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# Possibilities for management of coastal foredunes with deteriorated stands of *Ammophila arenaria* (marram grass)

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**Abstract.** *Ammophila arenaria* (marram grass) is the most important plant species for sand stabilization in European coastal foredunes. Stand degeneration due to poor supply of wind-blown sand enhances the susceptibility for wind erosion when successional species do not become established. Replanted *A. arenaria* often fails to become established.

In the present study we examined whether management practices such as mowing, fertilizing, burning or below-ground cutting of plants may be applied to re-establish the vigour of *A. arenaria*. Field experiments performed at exposed sites, where naturally succeeding plant species are not supposed to become established due to salt spray, showed that none of the applied methods resulted into enhanced tiller density of *A. arenaria*. Thus, further studies are necessary to solve this type of management problem.

At the leeward side of foredunes, the successional species *Festuca rubra* ssp. *arenaria* and *Elymus athericus* could be established successfully as both pre-grown seedlings and planted bundles of cuttings (all further experiments were fertilized). When planted in spring, cuttings of successional plant species established less than those planted in early winter. Water repellency of the sand surface is supposed to be the main cause for this. Pre-grown seedlings were less susceptible for the season of planting. Direct sowing was not effective. Rabbit browsing had to be omitted to obtain successful establishment. When living rhizomes of successional plant species were still present in the soil profile, fencing alone turned out to be effective to re-establish vegetation at initially bare sites.

**Keywords:** Generative propagation; Planting time; Rabbit grazing; Sand stabilization; Succession; Vegetative propagation; Water repellency.

**Nomenclature:** van der Meijden (1990) for vascular plants; *Festuca rubra* ssp. *arenaria* is abbreviated as *F. rubra*.

## Introduction

For coastal defence purposes, the management of the Dutch foredunes is aimed at maintaining a minimum profile of sand. In narrow dunes, the minimum profile should be present in the outer foredune ridge, however, in wider dune areas, the minimum profile may also be present somewhere else in the outer dunes (de Ruig 1995). Plants are a major tool for sand stabilization and *Ammophila arenaria* (marram grass) is the most important species used for this purpose. Stabilizing of sand involves trapping of wind-blown sand from the beach, as well as fixation of the sand substratum of the foredunes. *Ammophila arenaria* is especially suited for catching sand and for surface stabilization in mobile dunes. When sand burial has stopped, *A. arenaria* may remain, even for decades (Desmukh 1979; Wallén 1980). Finally, however, gradual degeneration leads to its disappearance from the vegetation. The re-establishment of degenerated *A. arenaria* at stabilized foredune sites often fails as large percentages of the planting stock do not become established. Those plants that stay alive never become as vigorous as those that are subject to regular sand burial after planting (van der Putten 1990).

There are several possible explanations for the relationship between sand burial and the vigour of *A. arenaria*, which are summarized by Willis (1989). For example, sand deposits supply nutrients, eliminate competitors, and enable the plants to produce new roots in a substrate free of pathogens. When sand deposition diminishes, the stand as a whole degenerates. Degeneration of *A. arenaria* and its disappearance from the vegetation is caused by a combination of biotic and abiotic stress factors (van der Putten & Troelstra 1990; van der Putten et al. 1989). Plant parasitic nematodes and soil fungi seem to be the prime organisms involved in the stand degeneration (de Rooij-van der Goes 1995; Seliskar & Huettel 1993; van der Goes & van der Putten 1992; van der Putten et al. 1990). The pathogens are supposed to play an important role in the succession of foredune vegetation in general by differential tolerances among the successional plant species for their respective pathogens (van der Putten et al. 1993). At stable sites, replanted *Ammophila* sp. may not be as successful because of root pathogens, however, natural successors better adapted to the local soil-borne pathogens, will have greater chances of becoming established.

A number of studies have dealt with the establishment of *Ammophila* sp., only a few studies however, (e.g. Adriani & Terwindt 1974; Seliskar 1995) have examined management possibilities to prevent degeneration

