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Intraspecific variation in seedling growth responses of a relict tree species *Euptelea pleiospermum* to precipitation manipulation along an elevation gradient

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Abstract Improving the accuracy of predictions regarding how plants respond to climate change is crucial to protecting biodiversity. However, little is known about the effects of seed source and elevation on the response of mountain plant species to reductions in precipitation. Here, we collected seeds of a tree species (*Euptelea pleiospermum*) from three seed sources and carried out a two-growing-season reciprocal transplant experiment with precipitation manipulation at three sites along an elevation gradient in the Shennongjia Mountains, central China. Variations in whole-plant traits, leaf traits, and root traits were investigated. We found that most plant traits of *E. pleiospermum* seedlings were affected by reductions in precipitation, and responses varied among different elevations and seed sources. Whole-plant traits, root biomass, and leaf traits related to photosynthesis capacity decreased under reduced precipitation treatments at mid and high elevation sites. Thus, climate change induced drought will likely have a negative influence on seedling growth at mid and high elevation regions. In addition, a home-site advantage in whole-plant traits and root traits was observed. However, the responses of leaf traits in most cases were not affected by seed source because of higher phenotypic plasticity. Our results suggested that both local adaptation and phenotypic plasticity were important in seedling growth responses to reduced precipitation. We also highlight the importance of taking intraspecific variation into account when studying the response of plants to changes in climate.

Keywords Climate change · Elevation gradient · Local adaptation · Phenotypic plasticity · Precipitation manipulation · Reciprocal transplant

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Introduction

The average global temperature is predicted to rise 2–4 °C by the end of this century (IPCC 2014). At the same time, precipitation patterns will likely be altered, and an increase in the frequency and severity of drought events is expected across the globe (IPCC 2014). A large number of studies have demonstrated that climate change will affect plant growth, reproduction, phenology, and overall species distributions (Walck et al. 2011; Usinowicz and Levine 2018; Piao et al. 2019). These changes will, in turn, increase the risk of species extinction and accelerate the loss of global biodiversity (Thomas et al. 2004; Urban 2015). Therefore, learning to predict how species will respond to current and future climate change is critical for biodiversity conservation, and has become one of the most important research challenges (Parmesan and Hanley 2015; Ettinger et al. 2019).

Manipulative field experiments are a highly effective tool used to explore the response of plants to climate change (Rustad 2008; Wu et al. 2011; Kreyling et al. 2017). Early studies focused primarily on the effects of a single isolated climate change factor, such as elevated atmospheric CO_2, warming, or altered precipitation (Zanetti et al. 1996; Hartley et al. 1999; Nepstad et al. 2002). Subsequently, ecologists have begun to recognize the importance of studying plant responses to multiple interactive climate change factors (Norby and Luo 2004; Rustad 2008; Volder et al. 2010), and particularly the interaction between temperature and precipitation (Niu et al. 2008; Charles and Duke 2009; Grossiord et al. 2017). For example, Taeger et al. (2015) found that the effects of climate warming on the growth and phenology of *Pinus sylvestris* seedlings was strongly dependent on water availability. Likewise, warming may increase the sensitivity of seedling growth to precipitation in temperate deciduous tree species (Rodgers et al. 2018).

Recently, the importance of intraspecific variation has gained attention in global change biology (Moran et al. 2016; Midolo and Wellstein 2020). Most studies on plant responses to warming and altered precipitation regimes have not accounted for among-population variation and therefore may not be generally relevant (Taeger et al. 2015; Henn et al. 2018). Because populations tend to be locally adapted, and show phenotypic plasticity across environmental gradients, the responses of different populations to climate change are not always consistent (Hsu et al. 2014; Valladares et al. 2014; Gugger et al. 2015). For instance, alpine populations of *Erysimum capitatum* were found to be more sensitive to climate warming than low-elevation populations, likely as a result of local adaptation to high elevation sites (Kim and Donohue 2013). In addition, De Villemereuil et al. (2018) found that two high-elevation populations of the alpine plant species, *Arabis alpina*, lacked phenotypic plasticity compared to populations from lower elevations. Such studies highlight the need to take intraspecific variation into consideration when exploring how plant species respond to a rapidly changing climate. Such knowledge will help us to predict population dynamics and species demographics more accurately, so as to implement more effective and specific protection schemes for different populations.

Euptelea pleiospermum (Eupteleaceae) is a Tertiary-relict species distributed between 760 and 3200 m a.s.l. in montane forests of China (Fu and Jin 1992). The species is a deciduous broad-leaved tree that grows generally along the edge of river valleys in mountainous areas (Wei et al. 2010). It was listed as a rare species in the China Plant Red Data Book (Fu and Jin 1992). Like *E. pleiospermum*, there are many other rare or endangered Tertiary-relict tree species in montane riparian plant communities across the world (Hampe and Arroyo 2002; Tang and Ohsawa 2002; Mejías et al. 2007; Wei et al. 2010). As montane streams are primarily sourced from rainfall, changes in precipitation are bound to affect their hydrological conditions and associated vegetation communities (Garssen et al. 2014). As is well known, seedlings are the most vulnerable stage in a plant's life cycle, and seedlings are thus highly sensitive to environmental changes (Lloret et al. 2004; Dalgleish et al. 2010). As a result, seedlings are one of the important bottlenecks in the population recruitment and species persistence of rare plant species (Zimmer et al. 2014; Wright et al. 2018). With the rapid rise of global temperatures and increasing frequency of droughts, it is urgent to understand how seedling growth of montane riparian plant species responds to future climate change.

As temperatures gradually decrease at higher elevations, elevation gradients can be used as a proxy for temperature gradients in many situations (Körner 2003). Therefore, comparing the response of plant performance to precipitation treatments at different elevation sites is a good way to study the effects of interactions between temperature and precipitation on plant growth (De Boeck et al. 2016). We carried out precipitation manipulation treatments on seedling growth of *E. pleiospermum* along an elevation gradient in the Shennongjia Mountains, central China. Specifically, we used reciprocal transplant experiments to study the effects of seed source on seedling growth responses to variation in temperature and precipitation. We sought to address the following questions: (1) How does seedling growth respond to precipitation-reduction across different elevation sites? Is there an interaction between the elevation of transplant site (representing temperature) and precipitation? (2) Is the response of seedling growth to elevation and precipitation affected by seed source?

