

Hybridization in the genus *Atriplex* section *Teutliopsis* (Chenopodiaceae)

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ABSTRACT

A study based on experimental hybridization, culture and field work reports the occurrence of *Atriplex* hybrids in the flora of the British Isles, and discusses the taxonomic implications of these findings. The following hybrids were synthesized experimentally: *Atriplex littoralis* × *longipes*, *A. littoralis* × *praecox*, *A. littoralis* × *patula*. Segregation of wild *A. littoralis* × *prostrata* hybrids collected from two localities in W. Norfolk, v.c. 28, was observed in the botanic garden. Some of the segregants were similar in leaf morphology to *A. patula*, and others were identical to the formerly recognized taxon *A. littoralis* var. *serrata*. Evidence is presented that *A. calotheca* (Raf.) Fries, a species endemic to Scandinavia and the Baltic coasts of adjacent countries, did not originate from *A. littoralis* × *A. prostrata* as claimed by G. Turesson. Literature reports of the putative hybrids *A. glabriuscula* × *littoralis* and *A. patula* × *prostrata* in the British Isles are probably wrong.

INTRODUCTION

Section *Teutliopsis* Dum. includes all the native British *Atriplex* species except *A. laciniata* L. The members of this section are morphologically similar, genetically highly variable and phenotypically plastic. Because of this, the recognition of hybrids can be extremely difficult. Without evidence from carefully controlled experimental hybrids, assumptions about hybridization in *Atriplex* can be no more than speculation.

Turesson (1925) produced the first artificial hybrids in *Atriplex*. He used two techniques: one, which he called "free crossing", consisted in surrounding a plant of one species with several plants of another species; the other was to isolate the inflorescences of the parent species together in the same pergamin bag. He used these uncontrolled techniques because, as he stated, "... castrations unfortunately cannot be made in the genus *Atriplex* because of technical difficulties..." (Turesson 1925). Hulme (1957, 1958), however, succeeded in producing controlled experimental hybrids.

Gustafsson (1972, 1973a, 1973b, 1974) made a large series of carefully controlled experimental hybrids between all the members of the *A. prostrata* group in Scandinavia. He examined the cytology and fertility of natural and artificial hybrids and variation in hybrid offspring. He later (Gustafsson 1976) provided morphological descriptions of the species in this group with notes on the morphology, frequency and distribution of the hybrids in Scandinavia. The Scandinavian representatives of the group include all those found in the British Isles and an additional species, *A. calotheca* (Raf.) Fries, indigenous to the Baltic region. Gustafsson's studies form the basis for understanding this complex as it exists in Britain.

Partially fertile artificial hybrids have been made between species of sections *Teutliopsis* and *Sclerocalymma*, but none have been found in nature (Björkman *et al.* 1969, 1971). Nobs (1976) summarized the results of a number of attempted intersectional crosses (including *A. prostrata* × *A. laciniata* and *A. glabriuscula* × *A. laciniata*) which produced strong F₁ progenies, but these were less than 10% fertile. The other results were highly variable with some crosses yielding a strong F₁ but others producing no seed or only a sub-lethal F₁. None of the crosses, however, was sufficiently fertile to produce a second generation.

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The present study is based on experimental hybridization and culture work in the botanic garden and on field studies in Britain between 1974 and 1978. It examines the crossing relationships between *A. littoralis* and other members of the section *Teutliopsis* occurring in Britain and elsewhere. It reports on segregation in hybrid specimens of the *A. prostrata* group collected in northern and western Scotland and it discusses the taxonomic implications of the results of these studies.

MATERIALS AND METHODS

EXPERIMENTAL HYBRIDS

The technical difficulties of making artificial crosses in *Atriplex* involve: a) the small flower size (c. 1 mm just before anthesis); b) the close proximity of the staminate to the pistillate flowers (both types occur together in tightly compressed glomerules); and c) the ease with which self-pollination can occur in this self-fertile, primarily autogamous group.

Two characteristics of *Atriplex* floral development make experimental crossing possible: the occasional production of isolated axillary pistillate flowers, and the occurrence in some species of a degree of protogyny.

The plants used as female parents in these experiments were all at least slightly protogynous. Some also produced exclusively pistillate flowers in the upper leaf axils. The branches of these plants, all of which would have produced terminal inflorescences, were clipped before the flowers opened. Only two or three branches were left for controlled crossing. The staminate buds, which in normal glomerules occurred immediately above the pistillate ones, were removed with fine forceps. Pollen, freshly collected from mature newly-opened flowers, was applied to the receptive stigmas of the female parent with a no. 000 fine sable hair brush. Each morning the inflorescences were examined before 08:00 hours with a $\times 14$ lens, and successively forming staminate buds removed. After each examination the emerging new stigmas were repeatedly brushed with fresh pollen. The process was continued for about five weeks by which time the first seeds were beginning to ripen and flower formation had ceased. Plants used as female parents were isolated in separate, screened greenhouse cubicles. Emasculated plants, not pollinated, did not develop seed.

