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Improving seed germination of native species for camel rangeland restoration: effects of cold stratification and temperature

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33 **Running title**

34 Germination of Saharan native plants

35 **Data availability statement**

36 The data that support the findings will be available in Zenodo at [<https://zenodo.org>]
37 following a [6 month] embargo from the date of publication.

Improving seed germination of native species for camel rangeland restoration: effects of cold stratification and temperature

Native plants of the Sahara are remarkably resistant to prolonged droughts and are important sources of forage, food, and medicine. Their regeneration from seeds after strong anthropogenic disturbances is a challenging step toward their conservation and to mitigate desertification. We studied the germination responses of 43 dominant native species of the Sahara desert that could be propagated from seeds for future ecological restoration projects, exploring the effects of cold stratification and temperatures on seed germination. Seeds were stratified at 4°C for 3 days and then tested for germination at 5, 10, 15, 20, 25, 30, 35, and 40°C. While cold stratification negatively affected four species, it improved the germination of 36 species. Five of these species required cold stratification to germinate. Temperatures during the germination trial significantly influenced seed germinability. Twenty-three species (54%) germinated to higher percentages at intermediate temperatures (20 to 30°C) similar to the maximum temperatures of the rainiest months, when germination in the field is high. Thirteen species (30%) also germinated at a higher temperature (40°C). Seven species (16%) germinated best at low temperatures (5 to 10°C). Our results suggest that cold stratification is an efficient and easy treatment to apply prior to sowing seeds in the field for restoration.

Keywords: native plants; camel rangelands; ecological restoration; Sahara desert; seed germination; seed dormancy.

African Plant Database (version 3.4.0). Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria, from <http://africanplantdatabase.ch>

Introduction

Desertification is a gradual process of soil and vegetation degradation, often attributable to climate change and/or to direct human activities such as overgrazing and deforestation. Desertification threatens biodiversity and the survival of human populations, and is considered one of the environmental issues of greatest concern for the twenty-first century. The United Nations has set up a Convention to Combat Desertification (UNCCD), one of whose objectives is mitigating drought effects by restoring degraded land (UNCCD 2014).

Ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed (Gann et al. 2019). To improve degraded areas and fight against desertification, vegetation cover can be increased by sowing or planting a local and diversified set of species adapted to an arid climate (Toumi et al. 2017). Moreover, a pre-requisite for all ecological restoration projects is the use of native species (Gann et al. 2019), which requires accurate information on plant establishment and growth conditions, starting with seed germination.

Restoration success fundamentally depends on knowledge of seed biology, seeds being the primary tool for plant reintroductions (Gann et al. 2019). However, seeds are not always available and there is often a lack of information on the conditions required for germination and seedling establishment (Broadhurst et al. 2008; Dayrell et al. 2016). Seed germination is a crucial stage in the life cycle of plants, enabling the establishment of new individuals (Bewley and Black 1982; Baskin and Baskin 2014; Gurvich et al. 2017; Penfield 2017). In desert environments, temperature is a key factor in seed germination (Flores and Briones 2001; Pérez-Sánchez et al. 2011; Baskin and Baskin 2014; Gurvich et al. 2017). It affects, mainly or incidentally, dormancy-break and germination percentage (Baskin and Baskin 2014; Gurvich et al. 2017; Fallahi et al.

2017; Ostadian Bidgoly et al. 2018). Seed dormancy, defined as the inability of seeds to germinate under apparently favorable conditions, helps limit seed germination in a given habitat to the most appropriate time for seedling survival and plant development. At maturity, the seeds of most Mediterranean and desert species are dormant, which prevents germination immediately after dispersal (Schütz and Milberg 1997) and thus allows for unpredictable rainfall events. Naturally, dormancy-break occurs either *via* dry ripening at high summer temperatures or during cold (moist) stratification in winter, depending on the species and its life cycle. Temperature is therefore a major factor controlling dormancy-break. After dormancy is broken, temperature is also important in determining when seeds germinate, provided that the soil is moist. If seeds become non-dormant during the winter, they germinate in spring, which in desert areas is a time when rain is likely. Knowing seed requirements for germination is therefore essential to making optimal use of this important resource. This applies particularly to the seeds of unstudied species, such as a wide range of desert and Saharan species.

The North Saharan xeric steppe and woodland ecoregion acts as a transition zone between the North African Mediterranean ecosystems and the Sahara desert (Naia and Brito 2021). In Algeria, the largest country in Africa (2 381 741 km²), the various Saharan ecoregions occupy about 4/5 (2 000 000 km²) of the country. Among the main native ecosystems are open camel rangelands composed of native vegetation. When well-conserved, these rangelands are characterized by a great diversity of native Saharan plants, many endemic (Quézel and Santa 1962-1963; Ozenda 2004; Chehma 2006), which are used as medicines and nutritive fodder (Abdelguerfi 2004; Chehma 2005; Senoussi and Bensemaoune 2011; Baameur et al. 2015; Telli et al. 2016). In this area, the risk of desertification comes from drought combined with anthropogenic activities, such as overgrazing, clearing of rangelands, and the installation of cereal

center-pivot irrigation plots (Marfoua et al. 2010; Eddoud et al. 2018), all of which put certain plant species at risk of disappearing (Ayyad 2003; Darkoh 2003).

In the Saharan regions, there are few reliable data on the recovery of natural ecosystems after degradation (Aronson et al. 1993a; Aronson et al. 1993b). After overgrazing, arid and semi-arid rangelands may not recover for several years post-fencing against livestock (Kassahun et al. 2009). In situations where the degradation of rangelands has reached an irreversibility threshold and where resilience is no longer possible (e.g. after cereal cultivation), restoration actions *via* seeding or planting are necessary. Most attempts to seed rangelands with introduced herbaceous species and exotic shrubs have failed due to poor adaptation of these species to local environmental conditions (Ben Salem et al. 2008).

Because the restoration needs in this region are huge and urgent, research on the seed biology of native species is vital: their phenology, development, maturation, viability, and dormancy need to be explored to optimize restoration outcomes (Merritt and Dixon 2011). This study sought to define the germination ecology of 43 Saharan dominant native plant species from open camel rangelands, aiming to improve germination rates for future restoration projects in the northern Algerian desert. We focused on determining the effects of cold stratification and incubation temperature on these species' seed germination.

Material and methods

Study area

Our study area was located in Ouargla province in the Northeastern Algerian Sahara (Figure 1). Camel rangelands in the area are characterized by large areas of sand called *Oriental Ergs*, *Hamadas* (rocky plateaus), *Regs* (gravel zone), depressions (*Daya*, *wadi*

beds, Sebkha and Chott), and valleys (fossil valley from Oued Mya and Oued Righ Valley) (Ozenda 2004).

To characterize the climate of the study area, we selected a reference station (#31750: 31°41'28.321" N, 5°0'0" E) providing data over a 35-year period from 1979 to 2014 (Table 1). Temperatures are very high in summer (June to August in the range of 30.8°C and 32.5°C, respectively). The monthly average of the hottest month (July) is 33.0°C while that of the coldest month (January) is 10.67°C. The thermal amplitude between January and July is 37.3°C. Annual total precipitation is 59.2 mm. Most of the precipitation occurs from January to March, varying between 0.1 mm and 10.6 mm (February is the wettest month and July the driest) (Global Weather Data 2018).

Seed collection

We gathered seeds of 43 native species dominant in camel rangelands of the study area (Table 1) along three transects (Figure 1). The species included 18 families and 38 genera. The predominant families were Asteraceae (six species), Amaranthaceae, Brassicaceae, Fabaceae (five species each) and Poaceae (four species). Three species belonged to the Caryophyllaceae family and two species to Apiaceae, Boraginaceae and Zygophyllaceae. Only one species each belonged to Asclepiadaceae, Asphodelaceae, Cistaceae, Cleomaceae, Euphorbiaceae, Geraniaceae, Neuradaceae, Plantaginaceae and Plumbaginaceae.

Mature fruits containing seeds were gathered at random from 5-10 mother plants of each species with pruning shears and placed in paper bags. Each sample was labeled with the site, the name of the species, the date and place of harvest (*Oueds, Erg*, etc.). Species identification was performed using floras, namely Quézel and Santa (1962-1963), Ozenda (2004) and Danin and Fragman-Sapir (2022).

