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On the seed bank of the xerosere of the dry coastal dunes in the atlantic province of Europe

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Abstract

In eight sites, four in the northern and four in the southern part of the Atlantic province of Europe, in five places from the outer dunes towards the inner dunes of the xerosere, samples were taken from the germinable seed bank. Species only present in the seed bank were considered to have a persistent seed bank, whereas species only present in the established vegetation were referred to as having a transient seed bank.

All species found in all sites revealed that 71% had a transient type of seed bank and 16% a persistent type of seed bank. A decreasing proportion of species with a transient seed bank was found from the outer dunes towards the inner dunes, whereas the proportion of species with a persistent seed bank increased.

All species found in all sites revealed a higher proportion with a transient seed bank in the northern than in the southern part of the Atlantic province of Europe. This is the case in all sites from the outer dunes towards the inner dunes.

Zusammenfassung

Der keimfähige Samenvorrat ist an fünf Stellen in einer Reihe von Weissdünen zu Graudünen untersucht worden, davon vier im nördlichen Teil und vier im südlichen Teil der Atlantischen Provinz Europas. Arten, die nur im Samenvorrat vorhanden waren, wurden gekennzeichnet als „persistent". Arten, die nur in der etablierten Vegetation aufgefunden wurden, sind als „transient" gekennzeichnet.

Von allen Arten zusammen hatten 71% einen „transienten" Samenvorrat, 16% einen „persistenten" Samenvorrat. Der Anteil der Arten mit einem „transienten" Samenvorrat nahm ab von den Weissdünen zu den Graudünen; der Anteil der Arten mit einem „persistenten" Samenvorrat nahm zu.

Arten mit einem „transienten" Samenvorrat treten vermehrt im nördlichen Teil und weniger im südlichen Teil der Atlantischen Provinz auf. Das bezieht sich auf alle Bereiche von den Weissdünen bis zu den Graudünen.

1. Introduction

According to the generally accepted definition of vegetation: „... a system of largely spontaneously growing plant populations, growing in coherence with their sites and forming an ecosystem with these sites" (WESTHOFF & VAN DER MAAREL, 1973), the seed bank is part of the vegetation. As a consequence the study of the seed bank is an important task for vegetation science (WILLEMS, 1983). Indeed, the number of papers concerning the role of the seed bank as part of the ecosystem is increasing: 144 papers from 1900 until 1959, 144 papers in the 1960's, 99 papers in the 1970's, 176 papers in the 1970's and 416 papers from 1980 to 1988 (VYVEY, 1988-1989). Remarkable little is known about seed banks of dune plant communities. From VYVEY's list of 845 papers only seven deal with inner dunes (ALTAMIRANO & GUEVARA, 1982; BAKKER, 1985; SYMONIDES, 1978; 1979; VAN BREEMEN & VAN LEEUWEN, 1983; WATKINSON, 1978; WATKINSON & DAVY, 1985) and none with the outer dunes. HARPER

(1977) does not go into the seed bank of dune species. GRIME et al. (1988) do not deal with outer dune species, only with species also occurring in inland communities. Also specialized books or papers on dune systems do not deal with seed banks (RANWELL, 1972; WESTHOFF, 1989; WESTHOFF & VAN OOSTEN, 1991).

THOMPSON & GRIME (1979) distinguished two main types of seed bank, based on sampling throughout the year. Species found in the germinable seed bank for only a short period of time are referred to as having a transient type of seed bank, whereas species found throughout the year are considered to have a persistent type of seed bank.

In an earlier paper some aspects of the phytogeographical variation of the vegetation of the outer dunes in the Atlantic province of Europe was described (BAKKER, 1976). In order to get an idea of the seed bank of the plant communities occurring, some soil samples of the germinable seed bank were collected. The present paper deals with two questions: (i) which are the characteristics of the seed bank of the outer dunes in the Atlantic province of Europe, and (ii) does this germinable seed bank reveal some geographical variation in the Atlantic province?

