

ESTABLISHMENT OF *AMMOPHILA ARENARIA* (MARRAM GRASS) FROM CULMS, SEEDS AND RHIZOMES

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SUMMARY

(1) A study was made of three different methods of establishing *Ammophila arenaria*: planting bundles of culms (the traditional method), sowing seeds, and disc-harrowing rhizomes. The effects of applying slow-release fertilizer were also examined.

(2) A preliminary experiment examined the relative effects of straw, carboxy methyl cellulose, compost, reed, and a mixture of crop species in stabilising the sand. Only straw was effective.

(3) Sowing seeds at 200, 400, and 600 m⁻² and rhizomes (fragments 15 cm long, each with at least two buds) at 20, 40, and 60 pieces m⁻², showed that higher rates resulted in higher numbers of seedlings and primary shoots. However, after one growing season, production of biomass and tillers was only increased by fertilization.

(4) Although the recovery in above-ground plant parts of N and P was fairly low, slow-release NPK fertilizer (80-20-20 kg ha⁻¹) increased biomass significantly. Fertilizing rhizomes with 160-40-40 kg NPK ha⁻¹ produced significantly more dry matter than with 80-20-20 kg NPK ha⁻¹, but this had no effect on sown or planted *A. arenaria*.

(5) Rhizomes produced more tillers and biomass than bundles of culms and seedlings when fertilizer was applied. Without fertilizer, culms gave most biomass production, but seedling growth was very poor.

(6) A germination experiment in the laboratory showed that a high rate and percentage of germination was obtained at fluctuating temperatures and by supplying light. At fluctuating low temperatures, stratification increased germination of seeds. At fluctuating high temperatures, seeds germinated well and stratification gave no improvement.

INTRODUCTION

Ammophila arenaria (L.) Link (Marram grass) is a species that dominates the foredunes of north-western Europe, the Mediterranean, Australia, and the west coast of the U.S.A. (Knutson 1978; Huiskes 1979). Because of its natural ability to colonize and stabilize sand dunes, *A. arenaria* is often used for erosion control. Traditionally, bundles of *A. arenaria* with 3-6 culms (usually collected from vigorous stands in foredunes) are planted in 15-20 cm deep holes in a grid, 30-60 cm apart. New plants then emerge from basal stem buds. The tradition of planting *Ammophila* is very old, and is applied in many parts of the world (Brown & Hafenrichter 1948a, b, c; Augustine *et al.* 1964; Lux 1969; Atkinson 1971; Adriani & Terwindt 1974; Knutson 1978; Hobbs, Gimmingham & Band 1983; Ranwell & Boar 1986). As clearly as 1423, *A. arenaria* was planted on the island of Voorne in the Netherlands to protect the dunes from wind erosion (Pilon 1988).

At present, large parts of the foredunes in the Netherlands have to be raised and subsequently planted with *A. arenaria* to stabilize the sand-surface. These works are being carried out under the so-called Delta Act, which was enacted after flooding of the south-western Netherlands in 1953. The traditional planting method is very expensive, as it is

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done by hand. The method could be improved by mechanically harvesting and planting (Atkinson 1971; Knutson 1978) and by planting the stems horizontally (Hobbs, Gimingham & Band 1983). In large-scale dune reconstructions, however, there is often a shortage of plant material.

As seeds and rhizomes can also be used for propagation, more planting material could be collected from natural stands of *Ammophila* than is obtained when only the traditional planting method is used. Sowing *A. arenaria* seeds has been done with reasonable success (Adriani & Terwindt 1974; Tsurieil 1974; Mitchell 1974; Barr & McKenzie 1976). On very exposed sites however, establishment failure often occurs owing to wind erosion (Mitchell 1974). Temporary sand stabilization after sowing should be done, e.g. by spraying emulsions of bitumen (Tsurieil 1974) or disc-harrowing in straw (Mitchell 1974; Adriani & Terwindt 1974).

Underground vertical stems—rhizomes according to Wareing (1964) and Berg (1972)—have never been used for establishing *A. arenaria*. A recently developed method consists of disc-harrowing *A. arenaria* rhizomes (Van der Putten & Van Gulik 1987). This simulates the natural colonization of the beach by rhizome pieces with axillary buds, which can regenerate by forming primary shoots after fragmentation by waves, dispersal, and sand burial (Gemmell, Greig-Smith & Gimingham 1953; Maun 1984). Natural regeneration from *A. arenaria* rhizomes has not been studied, but similar studies have been done on *A. breviligulata* (Maun 1984) and *Elymus farctus* (Harris & Davy 1986). Although the regeneration percentage of buds is highest on single-bud fragments, most primary shoots that actually emerge originate from fragments with 2–5 buds (Maun 1984; Harris & Davy 1986).

