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Physical dormancy in *Geraniaceae* seeds

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Abstract

Seed dormancy was analysed in *Geraniaceae*, testing 29,103 seeds of 35 species for seed-coat impermeability to water. Seeds of wild and cultivated species from a number of different climatic/ecological zones (northern Germany, the Canary Islands and South Africa) were investigated. Seeds from cultivated plants and natural populations had similar (±2%) percentages of water-impermeable seeds. The percentages of impermeable seeds at maturity were also mostly constant (±2%) for two different years. The species analysed contained from 0 to 100% impermeable seeds at maturity, and could be classified into three quantitative types of physical dormancy: four species with no impermeable seeds (PY^0), 10 species with a maximum of 80% impermeable seeds (PY^{80}), and 21 species with more than 80% impermeable seeds (PY^{100}). Species with different life cycles and from very different habitats, e.g. *Geranium pratense* or *Pelargonium capitatum*, belonged to the PY^{100} group. However, all of the succulent shrubs investigated from the genus *Pelargonium* were PY^0 species. Five years of dry storage at 20 ± 5°C decreased physical dormancy in a species-dependent fashion. *Erodium cicutarium*, for example, had 95% impermeable seeds at maturity; all of them became permeable during the dry storage and began to germinate immediately after placing them on a moist substrate. Physical dormancy of other species, e.g. *Pelargonium zonale*, *Pelargonium vitifolium* or *Geranium pratense*, was not affected by dry storage. Thus, physical dormancy is a diversely differentiated feature in *Geraniaceae* with regard to both percentages of impermeable seeds at maturity and maintenance of dormancy under particular conditions.

Keywords: physical dormancy, hardseededness, *Geraniaceae*, seed coat

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Introduction

Physical dormancy is caused by seed-coat impermeability to water and occurs in different plant families, such as the *Anacardiaceae*, *Fabaceae*, *Geraniaceae* and *Malvaceae* (Baskin and Baskin, 1998). Many investigations of this phenomenon have been concerned with the histological characteristics of testa impermeability (Christiansen and Moore, 1958; Rolston, 1978; Harris, 1983; Bhalla and Slattery, 1984; Egley *et al*., 1986; Bevilacqua *et al*., 1987; Kelly *et al*., 1992; Serrato-Valenti *et al*., 1992; Meisert *et al*., 1999) and with methods to overcome the impermeable barrier (Mott and McKeon, 1979; Graaf and van Staden, 1983; Patil and Andrews, 1984; Kelly and van Staden, 1985).

Environmental factors can alter seed-coat impermeability. High temperatures (McKeon and Mott, 1982; Rice, 1985), drying (Baskin and Baskin, 1974), fire (Abrams and Dickmann, 1982), low winter temperatures and effects of animals (Baskin and Baskin, 1998) have been cited as ecologically relevant. Baskin and Baskin (2000) argue for specific dormancy-breaking factors to ensure that germination begins under suitable climatic conditions with regard to increasing fitness. For instance, they analysed drying as the main controlling factor of physical dormancy in *Geranium carolinianum*, enabling this autumn-germinating species to develop following a dry summer (Baskin and Baskin, 1974). Independent of dormancy-breaking factors, it is of ecological interest to compare the extent of physical dormancy in species adapted to different habitats, identifying environmental conditions where testa impermeability has evolved as a successful type of dormancy. Information concerning the quantitative aspects of water-impermeable seeds in different species is limited. The feature 'physical dormancy' or so-called 'hardseededness' is mainly described in individual species occurring in arid or semi-arid habitats (Williams and Elliott, 1960; Baskin and Baskin, 1974).

