

Ecophysiology of seed germination in Mediterranean geophytes. 1. *Muscari* spp.

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Abstract

Ecophysiological aspects of seed germination were investigated in four Mediterranean geophytes of the genus *Muscari* (*Liliaceae*): *M. comosum* (tassel hyacinth), *M. neglectum* (common grape hyacinth), *M. commutatum* and *M. weissii*. Experiments were performed at constant temperatures in the dark and under temperature and light conditions simulating those prevailing in nature during November–January, i.e. well into the rainy season of the Mediterranean climate. In all species, no primary dormancy was revealed, and germination occurred in a rather narrow range of cool temperatures (optimum at 10 or 15°C) and at a remarkably slow rate; both germination characteristics seem to be associated with autumn/winter seed germination and seedling establishment. Such a postulated strategy is ecologically advantageous within an unpredictable rainfall regime, known to prevail during the start of the rainy period of the Mediterranean climate. This strategy may also explain the spread of germination of *M. comosum* seeds over two consecutive years, observed by Theophrastus. Far-red light, simulating light conditions under a dense canopy, resulted in only a slight delay of germination compared to dark controls. Diurnal white light, qualitatively simulating natural daylight, caused a significant decrease of the germination rate in all four species studied. Moreover, white light was found to suppress considerably final seed germination (photoinhibition) in *M. weissii* and *M. neglectum*; in the latter species, prolonged imbibition under white light also led to the induction of secondary dormancy.

Keywords: common grape hyacinth, fire, germination rate, light, *Liliaceae*, Mediterranean geophytes, *Muscari commutatum*, *Muscari comosum*, *Muscari neglectum*, *Muscari weissii*, photoinhibition, secondary dormancy, seed coat, seed germination, tassel hyacinth, temperature

Introduction

Muscari (grape hyacinth), a genus comprising four subgenera and c. 40 bulbous perennial species, grows mainly in the Mediterranean region, but its area of distribution extends into Russia and Iran. The name *Muscari* derives from the Arabian word ‘*muscarimi*’, which in turn originates from the Greek word ‘*moschos*’ referring to the fragrance emitted by certain species. Two of the species investigated in the present study, *Muscari comosum* (L.) Miller and *Muscari weissii* Freyn belong to the subgenus *Leopoldia* (Parl.) Rouy while the other two, *Muscari neglectum* Guss. ex Ten. and *Muscari commutatum* Guss., belong to the subgenus *Botryanthus* (Kunth) Rouy (Davis and Stuart, 1984).

M. comosum (tassel hyacinth) is a distinctive, widespread plant, easily recognized by its purple or electric-blue ‘tassel’ made of small infertile flowers with long stalks. The fertile flowers are brown with pale yellowish-brown teeth. The species is a Mediterranean element and the most variable one in the subgenus *Leopoldia*; it grows from sea level up to 2000 m and is distributed over south-western and central Europe, the Mediterranean area and eastwards to Iran and Arabia. In some regions, especially Greece, the edible bulbs are still collected from the wild and can sometimes be seen in local markets.

M. weissii is similar to *M. comosum* but the teeth of the fertile flowers are yellowish. The species is an eastern Mediterranean element and grows from sea level up to 800 m in the Cyclades, the eastern Aegean islands, Crete and south-western Anatolia.

M. neglectum (common grape hyacinth) is a widespread polymorphic species. The uppermost flowers are usually light blue, small and sterile, whereas the flowers below are blackish blue with white recurved teeth. It grows from sea level up to 2300 m in northern Africa, Europe and western Asia.

M. commutatum is very similar to *M. neglectum*, but has fragrant flowers with blackish-violet teeth. It is an eastern Mediterranean element and grows near sea level in Italy, Sicily, the Balkans and the Aegean.

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Theophrastus (4th century BC) in both his plant treatises [*Historia Plantarum* (HP) and *De Causis Plantarum* (CP)] refers numerous times to *M. comosum*, known as 'bulbs' (which is still the current vernacular name of the plant in Greece). The plant is accurately described (e.g. HP 1.10.7; HP 7.13.1; see also Negbi, 1989), perhaps the consequence of its importance as a food source and its apparent cultivation. Indirect support for the latter are Theophrastus' passages about a method to increase the size of the edible bulb (HP 7.12.2) and the 'paradox' of seeds that germinate in two consecutive years: 'It is a characteristic of "bulbs" that not all seeds germinate together but some this year and the rest during the next (season), similarly to, as they say, the aegilops, trefoil and sugar beet' (HP 7.13.5; CP 4.6.1).

