Soil Property Plays a Vital Role in Vegetation Drought Recovery in Karst Region of Southwest China

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Abstract Southwest China is the world's largest continuous karst region, where drought events are expected to intensify in the future. Understanding the postdrought recovery of vegetation growth sheds light on the resilience and stability of ecosystems and is of great importance to the sustainable management. However, the effects of the soil properties, beyond the climate variations, on the vegetation postdrought recovery are often overlooked and remain unknown. In this study, we characterized both the patterns and the underlying processes governing the postdrought recovery trajectories of vegetation growth after extreme droughts in karst regions of southwest China. Linear mixed-effects model analyses revealed that higher mean Normalized Difference Vegetation Index (NDVI) preceding the spring/summer drought leads to shorter drought recovery time for both forests and grasslands, while opposite pattern appears in autumn/winter drought, particularly in forests. Significant effects of precipitation during recovery period were only found in grasslands but not in forests. More importantly, we discovered a crucial impact of the depth to bedrock on vegetation postdrought recovery in forests but not in grasslands, with deeper depth to bedrock associated to a shorter drought recovery. The field capacity is more important for postdrought recovery in karst regions than in nonkarst regions, which can be most likely attributed to differences in the water-holding capacities and water use strategies of vegetation. Our understanding of the postdrought recovery of vegetation growth in karst regions will facilitate the reasonable prediction of ecosystem resilience and health to extreme climate events in such fragile ecological environments.

Plain Language Summary Intensified extreme droughts have crucial effects on vegetation growth. Thus, comprehensive understanding of the postdrought recovery of vegetation growth is critical for predicting ecosystem resilience. While the effects of variations in climate conditions on postdrought recovery are well understood, little is known about the role of the soil properties in the vegetation postdrought recovery, particularly in regions with complex geomorphology. In this study, we investigated both the patterns and the underlying processes governing the postdrought recovery of vegetation growth after extreme droughts in karst regions of southwest China. We found that better growth condition preceding the spring/summer drought leads to shorter drought recovery time for both forests and grasslands, while opposite pattern appears in autumn/winter drought. Significant effects of precipitation during recovery period were only found in grasslands but not in forests. More importantly, we discovered that the depth to bedrock is crucial for vegetation postdrought recovery in forests but not grasslands, with deeper depth to bedrock associated to shorter drought recovery. The field capacity is more important for postdrought vegetation recovery in karst regions than in nonkarst regions. These findings highlight the important role of soil properties in controlling the postdrought recovery should be comprehensively evaluated.

1. Introduction

Extreme drought is a recurring phenomenon that has crucial impacts on both structures and functions of terrestrial ecosystems (Allen et al., 2010; Andergge et al., 2013; Ciais et al., 2005; van der Molen et al., 2011). It is one of the most widespread and devastating extreme climate events and has profound impacts on vegetation growth and the consequent land carbon sinks (Schwalm et al., 2012; Sheffield et al., 2014). Intensified extreme drought events have triggered widespread declines in vegetation growth or have even enhanced tree mortality through hydraulic failure and carbon starvation interplayed with other drivers and disturbances (Allen et al., 2010, 2015; Breshears et al., 2005). Extreme drought could exert lagged effects on the growth/productivity of woody and herbaceous plants within 1–4 years depending on a wide range of factors, including local climate and edaphic conditions, ecophysiological properties, and species-specific drought adaptation ability, which is referred to as the...
drought legacy effect (Anderegg et al., 2015; Wu et al., 2018) and significantly affects the vegetation postdrought recovery. More seriously, it is expected that more frequent and severe extreme droughts will occur in a warmer climate regime (Field et al., 2014), which potentially expose terrestrial ecosystems into sequential and repeated droughts and have a more deleterious impact on vegetation growth (Anderegg et al., 2020). Therefore, quantifying the vegetation recovery time (VRT), that is, how long it takes for ecosystems to return to their functional state before drought, after extreme drought is crucial and as a prerequisite to understand ecosystem vulnerability and resilience to extreme droughts (Anderegg et al., 2015).

Vegetation recovery time is a key indicator of drought impacts (Schwalm et al., 2017). With the increasing drought frequency, regions with longer VRT are more likely to be exposed to new drought events before they are fully recovered, so they may experience plant death and transition to a new state (Luo et al., 2015). If the VRT exceeds the drought interval, the ecosystems may be more susceptible to future droughts because repeated droughts will lead to the gradual loss of vegetation drought resilience and cavitation fatigue (Anderegg et al., 2020; Hacke et al., 2001; Huang et al., 2015). A recent study confirmed that the combined effects of drought severity and the length of drought recovery have deteriorated the ecosystem net primary production deficits (Gazol et al., 2018; Machado-Silva et al., 2021).

