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A Study of the Dynamics of the Seed Banks in a Complex Dune System, with the Aim of Restoration

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ABSTRACT

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To assess the possibility of restoring the original plant community of grey dune from a pine plantation, a synchronic study of the seed banks of three habitats, the grey dune, the pine plantation, and a clearing, was conducted at Quiberon (France). Five stations were selected: a Grey dune, Pine plantation 1, Pine plantation 2, Clearing 1, and Clearing 2. In contrast to the pine plantations, clearing 1, subject to heavy human disturbance, had a great similarity between its seed banks and its established vegetation. The larger clearing (C2) tend to resemble the grey dune, whereas the other was dominated by ruderal species.

The analysis of the seed banks demonstrated differences between the clearings and the pine plantations from which they were derived. The potential vegetation of the clearings was closer to that of the grey dune and had a larger number of species with a short life cycle than the pine plantations.

The seed banks of the pine plantations were not similar to that of the grey dune, but also differed from that of closed vegetation. This study suggested that it may not be possible to obtain a short term restoration of a grey dune after just clear felling only with the help of seed banks. On the other hand, seed dissemination could facilitate a restoration in a larger time scale as for clearings.

ADDITIONAL INDEX WORDS: *Dune, pine plantation, clearing, established vegetation, potential vegetation, synchronic dynamics.*

INTRODUCTION

In the 18th century, the dunes along the Atlantic coast of France, exploited for agriculture or sand reserve (GUILCHER and HALLEGOUET, 1991), were almost bare of vegetation. Submitted to important winds, they had become very mobile. Various works were undertaken to fix them, especially in the dunes of Gascony, first by private initiatives and then by the State (JACAMON, 1975). Afforestation that was started by the Danes and Germans, reached a peak in France in the 19th century (MCDONALD, 1954). Growing forests then became not only a means of protection but also the rule for managing dunes.

The high conservation value of grey dunes within dune complexes has been demonstrated by many publications (WANDERS, 1987; DE RAEVE, 1989; DUPONT, 1993). Within this type of biotope they are the only priority habitat that has been retained by Natura 2000 network "Fixed coastal dunes with herbaceous vegetation (grey dunes) 2130" (ROMAO, 1996). They are now well protected but their small area makes them vulnerable. The enlargement or recreation of

grey dunes from pine plantations would be beneficial for their conservation. From an ecological viewpoint, the afforestation of dunes has led to species-poor plant communities consisting mostly of common plant species (OVINGTON, 1950; RANWELL, 1972; HILL and WALLACE, 1989). Pine plantations are listed in the Natura 2000 habitat directive under the term of "Wooded dunes with *Pinus pinaster* 2270" and are not a conservation priority. The history of afforestation and the great human effort to maintain them has resulted in land managers becoming very attached to French forested dunes over the centuries. With the growing awareness of the biodiversity and of the value of dune habitats, the species-poor communities of pine plantations were regarded of low conservation interest. In the United Kingdom, large portions of pine plantation have already been removed from the Sefton Coast site (STURGESS, 1991; STURGESS and ATKINSON, 1993). Before envisaging clear-felling of French pine plantations, detailed studies need to be made of the capacities for grey dunes to be re-established from wooded dunes.

Pine plantations have led to major functional changes (OVINGTON, 1950; OVINGTON, 1951; RANWELL, 1972; VANDEN BYGAART and PROTZ, 1995). The restoration of "grey dune" habitat requires that its functional characteristics are also restored. ARONSON *et al.* (1995) produced a list of the vital attributes describing how ecosystems function. Among

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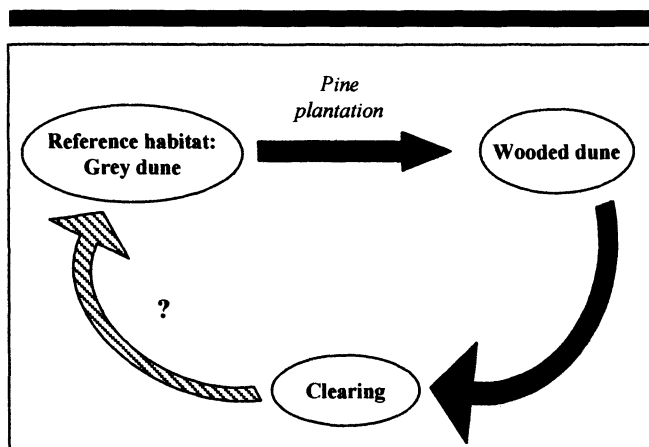


Figure 1. Dynamic position of the three habitats of a single dune ecosystem.

these, the stock of viable seeds in the soil is an expression of the potential vegetation. THOMPSON and GRIME (1979), and later TOUZARD (1999) used seed banks to analyse the mechanisms acting on biodiversity. Several authors have been interested in this potential vegetation for restoring steppes (NEFFATI *et al.*, 1996), dry grassland (BAKKER *et al.*, 1996), moist grasslands (BAKKER *et al.*, 1995), and flooded meadows (MCDONALD, BAKKER, and VEGELIN, 1996).

