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Taxonomy of *Atriplex* species indigenous to the British Isles

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ABSTRACT

A biosystematic study of the genus *Atriplex* (Chenopodiaceae) based on field, culture, experimental hybridization, herbarium and cytological work delineates the taxa of this genus indigenous to the British Isles. Detailed morphological descriptions are given and distribution maps and illustrations provided for *A. prostrata* Boucher ex DC., *A. glabriuscula* Edmondston, *A. longipes* Drejer, *A. praecox* Hülphers, *A. littoralis* L., *A. patula* L., and *A. laciniata* L. The habitats and reproductive biology of the species are discussed and the chromosome numbers reported. Hybrid derivatives between *A. longipes* and *A. glabriuscula* and between *A. longipes* and *A. prostrata* are common in many areas of the coast. The following hybrids are also reported: *A. glabriuscula* × *A. praecox*, *A. glabriuscula* × *A. prostrata*, *A. littoralis* × *A. prostrata*, and *A. littoralis* × *A. patula*.

INTRODUCTION

The most recent treatment of *Atriplex* occurring in the British Isles is that of Aellen (1964) in *Flora Europaea*. According to Aellen the following species are native: *A. laciniata* L., *A. patula* L., *A. littoralis* L., *A. prostrata* Boucher ex DC. (*A. hastata*), *A. glabriuscula* Edmonston and *A. longipes* Drejer.

Atriplex laciniata is placed in section *Sclerocalymma* Aschers., and the remaining species in section *Teutliopsis* Dum. Within this section *A. prostrata*, *A. glabriuscula* and *A. longipes* form a recognizable unit, the *A. prostrata* group or *Hastata* complex.

The taxonomic problems in British *Atriplex* species have been concerned with the members of section *Teutliopsis* and in particular with the *A. prostrata* group. In section *Teutliopsis*, the number of species recognized in British floristic works has varied from one in Bentham & Hooker (1896) to nine in Babington (1841). Druce (1928) recognized 21 native taxa of which six were treated by him as species and one was considered a hybrid. The considerable variation within the *A. prostrata* group is reflected in the taxonomic treatment it has received from British authors. In 1860, C. C. Babington wrote that G. Bentham believed *A. glabriuscula* to be indistinguishable from *A. prostrata* (A. M. Babington 1897). This difference of opinion resulted in different treatments of these plants in two important British floras – that of Babington (1843) and of Bentham & Hooker (1896). Hulme (1957) did not distinguish between the coastal forms of the *A. prostrata* group, referring to them as "*hastata-glabriuscula*". Tutin (1962), while treating *A. glabriuscula* as a species distinct from *A. prostrata*, added the remark that *A. glabriuscula* is "probably best regarded as a subspecies of it".

Until recently only *A. prostrata* and *A. glabriuscula* were recognized as occurring in Britain. Hulme (Aellen 1964) mentioned *A. longipes*, which was said to be "widespread in the British Isles", but other authorities (Gustafsson 1972) doubted its presence here and no material was available for study. Jones (1975) observed plants resembling *A. longipes* in a few localities in Britain and she suggested that this taxon was present here. In 1977, I reported the presence of *A. praecox* Hülphers in the British Isles and confirmed the presence of *A. longipes* (Taschereau 1977). Taxonomic ranking within the *A. prostrata* group, previously concerned only with *A. glabriuscula*, must now consider these two additional members of the group.

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Although many authors have written about *Atriplex*, relatively few have contributed much to our understanding. Moss & Wilmott (1914) provided a well-illustrated and helpful monographic account of the *Atriplex* species occurring in Britain. Aellen (1960) dealt with the taxonomy, distribution, ecology and economic uses of European *Atriplex*, and in 1964 he provided a revised account of their taxonomy and distribution.

Biosystematic studies have been extremely important in elucidating the taxonomy of species in section *Teutliopsis*: Turesson (1922a, 1922b, 1925), in a series of pioneer studies, demonstrated the value of extensive cultivation experiments and experimental hybridization in understanding the complexities of this group. Hulme (1957, 1958) produced the first controlled experimental hybrids in *Atriplex* thereby demonstrating the feasibility of this approach to the study of the genus. Her work was of key importance in understanding the taxonomy of section *Teutliopsis* in North America as well as in Britain. Hulme's experimental findings supported the taxonomic separation of the tetraploid *A. patula* from the diploids *A. littoralis* and *A. prostrata* and the maintenance of these taxa at the level of species. Bentham & Hooker (1896) had united them as intergrading variants of *A. patula*. Although by 1957 most British and European authors were treating all three taxa as separate species, this was not the case in North America. Since Gray (1868), North American taxonomists had regarded the members of section *Teutliopsis* including *A. prostrata* and *A. littoralis* to be intergrading varieties of *A. patula*, and they continued to do so until convinced otherwise by Hulme's data and subsequent studies (Taschereau 1972). (The confusion resulting from this traditional taxonomic treatment is still evident in ecological papers from North America in which *A. patula* is referred to as a halophyte and a component of salt marsh communities. In North America, as in Britain and elsewhere, *A. patula* is a ruderal and colonizer of disturbed soil, relatively salt tolerant but not a halophyte and never a component of salt marsh communities.)

Minor contributions to the experimental taxonomy of section *Teutliopsis* were made by van der Meijden (1970) in the Netherlands, and by Jones (1975a, 1975b) in Britain. Neither author did extensive cultivation experiments nor attempted to make hybrids.

The most extensive and important biosystematic studies in *Atriplex* are those by Gustafsson (1972, 1973a, 1973b, 1974, 1976) of the *A. prostrata* group in Scandinavia. They provide a foundation for understanding the group as it occurs in the British Isles. Without Gustafsson's many experimental hybrid specimens for reference, accurate identification of the hybrid derivatives that comprise so much of the British coastal *Atriplex* flora would have been impossible.

MATERIALS AND METHODS

The present work is based on a four-year study of the genus in the field, laboratory and botanic garden.

FIELD STUDIES

Great Britain

Areas within each of the major plant regions of Britain (Heath & Scott 1974) were examined at least once between 1974 and 1978. 75 sites covering 27 vice-counties were visited. The areas included 61 coastal and estuarine habitat sites, three inland salt marshes and eleven inland sites on disturbed ground. The location of these sites is given in Fig. 1.

Samples were taken from 255 populations and collections made comprising approximately 1,270 pressed herbarium specimens. All but three of my locality records cited in this paper are supported by voucher specimens filed in **MANCH**.

In 1977, a comprehensive survey of the *Atriplex* taxa on the coasts of the British Isles was undertaken through the Botanical Society of the British Isles in cooperation with the Biological Records Centre, Monks Wood. The 251 herbarium specimens collected by the participants and 80 data cards were sent to me for identification and checking. Data were obtained from 36 vice-counties representing all coastal regions except south-western England and the coasts of Ireland. The areas from which specimens were received are shown in Fig. 1.

Sweden

Three coastal localities in the province of Skåne in southern Sweden were examined with M. Gustafsson in 1975: Bunkeflo and Skanör Harbour south of Malmö, and Torekov near Ängelholm

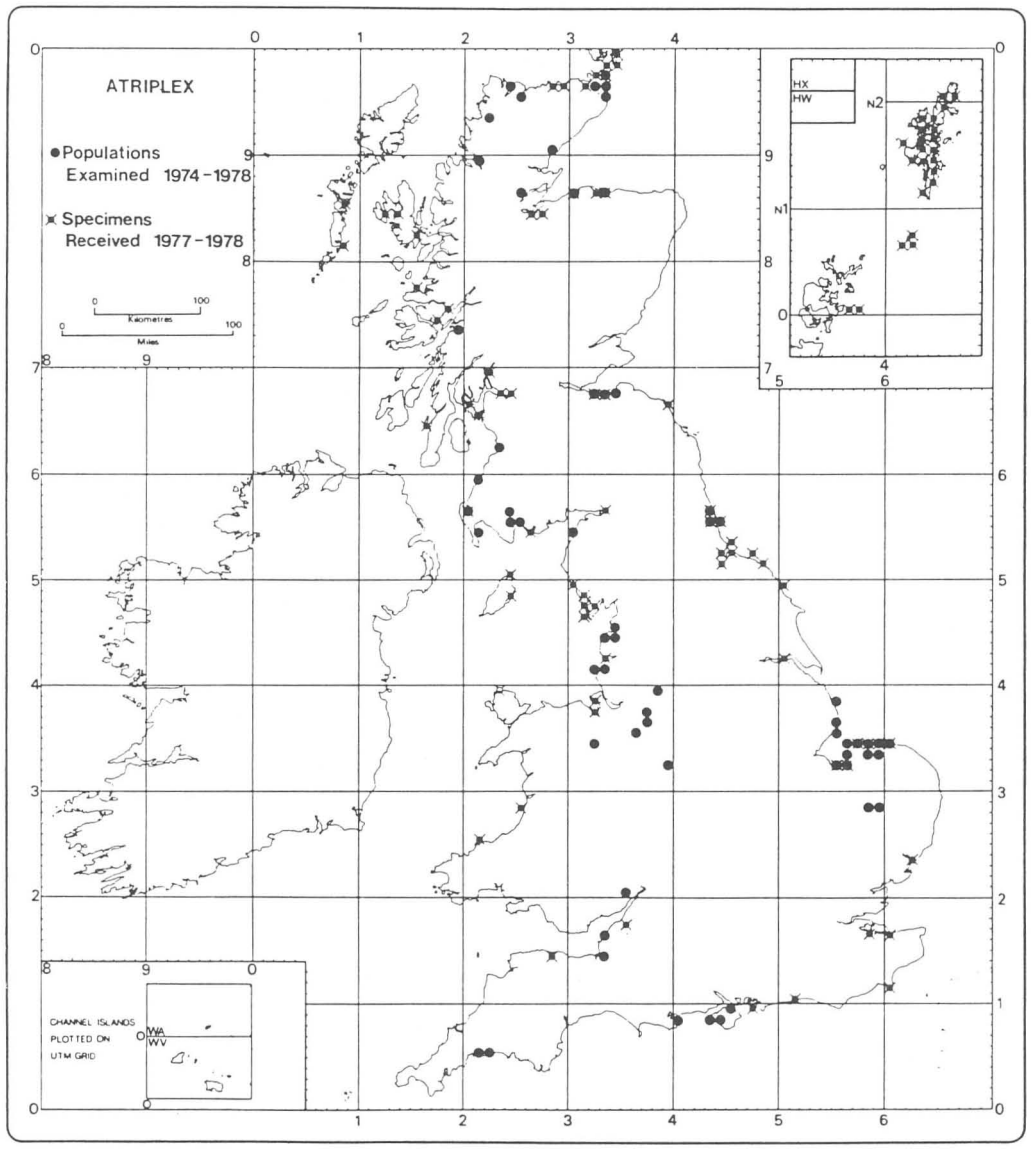

FIGURE 1. Localities from which *Atriplex* plants were examined.

on the south-western coast. The Torekov site was studied by Turesson (1925) in his work on the genus *Atriplex*, and all the localities visited provided material for the *Atriplex* investigations by Gustafsson (1976).

In 1976, three localities were examined on the coasts of the Baltic Sea: Kalmar on the mainland, Stora Rör and Ottenby on the island of Öland. Ottenby is the restricted type locality of *Atriplex hastata* L. (Stearn 1973). In total, six Swedish sites were examined and three populations were sampled, the taxa comprising five species and four hybrids.

