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Seed germination in *Launaea arborescens*: a continuously flowering semi-desert shrub

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Achenes (seeds) of the perennial shrub *Launaea arborescens* (Asteraceae) germinated under a wide range of environmental conditions. None of the seeds were dormant, nor was there any evidence that dormancy could be induced. Apparently, this semi-desert species has no means of preventing immediate germination. Achenes are produced and dispersed throughout the year, and we suggest that the timing of germination is regulated by the duration and degree of wetting and the presence of moderate soil temperatures. This germination behaviour suggests that there is no mechanism by which the germination of seeds formed one year can be delayed until subsequent years. By contrast, most desert plants accumulate persistent seed banks. The germination strategy of *L. arborescens* must be considered opportunistic, and we suggest that the survival of populations is ensured by other life history traits like continuous iteroparity and effective dispersal by wind.

Keywords: *Launaea arborescens*; germination; seed dormancy; continuous iteroparity; Asteraceae

Introduction

Continuous iteroparity, i.e. when flowering occurs throughout the year, is a widespread plant trait in humid tropical regions (e.g. Knapp, 1973). In seasonal environments, however, where water availability or temperature restricts the length or timing of the growth period, it is a much rarer phenomenon. For example, in the Province of Almeria in SE Spain, only 1·3% of the native and naturalized flora for which data on flower phenology (2470 taxa) are available can be found flowering throughout the year (Sagredo, 1987). Many of these species are short-lived ruderals, and nine species are dwarf-shrubs or shrubs.

One consequence of such a life history is that seeds are dispersed, or available for

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dispersal, throughout the year. Furthermore, in seasonal environments, the dispersed seeds can face drastically different conditions depending on when seed production occurs. Most such conditions will be suboptimal for seedling establishment and survival. Based on this reasoning, one could assume that it would be advantageous for continuously iteroparous species in seasonal regions to have a dormancy mechanism allowing germination to be delayed until conditions are favourable. That this assumption is valid is supported by documented differences in dormancy characteristics related to the timing of seed production (e.g. Hacker, 1984; Fenner, 1991; Gutterman, 1993).

This was the starting point for our investigation into the germination ecology of *Launaea arborescens* (Batt.) Murb. (Asteraceae), a continuously iteroparous, semi-desert shrub. Our main questions were: (i) Are the seeds dormant at dispersal? (ii) Do seeds differ in dormancy depending on when during the year they are produced? (iii) Are there differences in dormancy between seeds produced in different years? (iv) Are there any moisture-, light- or temperature-mediated mechanisms preventing germination under unfavourable conditions?

Materials and methods

Natural history of the species

Launaea arborescens is an almost leafless, xerophilous, perennial shrub reaching a height of 50–150 cm (Sagredo, 1987). It occurs in matorrals and on the banks and bottoms of temporary streams and often grows on extreme soils. The species has a semi-ruderal character and often rapidly recolonizes stream beds and abandoned fields (Freitag, 1971; pers. obs.).

Abundant flowering occurs from May to August, but flowers and achenes (hereafter called seeds) are produced throughout the year (Sagredo, 1987). Seed production is substantial, although the percentage of filled fruits varies from 60–90%. Seeds are black, 3–4 mm long and 0·6–1·0 mm wide, and have an average weight of 1·1 mg. They have a well developed pappus and are readily dispersed by wind.

Launaea arborescens is a Saharo-Canarian phytogeographical element but is also indigenous to the semi-desert of south-eastern Spain. Here, its distribution is restricted to the frost-free coastal area of the Almeria Province where annual precipitation is less than 400 mm (Freitag, 1971).

The collection site (02°20' E, 36°51' N; 20 m elevation) is close to Cabo de Gata, where the mean annual precipitation is 178 mm (period 1950–74) of which 79% falls from October to March. The variation in amount of rainfall among years can be considerable. The mean annual temperature is 18·1°C, with an absolute minimum air temperature above 0°C (Capel Molina, 1977). Of the years encompassed by this study, precipitations were 269 mm in 1992, 217 mm in 1993, 189 mm in 1994 and in 1995, 66 mm until September.

