Acta Bot. Neerl. 32(3), May 1983, p. 203–212.

GERMINATION ECOLOGY OF SOME DUNE SLACK PIONEERS

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SUMMARY

The effects of temperature, light, burial and salinity on the germination of *Centaurium littorale* (Turner) Gilmour, *Samolus valerandi* L. and *Parnassia palustris* L. are compared. Each species exhibits an almost absolute requirement for light. Germination does not occur below a day temperature of 15°C. The enforced dormancy, imposed by salinity is too weak to prevent germination at moderate salinity levels, which may cause considerable mortality after germination.

Samolus valerandi and *Parnassia palustris* exhibit innate dormancy, which is rapidly broken by cold stratification. None of the species is liable to induction of secundary dormancy by adverse environmental conditions. The seed variability is remarkably low, implying that under almost any set of environmental conditions the germination will be either rapid and complete, or completely inhibited.

The germination behaviour is discussed in relation to habitat and seed characteristics. It is argued that very different types of germination strategies may be successful in dune slack habitats.

1. INTRODUCTION

Environmental control of germination is an extensively reviewed subject (e.g. ANGEVINE & CHABOT 1979; KOLLER 1972; MAYER & POLJAKOFF-MAYBER 1975). Specific types of germination strategies are believed to have evolved in response to specific patterns of seedling mortality risk. These patterns may be largely determined by habitat characteristics (ANGEVINE & CHABOT 1979; GRIME 1979; HARPER 1957, 1977), implying that ecologically related species should exhibit more or less similar germination requirements (ANGEVINE & CHABOT 1979). This concept of habitat-specific "germination syndromes" may be very useful in comparing different habitats, especially fairly extreme habitats, in which the pattern of mortality risk is largely determined by a small number of stress factors (ANGEVINE & CHABOT 1979). Yet, even co-occurring desert annuals exhibit considerably different types of environmental control of germination (MAYER & POLJAKOFF-MAYBER 1975; WENT 1949; WENT & WESTERGAARD 1949), which may lead to strong annual fluctuations in dominance patterns (BREMAN et al. 1980). In general, co-occurring species may be expected to exhibit at least some variation in germination controlling mechanisms. Firstly, the same temporal pattern of germination may be achieved by different physiological mechanisms (HARPER 1957). Secondly, the pattern of seedling mortality risk depends on specific tolerances, which may strongly differ between species. Thirdly, the pattern of seedling mortality risk depends on the amount of carbohydrates and/or mineral nutrients which are stored in the seed (WERNER 1979). Fourthly, adaptation to unpredictable patterns of mortality risk may be achieved by dispersal in time as well as dispersal in space (COHEN 1966; GRIME 1979; HARPER 1977; MACARTHUR 1972; WERNER 1979). Finally, the necessity to prevent (occasional) heavy losses of offspring depends on other life-history parameters (monocarpy *v.* polycarpy; annuality *v.* perenniality).

The present study aims to describe the germination strategy of three species which often co-occur within the *Centaurio-Saginetum moniliformis* Diemont, Siss. et Westhoff 1947, a common pioneer association from dune slacks and beach plains in the coastal area of North-Western Europe (FREIJSEN 1967a). This association usually occurs within unstable transitional zones between wet and usually brackish slack bottoms and dry, non-saline dune slopes (FREIJSEN 1967a, b). These zones are characterized by fairly strong unpredictable fluctuations in soil salinity and soil water content (BEEFTINK 1977; FREIJSEN 1967a; SCHAT 1982), often leading to "catastrophic" mortality patterns (SCHAT 1982).

2. MATERIALS AND METHODS

The seeds were harvested from a beach plain called "Strandvlakte", located at the eastern side of the island of Schiermonnikoog (latitude 53°29′, longitude 6°12′).

The experiments were performed in germination cabinets at a daily light period of 14 hours. The light intensity at plant level was 14 W/m^2, unless otherwise stated. The seeds were placed on filter paper, lying on water soaked foam rubber, floating on a volume of demineralized water in translucent plastic boxes (10 × 10 × 10 cm), fifty seeds to a box. In the experiments with NaCl, the lid of the trays was sealed with vaseline, in order to avoid evaporation. The experiments concerning the effect of burial were performed using fine sand, of which the water content was kept at water capacity. The seeds were buried enclosed in fine-meshed nylon cloth, in order to facilitate their recovery.

