Perspectives in Plant Ecology, Evolution and Systematics 21 (2016) 31–40

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

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

Research article

Plant size and leaf area influence phenological and reproductive responses to warming in semiarid Mediterranean species

Enrique Valencia[a,b,*], Marcos Méndez[a], Noelia Saavedra[a], Fernando T. Maestre[a]

[a] Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, C/Tulipán s/n, 28933 Móstoles, Spain
[b] Department of Botany, Faculty of Science, University of South Bohemia, Branišovská 31, České Budějovice, Czech Republic

ARTICLE INFO

Article history:
Received 13 October 2015
Received in revised form 21 May 2016
Accepted 25 May 2016
Available online 26 May 2016

Keywords:
Climate change
Drylands
Functional group
Functional traits
Open top chambers
Phenology

ABSTRACT

Changes in vegetative and reproductive phenology rank among the most obvious plant responses to climate change. These responses vary broadly among species, but it is largely unknown whether they are mediated by functional attributes, such as size or foliar traits. Using a manipulative experiment conducted over two growing seasons, we evaluated the responses in reproductive phenology and output of 14 Mediterranean semiarid species belonging to three functional groups (grasses, nitrogen-fixing legumes and forbs) to a ~3 °C increase in temperature, and assessed how leaf and size traits influenced them. Overall, warming advanced flowering and fruiting phenology, extended the duration of flowering and reduced the production of flowers and fruits. The observed reduction in flower and fruit production with warming was likely related to the decrease in soil moisture promoted by this treatment. Phenological responses to warming did not vary among functional groups, albeit forbs had an earlier reproductive phenology than legumes and grasses. Larger species with high leaf area, as well as those with small specific leaf area, had an earlier flowering and a longer flowering duration. The effects of warming on plant size and leaf traits were related to those on reproductive phenology and reproductive output. Species that decreased their leaf area under warming advanced more the onset of flowering, while those that increased their vegetative height produced more flowers. Our results advance our understanding of the phenological responses to warming of Mediterranean semiarid species, and highlight the key role of traits such as plant size and leaf area as determinants of such responses.

© 2016 Elsevier GmbH. All rights reserved.

1. Introduction

Ongoing global warming is modifying plant vegetative and reproductive phenology in terrestrial habitats worldwide (Parmesan and Yohe, 2003; Gordo and Sanz, 2010; Körner and Basler, 2010). These changes have multiple consequences for ecosystem structure and functioning, including potential temporal asynchronies between plants and insects, modification in flower quality and seed mass, or reduced survival of plants (Goulden et al., 1996; Walther et al., 2002; Aerts et al., 2004; Williams et al., 2007; Inouye, 2008; Hegland et al., 2009). Vegetative and reproductive phenological responses to warming have been relatively well studied in temperate habitats (Dunne et al., 2003; Parmesan and Yohe, 2003; Sherry et al., 2007; Rollinson and Kaye, 2012), where temperature is often a limiting factor for plant growth and development (Parmesan, 2007; Liang et al., 2013). In these areas, both observational and experimental studies have shown that warming promotes an earlier and longer flowering season (Dunne et al., 2003; Menzel et al., 2006; Parmesan, 2007; Hovenden et al., 2008; Kardol et al., 2010).

Phenological studies often show a latitudinal variation in their responses, with extended growing seasons and a more advanced flower phenology in warmer compared to milder ecosystems (e.g., Menzel et al., 2006; Gordo and Sanz, 2009). However, few experimental studies have been conducted in arid, semi-arid and dry-subhumid environments (drylands hereafter, *sensu* UNEP, 1992), particularly when compared to the number of studies conducted in temperate ecosystems (Arft et al., 1999; Wolkovich et al., 2012; but see Liancourt et al., 2012). This is a worrying knowledge gap because drylands occupy ~41% of the Earth's surface (Safirel and Adeel, 2005), are a key biome for global plant diversity (White and Nackoney, 2003), and are currently threatened by climate change and desertification (Reynolds et al., 2007; Maestre et al.,

---

* Corresponding author at: Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, C/Tulipán s/n, 28933 Móstoles, Spain.
E-mail address: valencia.gomez.e@gmail.com (E. Valencia).

http://dx.doi.org/10.1016/j.ppees.2016.05.003
1433-8319/© 2016 Elsevier GmbH. All rights reserved.

2012). In addition, the phenological impacts of warming in drylands are likely to differ from those observed in temperate ecosystems. In water-limited environments, warming could advance flowering, but may decrease both the number of flowers/fruits and seed mass (Liancourt et al., 2012) due to reductions in soil moisture (Luo et al., 2001; Peñuelas et al., 2004).

Despite the large body of literature on phenological responses to warming, we do not fully understand why observed responses differ so widely across species (Arft et al., 1999; Peñuelas et al., 2002). To address this variability, such responses have been studied in relation to factors such as soil moisture, vernalization or photoperiod (Partanen et al., 1998; Boss et al., 2004; Turck et al., 2008; Körner and Basler, 2010). Clear connections between flowering time and advances in flowering phenology induced by warming have been found only in some cases (Fitter et al., 1995; Peñuelas and Filella, 2001; Root et al., 2003; but see Liancourt et al., 2012; Whittington, 2012). Plant functional groups, i.e. sets of species that encompass a variety of common functional attributes (Díaz and Cabido, 1997; Gitay and Noble, 1997), allow generalizing how species respond to environmental changes (Wilson, 1999). For example, annual grasses have an earlier flowering time than forbs (Cleland et al., 2006). Sherry et al. (2007) showed that early-flowering species showed an advancement of flowering in response to warming, while late-flowering species did the opposite. However, no previous studies have evaluated whether the same pattern applies to early- or late-flowering functional groups. Changes in the flowering time with warming could modify the coexistence of different species or functional groups within plant communities (i. e. phenological complementarity; Rathcke and Lacey, 1985).

