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Title page

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MG, GT and CD designed the experiment. MG performed the experiment. MG, GT and BG performed data analysis and wrote the manuscript.

Highlights

- Germination capacity of two Ludwigia congeners was tested at 24 and 27°C.
- Five of the ten tested populations reached final germination percentages >80%.
- Germination patterns of *L. hexapetala* depend on geographical origin of the seeds.
- The 3°C warming treatment accelerated the time to germination.
- It also increased germination percentage of *L. hexapetala* populations from France.

Abstract

Environmental temperature is the primary regulator of germination. Global climatic warming may substantially change seed dormancy and germination responses of wetland and riparian plant species. The potential for increased germination capacity, seed dispersal and geographic range expansion of invasive plant species is a particular concern relevant to the conservation of native biodiversity. The aim of this study was to compare the germination capacity of *Ludwigia hexapetala* and *Ludwigia peploides* subsp. *montevidensis* from two invaded ranges under 3°C warming predicted in climate change models. Germination of seeds collected from two invaded ranges was tested in controlled conditions at two air temperature regimes, 24°C/14°C and 27°C/17°C. Regardless of temperatures, the germination rates of studied species were greater than 80% for *L. hexapetala* from California, and for two populations of *L. peploides* from France. Seeds of *L. hexapetala* from California germinated two-fold more than seeds from France, while *L. peploides* from California germinated less quickly and at lower rates than two of three populations from France. The variation observed between invaded ranges could be interpreted as an adjustment of the germination responses of water primroses populations due to provenance environmental characteristics. The 3°C warming treatment accelerated the time to germination of water primrose seeds from California and France, and was a driving factor in final germination percentage for *L. hexapetala* populations from France. This study confirms that sexual reproduction can contribute to invasiveness of *Ludwigia* spp. and germination capacity will be maintained with 3°C temperature warming.

Keywords: aquatic plants, climate change, freshwater macrophytes, invasive species, *Ludwigia*, temperature

1. Introduction

As an adaptation to variable environments, wetland plant species often have both asexual and sexual reproduction. Clonal reproduction is common, and the rapid hydrochorous dispersal of vegetative fragments within watersheds has been broadly investigated (Barrat-Segretain and Bornette 2000; Riis and Sand-Jensen 2006; Vári 2013). The capacity for sexual reproduction contributes to the spread of plant species, and so for exotic species, promotes invasion (Forman and Kesseli 2003; Barrett *et al.* 2008) through regeneration from seed banks (D'Antonio and Meyerson 2002) or by the establishment of new populations (Dong *et al.* 2006). Indeed, long-distance colonization of macrophytes to distant watersheds is a potential mechanism for spread of invasive species, and waterfowl and other wildlife are known to be vectors of seed to novel environments (Viana *et al.* 2013; Bonilla and Pringle 2015; García-Álvarez *et al.* 2015). Moreover, sexual reproduction can increase genetic variation and the capacity for species for rapid adaptive evolution (Barrett *et al.* 2008). Classic studies of wetland seed banks document the importance of this reproductive mode for community assembly (van der Valk 1981; Capon and Brock 2006) yet germination ecology and seed dispersal of amphibious plants have more rarely been considered.

As environmental temperature is the primary regulator of germination (Bradford 2002), the expected climate warming may substantially change seed dormancy and germination responses of wetland and riparian plant species (Donohue *et al.* 2010), and is expected to have severe effects on riverine systems, including lower water levels (Capon *et al.* 2013). The moist soil areas exposed by these expected drawdowns may favor seed bank germination and so promote the maintenance of species that reproduce by sexual reproduction (Bornette and Puijalon 2010). Furthermore, future climate change could alter the reproductive strategies of aquatic plants, by promoting a shift from clonal spread to greater sexual reproduction (Gardner and Mangel 1999; Li 2014).

While freshwater ecosystems are widely threatened by both climate warming (Carpenter *et al.* 1992) and biological invasions (Dudgeon *et al.* 2006; Bellard *et al.* 2013), relatively little is known about the germination of invasive macrophytes. Managing an invasive species requires the greatest possible knowledge on its ecology, so it appears necessary to fill the knowledge gap regarding the germination dynamics of invasive macrophytes, especially in the context of increasing temperature. Data on the capacity of seeds to germinate with changing temperature can inform climate change predictions and invasive species risk assessments.

