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THE INFLUENCE OF MINERAL NUTRIENTS ON THE GROWTH OF *AMMOPHILA ARENARIA*

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INTRODUCTION

Differences in vigour of marram grass, *Ammophila arenaria* (L.) Link, growing in different parts of sand-dune systems, are well known and have been frequently recorded (Carey & Oliver 1918; Tansley 1949; Salisbury 1952; Willis, Folkes, Hope-Simpson & Yemm 1959b; and others). Characteristically marram is vigorous in the fore dunes, especially in areas receiving abundant supplies of blown sand, but grows poorly, often ultimately degenerating to the point of dying, in the inland parts of dune systems where there is much less sand movement and where the vegetation cover may be considerable.

The chief suggestions which have been made regarding the basis of these differences in vigour involve aeration, water regime, nutrient regime, organic matter content of the sand, the presence of toxic substances and competition. The possible importance of the effects of the levels of essential mineral nutrients was explored in the investigations reported here, which were carried out in conjunction with studies of the mineral nutrient status of the dune soils of Braunton Burrows, north Devon (Willis & Yemm 1961), and of the influence of the addition of mineral nutrients to various types of vegetation on the dunes (Willis 1963).

Results bearing on the problem of the vigour of marram were obtained from two approaches. Mineral nutrients were added at various intervals to an area of pure *A. arenaria* growing on the slope of a high dune at Braunton Burrows and the effect of this treatment was assessed by measuring the marram periodically and finally cutting and weighing it. The general procedure adopted here was that described by Willis (1963). In a second approach, marram seedlings were transplanted into pots containing sand from Braunton Burrows and grown under glasshouse conditions. They were subjected to a number of mineral nutrient regimes over a period of 3 years and measurements of growth were made on a number of occasions. In this experiment not only was the effect of a range of mineral nutrient treatments studied, but also the effect of the addition of sand to the pots when the marram had been growing for about 15 months.

EXPERIMENTAL METHODS

Field experiments

Two sites at Braunton Burrows supporting *Ammophila arenaria* were studied. One of these areas was dry dune pasture with relict marram and the results of this investigation have already been reported (Willis 1963). The second site was on a rather flat part of the windward slope of a large dune; here there was appreciable sand movement and in the experimental area marram was the only vegetation, and formed a fairly uniform stand of quite well established plants.

On the high dune an extremely simple experimental lay-out of a 2×2 Latin square was adopted. The square, which was permanently marked, was of 13·5 ft (4·11 m) side, and the units were 6 × 6 ft (1·83 × 1·83 m); access strips of 1·5 ft (45·7 cm) wide were employed. Larger sized squares than used elsewhere were chosen in view of the growth form of marram, with its far-ranging rhizome and root system. Major mineral nutrients were added to two of the units of the square (one to windward and one to leeward), the other two serving as untreated controls. The marram initially was of rather low vigour, and differed little from square to square; however, the control squares were selected so as to contain the marram which appeared healthiest.

The experiment ran for 2 years (June 1959 to June 1961), and major mineral nutrients were added on six occasions (in 1959 in June and October, in 1960 in April, June and October, and in 1961 in early May). The composition of the mixture of salts used was the same as that described previously (Willis 1963). It contained (quantities in g/m²): $(NH_4)_2HPO_4$, 25·4; $(NH_4)_2SO_4$, 12·7; K_2SO_4, 25·4; $MgSO_4.7H_2O$, 50·7. No calcium was added in view of the large amounts already present in the sand nor were minor nutrients included. The crushed, thoroughly mixed salts were spread as evenly as possible on the treated areas by hand, and were incorporated into the top 0·5 cm of the sand so that loss of salts by wind action and spread to the control squares were minimized. No plants other than marram were growing in the area at the start of the experiment and there was much bare sand between the shoots.

Observations concerning the growth and vigour of the marram were made on all the occasions when salts were added, and detailed records were taken initially in June 1959, in June 1960, and when the experiment ended in June 1961. The number of plants, of tillers and of leaves was counted, and the maximum height reached by each tiller measured. In June 1961 the shoots were all cut off at ground level and their fresh weight determined; the rhizome and root systems were also examined.

Glasshouse experiment

Small plants of *A. arenaria* were collected from the beds of seedlings occurring naturally on the dunes at Braunton on 22 April 1959, care being taken to secure uniform material and to lift the young plants so that damage to the root systems was minimal. The average height of the plants was about 25 cm, and most of them, probably having germinated in the previous spring, were about a year old.

