

Fruit development and performance of *Schoenus nigricans* in coastal dune slacks of Europe: an extension of H. G. Baker's seed mass–altitude to a seed mass–latitude relationship

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SUMMARY

The development fruits (nutlets) and seeds of *Schoenus nigricans*, a perennial sedge of wet coastal dune slacks, was compared between populations of the Mediterranean Sea and the North Sea, to examine the hypothesis of adaptation in a geographical gradient (Baker 1972). The development period of nutlets and seeds lasted several months. The serial insertion of nutlets on the spikelet caused a negative mass gradient from adaxial to abaxial nutlets. Final nutlet mass (first adaxial spikelet position) of Mediterranean plants was 30% higher than that of North Sea plants, extending Baker's hypothesis of the inverse relationship between seed (nutlet) mass and geographical altitude to geographical latitude.

The difference in final nutlet mass between plants from populations of the Mediterranean and North Sea persisted, when plants were grown under the climatic conditions of the North Sea plants. However, the nutlet mass, but not the seed mass of the Mediterranean plants, grown under Dutch climatic conditions, was less than at their original size. Start of flowering of the Mediterranean plants under Dutch climatic conditions was delayed by 1–2 months, compared with their flowering at the Mediterranean sites. Nutlets of Mediterranean plants ripened later than those of Dutch plants under the Dutch climatic conditions.

The differentiation in nutlet and seed masses and plant height in the geographic gradient in Europe and its persistence under experimental conditions indicates a strong genetic component of population differentiation. The data do not support the hypothesis of 'general-purpose genotypes' (Schmid 1992) in this wet dune slack species.

Key-words: climatic gradient, nutlet development, population differentiation, wet dune slacks, *Schoenus nigricans*, *Glyphipteryx schoenicolella*.

INTRODUCTION

Baker (1972) has postulated that seed mass (*sensu lato*, including fruits such as achenes, caryopses and nutlets) within a single plant species declines from the coast to the

mountain along a geographical altitudinal gradient. A possible explanation may be the decline in the length of the growing season. A similar effect may be caused by a latitudinal gradient; seed mass may increase by going from north to south in the Northern Hemisphere. However, it has been demonstrated that plants present in a geographical gradient can avoid the impact of climatic changes by restricting their life cycle to a certain period of the year, thus avoiding exposure to unfavourable climatic conditions. This latter behaviour is shown by winter annuals such as *Phleum arenarium* in Europe (Ernst 1991) and by the agricultural weed *Amaranthus retroflexus* (McWilliams *et al.* 1968).

Theoretical considerations predicting a single optimum seed size (Smith & Fretwell 1974; McGinley *et al.* 1987) are often in conflict with empirical data. Plants are obviously not capable of producing a uniform seed quality (Winn 1991), although seed-size variation within species has traditionally been regarded as low (Harper *et al.* 1970). Often seed size variation within plants is related to seed packaging (Mehlman 1993) and as a consequence to seed number. Thompson (1981) has earlier demonstrated that a wide variety of seed sizes may enhance survival of the local population. Unfortunately, all theoretical models do not account for the biological reality, so that only a very small number of the countless amount of seeds has a chance to germinate and survive the seedling stage. Survival, however, is not related to seed mass (Weller 1985). Therefore, seed size variation may be pleiotropically related to other plant attributes (Westoby *et al.* 1992) and seed size is often more related to plant height, growth form and dispersal mode than to fitness (Leishman & Westoby 1994).

Perennial plant species with evergreen shoots and leaves which are exposed to the local climatic conditions throughout the year, may be ideal to extend Baker's altitudinal hypothesis experimentally to the relationship between diaspore mass and geographical latitude. In a previous study it was shown that *Schoenus nigricans*, a characteristic perennial sedge of wet coastal dune slacks in Europe that is frequently threatened by water extraction (Grootjans *et al.* 1988; Stuijfsand *et al.* 1993), does indeed have a strong geographical gradient in fruit mass (Ernst 1991). Such differences in fruit mass may be caused by the length of the growing season and/or by the amount of radiation if the time necessary for seed development is variable between populations. The 'general-purpose genotype' *sensu* Schmid (1992) may also operate under latitudinal conditions, i.e. a genotype which can perform under a variety of environmental conditions by phenotypic flexibility.

To test the impact of the length of growing season, the nutlet and seed development of *S. nigricans* was analysed from flowering to nutlet ripeness in populations from dune slacks at the Mediterranean and North Sea coasts. Whether differences were purely phenotypic or genetically determined was tested by growing plants from the Mediterranean populations under the conditions of plants from the North Sea coast. The ecological consequences of differences in nutlet and seed masses are discussed.

