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CHANGES IN COMPETITION INTENSITY, HERBIVORY AND STRESS ALONG A SOIL DEPTH GRADIENT IN AN OLD FIELD

Teri M. Keogh

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Abstract

Four herbaceous plant communities were described along a natural soil depth gradient in an old field. Biomass and canopy height increased with soil depth. Species richness showed a quadratic relationship, whereas the proportion of native species increased with soil depth. The limiting resource was found to be nutrients, not water, even though the year was abnormally dry. I hypothesized that competition was the main factor structuring these communities. The relationship between competition intensity and soil depth was determined through experimentation using two phytometer species, *Liatris spicata* and *Lythrum salicaria*. Competition intensity decreased with soil depth across the four communities, which contradicts the Competitor/Stress-Tolerator/Ruderal Hypothesis (CSR) of Grime and Tilman's Resource Ratio hypothesis. Competition in this old field was primarily below ground. Herbivory from large herbivores did not change along the gradient, whereas stress was found to be greatest at both ends of the gradient.

Résumé

Quatres communautés de plantes herbacées ont été décrites en fonction d'un gradient naturel de profondeur de la terre dans un vieux champ abandonné. La biomass et l'hauteur de la voûte ont augmenté avec la profondeure de la terre. La richesse des espèces a démontré une relation quadratique avec la profondeure de la terre, tandis que la proportion d'espèces natives augmentait avec la profondeure de la terre. La ressource limitante était les nutriments du sol et non pas l'eau, malgré le fait que l'année en question était anormalement sèche. J'ai proposé que la competition est le facteur principale qui contrôle la structure de ces communautés. La relation entre l'intensité de la compétition et la profondeur de la terre a été examinée au cours d'expériences avec deux phytomètres, *Liatris spicata* et *Lythrum salicaria*. L'intensité de la compétition a diminué avec la profondeur de la terre à travers les quatres communautés végétatives, ce qui est en contradiction avec le "Competitor/Stress-Tolerator/Ruderal" (CSR) hypothèse de Grime et le "Resource Ratio" hypothèse de Tilman. La compétition dans ce vieux champ est surtout dans le sol. L'herbivorie n'a pas changé le long du gradient et le stresse a été plus sévère aux deux bouts du gradient de profondeur de la terre.

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General Introduction

Ecology is the science of the natural environment and of how organisms relate to each other and their surroundings. One branch of this science, plant ecology, studies the factors that influence the distribution and abundance of plants (Crawley 1997). Some such factors are rainfall, nutrients, other plants, herbivores and of course humans. In fact, one could argue that man has had more effect on the distribution and abundance of plants than any other factor. Therefore, the onus is on plant ecologists, and people in general, to learn about the world around them if we ever hope to lessen our impact. With that in mind, this project tackles an aspect of plant distribution and abundance.

If nature has one unifying principle, it is endless change in time and space. However, many studies make the assumption of a homogeneous environment, though such a thing rarely exists. It is far better to accept nature as heterogeneous and incorporate that into research. One way to accomplish this is to use gradients, where the variation is organized (Pielou 1975).

An old field in central Ontario, Canada was chosen as the study site in that it contains a natural productivity gradient as a result of varying soil depth. Old fields are the result of abandoned farmland slowly converting back to a natural state through succession. Many areas of eastern North America have old fields that are slowly reverting to deciduous forest, often dominated by goldenrods, asters and grasses. These are a relatively new type of habitat, created in many cases only a few hundred years ago. Old fields are similar to prairie, grassland, meadows and other habitats dominated by herbaceous vegetation but it is their origin as agricultural land which sets them apart.

Early ecologists spent most of their time describing species and habitats. Now the tendency is to focus more on quantifying ecology as opposed to qualitative description. However, there is still a need to describe a habitat, especially before using it to conduct an experiment. Description can be a powerful tool and often may help interpret the results of a quantitative experiment (see Fowler and Antonovics 1981). Therefore, the first chapter describes the old field, its soil depth gradient and its limiting resources.

The quantitative part of this study explores competition, which is defined as the negative effects that one organism has upon another by consuming, or controlling access to a resource that is limited in availability (Keddy 1989). Many studies have found evidence of competition in natural systems (Tansley 1917, Clements *et al.* 1929, Fonteyn and Mahall 1978, Connell 1980, Berendse 1983, Gurevitch *et al.* 1992) and specifically in old fields (Fowler 1982, Whigham 1984, Goldberg 1987, Goldberg and Landa 1991, Keddy 1991). Competition, along with predation and mutualism, are the three fundamental forces that connect organisms in living systems (Keddy 1989). Therefore, it is important if one wants to study a community or ecosystem completely to know if competition occurs, how it occurs, when and what are the impacts. There has been an enormous amount of research into competition between all sorts of organisms, from insects to trees. However, there are still no unified bodies of theories or laws of competition and these are things that any science needs to develop. Specifically, the question of whether or not competition changes in time and space needs to be explored. An aspect of that question is the focus of the second chapter, which explores the relationship between competition intensity and productivity, while also looking at herbivory and stress along the gradient.

Chapter 1

Patterns in vegetation and limiting resources along a soil depth gradient in an old field

Introduction

Old fields are the result of abandoned farmland slowly converting back to a more natural state and have long been studied by plant ecologists. This ecosystem has been used to study many different ecological processes including succession (Parrish and Bazzaz 1982, Hils and Vankat 1982, Tilman 1987, Olff *et al.* 1994b), resource limitation (Bakelaar and Odum 1978, Carson and Pickett 1990), disturbance (Armesto and Pickett 1985, Goldberg and Gross 1988, Carson and Pickett 1990), competition (Goldberg 1987, Reader and Best 1989, Cahill 1999), species diversity patterns (Olff and Bakker 1991, Goldberg and Miller 1990, Huberty *et al.* 1998) and herbivory (Baker 1937, Bonser and Reader 1995). Often these studies can be related both botanically and ecologically with investigations of other vegetation types dominated by herbaceous species. Some examples are farmland (C.J. Keddy *et al.* in prep., Epp and Aarssen 1989), pasture (Thomas and Dale 1977), grasslands (Tansley and Adamson 1925, Fowler 1980, Puerto *et al.* 1990, Wedin and Tilman 1993, Olff *et al.* 1994a), prairies (Dix and Smeins 1967, Burger and Louda 1995), alvars (Catling *et al.* 1975, Belcher *et al.* 1992, 1995), meadows (Abrahamson and Gadgil 1973), savanna (Inchausti 1995), and rock outcrops (Sharitz and McCormick 1973, Houle 1990, Wiser *et al.* 1998).

Natural gradients within old fields are rarely studied; in fact, the assumption is that old fields are homogeneous. The old field used in the following study, however, is an exception. It is located in Lanark County, Ontario, which is made up of either Precambrian rock of the Canadian Shield or limestone plains. The Shield is characterized by rocky, acidic soils and the limestone by deeper, alkaline soils (Shilts and Kettles 1989). The old field is located on the ecotone between these two areas. It is almost a mix of the two with more acidic rock outcrops and deeper more alkaline soils. The most important event in the natural history of Lanark County, the melting of the ice sheets, occurred a mere 12 000 years ago and shaped the physiography of the study site.

Humans have created the abandoned fields and pastures found in Lanark County. Originally, almost the entire county was forested until it was cleared by settlers for farming in the early to mid 1800's. First crop plants were introduced, then this field was abandoned in the early part of the 1900's and since then has been used for grazing and haying in an opportunistic fashion. When these areas were cleared, plants re-invaded the area. Many of the species were exotics that originated from Europe as seeds or with livestock. Some examples are the ox-eye daisy (*Chrysanthemum leucanthemum*), orange hawkweed (*Hieracium aurantiacum*) and evening primrose (*Oenothera lamarckiana*) (Keddy, P.A. personal communication). The first two of these species are found in the study site. However, many native species, such as goldenrods and asters, which were previously growing in dry open rock barrens (Catling and Brownell 1999) and alvars (Belcher *et al.* 1992), also invaded this new open habitat. The old field contains many golderod and aster species, such as *Solidago canadensis, Solidago nemoralis, Aster novae-angliae* and *Aster lanceolata.*

Patterns along gradients in old fields have received less attention partly because obvious gradients are uncommon in the normal tilled and deep soils. Yet gradients are important for causal analysis and have been experimentally produced to study how vegetation processes change along them. For example, Parrish and Bazzaz (1982) created an experimental nutrient gradient to study plants from three successional communities. Gurevitch *et al.* (1990) created a fertility gradient by using different amounts of fertilizer to investigate competition among old field perennials. Wilson and Tilman (1991) created an experimental nitrogen gradient to look at the components of plant competition in an old field. Stevens and Carson (1999) established an experimental productivity gradient in a first year old field to explore the relationship between plant density and species richness. Although some studies have explored natural gradients, such as a lakeshore (Wilson and Keddy 1986), water depth in a marsh (Shipley *et al.* 1991) and elevation between a riparian and upland forest (Lyon and Sagers 1998), few have done so in old fields. The choice between a natural or artificial gradient can alter the results of an experiment, for example how competition relates to the change in productivity along the gradient (Kadmon 1995).

Natural gradients can be the result of historical events in the area, such as volcanic eruption, glaciation or flooding. An example of the latter is a rock knob and clay plain physiography described by Chapman and Putnam (1966) for Southern Ontario as shown in Figure 1.1, which occurs in the study site. The underlying bedrock is composed of Pre-Cambrian granite that was shaped by glaciers approximately 12 000 years ago. As the glaciers melted and receded, till (silt/sand/gravel) was left covering the bedrock. The till is covered by clay that was deposited in the depressions that were created by the weight of the glacial ice. The origin of the clay, in the study site, could be either lacustrine (freshwater), marine (saltwater) or a combination of both, as there was first a lake in the area and then the Champlain Sea (Anderson 1989). A gradient of soil depth radiates outwards from the granite knobs as one moves out into the clay flats (Chapman and Putnam 1966).

This chapter describes an old field that contains a natural soil depth gradient due to a rock knob clay plain physiography. This gradient, and selective senescence from drought, results in visually distinct communities, providing a rare opportunity to study vegetation processes as they change along gradients in fields. Further, experimental resource additions determined how limiting resources change along this gradient.

Methods

Study Site

The study site was an old field in Lanark County west of Carleton Place and south of highway 7 in Ontario, Canada (45° 12' N, 76° 30' W), which is briefly described in the introduction. This field is approximately 150,000 m^2 and is surrounded by a deteriorating fence and deciduous trees. It is typical of many fields of eastern North America in that it was originally deciduous forest, cleared ca. 150 years ago. Formerly, the field was used for agricultural purposes including grazing and mowing for hay. An adjoining abandoned farm site had an influence on the property, including some escaped cultivated plants, piles of rocks and fences. Three years ago the entire field was mowed to eliminate woody plants and it is now dominated by herbs and grasses. The field is undergoing the early stages of succession, with young woody plants including *Pinus strobus, Fraxinus alba, Juniperus virginiana* and *Rubus* sp. Table 1.1 shows the dominant species (by Braun-Blanquet abundance) in this field compared to dominants in other old fields obtained from the literature.

This field has a rock knob and clay plain physiography as outlined in Chapman and Putnam (1966, Fig. 1.1). In places the gneiss rock is bare with crustose lichens and radiating out from these rock knobs are bands of progressively deeper soil. This formation produces a soil depth gradient from zero in the Rock Outcrops to greater than 100 cm in the deep clay areas. The varying soil depth produces vegetation zonation and four distinct plant communities. The first has very shallow soil, with expanses of bare rock and is typified by *Hieracium pilosella* and *Potentilla argentea.* The second has a complete cover of shallow soil and is dominated by grass species such as *Danthonia* *spicata* and *Phleum pratense*. The third has fairly deep soil, much more biomass and is dominated by *Solidago* and *Aster* species. The fourth has the deepest soil, is inundated by water in the spring, and is dominated by *Lythrum salicaria* and sedges. These four communities will be referred to as the Rock Outcrop, the *Danthonia*, the *Solidago* and the *Lythrum* communities.

Quantitative Description

The descriptive inventory of the field began in August 1998; all species encountered were identified and voucher specimens were obtained. Field identifications followed Gleason and Cronquist (1963). Dr. Paul Catling (Agriculture Canada) verified voucher specimens in order to ensure field identifications were done correctly.

Forty 0.25 m^2 quadrats were selected in a partial random design. First one of the four communities was located and then the area in which the quadrats would be placed was selected 100 cm from the edge of the community. However, most of the communities within the field were used, so the areas to place the quadrats could not be chosen randomly. There were ten representative quadrats for each of the four community types. In these quadrats, estimates of both biotic and abiotic factors were obtained during September 1998. First, a list was made of all the species rooted within each quadrat. Each species was then assigned a Braun-Blanquet abundance score between one and five as outlined in Mueller-Dombois and Ellenberg (1974). The scores are determined based on the percent cover of a particular species within a defined area. A score of one corresponds to 5% cover or less, two a 5 to 25% cover, three 25 to 50%, four 50 to 75% and five 75% or greater. The number of native and non-native species in each community was then determined using floras. Next, the height of the five tallest plants was measured and averaged to estimate maximum canopy height. All of the above ground plant material was clipped, placed in paper bags, dried in a drying oven at 80° C for 24 hours, and then weighed in order to estimate biomass. Finally, soil depth was measured with a soil auger, in the centre of each quadrat and in each of the four corners up to a maximum value of 50cm. These five measures of soil depth were then averaged to give one value per quadrat. These measurements provided species richness, Braun-Blanquet scores, canopy height, aboveground biomass and soil depth estimates for forty 0.25 m^2 quadrats within the field. Regression analysis was used to explore relationships between biomass and soil depth, species richness and soil depth, and species richness and biomass. Principal component analysis identified patterns in richness, canopy height and biomass. Differences in the proportion of native species in each community were not analyzed statistically because this was count data without any variation required to generate a p value.

