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PHENOTYPIC PLASTICITY OF WETLAND SPECIES OF *CAREX*

By

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ABSTRACT

The ecology hypothesis has been forwarded to account for differences in plasticity both among related species, and among different populations of a single species. It states that there is a correlation between the extent of heterogeneity in a habitat and the amount of plasticity in the species occupying that habitat. This hypothesis has been applied to habitats along successional sequences in which the early successional habitats are more heterogeneous in resource distribution, than late successional habitats. Experimental evidence suggests that at least some early successional species exhibit more phenotypic plasticity than late successional species presumably due to selection pressures in heterogeneous pioneer habitats. The succession process of interest in this study, the succession of fens and bogs, is driven to a large extent by the lowering of the water-table level as *Sphagnum* moss and vascular plants invade the habitat. I used a plasticity experiment to compare the phenotypic responses of two groups of sedges (*Carex*; Cyperaceae) to a water-table gradient: a group of pioneer species, *C. aquatilis*, *C. oligosperma* and *C. rostrata*, that also persist throughout the succession sequence and a group of late-invading species, *C. michauxiana*, *C. paupercula* and *C. vaginata*. The genotypes in the study exhibited largely uniform, adaptive responses on seven functional response variables, but were stable for total biomass, an estimator of fitness. The percentage of significant environment main effects per species and the magnitudes of genotypic coefficients of variation suggested greater plasticity in the late-invading species while reaction norms indicated no difference in pattern of plasticity between the groups. A second experiment made an intra-specific comparison of morphological response between early and late successional populations of both *C. aquatilis* and *C. rostrata* to a continuous water-table gradient. The water-table gradient had a significant effect on direction of rhizome growth, tiller growth rates, stem diameter and root porosity. Clones from early successional habitats responded more strongly to the water-table gradient than clones from late successional habitats.

RESUME

Des données experimentales suggèrent une plus grande plasticité phénotypique chez certaines espèces pionnières que chez les espèces de fin de succession. La succession laisant l'ojet de la présente étude, est celle d'une tourbière soumise à un abaissement de la nappe phréatique dû à l'envahissement progressif de l'habitat par la mousse de *Sphaigne* et les plantes vasculaires. Une expérience compara la plasticité phénotypique de deux groupes de *Carex*: (Cyperaceae) le long d'un gradient de niveau de nappe phréatique: un groupe d'espèces pionnières et qui se maintiannent jusqu' à la fin de la succession, soit *C. aquatilis, C. oligosperma* et *C. rostrata* et un groupe qui s'établit seulement en fin de sucession, soit *C. michauxiana, C. paupercula* et *C. vaginata*. Les génotypes utilisés dans l'expérience réagirent de façon uniforme quant à sept variables morphométrique, mais leur biomasse, indice de leur amplitude demeura stable. La proportion d'effets environmentaux significatifs par espèce et les coèfficients de variations génotypiques sont plus élevés chez les espèces de fin de succession, tandis que les normes de réactions n'indiquent aucune différence entre les deux groupes. Une deuxième expérience compara la plasticité phénotipique d'une population pionnière avec celle d'une population de fin de sucession, chez deux espèces de *Carex*: *C. aquatilis* et *C. rostrata*. Le gradient eut un effet significatif sur l'orientation des rhizomes, le taux de croissance, le diamètre de la tige et la porosité des racines. Les plantes pionnières réagisant davantage au gradient que les plantes de fin de succession.

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LITERATURE REVIEW

With the exception of vegetative spreading in clonal plants and the dispersal of propagules, individual plants cannot easily migrate from habitats that become unfavorable, making the ability to cope with changing conditions evolutionarily advantageous. The ways in which plants cope fall into two categories: populational and individual buffering. Populational buffering refers to genetic diversity among members of a population, upon which selection can act, while individual buffering refers to the concept of phenotypic plasticity (Moran et al., 1981). Phenotypic plasticity is the differential expression of a single genotype in the face of changing environmental conditions (Bradshaw, 1965). Thus a single genotype, upon encountering a series of environments, as in experimental conditions, or a variable environment, in natural conditions, can produce a range of phenotypes. The range of phenotypes is referred to as the norm of reaction (Schmalhausen, 1949). Populational buffering is an important mechanism of adaptation in the context of environmental changes that span more than one generation. Phenotypic plasticity is the mechanism by which adaptation occurs when the impact of environmental variation happens within the lifespan of one generation (Bradshaw, 1965).

The evolution of phenotypic plasticity

i)The conceptualization of phenotypic plasticity

Controversy exists regarding the conceptualization of phenotypic plasticity (Via et al., 1995). This results in further controversy regarding the mechanisms for evolution of phenotypic plasticity. One school of thought holds that phenotypic plasticity evolves separately from the character that it modifies. This group maintains that there are separate genes for plasticity (Schlichting and Levin, 1984; Scheiner and Lyman, 1991). However others argue that plasticity does not evolve independently from the character that it modifies. They believe that plasticity results from selection on the character states within each environment. This line of thinking was developed in a quantitative genetic model for the evolution of phenotypic plasticity developed by Via and Lande (1985). Given genetically identical shoots of a plant in two different environments, any trait of these shoots expressed in the two environments is viewed as two different characters that are

potentially genetically correlated. Therefore the resulting norm of reaction is a by-product of selection in each of these environments. This is contrary to the first group of researchers who believe that selection acts directly on the norm of reaction via genes for plasticity. Despite the controversy, it is agreed that plasticity, whether a separate trait or not, responds to selection and numerous studies have shown this to be the case (Scheiner, 1993).

ii) Genetic mechanisms of phenotypic plasticity

Despite the volume of literature that addresses the evolution of phenotypic plasticity, little is known about the underlying genetic mechanisms that enable the existence of phenotypic plasticity. Researchers from both evolutionary schools of thought have agreed that there are two categories of genetic effects that mediate plastic response to the environment. The first is termed allellic sensitivity, meaning that the effect of a single allele on the phenotype may change depending on the environment. The second category includes regulatory loci that cause genes to be expressed or not depending on the environment (Via et al., 1995).

Heterozygosity, though not a mechanism through which plasticity acts, may have a direct influence on plasticity. One hypothesis holds that as heterozygosity increases the amount of phenotypic plasticity should decrease since these two phenomena represent alternate strategies for dealing with environmental heterogeneity: genetic variation versus phenotypic plasticity (Marshall and Jain, 1968). The same inverse relationship is hypothesized, but for a different reason, by Lerner (1954), who pointed out that as inbreeding increases, the number of homozygous recessive loci increases and the organism becomes more developmentally unstable. This hypothesis, however, equates developmental instability with phenotypic plasticity which may not be accurate (Schlichting, 1986). A direct relationship between genetic variation and phenotypic plasticity has also been proposed. The rationale for this hypothesis is that phenotypic plasticity could act to protect genetic variation from selection pressures (Stewart and Nilsen, 1995).

iii)The measurement of phenotypic plasticity

Phenotypic plasticity is typically measured by establishing replicates of several genotypes or full/ half-sib families in a series of environments that vary along a gradient

over which a plastic response is expected. Comparisons in plastic response can be made at different taxonomic levels, so that genotypes or sibs may be from different families within a population, different populations within a species, or different species within a genus (Fry, 1992).

Experiments of this type can be analyzed with a two-way mixed ANOVA using the following model where genotype is random and environment is fixed:

$$y_{ijk} = \text{environment}_i + \text{Genotype}_j + G \times E_{ij} + \varepsilon_{ijk}$$

The environment main effect in the ANOVA model reveals the extent to which genotypes alter their phenotype in response to the environment; it provides a measure of mean plastic response. It does not include any heritable component of plasticity (Via, 1994). The genotype main effect indicates how much of the total phenotypic variation is due to genetic differences among the genotypes (Via, 1994).

The interaction between the two main effects provides an estimate of heritable plasticity. A significant genotype-by-environment interaction term (GXE) indicates the extent to which the genotypes differ in their plastic responses. If the GXE term is not significant, then the reaction norm, that is the range and pattern of phenotypic responses, cannot evolve within a population because there are no differences in plastic response among genotypes on which selection can act (Schlichting, 1986). Another indicator of the potential for evolution of the reaction norm are between-environment genetic correlations. If genetic correlations are high, then phenotypic expression across environments is under a high degree of genetic control. This implies that there is little room for evolution of the range of phenotypic response (Via and Lande, 1985).

Once the variance components associated with the main effects of genotype and environment and their interaction have been determined by ANOVA, they can be used to construct various measures of plasticity. Some authors have suggested that the variance component associated with the effect of environment itself can be used as a measure of plasticity (Marshall and Jain, 1968). This measure of plasticity does not present the complete picture because it ignores the effect of genotype and gives no indication of heritability.

Thompson (1991) suggested that the variance component associated with the GXE can be used as a measure of plasticity. As Scheiner (1993) pointed out however, the

magnitude of this variance is affected by two things: the changing order of genotypes across environments, and the amount of genetic variance within each environment. As an alternate measure, Scheiner and Goodnight (1984) suggested summing the environment and GXE variance components in order to derive what they term total plastic variance. This measure is problematic however because it is the sum of the mean and the variance of population plasticity and Schlichting (1986) stated that it is more logical to present them separately. Coefficients of variation (CVs) can also be calculated as estimates of the total amount of plasticity; they are simply the standard deviation of a treatment divided by the mean of a treatment (Schlichting and Levin, 1984, Taylor and Aarssen, 1988). The same problem exists with this measure however in that it combines mean plastic response with variation in plastic response. This difficulty can be overcome by calculating CVs separately for each genotype and taking the mean CV of the genotypes as a measure of plasticity.

Stability analysis is also used to assess plasticity. In this method the mean of each genotype in each environment is regressed onto the mean of all genotypes in each environment resulting in a regression line for each genotype (Finlay and Wilkinson, 1963). Genotypes with responses identical to that of the mean genotype will have a regression slope of one. Stable, or non-plastic genotypes will have a slope of less than one and unstable or plastic genotypes will have a slope greater than one. This method is not without problems since environmental responses by organisms are not necessarily linear as is assumed by this method (Hardwick, 1981). Yet another method of determining genotype stability involves the decomposition of the GXE variance into portions ascribable to each genotype (Dutilleul & Potvin, 1995). These portions are called stability variance components and a genotype is considered stable (non-plastic) when its stability variance component is equal to the within-environment variance. These indices are useful in that they allow statistical testing to determine if a genotype is stable. They also enable the researcher to rank the genotypes in terms of stability. They do not, however, allow pairwise testing between genotypes.

The above methods are useful to consider amount of phenotypic plasticity; however, a plastic response also demonstrates a pattern or direction. There are several methods to look at pattern of a plastic response, the most straightforward one being by

drawing the norms of reaction (Schmalhausen, 1949). The environments are plotted along the X-axis, and the response variable is plotted along the Y-axis. All of the genotypes in an experiment are superimposed onto the same graph and each genotype is represented by a single line. It is important to consider pattern of plastic response because measures of amount of can be misleading when considered in isolation. A non-significant environment main effect can either mean that the genotypes are not changing their phenotype in response to the environment or that they are changing their phenotypes in opposite directions with equal magnitude (Lewontin, 1974). The same ambiguity exists when using the coefficient of variation as a measure of plasticity. The norms of reaction enable one to distinguish between the two scenarios.

There are many methods of measuring phenotypic plasticity. When a method is chosen it is important to consider whether it reveals both amount and pattern of plastic response. The limitations of the method should also be considered specifically in regard to the question being asked.

Conditions favoring the evolution of phenotypic plasticity

i) Selection Pressures

Schlichting (1986) divided the forces behind the evolution of phenotypic plasticity into the categories of selection, drift and disruption of the genetic system. The category of selection includes cases where there are differences in pattern or amount of phenotypic plasticity in two species or populations due to the different selection forces operating in the two habitats in which the groups are found. This is a recurring theme in the plasticity literature. Many researchers have looked for differences in phenotypic plasticity in a group of plants growing in a stable habitat versus a group of plants growing in a habitat that is variable on a spatial or temporal scale relevant to the lifespan of a single individual. It is thought that individuals in a highly variable environment are under selection pressure for enhanced ability to adapt and will therefore exhibit greater phenotypic plasticity than individuals in a stable habitat. Research of this type has been done from both an inter-specific and an intra-specific perspective with mixed results.

Schlichting and Levin (1984) termed this phenomenon the ecology hypothesis and hypothesized that differences in the plasticity of two populations or congeneric species is partially a function of the difference in the ecology of their two habitats. They found

partial support for this hypothesis in their 1984 study of annual *Phlox* species, but the effect of ecology could not be conclusively separated from other effects in the experiment. Other authors have, however, found strong evidence for the ecology hypothesis. Macdonald et al.(1988) looked at species within the *Stellaria longipes* complex that grew in four distinct habitats: montane, boreal, tundra and prairie. They found that across the species, plants from the same habitat showed distinct patterns and amounts of plasticity and presented this as direct evidence for the ecology hypothesis. In another study supporting the ecology hypothesis, Caldwell et al. (1981) found that *Agropyron desertorum* was better able to tolerate grazing than *Agropyron spicatum.* This was found to be due largely to greater plasticity in resource allocation in the former species following defoliation. This difference in plasticity was attributed to the relatively longer history of herbivory pressure on *A. desertorum* that caused a selection pressure for plastic resource allocation.

The ecology hypothesis is also relevant to conspecific populations. Mooney and Roy (1982) grew individuals from two populations of *Heliotropum curassavicum* in a growth chamber and subjected them to different humidity conditions. They found that individuals from the desert population, where humidity is variable, were more plastic in their stomatal and photosynthetic response than were individuals from the coastal population, where humidity is constantly high. The ecology hypothesis has also been demonstrated among populations of *Solidago virgaurea* (Bjorkman and Holmgren, 1963), *Ranunculus flammula* (Cook and Johnson, 1968), *Agropyron repens* (Taylor and Aarssen, 1988) and *Solanum ptycanthum* (Hermanutz and Weaver, 1995), and among varieties of *Linum usitatissium* (Khan and Bradshaw, 1976).

The ecology hypothesis has been applied to conspecific populations and congeneric species that occur in early versus late seral stages along a successional sequence in cases where the early populations are subject to conditions that are spatially and temporally more variable than those to which late populations are subject. Gray (1985) compared the conditions in a population of *Puccinellia maritima* that was growing in a young salt marsh to the conditions in a population of the same species that was growing in a mature salt marsh. He noted that survival in early successional habitats depends upon the ability to adjust to harsh and changing conditions while survival in late

successional habitats depends upon the ability to compete in density dependent conditions. The variability in the first environment resulted in selection for phenotypic plasticity.

Some studies have found differences in plastic response in early versus late successional populations. Houssard and Escarré (1995) compared populations of *Rumex acetosella* dispersed along a successional gradient in an old field. Genotypes from both early and late successional populations were planted over a range of different planting densities to simulate various levels of competition. Plants from the pioneer population possessed a greater capacity for individual buffering, *i.e.* plasticity, to cope with environmental variation.

Thompson et al. (1991 a, b, c) conducted one of the most thorough studies on phenotypic plasticity in populations in different seral stages. They noticed that in natural populations of *Spartina anglica* occurring in salt marshes of different successional status, there was high among-population morphological variation. To test whether this variation was the result of genetic differences among the populations or of phenotypic plasticity, they planted clones from ten populations of different successional status in a common garden experiment (1991a). They found that the clones grown under uniform conditions exhibited very little morphological variation. They interpreted this as meaning that the variation seen among plants in different habitats was a result of plasticity and not genetic differentiation. To complement this experiment, they did reciprocal transplants of clones from three successional populations and found significant differences among the populations in their plastic response (1991b). In the third part of their study, they planted clones from the same populations as in the first study over a substrate gradient in a greenhouse and found that the pioneer populations showed greater response to the gradient (1991c). This set of experiments demonstrated the existence of intra-specific variation in phenotypic plasticity in populations of different successional status.

Differences in plastic response have also been found between early versus late successional congeneric species. Chazdon (1992) compared two *Piper* species for plastic response over a light gradient. One of them, *P. arieanum*, is a species common in the understory of late successional forests, while the other, *P. sancti-felicis*, is a pioneer species in forest gaps and clearings. The pioneer species showed a plastic response that

was four times greater than the late successional species in photosynthetic capacity and leaf nitrogen content across the gradient. Similarly, Zangerel and Bazzaz (1983) found that *Polygonum pensylvanicum*, an invader into early successional habitats, was more plastic in resource allocation than *Polygonum virginianum*, an understory species in mature forests. It has also been shown experimentally that early successional grassland species germinate and grow over a wider range of moisture conditions (Parrish and Bazzaz, 1976) and nutrient conditions (Parrish and Bazzaz, 1982) than late successional species.

Different selection pressures at the extremes of a successional gradient are often a feature of successional sequences and can result in pioneer species having greater plasticity than late successional species (Gray, 1985). However many pioneer species are able to persist throughout successional sequences and are also found in established habitats. A decline in the number of genotypes of these persistent species has been proposed as a feature of succession (Gray, 1984). Gray's theory, termed the biotype depletion hypothesis, proposes that many genotypes of species that persist throughout the succession sequence are eliminated due to competition and reduced seedling establishment as density-dependent conditions increase. Evidence for decrease in genotypes over time in persistent pioneer species has been found in *Lolium perenne* (Kay and Harper, 1974), (McNeilly and Rose, 1984), (Aarssen and Turkington, 1985), *Trifolium reprens* (Aarssen and Turkington, 1985), *Puccinellia maritima* (Gray, 1985), *Dactylis* and *Phleum* spp. (Charles, 1961, 1964, 1966) and *Carex lasiocarpa* (McClintock and Waterway, 1993). The reduction in number of genotypes throughout the successional sequence may act to reduce the relatively high numbers of phenotypically plastic genotypes of pioneer species that existed in the early successional habitats. As a result, individuals of pioneer species, that have persisted throughout the successional sequence, may exhibit no greater plasticity in the late successional habitats than species that only establish late in the successional sequence.

ii) Perennial plants

Plasticity is the response of an individual to environmental heterogeneity that occurs within an individual's lifetime (Bradshaw, 1965). As a result plasticity tends to be an important strategy for adaptation in long-lived perennials because they are likely to

encounter temporal variation. They are also likely to encounter spatial variation since many of them are able to spread over considerable distances by rhizomes and other means of vegetative propogation (Bradshaw, 1965; Macdonald et al., 1988; Stewart and Nilsen, 1995). Phenotypic plasticity has been demonstrated in a wide variety of perennial species including: *Polygonum virginianum* (Zangerl and Bazzaz, 1983), *Carex flacca* (Heathcote et al., 1987), *Agropyron repens* (Taylor and Aarssen, 1988), the *Stellaria longipes* complex (Macdonald and Chinnappa, 1989), *Carex lyngbyei* (Smythe and Hutchinson, 1989), *Cyperus* species (Aldous, 1994) and *Vaccinium macrocarpon* (Stewart and Nilsen, 1995).

Phenotypic plasticity combined with the clonal growth form, in which ramets are connected by rhizomes or stolons, enables clonal plants to engage in a strategy of growth referred to as foraging (de Kroon and Schieving, 1990). Foraging refers to the selective placement of ramets into favorable patches when a habitat is heterogeneous (Slade and Hutchings, 1987). Foraging in clonal plants is made feasible via plasticity in three morphological traits: branching frequency of rhizomes or stolons (spacers), distance between ramets and angle of spacer growth (Evans and Cain, 1995).

Foraging is a strategy employed in heterogeneous habitats. Steufer (1996) described components of heterogeneity that are important to consider when examining clonal response to variable habitats. First, the contrast or degree to which favorable patches differ from unfavorable patches must be sufficiently large to be perceived by the plant. Second, the scale over which conditions are variable must fall within the range that the plant in question can perceive. This scale refers to both spatial and temporal heterogeneity. Variation that is too finely grained or too coarse will result in a habitat that is functionally homogeneous for the plant and thus foraging will not be a feasible strategy. Wijesinghe and Hutchings (1997) demonstrated that the ability to forage for nutrients was patch-size dependent in *Glechoma hederacea*. They planted ramets of one clone into boxes that held the same total nutrient content but in different sized patches. The treatment with the largest patch size had four times as much root biomass in the rich patch than in the poor patch, whereas in the treatment with the smallest patches there was no significant difference in root biomass found in rich versus poor patches.

The term foraging has been used in the literature to refer to two related but different phenomena. Grime et al.(1986) used the term to describe the placement of roots and leaves into favorable environments. This definition is equally applicable to clonal and non-clonal plants. The definition of de Kroon and Schieving (1990) is different in that it refers to plasticity in characteristics of rhizomes or stolons that allows selective placement of ramets into favorable habitats; this latter definition is applicable only to rhizomatous clonal plants. There is controversy among researchers regarding whether foraging, as defined by the latter definition, actually occurs.

De Kroon and Hutchings (1995) reviewed research on the response of fifteen different clonal species to habitats that were heterogeneous with respect to nutrients. In only two cases did the space between ramets shorten in response to conditions of high nutrients, which implies selective tiller placement in favorable patches. However, almost all studies report an increased production of ramets in favorable patches. De Kroon and Hutchings used these findings to re-formulate the concept of clonal foraging. They think that there is little evidence for selective placement of ramets via plasticity in spacer growth characteristics but rather that foraging results from plasticity in stems, leaves and roots. This type of foraging is synonymous to foraging as described by Grime et al. (1986) in both clonal and non-clonal plants. De Kroon and Hutchings (1995) pointed out that spacer length between ramets is largely unresponsive to habitat heterogeneity across many species. As a result they feel that spacers in clonal plants are more likely to function as continuous habitat search organs regardless of environmental patchiness, than as promoters of selective ramet placement.

Ironically, in the same year that this re-formulation of clonal foraging was published, Evans and Cain (1995) published "direct evidence" that the clonal plant used in their study, *Hydrocotyle bonariensis*, was able to preferentially place ramets in favorable patches. They grew their study plant in trays under three conditions: alone, with continuous grass cover and with patchy grass cover. They found that the clone was able to respond to habitat patchiness by placing ramets in grass-free patches. As additional evidence for clonal foraging (*sensu* de Kroon and Schieving) they note that the three morphological characteristics that are crucial to foraging: spacer length, angle, and branching intensity, exhibited plasticity in their study. Macdonald & Lieffers (1993)

found preferential clonal expansion of *Calamagrostis canadensis* into favorable patches: warm soil, unshaded, free of intra-specific competition. Two other authors, Kelly (1992) and Salzman (1985), also reported conclusive evidence for clonal foraging.

Regardless of whether selective placement of ramets by clonal plants actually occurs in nature, the literature on clonal foraging has demonstrated that plasticity is an important mechanism of adaptation in clonal plants.

Conclusion

Phenotypic plasticity is an important mechanism of adaptation when environmental heterogeneity occurs on a spatial or temporal scale within the lifespan or geographic reach of individual plants. Evidence suggests that genotypes from populations or species originating in variable habitats may have greater capacities for phenotypic plasticity due to selection under shifting conditions. Plasticity is an important means of adaptation in genotypes of clonal plants because they can be long-lived and cover considerable area via vegetative spreading and are thus likely to encounter both temporal and spatial heterogeneity.

INTRODUCTION

The ecology hypothesis proposes that, as the difference between two habitats grows, so does the difference in the plasticity of the species or populations in the respective habitats (Schlichting and Levin, 1984). As discussed in the literature review, the ecology hypothesis has been applied to groups of plants that are from different seral stages along a succession gradient. The purpose of this study was to test the ecology hypothesis on congeneric species and conspecific populations within the genus *Carex* L., (Cyperaceae). The distribution of *Carex* species along the successional gradient of wetland habitats makes this genus ideal for both inter- and intra-specific comparisons of phenotypic plasticity.

The role of *Carex* species in wetland succession

The genus *Carex*, with more than two thousand perennial species, is an important genus in many temperate habitats as well as in many boreal and arctic wetlands (Bernard, 1990). The vigorously rhizomatous growth habit of some *Carex* species enables them to play an important role in wetland succession that proceeds by infilling (Bernard and Gorham, 1978).

Infilling refers to the centripetal invasion of a body of water by plants. The process can continue until the surface of water is entirely covered with live and decaying plants (Wells & Pollett, 1983). Rhizomatous species of *Carex* are important contributors to this process because they are able to invade open water by means of spreading rhizomes and establish themselves on the false bottoms that are created by planktonic sediments often found in ponds or small lakes (Tarnocai et al., 1988). Once the pioneer sedges have established a floating rhizomatous mat on the water surface, they facilitate invasion by other plant species and especially species of *Sphagnum* moss (Vitt, 1994). Plants accumulate and may decompose slowly on the sedge mat and this accumulation results in the uppermost layers of vegetation being elevated above the water, so that the plants are no longer growing in submerged conditions. Eventually the habitat can reach the stage of a *Sphagnum*-dominated bog in which the water table level may have fallen many centimeters below the surface of the vegetative layer (Wells and Pollett, 1983).

Many of the *Carex* species that are able to invade open bodies of water and dominate in pioneer habitats are also able to persist, but not dominate, at the drier

extreme of the successional gradient. In contrast, some *Carex* species cannot invade open bodies of water, but are able to establish in the wetland during later stages of succession when the water-table level begins to fall relative to the surface layers of vegetation. These two groups of species, the persistent pioneers and the late-invaders form the basis for the inter-specific comparison of plasticity in this study. The plastic response over an artificially established water-table gradient in three persistent, pioneer species was compared to that of three late-invading species. The most important difference between these two groups of species is that, although all six occur in established habitats, the late-invaders never grow submerged, nor form part of floating rhizomatous sedge mats. The three pioneer species used were: *Carex aquatilis* Wahlenb., *Carex oligosperma* Michx. and *Carex rostrata* Stokes, while the three late-invading species were: *Carex michauxiana* Boeckeler, *Carex paupercula* Michx., and *Carex vaginata* Tausch.

