Seed Science Research (2012) **22**, 161–167
doi:10.1017/S0960258512000037
© *Cambridge University Press 2012*

REVIEW PAPER

Incidence and ecology of very fast germination

R.F. Parsons*
Department of Botany, La Trobe University, Bundoora, Victoria 3086, Australia

(Received 5 December 2011; accepted after revision 31 January 2012; first published online 6 March 2012)

Abstract

A group of flowering plant species is known to germinate in less than 24 h from imbibition, but this phenomenon is often overlooked in the current literature. Here, I review this topic by searching the literature published since 1967 and listing the 28 most detailed cases found. Of these, 20 are species of Amaranthaceae (all formerly treated as Chenopodiaceae); 15 of these are from the subfamily Salsoloideae, which is characterized by the possession of spiral embryos. The non-chenopods listed are small numbers of species from the families Acanthaceae, Cruciferae, Gramineae (one species) and Salicaceae (*Populus* and *Salix*). Seeds of the Salsoloideae contain fully differentiated embryos. On imbibition, the embryo cells elongate and the spiral embryo uncoils and ruptures the thin seed coat. This can occur in as little as 10 min. Nearly all of the families showing very fast germination have small to very small seeds and little or no endosperm. Most species have soft, thin seed coats that imbibe water readily. All are from high-stress habitats, either arid or saline or from active floodplains, where they can rapidly exploit temporarily favourable conditions for germination. They exhibit one of two contrasting germination behaviours, either having seeds which all germinate within a very short time of wetting or having seed persistence whereby small amounts of rain cause germination of small fractions of seed from a long-living soil seed bank. Serious confusion in the literature in the use of the term 'opportunistic' is pointed out and clarified.

Keywords: dimorphic seeds, embryo, mucilage, opportunistic strategy, pioneer, seed size

*Correspondence
Fax: + 61(0)3 94791188
Email: r.parsons@latrobe.edu.au

Introduction

Using the definition of seed germination in flowering plants as the emergence of the radicle or shoot from the seed coat, germination speed is the time that event takes from the start of imbibition (Baskin and Baskin, 1998). The questions of which species germinate most quickly and how fast they germinate are hardly touched on in the excellent review text on germination by Baskin and Baskin (1998). Here, I briefly review the widely scattered literature on these subjects.

For a temperate flora, Grime *et al.* (1981) used the term 'rapidly-germinating' for species germinating in less than 4 d, while for desert annuals, Gutterman (2001) classified germination speed as (a) fast – less than 1 d; (b) intermediate – 1–2 d; (c) slow – more than 2 d. Because, in general, desert annuals germinate very quickly compared to other groups (see Grime *et al.*, 1981), here I will use the phrase 'very fast' to refer to species germinating in less than 1 d.

From the cases studied in detail, it is clear that fast germination can be of profound ecological significance in minimizing seedling mortality in a range of stressful habitats. Examples include both desert annuals in areas where droughts are common (Gutterman, 2003) and pioneer tree species of *Populus* and *Salix* from well-watered, temperate floodplains where the main causes of seedling mortality are seasonal desiccation and removal of seedlings by floods (Karrenberg *et al.*, 2002). Here, my aim is to further clarify the role of fast germination by giving an overview of its incidence in flowering plants and its relationship to habitat factors.

Methods

Because the first detailed account of very fast germination and its causes is that of Wallace *et al.* (1968), literature published from 1968 to the present was searched for records of flowering plant species for which the seeds germinate in less than 24 h. The papers

https://doi.org/10.1017/S0960258512000037 Published online by Cambridge University Press

by Faust (1936) and Williams (1960) are included for some minor points they make in passing. The databases searched were Biological Abstracts, Ingenta connect and ISI Web of Knowledge, using the search string: ((rapid or fast or 'very fast') and seed germination). I also used (time to germination). This was supplemented by using references from the author's personal database and papers cited therein. Values for minimum time to germination were often gleaned from tables and figures from diverse literature with a variety of main aims. The aim was not to provide an exhaustive list but to cover enough literature to indicate the main families and genera in which very fast germination is found. The data on grasses refer to germination of caryopses, while those on Amaranthaceae can include cases where the seed is covered by persistent fruit layers. For simplicity, such cases are treated as seeds here. Nomenclature for families and genera follows Mabberley (2008), while use of species names for *Salsola* follows Mosyakin (2003). Authors for species names are given in Table 1; those for species extra to Table 1 are given in the text.

Results

For species showing very fast germination, the survey eventually recorded 20 species of Amaranthaceae (all formerly treated as Chenopodiaceae), three species of Salicaceae, two of both Acanthaceae and Cruciferae and one Gramineae (Table 1).

