Road de-icing salt and the invasion of verges by halophytes.

Thesis

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I declare that this work is a result of my own investigation and has not been submitted for any other degree at this or any other University.

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Contents

Summary.

The halophytes invading roads are mostly from maritime habitats and their invasion appears to be a response to the heavy use of de-icing salt which began in the 1960's. The most widespread species, *Puccinellia distans* now occurs extensively in the north and east of England and Wales. Other maritime species occur mostly near the coast and include *Aster tripolium*, *Cochlearia officinalis*, *Puccinellia maritima* and *Spergularia marina*. Experiments and observations indicated that seed of invading populations is carried from the coast to roadsides on vehicles and once there is swept along in vehicular slipstreams. Rates of invasion, estimated by comparing the present distribution with that in 1975, were highest for species adapted to disturbed saline sites.

Levels of salt in roadside soils varied between sites. Well drained soils had lower salinities than clay soils, some of which had salinities higher than previously recorded on roadsides in Britain. There were peaks in winter during salt application and at some sites in early summer due to evaporation. Soil salinity levels proved to be significantly correlated with salt application rates, site exposure to the prevailing wind and traffic volume.

Species occured in distinct zones with maritime species confined to the saline road margin. This confinement was partly due to competition as glycophytes eliminated maritime species from non-saline experimental plots but was also due to a requirement for salt by the maritime species when growing on roadside soil.

Salt affected the resistance of maritime species to stress. For example the application of salt increased the freezing resistance of four of the species but decreased it in one. In trials using roadside soil protection from drought increased the survival of maritime species not treated with salt. Treatment with nutrients and other solutions containing ions easily assimilated by plants overcame the requirement for salt.

Two of the maritime grasses, _Puccinellia distans_ and _P. maritima_ proved to be suitable for reclaiming areas of roadside verge damaged by de-icing salt.

Chapter One. Introduction

De-icing salt has been used on roads since the 1940´s (H.M.S.O. 1953) but the present heavy applications and widespread use did not begin until the 1960´s (H.M.S.O 1968). As some of the salt is splashed onto the verges this heavy use has resulted in high salinities in roadside soils. Reports of high soil salinities began to appear in the late 1960´s, particularly in North America (e.g Westing 1969), but also in Britain (e.g. Davison 1971). A model has been developed for predicting soil salinity levels from salt application rates and climatic data (Thompson et al. 1979).

High soil salinity has damaged roadside vegetation in many areas, resulting in open swards and in some cases strips of bare ground adjacent to the road (Davison 1971; Catling and McKay 1980). Such bare patches are often referred to as "saltburn". It is into these open habitats that species, new to roadsides have invaded. Most of these species are usually associated with one or more maritime habitats, although some of them are also known from certain other habitats. Because of the difficulty of finding a suitable adjective to describe this group of species, in this thesis the term "maritime" is used, without implying that the species are restricted to such habitats. These species are all also ´halophytes´ according to the definition of Flowers, Troke & Yeo (1977), in that they are able to complete their life history in habitats with high salinity.

The first report of such species invading British roadsides was for north-east England (Matthews and Davison 1976). Since then there have been reports of similiar invasions elsewhere in Britain (Badmin 1979; 1981; Dony and Dony 1979; Feltwell and Philp 1980; Hyde et.al. 1981; 1982; 1983; Halliday 1983; and Kitchener 1983). There have also been reports of such invasions in the rest of northern Europe (e.g. Bresinsky et.al. 1980) and North America (e.g. Butler et al. 1971).

The grass genus Puccinellia is particularly successful in this new habitat. P.distans, P.maritima, P.fasciculata and P.rupestris now occur on British roadsides, with P.distans being by far the most widespread of any of the invading maritime species. The list of maritime species on roadsides is now long (Scott and Davison 1982; Kitchener 1983) and includes those associated with several different coastal habitats (Beeftink 1977). These habitats include saltmarshes (e.g. Aster tripolium and Suaeda maritima), dune systems (Cochlearia danica and Elymus pycanthus), the strand line (Atriplex littoralis) and disturbed saline sites (Puccinellia distans and Spergularia marina).

There is also at least one halophyte species invading British roadsides which is not of maritime origin. This is Hordeum jubatum which is a native of North America where it grows in salt-pans (Unger 1974; Best et.al. 1978) and which was first reported on British road verges by Lousley (1970). There are also several non-maritime species which have been able to survive in moderately saline soils on roadsides. They include such species as Senecio vulgaris, Atriplex spp., Matricaria ma ritima, and Polygonum spp which are frequently found in large numbers on roadsides. These species can occur in association with the invading maritime species (Feltwell and Philp 1980). Interestingly, they also sometimes occur in certain maritime habitats (Tansley 1939).

The invasion of newly created man-made habitats has occurred repeatedly over previous centuries and several cases have been well documented in general terms (Lousley 1953; 1970). One of the best known is that of Senecio jacobea which was introduced from Italy last century and spread throughout Britain along the railway network (Kent

1956a, 1956b, 1960, 1964). However, no invasion has been investigated in any detail while it was in progress so the present invasion of roadsides presents an excellent opportunity to do this.

The first objective of the study was to establish the present extent of the invasion in Britain. The recording of the distribution of species in north-east England, as part of this, also allowed an assessment of rates of invasion since the distribution was last recorded in the 1970's. This area was also suitable for the closer study of the nature of the invasion as there are particularly extensive areas of damaged roadside and a long list of maritime species now present on them (Matthews and Davison 1976; Scott and Davison 1982). Another objective of recording species distribution was to establish the likely sources of seed and methods of seed dispersal. There have been several suggested answers to these questions (Matthews and Davison 1976, Catling and McKay 1980, Feltwell and Philp 1980) but only Wace (1979) actually investigated the subject. He showed that, in Australia, large numbers of seed were carried on vehicles and that some seeds were carried considerable distances. This suggests that seed may be picked up by cars at the coast and then carried to saline verges.

As well as studying the distribution and means of invasion of these species it was also decided to investigate other aspects of their ecology. The investigation of a species in a new habitat allows, by comparison of that habitat with the old one, some insight into the requirements and tolerances of that species. There have been many studies in the past of maritime habitats, particularly of salt marshes (e.g. the volume edited by Jefferies and Davy 1979) and the study of the same species in the new roadside habitat could add to the understanding of natural ecosystems.

In north-east England there are very obvious differences in the occurrence of maritime species on verges, in terms of both the number and relative abundance of the species present at any particular place. As the invading species come from a range of maritime habitats (Beeftink 1977) in which there are different environmental conditions it was thought that the differences in occurence on roadsides might reflect variations in the habitat and differences in species physiology. An attempt was made to examine this variation by investigating correlations between species occurence and variation in environmental factors.

The vegetation on roadsides also tends to be zoned (Cusick 1982; Scott and Davison 1982). While some of the species are confined to the part of the verge adjacent to the road and heavily affected by salt, others occur some distance from the road in less saline soil. Similar gradients were described by Lee (1977) around inland salt marshes in Britain and by Unger (1979) for the saltpans of the United States. The usual explanation for such a discrete zonation is in terms of salinity tolerance and competition; salt tolerance determining how close to the road or salt source a species can exist and competition from glycophytes controlling the invasion of salt-tolerant species into the non-saline zone. Most workers agree that the exclusion of halophytes from non-saline soils is not due to any form of requirement for salt but simply to an inability to compete with glycophytes (for instance Barbour 1970, Waisel 1972, Wainright 1980). However, inspection of some road verges at the start of the study showed places where maritime species were apparently confined to the verge even though they were adjacent to the non-saline areas with no or little competition. Consequently another objective of the study was to investigate whether competition was the sole explanation for the confinement of maritime species to the immediate roadside or whether other factors were involved

Salt damage to roadsides can be unsightly, especially where the damage extends far from the road. The final aspect studied,albeit superficially, was the possibility of using some of the maritime roadside species to reclaim salt damaged verges and to sow on new roads that are likely to be heavily salted. There are many reports in the literature of grass trials on roadsides to assess species ability to withstand salt. Most of these have involved salt tolerant varieties of agricultural or amenity grass species (Roberts and Zybura 1967; Cordikes 1968; Humphries 1979) but some workers have tried salt tolerant species (e.g. Dudeck 1969) and one group has developed a variety of Puccinellia distans (Fults 1972; Hughes, Butler & Sanks 1975; Butler 1977), which is now commercially available in the United States for sowing on saline soils. On some roads in north-east England there are extensive areas of salt damaged verges not yet invaded by the maritime species and the local authorities have expressed concern over their unsightly nature. It was decided, therefore, to try using some of the invading maritime grass species for the reclamation of these areas and also for use in an amenity mixture for sowing onto new roadsides.

Chapter Two. Materials and methods

Experimental Sites

The position and description of all the experimental sites referred to in this thesis is given in Table 2.1.

Seed Collection and Sowing

Seed was collected from four roadside sites in north-east England; sites and the species collected at each are shown in Table.2.2. The only species collected from more than one were the *Puccinellia* spp. but, except for the reclamation trials (Chap. 8), only seed from Seaton Burn was used in experiments. Newly collected seed was air dried and then tested for viability on moistened Whatman Grade 182 9cm filter paper in covered petri dishes. Viable seed was then stored in a deep freeze and viability was re-assessed before use in experiments. Seed stores were replaced each season with new collections.

Commercial varieties used in experiments were *Festuca rubra* cv S59, *Lolium perenne* cv S23, *Festuca rubra* cv "Hawk" (a drought and salt tolerant variety which was being developed at the Welsh Plant Breeding Station and which was donated by Dr M.O.Humphreys) and *Puccinellia distans* cv "Fults" donated by Northrup King and Co., Minneapolis, USA. The amenity grass seed mixture was based on that recommended by the Ministry of Transport (1963) for roadsides and was donated by Newcastle City Parks Department and Northumberland County Council Highways

Table 2.1 Details of experimental sites

Experiment		Road & Locality	Grid Reference	Direction Carriageway.Road (see note A)	Road type (see B)	Age of verge	Traffic Density 24hr ave	Soil Salinity m siemens (see C)
Plantago Populations ((Chap. 3)								
	1	Al Morpeth By-Pass	NZ 176.856	S.B.C. NW/SE	dc, m, c	1970	3880	2.4
	2	,,	NZ 199.830	S.B.C. NW/SE	dc, m, e	,,	,,	3.5
	3	,,	NZ 180.849	S.B.C. N/S	dc, m, c	,,	,,	2.3
	4	,,	NZ 177.863	S.B.C NE/SW	dc, m, c	,,	,,	2.5
	5	,,	NZ 178.854	N.B.C. NE/SW	dc, m, c	,,	4600	2.0
	6	,,	NZ 176.856	N.B.C. NW/SE	dc, m, c	,,	,,	2.5
	7	,,	NZ 176.865	S.B.C. NE/SW	dc, m, c	,,	3880	2.4
	8	,,	NZ 182.883	S.B.C. NE/SW	dc, m, e	,,	,,	3.1
Seed trap sites (Chap. 4)								
P.distans	1	Al Arcot Hall	NZ 245.748	W&E.B.C. W/E	dc, m, c	1967	5500	4.1 & 2.8
	2	A69 Throckley	NZ 145.677	W&E.B.C. W/E	dc, m, c	1976	7400	2.9 & 3.1
P.maritima	1	Al Morpeth By-Pass	NZ 176.856	N.B.C. NW/SE	dc, m, c	1970	4600	2.4
	2	,,	NZ 176.865	N.B.C. NE/SW	dc, m, c	,,	,,	2.4
	3	,,	NZ 177.862	S.B.C. N/S	dc, m, c	,,	3880	2.3
	4	,,	NZ 190.835	S.B.C NW/SE	dc, m, e	,,	,,	3.4
	5	,,	NZ 176.856	N.B.C. NW/SE	dc, m, c	,,	4600	2.4
	6	,,	NZ 182.874	N.B.C. NE/SW	dc, m, e	,,	,,	2.3
	7	,,	NZ 178.863	S.B.C. N/S	dc, m, c	,,	3880	2.1
	8	,,	NZ 190.836	S.B.C. NW/SE	dc, m, e	,,	,,	3.1

Cont.

Table 2.1 Details of experimental sites (cont.)

Experiment	Road & Locality	Grid Reference	Direction Carriageway.Road	Road type	Age of	Traffic Density	Soil Salinity
Roadside Colonisation Trials (Chap. 5)							
1	A1 Morpeth By-Pass	NZ 181.862	S.B.C. NE/SW	dc, e	1970	3880	3.8
2	A1 Seaton Burn	NZ 229.756	S.B.C. N/S	dc, m	1971	11042	16.8
3	A69 Throckley	NZ 139.678	W.B.C W/E	dc, m, e	1976	7400	2.9
Reclamation Trials (Chap.8)							
1	A1 Shiremoor	NZ 317.692	S.B.C. N/S	dc, m, e	1967	9511	8.8
2	A197 Morpeth	NZ 209.868	S.B.C. NE/SW	c	-	2014	5.1
3	A696 Newc´ Airport	NZ 183.717	W&E.B.C. W/E	dc, m	-	11000	4.1-8.7
4	A696 Kenton	NZ 214.676	W&E.B.C. W/E	dc, m	1982	13000	6.1-9.5
Soil salinity Sites (Chap. 4)							
1	A1 Seaton Burn	NZ 231.753	S.B.C. N/S	dc, m, c	,,	11042	-
2	,,	NZ 230.755	S.B.C. N/S	dc, m, c	,,	,,	-
3	A1 Seghill	NZ 275.743	S.B.C. NW/SE	dc, m, e	,,	8546	-
4	A1 Morpeth Bye Pass	NZ 181.870	S.B.C. SE/NW	dc, e	,,	3880	-
5	,,	NZ 182.873	S.B.C. SE/NW	dc, e	,,	,,	-

Note A S.B.C. = South Bound Carriageway, N.B.C. = North Bound Carriageway, etc.

Note B d.c.=dual carriageway, m = with median, c = in cutting, e = on embankment

Note C Soils collected in April 1982 from 0.5m from road.

Department. The specification for the mixture is given in Table 2.3. The amenity grass seed mixture was sown on roadsides and at the University garden at the same rate as used by the Local Authority (60 g m-2). Other species mixtures used for roadside verge reclamation were also sown at this rate. All other sowings both of roadside trials and those at the Univerity garden were at double this rate (120 g m-2).

Culture Techniques

Seeds were germinated on moistened Whatman Grade 182 9cm filter paper. Emerging seedlings were transplanted five to an 11cm plastic Monocup containing river washed sand or, in certain experiments, soil. Pots were placed on capillary matting and regularly mist sprayed during the first two weeks to assist establishment. Seedlings were then thinned to three per pot and treatments commenced. In the freezing resistance trials, because of limited space, seven seedlings were planted in smaller (9cm) Monocups. These were then thinned to five. In all experiments, except those investigating the interaction of nutrients and salt (Chap. 5), each treatment was kept in separate 35.5 x 21.5cm seed trays lined with capillary matting, one replicate of each species per tray and trays positioned at random. Trays and matting were rinsed out once every week and re-randomized. In the nutrient/salt interaction experiment pots stood on a suspended wire mesh.

Salt and nutrient treatments

In all experiments in which plants were grown in pots under controlled conditions (Chs. 5,6,7) treatment solutions and growing

Table 2.2 Seed Collection Sites

Road & Locality	Grid Reference	Species Collected
Al Morpeth By-Pass	NZ 182.875 to 178.853	Plantago maritima, Puccinellia distans.
Al Seaton Burn	NZ 220.775 to 234-740	Agropyron repens, Cochlearia offinalis, Hordeum jubatum, Puccinellia distans, P.maritima, Spergularia marina.
Al Annitsford	NZ 275.744	Puccinellia distans, P.maritima, Suaeda maritima.
A1058 Wallsend	NZ 283.671	Aster tripolium.

Table 2.3 Composition of roadverge amenity mixture

Lolium perenne cv. S.23	60%
Festuca rubra cv. S.59	20%
Cynosurus cristatus	10%
Trifolium repens cv. S100	10%

conditions were as follows. Salt solutions were made up dissolving B.D.H. NaCl in distilled water. Essential elements were supplied by application of 4 g per litre of Chempak No.3 (table 2.4) in distilled water. Controls were given distilled water alone. In the basic treatment regime, plants were watered with the saline treatment solution twice a week, on Tuesday and Friday mornings. The solutions were applied at a rate of approximately 50 ml per pot using a fine-rosed watering can. On Mondays and Thursdays the pots were watered with aproximately 100ml of distilled water to prevent any concentration of salt and in the afternoons watered with Chempak nutrient solution at 50ml per pot.

Two types of controlled environment chambers were used, a large walk-in growth room and three Fisons growth cabinets. All were kept, unless stated otherwise, at 20^{o}C with a 16 hour day and a photon fluency rate of 505 μ mols $m^{-2}sec^{-1}$(P.A.R) in the large growth room and 640 μ mols $m^{-2}sec^{-1}$(P.A.R.) in the Fisons cabinets. At the end of the experiments plants were harvested, dried in an oven at 100^{o}C and then weighed.

Freezing resistence

The chambers used to test freezing resistance consisted of modified deep freezes with double glazed glass panel inserted into the lids. They were set beneath artificial lighting with an photon fluency rate of 225 μ mols $m^{-2}sec^{-1}$(P.A.R.) and 10 h daylength. Pots were placed on a wire mesh 40 cm from the cabinet bottom and above a fan to circulate the air. Using a cam operated temperature control the rate of temperature drop and rise was controlled at 2 C^{o} h^{-1} and the test temperature was held for four hours. To check that all parts of the cabinet and all parts of the plants were reduced to the test temperature, a Comark multi-probe thermocouple thermometer was used. Probes were placed in different parts of the cabinet and in different positions in several pots, in the sand, on the sand surface and in the leaf canopy. The cabinets were borrowed from Dr W.S.Stewart of the Agricultural Biology department.

Roadside trials

Several trials were conducted on roadsides in which the effect of salt and competition were studied. Where vegetation had to be removed the herbicide "Roundup" manufactured by Monsanto Ltd. was sprayed on to the vegetation at a rate of 5 l ha^{-1} using a CP3 knapsack sprayer. The dead vegetation was hand raked from the sites.

Table 2.4 Composition of Chempak No.3 Fertilizer

Active ion	Weight per Kilogram
Nitrogen	200g
Phosphorus	174g
Potassium	166g
Magnesium	225g
Iron	1.68mg
Manganese	0.85mg
Copper	0.85mg
Zinc	0.30mg
Boron	0.44mg
Molybdenum	0.011mg

Trials using roadside turves.

The turves used in Chap. 7 were cleared in the same way as above and then cut and placed in 33cm x 26cm x 11.5cm plastic washing up bowls with five 2cm diameter holes drilled in their base. These bowls were kept at the Universty Garden in a gravel filled frame.

The treatments for these trials included a seed fungicide treatment which consisted of a mixture of Cerasan and Thiram applied to seeds before sowing. The frost protection equipment was a low wattage soil warming cable. This was positioned just beneath the soil surface in three loops in each bowl so that no part of the soil surface was more than 5cm from the cable. The same cable served all replicates of this treatment and was controlled by a thermostat placed just beneath the soil surface and 5cm away from the warming cable. The trickle watering system consisted of a 150 l tank fed by a stopcock-controlled mains water outlet. From this an Otter pump delivered water into a Cameron irrigation system with two drip watering sticks in each replicate bowl of the treatment. This system was adjusted to give a two metre head of water. The pump was controlled by a time switch which turned the system on for 15 minutes at 8am and 4pm each day. The whole system was turned off during periods of wet weather. The solution used for the nutrient treatment was that of Hewitt (1952).

Vegetation recording

Recording by point quadrats (Chap. 5) used a 1mm diameter needle lowered vertically into the sward at randomly chosen points. Each contact was recorded. The position of each point qua drat was found using a one metre frame with a marked metre sliding bar.

Recording by local frequency (Chaps. 4 and 5) used a metre square quadrat divided into 100 cm compartments by fine wire.

Exposure scale

As part of the principal survey in chapter five the exposure of each site was estimated using the following scale.

1. verge very sheltered, in deep cutting.
2. verge sheltered by cutting or dense trees or houses on both side.
3. verge sheltered but shelter incomplete.
4. verge sheltered but shelter with many gaps.
5. some shelter by trees or houses.
6. little shelter by trees or houses.
7. verge exposed, occasional trees or house.
8. verge exposed open fields both sides.
9. verge exposed and on embankment.
10. verge very exposed, on high embankment with no shelter at all.

Soil Salinity Analysis

A large variety of methods have been used for roadside soil analysis in the past (Table 2.8), and the results obtained are not always easily comparable. It was therefore necessary to investigate the available methods to ascertain which to use and to be able to compare results with those of other workers.

Sample Collection

Richards (1954) and Jackson (1958) both recommended the use of augers for soil sampling for salinity analysis. They, however, were referring to agricultural soils. Roadside workers have only used augers where sampling with depth was attempted (e.g. Prior & Berthoux 1967). Where samples of only the top 5cm or 10cm are being collected a simple mechanism of core collecting is adopted. For instance Thompson et al. (1979) used upturned metal cups. Ranwell et al. (1973) emphasized the large variability of soil salinity within any given area and the resulting need for a high level of sample replication. They took ten parallel transects, bulking each set of ten samples. Colwill, Thompson & Rutter (1976) also took ten samples but bulked them into two samples and measured both. Roberts and Zybura (1967) and Davison (1971) used three. No-one gives actual evidence for the variability of soil salinity apart from Ranwell who quotes a paper (Ranwell et al. 1958) on soil salinity in saltmarshes. However, he gave no evidence that the variability of roadside and saltmarsh soils was comparable.

No references to storage effects have been found. Jackson (1958) stated that soil samples to be used for a saturated paste may be field moist or air dry but not oven dry.

Salinity measurements: conductivity/resistance measurements

Workers on American dry land salinity have come to accept electrical resistance and conductivity measurements as the standard technique. Resistance is measured on a saturated soil paste. Although results are reproducible, the method has not been developed to the same extent as the conductivity method. It is usually used only for approximate measurements in the field (Richards 1954).

Conductivity is the reciprocal of resistance and is the more logical choice for the measurement of salinity, as it increases with salt concentration. Conductivity is usually expressed per centimeter and the specific conductance is the conductance corrected to 25^{o}C. Although it is possible to read conductivity direct on a saturated paste, it is more common and satisfactory to extract soil moisture and make the measurement on that. This is because direct readings are influenced by bound sodium. Magistad et al. (1945 in Jackson 1958) found that a direct reading can give a conductivity of 0.5 to 4.8 times that of the corresponding extracted solutions. Extraction of soil can be done at the field moisture content, but this is laborious and reserved usually for more exacting studies, and as a means of checking how much results are affected by extraction procedures. Both Richards (1954) and Jackson (1958) recommend using a filtered, saturated soil paste

The saturated soil moisture content has been defined (Scofield 1932 in Richards 1954) as "the maximum amount of water held in the puddled soil without free water collecting in a depression made in the soil mass". Distilled water is gradually added, while stirring with a spatula, until the characteristic end point is reached. Scofield's definition relies on the presence of free water and to check this it is usual to leave a sample half an hour to see if any collects. It is possible however, for an experienced worker to identify the end point without leaving the soil to stand. To this end Jackson (1958) suggests these criteria: "the soil barely flows together into a hole made with a spatula, the surface is wet enough to glisten and the mixture just slides off a spatula".

The saturated soil paste method was used by Davison (1971) in Britain, but surprisingly none of the American roadside workers who have made conductivity measurements used it. Instead, most use a 1:2

soil water extract (eg Roberts & Zybura 1967, Prior & Bertheoux 1967). Richards (1954) gives details of this method also. Soils are oven dried and then added to distilled water to give a 1g-2ml ratio. Mixtures are stirred, left to stand half an hour and then filtered.

Salinity Measurements:Ion exchange methods

Soil sodium content has been used by two groups of British workers (Ranwell, Winn & Allen 1973, Collwell, Thompson & Rutter 1976, Thompson, Rutter, Ridout & Glover 1979). Soil is oven dried, diluted by a known volume of distilled water (usually 1:2 soil-water) and exchangeble sodium is brought into the solution with the use of a leaching agent. Both groups quote Allen (1974) as the source of methods. This author recommends a number of leaching agents. 1N Ammonium acetate (as used by Thompson's group), 2.5% acetic acid or distilled water alone (as used by Ranwell, Winn & Allen). The sodium content of extracted solutions is assayed using a flame photometer or atomic absorption spectrophotometer. All workers have expressed their results as ppm dry soil.

Chloride analysis has been used less frequently. Voorde et al. (1973) used a similar method to that given above for sodium, but using CaSo4 as a leaching agent, a method of Jackson(1958). Chloride was assayed by the Volhard method (Shoog & West 1966 in Voorde 1973). Thomas (1967) also measured chloride ion levels, but used titration with 5% silver nitrate. This technique allowed him to assay a large number of soils, but gave only relative results. He expressed results in terms of salinity next to the road compared with the soil some distance away.

Extraction procedures

Extraction of saturated pastes and 1:2 mixtures has usually been done by suction filtration. For a 1:2 extract, suction filtration is comparatively easy, but for a saturated paste it can be more difficult. It is essential when measuring conductivity to exclude fine clay particles from the filtrate, and these can pass through a cellulose filter. Richards (1954) states that colourisation due to dissolved organic matter does not appreciably effect the conductivity, but turbidity caused by clay particles may lead to appreciable error. Davison (1971) therefore adopted the use of Millipore filtration. This, however, can take a long time and several filter changes to give sufficient filtrate from a high clay soil. An alternative method is centrifugation as used by Voorde et al. (1973).

Results obtained with the use of the saturation method have usually been expressed as conductivity of the extracted solution. Both Jackson (1958) and Richards (1954), however, gave graphs and formulae (detailed later), for conversion to percentage, ppm, or osmotic pressure of the solution or (using the saturation percentage of the soil) to percentage soil weight. Results from the soil 1:2 water extract method have been expressed as salt soil content on a dry weight basis.

Soil salinity: discussion of methods

Sampling

As there was no intention to sample soils any deeper than 5cm a simple method such as that used by Thompson et al. (1979) was sufficient. It would seem necessary from the work of others to collect parallel transects of soil samples to allow for possible variation in soil salinity. To allow the calculation of the number of sub-samples to use, an investigation of the variability of two roadside soils was undertaken.

Extraction and Analysis

The most important choice was not between the methods of assay but between the methods of extraction; between those methods which use a set volume of extractant and the saturated soil paste method. All methods, except the soil paste, involve drying the soil and then extracting with a set volume of extractant, whether distilled water or a leaching agent, and their final results are expressed as salt per dry weight of soil. These methods suffer from two major criticisms.

Firstly, extracts of soil particularly those made with high water-to-soil ratios are less accurate measurements of the available salt content of the soil because salt which is bound at field moisture content may come into solution when the soil is diluted further (Jackson 1958). Wadleigh, Gallet and Kolish (1951) compared the conductivity of a saturated soil paste, a 1.2 and a 1.1 soil-water extract with measurements made directly on a saturated soil. They found the values recorded for the dilution methods much higher than the saturated soil paste and the direct reading, both of which were similar. The use of leaching agents or oven drying will make this problem worse by bringing further bound ions into solution.

The second criticism is that with these methods salt content is expressed in relation to the dry soil (i.e. p.p.m. or %). This, however, is not related in any simple way to the toxicity to plants. Jackson (1958) gives the example of two soils, one a loamy sand and the other a clay, both with the same salt content on a dry soil basis.

However, the salt content of these two soils at wilting point was very different, approaching ten times as high in the sandy soil. This was because at wilting point a sandy soil contains one tenth of the water of that of a clay soil.

The saturated paste method avoids these problems as it does not involve oven drying, leaching agents or excessivly diluting the soil, all of which may bring bound sodium into solution. As it uses a soil moisture state directly related to the field moisture range of soil, any measurements can be directly related to the affects on a plant growing in that soil. Richards (1954) gives convincing evidence of this. For a number of soils he calculated the saturation percentage (SP), a measurement of the amount of water in a soil at saturation and the 15 atmosphere percentage (FAP), an easily measured point closely approximating permanent wilting point. From these two values he calculated the ratio SP/FAP. He then divided the soils into four groups, coarse, medium, fine and organic. The SP/FAP ratio of the medium soils proved to be four, with a small standard deviation. Fine and organic soils had ratios just under four and again low standard deviations. Coarse (i.e. sandy) soils had higher ratios averaging 6.3. He thus concluded that with the exception of coarse soils the saturated paste will always contain approximately four times the amount of water as the same soil at its wilting point and thus twice that of the soil at its field capacity. This method can therefore be relied on to give results which are directly relatable to the stress a plant will be subjected to in that soil.

It was therefore decided to adopt the saturated paste method. While it would be possible to assay extractions using this method by means of sodium or chloride analysis, previous work using soil pastes has always involved conductivity measurements. As this method is both simple and well documented, it was also adopted.

The extraction of water from a saturated soil paste can be difficult, in particular when working with heavy clays. There are a number of alternative methods available. Davison (1971) found that filtering required a vacuum pump, but even then there can be problems. Cellulose filters often result in cloudy extracts and finer Millipore filters can be blocked by heavy clays. Centrifugation offers an alternative. It was decided to test all these methods on a number of roadside soils.

Experiments and results: variability of roadside soil salinity.

At three sites a continuous line of 25 5cm diameter samples were collected parallel to the road. The salinity of each sample was tested using the method detailed at the end of this chapter and recorded in Table 2.5. The variation was not as great as would have been expected from the literature.

A statistical investigation of these results, clumping sets of four or five contiguous samples and calculating coefficients of variation, produced no coefficient above 0.2 for any set of five adjacent samples. This is low enough to justify adopting the bulking of a set of five adjacent contiguous samples as a standard method. These results also show that a soil sample from immediately adjacent to a quadrat is a reasonable indication of the soil salinity of that quadrat.

Comparison of extraction methods.

Large amounts of six roadside soils were collected, thoroughly mixed and then divided into 25g samples. Two samples of each soil were analysed using each method. Each sample was brought to a saturated

Table 2.5 Salinity (m siemens) of saturated extracts of adjacent soil samples collected from two sites.

SITE	A1 Seaton Burn South bound carriageway (NZ 231.753)		A1 Morpeth By-Pass South bound carriage way (NZ 182.875)
DATE OF COLLECTION	15/3/1980		1/4/1980
DISTANCE FROM ROAD	0.5m	2.5m	1.5m
SAMPLE			
1	5.7	3.0	0.68
2	4.7	3.5	0.57
3	5.9	3.7	0.60
4	5.6	2.7	0.87
5	6.3	4.1	0.46
6	4.6	3.5	0.73
7	4.3	4.1	0.65
8	4.5	3.7	0.68
9	4.7	3.3	0.63
10	4.3	2.8	0.83
11	5.1	2.5	0.89
12	4.6	2.7	0.79
13	4.9	2.8	0.83
14	4.2	3.6	1.00
15	6.0	2.9	0.67
16	4.4	3.2	0.80
17	3.8	3.3	0.58
18	4.4	3.2	0.80
19	4.9	3.9	0.67
20	4.8	4.4	0.56
21	4.2	3.1	0.54
22	4.3	2.9	0.80
23	3.4	3.6	0.69
24	3.6	3.4	0.58
25	4.1	2.8	0.82
MEAN	4.69	3.31	0.69
S.D.	0.73	0.50	0.13
COEF OF VAR	0.15	0.10	0.19

paste, extracted, and the resulting extract made up to 10 ml with distilled water. Conductivities of final extracts were measured using a direct reading conductivity meter and corrected to 25 ^{o}c. The cellulose filters used were Whatman No.1. The vacuum pump was an Edwards High Vacuum pump model ED50, and the centrifuge an M.S.E. High Speed 18.

The extraction procedures and the results obtained using each are shown in Table 2.6. The variation in readings for the same soils using different methods is striking. There are a number of likely reasons for this. The use of a cellulose filter often results in a cloudy extract and Richards (1954) reported that such contaminated extracts can give lower readings as salt can be bound to these clay particles. This may explain why cellulose filters consistently gave the lowest readings. Millipore filters did not give cloudy extracts but produced very small volumes and no extract at all from the heavy clays. Soils which were passed through a cellulose filter followed by a Milipore one also gave very small extracts. The vacuum pump gave faster results than the Buchner pump but did not solve any of the problems. The very high readings using a vacuum pump with cellulose then Milipore filters may have been due to evaporation or absorption of the water. Centrifugation gave consistently large volumes and repeatable results. The lower rotor speed proved insufficient to obtain an extract from the soil with the highest clay content. It was decided to adopt centrifugation at the higher rotor speed as the standard extraction procedure.

Soil salinity: summary of method adopted

Five samples were collected at each site, samples were adjacent to each other and parallel to the road. A 5 cm diameter metal pipe

Table 2.6 Salinity of saturation extracts of soil samples using different separation methods

METHOD	SALINITY (m siemens)					
Site Grid ref.	Seaton Burn NZ 231.733				Morpeth By-Pass NZ 182.875	
Distance from road	0.5m	1.5m	2.5m	3.5m	0.5m	3.5m
Cellulose filter + Buchner pump	8.2 5.8	6.8 8.4	4.2 4.5	0.4 0.7	0.9 1.0	0.8 0.6
Milipore filter + Buchner pump	no extract	12.1 10.0	10.2 15.1	4.8 5.8	1.4 1.6	1.2 0.6
Cellulose filter +Milipore filter +Buchner pump	no extract	no extract	6.1 7.1	1.1 1.4	1.7 1.3	1.3 1.4
Cellulose filter + Vacuum pump	6.7 5.8	11.2 10.1	7.2 7.6	1.6 1.5	1.8 1.7	1.3 1.4
Milipore filter + Vacuum pump	no extract	no extract	6.2 5.5	1.5 1.6	1.7 1.6	1.4 1.3
Cellulose filter +Milipore filter + Buchner pump	22.0 28.0	65.0 72.5	6.6 6.8	1.6 1.6	1.9 1.8	1.8 1.8
Centrifuge 4,000 rpm. 30 mins	no extract	15.0 14.6	7.5 7.2	1.8 1.8	1.9 1.9	1.8 1.7
Centrifuge 12,000 rpm. 15 mins	11.7 11.5	13.5 13.8	8.1 8.0	1.8 1.9	2.0 2.1	1.7 1.8

marked to 5 cm depth was used to obtain samples which were then bulked and thoroughly mixed. Samples were stored in a cold room for no longer than a month before analysis. A 25 g sub sample was used which was brought to a saturated paste using distilled water. This paste was then spun at 12,000 r.p.m. on a M.S.E. high speed 18 centrifuge for 15 minutes. 10 ml. of the resulting extract was then tested for conductivity in a direct reading conductivity meter. Readings were corrected for temperature using the formula given by Richards (1954) (i.e. +2% for every $1^{\circ}c$ below $25^{\circ}c$).

Conversion and comparison of results

As a saturated soil paste bears a direct relationship to the normal range of soil water content it is possible to relate salinity measured by this method directly to the effect on vegetation. Bernstein (1958) defined a saline soil as any with a conductivity of the extracted extract above 4 mmhos (= m siemens). Bradshaw and Chadwick (1980) define a saline soil as having over 8mmhos in soil solution at field capacity, which is 4mmhos in a saturated paste extract. Jackson (1958) gave a table, redrawn here (Table 2.7) which classifies soils according to the conductivity of a saturated paste extract. Other tables which use only exchangeable sodium readings from dry soil/water extracts such as that given by Ranwell Winn & Allen (1973) are invalid. They do not take into account differences in soil saturation percentage which affects the dilution of the salt, and so its toxicity to the plant.

It is possible to convert conductivity into other units for expressing soil salinity. Both Jackson and Richards give graphs and formulae for conversion of conductivity readings into milliequivalents per litre, g per g of water and osmostic pressure of soil water. It is

Table 2.7 Scale relating plant response to soil salinity (adapted from Richards (1956)

Specific conductance of the saturation extract of soil (m siemens)

0 – 2	2 – 4	4 – 8	8 – 16	16 –
Nonsaline	Very slightly saline	Moderatly saline	Strongly saline	Very strongly saline
Salinity effects mostly negligible	Yields of very sensitive crops may be restricted	Yield of many crops restricted. Alfalfa, sugar beet and cereals adapted.	Only tolerant crops yield satisfactorily. Bare spots appear because of injury to germination.	Only a few very tolerant crops yield satis-factorily. Only salt tolerant grasses, herbs, shrubs and trees grow.
0 – 0.1	0.1 – 0.3	0.3 – 0.5	0.5 – 1.0	1.0 –

Percentage of salts in moisture saturation extract.

also possible, knowing the saturation percentage of the soil, to convert the result into g salt per g dry weight of soil using such graphs as Fig. 2.1, which follows Richards (1958) or the formula he also gives:

$$\%\text{salt in soil} = L \times 0.064 \times \%\text{ water in soil extract.}$$

Where L = Electrical conductivity of solution.

While it is thus possible to convert conductivity readings for a saturated paste extract into ppm of dry soil, such a converted result can not be reliably compared with results for other soils expressed in this way, unless the saturation percentage of these soils is also given. This is also true for comparisons between results of different workers using these methods. If the saturation percentage is given, it is possible to convert these results to equivalent conductivities and to assess soil toxicity using Fig 2.1.

Table 2.8 lists previous workers' measurements of roadside soil salinities. It can be seen that many different methods have been used and that most of the workers who give their results in terms of percentage of dry soil weight do not give saturation percentages for the soils.

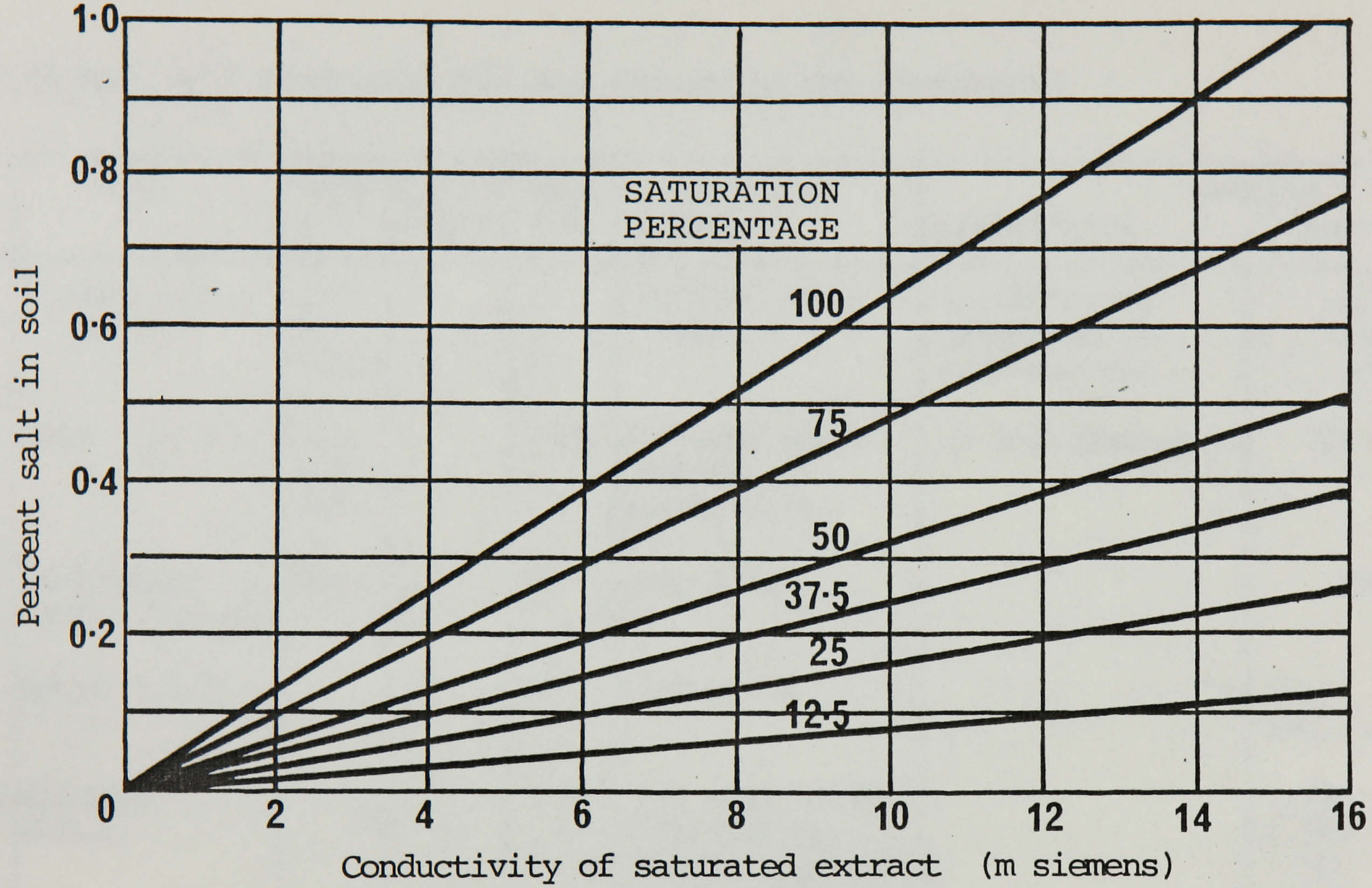


Fig. 2.1 Relation between the percentage salt in the soil and the electrical conductivity of the saturated extract. (Redrawn after Richards 1954)

Table 2.8 Roadside soil salt concentrations and methods in the literature.

Author(s)	Site	Date	Dist´to road(m)	Depth (cm)	Analytical method	Results: Conductivity	Results: ppm NaCl in soil	Further information
Prior and Bertheuox (1967)	Connecticut U.S.A.	Jan. Feb. Feb.	8 1.5 8	0 0 0	1:2 soil water extract	conductivity converted to soil content	410 ppm NaCl 450 ,, 60 ,,	
Roberts and Zybura (1967)	Iowa U.S.A	Jan. and Feb.	-	0-8	1:2 soil water extract conductivity	1.5-2.25mmhos/cm	720-12000 ppm NaCl	
Thomas (1967)	Washington D.C. U.S.A.	Jan.	-	-	not given		996-3,660 ppm Cl	
Hutchinson (1970)	Maine U.S.A.	-	0	15	not given		ave. 281 ppm Na max. 1,056 ,,	
Butler, Hughes Sanks and Craig (1971)	Chicago U.S.A.	- - - -	- - - -	0-4 ,, 0-10 ,,	1:5 soil water extraction Atomic absorption and conductivity		7,280 ppm 76,800ppm 2,160 Na 12,800salts 3,780 ,, 19,000 ,, 14,580 ,, 38,400	soils beneath bare ground amenity mix P.distans P.distans
Davison (1971)	Morpeth Al North/d Blaydon Al North/d Ovington North/d	April Sept. April Sept. Oct. Oct.	0.03 ,, ,, ,, 0.1 ,,	- - - - 0-5 10-15	Filtered saturated soil paste Conductivity reading	3.05 mmhos/cm 1.23 ,, 3.10 ,, 1.46 ,, 6.31 ,, 13.60 ,,		

Cont.

Table 2.8 Roadside soil salt concentrations and methods in the literature. (cont)

Ranwell, Winn and Allen (1973)	York A1 Not,s. A1 Derby M1 Norfolk A146 ,, Camb´s. A505	April March Sept. March Sept. Feb	0-1 ,, ,, ,, ,, ,,	- -	Oven dried extracted 1hr with distilled water Flame photometer		904 ppm Na (ave.) 656 ,, 390 ,, 636 ,, 266 ,, 244 ,,	
Voorde, Nigs and Van Dijck (1973)	Louvain Belgium	Jan. ,,	10 ,,	0-20 20-40	1:1 soil water centrifuged Vollard method		185-202 ppm Cl 134-269 ,,	
Colwill et al (1976)	Oxford M4	March	0.5	-	as Thompson et al (1979)		102 ppm Na	
Foster and Mann (1979)	London Canada	March July	1 ,,	0-8 ,,	1:10 soil 1M HNO vacum filter atomic absorption	0.35 Na 0.38 Cl 0.05 ,, 0.15 ,,		
Brod (1979)	Dortmund West Germany	-	-	0-15 ,,	?	0.2-1mmhos/cm 1.5 ,,		from roadside from cent.res.
Pitelka and Kellog (1979)	Maine U.S.A.	Spring & Fall	3 to 11	5	Comparing conductivity with known sample		487 ppm all salts	
Thompson, et al. (1979)	The Pennines M62	April	0.5	-	1:? 1N Ammonium acetate atomic absorption		1564-4101 ppm Na	
Catling and McKay (1980)	S.Ontario Canada	Early winter	- -	- -	1:? 1N Ammonium acetate flame photometry		500-6,375 ug/g Na 996-3,660 ,,	from roadside from beneath snowdump
Reznicek (1980)	Michegan U.S.A.	-	-	-	as Catling & McKay (1980)		996-3,660 ug/g Na	beneath roadside halophyte

Chapter Three Distribution and Invasion

Introduction

The maritime plants of the roadsides of north east England were originally surveyed by Paul Matthews in 1976. By re-surveying the same area at the beginning of this project it was possible to assess how far they had spread in the intervening years and whether there were any new records. As well as this local survey, it was decided to record the roadside distribution of maritime species for the whole of Britain. Non-roadside inland records of the maritime species were also researched in the hope that they might help reveal the origin of roadside populations, and give some insight into their habitat requirements. Finally, a literature search was undertaken to find out if similar roadside invasions were occurring elsewhere in the world.

The local survey allowed assessment of the invasion rate of each species. As the results also suggested that dispersal was affected by traffic direction some seed trapping experiments were undertaken.

Roadside Distribution

All major roads in north-east England were surveyed for maritime plants in 1980. This was done principally by car, stopping at all signs of salt damage on the roadside. The area known from Paul Matthew's survey to have maritime species was surveyed more thoroughly with all the un-paved major roads within 25 km of Newcastle inspected from a slow moving motorcycle. Areas which proved to have interesting assemblages of plants were later surveyed on foot. All known coastal sites for the same species in Tyne and Wear and Northumberland were also inspected. Any populations found during subsequent work were added to these records.

Elsewhere in Britain, roads could only be surveyed much less intensely. So, to widen the search area, a request was sent to members of the Botanical Society of the British Isles for roadside records of maritime species. These records were combined with those from the literature. Distribution maps were published (Scott and Davison 1982, Scott 1984) and exhibited in the hope that this would stimulate other botanists to return records for their local roads.

The maritime species with the most extensive roadside distribution is Puccinellia distans. The first roadside report was for north east England (Matthews & Davison 1976). This was followed by reports for Kent (Badmin 1979, Kitchener 1983), Bedford (Dony 1979, Dony & Dony 1979) Warwickshire (Badmin 1981), Suffolk (Hyde et al. 1981,1982,1983) and Cumberland (Halliday 1983). These and other records are summarised in Fig. 3.1, which shows the presence or absence of Puccinellia distans on roadsides using the 10 km squares of the National Grid.