Intra-specific comparisons for morphological response along a continuous water gradient were also made for early versus late successional populations of both *C. aquatilis* and *C. rostrata.*

Habitat heterogeneity in early successional wetlands

Pioneer and established wetland habitats differ on several abiotic components including nutrient availability and pH, however in order to clearly see differences in plasticity, the experiments were done over a single gradient. A water-table gradient was chosen because it is an important aspect of the difference between pioneer and established wetland habitats and it is readily measured in the field. Clones in the early stages of wetland succession encounter much variability in water-table levels, variability of both a temporal and a spatial nature. The habitat varies spatially along a gradient from the shoreline to the centre. The substrate near the shoreline is more solid allowing the roots and rhizomes of the sedge to be more firmly anchored than in the middle of the water body. Deeper in the body of water, the substrate becomes progressively less solid making establishment more difficult. Also, as the sedges spread from the edge of the water to the centre, they have to cope with growing in an increasingly anoxic environment (Crum, 1988).

This habitat also varies temporally in two ways. First, the habitat may change dramatically during different seasons in the year. The sedge mat may float on the surface

of the water during the wet season and advance along the floor of the pond or lake during the dry season. Second, although it takes thousands of years for succession to progress to the formation of a domed peat bog, the process of infilling occurs over a much shorter time frame. *Carex* clones have been estimated to persist as long as two thousand years in alpine regions (Steinger et al., 1996). Although clones in wetland areas may not be as long-lived, they still have the potential to survive for decades or possibly even hundreds of years. Infilling could therefore have an impact on environmental heterogeneity within the generation time of a single clone or the overlapping generation times of closely related clones.

Response variables

Allocation variables:

a)Root to shoot ratio: "An increase in root-to-shoot ratio is a common and well documented response to drought" (Sultan and Bazzaz, 1993b). Increasing the allocation of biomass in the favor of the roots advantages the plant in a situation of reduced water because there is a greater surface area of root tissue providing water for a reduced area of above ground tissue. Root to shoot ratio has been shown to be plastic in response to changes in moisture conditions in *Polygonum persicaria* (Sultan & Bazzaz, 1993b), *Carex flacca* (Heathcote et al., 1987), *Calamagrostis canescens*, *Carex gracilis*, and *Carex vesicaria* (Soukupová, 1994).

b) Number of roots: As a result of increase in allocation to the rooting system, it was expected that there would be an increase in number of roots in the low water-table treatment.

c) Mean leaf area: Shift in allocation also has the result that the leaf area is reduced on the plant, which is also advantageous, because there is less opportunity for water loss via transpiration (Setter, 1990).

d) Leaf area ratio and specific leaf area: These variables, measured as total leaf area/total plant biomass and total leaf area/total leaf biomass respectively, have been found to increase with increasing water availability in *Polygonum persicaria* (Sultan & Bazzaz, 1993b) and *Calamagrostis canescens*, *Carex gracilis*, and *Carex vesicaria* (Soukupová, 1994).

Growth Rate: In general, flooding is thought to decrease shoot growth (Jackson & Drew, 1984). However aquatic and marsh plants, as well as other flood resistant species have been found to have a faster growth rate under water. Accelerated growth of stems and petioles enables the plant to quickly put leafy tissue back into contact with a more favorable aerial environment and continue its normal functioning (Blom et al., 1994). This has been shown in many *Rumex* species (Perik et al., 1989; Voesenek and Blom, 1989; Voesenek et al., 1990). Ridge (1985) tested the growth rate of 20 species which are commonly found in marshes and found that in 90% of the cases, shoot extension was faster in submerged conditions than in well aerated conditions.

Stem diameter: Aerenchyma are parenchyma tissues with numerous longitudinal gas-filled channels. Aerenchyma is formed in the cortex of plant roots and in the above ground plant tissue; it functions to increase aeration in plants growing in anaerobic conditions (Crawford, 1993). The facultative formation of aerenchyma is a well-documented adaptive response to flooding in many plant species: *Carex gracilis* (Koncalova et al., 1988), *Typha latifolia* (Constable et al., 1992), *Rumex maritimus* and *Rumex crispus* (Laan et al., 1989), *Rumex palustris* (Blom et al., 1994), *Zea mays* (Sachs et al., 1996), *Alnus japonica* seedlings (Yamamoto et al., 1995) as well as in four species of tropical forage grasses (Baruch & Merida, 1995). It has been shown in emergent macrophytes that aerenchyma in leaf and stem tissue can occupy up to 50% of the cross-sectional area (Constable et al., 1992). It is known that gas spaces in leaves and stems of many wetland plant species are important for aeration of the plant (Teal and Kanwisher, 1966). Field data indicates a relationship between increasing stem diameter and increasing water-table level for *C. rostrata* (r^2=0.35; p=0.0017) and *C. aquatilis* (r^2=0.31; p=0.0001) (Gold, unpublished data). This relationship is probably due to the increased need for aeration at higher water table levels.

Based on the previous studies cited above, I expected that leaf area ratio, mean leaf area, specific leaf area, stem diameter and tiller growth rate would increase with increasing water-table level while the number of roots and the root to shoot ratio would decrease with increasing water-table level.

Objectives

Two experiments were performed in this study. A plasticity experiment was used to make an inter-specific comparison of phenotypic plasticity between two groups of *Carex* species that differ in their role during succession. The hypothesis tested in this experiment was that the group of persistent, pioneer species would exhibit greater phenotypic plasticity in response to a discrete water table gradient than would the group of late-invading species. It was therefore expected that the treatment (water-table levels) would have a significant effect on a greater proportion of the variables in the pioneer species than in the late-invading species. Furthermore it was expected that the pioneer species would have higher mean genotypic coefficients of variation, a measure of plasticity, on the variables than the late-invading species.

A continuous-gradient experiment was used to make an intra-specific comparison between populations from different seral stages. This experiment was used to test two hypotheses: 1) that clones from early successional habitats would colonize the experimental area, a large wooden box, to a greater extent than clones from late successional habitats, and 2) that clones from early successional habitats would show a greater range of morphological response than clones from late successional habitats in response to a continuous water-table gradient.

METHODS

Two main experiments were performed for this project, the plasticity experiment and the continuous-gradient experiment. Both of these experiments involved planting *Carex* tillers at different water-table levels. Three discrete treatment levels were used in the plasticity experiment: -35 cm, -10 cm and +5 cm. In the second experiment, the tillers were exposed to a continuous water-table gradient (-50 cm to +10 cm) that had been established within a large wooden box, these water-table levels were chosen because they fall within the range encountered by the pioneer species throughout the successional sequence.

An important feature of the design of the plasticity experiment is that the genotypes used for all six of the species were taken from sites that were similar in terms of successional status, in other words all six species were collected from late successional habitats. This was to ensure that any differences seen between species were not due to field site effects.

The continuous-gradient experiment was done twice, once with *C. aquatilis* and once with *C. rostrata*. This experiment was designed to compare the colonization patterns and morphological response of early and late successional populations of a single species collected from different sites. The successional status of the sites from which plants for both experiments were collected was ascertained using the ordination described below.

Identification of site status

The plants used in both experiments were collected from several sites in the area around Schefferville, Quebec (54°48'N, 66°48'W), during the months of July and August, 1998. The Schefferville area was chosen because it contains many undisturbed wetland areas at different stages of succession.

To characterize the sites, abundance data for all vascular plants were collected from thirty circular vegetation plots, 30 cm in diameter, within each site. I placed the plots on a transect along the long axis of each site. There was a plot in each ten-meter segment of the transect, however the position within this ten-meter segment was random. When the site was not long enough to allow thirty plots to be laid out in this manner, additional plots were laid out along a second axis, parallel to the first and at least 10 m from it. The vascular species found within these plots were each given an abundance

score using the Braun-Blanquet scale of abundance based on percentage cover of each species (Braun-Blanquet, 1932). Non-vascular species within the vegetation plots were grouped into categories of *Sphagnum*, mosses, lichens and fungi. The vegetation abundance data were analyzed using the Bray-Curtis ordination option available in version 3.11 of PC-ORD (McCune and Mefford, 1999).

The six species used in the plasticity experiment were each collected from a different site. *Carex rostrata* and *C. aquatilis* were also collected from twelve additional sites for use in the continuous-gradient experiment. One species that was slated for use in the plasticity experiment, *C. rariflora*, did not keep pace with the other five species in tiller production. To avoid delaying the start of the plasticity experiment, this species was replaced with *C. michauxiana*, which was collected from a bog in the Laurentians (46° 26' N, 74° 25' W). A complete list of the sites from which plants were collected and their locations, as determined by GPS, can be found in Table 1.

Propagation of Shoots

Within three days of my return from Schefferville in mid-August, 1998, I planted the plants in standard six-inch pots in a mixture of one-third peat moss and two-thirds black earth. Plants that originated from the same clone in the field were separated and planted in different pots to maximize tiller production in each of the clones. They were placed in the greenhouse with a 12h/ 12h photoperiod. The plants were watered daily and fertilized once every three weeks with 20-20-20 nitrogen-phosphorous-potassium (NPK) fertilizer at a concentration of 3g/L. To encourage the rapid propagation of shoots, plants were further separated into different pots as shoots were produced.

Table 1: Populations sampled to provide tillers for the experiments.
Unless otherwise stated, all populations are in the area around Schefferville, Quebec.

Population	Location	Species collected	Experiment
1. Ares Fen	54° 46' 53" N, 66° 47' 18" W	*C. aquatilis*	Continuous-gradient
		C. rostrata	Continuous-gradient
2. Astray Fen	54° 40' 15" N, 66° 36' 12" W	*C. aquatilis*	Continuous-gradient
3. Beagle Fen	54° 49' 28" N, 66° 49' 33" W	*C. aquatilis*	Continuous-gradient
4. Capricorn Fen	54° 47' 09" N, 66° 48' 40" W	*C. aquatilis*	Plasticity
5. Far Away Fen	54° 47' 33" N, 66° 47' 59" W	*C. aquatilis*	Continuous-gradient
6. Fen at Km 9 on Mine Road	54° 51' 31" N, 66° 57' 59" W	*C. aquatilis*	Continuous-gradient
7. Menihek Road Fen # 1	54° 32' 22" N, 66° 42' 18" W	*C. aquatilis*	Continuous-gradient
8. Railroad Fen	54° 50' 26" N, 66° 51' 06" W	*C. aquatilis*	Continuous-gradient
		C. paupercula	Plasticity
		C. rostrata	Continuous-gradient
9. Satellite Fen	54° 48' 14" N, 66° 51' 12" W	*C. aquatilis*	Continuous-gradient
		C. rostrata	Continuous-gradient
10. Pelletier Fen	54° 50' 26" N, 66° 51' 09" W	*C. oligosperma*	Plasticity
11. Airstrip Fen	54° 48' 34" N, 66° 48' 40" W	*C. rostrata*	Plasticity
12. Airstrip Fen Pool	54° 48' 41" N, 66° 48' 38" W	*C. rostrata*	Continuous-gradient
13. Floating Sedge Mat	54° 48' 43" N, 66° 48' 39" W	*C. rostrata*	Continuous-gradient
14. Menihek Road Fen # 2	54° 33' 41" N, 66° 43' 36" W	*C. rostrata*	Continuous-gradient
15. Red Bog #1	54° 49' 58" N, 66° 49' 43" W	*C. rostrata*	Continuous-gradient
16. Red Bog #2	54° 49' 53" N, 66° 49' 34" W	*C. rostrata*	Continuous-gradient
17. Forest Fen	54° 48' 06" N, 66° 48' 36" W	*C. vaginata*	Plasticity
18. Beaulieu Lake Mont Tremblant, Qc	46° 26' 06" N, 74° 25' 16" W	*C. michauxiana*	Plasticity

Verification of Clones

The six species used in the plasticity experiment were collected from six separate sites. All the genotypes required for each species were collected from the same site. Since five of the species used in the experiment are capable of spreading rhizomatously over considerable distances it was necessary to show that the tiller of these species were members of different clones.

For all species except *C. michauxiana,* which is cespitose, allozyme markers were used to verify that each tiller used in the experiment came from a distinct clone. Tillers that differed for at least one enzyme-coding locus were assumed to belong to different clones. Standard techniques of starch gel electrophoresis were used to assay the allozyme markers (Wendel and Weeden, 1989). I extracted enzymes by grinding fresh leaf material in Gottlieb buffer (Gottlieb, 1981). Wicks made of Whatman #3 filter paper were used to soak up the extract and these wicks were stored at -80 ° C until needed.

Histidine pH 6.5 buffer was used in conjunction with enzyme systems DIA (diaphorase), EST (esterase), IDH (isocitrate dehydrogenase), MDH (malate dehydrogenase), MDR (menadione reductase), 6-PGD (6-phosphogluconate dehydrogenase), PGM (phosphoglucomutase), PRX (peroxidase), and SKDH (shikimate dehydrogenase). Lithium borate pH 8.1 buffer was used in conjunction with enzyme systems AAT (aspartate amino transferase), ACP (acid phosphatase), ADH (alcohol dehydrogenase), GPI (glucose-6-phosphate isomerase), ME (malic enzyme) and TPI (triose-phosphate isomerase).

Preliminary experiment

In order to determine appropriate water-table levels for the subsequent plasticity experiment, I conducted a preliminary water-table experiment in the winter of 1998. Three species were used in this experiment, *C. aquatilis, C. oligosperma* and *C. rostrata.* These plants were collected in the area around Schefferville, Quebec in August, 1997.

Nine replicates of each of the three species were planted at two water-table levels, -13cm and -25 cm. Each tiller was planted in a separate opaque PVC tube, 65cm in height and 7.6cm in diameter. The water levels were maintained in each tube using the same irrigation system that is described in the following section.

The experiment was harvested after 60 days. At that point some of the tubes were crowded with new tillers to the point where there might have been competition effects. Upon harvest the following morphological measurements were taken: shoot length, length of longest root, number of roots, and fresh mass. In addition the plants were partitioned into above and below-ground components. The plant material was then dried at 65 °C for 48 hours. The above and below-ground components were measured and a root to shoot ratio was calculated.

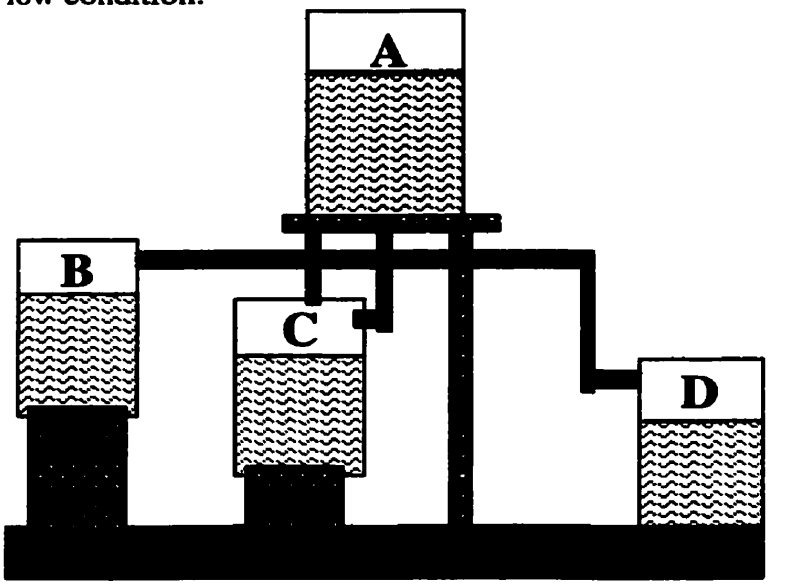
The following response variables: absolute change in length of planted shoot, root to shoot ratio, and change in root number, were analyzed, separately by species, with a one-way ANOVA. The sole factor in the ANOVA model was water level.

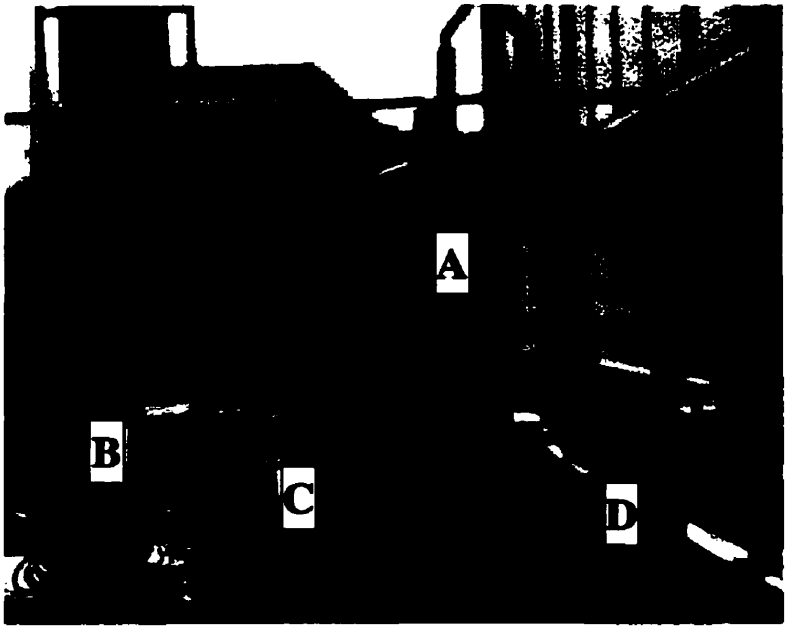
Plasticity experiment

Experimental design and set-up: Six genotypes of each of the six species were used in the plasticity experiment, they were planted in three water-table levels. The treatment levels were: -35cm (low), -10cm (medium) and +5cm (high). Three species, *C. aquatilis, C. oligosperma* and *C. rostrata* were persistent, pioneer species. The other three, *C. michauxiana, C. paupercula* and *C. vaginata* were late-invading species. However all six species were sampled from sites of approximately equivalent successional status, in order to control site effects on plant growth, based on an ordination of vegetation data from each site.

The plants were arranged in a randomized complete block design with three blocks and 108 plants, or a complete replicate per block. Additional non-experimental plants were placed around the border of each of the blocks in order to reduce edge effects. Nine tillers were required from each genotype to provide three replicates in each of three treatments for use in the experiment. Blocks of the experiment were planted as tillers became available; thus, the experiment was blocked in time with the blocks being planted 4 weeks apart. Throughout the experiment the greenhouse room was kept under constant conditions of 14 hour day length, 17 degree days and 10 degree nights, to reflect late summer conditions in Schefferville where most of the plants were native. Each block was planted in the center of a separate greenhouse bench (Fig. 1).

Figure 1: This irrigation system was used in the plasticity experiment. This set-up, which was repeated for each block, consisted of a large water reservoir (A) that supplied smaller reservoirs (B, C and D) which in turn supplied water to the individual shoots in each tube, as seen in photograph underneath. Reservoir B supplied all of the tubes in the high condition, C supplied those in the medium condition and D supplied the tubes in the low condition.





The treatments were maintained by an irrigation system that held the water-table levels constant using the effect of gravity (Fig. 1). Each tiller in the experiment was planted into a separate tube made of opaque PVC plastic, 50cm in height. The tubes were filled with black earth that was harvested from the lower layers of a peat bog near Alexandria, Ontario. A layer of gravel 5cm deep was first added to the bottom of the tubes. The irrigation tubing was nestled in this gravel in order to prevent the fine particles of the peat from clogging the holes in the tubing. The tubes were sealed water-tight at the bottom by means of a tightly fitting plastic cap and water-proof glue. Each tube was attached, via rubber tubing, to one of three water reservoirs. Each water reservoir corresponded to one of the three water-table treatment levels. The water level in the tubes attached to a given water reservoir was maintained, by gravity, at the same level as the water in the reservoir. Each of the three water reservoirs was fed by a single, larger water reservoir. This whole system, one large water reservoir feeding three smaller water reservoirs feeding 108 tubes, was repeated for each block .

Each block of the experiment was planted on a single day. Before planting the tillers, the following morphological measurements were taken: fresh mass, shoot length, length of longest root, number of roots and number of rhizomes. Tillers were selected to be as close in size as possible within a species. Each tiller was planted into a dry column of peat and then given 500mL of water. The day following the planting of each block, the irrigation system was connected and the water levels established within each tube. For the first week after planting, the high and medium treatments were kept at the same level (-10cm) to allow the tillers in the high condition to establish before the onset of flooded conditions. The tillers in the low water-table level were not treated this way because of concern that the peat in the enclosed column would not dry out after the water-table level had been lowered to the treatment level.

Throughout the course of the experiment, each tube was monitored every three days. The length of the planted tillers and the above-ground lengths of any newly-emerged tillers were recorded.

Harvest: I harvested each block 60 days after its planting date. Each harvest took three days. On the first day I cut the originally planted shoot from each tube at the level of the soil. These shoots were weighed and measured, their stem diameters were

measured using a Vernier caliper and their leaves were counted and then pressed flat in a plant press so that the leaf areas could be measured at a later date. On the second day, I cut all tillers at the level of the soil surface and the same measurements were taken for each. On the third day, I emptied each of the tubes and rinsed away excess peat. I then soaked the root systems in hot soapy water for an hour in order to loosen the remaining peat. The clean root systems were then rinsed, patted dry and weighed. The number of roots was counted and the length of the longest root was measured. All rhizomes were counted and measured. In the days that followed, the leaf areas of the originally planted shoots and all the tillers were measured using a Li-Cor 3100 leaf area meter. All above and below-ground plant material was then dried for 48 hours at 65°C, allowed to cool, and weighed.

Data analysis: Eight response variables were analyzed in the plasticity experiment (Table 2). These variables were analyzed with a mixed two-way ANOVA model or, for two variables, an ANCOVA model. For these two variables, number of roots and dry mass at harvest, it was possible to measure a logical covariate before planting: number of roots prior to planting and fresh mass prior to planting. All statistical analyses were done using the SAS system for windows, version 4.0. The six species were analyzed by separate models resulting in eight AN(C)OVAs done for each of six species. This resulted in an inflation of the Type I error due to repeated tests on the same data set. To account for this, the alpha level was adjusted with the Bonferroni correction and accordingly set at $0.05/8 = 0.00625$.

A common problem of plasticity data sets is the violation of the homoscedasticity assumption of ANOVA, *i.e.* the assumption of equal variance in all treatments. This violation is caused because typically the variable means increase or decrease across the treatments and, as Steel and Torrie (1980) point out, variance tends to increase as a function of the magnitude of the mean. Dutilleul and Potvin (1995) developed a transformation specifically designed for plasticity data sets that allows the removal of the among-environment heteroscedasticity while preserving the treatment means. To determine whether the use of this transformation was appropriate, I calculated Box's epsilon according to the method of Dutilleul and Potvin (1995) for each species per variable. Box's epsilon provides an estimate of the extent to which the homoscedasticity

assumption has been violated. It ranges from 1/1-p to 1, where p is the number of treatments. Values of epsilon near the bottom of the range indicate violation of the assumption of homoscedasticity.

In order to remove among-environment heteroscedasticity, the transformation sets the genetic variance within an environment to one, where one was chosen arbitrarily for ease of calculation. Dutilleul and Carrière (1998) suggested a modification of this transformation in which the genetic variance of the environments is set to an intermediate value: the geometric mean of the genetic variances in each of the environments. I carried out the transformations following this modified method.

Table 2: Definition of variables and covariates for analysis of variance of plasticity data.

Variable	Definition	Covariate	Definition
Dry mass	Dry mass of entire tiller	Initial fresh mass	Initial biomass of the entire tiller at time of planting
Leaf area ratio	Area of leaves divided by fresh mass of the entire tiller	None	
Mean leaf area	Area of leaves divided by number of leaves	None	
Number of roots	The number of roots at harvest	Initial # of roots	The number of roots attached to the tiller before planting
Root: shoot	Ratio of dry mass of roots and rhizomes to dry mass of the shoot	None	
Specific leaf area	Area of leaves divided by above-ground fresh biomass	None	
Stem diameter	Stem diameter at harvest of oldest tiller (excluding the tiller originally planted)	None	
Tiller growth rate	Growth rate of tiller for the first 9-12 days after emergence (cm/day)	None	

Table 3: AN(C)OVA model used in analysis of plasticity experiment

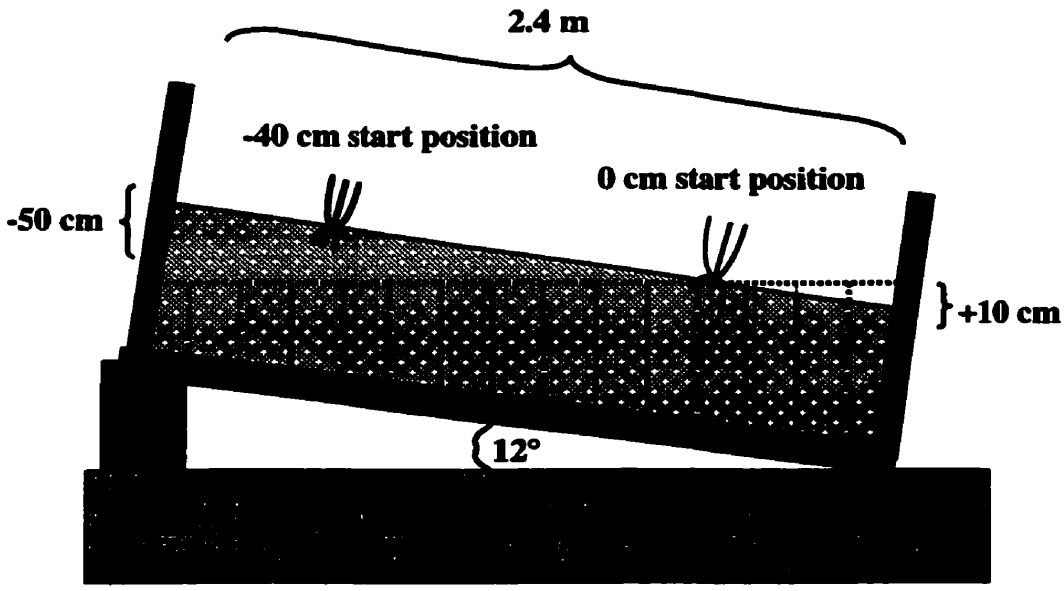
Effect	Fixed/Random	Error Term	Degrees of Freedom
Environment	Fixed	G X E	2
Genotype	Random	Error	5
G X E	Random	Error	10
Block	Random	Error	2
Covariate		Error	1

In addition to analysis of variance and covariance, coefficients of variation (CVs) were calculated for each genotype. These CVs resulted in six values per species per variable. For each variable, the thirty-six coefficients of variation were analyzed by Kruskal-Wallis analysis of variance by ranks since the data were proportions (Zar, 1984), to determine if the species differed significantly in the magnitude of their genotypic coefficients of variation. Mann-Whitney U tests were used in order to determine which species differed significantly from each other.