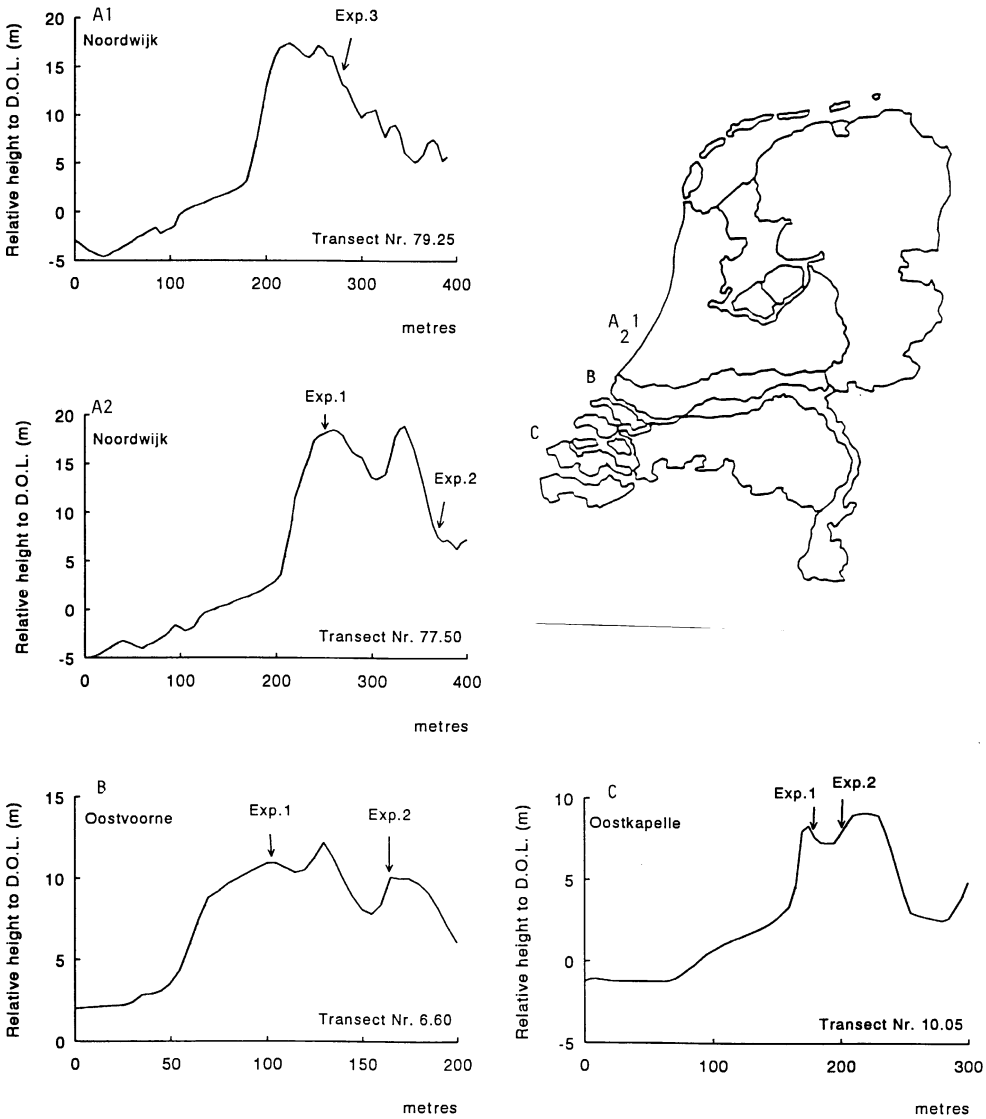


**Fig. 1.** Locations of the experimental fields along the North Sea coast of the Netherlands.

of *Ammophilla* sp. stands. In the present study, a number of management practices were applied at degenerated stands of *A. arenaria*. In addition, possibilities to establish a number of natural successors of *A. arenaria* were studied in field experiments in relation to the type of planting material, planting date and the effect of exposure to browsing animals (predominantly rabbits).

## Methods

### *Experiments that were carried out*

As the natural variation along the Dutch coast is large, three locations were chosen to carry out field Experiments 1 and 2 varying in exposure, foredune height and history (Fig. 1). All sites concerned calcareous foredunes where the management of stand vigour of *A. arenaria* failed, due to degeneration at both exposed and unexposed sites. The first experiment concerned the re-establishment of vigour of degenerated *A. arenaria* at exposed sites where natural succession is supposed to be prevented by e.g. salt spray. The second field experiment to examine the artificial establishment of natural successors was done at less exposed parts of the foredune at all three experimental sites. As the results of the planting of natural successors were rather poor everywhere, an additional, more extensive, third field experiment was performed at the Noordwijk site, where the management problems were most severe. For three successional plant species that were expected to be successful according to Experiment 2, it was examined how the effects of protection against rabbit browsing, of planting date and of type of planting material could be optimized. The experiments are listed in Table 1.

*Site descriptions*

At Oostvoorne (OV) between 1985 and 1988, the foredune was raised and strengthened artificially by sand dredged from the sea floor (van der Putten & Kloosterman 1991). The grain size distribution was heterogeneous and some sand deflation has locally resulted in a desert pavement of shells. At the study site, the dunes were between 8-10 m above Dutch Ordinance Level (DOL). According to visual observations, both experimental fields were not exposed to sand deposition (Fig. 1). In the winter of 1985-1986, the *A. arenaria* stand was planted and after initial vigorous growth (van der Putten & Kloosterman 1991), the productivity of the stands has declined strongly. A number of successional plant species have established, although their contribution to the soil cover is low. During the course of the study the outer slope of the foredune at Oostkapelle (OK) was subject to erosion. Field Experiment 1 was subjected to moderate (± 10 cm/year) sand deposition. The foredune is situated between 7-9 m above DOL (Fig. 1). The site of the planting experiment had been raised in the winter of 1983-1984 by sand collected from a large dune top in the inner dune area. Thereafter, the site was planted with *A. arenaria*, but most plants failed to establish. At Noordwijk (NW) the foredune was 18 m above DOL and none of the experimental fields was subjected to regular deposition of windblown sand (Fig. 1). This foredune has been relatively stable for a long period and already at the top the dominance of *A. arenaria* was taken over by *Festuca rubra* and *Carex arenaria*. At the leeward slope, shrubs of *Hippophae rhamnoides*, *Sambucus nigra*, *Ligustrum vulgare*, and *Salix repens* occurred. Between these shrubs, there were many bare areas that were planted with *A. arenaria* and brushwood of *H. rhamnoides*. Most of the *A. arenaria* planted by the local manager failed to establish. Because of the large number of relatively small bare patches at Noordwijk, Field experiment 2 was performed in two subsites, approximately 500 m apart.

**Table 1.** Summary of the three experiments, their objectives and the site of application.

| Experiment / Objective | Oostvoorne | Noordwijk | Oostkapelle |
|---|---|---|---|
| 1 Management of degenerated *Ammophila arenaria* at exposed sites | × | × | × |
| 2 Enhancement of succession of degenerated *A. arenaria* at unexposed sites by planting successional species | × | × | × |
| 3 Examining the effect of time of planting, planting material and rabbit browsing of most the successful species from Experiment 2 | | × | |

*Field experiments*

*1. Management of degenerated Ammophila arenaria*

In March 1990, field trials were installed near Oostvoorne, Oostkapelle and Noordwijk (Fig. 1, Table 1). At exposed sites where *A. arenaria* was no longer optimal, 16 plots of 5 m × 10 m were layed out parallel to the shoreline. In four blocks (i.e. replications), three treatments were randomly applied and the development of the shoot production of *A. arenaria* was compared to that in untreated plots. At Oostvoorne and Noordwijk, the treatments were (1) mowing by bush-mower at 0.05 m above the soil surface and removing the plant material, (2) thinning of the stand as is done when plant material is collected from natural vegetation: 80 % of the above-ground plant parts was removed by cutting the plants at about 0.1 m below the soil surface by hand-shovel, and (3) burning the old above-ground plant parts. At Oostkapelle, treatment 3 (burning) was replaced by fertilization with 40 kg of N, 20 kg of P and 20 kg of K per ha of Osmocote (9-12 months active).