Amaranthaceae

The group of species that was formerly Family Chenopodiaceae is mostly made up of shrubs and herbs, especially from arid and semi-arid areas. Seed size for the species in Table 1 ranges from 0.9 mm to 2 mm, which is small to medium using the categories of Ellis *et al.* (1985). True endosperm is nearly or quite absent; when perisperm is absent too, the embryo entirely fills the seed coat (Wallace *et al.*, 1968; Cronquist, 1981). Mucilaginous seeds are only known in *Beta* and *Spinacia* (Heydecker *et al.*, 1971; Kuhn, 1993; Kreitschitz, 2009; Western, 2011).

Wallace *et al.* (1968) highlighted the fact that the pioneer annual weed *Salsola tragus* (Amaranthaceae; given as *S. kali*) can germinate in less than 29 min. This is a case where, before imbibition, the seeds contain fully differentiated embryos coiled in the form of a spiral. On water addition, germination consists merely of the uncoiling of the spiral embryo as the embryo cells elongate so that the embryo ruptures the seed coat (Wallace *et al.*, 1968). *Salsola tragus* is a member of subfamily Salsoloideae which is the only subfamily in the family characterized by possession of spiral embryos (Kuhn, 1993). The subfamily includes at least 15 species showing very fast germination, by far the largest such group (Table 1). For one of the group, the Sahara Desert species *Anabasis aretioides*, its early development is described: 'Saturated with water after a rain shower, seeds of *Anabasis aretioides* unfold their embryos in ten minutes. Ten hours later, their roots are anchored in the soil and the spread green cotyledons are capable of photosynthesis.' (Grenot, 1974). Ten minutes is the fastest time for germination I recorded (Table 1). Of the genera in Table 1, *Salsola* is the one for which most data are available; they are partly summarized here. An extremely short life cycle of within 3 months is known for *S. tragus* (as *S. kali*; Johnson, 1998). For the same species, it has been suggested that the unwinding of the embryo at germination is important in forcing the radicle into the soil (as *S. kali*; Wallace *et al.*, 1968). Finally, in a study of the germination of fresh seeds of species from a cold desert in China, of the eight species of annuals, only *Salsola collina* Pall. (the sole species of Salsoloideae studied) germinated at high percentages. The other annuals, including *Chenopodium album* L. and *C. vulvaria* L. from subfamily Chenopodioideae in the Amaranthaceae, required dormancy-breaking treatment (Wesche *et al.*, 2006). This striking difference in germination strategy requires elucidation in this context.

At least five of the species of Salsoloideae in Table 1 have dimorphic seeds. The best-understood case is that of *Suaeda acuminata* of central Asian deserts. It has both large, brown, soft-coated seeds and smaller, black, hard-coated (but water-permeable) seeds. Fresh brown seeds are non-dormant, imbibe water readily and most have germinated 6 h from imbibition. Fresh black seeds have physiological dormancy, imbibe water slowly and, even after 20 d, less than 7% have germinated. Both morphs have fully developed embryos before imbibition (Wang *et al.*, 2012). A closely analogous case is that of *Suaeda salsa* (Table 1; Song *et al.*, 2008). The case of *Halogeton glomeratus* is also closely analogous (Williams, 1960) except that, strangely, the seed coat colours are reversed, i.e. the black morph is the non-dormant, fast-germinating one. The similar cases in *Salsola* involve very fast germinating, large, non-dormant, green seeds and slow germinating, small yellow seeds which are dormant when fresh (Negbi and Evenari, 1961; Negbi and Tamari, 1963; Wei *et al.*, 2007). In *S. affinis*, the two behaviours are described as 'opportunistic' (green seed) and 'cautious' (yellow seed) (Wei *et al.*, 2007). Clearly, having two such complementary behaviours means that a single seed batch can provide seedlings over a longer period and a wider range of conditions than either behaviour alone can (Wei *et al.*, 2007). Very fast germination behaviour requires extreme embryo and seed coat specializations which may be incompatible with a longer-term, more cautious strategy, thus

https://doi.org/10.1017/S0960258512000037 Published online by Cambridge University Press

https://doi.org/10.1017/S0960258512000037 Published online by Cambridge University Press

Table 1. Minimum time to germination, life form, natural range and habitat for flowering plants that can germinate in less than 24 h from imbibition

