

# Population differentiation in the life-history characteristics of salt-marsh annuals\*

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## Abstract

Coastal salt marshes are heterogeneous spatially but predictable temporally. Genetic differentiation between populations on different parts of a marsh in response to this combination of circumstances has been well documented in several perennial species; differentiation has been evident in certain features of the life cycle that contribute to overall fitness.

Our studies of the annuals in the marshes of the north Norfolk coast of Britain have shown that there are distinct populations, that have particular micro-habitats and different vegetational affinities, within the annual species *Suaeda maritima* and within the complex of several closely related species of *Salicornia*. Consequently, three sequential questions about these annuals may be posed: 1. What is the extent of genetic differentiation? 2. What features of the life history show differentiation? 3. Can any of this variation be demonstrated to have adaptive value?

This paper reviews evidence for the upper- and lower-marsh populations of (diploid) *Salicornia europaea* agg. at Stiffkey, U.K. The six main approaches described comprise collateral cultivation, perturbation of the field environment, isozyme analysis and three types of reciprocal transplantation. The value of these complementary methods is discussed, and they are used to demonstrate that there is considerable genetic differentiation between the two populations; it is manifested in the phenology of growth, mortality and density-dependent fecundity. In terms of the ability of individuals to leave descendants, there is a dramatic reduction in fitness of each population when it is grown in the reciprocal environment. This finding indicates that the genetic differentiation has clear adaptive value.

## Introduction

The characteristics of coastal salt marshes are such that we might predict, a priori, the development of local differentiation in the genetic structure of plant populations within them. Salt marshes are heterogeneous in space but they vary in a cyclic,

largely predictable, manner in time (Gray, 1974; Jefferies *et al.*, 1979). The local selection pressures are broadly consistent from year to year and therefore consistent for any particular phase in an annual life cycle or for any phenological stage in a perennial one. Salt marsh perennials have been the subject of intensive genecological study from the seminal work on *Plantago maritima* (Turesson, 1922; Gregor, 1938) to recent detailed investigations on *Aster tripolium* (Gray, 1974) and *Puccinellia maritima* (Gray & Scott, 1980). There is ample evidence of genetically determined variation for many of the life-cycle characteristics that ultimately contribute

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to evolutionary fitness in plants (Solbrig, 1980). The annual plants of salt marshes might be expected to have responded particularly rapidly to selection pressures, because of their short generation time, but examination of the components of their life histories has received little attention until recently (Jefferies *et al.*, 1981; Davy & Jefferies, 1981).

The major features of the environmental heterogeneity at Stiffkey salt marsh, on the north Norfolk coast of Britain, have been described by Jefferies *et al.* (1979). Essentially, a relatively ancient area of marsh (upper marsh) is separated from a much more recently accreted lower marsh to the seaward, by a shingle bank. Except in rare storm surges, the tide does not overtop the bank. The main creek passes round the end of the shingle bank such that water overflows from the creek system onto the upper marsh with the flowing tide and drains back into it with the ebbing tide.

In contrast, water moves more directly up and down the lower marsh with the tide. This pattern tends to restrict the fluxes of seeds between the upper and lower marshes. Superimposed upon this major discontinuity is the pattern of pans, creeks and their levees, as well as microtopographic heterogeneity.

The lower marsh is flooded by most of the twice-daily high tides each year, whereas the upper marsh is completely covered only by spring tides, and is not covered at all for two four-week periods either side of the summer solstice. During these periods evapotranspiration usually exceeds precipitation, and this leads to very hypersaline conditions on the upper marsh. The greater amplitude of the annual variation in salinity on the upper marsh and the resulting low sediment water potentials in summer have been documented in detail by Jefferies *et al.* (1979). The smaller-scale differences in environment between other parts of the marsh are less obvious and are still being characterized.