Water primroses *Ludwigia hexapetala* (Hook. & Arn.) Zardini, H. Y. Gu & P. H. Raven. (syn. *L. grandiflora* subsp. *hexapetala, L. uruguayensis*) and *Ludwigia peploides* subsp. *montevidensis* (Sprengl) P.H. Raven (Onagraceae) are amphibious species from South America that have naturalized in Europe and in the US. Cross-latitudinal studies provide an outstanding approach to study climate warming effects on vascular plant species (De Frenne *et al.* 2013). We compared germination dynamics of seed from populations of water primroses naturalized in western France and California. Environmental differences in the invaded ranges where the seed was produced presents an opportunity to investigate and compare the variation in the germination capacity of seeds produced under different climatic conditions from two invasive *Ludwigia* congeners. In the native South American range, populations of both taxa are observed to produce capsules and seeds (Grewell, pers. obs.), but germination details are unknown. In California, all studied populations produce mature fruits with viable seeds, though differences in seed production are noted between taxa and from populations in contrasting resource environments (authors, personal obs.). In France the number of fertile populations is thought to have increased over the past 15 years, raising concerns about the future invasiveness of the taxa (Ruaux *et al.* 2009; Haury *et al.* 2014). The development of seed banks by invasive water primroses can support the persistence of populations, by ensuring their regeneration by seed after disturbances such as managed control efforts (Haury

et al., 2012). In this study we investigated the effects of temperature increase on the seed germination of water primroses from two invaded ranges. Global surface temperatures are predicted to increase between 1 and 4°C by 2100 (IPCC 2013). We hypothesized that i) an increase of 3°C will enhance *L. hexapetala* and *L. peploides* subsp. *montevidensis* germination capacity, and ii) seeds from California will have a greater germination capacity than seeds from France because populations in the invaded California range have established under higher temperature regimes.

2. Materials and methods

2.1. Study species

L. hexapetala, a decaploid species (2n=80), was introduced to France in 1830 in the southern part of the country, and reached the Loire basin by the late 1970s (Ruaux *et al.* 2009). The diploid congener (2n=16), *L. peploides* subsp. *montevidensis*, hereafter *L. peploides*, was observed in France for the first time around 1830 (Dandelot *et al.* 2005). In the US, the first records of *L. hexapetala* on the West Coast are from the 1940s, while earliest records of *L. peploides* are from 1863-1893 (Grewell *et al.*, 2016). Once established, both taxa have spread widely through water bodies as clonal fragments, forming dense mats under and above the water surface (Thouvenot *et al.* 2013). *Ludwigia* spp. are also capable of sexual reproduction (Okada *et al.* 2009; Ruaux *et al.* 2009), and all from section Jussiaeae are also thought to be self-compatible (Wagner *et al.* 2007). Okada *et al.* (2009) showed that populations of *L. hexapetala* in California watersheds have limited genetic variation, inferring their spread is almost exclusively clonal. Yet, sexual recombination was also detected within populations with disturbance, which indicates recruitment from seeds (Okada *et al.* 2009). Recent experimental studies confirm that seeds of aquatic *Ludwigia* spp. have the capacity to germinate following dispersal in waterbird guts (García-Álvarez *et al.* 2015), which may explain the spread of populations between distant watersheds throughout native and invaded

ranges. Seed bank emergence assays from *L. hexapetala* population sites also support the importance of seedling recruitment in California (Grewell *et al.*, 2016).

2.2. Study sites: two contrasted invaded ranges

Water primroses tolerate a broad range of environmental conditions. The climate at invasive *Ludwigia* population sites in California and northwestern France is quite different. In coastal northern California, the Russian River watershed is dominated by a temperate Mediterranean climate, with rainy winters and dry summers (Fig 1a). Low precipitation combined with hot air temperature in summer lead to recurring seasonal drought. In France, the middle Loire River experiences an oceanic temperate climate. Precipitation is evenly dispersed over the year, but more abundant in winter (Fig 1b). Winters are mild, and summers are relatively warm, with occasional hot events.

