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Teague, Macall

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Growth and functional responses to precipitation in the desert phreatophyte *Sarcobatus vermiculatus*  
following consecutive years of drought

By

MACALL TEAGUE  
THESIS

Submitted in partial satisfaction of the requirements for the degree of

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in

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DAVIS

Approved:

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Troy Magney, Chair

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Rebecca Hernandez

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Michael Aspinwall

Committee in Charge

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## ABSTRACT

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Sand motion and dust emissions in arid environments contribute to increased amounts of fine particulate matter suspended in the atmosphere, with possible negative consequences for human health at the local and regional scale. Prior to implementation of dust control measures in 2002, dust emissions from Owens (dry) Lake, California were the single largest source of fine aerosol particulate matter with a diameter less than 10  $\mu\text{m}$  ( $\text{PM}_{10}$ ) in the United States. *Sarcobatus vermiculatus*, a deep-rooted woody phreatophyte shrub, stabilizes the dune system surrounding Owens Lake and is highly effective at reducing sand motion and trapping wind-blown dust during high-wind events. Declines in *S. vermiculatus* growth or health due to drought or other disturbances that reduce resource availability could contribute to destabilization of the dune system and greater likelihood of erosion and poor air quality. Nonetheless, relationships between *S. vermiculatus* health and function and resource availability are not well understood in the Owens Lake vegetated dune system. The purpose of this study was to investigate the effects of surface water inputs (precipitation, runoff) on the growth and function of *S. vermiculatus* after consecutive years of drought. The southwestern United States has been in the grips of a megadrought since 2000, with 2021 marking an exceptionally dry year. As surface conditions become increasingly dry, many plants invest in deeper roots for accessing water, assuming adequate carbon reserves are available for root growth. However, previous studies in *S. vermiculatus* have demonstrated strong co-limitation of plant growth by water and nutrients (which typically arrive from surface inputs), such that the species might maintain a mostly shallow root system to capture pulses of water and nutrients. Though, a complete shift in root distributions for *S. vermiculatus* is unlikely due to the presence and availability of regional shallow groundwater. To understand the vertical distribution of *S. vermiculatus* roots we collected soil cores across eight dune locations (depth range 1.8 to 7.6 m) and extracted roots at intervals of 30 and 45 cm. To understand spatiotemporal dynamics in soil moisture, especially in relation to surface water inputs, we carried out monthly neutron probe readings over 13 months across the same dune locations, with

readings occurring at the same depth intervals as root sampling. Neutron probe data were converted to volumetric water content (VWC) using calibration equations. To understand spatiotemporal dynamics in shrub function, in relation to key environmental drivers, we collected predawn and midday stem xylem water potential ( $\Psi$ ), predawn and midday chlorophyll fluorescence ( $F_v/F_m$ ,  $\Phi_{PSII}$ ) and midday leaf gas-exchange (net photosynthesis [ $A_{net}$ ], stomatal conductance to water vapor [ $g_s$ ]) on 48 shrubs spread across eight dune locations (6 per dune location) at six timepoints. Fortuitously, our data collection spanned markedly different environmental conditions, capturing both the tail end of a multi-year drought and above-average summer precipitation. Across locations and timepoints, we found that VWC increased following precipitation and runoff events and VWC in the top 0.9 m of soil was positively correlated ( $R^2 = 0.76$ ,  $p < 0.0001$ ) with predawn stem water potential ( $\Psi_{pd}$ ). This indicated that shrubs respond to and utilize surface soil moisture even after periods of prolonged drought. Increased  $\Psi_{pd}$  was associated with higher midday  $A_{net}$ ,  $g_s$ , and chlorophyll fluorescence, though leaf temperature and vapor pressure deficit (VPD) were the most important drivers of  $A_{net}$  regardless of  $\Psi_{pd}$ . Additionally, following a significant late summer rain event in September 2022, shrubs produced substantial new growth. This new growth and combined with increased C fixation could increase C availability for growth and reproduction leading into the next growing season. Collectively, our data suggest that surface water is a key resource for *S. vermiculatus* and, although shrubs access deep soil moisture and groundwater, precipitation events seem to be a key driver in their growth and function.

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# 1 INTRODUCTION

Plant species differ in their water-use strategies, including considerable variation in the utilization of summer precipitation by perennial plants in arid ecosystems (Williams and Ehleringer 2001; Snyder et al. 2004; Kray et al. 2012). These differences are driven primarily by climate and regional soil properties (Williams and Ehleringer 2001; Chimner and Cooper 2004), root morphology and root depth distributions (Schenk and Jackson 2002), and various physiological adaptations evolved to withstand water stress (Hacke et al. 2000). There is limited knowledge regarding the effects of precipitation on the desert phreatophytic shrub *Sarcobatus vermiculatus* (Hook.) Torrey (Chenopodiaceae; common name black greasewood) found growing throughout the Great Basin, United States (Romo and Haferkamp 1989; Snyder et al. 2004; Kray et al. 2012). In the context of a changing climate, the Great Basin is expected to experience increased temperature, more widely spaced precipitation events, and more intense and long-lasting drought events (Snyder et al. 2019). Here, we seek to understand the effects of precipitation on the growth and function of *S. vermiculatus* near the warmest and driest limit of its distribution.

Dust storms caused by wind erosion, or the aeolian-transport of soil particles, occur primarily across arid and desert ecosystems (Abdul-Wahab 2006; Kolesar et al. 2022). Wind erosion is affected by many factors, including climatic (e.g. wind speed, precipitation) and land-surface characteristics (e.g. vegetation cover, soil texture) (Shao 2009). Desert dust storms increase levels of soil-derived mineral dust and PM<sub>10</sub> (fine aerosol particulate matter with a diameter less than 10 µm) within the atmosphere, causing air-quality hazards and threats to human health (Goudie and Middleton 2006; Shao 2009). Increased levels of PM<sub>10</sub> in the atmosphere are associated with increased levels of pediatric and adult respiratory disease on both a regional and local scale (Gyan et al. 2005; Kar and Takeuchi 2004; Kim et al. 2015).

Strong winds at the Earth's surface drive the emission, transport, and deposition of fine grain particles on open, arid lands (Abdul-Wahab 2006; Kolesar et al. 2022). Fugitive dust (eolian sediments released as aerosols from anthropogenically disturbed lands) is primarily introduced into the atmosphere

after being struck by larger, high-energy particles called saltators (Cahill et al. 1996; Lancaster and Baas 1998; Kolesar et al. 2022). Saltators are typically sand-sized particles (0.05-2.0 mm) that are blown across the soil surface in a process known as saltation (Shao et al. 1993). The amount of time that a particle is suspended in the atmosphere is determined by its particle size (Anderson 1987), with small dust particles (<20  $\mu\text{m}$ ) being suspended longer than larger particles (Kulkarni et al. 2011). These small dust particles can travel hundreds to thousands of kilometers from the emission source, negatively impacting the health of surrounding communities (Reid et al. 1993; Shao et al. 2011; Kolesar et al. 2022).

Dune complexes are a common feature of arid ecosystems and can act as both sand sources and depositional sinks (Lancaster et al. 2015). Vegetation is an important factor for soil stability in desert dune systems (Buckley 1996) and the effectiveness with which they prevent saltation is directly related to plant size, structure, and landscape positioning (Musick and Gillette 1990; Stockton and Gillette 1990; Miri et al. 2017). Vegetation helps to dampen the effects of saltation through physical protection of the soil surface, reduction of the momentum of airflow and shear stress on the soil surface, and by trapping wind-blown saltators and creating sites of deposition and accumulation (i.e., dunes) (Wolfe and Nickling 1993; Lancaster and Baas 1998; Richards et al. 2022). The type and abundance of vegetation in these dune complexes are influenced by surface and subsurface hydrology which influence the availability of water to vegetation (Noy-Meir 1973; Richards et al. 2022). The stability or instability of desert dune systems depends on the interaction between precipitation, surface and vadose zone soil moisture, flash flood events, vegetation cover, and active sand motion (Barchyn and Hugenholtz 2013; Richards et al. 2022).

The southern Great Basin is one of the driest regions within the United States and has high variability in the distribution and timing of precipitation. Vegetation throughout the Great Basin includes deep rooted shrubs interspersed with perennial grasses and forbs on coarse, well-drained soils (Dobrowolski et al. 1990). A general pattern has been proposed in which shrubs and forbs primarily access moisture from deep soil horizons thereby escaping competition from the shallower rooted grasses and

annuals (Dobrowolski et al. 1990). During dry periods, desert ecosystems are essentially in an inactive or steady state and the uptake of nutrients from soil by plant depends upon soil water content (Noy-Meir 1973, Misra and Tyler 2000). Desert soils are often weakly developed, alkaline, and, depending on texture, have low cation exchange capacity (Drenovsky and Richards 2005). This, in addition to receiving limited precipitation, results in desert ecosystems containing soils low in available N and P and organic matter (Schlesinger and Peterjohn 1991; Cross and Schlesinger 1999; Breen and Richards 2007). Infrequent yet concentrated rainfall occurs throughout the Great Basin which brings considerable amounts of sediment from the surrounding alluvial fans to the valley floor (Mabbutt 1979). The primary types of vegetation in the Great Basin are perennial grasses, woody shrubs, and small trees which survive by adaptations to restrict transpiration loss and withstand osmotic stress (Dobrowolski et al. 1990).

This study focuses on the vegetated dune areas (VDAs) surrounding the northwestern and northeastern shores surrounding Owens (dry) Lake (Figure 1), including the Lizard Tail, Swansea, and Keeler dune complexes. Maintaining vegetation cover on these dunes is essential, as reductions in cover lead to increased saltation and subsequent PM<sub>10</sub> emissions (Richards et al. 2022; Schmid et al. 2022). PM<sub>10</sub> emissions coming from the Owens (dry) Lake lakebed (playa), located in the southwestern Great Basin, United States increased considerably after dewatering of the lake began in 1913 (Reheis 1997). Prior to desiccation, Owens Lake was a large, shallow body of water in the southwestern portion of Owens Valley fed by the Owens River. It is a terminal lake, meaning that it exists within a depression that has no outlets (Cahill et al. 1996). Therefore, the volume of water contained within the lake was dependent on a balance between inflow of precipitation and snowmelt from the surrounding mountains and the rate of evaporation (Gale 1914). Since the lake was large, shallow, and situated in an arid environment, variations in precipitation would lead to large fluctuations in shoreline elevations (Gale 1914). Additionally, due to high rates of evaporation, lake water contained large amounts of salts in solution which, upon drying, resulted in salt-rich playa dust and saline soils vulnerable to erosion (Gale 1914; Cahill et al. 1996).

The prevalence of high winds throughout Owens Valley coupled with the increased area of wind-erodible sediments resulted in desertification and large-scale dust storms throughout Owens Valley (Dahlgren et al. 1997; Reheis 1997). Subsequently, Owens Lake became the single largest source of fugitive dust in the United States until dust control measures were implemented in 2002 (Gill and Gillette 1991; Cahill et al. 1996; Gill 1996; Lancaster et al. 2015). Adverse health effects due to emissions were documented in neighboring towns, such as Keeler, CA, and throughout the valley (Saint-Amand et al. 1986; Cahill et al. 1996; Gill 1996).

The purpose of this research was to investigate the response of *Sarcobatus vermiculatus* shrubs growing around Owens Lake to surface water inputs after consecutive years of drought. *S. vermiculatus* might show contrasting responses to surface water inputs for a few reasons. Given the phreatophytic nature of *S. vermiculatus* (access deep soil moisture and shallow groundwater), the low and infrequent nature of precipitation in the southern Great Basin, and ongoing megadrought conditions impacting the region (Stahle 2020; Williams et al. 2022; Strange et al. 2023), abundance of surface roots involved in resource uptake may be low which might limit responsiveness to surface water inputs. Root production often follows a “wave-like” pattern where, as the surface soil layers dry, root production occurs at progressively deeper depths (Fernandez and Caldwell 1975). Additionally, similar research conducted on *Ericameria nauseosa*, another deep-rooted perennial shrub within the Great Basin, showed little to no uptake of summer precipitation for this species (Ehleringer and Dawson 1992; Donovan and Ehleringer 1994). Alternatively, *S. vermiculatus* has been shown to be co-limited by water and nutrient inputs in previous studies in other parts of its distribution (Drenovsky and Richards 2004; Drenovsky and Richards 2006). This suggests that *S. vermiculatus* could maintain a high proportion of surface roots to take advantage of infrequent but important pulses of water and nutrient inputs. Due to the high energetic costs associated with the annual replacement of fine, diffuse roots in these cold desert ecosystems

(Dobrowolski et al. 1990), does *S. vermiculatus* invest scarce resources to maintain these shallow root systems to capture available surface soil moisture?

## 2 MATERIALS AND METHODS

### 2.1 STUDY AREA

Owens (dry) Lake is situated at the southern end of Owens Valley, California within the Great Basin region of the southwestern United States. The 280 km<sup>2</sup> dry lakebed is bounded by the Sierra Nevada range to the west, the Inyo and White mountain ranges to the east, and the Coso range to the south. Owens Lake is situated within the rainshadow of the Sierra Nevada mountains, lying immediately east of the highest peak in the continental United States, Mount Whitney (4,421 m). The valley floor ranges in elevation from roughly 1,100 to 1,250 m. Owens Valley is characterized by cold winters (mean temperature in January is 4.5 °C) and hot, dry summers (mean temperature in July is 28.9 °C). Mean annual temperature (January – December) is 15.9 °C (2002-2023) (California Irrigation Management Information System, CIMIS). Mean annual precipitation on the valley floor, near the lake, is 6.25 mm (2002-2023) (CIMIS), with most precipitation occurring between November – April. Recharge from the Sierra Nevada snowpack supplies most of the groundwater recharge within the valley. So, although precipitation is limited, groundwater is abundant (Sorenson et al. 1991).

The vegetated dune areas (VDAs) selected for this study all exist at or above the 800-year-old historic shoreline of Owens Lake (Bacon et al. 2018). These dunes exist at the base of alluvial fans formed along the Inyo, Coso, and Sierra Nevada mountain ranges (Blanton et al. 2022). The 800-year-old shoreline is where the maximum dune development exists and therefore where the highest rates of cover are found. Eight representative VDA locations were selected for detailed characterization: VDA01A, VDA01B, VDA02A, VDA02B, VDA03B, VDA05A, VDA08A, and VDA08B (Figure 1). Each site consisted of major vegetated dune complexes at or above the 800-year-old shoreline which are dominated by *S. vermiculatus*.

VDA01A and VDA01B are located on the northwest shore of Owens Lake and contain the most diverse vegetation communities of all eight sites. At these sites, the vegetated dunes are large and run parallel to the historic shoreline of Owens Lake (Bacon et al. 2018). These dunes are situated between the lacustrine plain to the north and the historic playa to the south. At these sites, most *S. vermiculatus* shrubs occur on dunes between the ~360 (1,099-1,101-meter elevations) and ~800 (1,103-meter elevation) year old shorelines (Bacon et al. 2018). Average depth to groundwater at these sites is 4.7 and 6.8 meters, respectively.

VDA02A and VDA02B are located on the northeast side of Owens Lake and are both a part of the Lizard Tail dune complex (Lancaster et al. 2015). The majority of *S. vermiculatus* shrubs occur above the ~800-year shoreline (1,103-meter elevation). There is a steep south-facing slope below the ~800-year shoreline at these sites which also contain *S. vermiculatus* shrubs. Average depth to groundwater at these sites is 4.3 and 6.8 meters, respectively.

