De-icing salt and the invasion of road verges by maritime plants

N. E. SCOTT and A. W. DAVISON

Department of Plant Biology, The University, Newcastle upon Tyne

ABSTRACT

The distribution of maritime species on British roadsides is described, and that of the most widespread species, *Puccinellia distans*, is mapped. Other species reported are *Aster tripolium*, *Atriplex littoralis*, *Cochlearia danica*, *Hordeum marinum*, *Plantago maritima*, *P. coronopus*, *Puccinellia maritima*, *Spergularia marina*, *S. media*, *Suaeda maritima*, and the North American adventive *Hordeum jubatum*. The roadside distribution of maritime plants in north-eastern England is brought up to date with two further species, *Cochlearia officinalis* and *Puccinellia fasciculata*, added. The latter was previously unknown north of Norfolk. To evaluate rates of invasion the present distribution in north-eastern England is compared with that of 1975. The occurrence of maritime species on roadsides is associated with the use of de-icing salt and is also occurring in North America and northern Europe. Observations are made on the habitat and associated plants.

INTRODUCTION

The first report of maritime plant species invading British roadsides was for north-eastern England by Matthews & Davison (1976). Since then there have been reports of similar invasions elsewhere in Britain (Badmin 1979, Dony 1979, Dony & Dony 1979, Feltwell & Philp 1980, Badmin 1981). These reports and other records are summarized in this paper to give the present known distribution of maritime species on British roadsides. Also, the original work of Matthews & Davison on the maritime roadside flora of north-eastern England is updated.

The invasion by maritime species is related to the heavy application of de-icing salt to major roads. High salinities in roadside verge soils (Davison 1971, Thompson *et al.* 1979) have resulted in open swards and in some cases strips of bare ground adjacent to the road. Such bare patches are often referred to as 'salt burn'. It is in these open habitats that the maritime species have been successful.

Particularly successful is the grass genus *Puccinellia*.* *P. distans*, *P. maritima* and *P. fasciculata* are all now found on roadsides, with *P. distans* being the most widespread of any of the maritime species. Apart from *Hordeum marinum*, the rest of the maritime species on inland verges are dicotyledons which otherwise occur in saltmarshes (*Aster tripolium*, *Cochlearia officinalis*, *Plantago maritima*, *Spergularia media*, *Suaeda maritima*) or other maritime sites (*Atriplex littoralis*, *Cochlearia danica*, *Plantago coronopus* and *Spergularia media*). Many of the common roadside species, such as *Hordeum jubatum*, *Atriplex* spp., *Matricaria perforata*, *Senecio vulgaris* and *Polygonum* spp., which occur in association with these maritime species, are also known from saline coastal habitats and presumably have a degree of salt tolerance.

Puccinellia distans is now present on roads throughout much of northern, central and eastern England (Matthews & Davison 1976, Dony & Dony 1979, Badmin 1981) but the other maritime species occur principally on roads in the north-east (Matthews & Davison 1976), and in Kent in the south-east (Badmin 1979, Feltwell & Philp 1980). Similar invasions are occurring on the major roads of northern Europe (for instance see Bresinsky *et al.* 1980) and North America (Butler *et al.* 1971).

There are many interesting questions that arise concerning this invasion and the authors have begun a number of experiments in an attempt to answer some of them; the existing information is discussed at the end of this article.

*nomenclature follows that of *Flora Europaea*

DISTRIBUTION

The maritime species with the most extensive roadside distribution is *Puccinellia distans*. The first roadside report was for north-eastern England (Matthews & Davison 1976). This was followed by reports for Kent (Badmin 1979), Bedford (Dony & Dony 1979) and Warwickshire (Badmin 1981). It was discovered at other roadside sites by the authors in 1979 and 1980, while further records have kindly been reported in answer to a request to the B.S.B.I. Figure 1 maps the distribution of *Puccinellia distans* on roadsides in the British Isles.

P. distans is very distinctive at anthesis and it can be recognized at some distance. As a result, many of the records were initially noticed from cars. The only surveys on foot have been by Feltwell &