The seeds were transported to the laboratory and stored under ambient laboratory conditions (18–30 °C, 20–30% relative humidity) until used. Germination tests were conducted during the month following the gathering. For *Atriplex dimorphostegia*, since each plant carries several types of seeds with different dormancy (Sukhorukov 2007), we used humped seeds (*sensu* Koller 1957) after removing the bracts.

Classification according to seed dormancy

We classified 43 species according to Baskin and Baskin (2004) in different seed dormancy classes based on a literature search, as follows: Non-Dormant, Morphological Dormancy, Morphophysiological Dormancy, Physiological Dormancy, Physical Dormancy, Combinational Dormancy. When we could not find a species, we looked at other species of the same genus (Table 3).

Germination trials

First, the seeds were cleaned of all impurities (plant debris, infected or empty seeds), either manually or using tweezers or, for very small seeds such as *Ifloga spicata* (Forssk.) Sch.Bip. (Asteraceae), using the binocular magnifier or the stereoscope. Then, the seeds were disinfected as per Ouhaddach et al. (2014), by soaking them in dilute sodium hypochlorite solution (10%) for 10 minutes then rinsing 3 times with distilled water to remove all traces of sodium hypochlorite. Seeds were checked to determine whether they contained any embryos.

To determine the effects of cold stratification on dormancy-break and germination, half the seeds were stratified at 4°C: they were placed on a wet substrate, i.e. filter paper moistened with water, in darkness, for three days. After this period of cold stratification, cold-treated seeds and control seeds (i.e. not subjected to a cold

stratification treatment) of the 43 species (Table 2) were placed in sterile Petri dishes, 90 mm in diameter and 15 mm in height, containing two layers of filter paper previously soaked in distilled water. There were 10 seeds / Petri dish and three repetitions. The seeds were incubated in phytotrons (SNIJDERS Labs Economic Lux Chamber VF 475, The Netherlands) in a growth chamber (Laboratory of Plant Physiology, University of Laghouat). The germination temperatures tested were: 5, 10, 15, 20, 25, 30, 35, or 40°C, with a photoperiod of 12/12 h regime. Germination was monitored daily for 8 weeks. Seeds were considered germinated when the seed radical (primary root) grew to 2 mm (Nin et al. 2017). The effect of each treatment (with or without cold stratification) on seed germination was measured as the seed Germination Percentage (GP %) (Ranal and Santana 2006; Ranal et al. 2009; Soltani et al. 2015). It was calculated according to the following formula (A):

$$\text{Germination Percentage in each Petri dish} = (\text{GS} / \text{TS}) * 100 \quad (\text{A})$$

Where: **GS** is the number of the Germinated Seeds; **TS** is the Total number of sown seeds = 10.

Statistical analyses

Seed germination was analyzed using Generalized Linear Models (GLM) fitted with a quasibinomial error distribution. The factors were “temperature” and “cold stratification”. Then pairwise comparisons were performed with a Tukey adjustment. All statistical analyses were performed using the R 3.6.0. statistical package (R Core Team 2020).

Results

Germination without cold stratification (control experiment)

Five out of the 43 species (12%, from five different families) did not germinate without cold stratification and eight species (19%) had a very low germination rate without cold stratification (Table 3). Twelve species (28%) displayed bell-shaped germination percentage curves with increasing temperature, germinating better at intermediate temperatures (between 15°C and 35°C depending on the species) (Figures 2 to 8). Seven species (16%) germinated better at lower temperatures (5°C to 20°C), while ten species (23%) germinated better at higher temperatures (30°C to 40°C) (Table 3).

Germination improved by cold stratification treatment

Overall, seed germination was significantly improved by cold stratification ($F=64.9$; $P<0.001^{***}$) and was best at between 20°C and 35°C ($F=52.0$; $P<0.001^{***}$) (Supporting information Figure S1). Cold stratification significantly increased the germination percentage of the 13 species that germinated <20% in the control experiment (Table 3) (Figure 2, 3). Among the five species that did not germinate without cold stratification, *Echium trygorrhizum*, *Fagonia glutinosa*, and *Neurada procumbens* had a better germination percentage at intermediate temperatures while *Pergularia tomentosa* and *Perralderia coronopifolia* germinated better at temperatures above 30°C (Figure 3). Among 13 species germinating <20%, eight (62%) had a significantly lower germination percentage at low (5, 10, 15°C) and very high (40°C) temperatures (Table 3; Figures 2, 3). Three species (*Foeniculum vulgare*, *Pergularia tomentosa*, and *Perralderia coronopifolia*) had a significantly lower germination percentage at low temperatures (5, 10, 15°C) but germinated well up to 40°C (Figures 2, 3). Finally, two Amaranthaceae species (*Agathophora alopecuroides* and *Cornulaca*

monacantha) germinated better at low temperatures (10°C to 15°C) (Figure 2).

Among the 30 species that germinated better under cold stratification (>20%; Table 3), the germination increase was significant for 23 species (77%; Figures 4 to 6). Eight (8) of these 23 species (35%) displayed bell-shaped germination percentage curves with increasing temperature, germinating best at intermediate temperatures (between 15°C and 35°C depending on the species) (Figures 4 to 6). Another eight species (e.g. *Eremobium aegyptiacum*, *Henophyton deserti*) showed significantly lower germination at low temperatures (5, 10, 15°C) and germinated well at a higher temperature (40°C) (Figures 4 to 6). Finally, six species (e.g. *Scorzonera laciniata*) germinated better at low temperatures (10°C to 15°C) (Figures 4 to 6).

Germination not improved by cold stratification treatment

Among the 30 best-germinating species (>20%; Table 3), cold stratification did not affect the germination of *Helianthemum lippii* and *Stipagrostis pungens* (Figure 8). It had mixed effects on *Asphodelus tenuifolius*, where germination percentage after cold stratification increased when incubated at 10°C and 25°C and reduced when incubated at 5°C and 30°C (Figure 8). Cold stratification reduced the germination rate of *Launaea nudicaulis* at 5°C and 25°C, of *Limoniastrum guyonianum* at between 5°C and 15°C (Figure 7), of *Erodium glaucophyllum* at 25°C, and of *Paronychia arabica* at 30°C (Figure 7). Overall, these four species germinated better at 25-30°C (Figure 7).

Discussion

Effect of cold stratification on seed germination

Cold stratification is known to break physiological dormancy, i.e. cold treatment increases the growth potential of the embryo, enabling it to push open the seed coat

(Baskin and Baskin 2014). In our study, the germination of some species with physiological dormancy appeared to be positively affected by cold stratification. Similar effects have been reported in the literature for *Atriplex dimorphostegia* (Koller 1957), *Peganum harmala* (Hammouda and Bakr 1969), and *Spergularia salina* (Bakker et al. 1985). Our results are also consistent with a study on *Peganum harmala* where dormancy was broken by cold stratification (Zhen et al. 2011). In addition, cold stratification has been found to have a positive effect on other species, likely because their seeds share the physiological dormancy documented for species of the same genera (Table 3): *Agathophora* (Khan et al. 2011), *Cleome* (Sen and Chatterji 1968; Hammouda and Bakr 1969; Cane 2008; Muasya et al. 2009; Baskin and Baskin 2014), *Echium* (Carqué-Álamo et al. 2003), *Euphorbia* (Baskin and Baskin 2014), *Fagonia* (Sen and Chatterji 1968; Hammouda and Bakr 1969), *Takhtajaniantha pusilla* (Tang et al. 2009), *Pergularia*, *Plantago* and *Sisymbrium* (Baskin and Baskin 2014). Physiological dormancy is also documented for the seeds of several *Stipagrostis* species, such as *Stipagrostis ciliata* (Neffati et al. 1996) and *Stipagrostis pennata* (Bahrani and Khartegh 2006). In our study, one *Stipagrostis* species, *Stipagrostis plumosa*, responded positively to cold stratification, indicating the physiological dormancy of its seeds, while *Stipagrostis pungens* was not affected. Finally, *Asphodelus tenuifolius* was little affected by cold stratification although this species was shown to have morpho-physiological dormancy (Koller 1957). Most of the species that we classified as having physiological dormancy in this study likely come into the non-deep physiological dormancy category, since our short cold-stratification treatment improved their germination (Baskin and Baskin 2004; Table 3).