In this paper, the traditional planting method (1) is compared with the application of seeds (2) and rhizomes (3) of *A. arenaria*. Because the latter two methods require effective stabilization of the sand surface (Van der Putten & Van Gulik 1987), a preliminary field trial (experiment 1) was done in which several ways of temporary sand stabilization were compared. The best method of temporarily stabilizing the sand was used in a field trial to compare the traditional planting method with sowing seeds and disc-harrowing in rhizomes, using different levels of addition of plant material and of slow-release fertilizer (experiment 2). During experiment 1, seed dormancy considerably delayed seedling emergence. In experiment 2, however, dormancy was much lower. To clarify these differences in seed behaviour, a germination experiment was done in the laboratory (experiment 3).

MATERIALS AND METHODS

Experimental area

The field experiments were done on the coastal foredune ridge of the island of Voorne, the Netherlands (51.5°N, 4.05°E). As a part of the Delta-works, this foredune had been raised with sand dredged from the sea. Vegetative material and seeds were collected from the foredune before its reconstruction was finished.

Experiment 1

In May 1984, protective cover by nurse crops and short-term sand fixation were studied in a preliminary field experiment by measuring emergence and establishment of *A. arenaria* seedlings. Plots 3 × 6 m were arranged in a Latin square design with three replicates. Seeds of *A. arenaria*, collected the previous year and stored dry at 12 °C, were

sown at a rate of 580 seeds m^{-2} (20 kg ha^{-1} ; maximum germination percentage 95%). One half of each of the plots was sown with a mixture of five nurse crops, which were supposed to emerge quickly and protect the seedlings of *A. arenaria*. The mixture (241 kg ha^{-1}) contained *Secale cereale* (70 kg ha^{-1}), *Hordeum vulgare* (70 kg ha^{-1}), *Triticum aestivum* (70 kg ha^{-1}), *Lupinus perennis* (30 kg ha^{-1}), and *Trifolium repens* (1 kg ha^{-1}). The seeds were buried by harrowing the sand.

Five methods of short-term sand stabilization were examined: (i) disc-harrowed straw (0.5 kg m^{-2}); (ii) bundles of dry seed (*Phragmites australis*) planted in a 50 × 75 cm grid; (iii) compost ('edelcompost' type, 4 kg m^{-2}), (iv) carboxy methyl cellulose (CMC, 'average viscosity' type, 4 g m^{-2}); (v) controls (no treatment). Both compost and CMC were suspended in water and sprayed on the sand surface.

In August and November 1984, and in August and September 1985, emerged seedlings were counted in a 0.5 × 1.0 m^2 patch selected at random in each plot.

Experiment 2

Experimental design

In March 1987, *A. arenaria* was established at experimental field plots of 5 × 5 m^2 (excluding a 1-m margin all around) from culms (traditional method), seeds, and rhizomes. The traditional method was carried out at one density. Seeds were sown at 200, 400 and 600 seeds m^{-2} (7.5, 15 and 22.5 kg ha^{-1} , respectively). Rhizomes were planted at 20, 40 and 60 15-cm pieces m^{-2} . Before planting culms, sowing seeds, or disc-harrowing rhizomes, a slow-release fertilizer was broadcast at three levels: 0, 80-20-20, and 160-40-40 kg NPK ha^{-1} . All treatments (combinations of planting method, density, and fertilizer level) were carried out in four replicates.

Methods of establishing *A. arenaria*.

Culms of *A. arenaria* were cut 10 cm below the soil surface from a vigorous stand. Bundles (each of thirteen culms) were planted in holes 15-cm deep in a 50 × 75 cm grid. Ninety-five per cent of the tillers had at least two apparently viable buds. Seeds of *A. arenaria* (from the same batch used in the germination experiment) were mixed with sand to improve their distribution, and sown. The sand surface was disc-harrowed superficially to bury the seeds 3-5 cm deep. Rhizomes were collected from the top 2-m soil layer in a vigorous stand of *A. arenaria*. To obtain pieces with 2-5 viable buds (Maun 1984), the rhizomes generally had to be cut into pieces approximately 15 cm long. This was done by disc-harrowing the sand surface after the rhizomes had been spread, which chopped off the rhizomes and buried them 10-15 cm deep.

Fertilization and sand stabilization

The applied 24-6-6 NPK slow-release fertilizer ('Osmocote', active for 12-14 months at a soil temperature of 21 °C) consisted of 14% N as urea, 10% N as ammonium nitrate and ammonium phosphate, 6% P_2O_5 as ammonium phosphate and calcium phosphate, and 6% K_2O as potassium sulphate. Hereafter, P and K will be used to indicate P_2O_5 and K_2O .

The fertilizer was broadcast before establishing *A. arenaria* and disc-harrowed to a depth of 10-15 cm. After applying all treatments the sand surface of all plots was 'fixed' by disc-harrowing to 5 cm depth of 0.5 kg m^{-2} of straw. Finally, the culms were planted. In some additional plots, fertilizer was applied directly in the planting holes instead of by

broadcasting; in this case two levels of NPK were supplied, 80-20-20 and 120-30-30 kg NPK ha⁻¹.