MATERIAL AND METHODS

Nutlet and seed mass of Schoenus nigricans in a latitudinal European gradient

For extending Baker's altitude-seed mass hypothesis to a latitude-(nutlet) seed mass hypothesis, nutlets and seed sizes were tested for 11 European populations from wet coastal dune slacks. Five Mediterranean populations of *Schoenus nigricans* L. were

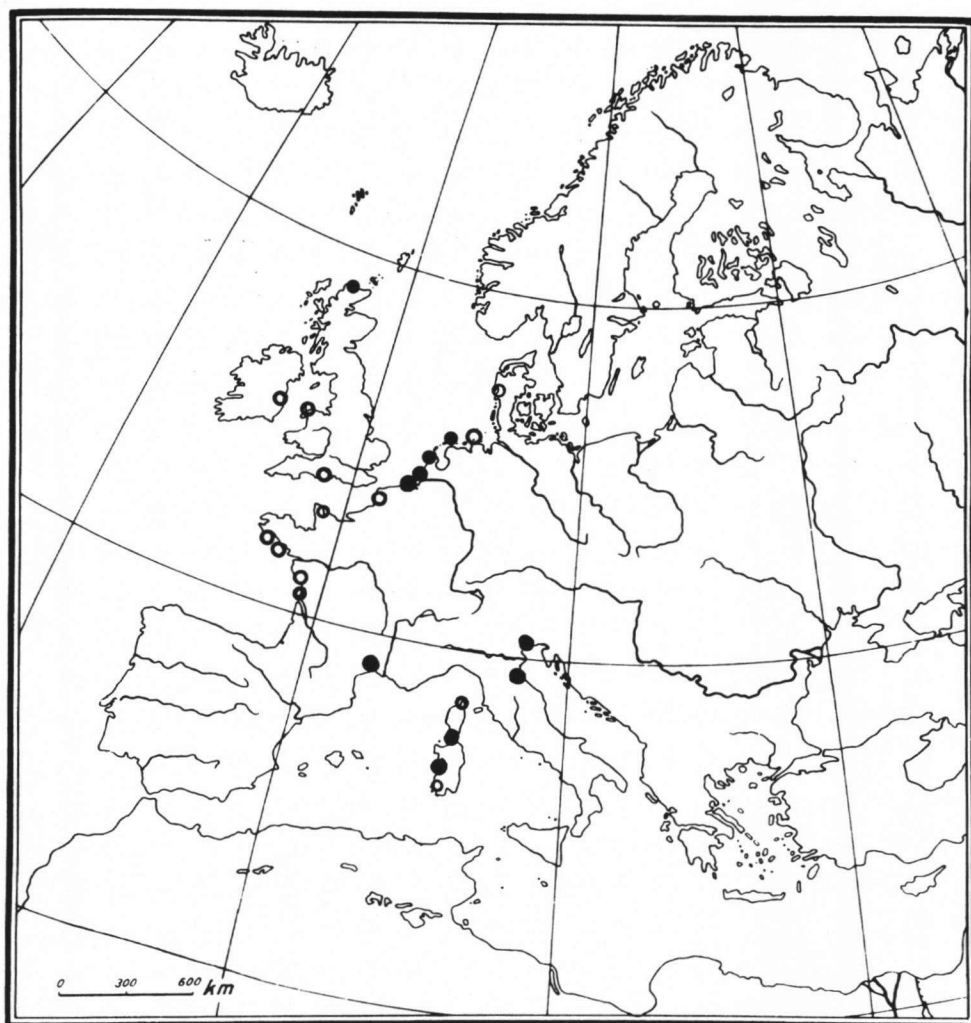


Fig. 1. The occurrence of *Schoenus nigricans* in wet coastal dune slacks in Europe. The filled circles indicate the populations studied.

investigated: Sinis near Oristano (Sardinia) 39°48'N, 8°28'E (Bocchieri *et al.* 1987); Figari (Corsica) 41°2'N, 9°8'E (Paradis & Piazza 1992); Salin de Giraud (Camargue) 43°02'N, 4°23'E; Bardello (north of Ravenna) 44°32'N, 12°17'E (Piccoli & Merloni 1989); and Alberoni (near Venice) 45°17'N, 12°18'E. Infructescences from six populations around the North Sea were collected: Goedereede (South Holland) 51°50'N, 3°54'E; De Zilk 52°18'N, 4°31'E; Oceaen 52°33'N, 4°35'E; Egmond (North Holland) 52°36'N, 4°31'E; Schiermonnikoog (Frisian Wadden island) 53°30'N, 6°12'E and Betty Hill (North Scotland) 58°34'N, 3°37'W (Fig. 1).

