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Monitoring Bryophytes and lichens dynamics in sand dunes: example on the French Atlantic coast

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Abstract

Bryophytes and lichens communities growing on nine non-forested coastal dunes along the Atlantic seaboard of France were studied from vegetation surveys during three years. Coastal dune systems provide opportunities for the study of plant successions and colonisation processes. The distribution of species and the relationships between bryophytes and lichens *versus* pedologic factors has been investigated on 1x1m permanent plots and were analysed by multivariate analyses. This study has shown that the different species are distributed in five groups in the different dune habitats. These groups are composed with several Mediterraneo-Atlantic species which distinguished them from other communities described in bryophytes and lichens successions in Europe. The significative relationships between the five groups and pedologic factors such as pH-water, percentage of total calcium and total nitrogen permit to evaluate the chemical variations of the soil along the dune-transect. The knowledge of relationships between the responses of the species and the abiotic variations of the soil determine functional groups. The monitoring of these functionnal groups is a good tool to understand evolutionary processes of dune-ecosystems and their management.

Keywords: Vegetation survey; Communities; Succession; Functional groups; Management.

Introduction

The management of the Atlantic littoral dunes is supported by the identification and monitoring of indicator species that make it possible to evaluate the modifications of the ecosystem (Favennec *et al.,* 1996; Favennec, 1997; 1999) The 'biomonitoring' is a follow-up in time of the state of the vegetation and utilises the response of species or associations of plants in order to detect or to predict the changes of the environment and to follow its evolution. The idea of biomonitoring appeared at the end of the 19th century hen Nylander (1866) used the abundance of lichens to measure the effects of air pollution. The various aspects of biomonitoring were summarized by Arndt *et al.* (1987) and Arndt (2000) classifying indicators as 'reactive' (sensitivity) and 'accumulative' (potential of accumulation) bioindicators.

The 'biointegrator' concept (sensu Garrec and van Haluwyn, 2002) is based on the study of populations or communities. Changes in specific composition, the appearance or disappearance of species and changes in density inform about the state of the ecosystem. This concept was previously developed by Blandin (1986) to designate plants which 'by their qualitative and/or quantitative characteristics testify to the state of an ecological system and which by variations of these characteristics, make it possible to detect possible modifications of this system'. The cartography of lichenous diversity is used at the European level as indicator of environmental quality (Asta *et al.*, 2003).

The vascular plant vegetation of French dunes has been studied intensively (Duffaud, 1996; Géhu, 1993, 1977; Despeyroux, 1984; Lahondère, 1980). Some studies on bryophytes (Pierrot, 1980, 1974; Bonnot, 1971; Fustec-Mathon and Mathon, 1960; Turmel, 1950; Duchauffour, 1948; Camus and Charrier, 1911) and lichens (Botineau and Houmeau, 1980; des Abbayes, 1951; Piquenard, 1904) have described distribution patterns on different parts of dunes. However, no recent study specifically studying the ecology of mosses and lichens developing in the littoral dunes in France is available.

During the year 2001, an observatory of the mosses and lichens on nine non-forested dunes of the Atlantic coast of France was set up – in collaboration with personnel from the French National Forests Commission (ONF) – in order to identify the distribution patterns of the mosses and lichens in relation to the dynamics of the dunes (environmental factors), and to relate the edaphic parameters to these patterns.

Materials and methods

Study area

The study area consists of nine sites of littoral dunes. The sites were selected on the basis of the patrimonial interest of the vegetation. Each site has already been the subject of several floristic, geomorphological, landscape studies, and inventories (Natural Zone of Faunistic Floristic and Ecological Interest, Important Birds Area).
The sites were distributed from Brittany to the south of Les Landes (Fig. 1): in Morbihan (administrative department 56): the domanial dune of Quiberon, Plouharnel; in the Loire-Atlantique (44): pointe de Pen Bron (la Turballe); in the Vendée (85): the pointe d'Arçay (la Faute/mer); in Charente Maritime (17): dunes de St Trojan on the Oléron island and the Pointe Espagnole (la Tremblade); in Gironde (33): the dune of le Flamand (Vendays-Montalivet) and the dunes of the Cap Ferret; in Les Landes (40): domanial dunes of Mimizan and Tarnos.

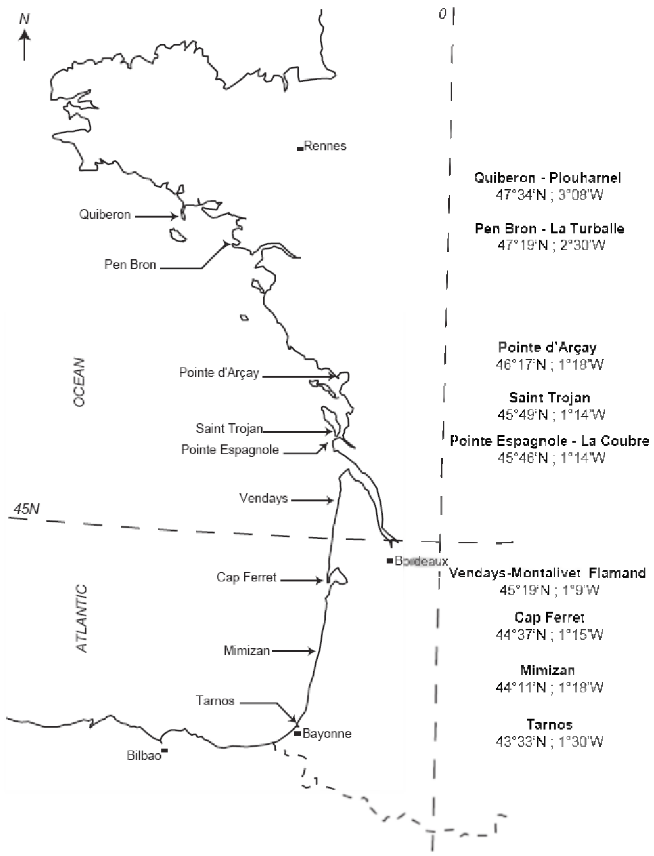


Fig. 1. Study area: location of the observatory composed of nine non-forested dunes on the French Atlantic coast.