P.distans is very distinctive at anthesis and it can be recognised at some distance. As a result, many of the records were initially noticed from cars. Apart from the author's own surveys, the only surveys on foot were by Feltwell and Philp (1980) on the M20 in Kent. Because of this, populations could easily have been missed on many roads. In addition, the number of roads which were visited varied in different areas. North east England, Bedfordshire and Kent were surveyed thoroughly, but in other areas only the major roads were searched and usually just the motorways and the primary trunk roads. Thus it is likely that the roadside distribution of P.distans is greater than is shown here. As major roads were, however, visited in most areas likely to have a roadside maritime flora the basic outline of the distribution is thought to be correct.

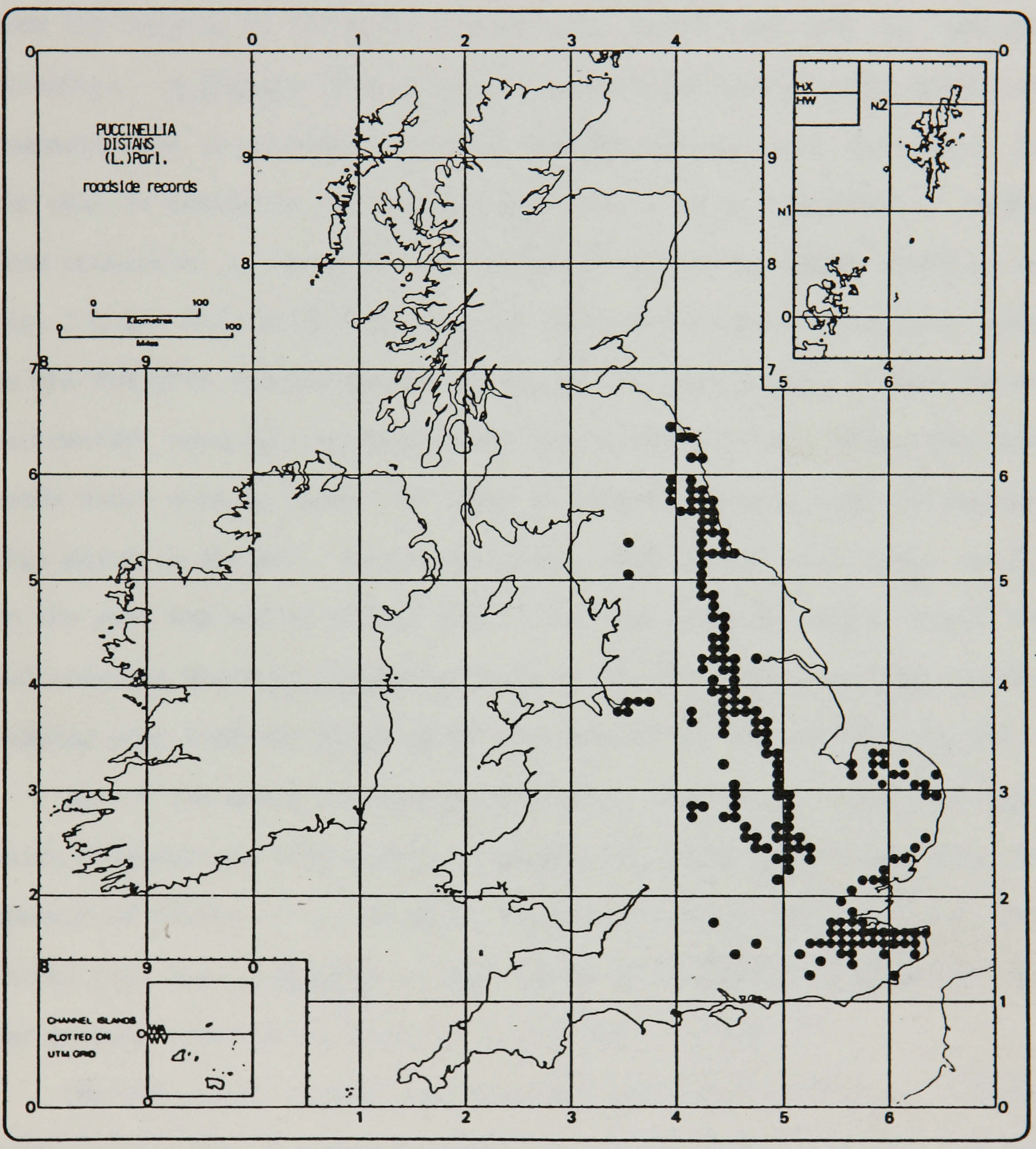


Fig 3.1 The distribution in the British Isles of Puccinellia distans on roadsides. 1984.

Only a few of the records shown on Fig. 3.1 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 is confined to the Al between Morpeth and Berwick. To the west it occurs on the A69 and A68 as well as on the B6341. South from Newcastle, it is on the Al (National Grid 10 km square 45/24 as in Fig. 1), and A19 (45/44) and some of the roads between these two, such as the A66 from Middlesborough to the Al at Darlington. From there southwards, records are confined to the Al until 44/45, when the A58 heads south west to Leeds. The line of records crossing east to west at this point is the M62. From here south, records form two lines, the Al on the east and the Ml 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 Ml at 42/46 are records for the A45 and the M62.

All of the above records are virtually continuous; the few gaps which do occur are more likely to be due to under-recording than to absence of plants. For instance, the gaps on the Ml are probably due to the fact that P.distans is more scattered there and is often only on the central reservation where it is difficult to record.

The remaining records form obviously discrete populations. Those leading away from the Mersey (33/68) are on the M56. The two records in Cumbria are on the A6 where it crosses Shap Fell and on the M6 near Penrith and those in Derbyshire (in 43/16) are on the A515. The records in East Anglia are on the A149 near Kings Lynn around Norwich on the A47, A148, A1065 and A146 and on the A12 between Woodbridge and Chelmsford. The records in south east England are in Kent on the A2, M2, A20, M25 and M26 and the adjacent minor roads. The single record in Sussex is on the A3 and those in Surrey on the A24 and at intersections on the M23 and M25. The record 44/17 is on the M4 east of Oxford and those beneath this in Hampshire are on the M3 and A30.

Most of the other maritime species that have invaded British roads are confined to two areas. For north east England, Matthews and Davison (1976, from a 1975 survey) recorded the following species: Puccinellia distans, P.maritima, Spergularia marina, S.media, Suaeda maritima, Aster tripoliim, Plantago maritima and P.coronopus. More recently two further species have been found, namely Cochlearia officinalis and Atriplex littoralis. The former was found in 1978 on the central reservation of the A1 north of Shotton Grange (NZ 226.767). The plants have set seed every year and now number over 30 individuals. The species is still confined to this one site. The distribution of Atriplex littoralis is more extensive, as it occurs on the A1, both near Seaton Burn and on the Morpeth by-pass. It was probably present for some years but remained unrecognised because it grows amongst Atriplex patula and A.hastata. The three species are difficult to distinguish on roadsides because they are usually severely infested with gall-forming insects. Another recent find is the fungus Agaricus bernardii (det. D.A.Reed of Kew). This species is usually associated with saltmarshes but has been found on saline roadsides before (Phillips 1982).

Amongst the most recent records for north-east England are two which are isolated and some way inland. These are both near places regularly visited by the vehicle used for the experiments on maritime plants, so that it is considered that they were inadvertantly spread by the author. The records are for Puccinellia distans on a road in the author's village (Elsdon NT 936.934) and for Spergularia marina near a salt dump on the A68 (NT 935.777) which is used as a source of salt for experiments. Both populations are approximately 40 km inland and 20 km from the nearest other population of the same species.

The other area with a large maritime flora is Kent (Badmin 1979, Feltwell & Philp 1980, Burton 1983, Kitchener 1983 and pers. comm.) where are found Armeria maritima, Aster tripolium, Atriplex littoralis, Bupleurum tenuissimum, Cochlearia danica, Desmazeria marina, Elymus pycanthus, Halimione portulacoides, Hordeum marinum, Juncus gerardii, Parapholis strigosa, Puccinellia distans, P.fasciculata, P.rupestris and Spergularia marina. Cochlearia danica has also been found nearby in Surrey where it grows along 11 km of the A3 (J.Smith pers. comm.).

Recently, maritime plants were also found in East Anglia. Cochlearia danica was found along the A45 leading from Ipswich inland on the A11 and A12 (Hyde et.al. 1982,1983), Juncus gerardii and Spergularia marina were found on the A146 near Norwich (Daniels 1984). Parapholis strigosa was found on the A1065 near Norwich (G.Kitchener pers. comm.) and with Armeria maritima on the A12 in East Suffolk (E.M.Hyde pers. comm.).

There are a few records from elsewhere in Britain. In Yorkshire Atriplex littoralis has been reported from the A1 (C.S.V.Yeates pers.comm.) and Armeria maritima has been found on the A40 near Oxford (H.J.Bowman pers.comm.). Spergularia marina was reported on the A833 near Inverness. This is the first report of a maritime species beside a Scottish road which appears to be related to the use of de-icing salt. However C.S.V.Yeates also reports that this population is now extinct due to road improvements.

There are roadside records for maritime species which do not appear to be associated with the use of de-icing salt. 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, McAllister & Fearn 1978), which are both associated with local limestone, are good examples of this. The invasion by Cochlearia officinalis of roads in south west 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.

The status of Plantago coronopus, which is known from a number of roadside sites in the south, is also uncertain. Feltwell and Philp (1980) reported it on the M20 and Kitchener (1983) on the east Kent roads. The author has recorded it beside the A272 in Sussex (SU 862.815) where the conductivity (0.5 m from the road 0.88 m siemens; 1.2 m from the road 0.29 m.siemens) showed that there was salt influence. However, this species is known inland elsewhere in the south on sandy soils and as all these roadside records are near, or on, heathland any association with saline roads may be coincidental.

The roadside records of maritime species other than Puccinellia distans were mapped using the 10 km squares of the national grid (Fig. 3.2). Where it was questionable whether an invasion was associated with the use of salt, such as with Cochlearia officinalis and Plantago coronopus, records were not included. It is to be noted that with the one exception of the A40 record of Armeria maritima, records are confined to 100 km of the east coast.

Another species often found growing on saline roadsides is Hordeum jubatum. This adventive is a native of North America (Best et al. 1978) and was first recorded from southern Britain at the beginning of the century when it was reported as being introduced in bird seed. H.jubatum seems to have moved onto major roadsides in southern Britain in the early 1960's but as this did not result in new vice-county records it is difficult to find precise dates. In the late 1960's it began to appear on midland and northern roads resulting in such new

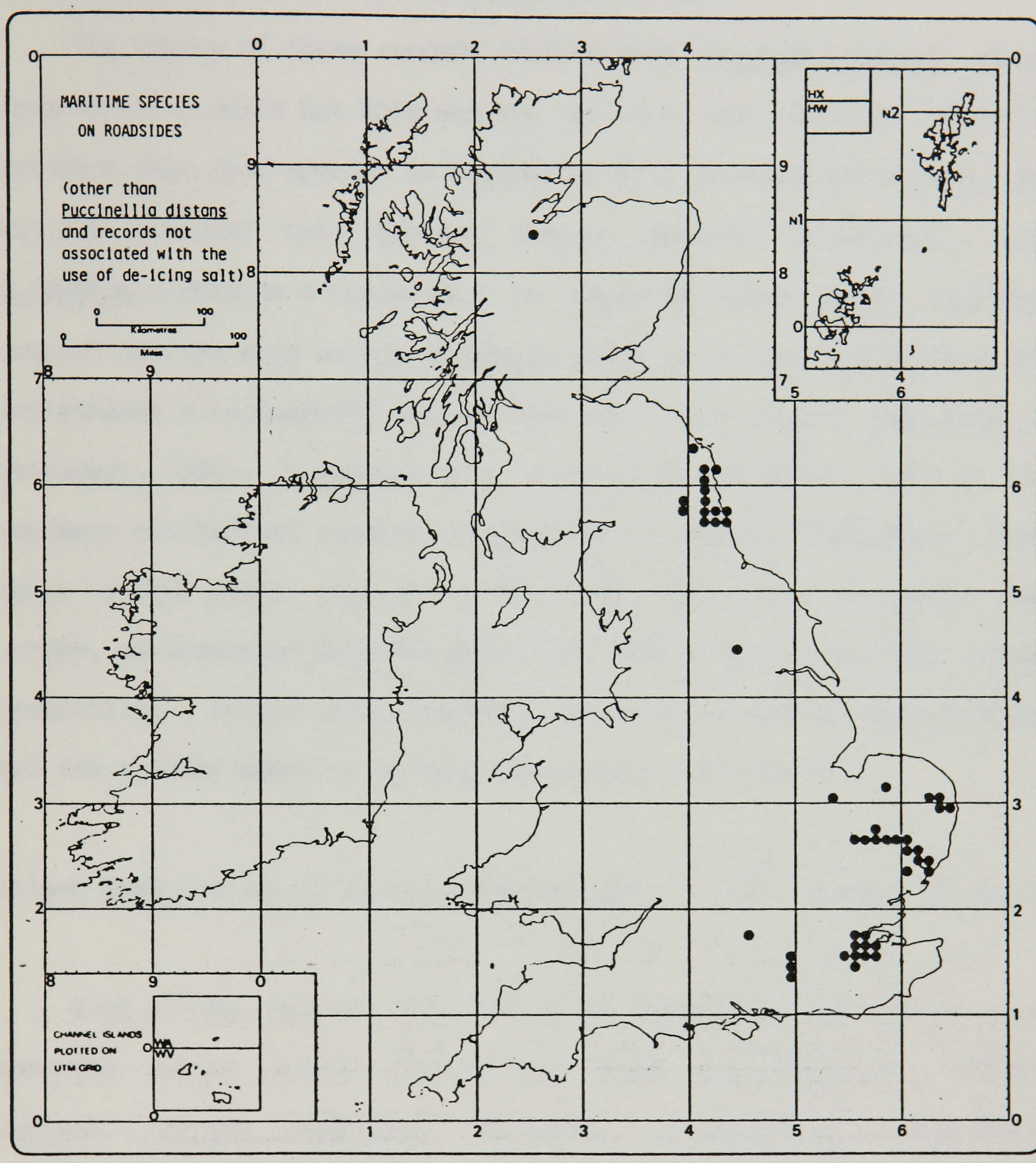


Fig 3.2 The distribution in the British Isles of coastal species on roadsides other than Puccinellia distans and records unlikely to be associated with the use of de-icing salt. 1984.

vice-county roadside records as North Lincolnshire (1963), Durham (1976), Rutland (1969), Cumberland (1969), Leicestershire (1971), Warwickshire (1974), West Yorkshire (1974), South Northumberland (1976), Westmorland (1978), Roxburghshire (1980).

The timing of these records implies that Hordeum jubatum spread from south to north but this may not be the case because there is evidence that this species is introduced with imported grass seed. The N.I.A.B. official seed testing station reported (pers.comm.) that H.jubatum occurs as a contaminant in imported grass seed, including seed of species such as Poa pratensis which is in the Department of the Environment's recommended seed mixture for road verges (Ministry of Transport, 1963). H.jubatum is a short-lived perennial and in the southern and midland roadside 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.

Inland distribution of maritime species prior to the invasion of roads.

Some of the species now known on roadsides have never been recorded inland before (information from the Biological Records Centre). Elymus pycanthus, Halimione portulacoides, Parapholis strigosa, Puccinellia fasciculata, P.rupestris, Spergularia media and Suaeda maritima were only known previously from coastal, saline sites. Puccinellia maritima has only been recorded away from the coast on saline sites. These sites consist of inland saltmarshes and the saline soils associated with the salt industry (Lee 1977). Puccinellia distans, Aster tripolium, Spergularia marina and Plantago maritima are also known today from such sites. These sites are associated with outcrops of the Keuper saliferous beds and occur principally in Cheshire, Staffordshire and Worcestershire. One of these sites, which is of particular interest, is the salt mine at Winsford. This is the major source of de-icing salt in Britain and supplies most of the salt used on British roads. A thorough search of the site revealed Spergularia marina and Puccinellia distans growing in some quantity around the works and Aster tripolium growing on the nearby settlement ponds. No other maritime species could be found.

The species known from non-saline soils can be divided into two groups. First, there are the species which occur away from saline soils only as casuals or introductions; these are Atriplex littoralis, Cochlearia danica, Desmazeria marinum, Hordeum jubatum, H. marinum, Puccinellia distans and Spergularia marina. The species Aster tripolium and Juncus gerardii probably also belong to this group. The casual sites for these species are few and local, except for Cochlearia danica which invaded railways in the last century, in much the same way as it is now invading roads.

The other group, consisting of Armeria maritima, Bupleurum teuniussimum, Cochlearia offinalis, Plantago coronopus and Plantago maritima, is of species thought to have been growing on non-saline soils prior to man´s influence. The inland sites (Perring and Walters 1962) for Bupleurum tenissimum are no longer extant. The records for Plantago maritima and Armeria maritima are mostly montane, in the Pennines and the Scottish mountains. Cochlearia offinalis has a similar but more widespread distribution. The only native location for any of these species near one of the roadside sites is the population of Plantago maritima on the Magnesium limestone of County Durham. Plantago coronopus, however, occurs on many sandy and gravel soils inland in the south and all of the reported records are from roadsides on or near these native soils.

Some of the species which are not confined to saline soils nevertheless appear to be confined to particular soil types. For instance Plantago maritima and Armeria maritima tend to occur on calcerous or heavy-metal contaminated soils (Tutin et al. 1972;1976), such as the limestone of the Pennines, the heavy metal wastes of the river Tyne and the limestones, micashists and serpentine of the Scottish mountains. Some of the casual records are also associated with the same rock types, either as quarries or spoil heaps. Most of the other casual records are for urban sites.

Abroad

Some foreign reports of roadside maritime plants have been found but this review may well be incomplete as it is difficult to trace articles on this subject because they are usually in local natural history publications.

Puccinellia distans now occurs on roads throughout most of northern Europe. Adolphi (1975), Seybold (1977), Lienbecker (1979), Krach & Koepff (1980) and Bresinsky, Schunfelder and Schulwerk (1980), all detail its spread in different areas of West Germany. Fukarek, Knapp, Rauschert and Weinert (1978) reported P.distans on roadsides in East Germany and it has also been found in the Netherlands (Vallei 1979), Poland (Mirek & Trzcnska-Tacik 1981), Denmark (Vestergarde, pers.comm.) and Sweden (Jerling, pers.comm.). Badmin (1980) discovered it in Northern France.

Weinert mentions in correspondence the more local occurence in East Germany of Aster tripolium and Plantago maritima. Jerling reported (pers.comm.) that Plantago maritima also occurs on roads near Stockholm while Wieyers reported Armeria maritima, Cochlearia offinalis and Plantago maritima on roads near Rotterdam. Seybold (1977) has recorded Hordeum jubatum on roadsides in southern Germany and Switzerland and Haperen and Kogel (1981) in the Netherlands.

In North America Puccinellia distans was discovered on expressways around Chicago by Butler, Hughes, Sanks and Craig (1971) and is reported as having spread rapidly since (Butler 1977). It is not a native species to America but was introduced from Europe and has become widespread on saline agricultural soils (Fernald 1950). It has also been reported from Michigan (Voss 1972) and Pennsylvania (Wherry, et al. 1979) More recently Cusick (1982) has described the invasion of Ohio´s roads by P. distans. The first herb rium record for the state dates from 1963 and there was only one other during the 1960´s. Since 1972, however, spread along roadsides has been rapid so that by 1982 it had been recorded from 35 of the 88 counties. Cusick speculates that it probably occurs undiscovered on the roadsides of other American states. In Ohio P.distans was found growing at some localities with Spergularia marina, S. media and Carex praegracilis. A larger maritime flora has been found on the roadsides of Michigan (Reznicek 1980) and southern Ontario (Catling and McKay 1975, 1980). Species include Aster spp., Atriplex littoralis, Carex praegracilis, Juncus gerardii, Puccinellia distans, Spergularia marina, S.media and Suaeda calceoliformis. Many of these species are believed not to be locally native but to have invaded the area in the late nineteenth century when they were associated with the new salt industries (Catling and McKay 1981). They were also known from salt piles at railway yards which perhaps indicates that they were originally brought inland in railway ballast. There are species now on roadsides that originated from the east and west coasts of North America as well as adventives from Europe (Reznicek 1980)) Other species invading saline roadsides are native to the areas, such as Hordeum jubatum which occurs in the edges of saline pools and salt pans (Ungar 1974). As well as P. distans, Carex praegracilis appears to be particularly successful on roadsides (Reznicek, Catling & McKay 1976).

Rate of invasion

In order to assess the relative success of the different maritime species, all the major roads within 40 km of Newcastle were re-surveyed in 1980 and the distributions compared with those recorded by Paul Matthews in 1975. The maps were further updated in 1982. The presence or absence of the various species was plotted using the 1 km squares of the National Grid for an area which covers north Tyne and Wear and south-east Northumberland (Figs. 3.3 & 3.4). Only Puccinellia distans, P.maritima and Spergularia marina are known to occur on north-east roads outside this area. Both Puccinellia species are present on the A1 north to Berwick, P.distans and Spergularia marina occur to the west on the A68 and A69 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 remote, however, since the 1975 survey was thorough, with all the relevant roads being walked, and as all new discoveries were 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 were not present in the recently discovered populations.

Using these results it is possible to place the invading maritime species into one of three categories. Those which are spreading rapidly: Puccinellia distans (Fig. 3.3) and Spergularia marina (Fig. 3.3). Those which, although not spreading as rapidly, are relatively widely distributed: Puccinellia maritima (Fig. 3.3) and Plantago

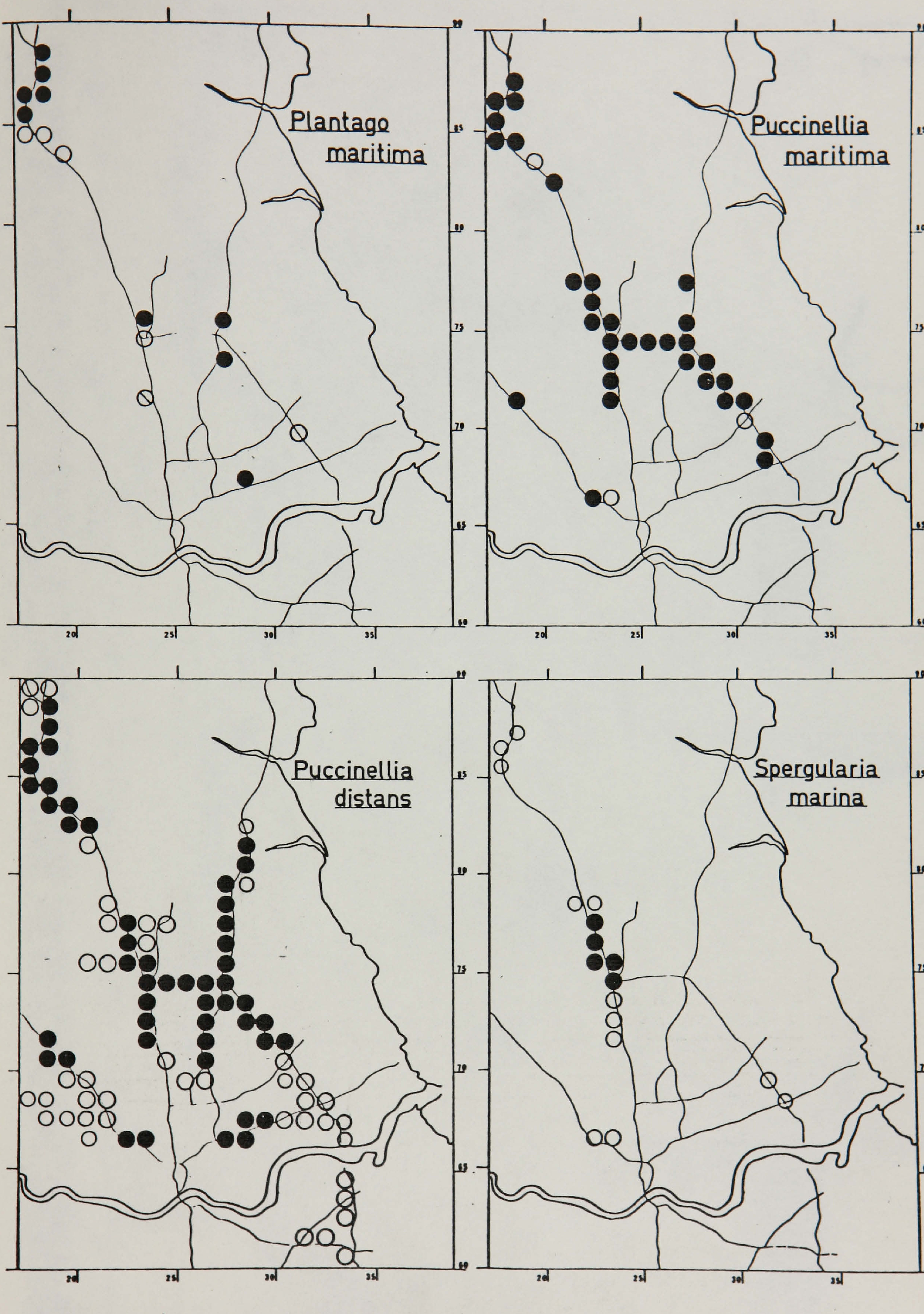


Fig 3.3 The roadside distribution in N.E.England of maritime species using the 1km squares of the National Grid. Closed symbols (●) present both in 1982 and 1975, open symbols (O) present in 1982 only, crossed symbols (⊘) present in 1975 only. The river shown is the Tyne.

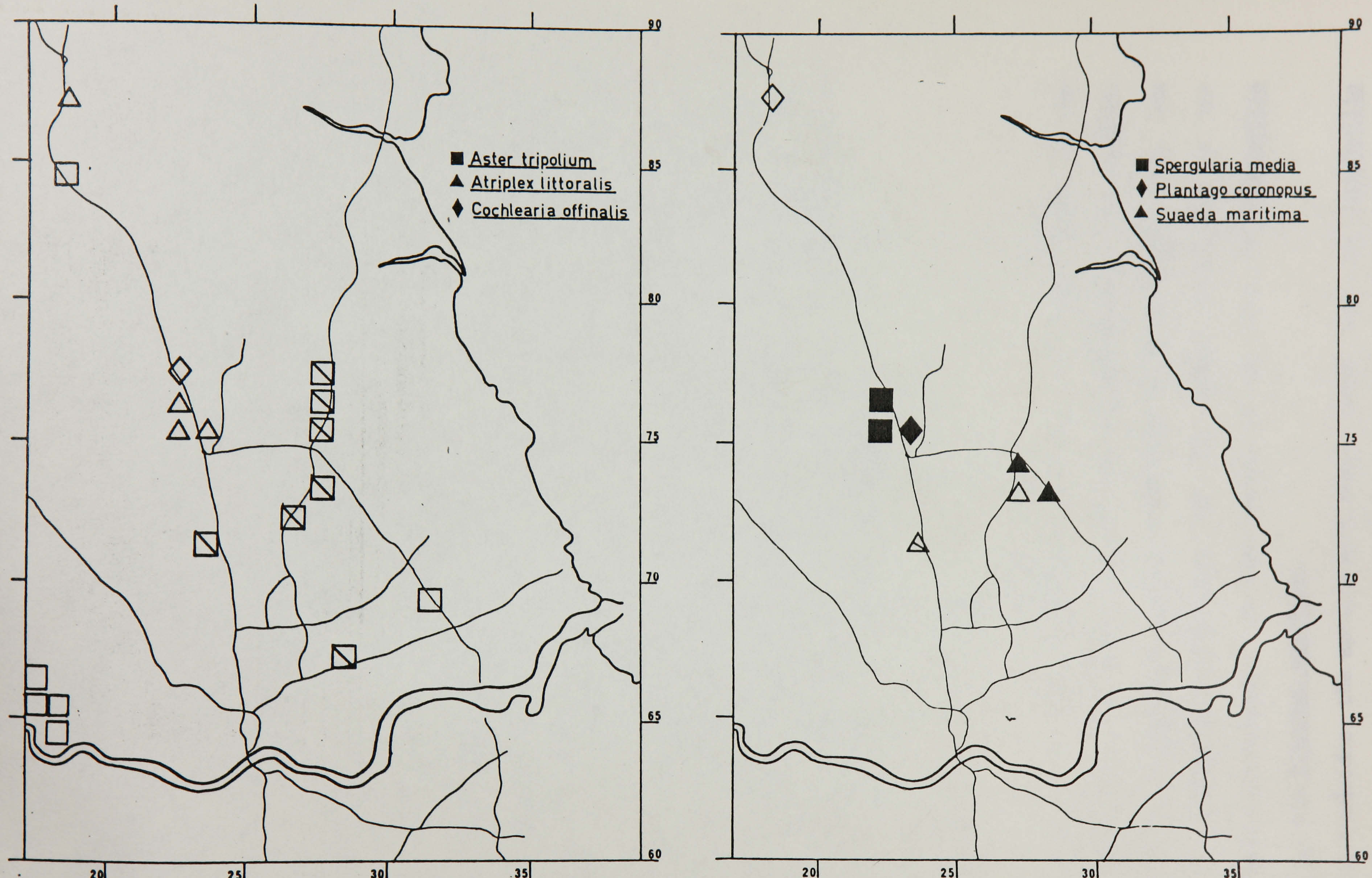


Fig 3.4 The roadside distribution in N.E.England of maritime species using the 1km squares of the National Grid. Closed symbols (■▲♦) present both in 1982 and 1975, open symbols (□△◇) present in 1982 only, crossed symbols (⊠▲◈) present in 1975 only. The river shown is the Tyne.

maritima (Fig. 3.3). Finally, there are those species which have not spread at all or very little since 1975: Spergularia media, Suaeda maritima and Plantago coronopus (Fig. 3.4) fall into this category.

All the original 1975 populations of Aster tripolium were extinct by 1983 but others had appeared on different stretches of road (Fig 3.4). From site observations and from observations of seedlings grown 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 probably prevented successful seed set and this therefore led to rapid extinction. Aster tripolium is also lost from heavily grazed saltmarshes (Chapman 1960). Continual re-introduction of this species onto roadsides in north eastern England may be facilitated by its occurrence on the banks of the river Tyne within Newcastle upon Tyne. One of the recently discovered populations was only 400 metres from a riverside site.

Distribution of individuals.

Most of the new records shown in Fig. 3.3 were found in the direction of traffic flow, away from the old populations. For example, the spread of Spergularia marina south down the Al at Seaton Burn was on the southbound carriageway but the spread north was on the northbound carriageway. The same tended to be true of Puccinellia maritima and Plantago maritima.

On roadsides, the species with small seeds such as Puccinellia distans and Spergularia marina tend to occur as long, continuous

Fig 3.5 Distribution and size of individuals in a roadside colony of Plantago maritima. Individuals drawn on a scale 5x that of axes. (NZ 176.856)

Fig 3.5 Distribution and size of individuals in a roadside colony of Plantago maritima. Individuals drawn on a scale 5x that of axes. (NZ 176.856)

populations. In contrast, the much larger seeded Plantago maritima tends to occur in discrete colonies and these show a distinct pattern of spread from founder plants. Fig. 3.5 shows a plan view of the distribution and size of individuals in a typical roadside colony of this species on the Morpeth by-pass. The smaller and younger plants were of highest density in the direction of traffic flow. This is also shown in Fig. 3.6 where the size of individuals is plotted against position along eight separate transects, parallel to the road. All populations show the same skewdness

Seed dispersal.

The previous results indicated that the slipstream of passing cars effects the distribution of seed. To quantify this, seed traps were set up on roadsides around point seed sources of two species, Puccinellia distans and Plantago maritima. Colonies of Plantago maritima on the Morpeth by-pass proved ideal for this and eight were chosen for study, four on each side of the road. As Puccinellia distans tends to form continuous populations, point sources of seed were created and this was done in two ways. On the A1 at Arcot Hall there are only occasional clumps of Puccinellia distans. Two of these on opposite sides of the road were chosen and all other plants were prevented from seeding by regular removal of the flowering panicles. There were no populations of Puccinellia distans on the A69 at Throckley and on this road clumps of the species were transplanted from the A1 to opposite sides of the road.

Two forms of seed trap were used, sunken plastic trays of sterilised soil and square metal sheets covered with a layer of glycerine, which were nailed to the ground (see ch.2 for details). Both were set up on verges for three months during seed shedding. The

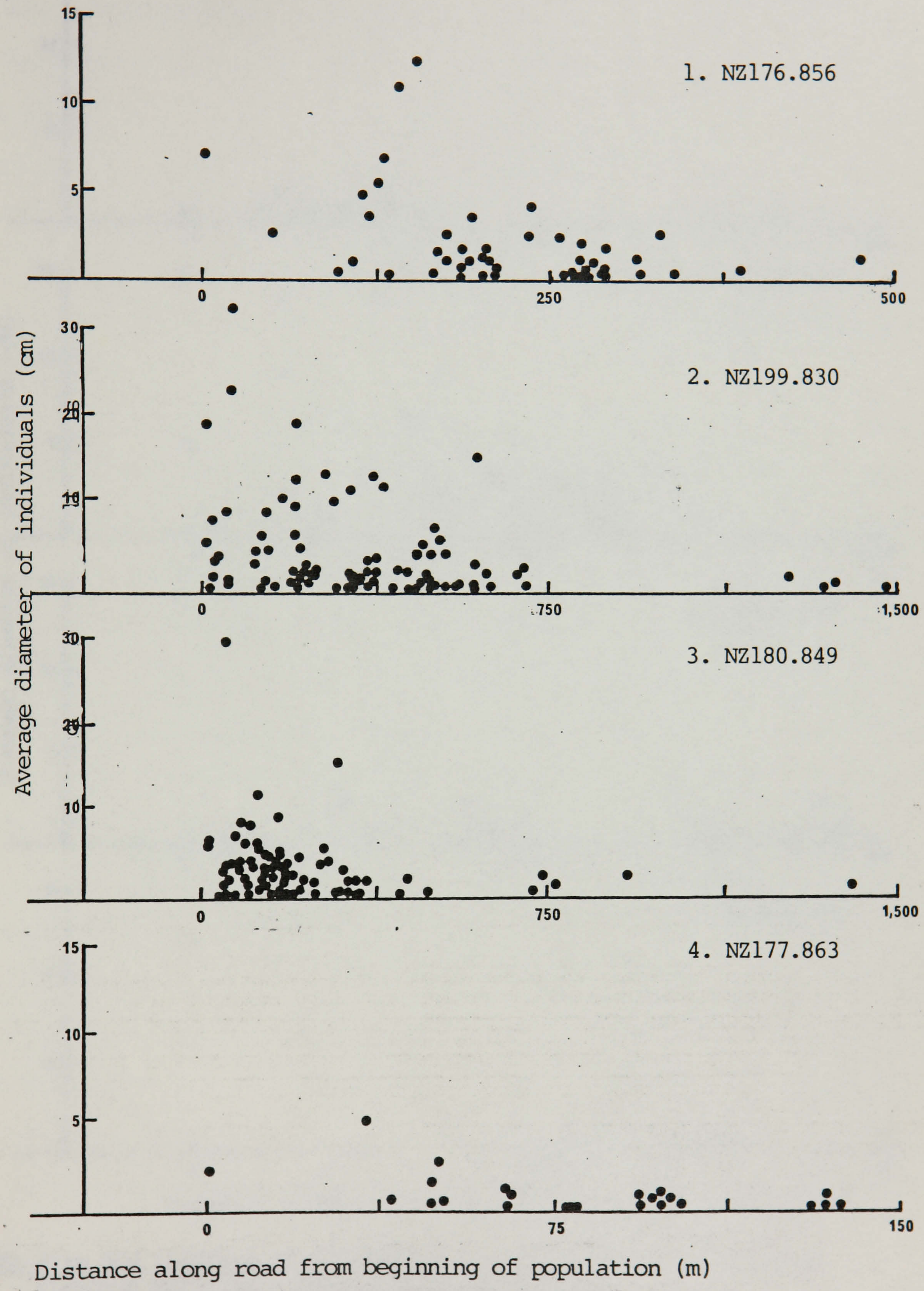


Fig 3.6a Size and location of individuals in four roadside colonies of Plantago maritima. South bound carriageway.

----- TRAFFIC FLOW ------>

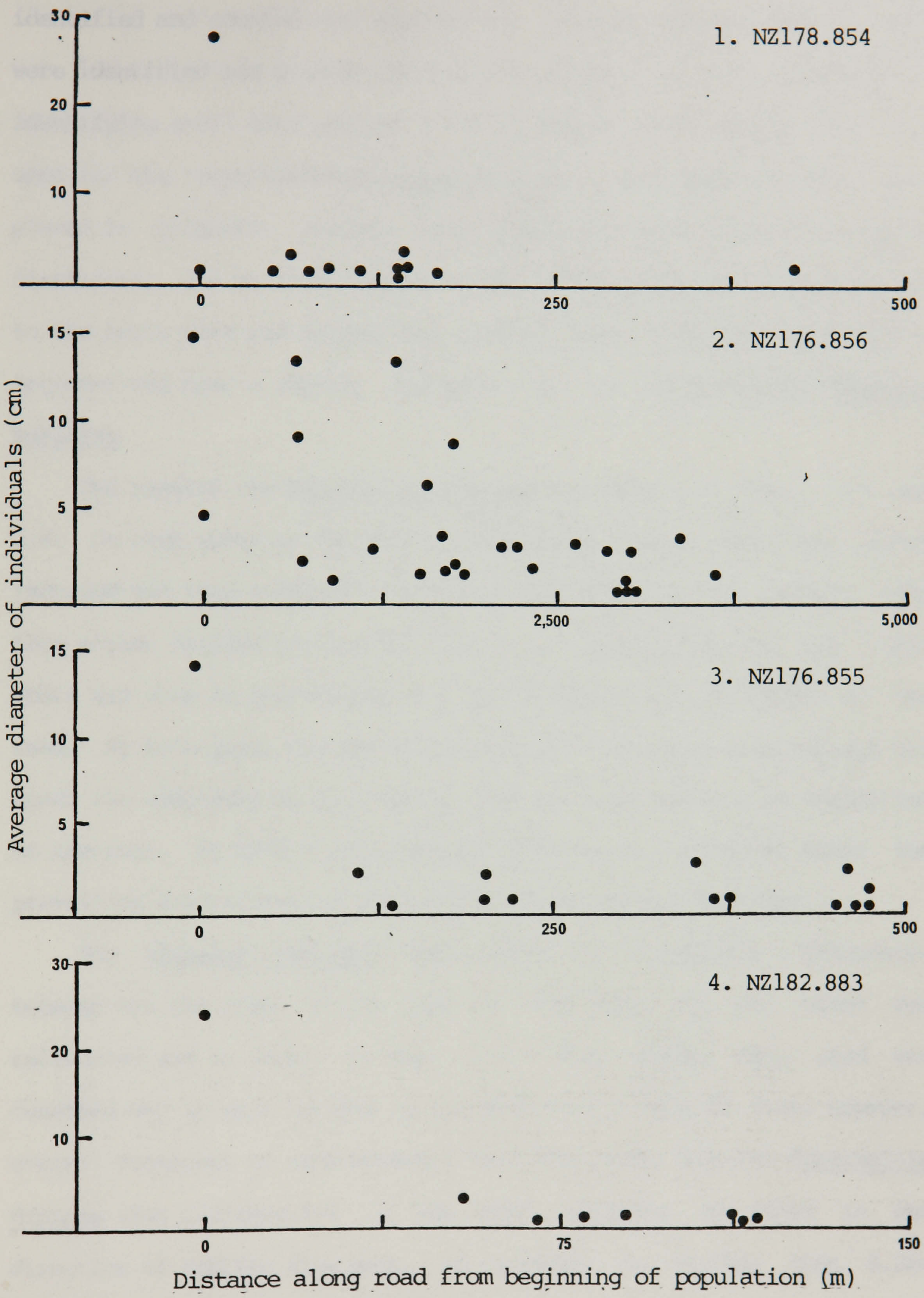


Fig 3.6b Size and location of individuals in four roadside colonies of Plantago maritima. North bound carriagway.

----- TRAFFIC FLOW ------>

trays were then returned to the laboratory, watered and seedlings identified and counted over six months. With the sticky sheets seeds were identified and counted directly but because of the problems of identifying small seed amongst a lot of debris this method was only used for the large-seeded Plantago maritima. Both types of trap were placed in transects leading away from the seed source in three directions; one at right angles to the traffic flow and two parallel to the road, with and against the traffic flow. Traps were put closer together and over a shorter distance for the large-seeded Plantago maritima.

The results for Puccinellia distans are shown in Figs. 3.7 and 3.8. On both sides of the road at both sites there were more seeds recorded and they travelled further in the direction of traffic flow than either against the traffic flow, or at right angles to the road. There was also an interesting difference between the two sides of the road. At both sites the prevailing wind is west-south westerly and the roads run east-west in cuttings so that the wind tends to be channelled to the east. At both sites dispersal distance was greatest where the prevailing wind direction and traffic direction were the same.

For Plantago maritima there were no discernible differences between the two sides of the road so the mean for all sites was calculated and is shown in Fig. 3.9. Once again, more seed was recorded and it went further in the direction of traffic flow, however, overall distances of seed movement were much lower than for Puccinellia distans (for instance 50% of the seed collected in trays in the direction of traffic flow went, on average, no further than 0.26m compared to 0.94m for P. distans).

Far fewer seed were found using the sticky metal sheet technique, although there was still significantly more in the direction of traffic flow (Fig. 3.9). It was noticed that after a few weeks on the roadside the sheets were completely covered in debris and thus no longer sticky and this probably explains the lower number of seed counted with this technique.