Evaluation

The experiment was recorded twice. In July 1987, numbers of emerged seedlings, primary shoots (i.e. emerged buds of the rhizomes), and tillers (from culms and rhizomes) were counted. Plant parameters were determined by a stratified random sampling method. The sampled area, or numbers of plants counted, depended on the variability within the treatment. In every plot with seedlings, five subplots of 1 m² were examined; in every plot with rhizomes, eight subplots of 0.18 m²; and twenty-five bundles were examined in every plot with planted culms. Numbers of tillers per bundle were estimated for each level of NPK by linear regression of the circumference on the numbers of tillers per bundle.

In October 1987, a strip of 3 × 1 m was cut at ground level in each plot with seedlings or rhizomes, and the total amount of fresh material was weighed. A subsample was weighed fresh and the numbers of tillers were counted before drying for 48 h at 70 °C to determine the percentage dry matter. Numbers of tillers of the bundles of culms were assessed as above and dry weight was estimated by linear regression.

Plant samples were dried at 70 °C and ground through a 1-mm mesh. After digestion of a subsample in a concentrated sulphuric acid/salicylic acid mixture with hydrogen peroxide, N and P were determined colorimetrically (indophenol-blue method and molybdenum-blue method, respectively), and K by atomic absorption.

Recovery of N, P, and K via above-ground plant parts was determined in order to assess effectiveness of the applied slow-release fertilizer. Recovery of N, P, and K was calculated from:

$$R = 100\% \times (U - Z) \times (Y - X)^{-1}$$

where R = % recovery, U the uptake of N, P, or K (g m⁻²) in a fertilized plot, Z the uptake of N, P, or K (g m⁻²) in an unfertilized plot, Y the amount of N, P, or K in the applied slow-release fertilizer (g m⁻²) X the amount of N, P, or K in the slow-release fertilizer (g m⁻²) still present after one growing season. Fertilizer grains were collected in April 1988 and digested and analysed as described for plant material.

The results were statistically analysed by analysis of variance after Cochran's test for homogeneity of variances (Sokal & Rohlf 1981). If necessary, homogeneity of variances was obtained by logarithmic or square root transformation of data.

Seed germination experiment

Spikes of *A. arenaria* were collected in July 1986, air-dried and threshed. After dry storage for 5 months at 12 °C, batches of forty caryopses ('seeds') were placed in Petri dishes on filter paper. Mean weight per seed was 3.6 mg. The effects of seed pre-treatments, temperature and illumination on germination were examined. A 10 × 3 × 2 factorial experiment was done with three replicates per treatment. Petri dishes with seeds were stored at 4 °C, either moistened with demineralized water ('stratification') or kept dry ('dry cold'), for 0, 2, 3, 5 or 7 weeks. After the period of storage, the pre-treated seeds were exposed to three night/day (16/8 h) temperature regimes: 20/20 °C, 10/20 °C, and 20/30 °C. Half the Petri dishes were wrapped in light-proof bags, and the others were exposed to light during the 8-h period of high temperatures. Apart from the germination experiment, six extra Petri dishes were each filled with forty seeds, from which palea and

lemma had been removed. In three dishes (replicates) an incision was made in the seed coat without damaging the embryo. Seeds were germinated in light/dark at 8/16 h 20/10 C.

The dry seeds were moistened immediately before the experiments started, and demineralized water was supplied every other day if necessary. To determine the percentage germination, seeds were counted and removed when the plumula became visible. Moistening and counting of all seeds was carried out in green light (Blom 1978) to protect the seeds of the 'dark' treatment from illumination (Wesson & Wareing 1969).

RESULTS

Experiment 1

Table 1 shows that very few seedlings established in 1984. A new germination flush occurred in 1985 in the plots stabilized by straw. In the plots with reed, CMC, and compost, all seedlings had disappeared by 1985. The highest emergence of nurse crops occurred in plots with sand fixation and 15-cm stubbles remained until the end of 1985. Their presence did not, however, affect the number of *Ammophila* seedlings.

Experiment 2

Sowing rate of seeds and planting density of rhizomes had a significantly positive effect on the emergence of seedlings and primary shoots in July 1987 ($P < 0.001$; Table 2). The intermediate sowing rate resulted in significantly more seedlings than the low rate, but the high sowing rate gave no further increase. Fertilization increased seedling numbers ($P < 0.05$). In July 1987, the rhizomes produced significantly more tillers when rhizome density and NPK-level were increased ($P < 0.001$; Table 2). Fertilization also increased tiller production of the bundles. There were no significant differences between broadcast and plant-hole application of NPK.

In October 1987, after one growing season, the above-ground dry matter production, the number of tillers, and the weight per tiller were no longer affected by sowing rate or

TABLE 1. Mean numbers of seedlings* of *Ammophila arenaria* in plots with and without short-term sand stabilization and protection crops

Sand fixation	Nurse crops†	Seedling numbers (m ⁻²)			
		1 August 1984	14 November 1984	1 August 1985	24 September 1985
None	+	14 (4-32)	6 (0-26)	0	0
Reed/CMC/Compost‡	-	24 (8-64)	6 (0-28)	0	0
Reed/CMC/Compost‡	+	34 (6-78)	16 (0-36)	0	0
Straw	-	58 (50-66)	16 (12-22)	114 (86-142)§	112 (78-148)§
Straw	+	32 (18-62)	8 (0-14)	158 (66-290)¶	142 (34-326)¶

* Means from three counts, with ranges in parentheses.

