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Response of Three Plant Communities to Trampling in a Sand Dune System in Brittany (France)

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ABSTRACT / Dunes that are protected because of their very rich and diverse plant communities are often exposed to excessive visitor pressure. The effects of trampling on the habitat must be known from a conservation viewpoint but also are important for management. To determine the response of plant assemblages to trampling by people, an experimental study was conducted on the state-owned dunes at Quiberon (Brittany, France). Indices of resistance and resilience were used to compare three typical plant communities belonging to the various landscape units: mobile dune, semifixed dune, and fixed dune. The strong contrasts between communities belonging to different successional stages reflect their ecological functioning. The mobile dune and semifixed dune with their low resistance contrasted with the fixed dune. Only the vegetation cover of the semifixed dune benefited from long-term trampling and had a very high resilience (134%). This response could be explained by a good balance of two opposite factors: soil compaction increasing soil stability and moisture content, and vegetation destruction. Because of their low resilience, trampling seems to be harmful for fixed dunes in the long term. The tourist pressure seems easier to integrate in to the mobile dunes and the semifixed dunes if periods of recovery are included in the management.

During the 20th century, human activities linked to tourism have affected and damaged many coastal areas (Liddle and Greig-Smith 1975, Paskoff 1989, Van der Meulen 1997, Olsauskas 1996). The interest in seaside recreation and living has led to the construction of seaside resorts, including hotels, apartments, campsites, and golf courses on the seafront (Doody 1989, Priest and others 1997). Dunes, reduced to small areas, have become habitats that are valuable not only because of their rarity, but also because of their great biodiversity (Wanders 1987, De Raeve 1989, Dupont 1993). Managers are now aware of the need to conserve sand dunes; they are protected from the most destructive activities such as sand extraction, or motorcycling (Guilcher and Hallégouët 1991). They do, however, receive large numbers of tourist visitors, and trampling becomes a problem as it represents the major disturbance affecting dune vegetation. It is therefore important to know how resistant dune vegetation is to trampling and its ability to regenerate.

Trampling is an integral part of the problems of conservation management of natural areas that are attractive for tourists (Gomez-Limon 1995, Toullec 1997, Toullec and others 1999, Gallet and Rozé 2001, 2002). The coastline is affected and many authors have chosen sand dunes to study the effect of trampling on vegetation (Liddle and Greig-Smith 1975, Slatter 1978, Hylgaard and Liddle 1981, McDonnell 1981, Bowles and Maun 1982, Andersen 1995, Lemauviel 2000).

Excessive visitor pressure can damage dunes and lead to the degradation of vegetation, which exposes the sand to rain and wind erosion (Doody 1989). Moderate trampling can have a positive effect on species diversity (Van der Maarel 1971). Disturbances such as that caused by grazing rabbits conserve mature dunes as small grasslands (Thomas 1960, ten Harkel and Van der Meulen 1996, Novo and Merino 1997). Trampling could also prevent scrub encroachment of coastal habitats (Goldsmith and others 1970, Andersen 1995) and retain the young sand dune successional stages.

Trampling can be studied in two ways, from a conservation viewpoint or as management tool, but before drawing any conclusions, its effects on the habitat must be better understood. This paper describes the results of an experiment conducted on a site that is heavily frequented in summer: the state-owned dune at Quiberon (Brittany, France). The purpose of the research is to study the response to trampling of three plant communities representing the different dune landscape units: mobile dune, semifixed dune, and fixed dune.

KEY WORDS: Sand dune; Resilience; Resistance; Trampling; Vegetation

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Materials and Methods

The state-owned sand dune at Quiberon in the south of Brittany, France (47°30′N, 3°10′W) consists of a long range of dunes extending from Gâvres to Quiberon (Guilcher and Hallégouët 1991). Recognized for its great diversity of flora (Lahondère and Bioret 1997), the dune has been the subject of a European project (LIFE) and forms part of the Natura 2000 network (Romao 1997).

