant water status during the majority of precipitation events, which, as noted previously, generally do wet foliage but do not substantially increase soil moisture.

METHODS

Our experiments were conducted at the Mesita del Buey site on Los Alamos National Laboratory, near Los Alamos, New Mexico, USA (35°51′ N, 106°16′ W; Breshears 2008). The site is at an elevation of 2140 m; has annual precipitation of ~400 mm, mainly in the form of winter snowfall and late-summer precipitation; mean ambient air temperature of ~9°C, ranging from −2°C in January to 21°C in June; and soil depths varying between 33 to 125 cm. Tree canopy cover was ~50%, divided roughly equally between *Juniperus monosperma* and *Pinus edulis* at the time of the study (Breshears et al. 1997, Wilcox et al. 2003a).

Our design for water exclusion, consisting of a sealed but ventilated plastic water barrier on the ground surface of a roughly 50 × 50 m plot paired with a control plot, allowed us to evaluate the response of plant water potential of *J. monosperma* to rainfall interception when soil infiltration was excluded (Fair and Breshears 2005). During summer 2002, we tracked precipitation, soil water content at 0–30 cm (using time-domain reflectometry), and predawn plant water potential (methods were similar to those described in Breshears et al. 1997). Water was excluded from the plot by a composite plastic sheet of white vinyl-coated polyester truck tarpaulin (mass ≥ 470g/m²; Shelton, Reynolds,

Incorporated, Milwaukee, Wisconsin, USA) with smaller tarp sections fitted and glued together in the field with vinyl glue. Special sections were fabricated for installation around the base of each woody plant. These pieces were fit snugly around the stems of the woody plants and were bound tightly to the stem with a section of elastic cord. The water exclusion plot had a ventilation system beneath the plastic sheet that consisted of ~10 cm diameter perforated plastic drain pipes. The pipes were placed on the ground surface every 5 m along the plot and parallel to the slope, running from the top of the plot downslope to the bottom (to encourage air flow); pipe sections (3.05 m length) were fit together and placed on the ground surface such that the ventilation holes were not covered by ground or plastic, with the ventilation tubes remaining exposed at the upslope and downslope ends of the plot. Probes for measuring soil water content by time-domain reflectometry were installed throughout the plot (n = 50). Any probe that indicated an increase of >3.5% volumetric water content during any interval of the study was assumed to be detecting a nearby leak (n = 11 that were generally colocated), and that probe and all trees within 10 m of that probe were excluded from analysis. Therefore, all trees in the analysis had an exclusion buffer of at least 10 m all directions, which we believe is at least 2 m greater than the estimated rooting neighborhood, based on the limited available rooting data (Breshears 1993). Soil water content from the remaining probes never exceeded 12% volumetric water content, corresponding to a soil water potential of <−10 MPa (Breshears et al. 1997). Predawn plant water potential was measured to the nearest 0.05 MPa simultaneously for two shoots (using a PMS Model 1000 pressure chamber; Corvallis, Oregon, USA). Sample sizes for soil water content were 159 for the control plot and 41 for the water-exclusion plot, and for plant water potential were six trees for the control plot and five for the treated plot. Plot installation was completed and monthly soil and plant water status measurements were initiated mid May 2002. Plot results were analysed with a two-way ANOVA with repeated measures using a Bonferroni test for contrasts.

We conducted four shoot-scale experiments designed to test for water uptake via foliar absorption. Plant water potential was measured during daylight hours for each of four shoot experiments (shoot size ~8 cm), as described for the plot experiments. For the first experiment, shoots were designated as control or treated (n = 16 each) and then measurements of initial plant water potential were obtained for both categories. After obtaining initial plant water potentials from shoots on each subject tree, water in a beaker was poured over eight randomly selected shoots that were still on the tree (~300 mL poured over foliage in less than 60 s, repeated five times), allowing foliar interception by these treated shoots only (excess water was captured in a pan held beneath the treated shoot). The treated shoots were left intact for 5 minutes, the treated and control shoots were