The marram was planted, at a depth of about 10 cm, in coarse, freshly blown sand from the Burrows (soil A, Willis & Yemm 1961), in drained polythene containers of top diameter 22 cm and depth 20 cm. Six young plants were transferred to each container, four (or in one instance five) containers serving as replicates for the five different mineral nutrient treatments investigated. A control series of four pots which received deionized water only was also included. The five mineral nutrient regimes were as follows: complete culture solution; complete except for nitrogen (−N); complete except for phosphorus (−P); complete except for potassium (−K); lacking nitrogen, phosphorus, and potassium (−NPK). The composition of the nutrient solutions is given in Table 1. All solutions were prepared from pure reagents and deionized water; a source of iron was added to the solutions to give approximately 0·05 g iron/10 l. (ferric versenate, or, in the case of −N and −NPK solutions, ferric citrate) and a supply of trace elements (Mn, Cu, Zn, B, Mo), as appropriate, in the form and quantities given by Hewitt (1952, p. 189).

The plants were grown in a glasshouse in normal daylight; the temperature in winter did not fall below 12° C. After the plants had been set in the containers, they were kept in the shade for 2 days to help their establishment and then were transferred to normal glasshouse conditions (25 April 1959). The cultures were usually watered in alternation with the appropriate nutrient solution and deionized water; at first about 300 ml nutrient solution and 300 ml deionized water per container per week was adequate, but at later stages, especially during the summer months, somewhat greater quantities were required, especially in those cultures where considerable growth had been made. The plants were not allowed to become desiccated, nor did appreciable leaching occur from the pots. On 27 July 1960, more sand, collected from the same site as the sand in which the marram was growing, was added to the containers to increase the level by about 5 cm (*c.* 2·2 kg dry sand). By this treatment it was hoped to obtain some indication of the importance, in influencing the growth of marram, of sand accretion such as might occur under natural conditions.

Table 1. *The composition of mineral nutrient solutions added to* Ammophila arenaria *grown under glasshouse conditions*

	Complete	−N	−P	−K	−NPK
KNO_3	2·02	–	2·02	–	–
$Ca(NO_3)_2$ anhydrous	6·56	–	6·56	6·56	–
$NaH_2PO_4.2H_2O$	2·08	2·08	–	2·08	–
$MgSO_4.7H_2O$	3·69	3·69	3·69	3·69	1·84
$CaCl_2.6H_2O$	–	8·76	–	–	4·38
KCl	–	1·49	–	–	–
NaCl	–	–	–	–	1·17
$NaNO_3$	–	–	–	1·70	–

The figures give g/10 l. of culture solution. Only the major nutrients are listed here.

Records were made of the numbers of leaves and tillers, and of the maximum height of the living leaves on 1 May 1959, 2 June 1959, 8 July 1959, 15 October 1959, 27 July 1960 and finally after a very considerable period on 12 April 1962. Samples were also taken for determination of fresh and dry weights initially and on the last four occasions listed above. Two plants per container were removed on 8 July 1959, two on 15 October 1959 and one each on 27 July 1960 and 12 April 1962. In sampling, care was taken to avoid damage to the plants remaining in the pots.

EXPERIMENTAL RESULTS

The effects on the growth of Ammophila arenaria *of the addition of mineral nutrients to dune sand under natural conditions*

When major mineral nutrients were added to sand on a dune slope at Braunton Burrows bearing a pure stand of *Ammophila arenaria* a marked improvement in its growth was observed. The most important effects of the addition of mineral nutrients were the increased density of the shoots of the marram, the taller growth and the general improvement in vegetative vigour of the plants. Initially the marram of the experimental area was of low vigour, but the plants made progressive improvement and by the end of the 2 year period were very flourishing. Nevertheless, flowering did not take place in these plants.