Three vegetation communities are included in the study. The mobile dune or yellow dune is an open tall grassland dominated by *Ammophila arenaria* corresponding to the phytosociological association *Euphorbio-Ammophiletum R. TX. 1945* (Géhu 1994). It develops on the foredune where the dominant factor is sand mobility. When the relief decreases inland, the semifixed dune also called a transition dune replaces this grouping. It is an open and short grassland belonging to the *Festuco-Galietum* Géhu 1964 group (Géhu 1994). More inland, the fixed dune or grey dune colonizes the flat part of the landscape. It is a close and short grassland very rich in species corresponding to the *Roso-Ephedretum* (Kühnholtz-Lordat 1923, Vander Berghen 1958, Géhu 1994).

The experimental protocol was based on that of Cole and Bayfield (1993) and adapted to our study area. For each community, five simulated foot paths 5 m long and 50 cm wide, were delineated in an homogeneous area. Mobile dunes are characterized by their relief and a structure that changes from the beach toward the rear dune. To minimize any effect of slope, foot paths were chosen parallel to the coastline along the top of a dune ridge. For the other communities, foot paths were chosen perpendicular to the coast line. Five trampling treatments were conducted on each of the five foot paths. Control areas were selected in each zone to be used as a baseline for comparing the effects of trampling. The intensity range of trampling treatments varied, depending on the communities because their immediate responses were very different. The highest number of passages was first determined so as to cause more than 50% reduction of the vegetation cover. Then, intermediate values were assigned to the other foot paths. Intensity of trampling varied from 0, 50, 150, 500 to 1500 passages for the mobile dune, from 25, 50, 75 to 125 passages for the semifixed dune, and from 250, 500, 750 to 1000 passages for the fixed dune. The foot paths were trampled on a single date in June 1998.

The vegetation was monitored using permanent lines (Daget and Poissonet 1971, Forgeard and Touffet 1980). Twenty permanent points are spaced 5 cm apart in five contiguous 1-m-long permanent lines, in the middle of each foot path. Each plant species in contact with each of the permanent points was recorded so as to estimate their frequency. The first measurement was made immediately before trampling to determine the initial state of the vegetation. Plants do not die immediately after trampling, so Cole and Bayfield (1993) suggested that the effects of trampling should be measured several weeks later. The second measurements were therefore made two weeks after the disturbance. This timing is well adapted to herbaceous vegetation, which changes very quickly at this season but is insufficient for the moss-lichen stratum, which was therefore excluded from our observations. The final measurement was made one year after trampling to determine the extent that the plant cover had regenerated.

The results were expressed as the relative frequency (*RF*) compared to the control by using the equation of Cole and Bayfield (1993):

$$RF\,(\%) = \frac{\text{Frequency at time } t}{\text{Initial frequency}} \times cf \times 100$$

where cf is the initial frequency in the control divided by the frequency at time t in the control.

As advocated Cole and Bayfield (1993), relative frequency is based on the sum of the frequency of all species. Relative frequency is more informative than just a frequency of total vegetation as it integrates a possible superposition of the vegetation layers. Relative frequencies were compared by the Kruskal-Wallis test (Scherrer 1984) in order to test the statistical effect of an increasing intensity of trampling. This nonparametric test was chosen because the data did not fit a normal distribution.

To determine the response of plant communities to trampling, two indices were chosen: resistance (Liddle 1975)— the ability of a community to not change after a disturbance—and resilience (Cole and Bayfield 1993)—the ability to regenerate after a disturbance. Each of the graphs plotting the relative frequency against the trampling intensity were fitted to a polynomial regression. Analyses of variance (Sokal and Rohlf 1981) were used to compare calculated data with observations.