Amongst the annual species, several morphologically and phenologically distinct populations occur both within the upper and lower marshes. The predominant *Salicornia* in the upper marsh corresponds with *Salicornia ramosissima* and that on the lower marsh with *Salicornia europaea* s. str. The distinctive diploid *Salicornia pusilla* also occurs on the upper marsh. The pioneer community on the sandflats on the seaward fringe of the marsh is

dominated by the tetraploid *Salicornia dolichostachya* and two further tetraploid types also occur in distinct micro-habitats within the upper and lower marshes. There are two distinct forms of *Suaeda maritima* on the upper marsh and one on the lower. Lower marsh forms of both *Salicornia* and *Suaeda maritima* occur sporadically on upper-marsh strandlines. To analyze the upper-marsh vegetation species ordination, based on 180 systematically arranged 50 × 50 cm quadrats was carried out, using Detrended Correspondence Analysis (Hill, 1979) (Fig. 1). Although the annuals form a distinct group, all of them, including two types of *Salicornia*, distinguishable at the time of year the marsh was surveyed (July) only by their differing pig-

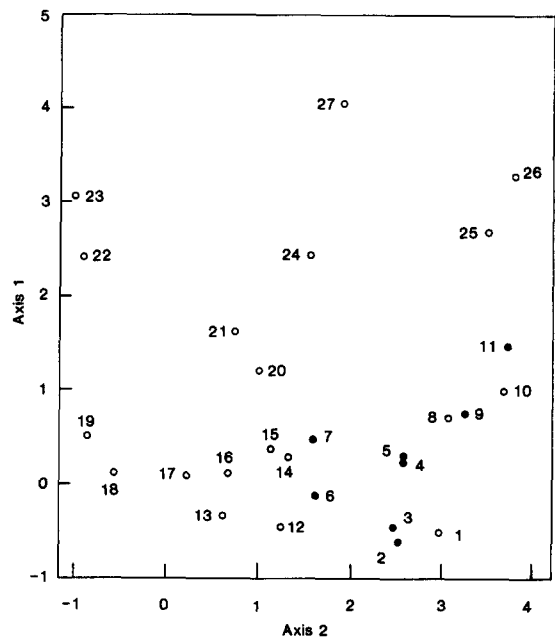


Fig. 1. Detrended Correspondence Analysis of species in 180 systematically arranged quadrats on the upper marsh at Stiffkey, U.K. Annuals (●); perennials (○). Species code numbers: 1, *Spartina anglica*; 2, *Salicornia* (red-pigmented form) – see text; 3, *Spergularia marina*; 4, *Suaeda maritima* (early flowering form); 5, *Salicornia pusilla*; 6, *Salicornia* (green form) – see text; 7, *Suaeda maritima* (upper-marsh form); 8, bare ground; 9, *Salicornia europaea* s. str.; 10, *Suaeda vera*; 11, *Suaeda maritima* (lower-marsh form); 12, *Spergularia media*; 13, *Armeria maritima*; 14, filamentous green algae; 15, *Limonium vulgare*; 16, *Triglochin maritima*; 17, *Plantago maritima*; 18, *Arthrocnemum perenne*; 19, *Bostrychia scorpioides*; 20, *Puccinellia maritima*; 21, *Aster tripolium*; 22, *Festuca rubra*; 23, *Artemisia maritima*; 24, *Halimione portulacoides*; 25, *Cochlearia anglica*; 26, *C. officinalis*; 27, *Elymus pycnanthus*. Axes are scaled in standard deviations.

ments, have somewhat different vegetational affinities. Similarly, examination of the corresponding stand ordination reveals that, for example, the red-pigmented *Salicornia* (the upper-marsh form considered in detail in this paper) occupies a very cohesive group of stands that show little of the overall vegetational variation (Fig. 2).

This apparent diversity of populations raises three important issues:

1. To what extent are the populations within species (or micro-species within species aggregates) genetically differentiated?

2. What features of the annual life history show differentiation?

3. Can any of this variation be demonstrated to be adaptive in the sense of conferring fitness to local environments?

This paper will be concerned with discussing the types of evidence necessary to resolve these questions, with reference to the two populations about which we know the most: populations of the diploid

*Salicornia europaea* agg. on the lower (*S. europaea* s. str.) and upper (*S. ramosissima*) marshes at Stiffkey. *Salicornia* is believed to be substantially cleistogamous (Ball & Brown, 1970) and so there is probably less gene exchange between populations via pollen than there is through seed fluxes. The density of *Salicornia* populations in the field varies both in time and space and they are regulated by a combination of density-dependent and density-independent factors (Jefferies *et al.*, 1981). The intricacies of the population biology, in the context of a complex physical environment, render it unlikely that any single experimental approach will provide complete answers to the three questions formulated earlier. Consequently, the rationale of this paper is to consider the contribution and limitations of a variety of techniques which have been brought to bear on these problems: collateral cultivation, environmental perturbation, iso-enzyme analysis and three approaches to reciprocal transplantation experiments.

