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Leaf trichomes can alleviate water deficit stress and maintain diurnal photosynthesis by increasing leaf wetness and water absorption in *Metrosideros polymorpha*

Gaku Amada^{1,2,3} | Yoshiyuki Miyazawa⁴ | Yuji Kominami³ |
Kanehiro Kitayama^{1,5} | Yusuke Onoda¹

¹Graduate School of Agriculture, Kyoto University, Kyoto, Japan

²Institute of Arctic Climate and Environment Research, Research Institute for Global Change, Japan Agency for Marine-Earth Science and Technology, Yokohama, Japan

³Forestry and Forest Products Research Institute, Forest Research and Management Organization, Tsukuba, Japan

⁴Faculty of Agriculture, University of Ryuky, Nishihara, Japan

⁵Faculty of Tropical Forestry, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia

Correspondence

Gaku Amada, Graduate School of Agriculture, Kyoto University, Kyoto, 606-8502, Japan.
Email: amada.gaku@gmail.com

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Abstract

Leaves frequently become wet throughout their lifetime, and leaf wetting affects the physiological activities of leaves. Leaf trichomes, which are often observed in plants inhabiting dry areas, may prolong the duration of leaf wetness and increase foliar water uptake (FWU), thereby contributing to greater carbon gain through improved leaf water status. However, the effects of leaf trichomes on leaf wetness and physiological activities have not been examined across a wide range of environmental conditions. We focused on *Metrosideros polymorpha*, a dominant tree species that exhibits significant variation in the amount of abaxial leaf trichomes across diverse environmental gradients in the Hawaiian Islands. Pubescent individuals are abundant in dry areas, whereas glabrous individuals are common in moderately wet areas. In the field, the presence of a greater amount of hydrophilic leaf trichomes significantly prolonged the duration of leaf wetness, by up to 100 min/day. When nighttime leaf wetting was experimentally prevented, the duration of high shoot-level photosynthetic rates decreased, suggesting that nighttime leaf wetness can increase the duration of high stomatal openness during the daytime. In laboratory experiments, the FWU ability was greater in pubescent individuals inhabiting dry, cold areas than in glabrous individuals inhabiting wet, warm areas. These findings suggest that the leaf trichomes of *M. polymorpha* improve leaf water status and increase carbon gain by increasing the duration of leaf wetness and FWU, which may contribute to the fitness of this species in dry environments.

KEYWORDS

environmental gradient, foliar water uptake, Hawaii, leaf hair, midday depression

1 | INTRODUCTION

Plant leaves can become wet due to precipitation, fog, and nighttime dew. Leaf-wetting events are considered to have both benefits and costs for plant functions depending on the plant species and their habitat environments (Dawson & Goldsmith, 2018). Leaf wetness improves leaf water status (Berry et al., 2019; Eller et al., 2016; Goldsmith et al., 2013) and enhances photosynthesis and growth (Eller et al., 2013; Zhuang & Ratcliffe, 2012), whereas other studies suggest that leaf wetness can have adverse effects on photosynthesis (Hanba et al., 2004; Ishibashi & Terashima, 1995) and promote pathogen growth and spread on the leaf surface (e.g., Huber & Gillespie, 1992).

The uptake of water from the leaf surface into leaves, commonly referred to as foliar water uptake (FWU), is a key process in improving leaf water status. While FWU ability has been commonly observed across a wide range of plant taxa and habitats (Berry et al., 2019; Dawson & Goldsmith, 2018; Rundel, 1982), FWU is more critically important for plants under water deficit stress; in arid areas (e.g., Agam & Berliner, 2006), early successional areas (e.g., Vitousek et al., 1992), anaerobic bog areas (e.g., Armstrong & Boatman, 1967), and saline areas (e.g., Hayes et al., 2020). FWU is also important for tall trees, which are prone to desiccation due to hydraulic resistance (e.g., Simonin et al., 2009). Moreover, FWU is linked with the duration of leaf wetness; that is, longer leaf-wetness duration enables leaves to take up more water from the leaf surface (Boanares, Ferreira, et al., 2018; Liang et al., 2009; Ohrui et al., 2007; Stone, 1963).

Leaf trichomes, which are found on the leaf surfaces of various plant species, play important roles in both leaf wetness and FWU (Bickford, 2016; Johnson, 1975; Li et al., 2023; Liu et al., 2017). The effects of leaf trichomes on leaf wetness differ across species and depend on the morphology and chemical components of trichomes (Brewer & Smith, 1997; Fernández et al., 2014). Some leaf trichomes are hydrophilic and can increase water retention on the leaf surface, whereas others are hydrophobic and can increase water repellency (Brewer & Smith, 1997; Fernández et al., 2014). Dense leaf trichomes can promote dew condensation in a trichome layer by decreasing saturation vapor pressure via surface effects (i.e., capillary condensation) and by promoting the deposition of hygroscopic aerosols that may become deliquescent (Konrad et al., 2015). Although FWU is linked with the duration of leaf wetness (Boanares, Ferreira, et al., 2018; Liang et al., 2009; Ohrui et al., 2007; Stone, 1963), the effects of leaf trichomes on the duration of leaf wetness have not been examined in plants with large variations in the amount of leaf trichomes that can be seen across large environmental gradients. Moreover, leaf trichomes can also

serve as a major FWU pathway along with the stomata, cuticle, and hydathode (Berry et al., 2019; Schreel & Steppe, 2020). FWU through leaf trichomes has been determined or discussed in a wide range of plant taxa (Araújo et al., 2024; Boanares, Ferreira, et al., 2018; Boanares, Isaias, et al., 2018; Eller et al., 2016; Fernández et al., 2014; Grammatikopoulos & Manetas, 1994; Nguyen et al., 2017; Ohrui et al., 2007; Pina et al., 2016; Schreel et al., 2020; Vitarelli et al., 2016), while some leaf trichomes in several plant species cannot function as FWU pathways (Burrows et al., 2013; Grammatikopoulos & Manetas, 1994).

FWU can increase the carbon gain by increasing stomatal conductance (Berry et al., 2014; Eller et al., 2013; Simonin et al., 2009), likely by increasing the turgor of stomatal guard cells (Schreel & Steppe, 2020) and by reducing root water deficit stress by supplying water to the roots (a sap flow reversal; Eller et al., 2013). In addition to these effects of FWU on stomatal openness, wet trichomes can maintain high air humidity in the trichome layer, which theoretically increases stomatal conductance (Konrad et al., 2015). Since the photosynthetic rate is strongly regulated by stomatal conductance as well as other environmental factors throughout the day (Jones, 2014), FWU can increase daily carbon gain by prolonging the duration of increased stomatal conductance especially under water deficit stress conditions (Ben-Asher et al., 2010; Berry et al., 2014; Eller et al., 2013; Zhuang & Ratcliffe, 2012).