Materials and methods

Study area and species

The study was carried out in the Shennongjia Mountains (31°15′-31°57′N, 109°56′- 110°58′E) of central China. The highest peak is 3105.4 m a.s.l.. The climate in this area is described as subtropical monsoon, with mild, wet summers and cold, dry winters (Dang et al. 2013). Based on the climate data records (1952–2004) from the Badong meteorological station (295.6 m a.s.l.) in the Shennongjia Mountains, the mean annual temperature was 17.4 °C and the mean annual precipitation was 1089.6 mm (Dang et al. 2013). The mild and humid climatic conditions in this region provide a good growth environment for rare and relict plant species. Vegetation surveys indicate that a large number of rare and relict plant species (*Cercidiphyllum japonicum*, *Tetracentron sinense*, *E. pleiospermum*, etc.) are distributed in the riparian forests of the Shennongjia Mountains (Jiang et al. 2002; Shen et al. 2004; Wei et al. 2010). In this area, *E. pleiospermum* has a wide distributional range in terms of elevation, primarily between 900 and 2100 m a.s.l. (Jiang et al. 2002; Wei et al. 2008), which makes it a good species for studying seed source effect on seedling growth response to altered climatic conditions.

Seed collection and sowing

In autumn of 2016, we collected mature seeds of *E. pleiospermum* from low-elevation (1100—1200 m), mid-elevation (1500—1600 m), and high-elevation (1900—2000 m) populations (referred to as L, M and H seed source, respectively). Seeds were randomly collected from ten healthy mother trees at each seed source. Seeds from the same seed source were thoroughly mixed and air-dried for approximately one month in the laboratory. After drying, the seeds were stored at 4 °C for nearly 4 months until sowing.

In late March 2017, a nursery (3 m × 2 m) was established at the National Observation and Research Station for Forest Ecosystem in Shennongjia (31.323°N, 110.485°E, 1286 m a.s.l.), China. The nursery was evenly divided into three plots (1 m × 2 m). Seeds from different seed sources were separately sowed into the three plots. Plots were watered to ensure seed survival and proper germination.

Experimental setup

We established three reciprocal transplant sites along an elevation gradient in the Shennongjia Mountains. These sites were located at low (~ 800 m), mid (~ 1500 m), and high (~ 2200 m) elevations in open areas with relatively flat ground. All sites were facing south to keep the light conditions as consistent as possible. We refer to transplanting sites as L, M and H site, respectively. Geographical information and a map of these sites are shown in Table S1 and Fig. S1. Within each site, three 4 m × 2.5 m plots were established. The three plots, about 5 m apart, were associated with three different precipitation reduction treatments. The treatments were ambient precipitation (P0), 20% reduction (P1), and 40% reduction (P2). In addition, each plot consisted of three subplots (1 m × 1.5 m) (Fig. S2) used to plant seedlings. To prevent animal damage (grazing or trampling), 0.75 m tall wire netting was placed around each plot.

Precipitation manipulation

Precipitation reduction treatments were accomplished using a device composed of a supporting frame and interception roof (Fig. S3). This device was called rain-out shelters and have been widely used in precipitation manipulation experiments (Yahdjian and Sala 2002; Grossiord et al., 2016; Zhou et al. 2018). The supporting frame consisted of a trestle built around the plot with stainless steel pipes. There was a height difference of about 40 cm between the front and the back pipes installed in the horizontal direction, resulting in an incline that enabled the intercepted rain water to flow away from the experimental area (Fig. S3). The mean height of the frame was about 1.8 m to allow adequate space for seedling growth.

Transparent U-shaped PC (polycarbonate) sheets were evenly mounted on the frame to intercept rain water, which was used as the precipitation interception roof (Fig. S3). The U-shaped PC sheet was 2.5 m in length and 5 cm in width. We used 16 and 32 sheets, at a distance from each other of 20 cm and 7.5 cm, to attain P1 and P2 treatments, respectively. For example, the 20% precipitation reduction treatment (P1) had 16 sheets located regularly at a distance of 20 cm, for covering 20% of the plot area (2.5 m × 4 m) (Fig. S3).

In addition, we installed barriers of plastic sheets (0.5 m height) around the seedling areas: 0.3 m reaching down the soil to prevent lateral movement of soil water between the experimental seedling areas and their surroundings, and 0.2 m above the ground to avoid lateral surface runoff (Fig. S3) (Hoeppner and Dukes 2012; Kreyling et al. 2017).

Seedling transplanting

Because local soil conditions can alter the seedling responses to climate (Ford and HilleRisLambers 2019), we removed 30 cm of soil at each experimental area and filled them with a uniform transplant soil. This was done to eliminate the potential effects of soil heterogeneity on seedling growth. The transplant soils used in this study were similar to natural soils of the species. They were humus soils collected under forest stands in this area.

In June 2017, seedling transplanting began two months after seedlings emerged when they were approximately 5 cm in height. We selected seedlings that were similar in size for planting at the experimental sites. Five seedlings from each seed source were randomly planted within each subplot, and the distance between seedlings was 20 cm. The overall experimental design included 3 elevation treatments × 3 precipitation treatments × 3 seed source treatments × 3 subplots × 5 seedlings/ subplot = 405 seedlings in total. In addition, we planted one seedling with the same planting distance in the periphery of the target seedling area to reduce edge effect (Fig. S2). To ensure that seedlings grew over a similar time period, seedling transplanting was completed within three days. After transplanting, manual management (e.g. watering) was carried out for 2 weeks to ensure survival of seedlings.

Data collection

Soil moisture and temperature were measured by the 5TM sensor (Decagon, USA) during the second growing season. In May 2018, sensors were installed 15 cm below the soil surface at each plot and were connected to Em50 loggers (Decagon, USA). Soil moisture and temperature data were recorded every 15 min.