VDA03B is at a lower elevation (1,099-1,101-meter elevation) than VDA02, with a majority of *S. vermiculatus* shrubs existing on stony soils above the ~800-year shoreline. The shrubs at this site are relatively small and scattered. A distinct feature of this VDA is evidence of significant flood flow into the dunes from a large alluvial fan positioned upslope from the VDA. These inputs are essentially absent from VDA01 and VDA02. During the installation of neutron probe access tubes, a confining (i.e., cemented caliche) layer was encountered at many locations, with depth to the confining layer decreasing as proximity to the playa increased. Average depth to groundwater at this site is 1.5 meters.

VDA05A is located on the east side of Owens Lake at the Dolomite Mine Historic Marker. The vegetated dunes at this site occur between the ~800-year (1,103-meter elevation) and ~3,560-year (1,108-meter elevation) shorelines. A large dune, likely created in part by the ~3,560-year shoreline and the activation of the Keeler Dune complex (Richards et al. 2022), bisects this VDA. Average depth to groundwater at this site is 5.9 meters.

VDA08A and VDA08B are located within the Keeler Dune complex. The dunes in this VDA exist above the ~800-year (1,108- meter elevation) shoreline and are semi-unstable due to the installation of chevron berms within the adjacent Slate Canyon alluvial fan (Richards et al. 2022). Evidence from studies done on the Keeler Dune complex show that these dunes have existed since at least 1944 (Schmid et al. 2022) and are accumulating sand and growing quickly (Schaaf et al. 2021). Similar to VDA03B, VDA08 has strong evidence of flood flows onto the area above the semi-stabilized dunes. Average depth to groundwater at these sites is 5.2 and 4.6 meters, respectively.

**FIGURE 1. OVERVIEW OF THE VEGETATED DUNE AREAS SURROUNDING OWENS LAKE, INCLUDING THE LOCATION OF PIEZOMETERS, NEUTRON PROBE ACCESS TUBES, AND *S. VERMICULATUS* SHRUBS MARKED FOR ROUTINE MONITORING.**



## 2.2 SPECIES

*Sarcobatus vermiculatus* (Hook.) Torrey (Chenopodiaceae; common name black greasewood) is a winter-deciduous, salt-tolerant shrub. The species is considered a deep-rooted halophytic and facultative phreatophyte and facultative upland species (Romo and Haferkamp 1989; Trent et al. 1997). *S.*

*vermiculatus* shrubs, which display leaves from late spring to early autumn, persist in environments where precipitation is low, unpredictable, and often occurs during the winter when temperatures are too low to facilitate growth (Romo and Haferkamp 1989; Trent et al. 1997). Additionally, they are often found in environments that have halomorphic soils, which induce intense osmotic stress (Donovan et al. 1996). The distribution of *S. vermiculatus* is spread throughout much of western North America, with its range spanning from western Canada to Mexico and from the Great Plains to eastern California (Hickman et al. 1993; Drenovsky et al. 2011).

*S. vermiculatus* often colonizes areas where the groundwater table is sufficiently high (Robinson 1958; Rickard 1967; Groeneveld 1990; Trent et al. 1997). It is a desert halophyte, meaning it can survive and reproduce in soils with high salinity (Flowers et al. 1977; Skougard and Brotherson 1979), and has evolved special ion physiology characteristics that enable survival in these environments which face nutrient limitations and osmotically reduced water availability (Donovan et al. 1997, Flowers and Colmer 2008). An adaptation of halophytes which aids in survival is their ability to uptake and transport greater amounts of Na to leaves which maintains water potential gradients needed to drive water uptake and maintain turgor pressure (Donovan et al. 1997; Flowers and Colmer 2008). Monovalent ions, such as Na<sup>+</sup> or Cl<sup>-</sup>, are often toxic at the concentrations needed for osmotic adjustment (Flowers and Colmer 2008). *S. vermiculatus* has evolved physiological modifications which enable them to sequester Na<sup>+</sup> in vacuoles and balance the charge with glycinebetaine which maintains tolerable ion concentrations within the cytoplasm (Hadley and Szarek 1981; Donovan et al. 1997; Drenovsky and Richards 2004). The production of glycinebetaine requires large investments of N which, combined with limited N available in desert soils, results in N-limitations within *S. vermiculatus* (Donovan et al. 1997; Hadley and Szarek 1981).

Both the amount of N stored in soils and the rate at which biological N cycling occurs vary with climate (Amundson et al. 2003). As rainfall decreases, so does N storage and rates of biological N cycling (Jenny and Leonard 1934; Noy-Meir 1973; Post et al. 1985). Additionally, in arid environments the low

available soil moisture constrains net primary productivity which leads to low N uptake by desert plants and low carbon inputs to the system (Post et al. 1985). Limited soil moisture reduces leaching throughout the soil profile resulting in an accumulation of inorganic N salts (Post et al. 1985). Collectively, these lead to a low carbon to nitrogen ratio which reduces microbial activity, decomposition, and nutrient turnover in the soil (Post et al. 1985). Therefore, nutrient conservation is an important feature for plants growing in low-fertility environments (Eckstein et al. 1999). The main mechanisms for minimizing nutrient loss in these environments is by extending the life span of plant tissues and resorption of nutrients from abscised plant parts (Eckstein et al. 1999).

## **2.3 METEOROLOGICAL DATA COLLECTION**

Six relative humidity and temperature sensors were installed at VDA01A in June 2022 (HOBO MX2300, Onset, Bourne, MA, USA). Sensors were secured to T-posts and situated proximal to the canopy of each shrub marked for routine monitoring. Measurements were collected at five-minute intervals and data was downloaded from the sensors monthly. Precipitation data was obtained from CIMIS Station 183, Owens Lake North (36.488611, -117.91944), which is owned and operated by Los Angeles Department of Water and Power (LADWP).

## **2.4 GROUNDWATER ELEVATION MONITORING, SOIL MOISTURE, AND ROOTZONE CHARACTERIZATION**

### **2.4.1 GROUNDWATER, SOIL PROPERTIES, AND ROOTZONE CHARACTERIZATION**

Along with atmospheric drivers, many landscape-level factors affect dune vegetation health and vigor. These factors include soil characteristics (soil moisture, salinity, texture, nutrient availability), groundwater depth and quality, flood flow input (water, sediment, litter), and aeolian deposition and/or erosion. The objective of this effort was to characterize the soil profile, lithology, moisture content, root density distribution, and groundwater levels under the *S. vermiculatus* shrubs dominating the dunes.

In 2020, piezometers were installed to measure groundwater depth at each of the VDA locations using a combination of hand and mechanical drilling. Descriptions of root distribution, soil layering, soil texture, structure, and color were recorded during soil sample collection. For sites that were hand augured (VDA01A, VDA02A, VDA02B, VDA08A, VDA08B), soil and root samples were collected at 30 cm intervals. For sites that were installed with a rig (VDA01B, VDA03B, VDA05A), samples were collected with a split spoon at 45 cm intervals. Additional soil samples were collected via hand-auger on top of the vegetated dunes in VDA03B, VDA08A, and VDA08B in order to capture the root distribution on top of the dunes in addition to the dune interspaces where piezometers were installed. Augering ceased once groundwater or refusal due to a confining layer was reached and piezometers were inserted into the boreholes. The boreholes were then sealed with sand and bentonite. Pressure and temperature transducers were installed in each of the piezometers which enabled continuous monitoring of depth to groundwater surface. Data from these transducers were downloaded monthly.

In the field, a set volume of soil (0.5-1 liter) was collected from each 30 cm interval and sieved to collect roots. Coarse roots (> 3mm in diameter) and fine roots (< 3 mm in diameter) were removed with tweezers from progressively finer sieves (4 - 0.2 mm). All material passing through the finest sieve (0.2 mm) was carefully inspected for roots, within which only a few root fragments were found. Coarse and fine root samples from each depth and location were individually bagged in the field and taken to the lab for washing and soil removal. Cleaned roots were dried at 70 °C and weighed to determine dry mass. Root dry mass per depth interval were corrected for the volume sampled so all depths were related to the same volume across all depths and boreholes. Relative root density was calculated for each borehole and depth as the quotient of the root mass to the total mass of soil for that borehole. Using these data, relative distributions of fine roots and coarse roots throughout the soil profile were quantified. Root distribution data for each depth and VDA were averaged to determine the overall and general rooting profile of *S. vermiculatus* across all VDAs.

## 2.4.2 ACCESS TUBE INSTALLATION

To monitor vadose zone soil moisture over time, especially in relation to surface water inputs, neutron probe access tubes were installed near existing piezometers at all VDA locations in May/June 2022. To install access tubes, holes were hand-augered using a 4.45 cm auger bucket and 1.52 m extension rods. Bulk density (BD) and texture samples were collected at intervals of 15 cm, 30 cm, 45 cm, and 45 cm increments thereafter until reaching a confining layer or groundwater. Afterwards, a 5.08 cm diameter PVC well casing (hereafter, access tube) was installed in the hole and bentonite was added to the bottom to prevent upwelling of groundwater. Care was taken to ensure that the access tube fit snugly into the hole as voids can introduce error into neutron probe measurements (Chanasyk and Naeth 1996). The access tube was then sealed with a well cap and left to equilibrate for 72 hours. BD samples were collected using a 49.9 cm<sup>3</sup> volumetric bulk density corer. These samples were quickly bagged and weighed in the field to determine wet mass. Samples were then dried at 105 °C for 48 hours in a lab oven and weighed to determine dry mass. Volumetric water content (VWC,  $\Theta$ ) was calculated as the ratio of water volume per unit soil volume (1 g H<sub>2</sub>O = 1 cm<sup>3</sup> H<sub>2</sub>O). BD (g cm<sup>-3</sup>) was calculated as soil dry mass per unit soil volume. Texture samples were collected and processed in the laboratory to determine the relative proportion of sand, silt, and clay.

At certain depths, it was not possible to collect samples for accurate BD measurements. At these depths, gravimetric soil water samples were collected instead. These samples were bagged, weighed in the field for fresh mass determination, and lab dried to determine dry mass. BD of gravimetric samples were predicted using a linear function describing the relationship between percent silt and BD; this is the same approach used for predicting BD of samples collected during piezometer installation. The empirical function was developed using soil texture and BD data collected during neutron probe installation in May and June 2022, and soil texture and BD data collected during piezometer installation in August 2020. All VDAs and a range of soil depths were represented in this dataset. A total of 86 observations were used to

develop the linear model. The final model was:  $BD \text{ (g cm}^{-3}\text{)} = 1.57 - (0.00504 \times \% \text{Silt})$ ;  $R^2=0.31$ ,  $P < 0.0001$ , RMSE = 16%). With predicted BD, we then estimated VWC of these samples and added them to the neutron probe calibration dataset (described in Section 2.4.3).

Starting in May 2022, we used a neutron probe (503 ELITE Hydroprobe, InstroTek Inc., Research Triangle Park, NC, USA) to measure neutron counts at each depth within each access tube. Neutron probe measurements were repeated on a monthly-basis from May 2022 to May 2023. Measurements were collected at intervals of 15 cm, 30 cm, 45 cm, and 45 cm increments thereafter until the bottom of the access tube was reached. Standard counts were also taken at the beginning and end of each day and neutron count ratios were calculated (average neutron count/average standard count). Count ratio was subsequently used to predict VWC, as described in Section 2.4.3 below.

In September 2022, three additional access tubes were installed at select VDAs for the purposes of collecting more data for neutron probe calibration. The locations of these access tubes were selected to represent the range of soil texture across the VDAs. Dry BD samples were collected and processed as described above and neutron probe readings were immediately taken in the newly installed access tubes. An infiltrometer, consisting of a 175 cm diameter ring of flexible sheet metal (75 cm wide), was then installed around the access tube and roughly 160 gallons of water was added to saturate the entire soil profile. After water was allowed to infiltrate the soil for several hours, we returned to the access tube and took neutron probe readings to determine water movement through the soil profile to assess whether infiltration was complete. Once the wetting front had infiltrated the entire soil profile, “wet” neutron probe readings were collected. Immediately following the collection of the “wet” neutron probe reading, four soil cores were augered around the access tube and BD samples were collected and processed as described previously.

### 2.4.3 NEUTRON PROBE CALIBRATION EQUATION

The neutron probe provides estimates of neutron counts. To convert these counts to VWC, a linear relationship must be derived from soil physical properties and neutron count ratios at each measurement depth. Collection of calibration data occurred in two phases: an *in-situ* calibration in May/June 2022 and a calibration-specific event in September 2022. We created two separate calibration equations; one for the surface (top 45 cm) and one for the subsurface (all depths > 45 cm). Two separate equations were developed because, within the top 45 cm of soil, fast neutrons escape into the atmosphere leading to a different VWC prediction than the subsurface (Chanasyk and Naeth 1996). Additionally, soil texture often has a large effect on VWC estimations and must be considered as a covariate (Dong and Ochsner 2018).

For each calibration access tube, a surface and subsurface equation was developed by building a linear regression between the count ratio (neutron count divided by standard count) and VWC. Analysis of covariance (ANCOVA) was used to determine whether surface and subsurface equations were significantly different among calibration tubes (i.e., sites). ANCOVA tests revealed that equations were not different between tubes/sites, such that a single surface and subsurface equation, respectively, could be used across all tubes/sites. We then determined whether soil texture (%Sand, %Silt, %Clay) explained additional variation in VWC not explained by count ratio. For both surface and subsurface models, we tested the relationship between VWC and count ratio, with texture included as a covariate. For the surface calibration model, no soil texture variable (e.g., %Sand, %Silt, %Clay) was significant; only count ratio was an important predictor of VWC. For the subsurface, %Clay was a significant covariate ( $P=0.0025$ ) and was therefore included in the equation. The final surface equation is  $y = (0.288 \times \text{Count Ratio}) - 0.038$  (adjusted  $R^2 = 0.85$ ,  $P < 0.0001$ ). The final subsurface equation is  $y = (0.435 \times \text{Count Ratio}) + (0.007 \times \% \text{Clay}) - 0.0849$  (adjusted  $R^2 = 0.82$ ,  $P < 0.0001$ ). For depths and access tubes where texture data was not collected for any reason, texture values were appended with data collected at each VDA during piezometer installation in

2020. Neutron counts collected outside of calibration events (during routine monitoring) were then converted to VWC using the calibration equations.

#### **2.4.4 CONVERSION OF VOLUMETRIC WATER CONTENT TO PLANT AVAILABLE WATER**

In order to evaluate only the plant available water (PAW) of VWC, or the amount of water between field capacity (FC) and permanent wilting point (PWP), VWC measurements were converted to estimations of FC and PWP using pedotransfer functions. Pedotransfer functions are statistical tools used to estimate unknown soil properties from empirically measured soil properties (Oschner 2022). Soil samples collected during piezometer installation were analyzed for water content of the soil at FC (-0.033 MPa) and PWP (-1.5 MPa) (IAS Laboratories, Phoenix, AZ). Two pedotransfer functions were developed by building multi-linear regressions between soil texture (%Sand, %Silt, %Clay) and water holding capacity at FC and at PWP. For both equations, %Sand and %Clay were found to be significant. The final equation for FC was  $y = 62.727 - (0.546 \times \%Sand) + (0.314 \times \%Clay)$  (adjusted  $R^2 = 0.84$ ,  $P < 0.0001$ ). The final equation for PWP was  $y = 16.993 - (0.136 \times \%Sand) + (0.358 \times \%Clay)$  (adjusted  $R^2 = 0.83$ ,  $P < 0.0001$ ). These equations were then used to calculate FC and PWP for each soil layer at which neutron probe measurements were taken. To calculate PAW for each soil layer, the minimum value between VWC and FC was selected as the upper limit. This is because any water present in the soil above FC is essentially unavailable to plants, as is subject to drainage by gravity. PAW was then calculated by subtracting PWP from the upper limit. If the resulting soil water content was less than PWP, PAW was set equal to zero. PAW storage by soil layer was then calculated by multiplying PAW by the depth interval (15 or 45 cm).