To investigate the ecological significance of leaf trichomes in relation to leaf wetness, we studied *Metrosideros polymorpha*, an endemic dominant tree species across wide environmental gradients in the Hawaiian Islands: mean annual temperature ranges from 5 to 25°C, mean annual precipitation from a few hundred to over 10 000 mm yr⁻¹, and soil age from a few decades to over 4 million years (Cordell et al., 1998; Cornwell et al., 2007; Kitayama & Mueller-Dombois, 1995). Leaf trichomes mostly occur on the lower leaf surface (i.e., abaxial side) in amounts ranging from 0 (glabrous) to ~150 g m⁻² in *M. polymorpha* (up to 40% of leaf mass; Joel et al., 1994; Tsujii et al., 2016). Glabrous-leaved trees are often dominant in moderately wet areas, whereas pubescent-leaved trees are more dominant in low precipitation, early successional, or anaerobic bog areas (Stacy et al., 2014; Tsujii et al., 2016; Vitousek et al., 1992), where water uptake from roots is difficult. The greatest amount of leaf trichomes is found in dry alpine areas on Mauna Loa (Amada et al., 2017, 2023; Hoof et al., 2008; Tsujii et al., 2016), where the ratio of fog to rain is high (up to 75% of the summed amount of fog and rainfall; Juvik & Ekern, 1978). The leaf trichomes of *M. polymorpha* are dense and woolly (Amada et al., 2017; Hoof et al., 2008), which may effectively capture fogs and retain the water in its trichome layer.

In the present study, to evaluate the potential advantage of leaf wetness and FWU in pubescent leaves, we compared leaf wetness between intact and trichome-removed leaves at seven sites on the island of Hawaii where our previous study found large variations in the amount of leaf trichomes (Amada et al., 2020). We also evaluated the effects of leaf wetness on diurnal photosynthetic rates by preventing nighttime dew under field conditions. Laboratory experiments were conducted to compare FWU availability between pubescent and glabrous shoots. Specifically, we addressed the following three questions: (i) Do leaf trichomes prolong the duration of leaf wetness? (ii) Does leaf wetness promote FWU in pubescent leaves more than in glabrous leaves? (iii) Does leaf wetness prolong the duration of photosynthesis under field conditions?

2 | METHODS

2.1 | Study sites

To evaluate the effects of leaf trichomes on the duration of leaf wetness under various environmental conditions, we used seven sites that differed in elevation and environmental conditions on the slope of Mauna Loa on the island of Hawaii (Table 1; Figure S1): six sites at 100, 700, 1280, 1800, 2000, and 2400 m a.s.l. on the east slope (E100, E700, E1280, E1800, E2000, and E2400, respectively) and one dry warm site at 700 m a.s.l. on the west slope (W700). The alpine areas on Mauna Loa are drier than the lower-elevation areas because of the cold dry descending air of the Hadley cell circulation (the mean base height of the trade-wind inversion zone is 2255 ± 497 m; Cao et al., 2007; Giambelluca et al., 2013). The ratio of fog to total water (fog + rainfall) is known to be high at 2500 m a.s.l. on the east

slope of Mauna Loa (near the E2400 site) and reaches 75% in the dry season, whereas the ratio is <10% in both wet and dry warm areas (Juvik & Ekern, 1978). The soils at all the sites are generally immature (150- to 3000-year-old lava flows) and particularly undeveloped at colder and drier sites compared with warmer and wetter sites because of slower mineral weathering (Vitousek et al., 1992).

For Question I, we examine the effects of leaf trichomes on the duration of leaf wetness in all seven sites. In particular at the E2000 site where the largest variation in the amount of leaf trichomes was observed (Table 2), we examined the association between the prolonged leaf wetness due to the trichomes and the amount of leaf trichomes. For Question II, we compared the FWU ability between pubescent and glabrous shoots at the driest E2000 site and the wettest E700 site (see aridity index in Table 1). For Question III, we evaluated the effect of leaf wetness on the diurnal variation in photosynthetic rates at the driest E2000 site only due to logistic reasons—this site was relatively easy to access whereas the other sites were remote and required a long hike with heavy equipment.

2.2 | Field measurements

2.2.1 | Monitoring leaf wetness

To examine the effects of leaf trichomes on the duration of leaf wetness, we monitored leaf wetness on the lower side of the leaves with and without trichomes using the novel wet-monitoring method. We used water-sensitive paper (KN37-10, Kuretake Co. Ltd., Nara, Japan), whose color becomes darker through the absorption of water and returns to white after drying. We attached a few pieces of the paper, which were cut into $\sim 2 \times 5$ mm pieces, to the

TABLE 1 Environmental conditions and dominant phenotypes of *Metrosideros polymorpha* at our study sites.

Sites	Latitude	Longitude	MAT ^a (°C)	MAP ^a (mm yr ⁻¹)	PET ^a (mm yr ⁻¹)	AI ^b	Soil age ^c (ca. years)	Dominant
E100	19°42'12" N	155°05'46" W	22.9	3904	2476	1.58	150	Pubescent
E700	19°41'40" N	155°41'40" W	18.0	5934	1599	3.71	150	Glabrous
E1280	19°41'13" N	155°17'44" W	15.4	3503	1550	2.26	150	Pubescent
E1800	19°39'45" N	155°22'10" W	13.3	2260	1305	1.74	150	Pubescent
E2000	19°40'25" N	155°28'01" W	11.7	1042	2842	0.37	1500	Pubescent
E2400	19°35'20" N	155°27'40" W	10.0	1021	1856	0.55	1500	Pubescent
W700	19°49'39" N	155°49'13" W	19.4	585	1300	0.45	150	Pubescent

Note: The site locations are shown in Figure S1.

Abbreviations: AI, aridity index; MAP, mean annual precipitation; MAT, mean annual temperature; PET, mean annual potential evapotranspiration.

^aGiambelluca et al. (2014).

^bAI = MAP/PET.

^cSherrod et al. (2007).

TABLE 2 Leaf traits of *Metrosideros polymorpha* at the seven study sites where leaf wetness was monitored.