Continuous-gradient experiment

In this experiment, *C. rostrata* tillers were planted over a continuous water-table gradient. This gradient was established by planting tillers inside a wooden box 240cm long by 120cm wide by 90cm deep, lined with plastic sheeting (Fig. 2). The box was lined with 5cm of gravel, the irrigation tubing was installed and then the box was filled to a depth of 60cm with peat from the same source as was used in the plasticity experiment. The box was then placed on an angle of 12°, and a water-table was established inside by connecting the irrigation tubing to a large water reservoir. The reservoir was initially elevated to start the water flow. The water level remained parallel to the ground and since the box itself was on an angle, this created a continuous water-table gradient. *Carex rostrata* tillers were planted in the box and given two weeks to establish before the water-table gradient was created. During these two weeks the peat surface in the box was watered with five liters of distilled water every other day. Five liters of 20-20-20 NPK

Figure 2: Side view of the set-up for the continuous-gradient experiment, in which a water-table gradient was established within a wooden box. The dashed lines represent the water-table level. The two plants mark the positions along the gradient, 0cm and -40cm, at which rows of tillers were initially planted. The gradient ranged from +10cm at the wet end, to -50cm at the dry end.



fertilizer at a concentration of 3g/L was applied to the peat surface one week before the water-table gradient was established.

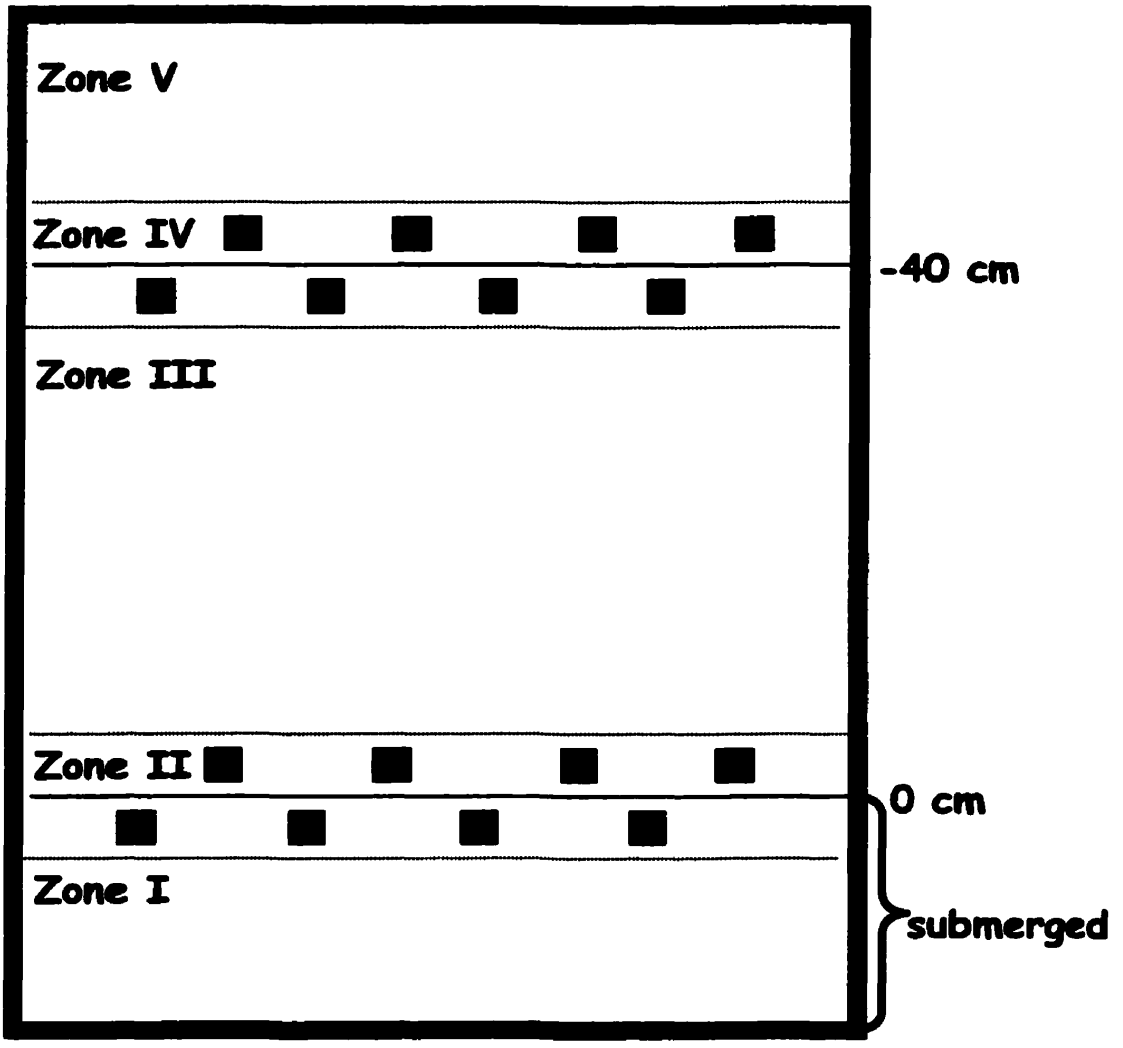
Eight *C. rostrata* clones were used in the experiment. These eight clones came from eight different wetland sites: four were early successional sites and four were late successional sites as determined by the previously described ordination. Two tillers were taken from each clone and one was planted 60cm from each end of the box (Fig. 3). Once the water-table gradient was established, these positions corresponded to approximately 0cm and -40cm water-table depths.

Throughout the course of the experiment, the shoot lengths of all the planted tillers were measured every three days. The positions of new tillers that emerged during the course of the experiment were mapped and the dates of emergence were noted. Each tiller was assigned a number. The stem diameter of each tiller was measured forty-five days after emergence. An identical experiment was run concurrently using *C. aquatilis.*

Harvest: The experiment ran for six months and was harvested on May 25 -26 , 1999 (*C. aquatilis*) and June 1-June 2 (*C. rostrata*). Prior to harvest, every tiller in each box was tagged and identified with its previously assigned number. In excavating the box, each of the sixteen original shoots was used as a starting point. From these starting points all connected rhizomes and tillers were removed from the box as a whole. The roots had formed a continuous mat at the bottom of the box and were impossible to attribute to each of the sixteen plants. For each of the sixteen plants (eight clones) removed from the box, the following data were recorded: length and fresh mass of all rhizomes and length, fresh mass and number of leaves for each shoot. The stem diameter of each tiller was also measured using Vernier calipers. The leaves were pressed and the leaf area was measured for each shoot the following week. All rhizomes and leaves were then dried for forty-eight hours at 65°C and their dry mass recorded.

While the tillers and rhizomes were being extracted from the box, samples of root and rhizome tips randomly chosen from the extreme ends of the box were also collected. These were identified according to which tiller they had been taken from, wrapped in wet paper towel and put on ice for no more than six hours while the box was being emptied. The porosity of each of these root and rhizome samples was measured using a 25mL pycnometer following the method of Jensen et al. (1969).

Figure 3: Diagram of the set-up of the continuous-gradient experiment. The squares represent the starting position of the sixteen plants. In order to maximize the initial amount of space between a plant and its neighbor, the plants were started along two parallel lines at the dry and wet starting positions. These lines were spaced 7.5 cm apart.



Data Analysis: The data from this experiment were analyzed using entire plants, individual rhizomes, and individual tillers as experimental units. In the first case each of the sixteen plants in the box (eight clones at two starting positions each) was treated as an experimental unit. The effects of starting position (wet versus dry) and the type of site from which the clone had originally been collected in the field (early succession versus late succession), as well as the interaction between these two main effects were examined using the ANOVA model (Table 4). One allocation variable: rhizome mass/ shoot mass, and four productivity variables: dry mass of rhizomes, total leaf area, dry mass of above ground biomass and total dry biomass were assessed.

Table 4: Model for analysis of Continuous Gradient Experiment using clones as the experimental unit.

Effect	Fixed/ Random	Error Term	Degrees of Freedom
Starting position (SP)	Fixed	Error	1
Site	Fixed	Error	1
SP*site	Fixed	Error	1

In the second analysis, individual rhizomes were used as experimental units. Two variables were analyzed: gradient distance and length of the rhizome/ gradient distance. Gradient distance refers to the total distance a rhizome covered along, *i.e.* parallel to, the water gradient. Rhizome length divided by gradient distance is thus a measure of the directness of the path taken by a rhizome relative to the water gradient (Fig. 4). This analysis was used to determine if initial starting position, site type, or the direction in which the rhizome was spreading had an effect on these variables. The ANOVA model for this analysis is in Table 5.

Figure 4: Illustration of the terms gradient distance and rhizome length/gradient distance. Rhizome length refers to the actual total length of the rhizome, tiller to tiller. Gradient distance refers to the distance traveled, by the rhizome, along the gradient.

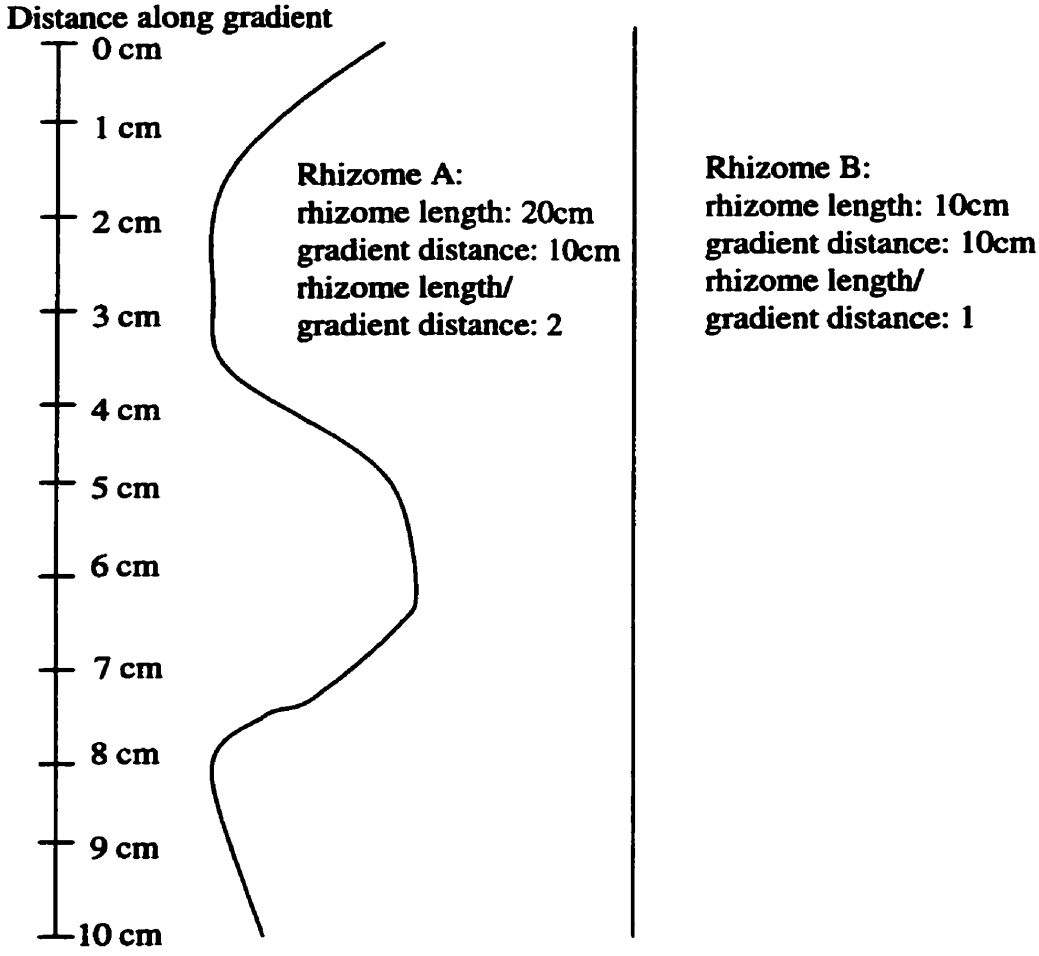


Table 5: Model for the analysis of Continuous Gradient Experiment using rhizomes as the experimental unit.

Effect	Fixed/ Random	Error Term	Degrees of Freedom
SP	Fixed	SP*direction	1
Site	Fixed	Error	1
Direction	Random	Error	1
SP*direction	Random	Error	1

Two variables were assessed in the analyses that used tillers as the experimental unit: stem diameter 45 days after emergence and growth rate of the tiller during the 10 days after emergence. In analyzing these two variables, the surface area enclosed by the wooden box was divided into five zones separated by imaginary lines drawn perpendicular to the water-table gradient (Fig. 3). Zone II included the eight starting positions of the clones planted in the wet portion of the box and zone IV included the eight starting positions of the same clones planted in the dry portion of the box. Zone I was the submerged end of the box, zone V was the extreme dry end of the box and zone III was in between zone II and IV and covered the middle portion of the box. In an attempt to have an equal number of tillers in each zone for analytical purposes, the zones were not created equal in size. The main effects in the model were zone and site type (Table 6).

Table 6: Model for the analysis of Continuous Gradient Experiment using tillers as the experimental unit.

Effect	Fixed/ Random	Error term	Degrees of Freedom
Zone	Random	Error	1
Site	Fixed	Zone * Site	1
Zone * Site	Fixed	Error	1

The porosity data were analyzed separately from the above data because they were sampled differently. The rhizomes and roots were each analyzed by ANOVA with water table level as the single main effect.

RESULTS

Preliminary Experiment

This pilot study was done to determine what range of water-table levels would be appropriate for use in the plasticity experiment. Three variables were analyzed using an ANOVA model with water-table level as the sole factor: change in total length of shoots (including growth of the originally planted shoot and any new tillers that were produced), change in number of roots, and root to shoot ratio. I expected to see an increase in root to shoot ratio as the water table dropped, as well as a decrease in total length of shoots and an increase in number of roots. This experiment was done to determine if a difference of 12 cm in water table would cause significant differences for these three variables.

Carex rostrata showed a significantly greater increase in root number at the higher water table (Table 7). This result is surprising as I expected to see an increased number of roots in the lower water table treatment as a result of the plant expending more energy in below-ground growth to increase water uptake. *Carex rostrata* did show a higher root to shoot ratio in the low treatment, although this difference was not significant (Table 7). Perhaps the greater root to shoot ratio was achieved through more extensive branching of the roots rather than an increase in root number. *Carex aquatilis* showed a significantly higher mean root to shoot ratio in the low treatment, as expected (Table 7). The alpha level was corrected to account for multiple testing.

As a consequence of these results it was decided to increase the differences in water-table level among treatments in the plasticity experiment to increase the probability of detecting environment effects. The difference between the two extreme treatments in the plasticity experiment was more than triple the difference in the preliminary experiment and it corresponded approximately to the extremes that the pioneer species would encounter in the field.

Table 7: ANOVA testing the effect of water-table level on variables from preliminary experiment

(** = p<0.001, * = p<0.00556)

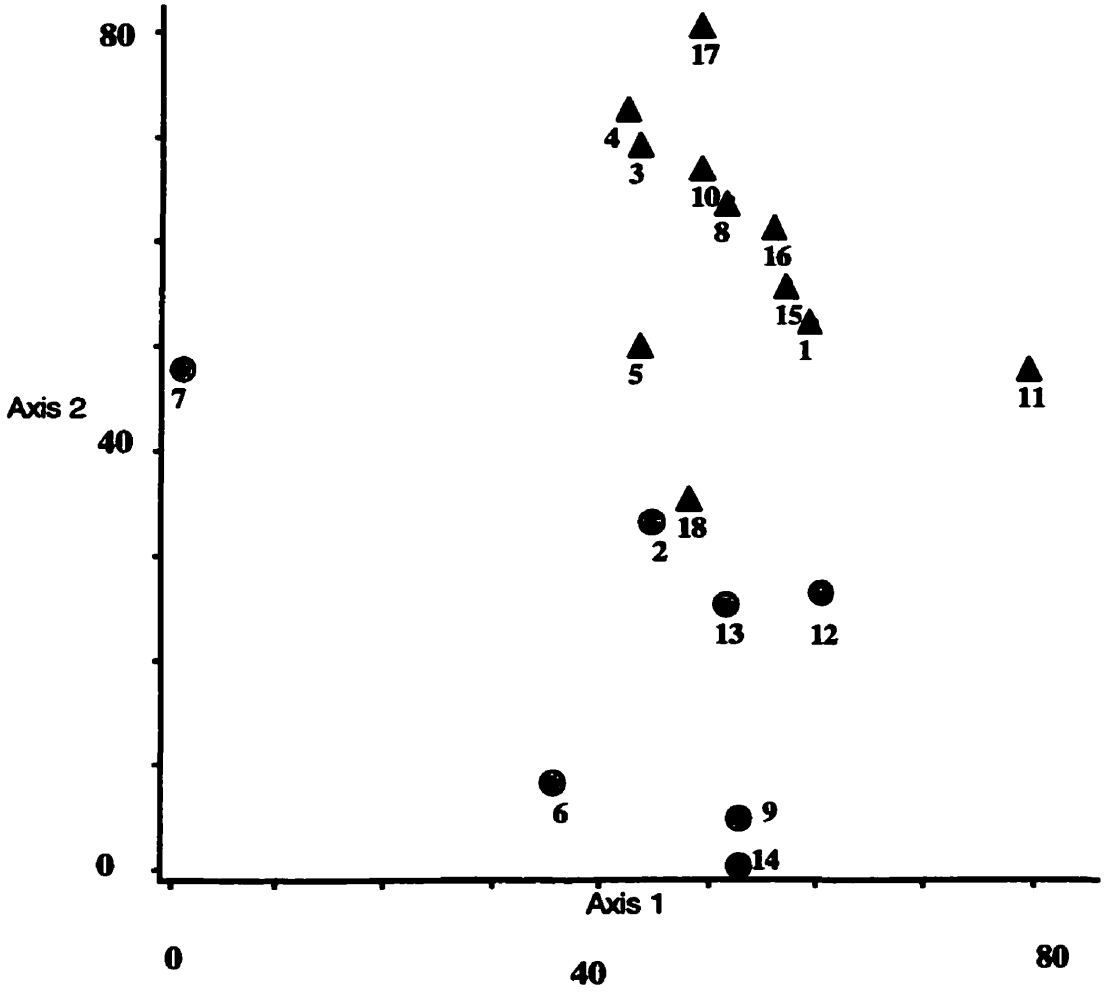
Species	Variable	F
C. aquatilis	Δ shoot length	1.22
	Δ number of roots	3.95
	root: shoot	6.14*
C. oligosperma	Δ shoot length	3.65
	Δ number of roots	0.02
	root: shoot	3.63
C. rostrata	Δ shoot length	1.15
	Δ number of roots	14.66**
	root: shoot	0.61

Identification of site status

The species abundance data from the eighteen sites from which clones were collected were submitted to Bray-Curtis ordination, which separates the sites along two axes based on similarity of composition (Figure 5). The numbering of the plots in the ordination follows the same numbering scheme as Table 1 in the Methods section. Sites that were deemed to be early successional for the purposes of the experiments are marked with a circle, while sites that were deemed to be late successional are marked with a triangle. The scatterplot indicates separation of the two site types along the axes. The first two axes extracted a total of 47.10% of the variance in the original data.

Carex michauxiana was collected from site 18 for the plasticity experiment and therefore this site was deemed, for experimental purposes, as late successional. In the scatterplot of the ordination however, it is closer to the pioneer sites than to the late successional sites. This was the only southern site used in the study and therefore it contained species not found in any other site which may account for its distance from the cluster of late successional sites. This site does however, have important features in common with the other late successional sites: a greater number of species than all of the early successional sites and a lack of open water. Site 7, which was a pioneer site in

Figure 5: Ordination of field sites based on vegetation abundance data. The numbering scheme is that of Table 1. All sites that were deemed to be early successional for experimental purposes are marked with a circle; late successional sites are marked with a triangle. The first Bray-Curtis axis extracted 15.08% of the variance from the data; the second axis extracted 32.02%. Total variance extracted by the two axes is 47.11%.



the continuous gradient experiment lies far from the cluster of early successional sites. Only 2 species were present at this site, *Carex rostrata* and *Menyanthes trifoliata*. A minimum of 7 species were present in every other early successional site; this difference may have caused the separation of site 7 from the other pioneer sites. However site 7 shared important features with the other early successional sites: it was dominated by a floating rhizomatous sedge mat and had much open water.

Verification of clones

Five of the species were assayed for genetic differences in allozymes in order to ensure that the tillers sampled at the sites were from different clones (Fig. 6). This was not necessary for *C. michauxiana* since it is a non-rhizomatous species and only one tiller was collected from any given cespitose clump. *Carex aquatilis, C. paupercula* and *C. vaginata* were cleanly separated into the required six genotypes. *Carex oligosperma* and *C. rostrata* did not show as much allozyme variation and could only be separated into three and four genotypes respectively on the basis of the allozyme phenotypes. In both cases I chose the remaining genotypes by selecting tillers that had been sampled as far as possible from each other and from the genotypes separated by allozyme variation.

Plasticity experiment

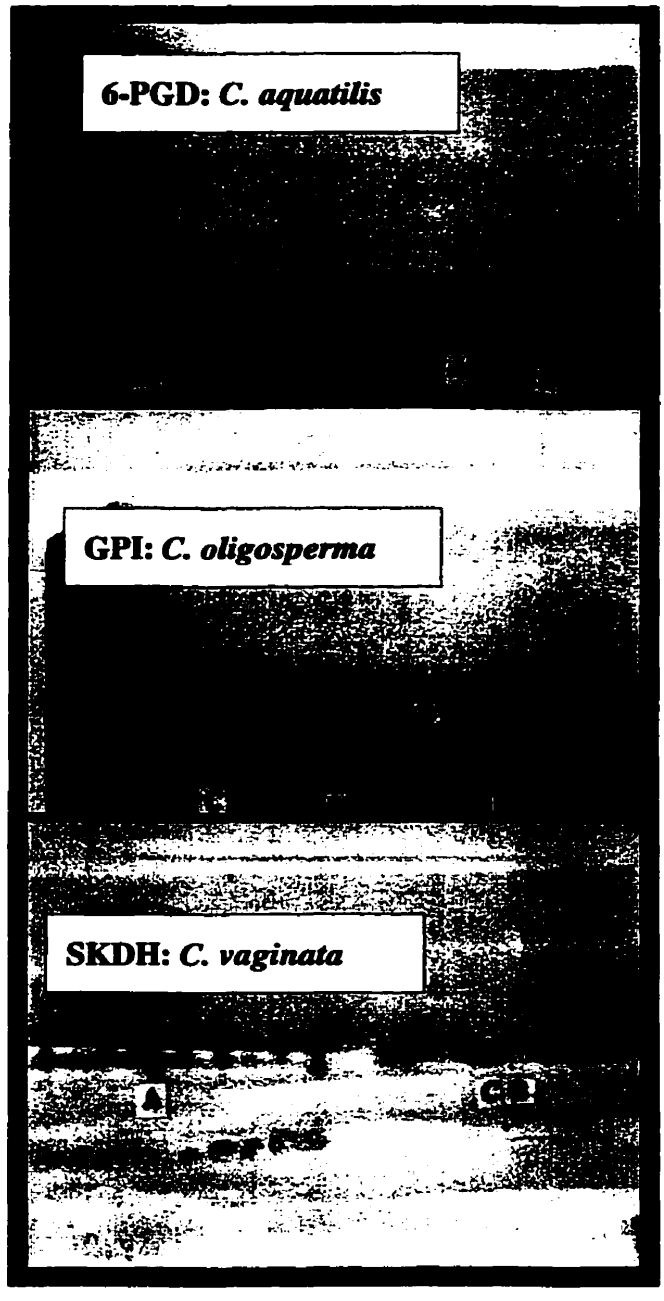
Effects of the transformation for environmental heteroscedasticity: The first step in analyzing the plasticity data was to calculate estimates of Box's epsilon for raw data and for transformed data from which environmental heteroscedasticity had been removed. An epsilon value of 1 indicates that the observations are both independent and free of among-treatment heteroscedasticity. I did not expect these values to reach one with the transformation since the same genotypes were used in each environment, which means that the observations are necessarily not independent. However in 70% of the cases, the epsilon values did rise indicating that the transformation successfully reduced the effect of heteroscedasticity (Table 8). In those cases where the epsilon value decreased as a result of transformation, the decrease was usually less than 5%; in only three cases was the decrease greater than 10%. Overall the transformation resulted in an average increase of 6.3% (± 10.4%) in the epsilon value. Thus the transformation was used on all of the data prior to analysis by ANOVA or ANCOVA.