This study, conducted on the State-owned dune at Quiberon (France), is a chronosequence approach. A single ecosystem was studied at different stages in its succession: the grey dune, the wooded dune and clearings (Figure 1). In the absence of successional data on the species replacement that would take place after clear felling a wooded dune, the clearing habitat provides some idea of what these changes may be. The aim of the present study was to compare three habitats in a chronosequence on the basis of their potential and established vegetation. This should enable us to evaluate the possibilities of restoring a grey dune from the seed banks of a planted habitat.

METHODS

Study Area

The dune at Quiberon forms part of a large dune complex stretching from Gâvres to Quiberon (GUILCHER and HALLEGOUET, 1991). Situated in southern Brittany (France 47°30'N, Long 3°10'W), it forms a tombolo connecting the island of Quiberon to the mainland. Part of the dune complex was afforested at the end of the 1850s, but a large section of grey dune has remained intact. Few clearings are speeded in

the forest. Some of the soil properties in the three study habitats are shown in Table 1 (LEMAUVIEL, 2000). The soils of the three habitats have the same physio-chemical matrix and their calcium carbonate contents are similar. On the other hand, the nitrogen and carbon contents differ greatly between the different habitats. The accumulation of litter has led to an increase in the C/N ratio in the pine plantations (OVINGTON, 1950). In contrast, the incorporation of organic matter into the soil and its more intensive mineralisation in the clearings has led to a decrease in this ratio (KLIMO and GRUNDA, 1989).

Five stations were defined in the south of the dune complex (Figure 2). The reference habitat is the grey dune (station D). This station is located in the largest area in which the plant community is a typical grey dune of southern Brittany (LEMAUVIEL, 2000). Two clearings C1 and C2 were chosen within the 2 pine plantation stations P1 and P2. Clearing 1 (40 m × 20 m) is close to the access road and is subject to frequent visitor disturbance. There is no longer any trace of former forest. Clearing 2 (100 m × 40 m), is situated in the middle of the forest, and is rarely visited by tourists. Remaining tree stumps are an indication that it was formerly wooded. Unfortunately no information is available on the dates when the clearings were produced.

Analysis of the Established Vegetation

The established vegetation at each of the stations was surveyed in March 1998. The end of the winter corresponds to the period of higher species richness for the southern Brittany' grey dune (LEMAUVIEL, 2000). These surveys involved listing all the species occurring in three 1 m² quadrats. Nomenclature follows TUTIN *et al.* (1964–1980). Each species was given an abundance-dominance score (BRAUN-BLANQUET, 1965).

Analysis of the Seed Bank

A preliminary attempt to identify seeds from the soil under a binocular microscope proved to be unusable. The method of studying the seed banks by monitoring germination of seedlings from soil samples incubated in a greenhouse was therefore chosen. This method is widely used (THOMPSON and GRIME, 1979; GROSS, 1988; LOONEY and GIBSON, 1995; TOUZARD, 1999; COMBROUX *et al.*, 2001). Nevertheless, some seeds whose dormancy is difficult to break may not appear.

The seed banks contained in the soils of the 5 stations were analysed in November 1997. Five samples were collected at random from each station using cylinders 6 cm in diameter and 5 cm tall. Three strata were distinguished: 0 to –5 cm,

Table 1. Soil properties in three dune habitats, average ± standard error (n = 5). Different letters indicate differences (p < 0.05) between habitats.