CULTIVATION

Large numbers of plants were cultivated to study regional variation and phenotypic plasticity. Plants were also cultivated to confirm identification, to facilitate observations on reproductive biology, to make artificial hybrids and to observe segregation in natural and artificial hybrid progeny. From 1974 to 1978, approximately 2,650 plants were cultivated either in the greenhouse or in outdoor plots in the botanic garden. Of these, about 1,280 were grown to maturity. These included 27 taxa comprising representatives of all the four European sections of the genus. For reference and study, 380 specimens of pressed plants consisting of stems, leaves, bracteoles and fruit were prepared from the cultivated material, as well as 75 specimens consisting only of bracteoles and fruit.

Seeds were sown in trays of John Innes Seed Compost in the autumn and placed in an unheated greenhouse over winter. In this way the dormancy encountered in several species was overcome. The seedlings were later transferred to individual pots containing John Innes Potting Compost. Dormancy in almost all seeds could be overcome by placing the moistened seeds in a controlled cycling environment (Ignaciuk & Lee 1980) where they were exposed to 9 hours dark at 10°C and 15 hours light at 30°C. Germination then occurred within two weeks. In a few cases, however, seeds in the controlled cycling environment germinated only after the seed coat was also removed.

CYTOLOGY

The chromosomes are small (2–3 μm), metacentric to submetacentric, and morphologically similar. The basic number in the genus is x=9. Endomitosis, the formation of cells containing multiples of the normal somatic number, is a phenomenon encountered in *Atriplex* root-tips, and one that complicates chromosome counting. Diploid, tetraploid and octoploid cells are commonly present in the same root-tip preparation. Polyploid cells increase in number along the root-tip. They can be largely avoided in cytological preparations by utilizing only a minute section of the root behind the root-cap.

Root-tips obtained from vigorous young plants cultivated in pots in the greenhouse were pre-treated overnight in 0.2 mM solution of 8-hydroxyquinoline at 5°C then fixed in absolute alcohol-glacial acetic acid (3:1) for 24 hours. The material was then transferred to 70% alcohol and stored in the deep freeze until use. The tips were hydrolysed in 1N HCl for 9 minutes at 60°C then stained in Feulgen for 2 hours. The excised tip was tapped and squashed in lacto-propionic orcein.

Meiotic preparations were made by fixing very young buds in a mixture of absolute alcohol, chloroform and glacial acetic acid (6:3:1) for 24 hours in the deep freeze. The fixed buds were transferred to 70% alcohol before use then dissected out in 45% lacto-propionic acid and squashed in lacto-propionic orcein.

HERBARIUM

Descriptions and other taxonomic data presented in this study are based almost entirely on specimens I collected between 1974–1978 or collections made by others during that period and sent to me. Herbarium studies were used primarily to supplement and confirm these data and to establish the extent of variation within taxa from widely separate geographic regions. My distribution records of *A. patula*, *A. prostrata*, *A. littoralis* and *A. laciniata* are supplemented by data provided by the Biological Records Centre. Additional distribution records of *A. glabriuscula* and *A. praecox* are based only on herbarium specimens I identified.

Material from the following herbaria was studied: **ABD**, **ANK**, **BM**, **C**, **CGE**, **DBN**, **E**, **K**, **LD**, **LIV**, **LIVU**, **MANCH**, **NMW**, **OXF**, **SLBI**, **TCD** (abbreviations according to Kent & Allen (1984) and Holmgren *et al.* (1981)). Herb. B. Hulme at **LIV** was also examined.

Specimens are not cited in this paper. I have, however, annotated the entire holdings of the following major British and Irish herbaria: **ABD**, **CGE**, **DBN**, **E**, **LIV**, **LIVU**, **TCD**. Also, approximately half of the large holdings of **NMW** have been annotated by me.

DIAGNOSTIC CHARACTERS

The diagnostic characters used in *Atriplex* identification differ from those used in other chenopod genera. The inflorescence provides few characters, and the flowers virtually none. Even seed surface

sculpturing, a character found so useful for separating closely related species of *Chenopodium* (Cole 1961), has so far not proved helpful in *Atriplex*.

Within a species, the leaf outline can vary from one biotype to another in the same habitat and from one node to the next on the same plant. Within a species, colour, vestiture and habit can vary due to genetic difference or because of environmental factors. Leaf colour outline and vestiture can also change with the maturity of the plant. Younger leaves or those remaining on the plant at maturity can differ greatly from mature leaves or the earlier-formed leaves that may have dropped off the plant by maturity.

Most characters are to some extent variable. In some cases, the phenotypic plasticity is such that particular environmental factors can cause plants of one species to resemble the phenotype of another, genetically different species.

The most important diagnostic characters are those of the lower principal leaves and of the fruiting unit. The latter consists of the seed with surrounding pericarp and the pair of bracteoles within which they are enclosed. Separation of species in section *Teutliopsis* depends essentially on the existence of a consistent correlation between the characters of the lower leaves and those of the fruiting unit.

Some species have a restricted range in Great Britain and some occupy relatively specific habitats. Information about the habitat and locality is particularly useful in this group.

Special terms used in the key and descriptions are illustrated in Fig. 2 and explained along with the major diagnostic characters below.

HABIT

Atriplex may be erect with branches ascending or outspreading, or prostrate (decumbent or procumbent). My experiments and those of Turesson (1919) indicate that environment, particularly light, nutrient and moisture, has a considerable effect on the habit of some species. In several species two variants exist: a hereditary prostrate kind and a modificatory prostrate kind. In the latter, intense light induces a plagiotropic response in a normally erect plant; and in the former, shading causes the branches to turn upwards (Turesson 1919).

Though variable in some species, the habit is often distinctive. *A. littoralis* in Britain is consistently erect. *A. glabriuscula* is characteristically procumbent on exposed beaches, becoming decumbent to weakly erect when crowded at the landward margin of the beach, but also possessing a less common erect variant. *A. patula*, commonly erect though often spindly and falling over, has hereditary and modificatory prostrate variants. *A. prostrata* has erect and prostrate kinds.

LEAVES

Lower Principal. The lower principal leaves are the earlier-formed leaves on the central axis in the middle to lower part of the plant, at approximately nodes 4 to 8 up from the base, between flowering and the development of mature fruit. They often differ considerably in size and form from the later-developing upper leaves and they frequently drop off before the bracteoles and seed are fully mature. The lower leaves on *A. longipes*, for example, are elongate-triangular with basal lobes while the upper leaves that develop on older specimens are lanceolate to linear and frequently entire. By the time the plants reach maturity, the only leaves that remain on them may be the lanceolate to linear ones.

Outline. The leaf outline, although extremely variable within some species, is an essential diagnostic character. The outline of the lower principal leaves is less variable and it is these that are taxonomically significant.

Base. The leaf base angle of the lower principal leaves, cautiously employed, can provide a useful secondary character. It is too variable to be used alone to separate *A. glabriuscula* from *A. prostrata* but other species have a characteristic base. In *A. patula* and *A. praecox*, for example, the leaf base is cuneate and in *A. longipes* it is cuneate to obtuse. The leaf base often serves as a useful character for detecting hybrids between species with truncate leaves and those with cuneate leaves. Between the upper and lower leaves on the same plant, the leaf base angle is often very different, and in some individuals it varies greatly even from one node to the next.

Succulence. Leaf succulence has little diagnostic value, although some individuals of *A. glabriuscula* may have extremely succulent leaves. Specimens of the hybrid *A. littoralis* × *A. prostrata* are usually extremely succulent, perhaps as a result of positive heterosis.

Colour. Betacyanins (Dreiding 1961) are responsible for the red colour in *Atriplex*. As a taxonomic

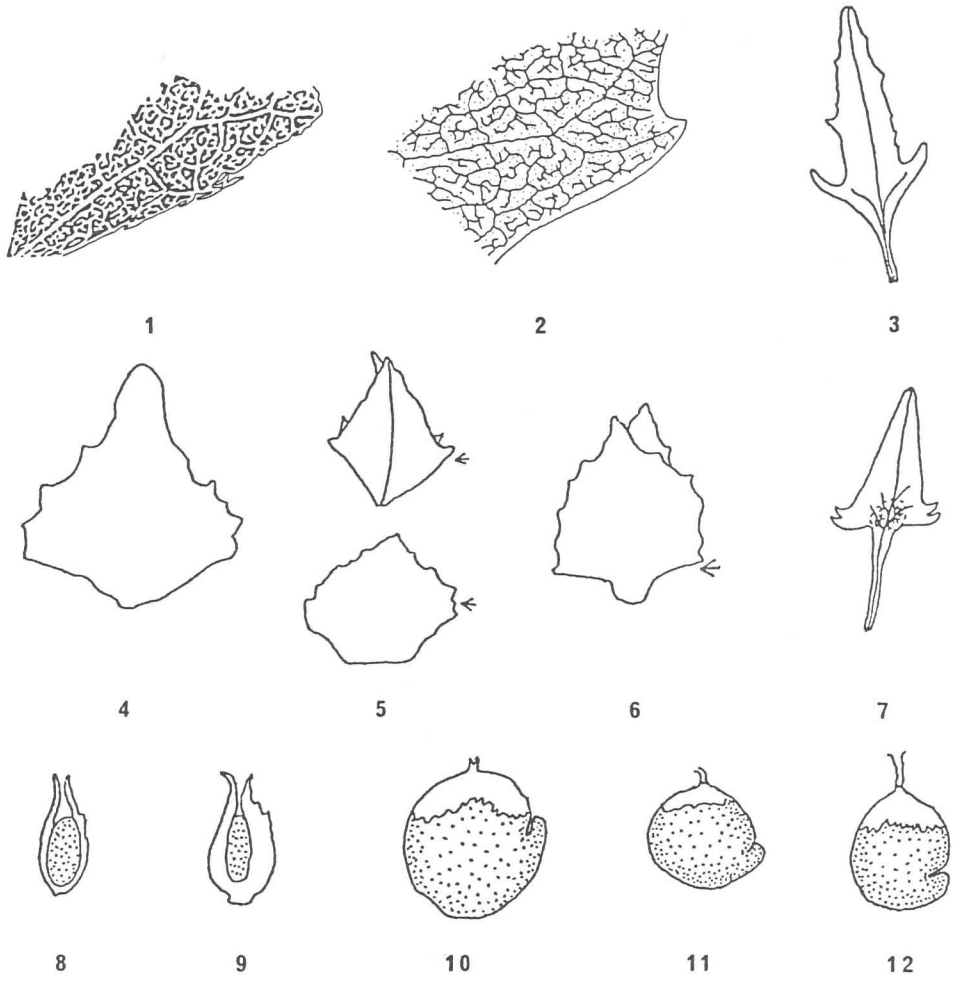

FIGURE 2. Diagnostic characters used in *Atriplex*.
1. Kranztypus leaf venation (section *Sclerocalymma*); 2. Normal dicotyledonous leaf venation (section *Teutliopsis*); 3. Forward-curving basal lobes; 4. Lingulate apex; 5. Bracteole margins united up to the middle (arrow); 6. Bracteole margins united only at the base (arrow); 7. Stalked bracteole; 8. Bracteoles thin or evenly-thickened; 9. Bracteoles spongy-thick from the middle to the base; 10. Seed radicle strongly up-pointing; 11. Seed radicle obliquely up-pointing; 12. Seed radicle out-pointing.

character colour is of secondary importance. The red colour in some individuals may be the result of a genetic difference, but the development of red may depend largely on environmental factors. *A. praecox* in Britain is characteristically red but in *A. glabriuscula*, reddish and entirely green plants commonly occur together in the same population. *A. littoralis* may be green or reddish and in *A. patula*, a species which is usually entirely green, reddish strains occur. The leaves of *A. longipes* frequently turn bright yellow at maturity but so do those of some of its hybrids with *A. prostrata*.
Vestiture. Young *Atriplex* leaves are covered with stalked, oblong, fluid-filled vesicular hairs. These, as the leaf matures, dry and form a scaly or mealy surface. As a taxonomic character, the density of the scales and their distribution on the leaf surface has limited usefulness. For example, the abundant mealiness on the leaves of some coastal species gives them a distinctive whitish appearance. *A. patula*, by contrast, has only a sparse, hardly discernible covering of fine mealy particles on the younger leaves.

