The relative importance of disturbance and environmental stress at local and regional scales in French coastal sand dunes

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Abstract
Questions: 1. Is there a primary role of disturbance at local scale and of environmental stress at regional scale? 2. Does disturbance increase or decrease environmental stress at local scale?
Location: The Atlantic coastal dune system of the Aquitaine Region (France).
Methods: Species biomass and 16 environmental variables were sampled in 128 quadrats along a local beach-inland gradient and a regional North-South gradient. Environmental data were analysed with ANOVAs and vegetation-environment relationships with Canonical Correspondence Analysis.
Results: At the local scale community composition was primarily driven by disturbance due to sand burial, whereas water and nutrient stress better explained regional differences. However, random biogeographical events are very likely to also affect community composition at the largest scale. The main interaction between environmental stress and disturbance was the mitigation of nutrient stress induced by disturbance at a local scale. This was due to a positive direct effect of sand burial and a positive indirect effect of wind (decrease in VPD by ocean spray). Although wind had also a significant effect on soil conductivity and pH, there was no evidence that these factors had any role in community composition.
Conclusions: Our results support the hypothesis that disturbance had a primary role at local scale and environmental stress at regional scale but further research is needed to separate the effect of stress from that of dispersal at regional scale. We also demonstrated that environmental stress in primary succession may not always decline with decreasing disturbance.

Keywords: CCA; Community composition; Nutrient stress; Primary succession; Sand burial; Vegetation-environment relationship; Water stress; Wind.


Abbreviations: CCA = Canonical Correspondence Analysis; VPD = Vapor Pressure Deficit.

Introduction

Most plant ecologists agree that, among the three main filters of community assembly theory (Huston 1994; Grime 1998; Lortie et al. 2004), environmental conditions are prevalent at intermediate scales (i.e. local and regional scales; Grime 1973; van der Valk 1981; Keddy 1992), whereas biotic interactions and chance biogeographical events are the more important at either the smallest (patch) scale or the largest (i.e. continental) scale (Grime 1973; Zobel 1992; Huston 1999; Mittelbach et al. 2001). Environmental conditions include stress and disturbance, which have been well identified as different factors in theoretical community models (Grime 1973, 1979; Huston 1979; Tilman 1982). According to Grime (1979), stress includes all constraints limiting community productivity, whereas disturbance is a mechanism limiting plant biomass by causing its partial or total destruction (see White & Jentsch 2001 for a review). Disturbance is also defined as a stochastic event in opposition to environmental stress which is predictable and rather continuous. Most common stress factors are drought, cold, shade and nutrient deficiency (Grime 1979), whereas examples of disturbance are multiple and include biotic disturbances (e.g. herbivory) and physical and/or anthropogenic disturbances (e.g. flooding, fire, ploughing or mowing).

A large number of previous studies have attempted to focus on single gradients where environmental stress or disturbance were easily manipulated or accessible like, for example, temperature along an elevation gradient in mountain ranges (Callaway et al. 2002; Sanchez-Gonzalez & Lopez-Mata 2005), flooding in wetlands (Toner & Keddy 1997; Touzard et al. 2002), mowing and grazing in grasslands (Verrier & Kirkpatrick 2005) or water availability in arid environments (Maestre et al. 2005; Westbrooke et al. 2005). However, because of the complex nature of environmental gradients, stress and
disturbance are often intermingled in natural landscapes, which render the separation of the effects of both of these direct factors, difficult as suggested, for example, by Choler et al. (2001) for elevation gradients or Goldberg & Barton (1992) for productivity gradients in general. Additionally, environmental stress and disturbance are known to interact strongly along complex environmental gradients (Ryser & Urbaś 2000; Craine et al. 2001). According to the two main successional models of the literature (see Connell & Slatyer 1977 and Finegan 1984 for a review), disturbance may either be positively or negatively correlated to environmental stress, depending on the harshness of the physical environment. In physically severe environments the positive effect of dominant pioneer species has been found to decrease environmental stress with decreasing disturbance (autogenic succession, Clements 1916; Chapin et al. 1994), whereas in benign environments dominant pioneer species are expected to increase environmental stress with decreasing disturbance (individualistic succession, Mc Arthur & Wilson 1967; Grime 1979; Tilman 1982).

