https://doi.org/10.5194/bg-2022-50
Preprint. Discussion started: 15 March 2022

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

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Abstract. Stomatal conductance (gs) of all co-existing species regulates transpiration in arid and semi-arid grasslands prone to droughts. However, the effect of drought stress on gs is debated, and the interaction effects of abiotic and biotic constraints on canopy gs remain poorly understood. Here, we used ^{18}O enrichment of leaf organic matter above source water ($\triangle^{18}O$) as proxy for gs per leaf area to increase understanding of these effects. Three grassland transects were established along aridity gradients in Loess Plateau (LP), Inner Mongolian Plateau (MP), and Tibetan Plateau (TP) which differ in radiation and temperature conditions. Results showed that canopy gs consistently decreased with increasing aridity within transects. The order of gs at a given aridity index was LP>MP>TP, due to suppressed effects of excess radiation and low temperatures among transects. Primary determinant of drought stress on gs was soil moisture (SM) in LP and MP, and vapor pressure deficit (VPD) in TP. Radiation exhibited consistently negative effect on gs via drought stress within transects, while temperature had positive effects on gs in LP, no effects in MP, and negative effects in TP. Adding the interaction of leaf area and abiotic factors increases the percent of explained variability in gs by 17 and 36% in LP and MP, respectively, but not in TP due to an overwhelming effect of climate. The results highlighted the need to integrate multiple stressors and plant properties to determine spatial variability in gs.

Keywords: stomatal conductance, oxygen isotope, drought stress, excess radiation, high temperature, grassland

1 Introduction

Stomatal conductance (gs) of all co-existing species plays a significant role in water loss (transpiration) and carbon uptake (photosynthesis) at ecosystem level, thereby coupling water and carbon cycles (Jarvis & McNaughton, 1986; Zhu *et al.*, 2015; Martin-StPaul *et al.*, 2017; Wang *et al.*, 2021a). The model linkages between gs and photosynthesis mean that the biophysical response of gs varies depending on water, radiation, temperature and leaf economic traits at leaf level (Farquhar *et al.*, 1980; Leuning, 1995; Wright *et al.*, 2004; Buckley, 2019; Carminati & Javaux, 2020). However, experimental evidence suggested that the strength of gs responses to changing environment factors varies with species (Galmes *et al.*, 2007), and changes in

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environment factors can have interactive effects on the variability in gs (Zeuthen *et al.*, 1997; Costa *et al.*, 2015; Doupis *et al.*, 2020). Community in field is simultaneously affected by a variety of environmental stressors, and canopy gs is the cumulative rate over time of co-occurring species (Xia *et al.*, 2015). However, how interactive effects of multiple environment stressors and community traits regulate the spatial patterns of canopy gs remain largely unknown (Maxwell *et al.*, 2018).

Drylands cover 41% of the Earth's surface (Yao *et al.*, 2020; Xu *et al.*, 2021b), and drive the variability in global terrestrial carbon sink (Ahlstrom *et al.*, 2015). The survival, transpiration, and productivity of plants growing in this region is simultaneously stressed by drought (Hoshika *et al.*, 2018; Peters *et al.*, 2018; Flo *et al.*, 2021), 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; Aguirre-Gutierrez *et al.*, 2019); this may ultimately affect gs (Wang *et al.*, 2021b). Thus, canopy gs in drylands was expected to influenced by the interaction of drought, high radiation, high temperature and biotic factors.

Canopy gs should be primarily limited by drought in drylands, which is often characterized as low soil moisture (SM) and high vapor pressure deficit (VPD). It is generally assumed that increased drought stress reduces gs at leaf level (Hoshika *et al.*, 2018; Peters *et al.*, 2018; Stocker *et al.*, 2019; Flo *et al.*, 2021). The limitation of SM and VPD on gs involves two independent mechanisms; in one, low SM (available water in the soil for plant root uptake) reduces soil water potential and hinders transport of soil water to leaf; in the other, high VPD reduces leaf water potential and increases transpiration demand (Oren *et al.*, 1999; Buckley, 2017; Zhang *et al.*, 2021). However, there is an ongoing debate on the relative role of SM and VPD in determining the response of canopy gs to dryness (Liu *et al.*, 2020). For instance, a global analysis demonstrated that SM stress is the dominant driver of productivity in semi-arid ecosystems (Liu *et al.*, 2020). Howecer, anonther study demonstrated that VPD stress is the dominant influence on surface conductance (Konings *et al.*, 2017). Yet, these studies lack direct biological evidence, because canopy gs cannot be measured directly, especially at large scales.