2.3. Germination experiment and assessment

Seed capsules were collected when ripe during late summer in northern California and in western France, from 3 sites in both invaded ranges for *L. hexapetala*, and from 3 sites in France and 1 site in California for *L. peploides* (Table 1). In France, the 5 sites located on the Loire River are oxbows, separated by 2 to 10 km, and the remaining site is a series of ponds in the Vilaine watershed. This last site was selected because the observation of fruit production by *L. hexapetala* at this site is recent, and because no other sites with a sufficient amount of capsules of *L. hexapetala* were found in the area of study on the Loire river. In California, collections sites of *L. hexapetala* in the Russian River were separated by 15 to 70 km; and *L. peploides* was collected in a tributary to the Napa River. All collection sites in both invaded ranges were discrete, widely separated and characterized by dense vegetation beds of water primroses with no co-occurrence of the two species. We consider each sampled site as a population in this study, as locally the species were submitted to different conditions between each site. Where possible, seed capsules were collected from population patches separated by

at least 10 m in an attempt to collect from discrete individuals, and a maximum of three fruits were collected per each erect stem. Capsules were dried at ambient temperature and stored in the dark. Fifteen capsules were used per population, 20 seeds were randomly extracted from each capsule. Seed surfaces were sterilized by immersion in a sodium hypochlorite solution (5%) for 30 seconds, and then seeds were gently washed with distilled water. Petri dishes (90 mm diameter) were sterilized in a sodium hypochlorite solution diluted with boiling tap water, for 15 minutes. The bottom of each dish was covered with a layer of glass beads, a filter paper disk and 15 mL of distilled water. To avoid capsule effect, the 20 seeds extracted from a capsule were distributed with 2 seeds per capsule distributed in each of 10 petri dishes, for each population, for a total of 30 seeds per petri dish. Population CALH1 of *L. hexapetala* from California didn't produce enough seeds per capsule to allow us to follow this protocol. For these populations, 6 seeds (or 12 when possible) from each capsule were distributed in 6 petri dishes, up to 25 seeds per container. Petri dishes with seeds were stored at 4°C in the dark for 15 days in order to break seed dormancy. They were then split in two equivalent groups of five replicated dishes per population (three for population CALH1), and distributed randomly in two growth chambers (Percival AR-41L3). Growth chambers were set at two temperature regimes, 24/14 °C and 27/17°C (day/night) with a photoperiod 12/12 (25 $\mu mol.m^{-2}.s^{-1}$). In both invaded ranges, germination of *Ludwigia* spp. occurs over an extended time period from spring to summer. A preliminary experiment conducted at 16 and 19°C showed no germination of the seeds from California (unpublished data). In order to test the seed germination for both ranges at the same temperatures, we chose higher temperature for this experiment, with a control temperature regime of 24/14°C. Thereby the 24/14°C temperature regime represents high summer temperatures in northwestern France and high late spring temperatures in northwestern California. The 27/17°C temperature regime corresponds to an increase of 3°C, an increase consistent with predictions from the IPCC

climate change models (IPCC 2013). Seed germination was monitored three times a week for 7 weeks. A seed was considered germinated once the radicle protruded the testa, and was then removed from petri dishes. The water level was maintained throughout the duration of the experiment, by addition of distilled water.

Three germination indices were determined: final germination percentage (FGP), mean time to germination (MTG) and germination index (GI). MTG was calculated using the following equation (Luque *et al.* 2013):

$$MTG=(\Sigma nD)/N$$

Where n is the number of seeds which germinated on day D, D is the incubation period until counting, in days, and N represents the total number of seeds germinated during the experiment. GI was calculated according to the Association of Official Seed Analysts (Javaid and Tanveer 2014):

$$GI=\Sigma(n/D)$$

where n is the number of seeds which germinated on day D, and D is the incubation period until counting, in days. The GI reflects both the amount of germination and the germination velocity. In this study, the maximum GI possible is 10. A high GI means that many seeds germinated early and a low GI suggests a late germination or few germinated seeds.