Figure 6: Examples of allozyme gels used to differentiate among clones. Photograph i shows 6-phosphogluconate dehydrogenase (6-PGD), which was used to separate three clones (A,B and C) of *C. aquatilis*. Photograph ii shows glucose-6-phosphate isomerase (GPI), which was used to separate three clones (A,B and C) of *C. oligosperma*. Photograph iii shows shikimate dehydrogenase (SKDH), which was used to separate three clones (A,B and C) of *C. vaginata*.

i)

ii)

iii)



Results of analysis of variance and covariance: The statistical testing was done separately for each species. Eight variables were tested for each species, three of which had covariates and five of which did not. To correct for the multiple testing done within each species, the alpha level was set at 0.05/8 = 0.00625. The model was initially run including interactions between block and environment and block and genotype. These interactions were significant less than 0.1% of the time and thus eliminated from the model. In cases where the block effect was not significant, the model was re-run without it.

i) Environment main effects

The environment main effect was significant for 13 of 48 cases, or 27.1% of the time (Tables 9A-G). The pattern of significant effects across the species is somewhat surprising. The three late-invading species: *C. michauxiana*, *C. paupercula,* and *C. vaginata* had 3, 5 and 2 significant environment main effects respectively while the three pioneer species: *C. aquatilis*, *C. oligosperma* and *C. rostrata* had 2, 0 and 1 significant effects respectively. This is opposite to what I had predicted in that I expected to find a greater number of variables exhibiting a plastic response in the pioneer species.

The pattern of significant effects across the variables is interesting in that dry weight, an estimator of fitness, was never significant. The effects were limited to the seven variables that measured adaptive response to the water table levels; total dry weight was never significantly affected by the environment. Specific leaf area was significant in four species, growth rate and root to shoot ratio in three, stem diameter in two and leaf area ratio, mean leaf area and number of roots were each significant in one species.

Table 8: Epsilon values by species, per variable, before and after transformation. Epsilon values range from 1/1-p - 1. The closer the value of epsilon to 1, the less the violation of the assumption of homoscedasticity.

Variable	Dry weight		Leaf area ratio		Mean leaf area		Number of roots	
Species	Before	After	Before	After	Before	After	Before	After
C. aquatilis	0.9910	0.9811	0.8819	0.9657	0.8532	0.8907	0.9824	0.9217
C. michauxiana	0.8491	0.7442	0.7526	0.9653	0.9743	0.9643	0.9189	0.8802
C. oligosperma	0.7148	0.8082	0.6046	0.8841	0.7844	0.9001	0.7767	0.8027
C. paupercula	0.8066	0.8878	0.8119	0.9772	0.6839	0.7926	0.6775	0.9317
C. rostrata	0.6035	0.6484	0.6481	0.7134	0.6375	0.6411	0.8695	0.8139
C. vaginata	0.5946	0.6780	0.8004	0.9900	0.9099	0.8481	0.8533	0.8912

Variable	Root: shoot		Specific leaf area		Stem diameter		Tiller growth rate	
Species	Before	After	Before	After	Before	After	Before	After
C. aquatilis	0.7227	0.9207	0.6658	0.7834	0.6265	0.7004	0.7137	0.7228
C. michauxiana	0.9940	0.8514	0.6582	0.6313	0.7925	0.6976	0.6110	0.6672
C. oligosperma	0.8370	0.9372	0.7965	0.9414	0.8651	0.8574	0.9263	0.9840
C. paupercula	0.7375	0.8549	0.9180	0.9450	0.6237	0.6608	0.5078	0.5012
C. rostrata	0.9436	0.9728	0.6767	0.8102	0.7673	0.8506	0.6730	0.7910
C. vaginata	0.9283	0.9183	0.8435	0.9422	0.9743	0.9451	0.9366	0.9946

Table 9A: AN(C)OVA results from plasticity experiment for *Carex aquatilis*, a pioneer species. (* = p< 0.00625)

Variable	Genotype		Environment		G X E		Block		Covariate	
	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F
Dry weight	0.26	0.9324	1.37	0.2655	0.83	0.5996	5.03	0.0124	**18.23**	**0.001***
Leaf area ratio	2.20	0.0717	4.43	0.0179	1.27	0.2877	**9.69**	**0.0005***	None	
Mean leaf area	0.96	0.4500	0.41	0.6665	0.43	0.9229	0.03	0.9702	None	
Number of roots	0.46	0.8014	1.29	0.2845	1.38	0.2312	0.54	0.5857	0.07	0.7893
Root: shoot	0.55	0.7340	**14.6**	**0.0011***	0.56	0.8376	0.80	0.4561	None	
Specific leaf area	1.46	0.2239	**8.52**	**0.0008***	1.98	0.0680	**10.37**	**0.0002***	None	
Stem diameter	1.85	0.1277	1.06	0.3562	0.89	0.5516	0.61	0.5581	None	
Tiller growth rate	0.33	0.8927	1.06	0.3562	1.10	0.4014	1.43	0.2612	None	

Table 9B: AN(C)OVA results from plasticity experiment for *Carex michauxiana*, a late-invading species. (* = p< 0.00625)

Variable	Genotype		Environment		G X E		Block		Covariate	
	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F
Dry weight	1.42	0.2343	0.75	0.4782	0.92	0.5284	4.24	0.0230	**26.17**	**0.0001***
Leaf area ratio	0.76	0.5822	0.12	0.8853	1.66	0.1279	2.70	0.8180	None	
Mean leaf area	**3.85**	**0.0053***	**7.55**	**0.0015***	5.96	0.0198	4.39	0.0201	None	
Number of roots	1.07	0.3891	3.43	0.0409	0.98	0.4826	6.08	0.0066	**27.57**	**0.0001***
Root: shoot	3.54	0.0395	4.23	0.0466	0.84	0.5975	1.97	0.1552	None	
Specific leaf area	1.64	0.1673	**7.08**	**0.0021***	7.32	0.0110	3.84	0.0313	None	
Stem diameter	2.83	0.0278	3.31	0.0466	0.87	0.5707	1.90	0.1676	None	
Tiller growth rate	**3.97**	**0.0050***	**6.83**	**0.0027***	3.20	0.0841	0.77	0.4745	None	

Table 9C: AN(C)OVA results from plasticity experiment for *Carex oligosperma*, a pioneer species. (* = p< 0.00625)

Variable	Genotype		Environment		G X E		Block		Covariate	
	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F
Dry weight	0.51	0.7638	3.71	0.0327	1.27	0.2883	**52.54**	**0.0001***	**71.37**	**0.0001***
Leaf area ratio	1.25	0.3012	0.44	0.6456	0.52	0.8669	.32	0.1135	None	
Mean leaf area	0.70	0.6259	0.85	0.4334	0.80	0.6330	0.43	0.6537	None	
Number of roots	0.58	0.7166	2.46	0.0968	0.42	0.9262	5.15	0.0299	5.13	0.0284
Root: shoot	0.64	0.6694	0.24	0.7900	0.77	0.6542	1.94	0.1599	None	
Specific leaf area	1.33	0.2684	1.19	0.3132	0.78	0.6495	0.83	0.4453	None	
Stem diameter	1.01	0.4258	0.11	0.8981	1.11	0.3846	0.07	0.9320	None	
Tiller growth rate	1.17	0.3417	5.03	0.0118	1.91	0.0899	**9.92**	**0.0006***	None	

Table 9D: AN(C)OVA results from plasticity experiment for *Carex paupercula*, a late-invading species. (* = p< 0.00625)

Variable	Genotype		Environment		G X E		Block		Covariate	
	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F
Dry weight	1.96	0.1026	1.70	0.1950	0.93	0.5169	1.65	0.2081	**49.52**	**0.0001***
Leaf area ratio	1.83	0.1341	**9.14**	**0.0007***	0.59	0.8105	**9.37**	**0.0006***	None	
Mean leaf area	0.57	0.7205	0.84	0.4370	1.38	0.2281	1.43	0.2532	None	
Number of roots	1.36	0.2556	**9.71**	**0.0003***	0.48	0.8906	0.02	0.9833	**22.70**	**0.0001***
Root: shoot	0.64	0.6673	3.57	0.0675	2.03	0.0607	**6.17**	**0.0052***	None	
Specific leaf area	1.42	0.2351	**30.24**	**0.0001***	0.28	0.9828	1.31	0.2837	None	
Stem diameter	1.95	0.1121	**9.70**	**0.0005***	1.60	0.1664	0.18	0.8330	None	
Tiller growth rate	1.53	0.2078	**24.74**	**0.0001***	0.75	0.6704	**3.99**	**0.0014***	None	

Table 9E: AN(C)OVA results from plasticity experiment for *Carex rostrata*, a pioneer species. (* = p< 0.00625)

Variable	Genotype		Environment		G X E		Block		Covariate	
	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F
Dry weight	2.94	0.0224	1.47	0.2416	0.73	0.6901	1.91	0.1643	**29.85**	**0.0001***
Leaf area ratio	1.11	0.3658	0.28	0.7581	0.97	0.4857	2.65	0.0851	None	
Mean leaf area	**4.34**	**0.0026***	1.75	0.1857	0.84	0.5929	2.84	0.0722	None	
Number of roots	2.54	0.0423	4.46	0.0174	0.48	0.8900	**7.66**	**0.0014***	**10.63**	**0.0022***
Root: shoot	2.33	0.1115	2.72	0.0839	0.43	0.9221	2.79	0.0758	None	
Specific leaf area	1.11	0.3658	5.41	0.0078	0.97	0.4867	1.89	0.1667	None	
Stem diameter	1.26	0.3011	**5.94**	**0.0054***	0.26	0.9864	3.69	0.0370	None	
Tiller growth rate	3.09	0.0189	5.29	0.0092	0.40	0.9355	**10.00**	**0.0003***	None	

Table 9F: AN(C)OVA results from plasticity experiment for *Carex vaginata*, a late-invading species. (* = p< 0.00625)

Variable	Genotype		Environment		G X E		Block		Covariate	
	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F
Dry weight	3.50	0.0094	0.07	0.9369	1.43	0.2085	2.11	0.1368	**18.62**	**0.0001***
Leaf area ratio	1.11	0.3658	0.28	0.7581	1.03	0.4365	4.65	0.0167	None	
Mean leaf area	1.64	0.1687	1.87	0.1655	1.09	0.3992	1.28	0.2919	None	
Number of roots	3.46	0.0100	1.28	0.2887	1.73	0.1120	0.31	0.7328	3.15	0.0827
Root: shoot	1.44	0.2453	7.09	0.0121	1.02	0.4493	0.33	0.7200	None	
Specific leaf area	0.60	0.6971	**14.91**	**0.0001***	0.81	0.6208	3.86	0.0311	None	
Stem diameter	2.14	0.0793	0.28	0.7549	0.47	0.8977	0.02	0.9851	None	
Tiller growth rate	1.56	0.1937	**9.21**	**0.0005***	0.94	0.5151	1.25	0.3021	None	

It was expected that leaf area ratio, mean leaf area, specific leaf area, stem diameter and tiller growth rate would all increase with increasing water-table level and that root to shoot ratio would decrease with increasing water-table level for the reasons stated in the introduction. In the majority of cases the treatment means followed the expected patterns of adaptive response (Tables 10A-G). In the case of the root to shoot

ratio, for example, the low treatment yielded a higher mean root to shoot ratio than the high treatment for every species. Likewise, the same pattern was seen in stem diameter and growth rate in which the high treatment always (with the exception of stem diameter in *C. oligosperma*) produced the highest mean. Although the relative position of the extreme treatments usually followed the expected pattern, the ranking of the intermediate treatment was quite variable across the species and variables.

When the environment main effect was significant, the expected pattern of treatment means was seen with two exceptions: leaf area ratio in *C. paupercula* and mean leaf area in *C. michauxiana*. In these two cases the relative ranking of the two extreme treatments was the opposite of the predicted pattern. Generally the patterns of response were as expected, and similar across the six species. It cannot be said that the pattern of response differed in the two groups.

Table 10A: Treatment means and standard deviations for dry weight (g), this variable was never significantly affected by the environment.

Species	High	Medium	Low
C. aquatilis	3.132 ± 1.882	3.286 ± 1.651	3.028 ± 1.160
C. michauxiana	1.060 ± 0.665	0.945 ± 0.484	0.853 ± 0.597
C. oligosperma	0.736 ± 0.455	0.578 ± 0.316	0.782 ± 0.338
C. paupercula	0.637 ± 0.235	0.440 ± 0.193	0.526 ± 0.248
C. rostrata	1.839 ± 1.491	1.630 ± 0.902	1.703 ± 0.943
C. vaginata	0.697 ± 0.327	0.666 ± 0.334	0.671 ± 0.179

Table 10B: Treatment means and standard deviations for leaf area ratio (cm^2/g). Species-variable combinations that showed a significant environment main effect are marked with an asterisk (*).

Species	High	Medium	Low
C. aquatilis	7.247 ± 1.606	5.836 ± 1.967	5.954 ± 1.601
C. michauxiana	13.404 ± 2.557	13.696 ± 4.707	10.071 ± 3.174
C. oligosperma	7.625 ± 1.608	7.182 ± 2.094	8.036 ± 6.227
C. paupercula *	13.603 ± 5.605	12.431 ± 3.984	13.952 ± 7.802
C. rostrata	10.823 ± 2.401	10.220 ± 1.976	10.431 ± 3.198
C. vaginata	12.681 ± 3.505	11.261 ± 5.862	9.159 ± 3.091

Table 10C: Treatment means and standard deviations for mean leaf area (cm^2)

Species	High	Medium	Low
C. aquatilis	4.032 ± 1.265	3.617 ± 1.112	3.713 ± 1.133
*C. michauxiana**	2.448 ± 0.617	1.987 ± 0.537	2.626 ± 0.496
C. oligosperma	1.678 ± 0.678	1.567 ± 0.684	1.419 ± 0.442
C. paupercula	1.778 ± 0.631	1.491 ± 0.533	1.551 ± 0.951
C. rostrata	3.414 ± 1.678	2.840 ± 1.071	3.072 ± 0.676
C. vaginata	1.500 ± 0.474	1.185 ± 0.465	1.346 ± 0.565

Table 10D: Treatment means and standard deviations for number of roots

Species	High	Medium	Low
C. aquatilis	33.8 ± 12.8	37.9 ± 10.1	32.1 ± 10.3
C. michauxiana	31.9 ± 16.3	28.8 ± 15.2	29.7 ± 12.6
C. oligosperma	14.8 ± 7.0	11.0 ± 5.6	14.0 ± 6.4
C. paupercula *	12.2 ± 7.2	6.8 ± 2.6	8.1 ± 4.0
C. rostrata	23.2 ± 10.3	22.6 ± 13.7	16.7 ± 8.1
C. vaginata	23.7 ± 11.7	20.6 ± 9.6	18.7 ± 9.7

Table 10E: Treatment means and standard deviations for root: shoot

Species	High	Medium	Low
C. aquatilis *	1.344 ± 0.361	2.086 ± 0.641	2.024 ± 0.806
C. michauxiana	0.426 ± 0.158	0.533 ± 0.107	1.075 ± 0.230
C. oligosperma	0.719 ± 0.194	0.782 ± 0.438	0.741 ± 0.315
C. paupercula *	1.039 ± 0.541	1.680 ± 0.747	1.775 ± 0.994
C. rostrata	0.960 ± 0.240	1.146 ± 0.274	1.119 ± 0.283
C. vaginata *	1.116 ± 0.491	1.652 ± 0.681	1.878 ± 0.756

Table 10F: Treatment means and standard deviations for specific leaf area (cm^2/g)

Species	High	Medium	Low
C. aquatilis *	23.218 ± 4.984	29.192 ± 7.442	28.591 ± 4.906
*C. michauxiana**	24.012 ± 4.741	28.617 ± 5.489	26.303 ± 2.938
C. oligosperma	18.200 ± 2.420	19.508 ± 3.921	19.856 ± 4.328
C. paupercula *	34.456 ± 10.513	55.303 ± 11.518	62.483 ± 12.432
C. rostrata	28.294 ± 2.584	32.211 ± 5.664	32.560 ± 5.589
C. vaginata *	33.061 ± 6.491	47.523 ± 8.932	44.581 ± 9.446

Table 10G: Treatment means and standard deviations for stem diameter (cm)

Species	High	Medium	Low
C. aquatilis	0.80 ± 0.54	0.79 ± 0.43	0.76 ± 0.36
C. michauxiana	0.84 ± 0.36	0.76 ± 0.33	0.76 ± 0.30
C. oligosperma	0.68 ± 0.26	0.58 ± 0.35	0.69 ± 0.27
C. paupercula *	0.67 ± 0.36	0.41 ± 0.32	0.46 ± 0.25
C. rostrata *	1.04 ± 0.46	0.99 ± 0.19	0.80 ± 0.36
C. vaginata	0.60 ± 0.17	0.59 ± 0.14	0.52 ± 0.22

Table 10H: Treatment means and standard deviations for tiller growth rate (cm/day)

Species	High	Medium	Low
C. aquatilis	0.81 ± 0.26	0.64 ± 0.26	0.52 ± 0.25
*C. michauxiana**	0.51 ± 0.23	0.36 ± 0.15	0.48 ± 0.14
C. oligosperma	0.42 ± 0.17	0.35 ± 0.14	0.30 ± 0.11
C. paupercula *	0.43 ± 0.18	0.24 ± 0.12	0.14 ± 0.072
C. rostrata	0.56 ± 0.28	0.39 ± 0.18	0.43 ± 0.15
C. vaginata *	0.30 ± 0.13	0.20 ± 0.16	0.12 ± 0.093

ii) Genotype main effects and Genotype by Environment interaction effects

A surprising aspect of the results was the low number of genotype main effects and the complete absence of significant GXE effects. There were only three significant genotype main effects, or 6.25% of the total. Two of them were in *C. michauxiana* and one in *C. rostrata*. This absence of significant effects cannot be attributed to the rather conservative level at which these effects were tested. Had the alpha level been left at 0.05, *i.e.* left uncorrected for multiple testing, there would only have been six additional genotype main effects and two significant GXE effects.

iii) Block effects

There were eight significant block effects, or 16.7% of the total. These block effects were probably due to environmental heterogeneity within the greenhouse room. A log of environmental data for each of the blocks was kept during the plasticity experiment. This log (Appendix I) included data from a Photosynthetically Active Radiation (PAR) meter as well as soil temperature for each treatment in each block. These data indicate that block II was receiving less light and had lower soil temperatures across all three treatments than either blocks I or III. The patterns of means seen across the blocks supports the notion that the significant block effects could have been caused

by the lower temperatures and light conditions in block II. Variable means by block are found in Appendix II. Variables such as growth rate, increase in number of roots and leaf area ratio, which one would expect to have smaller means under conditions of lower light and temperature, were significantly affected by blocking in several species and these variables had the smallest means in block II (Fig. 7).

iv) Covariate Effects

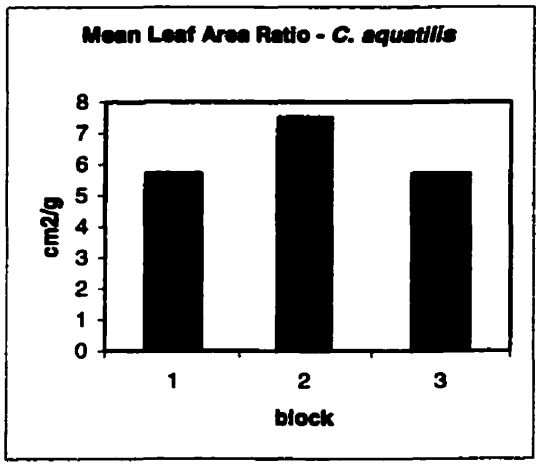
The effect of the covariate was significant 9 out of 12 times. Significant covariate effects were strongly associated with the variable dry weight. In every species, the covariate fresh weight at planting, had a significant effect on dry weight at harvest. This indicates that this was an appropriate choice for a covariate for this variable.

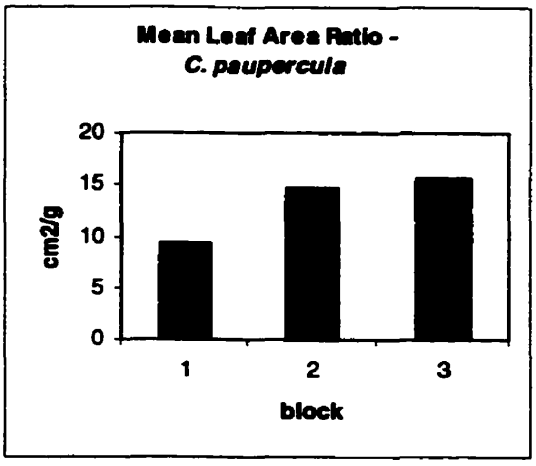
Reaction Norms

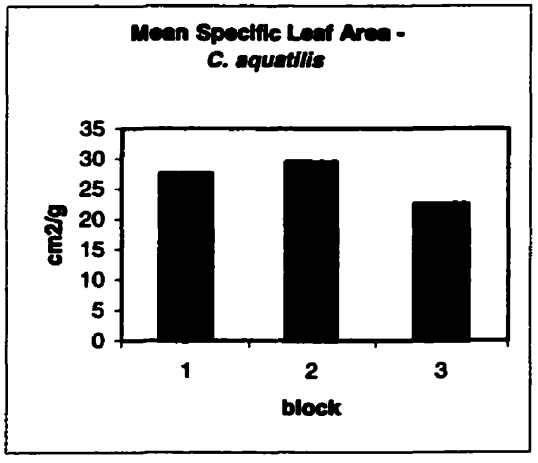
The pattern of response of the species to the environments can be examined using the reaction norms (Fig. 8 A-H). They are arranged by variable, with all of the species on the same page. For comparison purposes, the scale of the Y-axis is the same for all six species for a given variable. The pioneer species are in the left column and the late-invaders are in the right column. The reaction norms again show that in the majority of cases the predicted response was seen. The reaction norms for stem diameter, growth rate and mean leaf area, for example, generally show for all species an increase in value from the low treatment to the high treatment.

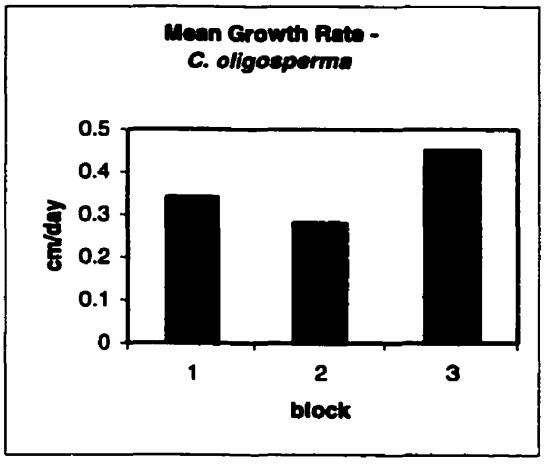
In every case the genotypic lines in the reaction norms cross each other, in some cases quite extensively. This is normally indicative of a significant GXE effect. I have included error bars on these reaction norms to illustrate why, despite the non-parallel nature of the genotypic lines in the reaction norms, the interactions are not significant. In every case the error bars overlap indicating that there was much variability within each of the genotypes within the environments. The magnitudes of the error bars on the norms of reaction are illustrated in Figure 9 where the reaction norm for specific leaf area in *C. aquatilis* has been decomposed by genotype. It appears that the magnitude of the within-genotype, within-environment variability has made it impossible to detect interaction effects.

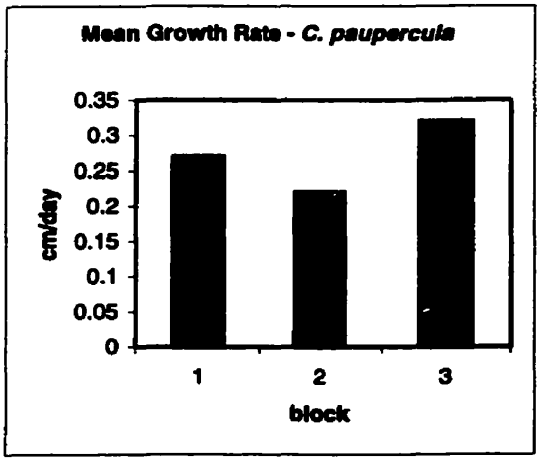
Figure 7: Histograms illustrating selected significant block effects. Environmental data indicate that block 2 experienced conditions of lower light and colder soil temperatures.