The timing of extreme drought is crucial to determine the drought impacts on vegetation recovery. The seasonality of extreme drought occurrence is shifting dramatically accompanying with asymmetric seasonal warming and shifts in seasonal precipitation distribution, reshaping the ecosystem structure and functioning (Samaniego et al., 2018; Xu et al., 2020). Increasing number of studies have investigated the impacts of drought timing on vegetation growth, ecosystem productivity, drought recovery, etc. Previous finding revealed the spring drought significantly reduced the annual carbon balance of forests in southern France, while the increase in the severity and/or duration of the summer drought seems unlikely to have a negative impact on the average carbon budget of the ecosystem (Allard et al., 2008). Notably, the integrated legacy from dry season droughts was about nine times the magnitude of that from wet season droughts at the global scale (Huang et al., 2018). Despite the great efforts, less is understood for the potential divergent impacts of drought timing on vegetation growth and recovery, particularly in regions suffering from strong and frequent seasonal drought stress.

Southwest China has experienced intensified seasonal extreme droughts, causing serious economic losses and ecological damages (Liu et al., 2016; Wang et al., 2018). Notably, this region is experiencing a clear interdecadal transition from wet to dry in autumn since mid-1990s (Wang et al., 2018). In this region, abundant rainfall during the rainy season is difficult to be stored in the soil, and most of the water is lost through underground runoff, which is mainly attributed to widespread karst geomorphology (Heilman et al., 2014; Liu et al., 2016). The karst region in southwest China is characterized by widespread rocky desertification, with a high ratio of bedrock outcrops to shallow soil and a low vegetation coverage (Li et al., 2016; Liu, Liu, Guo, Wang, et al., 2016, Liu, Liu, Guo, Zhao, et al., 2016). Affected by the unique hydrogeological structures in karst regions, differences in water availability cause plants to colonize different landscape positions (Efe, 2014). Different plant species in this region are characterized by diverse water use strategies in wet and dry seasons. For example, water uptake for Rademacheria sinica growing on the continuous outcrops shifted from rainwater stored in rock fissures of the unsaturated zone in the early dry season to deep water sources in the late dry season. In contrast, Alchornea trewioides growing on outcrops always relied on recent rainwater (Nie et al., 2012).

However, the potential roles of edaphic properties beyond the climate variations, such as the depth to bedrock, field capacity, etc., on the responses of vegetation growth to seasonal extreme droughts remain unknown. The edaphic properties should have important impacts on the drought response of vegetation in karst regions, owing to spatially diverse geomorphic conditions and the associated variability in soil water contents and nutrition supply. Ecosystem productivity in this region was largely limited by low water availability and the shortage of soil nutrients resulting from the shallow soil (Guo & Dong, 2009; Zhang, 2009). Previous study shows that soil in karst region had higher microbial respiration rates than those in the nonkarst region, which directly affects the release and retention of soil nutrients, and then affects plant growth (Chen et al., 2018). Therefore, comprehensive understanding of the potentially crucial roles of edaphic properties in regulating the vegetation growth recovery from extreme droughts is a prerequisite for better predicting the ecosystem stability in a more extreme climate in this region and other regions alike.
Here, we performed a study aiming to identify the underlying processes governing VRT in karst regions of Southwest China, particularly emphasizing the effects of drought timing and edaphic properties. Specifically, this study aims to (1) identify the potential divergent effects of extreme droughts that occurred in different seasons on VRT, and (2) determine the differentiating roles of edaphic and climate factors governing the postdrought VRT between forests and grasslands.

2. Materials and Methods

2.1. Study Region

Southwest China spans from 20°53′49″N to 34°18′46″N and from 97°21′22″E to 112°3′24″E. It is composed of five provinces, including Sichuan, Chongqing, Guizhou, Yunnan, and Guangxi (Figure 1). It is a typical subtropical region dominated by south Asian monsoon system, with cold, dry winter, and warm, wet summer. The mean annual temperature ranges from 14.9 to 22.2°C. The mean annual precipitation varies from 1,000 to 1,300 mm, with most of it fallen in summer. Forest, savanna, cropland, and grassland are the typical ecosystem types in this region, occupying 29.8%, 26.8%, 25.5%, and 12.1% of the land area, respectively, according to the moderate resolution imaging spectroradiometer (MODIS) land cover map (https://neo.sci.gsfc.nasa.gov/view.php?datasetId=MCD12C1_T1).

