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Germination response to light and temperature in eight annual grasses from disturbed and natural habitats of an arid Arabian desert

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ABSTRACT

It has been hypothesized that annuals of unpredictable arid deserts produce dormant seeds as a strategy for risk spreading, but weedy annuals have lower dormancy and positively photoblastic seeds. I tested this hypothesis by comparing dormancy, and photoperiod and temperature requirements during germination in annual grasses of unpredictable arid deserts and other grasses from disturbed sites. Seeds were collected from four annual grasses of natural sandy deserts and other four from disturbed sites of an arid Arabian desert. Seeds were germinated in three incubators adjusted at daily night/day temperature regimes of three temperatures in both continuous darkness and alternating 12 h light/12 h darkness. The four sandy desert grasses had greater dormancy, compared to those of disturbed sites. Light and temperature ranges of germination were narrower and species specific for sandy desert grasses. Seeds of the grasses of disturbed sites germinated at wider range of temperatures and all were positively photoblastic, except Chloris virgata. Negative photoblastism was very rare, recorded only in seeds of Coelachyrum brevifolium at lower and moderate temperatures. Seed photoblastism depended more on habitat types than seed mass. The light and temperature requirements of the studied grasses can explain their adaptation and distribution in natural habitats.

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1. Introduction

Desert environments are very heterogeneous and unpredictable both in space and time. The habitats are patchy and rainfalls vary substantially both in amount and timing within and among years ([El-Keblawy, 2017a; El-Keblawy et al., 2015a\)](#page--1-0). Desert annuals, in particular, reproduce or die depending on the amount and pattern of the unpredictable rainfall events. In response to such temporal and spatial uncertainties, annuals retain a fraction of dormant seeds for possible future germination opportunities in potentially more favourable years ([Venable and Brown, 1988; Milberg et al.,](#page--1-0) [2000; Saatkamp et al., 2014\)](#page--1-0). Such a bet hedging strategy could be understood as an insurance against reproduction failure, which could increase long-term fitness [\(Levy et al., 2012](#page--1-0)). It could also be explained as a form of risk spreading in temporally variable, unpredictable environments. Delaying the germination to start during favourable periods for seedling establishment maximizes fitness of both mother plant and offspring [\(Fenner and Thompson, 2005\)](#page--1-0). In

addition, delaying and spreading germination could reduce sibling competition and competition between seedlings and maternal plants [\(Cheplick, 1992\)](#page--1-0).

Desert plants develop different types of seed dormancy that could only be broken as soon as they are exposed to the proper environmental signals that enhance seedling establishment ([Finch-](#page--1-0)[Savage and Footitt, 2012\)](#page--1-0). Dormancy release or germination induction in seeds of desert plants are influenced by several factors, including alternating temperatures, light and dormancy regulating chemicals ([Bewley and Black, 1994; El-Keblawy, 2014; El-Keblawy](#page--1-0) [and Gairola, 2017](#page--1-0)). Temperature, for example, is a critical environmental factor that regulates seed dormancy break and induces germination ([Baskin and Baskin, 2014\)](#page--1-0). In addition, seasonal temperature fluctuations play a major role in regulating the loss of primary dormancy and inducing secondary dormancy ([Probert,](#page--1-0) [2000\)](#page--1-0). Even after dormancy break, temperature is the major determinant of germination capacity and speed. In seasonal climates, temperature is a good indicator of the time of year, and therefore, it is strongly implicated in timing of germination ([Fenner](#page--1-0) [and Thompson, 2005; Baskin and Baskin, 2014; El-Keblawy et al.,](#page--1-0) [2015b](#page--1-0)). The uppermost soil layer in deserts serves as the major germination bed and experiences wide daily and seasonal fluctuations in light and temperature conditions, especially in the

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unpredictable arid deserts [\(El-Keblawy et al., 2011; El-Keblawy and](#page--1-0) [Gairola, 2017](#page--1-0)). Consequently, germination of many desert plants occurs only when the particular combinations of light, temperature and soil moisture are optimal for plant growth ([El-Keblawy, 2013,](#page--1-0) [2017b\)](#page--1-0).

Seed responses to light are also important for preventing the occurrence of germination in places and at times that are unfavorable for seedling establishment ([Flores et al., 2011\)](#page--1-0). Plants can be classified in terms of their responses to light for germination as positive photoblastic (require light to germinate), negative photoblastic (require darkness) and neutral photoblastic (neutral to light) ([Baskin and Baskin, 2014](#page--1-0)). Several theoretical models and empirical studies have reported that smaller seeds tend to be positively photoblastic and to form persistent seed bank, their germination is independent of light, and they produce a short-lived seed bank ([Venable and Brown, 1988; Milberg et al., 2000](#page--1-0)). The importance of light for small seeds buried in the soil is to help them recognize their position near the soil surface [\(Milberg et al., 2000\)](#page--1-0). Exposure of small seeds to light initiates the germination process, provided that all other conditions for seedling survival are available [\(Baskin](#page--1-0) [and Baskin, 1988; Milberg et al., 2000\)](#page--1-0). Such a light sensing mechanism is to avoid germination in deep soil, where emerged seedlings would deplete seed nutrients before reaching light for photosynthesis [\(Bewley and Black, 1994; Pons, 1992\)](#page--1-0). As the physiologically and ecologically effective light rarely penetrates more than 4-5 mm through the soil [\(Tester and Morris, 1987\)](#page--1-0), germination is expected to commence at that shallower depth for both neutral and positive photoblastic seeds.

