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THE EFFECTS OF HABITAT PERTURBATION ON LEAF POPULATIONS OF AMMOPHILA ARENARIA (L.) LINK[1]

A. H. L. HUISKES[2]

School of Plant Biology, University College of North Wales, Bangor, Gwynedd LL57 2UW, U.K.

SUMMARY

The effects of various perturbations on leaf populations of *Ammophila arenaria* in various stages of a sand dune sere were studied over a period of almost two years. Fertilizer application markedly increased both the density and flux of leaves in young slack and old slack populations, where associated species were absent or rare; there was no change in population size or flux in more closed vegetation where a number of associated species were present.

Sand accretion temporarily increased the flux in but not the density of the leaf populations. It is suggested that the decline in density of *Ammophila* in stabilizing dune seres is caused by the monopolization of nutrients by more shallowly rooting species.

1. INTRODUCTION

In a previous paper (Huiskes & Harper 1979) it was shown that the leaf was a convenient basic growth module to study the population biology of clonal plants. The results found by looking at leaf populations are also representative for populations of *Ammophila* plants. In a study of *Ammophila* on a coastal dune system, it was shown that the density of live leaves per unit area decreased with increasing fixation of the dunes, while the population flux remained largely unaltered. The density of leaves as well as the birth and death rates showed a strong seasonal rhytm. It was suggested that as the dune system becomes fixed, interference from other species is responsible for the decrease in population density of *Ammophila.*

The shortage of mineral nutrients is thought to place severe limits on the biomass production of dune vegetation (Willis & Yemm 1961). In fixed areas of the dunes bearing closed vegetation, water may also be limiting (Willis et al. 1959).

The present study was designed to determine the effects on natural populations of *Ammophila* of a series of perturbations:

1. Removal of associated species;

[1] Communication nr. 186 of the Delta Institute for Hydrobiological Research, Yerseke, The Netherlands.

[2] Present address: Delta Institute for Hydrobiological Research, Vierstraat 28, 4401 EA Yerseke, The Netherlands.

2. Controlled accretion of sand;
3. Addition of nutrients (NPK) to the soil;
4. Addition of nutrients (NK) to *Ammophila* only, as a foliar spray.

2. MATERIALS AND METHODS

Experimental and control plots were marked out along two transects across the dune system of Newborough Warren National Nature Reserve, Isle of Anglesey, U.K. (Nat. Grid Ref. SH 415 625). The soil conditions (*table 1*), vegetation and behaviour of *Ammophila* on these sites have been described by HUISKES (1977b) and HUISKES & HARPER (1979). The experimental areas were sited to include a mobile young wet slack (i.c. a dune valley formed by wind erosion, blown out to a depth close to the phreatic water level) (HUISKES 1977a), a second (semi-fixed) dune ridge, a fixed wet slack, a dune grassland, and an old fixed dune and an old dry slack which was not as deeply eroded as the wet slack, with a sparse vegetation. There were no plots situated on the first dune ridge, as these would attract too many visitors, which was disadvantageous for the vegetation. At each site, on each transect, there were five plots of 1 m^2, one of which was treated as a control and the remainder were treated as follows:

(I) All vegetation except *Ammophila* was removed; above-ground parts were removed completely but the underground parts were mainly left in place to avoid disturbing the roots of *Ammophila*. This weeding process was repeated approximately monthly.

(II) A layer of sand c. 5 cm deep was sprinkled over the plot. The first application of sand was made on 13 August, 1975 and further 5 cm layers were applied on 22 March, 1976 and 20 September, 1976.

Table 1. Soil characteristics of the top 20 cm of the study sites along one of the two transetcs across the dunes of Newborough Warren NNR. The data given for loss-on-ignition (measured after glowing a dried sample of 5 grams for 90 minutes at 425 °C) and moisture content (measured after drying 5 grams at 105 °C for 16 hours) are the means of two measurements on each sample; the total N-figures (measured by means of an automatic azotometer (MERZ 1968)) and the exchangeable K, Na, Ca, Fe, Mg, and P (measured by atomic absorption spectrophotometry after extraction with 1N ammonium acetate) are the means of three measurements on each sample. Each soil sample was a mixture of four cores taken from each study site.