	Grey Dune	Pine Plantation	Clearing
Calcium carbonate (%)	3.21 ± 0.06 a	3.07 ± 0.60 a	2.77 ± 0.16 a
Total carbon (%)	1.99 ± 0.34 b	2.15 ± 0.11 b	0.98 ± 0.18 a
Total nitrogen (%)	0.22 ± 0.04 b	0.13 ± 0.03 a	0.08 ± 0.00 a
C/N	8.87 ± 0.24 a	18.74 ± 4.62 b	12.39 ± 2.51 ab

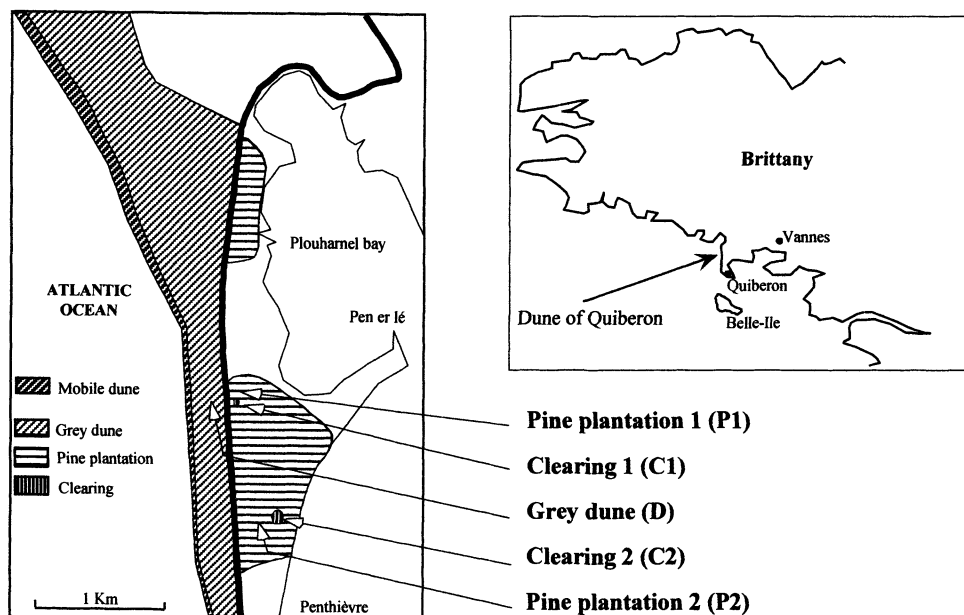


Figure 2. Location of the five experimental stations.

–5 to –10 cm and the litter that was only present in the pine plantation stations.

Trays (12 × 17 cm) were filled to a depth of 3 cm with sand sterilised at 105°C for 48 h. The soil samples were stored at 4°C for 48 h to break any dormancy. Then each sample was spread over the sand and placed in an unheated greenhouse. The trays were watered frequently to maintain constant moisture content.

Germination of seedlings was monitored 3 times a week during five months. Individual seedlings were identified and then removed from the trays.

Data Processing

JACCARD'S (1908) coefficient was used to compare the seed banks at the stations with their established vegetation and also the seed banks of pine plantation and clearings stations with the potential and established vegetation of the grey dune.

$$J = c/(a + b - c)$$

where:

a = Number of species in sample A

b = Number of species in sample B

c = Number of species found in both samples

Mosses and lichens, which do not produce seeds, were excluded from the calculation.

—The species richness of the established vegetation was estimated from the mean number of species per quadrat, and that of the seed banks from the mean number of species per sample.

The effect of the station factor was tested by several seed

bank descriptors. A preliminary analysis of the data using the Wilk-Shapiro test with a probability of 90% showed that some data did not have the normal distribution required for parametric tests, so Kruskal-Wallis tests were used (SOKAL and ROHLF, 1981).

RESULTS

Established Vegetation

The current floristic composition of the five stations is shown in Table 2. The grey dune, clearings, and pine plantations differed from one another in their bryophyte/lichen, herb, and shrub strata; only two species, *Rosa pimpinellifolia* and *Sanguisorba minor* occurred equally in all three habitats. The pine plantations had a low diversity. Pine plantation 1 was typified by the presence of *Ligustrum vulgare* and *Iris foetidissima*, whereas the pioneer forest species *Rubia perigrina*, *Lonicera periclymenum* and *Hedera helix* characterised pine plantation 2.

The grey dune had the largest number of species. Its bryophyte/lichen stratum was dominated by lichens of the genus *Cladonia*. *Rosa pimpinellifolia* and *Ephedra distachya* are the characteristic species of the “*Rosa spinosissima*-*Ephedretum distachyae*” phytosociological grouping (GEHU, 1994). The floristic assembly was very rich in winter annuals such as *Omphalodes littoralis*, *Cerastium diffusum*, *Mibora minima*, *Cochlearia danica*, *Erophila verna* and *Saxifraga tridactylites*.

