

Slope-aspect induced climate differences influence how water is exchanged between the land and atmosphere

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Abstract

High resolution air temperature, relative humidity, soil moisture, insolation, and sap velocity observations on 14 madrone trees spanning adjacent north and south slopes at the University of California’s Angelo Coast Range Reserve show that cross-slope climate differences in the mid-latitudes are ecologically important, and impact vegetation-mediated water balance between the earth surface and the atmosphere. In this paper, we describe the cross-slope differences in direct observations of vapor pressure deficit (VPD) and sap velocity, which we use as a proxy for transpiration. We use a hybrid observation/model approach to estimate cross-slope insolation variations. We show that trees on opposing slopes do not follow a shared pattern of physiological response to transpiration drivers, meaning that the observed sap velocity differences are not due entirely to observed microclimate differences, but also due to population-level physiological differences, which may indicate acclimation to inhabited microclimate. While our present dataset and analytical tools do not positively identify any mechanism of possible acclimation, we speculate that differing proportions of sun-adapted and shade-adapted leaves, differences in stomatal regulation, and cross-slope root zone moisture differences could explain some of the observed and modeled differences.

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7 **Key Points:**

- 8 • Solar radiation differences generate different microclimates across adjacent north-
9 and south-facing slopes in the midlatitudes
- 10 • Continuous high frequency measurements document microclimatic differences and
11 covarying tree water use across a hillslope divide over a dry Mediterranean sum-
12 mer
- 13 • Transpiration of a single evergreen tree species is higher on the drier sunnier south-
14 facing slope, suggesting different water use and adaptation strategies.

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Abstract

High resolution air temperature, relative humidity, soil moisture, insolation, and sap velocity observations on 14 madrone trees spanning adjacent north and south slopes at the University of California’s Angelo Coast Range Reserve show that cross-slope climate differences in the mid-latitudes are ecologically important, and impact vegetation-mediated water balance between the earth surface and the atmosphere. In this paper, we describe the cross-slope differences in direct observations of vapor pressure deficit (VPD) and sap velocity, which we use as a proxy for transpiration. We use a hybrid observation/model approach to estimate cross-slope insolation variations. We show that trees on opposing slopes do not follow a shared pattern of physiological response to transpiration drivers, meaning that the observed sap velocity differences are not due entirely to observed microclimate differences, but also due to population-level physiological differences, which may indicate acclimation to inhabited microclimate. While our present dataset and analytical tools do not positively identify any mechanism of possible acclimation, we speculate that differing proportions of sun-adapted and shade-adapted leaves, differences in stomatal regulation, and cross-slope root zone moisture differences could explain some of the observed and modeled differences.

Plain Language Summary

The transfer of water from plants to the atmosphere is determined by the interaction between plant physiology and local microclimate. We made high frequency observations of sap velocity in two populations of Pacific madrone trees across a hillslope divide containing a strong microclimatic gradient. The differences in sunlight between the two slopes lead not only to different temperatures and humidities, but also to differences in energy available for photosynthesis, and hence transpiration. As a result, trees on the south-facing slope transpire 20% more water over the dry Mediterranean summer. Furthermore, we found that water use by trees on the north slope bears a different relationship to environmental conditions than water use by trees on the south slope.

1 Introduction

Plant transpiration is a major conduit for the transfer of water from the land to the atmosphere (Jasechko et al., 2013), and our understanding of how complex and sensitive the leaf-to-atmosphere link is to localized feedbacks, such as slope exposure and

46 associated conditions, is increasing (e.g., P. Link et al. (2014); Harrison et al. (2020); Ami-
47 trano et al. (2019)). Slope aspect influences microclimate (ambient air temperature (T),
48 vapor pressure deficit (VPD), soil moisture, and light) directly via insolation differences,
49 and this effect varies depending on latitude and slope characteristics. Cross-slope mi-
50 croclimate differences provide a natural laboratory for investigating the physiological re-
51 sponse of vegetation to altered T, VPD, and light regimes, as other environmental fac-
52 tors such as precipitation, underlying lithology and soil type, and cloud cover are com-
53 parable between adjacent hillslopes. Investigation of water dynamics in this setting yields
54 insights into how vegetation–atmosphere water cycle interactions may evolve under fu-
55 ture climates with different temperature and VPD regimes, which contributes to more
56 accurate projections of anticipated water fluxes under an altered climate.

57 The influence of natural microclimatic variations that can be associated with to-
58 pographic position on vegetation water dynamics is poorly understood, and hence of-
59 ten omitted in models, due to a lack of data (Mencuccini et al., 2019). No prior work
60 has, to our knowledge, investigated cross-slope transpiration dynamics in any of North
61 America, nor in a Mediterranean ecosystem, nor with such density of sap velocity ob-
62 servations focused a single species. Prior work which investigated interspecies transpi-
63 ration differences among five dominant tree species at our site reveals the importance
64 of controlling for species in order to accurately capture the species-specific signatures of
65 transpiration timing and volume, which can be large in this ecosystem: at the extreme,
66 differences in forest composition in the North Coast Range could alter anticipated sur-
67 face temperatures by up to 3°C during the hottest summer months (P. A. Link, 2015).

68 We present a set of field observations and modeling exercises designed to investi-
69 gate the effect of disparate microclimates on water fluxes from a single species of deeply-
70 rooted drought-tolerant broadleaf evergreen tree. We use the climatic gradient created
71 by differences in solar radiation on adjacent north- and south-facing slopes of a hill to
72 explore the impact of variable microclimate on sap velocities, and thus transpiration, in
73 this single species of tree. We define microclimate by ambient air temperature and hu-
74 midity beneath the canopy, incoming solar radiation adjusted for the slope and aspect
75 of the closed canopy, and soil moisture measured at 30 cm.

76 In the following sections, we describe the research site and our network of direct
77 observations, including our hybrid observation/model approach to simulating sunlight.

78 We then give a detailed analysis of the climatic features and sap velocity measurements
79 of the two slopes, and present our parameterization of a transpiration model based on
80 these cross-slope differences in microclimate and sap velocity. We conclude by explor-
81 ing the implications of cross-slope differences in ecological response parameters for for-
82 est resilience in this region under future climates, including a discussion of the limita-
83 tions of our analysis and proposed next steps.

84 **2 Methods**

85 **2.1 Site description**

86 At the University of California’s Angelo Coast Range Reserve (39.729167, -123.644444),
87 a site with large variation in year-to-year precipitation (e.g., 1027 mm in 2013-14, 2991
88 mm in 2016-17), there exists a heavily instrumented site spanning a forested north-facing
89 slope. The forest is composed of mixed broad-leaf and needle-leaf evergreen trees typ-
90 ical of the Douglas fir Pacific alliance (USDA, 2008). Over a 8000 m² area, slightly larger
91 than a standard soccer field, over 1000 instruments have been collecting data since 2009.
92 Weather stations, wells, soil moisture probes, sap velocity sensors, streamflow gauging
93 stations, hanging arrays of temperature and humidity sensors, and a deep (25 m) lat-
94 eral rock moisture sampling apparatus shed light on the path of water through this ecosys-
95 tem.

96 For the first time at the site, our installations take the observations to the south
97 slope. Because of the near-direct north–south orientation of the hillslope, the microcli-
98 matic differences between the two slopes are pronounced. The north slope of the hill is
99 cool and moist and has a river (Elder Creek) at the bottom. The south slope of the hill
100 is comparatively hot and dry and has no river. Our direct observations show that the
101 south slope can be nearly 7°C hotter and experience VPDs of up to 1.8 kPa greater dur-
102 ing late September mornings (see Table 1). There is a visible transition in tree species
103 composition across the ridge of the hill (see Figure 1). Because these are two sides of the
104 same hill, we assume precipitation inputs and cloud-induced variations in solar radia-
105 tion are identical.

106 For the purposes of examining cross-slope differences in sap velocity, we focus on
107 the dry months (June–October). This is because the seasonal drought in California’s Mediter-
108 ranean climate simplifies our environmental conditions firstly by avoiding potential post-

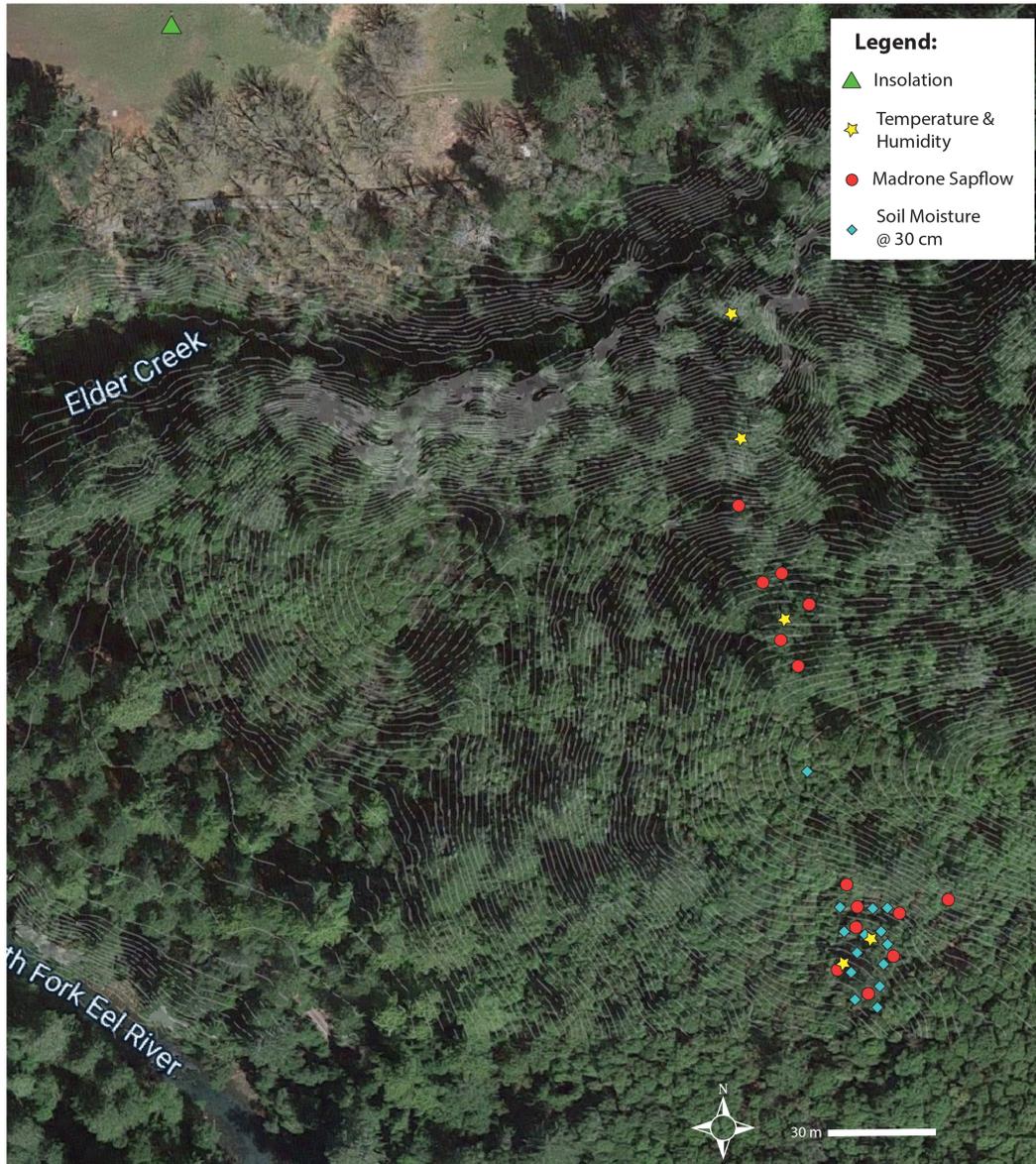


Figure 1. A map of the Rivendell field site in Northern California (39.729167, -123.644444), and the locations of data for this analysis. The canopy covering the north slope is largely made up of Douglas fir (*Pseudotsuga menziesii*), bay (*Umbellularia californica*), and evergreen oak tree species (Tan oak *Notholithocarpus densiflorus*, Coastal live oak *Quercus agrifolia*, Canyon live oak *Quercus chrysolepis*), with some Pacific madrone trees (*Arbutus menziesii*) in the upper half of the hillslope. In contrast, the south slope is mostly populated with Pacific madrone trees, with a few Douglas fir and oak trees primarily occurring in the upper half of the slope near the ridge. 1 m topographic lines are shown in light gray. Underlying high-resolution satellite imagery is from Maxar Technologies, accessed through Google Earth Engine (Gorelick et al., 2017).

109 rain leaf wetness (leading to possible sunny conditions with low transpiration), and sec-
110 ondly by simplifying the correlation of 30 cm moisture dynamics with those of deeper
111 moisture layers, which the trees at this site are accessing (Oshun et al., 2016). Thirdly,
112 during a time of continuously declining subsurface moisture availability, we hypothesize
113 that above-ground microclimatic variations may have the largest impact.

114 We focus on Pacific madrone (*Arbutus menziesii*) for two reasons: Firstly, their preva-
115 lence on both slopes at our site in particular allows for higher rates of same-species sam-
116 pling. Secondly, prior work on the north slope at this site (P. Link et al., 2014) has shown
117 that madrone trees reach their peak sap velocities latest in the dry season, around mid-
118 to late-July, compared to other neighboring evergreen species on the site, which reach
119 their peak sap velocities up to two months earlier when soils are wetter. Thus, madrone
120 trees experience their sap velocity peak during the highest VPD conditions in combina-
121 tion with the lowest soil moistures of any other tree species at our site. We hypothesized
122 that this would make madrones trees more sensitive to strong above-ground climate gra-
123 dients, potentially resulting in a larger cross-slope signal in the sap velocity data.

124 **2.2 Instrumentation**

125 The field study collects 1) sap velocity measurements on Pacific madrone trees; 2)
126 ambient understory temperature and humidity microclimate; 3) incoming solar radia-
127 tion to an open meadow adjacent to the site; and 4) soil moisture at 30 cm (Figure 1).

128 Sap velocity sensors (Dynamax Granier-style Thermal Dissipation Probes, as in Granier
129 (1985) and Granier (1987)) are installed into 14 madrone trees, 8 on the south slope and
130 6 on the north slope (Figure 1, red dots). Each tree has two 80 mm long sensors with
131 thermocouple junctions at 15 and 70 mm, and sensors are placed approximately 180° apart.
132 We consider only data from the outer thermocouple junctions, at 15 mm depth, result-
133 ing in 16 and 12 data streams on the south and north slopes, respectively. Sixteen soil
134 moisture sensors (Campbell Scientific CS650) monitor surface soil moisture at 30 cm in
135 a network that covers the south slope and ridge area (Figure 1, blue diamonds). Unfor-
136 tunately, similar soil moisture observations on the north slope were compromised dur-
137 ing the study period, and are therefore not used in this study. Three temperature and
138 humidity sensors (Campbell Scientific CS215) are installed 4-6 ft above the ground in
139 weather stations on the north slope, while eleven exist on the south slope, ten of which

140 hang in a vertical string from the canopy to the ground, and the last of which is installed
141 4-6 ft above the ground in a weather station (Figure 1, yellow stars; vertical string rep-
142 resented as one point). A weather station in an adjoining meadow provides information
143 about incoming radiation, wind speeds, and precipitation (Figure 1, green triangle).

