The reaction of some sand-dune plant species to experimentally imposed environmental change: a reductionist approach to stability*

R. R. Page, S. G. da Vinha & A. D. Q. Agnew
Department of Botany and Microbiology, University College of Wales, Aberystwyth, Wales, SY23 3DA, U.K.

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Abstract

Coastal dunes in western Europe have long been under grazing and recreational pressure, but the vegetative cover appears to be remarkably resilient. In a series of experiments on Ynyslas Dunes, Cardigan Bay (Wales, U.K.), trampling, protection, fertiliser, and herbicide treatments were monitored using non-destructive and destructive sampling methods. This paper discusses the behaviour of 12 important species after these treatments on three major dune habitats: *Agrostis tenuis, Ammophila arenaria, Bellis perennis, Festuca rubra, Galium verum, Leontodon taraxacoides, Ononis repens, Plantago lanceolata, Poa subcaerulea, Thymus praecox, Homalothecium lutescens, Tortula ruraliformis.*

Although stability is usually thought of as a feature of the community, a reductionist approach suggests that grasses react quickly but temporarily, dicotyledonous forbs often show slower reaction times, each species reacting in its own way to changes in the environment. A tentative classification of our study species is possible.

Introduction

Ynyslas Dunes (Fig. 1) are a western dune system associated with the mouth of the Dovey Estuary in Cardigan Bay, Wales. The dunes are calcareous ($CaCO_3$ content 3–5%) and have grown extensively in the last 100 years. They show a series of classical dune vegetation types (Ranwell, 1972) of strand plants, embryo dunes, mobile dunes with much open sand between *Ammophila arenaria* tussocks, semi-fixed mossy dunes with *Tortula ruralis* ssp. *ruraliformis, Homalothecium lutescens* and *Peltigera canescens/rufescens,* and fixed grey dunes where plant cover reaches 100% and *Festuca rubra* is often dominant. There is no dune heath since the dunes are too young and calcareous but some acidity does develop in the winter-flooded slacks and on the older dunes where *Rhytidiadelphus triquerus* is an indicator of such conditions.

The area is a National Nature Reserve but is not closed to the public and research was set up in 1974 with the aim of providing information helpful to the management of increasing recreation pressure on the dune system. Visitors are on foot, often using the dunes as a passageway to the open beaches, and often as an educational facility. Over 500 000 person-days were recorded in 1974–75, and it was clear that damage was being done. At the same time the rabbit population recovered from the effects of myxomatosis and grazing was increasing.

The first research objective was to separate and quantify the effects of human trampling and rabbit grazing by means of exclosures and experimental treatments. The second was to investigate the effects of the management tools of fertilisers and selective herbicides. This is not a new approach, having been extensively reported (Blom, 1977; Hyl-

* Nomenclature follows Smith (1978), for bryophytes and Clapham, Tutin & Warburg (1962), for angiosperms.

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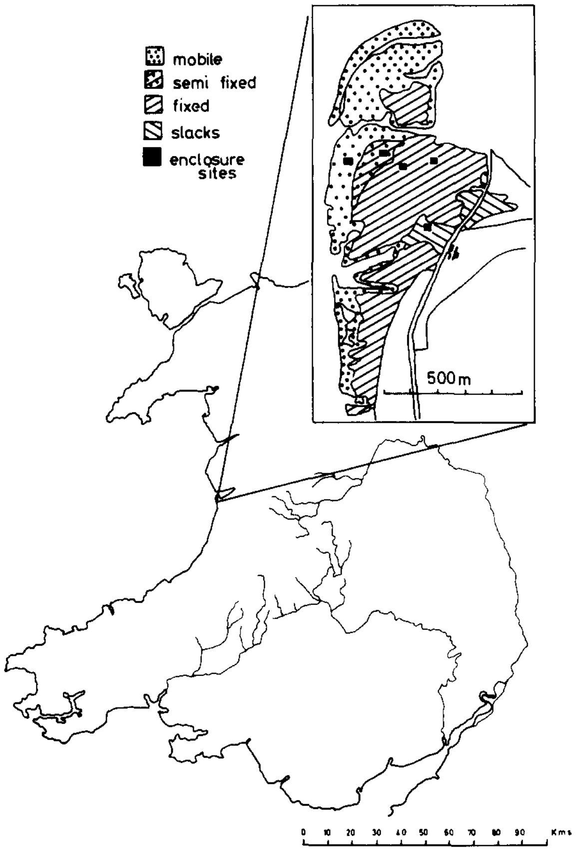