In late September 2018, we collected seedling samples from one randomly selected subplot within each plot. Due to the death of a few seedlings throughout the experiment, 3–5 seedlings from each seed source were collected in each subplot and a total of 105 seedlings were sampled. Before sampling, stem height and leaf chlorophyll concentration were recorded. The mean height of seedlings grown at low-, mid- and high-elevation sites were 110.6 cm, 66.0 cm and 19.9 cm at harvest, respectively. We measured chlorophyll concentration three times as a replication for each leaf and for three leaves per individual using a SPAD-502 chlorophyll meter (Konica-Minolta, Japan). We clipped seedlings at ground level and measured aboveground biomass. Then, we carefully dug up seedling roots and washed them with clean water. After the water on the surface of the root was air-dried, root biomass and maximum root length were measured. We also calculated total biomass as the sum of aboveground biomass and root biomass. Next, aboveground and root samples were dried in an oven at 70 °C for 48 h to constant weight to measure dry biomass. Then, the root-to-shoot ratio was determined using the root dry mass divided by the aboveground dry mass.

In addition, we collected five to ten healthy leaves from each seedling to measure leaf traits. Fresh leaves were collected and immediately weighed and scanned without the petiole, and leaf area was calculated using an image analysis software (Digimizer; Medcalc software, Mariakerke, Belgium). Leaf thickness was measured using Vernier calipers. Leaves were then dried at 70 °C for 48 h and weighed. Specific leaf area (SLA) was calculated as leaf area divided by leaf dry mass. Leaf dry matter content (LDMC) was determined by leaf dry mass divided by leaf fresh mass. Leaf density was calculated by dividing the inverse of

SLA by thickness (Vitasse et al. 2014). These leaf traits, including the chlorophyll concentration measured earlier, were averaged for each individual seedling. Afterwards, we separately ground the dried leaves of each seedling and analyzed them for leaf nutrient concentration. Leaf nitrogen concentration (LNC) was analyzed with a stable isotope mass spectrometer (Isotope–MS, delta V advantage; ThermoFisher Scientific, Darmstadt, Germany). Leaf phosphorus concentration (LPC) was analyzed with an inductively coupled plasma optical emission spectrometer (ICP-OES) (Optima 8000, PerkinElmer, USA).

Statistical analysis

The main and interaction effects of transplant site elevation and precipitation treatment on the measured plant traits were tested using linear mixed effects models (Vitasse et al. 2014). The fixed effects included site elevation, precipitation and their interaction. The seedling nested within seed source was treated as a random effect. The above analyses were carried out by the "lme" function in "nlme" package and "anova" function with the statistical program R version 3.1.3 (R Development Core Team, 2015; http:// www.r-project.org/).

In addition, the effect of precipitation treatment on soil moisture and temperature at each site, whole-plant traits, leaf traits, and root traits of seedlings from the same seed source at each site was estimated using one-way ANOVA, and multiple comparisons were conducted using Tukey's post-hoc test. The same analysis method was used to evaluate the effect of seed source on whole-plant traits, leaf traits and root traits of seedlings under the same precipitation treatment at each site. Before statistical analyses, a Shapiro–Wilk test and Levene's test were used to test whether the data satisfied the assumption of normality and homogeneity of variance. Prior to the analyses, aboveground biomass, total biomass, stem height, LPC and root biomass were $\log_{10}$ transformed. These statistical analyses were carried out using the SPSS software (version 21.0; IBM SPSS Statistics for Windows, Chicago, IL, USA).

Results

Soil moisture and temperature

Soil moisture at 15 cm depth declined significantly under the precipitation reduction treatments within the same transplant site (Table 1; Fig. S4). Among the sites, the effectiveness of reduced precipitation manipulation at the M site were most pronounced in terms of soil moisture content, but with few differences between P1 and P2 treatments (Table 1). Average soil moisture content decreased with the increasing of precipitation reduction at both L and H sites (Table 1).

Within the same transplant site, average soil temperatures had marginal differences among different precipitation treatments (Table 1). As expected, within the same precipitation treatment, average soil temperature decreased with the increasing elevation (Table 1).

Whole-plant traits

Response of whole-plant traits to reduced precipitation varied among different elevation sites, as the main and interactive effects of elevation and precipitation on these whole-plant traits were significant (Table 2). At the L site, precipitation reduction resulted in a significant increase in aboveground biomass, total biomass, and stem height in seedlings from the L seed source (Fig. 1A, D, G). At the M site, these traits reduced under precipitation reduction treatments for all three seed sources (Fig. 1B, E, H). At the H site, whole-plant traits decreased under reduced precipitation treatments only for seedlings from the L seed source (Fig. 1C, F, I).

Within the same reduced precipitation treatment, whole-plant traits were also affected by seed source, and seedlings from L and M seed sources attained a better performance in terms of biomass in their locations of origin. At the L site, aboveground biomass and total biomass of seedlings from the L seed source were significantly higher than for seedlings from the M and H seed sources under the P1 and P2 treatments (Fig. 1A, D). Similarly, at the M site, aboveground biomass and total biomass of seedlings from the M seed source were significantly higher than for seedlings from the other two seed sources under the P1 treatment (Fig. 1B, E). At the H site, total biomass and

Table 1 Moisture and temperature of soil at 15 cm depth for each precipitation treatment at the three sites (Mean ± SE). Measurements were taken during the growing season (May to November) in 2018

Precipitation treatment	L site		M site		H site	
	Moisture (%VWC)	Temperature (°C)	Moisture (%VWC)	Temperature (°C)	Moisture (%VWC)	Temperature (°C)
P0	26.7 ± 0.031a	19.9 ± 0.033b	28.0 ± 0.026a	17.4 ± 0.032a	31.7 ± 0.021a	13.5 ± 0.033a
P1	23.3 ± 0.053b	20.3 ± 0.033a	15.5 ± 0.019b	17.3 ± 0.028b	24.1 ± 0.022b	12.9 ± 0.031c
P2	18.9 ± 0.037c	19.6 ± 0.031c	14.7 ± 0.015c	17.2 ± 0.031c	20.6 ± 0.018c	13.0 ± 0.033b

Different letters indicate significant differences among precipitation treatments ($p < 0.05$) at each site

SE: standard error; *VWC:* volumetric water content. Precipitation treatments: *P0*: ambient precipitation; *P1:* 20% precipitation reduction; *P2*: 40% precipitation reduction

Table 2 Effects of transplanting elevation, precipitation, and their interactions on whole-plant traits of *Euptelea pleiospermum* seedlings

Factor	*df*	Aboveground biomass		Total biomass		Stem height	
		F	*p*	F	*p*	F	*p*
Elevation (Ele)	2	426.44	**< 0.001**	461.42	**< 0.001**	677.63	**< 0.001**
Precipitation (Pre)	2	8.79	**< 0.001**	8.95	**< 0.001**	3.64	**0.030**
Ele × Pre	4	14.29	**< 0.001**	11.43	**< 0.001**	8.89	**< 0.001**

The significant *p*-values were shown in bold ($p < 0.05$)

stem height of seedlings in the P2 treatment from the H seed source were significantly higher than for seedlings from the L seed source (Fig. 1F, I).