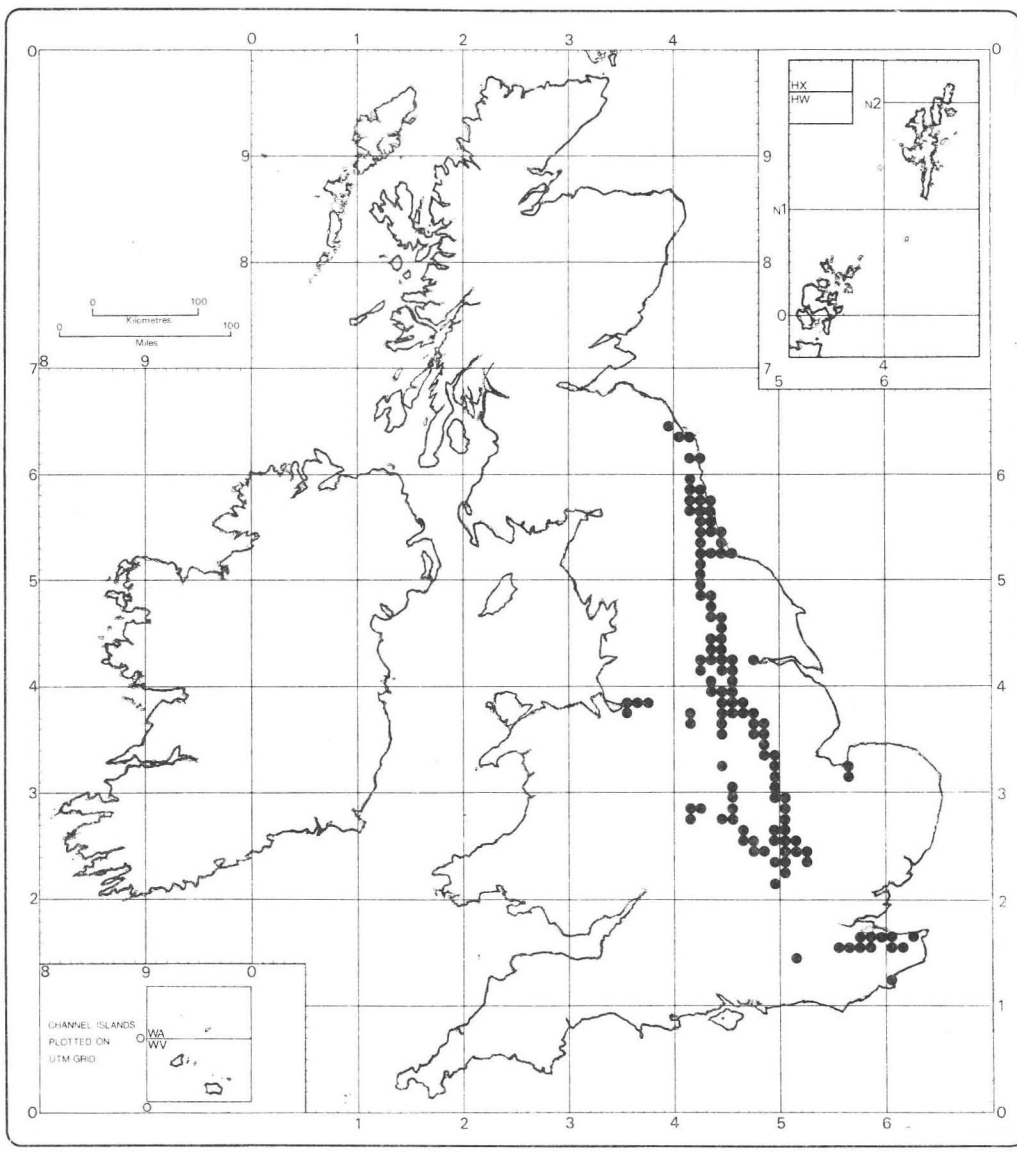

FIGURE 1. The distribution in the British Isles of *Puccinellia distans* on roadsides.

Philp (1980) on the M20 in Kent and by the present authors on roads around Newcastle. Because of this, populations could easily have been missed on most surveyed roads. In addition the number of roads which have been visited varies in different areas. North-eastern England, Bedfordshire and Kent have been surveyed well, but in other areas only the most major roads have been searched, usually just the motorways and the primary trunk roads. Thus it is more likely that the roadside distribution of *P. distans* is greater than is shown here. The authors feel, however, that, as major roads have been visited in all areas likely to have a roadside maritime flora, this mapped distribution is not likely to be greatly different in outline from the actual roadside distribution.

Only a few of the records shown on Fig. 1 are of isolated populations. Most are part of nearly continuous populations spread linearly along the verges. Most of the distribution from the Scottish border to Bedfordshire is continuous and, although it may have resulted from the merging of different populations, there are now no obvious divisions. *P. distans* occurs on many roads immediately to the north of Newcastle, but only on the A1 between Morpeth and Berwick. South from Newcastle, it is on the A1 (National Grid 10 km square 45/24), the A19 (45/44) and some of the roads between these two, such as the A66 from Middlesborough to the A1 at Darlington. From there southwards, records are confined to the A1 until 44/45, when the A58 goes south-west to Leeds, and just south of this where the records crossing east to west are on the M62. South from this records form two lines, the A1 in the east and the M1 in the west, until the records merge again in Bedfordshire, where *P. distans* has been found on a number of other roads. Leading west from the M1 at 42/46 are records for the A45 and the M42. All of the above records are virtually continuous; the few gaps which do occur are more likely to be due to under-recording than absence of plants. For instance, the gaps on the M1 are probably due to the fact that *P. distans* is more scattered there and often only on the central reservation, and thus difficult to record.

The remaining records form obviously discrete populations. The dots leading away from the Mersey (33/68) are on the M52. Those in Derbyshire in 43/16 are on the A515 and those in Norfolk in 53/62 are on the A149 near King's Lynn. The records in south-eastern England are in northern Kent on the M2, A2, M26 and A249 but also on the A20 going into southern Kent. The one dot in Surrey is an isolated record on the A24.

Fig. 2 shows the records for *Puccinellia distans* in Perring & Walters (1962). None of these records is for roadsides, so it can be seen that *P. distans* does occur elsewhere inland. These inland records are either recent and for disturbed ruderal sites, such as dumps and quarries, or from saline sites, such as the inland salt-marshes and old brineworks. Information from vice-county recorders indicates that many of these inland populations away from roadsides, especially the casual ones, are no longer extant.

Most of the other maritime species that have invaded British roads are confined to two areas. For north-eastern England, Matthews & Davison (1976, from a 1975 survey) recorded the following species: *Aster tripolium*, *Plantago maritima*, *P. coronopus*, *Puccinellia distans*, *P. maritima*, *Spergularia marina*, *S. media* and *Suaeda maritima*. More recently two further species have been found, namely *Cochlearia officinalis* and *Puccinellia fasciculata*. The former was found in 1978 on the central reservation of the A1 north of Shotton Grange (46/226.767). The plants have set seed every year and now number over 30 individuals. The species is still confined to this one site. *Puccinellia fasciculata* (det. C.A. Stace) is also known from only one site but as this species can be hard to detect growing amongst other *Puccinellia* species it may be more widespread on roadsides. The individuals found seem to be referable to the taxon *pseudodistans*, which is variously treated between the ranks of species and forma. It was discovered in 1980 growing amongst *P. distans* and *P. maritima* on the A1 near Seaton Burn (46/230.754). Previous to this discovery, this species was not known any further north than Norfolk and its discovery on the roads of north-eastern England is obviously important in the understanding of the origin of maritime road verge plants.