In regard to seed dispersal, *M. comosum* and *M. neglectum* are described as rain ballists and anthropochorous (Müller-Schneider, 1986), while the latter species is additionally referred to as myrmecochorous (Müller-Schneider, 1983).

Little information is available on the germination of geophytes (Baskin and Baskin, 1998). Apart from karyological and cytotaxonomical studies on the genus *Muscari* (Bentzer, 1969, 1972a, b, 1973; Stuart, 1970; Garbari, 1984; Karlén, 1984; Dalgic, 1991), information concerning the overall reproductive biology of the studied taxa is scarce (Valdés and Mejias, 1988).

The present study is a contribution towards filling this gap of knowledge and investigates the ecophysiology of the germination behaviour in four Mediterranean species of *Muscari*. More specifically, the following aspects are examined: (1) germination in the dark and dormancy status of the seeds; (2) temperature range and rate of germination; (3) germination characteristics under simulated natural conditions; (4) the role of light (and seed coat) on germination; and (5) the potential induction of secondary dormancy.

Materials and methods

Plant material

Seeds of *M. comosum* and *M. neglectum* were collected in July 1991 from a burned pine forest at Mt. Parnes, Attica [400–450 m above sea level (a.s.l.)] during the second postfire year (Thanos *et al.*, 1996). The seeds of *M. neglectum* used in the experiments presented in Fig. 3 (right-hand column) were collected from the same site in June 1994. Seeds of *M. commutatum* were collected in June 1992 from a burned pine forest in Avlona, Attica (480 m a.s.l.) during the first postfire year. Seeds of *M. weissii* and the three lots of *M. neglectum* used in the experiment reported in Table 1

were collected in Karpathos and Crete and were kindly provided by the Botanic Garden of Berlin. The average, air-dry seed weights for *M. comosum*, *M. commutatum* and *M. weissii* were, respectively: 5.8 ± 0.1 ($n = 50$), 2.6 ± 0.1 ($n = 50$) and 4.7 ± 0.3 mg ($n = 9$). The mean seed weights for the two lots of *M. neglectum* (1991 and 1994) were 4.3 ± 0.1 ($n = 50$) and 2.9 ± 0.1 mg ($n = 50$), respectively. The seeds were stored in light- and waterproof plastic boxes, at room temperature ($20 \pm 5^\circ\text{C}$). Experiments with *M. comosum* and *M. neglectum* shown in Figs 1 and 2 and the left-hand column of Fig. 3 were performed after 3 months of storage, while those in the right-hand column of Fig. 3 were performed after 2 years of storage; experiments with *M. commutatum* (Figs 1 and 3) were performed after 3.5 years of seed storage.

Nomenclature follows Tutin *et al.* (1980), and distribution data are based on both *Flora Europaea* (Tutin *et al.*, 1980) and *Flora of Turkey and the East Aegean Islands* (Davis and Stuart, 1984).

Germination conditions

Germination tests were performed in glass Petri dishes (7 cm in diameter) lined with two filter-paper discs and moistened with 3 ml of distilled water. The criterion of germination was visible radicle protrusion and, after each count, germinated seeds were discarded. The tests were terminated when no additional seeds germinated. All manipulations of imbibed seeds were carried out under a dim, green safelight. Unless otherwise indicated, each value is the mean of five replicates of 25 seeds \pm standard error (SE). T_{50} is the time needed for 50% of the final germination value, and is calculated by linear interpolation from the two germination values closest to median germination. Chipping of *M. comosum* seeds was carried out under a stereomicroscope: seeds were handled with forceps and a sharp scalpel was inserted 0.5 mm deep into the radicle end of the seed; with a slight twist, part of the seed coat and a small section of the endosperm were cut away to expose (but not damage) the radicle.