Fig. 1. The location of Ynyslas Dunes, Wales, with dune habitat types diagrammatically represented. Experimental sites are shown as black blocks.

gaard, 1981; Liddle & Greig-Smith, 1975; Liddle & Moore, 1974; Streeter, 1971 are the more recent references on this topic). Nevertheless, there is a need to repeat experiments and validate predictions for specific areas. This paper summarises some aspects of reports by Page (1980) and Da Vinha (1981) on research undertaken from 1975–80.

Methods

The study of this dune system was started with an investigation of trampling impact in four ways: 1) the comparison of soil and species differences on long-established paths and undisturbed areas, 2) experimental increase of the trampling on existing paths, 3) the experimental trampling of undisturbed areas, and 4) the protection of paths from further trampling. For these four series of investigations human passage was monitored using pressure sensitive counters in paths, as well as trip pins (Bayfield, 1971) and direct observation, while plant species occurrence was estimated as cover percentage in small permanent quadrats, never larger than 30 × 30 cm. Path trampling was measured in units of person per metre transect across the path. For example, 30 people using the central 25 cm cross section of a path are said to be 120 people m ^{1}. In this way various problems of standardisation were overcome. Paths were monitored for 40 summer days in the study of established paths and all year for the experiment on increased trampling of paths.

For the experimentally increased use of established paths trampling (in soft soled walking shoes, exerting some 150 g m cm ^{2}) was applied at multiples of current recreational use of the paths. The experiments lasted one year starting in the summer of 1974, with vegetation cover being estimated at the start and finish and soils analysed upon completion.

Exclosures of nearly 20 m^2 area were constructed in 1973, half inside rabbit-proof wire mesh and the rest only restricting human access. Cover estimation in small quadrats was again used to monitor the effect of protection. These areas were afterwards (April 1977) used to follow the reaction of species to release from competition (by a single application of selective weedkillers) combined with fertiliser treatments. Here the standing crop was harvested from random quadrats of 15 × 15 cm. The subdivision of such fragmentary material into species contributions only proved possible for the more abundant species, and this part of the record is incomplete.

In field experiments natural population fluctuations may easily override treatment effects. In these studies control areas were designated and experimental results related to concurrent changes in the controls. Clearly, this assumes that the latter are due either to the current weather (for instance 1975 and 1976 had dry summers), or to the continuation of general vegetation change in the area of the experiment. Although open to criticism, we feel that this approach is better than using a starting population as the only control value against which to measure change.

Soils were analysed by taking replicated cylindrical cores of 4.7 cm diameter and 5 cm depth. Combustion and oven drying were used to measure organic matter and soil moisture content respectively, and dry bulk density by displacement with acetone (Gupta, 1933). Using these data percentage saturation of pore space was also calculated. All cores were taken after a period of heavy rain followed by twelve dry hours in which state they should be near field capacity (Warkentin, 1971).

Species performance

Great quantities of data were gathered during the six years of the investigation. Two species, *Ononis repens* and *Galium verum,* are taken as examples because data on these two are relatively complete and are reported on in detail.

Ononis repens

General distribution

The mean % pore space, organic matter and moisture levels at which this species occurs are in the middle of the range of species reported on (Fig. 2), reflecting its widespread distribution. On untrampled soils, although common, its percentage cover is negatively correlated with soil moisture when all fixed and semi-fixed sites are included in the analysis ($r = -0.62$, Table 1) and with a greater correlation coefficient ($r = -0.82$) when fixed dune sites are analysed separately. Now on paths there is more *Ononis* on the drier semi-fixed dunes, even though path soils are moister than untrampled soils, and there is no correlation between *Ononis* cover and soil moisture on paths. However, it is only on the fixed dunes that there is a negative relationship between trampling and soil moisture, and the most trampled semi-fixed dune paths are used by fewer people than the most trampled fixed dune paths. Since *Ononis repens* is apparently unable to resist high levels of trampling (see below), its cover is low on the driest fixed-dune soils and high on the inherently dry semi-fixed dunes.