The karst ecosystem in Southwest China is one of the largest exposed carbonate rock areas in the world. It covers more than 0.54 million km². Karst landforms, characterized by severe soil and water loss, are widespread in this region and are highly vulnerable to human disturbances and climate change, particularly seasonal drought stress. Previous studies have shown that there has been an interdecadal transition from wet to dry in autumn since 1994, and shifts in autumn precipitation are the main triggers of the dry-wet decadal transition and intensified extreme droughts in recent decades (Wang et al., 2018). Incremental studies have consistently revealed that seasonal extreme drought events have led to a pervasive decline in vegetation growth and weakened terrestrial carbon uptake in Southwest China (Liu et al., 2016a; Wang et al., 2015). For example, extreme drought in the summer of 2009 to winter of 2010, particularly the spring drought of 2010, led to a significant decline in the vegetation greenness and primary productivity in Southwest China (Li et al., 2019; Song et al., 2019; Zhang et al., 2012).

Figure 1. Major land covers and distribution of karst regions in Southwest China. (a) Spatial distribution of major land covers in Southwest China. The land cover map was derived from MODIS in 2010 (https://neo.sci.gsfc.nasa.gov/view.php?datasetId=MCD12C1_T1). (b) The geographical distributions of karst landforms (https://digital.lib.usf.edu/SFS00534200001) in Southwest China. The inlets in (a and b) show the location of Southwest China.
2.2. Data Sets

2.2.1. NDVI Data Set

We used satellite-derived Normalized Difference Vegetation Index (NDVI) to investigate variations in vegetation greenness/growth in this region. The NDVI derived from the Advanced Very High Resolution Radiometer observations during 1982–2015 was produced by the Global Inventory Modeling and Mapping Studies (GIMMS) group (i.e., GIMMS NDVI3g) (Li et al., 2019; Wu et al., 2018). The GIMMS NDVI3g has a spatial resolution of 1/12° and a 15-day temporal resolution. This data set has been widely used to investigate the changes in vegetation growth and productivity in diverse ecoregions globally (Ye et al., 2021). The GIMMS NDVI3g is then aggregated to a spatial resolution of 0.25° and monthly values to match other climate and soil property data sets.

2.2.2. Climate and Soil Moisture Data Set

Monthly gridded air temperature (AT) and precipitation (TP) data from 1982 to 2015, with a spatial resolution of 30 arc sec, were obtained from the ECMWF (European Center for Medium-Range Weather Forecasts, https://www.ecmwf.int/en/forecasts/dataset/ecmwf-reanalysis-v5). We aggregated them into a spatial resolution of 0.25° to match the NDVI data. The root-zone soil moisture data were obtained from the Global Land Evaporation Amsterdam Model (GLEAM) version 3.0a with a spatial resolution of 0.25° (Martens et al., 2017). In vegetated regions, root-zone soil moisture is a link between surface phenology and subsurface water storages, and it strongly influences surface water balance and energy partitioning due to evapotranspiration. Root-zone soil moisture also controls surface vegetation health conditions and coverage, especially in regions suffering from seasonal or year-long drought stress, where water is one of the main controlling factors for vegetation growth (Wang et al., 2007).

2.2.3. Land Cover and Landform Data Set

A land cover classification map was obtained from MODIS products (i.e., MCD12C1). This data set recognizes 17 categories of land covers following the International Geosphere-Biosphere Program (IGBP) scheme (Loveland & Belward, 1997). This set of land cover types includes 11 categories of natural vegetation covers broken down by life form, three classes of developed and mosaic lands, and three classes of nonvegetated lands. The spatial distributions of major land cover types in our study region are shown in Figure 1a. In this study, we considered two major natural vegetation covers, including forests and grasslands, where forests are regrouped as evergreen needleleaf forests, evergreen broadleaf forests, and mixed forests and grasslands are regrouped as woody savannas and grasslands.

The karst landform map is obtained from the World Map of Carbonate Rock Outcrops v3.0 (https://digital.lib.usf.edu/SFS0055342/00001), which is produced by the University of Auckland, using a multitude of sources, the most important of which are acknowledged in Williams & Ford (Ford & Williams, 2007a; Williams, 2008a). It defines karst as comprising terrain with distinctive hydrology and landforms that arise from a combination of high rock solubility and well developed secondary (fracture) porosity (Ford & Williams, 2007b). This v3.0 revision is in greater detail and attempts to differentiate those areas where carbonate rocks are relatively pure and continuous from those where they are abundant but discontinuous or impure.

