

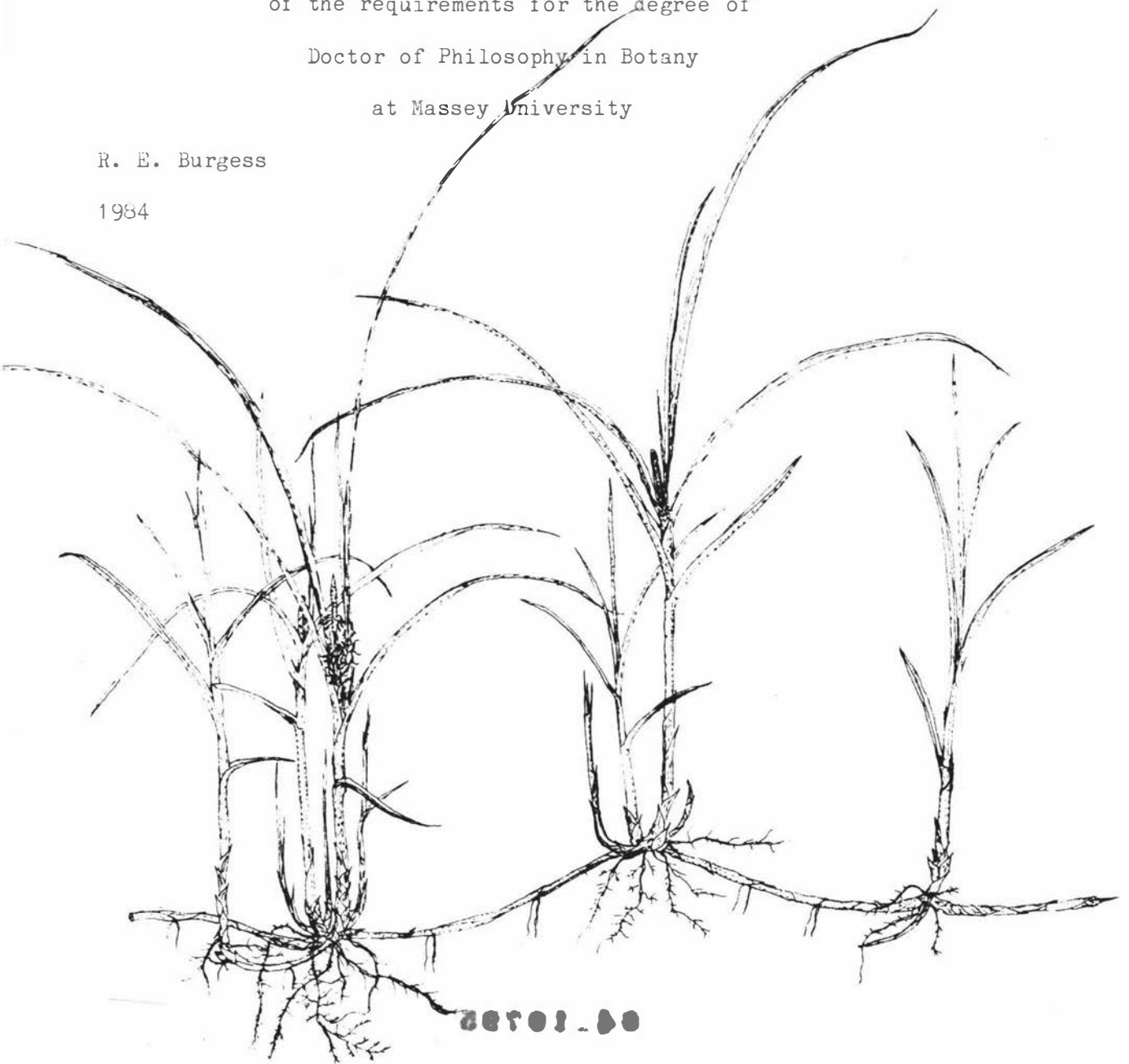
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The life history strategy
of Carex pumila Thunb. (Cyperaceae),
a rhizomatous perennial pioneer species
on the sand plains of the dune system
of coastal Manawatu

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presented in partial fulfilment
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ABSTRACT

The life history strategy of Carex pumila Thunb. (Cyperaceae), a major colonist of raw moist sand on the sand plains of coastal Manawatu, New Zealand, is outlined. By virtue of the continuous formation of sand plains, sites suitable for colonization are a permanent feature of this habitat and vegetation of increasing seral maturity is represented at any one time across a series of adjoining deflation hollows and low dunes. It is proposed that the species is an r-strategist well suited to exposure, nutrient stress and seasonal flooding. Amelioration of these conditions by deliberate perturbation treatments resulted in this seral species responding in a way that ultimately lead to its more rapid demise.

The species has a rhizomatous perennial growth habit. The modular construction of its rhizome system is described for the first time. Similarly, the occurrence of both long and short sympodial rhizome branches and of large-diameter sinker roots have not been previously described in the literature on this species. Its floral development appears to be environmentally cued. Emergence of inflorescences occurs in early October. Maximum size of dissemules is obtained by early January. Subsequently seeds are shed and the shoots bearing them die. The species is essentially allogamous, although in a laboratory experiment, it was found to be partially self-compatible. Self-pollination must be expected in the field since neighbouring shoots are likely to be part of the same genet.

Field studies are reported in which the performance of Carex pumila was monitored, firstly at sites of increasing seral maturity both in space and in time, and secondly in response to perturbation treatments. Populations showed a pattern of development that included

a juvenile phase of rhizome expansion, an adolescent phase of increasing shoot density, a mature phase in which a proportion of the shoots were reproductive, and a senile phase of diminished growth and seed production. Phasic development was more protracted on the more stressed and more exposed sites. Other species more rapidly filled the space made available by the death and decay of Carex pumila shoots, than the colonist itself. As a pioneer, the species is doomed to extinction on the sites it colonizes.

In a perturbation experiment, the sward mass of the total vegetation per unit area was increased at all sites by nitrogen fertilizer, applied as ammonium ions at a rate of 50 kg N / ha. Where the Carex pumila population was in a senile phase in an old deflation hollow, the increase was made mainly by other species. In younger populations on a low dune, the density of shoots and expanding buds of Carex pumila were markedly increased by the fertilizer treatment. Associated with this, a significant increase occurred in the proportion of the total dry weight of vegetative branches in rhizomes and in green leaves.

A nitrogen limitation to seed yeild was indicated at the older low dune site. Here nitrogen fertilizer addition increased seed output per unit area by increasing both seed number per culm and seed size. By contrast on the younger low dune site, seed output per unit area was unchanged by the perturbation. In this population, reallocation of resources within fertile shoots, which was seen as an increased number of seeds per culm, was offset however by a reduction in fertile shoot density.

Seed reproductive effort varied between 0 and 16% of total biomass, whereas rhizome allocation was more variable; up to 100% of biomass where the species was invading an embryonic deflation hollow. As a proportion of the biomass of fertile shoots alone, seed reproductive effort estimates of up to 32% were obtained.

The post-anthesis photosynthetic contribution of female spikes to final seed weight was estimated at 26%, in a growth room experiment. This estimate is considered conservative given that final seed weight was not significantly reduced by defoliation and shading of the culm. Thus, the allocation of biomass to seeds cannot be considered a drain on the carbon resources of the plant that might otherwise be allocated to growth or some other plant function.

Total nitrogen concentrations were dissimilar in different plant parts and, for comparable organs, between populations of different ages. Thus, allocation patterns to component parts based on dry weight and total nitrogen were different. Given that nitrogen was seen to be limiting growth in this seral habitat, the allocation of this resource is likely to be of greater significance in the evolution of life history strategies than is that of dry weight.

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CHAPTER ONE

Introduction

- 1.1 Life histories, allocation of resources and reproductive effort.
- 1.2 Successional trends of reproductive effort.
- 1.3 Quantification of life history strategies.
- 1.4 Sand plains and waterlogged soils.
- 1.5 Carex pumila Thunb.
- 1.6 Aims of the study.

This thesis describes aspects of the life history strategy of Carex pumila, a rhizomatous perennial plant species, a colonizer of the seasonally flooded sand plains of the Manawatu coastal dune system.

Carex pumila plays a pivotal role in the early development of these sand plains (Esler 1978). Thus, the behaviour of this species may not only reflect the early stages of development of the sere, but may also be a causal influence in the process. In this study, the life history strategy of Carex pumila on the sand plains is described in terms of the allocation of both biomass and mineral nutrients over time, along with the changes in reproductive effort of the species as the sere progresses.

1.1 Life histories, allocation of resources and reproductive effort

Reproductive effort was originally defined by Harper and Ogden (1970) as the efficiency of a plant as a "seed-producing machine". The energy input of the machine was seen as the total assimilated carbon or gross production plus the energy stored in the original seed from which the plant grew. The energy output was the energy contained in the seeds produced. The machine efficiency or reproductive effort was simply the ratio between input and output. The measurement of reproductive effort therefore involved the determination of gross production, starting capital and that fraction which was seeds or vegetative propagules. Detailed energy budgets, ideally expressed in energy units rather than grams dry weight, over the entire life cycle of the plant were thus required.

The measurement of reproductive effort in plants stemmed from the concept of energy allocation (Cody 1966); that is the idea that organisms have a limited quantity of time or energy (or other resource) to partition between the various life activities of growth, maintenance, predator avoidance and reproduction. The expenditure of resources on any one of these necessarily means a decreased amount available for expenditure on others. The way in which an organism allocates its resources between these functions was seen to be a characteristic of ecological and evolutionary significance. Reproductive effort as defined above is a measure of the energy allocation to reproduction, as opposed to the allocation to development of a competitive growth form or defense against predators, and thus has been seen as a quantifiable measure of the "relative value which natural selection has placed upon that function" (Harper and Ogden 1970). Monocarpic grain crops and wild annual species have a high reproductive effort, usually greater than 20% and up to 40% of their annual net assimilation, whereas in ^{polycarpic}~~polycie~~ herbaceous perennials and forest trees it may be less than 5% (Harper et al. 1970).

The quantitative pattern of resource allocation integrated over the entire life of an individual is a means by which the life histories of different organisms can be compared. The resource allocation pattern will be a reflection of the individual's genotypic programme or strategy and is determined by the interaction of that strategy with the environment. A single strategy may include a range of developmental pathways as seen in plants by the plastic response of an individual to fluctuations in the environment (Heslop-Harrison 1964). This developmental flexibility has itself been moulded by natural selection. Thus, the range of life history strategies

displayed by plants is considered to be adaptive, reflecting the sets of selective pressures under which these organisms have evolved.

Examination of the literature reveals that the types of life histories encountered in nature, as with the types of physical and biological environments, are limited. For example, Dobzhansky (1950), working with birds, distinguished between the ways in which natural selection acted in the tropics and at higher latitudes. He argued that in temperate zones physical environmental factors which are density-independent tend to limit population growth whereas in the tropics biological (density-dependent) interactions predominate. He argued, further, that this led to selection for early onset of sexual maturity and larger clutches in temperate zones as opposed to selection for the ability to compete and to avoid predation in the tropics. MacArthur and Wilson (1967) developed these ideas, coining the term 'r-selection' for selection in uncrowded situations favouring rapid population expansion and 'K-selection' for selection in saturated or crowded situations favouring ability to compete. During the last 15 years the meaning of r- and K-selection has developed and broadened to include selection in relation to the degree of environmental uncertainty or habitat disturbance (Gadgil and Solbrig 1972) and also in relation to the degree of density-dependent mortality (McNaughton 1975). It has also been used erroneously to describe the combinations of life history characteristics that it has brought about.

r-K-selection theory predicts the association of life-history traits into two groups (1) resulting from r-selection: early age at first reproduction; large clutch size; once only reproduction; no parental care; large reproductive effort; many, small progeny; low assimilation efficiency; and short generation time (a specific

combination of which is a single r-strategy) and (2) resulting from K-selection: delayed reproduction; repeated reproduction; small clutches; parental care; smaller reproductive effort; few, large progeny; and high assimilation efficiency (a specific combination of which is a single K-strategy) (Stearns 1976). The use of the terms r- and K-selection to refer to selection in relation to the amount of density-dependent mortality and degree of habitat stability in addition to the original meaning of selection in relation to the degree of crowding (competition) has led to considerable confusion. If crowding results in density dependent mortality through depletion of resources or conversely if crowding is prevented by density-independent mortality factors, or if the stability of the habitat affects the degree of crowding then the life history consequences may be predicted by r-k selection theory. The confusion arises, however, where the selective effects of these environmental factors are not mediated by their effect on crowding but where instead they directly affect life history parameters. For example, where the density-dependent source of mortality is predation, the life-history consequences are not likely to be the same as those that result from crowding (Wilbur et al. 1974; Wilbur 1976).

Reproductive effort has been the life history trait most commonly used to place a population on the r-K-strategy continuum for the purpose of comparison with populations living in other environments (e.g. Gadgil and Solbrig 1972; Gaines et al. 1974; Abrahamson 1979). More recently, however, Parry (1981) deemed that reproductive effort should not be used as an index of r- and K-selection. In support of this view he pointed to the lack of association between reproductive effort and egg size in both plants and other organisms (Wilbur 1977; Bostock and Benton 1979); egg size being a life

history trait fundamental to r-K-selection theory. Further, Parry has questioned the explanations given by Gadgil and Solbrig (1972) and Gaines et al. (1974) for differences in reproductive effort between populations where the degree of density-dependent/density-independent mortality was inferred but not actually measured. He indicated that other causes of these population differences, for example, differences in adult as opposed to juvenile mortality rates, were not considered. The life history consequences of such differences in mortality schedules are discussed below. The possibility remains that r-K-selection which assumes constant mortality in both adults and juveniles, need not have been invoked.

Alternative explanations for those groupings of life history attributes that have become known as r- and K-strategies and for other groupings of traits, have been hypothesized. "Bet-hedging" or stochastic models which deal with the consequences of fluctuations in juvenile and adult mortality and fecundity schedules (Schaffer 1974) predict that when juvenile mortality or birth rate fluctuates more than adult mortality, a syndrome of delayed maturity, reduced reproductive effort, fewer young and longer life should evolve; whereas when adult mortality fluctuates more than juvenile mortality or birth rate then earlier maturity, larger reproductive effort and more young should evolve (Stearns 1976,1977). Measurements of reproductive effort in situations where adult and juvenile mortality schedules have been estimated, confirm that higher adult mortality is correlated with high reproductive effort and lower adult mortality with lower reproductive effort (Calow 1979; Primack 1979).

Grime (1977) recognized stress (conditions that restrict production, e.g. mineral nutrient or water deficiency) and disturbance (conditions associated with the destruction of plant biomass e.g. wind or herbivores) as factors which limit plant biomass in any habitat. He proposed the existence of three primary strategies in plants: the competitive (C) strategy associated with low stress and low disturbance conditions, the stress-tolerant (S) strategy with high stress and low disturbance, and the ruderal (R) strategy with low stress and high disturbance. Secondary strategies in response to combinations of these conditions were also recognised. It is evident, therefore, that selection regimes that determine plant strategies have many dimensions (Wilbur 1976), one of which is the continuum from r- to K-selection (sensu MacArthur and Wilson 1967). Others include seasonality (Boyce 1979), degree of habitat disturbance (Gadgil and Solbrig 1972), environmental stress (Grime 1977) and predation (Wilbur et al. 1974). Thus, the explanation for the evolution of all observed combinations of life history characteristics on the basis of just one of these dimensions (e.g. r- and K-selection) will probably be an over-simplification and this has prevented the formulation of precise predictions which may be empirically tested; the theory therefore has become imprecise.

1.2 Successional trends in reproductive effort

Harper (1967) questioned whether the proportion of a plant's output that is devoted to reproduction is higher in colonizing species than in those of more mature habitats. It has been suggested that ecological succession involves a shift from r- to K-selection with increasing age or maturity of the community (Wilbur et al. 1974). r-K-selection theory predicts that r-selection will produce a specific

combination of life history traits (a specific r-strategy) and K-selection another (a K-strategy) (Gadgil and Solbrig 1972). Thus, seral species are predicted to possess more rapid growth to reproductive maturity, higher reproductive effort and more copious production of smaller, often wind dispersed seed (typical of r-strategists) than species which replace them as the sere progresses (K-strategists).

Attempts to answer Harper's question conform to a common pattern : reproductive allocation decreases with increasing maturity of the sere (Gadgil and Solbrig 1972; Abrahamson 1975b; Gaines et al. 1974; Hickman 1975; McNamara and Quinn 1977; Roos and Quinn 1977; Newell and Tramer 1978; Abrahamson 1979). For example, in a study with goldenrods (Solidago species) Abrahamson and Gadgil (1973) followed the distribution of dry matter between reproductive and vegetative tissues in four perennial species from a series of sites that they ranked according to successional maturity : an immature, dry open and heavily disturbed site; a wet site of intermediate maturity; and a mature hardwood site that was relatively undisturbed. Although not all species occurred at all sites, the appropriate comparisons between sites confirmed their prediction that reproductive effort would decline with increasing successional maturity of the community. However, Bradbury and Hofstra (1975) were unable to show that the difference in reproductive effort between two Solidago canadensis populations from sites of different successional maturity was significant.

In such studies with field populations there is no way of knowing whether the observed differences were environmentally-induced plastic differences or genetically based. Only where comparison of different populations in a greenhouse or common site has been carried out have

these components of variation been distinguished. Hickman (1975) found that for the annual, ^{Polygonum}~~Polygonum~~ cascadense, the trend of increasingly greater reproductive effort in populations from successively harsher, more open habitats found in the field, was not found in the greenhouse. Hickman concluded that the field differences were directly attributable to environmental effects rather than to genetic differentiation between the populations. A similar result was obtained by Raynal (1979) in studying field and greenhouse population of Hieracium florentinum: field differences in reproductive effort disappeared when populations were grown under identical glasshouse conditions. Roos and Quinn (1977) showed field differences in reproductive effort in the predicted direction between populations of the grass Andropogon scoparius at sites of varying age. In the greenhouse differences in the same direction were found although these were small and often not significant. They concluded that there appeared to be at least a possibility that genetic differentiation existed between young and old field populations in terms of reproductive effort. Thus the results to date are no more than suggestive that ecotypic differentiation in terms of resource allocation to reproduction has occurred between populations of a single species at various seral stages. The adaptive strategy in early plant succession therefore appears to be high reproductive effort and copious production of small highly vagile offspring (Horn 1974). A similar pattern was described for birds colonizing islands (Diamond 1975). Diamond termed the pioneers "supertramps" which were not particular about their choice of habitat and were prolific and dispersive.

The perennial rhizomatous growth habit is frequently encountered in plans of pioneer and early seral communities particularly where continual renewal of the substrate is occurring such as on sand dunes (Ogden 1974a). In the harsh unstable environments of dune slacks in coastal New Zealand, native herbs possessing the rhizomatous habit and tolerance of prolonged inundation with water predominate (Esler 1978). The strategy of these plants which usually allows for both long distance dispersal by seeds and for rapid extension by rhizomes into newly exposed adjacent areas which may be unfavourable for seed germination, does not conform to the suite of life history characteristics predicted under r-selection for colonizing species. The strategy of rhizomatous perennials differs from that of annual r-strategists in that the strategy does not ^{preclude} ~~prede~~ competition with other species which occurs in seral habitats. The rhizomatous perennial may produce a dense stand of ramets which resists invasion and so persists as a long-lived seral mono-culture. Such an efficient use of biological space by clonal perennials has been attributed to the lack of self-thinning within the stand (Hutchings 1979). Hutchings found that shoot numbers remained relatively constant throughout the growing season and an increase in shoot size stopped when the "thinning line" (Yoda et al. 1963)* was reached. However, when shoots subsequently died Hutchings observed no further

*Footnote: The thinning line, with a gradient of $-3/2$, represents the changes through time of mean plant weight and plant density of populations of genets of a wide variety of species undergoing thinning.

accumulation of biomass. This lack of self-thinning was considered an important aspect of the efficient system of utilization and re-distribution of resources within the clone. It is this aspect which results in the development of closed stands of clonal perennial plants.

Alternatively, the rhizomatous perennial may escape to new areas through seed production. This choice "depends in part on decisions made by natural selection governing the changes in pattern of resource allocation in response to shoot density and in particular the relative proportions devoted to seeds and rhizomes" (Ogden 1974a). Allocation has been shown to favour seed production as opposed to vegetative spread as the density of the clone increases in both Tussilago farfara (Ogden 1974a) and Rubus spp (Abrahamson 1975); an adaptive response to low fertility conditions in open habitats (S-selection of Grime 1977).

This view that allocation to seeds (sexual reproduction) and to rhizomes (clonal growth) may be alternatives has also been suggested by the work of Tripathi and Harper (1973) who compared the number of seeds and rhizome buds produced per plant for two congeners, Agropyron repens and A. caninum of contrasting growth habits. A. repens produces an extensive rhizome system whereas A. caninum forms a closed tussock by production of intravaginal tillers. Although the estimates of seeds and buds were widely different between the two species, the sum of seeds plus rhizome buds per plant were remarkably similar.

Seral perennials are also found in ruderal or disturbed habitats. For example, Plantago major in ruderal habitats has been found to allocate from 10 to 28% of its total biomass to seeds (Kawano 1975; Hawthorn and Cavers 1978), whereas other perennials from less

disturbed habitats generally have a lower seed reproductive effort (Kawano 1975). The dry weight allocation to ^{clonal growth} ~~clonal growth~~ in Plantago major was found to overlap the range found in the rhizomatous perennial Tussilago farfara of seral habitats namely 0-22% (Ogden 1974a) and was similar to that (18%) found after 10 weeks growth in the stoloniferous perennial Trifolium repens of relatively open, disturbed habitats (Turkington and Cavers 1978). Trifolium repens is adversely affected by low light levels. It has thus been suggested that stolons in this species may have evolved permitting the species to escape the effects of interspecific interference (Turkington and Cavers 1978). Such a growth habit would allow the species rapid local spread so effectively monopolizing available resources and thereby excluding other species (K-strategy of MacArthur and Wilson 1967). A similar explanation can be given for the rhizomatous growth habit of seral perennials of low fertility sand dune and sand slack habitats.

A characteristic feature of seral rhizomatous perennial species of nutrient deficient habitats is the linear clonal growth habit (e.g. Carex acutiformis of marshlands in the British Isles, Grime 1979; and Ammophila arenaria in sand dunes, Raunkaier 1934). The adaptive significance of linear clonal growth in such habitats may be related either to (1) the efficient capture of nutrients by the roots of extending rhizomes and the efficient transport of these nutrients to other parts of the clone or (2) the recycling of nutrients from the older to the more juvenile parts of the clone (Noble and Marshall 1983). Noble and Marshall found little evidence of basipetal movement of nitrogen and phosphorus, in one such species, Carex arenaria, in either field or glasshouse experiments, even when older basipetal shoots were severely nutrient-stressed. On the contrary, preferential movement of nutrients taken up from the soil and from older parts of

the clone was found towards the younger, developing parts at the front edge of the clone. Such acropetal movement also applied to assimilate re-distribution in both this and other studies (e.g. Forde 1966, in Agropyron repens). Thus, the linear rhizomatous habit of Carex arenaria allows for the continual extension into previously uncolonized sands and the exploration of scarce nutrient resources (Noble and Marshall 1983).

It is apparent, however, that there is only limited redistribution of water, nutrients or assimilate in Carex arenaria. Tietima (1979) found no long distance water or mineral nutrient translocation along the rhizome in this species. He concluded that redistribution via the phloem is limited to the extent that the plant could not use this supply to maintain a high growth rate in those plant parts not directly supplied by an external source of mineral nutrients.

The explanation of life history strategies in seral species will involve estimation of environmental parameters, variabilities in adult and juvenile mortality schedules, the degree of density dependent versus density independent mortality and the degree of environmental stress (Stearns 1977).

1.3 The quantification of life history strategies

In section 1.1, the idea was developed that the life history of an organism represents a series of compromises to a set of physical and biological environmental conditions. A life history has many components. The battery of tactics that makes up a life history strategy enables a plant to survive and reproduce; that is, it implies a set of adaptive responses that have been put together over

evolutionary time (Wilbur 1976).

The important components of a life history strategy according to Solbrig (1980) include:

1. soil seed pool, seedling and adult mortality.
2. age at first reproduction
3. reproductive life span
4. proportion of fertile to vegetative individuals at any one time.
5. fecundity, seed production which depends upon flower number and pollination rates.
6. fecundity-age regression
7. reproductive effort.

The quantification of a life history strategy of one plant population is thus a formidable task. In any one study only a sample of life history parameters can be measured. The choice is for the worker to decide the most efficient means by which to quantify a strategy.

As noted previously, reproductive effort has been the life history parameter most commonly used to quantify the life history strategy of a population for the purpose of comparison with populations living in other environments.

Measurement of reproductive effort

Harper and Ogden (1970) have indicated that the ideal measurement of reproductive effort involved the calculation of detailed energy budgets, expressed in energy units over the entire life of the plant:

Gross reproductive effort =

$$\frac{\text{Total energy as propagules}}{\text{Total energy}}$$

$$\frac{\text{of seed from which plant grew} + \text{Gross assimilation}}{\text{Total energy}}$$

Because of the difficulties in measuring plant respiration in the field, especially that of subterranean parts, the budget is usually of the energy remaining after the respiratory demands both for growth and maintenance of the organisms are met. Thus

Net reproductive effort =

$$\frac{\text{Total energy as propagules}}{\text{Total energy}}$$

$$\frac{\text{of original seed} + \text{Net production}}{\text{Total energy}}$$

If the metabolic efficiencies of different plant organs were similar then net reproductive effort would be a simple overestimate of gross reproductive effort. This however is probably an unreasonable assumption. In one of the few studies involving the direct measurement of both plant growth and maintenance respiration, Hansen and Jensen (1977) showed that for Lolium multiflorum swards, the respiratory demands of roots were higher than those of the aerial fraction (leaves). Further, where per gram energy values are more or less similar in all plant organs, estimates of dry weight would at least be proportional to net production (Harper and Ogden 1970). Hickman and Pitelka (1975) showed that for plants with largely

carbohydrate seed reserves, and therefore an approximate equivalence of energy values between vegetative and reproductive structures; significant allocation pattern differences between populations could be reflected equally well by dry weight as by energy measures. They concluded therefore that time-consuming energy determinations were unwarranted for such studies.

Thus, by taking into consideration the loss of plant parts and by ignoring the original seed weight as negligible compared to total dry weight, reproductive effort can be estimated by the ratio of total weight of seeds produced to total plant weight at time of maturity. This ratio should include underground parts and thereby will differ from measurements of "harvest index" (*sensu* Donald 1962) (Harper and Ogden 1970). No other technique for estimating reproductive effort has proved superior for field studies requiring large sample size (Primack 1979).

Problems have been encountered however in the quantification of reproductive effort in rhizomatous perennial species. There has been a dichotomy of views over whether the allocation to rhizomes is more properly viewed as allocation to (clonal) growth (Harper 1977) or as allocation to (asexual) reproduction (Abrahamson 1979). At a more practical level problems are encountered with parts continually dying (and thus being liable to be lost) redistribution of assimilate (other resources) within a plant between different organs and shedding of parts such as seed prior to harvest. It has often been necessary to estimate the loss of seed (and other parts), for incorporation into the budget, by the regression of seed weight (or that of other part) on the size of a plant part not liable to be lost (e.g. receptacle; Harper and Ogden 1970).

It is through viewing reproductive effort as a measure of the 'cost of reproduction', that is, a measure of a plants resource allocation to reproduction as a whole, that many of the attempts to measure reproductive effort have differed from that of Harper and Ogden (1970). They measured that proportion of resources allocated to seeds and, in fact, adopted the loose definition of a seed as the dispersal unit and so the whole achene of the composite Senecio vulgaris was taken as the "seed" in their study. Similarly, in many other studies, the estimation of reproductive effort has involved the calculation of the allocation to disseminules or diaspores (the units of dispersal) rather than that to seeds alone (e.g. Handel 1978). The use of the ratio of weight of "seed" output to total plant weight at maturity allows a simple comparison of the efficiencies of plants with diverse morphologies as seed producers (Harper and Ogden 1970). The redefinition of reproductive effort and the failure of workers to actually measure seed weight in the study of dry weight allocation in plant populations (e.g. Hawthorn and Cavers 1978) precludes the possibility of such comparisons.

The proportion of resources allocated to seeds, the "reproductive effort" of Harper and Ogden is a fundamentally different quantity from that devoted to flowers, ("reproductive effort" of Abrahamson and Gadgil 1973) or to flowers and flower stalks, ("reproductive effort" of Hawthorn and Cavers 1978). No consensus has developed as to what should be included in this ratio. Trivedi and Tripathi (1982) for example calculated three different "reproductive effort" values (the allocation to seeds, to flowers and to flowers plus ancillary reproductive structures) in order to make comparisons with previous studies.

Thompson and Stewart (1981) argued that allocation to all reproductive structures, that is "total reproductive effort", is a more realistic estimate of the resources actually committed to reproduction than is seed output. It becomes a matter for the worker to decide therefore whether or not a structure is reproductive, or ancillary to reproduction. Thompson and Stewart stated that they had no wish to be dogmatic on this issue. By measuring allocation to flower stems and/or flowers workers are no longer measuring the efficiency of a plant as a seed producer, (reproductive effort sensu Harper and Ogden): rather they are attempting to measure a far more elusive quantity, namely the resource cost to a plant of seed reproduction. The cost to the plant of the production of structures ancillary to reproduction are quite rightly incorporated into this cost analysis.

If a plant is viewed as the means by which one seed produces more seeds then the whole plant body could be argued to be ancillary to reproduction and total reproductive effort becomes 100% for all plants and thus meaningless as a concept. A less extreme point of view has been to include flowers and supporting structures not present in the vegetative plant body in the measurement of the 'effort' involved in reproduction.

A difficulty arises in the measurement of total reproductive effort because many reproductive structures, including flowers in many species and even the disseminules themselves are photosynthetic and therefore can be expected to contribute to their own increase in dry matter or energy (Bazzaz and Carlson 1979). For example, in wheat, estimates of the contribution of ear photosynthesis to final grain weight ^{may} be as much as 60% (Evans et al, 1975). In such instances, the production of those reproductive structures is not a cost to the

plant in the sense that Cody (1966), in developing the concept of energy allocation, visualized the production of eggs being a cost or drain on the birds limited energy pool. Where reproductive photosynthetic assimilation is occurring the drain of carbon to reproductive structures is being met by the increase in overall size of the pool of that resource.

From an evolutionary point of view, the budget of a resource the very act of allocation of which leads to an increase in the size of the pool of that resource, is of little value since the allocation of such non-limiting resources will not allow estimates of the true costs of particular structures or functions and thus cannot be expected to shed light on the value natural selection has placed on those structures or functions (Calow 1979). Harper and Ogden recognized that their selection of the net energy budget as the basis for describing the plants resource allocation was arbitrary and acknowledged that the allocation of some other limited resource, for example, nitrogen might be more important in the evolution of life history or reproductive strategies. As Harper (1977) stated the cost of reproduction cannot be measured without knowing the appropriate currency. It is to be expected that the relevant currency in which to measure resource allocation in plants may vary between species and between habitats since the resource that limits population growth in one set of circumstances is not likely to be the same in all situations.

Thompson and Stewart (1981) opine that the measurement of energy or dry matter allocation in plants is inherently wrong. They suggest that the appropriate currency for allocation studies in plants is mineral nutrients since minerals represent a plant resource that forms a limited pool which is not increased in size by the process of

allocation itself. The only justification they see for the study of energy or biomass allocation in plants is where it can be shown that mineral nutrient concentrations in vegetative and reproductive parts do not substantially differ. No equivalence has emerged between vegetative and reproductive structures for mineral nutrient concentrations. For example, Fagus sylvatica seeds contain six times as much minerals per gram dry weight as beech wood (Harper 1977). In an allocation study, Lovett Doust (1980b) showed for Smyrniolus atrum, patterns of allocation of dry matter and phosphorus, a mineral nutrient with a reputedly crucial role as a storage element in seeds, to be quite different. Similarly, van Andel and Vera (1977) found that neither nitrogen, phosphorus, nor potassium allocation patterns reflected the dry matter allocation in either Senecio sylvaticus or Chamaenerion angustifolium, but by taking the three nutrients together, a good approximation was obtained. It is reasonable, however, to suggest that the allocation of, for example, limited nitrogen to plant roots which would allow for further growth of this fraction and thus the further uptake of nitrogen so increasing the pool of this resource, is the same as that involving the allocation of dry matter (energy) that Thompson and Stewart (1981) find irrelevant to the study of the evolution of life history strategies in plants.

1.4 Sand plains and waterlogged soils

Sand plains

Very little work has been carried out on the ecology of sand plain systems other than in the British Isles and Holland (Ranwell 1972). Sand plains elsewhere in America, Eurasia and Australasia remain largely undescribed and in New Zealand at least the possibility of describing these unique vegetation stands and associated fauna is rapidly diminishing due to their annihilation by the invasion of exotic plants (Esler 1978) principally as a result of the efforts to crop these waterlogged lands (see for example 'Round Bush Management Plan' 1982).

Esler's studies (1969, 1970) described the interplay of sand, plants, moisture, wind and topography in shaping the sand dune system of coastal Manawatu. In this harsh, unstable environment, influenced by salt, seasonal submergence and drought, the strong persistent west to north-west winds constantly move dry sand. The characteristic parabolic high dunes of the area form a complex pattern with often extensive low-lying plains enclosed between them and the foredune. When bare of vegetation, the parabolic rear dune is blown inland as a result of the removal of dry sand at the base of its windward slope (windsweep) down to the level of moist sand just above the water table. The damp hollow so formed at the base of the windsweep is colonized by several small rhizomatous plant species: Limosella lineata, Eleocharis neozelandica, Ranunculus acaulis, Selliera radicans (the Manawatu sand plain form as opposed to the long-leaved salt marsh form, Ogden 1974b) and Myriophyllum votschii. Around the edge of this hollow Esler describes Carex pumila forming a continuous fringe. This species of Carex has the ability to accumulate sand and

so form a low dune approximately 0.3 metres higher than the hollow. The hollows so formed are characteristically bow-shaped. A number of sand dune species including the introduced Ammophila arenaria and the native Desmoschoenus spiralis germinate in the warm, damp sand and soon appear on the low dune, building it higher and eventually replacing Carex pumila.

As this is occurring, the rear dune will have moved further inland exposing more damp sand at the the base of the windsweep, allowing the colonization and development of a new damp hollow. The process is thus repeated producing a sequence, both in space and time of small arcuate damp hollows separated by similarly shaped low hummocks within the more extensive sand plain. The youngest hollow of the chronotoposequence will be closest to the base of the windsweep of the inland moving rear dune, with progressively older hollows of greater distances seawards. Esler has described the development of vegetation in the older hollows with Leptocarpus similis becoming dominant, and Schoenus nitens and other species present. Further vegetational development in these hollows may involve Cortaderia toetoe, Cordyline australis and, where deposition of sand causes the plain to become dry, Scirpus nodosus. On the older, higher, drier parts of the plain Lupinus arboreus, Hypochaeris radicata, Leontodon taraxacoides and annual grasses and legumes form a more or less sparse cover (Esler 1978).

Waterlogged soils

Frequent, seasonal or permanent waterlogging as a result of high rainfall, topogenic water accumulation or poor drainage leads to the formation of hydromorphic soils (Armstrong 1975). Hokio series soils of the Manawatu sand country (Cowie et al. 1967) fall into this

category. Waterlogging and the ability to cope with these conditions will determine the nature and development of the vegetation in wetlands (see for example Willis et al. 1959; Jones 1972) and thus the continuing development of the soil.

In response to soil flooding, respiring aerobic micro-organisms will reduce oxygen concentration to zero within a few hours (Scott and Evans 1955) and subsequently will be replaced by a population of anaerobic organisms. The diffusion rate of oxygen into oxygen-depleted soil is usually insufficient to maintain aerobic organisms except within a few centimetres of the surface of the flooded soil. For example, Ranwell (1959) found that where the soil was waterlogged at the surface, but not flooded, completely anaerobic conditions were found only 3cm below the soil surface. Where the water table drops below the surface, anaerobic conditions can be expected to prevail even above the ground water level due to capillary action (Boggie 1972).

The sequence of events that might be expected in a mineral soil as a result of flooding (Patrick and Turner 1968), starts with a decline in oxygen concentration followed by the chemical reduction of nitrate, then manganese, then iron, then sulphate. Where organic matter is present, the concentrations of the diverse organic products of anaerobic microbial metabolism and of carbon dioxide will also increase, although because carbon dioxide has a very high solubility in water it will be dispersed more rapidly from its site of production than the opposite movement of oxygen. Thus, the adverse effects of waterlogging on plant growth and survival are rarely the result of carbon dioxide toxicity. Little is known of the effects on plants in waterlogged habitats of the products of anaerobic microbial metabolism although ethylene has been implicated in the reduction of

transpiration, wilting and leaf abscission that accompanies flooding (Jones and Etherington 1970).

At positive redox potential certain facultative anaerobic micro-organisms can use nitrate as an electron acceptor in respiration resulting in denitrification by the evolution of gaseous nitrogen or di-nitrogen oxide. Patrick and Tusneen (1972) found large losses of nitrogen from continuously flooded soils in which a narrow surface aerobic layer remained overlying an anaerobic layer. They explained these losses as the result of the downward movement of nitrate formed in the surface layer by nitrification into the underlying layer where denitrification took place. In addition, the loss of nitrogen from alternately flooded and drained soils as a result of denitrification has long been recognized (Russel 1961).

In waterlogged soils nitrogen usually reaches the roots of plants as ammonium ions derived from decaying organic matter, although nitrogen-fixation by free-living microorganisms may also be important for example in rice paddies where both blue-green algae and bacteria have been demonstrated to fix nitrogen (McRae and Castro 1967). Nitrogen fixation by autotrophic blue-green algae (e.g. Nostoc and Anabaena species) is widespread (Mulder et al. 1969) and important in raw soils as they pioneer the series of N-fixing microorganisms (Etherington 1975). Azotobacter bacteria may be ecologically important N-fixers in highly deficient habitats such as on sand dunes where it is found in the rhizosphere zone of Ammophila arenaria which supplies organic metabolites to the bacterium and is provided with survival levels of nitrogen (Etherington 1975).

At increasingly lower redox potentials manganese and then iron will be reduced causing an increase in the concentration in the soil of exchangeable/soluble ions of both these elements. Since soils usually contain more iron than manganese, the dominant redox couple in soils is that of iron (FeIII/FeII). High concentrations of both divalent iron and manganese (soluble reduced forms) are toxic to plants. Thus, plants in regularly or permanently waterlogged habitats where high concentrations of these ions prevail must possess some means of protection against these effects. For example, the differential ability of sand slack species, Carex nigra and Agrostis stolonifera, to survive otherwise toxic concentrations of ferrous and manganous ions which occur in the slack habitat during periods of maximum growth of the vegetation in spring and early summer appears to be related to their ability to exclude these ions (Jones 1972a,b).

The deposition of ferric ions adjacent to roots in a waterlogged soil in an otherwise reduced (ferrous) state (Armstrong 1967) supports the view that plants may protect themselves from this hostile soil environment by leaking oxygen from the roots (radial oxygen loss, ROL). The formation of an oxygenated rhizosphere sheath by ROL requires a gas exchange pathway between root cells through the plant to the leaves and stomata. This pathway will be enhanced by the provision of air-space tissue which in wetland species may be up to 60% by volume of the plant body compared with 2-7% pore space typical of mesophytes (Armstrong 1975). The formation of large air spaces (lacunae) in various tissue (aerenchyma) in grasses and sedges may result from cell collapse.

Leaf and stem xeromorphy is a common feature of many species of waterlogged habitats (e.g. Carex pumila, Pegg 1914; Juncus and Erica spp, Armstrong 1975) despite what might be expected of plants growing in aquatic conditions. Armstrong (1975) suggested that "it seems likely that the primary function of xeromorphism in these plants is not [that] of water conservation per se but rather to reduce the velocity of water movement to the root surface... [thus] the time available for oxidation of phytotoxins in the rhizosphere zone of oxygenation will be increased". The observation by Jones (1971) that antitranspirants improved survival under waterlogging and limited iron uptake in normally waterlogging sensitive Erica cinerea, supports this view.

Other adaptations to waterlogging include those involving the root system. Under permanent waterlogging adventitious roots may become orientated horizontally close to and even above the surface (e.g. Burgess 1974) presumably within a tolerable redox zone. Where the soil water table fluctuates, a shaving brush effect in the root system has been observed as rising water kills the root apices but not the bases from which new laterals grow. This flux of death and recruitment of root apices produces a mass of brush-like roots (Armstrong 1975).

1.5 Carex pumila Thunb

The genus Carex has 73 species in New Zealand falling into 17 sections within three subgenera (Moore and Edgar 1970). Carex pumila Thunb. Fl. jap. 1784, 39. C. littorea Labill. Nov. Holl. Pl. Sp. 2, 1806, 69, t.219. C. pumila Thunb. subsp. littorea (Labill) Kuk. in Engl. Bot. Jb. 27, 1899, 551, is one of the two New

Zealand members of the section Paludosae of the subgenus Carex. Moore and Edgar (1970) describe Carex pumila as quite unlike other members of the genus in New Zealand having rather coarse tufts of keeled, blue-green leaves up to 40cm long growing from a long, creeping, slender (c.2mm diameter) rhizome and large (c7 x 3 mm) smooth, corky, turgid utricles enveloping each fruit. Carex pumila is monoecious with a terminal cluster of male flowers with usually several predominantly female flower clusters lower on the culm or stem which may extend up to 20cm above ground (Moore and Edgar 1970). Carse (1916) found specimens with leaves and culms up to double the lengths described above. In Carex, the flower clusters are morphologically spikes and each "flower" is a spikelet.

In New Zealand, Carex pumila is found on coastal sands throughout the North Island (but rarely between Kawhia and Wanganui on the west and Tokomaru Bay and Porangahau on the east) and South Island (although rare on the west coast) and Chatham islands. Beyond New Zealand the species is recorded from Chile, Korea, China, Japan (type locality), Lord Howe island, Australia and Tasmania (Moore and Edgar 1970). In Japan, it is an element of the warm temperate region found in the littoral zone, in sandy places along the seacoast where it is common (Flora of Japan). In Australia, it grows in southern and eastern coastal regions and, an interesting feature, at inland locations in the Flinders Ranges and Southern Lofty regions of South Australia (Black 1978).

Carex pumila has received only brief mention in the New Zealand ecological literature principally as a sand-binding species confined to the sand plains of coastal dunelands (Cockayne 1911) where it has great ability to collect sand (Esler 1969). Its appearance "contrary to what might be expected from the fact that the plant grows in moist

hollows" is that of a xerophyte (Pegg 1914). However Cockayne commented that its water requirements (a factor that Esler cites as having has a "critical influence" on species-distribution on the sand plain) may be greater than those of the sand-binding dune species, Spinifex hirsutus and Desmoschoenus spiralis. This view is supported by Esler's figure 2 which shows that the local distribution of Carex pumila on a Manawatu sand plain extends below the level of the mean summer water table, unlike the distribution of dune species, such as Desmoschoenus, which when found close to the mean summer water table occur mainly as seedlings. Adult plants of these dune species are also found on the sand plains but only as relics of vegetation of the dunes which covered the area before deflation (sand removal by wind) (Esler 1969).

Morphological variation within and between stands of Carex pumila in New Zealand undoubtedly exists (Moore and Edgar 1970; Carse 1916; Esler 1969). Variation in both plant size and seed production occurs within a single patch which suggested to Esler (1969) responses to differences in micro-habitat.

The ability of Carex pumila to stabilize sand is crucial in its role in the development of the sand plain. The series of arcuate hummocks that are found on the sand plain separating the chronosequence of similarly-shade damp hollows in the wake of the receding rear dune are formed as a result of the sand-collecting ability of this pioneer species (see section 1.3 and Esler 1978).

1.6 Aims of the study

The aim of the present study was to investigate the behaviour of Carex pumila from sites representative of the early stages of seral development on a sand plain within the Manawatu coastal dune system. The species plays a pivotal role in the process whereby a catenary system of damp deflation hollows and low-lying dune ridges of increasing age at increasing distance from the rear dune is initiated on these sand plains (Esler 1978).

In chapter 2, the growth habit of the species is outlined (section 2.1) along with observations on seed and clonal material collected in the field and grown at Palmerston North under a series of conditions. Attempts were made to germinate seed (section 2.2), to observe shoot phenology (section 2.3), to induce flowering (section 2.4), to test compatibility (section 2.5) and to estimate reproductive assimilation, ie the photosynthetic contribution of female inflorescences to seed weight (section 2.6).

Initial field studies (chapter 3) involved a description of the sand plain habitat (section 3.1) and of aspects of the behaviour of naturally-occurring Carex pumila topodemes (henceforth called populations) on the sand plain at closely adjacent sites at increasing distances from the rear dune (section 3.2). Phasic development of Carex pumila on the sand plain is described (3.2.1) and the rates of clonal spread (3.2.2) and of leaf litter decomposition (3.2.3) estimated.

The major thrust of the investigation involved an attempt to influence the behaviour of the species in situ by applying to them a series of perturbation treatments (chapter 4). It was considered that through such manipulations causal factors in the development of the

sere could be investigated. The approach taken in the perturbation experiments was to describe the life history strategies of the Carex pumila populations at the various sites under the contrasting experimental regimes in terms of the the distribution patterns of both dry weight and crude total nitrogen to component shoots and organs over time. This was done over four successive summers. During these three years successional trends were expected to become apparent at each site as the resident population aged. Thus, the development of the sere was monitored both in space, across the chronotoposequence of low dunes and hollows on the sand plain, and in time, over the four growing seasons. The specific allocation to seeds (reproductive effort sensu Harper and Ogden 1970), to all reproductive structures (total reproductive effort sensu Thompson and Stewart 1981) and to rhizomatous and aerial spread was determined at each site for comparison one with another and against that for other species in seral communities. The allocation of nitrogen in this pioneer herb was determined as it was considered that this nutrient would be likely to limit plant growth on these recently exposed raw sandy soils. Its allocation was therefore considered an appropriate currency for the determination of the life history strategy of this species. Energy and percentage lipid determinations were made on various organs including seed. The values obtained gave validity to the assumption that biomass measurement would be a good approximation of that of net production. Since the inflorescence of Carex pumila including the disseminules (morphologically 'utricles') themselves, remain green for an extended period during their development, an estimate was made of reproductive assimilation (see above) to enable a more complete estimation of the cost of sexual reproduction in this species. Further, since Carex pumila grows in a sandy substrate, the underground parts including both roots and rhizomes were readily

excavated for inclusion in the resource allocation budgets.

CHAPTER TWO

Aspects of the biology of Carex pumila

- 2.1 Growth habit
- 2.2 Germination
- 2.3 Seedling morphology
- 2.4 Shoot phenology
- 2.5 Self incompatibility
- 2.6 The contribution of reproductive assimilation to seed production

2.1 Growth habit

The concept of plant architecture and the modular construction of plants is essential to an understanding of all branched structures in plants (White 1980). A module ('article' in the original, French) is an axis whose meristem creates all the differentiated structures of a shoot from inception to flowering (Halle and Oldeman 1970). In rhizomatous species, the modular unit is a single aerial shoot and its associated rhizome and adventitious roots. Growth of such clonal species is usually horizontal and involves the continual serial addition of new modules or 'ramets'. Collectively, the ramets make up the genetically distinct individual or 'genet' which is ultimately derived from a single zygote.

The adaptive significance of differences in growth forms of perennial plants between those clonal species that expand laterally and often fragment, and those that attain height and the physical integrity is usually maintained (most trees), has been discussed by Harper (1977). Light is seen to play the dominant role in selection for the vertical strategy whereas grazing or shortage of water or nutrients (as in sand dune communities) are significant in selection for the horizontal strategy.

The genetically-determined growth plan of a plant which determines its form is called the architectural model. Over twenty such models have been recognised in tree species (White 1980) whereas in rhizomatous plants Bell and Tomblinson (1980) recognized three basic types: octagonal, hexagonal and linear. These various, yet geometrically precise configurations, determined by characteristic angles of branching and patterns of bud growth are believed to confer certain advantages in terms of substrate exploration and exploitation

(Bell and Tomblinson 1980).

The adaptive significance of differences in architecture between species within each of the three rhizomatous strategies may be more difficult to explain. For example, the rhizome system of the sand sedge Carex arenaria, which Noble (1982) showed to allow for continual extension into bare sand and exploration for scarce nutrients, departs from strict linearity by branching at infrequent and irregular intervals at an average angle of 15 degrees. The adaptive significance of this departure from linearity may be appropriate to a mobile substrate which forms narrow bands (Bell and Tomblinson 1980).

Variation of the geometric pattern of rhizomatous growth within a clonal species also occurs. Branching pattern may be altered directly by alteration of environmental conditions such as changes in amount of sand accretion (Marshall 1965) or may be seen to differ genetically between population within a species (Harris 1970). Further, variation within a clone may exist as seen in the various phases of clonal development, which reflects variation in age of rhizomes (Watt 1947; Noble et al. 1979). Thus, rhizomes at the leading edge of a clone behave differently from those in older parts of the clone.

In this section, the growth habit of Carex pumila is described and compared and contrasted with that of carices growing elsewhere.

Observations

Carex pumila is a rhizome geophyte in the sense of Raunkiaer (1934). It possesses a more or less elongated horizontal axis, called a rhizome, which superficially has a monopodial character. In fact, the rhizome is a sympodium, an axis made up by the serial addition of the basal portions of successive individual branches or shoot modules.

Normally, the rhizome is transversely geotropic, growing at right angles to gravity, and at some later stage of its development it becomes negatively geotropic. Thus, the apical portion of each module grows vertically, projecting into the air bearing foliage leaves and in some cases becoming reproductive (figure 2.1).

A feature of the sympodial rhizome system of Carex pumila is its ability to change direction of growth in the vertical plane, so that its buds are ^{continually} ~~continue~~ at a characteristic depth immediately below the soil surface. Thus, the rhizome may grow more or less vertically upwards for some distance (figure 2.2) and when the shoot apex arrives close to the surface the rhizome will revert to a horizontal direction of growth. This behaviour is characteristic of many rhizome geophytes (Raunkiaer 1934) particularly those of sand dunes, peat bogs and other habitats where rapid accretion of the substrate occurs. It is probably this ability which allows Carex pumila to tolerate moderate levels of sand accretion but which ultimately leads to its demise in the presence of more prolific sand accumulators such as Ammophila arenaria and Desmoschoenus spiralis.

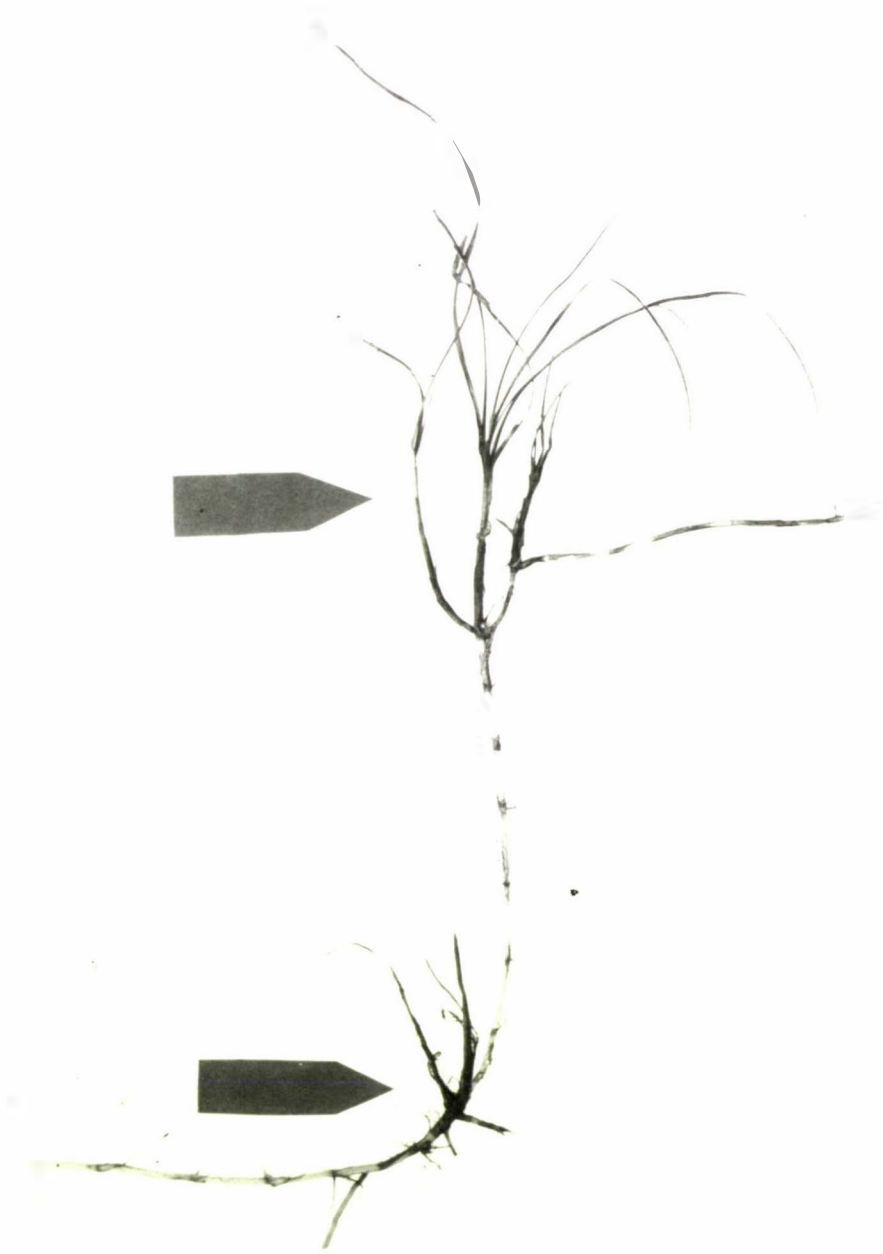
Should the rhizome of Carex pumila become exposed to the atmosphere, it will grow obliquely downwards until the apex becomes buried in the substrate where it resumes normal horizontal growth (figure 2.3). Through such changes in direction of growth a loop formation may occur.

Two types of shoot module can be distinguished in Carex pumila: one associated with long, the other with short or dwarf rhizome branches (figure 2.2). The adnation of long rhizome modules makes up the basic linear pattern of rhizome architecture. Branching of the long rhizome occurs at irregular intervals along this linear structure

Figure 2.1 A drawing of the primary rhizome axis of Carex pumila illustrating its basic morphology.



0 25 cm



2.2 Vertical growth of a primary rhizome axis of Carex pumila



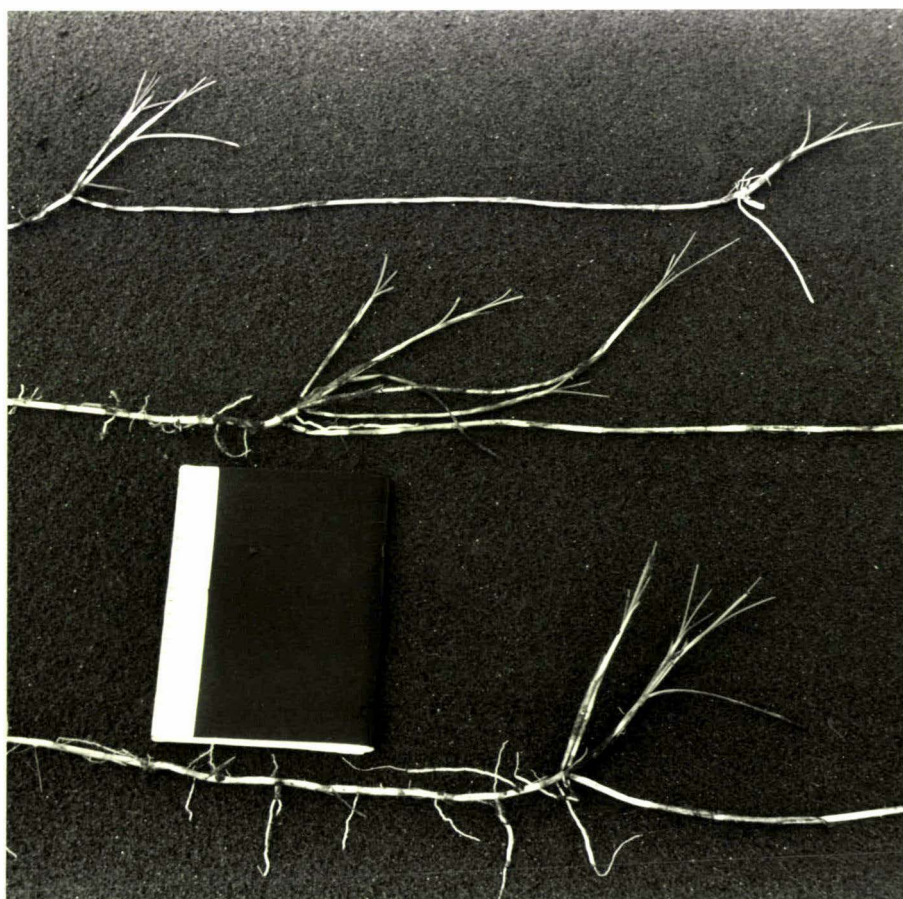
2.3 Carex pumila rhizome looping down into the substrate.

(figure 2.3). Long branches grow out from each other at angles between 9 and 21 degrees (mean 15.3 degrees; cf. branch angle of 15 degrees for Carex arenaria quoted by Noble 1982) and may continue to grow more or less parallel to each other. In some instances more than two long rhizome branches may grow out from the base of the aerial portion of a single long shoot module. Despite this, no branching of the rhizome was found from nodes further back along the parent rhizome; that is, branching appears to be acropetal.

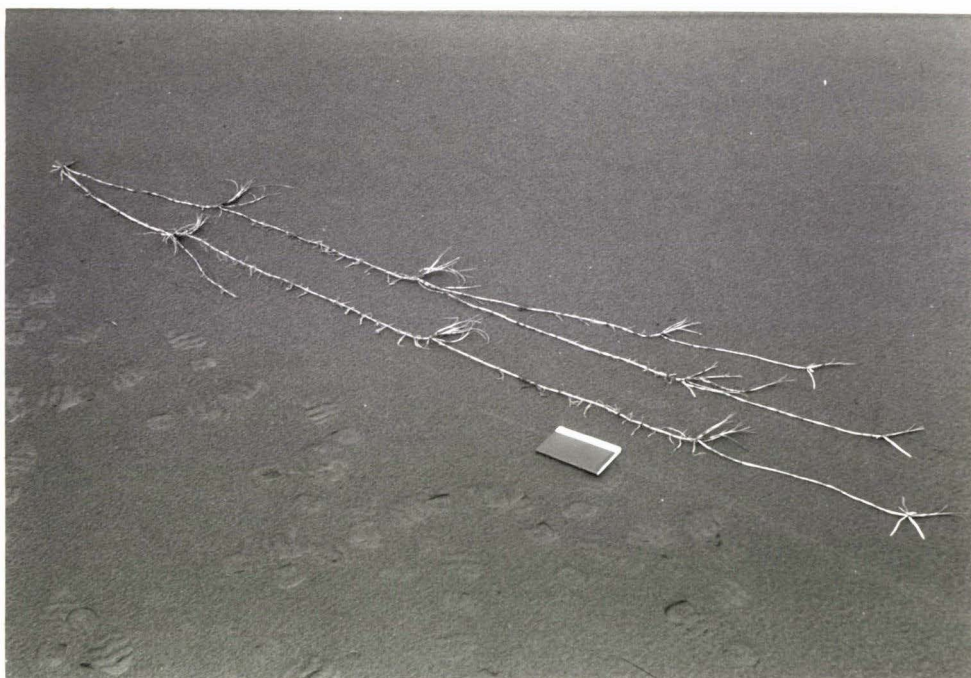
Superimposed upon this pattern of long branches, short branch modules arise from around the base of the orthotropic phase of a long branch module so forming a tuft of loosely packed aerial shoots (figures 2.2 and 2.4). These dwarf shoots, like long shoots, grow out through the overlapping brown scale leaves at the base of the aerial portion of the parent shoot giving a similar appearance to extravaginal grass tillers. Whereas the pattern of branching of long shoot modules determines the shape of this rhizomatous species (figure 2.5), the frequency of branching of both branch types determines the density of the clone (chapters 3 and 4).

The diameter of dwarf rhizome branches is less than that of long branches (figures 2.4 and 3.21), although in some instances dwarf segments may become extremely elongated, obscuring the distinction between these two branch types (figure 2.6).

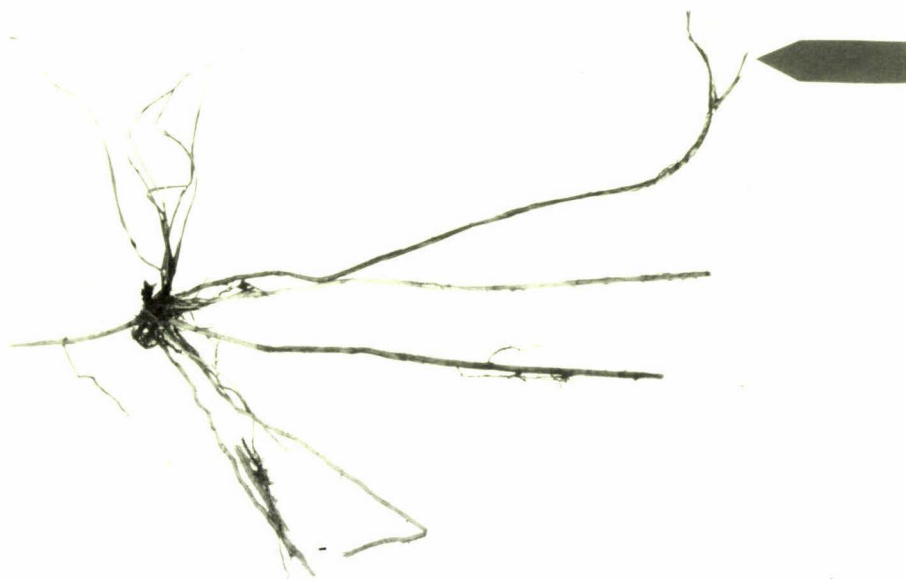
The number of internodes per sympodial unit was variable within each of these two branch types (in contrast to Carex arenaria, Noble et al. 1979). The precise number of internodes per rhizome branch module was difficult to estimate due to (1) the shortening of rhizome internodes during the transition from horizontal to orthotropic development of the branch and (2) the merging between



2.4 Short branch modules of Carex pumila



2.5 Basic linear pattern of rhizome architecture.



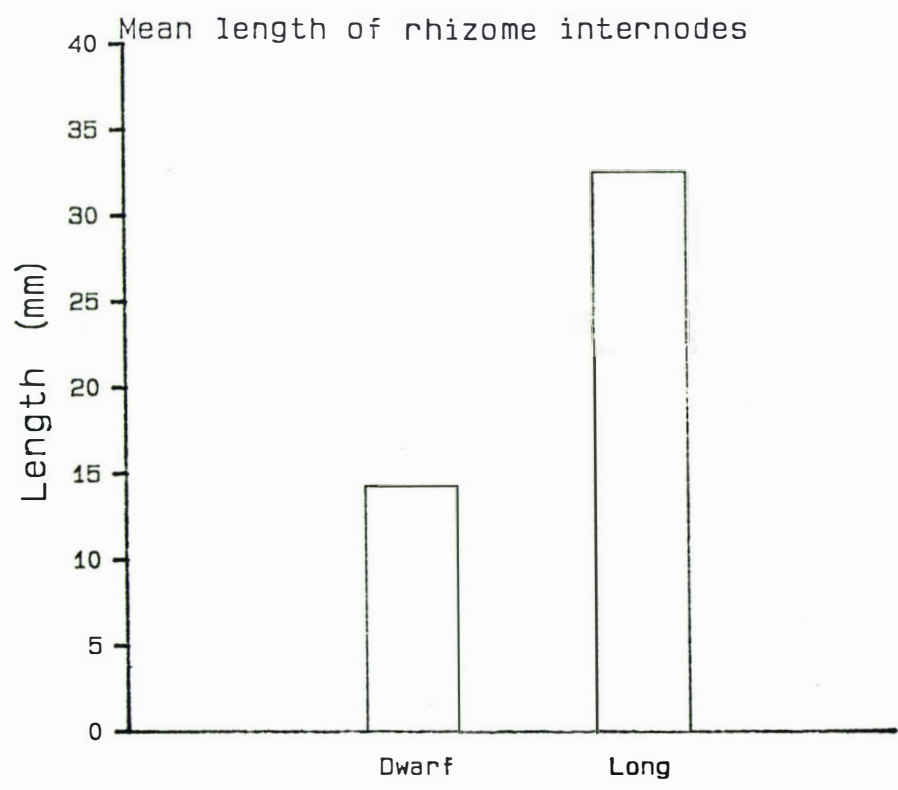
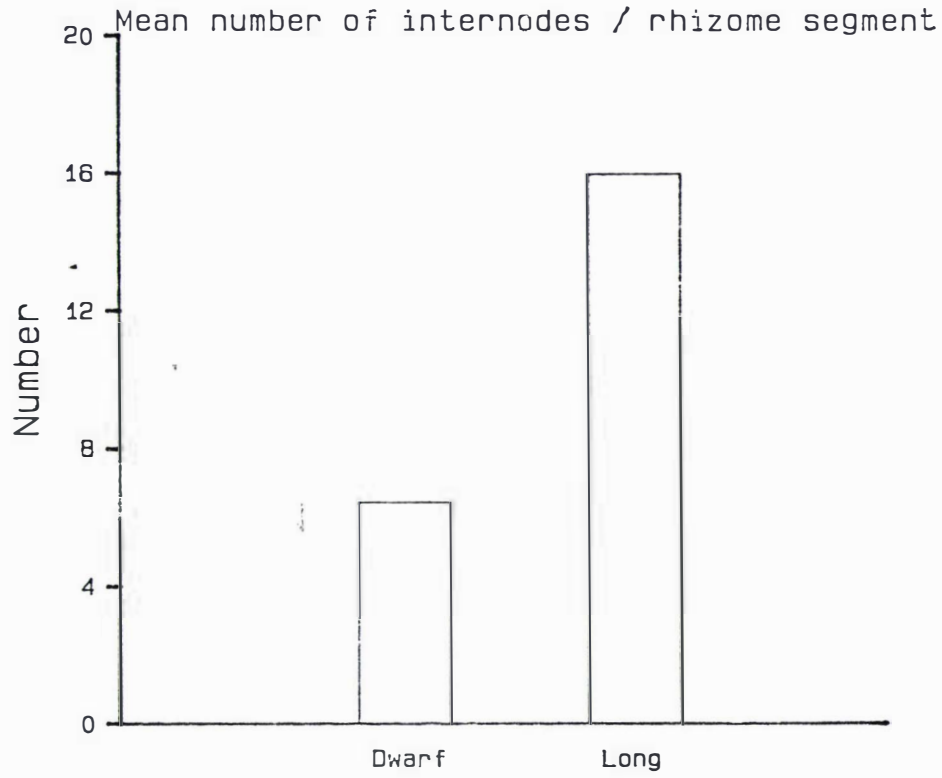
2.6 Short branch module (arrowed) abnormally elongated.

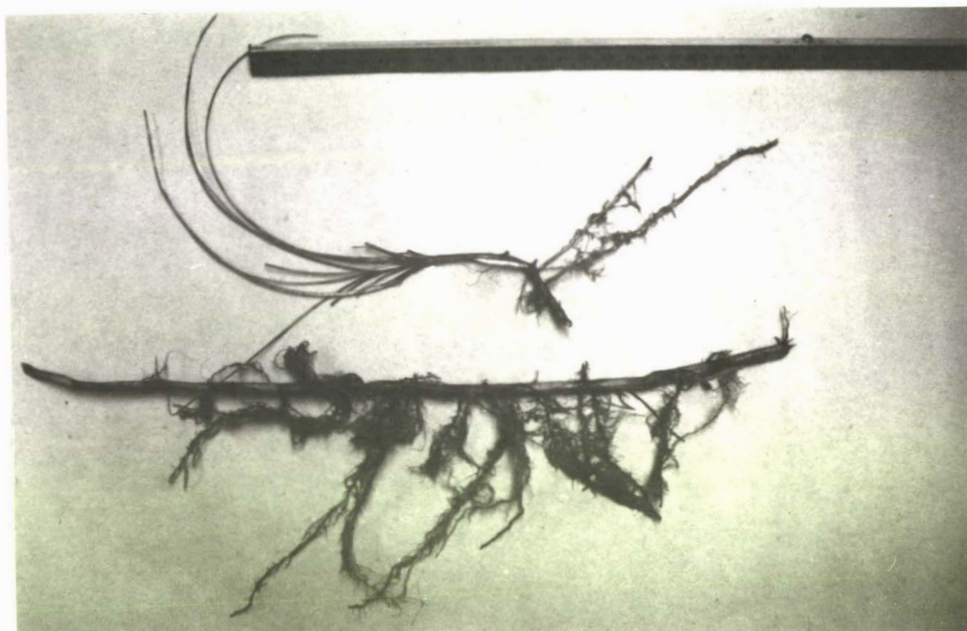
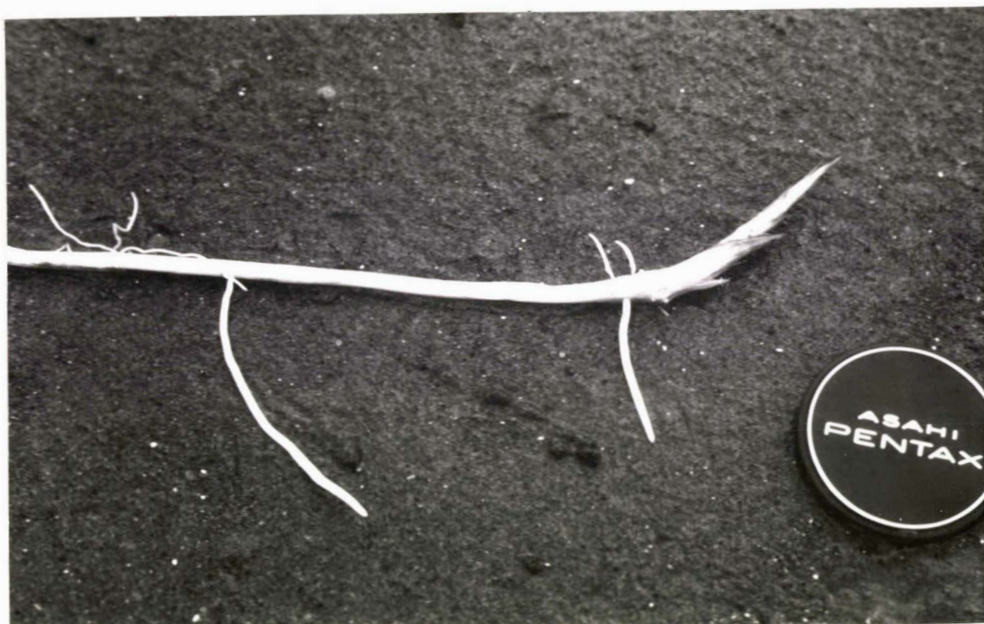
(rhizome) scale leaves and the true foliar leaves with differentiated sheath and lamina (figure 2.1 and figure 2.8a). However, the number of internodes making up dwarf rhizome branches was considerably fewer and the internodes were on average considerably shortened compared with those of long rhizome branch modules (figure 2.7).

A characteristic of Carex pumila not previously noted in the literature is the dimorphism displayed by its roots. Large diameter white sinker roots grow out from the developing rhizome along with finer roots from the more distal nodes of long rhizome branch units (figure 2.8a). Sinker roots in Carex pumila are not restricted however to the base of each orthotropic shoot as in Carex arenaria (Noble 1982). In Carex pumila both types of root turn brown with age. Sinker root diameter was variable (range 1.3 to 2.9mm, mean 2.28mm). The development of the finer, much branched roots of Carex pumila which form a dense mat in the zone immediately below the soil surface (figure 2.8b) proceeds that of the sinker roots (figure 2.8a).

Root swellings have been reported in several genera of the Cyperaceae including a number of species of Schoenus, Cladium, Kobresia and of Carex (Davies et al. 1973). In all cases the species were found in sand slack habitats where an organic layer on the soil surface had developed. The phenomenon, however, may not be universal to all carices of dune hollows. It was searched for in Carex pumila carefully excavated from moist dune hollow habitats and although there was variation in width of single sinker roots (figure 2.8a), the excrescences of fine laterals observed by Davies and co-workers were not evident.

Figure 2.7 Mean number and length of internodes on dwarf and long rhizome segments of Carex pumila





2.8 Adventitious roots of Carex pumila

(a) sinker roots and (b) mass of fine branched roots.

2.2 Germination

Observations

Seedlings of Carex pumila were rarely observed in the field. This lack of observed field germination and the difficulty experienced in germinating seeds of this species in the laboratory are characteristic of creeping sedges (Salisbury 1942). More recently, however, Noble (1982) has reported germination requirements of Carex arenaria to be less than exacting. Provided unlimited moisture and suitable temperature variation (e.g. 30/19°C, 20/15°C or 15/8°C) between 70 and 80% germination was achieved in this species. Attempts were made to germinate recently-fallen (mature) seed of Carex pumila under 30/20°C 16/8 hr day/night by staff at the Seed Technology Centre, Massey University. After three weeks no seed had germinated. Successful germination was achieved under uncontrolled conditions with this seed. Seed was kept moist in a plastic container at uncontrolled temperatures, adjacent to a radiator heater on a window sill at Palmerston North. Wide temperature fluctuations must have been experienced by these seeds. Of the 4940 seeds collected, 16.46% germinated. Shoot emergence was observed in the bulk of these seedlings over a period of two weeks from 1 October 1979, almost five months from the date of seed collection.

The period leading to the onset of germination may have been a phase of (1) protracted imbibition or (2) softening of the corky utricle. The possibility that this may also have been a period of post-ripening dormancy, as suggested for most Carex species by Jermy and Tutin (1968), could not be discounted. The subsequent rapid germination reaching an asymptote within two weeks was also reported

by Noble (1982) for Carex arenaria.

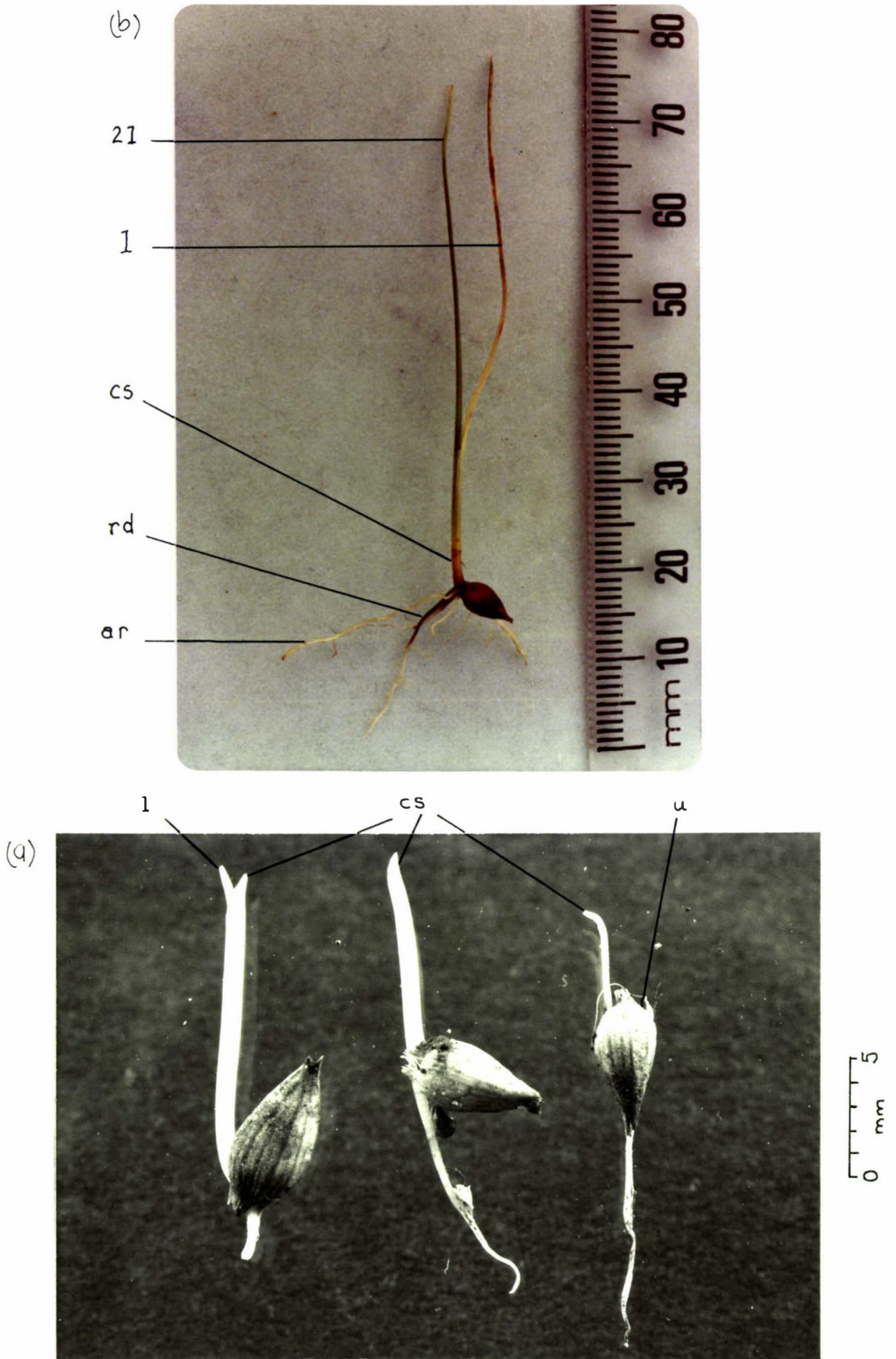
2.3 Seedling morphology

Observations

Figure 2.9 shows stages in the development of Carex pumila seedlings (a) less than one-week-old and (b) approximately two weeks old. In each of the seedlings, the shoot and root have emerged from the basal end of the intact utricule, the bifid beak of which can be seen at the narrowed distal end. In this figure u = utricule; c = cotylar sheath; l = first leaf; 2l = second leaf; m = mesocotyl; r = radicle; ar = adventitious root.

2.4 Shoot phenology

Phenological patterns have been studied in both tropical and temperate areas with records of such phenophases as active vegetative growth, presence of flower buds, flowering, fruiting and die-back of shoots, being kept at regular intervals (Kalin Arroyo et al. 1981). Of these phenophases, the time of flowering has probably received most attention with, in natural communities in temperate zones, temperature, photoperiod and soil moisture being the important variables that act as environmental stimuli entraining this phenomenon (Evans 1971). However, once floral initiation has occurred, biotic factors such as the behaviour and abundance of pollinators must also be important in determining the patterns of flowering phenomena.



2.9 Seed and seedling morphology of Carex pumila

Observations

Observations were made on shoots of Carex pumila raised from spring-germinated seed (section 2.2). Seedlings less than one week old (figure 2.9) were planted in pure beach sand without fertilizer in three 40x30cm plastic trays (60 seedlings per tray) and kept in an unheated glasshouse. Three-, 19- and 27-day-old seedlings were observed to possess on average 1,3 and 4 leaves, respectively, giving a rate of leaf emergence of one leaf per week for seedlings up to one month old.

As rhizomes began to develop and daughter shoots were produced (2-4 months old), genet were transferred to 20x20cm plastic planter bags (one genet per bag) containing pure sand without fertilizer and placed outdoors where the plants were observed over four successive summers.

By the second summer (1980-81) the original shoot had died and been replaced by two or more daughter tillers which in general remained vegetative. On those few shoots that were seen to be reproductive (less than 1% of total number of live shoots) male spikes were observed, but female spikes did not emerge. No seed was produced.

By the third summer (1981-82) a dense canopy of large shoots up to 40cm at collar height, many of which were fertile, had developed, resembling the most vigorous growth of the species observed on the sand plains (chapters 3 and 4). The density of shoots was estimated at 500 shoots per m². Extending rhizomes penetrated the walls of the plastic planter bags and had produced shoots on the surrounding ground.

By the fourth summer (1982-3) the majority of shoots were dead. The few live shoots present were either large but otherwise senescent fertile shoots with few seed, survivors of the previous autumn cohort, or young vegetative shoots penetrating the now flattened dense canopy of dead shoots that had formed the live standing shoot population of summer 1981-82.

Flowering

The phenology of flowering was followed on fertile shoots collected in turves from the field in spring 1979. Shoots were monitored daily over the critical period of stigma protrusion and anthesis. The sequence of events to emerge to which the following stages of development were applied (after Waldren and Flowerday 1979) was:

Stage	Description	Days from
		30 September
5	Culm elongating. Terminal (male) spike emerges.	13
	Emergence of uppermost female spike.	20
6	Protrusion of stigmas. Culm elongation stopped.	27
	Exsertion of anthers.	30
7	End of anthesis. Swelling of utricles begins.	37
8	Swelling of utricles. (Upper leaves, culm and utricles green).	
9	Utricles turn yellow, red-brown	60
10	Maturity. (Shedding of utricles; vegetative parts dead)	70-120

These observations suggest that fertile shoots of Carex pumila are protogynous although on a given shoot, stigmas remain white and apparently receptive to pollen throughout anthesis (figure 2.10). On some shoots, culm elongation ceased before any of the female spikes had emerged. On these shoots, normal development of the male spike proceeded giving the impression of male development prior to that of female development (protandry). Within both male and female spikes, the sequence of development of spikelets (flowers) appeared to be acropetal (figure 2.10), although on male spikes the first anthers to emerge were those halfway along the length of the spike (figure 2.11). Anthers were exerted over a period of about a week although most pollen was shed within 1-2 days.

Induction of flowering

The observations on flowering show that culm elongation and subsequent development of male and female spikes are co-ordinated suggesting that these phenomena are environmentally cued. Further observations, made in the field, of the similar timing of floral development in each of three summers (1978-79, 1979-80 and 1980-81; section 4.3.5) support this view.

Shoots of species in which the initiation of inflorescence primordia have been shown to be under environmental control may enter the terminal reproductive phase in autumn/winter although it is not until the following spring/summer that flowers emerge and reproductive output is realised. In attempting to induce floral initiation in Carex pumila, therefore, young shoots were used that could not have already undergone environmental induction of flowering.



2.10 Stages in flowering and seed production of Carex pumila. Top left: Terminal male spike and two female spikes; stage 6, preanthesis, stigmas emerging, stigma divided into three. Top right: Stage 7, end of anthesis. Bottom left: Stage 8, post anthesis, utricles green and swollen; note female flowers at base of terminal male spike. Bottom right: Stage 9-10, utricles yellow, red-brown, vegetative parts brown.



2.11 Male spike with anthers exerted.

wind-pollinated species the pattern of pollen flow is a rectangular hyperbola (Griffiths 1950) and consequently effective pollen flight distances are highly restricted (Handel 1976b).

Within the genus Carex, compatibility tests have been carried out on relatively few species. Of these, only Carex pendunculata, a myrmecochore from North America, is confirmed as being self-compatible (Handel 1976a). Faulkner (1973) tested a range of north-west European species of the section Acutae including those previously reported by Jermy and Tutin (1968) to be self-compatible and found that all but one of over 50 plants were more or less self-incompatible. The single compatible individual found by Faulkner was a member of the species Carex paleacea in which the inflorescences are considerably shorter than the leaves, an arrangement that appears to promote self-pollination in nature.

The following experiment was designed to test compatibility in Carex pumila (section Paludosae). Outwardly, the species appears to be open-pollinated with a conspicuous staminate spike terminally situated on each culm, many small light pollen grains and a lag between the protrusion of stigmas and the onset of anthesis (section 2.4).

Methods and materials

A 30 x 30 cm turf from an area at which Carex pumila was growing in monoculture on the sand plains near Tangimoana (1 km north of the area described in section 3.1) was removed to an unheated glasshouse in Palmerston North on 1 November, 1979. A large proportion of the shoots were fertile, at a stage of development proceeding male spike emergence but prior to stigma protrusion and anthesis. Shoots were closely monitored so that immediately before stigma protrusion and

subsequent anthesis, entire individual culms were enclosed in a paper "pollinating" bag which was loosely tied at the base of the culm. Eleven tagged and numbered shoots were bagged in this way on 6 November, 1979. Most pollen release occurred on the 7 and 8 November. The bags were removed along with staminate spikes on all shoots on 24 November after the utricles on the control shoots had begun to enlarge.

The experiment was terminated after two months on 7 January 1980 when the vegetative portion of the fertile culms had turned brown. Utricles and associated rhachillae on some shoots in both control and bagged treatments were still green. The number of female spikes per inflorescence, utricles per spike and utricles containing mature seed on each inflorescence were counted, and utricles bulked for each shoot (inflorescence) dried at 80 °C for 24 hours and weighed. The 11 bagged shoots and 25 of more than 30 untreated shoots on the turf were processed in this way. From these data the percentage of utricles containing mature seed and the mean dry weight per utricle were calculated for each shoot.

The significance of differences between treatments, for utricle number and weights per shoot, one thousand utricle weight and percentage of utricles containing mature seed were tested by one-way analysis of variance (treatments = 2, open-pollinated and bagged shoots; number of replicates per treatment = 25 and 11 respectively).

In addition, at the termination of the experiment, the turf was washed under a jet of water to remove sand from the roots and rhizomes. Rhizome interconnections between the aerial shoots were thus revealed. Two equal-sized sets of interconnected shoots (18 in each) were found which were designated G1 and G2, within which four

(4) and seven (7) shoots respectively were self-pollinated. G1 and G2 may be portions of different genets (clones) or they may be different portions of one genet severed when collecting the turf. Further analyses of variance for utricle number per shoot and dry weight per utricle were applied and the significance of differences between all pairs of the four treatment x genet group means was determined by applying the student-Newman-Keuls test for multiple comparisons among means based on unequal sample sizes (Sokal and Rohlf 1969).

Results

The effect of bagging individual shoots of Carex pumila at the time of anthesis to prevent open-pollination in the glasshouse was to reduce the mean dry weight of utricles produced per shoot (table 2.1). Since no significant ($p > .05$) differences were found between any of the four treatment X genet combinations for mean number of seeds per shoot (table 2.2), this reduction in utricle weight in response to bagging resulted from the reduction in mean dry weight per utricle (table 2.3). Each mean in table 2.3 (dry weight per utricle) was found to be significantly ($P < .05$) different from each of the other means.

Table 2.1 Dry weight of utricles per shoot (g)

	Mean	SD	n
Self-pollinated shoots	.21447	.0962	11
Open-pollinated shoots	.28934	.0943	25

Means differ, $P < .05$.