The flowers of *Schoenus nigricans* are said to be arranged in a 1–4 flowered spikelet (Reichgelt 1956; exceptionally 7-flowered, Hegi 1966), but a preliminary survey of several European populations has shown that up to 6 flowers per spikelet can be present in all populations (Fig. 2). Only the nutlets and seeds at the first and second spikelet

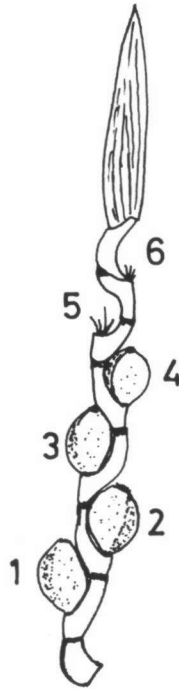


Fig. 2. Spikelet of *Schoenus nigricans* with fully developed nutlets at positions 1 to 4, and remnants of male flowers at position 5 and 6.

positions were considered for comparison of the European populations, because nutlets at the third position were often not developed and those at the fourth position were often absent (cf. Table 2). In addition, predation of the nutlets by the monospecific microlepidopteran larvae of *Glyphipteryx schoenicolella* Boyd may affect the biomass of nutlets and seeds (Ernst & van der Ham 1988). Therefore, infructescences with more than one infected spikelet were discarded.

The nutlets were removed from the spikelet with a pair of tweezers, collected per spikelet position and dried at 60°C for 14 hours. After weighing on a microbalance (1 µg sensitivity, Mettler ME30), nutlets were carefully broken up with a setting pin; the seed was removed with a pair of tweezers. The seeds were dried at 60°C for 34 hours and weighed. Per population, at least 50 nutlets and seeds at the first and second spikelet positions were analysed, two infructescences per each of 10 plants. Nutlets were harvested in late August to early September.

Nutlet and seed development in dune slacks at the Mediterranean and North Sea coasts

To analyse the differences in time of development of nutlets and seeds on the spikelet, the inflorescences were investigated during the growing season (1992) at a Mediterranean and North Sea site. The populations of *Schoenus nigricans* were studied at the wet dune slacks of the coastal North Sea dunes at Egmond, North Holland (Ernst & van der Ham 1988; Van Beckhoven 1992) and the Rono delta dunes at Bardello, Northern Italy (Piccoli & Merloni 1989). Some climatic data of weather stations at some distance of both sites during the study are given in Fig. 3.

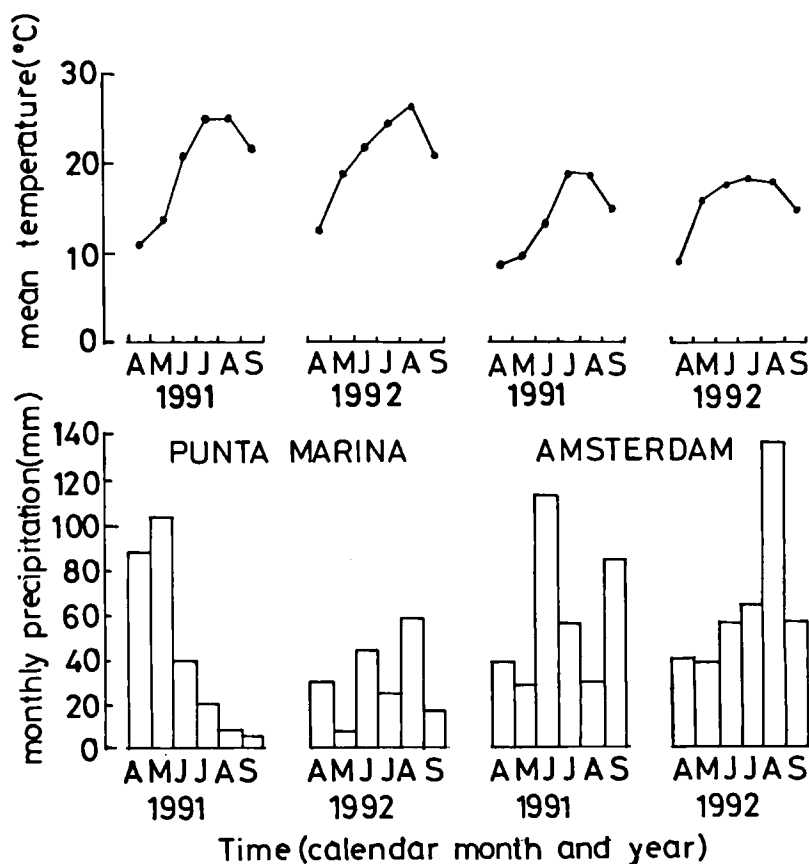


Fig. 3. Mean monthly temperature and precipitation during the period of flowering and fruit development of *Schoenus nigricans* near the Mediterranean (Punta Marina) and North Sea (Amsterdam) sites of the two investigated populations during 1991 and 1992.