Cold stratification can also make seeds with physical dormancy (i.e., a water-impermeable seed coat) sensitive to dormancy-break when temperatures increase in

spring (Van Assche et al. 2003). In our study, cold stratification positively affected the germination of one species with physical dormancy: *Argyrolobium uniflorum* (Neffati et al. 1996). A positive effect of cold stratification has previously been found for species whose seeds likely share the physical dormancy of other species of the same genera: *Astragalus* (Hammouda and Bakr 1969) and *Launaea* and *Scorzonera* (Baskin and Baskin 2014). Zhou et al. (2012) showed that cold stratification doubled the germination rate of *Astragalus mongholicus* seeds. In our study, *Helianthemum lippii*, with physical dormancy (Neffati et al. 1996), did not respond to cold stratification, consistent with the findings of Zaman et al. (2009). While several species of the genus *Erodium* are documented as showing physical dormancy (*E. boissieri*, *E. botrys*, *E. cicutarium*, *E. malachoides*, *E. moschatum*, *E. stephanium*; Baskin and Baskin 2014), *Erodium glaucophyllum* here responded negatively to cold stratification.

All the species classified as non-dormant (Table 3) responded positively to cold stratification. One species with morphological dormancy, *Foeniculum vulgare* (Thomas 1994), also responded positively to cold stratification, consistent with the study of Tahaei et al. (2016) where moist cold stratification at 4°C applied for 15 days improved germination.

Regarding the seven species in which cold stratification produced either a negative effect (*Erodium glaucophyllum*, *Launaea nudicaulis*, *Limoniastrum guyonianum*, *Paronychia arabica*), no effect (*Helianthemum lippii*, *Stipagrostis pungens*), or a mixed response (*Asphodelus tenuifolius*), we may have applied insufficiently cold temperatures for insufficiently long durations. Weather data show that the coldest winter months are December, January, and February. Each year on average during these 90 days, while there is less than one day when minimum temperatures are below 0°C, there are eleven days when minimum temperatures are

between 0°C and 2.99°C and twenty days when minimum temperatures are between 3°C and 4°C. It is therefore possible that colder temperatures or longer cold stratification treatment would yield better germination results.

Effect of temperatures on seed germination

In our study area, the rainy season ranges from January to March, accumulating in three months half the total annual rainfall (27.32 mm) (Table 1). During that rainy season, minimum temperatures range from 5.4°C to 10.2°C and maximum temperatures from 16°C to 23.9°C.

In this experiment, seven species germinated at relatively low temperatures. Three of them belong to the Amaranthaceae family, whose species have been shown to germinate fast to take advantage of temporarily favorable conditions for germination (Parsons 2012). *Scorzonera laciniata* and *Asphodelus tenuifolius* are eurymediterranean species (Eddoud et al. 2018), which may germinate at lower temperatures than most Saharan species. On the other hand, *Savignya parviflora* subsp. *longistyla* and *Plantago ciliata* are Saharo-Arabian species (Eddoud et al. 2018), meaning that they may germinate in the colder months (December through February; Table 1) better than most naturally co-occurring species, although this would need to be confirmed by further research.

Ten species germinated well at high temperatures (30, 35, 40°C). All these species, except *Foeniculum vulgare*, are Saharan or Saharo-Arabian species, most likely adapted to germination at high temperatures. These species may germinate outside the main rainy season, but this would need to be confirmed in the field. The months with maximum temperatures (between 30°C and 40°C) but still some rainfall are April, May, September, and October.

Finally, most of the species (17) germinated best at intermediate temperatures (between 20°C and 35°C, depending on species). This may be because these species' optimum germination temperatures coincide with the average rainy season temperatures of their local habitats (Gurvich et al. 2017), which in our study area range from 19.0°C to 23.9°C in February and March, respectively.

Conclusion

The timing of seed germination in the field determines the conditions to which seedlings will be exposed immediately after germination, thus strongly influencing the success of seedling establishment. This makes pre-treatments to overcome seed dormancy essential to the successful use of direct seeding in restoration projects. Our results demonstrate that cold stratification has a positive effect on the germination of more than 80% of the studied species. Thus, we recommend a cold stratification treatment prior to sowing, except for *Erodium glaucophyllum*, *Launaea nudicaulis*, *Limoniastrum guyonianum*, and *Paronychia arabica*. We acknowledge that programming seed sowing at optimal germination temperature, and thus at three different dates according to the three species groups identified (those germinating well at low, intermediate, or high temperatures), may not be practical. Nevertheless, studying germination in the field could confirm the benefits of such a protocol. An easier alternative would be to sow all species in January, so that the relatively short rainy season in the study area can ensure their germination and establishment. In any case, these three species categories classified by ideal germination temperatures can be applied in plant propagation.

Most of the best-germinating species also germinated over a wide range of temperatures, and are perennials: *Limoniastrum guyonianum*, *Polycarpaea robbairea*, *Eremobium aegyptiacum*, *Helianthemum lippii*, and *Moltkiopsis ciliata*. Other studies

have shown that species with these characteristics can become dominant in landscapes and can be particularly important in ecological restoration projects, especially where the aim is to protect the soil from erosion. Depending on species establishment in the field, the percentage of such species in the seed mix can be adjusted to the desired cover.

As part of future projects to restore and preserve the biodiversity of the Saharan spontaneous flora, further studies are needed to determine the ecological requirements of the seeds of other Saharan species. For the species studied here, germination in the field should also be investigated along with distinctive features, such as seed heteromorphy (e.g. *Atriplex*; Sukhorukov and Danin 2009), which can lead to differences in germination conditions.

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Disclosure statement

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Author contributions

MM, SBB, AE conceived and designed the research; AB helped with GIS and maps; MM conducted the experiment; MM, EB analyzed the data; MM, EB wrote the manuscript; all authors contributed to revision of the text.

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Table 1. Climate data for the study area, from station (#31750: 31°41'28.321" N, 5°0'0" E) (Global Weather Data 2018).

Month	1	2	3	4	5	6	7	8	9	10	11	12
Max Temperature (°C)	16.0	19.0	23.9	28.9	34.2	39.7	42.7	42.0	36.9	30.3	22.2	16.9
Min Temperature (°C)	5.4	7.0	10.2	13.7	17.8	21.9	23.3	22.9	20.2	15.6	9.9	6.3
Precipitation (mm)	9.3	10.6	7.4	5.7	5.2	1.4	0.1	0.3	2.4	6.0	6.0	4.7
Relative Humidity (%)	0.6	0.5	0.4	0.3	0.2	0.2	0.2	0.2	0.3	0.4	0.5	0.6
Solar radiation (kWh/m²/d)	12.4	16.0	20.5	24.9	27.0	27.8	27.8	25.6	21.6	17.2	13.2	11.4

Table 2. List of species studied for the effect of cold scarification on seed germination and dormancy. **Chorotypes:** T = Therophyte, C = Chamaephyte. The nomenclature follows version 3.4.0 (2014) of the African Plant Database. Chorotypes and life forms come from (Quézel and Santa 1962-1963; Ozenda 2004; Danin and Fragman-Sapir 2022).

Family	Updated scientific name *	Chorotypes	Habitat	Seed collection
<i>Amaranthaceae</i>	<i>Agathophora alopecuroides</i> (Delile) Fenzl ex Bunge	C	Sandy, gravelly ground of <i>Regs</i> .	March-July
<i>Amaranthaceae</i>	<i>Anabasis articulata</i> (Forssk.) Moq.	C	Stony soils.	October-November
<i>Amaranthaceae</i>	<i>Atriplex dimorphostegia</i> Kar. & Kir.	T	Silty areas, wetlands and oases of the northern Sahara.	February-May
<i>Amaranthaceae</i>	<i>Bassia muricata</i> (L.) Asch.	T	Common throughout the Sahara, especially in clay soils.	February-June
<i>Amaranthaceae</i>	<i>Cornulaca monacantha</i> Delile	C	Sandy areas and <i>Regs</i> , in isolated individuals and in populations.	August-November