Vegetation survey and sampling data

Synchronic study

In Autumn 2001, the mosses and lichens were inventoried on the entire non forested dune (from the beach to the *Pinus* plantations). The sampling design takes account of the geographical characteristics of the zone of study and the different habitats of the dunes. Two or three transects were selected per site, each transect comprising three permanent plots per habitat (semi-fixed dune SFD, fixed dune FD, rear fixed dune RFD). One hundred and twenty four (124) plots were taken using a removable quadrat (1x1m) with square mesh of 10cm. This method makes it possible to provide quantitative information on the relative frequency of species (Greig-Smith, 1964; Gordon, 1969; Poissonnet, 1969; Clément, 1987). The percentage cover of species was measured on each quadrat; 10 classes of values were recorded (1: presence; 2: 1-10%; 3: 11-20%; 4: 21-30%; 5: 31-40%; 6: 41-50%; 7: 51-60%; 8: 61-70%: 9: 71-80%: 10: 81%) or more.

Diachronic study

A vegetation survey was carried out on 77 permanent plots (1x1m) in order to follow the modifications within the mosses and lichens communities over time. The analysis of the average (± standard deviation) of the relative frequency of the species makes it possible to highlight dynamic fixation processes. The readings were taken every year in autumn during 3 years. Percentage cover was measured in three habitats of the dune: semi-fixed dune (n=15), fixed dune (n=32), rear fixed dune (n=30).

The life-strategies

The species are classified according to During (1979, 1992). Important traits of species which are observed in the system of 'life-strategy' are the vegetative form, reproduction, life-span, and effects of the environment (constant or fluctuating) on these traits. In order to obtain a result at community level, the system was modified by supposing *a priori* that the life-strategy of each species identified in the community tends to be standardized at its community level (highlighting of common traits), even if each species taken separately has its own life-strategy.

Environmental factors relating to the distribution

Each plot (n=124, 1x1m) was characterized by five environmental parameters related to its distribution on the littoral dune:
(1) The Atlantic coast (Z-L) divided in three parts: the south of Brittany (1), the Middle West (2), and Aquitaine (3).
(2) The position of the plot in relation to the habitats of the dune (Z-T): coefficient 1 for the semi-fixed dune (DT), 2 for the fixed dune (DF), 3 for the rear fixed dune (ADF).
(3) Species Richness (NbSp) corresponds to the total number of species of mosses and lichens listed on the quadrat.
(4) The percentage of bare sand ('sable nu') is the relative frequency measured on the square. (5) The percentage of cover of the vascular vegetation (Phan) is also taken from the relative frequency measured on the quadrat.

Soil analyses

As bryophytes and lichens have no roots, they are in direct contact with the superficial soil layer (Ketner-Oostra and Sykora, 2000). Soil analyses were carried out on 142 relevés. The sand samples were collected in autumn 2001 from the surface soil layer (0 to 5 cm depth) on microstations of 10x10cm. The vascular plant vegetation was recorded (presence/absence) for each sample. A minimum of 15 samples per community is used for the analyses. The cover of bryophytes and lichens was recorded at each station. Analyses were conducted on samples that were dried in an oven at 65°C for 24h and then sieved through a 2mm sieve.

- The pH-H_20 was measured on suspension of 10g of air-dried soil in 25ml of distilled water, after shaking for 1 min and leaving to stand for 1min (Forster 1995).
- The conductivity was measured with a conductivity meter on the supernatant of 10g of soil suspended in 50ml of distilled water, after shaking for 45min (Baize, 1988).

- The percentage organic matter (%OM) in the soil was determined by measuring the total ash content (Aubert, 1978). The soil was dried in an oven at 105°C for 24h. The samples were then combusted in a muffle furnace for 24h at 430°C. After weighing (W1 initial dry weight and W2 dry weight after combustion), the result is given by the formula: %OM=((W1-W2)/W1)x100.
- The percentage of total calcium (%Ca) was determined using the Bernard calcimeter method (French standard AFNOR X31-105).
- The percentages of carbon and total nitrogen (%C,N) were measured using a Perkin Elmer Series II 2400 CHN analyser, on 30-40mg of soil samples dried at 105°C and homogenised by grinding.

Data analysis

The species of mosses and lichens growing on the ground or the litter layer were recorded in autumn 2001. A data matrix of 124 quadrats (1x1m) including 29 species of mosses and lichens was analysed by Detrended Correspondance Analysis. (DCA, Benzecri, 1973; Ter Braak, 1996) to define vegetation patterns.

To examine the relations between the environmental factors and the distribution of the vegetation, the data matrix of 124 quadrats and the 29 species of mosses and lichens and five environmental factors were analysed with Canonical Correspondence Analysis (CCA). The importance of the relation between the species and the parameters taken separately, was tested with a Monte-Carlo permutation test.

The means and the standard deviations of each soil factor were calculated for each community; and were compared by a one way analysis of variance (ANOVA); the communities were compared pairwise by a Tukey test (Glantz and Slinker, 1990).
The relationships between the soil characteristics and the distribution of the communities were examined. A matrix of 142 samples (6VE) including the five groups of species of mosses and lichens was analysed by Canonical Correspondence Analysis (CCA). The importance of the relation between the groups of species and measured parameters taken separately was tested by the Monte-Carlo permutation test.

Results

Vegetation patterns

The results of the DCA (matrix of 124 quadrats x 29 sp) is shown in Fig. 2. The first three axes account for 28.1% of total inertia. The first axis (16.7%) reflects a gradient of dune fixation related to the distance from the beach. From the score of the species on axis 1 of the DCA and the analysis of the scattergram, five groups are distinguished.

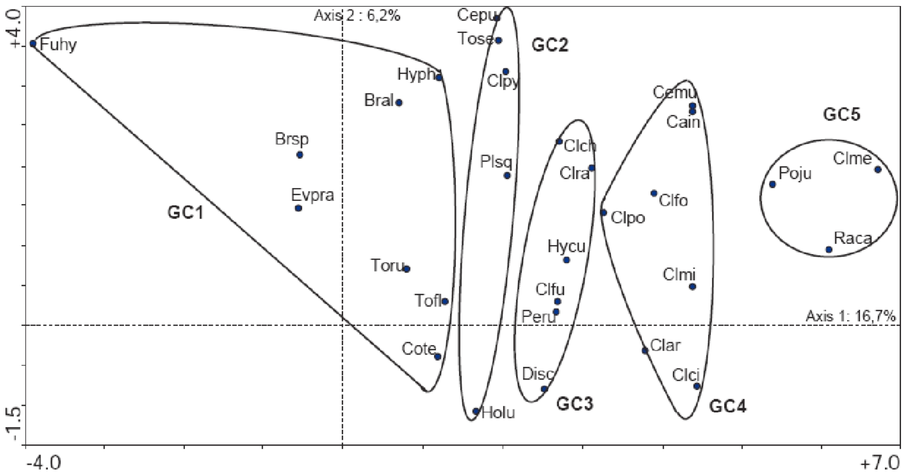


Fig. 2. Scatterplot of the two first axes (axis 1: 16.7%; axis 2: 6.2%) of Detrented Correspondance Analysis. Diagram shows the 29 species in five groups: GC1, GC2, GC3, GC4, GC5. See Table I for the code of the species.