Table 2.2 Number of seeds per shoot

	Mean	SD	n
G1 Self-pollinated	98.5	21.73	4
G1 Open-pollinated	96.0	20.57	14
G2 Self-pollinated	80.0	27.99	7
G2 Open-pollinated	72.82	22.07	11

Means not different. $P > .05$

Table 2.3 Dry weight per utricle (mg)

	Mean	SD	n
Self-pollinated	2.34487	.5785	11
Open-pollinated	3.38102	.5700	25

Means differ, $P < .01$

Although dry weights of individual utricles were not measured, it was apparent that the reduction in mean utricle weight brought about by bagging resulted from the failure of a significant ($P < .001$) proportion of utricles on each shoot in this treatment to produce mature seed (table 2.4). Utricles of Carex pumila enclose a single pistil containing a solitary ovule. When the ovule is fertilized and the seed mature, the enveloping utricle is thick, corky and turgid, whereas unfertilized pistils remain thin and flaccid.

Table 2.4 Percentage of utricles containing mature nuts.

	Mean	SD	n
Self-pollinated shoots	60.84	17.6 309.71	11
Open-pollinated shoots	94.00	5.22 27.25	25

Discussion

The result of this experiment suggest that Carex pumila is partly self-compatible. The percentage of utricles with mature seed and consequently the mean dry weight per utricle was reduced by about 30% on self-pollinated shoots in the glasshouse. If self-incompatibility is the total failure to set seed on selfing then Carex pumila cannot be considered self-incompatible. However, such a strict definition of self-incompatibility may no longer be warranted considering the accumulating evidence of multigenic systems determining incompatibility in plants (Lewis 1979). Certainly, the strength of the self-incompatibility reaction varies in different taxa (Ganders 1979) and in some it is very weak with a high percentage of seed set with selfing, as in Nymphoides (Ornduff 1966). The results of the present experiment suggesting only weak self-incompatibility in this New Zealand member of the section Paludosae are at variance with those of Faulkner (1973) for north west European species of section Acutae of the same subgenus, Carex. Faulkner, by enclosing the female inflorescences on test plants with a glassine sleeve so that only by artificially applying pollen were any seed set, found that self-pollination resulted in extremely low seed set, between 0-20% in all but one plant tested. The higher seed set in self-pollinated shoots of Carex pumila than in other self-incompatible members of the subgenus may be the result of apomixis, although this is unlikely considering the observation that isolated fertile shoots of Carex

pumila on the sand plain at Tangimoana set few seed as reflected by their reduced mean seed weights (see Ch.4). Apomixis is unknown elsewhere in the genus (Handel 1976).

Self-pollination may not be avoidable in Carex pumila in the field despite features, both structural and phenological, that are normally associated with outcrossing : monoecy, protogyny and the conspicuous location of the male spike on the terminal portion of the culm. Although stigmas are exerted before anthers there is overlap between pollen release and receptivity of the stigmas on the same shoot (section 2.4). Even the transfer of pollen between neighbouring Carex pumila shoots in the field may not involve cross-pollination since such shoots are likely to be part of the same genet in this clonal species. In Anthoxanthum odoratum, a protogynous, self-incompatible wind-pollinated grass species, Snaydon and Davies (1976) showed that pollen flow rapidly declined to a low level at 2 metres.

Protogyny and protandry in self-incompatible species is considered by Connor (1979) an unnecessary phenological action, except perhaps as legacies of the past or to reduce pseudo-compatibility. The latter may be the explanation of the combination of protogyny and weak self-incompatibility in Carex pumila, a species that must be described as essentially allogamous.

2.6 The contribution of reproductive assimilation to propagule production

The photosynthetic contribution of reproductive structures (reproductive assimilation) to seed- or grain-filling has been the subject of numerous investigations particularly in economic species including wheat, barley, maize and rice. Quantitative estimates of this contribution vary considerably not only according to genotype but also to the methods employed in their determination. In wheat, for example, shading, excision, [^{14}C]CO₂ feeding and infra-red gas analysis techniques have all been used (Thorne 1966) with estimates of the contribution of ear photosynthesis to final grain weight ranging from 10% to 60% (Evans et al. 1975).

Although shading and excision continue to be used as means of estimating the contribution of plant parts to propagule production, they may give somewhat biased estimates since these treatments are likely to have effects besides reducing or blocking photosynthesis in the shaded or excised tissues. For example, shading and excision may result in (1) a change in temperature, (2) a reduction in transpiration, (3) an increase in respiration or (4) the induction of compensatory changes in assimilate distribution within the plant. Thus propagule weight may be affected through treatment effects on translocation and photosynthesis in other organs.

Using this technique Archbold (1945) concluded that grain growth in wheat is largely based on concurrent photosynthesis rather than previously accumulated reserves. Thus, shading or defoliation after anthesis usually reduces wheat grain yield (e.g. Bremner 1972) although this may not always be the case (e.g. Fischer 1975). Evans et al. (1975) suggest that 90-95% of the carbohydrate in wheat grains

comes from photosynthesis after anthesis. In Proctor barley on the other hand Briscoe et al. (1975) have estimated only 47% of final grain weight is contributed by post-anthesis photosynthesis (34% was attributed to flag leaf photosynthesis and 13% to reproductive assimilation i.e. photosynthesis in the ears). In Ambrosia trifida, an annual colonizer of disturbed habitats in Illinois, Bazzaz and Carlson (1979) have estimated, by means of excision experiments and measurements of CO₂ flux, that reproductive assimilation accounted for 41% and 57%, respectively, of the carbohydrate required to produce male and female inflorescences on intact plants.

Thus, for the accurate analysis of reproductive effort, that is the cost to a plant of producing reproductive structures, reproductive assimilation should be taken into consideration (Bazzaz and Carlson 1979). Reproductive assimilation is likely to be significant in sedges in which the sexual reproductive propagules contain chlorophyll and remain green for an extended period during their growth and development.

The following is an experiment designed to estimate the photosynthetic contribution of female inflorescences to propagule filling and reproductive effort in Carex pumila. The experiment followed the elaboration of "seed" (nut enclosed in a green pericarp or utricle) by pollinated female inflorescences on intact shoots under various shading and defoliation treatments, imposed after anthesis at the time rapid increase in seed weight was expected.

Methods and materials

Nine 30 x 30 cm turves were removed on 13 October, 1979 from an area on which Carex pumila was growing vigorously in monoculture on the sand plains near Tangimoana (1 km north of the study area; see

section 3.1) to an unheated glasshouse in Palmerston North. Each turf included between 9 and 52 fertile shoots, all at a stage of development around male spike emergence but prior to stigma protrusion and anthesis. All vegetative shoots were cut at ground level and removed and any that appeared subsequently were similarly removed. As anthesis was reached, shoots were tagged and assigned to one of four groups for subsequent treatment. An attempt was made to include all four treatment groups on each turf. Turves were then removed to a controlled environment room at the DSIR Climate Laboratory at Plant Physiology Division, Palmerston North. Conditions in the room were:

Temperature	$18^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ constant day and night
Relative humidity	$52/81 \pm 5\%$ day/night with corresponding
Vapour pressure deficit	10/4 mb day/night
Photosynthetic irradiance	$155 \pm 5 \text{ w m}^{-2}$ (equivalent to a photosynthetic photon flux density of $630 \pm 20 \text{ uE m}^{-2} \text{ sec}^{-1}$)
Daylength	14 hours (full lights)
Lamp combination	4 x 1000W Sylvania "Metalarc" high pressure discharge lamps plus 4 x 1000W Philips tungsten halogen lamps

The sandy substrate was kept permanently above field capacity by maintaining the turves in water-filled trays.

Between seven and fourteen days after anthesis at the time rapid increase in seed weight was expected, the following shading and defoliation treatments were imposed:

ES: Terminal section of the culm including the female inflorescence was shaded

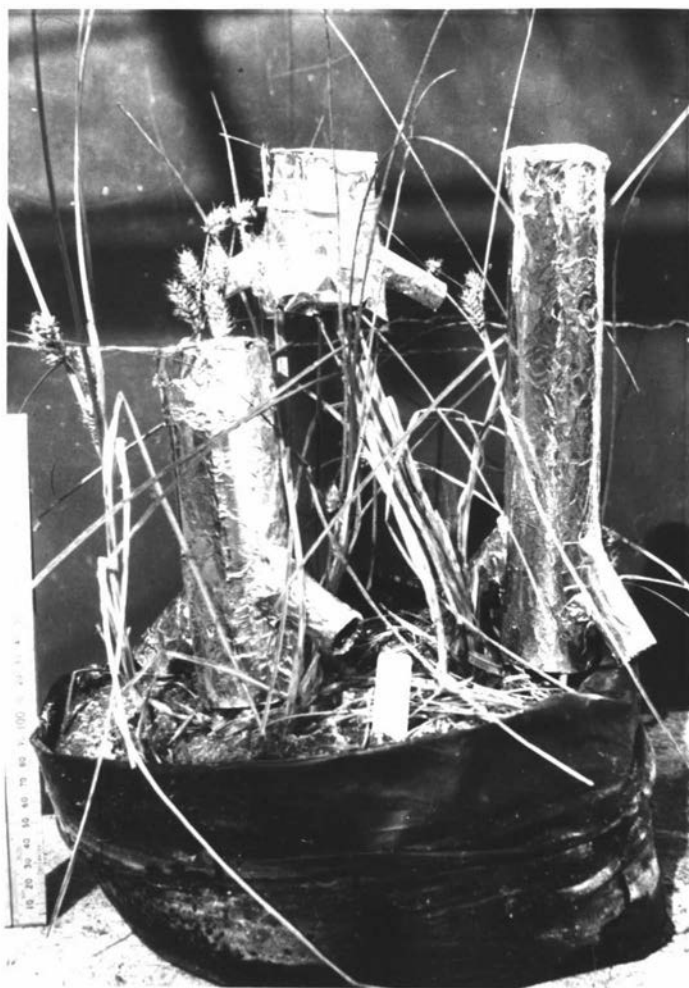
SS: Green leaf laminae were removed at the junction between sheath and lamina and the shoot, excluding the terminal fertile section with attached female and male spikes, was shaded

D : Green leaf laminae were removed as above and the entire shoot was shaded

C : Shoots were left untreated (control treatment).

These treatments allow two estimates to be made of the photosynthetic contribution of the inflorescence to the increase in seed weight firstly by the comparison of treatments ES and C and secondly by comparison of treatments D and SS. No attempt was made to prevent the translocation of stored assimilate from rhizomes to seeds.

Shades were made from black cardboard folded to form a 100mm diameter cylinder enclosed at one end and covered with aluminium foil (figure 2.12). Cylinders were attached to stakes pushed into the turves. A maximum of four shoots were enclosed within any one shade. An aluminium foil covered black cardboard disc with holes cut to accomodate the culms was used to cover the basal end of each cylinder in treatment ES.



2.12 Defoliation and shading treatments. Left to right: Treatment C, control; treatment SS, shoot defoliated and stem shaded; treatment ES, inflorescence shaded; treatment D, shoot defoliated and completely shaded.

At the beginning of the experiment between 16-22 November 1979 all plant material removed as part of the treatment was weighed along with a set of control shoots from each turf. These shoots (aerial parts only) were divided into their constituent parts, dried at 80°C for 24 hours and weighed, and numbers of female spikes per culm and seed per spike counted. The experiment was terminated on January 29-30 1980 by which time most shoots were dead. The sandy substrate was removed by washing and complete shoot modules (including the underground fractions) were separated, divided into constituent parts, dried as above and weighed. Numbers of seeds per inflorescence were counted.

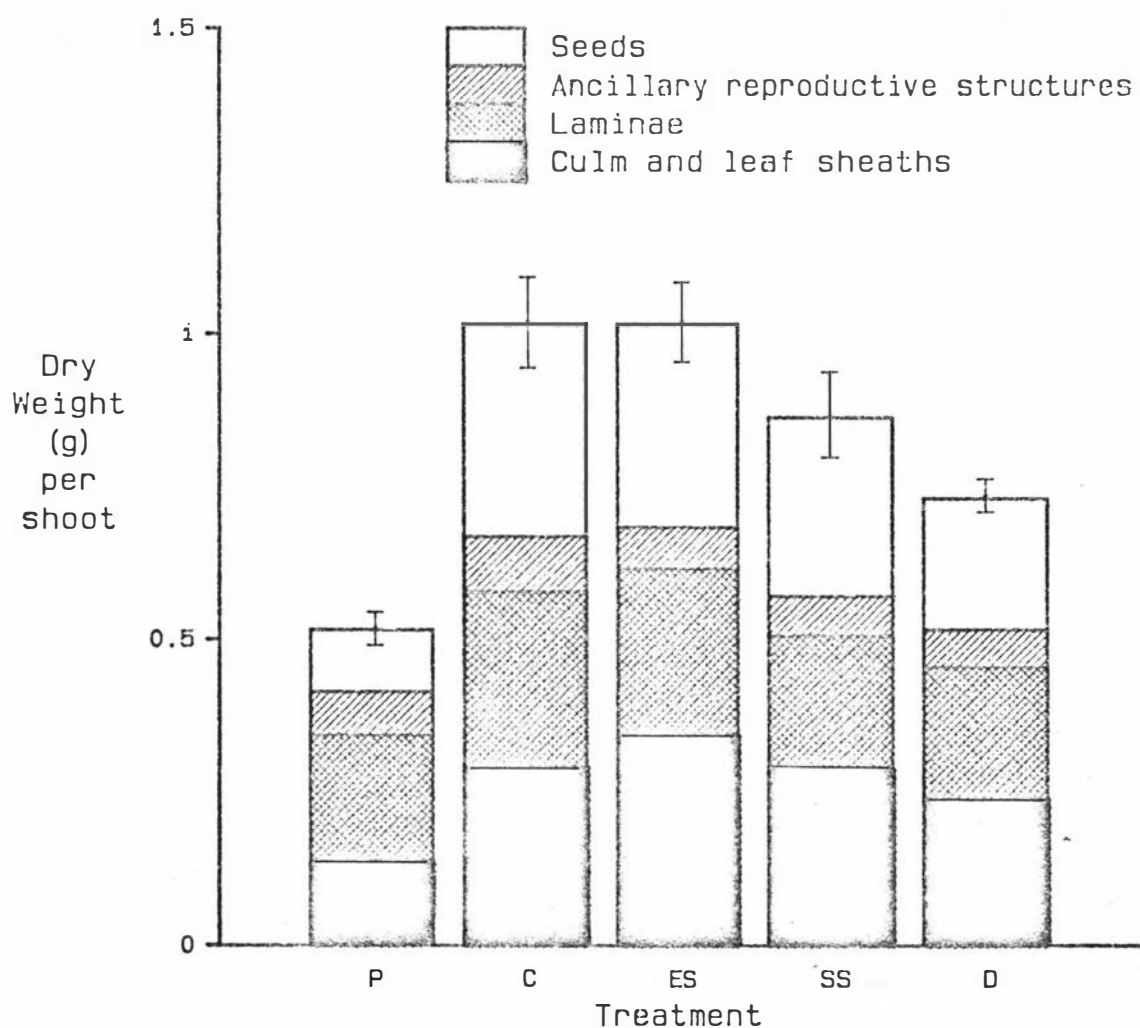
Statistical Analysis

Since a variable number of fertile shoots were found on each of the nine turves collected, equal numbers of shoots per treatment could not be ensured. Apart from the controls most treatment groups possessed three shoots per turf (average 3.74, range 2 to 7 shoots). Means were obtained for each treatment on each turf for (1) dry weight per module for each shoot component, (2) number of seeds per shoot, (3) 1000 seed weight and (4) the proportion of the total branch or total aerial shoot weight as propagules. Comparisons of these means were carried out by analysis of variance or Students t-test. Where significant treatment differences were revealed by use of the Students t-test, no more sophisticated statistical procedure was deemed necessary.

Results and discussion

Figure 2.13 shows the effect of post-anthesis shading and defoliation on the distribution of dry weight in aerial shoots of

Figure 2.13. Distribution of the aerial dry weight (grams/shoot) of fertile shoots of *Carex pumila* to component structures under contrasting defoliation shading treatments (P = pre-experiment control; C = untreated control; ES = inflorescence shaded, intact plant; SS = vegetative portion shaded; defoliated plant; D = whole shoot shaded, defoliated plant). Vertical bar denotes $\pm$ variance of means.



Carex pumila. The mean aerial dry weight per shoot increased over the duration of the experiment in all four treatments compared to the pre-experiment control (treatment P). This increase was shared between the fertile and vegetative components of these reproductive shoots. The increases in each vegetative component (that is, in culm and sheaths and in leaf laminae) and in the major fertile component (that is, in seeds) were highly significant in all treatments ($P < .01$; table 2.5). Figure 2.13 shows a greater proportional increase occurred in the fertile portion than in the vegetative portion of these shoots ($P < .001$; table 2.6). Figure 2.13 suggests that at the termination of the experiment only defoliation and shading of at least the vegetative portion of the aerial shoot (treatments SS and D) had any effect on reducing the mean dry weight of shoots. Inflorescence shading (treatment ES) had no effect on this parameter. When aerial shoot components were divided into their constituent parts, however, the only significant treatment effect was a reduction of the dry weight of seeds per shoot in response to defoliation and complete shoot shading (treatment D, $P < .05$, figure 2.14 and table 2.7). This effect was seen to be due to the reduction in mean dry weight per seed (figure 2.15); the number of seeds per inflorescence was similar in all treatments (table 2.7). The uniformity in seed number per shoot was expected since the treatments were not imposed until one to two weeks after anthesis at a time that seed numbers would have been determined. Earlier imposition of the shading/defoliation treatments was avoided since this has been seen to affect seed number (Bremner 1972; for wheat).

Table 2.5 Analysis of variance

Analysis of variance	F	Level of significance
Culm and sheaths d.w./shoot	4.62	P<.01
Leaf laminae d.w./shoot	5.276	P<.01
Seeds d.w./shoot	8.355	P<.001
Reproductive effort	6.6704	P<.001
Seed number/shoot	0.4466	ns
Seed weight	22.809	P<.001

ns = not significant

Table 2.6 Reproductive effort: the proportion of dry weight of (a) aerial shoot and (b) total (aerial plus underground) branch modules as propagules ("seeds").

Reproductive effort (%)

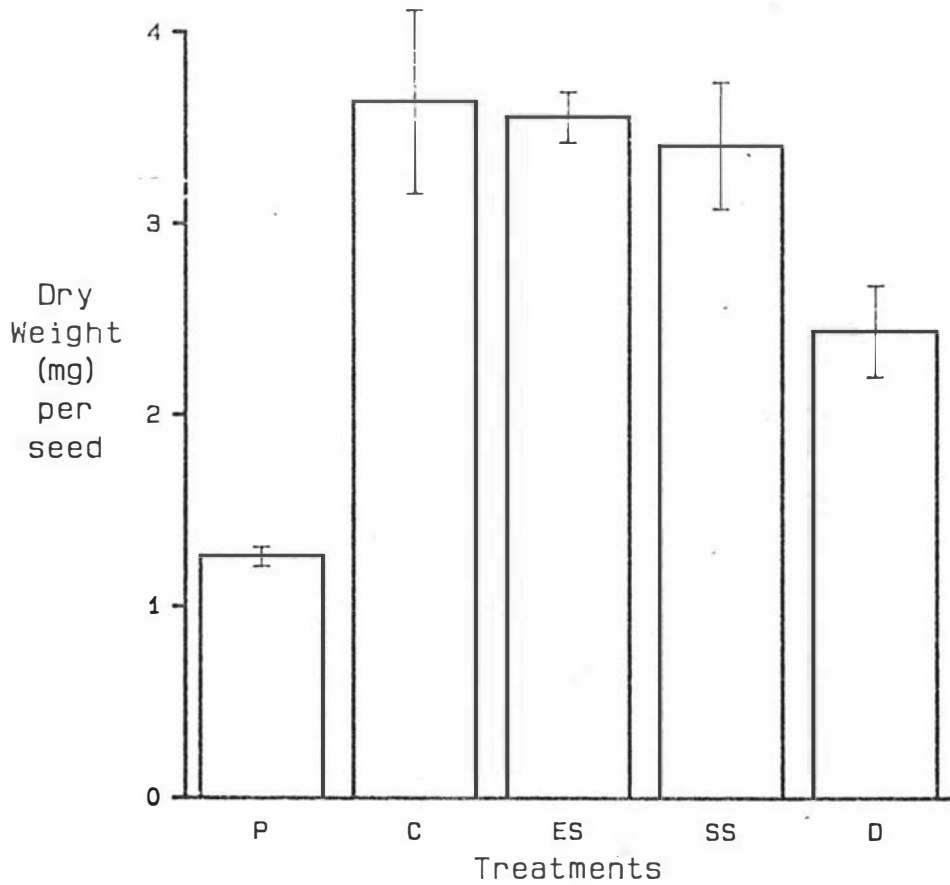
Treatment	(a)Aerial	(b)Total
Control (C)	32.98 $\pm$ 1.40	27.53 $\pm$ 1.32
Inflorescence shaded (ES)	32.94 $\pm$ 1.59	24.27 $\pm$ 1.95
Vegetative portion shaded (SS)	34.52 $\pm$ 1.91	29.48 $\pm$ 2.42
Complete shoot shaded (D)	29.23 $\pm$ 1.72	25.59 $\pm$ 2.11
Pre-experiment control (P)	21.94 $\pm$ 1.89	-

Figure 2.14 Female spikes at the end of the defoliation and shading experiment.



Increase in temperature from 15/10 (day/night) through 21/16 °C to 30/35 °C has been shown to decrease both the duration of propagule filling and final propagule weight in wheat (Sofield et al. 1974). The main temperature effect on duration of propagule filling in this species is attributed to day as opposed to night temperature (Evans et al. 1975). Phytotron experiments have also shown that temperature rather than radiation has the predominant effect on duration of grain filling in wheat (Evans et al. 1975). The temperature regime in this experiment, namely 18°C constant day and night, was chosen to ensure a relatively prolonged duration of propagule filling and so maximal final propagule weight. Air temperature (and CO₂ concentration) may have been increased above ambient within the enclosed cylinders (figure 2.12), especially in treatment D, despite the covered openings which were designed to allow the passage of air but only a minimum of light. This may account at least in part for the reduced seed weight and shortened duration of propagule filling (as seen in numbers of

Figure 2.15 Mean dry weight (mg) per seed of Carex pumila under contrasting defoliation and shading treatments (see figure 2.13 for key to treatments). Vertical bar indicates $\pm$ variance of means.



shed seed) in treatment D at the end of the experiment compared to the other treatments.

Table 2.7 Parameters of shoots under contrasting defoliation and shading treatments.

(a)		Mean (<u>±</u> SE)		
Treatment		No. of seeds	Seed weight	Seed weight
		per shoot	(mg)	per shoot (g)
Control	(C)	94.7 <u>±</u> 8.2 a	3.6408 <u>±</u> .2451a	.347 <u>±</u> .0439a
Spikes shaded	(ES)	87.7 <u>±</u> 9.9 a	3.5615 <u>±</u> .1481a	.332 <u>±</u> .0352a
Culm shaded	(SS)	89.1 <u>±</u> 11.6a	3.4071 <u>±</u> .2161a	.293 <u>±</u> .0293a
Shoot shaded	(D)	91.7 <u>±</u> 8.7 a	2.4414 <u>±</u> .1842b	.215 <u>±</u> .0226b
Pre-expt control	(P)	76.9 <u>±</u> 8.6 a	1.2572 <u>±</u> .1012d	.101 <u>±</u> .0166d
(b)		Mean (<u>±</u> SE)		
Treatment		Culm and sheath	Rhizome DM per	
		DW per shoot (g)	dwarf segment (g)	
Control	(C)	.3439 <u>±</u> .0366a	.0663 <u>±</u> .0095a	
Spikes shaded	(ES)	.2907 <u>±</u> .0518ab	.0554 <u>±</u> .0075ab	
Culm shaded	(SS)	.2900 <u>±</u> .0213ab	.0461 <u>±</u> .004 b	
Shoot shaded	(D)	.2378 <u>±</u> .0231b	.0445 <u>±</u> .0052b	
Pre-expt control	(P)	.1365 <u>±</u> .0231c		

Within each column, letters indicate Duncan's multiple range test;

a>b, P<.05; b>c, P<.01; b>d, P<.001.

Maximal seed weights achieved in this experiment were found on control shoots (figure 2.15; mean 3.6408 ± 0.2451 mg per seed). Estimates of the various contributions to this final seed weight which have been calculated by comparisons of the ~~treatm~~^{treatment} means from figure 2.15, are shown in table 2.8. At the time of imposition of the treatments, mean dry weight per seed was $1.2572 \pm .1012$ mg, a little more than one-third of the final weight achieved in the control shoots ten weeks later. Seed weight increased over the duration of the experiment in all treatments, including that in which the shoots were defoliated and the entire shoot shaded (treatment D). This latter increase which corresponds to about one-third of final seed weight in the control shoots (C) must be attributed to translocation of pre-formed assimilate, since photosynthesis in treatment D shoots may be assumed to be negligible.

Table 2.8 Contributions to propagule weight in Carex pumila

		Proportion of control mean seed weight (%)
Untreated control	(C)	100.00
Inflorescence photosynthesis (a)	(C - ES)	2.18
	(b) (SS - D)	26.52
Vegetative photosynthesis	(C - SS)	6.42
Whole shoot photosynthesis	(C - D)	32.94
Translocated/pre-formed assimilate	(D - P)	32.52
Pre-experiment control	(P)	34.53

The source of pre-formed assimilate in this experiment must ultimately be the underground fraction rather than the stem, as suggested by Briscoe et al. (1975) for barley. The mean dry weight of stems (and sheaths) actually increased over the duration of the experiment in all treatments compared with the pre-experiment control (treatment P, figure 2.13). The only possible source of assimilate leading to such an increase in treatment D must be translocation from the rhizomes. Unfortunately, no data are available for pre-experiment rhizome weights for comparison with those at the end of the experiment. However, at that time, the lowest mean dry weight of dwarf rhizome branches was obtained for treatment D, in which the drain of rhizomatous reserves was expectedly greatest (table 2.7).

The remaining (one-third) contribution to final seed weight is that of concurrent photosynthesis during the post-anthesis period. Two estimates of the photosynthetic contribution of the inflorescence to propagule production were obtained by calculating the reduction in seed weight with inflorescence shading, firstly, in intact shoots (comparison of treatments ES and C) and, secondly, in defoliated shoots (comparison of treatments SS and D). The discrepancy between these two estimates (table 2.8) indicates the ability of fertile shoot modules of this clonal species to compensate for reductions in photosynthesis in various component organs in the development of seeds. This ability to compensate for reductions in photosynthesis would suggest that, in an intact plant, the estimate of the contribution of pre-formed assimilate to final seed weight of about one-third may be an over estimation and therefore the estimation of concurrent photosynthesis to be correspondingly conservative. Likewise, the estimate of reproductive assimilation over this post-anthesis period to final seed weight (of 26%) may be an

underestimation. The similarity of final seed weight in treatments C and SS could be interpreted as an almost complete reliance by the seeds on reproductive assimilate with little demand for leaf or culm assimilate. A similar conclusion was reported by Evans and Dunstone (1970) for low-yielding primitive wheats. However, the acceptance of a value greater than 26% for the contribution of post-anthesis reproductive assimilation to propagule filling would require further experimentation involving more direct measures of reproductive assimilation and inflorescence respiration (by infra red gas analysis) and by the use of $[14-C]CO_2$ to trace the fate of assimilates formed in different parts of the sedge shoot.

CHAPTER THREE

Initial field studies

3.1 Description of the habitat

3.1.1 The study area

3.1.2 Climate

3.1.3 Wind speeds

3.1.4 Vegetation cover

3.1.5 The water table

3.1.6 Soil water profile

3.1.7 Soil nutrient and organic matter status

3.1.8 Nitrogen fixation

3.2 Carex pumila on the sand plains

3.2.1 Phasic development

3.2.2 Rates of clonal spread

3.2.3 Leaf litter decomposition

3.1 Description of the habitat

3.1.1 The study area

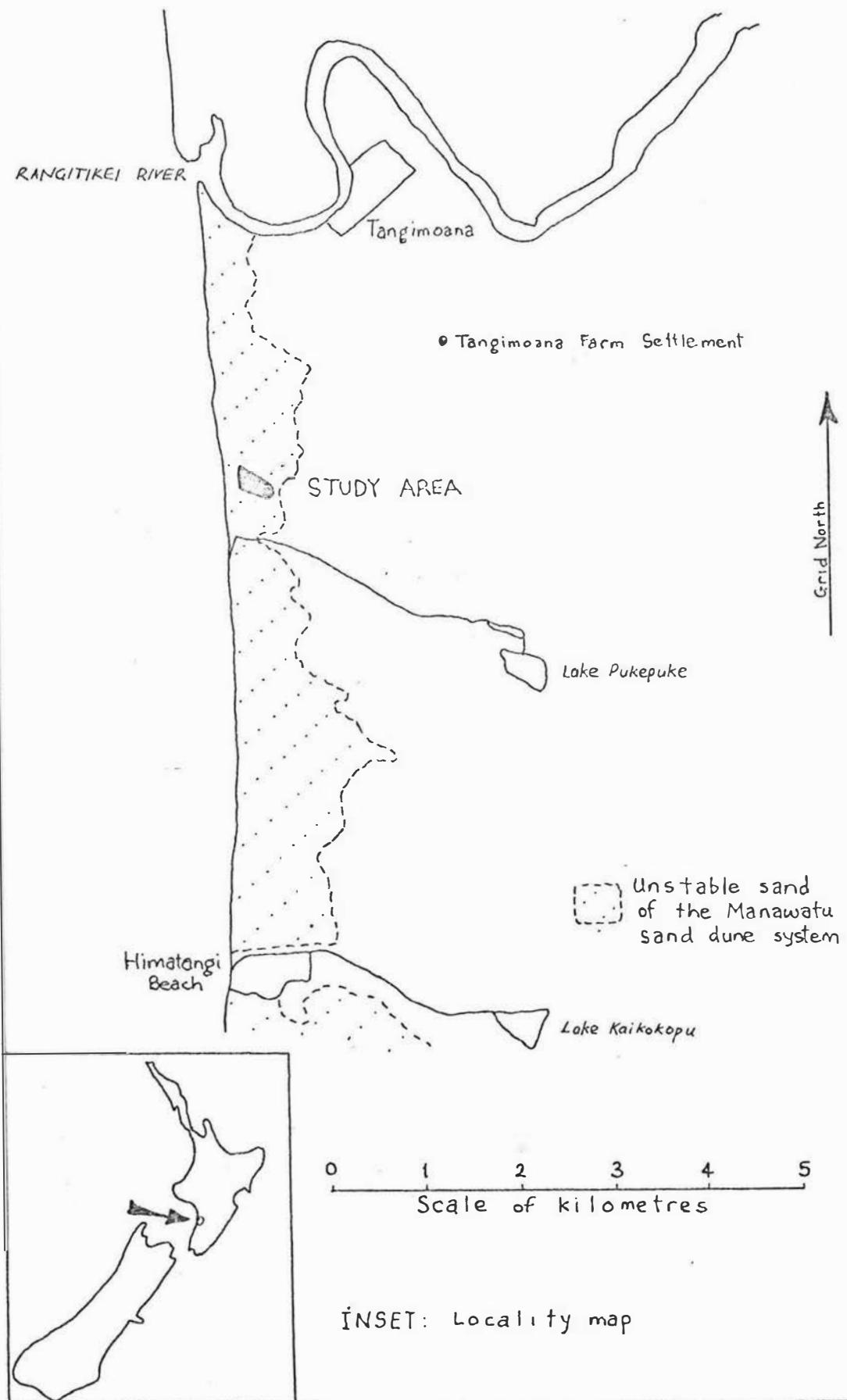
The study area was established on a sand plain near the northern end of the Manawatu sand dune system, 3 km south of Tangimoana beach on the west coast of the north island of New Zealand (40 degrees 19' 38"S, 175 degrees 14'E; figure 3.1). The area was situated at the landward end of the sand plain within 500 m of the coastal foredune, at the base of the windsweep of a landward moving parabolic rear dune and sandwiched between two parallel longitudinal dunes (the trailing arms of the parabolic rear dune) (figure 3.2). The dunes framing the study area rose 6-8 m above the level of the sand plain. The study area straddled a putative chronotopological series of damp deflation hollows (dune slacks) separated from each other by low arcuate dune ridges (figure 3.2) presumed to have been formed in the wake of the receding rear dune (Esler 1978 and section 1.4). The youngest hollow of this catenary system was closest to the rear dune with successively older hollows at progressively greater distances moving seawards.

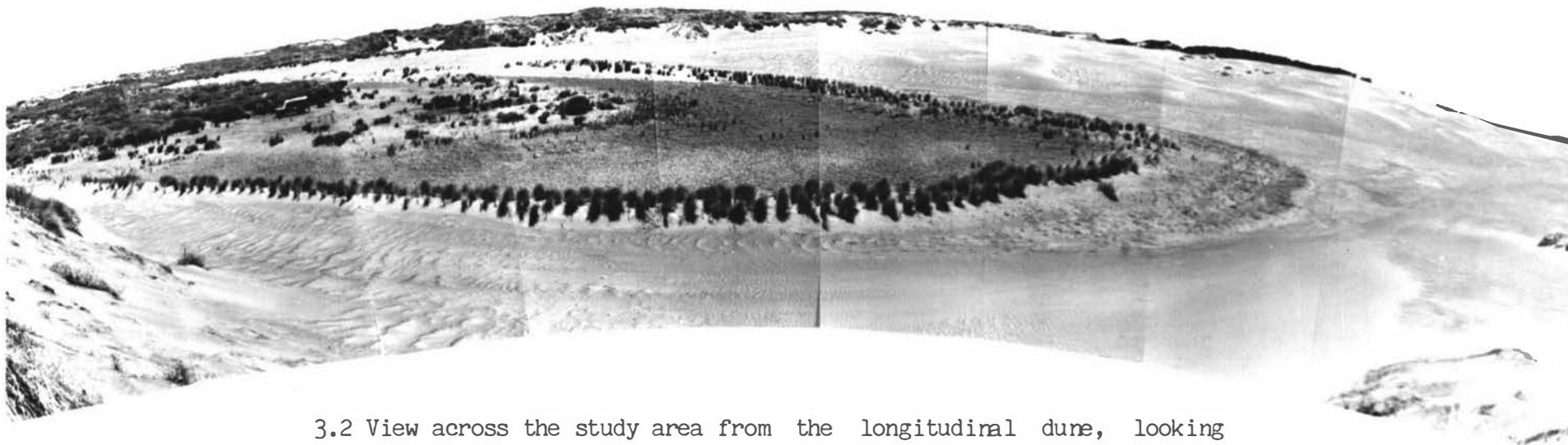
Five field sites were chosen in December 1977 at progressively greater distances from the youngest (terminal) hollow (figure 3.3) to represent sites of successively increasing age or seral maturity. The sites, which were numbered according to their relative distance from the terminal hollow, were:

Site 0 (S0) in the embryonic terminal deflation hollow was bare of vegetation in December 1977 and remained so until the end of the following summer (1978-79).

Site 1 (S1) on the edge of the adjacent low dune ridge

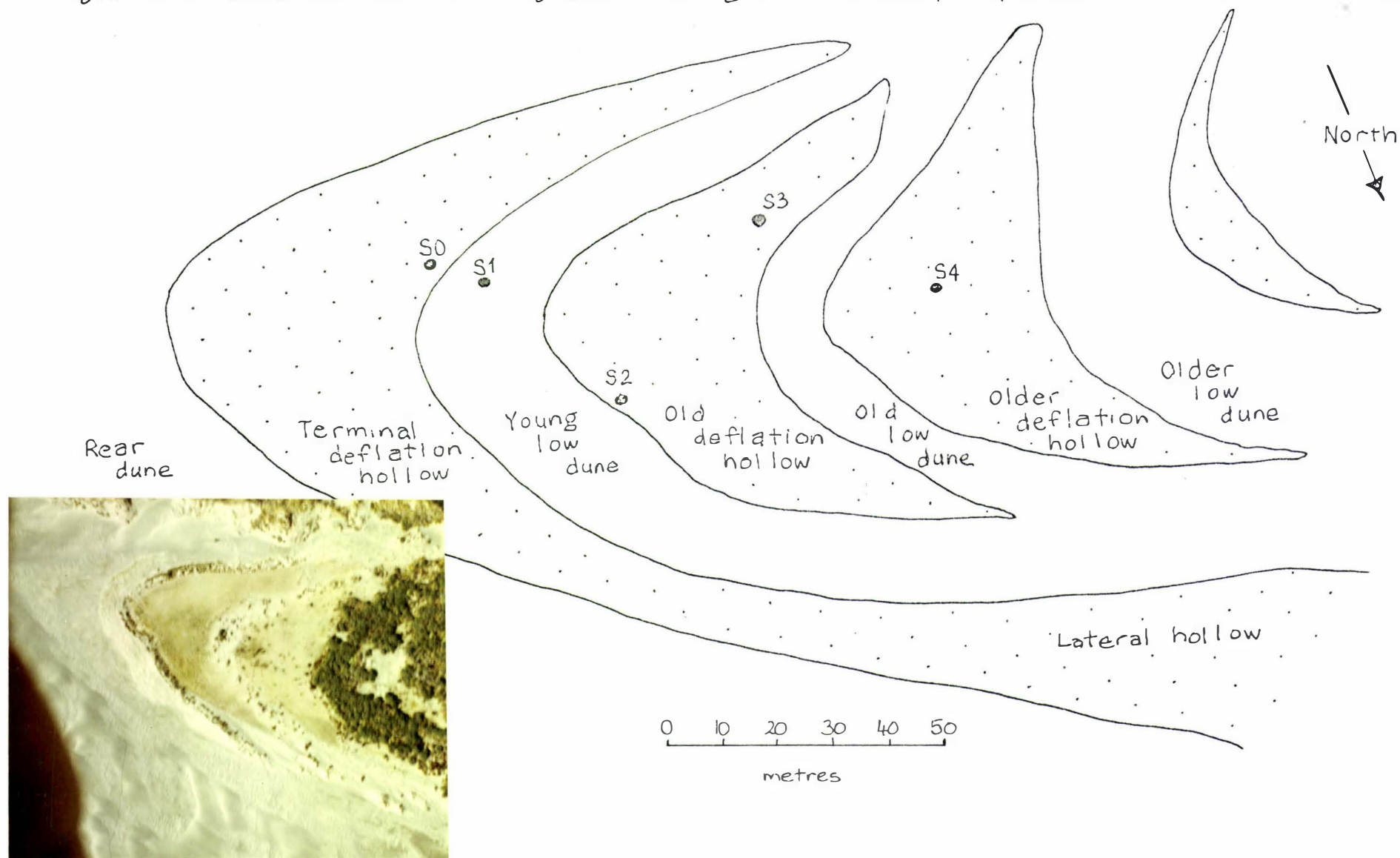
Figure 3.1

Location of the study area



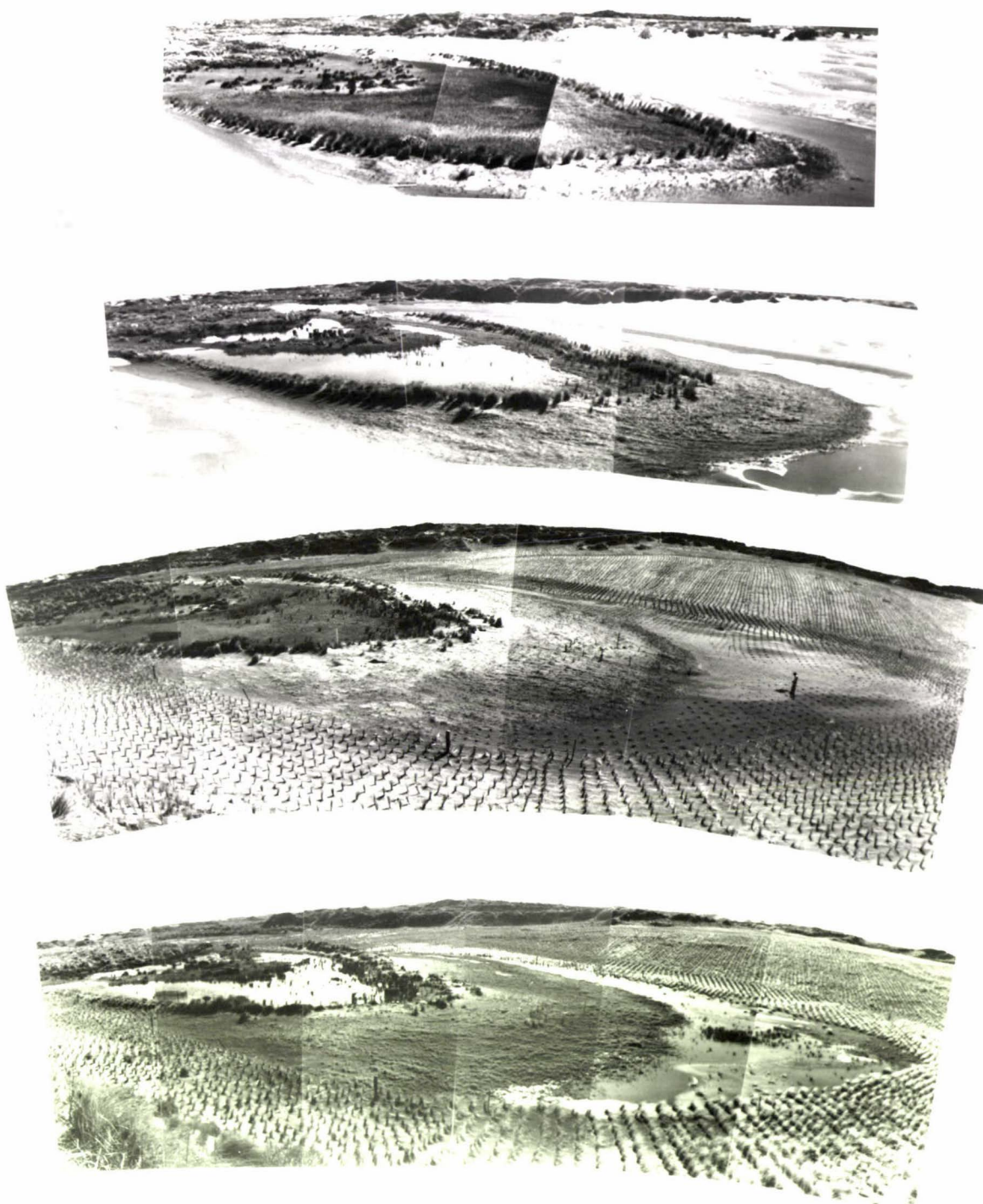
3.2 View across the study area from the longitudinal dune, looking north. Coast on extreme left.

Figure 3.3 Plan view of the study area showing the chronotoposequence of hollows and low dunes



included the front of Carex pumila rhizomes growing into the uncolonized terminal hollow. By the summer of 1978-79 S1 was about 5m behind this advancing front and sand had accumulated at the site so that the surface was approximately 30 cm higher than that of the terminal hollow. In this way, the low dune continued to encroach upon the terminal hollow (figure 3.4). By October 1979 S0 had been incorporated into the low dune and represented a similar juvenile phase of development (see section 3.2.1) to S1 nearly two years previously.

Sites 2,3 and 4 (S2, S3 and S4) were situated on more stable parts of the sand plain, within the two successively more distant (older) damp deflation hollows which became ponds during the winter (figure 3.4). Within these hollows extreme variation in plant vigour and seeding capacity was found, typical of Carex pumila on the sand plains of the Manawatu coastal dune system (Esler 1969). The sites were chosen to represent the extremes in this variation range (figure 3.5). S2 and S3 were found within 50m of each other on the old hollow behind the low dune ridge on which S1 was situated (figure 3.3). S4 was found in the older hollow further from the rear dune and separated from S2 and S3 by another, older, low dune ridge (figure 3.3).



3.4 Panorama of the study area over time. Top to bottom: December 1977; May 1979; October 1980; August 1981.



3.5 The field sites in December 1977. Top right: S1 on edge of the low dune. Bare moist sand of terminal hollow (S0) in background. Top left: S2 in old deflation hollow, showing dense stand of Carex pumila. Bottom right: S3 in old deflation hollow. Bottom left: S4 in older deflation hollow. Note depauperation of Carex pumila on older deflation hollow sites.

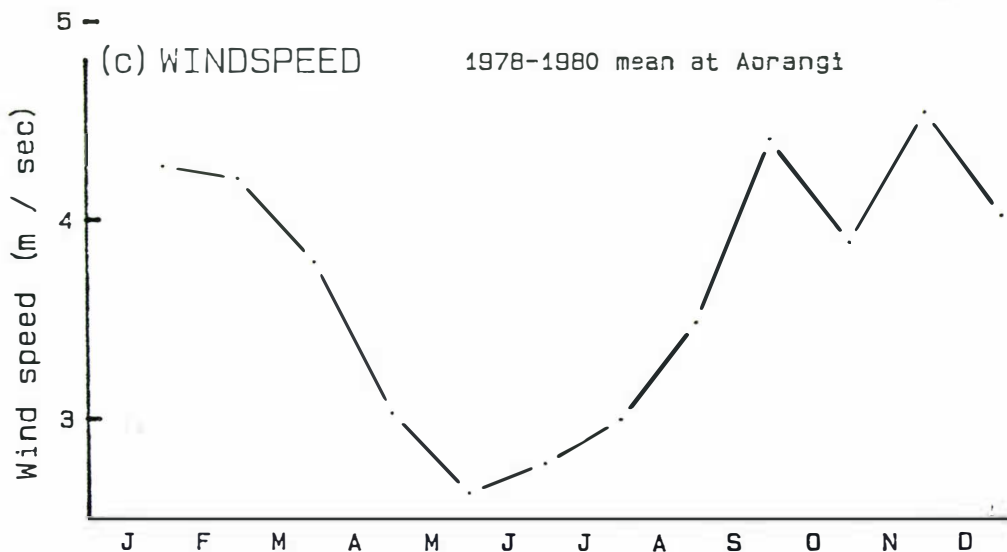
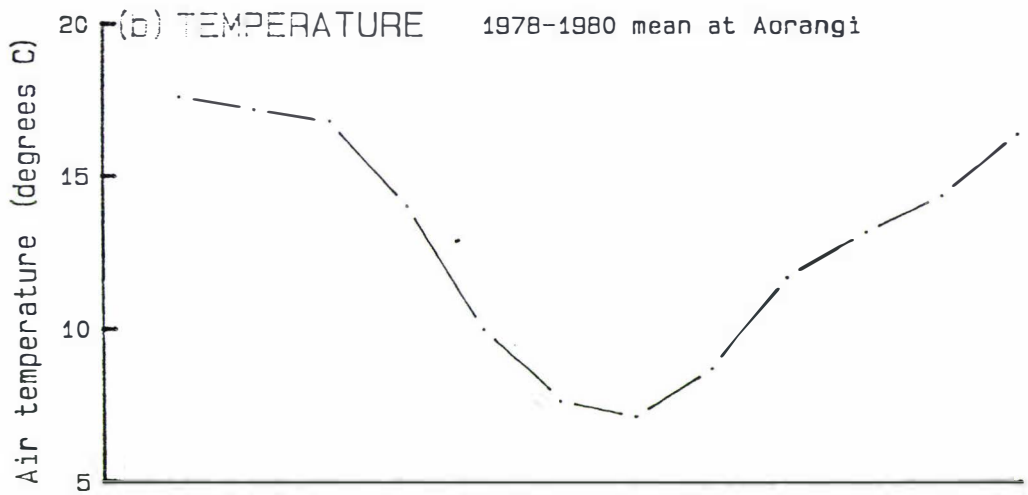
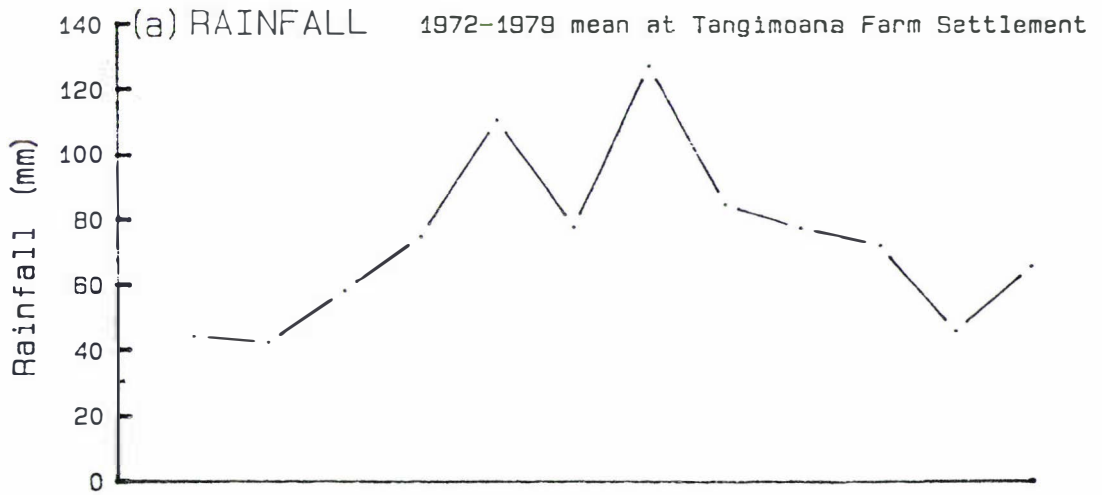
3.1.2 Climate

The climate of the Manawatu coastal sand country is characterised by warm summers and mild winters, a low mean annual rainfall distributed throughout the year and frequently gale force predominantly west to northwest winds (Robertson 1959). Figure 3.6 shows the mean monthly rainfall (1972-1979) at the Tangimoana Farm Settlement, a site approximately 2.5 km north-east of the study area (figure 3.1). February (late summer) was the driest month with an increase in rainfall in April and May (autumn). July (mid-winter) was the wettest month. The subsequent decrease in mean monthly rainfall through spring to the late summer low in February shows fluctuations in both October (spring) and December (summer). The mean annual rainfall recorded at this site (1972-79) was 899 ± 155 mm, typical for this coastal region.

Air and soil temperatures reach a maximum in late summer (January-February) and a minimum in mid winter (July), although there is no great variation in mean monthly temperature (figure 3.6 and Cowie et al. 1967). On the sand plains, a wider range of soil temperatures can be expected upon the sparsely covered low dunes than in the vegetated hollows where Cockayne (1911) noted surface temperatures in excess of 38 degrees C as the surface sand dried out during summer.

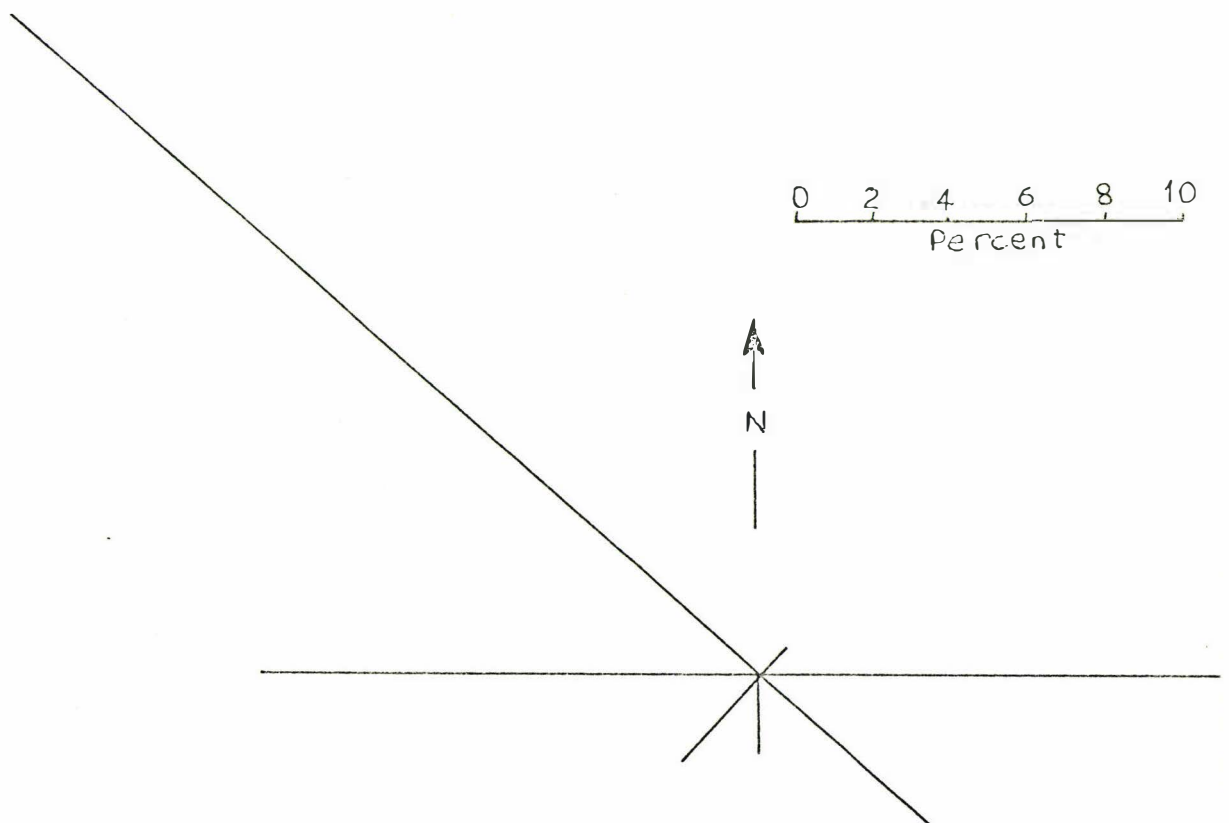
The winds in the region are variable. The predominant often strong and gusty winds of the Manawatu coast (figure 3.7) correspond to the direction of movement of the rear dune and the orientation of the longitudinal dunes (namely, from west of north-west to east of south-east; figure 3.2). Figure 3.6 shows spring and summer to be the windiest period of the year with mean daily windspeeds, based on

Figure 3.6 Mean monthly (a) rainfall, (b) temperature and (c) windspeed, at sites on the Manawatu plains.



the mean daily run of the wind for each month, of 4 to 4.5 m/sec. Autumn and winter (April to July) with mean daily windspeeds of less than 3 m/sec (figure 3.6) is characterised by prolonged periods of calm or light winds (Cowie et al. 1967). However, over the study period (1978 to 1980), wind gusts of at least 3 seconds duration of between 20 and 30 m/sec were recorded in every month of the year, at Ohakea 19 km northeast of the study area. Also, highest mean daily windspeeds in each month may be two to four times the value plotted in figure 3.6. For example, the maximum mean daily windspeed for the calmest month of the year (May) at the same site and over the same period on which figure 3.6 data were based, was 10.17 m/sec, only about 1.5 m/sec less than the maximum for any month over this three year period (Meteorological Observations 1978-1980).

Figure 3.7 Percentage frequency of surface wind directions (redrawn from table 3, Cowie et al. 1967).



On the sand plains of the Manawatu coastal dune system wind causes the movement of dry sand resulting in its local accumulation around plant shoots or in local deflation as in the formation of the terminal hollow. These effects of the movement of sand by wind on the study area were most evident during the more windy months of spring, summer and early autumn. The area was more stable during the winter months.

3.1.3 Wind speed on the sand plain

At each visit to the study area between December 1979 and September 1980, determinations of the velocity of the wind at 300mm above the soil surface were made at four sites. The mean wind speed at each site was obtained by recording the wind run during five consecutive 60-second intervals using a hand-held tachometer facing the direction of the wind. Wind velocity close to the ground will be influenced by micro-topography and plant cover and although they are likely to be substantially less than at the standard height for meteorological stations (5m), they are more likely to reflect those wind velocities that influence the growth of small herbaceous plants.

On the occasion of three visits to the study area wind velocity at 300mm was too low to be measured accurately with the device used. Wind speeds varied between dates, between sites across the study area and between sheltered and control plots (chapter 4). The variation between dates was due to the differences between mean wind velocity on the days measurements were made. Site differences resulted from differences in the topography and plant cover across the sand plain. No significant difference in wind speeds was found between the sparsely vegetated sites on the low dune (S0 and S1) and in the old

deflation hollow (S3). However, within the old hollow, wind velocity was substantially ($P < .001$) reduced at S2 (table 3.1) where the vegetation formed a more or less closed canopy between 20 and 30 cm above the slack surface (section 3.1.4).

Table 3.1 Wind speed at four sites on the sand plain under two treatments (with (S) and without (C) shelter).

	Mean velocity (m/sec)			
	S0	S1	S2	S3
Control (C)	3.03	3.181	1.713	3.094
With shelter (S)	1.345	0.4	0.198	1.35

Each value is mean of 5 x 60-second replicates on each of five dates during summer 1979-80

The maximum mean wind velocity at any site recorded at the study area was measured at 7.56 m/sec in the old hollow at S3 during a westerly. This corresponded to a daily wind run of 641 km recorded at the meteorological station at Grasslands Division of the D.S.I.R. near Palmerston North.

Wind breaks (exclosures) were erected at four sites on the sand plain in spring 1979 (section 4.1). These nylon-mesh structures significantly ($P < .001$) reduced wind speeds at 300mm above the surface at all sites (table 3.1) although mean values within an intact exclosure could still be high on a windy day. For example, during the westerly gale on 17 September, 1980, a mean speed of 5.08 m/sec was

recorded within the enclosure on the old hollow at S3, compared with 7.56 m/sec on the control plots. The effectiveness of the enclosures in reducing wind speed was not equal at all sites (table 3.1). At S0 and S3, wind speed was reduced by only about 56% by the shelters compared with almost 90% reduction at S1 and S2. The effectiveness of the shelters was considerably reduced at the two former sites by wind damage to these structures which required continual maintenance throughout the summer of 1979-80.

3.1.4 Vegetation

The vegetation cover (sensu Greig Smith 1957) at five sites on the sand plain in November 1980, was determined by point analysis (table 3.2) by sampling 225 points at each site.

It is evident from table 3.2 that the species composition at S0 and S1 on the low dune was dissimilar to that at the other three sites. Not only was Carex pumila either the only species present (S0) or the only one present in quantifiable proportions (S1), but also there was a greater percentage of bare sand uncovered by plant leaves, compared to S2, S3 and S4. The cover provided by all species at the dry low dune site (S1), which was colonised in summer 1977-78 by the advancing front of Carex pumila rhizomes, was only 12 percent, the lowest of all sites studied on the sand plain. By comparison the cover provided by the sole species at S0 on the edge of the low dune was more than double this, namely 25 percent. S1 was distinguished by the presence of five sand dune species which, with the exception of Gnaphalium luteo-album, are all introduced (table 3.2). By contrast, all but Largurus ovatus and ^{Leontodon}~~Leodon~~ taraxacoides of the 12 species found on the deflation hollows are native to New Zealand.

Table 3.2 Percentage cover at five sites on the sand plain in November 1980

Species	S0	S1	S2	S3	S4
<i>Selliera radicans</i>	NP	NP	9	35	37
<i>Leontodon taraxacoides</i>	NP	NP	9	3	7
<i>Bryum campylothecium</i>	NP	NP	NP	NP	12
<i>Eleocharis neozelandica</i>	NP	NP	23	5	22
<i>Lobelia anceps</i>	NP	NP	8	P	5
<i>Epilobium billardierianum</i>	NP	NP	8	NP	1
<i>Carex pumila</i> live shoots	23	4	13	0.4	P
dead shoots	2	8	31	1	3
<i>Lagurus ovatus</i>	NP	NP	6	P	3
<i>Scirpus nodosus</i>	NP	NP	5	P	2
<i>Leptocarpus similis</i>	NP	NP	2	P	P
<i>Cortaderia toetoe</i>	NP	P	P	NP	NP
<i>Senecio elegans</i> I	NP	P	NP	NP	NP
<i>Gnaphalium luteo-album</i>	NP	P	NP	NP	NP
<i>Ammophila arenaria</i> I	NP	P	NP	NP	NP
<i>Hypochaeris glabra</i> I	NP	P	NP	NP	NP
<i>Lactuca serriola</i> I	NP	P	NP	NP	NP
Blue-green algal crust	NP	NP	2	0.4	0.4
Total vegetation cover	25	12	116	44.8	92.4
Bare ground	75	88	2.3	57	31

NP=not present; P=present, but not in sample; I=introduced species

The total vegetation cover on the dune slacks (S2, S3 and S4) was higher than that on the low dune at S0 and S1 (table 3.2). Further, species diversity was greater on the slacks than on the low dune. Nine species were common to S2, S3 and S4. Dune slack species missing from at least one deflation hollow site were the moss Bryum campylothecium, found only at S4 where it formed a more or less continuous mat over much of the oldest deflation hollow; Cortaderia toetoe, found both on the drier parts at the landward end of the old hollow where some sand accumulation had occurred (S2) and on the low dune at S1; and Epilobium billardierianum which was absent from S3. This absence is probably the result of the high wind speeds on this part of the old hollow (section 3.1.3) where the vegetation cover was low. The hoary capsules of this wind dispersed species would not readily settle and become lodged under these conditions.

The percentage cover provided by the dune slack species that were common to all three deflation hollow sites differed between S2, S3 and S4. The greatest cover provided by any species on the sand plain was obtained for Selliera radicans* which covered more than one-third of the ground at both S3 and S4. Cover provided by live shoots of Carex pumila at S2, was estimated at 13 percent, although with dead shoots of this species taken into account, this value increased to 44 percent. Eleocharis neozelandica covered almost one-quarter of the surface at both S2 and S4. At S2, the percentage of bare ground was only 2.34 percent, the lowest of all sites studied on the sand plain.

* Footnote: In addition to its ability to produce seed and to colonise locally by extension growth of a rhizome, Selliera radicans produces thickened almost globular leaves which when separated from the parent plant may grow as an independent individual (ramet).

The dune slack species that provided more cover at S2 than at either of the two other deflation hollow sites (S3 and S4), namely Scirpus nodosus, Lobelia anceps, Epilobium billardierianum and Leptocarpus similis, are all tall-growing species with the ability to reach at least to the top of the canopy formed by Carex pumila. By contrast the prostrate Selliera radicans whose stolons and leaves form a mat closely adpressed to the soil surface provides considerably reduced cover at S2, compared with that on the more open parts of the old hollows at S3 and S4.

The total vegetation cover plus the proportion of sample points where no leaves were found (bare ground) was greater than 100 % at S2, S3 and S4 indicating the overlap of leaves of different species at each of these old deflation hollow sites. This overlap which resulted from a stratification within the herbaceous vegetation (figure 3.8) was more pronounced at S2 and S4. The lower stratum of Selliera radicans, Leontodon taraxacoides and at S4 only Bryum campylothecium, which lies close to the soil surface, was overlain by the more erect leaves of Eleocharis neozelandica which in turn were overlain by leaves and stems of Lobelia anceps, Epilobium billardierianum, Carex pumila and Lagurus ovatus. Leptocarpus similis and Scirpus nodosus were the tallest members of the vegetation although these tended to form a dense erect clump with little lateral spread. At S3 and S4, the greater percentage cover was provided by species of the lower strata compared with the upper stratum (66 and 14 %, respectively) whereas at S2 the relative importance of these strata were reversed (46 and 72 %, respectively).



3.8 Stratification of the vegetation.

3.1.5 The water table

Measurements of the vertical distance of the free water table to the soil surface were made at S0, S1, S2, S3 and S4 and at a sixth site midway between S3 and S4, within the study area. In the slacks or hollows between the arcuate low dune ridges the ground water level was in close proximity to the surface throughout the year. The soil immediately above the free water table was waterlogged so that aeration of the soil would have been reduced, the rate of organic matter decomposition lowered and the carbon to nitrogen ratio increased (Ranwell 1972). Further, surface leaching during the drier summer months would have been offset by the return of bases to the surface layer when the water table rose in the winter (Ranwell 1959). It was apparent from the distinctive vegetation in the slacks and on the associated low dune ridges in the present study (see table 3.2) that the ^{distance}~~dist~~ of the free water table from the ground surface, or one of its associated variables, was a controlling factor in the development of the vegetation on the sand plain.

In August 1978 at each of six sites, a 1.0 m length of alcathehene pipe (22mm internal diameter) was planted into the ground to a depth of 950mm. A cork attached to a length of cotton thread was used to record the level of water in the pipes. Because of the difficulty of keeping the pipes clear even with the use of a soil auger, this method of recording the distance to the water table was discontinued after 12 months in favour of simply excavating to the level of the water table and replacing the soil after measurements had been made. Water table levels at each site were recorded at irregular intervals on the occasion of each visit to the study area between August 1978 and October 1980.

Variation in water table levels was evident between sites on the sand plain due to differences in their elevation. These differences however were not constant over the duration of the study as a result of the seasonal movement of dry sand across the area causing local deflation and accumulation, especially on the younger part of the system closer to the rear dune. The mean summer (November 1978-March 1979) water table levels at each site given in table 3.3. Assuming that the water table was horizontal across the study area and that there was no significant accretion or erosion of the surface at these sites over this period then the data in table 3.3 can be used to determine the topographic profile across the study area (figure 3.9). Since the water table level will rise slightly at the edge of an individual dune slack (hollow), although it will not follow the steeper profile of the dune (Ranwell 1972), the present method will underestimate the elevation of the low dunes. The estimated levels of the sand surface in the two older deflation hollows at S3 and S4 were similar. The level was slightly raised at the landward end of the old hollow at S2. The sand surface was further elevated in the terminal hollow. The difference in elevation between the old and the young terminal deflation hollow was greater in early summer (November, December 1978; c 90mm) than later in summer (January, February 1979; c 20mm). This difference is accounted for by the continued wind deflation of the uncolonized terminal hollow, but not of the vegetated old hollow, during this period as the water table level dropped (see below) and the surface sand dried.

Figure 3.9 Topographic profile of the study area

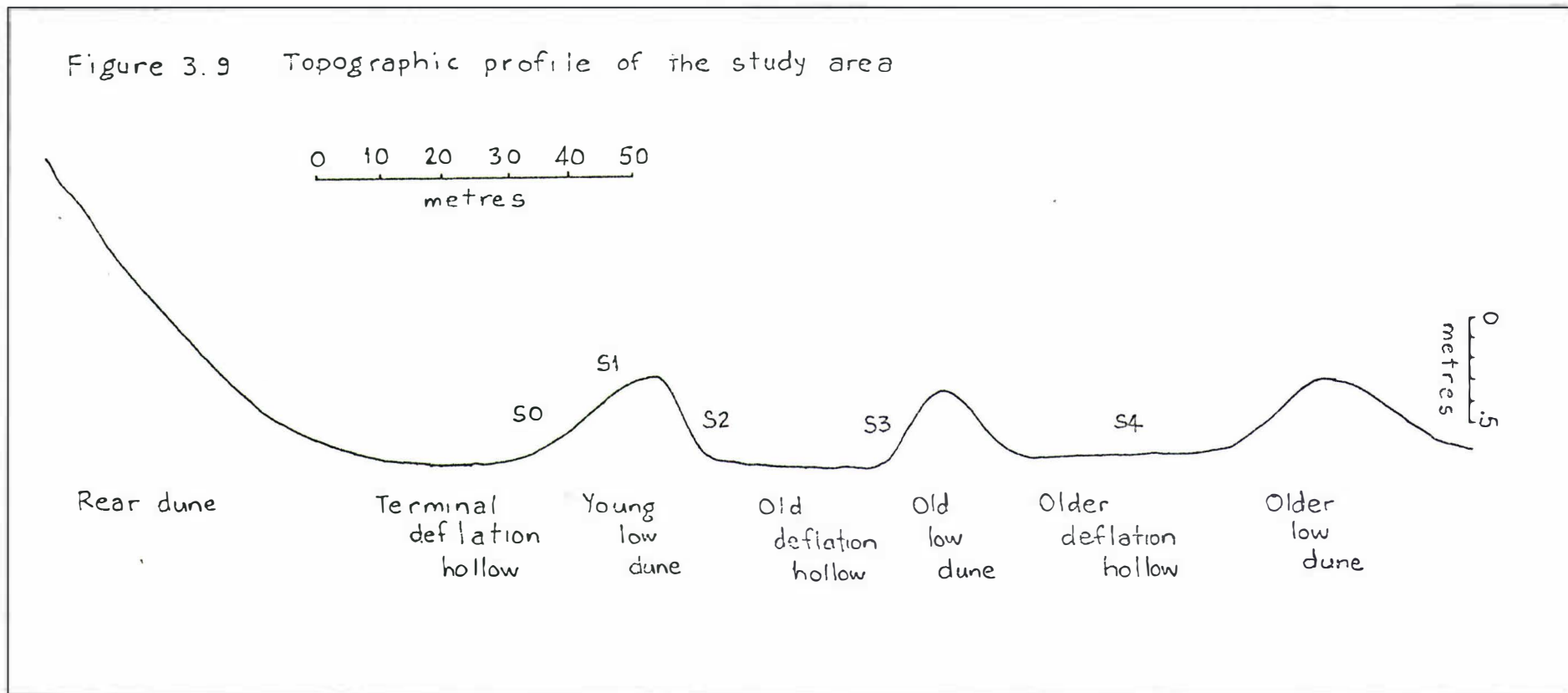


Table 3.3 Mean summer water table levels at six sites on the sand plain, November 1978 to February 1979.

Site	Distance below surface (mm)
S0 Terminal hollow	466.1
S1 Low dune ridge	748.9
S2 Old deflation hollow	393.4
S3 " " "	366.5
Older low dune ridge (between S3 and S4)	746.6
S4 Older deflation hollow	360.7

The elevation of the old low dune and the young low dune at S1 was remarkably similar, despite the variable heights of these low dunes above the adjacent deflation hollows. Ammophila arenaria which has the ability to build the low dunes higher (Esler 1978) was absent from both the old low dune and from S1. This species however was present elsewhere on the young low dune forming an arcuate band (figures 3.2 and 3.4) where by summer 1978-79 it had accumulated sand to a greater height than at S1 at which Carex pumila was the only species present.

Ranwell (1972) showed that the overall shape of the water table in a large isolated dune system is dome-shaped as a result of the more rapid drainage on the periphery of the dune system. Should the water table in the Manawatu sand dune system conform to this shape, the scale of variation over the study area is likely to be only small since the field sites were all within 100m of each other.

Generalised seasonal changes in water table levels on the study area were evident (figure 3.10). The water table levels were high during the winter often resulting in surface flooding in the hollows, steadily dropped during spring and summer with some fluctuation to a low in February-March, and rose more sharply in the autumn. This autumn rise in water table levels coincided with the death of the fertile shoot cohort of Carex pumila. Each winter, with the exception of 1978 when the first half of the year to mid winter was uncharacteristically dry (rainfall was 218mm compared with the 1972-79 mean of 409mm), the water table in the hollows rose to the surface so that there was either surface puddling (1980) or actual flooding (1979 and 1981). The annual range in water table levels was between 600 and 700mm, approaching that described by Ranwell (1959) for slacks in a dune system on Anglesey in North Wales where the annual rainfall was also similar to that on the Manawatu coast.

Short term fluctuations in water table levels were super-imposed upon these seasonal trends and show a similar pattern to that described by distribution of rainfall (figure 3.11). For example between 10 and 14 November, 1978, the water table rose 130-135mm in the two more mature old deflation hollow sites. The water table level rise over this period was not as evident on the low dune and on the immediately adjacent old hollow (S2) where sand accretion occurred concurrently on these parts of the sand plain. The sharp rise in the water table level over this period coincided with the thunder storm of 11-12 November 1978 when 27.4mm of rain fell. Between the 10 and 14 November 30.8mm of rain was recorded. Given a pore space of 40% for the soil in the older hollows (see section 3.1.6) this rainfall accounted for only about one-half the observed rise of the water table in the older hollows. The remaining rise must have been the result of

Figure 3.10 Water table levels in the old deflation hollows over time (averaged over S2, S3 and S4)

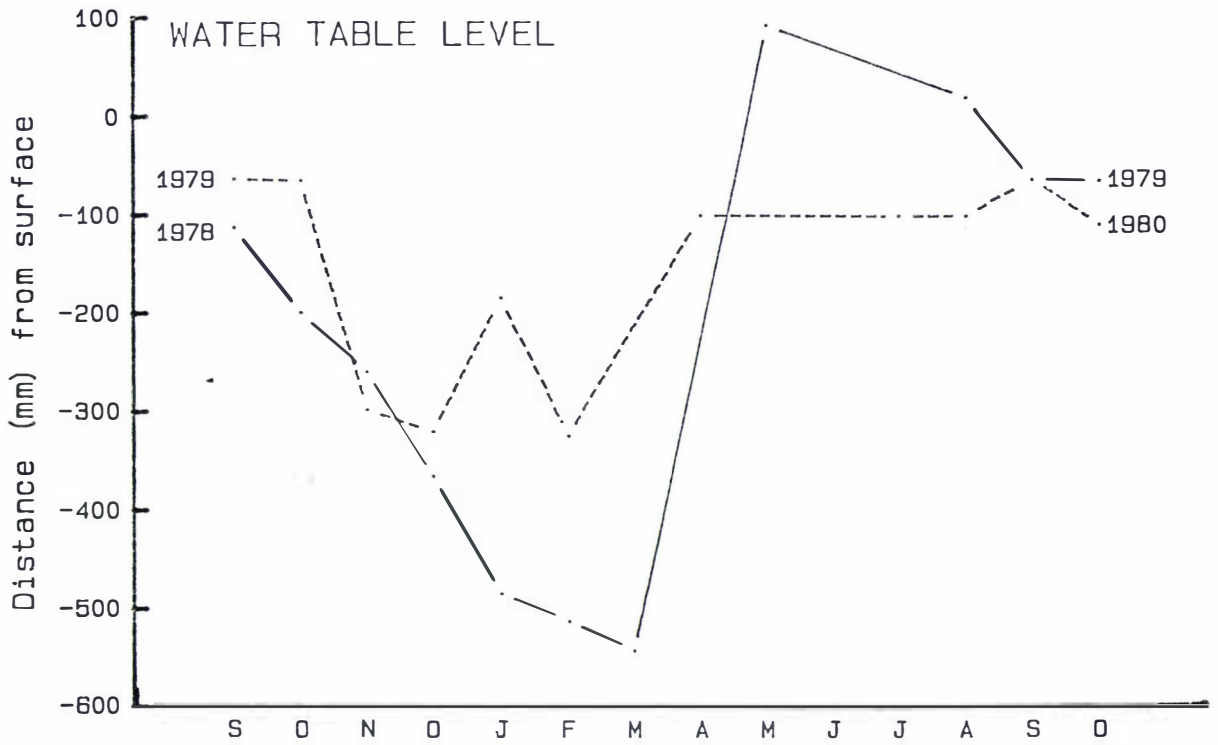
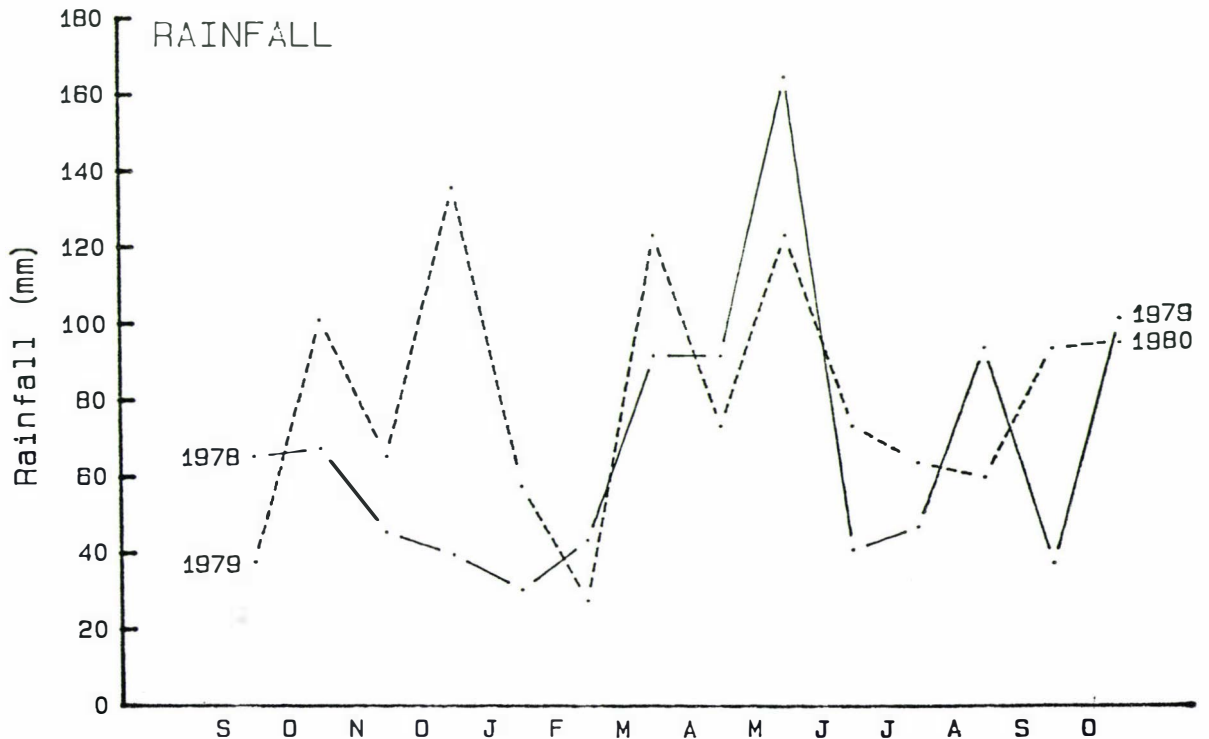


Figure 3.11 Total monthly rainfall at Tangimoana Farm Settlement #, 1978-1980.

(#2 km further inland and 1.6 km north of the study area)



topogenic water accumulation on the sand plain from the ~~sounding~~ ^{surrounding} high parabolic dune.

3.1.6 Soil water profiles

At the end of the winter (September) 1978 ten replicate soil samples were taken from each of five sites on the sand plain to determine the soil moisture profile. Sample cores (20mm diameter) were taken at successive 10mm depths until the water table was reached. Each 100mm-long sample core was removed, placed into a plastic bag, sealed and labelled and taken to the laboratory for weighing, drying at 105 degrees C for 16 hours and reweighing. The volume of dry sand in each sample was also measured. The dry sand from each of the three old deflation hollow sites was placed in a 500 degree C oven for 24 hours to determine the organic matter fraction and then passed through a series of seven sieves (63-4000 μm) to determine the various particle size fractions. A hand magnet was used to remove the ferreous fraction.

The water content of the sand down the profile at each site, expressed as a percentage of the volume of wet sand, is shown in figure 3.12. At each of the three sites within the old deflation hollows, only one 100mm-deep soil core sample was required to reach the water table. At these sites where the soil from the surface to the free water-table level was completely saturated, water made up more than one-third of the volume of wet sand. This volume is called the pore space of this sandy soil. The water holding capacity of the soils across the study area was expectedly low as a result of the extremely low organic matter contents (table 3.4) of these raw or relatively undeveloped soils.

Figure 3.12 Soil moisture profiles at five sites on the sand plain, in September 1979.

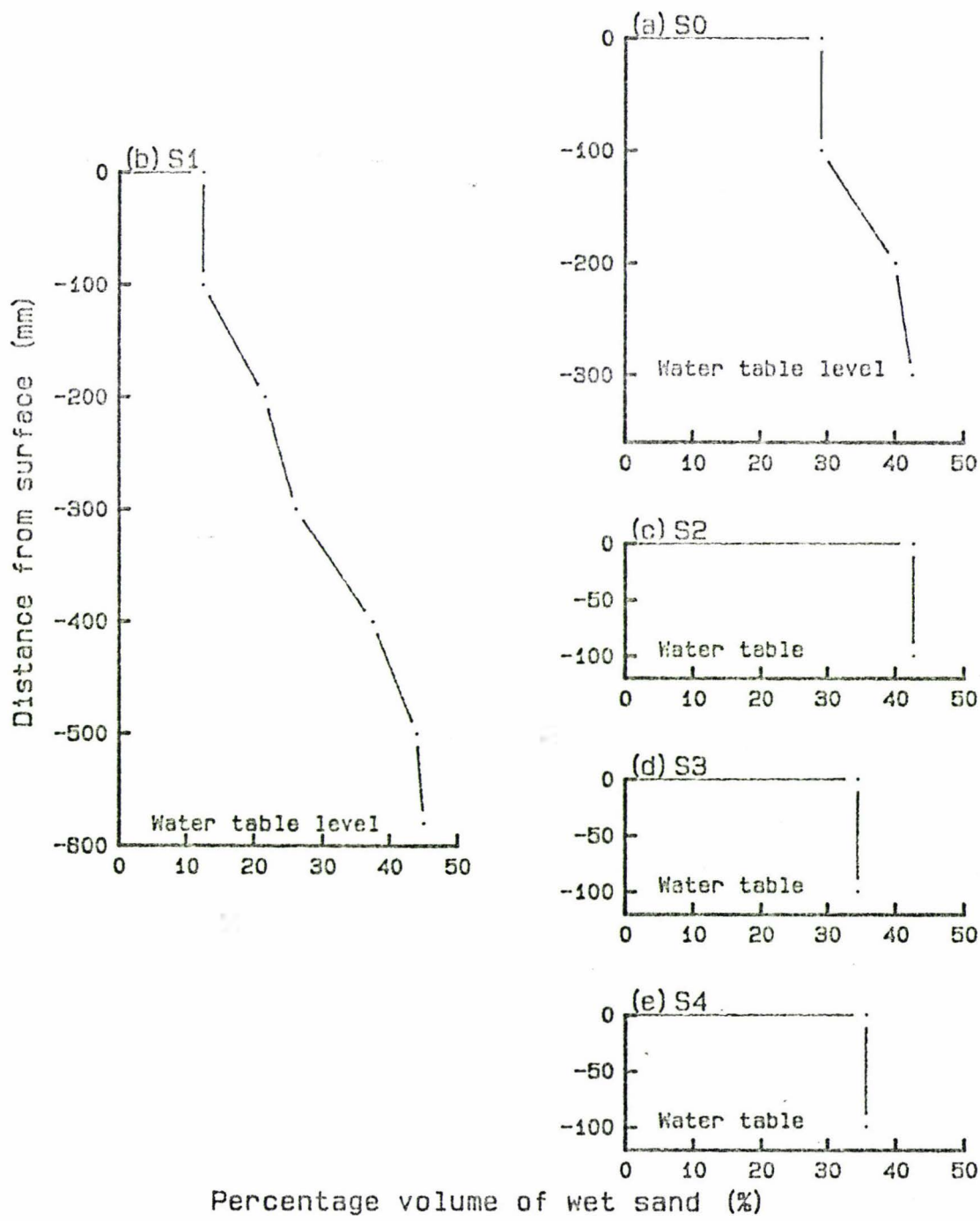


Table 3.4 Percentage of total oven dry weight of various particle size classes of sand at 0-100 mm depth at three deflation hollow sites on the sand plain near Tangimoana.

Particle size class (μm)	Percentage (%) of total dry weight		
	S2	S3	S4
>4000	-	-	-
1000-4000	.82	.44	.3
500-1000	1.17	1.4	1.4
250-500	37.72	11.34	14.6
125-250	55.14	79.2	74.3
63-125	4.79 (1.51)	6.39 (1.65)	8.2 (2.4)
<63	.22	.6	.6
organic matter	.16	.6	.7

(Percentage of ferreous fraction in brackets)

The difference in water content of the saturated soils in the deflation hollows between S2 and S3 and S4 (figure 3.12) was attributed to the difference in mechanical composition of the sand (table 3.4). At S3 and S4 where there was a greater percentage of smaller sand particles than at S2, there was also a reduced pore space as indicated by the reduced water content of the saturated soil (figure 3.12). The ferreous fraction of the ~~deflon~~^{deflation} hollow soils was confined to that fraction of "fine" sand between 63 and 125 μm diameter and accounted for from 1.5% to 2.4% of the total soil dry weight. This is comparable to the 3% "opaques" quoted by Gibb (1977) for beach sample at Tangimoana Beach, a value considerably less than

the 80-90% opaques in beach sand further north on the west coast of the north island at Patea.

3.1.7 Soil nutrient and organic matter status

Frequent, seasonal or permanent waterlogging on the sand plains of the Manawatu coastal dune system, largely as a result of topogenic water accumulation has led to the formation of hydromorphic soils on the low-lying areas classified by Cowie et al. (1967) as Hokio series. Soils on the associated dunes derived from the same wind-blown parent material are mapped as Waitarere sand. Soils of the plains in which a more diverse and vigorous vegetation develops (Esler 1969, 1970, 1978) might be expected to be enriched by the leaching of minerals from the surrounding dune ridges (Salisbury 1952).

Within the study area, the soil was still very young with little profile development except for a darkening of the upper 1-2cm by organic matter in the older hollows. The soil in the originally bare terminal deflation hollow was raw sand and could be taken as "time-zero" in the chronotoposequence of soil development on the sand plains. The soil nutrient, pH and organic matter status at different stages in the sere were determined by sampling at five sites (at increasing distances from the terminal hollow) in spring (September) 1978. Fifteen replicate soil cores (20mm diameter x 100mm depth) were taken at each site, bulked, oven dried for 48 hours at 70 degrees C and analysed for calcium, potassium, phosphorus and magnesium available for plant growth, and percentage carbon. From the latter, percentage organic matter (carbon x 1.7 approximately, Von Bemmeln's factor; Ranwell 1959) and percentage nitrogen (C/N ratio = 20; Cowie et al. 1967; Noble and Marshall 1983) were determined. Two years

later in spring (September) 1980, the pH of the soil water was determined visually using a soil indicator solution ("BDH soil testing reagent"). Twenty five ml samples of soil water were taken at each site, two drops of indicator solution added to each and the colour compared to a standard chart. The pH determination in the field were confirmed on return to the laboratory using a pH meter ("Radiometer Copenhagen type 28").

The alkaline soil pH was relatively invariable across the sites studied (table 3.5). The pH varied minimally between sites of at increasing successional maturity at increasing distances from the terminal hollow and by 1980 had changed little since the determinations two years previously (table 3.5). Weathering of shell fragments evident throughout the sand in the study area together with the lack of organic acids in the soil resulting ^{from the} ~~from the~~ lack of soil organic matter (see below) accounts for the basic nature of the soil solution. The continued weathering of shell fragments especially in the older deflation hollows could explain the slight apparent shifts upwards in pH over the two year period to September, 1980.

Table 3.5 Soil pH at five sites on the sand plain in spring.