Radiation and temperature may indirectly regulate canopy gs by influencing photosynthesis (Aasamaa & Sober, 2011; Medlyn *et al.*, 2012) and adjusting drought stress (Ciais *et al.*, 2005). However, previous studies conducted at leaf level showed that the direction and intensity of radiation and temperature on gs strongly depend on their distribution range and the relationship with aridity. For example, the response of gs to radiation and temperature generally shows an increasing trend up to optimum values (Xu *et al.*, 2021a), while excess radiation in combination with drought stress suppresses gs (Zeuthen *et al.*, 1997; Costa *et al.*, 2015; Doupis *et al.*, 2020). In addition, increasing temperature may result in high VPD or low SM (Seneviratne *et al.*, 2010). However, these effects were obscured by drought stress in natural conditions, which alone caused a gs reduction (Fu *et al.*, 2006; Duan *et al.*, 2008). Consequently, it is difficult to disentangle whether the decline in gs at community level with increasing aridity is simply a consequence of drought stress or an interaction of multiple stressors.

Additionally, environmental stressors should have an indirect effect on canopy gs by regulating community morphological traits. However, few studies have addressed this topic at the community scale considering both environmental

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and plant regulators. Communities change their morphological functional traits to tolerate environmental stress (Anderegg *et al.*, 2018), including leaf area (LA) and specific leaf area (SLA) (Wright *et al.*, 2017). LA and SLA determine plant capacity for capturing light (Poorter *et al.*, 2009), leaf heat exchange (Wright *et al.*, 2017), and length of water pathway through leaves (Kang *et al.*, 2021), all of which are closely related to transpiration and photosynthesis. Previous studies 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 in woody species in eastern Qinghai-Tibet, China showed that LA and stomatal size co-varied with temperature (Kang *et al.*, 2021), indicating that the changes in LA and SLA may play important roles in regulating canopy gs.

To investigate the interactive effect of environmental stressors and biotic factors on canopy gs, three grassland transects along aridity gradients were established in three plateaus with different radiation and temperature conditions, i.e., Loess Plateau (LP), Mongolian Plateau (MP), and Tibetan Plateau (TP) across arid and semi-arid regions in China. Given that the order of mean annual temperature and radiation is LP>MP>TP and LP<MP<TP, respectively (Ren *et al.*, 2021), the differences in radiation and temperature across three plateaus provide an ideal platform for exploration of interaction effects of multiple stressors and biotic factors on canopy gs. We hypothesized that: (1) increasing solar radiation and/or air temperature along aridity gradient will exacerbate drought stress impacts on gs within transects, (2) excess solar radiation and low temperatures will result in differences in gs among transects, (3) integrating environmental stress and community functional traits will significantly improve the capacity for predicting gs.

Bulk leaf $\delta^{18}O$ and aboveground biomass of all co-existing species were determined. Theoretically, the change of $\delta^{18}O$ in organic matter is affected by gs based in steady-state leaf water ^{18}O enrichment (Farquhar *et al.*, 1998; Barbour *et al.*, 2000; Barbour, 2007). Negative relationship between $\delta^{18}O$ (or the ^{18}O enrichment of organic matter above source water, $\triangle^{18}O$) and gs expected relationship has been observed intra- (Cernusak *et al.*, 2009; Cabrera-Bosquet *et al.*, 2011) and inter-species (Barbour *et al.*, 2000; Grams *et al.*, 2007; Cernusak *et al.*, 2009; Moreno-Gutierrez *et al.*, 2012), and among communities along a climate gradient (Keitel *et al.*, 2006). $\delta^{18}O$ or $\triangle^{18}O$ is now widely used by plant eco-physiologists to infer the spatial and temporal variation in gs (Flanagan & Farquhar, 2014; Maxwell *et al.*, 2018; Guerrieri *et al.*, 2019; Levesque *et al.*, 2019). To exclude the influence of variation in $\delta^{18}O$ of the source water, we calculated the $\triangle^{18}O$ (Keitel *et al.*, 2006). Combining with aboveground biomass, $1/\triangle^{18}O$ was upscaled from leaf to community levels (Flanagan & Farquhar, 2014; Wang *et al.*, 2021b). Proxies for drought (i.e., SM and VPD), air temperature (i.e., mean, maximum and minimum) and solar radiation were derived from global or regional datasets.