## **2.5 PHYSIOLOGY**

At each of the eight locations, six mature shrubs were selected for routine physiological measurements, resulting in a total of 48 shrubs. All shrubs were positioned near an existing piezometer (Section 2.4.1) to better understand the relationship between groundwater levels and shrub function within the VDAs.

### 2.5.1 XYLEM WATER POTENTIAL

Predawn and midday stem water potential ( $\Psi_{pd}$  and  $\Psi_{md}$ , respectively) were measured across all VDAs at six timepoints to determine shrub water status (May 2022, July 2022, September 2022, November 2022, March 2023, and May 2023).  $\Psi_{pd}$  and  $\Psi_{md}$  (units of MPa) were each measured on one upper canopy stem per shrub using a Scholander pressure chamber (PMS Instruments, Corvallis, OR, USA).  $\Psi_{pd}$  measurements were collected between 03:00 – 06:30 PST, with measurements ceasing at first light (roughly 30 minutes before sunrise).  $\Psi_{md}$  measurements were collected between 11:30 – 14:30 PST approximating midday conditions. Due to the logistic difficulties of measuring shrubs across many different sites,  $\Psi_{pd}$  and  $\Psi_{md}$  measurements were split across two days. Stem samples were collected by first enclosing the sample in a thin plastic bag to minimize evaporation loss from the cut surface. The exposed portion of the stem was then cut using a razor blade and quickly placed in a larger bag and sealed. Samples were placed in a cooler and immediately taken to the pressure chamber. Samples were measured within five minutes of removal from the shrub.

### 2.5.2 LEAF GAS-EXCHANGE

Midday leaf gas-exchange and predawn and midday leaf chlorophyll fluorescence were measured at six timepoints between May 2022 and May 2023 to determine temporal and spatial variation in shrub function. At each timepoint, a LI-6400XT portable photosynthesis system (Li-Cor Inc., Lincoln, NE, USA) was used to record steady-state measurements of light-saturated net photosynthesis ( $A_{net}$ ) and leaf stomatal conductance to water vapor ( $g_s$ ) on one cluster of upper canopy, sun-exposed leaves per shrub. The ratio of  $A_{net}$  to  $g_s$  was calculated as a measure of intrinsic water use efficiency (iWUE,  $\mu\text{mol mol}^{-1}$ ). Leaves typically reached steady-state within 7–10 min of being enclosed in the cuvette. Measurements were made between 11:00 and 15:00 PST and were generally split across two days given the logistic difficulties of measuring shrubs located across many sites. Gas exchange measurements collected in September and November were sampled from both new growth and mature leaves.

For all measurements, flow rate was held constant at  $500 \mu\text{mol s}^{-1}$ , reference  $[\text{CO}_2]$  was set at  $415 \mu\text{mol mol}^{-1}$  using the  $\text{CO}_2$  mixer, and light intensity inside the chamber was maintained at  $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$  photosynthetic photon flux density (PPFD) using the red/blue LED light source. Block temperature was set at ambient midday air temperature, although leaf temperature varied within each measurement day according to ambient air temperature changes and water fluxes from the leaves. Relative humidity in the chamber was controlled near ambient external conditions, but also varied depending upon water vapor fluxes from the leaf such that the leaf-to-air vapor pressure deficit ( $\text{VPD}_{\text{leaf}}$ ) varied among and within measurement days.

After leaf gas-exchange and corresponding environmental data (leaf temperature,  $\text{VPD}_{\text{leaf}}$ ) were logged, the measured leaves were removed from the stem, placed in sealed plastic bag, and stored in a cooler until leaf area image analysis could be completed to correct the fluxes based on actual one-sided leaf area inside the chamber. Leaf samples were processed at the end of the measurement day by photographing leaves of each individual shrub against a blue background with a  $4 \text{ cm}^2$  red square placed adjacent to the leaves for scaling purposes. Leaf area images were processed in Image J software using standard techniques. The leaves were then oven dried for 72-hours and weighed using a microbalance. Specific leaf area (ratio of leaf area to dry mass) was then calculated and used to calculate gas exchange rates per unit area.

### **2.5.3 LEAF CHLOROPHYLL FLUORESCENCE**

Dark-adapted ( $F_v/F_m$ ) and light-adapted ( $\Phi_{\text{PSII}}$ ) chlorophyll fluorescence measurements were taken at the same timepoints as  $\Psi_{\text{pd}}$  and  $\Psi_{\text{md}}$  using a portable porometer with a Pulse-Amplitude Modulated (PAM) fluorometer (LI-600, LI-COR Biosciences, Nebraska, USA). All measurements were collected using the manual gsw+F configuration. Leaves were placed side by side (non-overlapping) to create a continuous surface then enclosed in a  $0.75 \text{ cm}^2$  aperture clamp, ensuring that the entire aperture was covered. For  $\Phi_{\text{PSII}}$ , leaves were held in their natural orientation to incident sunlight during

measurement. Photosynthetically active radiation (PAR) ranged from  $223 \mu\text{mol m}^{-2} \text{s}^{-1}$  in November 2022 to  $2,618 \mu\text{mol m}^{-2} \text{s}^{-1}$  in July 2022. Three measurements were taken per shrub and averaged for each timepoint excluding May 2022, where a single measurement was taken per shrub.

#### **2.5.4 STEM GROWTH**

For each of our 48 shrubs, one axillary stem was measured in May 2022 and flagged for repeated growth measurements. In May and July 2022, measurements were taken from the base of these stems to the tip of the apical leaf. In September, five new axillary stems per shrub were selected at random for measurement. The mean of these five measurements was calculated and recorded. In November, three new axillary stems per shrub were selected at random for measurement. The mean of these three measurements was calculated and recorded. In early March 2023, prior to budburst, two axillary stems (one northerly, one southerly) were measured and flagged for repeated growth measurements. The mean of these two measurements was calculated and recorded. These same stems were measured again in late March 2023 and May 2023.

#### **2.5.5 LEAF NITROGEN CONTENT**

Leaves from all 48 shrubs were collected across three timepoints (May 2022, September 2022, March 2023) and analyzed for leaf N, C, and isotope composition ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ). Once collected, leaves were washed three times with distilled water and left to air dry. These samples were submitted to the University of California, Davis Analytical Lab where they were dried, ground, and encapsulated. Samples (4.02 – 4.91 mg) were then submitted to the University of California, Davis Stable Isotope Facility (UCD SIF) where they were analyzed for %N, %C,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$  using an Elemental Analyzer Isotope-Ratio Mass Spectrometry system. Natural signatures of  $\delta^{15}\text{N}$  provide insight into N cycling, especially variability in N cycling among plants, sites, and over time. Although many factors can influence  $\delta^{15}\text{N}$  signatures and caution is needed with interpreting such data (Hogberg 1997), a depleted signature of  $\delta^{15}\text{N}$  is generally thought to indicate a more open nitrogen cycle, with smaller losses of N (e.g., gaseous) relative to turnover

(Austin and Vitousek 1997). Enriched signatures of  $\delta^{15}\text{N}$ , on the other hand, are thought to indicate a more closed N cycle with greater losses of N relative turnover.

Signatures of  $\delta^{13}\text{C}$  in leaf tissue provide a time-integrated measure of iWUE (Farquhar et al. 1989).  $\delta^{13}\text{C}$  is calculated as  $(\text{Sample } 13\text{C}/12\text{C} / \text{Standard } 13\text{C}/12\text{C} - 1) \times 1000$ , where Sample  $13\text{C}/12\text{C}$  is the abundance ratio of the tissue sample and Standard  $13\text{C}/12\text{C}$  is the abundance ratio of the standard (Vienna Pee Dee Belemnite).  $\delta^{13}\text{C}$  is inversely proportional to the ratio of intercellular  $\text{CO}_2$  ( $C_i$ ) to atmospheric  $\text{CO}_2$  ( $C_a$ ). Leaves achieve high  $C_i/C_a$  when carbon fixation per unit stomatal conductance is low (low intrinsic water use efficiency). As a result,  $\delta^{13}\text{C}$  is positively associated with iWUE.

### **2.5.6 STATISTICAL ANALYSES**

A two-way repeated-measures analysis of variance (ANOVA) was used to test the effects of measurement Date, VDA location, and the Date  $\times$  VDA interaction on all physiological variables described in Section 2.5. When VDA or measurement Date  $\times$  VDA interactions were statistically significant ( $P < 0.05$ ), Tukey post-hoc tests were used to compare VDA means, overall or within individual measurement events.

## **3 RESULTS**

### **3.1 METEOROLOGICAL DATA**

Between May 2022 – May 2023, temperatures ranged from  $-9.3^\circ\text{C}$  to  $46.0^\circ\text{C}$  (Table 2) (HOBO MX2300, Onset, Bourne, MA, USA). The highest temperatures occurred during July 2022, with mean and maximum midday temperatures of  $40.0$  and  $48.4^\circ\text{C}$ , respectively. The lowest temperature recorded occurred during November 2022, with a daily minimum temperature of  $-9.3^\circ\text{C}$ , although mean monthly temperatures were lowest in December 2022 and January 2023 at  $4.2^\circ\text{C}$  (Table 2). Total precipitation during our study was  $109.2\text{ mm}$  (Table 1), with  $35.6\text{ mm}$  of precipitation occurring between July – September 2022.

**FIGURE 2. SHRUB-LEVEL MINIMUM, MAXIMUM, AND MEAN DAILY TEMPERATURE (°C), SHRUB-LEVEL MINIMUM, MAXIMUM, AND MEAN VAPOR PRESSURE DEFICIT (kPa) AND PRECIPITATION (mm) MONITORED BETWEEN JUNE 2022-MAY 2023. TEMPERATURE AND VAPOR PRESSURE DEFICIT DATA WERE RECORDED USING HOBO MX2300 DATA LOGGERS. PRECIPITATION DATA WAS DOWNLOADED FROM CIMIS STATION 183 – OWENS LAKE NORTH.**

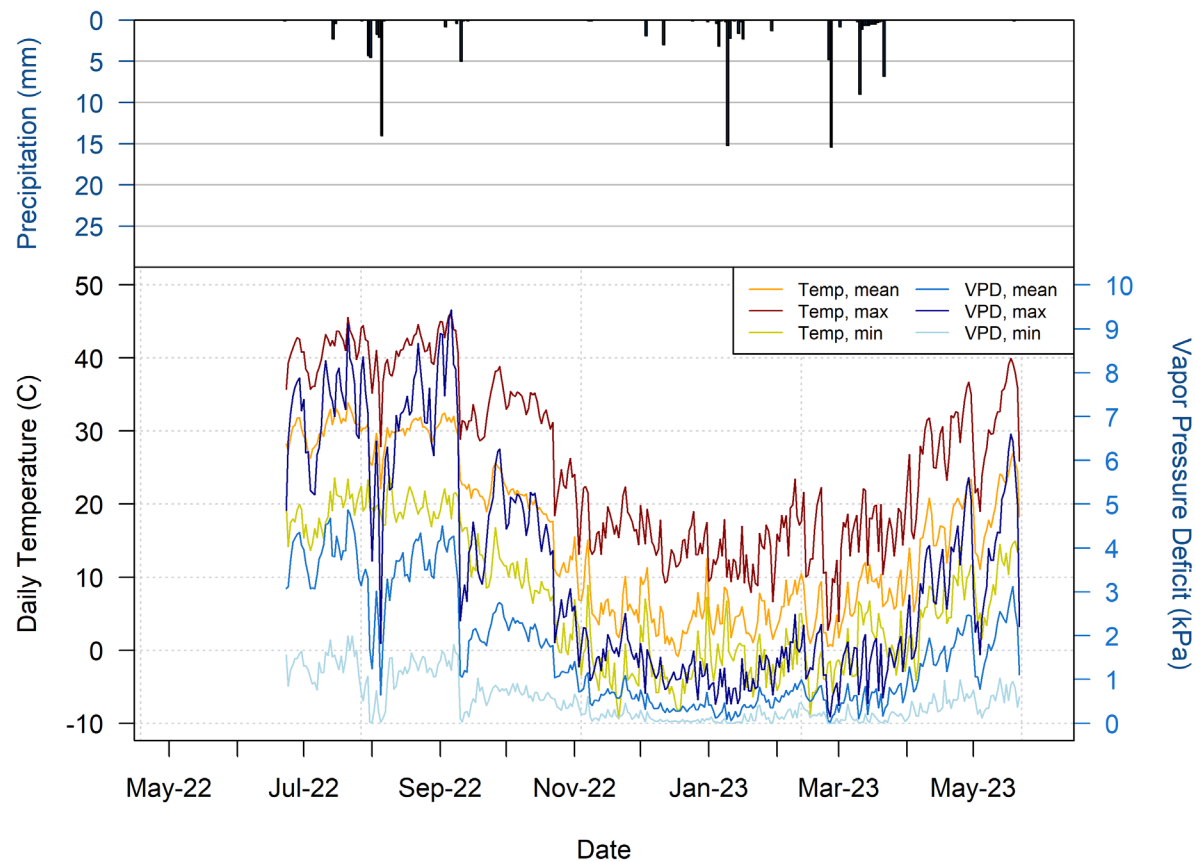


**TABLE 1. TOTAL MONTHLY PRECIPITATION (mm) FROM MAY 2022-MAY 2023 FOR OWENS (DRY) LAKE. DATA WERE DOWNLOADED FROM CIMIS STATION 183 - OWENS LAKE NORTH.**

| Month          | Precipitation (mm) |
|----------------|--------------------|
| May 2022       | 0.0                |
| June 2022      | 0.0                |
| July 2022      | 11.68              |
| August 2022    | 17.78              |
| September 2022 | 6.35               |
| October 2022   | 0.0                |
| November 2022  | 0.0                |
| December 2022  | 5.08               |

|               |       |
|---------------|-------|
| January 2023  | 26.92 |
| February 2023 | 20.32 |
| March 2023    | 21.36 |
| April 2023    | 0.0   |
| May 2023      | 0.0   |

**TABLE 2. MONTHLY MEAN MINIMUM, MEAN MAXIMUM, AND MEAN TEMPERATURES (°C) BETWEEN MAY 2022 AND MAY 2023. MAY 2022 DATA WERE DOWNLOADED FROM CIMIS STATION 183. JUNE 2022-MAY 2023 WERE MEASURED USING HOBO MX2300 DATA LOGGERS LOCATED IN VDA01A.**

| Date           | Daily Minimum Temperature (°C) | Daily Maximum Temperature (°C) | Mean Monthly Temperature (°C) |
|----------------|--------------------------------|--------------------------------|-------------------------------|
| May 2022       | 2.5                            | 35.0                           | 19.7                          |
| June 2022      | 14.3                           | 44.5                           | 30.3                          |
| July 2022      | 13.7                           | 46.0                           | 30.7                          |
| August 2022    | 17.0                           | 44.4                           | 29.5                          |
| September 2022 | 8.4                            | 45.7                           | 25.2                          |
| October 2022   | -0.5                           | 34.9                           | 17.5                          |
| November 2022  | -9.3                           | 24.6                           | 6.5                           |
| December 2022  | -8.3                           | 19.9                           | 4.2                           |
| January 2023   | -6.6                           | 16.4                           | 4.2                           |
| February 2023  | -8.5                           | 20.2                           | 5.1                           |
| March 2023     | -3.7                           | 21.6                           | 7.6                           |
| April 2023     | -4.9                           | 34.2                           | 15.1                          |
| May 2023       | 6.2                            | 33.2                           | 19.7                          |

## 3.2 SOIL PHYSICAL PROPERTIES

Soil samples analyzed were dominated by sands (0.05 – 2 mm) with layers of silt and clay interspersed throughout the soil profile. 108 out of 129 samples collected contained at least 90% sand sized particles. VDA01A had an average sand content of  $95.9 \pm 0.6\%$  (mean  $\pm$  SE; range 93.0-99.2%) and an average BD of  $1.6 \pm 0.03 \text{ g cm}^{-3}$  (range 1.45-1.76  $\text{g cm}^{-3}$ ). VDA01B had an average sand content of  $96.8 \pm 0.6\%$  (range 91.7 – 98.4%) and an average BD of  $1.6 \pm 0.3 \text{ g cm}^{-3}$  (range 1.56 – 1.72  $\text{g cm}^{-3}$ ). VDA02A had an average sand content of  $84.8 \pm 3.3 \%$  (range 69.1 – 97.8%) and an average BD of  $1.51 \pm 0.03 \text{ g cm}^{-3}$  (range 1.29 – 1.86  $\text{g cm}^{-3}$ ). VDA02A had prominent silt (0.05 to 0.002 mm) layers at 1.37 m (24.8%), 2.29 m (18.6%), 2.74 m (27.0%), 3.2 m (24.5%), and 4.12 m (24.3%) and an average BD of  $1.51 \pm 0.06 \text{ g cm}^{-3}$ .