2. Material and methods

2.1. Study area

The study area includes eight sites in the outer dunes of the Atlantic province of Europe (Fig.1) according to MEUSEL et al. (1965) and ROISIN (1969). For the present study the four southern sites are lumped as the southern part, the four northern sites as the northern part of the Atlantic province (Table 1). Climatological data and soil characteristics of the outer dunes

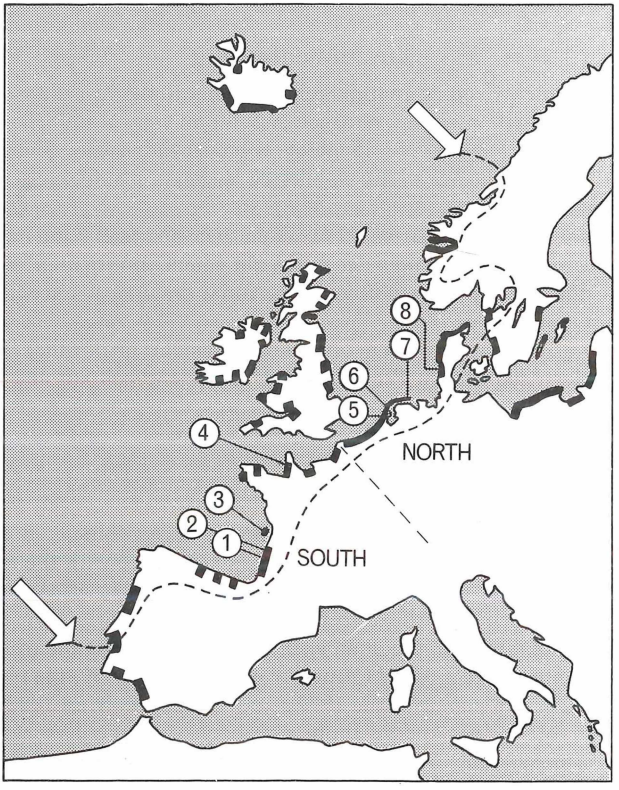

Fig.1: The Atlantic province of Europe and the lay-out of the study sites.

are summarized by BAKKER (1976) (Fig.2). It is obvious that the most southern site, south of the river Gironde, and the three most northern sites, north of Bergen in the Netherlands, can be assigned to the area poor in lime of the Atlantic province.

Table 1: Study sites in the Atlantic province of Europe (see Figure 1)

1	Vendays (F)	poor in lime
2	St. Trojan (F)	rich
3	Pte. Espagnol (F)	rich
4	Portbail (F)	rich
5	Castricum (NL)	rich
6	Bergen (NL)	poor
7	Schiermonnikoog (NL)	relatively rich
8	Vejerstrand (DK)	poor

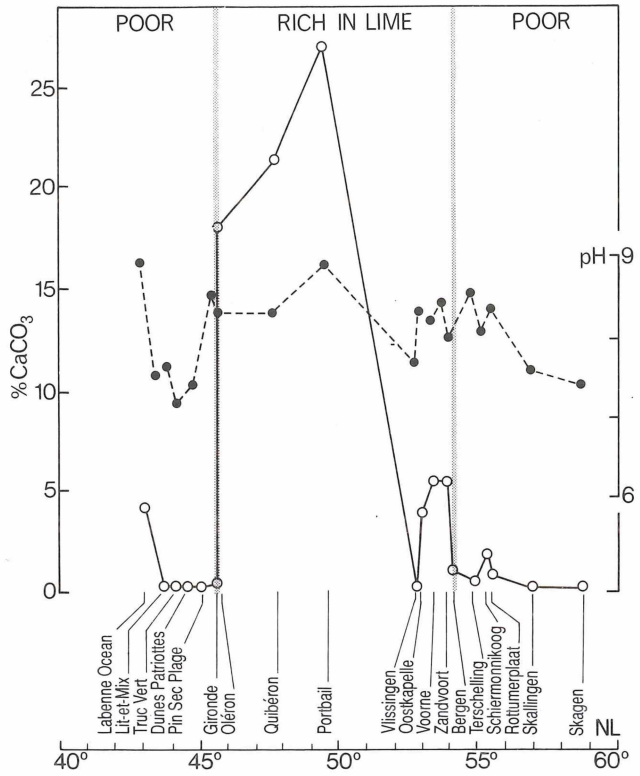

Fig.2: Percentage $CaCO_3$ and pH of the topsoil in outer dune sand from southern France towards northern Denmark (from BAKKER, 1976).