Leaf traits

The effect of precipitation treatment on leaf traits varied under different elevation sites, as the main and interactive effect of elevation and precipitation on most leaf traits was significant (Table 3). At the L site, SLA, LDMC, leaf density, and LNC of seedlings from the three seed sources did not vary significantly with different precipitation treatments (Fig. 2A, D, G; Fig. 3A), while LPC and leaf chlorophyll concentration of seedlings from L seed source were higher under P2 treatment (Fig. 3D, G). At the M site, LDMC and leaf density of seedlings from L seed source increased significantly under P2 treatment (Fig. 2E, H); LNC, LPC, and leaf chlorophyll concentration decreased significantly under precipitation reduction treatments, regardless of seed source (Fig. 3B, E, H). At the H site, SLA of seedlings from L seed source was higher under P2 treatment (Fig. 2C); leaf density of seedlings from M and H seed sources decreased significantly under P2 treatment (Fig. 2-I).

Within the same precipitation treatment, leaf traits were not affected by seed source in most cases, and the home-site advantage was not detected except for LPC. At the L site, SLA of seedlings from H seed source and LPC of seedlings from L seed source were higher than the other two seed sources under the P0 and P2 treatment, respectively (Fig. 2A; Fig. 3D). At the M site, SLA of seedlings from H seed source, LDMC and leaf density of seedlings from L seed source were higher than the other two seed sources under the P2 treatment (Fig. 2B, E, H). At the H site, all leaf traits did not vary among different seed sources under the same precipitation treatments.

Root traits

Root traits responded differently to precipitation reduction among the three sites, as the main and interactive effects of elevation and precipitation on root traits were significant in most cases (Table 4). At the L site, root biomass and maximum root length of

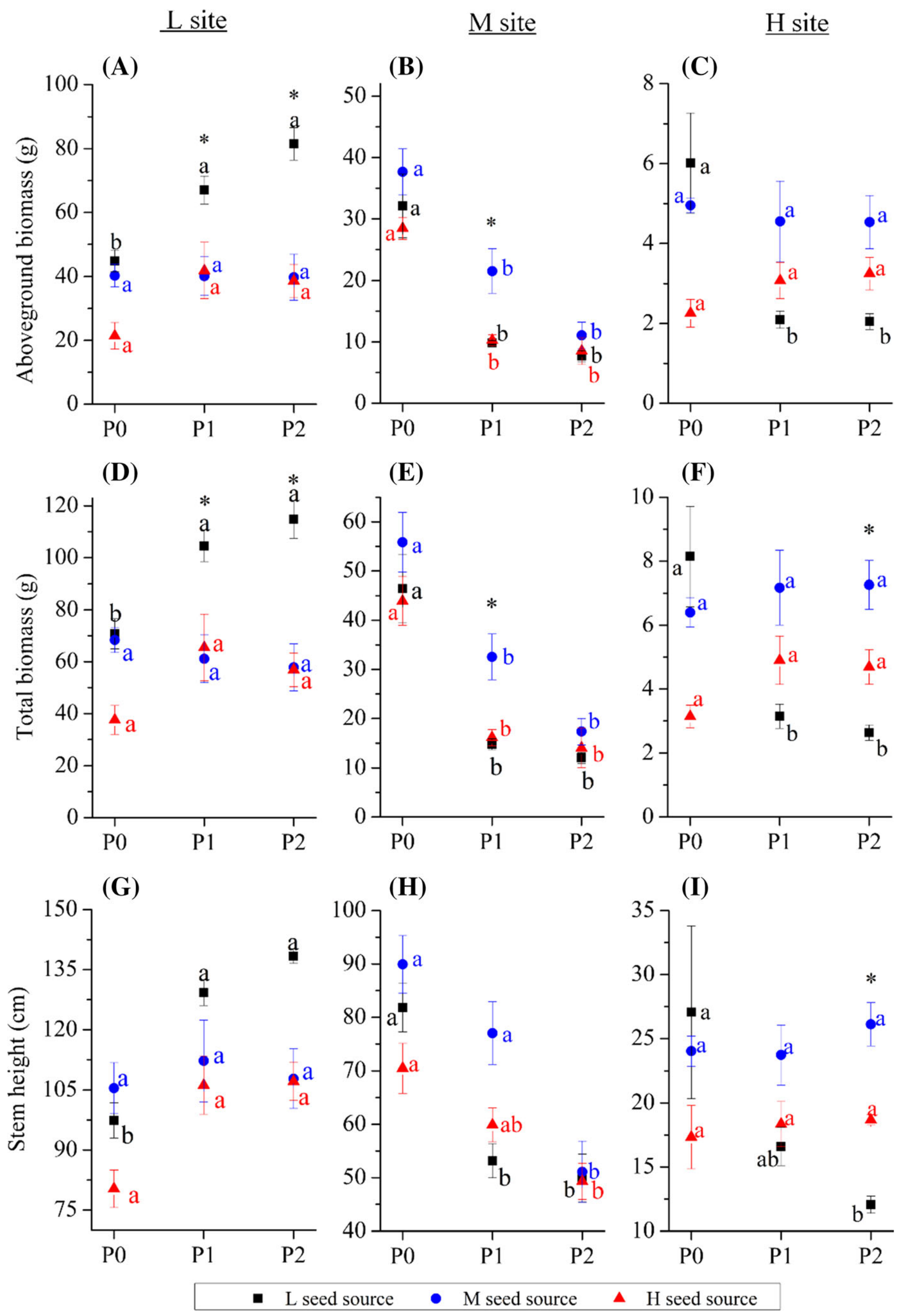

Fig. 1 Response of whole-plant traits of *Euptelea pleiospermum* seedlings from different seed sources to precipitation treatments at the three sites (mean ± SE). **A**-**C**, aboveground biomass; **D**-**F**, total biomass; **G**-**I**, stem height. Precipitation treatments: P0, ambient precipitation; P1, 20% precipitation reduction; P2, 40% precipitation reduction. *L:* Low elevation; *M*: Mid elevation; *H:* High elevation. Different letters indicate significant differences among precipitation treatments within the same seed source ($p < 0.05$); asterisk indicates significant differences among seed sources within the same precipitation treatment ($p < 0.05$)