For germination experiments in darkness, seeds were incubated within lightproof, metal containers in controlled temperature cabinets (Model BK 5060 EL, W.C. Heraeus GmbH, Germany) where temperature was kept constant within $\pm 0.5^\circ\text{C}$ of the value set. Seed germination experiments under various light regimes were performed in temperature- and light-programmable growth units (model GB48, Conviron, Controlled Environments, Winnipeg, Canada) equipped with a lamp canopy of 48 incandescent bulbs (Sylvania 50A19, 50 W, 277 V) and 10 fluorescent tubes (Sylvania Cool White FR96T12/CW/VHO-235/1). In order to simulate the natural conditions encountered during November–

January, temperature and light programmes were automatically changed according to the average climatic data (period 1955–1987) of the Athens Airport Meteorological Station (Thanos *et al.*, 1991). In the experiments presented in Fig. 3, temperature and light programmes were updated every day (left) or every week (right-hand column), respectively. Temperature was programmed to change every 3 h, and lights were turned on 30 min before official sunrise and off 30 min after official sunset, while both the quality and quantity of light were automatically adjusted several times during the 'day' (Thanos *et al.*, 1991). Light measurements were made with a portable spectroradiometer (LI-1800, Li-Cor, Lincoln, NE, USA); calculations of flux densities and values of ζ and ϕ were made using a previously described software application (Thanos *et al.*, 1994). White light (W) had a value of ζ (660/730 nm photon ratio) equal to 1.031, while the phytochrome photostationary state ratio ($\phi = [Pfr]/[Ptot]$) was 0.635, and the total photon flux density in the visible range (400–800 nm) was $124.9 \mu\text{mol m}^{-2} \text{s}^{-1}$. When this light was filtered through three sheets of Plexiglas filters (two blue, 627, and one red, 501, 3-mm thick each; Röhm GmbH, Germany) a 'canopy simulating', far-red-rich light (FR) was obtained. In this case, the values of ζ , ϕ , and total flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$) were 0.001, 0.039 and 19.8, respectively.

Results

The germination time courses at various constant temperatures, in the dark, as well as the effect of temperature on final, dark germination for *M. comosum*, *M. neglectum* and *M. commutatum* are illustrated in Fig. 1. Germination of *M. comosum* seeds occurred very slowly, at a rather narrow range of cool temperatures (5–15°C), and it was sharply suppressed above 15°C in the dark. However, having imbibed at inhibitory temperatures for 1 month, ungerminated seeds were induced to germinate fully upon a subsequent transfer to the optimal temperature, 15°C. In *M. neglectum*, both rate and final values of dark germination, as well as temperature range, were similar to those of *M. comosum*, with one significant exception: at 5°C germination was nil. Seeds unable to germinate at the suboptimal temperatures 20 and 25°C could be induced to germinate fully upon transfer to the optimal temperature 10°C (3 months after onset of imbibition). Full recovery of germinability did not take place in seeds imbibing for 1 month at 5°C: final germination scored upon transfer to the optimal temperature was about 60%. Seeds of *M. commutatum* germinated optimally at 10–20°C, while germination was abruptly suppressed at 5 and 25°C. Ungerminated seeds could be induced

to germinate fully upon a subsequent transfer to the optimal temperature, 15°C. On the basis of germination rate, *M. commutatum* germinated faster compared to the two other species, while its optimal temperature range was shifted to somewhat warmer values (15–20°C).

In a preliminary attempt to investigate the role of seed coat on *Muscari* germination, dry seeds of *M. comosum* were chipped and then both chipped and intact (control) seeds were incubated in continuous darkness at 10°C. Chipping resulted in only a slight increase of germination rate (by 3–4 d) (Fig. 2).

