Excess radiation exacerbates drought stress impacts on canopy conductance along aridity gradients

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Abstract. Stomatal conductance ($g_s$) of all coexisting species regulates transpiration in arid and semiarid grasslands prone to droughts. However, the effect of drought stress on canopy conductance ($G_s$) is debated, and the interactive effects of abiotic and biotic constraints on $G_s$ remain poorly understood. Here, we used $^{18}$O enrichment above the source water ($\Delta^{18}$O) of leaf organic matter as a proxy for $G_s$ in order to increase the understanding of these effects. Three grassland transects were established along aridity gradients on the Loess Plateau (LP), the Inner Mongolian Plateau (MP), and the Tibetan Plateau (TP), which differ with respect to solar radiation and temperature conditions. Results showed that $G_s$ consistently decreased with increasing aridity within transects. $G_s$ on the TP was lower than that on the other two plateaus for a given level of aridity due to low temperature and high radiation. The primary determinant of drought stress on $G_s$ was soil moisture (SM) on the LP and MP, whereas it was the vapor pressure deficit (VPD) on the TP. Solar radiation exhibited a consistently negative effect on $G_s$ via drought stress within transects, while temperature had negative effects on $G_s$ on the TP but no effect on the LP or MP. Adding the interaction of leaf area and abiotic factors increases the percentage of explained variability in $G_s$ by 17 % and 36 % on the LP and MP, respectively, although this is not the case on the TP, where the climate exerts an overwhelming effect. These results highlight the need to integrate multiple stressors and plant properties to determine spatial variability in $G_s$.

1 Introduction

Stomatal conductance ($g_s$) of all coexisting species plays a significant role in water loss (transpiration) and carbon uptake (photosynthesis) at the ecosystem level, thereby coupling the water and carbon cycles (Jarvis and McNaughton, 1986; Martin-StPaul et al., 2017). Model linkages between $g_s$ at the species level and photosynthesis indicate that the biophysical response of $g_s$ at the species level varies depending on water, radiation, temperature, and leaf economic traits (Buckley, 2019; Farquhar et al., 1980; Leuning, 1995; Wright et al., 2004). However, experimental evidence has suggested that the strength of the $g_s$ species-level responses to changing environmental factors varies with species (Galmes et al., 2007) and that changes in environmental factors can have interactive effects on the variability in $g_s$ at the species level (Costa et al., 2015; Douphis et al., 2020; Zeuthen et al., 1997). Plant communities are simultaneously affected in the field by a variety of environmental stressors, and canopy conductance ($G_s$) is the cumulative rate of $g_s$ over time for co-occurring species (Xia et al., 2015). Nevertheless, how interactive effects of multiple environmental stressors and community
traits regulate the spatial patterns of \( G_s \) remains largely unknown.

Drylands cover 41 % of the Earth’s surface (Yao et al., 2020) and drive the variability in the global terrestrial carbon sink (Ahlstrom et al., 2015). The survival, transpiration, and productivity of plants growing in dry areas are simultaneously stressed by drought, high solar radiation, and temperature (Peguero-Pina et al., 2020). In addition, communities respond to drought, solar radiation, and temperature stressors by changing their functional traits (Fyllas et al., 2017; Martin-StPaul et al., 2017); this may ultimately affect \( G_s \). Thus, \( G_s \) in drylands is expected to be influenced by the interaction of drought, high radiation, high temperature, and biotic factors.

\( G_s \) should be primarily limited by drought, which is often characterized by low soil moisture (SM) and a high vapor pressure deficit (VPD), in drylands (Liu et al., 2020). The limitation of SM and the VPD on \( g_s \) at the species level involves two independent mechanisms: (1) low SM (available water in the soil for plant root uptake) reduces the soil water potential and hinders the transport of soil water to leaf; (2) a high VPD reduces the leaf water potential and increases the transpiration demand (Buckley, 2019; Oren et al., 1999). However, there is an ongoing debate regarding the relative role of SM and the VPD in determining the response of \( G_s \) to drought (Kimm et al., 2020; Liu et al., 2020; Novick et al., 2016). For instance, a global analysis demonstrated that SM stress is the dominant driver of \( G_s \) in xeric ecosystems (Novick et al., 2016). However, another study demonstrated that the variability in \( G_s \) in rain-fed maize and soybean over a precipitation gradient (283 to 683 mm per growing season) was mainly determined by the VPD stress (Kimm et al., 2020).