Experimental changes in trampling and grazing pressure

There are a number of suggestions, arising from field experiments, that competititve effects are important in determining cover of this species. For example, in Figure 3 is shown *Ononis* cover after trampling was imposed on 2 undisturbed sites over one year. In the absence of any treatment, cover changed to 156% and 77% of starting (1974) values for semi-fixed and fixed dunes respectively. 1974 had 29% more days with over 2 mm of rain than 1973, and the increase in cover of *Ononis* probably reflects its better performance during moist weather in the open vegetation of the semi-fixed dune.

Thus, on two fixed dune paths monitored during the same year, soils were as dry as in the dry semi-fixed dune site used for the trampling but grasses (mainly *Festuca rubra* and *Ammophila arenaria*) were co-dominant with *Ononis repens* which declined significantly during the year.

These observations and experiments suggest that

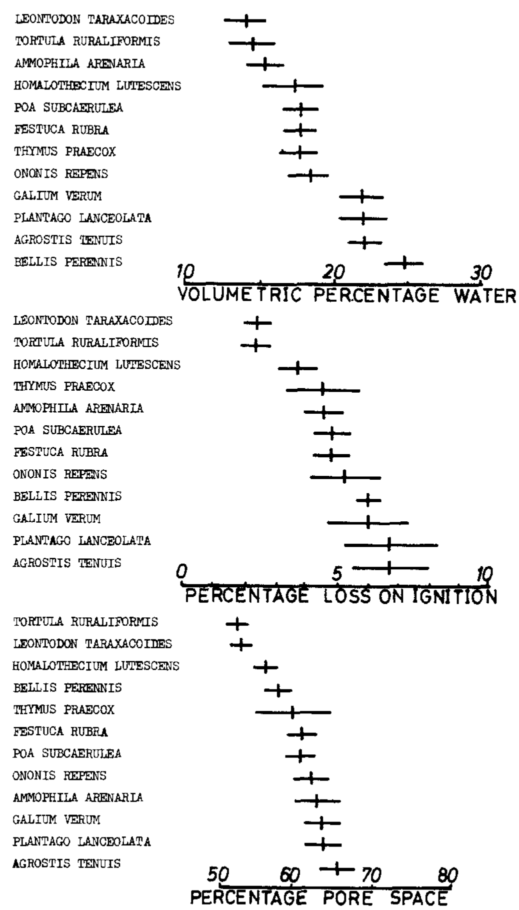

Fig. 2. Ranked species occurrence along ranges of the various soil factors which are associated with trampling, from 40 monitored sites which do not all correspond with experimental areas used in Figures 3 and 4. the mean value and one standard deviation either side of it is represented.

Table 1. Significant species correlations in random quadrats on and off paths with soil factors. LOI, loss on ignition; PS, percentage pore space; MFS, percentage moisture at field capacity; NS, no significant correlation; +, correlation positive; -, correlation negative.

	Untrampled soils	Path soils
Agrostis tenuis	+: LOI, PS, MFS	+: LOI, MFS
Ammophila arenaria	+: LOI, PS	NS
Bellis perennis	NS	NS
Festuca rubra	+: LOI, PS, MFS	NS
Galium verum	NS	+: LOI, PS, MFS
Leontodon taraxacoides	NS	NS
Ononis repens	-: MFS	NS
Plantago lanceolata	NS	+: LOI, PS, MFS
Poa subcaerulea	+: PS	+: LOI, PS, MFS
Thymus praecox	-: LOI, PS	NS
Trifolium repens	NS	+: LOI, MFS
Tortula ruraliformis	-: LOI, MFS	-: LOI, MFS

competition is related to moisture supply in determining cover of *Ononis repens*, but the summer of 1975 was particularly dry after April and the trampling experiments were terminated earlier than the exclosure experiments, thus making prediction difficult. Table 2 shows changes in *Ononis* cover during 1974/1975 in an exclosure on a fixed dune area previously little used by the public. *Ononis* fared worst in the control, increased in the rabbit-proof part and in the part simply protected from human trampling was intermediate in its response. Relative to the control here, there was no significant change in total cover of all species or grasses taken alone. However, cover of some species such as *Festuca rubra* whose mean cover in the exclosure at the start of the experiment was 30.9% increased relative to the control in the rabbit-grazed but not in the rabbit-proof parts, whilst others such as *Agrostis tenuis*, *Ammophila arenaria* and *Holcus lanatus* (whose total mean cover in the exclosures at the start of the experiments was 6.1%) declined in both exclosures, but only significantly in the rabbit-proof treatment. Soil moisture content and compaction levels were slightly, but significantly, lower in the rabbit-proof than the rabbit-grazed treatment and control soils. Broadly speaking then, the changes in cover of *Ononis repens* could be explained by assuming that trampling was so important that release from its suppressive effect allowed *Ononis* to compete successfully with grasses, but the greater resistance to trampling on the fixed dunes (Fig. 3) may relate to reduced competition from grasses combined with the more equable microenvironment and soil conditions.