A detailed description of the driftline-, the *Elymus athericus*-, the initial -, and the terminal *Ammophila arenaria* dune plant communities is given by BAKKER (1976). A syntaxonomical overview of the vegetation in the xerosere, including white-, yellow- and grey dunes (SALISBURY, 1952) can be derived from GÉHU (1969) and WESTHOFF & DEN HELD (1969). The syntaxonomy of the vegetation of the xerosere is complicated. Therefore, the comparison of different stages in dune building according the the landscape ecological approach proposed by DOING (1988) is preferable, since it includes geomorphological features. The outer dunes of

the xerosere feature the *Ammophila*-, the *Koeleria*-, the *Rubus*-, the *Hippophae*- and the *Corynephorus*-landscapes, respectively.

The *Ammophila* (A) landscape features the beach and blowing sand dunes with the characteristic species *Ammophila arenaria, Elymus farctus* and *Calystegia soldanella*. It occurs all over Europe. The *Koeleria* (K) landscape features dry, open, moderate Ca-rich, humus-poor dunes with intermediate sand blowing and the characteristic species *Koeleria macrantha, Sedum acre, Helichrysum stoechas* and *Tortula ruraliformis*. It occurs all over Europe. The *Rubus* (R) landscape features young, Ca-rich, relatively humus-rich dunes with little sand blowing and the characteristic species *Rubus caesius, Sambucus nigra* and *Ononis repens*. It is found in Belgium and in the Netherlands. The *Hippophae* (H) landscape features young, relatively Ca-poor, humus-poor dunes without sand blowing and with the characteristic species *Hippophae rhamnoides, Calamagrostis epigejos* and *Cynoglossum officinale*. It is found in northern France, in Belgium and in the Netherlands. The *Corynephorus* (C) landscape features dry, open, Ca-poor dunes with littele sand blowing and the characteristic species *Corynephorus canescens*, *Carex arenaria,* mosses and lichens. It occurs in the Ca-poor part of the Atlantic province (DOING, 1988)..

The lay-out of the different types of landscapes in most of the study sites is shown in Fig.3. It features the general sequence, from the beach towards the inner dunes, of *Ammophila-, Koeleria- and Corynephorus* landscape.

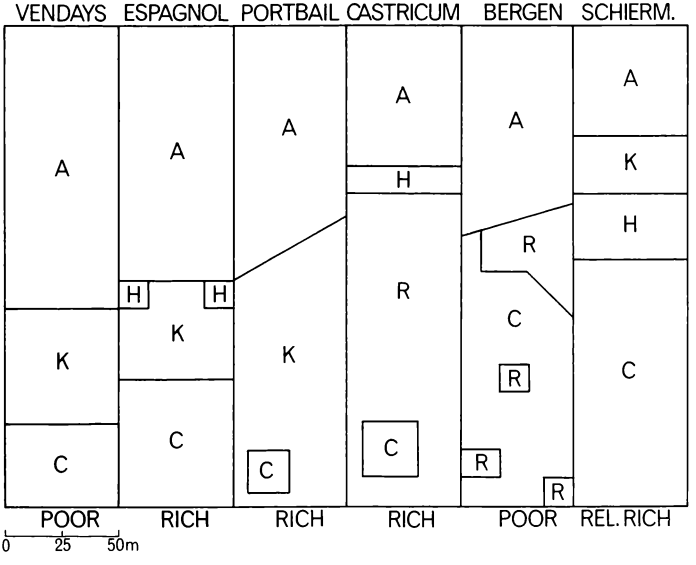

Fig.3: Maps of the landscapes according to DOING (1988) in several sites (see Table 1) along the Atlantic coast.

2.2. Seed bank characteristics

Five relevés (2x2)m² were made in each of the eight sites in a transect from the *Ammophila*- to the *Corynephorus* landscape. The relevés were made from the end of May 1980 in the southern part of the Atlantic province until mid June in the northern part of the Atlantic province.