The other area with a large roadside maritime flora is Kent (Badmin 1979, Felwell & Philp 1980), where are found *Aster tripolium*, *Atriplex littoralis*, *Hordeum marinum*, *Puccinellia distans*, *P. fasciculata* and *Spergularia marina*.

There are other roadside records for maritime species, but most of these do not appear to be examples of the same phenomenon. They are usually long-established stable populations and are on minor roads which do not receive much, if any, de-icing salt. The Durham roadside populations of *Plantago maritima* and the Cheshire roadside population of *Cochlearia officinalis* (Gill *et al.* 1978), which are both associated with local limestone, are good examples of this. The invasion by

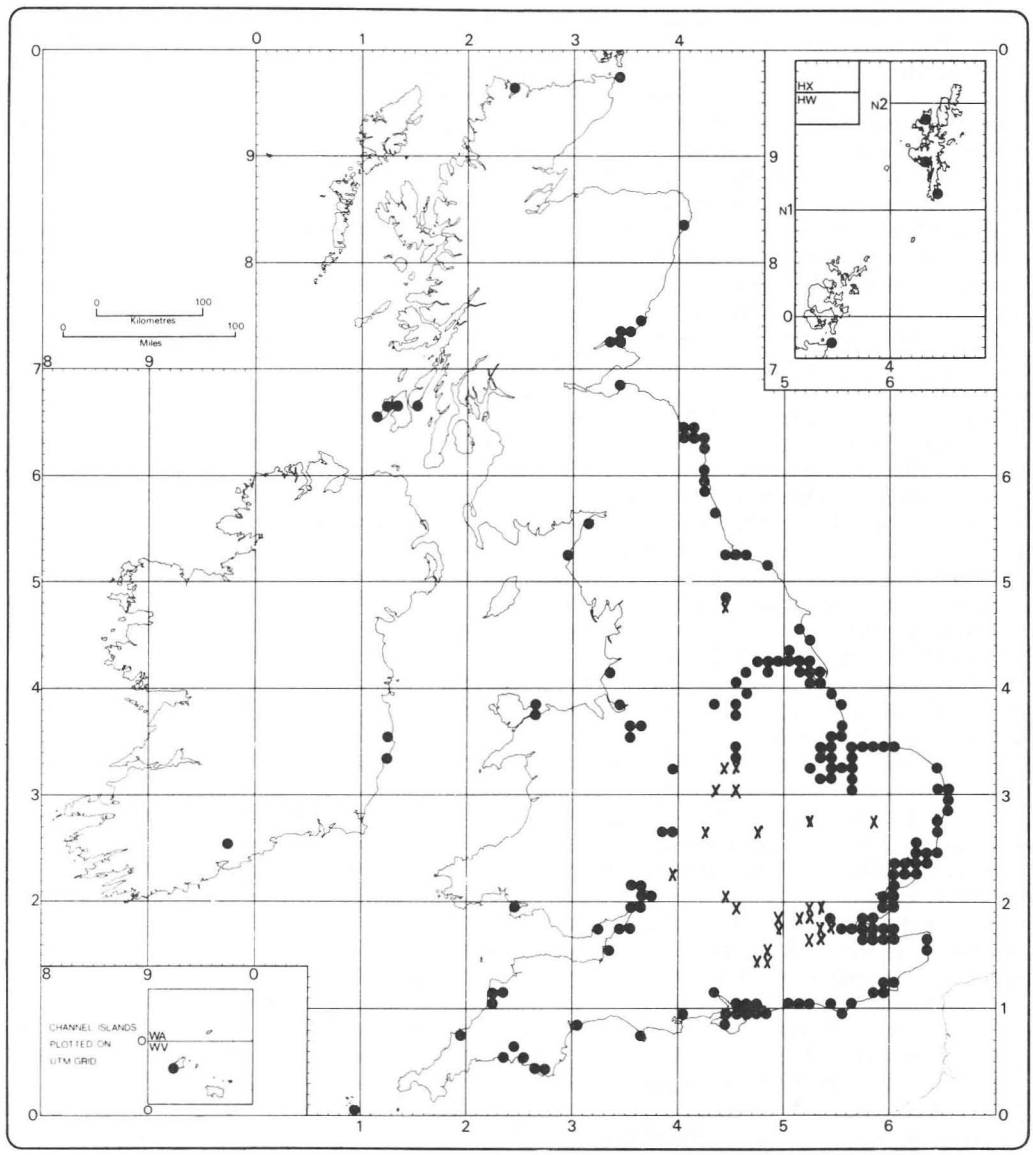

FIGURE 2. The distribution in the British Isles of *Puccinellia distans*, taken from Perring & Walters (1962). 1930 onwards •; Casual only ×.

Cochlearia officinalis of roadsides in south-western Wales (Chater 1975) would also seem to fall into this category. For whilst this invasion is recent the plants occur in mature grass swards on roadside banks on both minor and major roads in an area which uses little de-icing salt. However, the occurrence of *Cochlearia danica* (E.M. Hyde pers. comm.) on the A10 in Norfolk (52/710.722–708.717) would seem to be related to the use of de-icing salt. The population occurs on the bare margin of the verge and the road is quite heavily salted. *Plantago coronopus* is known from a number of roadside sites in the south: Feltwell & Philp (1980) report it on the M20, N.E. Scott has recorded it on the A272 in Sussex (41/862.215), and it has been reported as occurring on a roadside on Blackheath, London by O. L. Gilbert. This species is common inland in the south, associated with

sandy soils and all three roadside records are near to heathlands. However, all these roads are salted and it will be worthwhile examining these sites more closely.