Site	Sept 1978	Sept 1980
S0 Terminal hollow	8.1	8.0
S1 Low dune	8.0	8.0
S2 Old deflation hollow	8.1	8.3
S3 " " "	8.1	8.6
S4 Older deflation hollow	8.0	8.2

Shell fragments mixed with the sand provide a rich source of calcium available for plant growth which was found to be high in the older deflation hollow soils (table 3.6). These had undergone more weathering than those younger soils closer to the receding rear dune (S0 and S1). Similarly, available potassium and magnesium were higher in the more aged soils of the older hollows, although like phosphorus which did not vary between sites, the supplies of these minerals available for plant growth were relatively low (table 3.6). The sands of the Manawatu coastal dune system contain only small quantities of micaceous minerals (Cowie et al. 1967) which accounts for the limited amounts of available potassium found.

The organic matter content of the soils on the study area was extremely low, although it increased at sites of increasing seral maturity (table 3.6). Thus, in the oldest deflation hollow at S4, percentage organic matter of the soil (OM) was three times that of the soil of both the young terminal deflation hollow (S0) and the young low dune (S1). In spring 1978, soils at both S0 and S1 were raw. The organic matter content of the soils in the older hollows was comparable to that described by Cowie et al. (1967) for the youngest dune phase soils (Waitarere sand of the Manawatu coast) and to that found in a young coastal slack soil in a dune system on Anglesey, northwest Wales by Ranwell (1959). These OM values are however lower by at least an order of magnitude than those found in more mature sandy soils under Carex ~~pumila~~ arenaria on the same dune system on Anglesey (Noble and Marshall 1983) and on the Manawatu sand country (Cowie et al. 1967, table 9).

Table 3.6 Available nutrient status and percentage carbon, organic matter and nitrogen of the soil at five sites on the study area, in September 1978.

		Available				Percentage		
		Ca	K	P	Mg	N	C	OM
		(ppm soil)						
Young terminal hollow	(S0)	375	40	1	35	.0015	.03	.051
Young low dune	(S1)	375	40	1	35	.0015	.03	.051
Old deflation hollow	(S2)	875	80	1	50	.003	.06	.102
Old deflation hollow	(S3)	1000	80	1	75	.004	.08	.136
Old deflation hollow	(S4)	750	80	1	65	.0045	.09	.153

Percentage nitrogen in the soils sampled in September 1978 which was calculated on the basis of a C/N ratio of 20, was extremely low. These estimated values were lower than the bottom end of the range of soil nitrogen levels found by (Noble and Marshall 1983) using direct measurements of total soil kjeldahl nitrogen on a sand dune soil under Carex arenaria (range 0.0005 to 0.02%). These latter soil nitrogen levels of Noble and Marshall coupled with the directly-estimated OM levels allow the calculation of C/N ratios for these soils by use of Bremeln's factor. The values obtained (range 53.5 to 134.5) were between three - and ten-fold greater than the high value (15), indicating little decomposition and a raw type of organic matter, quoted by Cowie et al. (1967) for Waitarere and in the Manawatu sand country.

The presence of nitrogen in the soil on the developing sand plain near Tangimoana was attributed to the activity of nitrogen-fixing bacteria and blue-green algae. Nostoc spp. which were observed to form characteristic ball-shaped colonies of variable diameter (up to 10mm on the study area) and Anabaena spp. which form a gelatinous bloom were found in the older moist deflation hollows throughout the study. At the end of winter 1981, large quantities of Anabaena bloom were found in the flooded terminal hollow (figure 3.13). The presence of nitrogen on the study area may also have resulted from leaching from the surrounding area. Nitrogen fixing Lupinus arboreus was plentiful across the sand plain on which the study area was situated (figure 3.2). Further, non-symbiotic nitrogen fixing bacteria of the rhizosphere zone of Ammophila arenaria, a species abundant both on the low dune ridges on the study area and on the surrounding high dunes, have been implicated in the presence of nitrogen in sand dune communities elsewhere in New Zealand (Gadgil 1969).

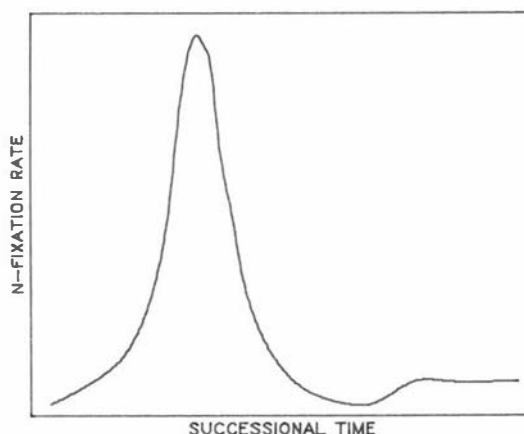
Figure 3.13 Anabaena bloom in the flooded terminal deflation hollow, in August 1981



3.1.8 Estimation of nitrogen-fixation by acetylene reduction

Stevens and Walker (1970) state that in most chronosequence studies, atmospheric nitrogen-fixing plants will be present at some early stage in the vegetation succession, although not always at the pioneer stage, and that, with increasing successional time, these plants will be eliminated by those that utilize the accumulated nitrogen. Thus, the predicted pattern of nitrogen fixation rates in primary succession will show an early peak and subsequent decline (figure 3.14).

Figure 3.14 Predicted nitrogen fixation rates during primary succession (redrawn from Gorham et al. 1979).



Nitrogen ^{fixation} ~~fixation~~ rates can be measured in the field by an acetylene reduction assay technique in which acetylene is specifically converted to ethylene by the nitrogenase enzyme of nitrogen-fixing organisms (Hardy et al. 1968). As nitrogenase activity of blue-green algae is believed to be intimately associated with photosynthesis possibly through the direct photosynthetic supply of either the reductant or the ATP (Waughman 1977), conditions that alter rates of photosynthesis such as light, temperature and moisture are likely to influence the acetylene reduction reaction (Lawrie 1981).

It has been reported that appreciable quantities of nitrogen are assimilated on moderately alkaline sand dune slack soils rich in blue-green algae, such as Nostoc spp. (Stewart 1967). Further, desiccation of these natural blue-green algal populations as a result of lowering of the water table in summer is at least partly responsible for the summer decrease in nitrogen-fixation. In the present study, blue-green algae (Anabaena and Nostoc spp.) presumed to be capable of fixing molecular nitrogen were found in the old deflation hollows (sand dune slacks). Further, conditions in the hollows (ie pH 8 and probable anaerobiosis indicated by brown iron oxide staining of the sand and more or less permanent dampness) were similar to those described by Waughman (1972) as suitable for free-living nitrogen-fixing bacteria. Thus, a preliminary investigation of nitrogen-fixation using the acetylene-reduction technique was carried out on the sand plain, on soil and blue-green algal samples.

Methods and materials

The apparatus and method used was based on that outlined for field use by Waughman (1971), except that it was considered unnecessary to replace the air in the incubation chamber with an inert gas before injecting the acetylene (Sprent 1979). Samples gathered in spring (September) 1979 from the flooded old hollow shortly after midday, either up to 3 gram fresh weight of Anabaena and Nostoc spp. or 25mm diameter soil cores to a depth of 25mm, were placed into rubber capped, sealed 30ml McCartney bottles. Using a syringe, 3 ml of air from each bottle was replaced by an equal volume of acetylene (carried in the field in a football bladder). The bottles were incubated on the ground in the deflation hollow, out of direct sunlight. At the end of the incubation period of one (1) hour, a gas

sample of approximately 10m. was removed and stored either in the syringe with the needle pushed into a rubber bung or in an empty serum bottle for laboratory analysis. Small (0.2ml) volumes of this gas were assayed by gas-liquid chromatography (Fountain pers comm). The ethylene produced as a result of the acetylene reduction reaction in the incubation chamber per hour per gram fresh weight of tissue (or per gram of soil) was calculated from the peak height ratio (gas chromatographic peaks) of ethylene to acetylene in the sample compared to their ratio in a standard mixture of the two gases. Two further controls were considered necessary to check for endogenous ethylene production; firstly a sample in the incubation chamber without acetylene and secondly killed plant material in the chamber with acetylene.

To enable comparisons with other published results, the theoretical ratio of C_2H_2 reduced to N_2 fixed of 3:1 was applied to the data, despite the controversy which surrounds the ratio believed to be most accurate (Lawrie 1981).

Results and Discussion

The rates of acetylene reduction in soil and unialgal samples obtained from a moist sand dune slack on the Manawatu coastal dune system are shown in table 3.7. It is apparent that acetylene reduction rates, and corresponding rates of nitrogen fixation, differed significantly between each of the three sample types. The value obtained for Anabaena, the highest of the three samples assayed, was somewhat lower than that for pure cultures of a member of this genus grown in laboratory conditions at 15 degrees C and high light intensity (Waughman, 1977). It is unlikely that higher values of nitrogen-fixing capacity for the local Anabaena collected as unialgal

samples in the field could have been achieved through artificially growing it as a pure culture. Granhall (1975) reported no difference in rates of acetylene reduction between unialgal cultures isolated from soils and pure cultures. The estimated rate of nitrogen fixed per unit area of sand dune slack in the present study, $1.65 \text{ mg N / m}^2 \text{ / hr}$ for the soil sample to 25mm depth assuming 8-12 hours of nitrogenase activity at this rate per day, is in the range for random samples of natural populations of blue-green algae, principally Nostoc, in a dune slack region reported by Steward (1965). Extrapolation of the limited data of the present study however must be tentative since measurements of such factors as oxygen tension, soil moisture, light intensity, soil temperature, pH and salinity, many of which have been shown to affect the acetylene reduction response (eg Waughman 1977), were not continuously monitored.

Table 3.7 Rates of acetylene reduction and corresponding values for N-fixation of soil and unialgal samples from a moist sand slack on the Manawatu coastal dune system, September 1979.

	n	C ₂ H ₂ reduced nmol/(g fresh wt . hr)	N ₂ fixed ugN/(g fresh wt . hr)
Soil	4	6.0 $\pm$ 0.7	0.056 [#]
Anabaena	11	56.3 $\pm$ 26.5	0.524
Nostoc	13	19.1 $\pm$ 5.5	0.178

The theoretical 3:1 ratio for C₂H₂ reduced : N₂ fixed was used.

[#]This value is equivalent to $1.65 \text{ mg N/m}^2\text{/hr}$ for the soil core to a depth of 25mm.

Diurnal as well as seasonal fluctuations in acetylene reduction in the field have been related to fluctuations in temperature, light and soil moisture. Lawrie (1981), for example, showed that daily and seasonal maxima in acetylene reduction in the sand dune habitat were achieved in early afternoon and in early summer respectively when both temperature and light intensity were high and ample moisture still available. Reduction in rates of acetylene reduction later in the summer Lawrie attributed to desiccation. Maximum daily temperature and light intensity and therefore nitrogenase activity could have been expected in the deflation ^{hollow} ~~he~~ shortly after midday at the time of day the assay was applied in the present study. However, both these factors were lower at this time of the year (September) than those that could be expected later in the spring/early summer but when the surface soil layer was still likely to be moist. Thus, nitrogen fixation rates obtained here for Anabaena and Nostoc spp. and for soil cores can be expected to underestimate local maxima for this stage of seral development on the sand plain. Later in the summer, lowering of the water table in the old hollow resulted in the soil surface drying out, especially where the vegetation cover was sparse. Under these conditions when dry algal crusts were observed, nitrogenase activities can be expected to be decreased.

Differences in the estimated rates of nitrogen fixation between the two blue-green algal samples may in part be attributed to differences in environmental moisture stress. Although the two algae were samples from the same deflation hollow slight differences in elevation and therefore dryness were apparent across the hollow. The Nostoc balls were found on the somewhat raised, drier parts of the hollow floor compared to the puddles in which the Anabaena bloom with higher estimated rates of N-fixation was collected.

3.2 Initial field studies

3.2.1 Phasic development

Where Carex pumila grew on the sand plain, both on the low dune bordering the terminal deflation hollow and on the moist deflation hollows themselves, distinctive zones in the vegetation could be seen. The descriptive terms (pioneer, building, mature and degenerate) first applied by Watt (1947) to phasic development in bracken (Pteridium) and several other species, were applied to these zones. Watt showed that the productivity of the vegetation in each case followed a generalized curve with a progressive increase from pioneer through building to the mature phase and a subsequent decline in the degenerate phase. The significant feature in the case where bracken was invading grassland was the progressive increase in rhizome age from the leading edge of the clone back to the hinterland where the oldest parts of the rhizome had decayed causing the clone to become fragmented. In the hinterland, the rhizomes were initially older and the shoots smaller than towards the margin where a large density of young, even-aged rhizomes were oriented more or less parallel to each other producing a zone of larger more vigorous shoots, than in the hinterland. Thus, a marked marginal effect was observed.

Phasic development in perennial species may be of general occurrence (Kershaw 1964), although in rhizomatous species where the phases intergrade along the rhizome axis and where the rhizome apices are buried at some depth below the surface, the phases may be difficult to define accurately (Noble et al. 1979).

Observations

A marked marginal effect in the vegetation was seen in the present study where *Carex pumila* was invading an uncolonized embryo deflation hollow from a low dune ridge (figure 3.15). The phasic classification applied to this continuum of development in *Carex pumila* was that proposed by Noble et al. (1979) in describing zonation in *Carex arenaria* growing at the base of mobile sand dunes on Anglesey, North Wales:

1. the 'juvenile' phase representing the marginal band at the leading edge of the clone
2. the 'adolescent' phase of predominantly vegetative shoots which approached the maximum density for the site
3. the 'mature' phase in which maximum density had been reached and distinguished from the adolescent phase by the higher proportion of fertile shoots
4. the 'senile' phase behind the mature phase and where the aerial shoot population was reduced in density and stature

This terminology was preferred to that of Watt (1947) because it conforms more to an age classification appropriate to population studies (Noble et al. 1979).

As in the study of *Carex arenaria*, the phases of development of *Carex pumila* across the low dune ridge represented a continuum in species diversity. On the edge of the low dune in the juvenile and adolescent phases, *Carex pumila* was the only species present whereas species diversity increased in the mature and senile phases higher on the low dune, where *Carex pumila* was ultimately replaced by marram

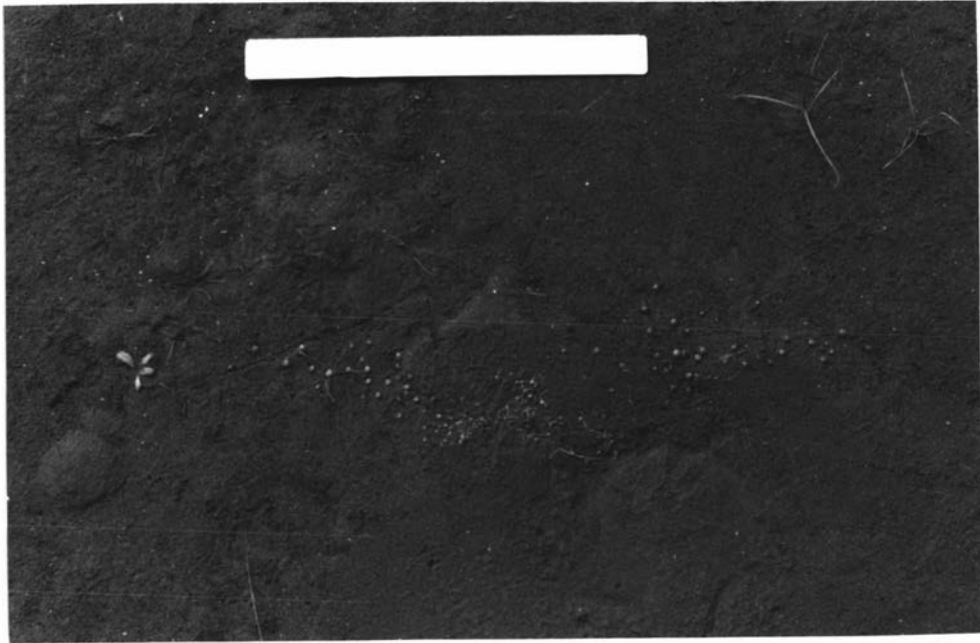


3.15 Carex pumila invading the terminal hollow.

(Ammophila arenaria) (see section 3.1).

Within the series of damp deflation hollows of increasing age at increasing distance from the terminal hollow, a second series of zones or phases of development of Carex pumila could be readily detected. The phases of development in this series did not intergrade as on the low dune ridge but were physically separated within the different hollows, thereby forming a stepped cline. In the summers of 1977-78 and 1978-79, the juvenile and adolescent phases of this series were absent. The terminal hollow, apart from the slow encroachment of Carex pumila rhizomes from the low dune, remained bare of vegetation. With the establishment of Carex pumila (and other species) from seed in this hollow in summer 1979-80, the younger phases were finally represented. The mature and senile phases of this age classification were represented in the summer of 1977-78 at S2 (mature), S3 (mature-senile) and S4 (senile) in the older hollows further from the base of the rear dune.

As on the low dune, the phases of development of Carex pumila within the moist hollows represented a continuum in species diversity. In December 1977, Lobelia anceps and Carex pumila were the only species present at the mature site in the old hollow (S2), whereas several species including Selliera radicans, Eleocharis neo-zelandica, Scirpus nodosus and Carex pumila were present in the more senile phases at the older more distal S3 and S4. When vegetation first became established from seed on the terminal hollow in summer 1979-80 (juvenile phase) isolated monospecific patches were found (figure 3.16). Although several species were represented they remained locally discrete until the following year by which time the vegetation was entering a more mature phase (figure 3.16).



3.16 Colonizing stages on the terminal deflation hollow. Top: winter 1980, showing seedlings; note bare ground. Bottom: winter 1981, showing increased cover by the young vegetation.

Clonal vigour

Aerial shoot density and plant performance (such as shoot weight or shoot height), which constitute measures of the vigour of a clonal species at a particular site and therefore the suitability of the site for growth of that species (Noble et al. 1979) varied, firstly across the low dune ridge (figure 3.17) and, secondly, between the deflation hollow sites (see figure 4.1). Both followed the characteristic n-shaped curves for phasic development described by Watt (1947) and others since.

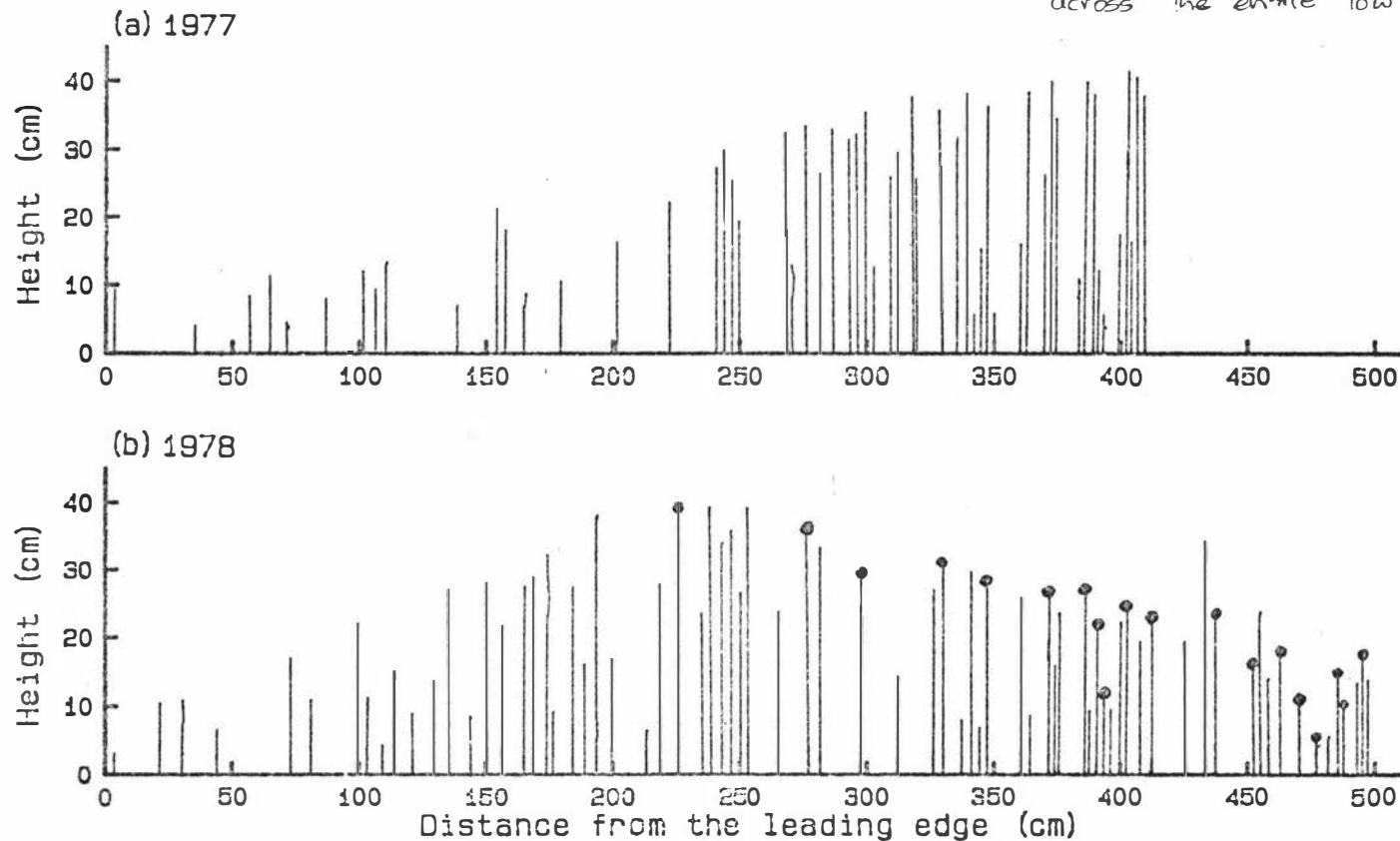
Various other measure of vigour have been applied to clonal species displaying phasic development. Noble (1982) suggested that the most reliable indication of vigour in Carex arenaria was given by the percentage of dormant buds per unit number of sympodial modules taken from primary rhizome axes. In the present study, an estimate of the size of this bud bank was obtained by releasing buds from dormancy by the addition of nitrogen fertilizer (section 4.3.7). The increased density of shoots three months after the nitrogen perturbation treatment (see section 4.3.1) was used as an estimate of the density of dormant buds present at the time of perturbation. Other measures of vigour include the relative proportion of dwarf to long branches (Noble 1982) and the ratio between aerial shoot biomass and rhizome biomass (Noble et al. 1979).

In May and July 1980 several primary rhizome axes were excavated from the edge of the low dune bordering the terminal hollow.

These large rhizome fragments of Carex pumila which included the terminal sympodial unit and at least one (May) or two (July) successive sympodial units were measured, divided into constituent parts, dried and weighed. In neither May nor July were dwarf shoots

Figure 3.17 Height of Carex pumila shoots on the edge of the terminal hollow. (a) December 1977 and (b) December 1978.

Neither (a) nor (b) represents the transect across the entire low dune.



associated with any of the terminal long branch units which also showed no orthotropic or adventitious root development. Relatively few dwarf branches were associated with penultimate long branch modules and contributed little to total (aerial plus underground) and even less to aerial biomass in either May or July (table 3.8). Further back along the primary rhizome axis, dwarf branches associated with antepenultimate long branch units outnumbered long branch modules and contributed almost 50% of the combined aerial biomass (July; table 3.8). A similar trend was shown on a genet excavated from the terminal hollow in July 1980. This genet included two primary rhizome axes each including four successively older long branch units. Thus, on these parts of the sand plain where the Carex pumila population was in a juvenile phase, the ratio of dwarf to total (dwarf plus long) shoot (density, total biomass or aerial biomass) may be used to estimate age of the clone.

Table 3.8 Characteristics of excavated portions of Carex pumila genets in winter 1980. LD = low dune; TH = terminal hollow.

				Number of			
				long branch units from terminal module			
				0	1	2	3
(A) Long rhizome branch unit							
(i) mean length (cm)	MAY	LD	24.33	38.0	ne	ne	
		JULY	LD	35.14	53.7	40.9	ne
				(+18.09)	(+22.77)	(+22.94)	
		TH	82.0	54.5	43.5	19	
				(+0)	(+3.54)	(+4.95)	
(ii) Dry weight (mg/cm)	MAY	LD	9.863	24.868	ne	ne	
		JULY	LD	9.715	16.14	13.53	ne
		TH	8.943	9.908	8.966	6.316	
(B) Dwarf/total ratio							
(i) ABD/ABMS	MAY	LD	0		ne	ne	
		JULY	LD	0	0.035	0.478	ne
		TH	0	0.343	0.641	0.801	
(ii) BD/BMS	MAY	LD	0	0.09	ne	ne	
		JULY	LD	0	0.005	0.234	ne
		TH	0	0.154	0.364	0.627	
(iii) #D/#T	MAY	LD	0	0.455	ne	ne	
		JULY	LD	0	0.182	0.727	ne
		TH	0	0.66	0.818	0.80	

0 = terminal, 1 = penultimate, 2 = antepenultimate, 3 = ante-ante-penultimate long branch module; ne = not estimated. (Figures in brackets are standard errors).

It is clear that the increasing density and aerial biomass of Carex pumila at increasing distances from the leading edge of the clone (figure 3.17) results from the increasing contribution of dwarf branch modules relative to that of long branch modules.

3.2.2 Rates of clonal spread

The rate of spread of the clone of Carex pumila growing from the low dune into the terminal deflation hollow was estimated by continually plotting the position of the advancing front along a fixed axis.

Observations

The front of the clone was found to have advanced 18m into the terminal hollow over three and a half years (table 3.9) giving an average rate of spread of 1.394 cm/day, for this period or 508.9cm annually. From successive measurements, the rate of spread of the clone for the intervening periods was calculated (table 3.9). This table shows that the rate of spread of the clone increased in spring to a maximum in early summer (November/December) of 2.432 ± 0.072 cm/day (averaged over three years). The autumn/winter (April to July) value were somewhat reduced (1.196 ± 0.243 cm/day averaged over four years). Both the higher summer rate and the continuation of extension growth of the clone of Carex pumila in winter, although at a reduced rate, accounts for the greater annual spread of this species into the deflation hollow on the Manawatu coastal sand dune system than that calculated for Carex arenaria growing either into a deflation hollow or into a dune face on Anglesey, North Wales (0.914 and 0.741 cm/day, respectively; Noble pers comm).

Table 3.9 Spread of the clone into the terminal hollow over time

Cumulative					
		distance	Time##	Rate#	
		travelled (m)	(days)	(cm/day)	
1978	25 JAN - 10 NOV	3.925	282	1.392	Winter
	10 NOV - 22 DEC	4.96	324	2.464	Summer
	22 DEC - 18 MAR	6.09	410	1.314	
1979	18 MAR - 28 AUG	8.10	573	1.233	Winter
	28 AUG - 30 OCT	9.2	636	1.746	
	(30 OCT - 20 NOV)			(1.905)	
	30 OCT - 27 FEB	12.0	756	2.333	Summer
1980	27 FEB - 28 JUL	13.2	908	0.789	Winter
	28 JUL - 7 NOV	13.7	1010	0.490	
	7 NOV - 17 DEC	14.7	1050	2.5	Summer
1981	17 DEC - 15 AUG	18.0	1291	1.369	Winter

Days from 25 JAN 1978.

During given period.

The calculated rates of clonal spread determined above by measuring the linear distance travelled by the advancing front of the clone, will underestimate the rate of elongation of primary rhizome axes. This deviation however, which is proportional to the deviation of these rhizome axes from strict linearity, may not be great, since long rhizome axes of Carex pumila excavated from the edge of the low dune in August 1979 (figure 2.5) showed branch angles to be small (in

the range 9-21 degrees, mean 15.3 degrees, section 2.1) and long branches, subsequently, to grow more or less parallel to each other. Excavation of and measurements on underground parts of Carex pumila (section 3.2.1) allowed an estimation of the rate of elongation of long rhizome axes where Carex pumila was growing into the terminal deflation hollow from the low dune.

The mean length of individual rhizome segments (including the terminal and successively older sympodial units) for primary rhizome axes excavated from within and from the edge of the terminal hollow in winter (May and July) 1980 is shown in table 3.8. Assuming the terminal sympodial units (length L_0) of May 1980 became the penultimate sympodial units (length L_1) of July 1980, then the rate of increase in length of the long rhizome axes (I) is given by

$$I_{t_1-t_0} = ((L_{1_{t_1}} - L_{0_{t_0}}) + L_{0_{t_1}}) / (t_1 - t_0)$$

which for the May - July 1980 period is

$$\begin{aligned} &= ((53.7 - 24.33) + 35.14) \text{ cm} / 80 \text{ days.} \\ &= 8.064 \text{ mm/day.} \end{aligned}$$

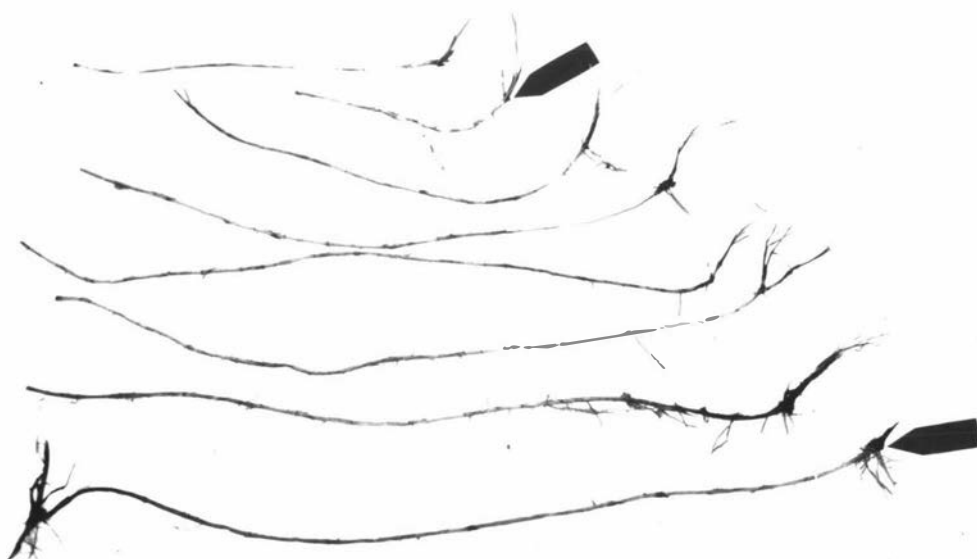
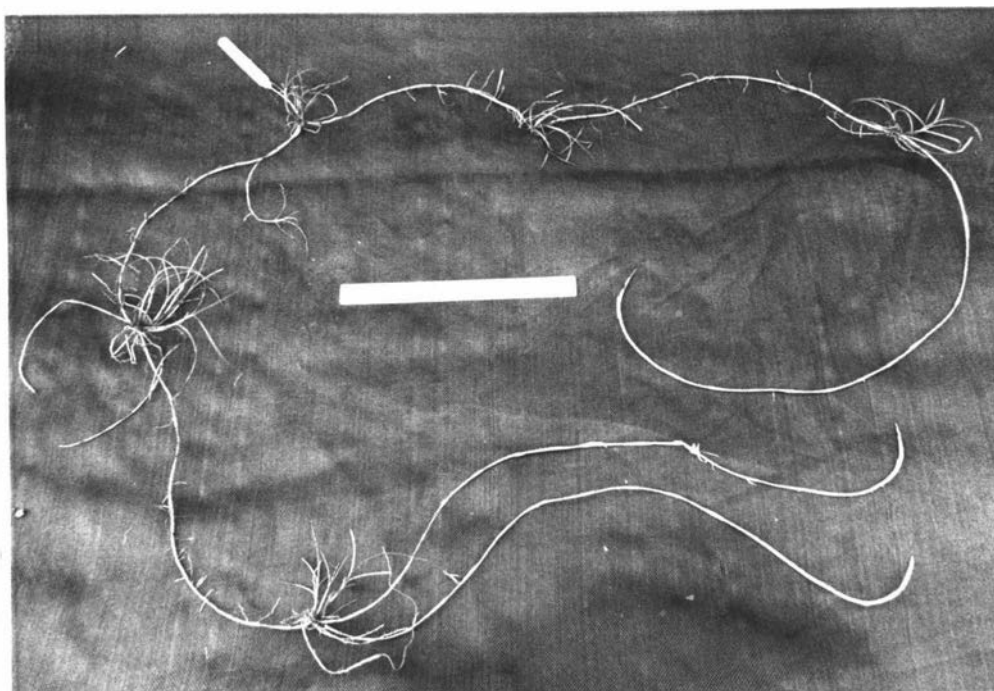
This rate of increase in length for the primary rhizome axes over this winter period is only slightly greater than the estimated rate of linear spread of the clone over this same period (table 3.9). Total rhizome growth and linear distance travelled by the clone into the terminal deflation hollow between May and July 1980 (64.51 and 63.12 cm, respectively) are very similar only as are expected from the measured frequency of branching and small branch angles for primary rhizomes on this part of the sand plain. Given this divergence the rates of growth of primary rhizome axes over the entire study can be estimated from table 3.9.

In the absence of direct measurements, the rate of extension growth of primary rhizome axes in the terminal hollow were assumed to be similar to those calculated above for rhizomes growing into the terminal deflation hollow from the low dune. The time at which each rhizome segment on the genet is calculated to have started growth (t_0) is shown in table 3.10. Germination of this genet can be presumed to have occurred in spring/early summer 1979-80 and to have arisen from a seed produced during the previous summer 1978-79.

Table 3.10 Mean length and time of initiation of growth of successive long branch units on a genet excavated from the terminal hollow in July 1980 (figure 3.18a).

	Mean Length	
	(cm)	t_0
Terminal	82	14 Feb 1980
Penultimate	54.5	21 Jan 1980
Antepenultimate	43.5	2 Jan 1980
Ante-antepenultimate	19.0	25 Dec 1979

In spring 1979 measurements were also made on excavated rhizome portions of Carex pumila from several sites on the sand plain. The length of long rhizome segments separating successive aerial shoot modules along primary rhizome axes varied within sites between consecutive sympodial modules (figures 3.18 and 3.19), between sites (figure 3.20) and between years. Mean length of rhizome segments of comparable long branch modules on the edge of the low dune was considerably greater in 1979 (figure 3.19a) than in 1980 (table



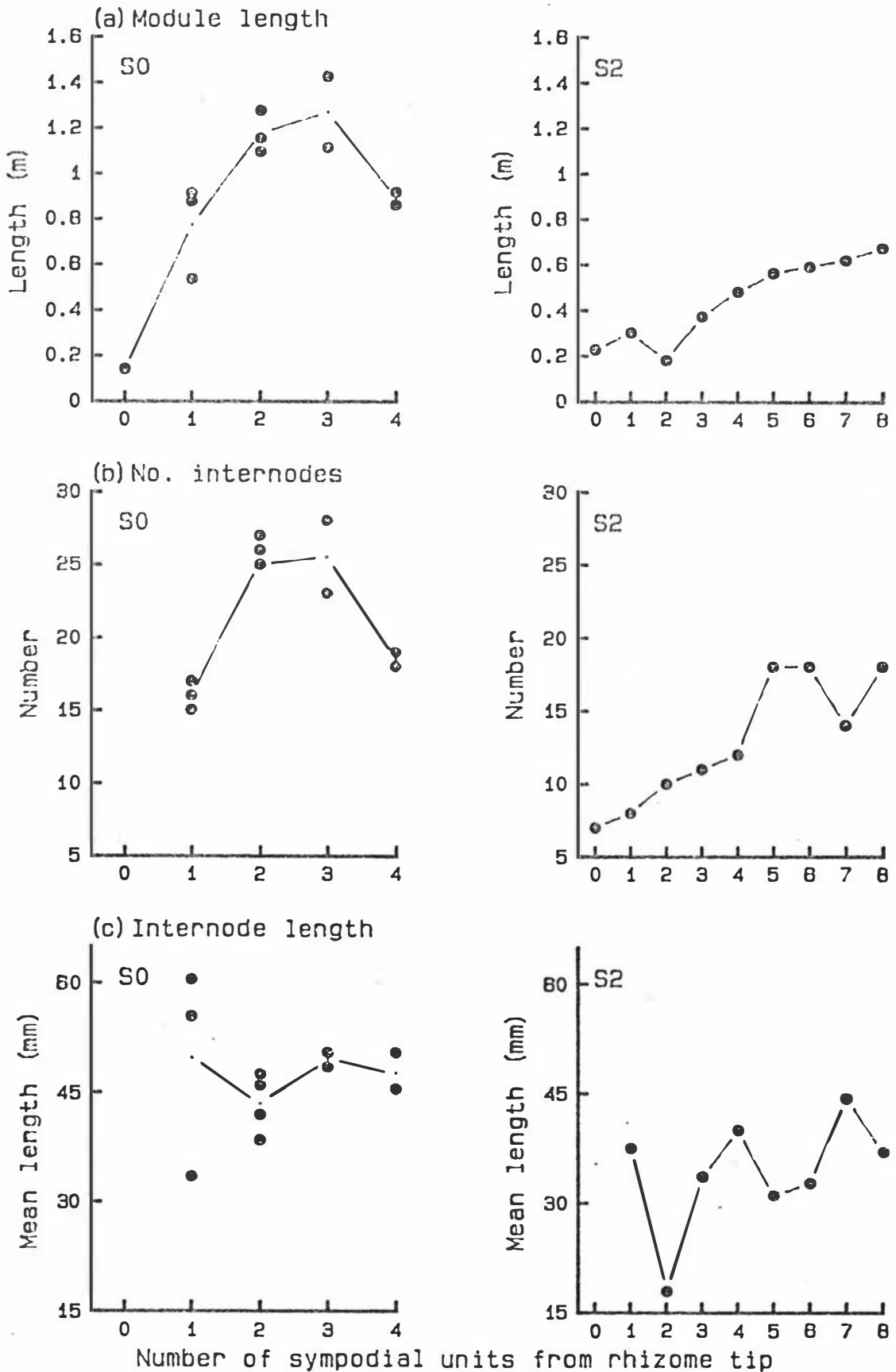
3.18 Portions of single genets of Carex pumila excavated from (a) terminal hollow July 1980 and (b) old deflation hollow September 1979.

3.8Ai).

The variation in length of the rhizome portions of successive sympodial units along a single primary rhizome axis can be attributed to seasonal environmental fluctuation. The rhizome system of Carex pumila excavated from the edge of the low dune in August 1979 came from a single genet and incorporated several primary rhizome axes (figure 2.5). Given the rate of spread of the clone on this part of the sand plain (table 3.9) and the difference between the linear spread of the clone and total rhizome growth, the age of successive long branch modules back from the rhizome front can be calculated. Figure 3.19a shows that the longer long rhizome branch modules were produced in the mid-late summer 1978-79 and autumn 1979 whereas the shorter long branch modules were produced in the winter 1979 and spring and early summer 1978. The proliferation of the entire rhizome system shown in figure 2.5 was estimated to have taken 9.5 months.

Figure 3.19 (a-c) shows that on this part of the sand plain (S0) the number of internodes per rhizome unit had a greater effect on determining total rhizome length per module than internode length which was variable but not in a manner consistent with total rhizome length per long module. A similar comparison on the old hollow (figure 3.19 d-f) shows that as the number of internodes per long rhizome module declined as the genet aged (as the rhizome module number behind the apex decreased) so total rhizome length per module decreased. Mean internode length per module at successive sympodial units along the primary rhizome axis on the old hollow was seen to fluctuate (figures 3.18b and 3.19f). Assuming that four to five successive sympodial units along the log rhizome axis in the old hollow represents the annual increment, as on the edge of the low dune, then the fluctuation in internode length would appear to be

Figure 3.19 Statistics of successive sympodial units along primary rhizome axes, at two sites (S0 and S2) on the sand plain. (a) Total length, (b) total number of internodes and (c) mean internode length per module

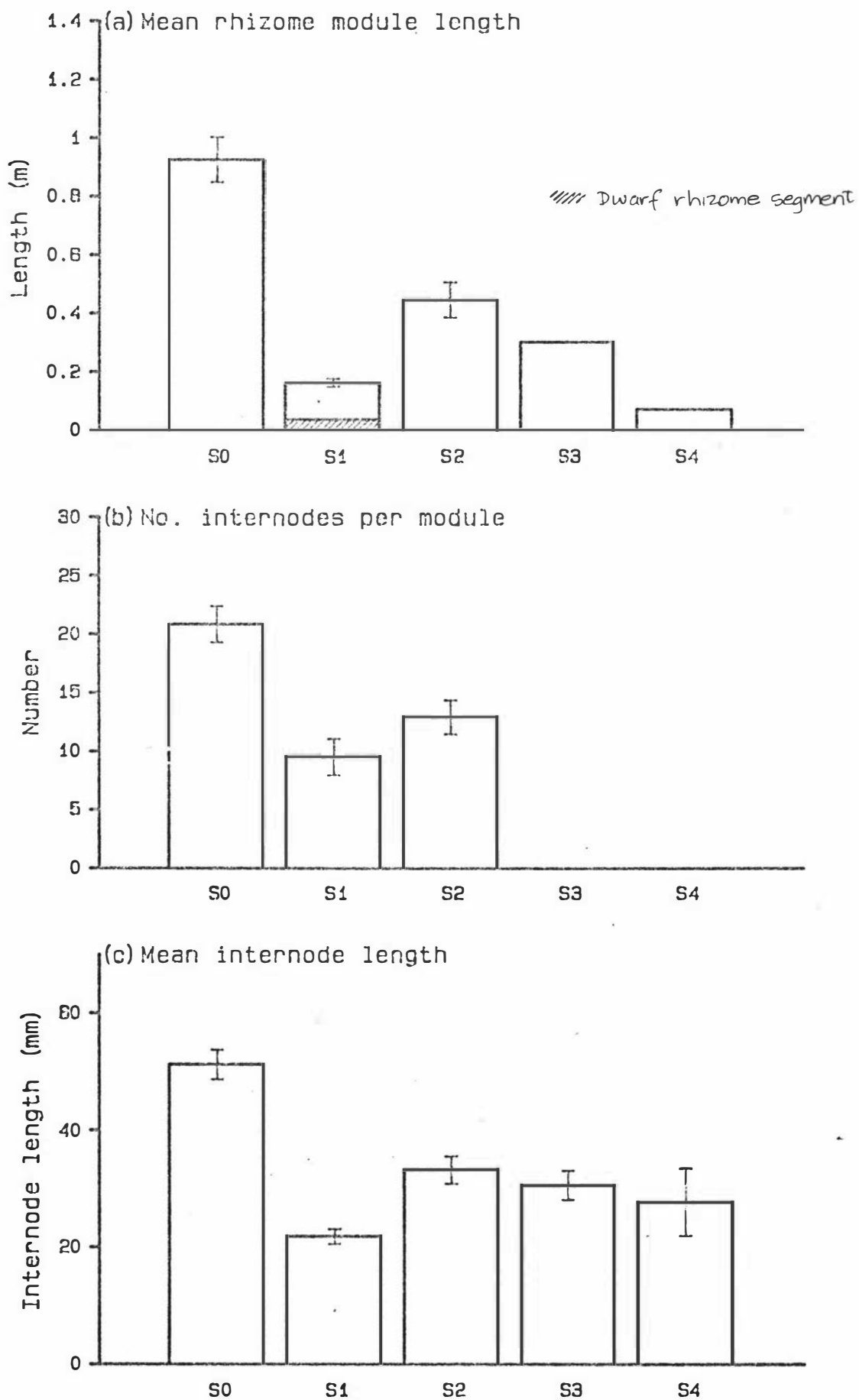


seasonal with decreased values in winter when the hollow soil was waterlogged. This contrasts with the variation in internode length found on the edge of the low dune which appeared to be independent of season.

The genet portion excavated from S2 in the old hollow in August 1979 included 9 successive long branch units. The mean length of the youngest rhizome units presumed to have been produced in winter 1979 was only half that of units presumed to have been produced the previous winter. This observation was attributed to the decline in suitability of the habitat for Carex pumila growth as the site aged. A similar difference in mean length of long branch units was observed between years on the edge of the low dune. In winter 1980, several primary rhizome axes were excavated from this site (table 3.8). The mean length of those (penultimate) branch units produced between May and July 1980 were shorter than those shown to be produced over a similar period during 1979 (figure 3.19a).

Site differences were also evident for the length of the rhizome portion of shoot modules (figure 3.20). The most extensive elongation of the rhizome of long sympodial modules was found in the juvenile phase on the edge of the low dune where Carex pumila was invading the embryonic terminal deflation hollow (S0). At the adjacent (older) site higher on the low dune (S1), mean rhizome length per sympodial unit was considerably reduced (figure 3.20a). It was here that vertical growth of long rhizome units was evident (figure 2.2); a response to the burial of rhizome buds of Carex pumila resulting from the accumulation of sand around shoots of this species. On the old hollow at S2, mean rhizome length per sympodial module was less than half that on the edge of the low dune and progressively reduced at sites of increasing distance from the rear dune. This probably

Figure 3.20 Statistics of long sympodial units at five sites on the sand plain, in September 1979. (a) Mean length (b) Mean number of internodes and (c) Mean internode length



reflects the greater age of the populations at greater distances from the rear dune and also the more prolonged periods of winter waterlogging in the hollows compared with the edge of the low dune. In the old hollow at S2 aerial looping of rhizomes was found, a phenomenon earlier linked with soil oxygen deficits under waterlogging (Raunkiaer 1934). Variation between sites in both number and length of internodes appears to contribute to the variation between sites in total length of rhizome per sympodial module (figure 3.20).

Measurements made on rhizome systems excavated from within and from the edge of the terminal hollow allowed the calculation of mean dry weight per unit length, for individual rhizome segments (sympodial units) in winter 1980 (table 3.8). The mean dry weight per unit length was lower in the terminal rhizome segments than in the penultimate segments. This difference was especially apparent on rhizomes growing into the terminal hollow in May following the reproductive period. Given the correspondance between sympodial modules in May and July (see arrows, table 3.8) it is apparent that a rhizome segment does not necessarily maintain a high dry weight (carbohydrate content) per unit length where the clone is continually expanding.

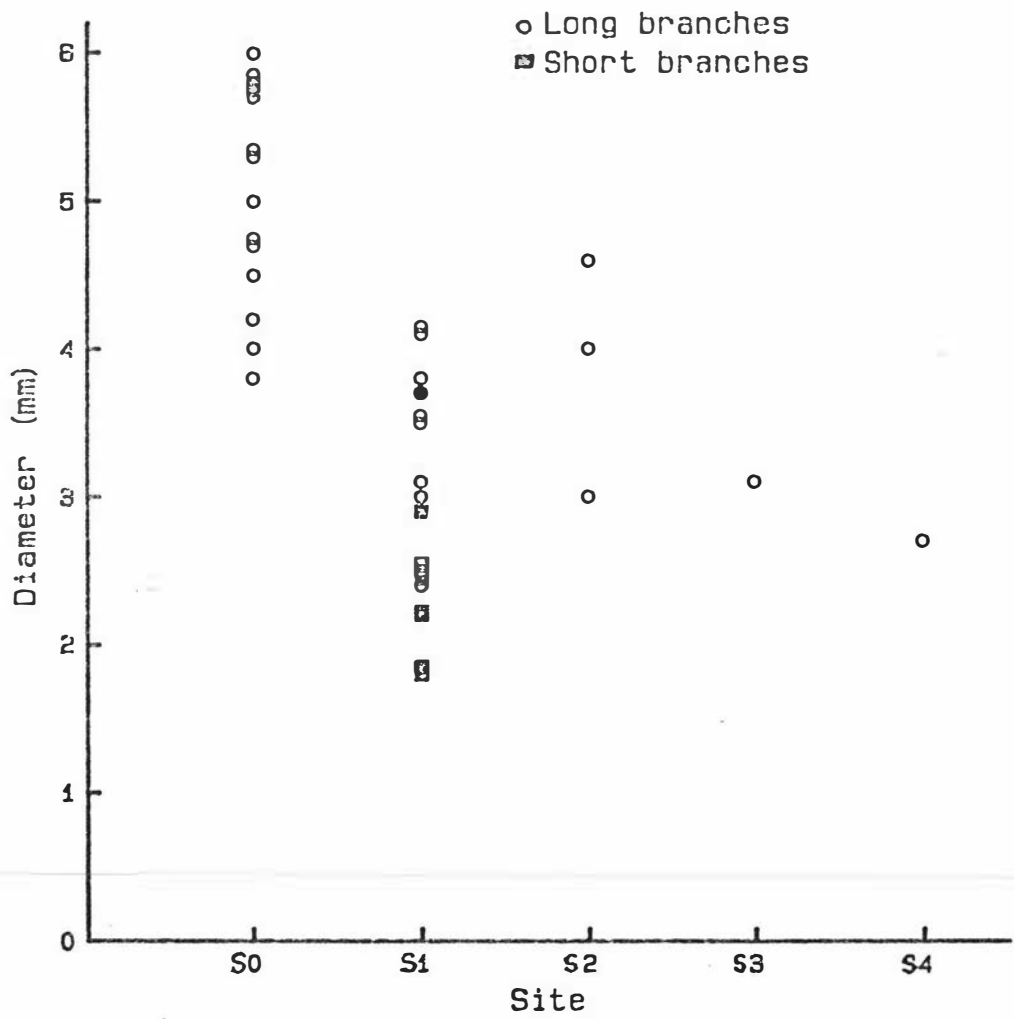
The generally low values obtained for all rhizome segments for the genet excavated from the terminal hollow in July may reflect the observation that the rhizome axes developed by this plant were in an active expansion phase unrestricted by other plants on the relatively bare terminal hollow. Further since few aerial shoot modules had developed on this genet the ability of this plant to generate large supplies of carbohydrate for storage was limited. By contrast, the distal rhizome segments on the edge of the low dune were connected to an ample carbohydrate generating capacity higher on the low dune.

Measurements of the diameter of rhizomes were also made in spring 1979. Figure 2.4 showed that the diameter of long rhizome branches was greater than that of dwarf rhizome branches and figure 3.21 although confirming this observation for branches at S1 shows that there was considerable overlap for this character. Similarly wide variability was found both within and between sites representing various phases of development for diameter of long rhizome branches (figure 3.21). Rhizome diameter was greatest at the juvenile site (S0) where the mean value was almost three times that given by Moore and Edgar (1970) for the species in New Zealand. The diameter of long rhizome branches at S4 (at the lower end of the range for rhizomes on the study area) was still greater than that given by Moore and Edgar. This low value at S4 and those low values for long rhizomes at S1 probably reflect the observation that many long rhizome branches at these sites have resulted from the continued growth of short (generally lower diameter) branches.

In August 1979, measurements were also made on the length of dwarf rhizome branches at S1. At this site, dwarf branches often became extended, and so the distinction between long and dwarf rhizome branches was not as clear-cut as at other sites. However, dwarf branches were on average still significantly shorter than long branches (figure 3.20).

3.2.3 Leaf litter decomposition

Most aquatic decomposition studies have involved allochthonous organic material, from neighbouring terrestrial sites, principally in streams and rivers where the action of moving water causes fragmentation of the litter and an apparent increase in breakdown

Figure 3.21 Rhizome diameter, Carex pumila

rates. Only recently have decomposition rates of wetland species in relatively stationary aquatic conditions been measured (e.g. Mason and Bryant 1975; Danell and Sjöberg 1979). While Carex pumila on the sand plain in the Manawatu sand dune system cannot be described as a hydrophyte, neither is it a truly terrestrial species since its habitat may be flooded for extended periods throughout the year. The aim of the present study was to measure the decomposition rate of Carex leaf litter within a moist sand slack using nylon mesh litter bags to enable comparisons with similar studies in both terrestrial and aquatic ecosystems and to enable more accurate estimates of net production of Carex pumila on the sand plain.

Methods and materials

The decomposition rate of Carex pumila litter was measured using 1.3 x 1.3mm-mesh nylon litter bags (figure 3.22) measuring 15cm x 10cm and containing between 7 and 8g dry weight of leaf material (table 3.11). The leaves were collected in autumn (April from the recently dead standing reproductive shoot cohort which had set seed during the previous summer. The leaves were air dried to a constant weight, chopped into 8cm lengths and accurately weighed amounts enclosed in a nylon mesh litter bag, along with a stainless steel numbered disc. The edges of the bag were secured with nylon fabric (bias-binding) and nylon thread, and the total weight (bag plus contents) measured. The 33 bags were soaked in water for several days to reduce fragmentation losses, then placed on the soil surface in the old hollow adjacent to S2, at 45cm spacing within an area 3m x 3m, on 9 May, 1980. The leaf material in each litter bag replaced an approximately equal quantity of litter which was removed from a 15cm x 10cm patch on the ground at which each bag was placed.

Figure 3.22 Litter bag on an old deflation hollow



Table 3.11 Outline of the procedure to determine the decomposition rate of Carex pumila leaves using litter bags in a deflation hollow on the sand plain.

			Total number of bags	Initial leaf dry weight (g / bag)	Number of bag removed after interval of			
Litter								
Starting date	type	n	Mean	SD	79	144	222	463 days
9 May 1980	dead leaves	33	7.6165	.2009	3	3	3	4

At each sampling on subsequent visits to the study area, at least three litter bags were chosen at random, placed into a plastic bag for transport to the laboratory where the litter bag and its contents were air dried to a constant weight, debris removed and the weight loss of the plant material calculated. When the experiment was terminated 20 bags remained in the field.

The model expressing the loss of dry weight due to decomposition in terrestrial ecosystems is given by

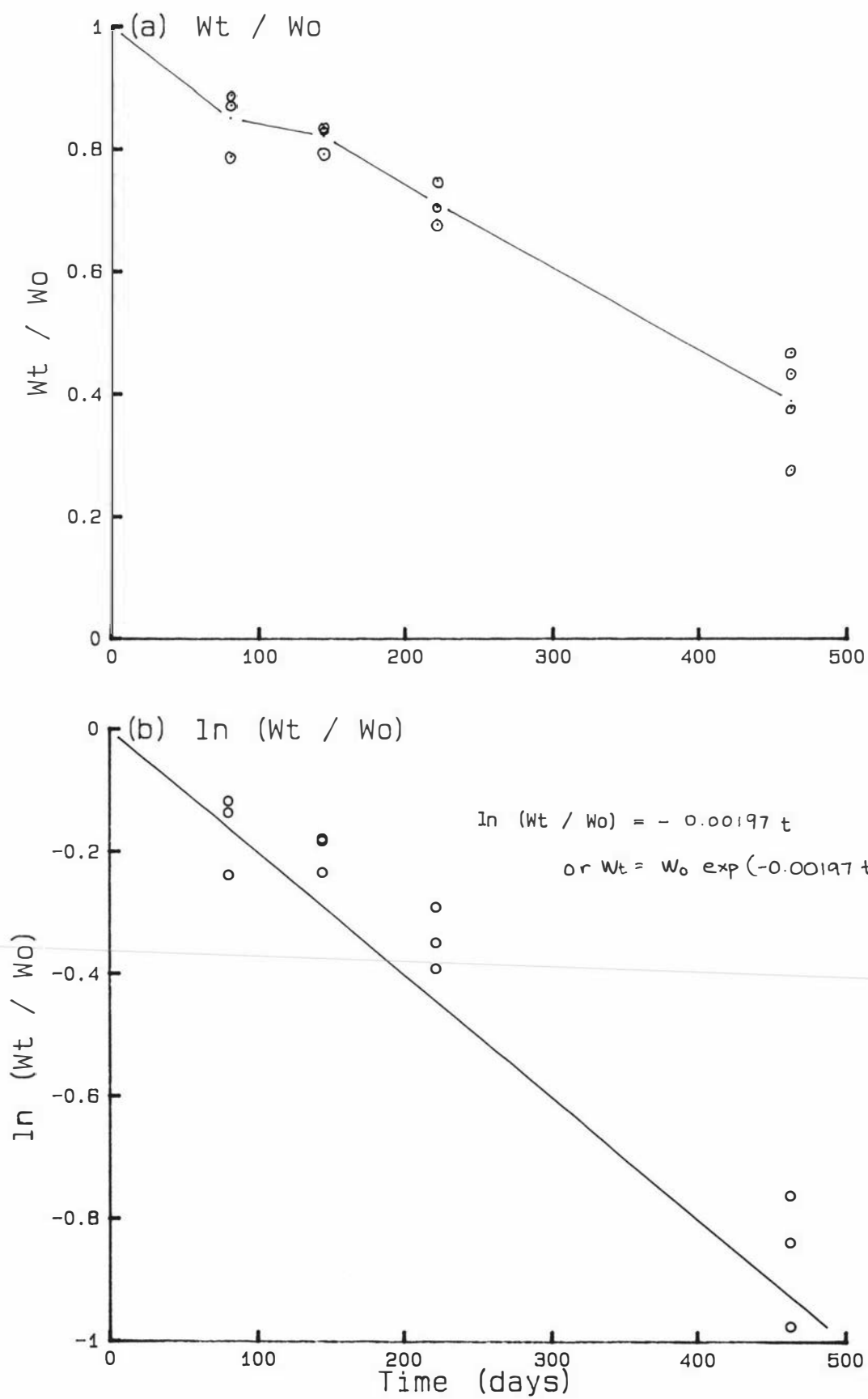
$$W_t = W_o \exp(-kt)$$

where t is time, w_t is the weight after time t , W_o is the initial weight, $\exp$ is the base of natural logarithms and k is a decomposition coefficient for the specific litter type (Olson 1963). Minderman (1968) claimed that the model does not hold for whole litter, although it may apply to individual litter constituents such as cellulose. To test whether $W_t = W_o \exp(-kt)$ holds for the Carex pumila data, the regression of $\ln (W_t/W_o)$ on time t was calculated and goodness of fit of the data to the model was tested by use of the F-ratio. The slope (k) of the regression of $\ln (W_t/W_o)$ on time will be an approximation, at the given level of probability, of the rate of decay of the material. The model, which assumes a rate of decay proportional to the amount of material decaying over time, can be applied to predict the times of 50% and 95% leaf breakdown ($0.693/k$ and $3/k$, respectively).

Results and discussion

Figure 3.23 shows the changes in dry weight of Carex pumila leaves resulting from decomposition in the moist sand slack habitat over time. The weight loss can be attributed to initial leaching which probably accounts for the apparent initially rapid decline in

Figure 3.23 Regression of dry weight of remaining litter of *Carex pumila* on time (t).



dry weight. This is followed by microbial decomposition which generally results in nitrogen-enrichment. However, Hodkinson (1975) found continual net loss of N from both Juncus and Deschampsia throughout his study. Predators such as nematodes soon appear which devour the fungi and bacteria. Larger invertebrates which normally, remove strips of plant material were probably excluded by the fine mesh of the nylon litter bags. Larger mesh sizes admitting larger fauna were not used to minimize inevitable losses through the mesh. The deviant observation at $t = 463$ days (figure 3.23) may reflect such losses.

The decomposition parameters obtained by applying the observed data to the model are given in table 3.12. The decay coefficient of $-0.002/\text{day}$ ($.72/\text{year}$) was equivalent to a 'slow' litter decomposition rate according to a classification proposed by Petersen and Cummins (Hodkinson 1975). However, this decay rate, which corresponds to predicted half life and 95% life values of .962 years and 4.326 years, respectively, was comparable to values obtained for litter of other monocotyledonous species in ponds and reed swamps where current action was not a significant factor causing physical fragmentation of the litter. For example, allochthonous litter of Deschampsia in beaver ponds (Hodkinson 1975) and Typha litter in a reed swamp (Mason and Bryant 1975) produced similar half-life values, although the decomposition of Phragmites in the reed swamp (Mason and Bryant 1975) and of Equisetum and Carex fluviatile in a lake in northern Sweden (Danell and Sjöberg, 1979) was measured at a faster rate. Thus, despite the apparent initially rapid decline in dry weight of Carex pumila (figure 3.23) approximately 80% of the litter remained after five months decomposition compared with only 50-60% of the Carex fluviatile litter in the Swedish study.

Table 3.12 Decomposition parameters for Carex pumila leaf litter
Decay

	coefficient	SD of decay		* 1/2-life	95%-life	
n	k (/day)	coefficient	F-ratio	(days)	(days)	P
13	-0.001973	0.000136	210	351	1579	<.001

* F-ratio = mean square of regression / mean square of the residual

Deviations of observed data from the model $W_t = W_o \exp(-kt)$ which are better observed on a log plot (figure 3.23) are apparent although they were not seen to be significant on the basis of the statistics used ($P < .001$). However, the four observations made at the end of the winter 1981 ($t = 463$ days) have a large influence on the predicted value of the decay coefficient (slope of the regression) (table 3.13). If the observations made throughout the study period accurately reflect the state of decay of Carex litter at those times then the rate of decay was not linear but changed over time. Both seasonal environmental effects and the stage in the decomposition process are probably involved. Decomposition involves a complex of factors such as leaching and the activities of bacterial and fungal decomposers and animal and plant predators (Bryant and Mason 1975). Environmental influences on the microfauna related to the degree of aeration of the litter which would have been determined largely by water table levels in the deflation hollow most probably affected decomposition rates. At no stage during the first winter (days 0 to 100) were the bags submerged since the water table did not rise above the surface over this period. However, during the following winter (1981, days 350 to 450, approximately) extensive flooding in the old deflation hollow occurred. Subterranean decomposition rates (of roots

and rhizomes) were not measured directly in this study, but are predicted to be lower than that estimated for leaves on the surface since below the surface, anaerobic conditions apply for a greater proportion of the year.

Table 3.13 Observed and predicted values of Y ($\ln Wt/Wo$), standard deviations of Y , residuals and standard residuals for Carex pumila leaf litter.

Time (days)	Y ($\ln Wt/Wo$)	Predicted Y value	SD of predicted Y	Residual	Std Residual	
463	-1.2929	-0.9136	0.0630	-0.3793	-2.98	RX
463	-0.9753	-0.9136	0.0630	-0.0617	-0.49	X
463	-0.8387	-0.9136	0.0630	0.0749	0.59	X
463	-0.7607	-0.9136	0.0630	0.1529	1.20	X

R denotes an observation with a large standard residual

X denotes an observation whose X -value gives a large influence

CHAPTER FOUR

Field perturbations

4.1 Introduction

4.2 Methods and materials

4.3 Results and discussion

4.3.1 Aerial shoot densities

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4.3.3 Age and size distributions

4.3.4 Dry weight, energy, elemental contents

1. Dry weight
2. Net biomass accumulation rates
3. Energy and elemental concentrations
4. Total nitrogen content per unit area

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4.3.6 Allocation of dry matter and total nitrogen

4.3.7 The effect of nitrogen fertilizer addition

4.1 Introduction

The sand plains of the dune system of coastal Manawatu provide a harsh environment for plant growth. External factors that are likely to limit growth in this habitat include (1) wind and shortages of both mineral nutrients and soil oxygen which restrict production and (2) the activities of wind, herbivores and pathogens which cause the partial or total destruction of plant biomass. This combination of stress and disturbance factors (sensu Grime 1977) precludes all but a small set of rhizomatous perennial herbs (Esler 1969).

In the field it is unlikely that causal relationships between organisms and their environment can be recognized without deliberate perturbation of the system. The field investigation outlined in this chapter involved three different perturbation treatments involving external factors considered to be of significance in the development of pioneer plant populations on the embryonic sand plain system: (1) the removal of seed and seedlings of Carex pumila, (2) the construction of wind breaks (shelters) and, (3) the application of nitrogenous fertilizer.

The aims of the study were twofold. Firstly, I wished to examine the behaviour and reproduction of Carex pumila and, secondly, to determine if within a particular seral stage the Carex pumila population could respond to a deliberate perturbation of the habitat in a way that would optimize reproductive output.

The selective pressures of the physical and biotic environment, the habit of the species and its life history pattern influence the nature and pattern of resource allocation by a plant to vegetative and reproductive structures (Snell and Burch 1975). Thus, the way in which a plant allocates its limited resources is of significance in

its ecological and evolutionary history as this will affect its survival and contribution to future generations (Abul-Fatih et al. 1979). Selection then may be thought of as having optimized, amongst other things, the allocation of resources between vegetative and reproductive functions in such a way that the organism's fitness is maximized. In the present study the patterns of allocation of the resources of dry weight and total nitrogen by Carex pumila populations over time were studied.

Answers to the following questions based on those originally posed by Harper (1967) were sought:

- (1) Is the proportion of the output of Carex pumila that is devoted to reproduction similar in the younger populations to those older populations further from the terminal hollow?
- (2) Is the proportion of dry weight and crude total nitrogen devoted to aerial growth greater in the more crowded populations?
- (3) Can the proportion of the output of Carex pumila that is devoted to seeds be altered by deliberate perturbation treatments?
- (4) Are the processes of clonal growth competitive with these involved in producing seeds? What is the relative expenditure of resources on seeds and clonal growth in the various populations?
- (5) What is the expenditure on organs ancillary to the seed?
- (6) Do the patterns of allocation of dry matter and of crude total nitrogen to component plant parts differ?

It was recognised that ^{this field} ~~this field~~ approach would be insufficient to distinguish between plastic and genetic population differences as the sere progressed in either space or time. To enable genetic differentiation to be demonstrated, populations raised from seed or shoots would need to be compared at a common site (Turesson 1922; Davies and Snaydon 1973).

Perturbation 1: Seed removal

In predictably changing habitats such as those of a primary succession, the increasing interference between plants may be a good cue for the decreasing favourability of the site for the pioneer species. In such habitats when density was low, clonal expansion would be possible. Clonal growth would be most advantageous as it would facilitate local spread and occupation of a site by a favoured genet. However, when population density became high due to crowding, dispersal through seed production would become advantageous as it would allow escape to new, perhaps more favourable sites (Abrahamson 1975). Thus, genets in seral habitats are predicted to exhibit a plastic reproductive response to increasing seral maturity, allowing them to switch from clonal growth to seed output depending upon the conditions.

Hawthorn and Cavers (1976) found that removal of spikes from fertile shoots of the perennial Plantago rugelii for two years in permanent quadrats in both old pasture and recently-disturbed pasture near London, Ontario, lead to reduced densities of this species. The degree of reduction of plant density in response to this perturbation can be considered to be directly proportional to the rate of new genet recruitment from the seed bank in the soil, relative to other means of maintenance of the population.

Carex pumila is a species with an apparent duality in the means by which it perpetuates itself. Under certain circumstances, it is a prolific seed producer, yet at the same time tenure at a site is maintained by the extension of rhizomes through the sandy substrate and the production of new aerial shoots. In clonal species such as Carex pumila, shoot density reduction through the removal of the source of new genets germinating in the soil seed bank may be offset by the vegetative production of new daughter shoots (ramets). In the experiment outlined below, both current and previous years seeds of Carex pumila were removed to investigate the role of sexual reproduction versus clonal growth in the establishment and/or maintenance of populations of this pioneer species at different stages of the sand plain sere.

Perturbation 2: Shelter

Wind has long been recognised by agriculturalists and more recently by ecologists as a factor affecting plant growth. Leonard Cockayne (1911) was the first to suggest that wind was an important ecological factor in the New Zealand environment noting that in windy places compact prostrate bushes of a similar growth habit to that resulting from divarication ^{predominated.} ~~dominated.~~

Wind exposure is a term used by ecologists to describe the stresses and disturbances experienced by plants growing in windy places. Exposure may be manifest as mechanical damage (Daubenmire 1959), anatomical and morphological changes or reduced plant yield (Grace 1977). Wind tunnel studies have shown high winds (7-12 m/sec) reduce relative growth rates, rate of leaf elongation and leaf area ratio, effects which have been attributed to reductions in leaf water potential (Grace 1974; Grace and Russell 1978). Similarly, the

anatomical and morphological changes (including smaller thicker leaves; shorter internodes; increased root/shoot ratios; increased amounts of vascular tissue; and increased number of stomata per unit leaf area) are like those features that develop in response to soil water deficits. Such responses to wind are primarily moisture stress effects (Hollows 1978). The reduction of leaf elongation and the increased incidence of sclerophylly brought about by increased wind speeds in the grass Festuca arundinacea have been shown to be less extreme when phosphorus supply to the plant was adequate (Pitcairn and Grace 1982). The possible role of nutrient stress in causing sclerophylly is further suggested by the observation of this feature in phosphorus deficient soils of Australia (Beadle 1954).

Amelioration of the effects of wind on plants by the use of wind breaks and shelter belts have been a practical means of increasing plant yield (Grace 1977). Wind breaks however, affect variables other than wind speed, such as temperature. Thus, there remains an uncertainty about the interpretation of results of shelter experiments in the field that are not complemented with controlled environment studies in a wind tunnel.

In coastal habitats wind, salt spray and nutrient and soil moisture deficits are likely to be important factors affecting plant growth. The problem of distinguishing between the effects of each is exacerbated by the observation that similar results may be achieved in response to all of these factors (Grace 1977). Thus, there remains an uncertainty about the suggestion of Turesson (1922,1925) that ecotypic differentiation of dwarf coastal populations in several plant species was the result of the lesser ability of such plants to trap salt carried by the wind.

An outstanding characteristic of the west coast of the north island of New Zealand is the large number of days per year with high wind gusts and in coastal Manawatu in particular the intensity and persistence of the highly directional winds which abound for most of the year (section 3.1). It is therefore possible that the magnitude of wind gusts which was seen to vary across the study area (section 3.1.8) could confer a degree of adaptive significance to the variation in vigour of Carex pumila across the same area. Thus, wind breaks were constructed across the sere to test this hypothesis.

Perturbation 3: Nitrogen fertilizer addition

It is well established that sand dune communities are under stress from low nutrient status of the soil. Rapid increases in productivity and turnover of ramets and individual plant parts have been observed when fertilizers are applied (Yemm and Willis 1961; Willis 1963; Huiskes 1979; Noble et al. 1979). Nitrogen and phosphorus are the elements most commonly found to be deficient in sand dune soils. For example, Smith (1977) reported "excellent growth responses to applications of nitrogen" and less marked responses to phosphorus, on sand country 7km north-east of the study area.

It is probable that soils of low-lying dune hollows are enriched by leaching from dune ridges that surround them (Salisbury 1952) and in this respect the hollows can be considered more favourable habitats for plants than the ridges. This view is confirmed by the experimental work of Jones (1975) who noted amongst the beneficial effects of waterlogging in relation to the development of dune slack vegetation, the increased availability of phosphorus and potassium. Thus, one might expect a diminished response to added fertilizer by vegetation in the less impoverished dune hollows compared with that of

vegetation on the more nutrient-stressed dune ridges. However, responses of sand dune communities to fertilizer apply to vegetation on both dune ridges and dune hollows, although these responses are not uniform to all species within these communities (e.g. Watkinson et al. 1979). The application of nitrogenous fertilizer was the final perturbation to the sand plain system. The objective was to determine the effect of this element, whose deficiency was suspected to be the major cause of stress in this pioneer sand plain community, on populations of Carex pumila, the major species present.

4.2 Methods and materials

Experiment 1: Seed removal

On December 26 and 27, 1977 all female spikes on fertile shoots and seed of Carex pumila on the ground were removed from two 2 x 2 m plots at each of four sites in the study area described above (section 3.1). Two similarly sized undisturbed control plots were also established at each site. The four plots at each of the old deflation hollow sites (namely, S2, S3 and S4) formed a square, replicate treatments diagonally opposite each other, with a 30cm wide pathway running each way between the plots. Since, on the edge of the low dune, the band of Carex pumila shoots invading the embryonic terminal hollow formed a relatively narrow band, the four plots at this site were established in a line, again with 30cm pathways between plots. Carex pumila seeds (each a nut encased in a corky utricle) which are buoyant were redistributed on the study area during the winter 1978 as a result of flooding and wind disturbance. Thus, seed was removed again from the ground on the treatment plots, in early spring 1978.

Harvesting programme and procedure

The harvesting programme for this experiment is given below:

Harvest number	26/27 December	1977 - Treatment established
1	25 January	1978
2	3 April	1978
3	10 August	1978
4	18 October	1978
5	1 November	1978
6	14 November	1978
7	29 November	1978
8	13 December	1978
9	27 December	1978
10	10 January	1979
11	19 February	1979
12	7 September	1979

At each harvest, on each of the 16 (4 sites x 2 treatments x 2 replicates) plots, one 30 x 30cm quadrat was harvested, initially towards the periphery and then with subsequent harvests progressively closer towards the centre of the 2 x 2m plot in order that trampling damage to unharvested plants be avoided. The aerial portion of all shoots, both living and dead, within each quadrat were removed at ground level and placed into a labelled bag. Below ground parts were sampled from the same areas used for the above-ground sampling by digging up all plant material in the quadrat to a depth of 30cm (up to 1m at S1 where sand accumulation occurred). A spade was used to sever the rhizomes at the edge of the quadrat. At S2, S3 and S4 in the old deflation hollows where the interweaving of rhizomes and matting of

roots had caused a turf to form, the below-ground samples were removed more or less intact for later separation. At S1 where a turf had not formed, the sand fell away from the roots and rhizomes. Underground plant parts were removed from the sandy substrate by washing. On return to the laboratory, all plant material from each quadrat (both aerial and underground fractions) was thoroughly washed in several changes of water and divided into constituent parts, dried at 80 degrees C in a forced ventilation oven for 24 hours and then weighed. Numbers of dead, vegetative and fertile shoots and of seed were counted. Roots may have been underestimated through loss in the washing and separating procedure; roots were also observed to penetrate below the sample depth. These errors are likely to be small (< 5%) since firstly, at S2, S3 and S4, the bulk of root material was associated with the mat of rhizomes in the upper 0-15 cm of soil, and secondly, Carex pumila roots do not penetrate the grains of the substrate (cf roots of species growing in clay soils). They were therefore easily separated from the sandy substrate, with little root damage or loss.

Experiment 2: Shelter wind breaks

On 1 October 1979, a 1 m high wind break was constructed around a 5 x 5 m area at each of four sites on the study area (S0, S1, S2 and S3) using 50mm mesh wire netting and hessian sack-cloth. All shelters, with the exception of that at S2 on the less exposed part of the study area (section 3.1.8), required renovation within two months when 6mm pore diameter Netlon wind break material was used. This too required continual maintenance during the latter part of the summer 1979-80.

Harvesting programme and procedure

The harvesting programme for the shelter experiment is given below:

Harvest number

	1 October 1979 - Windbreaks erected
13	17 October 1979
14	30 October 1979
15	6 November 1979
16	14 November 1979
17	27 November 1979
18	4 December 1979
19	11 December 1979
20	17 December 1979
21	8 January 1980
22	5 February 1980
23	5 April 1980
24	28 July 1980

The harvesting procedure differed from that outlined above for harvests 1 to 12. The 30 x 30 cm turves with aerial shoots attached were lifted and carried to the laboratory where the sandy substrate was removed by washing. This procedure facilitated the separation of intact branch modules, including the rhizome and adventitious roots. Vegetative, fertile and dead branch modules were counted and further separated into constituent parts. They were dried and weighed as above.

In addition to the counts of seed and of shoots taken previously each living shoot was placed in a size category according to the height to the ligule of the youngest fully-expanded leaf (collar

height). The number of both living and dead leaves per shoot were counted and the area of green laminae per shoot measured using an electronic scanner. On fertile shoots, the number of female spikes per culm and seeds per spike were counted, and the stage of development estimated.

Plant samples were collected from two contiguous 30 x 30 cm quadrats (ladder quadrats) within each treatment at S2 and S3. On the controls on the low dune (S0 and S1) four contiguous 30 x 30 cm samples were harvested. No samples were harvested from within the shelters at S0 or S1, although during this period measurements and counts of the aerial shoot population on these plots were made. Ladder quadrats (Pearsall and Gorham 1956) were used to avoid overestimation of biomass owing to clumping of the vegetation and edge effects. The limited area of the Carex pumila stands at each of the stages of development across the study area precluded replicate ladder sampling.

Experiment 3: Nitrogen fertilizer addition

In the spring of 1980 (September 17) ammonium sulphate fertilizer was applied by hand at a rate equivalent to 50kg of elemental nitrogen per ha to two replicate plots at each of three sites representing different stages of the sand plain sere. Two control plots (no added N) per site were established adjacent to the fertilized plots in such a position that it was unlikely fertilizer could be blown onto them.

Plots were established in the old hollow where the Carex pumila population was senile and formed only a small proportion of the total living biomass (S3) and at two contiguous sites on the low dune where the Carex pumila populations were in a mature (S1) or adolescent (S0) phase of development. The fertilized plots were not sampled at the subsequent harvest on 17 October, but were left undisturbed until the harvest on 17 December, 3 months after the application of nitrogen

when a single 30 x 30 cm quadrat was sampled from each plot. In addition two contiguous 30 x 30 cm quadrats were sampled from the old hollow at S2 to complete the temporal sequence at this site.

Harvesting programme and procedure

The harvesting programme for the nitrogen fertilizer perturbation experiment is given below:

Harvest number

	17 September 1980	N-fertilizer added
25	17 October	1980
26	17 December	1980

The turf from each 30 x 30cm quadrat was lifted intact, or where this was not feasible care was taken not to sever below-ground connections between aerial shoots within the sample and removed to the laboratory and treated as for harvests 12-24 allowing the separation of whole modules of both dwarf and long shoots into vegetative, reproductive and dead categories, for counting and further separation into components. Numbers of green and of dead leaves per living shoot, numbers of seed per 30 x 30 cm and numbers of live shoots within various size classes according to collar height were also counted.

Energy and lipid determination

Lipid determinations were made by ether extraction and energy determinations by use of a Gallenkamp adiabatic Bomb calorimeter. Energy determinations were carried out on constituent organs of Carex punila from S2 at harvest 1 and on seeds from S2 at harvests 7 to 10 and from each of four sites (S1, S2, S3 and S4) collected on 25 January 1979.

Crude total nitrogen

The determination of crude total nitrogen (%) of constituents organs of Carex pumila was carried out using the following reagents (Haselmore, pers comm):

1. Digestion mix. 100 g of potassium sulphate (AR) plus 1g of selenium powder were added to 1 litre of concentrated sulphuric acid (AR) in a large conical flask. This mixture was heated in a fume cupboard at c 300 degrees C for c 2 hours until a clear solution formed.
2. Hydrogen peroxide (AR), 30% (W/V).
3. Phenol reagent. 50g phenol (AR) plus 0.25g sodium nitroprusside (AR) was made up to 1 litre with distilled water in an amber bottle and kept in the refrigerator.
4. Hypochlorite reagent. 25g sodium hydroxide (AR) plus 56ml of 4% sodium hypochlorite was made up to 1 litre with distilled water and stored as for phenol.
5. Nitrogen standard. 2.360g ammonium sulphate (AR) was mixed with 100ml of distilled water to give a nitrogen concentration of 5 mg N per ml.

The procedure involved taking approximately 50mg of oven dried plant material passed through a 1mm mesh in a micro hammer mill, accurately weighed into digestion tubes (18 x 150mm, glass test tubes) to which 1 ml of digestion mix then 0.5ml of hydrogen peroxide was carefully added. The tubes were gently shaken to aid solubilisation. The samples, usually in batches of 48, were digested on an aluminium heat block initially set at 150 degrees C. They were then heated to

320 degrees C in about 2 hours and held at this temperature for a further 2 1/2 hours (4 1/2 hours total). The solubilisation and digestion were carried out in a fume cupboard. Safety glasses and gloves were worn when the digestion mix and hydrogen peroxide were added and the tubes placed on the heated digestion block. At the end of the 4 1/2 hour digestion period, the samples were transferred to a metal test tube holding block and left to cool, then 8 1/2 ml of distilled water added, mixed thoroughly and again left to cool. 50 μ l aliquots of this solution were transferred to a second set of test tubes then 1ml of phenol reagent and 1 ml of hypochlorite reagent were added, mixing thoroughly using a vortex mixer on the addition of each reagent. Samples were left for 1 hour at room temperature (or 20 minutes at 37 degrees C) then 8 1/2 ml of distilled water added, mixed thoroughly and read for absorbance at 630nm using a Hitachi spectrophotometer. A set of nitrogen standards containing 0, 0.5, 1.0, 1.5, 2.0 and 2.5mg N were taken through the entire procedure, with each batch of plant samples.

Absorbance at 630nm was linear over the range of nitrogen concentrations (0-2.5 mgN/ml) in the standards. Thus, a straight line was fitted to the plot of absorbance versus nitrogen concentration for the standards in each sample batch. The slope of this curve (straight line) was used to calculate the crude total nitrogen concentration (%) of each sample in that batch.

Component organs of Carex pumila shoots from harvests 1 to 26 were thus tested for percent crude total nitrogen. The total nitrogen content of this plant material in grams nitrogen per unit area of ground was then calculated from the dry weight data, so allowing the determination of the allocation of total nitrogen, as well as that of dry weight, to component organs and shoot types.

Other elements

Oven dried subsamples of constituent organs of Carex pumila were passed through a 1mm mesh in a micro-hammer mill. Accurately weighed samples (approximately 0.1g) of this finely milled material were ashed in a muffle furnace at 500 degrees C for more than two hours. The ash, approximately 0.01g per sample, was dissolved in 2 ml of constant B.P. 2 molar hydrochloric acid. This solution was decanted to remove any residue, resulting from incomplete combustion in the furnace.

Determinations were made on these samples of K and Na by flame photometry and of Cu, Zn, Fe, Ni, Mn, Mg and Ca by atomic absorption spectrophotometry. Standard solutions and blanks were run throughout the procedures along with the plant samples.

Raw data for dry weights, leaf areas, leaf, shoot and seed numbers and elemental concentrations have been placed on a magnetic tape held by the author.

Statistical analysis

At each harvest, the data were analysed by analysis of variance by use of Teddybear (Wilson 1979), a statistical package held at Massey University for use on the Burroughs B6700 Computer. For each variate analysed, means and within-treatment variances were calculated and tested for residual heterogeneity of variance (Bartlett's test), skewness (G1), kurtosis (G2 and A) and normality. Duncan's Multiple Range Test was performed to determine the significance of differences between level means within each factor, and a normality plot was calculated and printed. Where deviations from normality were indicated by these tests, transformations of the data were carried out. Log transformations were most frequently applied where the

frequency distribution was skewed to the right (G1 positive). Bartlett's test for heteroscedasticity is extremely sensitive to deviations from normality and thus a significant test result may merely indicate non-normality rather than heteroscedasticity (Sokal and Rohlf 1967). Thus, transformations to make the data normally distributed often resulted in a non-significant Bartlett's test (non-heteroscedasticity) where heteroscedasticity had previously been indicated. When transformation of the data did not show non-heteroscedasticity no further manipulation of the data (Sokal and Rohlf 1967, p.376) was attempted. Variates analysed included dry weight and total nitrogen content per unit area for individual and combined plant parts, ratios of various combinations of these, and dry weight and total nitrogen content of plant parts per branch module.

At the final harvest (H26), the unbalanced experimental design (control treatment only, at S2) required that the analysis of variance involve the partitioning of the sums of squares and degrees of freedom into arbitrary contrasts. The data were analysed by treating each site x experimental treatment combination as a different level of a single factor, "site". The sums of squares and degrees of freedom for this factor (site) were then partitioned into single-degree-of-freedom contrasts. The contrast coefficients are shown below:

Levels of factor "site"

		3C	3N	1C	1N	OC	ON	2C
Contrast name	A	1	0	-1	0	-1	0	1
	B	0	2	0	-1	0	-1	0
	D	0	0	1	1	-1	-1	0
	E	0	0	1	-1	-1	1	0
	F	0	0	1	-1	1	-1	0
	I	-2	-2	1	1	1	1	0

December 1980 harvest will therefore appear twice, first as a point in the temporal sequence (sections 4.3.1 - 4.3.6) and second, as a control for the nitrogen experiment (4.3.7).

4.3.1 Aerial shoot densities

Figure 4.1 shows the sum of the densities of vegetative, fertile and dead shoots of Carex pumila at four sites on the study area in January 1978. At sites of increasing distance from the terminal deflation hollow, the densities of living and of all shoots form n-shaped plots, reminiscent of those described for rhizomatous perennial species displaying phasic development (see references and further results in section 3.2.1). As a result of the nature of the formation of the sand plain, these sites form a chronoserries (section 3.1). The populations at the youngest and oldest sites, S1 and S4 respectively, had similar and reduced total living aerial shoot densities compared with the populations at sites of intermediate age, at S2 and S3. The populations at S1 and S4 could be distinguished by the proportion of dead shoots present in the total shoot population and by the ratio of fertile to vegetative shoots (figure 4.1). Dead and fertile shoots were absent from the juvenile Carex pumila shoot population at S1 on the edge of the terminal hollow. Vegetative shoot densities were remarkably similar at all four sites (figure 4.1).

Figure 4.2 shows the changes in living shoot densities of Carex pumila at each site monitored on the study area over time. In winter, spring and summer 1980, these shoots were divided into those attached

Figure 4.1 The sum of the density of vegetative , fertile and dead shoots of *Carex pumila* at four sites on the sand plain near Tangimoana, in January 1978. Vertical bar denotes $\pm$ variance of live shoot means.