Soil samples of 250 cc of the 5 cm topsoil, including litter, were collected in the same place and period as the relevés. The seed bank was measured as germinable seeds (THOMPSON & GRIME, 1979) kept for twelve months in a greenhouse providing day and night intervals at 20°C. The seed-containing soil was spread in a plastic tray filled with sterilized (to prevent germination of not sampled seeds) potting soil and watered daily. Emerged seedlings were removed after identification. Seedlings which could not easily be identified were grown separately. By

Table 2: Key for types of seed bank

1	–	Species absent from seed bank, but present in vegetation	*transient*
	–	Species present in seed bank	2
2	–	Species present in vegetation	*present*
	–	Speciens absent from vegetation	*persistent*

sampling in spring, it was assumed that the stratification demand of the species was met (BAKKER, 1989).

To characterize the type of seed bank in the present study, only data on presence/absence of species in the established vegetation and in the germinated seed bank are available. The seeds of species present in the seed bank, but absent in the established vegetation must be older than one year (if the seed samples were taken in spring) and are, therefore, referred to as persistent type of seed bank. The key for the assignement of types of seed bank is shown in Table 2.

Although all species found in the germinated seed bank are shown in the following tables, only species found in 3 or more sites out of the 40 sample sites (i.e. in >5%) are taken into account for the spectra of types of seed bank in different landscapes or parts of the Atlantic province.

The nomenclature of taxa follows the „Flora van Nederland" (VAN DER MEIJDEN et al., 1990), which is based on the „Flora Europaea" (TUTIN et al., 1964-1980), and „Les quatres flores de France" (FOURNIER, 1961).

3. Results

3.1. Types of seed bank

Species with a transient seed bank, i.e. only occuring in the established vegetation, are found in the *Ammophila* landscape (Table 3), but also further inland in the Koeleria- and the *Corynephorus* landscapes (Table 4). Other species are only found in the established vegetation in the majority of the sample points, but in some sample points both in the established vegetation and in the seed bank (Table 5). They do not occur in the *Ammophila* landscape and are mainly perennials, only the last four species listed in Table 5 are annual species. Another group of species is locally transient, locally persistent, i.e. only occurring in the seed bank (Table 6). These species also occur only in the more inner types of landscape. It should be mentioned that over 50% of this group of species is annual. *Leontodon saxatilis, Taraxacum* spec. and *Senecio sylvaticus* are anemochourous species. Only a few species have an exclusively persistent type of seed bank (Table 7). *Epilobium tetragonum* and *Erigeron canadensis* are anemochorous species. It is remarkable that all species of this group are not characteristic dune species, but seem to be ruderal species.

All species lumped from all 40 sites show that 71% can be assigned to the transient type of seed bank, 16% to the persistent type of seed bank and 13% can only be referred to as being present in the seed bank.

A decreasing proportion of species with a transient type of seed bank is revealed from the *Ammophila* landscape towards the inner dunes, whereas the proportion of species with a persistent type of seed bank increases (Fig.4).

3.2. Geographical variation in seed bank

Most of the species which are only found in the sites in the northern part of the Atlantic province can be assigned to the transient type of seed bank (Table 8). This is also the case for the majority of the species which are exclusively found in sites in the southern part of the Atlantic province, but some species have a persistent type of seed bank in all sites or in part of the sampled sites (Table 9).

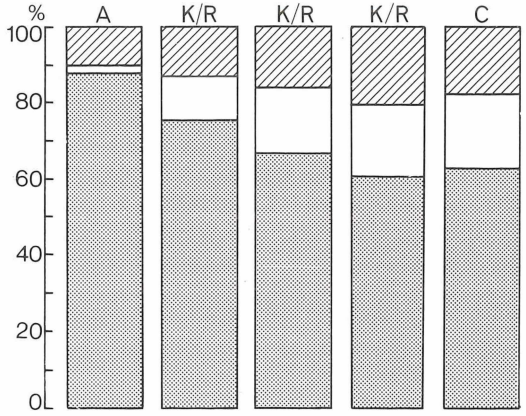

Fig.4: Seed bank type spectra in different landscapes in the xerosere of the dry dunes (dotted: transient; hatched: persistent: white: transient/persistent).

