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Reproductive performance of native and alien colonizing phanerogams on a glacier foreland, Iles Kerguelen

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Abstract The retreat of the Ampère Glacier, on Kerguelen, has left wide ice-free areas where five native and two alien vascular plant species are involved in primary colonization. The number of seeds produced by individual fertile plants has been determined for each species and germination capacity has been tested under different temperature and light conditions. *Colobanthus kerguelensis* and *Cerastium fontanum* produced the highest number of seeds per plant. No dormancy mechanism occurred in either species and they appeared to be the most successful colonizers during the early stages following the deglaciation. No seeds of *Azorella selago* and *Agrostis magellanica* had germinated after 2 months. Dormancy was demonstrated only in *Poa kerguelensis. Festuca contracta* was the only species which exhibited a negative photo-sensitivity. Germination of indigenous seeds required relatively high temperatures, whereas the optimum temperature for germination in the introduced *Poa annua* was 10°C. These results are compared with the few data available in the subantarctic literature and ecological implications are discussed.

Introduction

Glacier forelands are useful field laboratories for colonization and primary succession studies. However, most of these studies have been conducted in the Northern Hemisphere, in the arctic or alpine environments and few of them have provided good evidence for mechanisms of change (Matthews 1993). In the subantarctic province one of the few examples of such studies concerns the plant succession on chronosequences adjacent to glaciers snouts in South Georgia (Smith 1984). More information has been provided on the role of bryophytes in primary succession (Smith 1993), but no data are available on the true nature of the colonization processes in the subantarctic phanerogam species in relation to both environmental constraints and biological features.

The retreat of the glaciers in the Iles Kerguelen began at the end of the 18th century. Despite a cold oceanic climate this retreat has been accelerating since 1970, in response to increasing air temperature and shortage of precipitation recorded in this archipelago (Frenot et al. 1993). In consequence, areas of glacial debris have been recently exposed by glacier retreat. A multidisciplinary project investigating ecological changes along a chronosequence in front of the Ampère Glacier snout (Fig. 1) is currently in progress. This paper considers those biological features which are, in addition to the dispersal characteristics, fundamental to the understanding of the success or failure of the establishment of a species, i.e. seed production and germination capacity. Whereas different successionnal stages may be defined on the glacier foreland, only those communities with the highest densities were studied and the variability of these reproductive traits along the chronosequence is not discussed in this paper.

Twenty-one vascular plants species are indigenous to Iles Kerguelen. Little information about the reproductive behaviour, seed production and germination requirements of this flora on Kerguelen is available (Dorne 1968, 1977). Hennion (1992) provided an important account of the six species restricted to the Kerguelen Province, including one of the species (*Poa kerguelensis*) colonizing the vicinity of the Ampère Glacier. As proof of the simplicity of glacier forelands emphasized by Matthews (1993), only seven

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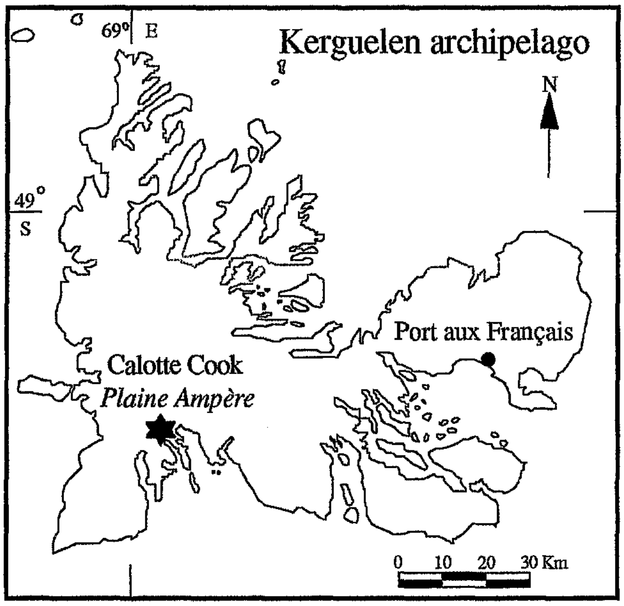


Fig. 1 Map of Kerguelen islands showing location of the study site in front of the Ampère Glacier, one of the largest outlets of the Calotte Cook ice sheet

phanerogam species are involved in primary colonization and all have a very scattered distribution on the fluvioglacial outwash plains. Seed production and germination capacity were determined for these seven species.

Materials and Methods

Plant species

Five of the seven species colonizing the newly deglaciated areas in front of the retreating Ampère Glacier are native: *Poa kerguelensis* Steud., *Agrostis magellanica* (Lam.) Vahl, *Festuca contracta* T. Kirk (Poaceae), *Colobanthus kerguelensis* Hook. f. (Caryophyllaceae) and *Azorella selago* Hook. f. (Apiaceae); the two others were probably introduced by whalers during the early 19th century: *Poa annua* L. (Poaceae) and *Cerastium fontanum* Baumg. (Caryophyllaceae). All these species are perennial.