Seed-coat impermeability in *Geraniaceae* was investigated previously in cultivated hybrids such as *Pelargonium zonale* 'Nittany Lion Red' or 'Sprinter' (Bachthaler, 1974), since the corresponding dormancy causes horticultural problems which could be

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overcome by scarification (Bachthaler, 1984). The typical *Geraniaceae* seed coat is endotestal–exotegmic (Boesewinkel, 1997), with the outer layer of the inner integument (the subpalisade layer) being lignified and functioning as the main mechanical layer. The inner layer of the outer integument (the palisade layer) is characterized by thick and lipophilic cell walls (Meisert *et al*., 1997; Meisert *et al*., 2001). This palisade layer and the closed chazal slit (Meisert *et al*., 1999) represent the structural basis of water impermeability. Testa histology of permeable and impermeable seeds within one species is uniform in structure and thickness, except in the chalazal region (Meisert, 1998).

Different *Pelargonium* hybrids (Schulz *et al*., 1991) show differences in the extent of physical dormancy and, thus, it is of special interest to analyse the percentage of water-impermeable seeds in naturally occurring *Geraniaceae* species. The *Geraniaceae* are especially suitable for comparative investigation because physical dormancy represents a conservative feature within the family (Baskin and Baskin, 1998; Meisert, 1998). Moreover, the family is widely distributed, both geographically and ecologically, from arid zones in South Africa to humid habitats in Europe. Therefore, the *Geraniaceae* can function as a model group to investigate the successful formation of water-impermeable seeds under different environmental conditions, and to analyse the relationship between the occurrence of physical dormancy in different species and their typical habitats.

Of particular interest was the question of whether *Geraniaceae* species constantly form a certain percentage of impermeable seeds, i.e. can these proportions be regarded as specific features? Furthermore, do the numbers of impermeable seeds differ among species? And finally, are there specific differences in the longevity of impermeable seeds, i.e. are there different patterns in breaking physical dormancy with regard to relevant environmental factors?

Materials and methods

Seeds from the following species were collected at seed maturity in 1995 and 1996 from natural populations in northern Germany (number of seeds collected in brackets): *Geranium dissectum* L. (2387), *G. molle* L. (1278), *G. palustre* L. (319), *G. pusillum* L. (1046), *G. pyrenaicum* Burm.f. (1722), *G. sylvaticum* L. (198) and *G. robertianum* L. (1230). Seeds were also gathered from cultivated plants in the Botanical Garden ('Berggarten') in Hannover/Germany over a period of 2 years (number of seeds collected in brackets), including: *Erodium manescavii* Coss. (337), *G. canariense* Reut. (459), *G. nodosum* L. (1064), *G. phaeum* L. (135), *G. renardii* Trautv. (313), *Pelargonium australe* Wild (3641), *P. capitatum* (L.) L'Hérit. (1113), *P. denticulatum* Jacq. (382), *P. hispidum* (L.f.) Willd. (584), *P. incrassatum* (Andr.) Sims (1904), *P. inquinans* (L.) L'Hérit. (1105), *P. mollicomum* Fourcade (932), *P. odoratissimum* (L.) L'Hérit. (898), *P. pseudoglutinosum* Knuth (580) and *P. vitifolium* (L.) L'Hérit. (1724). Additional species were cultivated in a greenhouse, and seeds were collected over two consecutive years (number of seeds collected in brackets). These included *P. candicans* Spreng. (2071), *E. botrys* (Cav.) Bert. (210), *E. chium* (L.) Willd. (1282) and *E. malacoides* (L.) L'Hér. (392). Seeds of the following species were harvested from natural populations on Tenerife/Canary Islands in 1996 (number of seeds collected in brackets): *E. botrys* (Cav.) Bert. (352), *E. chium* (L.) Willd. (229) and *E. malacoides* (L.) L'Hér. (111). Seeds from natural populations in South Africa were collected in 1997 (number of seeds collected in brackets): *P. capitatum* (L.) L'Hérit. (471), *P. carnosum* (L.) L'Hérit. (9), *P. inquinans* (L.) L'Hérit. (142), *P. peltatum* (L.) L'Hérit. (32), *P. tetragonum* (L.f.) L'Hérit. (2), *P. vitifolium* (L.) L'Hérit. (26) and *P. zonale* (L.) L'Hérit. (337). Fifty-five seeds were also collected from *P. carnosum* grown in greenhouses at the Botanical Garden in Münster/Germany. Thirty-one seeds of *P. laxum* (Sweet) G. Don were gathered in 2001 from greenhouse-grown plants at the Botanical Garden ('Berggarten') in Hannover/Germany.