2.2.4. Soil Property Data Sets

The gridded soil profile depth (DS) data were derived from a comprehensive soil characteristic data set of China with a spatial resolution of 30 × 30 arc sec (Shangguan et al., 2013). It includes the physical and chemical soil attributes derived from 8,979 soil profiles and the Soil Map of China (1:1,000,000). These depths of soil profiles are the depths to which the soils were examined, but in most cases, they are not the depth to bedrock. Field capacity is obtained from the soil hydraulic parameter data set and designed specifically for regional land surface modeling in China (Dai et al., 2013). This data set is available at a spatial resolution of 30 × 30 arc sec and with seven vertical layers. In this study, the summed field capacity in the seven soil layers was used to capture the maximum water-holding capacity of soil profile. Field capacity is the amount of water content retained in soil after excessive water has drained away under gravity and is regarded as the water content at about −33 kPa of suction pressure. We also use a depth to bedrock map of China with a spatial resolution of 10 km based on observations interpreted from borehole logs in China (Yan et al., 2020). This product is developed under an automated soil mapping framework. Observations were extracted from a global compilation of soil profile data (ca. 130,000 locations) and borehole data (ca. 1.6 million locations). The depth to bedrock was introduced to depict the spatial variations in regolith depth in this karst region, which is an important factor influencing the regolith water variability and...
the consequent vegetation growth (Jiang et al., 2020). We consistently aggregated the above three data sets into a spatial resolution of 0.25° to match the vegetation index and climate data sets.

2.3. Methods

2.3.1. Defining Single Drought Event and Vegetation Recovery Time

Considering the complex impacts of repeated droughts on vegetation growth, we only studied single extreme droughts. Drought event is tracked for all vegetated land pixels and is solely a function of the soil moisture metric. Drought stress is usually characterized by low soil moisture (SM) and high atmospheric water demand (i.e., vapor pressure deficit, VPD). Recent studies have demonstrated that SM, rather than VPD, is the main driving force that causes drought in most vegetation ecosystems and limits vegetation growth (Liu et al., 2020). As soil moisture is an important factor driving vegetation growth in karst areas, we used the GLEAM soil moisture data to identify the drought events in period of 1985–2013 in Southwest China.

First, we apply a 3-month forward-moving window to smooth the SM, NDVI and other climate time series. Then, a threshold of multiyear monthly mean minus two (−2) standard deviations is used for the SM to identify extreme droughts at monthly scale. We focused only on single drought event, that is, the severe drought events followed by another severe drought within 3 years are excluded from the analysis, and this will minimize the legacy effects of drought. Considering the different effects of drought timing (especially in the growing season and nongrowing season) on vegetation recovery time (Dietrich, 2016; Huang et al., 2018), we divided extreme droughts into two groups. Drought occurred within March to August is defined as a spring and summer drought, and drought occurred within September to February of the following year is defined as an autumn and winter drought. Recovery time is tracked starting at the first drought month. The NDVI is considered “recovered” when the postdrought 3-month NDVI returns to 90% of the multiyear monthly mean NDVI for their corresponding month (Figure 2).

2.3.2. Statistical Analyses

We performed the two-sample Kolmogorov-Smirnov test to evaluate the difference in the VRT between two vegetation types in two landforms under either spring/summer or autumn/winter drought. We applied linear mixed-effects models (LMM) to disentangle the underlying drivers governing the postdrought vegetation recovery in Southwest China. We included a list of six fixed-effect variables: mean temperature (AT) and total precipitation (TP) during the recovery period, mean NDVI in the 3 months preceding the extreme drought event, and three kinds of soil properties, including soil profile depth (DS), field capacity (TH), and depth to bedrock (DB), into the LMM. The preceding NDVI captures the predrought vegetation growth condition, and we did not consider the phenology effects on drought recovery of vegetation in our study because there is no clear seasonality in NDVI in this subtropical region.

Three separate LMM models were built to investigate the underlying drivers for VRT under different cases, while considering different random effect variables to account for the nested structure of the data. The first model was applied to compare and identify the important drivers for VRT under spring/summer and autumn/winter droughts, while considering vegetation type and landform as random effect variables. The second and third models were built for identifying and comparing the underlying drivers for VRT of two vegetation types under spring/summer and autumn/winter droughts and for VRT in karst and nonkarst regions under two drought timings, while taking landform and vegetation type as random effect variables, respectively. All fixed-effect variables are calculated into anomalies to eliminate the problem caused by different background values due to spatial heterogeneity. All covariates were standardized (centered and scaled) prior to performing the LMM to allow parameter estimates to be compared. Alternative models containing different combinations of fixed-effect variables and their interactions were compared to determine the best model through ranking of AICc (Akaike Information Criterion) values. All statistical analyses were performed in the R environment. The lmer function of the “lme4” package was used to fit the linear mixed-effects models. General expression for the linear mixed-effect model was:

\[ Y = X\beta + Zb + \varepsilon \]  