Table 3 Effects of transplanting elevation, precipitation, and their interactions on leaf traits of *Euptelea pleiospermum* seedlings

Factor	*df*	SLA		LDMC		Leaf density		Leaf N concentration		Leaf P concentration		Leaf chlorophyll concentration	
		F	*p*	F	*P*	F	*p*	F	*p*	F	*p*	F	*p*
Elevation (Ele)	2	16.56	**< 0.001**	61.40	**< 0.001**	8.54	**< 0.001**	2.57	0.082	99.82	**< 0.001**	46.86	**< 0.001**
Precipitation (Pre)	2	6.82	**0.002**	1.54	0.220	7.17	**0.001**	34.92	**< 0.001**	18.24	**< 0.001**	36.71	**< 0.001**
Ele × Pre	4	1.81	0.134	4.27	**0.003**	4.74	**0.002**	32.64	**< 0.001**	13.72	**< 0.001**	25.32	**< 0.001**

The significant p -values were shown in bold ($p < 0.05$)

seedlings from L seed source were significantly higher under the precipitation reduction treatments (Fig. 4A, G). In contrast, the root biomass and root-to-shoot ratio of seedlings from M seed source was significantly reduced at lower precipitations (Fig. 4A, D). At the M site, root biomass of seedlings from all three seed sources in the P1 and P2 treatments were significantly lower than in the P0 treatment (Fig. 4B). In contrast, the root-to-shoot ratio and maximum root length did not differ among treatments, regardless of seed source (Fig. 4E, H). Finally, at the H site, root biomass of seedlings from L seed source decreased under both precipitation reduction treatments (Fig. 4C), and the root-to-shoot ratio of seedlings from L and H seed sources were not different with the control (Fig. 4F).

Similar to aboveground biomass, root biomass of seedlings was affected by seed source within the same precipitation treatments (Fig. 4). At the L site, root biomass of seedlings from the L seed source were significantly higher than seedlings from the M and H seed sources under the reduced precipitation treatments (Fig. 4-A). At the H site, root biomass of seedlings from the L seed source was significantly lower than that of seedlings from the other two seed sources under the P2 treatment (Fig. 4C).

Discussion

Response of seedling growth to reduced precipitation across different elevation sites

Seedling growth of *E. pleiospermum* was significantly affected by the precipitation treatments. The response of measured plant traits to reduced precipitation varied across the different elevation sites, suggesting an interaction between temperature and precipitation on seedling growth. Rodgers et al. (2018) found that warming dramatically increased the sensitivity of seedling growth to precipitation. During periods of drought, higher temperatures lead to increases in vapor pressure deficit, resulting in higher plant transpiration and increased water loss (Breshears et al. 2013; Will et al. 2013). At the same time, soil moisture evaporation will increase at higher temperatures, leading to further water stress (Jung et al. 2010; Rodgers et al. 2018). However, our results were not exactly consistent with their findings. For example, whole-plant traits of seedlings planted at M site unexpectedly suffered the largest negative effects of reduced precipitation (Fig. 1B, E, H), although mean temperature at M site was not the highest (Table 1). It may be because soil moisture in this site had maximum reduction under the precipitation-reducing treatments among the three sites, which could be reflected in the soil moisture data during the second growing season (Table 1).

Whole plant traits of seedlings grown at the M and H sites decreased significantly under reduced precipitation treatments. This finding was largely consistent with several other studies (Gilgen and Buchmann 2009; Carón et al. 2015; Eziz et al. 2017). It had been found that a decrease in biomass and height was often the first response of plants to drought (Hsiao and Acevedo 1974; Ludewig et al. 2018), because reducing size could help plants minimize water consumption under drought condition (Rodgers et al. 2018; Kahl et al. 2019). Surprisingly, however, whole-plant traits of seedlings from L seed source increased with lower precipitation at the L site. This may be because the drought treatment promoted root biomass and