Some details of the changes resulting from the treatment with mineral nutrients are given in Table 2 and Fig. 1. At the start of the experiment, in June 1959, there was little difference in the numbers of plants in the four areas studied, but by June 1961 there was a

Table 2. *The effect of mineral nutrients on the growth of* Ammophila arenaria *on a dune slope*

	No. of plants	No. of tillers	Mean no. of tillers /plant	Mean max. height/plant (cm)	S.E. of mean max. height (cm)	Fresh wt of shoots (kg)
17 June 1959						
Area A	84	393	4·7	34·8	1·43	–
Area C	69	392	5·7	36·7	1·32	–
Area B	74	524	7·1	39·4	1·10	–
Area D	75	443	5·9	34·2	1·03	–
25 October 1959						
Area A	74	–	–	43·6	1·64	–
Area C	72	–	–	45·7	1·36	–
Area B	70	–	–	45·9	1·33	–
Area D	78	–	–	38·5	1·12	–
23 June 1960						
Area A	80	780	9·7	54·8	1·53	–
Area C	69	928	13·4	54·8	1·47	–
Area B	79	551	7·0	48·4	1·21	–
Area D	71	456	6·4	39·5	1·21	–
22 June 1961						
Area A	121	793	6·6	57·7	1·12	2·99
Area C	112	1297	11·6	58·7	1·54	3·55
Area B	87	545	6·3	50·5	1·17	1·48
Area D	97	556	5·7	40·5	1·14	0·67

Major mineral nutrients were added to areas A and C; areas B and D were untreated controls. Each area was 6 × 6 ft (1·83 × 1·83 m); for details see text.

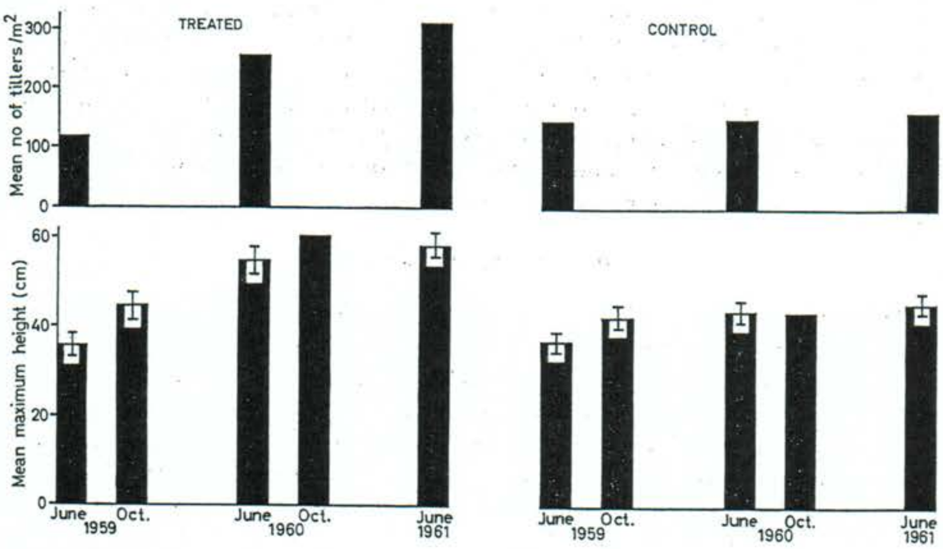

FIG. 1. The response of *Ammophila arenaria* to the addition of mineral nutrients under natural conditions. The effect of added major mineral nutrients on the density of tillers and on the height of the shoots is shown. The vertical lines indicate $\pm 2\times$ means of the standard errors of the mean maximum heights in the two treated and two control areas (further details in Table 2).

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very considerable increase in the treated squares, and also a small increase in the control areas. The changes in the numbers of tillers were much more striking, however. In the control areas the overall increase was about 14%, as compared with an increase of nearly 170% in the numbers of tillers in the areas receiving major mineral nutrients.

Some difficulties were encountered in estimating numbers of plants and of tillers; for example, where tillering took place well below the sand level so that tillers appeared at the surface of the sand clearly isolated from others they would have been scored as 'plants'. Furthermore, some fluctuations occurred as a result of the death of certain tillers (although the numbers were in no case considerable) and also of establishment of invading plants from seed. These considerations chiefly account for the small fluctuations in the numbers of plants recorded in Table 2, but in spite of these variations the substantial effects of added nutrients are clear.

Initially, in June 1959, the mean heights of the plants in areas C (treated) and D (control) were not significantly different, but the mean height of *Ammophila* in area A (treated) was significantly lower ($P = 0{\cdot}01$) than that of area B (control). After a single addition of mineral nutrients to the marram, however, the increase in height by October 1959 was such that there was now no significant difference between the mean heights of the shoots in areas A and B, and in area C the shoots were significantly ($P<0{\cdot}001$) taller than those of area D. Subsequently, on all occasions, the shoots receiving nutrients were significantly ($P<0{\cdot}001$) taller in both treated areas than in the two control areas.

