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Interpopulation variation in seed traits of five Polygonaceae

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Interpopulation variability in seed traits may drive the regeneration capacity of a species to colonize different environments. In the present study, we evaluated the variation in seed physical traits (mass / size, water imbibition, shape index) and physiological traits (germination) of five Polygonaceae species. Seeds of *Polygonum lapathifolium* var. *salicifolium*, *P. lapathifolium*, *Reynoutria japonica*, *Rumex trisetifer*, and *R. obtusifolius* were collected from two or three populations in Jiujiang, China. Physical seed traits were measured before germination tests conducted under different combinations of light and temperatures. Most species had a significant variation in seed physical and physiological traits, although populations are geographically close. Interpopulation variation in seed traits appeared to be species-specific, with the highest variation for *R. japonica* and lowest for *R. trisetifer* seeds. Germination response to temperature and light conditions also varied among species and populations, being mostly inhibited in the dark treatments. The light dependence of germination can be related to the small seed size, except for the round-seeded *Rumex*, depending on the temperature regime. Optimal temperature ranges mainly varied from 10/20°C to 25/35°C, with significant decreases in germination percentage at both coolest and warmest extremes. Germination requirements seem to be related to altitudinal gradients in populations of *P. lapathifolium* and *R. japonica* seeds.

KEYWORDS

intraspecific variation, *Polygonum*, population ecology, regeneration, *Rumex*, seed traits

Introduction

Variability in seed traits has been reported in different species, populations or individuals (see, e.g., Susko and Lovett-Doust, 2000; Lopez et al., 2008; Cervantes and Martín Gómez, 2019). Differences in seed (germination) traits among populations (i.e., within species) have been considered an effective evolutionary strategy that influence on species resilience by increasing the chances of reproduction under heterogeneous environmental conditions, thus minimizing the extinction risk (Venable and Brown, 1988). Hence, understanding interpopulation differences might help us addressing issues related to the evolution of variability patterns regarding plant regeneration from seeds. Seed physical traits (e.g., seed size/mass, shape, color, seed coat thickness, permeability, etc.), for instance, are directly or indirectly involved in regulating germination responses and many seed functions such as dispersal, type and level of dormancy, formation of the soil seed bank, seedling establishment, survival, and competitive ability (Eriksson, 1999; Larios et al., 2014; Larson and Funk, 2016; Saatkamp et al., 2019). Therefore, these traits have been related to plant fitness and species persistence across ecosystems

(Atis et al., 2011; Xu et al., 2014; Bhatt et al., 2016, 2021a; Bu et al., 2016). Evolutionary history, environmental context, genetic constraints, and plasticity are responsible for variation in seed traits at both intra- and inter-species levels (Violle et al., 2012; Ge et al., 2020).

Within species, interpopulation variation is vital to distinguish the ecological and evolutionary drivers shaping regeneration traits (Moreira et al., 2012). Interpopulation variability of ecological traits generally occur either due to (i) differences in environmental conditions among the different populations (Nicotra et al., 2010; Cochrane et al., 2014) or (ii) hereditary characteristics of populations (Cheptou et al., 2008; Cochrane et al., 2015). In addition, other factors can be responsible for shaping the interpopulation variability in seed traits, including local climate, habitat characteristics, inter- and intra-species competition levels, predation, resource provisioning, and epigenetics (Kleunen et al., 2001; Tautenhahn et al., 2008; Saatkamp et al., 2019). The variability in seed germination within a species, when seeds are collected from different populations, has been linked to spatial variability due to climatic and edaphic parameters or a differentiated gene pool (Elnaggar et al., 2019; Bhatt et al., 2021b,c). Most of the studies so far focused on testing interpopulation variation regarding seed mass or size and their effect on seed germination (Xu et al., 2016; Kołodziejek, 2017; Moya et al., 2017; Bhatt et al., 2019). However, few studies investigated interpopulation variation in other physical traits, like seed shape and color and their role in regulating seed dormancy and germination (but see Zhang and Maun, 1990; Mülken et al., 2005; Atis et al., 2011; Bhatt et al., 2016).

Generally, seed germination requirements are synchronized with the population's environmental condition to increase the possibility of seedling survival and establishment (Baskin and Baskin, 2014). Studies have shown that interpopulation variation in seed dormancy and germination is broadly correlated with abiotic factors, such as altitude, latitude, temperature, soil moisture, and habitat type (Wagmann et al., 2012; Fernández-Pascual et al., 2013; Cochrane et al., 2014; Pendleton and Pendleton, 2014). Because different populations among different localities may experience different natural selection pressure, they may lead to local adaptation over time. For instance, higher interpopulation variability in germination responses has been reported in populations living in unpredictable environmental conditions than those living in more stable (i.e., less variable) conditions (Meyer and Allen, 1999). Therefore, the same species growing in different populations can respond differently to the same environmental signals based on the selective pressures acting on the population (Oduor et al., 2016; Amini et al., 2017).