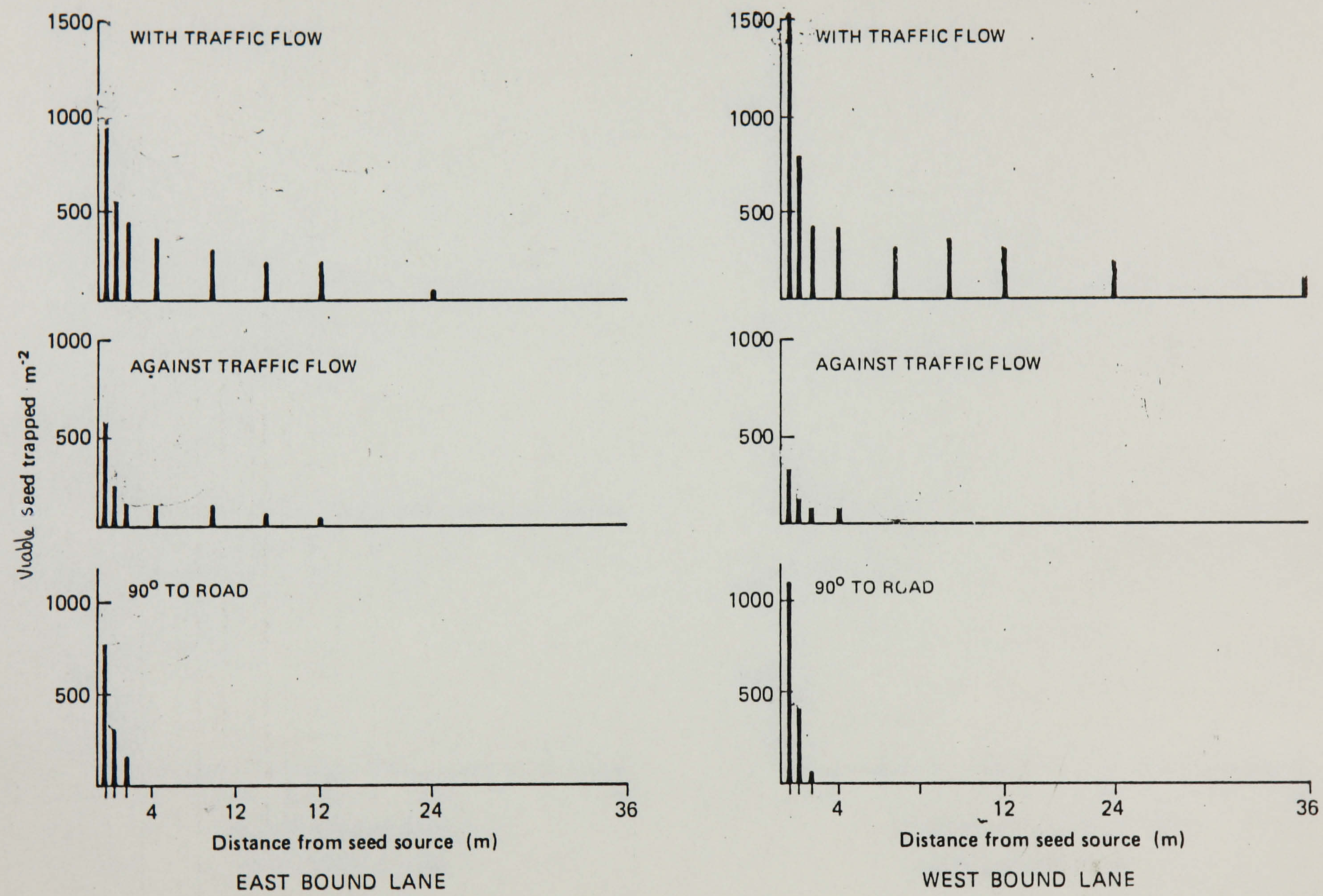


Fig 3.7 Numbers of seed trapped in trays of sterillised soil placed on transects through colonies of *Puccinellia distans*, on opposite sides of the Al at Arcot Hall (NZ 245.748)

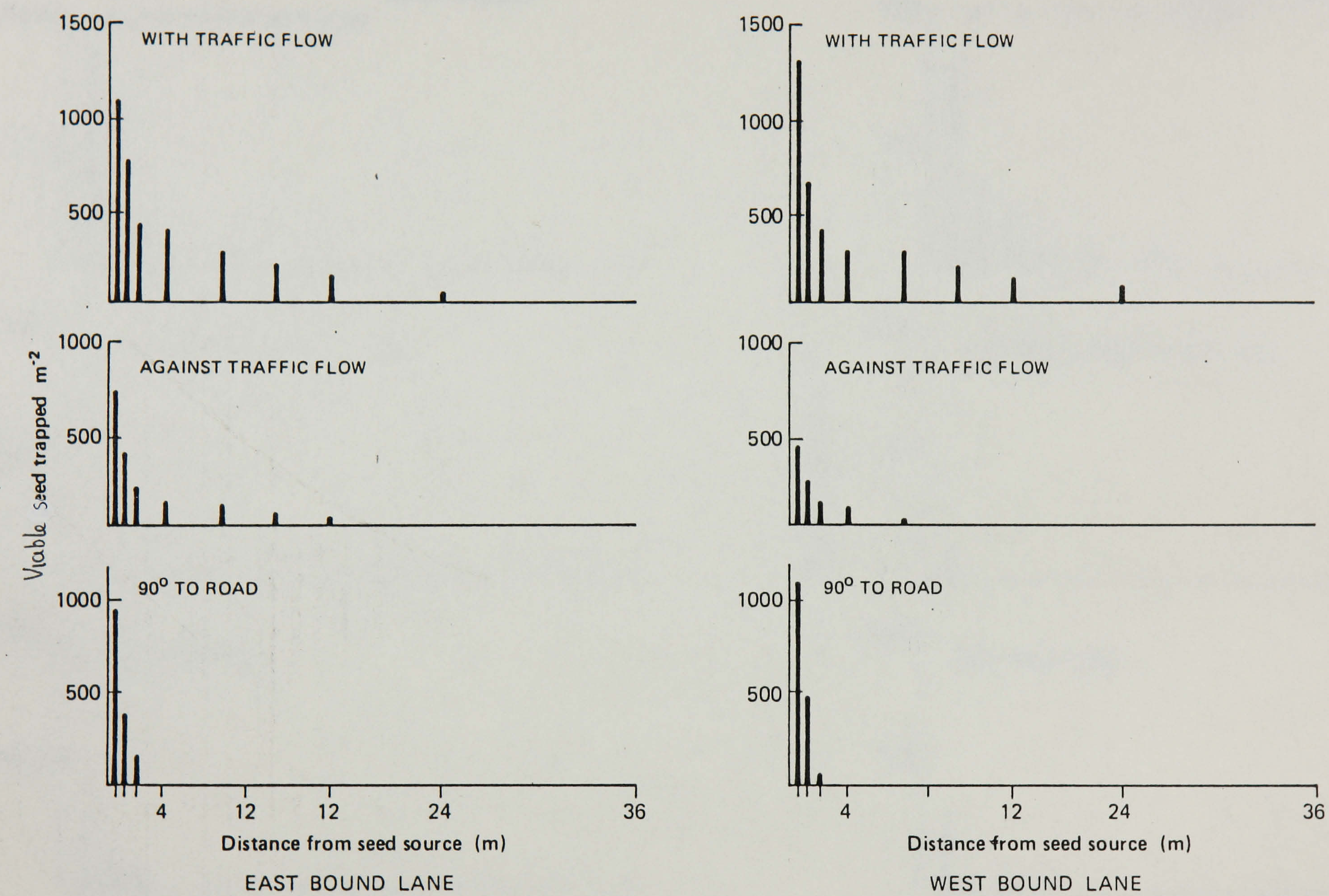
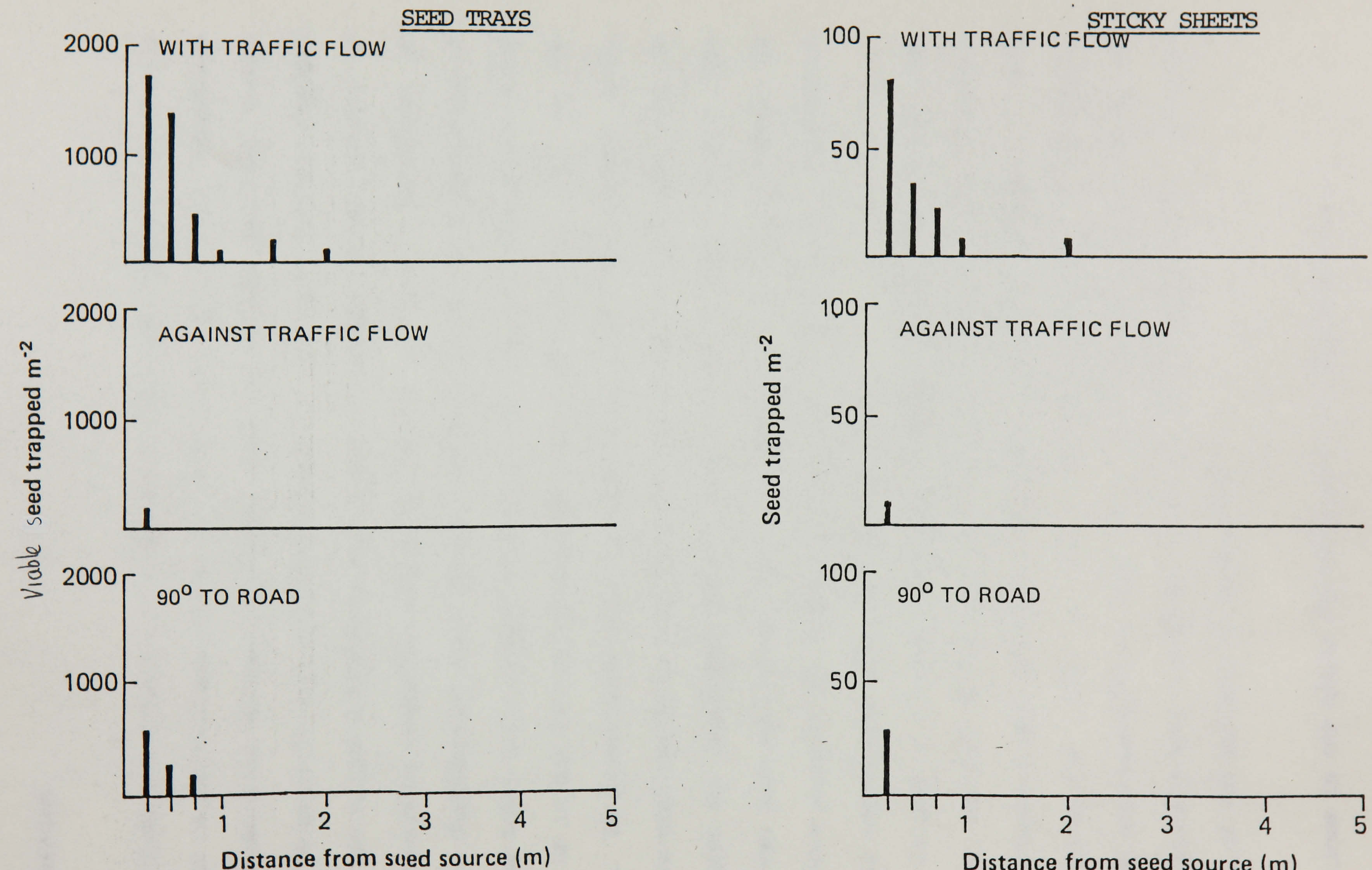


Fig 3.8 Numbers of seed trapped in trays of sterillised soil placed on transects through colonies of Puccinellia dis on opposite sides of the A696 at Throckley (NZ 145.677)



<u>Fig. 3.9 Mean numbers of seed trapped using two seed trap methods on transects through colonies of *Plantago maritima*, at 8 sites on the Morpeth by-pass</u>

Chapter Four. Soil salinity.

Introduction

Although the invasion of roadsides by maritime species is closely related to the increase in the use of de-icing salt, local variations in the abundance of species between sites can not be explained simply by differences in salt application rates. In north eastern England there are marked differences in species occurrence along lengths of road receiving nominally identical levels of salt. Variations in species distribution could be due to differences in the accumulation of salt by local soils, either because of differences in the nature of the soils or in the factors responsible for transfer of the salt to the verge. To investigate this the salinity of soils from several sites was measured regularly over the period of study. So as to be able to interpret any variations between sites and within sites, climatic data and local salt application rates were recorded. To allow results for the three years of the study to be put into a wider context information on salt use in previous years was researched.

As part of a survey of roadside vegetation described in the next chapter, the soil salinity of each site visited was also measured. This allowed a more extensive assessment of the variation in soil salinity at one point in time. In addition, other environmental factors were measured for each site. Correlations between these and soil salinity were calculated in an attempt to establish the principal causes of the salinity of these soils.

Variations in the use of de-icing salt in previous winters.

Most of the de-icing salt used in Britain comes from the salt

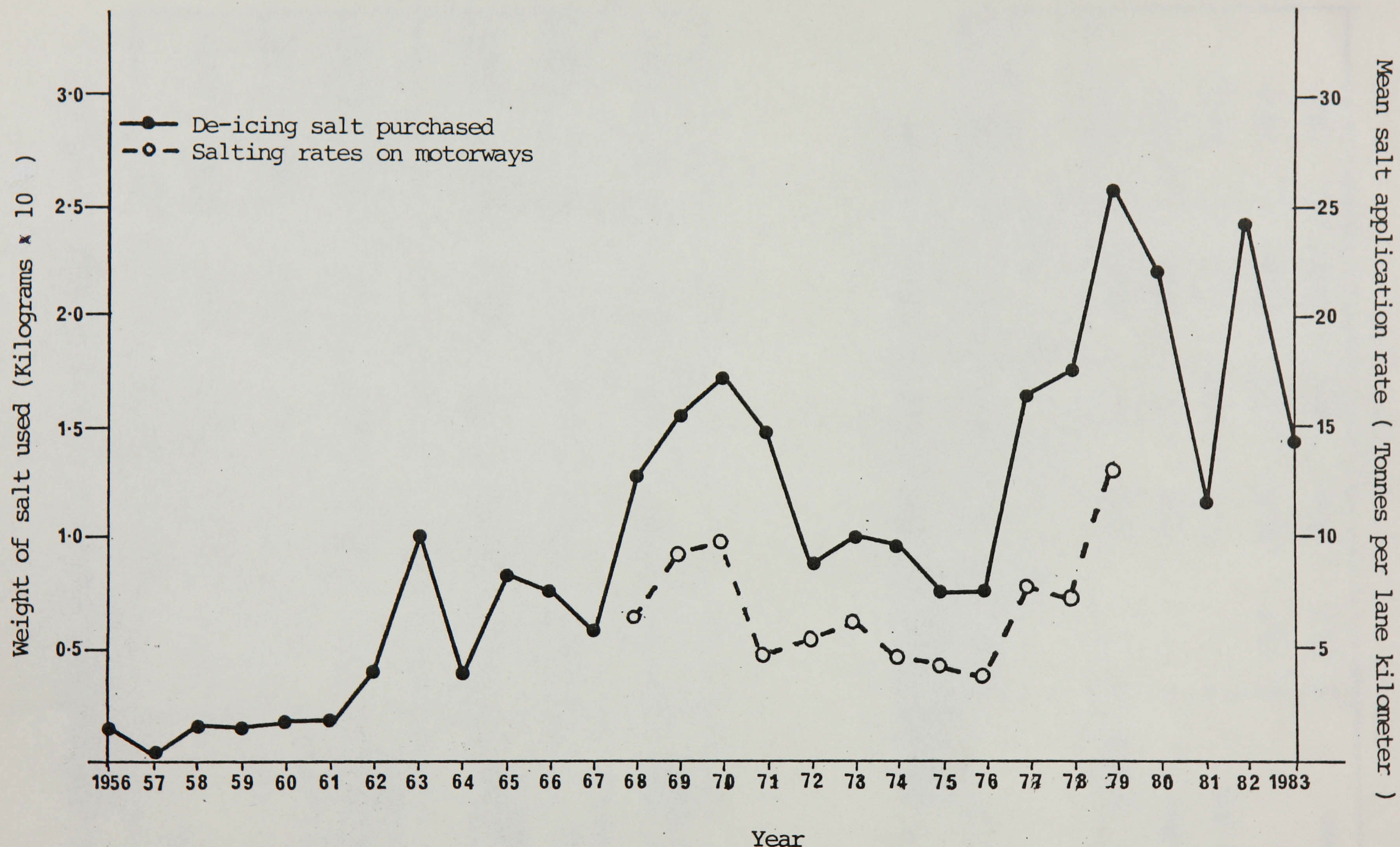


Fig. 4.1 Amounts of salt purchased annually for winter road salt maintenance in Britain (as estimated by the I.C.I. Salt Marketing Dept.) and the amount used on English motorways during the winters at the beginning of the years 1968-1979 (from Thompson et al. 1979).

Table 4.1 Tonnes of salt used annually by Local Authorities in the area of the study

Local Authority	Salt applied per winter (Tonnes)					
	78/79	79/80	80/81	81/82	82/83	83/84
Morpeth District Council	-	-	-	11,000	7,100	9,700
Northumberland County Council	-	50,000	29,500	29,500	33,000	25,000
North Tyneside City Council	8,500	6,000	8,000	11,000	5,500	6,800
Newcastle City Council	11,500	9,000	9,500	10,000	9,700	8,600
Tyne and Wear County Council	36,000	35,000	35,000	50,000	40,000	35,000

Table 4.2 Salt application and mean application rates to various sections of the Al

Section of Road	Salt applied per winter (Tonnes)				Application rate mean ($g\ m^{-2}$)
	79/80	80/81	81/82	82/83	
Morpeth by-pass	-	11.8	10.3	15.4	44.8
Seaton Burn	-	14.9	13.4	15.6	52.0
Holiday Inn	-	11.9	10.6	14.2	42.2
Seghill	11.7	15.6	18.4	11.6	39.9
Shiremoor	11.7	15.6	18.4	11.6	39.9

mine at Winsford, Cheshire owned by Imperial Chemical Industries. The salt marketing division of this firm have been estimating total sales of de-icing salt to British local authorities, from their own mine and other sources, since 1956. Most local authorities buy their salt during the summer to bring their stocks back up to set levels. In a harsh winter they may buy salt in the later part of the winter. Thus the sales of salt for each year, as estimated by I.C.I. (Fig 4.1), reflects the use of salt in the previous winter. This relationship is demonstrated by the strong similarity between these figures and those for the rate of salt application on English motorways during the winters 1967 to 1979, given by Thompson et al. (1979) which are also shown in Fig. 4.1. Salt usage by the local authorities covering the area of the project (Table 4.1) show that local use reflects the national use, except that the variation between years is less marked.

Soil salinity at five sites.

Soils were sampled from five roadside sites, two on the Morpeth by-pass (NZ 182873, NZ 182872), two at Seaton Burn (NZ 230755, NZ 231753) and one at Seghill (NZ 275743). The top 5cm of soil was collected, stored and the conductivity of a saturated extract measured following the methods described in chapter Two. At each site soils were sampled at 0.5m, 1.0m and 1.5m from the roadside. Sampling began in October 1979 and continued every two months until January 1981 when the frequency of sampling was increased to every month. Sampling ceased in October 1982 except for site 4 where sampling ceased in Febuary 1982 when this section of roadside was excavated by the Local Authority. The results are given in Figs. 4.2-4.6.

Of particular interest in the results are the peaks in soil salinity. These occur each year in winter and also, at some sites, in

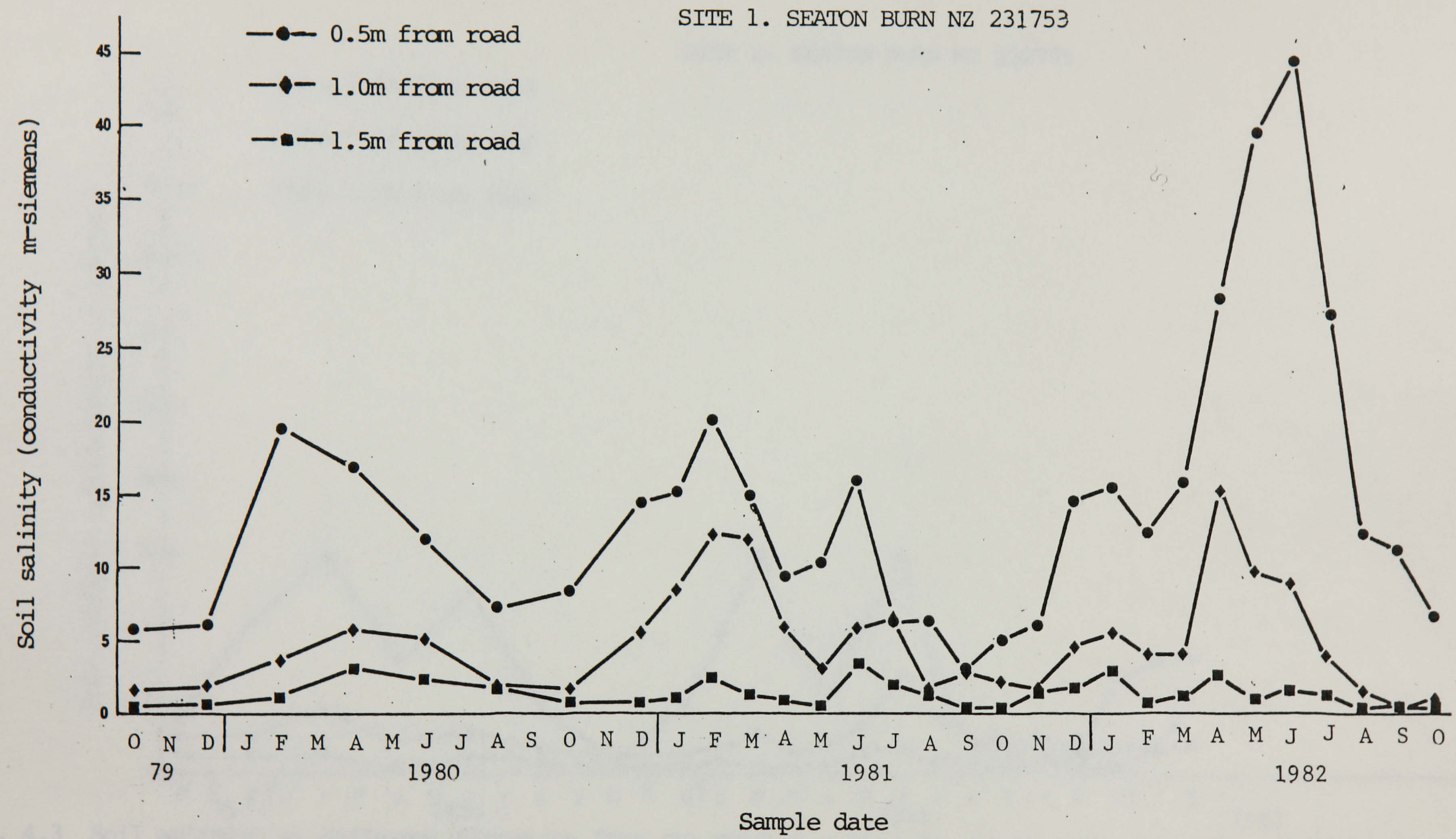


Fig. 4.2 Soil salinity at different distances from the road at a site on the Al next to the south bound carraigway. Site l Seaton Burn (NZ 231.753).

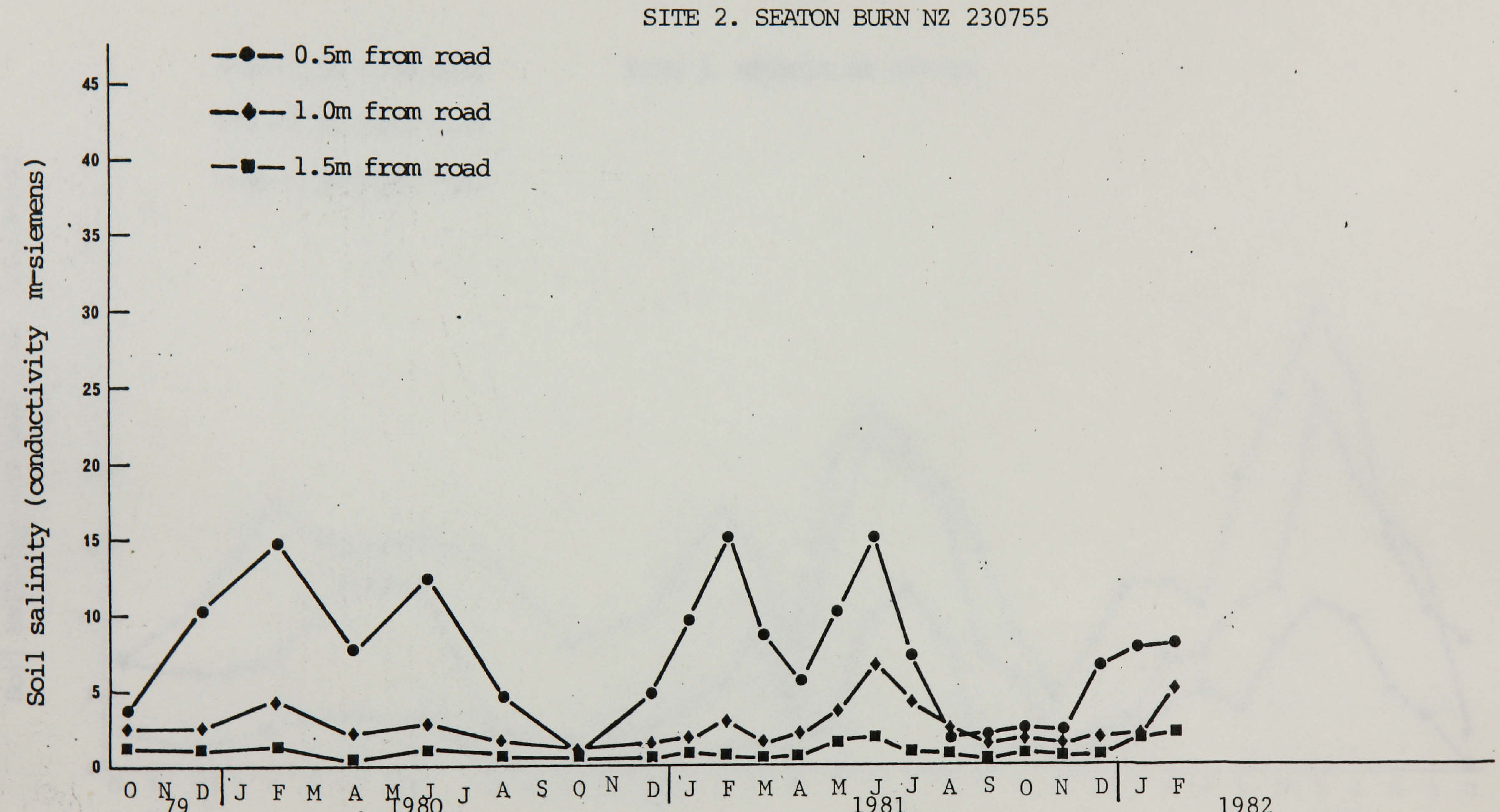


Fig. 4.3 Soil salinity at different distances from the road at a site on the Al next to the south bound carraigeway.
Site 2 Seaton Burn (NZ 230.755).

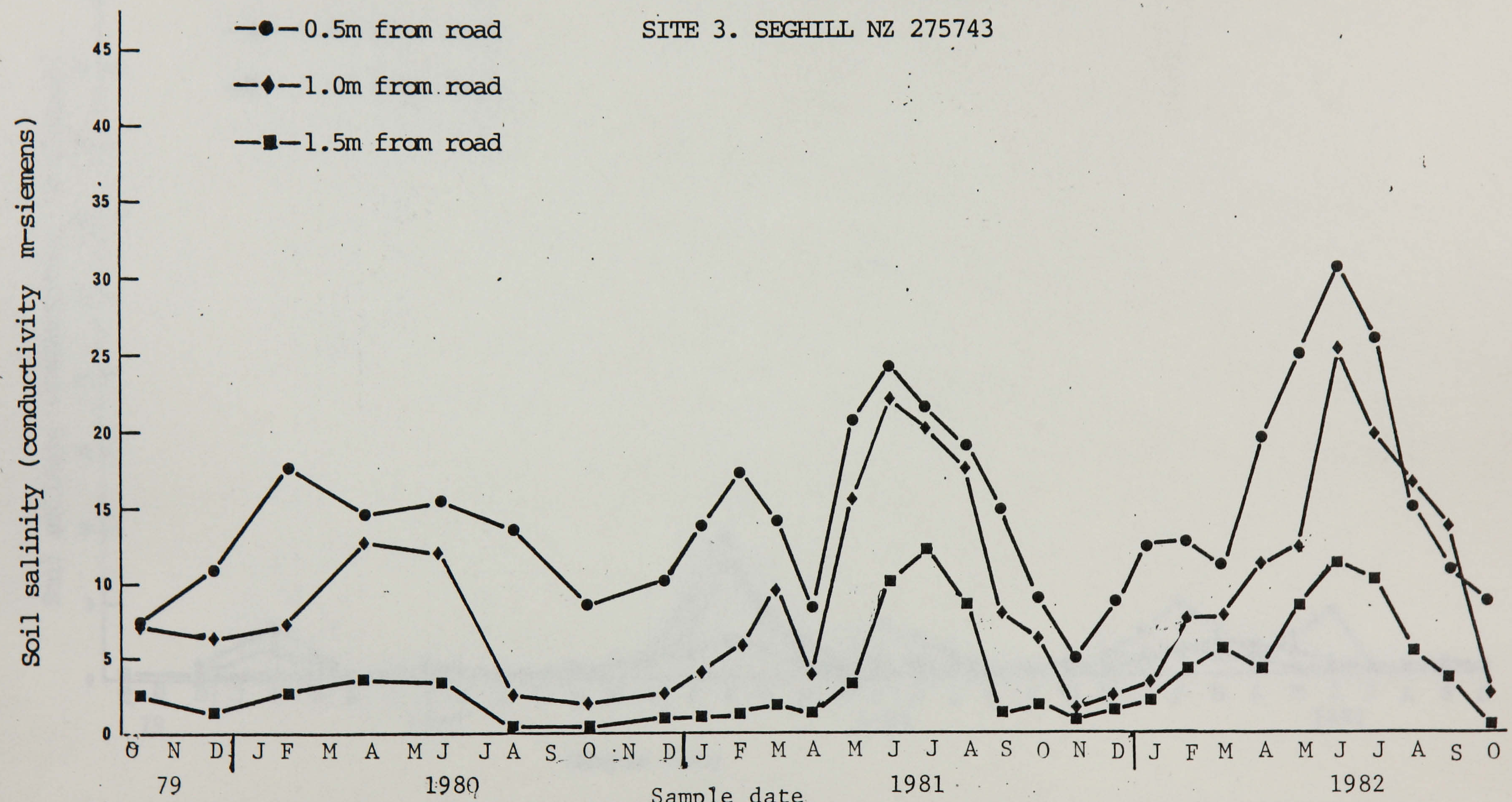


Fig. 4.4 Soil salinity at different distances from the road at a site on the A1 next to the south bound carraigway. Site 3 Seghill (NZ 275.743).

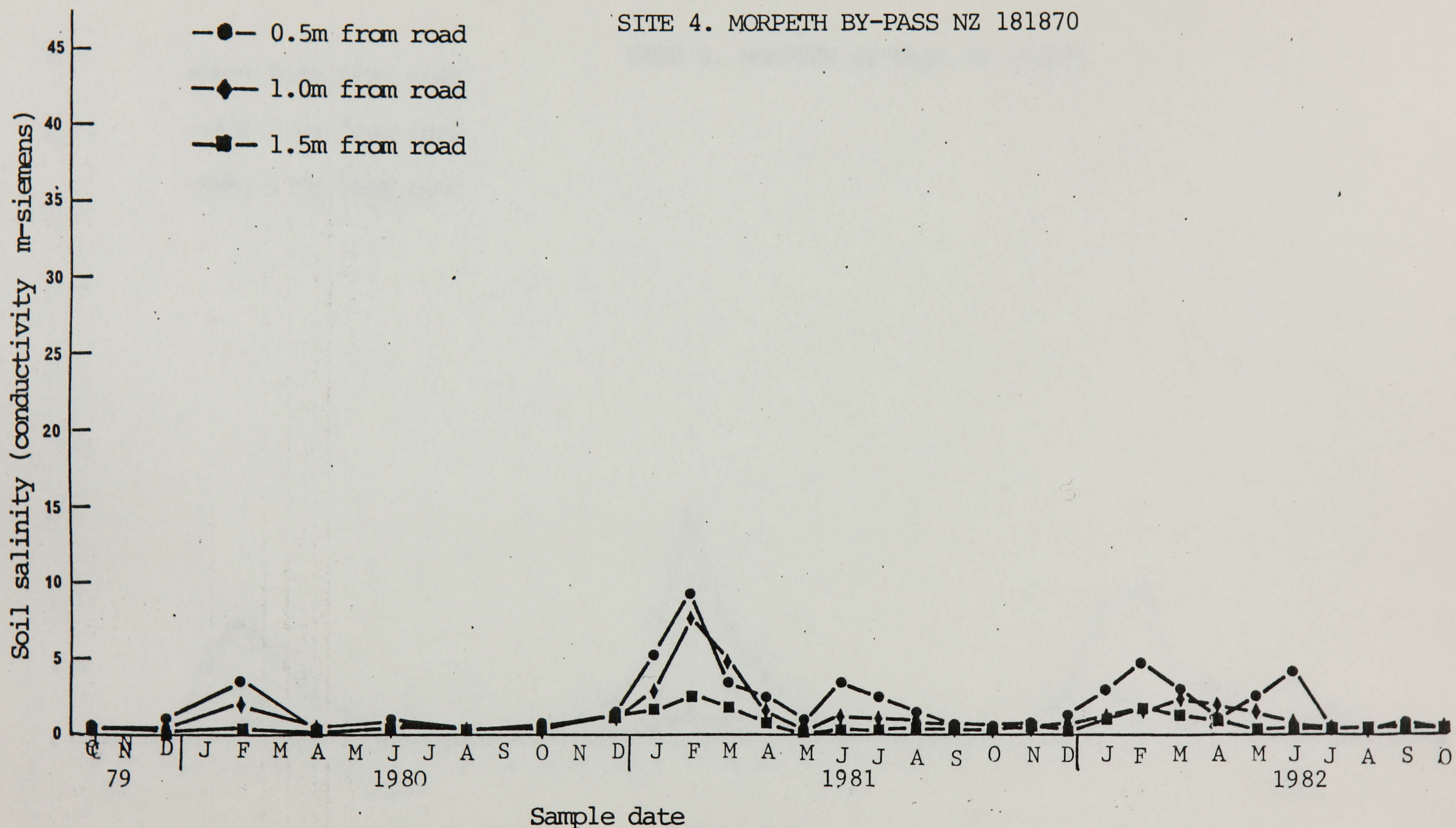


Fig. 4.5 Soil salinity at different distances from the road at a site on the Al next to the south bound carraigeway. Site 4 Morpeth by-pass (NZ 181.870).

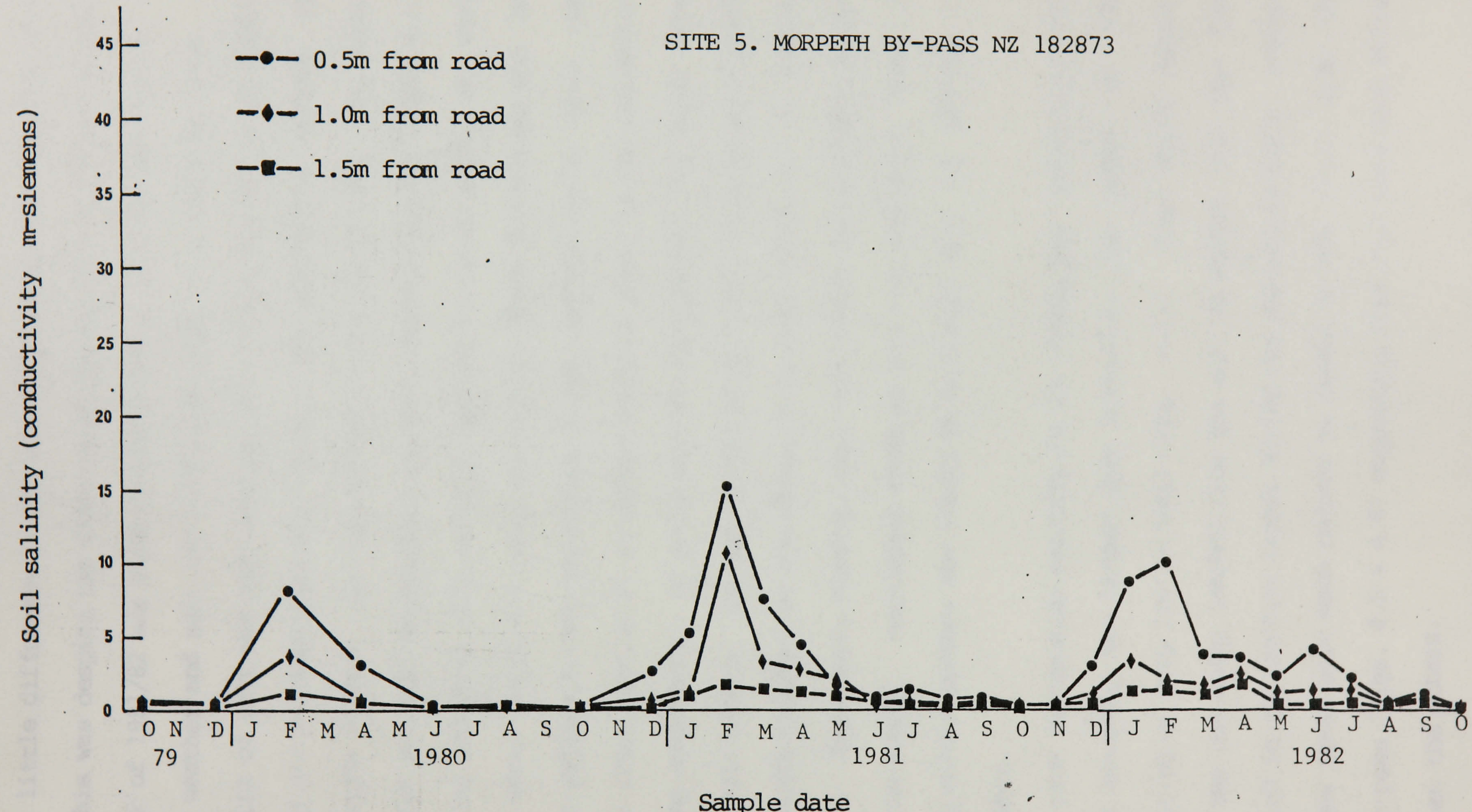


Fig. 4.6 Soil salinity at different distances from the road at a site on the Al next to the south bound carraigeway. Site 5 Morpeth by-pass (NZ 182.873).

summer. The winter peak occured at the time of salt application and there was little difference in the heights of this peak over the three years. This was despite the three years having very different winters. The winter of 1981/82 was a particularly harsh one with two periods of very cold weather and salt use in Britain (Fig. 4.1) reflects this. A large amount of salt was also used in 1979/80 but the winter of 1980/81 was a mild one and much less was used. The differance between the years is still evident but less marked in the figures for the amount of salt used by local authorities in north eastern England (Table 4.1). However, the amount of salt actually applied to the Al road, on which the sites were, (Table 4.2) does not reflect these differences and has a similiar pattern to the salinities of the roadside soils. This road is a major trunk road so it is salted whenever there is the possibility of freezing conditions. In north eastern England this can occur often even in a mild winter. In fact in the winter 1980/81 there were nearly as many frosts recorded at the Newcastle weather centre as in 1981/82 (Fig. 4.7). These were, however, much less severe and were more spread out over the winter. More minor roads in the area and major roads in areas with milder winters are likely to be salted only in periods of harsh weather.

The peak in roadside salinity in the summer was associated with periods of drought. The largest peak occured in the summer of 1982 after a spring of very low rainfall (Fig. 4.7). This would suggest that salt was not being leached from the soil in winter and was then concentrated in the surface layers during dry periods in early summer. These summer peaks were much reduced or absent in the soils from the Morpeth by-pass (Figs. 4.5 & 4.6) suggesting that they were much better drained than the others.

Regression coefficients for the relation between the soil salinity at the four sites for which there were complete data and several

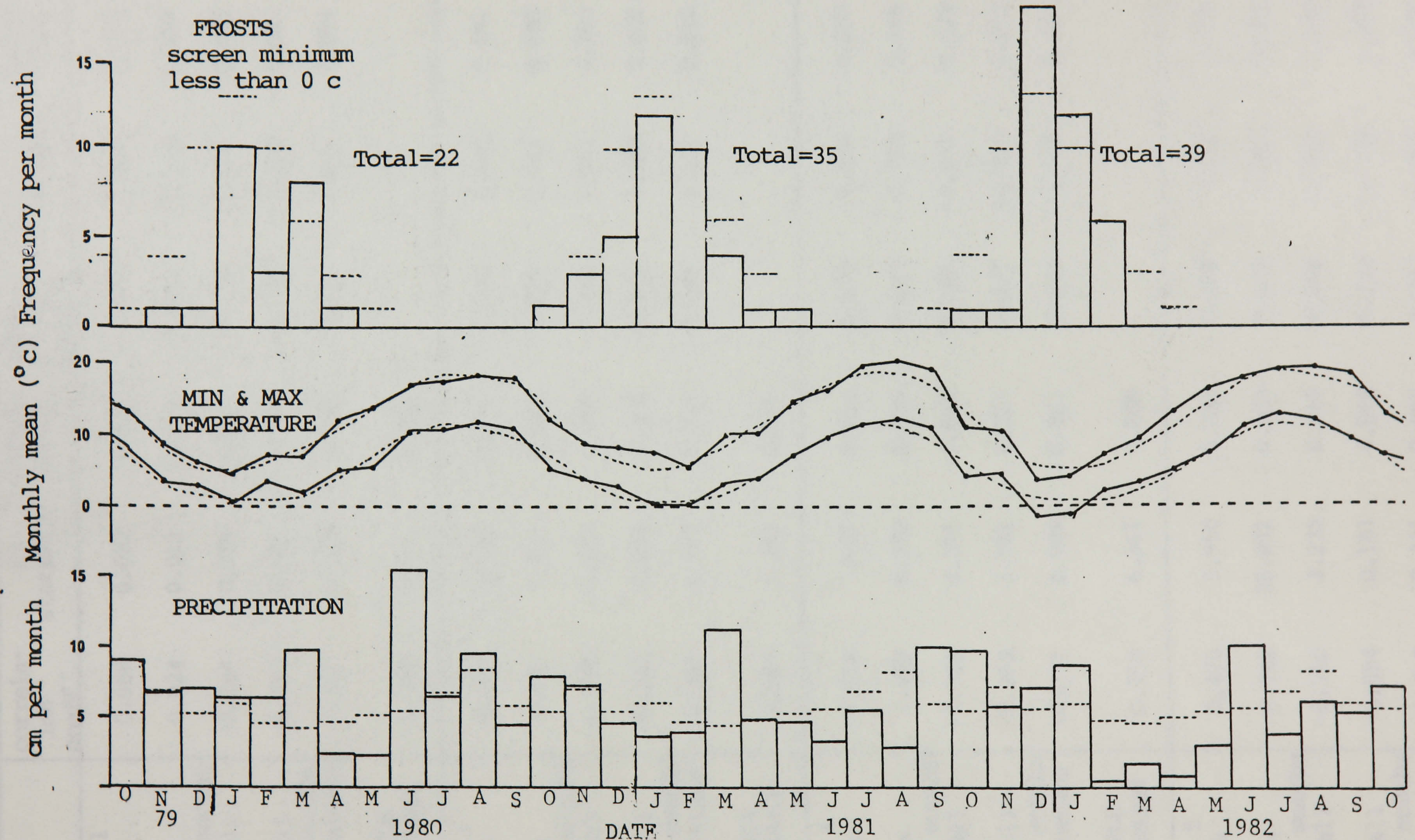


Fig. 4.7 Variations in monthly precipitation, temperature, and frequency of frost over period of study. Broken line (---), mean values 1956-1979

Table 4.3 Correlation between the soil salinity at four sites over three years and four climatic variables.

	correlation coeff´	F-statistic	probability	Partial correl´ coeff´	T-statistic	probability
SITE 1						
Frosts	0.066	0.092	0.763	0.324	1.820	0.073
Frosts pre 2 months	0.024	0.012	0.912	-0.031	0.624	0.989
Rainfall	-0.184	0.736	0.400	-0.314	1.621	0.088
Rainfall pre 2 months	-0.443	6.481	0.000	-0.552	3.200	0.003
Temperature	0.400	4.006	0.058	0.273	1.631	0.064
MULTIPLE REGRESSION	0.708	4.561	0.004			
SITE 3						
Frosts	0.493	6.760	0.016	0.263	1.440	0.181
Frosts pre 2 months	0.457	5.551	0.028	-0.029	0.147	0.884
Rainfall	-0.199	0.874	0.360	-0.206	1.051	0.303
Rainfall pre 2 months	-0.243	1.314	0.264	-0.572	3.480	0.002
Temperature	0.306	4.191	0.024	-0.047	2.310	0.816
MULTIPLE REGRESSION	0.587	3.251	0.028			
SITE 4						
Frosts	0.514	7.561	0.012	0.496	2.850	0.008
Frosts pre 2 months	0.499	6.972	0.015	0.294	1.574	0.248
Rainfall	-0.372	3.391	0.079	0.405	-2.541	0.039
Rainfall pre 2 months	-0.262	1.541	0.227	0.437	-4.020	0.013
Temperature	-0.471	6.006	0.023	0.214	1.075	0.293
MULTIPLE REGRESSION	0.754	6.361	0.000			
SITE 5						
Frosts	0.470	5.950	0.231	0.298	1.562	0.799
Frosts pre 2 months	0.742	25.831	0.000	0.628	3.887	0.000
Rainfall	-0.310	2.232	0.149	0.298	-1.421	0.130
Rainfall pre 2 months	-0.094	0.181	0.668	0.348	-1.798	0.075
Temperature	-0.6.8	12.321	0.002	0.287	-1.420	0.091
MULTIPLE REGRESSION	0.827	10.461	0.000			

climatic variables were calculated. The results (Table 4.3) show that the monthly soil salinity was significantly correlated with the number of frosts in each month and the monthly mean tempreture for three of the sites. Monthly soil salinity was also significantly correlated with the total rainfall in each month. In the sites from Seaton Burn and Seghill the partial correlation coefficents were higher for rainfall than for frost or temperature, in those of the Morpeth by-pass the coefficents for frosts are higher. This reflects the difference between the summer salinities of these soils. Combined in a multiple regression the climatic variables accounted for between 34% and 68% of the variation in site salinity at the sites.

Soil salinity of survey sites.

The differ nce between soils of the Morpeth by-pass and other sites are also shown in the average soil salinities of the sections of road covered in the survey (Table 4.4). These soils were collected from a point adjacent to the centre of the first quadrat (i.e. 0.2m from the kerb). The soils were sampled in August 1982 and as would be expected at this time of year those from the Morpeth by-pass had much lower salinities. Another difference of note is the consistently higher salinities of the soils from the south bound carriageways compared with those from the north bound carriageways.

A number of variables that were thought to influence soil salinity were also recorded or calculated for the two hundred sites of the survey. The first was the salting rate for each section of road during the previous winter (Table 4.2). This was calculated using information from local authority depots on the quantity of salt used each time the road was salted. The Morpeth by-pass, Seaton Burn and Holiday Inn sections of the Al are all salted as part of separate runs

Table 4.4 Mean values of environmental variables on different sections of road, August 1982. Standard errors in parenthesis.

	Seaton Burn	Holiday Inn	Seghill	Shiremoor	Morpeth By-pass
		SOUTH BOUND CARRIAGWAY			
Bare Ground (% cover)	10.8 (±0.2)	7.5 (±1.3)	19.1 (±0.8)	18.7 (±1.6)	13.3 (±0.4)
Exposure (scale 1-10)	4 (±0.05)	4 (±0.3)	6 (±0.09)	5 (±0.2)	6 (±0.08)
Salinity (m siemens)	5.23(±0.15)	4.31(±0.60)	19.50(±0.80)	13.20(±1.19)	2.42(±0.07)
Traffic volume (10) (24h ave)	7.70(±0.00)	7.19(±0.20)	9.53(±0.01)	9.25(±0.15)	2.44(±0.00)
		NORTH BOUND CARRIAGWAY			
Bare Ground (% cover)	2.5 (±0.06)	2.5 (±0.4)	1.7 (±0.2)	3.3 (±0.2)	2.7 (±0.3)
Exposure (scale 1-10)	3 (±0.05)	3 (±0.4)	6 (±0.6)	5 (±0.2)	6 (±0.09)
Salinity (m siemens)	2.06(±0.03)	1.09(±0.06)	2.48(±0.34)	3.26(±0.25)	1.28(±0.03)
Traffic Volume (10) (24h ave)	6.32(±0.00)	6.80(±0.20)	7.29(±0.00)	7.56(±0.02)	2.89(±0.00)

by the Morpeth depot of Northumberland County Council. The Seghill and Shiremoor sections are salted by the North Tyneside Depot of Tyne and Wear County Council as one run. Both authorities salt the roads at the same rate (Table 4.2), but the North Tyneside depot sent the salting wagons out more frequently. Local authorities also supplied the mean 24hr traffic volumes for each section of road for the period of the study (Table 4.4). The amount of wind crossing the site was also thought likely to affect the amount of salt which reaches the verge. So site exposure was estimated using the scale detailed in chapter Two and the alignment of the site was used to calculate the frequency at which the wind blew across the road onto the site. For this latter variable the percentage wind rose for the years 1979-1982 supplied by the Newcastle Weather Centre (Fig 4.8) was used. The figure for each site was taken as the frequency of wind of which the direction was at 90° or 45° to the road. Thus, if the road ran north-south, a site on the south-bound carriageway was scored with the total of the wind blewing from the west, north-west and south-west.

When regression coefficents were calculated site salinity proved to be significantly related to all of the environmental variables (Table 4.5). In a partial correlation analysis all the environmental variables remained significantly correlated with site salinity, although the coefficents of correlation were mostly reduced. Combined in a multiple regression they account for 35% of the variation in site salinity.

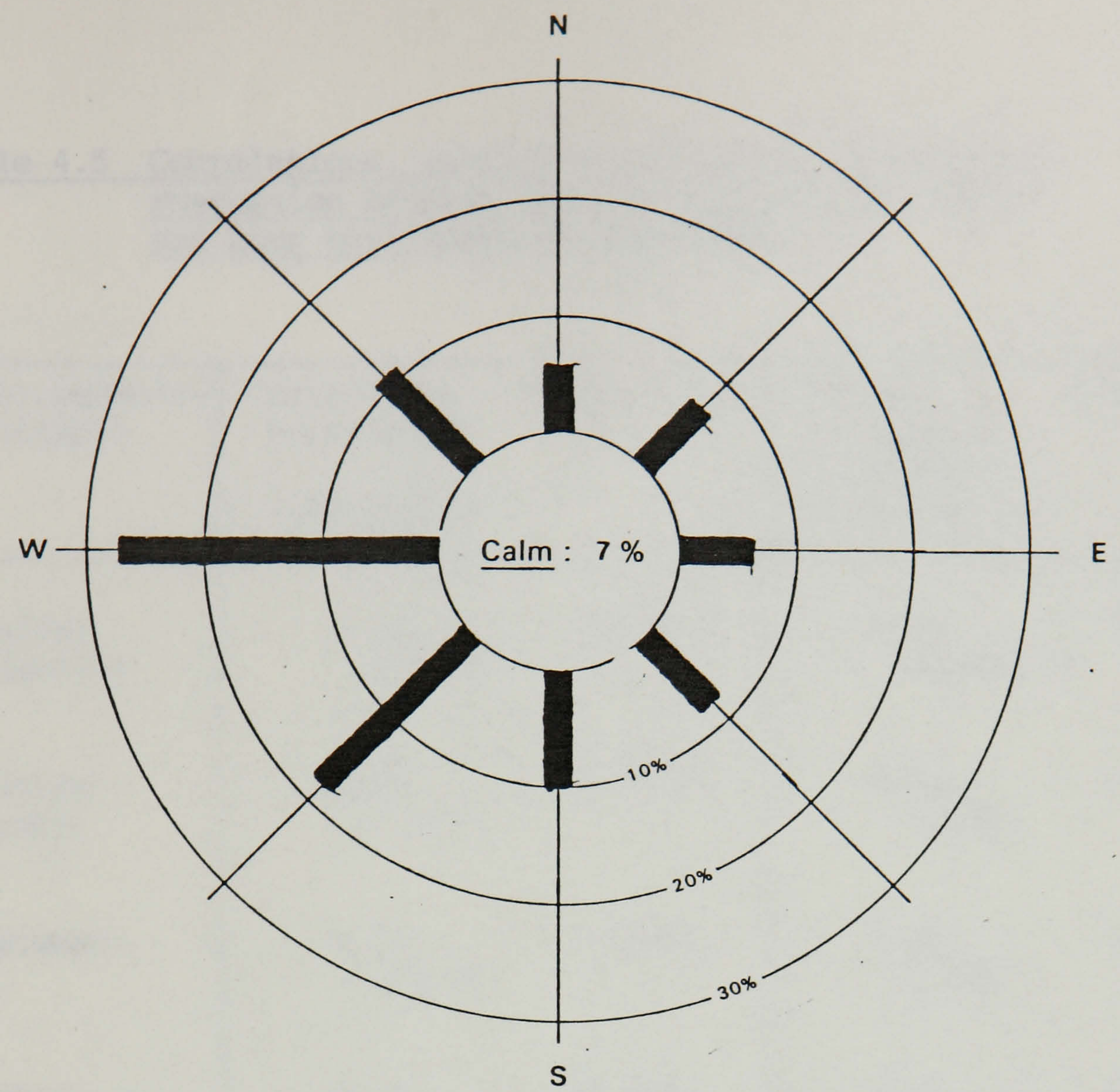


Fig. 4.8 Frequency of winds for various directions as a percentage of the total observations at the Newcastle Weather Centre, 1979-1982.