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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 semi-arid regions (i.e., Loess Plateau, LP; Inner Mongolian Plateau, MP; Tibetan Plateau, TP) in China (Lyu *et al.*, 2021). Transects were 600 km long in LP, 1200 km in MP, and 1500 km in TP. Differences in aridity (calculated as 1- mean annual precipitation/potential evapotranspiration) and growing season precipitation were not significant (P>0.05) among transects, while there are significant differences in growth season air temperature (LP>MP >TP) (Fig.1c) and solar radiation (LP<MP<TP) (Fig.1d) among transects. In each transect, we selected 10 sampling sites with increasing aridity index (Fig.1e) and growing season solar radiation (Fig.1h), and decreasing growing season precipitation from east to west (Fig.1f). More details about the characteristics of climate, soil and vegetation type in the 30 sampling sites can be found in (Lyu *et al.*, 2021).

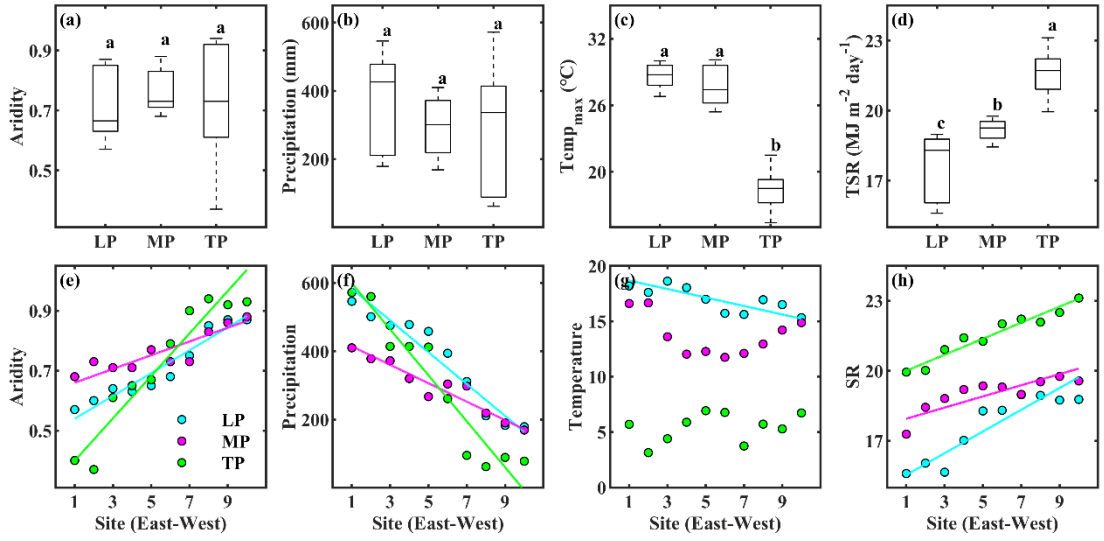

Figure 1. Comparison of aridity, growing season precipitation (mm), air temperature (°C), and radiation (MJ m^{-2} day^{-1}) (a) among three transects and (b) within transects. LP: Loess Plateau; MP, Inner Mongolia Plateau; TP, Tibet Plateau. Lowercase letters indicate significant differences among transects (P<0.05). Error bars indicate standard error of the mean.

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 30 sites, we delineated eight 1m× 1m plats in a 100m x 100m sampling area (Lyu *et al.*, 2021). Plant species (identified by experienced plant taxonomists), number of species and community structure were surveyed. Aboveground biomass was collected by species for dry mass and stable isotope analyses.

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2.2.2 Leaf area and SLA analysis

Three individuals were collected as replications for each species, six to ten fresh, healthy, and mature leaves were selected from individuals of each species, and leaf are (LA) was determined using a portable scanner (Cano Scan LIDE 110, Japan). Image J software was used to obtain LA values (Schneider *et al.*, 2012). Then, leaves were dried at 60℃ and weighed for leaf dry mass. SLA was calculated by dividing LA by leaf dry mass.