Seed production

Grass species

Inflorescences of each species were collected in a single site chosen according to the high density of individual plants. Date of sampling (between February and the beginning of March 1992 when seeds became mature), density and diameters of fertile plants for each species are shown in Table 1. Whereas there was a highly significant relationship between the size of *Azorella selago* cushions, i.e. the age of the plant, and the age of the deglaciation (Frenot et al. 1993), there was no relation between the diameter of grass clumps and their location along the chronosequence. However, this diameter is obviously related to the age of the plant. For this reason the whole range of grass diameters was sampled. The number of replicates are given in Fig. 2 (N values in the left column). The number of inflorescences, the number of spikelets per inflorescence and the number of flowers per spikelet were determined. In addition, seeds of *P. annua*, *P. kerguelensis* and *F. contracta* were examined with a binocular microscope to estimate the percentage of viable seeds on the basis of their morphological development (presence or absence of a well developed caryops between the lemma and palea). Finally the mean number of seeds produced per fertile plant was calculated to give an account of the fertility of the population studied.

Forbs species

The number of fruit per fertile plant was estimated for *C. fontanum* and *C. kerguelensis* from plants sampled on a 30 years old area where their abundances were maximum. The seeds contained in capsules of these species were counted. Fruit of *A. selago* were sampled in the oldest site of the chronosequence (about 200 years) where the largest cushions were observed.

Germination abilities

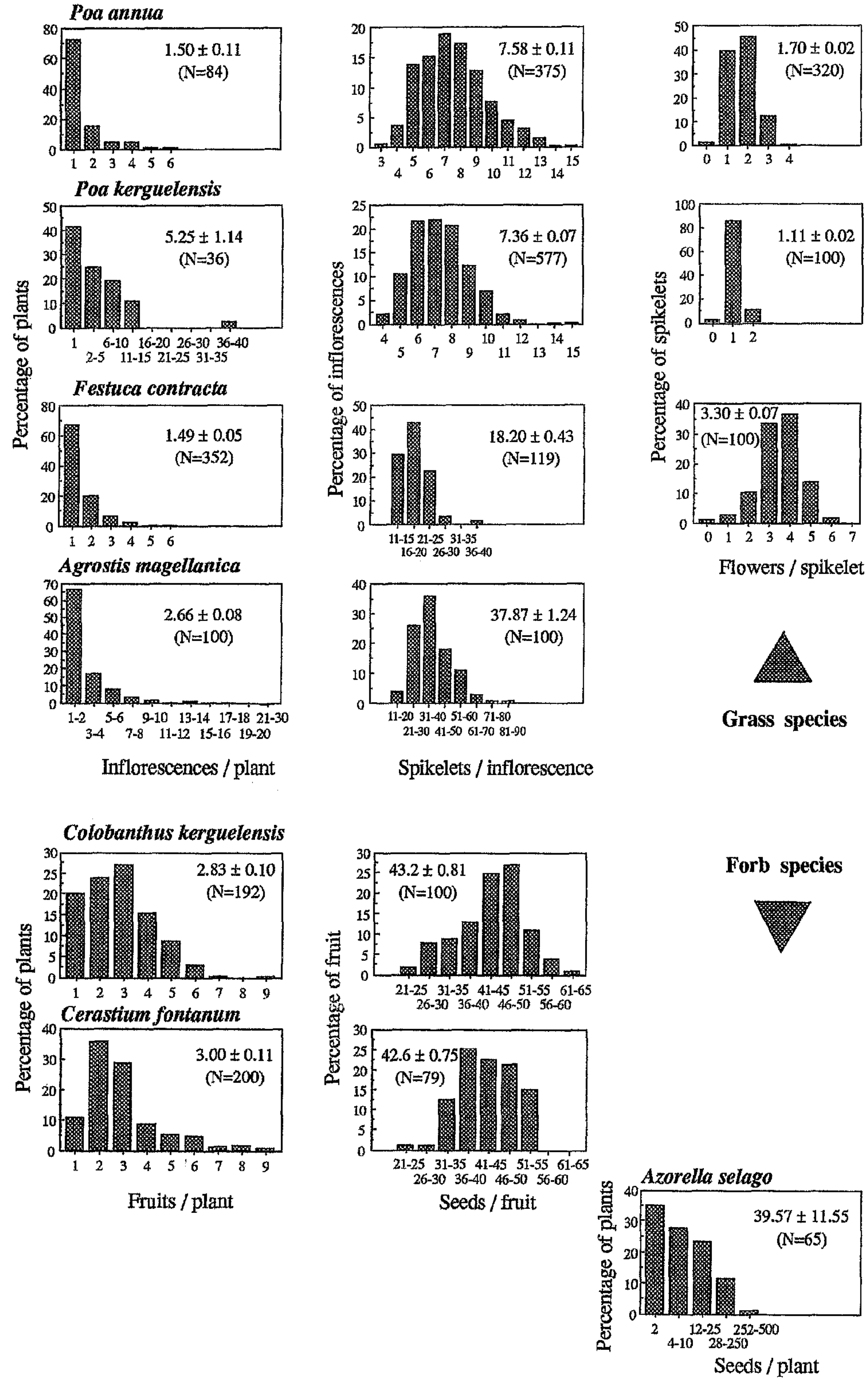
Air dried seeds were taken to the laboratory in France at ambient temperature and germination tests began about three months after their collection.