Table 4.5 Correlations, partial correlations and multiple regression between soil salinity at 200 sites and four environmental variables.

Environmental variable	Correlation coefficent (F-statistic)	Probability	Partial correlation coefficent (t-statistic)	Probability
Traffic density	0.38 (32.76)	<0.0001	0.32 (4.466)	<0.0001
Salting rate	0.21 (9.25)	<0.0027	0.26 (3.651)	<0.0002
Exposure	0.23 (11.38)	<0.0002	0.21 (2.893)	<0.0057
% Wind across road	0.34 (28.15)	<0.0001	0.31 (4.560)	<0.0001
COMBINED (multiple regression)	0.59 (23.58)	<0.0001		

Chapter Five. Roadside surveys.

Introduction

In north-eastern England there are marked differences in species occurrence along lengths of road receiving identical levels of salt. Both the number of maritime species present and their relative frequency vary. Also, at each site species, both maritime and non-maritime, are clearly zoned in relation to the distance from the roadside.

To investigate these observations it was necessary to establish the distribution of species in detail. There were two aspects to species variation which needed to be recorded: position in the zonation and differances in abundance at different locations. The initial survey involved visiting 200 sites over a few weeks in 1981. At each site species occurrence and position in relation to the road were recorded as well as percentage bare ground, soil salinity and site exposure.

The results from this survey were analysed in several ways. Initially mean local frequency of each species was calculated across transects on different sections of road in order to demonstrate zonation and to investigate the relationship between species position on the transect and site salinity.

Calculations of species density (numbers of species per unit area) across the transects, demonstrated a clear trend which occurred at most sites. To further investigate changes in species density across transects a second, much smaller survey, was undertaken at two of the sections of road examined in the first survey. In this, variation in species number, soil salinity and the dry weight of the standing crop and litter across transects at right angles to the road were measured.

To investigate differences in species occurrence between sites it was neccessary to undertake more complex analysis of the data from the main survey. Advice was taken on computer ordination techniques and two which appeared particurly promising were tried. The results of this analysis allows some insight into the possible causes for differences between sites.

Survey Design.

Two hundred sites were visited during August 1981, all on dual carriagway along 15 km of the A1 between the Tyne Tunnel and the north end of the Morpeth by-pass. All the roads were built in the same period using similar methods of construction. Sites were in pairs, one on either side of the road, each pair occurring at a random distance past every 10th drain along the road. Each site, 1m wide and 3m deep was divided into a transect of 9 quadrats of 0.33m x 1m. At each quadrat the percentage bare ground was estimated, and the presence or absence of each species recorded.

Species zonation.

Initial analysis of the data involved calculating the local frequency of species in each of the nine quadrats for all the sites on each section of road. Sections of road chosen for this type of analysis were those at Seaton Burn, Seghill, and the Morpeth by-pass. In the results shown here, only the more frequent species are included. At the Seaton Burn sites next to the south bound lane (Fig. 5.1) some maritime species, Puccinellia distans, Puccinellia maritima and

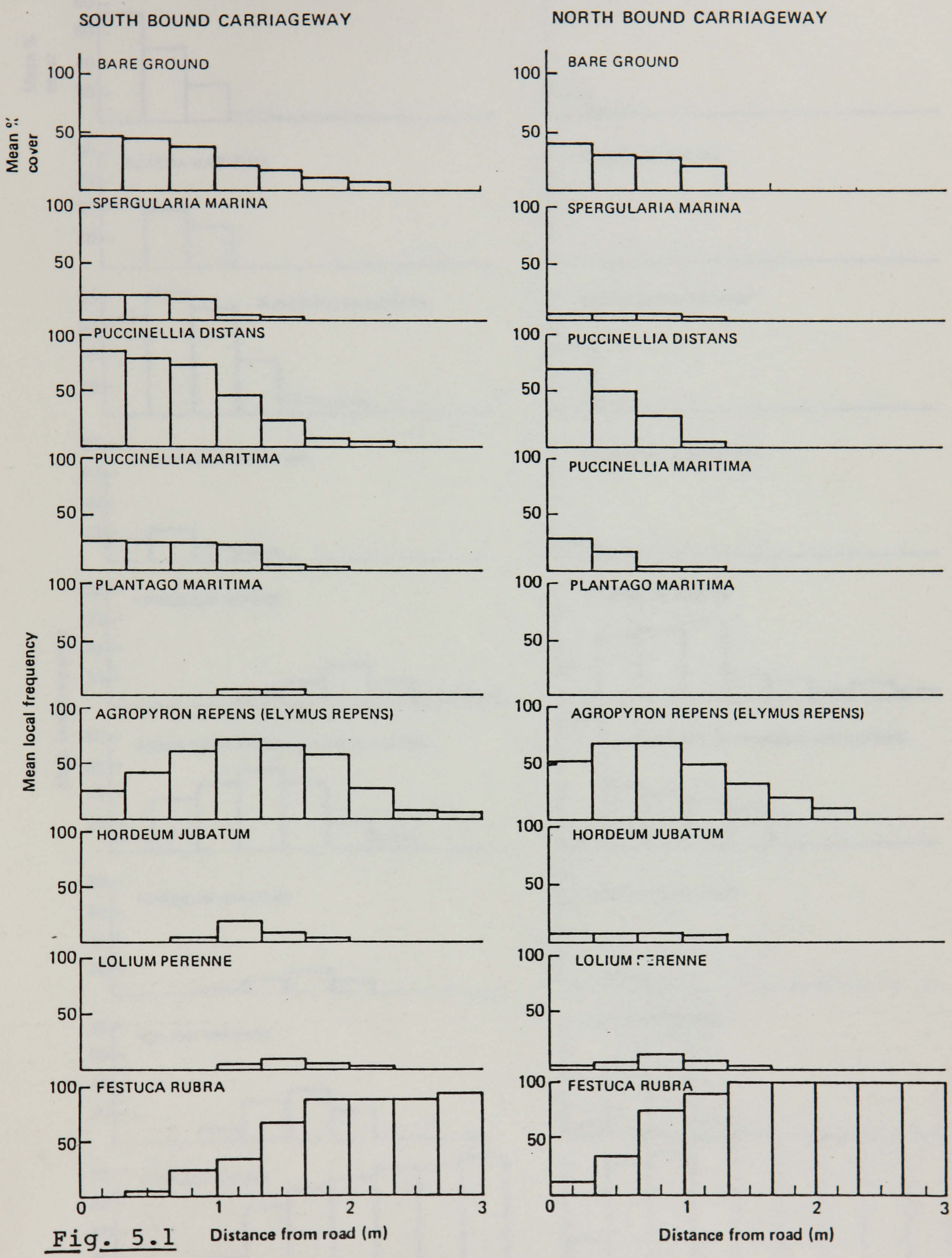


Fig. 5.1

MEAN LOCAL FREQUENCY OF SPECIES ALONG TRANSECTS AT 90° TO THE ROAD: A1, SEATON BURN

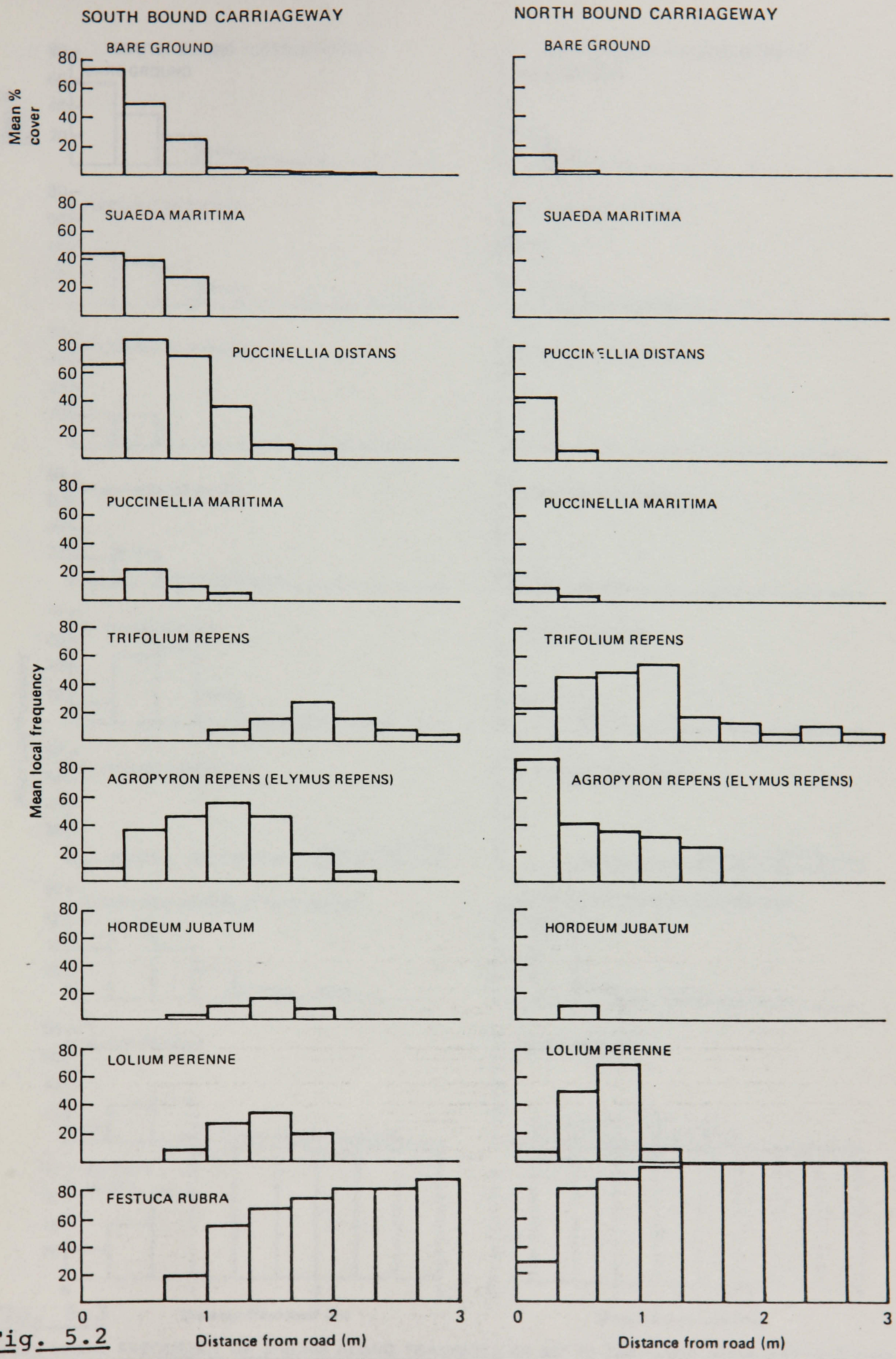


Fig. 5.2

MEAN LOCAL FREQUENCY OF SPECIES ALONG TRANSECTS AT 90° TO THE ROAD: A1, SEGHILL

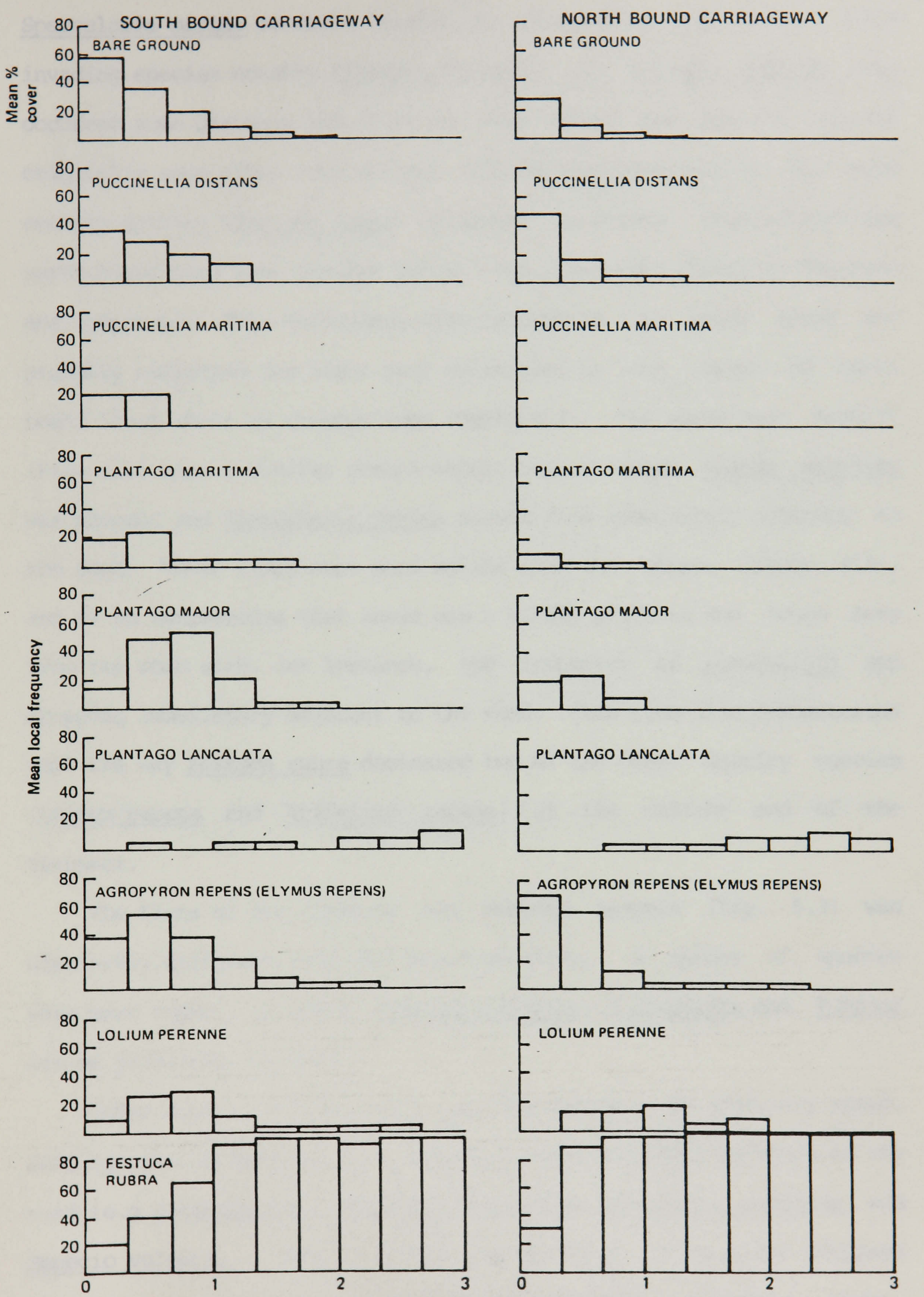


Fig. 5.3

MEAN LOCAL FREQUENCY OF SPECIES ALONG TRANSECTS AT 90° TO THE ROAD: A1, MORPETH BYPASS

Spergularia marina occurred immediately adjacent to the road. Other invading species notably Plantago maritima and Hordeum jubatum only occurred some distance away from the road among the amenity species originally sown after road making. Yet further back, one of the sown amenity species (Festuca rubra) dominated the others. Results from the north bound lane were similar but all the zones were closer to the road and compressed. This difference also occured at the other sites and probably reflected the lower soil salinities in the verges of north bound lanes shown in chapter four (Table 4.4). The sites near Seghill (Fig. 5.2) gave a similar result except that in these Suaeda maritima was present and Spergularia marina absent from immediately adjacent to the road. These sites were more saline than the others (Table 4.4), and it is interesting that there was a slight shift in the zones away from the road with, for instance, the frequency of Puccinellia spp dropping immediately adjacent to the road. This site also demonstrates well the way Festuca rubra dominated two of the other amenity species (Lolium perene and Trifolium repens) at the distant end of the transect.

The flora of the sites on the Morpeth by-pass (Fig. 5.3) was distinctly different from the other two sites. A number of species were more common, of these, Plantago maritima, P.lanceolata and P.major are of particular interest.

Other species occurring on roadsides tended to be similarly zoned. Some species occurred with the invading coastal species adjacent to the road (e.g Atriplex spp., Polygonum aviculare, Matricaria maritima and Senecio vulgaris). Others occurred further back, in the zone occupied by Hordeum jubatum (e.g. Leontodon autumnalis, Plantago major, Artemisia vulgaris) whilst others tended to occur just behind these (e.g Lolium perenne, Rumex spp., Taraxacum officinale and Achillea millefolium). Further back in the Festuca rubra dominated sward, the

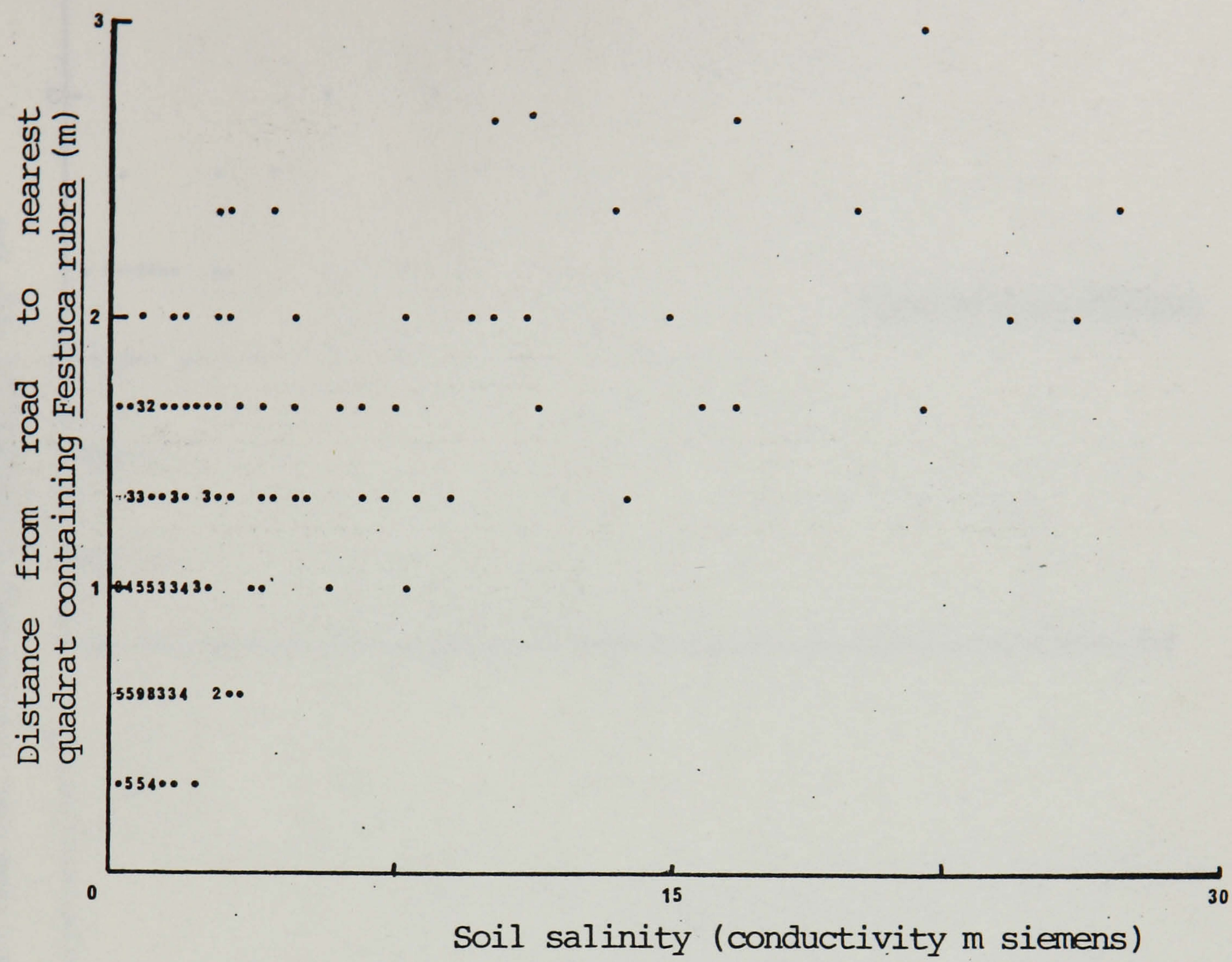


Fig. 5.4 The relationship between the minimum distance of Festuca rubra from the road and site salinity.

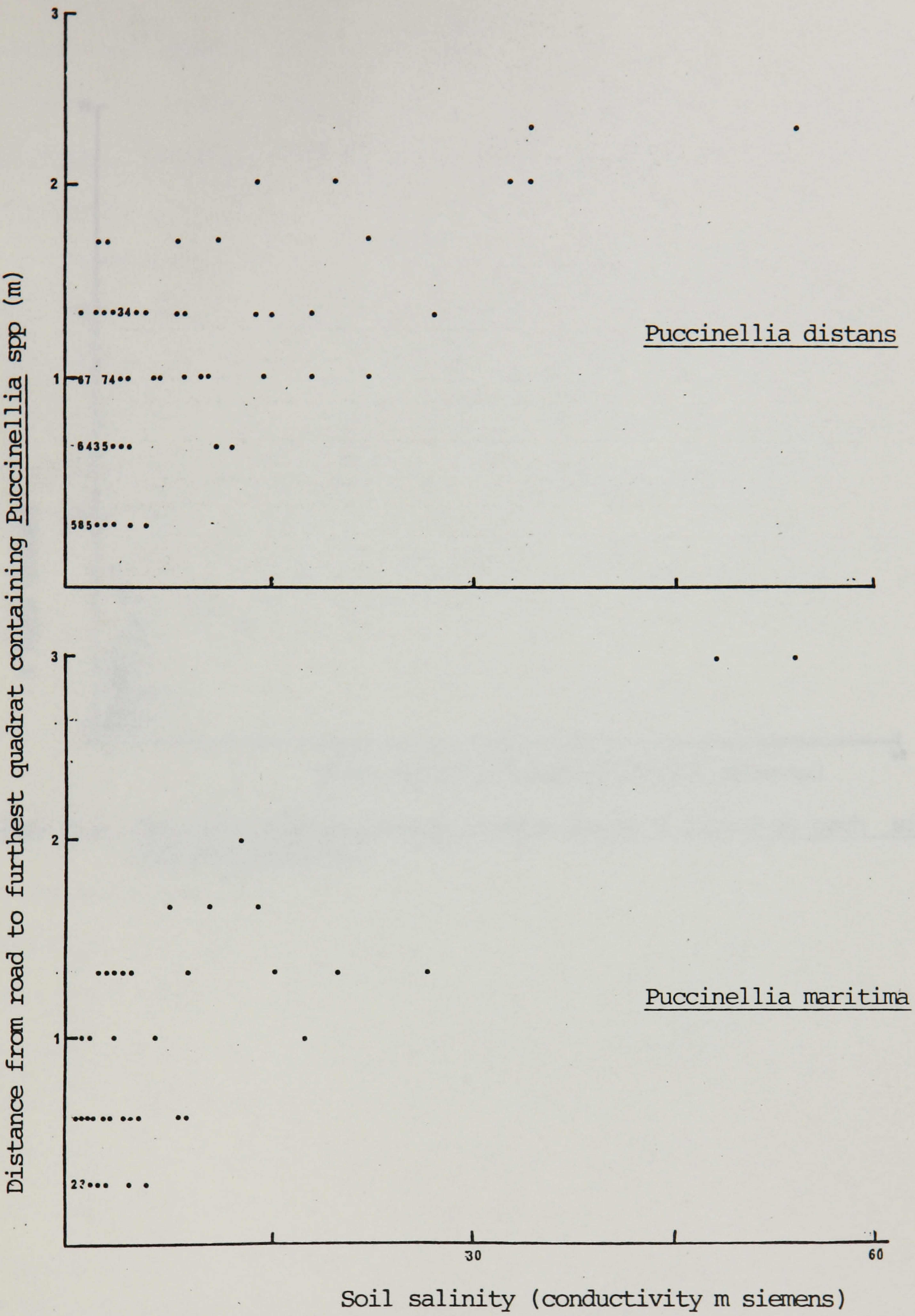


Fig. 5.5 The relationship between the maximum distance of Puccinellia spp. from the road and site salinity.

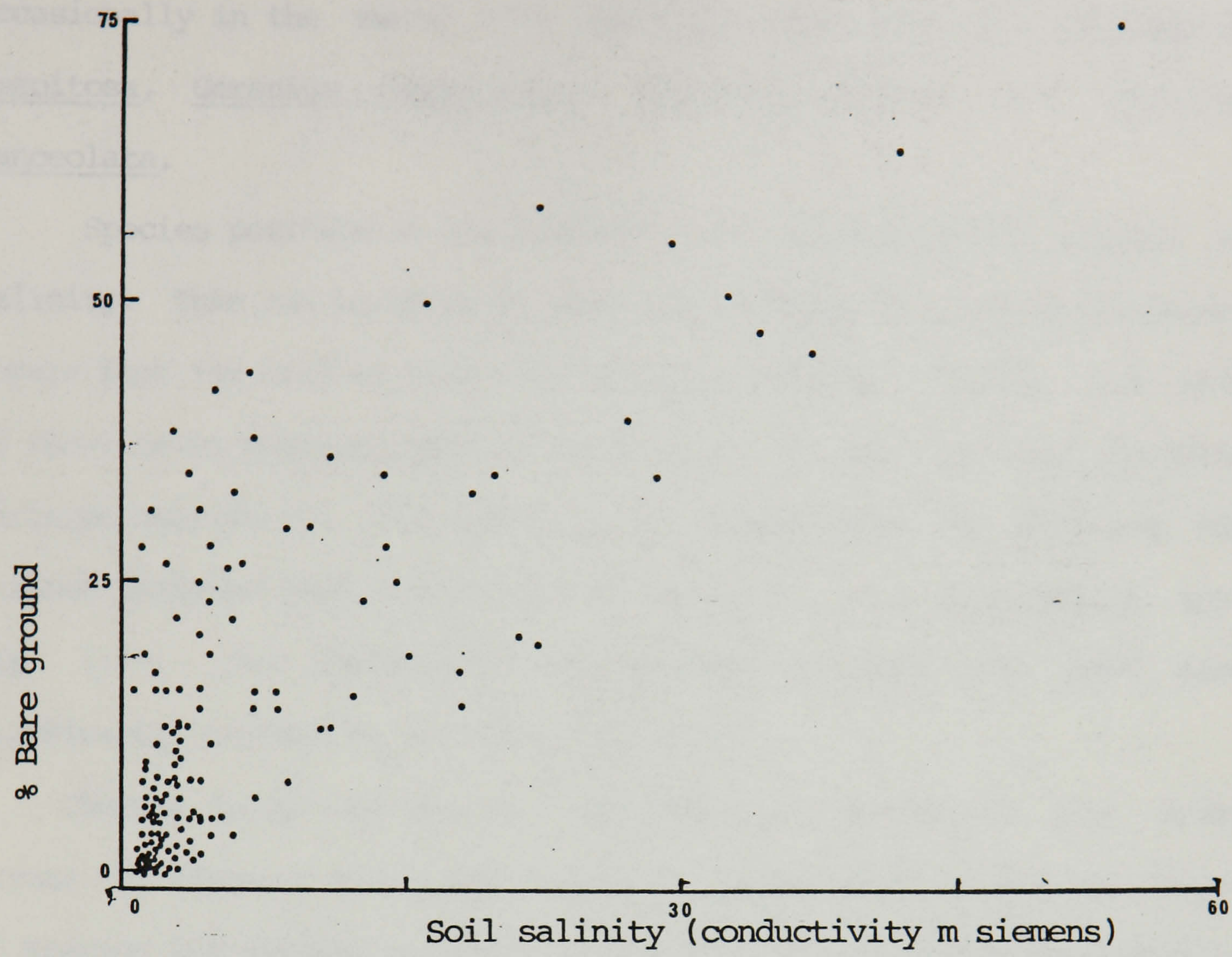


Fig. 5.6 The relationship between percentage bare ground at each site and site salinity.

numbers of species were constantly lower. Species occurring occasionally in the sward were Heracleum sphondyl ium, Deschampsia caespitosa, Geranium robertianum, Cirsium arvense and Plantago lanceolata.

Species position on the transect was significantly related to salinity. This can be shown by plotting the minimum distance a species occurs from the road at each site against salinity. In Fig. 5.4 this is shown using Festuca rubra as an example. In the case of invading maritime species the relationship is demonstrated by plotting the maximum distance from a road against salinity (e.g Puccinellia spp. Fig. 5.5). The percentage bare ground at each site was also signficantly related to salinity (Fig. 5.6).

Changes in species density (the number of species per unit area) across the transect were demonstrated by calculating the average number of species per quadrat as shown in Fig. 5.7 for the Seaton Burn section of the Al. In the second survey eight sites on the Al were examined. In recording species density in each quadrat, the dry weight of the standing crop, including litter, and the soil salinity were also calculated. Fig 5.8 shows the results for a transect across a particularly saline verge and demonstates how species density was related to the position of the quadrat on the transect, to the decline in salinity and to the increase in total dry weight of the standing crop. The peak for species density occurred in the region where salinity declined but where standing crop was just increasing. Also of interest is the way that the contribution of litter to the standing crop also increased with distance away from the road. Fig. 5.9 demonstrates this same relationship between species density and total standing crop for data pooled from the eight sites surveyed. This time there were 5 quadrats at each site at 0.5, 1.0, 1.5, 3.0, and 5.0 m from the road. The same peak appeared as in Fig. 5.8 with possibly a

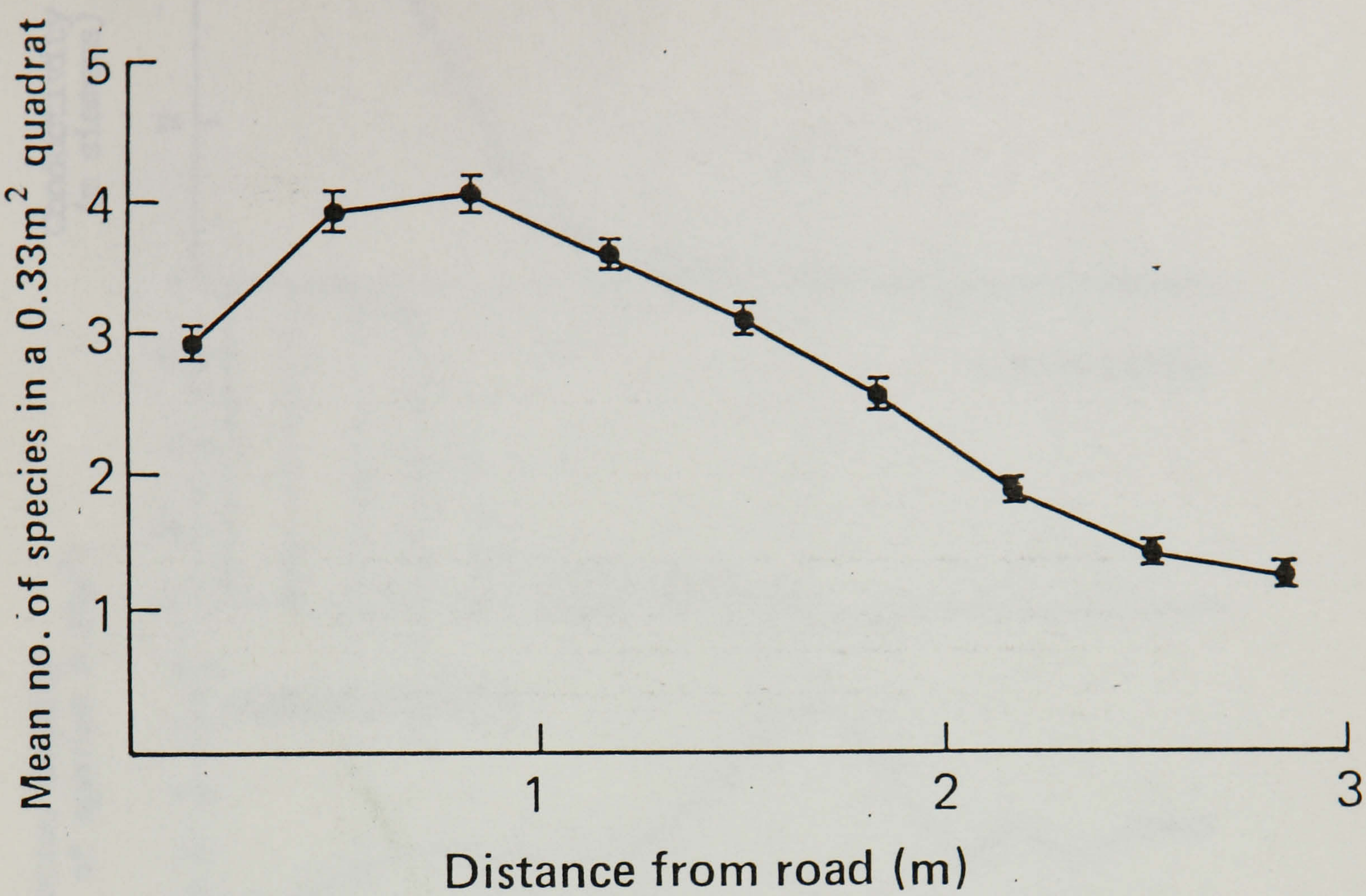


Fig. 5.7 Mean number of species in transects at right angles to the A1, Seaton Burn. Standard errors shown as bars.

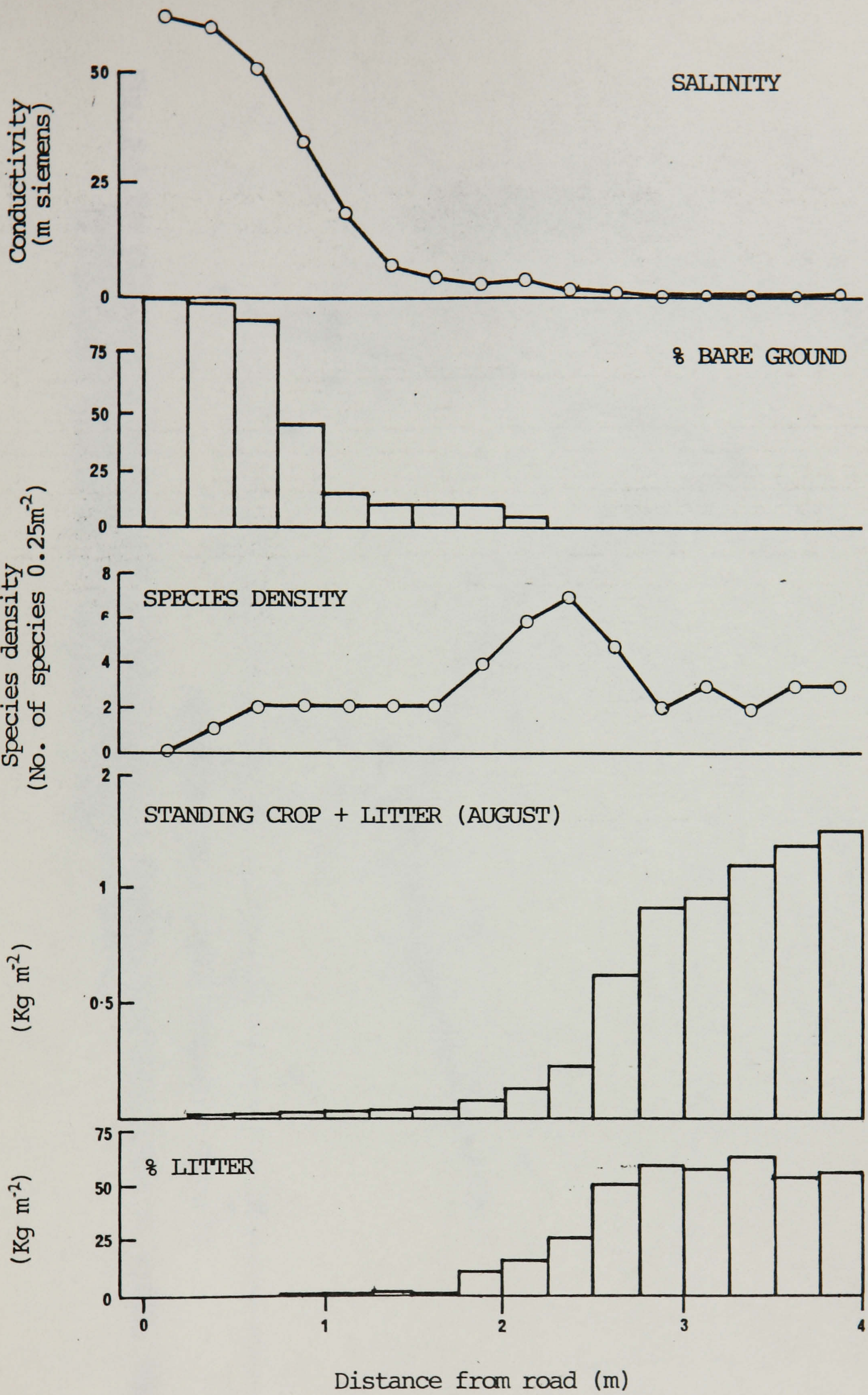
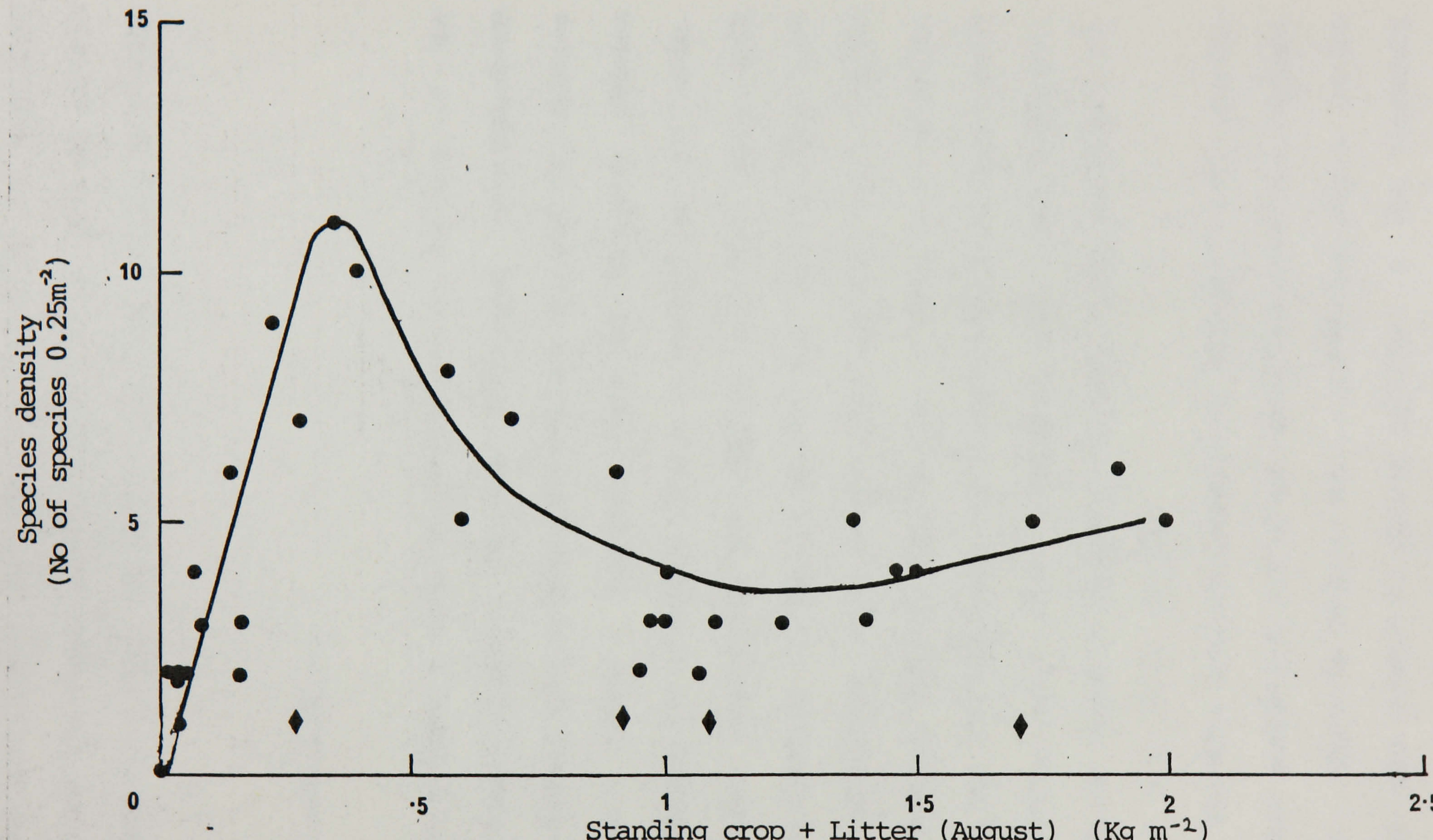


Fig. 5.8 Changes in salinity, % bare ground, species density, total standing crop plus litter and %litter in a transect at right angles to the Al, Seghill.



<u>Fig. 5.9 The relationship between species density and the standing crop-plus-litter in August, for samples at different distances from the Al at Seaton Burn and Seghill.</u>
(♦ = Quadrats containing only *Agropyron repens*)

further slight rise at the far end of the transect. Only one of the transects used for this figure had quadrats dominated by Agropyron repens. The results for these quadrats did not fit in with the pattern of the other quadrats. They are shown in Fig. 5.8 by different symbols.

Species and site ordinations.

Two computer ordination techniques were used for analysis of the data from the princepal survey. Decorana (DEtrended CORrespondence ANAlysis) is a sophisticated ordination technique designed for species in sample data (Hill 1979a). Twinspan (Two Way INdicator SPecies ANalysis) is a program for arranging data in an ordered two way table. This works by first classifying the samples and then using this classification to classify the species so that the results have some similarity to an ordination axis except that species with similar occurrences are grouped, and odd samples are placed in a discrete position which is not necessarily at the intermediate position it would occupy on an ordination axis. Both techniques were used throughout this project with the standard parameter settings (refer to manuals for discussion of use, Hill 1979a, 1979b).

Analysis of the data used the presence or absence of each species in each of the nine quadrats at the sites, in effect using the quadrats as separate sites. Using the data in this way, Twinspan gave a series of divisions which were related to species position in the transects (Fig. 5-10) and they reflected the groupings suggested by the use of local frequency. The species which tend to occur nearest the road were at one end and those which occur furthest away from the road at the other end. Position of species on the first axis produced by Decorana was also related to position in the transects (Fig. 5.11). Thus this

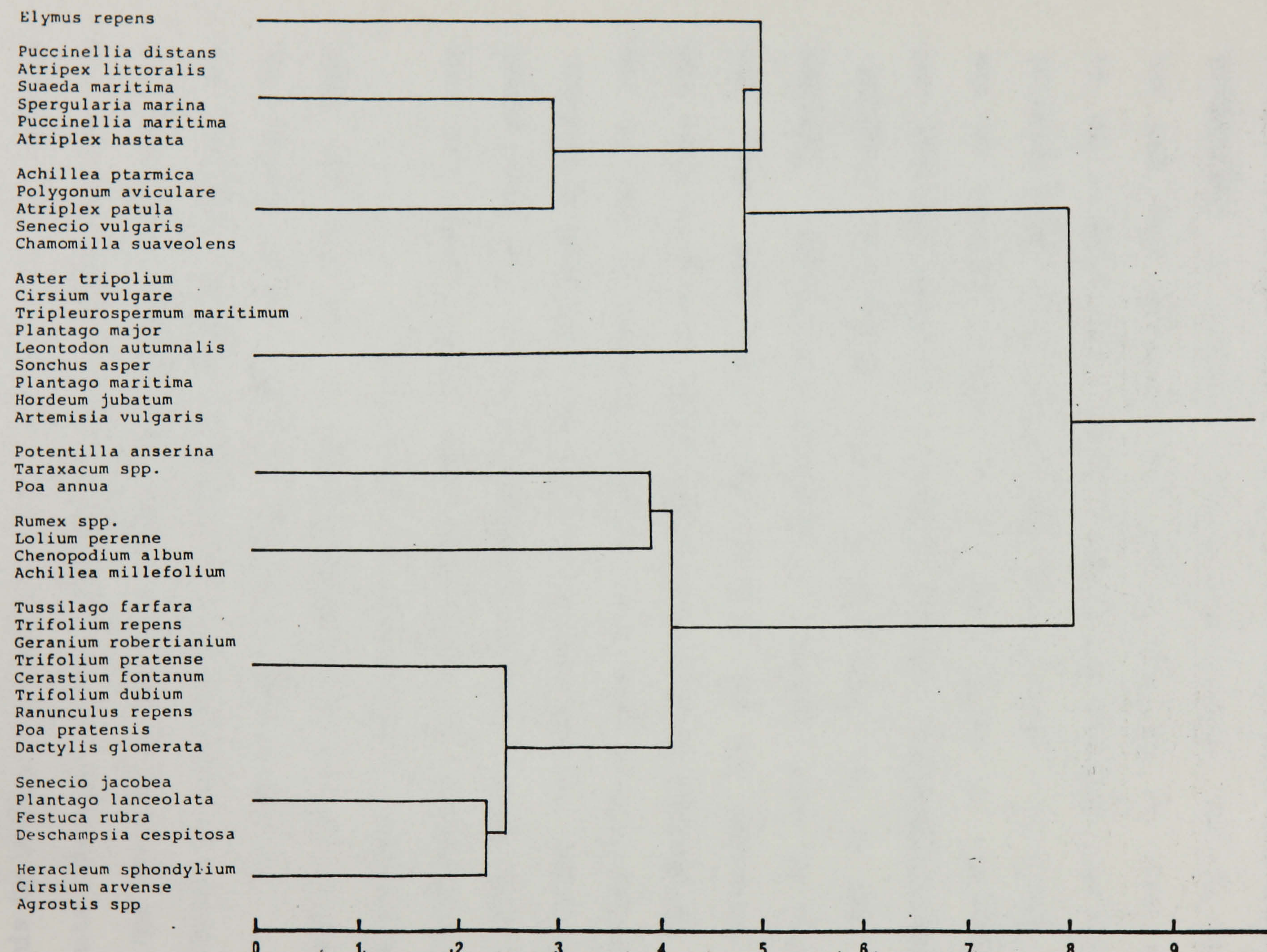


Fig. 5.10 Dendrogram illustrating twinspan anaylsis of species association using species presence in each quadrat.

axis would appear to be related to salinity. An attempt was made to confirm this by calculating the correlation between the co-ordinates for each site (the mean of the position of the nine quadrats for the site) and the salinity at the site. This demonstrates that the 1st axis is strongly related to salinity, while the 2nd or 3rd are not (Table 5.1). The 2nd axis may be related to soil water status, for species known to be tolerant of drought occur at the top and those known to be tolerant of waterlogging at the bottom.