then cut and lightly shaken to remove excess water, and water potential of the shoots was measured (blotting of foliage with paper tissue indicated there was little to no residual water on the foliage at the time of measurement). The second experiment was conducted to determine if any response observed from the first experiment was attributable to re-equilibration of leaf xylem with the stem xylem, due to halting of transpiration (Holbrook and Zwieniecki 1999, Snyder et al. 2003), rather than from foliar absorption. We replicated the experiment with control and treated shoots ($n = 10$ each) that were pre-cut to prevent re-equilibration and placed in the dark to minimize transpiration. Shoots were cut in the field, placed in the dark for at least 30 minutes, treated shoots were wetted as above, and both control and treated shoots were then placed in a dark container for an additional 30 minutes prior to measuring plant water potential. In the third experiment, an independent test of foliar water uptake was conducted by replicating the second experiment described above using spray water enriched in the oxygen isotope ratio ($\delta^{18}O$) and a two end member mixing model (Phillips and Gregg 2001). The sample size was nine paired control and treatment shoots collected in both the morning (08:00 hours MST) and afternoon (14:00 hours MST). Samples were handled as in the second experiment but were sprayed with the labeled water (prepared by diluting source water with ~500‰ $\delta^{18}O$ down to a target of ~50‰ $\delta^{18}O$; sprayed to entirely wet the twig using ~3 mL of labeled water applied in approximately three sprays applied within a ~5-s interval) and were immediately sealed in vials after water potential measurement. In addition, we tested if water potential measurements biased our results via pressing surface water into foliage. We did so by spraying an additional 18 shoots with labeled water, followed by water potential measurements on nine of these samples. Isotopic analyses were conducted at the Center for Stable Isotope Biogeochemistry at University of California–Berkeley on a Finnigan-Mat Delta Plus XL mass spectrometer (Finnegan MAT GmbH, Bremen, Germany). For the fourth experiment, measurements were made for shoots that were still attached to each of a larger set of trees ($n = 37$ trees): for each tree, measurements were obtained from shoots that were treated as in the first experiment (e.g., ~300 mL of water added five times, followed by a 5-minute period prior to sampling) and from control shoots. Responses were analyzed for the first three shoot experiments using paired t tests (P values reported if <0.05) and for the fourth shoot experiment using type II regression.

RESULTS

In the plot-scale experiment, we excluded precipitation input to soil via a ground surface cover, as confirmed by soil moisture measurements (Fig. 1A). Initial measurements on both the water-exclusion and control plots obtained following the onset of severe
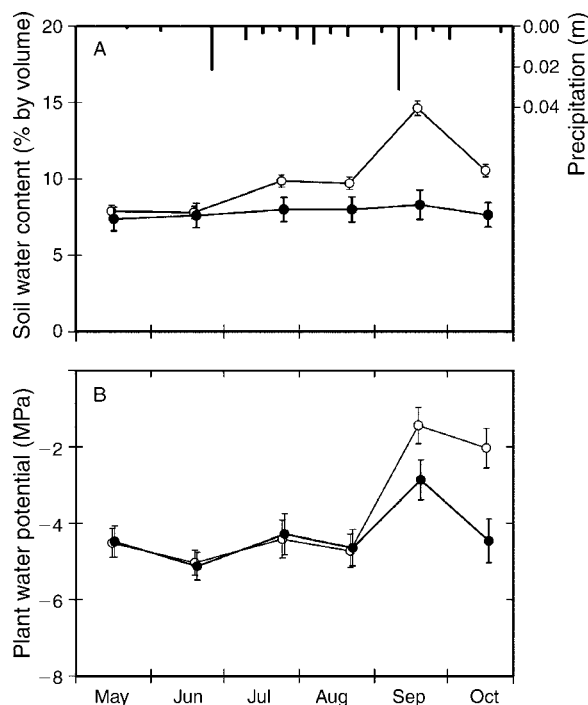

FIG. 1. Temporal dynamics for the control plot (open circles) and the water-exclusion plot (solid circles), showing least-squares means and 95% confidence intervals. (A) Precipitation (m) and soil water content (% by volume, 0–30 cm depth), measured by time-domain reflectometry, for both plots. (B) Predawn plant water potential for *Juniperus monosperma* trees on both plots. The increase in plant water potential on the water-exclusion plot in September, measured shortly after a large rainfall event, in concert with the lack of increase in soil water content on that plot, suggests that plant water stress was reduced by foliar absorption of water.

drought indicated low soil water content (Fig. 1A) and high plant water stress (Fig. 1B) in both the control and water-exclusion plots. Soil water content in the control plot increased after the arrival of monsoon precipitation in September, but soil water content in the water-exclusion plot remained constant due to its covered surface (Fig. 1A; $P < 0.001$). Notably, water stress of plants on the water-exclusion plot, as measured by water potential, also responded to September monsoon precipitation, despite the low and unchanged soil water content of that plot (Fig. 1B; $P < 0.001$).