When trampling was applied at a range of frequencies, but the same intensity (150 passages m^{-1} $year^{-1}$), the least damage was caused on both the fixed and semi-fixed dunes by spreading the trampling over one year at weakly rates that were a percentage of actual use made of a path by the public (Fig. 3). On the fixed dunes there was no

Table 2. Differences in percentage cover after 2 years of protection from trampling and grazing or trampling alone, in 3 sites. Control is an area which continued to receive use. Asterisk marks differences from control at 5% or better.

	Fixed dune high-use site			Fixed dune low-use site			Trampled slack site		
	Control	Trampling prevented	Grazing & trampling prevented	Control	Trampling prevented	Grazing & trampling prevented	Control	Trampling prevented	Grazing & trampling prevented
Agrostis tenuis	+3.0	-5.0*	-1.0*	+4.5	+1.0	-1.0*			
Ammophila arenaria				+1.5	+0.5	-2.5			
Poa subcaerulea	+1.5	-0.5	+1.5	-4.5	11.0	-1.5			
Festuca rubra	-7.5	-2.5	-6.0	-32.0	-15.0*	-25.0			
Bellis perennis							-2.0	-2.0	-4.0*
Galium verum	+4.5	+7.5	+5.0	-12.0	-15.0	-1.5			
Leontodon taraxacoides							+2.0	-11.0*	+3.0
Ononis repens				12.5	-6.5*	+12.0*			
Plantago lanceolata	15.5	-5.5	-8.5*						
Thymus praecox	+4.0	+17.5	-2.0	+7.5	+2.0	-2.0			