Table I presents the 29 species ordered according to their score on axis 1 of the DCA (= 16.7% of total inertia) as well as the five groups of species. The discriminating species of each group (in bold) are those whose presence is higher than 10% in the 124 plots and of which percentage cover (F.R.) is higher than 10%. *Racomitrium canescens* (GC5) is the only discriminating species whose presence lies between 5 and 10%. An adaptation of the system of life-strategy defined for the species by During (1992) is used. The result obtained proposes a life-strategy for each identified community.

Distribution of the species

The relations between the distribution of the species and the five environmental factors was examined by CCA (Fig. 3). The position on the transect (Z-T), the geographical distribution along the coastal zone (Z-L), the percentage cover by the phanerogams (Phan) and the species richness (NbSp) are the factors which have importance after the Monte-Carlo permutation test ($P<0.05$) (Table II). They were strong determinants for the graphical representation of the species. The first three axes account for 91% of inertia. The position on the transect, percent cover of vascular vegetation were determinants of axis 1 (58.7%). It represents a gradient of fixation/stabilisation. The distribution on the coatal zone was determinant of axis 2 (19.7%). It expresses a geographic gradient from North to South.

Table I. The five groups of mosses and lichens in relation with the life strategies system (During, 1992). The species are ordered by their scores along the first DCA axis (Fig. 2). The discriminating species of each group (in bold) are those whose presence is higher than 10% in the 124 permanent plots and of which the percentage cover (F.R.) is higher than 10%

Species	(DCA) Communities	Life-strategy of the Communities
Funaria hygrometrica (Fuhy)		
Evernia prunastri var. arenaria (Evpra)		
Bryum spp. (Brsp)		
Brachytecium albicans (Bral)	GC1	Ephemeral colonist
Tortula ruraliformis (Toru)		Colonist *stricto sensu*
Collema tenax (Cote)		(+ Opportunists)
Hypogymnia physodes (Hyph)		
Tortella flavovirens (Tofl)		
Homalothecium lutescens (Holu)		
Ceratodon purpureus (Cepu)		
Toninia sedifolia (Tose)	GC2	Colonist stricto sensu
Cladonia pyxidata (Clpy)		(+ Perennial stayers)
Pleurochaete squarrosa (Plsq)		
Dicranum scoparium (Disc)		
Peltigera rufescens (Peru)		
Cladonia furcata (Clfu)	GC3	Perennial stayers
Cladonia chlorophaea (Clch)		
Hypnum cupressiforme (Hycu)		
Cladonia rangiformis (Clra)		
Cladonia portentosa (Clpo)		
Cladonia arbuscula (Clar)		
Cladonia foliacea (Clfo)		
Cetraria muricatum (Cemu)	GC4	Perennial stayers /
Cladonia mitis (Clmi)		Strees tolerant species
Campylopus introflexus (Cain)		
Cladonia ciliata (Clci)		
Polytrichum juniperinum (Poju)		
Racomitrium canescens (Raca)	GC5	Strees tolerant species /
Cladonia mediterranea (Clme)		Colonist *stricto sensu*

Table II. Level of significance of parameters connected to the 29 species of 124 permanent plots, tested with Monte-Carlo permutation test. P<0.050 is the chosen significance margin; Z-T : position on the transect Z-L: geographic zone Phan : % cover of phanerogams NbSp: species richness in mosses and lichens Sable nu : % bare sand

Parameters	P	F
Z-T	0.005	12.76
Z-L	0.005	5.17
Phan	0.005	2.48
NbSp	0.005	2.28
Sable nu	0.100	1.49

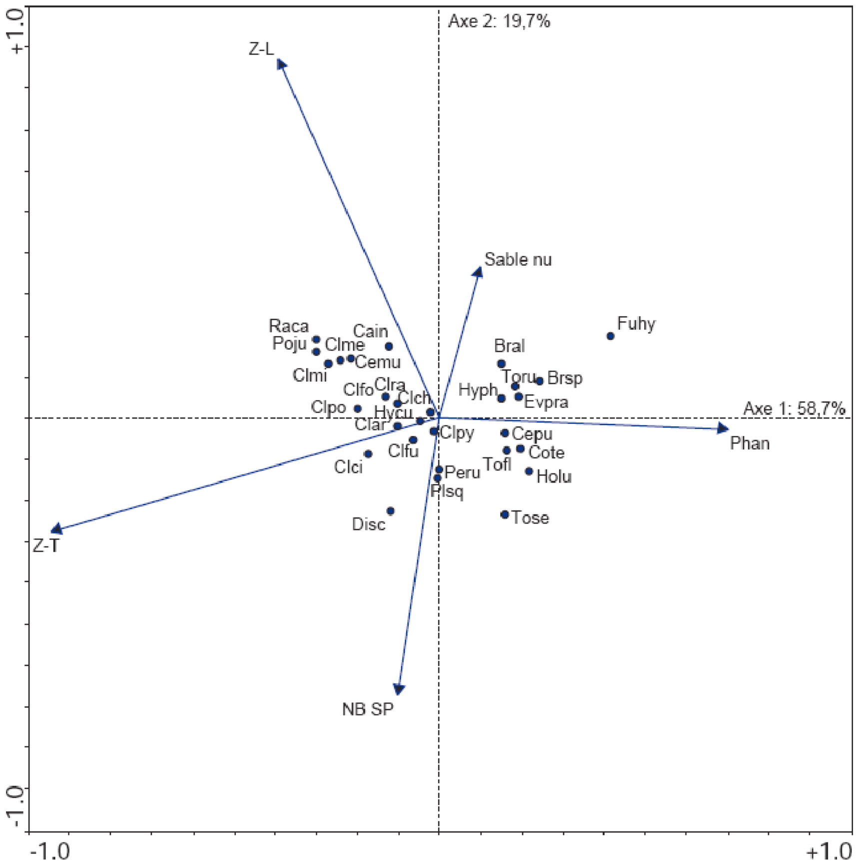


Fig. 3. Distribution of the species. Scattergram of the two first axes (axis 1: 58.7%; axis 2: 19.7%) of Canonical Correspondance Analysis CCA. Diagram shows the relation between the 29 species and the environmental parameters. See Table I for the code of the species.