Germination responses of light depend on habitat type. In environments where seeds are likely to be buried within the soil, covered with litter or present under the shade of nurse plants, light can be an important factor determining safer sites that enhance seedling establishment after germination ([Fowler, 1988\)](#page--1-0). In dense forest, for example, light requirement is recognized as a gapdetection mechanism to avoid germination in sites hinder seedling establishment, such as shaded environments under tree canopies or beneath accumulated litter ([Khurana and Singh, 2001\)](#page--1-0). However, in arid deserts that have sparse vegetation, the light effect might not be an important factor for determining germination. For example, [Flores et al. \(2016\)](#page--1-0) assessed seed photosensitivity for 12 desert species from the Southern Chihuahuan Desert and found that all species were neutral photoblastic. In addition, the author assessed the light requirements for seed germination of 16 perennial grasses of the Arabian deserts and found all of them also neutrally photoblastic [\(El-Keblawy, unpublished data, 2017](#page--1-0)b). However, little information is available about the role of light, as an environmental signal, in regulating germination of annual grasses of the arid deserts. In addition, little is known about the interaction between the light and temperatures in regulating germination in arid desert grasses.

Theoretical models and empirical data have reported that annual plants in unpredictable environments, such as arid deserts, have higher temporal variation in reproductive success and both higher dormancy and small seeds. Conversely, perennials have lower temporal variance in reproductive success and produce large seeds that are characterized by low dormancy ([Venable and Brown,](#page--1-0) [1988; Gremer and Venable, 2014\)](#page--1-0). In disturbed, but more predictable environment, however, selection favors less dispersal, and less dormancy follows because most seeds are in reliably favourable sites [\(Venable and Brown, 1988\)](#page--1-0). The aim of this study was to assess the effect of light and temperature and their interaction on germination of eight grasses from the arid environments of the United Arab Emirates (UAE). Four of the species grow naturally in highly heterogeneous, unpredictable sandy deserts (Aristida abnormis, A. adscensionis, Eragrostis ciliaris and Coelachyrum

brevifolium) and the other four are weeds of predictable environments of frequent, regular large-scale disturbed farms or road sides (Chloris virgata, Dactyloctenium aegyptium, Eragrostis barrelieri and E. papposa). Two species of the first group and one of the second have specialized structures for spatial dispersal, but the other five do not have such structures. In addition, there are big variations in seed masses and sizes among the selected species. I tested the hypothesis that annual grasses from more highly unpredictable and heterogeneous desert environments produce seeds with high dormancy, compared with those from more predictable, but disturbed, farms. Different light requirements is expected for seeds from natural deserts and those of disturbed farms; more light is expected to be needed for the germination of seeds of disturbed farms (i.e., their seeds are strong positive photoblastic), compared with seeds of natural deserts.

2. Materials and methods

2.1. Seed collection and variation in life history and seed traits

Mature seeds of eight annual grasses were collected during May-June 2013 from different locations in the Northern Emirates of the UAE; four from natural sandy deserts and the other four from disturbed habitats (farms and roadsides) ([Table 1](#page--1-0)). Seeds of each species were collected from 50 to 60 randomly chosen plants and mixed together in order to represent the genetic diversity of the populations of the studied grasses. Yellowish colored spikes were collected to ensure that collected caryopsis were fully ripened. Immediately after collection, spikes were air dried and threshed to separate caryopses (hereafter termed seeds) by using a hand-made rubber thresher. Seeds were cleaned from the surrounding structures and debris and stored in brown paper bags at room temperature until their use in the germination experiment in January 2014. For each tested species, the average seed mass was determined by weighing three replicates, each of 100 seeds. In addition, average seed size of each species was assessed by measuring the length of 50 seeds.

2.2. Germination experiment

Seeds of each species were germinated in three programmed incubators adjusted at daily night/day temperature regimes of 15/ 25 °C, 20/30 °C and 25/35 °C in both continuous darkness and alternating 12 h light/12 h darkness. The light period coincided with the higher temperature. In dark treatment, the Petri-dishes were wrapped in aluminium foil to prevent any exposure to light. The germination was conducted in 9-cm tight-fitting Petri-dishes containing one disk of Whatman No. 1 filter paper moistened with 10 ml of distilled water. Four replicates, each with 25 seeds, were used for each treatment. Seeds were considered to be germinated with the emergence of the radicle. Germinated seeds were counted and removed every alternate day for 20 days. However, seeds incubated in the dark were checked only after 20 days. Therefore, they were not exposed to any light during the incubation period.

2.3. Data analyses

Rate of germination was calculated with a modified Timson's germination velocity index: Σ G/T, where G is the percentage of seed germinated on every alternate day, and T is the total germination period. The maximum possible value for our data using this germination rate index (GRI) was 50. The higher the value the more rapid the germination. The GRI was only calculated for seeds incubated under light conditions.

Two-way ANOVAs were performed to assess the effects of light

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