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Geographic patterns and environmental drivers of seed traits of a relict tree species

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ABSTRACT

Seed traits related to recruitment can directly affect plant fitness and persistence. Phenotypic variability in seed traits among populations could increase species resilience and reduce the risk of extinction under climate change. However, seed trait variations along geographic gradients of relict mountain tree species remain poorly explored despite their vulnerability to environmental changes. Here, we collected seeds of *Euptelea pleiospermum* from 18 populations across its natural distribution in China, measured seed morphology and seed nutrients, and performed a germination test. We investigated geographic patterns of seed traits and analyzed the relationships between environmental factors and seed traits. We also analyzed the relationships between seed intrinsic attributes and seed germination percentage. In addition, we explored the direct and indirect effects of climatic and edaphic variables on seed germination percentage. We found substantial variation in seed traits of this species among populations. Seed mass decreased from low to high latitude, and seed size (length and width) decreased with longitude from west to east. Seed germination timing increased from low to high altitude. Temperature and soil phosphorus determined the geographic variation of seed traits. Seed mass and seed nitrogen had positive effects on seed germination percentage. Seed intrinsic attributes, rather than maternal environmental factors, were the dominant drivers of the variability in seed germination percentage. However, maternal environmental variables could indirectly affect the seed germination percentage through their effects on seed morphology and nutrients. These results demonstrate that among-population seed trait variations are mainly driven by climatic variables and soil nutrients, and indicate that climate warming is likely to alter seed germination patterns by shifting seed intrinsic attributes. Our study provides insight into how mountain tree species regulate seed traits and germination time to adapt to heterogeneous environments and improves our power to predict how relict plants may respond to climate change.

1. Introduction

Seed production is a crucial stage in a plant's life history and seed traits can directly affect plant fitness and persistence (Cochrane et al., 2015). Seed mass and seed germination timing play important roles in the early development of a plant, including germination (Baskin and Baskin, 1998), seedling establishment (Baraloto et al., 2005) and subsequent survivorship (Moles and Westoby, 2004; Simons, 2011). Plant species with wide distribution generally exhibit different degrees of phenotypic variation resulting from their adaptive differentiation to diverse environments (Uribe-Salas et al., 2008; Salmela, 2014). Many studies have demonstrated that intraspecific variability can improve plants' performance and facilitate their adaptability to local environmental gradients (Messier et al., 2010; Sides et al., 2014), but what if local environment changes? In recent decades, anthropogenic climate change has become a major threat to biodiversity and influenced a range of plant life-history phases, especially early developmental stages (Walck et al., 2011). Fortunately, plants have been evidenced to be flexible in their early life-history, and certain seed traits have the potential to help to cope with environmental changes and thus increase plant fitness (reviewed in Cochrane et al., 2015). Therefore, exploring seed trait variations and their driving factors will help us to understand species' adaptations to heterogeneous environments and to improve our prediction of plants' responses to rapidly changing climates, which can ultimately provide valuable information for species' management and conservation.

Seed trait variations widely exist within and across species and are strongly affected by geographic origins or environmental variables

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(Guo et al., 2010; Gorden et al., 2016). Numerous studies have shown that seed mass decreased along latitude from the equator to the poles (Murray et al., 2003; Moles et al., 2007; De Frenne et al., 2013), which evidenced the hypothesis that higher temperatures and greater solar radiation in low latitudes were beneficial for plants to obtain more photosynthetic products and subsequently produce larger seeds (Murray et al., 2004). Contrarily, other studies found a non-significant relationship between seed mass and latitude (Winn and Gross, 1993).

Seed nutrients are vital for seed germination and early seedling establishment (Pérez-Ramos et al., 2010; Carón et al., 2014). However, current knowledge about seed nutrient patterns along an environmental gradient and the possible causes are very limited. De Frenne et al. (2011) found that seed nitrogen (N) concentration of a widespread herb decreased with increasing latitude, which may have been driven by lower soil N availability in the north. While seed morphology and nutrient concentrations are affected by environmental variables, such as temperature, precipitation, solar radiation or soil nutrients (Murray et al., 2004; Valencia-Díaz and Montaña, 2005; De Frenne et al., 2011), some questions still remain. For example, what are the relative contributions of these environmental factors on seed trait variations?

Seed germination is the first step of population regeneration, which is often a serious bottleneck in the life cycle of plants (Donohue et al., 2010). Seed germination is closely associated with seed intrinsic attributes and environmental conditions experienced by the mother tree. Most studies have demonstrated that larger seeds generally show larger germination percentages (Hantsch et al., 2013) because of their higher resource reserves (Obeso, 1993). However, Eriksson (1999) found that seed germination had no relationship with seed mass, and Bu et al. (2007) reported that there was a negative significant correlation between them. Time to germination is a strategy for plants to spread risk over time to improve reproductive success (Venable, 2007). Theoretical models predicted that large seeds germinate faster than small seeds (Venable and Brown, 1988) and higher seed N concentration may accelerate seed germination (Hara and Toriyama, 1998). On the other hand, germination patterns can also reflect a response to environmental conditions experienced by the mother tree. For instance, Jorritsma-Wienk et al. (2007) reported that seed germination percentage and germination speed of a perennial herb varied among populations from different habitats. However, there is little research on seed morphology and nutrient traits in combination with seed germination traits, especially comparing the influence of the maternal environments, and seed intrinsic attributes on seed germination.