Relation between the communities and soil

Five communities were identified through analysis of the vegetation patterns. Table IV presents the average values (+ Standard Deviation) obtained for each soil analysis under the communities. The analysis of variance (ANOVA) is used to compare the various groups according to each parameter. The groups present statistically significant differences ($P<0.001$) for four factors analysed from the surface soil layer: pH, total calcium, the percentage of organic matter, and total nitrogen.

The relations between the edaphic parameters and the five communities were examined by CCA (Fig. 4). The pH (pH-water), the percentage of total nitrogen (%N), the total calcium rate (%Calcaire) and the percentage of total carbon (%C) are the significant edaphic factors (Monte-Carlo permutation test: $P<0.05$) (Table III). They were strong determinants for the graphical representation of the species. The first three axes account for 97% of total inertia. pH and calcium content were determinants of axis 1 (64.6%), reflecting a gradient of acidification and decalcification. The percentages of carbon and nitrogen were determinants of axis 2 (23.9%), represent a trophic gradient.

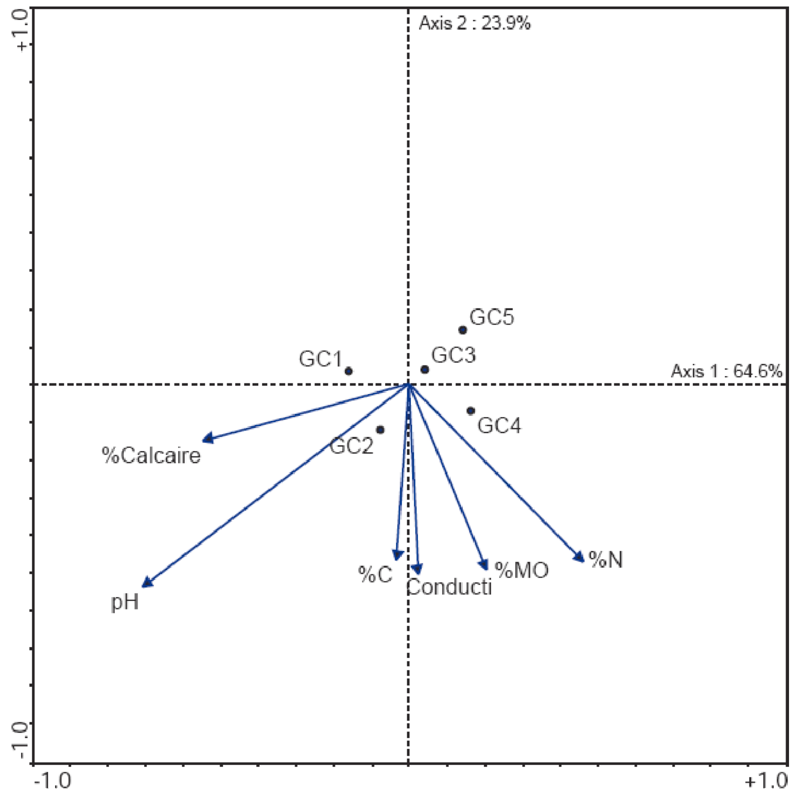


Fig. 4. Relations between the five communities and the soil. Scattergram of the two first axes (axis 1: 64.6%; axis 2: 23.9%) of Canonical Correspondance Analysis CCA.

Table III. Rate of significance of edaphic parameters connected to the five groups of species of 142 relevés of the soil surface, tested with Monte-Carlo permutation test ($P < 0.050$ is the chosen significance margin)

Parameters	P	F
PH	0.005	8.52
%N	0.005	6.24
%Calcaire	0.015	3.61
%C	0.030	2.52
Conductivity	0.420	0.98
%MO	0.845	0.37

Table IV. Results of the analyses of soil surface layer (N = 142; 0-5cm depth) for each community (n=5). The means (Moy) and the standard deviation (StD) are shown for each parameter (pH, Conductivity, Organic Matter, Carbon and Nitrogen Total, Calcium). There is a significant statististical difference between the different groups for pH, Calcium, Organic Matter and Nitrogen total

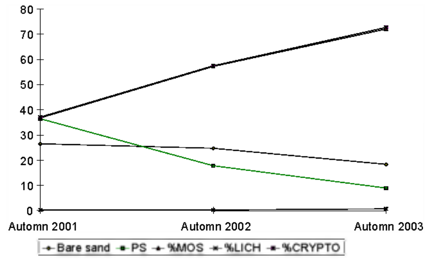
Groups	No. Relev.	pH Moy	StD pH	%Ca Moy	StD Ca	Cond Moy	StD Cond	%MO Moy	StD MO	%C Moy	StD C	%N Moy	StD N
GC1	42	7.80	0.65	7.16	6.86	69.90	16.98	1.29	1.88	1.32	1.02	0.02	0.01
GC2	22	7.88	0.40	4.59	3.90	68.53	15.81	1.47	1.43	1.21	0.65	0.03	0.02
GC3	33	7.17	0.83	3.92	6.03	62.62	40.75	1.25	1.60	1.14	1.33	0.03	0.06
GC4	30	7.14	0.87	3.10	4.09	82.30	58.08	2.36	2.26	1.59	1.62	0.08	0.10
GC5	15	6.77	0.75	0.16	0.26	49.45	21.78	0.90	0.48	0.48	0.25	0.03	0.01