144 There are several unique aspects of this field work: 1) the high resolution of sap
145 velocity measurements (2 sensors per tree and 14 trees); 2) the comprehensiveness of the
146 hydrological measurements, from ambient microclimate, sap velocities, soil moisture and
147 ground water fluctuations; and 3) the high frequency (<15 minutes) of the measurements
148 (Figure 4), a time scale that is commensurate with time steps of ecological processes in
149 state-of-the-art climate models.

150 **2.3 Data processing**

151 All data are collected at 1- to 15-minute intervals, and resampled to 5 minute in-
152 tervals, with no interpolation. Cleaning and analysis of field data was conducted with
153 Python 3.7.4.

154 **Sap velocity:** Granier-type sap velocity probes present challenges to error quan-
155 tification, especially with regard to sensor calibration (Davis et al., 2012), the choice of
156 constants in Granier’s empirically-derived sap velocity formula, which may be species-
157 specific (Sun et al., 2012), and fluctuations in sapwood heat capacity on time scales of
158 days to weeks (Ward et al., 2017). Additionally, asymmetries in tree tissues circumfer-
159 entially (Oliveras & Llorens, 2001) result in different sap velocities even when measured
160 at a constant depth. Our study trees ranged from 14-28” in diameter, and we used two
161 probes per tree installed 5.5-6.5 ft from the ground, which we infer based on our own prior
162 experiments is insufficient resolution to capture the true scale of radial variation in sap
163 velocity. Yet, because the probes intrude into critical water-transporting tissues, over-
164 saturating a tree with sensors may stress the tree, changing the degree to which the data
165 streams can represent an undisturbed population.

166 We confront these issues by assuming that any uncertainty introduced by varia-
167 tion in construction or calibration of sensors, or from incomplete sampling of radial sap
168 velocity variation, is randomly distributed in our data set. We also assume that, given
169 our focus on a single tree species, using sap velocity equation constants validated for madrone
170 in specific is unnecessary, as our data all received identical scaling and no cross-species

171 comparisons are made. Fluctuations in sapwood heat capacity are corrected via the stan-
 172 dard practice of continuously redetermining a unique local ‘zero flow’ over a particular
 173 window of time, to ensure comparability of data collected in different seasons during which
 174 tree tissues may have had differing water content (Ward et al., 2017).

175 Our sap flow data processing begins with applying the standard zeroing procedure
 176 to each data stream using a 5-day window. We then looked for outliers among the in-
 177 dividual sap velocity data streams, defined as having a mean sap velocity that is more
 178 than twice the interquartile range away from the mean sap velocity for the group of sen-
 179 sors representing a particular slope. One outlier on the north slope was identified and
 180 excluded, and all remaining data streams were averaged together by slope, resulting in
 181 a sap velocity time series for an average north slope madrone tree and an average south
 182 slope madrone tree. We assume that the number of remaining data streams on each slope
 183 (11 data streams for the north slope and 16 for the south slope) is enough to ensure that
 184 no systematic error remains from either endogenous sensor error or incompletely-sampled
 185 radial variation in sap velocity. We interpret the standard deviation of our average-tree
 186 data streams as representing total uncertainty in our measured sap velocity magnitude.
 187 This is illustrated in Figure 2.

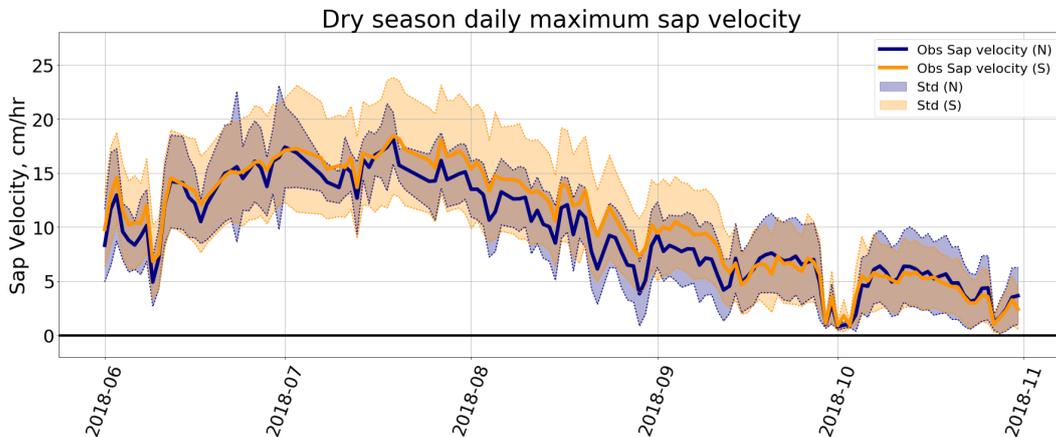


Figure 2. Daily maximum sap velocities for each slope, plotted with ± 1 standard deviation reflecting spread among the data streams for each slope’s tree population. While the south slope has faster peak velocities on average throughout most of the dry season up to the middle of September, during the end of the dry season the north slope experiences faster peak sap velocities on average. Nevertheless, as Figure 6 shows, the south slope transpires more water per sapwood area even during the month of October due to a longer diurnal cycle of transpiration.

VPD: Temperature and humidity are both reported by a single instrument (Campbell Scientific CS215, Figure 1, yellow stars). We averaged temperature and humidity data streams by slope, and then derived vapor pressure deficit (VPD) as:

$$VPD = SVP(1 - RH)$$

188 where SVP is the saturated vapor pressure (kPa) estimated as a function of tempera-
 189 ture by the Clausius-Clapeyron equation (Bolton, 1980), and RH is the directly sensed
 190 relative humidity.

191 **Insolation:** Unobstructed total (combined direct and diffuse) solar radiation is mea-
 192 sured in an adjacent meadow (LI-COR LI200X-L, Figure 1, green triangle). To derive
 193 the solar radiation on the north and south slopes, we first derived slope aspect from to-
 194 pographic maps. Because the slope undulates over the area enclosed by observations, we
 195 use the average aspect of each sampled tree’s location. The south slope’s aspect is 189.1° ,
 196 where 180° is due south; the north slope’s aspect is 344.2° , where 360° is due north. Thirdly,
 197 we measure the canopy slope from 12 LiDAR cross-sections of the vegetation (e.g. Lee
 198 et al. (2016)) on each slope, taken 10 m apart laterally along a N-S axis through the ob-
 199 servational footprint. For the north slope, on which broadleaf vegetation makes up a closed
 200 canopy understory to a sparse canopy of emergent Douglas fir trees, the slope of the broadleaf
 201 vegetation was measured. The south slope’s canopy has a slope of 21.97° , while the north
 202 slope is steeper, with a broadleaf canopy slope of 32.82° .

203 The clear-sky direct solar radiation for different times and days (solar zenith and
 204 azimuth angles) is calculated using python’s ‘solarradiation’ library (Stafford, 2018) that
 205 follows the formulation of Duffie and Beckman (1991). The calculation is done for a flat
 206 surface (S_{flat}) as well as for north and south slopes (S_N and S_S , respectively), using the
 207 latitude, canopy slope steepness, and slope aspect we have estimated for each slope. To
 208 obtain the total insolation for each slope, we scale the total radiation measured at the
 209 meadow by the scaling factor for each slope:

$$I_{North} = I_{meadow,Observed} \times \frac{S_N}{S_{flat}}$$

$$I_{South} = I_{meadow,Observed} \times \frac{S_S}{S_{flat}}$$

210 Figure 3 provides a visualization of the computed solar trajectories for the Riven-
 211 dell site and the scaling factors for each slope. The relative angles of the hillslopes and

212 solar trajectories illustrate why it is that early in the dry season, the north slope receives
 213 more afternoon sunlight than the south slope, and late in the dry season, the north slope
 214 gets very little direct sunlight at all. Late in the dry season, the south slope receives more
 215 sunlight than the flat meadow, while the north slope receives less.

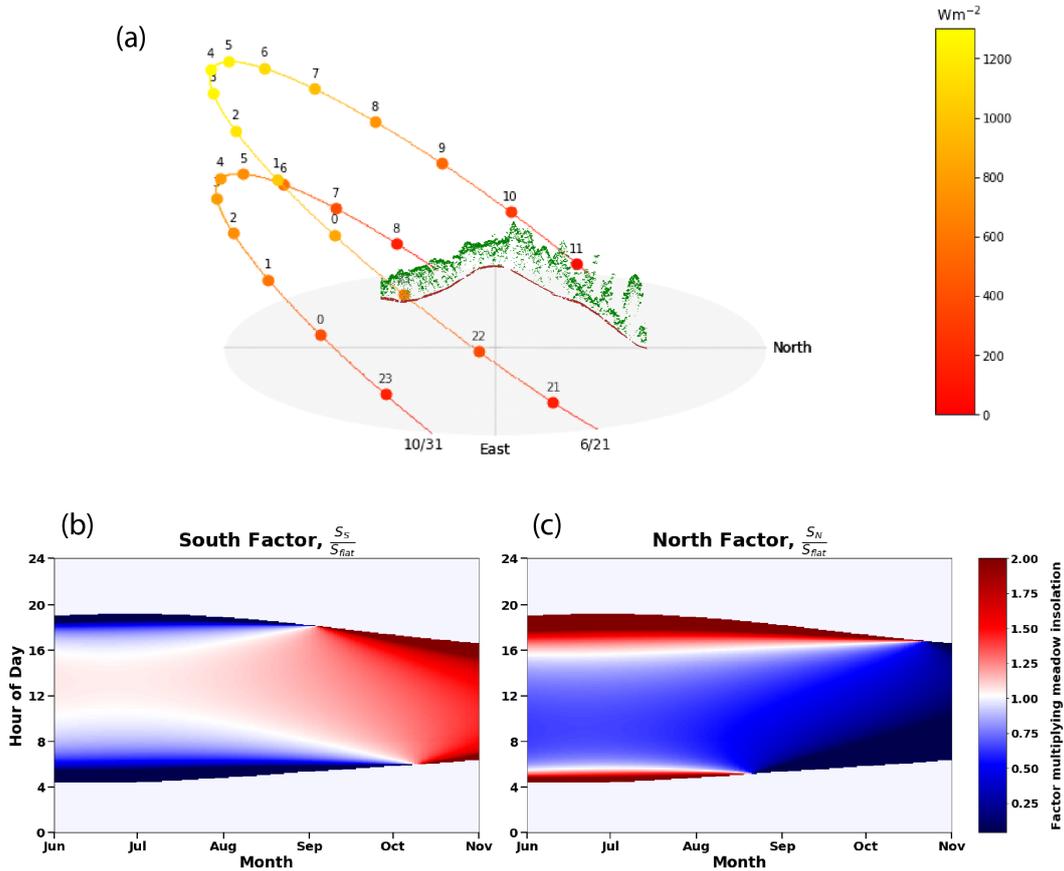


Figure 3. A summary of the solar model. Panel a: The solar trajectories at the latitude of the Rivendell site for the summer solstice (6/21) and the end of the dry season (10/31), showing that the sun rises and sets north of due East and due West for part of the dry season. The numbers indicate local time. A LiDAR cross section of the Rivendell site is provided for orientation. Panels b) and c): the scaling factor for each slope’s insolation, as it evolves throughout the day (y-axis) and the dry season (x-axis). The asymmetry in panels b) and c) reflects the slightly westward aspect of both slopes, also visible in Figure 1.

216 **Soil Moisture:** Our dense network of 14 soil moisture sensors at 30 cm (CS650
 217 Water Content Reflectometers, Figure 1, blue diamonds) shows large-magnitude vari-

218 ation in soil volumetric water content at a roughly 15 m length scale, independently con-
219 firmed by a limited amount of manual soil sampling. This variation in shallow soil mois-
220 ture is spatially organized, and appears to relate to the geomorphology and history of
221 shallow landslide disturbance in the area (W. Dietrich, private communication). This
222 variation does not appear to be correlated with variation in sap velocity magnitude of
223 proximate trees, suggesting lateral and vertical extents of the tree roots may be access-
224 ing moisture from a wider area and from deep moisture in weathered bedrock (Rempe
225 & Dietrich, 2018; Vrettas & Fung, 2017). Lacking observations to capture these deep mois-
226 ture reservoirs, we assume that the overall dynamics of root-zone moisture are correlated
227 with those of 30 cm soil moisture over the summer dry season (i.e., both show a steady
228 decline), and use a site-wide average of 30 cm soil moisture for both slopes.

229 **3 Results & Discussion**

230 **3.1 Microclimate and sap velocities on the north and south slopes**

231 To illustrate the high-frequency data stream, Figure 4 shows, for the dry season
232 and beginning of the wet season (June–October) of 2018, the average microclimate and
233 sap velocity data for the north and south slopes, as well as the averaged soil moisture
234 data for the south slope. While soil moisture shows a steady decline through the dry sum-
235 mer, sap velocities on both slopes peak in July when 30 cm soil moisture is generally around
236 10%, about 1-2 months after the start of the dry season.

237 Monthly climatologies of the diurnally cycling variables (i.e., all except soil mois-
238 ture) display the microclimate and sap velocity differences between the two slopes, and
239 provide a snapshot of how these variables evolve together throughout the dry season (Fig-
240 ure 5). In the diurnal cycle, both the south and north slopes show sap velocities that peak,
241 not surprisingly, around mid-day. However, the south slope sap velocity is substantially
242 faster than north slope sap velocity in late morning, while the north slope flows slightly
243 faster than the south slope in the late afternoon and early evening. The cross-slope dy-
244 namics of the sap velocity diurnal cycles are also descriptive of the cross-slope dynam-
245 ics of the diurnal cycles in above-ground microclimate.