In the first winter (1990-1991), the outer dune slope was washed away and the experimental field at Oostkapelle was buried by 0.1 m of wind-blown sand. At Noordwijk, part of the field was disturbed by machines. At Oostkapelle, all plots remained included, but at Noordwijk, the damaged field plots were excluded from further evaluation.

Per plot, two randomly situated permanent quadrats (PQs) of 1 $m^2$ were marked. In May, July, and October 1990 and in May and October of the two subsequent years, field evaluations were performed by counting the number of living tillers in the PQs. For each evaluation event, the data were statistically analyzed using oneway analysis of variances (ANOVA) with $P < 0.05$.

*2. Establishment of natural successors of A. arenaria*

In April/May 1990, field trials were started at all three experimental locations (Fig. 1). Above-ground vegetation was absent at the sites when the experiments were set-up. At each field, nine plant species were established by planting pre-grown plants, bundles of culms, or rhizomes. The plant species and their modes of establishment are shown in Table 2. The field was divided into four blocks and each species was planted individually at four replicate plots of 4 m × 4 m; one plot per block. In addition, four replicate plots were sown with a mixture of the grass species from Table 2 and the sedge *Carex arenaria*.

The 30 cm tall pre-grown shrubs of *H. rhamnoides* and *Ligustrum vulgare* were obtained from a nursery of the 'Haagse Duinwaterleidingbedrijf' at Scheveningen dune area. The *Salix repens* and *Sambucus nigra* stem cuttings were collected near Oostvoorne. All shrubs were planted at a density of three plants/$m^2$. The bundles of culms were collected from local natural stands. The plants were cut at 10 cm below the soil surface. Then, bundles of six culms, each with at least two viable dormant buds, were planted at a density of four bundles/$m^2$. The rhizomes were collected from natural stands of local origin. The rhizome material was loosely packed in containers, chopped into 20 cm-pieces and buried in 10-15 cm deep furrows which were 50 cm apart. About 1 L of rhizome material was applied per $m^2$. The rhizomes of *C. arenaria* contained shoots, that remained above the soil surface after the rhizomes were buried. The seeds originated from the foredunes near Oostvoorne. They were threshed mechanically and planted as caryopses (± 200/$m^2$).

Each experimental field was supplied with slow-release NPK-fertilizer (Osmocote, 9-12 months active) and 40 kg of N, 10 kg of P and 10 kg of K were applied per ha. The fields at Oostvoorne and Noordwijk were completely fenced to exclude rabbits. At Oostkapelle, two blocks were fenced and two not.

In the first year at the end of the growing season, the numbers of established plants were counted. In the two subsequent years, the percentage cover of the field plots was assessed and split-up for the (1) plant species established, (2) mosses and (3) naturally established vegetation (mostly *F. rubra*).

**Table 2.** Mode of establishing the plant species at the three field sites Oostvoorne, Noordwijk and Oostkapelle. B = bundles of culms, R = rhizomes, C = rootless cuttings from branches, and S = pre-grown seedlings; - = the species has not been applied.

| | Field site | | |
|---|---|---|---|
| Plant species | Oostvoorne | Noordwijk | Oostkapelle |
| *Ammophila arenaria* | B | B | B |
| *Calammophila baltica* | B | B | B |
| *Festuca rubra* ssp. *rubra* | R | R | B |
| *Carex arenaria* | R | R | R |
| *Elymus athericus* | R | B | B |
| *Calamagrostis epigejos* | B | B | B |
| *Salix repens* | C | - | C |
| *Sambucus nigra* | C | C | C |
| *Ligustrum vulgare* | - | S | - |
| *Hippophae rhamnoides* | S | S | S |

*3. Effects of date of planting, type of plant material and rabbit browsing*

Based on the poor establishment of the planted species in Experiment 2, Experiment 3 was designed to examine whether the establishment could be improved by varying the planting date (early vs. late in winter) or the effect of the type of planting material (bundles of culms vs. pre-grown seedlings). The experiment was done at a field near Noordwijk, where management problems were most severe probably due to the strongly water repellent sand. By performing the experiment in both fenced and unfenced fields, it was studied whether the effects of rabbit browsing differed between planting dates. In November 1991 and April 1992, the three most successful plants in Experiment 2 (i.e. *F. rubra*, *C. arenaria*, and *E. athericus*) had been established from vegetative, un-rooted plant parts and from pre-grown seedlings. The field trial was done at the leeward side of the coastal foredunes at Noordwijk (Fig. 1). Here, the stabilizing vegetation had disappeared completely and the surface sand was very water repellent (water drop penetration time 600 - 3600 sec according to the method of Dekker & Jungerius 1990). Half of the field was surrounded by a fence against rabbits. Within both the fenced and unfenced parts of the field, four blocks were situated along the altitude lines and served as replicates. Within each block, every treatment was applied once at a plot of 2 m × 2 m. In May 1992, all plots were supplied with slow-release fertilizer as in Experiment 2.

The seeds were collected near Oostvoorne, dried and threshed manually. They were germinated for about two weeks at day/night cycles of (16 h, 30 °C)/(8 h, 20 °C). The seedlings were grown for nine weeks in an unheated greenhouse before they were planted in November. The remaining seedlings were kept frost-free during winter in a greenhouse. They were 30 weeks old when planted in April 1992.