Plant functional traits can shed light on the responses of reproductive phenology to warming, but their influence has received little attention so far (Bolmgren and Cowan, 2008; Miller-Rushing et al., 2008; Richardson et al., 2010). For instance, plant size should correlate with flowering onset (Vile et al., 2006), but its relationship with other reproductive phenological variables is unknown. Thus, a better knowledge about the links between functional traits and phenological responses is needed to enhance our ability to predict plant responses to warming.

To fill current gaps in our understanding about the responses of Mediterranean semiarid species to climate change, we experimentally evaluated the reproductive phenology and reproductive output to warming of 14 Mediterranean semi-arid species belonging to different functional groups. Specifically, we assessed: (1) how warming affects key phenological events, such as flowering (onset, peak, cessation or duration) and fruiting (onset, peak), and reproductive output (number of flowers, fruits or seed mass), (2) whether responses to warming were consistent among the different reproductive phenology and reproductive output variables, and between years with contrasting environmental conditions, (3) the role of functional groups and functional traits on reproductive phenological responses, and how warming modifies them, and (4) whether the magnitude of intraspecific changes in functional traits modulate these responses to warming. We predict that warming would cause an advance of all components of reproductive phenology, an increase in flowering duration and a decrease in the number of flowers, fruits and seed mass (Liancourt et al., 2012). Warming will also result in less water availability compared with the control, and these differences will be especially marked at the end of the growing season (Valencia et al., 2016b). As a consequence, reproductive output might decrease with warming (Liancourt et al., 2012). We also hypothesized that phenological responses to warming will vary among plant functional groups (Cleland et al., 2006), and that these responses will be affected by functional traits such as plant size and leaf area (Vile et al., 2006; Sherry et al., 2007; Bolmgren and Cowan, 2008).

2. Materials and methods

2.1. Study species

We studied 14 species belonging to three broad taxonomical functional groups: grasses (*Cynodon dactylon* [L.] Pers., *Poa pratensis* [L.], *Agropyron cristatum* [L.] Gaertn., *Festuca ovina* [L.]), nitrogen-fixing legumes (*Hedysarum coronarium* [L.], *Dorycnium pentaphyllum* [Scop.], *Anthyllis vulneraria* [L.], *Medicago sativa* [L.], *Bituminaria bituminosa* [L.] C.H. Stirt.) and forbs (*Plantago lanceolata* [L.], *Sanguisorba minor* [Scop.], *Echium boissieri* [Steud.], *Echium plantagineum* [L.], *Asphodelus fistulosus* [L.]; Table S1). We selected these species because they typically coexist in grassland communities, abandoned fields and roadside slopes undergoing secondary succession in semi-arid Mediterranean areas (García-Palacios et al., 2010).

2.1.1. Experimental design

A microcosm experiment was conducted at the Climate Change Outdoor Laboratory, located at the facilities of Rey Juan Carlos University (URJC, Móstoles, Spain: 40°20′37″N, 3°52′00″W, 650 m a.s.l.) between April 1, 2011 and July 31, 2013. Microcosms consisted of plastic pots (depth 38 cm, internal diameter 28 cm) filled with 32 cm of natural soil (sand content: 73.5%, silt content: 18.5%, clay content: 8.0%) and 3 cm of expanded clay for drainage at the base. All the microcosms were initially watered with 500 mL of a soil microbial inoculum to recreate realistic microbial communities, as described in Maestre et al. (2005). All the pots were placed in holes in the ground, and kept under ambient light and rainfall to keep the most natural conditions.

The experiment was designed as a randomized block design, with two treatments: warming (control vs. ~2.9 °C annual temperature increase), and functional group (three levels: grasses, nitrogen-fixing legumes and forbs). Microcosms were arranged in four blocks containing a replicate of species per temperature treatment, resulting in 112 microcosms in total. A minimum distance between microcosms of 1 m was established to minimize the risk of sampling non-independent areas.

Seeds for this experiment were obtained from commercial sources (Intersemillas Ltd., Valencia, Spain). In April 2011, we randomly sowed seeds of each species within each microcosm. We planted a monoculture in each microcosm at a density of 160 individuals/m^2. This density is within the range found in semiarid ecosystems from central Spain (e.g., 131 individuals/m^2; Chacón-Labella et al., 2016). The microcosms were watered with 1 L three times per week during the first six weeks of the experiment, and once a week in July and August 2011, to ensure seed establishment. Weeds were regularly removed during the experiment. The warming treatment was set up on December 05, 2011, once all microcosms had an established population, and the experiment terminated in July 2013. We elevated the temperature in the warming treatment by using open top chambers (OTCs), which have been commonly employed in warming experiments (e.g., Marion et al., 1997; Hollister and Weber, 2000; Escolar et al., 2012; Liancourt et al., 2012). These were hexagonal chambers built of methacrylate plates, with sloping sides of 65-52-42 cm (Fig. S1). Methacrylate has high transmittance in the visible spectrum (92%), very low emission of the infrared wavelength (4%) and high energy transmission (85%; data provided by the supplier, Decorplax Metacrilatos S.L., Madrid, Spain). Chambers were open on their top to allow rainfall and air flow, and were raised 5 cm from the soil surface to achieve adequate air flow and avoid excessive heating. Air temperature and humidity were measured in warming and control plots using automated sensors (HOBO U23 Pro v.2 Temp/RH, Onset Corporation, Bourne, MA, USA). The OTCs employed raised temperature by an average of ~2.9 °C compared to control plots during our experiment (Fig.

Download English Version:

https://daneshyari.com/en/article/4400904

Download Persian Version:

https://daneshyari.com/article/4400904

Daneshyari.com