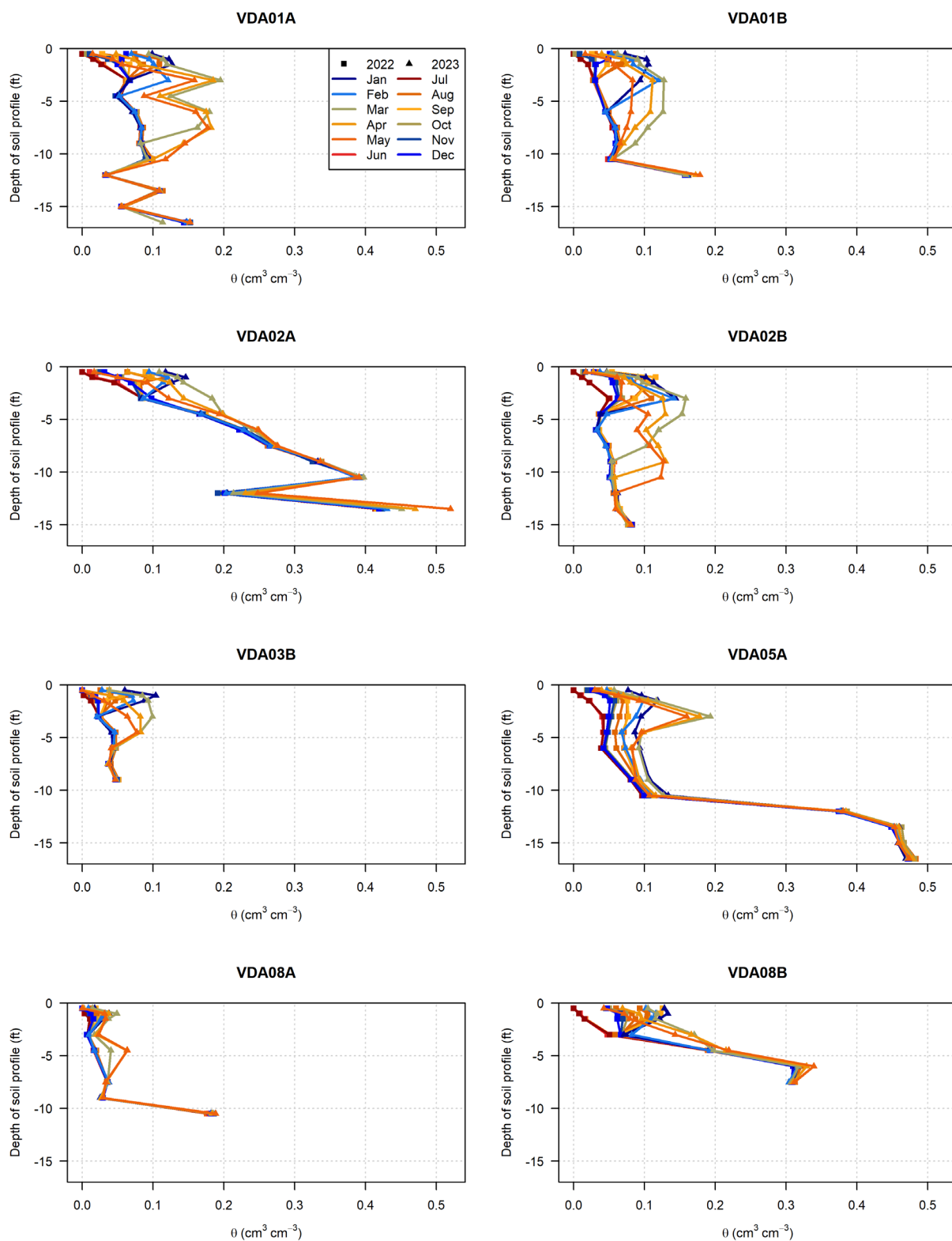
(range 1.29-1.86 g cm<sup>-3</sup>). VDA02B had an average sand content of 97.6 ± 0.4% (range 94.6 – 99.1%) and an average BD of 1.53 ± 0.02 g cm<sup>-3</sup> (range 1.45 - 1.65 g cm<sup>-3</sup>). VDA03B had an average sand content of 97.8 ± 0.3% (range 95.8 – 98.7%) and an average BD of 1.58 ± 0.02 g cm<sup>-3</sup> (range 1.56 – 1.65 g cm<sup>-3</sup>). VDA05A had an average sand content of 83.4 ± 5.2% (range 48.1 – 98.5%) and an average bulk density of 1.53 ± 0.03 g cm<sup>-3</sup> (range 1.33 – 1.74 g cm<sup>-3</sup>). VDA05A had prominent silt layers at 3.66 m (14.6%), 4.12 m (44.7%), 4.57 m (47.4%), and 5.03 m (40.1%). VDA08A had an average sand content of 63.6 ± 8.1% (range 29.9 – 98.5%) and an average bulk density of 1.46 ± 0.08 g cm<sup>-3</sup> (range 1.26 – 1.64 g cm<sup>-3</sup>). VDA08A had a prominent silt layer at 3.20 m (10.1%). VDA08B had an average sand content of 91.8 ± 5.7% (range 51.9 – 98.9%) and an average bulk density of 1.49 ± 0.05 g cm<sup>-3</sup> (range 1.31 – 1.71 g cm<sup>-3</sup>). VDA08B had prominent silt layers at 1.37 m (29%), 1.83 m (52.7%), 2.29 m (30.1%), and 2.74 m (39.7%).

### **3.3 SOIL MOISTURE**

During March 2023, maximum VWC was measured at all VDAs except for VDA08B, which had the highest measurements in January 2023 (Figure 3). At VDA01A, the highest VWC was measured at a depth of 0.91 m and the wetting front from precipitation infiltrated 2.44 m into the soil profile. At VDA01B, the maximum VWC was measured at a depth of 0.91 m and the wetting front from precipitation infiltrated 2.44 m into the soil profile. At VDA02A, the maximum VWC was measured at a depth of 3.96 m, with soil moisture increasing with depth. VDA02A has a shallow water table present at 4.27 m, so these measurements are likely capturing the capillary fringe (i.e. effects of capillary rise) rather than the influence of surface soil moisture. At VDA02B, the maximum VWC was measured at a depth of 0.91 m and the wetting front from precipitation infiltrated 2.74 m into the soil profile. At VDA03B, the maximum VWC was measured at a depth of 0.91 m and the wetting front from precipitation infiltrated 1.83 m into the soil profile. At VDA05A, the maximum VWC was measured at a depth of 4.88, though these measurements are likely capturing the capillary fringe. At VDA08A, maximum VWC was measured at 3.35 m, likely

capturing capillary fringe. At VDA08B, the maximum VWC was measured at one and 0.46 m with the wetting front from precipitation infiltrating 1.22 m into the soil profile.

**FIGURE 3. MONTHLY VOLUMETRIC WATER CONTENT MEASURED USING A NEUTRON PROBE ACROSS ALL VDAS BETWEEN MAY 2022 - MAY 2023**

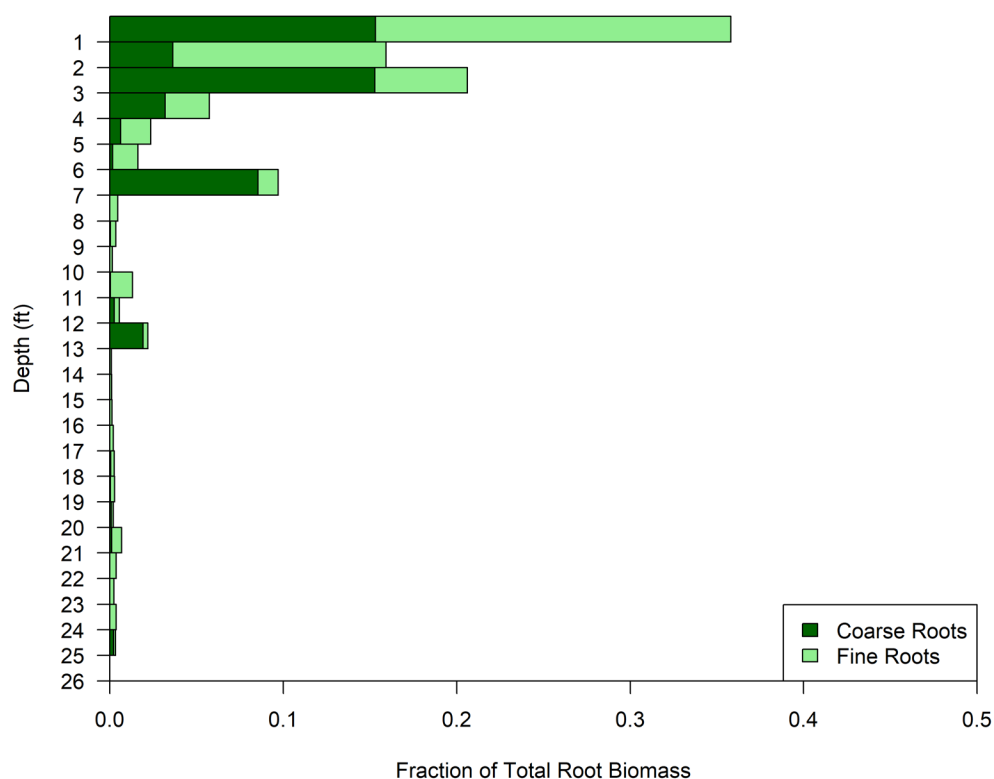


### 3.4 ROOT DEPTH DISTRIBUTION

In order to examine the effects of soil moisture on  $\Psi_{pd}$  and  $\Psi_{md}$ , depth bins were created based on coarse and fine root distribution throughout the soil profile using root distribution data collected during the 2020 piezometer installation. An aggregation of all coarse and fine root data (mass) was compiled across all VDAs. This was done, in part, to account for any sampling bias that may occur from attempting to describe root depth distribution throughout an entire VDA from a single borehole.

Based on this aggregation, the resulting depth bins were created from the cumulative sum of all coarse and fine roots to represent the depths within which most roots were found. These bins were 0 – 91 m, 91 – 2.13 m, and 2.13 – 4.89 m. Correlations between VWC and PAW values within the depth bins and  $\Psi_{pd}$  and  $\Psi_{md}$  were examined.  $\Psi_{pd}$  showed a significant positive correlation with both PAW and VWC measured at 0 to 91 m ( $R^2=0.40$ ,  $p<0.0001$  and  $R^2=0.57$ ,  $p<0.0001$ , respectively).  $\Psi_{md}$  also showed a significant positive correlation with PAW and VWC measured at 0 to 91 cm ( $R^2=0.47$ ,  $p<0.0001$  and  $R^2=0.63$ ,  $p<0.0001$ , respectively). Water potential values were not related to VWC or PAW in deeper portions of the soil profile. In general, relationships between PAW and  $\Psi$  were weaker than relationships between VWC and  $\Psi$ .

**FIGURE 4. ROOT DEPTH DISTRIBUTION FOR *S. VERMICULATUS* COLLECTED DURING THE INSTALLATION OF PIEZOMETERS IN LATE 2020. DATA SHOWN BELOW ARE AN AGGREGATION OF FINE AND COARSE ROOT MASSES ACROSS ALL VDAs.**



### 3.5 GROUNDWATER ELEVATION MONITORING

In total, 32 months of groundwater elevation data have been collected from the piezometers installed in the VDAs. Across all VDAs, average depth to groundwater ranged from 1.43 m (VDA03B) to 6.81 m (VDA02B). Seasonal trends in groundwater elevation are apparent, with periods of groundwater recharge occurring through the fall and winter (approximately October 1 – April 20) and groundwater decline occurring in spring and summer (approximately April 21 – September 30). The magnitude of these changes varies across VDAs. In VDA05A, groundwater elevation increases 92 cm on average each year (Table 3). Conversely, groundwater elevation increased only 2 cm on average for VDA02B (Table 3). Studies have shown that roots of *S. vermiculatus* can reach depths of up to 6 m (Shantz and Piemeisel 1940; Robertson 1983) indicating that shrubs within the VDAs likely have year-round access to groundwater and/or deep soil moisture due to capillary rise.