RATE OF INVASION

In order to assess the relative success of the different maritime species, their distributions in north-eastern England in 1980 were compared with those of 1975. The presence or absence of the various species is plotted using the 1 km squares of the national grid for an area which covers northern Tyne and Wear and south-eastern Northumberland (Figs 3-8). Only *Puccinellia distans* and *P. maritima* are known to occur on north-eastern roads outside this area. Both species are present on the A1 north to Berwick and *P. distans* occurs south on the A1 and A19.

It may be possible that some of the sites found since 1975 were overlooked in the original survey. This possibility is felt to be unimportant, however, since the 1975 (and the 1980) surveys were thorough, with all the relevant roads being walked, and all new discoveries have been either small populations or extensions to the range of known populations. Furthermore, with species in which the size of an individual is an indication of its age (as with *Plantago maritima* and *Puccinellia maritima*), large plants are not present in the recently discovered populations.

The rate of spread into new 1 km squares varies between the different species. *Puccinellia distans* (Fig. 3) and *Spergularia marina* (Fig. 5) seem to be spreading the most rapidly. *Plantago maritima* (Fig. 6) is spreading nearly as rapidly, especially in the north on the Morpeth by-pass. *Puccinellia maritima* (Fig. 4) and *Suaeda maritima* (Fig. 7) have spread much more slowly, while *Spergularia media* and *Plantago coronopus* (Fig. 7) have not spread into any new 1 km squares. At most sites known for *Aster tripolium* (Fig. 8) in 1975 the populations could not be rediscovered in 1980 and are presumed extinct.

The stretch of road with the greatest number of species is the A1 just north of Seaton Burn (Fig.

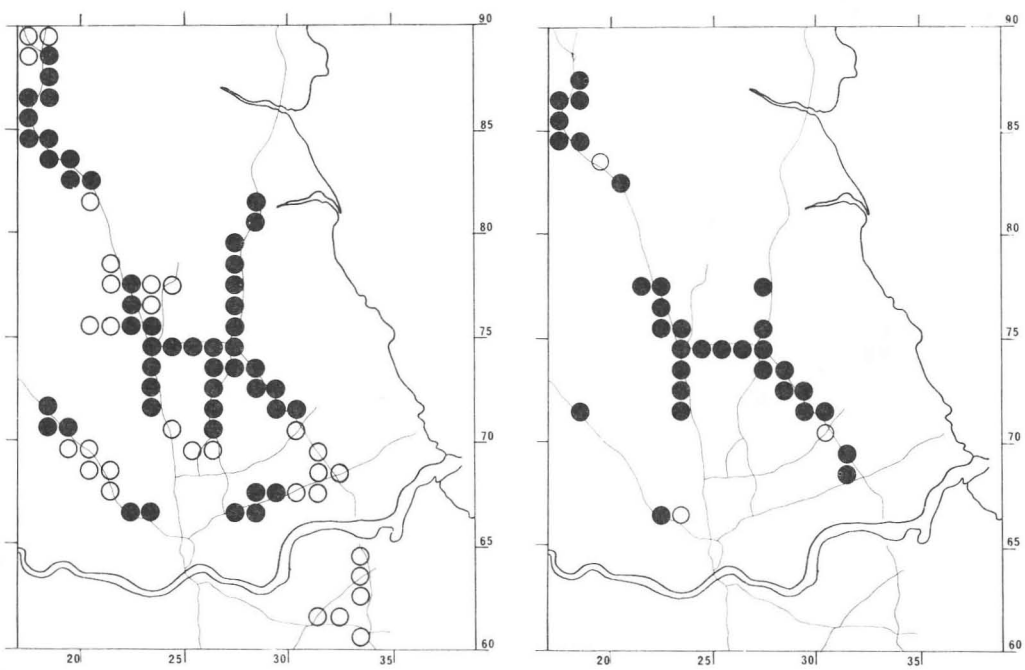

FIGURE 3. The distribution in north-eastern England of *Puccinellia distans* using the 1 km squares of the national grid. Present both in 1975 and 1980 ●; present in 1980 only ○.

FIGURE 4. The distribution in north-eastern England of *Puccinellia maritima* using the 1 km squares of the national grid. Present both in 1975 and 1980 ●; present in 1980 only ○.