The pericarp was removed from all of the collected seeds (= 29,103), and the seeds were placed on wet filter paper for 10 d at 14.5°C (=10-d test). Seeds that did not swell during the 10-d test were counted as impermeable. The water-impermeable fraction of several species from the 1996 harvest was tested again after storage for 5 years, using the same 10-d test. These were stored in small paper bags at 20 ± 5°C in a dark and dry storage room.

The thickness of the palisade and subpalisade layers was measured before storage on testa cross-sections. These measurements were carried out using a Zeiss Axiolab microscope analysing three impermeable seeds per species: *P. tetragonum*[1], *P. australe*[2], *P. candicans*[2], *P. capitatum*[2], *P. carnosum*[1], *P. denticulatum*[2], *P. hispidum*[2], *P. incrassatum*[2], *P. inquinans*[1], *P. mollicomum*[2], *P. odoratissimum*[2], *P. vitifolium*[2] and *P. zonale*[1] ([1] harvested South Africa, 1997; [2] harvested Berggarten, Hannover, 1996).

Results

Summing data from all harvests, percentages of water-impermeable seeds in the *Geraniaceae* varied greatly (Table 1). Four of the 35 species investigated did not form any water-impermeable seeds, and all the seeds of four other species were impermeable. The remaining 27 species exhibited water-impermeable fractions

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Table 1. Fraction of impermeable seeds at maturity in 35 *Geraniaceae* species (means of all collected data) and percentage of seeds within the hardseeded fraction remaining impermeable during 5 years of dry storage

Species	Percentage of impermeable seeds at seed maturity (%)	Type of physical dormancy	Percentage of seeds in the hardseeded fraction that remain impermeable during 5 years of dry storage (%)
E. manescavii	0		
P. carnosum	0	PY^0	
P. tetragonum	0		
P. laxum	0		
G. dissectum	20		0
G. molle	34		
P. australe	34		83
P. mollicomum	44		27
G. nodosum	57	PY^{80}	
G. pyrenaicum	66		0
G. pusillum	68		0
G. sanguineum	68		74
G. macrorhizum	69		35
G. palustre	70		
P. zonale	82		100
P. inquinans	85		100
G. renardii	87		
G. canariense	89		0
P. peltatum	91		
G. robertianum	93		59
E. botrys	94		
E. cicutarium	95		0
P. denticulatum	95		
E. chium	96	PY^{100}	
G. pratense	96		100
G. sylvaticum	96		
P. capitatum	98		98
P. pseudoglutinosum	98		
P. candicans	99		99
P. incrassatum	99		51
G. phaeum	99		100
E. malacoides	100		
P. hispidum	100		
P. odoratissimum	100		
P. vitifolium	100		100

ranging from 20 to 99%. Although the formation of testa impermeability in different species represents a continuum, a quantitative distinction can be made between different types of physical dormancy (PY) in the *Geraniaceae*: (1) the smallest group (PY^0) was represented by four species with only permeable seeds; (2) both permeable and impermeable seeds occurred in a group (PY^{80}) that included 10 species with impermeable seed percentages ranging from 1 to 80%; (3) the final category (PY^{100}) was characterized by species with more than 80% impermeable seeds, including 21 of 35 species representing all three genera of *Geraniaceae* investigated.

Comparing the water-impermeable seed fractions of three PY^{100}-*Pelargonium* species under natural conditions and in cultivated plants, there was little variation among them (Fig. 1). Nevertheless, in all three of these species, the hardseeded content of cultivated plants was always slightly higher than that of wild plants.