By these methods, 35 crosses within section *Teutliopsis* were made, 14 of which produced an F_1 generation. The following species were used: *A. littoralis* L. from England, Scotland, Finland, Norway, Romania and U.S.S.R.; *A. praecox* Hülphers from Scotland and Norway; *A. prostrata* Boucher ex DC. from England; *A. longipes* Drejer from England; *A. glabriuscula* Edmondston from England; *A. calotheca* (Raf.) Fries from Norway and Denmark; *A. patula* L. from England, Hungary and Argentina. The crossing combinations are given in Table 1. In addition, one intersectional cross between *A. littoralis* (Romania) of section *Teutliopsis* and *A. rosea* L. (Romania) of section *Sclerocalymma* was attempted, but no seed was produced.

NATURAL HYBRID SEGREGATION

A. littoralis \times *A. prostrata*

Three plants of this putative hybrid were collected from two localities in Norfolk. Seed was taken from each of these plants and sown separately in sterilized compost. A total of 332 F_2 plants was scored.

A. prostrata Group Hybrid Derivatives

Seeds of putative hybrid plants believed to involve *A. prostrata*, *A. longipes*, *A. glabriuscula* and *A. praecox* from three localities on the northern and western coasts of Scotland were sown in the botanic garden. About 40 plants from each hybrid were raised.

POLLEN AND SEED FERTILITY

Pollen fertility was estimated as the percentage of well-developed pollen grains deeply stainable with trypan blue in lactophenol. From 500 to 1,500 grains were counted for each individual. Seed fertility was estimated as percentage of seeds germinating. In addition to pollen and seed fertility, seed production was examined in the hybrids and hybrid progeny.

Voucher specimens of experimental hybrids, putative hybrids and hybrid segregants were deposited in MANCH.

TABLE 1. ATTEMPTED CROSSES WITH *A. LITTORALIS*
Origin of seed is given in parentheses after the species.

Female parent	Male parent	No. of attempted crosses	No. of crosses producing an F ₁	Total no. of F ₁ plants
Diploid 2n=18	Diploid 2n=18			
<i>A. littoralis</i> (England) ×	<i>A. prostrata</i> (England)	1	0	0
<i>A. littoralis</i> (U.S.S.R.) ×	<i>A. prostrata</i> (England)	1	0	0
<i>A. littoralis</i> (Finland) ×	<i>A. glabriuscula</i> (England)	1	0	0
<i>A. littoralis</i> (England) ×	<i>A. longipes</i> (England)	1	0	0
<i>A. longipes</i> (England) ×	<i>A. littoralis</i> (England)	2	0	0
<i>A. littoralis</i> (Finland) ×	<i>A. longipes</i> (England)	4	4	45
<i>A. littoralis</i> (Finland) ×	<i>A. praecox</i> (Scotland)	2	2	9
<i>A. praecox</i> (Scotland) ×	<i>A. littoralis</i> (Norway)	4	0	0
<i>A. littoralis</i> (Romania) ×	<i>A. calotheca</i> (Norway)	1	0	0
<i>A. littoralis</i> (U.S.S.R.) ×	<i>A. calotheca</i> (Norway)	7	0	0
<i>A. littoralis</i> (U.S.S.R.) ×	<i>A. calotheca</i> (Denmark)	2	0	0
<i>A. praecox</i> (Norway) ×	<i>A. littoralis</i> (England)	1	0	0
Diploid 2n=18	Tetraploid 2n=36			
<i>A. littoralis</i> (Romania) ×	<i>A. patula</i> (England)	1	1	13
<i>A. littoralis</i> (U.S.S.R.) ×	<i>A. patula</i> (Argentina)	1	1	32
<i>A. littoralis</i> (U.S.S.R.) ×	<i>A. patula</i> (England)	5	5	91
<i>A. littoralis</i> (U.S.S.R.) ×	<i>A. patula</i> (Hungary)	1	1	40

RESULTS AND DISCUSSION

EXPERIMENTAL HYBRIDS

A. littoralis × *A. prostrata* Group

The results of attempts to cross diploid *A. littoralis* with members of the diploid *A. prostrata* group are summarized in Table 1. The pollen fertility of the species and hybrids is compared in Table 2.

Although *A. littoralis* hybridizes with *A. prostrata* in nature, as discussed below, attempts to obtain artificial hybrids were unsuccessful. In all attempted crosses, however, the *A. prostrata* parents were inland ruderal biotypes. The natural hybrids involved only the coastal halophytic biotypes.