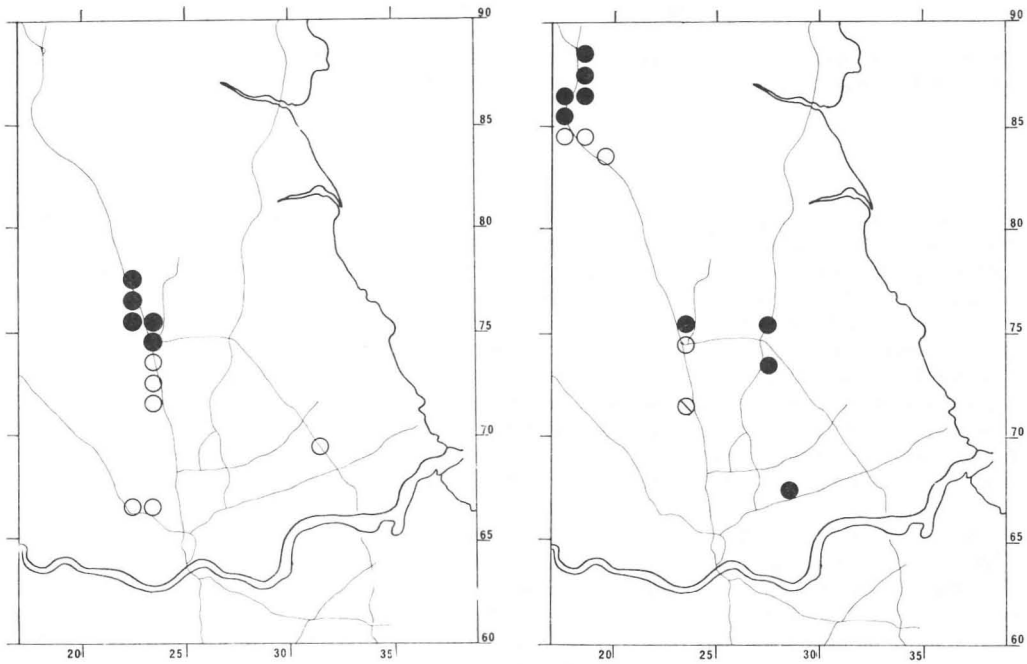

FIGURE 5. The distribution in north-eastern England of *Spergularia marina* using the 1 km squares of the national grid. Present both in 1975 and 1980 ●; present in 1980 only ○.

FIGURE 6. The distribution in north-eastern England of *Plantago maritima* using the 1 km squares of the national grid. Present both in 1975 and 1980 ●; present in 1980 only ○; present in 1975 only ⊘.

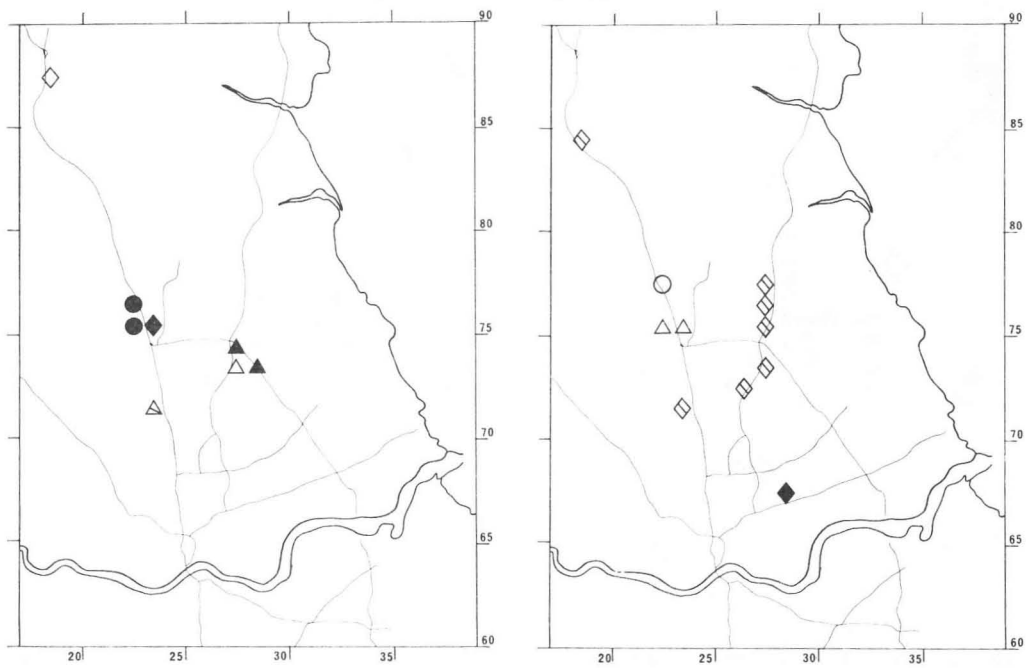

FIGURE 7. The distribution in north-eastern England of *Spergularia media* ●; *Plantago coronopus* ⧫; *Suaeda maritima* ▲. Present in 1980 and 1975, closed symbols; present only in 1980, open symbols; present only in 1975, crossed symbols.

FIGURE 8. The distribution in north-eastern England of *Cochlearia officinalis* ●; *Aster tripolium* ⧫; *Puccinellia fasciculata* ▲. Present in 1980 and 1975, closed symbols; present only in 1980, open symbols; present only in 1975, crossed symbols.

3–8, 23/75 – 24/75). Here, the south-bound verge has extensive areas of salt burn in which most of the roadside maritime species occur. The species not present are *Suaeda maritima*, *Aster tripolium* and *Cochlearia officinalis*. The last species occurs on the A1 less than a mile to the north and the other two species were found in a similar concentration of species some miles to the south on the A1 (Fig. 3–8, 23/71). These last populations were lost, however, when the verge was relaid in 1976. The juxtaposition of species perhaps indicates that these were original sites of introduction.

HABITAT

In north-eastern England, all roads with maritime species are heavily salted and, in other areas of invasion, whenever enquiries have been made, roads have also proved to be salted heavily. In fact the present distribution of the most widespread species, *Puccinellia distans*, reflects the quantities of salt used on motorways in different areas of England and Wales (J. R. Thompson pers. comm.).

With the exception of the examples discussed earlier, such as *Cochlearia officinalis* in Wales, all roads with maritime species show evidence of salt damage to the existing roadside vegetation. Grass swards are more open and in some cases the verge is completely denuded of vegetation for up to 3 m from the road. Roads with particularly high traffic densities show more vegetation damage, presumably because more of the salt is thrown onto the verge as spray. On the roads to the north of Newcastle there is a greater incidence of damage on the south-bound carriageway than on the north. This is because de-icing salt is usually applied in the early morning, and traffic density immediately after then is higher going south, because of the rush-hour traffic into Newcastle.