Comparing the data from two consecutive years with a minimum of 300 seeds per species for each year analysed (Fig. 2), 8 of 11 species produced similar percentages of impermeable seeds. For instance, *P. australe* (PY^{80}), produced 33% impermeable seeds in 1995 and 30% in 1996. Similarly,

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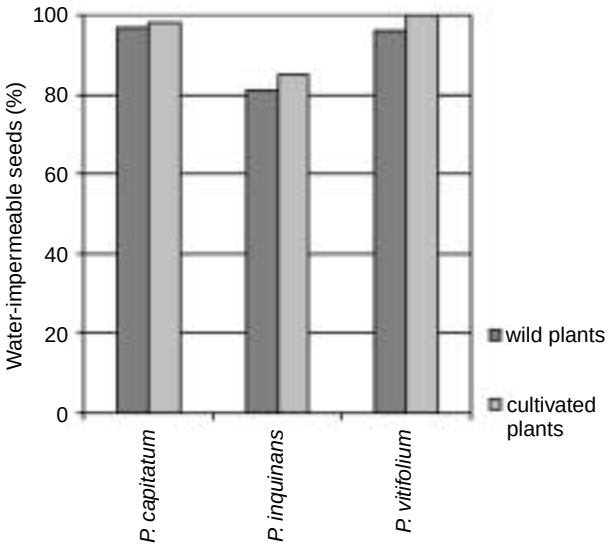


Figure 1. Comparison of impermeable seed content from cultivated and wild plants.

the water-impermeable fraction of *G. renardii* (PY^{100}) was 87% and 88% in these 2 years. Two additional PY^{100} species, *P. vitifolium* and *G. robertianum*, exhibited the same degree of physical dormancy in both years (100% and 93%, respectively). However, three species had notable differences in percentages of impermeable seeds when comparing the harvests of 1995 and 1996. *Pelargonium mollicomum* had 55% impermeable seeds in 1995 and only 31% in 1996, while the hardseeded fraction of *G. dissectum* decreased from 57% in 1995 to 11% in 1996. In *G. pyrenaicum*, impermeable seeds decreased from 100% to 48% in the same period.

The influence of dry storage for 5 years on physical dormancy varied among species (Table 1). Seeds of *E. cicutarium*, *G. canariense*, *G. dissectum*, *G. pusillum* and *G. pyrenaicum*, which were impermeable in 1996, lost impermeability completely after 5 years. On the other hand, hardseedness of other species was either not at all influenced by the long storage time (*G. pratense*, *G. phaeum*, *P. inquinans*, *P. vitifolium* and *P. zonale*), or exhibited only minor reduction (*P. candicans* and *P. capitatum*). *Pelargonium mollicomum*, where the percentage of impermeable seeds deviated remarkably for the 1995 and 1996 harvests, showed a gradual reduction in physical dormancy; only 27% of the hard seeds in 1996 were still impermeable in 2001. Seeds of the two species showing the highest deviation between 1995 and 1996 (*G. pyrenaicum* and *G. dissectum*) (Fig. 2) were completely permeable after 5 years of dry storage (Table 1). The pattern of impermeability alteration as a result of dry storage did not correlate with the quantitative type of physical dormancy. *Erodium cicutarium* and *P. vitifolium*, for example, are both PY^{100} species, but all hard seeds of *E. cicutarium* lost their impermeability,