Venation. Leaf venation in section *Teutliopsis* consists of the normal dicotyledonous type. Immature and densely lepidote specimens in section *Teutliopsis* can be immediately distinguished from *A. laciniata*, the only native species not in section *Teutliopsis*, by the leaf venation. *A. laciniata* possesses the highly distinctive Kranztypus venation (Fig. 2). This becomes readily visible with a hand lens when the leaf is scraped with a knife-blade.

BRACTEOLES

The breacteoles provide some of the most useful diagnostic characters. Within many species, however, there can be considerable variation. The variation may be due to genetic differences between biotypes of the same species or differences in the environmental factors acting on the same biotypes. Once the limits of variation are known within a species, the bracteole characters can be usefully employed. The following characters should be observed:

Outline. In most species the outline is either triangular, rhombic, ovate or some combination of these shapes.

Apex. In most species, the apex is usually either acute, acuminate, lingulate or produced to a thin foliose tip.

Base. In most species, the base is truncate, obtuse, or cuneate. The base, especially of bracteoles occurring in the axils of leaves or branches, should be examined for the presence of a stalk, a variable but important character whose presence is usually essential for the identification of hybrids involving *A. longipes*.

Margin. How far the bracteole margins are united up from the base is a major diagnostic character. The presence or absence of lateral angles is important. The degree to which the lateral angles are developed, whether the development is unilateral or bilateral, and whether the lateral angles are rounded or pointed are important characters. The degree of toothing and the position of the teeth are also significant.

Dorsal Surface. The dorsal surface is described as smooth, muricate or tuberculate, strongly reticulate-veined, 1-veined or obscurely-veined. Both smooth and tuberculate individuals may occur within one species, and the degree to which the veins are prominent varies within individuals of the same taxon, but once these limitations are known, the characters can be usefully employed.

Inner Surface. A layer of distinctive, brown or silvery-brown, spongy tissue of large air-filled parenchyma lines the inner surface of the bracteoles of certain species. Within a single taxon, this tissue may be undeveloped, developed only at the base, or developed over the entire surface. In *A. patula*, for example, it is never present, but it typically occurs in members of the *A. prostrata* group.

Substance. The bracteoles are described as membranous, herbaceous or spongy. Membranous bracteoles, such as often occur in *A. praecox* are so thin that the fruit, not merely its outline, can be seen within them. The bracteoles of *A. glabriuscula*, for example, are spongy, particularly in the basal portions. This spongy character is especially useful for distinguishing hybrids between *A. glabriuscula* and species that have membranous or herbaceous bracteoles.

SEEDS

The types of seeds present, their size, shape and position within the pericarp, provide important diagnostic criteria.

Dimorphism. On the same plant, two distinct seed types may occur: a brown type and a black type. The brown seeds are reddish to dark brown, usually larger than the black, flattened and disc-shaped, have a radicle that is distinctly produced, have a dull or pebbled-glossy surface with the radicle region often strongly striate-pebbled, and possess a softer outer coat. The black seeds in most species are generally smaller than the brown, are biconvex, have a radicle that is scarcely produced, have a smooth-glossy surface and possess a harder outer coat.

In some individuals, these morphological distinctions in seed type are relatively constant, but most taxa have many individuals in which numerous morphologically intermediate seed types occur. The relative abundance of the two seed types within the individual has slight taxonomic significance because the ratio may differ within strains of the same species. This is particularly true of *A. patula* and *A. littoralis*. In these species it is common to find that one or the other seed type predominates within a particular strain of plants.

The distinctions in radicle position and direction discussed below, as well as differences in seed shape, are much more apparent in the larger, brown and intermediate types than in the smaller black types.

Radicle Position and Direction. The position of the seed radicle and its direction are important taxonomic characters. Surrounding the seed is a loosely or firmly attached membranous pericarp with the vestiges of the style situated at the top. The outline of the radicle becomes visible on the seed margin when the lower part of the pericarp is teased away. The radicle may emerge from the middle portion of the seed margin ('median') or from the base of the seed ('basal'). The radicle apex may be directed upwards towards the style vestiges ('up-pointing'), or outwards at a right angle to the style axis ('out-pointing'), or at an angle between these directions ('obliquely up-pointing').

KEY TO THE SPECIES

1. Leaf venation appearing (at ×12) as a conspicuous, dark green, reticulate pattern (Kranztypus) when the leaf surface is scraped with a sharp blade; bracteoles cartilaginous and hardened in the lower half; seed transversely elliptical, light brown ..... 7. *A. laciniata*
1. Leaf venation appearing (at ×12) as the normal dicotyledonous type and not showing a dark green reticulate pattern when the leaf surface is scraped with a sharp blade; bracteoles herbaceous, membranous or spongy-inflated, not hardened in the lower half; seed ovate to orbicular, dark brown or black 2
2. Lower leaves linear or lanceolate 3
2. Lower leaves triangular or rhombic-ovate 4
3. The lower leaves linear without basal lobes; bracteoles ovate, thick, margins united only at the base, apices acute or lingulate and frequently reflexed at maturity. Coastal halophyte ..... 5. *A. littoralis*
3. The lower leaves lanceolate with forward-curving basal lobes; bracteoles rhombic, thin, margins united almost to the middle, apices acute to acuminate and never reflexed at maturity. Non-halophytic inland and coastal weed of disturbed ground ..... 6. *A. patula*
4. Lower leaves rhombic-ovate; mature plants small (mostly 8–10 cm high). Restricted to lower littoral zone of coastal beaches ..... 4. *A. praecox*
4. Lower leaves triangular; mature plants larger (mostly more than 20 cm high). Occurring throughout the littoral zone of coastal beaches and inland 5
5. Bracteoles rhombic, margins united up to the middle, spongy-thick from the middle to the base; seed radicle strongly up-pointing. Coastal halophyte ..... 2. *A. glabriuscula*
5. Bracteoles ovate or triangular, margins united only at the base, thin or evenly thickened; seed radicle out-pointing or obliquely up-pointing. Coastal and inland 6
6. Lower leaves deltoid-triangular, length less than twice the width, base truncate to subcordate (base angle more than 160°); axillary bracteoles infrequent, morphologically similar to terminal ones, thin or evenly thickened, none foliaceous; margins with pointed or rounded, weakly developed lateral angles; dorsal surface smooth or weakly veined towards the base; sessile. Coastal and inland in saline or weedy habitats ..... 1. *A. prostrata*
6. Lower leaves narrowly triangular, length about twice the width, base cuneate (basal angle less than 150°); axillary bracteoles frequent, morphologically different from terminal ones, thin, at least some of them foliaceous; margins with pointed, strongly developed lateral angles; dorsal surface strongly reticulate-veined towards the base; stalked (stalks 5–25 mm long). Restricted to estuarine salt marshes in tall vegetation ..... 3. *A. longipes*

DESCRIPTIONS

ATRIPLEX Section *TEUTLIOPSIS* Dumort., *Fl. Belg.*, p. 20 (1827).

Stems green with whitish, stramineous or red stripes. Venation normal dicotyledonous type. Flowers monoecious, the pistillate ones all bracteolate and lacking a perianth. Bracteoles united at the base or up to the middle at most, not becoming cartilaginous in fruit. Seeds exclusively vertical.

A. prostrata group. In the British Isles this group is represented by: *A. prostrata*, *A. glabriuscula*, *A. longipes*, and *A. praecox*. The species are morphologically similar and interfertile in varying degrees

and, except for *A. prostrata*, all are restricted to littoral or estuarine habitats. Many coastal populations are made up of hybrid derivatives variously intermediate between two or more species. 2n=18.

1. *A. PROSTRATA* Boucher ex DC., in Lamarck & De Candolle, *Fl. Francaise*, 3rd ed., p. 387 (1805). Lectotype: "Env. du Havre", h. DC. 386, marked "*A. prostrata* Boucher" in herb. DC. (**G**), fide M. Gustafsson in *Opera Botanica*, **39**:21 (1976).

A. prostrata Boucher, *Extrait de la Flore d'Abbeville et du départment de la Somme*, p. 76 (1803). Nomen nudum.

A. triangularis Willdenow, *Sp. Pl.*, **4**:963 (1806). (Lectotype: sheet number 3, "Ipse legi 1804 in Lido di Venezia" initialled "W" and marked "Atr. triangularis", in herb. Willdenow (**B**), fide Taschereau in *Can. J. Bot.*, **50**:1583 (1972)).

A. oppositifolia DC., *Rapports sur les voyages botaniques et agronomiques*, p. 12 (1813). (Lectotype: specimen h. DC. 390 marked "*Atriplex oppositifolia*" in herb. DC. (**G**), fide M. Gustafsson in *Opera Botanica*, **39**:23 (1976)).

A. latifolia Wahlenberg in *Svensk Botanik*, **9**:628 (1824). (Lectotype: Drawing No. 628, in *Svensk Botanik*, **9**:628 (1824), fide M. Gustafsson in *Opera Botanica*, **39**:23 (1976)).

A. deltoidea Babington, *Primitiae Florae Sarnicae*, p. 82 (1839). (Lectotype: Guernsey, Fort George, 1837, *C.C. Babington* (**CGE**), fide M. Gustafsson in *Opera Botanica*, **39**:23 (1976)).

A. hastata sensu Aellen in *Fl. Europaea*, **1**:97 (1964), and sensu auct. angl. non L. The species that Linnaeus called *A. hastata* is the plant presently called *A. calotheca* (Raf.) Fries. (Lectotype: sheet 1221.17 marked "hastata" (**LINN**), fide Taschereau in *Can. J. Bot.*, **50**:1585 (1972)).

Plants 10–100 cm, erect, ascending, decumbent or procumbent. Stems striate, subangular to angular, green and stramineous striped or ± reddish. Branches opposite or sub-opposite up to about two-thirds from the base. Foliage green or reddish, non-succulent; mature leaves finely farinose or glabrous; juvenile and upper leaves glabrous to finely farinose above, grey-farinose to densely white-lepidote below. Lower leaves 2–11 cm long, 2–10 cm wide, triangular with a pair of obtuse out-pointing basal lobes; margins entire, dentate or irregularly toothed; apex acute to obtuse; base truncate to subcordate or broadly obtuse. Upper leaves smaller, triangular or lanceolate, with or without basal lobes; margins entire or toothed. Inflorescence 2–9 cm long, spiciform, composed of contiguous or irregularly spaced glomerules, terminal on stems and branches and on short stems from the axils of upper leaves, leafless except at the base. Bracteoles 2–6 mm long, sessile, triangular to triangular-ovate; apex broadly acute; base truncate to obtuse; margins entire or dentate, united at the base, lateral angles rounded and not strongly developed; herbaceous and thin or ± thickened by the presence of spongy tissue; dorsal surface smooth or tuberculate, venation obscure or prominent. Two seed types present and distinct. Brown seeds 1.5–3.0 mm wide, orbicular; radicle sub-basal, obliquely up-pointing to out-pointing. Black seeds 1.0–2.5 mm; radicle basal, out-pointing. 2n=18. Fig. 3.