Solar radiation and temperature may directly regulate \( G_s \) (Buckley, 2019; Farquhar et al., 1980; Leuning, 1995) and adjust drought stress (Costa et al., 2015; Doupis et al., 2020; Zeuthen et al., 1997). However, previous studies have shown that the effects of the direction and intensity of solar radiation and temperature on \( g_s \) at the species level strongly depend on their distribution range and the relationship with aridity. For example, the response of \( g_s \) to solar radiation and temperature at the species level generally shows an increasing trend up to optimum values (Xu et al., 2021a), whereas excess radiation (Costa et al., 2015; Doupis et al., 2020; Zeuthen et al., 1997) and a high-temperature-associated high VPD or low SM (Seneviratne et al., 2010) would suppress \( g_s \). However, these effects are obscured by drought stress under natural conditions, which alone causes a reduction in \( g_s \) at the species level (Duan et al., 2008; Fu et al., 2006). Consequently, it is difficult to disentangle whether the decline in \( G_s \) with increasing aridity is simply a consequence of drought stress or an interaction of multiple stressors.

Given that \( g_s \) and photosynthesis are closely correlated at the species level (Leuning, 1995), environmental stressors should have an indirect effect on \( G_s \) by regulating community morphological traits. However, few studies have addressed this topic at the community scale, considering both environmental and plant regulators (Wang and Wen 2022a, b, c). Communities change their morphological functional traits to tolerate environmental stress, including leaf area (LA) and specific leaf area (SLA) (Wright et al., 2017). LA and SLA determine a plant’s capacity to capture light (Poorter et al., 2009), leaf heat exchange (Wright et al., 2017), and the length of the water pathway through leaves (Kang et al., 2021) – all of which are closely related to transpiration and photosynthesis. Previous studies have focused primarily on the patterns of LA and SLA along environmental gradients (Peppe et al., 2011; Wright et al., 2017). For example, small-leaved species prevail in dry, hot, sunny environments or at high elevations (Wright et al., 2017). SLA generally decreases with increasing radiation and drought stress and increases with decreases in temperature (Poorter et al., 2009). Recently, a study conducted on woody species in eastern Qinghai–Tibet, China, showed that LA and stomatal size varied with temperature (Kang et al., 2021), indicating that changes in LA and SLA may play important roles in regulating \( G_s \).

To investigate the interactive effect of environmental stressors and biotic factors on \( G_s \), three grassland transects were established along aridity gradients – one on the Loess Plateau (LP), one on the Inner Mongolian Plateau (MP), and one on the Tibetan Plateau (TP) – in arid and semiarid regions of China. The grassland transects span gradients of precipitation, SM, VPD, solar radiation, and temperature, and they provide an ideal platform for the exploration of the interactive effects of multiple stressors and biotic factors on \( G_s \) (Table S1 in the Supplement). In addition, the three grassland transects experience different solar radiation and temperature conditions at a given aridity, due to the differences in the geographical locations of the three plateaus. The order of the mean annual temperature and solar radiation across the sites is LP > MP > TP and LP < MP < TP, respectively. We hypothesized that (1) increasing solar radiation and/or air temperature along the aridity gradient will exacerbate drought stress impacts on \( G_s \) within transects, (2) high solar radiation and low temperatures will jointly suppress \( G_s \) at a given aridity among transects, and (3) integrating environmental stress and community functional traits will significantly improve the capacity for predicting \( G_s \). To test our hypotheses, time-integrated \( G_s \) was represented by community-weighted \( ^{18} \text{O} \) enrichment above the source water of leaf organic matter (\( \Delta^{18} \text{O} \)) (Cabrera et al., 2021; Hirl et al., 2021).