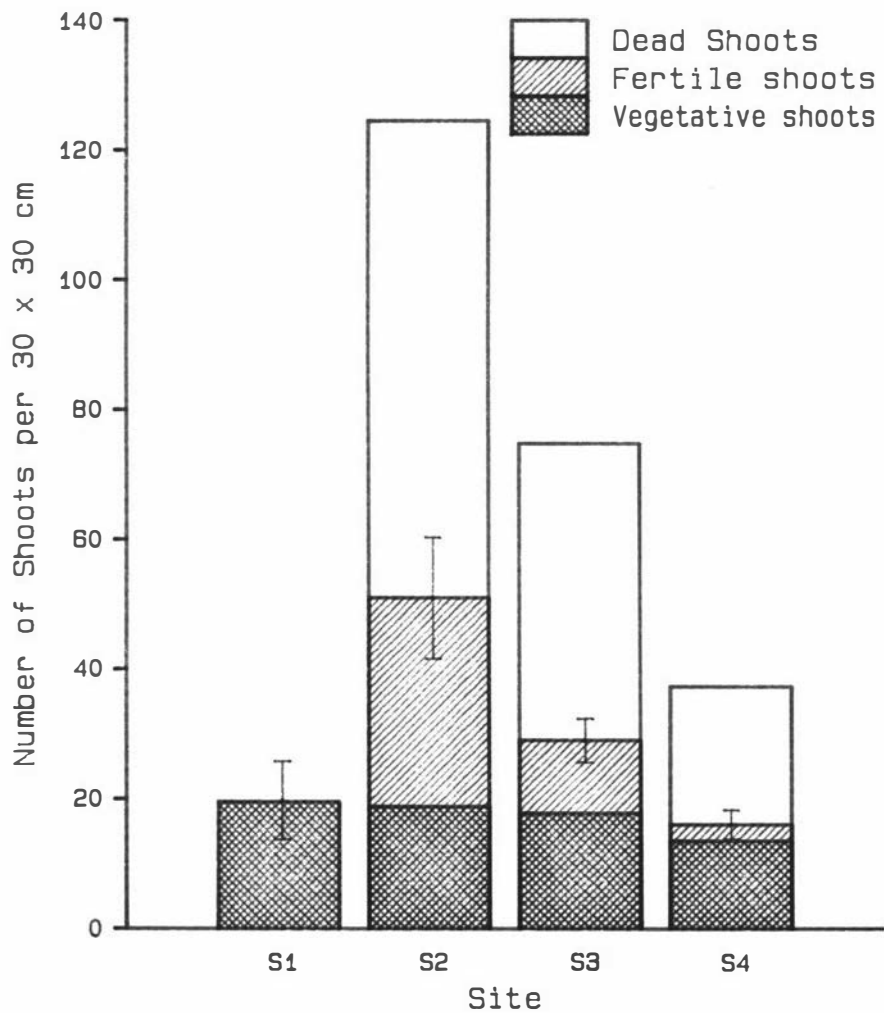
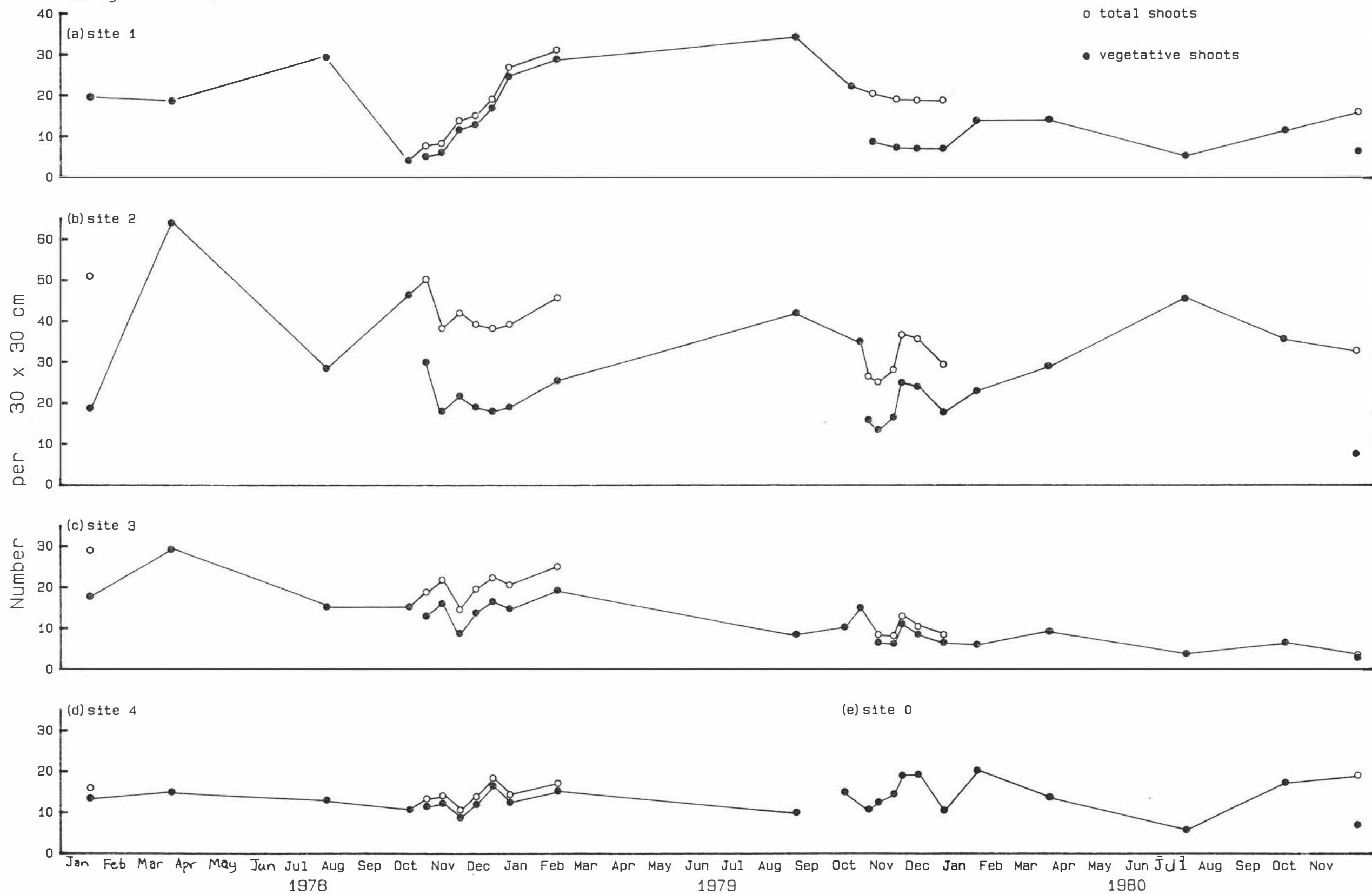


Figure 4.2 The sum of the density of vegetative and fertile shoots of *Carex pumila* over time at five sites on the sand plain, during 1978, 1979 and 1980

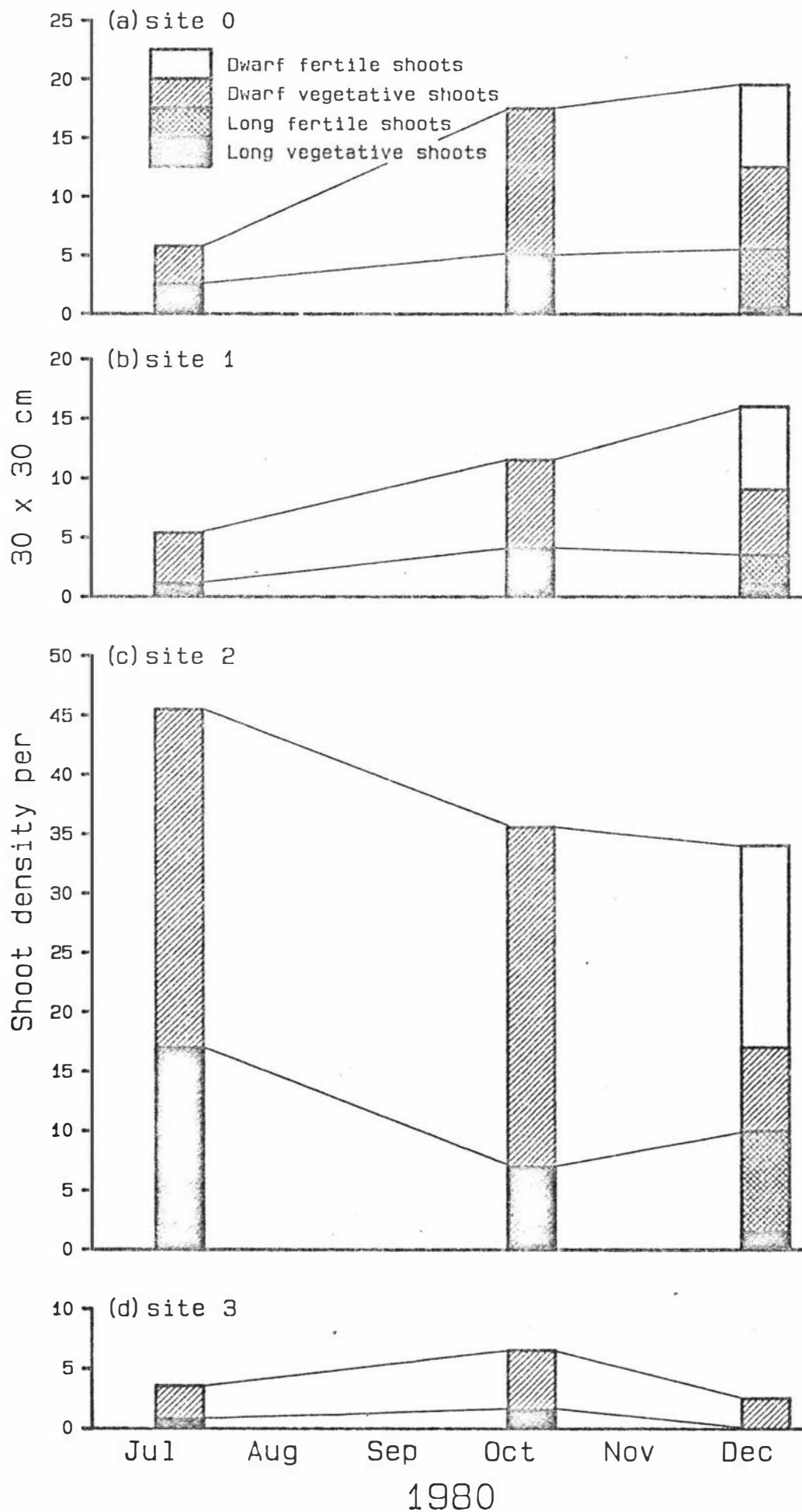


to dwarf and to long rhizome branches (figure 4.3). From the changes between successive harvests, new vegetative shoot recruitment and shoot mortality may be inferred. These data show two major trends, firstly of seasonal fluctuations and secondly, of longer term changes that could be predicted on the basis of population age, ie distance from the terminal hollow. In the younger populations on the edge of the low dune, shoot densities increased from year to year in contrast to the trend in the older populations, both on the deflation hollows and on the low dune, of declining shoot densities between years.

The seasonal fluctuations in density of Carex pumila shoots are not in phase for the populations on the low dune and on the deflation hollows. In conjunction with data on the distributions of shoot age at consecutive harvests (section 4.3.3), seasonal density fluctuations show shoot mortality to be most apparent in winter/early spring and again in mid-summer on the deflation hollows (S2, S3 and S4), and in both spring and summer on the low dune (S0 and S1). Shoot mortality also occurred in autumn at all sites on the study area, as the culmination of the events leading to flowering and seed production in these monocarpic shoots. Major periods of shoot recruitment occurred in autumn and spring on the deflation hollows, periods that coincided with more mesic soil conditions compared with those in summer (dry) and winter (flooded). On the low dune, where the winter water table levels remained below the surface, net shoot recruitment continued throughout winter. Thus, whereas a seasonal trough in shoot density was found in winter on the deflation hollows, a seasonal peak was found at this time of the year or early spring on the low dune.

Figure 4.3 The sum of the density of dwarf and long shoot populations of *Carex pumila* over time at four sites on the sand plain between July (winter) and December (summer) 1980

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The lack of appearance of new shoots above the surface at S1 during autumn 1978 was associated with a marked accumulation of about 300mm of sand at this site. Continuing growth of this juvenile Carex pumila population was however, not prevented (see section 4.3.4). When the sites on the study area were established in December 1977, S1 was at the edge of the low dune and included the front of Carex pumila rhizomes advancing into the terminal hollow. By the end of March 1978, the rhizome front had extended into the terminal hollow a further 0.8m and sand accretion had occurred around shoots at S1 which were then further behind the rhizome front (section 3.2.2).

Continuing vegetative shoot recruitment and the lack of shoot mortality over the winter at S1 lead to an increased total living shoot density by August 1978 (figure 4.2). Further building of the low dune, as a result of the deposition of dry wind-blown sand around Carex pumila shoots in spring 1978, resulted in a massive decline ($P < .01$) in the density of living shoots and a concomitant increase in that of dead shoots at this site between August and mid-October 1978 (figure 4.2). Figure 4.2 shows that the recovery of the living shoot density at S1 to the late winter 1978 peak took the whole of the subsequent 1978-79 summer, to February 1979.

Few shoots at S1 were seen to be fertile in the summer of 1978-79 (figure 4.2, difference between total living and vegetative shoot densities), although their density (24.6 / m² averaged over harvests 5 to 11) represented almost 50% of the spring nadir of total living shoots. The steady increase in vegetative shoot density at S1 over summer 1978-79 continued the following autumn and winter, so that by

spring (September) 1979 mean aerial living shoot density was the greatest yet seen at this maturing site (figure 4.2). In spring 1979, shoot density at S1 decreased. This decline was not as massive as that in 1978 (figure 4.2), when the site was closer to the edge of the low dune and so more vulnerable to sand deposition. However, the movement of sand by the strong seasonal winds continued across the site in summer 1979-80. In the face of this continuing site disturbance and increased moisture stress as a result of the lowered summer water table level, the ageing Carex pumila population at S1 showed a reduced ability to maintain itself; net vegetative shoot densities remained low over this period.

The density of fertile shoots at S1 in the summer 1979-80 was significantly greater than that of in the previous year, although as a proportion of the late spring 1979 living shoot density, it was similar to that proportion of the late spring 1978 shoot density found to be fertile in summer 1978-79, namely almost 50% (figure 4.2).

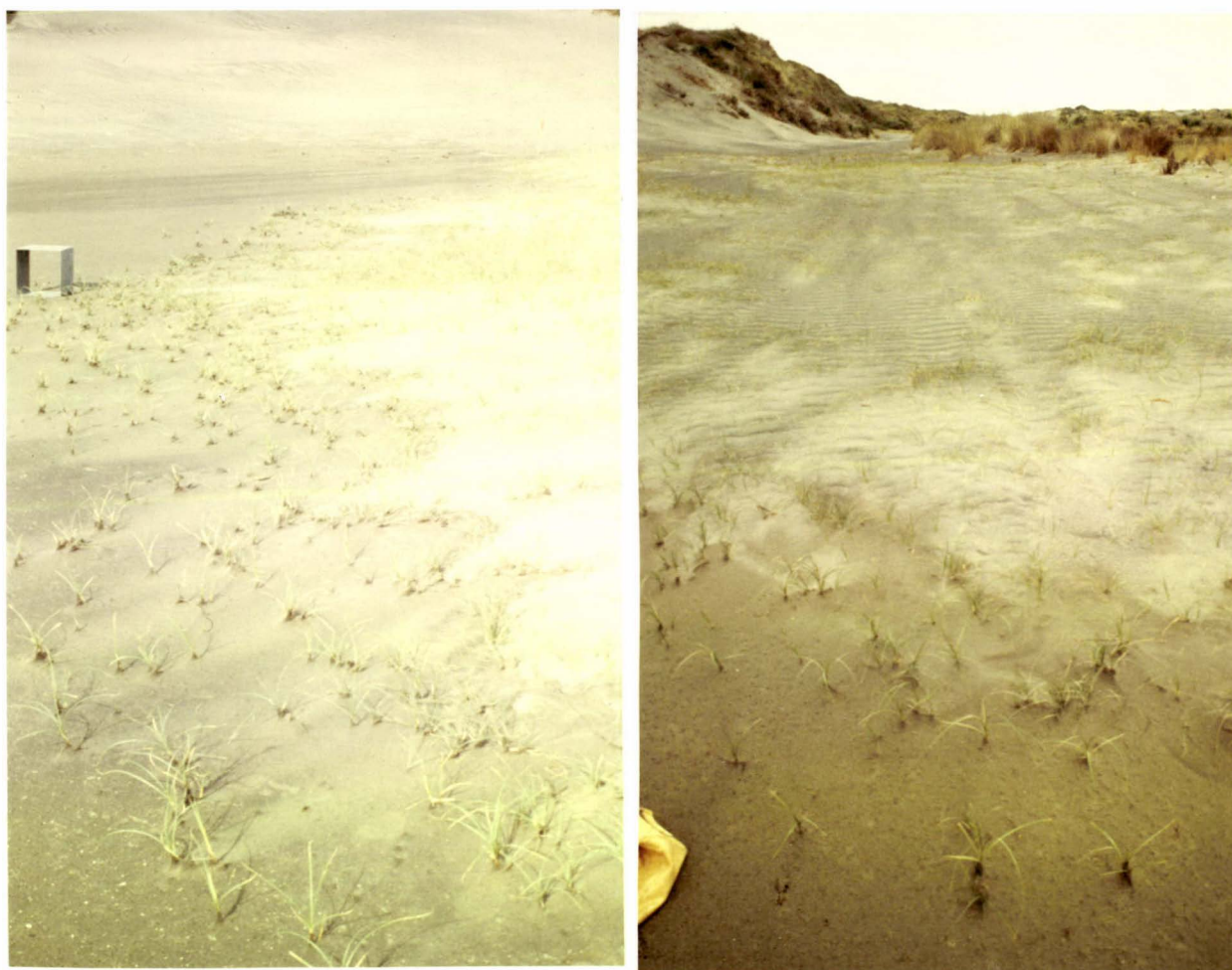
Recruitment of new vegetative shoots on the low dune at S1 later in the summer 1979-80 and the following autumn resulted in a net increase in vegetative shoot density to April 1980, although this increase was considerably smaller than that observed twelve months earlier. The increasing senility of this low dune population was reflected by the net decrease in living shoot density over the winter 1980, whereas during the two previous winters net shoot recruitment occurred. However, between mid-winter (July) and late spring (October) 1980, shoot density at S1 increased, whereas in previous years, the deposition of dry wind-blown sand on the low dune in spring was associated with net shoot mortality.

By December 1980, fertile shoot density on the control plots represented 100% of the living shoot population present at the site five months previously. This density was similar to that for fertile shoots observed at this site during summer 1979-80. The reduced spring/early summer shoot mortality on the low dune in 1980 was also reflected by the density of vegetative shoots at S1 which in December 1980 was no less than that observed in mid-summer twelve months previously. The senescence of the Carex pumila population on the low dune at S1 was retarded by the increased stability of the sand plain brought about by the artificial planting of Ammophila arenaria on the surrounding high dunes and lateral sand plains in spring between 20 August and 17 September, 1980 (figure 3.4). Thus, during the windy period of spring 1980 the supply of mobile sand was drastically reduced and the putative major cause of spring/early summer shoot mortality on the low dune was removed.

From spring 1979, a further site (S0), where Carex pumila rhizomes were extending into the terminal deflation hollow, was monitored. S0 was situated on the edge of the low dune in a comparable position to that of S1 when this site was laid down in summer 1977-78. The age distribution of the shoot population at S0 in mid-October 1979 (section 4.3.3) shows predominantly young shoots, with a few aged shoots, which were likely to have been recruited the previous autumn. This conclusion was supported by the observation in mid-summer 1979-80 of a small proportion of fertile shoots in the total shoot population. Aerial shoot density at S0 increased during spring 1979/early summer 1979-80 (figure 4.2), despite the accretion of wind-blown sand around Carex pumila shoots on this part of the low dune (figure 4.4). A large decline in total living shoot density was observed at S0 in midsummer 1979-80 between 17 December and 8 January.

At this latter date, dead vegetative shoots first appeared in the budget at S0. Continuing shoot recruitment at S0 in late summer 1979-80 resulted in a return to the earlier vegetative shoot density peak (figure 4.2).

Figure 4.4 Views of the low dune showing newly deposited (dry) sand, in (a) spring 1979 (left) and (b) autumn 1980 (right).



Subsequent deposition of large quantities of sand on the low dune by high winds during February 1980 resulted in shoots at S0 being buried by 21 February 1980 (figure 4.4b). At subsequent harvests on the edge of the low dune in autumn and winter 1980, the density of living shoots was reduced (figure 4.2). The surviving population in

July showed a more mature age structure than that at the site in April which was skewed to the right (section 4.3.3). Over the subsequent spring and early summer, the effect of recruitment of both dwarf and long shoots was evident with the total living shoot density reaching a plateau in December 1980 (figure 4.3). Of these shoots, more than 50% were fertile. The densities of both dwarf and long fertile shoots at this site in summer 1980-81 was significantly ($P < .05$) greater than that of the winter dwarf and long shoot populations present at the site in July. They were however, no different from that of the combined shoot plus shoot bud populations present at this time. The implication of this observation is that both long and dwarf underground shoots of Carex pumila that are present in winter and that have undergone little or no orthotropic development can develop during the subsequent spring and summer into fully fertile shoots, capable of producing ripe seed. This was confirmed by the monitoring of tagged shoots. An emerging shoot in spring was observed to have produced seed by the end of summer, four months later.

In the old hollows at S2, S3 and S4, the pattern of change in shoot densities observed over the duration of the study showed differences to those seen on the low dune site. Sand accretion which was associated with aerial shoot mortality on the low dune was not seen to be significant in the old hollows. Periods of shoot mortality in the old hollows other than that in autumn associated with flowering in these monocarpic shoots were identified during the winter and spring when the water table was close to or above the surface bringing about anaerobiosis/reducing conditions in the surface layers of the soil, and again in mid-summer. There were also two periods during the year that new vegetative ramet recruitment caused net increases in vegetative shoot densities on the old hollows; in spring-early summer

and again in late-summer autumn, as on the low dune at S1.

Mean vegetative shoot densities increased at the the three sites in the older deflation hollows over late summer/autumn to the end of March 1978 (figure 4.2). This net autumn recruitment of new vegetative shoots decreased in significance at sites of increasing age (distance from the terminal hollow). These site differences resulted partly from the difference in absolute density of total living shoots from which daughter tillers may be produced (figure 4.1), and partly by the difference in the proportion of these living shoots that, on average, gave rise to a new daughter ramet (table 4.1). Both of these factors showed decreases with increasing age of site.

The reduction in vegetative shoot densities at the three old deflation hollow sites over winter (April to August) 1978 mirrored the autumn increases, with decreased mortality both in terms of absolute numbers per unit area (figure 4.2) and relative rate (table 4.1) at sites of increasing senility. This result was similar to that of Noble et al. (1979) who found the greatest death rates of Carex arenaria shoots at sites where birth rates of shoots were also greatest.

Table 4.1 Change in vegetative shoot density of Carex pumila in autumn and in winter 1978 at four sites on the study area, relative to the combined fertile plus vegetative shoot density at these sites in January 1978.

Relative change in shoot density			
	January-April	April-August	Nett
S1	- .051 ns	+ .544 ***	+ **
S2	+ .887 ***	- .696 ***	+ *
S3	+ .397 *	- .483 *	- ns
S4	+ .094 ns	- .125 ns	- ns

Level of significance of the changes at each site are indicated: ns = not significantly different from zero; * = $P < .05$; ** = $P < .01$; *** = $P < .001$.

The effect of spring vegetative shoot recruitment was seen at S2 between August and mid-October 1978 when total living shoot density increased by an amount equivalent to the subsequent midsummer mean vegetative shoot density (figure 4.2). Similar increases in total living shoot densities at S3 and S4 later in spring, in October-November 1978, were smaller and due to large within-site variability were not statistically significant.

During the late spring 1978 and early summer 1978-79, mortality of larger and older, non-flowering ramets continued at S2, S3 and S4 in the older hollows, indicated by the decline in density of vegetative shoots (figure 4.2). The midsummer mean density of vegetative shoots at each of these sites was remarkably similar to that observed twelve months earlier. The recruitment of vegetative shoots in late summer 1978-79 was evident at each of the old hollow sites.

Between February and September 1979, a net increase in vegetative shoot density was observed at S2, in contrast to a net decline in density of these shoots at the more senile sites, S3 and S4. Since this was the net effect of autumn recruitment and winter mortality on the old hollows in 1978 (table 4.1), it was assumed that a similar pattern was followed in 1979.

Death of vegetative shoots on the old hollow continued into spring 1979, as in 1978. Shoot mortality at S2 and S3 between early September and mid October 1979 occurred mainly in the older, larger shoot cohort (section 4.3.3).

The pattern of change in vegetative shoot density in the old hollow during summer 1979-80 was similar to but more accentuated than that seen during the previous summer. Recruitment of new vegetative shoots resulted in a net increase in vegetative shoot density leading up to mid-summer at both S2 and S3 (figure 4.2). This was followed by a net loss in vegetative shoot density in late December-January as the vegetative shoot populations aged (section 4.3.3).

Late summer and autumn recruitment more than doubled vegetative shoot density at S2 between January and July 1980, following the pattern seen in the two previous years. In the more senile old hollow population at S3, a very much smaller net vegetative shoot density increase occurred between February and April 1980, although by mid-winter (July), shoot mortality had resulted in a net decline in density of living shoots. This net result of autumn recruitment and winter mortality at S3 in 1980 was observed in both of the two previous years. This accounts for the pattern of declining shoot density with increasing senility of this old population.

Spring shoot mortality at S2 saw the loss of most of the long shoots by October 1980 (figure 4.3). Those long shoots surviving were in the main reproductive. In the spring and early summer 1980-81, the decline in density of the combined dwarf plus long living shoot population at S2 was similar to that seen in 1979. The combined density of the surviving dwarf and long tillers, which were seen to be fertile was not significantly different from fertile shoot density found at this site in summer 1979-80. At the final harvest in December 1980, the density of the surviving vegetative shoot cohort, of predominantly dwarf tillers, was less than 80 / m², the lowest seen on this part of the old hollow at any time during the study.

Fluctuations in shoot density in the more senile old hollow population at S3 in spring and early summer 1980-81 were small and not statistically significant. As at S2, the density of the surviving vegetative shoot cohort of exclusively dwarf tillers in December 1980 was the lowest seen here during the entire study. The overall decline in living shoot densities at the two old hollow sites over the three years of the study is evident from figure 4.2.

The seasonal maximum density of fertile shoots of Carex pumila obtained at each of the old hollow sites monitored, which may be used as a crude measure of the fecundity of the population, was observed in 1977-78, the first summer of the study (table 4.2). In each successive year, as the resident population at each of these sites became progressively more senile, the mean density of fertile shoots averaged over the late spring and summer harvests declined asymptotically. Thus, whereas the differences at S2 and S3 between 1977-78 and 1978-79 and at S2 between 1978-79 and 1979-80 were large and significant ($P < .05$), later differences where the populations were in more advanced stages of senility were smaller in magnitude (table

4.2).

Table 4.2 Mean ($\pm$ standard deviation) density of fertile shoots of Carex pumila at five sites on the study area, in four consecutive summers.

	Density / 30 x 30 cm				
	S0	S1	S2	S3	S4
1977-78	ne	0	30.1 $\pm$ 1.5	13.4 $\pm$ 1.5	2.5 $\pm$ 1.77
1978-79	ne	2.2 $\pm$.3	20.2 $\pm$ 1.32	5.8 $\pm$.62	1.9 $\pm$.38
1979-80	0.25 $\pm$.08	11.7 $\pm$ 1.23	11.6 $\pm$ 1.32	1.9 $\pm$.48	ne
1980-81	12.00 $\pm$.71	9.5 $\pm$ 1.77	17.7 $\pm$ 6.	.8 $\pm$.42	ne

ne = not estimated

On the low dune at both S0 and S1, younger phases in the development of the resident populations were represented. Fertile shoot density at these sites increased between years. At S1 in 1977-78 and S0 in 1979-80, the shoot populations were almost exclusively vegetative. These represented the juvenile phase of the succession at these sites. In subsequent years, mean summer fertile shoot density increased to maxima in 1979-80 at S1 and in 1980-81 at S0 (table 4.2). These represented mature phases of the seral development on the low dune. The decline in fertile shoot density between summer 1979-80 and summer 1980-81 was only small. It was assumed however, to represent the beginning of the steeper decline in this parameter between years similar to that seen with the increasing senility of populations in the old deflation hollows (table 4.2).

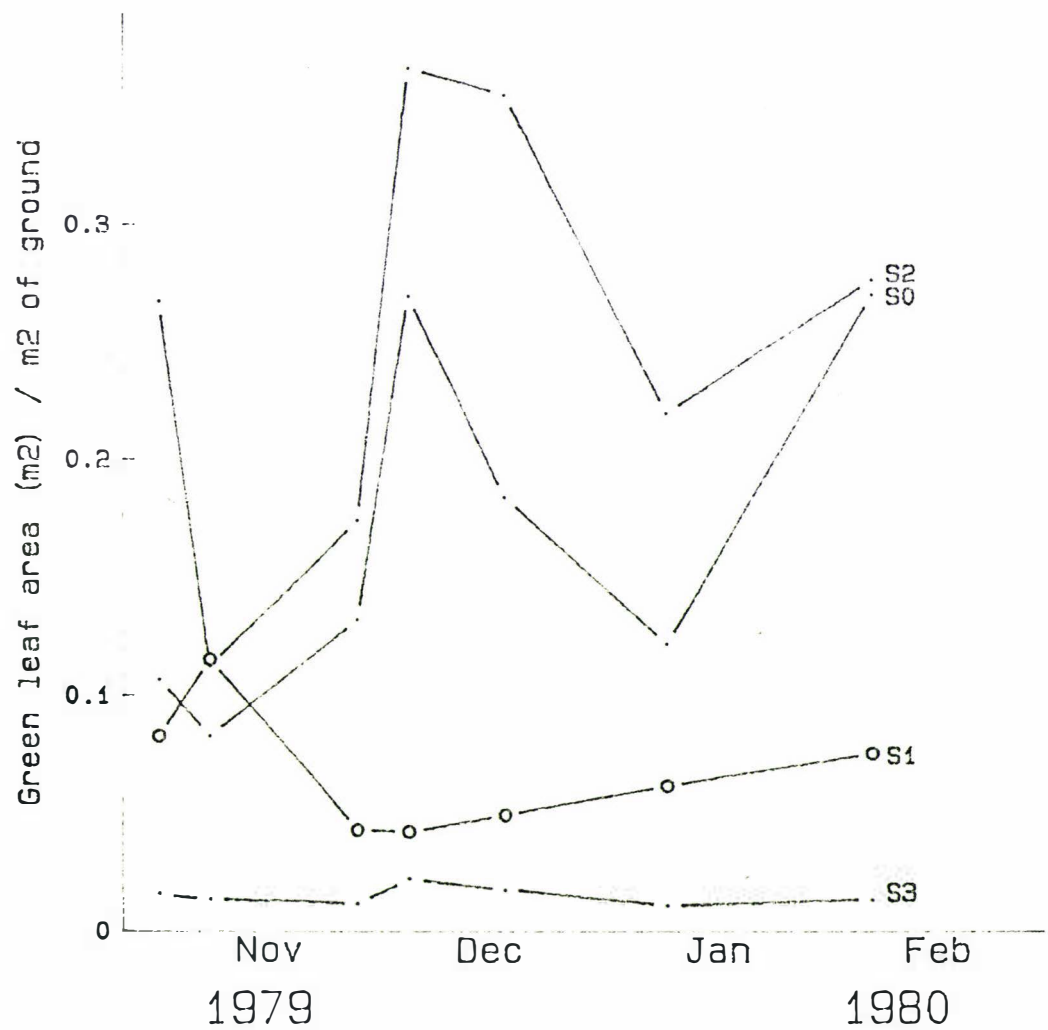
Ogden (1974a) predicted that for the rhizomatous perennial Tussilago farfara, the density of flowering shoots in one season would be closely related to the number of vegetative shoots in the preceding year. His data showed this was approximately the case, at least in some of his experimental treatments. The data for Carex pumila were equally equivocal. Where the populations were mature or early senile (as at S2 in each year of the study, S1 in 1979-80 and 1980-81 and S0 in 1980-81) this relationship was approximated. However, where the Carex pumila populations were in a more advanced stage of senility (S3 in 1980-81 and S4 in 1978-79), the density of flowering shoots was significantly less than the potential shown by vegetative shoot density in the previous summer. Net mortality of the following years potentially reproductive shoots over later summer, autumn, winter and following spring in the more senile populations accounts for this decline. The reduced density of fertile shoots in the adolescent populations on the low dune at S1 in 1978-79 was accounted for by the massive spring mortality of shoots associated with sand accretion on the low dune between August and October 1978. This fertile shoot density did however represent almost 50% of the surviving October population.

4.3.2 Leaf area

The green laminar area per unit ground area (leaf area index, LAI) of vegetative shoot populations monitored in summer 1979-80 ranged between 0.01 and 0.364 at S3 and S2, respectively (figure 4.5).

The LAI of vegetative shoots at S3, which remained less than 0.022 throughout the summer, was significantly lower than that at each of the other sites, at which LAI values were remarkably similar in

Figure 4.5 Green leaf area of vegetative shoots of *Carex pumila* per unit area of ground at four sites on the study area in summer 1979-80



early November (figure 4.5). The LAI of vegetative shoots generally increased over the summer at these three sites, paralleling the changes in shoot density (figure 4.2).

As fertile shoots mature, their green leaf area declines (section 4.3.5). At the beginning of summer 1979-80 (in November), the LAI of fertile shoots was estimated at 0.033 and 0.123 at S3 and S2 respectively. By early February 1980, the LAI of fertile shoots had declined to less than 0.013 at both sites.

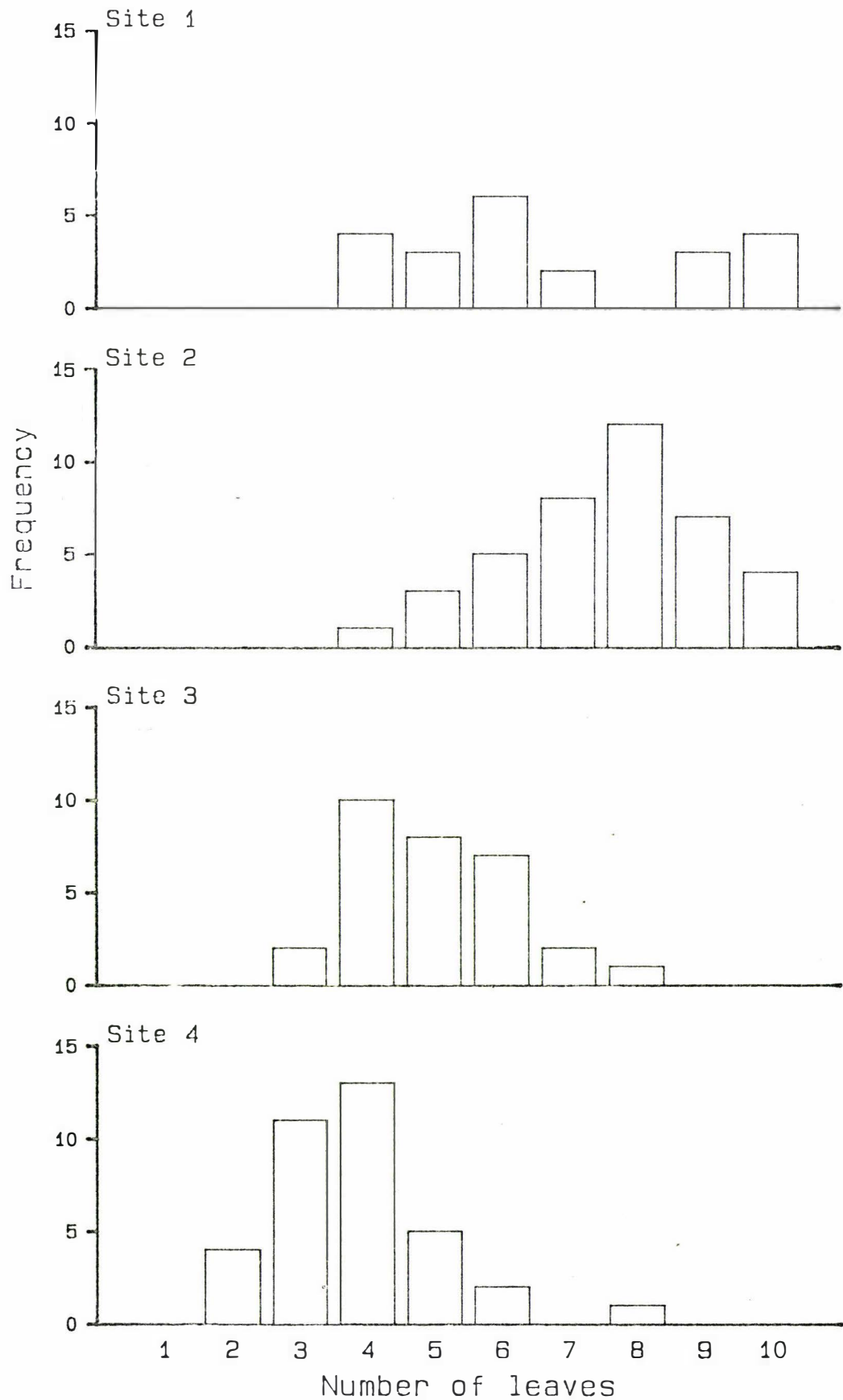
4.3.3 Age and size of shoot populations

1. Shoot size distributions

The frequency distribution of the total number of leaves per dead Carex pumila shoot at four sites in September 1979 (figure 4.6) shows that shoot mortality occurred in the progressively more senile populations when shoots possessed fewer leaves. This indicates lesser longevity of shoots and/or a less rapid rate of leaf production in the more senile populations.

Since variable numbers of leaves were produced by shoots by the time of shoot death, both within and between sites (figure 4.6), the absolute numbers of leaves per living shoot could not be taken as a satisfactory guide to shoot age. A better approximation was the ratio of the number of dead leaves to the total number of leaves per shoot. Shoots with few or no dead leaves suggested a young shoot with long life expectancy, produced a low dead/total leaf ratio value and so fell into the younger age classes. Shoots with predominantly dead leaves, suggested an older shoot with a shorter life expectancy, produced a high dead/total leaf ratio value and so fell into the older

Figure 4.6 The frequency distribution of the number of leaves per lead shoot at four sites in September 1979



age classes. As aerial shoots of Carex pumila emerged above the surface of the soil they were enclosed by scale-like leaves (bracts). These shoots were placed into age class 0 distinct from those older shoots which possessed expanded green leaf laminae, but no dead leaves (dead leaf to total leaf ratio = 0, age class 1).

2. Shoot age distributions

Figure 4.7 shows the age distributions of populations at each of five sites on the study area between September 1979 and December 1980. Notable features of this figure are:

1. In autumn/winter: the skewed (to the right) shape of the juvenile populations at S0 on the edge of the low dune in both years; the distinctly bimodal age structure of the more mature populations at S1 and S2 in both years; and the flattened (platykurtic) age distribution in the senile populations at S3 in both years and at S4 in 1979.
2. In the early spring: the rejuvenescence (skewing to the right) in all populations suggesting new vegetative shoot recruitment and/or mortality of old shoots.
3. Later in spring/early summer: the identification of fertile shoots within the more aged shoot classes.
4. During the summer (1979-80): the movement of the fertile shoot cohort at each site into the older age classes. A similar ageing of the vegetative shoot populations at each site was also apparent.

The living shoot population in the old hollow at S2 in July 1980 showed a bimodal age distribution of predominantly old, long shoots and predominantly young, dwarf shoots (figure 4.7). The young dwarf shoot age class in July, which included many shoots with up to four

Figure 4.7 Frequency distribution of age classes of Carex pumila shoots at four sites on the sand plain

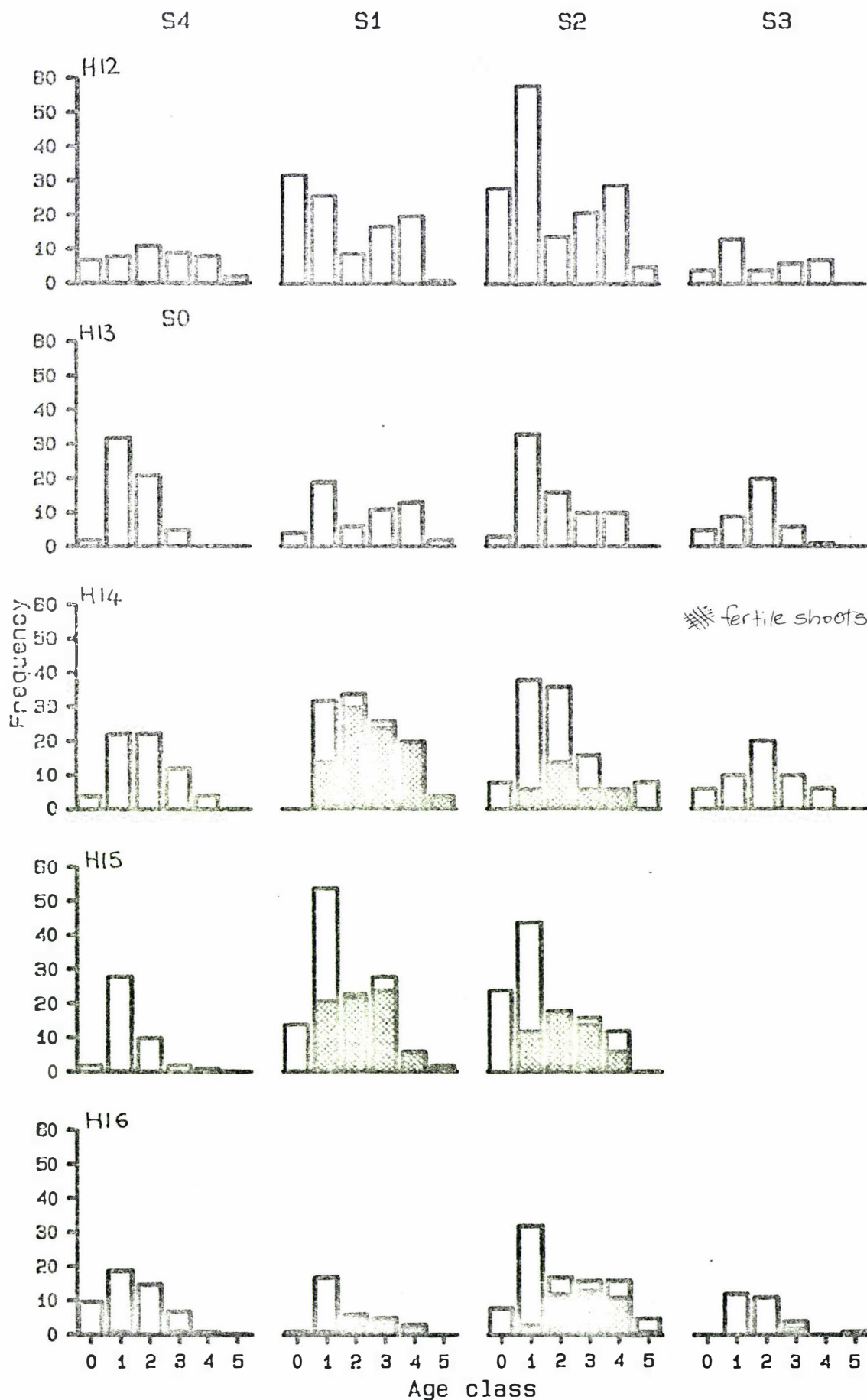


Figure 4.7 Age class distributions continued.

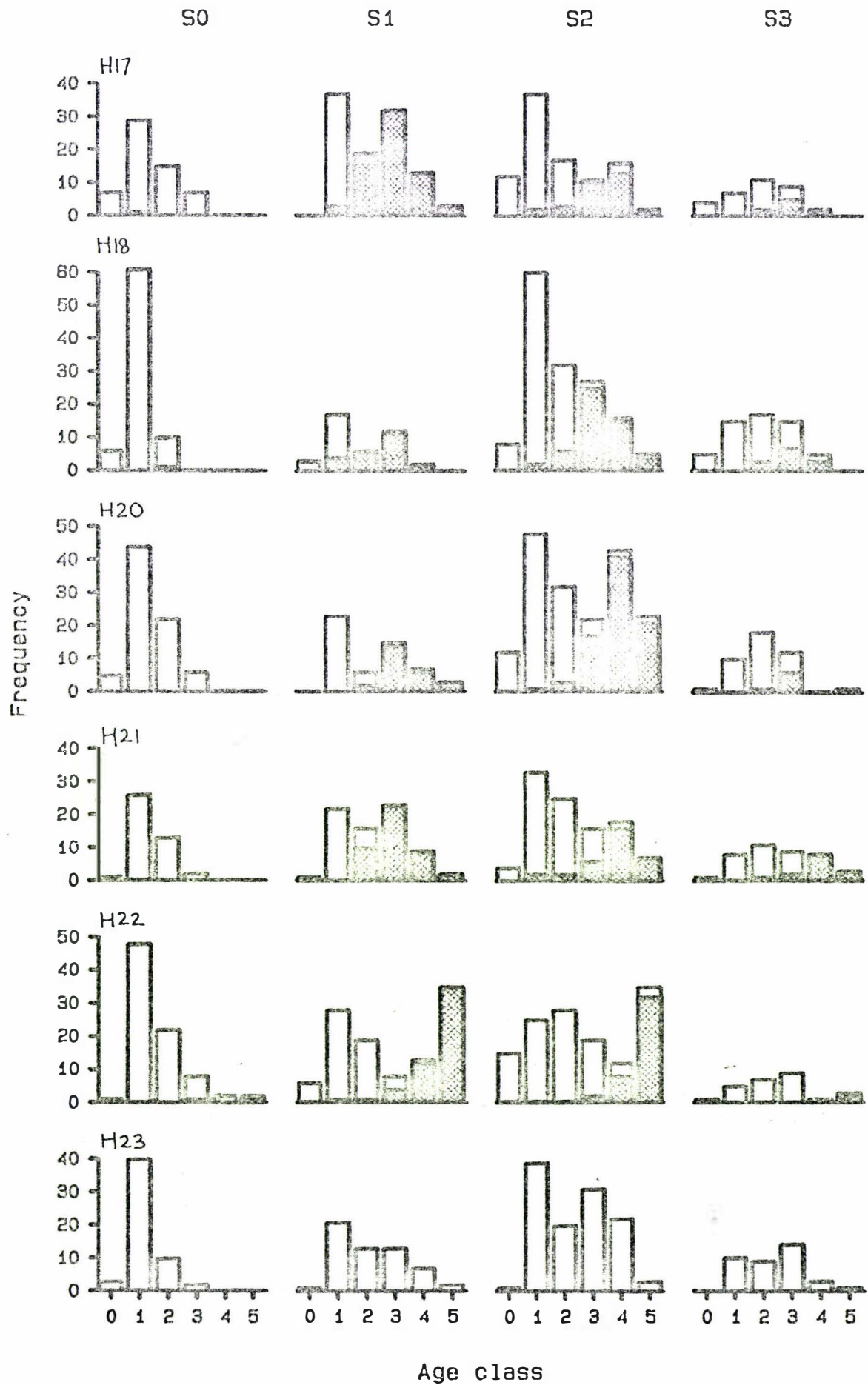
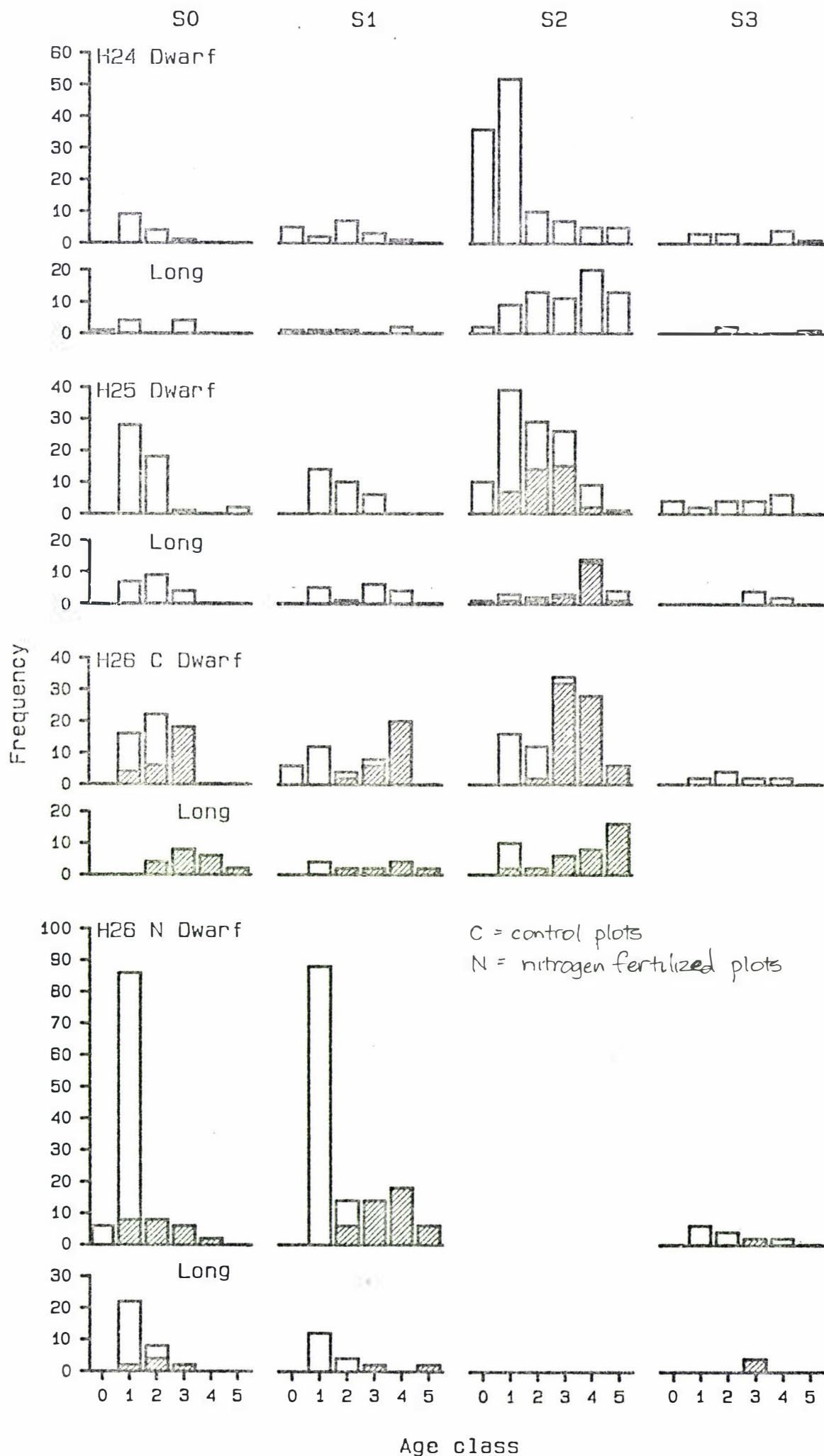


Figure 4.7 Age class distributions of shoots continued

140c



green leaves, accounted for the older vegetative dwarf shoot classes and the dwarf fertile shoot category three months later, in spring. The young age class of dwarf vegetative tillers in October 1980 included many new recruits since winter showing no leaf lamina expansion.

In midwinter 1980, no significant differences in mean age were observed between site populations averaged over all shoots (table 4.3). However, the data suggest that the population at S3 was more senile than the others. This difference became significant by October ($P < .05$, table 4.3). In October 1980, it was possible to identify fertile shoots at S2, which were significantly older than vegetative shoots ($P < .001$, mean age = 0.429 and 0.265, respectively).

Table 4.3 Mean age (ratio of dead to total number of leaves per shoot) at four sites on the sand plain, in winter and spring 1980.

	Mean ($\pm$ SE)	
	July	October
Site 0	0.222 $\pm$ 0.034b	0.193 $\pm$ 0.02 b
Site 1	0.292 $\pm$ 0.042b	0.287 $\pm$ 0.031b
Site 2	0.235 $\pm$ 0.045b	0.326 $\pm$ 0.025ab
Site 3	0.371 $\pm$ 0.059ab	0.408 $\pm$ 0.043a

a > b, $P < .05$

In July, more than 40% of shoots at S3 fell into the two oldest age classes (figure 4.7). Living shoots with fewer than five leaves cannot be included in the oldest age class 5. Thus, populations such as that at S3, where the total number of leaves per shoot was only infrequently greater than five, are likely to be under-represented in this oldest age class.

Dwarf shoots fell into lower age classes than long shoots at all sites in midwinter (July) 1980 (figure 4.7). This difference between long and dwarf shoot populations continued to be observed in both spring (October) and summer (December) 1980. However, the ultimate size that could be obtained by a shoot was not restricted by the type of rhizome segment to which it was attached. Shoots with the maximum number of leaves counted (11) and in the largest size category (collar height >20cm) were found attached to both long and dwarf rhizome branches.

As the populations aged at each of the four sites monitored during the second half of 1980, site differences emerged. New shoot recruitment between July and October at S0 and S1 on the low dune resulted in the mean age of these two populations averaged over all shoots in October remaining similar to that seen in July. By contrast on the old hollow at S2 and more markedly at S3, mean age increased over this period. At S2 in October, shoots that were seen to be fertile were on average older than the vegetative shoot population. However, the most senescent shoots (age class 5) were predominantly vegetative, in both dwarf and long shoot categories (figure 4.7). Aged vegetative shoots were absent from the living shoot population in December 1980.

By December 1980, the only shoots in the two oldest age classes were fertile except in the most senile population at S3. At all sites, vegetative shoots were predominantly those attached to dwarf as opposed to long rhizome modules and, with the exception of those at S3, predominantly young (figure 4.7). The increasing contribution of dwarf shoots to the total with increasing age was also shown in table 3.8 with the increasing age of the clone back along a single rhizome axis from the tip.

4.3.4 Dry weight, energy and crude total nitrogen per unit area of ground

1. Dry weight

As a pioneer of a primary succession, Carex pumila forms more or less monotypic patches. I have coined the term sward mass to express the dry weight of these swards at a given time. Sward mass includes both above- and below-ground parts of both living and dead material of the total vegetation. Figure 4.8 shows the sward mass obtained at four sites on the study area in January 1978. Although the bulk of the vegetation at all of these sites was Carex pumila, other species progressively increased proportionately at sites of greater putative age, at increasing distances from the terminal hollow.

The estimated age of the vegetation at S1 in January 1978 was 0-5 months (section 3.2.2). The sward mass at this site, which entirely comprised living shoots of Carex pumila, was low. The difference between this and each of the other three older sites could be attributed to the greater opportunity (time) for accumulation of dry matter. The decreasing suitability of the older deflation hollow sites for growth of the pioneer, Carex pumila, was reflected in (1) the decreased sward mass, (2) the increased proportion in other species (figure 4.8), (3) the decreased aerial biomass of Carex pumila and (4) the increased proportion of herbage mass of this species contributed by dead shoots (figure 4.9).

Dead aerial shoot modules of Carex pumila are continually being lost through decomposition and removal by wind and other disturbance factors. Thus, their herbage mass can be expected to be reduced at the older deflation hollow sites, since this will tend to reflect the herbage mass of living shoots of the species (figure 4.9). A

Figure 4.8 The sum of the sward mass of Carex pumila and other species, at each of four sites on the sand plain near Tangimoana, in January 1978.

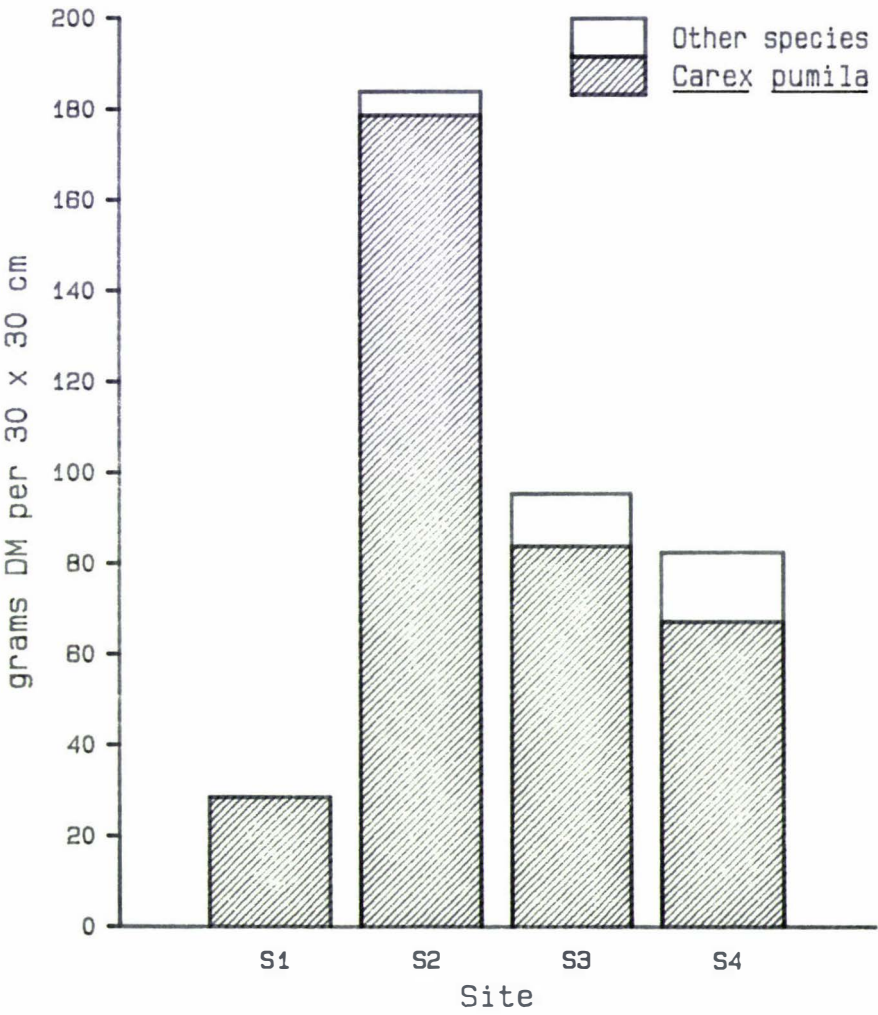
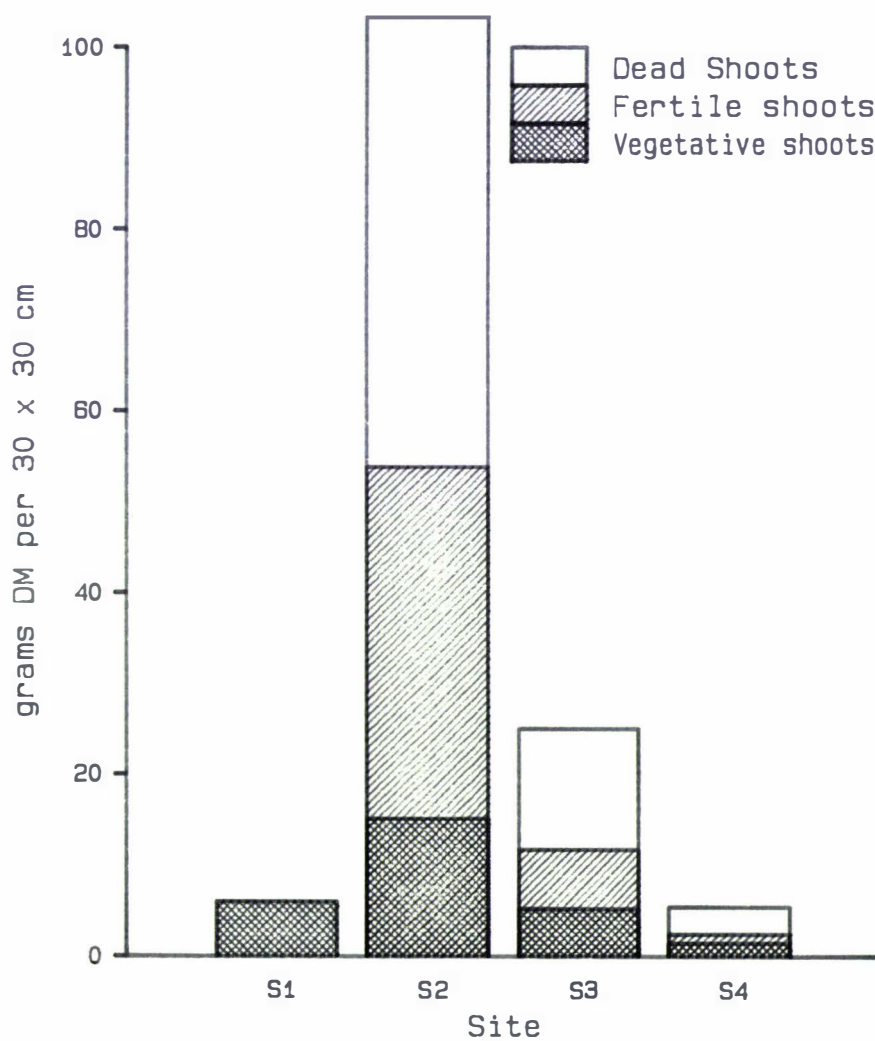


Figure 4.9 The sum of the herbage mass of vegetative, fertile and dead shoots of *Carex pumila* at four sites on the sand plain, in January 1978.



relatively slower rate of loss of underground parts than of aerial parts, through slower decomposition rates and/or the absence of removal by wind as a factor, would result in the greater accumulation of roots and rhizomes relative to herbage. This accounts for the difference in shape of the plots of sward mass and herbage mass for this species across the sand plain (figure 4.8 and 4.9 respectively). The shape of these plots, like that of shoot densities (figure 4.1), are suggestive of the n-shaped curve described by Watt (1947) expressing "the general course of change in total production" for vegetation displaying phasic development.

Living shoot populations of Carex pumila at these four sites, monitored at the beginning of the study, were also clearly distinguished by the mean size of aerial shoot modules (figure 4.10). Figure 4.10a described an n-shaped plot similar to that seen for herbage mass of these same live shoot populations (figure 4.9). Fertile shoot modules were on average larger than vegetative modules (figures 4.10a and b), indicating the greater average age of the former. This however, masks the diversity of both size and age of individuals within these populations (figure 4.7). Inclusion of roots and rhizomes in the comparison of mean size of branch modules results in the disappearance of the distinction between the juvenile (S1) and mature (S2) populations (figure 4.10b).

Figure 4.11 shows the standing herbage mass of living shoots of Carex pumila (aerial biomass, AB) at sequential harvests at each of four sites on the study area during 1978 and 1979. From aerial biomass and shoot density, the dry weight of aerial shoot modules at each site was calculated at each harvest and also plotted over time (figure 4.12). In spring and summer, fertile shoots were shown

Figure 4.10(a) The mean dry weight per aerial shoot module of Carex pumila at four sites on the sand plain in January 1978; for (i) vegetative, (ii) fertile and (iii) dead shoots (Vertical bars denote $\pm$ standard deviation)

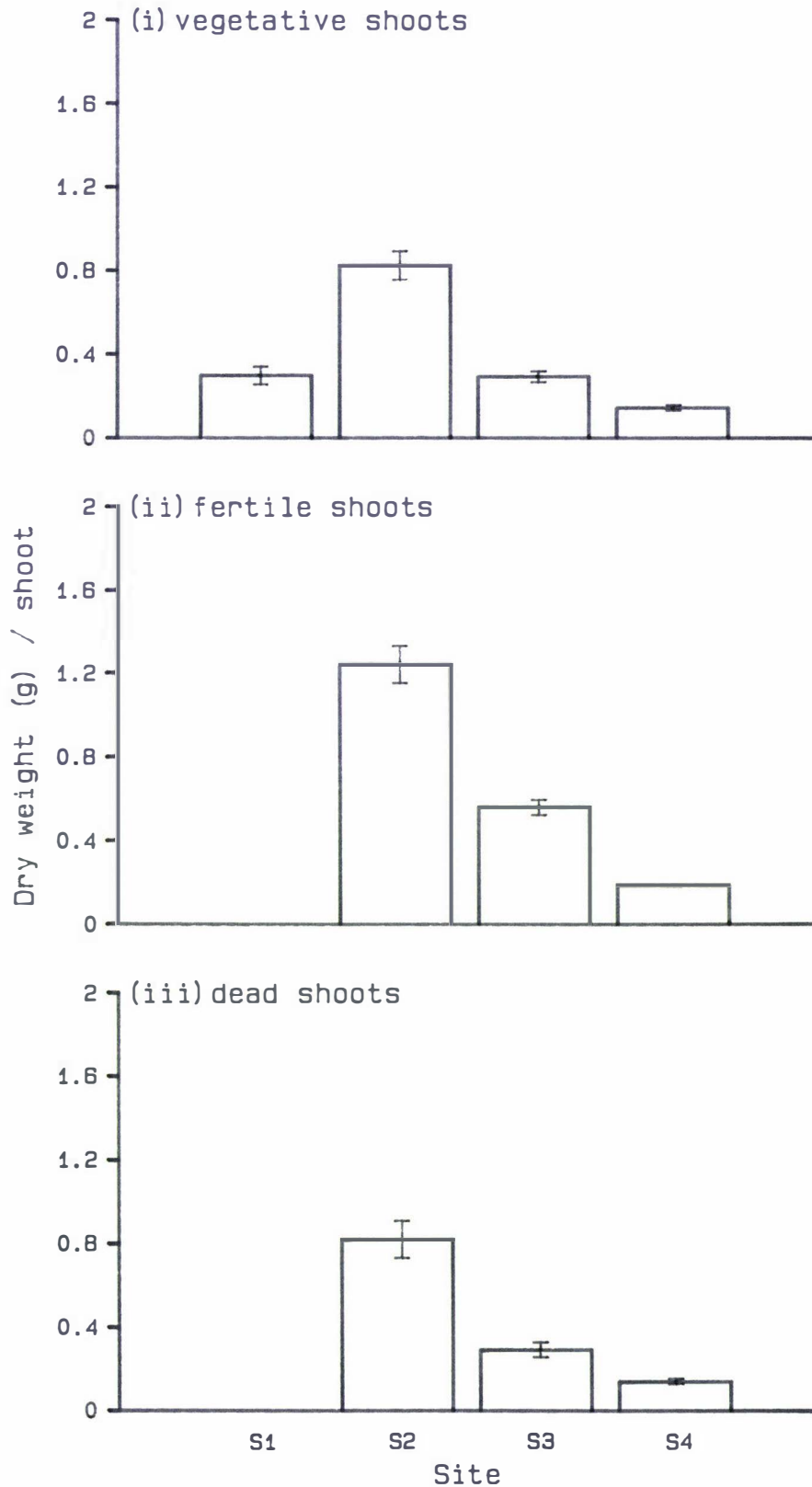


Figure 4.10(b) The mean dry weight per branch module (including underground parts) of *Carex pumila* at four sites on the sand plain in January 1978; for (i) vegetative and (ii) fertile shoots.

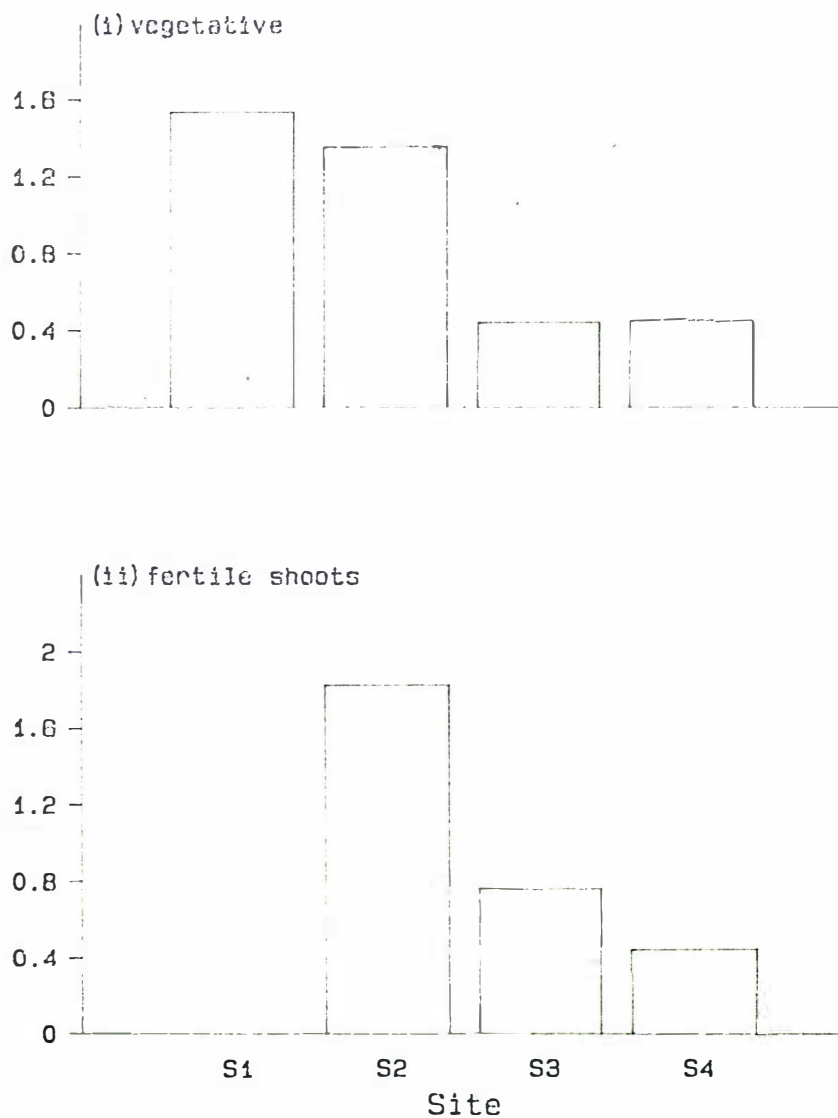


Figure 4.11 The sum of the aerial biomass of fertile and vegetative shoots on the sand plain, during 1978 and 1979

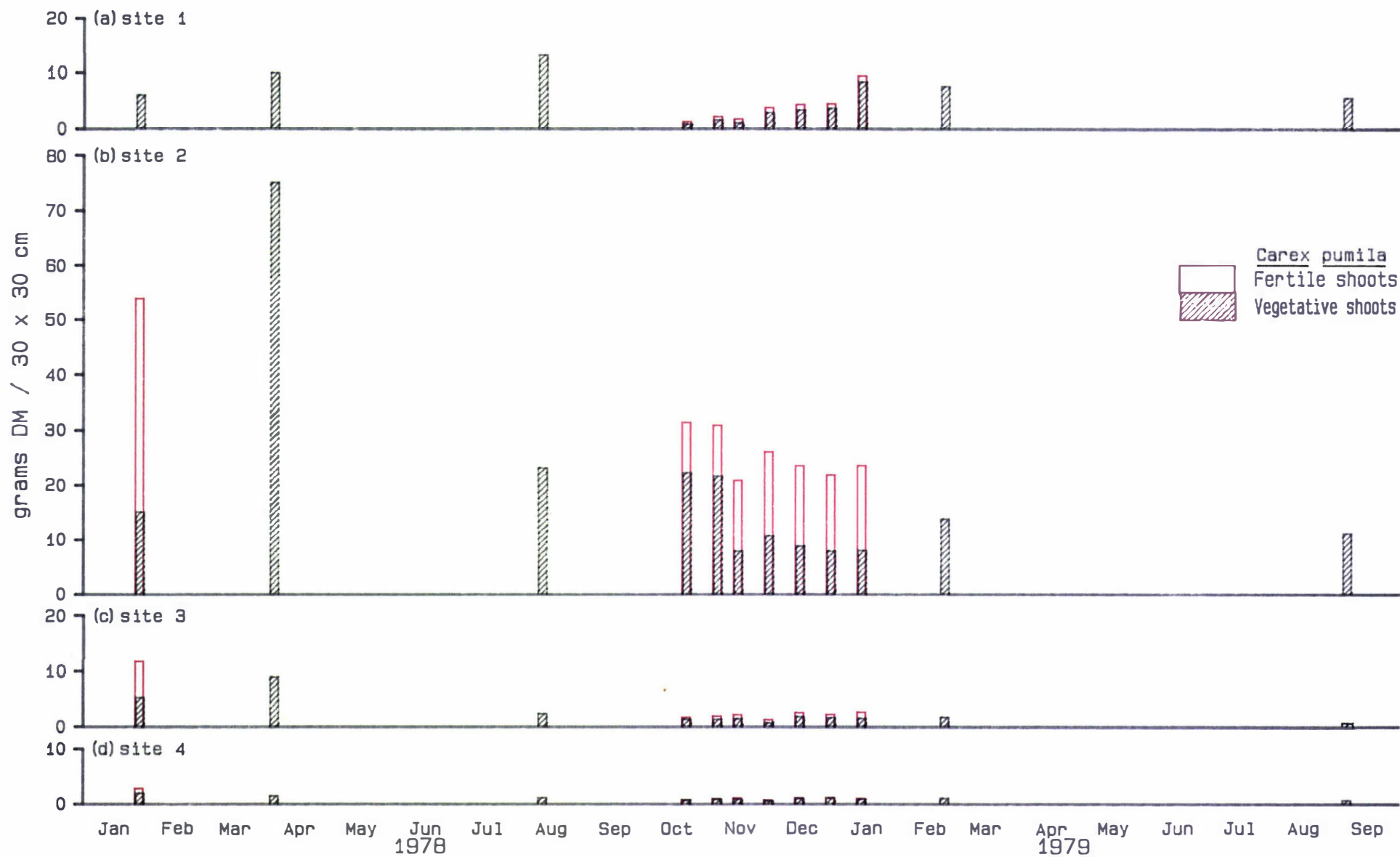


Figure 4.12 (a) Distribution of the aerial biomass per fertile shoot of *Carex pumila* to component parts over time at four sites during summer 1978-79

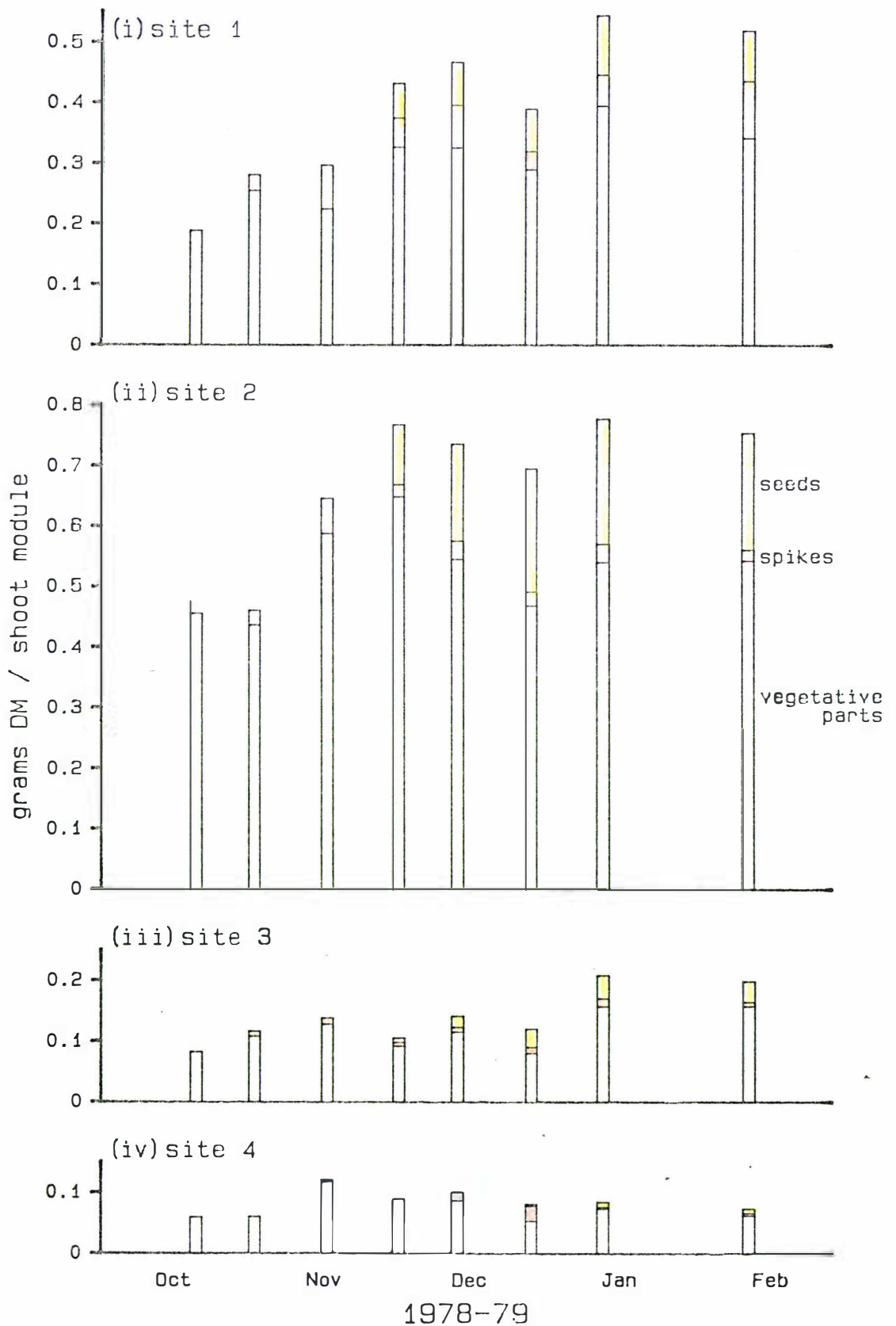
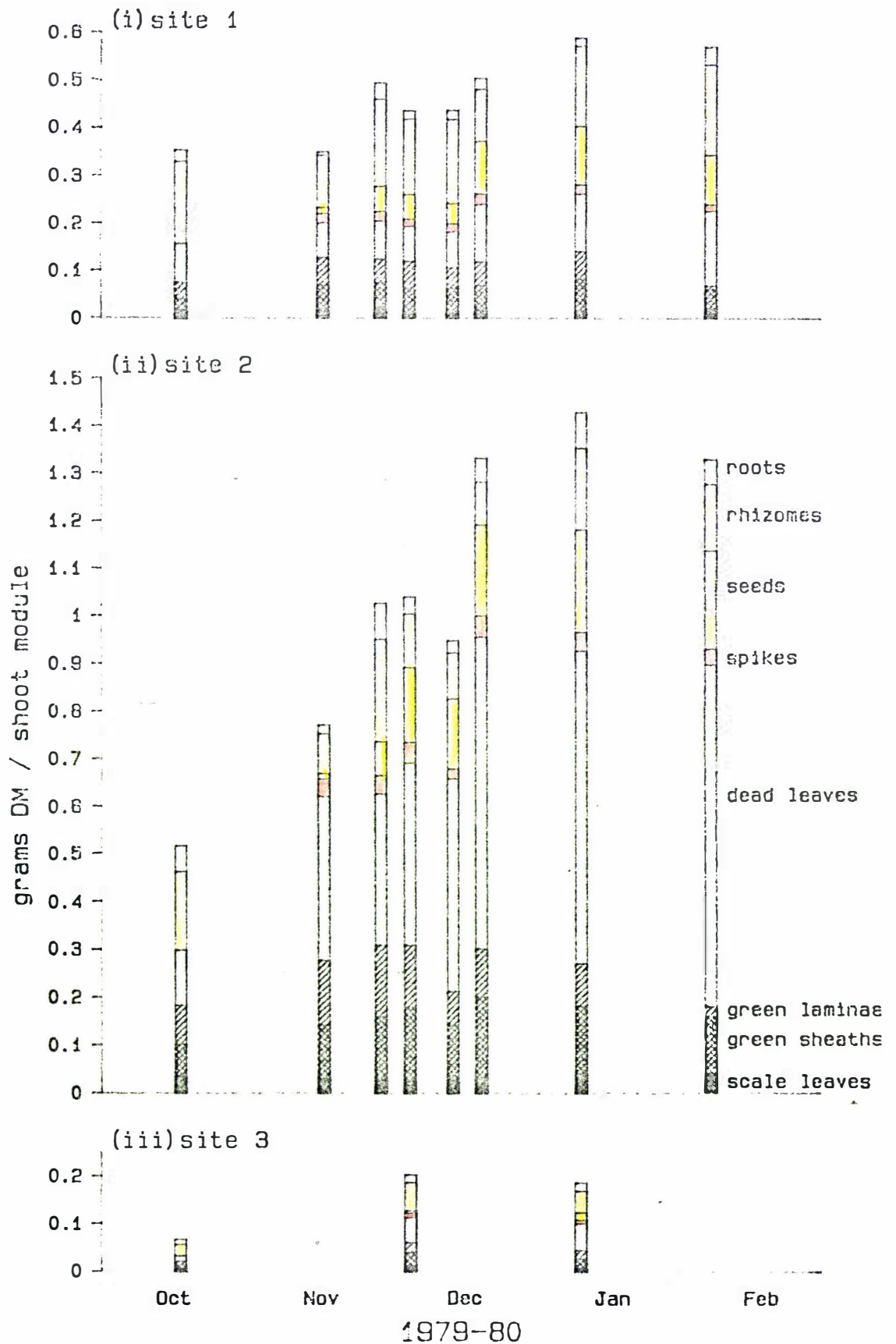


Figure 4.12 (b) Distribution of the biomass per fertile shoot of *Carex pumila* to component parts over time at three sites during summer 1979-80



separately from vegetative shoots in both figures 4.11 and 4.12. For those intervals that standing aerial biomass increased over time (figure 4.11), the mean dry weight per aerial module did not necessarily also increase (figure 4.12). The relative increases in shoot recruitment and growth of newly recruited shoots will account for this discrepancy. At harvests from September 1979, rhizome segments of Carex pumila, with attached adventitious roots, were separated with their aerial shoot portions intact. Thus, total (aerial plus underground) biomass of Carex pumila populations was subsequently followed over time (figure 4.13).

Figures 4.11 and 4.13 show seasonal fluctuations in biomass of Carex pumila. Longer term trends shown in figures 4.11 and 4.13 are similar to the changes in shoot densities of these same populations with time (figure 4.2) and of biomass differences between sites of increasing age at increasing distances from the terminal hollow (figure 4.9). Standing biomass of vegetative shoot populations of Carex pumila increased over autumn at all sites except where the population was in an advanced stage of senility. Increases were also seen in spring and early summer in the total shoot population. The latter increases can be attributed to vegetative shoot recruitment and growth, and to the growth in size of shoots which were fertile (figure 4.12). Net losses of biomass occurred in winter at all sites, except in the most juvenile populations.

Aerial biomass of vegetative shoots increased over autumn 1978, between January and April at each site, except S4 where the Carex pumila population was already in an advanced senile stage of development (figure 4.11). The average size of shoots at S2 also increased (figure 4.12). At S1 where the population was in a juvenile stage of development, the increase in aerial biomass continued to the

Figure 4.13 The sum of the biomass of fertile and vegetative shoots of *Carex pumila* at four sites on the sand plain, during 1979 and 1980

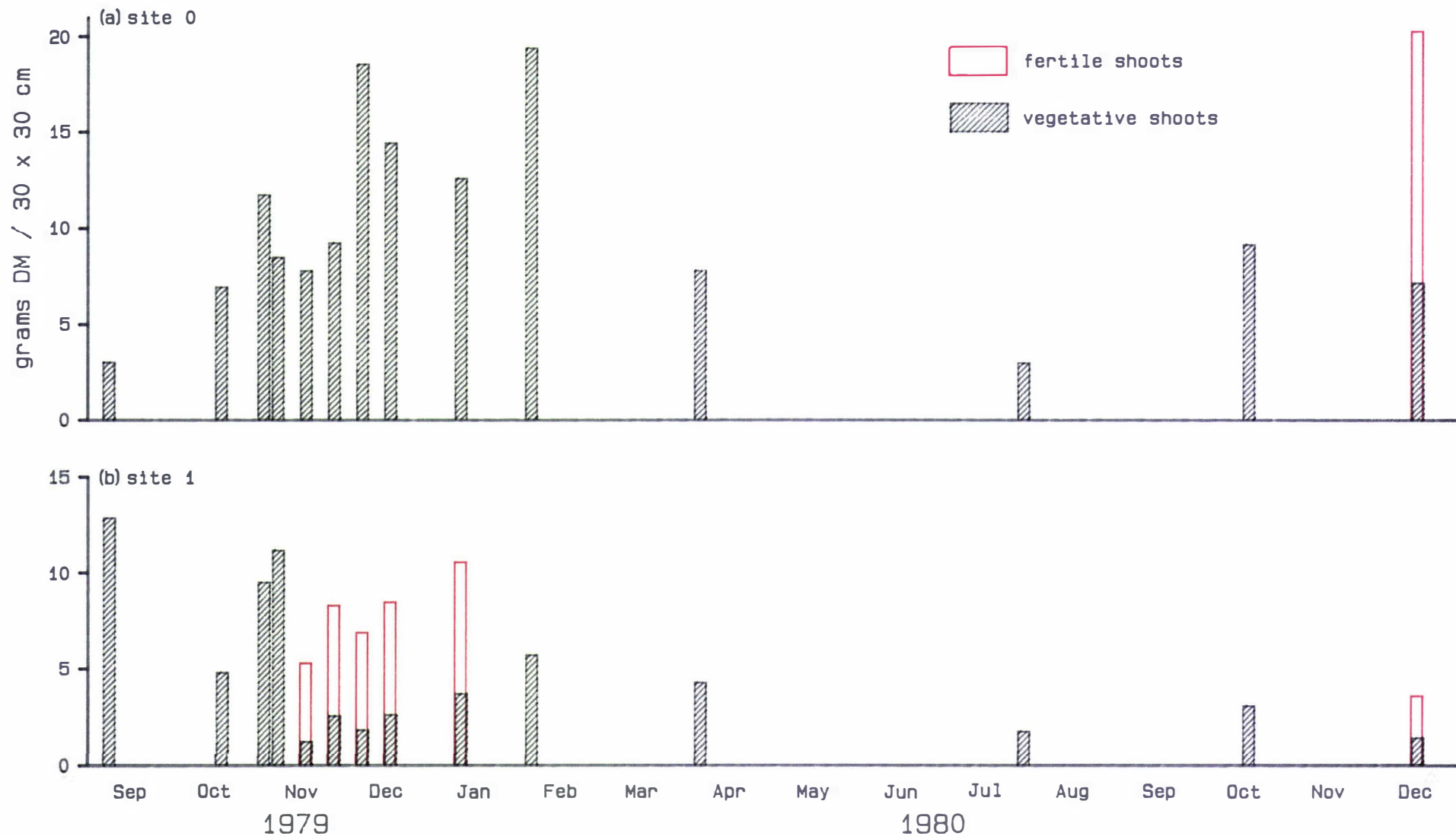
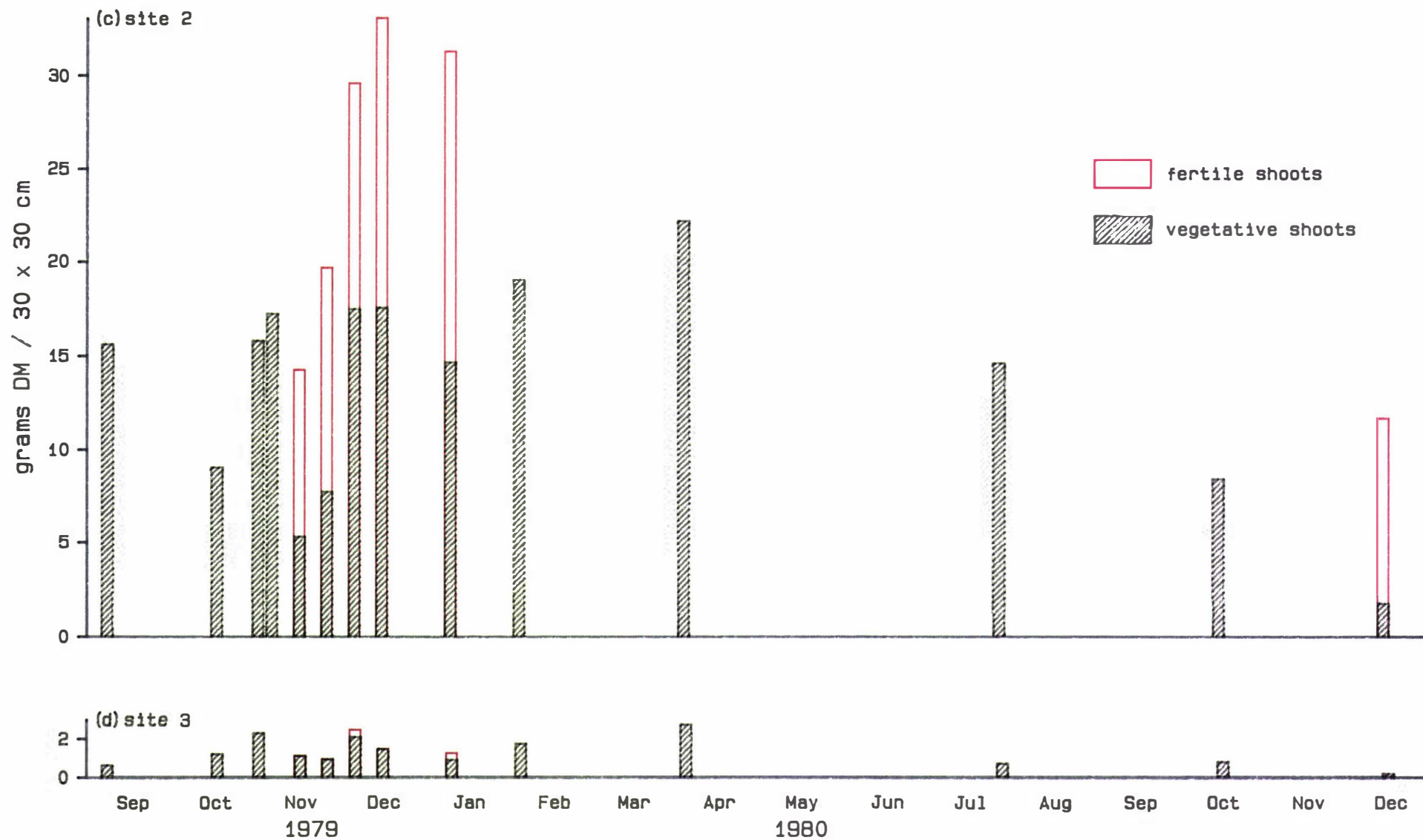


Figure 4.13 continued



end of winter 1978, whereas at the older sites in the damp deflation hollows, a net loss over winter was observed. A net loss of aerial biomass was subsequently observed in early spring 1978 at S1 associated with the inundation of the site by sand. The reduction of aerial biomass of Carex pumila in the deflation hollows (S2, S3 and S4) during the winter and early spring and on the low dune (S1) in early spring 1978 coincided with the mortality of principally old vegetative shoots (sections 4.3.1 and 4.3.3).