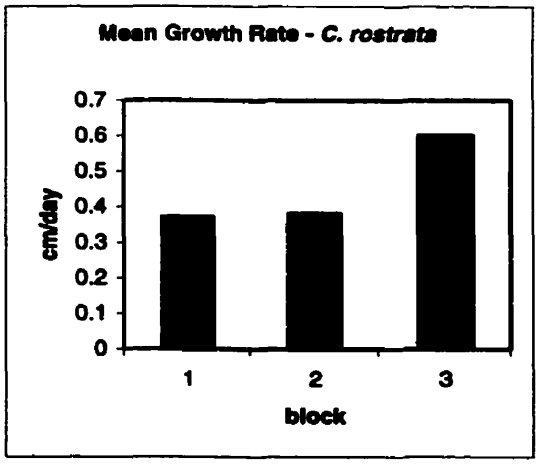
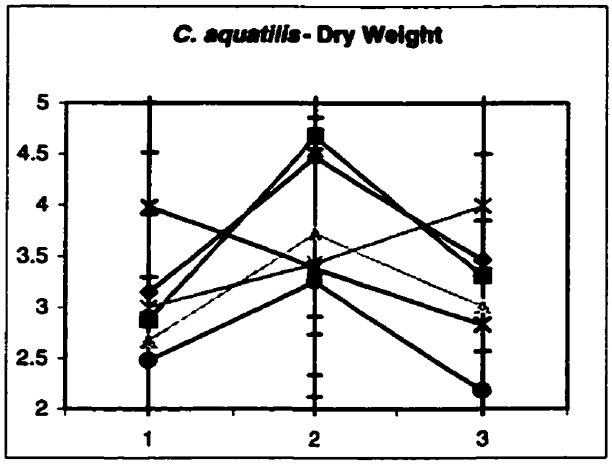
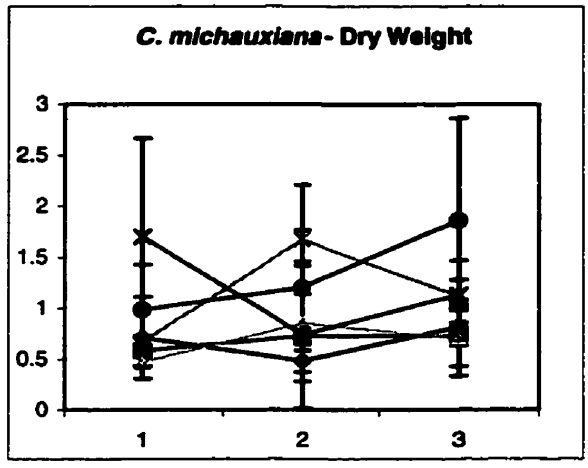
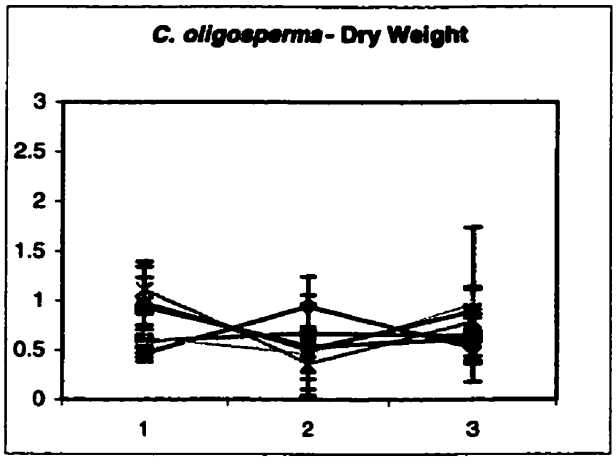
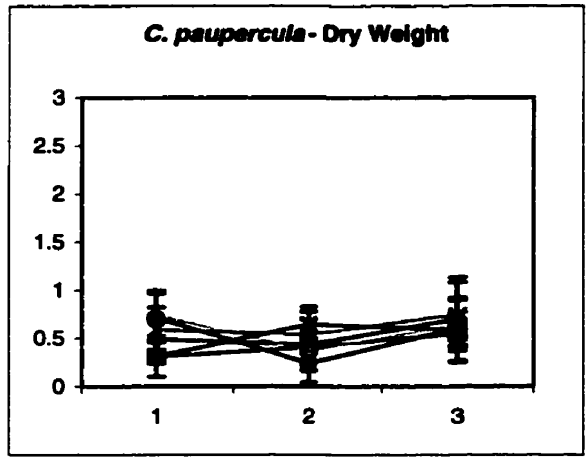


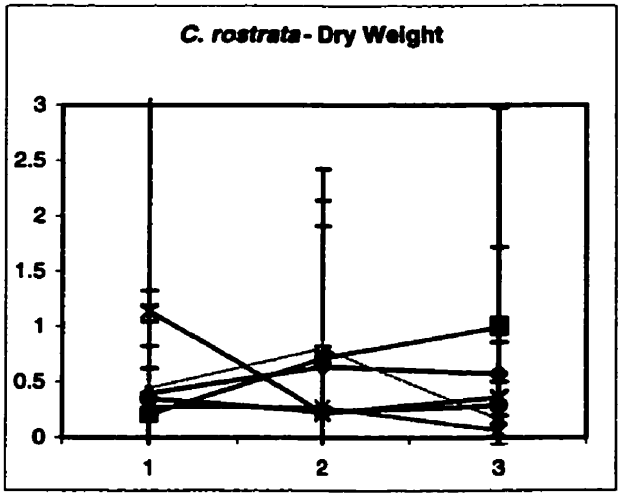
Figure 8A: Reaction norms for all species for the variable dry weight (g). Dry weight was not significantly affected by environment in any species. Each line in each figure represents a genotype. The environments, plotted along the X-axis are represented as follows: 1= Low (-35cm); 2=Medium (-10cm); 3=High (+5cm). Error bars around each point are equal to standard deviation.











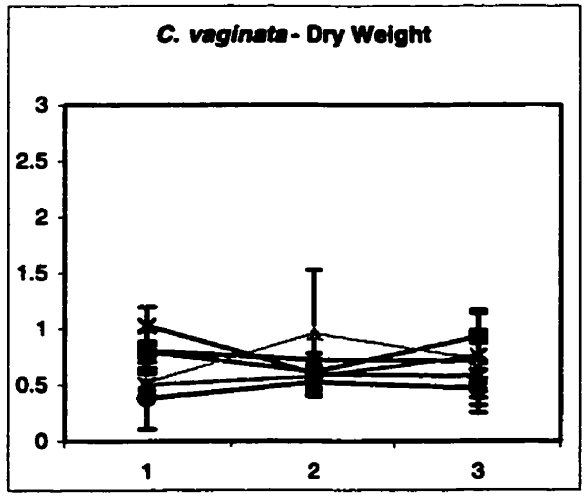
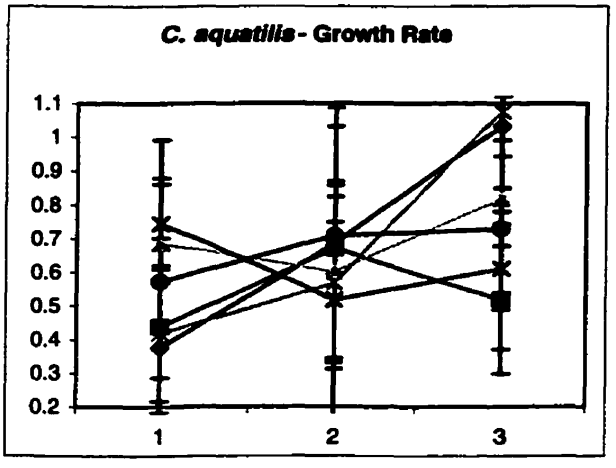
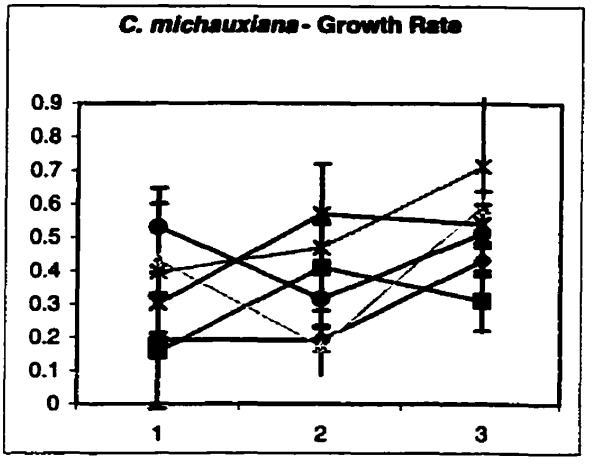
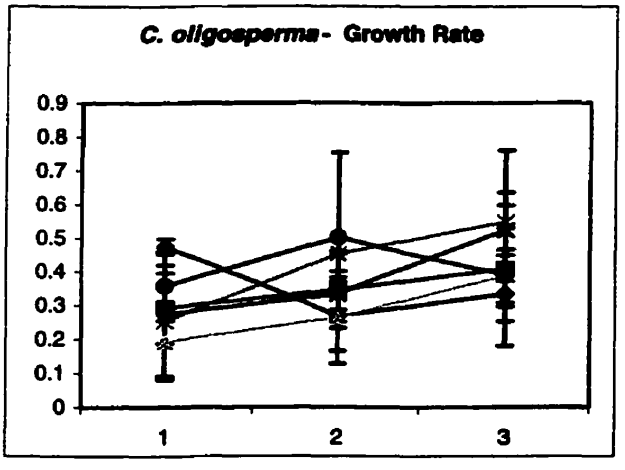
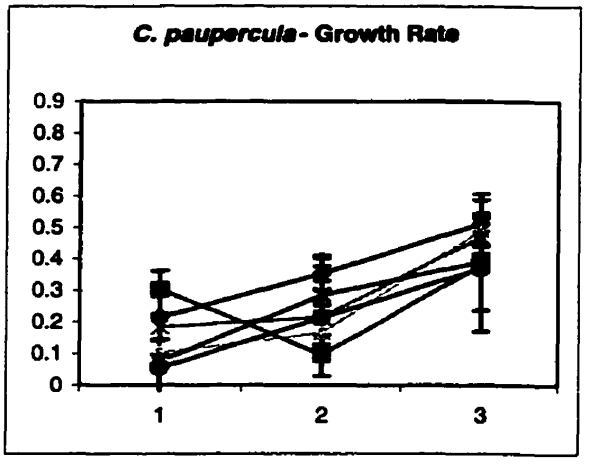


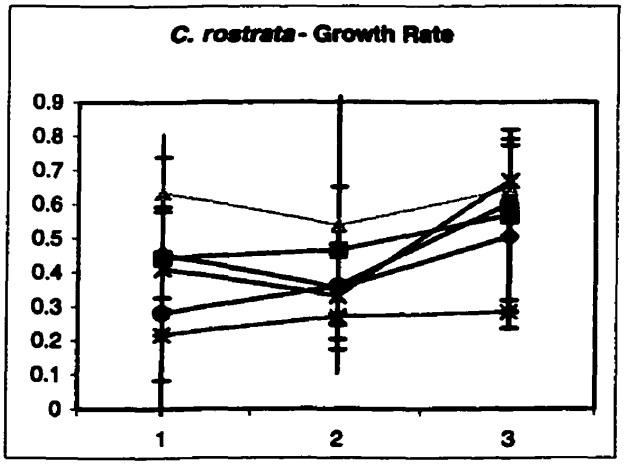
Figure 8B: Reaction norms for all species for growth rate (cm/day).











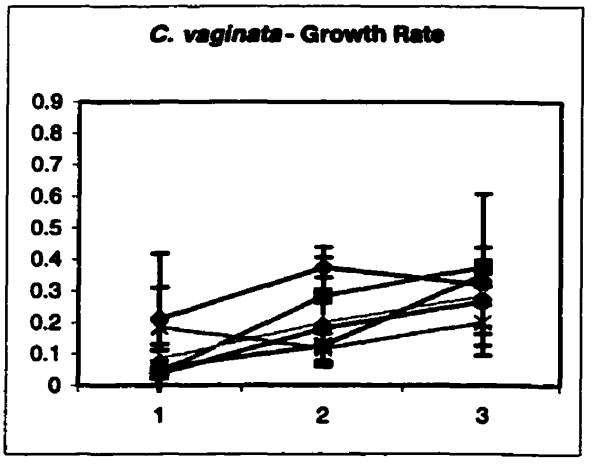


Figure 8C: Reaction norms for all species for leaf area ratio (cm^2/g)

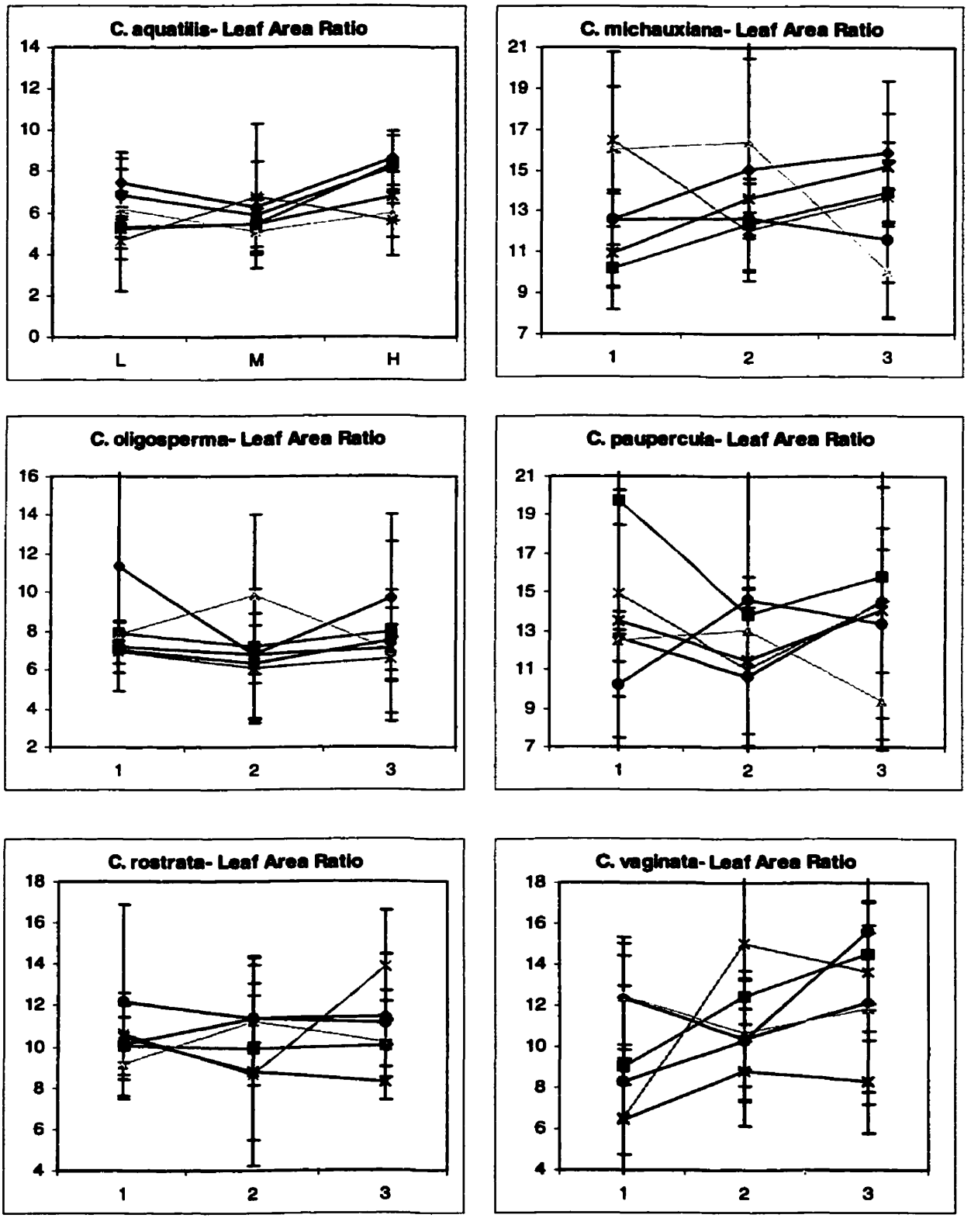


Figure 8D: Reaction norms for all species for mean leaf area (cm^2).

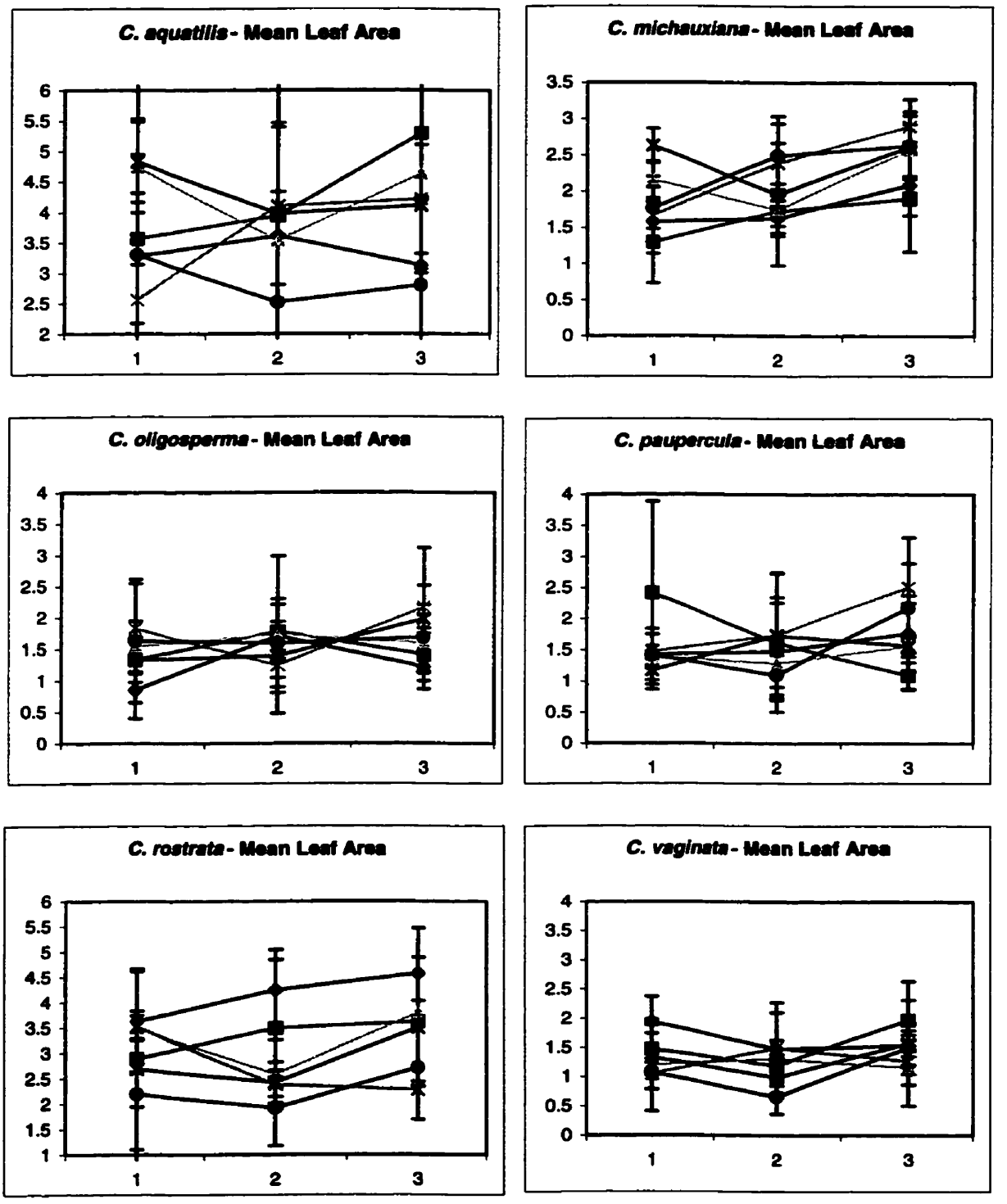
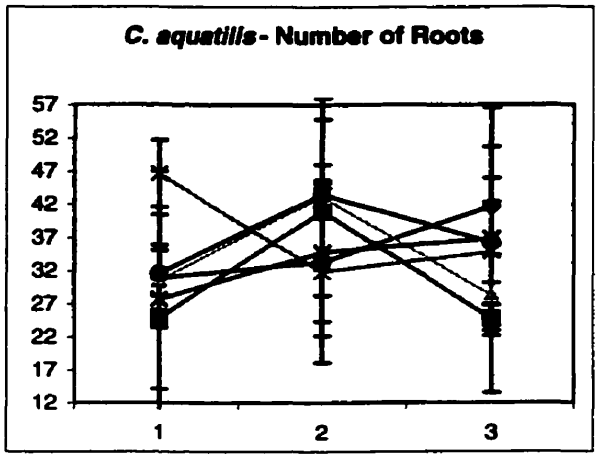
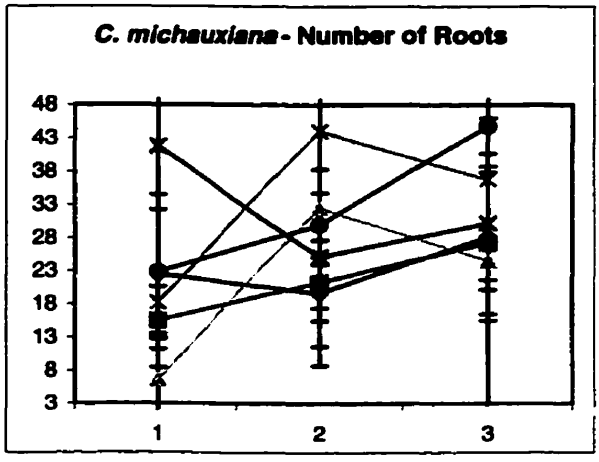
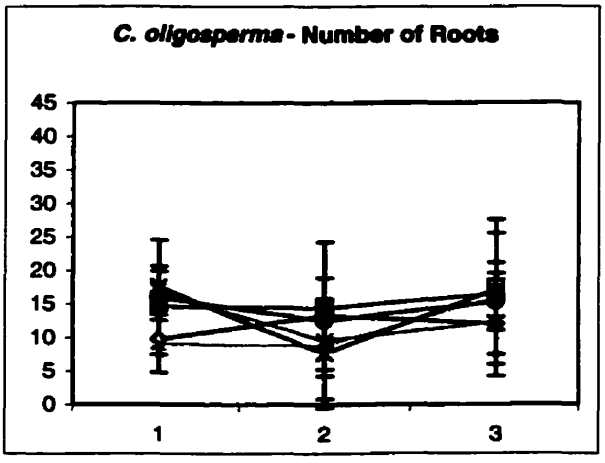
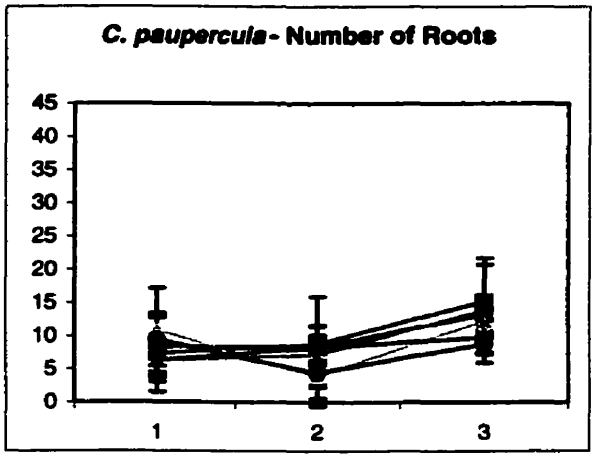


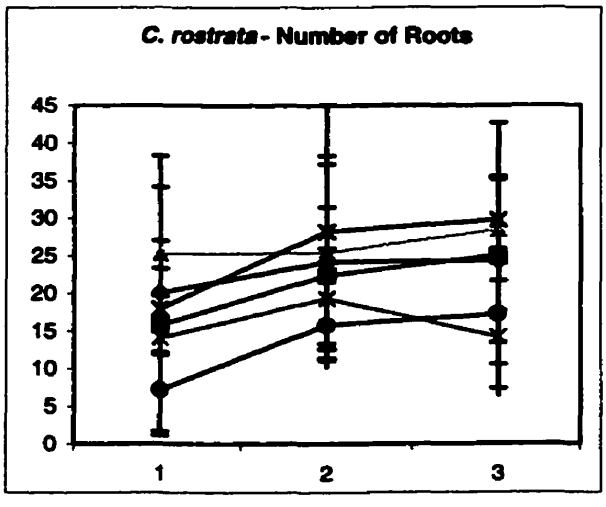
Figure 8E: Reaction norms for all species for number of roots.