During the growing season of 1992, two inflorescences c.q. infructescences of each of 20 plants were randomly collected in both populations at monthly or shorter intervals. This plant material was air-dried; infructescences from the Italian site were sent to Amsterdam for further treatment. For analysis of nutlet and seed development, all spikelets were cut off from the infructescence. For determination of nutlet and seed mass and the isolation of seeds from nutlets, the above described procedure was followed.

Length and diameter of 20 ripe nutlets from each spikelet position of the populations at Barello and Castricum, harvested from five plants in August and September 1992, respectively, were measured under a binocular (magnification 4×10) on a grid system with a subdivision of 0.1 mm and an ocular division of 10 grids for 0.1 mm.

Phenotypic plasticity and/or genotypic differentiation

To test the possibility of phenotypic or genotypic differences, plants were grown from nutlets collected from the North Sea populations at Egmond and Schiermonnikoog and from the Mediterranean populations at Oristano, Alberoni and Salin de Giraud. After germination in March and April 1991 seedlings were planted in dune sand (pH 7.2), two plants per plastic pot (10 cm high, 6 cm in diameter) and were kept in a glasshouse for

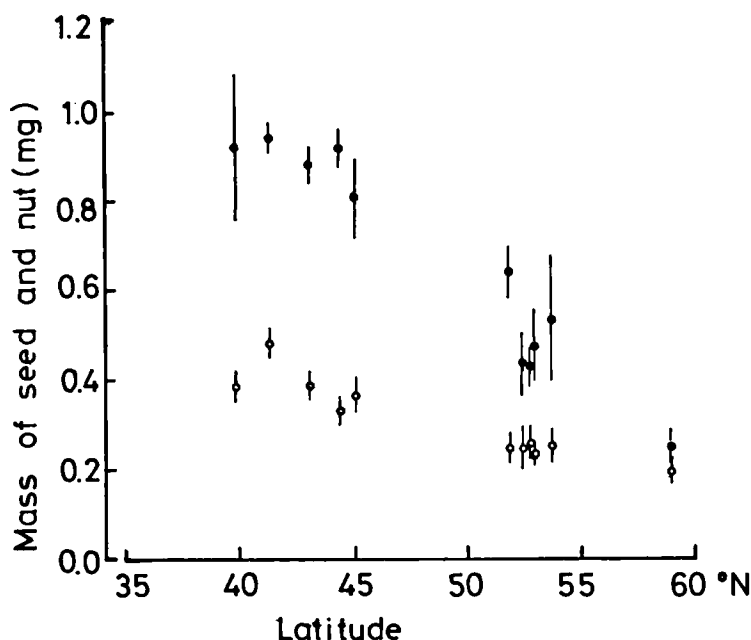


Fig. 4. Relationship between geographic latitude and the mean masses of ripe nutlets (closed symbols) and seeds (open symbols) of *Schoenus nigricans*, all at the first spikelet position. Per population 10 plants, two infructescences per plant were analysed. The mean (± 1 SE) is given.

the first 14 months ($20^{\circ} \pm 2^{\circ}\text{C}$, 60–80% relative humidity, additional radiation by mercury iodide lamps, providing a light intensity of $235 \mu\text{Einstein m}^{-2} \text{s}^{-1}$ at plant level). Due to the tall growth form, shoots of *S. nigricans* will receive their photosynthetic energy in the field from reflected and diffusive irradiation during late morning and early afternoon, but from direct radiation in the early morning and the late afternoon. It is difficult to simulate the change in radiation angle during the day in illumination experiments. Therefore, plants from all populations were transplanted in May 1992 under the same climatic outside conditions in the experimental plots at Amsterdam. In spring 1993 plants flowered. For the development of nutlets and seeds, nutlets were harvested every 2 weeks (five inflorescences resp. infructescences, each of one plant per sampling date) and prepared as described earlier.

Data analysis

Data were analysed by a factorial analysis of variance (ANOVA) and regression analysis (Sokal & Rohlf 1981).

RESULTS

Nutlet and seed mass of *S. nigricans* in a latitudinal European gradient

Nutlet and seed masses were negatively correlated ($n=950$, $r^2=0.956$; and $r^2=0.840$, $n=950$) with latitude along the European geographical gradient, with highest masses in the Mediterranean populations and lowest in the most northern population at Betty Hill in Scotland (Fig. 4). The mean nutlet mass of the utmost populations differed by a factor