Given that interpopulation variation usually reflects the environmental adaptation of species (Kyle and Leishman, 2009), the present study focused on interpopulation variation in seed physical (mass, size, shape, color, etc.) and physiological (germination responses) traits of five Polygonaceae species. Germination at species level has been previously investigated for this family, but mostly using seeds from a single population, as reported for seeds of *Polygonum lapathifolium* (Timson, 1965; Staniforth and Cavers, 1979), *Reynoutria japonica* (Mariko et al., 1993), and *Rumex obtusifolius* (Hand et al., 1982; Van Assche and Vanlerberghe, 1989; Benvenuti et al., 2001). In the present study, we hypothesized that different populations of species growing in different microclimates might also differ in their seed morphology and germination strategy. To test this hypothesis, we examined the following questions (i) is there a difference in seed physical traits (size, mass, shape, and color) according to the seed

population? (ii) are there any light and temperature mediated mechanisms affecting seed physiological (germination) traits under laboratory conditions? (iii) is there a different seed germination response to light and temperature among the seed populations within each study species?

Materials and methods

Seed collection

In 2020, we collected seeds of five species of Polygonaceae from two to three populations at the time of their natural dispersal to ensure that the seeds were physiologically in their mature stage (Table 1, Figure 1). We obtained permission from Jiujiang Forestry Bureau, China, for seed collection. The voucher specimens for each species were collected from each location and deposited in the herbarium of Lushan Botanical Garden, China. For each species and each population, seeds were collected from 25 to 30 randomly chosen plants to represent the genetic diversity. After collection, the seeds were cleaned and tested for germination within a week.

The seed collection areas fall under the wet subtropical monsoon climatic zone. The lower altitude of the mountain is subtropical with warm and humid climate, whereas the higher altitude is warm temperate with cool and humid climate. The mean annual temperature is 16–18°C and mean annual precipitation range between 1,000 and 1,600 mm. The average temperature of January is 4.4°C. The average temperature in July is 29.6°C, with an extreme maximum temperature of 40.2°C (Hong et al., 2013; Xie et al., 2013).

To determine the seed dispersal syndrome, we have taken into account fruit/seed morphology, the available literature, as well as our personal observations, and come to conclusion that seeds of all five species have a relatively high potential to be dispersed by more than one of these three dispersal modes (anemochory, hydrochory, and/or zoochory). These multiple dispersal vectors may facilitate seed dispersal even among fragmented populations.

Seed physical traits

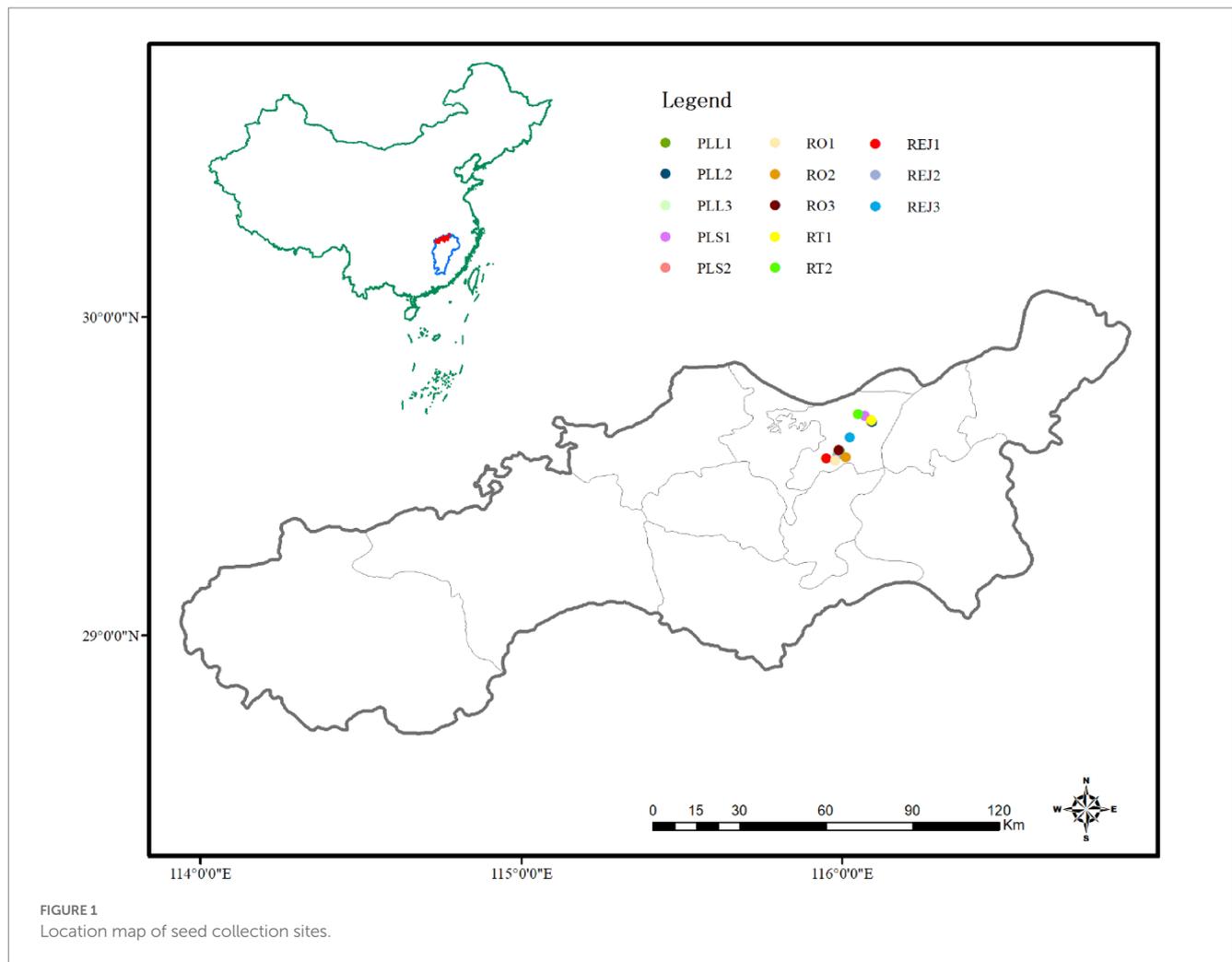
A Stereo Microscope (Nikon SMZ800N) fitted with a microscope camera IMG-SC600C was used to examine the shape, dimensions (length, width, and height), and color of the seed. Fifteen seeds were examined for each species/population by ventrally attaching them to filter paper using double-sided sticky tape. Seed mass was determined at the time of collection (fresh mass) from three 100-seed replicates per species, using a Sartorius electronic balance (Sartorius Co., Göttingen, Germany).