Although they differed from one another, the vegetation of the clearings was dominated by winter annuals, most of which also occurred in the grey dune station. Other species such as *Myosotis ramosissima*, *Festuca rubra* ssp. *arenaria*, and *Asperula cynanchica* are also typical of grey dunes. The annuals *Aphanes arvensis* and *Sagina apetala* that were pres-

Table 2. Floristic composition of the five stations. Intervals correspond to the minimum and maximum abundance-dominance score noted in the three quadrats.

	Grey Dune	Pine Plantation 1	Pine Plantation 2	Clearing 1	Clearing 2
Phanerogams					
<i>Cochlearia danica</i>	0-1				
<i>Ephedra distachya</i>	0-3				
<i>Anagalis tenella</i>	0+				
<i>Euphorbia portlandica</i>	+--				
<i>Lamium amplexicaule</i>	0-1				
<i>Omphalodes littoralis</i>	1-1				
<i>Sedum acre</i>	0+				
<i>Viola kitaibeliana</i>	+ -1				
<i>Cerastium diffusum</i>	3-4			0-3	
<i>Mibora minima</i>	4-5			1-3	
<i>Erodium cicutarium</i>	+--			0-1	
<i>Erophila verna</i>	+ -1			+ -2	
<i>Saxifraga tridactylites</i>	0+			1-1	
<i>Arenaria serpyllifolia</i>	0+			0-2	0+
<i>Geranium molle</i>	0-1				0+
<i>Carex arenaria</i>	0-1				0+
<i>Veronica arvensis</i>	1-1				0+
<i>Ligustrum vulgare</i>		0-2			
<i>Iris foetidissima</i>		0+			
<i>Rubus caesius</i>		+--	+ -2		
<i>Rubia peregrina</i>			0-1		
<i>Lonicera periclymenum</i>			0+		
<i>Hedera helix</i>			0-1		
<i>Juncus bufonius</i>		0+	0+	0-2	
<i>Viola riviniana</i>		0-1	+ -1		0+
<i>Sanguisorba minor</i>	0-3	+--	1-2		4-4
<i>Rosa pimpinellifolia</i>	0-1	1-2	1-3		2-2
<i>Allium sphaerocephalon</i>				+ -1	
<i>Myosotis ramosissima</i>				0+	
<i>Aphanes arvensis</i>				0-1	
<i>Sagina apetala</i>				2-2	
<i>Thymus serpyllum</i>					0-1
<i>Festuca rubra ssp. arenaria</i>					0+
<i>Sonchus oleraceus</i>					0+
<i>Asperula cynanchica</i>					0+
Mean species richness	13.3	4.7	6.0	8.7	5.7
Cryptogams					
<i>Homalothecium lutescens</i>	2-4				
<i>Cladonia spp.</i>	4-5				3-4
<i>Tortula ruralis ssp. ruraliformis</i>	1-4			4-4	0-1
<i>Pseudoscleropodium purum</i>		2-4	4-5	1-2	+ -5
<i>Hypnum cupressiforme</i>					1-5
Mean species richness	3.0	1.0	1.0	2.0	3.3

ent in station C1 reflect the ruderal nature of this station which is close to the road.

Potential Vegetation

Seed Distribution in the Soil

The largest proportion of seeds occurred in the top five centimetres of soil in the clearings and grey dune (Figure 3). The seed banks in the pine plantations were divided between the three portions. The top five centimetres contained less than 50% of seeds, the litter and the soil at a depth of 5 to 10 cm containing almost equal proportions of the remaining seeds.

The species richness appeared to be highest in the 0-5 cm layer (Figure 4) in all stations. With a few exceptions, the species present in the 5-10 cm layer did not differ from those

occurring in the 0-5 cm layer. *Amaranthus sp.* and *Poa annua* only occurred in the litter of the pine plantations.

In the analyses of the seed bank data, all the layers were combined and were expressed in terms of unit area.

Species Composition of the Seed Banks

The species compositions of the seeds in all soil layers combined are shown in Table 3. The organisation of the species in the table takes into account their occurrence in 1, 2 or 3 habitats. *Arenaria serpyllifolia*, *Euphorbia portlandica*, *Festuca rubra ssp. arenaria*, *Carex arenaria*, *Medicago littoralis*, and *Saxifraga tridactylites* form part of the plant assembly of grey dunes but were present in all five stations. Only *Sedum acre* occurred exclusively in the grey dune. The species that