Data on seed germination under 'late autumn' Mediterranean conditions for *M. comosum* and *M. neglectum* (lot 1991) are presented on the left-hand side of Fig. 3. Seeds were imbibed in diurnally alternating temperatures; white light was applied during the warm, 'day' period. Both the duration of the photoperiod and the temperatures of 'day' and 'night' were chosen to simulate those naturally encountered during November–December. The quality of the white light was similar to that of daylight, but its flux density was approximately 10% of the latter. Nevertheless, virtually total inhibition of germination (final level: 10%) was recorded for *M. neglectum*, while a considerable delay (c. 6 days) of germination was observed for *M. comosum* seeds. The pace of germination was shown once more to be slow for both species; germination started as the temperature gradually decreased and reached a favourable range. Furthermore, photoinhibition was obtained with a small number of seeds of *M. weissii* and three additional seed lots of *M. neglectum* (Table 1). In two out of three of the *M. neglectum* lots examined, germination under white light was considerably inhibited, while in *M. weissii* and the third lot of *M. neglectum*, a decrease of both the final extent and the rate of germination was recorded. When ungerminated seed samples of *M. neglectum* (those shown in the left-hand column of Fig. 3) that had remained under simulated natural conditions and diurnal alternations of white light and dark for 4 months ('November–February') were transferred to complete darkness at 10°C, only a further 10% germinated. Therefore, prolonged imbibition under white light not only inhibited germination but also led to an induction of secondary dormancy.

In the experiment presented in the right-hand column of Fig. 3, seeds of *M. comosum*, *M. neglectum* (lot 1994) and *M. commutatum* were imbibed under weekly average temperatures simulating those encountered during December–January. Dark germination of the first two species was considerably faster under these quite colder, winter conditions when compared with the autumn ones shown in the left-hand column of Fig. 3. On the basis of germination speed, *M. commutatum* was once more demonstrated