The co-ordinates for each site were plotted onto the same ordination (Fig. 5-12). This was done separately for the two verges and in each figure the sections of road have been indicated by numbers. The relative position of sites from different sections of the Al are distinct. The Morpeth by-pass sites would appear to be drier than the rest and reference to the original data shows that they are characterised by such species as Geranium robertianum, Plantago lanceolata, and on the more saline soils Matricaria maritima, Tripleurospermum maritima, Senecio vulgaris, Plantago maritima and Plantago major all of which occur in a similar position on the ordination (Fig 5.11). Much of this road has been built using material which is very well draining and prone to drought. The sites on the Al near Seaton Burn on the other hand are on heavy clay and are characterised by such waterlogging tolerant species as Deschampsia cespitosa, Heracleum sphondylium and in the saline soils Spergularia marina, Puccinellia maritima, Hordeum jubatum, Atriplex spps and Polygonum aviculare. All of which occur at the bottom of the ordination (Fig. 5.11). The ordination also indicates that the Seaton Burn sites tend to be more saline than most of the other sites, as they occur more to the saline end of Axis 1.

The sites from the other sections of the Al are more intermediate in position on Axis 2 and more variable in position on Axis 1. This

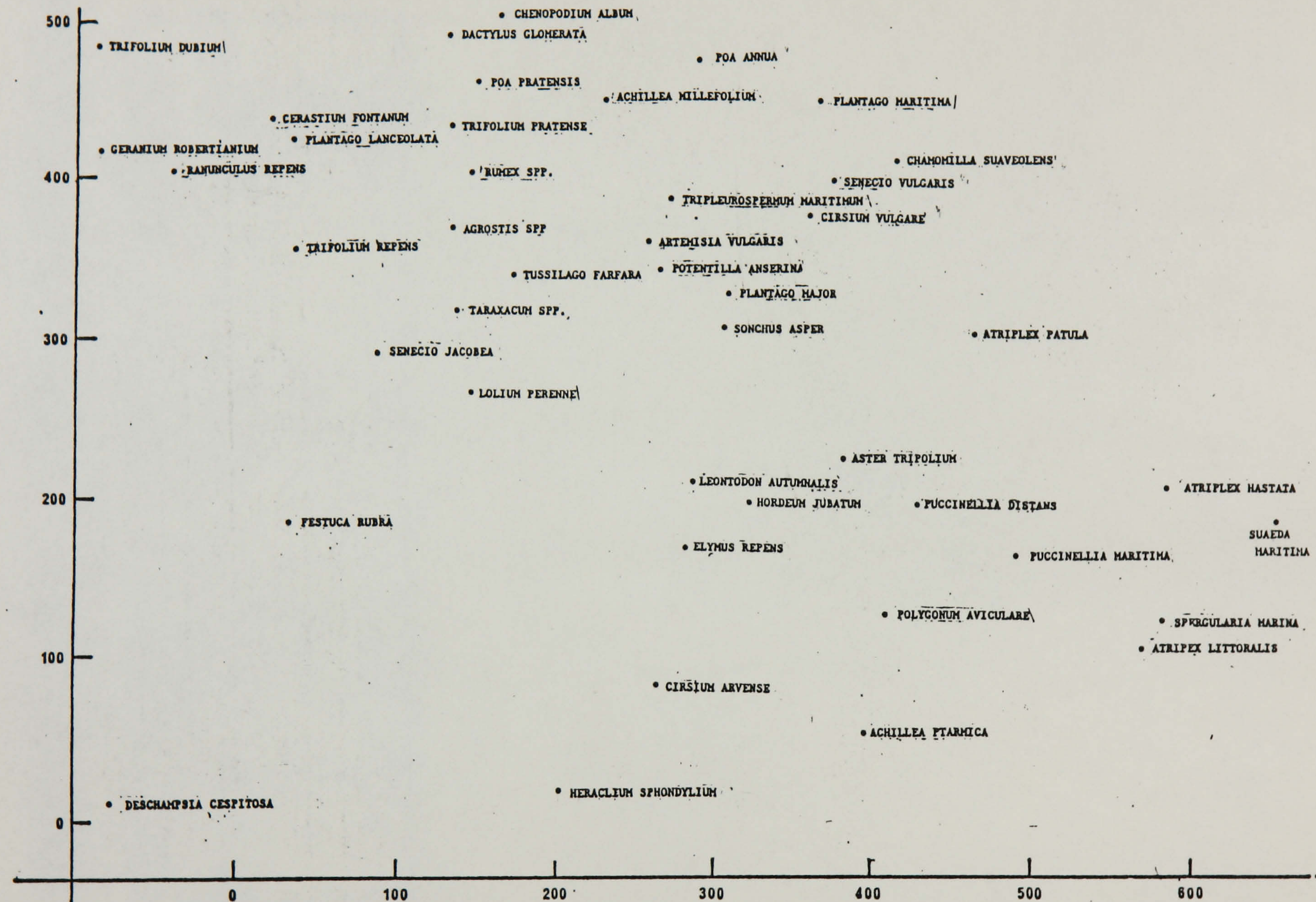


Fig. 5.11 Ordination of species on two axis by means of Decorana using species presence in each quadrat.

Table 5.1 Correlation between the position of 200 sites on the ordination axes shown in Fig. 5.11 and site salinity

Axis	Correlation coefficent	F-Statistic	Probability
1	0.583	101.78	0.0001
2	0.208	9.01	0.0030
3	-0.127	3.25	0.0727

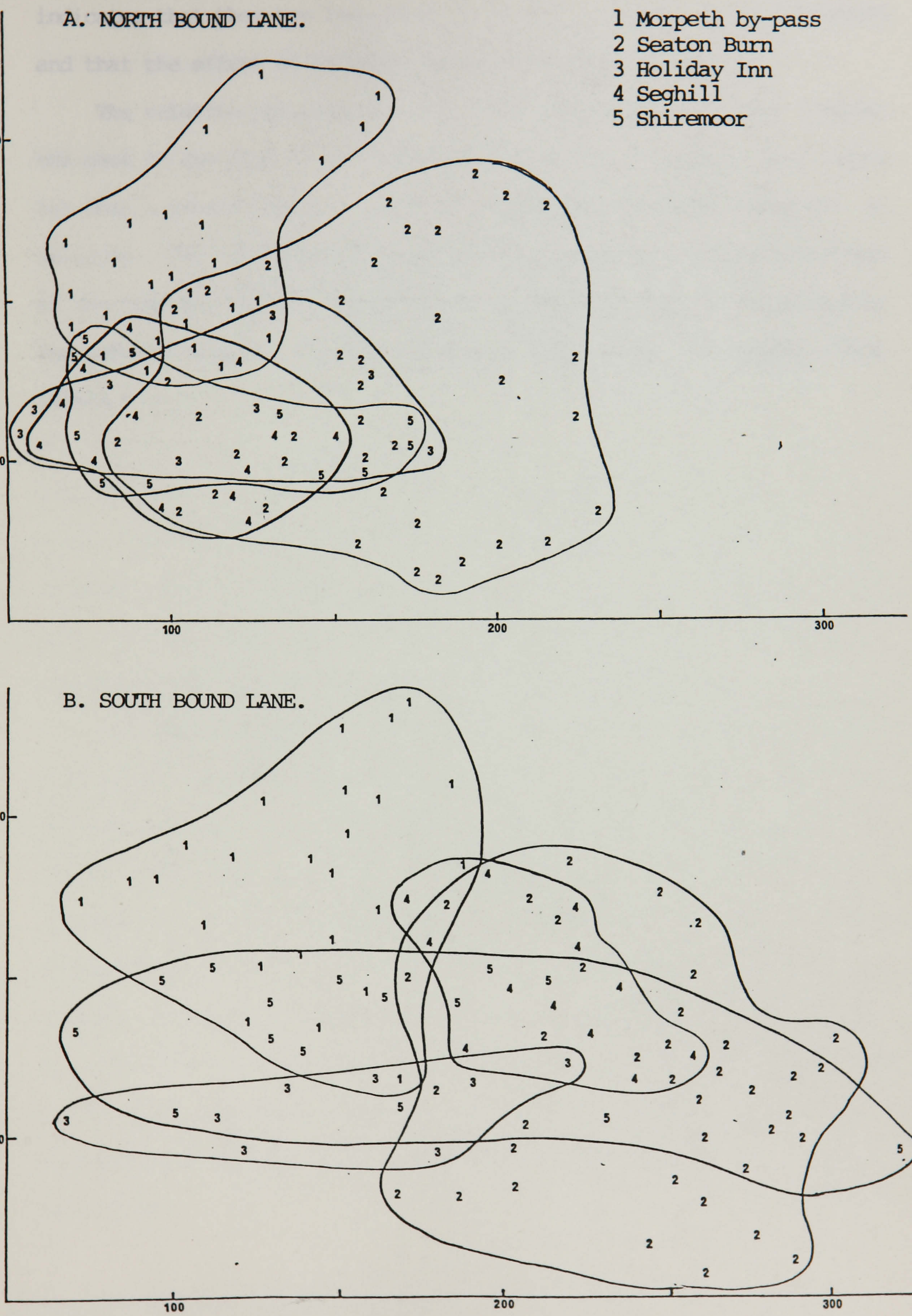


Fig. 5.12 Ordination of sites by means of decorana using species presence in each quadrat.

indicates that they are less prone to either drought or waterlogging and that the effect of salinity is more variable.

The relative position of sites from each section of road remains the same in the plot of the north bound lane sites except that there has been a general shift to the left indicating a general reduction in salinity. The difference in soil salinity between sites on either side of the road and between the different sections of road are confirmed by the average salinity for each section of road shown in chapter Four (Table 4.4).

Chapter Six. The effects of salt on establishment and growth.

Introduction

In Chapter Five it was shown that on saline roadsides species occur in distinct zones and that the zonation correlates with soil salinity. The simple and obvious explanation for such a distinct zonation is in terms of salinity tolerance determining how close to the road a species can exist, and competition from glycophytes controlling the invasion of salt tolerant species into the non-saline zone. There must be some doubt, however, whether competition is the sole factor restricting salt tolerant species to the saline zone because there are areas on roadsides where maritime species have not invaded bare, non-saline soil that is adjacent to the saline strip.

This chapter describes laboratory and field experiments which investigate the effects of salt and competition on the establishment of some maritime species. Initially the relative salt tolerance of species was examined using nutrient culture and varying salt treatments. Further experiments were on the effects of salt on the establishment of selected species in garden and roadside plots, in the presence and absence of competition. These experiments showed there was a difference in response of plants between the nutrient culture and field plot experiments so two additional experiments were then undertaken to examine the growth on garden and roadside soil in the laboratory.

Nutrient culture and salt response.

Eight roadside species were grown in sand culture and subjected to

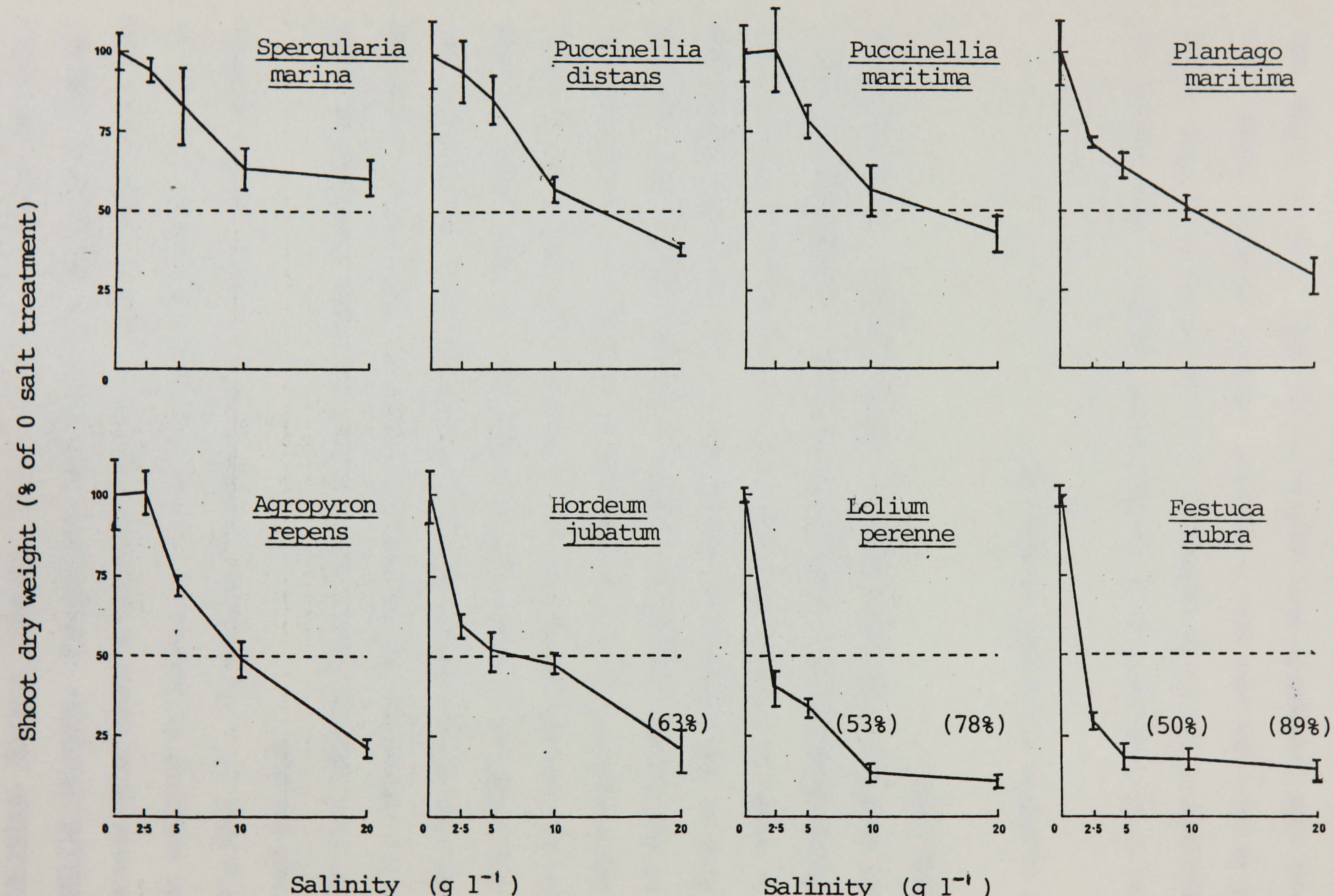


Fig. 6.1 Mean shoot dry weight of plants grown in sand culture supplied with 0,2.5,5,10 and 20 g NaCl l . Dry weights are shown as percentage of control; percentage dead plants are shown in brackets.

a range of salt treatments. The species used were Agropyron repens, Festuca rubra, Hordeum jubatum, Lolium perenne, Plantago maritima, Puccinellia distans, Puccinellia maritima and Spergularia marina. Plants were grown under artificial light in a growth room using the methods outlined in Chapter 2. The salt treatments were 0, 2.5, 5, 10 and 20 g NaCl l^{-1}. Plants were harvested after twelve weeks growth, dried and weighed.

The nine species showed significantly different reactions to salt (Fig 6.1). While the dry weight of all species fell with increasing salinity, the effect varied markedly between species. By plotting the final dry weight as a percentage of the weight on zero salt it was possible to rank the species tolerance to salt using the point at which final dry weight fell to fifty per cent of the control. Individuals of three of the species, Agropyron repens, Lolium perenne and Festuca rubra died at the highest salt treatments and in these cases percentage death is shown in brackets in Figure 6.1. The order of salt tolerance was: Spergularia marina > Puccinellia maritima = Puccinellia distans > Plantago maritima = Agropyron repens > Hordeum jubatum > Lolium perenne = Festuca rubra.

Growth in garden plots with competition

Two trials were set up at the University Garden. The layout of one replicate of the first experiment is shown in Fig. 6.2. The whole 2.5 x 2.5m plot was sown with a roadside amenity mixture (Chap. 2). Different salt treatments were applied to the four 1.25 x 1.25m sub plots and into each of the four 0.3 x 0.3m squares within each subplot were sown one of four maritime species, Plantago maritima, Puccinellia distans, Puccinellia maritima or Spergularia marina. The four salt treatments were 0, 250, and 750 g NaCl m^{-2} applied each fortnight. The

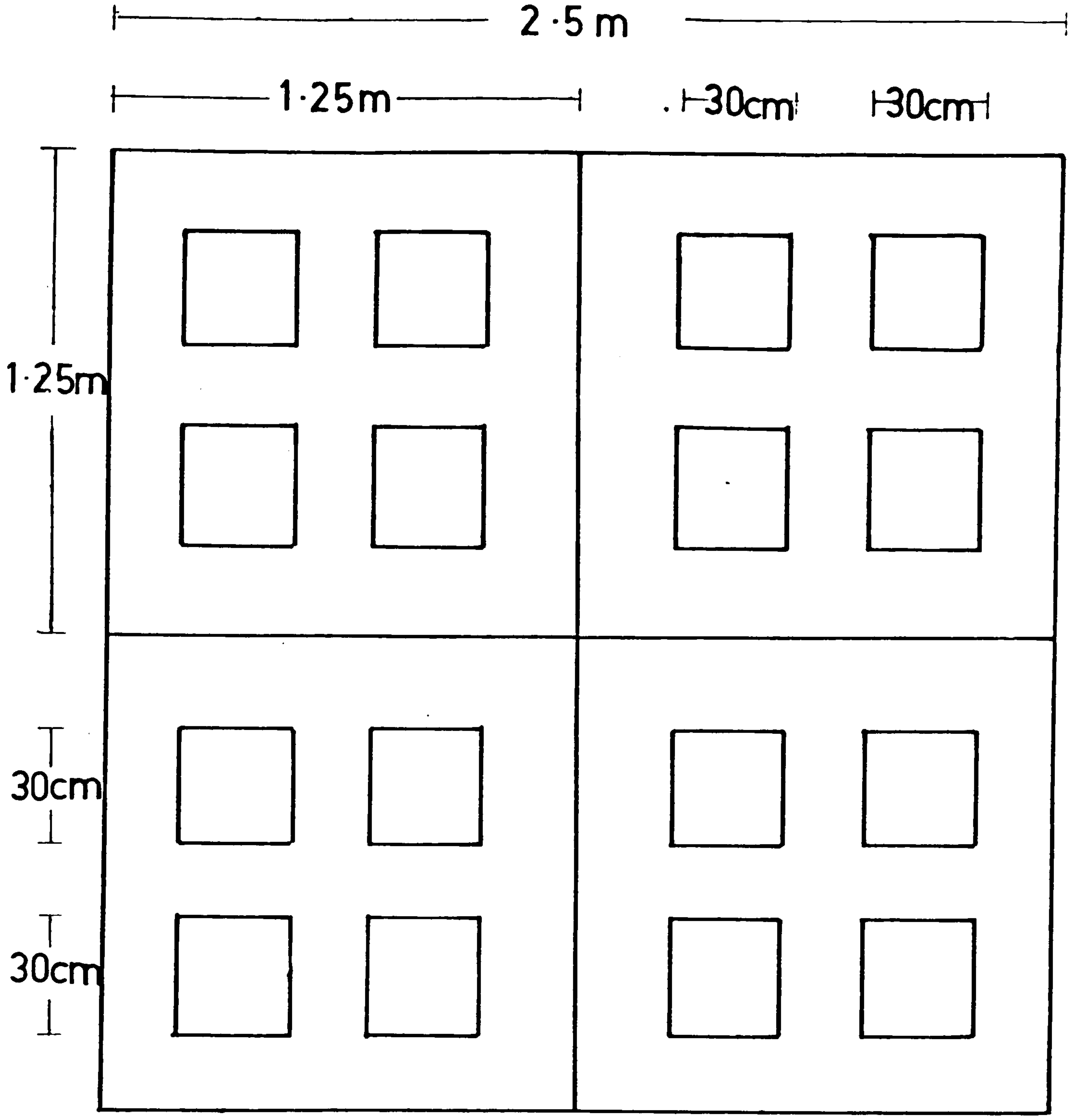


Fig. 6.2 Establishment of maritime species in a experimental grass sward treated with different levels of de-icing salt; layout of one replicate plot. The whole 2.5 x 2.5 m plot was sown with amenity mixture, each 1.25 x 1.25 m sub-plot received a different salt application and within each sub-plot one of four maritime species was sown in each of the 0.3 x 0.3 m squares.

position of treatments and species within plots was chosen at random.

The plots were sown in July 1980 with the amenity grass seed mixture (Chap. 2) and with the seed of maritime species in September. They were salted from 1st November until March 15th for the next two winters. The mean salinity (expressed as conductivity) of soil samples collected from each salt treatment is shown in Table 6.1. As expected, the conductivity correlated with salt application rate. The conductivities were similar to those of soil samples from roadsides as shown in Chapter 4. The conductivity of soils receiving the high salt treatment was similar to that of a roadside soil supporting only the maritime species while the conductivity of the low salt treatment was similar to that of a grass sward damaged but not killed by salt.

In June 1981 the cover of all species occurring in each of the squares originally sown with maritime species, was measured using mean local frequency. These results are also shown in Table 6.1. The cover of the original amenity sward was decreased by salt treatment. The small remaining cover of these species at the higher salt treatments was usually due to a few individuals surviving on the edges of the plots. Because of this it might be best to ignore cover of less than 5%. The maritime species established only in the grass swards that were treated with the two highest levels of salt (500 and 750 g per fortnight). Plantago maritima had significantly higher cover than the other three species. Puccinellia maritima was the only species that did not establish in the medium (500 g per fortnight) treatment.

Growth in garden plots without competition.

In parallel with the competition experiment, another trial was undertaken which examined establishment on bare garden soil treated with the same salt levels. Three maritime species were used, Plantago

Table 6.1 Establishment of maritime species in July, nine months after sowing in an amenity mixture grass sward treated with de-icing salt.

SALT TREATMENT (g m^{-2} per fortnight for 5 months)	0	250	500	750
SOIL SALINITY (conductivity m siemens)	0.28	4.4	7.5	15.2
MEAN LOCAL FREQUENCY: Original amenity mixture	100	98.1	74.0	11.2
MEAN LOCAL FREQUENCY: Plantago maritima	0	0	25.5	89.5
MEAN LOCAL FREQUENCY: Spergularia marina	0	0	2.5	58.7
MEAN LOCAL FREQUENCY: Puccinellia distans	0	0	1.25	44.5

maritima, Puccinellia distans and Spergularia marina, as well as the amenity seed mixture used to create the sward in the experiment just described. There were eight 20 m^2 replicate plots each divided into four salt treatments each of which contained four 250 cm^2 plots which were sown with a different species or the amenity seed mixture. The position of salt treatments and sown species was chosen at random.

The plots were sown in October 1980 and salted with the same levels of NaCl at the same frequency from then until March 15th 1981. Plots were weeded of all other species once a month from March onwards and recorded in July 1980. The cover of plots containing the maritime species was measured using 50 randomly placed point quadrats and the density of seedlings was measured by counting the number of individuals in each plot (or when numbers were high the number in two randomly positioned 10 cm quadrats within a plot). In plots containing the amenity mixture the local frequency of the species present was measured.

Soil samples were collected from each salt treatment within each replicate plot at the same time as the vegetation was recorded and later measured. The soil conductivities (Table 6.2) were significantly higher than those of the previous experiment. This may be because in that latter experiment the salt was applied to a grass sward. Decreased salinity in soils with vegetation cover was also noticed on the roadside and may be caused by the vegetation decreasing evaporation or by maintaining soil structure or drainage.

Application of salt reduced the establishment and growth of the species in the amenity mixture, as in the previous experiment. As the soil salinity was so variable within treatments the effects on the amenity species are most clearly seen by plotting the cover of each species against the soil salinity rather than the salt application rate (Fig 6.3). Lolium perenne showed the greatest salt tolerance,

Table 6.2 Establishment of maritime halophytes and an amenity seed mixture in garden plots treated with different levels of de-icing salt: soil conductivity.

TREATMENT	Control	Low Salt	Medium Salt	High Salt
SALT APPLICATION RATE (g per fortnight)	0	250	500	750
SOIL CONDUCTIVITY (m siemens)	0.51 (±0.02)	3.09 (±0.33)	8.4 (±0.71)	19.8 (±2.6)

Table 6.3 Germinating seedlings present in 100g of soil collected from roadside trials after incubation and watering with distilled water for six weeks followed by solution containing 8 g l^{-1} NaCl

PREVIOUS TREATMENT	Non salted		Salted	
WATERING REGIME	water	water +salt	water	water +salt
SEEDLINGS PRESENT				
Atriplex spp.	16	7	21	3
Festuca rubra	12	-	10	-
Trifolium repens	15	-	16	-
Spergularia marina	-	-	15	-
Puccinellia distans	-	-	4	-

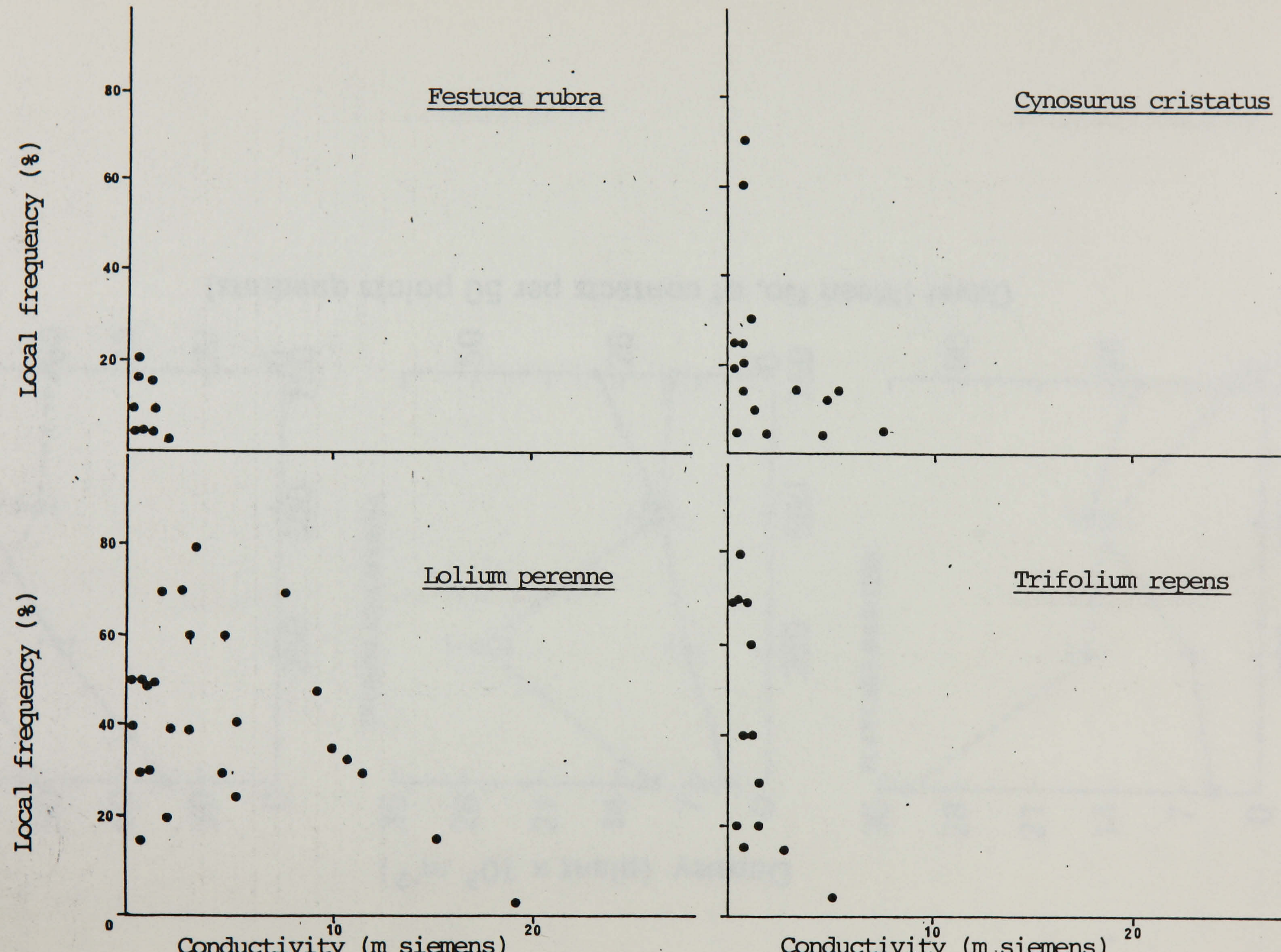


Fig. 6.3 Response of species in the amenity mixture to salt application. Local frequency is plotted against soil salinity (expressed as conductivity).

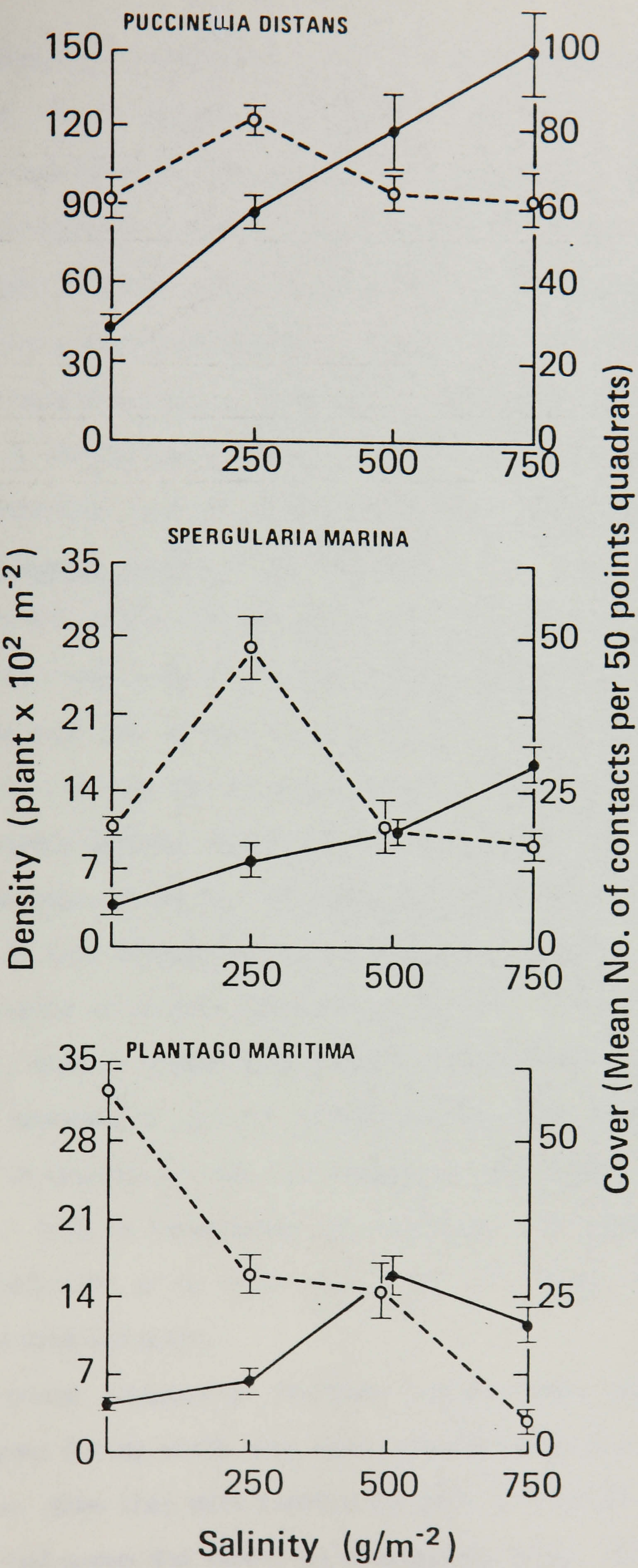


Fig. 6.4 Establishment of maritime species 9 months from sowing in bare garden plots treated with different levels of de-icing salt; cover(—●—) and density(-○-)plotted against salt application rate.

establishing and growing well in soils with conductivities of up to 10 m siemens while Cynosurus cristata established in soils with conductivities of up to 6 m siemens. The other t species declined in all salt treated soils as compared with the control. The maritime species were affected differently by the salt treatments (Fig 6.4). When the plots were recorded in July 1981, the control non-saline soils surported only very small seedlings, many of which were red. In contrast in the salted treatments individuals were larger and showed no red pigmentation. By the time of recording both Puccinellia distans and Spergularia marina were beginning to flower in the salted treatments but not in the control plots. The results of recording the cover using randomly placed point quadrats showed a difference between treatments with the cover rising as the salt treatment increased (Fig. 6.4). This rise was not as spectacular as the observable difference between plants because the density of individuals tended to fall with increasing salt treatment. Plantago maritima's density fell with each increase in salt treatment, while Spergularia marina and Puccinellia distans showed an initial increase in density with the lowest salt treatment, then it dropped with further increases (Fig 6.4).

The increase in size of individuals more than compensated for the decrease in density so that the biomass of each species increased with salinity. This is illustrated by plotting the ratio cover/density against salinity, as in Fig. 6.5. In all three cases the ratio increased with salinity.

The plots containing maritime species were maintained for a further year during which they were weeded monthly and salted at the same rate. When they were finally recorded in August 1982, Plantago maritima had grown and showed no more pigmentation. The cover in the unsalted plots (Fig. 6.6) was not significantly lower than that in the salted plots. The cover of the other two species was still

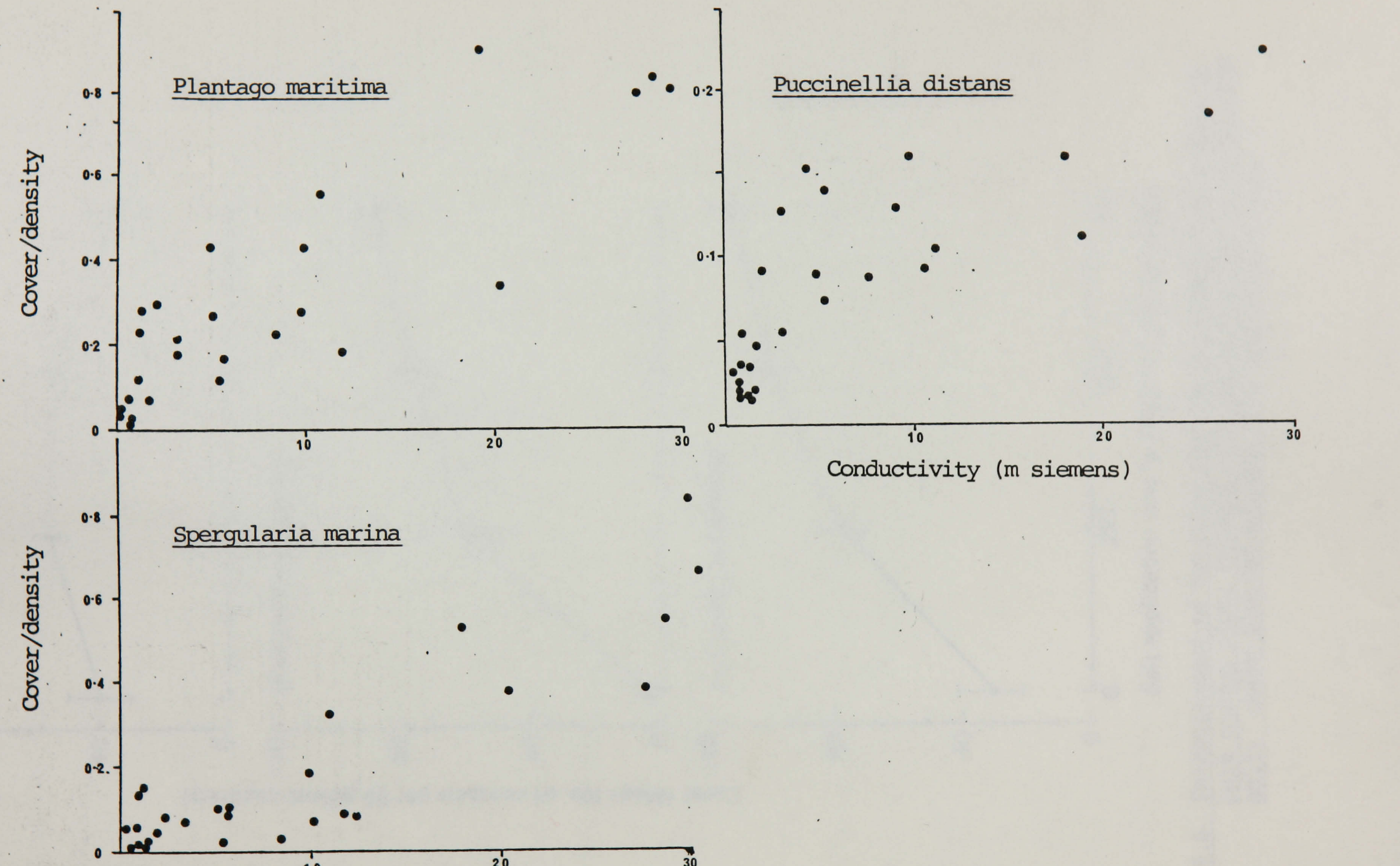


Fig. 6.5 Establishment of maritime species 9 months from sowing in bare garden plots treated with different levels of de-icing salt; the ratio cover to density plotted against soil salinity.

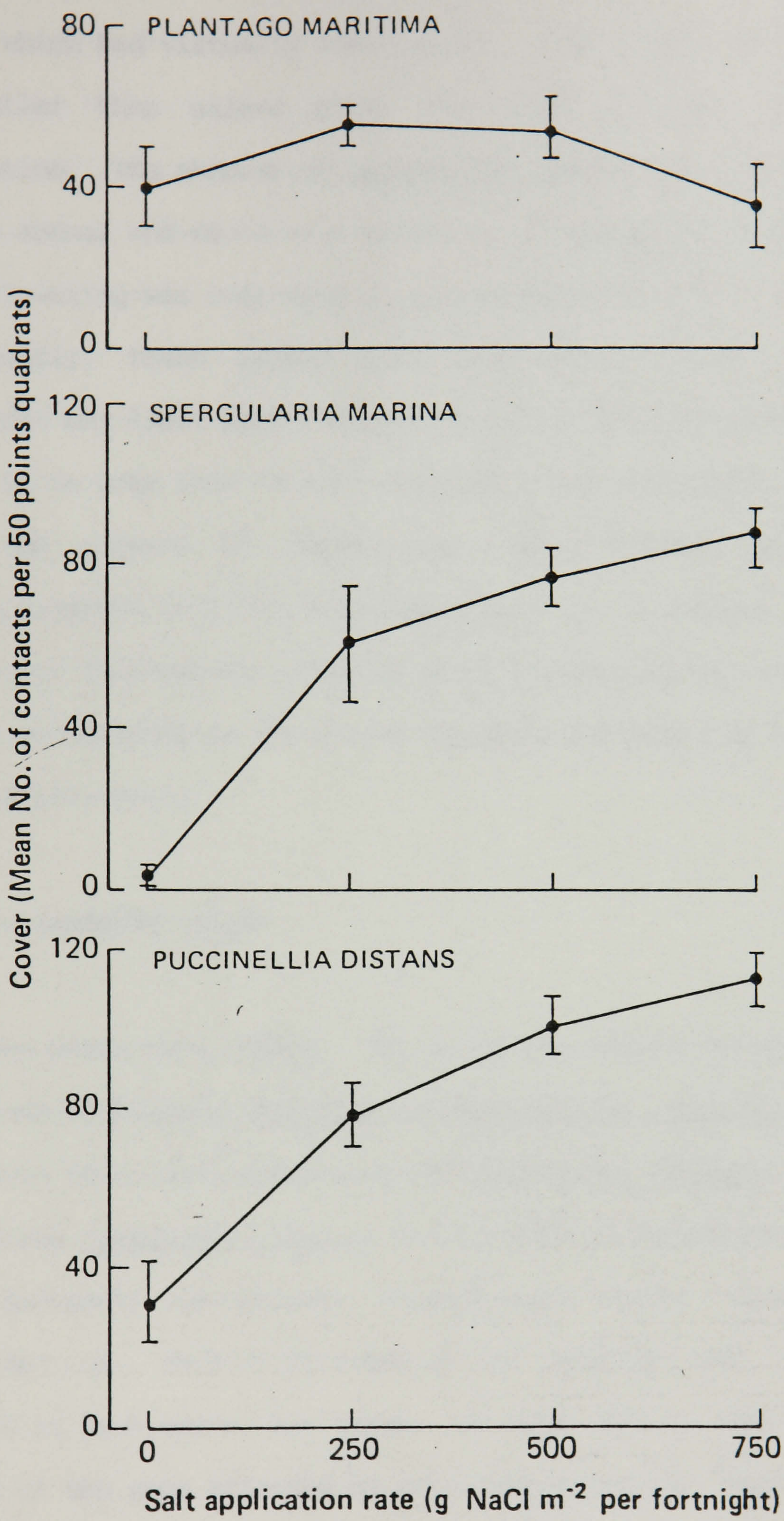


Fig. 6.6 Establishment of maritime species 21 months from sowing in bare garden plots treated with different levels of de-icing salt; cover plotted agianst salt application rate.

significantly lower in the unsalted plots especial for Spergularia marina, which had virtually disappeared. Individuals of both species were smaller than salted plots but they did not show much red pigmentation. The absence of Spergularia marina was presumably because it is an annual and would have needed to re-establish from seed. Very little flowering was ever seen in these unsalted plots.

Clearly, these garden plot experiments show that whilst competition may limit maritime species on non-saline soils, there also appears to be some form of salt requirement for successful establishment even in the absence of competition. The recovery of Plantago maritima suggests that the requirement may be transient. The first recording of these plots coincided with a period of drought and this may have contributed to the stress symptoms exhibited by individuals in the non-saline soils.

Growth in roadside trials

Three sites were chosen: The A1 at the Morpeth by-pass, which has populations of Plantago maritima and Puccinellia distans; the A1 at Seaton Burn which has populations of Puccinellia distans, Puccinellia maritima and Spergularia marina; and the A69 at Throckley which had no coastal halophyte populations. At each site, twenty strips, 9 x 1m were marked out. Each strip began at the roadside and ran at right angles to it back across the verge. At nine metres the strips were well out of the zone affected by salt from the road. Half the strips were cleared using a herbicide in June 1980. Any vegetation which survived this treatment was resprayed in August. The strips were in groups of four, one for each treatment combination (control, salt alone, salt and herbicide, herbicide alone). The salted strips were treated with 500 g NaCl m^{-2} per fortnight from November 1st 1980 until

March 15th 1981. The two sites with populations of maritime species were left to allow these plants to invade the strips naturally. The A69 site was sown with a seed mixture containing an equal quantity of Plantago maritima, Puccinellia distans and Spergularia marina in October 1980 at 120g m^{-2}.

The cover of all species present was measured in May 1981. For this, strips were divided into successive 50 cm wide quadrats running back from the road. Local frequency was recorded using a 1 m^2 quadrat divided into a 10 x 10cm grid. At the same time, soil samples were taken which were later tested for conductivity. The mean local frequency for species in each quadrat is shown in Figs. 6.7 to 6.9. All species are shown that had an average local frequency of more than 10% in at least one quadrat. The figures also show the salinity across the strips and the percentage bare ground for each quadrat.

The salinity of the salted strips was increased right across their lengths, but was highest next to the road due to the effect of salt splash from the road. The salinity of the unsalted strips was only high in the region affected by saltsplash, near to the road. The salted strips which were cleared of vegetation tended to have higher salinities away from the road than the uncleared strips. The vegetation in the uncleared strips appeared to have protected the soil from some of the salt as previously mentioned.