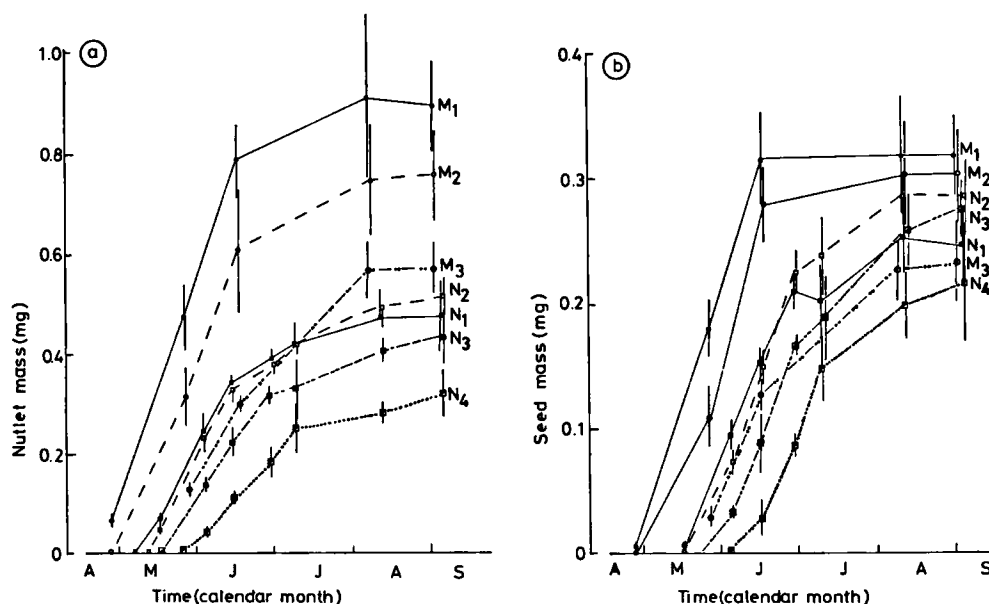


Fig. 5. Development of mass nutlets (a) and seeds (b) at the various spikelet positions of plants from the Mediterranean (circles) and North Sea (quadrats) populations of *Schoenus nigricans* at their natural site during the growing season 1992. M₁, M₂ and M₃ are the mean nutlet mass (± 1 SE) of the Mediterranean plants at spikelet positions 1, 2 and 3, N₁ to N₄ those of the North Sea plants at spikelet positions 1, 2, 3 and 4.

of 3 (940 μ g vs. 310 μ g) and seed mass by a factor of 2.3 (475 μ g vs. 210 μ g) in Figari and Betty Hill, respectively.

Nutlet and seed development in dune slacks at the Mediterranean and North Sea coasts

In the dune slack at Bardello flowering started in early April; this was 1 month earlier than in the dune slack at Egmond and lasted at both sites for 4 and 6 weeks, respectively. In plants of both populations flowering and nutlet development began at the most adaxial position of the spikelet. The flower and nutlet at the second position of the spikelet followed approximately 4–5 days later, with an additional 1–2 weeks for initiation of flower development at the third to fifth positions; nutlets at the fourth and fifth positions were often without seed (Fig. 2). Flowering started relatively synchronously among plants of the same population and could last up to 4 weeks.

As a consequence of this serial flowering at each spikelet, nutlet and seed masses possessed rather strong abaxial gradients on the spikelets (Fig. 5a). The most adaxial nutlets of plants from both populations had nearly the same mass increment (of approximately $7.2 \mu\text{g day}^{-1}$) during the early 4 weeks of development. After this period the increase in nutlet mass was significantly ($P < 0.01$) higher in Italian than Dutch plants. This resulted, after 4 months of nutlet development, in a final mass of $908 \pm 166 \mu\text{g}$ for nutlets at the first spikelet position, $742 \pm 108 \mu\text{g}$ at the second spikelet position, and $565 \pm 52 \mu\text{g}$ at the third spikelet position in the case of the Italian plants. In the Dutch plants nutlet mass at the first position was significantly lower ($P < 0.05$) than at the second spikelet position, $460 \pm 73 \mu\text{g}$ vs. $514 \pm 38 \mu\text{g}$. Although the development of the nutlet at the third spikelet position started 15–20 days later than at the first spiked position, it achieved nearly the same final mass, i.e. $433 \pm 57 \mu\text{g}$. The