(1)

where \( Y \) is the response variable VRT; \( X \) is the design matrix of fixed-effect variables; \( \beta \) is a vector of parameters for the fixed-effect variables; \( Z \) is the matrix for the random components of the model; \( b \) is the corresponding vector of parameters for the random components; \( \varepsilon \) is the residual terms.
3. Result

3.1. Spatial Patterns of Mean VRT in Period of 1985–2013

Overall, VRT is generally shorter than 6 months in 59.6% of the study region, and VRT is longer than 6 months in 5.4% of study region in both spring/summer and autumn/winter drought. No extreme drought events meeting our criteria were identified in the remaining 35% of our study region. The vegetation growth in most regions can recover from spring/summer drought within 4 months (Figure 3a). For autumn/winter extreme drought, the VRT in the southeastern part of the study area was much longer than other regions (Figure 3b). Overall, VRT from spring/summer droughts (2.75 ± 2.27) was significantly shorter than that from autumn/winter droughts (4.51 ± 3.90) (Figures 3 and 4).

We compared the VRT of forests or grasslands between karst and nonkarst regions and between forests and grasslands within either karst or nonkarst regions (Figure 4). VRT for forests ranges 1–19 months (2.5 ± 1.8) and 1–18 (3.7 ± 3.4) months in both karst and nonkarst regions in spring/summer and autumn/winter drought, respectively; whereas, VRT for grasslands ranges 1–21 months (3.1 ± 2.8) and 1–19 months (5.5 ± 4.3), respectively. In most cases, the VRT on nonkarst landforms is significantly (p < 0.05) shorter than that on karst landforms. More interestingly, we observed a significantly (p < 0.05) shorter VRT in forests than that in the grasslands in both karst and nonkarst regions, with such divergence more prominent in autumn/winter drought (Figure 4).
3.2. Effects of Variables on VRT Under Different Drought Timing

The LMM results for the VRT of spring/summer and autumn/winter droughts were displayed in Table 1. There exhibits clear difference in the important driving factors for the VRT between the spring/summer and autumn/winter drought. For spring/summer droughts, the mean temperature during recovery period is important \((p < 0.05)\) for controlling the VRT, with higher temperature associated with shorter VRT. The total precipitation during the recovery period significantly and negatively impacts the VRT under autumn/winter droughts (Table 1). More interestingly, we discovered a consistently and significantly negative impact of the depth to bedrock (i.e., deeper DB will lead to shorter VRT) on controlling the VRT for drought events in both spring/summer and autumn/winter (Table 1). It is worth noting that during the spring/summer droughts, the preceding NDVI also has a significant impact on the VRT, but this pattern did not show up in the autumn/winter drought. We further analyzed the difference in drivers underlying the VRT between the two vegetation types. The higher preceding NDVI will lead to more vigorous vegetation growth, which results in a shorter VRT under spring/summer droughts (Figures 5a and 5c). In contrast, higher preceding NDVI will postpone the recovery of vegetation growth, especially in forests under autumn/winter droughts (Figure 5b). More importantly, we discovered a crucial impact of the depth to bedrock on vegetation postdrought recovery in forests, with deeper depth to bedrock associated to a shorter drought recovery (Figures 5a and 5b). For forests, higher mean temperature during recovery period will shorten vegetation postdrought recovery under spring/summer droughts (Figure 5a), while for grasslands, higher precipitation is more conducive to vegetation recovery under both spring/summer and autumn/winter droughts (Figures 5c and 5d).

3.3. Effects of Variables on VRT of Different Landforms

For forests, climate variables are not significant for VRT in karst regions. While in nonkarst regions, the mean temperature during the recovery period and soil thickness exert significantly negative and positive effects on
VRT, respectively (Figure 6). More interestingly, we observed a significantly negative effect of the depth to bedrock (i.e., much deeper depth to bedrock leads to much shorter VRT) on VRT of forests (Figures 6a and 6b). For grasslands, the mean temperature and the total precipitation during recovery periods exert consistently positive and negative effects on VRT, respectively, at both karst and nonkarst regions (Figures 6c and 6d). Specifically, higher temperature during recovery period postpones grassland recovery, while higher precipitation shortens grassland recovery (Figures 6c and 6d). The preceding NDVI has a more negative effect (i.e., higher NDVI values lead to shorter VRT) on VRT in nonkarst regions than karst regions (Figure 6). Notably, the field capacity plays a more important role in VRT of grasslands in karst regions, while no significant role was observed in nonkarst regions (Figures 6c and 6d).