2 Materials and methods

2.1 Study areas

In this study, we established three grassland transects spanning a broad range of climatic conditions and grassland types.
in arid and semiarid regions (i.e., the Loess Plateau, LP; the Inner Mongolian Plateau, MP; the Tibetan Plateau, TP) in China (Lyu et al., 2021). Transects were 600 km long on the LP, 1200 km on the MP, and 1500 km on the TP. In each transect, we selected 10 sampling sites with increasing aridity from east to west (calculated as 1–mean annual precipitation/potential evapotranspiration). SR and the growing season VPD increased whereas growing season SM decreased with increasing aridity (Table S1). Among transects, differences in aridity (Fig. 1a), precipitation (Figs. 1b, S1a; Table S2), growing season SM (Fig. 1c), community leaf area (Fig. 1h), and SLA (Fig. 1i) were not significant (P > 0.05), whereas differences in the VPD (Figs. 1d, S1b; Table S2), SR (Figs. 1e, S1c; Table S2), and air temperature (Figs. 1f, S1d; Table S2) were significant. More details about the characteristics of climate, soil, and vegetation type at the 30 sampling sites can be found in Lyu et al. (2021).

2.2 Sampling and measurements

2.2.1 Sample processing

A field survey and sample collection were conducted during the peak growing season (July to August) in 2018. Within each of the 30 sites, we delineated eight 1 m × 1 m plots in a 100 m × 100 m sampling area. Plant species (identified by experienced plant taxonomists), the number of species, and the community structure were surveyed (Table S3). Aboveground biomass was collected by species for dry mass and stable isotope analyses.

2.2.2 Leaf area and specific leaf area analysis

Three individuals per site were collected as replications for each species, and 6–10 fresh, healthy, and mature leaves were selected from individuals of each species for LA determination with a portable scanner (CanoScan LiDE 110, Japan). ImageJ software was used to obtain LA values (Schneider et al., 2012). The leaves were then dried at 60 °C and weighed for leaf dry mass. SLA was calculated by dividing LA by leaf dry mass. Dried leaf samples were ground using a ball mill and then oven dried before 18O analysis.

2.2.3 Stable isotope analysis

An isotope ratio mass spectrometer in continuous-flow mode (253 Plus, Thermo Fisher Scientific, Bremen, Germany) coupled with an elemental analyzer (FLASH 2000 HT, Thermo Fisher Scientific, Bremen, Germany) was used to determine δ18O values (Wang et al., 2021a, b). Isotope ratios are expressed as per mil deviations relative to Vienna Standard Mean Ocean Water (VSMOW) (oxygen) standards. Long-term precision for the instrument was <0.2‰ for δ18O measurements. Leaf δ18O at the species level ranged from 12.07‰ to 35.35‰ on the LP, from 17.42‰ to 32.65‰ on the MP, and from 12.07‰ to 35.35‰ on the TP (Fig. S2, Table S4).

We expressed observed leaf δ18O as Δ18O at the species level (Δ18O_L) in order to remove the source water effects on leaf δ18O (Guerrieri et al., 2019; Helliker and Richter, 2008; Maxwell et al., 2018):

\[
\Delta^{18}O_L = \frac{\delta^{18}O_L - \delta^{18}O_S}{1 + \delta^{18}O_S/1000},
\]

where \(\delta^{18}O_L\) and \(\delta^{18}O_S\) are the δ18O of the bulk leaf at the species level and source water, respectively. Generally, data on the long-term stem water isotopic composition for each species are not available. As precipitation is the only or the main source of water in dryland ecosystems, we assumed that the amount-weighted δ18O of precipitation during the growing season can reflect the δ18O of source water (Guerrieri et al., 2019; Maxwell et al., 2018). The δ18O of monthly precipitation at each site was simulated using longitude, latitude, and elevation according to Bowen et al. (2005). Δ18O at the species level ranged from 21.69‰ to 43.89‰ on the LP, from 24.68‰ to 41.68‰ on the MP, and from 21.69‰ to 43.89‰ on the TP (Fig. S2, Table S3).