Water imbibition

Seed permeability to water was assessed by recording the mass of three 25-seed replicates before and after moistening them in 9-cm-diameter Petri dishes containing two sheets of Whatman No. 1 filter paper. Seeds were moistened for 24 h at room temperature (22 ± 2°C) using 10 mL of distilled water. The water uptake by seeds was calculated using the formula (Water absorption (%)) = [(W2 – W1)/

TABLE 1 Location and other details of the study species.

Species	Population	Collection month	Place	Latitude	Longitude	Altitude (masl)	Growth form	Habitat
<i>Polygonum lapathifolium</i> var. <i>salicifolium</i>	Pls1	July	Yujiahe town	29°41'23.55"	116°4'15.07"	5.39	Annual herb	Grassland
	Pls2		Gutang town	29°40'13.031"	116°5'33.815"	13.55		
<i>Polygonum lapathifolium</i>	Pl1	November	Guling town	29°34'46.2"	115°59'36.24"	1115.03	Annual herb	Grassland
	Pl2		Gutang town	29°40'15.159"	116°5'39.887"	26.41		
	Pl3		Guling town	29°32'55.974"	115°58'46.379"	1086.66		
<i>Reynoutria japonica</i>	Rj1	November	Guling town	29°33'20.706"	115°57'04.060"	687.86	Perennial herb	Forest
	Rj2		Guling town	29°33'55.612"	115°59'07.874"	1229.09		Forest
	Rj3		Northern road of Lushan	29°37'15.893"	116°1'28.350"	530.97		Streamside
<i>Rumex trisetifer</i>	Rt1	May	Weijia town	29°40'31.39"	116°5'29.14"	4.94	Annual herb	Streamside
	Rt2	June	Yujiahe town	29°41'38.05"	116°2'59.17"	2.29		Grassland
<i>Rumex obtusifolius</i>	Ro1	July	Guling town	29°32'55.88"	115°58'46.13"	1057.44	Perennial herb	Cultivated area
	Ro2	July	Guling town	29°33'34.65"	116°0'41.98"	979.76		Streamside
	Ro3	August	Guling town	29°34'55.36"	115°59'22.43"	1081.14		Cultivated area



$W1 \times 100$), where $W2$ is the mass of the seeds after imbibition for a given interval and $W1$ is the initial seed mass (Baskin et al., 2004).

Effect of temperature and light on seed germination (physiological traits)

Seeds were surface sterilized in 0.50% sodium hypochlorite for 1 min, then washed thrice with deionized water to avoid attack by fungi. To determine the effect of temperature and light, seed germination tests were conducted in incubators (Kesheng incubators, Model- DRX-800C- LED, China) set at five different alternate temperature regimes (5/10, 10/20, 20/30, 25/35, and 35/40°C) in 24-h darkness (dark treatment) and/or 12 h light/12 h darkness (light treatment). The incubators were fitted with cool white fluorescent tubes ($60 \mu\text{mol photons M}^{-2}\text{S}^{-1}$). These temperature regimes were chosen to stimulate the average temperature of natural habitat (seed collection site) for different months (i.e., 5/10°C—December to February; 10/20°C—March, April, and October, November; 20/30°C—May, June and September; 25/35°C—July and August). The highest temperature regime (35/40°C) was used to investigate the ability of seeds to tolerate the high temperature during germination. Seeds were

exposed to 12 h light at the highest temperature within each alternating temperature regime.

Seeds were sown in 9-cm Petri dishes containing three disks of Whatman No. 1 filter paper moistened with 10 ml of distilled water and placed in incubators. Darkness was achieved by wrapping Petri dishes in two layers of aluminum foil. Four replicates of 25 seeds each were used for each treatment. The seeds were considered to be germinated with the emergence of the radicle (≥ 2 mm). Germinated seeds were counted and removed daily for a 30-days period. However, seeds incubated in the dark regimes were checked only at the end of the test. At the end of the germination test, all the ungerminated seeds from the light treatment were dissected to evaluate the embryo status and viabilities of the nongerminated seeds (living and therefore white; turgid and brown and, therefore, dead) under a stereoscope.