Well developed and undamaged seeds were placed in Petri dishes (25 seeds per dish) on two sheets of moistened filter paper and stored in different conditions of constant temperatures (5, 10 and 20°C) and light: 24 h dark (dark sets) or 16 h light–8 h dark photoperiod (light sets). These conditions were determined in relation to the summer natural photoperiod and the monthly mean winter (2.0°C) and summer (7.6°C) temperatures recorded at Port-aux-Français. The meteorological station is located in a sheltered area and there is no doubt that a harsher climate occurs on the West side of the archipelago. However top soil temperatures in the Plaine Ampère frequently reached 18–20°C during the sunny days in summer.

Table 1 Dates of sampling, densities (Mean ± SE, N = 100 contiguous 1 m^2 plots) and diameters of fertile plants sampled (Mean ± SE, number of replicates: see N values in the left column of Fig. 2)

Species	Date of sampling	Density of fertile plants ind./m^2	Diameter of fertile plants cm
Festuca contracta	13/03/92	0.16 ± 0.04	6.80 ± 0.14
Poa kerguelensis	14/02/92	0.37 ± 0.10	4.22 ± 0.28
Agrostis magellanica	13/03/92	34.7 ± 1.51	2.70 ± 0.09
Poa annua	04/03/92	0.83 ± 0.12	1.76 ± 0.08
Azorella selago	10/03/92	0.68 ± 0.09	15.35 ± 0.73
Colobanthus kerguelensis	04/03/92	9.98 ± 0.70	–
Cerastium fontanum	04/03/92	28.94 ± 2.56	–

Fig. 2 Distribution of the main reproductive characteristics used to estimate the production of seeds for the seven colonizing species on the Plaine Ampère sandur. Mean, SE and number of replicates are given in each diagram



Each temperature treatment comprised four sets of 25 seeds. For the grass species, tests were carried out on seeds enclosed between the lemma and palea. One set was placed in dark. The three other replicates were submitted to the photoperiod regime. Dishes were examined daily for more than two months and at the same time watered with de-ionized water. When a distinct radical appeared, the seed was considered germinated and was removed from the dish.

In some species, no germination was observed at 5°C after 28 days. In this case the seeds were submitted to the following conditions: the seeds stored in the 5°C dark treatment were transferred to 20°C dark treatment; one light dish was kept at 5°C and the two other replicates were removed and placed respectively in the 10 and 20°C light treatment. The first month at 5°C was then considered as a cold pre-treatment for the seeds which never germinated at this temperature.

The species which did not produce germination at 10°C after 28 days were treated similarly: the 10°C dark dish was placed in the 20°C dark treatment, two light dishes were transferred to 20°C light treatment and the last one was kept in the 10°C light treatment.

The mean time of germination (T_m) was calculated in each test from the following formula:

$$T_m = \frac{1}{N}\sum in_i$$

where N is the total number of germinated seeds at the end of the experiment and n_i the number germinating by the ith day. In order to preserve the validity of this calculation T_m has been calculated only when seeds germinated without cold pre-treatment and when the percentage of germination was above 10%.

Comparisons of means were statistically performed using the t test (in respect of the normality of the distribution and the homogeneity of variances) or the non-parametric Mann Whitney test. The confidence intervals given in the text are standard error values (SE).

Results

Seed production

Grass species

All the gramineous species produce a small number of inflorescences per fertile plant (Fig. 2). Means vary from less than two for *P. annua* and *F. contracta* to more than five for *P. kerguelensis*. Despite these low mean numbers, some plants with high diameters may exceptionally produce many inflorescences, e.g. up to 28 for *A. magellanica* and 36 for *P. kerguelensis*. However, as indicated by the standard errors shown in Table 1, the fertile plants cover a narrow range of diameter. In consequence, the variability of the inflorescence number cannot be related to the only age of plants.

The two *Poa* species show a similar pattern of spikelet distribution in the inflorescences, varying from 3 to 15. This variability increases for *F. contracta* (11 to 36) and for *A. magellanica* (12 to 87).

A. magellanica has only one flower in each spikelet, as is common in the genus *Agrostis*. The number of flowers per spikelet in *P. kerguelensis* is significantly lower than in *P. annua* ($p < 0.001$, t test). In some inflorescences, a few spikelets have no flowers. A similar observation was made in *F. contracta* where the terminal spikelets are sometimes sterile. In this species the number of flowers per spikelet is higher and can reach six.

Visual examination of the seeds revealed that 58% of *P. annua*, 65% of *F. contracta* and 75% of *P. kerguelensis* flowers produce fertile seeds (Table 2). No data are available for *A. magellanica* owing to the difficulty of visually estimating the good development of seeds.

These results allow an estimation of the mean seed production per fertile plant for each species (Table 2). *P. kerguelensis* produces three times more seeds than *P. annua*. Despite the uncertainty on the percentage of fertile seeds in *A. magellanica*, it seems that this grass produces the highest number of seeds.

Forb species

The two Caryophyllaceae species have a similar pattern of fruit and seed production and the mean values do not differ significantly ($p > 0.05$, respectively t test and Mann Whitney). In consequence, the mean numbers of seeds produced by fertile plants are similar (Table 2).