TABLE 2. POLLEN FERTILITY (% STAINABLE GRAINS) IN SPECIES,
NATURAL HYBRID PROGENY, AND EXPERIMENTAL HYBRIDS
N=number of plants sampled

	0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	N
Species											
<i>A. littoralis</i>	—	—	—	—	—	—	—	—	1	3	4
<i>A. patula</i>	—	—	—	—	—	—	—	—	—	1	1
<i>A. praecox</i>	—	—	—	—	—	—	—	—	—	1	1
Wild hybrid segregants											
<i>A. littoralis</i> × <i>A. prostrata</i> F ₂	—	—	—	1	1	3	1	3	3	4	16
Experimental hybrids											
<i>A. littoralis</i> × <i>A. longipes</i> F ₁	—	—	5	8	7	5	1	—	—	—	26
<i>A. littoralis</i> × <i>A. praecox</i> F ₁	—	—	—	1	4	—	—	—	—	—	5
<i>A. littoralis</i> × <i>A. patula</i> F ₁	4	—	—	—	—	—	—	—	—	—	4
<i>A. littoralis</i> × <i>A. patula</i> F ₂	1	1	2	2	1	—	—	—	—	—	7
<i>A. littoralis</i> × <i>A. patula</i> F ₃	—	—	—	—	—	—	—	4	4	—	8

TABLE 3. *A. LITTORALIS* × *A. PATULA*: SEQUENCE OF PLANTS CULTIVATED 1975–1978 FROM A SINGLE CROSS

One cross yielding 40 hybrid plants	Number	%
F₁		
Plants cultivated to maturity	36	90
Plants surviving to produce some seed	12	33
Total seed production of all seed-bearing plants	35	
Seeds planted	35	100
F₂		
Seeds germinating	17	49
Plants surviving to produce some seed	17	100
Total seed production of all seed-bearing plants	c.900	
Seeds planted	20	2
F₃		
Seeds germinating	13	65

Attempts to synthesize the hybrid *A. littoralis* × *glabriuscula* were also unsuccessful.

A. littoralis was successfully crossed with *A. longipes* only when Finnish *A. littoralis* was used as the female parent and English *A. longipes* as the male parent. Reciprocal crosses using English plants only were unsuccessful. The F₁ hybrids were morphologically intermediate between the parent species and distinctly different from *A. littoralis* × *prostrata* hybrids.

A. littoralis (female) was crossed with *A. praecox* (male) and produced morphologically intermediate hybrids. Four attempts at the reciprocal cross failed. Crosses using two strains of *A. praecox* (one from Norway and one from Scotland) as the female parent produced many well-formed seeds but none of them germinated.

Unsuccessful attempts were made to cross *A. littoralis* with *A. calotheca*, a member of the *A. prostrata* group almost entirely restricted to the coasts of Scandinavia. This cross was of particular interest because of Turesson's (1925) belief, based on experimental findings, that *A. calotheca* itself originated from the hybrid *A. littoralis* × *A. prostrata*.

Except for *A. littoralis* × *prostrata*, discussed below, no hybrids between *A. littoralis* and members of the *A. prostrata* group have been found in nature.

A. littoralis × *A. patula* Crosses

All crosses between diploid *A. littoralis* (female) and tetraploid *A. patula* (male) were successful and 176 triploid F₁ plants were obtained (Table 1). In cultivation, the F₁ hybrids were large (up to

TABLE 4. *A. LITTORALIS* × *A. PATULA*: SUMMARY OF CULTIVATED PLANTS AND FERTILITY CHANGES IN THREE GENERATIONS

Total no. of crosses	8
Total no. F ₁ plants produced	176
Total no. F ₁ plants grown to maturity	140
Total no. F ₁ plants producing seed	18
% seed-bearing F ₁ plants	13
Range of seeds per F ₁ plant	(0–) 1–8 (–32)
Total no. of F ₂ plants grown to maturity	42
Total no. of F ₂ plants producing seed	33
% seed-bearing F ₂ plants	79
Range of seeds per F ₂ plant	(0–) 15–175 (–c.300)
Total no. of F ₃ plants grown to maturity	11
Total no. of F ₃ plants producing seed	9
% seed-bearing F ₃ plants	82
Range of seeds per F ₃ plant	(0–) c.300–c.1000 (–c.2000)