### Collateral cultivation

The first evidence that individuals from lower- and upper-marsh populations of *Salicornia* responded differently in a common environment came from glasshouse experiments, designed to examine the growth responses of a number of halophytes to nitrogen (Jefferies, 1977). Young seedlings were transplanted from the marsh to sand culture in individual spots. They were watered with dilute artificial seawater containing NaCl ( $2.5 \times 10^{-2}$  mol/l), MgSO<sub>4</sub> ( $2.5 \times 10^{-3}$  mol/l), NaH<sub>2</sub>PO<sub>4</sub> ( $2 \times 10^{-3}$  mol/l), CaCl<sub>2</sub> ( $10^{-3}$  mol/l), and KCl ( $10^{-3}$  mol/l); iron and trace elements were as used by Johnson *et al.* (1957). The nitrogen concentration in the nutrient solution was varied in different treatments between  $10^{-5}$  and  $10^{-3}$  mol/l, as nitrate (NaNO<sub>3</sub>) or ammonium (NH<sub>4</sub>Cl). After 55 days of growth, the upper-marsh plants had achieved dry weights (50–150 mg per plant, depending on treatment) that were consistently no more than half of those achieved by the lower-marsh plants (100–330 mg per plant). Plants of both populations showed a considerable growth response to increasing nitrate concentration and performed poorly when ammonium was supplied (Jefferies, 1977).

The observed divergence of growth rate between

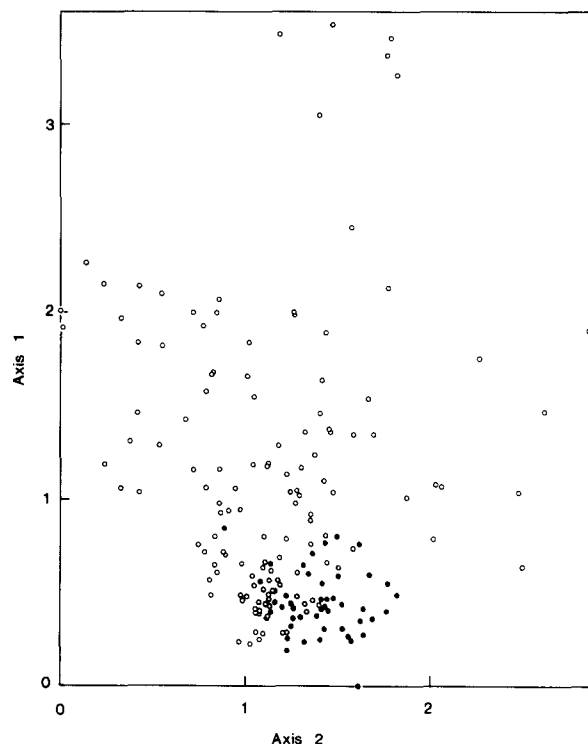


Fig. 2. Detrended Correspondence Analysis of 180 systematically arranged quadrats on the upper marsh, Stiffkey, U.K. The presence (●) or absence (○) of the red-pigmented form of *Salicornia* (see text) is shown. Axes are scaled in standard deviations.

the upper- and lower-marsh plants grown under similar conditions strongly suggests that there are genetic differences between them. It is well known, however, that environmental effects can be transmitted through seeds for several generations (e.g. Hill, 1967; Durrant, 1972). When, as here, seedlings have been transplanted from their natural habitats, there might also have been a carry-over effect from their seed bank and germination histories. Furthermore, it is a far from safe extrapolation back to the natural environment, where other factors may be of overriding significance. Plants may be responding to environmental cues not present in the glass-house and the members of a natural population would be interacting.