† A mixture of cereals (*Secale cereale*, *Hordeum vulgare*, *Triticum aestivum*), *Lupinus perennis*, and *Trifolium repens*. Presence of nurse crops is indicated with +.

‡ Because the numbers of seedlings in the treatments with reed, CMC, and compost were all low, these were averaged.

§ Slow-release NPK fertilizer (Osmocote) applied in May 1985 at § 40-10-10 kg NPK ha⁻¹ and at ¶ 120-30-30 kg NPK ha.

TABLE 2. Effects of fertilization and sowing rate or rhizome density on *Ammophila arenaria* from seeds, rhizomes and planted culms in July 1987

	Seeds		Rhizomes		Bundles of culms†	
	Emerged seedlings		Primary shoots	Tillers	Tillers	
					B	P
NPK (kg ha ⁻¹)						
0-0-0	50 a		21 a	31 a	14 a	
80-20-20	57 ab		21 a	70 b	38 ab	27 ab
120-30-30						45 c
160-40-40	67 b		25 a	77 b	49 c	
Seed/rhizome fragment density						
200/20 m ⁻²	36 a		12 a	33 a		
400/40 m ⁻²	62 b		22 b	57 b		
600/60 m ⁻²	69 b		33 c	87 c		
Factor	d.f.	F	F	F	d.f.	
NPK	2	5.14*	1.20 N.S.	38.9***	4	5.89**
Density	2	23.9***	31.4***	41.4***		
NPK × Density	4	2.63 N.S.	0.80 N.S.	1.01 N.S.		
Error (mean square)		183	42.8	0.81		138

Average numbers (m⁻²) of emerged seedlings, primary shoots, and tillers are presented as calculated over the main factors NPK and density. Figures in columns followed by the same letter were not significantly different ($P > 0.05$). *F*-values and degrees of freedom (d.f.) of emerged seedlings, and primary shoots and tillers from rhizomes were calculated from two-way analysis of variance with the factors NPK (fertilizer) and sowing rate (or rhizome density). *F*-values and degrees of freedom of tillers from bundles of culms were calculated by one-way analysis of variance with the factor NPK.

† Planted on a 50 × 75 cm grid. Fertilizer either broadcast (B) or placed in the planting holes (P). N.S., not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 3. Effects of fertilization and planting density on establishment of *Ammophila arenaria* from seeds and rhizome fragments in October 1987

Factor	d.f.	Seedlings			Rhizomes		
		Dry matter production	Tiller number	Tiller weight	Dry matter production	Tiller number	Tiller weight
		F	F	F	F	F	F
NPK	2	21.0***	20.1***	27.8***	35.1***	17.1***	9.25***
Density	2	3.16 N.S.	1.94 N.S.	2.87 N.S.	1.88 N.S.	0.55 N.S.	2.65 N.S.
NPK × Density	4	2.73 N.S.	0.80 N.S.	2.55 N.S.	0.31 N.S.	0.57 N.S.	2.92 N.S.
Error (mean square)		750	8.62	0.078	2587	14.3	0.021

F-values of dry matter production, numbers of tillers, and weight per tiller of seedlings and plants established from rhizomes were calculated by two-way analysis of variance with the factors NPK (fertilizer) and sowing rate (of rhizome density).

N.S., not significant; *** $P < 0.001$.