A. selago has two seeds per fruit, as is typical in species of Apiaceae. The number of seeds observed on the *A. selago* cushions is extremely variable (Fig. 2). No relationships between the cushion diameter and seed production were observed at the study site.

Germination capacity

Germination test without pre-treatment

A. magellanica and *A. selago* did not germinate at any of the temperature treatments. Seed of the five other species showed different germination abilities (Fig. 3a and Table 3):

F. contracta germinated only at 20°C (except for a single germination in 10°C light) and better results have been obtained in the dark. Whereas germination occurred over a long period in the light (between days 15 and 61), all seeds grown in the dark germinated between days 10 and 20 ($T_m = 12.9$).

P. annua exhibited an unusual pattern of germination: the highest percentages were observed at 10°C; at this temperature germination was higher in light but T_m was lower in dark (Fig. 3a and Table 3). At 20°C, only

Table 2 Data for flower and seed numbers in the seven colonizing species (estimation using the data shown Fig. 2)

Species	Fertile flowers per spikelet (%)	Number of flowers per inflorescence	Number of seeds per fertile plant
Festuca contracta	65	60.1	58.2
Poa annua	58	12.9	11.2
Poa kerguelensis	75	8.2	32.3
Agrostis magellanica	–	37.9	100.8
Colobanthus kerguelensis	–	–	122.3
Cerastium fontanum	–	–	127.8
Azorella selago	–	–	39.6

Fig. 3a, b Germination tests: **a** without cold pre-treatment; **b** with cold pre-treatment. The curves terminate at the time of the final germination. Continuous lines: light condition; dotted lines: dark condition; thick lines: tests performed at 20 °C

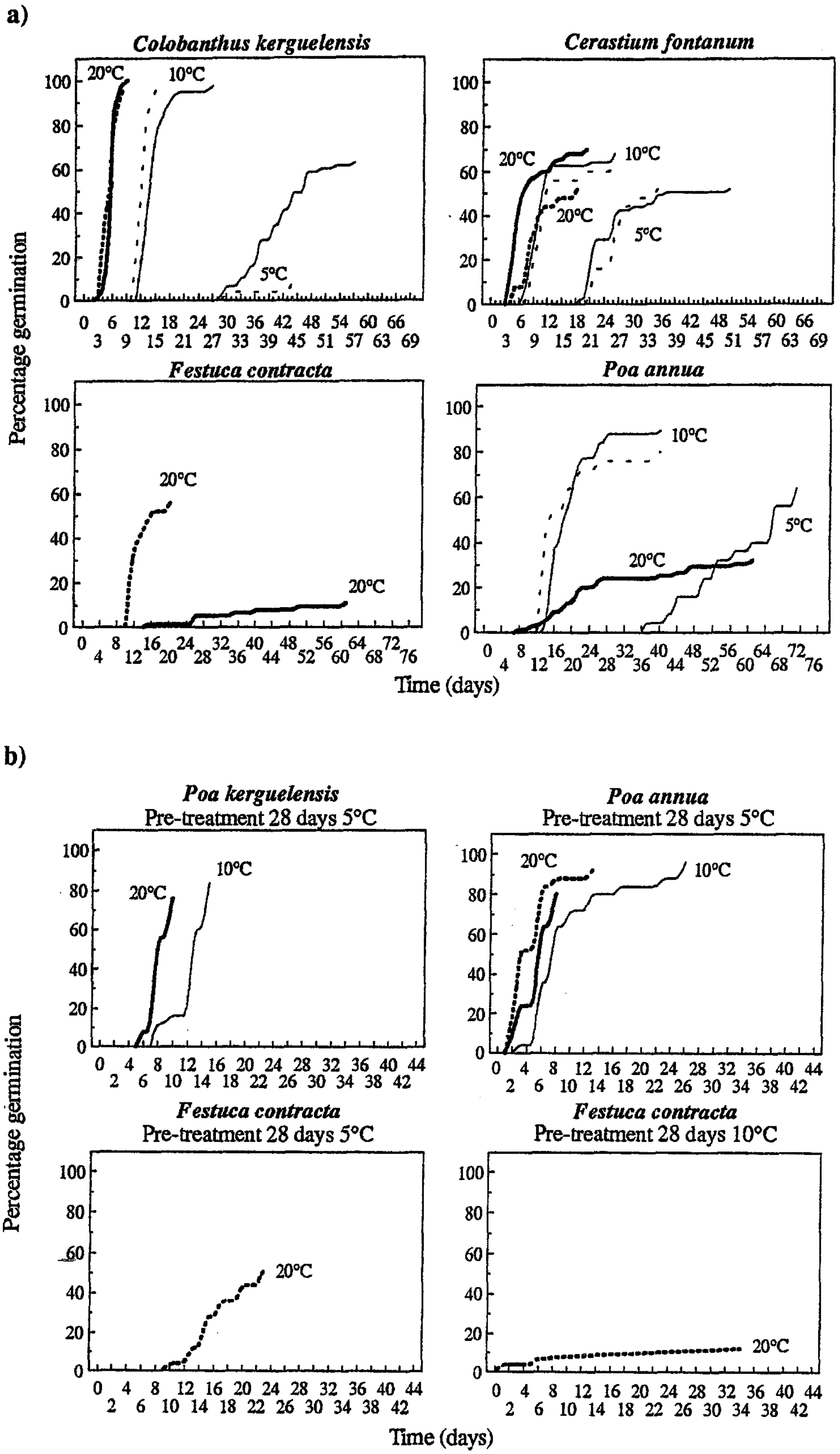


Table 3 Final percentage and mean germination time for seeds of four species germinating without cold pre-treatment. nc = T_m not calculated, owing to the low percentage germination (< 10%)