Many of the larger, older, living shoots present in the populations in early spring 1978 subsequently proved to be fertile. Figure 4.12 shows the changes in the average size of fertile shoots and of each component organ at each site over time, in summer 1978-79. The increases in mean aerial dry weight per fertile shoot over time can be attributed to increases in both vegetative and fertile fractions (figure 4.12). This may result from the mobilization of resources found in the rhizomatous fraction and/or the assimilation of carbon in both vegetative and fertile aerial shoot parts (section 2.6). From mid-summer, decreases in the mean dry weight of both vegetative and fertile shoot components were observed (figure 4.12). Decreases in the green leaf and stem fractions could be assumed to result from firstly, the senescence of these parts and concomitant increase in the dead leaf fraction and secondly, from the redistribution of resources to seeds. Decreases in dead leaves and in seeds could only be explained by loss.

The standing aerial (vegetative shoot) biomass at S1 in mid-summer 1978-79 was greater than that at either S3 or S4 and remained so during autumn and winter 1979 despite the net loss of herbage over this period at all of these sites (figure 4.11). The standing aerial biomass of Carex pumila was greater at S2 than at any

of the others, throughout the entire 20-month period shown in figure 4.11. This can be attributed firstly, to the larger net accumulation of herbage at this site in autumn 1978 and to a lesser extent in autumn 1979 despite the large losses also recorded, and secondly, to the greater proportionate allocation of biomass to aerial parts at S2 compared with other sites.

Over the period shown in figure 4.11, roots and rhizomes of Carex pumila were bulked for all shoot modules. Estimates of the biomass of roots and rhizomes attached to living shoot modules during this period were made by use of the ratio of the biomass of living to total living plus dead shoot modules (figure 4.14). At those sites where Carex pumila was a recent colonist all branch modules were living and the ratio equalled unity (S1 in January 1978 and S0 in October 1979). As the populations at these sites aged and Carex pumila modules died, an asymptotic decline in the ratio occurred. The ratio showed deviations from strict curvilinearity reflecting the balance of shoot births and deaths, and of decomposition and biomass accumulation.

At the late winter 1979 harvest, the standing biomass values of the Carex pumila populations at S1 and at S2 were similar (figure 4.13), despite the difference seen in figure 4.11 for standing aerial biomass. Total biomass at S1 and S2 was significantly ($P < .001$) greater than those values obtained elsewhere on the sand plain, at S3 and S4. Since biomass estimates in the two most aged Carex pumila populations were low, and reduced compared with the previous year, it was decided to discontinue harvests at one of these, namely S4.

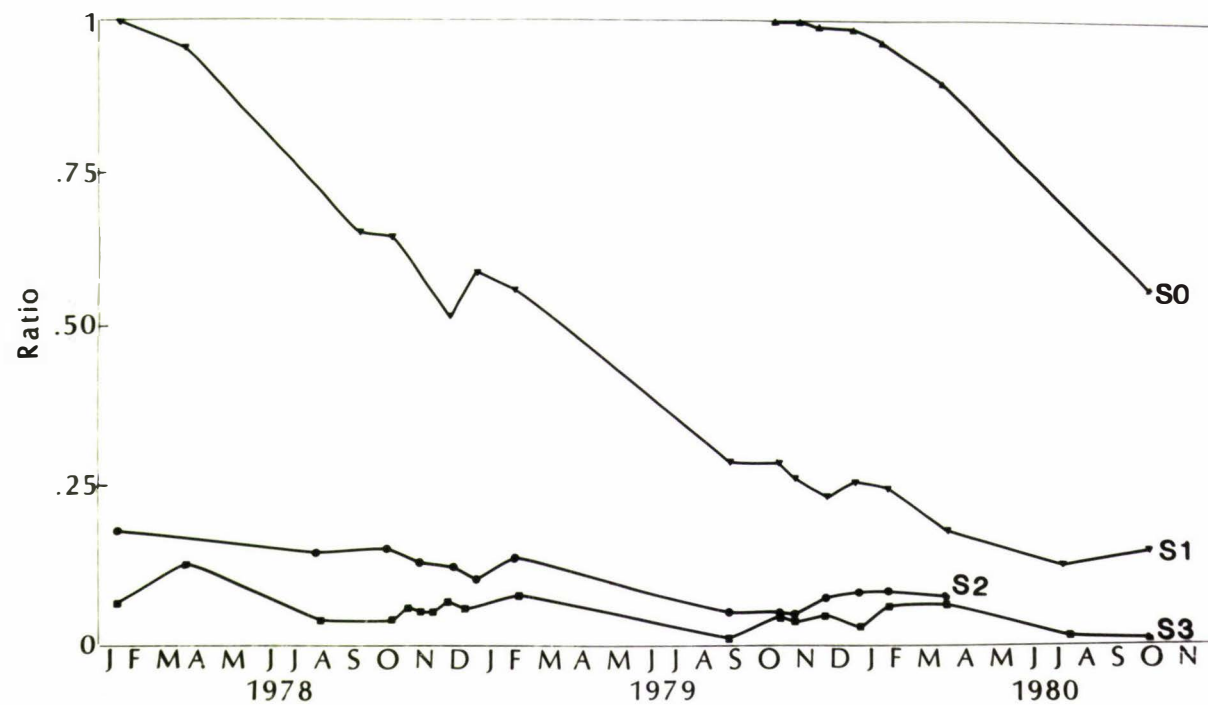


figure 4.14 The ratio of the dry weight of living to total (living plus dead) shoots of *Carex pumila* over time, at four sites on the sand plain

The net losses of biomass observed at all sites over the winter of 1979 in the aerial shoot fraction (figure 4.11), continued into the spring to mid-November 1979. These reductions seen in total biomass of living shoots between harvests at S1, S2 and S3 (figure 4.13) can be attributed to the mortality of principally older, larger vegetative shoots (see section 4.3.1 and 4.3.3) and mirror those described for aerial biomass during winter/early spring 1978 (figure 4.11). The subsequent spring 1979 and summer 1979-80 net increases in biomass of the vegetative shoot population at each site monitored (figure 4.13) also mirrored those seen for aerial biomass twelve months previously (figure 4.11).

At S0 not previously monitored, the net increases in biomass over spring and early summer 1979-80 resulted in the summer mean standing biomass of this juvenile population being similar to that found in the old hollow at S2 (figure 4.13). The S2 population was still distinguished however, by the standing crop of fertile shoots (figure 4.13). Fertile shoots were found only in some plots and at some of the summer 1979-80 harvests in this young population at S0. The vegetative shoot biomass at S1 and S3 in mid-summer 1979-80 was significantly reduced compared with that at both S0 and S2. The populations at S1 and S3 could also be distinguished from each other by the biomass of fertile shoots (figure 4.13).

During 1980, further net increases in biomass by vegetative shoots was seen over autumn at all but the newly monitored S0 on the edge of the low dune (figure 4.13). Deposition of wind-blown sand on the edge of the low dune during February 1980 (figure 4.4b) resulted in net loss of biomass at S0 between the late summer (February) and autumn (April) harvests. The Carex pumila population subsequently

observed at this site included numerous new young shoots. Net loss of biomass in early winter 1980 (April-July) was also evident higher on the low dune at S1 and on the waterlogged deflation hollow at both S2 and S3.

In winter and spring 1980, the living shoot population of Carex pumila at each site was divided into those attached to dwarf and long rhizome modules, and in the subsequent summer, each of these two types of shoot was further divided into fertile and vegetative modules. The mean size of the long shoot type was consistently higher than that of the dwarf type both on the basis of total (aerial plus underground) and aerial dry weight per branch module, throughout the period July to December 1980 (figure 4.16). This difference can be related to the relative ages of these populations (figure 4.7). The maximum size that could be obtained by an individual shoot attached to either a dwarf or long rhizome module was the same (section 4.3.3).

In July 1980, the biomass of dwarf and long shoots per unit area of ground was greater at S2 than at any of the other sites (figure 4.15), as a result of the density of each of these two types of shoots. The mean dry weight per shoot module for both dwarf and long shoots was no different between S2 and any of the other sites (figure 4.16), despite differences in age structure (figure 4.7).

In 1980, the now familiar spring/summer net increase in population biomass of Carex pumila began earlier on the low dune at S0 and S1 than on the deflation hollow (figures 4.13 and 4.15). The increased stability of the low dune in 1980 as a result of the planting of Ammophila arenaria on the surrounding dunes (figure 3.4) accounted in part for this difference. The increasing senility of the populations on the deflation hollows and the high water table in late

Figure 4.15 The sum of the biomass of dwarf and long shoot populations of *Carex pumila* (grams DM / 30 x 30 cm) over time at four sites on the sand plain between July (winter) and December (summer) 1980

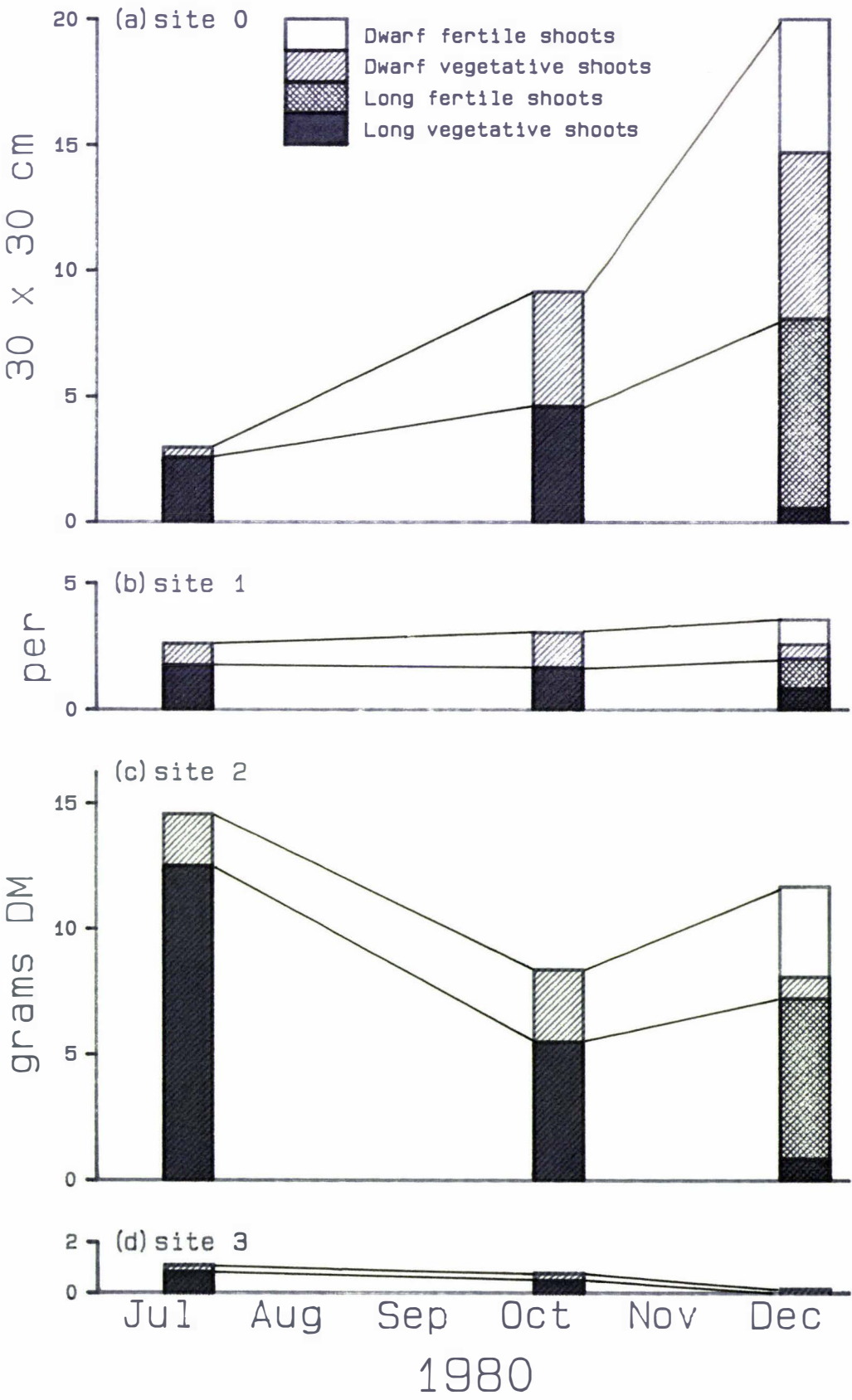


Figure 4.16 The distribution of biomass of component parts of (a) dwarf and (b) long branch modules of *Carex pumila* at four sites on the sand plain in July, October and December 1980

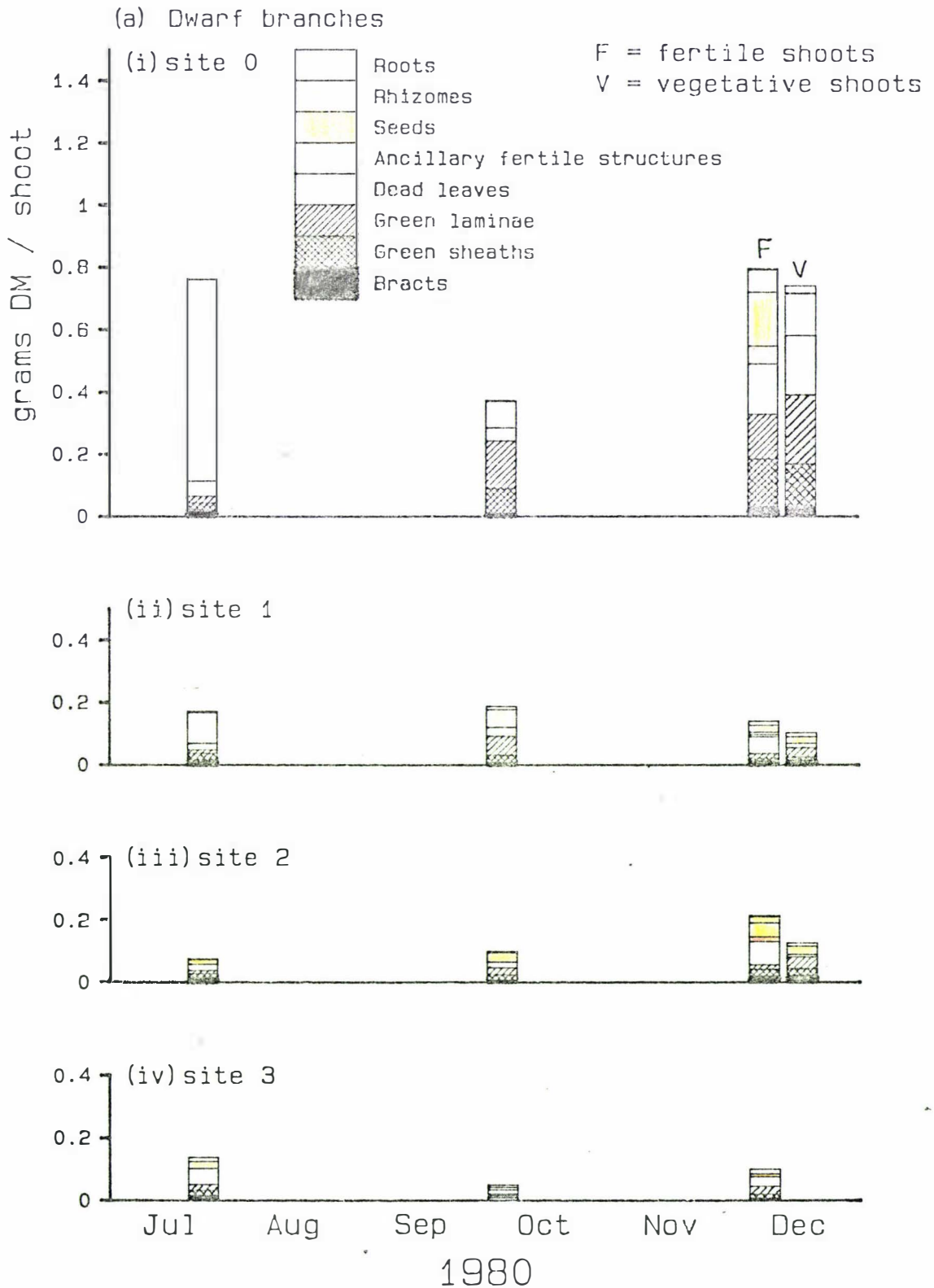
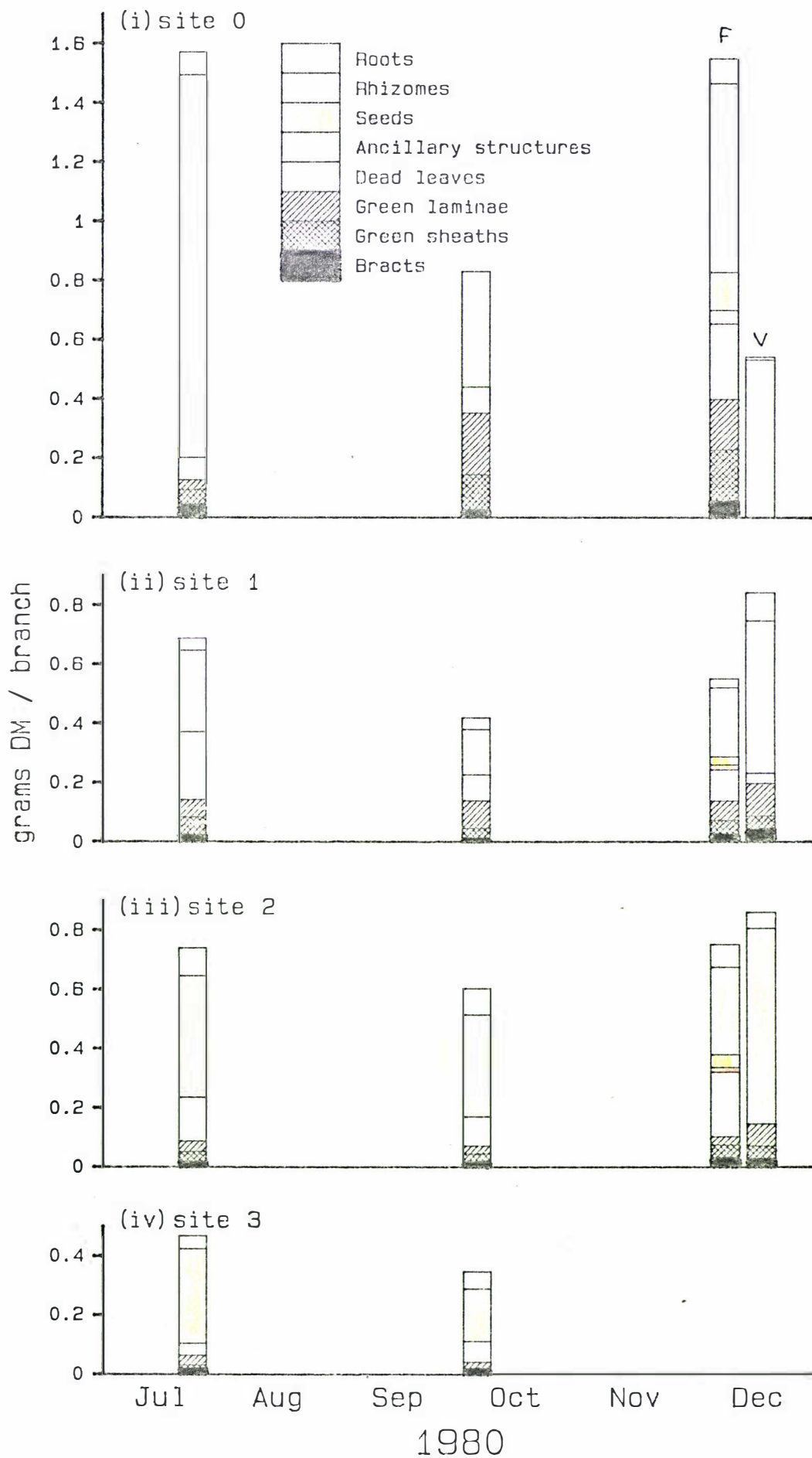


Figure 4.16 continued

(b) Long shoots

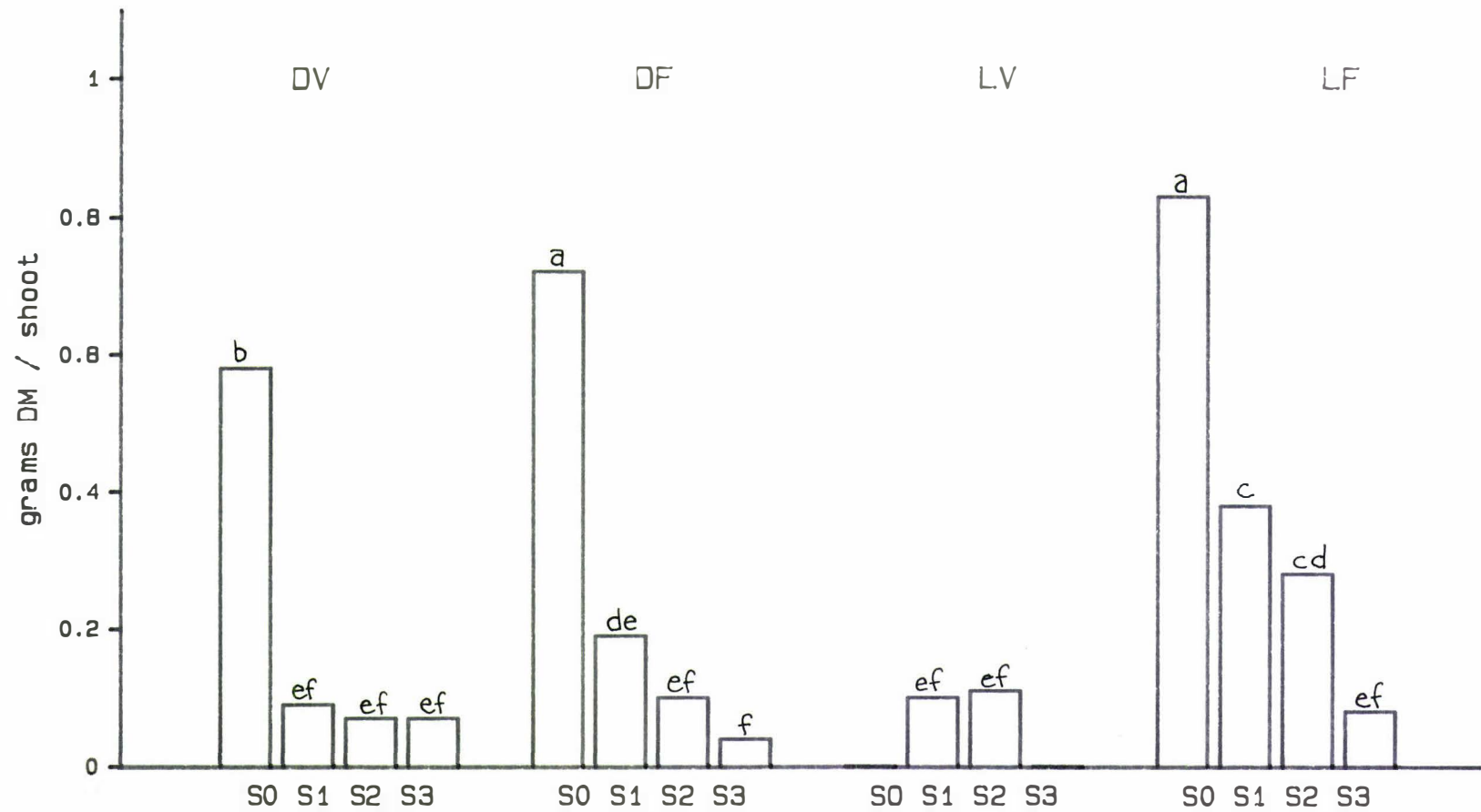


winter also contributed to this difference. The net biomass increases in the two older populations at S1 and S2 were small in both the dwarf and the long shoot components (figure 4.15).

By contrast, the increases in the younger population at S0 occurred at a higher rate than elsewhere on the sand plain, especially over the late spring/summer period from October to December 1980 (figure 4.15). The increases at S0 between July and October 1980 in both long and dwarf shoot components (figure 4.15) resulted from an increase in densities of these two shoot types (figure 4.3) and also from an increase in the average size of dwarf shoots (figure 4.16). The October-December 1980 increases (figure 4.15) were largely attributable to the increase in mean size of both dwarf and long shoots (figure 4.16). Thus, the standing biomass of Carex pumila at S2 was surpassed for the first time in the present study by that at another site, namely S0 (figures 4.13 and 4.15).

In December 1980, the mean dry weight per aerial shoot module was affected not only by the type of shoot (dwarf versus long) but also by their sexual state (vegetative versus fertile), by site (figure 4.17) and by nitrogen fertilizer addition (section 4.3.7). Averaged over the four sites, mean size of fertile shoots was greater than that of vegetative shoots ($P < .01$) and long shoots greater than dwarf shoots ($P < .01$), effects attributable to the relative ages of these shoot populations (figure 4.7). On the control plots (no added fertilizer) at the four sites studied, the mean size of aerial shoots was significantly greater at S0 than at all other sites, for each shoot category represented at S0 ($P < .001$; figure 4.17). These differences may also be a difference in the mean age of shoots. The age distribution of dwarf vegetative shoots at S0 in December 1980 indicated an older population than that at other sites (figure 4.7).

Figure 4.17 The mean aerial dry weight per shoot of dwarf (D) and long (L), fertile (F) and vegetative (V) shoot modules of *Carex pumila* at four sites on the sand plain in December 1980. Letters (a-f) refer to Duncan's multiple range test.



In summer 1979-80, no direct evidence was obtained for the redistribution of resources stored in rhizomes attached to fertile shoots during flowering and seed production. Over this period, no change was observed in mean dry weight of rhizomes per fertile shoot (see ^{above} ~~below~~, figure 4.12^b). Further, the mean dry weight of the rhizome fraction per branch module was no different between rhizomes attached to vegetative and to fertile shoots (table 4.4). These observations support the view that the rhizome of Carex pumila acts not so much as a storage organ releasing accumulated carbon to other shoot parts, but more as a migratory organ like that of other "creeping" sedges (Salisbury 1942) allowing local colonization and resource capture.

Table 4.4 Mean dry weight per rhizome segment attached to fertile, vegetative and dead shoots at four sites on the sand plain in summer 1979-80.

Shoot category	grams DM / branch			
	S0	S1	S2	S3
Vegetative	.446 a	.157 b	.139 b	.063 b
Fertile	-	.156 b	.129 b	-
Dead	.42 a	.564 a	.42 a	.565 a

a > b; $P < .001$; Duncan's multiple range test.

However, the estimation of mean dry weight of rhizomes per branch module during this summer was complicated, firstly by dwarf and long rhizome segments attached to live aerial shoots not being separated, and secondly by long rhizome sympodial segments being longer than the

dimensions of the quadrat laid down for sampling (figure 3.20).

In summer 1980-81 when dwarf and long rhizome segments were separated from each other, the evidence shows that the dry weight of rhizomes of fertile shoot modules was reduced compared with that of vegetative shoots (table 4.5). In Carex arenaria, a sand sedge of similar rhizome architecture to Carex pumila, up to two-thirds of the seasonal variation in dry weight of rhizomes could be accounted for by the variation in carbohydrate content (from figure 7, Noble 1982). Thus, given a similar determination of dry weight of rhizomes of Carex pumila by carbohydrate content, differences shown in table 4.5 might also be attributed to differences in stored carbohydrate. Likely major sinks for such reserves in older rhizomes include seeds and younger rhizomes in more distal parts of the clone.

Table 4.5 Mean dry weight per rhizome segment, December 1980.

C = control, N = nitrogen fertilizer treatment.

		Dwarf		Long	
		vegetative	fertile	vegetative	fertile
S0	C	.180	.071	.530	.638
	N	.091	.079	1.446	.79
S1	C	.022	.022	.515	.234
	N	.040	.039	.526	.145
S2	C	.025	.019	.440	.296

Differences obtained in spring and summer 1979-80 in terms of the dry weight of rhizomes (per unit length and per sympodial segment, tables 4.6 and 4.4 respectively) can be related to the proportion of long as opposed to dwarf rhizome segments in the populations. As the

populations aged, an increasing proportion of the live shoot population can be expected to be made up by dwarf as opposed to long shoots (table 3.8 and section 4.3.6). The diameter and length of dwarf or short rhizome segments were significantly less than that of long rhizome segments (section 3.2.2) and therefore the former can be expected to store less carbohydrate per unit length and per rhizome segment.

Thus, the mean dry weight per rhizome segment attached to vegetative shoots decreased at sites of increasing age (S0 to S3, table 4.4). At S0, where the Carex pumila population was in an adolescent stage of development (made up by predominantly long branch modules), the mean dry weight of rhizome segments attached to vegetative shoots was highly significantly greater than at each of the other three sites ($P < .001$; table 4.4) and comparable with the values obtained for long branch segments in December 1980 (table 4.5). In contrast in the oldest population at S3, rhizome weight was similar to that found for dwarf rhizome segments in December 1980 (table 4.5). Also, the mean dry weight per rhizome segment attached to dead shoots was greater than that of rhizomes attached to live shoots (table 4.4). At a given site, the dead shoot population can be expected to be made up by a greater proportion of long branch modules than the current live shoot population. The mean dry weight per rhizome segment attached to dead shoots at the three older sites studied was similar to that at S0 where the shoot population was made up of predominantly long branch modules.

In September 1979, rhizome segments attached to dead aerial shoots were found to be significantly heavier per unit length than those attached to green shoot modules at all sites except at S2 (table 4.6). Noble (1982) noted that in Carex arenaria, rhizomes may remain

alive and contain substantial amounts of starch for several years after losing their aerial shoots through death and subsequent decay. This may also apply to Carex pumila in which live dwarf branch modules were seen to be growing from old long rhizome segments, the aerial portions of which were decayed (figure 2.4). The mean dry weight per unit length of rhizome at S2 reflects the larger capacity of the shoots at this compared with other sites to generate supplies of carbohydrate for storage (see figures 4.10 and 4.12 for mean shoot size). The range of values for the dry weight per unit length of rhizomes obtained at S2 (namely 2-4 g/m) was similar to the maximum values reported by Noble (1982) for Carex arenaria.

Table 4.6 Mean dry weight per unit length (g/m) of rhizome segments attached to living and dead shoot modules at five sites on the sand plain, in spring 1979.

Dry weight of rhizome segments (g/m)		
	Live	Dead
Site 0	1.22 ab	-
Site 1	2.11 de	2.55 f
Site 2	2.72 f	2.55 ef
Site 3	1.13 ab	1.73 cd
Site 4	0.85 a	1.56 bc

Letters indicate Duncan's multiple range test, $P < .05$

2. Net biomass accumulation rates

Net herbage accumulation rate (NHAR) over a particular sampling interval may be calculated in many ways from standing herbage mass data obtained at sequential harvests. Trough-peak analysis of live

herbage material which involves the summation of positive increments in aerial biomass per unit area of ground (AB) between harvests (method 6a of Singh et al. 1975) may be expressed:

$$NHAR = \sum_{n=1}^k (AB_n - AB_{n-1})^* / (t_k - t_0) \dots\dots\dots(1)$$

where harvests are at times t_0 to t_k ; * indicates that only positive increments of aerial biomass are included.

Where standing herbage mass is divided into living and dead shoot components, then positive increments in dead material may be included in this calculation where they coincide with positive increments in live material; the rationale is that where live and dead materials increased over the same sampling interval then new production must have been rapidly transferred from the live to the dead component (Method 7 of Singh et al. 1975). This may be written:

$$NHAR = \sum_{n=1}^k ((AB_n - AB_{n-1})^* + (DH_n - DH_{n-1})^\#) / (t_k - t_0) \dots(2)$$

where DH is standing herbage mass of dead shoots and # indicates that positive increments of dead material will only be included where this coincides with positive aerial biomass increments. This calculation does not allow for losses by physical removal by disturbance factors such as grazing animals and wind, decay or translocation to underground organs.

NHAR of a single shoot cohort may be calculated similarly by summing positive increments in mean aerial biomass per shoot (ABS) between harvests and multiplying this by the mean shoot density of this shoot cohort ($\overline{SD}$):

$$NHAR = \sum_{n=1}^k (ABS_n - ABS_{n-1})^* \cdot \overline{SD} / (t_k - t_0) \dots\dots\dots(3)$$

Equation 3 will be useful in those situations where spatial variability in shoot density, results in the biomass per unit area showing a variability in space that is at least as large as the variations over time. The summation of positive increments in biomass per unit area between consecutive harvests (equation 1) will run the risk of inflating estimates of net herbage accumulation by creating a mythical population in which apparent increments in biomass between harvests, which may at least in part result from spatial variation, will appear to occur on a common unit area of ground.

Estimates of net herbage accumulation by vegetative shoot populations at each site were made by application of equation 1 between consecutive harvests in figure 4.11 (table 4.7a). Positive increments in dry weight of dead shoots per unit area that coincided with positive increments in aerial biomass of vegetative shoots (equation 2) were also calculated in 1978 (table 4.7b). By substituting total standing biomass (SB) for aerial biomass (AB), equation 1 was also applied to the total biomass of vegetative shoot populations during 1979 and 1980, using figures 4.13 and 4.15 (table 4.7c). From July 1980 dwarf and long branch modules were treated separately for this exercise. In summer 1978-79 and 1979-80, the analysis on fertile shoot populations was based on both equation 1 and equation 3 (table 4.7d). The latter estimate was the more conservative.

Table 4.7 Net accumulation of biomass of Carex pumila at sites (S0-S4) between successive harvests. - indicates net biomass loss.

(a) Herbage estimates for vegetative shoots based on equation 1

	grams DM / m2 / day			
	S1	S2	S3	S4
H1-H2	.64	9.79	.6	-
H2-H3	.28	-	-	-
H3-H4	-	-	-	-
H4-H5	.56	-	-	.16
H5-H6	.03	3.19	.19	-
H6-H7	1.55	3.87	-	-
H7-H8	.46	-	1.04	.33
H8-H9	.24	-	-	.08
H9-H10	3.92	1.39	.38	.02
H10-H11	.01	1.64	.06	.06
H11-H12	-	-	-	-

(b) Positive increments in dead shoots per unit area that coincided with positive increments in (a).

	grams DM per m2			
	S1	S2	S3	S4
H1-H2	1.67	-	-	-
H2-H3	53.89	-	-	-
H3-H4	-	-	-	-
H4-H5	-	-	-	-
H5-H6	-	-	16.24	-
H6-H7	-	-	-	-
H7-H8	-	-	47.22	-
H8-H9	11.36	-	-	5.06
H9-H10	92.44	-	-	-
H10-H11	-	22.89	-	-
H11-H12	-	-	-	-

(c) Total biomass increments for vegetative shoots based on equation 1 during 1979 and 1980.

	grams DM / m2 / day			
	S0	S1	S2	S3
H10-H11	-	-	2.32	0.136
H11-H12	-	-	-	-
H12-H13	(0.32)	-	-	0.158
H13-H14	4.07	4.01	5.82	0.94
H14-H15	-	2.63	2.25	-
H15-H16	-	-	-	-
H16-H17	1.24	1.13	2.09	-
H17-H18	14.74	-	15.48	1.86
H18-H19	-	-	-	-
H19-H20	-	1.45	0.11	-
H20-H21	-	0.45	-	-
H21-H22	2.71	0.79	1.74	0.33
H22-H23	-	-	0.58	0.19
H23-H24	-	-	-	-
H24-H25 Dwarf	0.57	0.07	0.11	0.002
Long	0.28	-	-	-
H25-H26 Dwarf	1.20	0.02	0.16	-
Long	0.11	0.07	0.16	-

(d) Seasonal herbage increments for fertile shoots based on (i) equation 1, (ii) equation 3 (figure 4.12) and mean shoot density and (iii) equation 1 (figure 4.15). ne = not estimated.

	grams DM / m2				
	S0	S1	S2	S3	S4
(i) 1978-79	ne	17.67	268.9	31.33	7.45
(ii) 1978-79	ne	7.61	96.85	9.12	0.50
1979-80	1.17	29.77	85.23	5.70	ne
(iii) 1980-81	44.00	-	17.22	-	ne

The greatest rates of net biomass accumulation that were estimated at any site during the study were found at S2 during autumn 1978 and spring 1979. The autumn 1978 increase measured at 9.79 g DM / m2 / day which represented a five-fold increase in standing herbage (figure 4.11) compares with rates of production of green material in sedge dominated wetlands in North America (Bernard and Macdonald 1974). The spring 1979 increase was greater (15.5 g DM / m2 / day), but included underground organs.

The estimated daily rates of net biomass accumulation for long and dwarf shoots of Carex pumila from July to October and from October to December 1980 are given in table 4.8. No significant differences were found between the two shoot types. The maximum rate estimated over these periods which were found at S0 to be 2.04 g DM / m² / day for the combined dwarf and long, vegetative and fertile shoot population was still considerably less than that estimated for aerial shoot growth in the old hollow at S2 in autumn 1978, or for total biomass at S2 in spring 1979.

Table 4.8 Estimates of aerial shoot growth rates of long and dwarf shoots at sites on the sand plain during spring and early summer 1980.

Aerial shoot rate of increase in size (mg DM / shoot / day)		
	July-October	October-December
S0 dwarf shoots	2.62	7.13
long shoots	2.72	6.34

During 1980 biomass accumulation at S0 was reduced by the effect of grazing by rabbits. This form of habitat disturbance was evident on young shoots, especially across the fringe of the low dune throughout the study. Figure 3.5 shows evidence of rabbits in mid-summer 1977-78. In late August 1980, almost one month after the winter harvest was taken, young shoots on the fringe of the low dune were extensively damaged by grazing (figure 4.18). At the spring 1980 harvest previously grazed shoots which could readily be identified were included in the sample at this site. The number of leaves per shoot to have elongated since grazing, and the increase in length of the longest leaf per grazed shoot are shown in table 4.9. No

differences between dwarf and long shoots both of which were grazed were apparent.

Table 4.9 Rates of leaf emergence and increase in leaf length at S0, between August and October 1980

	Rate of leaf emergence (number/60 days)	Rate of increase of leaf length (mm / day)
Dwarf shoots	3.0 $\pm$.223	5.05 $\pm$.483
Long shoots	2.95 $\pm$.25	5.33 $\pm$.296

On the low dune, the shelters erected in spring 1979 excluded mammalian grazers. Measurements of numbers of leaves per shoot and length of leaf laminae were made in October 1980. Where grazing had been prevented, shoots possessed up to eight leaves, cf five where grazing had previously occurred. The frequency distribution of length of leaf laminae indicated many more shorter (younger) leaves where grazing was prevented (figure 4.18). Little difference in maximum leaf length was apparent between the two treatments.

The estimated annual net biomass accumulation of Carex pumila shoot populations at the four sites on the sand plain from January 1978 are given in table 4.10. The estimates were based on (i) equation 1 and (ii) equation 2 for vegetative shoots, and equation 3 for fertile shoots.

Figure 4.18 The effect of rabbits grazing on the low dune
(a)



(b) The frequency distribution of leaf length in spring 1980, on sheltered and control plots

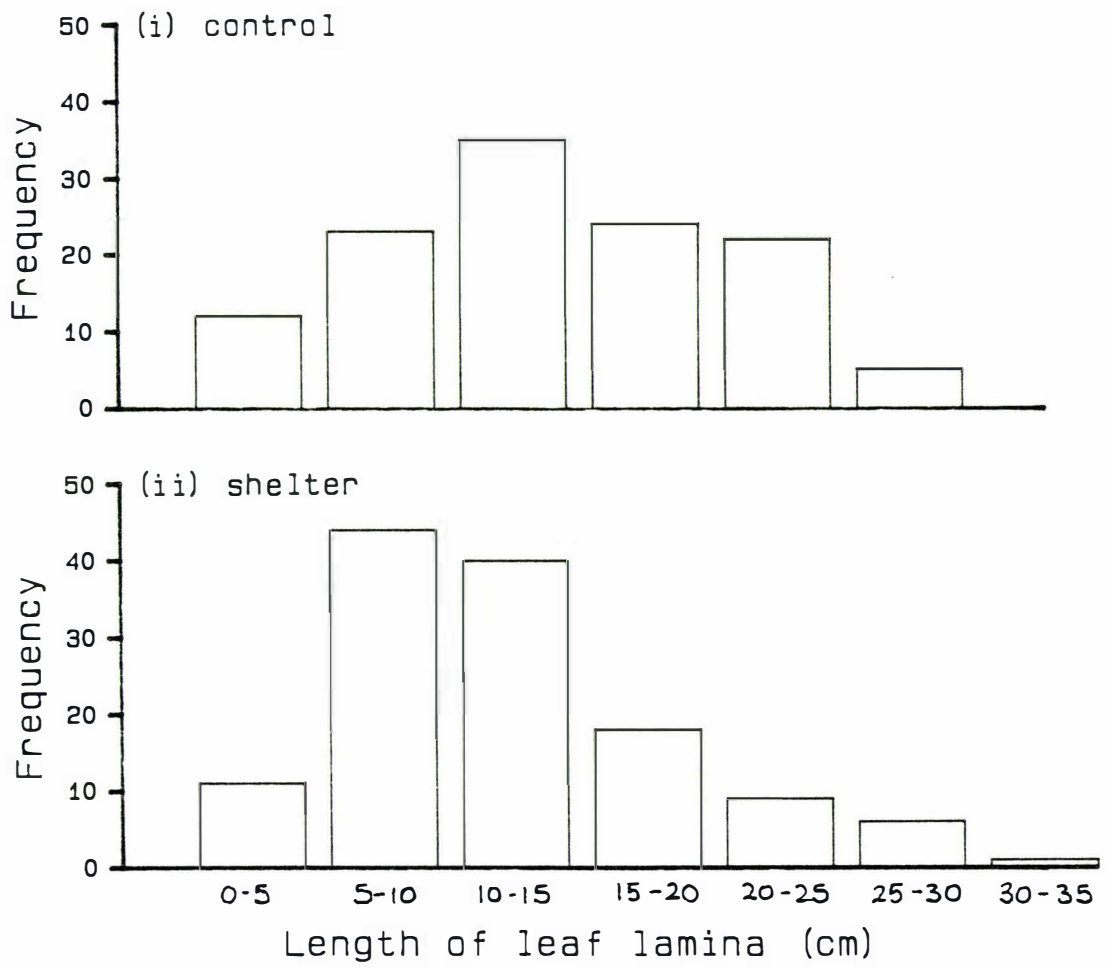


Table 4.10 Estimated rates of annual net biomass accumulation of Carex pumila (g DM / m² / year) at five sites on the sand plain, during 1978, 1979 and 1980.

		grams DM / m ² / year				
		S0	S1	S2	S3	S4
1978	(i)	-	409.71	1145.9	157.1	21.84
	(ii)	-	781.42	1211.1	311.95	33.98
1979		250.5	135.77	405.57	42.69	ne
1980		268.01	64.11	119.89	20.5	ne

(i) aerial and (ii) total biomass estimates for 1978

The standing biomass (SB) in midsummer was found to be positively related to the annual net biomass accumulation (ANBA) that occurred both subsequently and previously (figure 4.19). The equations for these relationships are:

$$\text{ANBA} = -22 + 1.16 \text{ SB}_1 \dots\dots\dots(4)$$

$$\text{and } \text{ANBA} = -19.9 + 1.91 \text{ SB}_2 \dots\dots\dots(5)$$

respectively; where SB₁ is the standing biomass at the beginning and SB₂ the standing biomass at the end of a twelve month period of net biomass accumulation. The estimated intercept on the ANBA axis (SB = 0) in each case is small and not found to be significantly different from zero. Further, the estimated slope coefficients for the ANBA/SB regression lines are significantly different from zero in both cases (P<.01). The simple ANBA - SB correlation coefficient (r) values suggest that the standing biomass in mid-summer is a better predictor of subsequent than of previous annual net biomass accumulation. However, comparison of the residual mean squares from the two analysis

of variance tables giving the sums of squares due to regression (table 4.11) shows that there was no significant difference between these two parameters as predictors of annual net biomass accumulation (F-ratio for 10 and 9 degrees of freedom was not significant).

Table 4.11 Analysis of variance of the regression of standing biomass (SB) on annual net biomass accumulation (ANBA). (SB1 and SB2 = SB before and after a period of biomass accumulation, respectively).

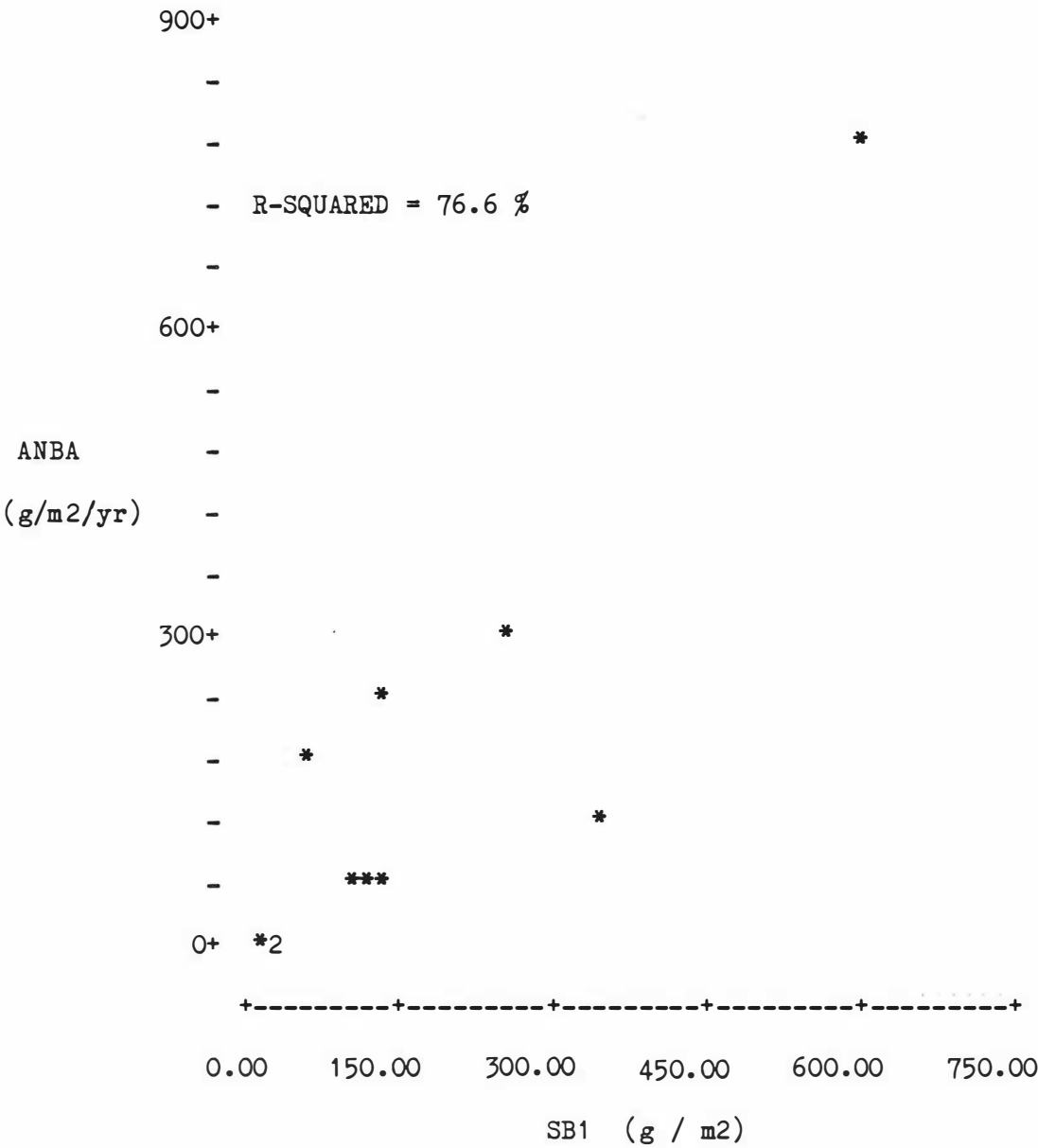
ANALYSIS OF VARIANCE ANBA vs SB1

DUE TO	DF	SS	MS=SS/DF
REGRESSION	1	413836	413836
RESIDUAL	9	126489	14054
TOTAL	10	540325	

ANALYSIS OF VARIANCE ANBA vs SB2

DUE TO	DF	SS	MS=SS/DF
REGRESSION	1	376822	376822
RESIDUAL	10	169134	16913
TOTAL	11	545957	

Figure 4.19 The relationship between annual net biomass accumulation and standing biomass of Carex pumila before a 12-month period of biomass accumulation.



Cumulative losses of biomass in the resident Carex pumila populations during 1978, 1979 and 1980 were greater than cumulative gains (net biomass accumulation) over these same annual periods, at all sites monitored on the study area, with the exception of S1 in 1978 and S0 in 1980. The standing biomass estimates of both fertile

and vegetative shoot populations at each of the former sites therefore were lower than those obtained at the same site twelve months previously (figures 4.11 and 4.13). This trend was also seen in tables 4.12 and 4.13 which show the mean dry weight per shoot module in each of the four summers of the study. The trend reflects the increasing age/senility of these seral populations.

The reductions in standing biomass (figures 4.11 and 4.13) were most marked in absolute terms at those sites at which net biomass (or herbage) accumulation had previously been greatest (as at S2 during 1978). The observation of Noble et al. (1979) that populations of Carex arenaria that have the highest rates of shoot births also had the highest death rates probably reflects a similar phenomenon. In less productive populations at other sites, the decline between years although less marked in absolute terms still represented large relative losses. For example, at S3 between 1978 and 1979, a five-fold decline in standing biomass occurred (figure 4.11).

The exceptions to the trend of overall net losses of biomass between years apply to those populations which were in a juvenile phase of development when first monitored. At S0, annual net biomass accumulation rate for 1980, which was probably underestimated due to site disturbance by rabbit-grazing in winter and sand deposition in autumn, was 50 per cent higher than that estimated for 1979 (table 4.10). However the expected mortality of older shoots and suppression of growth as a result of the movement of large quantities of sand onto the site did not eventuate in spring 1980 (see above). This resulted in a similarly increased standing biomass at this site in December 1980 compared with that twelve months previously (figure 4.13). The inundation of S1 by sand in spring 1978 resulted in the loss of about 95 per cent of live herbage in this juvenile/adolescent population

over this August-October period. Recovery of of this population later in the spring/early summer was reflected in the mid-summer 1978-79 aerial biomass value which surpassed that of January 1978, but did not show a continuing increase over the autumn and winter 1979 as in 1978 (figure 4.11). Thus, from autumn 1979, standing biomass values at this site were less than those recorded twelve months previously.

The declining biomass per unit area of the population at S1 over time between summer 1978-79 and 1980-81 was not paralleled by shoot density (section 4.3.1). The declining biomass was attributable to the depauperation of shoot modules (tables 4.12 and 4.13). The accretion of sand at S1 over the duration of the study not only caused disturbance to the plants, but also increased nutrient- and water-stress by removing them from ready access to the water table.

Table 4.12 Mean seasonal maximum aerial dry weight per shoot module of reproductive shoot populations of Carex pumila at five sites on the sand plain in each of four summers.

		grams DW / aerial shoot module				
		S0	S1	S2	S3	S4
1977-78		ne	0	1.24	.56	.185
1978-79		ne	.512	.777	.202	.120
1979-80		.932	.402	1.19	.126	ne
1980-81	Control	.762	.138	.251	0	ne

Table 4.13 Winter minimum and summer maximum mean dry weights per aerial shoot module of the vegetative shoot populations of Carex pumila at five sites on the sand plain in successive years, 1977-78 to 1980-81.

		grams DW / aerial shoot module				
		S0	S1	S2	S3	S4
(a) Winter minima						
1978	ne	0.19c	0.46a	0.08d	0.06d	
1979	0.17c	0.18c	0.27b	0.03d	0.03d	
1980	0.12d	0.12d	0.12d	0.06d	ne	
(b) Summer maxima						
1977-78		0.292	0.82	0.29	0.14	
1978-79		0.335	0.45	0.12	0.075	
1979-80	0.482	0.295	0.616	0.12	ne	
1980-81	0.65	0.12	0.21	0.075	ne	
a > b; P<.05		a > c; P<.01	b > c; P<.01	c > d; P<.05		

As shown in figure 4.8, species other than Carex pumila made up only a small proportion of the total sward mass in January 1978, although at sites of increasing distance from the terminal hollow this proportion increased. As the resident swards at each site on the sand plain aged over the three years of the study, the standing mass of other species in the sward increased (table 4.14). These increases in other species with time contrast with the decline in biomass of Carex pumila seen between consecutive years. The differences observed between sites on the sand plain at a given point in time then, parallel the successional changes with time and are consistent with the view that the populations at these sites form a successional series.

Table 4.14 Sward mass of species other than Carex pumila in 1979-80 and 1980-81 at two sites on the sand plain.

	grams DM / m ²	
	1979-80	1980-81
S2	29.1 $\pm$ 42	352.9 $\pm$ 252.1
S3	142.1 $\pm$ 57.1	196 $\pm$ 55.6

3. Energy and elemental concentrations

(i) Energy

The energy values determined for component organs of Carex pumila are shown in table 4.15. At S2, the mean energy value obtained for seeds was higher ($P < .05$) than that for each of the other plant parts assayed (except roots, table 4.15a). The energy content of seeds increased over the season suggesting the elaboration of high energy

containing compounds as seed weight increased. At S2, mature seed was seen to have a significantly higher ($P<.05$) mean energy value than that of seeds collected earlier in the season before grain filling had commenced (table 4.15b). There were also highly significant ($P<.001$) site differences for the energy value of seeds collected at the end of the season (table 4.15c). The lower energy values of seeds found at S1 and S4 compared with S2 and S3 were similar to that for immature seeds at S2 (table 4.15b). These reduced energy values for seed suggest incomplete seed development. This was confirmed by the reduced mean seed weights found at these sites compared with S2 and S3 (section 4.3.5).

Table 4.15 Mean ($\pm$ standard error) energy values (joules / gram DM) of Carex pumila (a) for component parts from S2 in January 1978, (b) for seeds from S2 at two different stages of fertile shoot development (November, 1978 and January, 1979) and (c) for seeds from four different sites in January, 1979.

(a) Plant part		joules/gram
	Roots	19334.4 $\pm$ 56.4
	Rhizomes	18426.1 $\pm$ 22.4
	Leaves	18761.0 $\pm$ 277.3
	Glumes/rhachillae	15023.0
	Male inflorescences	15600.7
	Seed	20234.4 $\pm$ 166.6
(b)Seeds	Stage of development	joules/g
	7-8 (seed filling)	18007.5 $\pm$ 26.0
	10 (maturity)	20305.6 $\pm$ 483.9
(c)Seeds	Site	joules/g
	S4	16986.2
	S3	20334.9 $\pm$ 142.9
	S2	20443.7 $\pm$ 98.9
	S1	18032.6 $\pm$ 312.3

Energy values of stored material dried at 80 degrees C and corrected for % dry weight.

The energy values for seeds (and other organs) of Carex pumila suggest that the lipid content of these organs is low. This was confirmed by a direct determination of percent lipid content on seeds from mature fertile shoots collected in January 1978; a value of $3.615 \pm 0.216\%$ fat by weight was obtained. These values contrast with

the energy content of seeds of other plant species which store much larger concentrations of lipids (Levin 1974).

It is unlikely that proportionate allocation patterns in Carex pumila to component shoots and organs based on joules would differ significantly from those based on dry weight. Working with Lupinus species, which store up to 15% lipids in their seeds, Hickman and Pitelka (1975) confirmed that the proportionate energy allocation patterns using both grams dry weight and stored energy units as measures of energy investment did not differ significantly. The preliminary energy values obtained for Carex pumila seeds (both percent lipid and joules/gram), the small differences between plant organs in terms of energy content/gram DM (table 4.15a) and the relatively high within-site variance for proportional plant part dry weights (section 4.3.6) suggest that a similar result would be obtained in this study. More extensive energy determinations were not therefore carried out.

(ii) Elemental concentrations

The elemental concentrations of Cu, Zn, Fe, Ni, Mn, Mg, Ca, Na and K of constituent organs of Carex pumila sampled from the mature population in the old hollow at S2 in October 1978 are shown in table 4.16. Variation between constituent organs was evident from this table. Further, compared with values quoted by Brooks for plant material generally, Carex pumila on the study area contained reduced amounts of Zn, Fe and Mn, and elevated amounts of Mg and Na. High concentrations of these latter two elements in this coastal habitat accounts for the massive plant concentrations. The prevailing west to north-west winds bring sea spray onto the coastal dunelands. The low plant concentration of Fe is interesting in that it reflects the low

concentrations in the substrate (table 3.6) in contrast to the sand immediately north of the study area, south of the Rangitikei River mouth which contains massive amounts of magnetic minerals (Gibb 1977). On this prograding coast, sand at inland sites can be expected to differ little in mineral composition from that on the beach (Oliver 1948).

Table 4.16 Mean ($\pm$ standard deviation) elemental concentrations of constituent organs of Carex pumila in October 1978.

	Concentration (ppm)				
	Cu	Zn	Fe	Ni	Mn
Roots	9.5 $\pm$ 3.5	13.0 $\pm$ 2.1	59.5 $\pm$ 14.3	3.8 $\pm$ 1.9	61.8 $\pm$ 13.8
Rhizomes	7.0 $\pm$ 1.4	20.0 $\pm$ 7.2	19.2 $\pm$ 5.1	3.8 $\pm$ 1.8	17.0 $\pm$ 6.2
Green lvs	10.5 $\pm$ 3.5	25.5 $\pm$ 8.1	11.0 $\pm$ 6.4	3.3 $\pm$ 0.8	91.2 $\pm$ 28.8
Dead lvs	6.5 $\pm$ 0.5	8.5 $\pm$ 1.5	14.5 $\pm$ 4.5	16.5 $\pm$ 13.5	87.0 $\pm$ 3.0
Bracts	7.0	10.0	38.0	1.0	39.0
###	9.0	70.0	500.0	3.0	400.0

	Mg	Ca	Na	K
Roots	2550 $\pm$ 10.30	6394 $\pm$ 1030	7052 $\pm$ 1733	5546 $\pm$ 1547
Rhizomes	1095 $\pm$ 183	3275 $\pm$ 957	3978 $\pm$ 1196	5627 $\pm$ 2579
Green leaves	1770 $\pm$ 262	4537 $\pm$ 482	2471 $\pm$ 599	9297 $\pm$ 1764
Dead leaves	2167 $\pm$ 1357	8175 $\pm$ 75	844 $\pm$ 120	979 $\pm$ 326
Bracts	1920	6825	1688	2936
###	700	5000	200	3000

Means for plant material generally, from Brooks (1972, table 11.2)

The allocation of limited minerals to different plant parts may be of greater significance in the evolution of plant strategies on these nutrient-stressed sand plains than that of dry weight. These data suggest that allocation patterns based on dry weight and minerals in Carex pumila will differ significantly. This was tested for crude total nitrogen.

(iii) Crude total nitrogen

In Carex pumila, percent crude total nitrogen (%TN) values for seeds and green leaf laminae were higher than that for green leaf sheaths, which in turn was higher than those of all other parts of

live branch modules (table 4.17). These differences, averaged over the four sites monitored during 1979-80, were highly significant ($P < .001$). Taking each component organ in turn, it was found that the %TN values for seeds and for green leaf laminae were similar at all four sites across the study area (table 4.18). By contrast, %TN of rhizomes, roots and bracts were significantly greater at S2 than at other sites ($P < .001$, $P < .001$ and $P < .05$, respectively). This observation probably reflects the greater concentration of available nitrogen in the soil in the old hollow than on the low dune, as a result of the activity of nitrogen-fixing blue-green algae (section 3.1.5). Despite the reduced amounts of nitrogen available for uptake on the low dune, the concentrations of this element in green leaf laminae and seeds were not reduced on these sites. The low percent nitrogen values found for roots, rhizomes and bracts on the old hollow at S3, where blue-green algae were also evident, suggest that the nitrogen available for plant growth was not taken up by Carex pumila. Other later seral species, where they are present as at S3 in 1979-80, are likely to preferentially absorb soil nitrogen (see also section 4.3.7).

Table 4.17 Percent crude total nitrogen content (%TN) of component organs of live and dead branch modules of Carex pumila, averaged over four sites, in summer 1979-80.

	% TN	
	Live shoots	Dead shoots
Roots	0.47 b	0.425 b
Rhizomes	0.53 b	0.284 b
Bracts	0.45 b	
Green sheaths	1.09 c	
Green laminae	1.73 d	
Dead leaves	0.56 b	0.568 b
Seeds	1.79 d	

Letters indicate Duncan's multiple range test, $P < .001$

Table 4.18 Mean ($\pm$ standard deviation) percent crude total nitrogen content (%TN) of component organs of Carex pumila.

Percent total nitrogen (%TN)				
(a) Living branch modules, 1979-80				
	S0	S1	S2	S3
Roots	.497 $\pm$.124	.419 $\pm$.114	.612 $\pm$.123	.350 $\pm$.062
Rhizomes	.449 $\pm$.159	.505 $\pm$.177	.758 $\pm$.188	.393 $\pm$.085
Bracts	.403 $\pm$.100	.426 $\pm$.088	.521 $\pm$.100	.437 $\pm$.067
Green sheaths	1.327 $\pm$.446	1.107 $\pm$.328	1.031 $\pm$.336	.882 $\pm$.239
Green laminae	1.920 $\pm$.474	1.963 $\pm$.340	1.582 $\pm$.430	1.447 $\pm$.155
Dead leaves	.621 $\pm$.187	.508 $\pm$.136	.598 $\pm$.145	.520 $\pm$.111
Seeds	1.935 $\pm$.827	1.497 $\pm$.342	1.618 $\pm$.461	2.110 $\pm$.488
(b) Dead branch modules, 1979-80				
	S0	S1	S2	S3
Roots	.378 $\pm$.030	.472 $\pm$.071	.380 $\pm$.154	.468 $\pm$.036
Rhizomes	.289 $\pm$.044	.404 $\pm$.076	.224 $\pm$.049	.220 $\pm$.008
Leaves	.514 $\pm$.136	.565 $\pm$.089	.609 $\pm$.080	(.582 $\pm$.444)
(c) 1978-79				
	S1	S2	S3	S4
Roots #	.326 $\pm$.049	.456 $\pm$.043	.356 $\pm$.124	.390 $\pm$.137
Rhizomes #	.250 $\pm$.037	.212 $\pm$.043	.157 $\pm$.051	.133 $\pm$.047
Green leaves	1.625 $\pm$.236	1.277 $\pm$.198	1.422 $\pm$.238	1.327 $\pm$.281
Dead leaves	.865 $\pm$.237	.689 $\pm$.118	.744 $\pm$.194	.714 $\pm$.164
# Underground parts attached to living and dead shoots				

In the harvest of 1978-79, the underground portions of individual shoot modules were not separated so that values of dry weight and consequently percent total nitrogen estimates were obtained for the total root and total rhizome fractions only. No difference between sites were found for percent nitrogen content of roots. However, there was a progressive increase in percent nitrogen values for total rhizomes from the oldest to the youngest site (table 4.18c). The greater percent total nitrogen values of total rhizomes at the younger sites may reflect a greater proportion of living as opposed to dead rhizomes in this total underground fraction. In summer 1979-80, the percent total nitrogen content of rhizome modules attached to live shoots was twice that of rhizomes attached to dead shoots (table 4.17). The depletion of nitrogen from live shoot modules can be seen by comparing values for green leaf laminae and sheaths with values for dead leaves (on both living and dead shoots; tables 4.17 and 4.18).

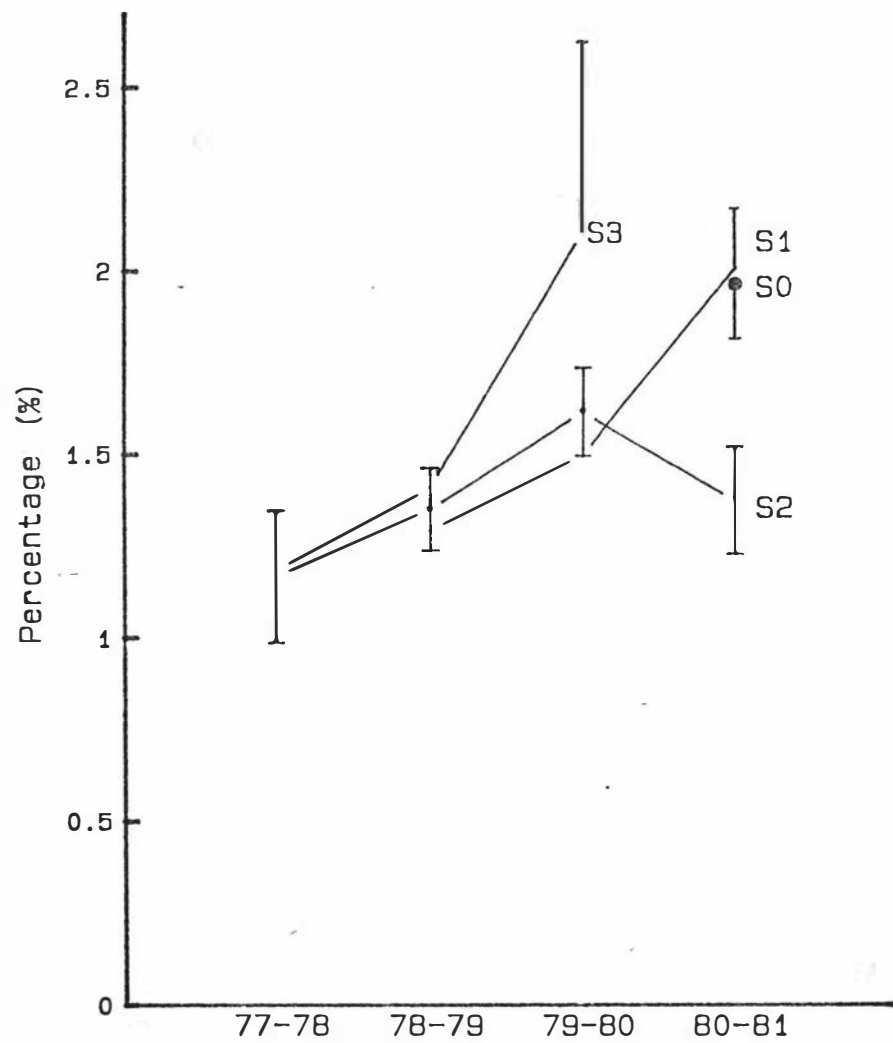
Figure 4.20 shows the effect of season (time) on the percent nitrogen content of seeds of Carex pumila at each of the sites monitored on the plain. The positive slopes of these curves reflect the increasing availability of nitrogen on the sand plain at the sites matured between 1977-78 and 1980-81. Free-living nitrogen-fixing blue-green algae (Nostoc and Anabaena species) found on the plain were probably responsible for the increases of nitrogen in the developing sand plain ecosystem. The subsequent decline in percent total nitrogen of seeds at S2 in the 1980-81 season (figure 4.20) reflects the decreasing suitability of the habitat for Carex pumila, as other species became abundant, interfering with the ability of the pioneer to accumulate resources. The fertile shoot population of Carex pumila at this site in summer 1980-81 was represented by a few depauperate shoots in contrast to the dense sward found in December 1977. Seed filling by this senescent shoot population was reduced compared with previous seasons (seed weight, section 4.3.5). In summer 1980-81, the percent nitrogen content of seeds at S2 was also significantly lower ($P < .001$) than those values at the two younger sites on the low dune.

The percent total nitrogen values for Carex pumila shoots in December 1980 differed substantially, not only between component organs and according to the maturity of the population (site), but also according to the vegetative or flowering state of the shoot and further whether the shoot was derived from a dwarf or a long branch. These differences are probably related to the depletion of nitrogen from shoots with age.

Table 4.19 shows the relative depletion of nitrogen from vegetative organs of fertile shoots of Carex pumila compared with vegetative shoots in December 1980. This observation reflects the greater maturity of the fertile shoot cohort and the onset of

Figure 4.20 Percent crude total nitrogen content of seeds of Carex pumila in four summers at three sites on the sand plain.

Vertical bars indicate 95% CI for site means based on pooled standard deviations



senescence in this part of the clone. Accompanying this senescence of vegetative parts is the growth and development of seeds which act as a store for nitrogen and other nutrient elements (Jefferies et al. 1979; Lovett Doust 1980). The channelling of nitrogen to seeds of Carex pumila resulted in a substantially greater concentration of this element in disseminules than in any other organ (approximately 5x that of rhizomes and 7x that of roots of fertile shoots, table 4.19). Structures already low in nitrogen in vegetative shoots (namely, bracts and roots) were not further reduced in fertile shoots.

Table 4.19 Mean percent crude total nitrogen content (%TN) of component organs of vegetative and fertile shoots of Carex pumila in December 1980.

Percent total nitrogen (%TN)		
Vegetative shoots		Reproductive shoots
Rhizomes	0.67	0.44
Rhizome tips	1.28	ne
Roots	0.38	0.29
Bracts	0.35	0.38
Green leaves	Sheaths	0.43
	Laminae	1.55
Dead leaves	0.68	0.50
Male spikes	-	0.79
Seeds	-	2.13

Although the percent nitrogen of the vegetative portion of fertile shoots was significantly ($P<.001$) different (lower) than that of vegetative shoots, the difference was not the same for all component organs (see significant 'state x organ' interaction term in

the analysis of variance, $P < .001$; table 4.20). Further, the significant 'state x site x organ' interaction ($P < .05$, table 4.20) indicates that the relative depletion of nitrogen from the component organs of fertile shoots compared with vegetative shoots was greater at S0 than at S1.

Table 4.20 Analysis of variance of percent total nitrogen content of component organs (or) of Carex pumila shoots at two sites (si) under two treatments (tr, + nitrogen fertilizer) in December 1980. Shoots were divided into vegetative and fertile states (st) and dwarf and long types (ty).

SOURCE	D.F. (M.V.)	S.S.	M.S.S.	F RATIO	
st	1	1.15	1.15	250.47	***
ty	1	0.11	0.11	22.97	**
st*ty	1	0.05	0.05	10.99	*
si	1	0.98	0.98	214.63	***
st*si	1	0.64	0.64	138.92	***
ty*si	1	0.08	0.08	18.06	**
st*ty*si	1	0.13	0.13	28.15	**
tr	1	0.02	0.02	3.72	ns
st*tr	1	5.104E-03	5.104E-03	1.11	ns
ty*tr	1	0.14	0.14	31.10	**
st*ty*tr	1	0.15	0.15	33.49	**
si*tr	1	0.04	0.04	7.70	*
st*si*tr	1	4.578E-05	4.578E-05	9.983E-03	ns
ty*si*tr	1	7.019E-04	7.019E-04	0.15	ns
st*ty*si*tr	1	0.03	0.03	6.11	ns
or	5	20.46	4.09	892.40	***
st*or	5	0.83	0.17	36.00	***
ty*or	5	0.11	0.02	4.90	ns
st*ty*or	5	0.01	2.118E-03	0.46	ns
si*or	5	0.33	0.07	14.27	**
st*si*or	5	0.25	0.05	10.75	*
ty*si*or	5	0.44	0.09	19.35	**
st*ty*si*or	5	0.06	0.01	2.45	ns
tr*or	5	0.24	0.05	10.38	*
st*tr*or	5	0.01	2.834E-03	0.62	ns
ty*tr*or	5	0.26	0.05	11.17	**
st*ty*tr*or	5	0.12	0.02	5.42	*
si*tr*or	5	0.26	0.05	11.52	**
st*si*tr*or	5	0.08	0.02	3.58	ns
ty*si*tr*or	5	0.05	0.01	2.32	ns
error	5	0.02	4.585E-03		

Estimated treatment means:

	st	ty	si	tr	or
Veg	0.82	Dw 0.74	SO 0.81	N 0.70	Rhiz 0.56
Fert	0.60	Lo 0.68	S1 0.61	C 0.72	Root 0.33
					Brac 0.37
					Shea 0.71
					Lami 1.70
					Dead 0.59
L.S.D. 5%	0.04	0.04	0.04	0.04	0.06
L.S.D. 1%	0.06	0.06	0.06	0.06	0.10
L.S.D. .1%	0.09	0.09	0.09	0.09	0.16

The fate of nitrogen in the vegetative plant parts lost during senescence (compare both dead with green leaves and vegetative components of fertile with vegetative shoots, table 4.19) was not directly monitored in the present study. However, the differential distribution of nitrogen amongst the component organs of Carex pumila shoots (table 4.19) suggests an acropetal direction of movement of this element through the plant and its accumulation in the distal parts, in the case of vegetative shoots in the green leaves and rhizome tips and in the case of fertile shoots ultimately in the seeds. Previous studies on other rhizomatous perennial species suggest only a very limited redistribution of resources between immediately adjacent shoot modules within the clone and a largely acropetal direction of movement of nutrients along the rhizome axis (Forde 1966; Tietima 1979; Noble and Marshall 1983). Even when older basipetal shoots were severely nutrient stressed, Noble and Marshall (1983) found little evidence of basipetal movement of nitrogen or phosphorus in Carex arenaria, a clonal species, in either field or glasshouse experiments.

In December 1980, the %TN averaged over all vegetative organs was significantly less at S0 than at S1 ($P < .001$, table 4.20). The %TN values at S0 were less than those at S1 for each component organ except bracts, which had uniformly low %TN values at both sites (significant 'site x organ' interaction, $P < .01$, in the analysis of variance, table 4.20). The effect of site was largely attributable to the low %TN values for reproductive shoots at S0 (significant 'state x site' interaction, $P < .001$, table 4.20) although the reduction of %TN of dwarf shoots between the two sites was greater ($P < .05$) than that of long shoots (significant 'type x site' interaction, table 4.20). These differences between the two sites reflects the more rapid

development and onset of senescence of dwarf and reproductive shoots at the younger site. At the older, drier low dune S1, development of these shoots was more prolonged.

The differences between sites for %TN for the various organs, were not all similar (significant 'state x site x organ', $P < .05$, and 'type x site x organ', $P < .001$, interactions, table 4.20). The overall reduction of nitrogen content of component organs at S0 was not evident for green leaf laminae of vegetative shoots (averaged over both shoot types and both treatments) nor for dwarf shoots (averaged over both states of shoot and both treatments). Further, the %TN of rhizomes of long shoots (averaged over both states and both treatments) was greater at the younger of the two low dune sites.

In Carex pumila, the percent crude total nitrogen values showed significant differences not only between plant parts and between sites, but also over time, between types of shoot (whether attached to dwarf or long rhizome segments), the sexual state of the shoot and in response to nitrogen fertilizer addition (section 4.3.7). These differences will alter estimates and comparisons of total nitrogen allocation from those based on dry weight alone. Since the percent nitrogen values differed by up to 7X between plant parts, it seems reasonable to expect that the allocation patterns based on total nitrogen and dry weight will differ significantly. This was tested directly (section 4.3.6).

The percent crude total nitrogen values for plant species other than Carex pumila obtained in the harvested samples were also determined (table 4.21). Since this sward mass was not divided into constituent species nor into aerial and underground parts, the values given in this table should not be compared with those obtained for

Carex pumila which apply to constituent plant parts.

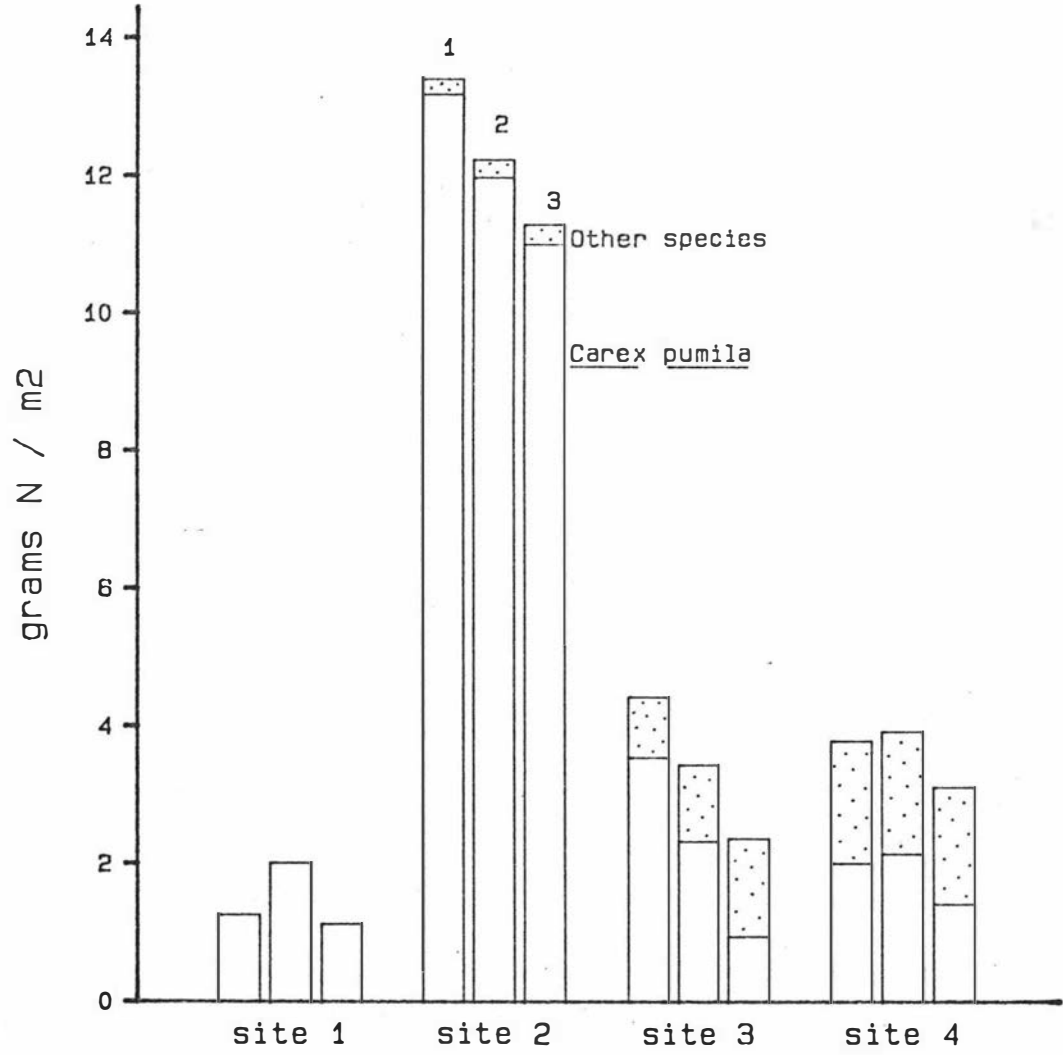
Table 4.21 Mean ($\pm$ standard deviation) percent crude total nitrogen content (%TN) of plant species other than Carex pumila found on the study area in December 1980.

Site	Treatment	%TN
S2	Control	1.06 $\pm$ 0.16
S3	Control	1.05
	Fertilizer	0.99

4. Total nitrogen content per unit area

At the beginning of the study the total nitrogen content of the sward mass was significantly ($P < .01$) greater at S2 in the old deflation hollow than that at any other site (figure 4.21) mainly as a result of the considerably larger sward mass at the former site (figure 4.8). Further contributing factors were (1) the proportion of sward mass in herbage, for which total nitrogen concentration was greater than other plant parts (table 4.17), was also greater at S2 than at other sites (section 4.3.6) and (2) percent total nitrogen values for several live shoot components were greater at S2 than at other sites (table 4.18). Dead aerial shoots of Carex pumila contributed a large and significant proportion of the total amount of nitrogen in the sward mass at the three old deflation hollow sites. This nitrogen would become available to growing plants only as a result of decomposition of this dead material. The time for 50% decomposition of dead Carex pumila leaves was shown in section 3.2.3 to be almost a year (351 days).

Figure 4.21 The distribution of the total nitrogen content of the sward mass to Carex pumila and other species at four sites in three successive years
1 = 1977-78, 2 = 1978-79, 3 = 1979-80



The fluctuations observed in terms of the total nitrogen content of the standing biomass of Carex pumila over time followed the changes already outlined for standing biomass on which the former values were based. The magnitude of the relative increases of the former parameter were however greater than those of the latter. At S2, the total nitrogen content of vegetative shoots increased 7-fold during autumn 1978 (table 4.22) whereas the dry weight increase although large (5-fold; figure 4.11) was not as great. Similarly at S1, total nitrogen more than trebled between January and August 1978 whereas the dry weight increase over this same period was less than double. No such discrepancy was found in the magnitude of the relative decline in dry weight and total nitrogen at for example, S2 over the winter to August 1978. The explanation for this difference lies in the percent nitrogen content of the plant tissues that were undergoing changes in standing dry matter. The initial increases in aerial biomass during 1978 at both S1 and S2 resulted from increases in live (green) herbage which possessed relatively high total nitrogen concentrations (table 4.17). The decreased standing aerial biomass over winter 1978 at S2, by contrast, resulted from leaf and shoot senescence. The percent total nitrogen content of dead leaves was considerably less than that of green leaves (table 4.17). The larger relative decrease of total nitrogen compared with that of dry weight at S1 during early spring 1978 can be similarly explained. Inundation of the site by sand removed green shoots that would otherwise have continued growing, rather than senescent shoots with a high proportion of dead tissue and lower N-concentrations.

Table 4.22 Total nitrogen content of the aerial biomass of Carex pumila during 1978.

	grams N / m ²	
	S1	S2
Summer 1977-78	.58	1.47
Autumn 1978	.96	10.20
Winter 1978	2.05	3.60
Spring 1978	.13	3.50
Summer 1978-79	.66	3.82

The increase in total nitrogen content of Carex pumila shoots during biomass accumulation depends upon nitrogen inputs from the surrounding area, even at those sites where nitrogen-fixing blue-green algae were apparent. The increase in total nitrogen by vegetative shoots at S2 during autumn 1978, equivalent to 8.73 g N / m², was somewhat greater than that that could be supplied by nitrogen-fixation in the soil (section 3.1.6). It was estimated that N-fixation in the surface layer of the soil to 25mm depth could have provided only 1.36 g N/m² over this autumn period (table 3.5). The balance can be attributed firstly to decomposition of Carex pumila and other plants in situ and secondly to topogenic accumulation from the surrounding high dunes and low dunes on the sand plain. Nitrogen fixation can be expected in the rhizosphere zone of Ammophila arenaria which provides a favourable environment for nitrogen-fixing bacteria (Hassouna and Waring 1964; Wahab 1975) and in Lupinus arboreus through its symbiotic association with Rhizobium bacteria. Both plant species were abundant on the plain and surrounding high dunes. Fixed nitrogen will subsequently be made available to other plants in the ecosystem through plant exudates and decomposition (Gadgil, 1971).

The differences in total nitrogen concentrations of the various plant parts resulted in changes in the levels of significance of differences between site populations for total nitrogen content compared with those seen for dry weight. Table 4.23 shows such a comparison for fertile shoot populations at S1 and S2 in December 1979. For those organs with low percent nitrogen values (roots, spikes and bracts), no significant differences were found between S1 and S2 for total nitrogen content, whereas these sites had been seen to differ when the comparison was based on dry weights (table 4.23). Conversely, for leaves and seeds (organs with significantly higher concentrations of nitrogen) the level of significance between the two sites for dry weight was increased when total nitrogen contents were considered (table 4.23).

