Ecology of the hybrid Marram Grass x *Calammophila baltica* in Britain*

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Abstract

Variation in growth habit between British populations of *Ammophila arenaria*, and its intergeneric hybrid, x *Calammophila baltica* was investigated. Competition between the two species was examined with a de Wit type competition experiment. The morphology of the species was found to be significantly different in terms of flowering, leaf dimensions, and tillering and branching patterns. It was found that they competed for the same space, except when nutrients were added and there was space for rhizome extension. These results imply that when planting for sand dune conservation, both species should be utilized in a mixed sward, with fertilizer added in a mulch.

Introduction

x Calammophila baltica (Flügge) Brand, the Hybrid, or Purple, Marram Grass, is also known as *x Ammocalamagrostis baltica* (Schrad.) P. Fourn., in the U.K., and as *Ammophila baltica* (Flügge) Link, in some parts of Europe. It is a sand dune species, common on northern European coasts, but rare in Britain, being found only in two east coast sites, around Ross Links in Northumberland, and along the East Anglian coast (Perring & Snell, 1978).

* Nomenclature follows Tutin *et al.* (1964–80), except in the use of *x Calammophila baltica* (Flügge) Brand (= *x Ammocalamagrostis baltica* (Schrad.) (P. Fourn.), see Rauschert (1977).

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x C. baltica is a naturally occurring, intergeneric hybrid between *Ammophila arenaria* (L.) Link, Marram Grass, and *Calamagrostis epigejos* (L.) Roth, Bush Grass or Wood Small Reed. Westergaard (1943) has determined that it occurs in three varieties, with different combinations of the parental chromosomes in each. Hubbard cited in Stace, (1975) has identified the British variety as var. *subarenaria*, a hexaploid which has a chromosome number of $2n = 42$, with 28 chromosomes from *A. arenaria* and 14 from *C. epigejos*. There are clonal differences between the two British populations, which indicate that they were formed in two separate hybridization events (Rihan & Gray, 1983).

Marram Grass is widely planted throughout Europe and the British Isles in sand dune conservation schemes. In appearance, *x C. baltica* is much more vigorous than *A. arenaria*, typically having longer, wider leaves than this parental species. Because of this, it is often planted in preference to *A. arenaria*, deliberately in the Netherlands (Adriani & Terwindt, 1974) and other north European countries, and by chance in the U.K. (Ellis, 1960). The biology of *A. arenaria* is described by Huiskes (1979), and

Vegetatio 61, 203–208 (1985).

the problem of the decline in vigour has been reviewed in a recent paper by Eldred & Maun (1981).

C. epigejos is known in the U.K. as a plant of damp woods and heavy soils (Hubbard, 1968), though its ecological distribution in mainland Europe appears to be rather different (Westergaard, 1943; Nygren, 1946).

In this paper we will describe some interim results of research into the growth habit and ecological distribution of the phenotype of *x C. baltica*, and its variation from *A. arenaria*. The consequences of these for sand dune management will be discussed in relation to the observations made on the British populations of *x C. baltica* var. *subarenaria*.

Materials and methods

In 1980, 163 randomly chosen 1 × 1 m quadrats were recorded, 100 on the Norfolk coast, between Horsey and Winterton (U.K., O.S. National Grid Reference TG 465243 to 495195); and 63 in Northumberland, on Holy Island, Ross Links and Budle Bay (U.K., O.S. National Grid Reference NU 118433 to 162360). Characters measured included the % cover of both *x C. baltica* and *A. arenaria*, the length and width of leaves of the tallest tiller of both species; and the number of flowers in each quadrat.

The variation in growth habit between the two species, as expressed by the horizontal spread of rhizomes, and the number of tillers produced on them, was measured in a blowout in Winterton which had been planted with a mixture of *x C. baltica* and *A. arenaria* in 1979. The plants had been spaced at approximately 1-m intervals, and had not yet merged into a uniform sward. The measurements were made in 1982.