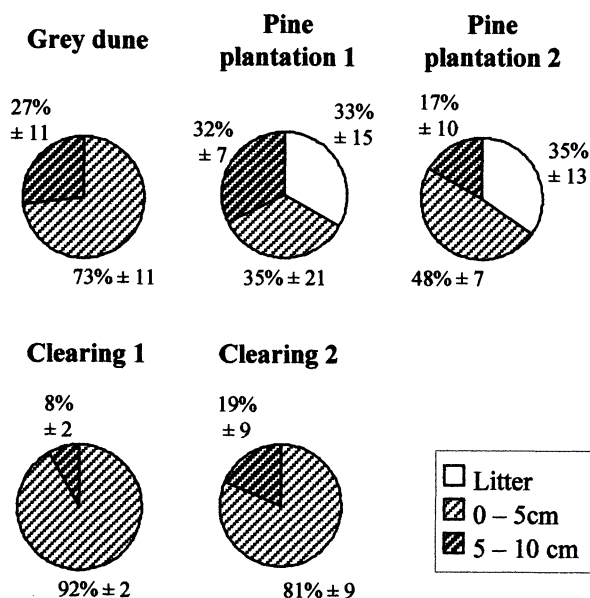


Figure 3. Seed distribution in the soil of the five stations. Values are means \pm standard error.

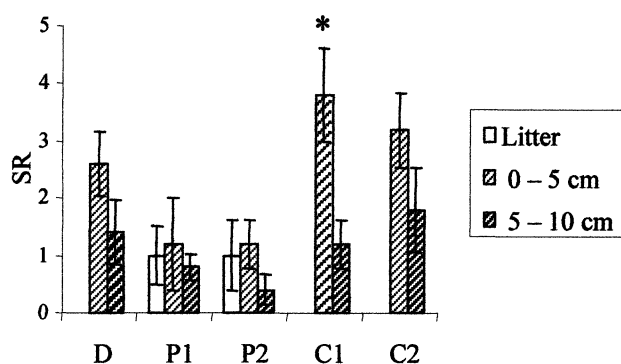


Figure 4. Species richness of the seed bank in each soil layer of the five stations. The bars show the standard error. * indicates a significant difference between the layers for each station.

were found in both the clearings and the grey dune were winter annuals characteristic of the plant community of grey dunes.

The seed banks of the clearings and pine plantations only had a few species in common: *Sanguisorba minor* typical of the grey dune, and *Juncus bufonius* a generalist.

Table 3. Mean species compositions (on a surface unit of 28.3 cm²) \pm standard error of the seeds in the soils of the five stations.

	Grey Dune	Pine Plantation 1	Pine Plantation 2	Clearing 1	Clearing 2
Grey Dune, Pine Plantation & Clearing					
<i>Arenaria serpyllifolia</i>	2.20 \pm 0.98	0.20 \pm 0.22		0.40 \pm 0.45	0.60 \pm 0.27
<i>Euphorbia portlandica</i>		0.80 \pm 0.42	1.00 \pm 0.50		0.20 \pm 0.22
<i>Festuca rubra ssp. arenaria</i>		0.20 \pm 0.22	0.20 \pm 0.22		
<i>Carex arenaria</i>	0.20 \pm 0.22	0.60 \pm 0.67		0.40 \pm 0.45	
<i>Medicago littoralis</i>		0.40 \pm 0.45	0.60 \pm 0.27		
<i>Saxifraga tridactylites</i>	2.40 \pm 0.90	1.80 \pm 2.12	0.20 \pm 0.22	1.40 \pm 1.34	0.60 \pm 0.27
Grey Dune					
<i>Sedum acre</i>	0.40 \pm 0.27				
Grey Dune & Pine Plantation					
<i>Viola kitaibeliana</i>			0.80 \pm 0.67		
Grey Dune & Clearing					
<i>Cerastium diffusum</i>				0.40 \pm 0.27	0.20 \pm 0.22
<i>Erophila verna</i>				0.40 \pm 0.27	
<i>Scleranthus annuus</i>					0.20 \pm 0.22
<i>Lamium amplexicaule</i>	0.40 \pm 0.45				0.60 \pm 0.67
<i>Veronica arvensis</i>	0.20 \pm 0.22			0.20 \pm 0.22	5.60 \pm 3.56
Pine Plantation					
<i>Poa annua</i>			0.40 \pm 0.45		
<i>Viola riviniana</i>		0.20 \pm 0.22			
<i>Holcus mollis</i>		0.40 \pm 0.45			
<i>Amarante sp.</i>			0.20 \pm 0.22		
Clearing & Pine Plantation					
<i>Sanguisorba minor</i>		0.40 \pm 0.45			0.40 \pm 0.27
<i>Juncus bufonius</i>		0.60 \pm 0.45		0.60 \pm 0.45	
Clearing					
<i>Allium sphaerocephalon</i>				0.20 \pm 0.22	
<i>Aphanes arvensis</i>				3.00 \pm 1.22	0.40 \pm 0.45
<i>Sagina apetala</i>				33.40 \pm 1.13	11.40 \pm 12.47
<i>Myosotis ramosissima</i>					0.80 \pm 0.67