Of particular interest is the difference in the occurrence between treatments of three of the maritime species, Plantago maritima, Puccinellia distans and Spergularia marina. At all three sites these species established in the full length of the salted strip cleared of vegetation. In the non-salted strips these species were confined to the soil adjacent to the road where the salinity was raised by salt splash. The other maritime species, Puccinellia maritima was confined to a zone in the salted strips not much larger than that of the

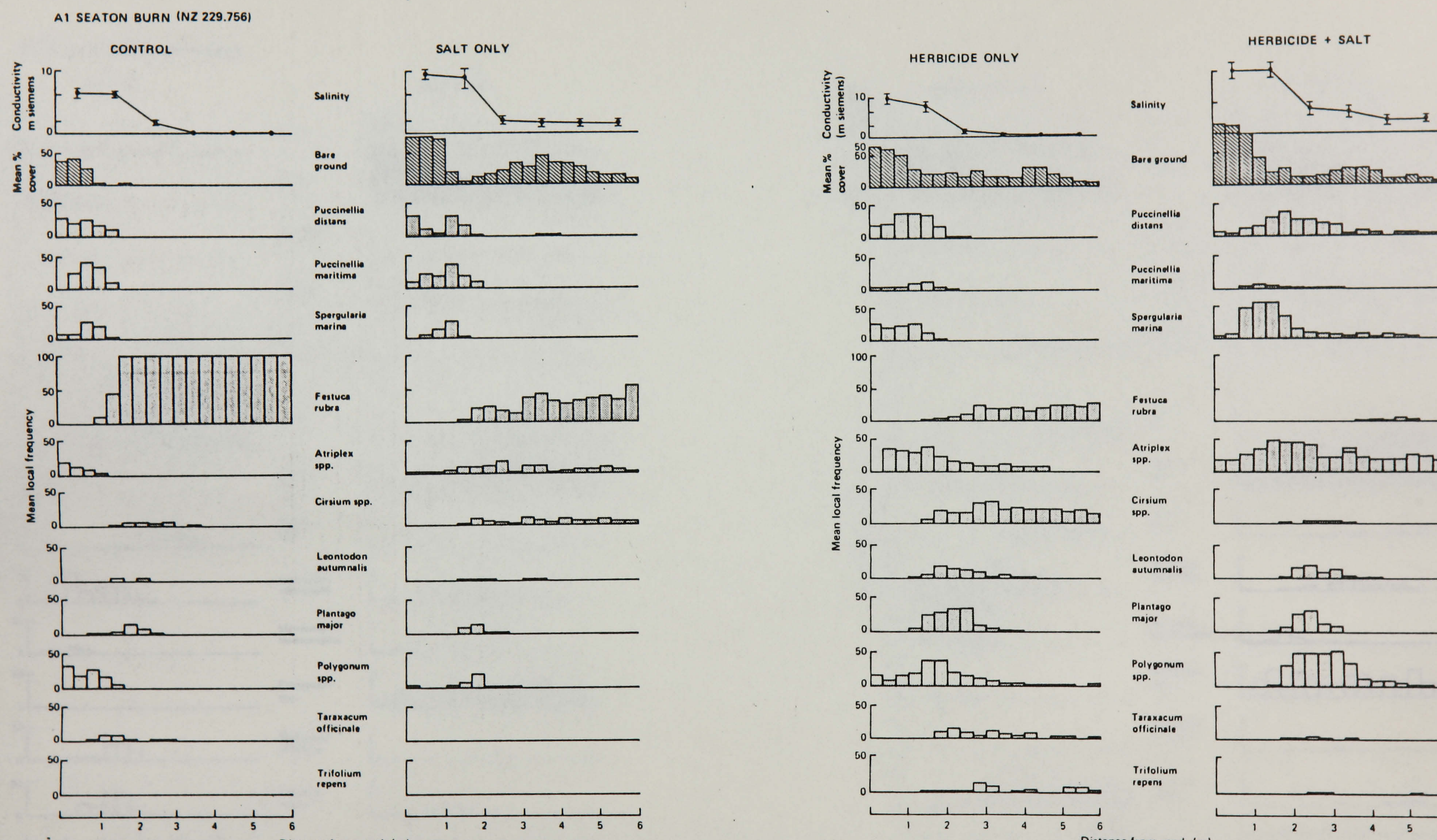


Fig. 6.7 Mean local frequency of species in metre wide strips running at right angles to the road which received one of four treatments (control, salt added at 500 g m per fortnight for 6 months, pre treated with herbicide to remove competition, salt and herbicide): A1 Seaton Burn (NZ 229.756).

Fig. 6.8 Mean local frequency of species in metre wide strips running at right angles to the road which have received one of four treatments (control, salt added at 500 g m per fortnight for 6 months, pre treated with herbicide to remove competition, salt and herbicide): Al Morpeth By-pass (NZ 181.862).

Fig. 6.9 Mean local frequency of species in metre wide strips running at right angles to the road which have received one of four treatments (control, salt added at 500 g m per fortnight for 6 months, pre treated with herbicide to remove competition, salt and herbicide): A69 Throckley (NZ 139.678).

unsalted strips. The strips which had not been cleared of vegetation prior to being salted contained fewer plants of maritime species in the zone outside the influence of saltsplash. Only Plantago maritima and Puccinellia distans established in these strips and both were infrequent, especially P.distans. There was no invasion away from the road in the control strips.

The other species occurring in the strips fell into one of three groups, depending on the response to the different treatments. The first group consisted of those species which normally only occur outside the saline zone. These species, Festuca rubra, Cirsium spp. and Plantago lanceolata (Figs. 6.7-6.9), declined or disappeared in the salted, uncleared strips and only occasionally re-established in the salted cleared strips, but re-established well in the unsalted, cleared strips. They would appear not to be tolerant of salt as they decline with its increase.

The second group of species consisted of, Leontodon autumnalis, Matricaria matricarioides, Taraxacum officinale, Plantago major and Trifolium repens. In the control strips, these species tended to occur adjacent to the road or just away from it. While they persisted or re-established in the salted treatments this tended to be further away from the road and their cover declined. In the unsalted, cleared strips they increased and invaded along the full length of the cleared area. Thus, these species which are normally confined to the road margin were able to spread when competition was removed. They would also appear not to be very tolerant of salt.

The last group consisted of Polygonum aviculare and Atriplex spp.. These species were confined in the control areas to a zone adjacent to the road. In the salt treatments, especially the cleared strips, cover of these species increased and they occurred across the full length of the strip. They established away from the road in the unsalted, cleared strips but not as successfully as in the salted strips. Thus these species were also confined to the road margin in the controls but unlike the previous group, they appeaed to be more tolerant of salt and consequently established and grew better when it was present. They are, presumably confined to the road margin by competition.

When these experiments were recorded invading seedlings were still small and there was still a considerable amount of bare ground. Although the sites were monitored once a month from when the germinating maritime species were first observed in the salted strips no seedlings of maritime species were recorded for the non-saline strips during this period. Thus, it would appear unlikely that it is competition which is excluding the seedlings.

After the sites had been recorded,100g samples of soil from the salted and unsalted cleared strips were taken into the laboratory. There they were kept moist in Petri dishes in the light and regularly turned. Any germinating seedlings were identified and recorded. After six weeks the soils were watered with a saline solution and recording continued. The results are shown in Table 6.3. While the maritime species appeared in the saline soils none appeared in the non-saline soils, even after these have been watered with a saline solution. This may have been because the seeds on the non-saline soils had germinated and died, and that they had not been inhibited by the lack of salt.

Growth on roadside and garden soil under laboratory conditions.

The experiments described so far demonstrated a remarkable reversal in the response of maritime species to salt treatments when growing on different substrates. Growth in nutrient culture was decreased by salt while for the same species on the roadside or in garden plots, it was increased. Consequently it was decided to grow two of the species, Plantago maritima and Puccinellia distans, on roadside and garden soil under laboratory conditions as well as in sand culture. The two species were planted as seedlings into pots of the three substrates, five individuals of one species per pot which were later weeded to three. There were four salt treatments (0, 1, 5, 15 g NaCl l^{-1}) and six replicates of each treatment/soil/species combination. All soils were treated using the regime described in Chapter 2 but the roadside and garden soil received no nutrients. The garden soil used was from a different part of the same plot as used in the previous experiment. The roadside soil came from the A69 at Throckley at three metres from the road and so was unaffected by salt. Saline soil was also collected from this site at 0.5 m from the road (i.e. from within the salt affected zone). This soil was also used in the experiment, but it received only the control treatment (0 NaCl).

In sand culture there was a significant decrease in final dry weight with increasing salt treatment for both species (Fig. 6.10). On the garden soil this was reversed with a significant increase in final dry weight over the control for Puccinellia distans at 5 g l^{-1} NaCl treatment and for Plantago maritima at 15 g l^{-1} NaCl. On the soil from the A69 there was no significant change in dry weight for Plantago maritima, and a significant decrease in final dry weight with increased salt for Puccinellia distans. For both species the final dry weight of plants grown on the saline soil collected adjacent to the road were significantly higher than any other treatment on either soil or sand culture. This soil was no more saline than the roadside soil treated with salt during this experiment (Table 6.4). Thus the remarkable difference in growth must have been due to some other property of the soil. One possibility is that this soil had a higher level of nitrogen due to input from passing vehicles. The plants grown in sand culture

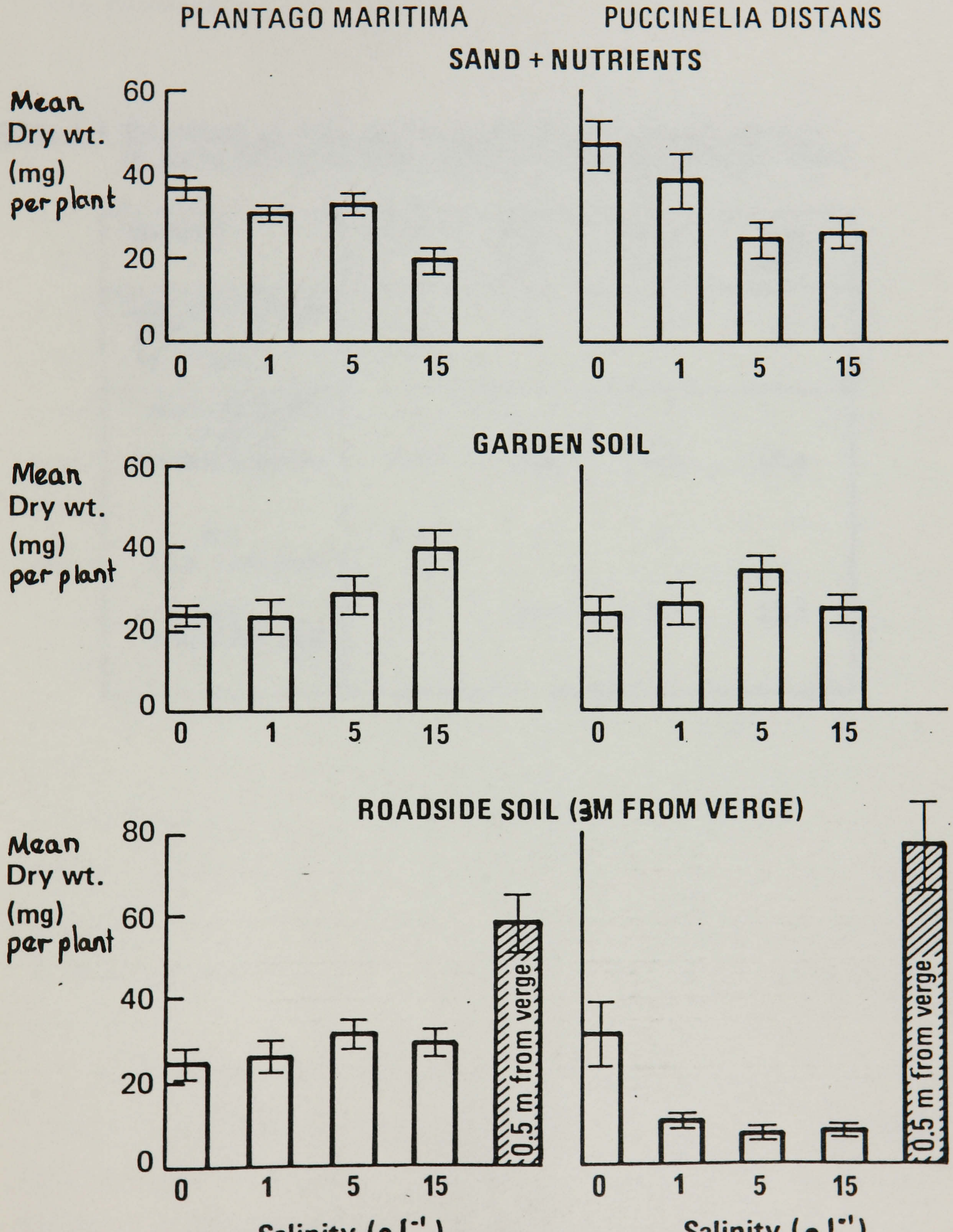


Fig. 6.10 Dry weight of two maritime species on garden and roadside soil, and in sand culture with different salinity regimes.

Table 6.4 The effect of salt on the growth of two coastal species on three different substrates: Soil conductivity.(m-siemens)

TREATMENT	Control	Low salt	Medium salt	High salt
SALT APPLICATION RATE ($g\ l^{-1}$ NaCl)	0	1	5	15
SOIL COLLECTED FROM:- Moorbank garden	0.65	1.9	5.2	13.4
A69 0.5m from road	4.8	-	-	
A69 8.0m from road	1.3	2.0	3.1	12.8

also received nitrogen as part of the nutrient treatment and it might be that it was the presence of nutrients which reversed the effect of salt treatments.

Nutrients and the effect of salt on growth.

To examine the effect of nutrients the previous experiment was repeated using the roadside and garden soils and two levels of salt treatment (5 and 15 g l^{-1} NaCl). Treatments were divided, half being given additional nutrients at 5 g l^{-1} per week. There were six replicates of each treatment combination. It was observed during the previous experiment that some of the salt-treated roadside soils dried out during the experiment, and once they had done so they did not re wet very well. It was thought that this may have been due to the salt causing deflocculation of the clay particles and with the resulting loss of soil structure. Drying-out of the roadside soils may have caused the decrease in final dry weight of Puccinellia distans. Because of this possibility, it was decided in this experiment to reduce the temperature of the Fisons cabinet by 5°C to 15°C and to increase the frequency with which solutions were applied. Additional applications of saline solutions were given on Wednesday, Friday and Sunday preceeded by waterings with distilled water to prevent build up of salt.

The final dry weights are shown in Fig. 6.11. This time there was a significant increase in final dry weight for both salt treatments over the control for both the garden and roadside soils. With the exception of Plantago maritima on the garden soil receiving 15 g l^{-1}NaCl the nitrogen-treated pots showed a reversal of this effect, with a decrease in final dry weight with increased salinity.

The relative final dry weights on the saline soil from beside the road were also of interest in this experiment. As in the previous experiment the final dry weight of both species was higher when grown on this soil than on the soil from three metres away from the road even when the latter was treated with salt. However, with additional nutrients the final dry weight of plants grown on the two roadside soils was not significantly different. This result suggested that the extra growth achieved by plants on the soil from beside the road was due to additional nutrients in the soil. The most likely nutrient to cause such an effect with these soils is nitrogen.

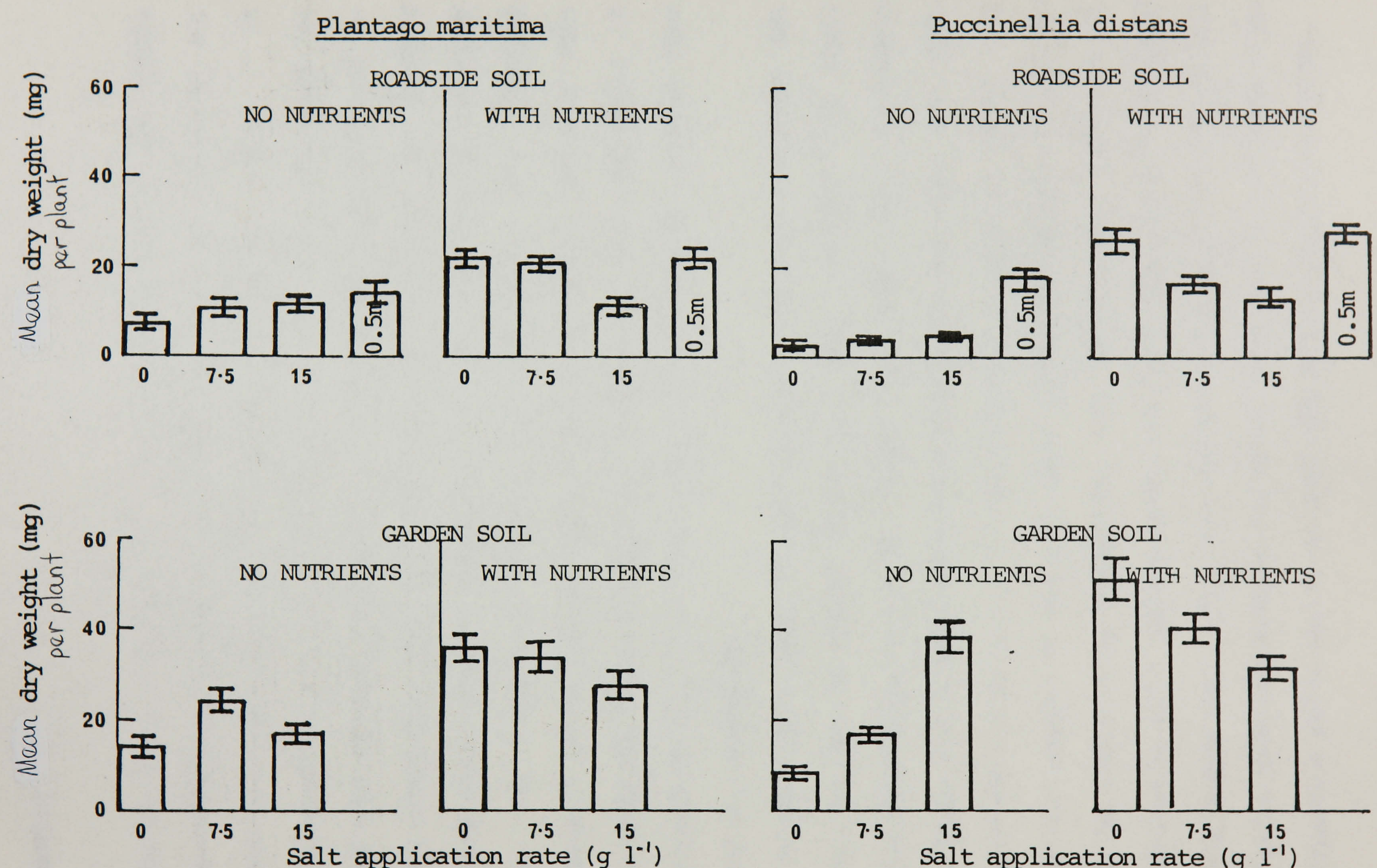


Fig 6.11 The effect of additional nutrients on the growth of two maritime species on two soils, under different salinity regimes.

Chapter Seven. The effects of sub-zero temperatures.

Introduction

The sea has a moderating infleunce on the climate of the nearby land so that plants of maritime salt marshes, dunes and cliffs are not subjected to the extremes that may occur even a few km inland . As winter temperatures are much less severe at the coast it might be expected that maritime plants would not have a very great tolerance to freezing conditions. This raises the question of whether low freezing resistance might limit the invasion of inland habitats by maritime species. To investigate whether this was likely the freezing resistance of all of the species for which seed was available were tested using the controlled freezing cabinets in the Department of Agricultural Biology. Two common non-maritime roadside species were included for comparison.

An additional reason for investigating freezing resistance was that salt is known to effect resistance to other stresses (see chapt 1). The observation in the last chapter that under field conditions plants given salt survived much better than those that were not given it may be related to this. A salt/freezing interaction might help explain some aspects of the confinement of maritime species to saline soils. To examine this possibility six species were selected for further work in which their freezing resistance was compared when grown with and without salt. In later experiments the effect of varying salt application rates was examined but during this work the equipment began to malfunction and it had to be abandoned without conclusive results.

Experiments and results

Eleven species were chosen for the initial testing of relative freezing resistance; the maritime species Aster tripolium, Cochlearia officinalis, Plantago coronopus, Plantago maritima, Puccinellia distans, P.maritima, Spergularia marina, Suaeda maritima and the American adventive Hordeum jubatum, together with the two common roadside grasses Agropyron repens and Lolium perenne. Seed was collected from roadside sites for all the species except Lolium perenne. In this case a commercial source was used, the cultivar S23, which is of known freezing resistance (Fuller and Eagles 1978; Davison and Bailey 1982). Plants were grown, five to a pot, in sand culture using the techniques described in Chapter 2. In this initial trial all species were placed in the same cabinet to ensure uniform conditions. After six weeks growth, plants were hardened for two weeks and then transferred to the freezing cabinet. The controls remained in the hardening regime. The cabinet was programmed to give nightly freezing cycles, each night going down to successively lower temperatures, starting at -1° C and going in 2°C steps to -11°C. After each night two pots of each species were removed and replaced in the hardening regime. Two days after the last pots had been removed, the cabinets were returned to the original growth conditions. Plants were maintained for four weeks and then scored for survival. New growth of tillers or adventitious roots was regarded as evidence of survival. The position of the species and treatments was chosen at random at all stages in the experiment. L.T. 50's (the temperature giving 50% kill) and 95% confidence limits were calculated using probit analysis. This technique, however, cannot be used where there is only one result between 100% and 0% survival and so there are no confidence limits for a few species. Survival curves are shown in Fig 7.1.

This initial trial had limited replication and the 95% confidence

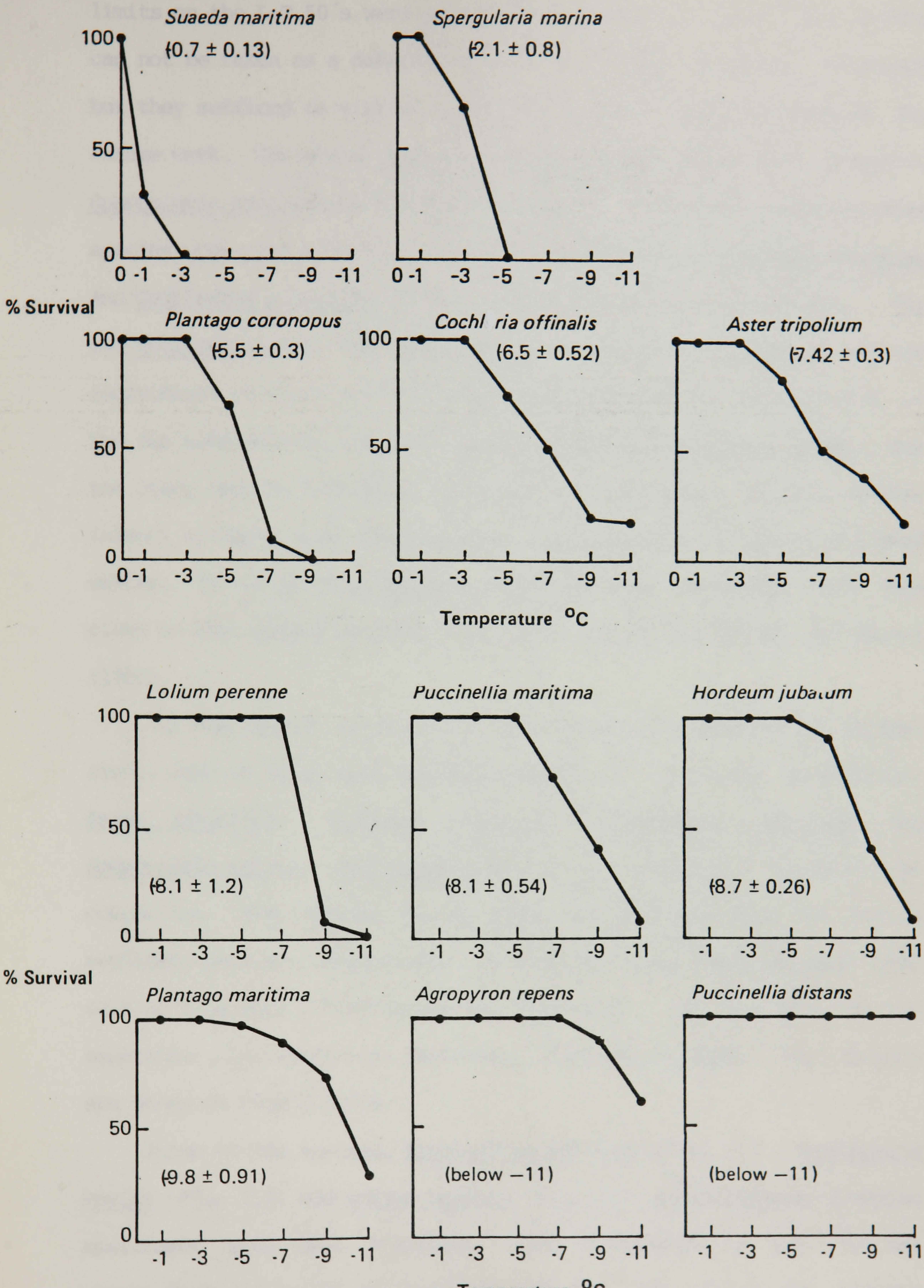


Fig. 7.1 Percentage survival of eleven roadside species at sub-zero temperatures. (L.T.50 in brackets)

limits on the L.T.50's were quite high. Because of this, these results can not be taken as a definitive test of species freezing resistance but they sufficed to give an indication of relative resistence for future work. The annual Suaeda maritima and the short-lived perennial Spergularia marina were the most sensitive. Many of the other maritime species were also sensitive including, surprisingly, Plantago maritima and Cochlearia offinalis, both of which grow in montane habitats. The two Puccinellia spp. were more tolerant, especially P. distans, all the individuals of which survived the lowest temperature. The L.T.50's of the two non-maritime species, Lolium perenne and Agropyron repens, put the other results into perspective as both regularly survive winters inland, although some individuals of L. perenne can be killed in a hard winter. The LT 50 of L. perenne cv S23 in this experiment was very close to that quoted by Fuller and Eagles (1980) and Davison and Bailey (1982).

Of the species in the first trial, five were selected for further study, four of which were maritime species of differing sensitivity: Aster tripolium, Plantago maritima, Puccinellia maritima and Spergularia marina. Lolium perenne cv. S23 was again included for comparison. With reduced species there was enough room for twelve replicate pots per temperature. Half of the pots were treated with salt at 2.5g NaCl l^{-1} throughout the experiment. At the end of the experiment, survivors were harvested, dried and weighed. The results are shown in Figs 7.2-7.6.

Three of the species, Puccinellia maritima (Fig. 7.2), Spergularia marina (Fig. 7.3) and Lolium perenne (Fig. 7.4) showed greater freezing resistance with salt treatment. The difference in L.T. 50 was particularly large for Puccinellia maritima. The final dry weights from these experiments, presented on the same figures also showed a decline with decrease in temperature. In the case of Puccinellia

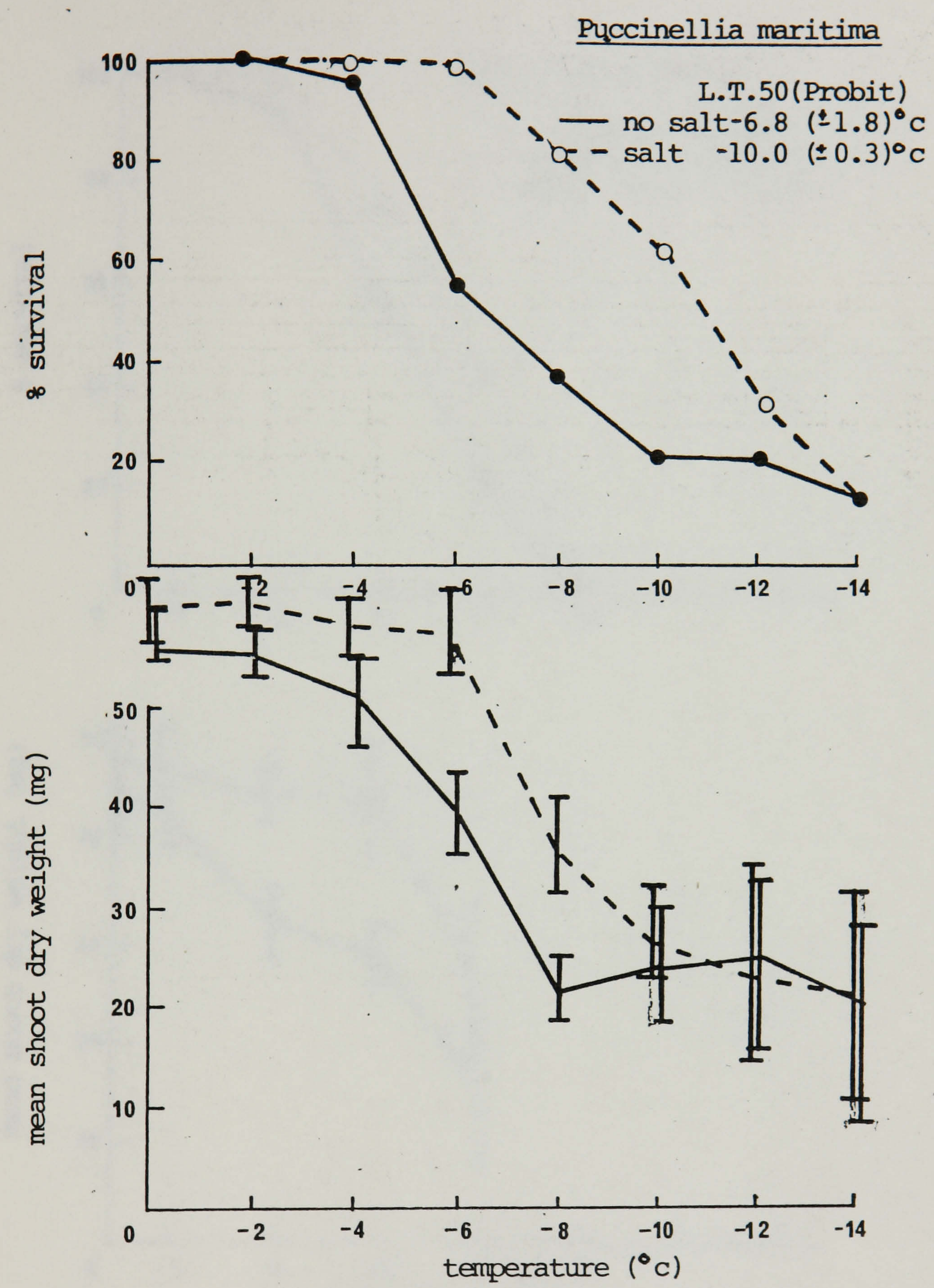


Fig. 7.2 Percentage survival and dry weight of shoots of Puccinellia maritima four weeks after exposure to sub-zero temperatures.
— no salt, - - salt.

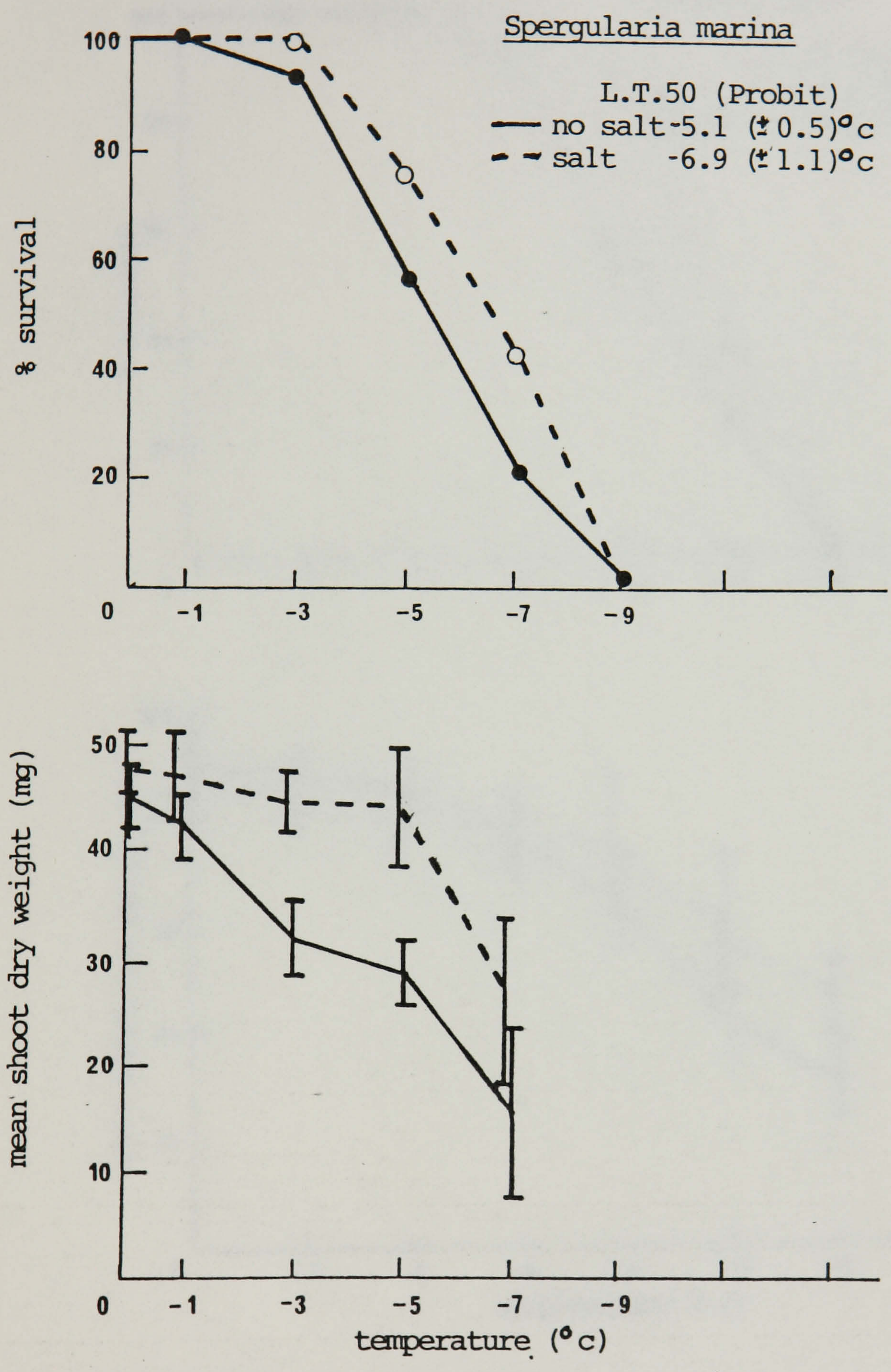


Fig. 7.3 Percentage survival and dry weight of shoots of Spergularia marina four weeks after exposure to sub-zero temperatures. — no salt, - - salt.

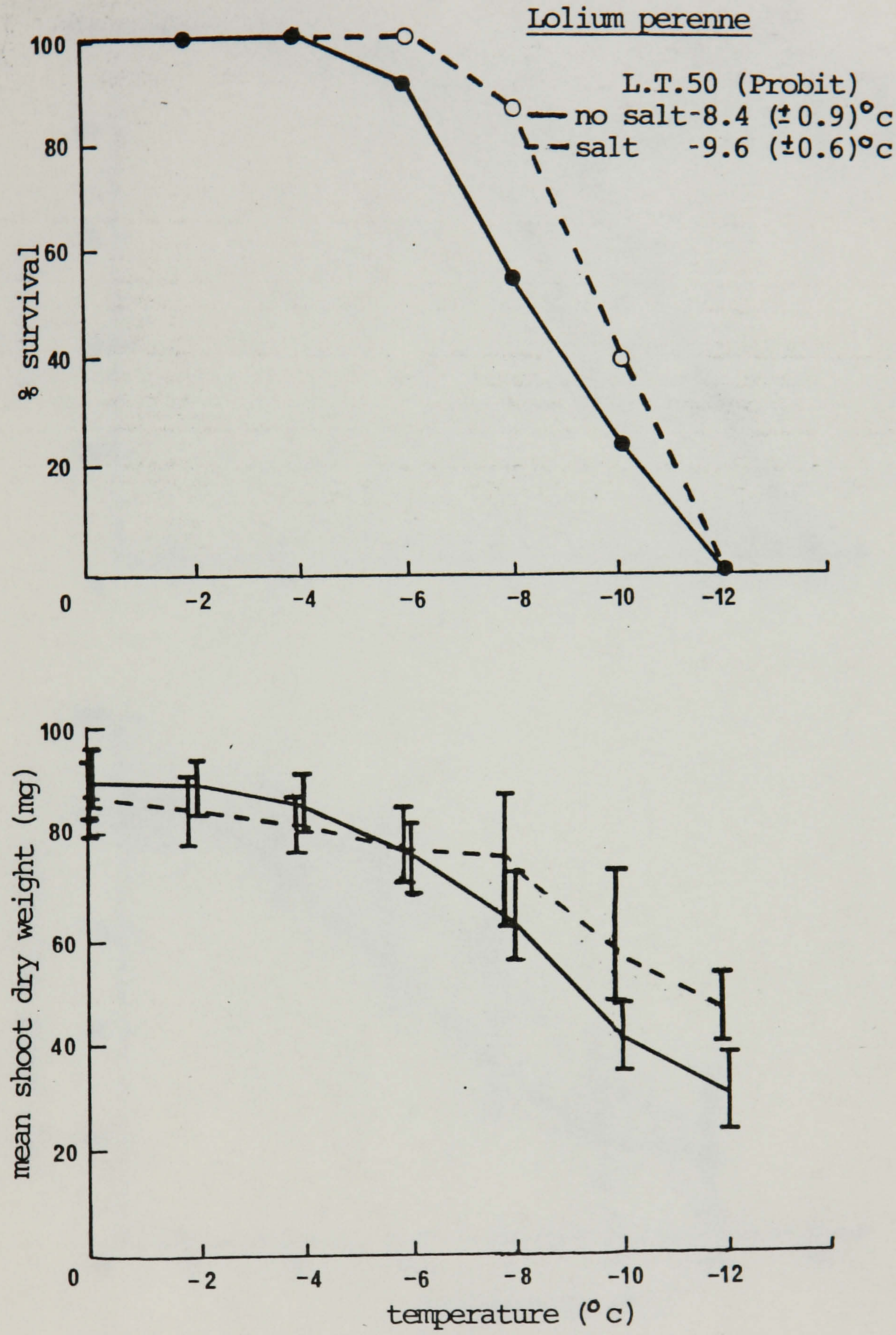


Fig. 7.4 Percentage survival and dry weight of shoots of Lolium perenne four weeks after exposure to sub-zero temperatures. —— no salt, - - salt.

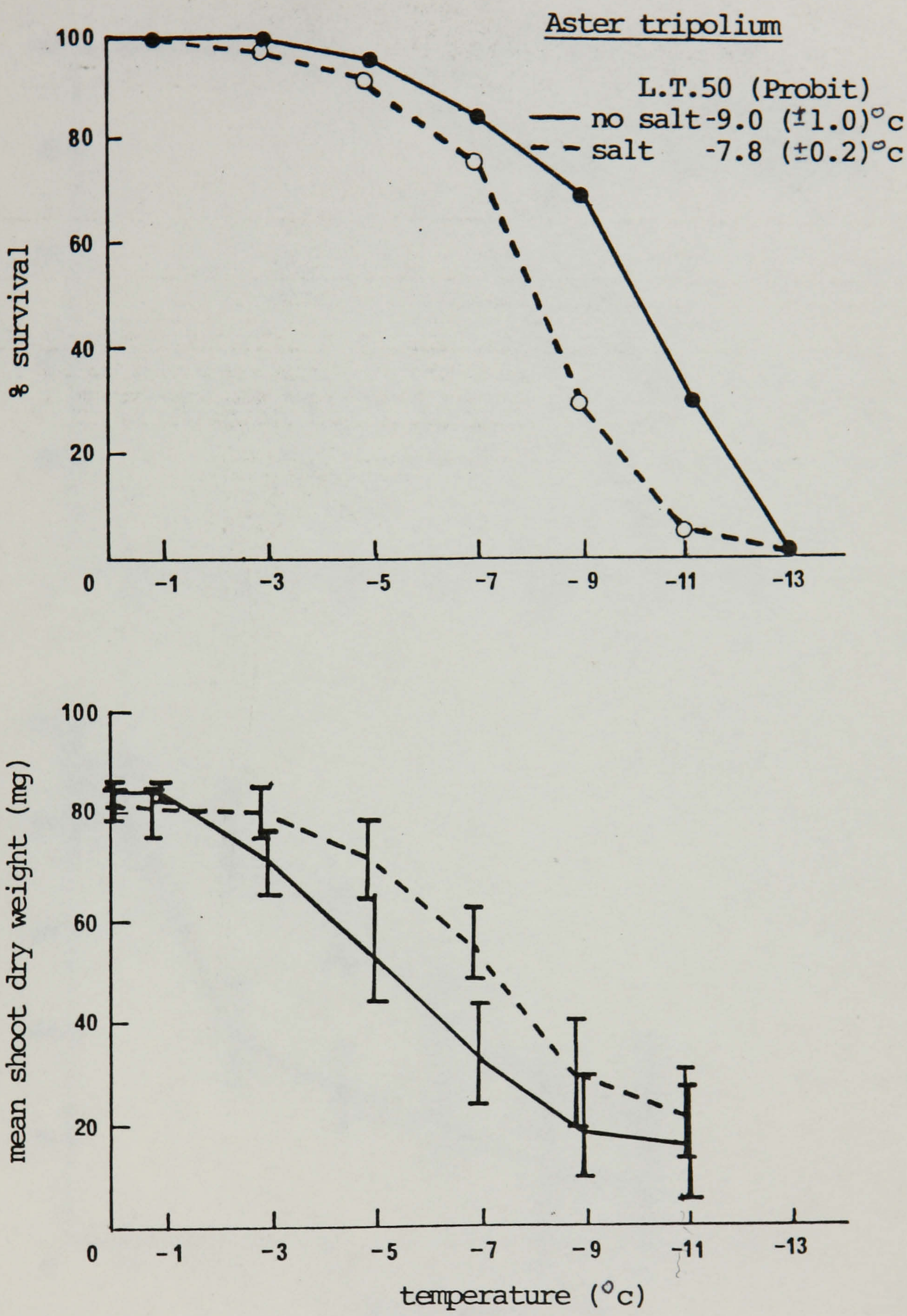


Fig. 7.5 Percentage survival and dry weight of shoots of Aster tripolium four weeks after exposure to sub-zero temperatures. —— no salt, - - salt.

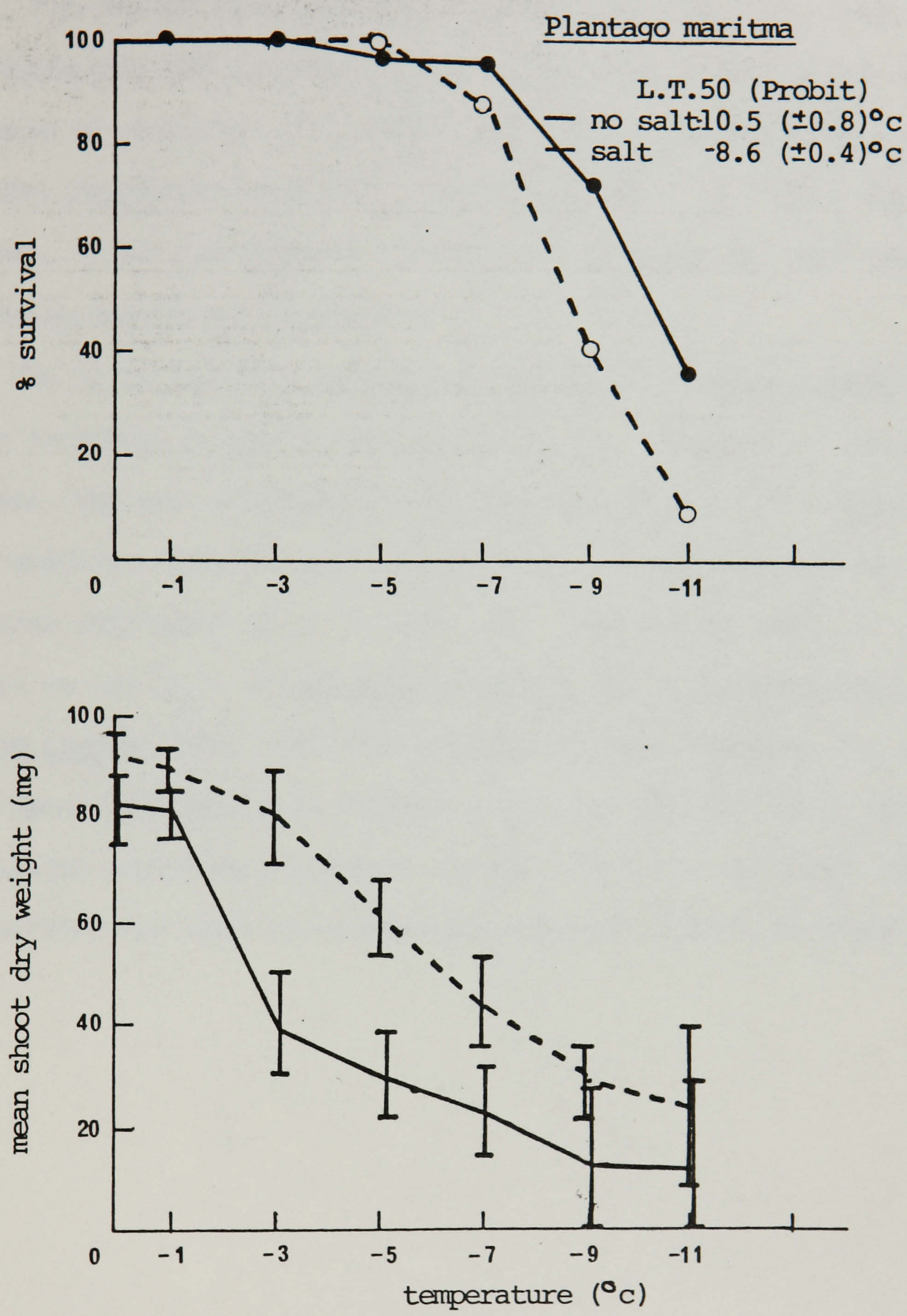


Fig. 7.6 Percentage survival and dry weight of shoots of Plantago maritima four weeks after exposure to sub-zero temperatures. — no salt, - - salt.

maritima and Spergularia marina, the addition of salt caused a significant improvement in the growth of the survivors.

In contrast both Aster tripolium (Fig. 7.5) and Plantago maritima (Fig. 7.6) showed lower survival with the application of salt, though the difference was only significant in the case of the latter species. In terms of shoot dry weight both were similar to the previous species, showing improvement with salt. The variability of final shoot dry weights, of all the species, tended to increase as the number of surviving individuals decreased.

Two of the species, Spergularia marina and Lolium perenne, were later re-tested using the same equipment and techniques. This time, however, the salt treatment was increased to 5g NaCl l^{-1}. The LT 50 of the unsalted plants of both species (Fig. 7.7) was the same as in the previous experiment (Fig. 7.3 and 7.4) However 5g NaCl l^{-1} had no effect on the LT 50 of Spergularia marina and it decreased the LT50 of Lolium perenne (Fig. 7.7). This suggested that response to salt is non-linear and complex so further trials to explore this effect of increasing salt were attempted. At this stage the equipment began to malfunction and the work on freezing resistance had to be abandoned.