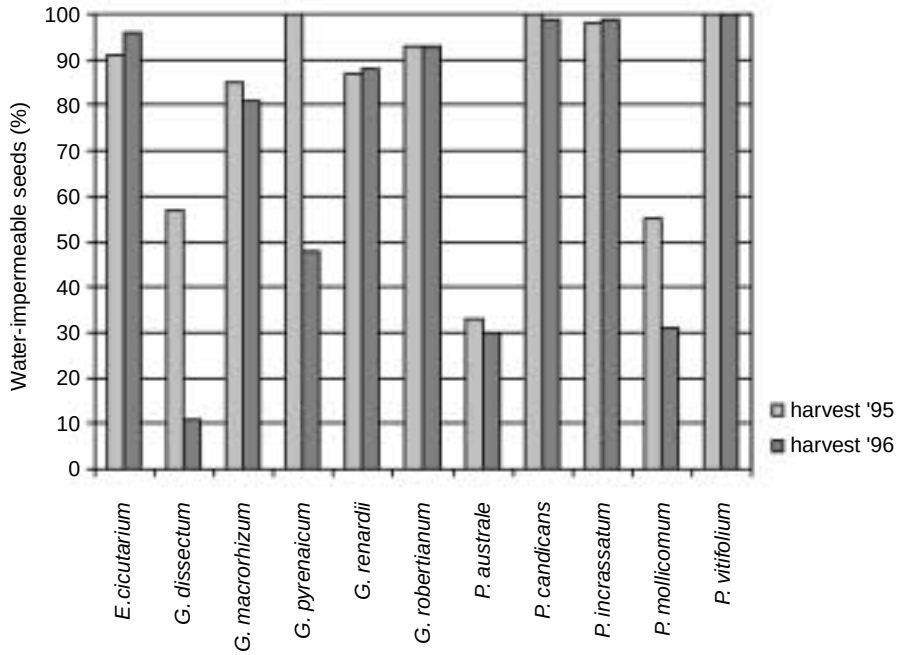


Figure 2. Comparison of harvests from 1995 and 1996.

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whereas all of the *P. vitifolium* seeds remained impermeable over the time period. Nevertheless, four of eight *Geranium* species and no *Pelargonium* species exhibited a total loss of hard seeds. The tendency to lose impermeability during storage was more prominent in *Geranium* than in *Pelargonium* species.

The thickness of the *Pelargonium* seed coats varied strongly, ranging from 9 to 25 μm for the palisade layer and from 15 to 48 μm with regard to the subpalisade layer. Comparing interspecific differences in layer thickness with the specific extent of physical dormancy (Fig. 3), all species with a minimum of 95% impermeable seeds had a palisade layer that is 15–25 μm thick (Fig. 3a), whereas thickness of the palisade layer in species with a hardseeded fraction of less than 50% was 9–14 μm. Similar results were observed with regard to the subpalisade layer (Fig. 3b). The thickness of this layer in seeds of species with less than 50% impermeable seeds was ⩽ 20 μm, whereas in those species with more than 90% impermeable seeds, the subpalisade layer thickness ranged from 21 to 48 μm. Thus, there is a clear, albeit non-linear, relationship between the proportion of impermeable seeds and the thickness of the palisade and the subpalisade layers.