Limiting Resources

In May 1999, another sixty quadrats (30 cm by 30 cm) were established (n=15 quadrats per community) in the same manner as outlined above for the other quadrats. Five quadrats in each community received additional water three times a week on average, depending on rainfall. Approximately four litres of water were poured on each quadrat with plastic watering cans, usually in the morning, unless it was raining at the time, in which case additional water was not added. Another five quadrats per community received slow release fertilizer pellets. Plant-prod® controlled release fertilizer, consisting of nitrogen (14%), phosphorus (14%) and potassium (14%) was applied once at the beginning of the growing season as directed on the package. Approximately 500 ml of the fertilizer was sprinkled over the surface of each quadrat at the beginning of May. The last five quadrats in each community that did not receive water or fertilizer served as controls. At the end of August 1999, the species composition and Braun-Blanquet abundance scores were assessed. Also, the dry above ground biomass was clipped, dried and weighed. Kruskall-Wallis ANOVA was used to test for significant differences within each community. Non-parametric statistics were used because of the small sample sizes.

Results

Soil depth, measured within quadrats, varied significantly among the four communities (Fig. 1.2, $R^2=0.913$, $p<0.001$). The Rock Outcrop community ranges in soil depth from 0-7 cm, the *Danthonia* from 8-15 cm, the *Solidago* from 35-49 cm and the *Lythrum* at <50 cm (Fig. 1.3a), as measured during the first growing season. During, the second growing season, a more accurate measure was taken with the soil auger and these measurements are used in Figure 1.2. Biomass also varies among communities, with the least in the Rock Outcrop (Fig. 1.3a, $R^2=0.672$, $p<0.001$). The communities with the most biomass are also the ones with a greater soil depth. The number of species per quadrat also changes among the four communities (Fig. 1.3b, $R^2=0.549$, $p<0.001$). The number of species does not seem to increase directly with soil depth because the *Danthonia* and *Solidago* communities have more species than the *Lythrum* community. Canopy height was also found to differ between the communities (Fig. 1.3c, $R^2=0.867$, $p<0.001$), with greater canopy height in communities with deeper soil. Finally, the Braun-Blanquet scores did not differ significantly between communities (Fig. 1.3d, $R^2=0.012$, $p=0.226$). The average score lay around 1.5, therefore most species occur infrequently regardless of the community.

A positive linear relationship existed between biomass and soil depth (Fig. 1.4a, $R^2=0.493$, $p<0.001$). There was a significant (polynomial) regression between species richness and soil depth (Fig. 1.4b, $R^2=0.491$, $p<0.05$) indicating a curvilinear relationship between the two variables. Canopy height also increased as soil depth increased, with a similar slope to the plot of biomass and soil depth (Fig 1.4 c, $R^2=0.763$, $p=0.001$). There was no clear relationship between species richness and biomass, even though the positive correlation is statistically significant (Fig. 1.4d, R^2=0.158, p=0.011), it explains very little of the variation. However, if the data points are coded by soil depth, it is evident that similar soil depths occupy similar areas on the graph. Using principal component analysis on species richness, canopy height and biomass, most of the variation was explained by the first factor (66.5%), which had high loadings from biomass (0.899) and canopy height (0.881), while factor two explained 25% of the variation and had a high loading from species richness (-0.755). A plot of factor one versus factor two showed that each community is relatively distinct (Fig. 1.4e). The percent of native species increased with soil depth; the *Lythrum* community had the greatest percentage of native species and the Rock Outcrop community had the least (Figure 1.5).

Braun-Blanquet abundance scores were plotted versus soil depth for some species, which occurred in more than two quadrats, to depict their distribution (Figure 1.6). Species that appear restricted mainly to the shallow soil or deeper soil could be considered habitat specialists. These species either grow only in the shallow soil, *Potentilla argentea* (Fig. 1.6a), *Rumex acetosella* (Fig. 1.6d) and *Solidago nemoralis* (Fig. 1.6g), or they grow more abundantly in the shallow soil, *Hieracium pilosella* (Fig. 1.6j). Other species grow only in the deeper soil, *Lythrum salicaria* (Fig. 1.6c), *Dactylis glomerata* (Fig. 1.6f) and *Solidago canadensis* (Fig. 1.6l), or more abundantly in the deeper soil, *Carex gracillima* (Fig. 1.6i). The figure also shows four species with a more even distribution that could be considered habitat generalists along the gradient. These species grow along the gradient at approximately the same abundance, *Poa compressa* (Fig. 1.6e), *Fragaria virginiana* (Fig. 1.6h) and *Chrysanthemum leucanthemum* (Fig. 1.6k) or with the same variation in abundance, *Danthonia spicata* (Fig. 1.6b).

The main limiting resource in this old field appeared to be macronutrients (NPK) since their additions lead to an increase in biomass (Fig. 1.7). In the Rock Outcrop and the *Solidago* communities, there was a significant difference among the biomass in the fertilizer treatment and the other two treatments, the control and watered treatment (p=0.009 and p= 0.0344 respectively, Fig. 1.7a,c). In the *Danthonia* community, there was a significant difference among both treatments, fertilizer and watered, versus the control (p=0.0118, Fig. 1.7b). The fertilizer, however, resulted in a slightly (but not statistically significant) higher biomass. In the *Lythrum* community, there was no significant difference among the treatments or control (p=0.075, Fig. 1.7d).

Discussion

Many of the variables measured, including biomass and canopy height, increased with soil depth or showed a humped back relationship (Figs. 1.3 and 1.4). In general, as productivity increases so does biomass (Mellinger and McNaughton 1975, Bakelaar and Odum 1978, Goldberg and Miller 1990, Foster and Gross 1998). The fact that biomass increased along this gradient indicates that soil depth is a good indicator of productivity. It is also not a surprise that canopy height would increase with soil depth because as the biomass increases, so does the pressure to be taller than neighbours in order to gain access to light. Further, as soil depth increases so does the availability of below ground resources, in which case, light may increasingly become the limiting resource. This may be further corroborated by the observation that in the *Lythrum* community, water and nutrients no longer appear to be limiting (Fig. 1.7 d).

Species richness showed a quadratic relationship with soil depth, similar to Grime's humpback model (Grime 1977) for diversity and productivity (Fig 1.4 b). Grime (1977) suggests that at high productivity, diversity is reduced by dominance of a few species. At low productivity, diversity is limited by the number of species capable of surviving the severe environmental stress or disturbance that is maintaining productivity at a low level in the first place. Therefore, it is at the intermediate levels of productivity that diversity is most high, as is seen in this field. However, the fact that flooding occurs in the *Lythrum* community, could be another cause of decreased diversity. Houle (1990) also explored a soil depth gradient radiating out from rock outcrop and found that richness increased with soil depth. However, the gradient in this case may not have reached a maximum point where richness would begin to decline, because the soil was not as deep as in the study site. More recently, Stevens and Carson (1999) reported a peak in diversity at a moderate level of productivity in an old field. They explain this peak through the assemblage thinning hypothesis which states that plant species richness along productivity gradients is influenced by total stem density. As fertility increases, individuals of all species tend to get larger and therefore crowd out or exclude subordinate individuals which will result in fewer species by chance alone. Regardless of which explanation is correct, there is support for a peak in diversity in this old field.

The abundance of some species varied as a function soil depth (Fig. 1.6). If the soil depth gradient did not exist and the soil was all uniformly shallow or deep, it appears likely that some of the specialists would not exist in this field. For example, if the whole field had deep soil, *Potentilla argentea* or *Solidago nemoralis* might not be found or if there was only shallow soil, *Dactylis glomerata* and *Lythrum salicaria* might no longer be present.

Pickett and Bazzaz (1978) hypothesized that a soil moisture gradient provided the basis for the co-existence of early successional old field species. Abiotic factors, as well as neighbours, were found to control the frequency of two grass species along an environmental gradient (Reader and Bonser 1993). More recently Reynolds *et al.* (1997) suggest that soil heterogeneity, such as variation in soil depth, water and nitrogen, contributes to the coexistence grassland annuals (see also Fowler and Antonovics 1981 and Fuhlendorf and Smeins 1998). This is a further indication that the soil depth gradient is affecting both the distribution and abundance of these herbaceous species, most of which are typical old field species.

Soil nutrients were the main limiting resource in this old field (Fig 1.7), especially in the Rock outcrop, *Danthonia* and *Solidago* communities. Bakelaar and Odum (1978) also found that fertilizer additions increased biomass in an old field in a floodplain near Athens, Georgia. In some terrestrial environments nitrogen may be the sole limiting resource (Tilman 1984, Tilman 1987, Huberty *et al.* 1998). In European grasslands, nitrogen is the major limiting nutrient and studies have found that when nitrogen fertilizer is no longer applied productivity decreases while diversity increases (Olff and Baker 1991, Olff *et al.* 1994a).

At our study site the increase in biomass with fertilizer addition becomes increasingly less apparent as soil depth increases (Fig. 1.7), probably in part because below ground resources are related to the volume of soil, which is a cubic function of depth. In the *Lythrum* community, the addition of fertilizer did not have a significant effect on biomass, which, as mentioned earlier, supports the suggestion that in that community, light may be limiting. However, the p value is close to the rejection level and a significant difference might have been detected if n was larger.

Water only had a significant effect on biomass in the *Danthonia* plot and even there fertilizer had more of an effect. This was unexpected because drought often produces visible senescence in the shallow soil around the outcrops. And 1999 was a drier, hotter year than the last ten years in that area of Lanark County according to an Environment Canada weather station in Appleton, Ontario, a town just outside Carleton Place, near the study site. According to Weatherhead (1986), short-term studies (one year or less) too often invoke unusual events to interpret data from field studies. Here, we report the opposite - - that despite an unusual event, a dry year, treatment affects of watering were minimal. Therefore, one might assume that in a normal year when more water was available, the vegetation might be more constrained by soil nutrients.

The changes in the percentage of native species along the gradient were not minor differences, ranging as they did from 15 to 65% (Fig 1.5). One potential explanation might be that the exotic species (*Hieracium pilosella, Potentilla argentea* and *Echium vulgare*) are more tolerant of shallow soil than of flooding or shade, however this would need to be tested. It also appears that in this old field, exotic species can more easily invade the shallow rock outcrops. Alternatively, native species are more successful at invading and surviving in the deeper soils. Fields, an open, sunny habitat, are not natural in this area, as it was almost entirely forest. Although there may have been a native flora associated with rock outcrops, this is inconsistent with the rock outcrops in the field having the most exotics.

The exotic species in the field, as mentioned in the introduction, mostly were brought over from Europe with the settlers. However, there are really only two possible sources for native species within the old field. One is the granite barrens to the west (Catling and Brownell 1999) and the other is the alvars to the east (Catling *et al.* 1975, Belcher *et al.* 1992, Catling and Brownell 1995). Both of these habitats could have acted as refugia for plants adapted to an open, sunny habitat. Granite barrens are naturally open habitats consisting of exposed granite rock with grassy areas, shrubs and scattered trees, which are spread throughout the Canadian shield region. *Aster ciliolatus, Danthonia spicata,* and *Solidago nemoralis* are just three examples of native species which are found in granite barrens and are also abundant in the study site (Catling and Brownell 1999). Alvars are areas of shallow soil over limestone with scant but unusual vegetation, which can be similar to rock outcrop communities. *Antennaria neglecta, Fragaria virginiana* and *Sisyrinchium montanum* are examples of native species found in alvars and the study site (Catling *et al.* 1975, Belcher *et al.* 1992, Catling and Brownell 1995). The source of the old field species, be it granite barrens, rock outcrops or the European flora, may potentially affect the distribution of native species within the field.

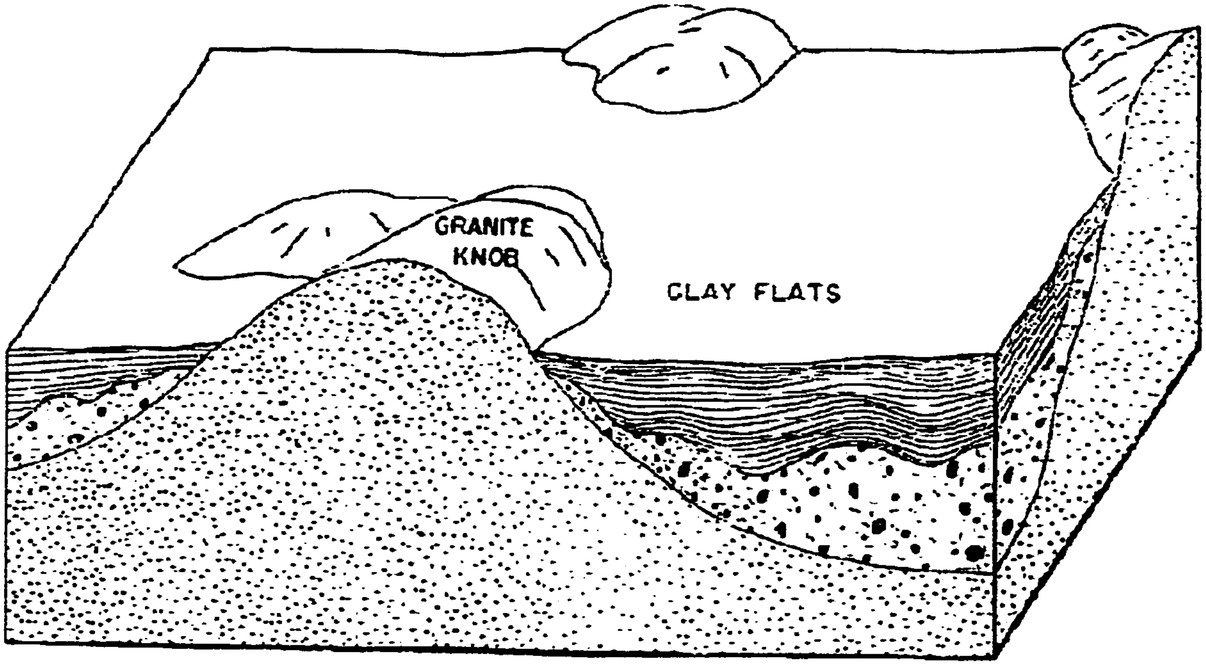
Tilman (1997a), while studying grasslands, found that areas of higher species richness were less easily invaded by new species and that invasibility was independent of total plant cover. He therefore suggests that exotic species might more easily invade areas of low species diversity than areas of higher diversity. However, Stohlgren *et al.* (1998), also looked at grassland ecosystems and they found that very productive sites, such as riparian zones, were more invasible and contained more exotic species. A relationship between invasibility and productivity does not yet seem clear, though this study seems to support Tilman's findings in that the less productive rock outcrops appeared more susceptible to invasion.