Given that leaf δ18O at the species level is affected by the leaf water evaporation process, variability in stomatal conductance (\(g_s\)) is expected to be evident in leaf δ18O (Barbour 2007; Barbour and Farquhar 2000; Farquhar et al., 1998). A negative relationship between Δ18O and \(g_s\) has been observed at both the species (Barbour and Farquhar, 2000; Cabrera-Bosquet et al., 2011; Grams et al., 2007; Moreno-Gutierrez et al., 2012) and canopy (Cabrera et al., 2021; Hirl et al., 2021) scales as well as among communities along soil (Ramirez et al., 2009) and climatic (Keitel et al., 2006) gradients. Consequently, we selected 1/Δ18O as a proxy for \(g_s\) at the species level in this study.

2.3 Community 1/Δ18O, LA, and SLA

Plant community parameters (1/Δ18O, LA, and SLA) were defined for each sampling site, and they were calculated as an average of eight quadrats. The respective 1/Δ18O, LA, and SLA were scaled from the leaf to community levels as follows:

\[
1/\Delta^{18}O = \sum_{i} BF_i \times (1/\Delta^{18}O_L)_i;
\]

\[
LA = \sum_{i} BF_i \times (LA_L)_i;
\]

\[
SLA = \sum_{i} BF_i \times (SLA_L)_i.
\]

Here, \(n\) is the species richness (number of species) of the community, and \(BF_i\) is the ratio of aboveground biomass of...
the $i$th species to the total aboveground biomass of the community. $\text{LA}_L$ and $\text{SLA}_L$ represent values of LA and SLA at the leaf scale. The aboveground biomass of each species was obtained by directly weighing the dried plant tissue per quadrat. Community $1/\Delta^{18}\text{O}$ was used in this study as a proxy for canopy conductance ($G_s$) (Cabrera et al., 2021; Hirl et al., 2021). We also derived $G_s$ from gross primary productivity (GPP) and the community ratio of intercellular to atmospheric CO$_2$ partial pressure (Cabrera-Bosquet et al., 2011).

2.4 Auxiliary dataset

Climate variables were obtained from the standard (19-variable) WorldClim Bioclimatic variables for WorldClim version 2 (1 km$^2$; https://www.worldclim.org/, last access: 3 September 2022; Fick and Hijmans, 2017). The growing season (April–October) and annual mean air temperature, maximum temperature, actual water vapor pressure, and cumulative precipitation were calculated from monthly values. The VPD was calculated from the actual water vapor pressure and temperature (Grossiord et al., 2020). The aridity index (calculated as $1 - \text{mean annual precipitation/potential evapotranspiration}$) was obtained from the Consultative Group for International Agricultural Research Consortium for Spatial Information (CGIAR-CSI; https://cgiarcsi.community/, last access: 3 September 2022). Solar radiation was derived from “A dataset of reconstructed photosynthetically active radiation in China (1961–2014)” (Liu et al., 2017). Soil moisture content within the top 10 cm depth was obtained from the remote-sensing-based surface soil moisture (RSSSM) dataset at a 0.1° spatial resolution (Chen et al., 2021) with an approximate 10 d temporal resolution.

2.5 Statistical analysis

Linear regressions were used to describe the patterns of climatic variables and $G_s$ along an aridity gradient (carried out in MATLAB, version 2018b; The Math Works, Inc., 2018). Differences in climate variables among the three transects were tested with a one-way ANOVA with Duncan’s post hoc multiple comparisons (SPSS Statistics 20; IBM Corp, 2011). To explore bivariate relationships between each of our hypothesized drivers (water variables and plant attributes) and $G_s$, we conducted a Pearson correlation analyses using IBM SPSS 20 software. We tested the differences in the slopes and intercepts of the linear regression between $G_s$ and aridity using standardized major axis (SMA) regression fitting (“smatr 3” package in R) (Warton et al., 2012). To determine the interactive effects of climate variables and plant properties on variability in $G_s$ along an aridity gradient, we fitted structural equation models using the “lavaan” package in R (R Foundation for Statistical Computing; R Core Team 2012) based on the current knowledge of the interactive relationships between climate variables, plant properties, and $G_s$ (Figs. S3, 4). We chose the final models with high-fit statistics: compar-