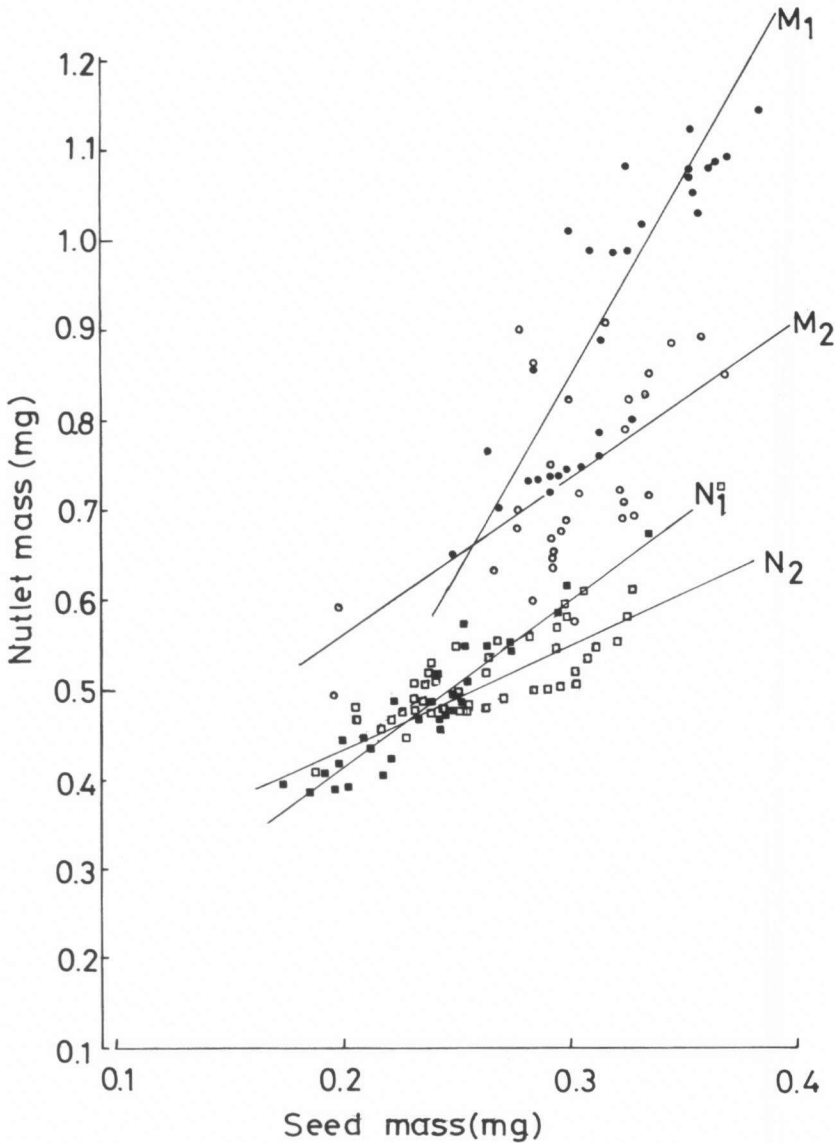


Fig. 6. Relationship between nutlet mass and seed mass of *Schoenus nigricans* at the first (1) and second (2) spikelet position. M=Mediterranean plants, N=North Sea plants.

mass gradient of seeds on a spikelet was less strong than that of the nutlets. The best developed gradient was present in the Italian plants (Fig. 5b). Whereas the nutlet mass was significantly ($P < 0.001$) different between both populations, the overall seed mass was not.

The ratio between nutlet mass and seed mass was linear at the first and second position (Fig. 6). Italian plants produced heavier nutlets with a relatively lower seed mass at the first spikelet position (M_1), whereas in the Dutch plants the increase of nutlet and seed mass (N_1) was nearly the same at the first spikelet position. At the second

Table 1. Length and diameter of nutlets of *Schoenus nigricans* (mean \pm 1 SE) from a Mediterranean and a North Sea population in relation to their position on the spikelet. Position 1 is the most adaxial, position 3 the most abaxial. Unlike superscripts indicate a significant ($P < 0.05$) difference between means. Number of nutlets for each spikelet position and population was 20, five plants per population

Nutlet character & population	Nutlet position on the spikelet		
	1	2	3
Length (mm)			
Bardello	1.57 \pm 0.09 ^a	1.50 \pm 0.07 ^b	1.40 \pm 0.14 ^c
Castricum	1.32 \pm 0.09 ^d	1.21 \pm 0.05 ^e	1.03 \pm 0.05 ^f
Diameter (mm)			
Bardello	0.08 \pm 0.06 ^a	0.88 \pm 0.06 ^a	0.85 \pm 0.02 ^{ac}
Castricum	0.82 \pm 0.04 ^{bc}	0.88 \pm 0.07 ^a	0.79 \pm 0.03 ^b

position (M_2 , N_2) mass increase was in favour of the seed in both populations. Differences in mass was mainly caused by an increased length of the fruits of the Italian plants at all positions of the spikelets (Table 1). Nutlet diameter showed much less difference between plants of both populations.

Phenotypic plasticity and/or genotypic differentiation

Duration of nutlet and seed development did not appear to differ greatly at the field sites in Italy and the Netherlands (cf. Fig. 5), and thus differences in nutlet and seed mass may be due to differences in irradiation intensity.