The different communities

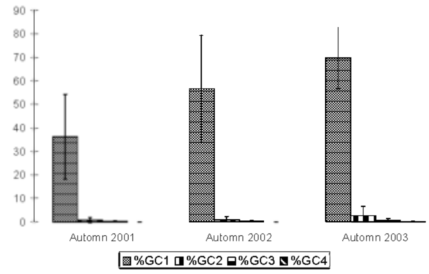
Group 1 (GC1) is composed of eight species. It is characterized by four acrocarpous mosses, like *Tortula ruraliformis, Bryum ssp, Tortella flavovirens*, and a pleurocarpous moss, *Brachytecium albicans*. These species have small sizes but are growing in height, they resist the weak sand accretion. The lichens are represented by *Collema tenax*, small lichen with gelatinous thallus, which colonizes in first of the parts of dunes recenty disturbed (James *et al.*, 1977), and two normally epiphytics lichens, *Evernia prunastri var arenaria* with fruticose thallus and *Hypogymnia physodes* with foliaceous thallus, here, they are terricolous. This group is in relation to a high pH (pH 7) and a high content of total limestone in sand. It is present on the whole of the sites in the semi-fixed dune (SMD). This group presents many species at strategy of transitory and colonizing colonizer in a strict sense (sensu, During, 1992). In this part of the dune, the mosses have an important role in the fixing of bare sand (Warming, 1909) and their presence makes it possible to appreciate a certain stability (progressive evolution) of this part of semi-fixed dune.

In Semi-fixed dune (n=15)

5a : Vegetation level

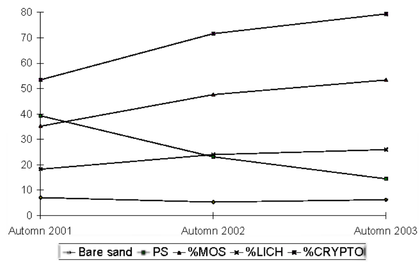


5b : Community level

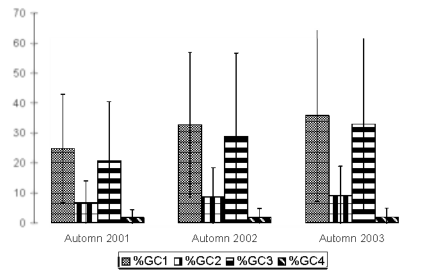


In Fixed dune (n=32)

5c :Vegetation level

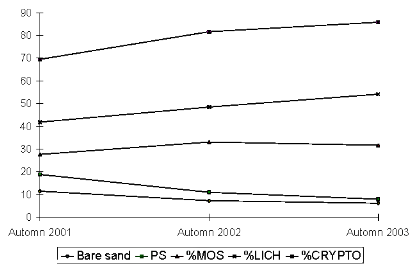


5d : Community level



In Rear fixed dune (n=30)

5e: Vegetation level



5f : Community level

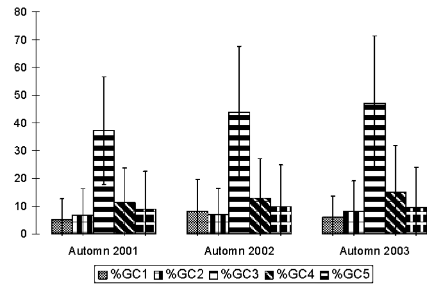


Fig. 5. Diachronic analysis of the percentage cover of mosses and lichens per habitat on 77 permanent plots; 5a and 5b Semi-fixed dune (SFD), 5c and 5d Fixed dune (FD), 5e and 5f Rear fixed dune (RFD).

This community presents by its discriminating species (*Tortula ruralifohurmis*) affinities with the bryolichenic cover of *Phleo - Tortuletum* in the 'black dunes' of the Western North of France (alternatives with *Brachytecium albicans* in dune in the process of decalcification and *Homalothecium lutescens* on sands more calcareous, both with pH 7) and of *Hornungio petraea - Tortuletum* (endemic) on dunes of Normandy and Brittany (Géhu and de Foucault, 1978). *Funaria hygrometrica* is an acrocarpous moss with fugitive strategy (During, 1992), it is characteristic of the soil disturbed by fire (Clement and Touffet, 1988, Esposito *et al.*, 1999), its presence remains limited in time and space for the dunes not undergoing this type of degradation.

Group 2 (GC2) includes five species. It is characterized by a pleurocarpous moss *Homalothecium lutescens* and two acrocarpous mosses, *Pleurochaete squarrosa*, mediterraneo-atlantic species, always observed without sporophyte on the Atlantic coast (Pierrot, 1980) and *Ceratodon purpureus*, accompanied by two lichens with squamulous thallus *Cladonia pyxidata* and *Toninia sedifolia*. The most part of the species of the group presents a strategy of colonist stricto sensu (During, 1992) and develops small carpets, forming a protective biological crust (Budel, 2001) from semi fixed dune (SFD) to the fixed dune (FD). It is influenced by a pH and a high rate of total limestone. *Cladonia pocilium* vicarious of *Cladonia pyxidata*, is indicating basic soil (James *et al.*, 1977). Certain species of this group are represented only on some sites, on the calcareous dunes of the Middle West and in the South Brittany in particular for *Toninia sedifolia*. It seems to be connected in *Fulgensietum fulgentis* Gams (James *et al.*, 1977) = *Toninio - Psoretum decipientic* Stordiek (Khalife, 1985) which is a community largely widespread (but threatened) in the center and the south of France (James *et al.*, 1977). This community requires a thorough study on the dunes.

Group 3 (GC3) includes six species, the lichens are dominant. *Cladonia rangiformis* and *Cladonia furcata*, *Cladonia sub-genus Cladonia* with fruticose complex thallus are often ubiquitous (James *et al.*, 1977) and a pleurocarpous moss *Hypnum cupressiforme* characterize this group and testify to a stop of powdering. An acrocarpous moss, *Dicranum scoparium*, and two lichens, *Cladonia chlorophaea* with complex thallus, and *Peltigera rufescens* with foliaceous thallus are also present. The latter testify to the presence of humus and by their development of the stop of a powdering. This group is influenced by the acidification, the increase in the nitrogen content (%N), factors related to the presence of humus. The presence of *Peltigera rufescens*, of which the photobiote is a cyanophyte, *Nostoc*, able to fix atmospheric nitrogen, sometimes being able to cover with broad surfaces, can be connected the increase in the percentage of measured total nitrogen, by leaching out in the medium (Scott, 1956). The species characteristic of this group have a strategy of perenial stayers (During, 1992). This group seems to translate, by its development, the passage of the semi-fixed dune at the fixed dune, dependent on weak variations of the ecological parameters (acidification, increase in the humus, stop of powdering). It is often represented the most on the studied dunes; it is present on broad surfaces on the parts of Fixed Dune (FD).