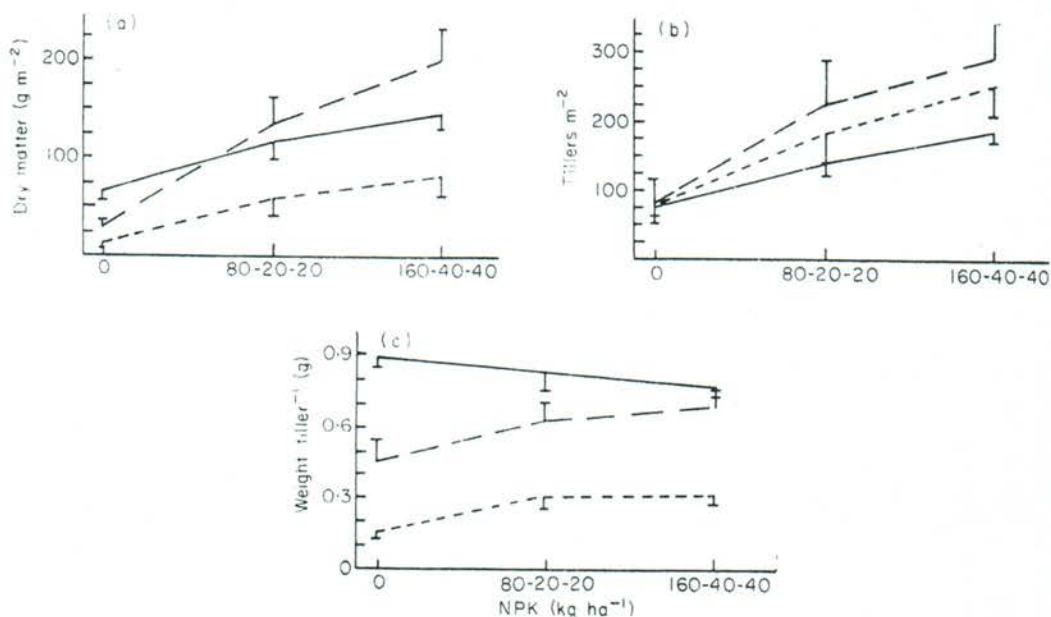


FIG. 1. Plant parameters in October 1987 after one growing season of bundles of culms (—), seedlings (---), and rhizomes (· · ·) at three levels of NPK: (a) above-ground dry matter production (g m^{-2}); (b) number of tillers (m^{-2}); (c) weight per tiller (g). Vertical bars represent 1 S.E.

density of rhizomes (Table 3). Only the application of NPK led to significant increases in these plant parameters ($P < 0.001$).

Without application of NPK, bundles of culms produced the most dry matter owing to the relatively high dry weight per tiller (Fig. 1). Mean tiller weight however, may have been overestimated because of remnants of the originally planted bundles. Since no significant differences were observed between plant-hole application and broadcast placement of NPK, data from the former are not shown. The application of 80-20-20 kg NPK ha^{-1} increased dry matter production and number of tillers in all cases, whereas weight per tiller only increased for seedlings and rhizomes. Doubling the amount of fertilizer to 160-40-40 kg ha^{-1} significantly increased dry matter production by rhizomes ($P < 0.05$), but did not significantly affect the number of tillers and weight per tiller. Tiller numbers and tiller weight responded to NPK fertilization similarly to seedlings and rhizomes. In the planted bundles, significant differences in dry matter production and number of tillers occurred only between the unfertilized stands and those supplied with 160-40-40 kg NPK ha^{-1} . Weight per tiller was not affected significantly by fertilizing. Rhizomes tended to produce most tillers, and bundles of culms the least. Seedlings produced the smallest tillers.

No urea-N was left in the fertilizer residue. Of the total amount of fertilizer applied, 9.4% of N, 40.5% of P and 52.4% of K were still present in the fertilizer granules after one growing season. Maximum recovery of N and P in the above-ground plant parts did not exceed 15% (Table 4). Recovery of K was very high however, and exceeded 100% in the case of rhizomes. The recovery of N, P, and K in above-ground plant parts from the rhizomes was generally 1.5-2 times higher than from the seedlings and the bundles of culms (Table 4). Doubling the amount of fertilizer to 160-40-40 kg ha^{-1} tended to reduce

TABLE 4. Recovery of nitrogen, phosphorus, and potassium in above-ground plant parts of *Amnophila arenaria* from seedlings, rhizomes, and bundles of culms in October 1987 after fertilizing with slow-release NPK fertilizer

Fertilization (kg NPK ha ⁻¹)	Recovery of N (%)						Recovery of P (%)						Recovery of K (%)														
	Seedlings			Rhizomes			Bundles*			Seedlings			Rhizomes			Bundles			Seedlings			Rhizomes			Bundles		
	B	P		B	P		B	P		B	P		B	P		B	P		B	P		B	P		B	P	
80-20-20	9	15	7	5	6	13	4	3	3	3	79	160	72	46													
120-30-30	7	11	10	8	4	9	5	3	3	59	122	79	57														
160-40-40																											

* Fertilizer applied by broadcasting (B) or placement in the planting holes (P).