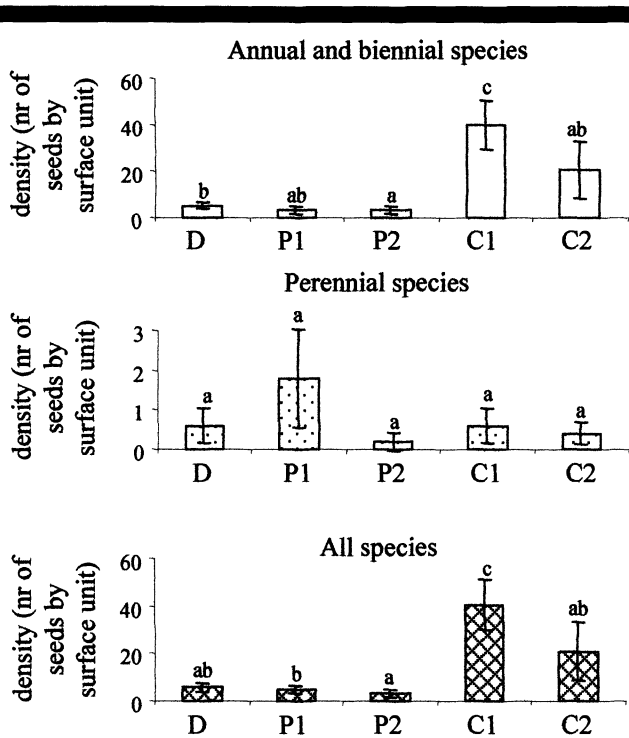


Figure 5. Seed density by functional group and total seed density in the five stations. The bars show the standard error. Different letters indicate significant differences among stations. (D: Grey dune, C1: Clearing 1, C2: Clearing 2, P1: Pine plantation 1, P2: Pine plantation 2).

The seed banks of the pine plantations included 4 woodland understorey or ruderal species.

Four species only occurred in clearings, two of them, *Aphanes arvensis* and *Sagina apetala*, were absent from pine plantations and the grey dune and characterised the "clearing" habitat.

Similarity between the Potential and Established Vegetation

The Jaccard coefficient was used to compare floristic composition of the seed banks and the existing vegetation. The seed banks of the grey dune and clearing 1 stations showed great similarities with the established vegetation 0.35 and 0.62 respectively. The value of this similarity index was low for clearing 2 (0.16) and the pine plantations only showed a slight similarity between the seed banks and the established vegetation, this was even zero for pine plantation 2 and 0.21 for pine plantation 1.

Characteristics of the Seed Banks

The variations in the density of seeds, in terms of their life history traits, are shown in Figure 5. According to the Kruskal-Wallis test, there was a station effect on the density of annual and biennial seeds ($\chi^2 = 13.38$, $p < 0.05$). The clearings had a higher density of species with a short life cycle than the other stations, this phenomenon being significant for clearing 1.

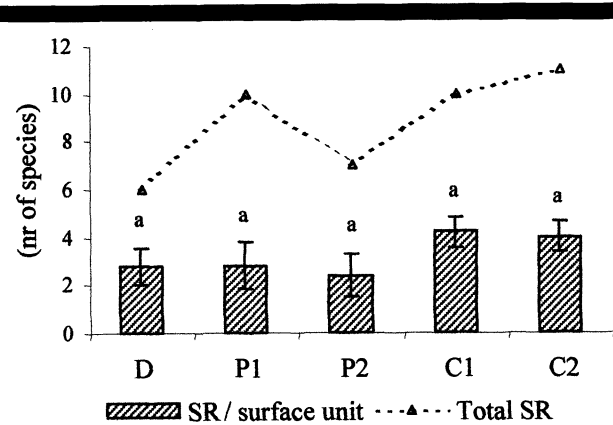


Figure 6. Mean and total species richness of the seed banks of the five stations. The bars show the standard error. Different letters indicate significant differences among stations. (D: Grey dune, C1: Clearing 1, C2: Clearing 2, P1: Pine plantation 1, P2: Pine plantation 2).