Under Dutch climatic conditions, plants originating from seeds of the Mediterranean populations produced nutlets with a higher mass at the first spikelet position (Table 2), compared with plants originating from seeds of the Dutch populations. Compared with the nutlets at their site of origin, the nutlet mass at the first spikelet position of the Mediterranean plants grown under Dutch climatic conditions was 79 (Oristano, Alberoni) to 83% (Salin de Giraud) of that of plants grown at their natural site. At the third and fourth spikelet position it was often the same in the Mediterranean and Dutch populations. Seed mass of the Mediterranean experimental plants (Table 3) was 25% higher than in the Dutch plants. In contrast to the nutlet mass it was similar or even slightly increased compared with plants growing at their original site. There was no significant ($P < 0.05$) difference in seed mass at the first and second spikelet positions.

DISCUSSION

Baker's (1972) hypothesis of a negative correlation between seed (fruit) mass and altitude in California was based on nearly 2500 taxa, with often low systematic affinity. Comparison between populations of one species in a geographical gradient are more reliable because most of the physiological reactions will be comparable, except the response to the supposed determining factor, e.g. the length of the growing season. Our data of nutlets of *S. nigricans* fit well into the general picture, that fruit and seed mass decreases with increasing geographical latitude, i.e. from the Mediterranean Sea to

Table 2. Nutlet mass of *Schoenus nigricans* at their natural sites (a) and at the experimental plots at Amsterdam (b) in the first year of flowering after 3 years of growth. Except for the experimental plants of the Oristano population, where only one plant was fruiting in the third year, for all other plants 50 spikelets were analysed. Data present the mean (± 1 SE). NP=not present. For the spikelet positions 1 and 2, 50 nutlets each per population and treatment were analysed; the measured nutlets at position 3 and 4 varied between 10 and 34

		Nutlet mass at spikelet position			
Population		1	2	3	4
<i>Mediterranean Sea</i>					
Oristano	a	909 ± 156	866 ± 233	655 ± 222	448 ± 124
(Sardinia)	b	722 ± 43	557 ± 59	524 ± 34	NP
Alberoni	a	805 ± 126	739 ± 45	581 ± 48	357 ± 100
(Po-delta)	b	638 ± 38	621 ± 39	577 ± 22	473 ± 51
Salin de Giraud	a	875 ± 36	885 ± 41	374 ± 104	NP
(Camargue)	b	725 ± 73	586 ± 140	354 ± 92	241 ± 12
<i>North Sea</i>					
Egmond	a	479 ± 86	496 ± 95	399 ± 138	305 ± 125
(North Holland)	b	460 ± 73	514 ± 38	433 ± 57	319 ± 52
Schiermonnikoog	a	588 ± 113	491 ± 75	NP	NP
(Wadden Island)	b	599 ± 41	605 ± 86	495 ± 46	327 ± 92

Table 3. Seed mass of plants of *Schoenus nigricans* at their natural sites (a) and at the experimental plots at Amsterdam (b) in the first year of flowering after 3 years of growth. For further explanation see Table 2

Population		Seed mass at spikelet position			
		1	2	3	4
<i>Mediterranean Sea</i>					
Oristano	a	339 ± 52	346 ± 45	287 ± 67	182 ± 37
(Sardinia)	b	386 ± 19	330 ± 20	285 ± 4	NP
Alberoni	a	367 ± 53	351 ± 32	320 ± 26	214 ± 55
(Po-delta)	b	403 ± 28	411 ± 22	411 ± 23	329 ± 50
Salin de Giraud	a	379 ± 25	380 ± 38	270 ± 67	NP
(Camargue)	b	377 ± 40	329 ± 78	325 ± 71	267 ± 36
<i>North Sea</i>					
Egmond	a	239 ± 16	286 ± 95	250 ± 50	198 ± 44
(North Holland)	b	255 ± 38	289 ± 25	295 ± 48	197 ± 27
Schiermonnikoog	a	267 ± 42	248 ± 25	NP	NP
(Wadden Island)	b	287 ± 26	320 ± 24	300 ± 23	227 ± 59