Few studies have assessed the relative importance of environmental stress and disturbance and their interactions at different spatial scales (Bamberg & Major 1968). We suggest that most disturbances, and in particular biotic (Tilman 1997) or physical disturbances generated by topography gradients (erosion, flooding, etc.) are more likely to prevail at smaller scales than stress factors generated by climate or substrate types. The main aim of our study is to analyse, in coastal sand dunes, the respective importance of environmental stress and disturbance for community composition at local and regional scales as well as interactions between both of these direct factors. Coastal sand dunes are severely constrained systems subjected to both high stress (salinity, drought, nutrient limitation) and important disturbances (sand burial, wind abrasion). However, because direct abiotic factors merge and change dramatically within a short distance along the successional gradient, the underlying causes of plant zonation still remain controversial. Furthermore, coastal sand dunes have been widely studied at local scales, i.e. along the complex beach/inland gradient, but fewer studies have searched for ecological mechanisms acting at a larger spatial scale (Rajaniemi et al. 2006), although contrasted patterns of community composition and diversity have been described at regional scales (Lemauviel 2000; Acosta et al. 2005).

We analysed the relationships between patterns of community composition and associated environmental factors (stress and disturbance) in order to understand the respective roles of these two components of the abiotic environment at two intermediate spatial scales, local scale (beach/inland gradient) and regional scale (240 km of the French Atlantic coast). Our main objective was to test the hypothesis that disturbance should have a primary role at the local scale and environmental stress at the regional scale. Our second objective was to search for interactions between these direct factors, both at the local and the regional scales, and in particular to test the dominant opinion of the literature that environmental stress and disturbance are positively related along the local complex successional gradient.

Material and Methods

Study sites

The study was conducted in the coastal sand dunes of the Aquitaine region (France) where dune systems stretched along 240 km of the Atlantic French coast, from the Gironde estuary in the North (45°33' N, 1°05' W) to the mouth of the Adour in the south (43°32' N, 1°30' W), close to the Pyrenees. The climate is temperate oceanic. Mean annual precipitations vary between 750 mm in the North to 1200 mm in the South of the Aquitaine coast (Meteo France data), with the rainiest period during winter. Tourism is highly developed in this area but concentrated in a few small towns which are separated by long stretches of hardly visited beaches (Favennec 2002). Most of the dune areas (180 km) are owned by the French government and managed by the National Forest Office (ONF). Coastal sand dunes are, in general, ca. 500 m-wide and delimited on their eastern edge by a maritime pine plantation since the 19th century. A 50-m wide zone of scattered stunted trees forms an ecotone between the forest and the herbaceous dune communities. From the beach to the inland tree-line ecotone, four geomorphological zones or dune types have been distinguished along a gradient of decreasing sand deposition (Lemauviel 2000): (1) foredunes occupying a narrow, ca. 20 m zone with a gentle slope; (2) white dunes, centred on a ridge up to 25 m high and ca. 100 m wide with a steep western slope; (3) transition dune on a second ridge with a similar elevation but a very gentle western slope contrasting with a steep eastern one; (4) grey dunes, ca. 200 m-wide and appearing as a quite flat area protected from the west by the two former ridges. This is the standard dune transect prevailing in the Central part of the Aquitaine coast, but flatter dunes may also be observed, especially towards the South.

Vegetation sampling

We used a preliminary study by the National Forest Office (O.N.F.) from the summer of 1997 to select the dominant community types of the whole area (See pictures in App. 1) for our vegetation-environment study. The 820 quadrats sampled by O.N.F. along the 240 km of Aquitaine coastal
dunes with Braun Blanquet’s standards (Braun-Blanquet & Pavillard 1928) were analysed with Correspondence Analyses (CA) followed by cluster analyses, using R software. Among the 23 plant community types identified with the cluster analysis along the Atlantic shoreline, we selected the 16 most common communities representative of the four successional stages: two foredune-, two white dune-, three transition dune- and nine grey dune- communities; covering all three geographical areas North, Central and South Aquitaine. Since our objective was to focus on the influence of natural disturbances (e.g. sand burial), we excluded communities highly influenced by recent human activities such as the deposit of a dense cover of pine branches by the forest managers. The number of selected communities increased from the foredune type to the grey dune type because β-diversity was more important inland than in disturbed pioneer conditions. Eight replicates of each community were randomly sampled in the whole distribution area of each community type with at least 1 km distance between sites. Furthermore, for community types occurring in the whole Aquitaine coast (e.g. foredune types), the eight replicates were distributed in the three regional areas.