Table 3: Species with a transient seed bank in the *Ammophila*-landscape

	Vegetation	Vegetation/ Seed bank	Seed bank	n
Ammophilia arenaria	100	0	0%	23
Elymus farctus	100	0	0%	5
Calystegia soldanella	100	0	0%	8
Eryngium maritimum	100	0	0%	5
Eurphorbia paralias	100	0	0%	3
Sonchus arvensis var. maritimus	100	0	0%	4
Galium arenarium	100	0	0%	4
Leymus arenarius	100	0	0%	2
Medicago marina	100	0	0%	1

Most of the species occurring in the whole Atlantic province show no differences with respect to their type of seed bank in both the northern and southern part. This is not true for six species (Table 10). These species reveal a tendency to have a persistent type of seed bank in more sites in the southern than in the norther part of the Atlantic province.

All species lumped from all 40 sites show a higher proportion of species with a transient type of seed bank in the northern than in the southern part of the Atlantic province, and accordingly a smaller proportion of species with a persistent type of seed bank (Fig.5). This trend is found in all sites from the *Ammophila* landscape towards the inner dune landscapes.

4. Discussion

The measurement of the germinable seed bank in the present study was not very intensive (sampling at one depth, at one moment and no replication at each sample point). Nevertheless the subdivision into transient and persistent types of seed bank seems to be in agreement with findings in the literature for many species. This is only true for species in the *Koeleria*- and the *Corynephorus* landscapes, since no data on species in the *Ammophila* landscape are available from the literature.

The assignment of *Cardamine hirsuta, Poa trivialis, Stellaria media* and *Cerastium fontanum* to the persistent type of seed bank, and of *Salix repens* and *Vulpia uniglumis* to the transient type of seed bank, is in agreement with GRIME et al. (1988). *Poa pratensis, Plantago lanceolata*

Table 4: Species with a transient seed bank in the *Koeleria* and *Corynephorus* landscapes

	Vegetation	Vegetation/ Seed bank	Seed bank	n
Ononis repens	100	0	0%	6
Euphorbia portlandica	100	0	0%	4
Lotus corniculatus	100	0	0%	14
Corynephorus canescens	100	0	0%	14
Hypochaeris radicata	100	0	0%	4
Crepis vesicaria ssp. taraxacifolia	100	0	0%	3
Viola curtisii	100	0	0%	8
Viola canina	100	0	0%	3
Rubus caesius	100	0	0%	9
Polygala vulgaris	100	0	0%	3
Rosa pimpinellifolia	100	0	0%	2
Hieracium pilosella	100	0	0%	2
Rumex acetosella	100	0	0%	2
Linum catharticum	100	0	0%	2
Anthyllis vulneraria	100	0	0%	2
Empetrum nigrum	100	0	0%	2
Cynoglossum offinale	100	0	0%	2
Hippophae rhamnoides	100	0	0%	2
Holcus lanatus	100	0	0%	2
Salix repens	100	0	0%	2
Cistus salviaefolius	100	0	0%	1
Thalictrum minus ssp. dunense	100	0	0%	1
Dactylis glomerata	100	0	0%	1
Antennaria dioica	100	0	0%	1
Anthoxanthemum odoratum	100	0	0%	1
Calamagrostis epigejos	100	0	0%	1
Crepis bulbosa	100	0	0%	1
Vulpia uniglumis	100	0	0%	12
Galium parisiense	100	0	0%	3
Vicia sativa ssp. nigra	100	0	0%	3
Vicia lathyroides	100	0	0%	2
Trifolium arvense	100	0	0%	2
Trifolium dubium	100	0	0%	2
Erodium cicutarum ssp. dunense	100	0	0%	1
Alyssum alyssoides	100	0	0%	1
Silene conica	100	0	0%	1
Helianthemum guttatum	100	0	0%	1
Filago minima	100	0	0%	1
Treesdalia nudicaulis	100	0	0%	1
Geranium molle	100	0	0%	1

and *Rumex acetosella* are reckoned among the transient type of seed bank in the present study, which is contradictory to the classification of GRIME et al. (1988). The assignment of *Koeleria macrantha* and *Bromus hordeaceus* to the transient type of seed bank, and of *Festuca rubra, Senecio jacobaea* and the annuals *Veronica arvensis, Arenaria serpyllifolia* and *Saxifraga tridac-*