The indices of resistance and resilience of the plant communities were calculated from the polynomial regression curves. The resistance index of Liddle (1975) is read on the after-trampling curve. It is the trampling intensity leading to a 50% reduction in the relative frequency of the vegetation. The resilience index is calculated, according to the definition of Cole and Bayfield (1993), with the help of the

Table 1. Initial floristic description of the three communities[a]

	Species *RF*		
	Mobile dune	Semifixed dune	Fixed dune
Ammophila arenaria	96.8 (1.4)		
Elymus farctus	4.2 (2.0)		
Atriplex hastata	0.2 (0.2)		
Crithmum maritimum	0.2 (0.2)		
Calystegia soldanella	0.8 (0.4)	0.6 (0.3)	
Vulpia membranacea	1.2 (1.2)	3.8 (0.9)	
Festuca rubra ssp. *arenaria*	8.2 (3.2)	2.6 (1.1)	0.4 (0.3)
Galium arenarium	5.6 (2.1)	0.4 (0.3)	1.2 (0.5)
Sedum acre		28.8 (3.0)	2.6 (1.0)
Mibora minima		9.8 (1.6)	3.4 (0.9)
Plantago coronopus		4.4 (1.5)	
Plantago lanceolata		2.6 (1.1)	0.6 (0.3)
Leontodon taraxacoides		1.6 (0.5)	0.2 (0.2)
Carex arenaria		1.6 (1.2)	
Herniaria ciliolata		1.6 (1.1)	
Geranium molle		1 (0.5)	
Ononis repens		0.2 (0.2)	
Rosa pimpinellifolia			85 (2.9)
Ephedra distachya			68.6 (7.0)
Homalothecium lutescens			41.8 (7.8)
Cladonia sp.			40.4 (8.1)
Tortula ruralis ssp. *ruraliformis*		2 (0.7)	9.2 (3.9)
Erodium cicutarium		5.2 (1.4)	16.2 (6.8)
Cerastium diffusum			5.8 (1.4)
Arenaria serpyllifolia			4.6 (1.7)
Euphorbia portlandica			2.2 (0.6)
Desmazeria marina			3.6 (1.0)
Linaria arenaria			1.8 (0.8)
Scleranthus annuus		0.2 (0.2)	1.2 (0.7)
Agrostis capillaris			0.8 (0.4)
Helichrysum stoechas			0.8 (0.5)
Eryngium campestre		0.2 (0.2)	0.6 (0.6)
Phleum arenarium			0.4 (0.3)
Asparagus officinalis			0.4 (0.4)
Bromus hordeaceus			0.2 (0.2)
Medicago littoralis			0.2 (0.2)
Torilis nodosa			0.2 (0.2)
Cynodon dactylon			0.2 (0.2)
Sum of all species *RF*	117.2 (3.9)	70.6 (5.5)	292.6 (16.9)
Species richness	2.32 (0.2)	5.6 (0.3)	5.84 (0.3)

[a]Means (and standard errors) correspond to all footpaths' permanent lines before trampling.

1-year-after trampling curve. It is the percent of change in relative frequency that occurs during 1 year following a 50% reduction in frequency caused by trampling.

Resistance (number of passages) : Intensity leading to $RF1 = 50\%$

$$\text{Resilience } (\%) = \frac{[RF2 \text{ (at the intensity of Resistance)} - 50]}{50} \times 100$$

where *RF1* is the relative frequency 2 weeks after trampling and *RF2* is the relative frequency 1 year after trampling.

Results

The initial vegetation composition of the three communities in all foot paths is given in Table 1. The species compositions of the mobile dune and fixed dune are quite different, while semifixed dune integrates many species existing in one of the other two

Table 2. Effect of trampling on relative frequency[a]

	Mobile dune		Semifixed dune		Fixed dune	
	T + 15 days	T + 1 year	T + 15 days	T + 1 year	T + 15 days	T + 1 year
H	16.26	11.05	12.00	12.16	13.37	10.46
P	<0.005	<0.05	<0.05	<0.05	<0.01	<0.05

[a]T: trampling; H: statistic of the Kruskal-Wallis test.