2.4. Statistical analyses

Statistical analyses were performed using statistical R™ 3.1.0 software (R Development Core Team 2013) with package multcompView (Graves *et al.* 2012). Plots were generated using packages ggplot2 (Wickham 2009), reshape2 (Wickham 2007) and cowplot (Wilke 2015). Normality and homogeneity of variances were tested prior to each parametric test, and data were transformed if necessary by arcsine-square-root, square-root or log10 transformation in order to meet statistical model assumptions. A two-way Analysis of Variance (ANOVA) with populations nested within invaded range was performed to test the effect of temperature,

population, and the interaction effect of those two factors on the three chosen germination indices. Tukey's HSD test was applied for multiple comparisons when p values were significant (<0.05) to determine differences in final germination percentage, mean time to germination and germination index.

3. Results

3.1. Final germination percentage (FGP)

For *L. hexapetala*, temperature, range, population within range and the interaction between temperature and range all had a significant effect on FGP (Table 2). Populations from California had a higher FGP (between 86% and 94%) than populations from France (maximum 50%) (Fig. 2a, 2b). Within French populations, two populations of *L. hexapetala* (FRLH1 and FRLH3) had the least final germination percentage, from 28% to 36% maximum. The FGP was higher at 27/17°C for populations from France, and there was no significant temperature effect on the FGP of populations from California (Fig. 3a).

FGP was strongly influenced by source populations of *L. peploides* seeds (Table 2) irregardless of temperature (Fig. 3b). FGP of the single California population ranged from 56 – 69%, which compares to the range of FGP measured from the French populations (~ 50%, 85% and 98%) (Fig. 2c, 2d).

3.2 Mean time to germination (MTG)

L. hexapetala's MTG was significantly influenced by temperature, range, and by population within range (Table 2). On average, French seeds germinated three-fold to eight-fold times slower than seeds from California populations (Fig. 4a). Within California population, CALH2 and CALH3 germinated 31% faster than CALH1, and the 3°C warming accelerated the germination of respectively 33%, 21% and 40%. French populations were all different regarding their germination velocity; at 24/14°C, FRLH1 germinated two-fold faster than

FRLH3, and 67% faster at 27/17°C (Fig. 4a). FRLH2 and FRLH3 germinated 30% and 25% faster respectively with a 3°C warming.

The MTG of *L. peploides* was strongly affected by both population within range and temperature (Table 2). FRLP3 seeds germinated three-fold faster than FRLP2 seeds (Fig. 4b). All *L. peploides* populations germinated faster at 27/17°C; 18% faster for CALP1 to 45% for the three French populations.

3.2. Germination Index (GI)

Regarding *L. hexapetala*, we observed a significant effect of temperature, range and population within range and the interaction between range and temperature (Table 2). The higher GI of CALH2 and CALH3 indicates these populations germinated significantly more than CALH1 in the first days of the experiment, at both tested temperatures (Fig. 2a, 2b, 5a). All tested populations germinated significantly more at 27/17°C in the first days of incubation. The French populations had a low GI, reflecting a slower but continuous germination (Fig. 2a, 2b, 5a)

The ANOVA indicated that the GI of *L. peploides* is affected by temperature, range, population within range, and by the interaction between population within range and temperature (Table 2). CALP1 and FRLP1 had a similar GI at 24/14°C, but were different from FRLP2 and FRLP3 for this temperature (Fig. 5b). The four populations were all different regarding their GI at 27°C (Fig. 5b). CALP1, FRLP1 and FRLP3 seeds had a higher and earlier germination with a 3°C warming during the first few days of incubation (Fig. 2c, 2d, 5b).

4. Discussion

4.2. Germination of Ludwigia spp. and invasiveness

To our knowledge, this study is the first to publish results about temperature warming and the germination capacity of invasive *L. hexapetala* and *L. peploides* subsp. *montevidensis.* A highlight of our results is that all populations of *L. hexapetala* from California and two populations of *L. peploides* from France reached particularly high final germination percentages (>80% of germination) at tested temperatures. Radford & Cousens (2000) suggest that high germination rates might be linked with invasion success. Moreover, seeds from the Apigné ponds germinated up to 30%, which is not very high but still important considering that mature seed capsule production by *L. hexapetala* has only been observed at this site in a few recent years. The germination rates we measured confirm the concerns regarding the possible future spread of invasive *Ludwigia* spp. by sexual reproduction. It appears that allocation of resources to sexual reproduction can be an effective way for water primroses to produce new propagules that can support invasiveness of the species. However, experiments conducted under controlled conditions are a first step, and may overestimate germination in natural environments. Literature reviews suggest germination is a plant trait that can evolve quickly in new environments or with changing environmental conditions (Donohue *et al.* 2010). To build from this study, germination capacity should be tested in outdoor experiments as well as in natural field conditions.