Data analysis

The seed physical traits (including seed mass, seed dimensions such as length, width, height, and water imbibition in 24 h) met the assumptions of both the Shapiro–Wilk normality test and Levene’s test for equality of variances. Therefore, depending on the number of studied populations (2

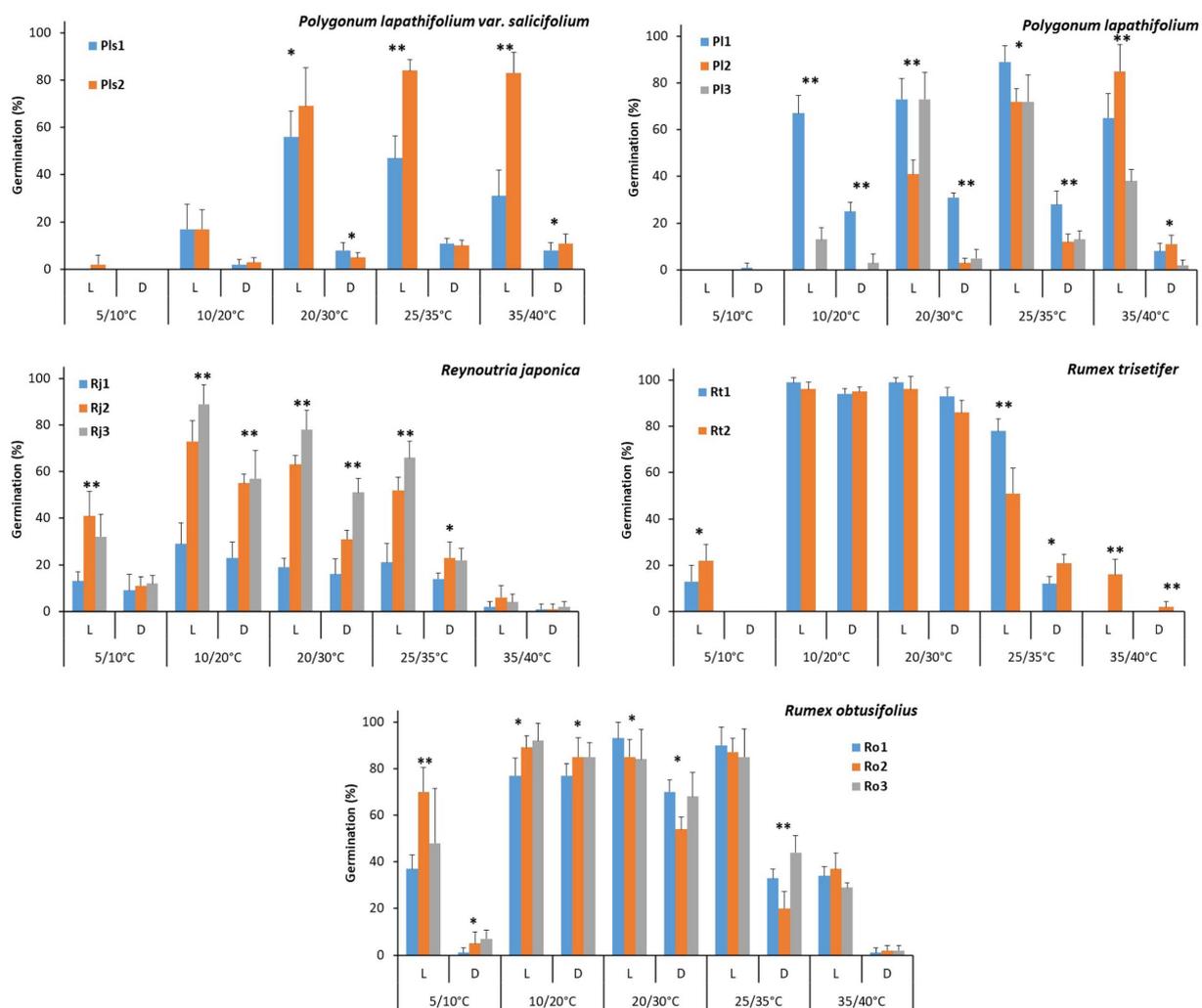


FIGURE 2

Influence of population, incubation temperatures, and photoperiod on mean seed germination percentage of five Polygonaceae species. Significance values of different factors are indicated in Table 2. Bars with * or ** signs indicate germination percentage differed significantly ($P < 0.01$ or < 0.001) between and/or among the populations at particular incubation conditions.

or 3) for each species, the independent-samples t -test or one-way ANOVA were used to compare interpopulation variation in seed physical traits. The physiological traits (germination data) did not meet the assumptions of normality and equality of variances; therefore, the relationship between mean percentage of germination (dependent variable) and the value of three predictors (population, incubation temperature and light) was compared for each species independently using a generalized linear model (GLM) with a Poisson probability distribution and identity-link functions. The effects of three predictors and their interaction in the model were tested by Wald Chi-square (X^2) values. All statistical analyses were performed using SPSS 16.