Family/species	Minimum time to germination	Life form	Natural range	Habitat	Notes	References*
Acanthaceae						
Blepharis ciliaris (L.) B.L. Burtt (as *B. persica*)	<50 min	Perennial herb	Eurasia, Africa	Arid; non-saline		17
B. sindica T. Anders.	<3 h	Annual	Asia	Arid; non-saline		18
Amaranthaceae						
(a) Subfamily Chenopodioideae; embryos annular or curved						
Bassia dasyphylla (Fisch. et Mey.) O. Kuntze	<12 h	Annual	Asia	Arid; non-saline dunes	Can be pioneer	1
Chenopodium quinoa Willd.	<2 h	Annual	South America	Semiarid, mesic; saline, non-saline		7
Kochia prostrata (L.) Schrad.	<1 d	Shrub	Eurasia	Arid, semiarid; saline		2
K. scoparia (L.) Schrad.	<1 d	Annual	Eurasia	Arid, semiarid; saline		2
(b) Subfamily Salicornioideae; embryos annular or curved						
Kalidium caspicum (L.) Ung-Sternb.	<12 h	Shrub	China	Arid; saline		3
(c) Subfamily Salsoloideae; embryos spiral						
Anabasis aretioides Moq. & Coss.	10 min	Shrub	Africa	Arid; non-saline	A cushion plant	20
Halogeton glomeratus (M. Bieb.) Mey.	< 1 h†	Annual	Eurasia	Arid, semiarid; saline, non-saline	Seeds dimorphic; can be pioneer	4
Haloxylon ammodendron (Mey.) Bunge	< 1 d	Shrub	Asia	Arid; saline and non-saline		5
H. persicum Bunge ex Boiss. et Buhse	<1 d	Shrub	Asia	Arid; non-saline		5
H. salicornicum (Moq.) Bunge	45 min	Shrub	Africa, Asia	Arid; saline		6
H. stocksii Hook. f. (as *H. recurvum*)	25 min	Shrub	Asia	Arid; saline		6
Salsola affinis C.A. Mey.	<4 h†	Annual	Eurasia	Arid; saline	Seeds dimorphic	13
S. tragus L. (as *S. kali*)	<29 min	Annual	Eurasia, Africa	Arid, semiarid; saline, non-saline	A tumble weed; pioneer	14
S. vermiculata L.	<1 d	Shrub	Eurasia, Africa	Arid, semiarid; saline, non-saline	Can be pioneer	15
S. volkensii Scheinf. & Asch.	<1 h†	Annual	Eurasia, Africa	Arid; non-saline	Seeds dimorphic; pioneer	16
Sarcobatus vermiculatus (Hook.) Torr.	<1 h; see text	Shrub	North America	Arid, semiarid; saline		8
Suaeda acuminata L.	6 h†	Annual	Asia	Arid; saline	Seeds dimorphic	9
S. monoica Forssk. ex J.F. Gmel.	<1 d	Shrub	Africa, Asia	Arid, semiarid; saline		10
S. physophora Pallas	<1 d	Shrub	Eurasia	Arid; saline		11
S. salsa (L.) Pallas	<1 d†	Annual	Eurasia	Mesic; saline	Seeds dimorphic	12
Cruciferae						
Anastatica hierochuntica L.	<5 h	Annual	Eurasia, Africa	Arid; non-saline	A resurrection plant	19
Diplotaxis harra (Forssk.) Boiss.	<1 d	Annual	Eurasia, Africa	Arid, semiarid; non-saline		21
Gramineae						
Schismus arabicus Nees	<4 h	Annual	Eurasia, Africa	Arid, semi-arid; non-saline	Can be pioneer	22
Salicaceae						
Populus deltoides Marsh.	<8 h	Tree	North America	Floodplains	Pioneer	24
P. grandidentata Michaux	<7 h	Tree	North America	Mesic woodlands	Pioneer	23
Salix interior Rowlee	<8 h	Tree	North America	Floodplains	Pioneer	24

* References: 1, Tobe *et al.* (1999); 2, Orlovsky *et al.* (2011); 3, Qu *et al.* (2008); 4, Williams (1960); 5, Tobe *et al.* (2000); 6, Sharma and Sen (1989); 7, Delatorre-Herrera and Pinto (2009); 8, Eddleman (1979); 9, Wang *et al.* (2012); 10, Waisel and Ovadia (1972); 11, Song *et al.* (2005); 12, Song *et al.* (2008); 13, Wei *et al.* (2007); 14, Wallace *et al.* (1968); 15, Creager (1988); 16, Negbi (1968); 17, Gutterman (1972); 18, Narita and Wada (1998); 19, Gutterman and Shem-Tov (1997); 20, Grenot (1974); 21, Tlig *et al.* (2008); 22, Gutterman (2003); 23, Faust (1936); 24, Noble (1979).

† Seeds dimorphic; this figure applies to the very fast germinating type.

favouring the evolution of dimorphic seeds with contrasting behaviour.