Figure 1. Comparison of aridity (a), growing season precipitation (b), soil moisture (SM) (c), vapor pressure deficit (VPD) (d), solar radiation (SR) (e), temperature (f), maximum temperature ($\text{Temp}_{\text{max}}$) (g), community leaf area (h), and specific leaf area (SLA) (i) among transects. The abbreviations used in the figure are as follows: LP – Loess Plateau, MP – Inner Mongolian Plateau, and TP – Tibetan Plateau. Lowercase letters indicate significant differences among transects ($P<0.05$). Error bars indicate the standard error of the mean; $n=10$.
3 Results

3.1 Variability in $1/\Delta^{18}O$ along aridity gradients

Bivariate linear regression between community $1/\Delta^{18}O$ and aridity showed that $1/\Delta^{18}O$ decreased linearly with increasing aridity within transects (Fig. 2a). The SMA regression fitting demonstrated that intercepts of SMA were significantly different from each other ($P<0.05$), whereas the slopes were not ($P>0.05$). The order of the intercepts was as follows: LP > MP > TP ($P<0.05$; Table S5). The intercepts of SMA significantly decreased with increasing growing season SR ($P<0.05$; Fig. 3b) and significantly increased with increasing growing season temperature ($P<0.05$; Fig. 3c). Significant differences in community $1/\Delta^{18}O$ were found among transects ($P<0.001$), and the order was LP > MP > TP (Fig. 2b).

3.2 Effects of SM and the VPD on the variability in community $1/\Delta^{18}O$

The Pearson correlation analysis showed that community $1/\Delta^{18}O$ was positively correlated with SM along aridity gradients within three transects ($P<0.05$; Table 1), while a significant relationship between $1/\Delta^{18}O$ and the VPD was only observed on the TP ($P<0.01$). Partial correlation analyses showed that $1/\Delta^{18}O$ was not related to SM ($P>0.05$) after controlling for the VPD, indicating that variability in $1/\Delta^{18}O$ on the TP was mainly determined by the VPD. SR exhibited negative correlations with $1/\Delta^{18}O$ on all three plateaus ($P<0.05$). Both mean temperature (Tempmean) and Tempmax were significantly and positively correlated with $1/\Delta^{18}O$ on the LP ($P<0.05$), but they were negatively correlated with $1/\Delta^{18}O$ on the TP ($P<0.05$); however, there were no significant correlations between either Tempmean or Tempmax and $1/\Delta^{18}O$ on the MP ($P>0.05$). Positive correlations were found between $1/\Delta^{18}O$ and LA on the LP and MP ($P<0.05$), and negative correlations were found between $1/\Delta^{18}O$ and SLA on the TP ($P<0.05$).

The interactive effects of environmental factors (Table 1) on community $1/\Delta^{18}O$ within transects were determined with structural equation models (SEMs) (Fig. 4a, b, c). SR, acting via SM, exhibited negative effects on $1/\Delta^{18}O$ on the LP (SPCI = −0.52, where SPCI denotes the standardized path coefficient of indirect effect) (Fig. 4a). Tempmax did not exert a significant effect on $1/\Delta^{18}O$ on the LP ($P>0.05$). SR exhibited a negative indirect effect on $1/\Delta^{18}O$ via SM on the MP (SPCI = −0.53) (Fig. 4b). The negative indirect effects of SR (SPCI = −0.49) and Tempmax (SPCI = −0.45) on $1/\Delta^{18}O$ via the VPD on the TP were similar (Fig. 4c).