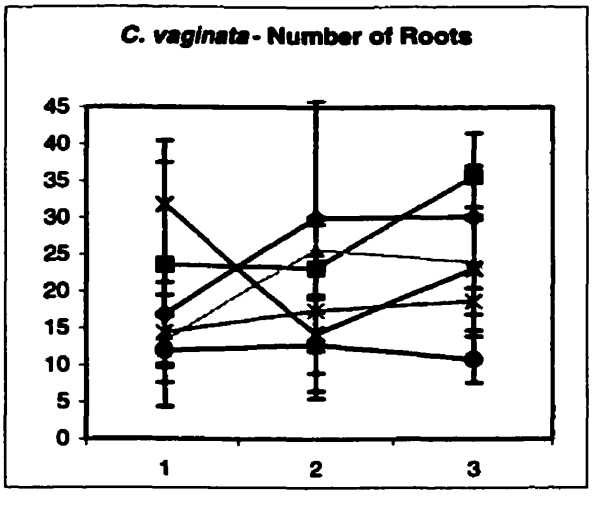
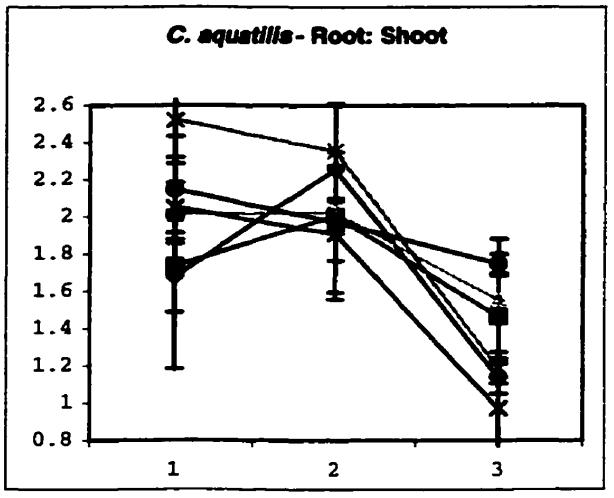
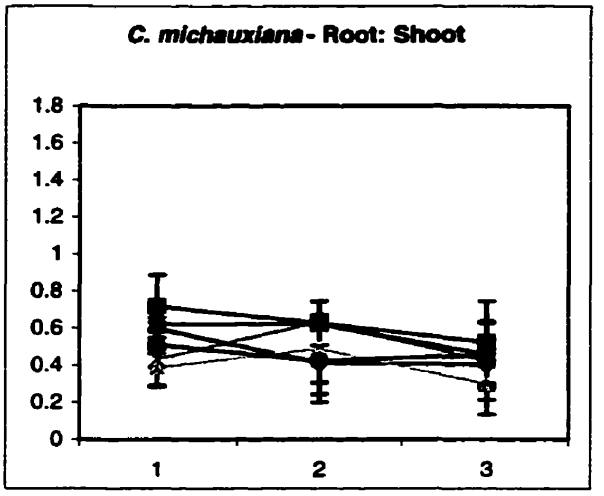
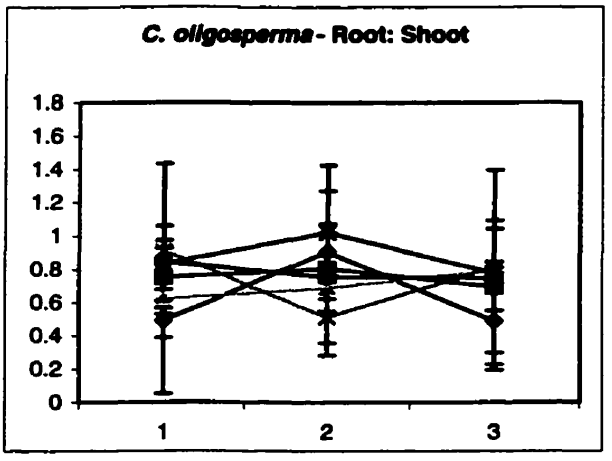
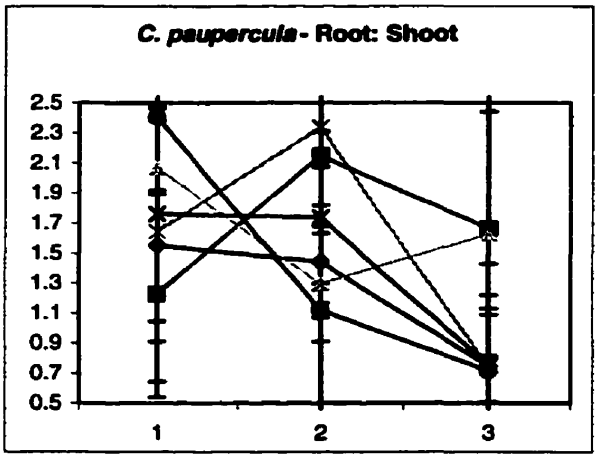


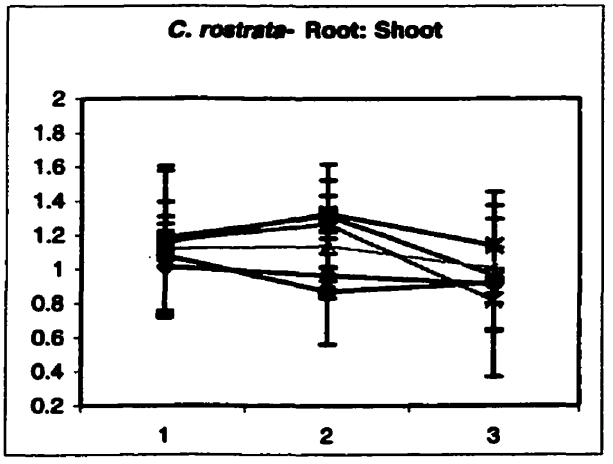
Figure 8F: Reaction norms for all species for root to shoot ratio.











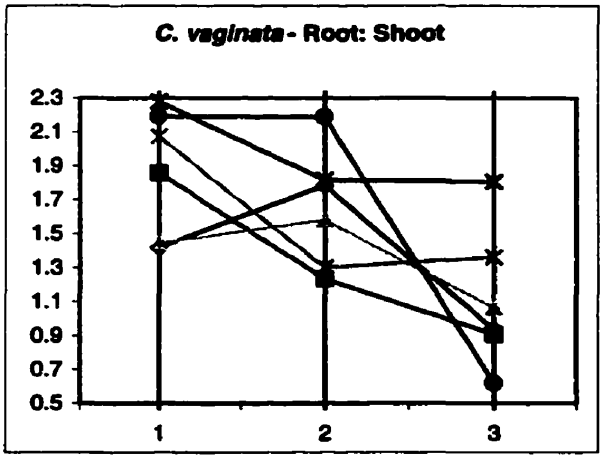


Figure 8G: Reaction norms for specific leaf area (cm^2/g).

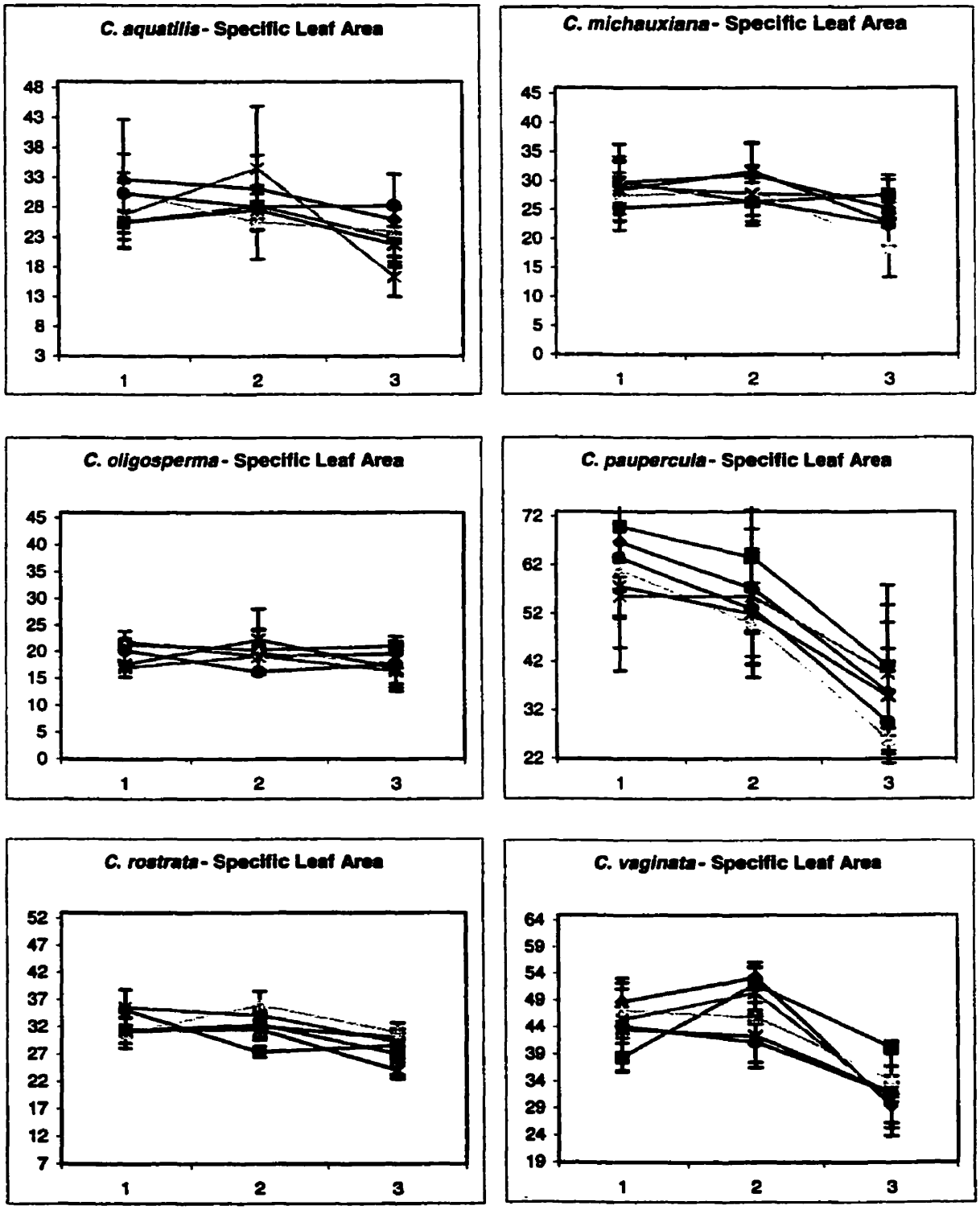


Figure 8H: Reaction norms for all species for stem diameter (cm).

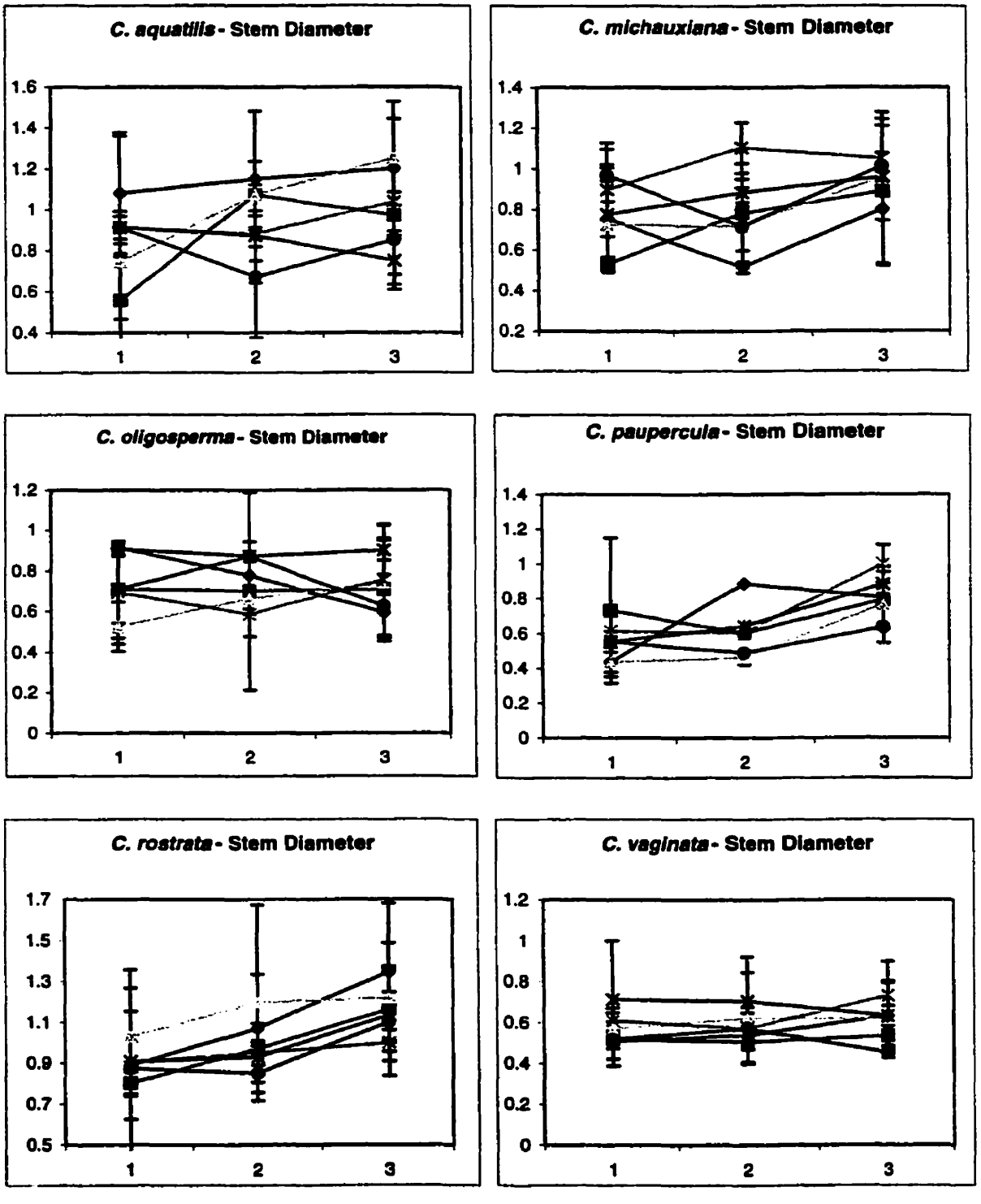
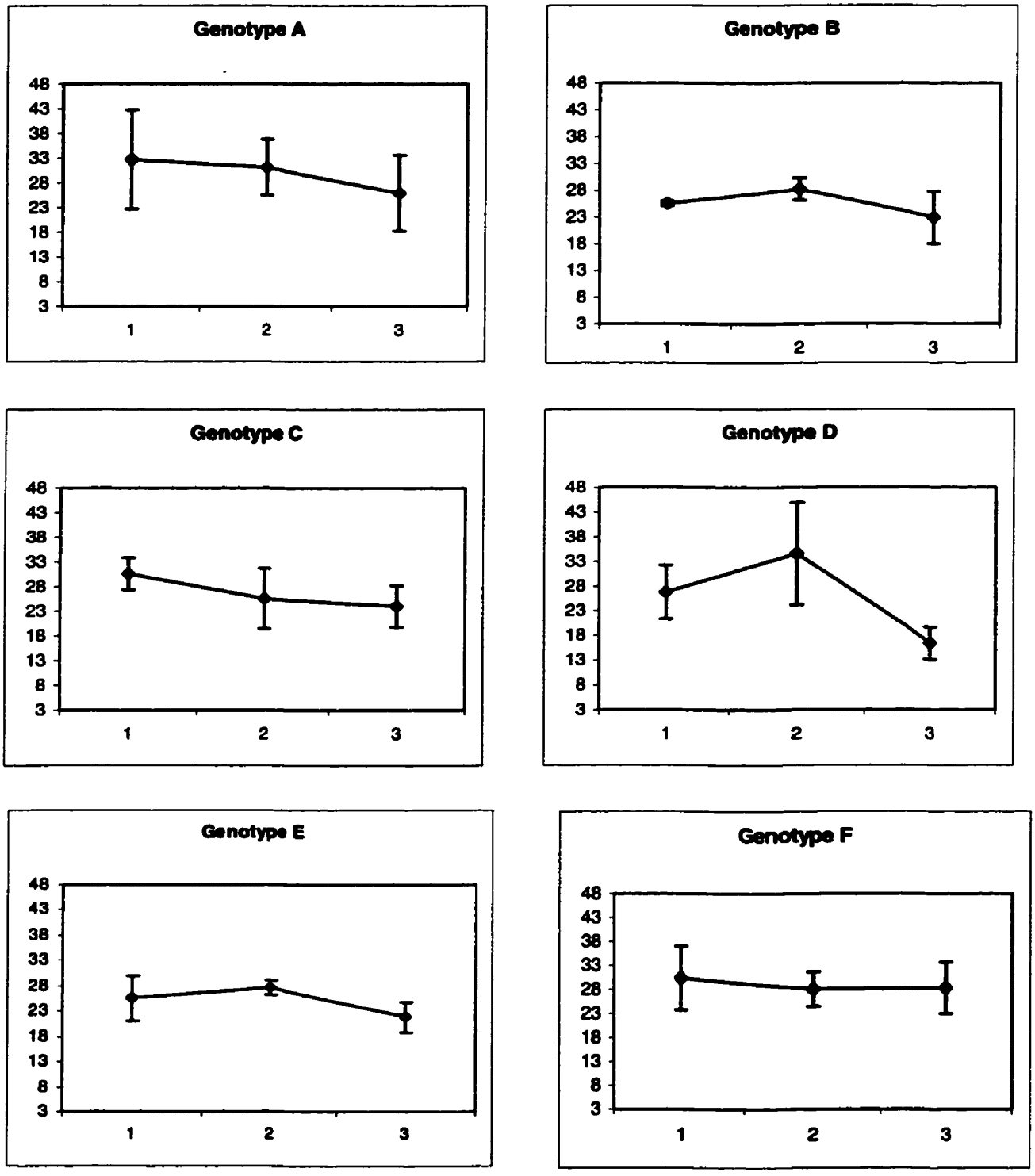


Figure 9: Separate reaction norms for specific leaf area in *C. aquatilis*, to illustrate the magnitude of the error bars.



Coefficients of Variation

There were significant differences among species in the amount of plasticity as measured by CVs for growth rate, root to shoot ratio and specific leaf area (Table 11). *Carex paupercula*, a late-invading species, had high mean CVs for the seven adaptive response variables, in six cases the highest and in the seventh case, the second highest. *Carex vaginata*, another late-invading species, had the highest mean for one variable and the second highest mean for three variables, all of which were adaptive response variables. However, for dry weight, *C. paupercula* and *C. vaginata* had the second lowest and lowest mean CV respectively. The four other species were fairly scattered in their rankings.

Table 11: Results of Kruskal-Wallis tests on genotypic coefficients of variation to determine if there were significant differences among the species for genotypic CVs. The letters under the results of the Mann-Whitney U test stand for the six species (pioneer species: *C. aquatilis* = A, *C. oligosperma* = O, and *C. rostrata* = R; late-invading species: *C. michauxiana* = M, *C. paupercula* = P, and *C. vaginata* = V). The values underneath the letters are the mean genotypic CV, a measure of amount of plasticity, for the variable indicated in the column on the left.

Variable	Kruskal-Wallis H p	Results of Mann-Whitney U Test
Dry weight	8.70 >0.05	R (56.4) O (54.2) M (47.8) A (46.0) P (45.0) V (35.3)
Leaf area ratio	12.11 >0.05	P (42.9) V (34.9) O (33.0) A (27.6) M (24.2) R (23.7)
mean leaf area	9.37 >0.05	P (40.3) O (38.0) V (36.1) R (34.3) A (30.0) M (25.9)
Number of roots	11.71 >0.05	P (55.4) M (53.2) O (50.2) R (49.7) V (41.9) A (33.1)
Root: shoot	**18.13 <0.01**	P (57.4) V (42.6) O (41.9) A (39.1) M (32.6) R (25.1)
Specific leaf area	**18.34 <0.01**	P (33.1) V (25.3) A (21.6) O (18.2) M (17.6) R (16.4)
Stem diameter	5.62 >0.05	P (28.2) A (27.3) O (27.1) M (26.6) R (21.3) V (21.0)
Tiller growth rate	**16.00 <0.01**	V (69.2) P (68.9) A (43.3) R (43.2) M (42.8) O (42.0)

Continuous-gradient experiment

The objectives of this experiment, stated in the introduction, were approached from two perspectives. First, entire plants were used as the experimental unit in order to compare overall productivity and allocation in early and late successional clones. Second, individual rhizomes and tillers were used as experimental units to look for evidence of morphological response to the water gradient.

In the analysis done using entire plants as experimental units, I expected clones from pioneer habitats would show more vigorous colonization than clones from established habitats. This would have been seen in a significant effect of site on the productivity variables: weight of rhizomes, weight of tillers, and leaf area. However in neither the *C. aquatilis* nor the *C. rostrata* experiment was such an effect seen (Tables 12 and 14). Treatment means and standard deviations can be seen in Tables 13 and 15. The effect of start position was included to determine if the overall water-table gradient was significantly affecting the productivity variables; it was never significant. There was one significant interaction between start position and site on tiller weight in *C. rostrata* (Fig. 10). The late successional clones produced a similar weight of tillers in both the wet and dry start positions while the clones from the early successional sites produced a far higher weight of tillers in the dry start position.

One allocation variable, rhizome weight/ tiller weight, was analyzed with the model using entire clones as the experimental unit. I expected that plants started in the dry position would allocate more energy towards rhizomes than shoot production compared to those in the wet position since I expected that those plants in the dry position would be spreading towards the wet end of the box. Also, an interaction was expected between start position and site whereby plants collected from pioneer sites would show a greater change in their allocation in response to the water table gradient to the two start positions than would plants from late succession sites. No significant effects were detected for this variable for either species.

Figure 10: Interaction between start position and site type on weight of tillers produced by *Carex rostrata* clones. The difference in dry weight of tillers was much larger between start positions for clones from early successional sites than for clones from late successional sites.

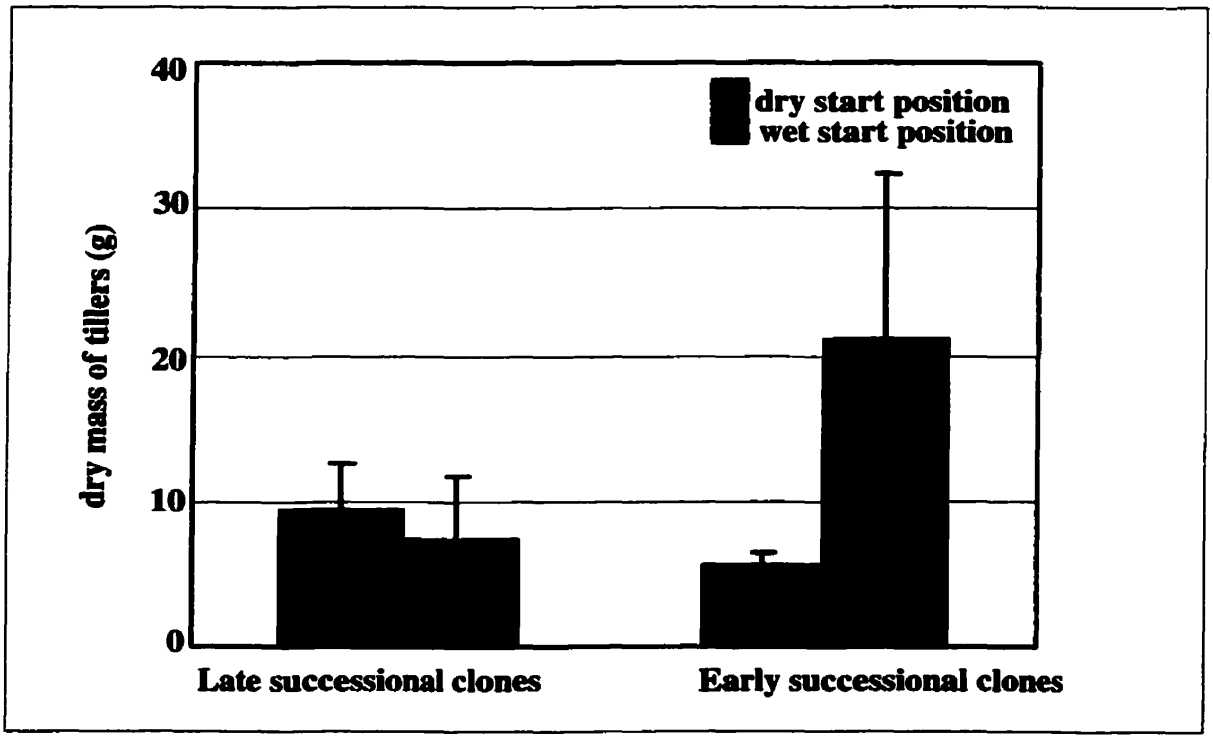


Table 12: ANOVA results using entire plant as experimental unit (*C. aquatilis*)

Variable	Site		Start position		Site * start position	
	F	Pr>F	F	Pr>F	F	Pr>F
Weight of rhizomes	0.13	0.7206	1.49	0.2458	0.00	0.9466
Weight of tillers	0.07	0.7894	0.89	0.3648	1.16	0.3030
Leaf area	0.28	0.6078	2.17	0.1664	1.19	0.2967
Rhizome wt/ tiller wt	0.23	0.6393	0.16	0.6947	1.30	0.2770

Table 13: Treatment means and standard deviations for variables using entire plant as the experimental unit. (*C. aquatilis*)

Factor	Condition	Weight of rhizomes (g)	Weight of tillers (g)	Leaf area (cm^2)	Rhiz. wt./ tiller wt. (g/g)
SP	Wet	2.365 ± 1.258	7.389 ± 2.551	614.1 ± 214.8	0.337 ± 0.173
	Dry	1.652 ± 0.887	5.872 ± 3.622	445.0 ± 234.9	0.299 ± 0.134
Site	Early Success.	2.113 ± 1.212	6.850 ± 2.404	559.8 ± 217.5	0.334 ± 0.176
	Late Success.	1.904 ± 1.081	6.411 ± 3.880	499.4 ± 261.3	0.302 ±0.131

Table 14: ANOVA results using entire plant as experimental unit (*C. rostrata*) (*=p<0.05)