	E100	E700	E1200	E1800	E2000	E2400	W700
LMA (g m^{-2})	191.2 $\pm$ 12.5	218.3 $\pm$ 6.4	283.4 $\pm$ 7.9	313.6 $\pm$ 10.2	340.0 $\pm$ 20.6	421.5 $\pm$ 8.0	248.2 $\pm$ 7.3
Trichome (g m^{-2})	22.1 $\pm$ 13.4	4.2 $\pm$ 5.5	48.0 $\pm$ 3.8	56.6 $\pm$ 4.7	113.1 $\pm$ 20.5	154.9 $\pm$ 11.0	65.8 $\pm$ 11.9
Lamina (g m^{-2})	159.6 $\pm$ 12.4	203.3 $\pm$ 9.8	220.3 $\pm$ 7.7	251.0 $\pm$ 2.8	254.9 $\pm$ 13.8	275.4 $\pm$ 12.9	185.7 $\pm$ 6.3

Note: The sample size (i.e., the number of individuals whose wetness was monitored) was $n = 5$ individuals at the E2000 site and $n = 3$ individuals at the other sites. Means $\pm$ standard errors.

Abbreviation: LMA, leaf mass per area.

leaves with instant resin glue (Figure 1). We randomly selected five individuals at the E2000 site and three individuals at the other sites. We chose one representative sun-exposed shoot with 18–24 leaves for each individual and carefully removed the leaf trichomes on one-half side of each leaf (separated by the midrib) using a rubber thimble (see Figure 1). Our previous study demonstrated that this trichome-removed treatment did not affect the leaf gas-exchange traits (Amada et al., 2023). For each shoot, we took time-lapse images every 10 min with digital cameras (WG-40, RICOH, Tokyo, Japan) at the E2000 site for 11 days in September 2017 and at the other sites for 5 days in July and August 2018. For each intact and trichome-removed side, we categorized leaf wetness into three “wetness levels” (0–2) on the basis of the proportion of wet leaves out of the total number of leaves. Wetness level 0 indicates that no leaves are wet, wetness level 1 indicates that 0%–50% of the leaves are wet, and wetness level 2 indicates that 50%–100% of the leaves are wet. We calculated the prolonged duration of leaf wetness due to leaf trichomes as the duration when the intact sides exhibit larger levels than the trichome-removed sides (Figure 1c). It is noted that our method is likely to provide conservative estimates of leaf wetness duration because we observed the water-sensitive paper attached to the surface of a trichome layer dried faster than trichomes themselves did. To assess the relationship between the variation in trichome mass and the prolonged leaf wetness duration under a given environment, we used the prolonged wetness duration of each individual (five individuals) for each measurement day (11 days) at the E2000 site. To compare the wetness duration or the trichome prolonged effects among the sites, we calculated mean values across the monitored individuals at each site for each measurement day. During wetness monitoring, the air temperature and relative humidity were measured every 10 min (TR-72WF-H, T&D Co., Matsumoto, Japan).

2.2.2 | Shoot-level photosynthesis

To determine the effects of leaf wetness on the temporal patterns of photosynthesis under field conditions, we

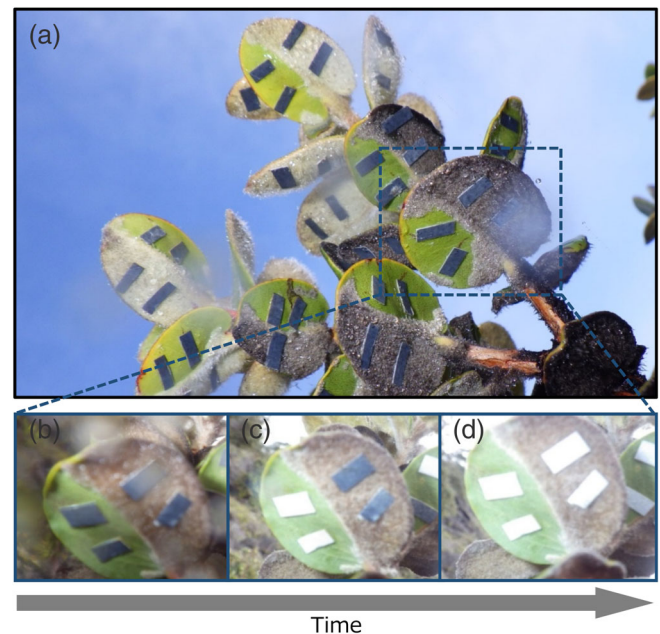


FIGURE 1 A representative image of leaf wetness monitoring using water-sensitive paper, whose color becomes darker by wetting but becomes white upon drying. For each monitored leaf, the leaf trichomes on one-half side were removed (green surfaces), and those on the other half side were kept intact (without removing the trichomes; gray surfaces). In the morning, the surface wetness of the leaves gradually decreased (from b to d). We calculated the prolonged duration of leaf wetness due to leaf trichomes as the increase in wet duration on the intact sides compared with the trichome-removed sides (i.e., c).

conducted a wetting exclusion experiment where individuals, which were lower than 2 m in height, were covered with waterproof sheets to prevent nighttime leaf wetting at the E2000 site. We confirmed that this cover treatment prevented leaf wetting by the water-sensitive paper utilized for monitoring leaf wetness duration. Using three control individuals and three wetting-prevented individuals, we measured the shoot photosynthetic rates throughout the day on seven sunny days in September 2018 (mean and standard deviation of photosynthetic photon flux density during measurements among measurement days: $1146 \pm 136 \mu\text{mol m}^{-2} \text{s}^{-1}$). We measured

the gas exchange rates of the shoots (approximately 10 cm in length) using a closed system consisting of an acrylic cylinder chamber for containing a shoot ($\phi 14.4 \times h 15$ cm), an infrared gas analyzer (LI-840, LICOR, Lincoln, USA), a pump (MP-2 N, SHIBATA, Tokyo, Japan), and a data logger (GL840, GRAPHTEC, Yokohama, Japan). To avoid damaging the infrared gas analyzer with high humidity, we attached a small cylinder with silica gels on a flow channel from the chamber to the gas analyzer (keeping the relative humidity lower than 60%). The photosynthetic rates were calculated from the slope of decreasing rates of CO_2 concentration ($R^2 > 0.99$) during the initial 30 s after a target shoot was placed in the closed chamber. The chamber volume, air temperature in the chamber, and total leaf area of each measured shoot (174 cm^2 on average) were taken into account to calculate the photosynthetic rate per unit leaf area. We repeatedly measured the photosynthetic rates of the six individuals every hour from 0530 to 1730 h. From the diurnal variations in photosynthetic rates, we calculated the duration of photosynthesis when the photosynthetic rates were above 25%, 50%, or 75% of the maximum rate for each shoot on each measured day (called “25%, 50%, and 75% photosynthetic durations”, respectively) (see Figure S2). Mean values across the three individuals for each treatment were used as representative values for each measurement day. In the preliminary experiment, we confirmed that there was no a priori difference between control and treated individuals (i.e., no sample bias) by applying the same measurements for the same six individuals without the wetting exclusion treatment (Figure S3). In this experiment, the transpiration rate was not assessed because water droplets in the trichome layer can lead to an overestimation of transpiration.