In the case of *Centaurium littorale* and *Samolus valerandi,* protrusion of the radicle was used as a criterion for germination. In the case of *Parnassia palustris*, protrusion of the plumule was used, because *Parnassia palustris* is one of the few species, in which the plumule protrudes before the radicle. Complete necrosis of the radicle was used as a criterion for seedling mortality.

3. RESULTS

3.1. Temperature

The rate and final percentage of germination of freshly harvested seeds at various temperature regimes is given in *table 1*. Fresh seeds of all species under investigation germinate only at temperature regimes with day temperatures of 15°C or more. *Samolus valerandi* prefers a cold night/warm day regime. At a lower day temperature (15°C) a cold night is absolutely necessary for germination. *Parnassia palustris*, on the other hand, shows a delayed and less complete germination

Table 1: Final germination percentage (f.p.) and arithmatic mean germination day (m.g.d.) for fresh seeds at various temperature regimes. The germination percentage was considered to be final after three weeks without additional germination. The values represent the mean of four replications with 50 seeds each; the difference between the mean and the maximally deviating replica is given between brackets.

Temp. (°C)	*Centaurium littorale*		*Samolus valerandi*		*Parnassia palustris*	
night/day	f.p.	m.g.d.	f.p.	m.g.d.	f.p.	m.g.d.
5/10	0	–	0	–	0	–
5/15	99 (±1)	12 (±3)	100	12 (±4)	0	–
8/18	100	8 (±1)	100	9 (±2)	38 (±14)	18 (±5)
5/25	100	7 (±1)	100	7 (±1)	18 (±12)	20 (±4)
10/10	0	–	0	–	0	–
15/15	100	8 (±2)	0	–	0	–
18/18	100	6 (±1)	14 (±6)	21 (±7)	48 (±13)	6 (±6)
25/25	100	6 (±1)	53 (±14)	11 (±3)	54 (±10)	15 (±3)

Table 2: Final percentage and mean germination day (between brackets) at various temperature regimes, after storing the seeds at different conditions in the dark (each value is based on two replications with 50 seeds each).

	Temp. (°C)	Storage conditions and storage period				
	night/day	dry (20°C) (20 weeks)	dry (4°C) (27 weeks)	moist (10°C) 12 weeks)	moist (15°C) (12 weeks)	moist (4°C) (4 weeks)
Centaurium littorale	5/10	0	0	0	0	0
	5/15	100 (9)	100 (8)	100 (7)	100 (6)	99 (5)
	5/25	99 (6)	100 (7)	100 (6)	100 (5)	98 (5)
	10/10	0	0	0	1	0
	15/15	100 (8)	99 (8)	100 (6)	100 (5)	100 (6)
	25/25	100 (5)	100 (7)	100 (5)	99 (5)	100 (5)
Samolus valerandi	5/10	0	0	0	not tested	0
	5/15	100 (8)	99 (9)	100 (10)		100 (6)
	5/25	100 (4)	99 (5)	100 (5)		100 (4)
	10/10	2	0	1		0
	15/15	100 (7)	100 (9)	99 (8)		100 (6)
	25/25	99 (5)	100 (7)	100 (6)		98 (5)
Parnassia palustris	5/10	0	0	not tested	not tested	0
	5/15	1	0			94 (17)
	5/25	3 (44)	23 (44)			92 (14)
	10/10	0	0			0
	15/15	0	5 (31)			89 (13)
	25/25	12 (33)	45 (19)			91 (10)

Table 3: Final germination percentage and mean germination day (between brackets) at a constant temperature of 25°C, at various levels of light intensity. Prior to the experiments the seeds were either dry stored at 20°C for three months (A), or stored on moist filter paper at 4°C for 2.5 months (B). The values are based on two replications with 50 seeds each. The percentages of germination at complete darkness were established after 1.5 months and are not necessarily final percentages.