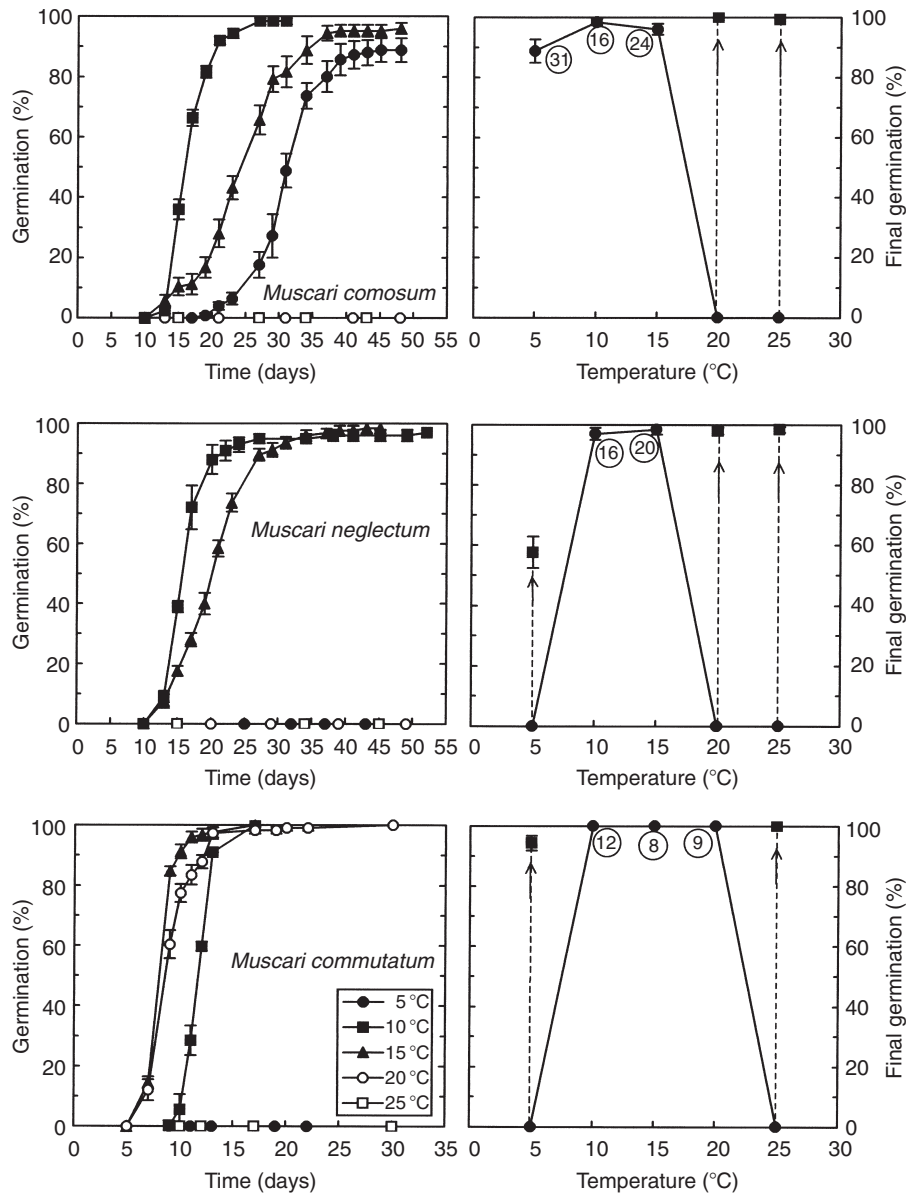


Figure 1. Time courses of seed germination (left-hand column) and final seed germination in continuous darkness (right-hand column), as a function of constant temperatures, for three species of *Muscari*. Circled numbers (right-hand column) are T_{50} values in days (time needed for 50% of final germination). The solid squares (right-hand column) correspond to final dark germination for the ungerminated seed samples (same samples shown in circles) upon transfer to the optimal temperature (10°C for *M. comosum* and *M. neglectum* and 15°C for *M. commutatum*). The transfer took place 1 month after onset of imbibition (in *M. neglectum* at 20 and 25°C: after 3 months). Vertical bars denote \pm SE.

to be the fastest among the three species. In all cases, far-red (canopy simulating) light, applied during the warm period, resulted in only a slight delay of germination compared to the dark control. Whereas a similar effect of white light (slight decrease of germination rate) was observed in *M. comosum* and *M. commutatum*, germination was dramatically inhibited

in *M. neglectum*, reaching only *c.* 10%. However, in this latter case no secondary dormancy was imposed; when ungerminated seeds that had remained under simulated natural conditions and diurnal alternations of white light and dark for about 1 month were transferred to 10°C in the dark, a further 80% germinated over a period of 30 days.

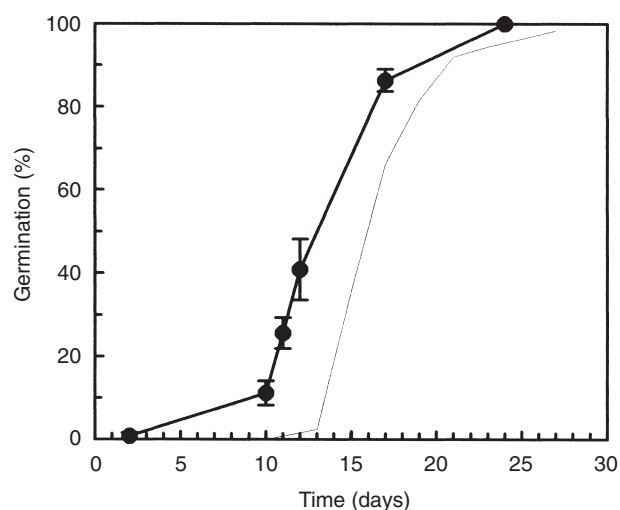


Figure 2. Time courses of germination for *Muscari comosum* seeds at 10°C, in continuous darkness. (●) Seeds that have undergone chipping, i.e. part of the seed coat and a small section of the endosperm have been cut away to expose the embryonic radicle. The thin line (right) corresponds to untreated, intact seeds (cf. Fig. 1). Vertical bars denote \pm SE.

Discussion

Temperature range and rate of germination

The temperature range of dark germination in the *Muscari* species studied seems typically Mediterranean (Thompson, 1970; Thanos, 1993; Skordilis and Thanos, 1995) and is consistent with the species origin and distribution. Full germination took place at relatively cool temperatures (5–20°C), with *M. neglectum* characterized by the narrowest range (10–15°C), while germination of *M. comosum* and *M. commutatum* was additionally manifested at 5 and 20°C, respectively. Due to the limited number of seeds, *M. weissii* was tested only at 15°C, where full germination was obtained with a T_{50} value of 14 days (Table 1). On the basis of germination speed, the optimal temperature was 10°C for *M. comosum* and *M. neglectum* and 15°C for *M. commutatum*. Although the temperature of 15°C is frequently recorded as optimal among species growing in regions with a Mediterranean climate, the particularly cool temperature of 10°C found in the present study is rather unusual. A similar case is that of the liliaceous geophyte, *Chionodoxa lochiaie*, where germination took place exclusively at 10°C with a T_{50} value of 53 days (Kadis, 1995). The low temperature optima for manifestation of germination were also demonstrated in the experiments carried out under simulated natural conditions (Fig. 3), where germination took