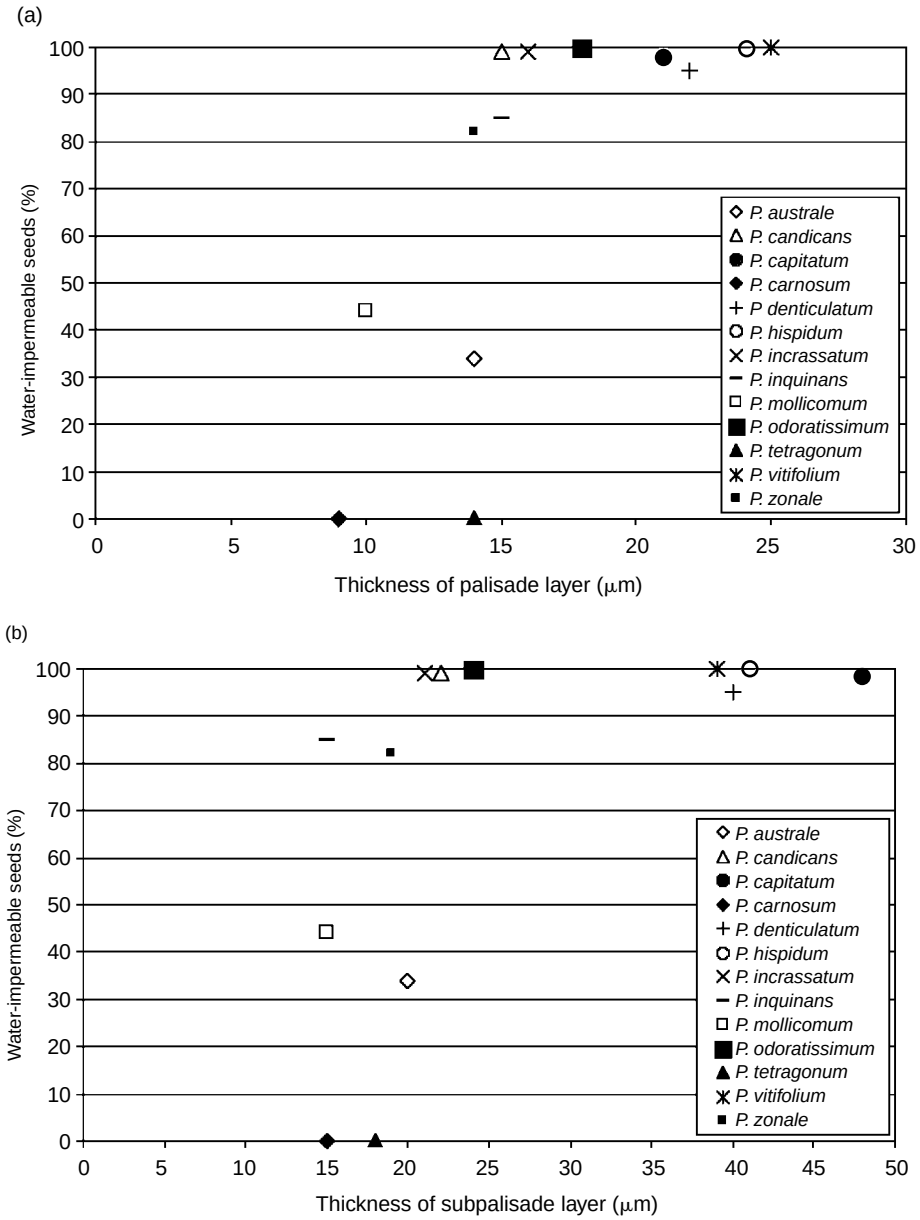


Figure 3. Average thickness of palisade (a) and subpalisade (b) layer in relation to the specific extent of physical dormancy.

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Discussion

Physical dormancy in *Geraniaceae* can be differentiated specifically in terms of the percentage of impermeable seeds at maturity, ranging from 0 to 100%. Most species investigated exhibited more than 80% impermeable seeds, classified as PY^{100} species, so that the formation of a large hardseeded fraction can be identified as a prominent strategy in *Geraniaceae*. Thus, the rule for physical dormancy in *Cistaceae*, that the majority of seeds in a given population are impermeable (Thanos *et al*., 1992), is also valid for many *Geraniaceae* species. The germination strategy in these PY^{100} species, for example *P. capitatum*, generally depends on specific dormancy-breaking factors. Two further strategies were also observed, as characterized by species with some (PY^{80}) or no (PY^{0}) impermeable seeds. The occurrence of PY^{80} species, e.g. *P. australe*, can be interpreted as a dual strategy, whereby permeable seeds germinate immediately, while impermeable ones remain in the soil to germinate later. Thus, seed germination of PY^{80} species takes place in a controlled way at two different times. The absence of impermeable seeds in PY^{0} species, such as *P. carnosum*, demonstrated that physical dormancy has become totally reduced in some *Geraniaceae* species. This is markedly different from the data on *Cistaceae*, where all 42 investigated species possessed 'hard-coated seeds' (Thanos *et al*., 1992). On the whole, the continuum of the degree of physical dormancy can be useful for subdividing species into quantitative types for identification of corresponding germination strategies.

There was little variation between wild and cultivated plants of *Pelargonium* species. The formation of hardseededness in *Pelargonium* is widely independent of habitat variations. These results contrast with grass populations, where dormancy varied with different habitat conditions (Allen and Meyer, 1998).