TABLE 5. HYBRID DERIVATIVES IN THE *A. PROSTRATA* GROUP.
SUMMARY OF CULTIVATION RESULTS

Hybrid	Locality	Progeny
<i>A. glabriuscula</i> × <i>praecox</i>	Tongue, v.c. 108	One of the progeny had bracteoles with stalks suggesting <i>A. longipes</i> may be involved
<i>A. × kattegatensis</i> (<i>A. longipes</i> × <i>prostrata</i>)	Ullapool, v.c. 105	No segregation. Plants very similar to each other
<i>A. glabriuscula</i> × <i>longipes</i>	Oban, v.c. 98	Parental characters apparent in several of the progeny, i.e., long-stalked, very thick bracteoles

1.5 m high) and robust, but mostly sterile. Pollen fertility varied from 5% to 9% stainable grains and the seed set varied from one to eight seeds per plant (to 32 in one plant). Only 13% of the plants produced any seed. Hulme (1957) examined the cytology of this hybrid and reported irregular meiosis: bivalents and univalents occurred and trivalents were frequent; tetrads contained from three to five units that varied considerably in size. In later generations (Tables 3 and 4), pollen fertility, seed production and fertility increased but this was not matched by an increase in vegetative vigour. The F_2 and F_3 plants were weak and morphologically distorted and probably would not have survived outside of greenhouse cultivation.

The experimental F_1 hybrid is readily made and vigorous. Therefore, one might expect the wild hybrid to be frequent in nature. This, however, is not the case. Despite careful searches in several coastal localities where *A. patula* and *A. littoralis* were observed growing together in disturbed ground, only one putative hybrid population was found.

The wild hybrids were much smaller than the experimental hybrids, with shorter leaves and much more condensed inflorescences. A characteristic feature of this hybrid was the presence on most inflorescences of one or two expanded, well-formed, fertile bracteoles that stood out amongst a mass of compressed, mis-shapen, sterile bracteoles.

NATURAL HYBRIDS

A. prostrata Group

Segregation in Putative Hybrids. Segregation in the putative hybrid offspring was not clear. The wild hybrids seemed to be hybrid derivatives rather than first generation hybrids and it was not obvious which of the four species in this group were involved. Their progeny often showed the same characters as the parents, only in different combinations. Characters derived from the original parent species were not seen together in any single offspring but could sometimes be observed in several plants derived from one hybrid. The development of stalked bracteoles on several plants indicated, for example, that *A. longipes* was involved. One progeny from Ullapool plants showed little variation and compared well with a relatively stable variant of *A. longipes* × *A. prostrata* that is common on the western coasts of Sweden. The results of cultivation are summarized in Table 5.

Effectiveness of Cultivation as a Technique. Previous authors have commented on the problems of using cultivation to determine the parentage of putative hybrids in the *A. prostrata* group. Turesson (1925), who raised up to 200 individuals from putative hybrids in the group, observed that segregation often took place only as regards subtle, small characters that allowed no conclusion to be drawn as to the parental species. Gustafsson (1973a) noted that most of the genes governing the taxonomic characters in this group, even those conditioning the different characters of the bracteoles, are inherited unlinked.

The following practical reasons limited the use of cultivation to investigate the parentage of wild hybrids in this group. Firstly, the progeny of hybrids were often extremely luxuriant, producing tangled masses of branches up to 1 m long, and requiring large areas for cultivation. Secondly, in this group it was essential to grow all the plants to maturity to study the characters of the bracteoles. These, however, were very easily lost from the plants. Indoors, the branches of adjacent plants became tangled and most of the bracteoles fell off in separating them; outdoors, birds removed most of the bracteoles.

TABLE 6. *ATRIPLEX LITTORALIS* × *A. PROSTRATA* NATURAL HYBRIDS, F₂ SEGREGATION AND SEED GERMINATION

Locality	% seeds germinating	No. of plants examined	No. of <i>prostrata</i> types	No. of intermediate types	No. of <i>littoralis</i> types	No. of sickly plants
Wolferton, Norfolk						
76-24A	86.5	82	10	61	5	6
76-24B	86.1	46	4	36	6	0
Burnham Deepdale, Norfolk						
76-20	50.7	204	56	85	7	56

Occurrence in the British Isles. *A. longipes* × *A. prostrata* is one of the most frequent hybrids on the coasts of Britain. A true-breeding variant is known from northern and north-western Scotland and Shetland where it occupies a habitat uncolonized by either of the parent species. Gustafsson (1973b) has made artificial hybrids between this variant and the following species: *A. longipes*, *A. praecox* and *A. prostrata*, but these hybrids have not been reported from nature. Field studies indicate that other hybrids and hybrid derivatives involving *A. longipes* are very frequent in Britain and of key importance in understanding variation in the *A. prostrata* group here.

A. littoralis × *A. prostrata*

Segregation in Putative Hybrids. *A. littoralis* × *A. prostrata* putative F₁ hybrids collected in nature were relatively fertile. About 70–80% of the bracteoles contained well-developed seed. Both large-brown and small-black seed morphs were frequent in the same plant and germination of both morphs was high (80 to 90%). Pollen fertility of F₂ plants is given in Table 2, and segregation is summarized in Table 6.