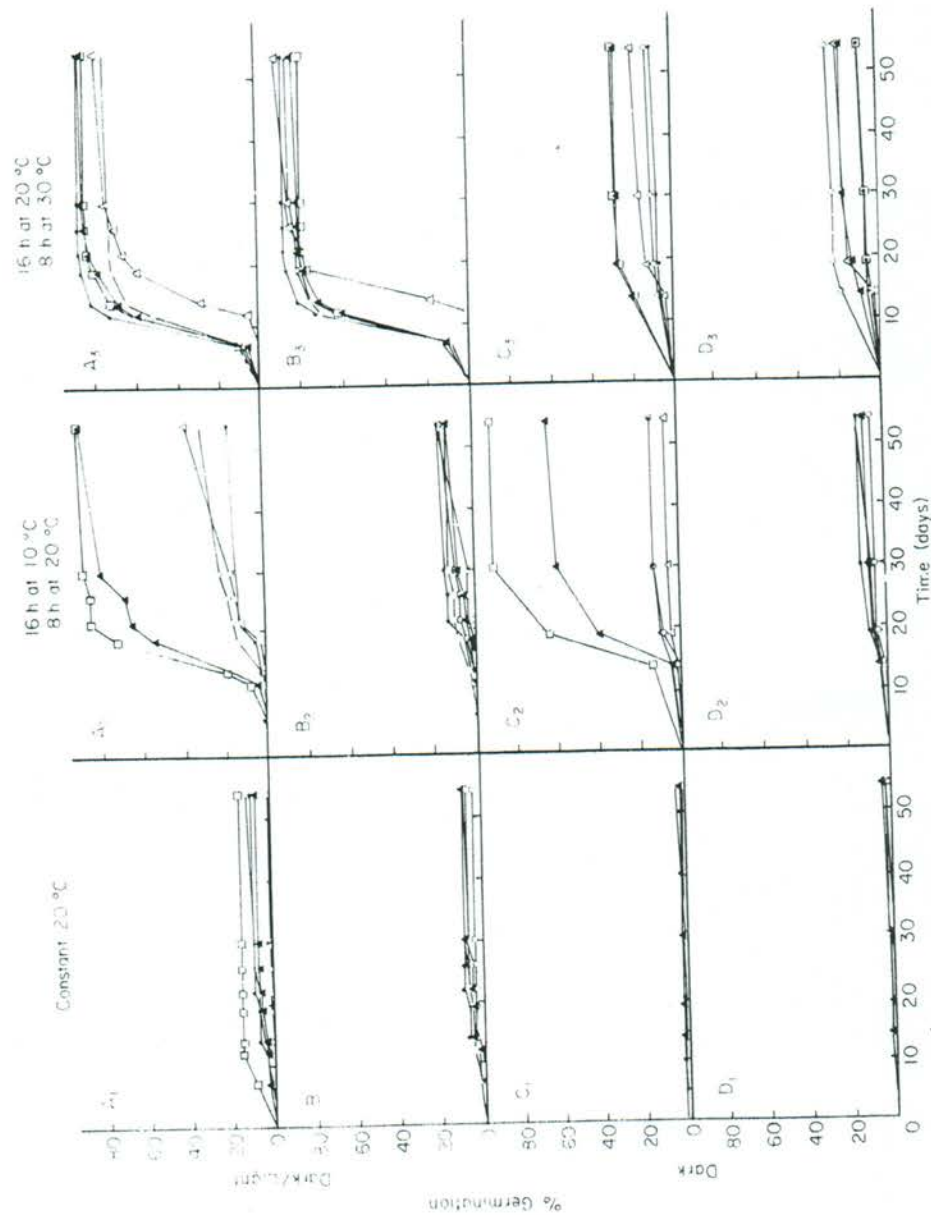


Fig. 2. Germination (%) of seeds of *Ammophila arenaria* with time (days) with different temperature regimes, illumination, and stratification pre-treatment (●, 0; △, 2; ▲, 3; □, 5; ○, 7 weeks, respectively) either moist (A + C) or dry (B + D). Seeds were illuminated during the 8-hour warm period (A + B) or kept in the dark (C + D).

the recovery of N and P from the seedlings and rhizomes. In planted culms however, recovery of N and P increased with increasing rate of fertilization.

Seed germination experiment

The effect of pre-treatment depended on the germination temperature. A stratification period of 5 and 7 weeks increased the percentage of germination only when the temperature fluctuated daily between 10 and 20 °C (Fig. 2). Dry cold storage had no effect on germination. After incision of the seed coat and a germination period of 22 days at 10/20 °C, germination was 94%, compared to 14% in untreated seeds (data not shown in Fig. 2).

All pre-treatments resulted in very low germination percentages at a constant temperature of 20 °C (Fig. 2). In light and at daily fluctuating temperatures of 20/30 °C, germination was 80% in 10–15 days, irrespective of pre-treatment of the seed. At a low daily fluctuating temperature of 10/20 °C, percentage of germination depended on the effectiveness of pre-treatment of the seed (see above).

Germination in darkness was generally considerably lower than in light (Fig. 2). Only with seeds that were stratified for 5 and 7 weeks, and that were subsequently exposed to fluctuating temperatures of 10 and 20 °C, was there a relatively high germination percentage in darkness.

DISCUSSION

Three methods of artificially establishing *A. arenaria* have been compared: planting culms, sowing seeds, and disc-harrowing rhizomes, while the effect of temporary sand stabilizers was also studied. However, temporary sand stabilization interacted with a poor germination rate due to seed dormancy. Only straw remained long enough to enable the seeds to germinate. In plots stabilized with CMC, compost or reed, the sand surface eroded during winter. Protective cover by nurse crops had no effect on numbers of seedlings. In another large-scale experiment, seed dormancy did not occur. In that experiment, compost lasted long enough to enable seedling establishment (Van der Putten 1989).