### **Perturbation of the natural environment**

Some of these difficulties may be overcome by observing the response of plants in the field to experimental perturbations. The slower growth of the upper-marsh plants coincides with the early summer period when hypersalinity and nitrogen deficiency are likely to develop in the upper-marsh sediments; their rate of growth increases appreciably in July and is maintained until flowering (Jefferies *et al.*, 1979, 1981). Slow growth during such an adverse period is clearly potentially of adaptive value. If the differences in growth rate were due substantially to plasticity it should be possible to eliminate them by the treatment of plots in the upper marsh with seawater and inorganic nitrogen during the hypersaline period. Various combinations of treatment were applied during two summers, including the spectacularly sunny and dry summer of 1976. Although plants on both marshes responded to the addition of nitrate- and ammonium-nitrogen, the considerable increase in dry weight of the upper-marsh plants was mainly in July and August; irrigation with seawater had little effect on the growth of upper-marsh plants. Thus the pattern of growth proved to be strongly determinate and it was not possible to modify significantly the delay in growth of the upper-marsh plants (Jefferies *et al.*, 1979, 1981).

This is further evidence for a substantial genetically determined component to the differences in growth and phenology between the plants of the two populations. Once again, the possibility of a

carry-over effect can not be discounted entirely, although this is unlikely. In this particular experiment we are furnished with no insight into the implications of the differentiation for regulatory processes in the populations. Perhaps the most serious limitation is that the adaptive value of delayed versus continuous growth can only be inferred from its concomitant variation with factors such as hypersalinity, but we have no direct evidence for causal relationships. However, inactivity or dormancy is widely and reasonably believed to be an appropriate response to adverse conditions (e.g. Harper, 1977, p. 62; Villiers, 1975).

### **Isozyme studies**

The electrophoretic analysis of 15 populations of the *Salicornia europaea* aggregate made by Jefferies & Gottlieb (1982), included collections from the upper and lower marshes at Stiffkey. 18 enzymes were investigated and a total of 30 isozymes was detected in all of the 800 plants examined. The electrophoretic mobilities of 24 isozymes were identical in all individuals. However the other 6 isozymes each had two electrophoretic variants and the plants could be divided into two groups on this basis, as each individual had either one set of 6 variants (type a) or the other set (type b). The genetic divergence at these loci is of the strongest type demonstrable by electrophoresis; they are fixed for different alleles at monomorphic gene loci. No heterozygotes were detected, which accords well with a high degree of inbreeding through cleistogamy.

Amongst the lower-marsh plants, 93% were of type a and 7% of type b; these proportions were almost exactly reversed in the upper-marsh sample. In the context of the accumulated knowledge of these isozymes in other species (Gottlieb, 1981, 1982), this represents very direct evidence for genetic differentiation in the absence of breeding experiments. Indeed, Jefferies & Gottlieb (1982) argue from the lack of genetic variability that they are distinct homozygous lineages rather than selections from a polymorphic population. It remains to be seen, for instance, how *Salicornia pusilla* and *S. dolichostachya* will relate to this clear-cut system, or whether this genetic divergence is of any adaptive value.

## Reciprocal transplant experiments

Reciprocal transplants between field sites, where the transplanted individuals experience the naturally occurring selection pressures that affect mortality, growth and reproduction, constitute the most powerful technique available for analysis of the evolution of life-history traits, genetic differentiation and the relative fitness of populations. Unfortunately, as Antonovics & Primack (1982) have stressed, such experiments are not without their difficulties and drawbacks. This is particularly true of the salt marsh environment where the mechanical energy of tide and waves creates special problems for the establishment of transplants. Mortality may be very high; in our earliest seed transplants several thousands of seeds disappeared without trace within days of being sown. Even in successful experiments the variation may be high, but with limited manpower a compromise must be struck between the size of the experiment and the error variance. In addition, the transplant sites are subject to invasion by the usual water-borne seed fluxes and yet we need to be able to identify the individuals in transplanted populations for the duration of the experiment. These issues have led us to three approaches which serve different purposes and suffer from somewhat different drawbacks.