Daily light period		14 hours	14 hours	14 hours	2 minutes	0 minutes
light intensity (W/m^2)		14	4	1	1	0
Centaurium	A	99 (8)	92 (10)	84 (12)	20 (28)	2
littorale	B	100 (5)	100 (5)	98 (5)	not tested	3
Samolus	A	98 (9)	28 (12)	4 (16)	2	0
valerandi	B	100 (5)	99 (7)	100 (9)	not tested	1
Parnassia	A	46 (16)	41 (16)	13 (14)	11 (34)	2
palustris	B	97 (11)	94 (9)	96 (10)	not tested	0

at low night temperatures. *Centaurium littorale* exhibits no clearcut preference for low or high night temperatures, at least not within the tested range of temperature regimes. As long as day temperatures are 15°C or more, germination is always rapid and complete.

3.2. Storage conditions

The effect of storage under various conditions on the rate and final percentage of germination can be established by comparing *tables 1* and *2*.

Four weeks of storage at 4°C on moist filter paper allows *Samolus valerandi* to germinate rapidly and completely at non-fluctuating temperatures of 15°C or more. Prolonged storage, irrespective of the storage conditions, produces a similar effect.

The germinability of *Parnassia palustris* is also strongly affected by storage. Four weeks of storage at 4°C on moist filter paper allows germination at 5/15°C and increases the rate as well as the final percentage of germination at each of the other tested temperature regimes, apart from 5/10 and 10/10°C, at which no germination occurs at all. The inhibitory effect of a low night temperature is less pronounced than in fresh seeds. Prolonged dry storage at a high temperature, however, strongly reduces the germinability. Dry storage at a low temperature as well as moist storage hardly affects the germinability.

The germination of *Centaurium littorale* is barely or not at all affected by seed storage, irrespective of storage conditions.

3.3. Light

The effect of light on the rate and final percentage of germination is given in *table 3*. Cold stratification apparently decreases the light requirement for germination. Complete darkness, however, almost completely inhibits the germination of dry-stored as well as cold-stratified seeds. The seeds that fail to germinate in the dark or at low light intensities, germinate after exposure to a high intensity, at a rate and to a final percentage, comparable to that of seeds, which have immediately been exposed to a high light intensity. Darkness apparently does not induce a secundary dormancy.

3.4. Burial

The effect of burial on the germination of dry-stored (20°C) as well as cold-stratified (4°C) seeds in given in *table 4*. The table shows that a sand cover of 5 mm is enough to prevent the germination of dry-stored seeds. After cold-stratification, however, the seeds are capable of germinating at a depth of 5 mm, at least partially. At a depth of 10 mm germination is almost completely inhibited. Similar to darkness, or low light intensity levels, burial does not induce a secundary dormancy. The high similarity between these results and those of the previous section indicate that the effect of burial is due to light interception by the sand cover.

3.5. Salinity

The effect of NaCl on the germination of cold-stratified (4°C) seeds is given in *fig. 1*. NaCl inhibits the germination, especially that of *Parnassia palustris*. Seeds which fail to germinate at NaCl-concentrations of 60 and 120 mmol/l, often seem to have lost their germinability, since most of them do not germinate even after a transfer to non-saline conditions (*fig. 1*). Seeds, which fail to germinate at 240 mmol/l, however, exhibit an almost normal germinability after a transfer to non-saline conditions. In the case of *Samolus valerandi* and *Centaurium littorale*, seeds which fail to germinate at 240 mmol/l remain very hard, whereas seeds which fail to germinate at lower concentrations become weak after some time. In many cases the seed coat looses its integrity. After transfer to non-saline conditions they become rapidly infected by fungi, which suggests that they have been killed by the salt during an early stage of the germination process.

All the species exhibit a considerable mortality after germination, which increases with salinity (*table 5*). The seedlings of *Parnassia palustris* are much more salt-sensitive than those of *Centaurium littorale* and *Samolus valerandi*.

Table 4: Percentage of germination (after 30 days) at various depths in a fine sand soil, at an air temperature of 5/25°C. Prior to the experiment the seeds were either dry stored at 20°C for three weeks (A), or stored on moist filter paper at 4°C for five weeks (B). The values are based on two replications of 50 seeds each.