**FIGURE 5. DEPTH TO GROUNDWATER IN METERS FROM NOVEMBER 2020 TO JUNE 2023. AREAS SHADED IN BLUE REPRESENT PERIODS OF GROUNDWATER RECHARGE (OCTOBER 1 - APRIL 20). AREAS SHADED IN RED REPRESENT TIMES OF GROUNDWATER DECLINE (APRIL 21 - SEPTEMBER 30). ALL DATA WERE DOWNLOADED MONTHLY FROM PIEZOMETERS WITHIN THE VDAS.**

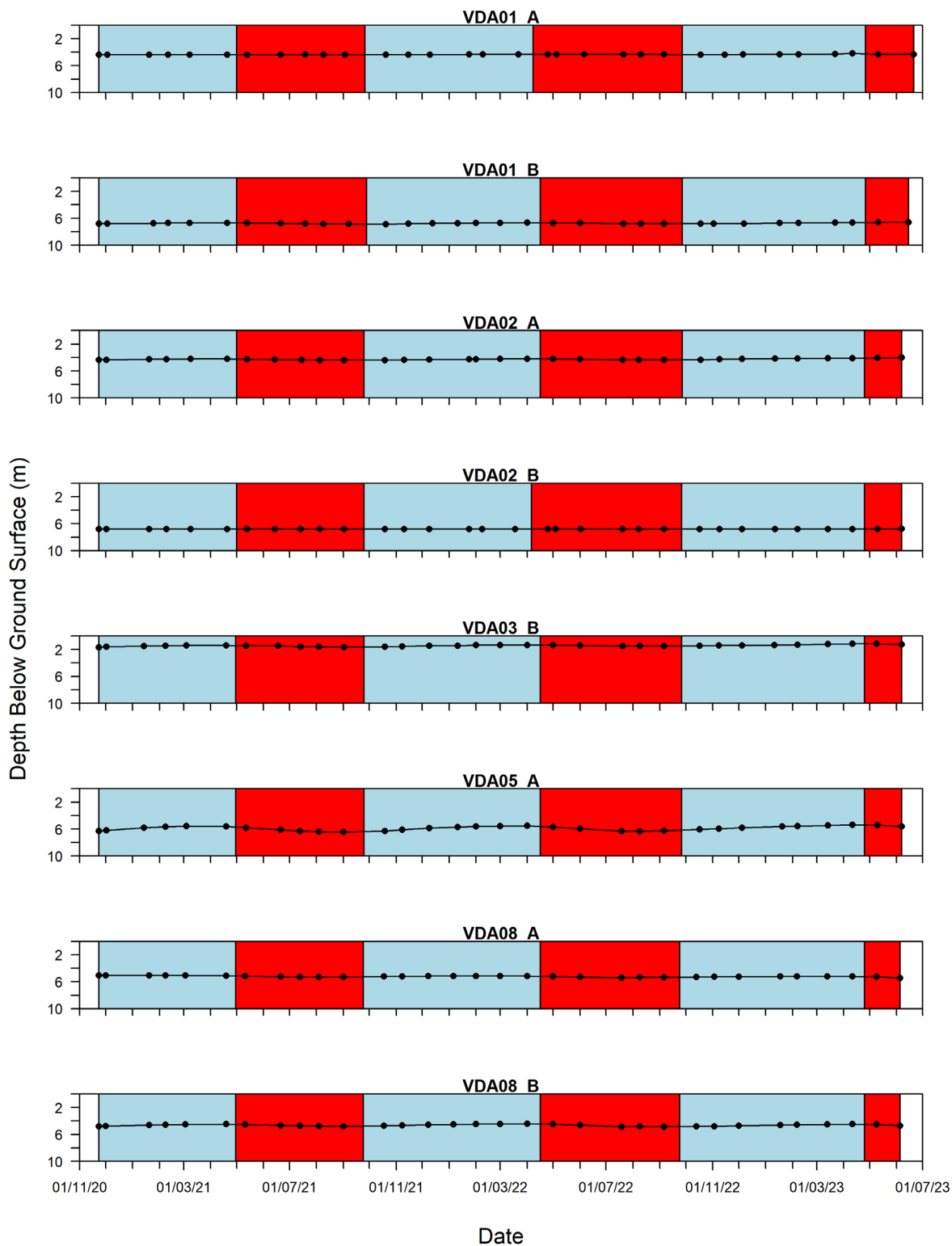


**TABLE 3. MINIMUM, MAXIMUM, AND MEAN DEPTH TO GROUNDWATER (DTW), MINIMUM, MAXIMUM, AND MEAN GROUNDWATER SURFACE ELEVATION (GWSE), AND SEASONAL GROUNDWATER ELEVATION CHANGE FOR DATA COLLECTED AT THE VDAS BETWEEN NOVEMBER 2020 - JUNE 2023.**

| Piezometer | Season   | Min DTW (m) | Max DTW (m) | Mean DTW (m) | Min GWSE (m-amsl) | Max GWSE (m-amsl) | Mean GWSE (m-amsl) | Max - Min (cm) |
|------------|----------|-------------|-------------|--------------|-------------------|-------------------|--------------------|----------------|
| VDA01A     | Decline  | 4.34        | 4.37        | 4.36         | 1096.50           | 1096.53           | 1096.51            | 3              |
|            | Recharge | 4.21        | 4.37        | 4.35         | 1096.50           | 1096.66           | 1096.52            | 16             |
| VDA01B     | Decline  | 6.68        | 6.84        | 6.77         | 1091.33           | 1091.49           | 1091.40            | 16             |
|            | Recharge | 6.65        | 6.87        | 6.74         | 1091.30           | 1091.52           | 1091.43            | 22             |
| VDA02A     | Decline  | 4.22        | 4.39        | 4.32         | 1095.41           | 1095.58           | 1095.48            | 17             |
|            | Recharge | 4.08        | 4.38        | 4.25         | 1095.41           | 1095.71           | 1095.55            | 30             |
| VDA02B     | Decline  | 6.81        | 6.82        | 6.81         | 1102.42           | 1102.43           | 1102.42            | 1              |
|            | Recharge | 6.80        | 6.82        | 6.81         | 1102.42           | 1102.43           | 1102.42            | 2              |
| VDA03B     | Decline  | 1.34        | 1.64        | 1.50         | 1096.31           | 1096.61           | 1096.45            | 30             |
|            | Recharge | 1.16        | 1.70        | 1.42         | 1096.25           | 1096.79           | 1096.53            | 54             |
| VDA05A     | Decline  | 5.72        | 6.46        | 6.16         | 1096.49           | 1097.23           | 1096.78            | 74             |
|            | Recharge | 5.38        | 6.30        | 5.78         | 1096.64           | 1097.56           | 1097.16            | 92             |
| VDA08A     | Decline  | 5.17        | 5.38        | 5.29         | 1100.93           | 1101.14           | 1101.02            | 21             |
|            | Recharge | 5.04        | 5.31        | 5.16         | 1101.00           | 1101.27           | 1101.15            | 27             |
| VDA08B     | Decline  | 4.50        | 4.81        | 4.67         | 1098.90           | 1099.20           | 1099.04            | 30             |
|            | Recharge | 4.42        | 4.84        | 4.61         | 1098.87           | 1099.29           | 1099.10            | 42             |

## 3.6 PLANT PHYSIOLOGICAL RESPONSES

### 3.6.1 XYLEM WATER POTENTIAL

From May 2022 to May 2023, the minimum predawn xylem pressure potential ( $\Psi_{pd}$ ) observed was -4.05 MPa and the maximum was -0.45 MPa (Figure 6). The minimum midday xylem pressure potentials ( $\Psi_{md}$ ) observed was -5.70 MPa and the maximum was -1.19 MPa (Figure 6). Across VDAs, mean  $\Psi_{pd}$  ranged from -0.67 MPa to -3.58 MPa and mean  $\Psi_{md}$  ranged from -1.67 MPa to -4.99 MPa.

A significant Date x VDA interaction was detected for  $\Psi_{pd}$  ( $F = 7.5$ ,  $P < 0.0001$ ) indicating that differences in  $\Psi_{pd}$  varied among VDAs over time. In May 2022, VDA05A had a significantly higher  $\Psi_{pd}$  ( $-1.85 \pm 0.10$  MPa) (mean  $\pm$  standard error) than VDA02A ( $-2.76 \pm 0.06$  MPa) and VDA02B ( $-2.51 \pm 0.12$  MPa). In July 2022, VDA03B showed significantly higher  $\Psi_{pd}$  ( $-2.83 \pm 0.21$  MPa) than VDA02A ( $-3.58 \pm 0.15$  MPa).

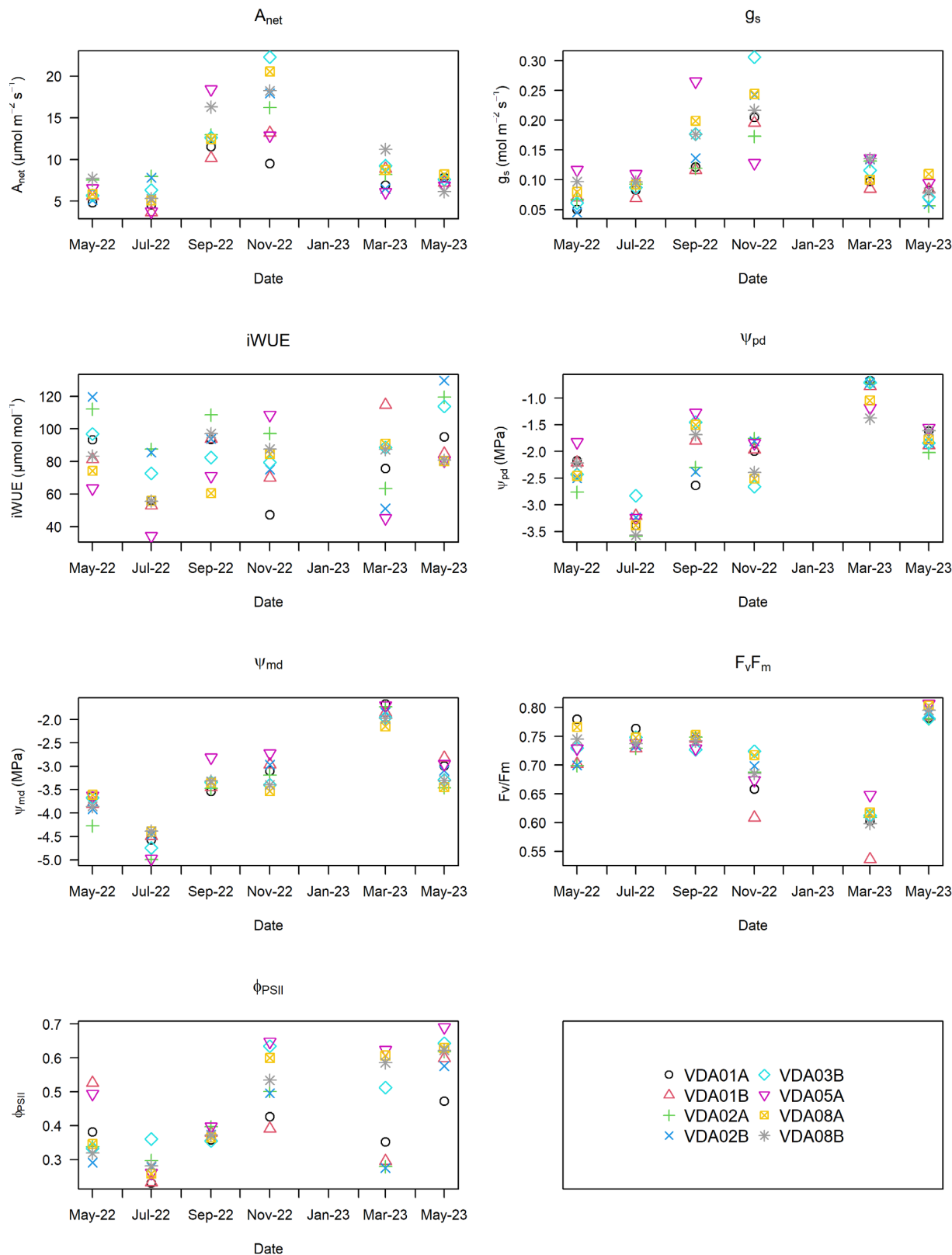
MPa) and VDA08B ( $-3.57 \pm 0.08$  MPa). In September 2022, VDA01B, VDA03B, VDA05A, VDA08A, and VDA08B exhibited higher  $\Psi_{pd}$  ( $-1.45$  to  $-1.80$  MPa) than VDA01A, VDA02A, and VDA02B ( $-2.30$  to  $-2.63$  MPa). In November 2022, VDA01A, VDA01B, VDA02A, VDA02B, and VDA05A exhibited higher  $\Psi_{pd}$  ( $-1.76$  to  $-1.99$  MPa) than VDA03B, VDA08A, and VDA08B ( $-2.39$  to  $-2.66$  MPa). In March 2023, VDA01A showed higher  $\Psi_{pd}$  ( $-0.67 \pm 0.07$  MPa) than VDA08B ( $-1.38 \pm 0.08$  MPa). There were no significant differences in  $\Psi_{pd}$  among VDAs in May 2023.  $\Psi_{pd}$  and  $\Psi_{md}$  were lowest in July 2022 ( $-3.30$  MPa and  $-4.63$  MPa) and highest in March 2023 ( $-0.90$  MPa and  $-1.86$  MPa) (Figure 6).

A significant Date x VDA interaction was observed for  $\Psi_{md}$  ( $F=2.83$ ,  $P<0.0001$ ) indicating that differences in  $\Psi_{md}$  varied among VDAs over time. Tukey post-hoc comparisons indicated that VDA differences in  $\Psi_{md}$  were only significant in November 2022. In November 2022, VDA08A had lower  $\Psi_{md}$  ( $-3.53 \pm 0.15$  MPa) than VDA05A ( $-2.73 \pm 0.07$  MPa).

**TABLE 4. ANALYSIS OF VARIANCE OF MEASUREMENT DATE, LOCATION (I.E. VDA), AND DATE X LOCATION EFFECTS ON LEAF-LEVEL PHYSIOLOGICAL VARIABLES MEASURED ON *SARCOBATUS VERMICULATUS* BETWEEN MAY 2022 AND MAY 2023. NUMERATOR AND DENOMINATOR DEGREE OF FREEDOM (DF) AND F-VALUES ARE PRESENTED FOR EACH DATE, LOCATION, AND DATE X LOCATION. F-VALUES FOUND TO BE STATISTICALLY SIGNIFICANT ( $P<0.001$ ) ARE DENOTED WITH “\*\*\*”. F-VALUES FOUND TO BE STATISTICALLY SIGNIFICANT ( $P<0.01$ ) ARE DENOTED WITH “\*\*”.  $G_s$  DATA WERE LOG TRANSFORMED TO FULFILL ASSUMPTIONS OF NORMALCY.**

|                              | Date |            | VDA |          | Date x VDA |         |
|------------------------------|------|------------|-----|----------|------------|---------|
| Variable                     | df   | F          | df  | F        | df         | F       |
| $A_{net}$                    | 5    | 79.41***   | 7   | 4.93***  | 35         | 2.31*** |
| $g_s$                        | 5    | 67.97***   | 7   | 5.13***  | 35         | 2.56*** |
| $\Psi_{pd}$                  | 5    | 353.21***  | 7   | 5.89***  | 35         | 7.48*** |
| $\Psi_{md}$                  | 5    | 415.84***  | 7   | 5.86***  | 35         | 2.83*** |
| $F_v/F_m$                    | 5    | 196.36***  | 7   | 7.44***  | 35         | 2.82*** |
| $\Phi_{PSII}$                | 5    | 140.20***  | 7   | 16.98*** | 35         | 7.55*** |
| Stem growth<br>(March – May) | 2    | 1055.04*** | 7   | 10.0***  | 14         | 2.54**  |

**FIGURE 6. MEAN MONTHLY VALUES OF  $A_{\text{net}}$ ,  $g_s$ ,  $i\text{WUE}$ ,  $\Psi_{\text{pd}}$ ,  $\Psi_{\text{md}}$ ,  $F_vF_m$ , AND  $\Phi_{\text{PSII}}$  FOR VDA01A, VDA01B, VDA02A, VDA03B, VDA05A, VDA08A, AND VDA08B. DATA WERE COLLECTED BETWEEN MAY 2022 AND MAY 2023.**



### 3.6.2 LEAF GAS-EXCHANGE

Across all timepoints,  $A_{\text{net}}$  was highest in November 2022 ( $16.35 \pm 4.27 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; mean  $\pm$  standard deviation) and lowest in July 2022 ( $5.55 \pm 1.68 \mu\text{mol m}^{-2} \text{s}^{-1}$ ).  $g_s$  was highest in November 2022 ( $0.21 \pm 0.05 \text{ mol m}^{-2} \text{s}^{-1}$ ) and lowest in May 2022 ( $0.07 \pm 0.02 \text{ mol m}^{-2} \text{s}^{-1}$ ). The mean values for  $A_{\text{net}}$  were  $6.10 \pm 1.07$ ,  $5.55 \pm 1.68$ ,  $13.34 \pm 2.69$ ,  $16.35 \pm 4.27$ ,  $8.22 \pm 1.69$ , and  $7.21 \pm 0.77 \mu\text{mol m}^{-2} \text{s}^{-1}$  for May 2022, July 2022, September 2022, November 2022, March 2023, and May 2023, respectively (Figure 6). The mean values for  $g_s$  were  $0.07 \pm 0.02$ ,  $0.09 \pm 0.01$ ,  $0.16 \pm 0.05$ ,  $0.21 \pm 0.05$ ,  $0.12 \pm 0.02$ ,  $0.08 \pm 0.02 \text{ mol m}^{-2} \text{s}^{-1}$  for May 2022, July 2022, September 2022, November 2022, March 2023, and May 2023, respectively (Figure 6).