When the experiment was ended in June 1961, the average fresh weight of the shoot systems in the areas receiving nutrients was just over three times as large as that of the shoots in the control areas. This difference reflects the greater shoot density, the taller plants and the wider leaves, resulting from the addition of mineral nutrients. Excavation of the root systems in the treated and control areas showed that there were pronounced effects of mineral additions on the underground parts of the marram. Whereas there was poor lateral fibrous root development in the untreated areas, a dense mat of fine roots was formed where mineral nutrients had been applied. The contrast between the sparse roots in the control areas and the massed roots binding the sand in the treated areas, especially at depths of 7·5–30 cm, was very marked (roots were more than four times as plentiful where mineral additions had been made).

A further feature of interest noted in this experiment relates to the growth of plants other than marram on the dune slope. Initially marram was the only vegetation, and apart from a few very small angiosperms (fresh weight < 5 g) in one square at the end of the experiment, marram remained the only vegetation in the control areas. However, in both squares receiving nutrients colonizing species were finally of much greater importance (fresh weights were 103 g and 43 g), the improved growth being attributable to the enhanced nutrient status of the sand. The invading species were *Anagallis arvensis*, *Cerastium atrovirens*, *Phleum arenarium*, *Sonchus asper*, *Taraxacum laevigatum* and *Viola canina*.

The effect of different mineral nutrient regimes on the growth of marram on dune sand under glasshouse conditions

Substantial differences in the growth of marram were observed when different mineral nutrient solutions were added to the dune sand. Cultures receiving complete nutrients made good growth, those receiving nutrients complete except for potassium or for phosphorus moderate growth, whereas cultures to which no nitrogen was added made little or no growth. However, even these cultures improved when dune sand was later added to the pots. No flowering occurred under any of the nutrient regimes.

The chief features of the results are shown in Fig. 2 and in Table 3. It is clear from Fig. 2 that, within a month after the addition of nutrient solutions, all of the cultures receiving solutions containing nitrogen showed considerable growth. At the time of the first addition of nutrients (1 May 1959), there were no significant differences in heights of the plants given different treatments, but by 2 June (and on all subsequent occasions) the plants receiving complete nutrients, the −K series plants and those of the −P series were significantly ($P<0{\cdot}05$) taller than the rest. No significant differences in heights were found

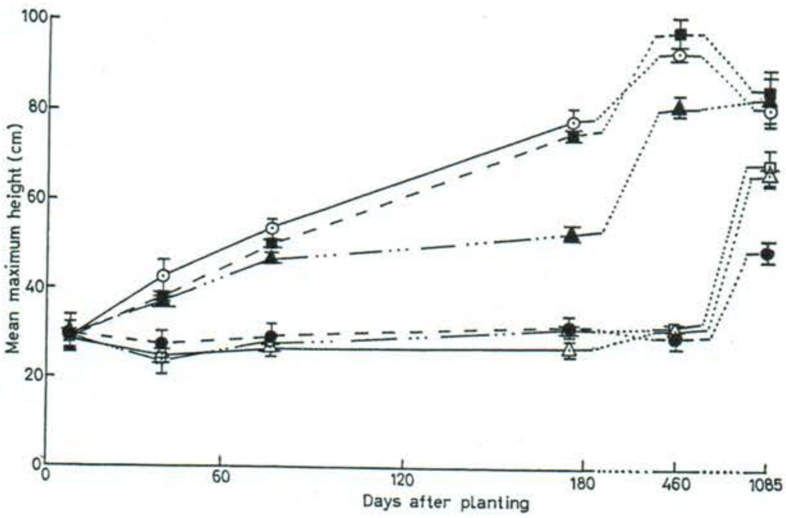

FIG. 2. The influence of added mineral nutrients on the growth of *Ammophila arenaria* in sand culture in a glasshouse. The mean maximum height per plant is shown for cultures receiving: complete nutrients, ⊙; complete except for nitrogen (−N), ●; complete except for phosphorus (−P), ▲; complete except for potassium (−K), ■; −NPK, ⊡; water only, ⚠. The vertical lines show the standard errors (±) of the mean values, and the dotted lines indicate the interrupted time scale.