A related aspect of Salsoloideae germination is that, at least in *Salsola volkensii* and *Suaeda monoica*, what protrudes first through the seed coat is the hypocotyl; radicle expansion and development are delayed. Hypocotyls are far better protected against dehydration than radicles by thick cuticular layers; this may be critical in allowing seedlings to survive the first few days after germination following light rain in desert areas (Negbi and Evenari, 1961; Waisel and Ovadia, 1972). It is not known whether this behaviour is widespread in other species of Salsoloideae.

Despite the small sample size and varying methods of assessing minimum time to germination, from the data in Table 1 it is possible that, in general, species of *Salsola* are able to achieve faster germination than those of *Suaeda*. If so, this can be associated with the fact that, while both genera have seeds with membranous pericarps, in *Salsola* the seed coat itself is membranous while in *Suaeda* it is 'shining black, crustaceous' (Stanley and Ross, 1983) which may reduce imbibition rates compared to those in *Salsola*. An exception to the generalization above is *Suaeda arbusculoides* L.S. Smith, which has a transparent, membranous seed coat (Stanley and Ross, 1983); establishing its germination speed would be an excellent way to test the hypothesis above. Turning to the other Salsoloideae, further relevant details to those in Table 1 are only available for *Sarcobatus vermiculatus* (Eddleman, 1979). The embryo is enclosed in a single transparent membrane called either a seed coat by Hils *et al.* (2003), who I will follow here, or a pericarp (Eddleman, 1979). On imbibition, germination normally occurs rapidly through ruptured or weak areas in the seed coat. However, in some seedlots, despite rapid imbibition, the seed coat does not rupture and the embryo remains trapped inside for at least 30 d unless the coat is ruptured with a needle. At the other extreme, in one seedlot, on many seeds the radicles were already protruding before imbibition. In this seedlot, the seed coat 'is not continuous around the embryo' (Eddleman, 1979). I have ignored this behaviour in Table 1 and simply put that germination takes less than 1 h. Turning to the subfamilies with annular or curved rather than spiral embryos (Table 1), *Kalidium* at least is like the Salsoloideae in having fully developed embryos in the seed before imbibition (Qu *et al.*, 2008).

Acanthaceae

Very fast germination is known in two desert species of *Blepharis*, both herbs (Table 1). Few other relevant data are known for these, except that germination is 'more orthodox' than the embryo-uncoiling type shown by *Salsola* (Gutterman, 1972). The family itself has very thin seed coats, no endosperm (in the subfamily which includes *Blepharis*) and large embryos which are straight or curved but not spirally coiled (Cronquist, 1981). For a mainly herbaceous family and in the context of the families in Table 1, seed size is large, e.g. 7.8 mg in *B. sindica* (Narita and Wada, 1998) and 5–10 mg in *B. linariifolia* Pers. (Elberse and Breman, 1989). In *B. ciliaris*, mucilaginous trichomes on the seed anchor the seed and seedling to the soil (Gutterman and Shem-Tov, 1997).

Cruciferae

Very fast germination is known in two annual desert species (Table 1). In this family, the embryo is strongly curved or variously folded. In some species, the cotyledons are spirally coiled (Appel and Al-Shehbaz, 2003), thus resembling those of the *Salsola* type. The behaviour of such spirally coiled embryos at germination has not been described. As in *Salsola*, the embryo is large, completely filling the seed (Rendle, 1938). In this family, the seeds are generally small; in Saharan species of *Diplotaxis* they can be dust-like (seed weight *c.* 0.05 mg) (Appel and Al-Shehbaz, 2003). Seed coats are thin and seed dormancy occurs in most species (Ellis *et al.*, 1985). Seed coats of some taxa become mucilaginous when wetted, including *Anastatica* and *Diplotaxis harra* (Gutterman, 2002).

Gramineae

The desert species *Schismus arabicus* is the sole monocot in Table 1; it is often a pioneer, has dust-like seeds and is 'one of the fastest maturing desert annuals'. It proceeds from imbibition to flowering in 4 weeks (Brooks, 2000); even shorter life cycles, from 8 to 10 d, from germination to seed production are known in the Saharan *Boerhavia repens* L. (Cloudsley-Thompson and Chadwick, 1964).

Salicaceae

Many papers document, in passing, the germination of species of *Populus* and *Salix* within 24 h (e.g. see the three cited in Karrenberg *et al.*, 2002), but few provide any details. In Table 1, I have simply included only the species with the three fastest values I could find. *Populus* and *Salix* species are usually pioneer trees on active floodplains. They produce very small seeds with very thin seed coats; in *Salix*, these are transparent. The seeds lack endosperm; the seed coats are entirely filled up by the embryo (Rendle, 1938; Karrenberg *et al.*, 2002). Unusually for temperate trees, seeds of most

https://doi.org/10.1017/S0960258512000037 Published online by Cambridge University Press

Populus and *Salix* species have no dormancy; this is associated with short seed longevity (Karrenberg *et al.*, 2002). Rendle (1938) believes that their rapid germination is associated with the development of mucilaginous hairs at the base of the hypocotyl (collet hairs involved in seedling anchorage; Noble, 1979) while the embryo is still in the seed.