Table 1. The Pearson correlation coefficients for correlations of community $1/\Delta^{18}O$ with environmental factors and with plant properties.

| Aridity   | Loess Plateau | Inner Mongolia Plateau | Tibetan Plateau |
|-----------|---------------|-------------------------|-----------------|
| SM        | −0.848**      | −0.843**                | −0.772**        |
| VPD       | −0.554*       | −0.384                  | −0.912**        |
| SR        | −0.639*       | −0.728*                 | −0.850**        |
| Tempmean  | 0.641*        | 0.303                   | −0.670*         |
| Tempmax   | 0.678*        | 0.038                   | −0.852**        |
| LA        | 0.757*        | 0.913**                 | 0.610           |
| SLA       | −0.519        | −0.576                  | −0.648*         |

3.3 Interactive effects of abiotic and biotic factors on the variability in $1/\Delta^{18}O$

When community LA and SLA were incorporated into the SEM, the community $1/\Delta^{18}O$ prediction significantly improved on the LP and MP, but there was no change on the TP (Fig. 5). In particular, LA had a positive effect on $1/\Delta^{18}O$ on the LP, and its effect (SPCD = 0.517, where SPCD denotes the standardized path coefficient of direct effect) was slightly larger than that of SM (SPCD = 0.430) (Fig. 5a). LA exhibited a positive direct effect on $1/\Delta^{18}O$ on the MP, whereas the effect of SM was not statistically significant (Fig. 5b). However, SLA did not directly affect $1/\Delta^{18}O$ on the TP ($P>0.05$; Fig. 5c).

4 Discussion

4.1 Radiation and temperature regulates variability in canopy conductance within transects via drought stress

Community $\Delta^{18}O$ in this study was relatively high (from a low of 26.8% on the LP to a high of 42.4% on the TP) (Fig. 2a, Table S1). A previous study conducted in a temperate grassland (mean annual precipitation was 753 mm) reported a $\Delta^{18}O$ of 28.2% at 30.53% (Hirl et al., 2021). This indicated that the canopy conductance ($G_s$), presented by community $1/\Delta^{18}O$, was relatively low in this study, and the community reduces $G_s$ in response to drought stress.

The decreasing $G_s$ with aridity within transects was mainly due to drought stress, coupled with the effects of high solar radiation and/or temperature. However, the relative roles of SM and the VPD in restricting $G_s$ along an aridity gradient were different across the three transects (Table 1).
In this study, we found that the variability in $G_s$ was limited by SM on the LP and MP, whereas it was mainly limited by the VPD on the TP. In addition, a global meta-analysis demonstrated that ecosystem conductance was mainly limited by low SM at xeric sites and by the VPD at mesic sites (Novick et al., 2016). This indicated that drought stress may be primarily controlled by SM on the LP and MP, but it may be limited by both SM and the VPD on the TP. An eddy covariance study conducted on the TP demonstrated that GPP in the growing season was significantly limited by SM and the VPD; however, the accumulated GPP was primarily determined by SM (Xu et al., 2021b). This may be because the dominant factors of drought stress differ at different spatial and temporal scales.

Solar radiation and temperature regulated within-transect variability in $G_s$ via drought stress (Fig. 4). Solar radiation exhibited consistently negative effects on $G_s$ because it increased with increasing aridity within the three transects (Fig. 1h, Table S1). These results are consistent with those of Fu et al. (2006), who demonstrated that the net CO$_2$ exchange in grasslands on the MP and shrublands on the TP was significantly reduced by high solar radiation. In this study, solar radiation exhibited a negative effect on $G_s$ via drought stressors (Fig. 4a, b, c). On the one hand, increas-
4.2 Interacting effects of abiotic and biotic factors on the variability in canopy conductance within transects

Our results indicate that solar radiation and temperature indirectly regulated variability in $G_s$ along an aridity gradient within transects via leaf morphological properties. Including LA increased the percentage of explained variability in $G_s$ by 17% and 36% on the LP and MP, respectively (Fig. 5a, b). Kang et al. (2021) noted that plants tend to balance light capture with light capture and heat exchange when examining spatial variability in $G_s$. To the best of our knowledge, this study is the first in which leaf morphological properties have been included to quantify the relative contributions of climatic and vegetation variables on $G_s$. Specifically, solar radiation exhibited negative effects on $G_s$ via LA on the LP and MP (Fig. 5a, b). Kang et al. (2021) noted that plants tend to balance light capture with
damage from high solar radiation. Solar radiation increased with increasing aridity on the LP and MP (Table S6). Consequently, our results demonstrate that communities on the LP and MP prevail by reducing LA to avoid damage at the expense of light capture.