2.2.3 Stable isotope analysis

In this study, we used $1/\triangle^{18}O$ in bulk leaves as proxy for gs. $\triangle^{18}O$ at species level ($\triangle^{18}O_L$) was calculated as (Wang *et al.*, 2021b):

$$\triangle^{18}O_L = \frac{(\delta^{18}O_L - \delta^{18}O_P)}{(1+\delta^{18}O_P/1000)} \quad (1)$$

where $\delta^{18}O_L$ is bulk-leaf $\delta^{18}O$ at species level; $\delta^{18}O_P$ is the amount-weighted $\delta^{18}O$ of precipitation during the growing season. $\delta^{18}O$ of monthly precipitation at each site was simulated using longitude, latitude, and elevation according to (Bowen *et al.*, 2005).

We measured $\delta^{18}O$ values in bulk leaves. Dried leaf samples were ground using a ball mill, and oven dried before analysis. Leaf samples were prepared in silver capsules for $\delta^{18}O$ analysis. An isotope ratio mass spectrometer in continuous-flow mode (Model 253 plus, Thermo Fisher Scientific, Bremen, Germany) coupled with an elemental analyzer (Model Flash 2000HT, Thermo Fisher Scientific, Bremen, Germany) was used to determine $\delta^{18}O$ values. Isotope ratios are expressed as per mil deviations relative to VSMOW (oxygen) standards. Long-term precision for the instrument was < 0.2‰ for $\delta^{18}O$ measurements.

2.3 Community $1/\triangle^{18}O$, LA and SLA

Plant community parameters ($1/\triangle^{18}O$, LA and SLA) were defined for each sampling site, and calculated as an average of eight quadrats. The $1/\triangle^{18}O$, LA, and SLA were scaled from leaf to community levels as follows (Wang *et al.*, 2021b):

$$1/\triangle^{18}O = \sum_{n}^{i} BF_i \times (1/\triangle^{18}O_L)_i \quad (2)$$

$$LA = \sum_{n}^{i} BF_i \times (LA_L)_i \quad (3)$$

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$$SLA=\sum_{n}^{i} BF_i \times (SLA_L)_i \quad (4)$$

where n is the species richness (number of species) of the community, and BF_i is the ratio of aboveground biomass of the ith species to the total aboveground biomass of the community. LA_L and SLA_L represent values of LA and SLA at leaf scale. Aboveground biomass of each species was obtained by directly weighing dried plant tissue per quadrat.

2.4 Auxiliary dataset

Climate variables were obtained from the standard (19) WorldClim Bioclimatic variables for WorldClim version 2 (1 km^2) (https://www.worldclim.org/) (Fick & Hijmans 2017). The growing season (April to October) and annual mean air temperature, maximum temperature, minimum temperature, actual water vapor pressure, and cumulative precipitation were calculated from monthly values. Vapor pressure deficit (VPD) was calculated from actual water vapor pressure and temperature (Grossiord *et al.*, 2020). Aridity index (=1-MAP/potential evapotranspiration) was extracted from the CGIAR-CSI (https://cgiarcsi.community). 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 extracted from remote-sensing-based surface soil moisture (RSSSM) dataset at 0.1° spatial resolution (Chen *et al.*, 2021), and approximately 10-day temporal resolution.

2.5 Statistical analysis

Differences in climate variables among three transects were tested with a one-way ANOVA with Duncan's post hoc multiple comparisons (SPSS, Chicago, IL, USA). To explore bivariate relationships between each of our hypothesized drivers (water variables and plant attributes) and gs, we conducted Pearson correlation analyses using IBM SPSS 20 software (SPSS, Chicago, IL). Linear regressions were used to describe the relationships between gs and aridity (Matlab, Version 2018b). We further tested the differences in slopes and intercepts of linear regression between gs and aridity using standardized major axis (SMA) regression fits (Wright *et al.*, 2006) (R Core Team 2012). To determine the interactive effects of climate variables and plant properties on variability in gs along an aridity gradient, we fitted structural equation models using the "lavaan" package in R statistical program (R Core Team 2012) based on the current knowledge of the interactive relationships between climate variables, plant properties, and gs. We chose the final models with high-fit statistics: comparative fit index >0.95, standardized root mean square residual < 0.08, and p-value > 0.8.

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3 Results

3.1 Variability in 1/△^{18}O along aridity gradients

Bivariate linear regression of 1/△^{18}O on aridity showed that 1/△^{18}O decreased linearly with increasing aridity within transects (Fig.2a). The standardized major axis (SMA) regression fits demonstrated that intercepts of SMA were significantly different from each other (P<0.05), while the slopes were not (P>0.05). The order of the intercepts was Loess Plateau (LP) < Inner Mongolia (MP) <Tibet Plateau (TP) (P<0.05, Table S1). The intercepts of SMA did not exhibited relationship with precipitation (Fig.3a, P>0.05), decreased with decreasing temperature (Fig.3b, P<0.01), and increased with increasing solar radiation (Fig.3c, P<0.05). Significant differences in gs were found among transects (P<0.001), and the order was LP>MP>TP (Fig.2b).