Cactaceae

This family does not qualify for Table 1, but shows some striking similarities with species of subfamily Salsoloideae in the Amaranthaceae. Species of Cactaceae usually have very small seeds (average 1–2 mm long) often with a thin seed coat (Barthlott and Hunt, 1993; Maiti *et al.*, 1994). The seeds are without true endosperm (Mabberley, 2008) and, in many species, show a lack of dormancy (Ortega-Baes *et al.*, 2010). The embryo may be curved or spirally rolled (Rendle, 1938). Given these characteristics, it is not surprising that, in most subfamilies, germination is fast and usually occurs within a week (Bregman and Bouman, 1983); this has been related to the thin seed coat by Maiti *et al.* (1994). Further work is needed to establish just how quickly germination can occur in such Cactaceae. As in the Cruciferae, seeds of some species produce a mucilage sheath on wetting (Barthlott and Hunt, 1993).

There are further species which fall just outside the 'less than 24 h criterion' used here for very fast germination. These are the two crucifers *Carrichtera annua* (L.) DC and *Erucaria microcarpa* Boiss. (as *Reboudia pinnata*) and *Plantago coronopus* L. (Plantaginaceae). These germinate in about 24 h or slightly longer (Gutterman and Shem-Tov, 1997).

Finally, I checked a tabulation of 'minimum days to germination' for about 550 species of Australian native flowering plants sown on to a variety of substrates. This yields just seven species for which the minimum is as short as 2 d. Of these, two are from Casuarinaceae, two from Compositae and the other three are from three different families. The Casuarinaceae and Compositae show a clear tendency for faster germination than the other families (Fox *et al.*, 1987). These possible family relationships need following up.

Discussion

Much remains to be discovered about the phenomenon of very fast germination. In the case of *Salsola tragus*, it is clear that it is mainly the result of water uptake leading to cell expansion. Cell division is not involved; the process is physical rather than physiological (Wallace *et al.*, 1968). However, this paper is the only one giving details of the process. Otherwise, all we know is that the other Salsoloideae have spirally coiled embryos like *Salsola*, with no details at all known for the other species listed.

Partly analogous behaviour is found in the germination of sporocarps of the arid-adapted fern *Marsilea*, where, on imbibition, hygroscopic mucilaginous tissue swells and within a few minutes a long wormlike structure splits the hard wall and emerges, when spores are released from it (Gifford and Foster, 1989).

In summary, all species in Table 1 (except *Schismus arabicus*) are from families in which the endosperm is absent or nearly so. Except for the Acanthaceae and *Chenopodium quinoa*, there are strong tendencies towards both small seed size (see also Grime *et al.*, 1981) and soft, thin seed coats which are often membranous or transparent and which imbibe water readily. A qualification to the point about seed coats applies to the five species of Salsoloideae with dimorphic seeds (Table 1). In the cases studied in detail, the thin-coated morph is non-dormant and germinates with the first rain while the thick-coated morph is dormant and provides a seed bank for future rain events (as discussed above). Except for the Gramineae (*Schismus*) and the Amaranthaceae (but with two exceptions), the families in Table 1 can produce mucilage on wetting, either from collet hairs at the base of the hypocotyl (in the Salicaceae; Rendle, 1938) or from the seed coat (in the other families). As well as its role in adherence to the surface soil, in the case of the seed coat, the mucilage envelope, by keeping water around the seed, can be crucial in speeding up germination (Gutterman, 2002; Kreitschitz, 2009).

Many species in Table 1 germinate over a very wide range of temperatures, leading Negbi and Evenari (1961) to state that, for some species, their germination is unusual in being 'independent of . . . temperature'. Some actual temperature ranges for germination for Table 1 species are: *Blepharis ciliaris*, 8–40°C (Gutterman, 2002); *Diplotaxis harra*, 5–30°C (Tlig *et al.*, 2008); *Salsola vermiculata*, 3–33°C (Sankary and Barbour, 1972); and *Sarcobatus vermiculatus*, 5–40°C (Romo and Eddleman, 1985). *Populus* and *Salix* also have wide ranges (Karrenberg *et al.*, 2002). Studies are needed to see if this is related to embryos being fully differentiated prior to germination, as is the case with *Salsola tragus* (Wallace *et al.*, 1968).