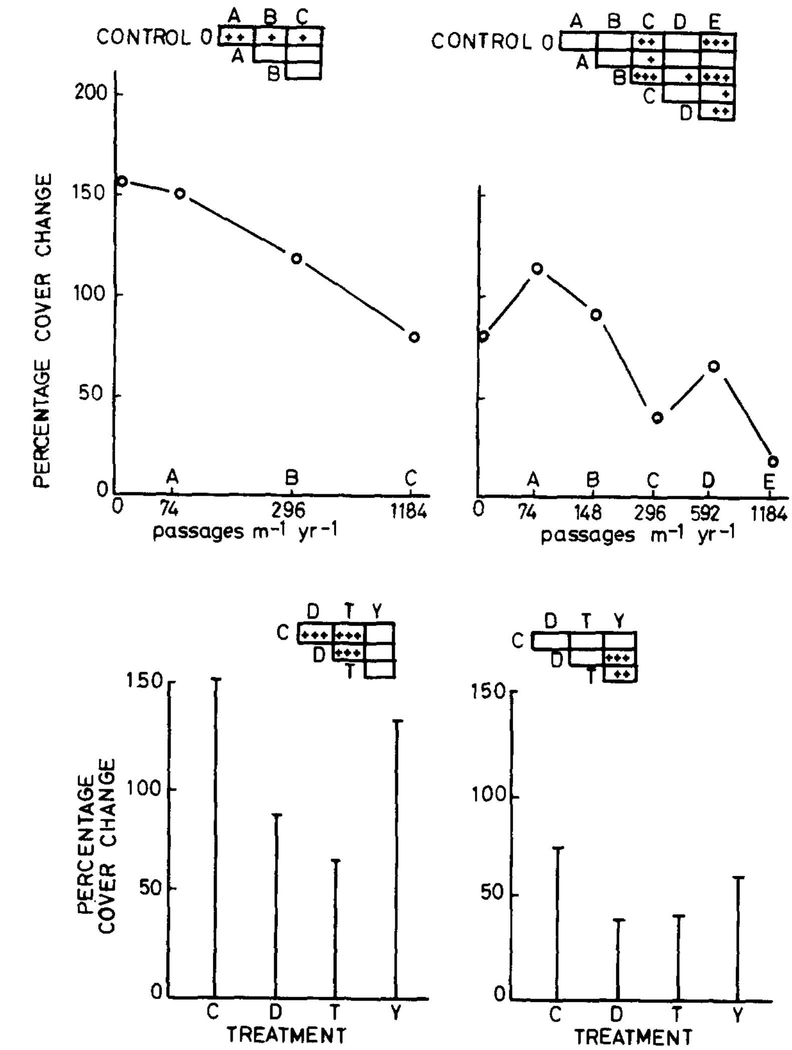

Fig. 3. Cover changes expressed as percentage of the starting value in *Ononis repens* populations after trampling treatments in previously undisturbed sites. Above are shown the effect of trampling increases on (left) a semi-fixed and (right) a fixed dune site. Below are shown the effects of different frequencies of application of trampling equivalent to 150 passages m^{-1} year^{-1}, as: C no trampling control; D, all in one day; T, all in one week; Y, distributed throughout the year. Triangular matrices give significance of t tests between means (+, $0.5 > p > 0.1$; ++, $0.1 > p > 0.01$; +++, $p < 0.01$) because heterogeneity of the populations precluded the use of variance analysis.

significant difference in relative cover from the control.

Application of the trampling over ten weeks or all in one day resulted in some reduction in relative cover in comparison with the control on both sites, but this was not significant in the fixed dunes. On the semi-fixed dunes the 'ten-week' treatment was the most damaging. It must also be repeated that the summer of 1974 in which the experiment started was particularly humid and 1975 included a period of drought. Under more average weather conditions results may have been different. When all the trampling was applied on one day the contemporary soil moisture condition was also probably very important. However, it was possible to find a relationship between the changes in *Ononis* in these experiments and changes in measured soil factors, of which compaction was the only one to be affected by the experiments on the fixed dunes. Cover of *Ononis repens* was not correlated with percentage pore space on paths or untrampled soils. The lack of any change in moisture levels was unexpected because a significant correlation between compaction and moisture levels was found in both long established paths and untrampled soils. The results, therefore, suggested that not all soil factors are in equilibrium with trampling pressure after one years' trampling.

Field manipulation of nutrients and competition

Disturbance resulted in considerably more change in the semi-fixed site (mossy dunes) than in the fixed dune site (Table 3), as would be expected, and this was reflected in the behaviour of *Ononis*. On both sites fertiliser addition combined with selective dicotyledonous removal resulted after two years in enhanced populations of *Ononis* (which reinstated itself very quickly from rhizomes). Only on the semi-fixed dunes was there a significant change in this species when monocotyledons were removed but an excessive variance in the fixed dune site may mask a real effect here. In both sites dicot removal alone resulted in apparently permanent damage to *Ononis* populations. Willis & Yemm (1961) found that *Ononis repens* was eradicated from turf transplants in the greenhouse (to which either complete nutrients, N + P + K or nitrate only were added) by the dense growth of *Festuca rubra*, but we have not confirmed this in the field. Here, fertiliser treatment alone had little effect but there was a chance absence of *Ononis* under this treatment in the semi-fixed dune site.

Table 3. Ononis repens above ground dry weight mean $g \cdot m^{-2}$ after treatment in April 1977 as follows: -M, monocotyledon selection herbicide and -M + F, with NPK fertiliser; -D, dicotyledon herbicide and -D + F, with NPK fertiliser; F, NPK fertiliser alone; C, control. Asterisks mark significances better than 5%. NP, species not present in this treatment.

A. Grey dunes, untrampled

Treatments	June 1977	August 1977	June 1978	F ratio
-M	18.4	23.5	45.3	1.3
-M + F	26.2	54.7	76.1	3.6
-D	11.3	17.4	8.0	0.6
-D + F	7.3	40.4	53.7	5.7*
F	68.4	73.7	92.5	0.7
C	13.6	50.9	47.3	4.0*
F ratio	4.7*	2.1	5.5*	

B. Semi-fixed dunes, previously trampled

Treatments	June 1977	August 1977	June 1978	F ratio
-M	13.1	11.7	88.2	4.1
-M + F	7.7	NP	17.2	2.6
-D	NP	1.0	5.8	0.8
-D + F	46.6	38.0	147.1	8.4*
F	NP	NP	NP	NP
C	66.4	60.4	106.2	1.3
F ratio	4.9*	6.3*	14.9*	