In each of the 128 (16 × 8) community replicates, above-ground vegetation was clipped at ground level within 1 m × 1 m quadrats. Every vascular plant species was identified and separately collected, whereas mosses and lichens were pooled in one group. Plant material was dried at 65 °C for 72 h and weighed.

**Environmental data**

Several environmental variables were measured in 2005 at each of the 128 sites in order to quantify environmental stress and disturbance. Sand deposition, the primary factor of disturbance in coastal sand dunes (Dech & Maun 2005), was recorded by measuring the height of stakes buried in sand, from December 2004 to June 2005 corresponding to the storm period when sand deposition is the highest. Wind intensity was quantified by leeward-edge erosion of tatter flags (180 mm × 360 mm cotton flags, Rutter 1965) in January 2005. Flags were placed at 30 cm height on stakes erected close to the quadrat. They were fixed by rings in order to rotate freely with the wind. After seven weeks of exposure, the lost flag area was measured and expressed in percentage of the initial area. Soil moisture was measured in March and in May 2005 at 10 and 30 cm-deep with a profile probe (profile PR1, Delta-T Devices). We used litter bags to assess the rate of litter decay and thus indirectly quantify nutrient availability and soil fertility (Swift et al. 1979). Three specific litter bags were realized with 4 g of dried leaf litter of three dominant dune species (Elymus farctus, Helichrysum stoechas and Corynephorus canescens). For each quadrat, the three specific litter bags were buried 3 cm deep within the soil in March 2005, at the beginning of the growing season. The size of the mesh bags was 20 cm × 15 cm with a 2-mm mesh, whose value is small enough to prevent losses of litter due to breakage, but large enough to allow the access of decomposers (Bocock & Gilbert 1957). After 3 months of burial, litter bags were removed in late May 2005 and the remaining litter was dried and weighed. Results were expressed in percentage of lost mass and compared with litters kept in the laboratory during the same period. Soil conductivity and pH were measured with a pH/conductivity meter (WTW ph/cond. 340i, Germany). For each plot, ten soil scores were taken from the upper 10 cm of dune soil and pooled before measurements; 25 ml of distilled water was added to 10 g of dried soil sample and mixed for 2 h with a magnetic agitator. Soil conductivity was expressed in µS.cm⁻¹. Granulometry was obtained by dry sieving of 400 g of sand. Samples were automatically sieved with a shaker for 10 minutes through a fifteen stacked column of sieves, with a maximum mesh size of 5 mm and a minimum mesh size of 63 µm.

In addition to these local environmental factors, we recorded two regional factors along the Aquitaine coast: atmospheric nitrogen deposition and rainfall. Atmospheric nitrogen deposition was measured with nitrogen dioxide (NO₂) passive diffusion tubes every fifteen kilometers along the coast (i.e. at 16 positions along the coast). The diffusion tubes were purchased at Gradko International Ltd (Winchester, UK) and sent back for analysis after field exposition. Triplicate tubes were fixed on a post at 1.5 m above the ground under a plastic shelter providing protection against rain and bird droppings. The posts were placed behind the dune to prevent any influence from the ocean and at least 1 m from the dune slope with no surrounding trees, to ensure a maximum airflow around the samplers. Atmospheric nitrogen concentrations (oxidized form NO₂ and reduced form NH₃) were sampled over 2 periods of 3 months (summer 2004 and winter 2005). The samples were exposed for 4 weeks on each site and immediately sent to Gradko for analysis together with an unexposed field blank. Annual means of NO₂ concentrations were calculated from the 6 monthly values and expressed in kg.ha⁻¹. We regressed regional position to NO₂ concentrations for the 16 atmospheric NO₂ measurement points, in order to affect a NO₂ concentration value to the 128 quadrats for the CCA. We also regressed regional position to annual rainfall measured at five weather stations (Météo France data), in order to affect an annual rainfall value to the 128 quadrats for CCA and to the 16 NO₂ measurement sites for ANOVA.