place only after the temperature decreased and matched the favourable range. All species were additionally characterized by a slow germination rate, with T_{50} values ranging between 8 and 24 days under optimal conditions. Having imbibed at warm inhibitory temperatures, seeds of *M. comosum*, *M. neglectum* and *M. commutatum* were able to germinate fully upon transfer to the optimum temperature in the dark. However, the chilling temperature of 5°C had diverse effects: slight suppression of germination in *M. comosum* and full inhibition for *M. commutatum* and *M. neglectum*. In the latter species, seeds that had imbibed for 1 month at 5°C germinated up to only 60% upon subsequent transfer to the optimal temperature of 10°C (Fig. 1), whereas after prolonged imbibition (3 months at 5°C), no germination took place upon transfer to the optimal temperature. When a tetrazolium test was applied, these ungerminated seeds were not stained, implying a loss of viability due to prolonged exposure to chilling temperatures. A similar adverse effect by prolonged chilling has been reported in the typical Mediterranean pine, *Pinus halepensis* (Skordilis and Thanos, 1995), as well as in the endemic geophyte of Cyprus, *Scilla morrisii* (Kadis, 1995).

A 'Mediterranean' temperature range of germination, similar to the one found in the present study, has been recorded in the Greek endemic, maritime geophyte, *Allium staticiforme* (10–20°C: Thanos *et al.*, 1991; Delipetrou, 1996), as well as in the endemic plants of Cyprus, *A. willeianum* and *A. autumnale* (10–15°C: Skordilis and Georghiou, personal communication). Likewise, in three endemic and endangered geophytes of Cyprus (*Scilla morrisii*, *Crocus hartmannianus* and *C. cyprius*), germination took place at 10 and 15°C in the first two species and only at 10°C in the latter. In all cases the pace of germination was notably slow, with T_{50} values ranging from 30 to 60 days (Kadis, 1995). Finally, data on germination as a function of temperature in geophytes of the Negev Desert highlands (Israel) are in agreement with the results of the present study [10–20°C for *Tulipa systola*, *Bellevalia eigii* and *B. desertorum* (Boeken and Gutterman, 1990); 10–15°C for *Allium truncatum* and *A. rothii* (Gutterman *et al.*, 1995)].

Timing of germination

The Mediterranean climate is characterized by a considerable unpredictability of temperature and precipitation. Water availability, in particular, is extremely variable, both within a single growing season and among consecutive years. The present experimental results (low germination rate and the requirement of a narrow range of cool temperatures) suggest that field germination of *Muscari* seeds is