2.3 | Laboratory experiments

2.3.1 | Leaf traits

To determine the leaf traits of the individuals used for wetness monitoring, we collected sun-exposed leaves from three to five individuals from each site. We measured the areas of six leaves per individual using an image scanner (GT-S630, Epson, Suwa, Japan) and ImageJ software (National Institutes of Health, Maryland, USA). These scanned leaves were dried in an oven (70°C) for more than 2 days, and their dry mass was measured with a digital scale. Leaf mass per area (LMA) was calculated as the leaf dry mass divided by the leaf area. For the measurements of trichome and lamina masses (here, “lamina” refers to leaf tissues without trichomes), we

used a shaving technique (Tsujii et al., 2016); we removed leaf trichomes using a rubber thimble on a leaf half (separated by the midrib) and punched out two 10-mm-diameter discs from both sides of the leaf. These leaf discs were dried in an oven (70°C) for more than 2 days. We calculated trichome masses per area from the differences in the dry weight of the discs with and without trichomes, and lamina masses per area from the dry weight of the discs without trichomes.

2.3.2 | Anatomical assay

To determine whether the leaf trichomes of *M. polymorpha* are hydrophilic and whether they function as part of the FWU pathway, we conducted an anatomical assay for pubescent leaves collected at the E2000 site. A fluorescent apoplastic tracer solution (1% lucifer yellow carbohydrazide dilithium salt aqueous solution), which is often used to assess water uptake via leaf trichomes (e.g., Eller et al., 2016), was applied to either the upper or lower surface of fresh mature pubescent leaves, and these leaves were kept under saturated-humidity dark conditions for 24 h. The leaves were subsequently washed with distilled water and thinly sliced with a razor for observation with a fluorescence microscope (BX53, Olympus, Tokyo, Japan).

2.3.3 | Foliar water uptake

To examine the difference in FWU ability between pubescent and glabrous leaves, we measured and compared the FWU between pubescent shoots collected from the driest site (E2000) and glabrous shoots collected from the wettest site (E700). The FWU ability is expressed on the basis of the total leaf area (FWU_S) and shoot relative water content (RWC_S) as follows (Limm et al., 2009):

$$\text{FWU}_S = \frac{FM_{\text{after}} - FM_{\text{before}}}{LA}, \quad (1)$$

$$\text{RWC}_S = \frac{FM_{\text{after}} - FM_{\text{before}}}{FM_{\text{before}} - DM}, \quad (2)$$

where FM_{after} and FM_{before} are the shoot fresh masses after and before wetting, respectively; LA is the total shoot leaf area; and DM is the shoot dry mass. Because the difference in shoot fresh mass before and after wetting ($FM_{\text{after}} - FM_{\text{before}}$) included not only water absorbed into leaf internal tissues but also water retained in the trichome layer, we determined the FWU as the water absorbed into leaf internal tissues, which was

calculated from the shoot water potential. We randomly selected nine individuals from each of the E2000 and E700 sites, and collected three shoots from each individual ($9 \text{ individuals} \times 2 \text{ sites} \times 3 \text{ shoots} = 54 \text{ samples}$). We rehydrated these shoots by soaking the cut ends in water under dark conditions overnight before the experiment. We measured the relationship between shoot water potential and shoot water content using a pressure chamber (Model 1000, PMS Instrument Company, Albany, USA) with gradual dehydration of shoots, that is, every 10–30 min in a dark room for at least four cycles (Figure S4). We defined FM_{before} as the fresh mass of shoots whose water potential was lower than the midday shoot water potential at each site (i.e., when the shoots experienced the strongest water deficit stress during the day at each site; -0.83 MPa in E700 and -1.26 MPa at E2000 on average). Then, we sprayed distilled water on the shoots and kept these wet shoots under saturated-humidity dark conditions for 1, 3, and 6 h. Next, we wiped the surface water of these shoots with paper towels and used them for the measurement of shoot water potential (the water potential for FM_{after}). During the experiment, we sealed the cut end with cellophane to prevent water loss. We estimated FM_{after} using the obtained relationships between shoot fresh mass and shoot water potential for each shoot (Figure S4). After the experiment, we measured LA and DM .

2.4 | Statistical analyses

All analyses were conducted in the R statistical package (version 4.3.3; R Foundation for Statistical Computing, Vienna, Austria). To compare the wetness duration (wetness level >0) or the prolonged wetness duration among the sites, the Kruskal–Wallis test was used, followed by pairwise comparisons using Dunn's test with Holm adjustment for multiple comparisons (the PMCMRplus package; $n = 11$ days for the E2000 site and $n = 5$ days for the other sites). A Spearman's rank correlation test was used to examine the association between the amount of leaf trichomes and the effect of leaf trichomes on the wetness duration at the E2000 site ($5 \text{ individuals} \times 11 \text{ days} = 55 \text{ samples}$). Two-way repeated-measures analysis of variance (ANOVA) was used to examine the effects of wetting treatment and wetting time on the shoot water potential and to examine the effects of site and wetting time on the FWU_S and RWC_S ($n = 9$ individuals for each treatment). A paired t -test was used to examine the effects of the wetting-exclusion treatments on the duration of photosynthesis ($n = 7$ days for each treatment).

3 | RESULTS

3.1 | Leaf wetness and leaf trichomes

During the period of our field census, the leaves often got wet due to precipitation, fog, and nighttime dew at the sites lower than 2000 m a.s.l. on the east slope of Mauna Loa (E100, E700, E1200, E1800, and E2000; Figure 2a). In particular, the leaves were wet (i.e., the wetness level 1 or 2) throughout a night at these sites due to almost saturated-humidity conditions. At the E2400 and W700 sites, where low humidity was maintained at night, we rarely observed leaf wetness (i.e., the wetness level 0 was mostly observed; Figure 2a).