Our earlier preliminary study (Wang and Wen 2022a) demonstrated that $g_s$ was significantly affected by LA on the TP at the species level. However, the effect of community LA on $G_s$ was weak ($P = 0.061$; Fig. S5a), and variability in $G_s$ along an aridity gradient was controlled by SLA (Fig. S5b, Table 1). This highlighted the difference in biological drivers of $g_s$ at the leaf and canopy scales. Contrary to the results from the dry grassland species in Mediterranean (Prieto et al., 2018) and karst communities in subtropical regions (Wang et al., 2021), community $1/\Delta^{18}O$ significantly decreased with SLA in this study (Fig. S5, Table S1). This indicates that the traditional leaf economic spectrum theory may not be supported at the community level on the TP due to multiple environmental stressors. SLA generally decreases with increasing solar radiation and increases with temperature and water availability (Poorter et al., 2009). In this study, community SLA was negatively related to soil moisture and positively related to maximum temperature (Table S6), indicating that changes in community SLA were mainly controlled by maximum temperature. However, the direct effect of SLA on $G_s$ in the structural equation was not significant (Fig. 5c). This effect may be obscured by drought stress.

### 4.3 Differences in canopy conductance among transects

Significant differences in community $1/\Delta^{18}O$ for a given level of aridity were found among transects (Fig. 2a). Among transects, only the differences in the VPD, solar radiation, and temperature were significant ($P > 0.05$; Figs. 1, S1). In general, plants decrease their $g_s$ at the species level to respond to an increasing VPD (Grossiord et al., 2020). The intercept of the linear regression between aridity and community $1/\Delta^{18}O$ decreased with a decreasing VPD among transects ($P > 0.05$; Fig. 3a). This indicated that the difference in the VPD was not a contributor to the difference in $G_s$ among transects.

The differences in $G_s$ among transects may be attributed to the direct effects of solar radiation and temperature on $G_s$ and photosynthesis (Yu et al., 2002). Solar radiation exhibited a negative effect on the intercept of the linear regression between aridity and community $1/\Delta^{18}O$ among transects ($P < 0.05$; Fig. 3b). Excess ultraviolet-B radiation (Duan et al., 2008), insufficient thermal dissipation, and enhanced photorespiration under high solar radiation (Cui et al., 2003) can decrease photosynthesis, ultimately reducing $g_s$ at the species level. For example, Yu et al. (2002) observed that photosynthesis in wheat on the TP was lower at the leaf level than that on the North China Plain due to the high solar radiation on the TP.

The transect with a low temperature exhibited a low intercept of the linear regression between aridity and community $1/\Delta^{18}O$ (Fig. 3c), indicating that $G_s$ differences among transects were also inhibited by low temperature. Generally, photosynthesis and $G_s$ increased with temperature below the optimum temperature (Xu et al., 2021a). For example, the rate of photosynthesis was lower in a cold than in a warm environment (Yu et al., 2002).

### 4.4 Using community-weighted $1/\Delta^{18}O$ as an indicator of canopy conductance

Positive relationships between community $1/\Delta^{18}O$ and $G_s$ derived from GPP by Cabrera-Bosquet et al. (2011) (LP: $r^2 = 68$, $p = 0.003$; MP: $r^2 = 0.76$, $p = 0.001$; TP: $r^2 = 0.67$, $p = 0.004$) indicated that community $1/\Delta^{18}O$ is an effective indicator of the growing-season-integrated $G_s$ along aridity gradients (Cabrera et al., 2021; Hirl et al., 2021). However, caution is advised for studies at large scales (Moreno-Gutierrez et al., 2012; Prieto et al., 2018) because leaf $\Delta^{18}O$ is influenced by multiple environmental conditions, such as the $\delta^{18}O$ of source water, temperature, and VPD (Song et al., 2011).