Summary of Ononis repens *performance*

Ononis repens is a conspicuous plant, easily observed and of wide distribution in Western Europe. There is much information and yet the picture of its ecology and behaviour in the face of a changing environment remains rather confused. From our analyses we can say that populations fluctuate widely, probably controlled by seasonal weather variables, and a rather complex interaction between soil moisture, trampling and competition. But the species is an opportunistic one, capable of rapid exploitation of temporarily favourable sites. Competition seems to play a key role in switching the species to occupy resources, as is indicated by its increase under protection from trampling in one site and when protected from competition with other dicotyledons after herbicide treatment. Again, grazing should be considered as an interactive effect.

Galium verum

General distribution

This species is confined to the fixed dunes. The significant correlations between percentage cover of this species and soil moisture, measured volumetrically, ($r = 0.58$) organic matter ($r = 0.61$) and pore space ($r = 0.50$) when all path sites, both on the fixed and semi-fixed dunes are included in the analysis is therefore to be expected (Table 1). There was, however, no significant correlation between percentage cover and any measured soil factor when fixed dune paths were analysed separately. *Galium verum* was present at too low a percentage cover on untrampled fixed dune sites to allow regression analysis to be undertaken.

Experimental trampling change

Galium verum is present on the most highly

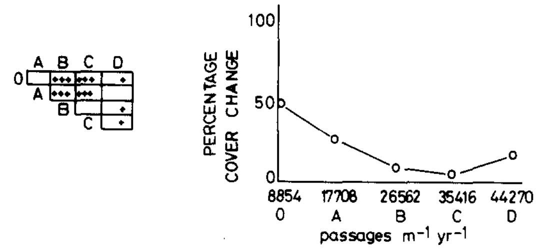

Fig. 4. Cover changes expressed as percentages of starting values in *Galium verum* after increasing the trampling of a previously used path. Significances shown as in Figure 3.

trampled path recorded on the dunes, used by 8 854 people m^{-1} $year^{-1}$, and although the mean percentage cover was only 1.7%, only three other dicotyledonous species had a greater cover. On this path there was an apparently steady decline in relative cover with experimentally increased trampling until a 300% in use was applied (Fig. 4).

Apart from a significantly higher moisture level in the experimental area suffering a 300% increase in trampling, which was probably not related to the treatment, there were no significant differences between measured soil parameters on the trampled area and the control, and the effect of increased trampling on the species in this experiment is most likely a direct one.

The difficulty of dealing with data from control sites is seen in the changes in *Galium verum* on control areas adjacent to enclosures (Table 2). On a moderately trampled fixed dune site percentage cover remained statistically unchanged between 1973 and 1975 whilst it declined over this period on a lightly trampled site. The difference in changes in percentage cover on controls is also seen in an experiment in which levels of trampling on paths is increased. On the heavily used path (Fig. 4) cover of *Galium verum* declined significantly over the experimental year, but remained statistically unchanged on a moderately trampled path in an experiment not reported here.

Relative to changes on the control, there was an increase in cover of *Galium verum* on a previously little trampled enclosure site (68% grass), only when rabbits as well as humans were barred access (Table 2), but on a previously more trampled site (20% grass), cessation of trampling and rabbit grazing had no effect relative to changes on the control.

Given the occurrence of *Galium verum* in relation to soil factors, it is probable that the relative increase (or rather failure to decline) on the previously little trampled site is related directly to cessation of grazing, and the difference between the changes on the two enclosure sites relates to competition from grasses.

Table 4. Galium verum above ground phytomass dry weight in g · m^{-2} in a fixed dune enclosure after 4 years of protection from trampling. Treatments as in Table 2. Below is shown ranges of values within which there are no significant differences at 5% or better. Asterisks mark significance at 5% or better.