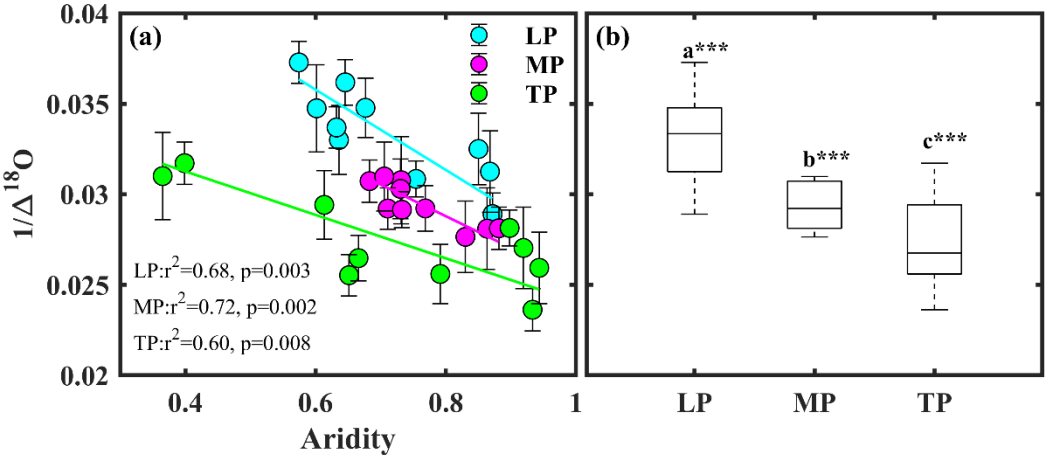

Figure 2. Patterns of 1/△^{18}O (a) along aridity gradient within transects, and among (b) transects. Different letters indicate significant differences (P < 0.001) among transects and grassland types. LP, Loess Plateau; MP, Inner Mongolia Plateau; TP, Tibet Plateau.

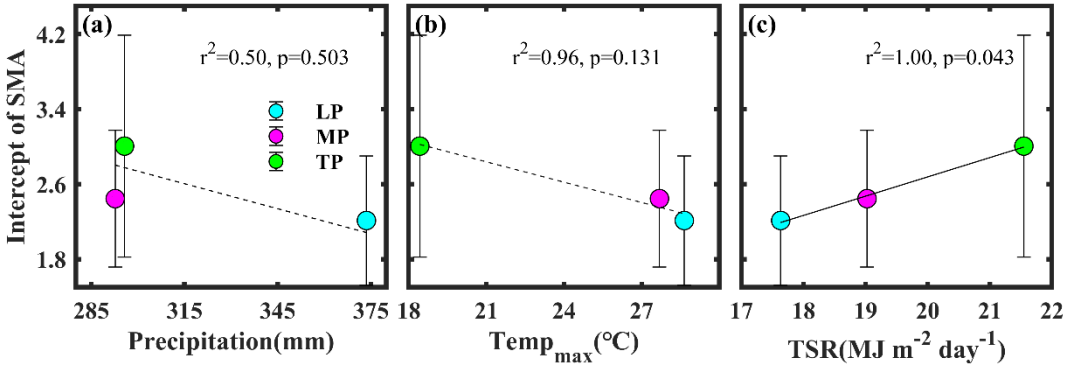

Figure 3. The relationship between the intercept obtained from standardized major axis analysis (SMA) and growing season (a) precipitation, (b) temperature, and (c) solar radiation (SR).

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3.2 Effects of SM and VPD on the variability in 1/△^{18}O

Pearson correlation analysis showed that 1/△^{18}O was positively correlated with soil moisture (SM) along aridity gradients within three transects (P<0.05, Table 1), while a significant relationship between 1/△^{18}O and vapor pressure deficit (VPD) was observed onlyin TP (P<0.01). Solar radiation (SR) exhibited negative correlations with 1/△^{18}O in all three Plateaus (P<0.05). Both mean ($Temp_{mean}$) and maximum ($Temp_{max}$) temperatures were significantly and positively correlated with 1/△^{18}O in LP, but negatively in TP. However, there were no significant correlations between both $Temp_{mean}$ and $Temp_{max}$ and 1/△^{18}O in MP. Positive correlations were found between gs and leaf area (LA) in LP and MP, and negative between 1/△^{18}O and specific leaf area (SLA) in TP (P<0.05).