Results

Polygonum lapathifolium var. *salicifolium*

No difference was detected regarding seed mass and seed length between the two populations (Pls1 and Pls2), but the other physical

traits (water imbibition, seed width, height, and shape index) differed significantly between populations ($p < 0.05$; Table 2). GLM revealed a significant effect of population, incubation temperature, light, and their interactions on the percentage of germination ($p < 0.001$; Table 3). Seeds of both populations had negligible germination ($< 12\%$) in the dark treatment (Figure 2). In the light treatment, optimum temperature regime differed for populations. Seeds of Pls1 reached maximum germination of 56% at 20/30°C, whereas seeds of Pls2 germinated at comparatively higher temperature regimes, reaching germination of 84 and 83% under 25/35°C and 35/40°C, respectively (Figure 2; raw data available at Supplementary Table S1).

Polygonum lapathifolium

There was significant interpopulation variation in seed mass, length, width, and seed shape index ($p < 0.05$). However, seed height and water imbibition were not significant among the

TABLE 2 Interpopulation variation in seed traits of five Polygonaceae species.

Species	Population	Seed mass (mg)	Water imbibition within 24h (%)	Seed length (mm)	Seed width (mm)	Seed height (mm)	Seed shape index	Seed color	Seed shape	Presence of dispersal structure (wing)
<i>Polygonum lapathifolium</i> var. <i>salicifolium</i>	Pls1	0.99	36.65 ^a	2.05	1.78 ^a	0.54 ^a	0.11 ^a	Dark-brown, brown	Broad-ovate	No
	Pls2	1.07	18.86 ^b	2.10	1.63 ^b	0.40 ^b	0.13 ^b	Brown, dark-brown, fulvous	Broad-ovate	
	Species mean	1.03	27.76	2.08	1.70	0.47	0.12			
<i>Polygonum lapathifolium</i>	Pl1	1.68 ^a	29.08	2.36 ^{ab}	1.67 ^a	0.40	0.17 ^{ab}	Reddish, brown, dark-brown	Oval, broad-ovate	No
	Pl2	0.93 ^b	29.96	2.27 ^b	1.58 ^b	0.38	0.15 ^b	Reddish, brown, dark-brown	Oval, long-oval, broad-ovate	
	Pl3	1.68 ^a	13.65	2.44 ^a	1.69 ^a	0.40	0.18 ^a	Reddish, brown, dark-brown	Oval, broad-ovate	
	Species mean	1.43	24.23	2.36	1.65	0.39	0.17			
<i>Reynoutria japonica</i>	Rj1	1.73 ^c	49.22	3.75 ^c	2.05 ^b	2.11 ^b	0.16 ^b	Dark-brown	Long-oval, oval	Yes
	Rj2	2.77 ^b	44.48	4.08 ^b	2.02 ^b	2.12 ^b	0.23 ^a	Dark-brown	Long-oval, oval	
	Rj3	4.44 ^a	36.23	4.56 ^a	2.34 ^a	2.36 ^a	0.28 ^a	Dark-brown	Long-oval, oval	
	Species mean	2.98	43.31	4.13	2.14	2.20	0.22			
<i>Rumex trisetifer</i>	Rt1	0.45	23.48	1.57	0.95	0.95	0.02	Reddish, brown	Oval	Yes
	Rt2	0.47	21.24	1.54	0.95	0.94	0.02	Milk-white, brown, black	Oval, long-oval	
	Species mean	0.46	22.36	1.56	0.95	0.95	0.02			
<i>Rumex obtusifolius</i>	Ro1	1.09	12.49 ^b	2.19	1.35 ^a	1.34	0.04 ^b	Dark-brown, brown	Broad-ovate	Yes
	Ro2	0.85	44.82 ^a	2.24	1.28 ^{ab}	1.28	0.05 ^a	Dark-brown	Broad-ovate, oval	
	Ro3	0.93	22.65 ^b	2.15	1.27 ^b	1.27	0.04 ^b	Brown	Broad-ovate, oval	
	Species mean	0.96	26.65	2.19	1.30	1.30	0.05			

Values with different letters in lower case represent significant difference ($p < 0.05$) at population level for respective trait of a respective species.

TABLE 3 Effect of population (P), incubation temperature (T), and photoperiod (L) on seed germination percentage of five Polygonaceae species.