Depth of burial (mm)	*Centaurium littorale*		*Samolus valerandi*		*Parnassia palustris*	
	A	B	A	B	A	B
0	100	100	100	100	22	92
2	68	82	42	100	24	68
5	2	16	0	100	0	1
10	1	0	0	0	1	0

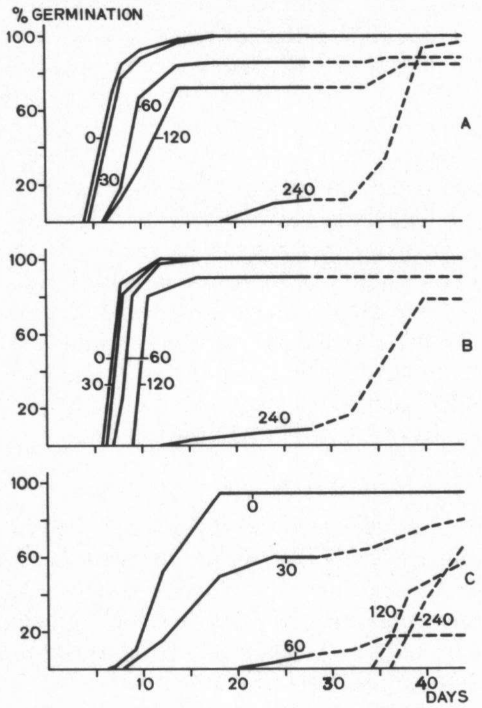

Fig. 1: Cumulative percentage of germination for *Centaurium littorale* (A), *Samolus valerandi* (B) and *Parnassia palustris* (C) at various salinity levels (solid lines) and after a subsequent transfer to demineralized water at the 28th day of the experiment (broken lines). Each experimental group contains 200 seeds, stratified for one month at 4°C on moist filter paper, prior to the experiment. The experiment was performed at 5/25°C.

Table 5: Percentage of dead seedlings at the 28th day after the start of the experiment concerning the effect of salinity on germination (see figure 1). Note that the time of exposure to NaCl after germination differs between individuals, species and concentrations.

	NaCl-concentration (mmol/l)				
	0	30	60	120	240
Centaurium littorale	0	2	78	89	100
Samolus valerandi	0	0	54	87	100
Parnassia palustris	0	72	100	–	–

4. DISCUSSION

The results of the present investigation reveal considerable interspecific differences with respect to germination strategy. Fresh seeds of *Samolus valerandi* and *Parnassia palustris* exhibit an innate dormancy, which is not absolute, but strongly restricts the range of environmental conditions, which allow their germination. This innate dormancy is rapidly broken by cold stratification, as demonstrated in many other species from temperate latitudes (ANGEVINE & CHABOT 1979; BARTON 1965). In the case of *Samolus valerandi*, the innate dormancy disappears with seed ageing, which is a common phenomenon (BARTON 1965). *Centaurium littorale,* on the other hand, hardly shows any innate dormancy at all.

At the beach plain of Schiermonnikoog the three species under study germinate almost exclusively in spring, usually in May (SCHAT 1982). Occasionally, however, seedlings of *Parnassia palustris* and *Centaurium littorale* have been encountered in the autumn, though in an extremely low density (less than one thousandth of the density in spring). These seedlings are always killed during the winter. *Samolus valerandi* has never been observed to germinate in the autumn. Demographic studies suggest that germination in the autumn would decrease the chance that a seedling survives until reproduction by a factor ten, at least (SCHAT 1982). *Samolus valerandi* and *Parnassia palustris* shed most of their seeds in September, whereas *Centaurium littorale,* which exhibits a much longer time-span between flowering and capsule dehiscence, does not shed its seeds until the last weeks of October. The inability of the seeds of the latter species to germinate below a day temperature of 15°C will therefore sufficiently prevent premature germination in the autumn, which may explain the absence of innate dormancy. In the case of *Samolus valerandi* and *Parnassia palustris,* on the other hand, the innate dormancy may often be necessary in order to avoid premature germination. A comparable reciprocity between innate dormancy and delayed seed release occurs in tropical forests with seasonal rainfall (GARWOOD 1977), which shows that similar temporal patterns of germination may be achieved by very different mechanisms (*cf.* HARPER 1957). Yet, *Centaurium littorale* seems to exhibit some geographical variation in germination behaviour, as massive germination in September has been observed in other parts of the Dutch dune area (Londo, pers. comm.). This is possibly the result of local climatic conditions, or edaphic factors (soil drainage, soil fertility), which may strongly affect the period of flowering and seed release (Schat, unpublished). Ecotypic differentiation or subspeciation may also play a role (FREIJSEN 1967a).