	Dark			Light		
	5°C	10°C	20°C	5°C	10°C	20°C
Festuca contracta						
Germinations (%)	0	0	56	0	1	11
Tm (days)	–	–	12.9	–	nc	34.9
Poa annua						
Germinations (%)	0	80	4	64	89	32
Tm (days)	–	17.2	nc	56.1	19.1	26.3
Colobanthus kerguelensis						
Germinations (%)	8	100	96	63	98	100
Tm (days)	nc	12.6	5.4	40.1	14.6	5.8
Cerastium fontanum						
Germinations (%)	52	64	52	51	68	69
Tm (days)	26.1	11.9	9.4	25.2	11.0	7.0

one germination occurred in the dark. Although the seeds grown at 20°C light quickly began to germinate, the number increased slowly to about 30% by day 61. At 5°C light, the onset of germination did not commence until day 37. By this time only one dish of seeds remained in this treatment, but the number of germinations increased more quickly than at 20°C and more than 60% of seeds had germinated 30 days later. No data are available for the dark set at this temperature.

P. kerguelensis had a very low success in germination since only 2 seedlings were observed at 4°C light, after 45 and 72 days, respectively.

C. kerguelensis germinated at all temperatures tested. At 20°C and 10°C, the percentage of germination reached nearly 100%, without marked differences between the dark or light conditions. At these temperatures germination occurred very quickly within a few days, i.e. between days 3 and 9 (20°C, $T_m = 5.4 - 5.8$) and between days 11 and 20 (10°C, $T_m = 12.6 - 14.6$), respectively; after this period, a single germination took place on the 27th day at 10°C light. At 5°C, the first germinations were observed after about one month and the final percentage germination was low. Very few seedlings developed in the dark at this temperature.

C. fontanum also germinated at all temperatures tested but germination success was lower than in *C. kerguelensis*. No differences were observed between the dark and the light treatments at 10 and 5°C. However, a positive photo-sensitivity, i.e. beneficial effect of light on germination, seemed to occur at 20°C.

Germination test with cold pre-treatment

This experiment was conducted using the set of seeds stored at 5°C or 10°C when no germination had been observed during the first 28 day period. In consequence, the conditions taken into account after cold pre-treatment was 20°C light, 20°C dark and 10°C light (Fig. 3b). All tests conducted on *A. selago* seeds have been negative.

In *F. contracta*, germination occurred only in the dark conditions. More than 50% of seeds stored at 5°C dark germinated between days 10 and 23 after their transfer to 20°C whereas the success of seeds stored at 10°C dark reached only 12% after 34 days.

P. annua exhibited high percentages of germination in the three sets of seeds transfered from 5°C to 10 and 20°C. Whereas the cold pre-treatment did not significantly modify the percentage of germination at 10°C, it markedly increased the number of seedlings at 20°C. Moreover, the pre-treatment allowed germinations in dark at 20°C.

Single seeds of *P. kerguelensis* stored at 10°C germinated when transferred to 20°C light and 20°C dark, respectively. The best results were obtained with the seeds stored at 5°C light and transferred to 10°C (84%) and 20°C (76%). Only one seed stored at 5°C dark germinated at 20°C.

Three seedlings of *A. magellanica* developed after the transfer of seeds from 5°C to 20°C (2 in light, 1 in dark).

Discussion

Data on the reproductive biology of the subantarctic angiosperm flora are almost negligible except for five species, *Acaena magellanica*, *Colobanthus quitensis*, *Deschampsia antarctica*, *Parodiochloa* (*Poa*) *flabellata* and *Festuca contracta* which have been studied in detail in South Georgia and in the maritime Antarctic (see review by Smith 1984). Of these species, *F. contracta* is the only one which colonizes the glacier forelands on Kerguelen. To our knowledge, very few studies have been carried out on the remaining four native species: *Agrostis magellanica*, *Poa kerguelensis*, *Colobanthus kerguelensis* and *Azorella selago*. However, there is an extensive literature on *Poa annua* because of its cosmopolitan status as a weed and turfgrass. In the subantarctic region *P. annua* and *Cerastium fontanum* are the most widespread introduced species (Walton 1975), but few data on their reproductive capacity in this biome are available.

Seed production

The mean number of seeds per fruit in *C. kerguelensis* (43.2 ± 0.8) is similar to that found by Hennion (1992) in other localities on Kerguelen (48 seeds/fruit). These values are higher than the number obtained in *C. quitensis* (9.5 to 23.4 seeds per capsule) by Holtom and Greene (1967) in culture.