Table 1 Pearson's coefficients among stomatal conductance (gs, using 1/△^{18}O as proxy for gs) and environmental factors and plant properties.

	Loess Plateau	Inner Mongolia Plateau	Tibet Plateau
Aridity	-.848**	-.843**	-.773**
SM	0.719*	0.707*	0.659*
VPD	-0.554	-0.384	-0.912**
SR	-0.639*	-0.728*	-0.850**
$Temp_{mean}$	0.641*	0.303	-0.670*
$Temp_{max}$	0.678*	0.038	-0.852**
LA	0.757*	0.913**	0.610
SLA	-0.519	-0.576	-0.648*

**, P<0.01; *, P<0.05. SM, soil moisture; VPD, vapor pressure deficit; SR, total solar radiation; $Temp_{mean}$, mean temperature; $Temp_{max}$, maximum temperature; LA, leaf area; SLA, specific leaf area.

The interaction effects of environmental factors (Table 1) on 1/△^{18}O within transects were determined with structural equation models (SEMs) (Fig.4a-c). SR, acting via SM, exhibited the strongest influence on 1/△^{18}O in LP (standardized path coefficient of indirect effect [SPCI]= -0.52) (Fig.4a). $Temp_{max}$ in LP showed a weak and positive indirect effect on 1/△^{18}O via SM (SPCI = 0.14). SR in MP exhibited a negative indirect effect on gs via SM (SPCI = -0.53) (Fig.4b). The negative indirect effects of SR (SPCI = -0.49) and $Temp_{max}$ (SPCI = -0.45) on gs via VPD in TP were similar (Fig.4c). The effect of

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SR on $Temp_{max}$ was inconsistent among transects: SR had a negative effect on $Temp_{max}$ in LP, a positive effect in TP, and no effect in MP.

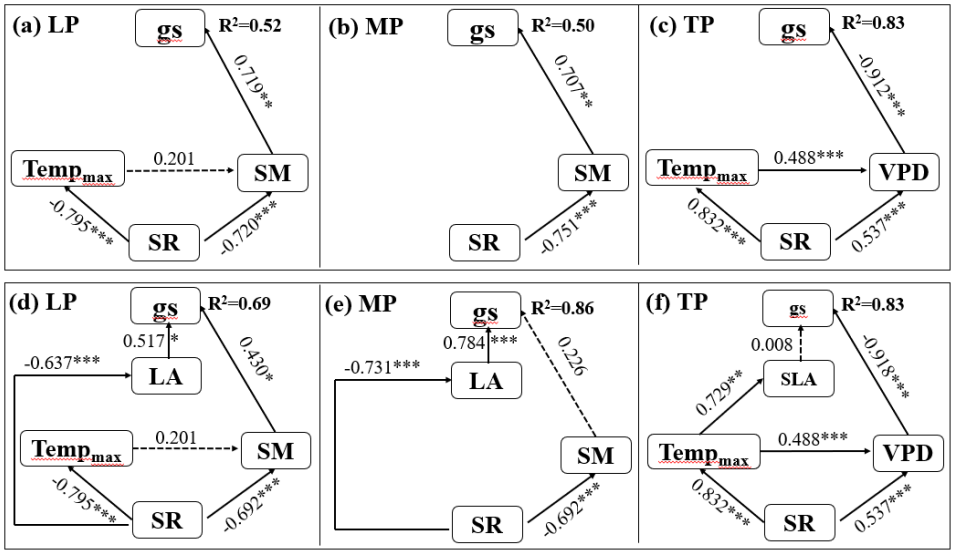

Figure 4. Structural equation models for stomatal conductance (gs). gs, stomatal conductance (using $1/\triangle^{18}O$ as proxy for gs); Tempmax: maximum temperature; SR, solar radiation; SM, soil moisture; VPD, vapor pressure deficit; LA, leaf area; SLA, specific leaf area; LP, Loess Plateau; MP, Inner Mongolia Plateau; TP, Tibet Plateau.