The cuttings were obtained from the surrounding natural vegetation in the same way as described for Experiment 2. Planting density of all plants was six plants/$m^2$. The numbers of tillers were counted in the central 1-$m^2$ area of each plot in June, August and October 1992, as well as in July 1993 and the results

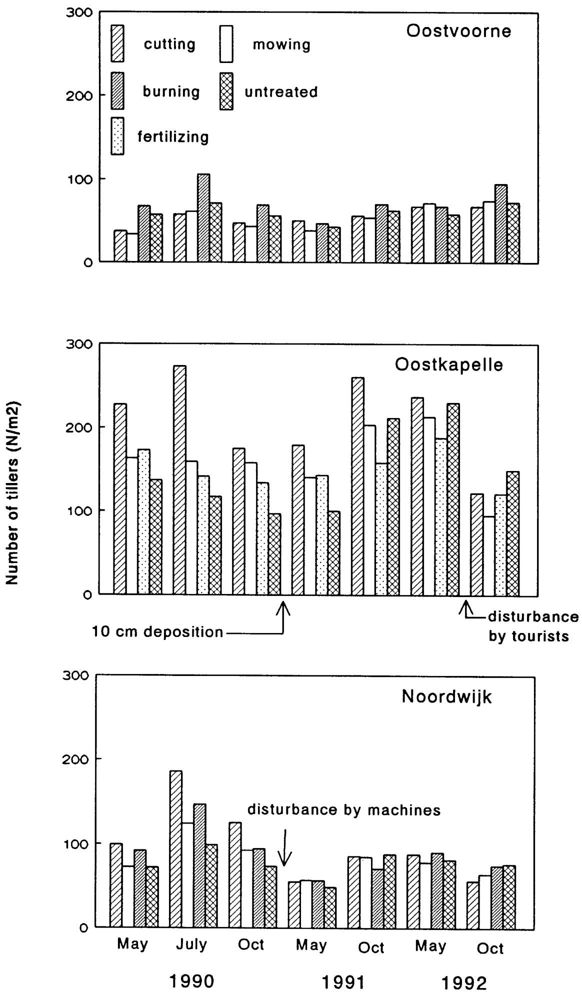


**Fig. 2.** Numbers of tillers/m$^2$ of *Ammophila arenaria* at the experimental fields Oostvoorne, Oostkapelle and Noordwijk as affected by different management practices.

were statistically analysed by ANOVA. As no plants survived in the unfenced area, a two-way ANOVA was performed for each plant species with factors 'plant material' and 'planting date'. Data were transformed to square roots when necessary to obtain homogeneity of variances. Averages were compared by Tukey's test with $P < 0.05$ (Sokal & Rohlf 1981).

## Results

### *Experiment 1. Management of degenerated Ammophila arenaria*

At Oostkapelle, the stand density of *A. arenaria* was about twice as high as at Noordwijk and the density at Oostvoorne was lowest of all (Fig. 2; differences among the experimental sites were not tested statistically). This rank in stand densities remained during the course of the study, although at the end the differences between Oostvoorne and Noordwijk had almost disappeared. The densities of the stands corresponded with the observed sand deposition, which was moderate at Oostkapelle, incidental at Noordwijk and absent at Oostvoorne.

In the first growing season, the only statistical effect of the management treatments was an enhanced tiller production after cutting of *A. arenaria* at the Oostkapelle field. In all other treatments and all other years, no significant effects of management were found (Fig. 2). Thus, taking into account that the stand at Oostkapelle still received some wind-blown sand and was the most dense of all three, the examined management practices were not successfully enhancing the tiller densities of the most severely degenerated *A. arenaria* stands.

### *Experiment 2. Establishment of natural successors of Ammophila arenaria*

The establishment of the planted bundles of culms, cuttings and rhizome material was poor. Hardly any of the planted seeds germinated and virtually none produced established plants. This treatment is, therefore, not presented in a figure. None of the cuttings of *S. repens* and *S. nigra* had produced roots and in September of the first growing season, they were all dead (Table 3). Previously planted cuttings of *H. rhamnoides*

**Table 3.** Percentage establishment of shrubs from unrooted cuttings (*Salix repens* and *Sambucus nigra*) and pre-grown seedlings (*Hippophae rhamnoides* and *Ligustrum vulgare*) and numbers of tillers (number/m$^2$) of five grass species and *Carex arenaria*. The data were recorded in September 1990, at the end of the first growing season, in all three experimental fields.

| Plant species | Field site: Oostvoorne | Noordwijk | Oostkapelle: fenced | unfenced |
|---|---|---|---|---|
| | % establishment | | | |
| *Salix repens* | 0 | - | 0 | 0 |
| *Sambucus nigra* | 0 | 0 | 0 | 0 |
| *Ligustrum vulgare* | - | 20 | - | - |
| *Hippophae rhamnoides* | 31 | 43 | 8 | 0 |
| | Number of shoots/m$^2$ | | | |
| *Ammophila arenaria* | 11 | 14 | 4 | 1 |
| *Calammophila baltica* | 17 | 18 | 4 | 7 |
| *Festuca rubra* ssp. *rubra* | 152 | 65 | 11 | 21 |
| *Carex arenaria* | 17 | 1 | 0 | 3 |
| *Elymus athericus* | 37 | 22 | 3 | 4 |
| *Calamagrostis epigejos* | 11 | 7 | 7 | 4 |