Samples of *x C. baltica* and *A. arenaria* were collected from the study beaches in September 1979, and *C. epigejos* was collected from Hickling Broad, Norfolk at the same time. These were grown for 1 year in pots in the University Botanic Gardens, then split into single tiller ramets to provide an even-age cohort for a de Wit type replacement series competition experiment (de Wit, 1960; de Wit & van den Bergh, 1965; Harper, 1977). The experiment was established in two environments: (1) at the University of Southampton Botanic Gardens at Chilworth, using a proprietary compost (7 parts loam to 3 of peat and 2 of coarse grit, with 2 kilos of base fertilizer, N P K = 9:7:3 + trace elements, per cubic meter of compost) in 7″ pots set in a gravel bed; (2) on a northeast-facing dune slope 100 meters from the sea at Studland, Dorset, on a site previously cleared of all other vegetation.

At each site, two treatments were used: with or without the addition of nutrient (Fisons 52 regular, a granular fertilizer with N P K = 20:10:10, applied at the rate of 30 g/m^2).

Six tillers were planted in each experimental unit, in series 6:0, 4:2, 3:3, 2:4, 0:6, with two replicates of each unit.

The experiment was set up in October 1980 to run undisturbed for 3 years. It was monitored at regular intervals by counting the number of tillers in each pot, measurements were also taken of other characters such as leaf length. In this paper, results after one-year growth are given, using tiller number to represent yield (Khan *et al.*, 1975).

Growth habit

Flowering

Because of breakdowns in the course of meiosis in micro- and macro-sporogenesis, described by Westergaard (1943) and Kubien (1965, 1970), *x C. baltica* is a sterile hybrid. Thus it is not able to increase its distribution by seed, and is confined to spreading by rhizome growth only. The species, however, still produces flowering culms, which are taller, with bushier panicles (Hubbard, 1968), though generally fewer in number, than those of *A. arenaria* in a comparable area ($p > 95\%$, Table 1).

Table 1. Flowering of *x C. baltica* and *A. arenaria* in quadrats where flowering occurs (quadrat data, *F* values and correlation coefficient (*r*) calculated for flowers/quadrat with % cover/-quadrat for both species).

	x *C. baltica*	*A. arenaria*
n	30	45
$\bar{x}$ Flowers/quadrat	3.9	11.6
$\bar{x}$ % cover/quadrat	20.4	26.1
F	9.51	5.60
r	0.504	0.339
p	0.001	0.05
$\bar{x}$ Flowers/cover	0.27	0.61
SEM	0.05	0.12

p = significance level; SEM = standard error of the mean.

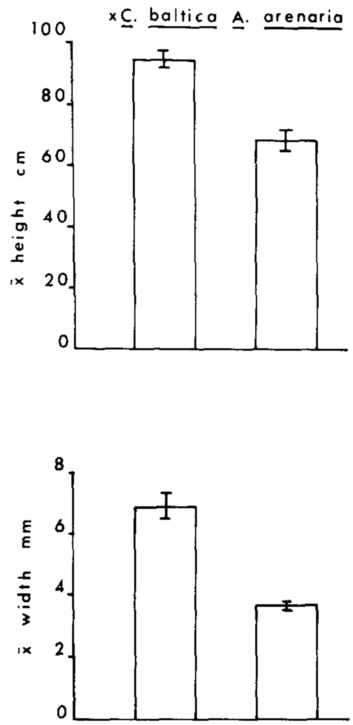

Fig. 1. Comparison of the leaf length and width of *x. C. baltica* and *A. arenaria* (quadrat data).
Bar indicates 95% confidence limits.

Leaves

When growing in a pure or mixed sward, the length and width of the leaves of *x C. baltica* are always greater ($p > 95\%$) than those of *A. arenaria* (Fig. 1). The greater width of the leaves of *x C. baltica*, plus a decrease in the sclerenchymatous strengthening tissues (Westergaard, 1943), means that they are also more lax than those of *A. arenaria*.

Rhizome and tillering pattern

The characteristic tussock appearance of *A. arenaria* is produced by a combination of horizontal rhizomes with long internodes (3–10 cm), giving rise to occasional areal shoots, which, under certain conditions, will branch to form vertical rhizomes, often with very short internodes (<2 cm), and forming a tuft of daughter tillers (Greig-Smith *et al.*, 1947; Gemmell *et al.*, 1953). *C. epigejos* tends to produce a more even sward, indicating that it has internodes of similar mean length, without vertical rhizomes, and with only one or two tillering branches at any given point.