Factors	<i>Polygonum lapathifolium</i> var. <i>salicifolium</i>		<i>Polygonum lapathifolium</i>		<i>Reynoutria japonica</i>		<i>Rumex trisetifer</i>		<i>Rumex obtusifolius</i>	
	Wald's χ^2	df	Wald's χ^2	df	Wald's χ^2	df	Wald's χ^2	df	Wald's χ^2	df
Population (P)	90.0**	1	186.0**	2	672.2**	2	0.490	1	3.81	2
Temp. (T)	978.4**	4	405.9**	4	2458.7**	4	1761.1**	4	1908.6**	4
Light (L)	1036.5**	1	1404.2**	1	295.1**	1	83.5**	1	586.5**	1
P×T	80.4**	3	193.4**	5	494.9**	8	20.8**	3	66.7**	8
P×L	90.1**	1	7.4*	2	114.4**	2	5.6*	1	19.9**	2
T×L	276.9**	3	85.1**	3	190.5**	4	87.7**	3	157.2**	4
P×T×L	74.9**	3	96.1**	5	89.9**	8	15.1*	2	23.0*	8

Significance level: * $p < 0.01$; ** $p < 0.001$. Data were modeled using a Generalized Linear Model (GLM) with a Poisson probability distribution and an identity-link function.

populations (Table 2). Populations, incubation temperature, light, and their interactions had a significant effect on seed germination ($p < 0.001$; Table 3). Dark treatment significantly inhibited germination compared to light treatment in most temperature regimes (Figure 2 and Supplementary Table S1). There was also a significant variation in the optimum germination temperature among populations (P11, P12, and P13). Seeds from P11 had a wide germination range, showing germination $>65\%$ from 10/20°C to 35/40°C, reaching 89% at 25/35°C (Figure 2 and Supplementary Table S1). A narrower germination window was found for P12 (germination ranged from 72 to 85% at warm temperatures of 25/35° and 35/40°C) and for P13 (72–73% at intermediate temperatures of 20/30° and 25/35°C).

Reynoutria japonica

Except for water imbibition, all other seed physical traits differed among populations, with a prominent 2.5-fold variation in seed mass ($p < 0.05$; Table 2). Furthermore, there was a significant effect of populations, incubation temperatures, light, and their interactions on the percentage of seed germination ($p < 0.001$; Table 3). The overall germination percentage varied 2 to 3 folds among populations (Rj1, Rj2, and Rj3). Seeds from Rj1 germinated a relatively low ($<30\%$) in all treatments, irrespective of dark and light conditions. The other two populations had maximum germination from 52 to 89% at temperature regimes from 10/20°C to 25/35°C in the light, with a decrease under the dark treatment, which varied from 52 to 22% (Figure 2 and Supplementary Table S1).

Rumex trisetifer

Unlike the other species studied, none of the seed physical traits of *R. trisetifer* varied significantly ($p = 0.85$) between the two populations (Table 2). Populations also had no effect on germination responses, but incubation temperature, light, and their interactions significantly affected germination ($p < 0.001$; Table 3). Seeds of both populations germinated from 86 to 99% in the temperature regimes

of 10/20° and 20/30°C, both in light and dark treatments (Figure 2 and Supplementary Table S1). However, germination decreased significantly in all other tested temperature regimes (5/10°C or $\geq 25/35^\circ\text{C}$), mainly in the dark.

Rumex obtusifolius

Three physical traits (water imbibition, seed width, and seed shape index) varied significantly among the populations ($p < 0.05$; Table 2), but no differences were found regarding seed mass, length, and height. Similar to *R. trisetifer*, populations had no effect on germination responses. However, incubation temperature, light, and their interactions significantly affected germination ($p < 0.001$; Table 3). At 10/20°C, all populations had a similar percentage of germination compared to light/dark treatments, ranging from 77 to 92%; dark conditions tended to decrease the percentage of germination at all other temperatures (Figure 2 and Supplementary Table S1). Optimal germination conditions differed among populations (Ro1, Ro2, and Ro3) in the light: germination of Ro1 reached $\geq 90\%$ at 20/30°C and 25/35°C, while germination of Ro2 and Ro3 varied from 84 to 92% in a broader range of temperature regimes of 10/20°C to 25/35°C. Even at the coolest temperature regime (5/10°C), 70% seeds of Ro2 germinated.

Discussion

Germination responses can be difficult to predict over time and space, as they are affected by several environmental factors such as temperature, light, and soil moisture (Baskin and Baskin, 2014; Bhatt et al., 2019, 2020, 2021a). Identification of the environmental factors that are responsible for maintaining phenotypic variation in nature is essential to understand the evolutionary mechanisms of plants (Larios et al., 2014; Manzano-Piedras et al., 2014). Existence of interpopulation variability in seed traits is commonly found, and important for enhancing the ability of species to persist against climatic variability (Cochrane et al., 2015). In this study, we found a relatively high

interpopulation variation in seed morphology and germination response (physical and physiological traits) of five Polygonaceae, although these species belong to the same family and were collected from geographically close locations (located approximately 4–32 km from each other). Despite the multiple seed dispersal vectors of the study species and relatively close distance between populations, it is important to note that the collected populations occur in a fragmented landscape, which may limit their gene flux from one population to others.

Intraspecific (interpopulation) trait variation could be due to environmental, genetic differences, or a combination of both genetic and environmental factors. Understanding the role of seed physical traits and their relationship with seed germination could thus be important for predicting which seed physical traits are more influential in affecting germination. However, until now, most of the studies mainly focused on the role of seed mass/size in germination responses (Wu and Du, 2007; Münzbergová and Plačková, 2010; Wu et al., 2011; Alstad et al., 2018; Chen et al., 2018). Despite differences between species, seeds of all studied species can be classified as small-sized, with a fresh mass varying from 0.45 to 4.44 mg. Small-seeded species have been recognized to be light-dependent (positively photoblastic) in different vegetation types worldwide, including temperate grasslands (Milberg et al., 2000), arid zones (Flores et al., 2011), and tropical rainforests (Aud and Ferraz, 2012). Such physical trait-germination relatedness may help to explain the germination patterns we found.