Collection and storage

Seeds were collected in the same area, from at least 50 individual shrubs in the second half of December during 3 consecutive years (1992–95). In the last year of this study, seeds were collected in December 1994 and in March and June 1995. Seeds were stored in paper bags in the laboratory at approximately 20°C and *c*. 50% air humidity until used.

Germination conditions

Germination tests at constant temperatures were carried out in incubators (Rubarth Apparatebau, Hannover, Germany). Each experiment consisted of three replicate Petri dishes (9 cm in diameter) with at least 50 viable seeds (pappus not removed). In dark treatments, the Petri dishes were wrapped in aluminium foil and stored in light-impermeable boxes in the incubators. Two experiments, i.e. germination at alternating temperatures and after warm stratification, were conducted in a thermo-gradient bar-incubator (described in detail by Ekstam & Bengtsson, 1993). Seeds were placed on strips of filter paper (Schleicher & Schüll, no. 595), wetted with deionized water, at locations in the incubator representing different temperature regimes. For each experiment, three batches of at least 50 viable seeds were placed at locations in the incubator representing the same temperature regime (replicates). Darkness was achieved by covering the transparent bar lids with light-impermeable, black tissue paper. Both types of incubators were equipped with a warm white light source providing 20–30 μmol $s^{-1}m^{-2}$ at seed level.

Germinated seeds were counted and removed daily or every second day in the light treatments and at the end of the experiment in dark treatments. A seed was considered to have germinated if its radicle had elongated. Viability of ungerminated seeds was determined after removing the seed coat. If the embryo was white and firm it was considered to be viable. Percentage germination was calculated excluding dead seeds. Before applying a one-way ANOVA, followed by the Tukey Honestly Significant Difference Test (HSD), germination percentages were arcsine transformed.

Temperature requirements

The first experiment was conducted to test germination at different constant temperatures: 3, 7, 10, 15, 20, 25, 30 and 35°C. In the second experiment the effect of diurnally fluctuating temperature (± 5°C) at different mean temperatures was tested: 7, 10, 15, 20, 25 and 30°C. In this experiment, maximum and minimum temperatures were maintained for 6 h each, with heating and cooling periods having the same duration. Both experiments were carried out with seeds that had been collected in 1993 and then kept in dry storage for 3 months.

Comparison of seeds produced in different seasons and years

Seeds collected in December in 3 consecutive years and dry-stored for 1–3 months were tested at three or four constant temperatures: 7, 10, 15 and 25°C. Seeds collected in December 1994 and in March, June and October 1995 were compared (only two replicates used for the June collection owing to a shortage of viable seeds) at constant temperatures of 15 and 25°C.

Changes during dry storage

To determine whether there had been an increase in dormancy during dry storage, seeds collected in December 1992 were tested after 2 and 50 months in the light at 7, 15 and 25°C.

Response to different photon fluence rates

The response of seeds, collected in March 1995 and dry-stored for 6–7 months, to high photon fluence rates was tested in a climate chamber. Seeds were placed at two different distances from two mercury lamps (Osram 'Power Star' HQI-T 400 Watt 'daylight') resulting in 400 and 1000 μmol $s^{-1}m^{-2}$ at seed level. Light was provided for 12 h per day. Seeds were put on filter paper placed on floating polyethylene granules in open dishes (9 cm diameter) with perforated bottoms. The dishes were floating in a tank containing water. The temperature at dish level fluctuated between 20 and 26°C. Germination was monitored for 14 days.

Germination after warm stratification

To ascertain whether a wet and warm stratification would have any effect on germinability, seeds were kept at 27, 33, 37 and 40°C, in both light and darkness, in the thermo-gradient bar-incubator. After 8 days seeds were transferred to lower temperatures (18–20°C). Germination was monitored for 20 days.