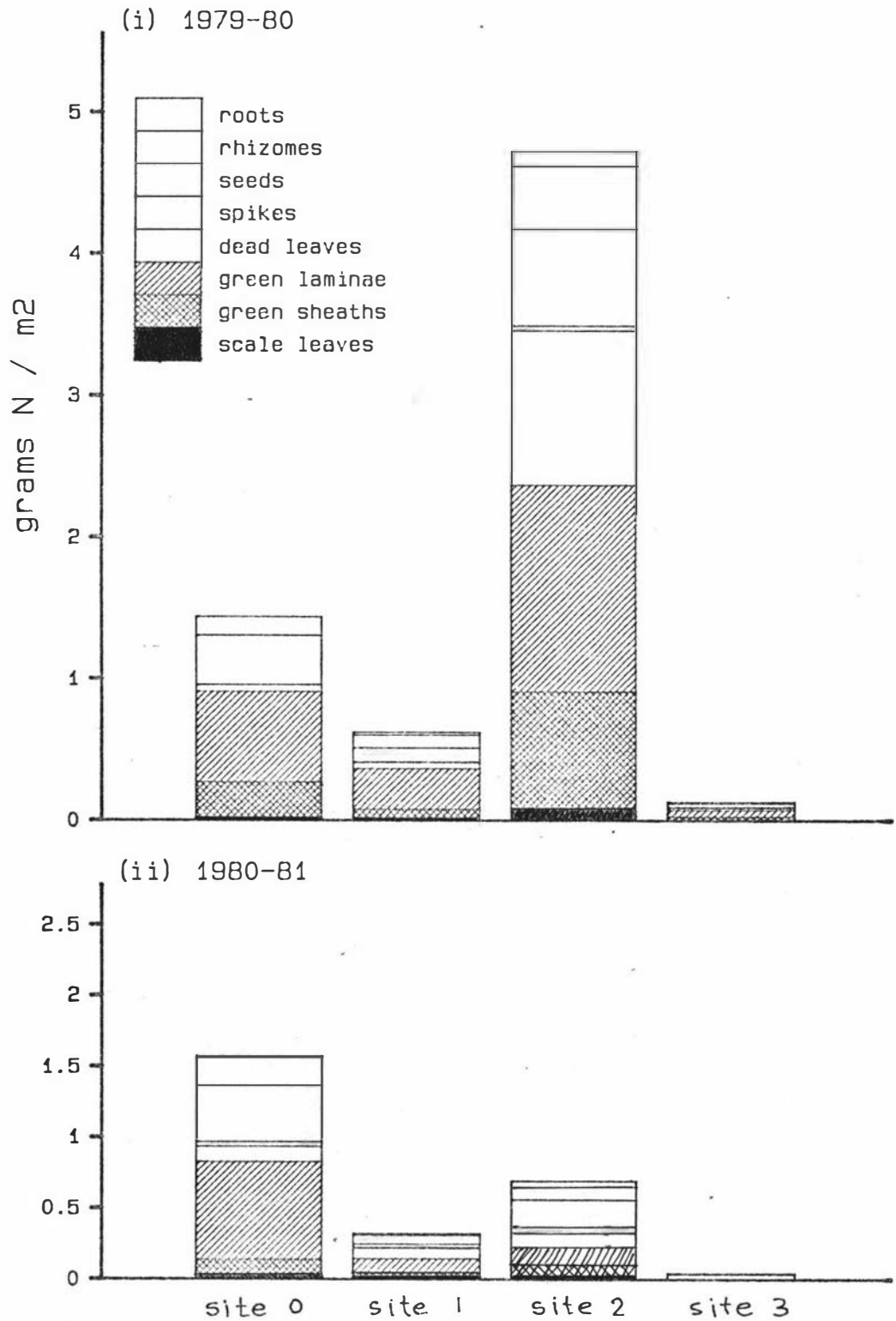
Table 4.23 The dry weight and total nitrogen content of component organs of fertile shoots per unit area, at S1 and S2 in December 1979.

	grams DW / m ²			grams N / m ²		
	S1		S2	S1		S2
Roots	2.33	**	9.00	.010	ns	.054
Rhizomes	9.00	ns	17.67	.046	ns	.134
Seed	6.67	**	42.22	.099	***	.683
Spikes	1.33	*	8.67	.006	ns	.034
Dead leaves	6.33	**	153.89	.032	***	.923
Green laminae	3.89	*	23.78	.076	**	.376
Culms & sheaths	3.00	*	39.56	.033	***	.408
Bracts	1.00	*	7.44	.004	ns	.039
Aer	22.22		275.50	.25		2.46
Total	33.44		302.11	.306		2.65

* P<.05; ** P<.01; *** P<.001; ns not significant

The difference between S2 and the other sites in terms of the total amount of nitrogen in the sward mass was maintained over the duration of the study. Over these three years, the Carex pumila component of sward mass or the living fraction of this at each of the old deflation hollow sites declined, both in terms of grams dry matter and total amount of nitrogen (table 4.24 and figure 4.22). These losses which reflected the increasing senility of these populations, were only partially balanced by the increases in both dry weight and total nitrogen of the 'other species' fraction (table 4.25). By contrast, at the two low dune sites, sward and live herbage mass and the total nitrogen contents of these parameters showed no such decline

Figure 4.22 Distribution of the total nitrogen content of *Carex pumila* biomass to component organs at four sites in summer 1979-80 and 1980-81



between the first and second summers in which these sites were monitored. Carex pumila was the only species included in the harvests at these two sites.

Table 4.24 Total nitrogen content (grams N per unit area) of the aerial biomass of Carex pumila at five sites on the sand plain between 1977-78 and 1980-81 (summer means).

	grams N / m ²				
	S0	S1	S2	S3	S4
1977-78	ne	0.58	5.61	1.22	0.23
1978-79	ne	0.65	3.82	0.29	0.14
1979-80	0.97	0.51	4.18	0.1	ne
1980-81	1.36	0.24	0.55	0.03	ne

In summer 1980-81, as in the previous summer, the total nitrogen content per unit area of living shoot modules (underground parts included) of Carex pumila was greater ($P < .05$) at the younger site towards the edge of the low dune than at the older site higher on the low dune (figure 4.22).

This greater quantity of plant nitrogen per unit area can be accounted for not by greater percentage levels of N, which were actually lower ($P < .05$) in shoots at the more adolescent site in 1980-81 (table 4.20) but simply by the greater living biomass at the younger of the two sites. By summer 1980-81, the total nitrogen content of the living shoot population at S2 in the old deflation hollow had declined substantially from that in the previous season (figure 4.22) as a result of the general senescence of the Carex

population at this site. Thus, although the total nitrogen content of live Carex shoots at the adolescent site on the edge of the low dune was greater than that at any of the other sites monitored in 1980-81 it was less than half that at S2 in the deflation hollow in summer 1979-80, the former value. The extremely low value obtained at S3 in the old deflation hollow in both 1979-80 and 1980-81 reflects the advanced stage of senescence of the Carex population on this part of the sand plain in both these years.

Table 4.25 Total nitrogen content of species other than Carex pumila

	grams N / m ²			
	S1	S2	S3	S4
1977-78	0	0.22	0.99	1.78
1978-79	0	0.26	1.11	1.67
1979-80	0	0.29	1.42	1.70
1980-81	0	3.53	1.96	ne

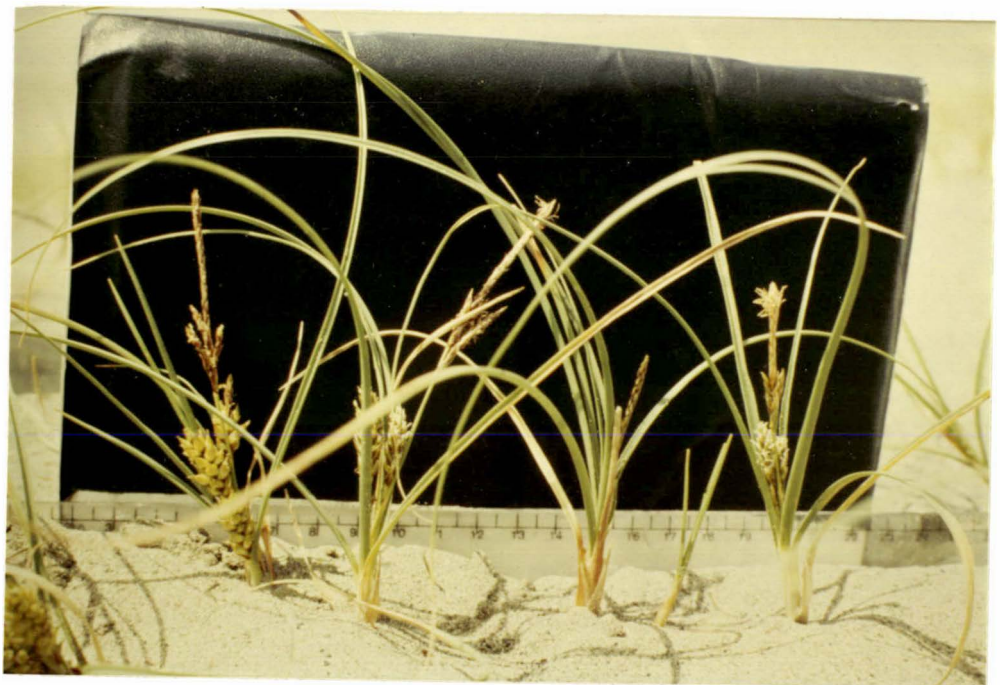
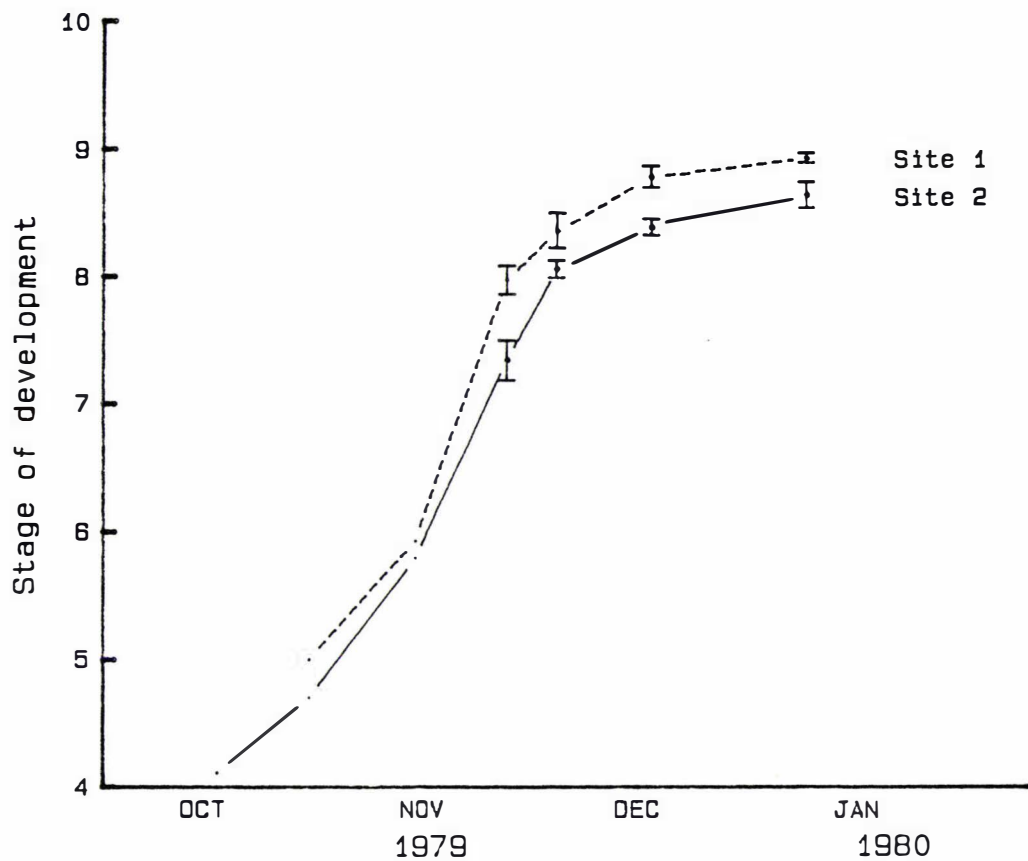
4.3.5 Flowering and seed production

At those sites at which fertile shoots of Carex pumila were present in the summers of 1978-79, 1979-80 and 1980-81, heading (the emergence of the terminal male spike from the mouth of the sheath of the youngest leaf; stage 5) occurred during October. In spring 1978, heading on the earliest fertile shoots at S1, S2 and S3 occurred between visits to the study area on 3 and 18 October whereas in 1979 earliest heading was between 6 and 13 October (at S1 and S2).

From spring 1979 the stage of shoot development was scored and leaf laminar area was measured on individual fertile shoots within the harvested samples. The changes in these parameters over time at S1 and S2 are shown in figure 4.23 and 4.24. Figure 4.23 may be compared with the phenology of flowering determined for fertile shoots removed to the laboratory in spring 1979 and monitored daily (section 2.3). Heading was reached between 30 October and 4 November. The uppermost female spike emerged (stage 5.5) as a result of continuing culm elongation six to eight days later. Within a further six days culm elongation ceased and stigmas were seen to have emerged and anthesis begun (stage 6). Anthesis was completed (stage 7) within another seven to nine days. Noticeable swelling of utricles (stage 8) occurred within another seven to nine days. The period of seed filling stages 7 to 9) extended for 5 to 6 weeks between the end of November and early January. Figure 4.23 b indicates the variability within a site population for stage of fertile shoot development.

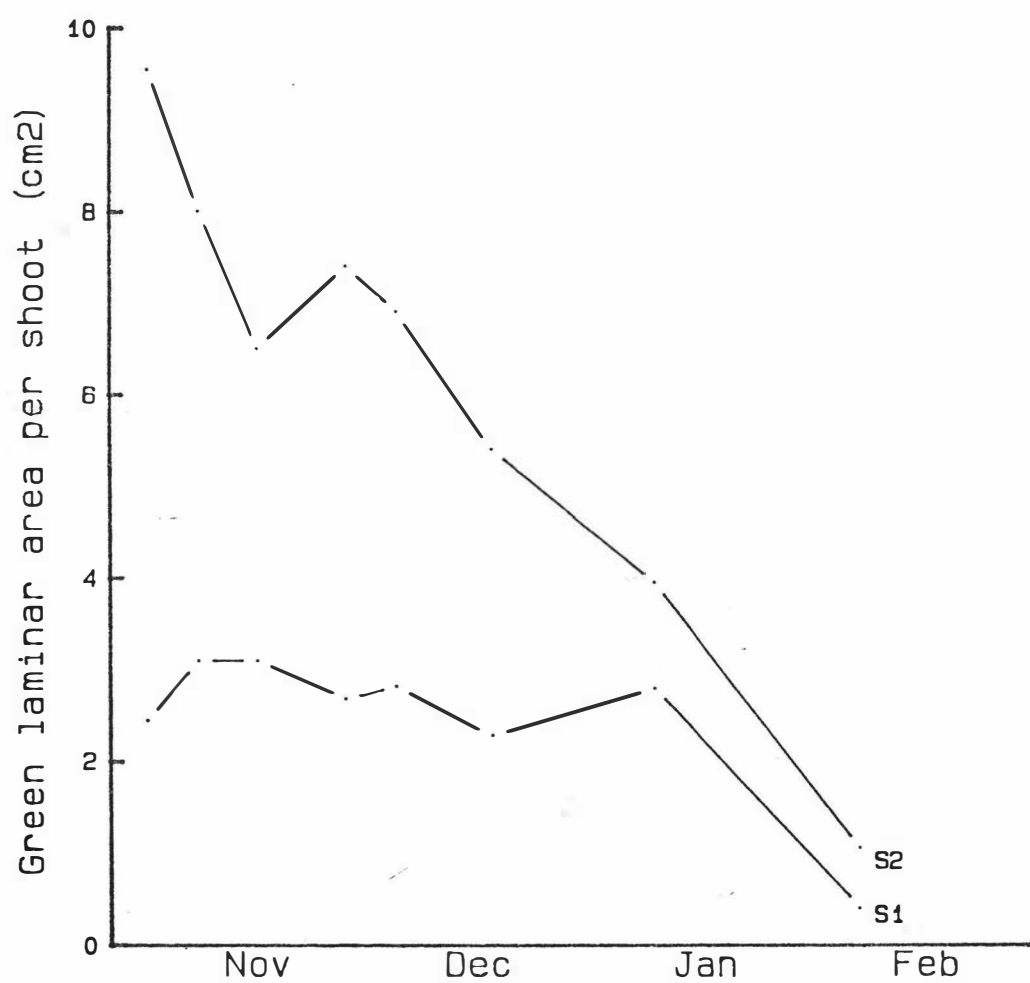
The development of fertile shoots of Carex pumila over the summer 1979-80 was accompanied by the gradual decline in the green leaf area per shoot (figure 4.24) and thus the ability of vegetative shoot parts to assimilate carbon. Since green laminar area was measured on individual shoots, this decline gives a more accurate picture of the onset of maturity in this coherent shoot cohort than the changes in dry weight of green leaf laminae per shoot, which were based on bulk leaf samples. Changes in green laminar area per fertile shoot between November 1979 and February 1980 mirrors the changes in stage of shoot development these shoots (figure 4.23).

Figure 4.23 (a) Mean ($\pm$ standard error) stage of development of fertile shoots of *Carex pumila* over time at two sites on the sand plain, during summer 1979-80.



4.23b Fertile shoots on the low dune, 27 November 1979. Left to right: stage 8-9; stage 7; stage 5; stage 6.

Figure 4.24 Mean area of green leaf laminae per fertile shoot over time at two sites on the sand plain, during summer 1979-80



The observation of the timing and duration of seed-filling determined from the visual score of stage of development was confirmed by direct measurement of the dry weight of seeds which when expressed on a per seed basis was seen to increase rapidly over December to maxima in early January (figure 4.25). The more precocious development of the fertile shoot population at S1 compared with that at S2 was evident throughout the spring/early-mid summer of 1979-80 (figure 4.23). Thus, by early January 1980, mean stage of development of fertile shoots at S2 in the old deflation hollow was similar to that found three to four weeks previously on the low dune site S1 (figure 4.23).

The rapid increase in mean dry weight of the inflorescence (figure 4.26) could be attributed to the increase in mean dry weight of seeds (figure 4.25) rather than the mean number of seeds. In both 1978-79 and 1979-80 mean number of seeds per inflorescence was observed to have reached a maximum at each site monitored by late November (figure 4.27). Earlier reduced estimates resulted from the incomplete elongation of the culm. More than one-third of the fertile shoots at S1 and S2 had not developed beyond stage 5 by mid-November 1979. Thus, female spikes on these reproductive shoots were still to emerge, accounting for the reduced mean number of female spikes per inflorescence at S1 and S2 at the mid-November harvest (figure 4.28). Further, the most distal female spike was observed to possess fewer spikelets than later-to-emerge spikes lower on the culm (table 4.26). Thus, although the full complement of spikelets was likely to have been present in early summer, the mean number of spikelets counted on emerged female spikes was lower in mid-November 1979 than that observed later in the summer (figure 4.29).

Figure 4.25 Mean seed weight of *Carex pumila* over time at three sites on the sand plain during summer (a) 1978-79 and (b) 1979-80.

Vertical bars denote $\pm$ standard errors of means

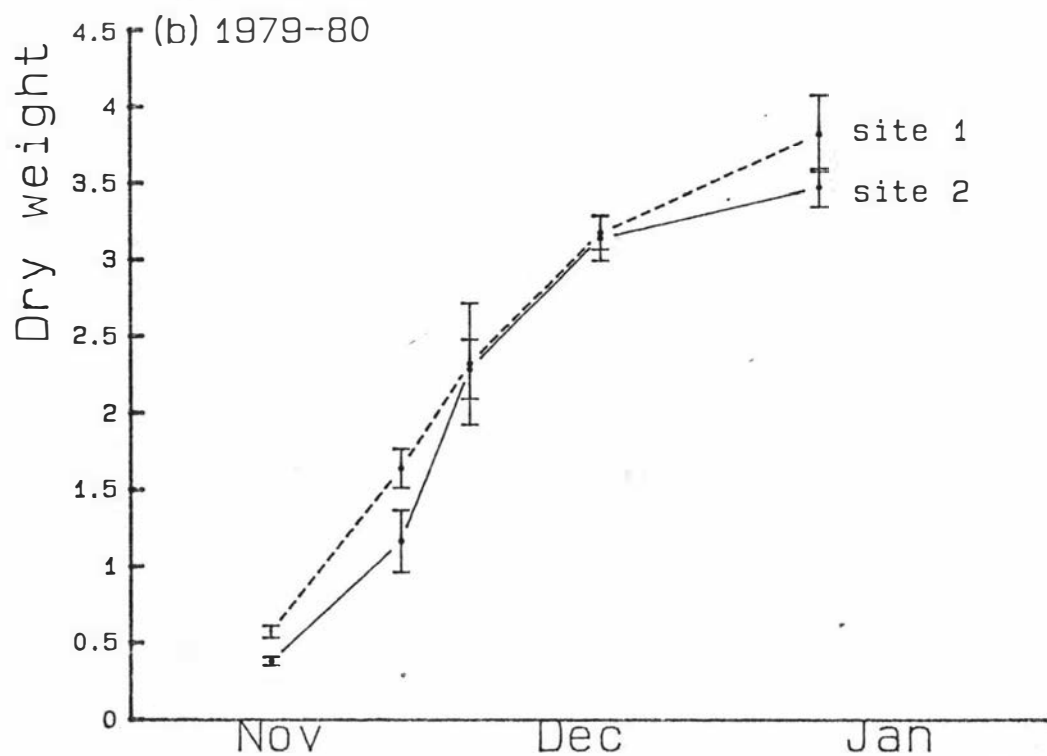
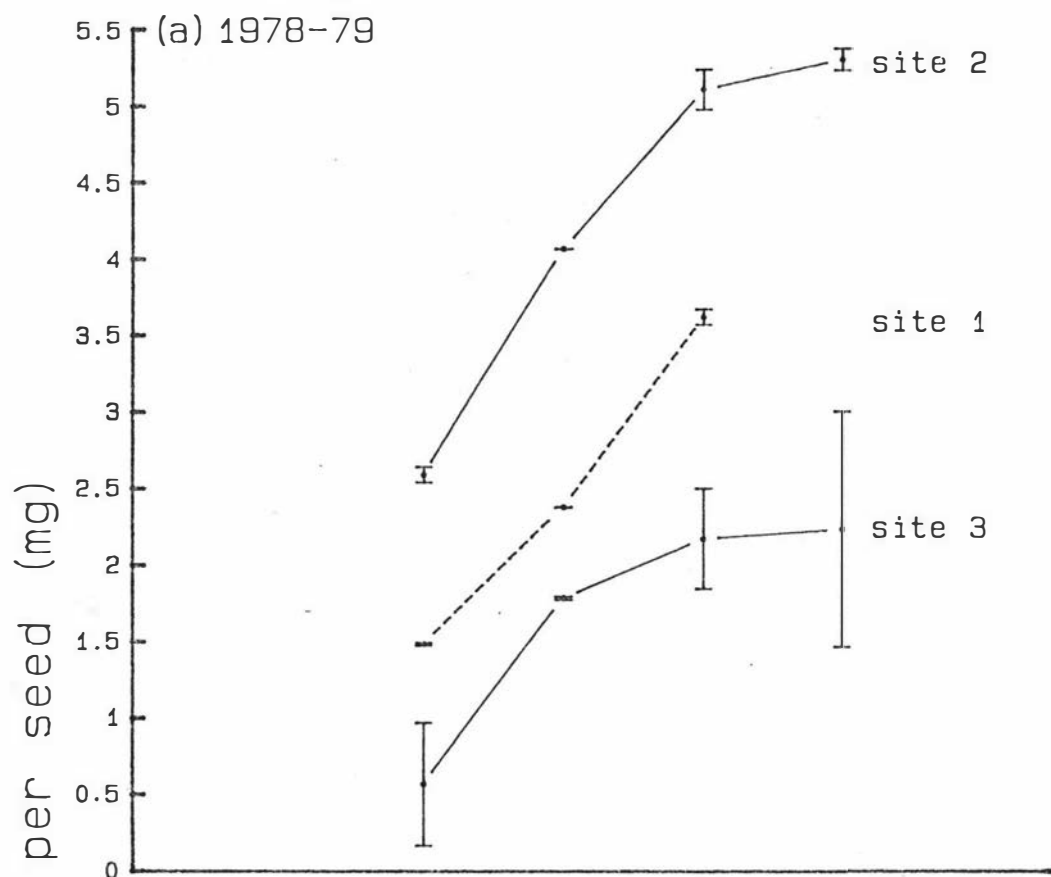


Figure 4.26 Mean dry weight of seeds per inflorescence of *Carex pumila* over time at three sites on the sand plain during summer (a) 1978-79 and (b) 1979-80.

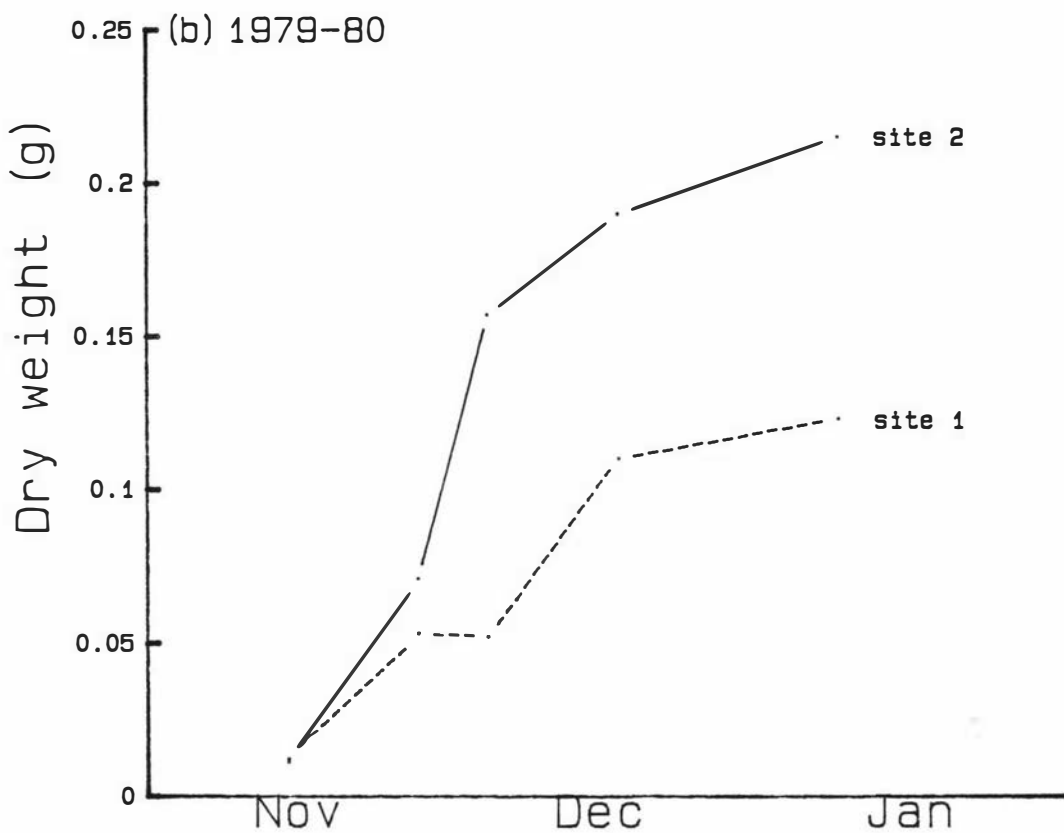
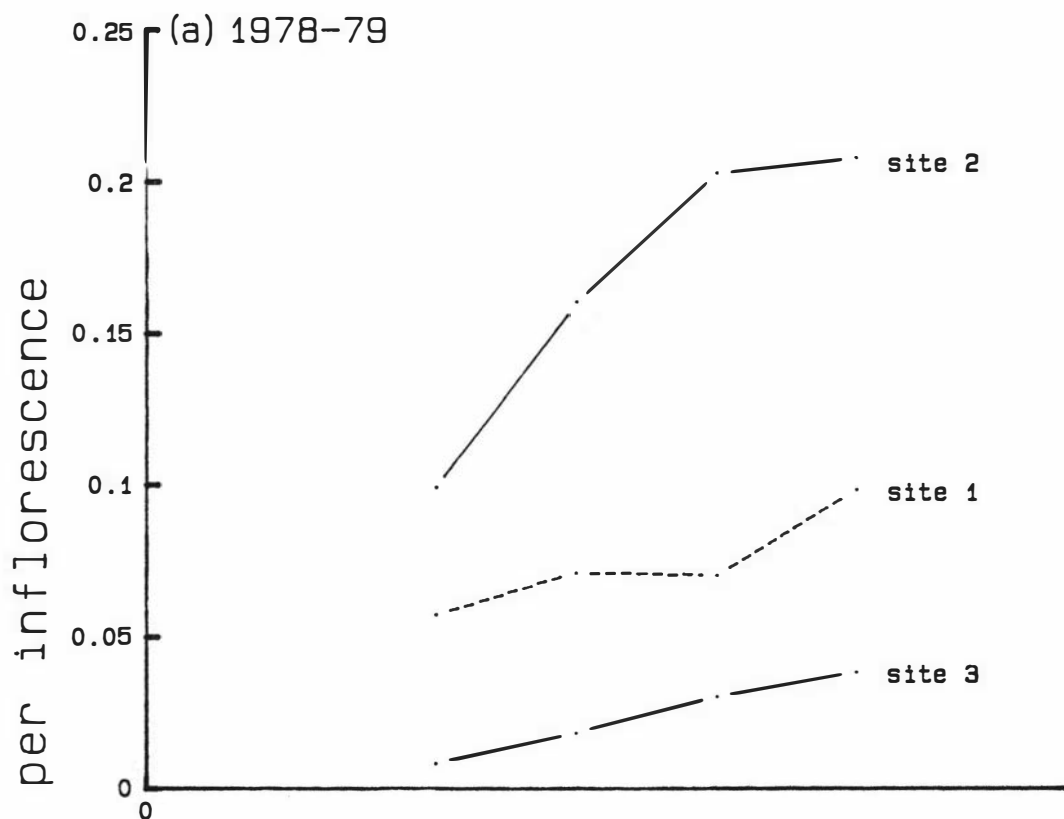


Figure 4.27 Mean ($\pm$ standard error) number of spikelets (seeds) per inflorescence over time, at three sites on the sand plain, during summer (a) 1978-79 and (b) 1979-80.

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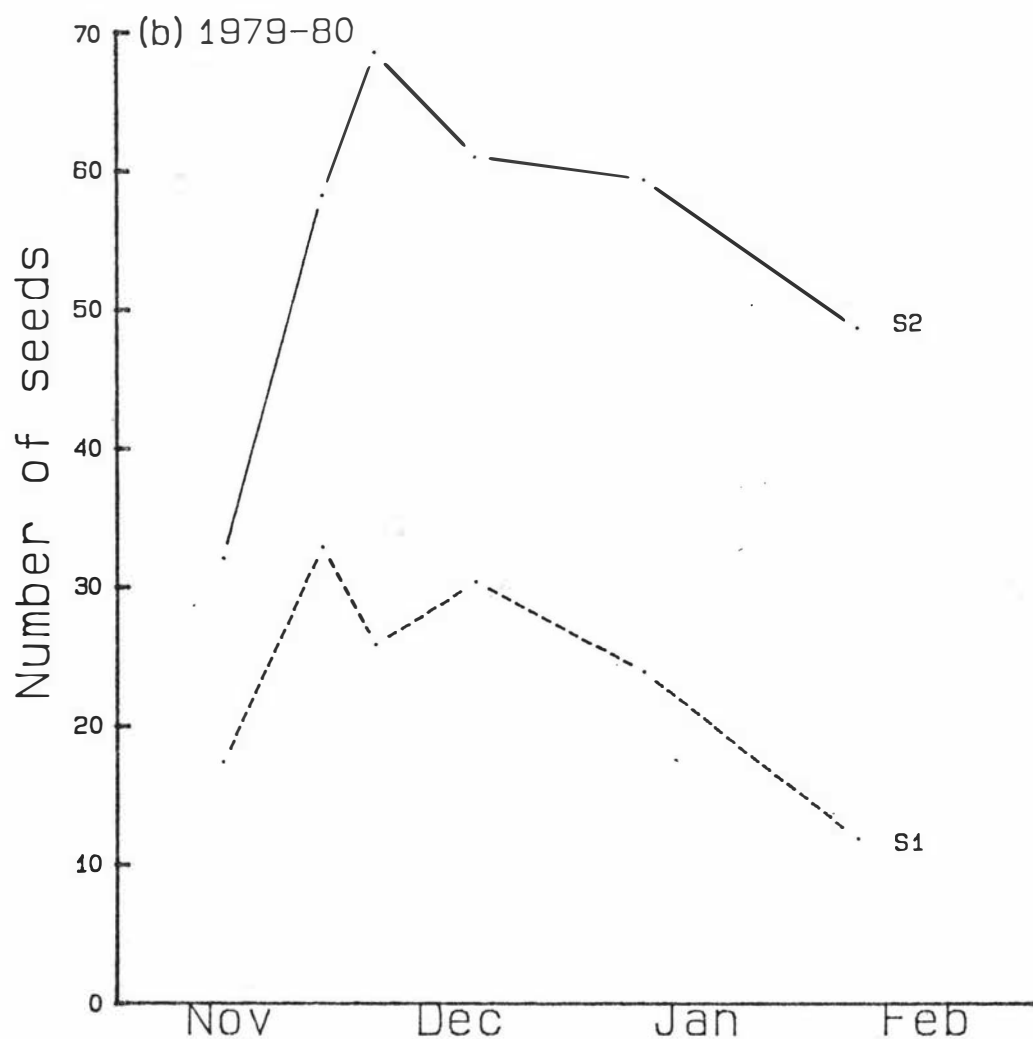
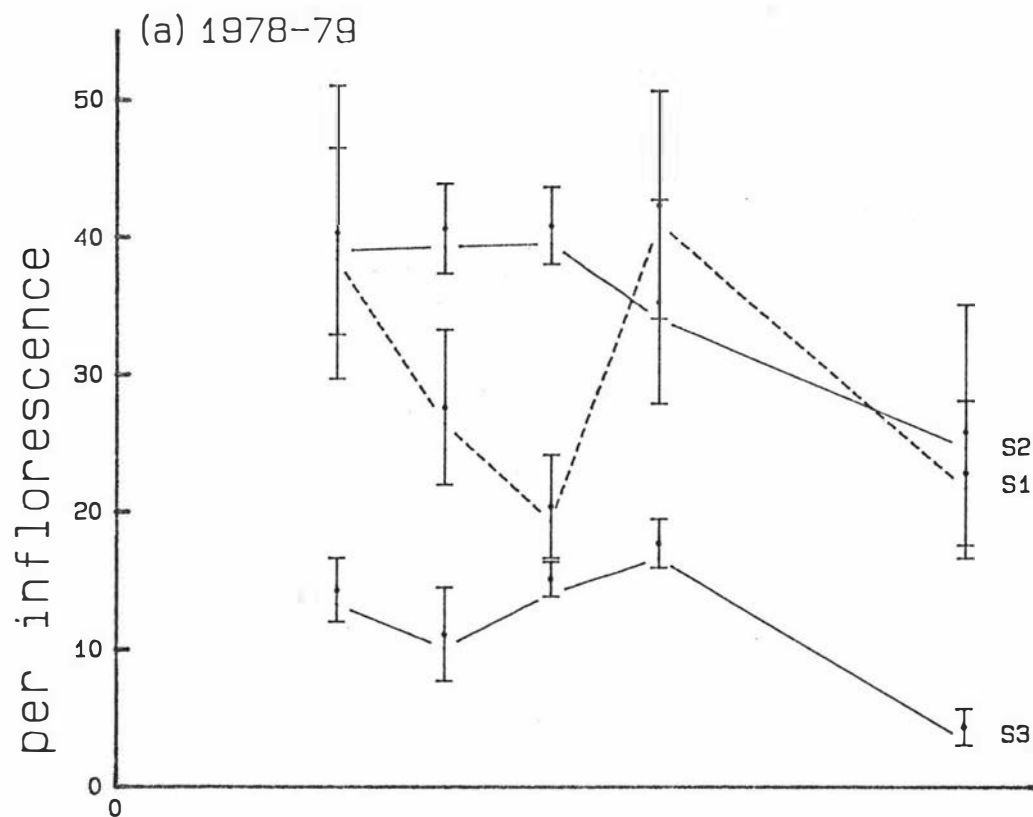


Figure 4.28 Mean ($\pm$ standard error) number of female spikes per inflorescence over time at three sites on the sand plain during summer 1979-80.

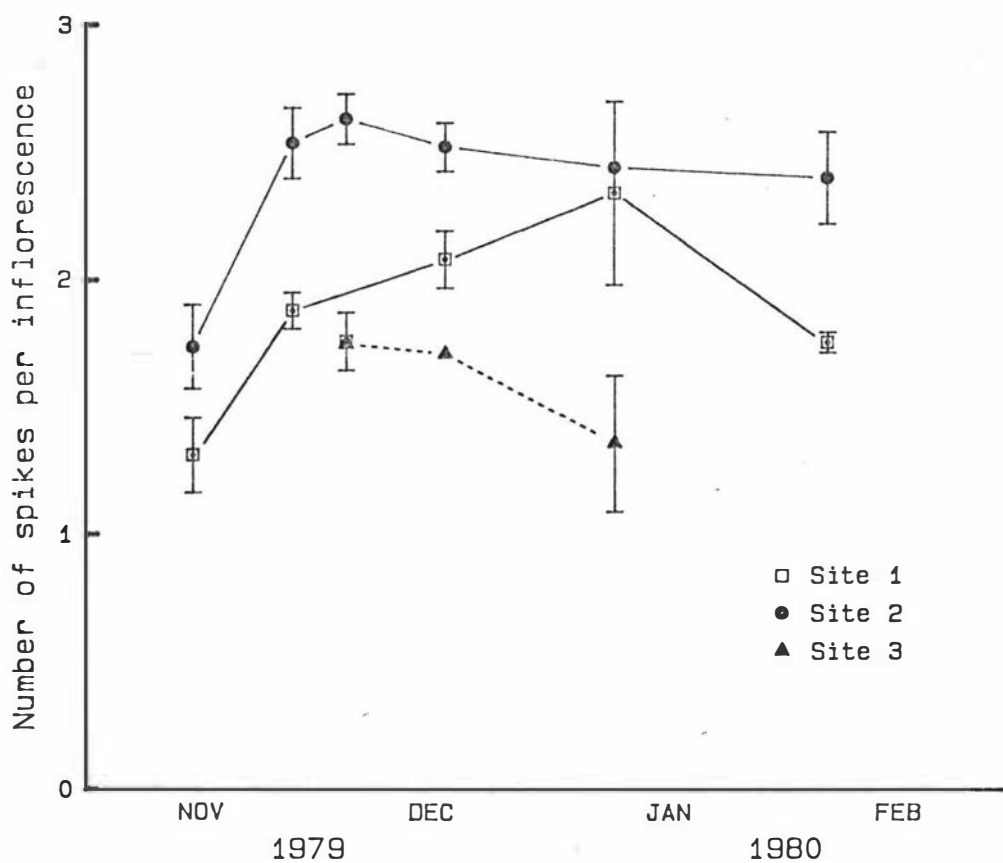
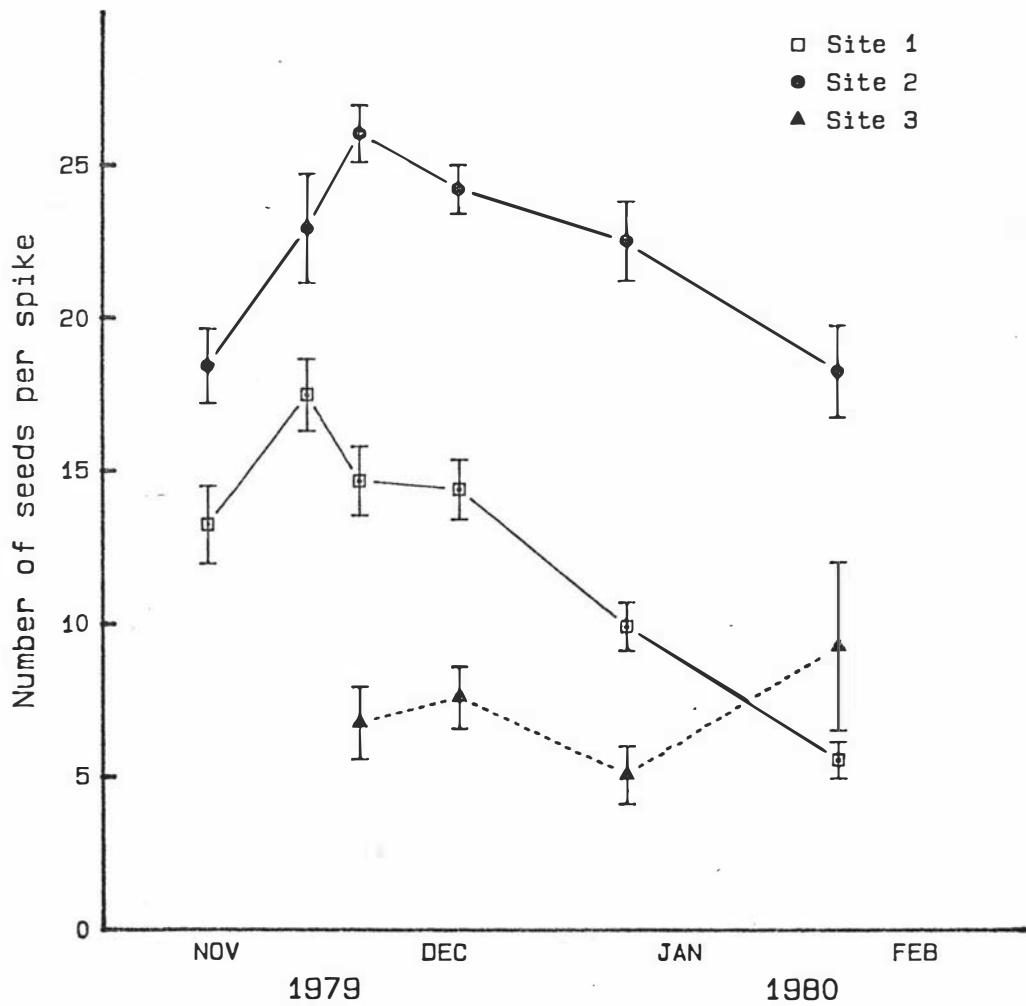


Figure 4.29 Mean ($\pm$ standard error) number of seeds (spikelets) per female spike over time at three sites on the sand plain during summer 1979-80.



Considerable variation was found both within and between sites in the size of inflorescences produced by Carex pumila, as a result of the number of female spikes that developed on each fertile shoot and the number of spikelets produced per spike. In mid-summer 1979-80, mean number of spikelets per inflorescence found on fertile shoots at S2 was greater than at S1. Both the number of spikelets per spike (figure 4.29) and number of female spikes per inflorescence (figure 4.28) contributed to this difference.

The terminal spike of Carex pumila is male, with occasionally ~~usually~~ one very small partly female spike at its base (figure 2.10). Such spikes produced few (0 to 5) seed. The remaining one to four spikes on shoots observed in the present study were female, although occasionally the most distal flowers on these spikes were male (figure 2.10). Female spikes produced up to 60 seeds each. Table 4.26 shows that the mean number of seeds per female spike varies very little for inflorescences with two, three or four female spikes. Where inflorescences possessed a single female spike, the number of spikelets was reduced. The average number of seeds produced by the largest inflorescences in the old hollow at S2 was comparable with that produced by Carex arenaria shoots with five well-developed spikes per inflorescence (Noble 1982).

Table 4.26 Mean number of spikelets (seeds) per female spike on fertile shoots of Carex pumila at four sites on the sand plain, in December 1979, (a) on the most distal and most basal female spikes on the culm and (b) on inflorescences with different numbers of spikes.

(a)	Number of seeds per spike			
	S0	S1	S2	S3
Most distal	18.0	13.0 $\pm$ 7.4	22.2 $\pm$ 11.2	3.8 $\pm$ 4.2
Most basal	25.0	16.2 $\pm$ 5.2	27.4 $\pm$ 10.5	8.7 $\pm$ 3.1

(b)	Number of spikes per inflorescence	Number of seeds per spike			
		S0	S1	S2	S3
	4	-	-	24.0	-
	3	23	17.5	26.48	8.33
	2	-	16.62	25.56	-
	1	-	12.8	19.0	6.00

The maturation of fertile shoots of Carex pumila during the late summer/autumn 1977-78, 1978-79 and 1979-80 was accompanied by a decline in the mean dry weight of seeds per inflorescence (figure 4.26). This decline was largely attributable to the shedding of mature seed seen in the decrease in mean number of seeds per inflorescence over this late summer period (figure 4.27). However, even where no seed was seen to be shed, as from fertile shoots at S2 between January and April 1978, mean seed dry weight still declined (figure 4.25). This decline was attributed to the decrease in dry weight of the utricle which during stages 7 and 8 was photosynthetic and turgid but turned brown during the latter stages of fertile shoot development (stages 9 and 10).

Where reduction of both mean number and dry weight of seeds per inflorescence over the late summer periods was evident, the mean dry weight per shed seed was estimated. Table 4.27 shows that shed seed was, on average, heavier than that retained by fertile shoots at each site monitored both in 1977-78 and 1978-79 (compare with figure 4.25). The estimated mean dry weight per shed seed at S3 in autumn 1978 was 7.436 mg (table 4.27), a value comparable with the maximum mean dry weight of seeds found in summer 1977-78 at S2 (figure 4.25). Dissemules shed at S4 in both 1977-78 and 1978-79 and at S3 in 1978-79, from the more senile old deflation hollow populations, although heavier than those remaining on shoots, were so light (table 4.27) that they were unlikely to contain viable seed.

Table 4.27 Estimated parameters of seed shed from time of seasonal maximum mean weight per seed (a) in 1977-78 to harvest 2 and (b) in 1978-79 to harvest 11 at various sites on the sand plain.

Seed shed				

Number per		Dry weight		
inflorescence		-----		
		mg/seed	g/infl.	g/30x30cm
(a) 1977-78				
Site 2	0	-	-	-
Site 3	20.71	7.4360	0.154	2.06
Site 4	16.29	2.1486	0.035	0.087
(b) 1978-79				
Site 1	6.32	6.9620	0.044	0.0972
Site 2	14.60	6.0274	0.088	1.7776
Site 3	9.10	2.2333	0.020	0.1183
Site 4	4.00	1.7500	0.007	0.0132

In summer 1979-80, the number of spikelets(seeds) on each female spike, and number of spikes per inflorescence were counted and length of each spike was measured providing more direct evidence for the shedding of seed from midsummer. The linear regression of spike length on number of seeds per spike in mid-December 1979 at each site monitored allowed the estimation of the number of seeds subsequently shed from those spikes on which it was apparent seeds were missing when harvested later in the summer. The linear regression equations used to estimate numbers of seeds shed are given in table 4.28.

Table 4.28 Regression equations used to estimate seed number per female spike (y = seed number per spike; x = spike length), in 1979-80

Site 1	$y = 1.211x + 2.769$	$r^2 = .551$
Site 2	$y = 1.431x - 0.033$	$r^2 = .873$
Site 2 Sheltered	$y = 1.117x + 4.62$	$r^2 = .742$
Site 3	$y = 1.288x - 0.621$	$r^2 = .894$

In early January 1980, more than one half of the spikes counted at S1 were found to have shed some of their seed. On average these spikes had lost 10.1 ± 1.49 seeds each (range 1 - 21 seeds / spike), which when averaged over all spikes in the sample was a mean loss of 5.82 ± 1.78 seeds/spike (table 4.29). This decrease from mid-December to early January was sufficiently large to be seen as significant when viewed indirectly through the mean number of seeds remaining on spikes (figure 4.29). Figure 4.29 also suggests a decline in seed number / spike at S2 in the old hollow, although this decline was not found to be statistically significant. The decline however, was real. At S2, a small proportion (c 5%) of the spikes sampled were observed to have lost some seed (range 3-37 seeds / spike), although when averaged over all spikes present in the sample the mean number of seeds lost per spike was small (table 4.29). The decline in seed number per spike average over all spikes present at S3 over this same period was similarly small (0.64 ± 1.11 seeds/spike) despite one-third of the spikes having lost seed. The mean loss of dry weight per spike, per inflorescence and per unit area as a result of the shedding of seeds was estimated on the basis that shed seed was on average equivalent to the mean dry weight/seed at the harvest preceding loss. The mean dry weight of seeds, per seed and per inflorescence continued to increase

at all sites monitored over this December-January period (figures 4.25 and 4.26) when mature seed was being shed. The dry weight of seeds lost will therefore be underestimated since shed seed tended to be the larger, heavier ones on the inflorescence. This was confirmed by the direct observation of the small proportion of dropped seed that was incorporated in the samples in January and February 1980. This proportion of recaptured seed gives an estimate of the vagility of Carex pumila dissemules.

Table 4.29 Mean loss of seeds (number and dry weight) from December 1979 to (a) early January 1980 and (b) early February 1980 ($\pm$ SD, n=4).

(a)	Number of seeds shed			
	/30 x 30 cm	/inflorescence	/spike	
Site 1	136.75 $\pm$ 17.77	13.34 $\pm$ 3.74	5.82 $\pm$ 1.78	
Site 2	25.75 $\pm$ 31.78	3.0 $\pm$ 3.12	1.06 $\pm$ 1.16	
Site 3	4.5 $\pm$ 7.79	1.13 $\pm$ 1.95	0.64 $\pm$ 1.11	
	Dry weight of seeds shed			
	g/30x30cm	g/inflorescence	g/spike	mg/seed
Site 1	0.45	0.044	0.019	3.2904
Site 2	0.081	0.009	0.003	3.1462
Site 3	0.006	0.002	0.001	1.3469
(b)	Number of seeds shed			
	/30 x 30 cm	/inflorescence	/spike	
Site 1	177.5 $\pm$ 53.39	12.41 $\pm$ 2.28	7.035 $\pm$ 1.02	
Site 2	86.0 $\pm$ 57.6	9.61 $\pm$ 7.72	4.07 $\pm$ 3.18	
	Dry weight of seeds shed			
	g/30x30cm	g/inflorescence	g/spike	mg/seed
Site 1	0.99	0.07	0.027	3.8286
Site 2	0.299	0.033	0.014	3.4766

The decline in mean number of seeds per spike estimated either directly from the regression of seed number on spike length (table 4.29) or indirectly from the mean number of seeds remaining on spikes (figure 4.29) continued over January to early February 1980. There is also evidence that at S1 whole female spikes were shed by fertile shoots over this same period. The mean number of spikes per inflorescence in early February 1980 was significantly ($P < .05$) lower than that observed at the previous harvests (figure 4.28). Assuming shed spikes at S1 each possessed 9.9 seeds (figure 4.29) then the loss of both number and dry weight of seeds from fertile shoots at site 1 over the late summer to February 1980 is shown in table 4.29. The loss of seeds from fertile shoots at S2 and S0 over this same late summer period was attributed solely to the shedding of mature seed from spikes and not to the loss of whole spikes (figure 4.28).

Seasonal maxima for mean seed dry weight and mean seed number were observed in December/January 1978-79 and 1979-80 (figures 4.25, 4.26, 4.27 and 4.29). Thus, the best estimates of these parameters in summer 1977-78 and 1980-81 would have been obtained at the harvests in January 1978 and December 1980. The seasonal maxima for mean dry weight of seeds per inflorescence and per seed and mean number of seeds per inflorescence at each of the old deflation hollow sites decreased from year-to-year as the resident Carex pumila populations aged (figures 4.30, 4.31 and 4.32 respectively), reflecting the increasing senility of these populations. At S0 and S1 at which the Carex pumila populations were juvenile when first monitored (in spring 1979 and summer 1977-78, respectively), seasonal maxima for mean dry

Figure 4.30 Seasonal maximum mean dry weight of seeds per inflorescence in four consecutive summers at various sites on the sand plain
Vertical bars denote $\pm$ standard error

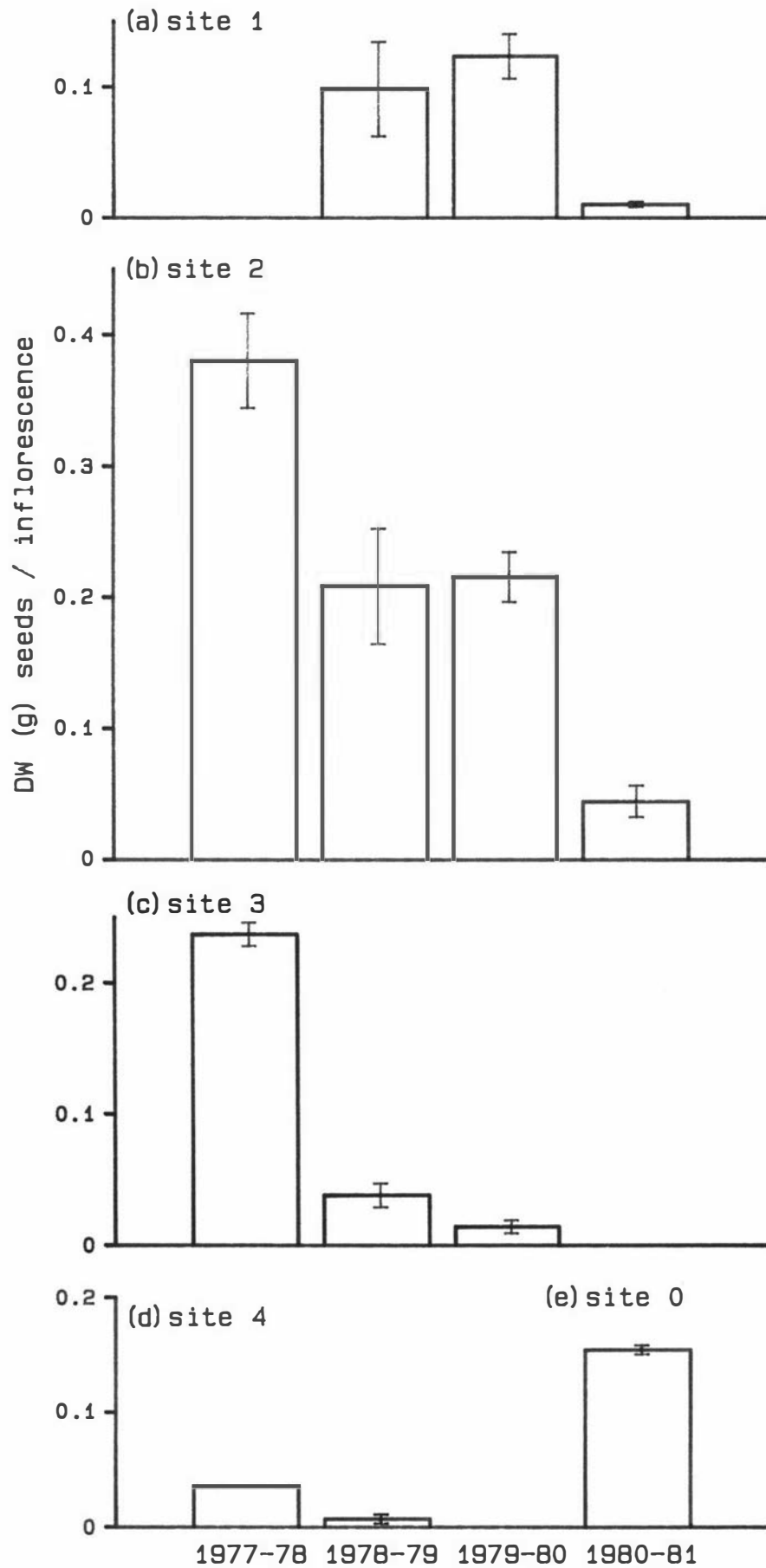


Figure 4.31 Seasonal maximum mean dry weight per seed of *Carex pumila* in four consecutive summers at five sites on the study area
Vertical bars denote $\pm$ standard error of means

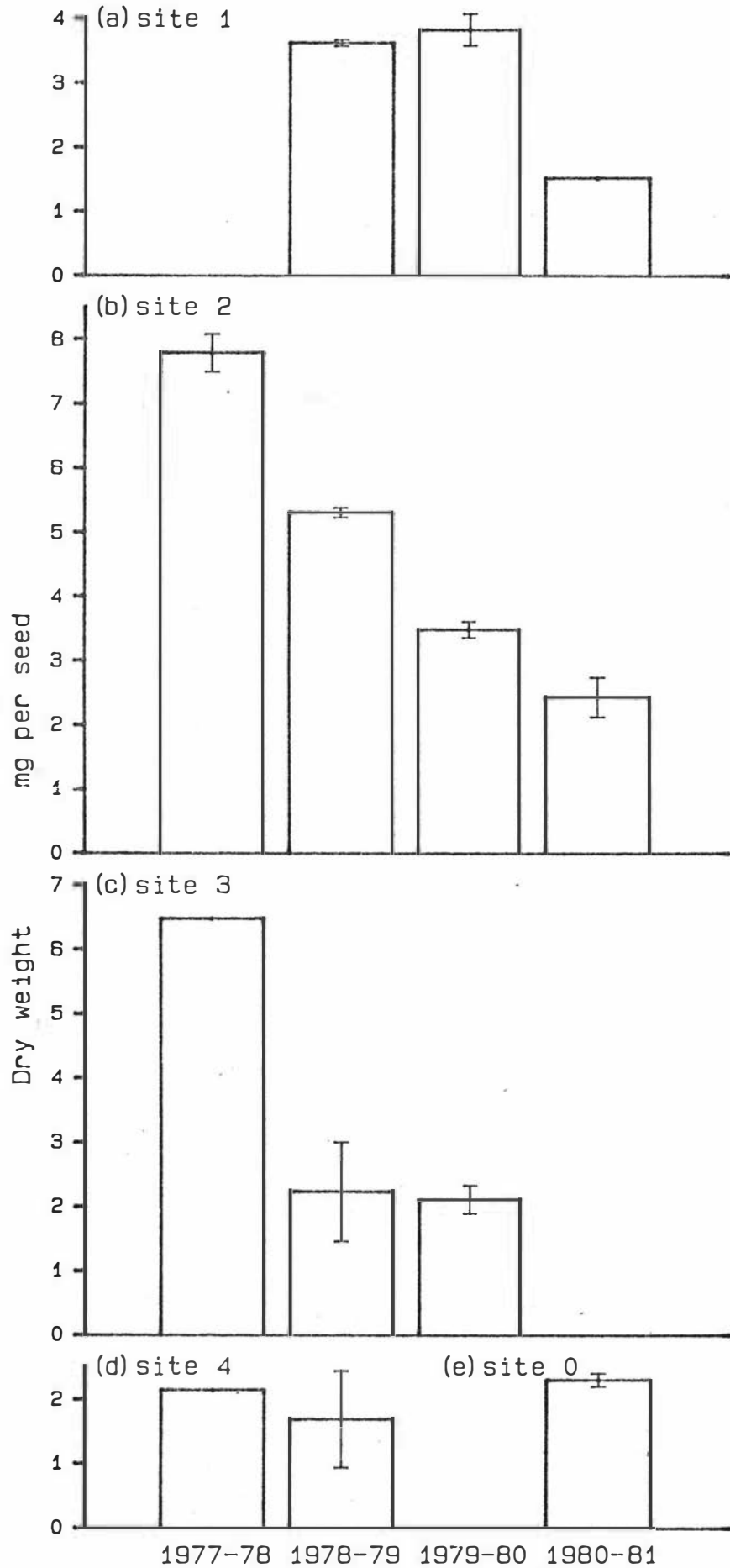
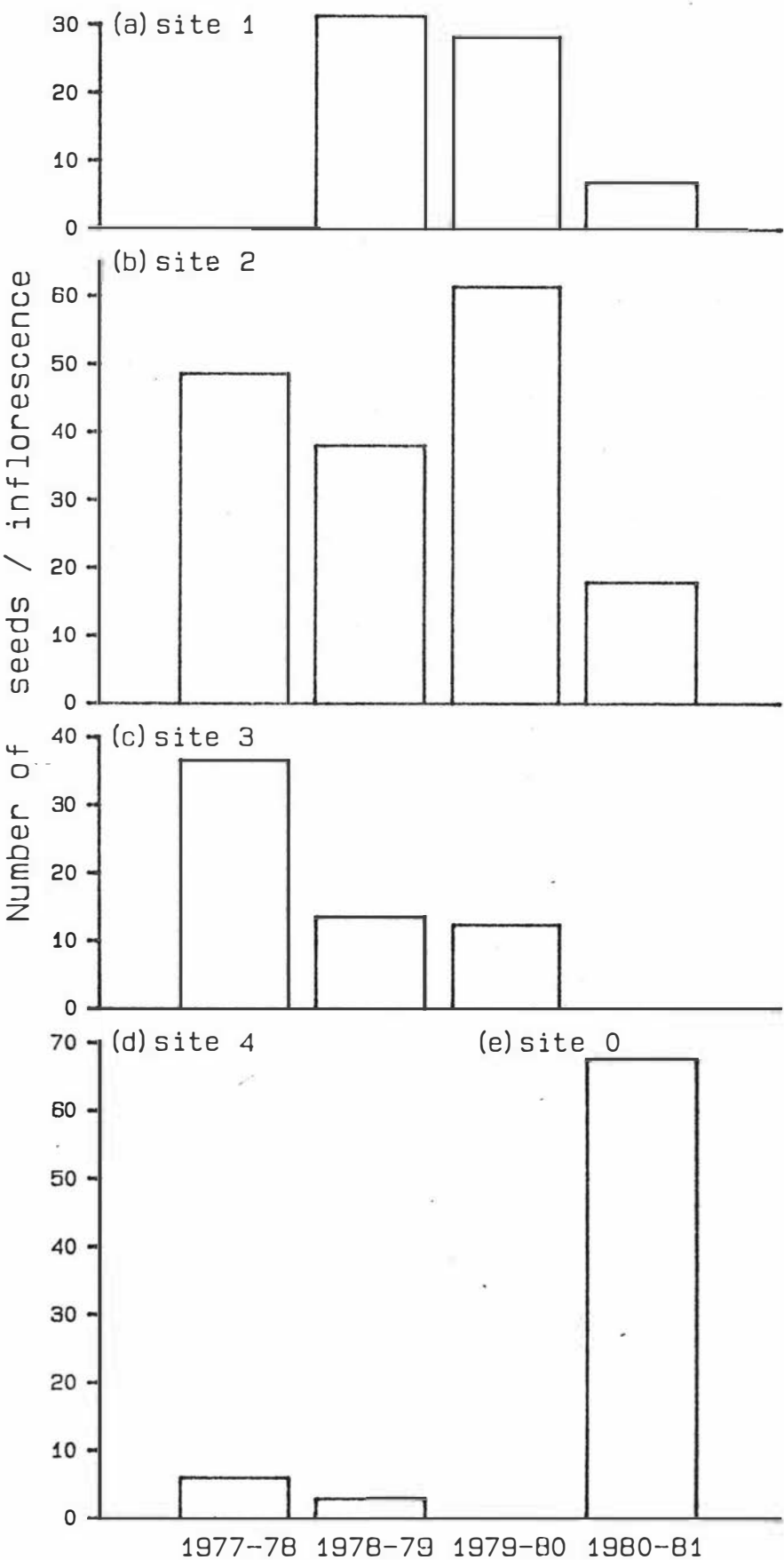


Figure 4.32 Seasonal maximum mean number of seeds per inflorescence of *Carex pumila* in four summers at five sites on the study area



weight of seeds per fertile shoot and per seed initially increased between years as the populations matured (between 1977-78, 1978-79 and 1979-80 at S1, and between 1979-80 and 1980-81 at S0; (figures 4.30 and 4.31). The maximum values obtained for these parameters on the low dune (at S1 in 1979-80 and S0 in 1980-81) were lower than local maxima obtained in the deflation hollows (at either S2 in 1977-78 and 1978-79 or S3 in 1977-78), reflecting the less favourable conditions for Carex pumila growth in the former habitat. As the population at S1 aged further in 1980-81, seed weight and number were considerably lower than that achieved in previous years (figures 4.30, 4.31, and 4.32) reflecting the senility of this population.

Within any one season, the maximum values obtained for these various seed dry weight and seed number parameters in the old hollow populations reflected the proximity of the site to the terminal hollow and therefore the putative age the population. With increasing distance from the terminal hollow, maximum mean seed dry weight per inflorescence and per seed and mean seed number per inflorescence and per female spike decreased in a manner similar to that seen between seasons at each of these sites. Younger phases of Carex pumila development on a deflation hollow site were not represented on the sand plain at any stage during the four summers of the present study. On the low dune however, such phases of development were represented. In 1977-78 and 1979-80 at S1 and S0 respectively, the Carex pumila populations were juvenile, producing no or few fertile shoots. Comparisons between S0 and S1 for seed parameters was possible in 1980-81, when the three seed parameters were reduced at the older (S1) compared with the younger (S0) population (figures 4.30, 4.31 and 4.32).

In summer 1979-80, shelter affected the development of fertile shoots of Carex pumila on the low dune at S1 differently from that on the deflation hollow at S2. At S1 shelter slowed the onset of maturity of fertile shoots, whereas the effect was reversed at S2. At S1, the effect was significant ($P < .01$) by mid-summer (table 4.30). In early February 1980, mean stage of development of fertile shoots on the control plots was 9.74, with all shoots scoring 9.5 or 10. A similar mean score was achieved on the sheltered plots in late February (nearly three weeks later) and even then 25% of fertile shoots scored 9.0 (figure 4.33). Further mean length of female spikes at S1 was increased by shelter (table 4.31) and consequently mean seed output of these spikes was also increased. Shelter had no effect on the number of female spikes found on fertile shoots at this or any other site.

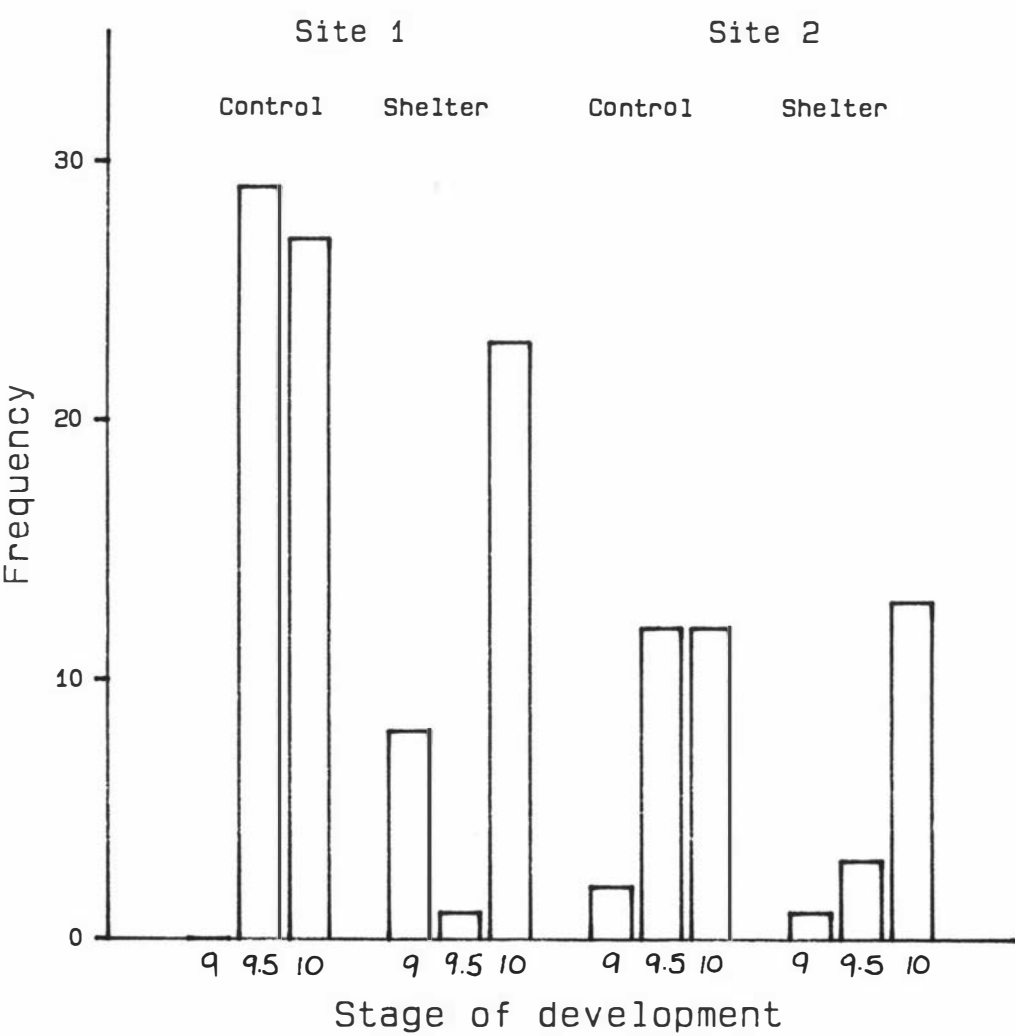
Table 4.30 The effect of shelter on the stage of fertile shoot development

	Mean stage of development					
	S1			S2		
	Control		Shelter	Control		Shelter
December	8.78	**	8.41	8.39	ns	8.25
January	8.93	**	8.60	8.64	ns	8.77
February	9.74		(9.73)	9.69	ns	9.85

(Estimate in brackets was obtained 3 weeks after that for control plots)

By contrast, shelter hastened the onset of maturity of fertile shoots on the old deflation hollow at S2. By early February, most fertile shoots on the sheltered plots at S2 had reached stage 10, whereas in the controls more than half were at stage 9.5 or 9 (figure

Figure 4.33 The frequency distribution of the stage of development of fertile shoots in February 1980, on sheltered and control plots



4.33). The mean difference however, was small and barely significant ($P=.10$). The main expression of the more advanced development of fertile shoots on the sheltered plots at S2, seen both in early January and early February 1980, was the significantly increased seed shedding. In early February 1980, the mean number of seeds remaining on spikes, which did not differ between treatments in December 1979, was highly significantly lower in the sheltered plots than in the controls.

Further, at S2 shelter affected both the slope and the intercept on the y-axis of the linear regression of spike length on number of seeds per spike. The effect was a more uniform number of seeds per spike; ie seed number for the larger than average spikes tended to be reduced, whereas for the shorter than average spikes, seed number per spike was increased by shelter.

Table 4.31 The effect of shelter on (a) mean spike length and (b) mean number of seeds/spike in December 1979 and (c) mean number of seeds/spike at S2 over time.

(a)	Mean spike length (mm)			
		Control		Shelter
	S1	11.52	a	17.32 b
	S2	17.48	b	15.73 b

(b)	Mean number of seeds / spike			
		Control		Shelter
	S1	13.57	a	23.7 b
	S2	23.67	b	25.83 b

(c)	Mean number of seeds / spike			
		Control		Shelter
	December	23.67		25.83
	January	24.02		20.98
	February	25.97		11.27

a < b; $P < .05$; Duncan's multiple range test.

The effect of shelter on fertile shoots at S2 was similar to the effect of increased temperatures on wheat development; namely, to shorten the duration of grain-filling by hastening the onset of maturity and therefore reduce maximum seed yields (Sofield et al. 1974). It is likely that an effect of increased shelter at S2 was to increase the already-elevated temperatures at this relatively calm old deflation hollow site. On the more exposed low dune (S1), the result of the reduced wind speeds within the shelters, to allow fertile shoots to continue growing into late summer, was probably related to

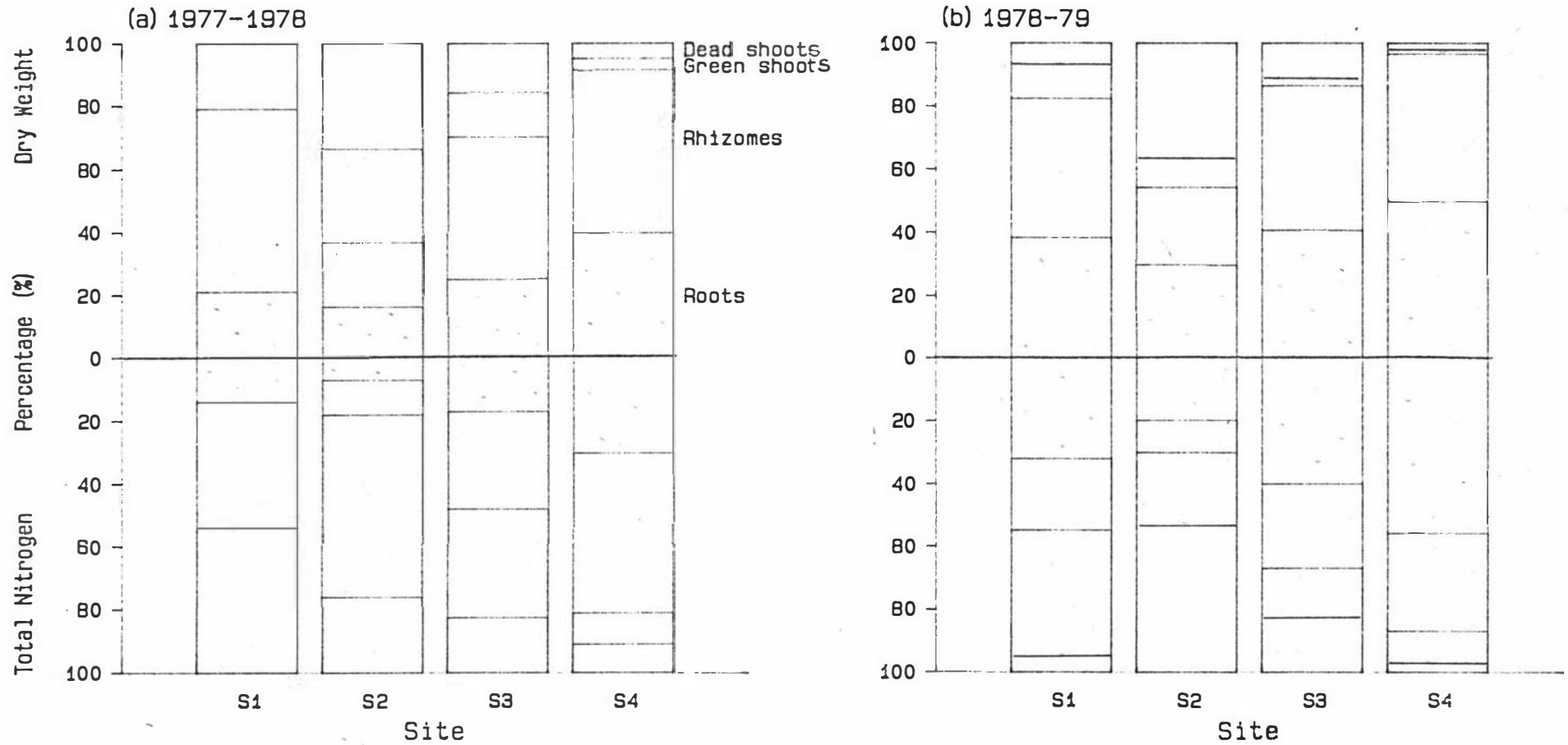
the amelioration of the water-stress conditions.

4.3.6 Allocation of dry weight and total nitrogen

1. Sward mass

In January 1978, the pattern of distribution of the dry weight of the Carex pumila sward to roots, rhizomes and herbage was similar at all sites monitored, with the exception of S2. At this latter site the resident population of Carex pumila was characterised by a large proportion (63%) of the total sward mass in herbage and a correspondingly small proportion (20%) in rhizomes. At the other three sites, S1, S3 and S4, the balance of herbage and rhizome mass was reversed, with less than 30% of the total sward mass in herbage, and between 45% and 60% in rhizomes (figure 4.34). The balance was found in roots. This difference can be related to soil fertility. It is well established that plants respond to low soil nutrient regimes by a decreased aerial:underground ratio (eg Lovett Doust 1980b). This response seen in rhizomatous perennial species as an increased proportional allocation to rhizomes allows the clone to remain and expand in situ in areas unfavourable to tall competitors (Ogden 1974a). Plant density remained high at the expense of extensive rhizome growth on the relatively fertile site, S2. The juvenile population at S1 could be distinguished from the other three populations by the proportion of herbage associated with live shoots - 100% at S1 in contrast to S2, S3 and S4 where at least 50% of the herbage was made up by dead shoots. The proportion of the sward attributable to live shoots (aerial biomass) was however still greater at S2 than at S1. At S3 and S4, at increasing distances from the terminal hollow, aerial biomass made up a decreasingly small

Figure 4.34 Proportional allocation of dry weight and total nitrogen of the sward mass of *Carex pumila* to aerial and underground components, at each of four sites (S1, S2, S3 and S4), in summer (a) 1977-78 and (b) 1978-79



proportion of the sward, reflecting the increasing senility of these populations.

The proportional allocation of the total nitrogen content of the sward mass of Carex pumila to aerial and underground components is also shown in figure 4.34. At all four sites, green shoots made up a greater proportion of the total than they did as dry weight while roots, rhizomes and dead shoots made up a correspondingly smaller proportion. This difference was the result of the higher concentration of total nitrogen in green and seed tissues.

Throughout 1978, the proportion of the Carex pumila sward found in herbage, measured both in dry weight and total nitrogen, continued to be greater at S2 than at all other sites. For instance, in April 1978, 80% of the total nitrogen of the Carex pumila sward at S2 was found in aerial shoots - 72% in live shoots. However, the proportion of the sward mass of Carex pumila found in herbage, and in particular aerial biomass, decreased at the three older sites between summer 1977-78 and 1978-79 (figure 4.34). As the maturity of the vegetation at S1 increased during 1978, herbage allocation increased (from 45% to 62% of total nitrogen between January and August 1978). The proportion of the sward mass at each site found in rhizomes in December 1978 was similar to that found eleven months previously, whereas that proportion found in roots had increased (figure 4.34). Aerial biomass as a proportion of sward mass was only 11.1% and 10.3% at S1 and S2 respectively (40% and 21% for total nitrogen). These values were significantly greater than those at either S3 or S4 (figure 4.34).

The decline in the proportional allocation of the sward to live shoots as the maturity of the population increased was also seen across the study area at sites at increasing distance from the terminal hollow in summer 1979-80 (figure 4.35). At sites of increasing age the proportion of the sward in live branches decreased. At S1 where in summer 1977-78 all shoots were living and vegetative, figure 4.35 shows that the total nitrogen apportioned to live branches was just 55% of the total and that 50% of this was apportioned to fertile shoots.

2. Biomass

The proportional allocation of biomass (live branches) of Carex pumila to rhizomes was greatest at those young sites towards the edge of the low dune where this species was spreading into the terminal deflation hollow. At the rhizome front 100% of the biomass of Carex pumila was underground, and almost entirely in the form of rhizomes. Adventitious root development usually follows the orthotropic development of branch modules (section 2.1). At S1 during 1978 and 1979 and at S0 during 1979 and 1980, more than 50% of biomass was allocated to rhizomes. At older sites both on the deflation hollows (S2, S3, and S4) and on the low dune (S1 in summers 1979-80 and 1980-81, and S0 in summer 1980-81) the proportion of biomass in rhizomes was considerably smaller (table 4.32).

Figure 4.35 The proportion of the total nitrogen content of the sward mass of *Carex pumila* found in vegetative, fertile and dead shoots, at four sites in summer 1979-80.

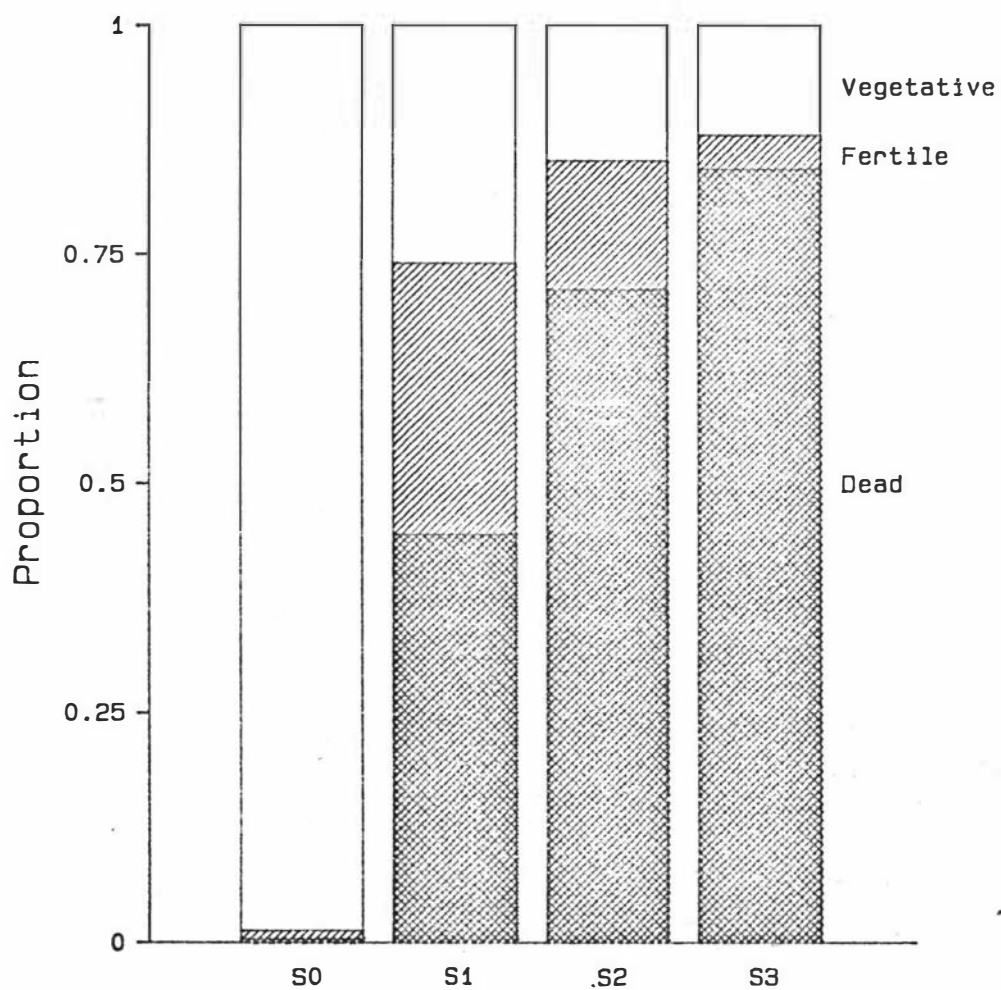


Table 4.32 Proportional allocation of standing biomass of Carex pumila to component parts, over time.

	Summer 1977-8	Winter 1978	Summer 1978-9	Winter 1979	Summer 1979-80	Winter 1980	Summer 1980-1
Site 1							
Roots	.213	.265	.265	.065	.051	.023	.09
Rhizomes	.579	.462	.52	.475	.320	.516	.372
Seeds	0	-	.002	-	.141	-	.028
Aerial	.209	.273	.218	.46	.488	.461	.510
Site 2							
Roots	.15	.162	.222	.06	.061	.113	.047
Rhizomes	.186	.214	.187	.237	.187	.499	.316
Seeds	.144	-	.089	-	.065	-	.100
Aerial	.521	.624	.494	.703	.687	.388	.537
Site 3							
Roots	.106	.170	.289	.255	.089	.195	.172
Rhizomes	.182	.314	.341	.361	.236	.448	.112
Seeds	.16	-	.025	-	.047	-	0
Aerial	.552	.516	.345	.484	.628	.357	.716
Site 4							
Roots	.29	.339	.361	.160	ne	ne	ne
Rhizomes	.377	.406	.359	.473	ne	ne	ne
Seeds	.011	-	.006	-	ne	ne	ne
Aerial	.322	.255	.274	.367	ne	ne	ne
Site 0							
Roots	ne	ne	ne	.050#	.123	.032	.026
Rhizomes	ne	ne	ne	.524#	.542	.737	.257
Seeds	ne	ne	ne	-	0	-	.100
Aerial	ne	ne	ne	.426#	.335	.231	.617
# Spring 1979							

Rhizome allocation in Carex pumila fluctuated seasonally being greater in winter/spring than in summer when aerial allocation reached a seasonal peak (table 4.32). This trend was obscured in the juvenile population at S1 where the initially high allocation to rhizomes was not superceded the following winter. As this population aged, the seasonal fluctuation became apparent. At S2, the proportional allocation of biomass to rhizomes, which was remarkably uniform in each of three successive summers (1977-78, 1978-79 and 1979-80) despite the winter increases, was significantly lower than that at other sites, and the aerial allocation significantly higher.

The proportion of dry weight devoted to aerial growth was greater in the more crowded populations compared with the less crowded populations. This was the case at S2 where aerial shoot densities were greater than at other sites. Aerial allocation also increased as populations increased in density with time on the low dune (table 4.32). Since aerial shoot parts contain higher concentrations of total nitrogen per gram dry weight than either roots or rhizomes (table 4.17), the increased proportional allocation to aerial parts in the more crowded populations, based on dry weights, was expectedly greater when based on total nitrogen.

The reduced aerial allocation at the two older deflation hollow sites (S3 and S4) compared with S2 can be attributed at least in part to the greater senility of the former sites. Likewise as the population at S2 became senile by December 1980, aerial allocation was decreased compared with that found at this site in previous summers. The winter/spring maximum proportional allocation to rhizomes at S2 in 1980 (55% of total DW) was more than double the previous site maximum obtained in winter 1979. Subsequently aerial growth did not occur to the extent observed in previous years.

The tendency towards a decreased aerial allocation as populations became increasingly senile was not apparent in all populations. As Carex pumila populations aged, shoot density become increasingly reduced. Whether an aerial shoot in such a population was attached to a dwarf or a long rhizome branch markedly affected the proportional allocation ratio. In the extremely depauperate population at S3 in summer 1980-81, all shoots on the control plots were attached to dwarf rhizome branches. Proportional rhizome allocation was 11% of biomass and aerial shoot allocation 72%. By contrast, on the nitrogen-fertilized plots at this site where the Carex population was

equally depauperate, but one-third of the aerial shoots were attached to long rhizome branches (section 4.3.7), the proportional allocation of biomass to rhizomes was markedly higher (24%), and that to aerial shoot parts lower (63%), than the controls.

Reproductive effort (RE), the proportional allocation of biomass to seeds (sexual reproductive effort, sensu Ogden 1974a), was minimal in young populations. At S1 in 1978-79, the Carex pumila population was sufficiently mature (up to 2 years old) that fertile shoots appeared in the budgets on most plots at all harvests, although at an extremely low density. Population RE (RE as a proportion of total biomass) at S1 at the time of maximum seed weight was only 0.2% (table 4.32). At S1 in 1977-78 and S0 in 1979-80 where the Carex pumila populations were less than one year old, fertile shoots were encountered only infrequently. At most harvests at these sites, all shoots sampled were vegetative. Thus, population RE was even smaller than that at S1 in 1978-79.

Maximum population reproductive effort found on the sand plain during the entire study (16% of biomass) was obtained in summer 1977-78 at S3 in the old deflation hollow. This value was approached only at S2 in the same summer (14.4% of biomass), and on the low dune as the populations matured, in 1979-80 at S1 (14.1%) and in 1980-81 at S0 (10%). In older populations, reproductive effort was reduced.

These data suggest an overall trend of increasing reproductive effort with population age over the first years from the time of colonization of a site followed by a period of declining reproductive effort as the population aged further, becoming more senile. At S0 and S1 this pattern was shown with increases over the first two and three years respectively followed by a decline at S1 in the fourth

summer. Only the declining phase of this pattern was shown in the deflation hollows at S2, S3 and S4. At the beginning of the study the resident populations at these sites were already mature showing maximal reproductive effort. The pattern between years (of an increase followed by a decline in reproductive effort with increasing seral maturity) was also seen in January 1978, by comparing sites at increasing distances from the terminal hollow.