Group 4 (GC4) is composed of seven species. It is characterized by a diversity of *Cladonia*, *Cladonia foliacea* with foliaceous thallus and *Cladonia* of the *Cladina* sub-genus (= *Cladina*) to fruticose complex thallus, *Cladonia ciliata*, *Cladonia mitis*, *Cladonia arbuscula*, *Cladonia portentosa* like *Cetraria muricata*, lichen with fruticose thallus. This group is influenced by the acidification and the decalcification of the substrate related to the increase in humus (%OM, %C). It translates the presence of parts of dunes acidifying themselves more than into fixed dune and decalcifying themselves, representing an evolution of the soil into a podzolisation (micropodzol sensu James and Wharfe, 1989). Only one moss is represented, *Campylopus introflexus*, classified invasive (Muller, 2001). The community is characterized by the species with strategies of competitor and stress tolerators developing on all the sampled sites of the dune fixed (FD) at the rear fixed dune (RFD).

Group 5 (GC5) is clearly distinguished in the graphical representation and includes three species. It is characterized by two acrocarpous mosses, *Racomitrium canescens* and *Polytrichum juniperinum*, with one *Cladina*, *Cladonia mediterranea*. This Mediterraneo-Atlantic species (des Abbayes and Duvigneaud, 1946) also tends to replace other *Cladonia* of the *Cladonia* sub-genus in the stage of *Quercus ilex* (Ozenda and Clauzade, 1970). This group is clearly influenced by the reduction in the pH in aged dune. It is only present in parts of acidified dunes and clearly or entirely decalcified (calcium below 0.5%) in stabilized dunes. It is a community which develops on dry sunny sands (Augier, 1966) with a strategy of stress tolerator and colonist (During, 1992). It is present in the most aged fixed dunes (FD) at the rear fixed dune (RFD).

Diachronic study on permanent plots per habitat

The trends in the change in cover of different mosses and lichens communities during three years are summerized in Fig. 5. The 77 Permanent plots (1x1m) on the dunes are subjected to disturbances.
The semi fixed dune is subjected to a powdering by sand and an average regular trampling, the rabbit by scraping exposes sand and of fires (reacrationnal activity) punctually disturb the surface of the sand. Fig. 5a presents the evolution of the mean of percentage of cover (n=15) at vegetation level. Bare sand decreases regularly as well as the phanerogams while the proportion of cryptogams (13 species) primarily represented by the mosses (eight species) almost doubled between 2001 and 2003 respectively from 37 to 72%. The lichens (five species especially *Collema tenax* and *Cladonia furcata*) are not very present (<1% in 2003). Fig. 5b presents the survey at community level. GC1 is the dominant community, *Tortula ruraliformis*, *Tortella flavovirens* and *Bryum spp.* quickly colonize the bare sand (36% in 2001 and 70% in 2003). Percentage cover of GC2 (*Ceratodon purpureus* and *Homalothecium lutescens*) and GC3 (*Hypnum cupressiforme* and *Cladonia furcata*) communities is less than 5% but increase. GC4 community is only established in 2003, represented by *Cetraria muricata* (<1%).

The fixed dune is subjected to low powdering, rabbit disturbances and a regular trampling. Fig. 5c presents the evolution of the mean of percentage of cover (n=32) at vegetation level. The bare sand is small (<10%) during the survey. The percentage of cover of phanerogams regularly decreases and cryptogams (21 species) is high (>50%). The covering of mosses (nine species) is the double of the lichens (12 species primarily of *Cladonia*). Fig. 5d presents the survey at community level. GC1 and GC3 are the dominant communities and are in extension (+10% between 2001 and 2003). Three other communities (GC2, GC4, GC5) are stable and increase slightly.

The rear fixed dune is subjected to an extreme regular trampling (recreational activity and hunting), an action of the rabbit and the wild boar (tilling) and a powdering intervene punctually. Fig. 5e presents the evolution of the mean of the percentage of cover (n=30) at vegetation level. The bare sand is small (<10%) during the survey. The percentage of cover of Phanerogams is low (<20%) and decreases, the cryptogams one (24 species) is very high (>70%). Lichens are dominant (12 species, especially *Cladonia* and *Cladina*) and increase, mosses (12 species, *Hypnum cupressiforme*, *Pleurochaete squarrosa*, *Racomitrium cnescens*) are stable (30%). Fig. 5f presents the survey at community level. All the communities are represented, GC3 is the dominant community and raises some (+10% of 2001 to 2003) with GC4 (light increase). The proportion of each community is stable and increases slightly.

Discussion

Vegetation patterns

The non-forested dunes of the Atlantic coast of France accommodate many species of mosses and lichens which present interesting biological characteristics. The populations develop on great surfaces in the fixed parts of the dune and densely cover the sand. They form a biological crust (Büdel, 2001) allowing the fixing of sand (stability). Mosses and lichens are distributed in five communities to identifiable life-strategies by their common biological-traits. The results obtained of the analysis of the soil surface layer confirm the observations of several authors; the dunes are characterized by a heterogeneous sandy substrate low in nutrients (Cowles, 1899; Olson, 1958; Géhu-Franck, 1978; Gerlach, 1993; Gerlach *et al.*, 1994; Berendse *et al.*, 1998). Each particular substrate tends to establish a characteristic uniform lichenous vegetation under the influence of similar ecological factors (James *et al.*, 1977; Ozenda and Clauzade, 1970) and the changes of the composition of the groups of species are connected significantly to certain edaphic factors in the dunes like Ketner-Oostra and Sykora (2000) showed. According to the studies carried out on the dunes (Watson, 1918; Richards, 1929, Brown and Brown, 1969; Tophan and Hitch, 1985), authors distinguished several factors so that the lichens constitute a significant part in the vegetation of the littoral dunes, such as the stability of sand, its moisture retention properties, the frequency and the permanence of the dewfall and the fog, and from the humus and calcium carbonate contents of sand (James *et al.*, 1977). The species of the communities highlighted are comparable with those described in the littoral dunes of the north of Europe (Ketner-Oostra and Sykora, 2000; Magnusson, 1983) but the communities present on the Atlantic coast of France a composition of Mediterraneo-Atlantic species like, *Tortella flavovirens, Pleurochaete squarrosa, Cladonia mediterranea* which also distinguish them compared to other groups described in the south of Europe (Gallego Fernandez *et al.*, 1995, Esposito *et al.*, 1999). The influence of the littoral microclimate is thus not to be neglected in the distribution of the communities in particular for factors like the sunning (heliophilous, thermophilous species) and of the relative humidity of the air.