Measurements of water potential for shoots that were attached to the tree at the time of wetting showed a significant response to foliar wetting relative to control shoots (Fig. 2A; $P < 0.001$). Re-wetted shoots showed an increase in water potential, corresponding to reduced water stress, that was much greater than changes in control shoots (Fig. 2B, $P = 0.001$). In the third experiment, replication of the water potential experiments using isotopically labeled water confirmed foliar uptake. Spray water $\delta^{18}O$ averaged 42.90‰ ± 0.05‰ (mean ± SE). Leaf water $\delta^{18}O$ averaged 15.2‰ (±0.43) and 16.9‰ (±0.29) for the control and
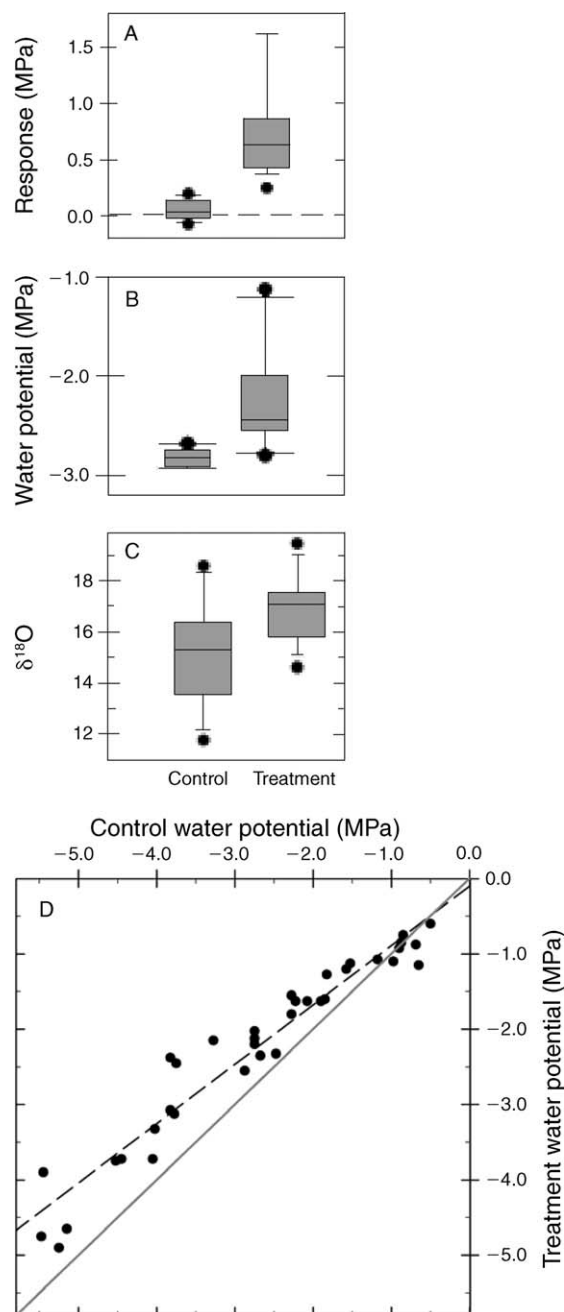
FIG. 2. Shoot-scale experiments evaluating foliar absorption using control shoots and treated shoots that received foliar wetting. (A) Change in plant water potential for in situ shoots relative to pretreatment samples (median in box of 25th and 75th percentiles, lines = 10th and 90th percentiles, points = extremes). (B) Water potential for control and treated shoots that were cut and in the dark prior to and following foliar wetting (box components as in panel A). (C) Stable isotope leaf water $\delta^{18}O$ for controlled shoots sprayed and treated shoots that were sprayed with labeled water ($\delta^{18}O$ of 42.90 ± 0.05 [mean ± SE]; box components as in panel A). (D) Control vs. treated shoots (dashed line, slope = 0.79; slope < 1.0: $P <$ 0.001, $R^2 = 0.93$). (The solid line is 1:1.) A slope significantly less than 1.0 indicates that the magnitude of response increases with plant water stress.

treatment samples, respectively ($P < 0.001$). This 1.7‰ change is equivalent to 6% change in leaf water $\delta^{18}O$ using the two-end-member mixing model Isoerror version 4.0 (Phillips and Gregg 2001). No difference was seen between morning and afternoon samples, or between samples sprayed and then measured for water potential verses samples sprayed and then immediately placed in vials. Mean water potential for the control shoots in the third experiment was −2.1 MPa (SE = 0.13). In the fourth shoot-scale experiment, measurements of changes in plant water potential for shoots attached to the tree at the time of wetting were obtained over a wide range of initial plant water potentials. The results show that the magnitude of the response in plant water potential to foliar wetting increased with water stress: water potential of treated shoots was correlated with water potential of control shoots with a slope that was significantly less than 1.0 (slope = 0.79, $P < 0.001$, $R^2 = 0.93$; Fig. 2D), indicating that the response was greater in plants that were more water stressed.