By 1982, in the planted area at Winterton, Norfolk, the total distance covered by rhizomes of *x C. baltica* was much greater than that of *A. arenaria* rhizomes, although the cover was not as dense. Secondary tufts were smaller, and the distances between them were also smaller ($p > 0.0002$ and 0.007 respectively when tested with the Mann Whitney U test) (Table 2, Fig. 2). In addition, in *x C. baltica* the central tussock, presumed to be the original planting stock, though covering a similar area in both cases, had significantly fewer tillers than *A. arenaria*. Two of the tussocks of *A. arenaria* had no apparent extended rhizome growth at all, and in one tussock of *x C. baltica* the center was not discernable. This suggests that *x. C. baltica* has fewer short internodes producing tussocks, and possibly a greater total number of long ones, than *A. arenaria*.

Competition

Competitive effects between *x C. baltica* and *A. arenaria*, which appear to share the same general niche, were examined in the de Wit type replacement series. There appear to be mutual competitive effects, the Relative Yield Totals (*RYT*), calculated

Table 2. Tiller and rhizome pattern of *x C. baltica* and *A. arenaria*, 3 years after planting (Winterton blowout).

		x *C. baltica*	*A. arenaria*
n original 'plants'		5	8
$\bar{x}$ diameter of central tussock	cm	10.50	18.12
	SEM	1.64	4.50
$\bar{x}$ tillers in central tussock		10.00	33.50
	SEM	1.63	5.95
apparent *n* outlying rhizomes		13	17
total distance covered	cm	543.01	343.99
n tufts		65	23
$\bar{x}$ distance between tufts	cm	8.35	14.95
	SEM	1.15	2.30
$\bar{x}$ tillers/tuft		1.55	2.96
	SEM	0.09	0.37

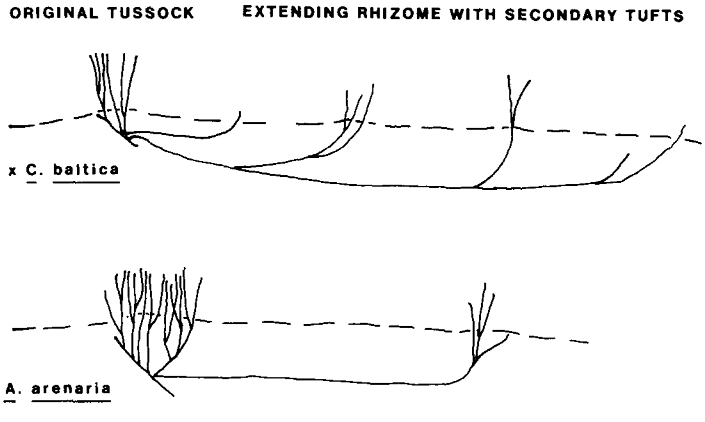

Fig. 2. Comparison of branching and tillering patterns in *x C. baltica* and *A. arenaria*, as indicated by the data given in Table 2. Pecked line shows sand surface.

for tiller numbers, were < 1.0, in all cases except for the Studland plot with added nutrient, in both sites this effect is greater in the untreated plots (Table 3). The graphs of the series (Fig. 3) show a model 3 reaction, with both species having an effect on the other, and the two species could be described as 'crowding for the same space' (de Wit, 1960). Again, the results for the fertilized plot at Studland do not agree with the rest, but appear to indicate that an abundance of nutrients will reverse the crowding effect.

It is of interest to note the differences in actual yield between the sand dune (roots and rhizome growth unrestricted) and pot (below-ground growth restricted) experiments. In the plots to which nutrients have been added, the yield of both species is substantially higher where the plants have the opportunity of radial spread. In the unfertilized plots the pot experiment has a slightly higher actual yield, which may result from the nutrients in the potting compost.

Table 3. Values of *RYT* for the 4 different treatments in the competition experiment (based on tiller number, for details, see text).