The distribution of each community in certain parts of the dunes seems to represent the modifications in the chemical composition of the soil surface layer by the description trophic of the gradients, acidification and decalcification of the beach to the forested dune. Fig. 6 summarizes the characteristics of the five mosses and lichens communities and lichens in relation to the edaphic gradients and their distribution on the non-forested coastal dunes.

Groups GC1 and GC2 are present in the zones at semi-fixed to fixed dune; they are communities with colonist life-strategy (During, 1992). The distribution of the species in these parts is thus related to the probability of being covered by sand (or resistance to burial for the arenicolous species) and the competition with the higher plants which present a strong covering.

Groups GC3, GC4 and GC5 are perenial stayers and stress tolerators; their presences reflect a low sand accretion rate. They are comparable in composition with mosses communities (Géhu and Géhu-Franck,1973; Augier, 1966) and lichens (James *et al.*, 1977; Gilbert, 2000) of the moors on sunny dry sands. The species of GC3 group (*Hypnum cupressiforme, Cladonia rangiformis, Cladonia furcata*), but especially of the GC4 (*Cladina*), of the GC5 (*Cladonia mediterranea, Polytrichum juniperinum*) are present in the relevés of three associations of dry moors of south-west France described by Géhu (1977) whose especially coastal moor with *Fustuca juncifolia* and with *Erica cinerea*. This one develops from the zone of contact between the grey dune with *Helichrysum stoechas* and the pine forest in back dune and penetrates towards the interior only of a few kilometers on the coasts of Les Landes and of la Gironde whose optimum is north of Adour at the south of Mimizan (Géhu, 1977).

The 'continental' vegetation thus influences the composition of vegetation in the littoral zone (border-effect), which can explain the diversification of the communities in the parts fixed on the dune by species with wide ecological amplitude. In fixed dune and rear fixed dune, zones fixed in the past by the vegetation, the ecological conditions change. A fall of the pH related to a decalcification like with the increase in the humus (James *et al.*1977) also influence the changes in the composition of the vegetation. Moreover, as Dawson *et al.* (1984) showed for the alpine tundras, the lichens compounds are mobile with the profile of the soil and they contribute to the formation of the soil and the other processes of evolution of the soil leading to a podzolisation. Communities (GC3, GC4, GC5) prefer a dry habitat little subjected to low disturbances. According to Gallego Fernandez *et al.* (1995, 1997) the presence of lichens and the height of the community are biological indicators.

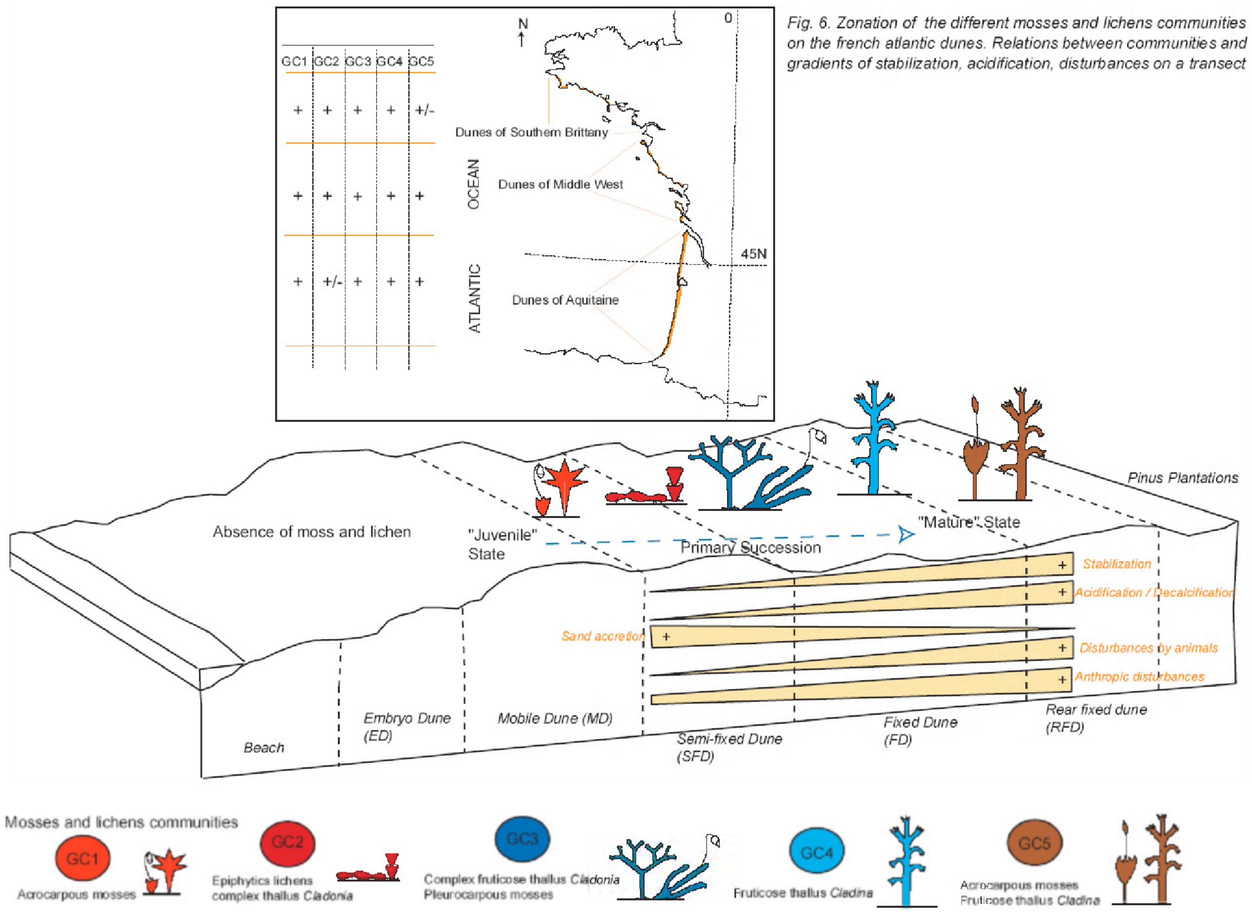


Fig. 6. Zonation of the different mosses and lichens communities on the french atlantic dunes. Relations between communities and gradients of stabilization, acidification, disturbances on a transect