The amount of leaf trichomes greatly varied among the study sites: the greatest amount of trichomes occurred at the E2400 site, which was the dry alpine area, and the lowest amount of trichomes occurred at the E700 site which was the wettest among the sites (Table 2; Figure 2b). This trend was consistent with the previous studies (Amada et al., 2020; Tsujii et al., 2016). The prolonged duration of leaf wetness due to these trichomes (i.e., the duration when the intact sides exhibit larger levels than the trichome-removed sides) significantly differed among the sites ($p < 0.001$). Longer duration, up to approximately 100 min, was observed at the E1280, E1800, and E2000 sites where abundant trichomes were found, but negligible at the E100 and E700 sites where little trichomes were found (Figure 2c). At the E2400 and W700 sites, leaf wetness itself was rarely observed during our field census period (i.e., the wetness level 0 was mostly observed; Figure 2). Within the E2000 site, the effect of leaf trichomes on the duration of leaf wetness was positively correlated with the amount of leaf trichomes (Figure 3; $p < 0.05$).

3.2 | Foliar water uptake

For both pubescent shoots from the E2000 site and glabrous shoots from the E700 site, the wetting treatment increased the shoot water potential, foliar water uptake on a shoot basis (FWU_S), and shoot relative water content (RWC_S). These effects increased with wetting time and were greater in pubescent shoots than in glabrous shoots (Figure 4).

According to the anatomical observations, the leaf trichomes had thick cell walls but no clear cuticle layer. The results of the tracer experiment revealed that the apoplastic water tracer strongly accumulated in the cell walls of the trichomes (Figure 5), indicating that the leaf trichomes of *M. polymorpha* had hydrophilic characteristics. However, the apoplastic water tracer was not observed in the mesophyll tissues probably because the tracer could not pass through the cell membrane (Figure 5).

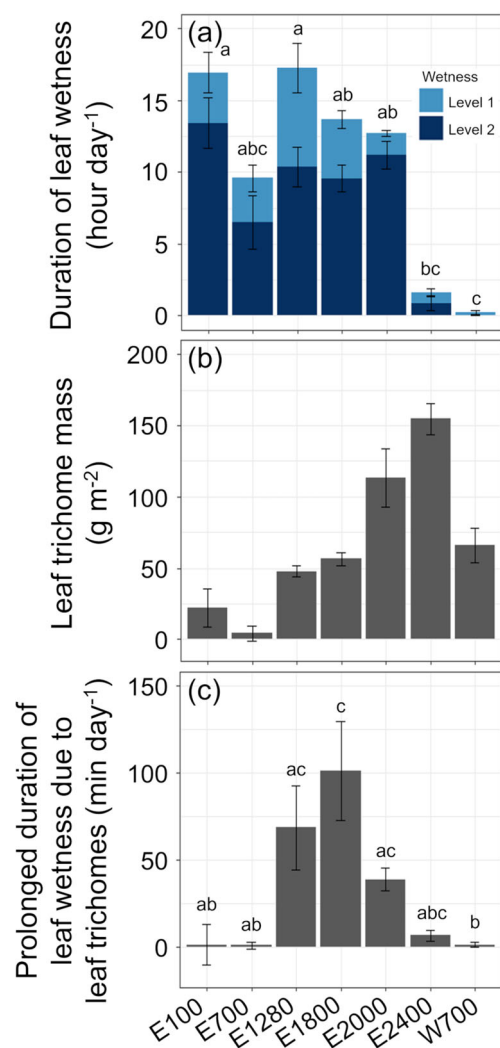


FIGURE 2 Duration of leaf wetness on intact surface, the amount of leaf trichomes, and the effect of leaf trichomes on the duration of leaf wetness among the study sites. In a, darker blue (wetness level 2) indicates durations when more than half of the leaves were wet on the basis of the proportion of wet leaves out of the total number of leaves on the intact side of the leaves, and lighter blue indicates (wetness level 1) durations when fewer than half of the leaves were wet. The prolonged duration of leaf wetness due to leaf trichomes (c) indicates the duration when the intact sides exhibit larger levels than the trichome-removed sides (Figure 1c). In a and c, the sample size was $n = 11$ days at the E2000 site and $n = 5$ days at the other sites, and different letters above the bars represent significant differences at the 10% level. The error bars represent standard errors.

3.3 | The rates and duration of shoot photosynthesis

While the peak rate of photosynthesis was not significantly different between the wetting-prevented and control individuals ($p > 0.10$; $4.23 \pm 0.24 \mu\text{mol m}^{-2} \text{s}^{-1}$), the 75% photosynthetic duration (per day) was significantly

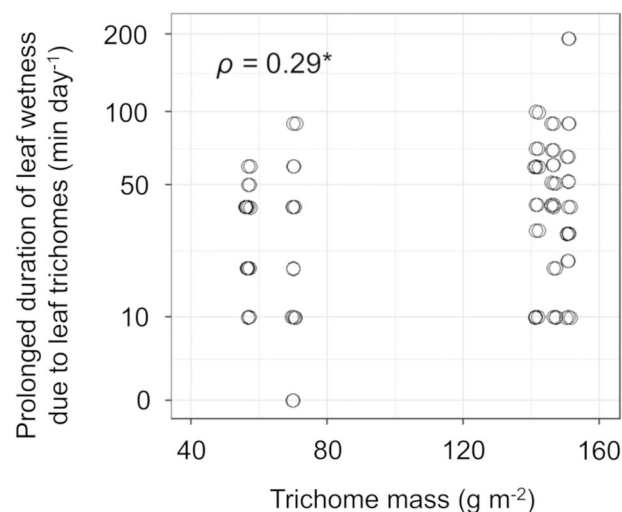


FIGURE 3 Relationship between the enhancement of the leaf wetness duration due to leaf trichomes and the amount of leaf trichomes at the E2000 site. The leaf wetness was monitored in five individuals for 11 days. Each point represents the prolonged wetness duration due to leaf trichomes in a single individual on a single measurement day. Points are slightly jittered to avoid complete overlapping. *: $p < 0.05$.

shorter in the wetting-prevented individuals than in the control individuals by ~ 100 min on average, whereas the 25% and 50% photosynthetic durations were not significantly different between the wetting-prevented and control individuals at the E2000 site (Figure 6a). A significantly shorter 75% photosynthetic duration in the wetting-prevented individuals than in the control individuals was observed both before (0530–1200 h) and after (1200–1730 h) noon (Figure 6b,c). The decrease in photosynthetic rates (midday depression) tended to be greater in the wetting-prevented individuals than in the control individuals (Figure 6d).

