Flora 229 (2017) 80–91

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.com/locate/flora

Propagule and seedling responses of three species naturalised in subtropical South Africa to elevated temperatures

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ARTICLE INFO

Article history:
Received 15 September 2016
Received in revised form 6 February 2017
Accepted 11 February 2017
Edited by Hermann Heilmeier
Available online 15 February 2017

Keywords:
Alien plants
Climate change
Germination
Invasion
Naturalised species
Seed mass
Seedling growth

ABSTRACT

The predicted 2–5 °C increase in global temperatures by the end of this century could enhance the invasive potential of some alien plant species. It is unclear whether aliens that originate from and/or are naturalised in warm areas are predisposed to respond positively to this increase. This study assessed the propagule and seedling responses of three alien plant species (*viz. Oenothera biennis*, *Syncarpia glomulifera* and *Petiveria alliacea*) naturalised in a subtropical region in South Africa to elevated temperatures. The species were characterised in terms of propagule (seed/achene) traits related to invasiveness before these were sown at ambient (daily maximum: 26.2 ± 0.3 °C; daily minimum: 17.9 ± 0.2 °C) and elevated (daily maximum: 30.6 ± 0.5 °C; daily minimum: 21.2 ± 0.3 °C) temperatures to assess germination capacity and rate. Seedlings subsequently produced were grown at these temperatures to assess growth and performance. Propagules of all species possess traits that facilitate persistent seed banks but their small size may not favour seedling survival under harsh conditions. Only *O. biennis* and *P. alliacea* exhibited high seed viability but elevated temperatures enhanced germination capacity and rate in all species. Seedlings of both *O. biennis* and *S. glomulifera* exhibited signs of stress at elevated temperatures (*e.g.* reduced biomass) though. However, while seedling production and survival were reduced at elevated temperatures in *O. biennis*, these parameters were enhanced at elevated temperatures in *S. glomulifera* (possibly due to increased shoot emergence rate). Elevated temperatures did not affect seedling production in *P. alliacea* but did enhance seedling survival, possibly by inducing biomass allocation patterns that enhance productivity. The ability of naturalised species to become invasive in a changing climate may be more dependent on phenotypic plasticity than the possession of a syndrome of invasive traits. Species that originate from, and are naturalised in, warmer climates may not be predisposed to respond positively to elevated temperatures.

1. Introduction

Globalisation has resulted in the movement of many plants and animals beyond their natural range and introduced novel environments for them to grow, reproduce and establish in (Cronk and Fuller, 1995). The distribution of alien plants is bounded by climate and climatic niches (Dukes and Mooney, 1999; Petitpierre et al., 2012). Changes in climate may influence the introduction, establishment, naturalisation (*i.e.* overcoming of various abiotic and biotic barriers to survival and regular reproduction (Richardson et al., 2000)) and invasion of alien plant species (Bradley et al., 2012; Walther et al., 2009). Increasing temperatures, in particular, are predicted to favour some aliens and invasive alien plants (IAPs), particularly those exhibiting superior phenotypic plasticity (Bradley et al., 2009; Richter et al., 2012). Alien and IAPs that are favoured may adversely affect indigenous flora (Chown et al., 2007; Dukes and Mooney, 1999; Walther et al., 2009) through allelopathy, competition and replacement (Davidson et al., 2011). Knowledge on alien plant responses to various climate change scenarios is therefore vital for managing ecosystems now and into the future since alien plant invasions impact on both human and ecosystem health (Simberloff et al., 2013).

Alien plants are more likely to thrive when introduced to novel environments with climatic conditions similar to those of their native range (Chown et al., 2007; Walther et al., 2009). This phenomenon of 'climatic niche conservatism' implies that alien species occupy similar distribution ranges, and survive under similar environmental conditions in native and invaded ranges (Peña-Gómez et al., 2014; Petitpierre et al., 2012). There are, however, areas of the world for which predicted changes in climate may either favour

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http://dx.doi.org/10.1016/j.flora.2017.02.013
0367-2530/

(Bradley et al., 2009) or disfavour (van Kleunen et al., 2010) alien and invasive alien plants.

Apart from niche conservatism a number of other factors influence and may promote invasions, *e.g.* specific functional traits (often related to reproduction and dispersal ability) as well as biotic interactions (Peña-Gómez et al., 2014; Simberloff et al., 2013). Species sharing the same ecological properties (*e.g.* life-history traits) might also respond in a similar way to change, thus making generalisations possible (Marini et al., 2012). A focus on plant functional traits that often trigger invasiveness in alien plants, such as high propagule viability, rapid growth, efficient biomass accumulation and allocation, and competitive ability (Daehler, 2003), may therefore be useful. Invasive alien species that exhibit these traits in a changing climate may alter abundances, richness and diversity of native species as a consequence of their superior competitive ability (Thuiller et al., 2006).

Climate changes such as the anticipated 2–5 °C global rise in temperature by 2100 (Christensen et al., 2007) have already, and will in the future, enable alien plants to expand into regions in which they previously could not survive and reproduce (Walther et al., 2009). Rising temperatures appear to facilitate IAPs by variably promoting their growth, reproduction, biomass production and competitive ability (van Kleunen et al., 2010). Invasion biologists must therefore aim to explain why some alien taxa may be better invaders than others under climate change scenarios such as elevated temperature. This will involve addressing a number of key questions, which include: (1) Is the invasive ability of alien taxa dependent on plant traits, habitat characteristics, or a combination of these (Thompson et al., 1995 and references therein) and (2) Is a species' ability to become naturalised in warm climates an indication that it will respond favourably to increasing temperatures? In this regard, there have been suggestions that alien plants originating from warm locations may increase in both abundance and geographical range with prolonged warming (Dukes and Mooney, 1999).