We also quantified for each quadrat the distance to the ocean (local scale) and to the South of Aquitaine (regional scale). Both distances were measured using GPS coordinates in cartography software (Arcview).
Statistical analyses

All statistical analyses were performed using R software (version 2.0.1, 2005). Relationships between vegetation quadrats and environmental variables were analysed with Canonical Correspondence Analysis (CCA, ter Braak 1987, ADE4 package in R software). A first CCA was performed on the whole data set (128 vegetation quadrats and 16 variables). In order to limit the number of variables (Lebreton et al. 1988), a second CCA was conducted only on the 13 variables (3 regional variables and 10 local variables) which had significant correlations with CCA scores in the first analysis. The three removed variables were Moisture 10 cm March, Moisture 10 cm May, Litter decay E. farctus. The significance of the relationship between floristic data and environmental variables was tested with Monte Carlo permutation tests (2000 permutations). For each dune type (foredune, white dune, transition dune and grey dune) of the three regional positions (North, Centre and South), we calculated the mean values and the 95% confidence limits of the quadrats scores on the first two CCA axes.

For each of the three regions (North, Centre and South), we conducted one way unbalanced ANOVAs on environmental factors (sand deposition, wind intensity, soil moisture, litter decay, soil conductivity, pH and granulometry), with dune type (foredune, white dune, transition dune and grey dune) as independent factor. We also performed one two-way unbalanced ANOVA with region and dune type as independent factor for each variable. For atmospheric nitrogen deposition and rainfall we also used ANOVA to test for regional effect. Two variables (sand deposition and granulometry) were log-transformed before analyses to meet assumptions of parametric tests. When an ANOVA effect occurred, Tukey’s HSD tests were used to determine significant differences among dune types or regions.

Results

Environmental factors

There was a highly significant variation in wind intensity due to both regional and local community positions, with the strongest wind intensities recorded in the foredunes and in the South of Aquitaine \( (p < 0.001 \) for both the regional and local effects in the two-ways ANOVA, Table 1). Additionally, there was a significant regional*local interaction \( (F_{6,127} = 4.2, p < 0.001, \text{Table 1}) \) due to weaker differences in wind intensity with local position in the South than in the two other regions; wind intensity was still very high in the grey dune of the South and not significantly different from the wind intensity recorded in the foredunes of the two other regions (Table 1). Similar patterns and results of the two-ways ANOVA were observed for pH and soil conductivity, with the highest values of both variables occurring in the foredunes and the South, and still very weak differences with local position in the South (Table 1). However, for soil conductivity this pattern was very true only when comparing the South to the Centre, because high values were also observed in the North (Table 1).

In contrast, sand deposition was primarily affected by local position \( (F_{3,127} = 20.8, p < 0.001 \) for the local effect in the two-way ANOVAs) with sand deposition values approximately a hundred times higher in foredunes than in grey dunes (Table 1), whereas the regional effect was weakly significant \( (F_{2,127} = 4.4, p < 0.01 \) ). Furthermore, results were opposite to those of the three previous variables, with much higher values in the North than in the South (Table 1). These results were strongly related to those of granulometry with much coarser sand particles in the South than in the two other regions. Additionally, there were no overall differences in granulometry with local position \( (F_{2,127} = 2.6, p > 0.05 \) for the local effect in the two-ways ANOVA).