An apparent compensation was seen between allocation to seeds and to new rhizomes in summer 1979-80. In December 1979, when seed weight was maximal, the sum of the proportional allocation of the total nitrogen content of Carex pumila biomass to seeds (dispersal) and to rhizomes of vegetative shoots (current local colonization) was closely similar at all four sites (table 4.33). These data apply to sites where the allocation of total nitrogen to dispersal and local colonization can be accounted for exclusively by rhizomes (at the juvenile site, S0), predominantly by seeds (at the mature sites, S1 and S2) or predominantly by rhizomes (at the senile site, S3).

Table 4.33 Proportional allocation of total nitrogen of Carex pumila biomass to seeds, rhizomes of vegetative shoots and the sum of the two, at four sites on the sand plain (a) in December 1979 and (b) in December 1980 with (N) and without (C) N-fertilizer addition.

(a) December 1979		Proportion of total nitrogen			
		S0	S1	S2	S3
Seeds		0	.143	.148	.047
Rhizomes (veg. shoots)		.249	.075	.066	.177
Sum		.249	.219	.215	.223
(b) December 1980					
		C N		C N	
		C	N	C	N
Seeds		.252	.120	.072	.099
Rhizomes (veg.)		.052	.209	.093	.158
Sum		.304	.329	.165	.256

The conclusion that rhizomatous extension and seed reproduction in Carex pumila are alternative processes is also supported by the summer 1980-81 data. In December 1980, the total allocation of total nitrogen to dispersal (seeds) and local colonization (rhizomes of vegetative shoots) was similar at those sites where the Carex population was not in an extremely impoverished condition (namely, at S0, S1 nitrogen-fertilized plots and at S2; table 4.33). In the old hollow at S3 and to a lesser extent on the control plots at S1, the allocation of total nitrogen to seeds plus rhizomes of vegetative shoots was somewhat reduced. At these two latter sites, soil nutrients were low and/or unavailable to Carex pumila as a result of the presence of later seral species. These data strongly suggest a soil-nitrogen limitation to clonal growth and seed reproduction in

Carex pumila.

Population reproductive effort in Carex pumila will be determined both by the proportion of fertile shoots in the total population and by individual reproductive effort, the proportion of fertile shoot biomass that is allocated to reproductive tissues, and finally to seeds.

3. Fertile shoot biomass

Figure 4.36 shows the proportional allocation of the standing aerial biomass of fertile shoots to component vegetative and fertile parts over time during 1978-79 and of the standing total biomass of fertile branches over time during 1979-80. In each season, reproductive allocation increased to a maximum in December / early January at all sites. Total individual reproductive effort (allocation to all reproductive structures, including seeds) reached a maximum somewhat earlier at S1 than at the other sites in the old hollows (figure 4.36). The more promiscuous development did not result in a continuing increase in reproductive allocation as at the other sites. In summer 1978-79, total RE (as a proportion of the aerial biomass of fertile shoots) was similar at S1, S2 and S3 (about 30% of dry weight) and higher than at S4 (figure 4.36). Given that maximum individual reproductive effort occurred in December / early January, the January 1978 and December 1980 estimates of reproductive effort can be expected to approximate seasonal maxima and may be compared with the 1978-79 and 1979-80 maxima. Figure 4.37 shows this comparison.

Figure 4.36 (a) Proportional allocation of aerial biomass of fertile shoots of *Carex pumila* to component parts over time in summer 1978-79.

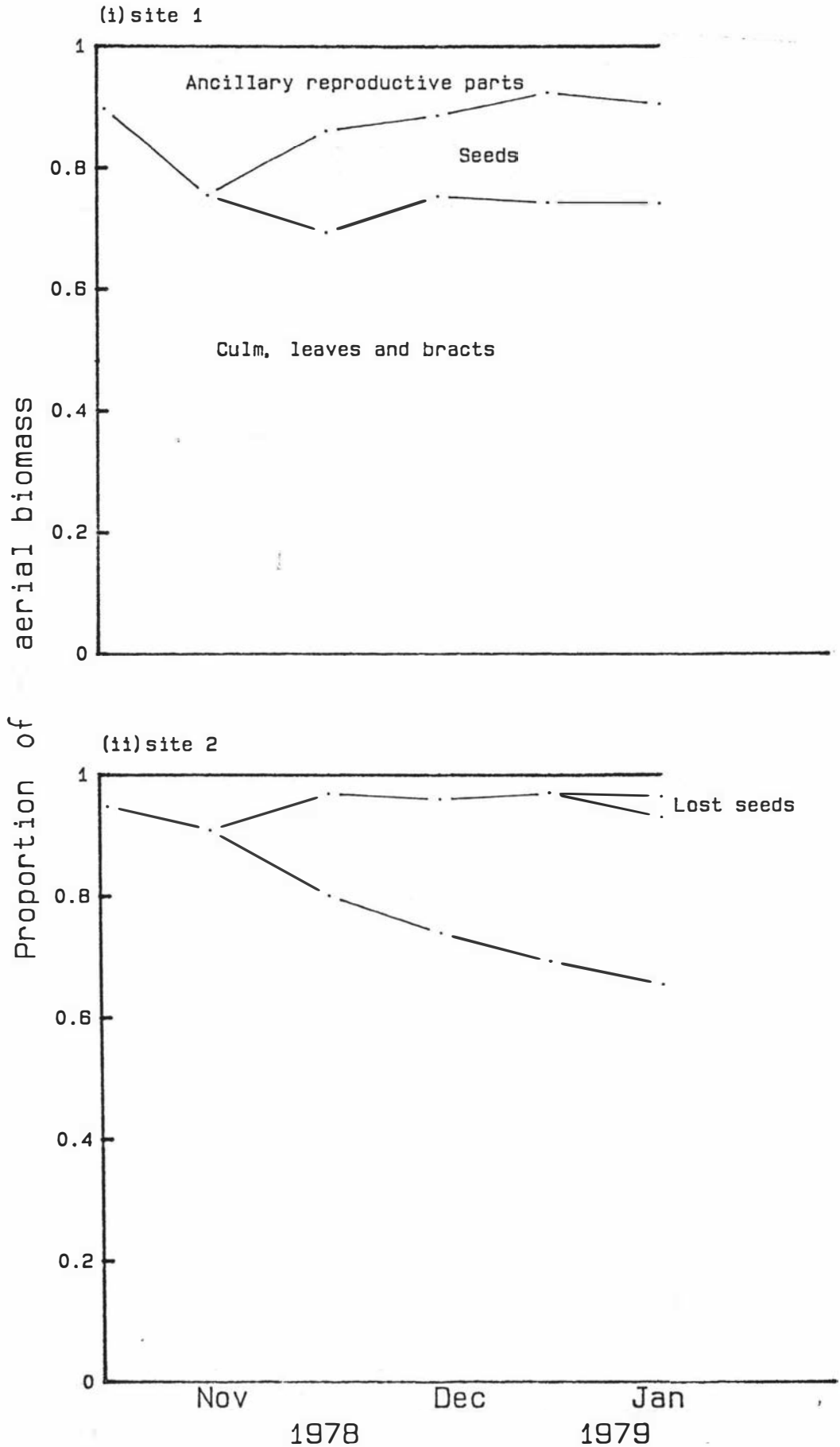
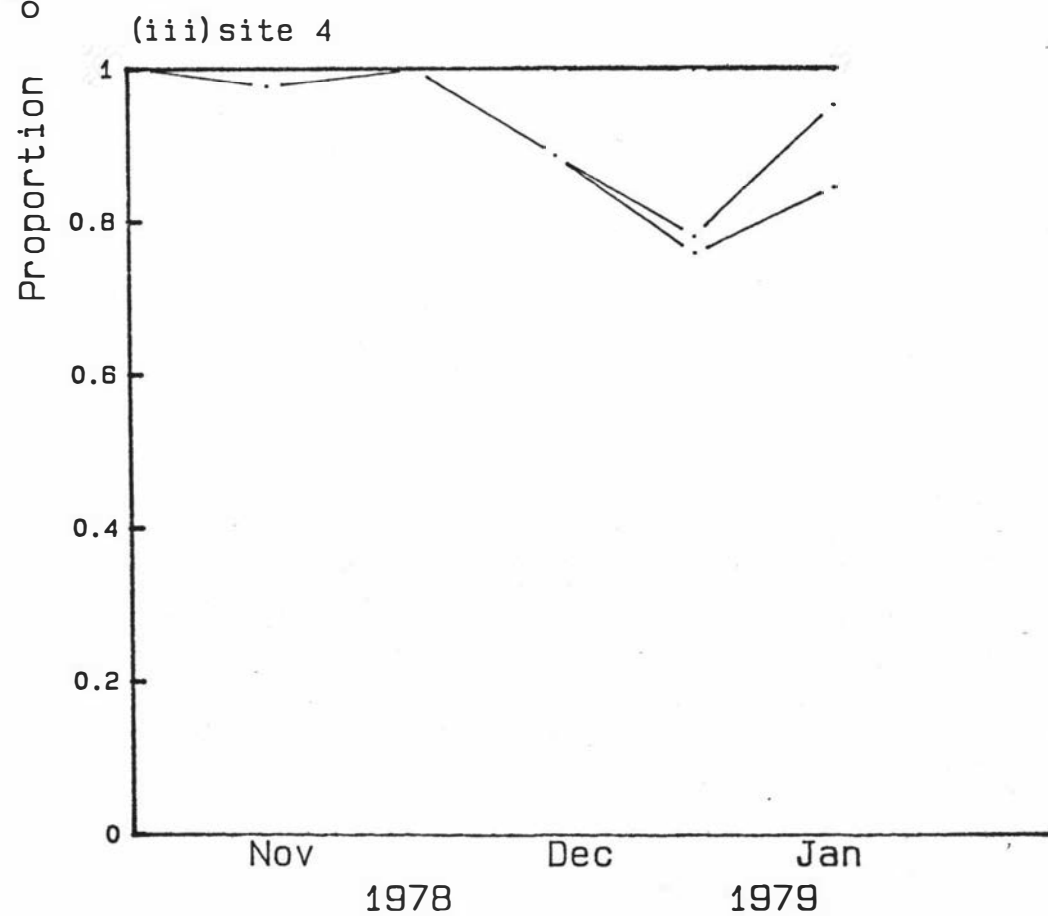
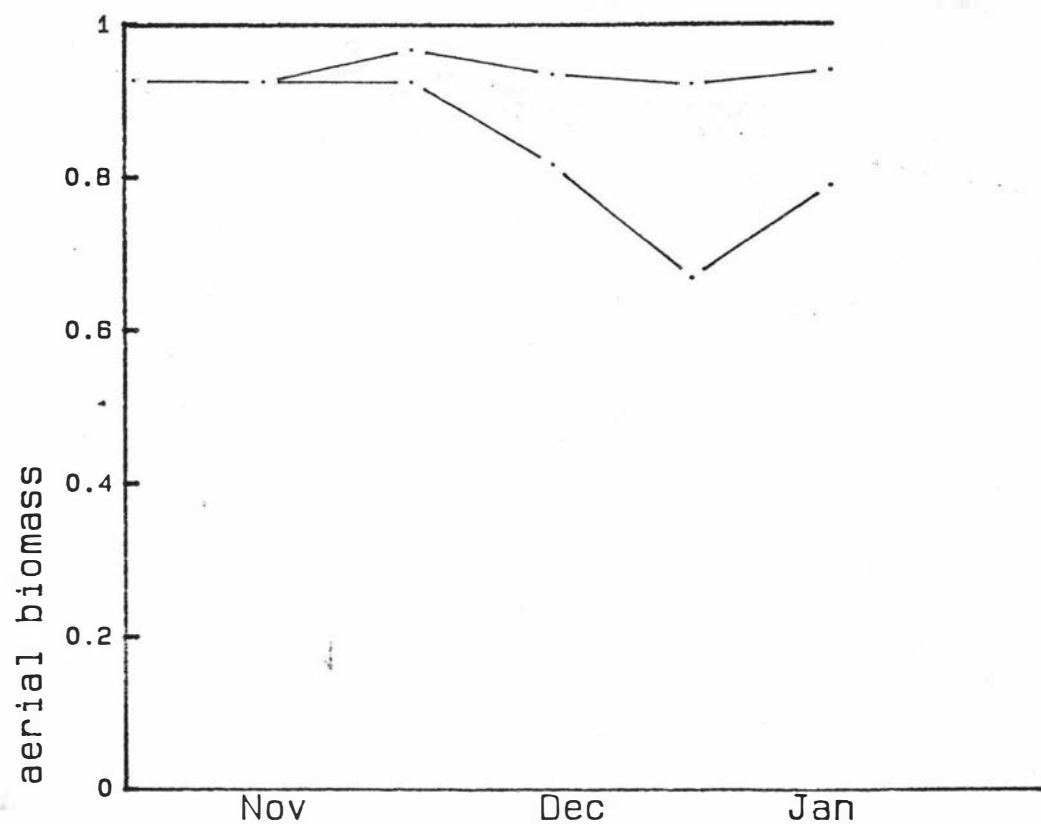


Figure 4.36 (a) continued: Allocation of aerial biomass
(iii) site 3



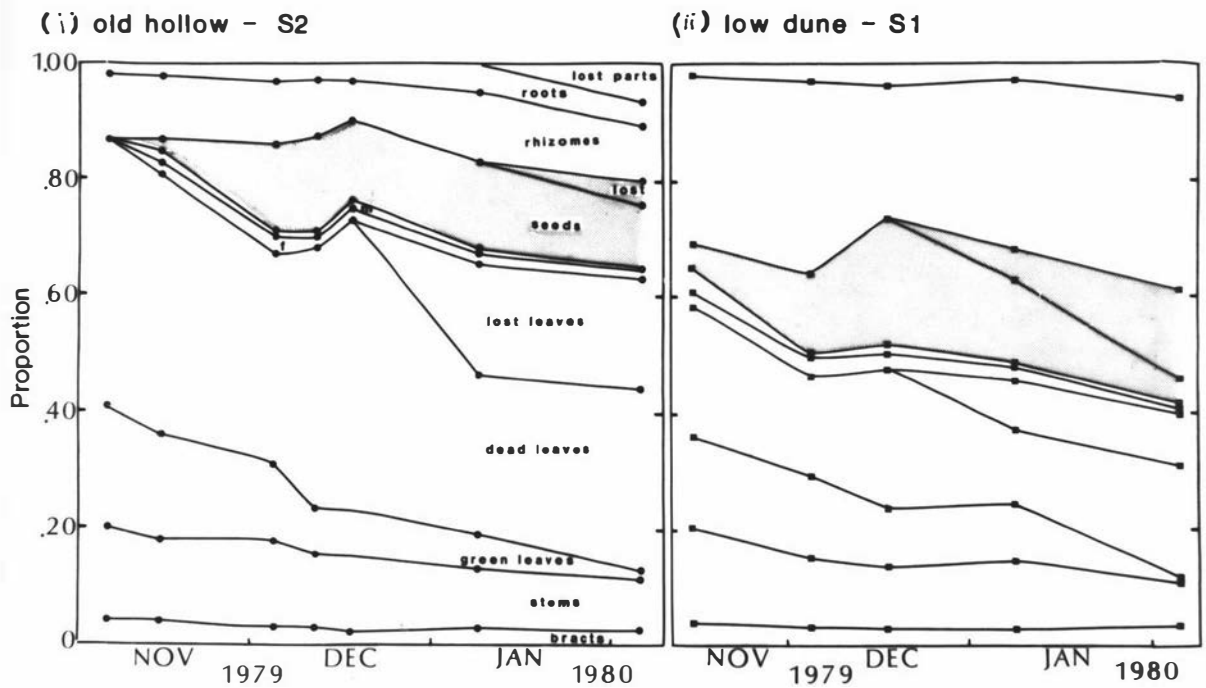
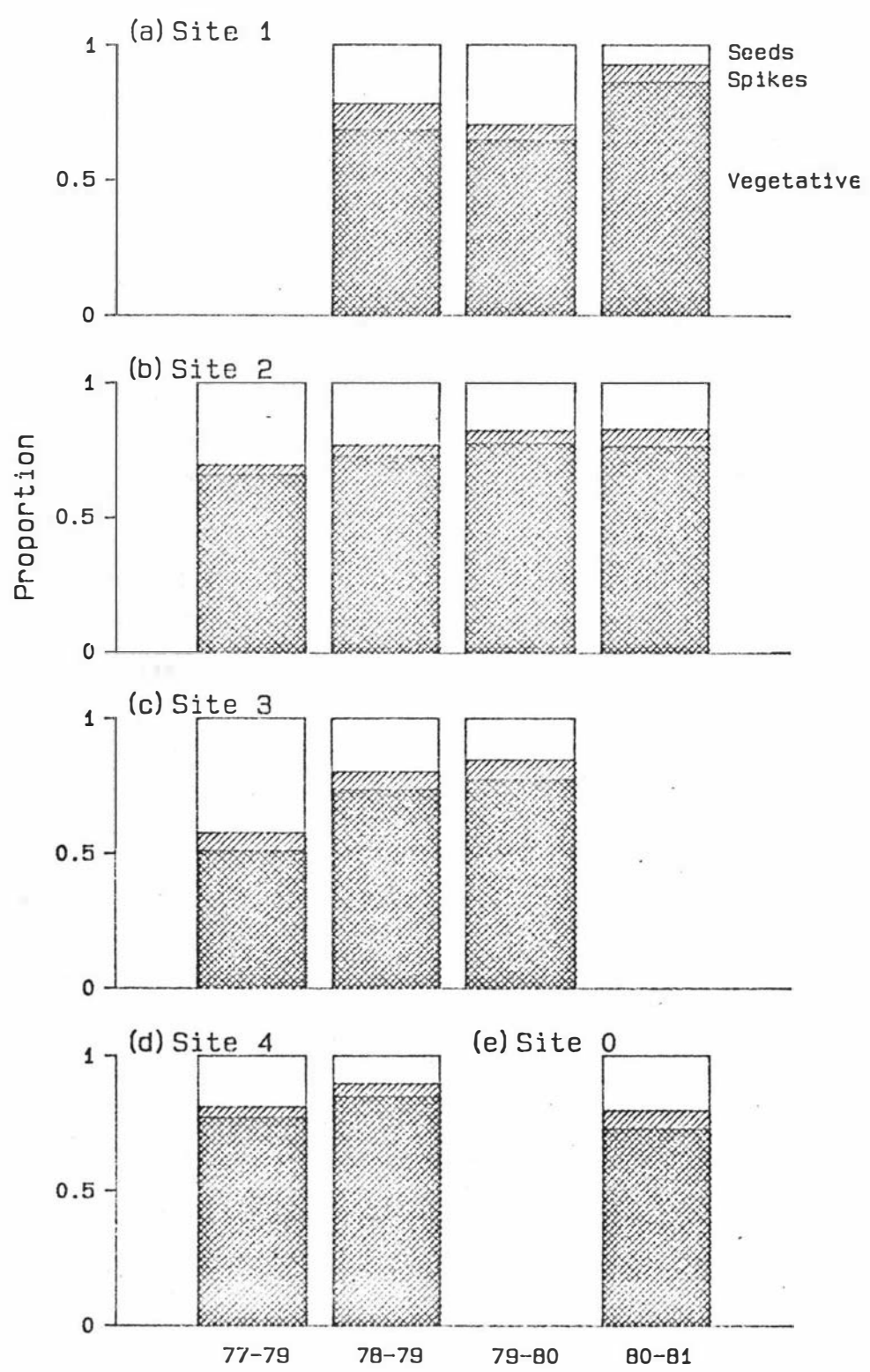


figure 4.36b Pattern of allocation of fertile shoot biomass of *Carex pumila* to component structures over time in summer 1979-80, at S1 and S2.

m = male spikes; f = female spikes (excluding seeds)

Figure 4.37 Proportional allocation of aerial biomass of fertile shoots of *Carex pumila* to component parts in mid-summer in four consecutive seasons



The greatest individual reproductive effort was seen at that site where population reproductive effort was also greatest, ie at S3 in summer 1977-78 when 49% of the aerial biomass of fertile shoots was apportioned to reproductive parts; 42% to seeds alone (figure 4.37). Seed RE, and as a consequence total RE, in January 1978 were highly significantly greater ($P < .001$) at S3 than at S2. Values at S4 were further reduced. No fertile shoots were present in the juvenile population at S1 in this first summer.

Individual RE was seen to increase between years at the two sites on the low dune that were juvenile when first monitored (namely, S1 and S0; figure 4.37). By contrast, at the old hollow sites where the resident Carex pumila populations had been mature (S2) or more or less senile (S3 and S4) at the beginning of the study, seasonal maximum individual RE progressively declined between years as the populations became more senile. Similarly at S1 between 1979-80 and 1980-81 where the Carex pumila population was entering a senile phase of development, individual reproductive effort declined (figure 4.37). This decline was a consequence of the inability of these depauperate shoots to channel resources into the development of sexual reproductive parts. This response reflects the demise of the species on these sites.

Figure 4.36b shows the proportional allocation of biomass (including roots and rhizomes) of fertile shoots to component parts over time during summer 1979-80. At both S1 and S2 seeds increased to a maximum in December when the allocation to rhizomes reached a low. Green leaf laminae and to a lesser extent stems and sheaths decreased over the entire duration (November to February). Rhizomes contributed a considerably larger proportion at S1 than at S2, and (dead) leaves contributed considerably more at S2 than S1. As a consequence of the

large contribution of underground parts to the total dry weight at S1 (25-35%), seeds made up a much smaller proportion of total biomass than they did as a proportion of the aerial biomass alone (18% and 30% respectively in mid-December). At S2 where aerial parts made up 85-90% of total biomass of fertile shoots, this discrepancy was not so apparent (seed RE = 14% and 16% as a proportion of total and aerial biomass of fertile shoots respectively in mid-December). Thus, whereas seed RE at S1 was seen to be highly significantly ($P < .001$) greater than at S2 when based on aerial biomass, the difference was not significant when based on total biomass.

At S1 and S2 individual reproductive effort as a proportion of the total biomass of fertile shoots was lower in December 1980 than in the previous summer. At the youngest site colonized 18 months previously, individual reproductive effort was similar to that at the mature site S1 in summer 1979-80. The development of fertile shoots in the younger population (S0) in December 1980 was delayed compared with that in the older population (S2). At S0 the proportion of dry weight of fertile shoots associated with green leaves and culms (29.3%) was significantly greater ($P < .05$) than that of S2 (13%) whereas the proportions were reversed for dead leaves (18.2% and 31% for S0 and S2 respectively; table 4.34). Despite the tardiness of development of fertile shoots at S0, it was unlikely that individual RE would have been substantially increased by subsequent seed filling.

Table 4.34 Proportional allocation of biomass of fertile shoots of Carex pumila to component organs in December 1980. (Controls only).

Proportion of total biomass of fertile shoots			
	S0	S1	S2
Roots	.03	.066	.073
Rhizomes	.273	.31	.287
Seeds	.141	.046	.111
Ancillary fertile parts	.048	.036	.013
Dead leaves	.182	.295	.31
Green leaf laminae	.142	.107	.047
Green sheaths	.151	.093	.083
Scale leaves	.034	.044	.049

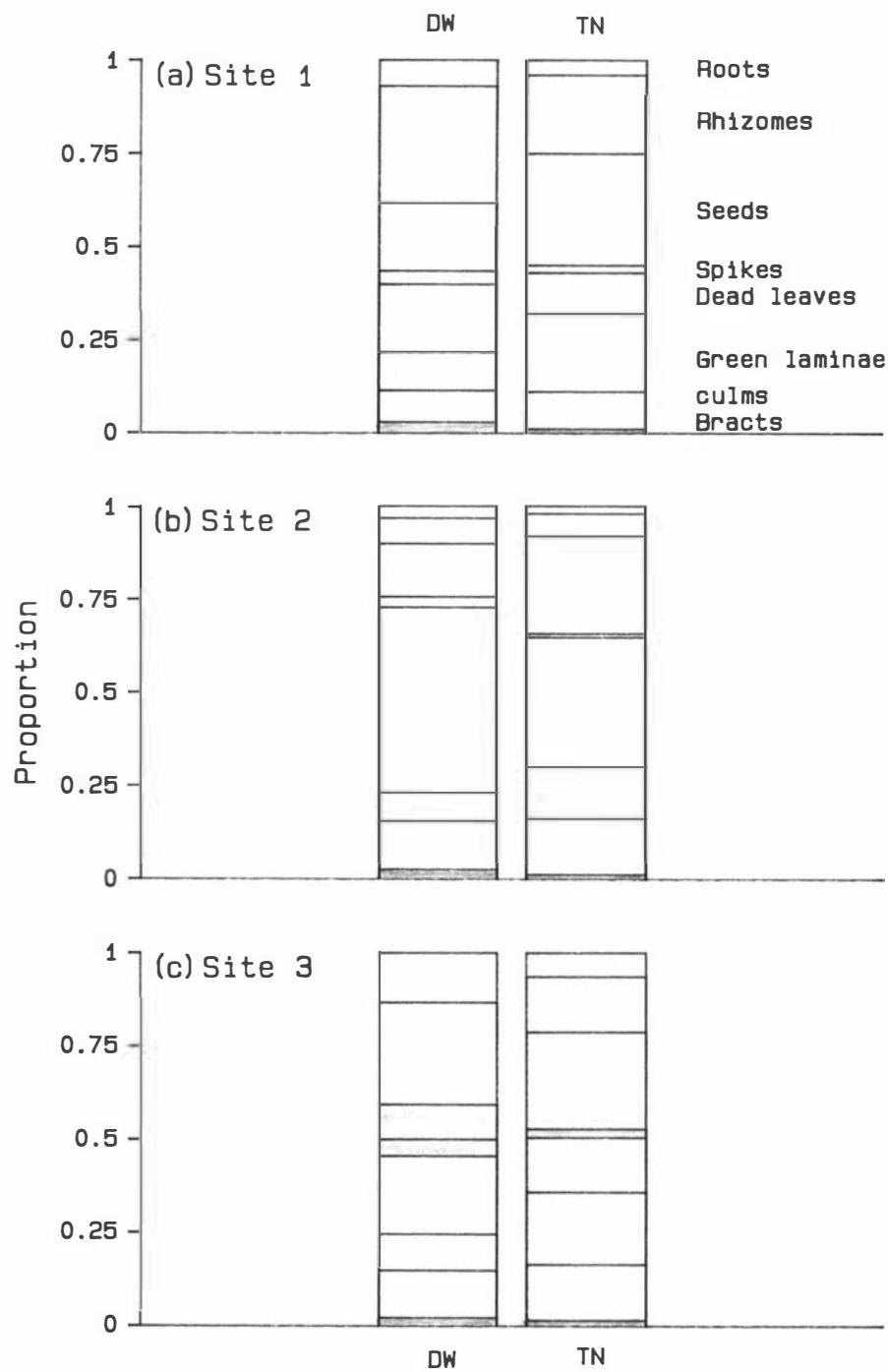
The pattern of dry weight partitioning between component parts of fertile shoots was significantly different from that based on total nitrogen content. In January 1978, individual seed RE as a proportion of aerial biomass was highly significantly less than that based on the total nitrogen content of these shoots (table 4.35a). Twelve months later in early January 1979 seed RE based on dry weight and total nitrogen showed similar discrepancies. Individual seed RE based on total nitrogen was 10% greater than that based on dry weight. At this harvest, the vegetative portion of fertile shoots was divided into green and brown (dead) fractions. The proportion of total nitrogen found in dead leaves was 10% less than that based on dry weight (table 4.35b) suggesting that the sink for labile nitrogen moving from leaves during their senescence was the seeds.

Table 4.35 Proportional allocation of total nitrogen (TN) and dry weight (DW) of the aerial biomass of fertile shoots of Carex pumila to component parts, in summer (a) 1977-79 and (b) 1978-79.

		Proportion of total														
(a) 1977-78		Site 2				Site 3										
		DW		TN		DW		TN								
Seeds		.31	**	.38		.42	**	.50								
Ancillary fertile parts		.03	ns	.02		.07	ns	.05								
Vegetative parts		.66	ns	.60		.51	ns	.45								
(b) 1978-79		Site 1		Site 2		Site 3		Site 4								
		DW		TN		DW		TN		DW		TN				
Seeds		.22	***	.32		.23	***	.33		.20	***	.30		.08	**	.13
Ancillary		.10	ns	.07		.04	ns	.03		.07	ns	.05		.04	ns	.03
Dead leaves		.65	***	.55		.64	***	.51		.71	***	.60		.83	**	.76
Green leaves		.04	ns	.06		.09	ns	.13		.03	ns	.05		.05	ns	.09

Again in summer 1979-80, the pattern of allocation to component organs of the fertile shoot population based on total nitrogen differed significantly from that based on dry weight (figure 4.38). Not only the allocation to seeds, which was between 8% and 15% greater when based on total nitrogen depending upon the site, but also the proportional allocation to green leaf laminae, dead leaves and rhizomes differed when based on total nitrogen from that based on dry weight (figure 4.38).

Figure 4.38 Proportional allocation of dry weight and total nitrogen of fertile shoot populations of *Carex pumila* to component parts at S1, S2 and S3 in December 1979



4. Fertile to vegetative shoot ratio

The ratio of fertile to vegetative shoots has been used as a measure of reproductive effort of natural populations of herbaceous species in seral habitats (Abrahamson 1975). Such an estimate can be made on the basis of shoot density (figure 4.39) or some resource such as dry matter (figure 4.40) or nitrogen. Figure 4.39 shows this ratio in four Carex pumila populations in January 1978. The ratio was greatest in the mature population at S2 and progressively decreased at sites further from the terminal hollow. These data suggest that the relative expenditure on reproduction (cf vegetative production of new tillers) was greater at the former site. A similar trend was shown in figure 4.40 for the proportional allocation of aerial biomass to vegetative and fertile shoots. By contrast, table 4.32 showed that population reproductive effort was greater at S3 than S2, in summer 1977-78.

Figure 4.40 shows the proportional allocation of standing aerial biomass at the time of maximum seed reproductive effort (figure 4.36) to vegetative and fertile shoots at various sites on the sand plain in each of four summers. It is apparent from figures 4.11 and 4.13 that maximum investment in fertile and vegetative shoot biomass occurred at different times of the year (namely, early summer and autumn, respectively) and, therefore, a simple fertile to vegetative shoot ratio at any one time of the year (such as figure 4.40) may not provide the most accurate measure of the relative importance of sexual reproduction and clonal growth in these populations.

The juvenile populations at S1 in summer 1977-78 and at S0 in summer 1979-80 stand out since the entire aerial biomass was apportioned to vegetative shoots. As these two populations matured

Figure 4.39 The ratio of the density of fertile shoots to vegetative shoots at four sites on the sand plain, in January 1978. Vertical bar denotes $\pm$ variance of the mean.

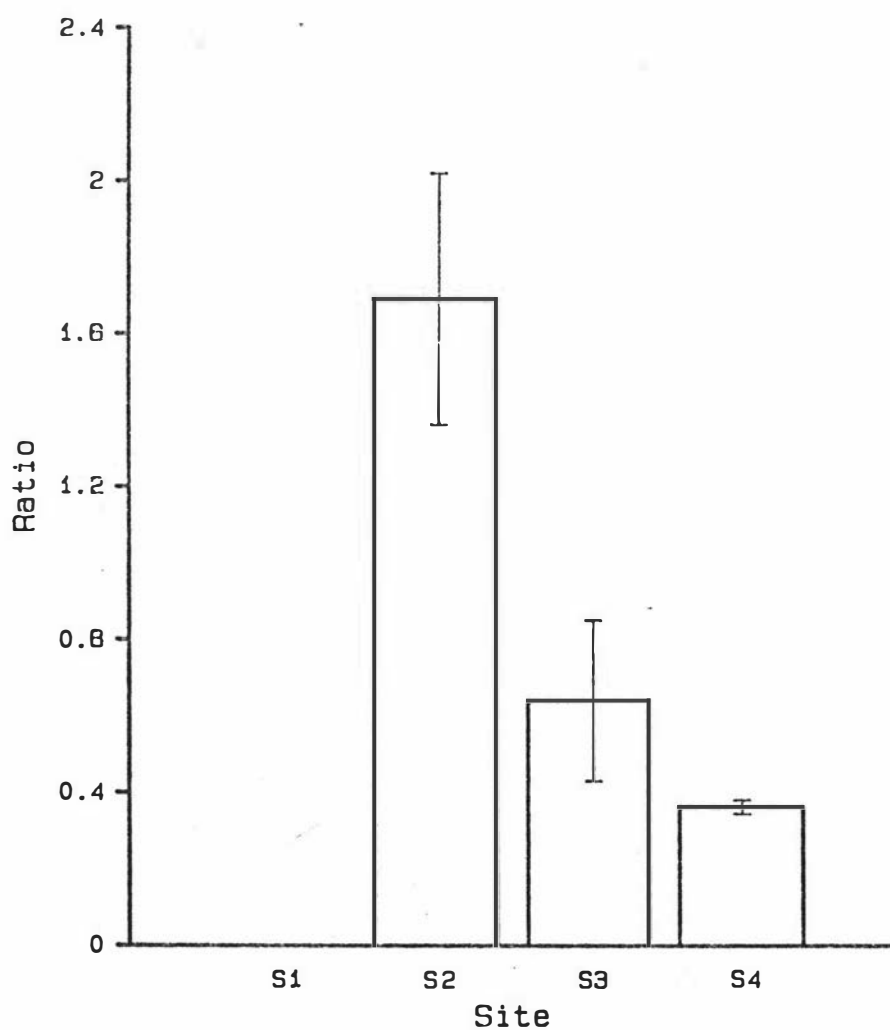
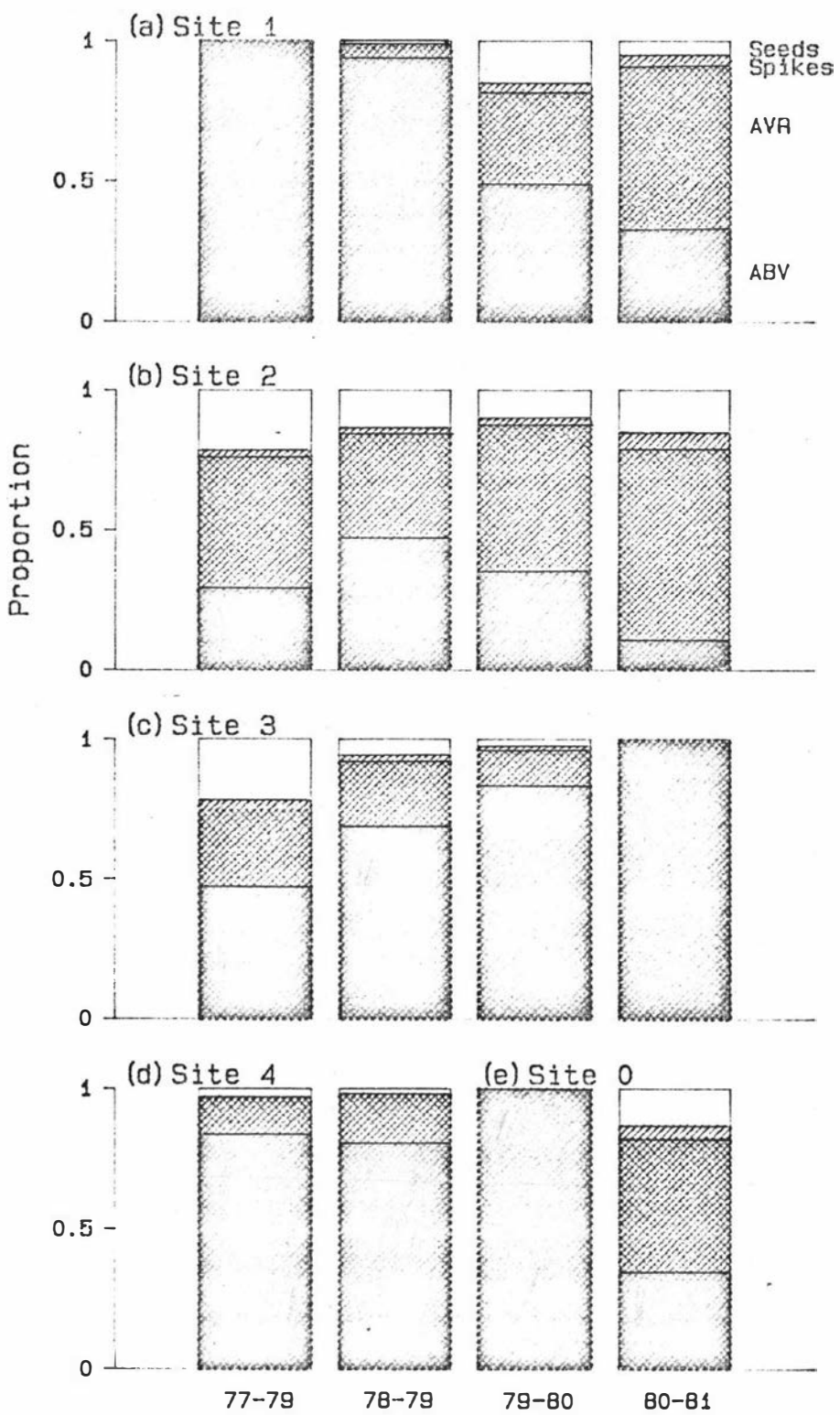


Figure 4.40 Proportional allocation of aerial biomass of *Carex pumila* to vegetative shoots (ABV) and to vegetative (AVR) and fertile fractions of reproductive shoots in four consecutive seasons



between years, the proportion of aerial biomass found in fertile shoots progressively increased (figure 4.40). This may be interpreted as an adaptive phenotypic response to increasing density and concomitant maturity by these populations. It is important to note that this shift from vegetative to fertile shoot growth as the populations aged, is not likely to have involved a change in the genetic structure of the resident populations: Carex pumila genets are long-lived, although individual ramets (branch modules) on the sand plain have a life expectancy of no more than 12 months. Such a phenotypic response by populations to increasing stand density and seral maturity have been noted elsewhere by Ogden (1974a; for Tussilago farfara), Thomas (1974; for Hieracium) and Abrahamson (1975; for Rubus spp).

The evidence in the old hollows at S2, S3 and S4 shows a different trend. In January 1978 the contribution of fertile shoots to total standing aerial biomass of Carex pumila decreased from S2 to S3 to S4 both in absolute terms (g DW / unit area; figure 4.9) and as a proportion (figure 4.40). The same ranking of these sites for allocation of biomass to fertile shoots was also seen in each of the three subsequent summers (figures 4.11, 4.13 and 4.40). S2, S3 and S4, which were sited at progressively increasing distances from the terminal hollow, represented sites of progressively increasing age.

A similar trend of decreasing reproductive effort over time was suggested at each of these sites by figure 4.37. Confirming this trend, figure 4.40 shows there was a decreasing proportion of aerial biomass in fertile shoots at both S3 and S4 between years. However, at S2 this proportion remained more or less similar for three seasons before balancing in favour of fertile shoots in summer 1980-81. This shift towards an increased "reproductive allocation" at S2 was however

more apparent than real. The elevated fertile to total aerial biomass ratio in December 1980 at S2 resulted from the lack of recruitment and growth of new vegetative shoots during the spring and early summer. The absolute size per fertile shoot and biomass per unit area of fertile shoots at S2 in December 1980 had decreased substantially compared with previous seasons (table 4.9 and figure 4.13 respectively), whereas the proportional allocation of aerial biomass of fertile shoots to seeds was no different from the low value found the previous year (figure 4.37).

The trend of decreasing reproductive allocation with time on the old hollows (between years at each site and across sites of increasing putative age in any one season) cannot be considered adaptive, but reflects the increasing senility of these Carex pumila populations which were being replaced on the sand plain by later seral species. In the senile Carex pumila populations (S1 in 1980-81; S2 in 1980-81; S3 in 1978-79, 1979-80 and 1980-81; and S4 in 1977-78 and 1978-79) few shoots showed signs of sexual reproductive development and on those that did, few seeds were produced (section 4.3.5). Shoots in these populations were depauperate compared with those in previous years (table 4.9) with a large proportion of their biomass associated with dead leaves. The young populations at which little or no fertile development occurred, by contrast, had a considerably larger proportion of their aerial biomass in green leaves.

5. Dwarf and long shoots

(a) Dwarf/total ratio

The proportion of the biomass of Carex pumila associated with dwarf as opposed to long branches varied between sites and over time between July (winter), October (spring) and December (summer) 1980

(table 4.36). It was shown above (section 3.2.1) that the ratio of the biomass of dwarf to total (dwarf plus long) branches increased with increasing age of the clone (table 3.8). At the July 1980 harvest the low BD/BMS ratio estimated at S0 (namely 15%; table 4.36) suggests the adolescence of the resident population. Rabbits which preferentially grazed young and therefore mainly dwarf aerial shoot modules (figure 4.18) contributed to the reduced BD/BMS value at this site. At S1, the BD/BMS ratio (65.9%) reflected the greater age and contribution of dwarf shoots to this population. Similarly, at S3 where the Carex population was senile, the BD/BMS ratio was high, although also more variable (larger standard deviation values) than at S0. The BD/BMS ratio was also low (15.7%) at S2. The S2 value reflected the relatively large contribution of old large long branch modules to the standing biomass. This population was not young.

Table 4.36 Ratio of the biomass of dwarf to total (dwarf plus long) branches of Carex pumila at four sites in July, October and December 1980.

	Proportion of total biomass in dwarf branches (BD / BMS)			
	S0	S1	S2	S3
July	.15	.659	.157	.689
October	.497	.455	.401	.301
December	.607	.432	.381	.492

At both S0 and S2 where the BD/BMS ratio had been low in July 1980, BD/BMS increased over the spring (table 4.36). At S0 this reflected increasing contribution of dwarf shoots to biomass increase. At S2, the increased BD/BMS ratio to October came about through the death of old large long shoots. Dwarf shoot biomass remained constant over this spring period (figure 4.15). BD/BMS remained more or less unchanged at S2 between October and December when both dwarf and long shoot biomass per unit area increased (figure 4.15).

The proportional contribution of dwarf shoots to total nitrogen content of biomass of Carex pumila in December 1980 (table 4.37) was greater than that based on dry weight (table 4.36). This effect was attributable to the greater proportional contribution of green leaves and seeds to biomass in dwarf branches compared with long branches (see part (b) below). These organs were found to have higher total nitrogen concentrations than all other plant parts (table 4.17). At S0 where the clone was vigorous and expanding, dwarf shoots accounted for a larger proportion of the total nitrogen content of biomass than at the three more senile sites (S1, S2 and S3). At sites of increasing distance from the terminal hollow, an increasing proportion of total nitrogen was found in fertile shoots.

The proportion of the total nitrogen content of biomass accounted for by dwarf and by long fertile shoots increased at sites of increasing age (table 4.37). Dwarf shoots at S3 do not fit this trend. Dwarf shoots at S3 that did not produce inflorescences formed an age structure similar to that for fertile shoots elsewhere. It is likely that the aged dwarf shoots of this most senile population were fertile but lacked the resources to express this condition.

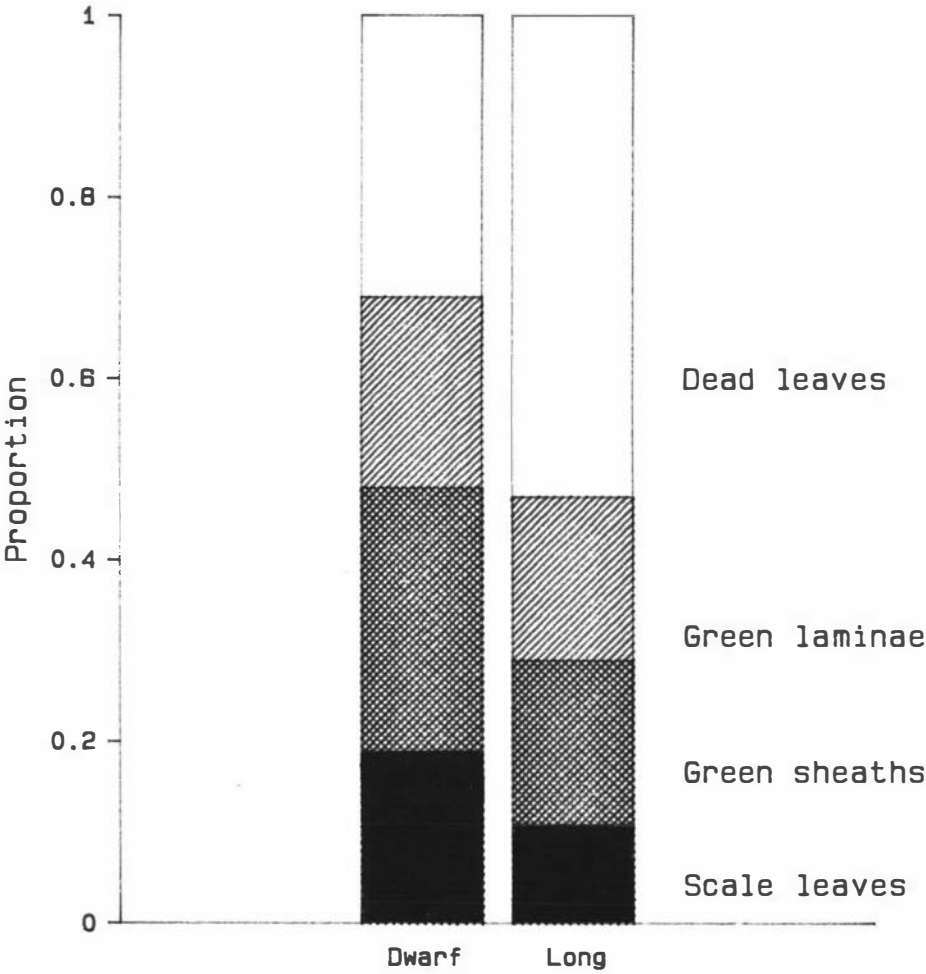
Table 4.37 Proportion of the total nitrogen content of the biomass of Carex pumila allocated to dwarf and to long branches at four sites in December 1980.

Proportion of total nitrogen content of biomass				
	S0	S1	S2	S3
Dwarf vegetative	.456	.192	.098	.521
fertile	.275	.324	.406	.071
Long vegetative	.017	.192	.057	.048
fertile	.253	.292	.440	.360

(b) Allocation to component organs

Dwarf branches were found to be significantly smaller than long branches (figure 4.16). This difference was attributable to the smaller mean dry weight per branch module of both aerial and underground fractions. The proportional distribution of the biomass of each shoot type to component parts also differed. Not only was the proportional allocation of biomass of each branch type to rhizomes notably greater for long branch populations but also the pattern of allocation within the aerial fractions differed (figure 4.41). Averaged over all four sites, dwarf shoots allocated a significantly greater proportion of their aerial biomass to both scale leaves and sheaths of green leaves, and a correspondingly smaller proportion to dead leaves, than long shoots, suggesting the younger average age of the former population. This was confirmed by the age distributions of these populations (section 4.3.3).

Figure 4.41 Proportional allocation of aerial biomass of dwarf and of long shoots of *Carex pumila* to component organs, averaged over four sites in July 1980



(i) Long shoots

In July 1980, the proportional allocation of biomass to component parts by long and by dwarf branch populations was not consistent between all sites (highly significant site x type interaction, $P < .001$ table 4.38). At S0, S2 and S3 the proportional allocation of long branch population biomass to rhizomes was highly significantly ($P < .01$) greater than rhizome allocation by dwarf branch populations whereas at S1, the two branch types did not differ significantly (table 4.38). Despite this similarity, the mean dry weight per long rhizome module at S1 was still greater ($P < .01$) than that per dwarf rhizome module (figure 4.16).

Table 4.38 Analysis of variance of the proportion of biomass of dwarf and of long branch modules in rhizomes, in July 1980

SOURCE	D.F. (M.V.)	S.S.	M.S.S.	F RATIO
site	3	0.12	0.04	3.01 ns
rep	3	4.905E-03	1.635E-03	0.12 ns
type	1	0.53	0.53	40.54 ***
site*type	3	0.43	0.14	11.01 ***
error	17 (4)	0.22	0.01	

Estimated treatment means:

	site	rep	type	
S3	0.50	0.49	Dwarf	0.33
S2	0.38	0.46	Long	0.62 ***
S1	0.48	0.47		
S0	0.55	0.50		
S0 > S2; $P < .01$			Long > Dwarf; $P < .001$	

Estimated means: The proportion of biomass of dwarf and of long branch modules in rhizomes in July 1980

	Dwarf	Long
Site 0	0.30a	0.80c
Site 1	0.57b	0.39a
Site 2	0.21a	0.56ab
Site 3	0.25a	0.75bc
a > b, $P < .01$; a > c, $P < .001$, b > c, $P < .05$		

Figure 4.42 shows that rhizomes contributed a greater proportion of long branch biomass than any other structure, at each of the sites monitored. As a proportion of the long branch population biomass, rhizome allocation was significantly greater ($P < .01$) at S0 than at S2 and S1. At S3 rhizome allocation was also significantly greater ($P < .01$) than at S1. The value at S3 was intermediate between and not significantly different from those at S0 and S2 (table 4.38).

Both mean dry weight of the aerial fraction per long shoot and the proportional allocation of long branch biomass to aerial parts was greater at S1 than at all other sites in July 1980 (figures 4.42 and 4.16). This was attributable to the greater proportional contribution of green and dead leaves to total long branch biomass at this site compared with other sites. Dead leaves at S2 also made up a significantly greater proportion ($P < .01$) of total long branch biomass than at S0 (figure 4.42).

At all sites the mean dry weight per long branch module declined between July and October 1980 although at S0 the mean aerial dry weight per long shoot (figure 4.16) and the proportional allocation of biomass of long branches to aerial parts (figure 4.42) were seen to increase over this period. At S1, S2 and S3, the proportional allocation of long branch biomass to component parts remained more or less constant (figure 4.42).

By December 1980 no living long shoots were found in the control plots at S3. At the other sites many of the long (and dwarf) shoots present in the winter and spring survived as fertile shoots. Long fertile shoots on the control plots allocated on average over S0, S1 and S2 11.4% of their aerial biomass to seeds, a significantly smaller proportion than dwarf shoots ($P < .05$; table 4.39). Differences

Figure 4.42 (a) Proportional allocation of biomass of dwarf branches of *Carex pumila* to component organs over time in July, October and December 1980.

F = fertile shoots; V = vegetative shoots in December.

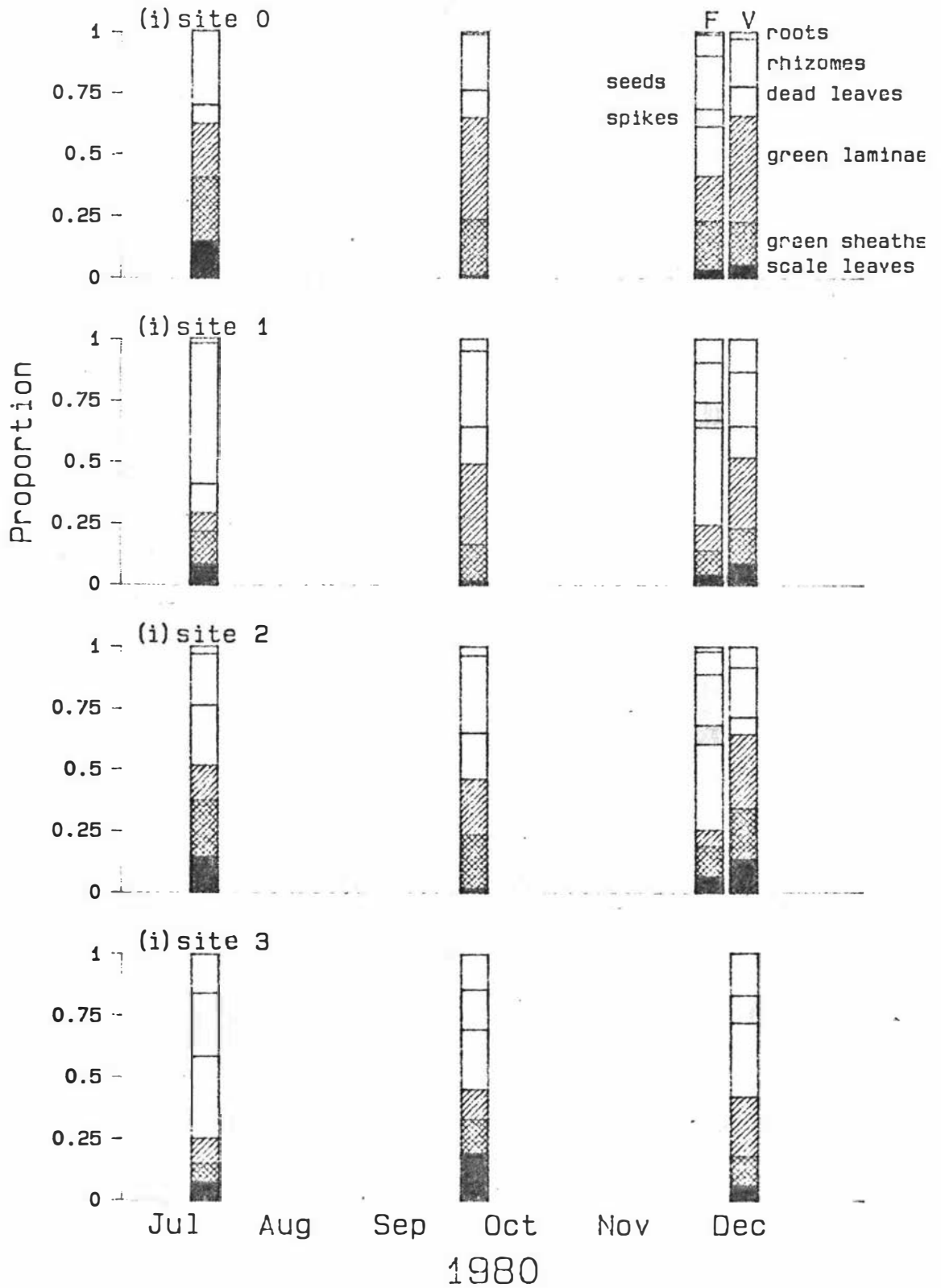
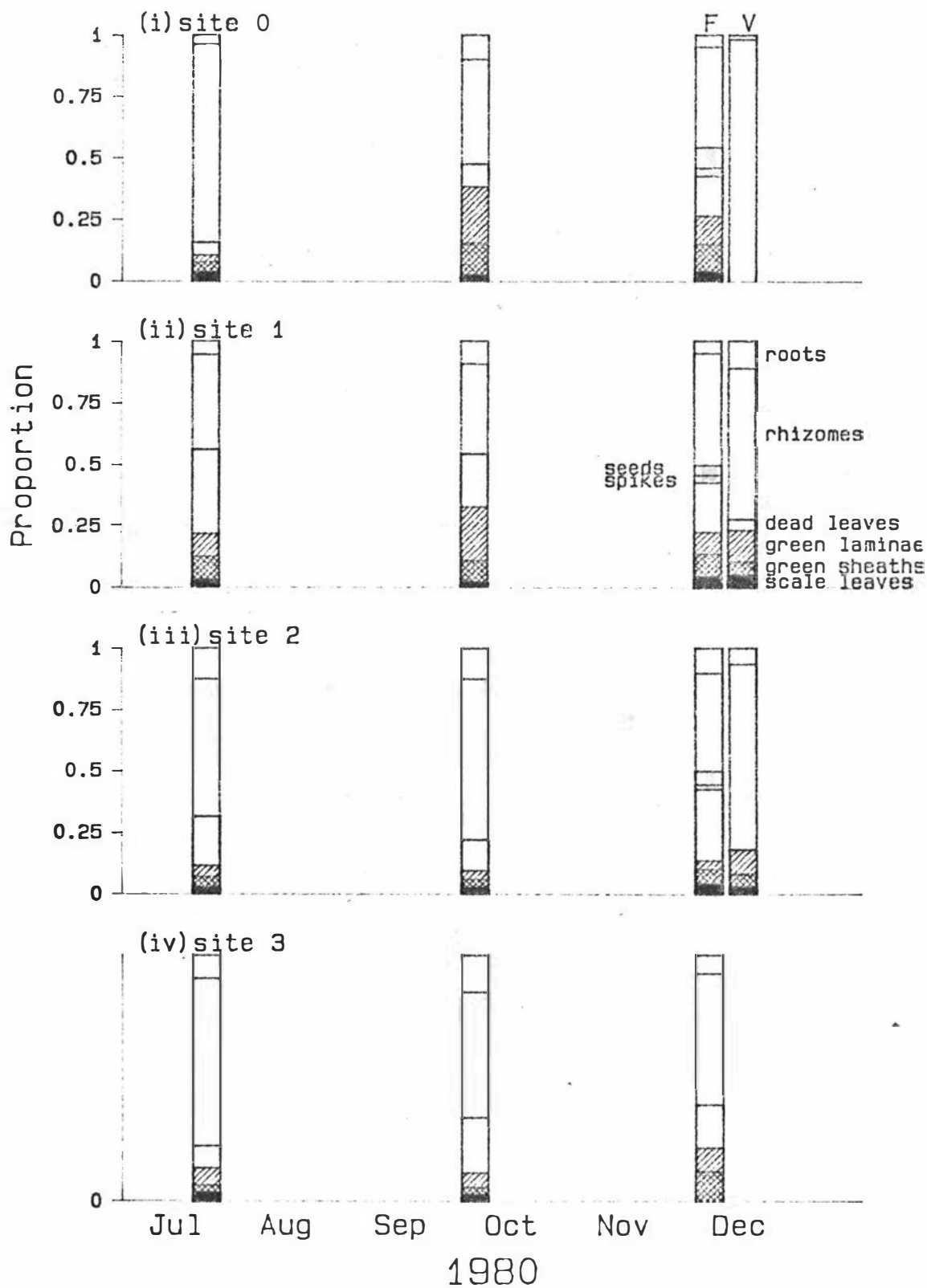


Figure 4.42 (b) Proportional allocation of biomass of long branches of *Carex pumila* to component organs over time in July, October and December 1980.

F = fertile shoots; V = vegetative shoots in December.



between the sites with regard to the allocation of aerial biomass of long shoots to sexual reproductive parts however were found (table 4.38), with that at S0 being greater ($P < .05$) than at either S1 or S2. There was no difference between long and dwarf shoots at S1 in their proportional allocation to sexual reproductive parts (table 4.40).

Table 4.39 Analysis of variance of seed reproductive effort as a proportion of aerial biomass of fertile shoots attached to dwarf and to long rhizome segments, in December 1980.

SOURCE	D.F. (M.V.)	S.S.	M.S.S.	F RATIO
site	2	0.03	0.02	29.07 **
rep	1	1.556E-03	1.556E-03	2.77 ns
type	1	0.01	0.01	24.86 **
site*type	2	8.753E-03	4.376E-03	7.79 *
error	5	2.809E-03	5.618E-04	

Estimated treatment means:

site	rep	type
S1 0.08	0.14	Dwarf 0.18
S0 0.20	0.16	Long 0.11
S2 0.17		

L.S.D. 5%	0.04	0.04	0.04
L.S.D. 1%	0.07	0.06	0.06
L.S.D. .1%	0.11	0.09	0.09

Estimated means: Proportion of aerial biomass

Rhizome type	Dwarf	Long
Site 0	0.24a	0.15b
Site 1	0.07c	0.08c
Site 2	0.23a	0.11bc

a > b, $P < .05$; a > c, $P < .001$; b > c, $P < .05$

A further difference between long fertile shoot populations (sites) in December 1980 was found in the proportional allocation of aerial biomass to dead leaves, which was significantly less at S0 compared with S1 and S2 (table 4.41).

Table 4.40 Total reproductive effort as a proportion of aerial biomass of fertile shoots attached to dwarf and to long rhizome segments, in December 1980.

Proportion of aerial biomass		
Rhizome type	Dwarf	Long
Site 0	0.32a	0.21b
Site 1	0.14c	0.13c
Site 2	0.32a	0.15c

a > b, $P < .01$; a > c, $P < .001$; b > c, $P < .05$

Table 4.41 Analysis of variance of the proportion of aerial biomass of fertile shoots attached to dwarf and of long rhizome segments in dead leaves, in December 1980. 19

SOURCE	D.F. (M.V.)	S.S.	M.S.S.	F RATIO
site	2	0.12	0.06	13.87 **
rep	1	1.605E-04	1.605E-04	0.04 ns
type	1	5.541E-03	5.541E-03	1.33 ns
site*type	2	0.06	0.03	6.75 *
error	5	0.02	4.164E-03	

Estimated treatment means:

	site	rep	type
S1	0.46	0.40	Dwarf 0.38
S0	0.27	0.41	Long 0.43
S2	0.49		
L.S.D. 5%	0.12	0.10	0.10
L.S.D. 1%	0.18	0.15	0.15
L.S.D. .1%	0.31	0.25	0.25

Estimated means:	Dwarf	Long
Site 0	0.23a	0.31ab
Site 1	0.53bc	0.39b
Site 2	0.39b	0.58c
c > b > a, $P < .05$; c > a, $P < .01$		

The mean December values for aerial and total dry weight per long fertile shoot at all sites which were greater than the corresponding values per long shoot in October (figure 4.16) indicate growth in individual shoot size over this period. At S0 and S1, the

distribution of biomass of these shoots to aerial versus underground parts was similar to that in October (figure 4.42) suggesting that sexual reproductive development resulted from the reallocation of aerial resources. The proportion of the biomass of long fertile branches in sexual reproductive parts (namely 7-11%; 4-8% in seeds alone) was similar to the early summer decrease in proportional allocation of biomass to green leaf laminae (figure 4.42). By contrast, at S2 the proportional allocation of long branch biomass to aerial parts increased between October and December at the expense of the rhizomatous fraction (figure 4.42).

At S1 and S2 where long vegetative branch modules were present in December 1980, the proportional allocation of biomass to rhizomes and the mean dry weight per long rhizome module were greater in long vegetative than in long fertile shoots. A further difference between these two long shoot populations, averaged over both sites, was that the former possessed a significantly reduced proportion and mean dry weight per branch module in dead leaves compared to the latter, confirming the difference in age of the two populations seen in section 4.3.3 at both sites.

(ii) Dwarf shoots

In July 1980, the mean dry weight per dwarf branch module was similar at all four sites monitored on the sand plain (figure 4.16). However, the distribution of biomass of these dwarf shoot populations differed between the sites. Dwarf branches at S1 possessed a significantly greater ($P < .01$) proportion of their total biomass in rhizomes, and consequently a smaller proportion in aerial parts, than comparable branches at S0, S2 and S3 (figure 4.42).

The greater senility of the dwarf shoot population at S3 compared with those at the other three sites was indicated by the greater proportional allocation of aerial biomass to dead leaves (more than one half aerial biomass at S3, cf less than one-third at each of the other three sites; figure 4.42). The proportional allocation of total biomass to roots was also larger at S3 (16%) than at other sites (0-3%; figure 4.42) further indicating the advanced age of this shoot population. No adventitious roots were found attached to dwarf rhizome branches at S0 where the population was young and in an adolescent phase of development. It was not surprising, therefore, to find that at S3, the mean dry weight per dwarf branch module declined over the early spring to October, while at other sites the mean size of dwarf shoots increased over this period (figure 4.16).

The increase in mean dry weight per dwarf shoot between July and October 1980 at S2 was only small and occurred more in the rhizome fraction than in other shoot parts. However, this increased proportional allocation of biomass to rhizomes at S2 portended the subsequent increase in mean aerial (and total) dry weight per dwarf shoot to December at this site (figure 4.16). At S0 and S1, where the July-October increases in mean dry weight per dwarf branch module were greater than at S2, the proportion of the total dwarf shoot biomass allocated to green leaf laminae increased from 21% and 7% to 41% and 33% respectively, significantly ($P < .05$) greater percentages than at either S2 or S3 (figure 4.42). This increased allocation to leaf laminae at S0 and S1 was balanced by a reduced proportional allocation to rhizomes and bracts (figure 4.42), although, at least at S0, the mean dry weight per dwarf rhizome branch increased over this period (figure 4.16).

By December 1980, reallocation of biomass within dwarf shoots in response to flowering and seed production was evident on the control plots at S0, S1 and S2 but not at S3 (figure 4.42). The mean dry weight per dwarf fertile branch module had further increased from the October values at S0 and to a lesser extent at S2, whereas at S1 dwarf fertile shoot mean size was less than that of the dwarf shoot population in October (figure 4.16).

The proportion of the aerial biomass of dwarf fertile shoots found in sexual reproductive parts, including seeds, was highly significantly ($P < .001$) greater at S0 and S2 than at S1 (tables 4.37 and 4.38; see also section 4.3.7 figure 4.48). This total reproductive effort is seen in figure 4.42 to have occurred between October and December more as a drain on the rhizome than on the vegetative aerial fraction although at S0 the proportional allocation to vegetative aerial parts by dwarf fertile shoots was also somewhat lower than that seen in October.

The dead leaf fraction of total biomass of dwarf fertile shoots in December was seen to have increased from the corresponding values in October, both as a proportion (figure 4.42) and in terms of mean dry weight per dwarf branch module (figure 4.16). In December, dead leaves made up a significantly greater proportion of aerial biomass of dwarf fertile shoots at S1 than at either S0 or S2 (table 4.41).

In contrast to their fertile counterparts, dwarf vegetative shoots showed a proportionately smaller allocation to dead leaves and a greater allocation both to green leaves and to rhizomes. This confirms the adolescence of the latter shoot cohort compared with the more mature fertile shoot population. This was also shown in figure 4.7, where at all sites, vegetative shoots were seen to belong to the

younger age classes, compared with fertile shoots.

Differences were also found between sites, in December 1980, in terms of the proportional allocation of dwarf vegetative shoot biomass to component parts (figure 4.42). At S0 green leaf laminae made up a significantly greater proportion of dwarf vegetative shoot biomass than at S1 ($P < .05$), whereas dead leaves and scale leaves together made up the balance at the latter site. Figure 4.7 indicates a greater range of age classes within the dwarf vegetative shoot population at S1 compared with S0 in December 1980, on the control plots. The greater mean proportional contribution of scale leaves and dead leaves to aerial biomass of dwarf vegetative shoots at S1 compared with S0 may reflect the contribution of very young (age class 0) and older (age class 3) shoots respectively in the population at S1. Dwarf vegetative shoots in these age classes were absent from S0 (control plots) at this harvest.

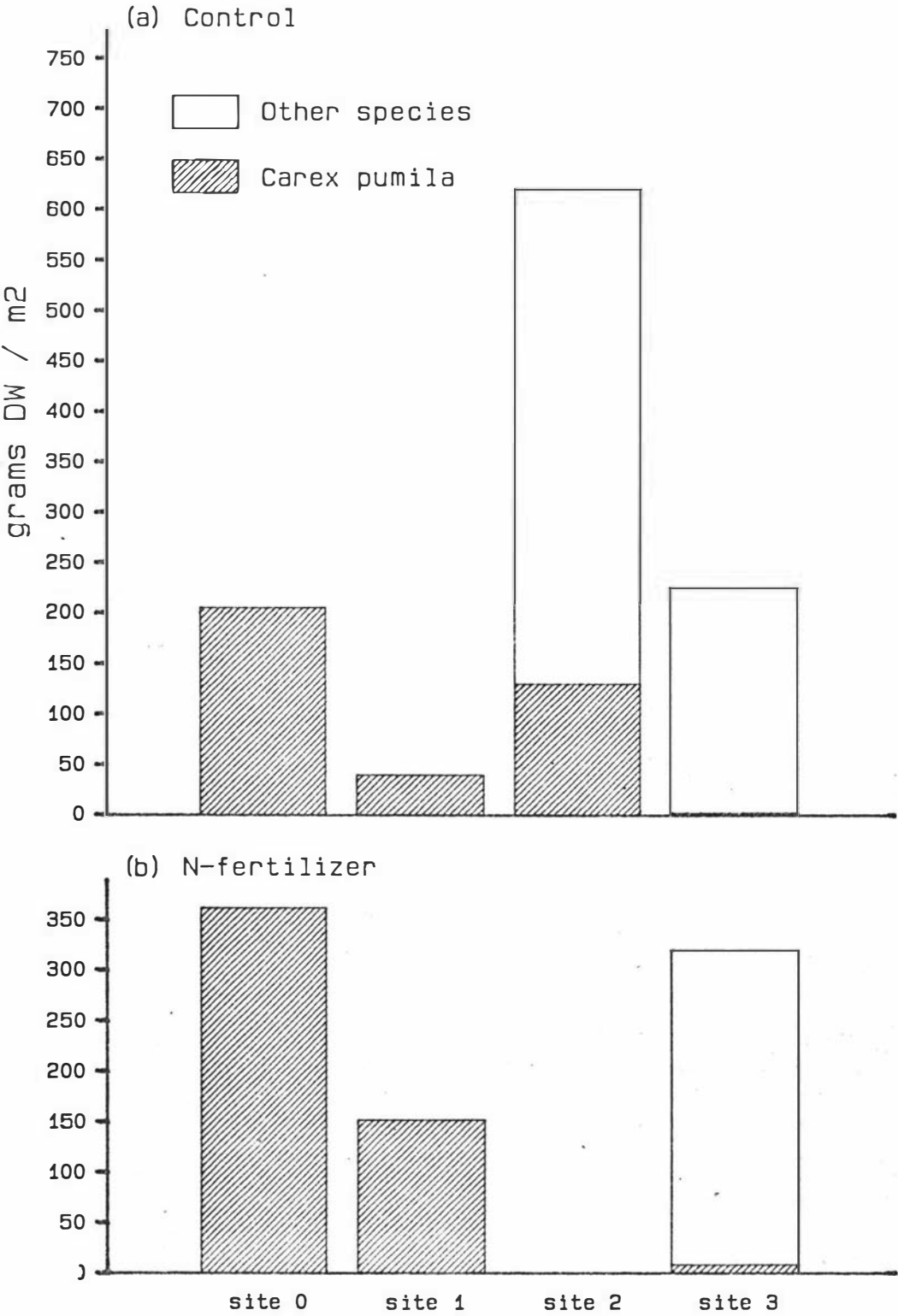
4.3.7 The effect of nitrogen fertilizer addition

1. Results

(a) Biomass

Nitrogen fertilizer addition (equivalent to 50 kg N / ha) in spring 1980 had by December of that year increased the sward mass at all sites relative to the controls (figure 4.43). However, significant differences were found between sites representing different stages in the sere, for components of these populations.

Figure 4.43 The distribution of biomass of the sward to *Carex pumila* and to other species with and without nitrogen fertilizer in December 1980



In the old hollow at S3, the depauperate Carex pumila population, which constituted only a minor fraction of the sward mass, showed little or no response to nitrogen fertilizer. The differences between the fertilized and control plots both in terms of biomass and shoot and shoot bud densities of Carex pumila were small and not statistically significant (figure 4.43 and table 4.42). At this site, species other than Carex pumila, notably Selliera radicans and Hypochaeris glabra, responded to fertilizer addition by increasing biomass (figure 4.43). However, the difference in amount of total nitrogen in the sward mass of the vegetation as a whole between control and fertilized plots at this site was equivalent to 9 kg N / ha, less than one-fifth of the nitrogen added.

Table 4.42 Shoot and shoot bud densities at S0, S1, S2 and S3 on the sand plain, in December 1980, with (N) and without (C) nitrogen fertilizer addition.

		Number of shoots or buds per 30 x 30 cm						
		S0		S1		S2	S3	
Shoot type		C	N	C	N	C	C	N
Dwarf	vegetative	7.0	21.0	5.5	24.0	7.0	2.5	3.0
	fertile	7.0	6.0	7.0	11.0	17.0	0.0	0.5
Long	vegetative	0.5	6.0	1.0	4.0	1.5	0.0	0.5
	fertile	5.0	2.0	2.5	1.0	8.5	0.0	1.0
Expanding buds		16.0	37.0	10.0	36.5	10.5	0.0	0.0
Dead shoots		1.5	0.5	11.0	4.5			

On the low dune at S0 and S1, nitrogen fertilizer increased biomass of Carex pumila (figure 4.43). At these sites other species were not found in the harvested samples. The magnitude of the increase in the more adolescent population at S0, which was 50% greater than that at S1, was equivalent to 1560 kg dry matter / ha or 20.7 kg nitrogen / ha (figure 4.44). The increase in total nitrogen represented almost half of the additional nitrogen applied three months previously. The increases in dry matter and total nitrogen at S1 (namely 1120 kg DM / ha and 13.1 kg N / ha) were more similar to those at S3 than at S0.

At S0, significant increases in dry weight (DW) and total nitrogen (TN) per unit area occurred in response to fertilizer in root ($P < .05$ for DW; $P < .01$ for TN), rhizome ($P < .05$ for DW and TN), culm including sheath ($P < .05$ for TN), and green laminar ($P < .05$ for TN) fractions. Both DW and TN of seeds were similar under the two treatments whereas dead leaves were reduced (figure 4.44). At S1, increases in DW and TN per unit area occurred in all branch components (figure 4.44). These increases were relatively small (cf S0) and only for TN of roots was the increase found to be statistically significant ($P < .05$). The magnitude of the increases in rhizomes, leaves and seeds were however, greater than those in roots.

(b) Total nitrogen concentrations, %TN

By bulking component shoot populations at each site, significant effects of fertilizer addition were masked. For example, nitrogen fertilizer did not affect the total nitrogen concentration (%TN) of Carex pumila shoots, averaged over all vegetative organs at both S0 and S1, and over both shoot types (those attached to dwarf and to long rhizome modules) and both states of shoot (vegetative and flowering;

Figure 4.44 Effect of nitrogen fertilizer on the distribution of (a) dry weight and (b) total nitrogen content of *Carex pumila* biomass to component organs at two sites in summer 1980-81

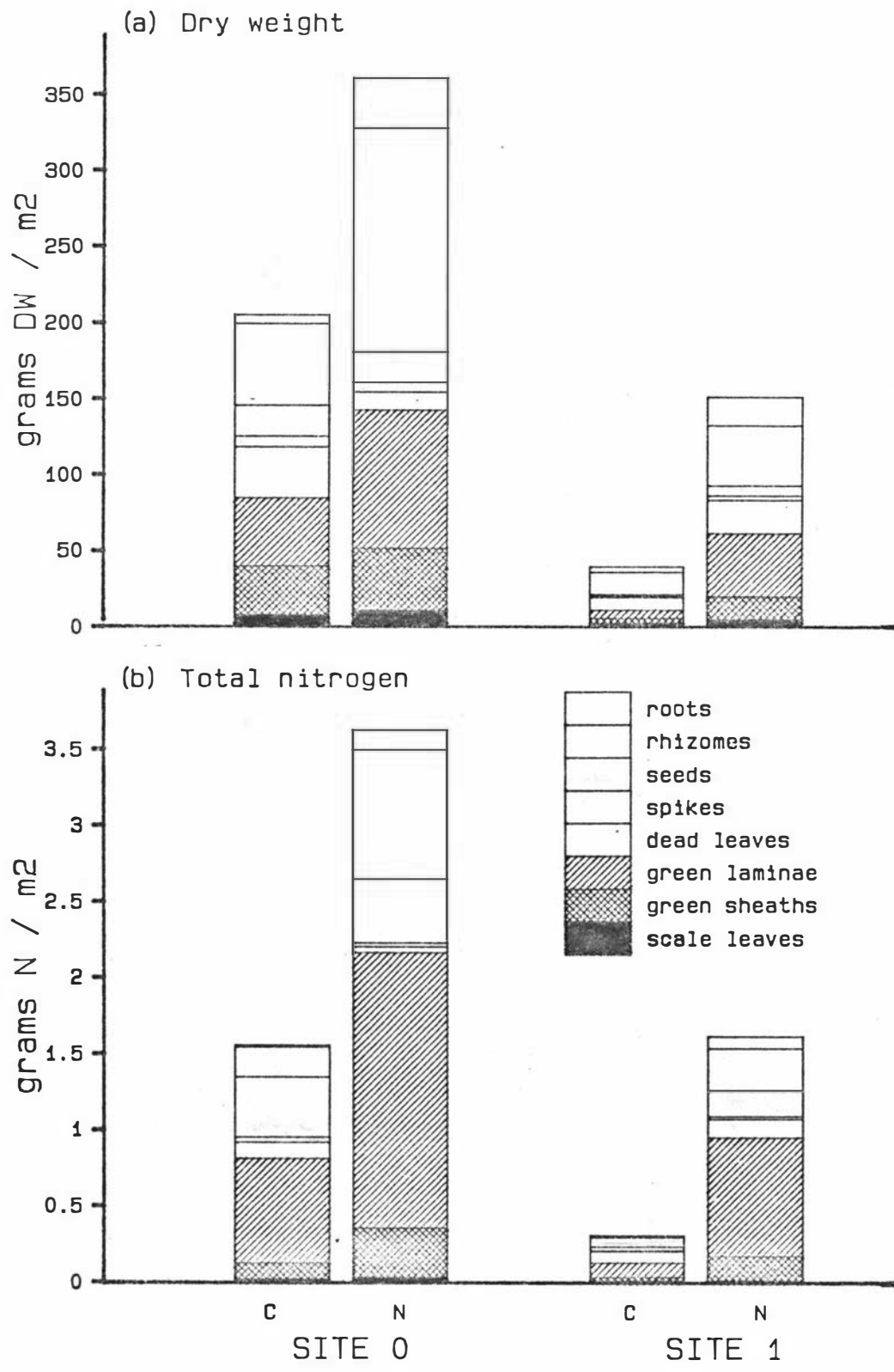


table 4.20). However, there was a differential effect of fertilizer on component organs which differed between sites and between dwarf and long shoots (see significant 'site x treatment x organ' and 'type x treatment x organ' interactions, $P < .05$, table 4.20). At the more mature site (S1), additional fertilizer increased the %TN of green leaves (laminae and sheaths) of dwarf vegetative shoots, and of underground organs, particularly rhizomes, attached to all but dwarf fertile shoots (table 4.43). At the younger site (S0), increases were seen in green leaves (both sheaths and laminae) of dwarf shoots. %TN values for long shoots remained constant or were decreased, as in the case of rhizomes attached to vegetative shoots at S0, and green leaf laminae and dead leaves at S1. %TN of seeds on shoots attached to both types of rhizome module were increased by the nitrogen treatment at S1 (table 4.43). No such effect occurred at S0.

Table 4.43 The effect of nitrogen fertilizer on the %TN of component parts of Carex pumila shoots at two sites on the sand plain.

		Rhiz	Root	Bracts	Green sheath	Green laminae	Dead leaves	Seeds
(a) Dwarf vegetative								
Site 0	Control	0.49	0.27	0.34	0.73	1.82	0.46	
	Fertilizer	0.61	0.44	0.27	1.17	2.33	0.53	
Site 1	Control	0.61	0.32	0.41	1.04	1.66	1.15	
	Fertilizer	1.20	0.55	0.44	1.37	2.09	0.68	
(b) Long vegetative								
Site 0	Control	0.94	0.40	0.39	0.95	1.76	0.56	
	Fertilizer	0.62	0.42	0.43	0.91	1.74	0.58	
Site 1	Control	0.35	0.29	0.22	1.02	2.00	0.96	
	Fertilizer	0.52	0.31	0.29	0.71	1.40	0.52	
(c) Dwarf fertile								
Site 0	Control	0.24	0.11	0.25	0.16	1.35	0.23	2.09a
	Fertilizer	0.32	0.13	0.41	0.24	1.62	0.15	2.16a
Site 1	Control	0.63	0.44	0.48	0.81	1.59	0.97	1.96a
	Fertilizer	0.65	0.42	0.40	0.71	1.81	0.51	2.32bc
(d) Long fertile								
Site 0	Control	0.29	0.19	0.42	0.12	0.99	0.34	1.84a
	Fertilizer	0.37	0.10	0.35	0.20	1.07	0.35	2.09a
Site 1	Control	0.38	0.39	0.45	0.55	2.10	0.76	2.07a
	Fertilizer	0.66	0.55	0.31	0.64	1.87	0.69	2.53c

a > b, $P < .05$; a > c, $P < .01$

(c) Density

Nitrogen fertilizer also affected the density and biomass of dwarf shoots differently from that of long shoots. Further, these responses differed between S0 and S1. This site x shoot type x treatment interaction can be summarized by the effect of fertilizer addition on the ratio of dwarf to total (long plus dwarf) shoots. On the basis of shoot density, the dwarf to total shoot ratio was increased by the nitrogen treatment at both S0 and S1 (table 4.44), suggesting that fertilizer application had a greater effect on dwarf than on long shoot densities.

Table 4.44 The effect of nitrogen fertilizer addition on the ratio of dwarf shoots to total (long plus dwarf) shoots; (a) density, (b) total biomass and (c) aerial biomass.

		RATIO	
		Dwarf / total shoot	
		Control	N-fertilizer
(a) Shoot density	S0	0.72	0.77
	S1	0.78	0.89
(b) Total biomass	S0	0.58	0.43
	S1	0.43	0.65
(c) Aerial biomass	S0	0.69	0.66
	S1	0.56	0.79
	S2	0.53	
	S3	0.76	

At both S0 and S1, fertilizer addition resulted in large increases in dwarf shoot and shoot bud densities in Carex pumila (table 4.42). By December, the bulk of the increased density of dwarf shoots was vegetative, although at S1 dwarf fertile shoot density was also increased by this treatment ($P < .05$). This latter increase is of interest in that to be fertile, these shoots must have been present before the application of fertilizer in spring. The density of fertile shoots at S0 and of shoots attached to long rhizome segments at both sites (S0 and S1) were not affected by this treatment. However, averaged over S0 and S1, the density of long shoots in which elongation of the culm and inflorescence development occurred was reduced by the nitrogen treatment ($P = .056$) with a concomitant increase in the density of long vegetative shoots ($P = .054$; table 4.42).

The density of dead shoots observed three months after nitrogen fertilizer application at S1 was reduced compared with the controls, whereas at S0 and S3 no such effect was seen (table 4.42).

At S0, the ratio of dwarf to total shoots based on biomass was decreased by nitrogen fertilizer, in contrast to that based on shoot density. At S1, the ratio was increased by the fertilizer treatment (site x treatment interaction significant, $P < .05$; table 4.44). This indicates a greater biomass response to nitrogen fertilizer addition by long relative to the dwarf shoots at S0, whereas at S1, the greater response was by dwarf shoots. This was confirmed when the biomass responses of component shoot populations to fertilizer addition were examined.

(d) Dry weight and total nitrogen of component populations and organs

Biomass of component shoot populations of Carex pumila was increased by the nitrogen treatment only where shoot densities were also increased. Significant effects were found in dwarf vegetative shoots at both S0 and S1, dwarf fertile shoots at S1, and long vegetative shoots at S0 (tables 4.42 and 4.45). The size of the increases in dwarf vegetative shoot biomass at the two sites were similar. Despite the increase of almost one order of magnitude at S1, which was clearly evident in the field (figure 4.45), the standing biomass of dwarf vegetative shoots on the fertilized plots was still less than that on the control plots at S0. The increase in biomass of the long vegetative shoot population at S0 ($P < .01$; table 4.45) was largely attributable to the increase by more than 30-fold of the rhizome fraction ($P < .01$; table 4.46). The fertilizer-induced increase seen in the aerial fraction of these shoots was smaller, but nonetheless significant ($P < .01$, table 4.45). The increased total and aerial biomass of dwarf fertile shoots at S1 in response to the fertilizer perturbation was attributable to large relative increases in rhizome, green leaf, dead leaf and seed fractions (table 4.46).

Figure 4.45 The effect of nitrogen fertilizer on the vegetation on the low dune.



Table 4.45 The effect of nitrogen fertilizer addition on (a) total and (b) aerial biomass of component shoot populations of Carex pumila on the sand plain, in December 1980.

	grams dry weight / 30 x 30 cm							
	S0		S1		S2		S3	
	C	N	C	N	C	C	N	
(a) Total								
Dwarf vegetative	5.08	*	9.2	0.56	*	4.99	0.86	0.17 ns 0.37
fertile	5.56	ns	4.56	0.98	*	3.45	3.60	0 ns 0.06
Long vegetative	0.27	**	14.51	0.84	ns	4.61	0.86	0 ns 0.09
fertile	7.55	ns	4.21	1.18	ns	0.57	6.37	0 ns 0.21
(b) Aerial								
Dwarf vegetative	3.95	*	6.41	0.37	*	3.50	0.61	0.12 ns 0.25
fertile	5.04	ns	4.19	0.72	*	2.87	3.201	0 ns 0.05
Long vegetative	0	**	3.59	0.23	ns	1.59	0.15	0 ns 0
fertile	4.11	ns	2.06	0.60	ns	0.41	3.18	0 ns 0.08

Table 4.46 Mean dry weight per unit area of component organs of Carex pumila populations in table 4.45.

	grams dry weight / 30 x 30 cm							
	S0		S1		S2		S3	
	C	N	C	N	C	C	N	
(a) Dwarf vegetative shoots								
Roots	0.14	0.465	.08	0.61	.075	.03	.08	
Rhizomes	0.985	2.335	.115	0.885	.175	.02	.04	
Dead leaves	0.625	0.06	.065	0.28	.07	.05	.065	
Green laminae	2.175	4.31	.16	2.29	.25	.04	.1	
Green sheaths	0.89	1.645	.085	0.7	.175	.02	.055	
Bracts	0.26	0.39	.055	0.225	.115	.01	.025	
(b) Dwarf fertile shoots								
Roots	0.02	0.01	.1	0.16	.075	0	.005	
Rhizomes	0.5	0.36	.155	0.425	.32	0	.005	
Seeds	1.213	1.278	.056	0.57	.757	0	0	
Female spikes	0.312	0.342	.019	0.156	.169	0	0	
Male spikes	0.085	0.07	.03	0.075	.11	0	.005	
Dead leaves	1.135	0.47	.385	1.23	1.25	0	.02	
Green laminae	1.01	1.05	.1	0.41	.23	0	.01	
Culms/sheaths	1.1	0.87	.095	0.35	.45	0	.01	
Bracts	0.18	0.11	.04	0.075	.235	0	0	
(c) Long vegetative shoots								
Roots	0.005	2.25	.095	0.92	.055	0	.005	
Rhizomes	0.265	8.675	.515	2.105	.66	0	.08	
Bracts	0	0.295	.04	0.075	.025	0	0	
Sheaths	0	0.795	.045	0.285	.045	0	0	
Green laminae	0	2.315	.11	0.955	.075	0	0	
Dead leaves	0	0.18	.035	0.27	0	0	0	
(d) Long fertile shoots								
Roots	0.355	0.255	.045	.01	.66	0	0.15	
Rhizomes	3.08	1.89	.53	.145	2.35	0	.115	
Seeds	0.632	0.508	.46	.028	.358	0	0	
Female spikes	0.168	0.127	.019	.017	.082	0	0	
Male spikes	0.06	0.025	.015	.015	.05	0	0	
Dead leaves	1.25	0.365	.255	.185	1.835	0	.035	
Green laminae	0.855	0.505	.11	.08	.235	0	.02	
Culms/sheaths	0.885	0.375	.1	.055	.375	0	.025	
Bracts	0.26	0.16	.055	.03	.25	0	0	

The effect of nitrogen fertilizer addition in increasing biomass of various component shoot populations of Carex pumila could not be attributed solely to the increases in density of these shoots. Increased growth of shoots also occurred in response to the fertilizer treatment. Table 4.47 shows the effect of nitrogen fertilizer on the mean size of both dwarf and long and fertile and vegetative shoots at three sites on the study area. Where nitrogen fertilizer did not affect shoot density or biomass per unit area, mean branch size also was not affected (table 4.47). Nitrogen fertilizer did however affect the distribution of biomass within all component shoot populations (see below).