4 | DISCUSSION

4.1 | Leaf trichomes and leaf wetness

To our knowledge, this is the first field-based study to explore the effects of leaf trichomes on the duration of leaf wetness across a large natural environmental gradient. We found that the leaf trichomes of *M. polymorpha* had hydrophilic characteristics (Figure 5) and demonstrated that the leaf trichomes contributed to a longer leaf wetness duration for up to ~ 100 min in the field (Figures 2 and 3). As mentioned in Section 2, this was likely a conservative estimate; thus, the actual effects of leaf trichomes on leaf wetness duration could be greater. The trichomes with thick cell walls and without a visible

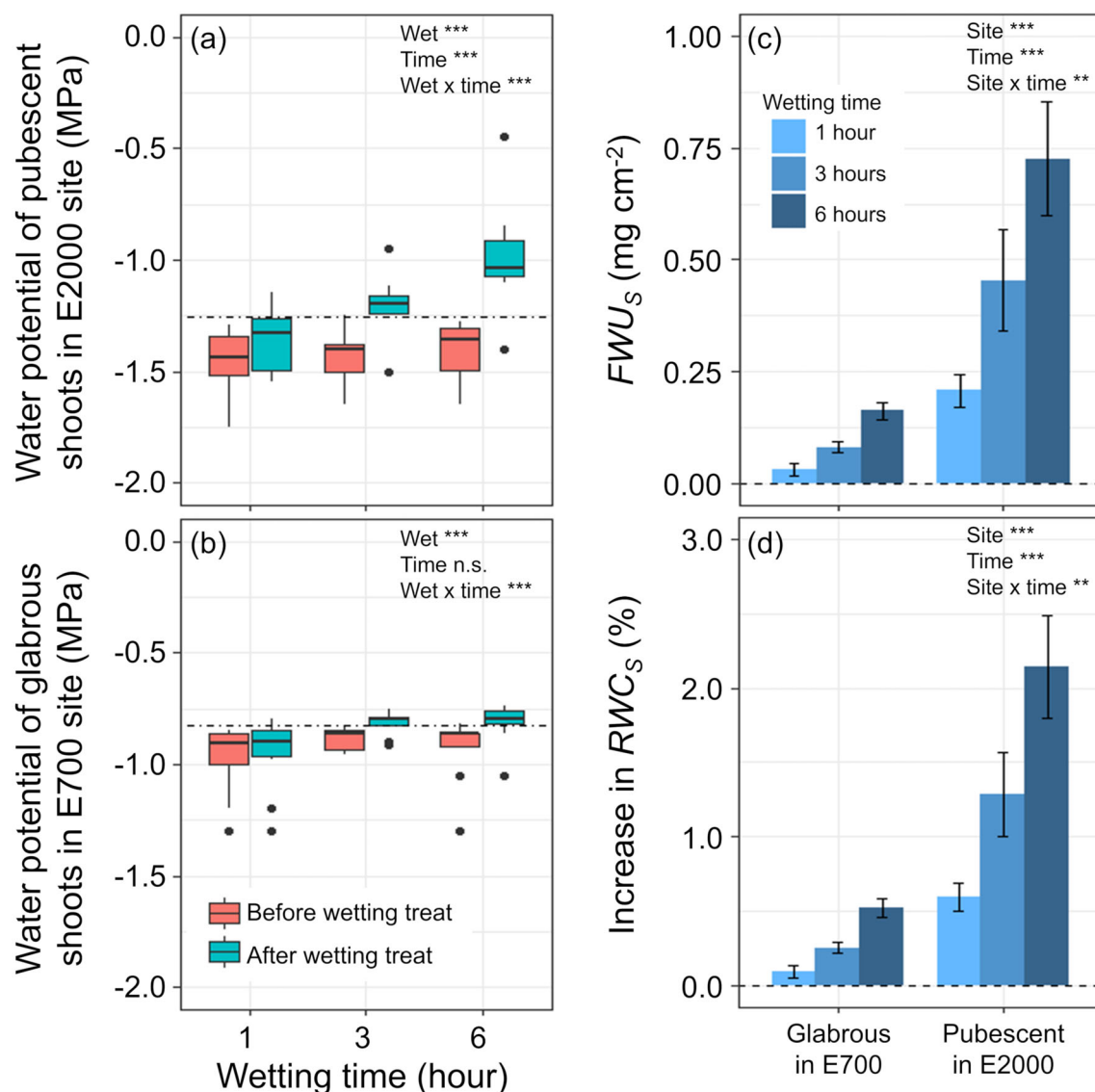


FIGURE 4 Water potential of pubescent and glabrous shoots before and after the wetting treatments and foliar water uptake per total leaf area on a shoot basis (FWU_s) and increases in shoot relative water content (RWC_s). The sample size for each treatment was $n = 9$ individuals. In a and b, dashed lines indicate the midday shoot water potential at each site. ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, †: $p < 0.1$, n.s.: $p \geq 0.1$.

cuticle layer in *M. polymorpha* are likely important for their hydrophilic characteristics. Moreover, the greater amount of leaf trichomes resulted in a longer duration of leaf wetness (Figure 3) probably because a thicker layer of dense trichomes can store more water and also can promote dew condensation (Konrad et al., 2015).

The prolonged duration of leaf wetness due to leaf trichomes depends on both the environmental conditions and the amount of leaf trichomes (Figure 2). The leaf trichomes prolonged the duration of leaf wetness at the E1280, E1800, and E2000 sites, where leaves had enough leaf trichomes and where wetting events often occurred because the site locations were under the base height of the trade-wind inversion zone (2255 ± 497 m; Cao

et al., 2007) (Figure 2). In contrast, we did not observe prolonged leaf wetness with trichomes at the dry alpine site (E2400) where the amount of trichomes was greatest. This was because few wetting events occurred during our field census period (Figure 2). The occurrence of wetting events is highly variable. Juvik and Ekern (1978) reported that the ratio of fog to rainfall is known to be highest at ~ 2500 m a.s.l. across the east slope of Mauna Loa, especially in drier seasons. Moreover, the fog ratio also depends on the base height of the trade-wind inversion zone (Juvik & Ekern, 1978), which can change daily, seasonally, annually, and interannually (Cao et al., 2007). Therefore, although the pubescent individuals at the E2400 site rarely receive water from the small amount of