A significant Date  $\times$  VDA interaction was found for  $A_{\text{net}}$  ( $F=2.3$ ,  $P<0.0001$ ) and  $g_s$  ( $F=2.6$ ,  $P<0.0001$ ) (Table 4), indicating that differences in gas exchange measurements for each VDA varied over time (Figure 6). In November 2022,  $A_{\text{net}}$  was higher in VDA03B ( $22.3 \pm 1.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; mean  $\pm$  standard error) and VDA08A ( $20.5 \pm 1.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) than VDA01A ( $9.5 \pm 0.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), VDA01B ( $13.2 \pm 1.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), and VDA05A ( $12.9 \pm 0.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). The differences observed in November 2022 were the greatest across the entire study period. Significant differences were also observed in September 2022, with VDA05A ( $18.4 \pm 3.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) being higher than VDA01B ( $10.2 \pm 2.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). No differences in  $A_{\text{net}}$  were found among VDAs in the remaining timepoints.

Temporal variation in  $A_{\text{net}}$  and  $g_s$  were partially driven by temperature and vapor pressure deficit (VPD). A cubic function described the peaked relationship between  $A_{\text{net}}$  and leaf temperature (Figure 7), with optimal conditions for photosynthesis occurring when leaf temperature was approximately  $20^\circ\text{C}$  ( $R^2=0.22$ ,  $P<0.0001$ ). A logarithmic function described the negative relationship between  $A_{\text{net}}$  and VPD, with the variability in  $A_{\text{net}}$  and the fitted model decreasing as VPD increases. The highest rates of  $A_{\text{net}}$  occurred when VPD was between 1 and 2 kPa (Figure 7). Additionally, a cubic function described the peaked relationship between  $g_s$ , leaf temperature, and VPD ( $R^2 = 0.23$ ,  $P < 0.0001$ ) (Figure 7) and ( $R^2 = 0.31$ ,

$P < 0.0001$ ) (Figure 7), respectively.  $g_s$  was highest when leaf temperature was approximately 20 °C and VPD was between 1 and 2 kPa. Across all timepoints, net photosynthesis increased as stomatal conductance increased (Figure 7). There was a weak but significant relationship between  $A_{net}$  and  $\Psi_{pd}$  ( $R^2 = 0.02$ ,  $P < 0.008$ ) and  $g_s$  and  $\Psi_{pd}$  ( $R^2 = 0.02$ ,  $P < 0.03$ ) (Figure 8) across all timepoints. Slightly more significant relationships were observed between  $A_{net}$  and  $\Psi_{md}$  ( $R^2 = 0.03$ ,  $P < 0.002$ ) and  $g_s$  and  $\Psi_{md}$  ( $R^2 = 0.02$ ,  $P < 0.007$ ) (Figure 8) indicating that increased midday water status is a significant factor affecting rates of photosynthesis and stomatal conductance.

**FIGURE 7. CORRELATIONS BETWEEN GAS EXCHANGE VARIABLES, INCLUDING  $A_{\text{NET}}$ , VPD,  $G_s$ , AND LEAF TEMPERATURE ( $^{\circ}\text{C}$ ) FOR DATA COLLECTED AT VDA01A, VDA01B, VDA02A, VDA03B, VDA05A, VDA08A, AND VDA08B BETWEEN MAY 2022 AND MAY 2023.**

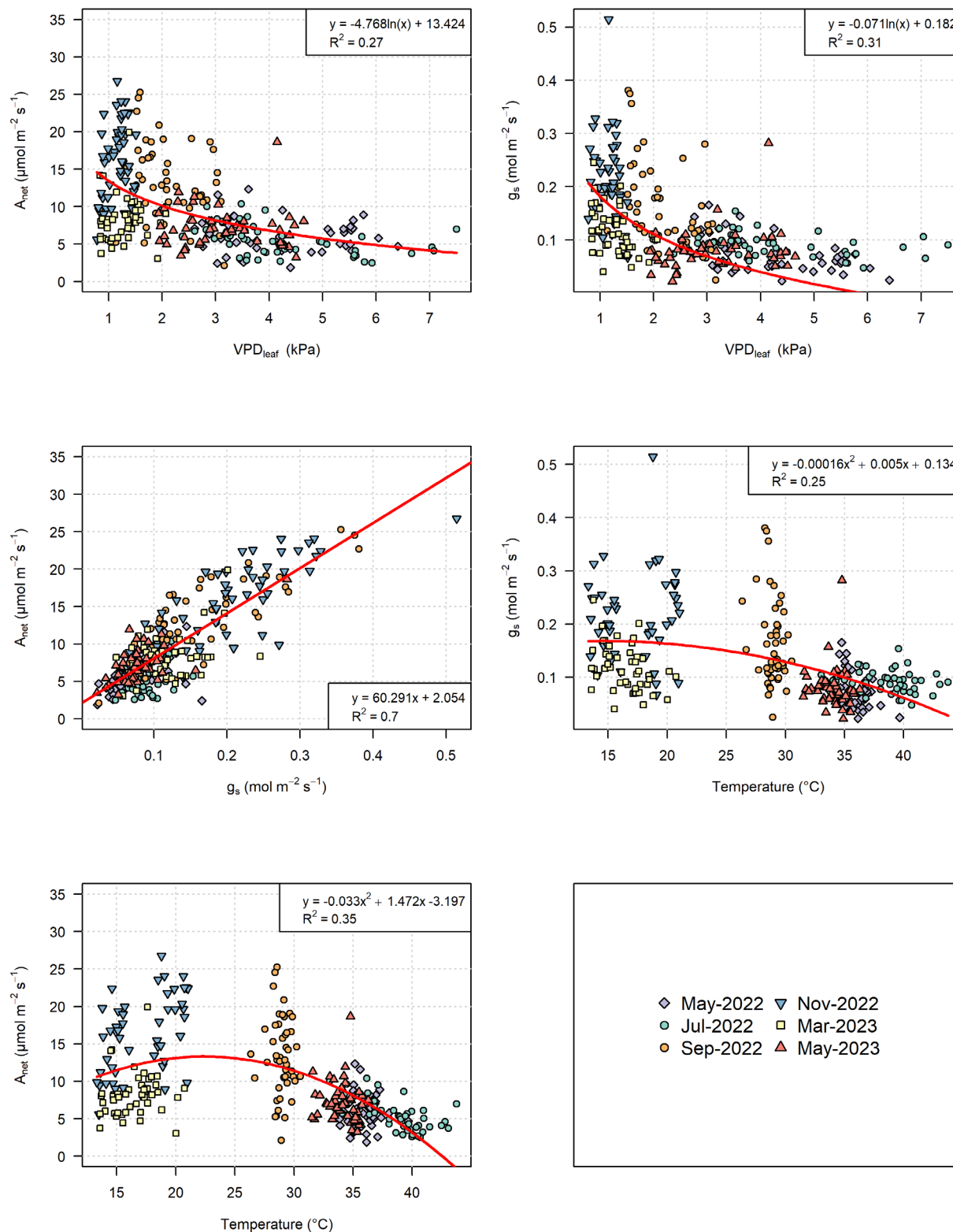
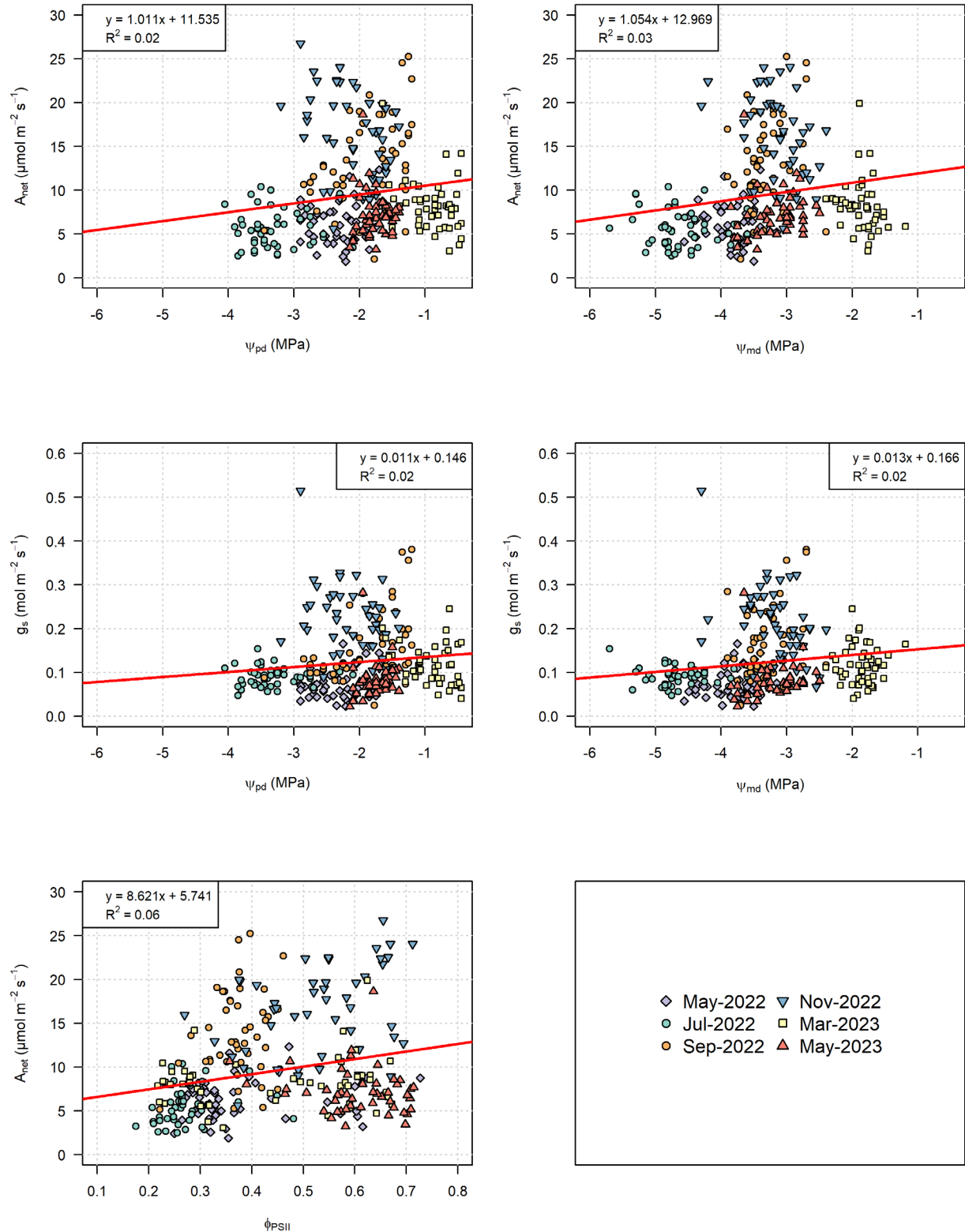


**FIGURE 8. CORRELATIONS BETWEEN GAS EXCHANGE VARIABLES INCLUDING  $A_{\text{NET}}$ ,  $G_s$ ,  $\Phi_{\text{PSII}}$ ,  $\Psi_{\text{PD}}$ , AND  $\Psi_{\text{MD}}$  FOR DATA COLLECTED AT VDA01A, VDA01B, VDA02A, VDA03B, VDA05A, VDA08A, AND VDA08B BETWEEN MAY 2022 AND MAY 2023.**



### 3.6.3 LEAF CHLOROPHYLL FLUORESCENCE

Across the six sampling dates, the minimum  $F_v/F_m$  value was 0.45, and the maximum was 0.82. The minimum  $\Phi_{PSII}$  value was 0.18 and the maximum was 0.73 (Figure 6). The average values for  $F_v/F_m$  were  $0.73 \pm 0.05$  (mean  $\pm$  standard deviation),  $0.74 \pm 0.03$ ,  $0.74 \pm 0.02$ ,  $0.68 \pm 0.05$ ,  $0.61 \pm 0.05$ , and  $0.79 \pm 0.02$  for May 2022, July 2022, September 2022, November 2022, March 2023, and May 2023, respectively (Figure 6). The average values for  $\Phi_{PSII}$  were  $0.38 \pm 0.12$ ,  $0.27 \pm 0.06$ ,  $0.37 \pm 0.05$ ,  $0.53 \pm 0.11$ ,  $0.44 \pm 0.16$ , and  $0.61 \pm 0.08$  for May 2022, July 2022, September 2022, November 2022, March 2023, and May 2023, respectively (Figure 6). Average  $F_v/F_m$  was lowest in March 2023 ( $0.61 \pm 0.05$ ) and highest in May 2023 ( $0.79 \pm 0.02$ ).

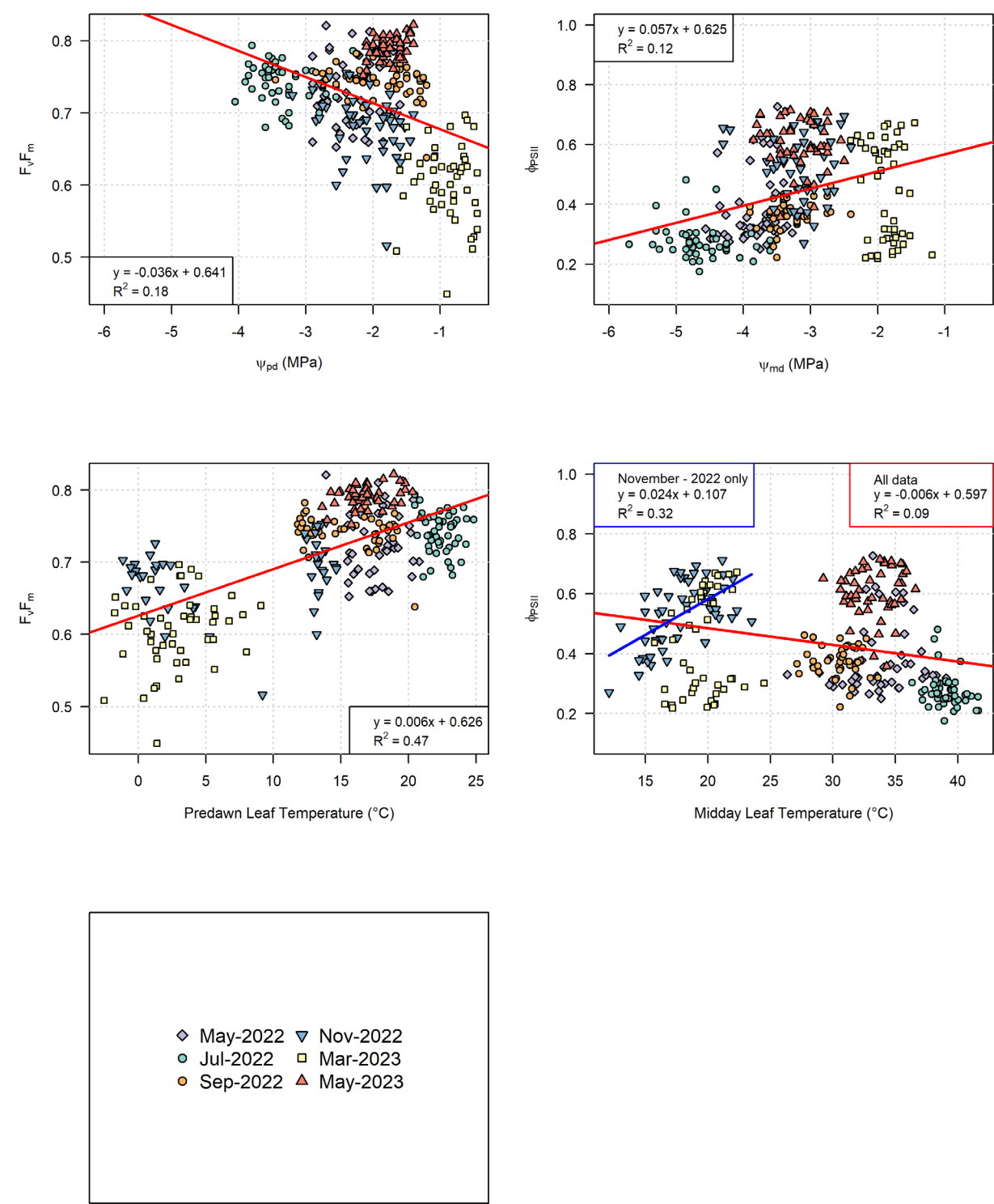
A significant Date x VDA interaction was observed for  $F_v/F_m$  ( $F = 2.83$ ,  $P < 0.0001$ ) suggesting that differences in  $F_v/F_m$  among VDAs varied over time. In May 2022, VDA01A showed significantly higher  $F_v/F_m$  ( $0.78 \pm 0.08$  (standard error)) than VDA01B ( $0.70 \pm 0.01$ ), VDA02A ( $0.70 \pm 0.01$ ) and VDA02B ( $0.70 \pm 0.01$ ) (Figure 6). No significant difference in mean  $F_v/F_m$  was found among VDAs for July or September 2022. In November 2022, VDA01B had the lowest  $F_v/F_m$  ( $0.61 \pm 0.02$ ) across all VDAs ( $0.69$  to  $0.72$ ) except for VDA01A ( $0.66 \pm 0.01$ ) and VDA05A ( $0.67 \pm 0.01$ ) (Figure 6). In March 2023, VDA01B exhibited lower  $F_v/F_m$  ( $0.54 \pm 0.03$ ) than VDA02B ( $0.62 \pm 0.01$ ), VDA03B ( $0.61 \pm 0.03$ ), VDA05A ( $0.65 \pm 0.01$ ), and VDA08A ( $0.62 \pm 0.02$ ). Mean  $F_v/F_m$  did not differ among VDAs in May 2023.