In north-eastern England, the maritime species usually occur in the completely bare areas of salt-burn. As the salt burn effect is confined to verges established since 1965, the maritime flora is usually found only on such recent verges. This is illustrated well on the north-eastern England distribution map for *Puccinellia distans* (Fig. 3), on which all the empty squares with major roads in them correspond to either older verges or built-up areas. The same is true in the area north of that covered by the maps, where, although much less road building has taken place recently, every record for *Puccinellia distans* corresponds to a post-1965 verge. It was in the mid 1960s that heavy applications of de-icing salt began. Major roads pre-dating then usually have *Elymus repens (Agropyron repens)* growing continuously along their length, mostly right up to the kerb, and salt appears to have had little effect on it. On more recent roads, however, *E. repens* is usually patchy or absent. The difference between the roads appears to be that when new roads were sown with the Department of the Environment recommended grass mixture, this was killed off in the first winter by salt. If the old roads were sown with such a mixture, salt applications were not high enough then to kill off the sward. It would seem that *Elymus repens* is able to invade a road verge and become dominant if the salt application is not high, and then is able to withstand increased applications of salt, but it is not always able to invade a verge already receiving levels of salt so high that it is causing salt burn. This is because the bare areas of salt burn will have suffered erosion, compaction and hence further increased salinity.

In other northern areas, where *Puccinellia distans* has invaded roads such as the M56, M62, M1 and A1, the habitat is similar to north-eastern England and populations are large. In the south, however, salt burn becomes less extensive and in Bedfordshire and Kent the maritime species are more scattered, in smaller populations on the margins of established verges. This difference is presumably a reflection of the larger amount of de-icing salt used in northern England, shown in the figures for motorways given by Thompson *et al.* (1979).

Species appear to differ in their ability to withstand water-logging. In north-eastern England some species are associated with certain roadside soil types. *Plantago maritima*, for instance, does well on the Morpeth by-pass (Fig. 6, 19/83 – 18/88), which has embankments made of an exceptionally well draining material. Most of its records are from these sites and there are many seedlings. The sites nearer Newcastle usually have only one or two older plants and very few seedlings and soils are usually mostly of clay and poorly drained. In contrast, *Spergularia marina* seems to occur only in such poorly drained sites, an observation which agrees with that of Sterk (1969) that natural populations often occur in and around transient saline pools. The only other species sufficiently widely spread for conclusions on soil preference to be made are *Puccinellia distans* and *P. maritima*. Both seem to be more catholic, though neither grows well or densely on the well drained soils of the Morpeth by-pass, perhaps indicating a susceptibility to water stress.

Some of the roadside maritime species are also known from non-saline inland sites, for example the mountain populations of *Plantago maritima* and *Cochlearia officinalis*, and *Puccinellia distans* which has been recorded as invading ruderal non-saline sites during much of the present century. Other species are not known away from saline soils, namely *Spergularia media*, *S. marina*, *Suaeda maritima*, *Puccinellia maritima* and *Puccinellia fasciculata*. It is generally assumed that this is due to the their inability to compete on non-saline soils, and the restriction of most of these latter species on roadsides to bare areas of salt burn appears to support this view. However, it has been noticed that, where bare ground leads away from the road and becomes non-saline, none of these maritime species goes beyond the saline strip parallel with the verge. Such transects of available open habitat are not common, and the few examples may be coincidental, but they may indicate some positive requirement by these species for salt. J. A. Lee (pers. comm.) mentions having noticed a similar situation on an inland saline pool at Sandbach, Cheshire, where *Spergularia marina* grows on otherwise bare saline muds but not on adjacent bare non-saline muds.

OTHER SALT-TOLERANT SPECIES

The other species which have invaded saline verges are also of interest. These species are adapted to the disturbed nature of the habitat and are presumably salt tolerant. Some of them also occur in maritime sites and the only difference between them and the 'maritime' species is that they also occur extensively inland. In north-eastern England at sites with the highest salinity the only additional species are *Atriplex* spp. and *Matricaria perforata*. In the less saline sites other species occur, such as *Polygonum aviculare*, *P. arenastrum* and *Senecio vulgaris*. All these species have been recorded by Feltwell & Philp (1980) on the M20 in Kent. It is significant that most of them are annuals and so will avoid the higher soil salinities of the winter. The *Atriplex* species can be difficult to identify as they are particularly prone to insect infestation on roadsides. In north-eastern England, only *A. hastata (A. prostrata)* and *A. patula* have been identified but in Kent *A. littoralis*, a maritime species, has also been reported.

Another species often found growing on saline roadsides is *Hordeum jubatum*. This adventive is a native of North America, (Best *et al.* 1978). Unlike the species mentioned above, *H. jubatum* is usually found growing in the grass sward. Its niche seems to be quite precise, because in the north-east it forms a strip growing parallel to the road which is normally no more than 1 m wide and from 0.5 to 1 m back from the road. Its natural habitat is the margins of saltpans where it also forms a precise band between the *Atriplex* zone and the non-saline meadow vegetation (Ungar 1979). It is also reported as occurring in saltmarshes in Newfoundland.

H. jubatum was first recorded from Britain in the south at the beginning of the century. It was reported then as being introduced in bird seed. *H. jubatum* seems to have moved on to major roadsides in southern Britain in the early 1960s but as this did not result in new vice-county records it is difficult to find precise dates. In the late 1960s it began to appear on midland and northern roads, resulting in such new vice-county records as N. Lincs., v.c. 54 (1963), Co. Durham, v.c. 66 (1967), Rutland, v.c. 55b (1969), Cumberland, v.c. 70 (1969), Leics., v.c. 55 (1971), Warks., v.c. 38 (1974), S.W. Yorks., v.c. 63 (1974), S. Northumb., v.c. 67 (1976), Westmorland, v.c. 69 (1978).