There is a clear relationship between very fast germination and high-stress habitats, with suites of Table 1 species variously adapted to arid, saline and active floodplain habitats. Allied to this is status as pioneer species (ten species in Table 1), including desert species like *Schismus arabicus* that become confined to disturbed areas as pioneers in the wettest parts of their range (Brooks, 2000). Species like *Halogeton glomeratus* (Williams, 1960), *Salsola tragus*

https://doi.org/10.1017/S0960258512000037 Published online by Cambridge University Press

(Wallace *et al.*, 1968) and *Schismus arabicus* (Brooks, 2000) can behave as highly invasive weeds. The essential ecology underlying the evolution of very fast germination is that seedling establishment can depend on rapid exploitation of temporarily favourable conditions (Grime *et al.*, 1981). For the desert species, after rain, fast germination can allow seedling roots to penetrate the surface soil before it dries out (Gutterman, 2003); for *Blepharis*, root length can reach 50 mm within 24 h of wetting (Gutterman, 2000).

There are two contrasting types of germination found in species with very fast germinating seeds. In one, all the seeds germinate within a very short time from wetting (e.g. *Blepharis* spp., Gutterman, 2002; *Populus* spp. and *Salix* spp., Karrenberg *et al.*, 2002; *Suaeda physophora*, Song *et al.*, 2005), while in the other, small amounts of rain cause germination of small fractions of seed from a long-living soil seed bank (e.g. *Schismus arabicus*, Gutterman, 2002). Possession of dimorphic seeds gives a species the ability to utilize both behaviours, one for each morph (see, for example, Wei *et al.*, 2007; Wang *et al.*, 2012), letting the species cope with more conditions than one behaviour alone. The main workers in this field refer to the two behaviours as strategies. Gutterman (2002) calls the first of them 'immediate germination' and the second one 'opportunistic strategy', while Wei *et al.* (2007) and Wang *et al.* (2012) call the first 'opportunistic strategy' and the second 'cautious strategy'. This confusion needs to be resolved. Brooks (2000) refers to the second strategy as 'bet-hedging' which, in my view, is a more apt term than opportunistic in such a context.

Further ramifications of very fast germination behaviour are: (1) that it may be crucial in conferring a competitive advantage, e.g. in the case of competition between *Salsola tragus* and other alien annuals in the Great Basin, USA (Young and Evans, 1972); and (2) that, because ants are said to collect seeds but not seedlings, rapid transition from seeds to seedlings allows escape from ant predation (Gutterman, 2000). Clearly, there is scope for much more work on fast germination.

Acknowledgements

I thank M. Bartley, T. Edwards, J. Morgan, I. Price, N. Scarlett and K. Watson for helpful discussions.

References

Appel, O. and Al-Shehbaz, I.A. (2003) Cruciferae. pp. 75–123 *in* Kubitzki, K. (Ed.) *The families and genera of vascular plants, vol. 5*. Berlin, Springer.

Barthlott, W. and Hunt, D.R. (1993) Cactaceae. pp. 161–196 *in* Kubitzki, K. (Ed.) *The families and genera of vascular plants, vol. 2*. Berlin, Springer.

Baskin, C.C. and Baskin, J.M. (1998) *Seeds: ecology, biogeography and evolution of dormancy and germination*. San Diego, Academic Press.

Bregman, R. and Bouman, F. (1983) Seed germination in Cactaceae. *Botanical Journal of the Linnean Society* **86**, 357–374.

Brooks, M.L. (2000) *Schismus arabicus* Nees. pp. 287–291 *in* Bossard, C.C. (Ed.) *Invasive plants of California's wildlands*. Berkeley, University of California Press.

Cloudsley-Thompson, J.L. and Chadwick, M.J. (1964) *Life in deserts*. London, G.T. Foulis.

Creager, R.A. (1988) The biology of Mediterranean Saltwort, *Salsola vermiculata*. *Weed Technology* **2**, 369–374.

Cronquist, A. (1981) *An integrated system of classification of flowering plants*. New York, Columbia University Press.

Delatorre-Herrera, J. and Pinto, M. (2009) Importance of ionic and osmotic components of salt stress on the germination of four quinua (*Chenopodium quinoa*) selections. *Chilean Journal of Agricultural Research* **69**, 477–485.

Eddelman, L.E. (1979) Germination in Black Greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.). *Northwest Science* **53**, 289–294.

Elberse, W.Th. and Breman, H. (1989) Germination and establishment of Sahelian rangeland species. I. Seed properties. *Oecologia* **80**, 477–484.

Ellis, R.H., Hong, T.D. and Roberts, E.H. (1985) *Handbook of seed technology for genebanks. Vol. II, Compendium of specific germination information*. Rome, International Board for Genetic Resources.