HABITAT AND DISTRIBUTION

Halophyte, ruderal and anthropophile, common in silt, sand and shingle on sea beaches and in salt marshes around the coast except in northern Scotland (Fig. 4, omitting unconfirmed, earlier northern records). It is a characteristic component of all inland salt marsh vegetation. The ruderal and anthropophilic biotypes, morphologically indistinguishable from the halophytic variants, are transient colonizers of freshly disturbed soil. They occur with *A. patula* along roadsides and edges of walkways and in waste ground by rubbish tips and on demolished building sites. In northern Scotland, Orkney and Shetland, *A. prostrata* has frequently been confused with hybrid derivatives between other members of the *A. prostrata* group. The species reaches its northern limits in Scotland in approximately the same latitudes as *A. littoralis*. On the east coast, the most northerly record is 3 km north-east of Dingwall, E. Ross, v.c. 106. On the west coast, the most northerly record is from Dumbuck, Dunbarton, v.c. 99. Two collections from disturbed ground on Fair Isle, Shetland, v.c. 112, are introductions of the ruderal biotype of the species and do not represent extensions of its natural range. The absence of *A. prostrata* further northward is coupled with the frequent presence of two hybrids: *A. longipes* × *A. prostrata* and *A. longipes* × *A. glabriuscula*.

FIGURE 3. *Atriplex prostrata*.

REPRODUCTIVE BIOLOGY

Facultatively autogamous and primarily wind pollinated but also visited by syrphid flies that feed on the pollen. Flowering August to September; seed set September to November. The staminate and pistillate flowers, closely clustered together in tight glomerules, mature and open almost simultaneously. This greatly lessens the opportunity for cross pollination. The seed, especially of the ruderal biotypes, consists mostly of the small black type. Unlike the small black seeds of *A. patula* these seeds show no differences in germination response. In *A. prostrata*, the small black seeds germinate at the same rate and to the same extent as the large brown seeds.

2. *A. GLABRIUSCULA* Edmondston, *Fl. Shetland*, p. 39 (1845).

Neotype: Keiss, near Wick, Caithness, 19.IX.1930, *M. L. Wedgewood* (**K**), fide M. Gustafsson in *Opera Botanica*, **39**:15 (1976). Excellent topotype material is: sheet 739, Baltasound, Unst, Shetland, 27.VIII.1887, *W. H. Beeby* (**SLBI**).

A. babingtonii Woods, *Tourist's Fl.*, p. 316 (1850). (Neotype: England, Isle of Wight, shore between Springfield and Nettlestone near Ryde, 26.VIII.1842, the left hand specimen (**K**). The description is probably based on a form of *A. rosea* sensu Babington *Trans. Proc. bot. Soc. Edinb.*, **1**: 13 (1841), fide M. Gustafsson in *Opera Botanica*, **39**: 15 (1976)).

A. glabriuscula var. *pseudocalotheca* Bennett, *Trans. Proc. bot. Soc. Edinb.*, **20**: 1 (1928). (Topotype material in herb. Arthur Bennett (**BM**)).

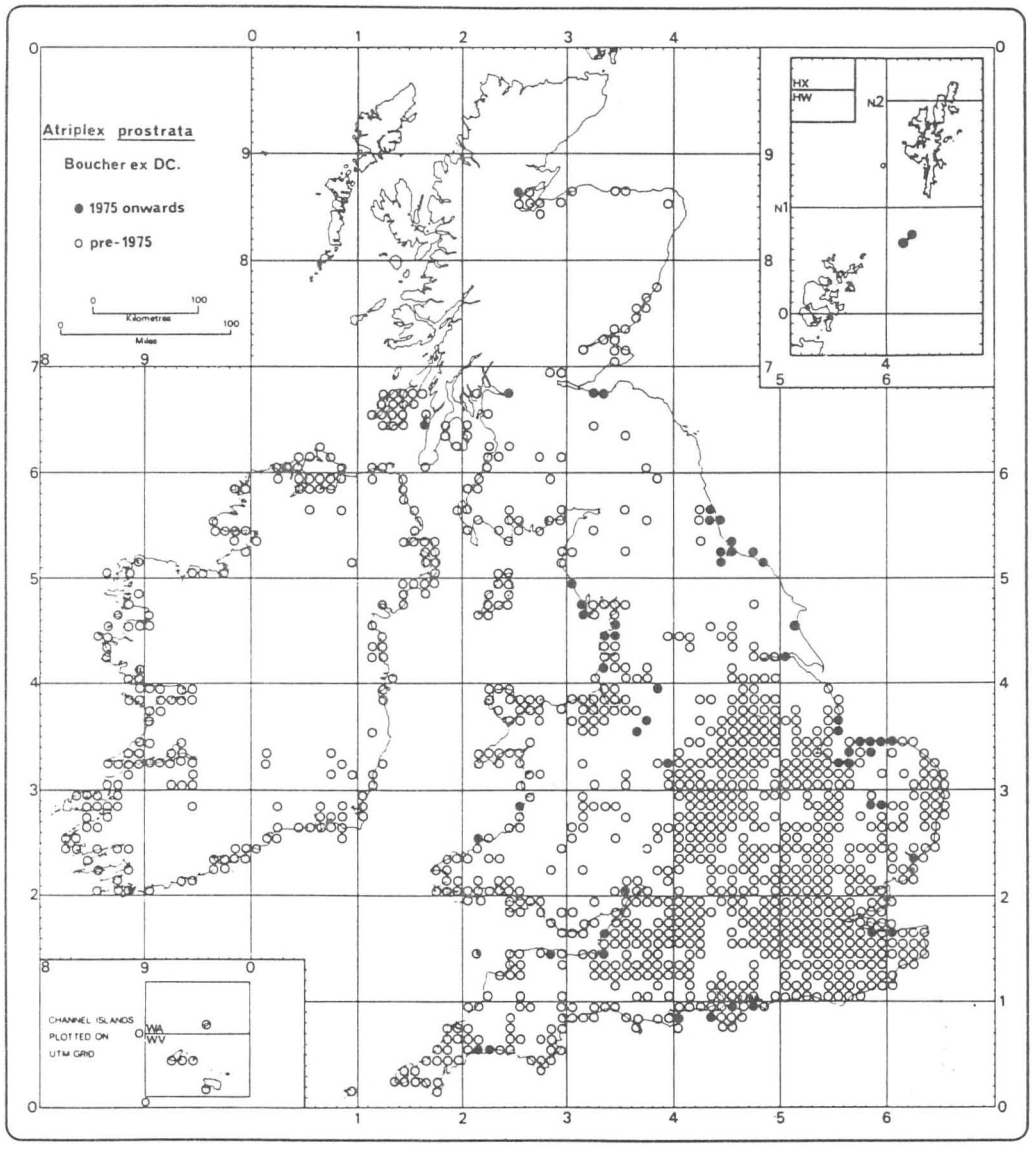

FIGURE 4. Distribution of *Atriplex prostrata* in the British Isles.

Plants 20–90 cm, prostrate, decumbent or less commonly erect. Stems striate, angular, green and stramineous striped, stout, tough-herbaceous. Branches opposite only at the base, swollen at attachment to the main stem. Foliage green, frequently succulent; mature lower and upper leaves glabrous or sparsely fine-farinose about the base of the main veins above and sparsely farinose below; the most juvenile leaves densely farinose above and below. Lower leaves 2–7 cm long, 2–6 cm wide, triangular with a pair of out-pointing to upcurving basal lobes; margins sinuate-dentate, irregularly toothed or rarely almost entire; apex acute to obtuse; base obtuse to truncate or rarely subcordate. Upper leaves smaller, outline highly variable, lanceolate or triangular, with or without basal lobes; margins entire or toothed. Inflorescence 2–15 cm long, spiciform, composed of loose, irregularly-spaced glomerules, terminal on upper stems and branches and from the axils of upper leaves, frequently with much reduced leaves subtending the glomerules up to about two-thirds from

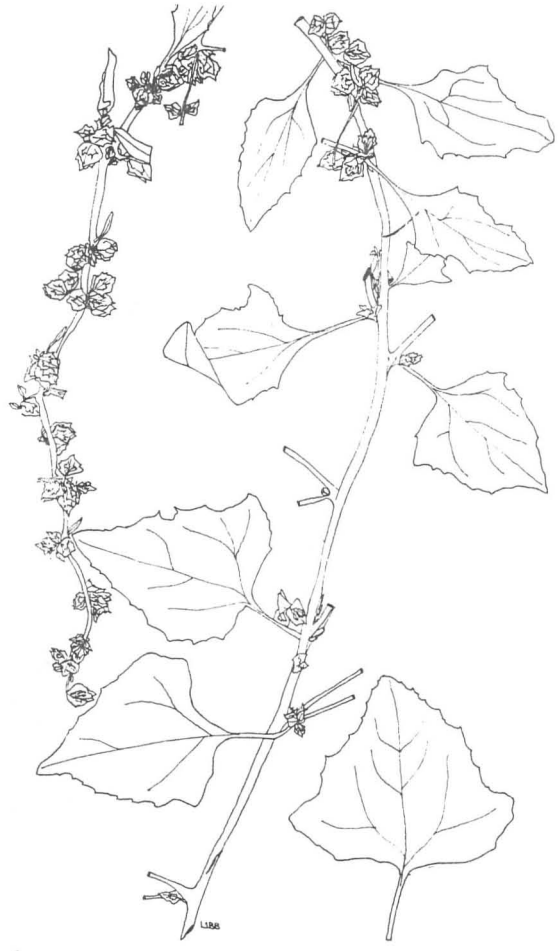

FIGURE 5. *Atriplex glabriuscula*.

the base. Bracteoles 4–10 mm long, sessile, rhombic; apex broadly acute; base broadly cuneate to obtuse or rounded; margins entire or dentate, united up to the middle; lateral angles rounded and not strongly developed; much thickened especially at the base by the presence of spongy tissue; dorsal surface tuberculate, muricate or smooth, venation obscure. Seeds 2.0–4.0 mm wide, mostly dark brown to black (rarely two types present), dull, smooth, ovate to orbicular, flattened or irregularly biconvex; radicle median and usually strongly up-pointing. 2n=18. Fig. 5.

HABITAT AND DISTRIBUTION

Obligate halophyte confined to the littoral zone of more or less exposed sand or shingle coastal beaches. Records of this species occurring inland (Chapman 1960; Perring & Walters 1962; Lee 1975) are erroneous. Because of the frequency with which this species has been confused with hybrid derivatives between other members of the *A. prostrata* group, all distribution records for it in the British Isles need to be re-examined. A partial distribution, based on my field work and the B.S.B.I. survey, is given in Fig. 6, but the species is much more common than the number of distribution dots would suggest. *Atriplex glabriuscula* is absent from the coasts of Yorkshire, Lincolnshire and Norfolk (v.cc. 61, 54, 53, 28, 27). The Yorkshire coast needs further investigation. The Lincolnshire coast is affected by severe habitat disturbance: intensive human recreational use, military use, extensive land reclamation, sea defence wall-building, cattle grazing and intensive rabbit grazing.