There were strong differences in litter decay rates among species \( (F_{2,380} = 103.8, p < 0.001 \) ) with the highest rate for the species of the foredunes, E. farctus, and the lowest for the species of the grey dunes, C. canescens (data not shown). Litter decay of H. stoechas was intermediate and is only shown in Table 1. Litter decay of H. stoechas was primarily affected by local position \( (F_{3,127} = 15.7, p < 0.001 \) for the local effect in the two-ways ANOVA) with higher decay rates in foredunes than in other dune communities (Table 1). There was also a significant regional effect \( (F_{2,127} = 3.2, p < 0.05 \) ) with higher litter decay rates in the South than in the two other regions (Table 1). Additionally, results of a two-way ANOVA conducted on grey dune data for the three litter types showed a highly significant regional effect due to a higher litter decay rates in the grey dunes of the South than in those of the two other regions \( (F_{2,215} = 5.8, p < 0.001 \) ).

Soil moisture values were higher at 30 cm-deep than at 10 cm \( (p < 0.001 \) ) both in March and May. At 30-cm deep in May (only shown in Table 1) there was only a highly significant regional effect with lower values in the Centre than in the two other regions \( (F_{2,127} = 14.4, p < 0.001 \) ).

Both rainfall and atmospheric nitrogen deposition rates were highly positively significantly affected by regional position, with the highest values of both variables in the South, intermediate significant values in the Centre, and the lowest values in the North (respectively \( F_{2,127} = 16.3, p < 0.001 \) and \( F_{2,127} = 154.5, p < 0.001 \) in one-way ANOVA, Table 1). Rainfall was 40% higher and atmospheric nitrogen deposition twice as high in the South than in the North.
Table 1. Means (± SE) and one-way ANOVA results (three upper set of lines) for 7 environmental variables (wind intensity, sand deposition, granulometry, pH, conductivity, litter decay for *H. stoechas*, soil moisture at 30 cm in May) recorded for 128 quadrats (left columns), and regional means (± SE) for the 2 environmental variables (atmospheric nitrogen concentration and rainfall) recorded along the Aquitaine coast (2 last columns). Results of two-ways ANOVA for the 8 environmental variables are displayed in the fourth set of lines. Asterisks indicate significance of ANOVA (* = p < 0.05, ** = p < 0.01, *** = p < 0.001, ns: non significant). Different letters indicate significant differences between dune types within regions, at p < 0.05 with Tukey’s tests following post-ANOVA. Lowercase letters refer to means within regions and capital letters to regional means. See App. 2 for detailed results of the analyses of the regional and local effect at the bottom of the Table.