Site	pH (water)	Loss-on-ign. % dry soil	Moist. cont. % dry soil	Total N % dry soil	K mg/100 g	Na mg/100 g	Ca mg/100 g	Fe mg/100 g	Mg mg/100 g	P mg/100 g
First dune ridge	8.8	0.28	7.46	< 0.01	1.9	3.3	156.1	0.4	2.5	< 0.5
Young wet slack	8.8	0.30	24.47	< 0.01	1.0	3.4	154.1	1.0	1.7	< 0.5
Second dune ridge	8.9	0.30	7.48	< 0.01	1.2	2.1	152.6	0.9	1.6	< 0.5
Fixed wet slack	8.5	1.10	9.01	0.03	2.6	3.7	143.4	1.2	3.8	< 0.5
Dune grassland	8.0	1.62	9.47	0.04	2.2	2.2	113.1	1.2	4.6	< 0.5
Old fixed dune	8.4	2.00	11.77	0.05	3.1	3.2	142.9	1.2	2.9	< 0.5
Old dry slack	8.8	0.71	7.54	0.01	1.5	2.3	150.9	2.1	1.9	< 0.5

(III) NPK fertilizer (12% N, 12% P, 18% K) was applied at intervals of six months at 167 g m^{-2}, representing a nitrogen application of 200 kg N ha^{-1}: a usual amount for semi arid nutrient-poor soils (Noble, pers. comm.) Each application of fertilizer was split into two doses 4–5 weeks apart to prevent fertilizer damage.

(IV) The leaves of *Ammophila* were sprayed with a solution of 100 ppm K and 200 ppm N (215 mg KNO_3 and 370 mg urea per litre) containing 0.33 ml $litre^{-1}$ of wetting agent. The leaves were sprayed until they were wet on both sides. Per plot an amount of 0.5–1 g N was sprayed on average depending on the density of *Ammophila*. Every care was taken to spray the leaves of *Ammophila* only.

The nutrient treatments were applied when the weather was judged appropriate. A dry day was chosen for the foliar spray, but "rain expected soon" was considered better for the fertilizer application. The dates of application were 25 March, 28 April, 19 August and 12 September 1975 and 24 March, 28 April, 20 September and 21 October 1976, respectively.

In each plot five clusters of tillers of *Ammophila* were chosen at random and individual leaves were marked with paints as they emerged so that their fate could be followed. In addition to this detailed study of subsamples, the total number of live leaves in each plot was counted at each recording date (generally every 4–8 weeks).

The data for leaves of the subpopulations in the two corresponding plots of each transect were pooled for analysis to obtain a reasonable sample size. Leaves produced ("born") between two subsequent recordings were treated as one cohort (BAZZAZ & HARPER 1977). The natality of the leaf cohorts was expressed as birth rate per month, using the formula:

$$a = \frac{30}{d} N$$

whereby a is the birth rate per month
d is the time in days between two subsequent recording dates;
N is the number of leaves formed between two subsequent recordings;
a month was regarded as having 30 days for convenience.

The death rates per month of the leaves in the (pooled) subsample were calculated for each cohort by dividing the initial number of leaves per cohort by the time in days lapsed between the first recording and the time when all the leaves had died; this value was then multiplied by 30. It gives only a mean death rate of the cohort. Generally the death rate changes markedly during the life span of a cohort.

3. RESULTS

Fig. 1 shows the changes in the number of live adult leaves present in the control and experimental plots in the different field sites. Only in the young slack and the old dry slack was there a marked change in the number of leaves per plot by the