Soil depth appears to affect the number of species that can grow, the height a plant can reach, the amount of primary production, the limiting resource and the percentage of native species, all resulting in four distinct communities. It seems reasonable to conclude that the soil depth gradient is the main factor controlling the distribution and abundance of vegetation. A logical next step would be to explore the plant interactions along the gradient, specifically whether or not competition intensity changes along productivity gradients.

Table 1.1 The dominant species in other studies of old fields obtained from the published literature compared to some of the dominant species found in the study site, Keogh in 1999. Dominance in the study site was determined by a Bruan-Blanquet score of two or greater. Note Bonser and Reader investigated four different old fields, (1) through (4).

Dominant Species	Tilman 1984	Armesto & Pickett 1985	Reader & Buck 1986	Goldberg 1987	Miller & Werner 1987	Epp & Aarssen 1989	Carson & Pickett 1990	Wilson & Tilman 1991	Belcher et al. 1992	Bonser & Reader 1995 (1)	(2)	(3)	(4)	Keddy et al. 1997	Keogh 1999
Agropyron repens	+			+	+	+								+	
Aster novae-angliae													+		
Carex gracillima															+
Danthonia spicata									+						+
Echium vulgare											+				
Fragaria virginiana							+							+	+
Hieracium pilosella															+
Hieracium pratense			+				+					+			
Linaria vulgaris													+		
Lythrum salicaria															+
Phleum pratense						+								+	
Plantago lanceolata					+										
Poa compressa			+							+	+				+
Potentilla recta											+				
Rumex acetosella							+								
Solidago canadensis		+		+			+					+	+		+
Solidago nemoralis								+							+
Trifolium pratense						+									
Vicia cracca														+	

Figure 1.1 The rock knob and clay plain physiography of the study site. As one moves away from the granite knobs a soil depth gradient exists (modified from Chapman and Putnam 1966).



GRANITE KNOB
CLAY FLATS

Figure 1.2 Soil depth compared between the four communities, Rock outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT) using one-way ANOVA. Each community is significantly different than the others based on soil depth ($n=20$, $R^2=0.913$, $p<0.001$). Error bars represent 95% confidence intervals and letters (a-d) are the result of Bonferroni post-hoc comparisons.

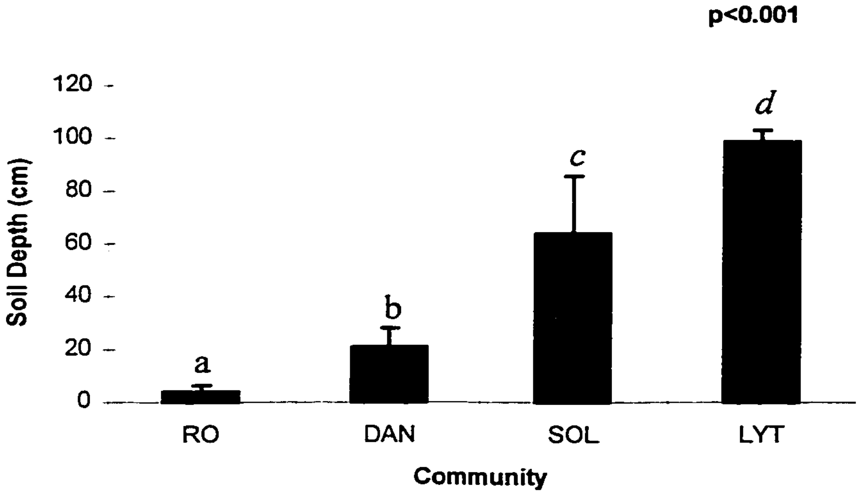
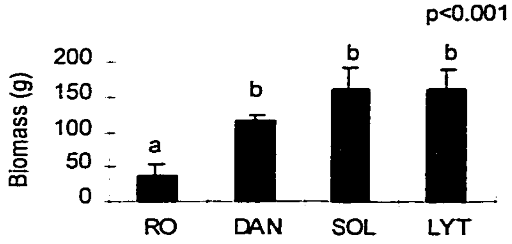
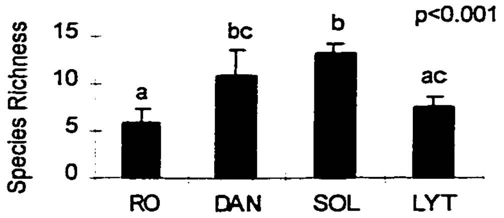

p<0.001
120
100
80
60
40
20
0
Soil Depth (cm)
a
b
c
d
RO
DAN
SOL
LYT
Community

Figure 1.3 A summary of the characteristics of the four communities, Rock outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT) with respect to a) biomass ($R^2=0.672$, $p<0.001$), b) species richness ($R^2=0.549$, $p<0.001$), c) canopy height ($R^2=0.867$, $p<0.001$) and d) Braun-Blanquet score ($R^2=0.012$, $p=0.221$). The analysis used was a one-way ANOVA, $n=40$, error bars represent the 95% confidence interval and letters (a-d) refer to Bonferroni post-hoc tests.

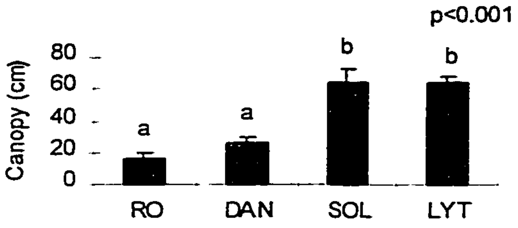
a)


p<0.001
Biomass (g)
200
150
100
50
0
a
b
b
b
RO
DAN
SOL
LYT

b)


p<0.001
Species Richness
15
10
5
0
a
bc
b
ac
RO
DAN
SOL
LYT

c)


p<0.001
Canopy (cm)
80
60
40
20
0
a
a
b
b
RO
DAN
SOL
LYT

d)

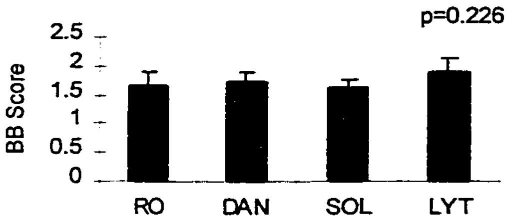

p=0.226
BB Score
2.5
2
1.5
1
0.5
0
RO
DAN
SOL
LYT

Figure 1.4 Relationships between the key variables in the old field a) a positive, linear relationship between soil depth and biomass ($n=40$, $R^2=0.493$, $p<0.001$), b) a quadratic regression of species richness versus biomass ($n=40$, $R^2=0.491$, $p<0.05$), c) a positive, linear relationship between soil depth and canopy height ($n=40$, $R^2=0.763$, $p=0.001$), d) the scatter of species richness versus biomass ($n=40$, $R^2=0.158$, $p=0.011$) coded by soil depth and e) factor 2 versus factor 1 coded by community from a PCA analysis ($n=40$, F1=66.5%, F2= 24.9%, F3=8.6%). Note factor one has large loadings from all three variables, especially biomass (0.899) and canopy height (0.881), whereas factor two has a large loading from species richness (-0.755).

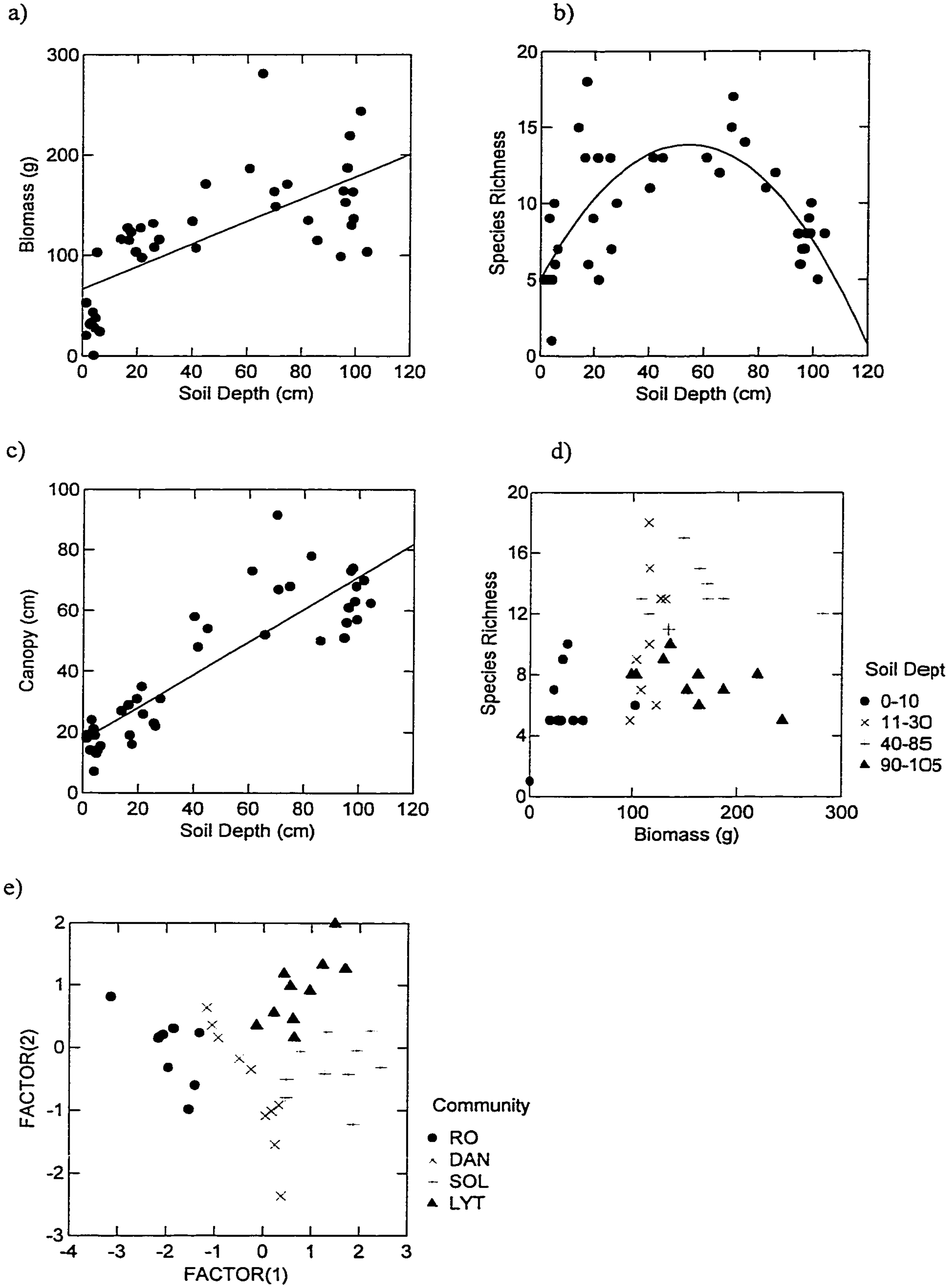

a)
Biomass (g)
300
200
100
0
0
20
40
60
80
100
120
Soil Depth (cm)
b)
Species Richness
20
15
10
5
0
0
20
40
60
80
100
120
Soil Depth (cm)
c)
Canopy (cm)
100
80
60
40
20
0
0
20
40
60
80
100
120
Soil Depth (cm)
d)
Species Richness
20
16
12
8
4
0
0
100
200
300
Biomass (g)
Soil Dept
● 0-10
× 11-30
– 40-85
▲ 90-105
e)
FACTOR(2)
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3
FACTOR(1)
Community
● RO
× DAN
– SOL
▲ LYT

Figure 1.5 The total percent native species in each community, Rock outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT). This was obtained from the species list for each community. Refer to Appendix 8.

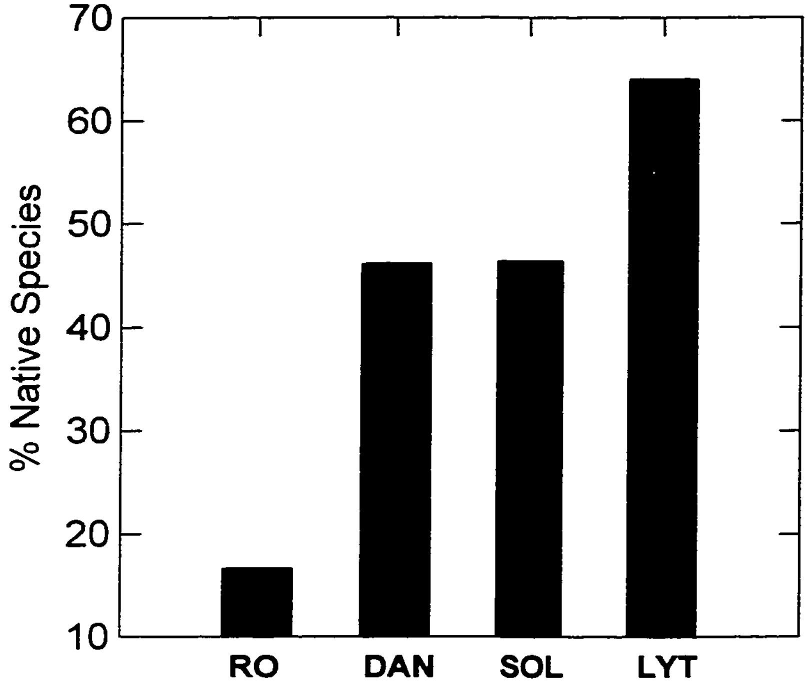

% Native Species
70
60
50
40
30
20
10
RO
DAN
SOL
LYT

Figure 1.6 The distribution and the abundance of some species in the old field. Distribution refers to position along the soil depth gradient and abundance refers to the Braun-Blanquet score. Each column is labeled with respect to habitat within the old field.