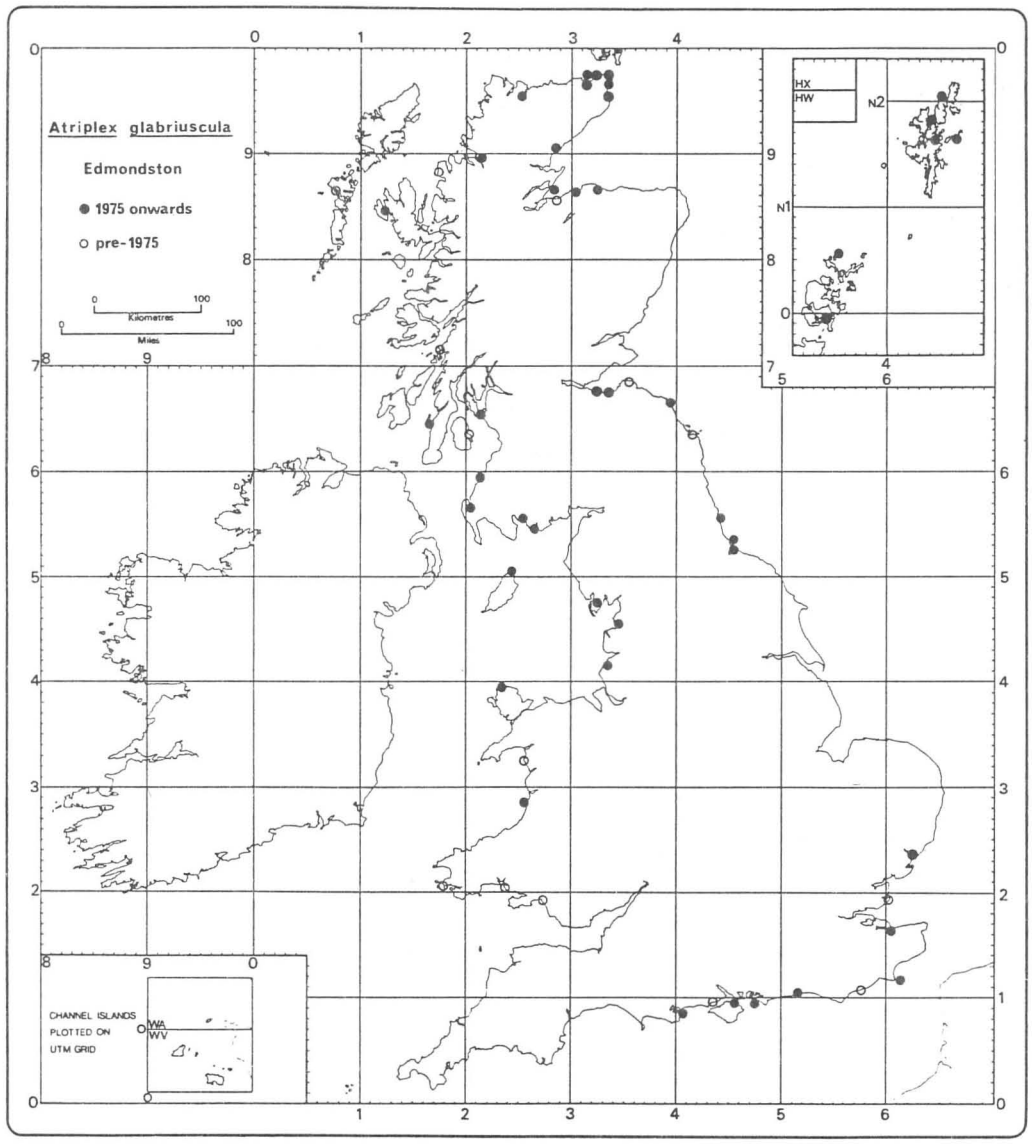

FIGURE 6. Distribution of *Atriplex glabriuscula* in the British Isles.

The northern Norfolk coast is also affected by reclamation, sea-wall defence and drainage, but other ecological factors may be influencing the distribution of *A. glabriuscula* here. Adam (1978) confirmed the distinctiveness of the northern Norfolk salt marshes. He noted that they show vegetational and floristic links with Mediterranean salt marshes. The ecological niche occupied by *A. glabriuscula* in other regions is here occupied by hybrid derivatives between *A. longipes* and *A. prostrata*.

REPRODUCTIVE BIOLOGY

Facultatively autogamous and primarily wind pollinated. Insects observed feeding on *A. glabriuscula* and crawling over the flowers probably play only a very minor role as pollinators in the

windy habitat where this species grows. Flowering July to August; seed set September to October. The staminate and pistillate flowers, closely clustered together at anthesis, mature and open almost simultaneously. This lessens the opportunity for cross pollination. *A. glabriuscula* is well adapted to dispersal by sea. The thick firm bracteoles, united up to about the middle, retain the seed while it is in the water. The large air-filled cells of spongy tissue at the base of the bracteoles give them high buoyancy. Under laboratory conditions 71% of the bracteoles examined were still floating after 24 days in continuously agitated sea water (Gustafsson 1973a). The seeds exhibit a marked dormancy. Those planted in the greenhouse will not germinate unless exposed for some time to the fluctuating weather conditions outdoors (Taschereau 1972, 1979). In the laboratory, the seeds can be induced to germinate within nine days by exposing them to alternating daily temperatures of 10°C and 30°C (Ignaciuk & Lee 1980). Seed germination on the north-western coast of England begins during the last week of April, four weeks after the equinoctial spring tides. The main germination occurs in May with a small amount in June. Ignaciuk & Lee (1980), who observed germination on the English coast, pointed out that the alternating temperature requirement of *A. glabriuscula* seeds delays germination until after the equinoctial tides, the period of greatest environmental instability. The amplitude of the diurnal temperature cycle, noted these authors, decreases rapidly with increasing sand depth. (In measurements by Ignaciuk it was halved with each 9 cm increase in depth). Thus, the

FIGURE 7. *Atriplex longipes.*

alternating temperature requirement also prevents the seed with its limited perisperm from germinating beyond depths greater than it can overcome.

3. *A. LONGIPES* Drejer, *Fl. Excurs. Hafniensis*, p. 107 (1838).
Lectotype: Denmark, Copenhagen, Flaskekroen, sheet L92/74 no. 1, *Drejer* (**C**), fide Jones in *Watsonia*, **10**: 250 (1975).
A. prostrata Boucher ex DC. var. *longipes* (Drejer) Meijden in *Gorteria*, **11**: 119 (1982).

Plants 20–90 cm, erect or spreading, stems striate, subangular, green and stramineous striped. Branches opposite only at the base or rarely higher in large specimens. Foliage green at maturity becoming yellow with senescence, succulent; mature and juvenile leaves glabrous. Lower leaves 4–6

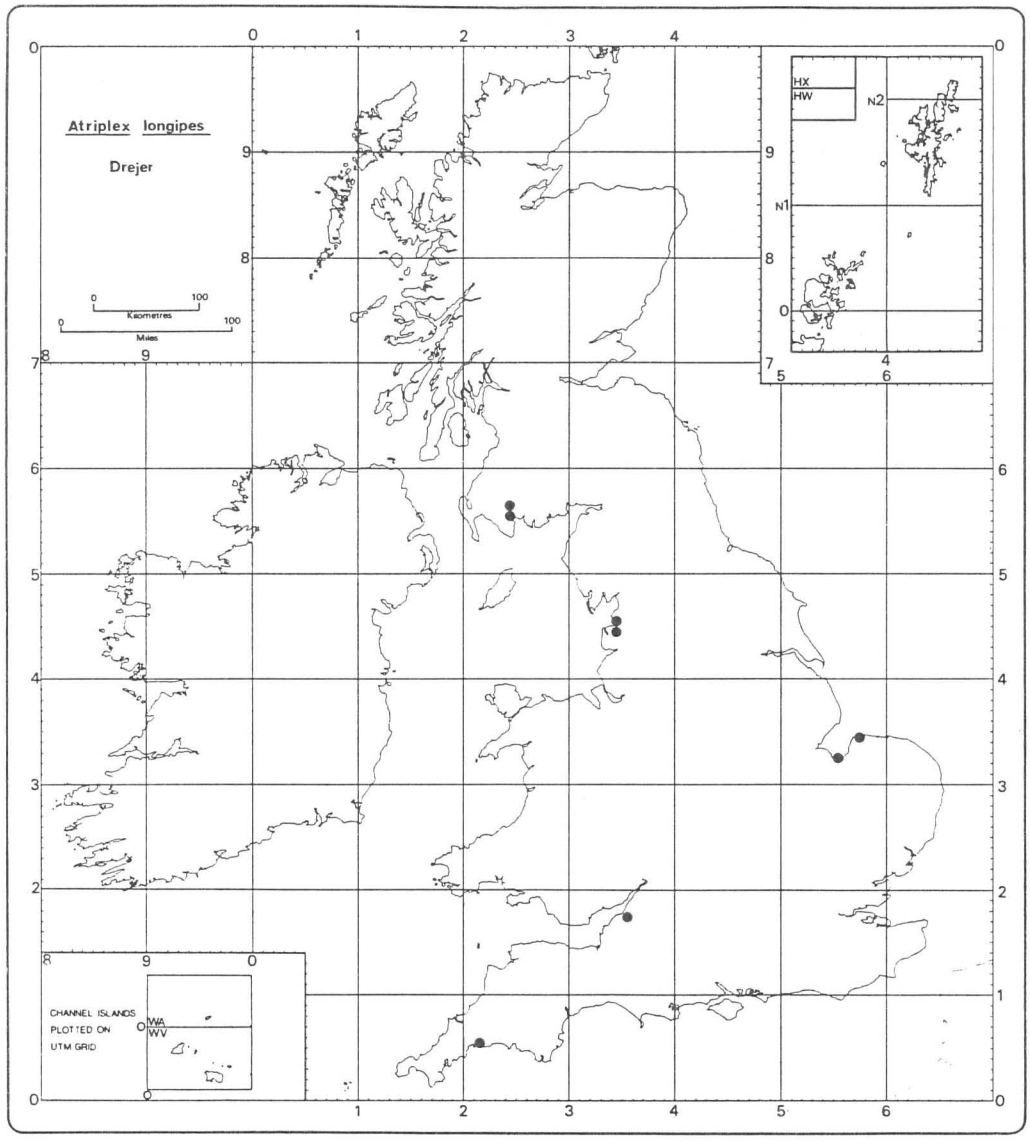

FIGURE 8. Distribution of *Atriplex longipes* in the British Isles.

cm long, 3–5 cm wide, narrowly triangular with a pair of out-pointing or forward-curving basal lobes; margins entire or irregularly toothed; apex acute; base cuneate. Upper leaves lanceolate to linear, without basal lobes or with one small lobe or a pair of weakly developed lobes; margins entire. Inflorescence 10–15 cm long, spiciform, composed of loose irregularly-spaced glomerules, terminal and in the axils of upper leaves and branches, frequently with much reduced leaves subtending the glomerules up to about two-thirds from the inflorescence base. Bracteoles consisting of two forms on the same plant: a smaller, shortly stalked to sessile, thin-herbaceous but non-foliaceous form occurring mostly in the terminal parts of the inflorescence; a larger, long-stalked, thin-herbaceous and frequently foliaceous form occurring in the mid to lower region of the inflorescence and particularly in the axils of the upper leaves and branches. Smaller bracteoles 5–10 mm long on stalks 0.5–1.0 mm long or sessile, rhombic or elongate-triangular; apex acute; base broadly obtuse or cuneate; margins mostly entire, united only at the base; lateral angles pointed, not strongly developed, dorsal surface mostly smooth, venation obscure or prominent. Larger bracteoles 10–25 mm long on stalks 5–25 (–30) mm long, ovate-lanceolate; apex acute; base cuneate to broadly obtuse; margins entire or with a few teeth, united only at the base; lateral angles pointed and strongly developed; dorsal surface smooth or slightly muricate; venation pronounced, forming a reticulate pattern towards the base. Two seed types present. Brown seeds 2.0–3.0 (–3.5) mm wide, orbicular; radicle basal to sub-basal, out-pointing. Black seeds 1.5–2.0 mm wide, orbicular; radicle basal, out-pointing. 2n=18. Fig. 7.