4. Discussions

4.1. Drought Timing Impacts Postdrought Recovery Time

We clearly reveal that the timing of drought events has differentiated impacts on the drought legacy effects on vegetation recovery, given that early drought mainly affects vegetation growth in the current year, while later drought reduces growth in the subsequent year (Kannenberg et al., 2019). Under autumn/winter drought, it will take much longer time to recover from the reduced vegetation growth (Figure 4). The longer VRT under autumn and winter drought could be partly attributed to the phenology effect, with this...
effect likely more prominent in temperate regions with clear vegetation phenology. On one hand, autumn and winter drought could delay the onset of spring phenology in this region (Ge et al., 2021), and a longer dormant period results in longer VRT. On the other hand, autumn and winter drought could exacerbate water stress in dry season, which decreases seasonal growth activity and leads to weaker seasonal biological carryover effects. The interacted effects of phenology changes and their biophysical feedbacks on vegetation growth reshape the drought recovery processes under different drought timing. For the 2009–2011 extreme drought event in Southwest China, extreme drought in winter and spring from 2009 to 2010 led to a decrease in enhanced vegetation index and productivity in the following spring and a decrease in NDVI and vegetation optical depth in summer; whereas, drought in the summer of 2011 led to an increase in vegetation productivity and an expansion of GPP/NPP in summer (Song et al., 2019), which partially validate our findings. Early drought will affect trees at the peak of biomass accumulation, resulting in a notable drought effect (D’Orangeville et al., 2018; Delpierre et al., 2016). In contrast, late drought may not give trees enough time to recover the lost branches and leaves, rebuild carbon

Figure 5. Linear mixed-effects model (LMM) for the vegetation recovery time (VRT) under spring/summer and autumn/winter droughts. LMM was performed for four groups: (a) forests under spring and summer droughts; (b) forests under autumn and winter droughts; (c) grasslands under spring and summer droughts; and (d) grasslands under autumn and winter droughts. Positive and negative factor effects indicate that higher values of corresponding factors will lead to longer and shorter VRT, respectively. AT, mean temperature during the recovery period; TP, total precipitation during the recovery period; NDVI, mean normalized difference vegetation index (NDVI) in 3 months preceding extreme droughts; DS, soil profile depth; TH, field capacity; DB, depth to bedrock. *p < 0.05; **p < 0.01; ***p < 0.001.
storage or repair embolism before senescence, thus affecting the leaf emergence and growth ability of trees in the next spring (Nathalie et al., 2006).

Interestingly, our study reveals that the vegetation growth condition before spring and summer droughts has a great impact on VRT. NDVI preceding the spring/summer drought makes up for vegetation growth after disturbance, while opposite pattern was observed in autumn and winter droughts (Table 1, Figure 5). The better the vegetation grows during spring and early summer most likely developed larger crowns, which might be able to still provide sufficient photosynthates to sustain growth during the drought period owing to the seasonal biological carryover effects (Lian et al., 2021). However, some other studies found that a lower resistance was associated with higher predrought growth rate (Bose et al., 2020), implying a potential divergent effect of preceding vegetation growth on drought resistance and recovery. Higher NDVI preceding the autumn/winter droughts might be associated with higher evapotranspiration during growing season in this region, which could exacerbate the drought stress on the subsequent spring phenology and growth activity in this karst region (Ge et al., 2021; Song

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Figure 6. Linear mixed-effects model (LMM) for the vegetation recovery time (VRT) in karst and nonkarst regions. LMM results for (a) forests in karst landform; (b) forests in nonkarst landform; (c) grasslands in karst landform; and (d) grasslands in nonkarst landform. AT, mean temperature during the recovery period; TP, total precipitation during the recovery period; normalized difference vegetation index (NDVI), mean NDVI in 3 months preceding extreme droughts; DS, soil profile depth; TH, field capacity; DB, depth to bedrock. *p < 0.05; **p < 0.01; ***p < 0.001.
et al., 2019), where is increasingly suffering from intensified autumn/winter drought stress, and thus leads to longer VRT. Nevertheless, comprehensive studies are urgently needed to disentangle the ecophysiological processes underlying this divergent pattern under different drought timings.