From 3% to 13% of the plants segregated toward *A. littoralis*, 9% to 27% toward *A. prostrata* and from 42% to 78% of the segregants were morphologically intermediate. The percentage of sickly and distorted plants ranged from 0% to 27%. In all three hybrids the number of progeny that segregated back toward the parental types left no doubt as to the parentage of the hybrid. Pollen fertility varied from less than 40% to more than 90%, but in 56% of the plants the fertility values were less than 80%.

In contrast to hybrid segregation in the *A. prostrata* group (Gustafsson 1973b), morphological segregation towards the parent species appears to be combined with the restoration of male fertility. With few exceptions, plants segregating toward parental types, including the *serrata* leaf form of *A. littoralis*, had pollen with well-formed, equal-sized grains and fertility values of over 90%. Morphologically intermediate plants showed considerable variation both in equality of grain size and stainability. Most of the plants in this category had pollen grains of unequal size with the amount of stained pollen ranging from 40% to 74%.

Segregants showing a wide range of character combinations occurred in cultivation and were observed growing with F₁ plants in the field. Many of the segregants were largely sterile and often weak-stemmed, but some were vegetatively very vigorous. The following three variants appeared in cultivation and were later found to be common where the hybrids occurred in nature:

1. *Patula*-leaf form (Fig. 1B). Plants with leaves like *A. patula* that possess the falcate basal lobes so characteristic of this species.
2. *Serrata*-leaf form (Fig. 1A). Plants with markedly sinuate-dentate leaves like extremes of plants formerly called *A. littoralis* var. *serrata*.
3. Gigantic form. Plants up to 1 m (2 m in cultivation) high with thick stems and gigantic leaves with ovate-lanceolate, irregularly-lobed laminae up to 15 cm long and 4 cm wide.

Occurrence in the British Isles. *A. littoralis* and *A. prostrata* commonly occur together. *A. littoralis* is frequently a dominant, forming dense stands, whilst *A. prostrata* is an associated subdominant. The two species are reproductively isolated from each other by differences in flowering time. *A. littoralis* flowers earlier. Cropping the terminal inflorescence in this species induces re-flowering in the new branches that arise. The later-flowering branches overlap in flowering time with *A. prostrata*. In cultivation, when the terminal inflorescences are removed, the axillary flowers that