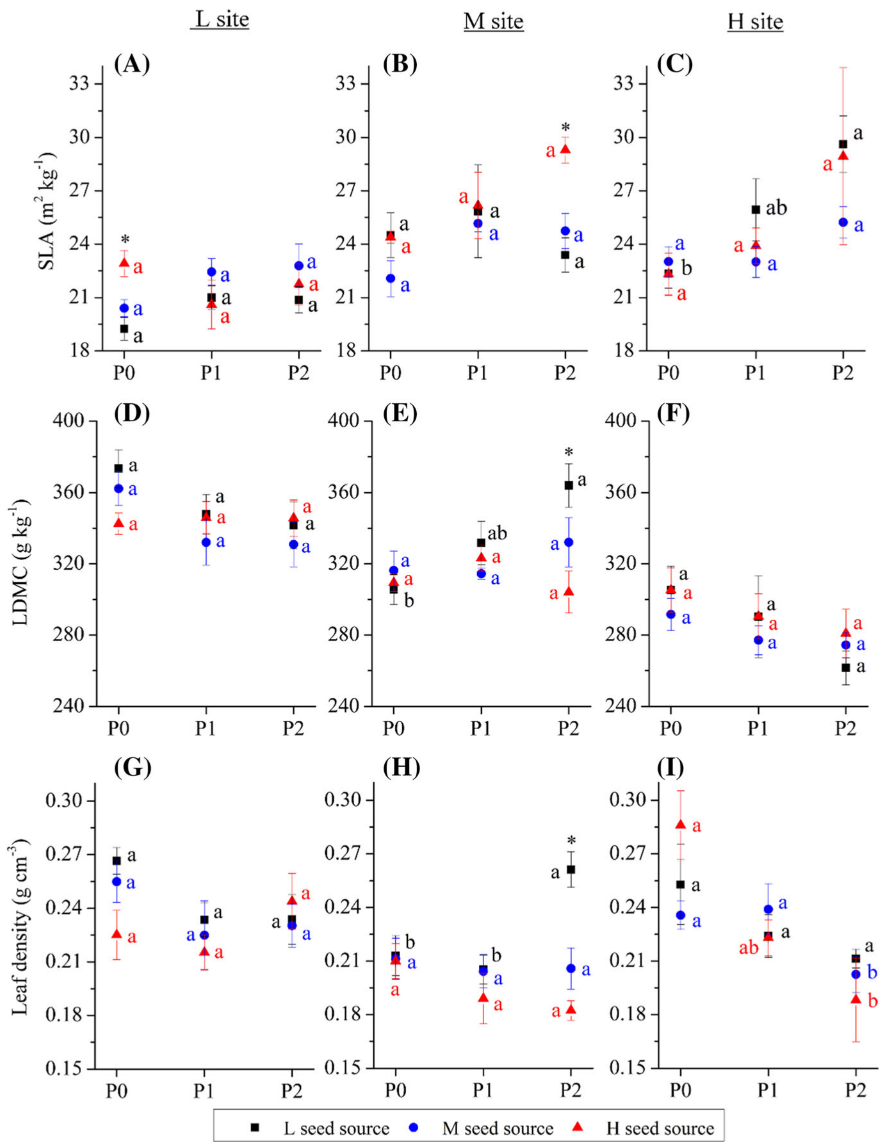

Fig. 2 Response of leaf traits (SLA, LDMC, leaf density) of *Euptelea pleiospermum* seedlings from different seed sources to precipitation treatments at the three sites (mean ± SE). **A**-**C**, SLA; **D**-**F**, LDMC; **G**-**I**, leaf density. Precipitation treatments: P0, ambient precipitation; P1, 20% precipitation reduction; P2, 40% precipitation reduction. *L:* Low elevation; *M:* Mid elevation; *H*: igh elevation. Different letters indicate significant differences among precipitation treatments within the same seed source ($p < 0.05$); asterisk indicates significant differences among seed sources within the same precipitation treatment ($p < 0.05$)

maximum root length (Fig. 4A, G), which promoted water absorption. In addition, LPC and leaf chlorophyll concentrations of seedlings from L seed source significantly increased under reduced precipitation (i.e. P2 treatment) at the L site (Fig. 3D, G), which could increase photosynthesis.

Leaf traits reflect plant resource acquisition and water use efficiency (WUE), and are known to be highly sensitive to environmental change (Wright and Westboy 2002; Wright et al. 2004; Jung et al. 2014). Generally, LNC, and leaf chlorophyll concentrations are closely related to photosynthesis capacity (Evans 1989; Reich et al. 1999; Gáborčík 2003). Likewise, LPC is typically associated with higher rates of leaf photosynthesis (Wright and Westoby 2001). In this study, the three leaf traits all declined with increased