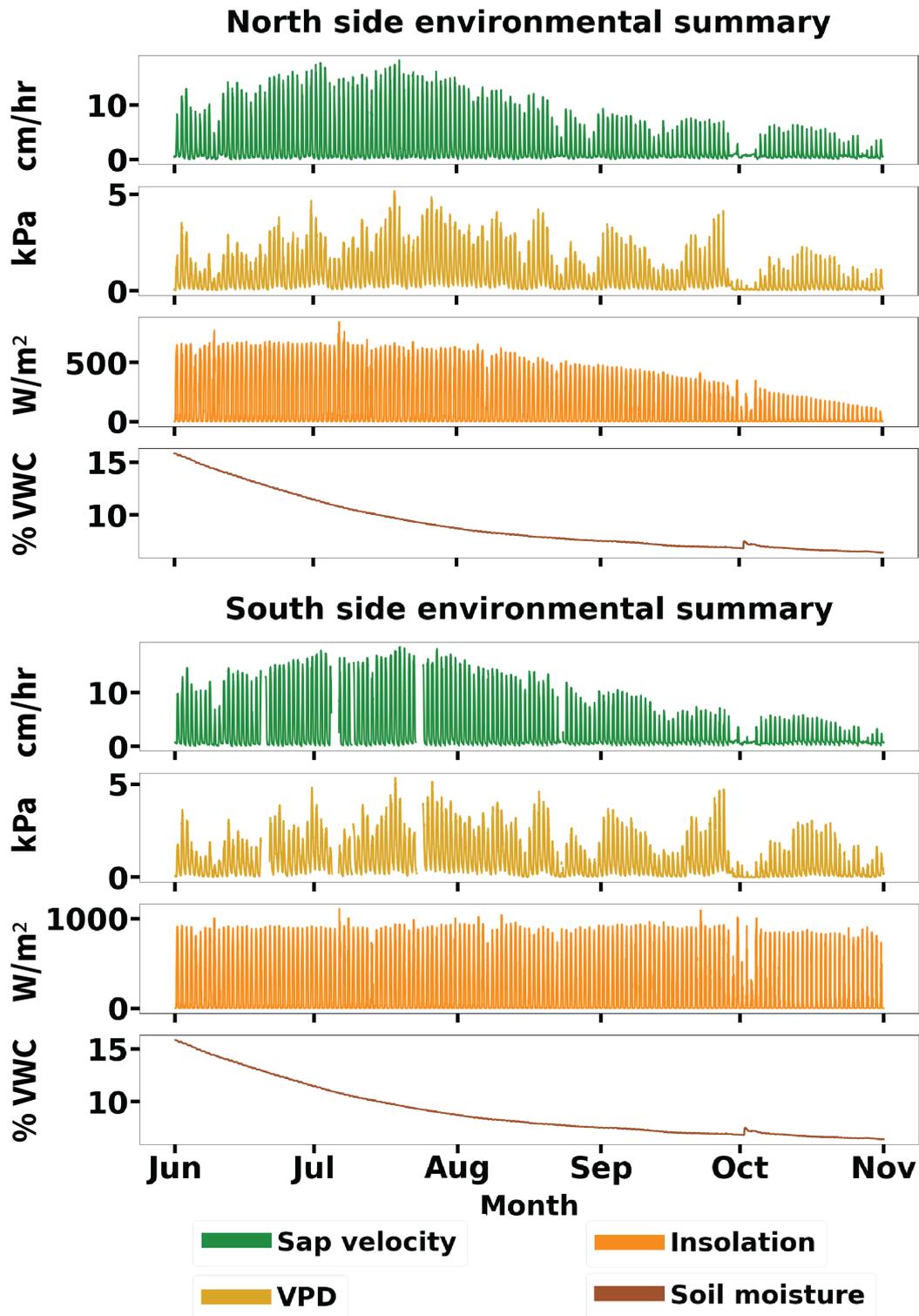


Figure 4. Time series of environmental drivers of sap velocity for each slope, showing what the MCMC parameterization process used as inputs. Soil moisture is identical for both slopes in this set up, though we tested other representations (see Figure 8). Sap velocities decrease to near zero during a rainstorm in early October when both insolation and VPD decline, and soil moisture increases. Thereafter both VPD and sap velocities picked up while soil moisture continues to decline. Day-to-day variations in VPD are large and show no significant trend through the dry season, but insolation varies substantially on the north slope over the dry season.

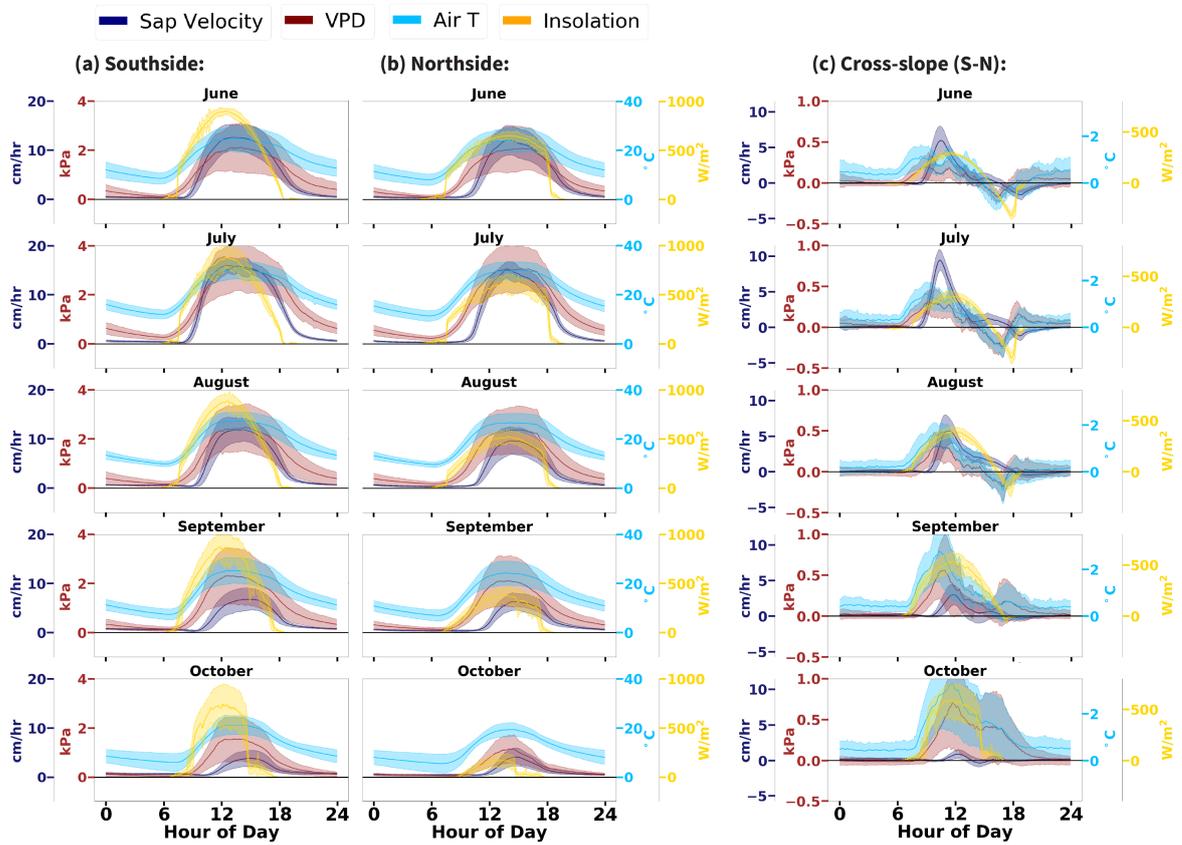


Figure 5. Monthly climatologies of diurnally cycling environmental drivers of sap velocity. Shading shows ± 1 standard deviation of the monthly climatology, and thus reflects the variability over the month. For all the months of the dry season and on both slopes, while air temperature (pale blue) rises and falls in close concert with the sun (yellow), the VPD diurnal cycle (burgundy) lags behind, and sap velocity (purple) lags behind even further. Though cross slope differences in sap velocity peak in July, the cross-slope microclimate differences peak in the late dry season, in September and October.

Table 1: A month-by-month summary of shifting environmental conditions on each slope. Rows labeled “Max” refer to the maximum value observed over the whole month, and values are reported with the date, hour, and minute recorded. “ClmMax” refers to the climatological maximum, i.e. the maximum of the average diurnal cycle of each variable observed over the whole month. The climatological maxima correspond with the climatologies shown in Figure 5, but the time series maxima show the extremes for the whole month, to help set the context. For instance, in late September and October, the south slope can become nearly 7°C hotter with 1.8 kPa higher VPD, and this climate difference occurs in the late morning-early afternoon. In contrast, in July, the month of peak sap velocity and cross-slope sap velocity differences, the largest cross-slope temperature and VPD differences are less than half the magnitude seen in October.

Sap Velocity (cm/hr) Maxima, by month:					
	June	July	August	September	October
Max (N)	16.44 06-30 15:55	18.22 07-19 13:55	13.51 08-02 13:45	9.30 09-01 14:00	6.40 10-08 14:25
Max (S)	16.65 06-30 15:35	18.45 07-19 13:00	16.01 08-02 13:40	10.48 09-04 14:05	5.83 10-14 15:10
Max (S-N)	9.54 06-30 10:05	11.35 07-25 10:20	9.16 08-01 10:50	5.79 09-04 11:25	2.38 10-04 12:55
Max (N-S)	3.23 06-23 18:45	3.11 07-01 18:50	0.94 08-07 19:45	2.41 09-20 14:25	1.53 10-19 14:25
ClmMax (N)	12.08 , 14:15	15.05 , 13:50	9.65 , 14:20	6.30 , 14:25	4.09 , 14:50
ClmMax (S)	12.62 , 13:05	16.00 , 12:35	11.89 , 14:05	6.77 , 14:55	3.83 , 15:00
ClmMax (S-N)	5.97 , 10:30	9.44 , 10:20	5.72 , 11:15	2.99 , 11:45	0.92 , 12:15
ClmMax (N-S)	1.66 , 18:45	1.19 , 18:40	0.46 , 19:40	0.27 , 18:40	0.32 , 14:30
VPD (kPa) Maxima, by month:					
Max (N)	4.66	5.13	4.21	4.13	2.27

	06-30 13:55	07-18 13:55	08-18 14:45	09-27 13:35	10-14 14:25
Max (S)	4.79 06-30 13:55	5.30 07-18 13:50	4.59 08-18 14:35	4.69 09-27 12:40	3.03 10-16 12:20
Max (S-N)	0.62 06-30 20:00	0.76 07-17 11:20	0.88 08-18 10:55	1.83 09-26 10:55	1.69 10-13 11:40
Max (N-S)	0.36 06-24 16:15	0.54 07-28 17:00	0.46 08-08 16:55	0.18 09-10 17:05	0.11 10-27 17:30
ClmMax (N)	2.07 , 15:25	3.05 , 16:00	2.37 , 14:50	2.09 , 13:50	1.15 , 14:00
ClmMax (S)	2.12 , 14:00	3.16 , 13:20	2.46 , 14:30	2.30 , 12:40	1.56 ,13:50
ClmMax (S-N)	0.20 , 09:10	0.30 , 09:05	0.32 , 10:25	0.56 ,10:45	0.71 ,11:45
ClmMax (N-S)	0.17 , 16:30	0.23 , 16:50	0.18 , 16:55	-0.001 , 06:10	0.01 , 05:40
Air Temperature (°C) Maxima, by month:					
Max (N)	34.53 06-30 14:35	35.95 07-18 14:00	32.21 08-18 14:50	32.22 09-27 14:10	23.46 10-13 14:15
Max (S)	35.20 06-30 13:55	36.83 07-18 13:10	33.38 08-18 14:15	34.34 09-27 12:35	27.76 10-13 13:15
Max (S-N)	2.54 06-23 00:25	2.38 07-01 08:05	3.17 08-18 11:00	6.34 09-26 10:55	6.61 10-20 11:30
Max (N-S)	1.97 06-17 15:50	1.57 07-28 17:00	1.71 08-21 15:30	0.89 09-05 18:25	0.78 10-22 17:10
ClmMax (N)	24.28 , 15:20	29.67 , 15:50	26.61 , 14:05	24.24 , 13:45	19.37 , 14:25
ClmMax (S)	24.73 , 12:55	30.37 , 13:20	27.34 , 14:15	25.28 , 13:20	21.29 ,14:15
ClmMax (S-N)	1.14 , 08:25	1.44 , 08:55	1.60 , 09:45	2.77 ,10:20	3.30 ,11:40
ClmMax (N-S)	0.82 , 16:30	0.90 , 16:55	0.79 , 16:55	-0.30 , 21:20	-0.41 , 05:10
Insolation (W/m²) Maxima, by month:					
Max (N)	774.4 06-09 16:35	841.9 07-06 14:55	654.5 08-05 13:50	475.9 09-01 13:30	347.5 10-04 13:55
Max (S)	1006 06-09 11:55	1108 07-06 11:55	1039 08-10 12:40	1096 09-22 12:15	1006 10-04 13:55
Max (S-N)	332.5 06-09 11:15	378.9 07-31 12:15	479.0 08-31 11:35	711.7 09-30 11:40	790.9 10-28 11:45

Max (N-S)	360.0 06-20 17:55	487.8 07-07 17:50	277.08 08-02 17:45	115.6 09-01 17:25	0.00 10-04 05:55
ClmMax (N)	650.5 , 14:10	613.8 , 14:55	524.4 , 13:50	380.1 , 13:20	171.9 , 13:20
ClmMax (S)	897.5 , 12:25	883.6 , 12:30	890.0 , 12:40	870.0 , 11:40	743.9 ,12:05
ClmMax (S-N)	288.7 , 11:20	300.5 , 11:55	391.0 , 11:45	534.8 ,11:40	593.2 ,10:50
ClmMax (N-S)	320.0 , 17:45	298.5 , 17:50	166.71 , 17:30	27.5 , 17:15	0.00 , 05:50

246 Figure 6 underscores the differences in timing and amount of sap velocity in the
247 diurnal cycle, both for the whole dry season (panel a) and for each month individually
248 (panels b-f). Cumulative integrals of the average sap velocity diurnal cycle show that
249 on average, south slope madrones transpire 20% more water per day over their combined
250 sapwood area during the dry season. August is the month with the peak percent cross-
251 slope difference in sap velocity, with south slope madrones transpiring on average 32%
252 more water per day over their combined sapwood area during this month. While for most
253 of the dry season the average south slope madrone tree moves water as fast or faster than
254 the average north slope madrone tree at their respective moments of daily peak sap ve-
255 locity, Figure 2 shows that late in the dry season the north slope madrone trees are slightly
256 faster, although they still transpire less per day.