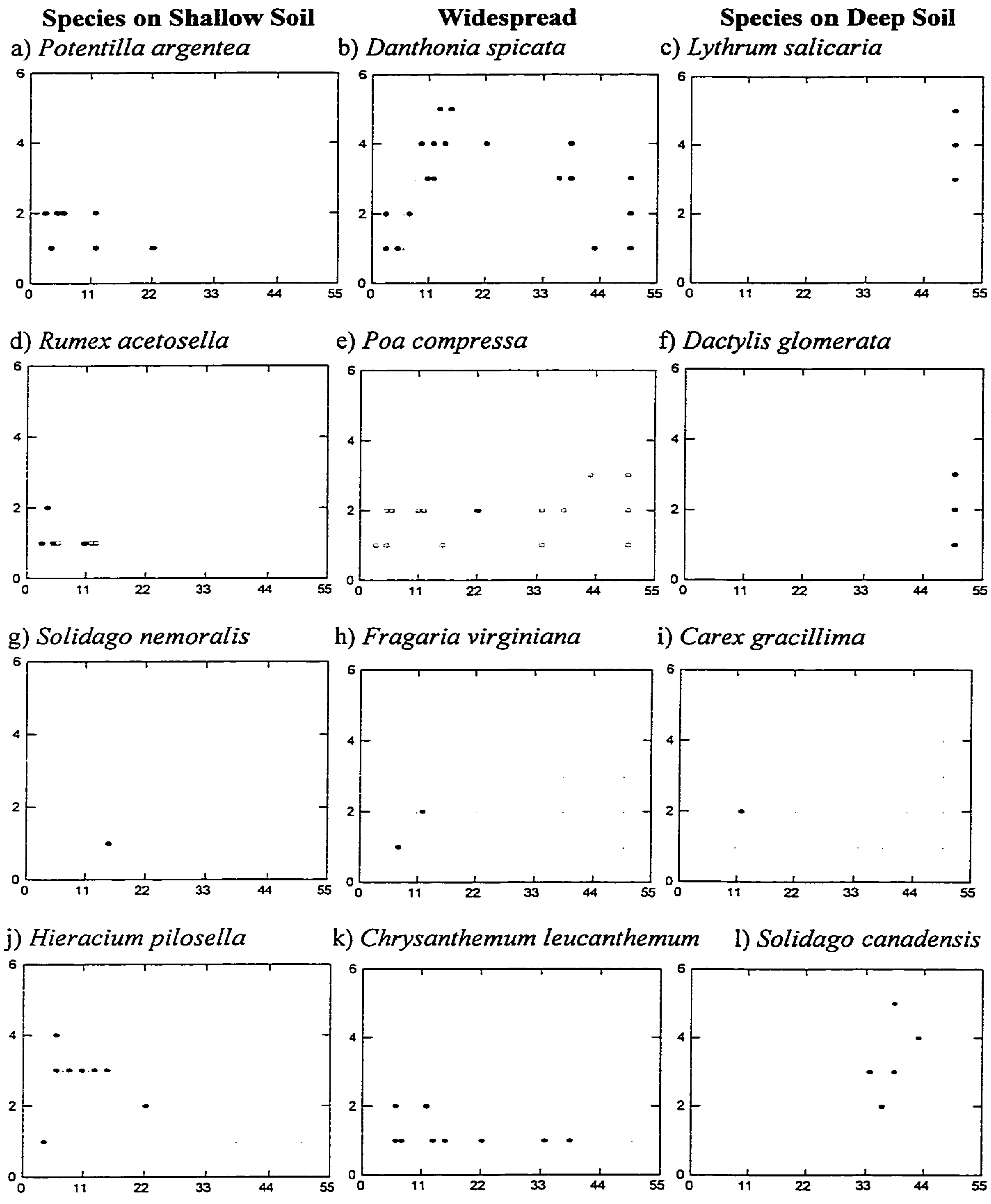
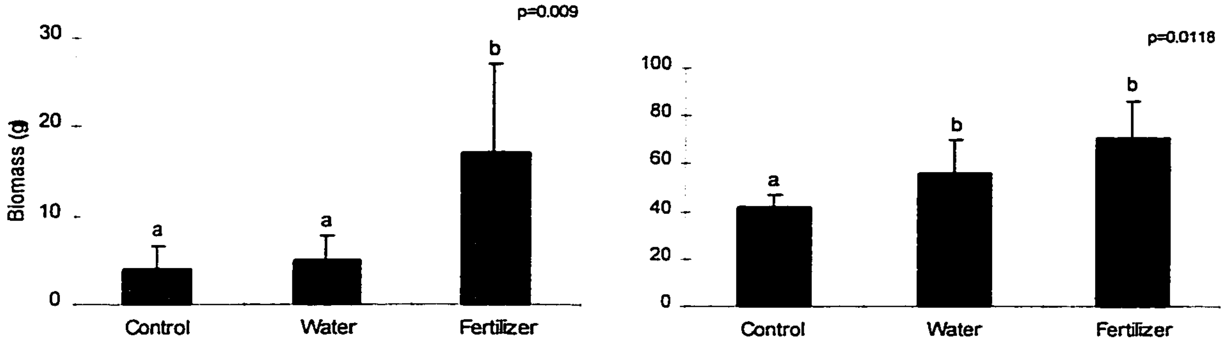
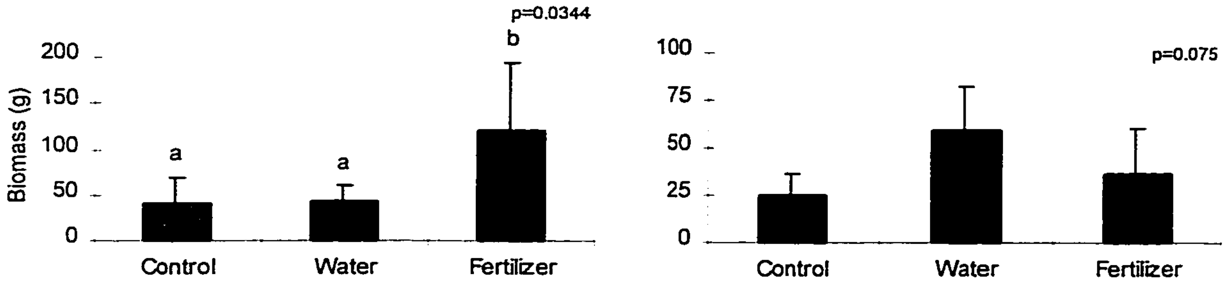

Species on Shallow Soil
Widespread
Species on Deep Soil
a) *Potentilla argentea*
b) *Danthonia spicata*
c) *Lythrum salicaria*
d) *Rumex acetosella*
e) *Poa compressa*
f) *Dactylis glomerata*
g) *Solidago nemoralis*
h) *Fragaria virginiana*
i) *Carex gracillima*
j) *Hieracium pilosella*
k) *Chrysanthemum leucanthemum*
l) *Solidago canadensis*
0
2
4
6
0
11
22
33
44
55

Figure 1.7 The biomass in each of the treatments compared to a control, separated by community. The error bars represent the standard deviation, n=15 and the p-values are a result of a Kruskall-Wallis ANOVA. The letters (a-d) are the result of Bonferroni post-hoc comparisons.


a) Rock Outcrop

b) *Danthonia*


c) *Solidago*

d) *Lythrum*

Chapter 2

Plant competition intensity along a soil depth gradient in an old field

Introduction

Plant species composition, diversity, biomass and growth form have all been shown to vary in nature with productivity (Whittaker 1975, Bakelaar and Odum 1978, Grime 1979, Silvertown 1980, Tilman 1988, Goldberg and Miller 1990). Productivity, which can be defined as the rate at which energy is bound by organic material created by photosynthesis (Whittaker 1975), has a large impact on plant communities. However, the question of whether or not biotic interactions, such as competition or predation, also change with productivity is far from resolved.

All plants, regardless of the productivity of the area in which they grow, require light, soil nutrients and water in order to survive. Almost without exception, plants growing in natural environments have neighbours and therefore must compete to gain access to these resources (Clements *et al.* 1929, Gurevitch *et al.* 1992, Tilman 1997b). Plants compete below ground for soil nutrients and water, while they compete above ground to acquire light.

This chapter explores one aspect of this competition for resources, competition intensity. Competition intensity is defined as the cumulative effect of all neighbours simultaneously on a given individual (Keddy 1989). In plant community ecology there is a large debate surrounding the question of whether or not competition intensity changes along productivity gradients (Reader and Best 1989, DiTomasso and Aarssen 1991, Miller 1996, Twolan-Strutt and Keddy 1996, Goldberg and Novoplansky 1997). According to Grace (1993), the importance of competition in ecological communities has been one of the most hotly debated and persistently contested issues throughout the history of ecological science.

Productivity gradients can be natural or experimental and can be represented in a variety of ways. Natural gradients could be percent plant cover, standing crop, soil depth, topography or even wave exposure (Wilson and Keddy 1986, Pantastico-Caldas and Venable 1993, Belcher *et al.* 1995, Kadmon 1995). Adding fertilizer, water or a specific nutrient, such as nitrogen can create experimental gradients (Whigham 1984, DiTomasso and Aarssen 1991, Wedin and Tilman 1993). All of these gradients affect the rate at which energy is bound by organic material created by photosynthesis. Therefore, they can be used to explore changes in competition with productivity.

There are three possible linear relationships between competition intensity and productivity. Competition intensity could be constant, increasing, or decreasing along the gradient. Figure 2.1 illustrates the three possible outcomes assuming linear responses. Though, the slopes of these lines are arbitrary and may vary among specific cases.

The reason for the debate over the relationship between competition intensity and productivity is the inconsistency in the literature. Nearly an equal number of studies found either an increase or no change in competition intensity with increasing productivity (Table 2.1). For example, the following two studies both looked at competition intensity along an experimental nutrient gradient in an old field, however conflicting results were reported. In 1991, Wilson and Tilman set up an experimental nitrogen gradient in an old field in Minnesota, they found that competition intensity did not vary significantly along the gradient. In contrast, Turkington *et al.*(1993) created an artificial nutrient gradient with old field species and found that competition intensity increased along the gradient. It is still not clear which of these outcomes is the most representative or if the outcome changes with each specific gradient. Therefore, this study was done to try and help resolve this debate.

Both herbivory and stress were also explored along this soil depth gradient. It has been suggested in the literature that herbivory may confound effects of competition in plant communities (Reader 1991, Burger and Louda 1994, Burger and Louda 1995, Rachich and Reader 1999). Taylor *et al.* (1997) actually found that herbivory was able to override the effects of competition and mask them completely. That work was done with three marsh grasses in areas of increasing salinity. Therefore, patterns in herbivory along the gradient were included. Stress, defined as any environmental factor potentially unfavourable to living organisms and normally imposes a metabolic cost (strain) on plants (Levitt 1972), was included because it can be looked at as the opposite of productivity. Since here there is an independent measure of stress, it allowed an opportunity to see how stress changes with productivity along a gradient of soil depth.

Purpose

The purpose of this research is to test whether plant competition intensity varies with soil depth, separated into above and below ground components. Also, the experiment examines whether or not there is also a relationship between herbivory and soil depth or stress and soil depth.

Hypotheses

1) CSR (Competitor, Stress-Tolerator, Ruderal) hypothesis (Grime 1973, 1979)

This hypothesis is from Grime's classification of plant strategies. He hypothesizes that a plant acts as a competitor (C), a stress-tolerator (S) or a ruderal (R). A competitor grows in areas of high productivity and maximizes its ability to capture resources. A stress tolerator grows in areas with low productivity (high stress) and does not compete with neighbors, but rather endures a continuously unproductive environment. A ruderal is a plant that grows in areas with high levels of disturbance and also does not compete with neighbours, but has a short life span with high seed production in order to re-establish following the disturbance. Therefore, in unproductive sites there are stress tolerators and in productive sites there are competitors. As productivity increases, plants have higher growth rates, produce increased amounts of biomass and have more interactions with other plants, which are all characteristics of a competitor. Consequently, stress tolerators are located at the unproductive end of the gradient.

2) Resource Ratio hypothesis (Tilman 1982, 1988)

According to Tilman, in unproductive sites plants compete for soil resources, whereas in productive sites, plants compete for light. Competition is primarily below ground in unproductive sites and primarily above ground in productive sites. Therefore, there is a qualitative change in competition, not a quantitative change.

3) Classical Exploitation Hypothesis (Oksanen *et al.* 1981, Crawley 1997b)

This hypothesis suggests that the importance of herbivory varies with productivity. Herbivory has little effect in unproductive environments, moderate impact in systems of intermediate productivity and low effect in areas of high productivity. At high productivity, there is enough energy to support larger predators to consume herbivores and at low productivity herbivores are food limited. This hypothesis assumes large spatial scales and the addition of a new trophic level as productivity increases.

Predictions

The research reported in this chapter tests an aspect of the CSR hypothesis using a soil depth gradient in an old field. The predictions follow the CSR hypothesis as opposed to the Resource Ratio hypothesis for a couple reasons. First, similar studies done by Keddy and other colleagues have found evidence to support Grime's theory. Second, Grime's explanation of plant strategies seemed a more plausible explanation for behaviour along a gradient. And finally, it is simpler to allow the null hypothesis to be of no difference as the Resource Ratio hypothesis predicts.

1) Competition intensity will increase as productivity increases along the gradient, according to the CSR hypothesis.

2) Both above and below ground competition intensity will increase with productivity, according to the CSR hypothesis.

3) Herbivory will increase along the gradient, after the Classical Exploitation hypothesis.

4) Stress will decrease along the gradient, also following the CSR hypothesis.