Whereas the number of flowers per spikelet in *F. contracta* on Kerguelen (3.30 ± 0.07) is similar to the results obtained in South Georgia by Greene (1964), it remains slightly higher than the number (2.6 ± 0.1) found by Tallowin (1977a) in the same island. However, the number of spikelets per inflorescence in the Kerguelen population (18.2 ± 0.4) is lower than on South Georgia, both in the sheltered (34 ± 2) and exposed (26 ± 2) areas (Tallowin 1977a).

The number of inflorescences produced per plant in *P. annua* varies greatly in the literature, reaching 450 in temperate pastures (Law et al. 1977). The very low value observed in Plaine Ampère (1.5 ± 0.1) is probably related to the low fertility of the soil and to climatic constraints. The number of flowers per spikelet generally varies between 3 and 5 in U.K. (Tutin 1957) or in the subantarctic islands (Chastain 1958, Greene 1964). When plants are submitted to strong perturbations, e.g. on golf courses, this number decreases to 1.7 (Lush 1988) which is identical to the value obtained in our study (1.70 ± 0.02), suggesting that the severe conditions of the glacier forelands could reduce flower development in this introduced species. Consequently, on the basis of our results, the number of seeds per inflorescence averages 12.9 compared with 61.9 ± 5.5 in plants grown on a poor artificial substrate in England Law (1981). The viability of *P. annua* seed seems to vary greatly between populations but generally appears to be high (Roberts 1964), ranging from 54.7 to 86.3%. On Australian golf courses, Lush (1988) also reported high percentage of viability (69 to 80%). The low percentage of fertile flowers obtained in Plaine Ampère (58%) may be another response to the harshness of the environment.

No published data are available on the seed production in the four other species. *P. kerguelensis* exhibits a higher percentage of fertile flowers and a higher number of inflorescences per plant than *P. annua*. In consequence, whereas the other parameters are very close in the two species, *P. kerguelensis* seed production per plant is three times higher. The number is greater in *A. magellanica* but this result is probably overestimated owing to the absence of information on the fertility of flowers in this species.

Germination

The absence of germination in *A. selago* confirms the observations made by Dorne et al. (1974) and Dorne (1977) who suggested a probable immaturity of the embryo. The very low number of seedlings obtained in *A. magellanica* may be the result of a dormancy which had not been broken during the experiment by the cold treatment, or possibly related to the immaturity of the embryo.

Three months after sampling, seeds of *F. contracta* germinated at 20°C and the cold pretreatment did not affect the final percentage of germination (52–56%), which is in accordance to the final value obtained by Tallowin (1977a). Nearly 50% of seeds sampled from plants growing on a fluvio-glacial sandy soil in South Georgia germinated three months after their collection between 15 and 20°C. In our experiments we were unable to verify the presence of a post seed fall ripening requirement in this species, as in South Georgia (Tallowin 1977a), or a one month post harvest dormancy, as mentioned by Smith (1984).

P. kerguelensis did not germinate without cold pretreatment: it is the only species in the experiment showing dormancy three months after harvest. When this dormancy is broken the germination reaches nearly 80% at 20°C and 10°C light. Hennion (1992) tested seeds from populations at four different sites on Kerguelen. She observed germination (about 10%) three months after sampling only in the coastal population whereas the seeds of the three remaining sites did not germinate over a range of 5–25°C. These conflicting results illustrate the post harvest dormancy variability in this species.

Such variability is also common in *P. annua*. Three months after their collection, no dormancy was demonstrated in the *P. annua* seeds sampled in the Plaine Ampère. Reports on the occurrence or absence of post-harvest dormancy in this species have been reviewed by Wells (1974). It varies considerably between collections by different authors and between ecotypes. Whereas freshly harvested seeds of a Maryland population germinated well at 10° (Standifer and Wilson 1988a), 12 weeks of dry storage were necessary before the first seeds germinated in another population (Standifer 1983). Koch (1968) showed that 50% of freshly harvested seeds were dormant but after storage for 4–6 wk in the laboratory, only 30% were dormant. Different conclusions were stated by the authors for each population studied, ranging from the presence of innate dormacy in the seeds (Howe and Chancellor 1983) to its absence (Froud-Williams 1985).

Maximum germination in the Kerguelen *P. annua* population was obtained at 10°C, but seeds also germinated at 5 and 20°C. Germination over a wide temperature range has been reported by numerous authors, but the optimum temperature differed between populations. Koch (1968) found germination increased from 38% at 2°C to 94% at 5°C and did not decline until temperatures exceeded 30°C. In some populations, germination was absent or marginal at 25°C (Standifer and Porche-Sorbet 1984). Our results are close to those obtained by Standifer and Wilson (1988b) for a population from Louisiana, i.e. 100% germination at 10 or 15°C and poor germination at 5 or 20°C. Similar observations were made at constant temperatures by Naylor and Abdalla (1982) but these authors pointed out that germination was always high with alternating temperatures, as in natural conditions. In some French populations 100% germination was obtained at 20°C, declining to 85% at 10°C (Darmency and Aujas 1988). The mean time of germination calculated by these authors at 10°C is quite similar to the results obtained in the Plaine Ampère population (14.6–15.0 and 19.1 days, respectively) but it differs greatly at 20°C (5.1–5.4 and 26.3 days, respectively).