Only seeds of *P. lapathifolium* and *R. japonica* had significant interpopulation variability in seed mass and seed length. The smallest seed size found in the Rj1 population proportioned a low percentage of germination regardless of light and temperature treatments. However, other seed traits, such as seed width, seed height, and seed shape index, varied significantly among populations of most studied species. Differences in the environmental conditions among populations can be responsible for seed trait variability, as suggested to vegetative and floral plant traits (Kuppler et al., 2020). But in our study, one must take in account that seeds of the different species were collected from populations growing geographically in close to moderate distance localities (4–32 km). Therefore, we argue that spatial heterogeneity in edaphic factors (i.e., nutrients) or differences in the gene pool among populations can contribute to determining the interpopulation variability, especially in geographically distance populations. In addition to subtle contrasts in environmental gradients, different populations are highly likely to be subjected to different selection pressures under natural conditions, leading to the evolution of interpopulation variability in seed traits as an adaptive response that allows the species to survive under spatially heterogeneous landscapes (Ge et al., 2020).

The exception was found for *R. trisetifer* seeds, with no difference in seed traits among the studied populations. Additionally, both *Rumex* species had the least light-dependent germination responses, despite their small seed size and round seed shape. Round and small seeds, due to their compact structure, should be more easily incorporated into soil seed banks and therefore subjected to dark conditions or minimal light penetration in the upper layer of the soil (Benvenuti, 2007; Saatkamp et al., 2014). Funes et al. (1999) reported that compact

seeds tend to persist for longer periods ungerminated in the soil. In contrast, in our case, the seeds of *R. trisetifer* and *R. obtusifolius* had the lowest shape index but high germination under both light and dark conditions, under optimal temperature. This indicates that their seeds would be promptly recruited rather form persistent seed banks. Factors other than seed physical traits may influence germination responses, such as adaptive responses and phylogenetic relatedness, regardless of population variability. Moreover, interactions of temperature and light have been pointed out as important drivers of the capacity of seeds to germinate depending on the species and specific temperature requirements (see Pons, 1992).

Seeds of all the five species were able to absorb water, indicating they do not show physical dormancy. Seeds of only two taxa (*P. lapathifolium* var. *salicifolium* and *R. obtusifolius*) had a significant variability in seed coat permeability (water imbibition) among populations. This variability in water imbibition among populations could be related to variation in coat hardness (thickness) due to spatial heterogeneity in habitat conditions, genetic background, and their interactions, which may be responsible for interpopulation variability in seed coat permeability as reported in other species (Jaganathan et al., 2019; Bhatt et al., 2021b). Bearing non-dormant seeds, all studied species were able to germinate immediately after dispersal, although the percentage of germination varied between or among populations and the tested temperature conditions. Fast germination could be related to the availability of sufficient precipitation throughout the year due to subtropical moist monsoonal climate in the seed collection sites (Kang et al., 2017). This contrasts with seasonal water restrictions, which are generally considered one of the main limitations for germination in most climatic conditions.

Temperature is one of the main environmental factors that regulate the germination, especially where availability of water is not a constraint for germination (Fenner and Thompson, 2005). Regarding thermal requirements, in the light, optimal germination ranges mainly varied from 10/20°C to 25/35°C, with significant decrease in germination percentage at both cooler and warmer extremes. However, some species, such as *Polygonum* spp., showed a marked variation in the optimal temperature requirement for germination depending on the population. Seeds of *P. lapathifolium* var. *salicifolium* from Pls2, for example, germinated equally well at the warmest tested temperatures, reaching >80% germination at 25/35°C and 35/40°C. Conversely, seeds from Pls1 attained maximum germination (56%) at a milder temperature regime (20/30°C). Seeds of *P. lapathifolium* also showed similar trends: The Pl2 population attained 85% germination under the warmest conditions (35/40°C), while Pl1 and Pl3 (both populations collected at elevation >1,000 m) attained maximum germination of 72–89% at temperatures 20/30°C and 25/35°C. Producing seeds with varying germination cues (temperature) may enhance fitness of these species in future climate change scenarios and reduce the risks of synchronizing recruitment in case of unfavorable conditions (Santo et al., 2015; Bhatt et al., 2020, 2021b).