Germination after cold stratification

The effect of a cold-wet stratification was assessed by placing seeds on wet filter paper in Petri dishes that were then stored in a refrigerator at 1·5°C. After 1, 2, 4 and 8 weeks at 1·5°C the Petri dishes were exposed to a constant temperature of 10, 15 and 25°C (three replicates each) in the light. First, however, seeds that had germinated in the refrigerator were counted and removed.

Duration of wetting required for germination and repeated dessication

The aim of this experiment was to find out if short periods of wetting, 12–62 h, were sufficient to initiate germination. Seeds collected in March 1995 and dry-stored for 7 months were put on sandy soil, originating from the collection site, in transparent plastic dishes with airtight lids. Each dish contained 115·0 g of sand and had been supplied with 25·0 ml of deionized water. The dishes were kept at 6 ± 1°C for 5, 13, 24, 40 or 62 h, after which the lids were removed and the dishes transferred to 25°C and 60% relative humidity. In this environment, the substrate lost most of its water within 20 h. Germination was recorded for 3 days.

Since there was no germination at all, probably because the soil dried out too quickly (within 20 h), all dishes were reallocated to new treatments. This time, after the soil had dried out completely in all dishes, the soil was wetted with 20·0 ml of water and the dishes were sealed with a lid. The lid was removed from three dishes after 12 h, and again after 24, 36, 48 and 62 h. Germination was recorded immediately after removing lids as well as after 12 and 24 h, by which time the dishes had dried up again.

To determine whether repeated desiccation of seeds could induce dormancy, the dishes were allowed to dry out again for 3 days and then rewetted with 20·0 ml of water. The dishes were kept closed, until no more seeds germinated. After 10 days ungerminated seeds were examined for viability and counted.

Osmotic potentials required for germination

Germination percentage was measured at various osmotic potentials at 25°C. The

osmotic potentials were obtained with polyethylene glycol 400 (PEG). The different potentials were adjusted with a freezing-point osmometer (Osmomat 030-D, Gonotec GmbH, Germany). This test was terminated after 3 weeks.

Outdoor emergence of freshly matured seeds and dry stored seeds

In the first experiment, freshly matured seeds were sown immediately after collection near the collection site. Batches of seeds were sown in pots and placed outdoors in a location that was not exposed to full sunlight. Half of the pots were covered light-tight with two layers of aluminium foil. The air temperature near the pots was monitored daily with a minimum–maximum thermometer.

In the second experiment, seeds were sown on 5 July 1995 in an experimental garden in Kiel during a spell of dry, warm weather. Half of the pots were placed under a dense leaf canopy, while the others were on a tray exposed to the sun. The soil surface temperature in one pot was monitored every 30 min with a sensor (Pt 100) connected to a data-logger (Squirrel 1200, Grant Instruments, Cambridge, Great Britain). Light was measured with a Licor quantum sensor at noon on a clear day and on an overcast day.

In both experiments six batches of 50 seeds were sown in plastic pots (8 cm diameter) filled with a sandy soil. The pots were placed outdoors in trays with a 2 cm layer of water. The trays were covered with fine-mesh nylon. Emerging seedling were counted and removed every second day until germination had ceased (the count for the dark treatment in the first experiment was made after 14 days).

Results

Temperature requirements

Seeds of *Launaea arborescens* germinated over a wide temperature range, i.e. from 1·5 to 30°C. However, germination was reduced at higher temperatures and in darkness, and at the highest temperatures tested little germination occurred (Fig. 1). Fluctuating temperatures did not stimulate germination. Instead, germination percentages were reduced at higher mean temperatures, probably because the seeds were exposed to high, inhibitory temperatures for part of the day. Germination proceeded quickest at 15–30°C, was somewhat slower at higher temperatures and was much slower at temperatures below 10°C (Table 1).

Comparison of seeds produced in different seasons and years

Generally, the seed batches collected in the 3 consecutive years of the study showed full germinaton at all temperatures tested. However, germination at 25°C in darkness was somewhat lower for seeds collected in March and June (85·5 and 90·3%, respectively) than for those collected in autumn and winter.