### *Seedling transplants*

This approach involves the transplantation of recently germinated seedlings before they are fully established, in much the same way as a horticulturist pricks out seedlings. Mortality may be appreciable and variable as a result of transplantation, and high densities are very difficult to achieve. It is not therefore an appropriate method for population studies where particular densities are required. However it is of value where spaced plants of defined position are to be harvested individually in order to follow the seasonal progression of dry weight. Such an experiment was described by Jefferies *et al.* (1981). It revealed that seedlings of *Salicornia* from the upper marsh showed the same determinate pattern of growth, with little growth in the early summer, irrespective of whether they were planted on the upper or lower marsh. Similarly, the lower-marsh seedlings showed the same pattern of continuous growth at both sites. This is consistent

with the previous findings that indicated genetically determined differences in the phenology of growth. In view of the accumulated evidence there can be little doubt that this is the case, but it should be remembered that seedlings which have survived and germinated under particular conditions conceivably could have a physiological 'memory' of this. If polymorphic seed is produced (e.g. Grouzis *et al.*, 1976; Ungar, 1976; Berger, 1985) with different germination behaviour there is also the danger of not taking into account one or more of the morphs, depending on when the experiment is established.

### *Turf transplants*

Another alternative requires the transplantation of shallow turves or cores of salt marsh sediment complete with their indigenous populations of annual plants, either established or in the seed bank. It is not usually feasible in practice to do this before germination; the uncertainty about the type and size of population which will develop is too great. However, if further germination takes place on the turves after transplantation, the new seedlings can reasonably be assumed to have come from the same seed bank as their earlier germinating neighbours. Population densities may be manipulated at this stage by thinning if necessary. Then quadrats are positioned on the turves and the plants within them mapped or counted; standard demographic methods pertain.

This method has been used to examine several features of the vegetative and reproductive phases of the life history of the upper- and lower-marsh *Salicornia*. In 1979, eight turves ( $10 \times 10 \text{ cm} \times 3 \text{ cm}$  deep) from each marsh were transplanted to the reciprocal site on 1 May (early transplants) and a further eight were transplanted on 1 June (late transplants). Ten turves were transplanted within their own site in each case on the earlier date. Each set of turves included a wide range of density and the plants in  $5 \times 5 \text{ cm}$  quadrats on them were monitored.

The relative survival (percentage mean survival for eight or ten quadrats in each case) between the date of the second transplant and harvest on 16 October is shown in Figure 3. The mortality in the lower-marsh plants was low during this period and transplantation to the upper marsh seemed to make

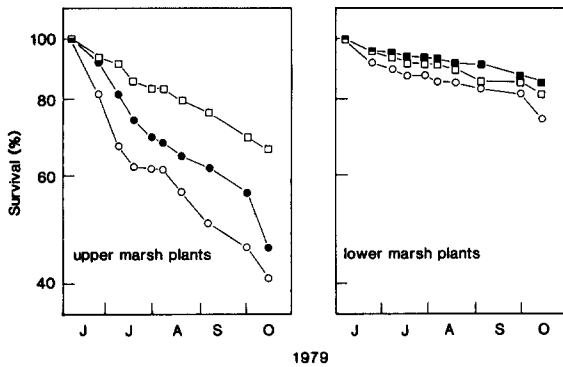


Fig. 3. Relative survival of upper- and lower-marsh populations of *Salicornia europaea* agg. transplanted reciprocally on turves in 1979, to the upper marsh ( $\square$ ,  $\blacksquare$ ) and lower marsh ( $\circ$ ,  $\bullet$ ). Open symbols represent early (1 May) transplants; closed symbols represent late (1 June) transplants. Survival is shown on a logarithmic scale; each point is the mean for eight  $5 \times 5$  cm quadrats.

little difference. Mortality was slightly higher in the upper-marsh populations at their own site, appreciably higher in the late transplant to the lower marsh and most acute in the early transplants there. The survival of upper-marsh plants was substantially reduced by moving them to the lower marsh, but not vice-versa. A similar experiment in 1980, in which all of the transplants were carried out at the

beginning of May and survival was monitored from 7 May to 9 October, showed essentially the same pattern of differential mortality.