Various authors proposed to group the species according to the common response (response-traits) to the environment or according to their common effects (effect-traits) on the processes of the ecosystem (Noble and Slatyer, 1980; Gitay and Noble, 1997; Lavorel *et al.*, 1997, McIntyre *et al.*, 1999). The monitoring on permanent plots allows observation of stabilization dynamics (fixing of sand) and the mechanisms of response to the disturbances which take part in it. The results suggest that the dynamic ones and the mechanisms vary according to the species, which have certain common response-traits (sensu Gitay and Noble, 1997), and according to the habitats, characterized by variations of the environmental conditions. These mechanisms allow the coexistence of the mosses and lichens populations, forming patches of the semi-fixed dune to the rear fixed dune. In a general way, an increase in the covering of the cryptogamic carpet with a season-effect was observed. This increase is more important during the winter, the local climatic conditions (cool and wet winters) seem to support photosynthesis for the growth and the reproduction. The summers being dry, the drying of the communities is accentuated by the wind, they reduce the periods of development.

Dynamic states

Although being frequently established in extremely unfavourable habitats, the lichens require very strict ecological conditions to develop (Clauzade and Rodon, 1966). This explains why there are close relationships between the bryolichenic vegetation of a determined zone on the dune and the ecological characters of this one, which makes it possible to use the mosses and lichens communities as biointegrators. The use of the biological traits is important to define the life-strategies of the species and the communities allowing a functional typology of habitats (Lavorel *et al.*, 1997). The results obtained in this survey (Jun *et al.*, 2004; Jun, 2005) show that the terricolous bryolichenic communities allow to carry out a typology of the ecosystem 'littoral dune' and to evaluate its states of dynamic. The various communities highlighted reflect three states of stability of the dune (Table V).
The bryolichenic communities highlight the dynamic stages of maturation (stabilization) of the dune by the passage of a juvenile state (conditioned by the abiotic processes) in dune of transition, dominated by the acrocarpous mosses (colonist), in a mature state in fixed dune and in rear fixed dune (characterized by the biotic interactions). The bryolichenic communities substitute themselves and diversify in these the last two habitats, in particular the populations of *Cladonia* and pleurocarpous mosses (perenial stayer), as soon as the physical disturbances of the medium (wind erosion and gradient of powdering by sand) decrease.

This phenomenon of diversification is conditioned and accentuated by the ecological characteristics of each site. The climate allows the development of Mediterraneo-Atlantic species. The animal and human disturbances as well as the stress factors of soil (pH and oligotrophy) and the dynamic states of degradation of the vegetations between the rear fixed dune and the forest border (with Ericaceae and Cistaceae and forests of protection with *Pinus pinaster*, *Querqus ilex* or *Q. suber*) condition the 'zones of contacts' (Delcayrou, 1997) and the diversity and the availability of the microhabitats. The cryptogamic communities of the rear fixed dune, especially *Cladina* and acrocarpous mosses (perennial stayer, competitor, stress-tolerator), reflect the multiplicity of the situations in the trajectories of evolution before the close vegetation translating to the forested dune. In a general way, the maximum of diversity out of mosses and lichens could be observed in sites presenting broad zones of semi fixed dune and fixed dune (one or more dune ridge), a minimum of anthropic disturbances (trampling) and a zone of contact to mixed forest (pines and oaks) of semi-diffuse type to diffuse.

Table V. The five communities of mosses and lichens show three states of stability of the dune: summary table

Communities	*Species*	State of Stability	*Habitat*
GC1 Acrocarpous Mosses & Epiphytics Lichens	*F. hygrometrica* *E. pr. var. arenaria* *B. spp.* *B. albicans* *T. ruraliformis* *C. tenax* *H. physodes* *T. flavovirens*	Juvenile State	*Semi Fixed Dune*
GC2 Mosses & small lichens	*H. lutescens* *C. purpureus* *T. sedifolia* *C. pyxidata* *P. squarrosa* *D. scoparium*	Juvenile State	*Semi Fixed Dune*
GC3 Cladonia & Pleurocarpous Mosses	*P. rufescens* *C. furcata* *C. chlorophaea* *H. cupressiforme* *C. rangiformis*	Mature substitution State	*Fixed Dune*
GC4 Cladina & Cladonia	*C. portentosa* *C. arbuscula* *C. foliacea* *C. muricatum* *C. mitis* *C. introflexus* *C. ciliata*	Mature diversified State	*Rear Fixed Dune*
GC5 Cladina & Mosses	*P. juniperinum* *R. canescens* *C. mediterranea*	Mature diversified State	*Rear Fixed Dune*

Monitoring and management

The analysis of the biotic interactions within the communities confirms that the lichens take a significant part in the processes of maturation of the ecosystem (Jun, 2005). For their precise distribution, their composition and their possible roles in the ecosystem, the terricolous mosses and lichens communities can be regarded as « keystone species » (sensu Aronson *et al.*, 1995) in the functioning of the fixed parts of the littoral dune called 'grey dunes', priority habitats of the European Directive Habitats. The monitoring of the communities obtained can contribute to obtain an ecological diagnosis on the dunes and make possible the management decisions of these lands. Mosses and lichens inform us about the functioning of the dunes by their distribution, and their capacities to resist to the disturbances.

Because of their size (from 0.5 to 5cm, even 10cm in height) smaller than the phanerogams, and their natural discretion, it is more difficult to take into account on the management of the dune, plants which patterns are complex or that present difficulties in the identifications. The natural dune dynamics are at the origin of the modifications of the favourable conditions for their development with a greater reactivity in the changes than for vascular vegetation. The 'health of an ecosystem' corresponds to its faculty of resilience after disturbance. The patches of the communities (mosaïc) of the carpet reflect the resilience of the habitats of the 'grey dunes'. Consequently, it is necessary to integrate the mosses and lichens communities in the reflections of management of these very vulnerable habitats and to allow the perenniality of the species in satisfactory population.

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Nomenclature

Purvis *et al.* (1992) for lichens.
Smith (1978) for bryophytes.
Tutin *et al.* (1968-1980) for vascular plants.

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