4.3. Effect of temperature increase

As global temperatures rise, increases in flood events and overall decreases in annual river flow will lead to changes in ecotonal habitat along riverbanks, and increased susceptibility to weed invasions (Palmer *et al.* 2008; Capon *et al.* 2013). This will create more suitable soil habitat exposed for seed bank germination, and increase opportunities for sexual recruitment of plants along riverbanks. Indeed, persistent soil seed banks can enable vegetation to respond

to unpredictable patterns of changing hydrologic patterns (Capon and Brock 2006). Our results suggest that *Ludwigia* spp. will be able to take advantage of these changing conditions through germination from seed banks: we showed that a 3°C warming had an impact on the germination pattern of water primroses from California and northwestern France, a result consistent with our first hypothesis. Indeed, the warming treatment we imposed allowed earlier radicle emergence for both taxa. This early timing of germination is very important, because the critical survivorship and establishment of germinants as seedlings directly depends on the environmental conditions following the initial germination event (Donohue 2005; Walck *et al.* 2011). Additionally, the timing of germination can have impacts on plant size and fecundity, since early germination provides a competitive advantage and can allow a longer period of reproduction (Donohue *et al.* 2010). The earlier germination (a few days) detected in our study under increased temperature might set up a priority effect, allowing water primroses seedlings to gain competitive superiority over later germinating species.

While the mean time to germination was reduced by increased temperature, the final germination percentages were slightly enhanced only for populations of *L. hexapetala* from France (+6% difference), and those of *L. peploides* were not influenced for both ranges. The limited impact of a 3°C warming on the absolute numbers of germinated seeds suggests that invasiveness of water primroses will be maintained under the tested range of increased atmospheric temperature, but won't be enhanced. Nevertheless, the maintenance of the same germination rate by invasive water primroses under increased temperature could confer a competitive advantage to these invaders over other species having a lower germination temperature threshold. Indeed, studies of invasive plant species have documented that species that germinate under a wider range of temperatures also develop wider geographic ranges than species with narrow germination temperature niches (Grime *et al.* 1981; Brändle *et al.* 2003). In this study, we considered only germination responses to temperature, while temperature

and moisture conditions are both important factors in natural conditions. Further investigation would be needed to bring a more exhaustive answer regarding the germination, and more broadly regarding the sexual reproduction of invasive *Ludwigia* spp. under climate change conditions.

4.4. Effect of ranges and population

Our results support our second hypothesis that seeds from populations of *L. hexapetala* sampled in California had a greater germination capacity, germinating between 37% to 66% more than French populations. These germination patterns clearly depend on the geographical origin of the seeds. According to Figuerola *et al.* (2005), variation in germination rate can be interpreted as adaptive responses of plants to adjust their germination patterns to habitat characteristics. Seeds from populations of *L. hexapetala* in California had high germination numbers early and quickly under experimental conditions. Selection pressures in response to local conditions may explain this rapid early germination: environmentally cued germination enables individuals to maximize their survival success by emerging as seedlings under favorable conditions with reduced risk of exposure to hostile conditions (Donohue 2005; Mayfield *et al.* 2014) such as heat during California summer. The germination pattern of *L. hexapetala* from populations from France contrasts with those of populations from California: seeds germinated lower, later and slower. In the field, the survivorship of seedlings from these populations is not jeopardized by high temperature if emerged in summer, which might explain why their seeds germinated more regularly. Consistent with our results, Hierro *et al.* (2009) found that non-native genotypes of *Centaurea solstitialis* from regions with a summer rain regime exhibited much lower germination fractions and rates than those from a region with summer drought.