257 In our data preparation, we eliminated one of the north slope data streams as an
258 outlier. If this outlier is included, the cross-slope differences in integrated sap velocity
259 are ordinarily the same for each time period considered, but of much smaller magnitude.
260 For instance, the dry season cross-slope percent difference in integrated sap velocity would
261 be 6.6%, rather than 20.1%, with the outlier included in the north slope average; and
262 August's cross-slope difference would be 13.7% instead of 32.4%. While we believe there
263 are legitimate reasons to exclude this outlier from the set of north slope data streams
264 due to the unique orientation of the canopy of that tree (which faces more westward than
265 northward, decoupling its solar access from the simulated sunlight we use in our anal-
266 ysis), we also believe that the data from the excluded sensor are accurate. This is illus-
267 trative of the fact that eleven high-frequency time series of sap velocity on the north slope
268 are inadequate for capturing the full range of possible variation on a steep slope. For this
269 reason, we do not provide a full error analysis for the cross-slope percentage differences

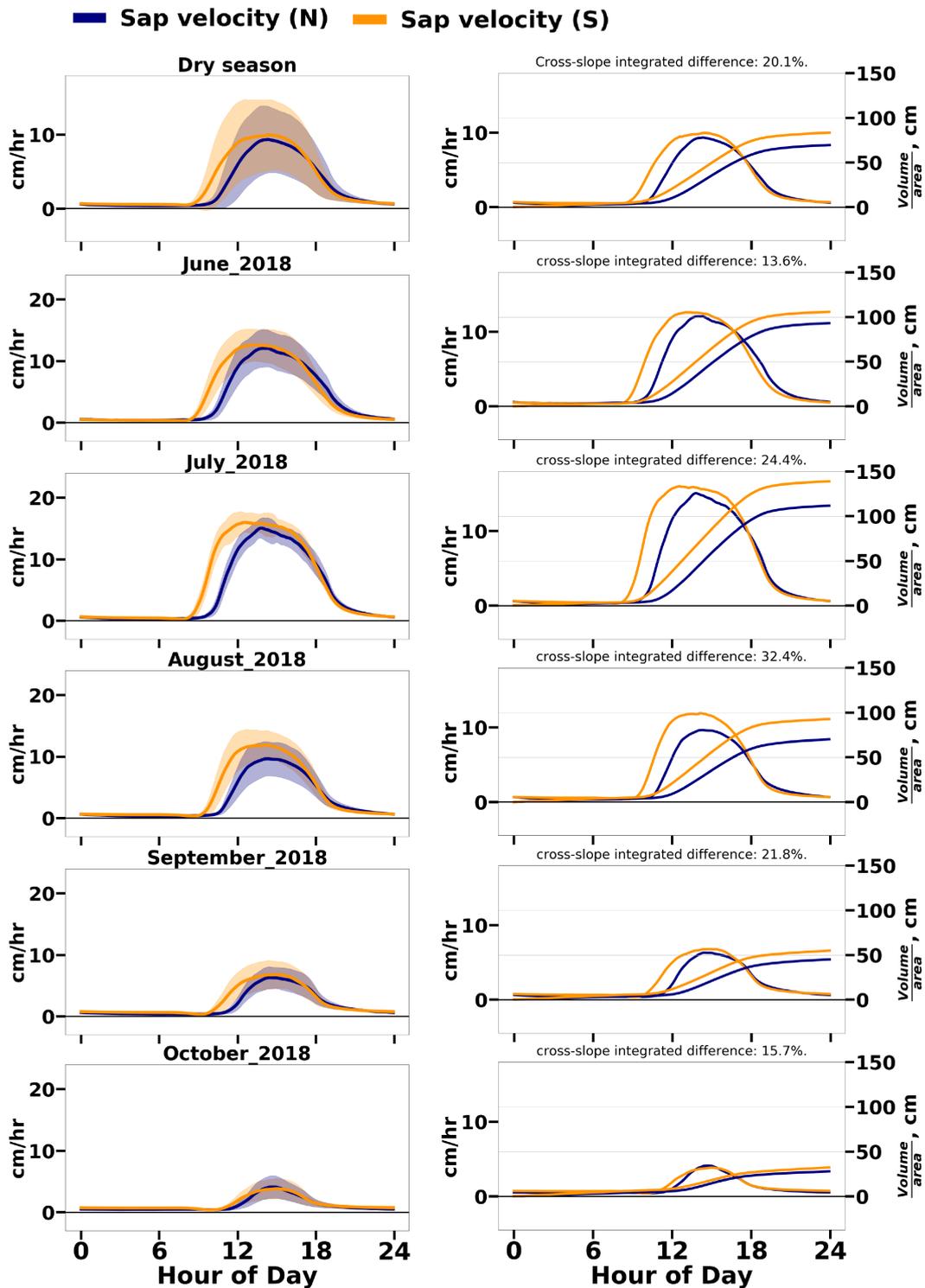


Figure 6. Average diurnal cycles (left panels) and cumulative integrals (right panels) of sap velocity for the entire dry season (June–October, panel a) and by month (panels b–f). The north slope is shown in purple and south slope is shown in orange; shading shows +/- 1 standard deviation of the climatologies, reflecting the variability over the time period (month or dry season). The south slope exhibits higher rates of time-integrated sap velocity, a proxy for transpiration, beginning earlier in the day and also experiencing a longer stretch of high sap velocity. Later in the dry season, the north slope experiences faster peak sap velocities, although it still produces less cumulative transpiration. See Figure 2.

270 in sap velocity, because more data is required to provide statistically meaningful esti-
 271 mates.

272 3.2 Description of sap velocity (transpiration) model

273 To understand the seasonal dynamics of daily maximum sap velocity across differ-
 274 ent tree species on the north slope of this site, P. Link et al. (2014) apply the concep-
 275 tual framework of the Jarvis model (Jarvis, 1976) in which the maximum bulk canopy
 276 conductance (g_{cmax}) under ideal conditions is modulated by ambient conditions to yield
 277 the instantaneous bulk canopy conductance, g_c . Furthermore, by assuming total tran-
 278 spiration E , approximated as $E = g_c \times VPD$, is proportional to the normalized sap
 279 velocity v_n with a proportionality constant α : $E = \alpha \times v_n$, they obtain the equation

$$v_n = \frac{g_{cmax}}{\alpha} \times VPD \times f_{VPD}(VPD) \times f_{\theta}(\theta) * \times f_I(I) \quad (1)$$

280 The forms of the functions are taken from Lohammar et al. (1980), Feddes et al.
 281 (1978), and Waring and Landsberg (2011):

$$f_{VPD}(VPD) = \frac{1}{1 + \frac{VPD}{D_0}}$$

$$f_{\theta}(\theta) = \frac{1}{1 + \exp(-\beta(\theta - \theta_0))}$$

$$f_I(I) = \gamma * (I - 1000) + 1$$

282 where D_0 , β , θ_0 and γ are parameters determined for each tree species using daily
 283 maxima of normalized observed sap velocity, VPD, insolation and soil moisture from Febru-
 284 ary 2009 to October 2011.

285 Equation 1, developed to investigate the seasonality of normalized daily maximum
 286 sap velocity across tree species on the same slope (and same microclimate), is not directly
 287 applicable for modeling the diurnal cycle during the dry season, where hysteresis in the
 288 response of sap velocity to VPD and insolation is observed (Zhang et al., 2014; Gimenez
 289 et al., 2019). We modify Equation 1 by allowing for a lag in the sap velocity response
 290 to diurnally cycling VPD and insolation of 1 and 2 hours previous. We assume no di-
 291 urnal variations in soil moisture θ , and thus we do not provide lagged terms for Φ_{θ} . We

292 further modified the approach by using averaged, rather than normalized sap velocities,
 293 which at substantive n (11 data streams on the north slope and 16 on the south slope)
 294 minimizes several potential sources of error that must be considered when using sapflow,
 295 and also provides the best match with the scale of our environmental data (see section
 296 2.3). Using averaged rather than normalized sap velocities and splitting the Φ_{VPD} and
 297 Φ_I expressions into three led to scaling differences in our parameters compared to P. Link
 298 et al. (2014), and in particular, our initial constant, the analog of g_{cmax}/α , has less re-
 299 lation to a theoretical maximum bulk canopy conductance, so for clarity we rename it
 300 ε . The resulting model is:

$$\begin{aligned}
 v_s(t) &= \varepsilon \times \Phi_{VPD}(VPD_t, VPD_{t-1}, VPD_{t-2}) \times \Phi_\theta(\theta_t) \times \Phi_I(I_t, I_{t-1}, I_{t-2}) \\
 &= \varepsilon \times \left(\frac{VPD_t}{1 + \frac{VPD_t}{D_0}} \times \frac{VPD_{t-1}}{1 + \frac{VPD_{t-1}}{D_{-1}}} \times \frac{VPD_{t-2}}{1 + \frac{VPD_{t-2}}{D_{-2}}} \right) \times \left(\frac{1}{1 + \exp(-\beta(\theta - \theta_0))} \right) \times \\
 &\quad \left((\gamma_0(I_t - 1000) + 1) \times (\gamma_{-1}(I_{t-1} - 1000) + 1) \times (\gamma_{-2}(I_{t-2} - 1000) + 1) \right) \quad (2)
 \end{aligned}$$

301 where t is time, t_{-1} and t_{-2} denote 1 and 2 hours previous, respectively. This re-
 302 sults in additional parameters in Equation 2, D_0 , D_{-1} , D_{-2} , γ_0 , γ_{-1} , and γ_{-2} , in ad-
 303 dition to β and θ_0 .

304 3.3 Slope-specific Parameters

305 To estimate the parameters in Equation 2 for the north and south slopes, we ran-
 306 domly selected 20% of the data (non-sequentially) and assigned it to a training data set,
 307 while reserving the remainder for testing. We used Hamiltonian Monte Carlo (Betancourt,
 308 2017), a type of Markov Chain Monte Carlo, and the No-U-Turn Sampler (Hoffman &
 309 Gelman, 2014) to derive our parameters for each slope. Parameter estimation used the
 310 pymc3 package in python (Salvatier et al., 2016). We repeated this procedure 5 times,
 311 to ensure that our parameter estimates did not change substantively depending on the
 312 sample assigned to the training data set. Our final reported parameters are the mean
 313 of all five runs for each slope. Figure 7 shows the mean parameters as well as the spread
 314 of parameters from each of the five runs.

315 We use the same priors (bounded normal distributions bound at zero; see Table
 316 2) for each model run, to ensure that emergent parameter differences arise from relations
 317 in the data and are not forced from priors. Choice of priors is informed through a com-
 318 bination of literature sources and empirical exploration of the data. The priors for the
 319 γ parameters are chosen so that the function Φ_I ranges roughly between 0 and 1 over
 320 the range of observed insolation. The prior for β is the most restrictive, and is chosen
 321 such that both slopes will fit into a tightly curved sigmoid. The south slope data set pre-
 322 dictably fits a tightly curved sigmoid even with an uninformative prior, but the north
 323 slope data set, appearing to be unconstrained by soil moisture, has the tendency to de-
 324 generate into a flat line (i.e., small β , arbitrary θ_0) if not constrained by the prior. The
 325 prior for θ_0 is chosen based on an empirically-informed guess at the critical soil mois-
 326 ture threshold that begins to constrain sap velocities. The priors for the D parameters
 327 are chosen such that Φ_{VPD} ranges roughly between 0 and VPD_{max} . The prior for ε is
 328 chosen to be of the correct magnitude to scale the other portions of the equation to a
 329 hypothetical maximum sap velocity. Table 2 shows the means and standard deviations
 330 of priors and posteriors for each parameter. The distributions of the parameters estimated
 331 for the north and south slopes, and their impact on sap velocities, are shown in Figures
 332 7 and 9.

Table 2: Priors for our MCMC parameterization, and the resulting posteriors. All runs began with identical priors. Posterior means and standard deviations are derived from five separate runs, each using a randomly selected 20% of datapoints.

MCMC parameters				
	Prior mean	Prior SD	Posterior mean	Posterior SD
South Slope Parameters:				
ε	6	60	900	26.0
D_0	3.0	1.0	0.380	1.88 E-2
D_{-1}	3.0	1.0	0.330	1.92 E-2
D_{-2}	3.0	1.0	0.223	9.61 E-3
β	160	6	163	2.32
θ_0	0.07	0.01	7.28 E-2	8.59 E-5
γ	6.0 E-4	2.0 E-4	6.83 E-7	6.81 E-7

γ_{-1}	6.0 E-4	2.0 E-4	8.30 E-4	2.89 E-6
γ_{-2}	6.0 E-4	2.0 E-4	1.20 E-6	1.20 E-6
North Slope Parameters:				
ε	6	60	779	30.5
D_0	3.0	1.0	0.216	1.42 E-2
D_{-1}	3.0	1.0	0.344	2.43 E-2
D_{-2}	3.0	1.0	0.801	3.02 E-2
β	160	8	163	5.94
θ_0	0.07	0.01	3.08 E-2	3.99 E-3
γ	6.0 E-4	2.0 E-4	4.30 E-4	1.00 E-5
γ_{-1}	6.0 E-4	2.0 E-4	6.08 E-4	1.43 E-5
γ_{-2}	6.0 E-4	2.0 E-4	5.05 E-4	1.76 E-5
Example Soil Moisture Experiment North Slope Parameters: Uniform +2%, Non-linear +5%				
ε	6	60	780	30.4
D_0	3.0	1.0	0.215	1.41 E-2
D_{-1}	3.0	1.0	0.344	2.42 E-2
D_{-2}	3.0	1.0	0.800	3.02 E-2
β	160	6	160	5.98
θ_0	0.07	0.01	6.94 E-2	9.62 E-3
γ	6.0 E-4	2.0 E-4	4.30 E-4	1.00 E-5
γ_{-1}	6.0 E-4	2.0 E-4	6.08 E-4	1.44 E-5
γ_{-2}	6.0 E-4	2.0 E-4	5.07 E-4	1.76 E-5

333 The resulting parameterizations for each slope show key differences in response to
334 environmental drivers. With the VPD parameters D_0 , D_{-1} and D_{-2} , a larger param-
335 eter value points to a greater sap velocity sensitivity to the variable (cf Equation 2). The
336 south slope has D_0 , D_{-1} and D_{-2} values of 0.380, 0.330, 0.223, respectively, suggesting
337 that south slope sap velocities are most sensitive to instantaneous VPD, but also to VPD
338 from 2 hours prior, though lagged VPD plays a slightly smaller role. The correspond-
339 ing values for the north slope are 0.216, 0.344 and 0.801, suggesting that on the north
340 slope VPD_{t-2} has the largest influence on sap velocities.