The density-dependent fecundity of plants in the 1979 experiment is shown in Figure 4. Linear regressions of mean seed production per plant (based on all of the plants present in  $5 \times 5$  cm quadrats, with the population densities shown) against the logarithm of density on 26 June are presented for purposes of comparison. Density at this date has been used because it gives slightly higher values of  $r^2$  than the density at harvest, presumably because of its influence at the onset of reproductive growth. An asymptotic model for this relationship is theoretically preferable and fits the behaviour of *Salicornia* excellently (see Watkinson & Davy, 1985) but has little advantage for data as variable as these. The responses of both upper- and lower-marsh populations in their own environments are similar to those observed on the in situ populations by Jefferies *et al.*, 1981; fecundity is much higher in the lower-marsh plants especially at lower densities. Upper-marsh plants on the lower marsh appear to perform better than in their own environment, although the regression coefficients are not significantly different. No useful distinction can be made between early and late transplants because of the

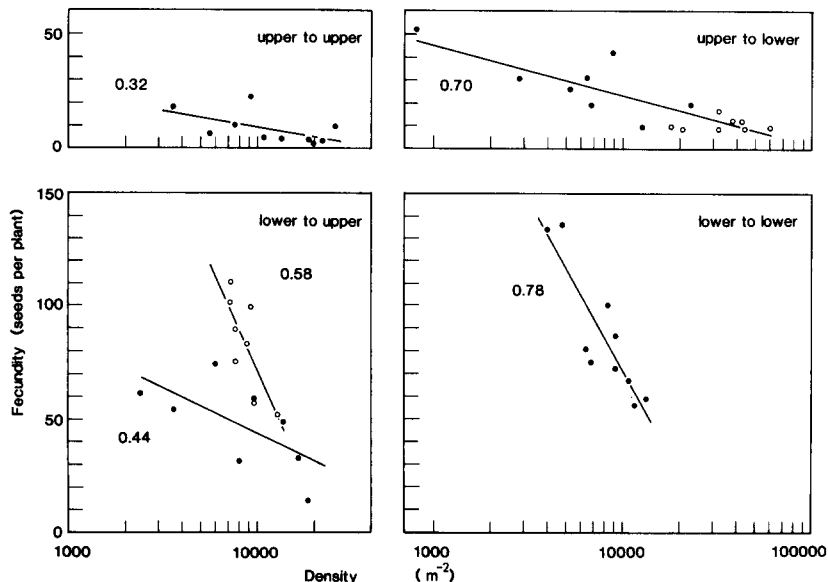


Fig. 4. Relationship between mean fecundity for all of the plants present in the  $5 \times 5$  cm quadrats and density (on 26 June) for plants transplanted reciprocally on turves in 1979. Early transplants - 1 May ( $\bullet$ ); late transplants - 1 June ( $\circ$ ). The proportion of variance accounted for by the regression ( $r^2$ ) is shown for each line.

restricted density range of the latter. Late transplants of lower-marsh plants to the upper marsh behave very similarly to those in their own environment; the early transplants, however, have a drastically reduced fecundity. Genetic differentiation clearly plays a major role in these differences but both populations show considerable plasticity of response as well.

There are indications that the selective forces against the upper-marsh plants on the lower marsh affect survival particularly, whereas those acting in the reciprocal arrangement affect fecundity particularly. However, this type of experiment only takes account of mortality in half the life cycle or less and some year-to-year variation depending on weather is probable. Also, the usual risk of a carry-over effect has been augmented by transferring part of the environment, in the form of sediment, with the plants.

#### Seed transplants

Transplants of seed are potentially of great value if the technical difficulties can be overcome: no sediment is transferred, mortality can be followed over the whole life cycle and estimates of relative fitness can be made. However this requires the planted seeds to be kept in position until they become part of the seed bank, and the natural influx

of seeds to be minimized. The approach may be exemplified as follows. Substantial areas are cleared of all annual plants by hand-weeding or glyphosate herbicide in August and September, before seed production. In October, fertile plants containing mature seed are collected, and a calibration of seed number per unit length of fertile branch or per number of fertile segments is constructed. Then appropriate numbers of fertile branches of known length are spread over  $10 \times 10$  cm experimental plots in the cleared areas to give the desired seed input. These branches are kept in position by placing  $10 \times 10$  cm squares of black plastic mesh (aperture width 4 mm) over the plots and fixing these to the sediment with hooked steel pins. The branches decompose in situ and release their seeds in the normal way. When germination occurs the new seedlings grow through the mesh without difficulty. Control plots are used to check that the seedlings are substantially derived from the seeds sown and not from an influx from the surrounding marsh.