Methods

The competition intensity experiment was set up in an old field during the summer of 1999. The old field is located in Lanark County west of Carleton Place, Ontario, Canada (Lat. 45°12'N, Long. 76°30'W). This is the same study site discussed in the previous chapter and its description can be found there.

As described earlier, there are four communities within the old field. Ten replicates of each phytometer, a plant that is used as a meter to measure something, such as competition intensity, were planted in each community for statistical and practical reasons. Indicator species or phytometers have been used for a long time in ecology (Clements and Goldsmith 1924, Clements 1935). Therefore, thirty plots of $1m^2$ were marked out, ten for each phytometer species, in each community, for a grand total of 120 plots.

Once it was determined, through germination trials, that there were enough viable seeds for each phytometer, the seedlings were started on April 8, 1999. Small peat pots of approximately 6 cm^2 and Premier® organic potting soil were obtained from Ritchie's Feed and Seed in Gloucester, Ontario. The peat pots were set up on large trays in the University of Ottawa greenhouse. Each pot was filled ¾ of the way with soil. Two hundred and thirteen pots were made for each phytometer, with 640 in total. In each pot, eight to ten seeds were distributed over the surface and then covered with 1 cm of soil. These seedlings were watered as needed, provided with sufficient sunlight and kept at 25°C. After two weeks of growth, the pots were continually weeded so that only four individual seedlings remained in each pot to prevent competition.

During the first three weeks of May, while the seedlings were getting established in the greenhouse, the treatments were being prepared. First, 10 $1m^2$ plots were randomly selected from the areas marked out previously in each community. Then within each plot there were four treatment subplots of $0.25m^2$ assigned. The treatments were 1) control, 2) no neighbours 3) below ground competition only and 4) a no herbivory treatment. The control treatment was essentially left unmanipulated. In the no neighbours treatment, the canopy was removed, the soil over turned to approximately 10 cm and then the subplot was sprayed with a non-residual herbicide, Wipeout®, with the active ingredient glufosinate ammonium. This was done to eliminate all neighbours roots and shoots. For the below ground treatment, a plastic net (mesh 1 cm^2) was used to pull back all the neighbouring shoots or above ground biomass so that only root competition could occur. The final treatment, no herbivory, had a wire cylinder (mesh ~ 2.5 cm^2) which was used to prevent small mammals and deer from being able to graze within the subplot. Unfortunately a mesh of this size could not prevent smaller herbivores, such as insects or snails from feeding. However, a mesh size small enough to prevent such herbivores would risk causing too much shading in the subplot. Figure 2.2 shows approximately what these four treatments looked like in the field.

During May 25 to 27, all of the phytometers were taken to the field and transplanted into the plots. In the centre of each subplot a phytometer was planted. The phytometers that were planted were selected for similarity in size to other individuals of the same species. However, there was inevitably some variation in initial size. Gerry and Wilson (1995) found that initial size had no influence on competitive response during the first summer of growth. Therefore, one could be confident that any slight variation would not affect the outcome of the competition experiment.

In each plot either *Lythrum salicaria* (purple loosestrife), *Liatris spicata* (dense blazing star) or *Avena sativa* (oats) were planted. Three phytometers were used because the choice of phytometer can affect the outcome of the experiment (DiTomasso and Aarssen 1989, Wilson and Keddy 1986a, Wilson in press). There were ten plots in each of the four communities, for each phytometer species, which resulted in 120 plots in total.

During the first two weeks of phytometer establishment, the plants were watered regularily as needed. It rained four times during the two weeks, so additional watering was done only three times. Also, during this establishment period, any phytometers that did not survive were replaced by other individuals of the same species. The oats had a very low initial survival rate and the majority had to be replanted. For the other two species, the initial survival rate was quite high and only about ten percent of the individuals of each species needed to be replaced. Any replaced plants were also kept moist for another two weeks following establishment. However, after phytometers were established none were watered and any mortalities were not replaced.

The no neighbour treatment was weeded twice a week to prevent any neighbours from invading. Also, the neighbours in the below ground only treatment were checked often to make sure they were still under the plastic netting. In addition to the individuals growing in the field, 30 phytometers (15 of each species) were left growing in the greenhouse. These were subjected to similar treatments as in the field in order to determine if there was an inherent effect of the plastic nets or cages on the phytometers. These plants were either surrounded by a net or cage made of the same material as in the field or left as a control. At the end of the summer, the above ground biomass was harvested, weighed and differences in biomass were used to determine if these treatments had an effect on growth.

During the summer, some abiotic measurements were taken. A rain gauge was set up in the field to measure rainfall through the course of the experiment. However, it was not possible to check it every day and was moved once through the course of the experiment. Therefore, it was decided that Environment Canada data from a nearby weather station would be more reliable. This was decided because the weather was reported there twice daily, included temperature, and was available for the past ten years. Ten soil samples of approximately 500 ml were obtained from each community in early August by taking a core of the top 10 cm. Half of each sample was analyzed by the Soil and Nutrient Laboratory at the University of Guelph for nitrogen ($NO_{-3}N$), phosphorus (P), potassium (K), magnesium (Mg) concentrations and pH. The other half was analysed for organic content. First, the dry weight of the sample was measured, then it was burned in a muffle oven for 48 hours at 550°C and finally re-weighed (Andrews 1973). Lastly, soil depth was measured with a soil auger in each of the experimental plots, ten times in each community for each phytometer.

On Sept. 1, 1999 the phytometers were all harvested by clipping at ground level. The below ground portion of the phytomter was not collected because roots are often difficult to separate from the soil without breaking or obtaining soil as well.

As the phytometers were clipped, they were placed in brown paper bags and taken back to the lab. Then, the bags were placed in the drying oven for 24 hours at 80°C.

Once the phytometers were dry, each was weighed in order to get biomass data. Biomass could then be used to calculate competition intensity, with the following formula:

$$\mathbf{CI_{TOTAL} = (P_{NN} - P_{NRS}) / P_{NN}}$$

$$\mathbf{CI_{ROOTS} = (P_{NN} - P_{NR}) / P_{NN}}$$

$$\mathbf{CI_{SHOOTS} = CI_{TOTAL} - CI_{ROOT}}$$

Where P_{NN} = phytometer in no neighbour treatment (no competition)

P_{NRS} = phytometer in neighbour roots and shoots treatment (total comp.)

P_{NR} = phytometer in neighbour roots treatment (belowground comp.)

Total pooled competition intensity was also calculated in order to increase the sample size. If the individual plant died in the no neighbour treatment, P_{NN} would equal zero. If there is a zero in the denominator, one cannot calculate CI_{TOTAL}. One could assume that outright death (as opposed to reduced growth) was due to a random event of planting a phytometer with reduced fitness, or at least was not due to competition. Therefore, we calculated the average biomass of all the individual phytometers that did survive in the no neighbour treatment and used this value in the following formula:

$$\mathbf{CI\ Pooled_{TOTAL} = (P\ average_{NN} - P_{NRS}) / P\ average_{NN}}$$

Herbivory and stress were also calculated using the phytometer biomass. Herbivory was calculated as the difference in growth between the treatment protected from herbivores with a cage and the similar treatment without a cage. The difference in biomass represents how much was consumed by herbivores. Stress was also calculated as a difference in growth between the no neighbour treatment and the average biomass of the ten largest phytometers of each species in the field. The ten largest phytometers, regardless of treatment, were used as an indication of the ideal size each species could reach. The difference in biomass represents how much growth was limited by stress. These were calculated according to the following formulas:

$$\textbf{Herbivory} = \mathbf{P_{CA} - P_{NRS}}$$

$$\textbf{Stress} = \mathbf{(P_{NN} - P_{MAX}\ average) / P_{MAX}\ average}$$

Where P_{CA} = phytometer in caged treatment

P_{MAX} = ten largest phytometers in any treatment.

Therefore, biomass data could be used to calculate competition intensity, herbivory and stress for subsequent statistical analysis. A one-sample t-test was used to determine if competition intensity differed significantly from zero. One way ANOVA's or the non-parametric equivalent, the Kruskall-Wallis, was used to compare all the variables among the four communities. Spearman rank correlations were used to explore the relationships between a variable and soil. Non-parametric tests, Kruskall-Wallis and Spearman Correlation, were used when sample sizes were low or when the data could not be transformed to meet parametric assumptions.

Results

Phytometer Survival

The survivorship of *Avena sativa* was very low, only approximately five individual phytometers survived, whereas for the other two species there was approximately 85% survival, during the initial two weeks. Therefore, *Avena* could not be included in any further analysis. All results are therefore based on the performance of the other two phytometer species, *Liatris spicata* and *Lythrum salicaria*. The survival of these phytometers, by the end of the experiment, generally increased along the soil depth gradient, regardless of the treatment in which the individual plant was grown (Fig. 2.3a,b).

Competition Intensity

The greenhouse trials, which looked at the effects of the nets and cages used in the field experiment (Fig. 2.4), found no significant difference among the two treatments and the control for either *Liatris* ($p=0.631$) or *Lythrum* ($p=0.670$).

Overall, the intensities of total competition ($p<0.001$) and belowground competition ($p<0.001$) were significantly greater than zero, whereas that of above ground competition was not ($p=0.298$ *Liatris*, $p=0.08$ *Lythrum*). This was true for both phytometers. There was a significant difference in total competition intensity (CI) between the communities (Fig. 2.5a,b) for both *Liatris* ($p=0.025$) and *Lythrum* ($p=0.048$), with a lower CI towards the deeper end of the gradient. Total CI also decreased significantly with soil depth for both phytometers (Fig. 2.5c,d, $r_s=-0.572$ *Liatris*,

r_s=-0.572 *Lythrum*, $p<0.002$). The same decreasing pattern occurred for below ground competition intensity both between communities (Fig. 2.6a,b, $p<0.001$ *Liatris*, $p=0.011$ *Lythrum*) and with soil depth (Fig. 2.6c,d, $p<0.001$ for both *Liatris* r_s=0.469 and *Lythrum* r_s=-0594.). Above ground competition intensity (CI) was different. *Liatris* showed no significant change in above ground CI across the four communities (Fig. 2.7a, $p=0.319$), however, for *Lythrum,* above ground competition increased only in the deepest soil of the *Lythrum* community (Fig. 2.7b, $p=0.022$). However, the correlations between above ground CI and soil depth were not significant (Fig. 2.7c,d, r_s=0.190, $p>0.5$ *Liatris*, $p>0.02$ *Lythrum*).

Similar results were found from the pooled competition intensity data. Again, there was a significant difference between the communities for *Liatris* (Fig. 2.8a, $R^2=0.312$, $p=0.003$) and *Lythrum* (Fig. 2.8b, $R^2=0.315$, $p<0.001$). Also, there was a significant decrease from the shallow to deeper soil communities and this was true for both species (Figure 2.8c,d, $p<0.001$). As the results for total pooled and unpooled competition were so similar, pooled data was not analysed for above or below ground competition intensity.

Herbivory and Stress

In addition to competition intensity, herbivory and stress were also examined for patterns along the soil depth gradient. Herbivory did not differ between the communities (Fig. 2.9a,b) for *Liatris* ($R^2=0.039$, $p=0.874$) or *Lythrum* ($R^2=0.029$, $p=0.894$). There was also no significant relationship between herbivory and soil depth, although the trend was towards higher herbivory in the deeper soil (Fig. 2.9c,d, $p>0..5$). The lowest stress occurred in the *Danthonia* community for both phytometers (Fig. 2.10a,b, R^2=0.595, p<0.001 *Liatris*, R^2=0.235, p=0.021 *Lythrum*), although, no significant correlation was found (Figure 2.10c,d, p>0.5 *Liatris*, p>0.1 *Lythrum*).

Abiotic Measurements

Soil organic content did not significantly differ among the four communities (Fig. 2.11a, R^2=0.045, p=0.645). pH increased from the Rock Outcrop to *Solidago* community, but then decreased again in the *Lythrum* community (Fig. 2.11b, R^2=0.614, p<0.001). The concentration of nitrate generally increased as the soil depth of the communities increased, except for a minimum in the *Danthonia* community (Fig. 2.11c, R^2=0.653, p<0.001). Phosphorus appeared to be more abundant as in the deeper soil communities, though there was more phosphorus in the *Danthonia* than the *Solidago* community (Fig. 2.11d, R^2=0.709, p<0.001). The *Solidago* community had the lowest concentration of potassium while the *Lythrum* community had the most (Fig. 2.11e, R^2=0.310, p=0.004). Magnesium concentration was lowest in the Rock Outcrop and greatest in the *Lythrum*, therefore Mg appears to increase with soil depth (Fig. 2.11f, R^2=0.836, p<0.001).

Using Environment Canada weather data the summer of 1999 had a higher average maximum daily temperature and had a lower average total daily rainfall than the last ten summers (Fig. 2.12a,b). For a comparison to the rain gauge see Appendix 11.

Discussion

General Implications

On the debate surrounding the relationship between plant competition intensity and productivity, there are two prevailing views in the literature. The first view predicts that competition intensity will increase with productivity because the unproductive end of the gradient is subjected to stress rather than competition (Grime 1973, 1979). The second view predicts that competition intensity will not change with productivity because there is a shift from below to above ground competition but overall total competition intensity remains the same (Tilman 1982, 1988). This study, however, found evidence for a third point of view, that competition intensity decreases with productivity, measured as soil depth.

Competition Intensity

There was evidence of strong competition occurring in the field, though the above ground competition was not significant. Competition in this field was primarily below ground. This would seem to indicate that the limiting resource is probably also below ground. The lack of above ground competition is consistent with Belcher *et al.*'s (1995) experiment in an alvar (see also Wilson 1988, Peltzer et al. 1998).