Treatments	June 1977	August 1977	June 1978	F ratio
-M	4.4	15.6	15.3	2.1
-M + F	21.7	89.2	62.8	10.4*
-D	4.9	10.6	9.8	0.9
-D + F	4.1	21.8	21.5	4.5
F	20.4	27.5	5.6	5.6*
C	14.2	21.1	21.0	1.0
F ratio	4.1*	10.1*	12.9*	

June 1977	-M + F	F	C	-D	-M	-D + F
August 1977	-M + F	F	-D + F	C	-M	-D
June 1978	-M + F	-D + F	C	-M	-D	F

Field manipulation of nutrients and competition

Galium was present only in one site in sufficient quantities for analysis of these manipulations. This is an area of heavily trampled and grazed fixed-dune vegetation which resembled a close cropped lawn in 1973 when enclosed. Considerable phytomass had accumulated by 1977 when treatments were applied to a totally protected section, although it was still more uniform and less tussocked than undamaged fixed-dune vegetation. Table 4 shows that it is only the fertilised treatment in which monocotyledons had been killed which showed enhanced growth of *G. verum*, but there is little sign of a return to normal level after 18 months.

Summary of Galium verum *performance*

There is much less evidence here than in the case of *Ononis repens*. This species is particularly associated with paths on the fixed dunes, and is resistant to trampling. It reacts very positively indeed when monocotyledons are removed, so that we suspect it is sensitive to competition with grasses as its morphology would suggest. Its performance fluctuated from year to year in the control of some experiments, yet in the perturbed fixed-dune site it was remarkably stable and recovery in the latter site was rather slow.

Discussion

The accounts of the two species' reaction to environmental change illustrate the complexity of the data base from which we work, and the difficulty of interpretation. A detailed survey of the reactions of every species would not only take a lot of space but would obscure an overview of the situation. For this reason, Table 5 has been prepared to display the overall features of the species' behaviour. Not all of the data base for this survey table has been figured in this paper, and reference must be made to Page (1980) and Da Vinha (1981) for the original analyses.

The semi-fixed funes, having a lower cover of plants, lower soil organic matter and drier soil, are conventionally considered to be less stable than the fixed dune areas. Here species should be opportunistic, capable of fast reaction to change and fast recovery from disturbance. Table 5 does not confirm this supposition.

While *Homalothecium lutescens* and *Tortula ruraliformis* are semi-fixed dune moss species which are associated with paths on the fixed dunes, there is no large group of species which is distributed in this way, and, apart from a short list of winter ephemerals, it is difficult to suggest others, except for *Leontodon taraxacoides* and *Plantago lanceolata*, where evidence is less clear. This merely confirms that paths, although developed through disturbance of fixed dune vegetation, are not comparable with a successional stage.

The fast recovery of *Festuca rubra* is of interest. This is a dominant species of fixed dunes. Willis (1963) has documented the same sort of reaction to increased NPK as we have here, but in this case the fertiliser inputs were sustained and the fast reversion to lower production was not observed. Our pulsed treatments allow us to distinguish between grasses and most dicotyledons in their rates of reversion to original biomass. Some dicotyledonous species are stress tolerant in the sense of Grime (1979) *(Ononis, Galium, Thymus)* and their slow recovery from perturbation is no surprise, but the instability of their resident populations is unexpected in this respect as is their response to the removal of grasses, taken to be competitors. We may attempt to categorise the species reported upon here as follows.

A. Those which have constant cover resistant to change and which reinstate quickly after release from stress. The grasses are examples of this type.

B. Those having cover varying from year to year with fast reaction to environmental change and, paradoxically, slow equilibration to the environment thereafter. The latter feature is possibly a matter of slow migration rates. *Ononis, Galium* and *Thymus* exemplify these.

C. Those with a particular advantage in certain types of environmental perturbation which overrides other characteristics. Here perhaps the remainder of our species belong: *Bellis, Leontodon, Homalothecium* and *Tortula*.

Finally, we turn to the community concept and stability. Our analysis so far has been of individual species, a reductionist approach. Competition for space must be taken into account in explanations of a species' behaviour following experimental treatment, as we have tried to show for *Ononis repens*, but competition and species' response is the link between species and the community. Is the behav-

Table 5. A summary of some species' reactions to environmental perturbation in Ynyslas Dunes, Wales. F is fixed, and SF is semi-fixed dune types. Habitat preferences are noted adjacent to each species name, the upper line referring to whether it occurs on or off paths, or neutral, while soil preferences are given as LO, MID, HI, being low medium and high values of P, LOI, M, being pore space, loss on ignition, moisture. N.A. = not applicable. N.D. = no data available.