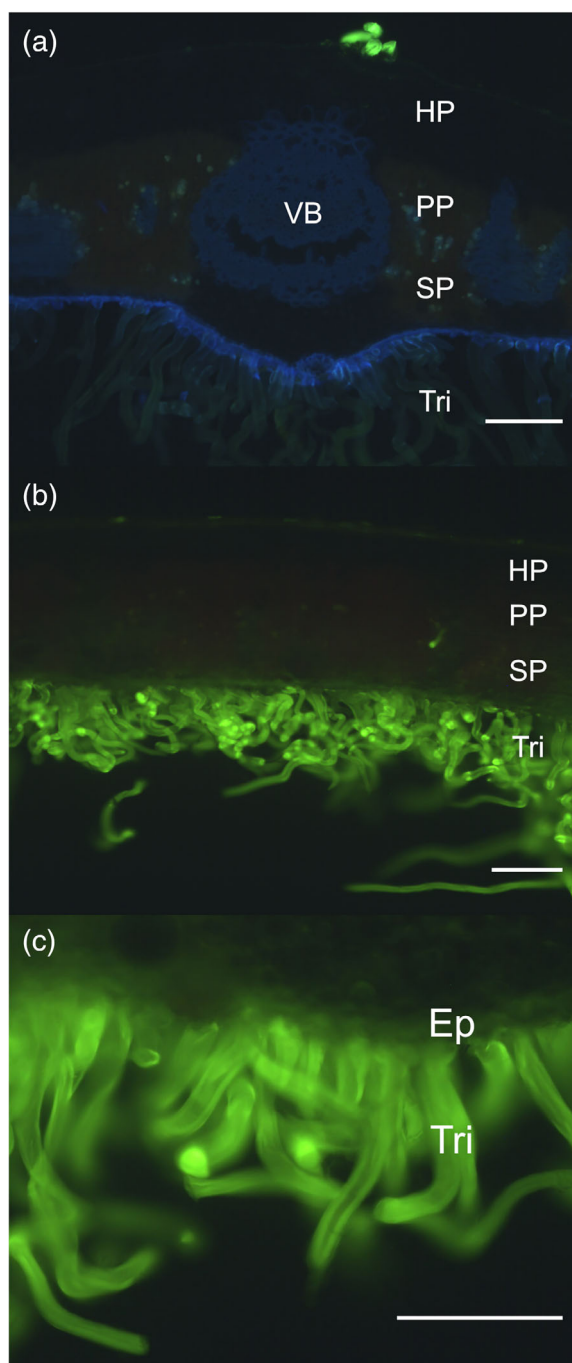


FIGURE 5 Anatomical assay for pubescent leaves at the E2000 site. In a and b, a fluorescent apoplastic tracer solution was applied to the upper and lower surfaces of fresh mature pubescent leaves, respectively. The apoplastic water tracer accumulated in the cell walls of the trichomes (b, c), whereas the tracer was not detected in mesophyll tissues when this tracer solution was applied to either the upper or lower leaf surface (a–c). Ep, epidermis; HP, hypodermal parenchyma; PP, palisade parenchyma; SP, spongy parenchyma; Tri, trichome. Scale bars indicate 100 μm .

precipitation, they may utilize the occurrence of fog to obtain some water. Besides, a greater amount of leaf trichomes is also found in bog areas (Stacy & Sakishima,

2019; Stacy et al., 2014), where trees have difficulties to take up water via roots because of the anaerobic conditions (Armstrong & Boatman, 1967; Canfield, 1990; Drew, 1983; Robichaux & Morse, 1990), but fog events often occur (Delay & Giambelluca, 2011; Juvik & Ekern, 1978). Thus, these leaf trichomes in such bog areas might also increase leaf wetness.

At the lower elevation sites, the leaf trichomes had negligible effects on the duration of leaf wetness. At the dry warm W700 site, the amount of precipitation is even lower than that at the E2400 site, and fog does not usually occur there, which may result in the lower amount of leaf trichomes compared with the individuals at the E2400 site. At the wet warm sites (E100 and E700), the small amount of leaf trichomes had no effect on the duration of leaf wetness even under wetting conditions. This thin trichome layer may not function in relation to increasing leaf wetness and may have other functions such as herbivory defense (Amada et al., 2020).

4.2 | Foliar water uptake

Leaves of *M. polymorpha* have FWU ability, as observed in many other plant taxa (Dawson & Goldsmith, 2018). This FWU ability can improve the water status of leaves but does not ameliorate root water deficit stress, as reversal of sap flow was not observed even at night when leaves were wet (Text S1; Figure S5; Clearwater et al., 2009; Eller et al., 2013; Skelton, 2017). A previous study showed sap flow reversal in *M. polymorpha* inhabiting cloud forests below the forest line on Haleakalā, Maui (Gotsch et al., 2014). The occurrence of sap flow reversal also depends on water potential in the rhizosphere (Eller et al., 2013). Thus, long-term monitoring of sap flow and soil moisture, particularly during periods of severe drought such as El Niño events, may be crucial for assessing the function of FWU on the root water status.

Foliar water uptake can be greater in pubescent individuals inhabiting dry, cold areas than in glabrous individuals inhabiting wet, warm areas (Figure 4). This difference may be attributed to differences in the FWU ability of leaves and in their habitat environments. Although the apoplastic water tracer was not transferred from leaf surfaces and trichomes to mesophyll or vascular tissues in *M. polymorpha* (Figure 5), it is likely that water moves into mesophyll or vascular tissues via symplastic pathways through trichomes in pubescent leaves. Similarly, previous studies suggest that several pubescent species can transport the absorbed water by leaf trichomes through symplastic pathways (Nguyen et al., 2017; Ohri et al., 2007). In addition, the differences in the midday water potential between the pubescent shoots at the E2000 site and the glabrous