<i>Apiaceae</i>	<i>Ammodaucus leucotrichus</i> Coss. & Durieu	T	Sandy beaches, <i>Oued</i> beds and rocky bottom depressions.	April
<i>Apiaceae</i>	<i>Foeniculum vulgare</i> Mill.	C	<i>Batha</i> , <i>Phrygana</i> , Disturbed habitats	July-November
<i>Asclepiadaceae</i>	<i>Pergularia tomentosa</i> L.	C	Common throughout the northern Sahara	February-April
<i>Asphodelaceae</i>	<i>Asphodelus tenuifolius</i> Cav.	T	Rocky soils, in <i>Oued</i> beds and silted depressions	February-April
<i>Asteraceae</i>	<i>Cotula cinerea</i> Delile	T	Depression, Saharan <i>Oueds</i>	April
<i>Asteraceae</i>	<i>Ifloga spicata</i> (Forssk.) Sch.Bip	T	Stony soils of depressions and beds of <i>Oueds</i>	March-May
<i>Asteraceae</i>	<i>Launaea capitata</i> (Spreng.) Dandy	T	Stony land, in depressions and beds of <i>Oueds</i>	March-April
<i>Asteraceae</i>	<i>Launaea nudicaulis</i> (L.) Hook. F.	C	Uncultivated fields and pastures in desert regions	April-May
<i>Asteraceae</i>	<i>Perralderia coronopifolia</i> Coss.	C	Rocky areas	April
<i>Asteraceae</i>	<i>Scorzonera laciniata</i> L.	C	Sandy habitats	April
<i>Boraginaceae</i>	<i>Echium trygorrhizum</i> Pomel.	T	Stony soils of depressions and beds of <i>Oueds</i>	April
<i>Boraginaceae</i>	<i>Moltkiopsis ciliata</i> (Forssk.) I. M. Johnst.	C	Sandy habitats	March-May

Brassicaceae	<i>Diplotaxis harra</i> (Forssk.) Boiss.	T	Clay-sandy soils of depressions and beds of <i>Oueds</i>	January-May
Brassicaceae	<i>Eremobium aegyptiacum</i> (Spreng.) Asch. & Schweinf. ex Boiss.	C	Sandy habitats	March-April
Brassicaceae	<i>Henophyton deserti</i> Coss. & Durieu	C	Desert rockeries, gypsum	April
Brassicaceae	<i>Savignya parviflora</i> subsp. <i>longistyla</i> (Boiss. & Reut.) Maire	T	Saharan pasture	January-April
Brassicaceae	<i>Sisymbrium reboudianum</i> Verl.	T	Saharan pasture (<i>Reg</i> , Depression), Saharan <i>Oueds</i>	April
Caryophyllaceae	<i>Paronychia arabica</i> (L.) DC.	T	Sandy habitats	February-May
Caryophyllaceae	<i>Polycarpaea robbairea</i> (Kuntze) Greuter & Burdet	T	Salty habitats, Saharan <i>Oueds</i>	January-April
Caryophyllaceae	<i>Spergularia salina</i> J. & C.Presl	T	Salty habitats	March-June
Cistaceae	<i>Helianthemum lippii</i> (L.) Dum. Cours.	C	Desert pastures, rock gardens, sand	February-April
Cleomaceae	<i>Cleome africana</i> Botsch.	T	Sandy habitats	April

<i>Euphorbiaceae</i>	<i>Euphorbia guyoniana</i> Boiss. & Reut.	C	Sandy habitats	April
<i>Fabaceae</i>	<i>Argyrobium uniflorum</i> (Dc) Jaub. & Spach	C	Common throughout the northern Sahara.	March-April
<i>Fabaceae</i>	<i>Astragalus arpilobus</i> subsp. <i>hauarensis</i> (Boiss.) Podlech	T	Sandy habitats	February-March
<i>Fabaceae</i>	<i>Astragalus boeticus</i> L.	T	Common throughout the northern Sahara	February-April
<i>Fabaceae</i>	<i>Astragalus gombo</i> Bunge	C	Sandy habitats	April
<i>Fabaceae</i>	<i>Astragalus mareoticus</i> Delile	T	Steppes, Saharan <i>Oueds</i>	April
<i>Geraniaceae</i>	<i>Erodium glaucophyllum</i> L'Héritier	C	Rocky clay soils	March-April
<i>Neuradaceae</i>	<i>Neurada procumbens</i> L.	T	<i>Oued</i> beds and sandy bottom depressions	February-April
<i>Plantaginaceae</i>	<i>Plantago ciliata</i> Desf.	T	Sandy and rocky ground of <i>Oued</i> beds and depressions	March-April
<i>Plumbaginaceae</i>	<i>Limoniastrum guyonianum</i> Boiss.	C	Sandy habitats	April

Poaceae	<i>Centropodia forsskalii</i> (Vahl) Cope	TH	Sandy habitats	April
Poaceae	<i>Sphenopus divaricatus</i> (Gouan) Rchb.	TH	Desert, Salty habitats	March-April
Poaceae	<i>Stipagrostis plumosa</i> (L.) Munro ex T. Anderson	CT	Sandy habitats.	April-May
Poaceae	<i>Stipagrostis pungens</i> (Desf.) De Winter	CH	Sandy habitats	April
Zygophyllaceae	<i>Fagonia glutinosa</i> Delile	TH	Sandy habitats	March-May
Zygophyllaceae	<i>Peganum harmala</i> L.	CH	Sandy habitats	March-April

Table 3. Germination results for the 43 studied species. **Germination (%)** is the average germination percentage over all treatments (with or without cold stratification, germination temperature). **Effect of treatment interaction** = cold stratification * temperature. **Effect of cold stratification** can be negative (lower germination after cold stratification compared to control), positive (higher germination after cold stratification compared to control), positive* (no germination in control) or mixed (positive and negative effects depending on temperature). **Germination temperature** can be highest at low temperatures (5 to 20°C), intermediate temperatures (20 to 35°C) or high temperatures (30 to 40°C). Species are classified in three groups: dark gray indicates species with a germination percentage above 40; light gray, species with a germination percentage between 40% and 20%; white, species with a germination percentage below 20%. Within these groups, species are listed in alphabetical order. **Seed dormancy classes** : ND = Non Dormant, MD = Morphological Dormancy, MPD = Morphophysiological Dormancy, PD = Physiological Dormancy, PY = Physical Dormancy, PY+PD = Combinational Dormancy (Baskin and Baskin 2004), * Type of dormancy is inferred. TBD = To be determined. ** For *Atriplex dimorphostegia*, since each plant carries several types of seeds with different dormancy (Sukhorukov 2007), we used humped seeds (*sensu* Koller, 1957) after removing the bracts.

Species	Germination (%)	Effect of treatment interaction	Effect of cold stratification	Germination temperature (°C)	Dormancy class	References	Physiological dormancy level
<i>Asphodelus tenuifolius</i>	40.0	p<0.001***	mixed	low	MDP	<i>Asphodelus tenuifolius</i> (Koller 1957)	NA
<i>Bassia muricata</i>	52.0	p<0.001***	positive	intermediate	PD	<i>Bassia scoparia</i> (Davis et al. 2016), <i>Bassia dasyphylla</i> (Li et al. 2006)	non-deep
<i>Diplotaxis harra</i>	47.5	p<0.001***	positive	intermediate	ND	<i>Diplotaxis harra</i> (Tlig et al. 2008)	NA
<i>Eremobium aegyptiacum</i>	59.0	p<0.001***	positive	high	TBD	TBD	NA

<i>Helianthemum lippii</i>	59.6	no effect	no effect	intermediate	PY	<i>Helianthemum lippii</i> (Neffati et al. 1996)	NA
<i>Henophyton deserti</i>	46.2	p<0.001***	positive	high	ND	<i>Henophyton deserti</i> (Gorai et al. 2014)	NA
<i>Launaea nudicaulis</i>	44.7	p<0.001***	negative	intermediate	PD & ND	<i>Launaea cornuta</i> (Baskin and Baskin 2014)	TBD
<i>Limoniastrum guyonianum</i>	66.1	p<0.001***	negative	intermediate	TBD: PD*		TBD
<i>Moltkiopsis ciliata</i>	57.8	p<0.001***	positive	intermediate	ND	<i>Moltkiopsis ciliata</i> (Tielbörger and Prasse 2009)	NA
<i>Peganum harmala</i>	45.8	p<0.001***	positive	intermediate	PD	<i>Peganum harmala</i> (Hammouda and Bakr 1969)	non-deep
<i>Polycarpaea robbairea</i>	64.4	p<0.001***	positive	intermediate	TBD: ND*		NA
<i>Scorzonera laciniata</i>	40.3	p<0.001***	positive	low	PD	<i>Takhtajaniantha pusilla</i> (Tang et al. 2009, as <i>Scorzonera pusilla</i>)	non-deep
<i>Stipagrostis pungens</i>	46.5	p<0.001***	no effect	intermediate	PD	<i>Stipagrostis ciliata</i> (Neffati et al. 1996), <i>Stipagrostis pennata</i> (Bahrani and Khartegh 2006)	TBD
<i>Ammodaucus leucotrichus</i>	22.1	p<0.001***	positive	high	TBD: PD*		non-deep
<i>Anabasis articulata</i>	23.3	p<0.001***	positive	intermediate	TBD: ND*		NA
<i>Argyrolobium uniflorum</i>	25.1	p<0.001***	positive	high	PY	PY: <i>Argyrolobium uniflorum</i> (Neffati et al. 1996)	NA
<i>Astragalus arpilobus</i>	22.6	p<0.001***	positive	intermediate	PY	PY: <i>Astragalus</i> (Hammouda and Bakr 1969)	NA
<i>Atriplex dimorphostegia**</i>	35.4	p<0.001***	positive	low	PD	PD: <i>Atriplex dimorphostegia</i> (Koller 1957)	non-deep