Variable	SP		Site		SP*site	
	F	Pr>F	F	Pr>F	F	Pr>F
Weight of rhizomes	2.52	0.3970	0.77	0.3970	3.36	0.0919
Weight of tillers	4.08	0.0664	2.94	0.1121	5.88	0.0320*
Leaf area	3.82	0.0742	2.98	0.1097	4.73	0.0504
Rhiz. Wt./shoot wt.	0.11	0.9051	0.16	0.6960	0.08	0.7765

Table 15: Treatment means and standard deviations for variables using entire plant as the experimental unit. (*C. rostrata*)

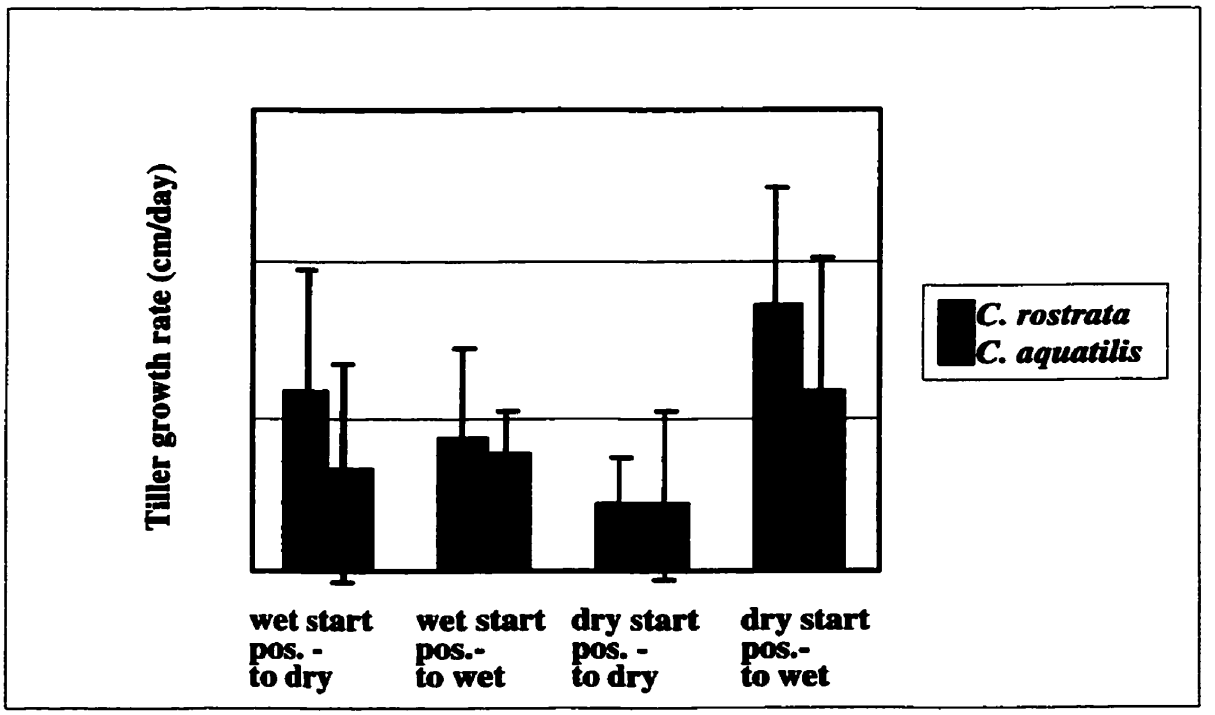
Factor	Condition	Weight of rhizomes (g)	Weight of tillers (g)	Leaf area (cm^2)	Rhiz. wt./ tiller wt. (g/g)
SP	Wet	2.279 ± 1.795	7.601 ± 2.749	737.4 ± 238.8	0.282 ± 0.141
	Dry	4.315 ± 3.459	14.537 ± 11.526	1439.3 ± 118.6	0.273 ± 0.137
SITE	Early success.	3.861 ± 3.373	14.014 ± 11.580	1398.3 ± 1163.7	0.263 ± 0.055
	Late success.	2.733 ± 2.336	8.124 ± 3.739	778.4 ± 398.0	0.293 ± 0.188

The next set of analyses used rhizomes as the experimental unit. Two variables were used to test differences: gradient distance and rhizome length divided by gradient distance. It was expected that to spread toward the water, tillers from plants that originated in the dry start position would produce rhizomes that moved farther along the gradient than those that began in the wet position. However in neither species was a significant effect of start position detected on the variable gradient distance (Tables 16-19).

There was a significant effect of direction on gradient distance for *C. aquatilis* and *C. rostrata*. The rhizomes spreading toward the wet end of the box had higher mean gradient distances than those spreading toward the dry end of the box. It was expected that rhizomes produced by plants in the dry start position would have a strong tendency to spread towards the wet end of the box, which was the case.

There was a significant interaction between direction and start position for *C. rostrata* (Fig. 11). Although the interaction for *C. aquatilis* was not significant, it is included for comparison purposes. *Carex rostrata* plants that were started at the wet end of the box produced longer rhizomes in the direction away from the water while plants started in the dry end of the box produced longer rhizomes in the direction toward the water. *Carex aquatilis* produced longer rhizomes in the direction toward the water from both start positions.

Figure 11: Interaction between start position and direction of rhizome spread on gradient length, the distance traveled parallel to the water-table gradient, of rhizomes for *Carex aquatilis* and *Carex rostrata.* The interaction is significant for *C. rostrata* only. In both species, the mean gradient distance of rhizomes spreading towards wetter conditions is longer than that of rhizomes spreading toward drier conditions.



Rhizome length/ gradient distance was analyzed because it gives an indication of the directness of the path taken by the rhizome. When a rhizome travels parallel to the water gradient, this ratio is equal to one; for every centimeter the rhizome spreads, it moves a centimeter along the gradient. It was expected that this might change with direction, *i.e.* that the rhizome might take a more direct path when moving in the direction of increasing water. No factors significantly affected this variable.

Table 16: ANOVA results using rhizomes as the experimental unit (*C. aquatilis*) (*=p<0.05)

Variable	Site		SP		Direction		SP*direction	
	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F
Gradient dist.	0.57	0.4549	0.45	0.5035	5.19	0.0270*	3.36	0.0718
Rhiz. len./gradient	0.57	0.4553	0.01	0.9341	2.18	0.1963	0.04	0.8448

Table 17: Treatment means and standard deviations for variables using individual rhizomes as the experimental unit. (*C. aquatilis*)

Factor	Condition	Gradient distance	Rhiz. Len./Gradient Dist
SP	Wet	14.25 ± 10.12	2.61 ± 5.27
	Dry	17.41 ± 16.68	3.65 ± 7.82
Site Type	Early success.	12.25 ± 11.30	3.06 ± 5.91
	Late success.	18.80 ± 13.63	2.77 ± 6.41
Direction	To dry extreme	11.94 ± 13.77	4.50 ± 9.04
	To wet extreme	17.97 ± 11.29	1.72 ± 1.05

Table 18: ANOVA results using rhizomes as the experimental unit. (*C. rostrata*) (**=p<0.01; *=p<0.05)

Variable	Site		SP		Direction		SP*direction	
	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F
Gradient	0.09	0.7617	0.17	0.6815	8.13	0.0057**	21.12	0.0001**
Rhiz.len./gradient	0.07	0.7967	2.43	0.1233	3.39	0.0700	2.80	0.0988

Table 19: Treatment means and standard deviations for variables using individual rhizomes as the experimental unit. (*C. rostrata*)

Factor	Condition	Gradient distance	Rhiz Len/ Gradient Dist
SP	Wet	20.67 ± 14.73	2.21 ± 2.23
	Dry	27.25 ± 17.93	4.28 ± 13.01
Site	Early success.	23.16 ± 16.25	4.03 ± 12.97
	Late success.	27.54 ± 17.98	2.63 ± 2.91
Direction	To dry extreme	16.10 ± 14.65	6.35 ± 16.58
	To wet extreme	30.17 ± 16.07	1.79 ± 1.43

The final set of analyses for this experiment was done using tillers as experimental units. Two variables were analyzed using this model: stem diameter and tiller growth rate. There were two main effects in the model: zone (as in Fig.4), and site type. Due to lack of sufficient spread of the plants across the water table gradient, only data from zones II and IV could be used. These were the zones in which the plants had been originally planted and these zones were the only two with enough replicates from each clone to be included in the analysis. I used this model to determine: first, if the water table gradient was sufficient to affect morphological response of the tillers, and second, if this response was greater in the clones from early successional sites.

Growth rate was expected to be higher in the wet zone since previous experimental evidence demonstrated that accelerated shoot growth is an adaptive response to flooding (see references in Introduction). Growth rate in *C. aquatilis* was not

significantly affected by zone (Table 20), although the mean growth rate in the wetter zone (II) was higher than in the drier zone (IV) (Table 21). However, interaction between zone and site type was significant (Figure 12). Clones from early and late successional sites showed opposite response to the water table gradient. The late successional clones decreased their growth rate slightly in the wetter zone, the opposite of the predicted response. The early successional clones showed a larger response to the water table gradient, and in the expected direction. Stem diameter was expected to be larger in the wet zone since facultative formation of aerenchyma in roots, stems and leaves is a common response to flooding (see references in Introduction). Mean stem diameter in *C. aquatilis* was smaller in the wetter zone, the opposite of the expected results; however, the difference was not significant. The interaction between site and zone was also not significant.

Table 20: ANOVA results using tillers as experimental unit. (*C. aquatilis*)
(* = $p<0.05$; **=$p<0.001$)

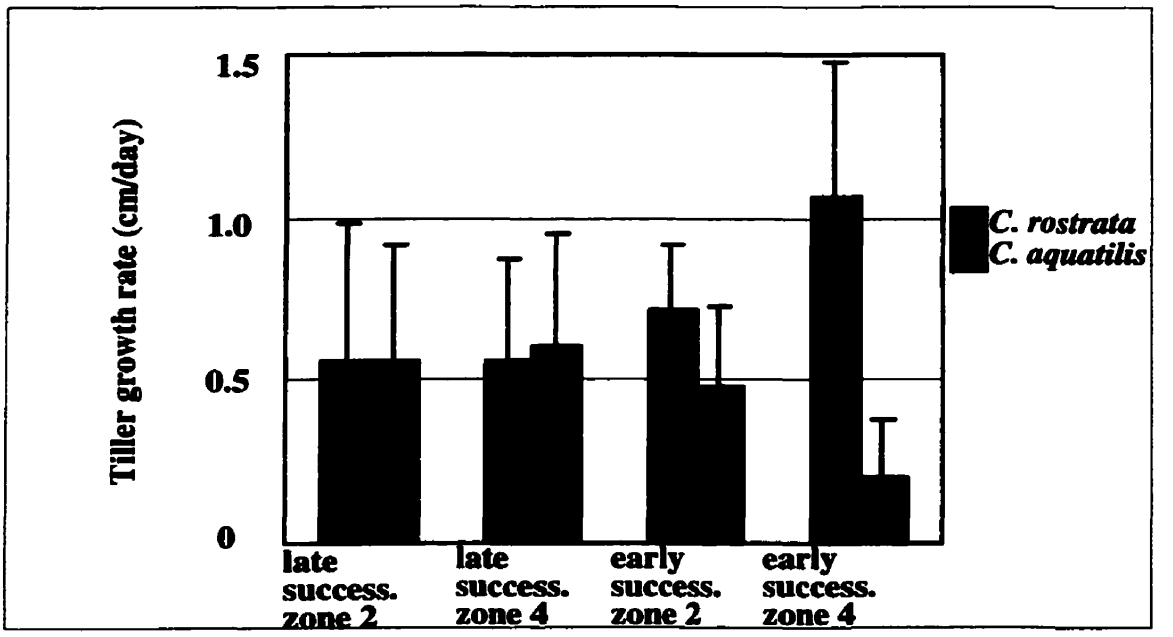
Variable	Site		Zone		Site * Zone	
	F	Pr>F	F	Pr>F	F	Pr>F
Growth rate (cm/day)	12.07	0.0009**	3.07	0.0841	5.46	0.0223*
Stem Diameter (cm)	4.17	0.0432*	0.71	0.4023	0.00	0.9641

Table 21: Treatment means and standard deviations for variables using tillers as the experimental unit. (*C. aquatilis*).

	Wet Zone (2)	Dry Zone (4)
Growth Rate (cm/day)	0.52 ± 0.31	0.34 ± 0.31
Stem Diameter (cm)	0.42 ± 0.14	0.44 ± 0.17

Stem diameter for *C. rostrata* was strongly affected by the zone in which the tillers emerged and the response was in the expected direction, with higher stem diameter

Figure 12: Interaction between zone of tiller emergence and site type on tiller growth rate for *C. aquatilis* and *C. rostrata*. The interaction was significant for both species. In both species the difference in growth rate between the two zones was much larger in the pioneer clones.



in the wet zone (Tables 22 and 23). Tiller growth rate was also significantly affected by zone in *C. rostrata*, however the response was opposite to the predicted direction. The interaction between site and zone was significant as well (Fig. 12).

Table 22: ANOVA results using tillers as experimental unit.
(* = p<0.05; **=p<0.001) (*C. rostrata*)

Variable	Site		Zone		Site * Zone	
	F	Pr>F	F	Pr>F	F	Pr>F
Growth rate (cm/day)	3.86	0.2996	4.43	0.0381*	4.60	0.0346*
Stem diameter (cm)	0.13	0.7220	11.61	0.0008**	0.66	0.4193

Table 23: Treatment means and standard deviations for variables using tillers as the experimental unit. (*C. rostrata*)

	Wet Zone (II)	Dry Zone (IV)
Growth Rate (cm/day)	0.62 ± 0.37	0.85 ± 0.45
Stem Diameter (cm)	0.57 ± 0.18	0.49 ± 0.14

The porosity data were analyzed separately from the rest of the continuous gradient data. In this case the treatment levels were simply the extreme wet end of the box versus the extreme dry end of the box. There was a significant effect on the percentage porosity for roots and rhizomes in *C. aquatilis* (Table 24). Porosity was higher, in both cases, in the wet end of the box (Table 25). Roots and rhizomes of *C. rostrata* in the wet end of the box had a slightly higher mean porosity than those in the wet end of the box (Table 24), but the difference was not significant (Table 25).

Table 24: ANOVA results for root and rhizome porosity. (*=p<0.05)

	Roots		Rhizomes	
Species	F	Pr>F	F	Pr>F
C. aquatilis	6.77	0.0151*	8.64	0.0135*
C. rostrata	0.01	0.9164	0.40	0.5431

Table 25: Treatment means for root and rhizome porosity (%).

	Water-table	Roots	Rhizomes
C. aquatilis	High	24.62 ± 5.15	25.66 ± 8.35
	Low	19.13 ± 6.05	15.32 ± 4.47
C. rostrata	High	21.63 ± 5.30	26.23 ± 5.10
	Low	21.40 ± 5.50	24.28 ± 4.80

DISCUSSION

Plasticity Experiment

The goal of this experiment was to determine if pioneer species of *Carex* exhibited greater plastic response to a water-table gradient than did late-invading species of *Carex* when the genotypes from both groups of species were collected from mature fens. The rationale for expecting greater plasticity in pioneer species is that the pioneer habitats of interest in this study are more variable, both spatially and temporally, in water-table gradient than are the established habitats. Since the variability is effective within the lifespan of a single generation, it is likely that there is selection pressure in these habitats for phenotypic plasticity.

Environment Main Effects

The eight response variables measured in the plasticity experiment fall into two categories, which will be discussed separately. Seven of the variables indicate physiological and morphological adjustments made by the plants in response to the water-table levels. The eighth variable, dry weight, is the only feasible estimator of fitness for this experiment. The time frame of the experiment was not conducive to the use of variables related to sexual reproduction as estimators of fitness. Shoots of *C. rostrata* require 18 - 24 months to flower depending on the season of emergence, and *C. aquatilis* shoots require 12 - 18 months (Gorham and Somers, 1973). Furthermore, northern species of *Carex* have been shown to have specific temperature and photoperiod requirements for flowering (Heide, 1997). Since the replicates in the experiment were blocked in time as well as in space, it was important to keep light and temperature conditions constant throughout the experiment. During the experiment less than 10% of the plants flowered, and 90% of the flowering plants were of the same species (*C. michauxiana*).

Number of tillers produced has been used as an estimator of fitness in other studies using perennial plants (Thompson et al., 1991c). This did not seem appropriate for this experiment since the number of tillers varied little across the treatments; in 87% of cases the number of tillers fell between 0 and 3. In addition, because the originally planted tillers continued to grow, total dry weight of the entire plant at harvest, with fresh weight of the original plant as a covariate, was a more accurate estimator of fitness.

The pattern of treatment means for the functional response variables was similar across the six species. The variables, leaf area ratio, mean leaf area, stem diameter and tiller growth rate, were expected to increase as water-table levels rose, for the reasons outlined in the introduction. In 20 of 24 cases, *i.e.*, four variables measured in six species, the mean value of these variables was higher in the wet treatment than in the dry treatment. The four cases in which the opposite was true occurred in three different species. The ranking of the medium treatment was variable. One of the variables, root to shoot ratio, was expected to decrease with increasing water-table level. In all six species the mean response was lower in the wet treatment than in the dry treatment, although again the ranking of the medium treatment was variable. This indicates that the plants in the experiment responded to the differences between the environments.

The environment main effect was never significant for total dry weight. This finding supports the notion that traits that underlie fitness, *i.e.* traits that enable the plants to survive and reproduce in a variety of conditions, tend to be plastic, and as a result of this, traits that estimate fitness are stable. In other words, plasticity in functionally adaptive traits allows for stability in components of fitness (Marshall et al., 1986; Bell, 1997).

Genotype by Environment Interactions

A surprising result of this experiment was the lack of significant G X E effects. The *p* values for the interaction term in the model were uniformly high; in only six of forty-eight cases were the values less than 0.1. This was unexpected, especially given that the genotypic lines in the reaction norms cross each other extensively which is normally indicative of significant interactions. It is important then to determine if G X E interactions were not detected due to flaws in the experiment.

There are several possible experimental flaws that may have contributed to the lack of significant interactions. It may be that the range of treatment levels was not sufficiently broad to allow for heritable plasticity to be detected. This is unlikely for several reasons. First, the range of water-table levels used in the experiment, -35cm to 5cm, is comparable to the range that the persistent pioneers encounter in natural conditions. Second, the environment main effects were significant 31.3% of the time, or 35% of the time if only the seven variables that were expected to be affected by the

treatment are considered. The pertinent question then becomes: is this percentage high enough to safely conclude that the treatment levels affected the physiology and morphology of the tillers? To answer this question, I compared the percentage of significant environment main effects found in this study to the percentage found by other researchers who did comparable experiments (Table 26). The percentage found in this study falls within the range found in the other experiments, in most of which significant G X E interactions were found. Finally, as previously mentioned, the species responded in similar, predictable directions on the variables measuring adaptive response, indicating that the treatments were effectively different.

The magnitudes of the error bars around each point on the norms of reaction are considerable and the error bars cross extensively (Figs. 8 and 9). Each of these points is the mean of three replicates of a single genotype in a single environment, so the error bars illustrate the within-genotype, within-environment variance or error variance. The genotypic lines on the norms of reaction cross extensively which normally indicates a significant interaction, but it appears in this case that the error variance is too large to allow the interaction to be detected. The magnitude of the error bars is due, in part, to the variability among the three blocks. Due to heterogeneous conditions in the greenhouse, the three blocks were under different light and temperature conditions and plant growth responded to these differences (Fig. 7). However the block effects are not the cause of insignificant interaction effects because block, when significant, was included as a factor in the model. Furthermore, large error bars do not always coincide with significant block effects for the 48 norms of reaction. There are many cases where, for a given variable, the error bars are larger in species with non-significant block effects than in species with significant block effects, for example dry weight in *C. aquatilis* versus dry weight in *C. oligosperma*. There must therefore have been another source of within-environment, within-genotype variability that was not factored into the model.

Table 26: Percent significant E and G X E effects found in previous plasticity experiments.

Authors	% sign. E effects	% sign. G X E effects
Andersson and Shaw, 1994	93.3	26.7
Heathcote et al., 1987	20	0
Hermanutz and Weaver, 1995	70.6	23.5
Macdonald et al., 1988	100	100
Nicotra et al., 1997	16.7	16.7
Schlichting and Levin, 1984	33	N/A
Sultan and Bazzaz, 1993a	100	40.9
Sultan and Bazzaz, 1993b	85	11.1
Sultan and Bazzaz, 1993c	72.7	0
Taylor and Aarssen, 1988	100	83.3
This study	27.1	0

The substrate, a natural peat source harvested from a local bog, was possibly an unintended source of variance. The peat was mixed prior to use in the experiment, but because a large volume was used, 1,145 L, perhaps the mixing was not sufficient to fully homogenize the large volume of peat. If this was the case, then the tubes may have not received uniform substrate and factors such as within-tube nutrient levels may have varied from tube to tube. This variation would have been randomly distributed with respect to the treatments and blocks. This would result in an increase in variability among the replicates that was impossible to factor into the model.

The species in this experiment were very responsive to increased nutrients during the propagation period (Gold, unpublished data). More specifically, *C. rostrata* has been shown to respond to addition of nitrogen and phosphorus with an increase in the rate of tillering as opposed to an increase in the growth of pre-existing tillers (Solander, 1983). *Carex aquatilis* responds to addition of nitrogen, phosphorus and potassium with an increased rate of tillering and an increase in leaf mass per tiller (Shaver and Chapin, 1995). Responses such as these would have an effect on the variables measured in the plasticity experiment. An increase in leaf mass per tiller would affect leaf area ratio,

specific leaf area and possibly the mean leaf area. Growth rate, which was measured on the first tiller to emerge, may have been slower in plants subject to a higher nutrient level since they were likely producing more tillers at a time than plants with lower nutrients. A decrease in root to shoot ratio as a response to an addition of nutrients has been demonstrated in many plant species (Zangerl and Bazzaz, 1983; Natr, 1988; Sultan and Bazzaz, 1993c). If this hypothesis of variable nutrient levels in the tubes is correct, not only was there a source of variance in the experiment that could not be factored out, but it is a source of variance that has a direct effect on the variables being measured.

An additional probable source of variance was tiller age. It was necessary to conduct this experiment starting with tillers rather than seeds in to eliminate variability in the genotype factor. Tillers culled from the mother plants being propagated in the greenhouse were chosen to be as uniform in size as possible, the assumption being that size is strongly correlated with age. However, since nine tillers were required per genotype, three at each of three different plantings, it was impossible to ensure that the tiller sizes be completely uniform. The coefficients of variation for initial tiller height ranged from 26.2 to 37.4 for the six species. Variance in response, caused by variation in tiller age, would add to the within-environment, within-genotype variance. Since evidence for G X E variance is provided by the extensive crossing of the genotypic lines on the reaction norms, the lack of significant G X E interaction effects is probably due to the large error variance caused by unintended and unavoidable sources of variation.

Differences in response between pioneer and late-invading species

The results provide several ways to compare phenotypic response in the two groups of species, including the proportion of significant environment main effects per species, the coefficients of variation, and the norms of reaction. I will discuss each in turn.

As mentioned in the literature review, the among-environment variance can be viewed as an estimate of phenotypic plasticity (Marshall and Jain, 1968). While it is true that this measure ignores any heritable component of plasticity, it does reveal the extent to which genotypes make phenotypic adjustments to the environment. Therefore a species with a greater number of significant environment main effects can be said to exhibit

greater plasticity than a species with fewer significant effects (Moran et al., 1981; Nicotra et al., 1997).

Coefficients of variation (CVs) have also been used as a measure of plastic response (Schlichting and Levin, 1984). CVs were calculated per genotype in order to examine the responsiveness at a genotypic level, while the environment main effects indicate responsiveness at the species level. These two sets of results, the proportion of significant environment main effects per species and the genotypic CVs, point to a higher phenotypic response in the late-invading species.

Andrus et al, (1983) provide an example in which bog species growing at low water-table levels have broader ranges of tolerance to water- table gradients than species growing at high water-table levels. The authors classified species of *Sphagnum* into those dominant on hummocks and those dominant on hollows. They found that hummock-dominant species had a broader vertical distribution along the gradient than did hollow-dominant species. They attributed this difference to relatively narrower tolerance of hollow species to the dry extreme of the hummock-hollow gradient. This division into hummock-hollow species is applicable to the *Carex* species used in the plasticity experiment. Although the pioneer species in this study were able to persist in drier, established habitats, within these habitats they tend to be found in hollows and depressions (Foster and King, 1984). *Carex paupercula*, a late successional species, is often found in hollows and depressions, but never in pools of water as are the pioneer species (Vitt and Slack, 1975). *Carex vaginata* is commonly found in boggy, spruce forests (Gleason and Cronquist, 1991), usually on hummocks (pers. obs.). *Carex michauxiana* is found on hummocks (pers. obs.) in wet meadows (Gleason and Cronquist, 1991). The larger plasticity seen in the late-invading species may be due to a lower tolerance of the pioneer species to the dry end of the water-table gradient.

The norms of reaction reveal similar patterns of response for the six species. The genotypic lines in the norms of reaction cross extensively for all species for all variables. Although certain species show visibly steeper response on some variables, for example *C. aquatilis* and *C. vaginata* for root to shoot ratio and *C. paupercula* for specific leaf area, these steeper responses are evenly distributed over the two groups of species. Thus

the norms of reaction do not indicate differences in response between the two groups of species.