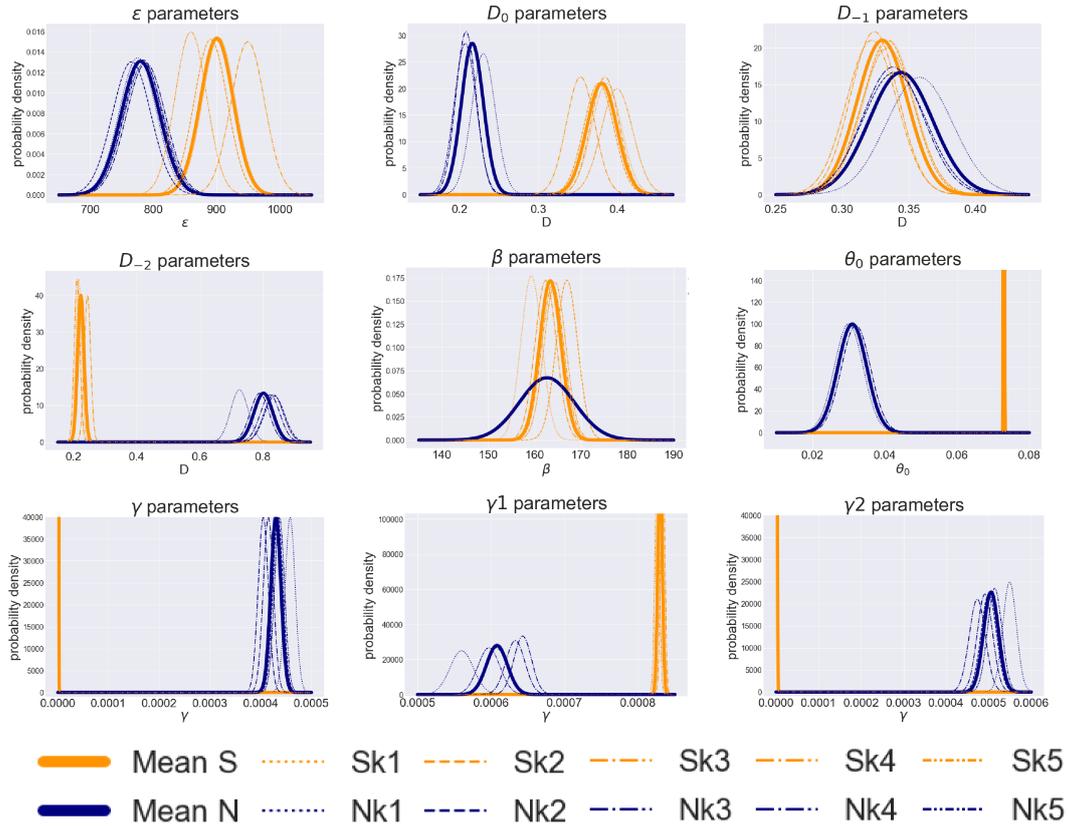


Figure 7. Posterior distributions of fitted model parameters for the north slope (orange) and south slope (blue). Results from each of the five randomly-selected training datasets are shown as dotted lines; and the mean as a bold line. Different subsets of data (k1-k5) used to parameterize the model result in very little difference in the fitted parameters, which is demonstrated in the narrow spread among the thin dotted lines.

341 The posterior estimates for all D parameters deviate from our prior D by roughly
 342 a factor of ten. This is compensated by the growth of ε away from our prior guess. Be-
 343 cause Φ_θ and Φ_I vary between 0 and 1, the scaling of modeled sap velocity depends on
 344 the product of Φ_{VPD} and ε , which is responsible for the inverse relation in their respec-
 345 tive deviations from our priors. Because smaller D parameters change the shape of Φ_{VPD}
 346 to a more curved shape, bending the function downward away from the $y = x$ line, and
 347 decreases the magnitude of the function overall, this relocation of modeled sap velocity
 348 magnitude away from Φ_{VPD} to ε implies that the effect of VPD on sap velocities seen
 349 in our observations is less linear, and “saturates” more quickly, than our prior param-
 350 eters allow. Based on the performance of the resulting models, we interpret that our pri-
 351 ors were broad enough to avoid unduly influencing the parameterization process, despite
 352 the strong deviation from prior to posterior.

353 For insolation, the γ_0 and γ_{-2} for the south slope are near zero, suggesting that
 354 sap velocities there respond mainly to insolation of the past hour (I_{t-1}). For the north
 355 slope, the results suggest that sap velocities are sensitive to contemporaneous insolation
 356 as well as insolation of the past two hours, as γ_0 , γ_{-1} and γ_{-2} have comparable values.

357 For soil moisture, β controls the slope of the sigmoid, and θ_0 controls the midpoint.
 358 β is similar between the two slopes, while θ_0 differs. The partial function Φ_θ (Figure 9
 359 panel b) shows that while soil moisture is a strongly limiting factor on south slope sap
 360 velocities after approximately 10% VWC, it does not cause any limitation for north slope
 361 sap velocities. Because soil moisture creates no constraint on sap velocities in the north
 362 slope model, there is less certainty in the exact parameter values, as seen in the larger
 363 spread of the north slope parameters compared to the south slope parameters (Figure
 364 7).

365 The lack of soil moisture observations on the north slope leaves uncertainty in the
 366 north slope sap velocity response to soil moisture. Our field experience suggests that north
 367 slope soils are less dry than the south slope, and while soil moisture is expected to de-
 368 cline through the dry summer, we do not have observations of its magnitude and rate
 369 of decline on the north slope. Therefore, we conducted several modeling experiments in
 370 which we artificially increased the soil moisture data stream used for the north slope pa-
 371 rameterization in both uniform and non-uniform ways: 1) Uniform +5%: we added a uni-
 372 form 5% increase to observed south-slope soil moisture; 2) Non-linear +5%: we adjusted

373 the rate of soil moisture decline to half of the observed rate, which amounted to a +5%
 374 difference in soil moisture by the end of the dry season; 3) Non-linear +7%: we adjusted
 375 the rate of soil moisture decline to one third of the observed rate, which amounted to
 376 a +7% difference in soil moisture by the end of the dry season; and lastly, 4) Uniform
 377 +2% and non-linear +5%: we added a uniform 2% increase to observed soil moisture,
 378 and then additionally adjusted the rate of soil moisture decline to half of the observed
 379 rate, which amounted to a +7% difference in soil moisture by the end of the dry season.
 380 We then re-ran the north slope MCMC parameterization process with these alternative
 381 soil moisture states. We found that between the standard and experimental runs, none
 382 of the final parameters changed substantively except θ_0 (Table 2). The changes in θ_0 ,
 383 in light of the co-occurring shift in hypothetical minimum soil moisture, do not under-
 384 mine the finding that soil moisture is not a limiting factor on the north slope. Put an-
 385 other way, changes to the representation of north slope soil moisture do not apprecia-
 386 bly change the shape of Φ_θ , but only shift it along the x-axis with changes in θ_0 (see Fig-
 387 ure 8). Thus, we conclude that, in our model, the sap velocities of the north slope are
 388 not constrained by soil moisture, and that this conclusion is not rooted in an imperfect
 389 soil moisture representation.

390 To compare the sensitivities of sap velocities on the two slopes to VPD and insola-
 391 tion, we computed mean diurnal cycles of VPD and insolation for July, and use the same
 392 mean cycles as inputs to Φ_{VPD} and Φ_I for each slope (cf Equation 2). Figure 9 shows
 393 the hysteresis loops in the sap velocity responses. For the same VPD diurnal cycle, the
 394 north slope model's Φ_{VPD} attributes more sap velocity amplitude variations to varia-
 395 tions in VPD than does the south slope model. This is visible in the greater functional
 396 range (plotted on the y-axis) of Φ_{VPD} over the same VPD range (x-axis). Also, at ev-
 397 ery value of VPD, the north slope model has a larger sap velocity response than the south
 398 slope model. This shows that the north slope model has both a higher baseline response
 399 to VPD as well as a higher proportional response to increases in VPD than the south
 400 slope model. The Φ_I functions show similar responsiveness to sunlight between the slopes,
 401 visible in the comparable functional range (y-axis) covered by Φ_I to the same insolation
 402 cycle. However, the south slope Φ_I has higher values over the range of observed sunlight.
 403 This implies that modeled sap velocity on the south slope has a higher baseline response
 404 to sunlight, although the two slopes show proportionally similar responses to increases
 405 in sunlight. Lastly, the south slope's soil moisture function shows that the south slope

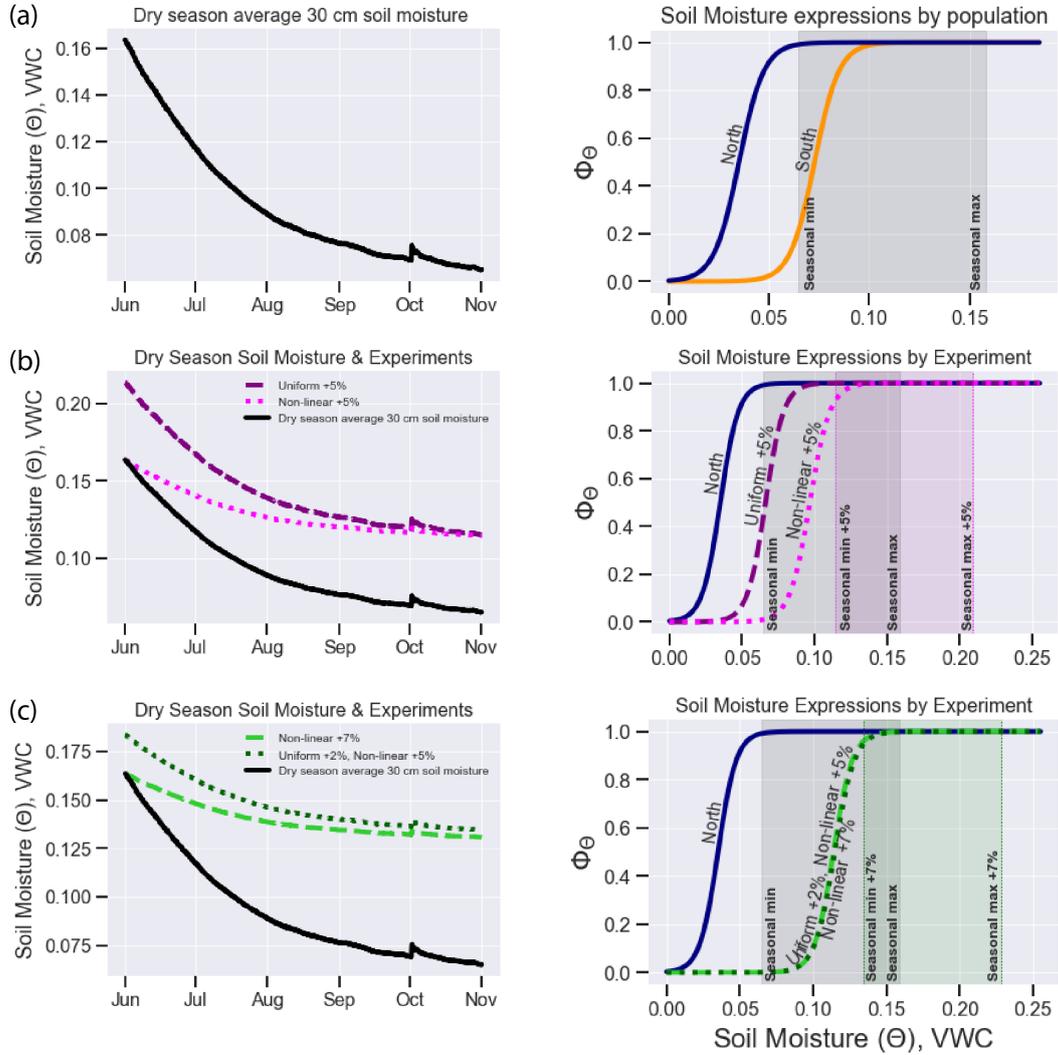


Figure 8. Experimental manipulations of north slope soil moisture time series reveal that under a range of hypothetical conditions, the MCMC parameters fitted for the north slope consistently indicate a lack of soil moisture constraint.

406 model uses soil moisture as a limiting factor on sap velocity while the north slope model
 407 does not, within the range of observed soil moisture over the whole season. Taken to-
 408 gether, the model results indicate population-level differences in response to environmen-
 409 tal drivers of transpiration. This is explored further in section 3.6.

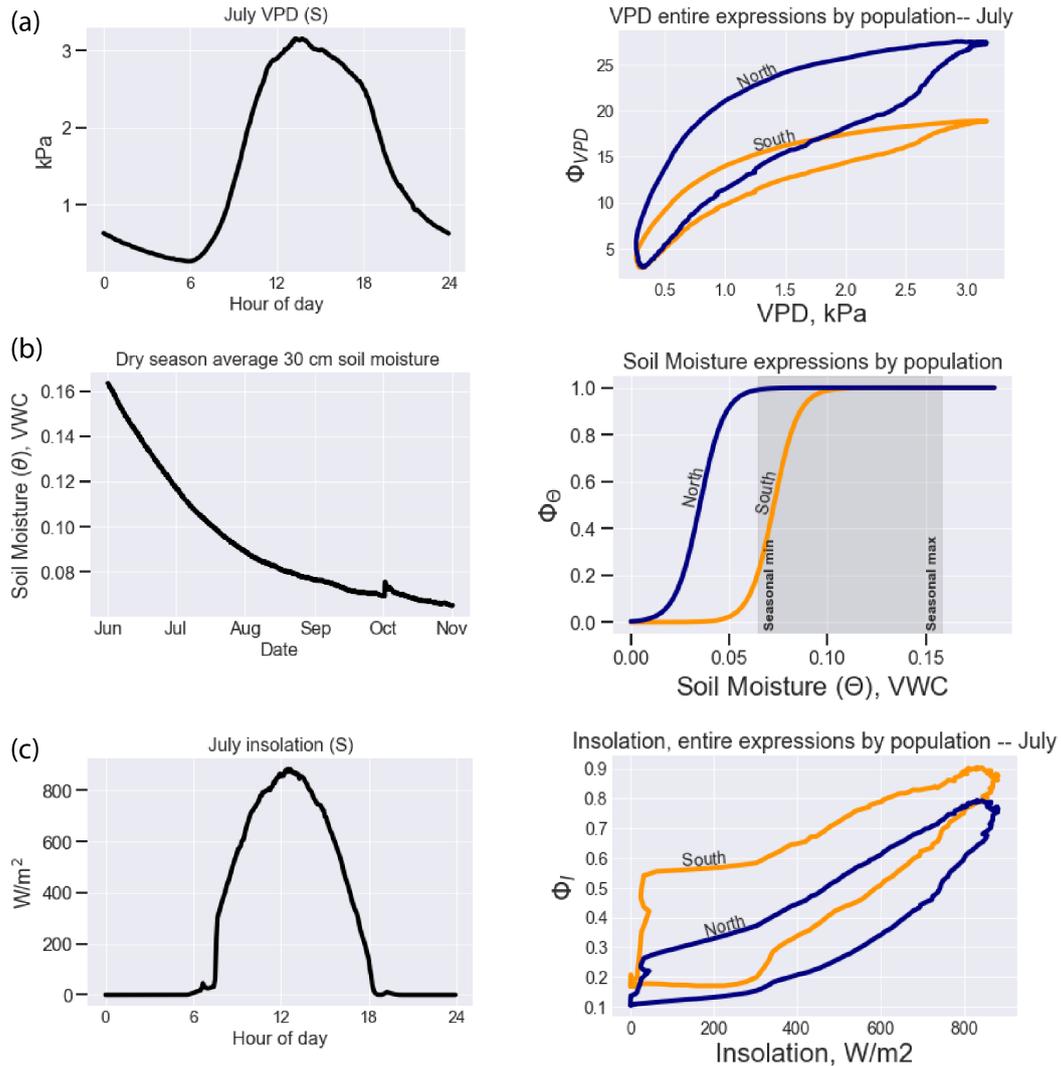


Figure 9. Partial expression plots of Equation 2 show differing sensitivity to environmental drivers among the two populations. The north slope model is more sensitive to VPD, and less sensitive to soil moisture and insolation, indicating that the trees on the north slope do not feel additional transpiration constraint from drying soils over the course of the dry season, beyond that imposed by the light limitation.