FIGURE 9. *Atriplex praecox*.

HABITAT AND DISTRIBUTION

Obligate halophyte confined to tall salt marsh vegetation bordering estuaries. *A. longipes* grows on a silty substratum in relatively undisturbed sites flooded with brackish water during the highest tides. It is associated with *Aster tripolium* in stands dominated by *Juncus maritimus* and at the margins of *Phragmites australis* stands. In Britain, it is widely distributed, occurring in Kirkcudbrightshire, Norfolk and Cornwall, but always it is local, usually rare and commonly associated with *A. prostrata* hybrids that make it difficult to detect. Distribution in the British Isles is given in Fig. 8.

REPRODUCTIVE BIOLOGY

Facultatively autogamous and primarily wind pollinated. Flowering (?) July to August. Fruiting mid-August to early September. The flowering times can only be inferred because only fruiting

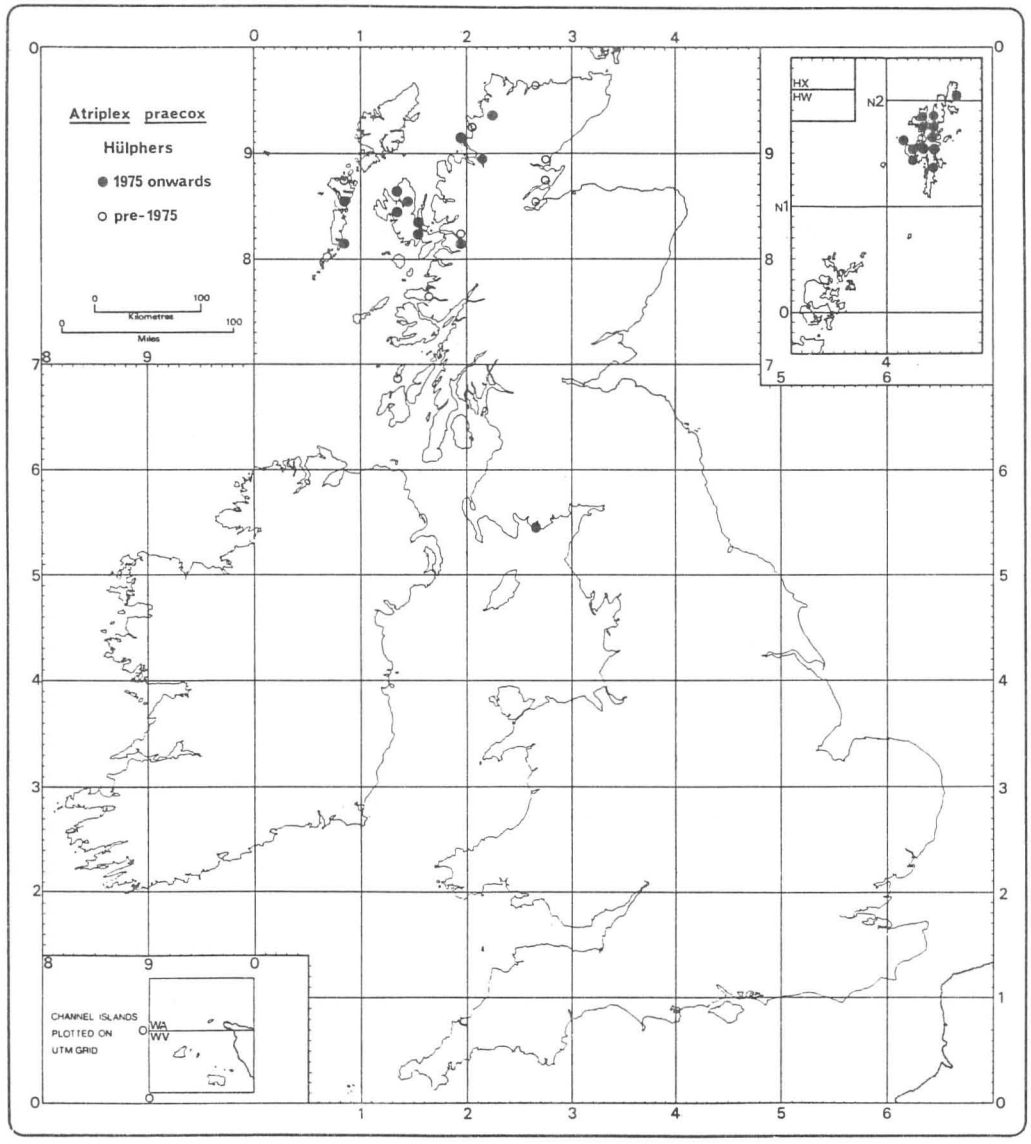

FIGURE 10. Distribution of *Atriplex praecox* in the British Isles.

material has been observed in the British Isles. Staminate and pistillate flowers occur together in the terminal inflorescence, but exclusively pistillate flowers occur singly or a few together in the upper stem and leaf axils. *A. longipes* in Britain, as in Scandinavia (Gustafsson 1972), exhibits distinct protogyny. The pistillate flowers in the leaf axils extend a pair of receptive stigmas several days before the staminate flowers open and shed their pollen. Thus, the opportunity for cross-pollination is increased.

4. *A. PRAECOX* Hülphers, in Lindman, *Svensk Fanerogamflora*, p. 228 (1918).
Lectotype: Sweden, Uppland, Ljusterö s:n, Särsö 18.VII.1912, *A. Hülphers* (marked *A. praecox*) (**S**), fide M. Gustafsson in *Opera Botanica*, **39**: 19 (1976).
A. nudicaulis Boguslaw, *Lesn. Zur.*, **1**: 30 (1846). (Type Locality: U.S.S.R., in the vicinity of Archangel). Type material inquired for unsuccessfully at **LE** by M. Gustafsson whom I have followed in listing this name as a synonym.
A. longipes Drejer subsp. *praecox* (Hülphers) Turesson in *Lunds Univ. Årsskr.*, N.F. Adv. 2, **21**(4): 6 (1925).

Plants 3–10 (–15) cm, erect or procumbent. Stems terete or sub-angular, green or red. Branches opposite up to about two-thirds from the base, the lowermost ones often long-spreading and sometimes longer than the central axis. Foliage bluish-green, often reddish tinged, succulent; mature leaves glabrous, juvenile and upper leaves finely farinose. Lower leaves 1.0–3.0 cm long, 0.5–1.3 cm wide, ovate or lanceolate with a pair of short, out-pointing basal lobes; margins entire or with a few short teeth; apex acute or obtuse; base cuneate to attenuate. Upper leaves smaller, lanceolate to linear, without basal lobes; margins entire. Inflorescence entirely axillary or also terminal, 1–3 cm long, composed of loose irregularly spaced glomerules, leafy throughout. Bracteoles 3–5 mm long, sessile or with stalks 0.5–1.5 mm long, rhombic-ovate or triangular-ovate; apex acute or acuminate; base cuneate, obtuse to truncate; margins entire, united at the base; lateral angles rounded, not developed or slightly unilaterally developed; thin-herbaceous or membranous; dorsal surface smooth, venation obscure. Seeds 1.5–3.0 mm wide, ovoid or sub-orbicular, 0.1–0.4 mm longer than wide, not distinctly dimorphic, black or dark brown, biconvex, lustrous, smooth or patterned; radicle sub-basal, obliquely up-pointing to out-pointing. 2n=18. Fig. 9.

HABITAT AND DISTRIBUTION

Obligate halophyte restricted to the margins of semi-protected sea inlets in northern coastal habitats. It occurs in shingle or sand in the low beach zone below the *Cakile-Atriplex* association, barely above the high water fucoid zone, in a region devoid of other terrestrial species. The most commonly reported habitat is close to the salt water in shingle bordering sea lochs. Here, *A. praecox* plants frequently form a distinctive red zone of very low, sparse vegetation clearly discontinuous from the strand plants of the middle beach. Distribution in the British Isles is shown in Fig. 10.

REPRODUCTIVE BIOLOGY

Facultatively autogamous and primarily wind pollinated. Flowering June to July; seed set August to September. The species is protogynous, the pistillate flowers extending receptive stigmas several days before the staminate flowers open and shed their pollen. *A. praecox* matures earlier than most other *Atriplex* species in Britain and disappears from its habitat before October. Reproductive isolation is probably facilitated to some extent by its earlier flowering time and by the specialized ecological niche which it occupies.

5. *A. LITTORALIS* L., *Sp. Pl.*, p. 1054 (1753).
Lectotype: L. 3613, No. 1 in herb. Royen (**L**), fide Taschereau *Can. J. Bot.*, **50**: 1581 (1972).
A. serrata Hudson, *Fl. Angl.*, p. 377 (1762). (Lectotype: drawing of *Atriplex angustifolia dentata* in the upper right hand corner of the page, t.7f.4. of J. Petiver's *Herbarij Britannici* (1712–15), cited by Hudson).
A. marina L., *Mant. Pl.*, p. 300 (1771).
A. littoralis var. *serrata* S. F. Gray, *Nat. Arr.*, p. 282 (1821).
A. patula var. *littoralis* A. Gray, *Man.*, 5th ed., p. 409 (1867) pro parte.

FIGURE 11. *Atriplex littoralis*.

Plants 30–150 cm, erect. Stems stout, striate, sub-angular, green and stramineous striped, frequently reddish. Branches opposite only at the base. Foliage green at maturity becoming yellowish or reddish with senescence, not or slightly succulent; mature lower and upper leaves glabrous; juvenile leaves slightly scurfy. Lower leaves 2–10 cm long, 0.5–1.5 cm wide, linear to linear-oblong, without basal lobes or with a varying number of leaves possessing one lobe or a pair of out-pointing to obliquely forward-pointing basal lobes; margins entire or irregularly repand-dentate; apex acute to acuminate; base attenuate. Upper leaves reduced, linear, without basal lobes; margins usually entire. Inflorescence long (up to 20 cm), interrupted spiciform, of densely packed glomerules widely spaced toward the base but becoming contiguous toward the apex, terminal and from the axils of upper leaves, leafless except at the base. Bracteoles 3–6 mm long, sessile, triangular-ovate; apex acute or lingulate, frequently recurved at maturity; base cuneate to obtuse, or truncate; margins denticulate, united at the base; lateral angles rounded, not or weakly developed; usually thick-spongy; dorsal surface muricate and commonly bi-tuberculate, venation obscure. Two seed types present but the black type usually more abundant. Brown seeds 2.0–2.5 mm wide, orbicular or transversely elliptic, radicle sub-basal, obliquely up-pointing to out-pointing. Black seeds 1.3–2.0 mm wide, orbicular or transversely elliptic, radicle sub-basal, out-pointing to obliquely up-pointing. 2n=18. Fig. 11.