Vegetatively propagated *A. arenaria* produced more robust tillers and more above-ground biomass than seedlings. Disc-harrowed rhizomes, if supplied with fertilizer, resulted in the highest biomass production and number of tillers (Fig. 1). Sixty rhizome pieces m^{-2} tended to produce more biomass than 40 or 20 m^{-2} , but the effect of rhizome density had disappeared after one growing season (Table 3). A similar effect has been observed with different densities of planted culms (Brown & Hafenrichter 1948b,c; Augustine *et al.* 1964). As planting is usually carried out in early winter, a planting density of at least 40 rhizomes m^{-2} is preferable to compensate for losses e.g. from frost damage.

Seedling establishment was significantly enhanced by fertilizing (Table 2). Low seedling survival observed by other authors (Huiskes 1977; Maun & Baye, 1989) may have been due to low nutrient concentrations in the soil. Plantings of *A. arenaria* can benefit from conventional fertilizers if supplied during the growing season (Brown & Hafenrichter 1948c; Augustine *et al.* 1964; Lux 1965; Adriani & Terwindt 1974). However, the application of conventional fertilizer at planting has not been successful due to leaching losses before the plants had even formed roots (Van der Putten & Van Gulik 1987). Application of slow-release fertilizer at planting resulted in a significantly increased biomass production, although recovery of N and P in above-ground biomass did not exceed 15% and was usually considerably lower (Table 4). High recovery percentages of

K were found, exceeding 100% with plants grown from rhizomes. This excess of absorbed K must have been derived from soil reserves. As the sand contained about 15 g K m^{-2} in the upper 20 cm, there was probably no direct need for K fertilization. Immobilization of nutrients due to straw decomposition can be virtually excluded as the fertilizer was applied at greater depth. Therefore, other factors such as leaching may be responsible for the low percentages of recovery, especially of N. Biomass production by bundles of culms with slow-release fertilizer either broadcast or applied in the planting holes did not differ significantly, suggesting the root system efficiently exploits the upper soil. Therefore, the release of nutrients from slow-release fertilizer should be improved to increase the efficiency of fertilization of dune grasses.

It was supposed that low germination of seeds in experiment 1 during the first season could have been due to the late start of the experiment (May) preventing the effects of some natural pre-treatment. To test this hypothesis, germination was studied in the laboratory. At low fluctuating temperatures ($10/20^\circ \text{C}$), seed germination of *A. arenaria* was improved by 5–7 weeks of stratification (Fig. 2), which is about twice as long as Mau & Baye (1989) recorded for *A. breviligulata*. Incision of the seed coat also improved the rate and percentage of germination of *A. arenaria*, which corresponds with observation for *A. breviligulata* (Laing 1958; Seneca 1969). These results suggest that the seed-coat of *Ammophila* spp. has to be pre-treated to enable imbibition (Spurný 1973). Germination in darkness of stratified seeds was found to be temperature-dependent. However, this may have been an artefact caused by the use of green light during watering and counting (Baskin & Baskin 1979; W.H. van der Putten, unpublished).

In practice, sowing of *A. arenaria* in winter or in early spring will result in a natural stratification, which was apparently the reason for germination in experiment 1. Although a lower light availability reduces germination of buried seeds (Huiskes 1979) this has to be accepted because superficially sown seeds are subject to wind erosion and desiccation (Huiskes 1977).

I conclude that good establishment can be expected from disc-harrowing rhizomes in combination with sand stabilization by straw and the application of slow-release fertilizer. However, other aspects are also involved, such as costs and long-term vegetation development in the artificial plantings. Therefore, at present the three methods of establishing *A. arenaria*, i.e. plantings of culms, sowing of seeds and disc-harrowing rhizomes, are being applied experimentally on a large scale in the Netherlands. The techniques and results will be reported in a subsequent paper.

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REFERENCES

- Adriani, M. J. & Terwindt, J. H. J. (1974). Sand stabilization and dune building. *Rijkswaterstaat Communications* 19, The Hague.
- Atkinson, W. J. (1971). Improved techniques to stabilize frontal and hind dunes after beach mining. *Journal of the Soil Conservation Service of New South Wales*, 27, 199–208.