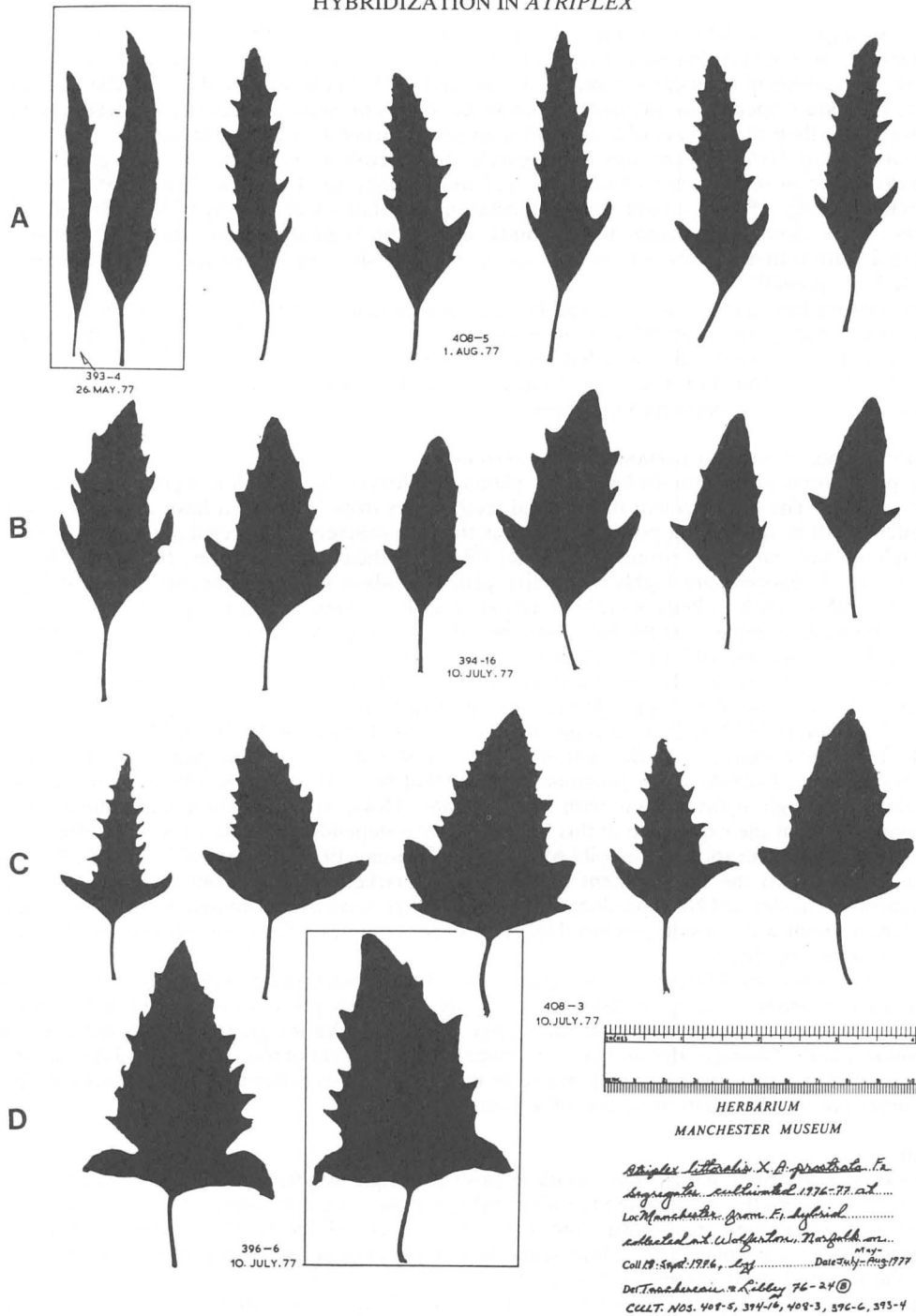


FIGURE 1. Leaf morphology of a variety of F₂ segregants cultivated from the wild hybrid *Atriplex littoralis* × *A. prostrata*. A, *A. littoralis* types (boxed) and leaves similar to those of the formerly recognized taxon *A. littoralis* var. *serrata*. B, Leaves morphologically ± identical to those of *A. patula*. C, Various intermediate leaf forms. D, *A. prostrata* types.

form are largely pistillate. In nature, this phenomenon coupled with protogyny would further favour out-crossing in *A. littoralis*. The hybrid *A. littoralis* × *A. prostrata* is known from the eastern and western coasts of England in v.cc. 28, 58, 60, and 66. It can be expected in disturbed habitats where the parent species are present in abundance: banks of estuaries recently dredged, earthen sea walls less than three years old, and salt marshes disturbed by rabbit cropping.

Resemblance of Hybrid Segregants to A. patula. In cultivation, numerous F₂ segregants of *A. littoralis* × *A. prostrata* were identical in leaf morphology to *A. patula*. Plants with this leaf morphology (Fig. 1B) were later found to occur in populations of wild hybrids in Britain. The plants bear a close resemblance to *A. patula* and in the vegetative state are very difficult to distinguish from that species. I have seen more than one sheet of the hybrid in British herbaria labelled "*A. patula*".

The mature hybrid plants may be readily distinguished from *A. patula* by the bracteoles. In the hybrid these are spongy-thick while in *A. patula* they are herbaceous and thin. Unlike the hybrid, *A. patula* does not grow in the same habitat as *A. littoralis*. The hybrid tends to be more succulent than *A. patula* and the lower leaves and branches on the hybrid are commonly alternate while in *A. patula* they tend to be opposite to subopposite.

ORIGIN OF SERRATE-LEAVED VARIANTS OF *A. LITTORALIS*

Most populations of *A. littoralis* have some plants with leaves that exhibit a degree of tothing on their margins. The development of marginal teeth varies from leaves that have only a few short irregular teeth in their distal portions to leaves that are coarsely and irregularly sinuate-dentate throughout and may have pronounced basal lobes. In their extreme form, the serrate-leaved variants of *A. littoralis* are highly distinctive plants. Hudson (1762), Linnaeus (1771) and pre-Linnean authors such as Petiver (1713) recognized such variants as distinct species.

For excellent examples, see the following sheets in the British herbarium BM: v.c. 15, Sandwich Bay, R. Meinertzhagen, 10.VIII.32; Pegwell Bay, A. J. Wilmott, 20/9/1912; v.c. 18, Bank of Thames at Tilbury Fort. There are also specimens from v.cc. 13, 16, 18. In LD there are specimens of this variant collected from Borgholm, Öland, Sweden by different collectors in successive years: 1874 by C. F. Elmqvist; 1912 by B. J. Holmgren; June 1932 by A. Vilke and July 1932 by H. Hylander.