4.2. Important Role of the Depth to Bedrock on VRT

We report a crucial role of the depth to bedrock in mediating VRT following extreme droughts in karst regions, with such effects more prominent in forests than grasslands. In regions with thin soil layers, when vegetation growth affected by drought, the faster the effective water moves in the rock formation, the more drought stress the vegetation will take (Cerda et al., 1998). By contrast, in regions with thicker soil layers, it can store more water in deep layers to sustain vegetation growth (Sternberg et al., 1996; Zhang et al., 2020).

In karst regions, forests often grow on bedrock outcrops, however the water sources used by the forests are not well understood (Nie et al., 2012). Some studies have revealed that the root system of vegetation can insert into bedrock, but it is still uncertain whether the bedrock depth or the soil depth plays a more important role in the nutrient absorption of the root system of vegetation (Fan et al., 2017). Our analysis implies that the depth to bedrock, rather than soil depth, has a more significant role in mediating the forest VRT, with deeper depth to bedrock leading to shorter VRT (Table 1 and Figure 6). The sharp change and obvious difference in hydraulic characteristics between soil and bedrock usually result in underground saturation at the soil bedrock interface (Katsura et al., 2009, 2014). Subsurface saturation at the soil bedrock interface can increase runoff generation and deeper bedrock recharge (Montgomery & Dietrich, 2002). Douglas fir in the Santa Catarina Mountains preferentially absorbs nonflowing deep soil water during drought (Dwivedi et al., 2020). In addition to storing water in the soil, physical evidence also shows that vegetation can utilize groundwater in weathered or fractured bedrock (Pelletier et al., 2013). Woody plants roots can penetrate into bedrock, and they usually get water from bedrock, rather than groundwater, for example, in California alone, 20 km³ of water can be extracted from bedrock by woody plants annually (McCormick et al., 2021). This way of utilizing water from the bedrock has also been demonstrated in Mediterranean areas and other dry climate environments in summer (Bornyasz et al., 2005; Dralle et al., 2018). The mycorrhizal fungal hyphae extending from the root of bedrock cracks to the surrounding weathered bedrock can promote the acquisition of bedrock groundwater (Bornyasz et al., 2005).

Woody plant roots extend deep into the substrate to access stored water when seasonal drought occurred (Schenk & Jackson, 2005). When bedrock is formed within this potential rooting depth, plant roots penetrate into rock fractures below the soil (Graham et al., 2010). Components in carbonate rocks such as limestone, dolomite and gypsum are easily dissolved by rainwater, which leads to crevices within the bedrock surface (Jiang et al., 2020). This allows vegetation to absorb water from bedrock during the drought episodes. On the other hand, these crevices promote the leakage and loss of water in regolith (Auler & Smart, 2003), which thus influences the regolith water-holding capacity (Buss et al., 2017). Changes in erosion rate will affect the responses of vegetation to soil properties (Wolf et al., 2016), and the regolith water loss rate may lead to the difference in vegetation growth and productivity. In addition, bedrock nutrients are also an important driving factor for vegetation growth in this region. Elements the fresh bedrock contains such as P, Ca, Mg, and K are not readily accessible to organisms due to mineral structure of bedrock. As weathering progresses, however, the porosity will increase and become a medium for organisms to obtain nutrients through the bedrock (Graham et al., 2010). The mineral nutrients derived from bedrock are extremely important for plant growth in karst regions (Dai et al., 2018). Previous studies have demonstrated that plants are sensitive to potential changes in nutrients from deeper bedrock sources (Castle & Neff, 2009). Although the underlying mechanism remains to be further explored, it is reasonable to believe bedrock composition can play a fundamental role in vegetation growth and affect the post drought recovery trajectories.

4.3. Vegetation Drought Recovery in Karst Landforms

The vegetation drought recovery is closely linked to the regolith features and the vegetation type-associated rooting systems (Ding et al., 2021). Vegetation growth mainly relies on the recent rainwater stored in the soil (Heilman et al., 2009). In hotter areas, such as Xishuangbanna, during the dry season of 2005, fog was the only source of water input (Liu et al., 2010). For grasslands with shallow root, in karst landform areas, lower soil water capacity could prolong the VRT, while in nonkarst landforms, the effect of soil water capacity is not significant.
Deep-rooted vegetation is often strongly controlled by interactions between vegetation water use and groundwater dynamics (Asbjornsen et al., 2011; Shen et al., 2013), although a drop in the groundwater level can increase the plant’s water stress, growth and mortality (Hember et al., 2017; McDowell et al., 2002). The difference in the coordination of regolith features and vegetation rooting systems most likely explain the shorter VRT and the significant role of the depth to bedrock in deep-rooted forests than in shallow-rooted grasslands (Figures 4–6).