The three sets of results in combination indicate that it is certainly not the case that the pioneer species had a higher plastic response to the water-table gradient than the late successional species. Other researchers, using similar means of comparison, have found no difference between early and late successional species. Moran et al., (1981) compared phenotypic plasticity in four races of *Xanthium strumarium* that differed in their colonization ability. They found no difference in environmental variance in response to a series of environments designed to represent the range of conditions that the races would encounter in natural conditions. They concluded that the ability to colonize was not related to phenotypic plasticity in this species but rather to differences in reproductive strategies. Similar results were found by Nicotra et al. (1997), who compared plasticity in response to a light gradient in two *Piper* species, one that invades forest gaps and the other that grows under the canopy of the mature forest. Their measures of plasticity included percent of traits measured with significant environment or G X E effects, magnitude of CVs and F ratios. No differences were seen in the plastic response of the two species based on these measures.

For successional sequences in which it is readily shown that early successional habitats are more variable than late successional habitats, the comparison between the plastic response of plants in these two habitat types is no different from the comparison between plants in any environmentally stable and variable habitats. Heathcote et al. (1987) compared plastic response to a flooding gradient of nine populations of *Carex flacca* that were collected from sites that differed in their flooding frequency. As in this study, all the plants in their experiment survived in all of the experimental conditions, and yield at harvest was not significantly affected by the treatments. Furthermore, the nine populations did not differ in response to the treatment. In another study that examined response to soil moisture, Sultan and Bazzaz (1993b) found no difference in the response among populations of *Polygonum persicaria* from habitats that differed in both amount and variability of soil moisture.

In response to other environmental factors such as soil toxicity, soil pH, nutrients and light, no difference has been found in species and populations of differing ecological

backgrounds by various researchers (McNaughton et al., 1974; Gibson and Risser, 1982; Nixon and McMillan, 1964; Ashmun and Pitkela, 1985; Sultan and Bazzaz, 1993a,c). In most cases, the lack of difference in response was attributed to lack of genotypic differentiation (applicable to comparison of populations only) and broad ecological tolerance of the genotypes. This may partially explain why the pioneer species did not exhibit a larger plastic response than the late-invaders. Although pioneers are subject to a far greater range of water-table levels under natural conditions than the late-invaders, the late-invaders do experience variability in water-table level in the established fen. Even within a mature fen, pools form and dissipate over time and while the late invaders do not survive and persist in the pools themselves, they are subject to the resulting fluctuations in moisture around the pools. This may result in broadly tolerant genotypes.

The design of this experiment called for all of the species to be collected from sites of approximately equal successional status because of the desire to control for site effects. Thus all species were collected from late successional sites. As discussed above, Gray (1984) has proposed that the reduction of the number of genotypes may be a feature of many successional sequences due to selection for biotypes that can survive in competitive conditions by aggressive vegetative reproduction.

Evidence for the biotype depletion hypothesis was found in a study that compared pioneer and established populations of *Carex lasiocarpa* (McClintock and Waterway, 1993). Higher genotypic diversity and smaller mean clone size was found in early successional sites than in established fens, bogs and woodlands. Since *C. lasiocarpa* is congeneric with the species used in this study and co-occurs with some of them in southern habitats, it is reasonable to expect that processes that affect *C. lasiocarpa* during succession, also affect the pioneer species in this study. If the biotype depletion hypothesis is applicable to the pioneer species in this study, than the relatively high proportion of phenotypically plastic genotypes in the population that result from selection pressures in variable pioneer habitats may be offset by the decline in number of genotypes throughout the successional sequence. Since this decline in genotypes is thought to result from selection pressure for genotypes that can compete with both other clones of the same species and clones of different species, perhaps genotypes that are

highly adapted to variable abiotic conditions are disfavoured as the succession sequence progresses.

In summary, the finding that pioneer species did not have a greater response to the water-table gradient in this study may be attributable to two factors, the existence of genotypes in both groups of species that are broadly tolerant of a wide range of ecological conditions, and the reduction in the number of genotypes of the pioneer species throughout the successional sequence.

Continuous-gradient experiment

While the purpose of the plasticity experiment was to make inter-specific comparisons in plastic response, the continuous-gradient experiment was designed to make intra-specific comparisons of morphological response of clones that originated from early and late successional sites. It was neither designed nor analyzed as a plasticity experiment. Although the same eight genotypes were planted at the high and low water-table start positions, the genotypes were not replicated. There were two specific goals of the experiment. First, to determine if there was a difference in extent of colonization between clones originating from the two types of sites. Second, to determine if the water-table gradient significantly affected morphological response of the clones and if so, if this response differed in clones from the two site types.

Extent of colonization

Colonization was measured on a per plant basis. The extent to which a clone colonized the experimental area was based on productivity variables: weight of rhizomes, weight of tillers and leaf area per clone. In other words, success of colonization was determined by the amount of biomass a clone could produce in the experimental area, given the water-table gradient. The extent of colonization did not significantly differ between early and late successional clones of either species.

Morphological response to the water-table gradient

Before considering whether there were differences in the response of early and late successional clones to the water-table gradient, it is important to consider whether the water-table gradient was sufficiently large to cause any significant morphological response to any of the experimental plants.

It was expected that the porosity of roots and rhizomes would be higher at the wet extreme of the water-table gradient than at the dry extreme since facultative formation of aerenchyma is a well-documented response to flooding (see references in Introduction). A significant effect of water-table gradient on porosity in both roots and rhizomes was detected in *C. aquatilis*, and the response was in the expected direction. This indicates that the tillers at the wet extreme of the water-table gradient were under conditions that were more anaerobic than tillers at the dry end of the gradient, *i.e.* that the two ends of

the box were effectively different. Response was also in the expected direction for *C. rostrata*, but the difference was not significant.

The effect of the zone in which the tillers emerged, on growth rate and stem diameter also provides an indication of whether the water-table gradient caused a significant morphological response. Stem diameter was measured as an index of aerenchyma production. It was expected that tillers emerging in the wet end (zone II) of the gradient would have larger stem diameters because of greater need for aeration. Stem diameter was significantly affected by zone in *C. rostrata*; the response was in the expected direction. Stem diameter was not significantly different in the two zones for *C. aquatilis*. Thus there is evidence in both species that the water-table gradient caused anaerobic stress: root and rhizome porosity were significantly affected in *C. aquatilis* while stem diameter was significantly affected in *C. rostrata*.

The effect of zone on growth rate was significant for *C. rostrata*; however, the direction of response was unexpected in that growth rate was significantly faster in the dry end of the box. Plants that were started in the dry position produced fewer tillers than plants that were started in the wet position. This may be the reason for the unexpected response: a plant from which several tillers are simultaneously growing would be expected to have a slower growth rate than a plant from which only one other tiller is growing.

Habitat preference as a response to the water-table gradient

Phytosociological studies in Labrador have shown that, within fens and bogs, *C. aquatilis* and *C. rostrata* are found most frequently in hollows and depressions (Foster and King, 1984) and on low ridges, wet sedges lawns and in deep pools (Foster et al., 1988). Given these findings, I expected both species to show a habitat preference for the wet end of the gradient. Two results indicate this preference. First, the effect of direction on gradient distance (distance traveled along the water-table gradient) was significant in both *C. aquatilis* and *C. rostrata*; in both species, rhizomes oriented towards increasing water depth tended to move farther along the gradient than did rhizomes oriented towards decreasing water depth. Only rhizomes that produced a tiller were included in this analysis because it was impossible to determine the orientation of rhizomes that were not anchored by a tiller during harvest. The movement of all of the rhizomes included in this

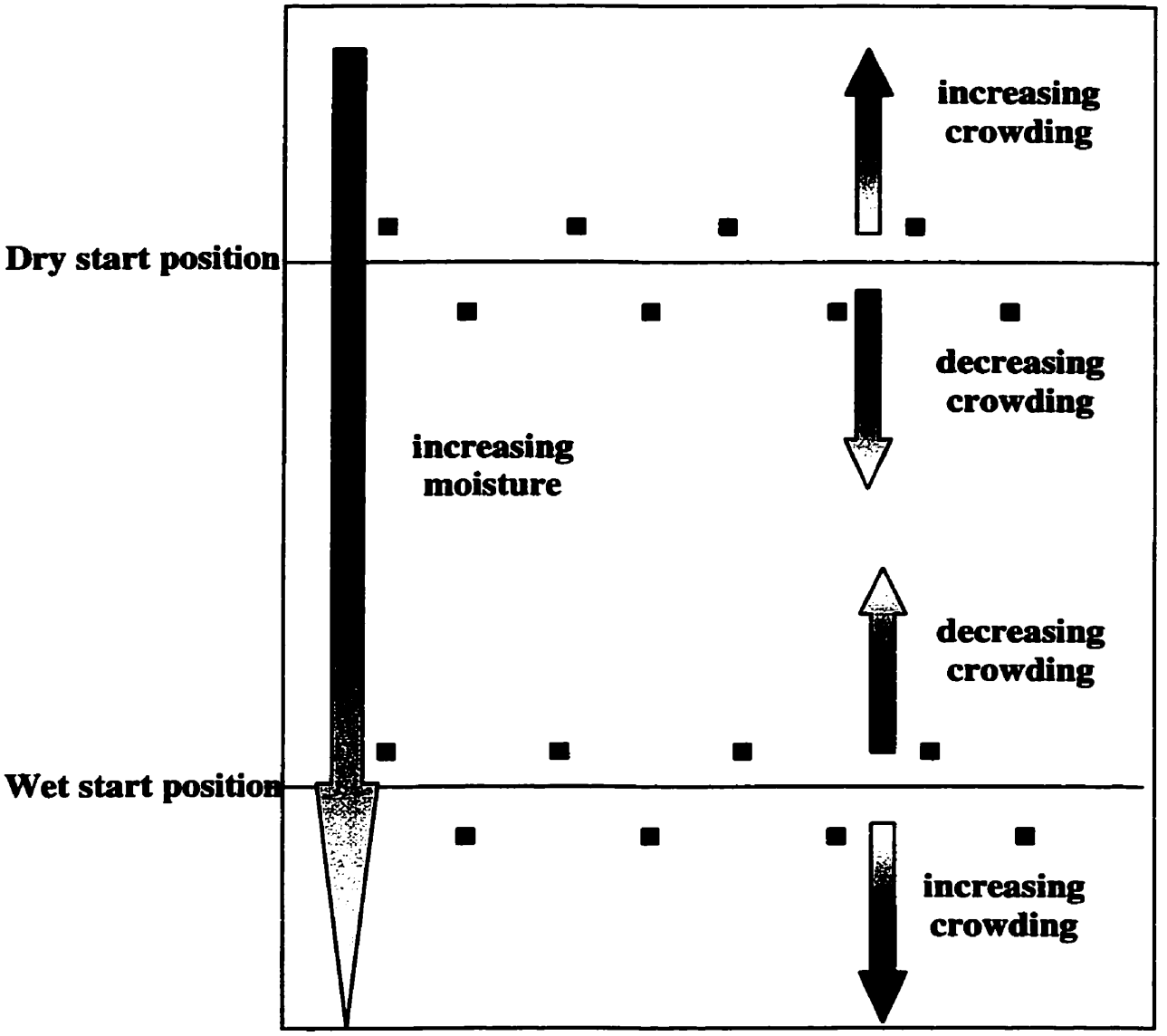
analysis therefore resulted in the placement of a tiller at a new position along the water-table gradient. Thus this significant result indicates a preference for placing tillers in moist conditions.

The second result that indicates habitat preference in this experiment is the interaction between start position and direction of rhizome spread on gradient distance, which was significant in the *C. rostrata* experiment (Fig. 11). In both species there was a strong tendency for plants in the dry start position to spread toward the wet conditions. In spreading toward the wet conditions, not only are the rhizomes moving towards a more favorable position along the water-table gradient, they are also spreading into an area of lower tiller density. Recall that the two originally paired planted rows of shoots were only 60cm from their respective ends of the box while the two sets of rows were 120cm apart. Therefore the area of lowest tiller density was, initially, between the two rows. In both species the mean gradient distance was shorter in plants that began in the wet starting position, indicating a weaker tendency to spread away from that starting point. There was little difference in mean gradient distance for rhizomes spreading towards wet and dry conditions from the wet starting position in both species.

The probable direction of rhizome spread is not intuitively obvious from the wet start position. Rhizomes that spread towards wetter conditions from this position are also encountering more crowded conditions, particularly later in the experiment. However, rhizomes that spread toward dry conditions encountered a lower tiller density but also a less favorable position along the water-table gradient (Fig. 13). The strong difference in direction of rhizome spread from the dry start position and the lack of a strong difference from the wet position indicate that the rhizomes that produced tillers were spreading to a more favorable position along the water-table gradient.

This phenomenon falls somewhere between the two definitions of foraging discussed in the literature review. Grime et al. (1986) used the term to refer to selective placement of roots and leaves in favorable patches, and as such, the definition applies to all plants. De Kroon and Schieving (1990) defined foraging as resulting from plasticity in rhizomes and stolons. Furthermore, by this definition, the plasticity must be found in very particular traits: branching frequency of rhizomes and stolons, spacer distance and angle of spacer growth (Evans and Cain, 1995). Thus foraging by this definition can only

Figure 13: Water-table and space gradients in continuous gradient experiment. The water-table increases from the top of the diagram to the bottom, space decreases toward both ends of the diagram since plants growing in these directions are encountering the ends of the box.



apply to clonal plants. The phenomenon found in this study can perhaps best be described as habitat selection in a clonal plant via rhizome sensitivity to moisture and, perhaps, competition.

Differences in morphological response between clones from early and late successional sites

A variety of evidence suggests that the clones responded morphologically to the water-table gradient, but were the responses of the early and late successional clones different? There were three significant interactions in the results that involved site of clone origin: site type X start position on dry weight of tillers in *C. rostrata*, and site type X zone of tiller emergence on growth rate in both *C. aquatilis* and *C. rostrata* (Figs. 10 and 12). In all three cases, clones from early successional habitats responded to a much greater extent to the water-table gradient than did the clones from the late successional habitats. It is likely the difference in magnitude of response between early and late successional clones that is causing the interaction to be significant (Figs. 10 and 12). The interaction between site and zone of tiller emergence on growth rate for both species is particularly striking. In both species, the change in growth rate between zones for late successional clones was minimal, while the change in early successional clones was large (Fig. 12). Thus it appears that the early successional clones responded to a greater extent to the water-table gradient than did the late sucessional clones.

As discussed with respect to the plasticity experiment, when considering response it is important to look at both magnitude and direction of response. The direction of response of growth rate in early successional clones to zone of tiller emergence is opposite in the two species. Growth rate was expected to increase in response to flooding at the wet extreme of the box since accelerated shoot growth has been shown as an adaptive response to flooding in several species (see references in introduction). Growth rate in *Carex aquatilis* increased from dry to wet conditions, while growth rate in *C. rostrata* decreased. So, while magnitude of response of early successional clones tended to be larger, the direction of the response was not always predictable.

SUMMARY AND CONCLUSIONS

The pioneer species in the plasticity experiment did not exhibit greater plastic responses than did the late-invading species. The pioneer species had an overall lower proportion of traits significantly affected by the treatment than the late successional species. Two of the late successional species, *C. paupercula* and *C. vaginata,* consistently had higher mean genotypic coefficients of variation than the other species. The greater plasticity in the late successional species may be due to the reduction of number of genotypes in pioneer species throughout the successional sequence. A three-way comparison in plastic response among late successional species, pioneer species from pioneer habitats and pioneer species from late successional habitats would test this hypothesis.

Results from the plasticity experiment support the notion that traits that are directly related to fitness will be stable while those that underlie fitness will be plastic (Marshall et al., 1896). The measure of fitness used in the experiment, dry weight at harvest, was never significantly affected by the environment while the other variables were significantly affected by the environment in 27.1% of species-trait combinations.

Results from the continuous-gradient experiment indicate that clones from both early and late successional habitats are equally able to colonize a resource gradient via vigorous rhizomatous growth. In addition, clones from both habitats were equally able to preferentially exploit the favorable end of the resource gradient and, as well, placed rhizomes in such a way as to reduce intra-specific competition.

A morphological response that increases an organism's ability to perform in spite of environmental stress can be construed as an adaptive response in that it increases the chance of persistence in the environment. This is particularly true in clonal plants where there is a trade-off between sexual and vegetative reproduction, which makes them less likely to employ the "flower and die" strategy, common in annuals, in response to stress. Adaptive morphological responses can be said to indirectly increase fitness because by prolonging an organism's existence in an environment, the chances of both sexual and vegetative reproduction are increased.

The tillers in both experiments exhibited adaptive morphological responses. The allocation variables measured in the plasticity experiment responded in the expected

direction, as did root porosity and direction of rhizome spread in the continuous-gradient experiment. Interestingly, the treatment had a significant effect on stem diameter in *C. rostrata* in both experiments. The fact that water-table level had a significant effect on this species in two experiments in which the gradient was established by different means, combined with field data and observations on stem diameter in *C. rostrata*, indicates that the facultative formation of aerenchyma is an important response to water-table levels in this species.

Together the experiments indicate broad ecological tolerance of these *Carex* species in response to variations in moisture. In the plasticity experiment, there was vigorous growth in all six species, in all three treatments, with very few exceptions. In the continuous-gradient experiment, the two boxes were densely colonized by both *C. aquatilis* and *C. rostrata*. Although a habitat preference was seen for the wet end of the gradient, tillers did emerge along the entire gradient. This broad ecological tolerance probably accounts for the plastic convergence (Sultan, 1987) that was seen in the norms of reaction of the plasticity experiment, and contributes to the lack of large differences between the two groups of species in the same experiment.

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Appendix I: Environmental conditions over the Blocks

Photosynthetically active radiation (PAR) measurements (u mol/m^2s)

Date	Time	Conditions	Block I	Block II	Block III
1-25	4:30pm	clear	72.441	62.531	65.021
	5:30pm	clear	53.868	45.143	50.752
	7:30pm	clear	51.398	47.033	47.030
	8:30pm	clear	56.930	45.790	51.402
1-26	9:00am	clear	101.25	91.279	109.36
	9:30am	clear	125.53	99.736	261.34
	10:00am	clear	190.27	123.62	142.30
	10:30am	snowing	166.57	131.07	157.74
	11:00am	snowing	169.06	135.03	174.04
1-27	7:00am	overcast	56.378	45.196	50.162
	7:30am	overcast	57.013	48.284	52.025
	8:00am	overcast	68.237	57.013	69.484
1-30	11:00am	partly cloudy	235.51	164.57	194.44
	11:30am	partly cloudy	259.11	318.85	265.36
	12:00pm	partly cloudy	460.06	150.02	163.03
	12:30pm	clear	556.72	143.44	179.54
	1:00pm	clear	476.82	140.26	162.65
	1:30pm	clear	500.96	158.63	336.76
	2:00pm	clear	290.74	251.55	364.75

Temperature Measurements (° C)

		Block I			Block II			Block III		
Date	Time	High	Med.	Low	High	Med.	Low	High	Med.	Low
1-25	4:30pm	16.3	16.2	16.0	15.0	13.9	14.1	16.0	16.5	16.8
	5:30pm	16.5	16.1	16.3	15.0	14.8	14.5	16.5	16.2	16.2
	7:30pm	16.3	16.1	16.3	14.8	14.5	15.5	16.2	16.2	16.8
	8:30pm	16.2	16.2	16.3	14.8	14.5	14.8	16.0	15.9	15.9
1-26	9:00am	13.8	13.8	13.5	13.0	12.9	12.8	14.1	14.0	14.0
	10:00am	14.2	14.4	13.9	13.1	13.1	13.4	15.2	14.8	15.4
	11:00am	14.5	15.3	14.6	14.0	14.4	14.2	15.3	15.4	15.5
1-30	11:00am	15.0	15.0	15.5	14.5	14.5	13.5	17.0	17.0	17.0
	12:00pm	16.2	15.5	15.5	15.0	15.5	15.2	17.2	17.0	17.0
	1:00pm	17.0	17.5	16.0	14.5	15.0	15.4	17.5	17.4	17.6
	2:00pm	16.5	16.5	17.5	15.0	15.2	14.5	18.0	17.5	18.0

Appendix II: Variable means and standard deviations by block per species.

Block means and standard deviations for dry weight (g)

Species	Block I	Block II	Block III
C. aquatilis	3.365 ± 1.599	2.254 ± 0.900	3.028 ± 1.160
C. michauxiana	0.861 ± 0.421	0.748 ± 0.333	0.853 ± 0.597
C. oligosperma	0.684 ± 0.490	0.617 ± 0.284	0.795 ± 0.329
C. paupercula	0.440 ± 0.218	0.659 ± 0.237	0.504 ± 0.210
C. rostrata	1.262 ± 0.597	1.572 ± 0.968	2.338 ± 1.417
C. vaginata	0.700 ± 0.254	0.655 ± 0.351	0.678 ± 0.248

Block means and standard deviations for leaf area ratio (cm^2/g)

Species	Block I	Block II	Block III
C. aquatilis	5.698 ± 1.186	7.513 ± 1.861	5.825 ± 1.807
C. michauxiana	12.090 ± 2.398	13.521 ± 2.852	5.652 ± 2.039
C. oligosperma	7.889 ± 6.254	8.342 ± 1.392	6.628 ± 1.851
C. paupercula	9.444 ± 6.394	14.956 ± 4.890	15.587 ± 4.529
C. rostrata	10.312 ± 2.580	11.554 ± 2.753	9.608 ± 1.950
C. vaginata	9.446 ± 2.563	10.419 ± 4.284	13.272 ± 5.244

Block means and standard deviations for mean leaf area (cm^2)

Species	Block I	Block II	Block III
C. aquatilis	3.721 ± 1.128	3.798 ± 1.056	3.844 ± 1.351
C. michauxiana	2.350 ± 0.598	1.939 ± 0.592	3.772 ± 1.298
C. oligosperma	1.501 ± 0.497	1.659 ± 0.774	1.511 ± 0.539
C. paupercula	1.475 ± 1.025	1.747 ± 0.471	1.598 ± 0.569
C. rostrata	2.677 ± 1.083	3.212 ± 1.155	3.437 ± 1.330
C. vaginata	1.461 ± 0.667	1.222 ± 0.477	1.348 ± 0.331

Block means and standard deviations for number of roots

Species	Block I	Block II	Block III
C. aquatilis	34.4 ± 13.8	32.1 ± 10.9	37.2 ± 8.1
C. michauxiana	23.6 ± 10.5	22.1 ± 10.6	35.6 ± 10.2
C. oligosperma	13.7 ± 8.2	11.1 ± 4.4	15.8 ± 5.9
C. paupercula	8.3 ± 4.4	9.7 ± 6.0	9.0 ± 5.9
C. rostrata	14.3 ± 5.5	21.9 ± 13.1	26.2 ± 10.3
C. vaginata	20.1 ± 10.3	21.9 ± 11.4	20.9 ± 10.0

Block means and standard deviations for root: shoot

Species	Block I	Block II	Block III
C. aquatilis	1.936 ± 0.704	1.771 ± 0.773	1.747 ± 0.703
C. michauxiana	0.469 ± 0.137	0.469 ± 0.210	1.735 ± 0.690
C. oligosperma	0.779 ± 0.366	0.627 ± 0.154	0.843 ± 0.374
C. paupercula	1.852 ± 0.965	1.540 ± 0.771	1.101 ± 0.592
C. rostrata	1.058 ± 0.289	0.980 ± 0.242	1.187 ± 0.263
C. vaginata	1.546 ± 0.762	1.660 ± 0.784	1.440 ± 0.617

Block means and standard deviations for specific leaf area (cm^2/g)

Species	Block I	Block II	Block III
C. aquatilis	27.372 ± 5.575	30.337 ± 7.211	23.291 ± 4.199
C. michauxiana	28.651 ± 3.377	25.153 ± 5.860	23.202 ± 6.250
C. oligosperma	19.953 ± 4.228	19.078 ± 3.821	18.527 ± 2.637
C. paupercula	47.420 ± 14.936	53.733 ± 13.076	51.090 ± 20.766
C. rostrata	31.539 ± 4.689	31.954 ± 6.589	29.571 ± 3.624
C. vaginata	41.193 ± 10.250	38.285 ± 10.604	45.686 ± 9.376

Block means and standard deviations for stem diameter (cm)

Species	Block I	Block II	Block III
C. aquatilis	0.70 ± 0.45	0.81 ± 0.41	0.84 ± 0.47
C. michauxiana	0.73 ± 0.094	0.66 ± 0.35	0.80 ± 0.48
C. oligosperma	0.56 ± 0.33	0.57 ± 0.27	0.85 ± 0.14
C. paupercula	0.52 ± 0.33	0.52 ± 0.34	0.50 ± 0.33
C. rostrata	0.92 ± 0.17	0.90 ± 0.40	1.02 ± 0.47
C. vaginata	0.58 ± 0.13	0.53 ± 0.23	0.59 ± 0.16

Block means and standard deviations for tiller growth rate (cm/day)

Species	Block I	Block II	Block III
C. aquatilis	0.66 ± 0.22	0.55 ± 0.31	0.74 ± 0.28
C. michauxiana	0.40 ± 0.14	0.36 ± 0.25	0.73 ± 0.31
C. oligosperma	0.34 ± 0.14	0.29 ± 0.13	0.45 ± 0.13
C. paupercula	0.27 ± 0.18	0.23 ± 0.15	0.32 ± 0.21
C. rostrata	0.37 ± 0.18	0.40 ± 0.20	0.60 ± 0.22
C. vaginata	0.24 ± 0.17	0.18 ± 0.14	0.21 ± 0.13