<i>Centropodia forsskalii</i>	35.9	p<0.001***	positive	intermediate	TBD: ND*		NA
<i>Cleome africana</i>	37.0	p<0.001***	positive	high	PD	PD: <i>Cleome</i> (Sen and Chatterji 1968; Hammouda and Bakr 1969; Cane 2008; Muasya et al. 2009; Baskin and Baskin 2014)	non-deep
<i>Cotula cinerea</i>	34.9	p<0.001***	positive	intermediate	ND	ND: <i>Cotula coronopifolia</i> (van der Toorn 1980)	NA
<i>Erodium glaucophyllum</i>	29.1	p<0.001***	negative	high	PY	PY: <i>Erodium boissieri</i> , <i>E. botrys</i> , <i>E. cicutarium</i> , <i>E. malachoides</i> , <i>E. moschatum</i> , <i>E. stephanium</i> (Baskin and Baskin 2014)	NA
<i>Euphorbia guyoniana</i>	20.6	p<0.001***	positive	high	PD (rarely ND)	<i>Euphorbia</i> (Baskin and Baskin 2014)	non-deep
<i>Ifloga spicata</i>	28.0	p<0.001***	positive	intermediate	TBD		NA
<i>Paronychia arabica</i>	39.5	p<0.001***	negative	intermediate	TBD: PY*		NA
<i>Plantago ciliata</i>	26.9	p<0.001***	positive	low	PD	PD: <i>Plantago</i> (Baskin and Baskin 2014)	non-deep
<i>Savignya parviflora</i>	32.0	p<0.001***	positive	low	PD	PD: <i>Savignya parviflora</i> (Bhatt et al. 2020)	non-deep
<i>Sisymbrium reboudianum</i>	29.5	p<0.001***	positive	intermediate	PD	PD: <i>Sisymbrium</i> (Baskin and Baskin 2014)	non-deep
<i>Spergularia salina</i>	29.4	p<0.001***	positive	intermediate	PD	PD: <i>Spergularia salina</i> (Bakker et al. 1985)	non-deep
<i>Stipagrostis plumosa</i>	34.7	p<0.001***	positive	intermediate	PD	PD: <i>Stipagrostis ciliata</i> (Neffati et al. 1996), <i>Stipagrostis pennata</i> (Bahrani and Khartegh 2006)	TBD

<i>Agathophora alopecuroides</i>	12.5	p<0.001***	positive	low	PD	PD: <i>Agathophora</i> (Khan et al. 2011)	non-deep
<i>Astragalus boeticus</i>	5.6	p<0.001***	positive	intermediate	PY	PY: <i>Astragalus</i> (Hammouda and Bakr 1969)	NA
<i>Astragalus gombo</i>	18.5	p<0.001***	positive	intermediate			
<i>Astragalus mareoticus</i>	7.1	p<0.001***	positive	intermediate			
<i>Cornulaca monacantha</i>	9.2	p<0.001***	positive	low	ND	ND: <i>Cornulaca monacantha</i> (Tielbörger and Prasse 2009)	NA
<i>Echium trygorrhizum</i>	3.1	no effect	positive*	intermediate	PD	PD: <i>Echium</i> (Carqué-Álamo et al. 2003)	non-deep
<i>Fagonia glutinosa</i>	13.2	no effect	positive*	intermediate	PD	PD: <i>Fagonia</i> (Sen and Chatterji 1968; Hammouda and Bakr 1969)	non-deep
<i>Foeniculum vulgare</i>	17.1	p<0.001***	positive	high	MD	MD: <i>Foeniculum vulgare</i> (Thomas 1994)	NA
<i>Launaea capitata</i>	5.5	p<0.01**	positive	intermediate	PD & ND	<i>Launaea cornuta</i> (Baskin and Baskin 2014)	TBD
<i>Neurada procumbens</i>	15.4	no effect	positive*	intermediate	TBD: PD*		non-deep
<i>Pergularia tomentosa</i>	5.7	no effect	positive*	high	PD	PD: <i>Pergularia</i> (Baskin and Baskin 2014)	non-deep
<i>Perralderia coronopifolia</i>	8.0	no effect	positive*	high	TBD: PD*		non-deep
<i>Sphenopus divaricatus</i>	19.2	p<0.001***	positive	intermediate	TBD: ND*		NA

Figure 1. Location of the study area.

Figure 2. Mean germination percentages of the eight species with a low germination rate ($<20\%$) which were positively affected by cold stratification. A. and B. Species germinating better at low temperatures; C. to G. Species germinating better at intermediate temperatures; H. Species germinating better at high temperatures.

Figure 3. Mean germination percentages of the five species with a low germination rate ($<20\%$) for which cold stratification was a pre-requisite to germination. A. to C. Species germinating better at intermediate temperatures; D. and E. Species germinating better at high temperatures.

Figure 4. Mean germination percentages of the eight species with a high germination rate ($>40\%$) which were positively affected by cold stratification. A. Species germinating better at low temperatures; B. to F. Species germinating better at intermediate temperatures; G. and H. Species germinating better at high temperatures.

Figure 5. Mean germination percentages of the eight species with a germination rate of between 20 and 40% which were positively affected by cold stratification and which germinated better at intermediate temperatures.

Figure 6. Mean germination percentages of the seven species with a germination rate of between 20 and 40% which were positively affected by cold stratification. A. to C. Species germinating better at low temperatures; D. to G. Species germinating better at high temperatures.

Figure 7. Mean germination percentages of the four species for which cold stratification had a slight negative effect. A. and B. Species with a germination rate of above 40%; C. and D. Species with a germination rate of between 20 and 40%.

Figure 8. A. and B. Mean germination percentages of the two species for which cold stratification had no effect. C. Mean germination percentage of the one species for which cold stratification had mixed effects.