Changes during dry storage

After 50 months of dry storage, seeds still showed 100% germination at all three temperatures tested (7, 15 and 25°C).

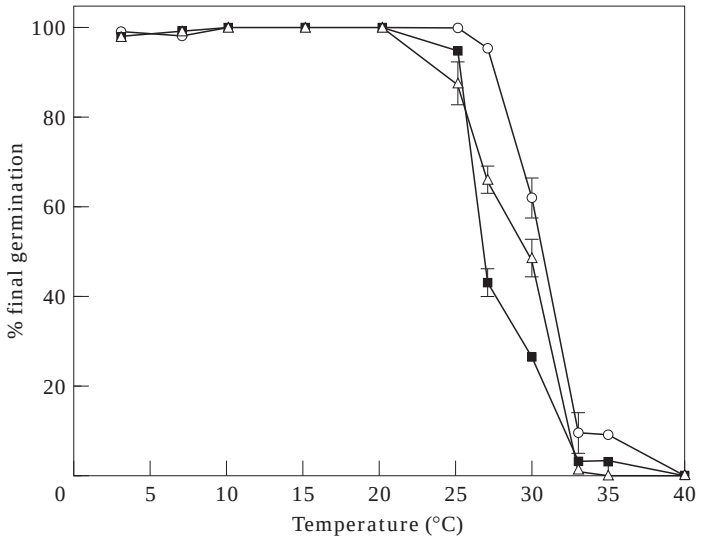

Figure 1. Mean germination percentages (± SE, given if > 3) of seeds of *Launaea arborescens* at different constant and daily fluctuating temperatures (amplitude 10°C). (○) = light, constant temperature; (■) = dark, constant temperature; (△) = light, fluctuating temperature.

Response to different photon fluence rates

Germination was not inhibited at 400 μmol $s^{-1}m^{-2}$, as indicated by the fact that all seeds germinated within 7 days. By contrast, at 1000 μmol $s^{-1}m^{-2}$ only 44·5% (± 1·5 SE) had germinated after 14 days.

Germination after warm stratification

Seeds stratified at 27, 33 and 37°C germinated without delay when transferred to lower temperatures. However, only a few seeds stratified at 40°C germinated. The remainder were heavily overgrown with mould and were considered dead since the embryo had become soft and slightly darker. Since all seeds died in a preliminary experiment in which seeds had been exposed to both high light intensities (1000 μmol $s^{-1}m^{-2}$) and high temperatures (40°/20°C) but were not overgrown by mould, we conclude that the high temperature caused most of the mortality.

Table 1. *Onset of germination, i.e. number of days until the first seed germinates, and number of days to 50% of final germination percentage (t_{50}) of* Launaea arborescens *seeds at different temperatures*

	Temperature (°C)								
	3	7	10	15	20	25	30	33	35
Onset	11	7	5	2	2	2	3	4	4
t_{50}	23	10	6	3	3	3	3	4	6

Table 2. *Germination percentages of* Launaea arborescens *after different time periods of wetting at 25°C. Means followed by the same latter are not significantly different at the 5% level (ANOVA, followed by a Tukey HSD test)*

Hours after imbibition	12	24	36	48	62
Final germination (%)	8·5a	18·0a	46·1b	64·0b	76·5b

Germination after cold stratification

Seeds exposed to a constant temperature of 10, 15 or 25°C after 1, 2 and 4 weeks of cold-wet stratification at 1·5°C germinated almost completely at all temperatures. After 6 weeks of stratification, 96·7% of the seeds had germinated during the period of stratification.

Duration of wetting required for germination and repeated dessication

In our first experimental design, no seeds germinated, probably because the soil dried up very quickly. However, a 12-h period during which the soil was constantly wet was sufficient to trigger germination in a few seeds (Table 2). Most germination took place during the moist period, with little germination occurring in the following dry period. In this experiment, no delay or inhibition of germination occurred after drying out the soils. When rewetted and kept wet after the end of the experiment, seeds germinated completely within 8 days.