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

When leaf area and specific leaf area were incorporated into the SEM, $1/\triangle^{18}O$ prediction significantly improved in LP and MP (Fig.4d-f), but there was no change in TP. In particular, LA had a positive effect on $1/\triangle^{18}O$ in LP, and its effect [SPC=0.517] was slightly larger than that of SM [SPC=0.430] (Fig.4d). LA exhibited a positive direct effect on $1/\triangle^{18}O$ in MP (Fig. 4d), while the effect of SM was not statistically significant (Fig.4e). However, SLA did not directly affect $1/\triangle^{18}O$ in TP ($P>0.05$) (Fig.4f).

4 Discussion

4.1 Different patterns of gs across transects

Stomatal conductance (gs, using $1/\triangle^{18}O$ as proxy for gs) consistently decreased with increasing aridity within the three transects; the order of gs at a given aridity value was Loess Plateau (LP) > Inner Mongolia Plateau (MP) > Tibetan Plateau (TP) (Fig.2a, Table S1). We attributed the differences among transects to the suppressed effects of excess radiation and low temperature due to the significant decrease in average growing season temperature (Fig.3b) and increase in solar radiation

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(Fig.3c) from LP to TP. Given that gs is typically correlated with photosynthesis (Aasamaa & Sober, 2011; Medlyn *et al.*, 2012)**,** radiation and temperature may indirectly regulate gs by influencing photosynthesis (Aasamaa & Sober, 2011; Medlyn *et al.*, 2012). Photosynthesis generally increased with increasing radiation and temperature until optimum values (Mercado *et al.*, 2009; Wehr *et al.*, 2017). Consequently, photosynthesis was lower in a cold than in a warm environment (Zhang *et al.*, 2018). In addition, excesses radiation would supress photosynthesis via photoinhibition (Demmigadams & Adams, 1992).

The relationship between intercepts of standardized major axis (SMA) and maximum temperature and solar radiation (Fig.3) further supports our view that excess radiation and low temperature interacted to exacerbate drought stress impacts on gs among transects. The intercepts of SMA significantly increased with decreasing temperature ($P<0.01$, Fig.3b) and increasing solar radiation ($P<0.01$, Fig.3c). Consequently, gs in TP was smaller than in LP and MP at given aridity conditions because the environment in TP is characterized by low temperature and high radiation.

4.2 Radiation and temperature regulates variability in gs via drought stress within transects

Based on results from this and earlier studies, we conclude that the decreasing gs with increasing aridity within transects was mainly due to drought stress, coupled with effects of high solar radiation or/and temperature. The relative roles of soil moisture (SM) and vapor pressure deficit (VPD) in restricting gs along an aridity gradient were different across the three transects (Table 1). Fu et al. (2006) found that the primary gs-limiting factor was drought stress. In this study, we found that the variability in gs was limited by SM in LP and MP, and co-limited by SM and VPD in TP. In addition, a global meta-analysis demonstrated that ecosystem productivity was limited by low SM regardless of VPD when drought stress was dominated by SM, and vice versa (Liu *et al.*, 2020). It meant that drought stress may be primarily controlled by SM in LP and MP, but may be limited by both SM and VPD in TP. An eddy covariance study conducted at an observation site in TP demonstrated that gross primary productivity (GPP) in the growing season was significantly limited by SM and 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 for different spatial and temporal scales.

Solar radiation and temperature regulated variability in gs within transect via drought stress (Fig.4). Solar radiation exhibited consistently negative effects on gs, because it increased with increasing aridity within three transects (Fig.1h, Table S2). These results were consistent with those of Fu et al. (2006), who demonstrated that the net CO_2 exchange of grassland in MP and shrubland in TP was significantly reduced by high solar radiation.

On one hand, increasing radiation decreased SM by regulating evaporation and transpiration (Zhang *et al.*, 2019). Solar radiation had negative effects on SM in the three transects in this study (Table S2). Meanwhile, increasing solar radiation can increase VPD by increasing temperatures (Grossiord *et al.*, 2020). However, a positive relationship between temperature and VPD was observed only in TP (Table S2).

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On the other hand, 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 gs. For example, photosynthesis in two herbaceous species in TP was reduced due to photorespiration in conditions of high photosynthetic photon flux density (Cui *et al.*, 2003).