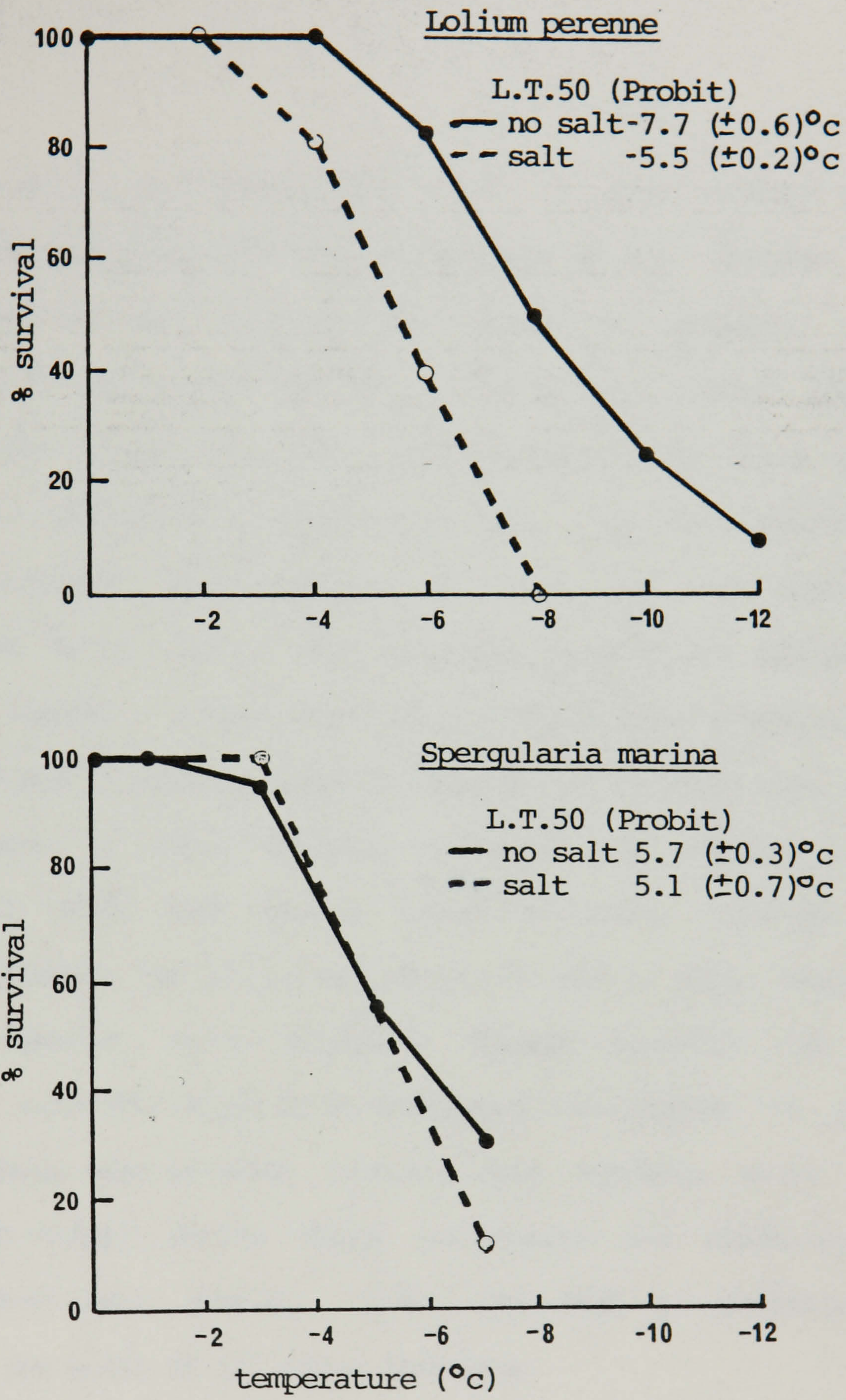


Fig. 7.7 The effect of an inreased salt application (5g NaCl l^{-1}) on the survival of *Lolium perenne* and *Spergularia marina* exposed to sub-zero temperatures. —— no salt, - - salt.

Chapter Eight. The nature of the requirement for salt.

Introduction

In Chapter 6 it was demonstrated that in sand culture under controlled conditions some maritime species grew as well without salt as with, but that the same species were unable to establish on a roadside unless it was treated with salt. There are several factors which were present in the field and not in the laboratory which might have caused this difference in response to salt. In the laboratory, plants were protected from stresses to which they are regularly subjected in the field, such as frost, drought, grazing and attack by pathogens. In Chapter 7 it was shown that salt treatment increased the freezing resistance of some maritime halophytes, so it might then also affect resistance to other related stresses. In addition most non-agricultural soils are low in major nutrients, whereas in laboratory experiments the plants were supplied with a high level of all essential elements. It was therefore thought possible that the availability of nutrients might have influenced the response to salt. In order to examine some of these possibilities roadside soils were taken to the University Garden where germination and establishment could be observed more clearly. This also made it possible to regularly weed the soils of all other seedlings.

Two trials were undertaken. In the first, several possible explanations for the response to salt in the field were investigated, including drought, frost, nutrient availability and pathogen attack on seedlings. The second trial followed the first and was a more detailed examination of the effects of nutrients and de-icing salt.

Trial 1

Soil was collected in October 1981 from the A69 at Throckley, one of the sites which had been used in the experiments described in Chapter 5. The site had been treated with a systemic herbicide in July. Complete turves 15cm deep were transferred intact from the site into large polythene washing-up bowls and cleared of dead vegetation. The bowls were placed in a sand filled plunge frame at the University Garden. There they were sown with the seed mixture used in the roadside trials (an equal quantity of Plantago maritima, Puccinellia distans and Spergularia marina).

Six different treatments were applied to five replicate bowls which were salted at 250 g m^{-2} per fortnight from November 1st to March 15th and five which were not. All bowls were kept weeded of all seedlings positively identified as other than the three sown species. Bowls were weeded in March, April and twice in June and July 1982. The treatments were:-

1. Control.

   No treatment.

2. Protection from pathogen attack prior to seedling emergence.

   All seeds were treated with a systemic fungicide (see chap. 2) before sowing.

3. Protection from frost.

   A thermostatically controlled low wattage heating cable was placed just beneath the soil surface. This was adjusted to prevent the soil and seedlings from being exposed to sub-zero temperatures.

4. Protection from possible harmful effects of the herbicide.

   It was possible that the systemic herbicide used to clear the roadside vegetation was killing the germinating seeds. A differential effect between salted and unsalted plots could have resulted from salt inhibiting germination. Turves from untreated areas of the A69 site were used, and they were weeded at least fortnightly of all but the three sown species.

5. Application of nutrients.

A nutrient solution (Hewitt 1952) was applied once a fortnight.

6. Protection from drought.

A trickle watering system was used, programmed to switch on twice a day and deliver surface moisture to prevent seedlings suffering from drought. During wet periods the system was turned off completely to prevent the bowls from waterlogging.

The position of all of the treatments was chosen at random. The experiment was allowed to run from October 1980 until July 20th 1981 when all above ground material was harvested. Individuals of each species were sorted, counted and then dried and weighed. Soil conductivity was tested in the spring and at the end of the experiment (Table 8.1). Because final dry weights in some of the unsalted treatments were very low, results were drawn on two different scales to improve visible comparisons. In Figs. 8.1-8.3 the lower histograms are of data for unsalted treatments drawn on a bigger scale. The results were tested statistically using analysis of variance with the studentised range test for comparison of means. In Table 8.1 the three important comparisons for each treatment are shown: between the salted and non-salted bowls of each treatment; between the non-salted treatment and the non-salted control; and between the salted treatment and the salted control. The statistical test for the non-salted comparison used only the results from the non-salted bowls as these results were much lower than the others.

By the end of the application of salt in April the soil conductivity of all the salted bowls had increased (Table 8.1). This

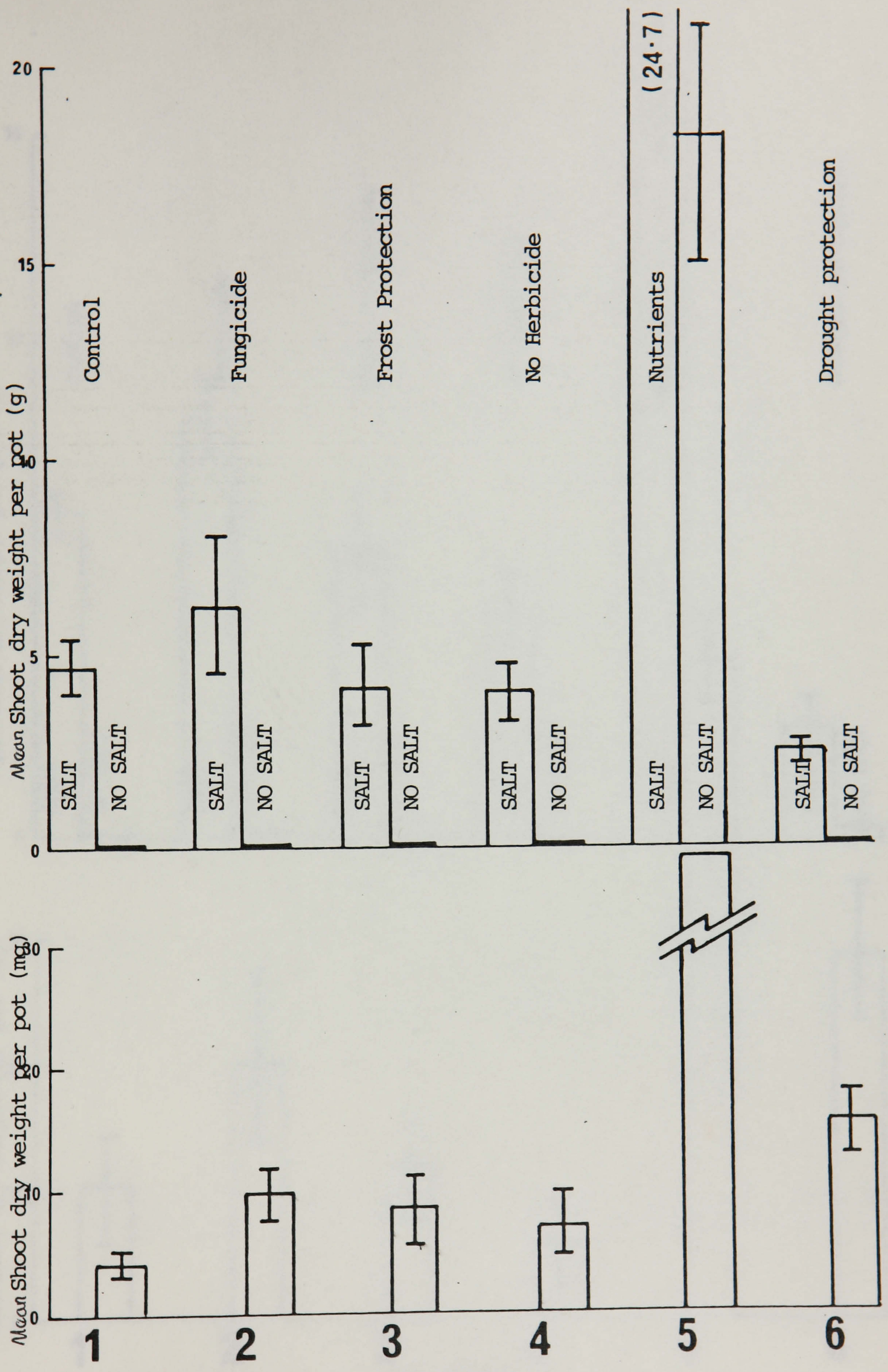


Fig. 8.1 The effect of six treatments on the growth of Puccinellia distans in a roadside soil treated and untreated with salt. The lower histogram shows the unsalted treatment again on a larger scale.

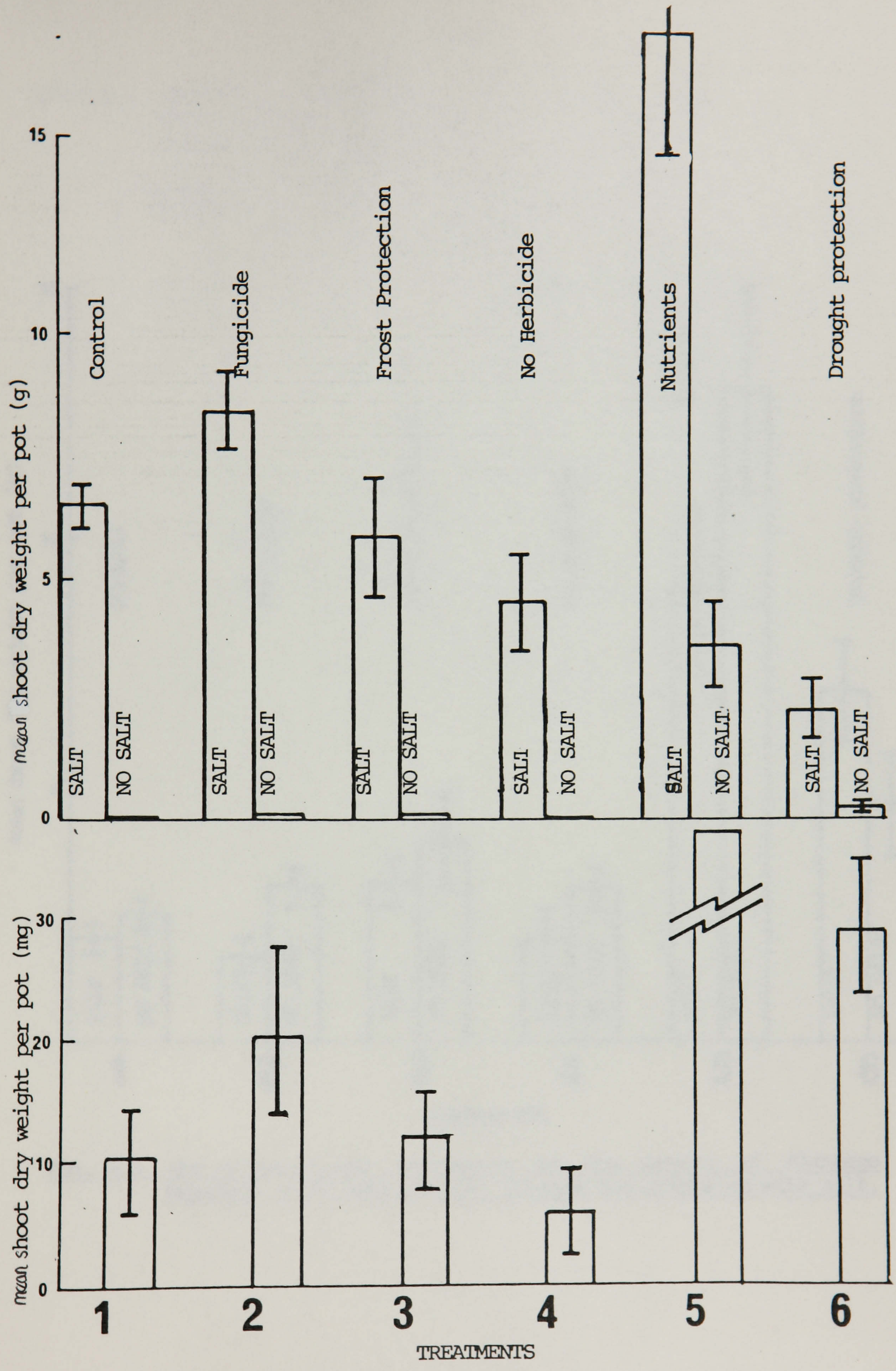


Fig. 8.2 The effect of six treatments on the growth of Spergularia marina in a roadside soil treated and untreated with salt. The lower histogram shows the unsalted treatment again on a larger scale.

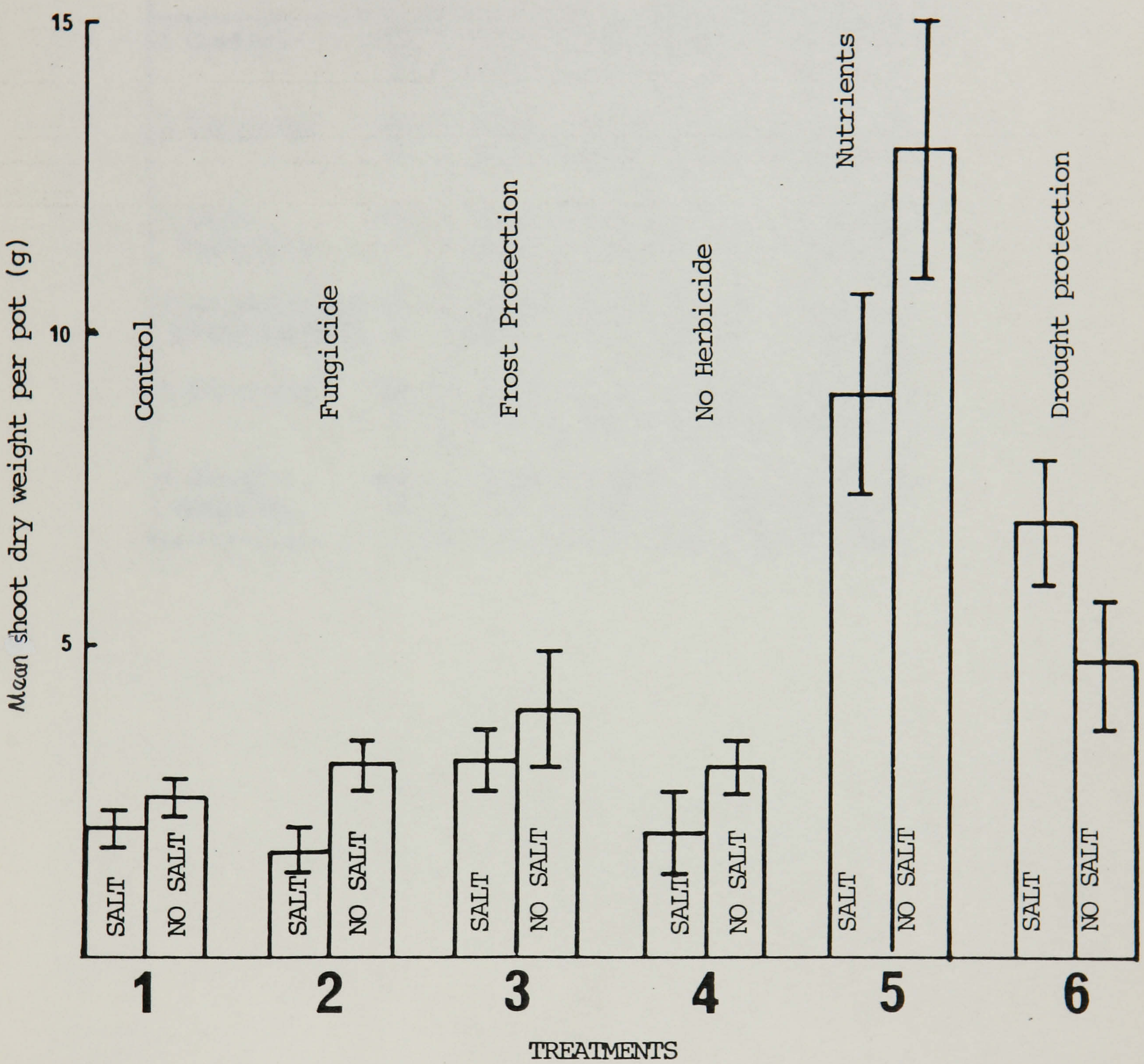


Fig. 8.3 The effect of six treatments on the growth of Plantago maritima in a roadside soil treated and untreated with salt.

Table 8.1 Conductivity (with standard errors) of soil 1 month after salt treatment finished (April 1982) and at harvest (July 1982).

Treatment S- salt NS- no salt		Conductivity (msiemens) April	July
1 Control	NS	0.32 (0.13)	0.14 (0.06)
	S	33.0 (3.0)	1.2 (0.51)
2 Fungicide	NS	0.52 (0.18)	0.16 (0.05)
	S	30.1 (2.8)	0.8 (0.53)
3 Frost Protection	NS	0.32 (0.2)	0.31 (0.21)
	S	28.4 (3.4)	1.1 (0.05)
4 No Herbicide Pretreatment	NS	0.30 (0.12)	0.14 (0.05)
	S	29.2 (4.4)	1.1 (0.32)
5 Nutrients	NS	4.84 (1.2)	2.54 (0.76)
	S	15.2 (4.6)	2.8 (0.21)
6 Trickle Watering	NS	0.08 (0.02)	0.06 (0.02)
	S	8.2 (3.2)	0.46 (0.14)

Table 8.2 Statistical significance of comparisons between the treatments of trial 1 (Figs. 7.1 - 7.3)

	Treatments 1 Control	2 Fungicide	3 Frost protection	4 No Herbicide	5 Nutrient	6 Trickle Watering
Puccinellia distans						
salted treatment against non-salted treatment	* *	* *	* *	* *	* *	* *
salted treatment against salted control		*			* *	*
non-salted treatment against non-salted control		* *			* *	*
Spergularia marina	1	2	3	4	5	6
salted treatment against non-salted treatment	* *	* *	* *	* *	* *	* *
salted treatment against salted control					* *	*
non-salted treatment against non-salted control					* *	* *
Plantago maritima	1	2	3	4	5	6
salted treatment against non-salted treatment		*			* *	* *
salted treatment against salted control					* *	* *
non-salted treatment against non-salted control					* *	* *

* = significant at 5%   * * = significant at 1%

increase was significantly less, however, for two of the treatments. Both treatments, the addition of nutrients and trickle watering, will have leached some of the salt from the soil. Both treatments also had significantly different soil salinities in the unsalted bowls than the control. Those receiving trickle watering had lower soil conductivities, presumably due to leaching, and those receiving nutrients had enhanced conductivities, presumably due to the addition of nutrient ions. By July the soil conductivities of the salted bowls for all treatments had markedly decreased due to leaching by rainwater, although they were still substantially higher that those of the unsalted bowls. The same two treatments had significantly different conductivities to the control. Those receiving trickle watering had lowered conductivities and those receiving nutrients had enhanced conductivities, presumably again due to leaching and the addition of nutrient ions.

In the control treatments of Puccinellia distans (Fig. 8.1) and Spergularia marina (Fig 8.2) the shoot dry weight from the unsalted bowls was very much lower than that from the salted bowls. By the time of the final harvest, seedlings in the control unsalted bowls had mostly died and those which remained were stunted and red in colour, their appearance suggesting a major nutrient deficiency. The plants in the salted bowls, in contrast were green and growing well. The five treatments also had a significantly greater shoot dry weight in the salted as opposed to the unsalted bowls. However some of these treatments gave a significantly different result than the control. Pre-treatment with fungicide increased the shoot dry weight. This increase was small though, and occurred in both the salted and unsalted bowls, and would thus appear to be unrelated to the effect of salt. The application of nutrients gave a large and significant increase to both the salted and unsalted bowls. The effect on the unsalted treatments was comparatively much greater than the salted treatment, and resulted in a shoot dry weight on the same scale as that of the treatment with salt. Thus the application of nutrients completely overcame the requirement for salt. There was a significant but much smaller increase in shoot dry weight in the unsalted bowls receiving trickle watering as compared to the control. Seedlings in these bowls appeared no larger than seedlings in the control but did not show the same signs of stress and many more survived. In the salted bowls there was a significant decrease compared to the control, which was probably related to the decrease in soil conductivity (Table 8.1). Trickle watering, therefore, only partially overcame the requirement for salt.

In contrast, Plantago maritima (Fig. 8.3) grew as well without salt as with in the control. On the roadside this species was unable to establish on these soils without salt. There must therefore be significant differences in the conductivities of this experiment and those of the previous one on the roadside.

This trial showed that it was possible to demonstrate a requirement for salt in Puccinellia distans and Spergularia marina. It also showed that the application of nutrients overcame the effects of the absence of salt, and that the elimination of drought reduced the visible symptoms of stress caused by the lack of salt but did not increase plant growth.

Trial 2

The full nutrient treatment in the first trial consisted of several major ions each of which could have caused the plant's response. In a second trial some of the major ions were applied as separate treatments with different accompanying cations and anions respectively. The two major ions of de-icing salt, Cl- and Na+, were similarly applied as different accompanying ions.

The turves for this trial were collected from the same roadside. They were treated with herbicide in May 1982 and collected, cleared of vegetation and sown at the beginning of August 1982. The same three maritime species were sown but this time bowls were divided into three, and one species sown per section. There were six replicate bowls per treatment and eleven treatments. Bowls were sunk into the same plunge frame as in the last experiment. Instead of applying de-icing salt to half of the replicates of each treatment, sodium chloride was applied in solution as a separate treatment. The treatments were:-

1. Control

Treatments investigating the effect of sodium chloride :-

2. Sodium chloride	$5.0\ g\ l^{-1}$
3. Potassium chloride	$6.3\ g\ l^{-1}$
4. Sodium sulphate	$6.0\ g\ l^{-1}$
5. Potassium sulphate (high)	$7.2\ g\ l^{-1}$

Treatments investigating the effect of nutrients :-

6. Complete nutrients	as Hewitt (1952)
7. Potassium nitrate	$1.04g\ l^{-1}$
8. Potassium phosphate	$0.17g\ l^{-1}$
9. Ammonium sulphate	$0.74g\ l^{-1}$
10. Trace elements	as Hewitt (1952)
11. Potassium sulphate (low)	$1.80g\ l^{-1}$

All treatments were applied fortnightly in 0.2 litres of water per replicate bowl. The control received water alone. Where possible applications were given during periods of rainfall. The concentrations of the salts used were calculated to give the same concentration of the ion of interest as occurred in the sodium chloride or complete nutrient treatment. Two control treatments of potasium sulphate were included, the higher to match the concentrations of K+ and SO4 - ions given in the potassium chloride and sodium sulphate treatments respectively and the lower to match those of potassium nitrate, potassium phosphate and ammonium sulphate.

Plants were grown from August until late October 1982 when the shoots were harvested and weighed. The shoot dry weights are shown in Fig. 8.4 and the results of an analysis of variance in Table 8.3. Shoot dry weight for all species were significantly lower in the control than the sodium chloride treatment. The difference was greatest for Puccinellia distans and Spergularia marina. Establishment and growth in the control was much better than in the previous experiment. This may have been due to the difference in weather. In 1982, April, May and June had considerable periods of high temperature and drought. There was only one such period during the second trial and that was short, the rest of the time the weather was mild and wet. It was only during this short drought period that the seedlings in the control looked under stress. At all other times they looked healthy although their rate of growth was low and they remained very small.

The application of potassium chloride gave results not significantly different from those of sodium chloride. The application of sodium sulphate also produced an increase in shoot dry weight, but this was significantly lower than that produced by sodium chloride or potassium chloride.

The complete nutrient treatment gave significantly higher shoot dry weights than either the control or the sodium chloride treatment. The application of each of the major nutrient ions produced, at least as great a response as that caused by sodium chloride, and for nitrogen the response matched that of the complete nutrient treatment. The application of trace elements did not produce a significant increase in shoot dry weight over the control. It is noticeable that treatments

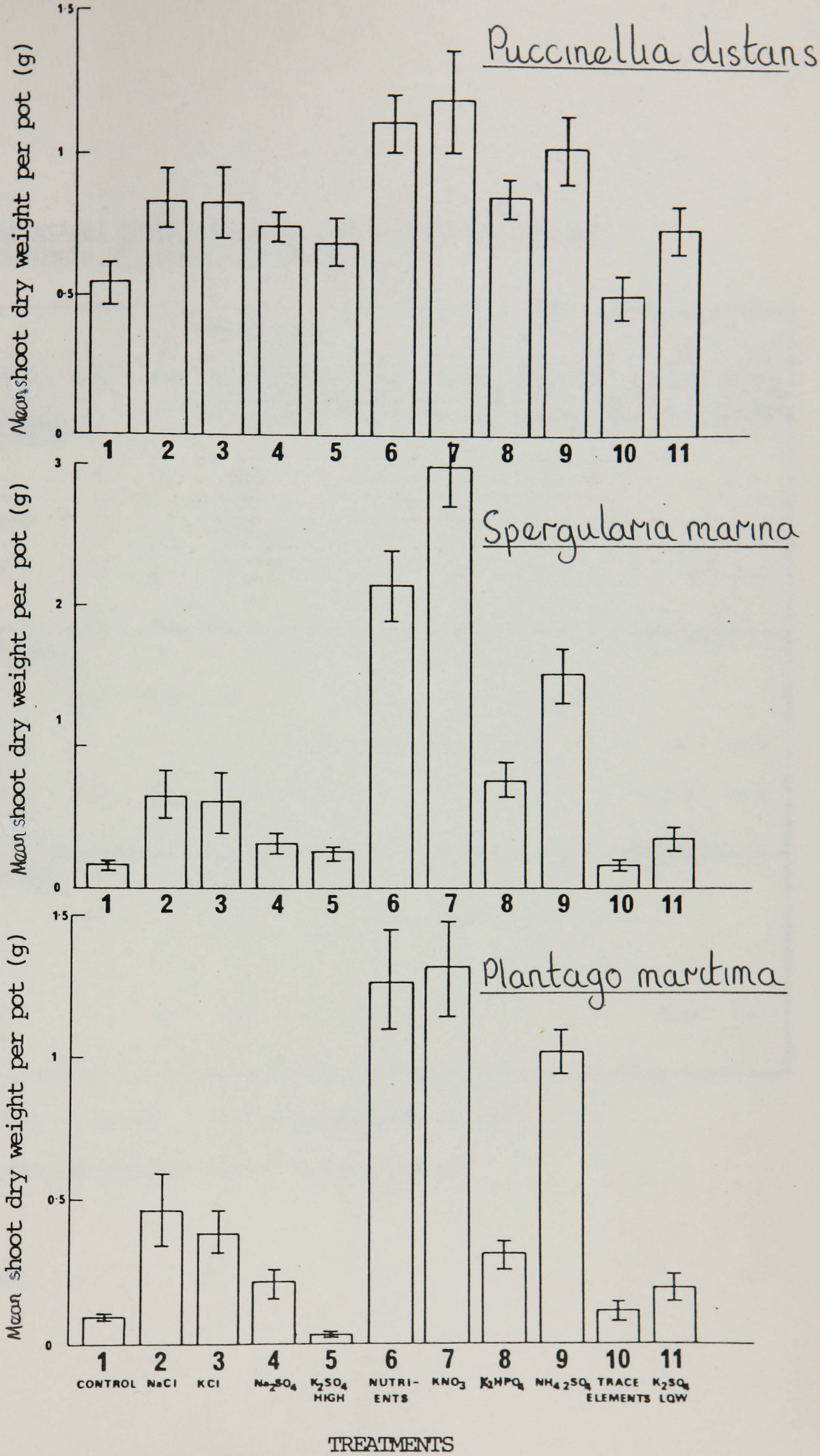


Fig. 8.4 The response to treatment with different salts of three halophytes growing on roadside soil.

Table 8.3 Statistical significance of comparisons between the treatments of trial 2 (Fig 7.4)

	Treatments										
	1. control	2. NaCl	3. KCl	4. Na_2SO_4	5. K_2SO_4 (high)	6. c.n.	7. KNO_3	8. KH_2PO_4	9. $(NH_4)_2$ SO	10. t.e.	11. K_2SO_4 (low)
Puccinellia distans											
1 Control		* *	*	*		* *	* *	* *	* *		
2 NaCl	* *			*	*	* *	* *		* *	* *	* *
3 Complete nutrients	* *	* *	* *	* *	* *		*	* *	*	* *	* *
Spergularia marina											
1 Control		* *	* *	*		* *	* *	* *	* *		
2 NaCl	* *				* *	* *	* *		* *	*	* *
3 Complete nutrients	* *	* *	* *	* *	* *			* *		* *	* *
Plantago maritima											
1 Control		*		*		* *	* *	*	* *		
2 NaCl	*						*		*		
3 Complete nutrients	* *		*	*	*					* *	*

* = significant at 5% * * = significant at 1%

c.n. = complete nutrients t.e. = trace elements which included an ion known to be not easily taken up by plants had comparitively lower results. This is particularly true of the treatments involving the sulphate ion, and to a lesser extent for those including the phosphate ion.

Chapter Nine. Reclamation of roadside saltburn using maritime grasses.

Introduction

Local authorities in north eastern England have expressed an interest in methods of reclaiming verges which have lost their vegetation cover because of salt damage. The invasion of salt damaged verges by maritime species, given time, results in a complete low-growing sward virtually indistinguishable from those of unaffected verges. The most important species in this colonisation process are Puccinellia maritima and P. distans and it was reasoned that it should be possible to use these grasses to reclaim damaged sites. To be economically worthwhile the method adopted would need to be simple and inexpensive and the species used would have to need little maintenance. The same authorities also expressed interest in a seed mixture which could be used to sow newly lain verges that were likely to suffer from salt damage. To this end, a number of trial formulations were tested.

For the reclamation of salt-damaged verges, seed of Puccinellia distans and Puccinellia maritima were collected from roadside populations in north eastern England. A commercial variety of Puccinellia distans named "Fults" was also included in the trials as well as a salt and drought tolerant Festuca rubra, named "Hawk". The basic amenity grass seed mixture which is usually sown on to the road verges was used for comparison. Three sites were selected, each representing different types of damaged verge. Site 1 was on the heavily used A1 road (NZ 317.692) and had extensive damage, with up to four metres from the road bare of vegetation. This site was on an embankment surrounded by flat fields and so it was very exposed. Site 2 was on the A696 near to Newcastle airport (NZ 183.717) and again it was heavily used. This site was not particularly exposed but did suffer from vehicles frequently mounting the verge and compacting the soil. Bare ground extended for an average of one metre. from the roadside. Site 3 was on a more minor road the A197 (NZ 209.868). It was located on a steep hill which was heavily salted. Bare ground on this site extended on average 0.5m. from the roadside. This road verge was used as a path by pedestrians

Trial 1

The area sown at each site included the bare ground next to the road and the area beyond which was usually patchily covered with vegetation. The lenghs of verge were divided into 5m sections. Alternative sections were sown at 60g m^{-2} with trial species or mixtures, each species or mixture sown into four replicate sections chosen at random. There were also four unsown controls. These sites were first sown in March 1980. The sites were raked over to break up the upper surface. They were then sown and raked over again to bury the seed. The first sowing of the exposed site 1 was unsuccessful as wind removed both the loosened soil and the seed. This site was resown during a wet period in April 1980, which proved more successful.

Trial 2

In this trial four seed mixtures, each based on the amenity mixture recommended for sowing road verges, were used on a newly lain verge. The composition of the four mixtures is shown in Table 9.1 The road used for this trial was an old section of the A696 in Newcastle which had just been substantially altered. Because of this, the verges and central reserve were raised by adding soil to a depth of 50cm. over the old grass sward. These roadsides had previously

Table 9.1 Seed mixtures used in trial Two

Mixture No.	Contents	rate per m
Mix 1	Amenity mixture	60 g
Mix 2	F.rubra cv. Hawk	4 g
	P.maritima	4 g
	P.distans	4 g
	Amenity mixture	48 g
Mix 3	P.distans	4 g
	Amenity mixture	56 g
Mix 4	P.distans	10 g
	Amenity mixture	50 g

suffered from salt damage and the City Council was concerned to achieve complete cover on the new verges. Two areas of the verge were used for the trial. One was a length along the south bound carriageway which was 5m wide and had previously been the most badly affected by salt damage. The other was the adjacent central reservation which was 15m wide. Each was divided into 10m sections, running at right angles to the road. Alternat e sections were sown with amenity grass mixture to separate the trial mixtures. The other sections were sown with one of the trial mixtures. Each verge had five replicates of each mixture and five replicates of the amenity mixture as a control, with positions chosen at random. This trial was sown in April 1982.

The sites of the first trials were monitored once a month for one year after sowing and recorded for percentage bare ground each October for four years. Figure 9.1 shows the results of these trials in October 1980,1981,1982 and 1983.

As the trials progressed some of the sown grasses invaded adjacent replicate strips. Puccinel a distans was most common, eventually occurring, at sites 2 and 3, at a low level in all of the strips and for some distance down the roadside away from the trials. Puccinellia maritima also occasionaly invaded other strips, but only those adjacent to those it had been sown into. This invasion explains the gradual increase in cover of the control strips at sites 2 and 3. These two sites also suffered from considerable disturbance during the trial. At site 3, at the Newcastle Airport, as well as cars mounting the verge there were several holes dug by the Gas Board. Site 2, at Morpeth, was walked on by pedestrians and there was also considerable erosion by water channelled along the foot path. It was noticable how rapidly Puccinellia distans was able to re-invade some of these disturbed areas.

The second trial was recorded in October 1982 and 1983, i.e. after

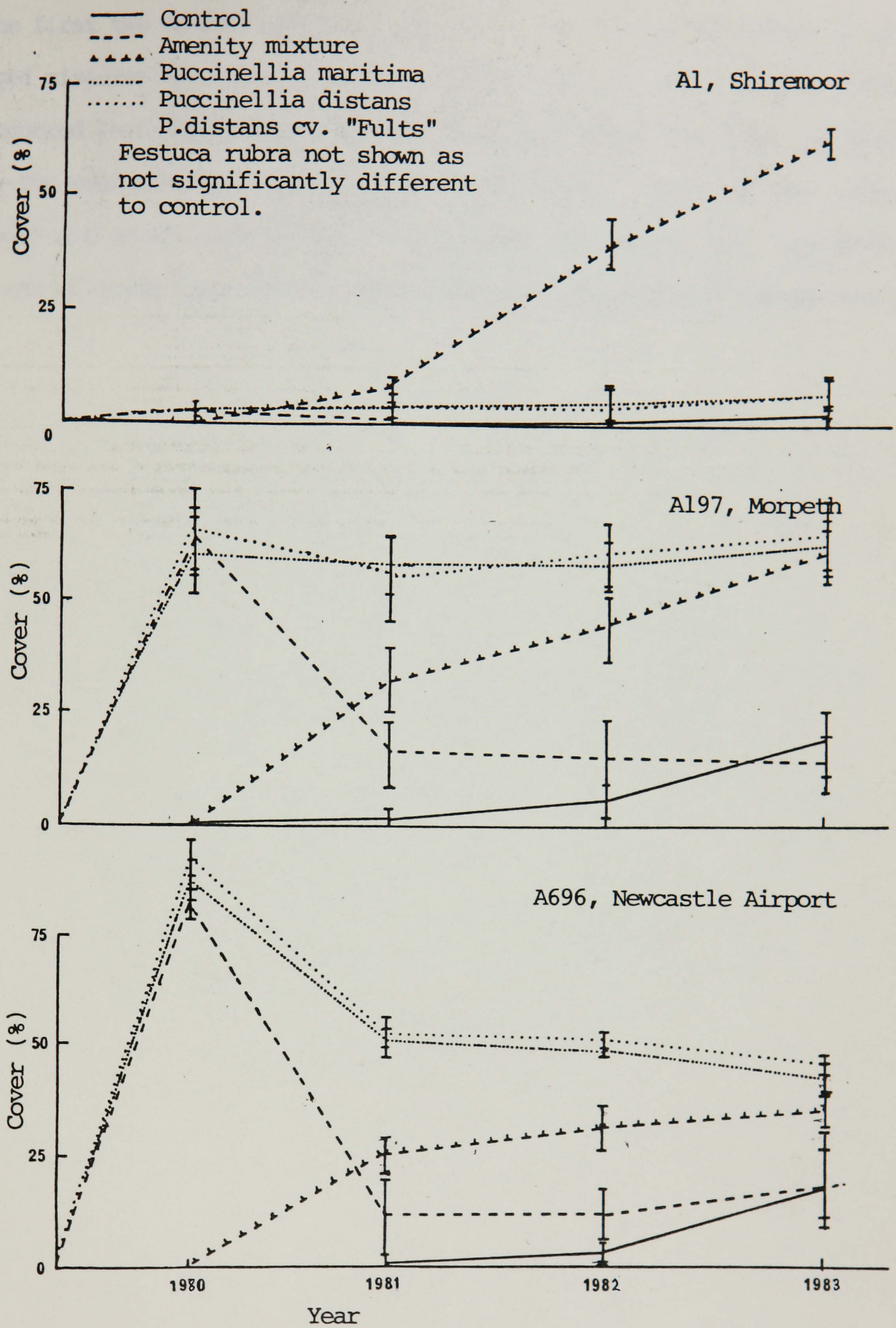


Fig. 9.1 Cover in succesive years of damaged roadside verges seeded with trial mixtures.

the first two seasons' growth (Table. 9.2). Initial establishment of all seed mixtures was poor, this was probably due to the drought which occurred in early summer the effects of which would have been enhanced by the poor clay soil used on the rebuilt verge. Much of the cover which did occur, especially in the control, was due to the occasional piece of grass from the old sward which had grown through the new soil.

Table 9.2 Cover of roadside verges one and two years after sowing with trial seed mixtures

Mixture No.	Cover %	
	1982	1983
Mix 1	11	13
Mix 2	14	24 *
Mix 3	16	15
Mix 4	19 *	17

(* probability of 0.05, ** of 0.01 of difference to mix 1 using analysis of variance)

Chapter Ten. Discussion.

Distribution.

The present distribution of Puccinella distans (Fig. 2.1) shows a distinct pattern, with all of the records confined to the north and east of England and Wales. This distribution is probably due to differences in the use and effect of de-icing salt in different parts of the country. In the west and south, the low use of salt is due to the lower incidence of frost, whilst the salinity of roadside soil is reduced further in the west by the higher rainfall (Thompson et al. 1979). The continued absence of P. distans from Scotland is more puzzling, for although less salt may be used than in northern England it is still enough to cause damage to verges on some of the main roads, and for Spergularia marina to have been found.

The other maritime species are more restricted in their roadside distribution. Fig. 3.2 shows how they are all confined to the east of Britain. In the rest of the world the occurrence of maritime species on roadsides is similarly restricted to areas where large amounts of de-icing salt are used. The reports described in chapter Three came from either northern North America or northern Europe which are the two areas of the world which have both cold winter weather and high volumes of traffic, and so are the only areas using large amounts of de-icing salt.

Relative success of species.

Puccinellia distans has now invaded virtually all of the major road verges around Newcastle (Fig. 3.3). In the rest of England this species may now have spread into all the areas where there are suitable saline habitats beside major roads, although further increase of populations is still likely within these areas. This remarkably rapid expansion 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 character species. He describes the association as forming ephemeral communities on saline soils, which are characterised by instability. Inland saltmarsh sites in which it also occurs (Lee 1975) are similar. Both inland and on coasts, the land is typically pastoral and only occasionally inundated with saline water. Inland saltmarsh sites are also disturbed, most of the maritime flora having been lost this century because of this disturbance (Lee 1975).

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, its rapid growth and flowering, high seed production and light seeds enable it to invade rapidly. The fact that seed are small and easily wind-blown means that it can be carried along in the slipstream behind vehicles.

Spergularia marina is another species of the same disturbed saline sites which is spreading rapidly on the roads of north eastern England. It is the other character species of the alliance Puccinellia-Spergularion salinae (Beeftink 1977), and it too is present in most of Britain's inland saltmarshes.

Most of the other maritime species on the roads of north eastern

England are from stable maritime habitats and all are spreading more slowly. Of these species the most widely spread are Plantago maritima and Puccinellia maritima. Neither of these species is associated with disturbed soils, but both have characteristics which may be advantageous in this new habitat. Seed production of Plantago maritima is high and the seeds are mucilaginous and sticky which may be an aid to rapid invasion. Puccinellia maritima has been described by Gray and Scott (1977a) and Weihe (1979), as acting as a pioneer plant on saltmarshes and mudflats. On roadsides it occupies a similar niche and although seed set is variable, with many plants not setting seed in a given year, it establishes in much more hostile environments than the other maritime species.

The other species on the roadsides are much more confined in their distribution and have spread little, if at all, since 1975. This is particularly true of Spergularia media which has not spread since the populations were discovered in 1975. This species is adapted to more stable maritime sites than S. marina (Sterk 1969). Although Plantago coronopus has spread little in north eastern England since 1975, in the south it is becoming frequent on roads. Kitchener (1983) reported that it is nearly as frequent as Puccinellia distans in Kent and suggested that an important factor in its success is its ability to set seed despite frequent mowing. It is questionable, however, whether this species should be considered as a true maritime species as it is common on inland sandy soils in the south, and it appears to be spreading onto road verges from there.

Neither Cochlearia officinalis or Atriplex littoralis were recorded from roadsides in north eastern England in 1975, so that no estimate of their rate of invasion has been possible. Atriplex littoralis is, however, quite widespread and is adapted to a disturbed saline site, the strand line. It is an annual, producing many seeds, and as A. patula and A. hastata are so successful on roadsides, it seems likely that A. littoralis may be so too. It was recently found on roadsides in Yorkshire and Kent.

Many of the species spreading rapidly elsewhere in Britain, but which do not occur in the north east, are also adapted to disturbed habitats. The annual Cochlearia danica now occurs on several roadsides in three different areas. Of the roadside flora of Kent, Kitchener has suggested that the annual Parapholis strigosa as well as Puccinellia fasciculata and P. rupestris all appear to be spreading and to have the potential for a wider distribution on roads. Once again these are species of disturbed saline habitats (Beeftink 1977). These species have a southern British maritime distribution (Adam 1978) which explains why they have not been found on the roads of north eastern England. The southern distribution might indicate a frost sensitivity or a requirement for higher summer temperatures which would limit their invasion to the roads of southern England.

Origins.

The first question which must be asked is that of when these species might have first invaded roadsides. The discovery of maritime plants on British roads has been reported on at least three occasions since 1975 (Matthews & Davison 1976; Dony & Dony 1979; Badmin 1979). The review in chapter three showed that discoveries have occurred from 1975 onwards in northern Europe and since 1971 in North America. 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 1960's (Fig. 4.1) 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 the area. Although P. distans is now widespread in Britain it is possible that this also could have occurred since the 1960´s, for as was demonstrated in Fig 3.3, this species is capable of very rapid invasion.

The roadside distribution of Puccinellia distans (Fig. 3.2) answers 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 1980). 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 existing inland populations. The British distribution of Puccinellia distans in Perring & Walters (1962) consisted of records prior to the invasion of roadsides. Some of the inland sites shown are near to some of the new roadside sites and 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 Steetley 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.

Some of the other maritime species on British roadsides are also on verges near to coastal sites with vehicular access. Good examples are Puccinellia maritima, which occurs along the A1 in Northumberland to within 4 km. of the Holy Island saltmarsh, and Cochlearia danica, which is spread along the A45 to within 5 km. of a coastal site near Felixstowe docks (E.M.Hyde pers.comm.). Although this is not so for the other species on roadsides, most are within 30 km. of a coastal site. One exception is the record of Armeria maritima on the M4 near Oxford, but as the species is common in gardens, this may have been the source of seed in this case. The other exception is the single record of Atriplex littoralis on the A1 in Yorkshire. Identification of this species on roadsides proved difficult in north eastern England, and it may be that the Yorkshire record is part of a wider yet unrecorded distribution.

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

In chapter Three it was reported that the N.I.A.B. official seed testing station listed Hordeum jubatum as a contaminant in imported grass seed and it seems likely that this is how this North American species is arriving on British roadsides. N.I.A.B. also reported the genera Puccinellia and Spergularia as contaminants in imported grass seed, but were not able to specify the species. In both genera there are species other than the ones invading roads which could occur as contaminants in grass seed. This is particurly so in the genus Spergularia in which the agricultural weeds S. arvensis and S. morisonii are more likely to occur than the maritime species. The other maritime genera that have invaded roadsides have not been found as contaminants.

Thus the introduction of some of the maritime species as contaminants in grass seed or de-icing salt can not be dismissed. However, 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, and that carriage on vehicles and in vehicular slipstreams has been demonstrated, means that the most likely explanation must be introduction from the local coasts.

Dispersal.

One of the characteristics of species of disturbed environments is the production of large numbers of light seed. The importance of this is shown in the results of the seed trap experiments (Fig. 3.7 - 3.9). These experiments showed that seed dispersal is enhanced by the slipstreams of passing vehicles. Puccinellia distans, which has much lighter seed than Plantago maritima, was carried much further. This difference is one reason why, on the roads around Newcastle, Puccinellia distans tends to occur as continuous populations along roadsides, and Plantago maritima as many small discrete colonies. Voort et al. (1979) found that species with light seed made the most rapid invasion along the verges of roads leading into new Dutch polders. The involvement of vehicles was indicated by the correlation between the extent of species invasion, and the traffic density.