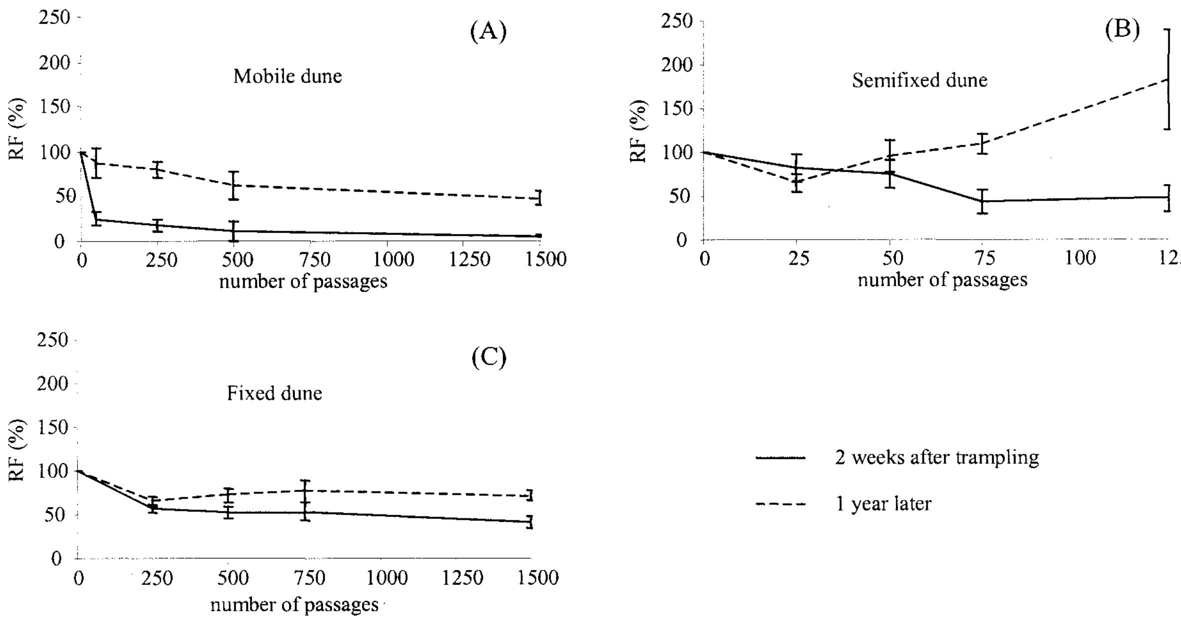

Figure 1. Relative frequency (*RF*) of the vegetation of the mobile dune (**A**), the semifixed dune (**B**), and the fixed dune (**C**) 2 weeks after trampling and 1 year later.

communities. *Ammophila arenaria* dominate the mobile dune community with a mean soil cover of 96.8%, while the frequency of other species are <10%. In the semifixed dune community, all species have low cover values except *Sedum acre* at 28.8%. The fixed dune community is codominated by four species: two woody plants, *Rosa pimpinellifolia* (85%) and *Ephedra distachya* (68.6%); a moss, *Homalothecium lutescens* (41.8%); and a lichen, *Cladonia* sp. (40.4%). Species richness increases from the mobile dune to the semifixed dune and to the fixed dune communities. The sum of the species frequency distinguishes the semifixed dune with a low value from the mobile dune and then the fixed dune with the highest value, 292.6% which reveals the important vegetation density.

In the three communities, trampling has a significant effect on the relative frequency of the vegetation 2 weeks after trampling as well as 1 year later ($P < 0.05$) (Table 2). The relative frequencies of all the vegetation of the mobile dune in relation to trampling intensity, 2 weeks and 1 year after trampling are compared in Figure 1A. The total relative frequency of the vegetation two weeks after the disturbance fell to 25.2% after just 50 passages, but as trampling increased, the relative frequency decreased only slightly from 17% at 250 passages to 5% at 1500 passages. One year after the disturbance, the relative frequency had returned to high values, but recovery was greatest in places where trampling was the least.