The apparent spread northwards could be coincidental, as there is evidence that *H. jubatum* is introduced with imported grass seed. The N.I.A.B. official seed testing station reports that *H. jubatum* occurs as a contaminant in imported grass seed including *Poa pratensis* seed, which is in the Department of the Environment's recommended grass seed mixture for road verges (Ministry of Transport 1963). *H. jubatum* is a short lived perennial and in the southern and midland road-side populations it usually disappears after three or four years. As such populations are often on newly sown verges, introduction with the grass seed would seem the most likely possibility. In the north, however, invasion has been of mature verges and the species seems to be more permanently established.

THE SITUATION ABROAD

Puccinellia distans also occurs on roads in northern Europe. Adolphi (1975), Seybold (1977), Lienbecker (1979), Krach & Koepff (1980) and Bresinsky *et al.* (1980) all detail its spread in different

areas of West Germany. Fukarek *et al.* (1978) report *P. distans* on roadsides in East Germany and E. Weinert (pers. comm.) mentions the more local occurrence of *Aster tripolium* and *Plantago maritima* on roadsides there. *P. distans* has also been reported in the Netherlands (Vallei 1979), and Badmin (1980) reports having noted it in northern France.

In North America *Puccinellia distans* was discovered on expressways around Chicago by Butler *et al.* (1971) and is reported as having spread rapidly since (Butler 1977). It is not a species native to America but is introduced from Europe and has become widespread on saline agricultural soils.

Hordeum jubatum is a native of North America and is common on roadsides there, forming similar narrow bands parallel with the road in at least some areas (observation by A. W. Davison in Quebec). Seybold (1977) has recorded *H. jubatum* on roads in southern Germany and Switzerland.

This brief review may be incomplete, as it can be difficult to trace articles on this subject since they are often in local natural history publications.

DISCUSSION

RELATIVE SUCCESS OF SPECIES

The remarkably rapid spread of *Puccinellia distans* along Britain's roads is a reflection of its adaptation to this new habitat. Its natural habitat would seem, from observations in Northumberland, not to be true saltmarshes, but rather the edges of saltmarshes or other saline maritime soils. Most sites are disturbed and often compacted, and many are poorly drained. This agrees with the habitat description by Beeftink (1977) of the alliance *Puccinellia-Spergularion salinae*, association *Puccinellia distantis*, for which *Puccinellia distans* is a characteristic species. He describes the association as forming ephemeral communities on saline soils, and states that these are characterized by instability. Inland saltmarsh sites in which it also occurs are similar (Lee 1975). Both inland and on coasts, the land is typically pastoral and only occasionally inundated with saline water.

Roadside sites have much in common with these natural sites as soils are often highly compacted and poorly drained as well as being highly saline. The roadside habitat is a recent one and the adaptation of *P. distans* to a disturbed habitat, and its short life cycle, high seed production and light seeds enable it to invade rapidly. The fact that its seed is small and easily wind-blown means that it can be carried along in the slipstream behind vehicles.

It is possible that other maritime species will eventually follow *Puccinellia distans* in colonising so much of Britain's major roadsides. *Spergularia marina*, which shares many of the characteristics of *P. distans*, would seem to be the most likely species. This species is spreading comparatively rapidly on the roads of north-eastern England and is present in Kent. It is also a species of disturbed habitats. It is the other characteristic species of the alliance *Puccinellia-Spergularion salinae* (Beeftink 1977), and is present in most of Britain's inland saltmarshes.

Both *Spergularia marina* and *Puccinellia distans* are spreading rapidly on the roads of north-eastern England (Figs. 1 & 3) and both are species adapted to a disturbed habitat. By comparison, the spread of *Puccinellia maritima* (Fig. 4), *Suaeda maritima* (Fig. 7) and *Plantago coronopus* (Fig. 7) is much slower. These species have heavier seed, *Puccinellia maritima* and *Plantago coronopus* live longer, and *Puccinellia maritima* has very variable seed-set with many plants not setting seed in any given year. *Spergularia media* (Fig. 7) is also expanding slowly, which is in marked contrast to *Spergularia marina*. Sterk & Dijkhuizen (1972) report that *S. media* is a species of more stable habitats than *S. marina*. While *S. marina* is an annual with lighter seed, *S. media* is a short-lived perennial with heavier seed. *Plantago maritima* (Fig. 6) has spread quite rapidly since 1975. The plants are long-lived and, although seed-set is good, seed is comparatively heavy. Seeds are, however, mucilaginous and sticky, and this may be an aid to more rapid invasion.

At most sites at which *Aster tripolium* (Fig. 6) was recorded in 1975, the plants could not be relocated in 1980 and the populations are presumed extinct. From site observations and from growing seedlings in the University gardens, the *Aster tripolium* plants on the roadsides would appear to be the high marsh ecotype as described by Gray (1974). Plants are short-lived, often monocarpic and usually fruit within the first two years. Flowering heads have large numbers of light fruits with gradual seed germination, which does not usually exceed 80%. Extinct populations were all on mown verges and, as the species has a tall flowering stem, regular mowing will probably have

prevented successful seed-set. With a short-lived plant, populations will have disappeared quickly. *Aster tripolium* is also lost from heavily grazed saltmarshes (Chapman 1960).