	Habitat		Natural cover fluctuation		Trampling resistance		Effect of trampling release		Effect of NPK treatment		Effect of competitor removal		Recovery speed	
	F	SF	F	SF	F	SF	F	SF	F	SF	F	SF	F	SF
Agrostis tenuis	on path HI:P, LOI, M	none	stable		resistant to 300% increase		decline	N.A.						
Ammophila arenaria	off path MID:P, LOI, HI:M		stable	stable	declines in all treatments		decline	increase	stable	stable	stable	stable	stable	stable
Poa subcaerulea	off path MID:P, LOI, M	off path	stable	stable		stable to 200% increase	stable		N.D.		N.D.		N.D.	
Festuca rubra	off path MID:P, LOI, M	off path	stable unstable	off path on path	stable	to 200% increase pulse decreases	stable	stable	increase		stable		fast	
Bellis perennis	on path MID:P, HI:LOI, M	none	unstable	N.A.	stable	N.A.	decline (slack) & grazing	N.A. effect	stable	N.A.	increase (slack)	N.A.	slow	N.A.
Galium verum	on path HI:P, LOI, M	none	unstable	N.A.	slight decline	N.A.	stable & grazing	N.A. effect	stable	N.A.	increase	N.A.	slow	N.A.
Leontodon taraxacoides	on path LO:P, LOI, M	off path	stable	stable	decline (slack)		increase	increase	increase (slack)	N.D.	increase (slack)	N.D.	fast (slack)	N.D.
Ononis repens	neutral MID:P, LOI, M	neutral	unstable		decline after threshold	decline no treshold	increase & grazing effect	increase	increase	N.D.	probable interaction with NPK	N.D.	slow	N.D.
Plantago lanceolata	on HI:P, LOI, M	off	unstable		steep decline		increase		stable		increase (slack)		slow (slack)	
Thymus praecox	on MID:P, LOI, M	neutral	unstable			resistant to medium levels	decline& grazing effect	increase	increase	increase	increase	increase	slow	slow
Homalothecium lutescens	on LO:P, LOI, M	off	unstable		steep decline	pulse increases cover	N.D.	stable	N.D.		N.D.		N.D.	
Tortula ruraliformis	on LO:P, LOI, M	neutral	stable	unless long trampled	steep decline	pulse increases cover	N.D.	increase	N.D.	increase	N.D.	stable	N.D.	unknown

Table 6. Variance ratio between dry weights in $g \cdot m^{2}$ under treatments as itemised in Table 3 for various categories of species. Significances of 5% or better are given by variance ratios greater than 2.62.

	Mobile dune		Semi-fixed dune 4 year enclosed path		Fixed dune untrampled		Fixed dune 4 year enclosed path		Slack	
June	'77	'78	'77	'78	'77	'78	'77	'78	'77	'78
Total lower plants	-	-	1.5	3.1	-	-	4.0	3.6	-	-
Total dicots	1.9	2.1	5.3	43.6	10.8	7.1	5.0	15.8	17.1	18.9
Total monocots	3.2	2.4	3.8	1.5	48.1	4.3	6.6	2.7	11.4	2.9
Total green	4.4	4.5	3.7	9.5	35.8	1.3	1.9	7.4	6.7	8.8
Litter	1.8	5.2	1.1	1.5	2.5	10.7	1.9	5.3	8.7	1.6
Total	3.4	5.0	1.8	3.5	6.6	11.3	1.3	1.9	4.4	7.2

iour of the community as a whole simply the sum of its parts, so that the species themselves are the units for which predictions can be made? Table 6 gives a summary of perturbation effects on five habitats of the dunes, and here there is evidence of overall community reactions to perturbation effects.

These variance ratios are between treatments which include a current control harvest, and show the intensity of the effect of treatments and the likely duration of these effects. The greatest effect of perturbation was found in the grey dunes, but this was almost entirely through grass growth, and there was fast recovery. Dicotyledons showed slow reaction (except on the grey dunes) and this was long maintained, while grasses showed the fastest recovery throughout. It is interesting that both path and semi-fixed dune vegetation seem to react similarly, while slacks and unfixed yellow dunes again behave in nearly the same way. These results seem much more confusing than those of Mellinger & MacNaughton (1975) after similar experimentation, and we present our data in the hope that generalisations can eventually be made about them.

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