Rocky desertification is common in karst landforms, with a high ratio of bedrock outcrops to shallow soil and low vegetation coverage (Jiang et al., 2020). The characteristics of rocky desertification and the dual conduit and diffusion flow system of the karst aquifer together promote rapid hydrological processes (rainwater quickly penetrates through the thin soil layer, and the connected fissures in the bedrock layer reach the rooting zone or below groundwater) (Nie et al., 2012). Bare bedrock, on the one hand, could increase the surface impervious area and hence promote rainfall runoff accumulation (Jukić & Denić-Jukić, 2009; Peng & Wang, 2012). Weathered bedrock has many physical characteristics that allow it to perform functions similar to soil, such as a high porosity, a saturated hydraulic conductivity, and a high water holding capacity (Rose et al., 2003). Because epikarsts have a high porosity and permeability and are able to store and transport water, even if the rainfall during the rain event during recovery is small, most rainwater is transported underground through fissures and fractures (Williams, 2008a). Meanwhile, although hard bedrock limits the downward growth of roots, deeper root exploration is possible due to the presence of cracks and dissolution karst features (cavities) in the rock. Cavities vary in size from pores to caves and can be empty or filled with soil (soil pockets) (Estrada-Medina et al., 2013). Therefore, the vegetation growing here has special water use strategies during different periods, which is also tree species specific. Deciduous plants such as Radermachera sinica mainly absorb recently stored rainwater in shallow fissures in summers with abundant rainfall and use surface-zone karst water in dry seasons. Evergreen plants such as Schefflera octophylla experience no changes in water sources (Nie et al., 2012). Another study found that evergreen fir (Cunninghamia lanceolata) mainly uses shallow soil water in the rainy season and groundwater in the dry season (McCole & Stern, 2007). Generally, shallow-rooted plants in karst landforms mainly absorb and use shallow soil water, while deep-rooted plants such as Eucalyptus grandis in karst regions often absorb water at different depths at the same time (Schwinning, 2008; Williams, 2008b). However, some other studies also show that karst evergreen trees are more likely to experience leaf hydraulic failure under extreme droughts than the deciduous trees (Tan et al., 2020). Our findings support the idea that intensified water limitation accompanying with a future climate drying could impose strong environmental filtering and/or selective pressures resulting in tight coordination between rooting depth, water use strategies, and the drought vulnerability across diverse karst communities.

5. Conclusions

In this study, we investigated both the patterns and the underlying drivers for the postdrought vegetation recovery time across different vegetation types and landforms in karst regions of southwest China, with emphasis on the regolith effects. It was found that higher mean normalized difference vegetation index (NDVI) preceding the spring/summer drought leads to shorter drought recovery time for both forests and grasslands, while opposite pattern appears in autumn/winter drought, particularly in forests. More importantly, we discovered a crucial impact of the depth to bedrock on vegetation postdrought recovery in forests but not in grasslands, with deeper depth to bedrock associated to a shorter drought recovery. The field capacity of soil is more important for postdrought vegetation recovery in karst regions than in nonkarst regions, which can be most likely attributed to differences in the water-holding capacities and water use strategies of vegetation. Karsts are widely distributed around the world, but the underlying processes and mechanism for the responses of vegetation growth to extreme climate events are not clear. Our results provide a baseline for the recovery of different vegetation types after extreme drought in a special landform. Future studies on the resilience of ecosystems should fully consider the crucial underground processes.
Data Availability Statement

All of the data sets used in this study can be freely accessible. The CIMMs-NDVI data were obtained from https://ecocast.arc.nasa.gov/data/pub/gimms/3g.v1f/. The land cover map was obtained from MODIS product MCD12C1 (https://modis.gsfc.nasa.gov/data/datasetpro). The monthly gridded climate data were obtained from the ECMWF (ECMWF, European Centre for Medium-Range Weather Forecasts, https://www.ecmwf.int/en/forecasts/dataset/ecmwf-reaanalysis-v5). The karst landform map was obtained from the World Map of Carbonate Rock Outcrops v3.0 (https://digital.lib.usf.edu/SFS0055342/00001). The gridded soil profile depth data were derived from a comprehensive soil characteristic data set of China (http://globalchange.bnu.edu.cn/research/soil1). Field capacity data were obtained from the soil hydraulic parameter data set (http://globalchange.bnu.edu.cn/research/soil3). The depth to bedrock data were obtained from the depth to bedrock map of China (http://globalchange.bnu.edu.cn/research/cdbf.jsp).

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