Table 5: Species with a transient/present seed bank

	Vegetation	Vegetation/ Seed bank	Seed bank	n
Sedum acre	90	10	0%	10
Poa pratensis	90	10	0%	19
Plantago lanceolata	88	12	0%	8
Koeleria macrantha	88	12	0%	17
Hieracium umbellatum	86	14	0%	7
Galium verum	67	33	0%	9
Galium mollugo	60	40	0%	5
Thymus pulegioides	50	50	0%	4
Senecio jacobaea ssp. dunensis	50	50	0%	4
Artemisia campestris ssp. maritima	40	60	0%	5
Myosotis ramosissima	87	13	0%	8
Bupleurum aristatum	67	33	0%	3
Bromus hordeaceus	50	50	0%	4
Phleum arenarium	47	53	0%	19

tylites to the persistent type of seed bank, respectively, are in most sample points in agreement with the classification of GRIME at all. (1988).

ROZIJN (1984) studied the longevity of seeds of seven winter annuals. She classified them as having a persistent seed bank, since 15 months after burial to 1 cm 8% of the seeds of *Myosotis ramosissima*, 19% of *Stellaria media*, 24% of *Aira praecox*, 35% of *Senecio vulgaris*, 43% of

Table 6: Species with transient/persistent seed bank

	Vegetation	Vegetation/ Seed bank	Seed bank	n
Jasione montana	33	33	33%	3
Herniaria maritima	80	0	20%	5
Festuca rubra	88	0	12%	16
Carex arenaria	71	21	8%	14
Helichrysum stoechas	42	50	8%	12
Veronica officinalis	0	50	50%	2
Leontodon saxatilis	37	25	38%	8
Taraxacum spec.	68	16	16%	6
Aira praecox	0	33	67%	6
Veronica arvensis	8	42	50%	12
Desmazeria rigida	16	38	46%	13
Mibora minima	10	50	40%	10
Saxifraga tridactylites	33	33	33%	3
Arenaria serpyllifolia	36	45	19%	11
Erophila verna	78	11	11%	9
Cerastium semidecandrum	36	54	10%	26
Senecio sylvaticus	22	44	34%	9

Table 7: Species with persistent seed bank

	Vegetation	Vegetation/ Seed bank	Seed bank	n
Epilobium tetragonum	0	0	100%	3
Erigeron canadensis	0	0	100%	3
Stellaria media	0	0	100%	8
Cerastium fontanum	0	0	100%	16
Cardamine hirsuta	0	0	100%	4
Poa trivialis	0	0	100%	2

Table 8: Species only occuring in the northern part of the Atlantic province

	Vegetation	Vegetation/ Seed bank	Seed bank	n
Rubus caesius	100	0	0%	9
Hierracium umbellatum	86	14	0%	3
Polygala vulgaris	100	0	0%	3
Senecio jacobaea ssp. dunensis	50	50	0%	4
Anthyllis vulneraria	100	0	0%	2
Empetrum nigrum	100	0	0%	2
Leymus arenarius	100	0	0%	2
Hippophae rhamnoides	100	0	0%	2
Holcus lanatus	100	0	0%	2
Salix repens	100	0	0%	2
Veronica officinalis	0	50	50%	2
Thalictrum minus ssp. dunense	100	0	0%	1

Cerastium semidecandrum, 62% of *Veronica arvensis* and 75% of *Erophila verna* were viable. The results of this experiment show that part of the seeds germinate within one year, another part after a longer period. This might explain the assignment to both the transient and persistent types of seed bank for many species in the present study.