Rock outcrops had the greatest competition intensity, with competition intensity decreasing in the communities with a greater soil depth (Figure 2.5). No other studies in the literature have reported a decrease in competition intensity along gradients of increasing productivity. However, Goldberg *et al.* (1999) did a meta-analysis on a group of papers that reported relationships between competition intensity and productivity. They used 294 cases in 14 studies and found that competition intensity significantly declined with increasing productivity when all of these data points were combined. The decreasing competition intensity with productivity was the result when final biomass and survival data were used, but not growth rate. They gave two possible explanations for this decrease. 1) The intensity of herbivory changed along the gradient and 2) the relationship between below ground and above ground (i.e. how the two variables are related in the competition intensity formula) affects the value of total competition intensity (Goldberg *et al.* 1999). The first explanation involving herbivory indicates that, if herbivores preferentially are consuming biomass in the more productive areas, this may actually decrease the competition among individuals to a level below what it is in the low productivity areas (see also Harper 1977). The second explanation points out that total competition, calculated as a sum of above and below ground competition, is therefore dependent on the values of these two variables. In this case the second explanation is more likely because above ground competition was not significantly different from zero, therefore total competition essentially equals below ground competition. However, even though mammalian herbivory did not appear to increase along the gradient, insect herbivory may have, though it was not measured.

Below ground competition intensity followed the same patterns as total competition intensity, i.e. it decreased along the gradient (Figure 2.6). It seems logical that below ground competition would decrease as the volume of soil and hence the amount of available resources increases. Above ground competition intensity did not change along the gradient, which is not surprising since it does not differ significantly from zero (Figure 2.7). Belcher *et al.* (1995), using the same design, also found no above ground competition in an alvar with a soil depth gradient. That result and the one from this study are both consistent with Tilman's model that competition will occur only where resources are most limiting (Tilman 1982). It appears that in the old field below ground resources were most limiting, though the effect decreased along the gradient. Another study (Aert *et al.* 1991) also found no net effect of above ground competition, only below ground between two species of dwarf shrubs and a grass species. Wilson (1993) found that it was below ground, as opposed to above ground competition that limited growth of the species examined in Australian grasslands and heath.

Cahill (1999) did find evidence of both above and below ground competition. He also found that below ground competition decreased while aboveground competition remained constant in an old field, as a function of fertility. Cahill measured both below and above ground competition directly and found that there was an interaction between the two variables. However, the gradient was not natural and the tubes used to construct the above ground only treatment, were inserted into holes drilled out by a soil auger, in which case the soil structure would be completely changed (Keddy, P.A. personal communication). In our study, independence was assumed and above ground competition was measured indirectly by the difference between total and below ground competition intensity. This could bias the results, which will be discussed later.

Not all studies found an interaction between above and below ground competition. Putz and Canham (1992) measured above and below ground competition directly in shrubs by reducing one then the other. They found that below ground competition was more intense on nutrient poor soils whereas above ground competition was more intense on good soil. However, the treatment that reduced both types of competition resulted in an additive increase in final biomass. Therefore, there was no evidence of an interaction between above and below ground competition, although, other studies have found evidence of a trade-off between above and below ground. Hutchings (1997) grew clones of the same species at different nutrient levels and found that as nutrients increased, biomass allocation to the roots decreased while it increased to the shoots.

There was mortality of some phytometers in the more unproductive end of the gradient. Whenever the phytometer did not survive in the no neighbour treatment, competition intensity could not be calculated. Therefore, the pooling process outlined in the methods was used to increase sample size and to see if different patterns emerged. Pooled data also demonstrated the decrease in competition intensity with productivity Figure 2.8). Pooling data in this manner is suspect to more uncertainty and underlying assumptions, therefore these results could not stand-alone. However, in combination with the results obtained with the unpooled data it is clear, that at least along this gradient, competition intensity is in fact decreasing.

Phytometers were grown in the greenhouse with cages, nets and a control to determine whether these objects had any inherent effect on the phytometers. It can be seen in Figure 2.4 a and b that there were no significant differences among the three treatments either *Liatris* or *Lythrum* species. From this one can therefore conclude that the cages or nets did not have an effect unto themselves.

Herbivory and Stress

Herbivory did not vary by community or along the soil depth gradient (Figure 2.9). Instead, grazing intensity appeared to be constant regardless of the amount of above ground biomass, which did increase along the gradient (see Chapter 1). However, due to the mesh size, it was only an estimate of mammalian herbivory. There is no way to determine if insect herbivory changed along the gradient, though there was very little evidence of chewed leaves. Therefore, herbivores in the field did not feed preferentially where there was more plant material to consume. Taylor *et al.* (1997) looked at changes in herbivory in coastal marshes that had a range of salinity. In two of the three grass species investigated, herbivory did not change significantly across the salinity gradient. In contrast to this result, a study in Mediterranean grassland found that grazing intensity increased with productivity along a trophic gradient (Puerto *et al.* 1990). Bonser and Reader (1995) also had a caged phytometer treatment to measure herbivory and found that grazing increased along a biomass gradient. Burger and Louda (1995) found similar results when looking at herbivory on prickly pear cactus. However, van de Koppel *et al.* (1996) found herbivory was most intense at intermediate levels of productivity. One explanation they gave for this was that at high productivity, grazing pressure was unable to keep biomass in check and this may therefore prevent herbivores from gaining access to the vegetation.

Stress differed significantly among the four communities for *Liatris,* with the least amount of stress occurred in the *Danthonia* community (Figure 2.10 a). The *Lythrum* phytometer also had the least stress in the *Danthonia* community, though it was not significantly different than the *Solidago* or *Lythrum* communities. This is an entirely unexpected result because the biomass, canopy height, species richness and soil depth (see chapter 1) all indicate that there is in fact a productivity gradient. One would expect the least stress in the *Lythrum* community. There was large phytometer mortality in the more unproductive end of the gradient compared to the more productive end. This certainly indicates that stress exists in the field and that it decreased along the gradient (Belcher 1992). However, stress does not seem to have been shown to decrease in the way that it was measured in this study.

Stress appears to be greatest at either end of the gradient, and lowest in the intermediate community. High stress in the Rock Outcrop community is easily attributed the lack of sufficient soil to acquire nutrients, water or physical support to remain upright. As for high stress in the *Lythrum* community, this could be attributed to spring flooding that occurs only in that community. However it is less obvious why stress is lowest in the *Danthonia* community. We suggest some possible explanations for this surprising result. The soil in the *Danthonia* community has the lowest organic content, the lowest concentration of nitrogen, a high concentration of phosphorus and the lowest concentration of magnesium. It is possible that the particular phytometers species prefer these conditions, particularly a low N:P ratio. Also, the field has been shown to be nutrient limited, therefore it is possible that phosphorus is limiting as opposed to nitrogen, which usually is limiting in terrestrial systems. The *Danthonia* community is also drier that the *Solidago* or *Lythrum* communities. *Liatris* grows naturally in dry areas and the *Danthonia* community may be closest to its soil moisture preferences, though this does not hold for the *Lythrum* phytometer. Mycorrhizal infection could be greater in the *Danthonia* community, though there is not other evidence for this. Herbivory is also lowest in the *Danthonia* community for *Liatris* and lower for *Lythrum*, though it is not a significant difference in either case and therefore unlikely. Another possible explanation is a result of shading. There are no effects of shading in the *Danthonia* community as the phytometers are taller than the canopy. The cleared plots, for the no competition and below ground only competition, in the other two communities should have eliminated shading. However, it is possible that these clearings were not large enough and the phytometers were in fact being shaded. In that case, shading stress would be higher in the *Solidago* and *Lythrum* communities, with the least stress in the *Danthonia* community. However, above ground competition, a consequence of shading was found to be very low within the field, making it improbable that this is the best interpretation. The most likely explanation is the differences in soil characteristics, particularly the high levels of phosphorus in the *Danthonia* community.

Soil analysis and Weather Data

The soil along the gradient also changed with respect to abiotic measurements (Figure 2.11). It is not surprising that different soil depths supported different plant species would have different soil characteristics. As an overall trend, the soil appeared to be more productive in the deeper areas of the gradient. There was a greater organic content, a shift towards more neutral soil and greater concentration of the nutrients measured. Therefore one could conclude that the soil depth gradient could also be a nutrient gradient and with both combined it is certainly a productivity gradient.

The Environment Canada and rain gauge data clearly indicate that the summer of 1999 had unusual weather compared to the last ten years. The summer the experiment was performed was hotter and drier than the last ten years. This probably increased the mortality of phytometers, especially in the shallower soils. However, water was still not shown to be the limiting resource (see Chapter 1). Vargas-Mendoza and Fowler (1998) found, in a pot experiment with *Ratibida columniferai*, that different amounts of competition but not water had a significant effect on final biomass. In this field as well, competition had a greater effect than water.

Choice of phytometers

Two of the three phytometers used were good choices. *Liatris spicata* and *Lythrum salicaria* survived in the field at all soil depths to some extent, showed variation in size along the gradient and were naturally found in similar habitats. However, *Avena sativa* was not a good choice. This agricultural species could not withstand the harsh conditions, compared to a fertilized and irrigated farm, in the old field. Mortality was so high that the species had to be excluded from the experiment. This suggests that oats and possibly other agricultural species are not well suited to being used as phytometers, at least not in old fields.

Liatris and *Lythrum* produced essentially the same results. These two species have a similar growth form and both occur in deeper soil. A good choice for a third phytometer might have been a species with a different growth form, for example a rosette species. Also, a rock outcrop species or at least a species found more on shallow soil might have also produced significant results. Using two species that both have similar soil depth preferences may have introduced a bias into the study. The *Liatris* and *Lythrum* may have had to compete more intensely in the communities where they are not naturally adapted to grow. If, for example, a deeper soil and a shallower soil species had been chosen and both had similar results then one could be more confident in concluding that the differences were not just due to more competition where the species was not adapted to grow. This might be one explanation as to why the competition was so intense in the *Danthonia* community. Also, a rosette species might have had a greater survival in the shallower end of the gradient, increasing the sample size in that area. Increased survival in the Rock Outcrop might occur because rosette species tend to be better adapted to dry environments as they often have a reduced surface area, they are low to the ground and protected from the wind, they often are hairy and sometimes succulent.

Limitations of the experiment

As in all field experiments there were some limitations of the study. First, the indirect measurement of above ground competition is one weakness. It is possible that above ground competition did differ significantly from zero but just was not detected (Cahill 1999). Also, the mortality of the *Avena* phytometer and the mortality in the Rock Outcrop community in general reduced the confidence in the overall conclusions. The experiment was only run for one growing season and it is possible that a longer-term study could have reported different results or at least the same results with more confidence (Wedin and Tilman 1993). Finally, the use of less powerful, non-parametric statistics decreases confidence in the overall results, particularly when no difference was found.

Practical considerations for future work

The debate surrounding the relationship between competition intensity and productivity gradients is still not resolved. Therefore, there is still more work to be done in this field. A few suggestions for a good experimental design are as follows. The above ground competition intensity should be measured directly (Cahill 1999). However, a less invasive method than the one used by Cahill would be preferable. Natural as opposed to artificial gradients are a better reflection of reality and should be chosen whenever possible. The greater the range of the gradient the more likely no patterns will be overlooked, therefore a longer gradient is always better. Belcher *et al.* (1995) also looked at a soil depth gradient but it only ranged from 0 to 17 cm and similarly Reader and Bonser (1993) looked at a gradient of 8-26 cm. The type of gradient and the range have been shown the affect the outcome of experiments (Kadmon 1995, Goldberg *et al.* 1999). It is better to use at least two phytometers in case the results are an exception because of an unusual response of one species. Using three species, with one having a different growth form, would be better still. Finally, current reviews seem to indicate that it is better to use no competition as opposed to a monoculture as a reference point (Miller 1996) and to calculate relative competition intensity as opposed to absolute competition intensity (Grace 1995). This experiment had a natural gradient, with a large range, used two phytometers and calculated relative competition intensity with no competition as a reference. More similar studies that measure above ground competition directly are required to finally resolve this issue in plant ecology.

Total and below ground competition decreased with soil depth, while there was little evidence of above ground competition. Mammalian herbivory did not change along the gradient. Stress was greatest at both ends of the gradient, i.e. the intermediate habitat, *Danthonia*, had the least stress (Figure 2.13). Overall, stress had the greatest negative effect on phytometer growth, then competition and finally herbivory (Figure 2.14).

Table 2.1 A summary of field experiments that have measured competition intensity (CI) along productivity gradients. For each the study site, the dependent variable (what was measured to determine competition intensity), the type of gradient (the indicator of productivity and whether it was natural, N, or experimental, E) and how competition intensity performed along an increasing gradient of productivity are reported (after Goldberg and Novoplansky 1997).

Reference	**Study Site**	**Dep variable**[1]	**Type of gradient**[2]	**CI along productivity gradient**[3]
del Moral 1983	subalpine meadow	D	snow melt/moisture (N)	I
Gurevitch 1986	grassland	B	topographic/moisture (N)	I
Wilson & Keddy 1986	lakeshore	B	wave action (N)	I
Gurevitch & Unnasch 1989	old field	D	nutrient (E)	I
McGraw & Chapin 1989	tundra	B	nutrient (N)	I
		R		d
		S		C
Reader & Best 1989	old field	R, S	nutrient (E)	I
			standing crop & light (N)	C
Gurevitch *et al.* 1990	glasshouse	B	resources (E)	C
Kadmon & Shmida 1990	desert	R	water (N & E)	I
		S		C
Reader 1990	old field	S	nutrient (E)	I
Wilson & Shay 1990	prairie	FS	biomass and nutrients (E)	C
DiTommaso & Aarssen 1991	old field	B	nutrient (E)	C
Wilson & Keddy 1991	wetland	S	nutrient (N)	I
Wilson & Tilman 1991	old field	B	nitrogen (E)	C
Campbell & Grime 1992	various	B	nutrient (E)	I
Pantastico-Caldas & Venable 1993	desert	S, R, B	moisture (N)	I
Turkington *et al.* 1993	old field	B	nutrient (E)	C
Wilson & Tilman 1993	old field	B	nitrogen (N)	C
			disturbance (N)	I
Reader *et al.* 1994	old field	B	plant biomass (N)	C
Belcher *et al.* 1995	alvar	B	soil depth (N)	C
Bonser & Reader 1995	old field & shoreline	B	biomass (N)	I
Kadmon 1995	desert	SR	water (N & E)	I
Wilson & Tilman 1995	old field	B	nitrogen (E)	C
Miller 1996	greenhouse	B	fertilizer: weak comp (E)	I
			strong comp (E)	C
Twolan-Strutt & Keddy 1996	wetland	B	standing crop (N)	I
Peltzer et al. 1998	grassland	G	nitrogen (E)	C
Cahill 1999	old field	B	nutrient (E)	C

[1] B= biomass, S= survival, FS= final size (circumference), G= growth rate, D= diversity, R= reproduction, and SR= survival & reproduction.