The disjunct populations which the larger seeded species such as Plantago maritima have, indicates that seed is not spreading just by means of vehicular slipstream. On a local scale, carriage on the blades of grass mowers, as proposed by Feltwell & Philp (1980), may be important. Such a mechanism seems most likely in the case of Plantago maritima, as this species has mucilaginous seeds which would easily stick to the mower blades.

On a bigger scale, other mechanisms may be involved, for some of the maritime species occur at sites a comparatively long distance from the nearest roadside or other seed source. Wace (1979) showed that in Australia large amounts of seed were carried on vehicles often for long distances. Evidence for the transport of maritime species on vehicles is suggested by the appearance of Puccinellia distans and Spergularia marina at two roadside sites in Northumberland which are comparatively remote from any seed source but which were visited regularly by the vehicle used in this study. Kitchener (1983) drew attention to a similar break in the distribution of many of the maritime species on Kent roads. He also suggested that carriage on vehicles could be responsible, and pointed out that the recent extensive work on the Thames flood barrier on the north Kent coast would have resulted in a lot of machinery working on coastal sites and then returning inland. Daniels (1984) reports that the seed of Spergularia marina has been found in mud washed from a lorry. In North America, Catling & McKay (1980) described how the maritime species were originally brought inland late last century in railway ballast and became established in saltpiles in railway yards. They spread from there into the saline sites created by the salt industry, and only recently spread along roads. They also proposed that carriage on vehicles and in vehicular slipstreams was responsible for the invasion of roads.

A much less likely means of carriage from coastal sites is on birds (Mathews and Davison 1976). Gulls and ducks are the most frequent carriers of seed and both could easily pick up seeds from the coast. Seed of at least one saltmarsh species, Suaeda maritima, has been found on a bird (Gillham 1970), but whether these birds are ever likely to drop the seed on a busy roadside is questionable.

Salt application rates.

The salt application rates used on major roads to the north of Newcastle (Table 4.1) are high compared with those for most of Britain (Williamson 1968; Ranwell et al. 1973; Thompson et al. 1979). They are of the same order as the heavily salted roads of northern Britain, West Germany (Thompson et al. 1979), Denmark (Vestegard 1971) and some areas of the eastern United States (Roberts and Zybura 1967; Hutchinson 1970). Roads around Chicago receive up to four times as much (Hughes, Butler and Sanks 1975).

Soil salinity.

The recording of soil salinity at five roadside sites (Fig. 4.1 - 4.5) showed that there tended to be two peaks in salinity in any one year. The first occurred in mid-winter and was associated with the application of de-icing salt to the road during periods of frost. The second occurred in early summer and was associated with the drying out of the soils and the resulting concentration of salt. Previous work on roadside soil salinities has only demonstrated winter peaks in salinity (for instance Prior & Berthouex 1967, Vestergaard 1971, Foster & Mann 1977, Brod 1979). Colwill et al. (1976) found at the most saline site they studied that this winter peak continued during one year into the early summer and put this down to an unusually cold and dry spring.

Separate summer peaks in salinity due to evaporation have, however, been demonstrated for saltmarshes in Britain (Jeffries et al. 1979), and in saltpans in North America (McMahon & Unger 1981).

The salinity of roadside soils in north eastern England was measured by Davison (1971) in 1969. Although some of his sites were on roads which were studied as part of this project they were all on sections of road now by-passed. The sites had salinities of 1.23 - 8.82 m-siemens, the highest reading was for a soil collected in October from a site bare of vegetation for up to 1 m from the road. The results are the same as those recorded as part of this project for similar roadsides at the same time of year. This indicates that these salinities have occurred on roadsides in north eastern England for at least 15 years.

The salinities found in the soils of the more saline roadsides are far higher than those ever found in agricultural soils. They are classified by Richards (1956) (Table 2.7) as strongly saline, or very strongly saline, on which only salt tolerant species can grow. The most saline soils recorded in north eastern England are well beyond the range of those quoted in Richards (1954) and are similar in salinity to saltmarshes (Jeffries 1977) and saltpans (Unger 1979).

It is difficult to compare the salinity of these roadsides with reports by other workers for other roads, because as pointed out in Chapter Two the methods used by most other workers produce data which make comparisons unreliable. If the results of this study are converted to p.p.m. using Table 2.2, comparisons can be made, but only approximately and with caution, with those of other investigations. To give some examples a typical conductivity of 10 m-siemens for the verge of the A1 at Seaton Burn which had a saturation percentage of 48.1 (mean for 10 samples), becomes 3,410 p.p.m. NaCl. A typical peak conductivity recorded in a dry period in summer is 45 m-siemens, which would become 15,100 p.p.m. NaCl. For the soil beside the Morpeth by-pass which had a mean saturation percentage of 38.2 and typical salinity of 3 m-siemens, the salinity becomes 710 p.p.m NaCl. The highest conductivity recorded during the study was 86 m-siemens on the Seghill section of the Al. This section had a mean saturation percentage of 52.2 and so the salinity becomes 28,000 p.p.m. NaCl.

These results are high in comparison with those of other workers (Table 2.8). The only recorded salinities in the same range are all for roads around North American cities (Roberts & Zybura 1967, Butler et al. 1971, Catling & McKay 1980). These are also the reports which mention extensive areas of bare ground caused by de-icing salt. The comparitively high levels of salt in the soils of this present study may be the reason why similar peaks of salinity in summer have not been described before. The few reported measurements of salinity throughout the year have been done on roads with lower levels of salt (Prior & Borthouex 1967, Vestergaard 1971, Foster & Mann 1977, Brod & Preusse 1980).

In Britain, roadside soil salinities in areas other than north eastern England have all been much lower. The highest recorded elsewhere were for the most exposed sections of the M62 and M63 where they crossed the Pennines (Colwill et al. 1976; Thompson et al. 1979). The salinities recorded there (the highest salinity recorded was 4,101 ppm Na at one site in April) were considerably lower than those recorded in this study for very exposed sites. Ranwell et al. (1973) recorded salinities on roadsides at several localities in England, the highest was for the Al in Yorkshire (904ppm Na) and others in Derbyshire, Norfolk and Cambridgeshire, were much lower.

The higher soil salinities in north eastern England occur despite the fact that these roads have salting rates no higher than on other major roads in northern England (Ranwell et al. 1973), and only half that applied to the M62 and M63 where they cross the Pennines (Thompson et al. 1979). This was confirmed by the I.C.I. Salt Marketing Division which reported that sales of salt are equally high to most of the counties of northern England. However, of the areas in north England with high traffic volumes the area around Newcastle has the lowest rainfall and it is probably this factor which is causing the extra high salinities. This agrees with the finding of Colwill et al. (1982) from the model they developed to predict roadside soil salinities from salt application rates and climatic data. They reasoned that both high salting rates and low rainfall would result in increased salinity and predicted that the highest salinity would occur in winter in soils beside roads in north central and north eastern England. The occurrence of a higher peak in summer they did not foresee.

Local variations in soil salinity.

The other interesting aspect of the soil salinity data is the difference between sites. The sites on the Morpeth by-pass tended to have lower salinities which fell quickly after the end of salting, and did not tend to have much, if any, of a peak in summer. The sites on the Seaton Burn and Seghill sections, in comparison, had high salinities, with the highest peaks occurring in summer. The soils of the Morpeth by-pass are very distinctive and unusual for the area; the embankments and some of the other verges are constructed from a well-drained substrate of shale. Salt is easily washed out of these soils so that soil salinity drops quickly after the winter and tends not to rise again in summer. The verges and embankments of the other sections of road are constructed from heavy clay. With high salt application clay soils deflocculate (Waisel 1972) and this results in the breakdown of soil structure and restricted water movement. Salt is not leached quickly and consequently builds up at the surface in summer due to evaporation (Westing 1969).

The differences in soil types also results in differences in the water relations of plants growing on them. The well-drained soils of the Morpeth by-pass tend to suffer from drought in the summer whereas the clays of the other sites, particularly those affected by high levels of salt (Waisel 1972) tend to be waterlogged during wet weather.

The ordination of the sites using Decorana demonstrated the differences between the sections of road. The first axis of the ordination was related to salinity and on this the Morpeth by-pass sites occurred towards the non-saline end. The second axis appeared to be related to the water relations of the site with drought tolerant species at the top and waterlogging tolerant species at the bottom. On this axis the Morpeth by-pass sites were distinctly nearer the drought end than those of the other sections of road. The soils of high salinity, from the sections other than the Morpeth by-pass were indicated as being prone to waterlogging.

Causes of soil salinity.

The soil salinity of sites was significantly correlated with all of the measured environmental variables. These were: the salting rates and traffic volumes on the adjacent road, the exposure of the site and the orientation of the verge in relation to the prevailing wind direction (Table 7.3). The connection between the salinity of roadside soils and salting rates is an obvious one. High traffic volumes result in higher soil salinities on roadsides because they increase the spray which throws the saline water onto the verge while cross winds enhance this effect on the downwind verge. The influence of wind and exposure explains the difference between the salinities of the verges beside the north and south bound carriageways of north-south orientated roads (table 4.4). This was also reflected by the results using mean species frequency (Fig. 5.1 - 5.3) and in the Decorana ordination (Fig. 5.12). The prevailing wind in the Newcastle area is from the west so that salt spray tends to be blown onto the south bound carriageways. Such an asymmetry in soil salinity has also been demonstrated for the M62 in the Peninnes by Colwill et al. 1976. They suggested that it could be caused either by the prevailing wind or by the incline of the road at the site. Sucoff (1975) has shown a significant effect of traffic volume on the salinity of roadside soils in Canada.

The multiple regression of the four environmental variables accounts for only 31% of the variation in soil salinity, so there must be other major variables involved. Variations due to sampling and measurement error will account for some variability. Also likely to be important is the effect of vegetation cover. In the growth experiments at the University garden (Chapter six), sites receiving identical amounts of de-icing salt had much lower soil salinities when covered with vegetation than when bare. Vegetation may maintain soil structure and so minimise waterlogging and allow the salt to be leached by rainfall. Although the amount of vegetation is, in turn, influenced by levels of salt spray, it is also influenced by other factors such as erosion and compaction due to vehicles leaving the road. Also of possible significance is the difference in traffic density during the day. De-icing salt is usually applied during the night or early morning and traffic flow after then is higher going south on all of the roads examined because of the rush hour traffic into the Tyneside area. Greater traffic density at this time will result in more salt being thrown onto the verges beside the south-bound lane.

Species zonation on roadsides.

The calculation of mean species frequency across transects away from the road (Fig. 5.1 - 5.3) demonstrated well how both the invading maritime species and other species on roadsides tend to be zoned. The position on the transect in which a maritime species tends to occur is related to the type of habitat it occurs in at the coast. Species described earlier as being from disturbed saline habitats occurred near to the road (Puccinellia distans, Spergularia marina, Atriplex littoralis), as did the species which act as colonisers in saltmarshes (Puccinellia maritima and Suaeda maritima). The other species from saltmarshes and those from stable saline habitats tended to occur further back from the road. Plantago maritima is a good example.

The non-maritime species were also zoned. A few of these occurred on the more saline soils, such as Atriplex spp., Polygonum spp., and Matricaria maritima. These species are also known to occur in coastal saline sites (Tansley 1939). Hordeum jubatum tends to occur in the same zone on roadsides as it does around saltpans (Unger, 1974), between the zones dominated by salt tolerant plants and the glycophytic grassland. In this zone species density was at its highest and there were many species which occurred only at this point. Good examples are Leontodon autumnalis, Plantago major, Sonchus asper and Artemisia vulgaris. This was also the point at which the species of the amenity mixture first appeared. Of these Lolium perenne tended to occur principally in this zone. Further away still from the saline zone, Festuca rubra dominated the sward to the exclusion of most other species.

The series of divisions in the dendogram created using Twinspan was related to species position on the transect. This method therefore gave the same kind of results as the analysis using mean species frequency but as it was not confined to a single section of road , it demonstrated the zonation of many more species on the transect.

Zonations in species density or performance across gradients in stress are well known. Zonation involving many of the same species as occur in the roadside transects have been described by Unger (1974) and Catling and McKay (1980) for saltpans in the United States and by Lee (1977) for inland saltmarshes in Britain. On the roadside, several stresses decrease with distance from the road, notably salinity, turbulence, abrasion and burial by road grit, compaction due to vehicles, insects, and pollutants such as N0x, hydrocarbons and lead. Although many of these stresses are without doubt of importance in this environment and will be discussed later, several observations and factors indicate that the gradient in soil salinity is the principal cause of the zonation. The analysis in chapter five showed that the distance of zones from the road is related to the salinity. Thus the more saline the site the further away from the road the invading maritime species are found (Fig 5.5). The ranking of these species according to their salt tolerance as measured in the laboratory in sand culture (Fig 6.1) was the same as the order in which these species occurred across roadside transects. Furthermore, the glycophytic species receded as the salinity increased (Fig 5.6) and the two grassland species which were included in the laboratory test of salt tolerance, Festuca rubra and Lolium perenne, had the lowest salt tolerance (Fig 6.1). Of the species originally sown in the amenity mixture Lolium perenne tended to occur nearest to the road, which agrees with the results of the trials at the University garden (Fig 6.3) in which it proved to be slightly more tolerant than the other species. The comparativly higher tolerance of this species was also noted by Beddeus (1967) and Fults (1972).

There are other important factors involved in the zonation of species across salinity gradients. In the literature as well as salinity tolerance, competition is seen as the other principal factor (Barbour 1970, Wainwright 1980); salt tolerance determining penetration into the saline zone, and competition from glycophytes controlling the invasion of salt tolerant species into the non-saline zone. On roadsides in north eastern England the competition is from the grassland species, particularly Festuca rubra, which dominates the glycophytic grassland sward.

Changes in species density.

Mean species density (number of species /unit area) was calculated for each quadrat in the transects (Fig. 5.7) described in chapter 5. Near the road, density was low, across the transect it rose to a peak and then fell. This pattern was strikingly similiar to the "humpback" model proposed by Grime (1973; 1979) to account for variation in density in relationship to gradients in disturbance or stress and competition (Fig. 10.1). According to this model where stress or disturbance is at its greatest only a few species, particularly tolerant of the conditions, are able to survive. As the stress or disturbance ameliorates, more species are able to survive and so density increases. When the stress or disturbance is so low that dominant species (in the sense of Grime, 1979) are able to grow they suppress other species and density decreases. Examples in the literature of such gradients are where there is; disturbance caused by frost shatter in a tundra area (Fox, 1981), disturbance caused by trampling next to a path (Grime, 1973), the stresses of lead on minespill heaps and of drought on limestone outcrops (Grime, 1973).

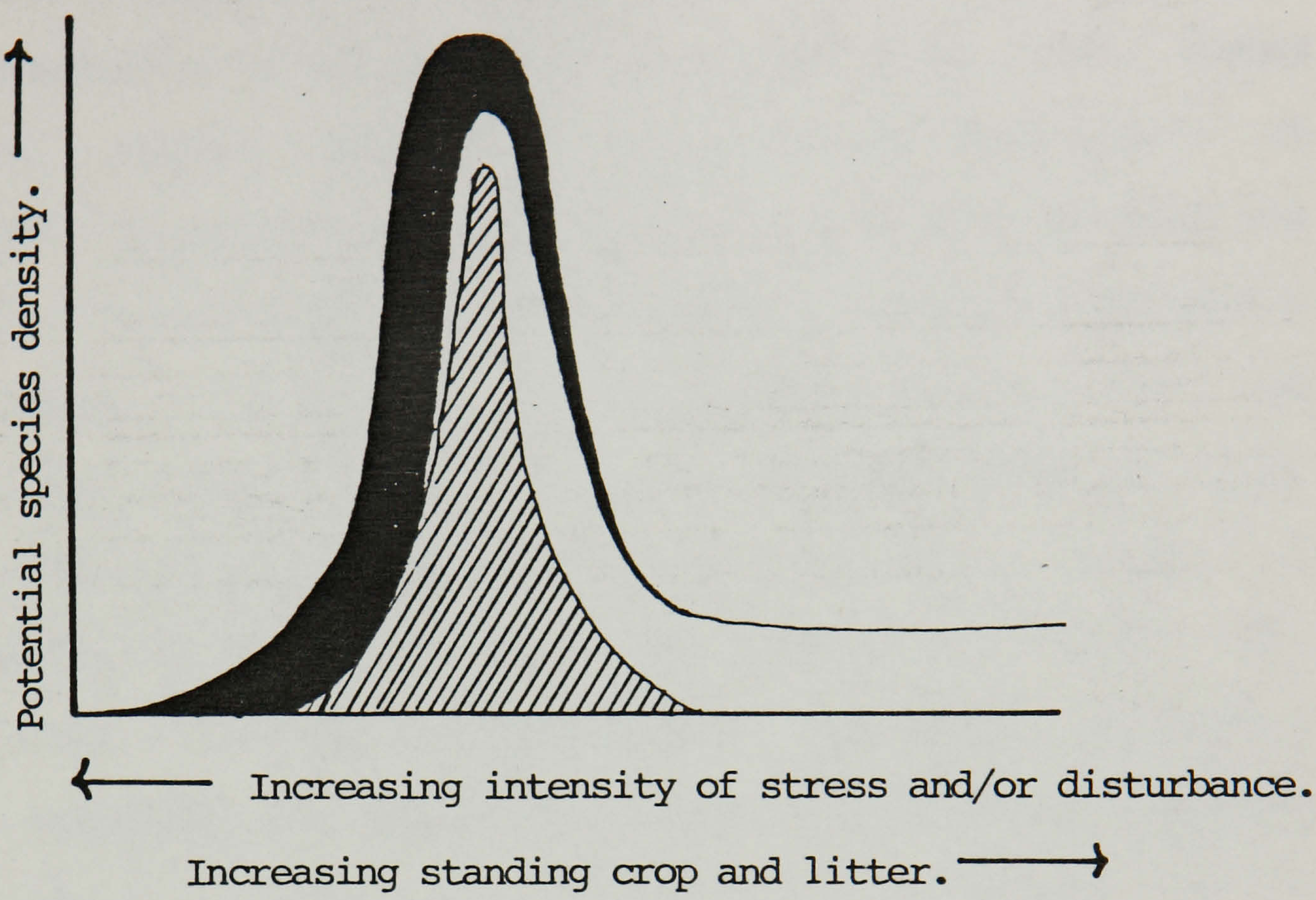


Fig 10.1 Model describing the impact of a gradient of increasing stress and/or disturbance upon the potential species density in herbacous vegetation; □ potential dominants; ■ species or ecotypes highly adapted to the prevailing form(s) of stress or disturbance; ▨ species which are neither potential dominants nor highly adapted to stress or disturbance (after Grime 1973; 1979).

On roadsides it is obviously the gradient in stress due to soil salinity which principally causes the zonation and initial variation in density. The invading maritime species which occur on the most saline soils are according to the classification used by Grime (1979), stress tolerators. However, there also appears to be some effect of "disturbance" using the term in the sense of Grime (1979) to mean the occurence of factors that limit plant biomass by causing its partial or total destruction. In some of the soils monitored (Fig 4.5, 4.6) the stress is ameliorated in summer as the salt is washed from the soil. Summer-annual species can thus avoid high soil salinities. Several of the annual species on these roadsides were classified by Grime (1983 and pers comm) as tolerators of disturbance. Such species as Senecio vulgaris, Polygonum spp., Matricaria maritima and Chamomilla suaveolens tend to occur on soils which have high salinities in winter and low ones in summer.

The species furthest away from roads are all competitive dominants in Grime´s (1979) classification. They have comparitively high dominance indices (Grime 1979 and pers comm.), which is an index derived from a summation of the relative growth rate, height, morphology and litter production (Grime, 1973; 1979). Two of the characteristics of this group described by Grime (1979) are high dry weight of standing crop, and high litter production. Several of the species in the glycophytic grassland sward have both of these characteristics, particularly Festuca rubra. In the transects described in chapter 5 as salinity decreased and allowed the dominants to grow, the total standing crop and litter increased (Fig. 5.8). When these two measurements reached a high level, the density of species decreased. This inverse relationship between total standing crop and species density was also demonstrated when the data for several sites were used to plot a scatter diagram (Fig. 5.9). The result was very similar to scatter diagrams published by Grime (1979) for several grassland habitats, including roadsides and by Oh and Kang (1983) for saltmarshes and grassland sites.

The maximum species density in the roadside transects was, however, lower than that found by other workers. This could be because the roadsides studied are a relatively recent habitat and have not yet achieved their maximum species density. Another difference is that there is a slight rise at the grassland end of the transect in species density. This is possibly due to the invasion of the grassland sward by species from the adjacent hedges or farmland. Many of the sites were next to uncultivated land containing a lot of tall herbs.

In both surveys described in chapter Five, quadrats containing Agropyron repens were distinctly different from the others (Fig 5.9, 5.10). On the roadside, this species occurs in relatively tall single species stands near to the road. It does not grow far back into the Festuca rubra dominated sward, although it is taller than most of the species in the sward. It appears, therefore, to be one of the species of the transition between the high salt zone and the grassland, with the unusual ability to dominate this normally high species density zone to the exclusion of other species. It is a species which does not compete well in dense grassland turf as it is rapidly eliminated from arable land when it is sown to pasture or meadow. Presumably it is out-competed by Festuca rubra on the non-saline soils on roadsides but as it is more tolerant of salinity than Festuca rubra it can occur nearer to the road. It is much less salt tolerant than the maritime species (Fig. 6.1), but despite this it often invades some way into the high salinity zone. This may be because its rhizomes allow water and nutrients to be transferred to the invading tillers.

Local variations in species distribution.

A number of observations in this study indicated that there are differences in the local distribution of species on the roads around Newcastle upon Tyne. Ordination using Decorana allowed a closer analysis of these differences and gave some indication of the possible causes.

The first axis of the ordination created using Decorana was related to salinity. The distribution of species along this axis was basically the same as that demonstrated using the methods of mean species frequency and Twinspan.

On the second axis, which was apparently related to the water relations of the sites, species associated with the Morpeth by-pass had a high loading. Many of the species described by Grime (1983 and pers comm) as disturbance tolerators are particularly common on the Morpeth by-pass, for instance Matricaria maritima, Chamomilla suaveolens, Senecio vulgaris, Poa annua and Atriplex patula. These species are mostly annuals and avoid high salinity by only growing in summer when the salt is washed from the soils of this section of road. The fact that these soils are also prone to drought may also act as a disturbance (in the sense of Grime, 1979) of the habitat. Catling and McKay (1980) described similar well-drained verges on the roads around Toronto which had some of the same species as the Morpeth by-pass. They also suggested that plants of this habitat avoid salinity by growing only in summer.

Most of the records of Plantago maritima were from the Morpeth section of road and it appears at the top of the ordination. Populations of this species on the Morpeth by-pass are often large with many seedlings, but those on other sections of road usually consist of one or two older plants with few seedlings. Species from this genus are known for their ability to withstand drought (Sagar & Harper 1964), and in fact both Plantago major and P. lanceolata are also frequent on this section of road, and occur higher on the second axis. Water stress, however, may not be the sole explanation for the difference in success on the two soil types. One adaptation Plantago maritima has to the high salinity of the upper saltmarsh in summer is to cease growth (Jeffries et al. 1979), but this strategy would not work on the heavy clays of the other sections of road as salinity on these soils, unlike saltmarsh soils, can remain very high all year round. This perhaps explains why this species is infrequent on heavy soils and why it never occurs in the more saline zone (Fig. 5.1), although it is known to grow on very saline soils in saltmarshes.

In contrast, Spergularia marina seems to occur only in sites which are periodically waterlogged and it is found lower on the ordination axis. Catling and McKay (1980) noted a similar distribution for this species and it also agrees with an observation of Sterk (1969) that natural populations occur in and around transient saline pools. The other maritime species on roadsides all have loadings on the second axis which tend to be low but not as low as Spergularia marina. Of these, the only two which are sufficiently widespread for conclusions on soil preference to be made are Puccinellia distans and Puccinellia maritima. Both seem to be more catholic. They tolerate waterlogged soils but also grow elsewhere, although neither grows well or densely on the well-drained soils of the Morpeth by-pass, perhaps indicating some susceptibility to water stress. Both species grow on waterlogged soils on the coast but are not confined to them (Brereton 1971, Beeftink 1977), and P. maritima's tolerance of waterlogged conditions has been demonstrated by Gray (1970). Hordeum jubatum grows in the same roadside soils as these two species and occurs at the same position on the ordination. It has been reported from other waterlogged soils (Dodd & Coupland 1967), and Wilson (1967) has shown how it competes most succesfully in saline and waterlogged conditions.

The effects of salt on growth.

The effect of treatment with salt on the growth of maritime species varied considerably in the different experiments performed in this thesis. When grown in sand in the laboratory, the application of increasing levels of salt reduced the final shoot dry weight of all species (Fig. 6.1). Other workers have grown some of the same species under broadly similar conditions with similar results (Lunt, Younger & Oertli 1961; Venables & Wilkins 1978). Some maritime species, including Suaeda maritima and Aster tripolium, have been found to grow slightly better in low-salt treatments than in the controls (Flowers, Troke & Yeo 1977; Rozema et al. 1983; Lee & Ignacuik 1984) but growth in the controls has never been so low as to lead to any suggestion of an obligate requirement for salt (Barbour 1970).

In the competition trials at the University garden (Table 6.1) maritime species were able to grow only when the sward was damaged by treatment with de-icing salt, suggesting that these species may be excluded from non-saline soils simply by competition. Similar results were found in competition trials by Gray & Scott (1977b). However,on the same soils without competition, the maritime species did not establish properly, and they exhibited marked symptoms of stress and remained small. The roadside trials (Figs. 6.7-6.9) gave a similar result in that the maritime species were completely unable to establish without additional salt. The two experiments strongly suggest that there is a positive requirement for salt under certain circumstances. On the other hand, other workers have had no difficulty establishing some of these species on garden soils (Hughes et al. 1975), although the soils involved would appear to have been more fertile than those used in the present work.

The subsequent trials investigating the growth of two of the maritime species on the same garden and roadside soils, but under controlled conditions (Figs. 6.10, 6.11) allowed a direct comparison of growth on these soils with that in sand culture. In controlled conditions, individuals grew on both substrates without salt, and there were no symptoms of stress. Growth was, however, still greater on the soils treated with salt. This indicates that the requirement for salt is partially determined by the external environment and partially by physical or chemical features of the substrate.

The application of nutrients in the second trial (Fig. 6.11) reversed the effect of salt. This may indicate that nutrients are important in some way to the requirement for salt in the field. It is to be remembered that plants growing in sand received a nutrient treatment. The effect of adding nutrients also indicates a possible cause for the enhanced growth in the soils from adjacent to the road as opposed to those from three metres back in the first trial (Fig 6.10). For when nutrients were added to the soils from three metres from the road the enhanced growth matched that achieved in the soils from adjacent to the road without added nutrients (Fig 6.11). This indicates that roadside soils may have enhanced levels of one or more nutrients. The most likely is nitrogen which could be washed into the soil from exhaust fumes, which contain high levels of nitrogen compounds (Mansfield 1979). High levels of nitrogen in the strip of soil beside major roads is also indicated by two other facts. Many of the plants associated with this habitat, such as Atriplex spp. and Polygonum spp. are associated elsewhere with soils of high nitrogen status, for instance the strand line (Salisbury 1952; Beeftink 1966; Lee et al. 1983) and urban sites (Ubrizsy 1951). Two of the strand-line Atriplex species have been shown to need high levels of nitrogen to withstand enhanced salinity (Rozema et al. 1983).

Secondly, it has been shown that herbivorous invertebrates occur in much greater numbers adjacent to the road than they do away from it (Pinnock 1976; Fluckiger et al. 1978; Port and Thompson 1980). Port and Thompson (1980) showed that this correlated with high levels of total nitrogen in roadside plants and they suggested that this was being taken up directly from exhaust fumes emmitted by passing vehicles. It could also be taken up by plants via the soil.

Freezing resistance.

The methods for the testing of freezing resistance have been investigated and perfected by several workers (eg. Lorenzetti et al. 1971; Fuller & Eagles 1978; Pearce & McDonald 1978), and are believed to provide a reasonably quantitative assessment. However, as there are a number of factors that differ between the laboratory and the field, two inland species were included in the trial for comparison. Agropyron repens proved to have an L.T. 50 lower than -11°C. This agrees with the fact that this species regularly survives winters inland without apparent damage. The L.T. 50 of the other species, Lolium perenne cv S.23, was -8.1°C, which is very close to that found by Fuller & Eagles (1980), and Davison & Bailey (1982) for the same species. Individuals of this species can be killed in a hard winter (Hides 1978).

As Agropyron repens and Lolium perenne both persist through most winters, their measured freezing resistance can be used as a comparison for maritime species. Those species with less resistance to freezing than Lolium perenne (ie. higher L.T.50's) are likely to be killed or severely depleted in a hard winter. These species are Aster tripolium, Cochlearia officinalis, Plantago coronopus, Spergularia marina and Suaeda maritima. Although the last two are summer annuals which will avoid most winter frosts, the particular sensitivity of Suaeda *maritima*, which had an L.T.50 of -0.7°C, would limit this species in north eastern England, where there are frequently early and late frosts that extend into the growing season. The freezing resistance of *Cochlearia officinalis* and *Plantago maritima* are very low for species known to occur on mountains. However, this would be explained if there are population differences in freezing resistance.

For those species with greater freezing resistance than *Lolium perenne*, sensitivity to frosts is unlikely to be important to their distribution inland in north eastern England. This is particularly true for *Puccinellia distans*, all the individuals of which survived the lowest temperature of -11° C. Butler (pers. comm.) has also investigated the freezing resistance of this species and found the L.T.50 was -27°C.

The effect of salt on freezing resistance.

The application of salt affected the freezing resistance of some of the species. There was a significant increase in survival and subsequent growth in *Lolium perenne*, *Puccinellia maritima* and *Spergularia marina*. This did not occur with *Aster tripolium*, and there was a significant decrease in survival for *Plantago maritima*. Increased freezing resistance caused by pre-treatment with another stress has been described before. Most examples involve drought (Cox & Levitt 1976; Chen & Li 1978; Steponkus 1980) but there are also examples involving salt (Maier & Kappen 1979; Kappen 1979). Sucoff *et al.* (1976a, 1976b) showed how pre-treatment with salt can have the opposite effect. *Malus* twigs sprayed with de-icing salt became more sensitive to freezing and they proposed that this was the cause of die-back in trees beside salted roads.

The hardening regime of two weeks that these plants received is believed to be sufficent to fully harden them (Lorenzetti *et al.* 1971; Fuller & Eagles 1978), but an alternative explanation is that the three species that showed an increase in resistance were not fully hardened and that treatment with salt had completed the hardening. The other two species could already have been fully hardened, and thus were unaffected by the salt treatment. It would be worthwhile trying the same experiment with varying hardening regimes.

The last experiment, in which the level of salt application was increased, needs to be repeated before any firm conclusions can be drawn. The results did indicate the importance of the level of salt application and a closer examination of this factor could also prove worthwhile. It may be that at a lower salinity *Plantago maritima* and *Aster tripolium* would show enhanced freezing resistance.

The relativly low freezing resistance of some of the maritime species and the enhancement of resistance by salt gives a reason for their confinement to the coast and to saline sites inland. However, the extent of the effect of salt on freezing resistance does not appear to be great enough on its own to explain the confinement of these species to saline soils. This is particularly so when it is considered that the interaction also occurs in a non-maritime species, *Lolium perenne*, and does not occur in two of the maritime species. This interaction will be discussed further after considering some of the other results.

The nature of the requirement for salt.

The experiments on the effect of salt on growth in chapter Six clearly indicated that, whilst competition may limit maritime species in non-saline soils, there also appears to be some form of requirement for salt for successful establishment and growth even in the absence of competition. These experiments also gave some important indications of what it might be. Firstly, the substrate the plant is growing on appears to be of importance. Plants were unable to grow properly without salt on soils from the roadside and the university garden but grew well in sand culture. Secondly, the extent of the requirement was greater in the field than on the same soils in the laboratory. Therefore, the requirement must be both associated with the form of substrate and with some aspect of the environment in the field. The recovery of Plantago maritima in the second year of the garden trials indicates that the requirement may be transient and only important during germination or establishment.

The trials in chapter Eight demonstrated that any treatment which supplied ions which are readily absorbed by the plant overcame the need for salt. Treatments which applied ions that were not so readily absorbed (e.g SO_4) had decreased effectiveness in overcoming the requirement. It would appear therefore that the requirement was not for any specific ion, but for any treatment which increases the available ions in the soil solution. Both the soils at the roadside and at the University garden were clays of low fertility and so likely to have very low concentrations of ions in solution. In comparison media used in laboratory experiments have a relatively high concentration of dissolved, readily absorbed ions. Even dilute standard culture solutions have remarkably high ionic concentrations (Fisher pers. comm.). This would explain why there was no requirement for salt when the same plants were grown in sand culture and why this rquirement has not been noted in other laboratory work. The results of Rozema et al. (1983) who found that the growth of four strandline species was stimulated by salt only when grown in media of low fertility could be an example of the same requirement.

The pattern of distribution of some of the maritime species in Britain also provides evidence for a requirement for soils with solutions of high ionic concentration. Plantago maritima occurs on saline soils by the coast and "base rich" soils inland (Tutin et al 1976). These soils are likely to have solutions with enhanced ionic concentration. For instance the magnesian limestone soils from beneath plants of Puccinellia distans and Plantago maritima at Pittington Quarry in Co. Durham had soil conductivities with a mean of 2.6 m-siemens. This is also true of the soils from the disturbed habitats that Puccinellia distans occurs in. The saline soils are heavily grazed saltmarshes or other disturbed saline sites; the non-saline soils are nearly all urban sites or quarries. These habitats often have soils with a high ionic concentration. Urban sites are often high in nitrogen and phosphorus (Davison 1971) and the quarries are often on base rich rocks. In North America Puccinellia distans appears to have a similiar distribution. Catling and McKay (1980), when describing the roadside distribution of this species in Ontario wrote that it grows equally well on calcareous soils and has been found growing along the chalk lines marking playing fields. In Czechoslovakia, P. distans has been reported growing on soils contaminated by industry with high levels of magnesium salts (Krippelova 1971).

In the immediate post ice-age period, many of today´s maritime species were considerably more widespread (Godwin 1975). They appear to have been common in the large areas of open vegetatation (Bell 1969) and it has been suggested that their present maritime and montane sites represent refuges during the interglacials (Godwin 1975). In the post glacial many soils may have had relatively high concentrations of dissolved ions because of the recent glacial action.

The correlation between distribution and a requirement for certain soil conditions is complicated, however, by competition.

Competition is obviously of primary importance in explaining the distribution of these species. Their low growth rates and perhaps other adaptations to stress may reduce their ability to compete on non-stressed soils. The view that competition is the sole explanation for their exclusion from non saline soils (e.g. Barbour 1970; Waisel 1972; Wainwright 1980) is however, obviously incorrect. It appears that the species are incapable of proper growth on such soils even in the absence of competition.

Another aspect of the requirement for salt is the interaction between salt treatment and resistance to other stresses. In the trials in Chapter Eight the prevention of drought increased the survival of the species but not their growth. In the freezing resistance trials (Chap. 7) salt increased the resistance of some maritime species to freezing. It would appear, therefore, that when these maritime species are grown in a medium of low ionic concentration they are unable to withstand other stresses. This would explain why they did not die when grown in roadside soils transferred to the stress-free controlled conditions of the laboratory and when protected from drought in the garden trials. In both situations the species survived but did not grow as well as when supplied with salt. Interaction between the hardening of a species to one stress and the hardiness to other stresses have been described by Cox and Levitt (1976), Chen et al. (1977), Chen & Li (1978), Maier & Kappen (1979) Steponkus (1980) and Smirnoff and Stewart (1984). Several workers have shown how different stresses can all result in increased production of proline (Palfi & Juhas 1970; Chu, Aspinall & Paleg 1974, 1976; Paquin 1977; Stefl et al 1978; Stewart & Larher 1980; Smirnoff & Stewart 1984). All the species which showed increased freezing resistance when treated with salt in chapter Seven are known to accumulate proline when under salinity stress (Stewart et al. 1979, Stewart & Larher 1980) and

Lolium perenne is known to accumulate proline in hardening to low temperatures (Draper 1971). Of the other two species, _Plantago maritima_ accumulates sorbitol in response to osmotic stress, and _Aster tripolium_ accumulates both methylated quaternary ammonium compounds and proline (Stewart _et al._ 1979). This might indicate that only those species which accumulate proline have a positive interaction between salt and freezing resistance. However, in the roadside trials _Plantago maritima_ was also unable to grow without salt.

It would appear possible that osmoregulatory agents are involved in the interaction between the hardiness to different stresses. Steponkus (1980) and Stewart & Larher (1980) have pointed out that frost, drought and salt stress all result in cell dehydration. The role originally proposed for osmoregulatory agents is the prevention of cell dehydration due to salinity (Stewart & Lee 1974). It seems possible that an increased concentration of any readily absorbed ion in the growth medium triggers the accumulation of these agents not the particular ions of sodium chloride. This has been demonstrated by Ahmed, Larher and Stewart (1981), who showed that polyethylene glycol 6000 had exactly the same effect on this accumulation in _Puccinellia maritima_ as an iso-osmotic solution of sodium chloride.

One hypothesis which would fit the facts known about the requirement for salt and which might be used as the basis for further work is that the physiology of these species is so adapted to the high concentrations of ions that they actually require a minimum level to function efficiently. Without this basic level the plant's growth is reduced, production of compatible solutes that act as protectants is low and so tolerance of other stresses is minimal.

Reclamation of saltburn.

All three sites used for the first reclamation trial proved to be subjected to other stresses as well as high salinity. The sites at Morpeth and Newcastle Airport were regularly disturbed and the soil compacted. At the former site this was caused by vehicles mounting the verge and at the latter by a combination of pedestrians using it as a footpath and erosion by water. The site at Seghill suffered from exposure. This site also had much higher salinity than the other two sites (Chap. 2).

Only the two Puccinellia species were able to establish properly on the bare soil at these sites. P. distans was successful at the Morpeth and Newcastle Airport sites. It was able to establish rapidly, achieving more than 50% cover in the first summer. It was also able to recover rapidly from the disturbance at these sites. In subsequent years it spread extensively onto adjacent saline verges. Butler (1977) had similar success establishing this species on roadsides in Ohio. It did not, however, establish properly on the exposed site at Seghill and Puccinellia distans did not create an ideal sward. The species is tufted, shallow rooted and so easily uprooted, and plants often die after seed set. Gray (1978) tried this species in sea bank trials and also found that it established and spread quickly, but concluded that it did not create a sward which would bind the soil well. Puccinellia maritima established well in all three sites. The complete cover of the sites took several years, however. The species did not appear in the first summer as the sowing was in spring and it needs a frost before it will germinate. The cover in the second year was much lower than the initial cover achieved by P. distans, but P. maritima has a spreading habit and in subsequent years it achieved the same cover as P. distans at the Morpeth and Newcastle Airport sites. It was also slow to recover from disturbance at these sites. The success of the species at the Seghill site was due to its spreading habit. Although, as with P. distans, only a few individuals established initially in this harsh environment, these were able to spread in the following years. The sward created by this species is matted and dense. This helps to bind the soil and prevent erosion. Gray (1978) also found this species successful in trials on the sea wall. It created a dense and stable sward which bound the soil.

The drought tolerant Festuca rubra cv. "Hawk" did not prove a success. In trials on the sea wall (Gray 1978) this variety proved tolerant of salt and drought. Thus it was surprising that in the roadside trials the cover achieved in the replicates was not significantly greater than in the control. This may indicate that seed was not germinating. Germination was good, however, in the laboratory before sowing, so its non-appearance at the sites is difficult to explain.

The amenity mixture was also not successful. Although it established well in the first summer at the two less saline sites, most of it was killed in the following winter.

The second trial was not a success. Although the maritime species established in places and achieved a slightly better cover than the amenity mixture, still most of the ground badly affected by salt was bare. This appeared to be because of the late sowing of the trial and the subsequent drought. This trial can not therefore be used as an assessment of the potential of a mixture of maritime species with amenity species.

The two Puccinellia species have complementary characters for the reclamation of saltburn. P. distans establishes and spreads rapidly both within the site and to other saline roadsides nearby. It is able to recover quickly from disturbance, something which occurs often on roadsides. Although P. maritima establishes a sward more slowly, it is able to do so in harsher habitats. The sward it does eventually create is much more matted and dense, and so harder wearing and better protection against soil erosion. Both species are low growing and so will need little maintenance. The ideal would be to sow the two species together. This would make use of the complementary characters of each species. Such a mixture could well prove successful on other saline soils, as it could be both quick in establishing and eventually dense and closely bound together. P. maritima is not, however, commercially available and would be difficult to harvest on a large scale. Flowering panicles are close to the plant and often grow laterally and near to the ground. Also seed production can be very variable. Both problems should be surmountable, but whether the potential market would make this worthwhile is questionable.

P. distans is available commercially as the variety 'Fults'. This North American variety proved successful on roads in Britain. The species has the added attraction that if introduced on one roadside in an area, it will rapidly spread to others with bare soil.

The simple method for sowing the species adopted in these trials proved successful as long as, if it was an exposed site, it was done in wet weather. The raking over of the verge before and after the sowing could be done on a larger scale mechanically by something such as a chain harrow. The second trial demonstrated the susceptibility of these sowings to drought in their initial stages. It would seem best, therefore, to sow verges during the winter, (if Puccinellia maritima is to be used,during early winter, to allow it to receive some low temperatures). An alternative method would be hydroseeding as described by Bradshaw and Roberts (1979) for roadside embankments. This method would bind the seed to the bare soil as well as giving a better medium for its initial establishment. A further alternative is the creation of turves using Puccinellia distans and a binding species, and transferring these to the roadside. Butler (1977) did this, and found that after a year on the roadside the binding species, Poa pratensis, had disappeared and Puccinellia distans remained as a good cover. Both of these alternatives would rapidly create a more dense sward. They would, however, be much more expensive than the simple method used in this study.

Concluding remarks and resume.

As this was the first detailed research into the invasion of roadsides by halophytes it had to be wideranging in its approach. Thus it gave rise to several different sets of conclusions and it highlighted several areas for possible future investigation. It was probably also the first time that the invasion of a man-made habitat by plants had been so fully investigated while the invasion was still occurring. This made it easier to demonstrate the probable origins of the invasion and mechanisms of dispersal. The evidence accumulated indicated that the invading species mostly originated from coastal sites and were carried to major roads on vehicles. Further quantitative evidence for this possibility could be sought using the methods developed by Wace (1979) who examined seed caught in car washes. If seed of maritime species is present on vehicles then it should be present in the sediment from any car wash near a road with maritime species on it.

Once the plants are on roadside seed is swept along in the slipstream of passing vehicles. Experiments using seed traps also demonstrated that lighter seeds are carried much further, perhaps explaining why species adapted to disturbed habitats, which produce a lot of light seed, are the most successful at invading roadsides. Of these Puccinellia distans has spread most rapidly and has probably invaded all the areas of England and Wales that currently have saline roadsides. Other species from disturbed saline habitats such as Spergularia marina, Cochlearia danica, Parapholis strigosa and other Puccinellia species are also spreading comparatively rapidly and may eventually be as widespread as P.distans. Further progress of the invasion will be recorded by requesting records through the B.S.B.I. and publishing updated distribution maps in their journal.

Roadside soil salinities recorded during this project were very high, some much higher than any previously recorded in Britain. Furthermore for the first time summer peaks in salinity were recorded. The high salinities were due to the large amounts of salt used in north eastern England and to the areas comparatively low rainfall. The years with the highest peaks in salinity were those with low rainfall in early summer. It is possible that such summer peaks would be found for other highly saline roadside soils if these were recorded all year round. As well as high salt usage and low rainfall several other influences on the level of soil salinity were demonstrated, such as high traffic volume which increases the spray throwing saline water onto the verge and crosswinds which enhance this effect on the downwind verge. Elsewhere it was also shown that poorly draining soils tend to accumulate salts to a greater extent than well draining ones and that vegetation cover can give some protection to the soil, possibly by improving the drainage.

The project demonstrated the potential of man-made habitats for investigating ecological problems. It produced several insights into the ecology of the invading species which will be of use in understanding their biology in natural ecosystems. Local distribiution on verges was influenced by soil drainage with some of the species confined to certain soil types. This pattern was mostly in agreement with the known distribution of these species in other ecosystems, but there were some interesting anomalies which would be worth further research. One such was the poor performance of Plantago maritima on highly saline soils and its preference for better drained soils where the salinity was alleviated during the summer. The laboratory growth trials in which halophytes were grown on roadside soils also gave some unexpected results which would be worth further investigation. These indicated that roadside soils contain higher levels of available nitrogen next to the road, which may be derived from the gaseous nitrogen emitted by vehicles.

Species were zoned across verges in relation to salinity gradients in the same way as on saltmarshes and saltpans. Examination of the data for species density, bare ground, total standing crop and litter across this zonation confirmed Grimes´ (1979) model for the change in species density across a gradient in stress. However, experiments in which competition was removed, and those in which seed was sown onto salted and unsalted soils in the field showed unequivocally that all of the species used had a requirement for salt. Even in the absence of competition seedlings did not invade non-salted areas and when sown in such soils they grew very slowly, their appearance was abnormal and eventually many died. This was unexpected and the most significant finding of the project because it conflicted with conventional views on the nature of the relationship between halophytes and salt. Almost all of the research on the reaction of halophytes to salt has been done in the laboratory and the general conclusion is that all will survive and grow without saline conditions but some show a positive response to low levels of added salt. It is usually thought that the failure of halophytes to grow on non-saline soils is due to competition from glycophytes. In view of the demonstration that under field conditions halophytes do require salt it is important that this aspect of their physiology should receive further attention.

A working hypothesis for the salt requirement is that halophytes are so adapted to media with a high ionic concentration or low osmotic potential that they require such conditions in order to function normally and deal with environmental stresses. For example, it may be that in media with low ionic concentrations the plants do not produce compatible solutes such as proline which have the role of acting not only as osmoregulatory agents but also protect enzymes against the stresses of heat, freezing and drought. As a next step it is necessary to culture seedlings in the laboratory in dilute media (with osmotic potentials similiar to that of a poor non-saline soil) and reproduce the symptoms seen in the field experiments. Tolerance of physical and perhaps biological stresses should be reduced in such plants.

The work on the reclamation of saltburn was the first time halophytic grasses had been used for this purpose in Europe. It demonstrated that they have potential as a cheap method of reclaiming salt damaged land. It would be well worth attempting further trials with the two Puccinellia species, both separately and together and to explore the possibility of mechanical collection of P. maritima seed.

The continued concern over winter road safety seems likely to ensure that road de-icing salt will be used for the forseeable future at levels at least as high as those of the present. Thus the roadside communities of maritime halophytes seem destined to continue to develop. Many of the species present on roadsides will probably become more widespread and new species may appear. With time these communities should completly colonise salt damaged verges covering the unsightly bare ground and allowing the partial re-invasion by some non-maritime species because of the improved substrate. Any use of maritime grasses for the reclamation of salt damaged verges will enhance this process. This invasion and the resulting communities are [illegible] field for further research.

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