A reciprocal transplant using this technique was set up using a wide range of input densities on 22 November 1979. Survival was followed during the subsequent year and the seed output per plant was established after harvest on 9 October 1980. It is possible to determine from this the average number of descendants produced by each seed sown, after exactly one generation (Fig. 5), and thus to derive a

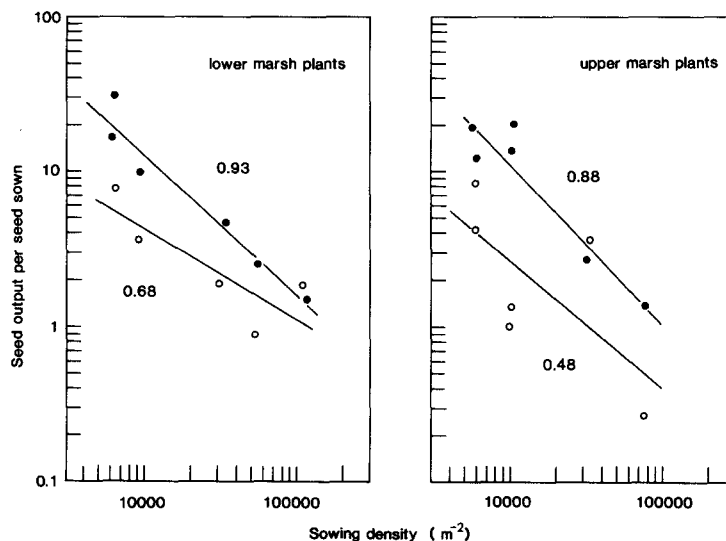


Fig. 5. Relationship between mean seed output per seed sown and sowing density in reciprocal transplants where branches containing mature seed were anchored to the marsh surface with plastic mesh squares. The experiment was set up in November 1979 and harvested in October 1980. Populations transplanted within their own sites (●) and to the reciprocal site (○). The proportion of variance accounted for ( $r^2$ ) by regressions is shown for each line.

measure of fitness. Seed output per seed sown is negatively density-dependent and significant linear regressions can be fitted to the logarithmically transformed variables. It is clear that for both populations this measure of fitness is greatly diminished by transplantation to the reciprocal site. Transplantation also introduces greater variability into the relationship in both cases. The relative fitness of each population at the reciprocal site can be expressed as the quotient of its two regression lines at any density (Fig. 6). As the pairs of regression lines are not parallel, relative fitness is also density-dependent, ranging from 18% at a density of 3 000/m<sup>2</sup> to 36% at 100 000/m<sup>2</sup> in the upper-marsh population and from 22% to 69% at the respective densities in the lower-marsh population. The increasing relative fitness with increasing density presumably reflects the increasing tendency of the density-dependent fecundity to offset the essentially density-independent mortality. Whether or not the presence of the plastic mesh had any influence on the natural mortality is difficult to ascertain, but the evidence for the adaptive value of the genetic differentiation between these two populations is very clear. This experiment closely simulates the natural invasion of each site by seeds or uprooted fertile plants of the other in areas where there is little competition with the indigenous populations. Presumably such competition would intensify the selective forces.

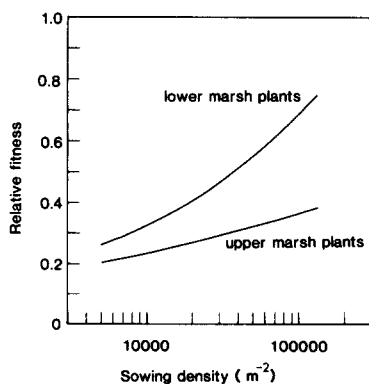


Fig. 6. Relationship between the relative fitness of populations when transplanted to the reciprocal site and sowing density for the experiment described in the legend to Figure 5. Relative fitness is derived as the quotient of the seed outputs estimated from the pairs of regression lines in Figure 5.

## Concluding remarks

A wide range of approaches has been reviewed. They provide complementary kinds of evidence and collectively are capable of answering the three questions posed initially, as has been demonstrated for *Salicornia europaea* agg. The upper- and lower-marsh populations show substantial genetic differentiation which is evident in their growth, phenology, and patterns of mortality and density-dependent fecundity. The relative fitness of each population in the two environments indicates that this genetic differentiation has a high adaptive value. More detailed analysis, examination of year-to-year variation as well as studies of the other *Salicornia* populations and *Suaeda maritima* are in progress.

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