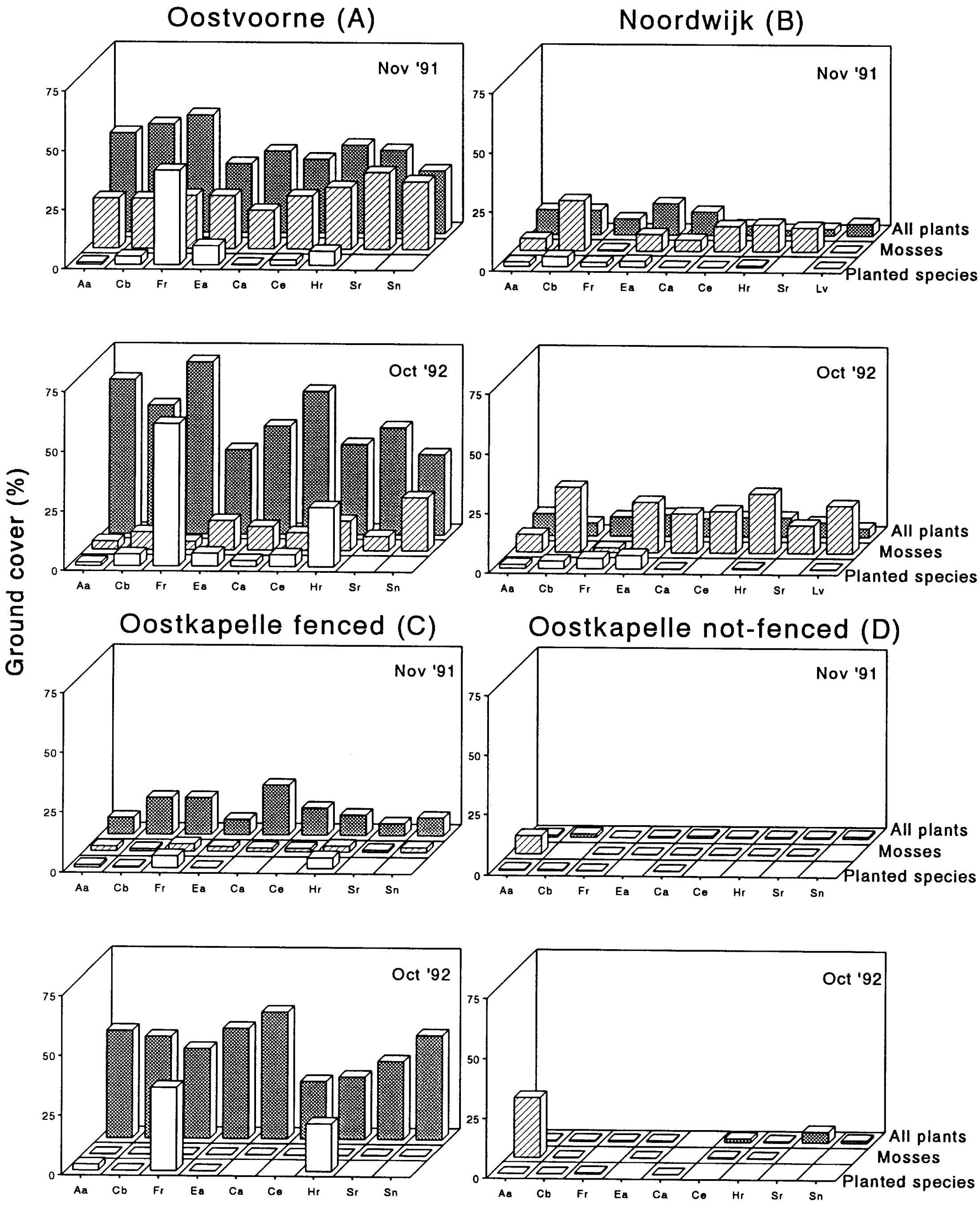


**Fig. 3.** Percentage ground cover (%) of all herbs, mosses, and the planted species at the experimental plots with planted *Ammophila arenaria* (Aa), *Calammophila baltica* (Cb), *Festuca rubra* (Fr), *Elymus athericus* (Ea), *Carex arenaria* (Ca), *Calamagrostis epigejos* (Ce), *Hippophae rhamnoides* (Hr), *Salix repens* (Sr), *Ligustrum vulgare* (Lv), and *Sambucus nigra* (Sn). Data were obtained from fields at Oostvoorne, Noordwijk and Oostkapelle (fenced and not-fenced).

at Voorne succeeded to establish (R. Dekker pers. comm.) which may have been due to their large size, the earlier planting date (approximately February), and to the relatively high water-holding capacity of the dredged sea sand in which the cuttings were planted which may have enabled the plants to form roots before drying out.

Less than half of the planted seedlings of the shrubs *L. vulgaris* and *H. rhamnoides* became established. The percentage survival was maximally 40 % (Table 3). At the unfenced part of the field at Oostkapelle, *H.*

*rhamnoides* did not establish, apparently because the young shrubs did not survive the browsing by rabbits, who also removed their bark. All grasses and *C. arenaria* established poorly. Production of new tillers was least at Oostkapelle, and the low numbers did not seem to differ between fenced and unfenced parts of the experimental field. Tiller production of *C. arenaria* was extremely poor, except at Oostvoorne. The few individuals that became established produced long rhizomes with the characteristic pattern of shoots sprouting from them. Establishment of *F. rubra* may have been over-estimated due to emergence of shoots from rhizomes that were presumably already present before the field trial was started. In the subsequent growing seasons, spontaneous regrowth occurred of especially *F. rubra* and, more sporadically, *A. arenaria*, *C. baltica*, *E. athericus*, *C. epigejos*, and *H. rhamnoides* (the latter through ingrowing rhizomes from shrubs that bordered the fields). The spontaneous development of the plants within the fenced area may have been due to a combination of the fertilizer and the exclusion of rabbits. At Oostkapelle, with fertilizer and without rabbits, generally more vegetation cover developed (Fig. 3C) than when rabbits were allowed in the fertilized plots (Fig. 3D). Apart from an extensive colonization of the experimental fields by *F. rubra*, mosses represented an important ground cover at Oostvoorne and Noordwijk (Fig. 3 A and B). At Oostkapelle, few mosses were present (Fig. 3 C and D). In August 1991, the planted *F. rubra*, *E. athericus* and *C. epigejos* produced flowering shoots at all fields except the unfenced near Oostkapelle. Although the general success of planting was low at all sites, we got the impression that the planting results may have been more effective. For optimizing the effects of the planting results, a restricted number of plant species was examined more extensively in a third field experiment, for logistical reasons carried out only at the site Noordwijk.