410 Because in our data preparation we excluded an outlier that substantially changed
411 the magnitude of the mean north slope sap velocity, we explored the impact of this out-
412 lier by repeating our MCMC analyses with the outlier included. Doing so led to some
413 slight changes in magnitude, but no ordinal differences, in the parameter differences found.
414 The largest differences were in Φ_{VPD} , with the outlier-inclusive average north slope sap
415 velocity even more responsive to VPD, but the conclusions regarding cross-slope differ-
416 ences in parameters are identical both with and without the outlier.

417 **3.4 Model performance**

418 With slope-specific parameters in combination with slope-specific microclimate data
419 streams, we computed model sap velocity data streams for north and south slopes. To
420 assess the performance of our models, we looked at four metrics: a) reproduction of the
421 dry season time series; b) reproduction of dry season time-integrated sap velocity; c) re-
422 production of dry season climatological sap velocity; and d) reproduction of dry season
423 climatological cross-slope differences in time-integrated sap velocities.

424 Each set of parameters was applied to its unique test data set, resulting in five sim-
425 ilar but separate estimates of the sap velocity time series. These estimates were then av-
426 eraged together to create our final modeled time series, which was the basis for the nRMSE
427 computed in the test of time series data reproduction (a, Figure 10) and the reproduc-
428 tion of time-integrated sap velocity (b, Figure 11). We also derived average parameter
429 means and standard deviations, which are reported in table 2 and were implemented in
430 our model runs which created our reproduction of dry season climatologies (c, Figure 12)
431 and cross-slope differences in time-integrated sap velocity (d, Figure 12). We opted for
432 presenting our results this way to adhere as closely as possible to the philosophy of keep-
433 ing our model tests free of any data that was used to derive parameters.

434 **3.5 Influence of parameters vs microclimate**

435 At the heart of our analysis is the question of whether cross-slope differences in sap
436 velocity are proportional to the cross-slope differences in microclimate, or whether population-
437 level differences in physiological function are also playing a role. Our parameter differ-
438 ences indicate population-level differences in physiological function, but as a way of more
439 intuitively visualizing the impact of parameter differences outside the influence of dis-

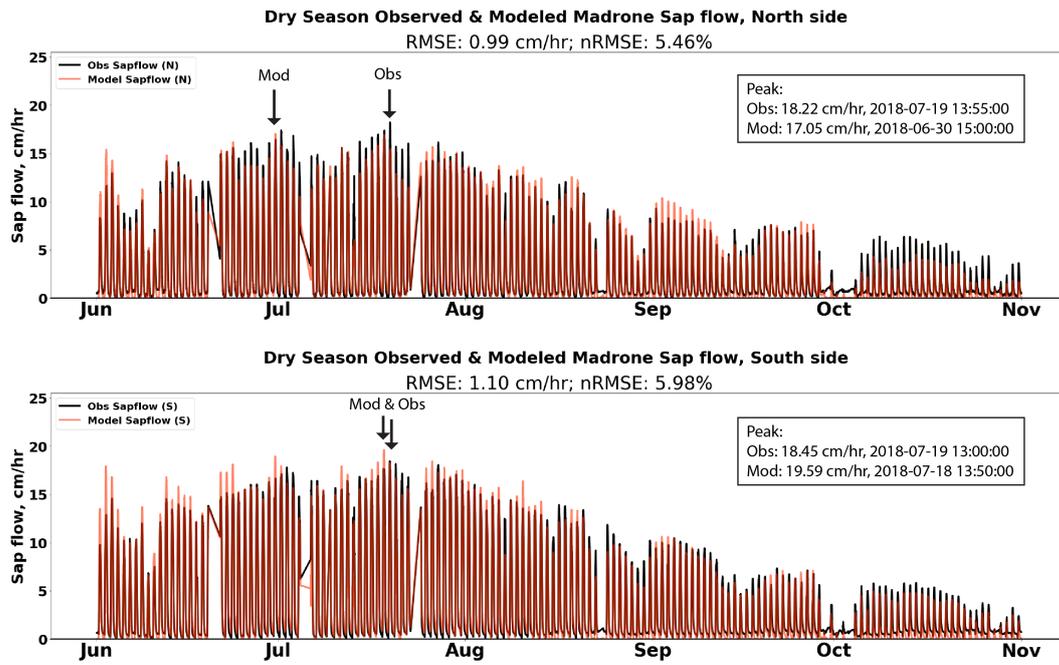


Figure 10. Performance assessment of the model reproduction of the dry season time series. Modeled sap velocity is in red, observations are in black. Model performance measured by nRMSE is similar for both slopes. The south slope model additionally comes close to accurately capturing the time period of seasonal peak sap velocity, while the north slope model is off by nearly a month. However, the month of October stands out as a period where the models systematically underestimate observations for both slopes. We consider reasons for this underestimation in section 3.7.

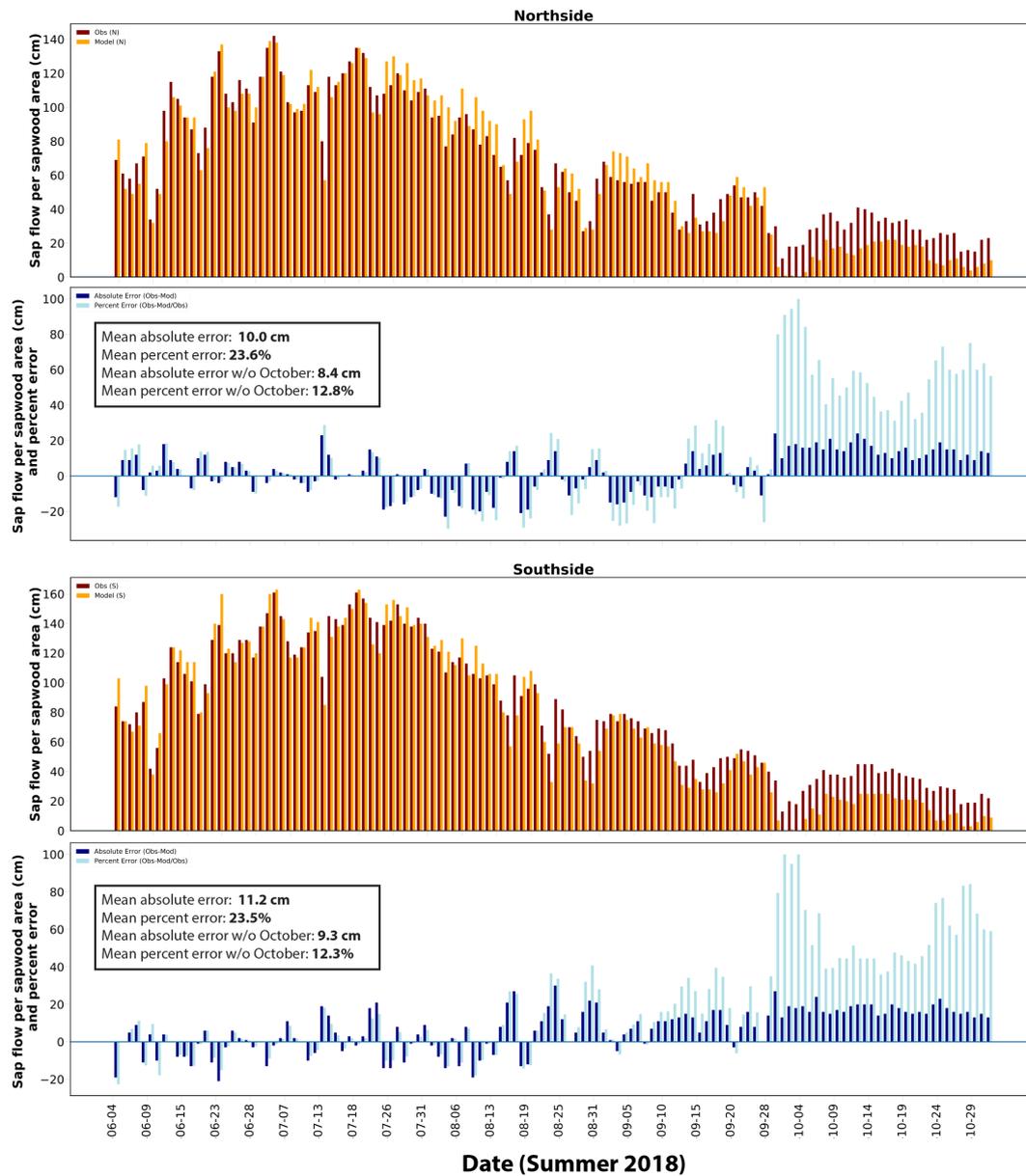


Figure 11. Daily integrals of modeled and observed sap velocities for each slope. The month of October is greatly underestimated due to seasonal shading of the light sensor positioned in the meadow, which is not representative of the tree environment. For the north slope, the model is able to capture 76% of dry season integrated sap velocity, and 87% of June–September integrated sap velocity. For the south slope, the performance is similar, with 76% of dry season integrated sap velocity and 88% of June–September integrated sap velocity represented.

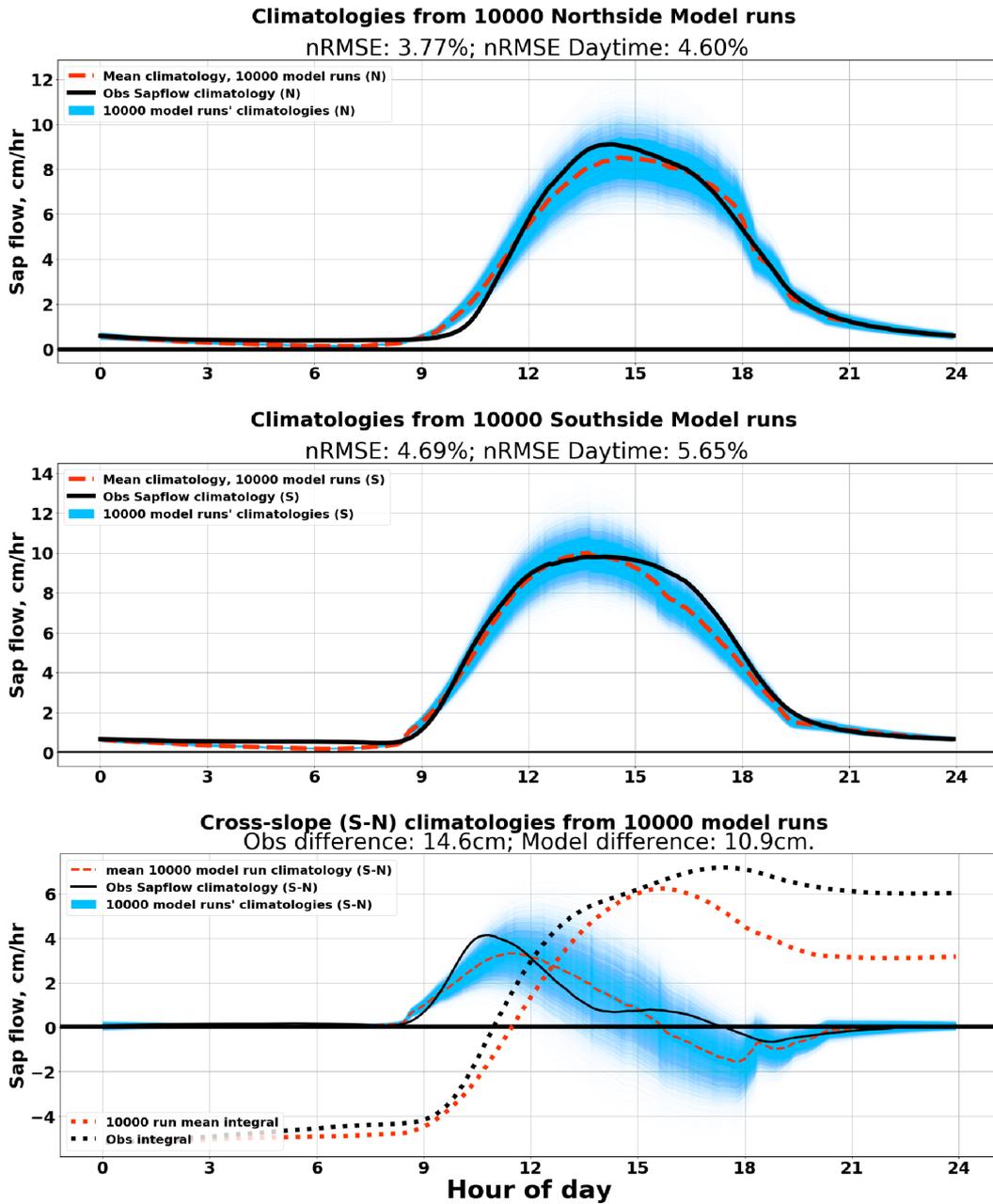


Figure 12. Performance assessment of models relative to the dry season average diurnal cycle. Dry season climatologies of 10,000 model runs are in pale blue, with the mean in red, and observed sap velocity in black. The spread among the 10,000 model runs is a visual indication of model uncertainty arising from spread in the parameter estimates. The normalized root mean square error (nRMSE) of the model comparison to observations is computed relative to the mean of the model runs, and is roughly 4% and 5% for the north and south slopes respectively (top two panels); if error is computed only over the active portion of the diurnal cycle (7am-10pm), this rises to 5% and 6% nRMSE for the north and south models respectively. The models are able to capture 75% of the observed difference in time-integrated sap velocity between the slopes (bottom panel).