on any occasion between the cultures to which complete nutrients were added and the cultures receiving nutrient solutions deficient in potassium. The heights of the plants to which culture solutions lacking phosphorus were added were significantly shorter, on the sampling occasions 15 October 1959 and 27 July 1960, than the heights of plants given complete nutrient solutions and potassium-deficient solutions. However, at the final sampling, after more sand had been added to the pots, there were no appreciable differences in height. Plants receiving water only and those of the −N and −NPK series made very little growth, and were not significantly different from one another, in respect of height, until extra sand was added to the cultures. Then all of these plants showed substantial increases in height; the marram receiving culture solution complete except for nitrogen was the shortest at the end of the experiment.

Tillering was clearly most extensive in the plants to which complete nutrients were added (Table 3), but the marram of the −K and −P series also showed a moderate amount of tillering. The differences in the degree of tillering are strongly reflected in the weights of the plants; at the end of the experiment the weight of the cultures receiving complete nutrients was significantly higher than that of all of the others, being more than twice that of the plants of the −K and of the −P series. Differences between the final weights of the −K and −P plants were not statistically significant, but the plants receiving potassium-deficient culture solution made considerably better growth during the early stages of the experiment. Obvious visual symptoms of deficiency were not seen in the leaves of these plants, although the leaf tips of the —P plants showed some die-back; the leaves were rather narrower than those of the plants receiving complete nutrients. The dry weights of the marram given water only, —N and —NPK treatments were not significantly different from one another at any stage, and were uniformly low. Tillering was slight and the leaves very narrow and pale, being yellow-green with scorched tips.

Table 3. *The effect on the growth of* Ammophila arenaria *of the addition of various mineral nutrients to sand cultures under glasshouse conditions*

	Treatment					
	Complete nutrients	−N	−P	−K	−NPK	Water only
After 76 days' growth (8 July 1959)						
No. shoots/plant	1·8	1·0	1·1	1·4	1·2	1·0
Leaf width (mm)	4·5	2·5	3·0	4·0	2·8	2·5
Fresh wt (g)/plant	3·24	1·46	1·65	3·09	0·88	1·09
Dry wt (g)/plant	1·06	0·55	0·67	1·03	0·41	0·49
After 175 days' growth (15 October 1959)						
No. shoots/plant	3·6	1·0	1·7	2·2	1·4	1·1
Leaf width (mm)	4·5	2·0	3·0	4·5	2·5	2·0
Fresh wt (g)/plant	7·87	1·37	2·32	8·46	1·21	0·91
Dry wt (g)/plant	2·97	0·57	1·02	2·59	0·52	0·41
After 461 days' growth (27 July 1960)						
No. shoots/plant	11·1	1·0	3·9	4·9	1·5	1·0
Leaf width (mm)	5·0	1·7	4·0	3·7	1·5	1·5
Fresh wt (g)/plant	28·21	1·52	8·48	20·42	1·50	0·89
Dry wt (g)/plant	11·64	0·78	3·77	8·91	0·74	0·44
After 1085 days' growth (12 April 1962)						
No. shoots/plant	8·8	1·0	3·3	3·0	1·0	1·7
Leaf width (mm)	3·8	2·5	3·5	3·5	2·5	2·0
Fresh wt (g)/plant	46·08	4·35	21·63	16·61	4·10	4·29
Dry wt (g)/plant	22·99	1·98	10·01	9·13	1·88	1·98

All of the results given are average figures. When transferred to sand culture (23 April 1959), each plant had only a single shoot and the mean dry weight per plant was 0·45 g.

It is of interest that the rate of increase in dry weight was enhanced in plants of the water only, —P, —N, and —NPK series after fresh sand had been added to the cultures. In particular, the plants receiving only water made very little growth indeed until the extra sand was added. The favourable effect of the added sand on growth of the marram was also indicated by the significant increases in heights of the plants of the water only, —N and —NPK series, as already indicated.

Examination of the root systems revealed several differences resulting from the nutrient regimes. In general the plants receiving complete nutrients and the potassium-deficient solution had plentiful intertwined roots of healthy appearance. Some of the roots were branched, thin (decorticated) and fibrous; others were little branched and thicker, with a substantial cortex. In contrast, the root systems of the other cultures were usually short and sparse. However, it was noticeable that some new roots had been initiated after the extra sand had been added to the cultures, and that these new roots were mostly formed above the existing roots, near the base of the freshly buried shoots.