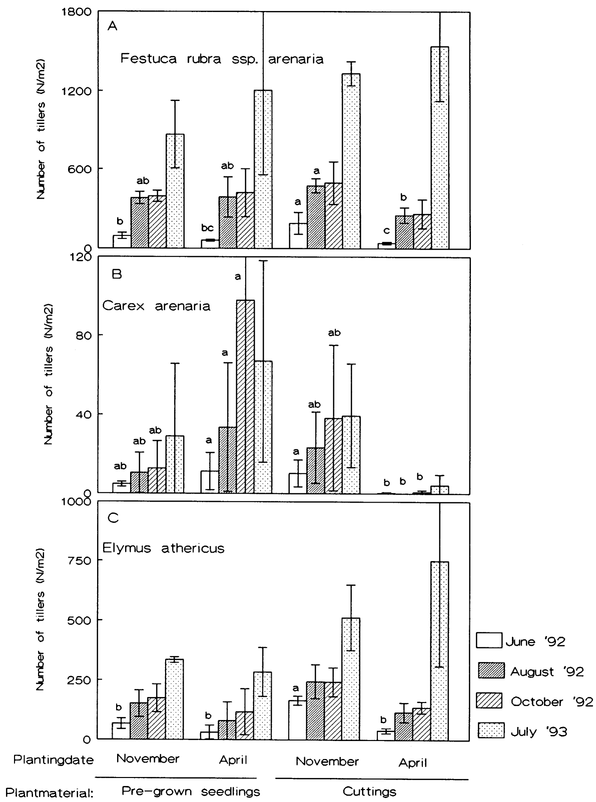


**Fig. 4.** Number of tillers/m² of *Festuca rubra, Carex arenaria* and *Elymus athericus* cuttings and pre-grown seedlings planted in November 1991 and April 1992. Error bars are standard deviations. Significant treatment differences per plant species per date of evaluation are indicated by different letters (a, b, etc.). The absence of letters above bars means that no differences were significant.

*Experiment 3. Effects of date of planting, type of plant material and rabbit browsing*

At the unfenced plots, none of the plants survived. The effect of rabbit browsing did not depend on the planting date. Therefore, only the results of the fenced plots are shown (Fig. 4).

*Festuca rubra*: In June and August, the result of the planted material depended on the date of planting (Table 4). Cuttings produced more tillers when planted in November than in April, but the time of planting was indifferent for the seedlings (Fig. 4A). In October, there were no significant differences anymore. In July 1993, cuttings had produced just significantly more tillers than seedlings ($P = 0.0455$; Table 4).

*Carex arenaria*: The numbers of new shoots were about 20 × and 10 × lower than those of *F. rubra* and *E. athericus*, respectively. Establishment had occurred quite irregularly and variation was, therefore, rather large. However, when established the plants started to migrate by producing rhizomes, which led to tillering. Cuttings that were planted in spring established poorly (Fig. 4B). Cuttings planted in November were far more successful than those planted in April. The seedlings were not affected by planting time (Fig. 4B). However, seedlings planted in November appeared to be more vulnerable to erosion of the sand surface than the seedlings of the other two plant species. The interacting effects between the type of plant material and the date of planting on the tiller production appeared also from the ANOVA results (Table 4).

**Table 4.** Two-way analyses of variances of *Festuca rubra* ssp. *arenaria*, *Carex arenaria* and *Elymus athericus* with factors plant material type (P: pre-grown seedlings and cuttings) and time of planting (T: early and late winter). Every evaluation was analysed separately. Df = degrees of freedom.

| | | *Festuca rubra* | | | *Carex arenaria* | | | *Elymus athericus* | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Evaluation date | Factor | df | *F* | *P* | df | *F* | *P* | df | *F* | *P* |
| June '92 | P | 1 | 1.50 | 0.2456 | 1 | 3.36 | 0.0915 | 1 | 13.03 | 0.0036 |
| | T | 1 | 35.7 | 0.0001 | 1 | 3.21 | 0.0986 | 1 | 36.49 | 0.0001 |
| | P × T | 11 | 12.1 | 0.0052 | 12 | 12.0 | 0.0047 | 12 | 5.27 | 0.0406 |
| Augustus '92 | P | 1 | 0.43 | 0.5275 | 1 | 2.99 | 0.1092 | 1 | 4.10 | 0.0657 |
| | T | 1 | 7.29 | 0.0207 | 1 | 0.48 | 0.5007 | 1 | 9.79 | 0.0087 |
| | P × T | 11 | 7.02 | 0.0226 | 12 | 9.07 | 0.0108 | 12 | 0.12 | 0.7369 |
| October '92 | P | 1 | 0.35 | 0.5654 | 1 | 2.03 | 0.1796 | 1 | 2.29 | 0.1564 |
| | T | 1 | 2.97 | 0.1126 | 1 | 0.35 | 0.5670 | 1 | 6.86 | 0.0224 |
| | P × T | 11 | 3.56 | 0.0857 | 12 | 10.3 | 0.0075 | 12 | 0.17 | 0.6878 |
| July '93 | P | 1 | 5.22 | 0.0455 | 1 | 1.77 | 0.2076 | 1 | 10.89 | 0.0063 |
| | T | 1 | 1.74 | 0.2163 | 1 | 0.03 | 0.8606 | 1 | 0.14 | 0.7184 |
| | P × T | 11 | 0.16 | 0.6975 | 12 | 7.65 | 0.0171 | 12 | 1.62 | 0.2274 |

*Elymus athericus*: In June 1992, cuttings planted in November produced more tillers than those planted in spring (Fig. 4C). There was no time-dependent effect in seedlings. This interaction between the effects of the type of plant material and the planting date on the number of tillers produced in June was significant (Table 4). During the rest of 1992, the plants established in November produced more tillers than those planted in April. In July 1993, cuttings on average produced more tillers than plants established from seedlings.