DISCUSSION

Our results collectively indicate that *Juniperus monosperma* exhibits foliar absorption as a function of plant water potential and that, under conditions of higher water stress, the effect of foliar absorption can be quite substantial, producing a change in water potential exceeding 1.0 MPa. With respect to our initial observations at the plot scale, it is unlikely that plants on the water-exclusion plot acquired water from beyond the plot boundary, which exceeds by at least 2 m the maximum horizontal rooting neighborhood, as estimated in the most relevant study—a previous tracer study located adjacent to the study site (Breshears 1993). Additionally, horizontal subsurface flow of water is insignificant in this ecosystem (Wilcox et al. 2003a). Hence, the reduction in plant water stress that occurred following precipitation and in absence of soil infiltration is most likely the result of foliar absorption of intercepted rain. A substantial precipitation event also occurred in June, but we did not measure plant water potential again for a few weeks and, not surprisingly, were not able to detect a reduction in plant water stress at that time (Fig. 1). The four shoot-scale experiments in the field and laboratory confirmed that the increases in plant water potential of *J. monosperma* on the water-exclusion plot could be explained by foliar absorption alone. The first shoot experiment (Fig. 2A) indicates improvement in plant water status that could result either from foliar absorption or from re-equilibration of leaf xylem with the stem xylem due to halting of transpiration (Holbrook and Zwienicki 1999). We excluded the latter mechanism in our second shoot-scale experiment by placing shoots in the dark (because *Juniperus* species exhibit minimal nighttime transpiration; Snyder et al. 2003) prior to addition of water. In this experiment, the shoot water potential response to rewetting (Fig. 2B) must be due to foliar absorption. The

isotope experiments confirm these findings, documenting foliar absorption even when the plants are not highly water stressed (average water potential of −2.1 MPa; Fig. 2C). Our fourth shoot-scale experiment demonstrates that the effect of foliar absorption on water potential is greater at lower water potential when the plant is experiencing greater water stress (Fig. 2D). Collectively, our shoot-scale experiments for *J. monosperma* build on our plot-scale experiment to indicate that foliar absorption of intercepted rainfall provides substantial improvement in plant water status, with the response to foliar uptake increasing with increasing amounts of plant water stress. Although additional research is needed to determine the persistence of the effect, which will of course depend on environmental conditions, the field observations (Fig. 1) suggest that the change in water potential can persist over more than a day.

There are several important implications of foliar absorption for dryland plants. The dependence of the magnitude of response on initial plant water potential may have contributed to discounting the importance of foliar absorption to date: our study included greater levels of plant water stress than most other such studies (e.g., <−2.0 Mpa; Figs. 1 and 2). Conditions of high water stress are more likely to occur in drylands and are likely to be most critical to plant survival during periods of extreme drought (Allen and Breshears 1998, Gutschick and BassiriRad 2003), the frequency and intensity of which are expected to increase as climate change progresses (Intergovernmental Panel on Climate Change 2002). Drought-induced mortality might result from embolism of the water transport elements due to water potential exceeding a cavitation threshold (Tyree and Sperry 1988). The range of plant water potentials observed for the plants in this plot study (Fig. 1B) were nearly always in excess of the *J. monosperma* threshold for initiation of embolism at ∼−3.5 MPa (Pockman et al. 1995). Hence, the foliar absorption documented here may be critical to plant survival during extended periods of drought. *J. monosperma* has been viewed as being more drought tolerant than its codominant woody species *P. edulis*, at first due to physiology, then additionally to rooting patterns determining plant water uptake (Breshears et al. 1997). Here we show another mechanism that also could be important that relates to both physiological response and water acquisition. In a recent drought, most *P. edulis* individuals at the Mesita del Buey site died, whereas most *J. monosperma* trees survived (Breshears et al. 2005). During the drought prior to *P. edulis* mortality, precipitation was limited to relatively few precipitation events that individually and collectively were insufficient to substantially increase soil moisture through a shallow depth interval overlapping with the active rooting zone (Breshears et al. 1997, 2005). These few precipitation events would have been sufficient to wet tree foliage and may have provided potentially important mitigation in plant water status of *J. monosperma* during a critical period of high water stress. The survival of *J. monosperma* individuals through conditions sufficient to result in mortality of most *P. edulis* individuals likely relates to the many ways the two species differ in physiology and associated water uptake patterns (Lajtha and Barnes 1991, Breshears et al. 1997). Additional research is needed to determine if *P. edulis* also exhibits foliar absorption, and if so, how such foliar absorption relates to the more limited range of plant water potentials observed in *P. edulis* (trees do not exhibit leaf water potentials lower than ∼−2.2 MPa [Breshears et al. 1997, Stimson et al. 2005]) and the greater change in plant water potential per unit change in foliar water content exhibited by *P. edulis* relative to *J. monosperma* (Stimson et al. 2005). Our results for *J. monosperma* suggest that foliar absorption could play an important role in mitigating water stress and in aiding survival during drought. The hypotheses that *P. edulis*, as well as other woody and herbaceous species, also exhibit foliar absorption of intercepted rainfall and that such absorption is a function of plant water potential require additional testing.