The two Caryophyllaceae species, *C. quitensis* and *C. fontanum*, have many germination features in common: absence of dormancy three months after the sampling of seeds, absence of photo-sensitivity, except apparently at 5°C in *C. kerguelensis* seeds (Fig. 3a), short mean germination times (Table 3) which decrease when temperature increases. Percentage of germinations in *C. fontanum* did not exceed 70%, whereas Williams (1983) noted rapid and complete germination in seeds of *C. fontanum* subsp. *glabrescens* from England. 100% germination was obtained in our experiment with *C. kerguelensis* seeds, confirming the results obtained by Hennion (1992). However, these results differ slightly from those obtained in *C. quitensis* from more southerly latitudes. In this latter species percentage germination increased with age of seeds from South Georgia (Holtom and Greene 1967), while germination is higher in seeds which have overwintered in a fresh state in Signy Island (Edwards 1974). Whereas no germination (Holtom and Greene 1967) or very low germination (Corner 1971) was obtained at 2–5°C in *C. quitensis*, we found more than 60% germination in *C. kerguelensis* at 5°C light. In *C. quitensis*, Holtom and Greene (1967) noted also a decrease in the amount of germination at 20°C and Corner (1971), in Argentine Islands, obtained very few seedlings at 25°C. This decrease was not observed in *C. kerguelensis* in which the maximum germination was observed at both 10 and 20°C. Hennion (1992) suggested that optimum temperature for *C. kerguelensis* germination is about 22.5–24°C, with 100% germination, whereas the maximum obtained in *C. quitensis* by Corner (1971) did not reached 25% at 12 or 20°C.

Conclusion

Vegetative reproduction plays a minor role in the primary colonization on the glacier forelands on Kerguelen. Warwick (1979) suggested that *P. annua* non-flowering tillers have the potential of becoming detached and establishing as separate individuals in Canada. Smith (1984) reported similar observations in *F. contracta*, and Tallowin (1977b) described vegetatively proliferated spikelets in this grass on South Georgia. None of these features has been observed on Kerguelen where it seems that only the products of sexual reproduction is involved in colonization of the glacier forelands. Consequently, studies on seed production and germination provide a good estimation of the reproductive capacity of these species.

The two Caryophyllaceae species produce the highest number of seeds per plant but the indigenous *C. kerguelensis* exhibits a higher rate of germination and a lower mean germination time than *C. fontanum*. No dormancy mechanism occurs in either species. From these points of view, these two species appear to be the most successful colonizing species on the glacier forelands.

Conversely, whereas the numbers of seeds produced by *A. magellanica* and *A. selago* are important, we cannot assess their reproductive capacity since no seeds germinated in the experiment. However, numerous seedlings of both species have been observed in the field, but the conditions required for post seed fall ripening and germination are not known.

F. contracta is the only species which exhibits a negative photo-sensitivity. The abundance of pebbles on the surface of the sandur provides many sheltered and dark microsites suitable for seed germination. *P. kerguelensis* is also the only species with a post harvest seed dormancy which was broken by cold pre-treatment; no germination was observed below 10°C. These results suggest that germination of seeds produced late in the season occurs in the following summer. The high temperature required for germination of *F. contracta* seeds indicates that a similar phenomenon probably occurs in this species, as was suggested by Tallowin (1977a) for South Georgian *Festuca*. More generally, the high temperature requirement for germination in subantarctic species, as in arctic and alpine plants (Billings and Mooney 1968), is an important delay mechanism which prevents young seedlings being exposed to low temperature during winter (Bliss 1985).

Even in the most severe conditions, populations of *P. annua* produce viable seeds, as demonstrated by Longton (1966) in Deception Island, South Shetland Islands. However, despite the great plasticity of *P. annua* emphasized by various authors (e.g. Tutin 1957; Wells 1974; Warwick 1979), it appears that the reproductive traits of this species on the glacier forelands on Kerguelen are very low: low number of inflorescences, low number of flowers per spikelet, low percentage of fertile flowers. Of all the species examined, *P. annua* exhibited the lowest seed production by each fertile plant. However, its seeds germinate well over a wide range of temperatures, and the optimum, in terms of rate (lowest T_m) and maximum germination, is reached at a lower temperature (10°C) than in the native species. Finally, no dormancy has been observed in the perennial form of *P. annua* on Kerguelen. This is in accordance with the general assumption that the tendencies towards post harvest dormancy are associated with the annual forms of this species (Gibeault 1971, in Warwick 1979).

The reproductive traits considered in this paper do not predict the capacity of plants to become established in the field but they are fundamental in understanding colonizing processes in recently deglaciated areas. Together with other life history traits they will be used in the future to determine the colonizing abilities of both native and introduced species and to develop, in relation to the environmental factors, a more comprehensive approach to the plant dynamics on subantarctic glacier forelands.