Another ecologically relevant phenomenon is the explosive nature of the germination process. The results with cold stratified seeds, or in the case of *Centaurium littorale*, even those with fresh seeds, show that there is only an extremely narrow temperature range, in which the germination percentage differs considerably from zero or one hundred. Moreover, the rate of germination is always extraordinarily high. The same conclusions apply to the germination of cold stratified seeds in a light intensity gradient. At the beach plain of Schiermonnikoog, germination is usually confined to a short period (less than one month), after which no germinable seeds are left, at least not on the soil surface (SCHAT 1982), whereas neighbouring species spread their germination over a much longer period. *Plantago coronopus*, for instance, germinates in September, October, April, May and June (SCHAT 1982), due to a pronounced seed polymorphism (SCHAT 1981). The absence of seed variability in the three species under study is remarkable, since it may easily lead to complete elimination of a whole year's offspring, at least locally (SCHAT 1982). This seems especially dangerous in the case of short-lived monocarpic species, such as *Centaurium littorale* and *Samolus valerandi*. Moreover, seed polymorphism is very common among short-lived species from unpredictable or transient habitats (HARPER 1977). The model presented by COHEN (1966) also suggests that seed polymorphism is an effective strategy in randomly fluctuating environments. Heterogeneity in space and dispersal between (sub)populations, however, are not incorporated in this model. The presence of small height gradients, for example, effectively prevents the extinction of *Centaurium littorale* and, though less effectively, that of *Parnassia palustris* from a whole dune valley, because the factors which threaten the maintenance of the population differ between height zones (SCHAT 1982). MACARTHUR (1972) demonstrates that in such a situation explosive germination in combination with extensive seed dispersal may be a better strategy than seed polymorphism. Field studies show that *Parnassia palustris* exhibits an extensive seed dispersal, whereas *Centaurium littorale* and *Samolus valerandi* seem to lack the capacity for it, in spite of their small seed size (FREIJSEN 1967b; SCHAT 1982). MACARTHUR's argument may therefore hold for *Parnassia palustris*, but probably not for *Centaurium littorale* and *Samolus valerandi*. It may be argued that the risks, which are brought about by a low seed variability, will be effectively reduced by storage of seeds in a subsoil seed bank, of which all the species under study seem to be capable, simply because of the their inability to germinate in the absence of light. At the beach plain of Schiermonnikoog, *Centaurium littorale* and *Samolus valerandi* are indeed represented in buried seed banks, at least locally. *Parnassia palustris*, however, is not, probably due to its soft seed coat (*cf.* COOK 1980). Anyway, the chance of successful recruitment from these banks is extremely small, at least within this area (Schat, in prep.). It is conceivable that the seed size may have consequences for the germination behaviour. The extremely small seed size of the species under study may, beside increasing the life-span of buried seeds (COOK 1980) and preventing seed mortality due to stagnating water during the winter (BINET 1968), restrict the period in which successful establishment in strongly seasonal environments is possible, due to the absence of a nutrient and energy reserve (ANGEVINE & CHABOT 1979; ERNST 1981; WERNER 1979). The latter may to some extent explain the phenomenon of massive germination within a short period.

The high mortality rate of the seedlings and germinating seeds at salt concentrations as low as 60 mmol/l, is rather surprising, in view of the fact that older individuals are able to survive and to grow at much higher concentrations

(SCHAT 1982). Seedlings are obviously much more salt-sensitive than adults. Field studies have shown that moderate salinity levels in May can completely destroy a whole year's offspring (SCHAT 1982). The latter risk is of course strengthened by the lack of seed variability, which prevents the maintenance of a readily available reserve of dormant seeds.

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