Like other tropical regions of Africa (Intergovernmental Panel on Climate Change [IPCC], 2007), South Africa is predicted to experience an increase in temperature by 2100 (Engelbrecht et al., 2011). The impacts of these changes on indigenous (Foden et al., 2007; Midgley and Thuiller, 2007) and alien (Rouget et al., 2004) flora in this region is receiving increasing attention at various taxonomic and spatial scales but more needs to be done. The costs of eradicating IAPs are exorbitant (Richardson and van Wilgen, 2004) and to better prioritise alien species for management/eradication, it may be useful to predict the responses of naturalised, emerging and invasive aliens to climate change.

This motivated the present study which investigated the propagule (seed/achene) and subsequent seedling responses of three phylogenetically distinct and phenotypically different aliens, of subtropical origin, that are presently naturalised in a subtropical area in South Africa to elevated temperatures. Propagule traits that can influence invasiveness (*e.g.* propagule mass and viability) and subsequent seedling responses to temperature related stress (Holm, 1994) were also compared across the three species. The present study was conducted on the propagules, specifically seeds of *Oenothera biennis* L. (Onagraceae) and *Syncarpia glomulifera* subsp. *glabra* Benth. (Myrtaceae) and achenes of *Petiveria alliacea* L. (Phytolaccaceae), and the seedlings produced by these propagules. For comparative purposes we selected three species that differ in terms of growth (life) form: *O. biennis* is a short-lived perennial herb that grows to ca. 1–2 m in height and is native to North America (Gimenez et al., 2013); *P. alliacea* is a perennial herb or woody shrub that is usually ca. 0.7 m high and native to the Amazonian region (Ochoa et al., 2013); and *S. glomulifera* is a tree that can grow to ca. 60 m in height over decades and is native to eastern Australia (Bean, 1995). Despite these differences in growth form all three species, which are of subtropical/tropical origin, have become IAPs in various subtropical/tropical parts of the world (Randall, 2012). All three species are naturalised (*sensu* Richardson et al., 2000) but are not invasive (South African Government, 2016) in the study area: eThekwini Municipal Area (EMA), located in KwaZulu-Natal, along the subtropical eastern coastal belt of South Africa.

Temperature like other environmental factors (*e.g.* rainfall) that control plant distribution acts at all stages of plant development (propagule, seedling and adult) and the environmental requirements at each of these stages can differ (Edkins et al., 2008). The focus on the propagule and seedling stage in the present study is based on the fact that seed germination, which is highly dependent on temperature and precipitation across all biomes (Walck et al., 2011), is the first step in the successful establishment of a plant and therefore influences the distribution of a species (Donohue et al., 2010). Furthermore, the ability of germinated seeds to establish as healthy, vigorous seedlings will ultimately determine the persistence of natural populations (Grice and Westoby, 1987). We hypothesise that species naturalised in subtropical/tropical parts of the world (1) display similarities in terms of the physical and germination characteristics of their propagules and (2) produce propagules and seedlings that will respond positively to elevated temperatures.

2. Materials and methods

2.1. Study area and plant material

Propagules used in the study were harvested from *O. biennis*, *S. glomulifera* and *P. alliacea* parent plants/trees growing within the EMA (ca. 2297 km^2; 26° and 31° S, 28° and 32° E). Care was taken in ensuring that fruits were collected from between 10–25 individuals within each population and these were pooled before selection of samples for all measurements and subsequent germination and seedling growth studies.

The exclusive selection of parent plants growing within the EMA as sources of propagules was based on the fact that this is a subtropical region that consistently displays an annual average daily maximum temperature of ca. 25.5 °C and an annual average daily minimum of ca. 16.7 °C (Durban Weather Office, 2011).

2.2. Propagule physical characteristics

Once harvested, mature fruits, as in *O. biennis* and *S. glomulifera*, or infructescences, as in *P. alliacea*, were immediately conveyed to the laboratory and characterised in terms of fruit size (n = 25), number of seeds in *O. biennis* and *S. glomulifera* and achenes in *P. alliacea*, per fruit/infructescence (n = 25). The achenes of *P. alliacea*, which are actually fruits that contain single seeds, will hereafter be referred to as 'seeds' owing to their seed-like appearance. As in other achene producing angiosperms, *P. alliacea* achenes display a hardening of the wall of the seed-vessel, which encloses the individual seed so tightly that it appears like an outer coat. It should also be noted that in nature *P. alliacea* plants disperse the entire achene (which contains a single seed) as the propagule. Seed size (n = 25) and mass (n = 25) were measured for all three species. Seed mass was measured using a balance with 0.00001 g precision whilst seed dimensions were measured using a calliper. Water content was measured for individual seeds (n = 25) gravimetrically using an electronic balance with a precision of 0.000001 g (Mettler, MT5; Germany) by weighing them before and after drying for 48 h at 80 °C. Water content was calculated on a dry mass (DM) basis (g H_2O g^{-1} DM).