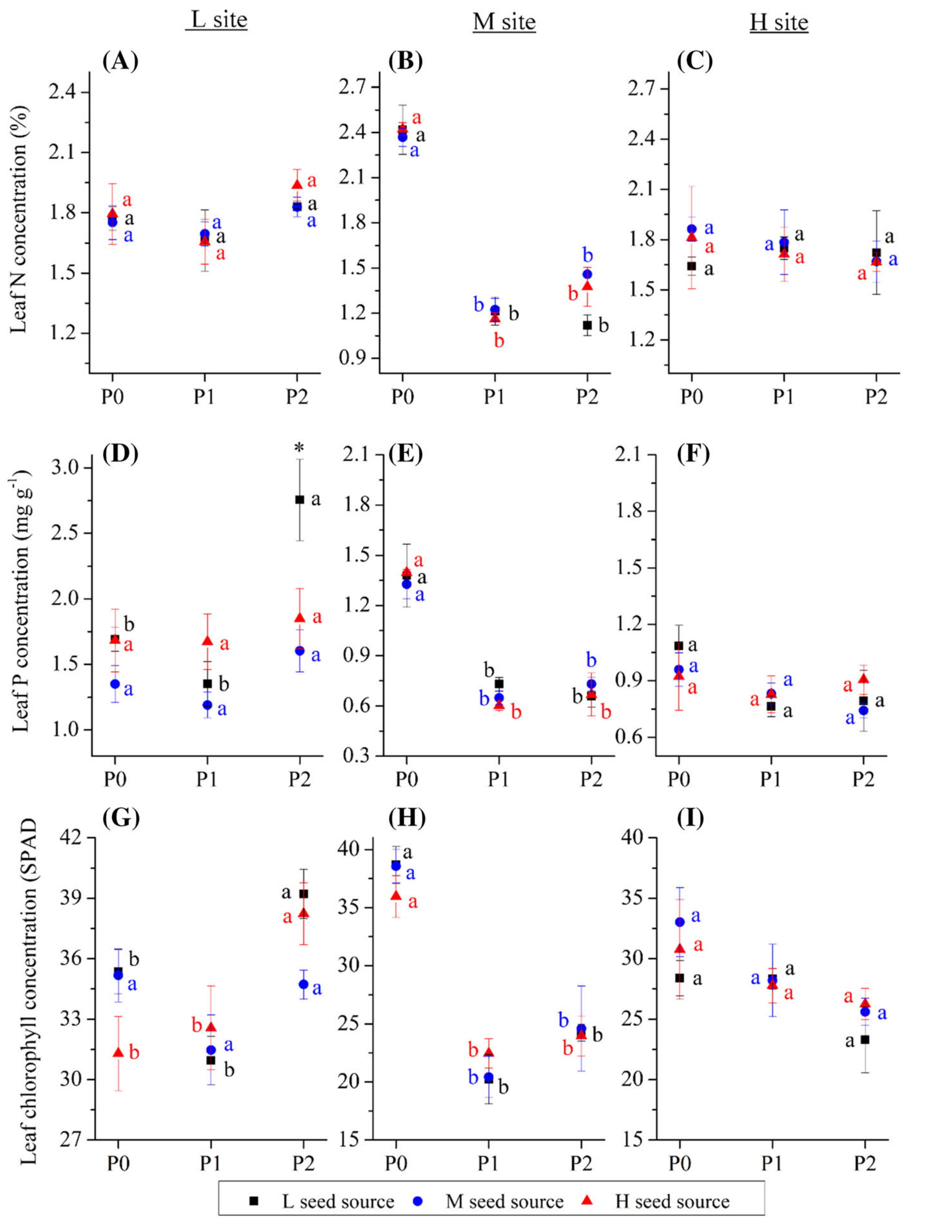

Fig. 3 Response of leaf traits (Leaf N, P and chlorophyll concentration) of *Euptelea pleiospermum* seedlings from different seed sources to precipitation treatments at the three sites (mean ± SE). **A**-**C**, leaf N concentration; **D**-**F**, leaf P concentration; **G**-**I**, leaf chlorophyll concentration. Precipitation treatments: P0, ambient precipitation; P1, 20% precipitation reduction; P2, 40% precipitation reduction. *L:* Low elevation; *M:* Mid elevation; *H:* High elevation. Different letters indicate significant differences among precipitation treatments within the same seed source ($p < 0.05$); asterisk indicates significant differences among seed sources within the same precipitation treatment ($p < 0.05$)

drought stress at the M site where soil moisture had the strongest reduction, regardless of seed source. This result indicates that water stress inhibits leaf N and P uptake and decreases overall photosynthetic capacity. These changes will almost certainly have a negative effect on seedlings fitness. Similarly, Deléglise et al. (2015) found that LNC of plants in a mountain grassland community declined under simulated drought conditions. However, it seems that these findings are not consistent with that LPC and leaf chlorophyll concentrations increased under reduced precipitation at the L site, where soil moisture declined

Table 4 Effects of transplanting elevation, precipitation, and their interactions on root traits of *Euptelea pleiospermum* seedlings

Factor	*df*	Root biomass		Root-to-shoot ratio		Maximum root length	
		F	*P*	F	*p*	F	*p*
Elevation (Ele)	2	383.51	**< 0.001**	3.27	**0.042**	67.27	**< 0.001**
Precipitation (Pre)	2	6.26	**0.003**	3.63	**0.030**	1.20	0.307
Ele × Pre	4	6.03	**< 0.001**	5.06	**0.001**	2.42	0.054

The significant *p*-values were shown in bold ($p < 0.05$)

less than M site. We infer that seedlings could enhance photosynthesis capacity to improve WUE under a small amount of soil moisture decline, but the leaf traits associated with photosynthesis were inhibited when drought stress was more severe (Wang et al. 2006). Plants generally have reduced SLA under drought conditions to reduce water evaporation and ultimately enhance WUE (Wellstein et al. 2017; Kahl et al. 2019). However, our results indicate that SLA of seedlings from L seed source exhibited an increasing trend under reduced precipitation at the H site. One possible explanation is that seedlings from L seed source may reduce construction costs of building leaves by increasing SLA (thin leaves) under adverse environments (e.g. drought stress, short growing season) at the H site (Kudo 1996; Sides et al. 2014).

Plants often invest in root traits under drought conditions (Poorte and Nagel, 2000; Erice et al. 2010; Eziz et al. 2017). As such, we expected to observe an increase in root biomass, root length, and root-to-shoot ratio under the precipitation reductions treatments. Ultimately, we found that the response of root traits to reduced precipitation was highly variable among sites. At the M and H sites, root biomass actually decreased under reduced precipitation treatments, suggesting that drought can have a negative effect on root growth. Moreover, the root-to-shoot ratio had no significant changes in most cases, and the possible reason was that aboveground and belowground biomass may reduce simultaneously under drought conditions. Other studies have also found that the root-to-shoot ratio of seedlings did not vary significantly across precipitation treatments, indicating that seedlings may not be able to allocate resources flexibly in response to water stress as adult plants can (Weißhuhn et al. 2011; Ludewig et al. 2018). However, the precipitation reduction treatments did promote maximum root length at the L site. This was in line with Koike et al. (2003), who found that root length of *Betula platyphylla* seedlings increased under drought conditions.

Effects of seed source on the growth response of seedlings to climate change

At the L site, whole-plant traits and root biomass of seedlings from L seed source were higher than those of seedlings from M and H seed sources under precipitation reduction treatments (Figs. 1 and 4). Likewise, the above traits of seedlings from H seed source were higher than those of seedlings from L seed source under drought treatments at the H site (Figs.1 and 4). Additionally, at the M site, whole-plant traits of seedlings from M seed source were higher than for seedlings from the other two seed sources in the P1 treatment (Fig. 1). These findings suggest a home-site advantage for seedlings that reflects local adaptation to elevation. Many studies have shown that local adaptation limits the ability of species to respond to environmental change (Bennington et al. 2012; Gugger et al. 2015). For example, Kim and Donohue (2013) found that alpine *Erysimum capitatum* seedlings suffered reduced seedling recruitment and higher mortality when transplanted to lower elevation sites. They attributed this to local adaptation to cold and humid environments at high elevation. Therefore, past adaptation to local environments at mid and high elevation mountains will constrain seedlings of populations in these areas to cope with altered environments, as climatic conditions in high-elevation regions are projected to become more similar to low-altitude environments under future climate change (e.g., climate warming, drought, etc.) (Kim and Donohue 2013; De Villemereuil et al. 2018).