A positive relationship was observed between  $F_v/F_m$  and predawn leaf temperature ( $R^2 = 0.47$ ,  $P < 0.0001$ ). Low temperatures in November 2022 and March 2023, some of which were below freezing ( $0^\circ\text{C}$ ), were associated with low  $F_v/F_m$  values. A negative relationship between  $F_v/F_m$  and  $\Psi_{pd}$  was observed across all data indicating that higher  $F_v/F_m$  values were associated with lower (more negative)  $\Psi_{pd}$ . This relationship is likely driven by the negative relationship between  $\Psi_{pd}$  and predawn leaf temperature ( $R^2 = 0.41$ ,  $P < 0.0001$ ).

Across the six sampling dates, minimum  $\Phi_{PSII}$  was 0.18 and maximum  $\Phi_{PSII}$  was 0.73 (Figure 6). Average  $\Phi_{PSII}$  was lowest in July 2022 ( $0.27 \pm 0.06$ ) and highest in May 2023 ( $0.61 \pm 0.08$ ). The average values for  $\Phi_{PSII}$  were  $0.38 \pm 0.12$ ,  $0.27 \pm 0.06$ ,  $0.37 \pm 0.05$ ,  $0.53 \pm 0.11$ ,  $0.44 \pm 0.16$ , and  $0.61 \pm 0.08$  for May 2022, July 2022, September 2022, November 2022, March 2023, and May 2023, respectively (Figure 6). A significant Date x VDA interaction was observed for  $\Phi_{PSII}$  ( $F = 7.55$ ,  $P < 0.0001$ ) suggesting that differences in  $\Phi_{PSII}$  among VDAs were not consistent over time. In May 2022, VDA01B and VDA05A ( $0.53 \pm 0.04$  and  $0.49 \pm 0.08$ , respectively) had the highest  $\Phi_{PSII}$  than all other VDAs (mean  $\Phi_{PSII} = 0.29 - 0.38$ ). No significant difference in mean  $\Phi_{PSII}$  was found among VDAs for July or September 2022. In November 2022, VDA01A had lower  $\Phi_{PSII}$  ( $0.43 \pm 0.03$ ) than VDA03B ( $0.63 \pm 0.01$ ), VDA05A ( $0.65 \pm 0.02$ ), and VDA08A ( $0.60 \pm 0.04$ ). In March 2023, VDA01A, VDA01B, VDA02A, and VDA02B had lower  $\Phi_{PSII}$  (mean  $\Phi_{PSII} = 0.28 - 0.35$ ) than the rest of the VDAs (mean  $\Phi_{PSII} = 0.51 - 0.62$ ). In May 2023, VDA01A had lower  $\Phi_{PSII}$  ( $0.47 \pm 0.04$ ) than VDA03B ( $0.64 \pm 0.01$ ) and VDA05A ( $0.69 \pm 0.01$ ).

Temporal variation in  $\Phi_{PSII}$  was not strongly correlated with temperature or plant water status. Across all measurements, a weak but significant negative relationship was observed between  $\Phi_{PSII}$  and midday leaf temperature, though leaf temperature only explained 9% of the variation in  $\Phi_{PSII}$  ( $P < .0001$ ) (Figure 9) meaning as temperature increased,  $\Phi_{PSII}$  decreased. In November 2022 a positive relationship was observed between  $\Phi_{PSII}$  and midday leaf temperature ( $R^2 = 0.32$ ,  $P < 0.0001$ ) (Figure 9). A positive relationship between  $\Phi_{PSII}$  and  $\Psi_{md}$  was observed across all timepoints, though  $\Psi_{md}$  explained only 12% of the variation in  $\Phi_{PSII}$  (Figure 9).

**FIGURE 9. CORRELATIONS BETWEEN  $F_v F_m$ ,  $\Phi_{PSII}$ ,  $\Psi_{PD}$ ,  $\Psi_{MD}$ , AND LEAF TEMPERATURE FOR VDA01A, VDA01B, VDA02A, VDA03B, VDA05A, VDA08A, AND VDA08B ACROSS SAMPLING POINTS BETWEEN MAY 2022 AND MAY 2023.**

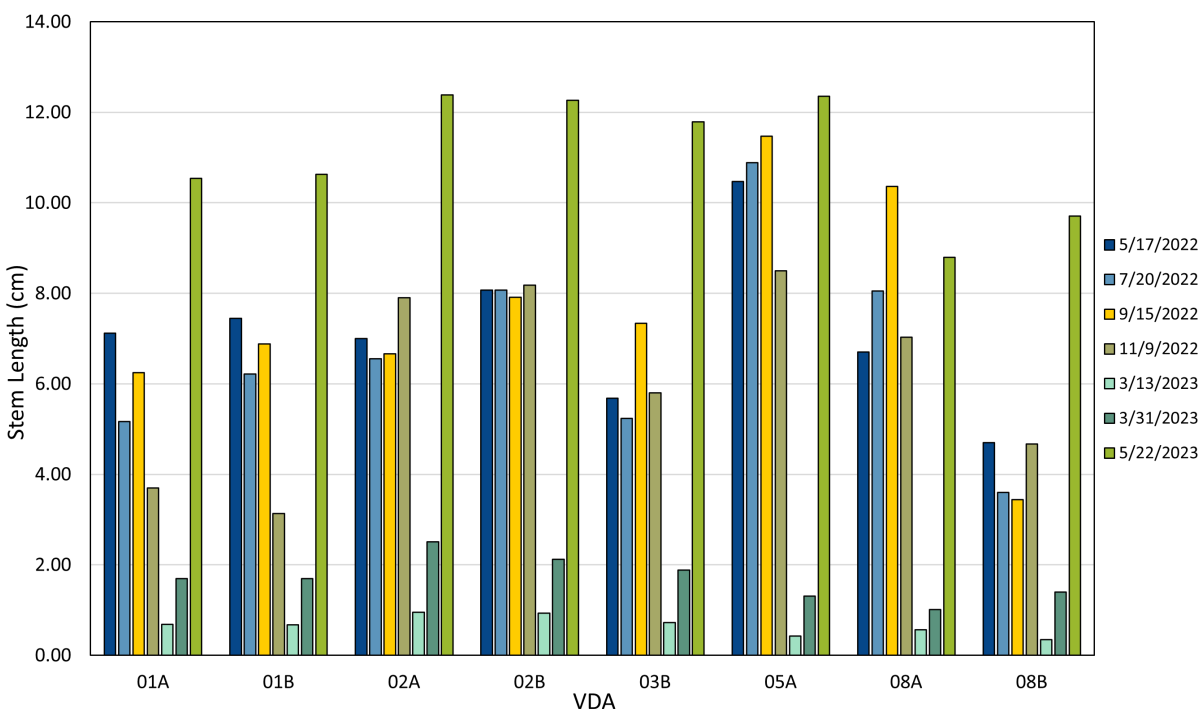


### 3.6.4 STEM GROWTH

From May 2022 to May 2023, the minimum stem length observed was 0.2 cm in March 2023 and the maximum was 22.60 cm in May 2023. Across all VDAs, mean stem length ranged from  $7.15 \pm 0.43$  (mean  $\pm$  standard error),  $6.72 \pm 0.54$ ,  $7.58 \pm 0.66$ ,  $6.11 \pm 0.40$ ,  $1.18 \pm 0.07$ , and  $11.06 \pm 0.56$  cm for May 2022, July 2022, September 2022, November 2022, March 2023, and May 2023, respectively. Average shoot length remained relatively constant between May 2022 and September 2022, indicating that growth had effectively ceased during the late spring and summer.

No significant Date x VDA interaction was found for shoot length during May 2022 – September or September – November. A significant Date x VDA interaction was found for shoot length between March – May 2023 ( $F= 2.54$ ,  $p= 0.003$ ). Small variations in shoot length were observed among the VDAs in early March 2023, with the longest initial length in VDA02A ( $0.95 \pm 0.03$  cm) and VDA02B ( $0.93 \pm 0.07$  cm) and smallest lengths in VDA08B ( $0.35 \pm 0.04$  cm). In the second March 2023 sampling period VDA02A ( $2.51 \pm 0.12$  cm) and VDA02B ( $2.12 \pm 0.17$  cm) had shoot lengths that were longer than VDA05A ( $1.31 \pm 0.27$  cm) and VDA08B ( $1.40 \pm 0.12$  cm). Shoot lengths did not differ between VDAs in May 2023.

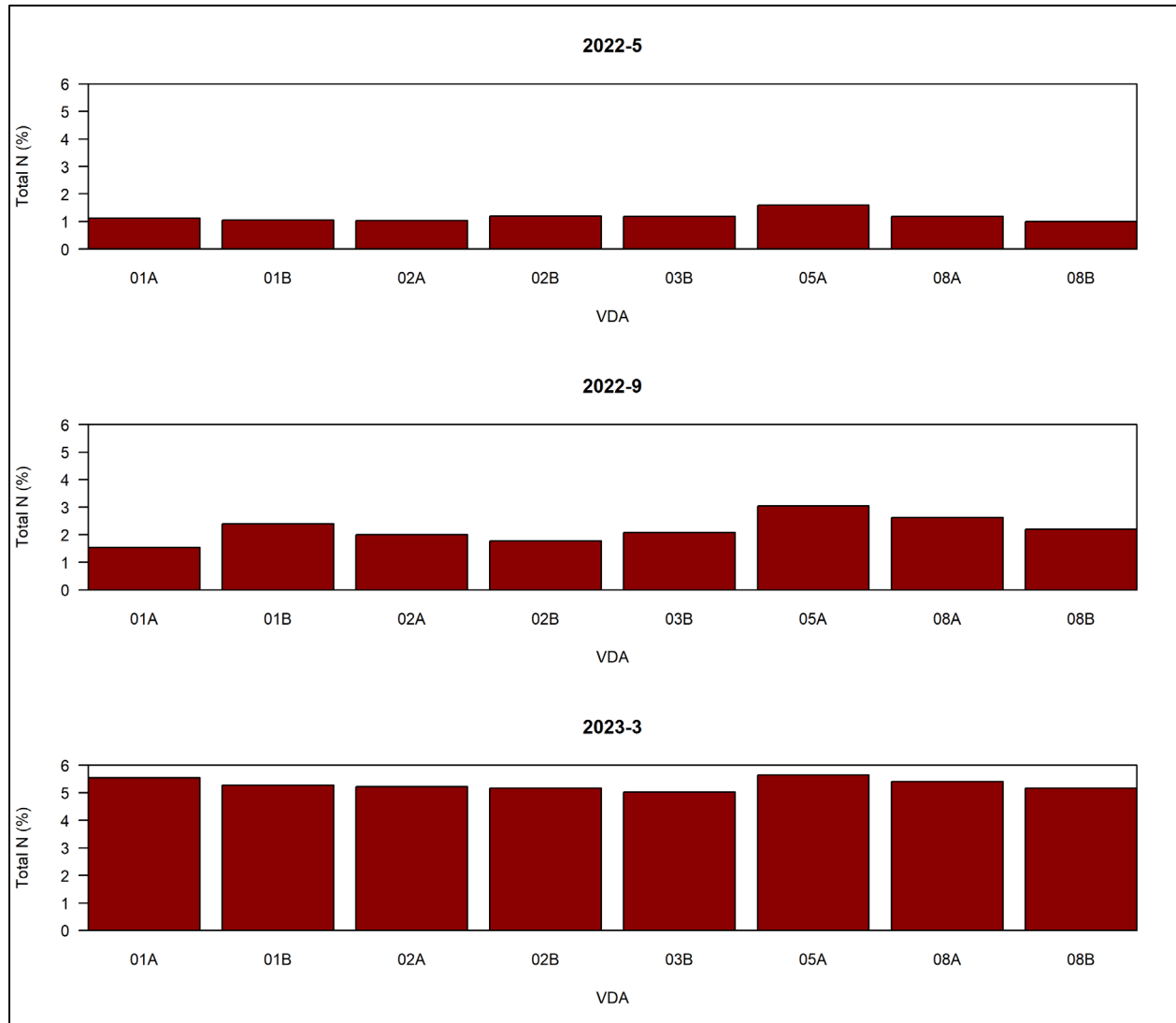
**FIGURE 10. MEAN VDA SHOOT LENGTH MEASUREMENTS (CM) COLLECTED BETWEEN MAY 2022 AND MAY 2023. THE SAME STEM WAS MEASURED IN MAY AND JULY 2022. FIVE NEW STEMS WERE MEASURED AND AVERAGED FOR SEPTEMBER. THREE STEMS WERE MEASURED AND AVERAGED IN NOVEMBER. TWO STEMS, ONE NORTHERLY AND ONE SOUTHERLY, WERE MEASURED IN MARCH AND MAY 2023.**



### 3.6.5 LEAF NITROGEN CONTENT

Percent leaf N increased nearly fivefold between May 2022 and March 2023 (Figure 11). Average percent N was  $1.17 \pm 0.31$  (mean  $\pm$  standard error),  $2.20 \pm 0.89$ , and  $5.31 \pm 0.43$  for May 2022, September 2022, and March 2023, respectively. The highest percent N (5.68%) was observed at VDA05A during March 2023. The lowest percent N (1.0%) was observed at VDA08B in May 2022. No significant Date  $\times$  VDA interaction was observed, indicating that differences in nitrogen content for each VDA did not vary over time.