[2] N= natural and E= experimental.

[3] I= increase, C= constant and d= decrease.

Figure 2.1 A simple model of the three possible relationships between relative competition intensity (CI) and productivity, assuming a linear relationship.

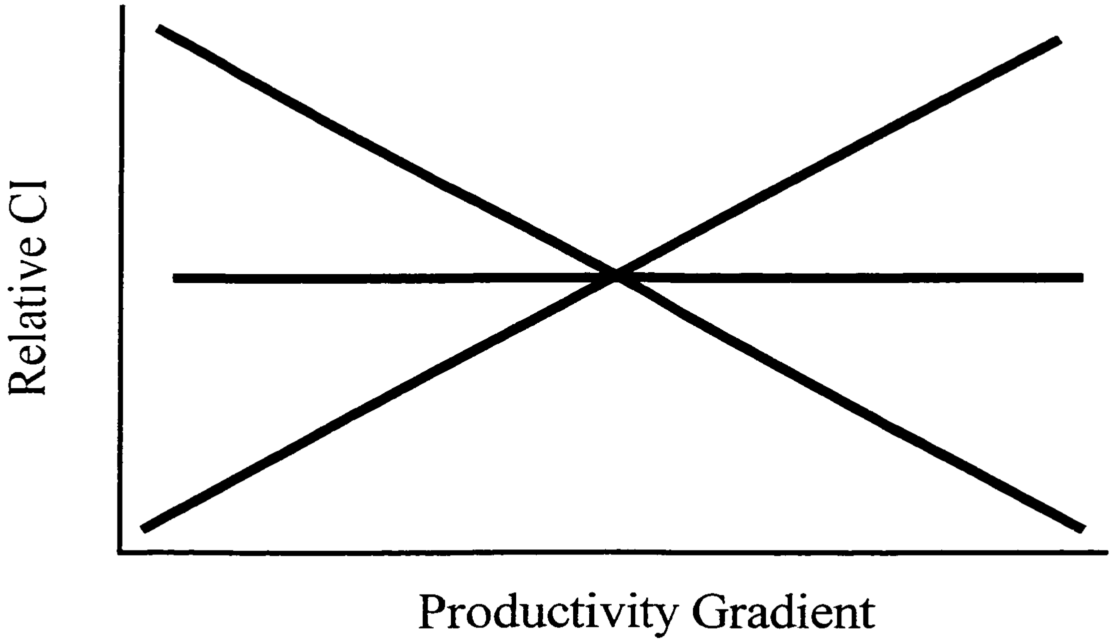
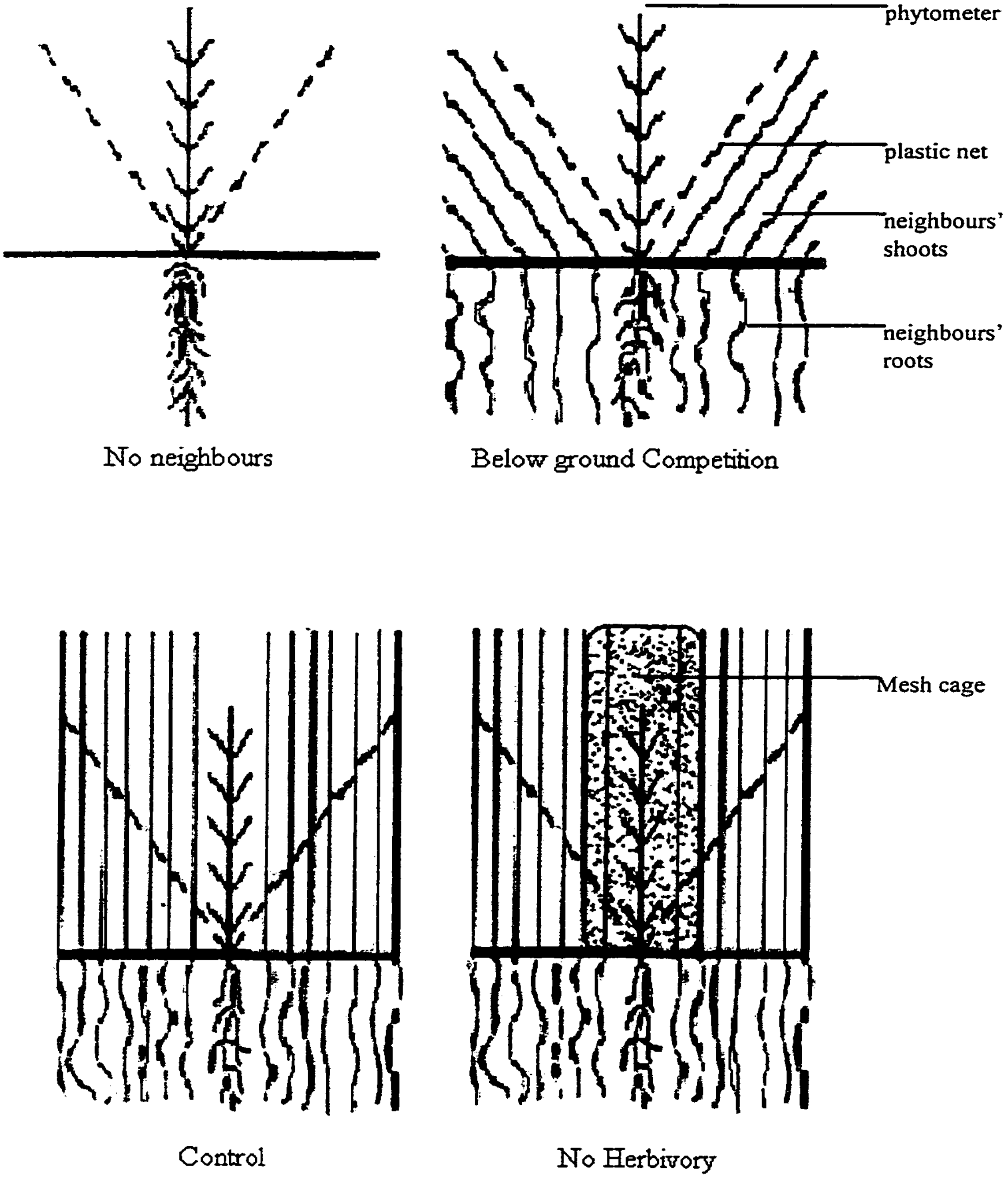

Relative CI
Productivity Gradient

Figure 2.2 The four treatments, no neighbours, below ground competition, control and no herbivory, used to measure competition intensity, herbivory and stress (adapted from Belcher et al. 1995).



No neighbours

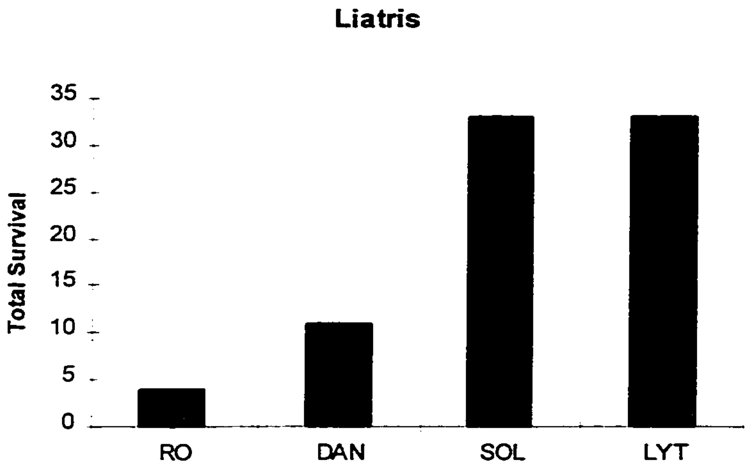
Below ground Competition

Control

No Herbivory

Figure 2.3 The total number of each phytometer that survived to the end of the experiment a) *Liatris spicata* and b) *Lythrum salicaria* in each of the four communities, Rock Outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT).

a)


Liatris
Total Survival
35
30
25
20
15
10
5
0
RO
DAN
SOL
LYT

b)

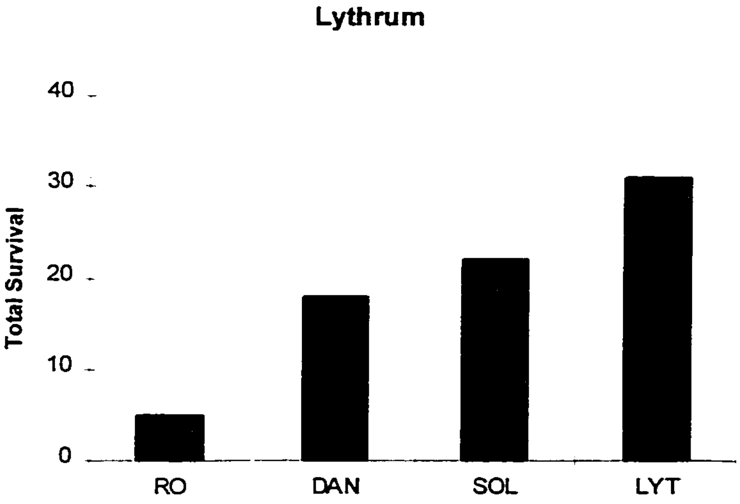
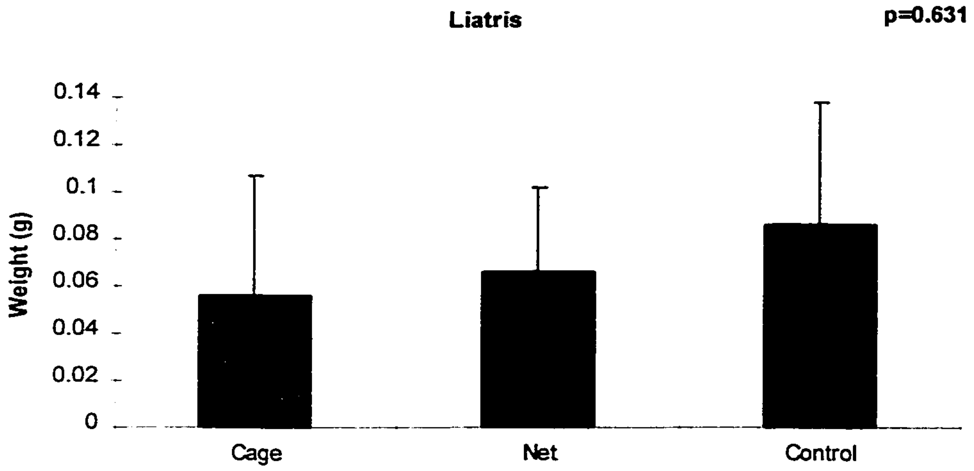

Lythrum
Total Survival
40
30
20
10
0
RO
DAN
SOL
LYT

Figure 2.4 The relationship among the three treatments, cage and net, versus control in the greenhouse experiment (n=15, Kruskall-Wallis ANOVA) for a) *Liatris* and b) *Lythrum*. Error bars are 95% confidence intervals.

a)


Liatris
p=0.631
Weight (g)
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
Cage
Net
Control

b)

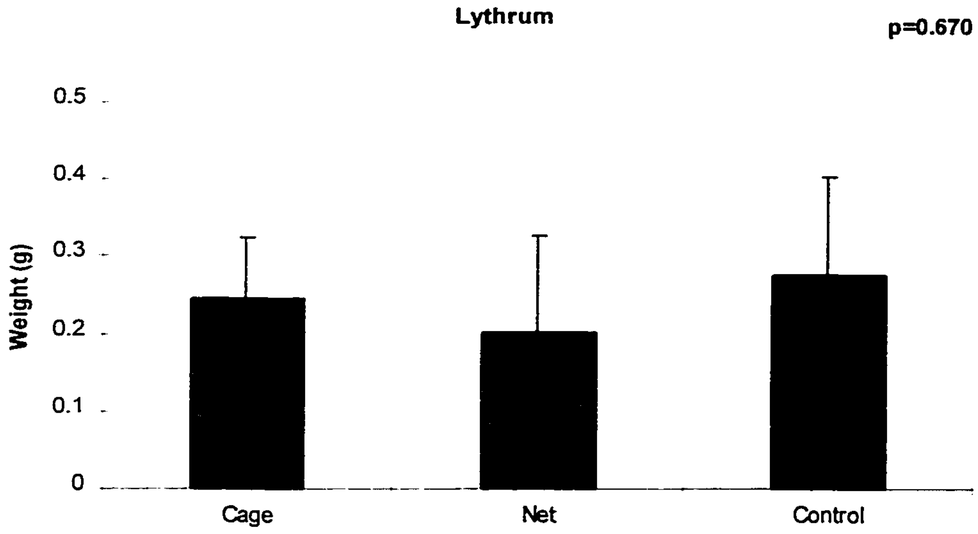

Lythrum
p=0.670
Weight (g)
0.5
0.4
0.3
0.2
0.1
0
Cage
Net
Control

Figure 2.5 The relationship among total competition intensity (CI) in the four communities, Rock Outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT), for a) *Liatris* (n=28, two outliers deleted, Kruskall-Wallis ANOVA), b) *Lythrum* (n=30, Kruskall-Wallis ANOVA). Also, between total competition intensity and soil depth again for c) *Liatris* (n=28, two outliers deleted, Spearman Rank Correlation, $0.002<p<0.001$) and d) *Lythrum* (n=30, Spearman Rank Correlation, $0.002<p<0.001$). Error bars are 95% confidence intervals.