440 parate microclimates, we put our model through a series of simple experiments in which
 441 we exchange some or all of the experienced microclimate between the slopes, and observe
 442 the response.

443 We see that the parameter differences lead to dissimilar responses when the mod-
 444 els are placed in the same microclimate. The north slope model substantially over-estimates
 445 observed sap velocity in the south slope microclimate (Figure 13 panel a), and the south
 446 slope model underestimates sap velocity in the north slope microclimate (Figure 13 panel
 447 b). Figure 13 (bottom four panels) further shows that while exchanging VPD environ-
 448 nment makes very little difference (Figure 13 panel c and d), exchanging the solar radi-
 449 ation environment makes a large difference (Figure 13 panel e and f), and artificially in-
 450 creasing soil moisture increases the sap velocities on the south slope but not the north
 451 slope (Figure 13 panel g and h).

452 The individual responses to environmental drivers, Φ_{VPD} , Φ_{θ} , and Φ_I (Figure 9)
 453 show that the over-estimation of the north slope model in the south slope microclimate
 454 is actually not associated with a stronger response to light from north slope trees, but
 455 instead with firstly a lack of moisture limitation on sap velocities, and secondly with a
 456 stronger response to VPD. Once the north slope model is freed from its light-limited en-
 457 vironment by using south slope insolation, the added vigor of its VPD response compared
 458 to the south slope model becomes clear.

459 **3.6 Interpretation of sap velocity model results**

460 The divergent parameterizations indicate different physiological responses to en-
 461 vironment between the two slopes, after controlling for inhabited microclimate. While
 462 none of the parameters in our model is a direct metric of a particular physiological prop-
 463 erty of the trees, we consider them to represent an aggregation of functional or “behav-
 464 ioral” differences, integrated across all mechanisms that influence sap velocity response
 465 to ambient environment, as in the interpretation of the formulas in Jarvis (1976) and Lohammar
 466 et al. (1980). We acknowledge that extrapolations of disparate physiological properties
 467 between the two tree populations from the differences in the models’ statistically-indicated
 468 controls on sap velocity can only be speculative, but we explore these speculations to be-
 469 gin a discussion about the degree and kind of acclimation that may exist between trees

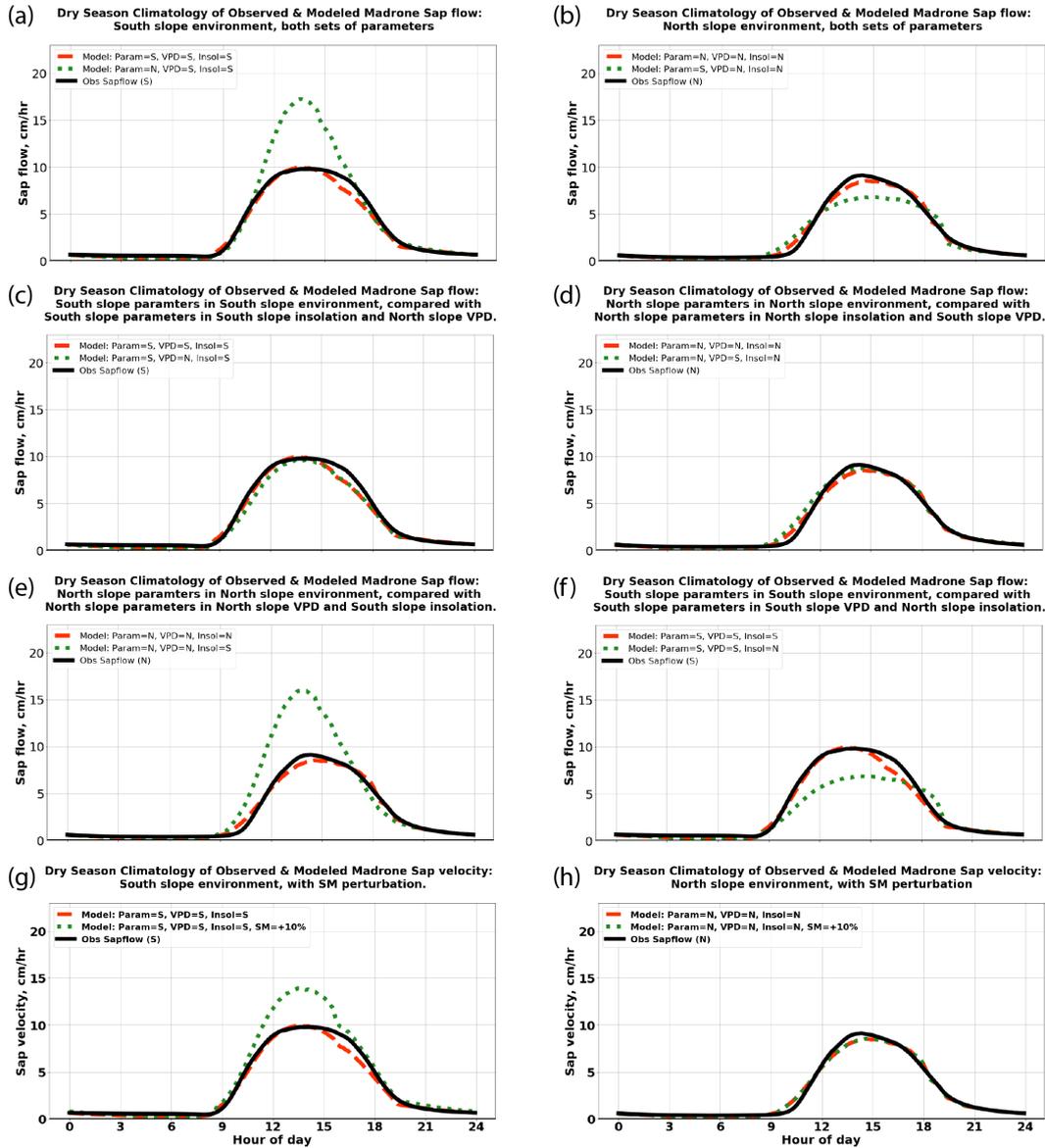


Figure 13. Using the slope-specific models in the opposite slope’s microclimate shows the differences in response generated by the two parameterizations to the same microclimate. Panels (a) and (b) show that the north slope model in a south slope microclimate has a more vigorous response than both the south slope model and the observations in the same microclimate, while conversely the south slope model underestimates both the north slope model and observations in the north slope microclimate. Panels (c) and (d) show that while exchanging only the VPD portion of the microclimate between the two slopes makes very little difference to the sap velocities estimated by each model, exchanging the solar radiation environment (panels (e) and (f)) makes a large difference. Panels (g) and (h) show that increased soil moisture increases sap velocities in the south slope model, but not in the north slope model. The estimation by the north slope model of faster sap velocities than the south slope model in the south slope microclimate is due in roughly equal measure to a lack of soil moisture constraint and a more vigorous response to VPD. The radiation exchange produces this result because it frees the north slope model from serious light limitation.

470 on differing slope aspects. We will consider the differences in each partial function Φ in
471 turn.

472 **VPD:** The parameterizations indicate that north slope madrones are more sensi-
473 tive to shifts in VPD than their south slope counterparts (Figure 9). Our intuition about
474 why this is the case is based on two population-level differences that we did not assess
475 in the field, but can presume are present to some degree. Firstly, because of the stark
476 differences in light environment between the two slopes of the hill, we expect that the
477 relative abundances of sun-adapted and shade-adapted leaves differ in the overall com-
478 position of the madrone canopies representing each slope's population, with the north
479 slope presumed to have more shade-adapted leaves than the south slope. There is a sub-
480 stantial body of literature describing the physiological differences between sun-adapted
481 and shade-adapted leaves (Boardman, 1977; Larcher, 1995), but because these differences
482 are usually described in terms of carbon assimilation rather than water use, directly re-
483 lating them to differences in transpiration dynamics between the two populations is chal-
484 lenging. To do this we would need information about relative water use efficiencies, which
485 leads to the second likely difference between the populations: differing canopy architec-
486 tures along the lines of what is typical of sun-rich vs. shade-rich populations likely lead
487 to differing light exposure regimes between the two populations. If, for instance, the pro-
488 portion of leaf area accessing direct sunlight as opposed to indirect light, or even sun-
489 flecks, is less on the north slope, the north slope transpiration dynamics could be expected
490 to be based on lower water use efficiencies, due to differing strategies of stomatal reg-
491 ulation (A. Knapp & Smith, 1987; Young & Smith, 1979). Woody vegetation using sun-
492 flecks as a light source have been shown to leave stomata open during moments of low
493 light in order to assimilate the most carbon when leaves are illuminated (Stokes et al.,
494 2010; Pearcy, 1998; A. K. Knapp & Smith, 1990). Thus, such differences in canopy ar-
495 chitecture could result in tighter coupling between sap velocity and VPD in north slope
496 canopies, due to the likely prevalence of exposed stomata on leaves that do not contin-
497 uously experience the top-of-canopy sunlight dynamics. While the impact of differing
498 proportions of sun-adapted vs shade-adapted leaves is obscured by an inability to resolve
499 the exact mechanisms involved, we do suspect that this also plays a role in shaping the
500 differences we observe. We thus speculate that, due to both lower light levels and dis-
501 rupted exposure to what light there is, north slope trees are comparatively profligate wa-

502 ter users even in the midst of the dry summer, preferring to maximize carbon assimilation rather than conserve water.

504 **Soil Moisture:** The parameterizations indicate that north slope madrones are not water limited over the dry season. In our model, artificially increasing soil moisture for the north slope (i.e., 'watering' the trees) does not lead to increased sap velocity (see Figure 13, panel h). Nor does artificially increasing the soil moisture availability in the data feeding into the MCMC algorithm alter the resulting north slope parameters in meaningful ways (Figure 8). We hypothesize that this is because there is greater plant-available moisture on the north slope. The north slope has a deep water table (20 m) and a thick layer of weathered bedrock, and it has been shown to store around 30% of subsurface moisture in the vadose zone (Rempe & Dietrich, 2018; Vrettas & Fung, 2017). While there is evidence that trees on both slopes use this deep 'rock moisture' in the vadose zone for part of the dry season (Oshun, 2016), we have less data about the subsurface structure on the south slope, and data on respective rooting depths between the two populations is inconclusive (Oshun, 2016). However, the stronger sunlight on the south slope leads to higher evaporation, and the sap velocity data shows that the south slope trees cumulatively extract more water. Even if the subsurface structures and rooting depths were similar, there would be differences in water availability due to different rates of evaporation and vegetation extraction. Also, the north slope madrones grow in closer proximity to Douglas firs, which are known to exhibit hydraulic redistribution (Brooks et al., 2002, 2006), although we have no direct observations of this at our site. This could be further contributing to increased moisture availability in the north slope rooting zone.

524 **Insolation:** The parameterizations indicate that south slope madrones have a slightly greater overall sensitivity to insolation, and their overall insolation response function is shifted upwards from the north slope function (cf. Figure 9 panel c). The slightly higher sensitivity in the insolation response on the south slope could be explained by factors similar to those influencing VPD response, namely a higher fraction of leaves exposed to direct light, leading to stomatal regulation strategies that are more in phase with changes in light than those on the north slope. The upwards shift in the magnitude of the response could be explained by higher proportions of sun-adapted leaves in the south slope trees, which, due to their enhanced stomatal area (Boardman, 1977), could have higher rates of water use at every level of light intensity. In sum, we interpret that the north slope trees appear to have a larger area of stomata exposed under certain combinations of con-

535 ditions (lower light, higher VPD) while the south slope trees appear to have a larger area
536 of stomata exposed under different combinations of conditions (higher light, and lower
537 VPD).

538 **3.7 Examination of residuals & limitations of analysis**

539 Because the month of October stands out as a period of systematic error in figures
540 10 and 11, we focus first on the model errors in October, and then consider the remain-
541 der of the season separately. Firstly, the representation in a rough terrain of sunlight on
542 the slopes scaled from a flat meadow observation becomes less accurate as the solar arc
543 becomes lower in the sky (i.e., closer to the winter solstice), as shading from neighbor-
544 ing hills, especially in early morning and late afternoon, is site-specific. In particular, we
545 are aware that the hill-shading received by our meadow-based light sensor begins sub-
546 stantially earlier in the day, in the late dry season, than the shading experienced by the
547 trees under observation, which are positioned at a higher altitude. Secondly, we note that
548 October began with a rain storm which was the only substantive moisture input dur-
549 ing the period under observation. This rain event likely altered the relationship between
550 surface and deep moisture reserves compared to the rest of the dry season, confounding
551 the representativeness of our θ data stream for the month of October.

552 Apart from the month of October, the errors seem randomly distributed. We looked
553 for, but did not find, correlations with wind speeds both in the time series and integrated
554 over days. However, we can identify loose correlations of the residuals with daily inte-
555 grated VPD. This suggests that there is a slight bias in our model towards overestimat-
556 ing sap velocity on exceptionally dry days, and underestimating it on more humid days.

557 Additionally, the model does not include variations of leaf area index through the
558 summer. Madrones are evergreen, with leaf lifetimes of approximately 14 months, so that
559 there are both old and new leaves between May and July (Ackerly, 2004). Studies have
560 shown that the old leaves often contain less nitrogen than the new leaves on Pacific madrone
561 (Adams, 1999), and it is thus reasonable to suppose that there are likely physiological
562 differences in photosynthetic capacity, water use efficiency, or both between young and
563 old leaves (e.g., as seen in Field et al. (1983)), which could be producing an effect not
564 accounted for by our model expression.

565 Lastly, we acknowledge that our field site is small and the microclimates represented
566 may not represent the extent of microclimatic variation across all north- and south-facing
567 slopes in the broader ecosystem.

568 4 Conclusions

569 It is known that different species of vegetation exhibit a wide range of responses
570 to ambient environment, which is pertinent knowledge to capturing several land-atmosphere
571 biogeochemical cycles. However, we show that even within a single species, substantial
572 variation can exist in the functional role that species plays in these biogeochemical cy-
573 cles, based on acclimation to inhabited microclimate. In particular, 1) There are sub-
574 stantive and quantifiable microclimate differences between slopes; 2) There are substan-
575 tive sap velocity differences between tree populations inhabiting the north and south slopes,
576 and these indicate substantive transpiration differences between slopes; 3) A sap veloc-
577 ity model parameterized only with ambient microclimatic conditions captures sap ve-
578 locity for our site well; and 4) The parameter differences in our sap velocity model rep-
579 resent different responses to ambient environment, and imply functional differences in
580 tree physiology, between the two populations. This is suggestive of acclimation to inhab-
581 ited microclimate.