<table>
<thead>
<tr>
<th>Dune types</th>
<th>Number of sampling points</th>
<th>Wind intensity (cm in 6 months)</th>
<th>Sand deposition (μm)</th>
<th>Granulometry (μm)</th>
<th>pH</th>
<th>Conductivity (μS cm⁻¹)</th>
<th>% Litter decay (% <em>H. stoechas</em>)</th>
<th>% Soil moisture (at 30 cm in May) (μg m⁻²)</th>
<th>Atmospheric N₂ (μg m⁻²)</th>
<th>Rainfall (mm)</th>
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<td>NORTH</td>
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<tr>
<td>Foredune</td>
<td>5</td>
<td>45.7 ± 2.9⁰</td>
<td>15.4 ± 5.3⁰</td>
<td>281.2 ± 20.7</td>
<td>8.3 ± 0.1⁰</td>
<td>333.2 ± 42.1⁰</td>
<td>55.8 ± 0.0⁰</td>
<td>8.2 ± 0.7</td>
<td>1.18 ± 0.07⁰</td>
<td>789 ± 16⁰</td>
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<td>White dune</td>
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<td>46.2 ± 2.4⁰</td>
<td>8.3 ± 4⁰</td>
<td>293.7 ± 10.8</td>
<td>8.2 ± 0.1⁰</td>
<td>249.2 ± 14.4⁰</td>
<td>29.4 ± 9.3⁰</td>
<td>10.5 ± 0.4</td>
<td>(number of replicates = 34)</td>
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<tr>
<td>Grey dune</td>
<td>24</td>
<td>27.5 ± 1.4⁰</td>
<td>0.1 ± 0⁰</td>
<td>316.3 ± 10.8</td>
<td>7.7 ± 0.1⁰</td>
<td>219.1 ± 9.7⁰</td>
<td>20.7 ± 1.9⁰</td>
<td>8.1 ± 0.4</td>
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<td>Local effect</td>
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<td>Foredune</td>
<td>7</td>
<td>47.7 ± 4.3⁰</td>
<td>11.2 ± 1.9⁰</td>
<td>316.4 ± 3.2</td>
<td>8.2 ± 0.0⁰</td>
<td>264.14 ± 7.7⁰</td>
<td>52.2 ± 3.9⁰</td>
<td>7.1 ± 1</td>
<td>1.73 ± 0.13⁰</td>
<td>885 ± 12⁰</td>
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<td>White dune</td>
<td>6</td>
<td>50.6 ± 4.7⁰</td>
<td>5.1 ± 1.9⁰</td>
<td>309 ± 5.6</td>
<td>8.3 ± 0.1⁰</td>
<td>196 ± 29.3⁰</td>
<td>28.6 ± 4.7⁰</td>
<td>6.5 ± 0.5</td>
<td>(number of replicates = 51)</td>
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<tr>
<td>Transition dune</td>
<td>14</td>
<td>34.0 ± 6.6⁰</td>
<td>0.6 ± 0.5⁰</td>
<td>318.9 ± 5.5</td>
<td>8.1 ± 0.1⁰</td>
<td>161.9 ± 20.7⁰</td>
<td>23.2 ± 4.3⁰</td>
<td>4.8 ± 0.4</td>
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<tr>
<td>Grey dune</td>
<td>24</td>
<td>33.0 ± 5.3³</td>
<td>0.1 ± 0.1³</td>
<td>327.45 ± 3.8</td>
<td>7.3 ± 0.1⁰</td>
<td>150.0 ± 14.0³</td>
<td>18.4 ± 3.0³</td>
<td>7.1 ± 0.5</td>
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<td>Foredune</td>
<td>4</td>
<td>54.8 ± 2.8⁰</td>
<td>2.0 ± 0.5⁰</td>
<td>596 ± 86.0⁰</td>
<td>8.6 ± 0.1⁰</td>
<td>232.2 ± 30.9</td>
<td>45.3 ± 0.8⁰</td>
<td>9.9 ± 0.9</td>
<td>2.48 ± 0.14⁰</td>
<td>1161 ± 13⁰</td>
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<td>42.7 ± 5.2⁰</td>
<td>2.8 ± 0.4⁰</td>
<td>485.4 ± 33.8⁰</td>
<td>8.6 ± 0.1⁰</td>
<td>226.7 ± 17.3</td>
<td>26.8 ± 2.4⁰</td>
<td>7.8 ± 1.8</td>
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<td>Transition dune</td>
<td>10</td>
<td>44.1 ± 3.8⁰</td>
<td>0.2 ± 0.1⁰</td>
<td>399.3 ± 12.9⁰</td>
<td>8.3 ± 0.0⁰</td>
<td>212 ± 28.8</td>
<td>28.3 ± 2.0⁰</td>
<td>10.2 ± 1.9</td>
<td>(number of replicates = 43)</td>
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<tr>
<td>Grey dune</td>
<td>24</td>
<td>45.3 ± 1.9⁰</td>
<td>0.0⁰</td>
<td>535.4 ± 20.5⁰</td>
<td>8.2 ± 0.0⁰</td>
<td>263.2 ± 9.1</td>
<td>31.5 ± 4.1⁰</td>
<td>10.1 ± 0.9</td>
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CCA

Eigenvalues of CCA-axes (Fig. 1) were 0.28 for axis 1, 0.22 for axis 2 and 0.15 for axis 3 (not shown). The Monte Carlo test with 2000 permutations indicated that the CCA ordination gave significant results ($p < 0.001$). Overall, the CCA ordination showed two important contrasts related to local and regional positions (Fig. 1c). These two contrasts were not parallel to the axes but rather oblique. However, because the local contrast was primarily related to axis 1 and the regional contrast to axis 2, for simplicity we will further refer to them as local and regional axes, respectively. The local axis opposed for the three regions the grey dunes to both the foredunes and the white dunes, whereas the regional axis opposed the dunes from the South to the dunes from both the Centre and the North (Fig. 1a).