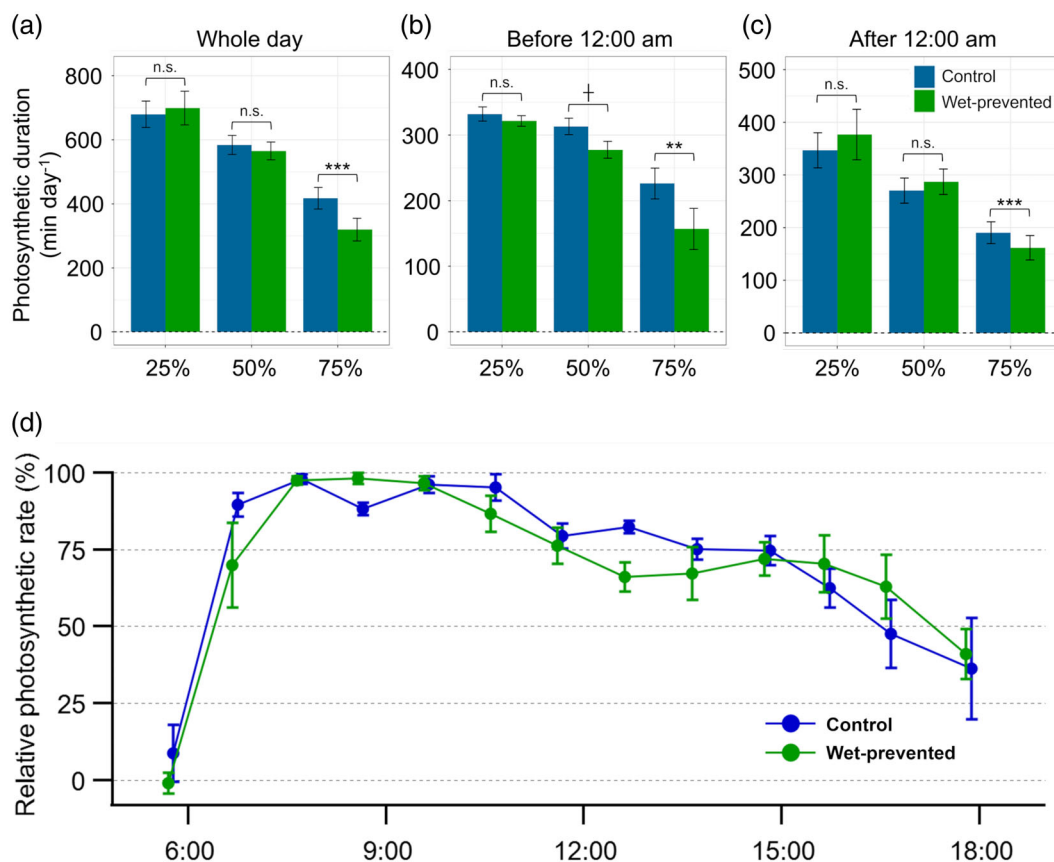


FIGURE 6 “Photosynthetic duration” during a day (a), before (0530–1200 h) and after (1200–1730 h) noon (b, c). The 75%, 50%, and 25% photosynthetic durations were defined as the times when the photosynthetic rates were above 75%, 50%, and 25% of the peak rate, respectively (see Figure S2). The sample size for each treatment was $n = 7$ days. An example of diurnal variations in relative photosynthetic rates in wetting-prevented and control individuals (with and without cover treatment, respectively) at the E2000 site (d). ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, †: $p < 0.1$, ns: $p \geq 0.1$.

shoots at the E700 site (Figure 4) may also be related to the differences in FWU ability. Compared with the glabrous individuals at the E700 site, the pubescent individuals at the E2000 site should have a lower midday water potential because of the lower water-retention capacity of a thin soil layer owing to slower soil development (Vitousek et al., 1992). In summary, FWU may be more important for pubescent individuals inhabiting dry, cold areas than for glabrous individuals inhabiting wet warm areas.

4.3 | Photosynthesis and leaf wetness

Leaves at the E2000 site often became wet during the night, and the sheet covering treatments prevented leaf wetting, which consequently decreased the duration of high photosynthetic rates without changing the peak rate of photosynthesis (Figure 6; Yokoyama et al., 2019). The longer duration of high photosynthetic rates caused by leaf wetness may have resulted from the longer duration of high stomatal openness caused by FWU (Figure 4; Berry et al., 2019;

Eller et al., 2016; Goldsmith et al., 2013). The wetness in the lower-side trichome layer may also contribute to the increase in stomatal openness through increasing humidity on the leaf surface (Konrad et al., 2015). In addition to this wetness effect, under cold conditions, dense leaf trichomes can provide thermal insulation and alleviate the temperature limitation of photosynthesis, thereby enhancing carbon gain (Amada et al., 2023). Overall, in dry alpine areas, leaf wetness enhanced by leaf trichomes can increase the carbon gain as well as improve water status through both FWU and water retention in the trichome layer.

5 | CONCLUSION

The present study suggests that the lower-side leaf trichomes of *M. polymorpha* can prolong the duration of leaf wetness and improve the leaf water status via FWU, which in turn can increase the duration of relatively high photosynthetic rates. Since leaf wetness is more beneficial under water deficit stress conditions, pubescent

individuals are more abundant at dry and early successional sites. In the dry alpine areas on the island of Hawaii, the largest amount of leaf trichomes up to 40% of leaf dry mass in *M. polymorpha* may reward an investment to capture fog and utilize the absorbed water efficiently for photosynthesis, although fog events occur infrequently. Their actual benefits for plant growth and fitness may be realized by more long-term field assessments.

Leaf trichomes can have multiple functions (Bickford, 2016; Johnson, 1975; Sack & Buckley, 2020): maintaining leaf temperature (e.g., Ehleringer & Mooney, 1978; Meinzer & Goldstein, 1985), avoiding photoinhibition (e.g., Skelton et al., 2012), and defending against herbivores (e.g., Dalin et al., 2008). In *M. polymorpha*, the large amount of leaf trichomes can increase diffusion resistance to heat fluxes on the leaf surface and contribute to increased carbon gain through increasing leaf temperature under alpine conditions (Amada et al., 2023). In addition, Amada et al. (2020) suggested that the leaf trichomes of *M. polymorpha* can impede gall formation in specialist psyllids (*Pariaconus* spp.), which increases water deficit stress in leaves and may decrease photosynthesis. This multifunctionality of leaf trichomes may be important for understanding the large geographical variation in the leaf trichomes of *M. polymorpha* across wide environmental gradients on the island of Hawaii.

AUTHOR CONTRIBUTIONS

Gaku Amada and Yusuke Onoda developed and framed the research questions. Gaku Amada, Kanehiro Kitayama, and Yusuke Onoda selected and established the study sites. Gaku Amada conducted all fieldwork and laboratory experiments. Gaku Amada and Yusuke Onoda developed the method for leaf wetness monitoring. Gaku Amada, Yoshiyuki Miyazawa, and Yuji Kominami developed the field measurement systems. Gaku Amada took the lead in writing the manuscript with contributions from all other authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ORCID

Gaku Amada  <https://orcid.org/0000-0001-8697-0689>

Yoshiyuki Miyazawa  <https://orcid.org/0009-0002-4092-1368>

Yuji Kominami  <https://orcid.org/0000-0001-9568-844X>

Kanehiro Kitayama  <https://orcid.org/0000-0002-6863-7118>

Yusuke Onoda  <https://orcid.org/0000-0001-6245-2342>

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SUPPORTING INFORMATION

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