Comparing harvests from two consecutive years (Fig. 2), most species exhibited uniform percentages of impermeable seeds. The minor degree of variation in 8 of the 11 species supports the interpretation that the percentages of impermeable seeds at maturity can be regarded as a constant and specific feature. These consistent results were observed for both PY^{80} (e.g. *P. australe*) and PY^{100} (e.g. *P. vitifolium*) species.

Despite the general observation of consistent proportions of impermeable seeds in many of the species studied, three species (*P. mollicomum*, *G. pyrenaicum* and *G. dissectum*) have a high deviation when comparing the harvests of two consecutive years. Thus, we need to clarify whether the interpretation of hardseeded content as a constant specific feature is false or whether the observed deviation is a measurement artefact. In this context it is useful to discuss possible effects of dry storage on seed dormancy. Seed-coat impermeability of many species, such as *P. vitifolium* and *G. pratense*, was not influenced by the long period of dry storage. Seeds of other species, such as *E. cicutarium*, *G. dissectum* and *G. pyrenaicum*, however, lost physical dormancy as a result of storage, consistent with the results of Baskin and Baskin (1974) on *G. carolinianum* L. Therefore, dry storage can cause dormancy loss in some species and not in others, and thus, the relevance of dormancy-breaking factors varies specifically in *Geraniaceae*. Comparing results on dormancy loss by dry storage and the described deviation of physical dormancy in two consecutive years, all species with a significant variation in percentage of physical dormancy are strongly influenced by dry storage. Indeed, seeds of *G. pyrenaicum* and *G. dissectum* lost their impermeability completely during the time of storage. Thus, the described variations in physical dormancy over 2 years may have resulted from the different times of dry storage before testing, since the harvested seeds were collected over a period of weeks before testing occurred. A possibly longer storage period in the second year might have resulted in dormancy loss and in a corresponding decrease in percentages of impermeable seeds. If this is correct, deviation in the extent of physical dormancy in *P. mollicomum*, *G. pyrenaicum* and *G. dissectum* is caused by non-standardized storage before testing. Therefore, storage parameters should be controlled carefully in future investigations.

The interpretation of hard seed content at maturity as a specific and constant feature was also confirmed by histological results. Palisade and subpalisade layers are thicker in PY^{100} than in PY^{0} species. Although impermeability is mainly regulated by the closed or open chalazal slit (Meisert *et al*., 1999), it is clear that thicker impermeable and mechanical layers are an associated barrier to imbibition. Therefore, species with a high percentage of impermeable seeds have a closed chalazal slit and form a thick mechanical and impermeable layer.

Starting from the assumption that the *Geraniaceae* species constantly exhibit percentages of impermeable seeds, and that the species can be usefully subdivided into three types of physical dormancy, the ecological significance of physical dormancy in *Geraniaceae* can be analysed. The results demonstrate that the PY^{100} type, with more than 80% impermeable seeds, is the most prominent of the investigated species. Many *Pelargonium* species naturally distributed in South Africa (e.g. *P. vitifolium*, *P. capitatum*, *P. candicans*, *P. zonale*, *P. inquinans* and *P. peltatum*) belong to this PY^{100} type. These *Pelargonium* shrubs occur in quite different habitats. *Pelargonium capitatum*, for example, grows on sand dunes along the coast, while *P. vitifolium* is found in partially

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shaded localities close to streams (van der Walt, 1977). Therefore, the PY^{100} type of physical dormancy as a successful strategy in *Pelargonium* is not restricted to particular environmental conditions. Many *Pelargonium* species are distributed in the winter-rainfall region of the south-western Cape Province (van der Walt and Vorster, 1988), where fire in summer is a natural part of the ecosystem. Protection against fire, or fire as an impermeability-breaking factor, could be one aspect to explain the ecological significance of physical dormancy in *Pelargonium* species, corresponding to results on *Geranium* species such as *G. bicknelli* (Abrams and Dickmann, 1982) and *G. bohemicum* (Granström and Schimmel, 1993). Moreover, fire as a relevant factor in dormancy breaking is compatible with the present results, showing that seed impermeability of all of the investigated PY^{100} *Pelargonium* species (except *P. incrassatum*) was not reduced by dry storage. Nevertheless, the influence of fire or other environmental factors on impermeable *Pelargonium* seeds under natural conditions still needs to be investigated.