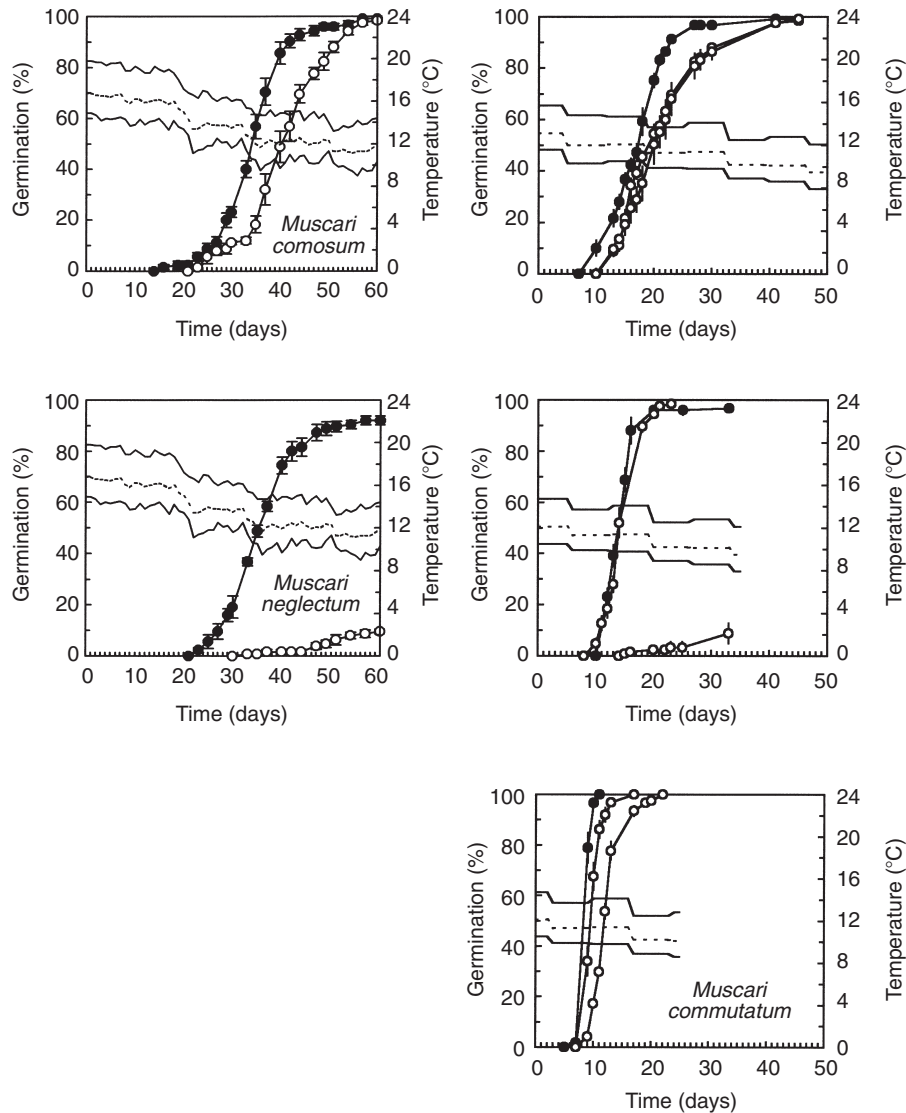


Figure 3. Germination time courses for three species of *Muscari* under simulated 'November–December' conditions (left-hand column; time 0 corresponds to '1 November') and 'December–January' conditions (right-hand column; time 0 corresponds to '1 December') for the upper diagram and '15 December' for the other two. Lines represent average values for daily (left-hand column) or weekly (right-hand column) temperatures (upper and lower solid lines: max. and min.; stippled line: mean). Solid circles, continuous darkness; open and grey circles, white light/dark and far-red/dark diurnal alternations, respectively. Vertical bars denote \pm SE.

tuned to take place well into the rainy season, in early winter, and provided that a quite lengthy, uninterrupted water supply is ensured. Such a 'delay mechanism' is considered an advantageous ecological adaptation towards the unpredictable rainfall pattern during the start of the rainy period in the Mediterranean climate (Thanos *et al.*, 1995).

Moreover, when higher temperatures coupled with water availability happen to prevail, germination is inhibited; however, no secondary

dormancy is imposed and, with a subsequent decrease of temperatures, germination can eventually take place (depending, of course, upon water supply). On the other hand, dry winter spells interrupting seed imbibition, in combination with the considerably slow pace of germination, may suppress radicle emergence in a fraction of the seed population, postponing germination until the next rainy season. Thus, it can be postulated that buried seeds of the *Muscari* species examined in the present study can

Table 1. Final seed germination (%) and germination rate (T_{50}) of *Muscari weissii* and three lots of *M. neglectum*, at 15°C. T_{50} is the time needed for 50% of the final germination. In all cases one sample of 25 seeds was used except for *M. neglectum*, Chania ($n = 50$)

| | Dark | | Continuous white light | |
|---------------------------------|------|-----------------|------------------------|-----------------|
| | % | T_{50} (days) | % | T_{50} (days) |
| <i>M. weissii</i> (Karpathos) | 100 | 14 | 56 | 36 |
| <i>M. neglectum</i> (Chania) | 100 | 17 | 80 | 24 |
| <i>M. neglectum</i> (Lasithi) | 96 | 15 | 8 | ≈ 40 |
| <i>M. neglectum</i> (Karpathos) | 80 | 16 | 24 | ≈ 50 |

persist in the soil (in the absence of appropriate cues), and germination can be distributed over more than one year. This hypothesis may well explain the observation by Theophrastus that *M. comosum* seedlings emerge in two consecutive years (HP 7.13.5). Similarly, seeds of *Muscari pulchellum* subsp. *clepsydroides* sown in a greenhouse in August were reported (Karlén, 1984) to start germinating in January and reach a final percentage of 51.2% at the end of April, while an additional 6.4% were found to germinate in the following 2 years. Finally, in *Muscari* subgenus *Leopoldia*, c. 50% of the seeds from intra- and interspecific crosses germinated during the first year and another 20% during the second (Bentzer, 1973).