## Discussion

At exposed sites devoid of fresh sand deposition, mowing, fertilizing or burning did not lead to any improvement of the vigour of degenerated *A. arenaria* (Experiment 1). Cutting plants below-ground was effective only at the most dense stand (Oostkapelle), but at both other sites no effect appeared. Therefore, previous results of Adriani & Terwindt (1974) with *A. arenaria* and Seliskar (1995) with the North American *Ammophila breviligulata* could not be applied to re-establish vigour of strongly degenerated stands of *A. arenaria*. Thus far, the only effective way to maintain vigour of *A. arenaria* is by enabling fresh wind-blown sand to be deposited in the vegetation (Huiskes 1979; Willis 1989). Further research is needed to formulate the management of stands of *A. arenaria* that degenerate due to insufficient burial by wind-blown sand at sites too exposed (e.g. to salt spray) for natural successors to become established.

When *A. arenaria* degenerates at lee-ward slopes, it is (at least in the Netherlands) usually succeeded by a vegetation type dominated by *F. rubra*, after which *H. rhamnoides* takes over the habitat. However, *F. rubra* is often succeeded by lichens instead of by *H. rhamnoides* (van Dieren 1934). These stages with lichens frequently occur at the leeward side of heavily managed foredunes of the Dutch mainland coast. As trampling causes breaking of the lichen crusts foredune managers fear for erosion of such sites. In severely damaged patches (Experiment 2), vegetation re-established spontaneously after fencing them (Fig. 5). The prerequisite is that the soil still contains rhizomes of perennials that are suppressed during most of the year. In Experiment 3, however, there was hardly any spontaneous re-establishment of plants due to the absence of living rhizomes in the soil profile (Fig. 6).

At the fenced sites, neither re-emergence from seed banks nor from planted caryopses of successional species was successful. Moisture is supposed to be one of the most constraining factors for seedling germination in foredunes (Huiskes 1977; Maun & Krajnyk 1989; Maun 1994). The sand surface of the lee-ward side of heavily managed foredunes, such as at the experimental fields 2 and 3 at Noordwijk, may be highly water repellent (Dekker & Jungerius 1990). At slopes, rain water may run off rather than penetrate the soil profile (Jungerius & Dekker 1990). Thus, at bare lee-ward slopes of foredunes without living rhizomes in the soil profile, natural vegetation re-establishment is not to be expected to occur immediately after omitting rabbits by fences. Probably, algae and mosses have to become established first (Pluis 1994) thus acting as nurse crops

**Fig. 5.** Experiment 2. Spontaneous regrowth of vegetation within the field at Noordwijk after two years of enclosure by gauze fences.

**Fig. 6.** Experiment 3 in July 1993. Establishment of *Festuca rubra*, *Carex arenaria* and *Elymus athericus* from planted seedlings and cuttings within gauze fences (in front) and no establishment without gauze fences (the bare sand area behind).

(*sensu* Maun 1994) enabling natural re-establishment of vascular plants from seeds.

When a vegetation cover is required at short term, successional plant species have to be introduced by planting. Our results show that pre-grown seedlings may be established throughout the whole winter, but that bundles of culms may be better planted early in winter to give them ample time for root production. In the second year, cuttings produced more tillers than seedlings, although differences were rather small. Both *F. rubra* and *E. athericus* developed well and large numbers of tillers, as well as flowering stems were produced (Fig. 6). *Carex arenaria* is less suitable for sand stabilization when applied alone, because its establishment is very variable and cuttings planted in spring hardly succeed to become established. However, *C. arenaria* may be very successful in recolonizing superficial blow-outs by vegetative expansion from established stands along the edges (W.H. van der Putten and B.A.M. Peters pers. observ.).

All experimental fields were supplied with fertilizers. Probably, fencing would have given less pronounced effects if no nutrients were supplied, as productivity of dune vegetation is strongly limited by nutrients (e.g. Willis 1963, 1965). However, rabbit browsing turned out to be a major constraint for re-establishment of vegetation. In the unfenced blocks of Experiment 2 at Oostkapelle percentage cover was lower than in the fenced blocks. And in Experiment 3, plants in the unfenced part of the field did not establish, even though at the time the experiments were performed, the local population of rabbits had decreased to 10-20 % of its expected population size. This was due to the Viral Haemarrhagic Disease, a new rabbit disease (Lucas & van der Hagen 1992). Rabbit browsing could not be excluded by varying the date of planting. The effects of rabbits on foredune vegetation is in line with their effects on strandline vegetation (Harris & Davy 1986) and on the vegetation of inner dunes (Boorman 1989).

Fertilization had a stimulating effect, but the release of nutrients lasted less than one year. After the first year, when the release of nutrients from the fertilizer had stopped, *F. rubra* remained dominant in the fenced fields and its percentage cover increased. In the unfenced field, the percentage cover remained low. Thus, all three conditions examined (rabbits, fertilization and planting date) were of major importance.

In conclusion, when vegetation has to be re-established at unexposed parts of coastal foredunes after degeneration of *A. arenaria*, the successive plant species *F. rubra* and *E. athericus* could be successfully established. These species do not only tolerate the soil-borne diseases of their predecessors (van der Putten et al. 1993); they could also be relatively easy established by planting bundles of culms or pre-grown seedlings. Rabbit browsing and planting date were important factors determining the success of plant establishment. When these factors are optimal, other plant species examined in Experiment 2, such as *C. epigejos*, *H. rhamnoides*, *S. repens* and *S. nigra* might be applicable as well. Further studies, however, are required to find a solution for the management of degenerated stands of *A. arenaria* at sites where successional plant species will be constrained by exposure to salt spray. Such conditions do occur at exposed sites where the transport of wind-blown sand from the beach is insufficient to maintain vigour of *A. arenaria*.