Faust, M.E. (1936) Germination of *Populus grandidentata* and *P. tremuloides*, with particular reference to oxygen consumption. *Botanical Gazette* **97**, 808–821.

Fox, J., Dixon, B. and Monk, D. (1987) Germination in other plant families. pp. 211–222 *in* Langkamp, P. (Ed.) *Germination of Australian native plant seed*. Melbourne, Inkata Press.

Gifford, E.M. and Foster, A.S. (1989) *Morphology and evolution of vascular plants*. New York, Freeman.

Grenot, C.J. (1974) Physical and vegetational aspects of the Sahara Desert. pp. 103–164 *in* Brown, G.W. (Ed.) *Desert biology*. New York, Academic Press.

Grime, J.P., Mason, G. and Curtis, A.V. (1981) A comparative study of germination characteristics in a local flora. *Journal of Ecology* **69**, 1017–1059.

Gutterman, Y. (1972) Delayed seed dispersal and rapid germination as survival mechanisms of the desert plant *Blepharis persica* (Burm.) Kuntze. *Oecologia* **10**, 145–149.

Gutterman, Y. (2000) Environmental factors and survival strategies of annual plant species in the Negev Desert, Israel. *Plant Species Biology* **15**, 113–125.

Gutterman, Y. (2001) *Regeneration of plants in arid ecosystems resulting from patch disturbance*. Dordrecht, Kluwer.

Gutterman, Y. (2002) *Survival strategies of annual desert plants*. Berlin, Springer.

Gutterman, Y. (2003) The inhibitory effect of Negev Desert loess soil on the fast germinating caryopses of *Schismus arabicus* (Poaceae). *Journal of Arid Environments* **54**, 619–631.

Gutterman, Y. and Shem-Tov, S. (1997) The efficiency of the strategy of mucilaginous seeds of some common annuals of the Negev adhering to the soil to delay collection by ants. *Israel Journal of Plant Sciences* **45**, 317–327.

https://doi.org/10.1017/S0960258512000037 Published online by Cambridge University Press

Heydecker, W., Chetram, R.S. and Heydecker, J.C. (1971) Water relations of beetroot seed germination, II. *Annals of Botany* **35**, 31–42.

Hils, M.H., Thieret, J.W. and Morefield, J.D. (2003) *Sarcobatus*. pp. 387–389 *in* Flora of North America Editorial Committee (Eds) *Flora of North America, vol. 4*. New York, Oxford University Press.

Johnson, N.C. (1998) Responses of *Salsola kali* and *Panicum virgatum* to mycorrhizal fungi, phosphorus and soil organic matter: implications for reclamation. *Journal of Applied Ecology* **35**, 86–94.

Karrenberg, S., Edwards, P.J. and Kollman, J. (2002) The life history of Salicaceae living in the active zone of floodplains. *Freshwater Biology* **47**, 733–748.

Kreitschitz, A. (2009) Biological properties of fruit and seed slime envelope: how to live, fly and not die. pp. 11–30 *in* Gorb, S.N. (Ed.) *Functional surfaces in biology, vol. 1*. Dordrecht, Springer.

Kuhn, U. (1993) Chenopodiaceae. pp. 253–281 *in* Kubitzki, K. (Ed.) *The families and genera of vascular plants, vol. 2*. Berlin, Springer.

Mabberley, D.J. (2008) *Mabberley's plant-book* (3rd edition). Cambridge, Cambridge University Press.

Maiti, R.K., Hernandez-Pinero, J.L. and Valdez-Marroquin M. (1994) Seed ultrastructure and germination of some species of Cactaceae. *Phyton* **55**, 97–105.

Mosyakin, S.L. (2003) *Salsola*. pp. 398–403 *in* Flora of North America Editorial Committee (Eds) *Flora of North America, vol. 4*. New York, Oxford University Press.

Narita, K. and Wada, N. (1998) Ecological significance of the aerial seed pool of a desert lignified annual, *Blepharis sindica* (Acanthaceae). *Plant Ecology* **135**, 177–184.

Negbi, M. (1968) The status of summer annuals in Palestine. *Israel Journal of Botany* **17**, 217–221.

Negbi, M. and Evenari, M. (1961) The means of survival of some desert summer annuals. pp. 249–259 *in Plant-water relationships in arid and semi-arid conditions. Arid zone research, vol. 16*. Paris, UNESCO.

Negbi, M. and Tamari, B. (1963) Germination of chlorophyllous and achlorophyllous seeds of *Salsola volkensii* and *Aellenia autrani*. *Israel Journal of Botany* **12**, 124–135.

Noble, M.G. (1979) The origin of *Populus deltoides* and *Salix interior* zones on point bars along the Minnesota River. *American Midland Naturalist* **102**, 59–67.