The results of the effect of trampling on the semifixed dune are shown in Figure 1B. The total relative frequency of the vegetation shortly after the trampling decreased slightly more at higher trampling intensities. One year later, on the 25-passages trail, the relative frequency decreased, but it increased on trails with more passages, reaching 181.5% on the trail with 125 passages.

The effects of trampling on the total relative frequency of the fixed dune are shown in Figure 1C. Two weeks after the trampling, the relative frequency fell to

Table 3. Resistance and resilience calculated from regression models[a]

Community	Date	Model	r^2	P	Resistance	Resilience
Mobile dune	T + 15 days	$66.9731 + 0.181365x - 9.37.10^{-5}x^2$	0.542	0.0002	95.7	
	T + 1 year	$96.856 + 0.0843392x - 3.42.10^{-5}x^2$	0.444	0.0016		78.2
Semifixed dune	T + 15 days	$102.288 + 0.943138x - 3.88.10^{-3}x^2$	0.396	0.0039	85.1	
	T + 1 year	$92.0719 + 0.646688x - 1.10.10^{-2}x^2$	0.355	0.0081		133.6
Fixed dune	T + 15 days	$92.0107 + 0.0959693x - 4.19.10^{-5}x^2$	0.583	0.000	585.1	
	T + 1 year	$91.4864 + 0.0516813x - 2.63.10^{-5}x^2$	0.135	0.0784		40.54

[a]The closeness-of-fit of the regressions was estimated by an ANOVA between the model and the experimental values.

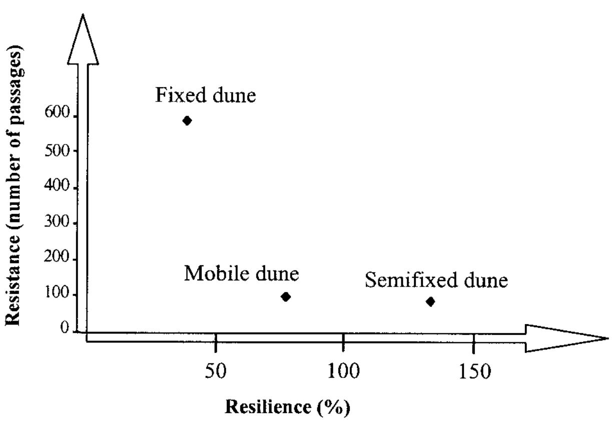

Figure 2. The relationship between resistance and resilience to trampling of three communities—a mobile dune, a semifixed dune, and a fixed dune.

almost half after 250 passages, but as the number of passages increases, the relative frequency shows no change. One year after the disturbance, the relative frequencies were higher than they were at 2 weeks, but no trail recovered to its pretrampling condition.

The curves showing variations in the relative frequency in relation to trampling intensity were modeled using polynomial regressions (Table 3). The curves were all fitted to equations of the type: $Y = a - bx + cx^2$. All the polynomials were second order and were significantly correlated with the original data ($P < 0.1$).

The polynomial equations were used to calculate the resistance (Liddle 1975) and resilience indices (Cole and Bayfield 1993) for each plant community (Table 3). The values obtained for the three communities are compared in Figure 2. The mobile dune and semifixed dune were rather similar with a very low resistance index, i.e., values of <100 passages. In contrast, the fixed dune community had a much higher resistance of nearly 600 passages. The semifixed dune, which had the lowest resistance value, also had the highest resilience value of 133.6%. The two other communities had resilience values well below 100%; the fixed dune had the lowest value followed by the mobile dune.

Discussion

The resistance and resilience clearly distinguished the different communities. The landscape units—the fixed dune, the semifixed dune, and the mobile dune—showed clearly different responses.