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## References

Adriani, M.J. & Terwindt, J.H.J. 1974. *Sand stabilization and dune building.* Rijkswaterstaat Communications no. 19: 68 pp.

Boorman, L.A. 1989. The influence of grazing on British sand dunes. In: van der Meulen, F., Jungerius, P.D. & Visser, J.H. (eds.) *Perspectives in Coastal Dune Management*, pp. 121-124. SPB Academic Publishing, The Hague.

Dekker, L.W. & Jungerius, P.D. 1990. Water repellency in the dunes with special reference to The Netherlands. *Catena suppl.* 18: 173-183.

de Rooij-van der Goes, P.C.E.M. 1995. The role of plant-parasitic nematodes and soil-borne fungi in the decline of *Ammophila arenaria* (L.) Link. *New Phytol.* 129: 661-669.

de Ruig, J. 1995. *De kust in breder perspectief. Basisrapport Kustnota 1995.* Ministry of Transport and Public Works, RIKZ 95.005, The Hague. (In Dutch.)

Desmukh, I.K. 1979. Fixation, accumulation and release of energy by *Ammophila arenaria* in a sand dune succession. In: Jefferies, R.L. & Davy, A.J. (eds.) *Ecological processes in coastal environments*, pp. 353-362. Blackwell Scientific Publications, London.

Harris, D. & Davy, A.J. 1986. Regenerative potential of *Elymus farctus* from rhizome fragments and seed. *J. Ecol*. 74: 1057-1067.

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). *J. Ecol*. 67: 363-382.

Jungerius, P.D. & Dekker, L.W. 1990. Water erosion in the dunes. *Catena suppl.* 18: 185-193.

Lucas, J.J.M. & van der Hagen, H.G.J.M. 1992. Nieuw dodelijk konijnenvirus in Meijendel. *Meijendel mededelingen* 24: 32. Department of Population biology, University of Leiden, Leiden. (In Dutch.)

Maun, M.A. 1994. Adaptations enhancing survival and establishment of seedlings on coastal dune systems. *Vegetatio* 111: 59-70.

Maun, M.A. & Krajnyk, I. 1989. Stabilization of Great Lakes sand dunes: effect of planting time, mulches and fertilizer on seedling establishment. *J. Coastal Res.* 5: 791-800.

Pluis, J.L.A. 1994. Algal crust formation in the inland dune area, Laarder Wasmeer, the Netherlands. *Vegetatio* 113: 41-51.

Seliskar, D.M. 1995. Coastal dune restoration: a strategy for alleviating dieout of *Ammophila breviligulata*. *Restor. Ecol.* 3: 54-60.

Seliskar, D.M. & Huettel, R.N. 1993. Nematode involvement in the dieout of *Ammophila breviligulata* (Poaceae) on the Mid-Atlantic coastal dunes of the United States. *J. Coast. Res.* 9: 97-103.

Sokal, R.R. & Rohlf, F.J. 1981. *Biometry. Their Principles and Practices of Statistics in Biological Research.* W.H. Freeman, New York, NY.

van Dieren, J.W. 1934. *Organogene Dünenbildung: eine geomorphologische Analyse der Dünenlandschaft der West-Friesischen Insel Terschelling mit pflanzensoziologischen Methoden.* Martinus Nijhoff, Den Haag.

van der Goes, P.C.E.M. & van der Putten, W.H. 1992. Nematode problems in *Ammophila arenaria* (marram grass). *Meded. Facult. Landbouww. RUGent* 57/3a: 847-856.

van der Meijden, R. et al. 1990. *Heukels' Flora van Nederland.* 21th ed. Wolters-Noordhoff, Groningen.

van der Putten, W.H. 1990. Establishment and management of *Ammophila arenaria* (marram grass) on artificial coastal foredunes in The Netherlands. In: Davidson-Arnott, R. (ed.) *Proceedings Canadian symposium on coastal sand dunes*, pp. 367-387. Associate Committee on Shorelines, National Research Council and Guelph University.

van der Putten, W.H. & Kloosterman, E.H. 1991. Large-scale establishment of *Ammophila arenaria* and quantitative assessment by remote sensing. *J. Coastal Res.* 7: 1181-1194.

van der Putten, W.H. & Troelstra, S.R. 1990. Harmful soil organisms in coastal foredunes involved in degeneration of *Ammophila arenaria* and *Calammophila baltica*. *Can. J. Bot.* 68: 1560-1568.

van der Putten, W.H., Maas, P.W.Th., van Gulik, W.J.M. & Brinkman, H. 1990. Characterization of soil organisms involved in the degeneration of *Ammophila arenaria*. *Soil Biol. Biochem.* 22: 845-852.

van der Putten, W.H., van der Werf-Klein Breteler, J.T. & van Dijk, C. 1989. Colonization of the root zone of *Ammophila arenaria* by harmful soil organisms. *Plant Soil* 120: 213-223.

van der Putten, W.H., van Dijk, C. & Peters, B.A.M. 1993. Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature* 362: 53-56.

Wallén, B. 1980. Changes in structure and function of *Ammophila* during a primary succession. *Oikos* 34: 227-238.

Willis, A.J. 1963. Braunton Burrows: the effects on the vegetation of the addition of mineral nutrients to dune soils. *J. Ecol.* 51: 353-375.

Willis, A.J. 1965. The influence of mineral nutrients on the growth of *Ammophila arenaria*. *J. Ecol.* 53: 735-745.

Willis, A.J. 1989. Coastal sand dunes as biological systems. *Proc. R. Soc. Edinb.*, 96B: 17-36.

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