- Augustine, M. T., Thornton, R. B., Sanborn, J. M. & Leiser, A. T. (1964). Response of American beachgrass to fertilizer. *Journal of Soil and Water Conservation*, **19**, 112-115.
- Barr, D. A. & McKenzie, J. B. (1976). Dune stabilization in Queensland Australia, using vegetation and mulches. *International Journal of Biometeorology*, **20**, 1-8.
- Baskin, J. M. & Baskin, C. C. (1979). Promotion of germination of *Stellaria media* by light from a green safe lamp. *New Phytologist*, **82**, 381-383.
- Berg, A. R. (1972). Grass reproduction. *The Biology of Utilization of Grasses*: (Ed. by V. B. Younger & C. M. Kell), pp. 334-337. Academic Press, London.
- Blom, C. W. P. M. (1978). Germination, seedling emergence and establishment of some *Plantago* species under laboratory and field conditions. *Acta Botanica Neerlandica*, **27**, 257-271.
- Brown, R. L. & Hefenrichter, A. L. (1948a). Factors influencing the production and use of beachgrass and dunegrass clones for erosion control. I. Effect of date of planting. *Journal of the American Society of Agronomy*, **40**, 677-684.
- Brown, R. L. & Hefenrichter, A. L. (1948b). Factors influencing the production and use of beachgrass and dunegrass clones for erosion control. II. Influence of density of planting. *Journal of the American Society of Agronomy*, **40**, 603-609.
- Brown, R. L. & Hefenrichter, A. L. (1948c). Factors influencing the production and use of beachgrass and dunegrass clones for erosion control. III. Influence of kinds and amounts of fertilizer on production. *Journal of the American Society of Agronomy*, **40**, 512-521.
- Gemmell, A. R., Greig-Smith, P. & Gimingham, C. H. (1953). A note on the behaviour of *Ammophila arenaria* (L.) Link in relation to sand dune formation. *Transactions and Proceedings of the Botanical Society of Edinburgh*, **36**, 132-136.
- Harris, D. & Davy, A. J. (1986). Regenerative potential of *Elymus farctus* from rhizome fragments and seed. *Journal of Ecology*, **74**, 1057-1067.
- Hobbs, R. J., Gimingham, C. H. & Band, W. T. (1983). The effect of planting technique on the growth of *Ammophila arenaria* (L.) Link and *Lymus arenarius* (L.) Hochst. *Journal of Applied Ecology*, **20**, 659-672.
- Huiskes, A. H. L. (1977). The natural establishment of *Ammophila arenaria* from seed. *Oikos*, **29**, 133-136.
- Huiskes, A. H. L. (1979). Biological flora of the British Isles. *Ammophila arenaria* (L.) Link. (*Psamma arenaria* (L.) Roem. et Schult.: *Calamagrostis arenaria* (L.) Roth) *Journal of Ecology*, **67**, 363-382.
- Knutson, P. L. (1978). Planting guidelines for dune creation and stabilization. *Coastal Zone 1978*, pp. 762-779. Proceedings of the Symposium on Technical, Environmental, Socioeconomic and Regulatory Aspects of Coastal Zone Management. ASCE, San Francisco.
- Laing, C. C. (1958). Studies in the ecology of *Ammophila breviflulata*. I. Seedling survival and its relation to population increase and dispersal. *Botanical Gazette*, **19**, 208-216.
- Lux, H. (1965). Flugzeugeinsatz zur Düngung der Amrumer Dünen. *Wasser und Boden*, **12**, 387-390.
- Lux, H. (1969). Zur Biologie des Strandhafers (*Ammophila arenaria*) und seiner technischen Anwendung in Dünenbau. *Experimentelle Pflanzensoziologie* (Ed. by R. Tüxen), pp. 138-145. Junk, The Hague.
- Maun, M. A. (1984). Colonizing ability of *Ammophila breviflulata* through vegetative regeneration. *Journal of Ecology*, **72**, 565-574.
- Maun, M. A. & Baye, P. (1989). The ecology of *Ammophila breviflulata* Fern. on coastal dune systems. *Reviews in Aquatic Science*, **1**, (in press).
- Mitchell, A. (1974). Plants and techniques used for sand dune reclamation in Australia. *International Journal of Biometeorology*, **18**, 168-173.
- Pilon, J. J. (1988). Kustafslag op Voorne in het verleden. *Waterschapsbelangen*, **8**, 255-259.
- Ranwell, D. S. & Boar, R. (1986). *Coast Dune Management Guide*. Institute of Terrestrial Ecology, Abbots Ripton.
- Seneca, E. D. (1969). Germination response to temperature and salinity of four dune grasses from the outer banks of North Carolina. *Ecology*, **50**, 45-53.
- Sokal, R. R. & Rohlf, F. J. (1981). *Biometry. The Principles and Practice of Statistics in Biological Research*. W. H. Freeman and company, New York.
- Spurný, M. (1973). The imbibition process. *Seed Ecology*. (Ed. by W. Heydecker), pp. 367-389. Butterworths, London.
- Tsuriell, D. E. (1974). Sand dune stabilization in Israel. *International Journal of Biometeorology*, **18**, 89-93.
- Van der Putten, W. H. (1989). *Establishment, growth and degeneration of Ammophila arenaria in coastal sand dunes*. Ph.D. thesis, Agricultural University, Wageningen, The Netherlands.
- Van der Putten, W. H. & Van Gulik, W. J. M. (1987). Stimulation of vegetation growth on raised coastal fore-dune ridges. *Netherlands Journal of Agricultural Science*, **35**, 198-201.
- Wareing, P. F. (1964). The developmental physiology of rhizomatous and creeping plants. *Proceedings of the 7th British Weed Control Conference*. British Crop Protection Council, Croydon.
- Wesson, G. & Wareing, P. F. (1969). The role of light in the germination of naturally occurring populations of buried weed seeds. *Journal of Experimental Botany*, **20**, 402-413.

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