However, plants may have differences in germination capacity or other indicators of fitness when under environmental conditions of provenance versus novel environmental conditions

due to reasons other than local adaptation (Kawecki and Ebert 2004, Hereford 2009, Hirst *et al*. 2016). Alternative factors that may interact and contribute to explain the difference of germination responses between the two ranges may include seed traits (i.e. seed size, nutrient reserves) that can vary due to differences in nutrient availability and other environmental characteristics among population sites (Galloway 2001, Baskin and Baskin 2014), or phenotypic plasticity of plants in source populations (Ghalambor *et al*. 2007, Byers and Hoffman 2009)

Our results also suggest a strong effect of population within range of origin on the germination capacity of *L. hexapetala*. Variance in germination characteristics between populations of *L. hexapetala* from France was higher than variance observed between populations from California. However the results from the population at Apigné pond were intermediate compared to the two populations located in the Loire River watershed. A similar result was observed between populations from California: the two populations in closest geographic proximity were not the most similar in their germination capacity.For *L. peploides* from France, our results suggest that source population influences germination rates and germination timing. We found a high degree of variation in germination of seeds from populations from the Loire River, despite the fact that they were collected from field sites in the same watershed region (3 to 15 km). These differences might be due to genetic drift, or to local environmental differences, such as variations in soil nutrient and water quality in the oxbow basins where capsules were formed and collected. The germination capacity of seeds from the population of *L. peploides* from California was either the same, higher or lower than the one of populations evaluated from France, depending on the population considered. It is difficult to draw conclusions about the germination capacity of *L. peploides* in California; we would need more populations from this invaded range for comparison. Because of the small sample size available to us from California, and a high variation in germination capacity

between populations from France, we cannot reach a conclusion about our second hypothesis for this species.

As parental environment can influence the germination patterns (Galloway 2001), in such circumstances, the comparability of the different water primroses origin (i.e. invaded range) is limited. It would be interesting to separate environmental and genetic effects with further experiments including seed material obtained from individuals grown under the same conditions (Baskin and Baskin 2014). At this time, genetic studies are underway but we do not have information about potential genetic differences between naturalized populations in France and California.

5. Conclusions

Invasive *L. hexapetala* and *L. peploides* have the capacity to establish *via* seed germination with predicted increases in climate warming. Our findings suggest a moderate effect of warmer temperature on seed germination of the evaluated populations. Both population and temperature contributed significantly to the amount and the velocity of germination of the invasive taxa, but population explained most of the variance. Moreover, time to germination was mostly distinguished by population site, even for California populations of *L. hexapetala.* These populations, produced in a warmer climate, germinated much more and quicker than those from France. The results of this controlled environment study should be considered the first sketch of how germination patterns of *L. hexapetala* might respond to predicted temperature increases. Further study that considers fitness consequences of germination dynamics, and both environmental and potential evolutionary effects is certainly needed to elucidate how this critical life stage operates under complex, natural environmental conditions. More information is needed about the sexual reproduction of these species, in their native range and throughout their naturalized range in order to fully understand the consequences of environmental change for the germination, colonization and spread of

invasive *Ludwigia* taxa. Improved understanding of mechanisms underlying reproductive strategies of these invasive plants can inform risk assessments, lead to adapted management strategies to counteract their range expansion and conserve native biodiversity.

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Table 1 – Location of the sites where capsules were collected. The first two letters of the site code correspond to the area of origin (CA=California, FR=France) and the two last letters indicate the species (LH=*Ludwigia hexapetala*, LP=*Ludwigia peploides* subsp *montevidensis*).

Species	Site code	Names of waterbody	Site name	GPS coordinates
L. hexapetala	CALH1	Russian River	Comminsky Station	38.886028, -123.055174
	CALH2	Russian River	Asti	38.763413, -122.966920
	CALH3	Laguna de Santa Rosa	Laguna Ranch	38.446701, -122.836557
	FRLH1	Apigné Ponds	Apigné	48.094956, -1.739948
	FRLH2	Loire River	Ile du Château	47.316483, 0.413346
	FRLH3	Loire River	Les Raguins	47.329167, 0.462044
L. peploides subsp. *montevidensis*	CALP1	Sage Creek	Sage Creek – Lake Hennessey	38.490237, -122.347488
	FRLP1	Loire River	Ile Joli Cœur	47.325036, 0.437465
	FRLP2	Loire River	Ile César, Ile aux boeufs	47.344959, 0.477065
	FRLP3	Loire River	Port de Vallières	47.386191, 0.605725