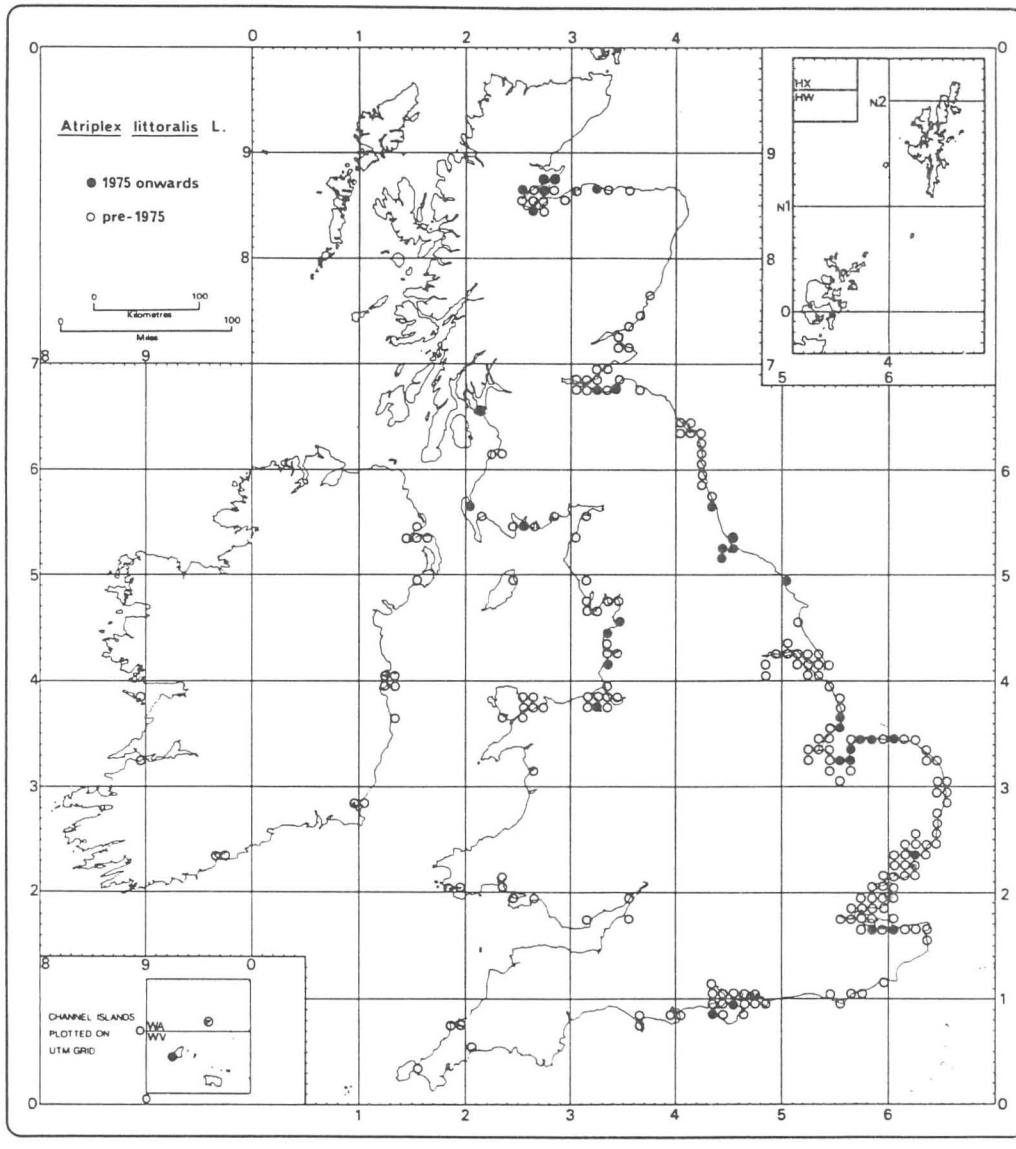

FIGURE 12. Distribution of *Atriplex littoralis* in the British Isles.

HABITAT AND DISTRIBUTION

Obligate halophyte confined to coastal habitats. *A. littoralis* is frequent in silt at the mouths of estuaries, in sand on more or less sheltered beaches and as a constituent of coastal salt marsh vegetation. With *A. prostrata*, it is frequently an early colonizer of earthen sea walls. Occasionally, *A. littoralis* is reported as a casual along roadsides inland, but such plants rarely persist more than one or two years. Distribution in the British Isles is given in Fig. 12. Here, *A. littoralis* reaches its northern limits in northern Scotland. On the east coast, the most northerly record is Balintore, E. Ross, v.c. 106. It is absent from Loch Fleet, about 15 miles further north in East Sutherland, v.c. 107. On the west coast, the most northerly record is Kilchattan Bay, Isle of Bute, v.c. 100. No specimens were seen from the Orkney Islands nor was the county recorder for that region able to find any. The distribution records from there in Perring & Walters (1962) may be a mistake.

REPRODUCTIVE BIOLOGY

Facultatively autogamous and primarily wind pollinated but also frequently visited by syrphid flies. Flowering July to August; seed set September to October. Staminate and pistillate flowers occur together in the terminal inflorescence but the flowers in the upper leaf axils are primarily and sometimes exclusively pistillate. Protogynous, the pistillate flowers extending a pair of receptive stigmas several days before the staminate flowers open and shed their pollen. The bracteoles in some strains remain attached to the inflorescence axis rather than falling with the seed. At maturity the tips of these bracteoles become recurved exposing the seed which is shaken out by the action of the wind on the rigid woody stalk. In other strains the bracteoles and seed fall together. In cultivation, *A. littoralis* seeds are the first *Atriplex* seeds to germinate but there is no information on the germination dates of plants in their natural habitat. The small black seeds are generally more abundant, comprising 70–80% of the seeds of most plants in Britain. The proportion ranges from 50–86% however, and some of the seeds categorized as brown are very dark brown and somewhat biconvex. In the laboratory, both black and brown seeds germinate readily at about the same rate within two weeks. There is no dormant period. A sweet, sticky exudate is produced in droplets on the stems and main branches of *A. littoralis* before and at flowering, but how this may be related to the reproductive biology is not known.

FIGURE 13. *Atriplex patula*.

6. *A. PATULA* L., *Sp. Pl.*, p. 1053 (1753).
Lectotype: No. 1221.19 in Herb. Linné (**LINN**), fide Taschereau in *Can. J. Bot.*, **50**: 1574 (1972).
A. erecta sensu Smith, *Fl. Brit.*, p. 1093 (1804).
A. angustifolia sensu Smith, *Fl. Brit.*, p. 1093 (1804).
A. patula var. *bracteata* sensu Moss and Wilmott, in *Camb. Br. Fl.*, p. 174 (1914). The taxon that Westerlund in *Sveriges Atripl.*, p. 57 (1861) called *A. patula* var. *bracteata* is a hybrid derivative between *A. longipes* and *A. prostrata*. (Lectotype: sheet marked "*Atriplex patula* Lin. – *bracteata* Westerl.," and initialed, "C.A.W." (**S**)).

Plants 15–100 cm, erect, ascending or prostrate. Stems angular, green and stramineous striped. Branches opposite to sub-opposite up to about two-thirds from the base. Foliage bright green at

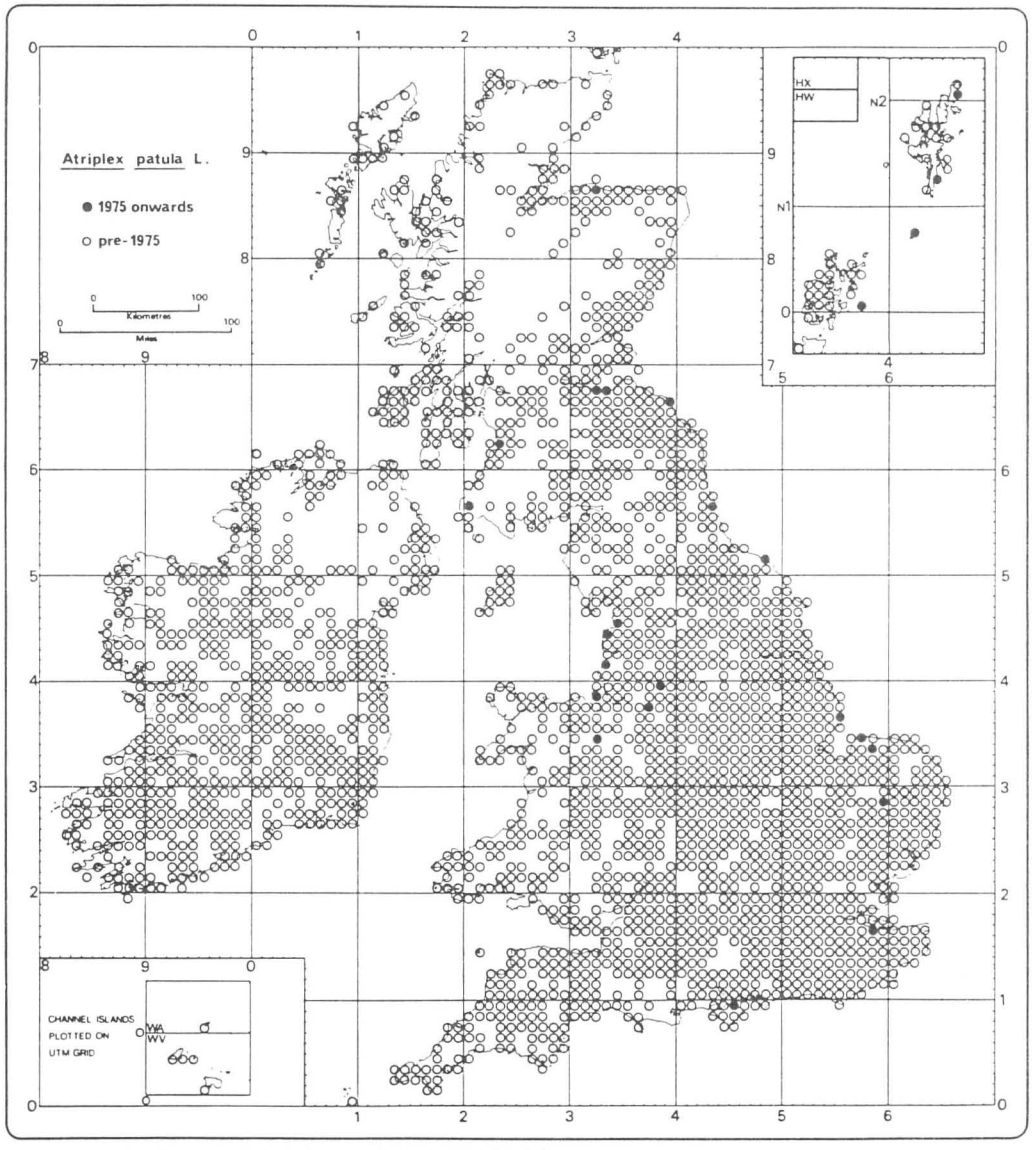

FIGURE 14. Distribution of *Atriplex patula* in the British Isles.

maturity, not changing with senescence, non-succulent; mature lower and upper leaves glabrous; juvenile leaves with fine, sparsely distributed farina (visible at ×12) on both sides but denser on the undersurface. Lower leaves 4–9 cm long, 1.5–4.5 cm wide, ovate-lanceolate with a pair of falcate, forward-pointing basal lobes or without lobes; margins irregularly serrate or entire; apex acute; base cuneate. Upper leaves smaller, narrowly lanceolate to oblong-linear without or with basal lobes; margins entire or irregularly serrate. Inflorescence 1–6 cm long, interrupted-spiciform, composed of densely packed glomerules becoming contiguous towards the apex, terminal and axillary, leafless or with reduced leaves in the lower portions. Bracteoles 3–7 (–20) mm long, sessile or with stalks 0.5–4.0 mm long, rhombic or triangular-rhombic; apex acute or acuminate; base cuneate to broadly obtuse; margins entire or with a few short teeth, united up to the middle; lateral angles pointed, often strongly developed; herbaceous and thin, sometimes becoming foliaceous, spongy tissue never present; dorsal surface smooth or with few irregular short laciniate appendages, venation obscure or prominent towards the base. Two seed types present but intermediate types are frequent and some strains produce mostly small black seeds. Brown seeds 2.0–3.5 mm wide, orbicular, radicle sub-basal, obliquely up-pointing. Black seeds 1.5–2.5 mm, orbicular; radicle sub-basal, out-pointing. 2n=36. Fig. 13.