The assignment to the transient type of seed bank of the species in the *Ammophila* landscape might be explained by the heavy blowing of the sand and hence burial of the plants. They seem to cope with this constraint by the perennial life-form and not by a persistent seed bank. Other explanations might be the deep burial of the seeds and the removal of seeds by the wind and little herbivores. Many species in the *Koeleria* and the *Corynephorus* landscape might store at least part of their seeds in a persistent seed bank. This seems functional from the point of view of irregular blowing of sand and hence burial of the seeds. MACK (1976) and WATKINSON (1978), however, think that the absence of a persistent seed bank of the annual species *Cerastium atrovirens* and *Vulpia uniglumis* might be related to the fact that the species occupies a habitat which is largely predictable. Probably similar life forms have different strategies to cope with constraints in their habitat (ROZIJN, 1984).

Which constraint could be responsible for the finding of the tendency of more sample points in the northern part of the Atlantic province to contain species with a transient type of seed bank than in the southern part is not clear. This interesting phytogeographical phenomenon needs more study by more intensive sampling of the germinable seed bank.

Table 9: Species only occuring in the southern part of the Atlantic province

	Vegetation	Vegetation/ Aeed bank	Seed bank	n
Calystegia soldanella	100	0	0%	8
Euphorbia paralias	100	0	0%	3
Galium arenarium	100	0	0%	4
Helichrysum stoechas	42	50	8%	12
Artemisia campestris ssp. maritima	40	60	0%	5
Crepis vesicaria ssp. taraxacifolia	67	0	33%	3
Euphorbia portlandica	100	0	0%	4
Vulpia uniglumis	100	0	0%	12
Desmazeria rigida	16	38	46%	13
Mibora minima	10	50	40%	10
Galium parisiense	100	0	0%	3
Bupleurum aristatum	67	33	0%	3
Cardamine hirsuta	0	0	100%	4
Medicago marina	100	0	0%	1
Hieracium pilosella	100	0	0%	2
Crepis bulbosa	100	0	0%	1
Cistus salviaefolius	100	0	0%	1
Poa trivialis	0	0	100%	2
Silene conica	100	0	0%	1
Helianthemum guttatum	100	0	0%	1
Filago minima	100	0	0%	1
Teesdalia nudicaulis	100	0	0%	1
Geranium molle	100	0	0%	1
Linum catharticum	100	0	0%	2

Table 10: Species with different types of seed bank in the northern and southern part of the Atlantic province

	Vegetation	Vegetation/ Seed bank	Seed bank	n
North Atlantic				
Festuca rubra	100	0	0%	12
Galium verum	67	33	0%	9
Phleum arenarium	87	13	0%	8
Cerastium semidecandrum	50	43	7%	14
Aira praecox	0	67	33%	3
Arenaria serpyllifolia	67	33	0%	3
South Atlantic				
Festuca rubra	50	0	50%	4
Galium verum	100	0	0%	2
Phleum arenarium	18	82	0%	11
Cerastium semidecandrum	21	64	15%	14
Aira praecox	0	0	100%	3
Arenaria serpyllifolia	25	50	25%	4

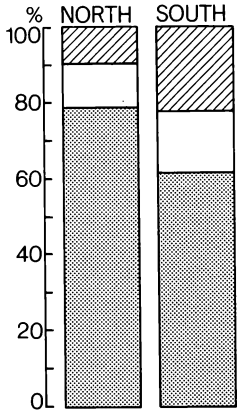

Fig.5: Seed bank type spectra in the northern and southern part of the Atlantic province of Europe (legend see Fig. 4).

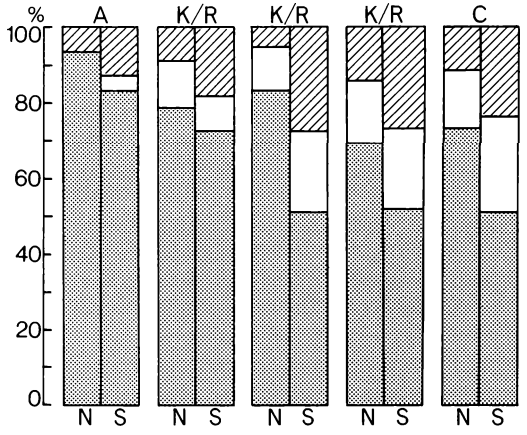

Fig.6: Seed bank type spectra in different landscapes in the xerosere in the northern and southern part of the Atlantic province of Europe (legend see Fig. 4).

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