The role of the seed coat

Chipping performed at a particular spot (point of radicle emergence) proved the most effective pretreatment for full germination in four liliaceous species, namely *Muscari atlanticum*, *Allium ursinum*, *Anthericum liliago* and *Asphodelus tenuifolius* (Newman, 1980). In the present study, chipping of *M. comosum* seeds resulted only in a slight enhancement of germination rate, since no primary dormancy was present. Therefore, the seed coat does not seem to be associated with the delay of germination in darkness, observed in the present study, as a factor of either water impermeability and/or mechanical restriction to radicle protrusion. Conversely, a quite plausible suggestion that merits further research is the post-maturation growth requirement of *Muscari* embryos, which are small, linear and apparently underdeveloped, as observed previously in many species of *Liliaceae* (Baskin and Baskin, 1998).

The role of light

Far-red light caused only a slight delay of germination in *M. comosum*, *M. neglectum* and *M. commutatum*, suggesting that germination in the field

is feasible even under dense leaf canopies. On the other hand, white light, simulating daylight in duration and quality, resulted in a decrease of germination rate in *M. comosum* and *M. commutatum*. Moreover, in *M. weissii* and *M. neglectum* a marked inhibition was observed, suggesting that under natural conditions germination of seeds exposed to direct sunlight, in gaps or open areas, is considerably restricted in the former species and almost totally inhibited in the latter. Furthermore, imbibition of *M. neglectum* seeds for a relatively long period under this unfavourable light regime leads to the induction of a secondary dormancy (photodormancy).

The inhibitory role of white light in the germination of geophytes has been demonstrated in several other cases: *Allium staticiforme* (under 'natural' white light, Thanos *et al.*, 1991; under white light/dark diurnal alternations, Delipetrou, 1996), *A. truncatum* and *A. rothii* (under naturally fluctuating temperatures, Gutterman *et al.*, 1995), *Bellevalia brevipedicellata* (under continuous white light, Delipetrou, 1996) and in *Pancratium maritimum* (at all temperatures suitable for germination, Keren and Evenari, 1974; under white light/dark diurnal alternations, Delipetrou, 1996).

The role of fire

The seeds of *M. comosum*, *M. neglectum* and *M. commutatum* of the present study were collected from populations thriving in recently burned areas. However, no primary dormancy was found and the germination took place without any fire-related stimuli. Similarly, a study of Californian and South African geophytes revealed a lack of fire-stimulated germination (Keeley and Bond, 1997). Germination of heat-treated seeds of two liliaceous species, *Calochortus splendens* (Keeley and Keeley, 1987) and *Zigadenus fremontii* (Keeley *et al.*, 1985), was decreased by 25% or more (Baskin and Baskin, 1998). On the other hand, geophytes are widely distributed in all mediterranean-climate regions, and many of them flower prolifically

after fire and recruit seedlings in the following years. *M. comosum*, *M. neglectum* and *M. commutatum* were recorded as common species in a burned *Pinus halepensis* forest of Mt. Parnes, Attica, during the initial (3-year long) postfire period (Thanos *et al.*, 1996). Thus, in fire-prone ecosystems, survival of *Muscari* species is due to resprouting, but seedling recruitment seems to take place very early in the postfire succession through a substantial increase of reproductive activity, possibly the result of reduced competition.

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Nitrogen Fixation: Global Perspectives

Edited by **T Finan**, *McMaster University, Canada*, **M R O'Brian**, *State University of New York*, **D B Layzell**, *Queen's University, Canada*, **J K Vessey**, *University of Manitoba, Canada*, and **W Newton**, *Virginia Polytechnic and State University, USA*

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