Figure 1

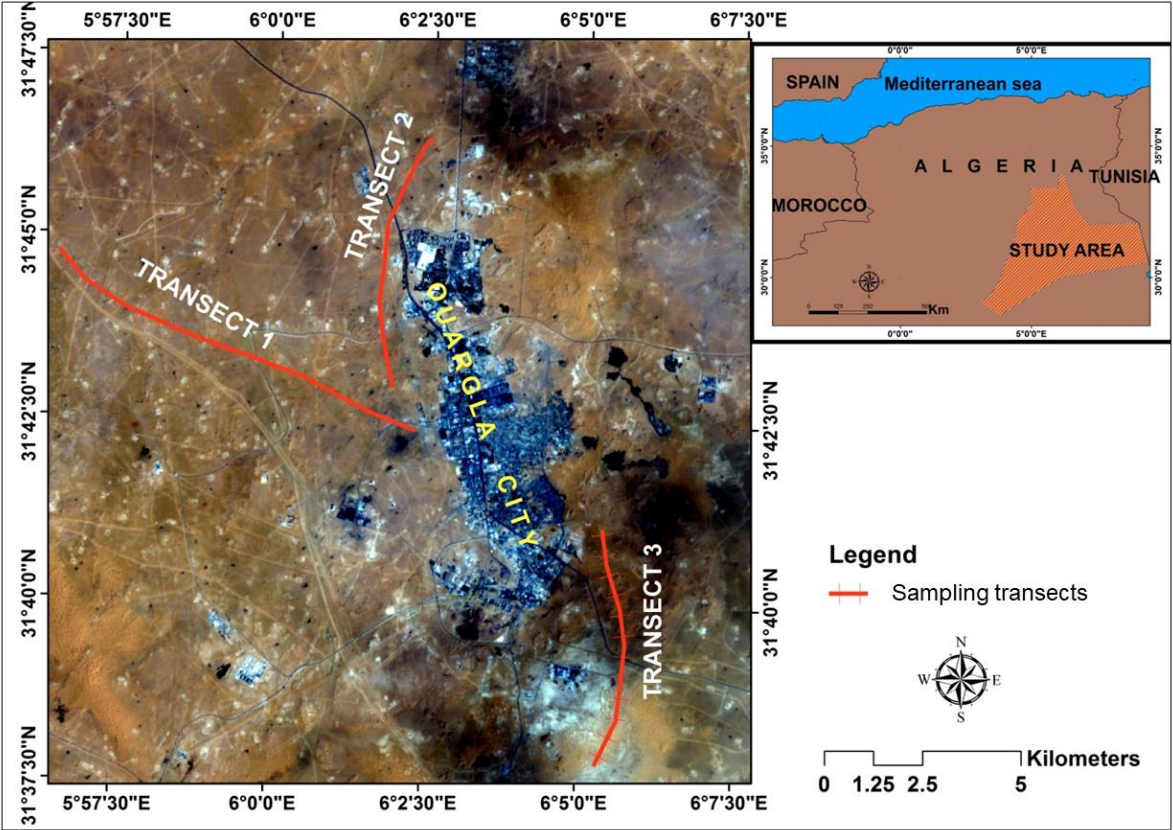


Figure 2

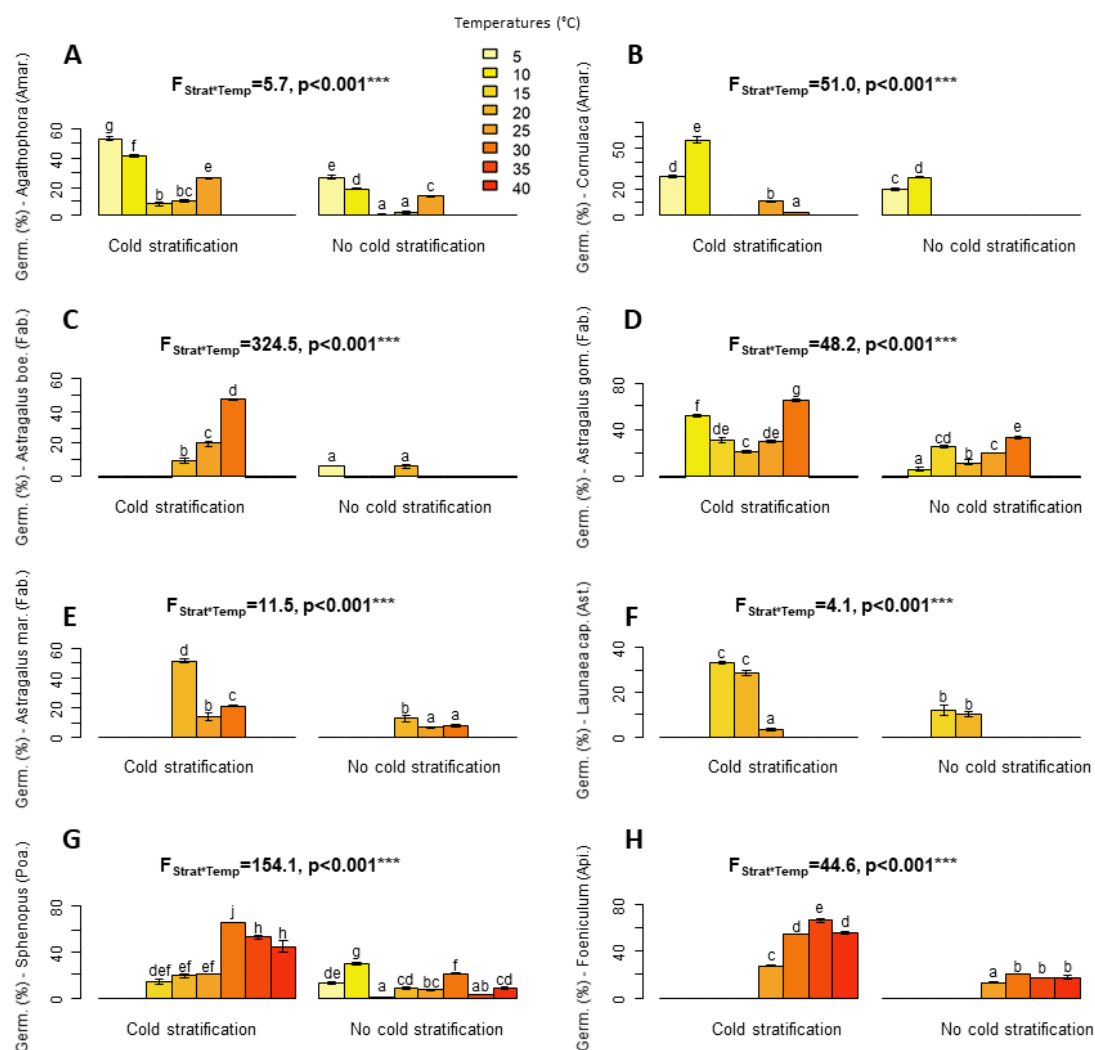


Figure 3

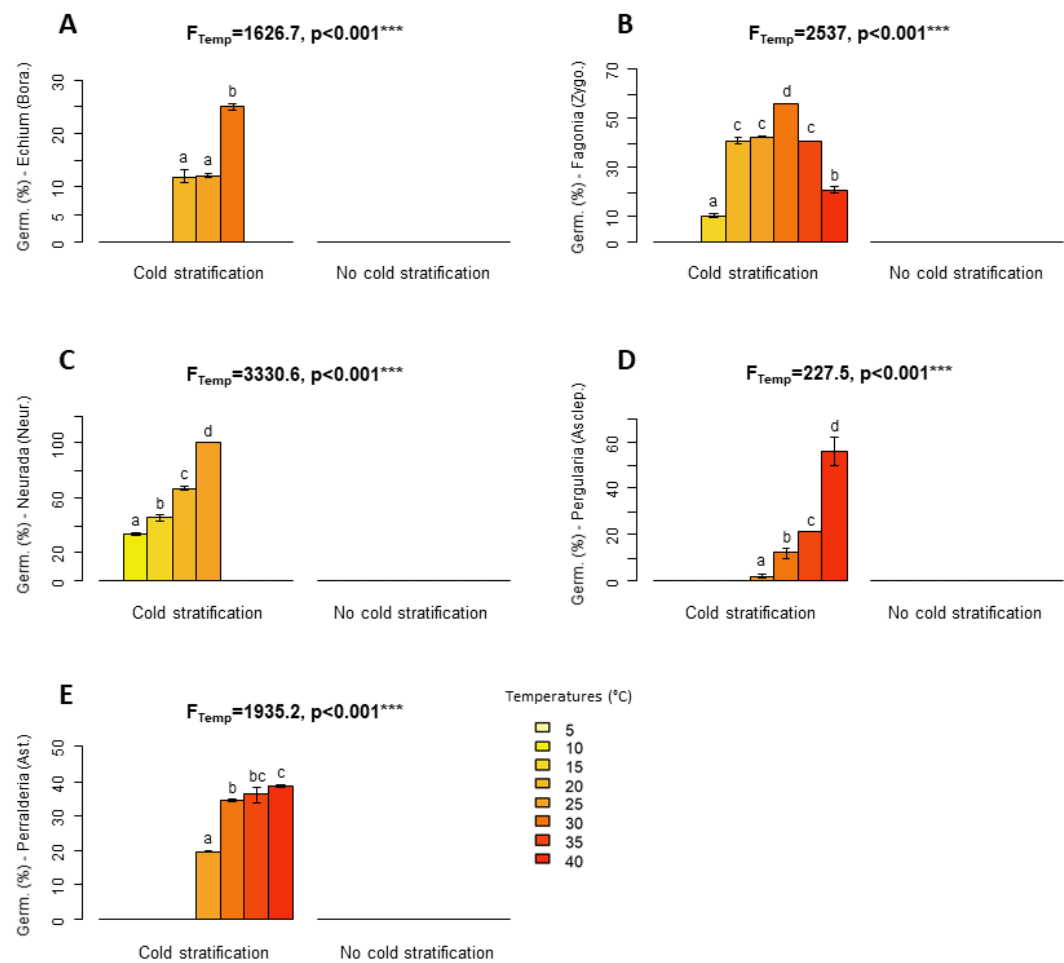


Figure 4

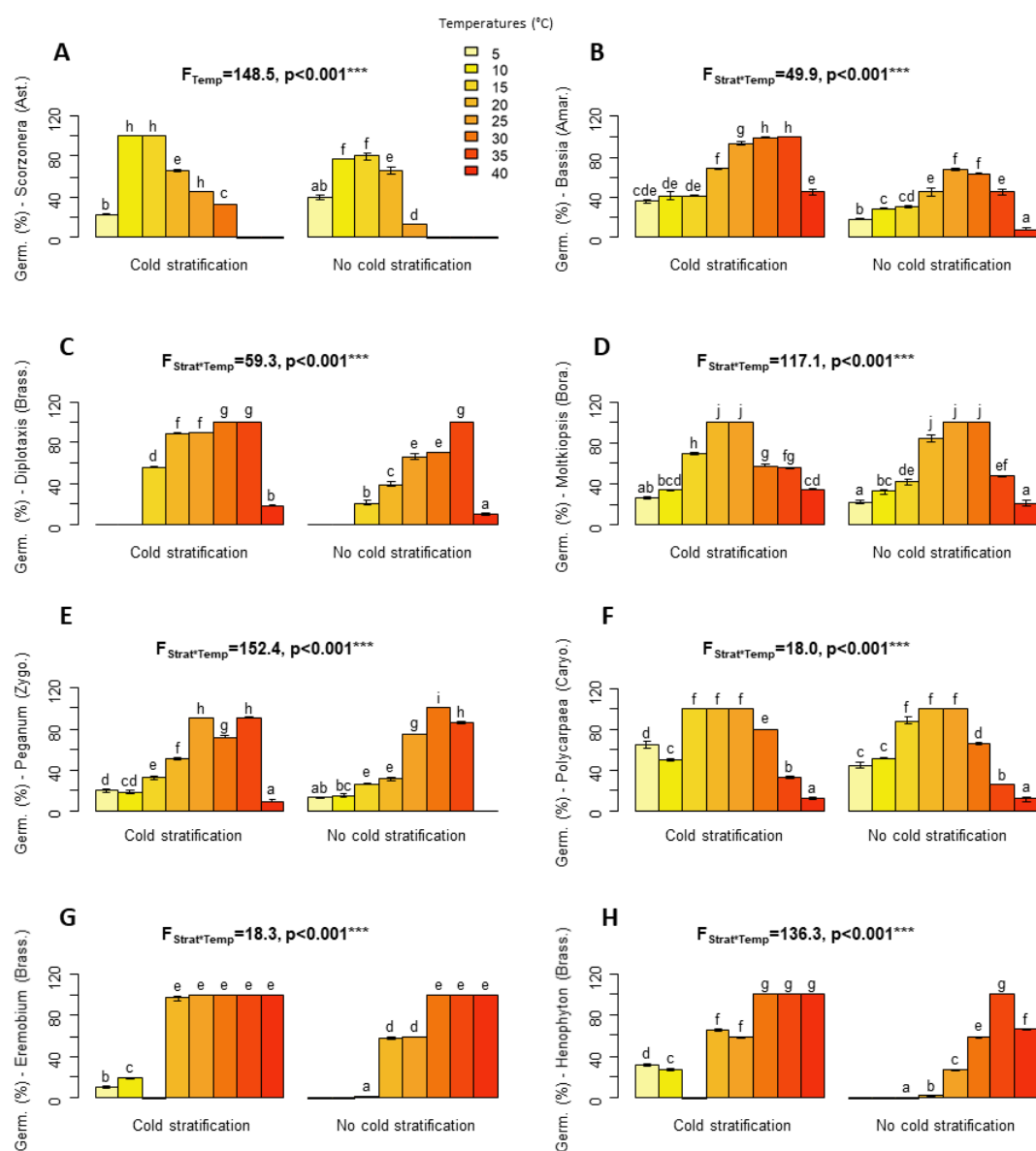


Figure 5