**FIGURE 11. TOTAL PERCENT NITROGEN FOR *S. VERMICULATUS* LEAF SAMPLES COLLECTED AT VDA01A, VDA01B, VDA02A, VDA03B, VDA05A, VDA08A, AND VDA08B DURING MAY 2022, SEPTEMBER 2022, AND MARCH 2023.**



## 4 DISCUSSION

The purpose of this research was to investigate the effects of surface water inputs on the growth and function of the phreatophytic shrub *S. vermiculatus* after consecutive years of drought. Given that these shrubs have access to deep soil moisture and the environment that these shrubs inhabit is typically one with erratic, low levels of precipitation do they, in times of prolonged drought, invest limited resources into shallow roots and utilize surface water to promote growth and function. We found a significant relationship between VWC and PAW within the top 0.91 m of soil and the water status of the

shrubs ( $\Psi_{pd}$  and  $\Psi_{md}$ ) and that values increased in timepoints following rain events. We also found that increased water status (higher, less negative  $\Psi$ ) was correlated with higher levels of  $A_{net}$ ,  $g_s$ ,  $F_v/F_m$ , and  $\Phi_{PSII}$ . These results suggest that although surface soil conditions have been predominantly dry throughout the recent megadrought, *S. vermiculatus* was able to capture available surface moisture in late 2022 and early 2023. Understanding the ways in which *S. vermiculatus* utilizes surface water is important for predicting the ways in which this ecosystem may be affected by shifts in precipitation patterns resulting from global climate change.

Increased soil water availability resulting from higher-than-average precipitation in both the summer of 2022 and the winter of 2023 resulted in increases in  $\Psi_{pd}$  and  $\Psi_{md}$ ,  $g_s$ , and  $A_{net}$  in *S. vermiculatus*. In the absence of rain, stem water potential declined by roughly 1 MPa from May 2022 to July 2022 across all VDAs. *S. vermiculatus* has deep tap roots that reach the capillary fringe and the shallow groundwater table measured throughout the VDAs. This suggests that  $\Psi$  should remain relatively constant regardless of surface water availability, as has been shown with other phreatophytes such as *Chrysothamnus nauseosus* (Drenovsky and Richards 2006; Flanagan et al. 1992), though this is not the case. One potential explanation as to why we found decreasing  $\Psi$  from May to July 2022 could be due to the bulk of *S. vermiculatus* roots being found roughly within the top 2m of soil, which saw a decrease in VWC between May and July 2022 (Figure 3). This resulted in little to no surface water being available for shallow roots to utilize therefore limiting their capacity for water uptake. Additionally, Donovan et al. (1996) suggested that deep roots of *S. vermiculatus* may have low hydraulic conductivity due primarily to unfavorable osmotic (rather than hydrostatic) gradients during periods of decreased transpiration, such as at night. This low conductivity may reduce the ability for *S. vermiculatus* to transport water from deeper soil layers, regardless of access to water, to keep up with high rates of evapotranspiration during dry periods, ultimately resulting in more negative  $\Psi_{pd}$  and  $\Psi_{md}$  in July. Interestingly, shrubs maintained relatively constant water potential gradients (i.e. differences between  $\Psi_{pd}$  and  $\Psi_{md}$ ) over time (Figure 6) regardless

of changes in soil moisture and evaporative demand. Franks et al. (2007) found a similar trend in *Eucalyptus gomphocephala* and suggests that whole-plant hydraulic conductivity is dependent on water potential gradients rather than absolute water potential. Further studies are needed to test this hypothesis in *S. vermiculatus*.

Between July and September, 3.58 cm of rain fell on the VDAs, resulting in a 1.43 and 1.30 MPa increase in  $\Psi_{pd}$  and  $\Psi_{md}$ , respectively. Although coarse roots of *S. vermiculatus* were found within reach of the regional surficial aquifer, a majority of the total cumulative root biomass was found within the top 0.9 m of soil. This is likely why there was a significant correlation between increased VWC and PAW in the 0.9 m of soil and increased plant water status. The advantages of this root morphology are twofold: 1) *S. vermiculatus* can capture and utilize pulses of precipitation and run-on when they occur and 2) when moisture is available in the vadose zone, plants can uptake inorganic nitrogen via mass flow (Trent et al. 1997). As PAW in the vadose zone declines, *S. vermiculatus* must obtain a larger fraction of its water from deeper in the soil profile or from groundwater. This may lead to N deficiencies in plants, as lower levels of inorganic N are present within the soil as groundwater is approached (Trent et al. 1997). The effects of summer precipitation on *S. vermiculatus* were apparent, as  $g_s$  and  $A_{net}$  nearly doubled from July to September 2022. The responses from *S. vermiculatus* suggest that this species does indeed utilize summer precipitation and surface soil moisture to drive growth. However, the increase in  $\Psi_{pd}$  and  $\Psi_{md}$  only accounted for 2-3% of variation in  $A_{net}$  and  $g_s$ , indicating that other factors aside from plant water status, such as nitrogen availability (Drenovsky and Richards 2004) and temperature stress (Hamerlynck et al. 2000), affect the ability of *S. vermiculatus* to assimilate carbon.

Substantial leaf drop and new shoot growth was observed in mid-September following the rains in July, August, and early September (Figure 10). New growth was evident on all 48 shrubs, but the growth ranged from small, swollen buds to fully elongated new shoots. In arid environments, precipitation and nutrients are co-limiting, with a majority of N bound in organic material leading to low levels of

productivity and seedling recruitment (Drenovsky and Richards 2004; Breen and Richards 2007). Pulses of precipitation are necessary to activate biological processes and stimulate nutrient cycling, as net primary productivity correlates with annual precipitation (Knapp 2001). Additionally, desert shrubs accumulate and concentrate dead organic matter beneath their canopy, creating “islands of fertility” where a majority of nutrient cycling occurs (Schlesinger and Bernhardt 2013, Schlesinger and Pilmanis 1998). This was evident at our sites, where we observed rainfall dislodging dead or dying leaves from branches and depositing them at the base of the shrubs. Events of this nature are likely a key source of organic matter and nutrient input to this system. Repeated pulses of summer precipitation are shown to drive high rates of nutrient cycling and nutrient availability in desert soils (Misra and Tyler 2000). Since *S. vermiculatus* are N-limited (Drenovsky and Richards 2004; Breen and Richards 2007), the increase in available N likely contributed to the onset of new shoot growth seen in September and November 2022. This new growth had higher N content than leaves measured in May and July 2022 (Figure 11), resulting in higher photosynthetic capacity and thus higher rates of  $A_{net}$ , since photosynthetic capacity is often determined by the N content in leaves (Evans 1989). Conversely, decreasing levels of N-availability results in reduced  $A_{net}$  and  $g_s$  (Farquhar and Sharkey 1982). This may explain why, as N became increasingly unavailable due to plant uptake, rates of  $A_{net}$  decreased, as observed of *S. vermiculatus*, between November and March.

Stomatal responses are driven largely by changes in the humidity of ambient air. Generally, increases in VPD lead to partial or full closure of the stomata (Farquhar and Sharkey 1982; Schulze et al. 1971). During this study, VPD ranged from 0.78 kPa in November to 7.51 kPa in July (Figure 2, Figure 7).  $g_s$  was highest during November and lowest in July, indicating that the optimal range of VPD for *S. vermiculatus* is 1-2 kPa (Figure 7). This may also help to explain why although  $\Psi_{pd}$  was slightly higher in May 2023 than November,  $g_s$  was lower. Average VPD in May 2023 averaged 3.17 kPa, which is beyond the optimal range for *S. vermiculatus*, resulting in lower  $g_s$  values. Additionally,  $g_s$  appeared to decrease once leaf temperature surpassed 30 °C, indicating that the stomata were partially closed. Interestingly,  $g_s$

was lower in March than it was in November, even though VWC and  $\Psi_{pd}$  was higher in March and VPD was within the optimal range (1.35 kPa). This could be partially attributed to variation in leaf age and development of shrubs measured between time points. In November, measurements were taken on fully elongated stems whereas in March 2023, shrubs had varying degrees of leaf maturity. Some sites, including VDA03B and VDA08B, had fully mature leaves during the time of measurement, while other sites, including VDA05A, had shrubs with small, underdeveloped leaves. By May 2023 leaf development across sites was comparable.

The effect of summer rains was evident on rates of photosynthesis, as  $A_{net}$  more than doubled between July and September. This is likely partly due to increased  $\Psi$  which increased  $g_s$  which, in turn, increased rates of  $A_{net}$ . Down-regulation of  $A_{net}$  has been observed in desert shrubs during times of water stress (Huxman et al. 2002). Therefore, the increase in  $A_{net}$  from July to September may be, in part, due to the alleviation of water stress brought on by summer precipitation (i.e. less negative  $\Psi_{pd}$  and  $\Psi_{md}$ ). Additionally, heat stress under drought conditions has been shown to reduce photosynthetic capacity of leaves (Huxman et al. 2002) which may have contributed to the low levels of  $A_{net}$  in July. Reduction of  $g_s$  during dry periods (i.e. May and July 2022) may be fundamental to maintaining tissue hydration in halomorphic soils (Trent et al. 1997). During our study, when temperatures exceeded 30 °C,  $A_{net}$  declined to approximately one half of the optimum rate and continually declined as temperatures increased.  $A_{net}$  was highest when VPD was between 1-2 kPa, as was  $g_s$ . This likely indicates that, in general, the highest rates of  $A_{net}$  occur when VPD is within the optimal range for  $g_s$ . Trent et al. (1997) showed that  $g_s$  declined to a greater extent than  $A_{net}$  in *S. vermiculatus* from above-average water year to a below-average water year. This indicates that  $g_s$  does not directly correlate with  $A_{net}$  in this species (Figure 7).

In March,  $\Psi_{pd}$ ,  $\Psi_{md}$ , VPD, and leaf temperatures were all within optimal ranges, similar to those seen in November (Figure 7, Figure 8), yet  $A_{net}$  was more than double in November than in March (Figure 6). This, in part, may be due to some levels of photoinhibition occurring due to freezing nighttime

temperatures that occurred in March. The collection of physiology data was split over the course of two days due to time constraints. In March, there was a freezing event between the first and second round of measurements. Frost was noted on leaves during predawn measurements, and frost damage (i.e. blackened leaves) was observed later during midday measurements. This frost likely damaged photosystems and reduced photosynthetic capacity, as a nearly two-fold difference can be seen in  $\Phi_{PSII}$  measurements across the data (Figure 6).

As with  $g_s$ , another compounding factor that may have affected  $A_{net}$  throughout the course of this study is differences in leaf age. In July 2022, leaves were fully mature and likely approaching senescence, as leaves were beginning to lose chlorophyll and appear yellow in color. In September, new growth was evident and by November most of those leaves had reached maturity. In March 2023, we captured early onset of juvenile leaves that were, in some cases, only slightly past budburst. Rates of photosynthesis change as leaves age. Rates of photosynthesis often begin slowly in young leaves, increase to maximum levels as leaves reach maturity and then decrease with increasing age (Freeland 1952). This pattern may explain why  $A_{net}$  was low in March even though environmental conditions (i.e.  $\Psi_{pd}$ ,  $\Psi_{md}$ , VPD, leaf temperature) were otherwise favorable.

$F_v/F_m$  showed a positive relationship with temperature, with values being lowest in November and March, likely due to below-freezing nighttime temperatures. Interestingly, a negative relationship was observed between  $F_v/F_m$  and  $\Psi_{pd}$  across all data. This suggests that higher  $F_v/F_m$  values are associated with lower  $\Psi_{pd}$ . This is likely due to the negative relationship between  $F_v/F_m$  and predawn leaf temperature ( $R^2 = 0.41$ ,  $P < 0.0001$ ), suggesting that time points with the highest  $\Psi_{pd}$  were also the coldest which is associated with low  $F_v/F_m$  values.  $\Phi_{PSII}$  had a positive relationship with  $\Psi_{md}$  across all timepoints ( $R^2 = 0.11$ ,  $P < 0.0001$ ), indicating that as water status declined, plants were under increasing levels of stress which in turn limited their capacity for photochemistry. This relationship is likely also influenced by the negative relationship between  $\Phi_{PSII}$  and midday leaf temperature that was observed across all data, except for

November. The positive relationship between  $\Phi_{PSII}$  and leaf temperature observed in November is likely caused by the large range in temperature (12.1 – 23.5°C) during measurements. As midday leaf temperature approached 20°C,  $\Phi_{PSII}$  increased. Interestingly, the highest values for  $\Phi_{PSII}$  were measured during May 2023.  $A_{net}$  was relatively low in May 2023 (similar to values in May and July 2022), indicating that although there was a high capacity for photosynthesis (i.e. high  $\Phi_{PSII}$ ) other factors were limiting its rate. This may be attributed to high midday leaf temperature (30-35°C) and VPD (2-4.5 kPa), both of which are outside of the optimal range for *S. vermiculatus*. A confounding factor of this study is that gas exchange measurements were taken across 3–4-hour windows and across two separate days, as evidenced by the large range in leaf temperature for November. During data collection, environmental conditions including VPD, temperature, and rates of evapotranspiration were subject to change. This may have contributed to differing results across gas exchange and fluorescence data.

The increase in growth,  $\Psi$ , and leaf gas exchange across all data indicates that summer precipitation is not only advantageous for *S. vermiculatus* due to its ability to alleviate drought-induced water stress, but it is important for driving nutrient availability and uptake. This increase in above-ground biomass and subsequent increase in  $A_{net}$  may provide a significant advantage to these shrubs by building photosynthate reserves for use during the next growing season. Increased C reserves can be used to drive production of additional fine roots, thus increasing the plant's ability to uptake water and nutrients in upper soil layers. *S. vermiculatus* behaves like an anisohydric plant, as they keep their stomata open at times where water potential is low enough to cause embolism to continue assimilating carbon (Martin-StPaul et al. 2017; McDowell et al. 2008). This is likely a result of selection pressures that led to xylem that are more resistant to negative water potentials. This allows stomata to stay open at water potentials much higher than that at which embolism can occur, which allows *S. vermiculatus* to maintain carbon assimilation during the dry summer months (Martin-Stpaul 2017). Although this is advantageous in water-limited systems, it also indicates that *S. vermiculatus* may be predisposed to cavitation as they have

smaller hydraulic safety margins if drought conditions are sufficiently severe and sustained (McDowell et al. 2008). As shallow roots cavitate (due to higher  $\Psi$  at the soil surface) functional rooting depth shifts deeper into the soil profile (Sperry and Hacke 2002). Therefore, if drought conditions are sustained over sufficiently long periods of time, *S. vermiculatus* may gradually invest more resources into deep tap roots rather than shallow fine roots.

## 5 CONCLUSION

The results of this study support our hypothesis that, even in times of drought, the phreatophytic shrub *S. vermiculatus* invests resources into shallow root production to capture surface soil moisture when available. Although they have roots that reach the capillary fringe and groundwater tables, uptake of shallow soil moisture increases access to N, a key limiting nutrient. Summer precipitation appears to be an important source of water input to the system and may provide a significant advantage going into the next growing season. VPD and temperature appear to be the most important drivers of  $A_{\text{net}}$  regardless of  $\Psi$ . Further research is needed to determine if *S. vermiculatus* consistently maintains roots in the upper soil layers during drought conditions, or if they have the ability to rapidly produce new roots once surface wetting occurs. The timing and ability to generate and/or activate surface roots when soil moisture is present would provide significant competitive advantages in this arid environment.

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