Osmotic potentials required for germination

Seeds imbibed in PEG solutions of different strengths showed a sharp decline in final germination percentage at osmotic potentials ≥ 0·5 MPa (Table 3). When wetted with distilled water, seeds in all treatments germinated if they had first been washed in tap water and transferred to Petri dishes.

Outdoor emergence of freshly matured seeds and dry stored seeds

Seeds sown immediately after harvest in Spain in December 1994 germinated completely within 2 weeks in light as well as in darkness. Mean daily minimum and maximum temperature during this period was 6·4°C and 22·2°C, respectively. In the second experiment, conducted in Germany, 96% of the seeds had germinated within 19 days, with a slight delay in the sun-exposed pots. The average temperature on the soil surface was 16·3°C in the shade and 19·6°C in the sun, whereas mean daily

Table 3. *Germination percentages of seeds of* Launaea arborescens *imbibed in PEG solutions of different strength (Ψ_s). Means followed by the same letter are not significantly different at the 5% level (ANOVA, followed by a Tukey HSD test)*

Ψ_s (MPa)	0	–0·25	–0·5	–0·75	–1
Final germination (%)	100a	76·9b	12·4c	7·7c	0·0d

maximum temperatures were 18·7 and 30·8°C, respectively. No ungerminated, viable seeds were found in any of the experiments.

The experiment in Germany compared germination in an exposed site with that under a leaf canopy. The exposed pots received 1050–1230 μmol $s^{-1}m^{-2}$ at noon on the clear day and 300–800 μmol $s^{-1}m^{-2}$ on the overcast day. The photon fluence rate in the shade was 4–5% of that in the sun.

Discussion

Seeds of *Launaea arborescens* appear to be constantly ready to germinate. Germination was complete in seeds sown directly after harvest, and none of our treatments induced a secondary dormancy. Nor did germination traits common in temperate species, such as the stimulatory effect of alternating temperatures and inhibition by leaf canopy (Baskin & Baskin, 1985, 1988), affect the germination of *L. arborescens*. Furthermore, there were no detectable differences in dormancy level between years. The ability to achieve full germination (90–100%) within a short period at a wide range of temperatures as well as in light and darkness seems to be rare in desert plants. Instead, the seeds of most Mediterranean and desert species have dormancy characteristics or structural properties that prevent immediate germination of at least a proportion of the seeds (Koller, 1956, 1957; Mott, 1972; Thanos *et al.*, 1989, 1991; Jurado & Westoby, 1992; Gutterman, 1993, 1994; Bell *et al.*, 1995). The ability of a considerable fraction of seeds not to germinate ensures the buildup and persistence of a soil seed bank which is considered vital for species in unpredictable environments (e.g. Venable & Lawlor, 1980). In a survey including 105 central Australian species, Jurado & Westoby (1992) found that for 103 of them, at least 20% of their seeds were still ungerminated after 10 days. Since seeds of all tested species were afterripened in their survey, the dormant fraction of fresh matured seeds is probably much higher in many species. In a study of numerous desert species, Gutterman (1993, 1994) reported that *Blepharis* spp. was the only species showing full germination over a temperature range comparable in width to that of *L. arborescens*. In *Blepharis* spp., however, seeds are retained on the mother plant and dispersed over a longer period which ensures the carry-over of seeds between rainfall events. Non-dormant seeds are also found in some species of *Atriplex*, but they are prevented from germinating by high contents of germination-inhibiting chloride in the bracteols (Beadle, 1952).

