



Climate warming and water primroses: Germination responses of populations from two invaded ranges



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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. *montevicensis* 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.

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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

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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-latitude 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 (Riaux 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 (Riaux 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 to 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; Riaux 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, collection 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 s, 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 min. 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

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