These contrasts were also easily detectable on the species diagram with three main groups of species (Fig. 1b).


rather an intermediate direction, and in particular wind intensity (positively correlated to both foredunes and the South), but pH and litter decay primarily explained the local contrast (positively correlated to foredunes and white dunes) and conductivity and NO$_2$ deposition the regional contrast (positively correlated to the South).

Discussion

The relative importance of environmental stress and disturbance changed with spatial scale in the French coastal dunes, and in accordance with our hypothesis there was a primary role of disturbance at the local scale along the beach-inland gradient, and a primary role of environmental stress at the regional scale. Furthermore, there were also strong interactions between environmental stress and disturbance occurring both at local and regional scales.

The primary role of disturbance at the local scale

Our results clearly demonstrate that disturbance by sand burial primarily drives species composition of sand dune communities at the local scale. Burial by sand acts as a strong selective force removing species not adapted to burial (Moreno-Casasola 1986, Maun 1998). The survival of foredune and white dune species (e.g. _E. farctus_ or _A. arenaria_) depends on their ability to produce roots and rhizomes in the burial deposit (Maun 1998). The primary role of sand deposition during early stages of plant succession in sand dunes has been demonstrated or put forward by several authors for different dune systems (van der Valk 1974; Moreno-Casasola 1986; Martinez et al. 2001; Dech & Maun 2005; Yura & Ogura 2006).

However, there has been a continuous controversy in the literature on the relative importance of salt spray and sand burial for local community zonation in these systems and some authors have rather emphasized the primary effect of salt spray (Oosting & Billings 1942; van der Valk 1974; Wilson & Sykes 1999). Although our ANOVA results showed that soil conductivity was significantly affected by local position, our CCA results showed that this variable was primarily correlated with regional position (see below the relation with wind intensity). In our dune system the highest values of conductivity did not exceed 334 μS.cm$^{-1}$. This corresponds to 0.075% of soil conductivity, whose value is below the threshold of toxicity of 1.5% in the rhizosphere proposed by Rozema et al. (1983) for _Cakile maritima_ and _Salsola kali_, two annual beach species. Soil conductivity was certainly too low in our coastal dunes to potentially act as a stress factor and significantly determine community composition, as shown by Yura & Ogura (2006) and Cakan & Karatas (2006). Salt spray may cover the plants of the foredune during important winter storms (E. Forey pers. obs.) but it is very unlikely to have a crucial role in plant zonation in oceanic temperate zones because regular precipitations wash the salt off the plants, as suggested by Maun & Perumal (1999). These arguments are supported by the high rarity of halophilous species in the communities of the Atlantic French coasts, even close to the ocean.

The primary role of environmental stress at the regional scale

Results of the CCA showed the primary role of environmental stress over disturbance for explaining differences in community composition among regions, in particular for grey dune communities. This is consistent with the results of Kammer & Möhl (2002) who found a primary role of stress (wind, solar radiation, soil nutrients, humidity, etc.) over disturbance (erosion, avalanches, herbivory, etc.) at the regional scale for alpine plant communities. Our CCA results emphasized the lower water stress of the dunes from the South, whereas ANOVAs on litter decay rate (an indirect measurement of soil fertility, Swift et al. 1979) showed that this region had also the lowest nutrient stress. Overall, coastal dunes are assumed to be highly limited by both water and nutrient stress because of their coarse sandy texture (Martinez & Psuty 2004). The relatively lower water and nutrient stress of dunes from the South may be explained in our system by both a higher rainfall and nitrogen deposition than the two other regions. This higher nitrogen deposition in the South of Aquitaine is likely due to the occurrence of important industrial activities in the North of Spain and to a higher number of towns and traffic than in the two other regions (Holland et al. 2005). Additionally, the important rainfall of the South of Aquitaine, induced by the vicinity of the Pyrenees mountain range, may both increase N deposition and indirectly lower the nutrient stress through a stimulation of decomposers with decreasing water stress (Michalet et al. 2001; Corcket et al. 2003).