The repeated appearance of this extreme variant as well as less extreme plants amongst the F₂ segregants of *A. littoralis* × *A. prostrata* suggests that the serrate-leaved plants of *A. littoralis* originated through hybridization with *A. prostrata*. However, cultivation experiments have demonstrated that the expression of this leaf character is dependent on relatively high nitrogen or optimum salt concentration in the soil (Ahmad in Taschereau 1979). For example, 50 mM NaCl in the nutrient led to the development of leaves with marked serrations but increasing the salt concentration to 400 mM NaCl produced plants with entire leaves. Control plants, grown in diluted standard nutrient without salt, produced leaves with a few short teeth such as are commonly found in *A. littoralis* populations.

Moss & Wilmott (1914) and various other authors have treated plants with more or less serrate leaves as a taxonomic variety: *A. littoralis* L. var. *serrata* (Huds.) S. F. Gray. Such plants occur in most populations of *A. littoralis* and the degree of tothing varies greatly within and between individual plants. Owing to this and the environmental component of the variation and the fact that there is no consistent correlation with bracteole morphology, it is better to recognize this variation in a description rather than by means of a formal epithet.

ORIGIN OF *A. CALOTHECA*

Tureson (1925) stated that *Atriplex calotheca* probably originated from the cross *A. littoralis* × *A. prostrata*. He based this on presumed artificial hybrids morphologically similar to *A. calotheca*. The pollen fertility of these plants was low and a great many of the bracteoles empty. Tureson suggested that the lacinate-leaved individuals he obtained originated from crosses of *A. prostrata* with the serrate-leaved variant of *A. littoralis*.

I was unable to find specimens in LD or S of the plants Tureson assumed represented the hybrid *A. littoralis* × *A. prostrata*. The photograph, however, in Fig. 8 and the drawings in Fig. 9 of Tureson's (1925) paper as well as the description are of specimens that are clearly identical to *A. calotheca*. They bear no resemblance to the plants I have described as *A. littoralis* × *A. prostrata*. The plants that Tureson described as this hybrid may have arisen by segregation from *A. prostrata*

plants that were themselves of hybrid origin involving *A. calotheca*. The following facts support this explanation. Firstly, hybrid plants in the *A. prostrata* group can resemble one or other of the parents (Gustafsson 1973a). When the seeds from such plants are cultivated, the effects of hybridization usually become evident in some of the progeny. Secondly, Turesson did not succeed in emasculating the parent plants, and in his attempt to obtain hybrids between *A. prostrata* and *A. littoralis* by 'free crossing', he harvested only the *A. prostrata* plants. Thirdly, introgressive hybridization between *A. prostrata* and *A. calotheca* is a common phenomenon in western Scandinavia and extensive hybrid swarms are frequent throughout the entire range of *A. calotheca* (Gustafsson 1976). The exact geographical origin of the plants Turesson used as parents is unknown, but hybrids between *A. prostrata* and *A. calotheca* are common at the sites Turesson investigated (M. Gustafsson pers. comm. 1975).

ERRONEOUS AND UNCONFIRMED REPORTS OF HYBRIDS

The identification of hybrid material in *Atriplex*, without evidence from experimental studies, is unsatisfactory. The following reports, all unconfirmed, are probably wrong.

A. glabriuscula × *A. littoralis*

Jones (1975) reported this hybrid based on plants she observed at Gibraltar Point, v.c. 54. My attempts to synthesize it were unsuccessful. Jones's report is probably incorrect because *A. glabriuscula*, one of the putative parents, is absent from Gibraltar Point. I searched carefully for it there in 1975 and the species later proved to be entirely absent from the coasts of Yorkshire, Lincolnshire and Norfolk, v.cc. 61, 54, 28, 27 (Taschereau 1979). The description of Jones's putative hybrid agrees with that of *A. littoralis* × *A. prostrata* and both of the parent species of this hybrid are present at Gibraltar Point. Jones (pers. comm. 1975) was herself not at all certain of her identification and was not aware of the existence of *A. littoralis* × *A. prostrata*.

A. patula × *A. prostrata*

Jones (1975) reported this hybrid as "very doubtfully recorded from v.cc. 3, 10 and 14 and from Germany on the basis of apparently intermediate specimens". *Atriplex patula* and *A. prostrata* very frequently grow together, often with their branches intertwined, in disturbed ground on vacant lots and demolished building sites throughout the British Isles. The hybrid was synthesized by Hulme (1957, 1958) who reported that the plants did not resemble any wild plants she had seen. Although the wild hybrid may yet be found in Britain, Jones's report is probably wrong. Despite numerous searches for the hybrid in situations where it might be expected, I have not found it. All specimens of apparently intermediate morphology, on cultivation, proved to be one of the species, usually *A. prostrata*. The basis for at least some reports of plants intermediate between *A. patula* and *A. prostrata* is probably the hybrid *A. longipes* × *A. prostrata*, only recently reported to occur inland in waste places (Taschereau 1985). Derivatives of this hybrid frequently have leaves with obtuse to cuneate bases that make them appear intermediate between *A. patula* and *A. prostrata*, previously the only taxa known from this habitat.