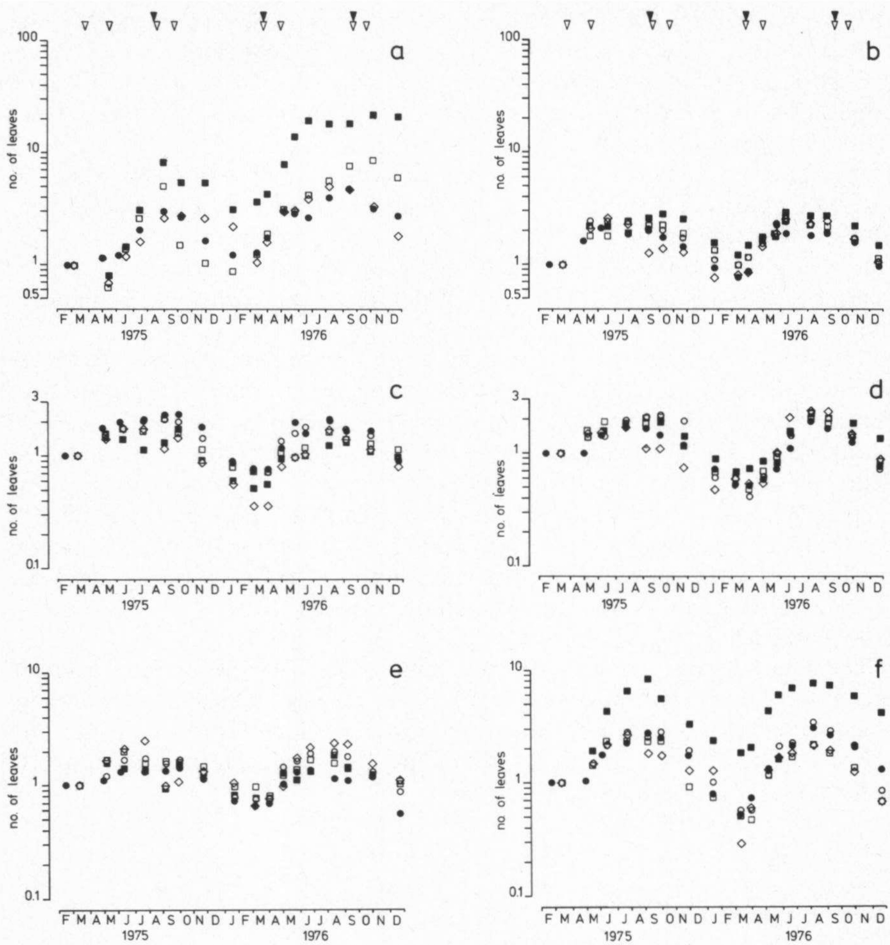

Fig. 1. The change in number of live adult leaves of *Ammophila arenaria* in two plots of 1 m^2 in various successional stages of the dunes of Newborough Warren NNR, subjected to various perturbations over almost two years.

a = young slack; b = second dune ridge; c = fixed slack; d = dune grassland; e = old fixed dune; f = old dry slack.

● = control, no treatment; ○ = upper ground parts of the associated species removed; ◇ = sand accretion of 5 cm every six months; ◆ = fertilizer applied every six months (167 g m^{-2} NPK (12–12–18) in two steps; □ = foliar spray applied twice every six months (KNO_3 + urea: 100 ppm K, 200 ppm N); ▼ = dates of the sand accretion treatment; ▽ = dates of the fertilizer and foliar spray treatments.

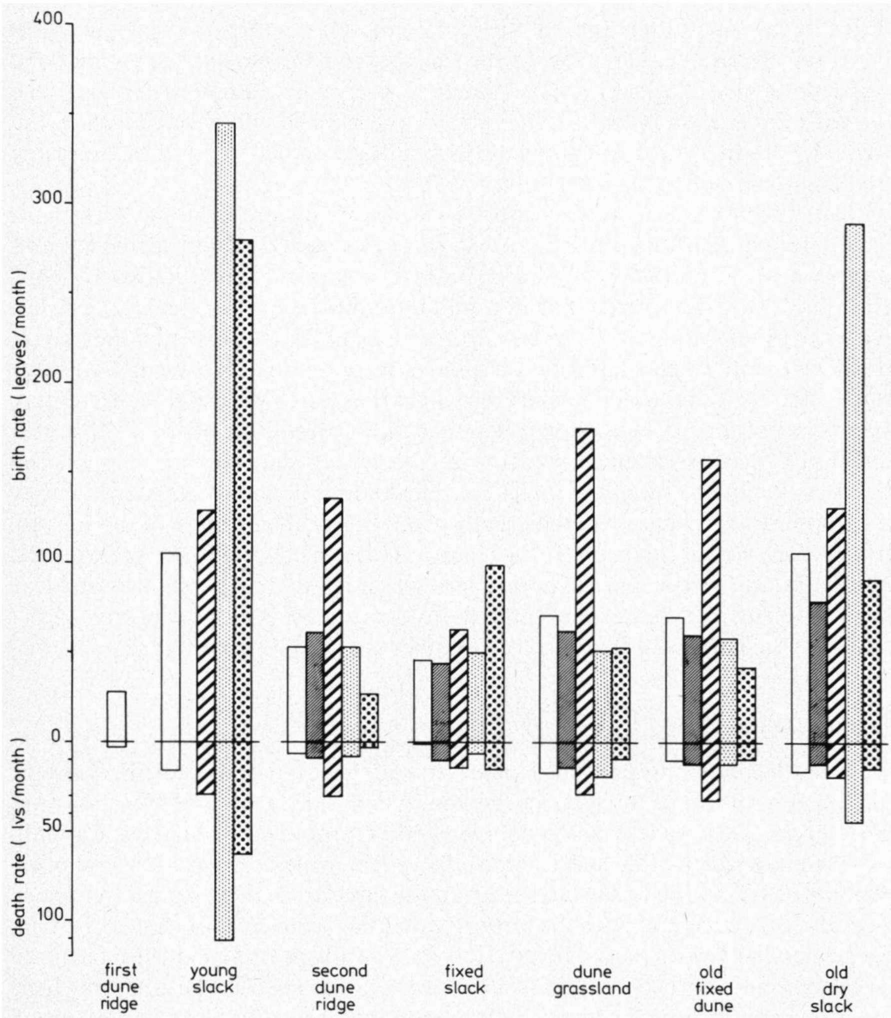

Fig. 2. The birth and death rates per month of leaf cohorts of *Ammophila arenaria* recorded in June 1976. The rates (an average of the rates in the two corrsponding plots) are recalculated for an initial standard population of 100 leaves. Open columns: control, no treatment; thinly hatched columns: upper ground parts of the associated species removed; heavily hatched columns: sand accretion of 5 cm every six months; thinly dotted columns: fertilizer applied every six months (167 g m^{-2} NPK (12–12–18) in two steps); heavily dotted columns: foliar spray applied twice every six months. As the vegetation in the young slack was a monoculture of *A. arenaria* the weeding experiment could not be carried out.