Northern Scotland. Therefore, it is possible to extend the fruit mass–altitude relationship as presented by Baker (1972) to a fruit mass–latitude relationship. The latter is also found for nutlets of *S. nigricans* on Sardinia, where the coastal population (5 m above sea level) has a mean nutlet mass of 772 ± 45 μ g, and that on a mountain fen (800 m above sea level) a mass of 453 ± 99 μ g (Bocchieri *et al.* 1987), which is comparable to the

nutlet mass of the Dutch populations. This negative relationship is not only restricted to the reproductive organs, but it could also be shown for shoot height of *S. nigricans* throughout Europe (Sparling 1968; Ernst 1991). A high genetic component in such a relationship was established by Clausen & Hiesey (1958) for populations of *Potentilla glandulosa*. In contrast to perennial plants, annual plants such as *Amaranthus retroflexus* in a North American latitudinal gradient (McWilliams *et al.* 1968) and *Phleum arenarium* in a European latitudinal gradient (Ernst 1991) can change their growth period in such a way that they remain exposed to similar environmental conditions at various latitudes, thus escaping the necessity of adaptation to a changing overall environment. In addition, a long period of seed and fruit development will integrate the environmental conditions, especially the irradiation, better than a short development time. The latter is very often associated with annual plants. Therefore, Baker's hypothesis should be restricted to perennial plants and annual plants, both with a long development time for the seed.

The length of the growing season as a determining factor for the negative relationship, as suggested by Baker (1972), does not hold for the various populations of *S. nigricans*. The development time of the Mediterranean plants from fertilization to a ripe nutlet is very similar to or even shorter than that of the North Sea plants. Based on the experimental results of the Mediterranean plants under Dutch climatic conditions, the Mediterranean plants are obviously adapted to a climate with high irradiation intensity and evaporation rate. Under a Dutch climate with less irradiations, the Mediterranean plants need time to reach the same performance of nutlets and seeds as at their natural site.

The strong gradient of nutlet and seed mass along the spikelet is not changed by different climatic conditions. Similar gradients within inflorescences affecting diaspore mass have been described for *Apium graveolens* (Thomas *et al.* 1979) and *Pastinaca sativa* (Hendrix & Trapp 1992). The serial insertion of nutlets on the spikelet of *S. nigricans* may favour resource competition. The most adaxial protogynous flower has the advantage of being fertilized first and thus they may have the best access to nutrients and water. All carbohydrates which are allocated into the nutlet and seed have to be imported from the shoot because the bracts do not photosynthesize, as known from inflorescences of other plant species. If the flow of minerals and carbohydrates is constant in time, it is quite reasonable to assume that the last initiated nutlet and seed will have less biomass.

Which are the ecological consequences of the nutlet position on the spikelet? First of all, infructescences of *S. nigricans* are often heavily infested by the larvae of the microlepidopteran *Glyphipteryx schoenicolella* (Ernst & van der Ham 1988). Each infestation starts at the most abaxial nutlet position, probably because it is easier for the larvae, hatching in early June under Dutch conditions, to consume the very young nutlets with as-yet unmineralized cell walls. Due to this feeding preference of the larvae, nutlets at the most adaxial (first) position have the greatest chance for survival. In addition, at the time of larval attack the high silica content of the nutlet may offer an impenetrable barrier. At the Mediterranean sites, rapid nutlet development and mineralization of the cell wall by silica (W. H. O. Ernst, unpublished) may hamper nearly all infestations.

A second consequence of the nutlet position on the spikelet is that of the release. It occurs by weathering from the top of the spikelet so that nutlets at the most abaxial position are released first, often as early as August at Mediterranean dune slacks and in

October and November at Dutch dune slacks. Once on the soil, the seeds with a soft nutlet are exposed to predation, especially by mites, and attack by decomposing fungi. In a very wet autumn they can germinate in early winter and will not survive a frost period in late winter. Nutlets at the most adaxial position build up an above-ground seedbank until the following spring, when dune slacks have the highest chance of being flooded (Ernst & van der Ham 1988). Similar differences in dispersal of diaspores due to their position at the infructescence are well documented from *Phleum arenarium* (Ernst 1981) and *Mesembryanthemum nodiflorum* (Guterman 1990).

A third consequence of serial insertion of nutlets on a spikelet is the impact of the nutlet position on the germination process. After nutlet release from the parent plant the thickness of the cell walls may determine the access of oxygen and water to the seed. Nutlets at the most abaxial position have the highest immediate germination rate (W. H. O. Ernst, unpublished data), whereas those at the adaxial position are characterized by a long dormancy period (Ernst & van der Ham 1988). This behaviour is similar to that of achenes from the tertiary and quaternary umbels of *Apium graveolens* (Thomas *et al.* 1979) and to that of the pseudocarps of *Pteranthus dichotomus* (Evenari *et al.* 1982). During a period of 6 months, germination of nutlets from Mediterranean plants was more delayed than that of the plants from the North Sea coast (Ernst 1991), thus emphasizing the latitudinal differentiation of *S. nigricans*.

The presence of great differences in seed and nutlet size does not fit theoretical considerations of optimalization of seed size (Smith & Fretwell 1974), but the cost of 'luxurious' production of seeds with low survival rates is low considering the carbohydrates and nutrients in *Schoenus nigricans*. From an evolutionary point of view, the optimalization process may still be in progress, therefore enabling high biodiversity.

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