The effect of temperature on variability in gs within transects differed among transects: drought stress effects on gs can be partly mitigated by lower temperatures in LP (Fig.4a), but exacerbated by higher temperatures in TP (Fig.4c). As with radiation, increases in temperature tend to increase evaporation and transpiration rates ultimately reducing SM, while VPD can be expressed as a curvilinear function of air temperature (Lawrence, 2005), always increasing with increasing temperatures (Oren *et al.*, 1999; Grossiord *et al.*, 2020).

gs exhibits a bell-shape response to air temperature (Li *et al.*, 2020). A leaf-level study conducted in TP showed that gs increased with increasing air temperatures until a maximum at 24.8 ℃, and then declined (Li *et al.*, 2020). Ecosystem-level studies also showed that high temperature at noon can result in a partial stomatal closure, ultimately limiting gs (Fu *et al.*, 2006; Zhang *et al.*, 2018). In TP, maximum temperature increased with increasing aridity, and was negatively related to SM and positively to VPD (Table S2, Fig.4c). Consequently, maximum temperature may exacerbate soil and atmospheric drought, and inhibit transpiration and photosynthesis, ultimately reducing gs along an aridity gradient. However, the maximum temperature decreased with increasing aridity in LP, and exhibited a positive effect on SM (Table S2). Under this hydrothermal synchronization effect, the maximum temperature exhibits a positive effect on gs.

4.3 Interacting effects of abiotic and biotic factors on the variability in gs within transects

Our findings indicated that radiation and temperature indirectly regulated variability in gs along an aridity gradient within transects through leaf morphological properties. Including leaf area (LA) increased the percentage of explained variability in gs by 17 and 36% in LP and MP, respectively (Fig.4d-e), compared to SEM models which excluded plant variables. This highlighted the need to integrate plant properties related to light capture and heat exchange when examining spatial variability in gs. To the best of our knowledge, this study was the first in which leaf morphological properties were included to quantify the relative contributions of climate and plant on gs. Specifically, solar radiation exhibited negative effects on gs via LA in LP and MP (Fig.4d-e). Kang et al. (2021) noted that plants tend to balance light capture with damage from high solar radiation. Solar radiation increased with increasing aridity in LP and MP (Table S2). Consequently, our results demonstrated that communities in LP and MP prevail by reducing LA to avoid damage at the expense of light capture.

Variability in gs along an aridity gradient in TP was controlled by specific leaf area (SLA) (Table 1). Although a significantly negative relationship was found between solar radiation and LA in this transect (Table S2), this negative effect did not transfer to gs (Table 1). We attributed this phenomenon to co-limitation of gs by radiation and temperature. Plants increase their leaf thickness to adapt to increasing temperature (Leigh *et al.*, 2012), and thick leaves have high heat capacity to avoid damage from high temperature (Leigh *et al.*, 2012). SLA integrates leaf area and thickness, and generally decreases

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with increasing radiation and drought stress, and increases with decreases in temperature (Poorter *et al.*, 2009). In this study, variability in SLA along an aridity gradient was significantly negatively corelated with maximum temperatures (Table S2). However, the direct effect of SLA on gs in the structural equation was weak (Fig.4f). This effect may be obscured by drought stress.

5 Conclusions

This study highlighted the need to integrate multiple stressors and plant properties when determining spatial variability in stomatal conductance (gs), and directly link species-level observations of physiological process (gs) to ecosystem-level observations of functions at a large spatial scale. Specifically, our results demonstrated that excess radiation and low temperature interacted to exacerbate drought stress impacts on gs among transects. Within a transect, radiation also exacerbated drought stress impacts on gs. Effects of drought stress on gs can be mitigated by decreasing temperatures in warm environments, and aggravated by increasing temperatures in cold environments. The primary determinant of drought stress on gs was soil moisture in LP and MP, and vapor pressure deficit (VPD) in TP. The ability to predict variability in gs could be significantly improved by integrating multiple stressors and leaf area in LP and TP, but not in TP due to an overwhelming effect of climate.

Data availability

Data availability. Requests for data or other materials should be directed to Xuefa Wen (wenxf@igsnrr.ac.cn).

Author contributions

JW and XFW planed and designed the research. JW performed experiments and analyzed data. All authors jointly wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests

The authors declare that they have no conflict of interest.

Acknowledgements

We thank the “Functional Trait database of terrestrial ecosystems in China (China_Traits)” for sharing all auxiliary plant and soil data. Ancillary meteorological data are available from China Meteorological Data Service Center (http://data. cma.cn/). This work was supported by the National Natural Science Foundation of China (41991234, 32001137).

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