DISCUSSION

That the growth of *Ammophila arenaria* is markedly affected under both natural and glasshouse conditions by the nutrient status of the sand is clearly indicated by the results of the present studies. The major limitation is of nitrogen supply, as is shown by the investigations of the growth of marram in pot cultures to which various additions of mineral nutrients were made.

The sand of Braunton Burrows is known to be of low nitrogen content (Willis, Folkes, Hope-Simpson & Yemm 1959a; Willis & Yemm 1961), and the limiting effect of these low levels is evident from the poor growth of marram in all of the pot cultures to which mineral nutrients lacking nitrogen were added (and in cultures receiving water only). Very low nitrogen contents have been found in the sand of the fore dunes of Ynyslas, Cardiganshire (Hassouna 1962; Hassouna & Wareing 1964), and nitrogen deficiency in this sand was shown to be a major factor limiting growth of marram and other sand-dune species in pot cultures. From these and other results there can be little doubt that for vigorous growth *A. arenaria* requires a substantial nitrogen supply. Hassouna & Wareing (1964) provide some evidence to suggest that where marram is luxuriant on fore dunes nitrogen-fixing bacteria, such as *Azotobacter*, are abundant in the immediate vicinity of the roots and play an important role in connection with the nitrogen nutrition of marram.

The rather low levels of phosphorus and potassium in the sand of Braunton Burrows have been shown to restrict growth of a number of plants (Willis & Yemm 1961; Willis 1963) and from the culture experiments reported here it is seen that marram also is limited by the low amounts of these nutrients in the sand when the nitrogen deficiency is made good. The content of phosphorus and also of potassium is not adequate to give optimal growth; on the other hand, the limitation of these nutrients in culture is not so severe as to produce clear visual deficiency symptoms in *Ammophila arenaria*.

Preliminary analyses of the shoot systems of marram harvested at the end of the glasshouse experiment show very low levels of potassium (1·95 mg K/g dry weight) in the tissues of the potassium-deficient cultures. These values are substantially smaller than the moderately low content (*c.* 5 mg K/g dry weight) in young plants taken directly from the dunes, and are in striking contrast with the levels in plants receiving complete nutrients or complete except for phosphorus (19·5 and 25·6 mg K/g dry weight respectively) where there appears to be 'luxury consumption' of potassium. It may be noted that the potassium levels in the tissues of the young marram from its natural habitat are lower than those at which a variety of plants exhibit deficiency symptoms (Goodall & Gregory 1947). On the other hand, phosphate levels in young plants from the dunes are not especially low (*c.* 1·0 mg P/g dry weight shoot), and plants in culture (where mycorrhizal development is probably less extensive) do not accumulate large quantities of phosphorus in the shoot systems even though phosphate is in plentiful supply at the roots. In particular, the level of phosphate in the shoots of the plants of the potassium-deficient cultures at the end of the glasshouse experiment (*c.* 0·6 mg P/g dry weight shoot) was well below that of young plants from the dunes, and suggests an important influence of potassium on the uptake of phosphorus. This result invites comparison with observations on micro-organisms in which, as discussed by Jennings (1963), potassium is known to stimulate phosphate uptake, and absorption over an extended period can continue only if potassium also is absorbed. Of interest in this connection is that increased absorption of phosphate in the presence of potassium and calcium has been demonstrated in seedlings of barley and pea by Mattson, Eriksson, Vahtras & Williams (1949). It is hoped that further light on such interaction of nutrients will be provided when more extensive analyses on marram have been completed.

The enhanced growth of *Ammophila* on the dunes shown when complete nutrients were added appears to be largely attributable to the increased level of nitrogen, although doubtless there was also some effect of the augmented phosphorus and potassium supply. The areas to which nutrient additions were made on the dunes were fairly large because of the growth form of the plant, as already mentioned; it is of note that although the addition of nutrients was spread over a period of 2 years, and rhizomes and roots extended from the treated areas to shoots some considerable distance away, the improvement in growth was fairly sharply confined to the squares receiving the nutrients. Nevertheless, some increase in height of the shoots in the adjacent control (untreated) areas was observed during the course of the experiment, which may be partly attributable to mineral nutrients being absorbed by roots in the treated squares and translocated out of these areas to a limited extent.