Our results can be compared with other published studies on the effects of trampling on dune vegetation. Among the experimental studies of the effects of trampling, Bowles and Maun (1982) compared two plant communities in the dunes of Pinery Provincial Park on the shore of Lake Huron, one an open grassland dominated by *Calamovilfa longifolia* and the other a grassland with abundant lichens of the genus *Cladonia*. These authors recorded a low resistance in the *Calamovilfa longifolia* grassland, which suffered heavy damage with only 50 passages, compared to the lichen-rich grassland, which survived the same trampling intensity despite some yellowing. Similarly, in communities more similar to those of French coasts, Liddle (1975) reported a resistance of 288 passages for a mobile dune and 344 passages for a dune grassland on the English coast. The results of our study were not entirely the same, since the resistance obtained for the mobile dune was 96 passages and 564–585 passages for the fixed dune. These studies do agree, however, in terms of the low resistance of the mobile dune and the higher resistance of the fixed dune.

Cole (1995a) established a negative correlation between resistance and resilience, we also found this in the Quiberon dune landscape. The fixed dune, with high resistance and low resilience, contrasted with the semifixed dune characterized by low resistance and higher resilience. These contrasts suggest that the various landscape units function differently, even though they are spatially close. Some of the vital attributes of these ecosystems (Aronson and others 1993, 1995) clearly differentiate them from one another and can explain their responses to disturbance. These include the species richness of plants, the total cover estimated by the total frequency, and the presence or absence of key species such *Ammophila arenaria* in the mobile dune or *Rosa pimpinellifolia* and *Ephedra distachya* in the fixed dune.

The mobile dune zone has the form of a tall and relatively dense grassland, almost exclusively dominated by *Ammophila arenaria*. This dune-building plant is the key species of the community in terms of geomorphology (Kühnoltz-Lordat 1923, Jungerius and Van der Meulen 1997) and in terms of biomass and species richness (Lemauviel 2000). The capacity of the community to resist trampling, therefore depends mainly on the physical properties of marram grass. It is a perennial Poaceae with robust erect leaves and stems and an extensive rhizome system. Erect herbs are the morphological type least resistant to trampling (Cole 1995a). The tufts of this tall grass break under the feet of walkers, so the immediate impact of the disturbance is a major destruction of the plant cover. Yorks and others (1997) studied the effects of the structure of the root system in the response of plants to trampling and did not find that rhizomes were an advantage in terms of resilience. However, the rhizomes of marram grass are very long and ramified and this property surely allows the plant to persist even if the aboveground parts are destroyed.

The semifixed dune, also called the transition dune, is covered with a short grassland similar to that of the fixed dunes, but is similar to the mobile dune in that it has a low resistance. The term semifixed dune in particular describes a very open dune community with an extremely low biomass compared to the mobile dune and the fixed dune (Lemauviel 2000). The plant community is very diverse and includes both annual and perennial species of short stature. The shallow rooted vegetation is easily uprooted at low trampling intensities. On the other hand, the species of the semifixed dune are "stress tolerant ruderals" according to Grime's (1979) definition. They are well adapted to disturbances such as being buried by sand and have a great capacity for regeneration. The initial relative frequencies were very low and resulted in high resilience values.

The fixed dune or grey dune is a relatively flat part of the landscape on a well-stabilized soil with a high organic matter content. It is a mature plant community (De Raeve 1989, Bonnot 1975). The flora is not exclusively coastal (Vanden Berghen 1964) and includes a large number of species with diverse ecological niches. The fixed dune is the richest zone of the landscape. In addition to herbaceous species, there is a dense carpet of mosses and lichens and woody species, forming a short grassland with a high cover. The flat topography and the presence of woody species give the fixed dune a resistance to mechanical disturbance such as trampling. The woody stratum, once damaged, can only regenerate slowly. Furthermore, soil movements that can result from trampling have an adverse effect on the plants of the fixed dune, which are maladapted to an unstable substrate.