An even higher interpopulation variability in maximum germination percentage was observed for *R. japonica* seeds—from 29% in Rj1 to 89% in Rj3, both at 10/20°C. Although Rj3

also germinated well (66%) at 25/35°C. This relatively wide temperature niche width (especially in Rj3) indicates such seeds (populations collected at elevation from 500 to 1,200 m) can better recruit when other environmental factors controlling seed germination (light &/or moisture) may be available beyond the normal window of seed germination season. Collection sites of *R. japonica* and *P. lapathifolium* populations had remarkable differences in altitude, which may be responsible for microclimatic contrasts. We argue that habitat heterogeneity and climatic variability contribute more toward determining the interpopulation variability rather than the geographic distance. Additionally, differences in germination requirements among populations of *P. lapathifolium* var. *salicifolium* could be attributed to the variation in competition, soil moisture, and mineral nutrition (Burton et al., 2000; Allison, 2002; Swain et al., 2006). Spatio-temporal heterogeneity in climatic conditions and edaphic factors among the population are reported to be the main driver for interpopulation variability (Kuppler et al., 2020), which ultimately lead to the interpopulation variability in seed morphology and germination traits (Baskin and Baskin, 2014; Hudson et al., 2015; Bhatt et al., 2021b).

Rumex species had less variation in germination percentage among the tested populations within their respective optimal ranges. Seeds of *R. trisetifer* germinated equally well at 10/20°C and 20/30°C ($\geq 96\%$), while *R. obtusifolius* germinated equally well at 10/20°C, 20/30°C, and 25/35°C (89%). The relatively broad thermal germination niche indicates that seeds of *R. obtusifolius* can germinate throughout the year, although the germination percentage was significantly reduced during winter (December to February). Similarly, *Polygonum* spp. can germinate outside their normal germination window, when the temperature ranges between 20 and 35°C. These results further support that seed recruitment in our study species is widely spread throughout the growing season, and this will increase their long-term fitness by spreading the risk of germination failure. Besides this, these species have higher possibility to establish in a broad environmental condition (Carlucci et al., 2015) and will be less affected by climate change as compared to those have specific temperature requirement for germination. For example, *R. trisetifer* and *R. japonica* have a specific temperature requirement and thus their germination may be restricted to the specific time (i.e., between March to June or between September to November for *R. trisetifer*, and between March to April or between October to November for *R. japonica*).

Overall, seed germination was significantly inhibited at the lowest temperature regime (except for Ro2), although different species showed interpopulation variability in terms of germination percentage. Avoiding germination in winter (December to February), when the temperature is around 5/10°C, could be a survival strategy for these species, as the chances of seedling successful establishment would be extremely low due to cold and frost. Low-temperature conditions may induce physiological dormancy, while the cold stratification period also helps seeds to synchronize germination with a favorable season, as reported in *Polygonum* and *Rumex* spp. (Totterdell and Roberts, 1979; Bouwmeester and Karssen, 1992; Batlla and

Benech-Arnold, 2005). However, at the highest temperature (35/40°C), one population of *P. lapathifolium* var. *salicifolium* (Pls2) and a population of *P. lapathifolium* (Pl2), both from the lowlands, germinated well ($>80\%$). For all other species/populations, germination percentage was significantly reduced at the warmest condition. These results indicate that tolerance to high and low temperatures during the germination stage can vary between/among populations, depending on species (Cochrane, 2016). Therefore, it could be imperative to test the interpopulation variability under a wider range of temperature, in order to model regeneration behavior regarding threshold models (Bradford, 2002).

Here, we found general patterns of seed and germination traits common to all five Polygonaceae, such as small seed size and predominant light-dependent germination (except *Rumex*). However, we also identified particularities of the studied populations. The optimal temperature requirements for germination varied according to the population of the seeds, mostly for *P. lapathifolium* and *R. japonica*, seeds collected from comparatively longer altitudinal gradients. Furthermore, interpopulation variability among the studied species could be linked to maternal effects (Luzuriaga et al., 2006; Kagaya et al., 2011; Bhatt et al., 2019, 2021b). Heterogeneity in maternal habitat conditions where populations grow is likely to be the main factor contributing to interpopulation trait variability. Phylogenetically related species have been reported to share similar traits in a general sense (Losos, 2008). For example, some studies suggest that related species share similarities regarding seed traits, dormancy, and germination characteristics (Moles et al., 2005; Norden et al., 2009; Carta et al., 2016). Other studies argue that seed traits, dormancy, and germination characteristics are regulated by environmental cues rather than the phylogeny (Vandelook et al., 2008; Arana et al., 2016; Fang et al., 2017). Therefore, it is important to compare the physical and physiological traits of closely related species to better understand which factors (phylogeny and/or environment) are responsible for influencing regeneration strategies, aiding to improve our predictive capacity to comprehend species distribution related to trait variability in changing environments.

Conclusion

Although seeds of the Polygonaceae shared similar physical traits, generally displaying small-sized seeds and light-dependent germination patterns. We found great variation in germination requirements between and/or among populations. For instance, optimal temperature regimes may change according to seed population, mostly in altitudinal gradients, as we show for *P. lapathifolium* and *R. japonica* seeds. Seeds of *Rumex* spp., on the other hand, seemed to be less affected by light availability, with similar responses regardless of the collection sites. Variability in regeneration traits can be crucial to comprehending the species' ability to colonize different areas, aiding in the identification of tolerant/sensitive populations affected by environmental changes.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary material](#), further inquiries can be directed to the corresponding author.

Author contributions

AB conceived and designed the experiments. AB and XC performed the experiments. AB and SP analyzed the data. AB, SP, and LD wrote the manuscript. All authors approve of this submission.

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2023.1093285/full#supplementary-material>

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