The densities of perennial seeds were very low in all stations. The pine plantations seemed to have the highest densities, but these differences were not significant ($\chi^2 = 2.55$, $p > 0.05$). There was a station effect for all seeds combined ($\chi^2 = 12.90$, $p < 0.05$). Pine plantation 2 had the lowest density and the clearing 1 the highest.

The mean and total species richnesses are shown in Figure 6. The large difference between the species richness per sample and the total species richness indicates that there was a great heterogeneity within the stations. The clearings, and especially clearing 1, seemed to have more species. However, the Kruskal-Wallis test conducted on the two series of samples did not reveal any significant station effect in terms of species richness ($\chi^2 = 4.69$, $p > 0.05$).

Similarity between the Seed Bank in Pine Plantations and Clearings and the Vegetation of the Grey Dune

The seed banks of the pine plantation and clearing habitats were compared with the potential and established vegetation of the grey dune by means of Jaccard coefficients. The similarity between the seed banks of these stations and that of the grey dune was greater than between the seed banks and the established vegetation of the grey dune. Clearing 1 and clearing 2 seed banks showed great similarity with grey dune seed bank, respectively 0.261 and 0.304, and also with grey dune established vegetation (0.25 the both). At the opposite, the pine plantations 1 and 2 showed low similarity with the grey dune vegetation, for seed bank (0.208 and 0.13) as well as for established vegetation (0.083 and 0.08).

DISCUSSION

Studies conducted in different habitats (THOMPSON and GRIME, 1979), and more specific studies on marshes (TOUZARD, 1999) and coastal vegetation (LOONEY and GIBSON, 1995) have demonstrated that there is little similarity between the established vegetation and seed banks. Clearing 2 and the pine plantations confirmed these studies by having only a slight or even no similarity between their established

and potential vegetation. In contrast, the grey dune, and especially clearing 1 had seed banks similar to the existing vegetation. This great similarity has been found in other studies on ploughed grassland (LEVASSOR, ORTEGA, and PECO, 1990), desert grassland (HENDERSON, PETERSEN, and REDAK, 1988), and in a freshwater tidal marsh (LECK and GRAVELINE, 1979). According to PECO, ORTEGA, and LEVASSOR (1995), the similarity between seed banks and established vegetation depends on the ratio of annual to perennial species, which was confirmed by our observations. Moreover, many species which develop in grey dune and clearings, *Arenaria serpyllifolia*, *Saxifraga tridactylites*, *Aphanes arvensis*, *Myosotis ramosissima* and *Veronica arvensis* have been found in seed banks. They all belong to the type III defined by THOMPSON and GRIME (1979) (GRIME, HODGSON, and HUNT, 1988) which means they are present both in persistent seed banks and in the transient ones. The seedling emergence technique was the best appropriated for this kind of milieu, but it is quite incomplete and may give special emphasis to the transient seed bank (PIERCE and COWLING, 1991) by favouring species with low dormancy mechanisms.

The low similarities of perennial communities are explained by the low contribution of the dominant perennials to the formation of the stock of seeds in the soil (PECO, ORTEGA, and LEVASSOR, 1995). In conifer forests, the seeds of the dominant species are generally absent or scarce in the soils (ARCHIBOLD, 1989). The case of *Rosa pimpinellifolia* clearly illustrates this mechanism, since it was present in nearly all the stations and was sometimes even dominant, but was never encountered in the seed banks. Its reproduction activities are low and some years completely absent, so its strategy to regenerate may involve vegetative processes and only a poor and short term transient seed bank. Clearing 2 was protected from human disturbance and the pine plantations were at an advanced successional stage and were not very exposed to perturbations. Among their plant assemblages they included species such as *Rubus fruticosus* and *Ligustrum vulgare* with a competitive strategy (sensu GRIME, 1979).

High similarities occur in disturbed environments where r-selected species dominate (LEVASSOR, ORTEGA, and PECO, 1990). Disturbances restrict the floral composition to the young stages of long-lived species (MOORE, 1980). The clearings and the grey dune shared a regime of intense disturbance resulting from wind and rabbit grazing. Clearing 1 differed by its heavy visitor pressure because of its proximity to the road. Its established and potential vegetation included ruderal species in the definition of GRIME (1979) such as *Aphanes arvensis* and *Sagina apetala*.