Leaf traits varied considerably across the different elevation sites and precipitation treatments. For the most part, these changes were not affected by seed

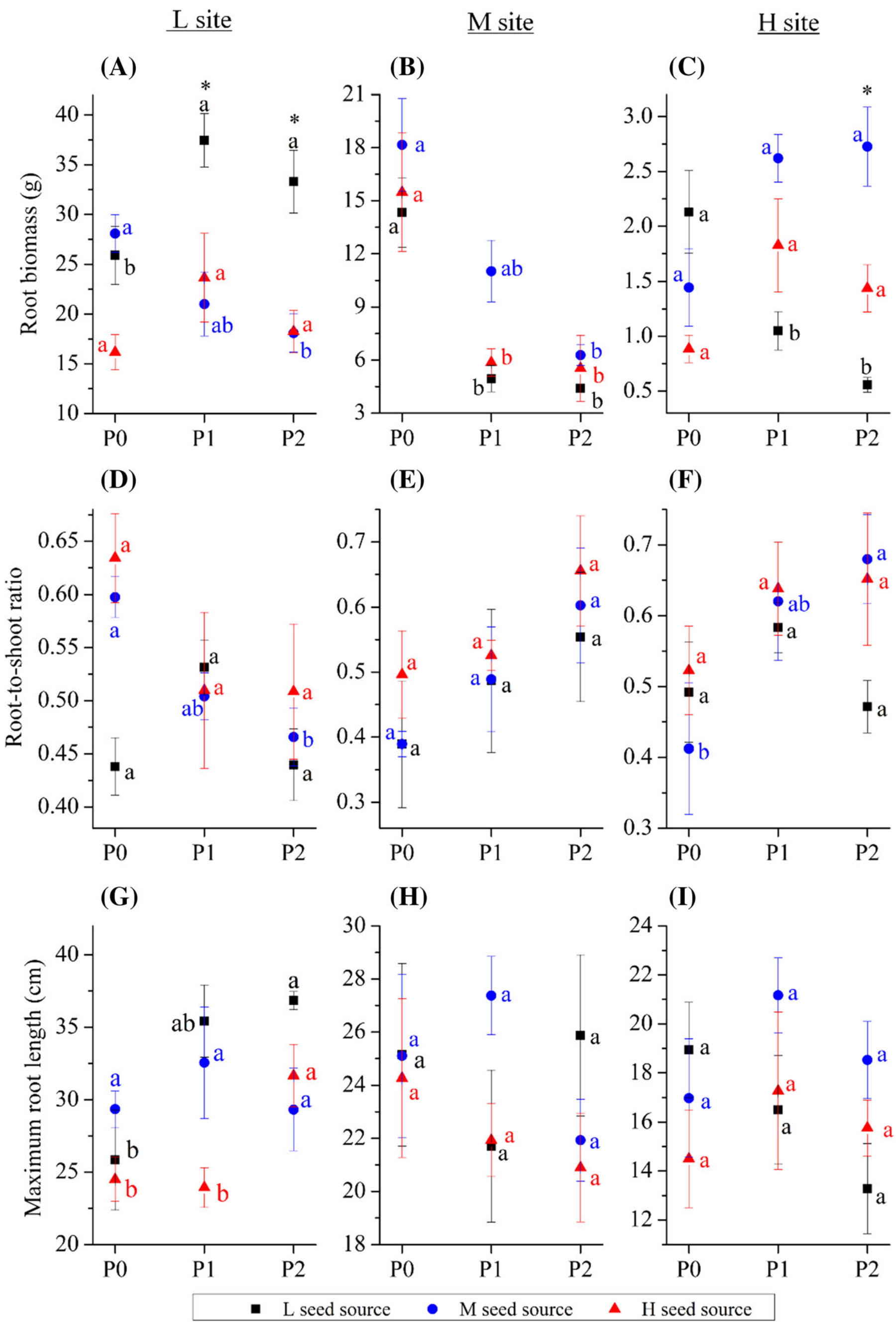

Fig. 4 Response of root traits of *Euptelea pleiospermum* seedlings from different seed sources to precipitation treatments at the three sites (mean ± SE). **A**-**C**, root biomass; **D**-**F**, root-to-shoot ratio; **G**-**I**, maximum root length. Precipitation treatments: P0, ambient precipitation; P1, 20% precipitation reduction; P2, 40% precipitation reduction. *L*: Low elevation; *M:* Mid elevation; *H*: High elevation. Different letters indicate significant differences among precipitation treatments within the same seed source ($p < 0.05$); asterisk indicates significant differences among seed sources within the same precipitation treatment ($p < 0.05$)

source, suggesting that leaf traits exhibit higher phenotypic plasticity than other plant traits. Ecologists have found that phenotypic plasticity generally helps plants adjust to new environments over a short period of time, which can allow them to buffer the negative effects of climate change (Ayrinhac et al. 2004; Nicotra et al. 2010; Anderson and Gezon 2015; De Villemereuil et al. 2018). For instance, Hamann et al. (2016) demonstrated that high phenotypic plasticity in SLA was conducive to overall fitness across multiple different habitats. Therefore, high phenotypic plasticity in leaf traits may help *E. pleiospermum* seedlings deal with the negative impacts of future climate change events. However, some studies also indicated that high phenotypic plasticity may imply metabolic costs that hinder species performance in resource-constrained environments (Liu et al. 2016; Bongers et al. 2017). In addition, Toledo-Aceves et al. (2019) found that plasticity in leaf traits had no effect on seedling survival in a cloud forest along an elevation gradient, while mean values did.

Conclusions

Most plant traits of *E. pleiospermum* seedlings were affected by reductions in precipitation, and responses varied considerably with elevation. This indicates that there is an important interactive effect between elevation and precipitation. Whole-plant traits, root biomass, and leaf traits related to photosynthesis capacity decreased under reduced precipitation treatments at M and H sites, suggesting that drought has a negative impact on seedling growth of this montane relict tree species at higher elevation regions. In addition, seedling growth responses to precipitation were significantly affected by seed source. There is local adaptation to elevation in whole-plant traits and root traits of seedlings, which may constrain their capacity to cope with future climate change. However, leaf traits were not affected by seed source in most cases and have higher phenotypic plasticity than whole-plant traits and root traits. Therefore, our results highlight the necessity to explore the role of local adaptation and phenotypic plasticity on relict tree species response to environmental changes. Ultimately, intraspecific variation should be taken into account when estimating how seedlings respond to climate change and more case studies are needed before general conclusions can be drawn.

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Author contributions MXJ, HW and XZW designed the study. HW and XZW carried out the field experiments and sampling. HW analyzed the data and wrote the original manuscript, with contributions from XZW and MXJ. All authors have given approval to the final version of the manuscript.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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