Orlovsky, N.S., Japakova, U.N., Shulgina, I. and Volis, S. (2011) Comparative study of seed germination and growth of *Kochia prostrata* and *Kochia scoparia* (Chenopodiaceae) under salinity. *Journal of Arid Environments* **75**, 532–537.

Ortega-Baes, P., Aparicio, M. and Galindez, G. (2010) Vivipary in the cactus-family: an evaluation of 25 species from northwestern Argentina. *Journal of Arid Environments* **74**, 1359–1361.

Qu, X., Baskin, J.M., Wang, L. and Huang, Z. (2008) Effects of cold stratification, temperature, light and salinity on seed germination and radicle growth of the desert halophyte shrub, *Kalidium caspicum* (Chenopodiaceae). *Plant Growth Regulation* **54**, 241–248.

Rendle, A.B. (1938) *The classification of flowering plants, vol. 2*. Cambridge, Cambridge University Press.

Romo, J.T. and Eddleman, L.E. (1985) Germination response of greasewood (*Sarcobatus vermiculatus*) to temperature, water potential and specific ions. *Journal of Range Management* **38**, 117–119.

Sankary, M.N. and Barbour, M.G. (1972) Autecology of *Salsola vermiculata* var. *villosa* from Syria. *Flora* **161**, 421–439.

Sharma, T.P. and Sen, D.N. (1989) A new report on abnormally fast germinating seeds of *Haloxylon* spp. – an ecological adaptation to saline habitat. *Current Science* **58**, 382–385.

Song, J., Feng, G., Tian, C. and Zhang, F. (2005) Strategies for adaptation of *Suaeda physophora, Haloxylon ammodendron* and *H. persicum* to a saline environment during seed germination stage. *Annals of Botany* **96**, 399–405.

Song, J., Fan, H., Zhao, Y., Jia, Y., Du, X. and Wang, B. (2008) Effect of salinity on germination, seedling emergence, seedling growth and ion accumulation of a euhalophyte *Suaeda salsa*. *Aquatic Botany* **88**, 331–337.

Stanley, T.D. and Ross, E.M. (1983) *Flora of south-eastern Queensland vol. 1*. Brisbane, Queensland Department of Primary Industries.

Tlig, T., Gorai, M. and Neffati, M. (2008) Germination responses of *Diplotaxis harra* to temperature and salinity. *Flora* **203**, 421–428.

Tobe, K., Zhang, L. and Omasa, K. (1999) Effects of NaCl on seed germination of five nonhalophytic species from a Chinese desert environment. *Seed Science and Technology* **27**, 851–863.

Tobe, K., Li, X. and Omasa, K. (2000) Effects of sodium chloride on seed germination and growth of two Chinese desert shrubs, *Haloxylon ammodendron* and *H. persicum* (Chenopodiaceae). *Australian Journal of Botany* **48**, 455–460.

Waisel, Y. and Ovadia, S. (1972) Biological flora of Israel, 3. *Suaeda monoica* Forssk. ex J.F. Gmel. *Israel Journal of Botany* **21**, 42–52.

Wallace, A., Rhoads, W.A. and Frolich, E.F. (1968) Germination behaviour of *Salsola* as influenced by temperature, moisture, depth of planting and gamma irradiation. *Agronomy Journal* **60**, 76–78.

Wang, H.-L., Wang, L., Tian, C.-Y. and Huang, Z.-Y. (2012) Germination dimorphism in *Suaeda acuminata*: a new combination of dormancy types for heteromorphic seeds. *South African Journal of Botany* **78**, 270–275.

Wei, Y., Dong, M. and Huang, Z.-Y. (2007) Seed polymorphism, dormancy and germination of *Salsola affinis* (Chenopodiaceae), a dominant desert annual inhabiting the Junggar Basin of Xinjiang, China. *Australian Journal of Botany* **55**, 464–470.

Wesche, K., Pietsch, M., Ronnenberg, K., Undrakh, R. and Hensen, I. (2006) Germination of fresh and frost-treated seeds from dry Central Asian steppes. *Seed Science Research* **16**, 123–136.

Western, T.L. (2011) The sticky tale of seed coat mucilages: production, genetics and role in seed germination and dispersal. *Seed Science Research* **22**, 1–25.

Williams, M.C. (1960) Biochemical analyses, germination and production of black and brown seed of *Halogeton glomeratus*. *Weeds* **8**, 452–461.

Young, J.A. and Evans, R.A. (1972) Germination and establishment of *Salsola* in relation to seedbed environment. I. *Agronomy Journal* **64**, 214–218.

https://doi.org/10.1017/S0960258512000037 Published online by Cambridge University Press