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References

Billings WD, Mooney HA (1968) The ecology of arctic and alpine plants. Biol Rev 43:481–529

Bliss LC (1985) Alpine. In: Chabot BF, Mooney HA (eds) Physiological ecology of North American plant communities. Chapman Hall, New York, pp 41–65

Chastain A (1958) La flore et la végétation des îles de Kerguélen. Mém Mus Nat Hist Nat, Ser B, Bot 11:1–136

Corner RWM (1971) Studies in *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv.: IV. Distribution and reproductive performance in the Argentine Islands. Br Antarct Surv Bull 26:41–50

Darmency H, Aujas C (1988) A genetic approach of germination: an example in *Poa annua* L. VIIIème Coll. Int. Biologie, Ecologie et Systématique des Mauvaises Herbes. INRA, Dijon, pp 25–32

Dorne AJ (1968) Note sur les conditions de germination en laboratoire de *Pringlea antiscorbutica* R. Br. CNFRA 23:17–24

Dorne AJ (1977) Analysis of the germination under laboratory and field conditions of seeds collected in the Kerguelen archipelago. In: Llano GA (ed) Adaptations within Antarctic Ecosystems. Gulf Publishing, Houston, Texas, pp 1003–1013

Dorne AJ, Devillez F, Courtemanche D (1974) La micro-radiographie des semences appliquée à certaines espèces récoltées dans les Terres Australes et Antarctiques Françaises. C R Acad Sci, Paris, Sér D 278:1491–1494

Edwards JA (1974) Studies in *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv.: VI. Reproductive performance on Signy Island. Br Antarct Surv Bull 39:67–86

Frenot Y, Gloaguen JC, Picot G, Bougére J, Benjamin D (1993) *Azorella selago* Hook. used to estimate glacier fluctuations and climatic history in the Kerguelen Islands over the last two centuries. Oecologia 95:140–144

Froud-Williams RJ (1985) Dormancy and germination of arable grass-weeds. Asp Appl Biol 9:9–18

Greene SW (1964) The vascular flora of South Georgia. Br Antarct Surv Sci Rep 45:1–58

Hennion F (1992) Etude des caractéristiques biologiques et génétiques de la flore endémique des îles Kerguelen. Thèse de Doctorat, Mus Nat Hist Nat, Paris

Holtom A, Greene SW (1967) The growth and reproduction of Antarctic flowering plants. Phil Trans R Soc Lond, Ser B 252:323–337

Howe CD, Chancellor RJ (1983) Factors affecting the viable seed content of soils beneath lowland pastures. J Appl Ecol 20:915–922

Koch W (1968) Environmental factors affecting the germination of some annual grasses. Proc 9th Br Weed Control Conf 9:14–19

Law R (1981) The dynamics of a colonizing population of *Poa annua*. Ecology 62:1267–1277

Law R, Bradshaw AD, Putwain PD (1977) Life history variation in *Poa annua*. Evolution 31:233–246

Longton RE (1966) Alien vascular plants on Deception Island, South Shetland Islands. Br Antarct Surv Bull 9:55–60

Lush WM (1988) Biology of *Poa annua* in a temperate zone golf putting green (*Agrostis stolonifera*/*Poa annua*). I. The above-ground population. J Appl Ecol 25:977–988

Matthews JA (1993) The ecology of recently deglaciated terrain. A geœcological approach to glacier forelands and primary succession. Cambridge University Press, Cambridge

Naylor RE, Abdalla AF (1982) Variation in germination behaviour. Seed Sci Technol 10:67–76

Roberts HA (1964) Emergence and longevity in cultivated soil of seeds of some annual weeds. Weed Research 4:296–307

Smith RIL (1984) Terrestrial plant biology of the sub-Antarctic and Antarctic. In: Laws RM (ed) Antarctic Ecology I. Academic Press, London, pp 61–162

Smith RIL (1993) The role of bryophyte propagule banks in primary succession: case-study of an Antarctic fellfield soil. In: Miles J, Walton DWH (eds) Primary succession on land. Blackwell Scientific Publications, Oxford, pp 55–78

Standifer LC (1983) Some effects of soil temperatures on dormancy of annual bluegrass (*Poa annual* L.) seeds. Meeting of the Weed Science Society of America: pp 60–60

Standifer LC, Porche-Sorbet R (1984) Seasonal changes in the germination of buried annual bluegrass seeds. Proc Southern Weed Science Society, 37th annual meeting, pp 301–301

Standifer LC, Wilson PW (1988a) Dormancy studies in three populations of *Poa annua* L. seeds. Weed Res 28:359–363

Standifer LC, Wilson PW (1988b) A high temperature requirement for after ripening of imbibed dormant *Poa annua* L. seeds. Weed Res 28:365–371

Tallowin JRB (1977a) Studies in the reproductive biology of *Festuca contracta* T. Kirk on South Georgia: II. The reproductive performance. Br Antarct Surv Bull 45:117–129

Tallowin JRB (1977b) Vegetative proliferation of *Festuca contracta* T. Kirk on South Georgia. Br Antarct Surv Bull 45:13–17

Tutin TG (1957) A contribution to the experimental taxonomy of *Poa annua* L. Watsonia 4:1–10

Walton DWH (1975) European weeds and other alien species in the sub-Antarctic. Weed Res 15:271–282

Warwick SI (1979) The biology of Canadian weeds. 37. *Poa annua* L. Can J Plant Sci 59:1053–1066

Wells GJ (1974) The biology of *Poa annua* and its significance in grassland. Herbage Abstracts 44:385–389

Williams ED (1983) Germinability and enforced dormancy in seeds of species of indigeneous grassland. Ann Appl Biol 102:557–566