Two contradictory factors seem to regulate the response of vegetation to trampling. The first effect is soil compaction, which increases the soil density, decreases porosity, and increases the soil moisture content (Liddle and Greig-Smith 1975, Blom 1976, Blom and others 1979, Maun 1993). In a dry soil, compaction can lead to greater plant growth because of both the higher moisture content and also the improved rooting (Liddle and Greig Smith 1975). Soil compaction can also favor seed germination because of the damper conditions. This is the case with some species of the genus *Plantago* (Blom 1976). In contrast, trampling adversely affects the vegetation by partially or totally destroying it. This destruction takes place in the short term, but trampling can also influence the vegetation in the long term. The destruction of perennial species will obviously have effects in subsequent years. The same is true for all those plants that are damaged before they can produce seeds.

In the mobile dune, any change to the soil would only be of short duration because of sand movements. More over, soil compaction cannot be considered as favorable on the mobile dune since the dominant species, *Ammophila arenaria,* is not only adapted to the instability but also grows faster with sand burying (Hutchings and de Kroon 1994).

The semifixed dune is characterized by a rudimentary soil that could benefit greatly from soil compaction produced by heavy trampling intensities. The increased moisture content and more stabilized soil could counterbalance the loss of plants. The semifixed dune vegetation cover benefited from the disturbance with its resilience of 134%. Soil compaction is much less of an advantage in the fixed dune. This plant community, with its high cover, has a deeper soil that retains moisture more effectively. The major destruction of the vegetation would therefore mask any beneficial aspects of compaction.

There is a curvilinear relation between trampling and the response of the vegetation. The three plant communities studied all fitted the same model, $Y = a - bx + cx^2$, which is in agreement with the modeling of Cole (1995b), but the curves differed in their appearance. It is interesting to note that for the semifixed dune, the curve of the relative frequency, 1 year after the disturbance, increased rapidly with increasing trampling intensity. The point of inflexion of the curve could therefore be an additional indicator for describing the response of the vegetation 1 year after the trampling. For a model of the type $Y = a - bx + cx^2$, the point of inflexion occurs near to the value 0 of the derivative, i.e., $Y' = -b + 2cx$, and therefore to the value $b/2c$ of x. This index $b/2c$ would tend toward zero in classical curves such as those of the mobile dune and fixed dunes, whereas it would approach a value of 1 in communities favored by trampling, such as the semifixed dune.

Goldsmith and others (1970) found that trampling could be beneficial in coastal habitats, in the absence of grazing, since it maintained an open vegetation. Andersen (1995) also recommended a reasonable intensity of trampling for maintaining mobile dunes in a young stage. Nevertheless, trampling can be a dangerous disturbance for an environment that has already been exposed to major stress (Slatter 1978). For example, Maschinski and others (1997) found that trampling, combined with adverse weather conditions, could lead to the complete disappearance of populations of sensitive species. The state-owned dunes at Quiberon are heavily grazed by rabbits, which could explain the strong immediate impact of trampling on the various landscape units. The resistance obtained for the mobile dune and the semifixed dune were very low. It was much higher for the fixed dune. The study site is very heavily visited, especially in July and August, and tourists concentrate in strategic areas close to the car parks that serve the beach. In the long term, trampling would seem to be very harmful for the fixed dune, which has a low resilience. Trampling will affect these communities for a long time. Andersen (1995) has described the greater vulnerability of fixed dunes compared to mobile dunes. This part of the landscape is therefore the community that should be given priority protection.

The resistance and resilience indices defined by Liddle (1975) and Cole and Bayfield (1993), respectively, have been used in recent works as tools for characterizing plant communities in terms of their responses to trampling (Cole 1995a, 1995b, Toullec and others 1999, Toullec 1997, Gallet and Rozé 2001, 2002). These indices are of value for managing the opening of sensitive areas to the public. The results obtained for the mobile dune and especially for the semifixed dune suggest that tourist pressure could easily be included in site management. Nevertheless, the concept of resilience only has meaning if the disturbance is halted and management includes periods of recovery.

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