ORIGINS

The most intriguing aspect of this work is the question of where these plants came from and how they got to their present sites. Firstly there is the question of when they might have first invaded these roads. The discovery of maritime plants on British roads has occurred separately on at least three occasions since 1975 (Matthews & Davison 1976, Dony & Dony 1979, Badmin 1979). Similar discoveries have occurred from 1975 onwards in northern Europe. While these plants could have been present but unrecorded on these roads long before their discovery, the evident association between invasion and the heavy application of de-icing salt, which began in the mid 1960s, would indicate that the invasion probably began after then. With the exception of a few populations of *Puccinellia maritima* and *P. distans*, the maritime species in north-eastern England are confined to roads built after 1967. This then would appear to be the earliest likely date of invasion in north-eastern England. *Puccinellia maritima* might be an exception to this, for despite its slow rate of spread (Fig. 4) its distribution is quite considerable, and there are some remarkably large plants (up to 3–4 m across) on some roads. Furthermore, it does occur on pre-1967 verges to the north of the area mapped. In contrast, except for *P. distans*, the other species are much more localized, even those spreading comparatively rapidly such as *Spergularia marina* and *Plantago maritima*. It seems, therefore, that these last two species, at least, were introduced more recently than *Puccinellia maritima* and possibly also later than the very widespread *P. distans*. So it would seem that in north-eastern England the introduction of different maritime species has not been entirely contemporaneous.

The disappearance of *Aster tripolium* is of interest at this point. The seed-set is so poor that populations have been unable to establish. This could mean that all of the small populations discovered in 1975 represented separate introductions, and that for at least one of the species introduction was not due to a single event.

The roadside distribution of *Puccinellia distans*, as shown in Fig. 1, indicates a possible answer to the question of the origin of these maritime species. Most populations of *P. distans* can be traced along major roads, with gaps between populations of no more than 10 km to coastal sites with vehicular access. Thus the populations on the A1, M1 and M62 could have come from saltmarshes at Holy Island in Northumberland and Cowpen Marsh south of Hartlepool. Roads cross both of these saltmarshes and lead to the A1 and A19 respectively. In Kent the A249 is lined with *P. distans* and leads from a coastal site on the Isle of Sheppey to the A2, M2 and M20 (Feltwell & Philp 1979). The population on the M56 and M6 could have originated in a similar way from the populations on the Mersey. Alternatively, some roadside populations could have originated from other inland populations shown on Fig. 2. Some of these records, particularly the casual ones, are for quarries or dumps which are used by vehicles. A good example is the record for the Streetly quarry in Nottinghamshire, which is near both the M1 and M62 and which supplies roadstone. The population on the M52 is very close to the inland saltmarsh and brine works sites of Cheshire.

Thus, it would be possible for most roadside populations of *P. distans* to have originated through seed being spread along roads carried in vehicular slipstreams. This is also true for the populations of *Puccinellia maritima* on the roads of north-eastern England which occur up the A1 to within 1 mile of Holy Island. This is not so, however, for the other maritime species on roadsides. Although all but one of these species occur on nearby coasts their distribution is not continuous along roads to these coastal sites. Seed must then have been carried to the roadsides. It has been shown by Wace (1980) that the number of seeds carried by vehicles can be high. As this is a roadside phenomenon, and as vehicles regularly cross local coastal sites, for these species, carriage on vehicles would seem the most likely means of transport. In fact, in the case of some of the more isolated roadside populations of *P. distans* (Fig. 1) elsewhere in the country, carriage on vehicles could also have played some part in its roadside distribution.

This simple explanation for the origin of the maritime species is marred by one fact, however: the discovery of what appears to be *Puccinellia fasciculata* on one roadside site in north-eastern England. This species was previously recorded only as far north as Norfolk and its presence on the roadsides of north-eastern England could mean that either it has been introduced from outside the area or that it

is present undetected on the coasts of the north-east. It can be difficult to distinguish growing amongst other species of *Puccinellia*, so that it is possible that it occurs on the local coast. In fact, as this paper was about to go to print, specimens of the same taxon (i.e. the variant *pseudodistans* of *P. fasciculata*) were discovered on the County Durham coast by Miss J. Hill (det. C. A. Stace), at the mouth of Castle Eden Burn (45/457.408). Although this find removes the major point against the possibility of introduction from the local coast, the likelihood of introduction from outside the area must still be considered. Matthews & Davison (1976) suggested a number of ways these species could have been introduced from outside the local area and these have been investigated further.

Matthews & Davison (1976) considered the possibility of the deliberate introduction of maritime species but after local enquiries dismissed this as unlikely, and no evidence has emerged since. The discovery since then of maritime species on roadsides in other areas of Britain and abroad confirms this conclusion. Seed could have been introduced as contaminant, either in the de-icing salt or in the grass seed mixtures used to sow the verge. Saltmarsh species do occur adjacent to the I.C.I. salt mine at Winsford, Cheshire (Lee 1975), from which most of Britain's de-icing salt originates. However, the only species recorded are *Puccinellia distans*, *Spergularia marina* and *Aster tripolium*. Matthews & Davison inspected a number of local salt-piles but found no maritime plants. Other salt-piles in the area have since been inspected and despite what would seem to be ideal habitats no maritime species have been seen.

To check on the possibility of seed as a contaminant in the grass seed mixture, enquiries were made with the N.I.A.B. official seed testing station and major seed importers. N.I.A.B. reports the genera *Puccinellia* and *Spergularia* as contaminants in imported grass seed without being able to specify the species. The other genera involved have not been found, and, in the genus *Spergularia*, there are other species more likely to occur in imported grass seed. Thus there is no direct evidence yet of maritime species being introduced from outside the local areas. This, combined with the fact that the occurrence of a large roadside maritime flora is confined to two counties (Northumberland and Kent) with major roads adjacent to the coast, means that at present the most likely explanation must remain introduction from the local coasts.

A number of experiments have been started to answer questions arising from this work. For instance, to try to ascertain the correct sources of origin for the seed, specimens have been collected from roadside sites and from some of the possible sources and these have been established at the University experimental gardens.

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The authors would welcome further reports of maritime species invading roads and also any corrections or comments on the information described here.

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