The time needed for the onset of germination under moist conditions in desert plants varies from 29 min in *Salsola kali* L. (Wallace *et al.*, 1968) to as long as 16 days in *Seriphidium sieberi* (Besser) Bremer & Humphy syn. *Artemisia sieberi* Besser (Gutterman, 1993). A 16-day imbibition period is relatively long for desert species, which are expected to germinate faster than those in moist habitats owing to the short periods of water availability. Therefore, conditions allowing germination of *S. sieberi* are only met once every several years, after a series of abundant rainfalls, whereas *S. kali* has the potential to germinate after one small rainfall event (Guttermann, 1993). The fact that *L. arborescens* seeds need 2–3 days between seed wetting and the onset of germination, as well as relatively wet soils with low osmotic strengths, suggests that low amounts of rainfall would do little to enhance germination, especially at high temperatures and in soils which dry up quickly. At intermediate levels of osmotic strength in the range of 0·5–1 MPa, Mediterranean and desert species (Batanouny & Ziegler, 1971; Thanos *et al.*, 1989) as well as many temperate species (Pons, 1986; Evans & Etherington, 1990; Schütz, unpublished data) have germination percentages higher than those of *L. arborescens*. However, several rainfall events or a single heavy rainfall causing intensive wetting of the soil may trigger a majority of *L. arborescens* seeds to germinate under natural conditions. In the area over which this species is distributed, wet soil conditions occur almost exclusively from October–April,

coinciding with relatively low temperatures and low light intensities, which both promote germination in *L. arborescens* seeds.

The germination of *L. arborescens* was strongly reduced after being exposed to high temperatures, high irradiance and wet conditions over several days. However, such conditions are not likely to occur together in the field, not even in deserts receiving summer rains, since warm soils dry up quickly (Gutterman, 1993).

Therefore, of the 12 mechanisms by which the germination of desert plants can be triggered according to Gutterman (1994), the duration of the wetting period seems to be the only one effectively regulating the germination of *L. arborescens* in the field. By contrast, other factors are relatively unimportant. The fact that only a fraction of the seeds germinated in the treatments with short wetting time suggests that this trait reduces the risk of seedling mortality to a certain extent. It could thereby function as a mechanism for carrying over seeds from one rain event to the next but probably not from one season to the next.

Furthermore, since *L. arborescens* has the potential to germinate throughout the year, it does not fit into the summer or winter desert floras described by Went (1948, 1949) based on their germination responses to temperature.

Due to its curious habit of producing and dispersing seeds throughout the year, *L. arborescens* does not fit into present groupings of desert plants, e.g. the five groups distinguished by Gutterman (1993) based on the timing of maturation, timing of dispersal and dispersal strategies. Nevertheless, *L. arborescens* can be characterized as using an opportunistic strategy for seed regeneration (continuous production of effectively wind-dispersed seeds) but a cautious strategy for vegetative survival (perennial shrub). Its opportunistic strategy is also reflected in its ability to recolonise temporary stream beds after heavy rains as well as its ability to colonise abandoned arable fields and waste lands (pers. obs.; Freitag, 1971).

Silvertown (1984) suggested that in unpredictable environments, dormancy, perenniality, dispersal and iteroparity are four means by which a species can successfully persist. They represent different means of escaping unfavourable conditions, either in time or space. As demonstrated by *L. arborescens*, species living in a fluctuating environment can effectively survive and spread by combining continuous iteroparity with the production of wind-dispersed seeds, even if they lack a long-lived seed bank.

The lack of dormancy makes it impossible to integrate *L. arborescens* in a scheme of various dormancy response patterns applied by Baskin *et al.* (1993, 1994) on 40 North American Asteraceae. This species showed different degrees of primary dormancy and gained the ability to germinate over a wider temperature range during afterripening. Baskin & Baskin concluded that climate is more important than the type of life cycle in determining the type of germination response pattern, since germination behaviour was strongly coupled to the climatic conditions of the place of origin of the species rather than to life cycle traits. However, the investigated species receive at least twice as much rainfall at their collection sites (Baskin *et al.*, 1993), and none of them is continuously iteroparous. Life cycle properties might be more important in determining the germination behaviour of Asteraceae occuring in arid environments than in humid or semi-humid environments.

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