	0 nutrient	+ nutrient
Studland	0.875	1.338
Chilworth	0.880	0.697

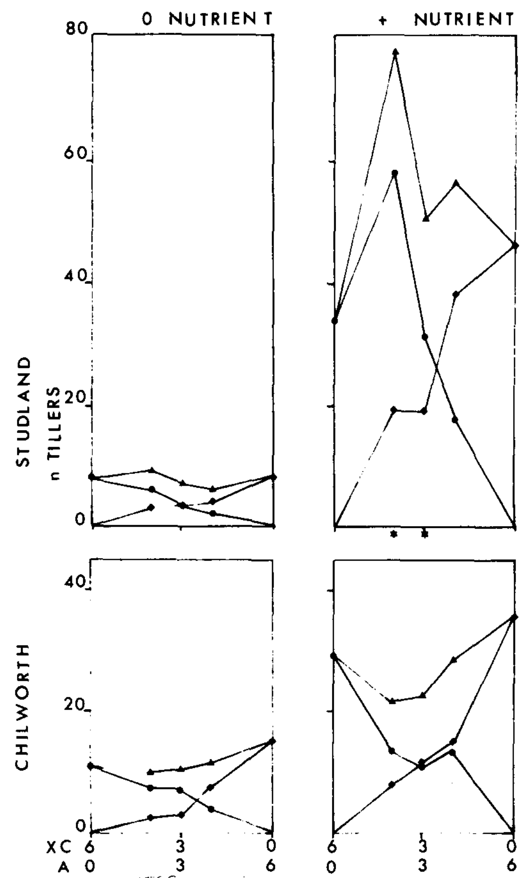

Fig. 3. The yield (as measured by number of tillers produced) of *x C. baltica* (X C) and *A. arenaria* (A) in replacement series, with and without added nutrients, at Studland (open sand) and Chilworth (pots).
* = only one replicate.

Discussion

In an actively accreting sand dune system, most of the sand movement is by sand creep and saltation, entrainment of the sand particle being a function of the shear velocity of the wind at the sand surface and the size of the grain (Bagnold, 1941). Sand particles may be lifted to heights of up to 1 m. at high wind speeds, but are commonly carried at a much lower height than this (Allen, 1970). The velocity of wind over a rough surface is proportional to the logarithm of the height above the surface, and is reduced to zero at a height Z_0 above the sand surface which varies according to the height and spacing of surface irregularities (see Ranwell, 1972, pp. 143–147, for a discussion of these points). Olson (1958) has shown that planting Marram can increase Z_0 thirty-fold from its value for bare sand. This means that most of the blown sand is trapped in the area of increasing Z_0 within a few meters on the leading edge of the vegetation (Fig. 4).

For dune conservation work, the important factors are to maintain a high value for Z_0 with an unbroken vegetation cover, to prevent erosion of sand already deposited; and, for sand dune building, or reconstruction, to have a comparatively wide area of increasing Z_0, with vegetation capable or rapidly growing up through freshly deposited sand.

Both *A. arenaria* and *x C. baltica* are capable of rapid growth through sand deposits. *A. arenaria*, despite its lower growth and narrower leaves, will provide a more dense vegetation cover, in terms of tiller number, than its hybrid. But, in endangered areas, the hybrid will spread faster, and the laxity of its leaves (which can be wind blown to the sand surface) may increase its effective density. Z_0 is likely to increase at a lower rate inland from the leading edge of a pure *x C. baltica* sward due to the lower tiller number, making this the more useful

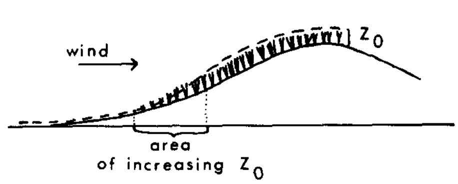

Fig. 4. The area of increasing Z_0 at the leading edge of dune vegetation.

species in areas where sand accumulation is required.

One aspect, other than its infertility, limiting the rate of spread of *x C. baltica* is its allocation of energy into flowering culms. Armstrong (1982) has suggested that up to 1/3 of the post maintenance energy of a rhizomatous plant may go into seed, rather than vegetative, production. Obviously this figure will not be so high for species such as *x C. baltica* which does not set seed, but it may still be a large portion of energy which would otherwise have gone into tiller or rhizome production.

The preliminary results of the replacement series experiment indicate that competition in a natural sward will reduce the yield of both *x C. baltica* and *A. arenaria*, but the addition of a suitable nutrient may reverse this effect, and substantially increase the total yield of both species.

Recommendations for sand dune conservation

In any planned planting of Marram, *A. arenaria* and *x C. baltica* should be planted in a mixed sward, the hybrid for fast cover, and *A. arenaria* for eventual thickness. The proportions of the species in the mixture should be varied according to the risk of wind erosion, and the need for sand deposition.

To increase the surface roughness, particularly in the years immediately after planting, as well as to add nutrient to the plants, the sand surface should be covered with a thick mulch (Adriani & Terwindt, 1974).

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