HABITAT AND DISTRIBUTION

Ruderal, fimicolous and anthropophilous weed of roadsides, pathways and barnyards, and a transient colonizer of freshly disturbed soil. This species frequently occurs in cities with *A. prostrata* on waste ground, at the margins of sidewalks, by rubbish tips and in disturbed soil on demolished building sites. *A. patula* rarely occurs in the littoral zone of coastal beaches. Along the coast it is primarily confined to the weedy ecotone between land and sea. It frequently occurs in soil on eroding coastal banks and about the nests of seagulls on coastal islands. Distribution in the British Isles is given in Fig. 14.

REPRODUCTIVE BIOLOGY

Facultatively autogamous and primarily wind pollinated but also visited by syrphid flies that feed on the pollen. Flowering mid-June to October; seed set September to November. The staminate and pistillate flowers are closely clustered together in tight glomerules. *A. patula* exhibits a slight protogyny, the female flowers extending receptive stigmas about one to four days before the anthers open. This species is the earliest flowering *Atriplex* in the British Isles. In Manchester, some plants begin flowering as early as 1st June. In the laboratory, the brown seeds germinate within about two weeks but few black seeds will germinate without being scarified and subjected to a period of alternating temperatures.

Section *SCLEROCALYMMA* Ascherson, *Fl. Brandenb.*, p. 578 (1864).

Stems whitish, pale brown or reddish. Venation kranztypus. Flowers monoecious, the pistillate ones all bracteolate and lacking a perianth. Bracteoles united up to the middle becoming cartilaginous in fruit. Seeds exclusively vertical.

7. *A. LACINIATA* L. *Sp. Pl.*, p. 1053 (1753).
Lectotype: in Hortus Siccus Cliffortianus (**BM**), fide Taschereau in *Can. J. Bot.*, **50**: 1591 (1972).
A. arenaria Woods in *Phytologist*, **3**: 593 (1849), non Nuttall.
A. maritima Hallier in *Bot. Z. Beitr.*, p. 10 (1863), non Crantz nec Pallas.
A. sabulosa Rouy in *Bull. Soc. bot. Fr.*, **37**: 20 (1890).

Plants 6–30 cm, decumbent with wide-spreading, ascending lower branches. Stems smooth or sub-angular, reddish or yellowish, more or less sparsely scaly, straight; much branched in a diffuse asymmetrical pattern. Lowermost one to three pairs of branches opposite or sub-opposite, the remainder alternate. Foliage whitish-green or greyish-green, non-succulent; mature and juvenile leaves covered with a fine scaly layer on both surfaces but more densely covered below. Lower leaves 1.5–4.0 cm long, ovate to lance-ovate, sinuate-dentate with larger basal lobes; base cuneate to a short petiole; apex obtuse. Upper leaves smaller, narrower, lanceolate or oblong, sinuate-dentate or entire, obtuse, mucronate. Inflorescence glomerulate in upper leaf axils. Bracteoles 6–7 mm long,

FIGURE 15. *Atriplex laciniata*.

sessile or with short stalks, broadly rhombic, whitish-green becoming scaly-black with maturity; apex acute; base cuneate; margins entire or with a few short teeth, united up to the middle, with lateral angles obtuse and strongly produced; cartilaginous, becoming thickened and hardened in the lower half, spongy tissue never present; dorsal surface smooth or with irregular pointed or flattened and wing-like tubercles or projections in the lower half, venation ± prominent. One seed type present: light brown, 3.5–4.0 mm wide, transverse-elliptic, dull, smooth; radicle median out-pointing to ascending, thick and prominent with apex strongly produced. 2n=18. Fig. 15.

HABITAT AND DISTRIBUTION

Coastal halophyte of sand or sand and cobble beaches. Widespread in the British Isles but often local. Where it occurs, it is usually present in low numbers as more or less widely-scattered individuals and after some years absence it may reoccur in a former locality. Observed in abundance only at Dunnet Bay, Caithness, Scotland. Distribution in the British Isles is given in Fig. 16.

REPRODUCTIVE BIOLOGY

Facultatively autogamous and primarily wind pollinated. Isolated plants grown in the greenhouse produced normal amounts of viable seed (Taschereau unpublished). Flowering August to September; seed set September to October. *A. laciniata* is well adapted to dispersal by sea. The cartilaginous bracteoles, united up to the middle, tenaciously retain the seed and soften little after soaking in sea water for several days. In the laboratory, bracteoles of this species floated in sea water for up to ten days (Taschereau 1970). Ignaciuk & Lee (1980) immersed bracteoles in constantly agitated salt water (600 mM NaCl). After five days, 20% of the bracteoles remained floating, but by eight days all had sunk. Ignaciuk & Lee (1980) found that seeds immersed in salt water (600 mM

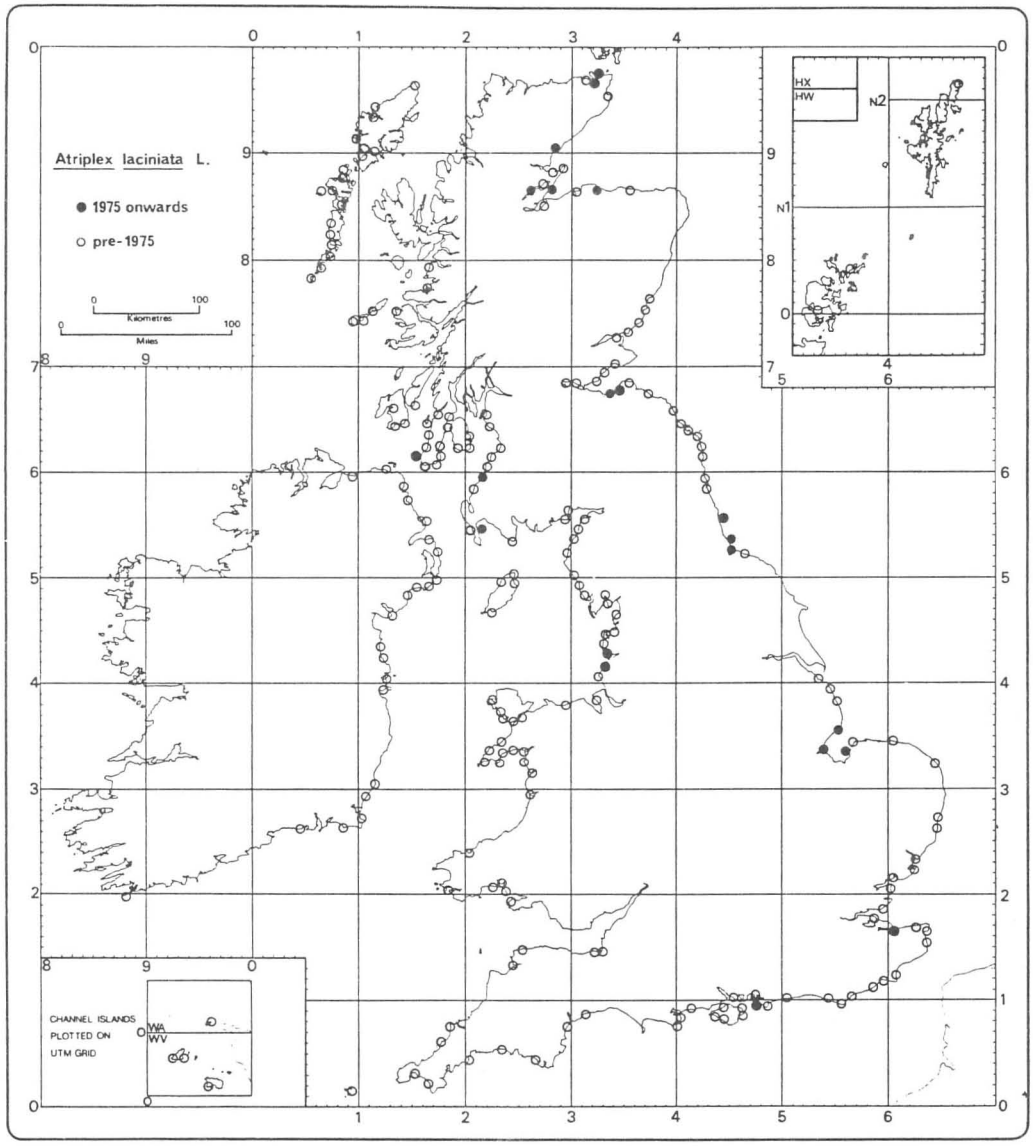

FIGURE 16. Distribution of *Atriplex laciniata* in the British Isles.

NaCl) for up to 30 days remained viable. Furthermore, these authors report that the seeds could germinate at this salt concentration and produce healthy seedlings although the growth rate of the plants was reduced. The seeds exhibit a marked dormancy. Those planted in the greenhouse will not germinate unless exposed for some time to fluctuating weather conditions outdoors (Taschereau 1970). In the laboratory, however, seeds readily germinate after being exposed to a period of alternating daily temperatures (Ignaciuk & Lee 1980). As in the case of *A. glabriuscula*, noted Ignaciuk & Lee (1980), the alternating temperature requirement of *A. laciniata* delays germination until after the spring equinoctial tides, the period of greatest environmental instability. This mechanism, they observed, also prevents the seed with its limited perisperm reserve from germinating beyond depths greater than it can overcome.

HYBRIDS

A. glabriuscula × *longipes*
Hybrid derivatives between *A. glabriuscula* and *A. longipes* are frequent on exposed coastal beaches in northern England and Scotland. They occur with *A. glabriuscula* in the habitat characteristic of that species in regions where *A. longipes* is absent.

A. glabriuscula × *praecox*
Rare in northern Scotland and Shetland. Occurring in the same habitat as the parent species.

A. glabriuscula × *prostrata*
Rare, from southern England to south-western Scotland and on the eastern coast of England. Occurring in the same habitat as the parent species. Earlier literature reports (Moss & Wilmott 1914; Jones 1975b) of its frequency are unconfirmed.

A. longipes × *prostrata*
Frequent wherever the parent species occur together; occasional inland in salt marshes and waste places. Hybrid derivatives between *A. longipes* and *A. prostrata* are common in sand and shingle on exposed coastal beaches in all regions of the British Isles, frequently in areas remote from one or both parent species.

Gustafsson's (1973b) experimental work with this hybrid in Sweden showed that it is present there as a more or less well-stabilized variant. Comparable plants are frequent in northern Scotland and occasional in Shetland where they occur on exposed coastal beaches, a habitat colonized by neither of the parent species. Occasionally found with *A. praecox* on the shores of somewhat less exposed sea inlets.

A. littoralis × *prostrata*
Occasional on the eastern and western coasts of England in disturbed habitats where both parents are present in abundance.

A. littoralis × *patula*
Known from only one locality in Midlothian, v.c. 83, where both parents were present in disturbed waste ground by the coast.

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