582 Our results strongly hint at acclimation in leaf and canopy structure and differing
583 stomatal regulation strategies (as in Wang et al. (2020)) between the two populations
584 of trees. We suggest that north slope trees, limited by sunlight rather than soil moisture,
585 have developed their canopies and stomatal regulation strategies to optimize for light
586 capture while spending water more profligately than their south slope counterparts. Through
587 this optimization, the north slope may be presumed to have different rates of carbon fix-
588 ation per area of leaf and unit water transpired. This has implications for understand-
589 ing water and carbon fluxes from forests today, and also for anticipating population-level
590 profiles of vulnerability to future conditions.

591 Climate change is expected to alter current regimes of temperature (increase, Romero-
592 Lankao et al. (2014)), VPD (increase, Grossiord et al. (2020)), precipitation (slight in-
593 crease, although with decreased water availability, Romero-Lankao et al. (2014); Zamuda
594 et al. (2013)), and cloudiness (unknown direction of change, Zamuda et al. (2013)) over
595 California. All three of these changes directly impact the environmental covariates in this

596 model. The model results suggest that the south slope trees become severely water lim-
597 ited by the end of the dry season, and thus further water limitation may either limit their
598 growing season, or create conditions that limit their performance. In contrast, on the north
599 slope, the trees do not appear to be water limited. However, it is unclear whether this
600 makes them more resilient to a hotter or dryer future. In our interpretation of param-
601 eter differences, north slope trees likely rely on much higher rates of water usage in or-
602 der to assimilate carbon. If water becomes a limiting resource in the north-slope micro-
603 climate in the future, and VPD levels continue to increase, these north slope trees may
604 be closer to crisis, choosing between cavitation or carbon starvation, than the south slope
605 trees would be under a more limited growing season (Wang et al., 2020; Grossiord et al.,
606 2020).

607 More measurements could help elucidate specific mechanisms underlying the pa-
608 rameter differences we have found. Direct measurements of photosynthesis/gas exchange
609 on the leaf level, or chemical analyses of leaf tissues including C:N ratios or isotopic com-
610 position, could help shed light on physiological differences in leaves between populations.
611 These measurements were not practical in our study given our lack of canopy access, but
612 more measurements on these trees, or parallel investigations in a greenhouse, could be
613 useful as a future study.

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626 **References**

- 627 Ackerly, D. (2004). Functional strategies of chaparral shrubs in relation to seasonal
628 water deficit and disturbance. *Ecological Monographs*, *74*(1), 25–44.
- 629 Adams, A. (1999). *Arbutus menziesii* and soils of the puget trough, washington. In
630 A. Adams & C. W. Hamilton (Eds.), *The decline of pacific madrone (arbutus*
631 *menziesii pursh): Current theory and research directions. proceedings of the*
632 *april 28, 1995 symposium held at the center for urban horticulture university*
633 *of washington seattle, washington subsequent research papers* (p. 139). Seat-
634 tle: Save Magnolia’s Madrones, Center for Urban Horticulture, Ecosystems
635 Database Development Research.
- 636 Amitrano, C., Arena, C., Roupahel, Y., De Pascale, S., & De Micco, V. (2019).
637 Vapour pressure deficit: The hidden driver behind plant morphofunctional
638 traits in controlled environments. *Annals of Applied Biology*, *175*(3), 313–325.
- 639 Betancourt, M. (2017). A conceptual introduction to hamiltonian monte carlo. *arXiv*
640 *preprint arXiv:1701.02434*.
- 641 Boardman, N. K. (1977). Comparative photosynthesis of sun and shade plants. *An-*
642 *nual review of plant physiology*, *28*(1), 355–377.
- 643 Bolton, D. (1980). The computation of equivalent potential temperature. *Monthly*
644 *weather review*, *108*(7), 1046–1053.
- 645 Brooks, J. R., Meinzer, F. C., Coulombe, R., & Gregg, J. (2002). Hydraulic re-
646 distribution of soil water during summer drought in two contrasting pacific
647 northwest coniferous forests. *Tree physiology*, *22*(15-16), 1107–1117.
- 648 Brooks, J. R., Meinzer, F. C., Warren, J. M., Domec, J.-C., & Coulombe, R. (2006).
649 Hydraulic redistribution in a douglas-fir forest: lessons from system manipula-
650 tions. *Plant, Cell & Environment*, *29*(1), 138–150.
- 651 Davis, T. W., Kuo, C.-M., Liang, X., & Yu, P.-S. (2012). Sap flow sensors: construc-
652 tion, quality control and comparison. *Sensors*, *12*(1), 954–971.
- 653 Duffie, J. A., & Beckman, W. A. (1991). *Solar engineering of thermal processes john*
654 *wiley & sons*. John Wiley & Sons.
- 655 Feddes, R., Kowalik, P., & Zaradny, H. (1978). *Simulation of field water use and*
656 *crop yield john wiley and sons*. New York, NY: John Wiley and Sons.
- 657 Field, C., Merino, J., & Mooney, H. (1983). Compromises between water-use ef-
658 ficiency and nitrogen-use efficiency in five species of california evergreens. *Oe-*

- 659 *cologia*, 60(3), 384–389.
- 660 Gimenez, B. O., Jardine, K. J., Higuchi, N., Negrón-Juárez, R. I., Sampaio-Filho,
661 I. d. J., Cobello, L. O., ... Chambers, J. Q. (2019). Species-specific shifts
662 in diurnal sap velocity dynamics and hysteretic behavior of ecophysiological
663 variables during the 2015–2016 el niño event in the amazon forest. *Frontiers*
664 *in Plant Science*, 10, 830. Retrieved from [https://www.frontiersin.org/](https://www.frontiersin.org/article/10.3389/fpls.2019.00830)
665 [article/10.3389/fpls.2019.00830](https://www.frontiersin.org/article/10.3389/fpls.2019.00830) doi: 10.3389/fpls.2019.00830
- 666 Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R.
667 (2017). Google earth engine: Planetary-scale geospatial analysis for everyone.
668 *Remote Sensing of Environment*. Retrieved from [https://doi.org/10.1016/](https://doi.org/10.1016/j.rse.2017.06.031)
669 [j.rse.2017.06.031](https://doi.org/10.1016/j.rse.2017.06.031) doi: 10.1016/j.rse.2017.06.031
- 670 Granier, A. (1985). Une nouvelle méthode pour la mesure du flux de sève brute dans
671 le tronc des arbres. In *Annales des sciences forestières* (Vol. 42, pp. 193–200).
- 672 Granier, A. (1987). Evaluation of transpiration in a douglas-fir stand by means of
673 sap flow measurements. *Tree physiology*, 3(4), 309–320.
- 674 Grossiord, C., Buckley, T. N., Cernusak, L. A., Novick, K. A., Poulter, B., Sieg-
675 wolf, R. T. W., ... McDowell, N. G. (2020). Plant responses to rising vapor
676 pressure deficit. *New Phytologist*, 226(6), 1550–1566.
- 677 Harrison, J. L., Reinmann, A. B., Maloney, A. S., Phillips, N., Juice, S. M., Webster,
678 A. J., & Templer, P. H. (2020). Transpiration of dominant tree species varies
679 in response to projected changes in climate: Implications for composition and
680 water balance of temperate forest ecosystems. *Ecosystems*, 1–16.
- 681 Hoffman, M. D., & Gelman, A. (2014). The no-u-turn sampler: adaptively set-
682 ting path lengths in hamiltonian monte carlo. *Journal of Machine Learning*
683 *Research*, 15(1), 1593–1623.
- 684 Jarvis, P. G. (1976). The interpretation of the variations in leaf water potential and
685 stomatal conductance found in canopies in the field. *Philosophical Transac-*
686 *tions of the Royal Society of London. Series B, Biological Sciences*, 273(927),
687 593–610. Retrieved from <http://www.jstor.org/stable/2417554>
- 688 Jasechko, S., Sharp, Z. D., Gibson, J. J., Birks, S. J., Yi, Y., & Fawcett, P. J.
689 (2013). Terrestrial water fluxes dominated by transpiration. *Nature*,
690 496(7445), 347–350.
- 691 Knapp, A., & Smith, W. (1987). Stomatal and photosynthetic responses during

- 692 sun/shade transitions in subalpine plants: influence on water use efficiency.
693 *Oecologia*, 74(1), 62–67.
- 694 Knapp, A. K., & Smith, W. K. (1990). Stomatal and photosynthetic responses to
695 variable sunlight. *Physiologia Plantarum*, 78(1), 160–165.
- 696 Larcher, W. (1995). *Physiological plant ecology, 3rd edition*. Springer-Verlag.
- 697 Lee, J.-H., Biging, G. S., & Fisher, J. B. (2016). An individual tree-based automated
698 registration of aerial images to lidar data in a forested area. *Photogrammetric*
699 *Engineering Remote Sensing*, 82(9).
- 700 Link, P., Simonin, K., Maness, H., Oshun, J., Dawson, T., & Fung, I. (2014). Species
701 differences in the seasonality of evergreen tree transpiration in a mediterranean
702 climate: Analysis of multiyear, half-hourly sap flow observations. *Water Re-*
703 *sources Research*, 50(3), 1869–1894.
- 704 Link, P. A. (2015). *Forests, water, and the atmosphere in northern california:*
705 *Insights from sap-flow data analysis and numerical atmospheric model simula-*
706 *tions* (Unpublished doctoral dissertation). UC Berkeley.
- 707 Lohammar, T., Larsson, S., Linder, S., & Falk, S. O. (1980). Fast: Simulation mod-
708 els of gaseous exchange in scots pine. *Ecological Bulletins*(32), 505–523. Re-
709 trieved from <http://www.jstor.org/stable/20112831>
- 710 Mencuccini, M., Manzoni, S., & Christoffersen, B. (2019). Modelling water fluxes in
711 plants: from tissues to biosphere. *New Phytologist*, 222(3), 1207–1222.
- 712 Oliveras, I., & Llorens, P. (2001). Medium-term sap flux monitoring in a scots pine
713 stand: analysis of the operability of the heat dissipation method for hydrologi-
714 cal purposes. *Tree Physiology*, 21(7), 473–480.
- 715 Oshun, J. (2016). *The isotopic evolution of a raindrop through the critical zone* (Un-
716 published doctoral dissertation). UC Berkeley.
- 717 Oshun, J., Dietrich, W. E., Dawson, T. E., & Fung, I. (2016). Dynamic, structured
718 heterogeneity of water isotopes inside hillslopes. *Water Resources Research*,
719 52(1), 164–189.
- 720 Pearcy, R. W. (1998). Acclimation to sun and shade. In A. S. Raghavendra (Ed.),
721 *Photosynthesis: A comprehensive treatise* (p. 250-263). Cambridge: Cambridge
722 University Press.
- 723 Rempe, D. M., & Dietrich, W. E. (2018). Direct observations of rock moisture,
724 a hidden component of the hydrologic cycle. *Proceedings of the National*

- 725 *Academy of Sciences*, 115(11), 2664–2669.
- 726 Romero-Lankao, P., Smith, J., Davidson, D., Diffenbaugh, N., Kinney,
727 P., Kirshen, P., . . . Villers Ruiz, L. (2014). North america. In
728 C. F. D. D. M. M. K. M. T. B. M. C. K. E. Y. E. R. G. B. G. E. K. A. L. S. M. P. M. Bar-
729 ros V.R. & L.L.White (Eds.), *Climate change 2014: Impacts, adaptation, and*
730 *vulnerability. part b: Regional aspects.* (p. 1439-1498). Cambridge, United
731 Kingdom and New York, NY, USA: Cambridge University Press.
- 732 Salvatier, J., Wiecki, T. V., & Fonnesbeck, C. (2016). Probabilistic programming in
733 python using pymc3. *PeerJ Computer Science*, 2, e55.
- 734 Stafford, B. (2018, September). *pysolar*. Zenodo. Retrieved from [https://doi.org/](https://doi.org/10.5281/zenodo.1461066)
735 [10.5281/zenodo.1461066](https://doi.org/10.5281/zenodo.1461066) doi: 10.5281/zenodo.1461066
- 736 Stokes, V. J., Morecroft, M. D., & Morison, J. I. (2010). Comparison of leaf water
737 use efficiency of oak and sycamore in the canopy over two growing seasons.
738 *Trees*, 24(2), 297–306.
- 739 Sun, H., Aubrey, D. P., & Teskey, R. O. (2012). A simple calibration improved the
740 accuracy of the thermal dissipation technique for sap flow measurements in
741 juvenile trees of six species. *Trees*, 26(2), 631–640.
- 742 USDA. (2008). *CALVEG zones and alliances: vegetation descriptions* (Tech.
743 Rep.). Retrieved from [http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/](http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev3_046448.pdf)
744 [fsbdev3_046448.pdf](http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev3_046448.pdf)
- 745 Vrettas, M. D., & Fung, I. Y. (2017). Sensitivity of transpiration to subsurface prop-
746 erties: Exploration with a 1-d model. *Journal of Advances in Modeling Earth*
747 *Systems*, 9(2), 1030–1045.
- 748 Wang, Y., Sperry, J. S., Anderegg, W. R., Venturas, M. D., & Trugman, A. T.
749 (2020). A theoretical and empirical assessment of stomatal optimization mod-
750 eling. *New Phytologist*.
- 751 Ward, E. J., Domec, J.-C., King, J., Sun, G., McNulty, S., & Noormets, A. (2017).
752 Tracc: an open source software for processing sap flux data from thermal dissi-
753 pation probes. *Trees*, 31(5), 1737–1742.
- 754 Waring, R. H., & Landsberg, J. J. (2011, 03). Generalizing plant–water relations
755 to landscapes. *Journal of Plant Ecology*, 4(1-2), 101-113. Retrieved from
756 <https://doi.org/10.1093/jpe/rtq041> doi: 10.1093/jpe/rtq041
- 757 Young, D., & Smith, W. (1979). Influence of sunflecks on the temperature and water

- 758 relations of two subalpine understory congeners. *Oecologia*, *43*(2), 195–205.
- 759 Zamuda, C., Mignone, B., Bilello, D., Hallett, K., Lee, C., Macknick, J., . . . Stein-
760 berg, D. (2013). *Us energy sector vulnerabilities to climate change and extreme*
761 *weather* (Tech. Rep.). Department of Energy Washington DC.
- 762 Zhang, Q., Manzoni, S., Katul, G., Porporato, A., & Yang, D. (2014). The hys-
763 teretic evapotranspiration—vapor pressure deficit relation. *Journal of Geo-*
764 *physical Research: Biogeosciences*, *119*(2), 125-140. Retrieved from [https://](https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1002/2013JG002484)
765 agupubs.onlinelibrary.wiley.com/doi/abs/10.1002/2013JG002484 doi:
766 10.1002/2013JG002484