It is also important to note that continental dryland ecosystems are characterized by a relatively low frequency of large precipitation events (Sala et al. 1992, Loik et al. 2004), with many precipitation events being intercepted by the canopy and not contributing to a substantial increase in soil moisture (Waring and Running 1998, Loik et al. 2004, Reynolds et al. 2004, Owens et al. 2006). Indeed, >35% of annual precipitation can be intercepted by juniper-dominated drylands, a large fraction of which results from medium to small precipitation events. Juniper interception storage reaches a maximum after only ∼5 mm precipitation (based on data in Owens et al. 2006; see also Collings 1966), and therefore the percentage of precipitation input intercepted is at or near maximum for a large proportion of precipitation events, which are often less than 5 mm (Wilcox et al. 2003b, Loik et al. 2004). Foliar uptake could therefore occur for a large fraction of precipitation events and is likely more important than previously appreciated. We speculate foliar absorption of intercepted rainfall may occur in other widespread species and could contribute to the recent finding that the amount of productivity among different ecosystems approaches a common rainfall-use efficiency during dry years (Huxman et al. 2004), which are characterized by a lack of large precipitation events (Sala et al. 1982). Overall, we speculate that foliar absorption is important both in mitigating plant water stress during drought and in providing frequent, small improvement in plant water stress in association with many precipitation events, whether or not they effectively contribute to a substantial increase in soil moisture.

The bypassing or supplementation of soil water uptake with foliar absorption of intercepted rainfall contrasts with an implicit assumption about plant water use in continental dryland ecosystems—that uptake of

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intercepted rainfall by foliar absorption is unimportant. This assumption is reflected in conceptual and predictive models in ecology, hydrology, and atmospheric science (Brooks et al. 1991, Waring and Running 1998, Bonan 2002). Foliar absorption could be important in these conceptual and predictive models, depending on the objective of interest. Differences in how and where various species or plant functional types obtain water are recognized as a fundamental determinant in conceptual and predictive models of vegetation dynamics (Walter 1971, Noy-Meir 1973, Breshears and Barnes 1999, Schwinning and Ehleringer 2001, House et al. 2003, Ogle and Reynolds 2004, Reynolds et al. 2004). In particular, the relationships between roots and soil water as a function of depth are central to all of these models, and hence the ability to at least partially bypass soil water uptake contrasts with one of their underlying assumptions. Further, major biogeochemical, hydrological, and atmospheric models assume that intercepted water is not absorbed via foliage, yet the changes in plant water potential that we have demonstrated in response to foliar absorption could be important because plant water potential is a fundamental constraint on water flux in these models (Brooks et al. 1991, Waring and Running 1998, Bonan 2002). Hence, if more widespread among dominant dryland species, foliar water absorption will need to be incorporated into these models when assessing atmosphere–land-surface interactions. Additionally, interpretation of previous climate or of sources of plant water uptake from plant isotopic signatures could be affected because it is based on the assumption that plants are using soil water, which might be isotopically different from rain water absorbed directly through foliage (Burke and Stuiver 1981, Roden et al. 2000).

In summary, our findings highlight three issues concerning foliar absorption. First, although foliar absorption is not currently included in most ecological, hydrological, and atmospheric models, it might need to be considered. Second, the occurrence of foliar absorption has implications for interpreting plant isotopic signatures. Third, foliar absorption can not only supplement water acquisition following increases in soil moisture associated with large or repeated precipitation events, but also enables plants to bypass soil water uptake and benefit from the majority of precipitation events, which wet foliage but do not increase soil moisture substantially. Therefore, foliar absorption could be more important than previously appreciated, especially during drought when water stress is greatest.

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