A. glabriuscula × *A. praecox*

Putative hybrids between *A. glabriuscula* and *A. praecox*, reported from Tongue, v.c. 108 and Ullapool, v.c. 105 (Taschereau 1977), remain unconfirmed. Plants grown from seed taken from these specimens yielded a range of variants (Table 5), none of which showed a clear segregation toward either of the putative parents. Other reports of this hybrid (Taschereau 1985) are based on plants clearly intermediate with small leaves morphologically identical to those of *A. praecox* and with bracteoles and seeds morphologically like those of *A. glabriuscula*.

A. glabriuscula × *A. prostrata*

This hybrid is not as common in the British Isles as Moss & Wilmott (1914) believed and as suggested by Jones (1975) who stated that intermediates between *A. glabriuscula* and *A. prostrata* "appear to be common in the British Isles where the two species are in contact. This occurs when weedy habitats are introduced into maritime areas by landslides or the building of sea-defences etc." Specimens I examined in BM identified by A. J. Wilmott as this hybrid were variants of *A. glabriuscula*.

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REFERENCES

- BJÖRKMAN, O., GAUHL, E. & NOBS, M. A. (1969). Comparative studies of *Atriplex* species with and without B-carboxylation photosynthesis and their first-generation hybrid. *Carnegie Inst. Washington Yb.*, **68**: 620–633.
- BJÖRKMAN, O., NOBS, M. A. & BERRY, J. A. (1971). Further studies on hybrids between C₃ and C₄ species of *Atriplex*. *Carnegie Inst. Washington Yb.*, **70**: 507–511.
- GUSTAFSSON, M. (1972). Distribution and effects of paracentric inversions in populations of *Atriplex longipes*. *Hereditas*, **71**: 173–194.
- GUSTAFSSON, M. (1973a). Evolutionary trends in the *Atriplex triangularis* group of Scandinavia, 1. Hybrid sterility and chromosomal differentiation. *Bot. Notiser*, **126**: 345–392.
- GUSTAFSSON, M. (1973b). Evolutionary trends in the *Atriplex triangularis* group of Scandinavia, 2. Spontaneous hybridization in relation to reproductive isolation. *Bot. Notiser*, **126**: 398–416.
- GUSTAFSSON, M. (1974). Evolutionary trends in the *Atriplex triangularis* group of Scandinavia, 3. The effects of population size and introgression on chromosomal differentiation. *Bot. Notiser*, **127**: 125–148.
- GUSTAFSSON, M. (1976). Evolutionary trends in the *Atriplex prostrata* group of Scandinavia, 4. Taxonomy and morphological variation. *Op. bot. Soc. bot. Lund.*, **39**: 1–63.
- HUDSON, G. (1762). *Flora Anglica*, p. 377. London.
- HULME, B. A. (1957). *Studies on some British species of Atriplex*. Ph.D. Thesis, University of Edinburgh.
- HULME, B. A. (1958). Artificial hybrids in the genus *Atriplex*. *Proc. bot. Soc. Br. Isl.*, **3**: 94.
- JONES, E. M. (1975). *Atriplex*, in STACE, C. A., ed. *Hybridization and the flora of the British Isles*, pp. 185–186. London.
- LINNAEUS, C. (1771). *Mantissa Plantarum*, p. 300. Stockholm. Facsimile reprint Weinheim, (1961).
- MOSS, C. E. & WILMOTT, A. J. (1914). *Atriplex*, in MOSS, C. E. *The Cambridge British flora*, **2**: 168–182, plates 172–188. Cambridge.
- NOBS, M. A. (1976). Hybridizations in *Atriplex*. *Carnegie Inst. Washington Yb.*, **75**: 421–423.
- PETIVER, J. (1713). *Herbarij Britannici*. London.
- TASCHEREAU, P. M. (1977). *Atriplex praecox* Hülpfers: a species new to the British Isles. *Watsonia*, **11**: 195–198.
- TASCHEREAU, P. M. (1979). *Taxonomy of the genus Atriplex in Great Britain*. Ph.D. thesis, University of Manchester.
- TASCHEREAU, P. M. (1985). Taxonomy of *Atriplex* species indigenous to the British Isles. *Watsonia* **15**: 183–209.
- TURESSON, G. (1925). Studies in the genus *Atriplex*. *Lunds Univ. Årsskr.*, N.F. Adv. 2, **21** (4): 1–15.

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