Because the most significant correlations with the regional CCA axis were found for complex factors (e.g. rainfall) primarily driven by geography but not for direct stress factors (litter decay and soil moisture), we suggest that regional patterns of community composition may also have been driven in part by chance biogeographical events in our study (dispersal and history). However, the importance of stochastic processes was not directly assessed in our study and further researches are needed to assess the relative importance of environmental stress and dispersal, as well as their interactions, for understanding regional patterns of composition in Aquitaine coastal dunes.
Interactions between disturbance and environmental stress

We observed a decrease in nutrient stress with increasing disturbance along the local successional gradient, and in particular in the most stressed regions, the North and the Centre (CCA and ANOVA results). This mitigation of stress may have been driven by a direct effect of disturbance by sand deposition on plant lifespan. This effect has been shown to reduce nutrient stress in a number of disturbed ecosystems through a relative nitrogen enrichment of plant individuals enhancing soil organic matter decomposition (Ryser & Urbas 2000; Craine et al. 2001). Another explanation of the increase in soil fertility towards the beach could be a mitigation of atmospheric water stress by the ocean spray brought by the wind. We conducted Vapor Pressure Deficit (VPD) measurements along the successional gradient in the Centre, i.e. the most stressed region; VPD was approximately 30% higher in the grey dunes than in the foredune (respectively 1.40 ± 0.02 KPa and 1.12 ± 0.04 KPa, p < 0.001, N = 4). This mitigation of atmospheric water stress by the wind may also have triggered litter decay and lowered nutrient stress in the foredunes. Wind is a complex factor which has been primarily considered as a stress factor, because in many continental systems, such as mountains and deserts, wind is dry and increases transpiration rates (Grace & Russell 1982). Wind was also a critical complex factor in our study, influencing a number of direct factors such as soil conductivity and pH, VPD and likely soil fertility. However, in our system it had an overall positive role on ecosystem functioning in interaction with sand deposition. This role was obvious at the local scale but the strongest wind occurring in the South may have also contributed to mitigate both water and nutrient stress in this region, and increased salinity as well.

Our results do not support the autogenic successional model which proposed an improvement of ecosystem functioning with decreasing disturbance during primary succession in continental dunes (Cowles 1899; Clements 1916). Following this influential model, French managers of coastal dunes (Favennec et al. 1998) and others (Lemaunviel 2000; Jun et al. 2004) also consider that environmental stress is highest in the foredunes, because diversity, biomass and soil organic matter, all increase inland, while soil conductivity decreases. However, although many other authors have also considered that an increase in total soil nitrogen or organic matter content indicates an increase in soil fertility in several dune systems (Kellman & Roulet 1990; Houle 2002; Toft & Elliott-Fisk 2002), this argument is not true in a number of constrained ecosystems where important values of both total soil N and C are indicating poor ecosystem functioning (e.g. Wardle et al. 1997). Furthermore, measurements conducted in the Central dunes by Forey (2007) showed that productivity was null in the grey dune and significantly increased along the local disturbance gradient. The occurrence of an inverse relationship between stress and disturbance has rarely been observed in constrained environments and may be specific to ecosystems where disturbance is due to a material deposit, such as sand in coastal sand dunes or silt in salt marshes (Pennings & Callaway 1992). In contrast, in most other constrained environments, such as arid or alpine systems, where disturbance is due to soil erosion, environmental stress has been shown to be positively related to disturbance (Choler et al. 2001; Michalet et al. 2002; Michalet 2006).

Although sand granulometry cannot be considered as a direct stress factor, regional variation in this complex factor induced regional variation in disturbance level. Although wind intensity was the highest in the South, sand deposition was the lowest because the coarser size of sand particles had very likely induced shorter sand displacements in the South than in the two other regions. Other authors have stressed the occurrence of interactions between complex stress factors and disturbance at the regional scale; for example, Bamberg & Major (1968) and Sheard & Geale (1983) have shown that changes in soil particle size induced by variation in substrate types may induce variation in cryoturbation (a crucial disturbance in arctic ecosystems) in Alpine and arctic ecosystems. These interactions have been shown to affect patterns of community composition, even at the regional scale; for example Bamberg & Major (1968) explained the contrasted patterns of diversity and composition of Alpine communities from calcareous and siliceous mountain ranges from the Rockies by these differences in cryoturbation related to mineral soil particle size.

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