Interspecific differences in rooting and water acquisition depth and phenology among coexisting species can lead to substantial differences in the $\delta^{18}O$ of their water sources (Moreno-Gutierrez et al., 2012). Previous studies have found that the depth of water uptake of co-occurring species in grasslands was commonly located in shallow soil layers throughout dry and wet periods (Bachmann et al., 2015; Hirl et al., 2019; Prieto et al., 2018). Differences in water acquisition depth could be ruled out as a major source of interspecific variation in leaf $\delta^{18}O$ in this study (Prieto et al., 2018). However, soil evaporation always exhibited increasing trends with increasing aridity and usually resulted in heavy enrichment in $\delta^{18}O$ in the remaining soil water used by plants (Lyu et al., 2021). Longer rainless periods and heavier evaporative enrichment of soil water along the aridity gradient could also contribute to a decreasing trend in community $1/\Delta^{18}O$. Consequently, our results may overestimate the decreasing trend in $G_s$ along the aridity gradient.

The decreasing trend in community $\Delta^{18}O$ along aridity gradients may originate from the temperature and VPD via their effects on evaporation and isotopic exchange between water and organic molecules (Barbour and Farquhar, 2000; Helliker and Richter, 2008; Song et al., 2011). For example, the equilibrium fractionation factor for water evaporation is dependent on temperature (Bottinga and Craig, 1968). Temperature and VPD gradients between leaf and ambient air influence the evaporative gradient from leaf to air (Helliker and Richter, 2008; Song et al., 2011). In addition, biochemical $^{18}O$-fractionation during cellulose synthesis is sensitive to temperature, and the proportion of oxygen in cellulose derived from source water is sensitive to humidity (Hirl et al., 2021).
The potential effects of temperature and the VPD on $\Delta^{18}$O via evaporation and isotopic exchange between water and organic molecules could be ruled out in this study. The growing season temperature variation was small along three transects (LP = 3.3°C, MP = 4.9°C, and TP = 3.8°C; Table S1). However, community $\Delta^{18}$O ranged from 3.89‰ on the MP to 7.78‰ on the LP (Table S1, Fig. 2a). Previous studies have demonstrated that the sensitivity of temperature to $\Delta^{18}$O was approximately 0.23‰ °C$^{-1}$ (Helliker and Richter, 2008; Song et al., 2011). It seems that the changes in temperature were not a main contributor to the large variability in community $\Delta^{18}$O. Meanwhile, a positive relationship between community $\Delta^{18}$O and temperature was observed on the LP ($P<0.05$), and a negative relationship was observed between community $1/\Delta^{18}$O and the VPD on the TP (Table 1). However, partial correlation analyses showed that community $1/\Delta^{18}$O was not related to temperature ($P>0.05$) nor the VPD after controlling for $G_s$ (data not shown). This indicates that the variability in community $1/\Delta^{18}$O was mainly determined by $G_s$.

5 Conclusions

This study highlights the need to integrate multiple stressors and plant properties when determining the spatial variability in $G_s$ and to directly link species-level observations of physiological processes to canopy-level observations of functions at a large spatial scale. Specifically, our results demonstrate that excess radiation and low temperatures interacted to exacerbate drought stress impacts on $G_s$ across transects, while solar radiation exacerbates drought stress impacts on $G_s$ within transects. The effects of drought stress on $G_s$ can be mitigated by decreasing temperatures in warm environments, whereas they can be aggravated by increasing temperatures in cold environments. The primary determinant of drought stress on $G_s$ was soil moisture in LP and MP, whereas it was the vapor pressure deficit on the TP. The ability to predict variability in $G_s$ could be significantly improved by integrating multiple stressors and leaf area on the LP and MP, although this would not be the case for the TP due to an overwhelming effect of climate.

Data availability. Requests for leaf $\delta^{18}$O and $\Delta^{18}$O data should be directed to Xuefa Wen (wenxf@igsnrr.ac.cn), and requests for leaf area and specific leaf area at the species level should be directed to Nianpeng He (Henp@igsnrr.ac.cn).

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