different treatments, fertilizer application to the soil (but not foliar application) increased the number of leaves. As the vegetation in the plots in the young slack was a monoculture of *Ammophila* a weeding experiment was not carried out. The seasonal fluctuation in leaf survivorship in the marked cohorts of leaves in the treated plots did not differ significantly from those studied in the untreated plots (see discussion in HUISKES & HARPER 1979).

Birth and death rates within cohorts of leaves are illustrated in *fig. 2*. Data for June were chosen for illustration because in this period of the year birth and death rates are high and differences between treatments emerge clearly; conclusions drawn, however, are valid for all the cohorts of all the recording dates. An analysis of variance of the birth rates and death rates of leaf cohorts was performed and, when significant differences were found, a Newman-Keuls test (DE JONGE 1964) was used to detect the values that were significantly different. A significant difference was shown between the birth and death rates of leaves under the various treatments except in the young slack. In all sites on the transects the birth rate of the leaves was increased following sand accretion but the response to fertilizer differed greatly according to the position of the sites on the transect. Foliar applied fertilizer increased leaf birth rate in the young slack but not in other sites. Application of fertilizer directly to the soil increased leaf birth rates in the young slack and the old dry slack but not in any of the intermediate positions. Removal of the other species had no effect.

4. DISCUSSION

None of the treatments produced major changes in population size (*fig. 1*) except for the application of fertilizer in the young and old slacks. It is clear that the parts of the dune system in which *Ammophila* responded to applied nutrients were those in which other species were absent (the young slack) or few (the open debilitated vegetation of the old slack). In the same areas the fertilizer treatment gave also an increase of both the birth rate and the death rates of the leaves. This phenomenon of an increased turnover rate (flux) after a treatment with fertilizer has also been described by NOBLE (1976) for *Carex arenaria*. The areas in which applied nutrients produced marked responses in *Ammophila* were largely free of associated species. This corresponds with the findings of LUX (1964), who did fertilizer experiments in newly planted *Ammophila* stands. In contrast, in the comparatively densely vegetated areas, it were the associated species, especially those with shallower root systems (e.g. *Festuca rubra*) rather than *Ammophila*, that were observed to react more strongly than *Ammophila* to applied nutrients, This increase of *F. rubra* was also found by FREYSEN & HEERES (ADRIANI 1970). This suggests that these associated plant species may be capable of depressing the growth of *Ammophila* by pre-empting nutrients on their passage down the soil profile. A pilot experiment carried out under greenhouse conditions gave a strong support to this suggestion (HUISKES 1977b). As the leaves of *Ammophila* are heavily cuticularized and the stomata are concentrated in furrows on the adaxial side of the often tightly inrolled leaves, these features probably prevented a foliar absorption of nutrients, which is most likely the reason why the foliar applied fertilizer had no effect.

After artificial sand accretion in the field, *Ammophila* completely recovered from burial within six months in all the successional stages of the dunes; during this period the population flux of the leaves was increased but no increase in leaf density could be detected. The associated species were severely depressed by this treatment. Only *F. rubra* emerged again within six months.

The results presented in this paper may suggest that the behaviour of (leaf) populations of *Ammophila* is dependent on the amount of nutrients available to the plants. More shallowly rooting species can effectively suppress *Ammophila* as the nutrients available to the vegetation as a whole get trapped by these more superficially rooting species. The low vigour – *Ammophila* found in the sparsely vegetated old slack is not so much an indication that competition does *not* cause loss of vigour but that the soil is too nutrient-poor to maintain a dense vegetation. Most of the nutrient supply in this area has to come from what little mineralisation there is, which is a relatively slow process under dry conditions. Other possible sources like salt spray, precipitation and sand accretion play a minor role in this part of the dunes: Input by salt-spray is only important in the most seaward dune ridge (VALK 1974) and sand movement is scarce in the fixed areas of the dunes. Most of the import of minerals will come with precipitation (HASSOUNA 1962; PEGTEL 1976; HUISKES 1977b) which is assumed to be insignificant. Fertilizer application has a tremendous effect here: Not only on the population size and flux of *Ammophila* but also on other species. Sand accretion may – temporarily – increase the population *flux* and rejuvenate the population, it may also increase the opportunity to produce more new – possibly better functioning – roots (MARSHALL 1965) but there was (at least within the study period) no evidence that it affected the population *size* of *Ammophila*.

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