Furthermore, geographic patterns of seed traits of relict mountain tree species remain poorly understood despite their sensitivity and vulnerability to environmental change. As phenotypic variations in seed traits among populations could improve species' fitness and persistence (Cochrane et al., 2015), there are an increasing number of studies on seed trait patterns and interacting factors. However, previous seed trait studies usually focused on annual, perennial herb (Murray et al., 2003; De Frenne et al., 2011; Gorden et al., 2016) or invasive species (Fumanal et al., 2007; Hantsch et al., 2013), with little attention paid to woody plants and/or rare species (Wang et al., 2014; Liu et al., 2017). *Euptelea pleiospermum* is a rare and relict tree species of mountain forests with a wide geographic distribution in China. Here, we investigated intraspecific seed trait variations of this species across its geographic distribution to predict that how relict mountain tree species respond to future climate change.

We collected seeds of *E. pleiospermum* from 18 populations, measured seed morphology (seed length, width and seed mass) and seed nutrients (seed C, N, and P), and performed a germination test. We examined the variation of seed traits among populations and analyzed the relationships between environmental factors (climate and soil nutrients) and seed traits. We also analyzed the relationships between seed intrinsic attributes (seed morphology and nutrients) and seed germination percentage. In addition, we explored the direct and indirect effects of climatic and edaphic variables on seed germination percentage. Specifically, we aimed to explore the following questions: (i) Are there substantial variations of seed traits among populations? If so, do seed traits vary significantly along geographic gradients? (ii) What are the relative roles of environmental factors (temperature, rainfall and soil nutrients) in directly driving seed trait variations? (iii) What is the major driver of seed germination percentage variation among populations? Maternal environments or seed intrinsic attributes?

2. Material and methods

2.1. Study species

Euptelea pleiospermum Hook f. et Thoms (Eupteleaceae) is a deciduous and broad-leaved Tertiary-relict tree species, mainly occurring in mountain riparian forests. It is endemic to China, India and Burma and is classified as a rare species in the China Plant Red Data Book (Fu and Jin, 1992). Adult grows up to 12 m in height and 20 cm in diameter at breast height. This species is wind-pollinated and flowers in early spring prior to leaf expansion (Endress, 1986); it then produces abundant fruits, which are gravity-, wind- and water-dispersed. The fruits are mostly double-seeded indehiscent samaras (in this study referred to as seeds), which scarcely crack under natural conditions, and the germinated fruits generally produce only one seedling (Wei et al., 2010).

2.2. Study areas and seed collection

The study area nearly covered the entire geographic distribution of *E. pleiospermum* in China (25.75–35.27°N, 100.02–119.43°E; Table 1 and Fig. 1), including the Qinba Mountains, Hengduan Mountains, Western Sichuan Plateau and Yunnan-Guizhou Plateau. Our sampling area spanned *ca.* 1060 km along latitude and *ca.* 1940 km along longitude. The altitude of the study sites ranges from 641 to 2770 m a.s.l. Mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm) across the area ranges from 6.5 to 13.7 °C and from 634 to 1631 mm, respectively. Seeds of *E. pleiospermum* were collected in 18 natural populations from September to October in 2016. We directly

Table 1
Site characteristics for the 18 populations of *Euptelea pleiospermum* across its geographic distribution in China.

Site code	Latitude (°N)	Longitude (°E)	Altitude (m)	*N*	Location information
YB	25.75	100.02	2690	5	Yangbi, Yunnan
QJ	27.22	103.12	2770	5	Qiaojia, Yunnan
DF	27.41	105.91	1623	4	Dafang, Guizhou
EMS	29.58	103.37	1460	5	Emeishan, Sichuan
TMS	30.36	119.43	1030	3	Tianmushan, Lin'an, Zhejiang
DBS	31.13	115.78	1002	3	Dabieshan, Jinzhai, Anhui
BPG	31.36	102.97	2660	5	Bipenggou, Lixian, Sichuan
LG	32.13	108.88	1363	5	Langao, Shaanxi
HL	32.76	103.99	2425	3	Huanglong, Songpan, Sichuan
BTM	33.49	110.93	1239	6	Baotianman, Neixiang, Henan
LY	33.59	106.29	1538	6	Lueyang, Shaanxi
FP	33.70	107.91	1553	5	Foping, Shaanxi
LS	33.75	110.83	1598	5	Lushi, Henan
TBS	34.08	107.69	1280	7	Taibaishan, Shaanxi
TS	34.39	106.08	1538	6	Maijishan, Tianshui, Gansu
HX	34.43	109.87	1200	8	Huaxian, Shaanxi
LX	34.77	106.67	1518	3	Longxian, Shaanxi
YC	35.27	112.44	641	5	Yangcheng, Shanxi

N, number of samples for each population.