A significant site x treatment interaction ($P < .05$) was found for mean size of dwarf vegetative shoots at S0 and S1. At S1, the mean size of these aerial shoots under the fertilizer regime was not significantly greater than that of the controls (table 4.47). By contrast, the mean size of dwarf vegetative shoots was decreased by the fertilizer treatment, at S0. At S1, the mean dry weight of green leaf laminae and mean number of green leaves per dwarf vegetative shoot module were significantly increased by the nitrogen treatment ($P < .05$, table 4.47 and figure 4.46 respectively). Figure 4.46 shows that most shoots at S1 including the new recruits arising during the period since nitrogen application had produced as many (3-6) or more (7-9) green leaves as the control shoots. The fertilizer-induced increase in aerial growth of dwarf vegetative shoots at S0 (where dwarf shoot recruitment was also increased) was insufficient for the average shoot to reach or surpass the mean size of the controls (table 4.47). The number and proportion of smaller than average shoots in the population was increased (figure 4.46). However, the mean size of dwarf vegetative shoots in the N-plots at S0 was still larger than

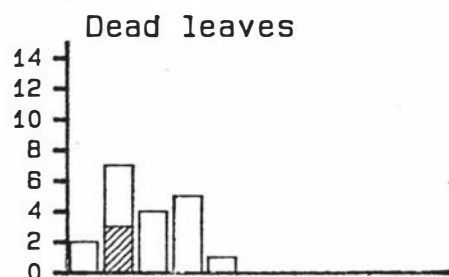
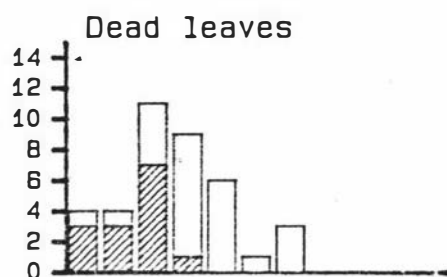
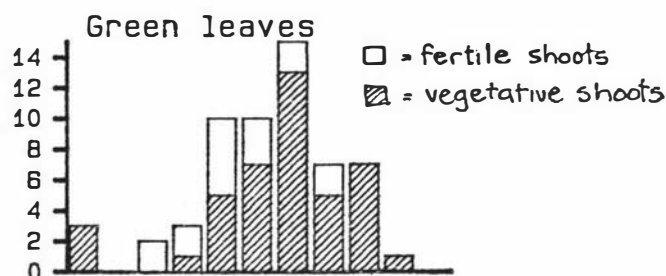
Figure 4.46 The frequency distributions of the number of green (G) and of dead (D) leaves per shoot of *Carex pumila* on (a) control and (b) N-fertilized plots, in December 1980

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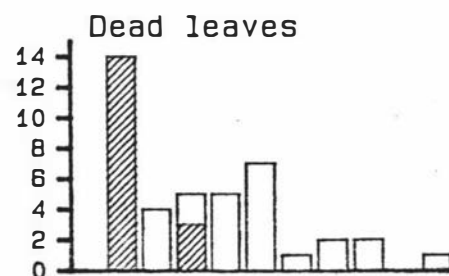
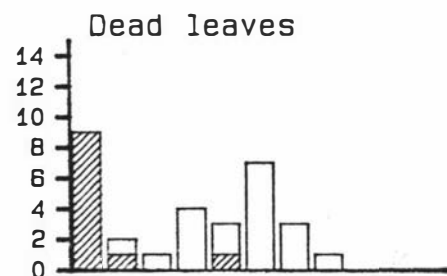
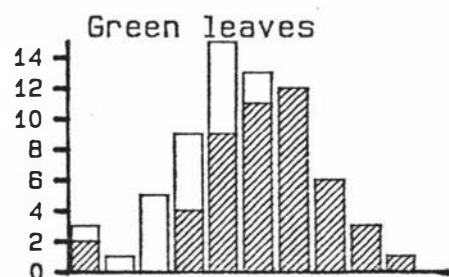
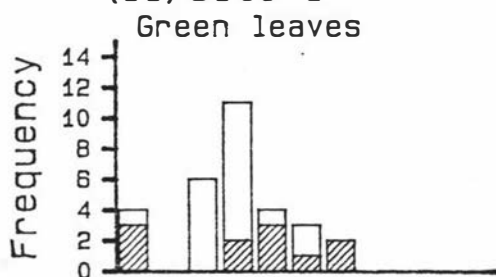
(a) CONTROL

(b) N-FERTILIZER

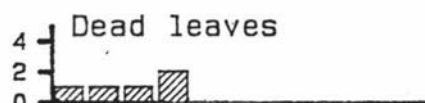
(i) Site 0



0 1 2 3 4 5 6 7 8 9 10
(ii) Site 1



0 1 2 3 4 5 6 7 8 9 10
(iii) Site 3



0 1 2 3 4 5 6 7 8 9 10

0 1 2 3 4 5 6 7 8 9 10

Number of leaves per shoot

that of dwarf vegetative shoots in the N-plots at S1 (table 4.47).

Table 4.47 The effect of nitrogen fertilizer on mean dry weight per branch module of component parts of Carex pumila shoots, in December 1980.

	grams dry weight / branch module							
	S0		S1		S2		S3	
	C	N	C	N	C	C	N	
(a) Dwarf vegetative shoots								
Total	.739	.475	.101	.21	.123	.099	.111	
Aerial	.58	.33	.067	.144	.087	.075	.075	
Roots	.019	.029	.013	.026	.01	.015	.024	
Rhizomes	.144	.113	.022	.04	.025	.009	.013	
Dead leaves	.088	.003	.013	.011	.009	.031	.025	
Green laminae	.318	.224	.03	.095	.037	.025	.026	
Green sheaths	.132	.086	.014	.029	.025	.013	.015	
Bracts	.036	.02	.009	.009	.017	.006	.009	
(b) Dwarf fertile shoots								
Total	.794	.772	.138	.311	.211	0	.11	
Aerial	.719	.691	.102	.257	.188	0	.09	
Roots	.004	.002	.014	.015	.004	0	.01	
Rhizomes	.071	.079	.022	.039	.019	0	.01	
Seeds	.173	.214	.008	.05	.045	0	0	
Female spikes	.045	.056	.003	.014	.01	0	0	
Male spikes	.012	.011	.004	.007	.006	0	.01	
Dead leaves	.162	.072	.054	.111	.074	0	.04	
Green laminae	.144	.178	.014	.037	.014	0	.02	
Culms/sheaths	.157	.143	.014	.031	.026	0	.02	
Bracts	.026	.017	.006	.009	.014	0	0	
(c) Long vegetative shoots								
Total	.54	2.352	.83	1.136	.557	0	.17	
Aerial	0	.565	.22	.38	.100	0	0	
Roots	.01	.341	.095	.23	.035	0	.01	
Rhizomes	.53	1.446	.515	.526	.422	0	.16	
Bracts	0	.049	.04	.019	.018	0	0	
Sheaths	0	.133	.045	.071	.03	0	0	
Green laminae	0	.353	.11	.239	.052	0	0	
Dead leaves	0	.03	.035	.068	0	0	0	
(d) Long fertile shoots								
Total	1.548	1.985	.549	.565	.751	0	.21	
Aerial	.826	1.01	.285	.41	.378	0	.08	
Roots	.084	.185	.03	.01	.077	0	.015	
Rhizomes	.638	.79	.234	.145	.296	0	.115	
Seeds	.126	.287	.023	.028	.043	0	0	
Female spikes	.034	.064	.009	.017	.01	0	0	
Male spikes	.012	.012	.008	.015	.006	0	0	
Dead leaves	.255	.193	.105	.185	.217	0	.035	
Green laminae	.17	.208	.065	.08	.028	0	.02	
Culms/sheaths	.175	.168	.048	.055	.045	0	.025	
Bracts	.052	.08	.023	.03	.029	0	0	

At S0, nitrogen was also seen to decrease both the mean number of dead leaves per dwarf vegetative shoot and the frequency of these shoots with two or more dead leaves each (figure 4.46). This latter effect cannot be attributed to the increased recruitment of dwarf shoots since the time of nitrogen application, but to a delay in the onset of leaf senescence by nitrogen. This conclusion is supported by the appearance in the treated plots (cf the controls) of dwarf vegetative shoots with more than seven green leaves each (figure 4.46). The change in response to nitrogen in the balance of dead and green leaves within dwarf vegetative shoots was also seen in the altered proportional distribution of the total dry weight of these shoots to green laminae and dead leaves (see below).

At S0 the mean size of long vegetative branches was increased over four-fold by the nitrogen treatment ($P < .01$, table 4.47), largely though an increase in the mean size of the rhizome fraction ($P < .01$), but also through the simple occurrence of aerial parts which were absent on the control plots. The samples taken from the control plots at S0 contained only a single 30cm portion of one long rhizome branch module. The dry weight of this rhizome portion was similar to that estimated for long rhizome segments attached to fertile shoots. No significant fertilizer effect was seen at this site for this latter parameter.

At S1, the mean size of dwarf fertile shoots was greater on the treated plots, than on the controls. This difference was attributed to increases in the rhizome fraction and all aerial shoot components. These increases did not occur equally in all branch components (see proportional allocation of biomass to component organs below). At S0, the mean size of fertile shoots attached to both dwarf and long rhizome branches showed no significant response to the nitrogen

treatment (table 4.47), although redistribution of dry weight within these shoots did occur (see below).

(e) Flowering and seed production

Nitrogen fertilizer application affected flowering and seed production at both low dune sites. These effects were due to in part changes in fertile shoot densities and in part the redistribution of resources within these shoots. The changes in fertile shoot densities were outlined in section (b) above.

Despite the reduced density of fertile shoots at S0 in response to the nitrogen treatment, there was no decrease in mean dry weight of seeds per unit area. This resulted from an increased mean number of seeds per reproductive culm ($P < .01$ for long fertile shoots; $P < .05$ for dwarf fertile shoots, table 4.48). At S0, mean size and nitrogen concentration of seeds on shoots attached to both dwarf and long rhizome branches were not significantly altered by the fertilizer treatment (table 4.48 and 4.43, respectively). Thus, the total nitrogen content per seed at this site also was not found to differ significantly between control and fertilized plots (table 4.48).

Table 4.48 The effect of nitrogen fertilizer addition on (a) mean seed weight, (b) mean number of seeds per inflorescence and (c) total nitrogen content of seeds of Carex pumila on shoots attached to dwarf and long rhizome branches, in December 1980.

(a) Mean seed weight

		grams/culm		mg/seed	
		Control	N-fertilizer	Control	N-fertilizer
S0	Dwarf	0.173	** 0.214	2.267	ns 2.436
S1	Long	0.126	** 0.287	2.324	ns 2.589
	Dwarf	0.008	** 0.057	1.307	* 2.152
	Long	0.023	ns 0.028	1.929	ns 2.667
S2	Dwarf	0.045		2.542	
	Long	0.043		2.219	

(b) Mean seed number/culm

		Control	N-fertilizer
S0	Dwarf	76.64	* 87.81
	Long	54.17	** 109.5
S1	Dwarf	5.68	** 22.69
	Long	11.5	ns 10.5
S2	Dwarf	17.24	
	Long	18.91	

(c) Total nitrogen content

		grams N / m2		mg N / seed	
		Control	N-fertilizer	Control	N-fertilizer
S0	Dwarf	0.282	0.307	0.0474	ns 0.0526
	Long	0.129	0.118	0.0428	ns 0.0541
S1	Dwarf	0.012	0.147	0.0255	* 0.0499
	Long	0.011	0.008	0.0399	ns 0.0675

At S1, the density of fertile shoots and their seed output per unit area of ground were extremely reduced and significantly lower than at S0 (tables 4.42 and 4.48). Nitrogen fertilizer addition increased both density of fertile shoots attached to dwarf rhizome branches and seed output per unit area, measured in both dry weight and total nitrogen. This was achieved through increases in both mean number of seeds per inflorescence and mean seed size on dwarf fertile shoots. The similarly sized increase in mean dry weight per seed on shoots attached to long rhizome branches at this site was not statistically significant.

At S1, %TN of seeds was significantly increased by the nitrogen treatment ($P < .05$ and $P < .01$ for dwarf and long fertile shoots, respectively, table 4.43). Thus, with the increased mean dry weight of seeds ($P < .05$ for dwarf shoots, table 4.48), their total nitrogen content was also significantly increased ($P < .05$) and was at least as great as that at S0 (for seeds borne on shoots attached to both types of rhizome module; table 4.48). Thus, the mean dry weight and total nitrogen content of seeds per inflorescence and per unit area were increased 5-10 fold by the nitrogen perturbation (tables 4.46 and 4.48). However, the seed output per unit area (grams DW and grams TN) at S1, even with the large relative increases in response to nitrogen fertilizer, was less than that at S0 by a factor of two (tables 4.46 and 4.48).

(f) Proportional allocation of biomass and total nitrogen

(i) Distribution of biomass (DW and TN) between component shoots and organs

Nitrogen fertilizer addition decreased the ratio of fertile shoot biomass to total biomass, based on both dry weight (DW) and total nitrogen (TN), at S0 and S1 (table 4.49). This reflects the greater increase in vegetative shoot biomass relative to that of fertile shoots, in response to this perturbation, at both these low dune sites. This response occurred largely as an increase in the proportional allocation to green leaf laminae and to rhizomes of vegetative shoots (table 4.50). As a proportion of the total population, green leaves and dwarf vegetative shoots, which are composed in a large proportion by green leaves (see below), constitute a considerably higher proportion of total nitrogen than dry weight (tables 4.50 and 4.49, respectively). At S0, the proportional

allocation to seeds (population seed reproductive effort) was lower on the fertilized plots compared with the controls. The sum of the allocation of total nitrogen of biomass to dispersal (seeds) plus local colonization (rhizomes of vegetative shoots) was similar on both treated and untreated plots at S0 and at S2. On the controls at S1, this sum was reduced, although it was increased in response to additional nitrogen. In the senile population at S3, this allocation to seeds and to rhizomes of vegetative shoots was further reduced (cf controls at S1; table 4.31).

Table 4.49 The effect of nitrogen fertilizer (N) on the proportional allocation of biomass based on (a) dry weight and (b) total nitrogen to component shoot populations, in December 1980. C = control

	Proportion of total			
	S0		S1	
	C	N	C	N
(a) Dry weight				
Dwarf vegetative shoots	.275	.283	.157	.366
Long vegetative shoots	.015	.447	.236	.338
Dwarf fertile shoots	.301	.14	.275	.253
Long fertile shoots	.409	.13	.331	.042
(b) Total nitrogen				
Dwarf vegetative shoots	.456	.357	.192	.529
Long vegetative shoots	.017	.378	.192	.196
Dwarf fertile shoots	.275	.184	.324	.249
Long fertile shoots	.253	.081	.292	.026

Table 4.50 Effect of nitrogen fertilizer (N) on the proportional allocation of biomass based on (a) dry weight and (b) total nitrogen of Carex pumila to component organs, in December 1980.

	Proportion of total			
	S0		S1	
	C	N	C	N
(a) Dry weight				
Roots	.028	.092	.09	.125
Rhizomes Fert	.192	.063	.189	.035
Veg	.07 * _k	.345	.18 _{ns}	.226
Seeds	.10 *	.055	.028 _{ns}	.044
Green laminae	.219	.252	.135	.275
(b) Total nitrogen				
Roots	.007	.035	.039	.048
Rhizomes Fert	.078	.019	.109	.015
Veg	.048 _{ns}	.215	.086 _{ns}	.157
Seeds	.252 * _{xx}	.115	.072 _{ns}	.099
Green laminae	.44	.498	.309	.481

(ii) Allocation of DW and TN within component shoot populations

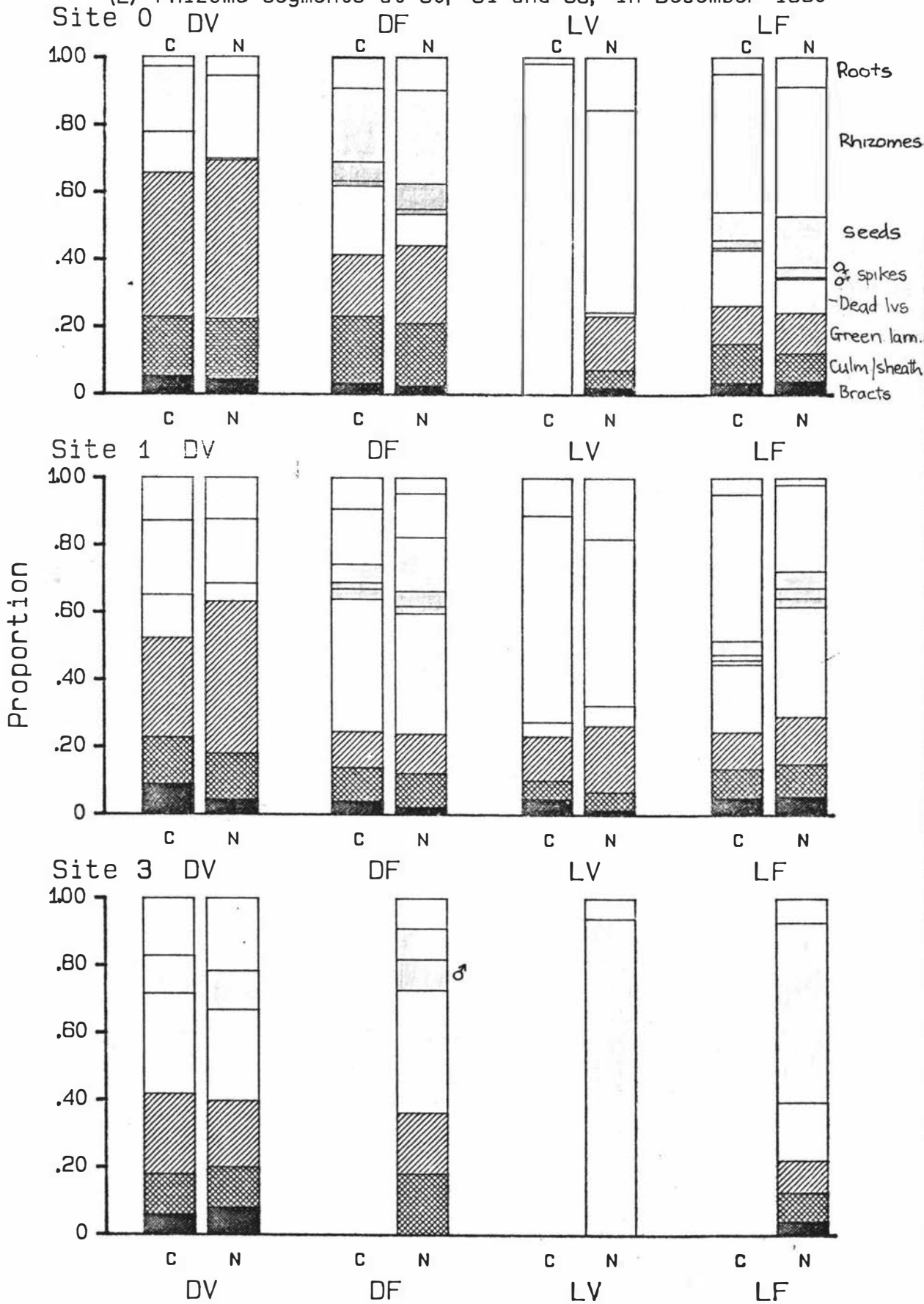
In December 1980, the proportional allocation of dwarf vegetative shoot biomass to component organs differed significantly from that of long vegetative shoots, at all sites and under both treatments (figure 4.47). The difference was attributable to rhizome allocation which was highly significantly greater in long than in dwarf vegetative shoot populations (table 4.51). Nitrogen fertilizer addition reduced the proportional allocation of vegetative shoot biomass to rhizomes in the long shoot population at S0, despite the large increase in the absolute allocation of biomass to this fraction (tables 4.46 and 4.47). In the control plots at this site, long vegetative shoots were represented by a portion of a single rhizome segment, whereas on the treated plots, aerial shoot modules attached to this branch type were found. As a consequence, the proportion of biomass of these branches in rhizomes was reduced.

Table 4.51 The effect of nitrogen fertilizer on the proportional allocation of biomass of (a) dwarf and (b) long vegetative shoot populations of Carex pumila to rhizomes, in December 1980.

Proportional allocation to rhizomes			
	Site	Control	N-fertilizer
(a) dwarf shoots	S0	.19 c	.25 c
	S1	.22 c	.19 c
(b) long shoots	S0	.95 a	.60 b
	S1	.58 b	.49 b

a > b, $P < .001$; b > c, $P < .01$

Figure 4.47 The effect of nitrogen fertilizer on the proportionate allocation of biomass of fertile (F) and vegetative (V) shoots attached to dwarf (D) and to long (L) rhizome segments at S0, S1 and S3, in December 1980



Long and dwarf vegetative shoots did not differ in the proportional allocation of their aerial biomass to individual aerial parts (bracts, sheaths of green leaves, green leaf laminae or dead leaves) at either S0 or S1 on either control or fertilized plots (figure 4.48). However, nitrogen fertilizer addition did increase the proportion of aerial biomass found in green leaf laminae, at both S0 and S1 and in both dwarf and long vegetative shoot populations (table 4.52). The increase in long vegetative shoots at S0 was small and not significant. On the nitrogen plots at both low dune sites, the proportion of the aerial biomass of long and of dwarf vegetative shoots found in green laminae ranged from 60 - 67%, values that were not significantly different from each other (table 4.52). The increased allocation of aerial biomass to green leaf laminae in response to the nitrogen treatment in the vegetative shoot populations occurred at the expense of the allocation to bracts at S1, and to dead leaves of dwarf shoots at S0 (figure 4.48 and table 4.52). The proportional allocation of aerial biomass to sheaths of green leaves was remarkably similar in all vegetative shoot populations in December 1980 on the low dune (figure 4.48).

Figure 4.48 (a) The effect of nitrogen fertilizer on the proportional allocation of aerial biomass of fertile shoots attached to dwarf (D) and to long (L) rhizome segments, December 1980.

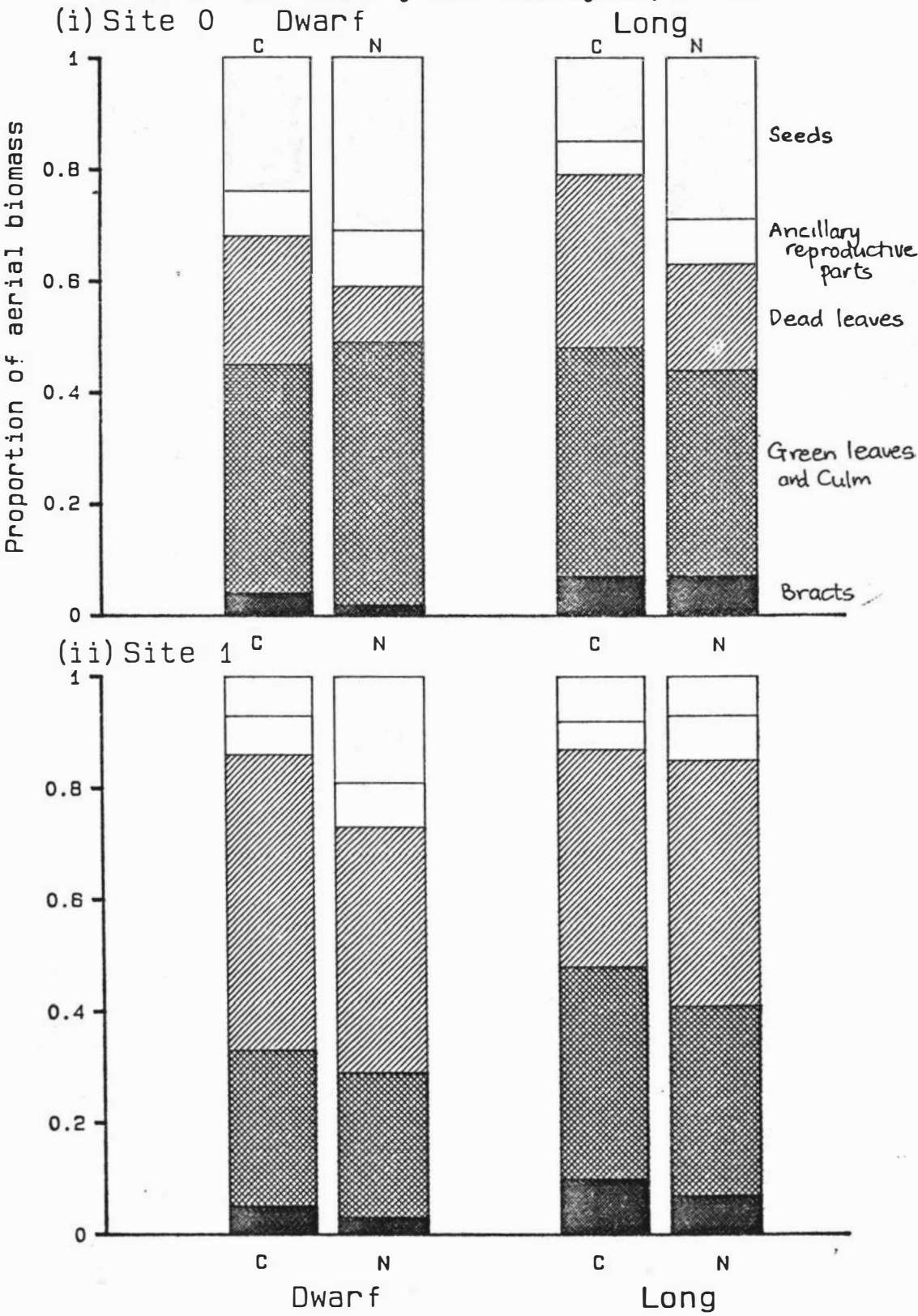
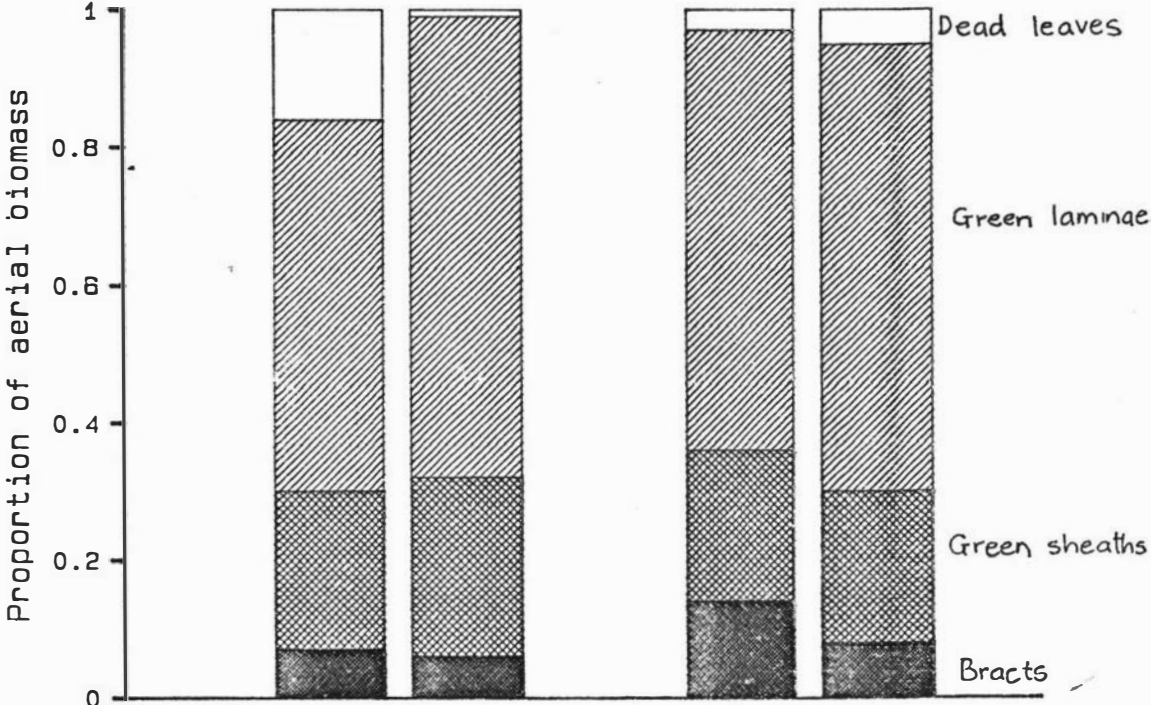


Figure 4.48 (b) The effect of nitrogen fertilizer on the proportional allocation of aerial biomass of vegetative shoots attached to dwarf (D) and to long (L) rhizome segments, Dec 1980.

(i) Site 0



(ii) Site 1

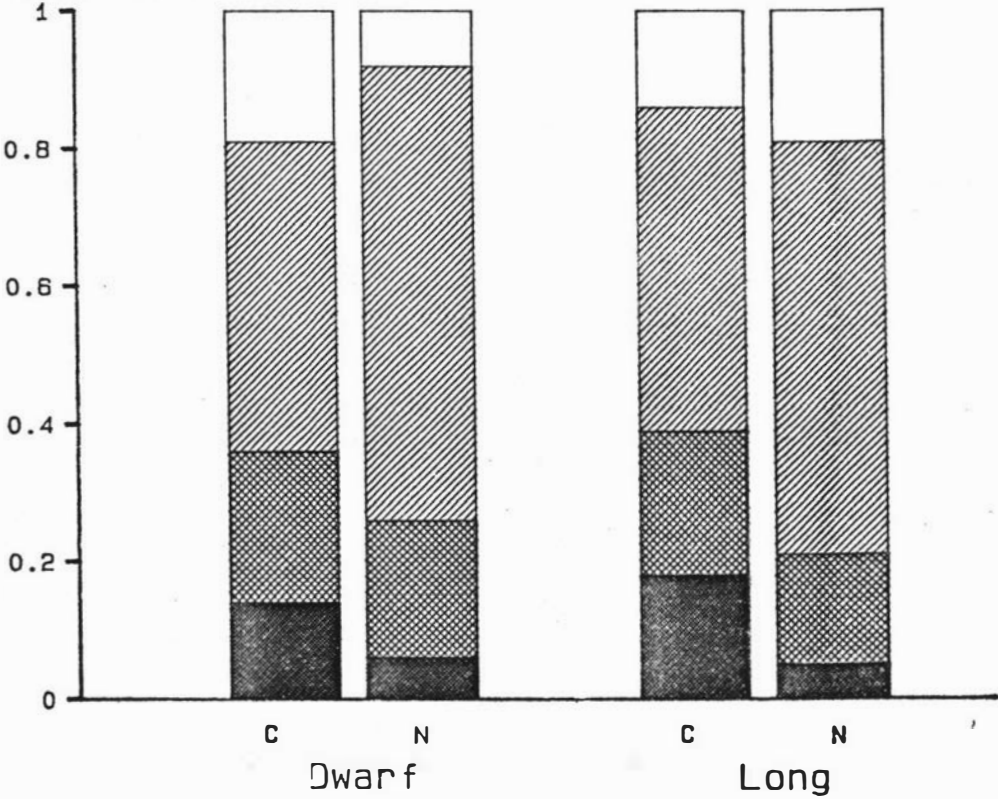


Table 4.52 The effect of nitrogen fertilizer (N) on the proportional allocation of aerial biomass of (a) dwarf and (b) long vegetative shoots of Carex pumila to component organs, in December 1980. C = control.

		Proportion of total dry weight					
		S0			S1		
		C		N	C		N
(a) Dwarf							
Green laminae	.55	**	.67		.45	***	.66
Green sheaths	.23	ns	.26		.22	ns	.20
Bracts	.07	ns	.06		.14	**	.06
Dead leaves	.16	*	.01		.19	ns	.08
(b) Long							
Green laminae	.62	ns	.65		.47	*	.60
Green sheaths	.22	ns	.22		.21	ns	.16
Bracts	.14	ns	.08		.18	**	.05
Dead leaves	.03	ns	.05		.14	ns	.19

Significance of differences are: * $P < .05$, ** $P < .01$, *** $P < .001$

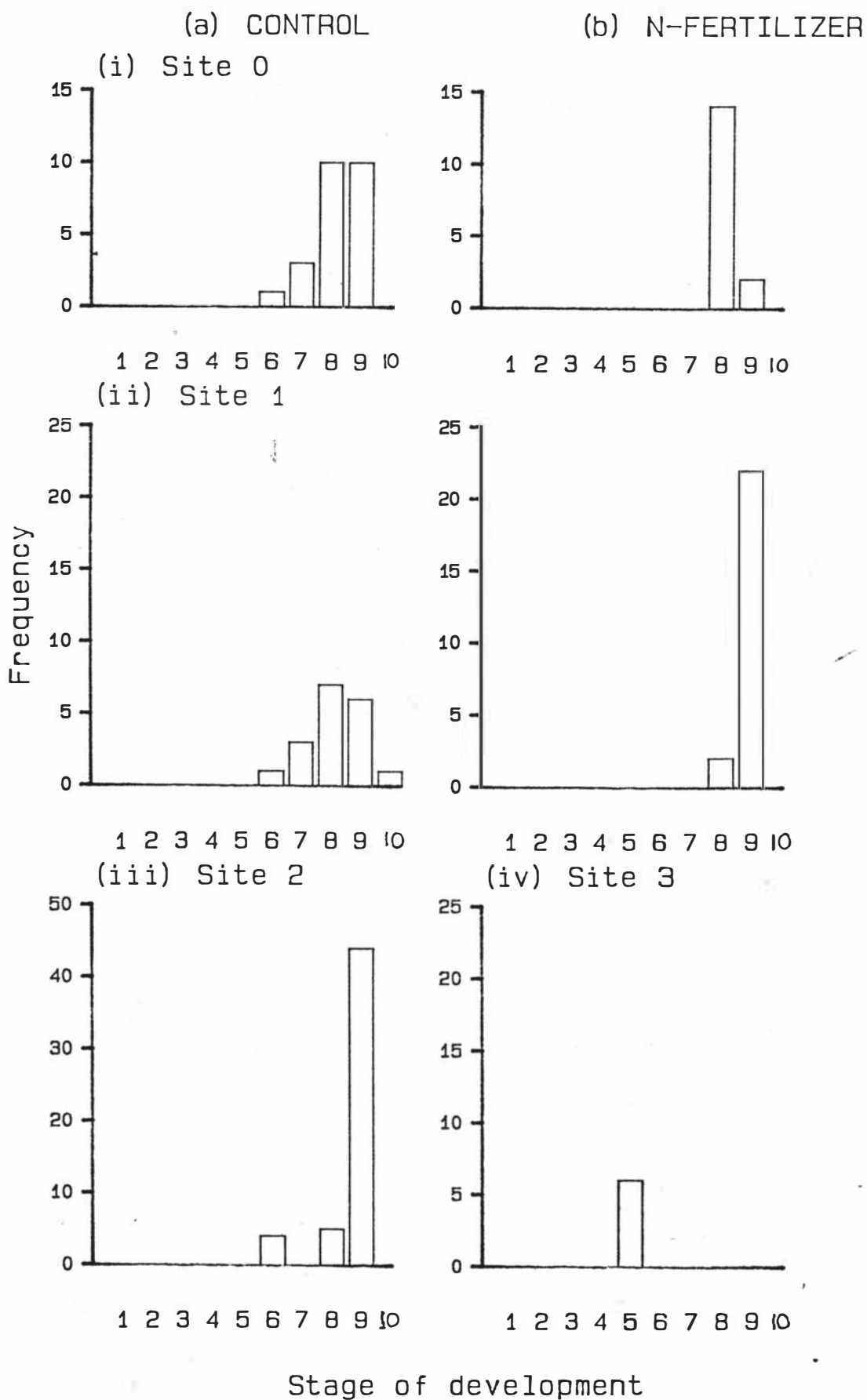
At S0 and S1, nitrogen fertilizer addition effected a redistribution of resources within fertile shoots (figures 4.47 and 4.48). This resulted in an increased total reproductive effort and seed reproductive effort, in fertile shoots attached to long and dwarf rhizome modules at S0 and to dwarf rhizome modules at S1. At S0, the dry weight and total nitrogen content of seeds per unit area was maintained on the fertilized plots (tables 4.46 and 4.48), despite the reduced proportion of the total population in fertile shoots (table 4.49). This redistribution of resources to reproductive structures at

S0, which occurred within shoots attached to both long and dwarf rhizome branches, appeared to be at the expense of other aerial shoot parts (figure 4.47). The greatest reduction in the proportional allocation of aerial biomass of fertile shoots at S0 was in the dead leaf fraction, for both shoot types (figure 4.48). At this site, the proportional allocation of dwarf fertile shoot biomass to green leaves was also increased by the fertilizer application. This juvenescence was associated with an increased number of green leaves per shoot (figure 4.46). The increase in the proportion of dwarf fertile shoots at stage 8 and a reduction of those at stage 9 at this site also suggest that the development of these shoots to maturity was retarded by the fertilizer treatment (figure 4.49).

At S1, nitrogen fertilizer increased the proportional allocation of dwarf fertile shoot biomass to sexual reproductive parts at the expense of the rhizome fraction (figure 4.47). This redistribution of resources was also seen as an increased mean number of seeds per inflorescence and an increased mean DW and TN per seed (table 4.48). At S1, reallocation of resources within long reproductive shoots also occurred in response to nitrogen addition. This also was manifest as a decreased allocation to rhizomes and an increased aerial shoot allocation (figures 4.47 and 4.48). However, unlike that in dwarf fertile shoots at this site, reproductive allocation within the aerial fraction was unchanged. The proportion found in dead leaves of long fertile shoots at S1 was increased.

At S3 in the old hollow, fertile shoots on the nitrogen fertilized plots had not developed beyond stage 5 by December 1980 (figure 4.49). Nitrogen may have delayed the senescence of these shoots. An equally plausible and not mutually exclusive explanation is that the stunted fertile shoots which were found only on the

Figure 4.49 The effect of nitrogen fertilizer on the frequency distribution of the stage of development of fertile shoots of Carex pumila, in December 1980



N-treated plots at this site simply lacked the vigour or resources of either stored reserves or assimilatory power for further elongation of the culm and female spike and seed development.

Table 4.53 compares the proportional allocation of the aerial biomass of component fertile shoot populations of Carex pumila to seeds based on grams dry weight with that based on grams total nitrogen as measures of resource investment. Since seeds were found to possess higher concentrations of total nitrogen than all other plant parts, with the exception of green leaf laminae, differences were expected between the two estimates. Seeds generally made up a higher proportion of the total nitrogen than of the dry weight of these fertile shoots.

Table 4.53 Proportional allocation of dry weight and total nitrogen of the aerial biomass of fertile shoots of Carex pumila to seeds, in December 1980.

(a) Means

Proportion of total in seeds					
Site	Shoot type	Treatment	Dry weight		Total nitrogen
SO	Dwarf	Control	0.24	***	0.53
		N-fertilizer	0.31	***	0.54
	Long	Control	.15	***	0.44
		N-fertilizer	0.29	***	0.62
S1	Dwarf	Control	0.07	ns	0.14
		N-fertilizer	0.19	**	0.43
	Long	Control	0.08	ns	0.15
		N-fertilizer	0.04	***	0.14

Significance of differences are: ** $P < .01$, *** $P < .001$

Table 4.53 (b) Analysis of variance

SOURCE	D.F. (M.V.)	S.S.	M.S.S.	F RATIO
type	1	0.03	0.03	11.94 **
site	1	0.39	0.39	138.42 ***
type*site	1	9.878E-03	9.878E-03	3.53 ns
treat	1	0.06	0.06	22.38 ***
type*treat	1	5.625E-03	5.625E-03	2.01 ns
site*treat	1	5.629E-05	5.629E-05	0.02 ns
type*site*treat	1	0.05	0.05	17.48 **
rep	1	0.01	0.01	4.96 *
res	1	0.29	0.29	102.87 ***
type*res	1	3.180E-04	3.180E-04	0.11 ns
site*res	1	0.05	0.05	18.17 ***
type*site*res	1	6.809E-03	6.809E-03	2.43 ns
treat*res	1	3.650E-03	3.650E-03	1.30 ns
type*treat*res	1	3.872E-04	3.872E-04	0.14 ns
site*treat*res	1	5.141E-03	5.141E-03	1.84 ns
type*site*trea*res	1	6.325E-03	6.325E-03	2.26 ns
error	13 (2)	0.04	2.798E-03	

Estimated treatment means and significance of differences between means

type	site	treat	rep	resource
Dwarf 0.31	S1 0.16	C 0.23	0.25	TN 0.37
Long 0.24	S0 0.39	N 0.32	0.30	DW 0.17
**	***	***		***

The analysis of variance showed that averaged over all site x shoot type x treatment combinations, the difference between dry weight and total nitrogen estimates was highly significant ($P < .001$), and that the magnitude of the difference was greater at S0 than at S1 averaged over the four shoot type x treatment combinations (site x resource interaction highly significant, $P < .001$). Table 4.53 shows that the estimates for all site x shoot type x treatment combinations to differ by a factor of two. At S0, all individual comparisons of dry weight and total nitrogen were highly significant ($P < .001$), and at S1 where nitrogen fertilizer significantly increased the proportionate allocation to seeds ($P < .05$ and $< .001$ for DW and TN, respectively), the difference was also highly significant ($P < .01$). For the other site x shoot type x treatment combinations at S1, the differences were smaller in magnitude and, although all in the expected direction, not found to be statistically significant (table 4.53).

The site x shoot type x treatment interaction term in the analysis of variance was highly significant ($P < .01$) indicating that the effect of fertilizer was not similar for both shoot types at both sites. Nitrogen fertilizer significantly increased the proportion of both dry weight and total nitrogen of fertile shoots in seeds, only in dwarf shoots at S1 and in long shoots at S0 (table 4.53). ~~In dwarf and long fertile shoots at S0 and S1, respectively, no such effect of fertilizer was observed ($P > .05$).~~

No significant difference was observed between dwarf and long fertile shoots in the proportionate allocation of either dry weight or total nitrogen of the aerial biomass to seeds, on the control plots at either low dune site. Only at S1, where nitrogen fertilizer significantly increased the proportionate allocation to seeds ($P < .05$ and $< .001$ for DW and TN, respectively), did such a difference become

apparent ($P < .001$).

2. Discussion

Nitrogen availability was found to be limiting plant growth in the study area. At all sites, each representing a different seral stage, nitrogen fertilizer addition increased both the sward mass and its total nitrogen content.

The effects of nitrogen fertilizer application on the growth of populations of rhizomatous perennial species in various stages of development on a sand dune sere have been reported elsewhere (Huskies 1979; Noble et al. 1979). On stands of both Carex arenaria and Ammophila arenaria, nitrogen-phosphorus-potassium (NPK) fertilizer increased the density and flux of shoots (Carex) and leaves (Ammophila) but only in situations where these pioneer species were the monopolist inhabitant. In well developed dune slack vegetation, other species were abundant and made the most visible response to the added fertilizer. The pioneers behaved as though little if any of the added nutrients were reaching their roots. Some of these observations were also made on Carex pumila in the sand plain sere in the present study.

In the old hollow where Carex pumila made up only a tiny fraction of the sward, other species, principally the round-leaf Manawatu sand plain form of Selliera radicans (Ogden 1974b) and Hypochaeris glabra, made most response to added nitrogen fertilizer. The differences between the nitrogen and control plots in terms of Carex pumila were very small. On younger sites where this species was the sole or major inhabitant, nutrient application greatly increased the number of buds recruited into active growth. By December three months after

fertilizer application, many of these had given rise to an aerial shoot. On the older site, where the population was entering a senile phase, these shoots had grown at least to the size of the controls. In the younger phase where Carex pumila was more vigorous, the nitrogen-induced cohort did not reach the size of their controls.

Evidence of the flux of leaves and shoots within the population was circumstantial. If the flux of either leaves or shoot modules were increased by fertilizer addition, then it should be possible to observe the net effect of this in a harvested sample of the standing crop: namely, an increase in the number of new shoots and leaves and an increase in the number of dead leaves per shoot or dead ramets per unit area, provided these dead units were not lost.

The evidence left no doubt that nitrogen fertilizer addition increased the birth rate of new aerial shoots on the low dune. However, the evidence for the increased death rate of leaves or ramets is equivocal. In the mature low dune phase additional nitrogen hastened senescence of reproductive shoots seen as an increase in the numbers of dead leaves per shoot and as an advance in the stage of shoot development (figure 4.49). In vegetative shoots, nitrogen fertilizer increased the frequency of shoots with at least one dead leaf (figure 4.46). However, the density of dead shoots at this site was reduced by the fertilizer application. This can be linked with the fertilizer-induced increase in density of reproductive shoots (table 4.42). These shoots predate the application of fertilizer. The response therefore can be attributed to the increased longevity of old dwarf shoots, that on the controls had died by December. This also accounts for the effect of nitrogen at this site of hastening the onset of maturity (death) in dwarf fertile shoots at this site, an effect not seen at S0 (figures 4.7 and 4.49).

In the younger low dune phase there was no evidence of increased death rates of either single leaves or whole shoots in response to nitrogen. On the contrary, the evidence at this site pointed to nitrogen retarding senescence by slowing the maturation of fertile shoots concomitantly reducing the numbers of dead leaves on both fertile and vegetative tillers (figures 4.46 and 4.49).

The conclusion that fertilizer increased the death rate of shoots of Carex arenaria (Noble et al. 1979) was based on results five to seven months after fertilizer application. At three months when observations of the effect of a similar treatment was made in the present study, Noble et al. (figure 8) show dead shoot density to be no different between the fertilizer treatment and the controls. It is probable that the increased birth rate of Carex pumila shoots in response to nitrogen fertilizer application on the Manawatu sand plain, precludes an increased death rate that was not seen at the December 1980 harvest, only three months after fertilizer application. On the sand plain, shoot mortality is associated with lowering water table levels in mid-late summer and flooding of the plain in winter. The December harvest was therefore probably too early to reflect major changes in dead shoot densities on either the treated or untreated plots.

This nitrogen effect at S0 which was closer to the water table than S1 is consistent with that often seen in crop species. Where ample soil water is available additional nitrogen leads to increased vegetative growth seen as a flush of new tillers and or an increased leaf area index (Scott et al. 1977; for wheat).

The fertilizer-induced increase in densities of both expanding buds and dwarf vegetative shoots was likely the result of nitrogen breaking bud dormancy. This phenomenon is known from other rhizomatous perennial species (McIntyre 1965) and was said to be responsible for the decrease in number of dormant buds in Carex arenaria populations in the younger phases of development in response to NPK fertilizer application (Watkinson et al. 1979). Late spring dormancy of Agropyron repens buds was attributed by Waring (1964) to the reduction of labile nitrogen in the rhizomes of this species as a result of the flush of aerial growth.

Seeds are a major sink for elemental nitrogen in plants (Jefferies et al. 1979). Thus where nitrogen is limiting plant growth, the number, weight or nitrogen concentration of seeds, or a combination of these, might be expected to be reduced. An increase in the availability of this nutrient through nitrogen-fertilizer application under such circumstances might therefore be expected to increase at least one of these parameters. On the low dune, nitrogen fertilizer increased the mean number of seeds per fertile culm. In the more senile of these populations at S1, fertile shoot density, mean seed weight and the nitrogen concentration of seeds were also increased. These effects strongly suggest that on the older part of the low dune Carex pumila is normally under stress from a limited supply of nitrogen. As a consequence, the allocation to seeds, which behave as a sink for nitrogen, is reduced. A similar conclusion was reported for Salicornia europaea, an annual coastal halophyte in Norfolk, England (Jefferies et al. 1979). In its coastal habitat, Salicornia is normally under stress brought about by a limited supply of nitrogen. In this situation seed numbers were reduced.

At S0, where the younger Carex pumila population was more vigorous, the evidence was not so unequivocal. Additional nitrogen did not affect the nitrogen concentration of seeds nor seed size. Despite the increased number of seeds per flowering shoot, seed output per unit area was unchanged by the nitrogen treatment. In perennial sedges and grasses, the proportion of reproductive shoots in the total population is an important component of the reproductive effort. At S0, the density of fertile shoots was reduced on the fertilized plots compared to the controls. Thus, it could not be concluded that soil nitrogen on this young part of the sand plain was limiting seed output. However, nitrogen was undoubtedly limiting vegetative growth in this young part of the clone.

Some other factor would appear to be limiting seed output. This view is confirmed by the nitrogen concentrations of constituent organs of the species which were greater at S0 than at other sites studied, including those in the old hollow where nitrogen-fixing blue-green algae were evident. This suggests that absorbed nitrogen is transported acropetally to younger expanding plant parts.

Reproduction is a lethal activity for Carex pumila shoots. At the same time vegetative growth, including rhizomatous spread, continues in adjacent parts of the clone. Some evidence was presented that within Carex pumila populations on the low dune, competition occurred for resources between vegetative expansion and sexual reproduction. At maturity, the biomass of fertile shoots becomes concentrated in the seeds, and nitrogen more so. Seed production appears then to deplete the shoot of limited nitrogen that might otherwise be used for other life activities. At S0, especially on the fertilized plots, where the clone was growing most vigorously, the depletion of nitrogen from the vegetative parts of fertile shoots and

its proportionate allocation to seeds was greatest.

CHAPTER FIVE

Discussion5.1 The sand plains

The sand plains of coastal Manawatu provide sites of particular ecological significance in that they are continuously in a state of succession. By virtue of the continuous nature of the formation of the sand plain (Esler 1978), sites suitable for colonization are a permanent feature of this habitat. Thus the youngest seral stages are readily encountered. It was on this basis that the study area was chosen.

Carex pumila is the major colonist in this habitat. The aims of the present study were to describe the pattern of development of Carex pumila in populations of increasing seral maturity on the sand plain, and to determine if within a particular seral stage the population could respond to a deliberate perturbation treatment. Sequential harvests were taken and the vegetation, which was dried and weighed, was divided into Carex pumila and other species. The former was further divided into component organs, including underground parts. Dead shoots were included and shed plant parts were estimated.

In December 1977, an area was selected at the base of a landward-moving rear dune which was bare of vegetation. The newly exposed damp sand had not had sufficient time or supply of germinable seed for plants to become established. It remained essentially bare

of vegetation for two years despite its appearance as an ideal environment for seedling establishment, especially in autumn and spring when the combination of moisture and augmented temperatures prevailed. However, during the winter months the water table rose at least to the surface whereas in summer the lowered water table levels resulted in drying of the sand surface and further deflation during windy periods. Thus, seedling establishment was not without hazard on this area. In summer 1978-79, seedlings of several species failed to survive on the terminal hollow. They had the sand on which they were established removed by wind. By winter 1980 seedlings of several species had established and with the greater stability of the area as a result of marram planting on the surrounding dunes in spring 1980, these plants remained at the site over the ensuing summer. Thus, by winter 1981, the terminal hollow had the appearance of a dense plant cover. The essential patchiness of the young vegetation with locally pure stands of several pioneer species including Carex pumila, Limosella lineata, Selliera radicans, Eleocharis neozelandica and Scirpus nodosus was seen. The presence of Selliera radicans on the terminal hollow may not result from seedlings but the establishment of a plantlet from a thickened, bulbous, succulent leaf broken off from the parent plant. Such leaves were seen especially in autumn, and appear characteristic of the Manawatu sand plain form of the species.

Thus, the colonization of the terminal hollow which was determined by chance factors of migration and establishment by seeds and plant fragments occurred too late during the study to allow anything but casual observation of the phenomena.

The field sites, chosen at increasing distances from the terminal hollow, represented sites of successively increasing age and seral maturity. Variation between sites in terms of quantifiable soil parameters was slight. A small degree of development of a humus layer on the surface in the old hollows, and nitrogen fixing blue-green algae were apparent in the old deflation hollows at the beginning of the study. However, it was not until winter 1981 that similar quantities of Anabaena bloom were found in the terminal hollow.

Plant available calcium, potassium, phosphorus and magnesium were greater in the older soils on the study area. Similarly percentage organic matter in the top 10cm increased with seral maturity. However, little decomposition had occurred and an extremely raw type of organic matter was present. The soil in the terminal deflation hollow and on the edge of the young low dune can be expected to have higher nutrient levels than raw beach sand, as a result of leaching of nutrients from the surrounding dunes (cf Salisbury 1952), but otherwise these soils are little different.

Variation in other physical environmental factors between sites was found that related to the topography of the sand plain. The relative shelter at S2 at the landward end of the old hollow adjacent to the young low dune was greater than at all other sites. Further, with the accretion of sand by Carex pumila on the low dune, the sites S1 and, in 1979 and 1980, S0 became less subject to fluctuations in water table levels. Sites in the old hollows (S2, S3 and S4) and in the terminal hollow (S0 in 1978 and 1979) were flooded in winter unlike low dune sites (S1 and, in 1980, S0) which were 300-500 mm higher, and out of reach of the water table.

The lowered water table levels in summer on the low dune would subject plants to long periods of moisture stress. Water table levels remained up to 1000mm from the low dune surface at the end of summer. Given that the capillary fringe from a free water surface in very fine sand (30-50 microns particle size) may be no more than 400mm (Ranwell 1972) and that most roots attached to live shoot modules are found within 300mm of the soil surface, it is unlikely that plants on the low dune were able to absorb water from the water table or its capillary fringe during dry summer periods. The soil moisture profile on the low dune in spring with the water table at 580mm from the surface, shows that water makes up a little over 10% by volume of the top 100mm of sand. The primary source of this water comes from rainfall, being held in the surface layer by the low moisture-holding capacity of the sand. The vegetation analysis reflects the drought conditions that prevail on the low dune.

Other ecosystem parameters, similar to those suggested by McNaughton (1975) to be important determinants of r- and K- selection, also showed wide variation between sites at the beginning of the study:

Interference (biomass, grams DW or TN / unit area)

Annual density variation (variance/mean shoot density)

These vegetation parameters are wholly or largely determined by the performance of Carex pumila.

5.2 Carex pumila on the sand plain

As a pioneer species, Carex pumila is doomed to extinction on the sites it colonizes. Thus, its success ultimately depends on its ability to put individuals into the early stages of the sand plain sere, elsewhere. Its strategy appears to be typical of that

encountered in plants of sand dune communities. It is successful in this highly disturbed, nutrient stressed habitat in that firstly, once present, it quickly expands to occupy the space available shutting-out other species, and secondly, it is continually escaping the interference from other more vigorous later seral species by either (1) spreading by rhizomes into adjacent uncolonized areas or (2) possessing a sufficiently large reproductive output that ensures the colonization by seedlings of newly exposed sites, elsewhere.

1. Basic morphology

The basic morphology and growth of Carex pumila on the sand plains of coastal Manawatu is remarkably similar to that of Carex arenaria, a sand sedge of coastal areas in Europe where it is abundant on mobile and semi-fixed dunes, but also found in moist dune slacks (Noble 1982). By contrast, Carex pumila is most abundant on the seasonally flooded slacks, but is also found on more elevated ground above the ground water table level.

The modular construction of Carex pumila was readily apparent. The modular unit is a single aerial shoot with its associated rhizome and adventitious roots which include both large diameter sinker roots, and finer more highly branched roots. Large diameter succulent roots are initiated in response to flooding in a variety of flood-tolerant plants (Keely 1979). The development of sinker roots preceded that of the finer root type, on young Carex pumila rhizomes invading the flooded terminal deflation hollow. The rhizome axis of Carex pumila is, then, a sympodium, made up by the serial addition of the basal portion of successive modules. Normally, the rhizome grows horizontally although, like other rhizome geophytes of habitats where rapid accretion of the substrate occurs, it may grow vertically until the

apex arrives close to the surface when it reverts to horizontal growth (Raunkiaer 1934). Carex pumila is replaced, however, by dune species such as Desmoschoenus spiralis which have a greater ability to accumulate sand.

Branching of the rhizome occurs at irregular intervals along its length, always at the base of the leafy orthotropic portion of a branch module. The length of each sympodial rhizome segment and the frequency of branching determine the density of the clone. On the edge of the low dune where Carex pumila was invading the terminal hollow, rhizome segments were often more than 1m long with infrequent branching whereas in the old hollow at site S2 branching was more frequent and rhizome segments much shorter (20-60cm). Contributing further to the density of the clone are short or dwarf modular units which arise like extravaginal grass tillers from the base of the aerial shoot modules described above. Thus, where aerial shoot density is low as on the low dune tufts of loosely packed aerial shoots will form a patchwork. On the old deflation hollow aerial shoot density was sufficiently high to produce a dense ground cover obscuring the patchiness of these tufts.

The linear rhizomatous architecture of Carex pumila like that of Carex arenaria (Noble and Marshall 1983), allows for continual expansion into bare sand and the appropriation of scarce nutrients. The branching along the primary rhizome axis at an angle of 15 degrees allows for the more complete coverage of the moist bare sand of the bow-shaped terminal deflation hollow. As the bare sand is colonized by Carex pumila and other rhizomatous species, the process repeats itself as the rear dune moves further inland exposing more damp sand at its base (Esler 1978). Thus a catenary system of damp hollows separated by similar arcuate low dune ridges is formed on the sand

plain.

The rhizome architecture and growth of Carex pumila allows for the rapid colonization and concomitant resource capture of the terminal hollow as the hollow is forming. The ability of this species to regenerate from seed allows for the more complete colonization of the growing area remaining unexploited by the rhizomatous spread of already existing clones at its edge. In winter 1980, a Carex pumila genet was excavated from the terminal deflation and measured. Two primary rhizome axes were evident, each with four successive long rhizome segments (sympodial units). The mean length of each 4-unit axis was 2m, which, given the estimated seasonal rates of rhizome extension, suggested a spring 1979 germination and establishment of the excavated genet.

Given time, clonal expansion may result in a single genet spreading over a considerable area, with the possibility that one or only a few genets may be responsible for the entire Carex pumila sward on the study area. This is not unreasonable given the infrequent observations of seedlings of this species on the sand plain during the study period.

Excavated rhizomes of Carex pumila on both the low dune and on the deflation hollows were seen to extend over 5m along a single rhizome axis, each of which may be branched one or more times over this distance. Fragmentation of the genet through decomposition of old buried rhizome segments prevented excavated rhizome axes being traced further back from the apex. The encroachment of the low dune by 18m onto the terminal hollow over the duration of the study, was the result of the contemporaneous extension of such branched rhizome axes onto the terminal hollow. The rate of extension of the rhizome

front, estimated at 5.08m per year, was greater than that determined for Carex arenaria growing into bare sand of either a dune face or a deflation hollow (Noble 1982). Given this rate of encroachment of the vegetation onto the moist bare sand at the base of the windsweep of the rear dune, the ages of the field sites in December 1977 were 0, 2.5, 5 and 16 years for S1, S2, S3 and S4, respectively. These estimates are subject to the uncertainty of rates of extension of the sand plain in previous years. Over the study period marked seasonal and year-to-year variation was found in rates of extension of the rhizome front into the terminal hollow. Further, the estimates of site age, at least of the two most distal sites (S3 and S4), may be inflated, given the manner in which the deflation hollows are colonized: ie not exclusively by the gradual systematic encroachment of rhizomes of Carex pumila, but also by chance migration and establishment of seeds and plant fragments, of this and other species.

2. Flowering and seed production

As a consequence of the pattern of formation of the sand plain new sites suitable for colonization by seedlings of Carex pumila are reliably close, either in space or time. At maturity, sexual reproductive disseminules of Carex pumila, weighing up to 8mg each, possess a corky covering (utricle). Thus, in winter they float on the ponds formed by the raised water table levels and are readily dispersed by wind. The direction of the prevailing west to northwest winds will tend to move disseminules in the direction of unexploited damp sand of a newly exposed or growing terminal deflation hollow.

Floral development in Carex pumila appears to be under environmental control. Heading (the emergence of the terminal male spike from the mouth of the sheath of the flag leaf) and subsequent

flowering phenomena occurred at the same time of the year in three successive years. From observations made on the sand plain in 1978, 1979 and 1980, heading began in the second week in October and continued into early November. An attempt to implicate photoperiod in the timing of flowering in Carex pumila by inducing floral initiation in seedlings less than one year old, was not successful. Seedlings placed in long days (continuous illumination) with and without prior cold treatment (30 days at 5 degrees C) did not initiate floral primordia. This does not of course preclude some other combination of temperature and photoperiod from being responsible for the entrainment of this phenomenon.

The changing soil moisture conditions in spring, resulting from the lowering water table levels may also be involved in the environmental entrainment of flowering phenophases in Carex pumila, although it is difficult to see that the precision of, for example, heading within such a narrow time span in each of three years could be entrained by an environmental variable as open to the vagaries of rainfall as water table levels. Despite this caution, the mean date of heading for the fertile shoot populations on the low dune and in the deflation hollow differed in the direction predicted on the basis of the hypothesis that culm elongation and, as a consequence, heading is determined by an environmental variable linked with the subsiding water table levels of spring. Soil moisture has been shown to be an important environmental variable, along with temperature and photoperiod, in the entrainment of the timing of flowering in natural communities in temperate zones (Evans 1971). The timing of floral events is such that anthesis occurred in this wind pollinated species during the most windy period of the year. Even at 30 to 60 cm above ground level, at the height of the male spike wind speeds of up to 7m/sec averaged over a five minute period were recorded on the sand plain. Thus, the chances of pollen transfer between fertile shoots

and so the chances of cross pollination are greater than if flowering occurred at a different time of the year.

Carex pumila must be described as essentially allogamous. It is monoecious and possesses a conspicuous staminate spike terminally placed on the culm, although it was found in a glasshouse experiment to be partially self-compatible (section 2.5). Individual shoots showed limited protogyny although synchronous protogyny over local site populations was not demonstrated. Thus, self-pollination may not be avoidable in the field, since neighbouring fertile shoots are likely to be part of the same genet of this clonal species. Further, pollen flow, despite anemophily, may be highly restricted (Handel 1976). Griffiths (1950) found gene flow in Lolium perenne to be less than 1% of maximum at a distance of 18.2m.

The precocity of heading on the more exposed, drier low dune compared with the deflation hollow might also be attributable to the poor soil fertility conditions at the former site. Although his data show no precocity in flowering in poor soil conditions, Ogden (1974a) suggested that from casual inspection of Tussilago farfara plants in spring this might be incorrectly inferred since shoots on low fertility soil possessed a greater proportion of empty receptacles than plants in more fertile soil.

The divergence in timing of heading of 14 days in 1979 between the low dune and the deflation hollow was not as great for subsequent floral events (emergence of stigmas, anthesis and grain-filling). Thus, maximum seed size was achieved at about the same time of the year in all fertile shoot populations (namely, early January). The more rapid increase in seed weight over late November/ early December at the deflation hollow site compared with the low dune site was expected given the higher temperatures that prevailed at the former

site as a result of the reduced wind speeds experienced. This effect of shortening the duration of grain-filling in response to increased temperatures has been established in economic species including wheat (Sofield et al. 1974). Further evidence that increased shelter hastens the onset of maturity of fertile shoots was found on the old deflation hollow in summer 1979-80. By early February most fertile shoots on the sheltered plots at this site were mature (dead) and shedding seed whereas on the control plots less than half the fertile shoots were mature and fallen seed made up in insignificant proportion of the total seed output.

Maximum seed output found on the sand plain was obtained in the old deflation hollow in summer 1977-78 (namely, 17000 seeds or 130.5 grams DW/m²). This is well in excess of that reported by Noble (1982) for Carex arenaria growing on sand dune soils in North Wales, although still somewhat less than that recorded for this same species in Breckland (7200 seeds or 7.92 grams DW/m² and 196000 seeds or 215.6 grams DW/m² respectively). By summer 1980-81, seed output of Carex pumila in the old deflation hollow was considerably reduced, especially in terms of dry weight per unit area (5028 seeds or 12.4 grams DW/m²).

Maximum seed output per unit area in summer 1980-81 which was found on the younger part of the low dune (8956 seeds or 20.5 grams DW/m²) was not affected by nitrogen-fertilizer application. Only on the more senile low dune site where seed output was comparatively depressed did additional nitrogen increase seed output (to 2928 seeds or 6.64 grams DW/m²). The marked increases in production of fertile shoots and seeds in response to nitrogen-phosphorus-potassium (NPK) fertilizer reported by Noble (1982) apply to a spring fertilizer application, administered the previous year. Seed output of Carex

pumila on the unfertilized plots on the younger part of the low dune in summer 1980-81 was still in excess of these NPK-fertilizer-augmented seed outputs reported by Noble (1982) for Carex arenaria.

3. Phasic development

Clonal expansion in Carex pumila results in several phases of population development being expressed on the ground at any one time and, at any one site, the resident population passing through similar phases of development over time. Similar patterns of development have been described in rhizomatous perennial species by several workers (eg Watt 1947; Thomas and Dale 1974; Noble et al. 1979). The pattern in Carex pumila includes a juvenile phase of rhizomatous spread on uncolonized moist sand, followed by an adolescent phase in which aerial shoot density increased. These initial phases involving expansion of the rhizome system, initially by the development of long rhizome branch modules followed by that of dwarf rhizome modules, occur to the exclusion of seed production. A mature phase follows in which a proportion of the locally high density of shoots ^{was} ~~were~~ fertile. The allocation of resources to seed production did not however occur to the exclusion of continuing rhizomatous growth and vegetative shoot development. In the senile phase which follows both rhizomatous and aerial growth, and seed production, were diminished to the extent that at the oldest old deflation hollow site at the end of the study period, fertile shoots of Carex pumila set no seed and none of the surviving depauperate shoots were attached to long rhizome branches. Thus, rather than showing increased density and sward mass (K-selection; McNaughton 1975) with increasing age of the population, n-shaped plots were found (cf Watt 1947).

The question was asked, what determines this pattern of response, and in particular the balance between rhizomatous spread, aerial growth and seed production? The response of Carex pumila to increasing plant-to-plant interference during increasing seral maturity can be viewed in terms of the population closing its ranks and persisting as a seral monoculture. Such a response has been suggested by Ogden (1974a) as an alternative to that of escape to new areas through seed production, or fragmentation of the genet and dispersal of these units.

The persistence of Carex pumila as an effective monoculture depends upon the extremely low nutrient resources normally available. The rhizome architecture and growth strategy of Carex pumila resulted in the spread of the species on the low dune to cover the available ground, appropriating the limited nutrients and effectively precluding the growth of other more vigorous species. On the low dune Carex pumila was the sole or major species present over the three years that harvests were taken. Thus, despite the relatively low plant cover afforded by Carex pumila, the species may be considered to have closed its ranks to other species as effectively as it had done on the deflation hollow at S2 in 1978 where the clone was considerably more vigorous and ground cover by this species was almost complete. Addition of nutrients to the low dune in spring 1980 resulted in increased density of shoots attached to dwarf rhizome branches and hence increased aerial growth. It also resulted in other more vigorous species that were capable of responding rapidly to the added nutrient (characteristic of more competitive-strategy species, Grime 1977), and that were normally precluded by the nutrient stress conditions, becoming established. Increased nutrient status of the soil by fertilizer addition therefore hastened the seral progression.

Where nutrient resources were more plentiful, as on the old deflation hollow at S2 in December 1977, the dense sward formed by the relatively young Carex pumila population also excluded almost exclusively other species. However, the demise of this population over time was more rapid than that on the more nutrient-stressed, younger sites on the low dune. The occupation of a site by Carex pumila may last several years (S4 where Carex pumila was almost totally replaced by December 1980, was estimated to be 19 years old), but as with all seral species, the occupation is only temporary.

Species other than Carex pumila contributed an increasing proportion of sward mass at increasingly older sites, both in time and space. Carex pumila is not completely replaced by these associated species. The demise of Carex pumila at the older deflation hollow sites then suggests the possibility that its decomposition may release compounds that are detrimental to the germination and/or growth of other species. The production of such compounds has been considered to form an important part of the competitive strategy of plants (Grime 1979). The leaching of inhibitory substances from live or dead and decaying parts of Carex pumila may also prevent the reinvasion of these soils by new rhizomes of this species (cf decomposition of Tussilago farfara; Ogden 1974a).

4. (iv) Allocation of resources to component parts

In Carex pumila allocation of resources can be thought of as being partitioned between the ecologically important ends of reproduction (dispersal to neighbouring sites by seeds), competition (exploitation of a given site by aerial shoot growth) and clonal spread (exploration of immediately adjacent sites by long rhizomes). The short rhizome segments of dwarf shoots are probably best

considered part of the allocation to competition in that they enable the more complete exploitation of a given site. The distinction between the latter two categories (namely, competition and clonal spread) is not absolute, as once colonization of an area by long rhizomes has been achieved, the subsequent aerial and adventitious root development of these branch modules leads to the capture of resources at that particular site. Further, dwarf rhizome branches may occasionally become greatly extended, giving the appearance of a long rhizome branch, albeit reduced in diameter (section 2.1).

The patterns of biomass allocation by Carex pumila populations showed seasonal fluctuations with the proportionate allocation of biomass to rhizomes reaching maxima at each site in winter, in contrast to summer aerial allocation maxima. This pattern is associated with the patterns of shoot mortality and recruitment. Major episodes of shoot mortality in Carex pumila were found in late summer, with the demise of the fertile shoot cohort, and during winter/early spring when soil conditions were anaerobic due to flooding. The main periods of shoot recruitment of Carex pumila, namely spring and autumn, can be related to the conditions that prevail in the surface layers of the soil which in turn are largely determined by the seasonal variation in the water table levels. In spring with the lowering of the water table, aerobic conditions returned to the soil surface which had been waterlogged (anaerobic) for several months during winter. In autumn the rising water table brought with it water-soluble nutrients back to the surface. The release of nutrients from the senescent fertile shoot cohort in autumn, may contribute to a flush of nutrients including nitrogen into the system at this time of the year, leading to the release of bud dormancy in other parts of the clone. Bud dormancy in summer was

likely to be caused by the depletion of labile nitrogen within rhizomes as a result of aerial shoot demands on this nutrient (^{Waring}~~Waring~~ 1964).

The proportionate allocation of biomass to rhizomes decreased with increasing age of the population. This was most marked on the low dune where Carex pumila was invading the bare sand of the continually growing terminal deflation hollow. At the rhizome front the entire biomass was in the form of rhizomes. Further back from the advancing front along the primary rhizome axes, an increasing proportion of total biomass was found in aerial parts. This increase was attributable to the increasing contribution of dwarf shoot modules to total biomass. The extreme in this trend was seen on the old deflation at S3 where at the end of the study all live shoots on the control plots were attached to dwarf rhizome branches. At maturity, a dwarf shoot size was no different from that of long shoots. However, the underground biomass of the whole branch module of each of these two branch types differed markedly. The most extreme divergence in the relative size of mature short and long rhizome units was found on the edge of the low dune in winter 1980 where long rhizome segments measured up to 1.4m. At this adolescent site 74% of population biomass was found in rhizomes. The high rhizome allocation in the more juvenile compared with more mature populations suggests the importance in the strategy of Carex pumila on the embryonic sand plain soils of plant parts devoted to the capture of below-ground resources. Where these resources were more plentiful, as on the old deflation hollow at S2, and when nitrogen fertilizer was applied, aerial allocation was significantly increased.

The trend of decreasing rhizome allocation with age when comparing sites of increasing distance (putative age) from the terminal hollow at any one time was obscured by the behaviour of the Carex pumila population at the sheltered site on the downwind end of the old deflation hollow at S2. The proportionate allocation of biomass at this site favoured aerial shoots whereas the balance was in the opposite direction at all other sites, including those older ones further from the terminal hollow. This increased aerial growth at S2 was attributable to the greater shelter and soil fertility at this site compared with others.

At S2 the tactics of Carex pumila are more that of a C-strategist (Grime 1977) than at other sites. Carex pumila was able to respond to the decreased stress/disturbance conditions by producing a dense cover of tall growing shoots. However, when the bulk of these had died by the end of summer 1978-79, recruitment of shoots of other later seral species was not prevented. These were more rapid than Carex pumila in occupying the space made available by the mortality of Carex pumila shoots, and by summer 1980-81 had largely replaced the latter (figure 3.8).

Since the energy values of component parts of Carex pumila were dissimilar, the allocation patterns to these components based on dry weight and on energy can be expected to differ. However, (1) the energy value of mature seeds of this species (namely, 20200 joules/gram /DW), the highest of all plant parts, was low relative to other species including those in which allocation patterns based on dry weight and energy were not seen to differ significantly (Hickman and Pitelka 1975; for Lupinus) and (2) the divergence in energy values between component organs in Carex pumila was low relative to the variances in proportional allocation to components between

replicates within treatments. Thus, dry weight and energy allocation pattern differences are unlikely to be significant. Further, Hickman and Pitelka (1975) predicted that allocation patterns based on dry weight and energy would not differ significantly in plants in which seeds stored only a moderate amount of lipid (up to about 15%). Seed lipid content of mature seeds of Carex pumila was 3.6% of dry weight. The same conclusion cannot be drawn for the comparison of allocation patterns based on dry weight and total nitrogen.

Total nitrogen concentrations in seeds of Carex pumila were 7x that of roots and 5x that of rhizomes. Values for green leaf laminae and sheaths were intermediate between seeds and underground parts and significantly different from both. Further differences were found between sites, averaged over all shoots, between long and dwarf shoots, and between vegetative and fertile shoots, for comparable structures. These differences probably reflect the declining percent total nitrogen values with shoot age. Thus, proportionate allocation patterns, within and between Carex pumila populations, based on dry weight and total nitrogen were expectedly different. These differences were most often highly significant.

The question now to be asked is whether nitrogen is a limiting resource in this seral habitat and, if so, whether the allocation of this resource is of more importance in the evolution of life history strategies on the sand plain than allocation of carbon (dry weight). The evidence is unequivocal. Nitrogen does limit the growth of the vegetation on the sand plain. However, it is only on the earlier seral stages that additional nitrogen fertilizer increased the growth of Carex pumila. On the old deflation hollow where the Carex pumila population was senile, and run-down compared with the resident Carex population at this site three years previously, other species

responded to the fertilizer addition. Carex pumila is then less of a C-strategist (sensu Grime 1977) than these other species, principally Hypochaeris glabra.

However, Carex pumila was able to respond to high nutrient levels in the soil on the deflation hollows. At S2 during 1978, the standing biomass and the estimated rates of biomass accumulation of this species were greater than at any other site during the course of the study.

The increase in the amounts of plant total nitrogen in Carex pumila shoots at S2 in autumn 1978 was more than 3x that estimated that could be supplied by nitrogen fixation in situ. This confirms the view that the vigour of Carex pumila can be attributed to the accumulation of nutrients from elsewhere on the sand plain. Sources of nitrogen include nitrogen-fixation in the rhizosphere zone of Ammophila arenaria and by Lupinus arboreus, species that were prominent on sites both within and immediately adjacent to the study area.

The amounts of plant total nitrogen in Carex pumila on the low dune were remarkable in that there was no immediately obvious source of this nutrient. Nitrogen-fixing blue-green algae, Anabaena and Nostoc spp., were confined to the deflation hollows and nitrogen-fixation in the rhizosphere zone of Carex pumila itself can probably be discounted. Such associations of bacteria with members of the Cyperaceae are unknown (Forde pers comm).

The differential distribution of concentrations of total nitrogen between plant parts within Carex pumila indicates an acropetal movement of this nutrient, ie the efficient channelling of this scarce resource to the continuously growing rhizome front. However, Noble

and Marshall (1983) contend that cut off from a supply of a limiting nutrient, continued extension of rhizomes (of Carex arenaria) would not be possible. Thus, the efficiency of redirecting nutrients within the clone from senescing shoots to new growing points may be high in stress tolerators such as those in sand dune communities but is not absolute. Nutrients may be absorbed directly from the soil by rhizomes, as in the absorption of phosphate by buried stolons of Trifolium repens (Hay and Dunlop 1982). In winter 1981, a new source of nitrogen in the terminal hollow was apparent with the presence of the Anabaena. Prior to this seepage of nitrogen fixed in the rhizosphere zone of Ammophila arenaria on the adjacent low dune and surrounding high dune seems the most likely source of this nutrient used by Carex pumila on the edge of the terminal hollow.

5. (✓) Seed reproductive effort

Like many plant species, the sexual reproductive structures of Carex pumila remain green and photosynthetic for an extended period of their development. Not until the major period of increase in dry weight of seeds is complete does the outer covering (utricle) lose its green colour, turning yellow or red-brown. The photosynthetic contribution of female spikes of Carex pumila to final seed weight was estimated at 26%. This value must be considered conservative due to the apparent maintenance of final seed weight in the face of post-anthesis defoliation, and shading of all but the inflorescence (section 2.6). In the field, Carex pumila shoots are often buried by sand. Thus, the elaboration of seed in such instances may occur as a result of the translocation of pre-formed assimilate from other parts of the shoot, or clone, or as suggested in the defoliation experiment, from reproductive assimilation. Whatever the contribution of photosynthesis in female spikes to post-anthesis increase in seed

weight (26-100%), reproductive effort estimates in Carex pumila (based on dry weight) cannot be considered a drain on carbon resources of the plant, in the same way that the production of progeny by animal species draws on a finite pool of resources within the individual. As concluded by Thompson and Stewart (1981), the allocation of nutrients may be of more fundamental significance in the evolution of life history strategies in plants than the allocation of carbon.

Seed reproductive effort as a proportion of the total living population biomass (SRE2) of Carex pumila was in the range 0-16% of total dry weight; 10-16% for mature populations that were neither juvenile nor senile. This puts Carex pumila midway along the r-K-strategy continuum between monocarpic grain crops and wild annual species, in which seed reproductive effort is characteristically 20-40% of annual net assimilation, and polycarpic herbaceous perennials and forest trees (seed RE <5%; Harper et al. 1970). These values are greater than those found by Ogden (1974a) for another seral perennial, Tussilago farfara, in which 3-8% of annual net production was found in seeds.

Such estimates of reproductive effort, based on total population biomass, will differ from those based on fertile shoots alone, according to the proportion of the stand made up by non-flowering individuals. Seed reproductive effort as a proportion of the biomass of fertile shoot populations of Carex pumila varied from 0 to 31.6%. This maximum was obtained in the old deflation hollow at S3 in January 1978 where population seed reproductive effort was also maximal. At the more fertile and sheltered old deflation hollow site, reproductive shoots had undergone considerably more shoot growth (mean size was 1.24g/aerial shoot cf 0.56g/shoot at S3) and had allocated a larger proportion of this total to vegetative parts. Total reproductive

effort (sensu Thompson and Stewart 1981) expressed as a proportion of biomass of fertile shoots was 36.5% at that site where seed effort was maximal. This proportion includes the dry weight of the terminal male spike and rhachillae and glumes of female spikes. The culm was included with leaves as vegetative.

These values of seed and total reproductive effort may be compared with those presented by Abrahamson (1979) which apply to randomly chosen flowering or fruiting plants from populations of 50 species of wildflowers from earlier (field) and later (woodland) secondary successional communities. The greatest reproductive effort values for Carex pumila were within the upper end of the range found by Abrahamson (1979) for field populations of perennial species.

Reproductive effort (RE) of Carex pumila in the old deflation hollow at S3, in January 1978

	Proportion of total	
Population seed RE (after Ogden 1974a)	DW	16%
Individual seed RE (after Abrahamson 1979)	"	31.6%
" total RE (after Thompson and Stewart (1981) "	"	36.5%
Harvest index (seeds as a proportion of aerial parts)	"	42%
" " " " "	TN	50%

Other estimates of the "reproductive effort" of this Carex pumila population have been made to enable comparison with other studies. Seed effort as a proportion of grams dry matter and total nitrogen content of aerial shoot biomass (equivalent to harvest index; Donald 1962) was 42% and 50%, respectively.

Abrahamson (1980) arguing from the behaviour of perennial rhizomatous species in sand dune communities predicted that with increasing shoot density there will be a shift from vegetative reproduction (sic) to seed production enabling dispersal to new favourable sites. The increasing interference between shoots with increasing density was suggested to be a reliable cue to the decreasing favourability of the site for seral perennials. In Carex pumila such interactions between shoots as the population passes from a juvenile to an adolescent and to a mature stage of development are intraspecific and most probably intraclonal.

The shift involving an increased reproductive effort with increasing density, as predicted by Abrahamson, was observed by comparison (1) of shoots on the low dune at increasing distances back from the leading edge of the clone, (2) of sites at increasing distances from the terminal hollow in January 1978 and (3) of populations at both low dune sites over time. In populations of increasing senility (as on each of the deflation hollow sites over time, and between old deflation hollow sites in 2nd, 3rd and 4th summers of the study) reproductive effort decreased. At these sites interspecific interference of Carex pumila populations was increased. The response by this seral species was to decline.

The shifts in reproductive effort of Carex pumila as populations matured and subsequently became more senile must be considered phenotypic. Genetic differentiation with respect to resource allocation between Carex pumila populations across the study area can be excluded. The oldest population studied was at most 16-18 years and although rapid population differentiation has been demonstrated in outcrossing, wind-pollinated species within short time spans (Bradshaw 1959; Antonovics 1971; Davies and Snaydon 1973), the low rate of

turnover of Carex pumila genets on the sand plain would preclude this phenomenon, given the infrequency that seedlings of this species were observed. The mode of growth of Carex pumila indicates that one or few genets can expand to occupy the space available and, despite the rapidity of turnover of individual ramets (few emerging shoots tagged were living 12 months later), are likely to remain until the demise of the population at that site. A single genet therefore must withstand a wide range of environmental conditions both at a given site on the sand plain and across a wide area. This ability coupled with the possibility of limited genetic recombination during sexual reproduction as a result of restricted pollen flow between genets, may bring about the evolutionary conservatism of this open pollinated species. A similar conclusion was reached by McWilliam et al. (1971) for one such species, Phalaris tuberosa, in Australia. The ability to alter reproductive effort (or any of character) in response to environmental changes is nonetheless under genetic control. In Carex pumila reproductive effort was altered by habitat perturbation.

Nitrogen was shown to limit seed output on the more mature site on the low dune in summer 1980-81, but not on the younger low dune site where Carex pumila was in a more adolescent phase of development. At the more senile site, additional nitrogen increased mean seed size and total nitrogen content per seed (partly through increasing the levels of total nitrogen in seeds) on fertile shoots attached to dwarf rhizome branches. The density of these fertile shoots was also increased by the nitrogen perturbation, an effect attributable to the delay in senescence of older shoots which had died on the control plots by December 1980. The timing of the nitrogen application (spring 1980) precluded any newly recruited shoots undergoing floral development and seed production by the time of harvest in December.

The main effect of increased elemental nitrogen on the components of seed output was an increase in the number of mature seed set by a fertile shoot at both low dune sites. Again because of the timing of the nitrogen application, numbers of floral primordia were unlikely to be affected by this treatment. Thus the increased seed output, through an increase in numbers of seed counted per culm was an effect of the increased nitrogen allowing the normal development of a greater number of preformed ovules. On the control plots where nitrogen levels were low, normal development of many ovules would have been prevented, or arrested prematurely, so accounting for any reduction in seed weight. At the younger low dune site, additional nitrogen increased the seed number per fertile shoot, without affecting seed output per unit area. At both low dune sites, additional nitrogen decreased the proportion of shoots attached to long rhizome branches that became reproductive, without altering the total density of long shoots.

The nitrogen fertilizer perturbation affected vegetative shoot populations of Carex pumila more greatly than fertile shoot populations three months after nitrogen fertilizer application; ie the greater response was in the younger portion of the clone at each site. The proportionate allocation of both dry weight and total nitrogen of the population as a whole to vegetative shoots was increased by this perturbation. Vegetative shoot size, numbers of leaves per shoot and shoot density all increased. The latter can be explained as a result of the increased amounts of nitrogen in the plant releasing the dormancy of shoot buds. The proportionate allocation of total population biomass to seeds was little affected by the treatment. Ogden (1974a) also observed an unresponsiveness of total population seed reproductive effort to soil fertility

differences by a seral rhizomatous perennial of low fertility habitats, namely Tussilago farfara.

By contrast to Tussilago farfara under high and low soil fertility conditions (Ogden 1974a), Carex pumila was not found to decrease the allocation of biomass to rhizomes under the higher fertility regime in ~~any~~^{all} populations. In the senile low dune population fertilizer addition did reduce the proportionate allocation to rhizomes, while increasing that to the aerial fraction, principally through increased dwarf vegetative shoot recruitment. In the younger low dune population, despite the increased dwarf vegetative shoot recruitment and growth brought about by the additional fertilizer, a large increase in the proportionate allocation to rhizomes occurred. It is likely that the timing of the fertilizer application and the measurement of the response in the present study accounts for this difference. Twelve months after fertilizer application casual observation of the study area showed that aerial shoot growth on the younger low dune site had been more greatly increased by the perturbation than that found at three months. It is possible that the allocation of annual net accumulation to rhizomes at this young site was decreased by the fertilizer treatment in contrast to that finding above, only three months from the time of nitrogen application.

The pattern of an increased proportionate allocation to rhizomes in poorer soils, a response that maintains the plant in an area unfavourable to taller growing species (Ogden 1974a), was confirmed in the present study by comparison of the Carex pumila populations on the more fertile part of the old deflation hollow at S2 and elsewhere. At S2 where soil fertility conditions were improved of other sites, density and both absolute and proportionate allocation of biomass to aerial shoots were greater and the proportionate allocation to

rhizomes considerably lower than at other sites.

Despite the reduction in the proportion and density of fertile shoots in the total population in response to fertilizer application, seed output per unit area was maintained. This came about through reallocation of biomass within fertile shoot populations, a result manifest in the increased number of seeds per fertile culm and, on the senile low dune site where mean seed weight was reduced on the controls, increased mean seed weight.

The total expenditure of dry weight by Carex pumila on seed production and rhizomatous growth was similar to that apportioned to seeds alone by seral annuals (cf Turkington and Cavers 1979). This total was achieved by a larger relative expenditure on rhizomes than on seeds. Since seeds were found to store a considerably greater concentrations of plant total nitrogen, this balance between seeds and rhizomes in mature populations was reversed when based on total nitrogen. Thus although the processes of sexual reproduction and rhizomatous growth are fundamentally different, they may be considered to be competing for the same limited resources within the plant.

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