Improvement in vigour of the marram to which complete nutrients were added on the dune slopes was reflected in increased numbers and heights of the shoots and greatly enhanced dry weights, although no flowering occurred. It was earlier reported (Willis 1963) that the addition of complete nutrients to dry dune pasture with relict marram at Braunton Burrows led to greater numbers of shoots of greater average weight than those in control areas. The experiments on the relict marram site and the dune slope were similar with respect to the mineral nutrients added and the period over which the additions were made, but the response by the marram differed to an appreciable extent. A greater improvement in growth was found in the marram of the dune slopes. Here the final average increases (as compared with the controls) in respect of number, maximum height and dry weights of shoots were 90%, 28% and 206% respectively, as compared with increases of 35%, 22% and 54% in the relict marram site. Two considerations likely to be of significance with regard to these differences are the contrast in rates of sand accretion at the two sites and the lack of associated plants on the dune slope as compared with the fairly complete cover of varied species in the relict marram area.

The capacity of marram to form new roots differs considerably in areas of very little sand accretion and in sites where appreciable sanding occurs. It was found that on the dune slopes a dense mat of roots was formed as a result of the addition of complete nutrients, so that the absorbing capacity of the marram was probably substantially increased. Initiation of new roots tends to be localized near the sand surface, and to occur especially in freshly buried bases of the shoots. This was demonstrated in the pot cultures to which sand was added after the plants had been growing for some time. The cultures showed increased rates of growth after the sand addition, and it is of note that the increases were greater than expected merely from the addition of the small quantity of nutrients present in the sand.

The importance of the failure of adventitious root development has been stressed by Marshall (1963) in relation to the decline in vigour of *Corynephorus canescens* on stable dunes. In this vertically growing perennial grass, the site of new root production is positioned higher up the axis with time, and on stable dunes these sites are above the sand surface and no new adventitious roots are formed. Marshall (1963) suggests that the decrease in vigour of *Ammophila arenaria* in the absence of sand accretion may result from a low rate of replacement of old by new roots because of competition for water by other plants in the surface sand layers, the site of adventitious root production. In areas where accretion occurs and competition is absent, the additional volume of moist sand may allow ready development of new roots. The evidence provided by the present study is essentially in keeping with these suggestions. Maintained vigorous growth in natural habitats doubtless depends on the continuous development of the root system, with the production of new roots exploiting a large volume of sand; the sand is frequently of low nutrient status, but the exploitation of extensive accretions may in part compensate for this. In contrast, under cultural conditions good growth is made possible by supply of relatively high levels of nutrients, particularly nitrogen, to a small volume of sand. On the dunes themselves, although the addition of mineral nutrients leads to increased branching of existing roots of the marram, there is little evidence that many new roots are initiated on old rhizomes which usually already bear the normal complement of two roots per node (Waterman 1919). On sites where sand accretion is considerable, and the shoots become progressively buried, there is a continued capacity for new root production, whereas in a stable area this is not so; it seems likely that marram declines in vigour in these sites at least partly because of failure of the root system.

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SUMMARY

1. The effect of the levels of major mineral nutrients on the growth of marram grass, *Ammophila arenaria*, in dune sand was investigated. Additions of mineral nutrients were made on a dune slope bearing a pure stand of marram and on dune pasture with relict marram at Braunton Burrows, north Devon. Small uniform plants were also collected from these dunes and grown in a glasshouse in sand to which various solutions of mineral nutrients were added.

2. When major nutrients were supplied to marram growing on the dunes the plants showed a considerable increase in vigour, with more frequent tillering, increased heights and substantially greater weights. The response to the augmented supply of nutrients was larger in the marram on the dune slopes, where rates of sand accretion were considerable, than on the dune pasture.

3. In sand culture in a glasshouse *A. arenaria* grew vigorously when complete nutrients were added, but very little when no nitrogen was supplied. When nutrients complete except for phosphorus and potassium were added, marram made moderate but limited growth in the sand from Braunton Burrows. Addition of sand to the pots after the plants had been established for some time enhanced the growth in all cultures.

4. Marram, although often found in sand of low nutrient status, requires substantial levels of nitrogen, phosphorus and potassium for good growth. At Braunton Burrows the chief limitation is of nitrogen. The success of marram in areas receiving much blown sand is discussed; here the influence of the accreting sand on root growth appears to be important.

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