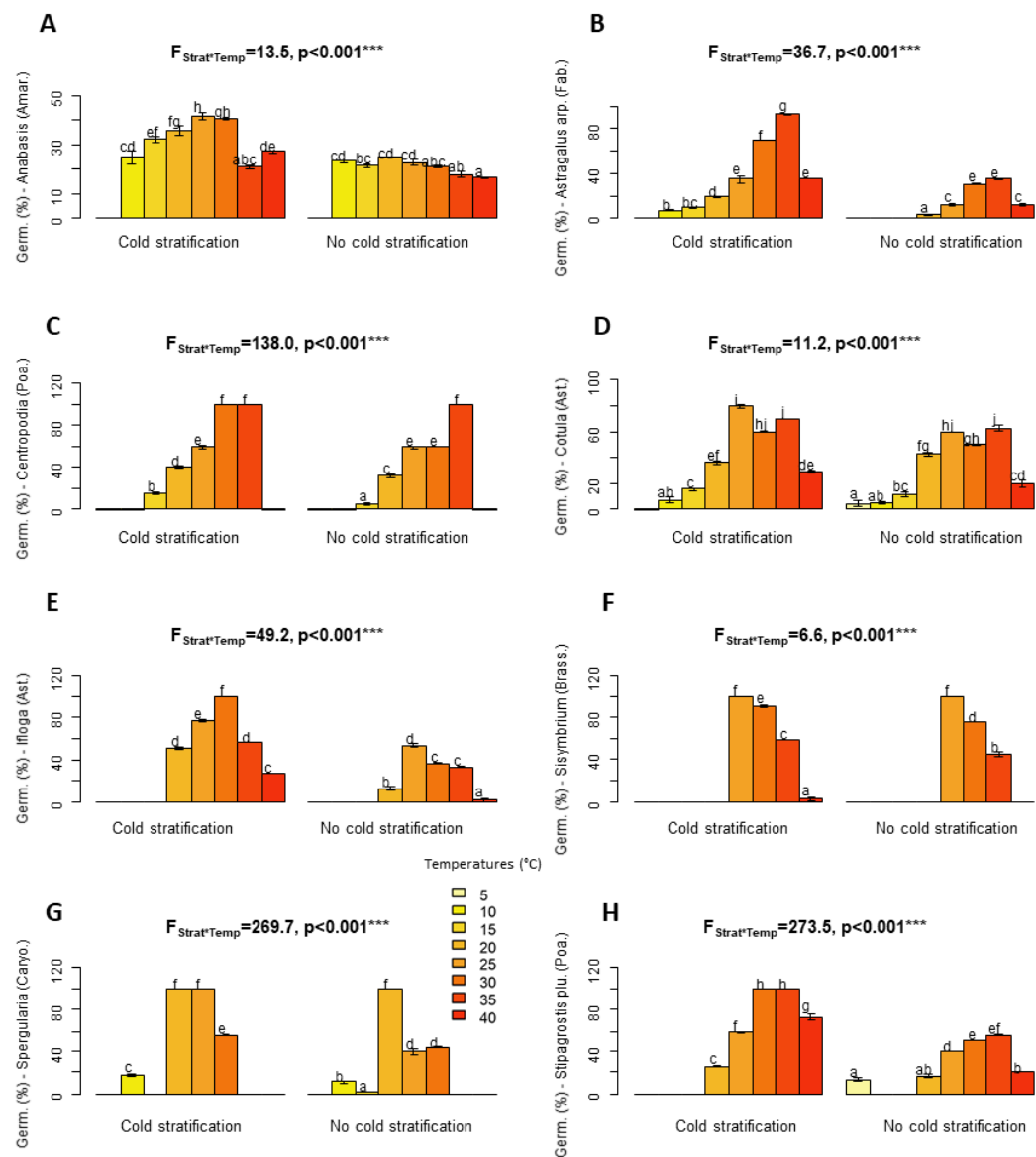


Figure 6

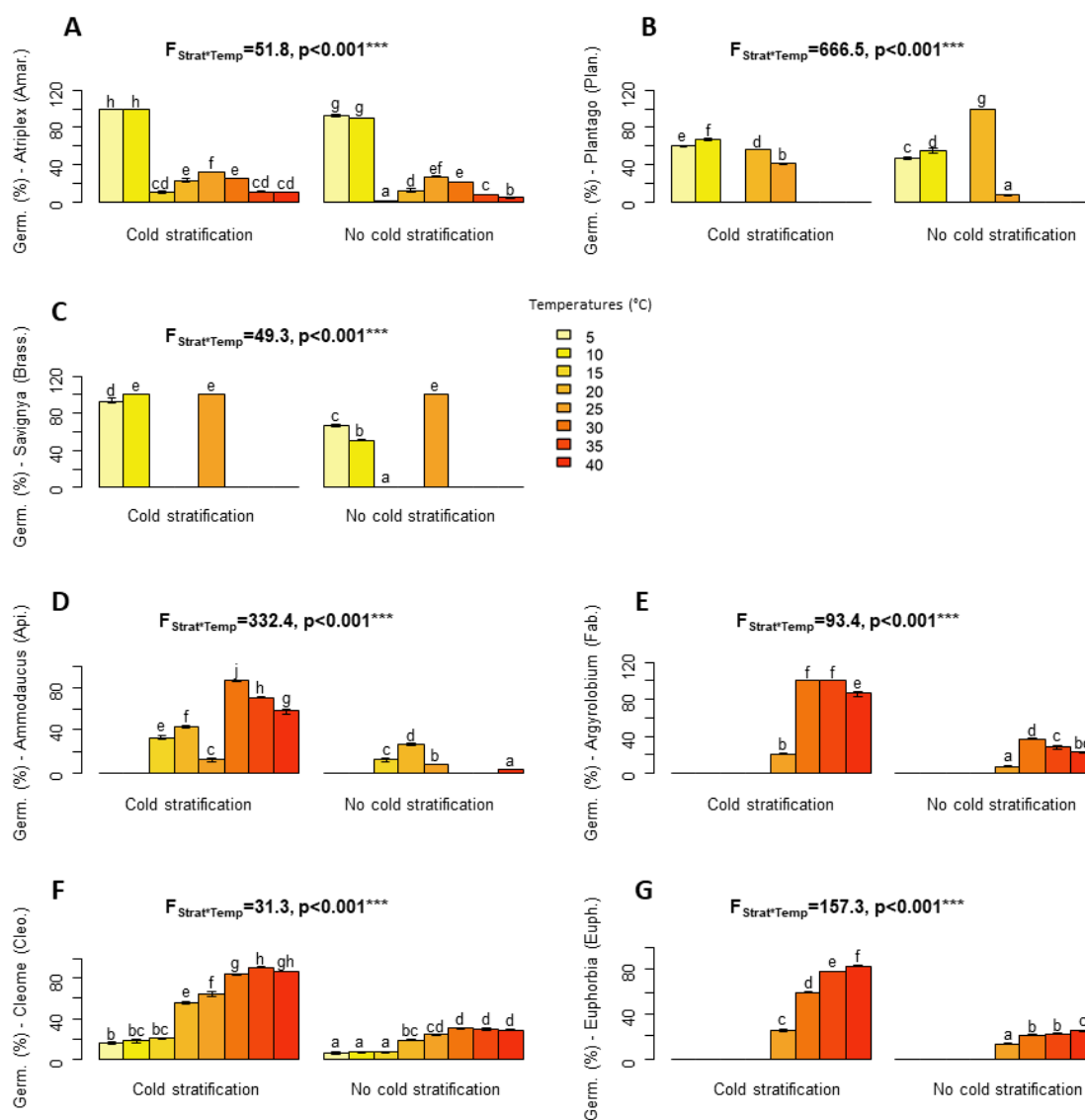


Figure 7

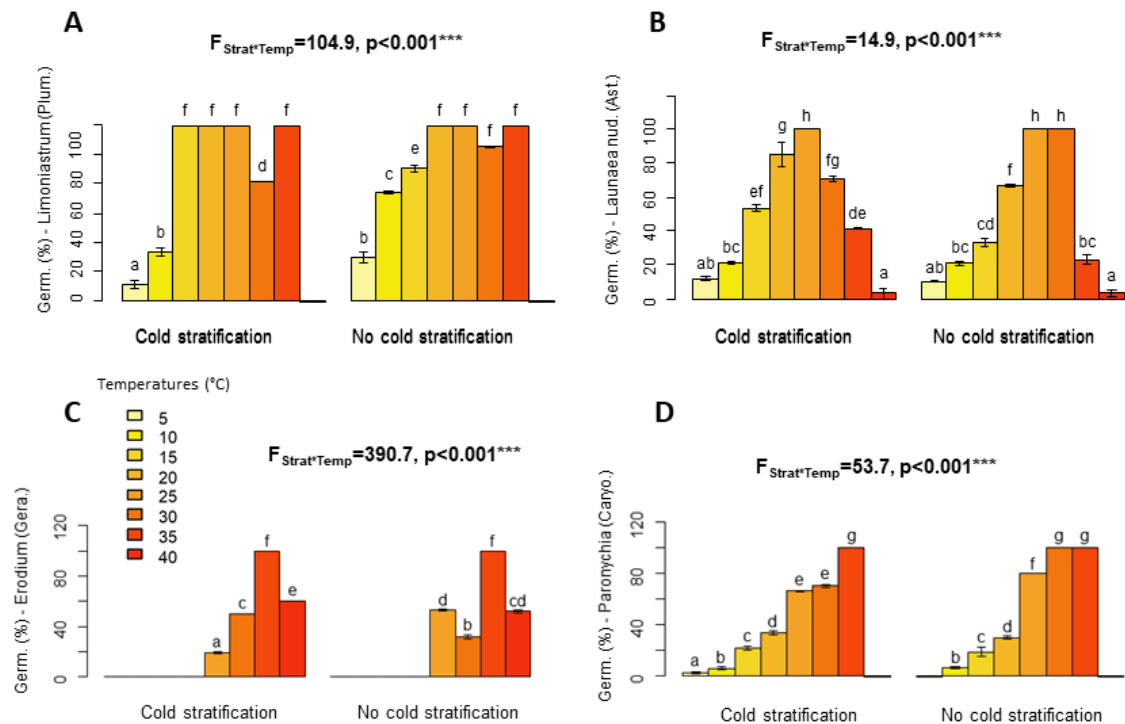
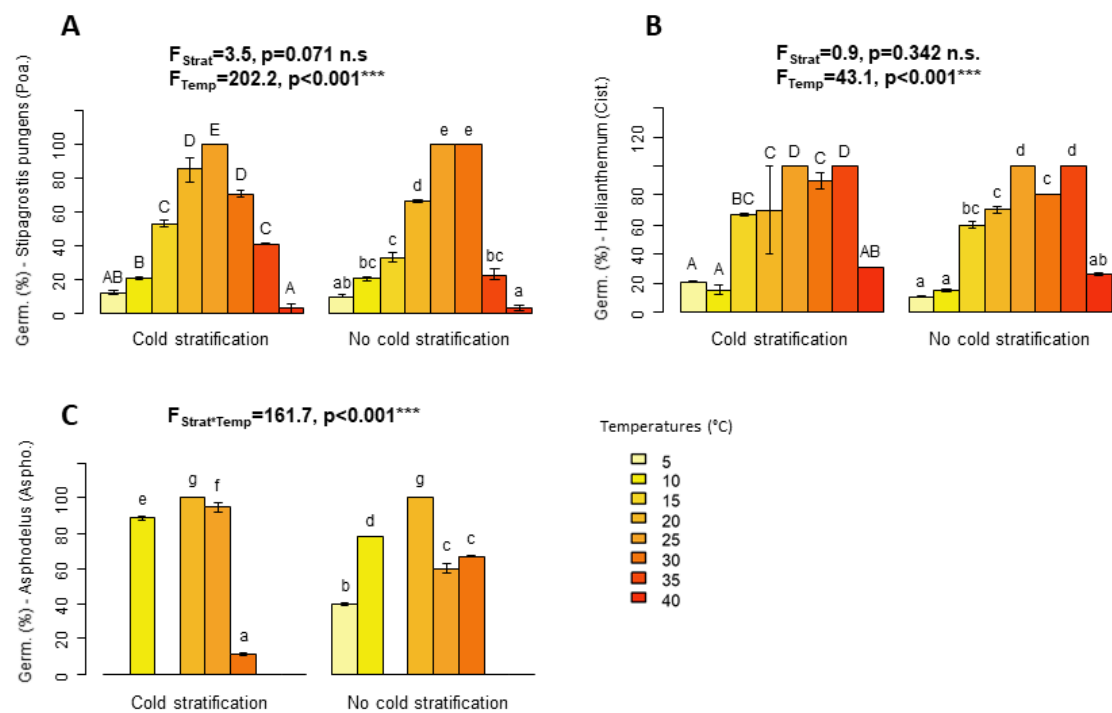


Figure 8



Supporting information

1. Overall effect of cold stratification and temperatures

Figure S1. Mean germination percentages of all 43 studied species depending on whether or not subjected to a cold stratification treatment prior to germination and on temperatures during the germination trial.