Although the clearings shared a high species richness, a higher density of seeds than the other stations, clearing 1 was significantly different by being much more extreme in these respects. The seed bank of this station was very unbalanced. Most of the species were only present in small quantities, whereas the seeds of *Sagina apetala* which possesses a persistent seed bank (GRIME, HODGSON, and HUNT, 1988) were very abundant. The size of the clearings and their distance from the grey dune played an important role in their floristic composition (LEMAUVIEL and ROZÉ, 2000). Clearing 2 had a large area, and was almost free from the microclimate effects

produced by the proximity of trees that has been described by JACAMON (1975) under the term "forest ambiance". Its mainly xerophilic edaphic conditions were similar to those of the grey dune. The vegetation resembled that of the grey dune by its carpet of bryophytes and lichens. Clearing 1 was small, and was shaded by pines for much of the day. Being close to the road it received a great influx of seeds.

The ratio of species with a short life cycle compared to perennials was much higher in the clearings than in the pine plantations. GRIME *et al.* (1981) demonstrated that storage under dry conditions favoured the germination of vernal annuals such as *Erophila verna*, *Myosotis ramosissima*, and *Saxifraga tridactylites*. These species were present in the seed banks of the clearings and of the grey dune. They experienced a dry summer season, or in any case much drier conditions in these open habitats than under the cover of the pine canopy. Their emergence and that of other vernal annuals was favoured in the grey dune and clearing habitats.

Studies conducted in wetlands have revealed a high concentration of seeds in the top few centimetres of soil (BONIS and LEPART, 1994). In this dune ecosystem, the seeds are distributed to a greater depth and their vertical distribution varies from one habitat to another. In agreement with the result of STURGESS and ATKINSON (1993), the more abundant seeds in the grey dune and clearings occurred mainly in the top five centimetres of soil, whereas the less abundant seeds in the pine plantations were distributed to at least a depth of 10 centimetres and were also contained in the litter. The floral composition did not vary with depth in the soil in any of the stations, but the top five centimetres had the greatest species richness. The pine plantations are quite young and many seeds have persisted in the soil while organic matter was accumulating on the top soil. For example, *Juncus bufonius* is well known as a species which possess a large amount of long term persistent seeds (GRIME, HODGSON, and HUNT, 1988; BAKKER and BERENDSE, 1999).

This study demonstrated that the pine plantation has not retained any traces of the former grey dune. The seed bank of the pine plantations only show a slight similarity to the potential and established vegetation of the grey dune. It could not therefore be used as a source of the original vegetation. Several studies on the restoration of grasslands report the same phenomenon (GRANSTRÖM, 1988; BAKKER *et al.*, 1995, 1996; McDONALD, BAKKER, and VEGELIN, 1996; MILBERG, 1995).

Clearings were studied as an alternative to monitoring changes after clear felling. Their seed banks were unlike those of the pine plantations from which they were derived and differed from one another but they are both enriched with species typical of grey dune plant communities. After clear felling, clearings have become open habitats dominated by species with a short life cycle and tending to resemble the short grassland of grey dunes.

This study stresses on the absence of any seed bank in the pine forest to restore grey dune vegetation communities. It suggested that it may not be possible to obtain a short term restoration after just clear felling only with the help of seed banks. On the other hand, seed bank represents one facet of the potential vegetation, and for many grey dune species, seeds

are disseminated by the wind or transported by animals. In a longer term, species could colonise the milieu and then permit a restoration, as for clearings. The absence of any dating for the clearings is however a limiting factor, preventing us from placing the events within a defined time scale.

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□ FRENCH SUMMARY □

Afin d'évaluer les possibilités de restauration d'une communauté végétale de dune grise après un abattage des pins, l'étude d'une chronoséquence de la banque de semences de trois habitats, la dune grise, la pinède et la clairière, a été menée sur le site de Quiberon (France). Cinq stations ont été sélectionnées: Dune grise, Pinède 1, Pinède 2, Clairière 1, Clairière 2. Contrairement aux pinèdes, la clairière 1, exposée à un régime important de perturbations anthropiques, présente une forte similarité entre sa banque de semences et la végétation actuelle. Les deux clairières sont différentes, la plus grande (C2) tend à ressembler à la dune grise, l'autre est rudéralisée.

La végétation potentielle des clairières se rapproche de la dune grise et accueille un plus grand nombre d'espèces à cycle de vie court que les pinèdes.

La banque de semences des pinèdes ne correspond pas à celle d'une dune grise mais ne s'assimile pas non plus à une végétation fermée. L'étude montre qu'à court terme, une restauration de dune grise après un abattage des pins ne pourra se faire seulement sur la base de la banque de semences. Les clairières tendent à se rapprocher de la dune grise et rendent compte de la possibilité d'une restauration à long terme par le biais la dissémination des semences.