The PY^{100} type of physical dormancy also includes many *Geranium* and *Erodium* species with different life cycles and from very different habitats. For instance, *E. cicutarium* is an annual or biennial with a wide distribution in semi-arid sandy environments, with 95% impermeable seeds. These seeds became completely permeable following 5 years of dry storage. The occurrence of physical dormancy in this spring-flowering species, which is adapted to a Mediterranean climate, may enable seeds to remain dormant during the final phase of a rainy spring. After this wet period seeds probably lose their impermeability by drying during the summer. However, this dormancy-breaking pattern still has to be confirmed by investigations of seed behaviour under natural conditions (see chapter 2 in Baskin and Baskin, 1998). In this context there is an open question, because the ecological significance of dormancy breaking in summer is meaningful for autumn-germinating plants (Baskin and Baskin, 2000), but questionable for spring-germinating ones.

To explain the occurrence of impermeable seeds in *G. pratense* (PY^{100}) or *G. palustre* (PY^{80}), both herbaceous perennials growing in moist meadow environments, the advantages of physical dormancy under humid climatic conditions should be considered. A higher resistance against mechanical or microbial attack could increase the probability of survival in moist soil conditions. This particular adaptation to humidity of *G. pratense* is also recognizable by the maintenance of seed impermeability after dry storage. Such a form of dormancy breaking would be redundant under conditions of constant humidity. However, further investigations are required to determine whether, for example, all *G. pratense* seeds become permeable before the next spring, or whether some of them remain in the soil for several years. The ability to remain viable over long periods has been demonstrated impressively for seeds of *G. bohemicum*, which germinated after 129 years of dry storage (Milberg, 1994).

The investigations on PY^{80} species, such as *P. australe* or *P. mollicomum*, demonstrated that some species only exhibit a reduced hardseeded fraction. As some of both species began to germinate immediately in the 10-d tests, we can conclude that this softseeded fraction is able to germinate as soon as enough water is available. *Pelargonium australe*, for instance, is naturally distributed on sand dunes and granite outcrops along the south coast of Australia, where rainfall occurs more or less throughout the year (van der Walt and Vorster, 1988). However, the duration of rainfall in this area is often very short, and the number of seedlings can easily become reduced as a result of the lack of water. Thus, the formation of dormant seeds, which remain in the soil, could be an important strategy to ensure the survival of the population. As the impermeable seeds of *P. australe* are not influenced by 5 years of dry storage, they may be able to remain in the soil for a long time. Altogether, the PY^{80} type of physical dormancy can be interpreted as the strategy to produce both seeds for immediate propagation, and seeds for securing the long-term survival of the species.

The occurrence of PY^{0} types, such as *P. carnosum* and *P. tetragonum*, is of special ecological interest, because all investigated stem succulents belong to this group. The absence of physical dormancy in these species would appear to represent a special form of adaptation to their arid habitat, which is characterized by short and irregular periods of rainfall. In such a climate seeds have to germinate as soon as rainfall occurs, and thus, any form of water-impermeable barrier would decrease fitness. Therefore, physical dormancy is not a useful feature in this unpredictable environment, qualifying Fenner's hypothesis that 'the ability to remain dormant for a long period is associated with seeds of species from unpredictable environments' (Fenner, 1985, p. 72).

In summary, physical dormancy is a diversely differentiated feature in *Geraniaceae*, with regard to both percentage of impermeable seeds at maturity and maintenance of dormancy under particular conditions. Fundamentally different strategies can be identified and classified as PY^{0}, PY^{80} and PY^{100} types of physical dormancy. The ecological significance of both the PY^{80} and PY^{100} strategies requires further investigation with regard to dormancy loss under natural conditions. The present data provide an essential basis for selection of

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suitable species for investigations on seed behaviour in the field.

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