Table 2 – ANOVA results for final germination percentage (FGP), mean time to germination (MTG) and germination index (GI) for seeds from six populations of *Ludwigia hexapetala* and four populations of *Ludwigia peploides* subsp. *montevidensis* exposed to two temperatures (24°C and 27°C) for 7 weeks. ns = not significant (p>0.05)

Species	Index	Effect	Sum Square	F value	P value
Ludwigia hexapetala	FGP	Temperature	144	6.50	0.014
		Range	38864	1760.91	<0.001
		Pop within Range	1679	19.01	<0.001
		Temp:Range	96	4.35	0.042
		Temp:Pop within Range	39	0.43	ns
		Residuals	971		
	MTG	Temperature	0.124	43.95	<0.001
		Range	6.061	2151.55	<0.001
		Pop within Range	0.420	37.36	<0.001
		Temp:Range	0.005	1.75	ns
		Temp:Pop within Range	0.015	1.32	ns
		Residuals	0.124		
	GI	Temperature	0.791	125.31	<0.001
		Range	45.372	7185.14	<0.001
		Pop within Range	1.054	41.74	<0.001
		Temp:Range	0.087	13.83	<0.001
		Temp:Pop within Range	0.020	0.77	ns
		Residuals	0.278		

Ludwigia peploides subsp. *montevidensis*	FGP	Temperature	0.00011	2.26	ns
		Range	0.00065	13.82	<0.001
		Pop within Range	0.00447	47.41	<0.001
		Temp:Range	0.00012	2.61	ns
		Temp:Pop within Range	0.00001	0.16	ns
		Error or residuals	0.00151		
	MTG	Temperature	2.439	29.85	<0.001
		Range	0.001	0.02	ns
		Pop within Range	11.997	73.42	<0.001
		Temp:Range	0.194	2.38	ns
		Temp:Pop within Range	0.094	0.58	ns
		Residuals	2.614		
	GI	Temperature	22.052	126.41	<0.001
		Range	7.813	44.79	<0.001
		Pop within Range	144.683	414.69	<0.001
		Temp:Range	0.033	0.19	ns
		Temp:Pop within Range	5.537	15.87	<0.001
		Residuals	5.587		

Fig. 1. Climatic diagrams of Santa Rosa in California, USA (a) and Tours in France (b), representing the local climate. Light grey bars represent the monthly rainfall in mm, the lines depict the average high (in black) and low (in grey) temperature per month, in Celsius degree (data source: Météo-France and USclimatedata.com)

Fig. 2. Cumulative germination percentage of *Ludwigia hexapetala* (a,b) and *Ludwigia peploides* subsp. *montevidensis* (c,d) seeds during 49 days under two temperature regimes 24/14°C day/night (a,c) and 27/17°C (b,d), for experimental populations from two invaded ranges

Fig. 3. Means (±SD) for final germination percentage of *Ludwigia hexapetala* (a) and *Ludwigia peploides* subsp. *montevidensis* (b) under two temperature regimes. Different capital letters above bars represent significant differences between populations. The symbol * highlights an overall temperature effect with higher FGP due to higher temperature. ($P<0.05$, Tukey HSD test)

Fig. 4. Mean time to germination (±SD) of *Ludwigia hexapetala* (a) and *Ludwigia peploides* subsp. *montevidensis* (b) under two temperature regimes. Different capital letters represent significant differences between populations. The symbol * highlights an overall temperature effect with higher MTG due to lower temperature. ($P<0.05$, Tukey HSD test)

Fig. 5. Germination index (mean ±SD) of *Ludwigia hexapetala* (a) and *Ludwigia peploides* subsp. *montevidensis* (b) under two temperature regimes. Different capital letters represent significant differences between populations. The symbol * highlights an overall temperature effect with higher FGP due to higher temperature. Different small letters indicate significantly different values. ($P<0.05$, Tukey HSD test)