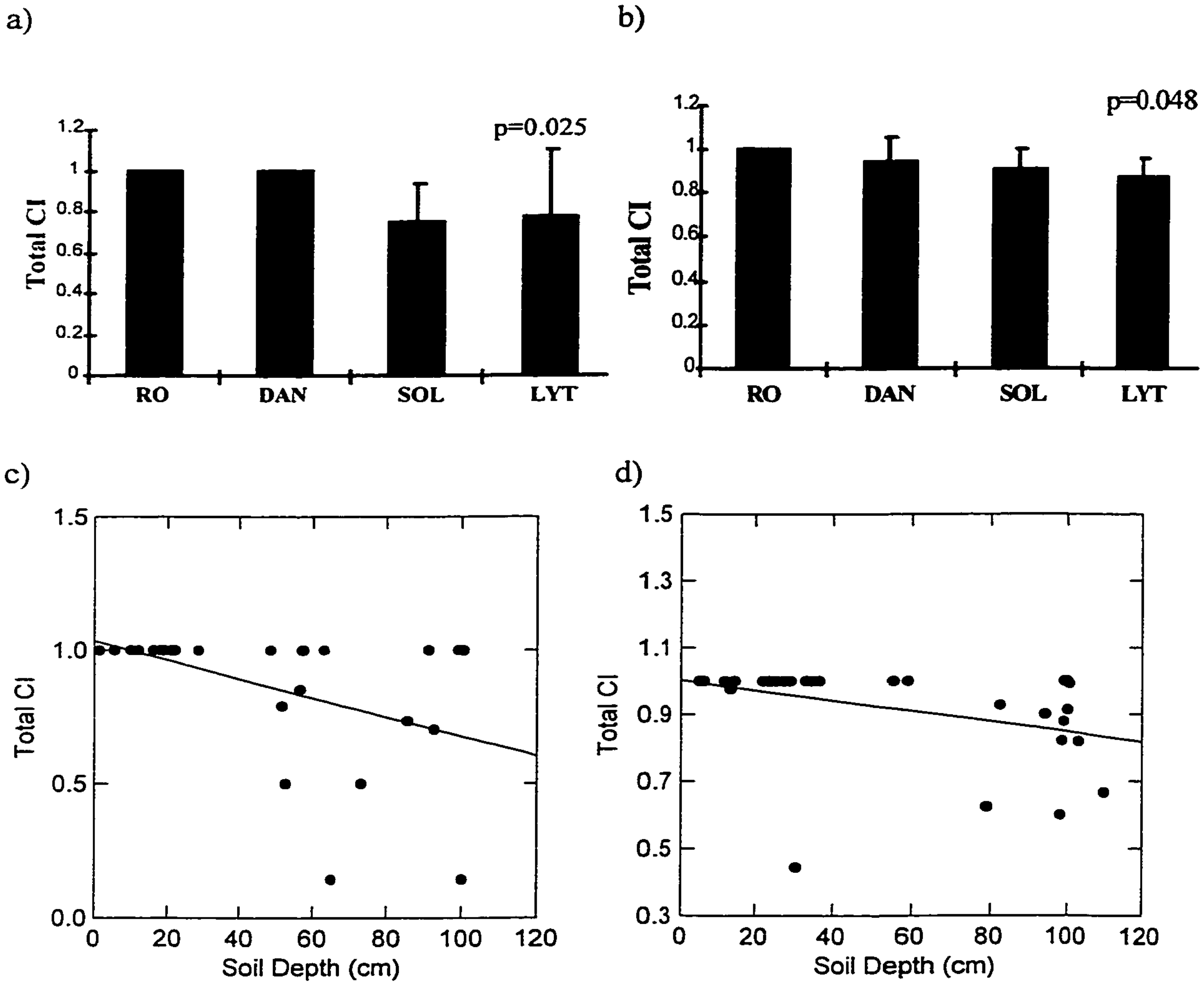

a)
b)
p=0.025
p=0.048
Total CI
1.2
1
0.8
0.6
0.4
0.2
0
RO
DAN
SOL
LYT
c)
d)
1.5
1.0
0.5
0.0
1.3
1.1
0.9
0.7
0.3
0
20
40
60
80
100
120
Soil Depth (cm)

Figure 2.6 The relationship among below ground competition intensity (CI) in the four communities Rock Outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT) for a) *Liatris* (n=30, Kruskall-Wallis ANOVA), b) *Lythrum* (n=30, Kruskall-Wallis ANOVA). Also, between below ground competition intensity and soil depth again for c) *Liatris* (n=30, Spearman Rank Correlation, p<0.001) and d) *Lythrum* (n=30, Spearman Rank Correlation, p<0.001). Letters (a-b) are the result of Bonferroni post-hoc comparisons and error bars are 95% confidence intervals.

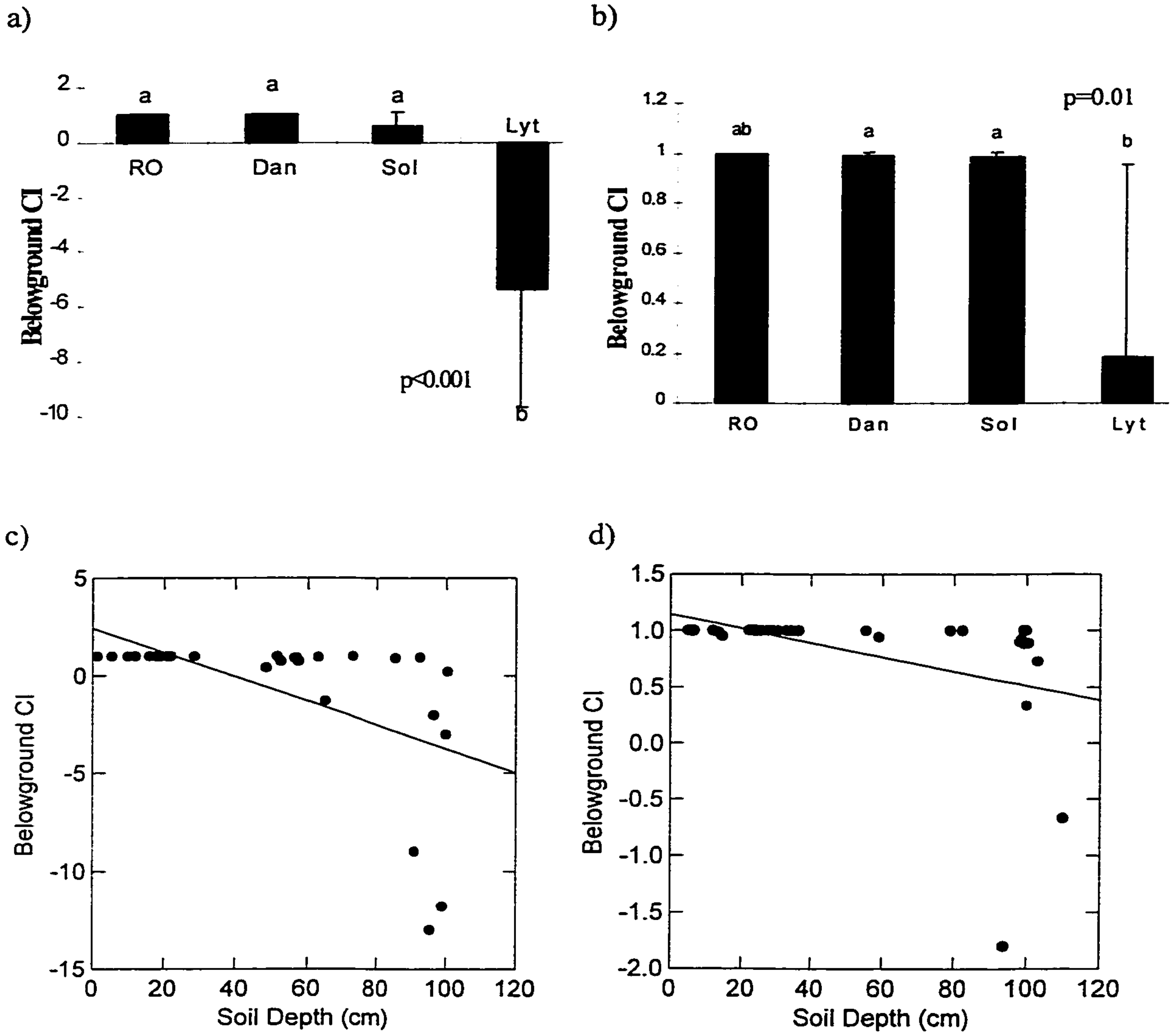

a)
b)
c)
d)
Belowground CI
RO
Dan
Sol
Lyt
a
a
a
b
ab
a
a
b
p<0.001
p=0.01
Soil Depth (cm)

Figure 2.7 The relationship among above ground competition intensity (CI) in the four communities Rock Outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT) for a) *Liatris* (n=30, Kruskall-Wallis ANOVA), b) *Lythrum* (n=30, Kruskall-Wallis ANOVA). Also, between above ground competition intensity and soil depth again for c) *Liatris* (n=30, Spearman Rank Correlation, p>0.50) and d) *Lythrum* (n=30, Spearman Rank Correlation, 0.50<p>0.20). Letters (a-b) are the result of Bonferroni post-hoc comparisons and error bars are 95% confidence intervals.

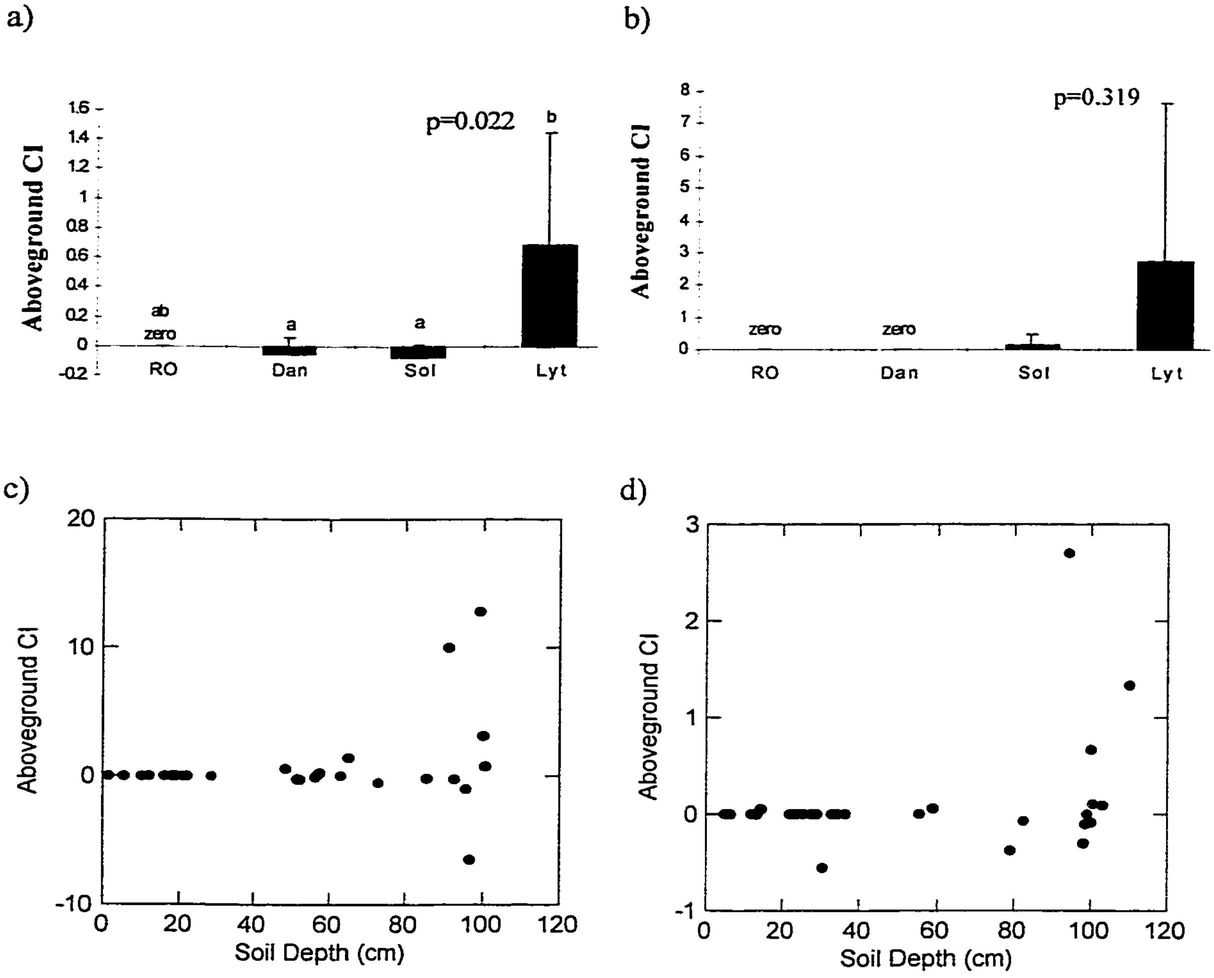

a)
Aboveground CI
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
p=0.022
ab
zero
a
a
b
RO
Dan
Sol
Lyt
b)
Aboveground CI
8
7
6
5
4
3
2
1
0
p=0.319
zero
zero
RO
Dan
Sol
Lyt
c)
Aboveground CI
20
10
0
-10
0
20
40
60
80
100
120
Soil Depth (cm)
d)
Aboveground CI
3
2
1
0
-1
0
20
40
60
80
100
120
Soil Depth (cm)

Figure 2.8 The relationship among total pooled competition intensity (CI) in the four communities Rock Outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT) for a) *Liatris* (n=30, ANOVA, R^2=0.312, p=0.003), b) *Lythrum* (n=30, ANOVA, R^2=0.315, p<0.001). Also, between total pooled competition intensity and soil depth again for c) *Liatris* (n=30, Spearman Rank Correlation, p<0.001) and d) *Lythrum* (n=30, Spearman Rank Correlation, p<0.001). Letters (a-b) are the result of Bonferroni post-hoc comparisons and error bars are 95% confidence intervals.

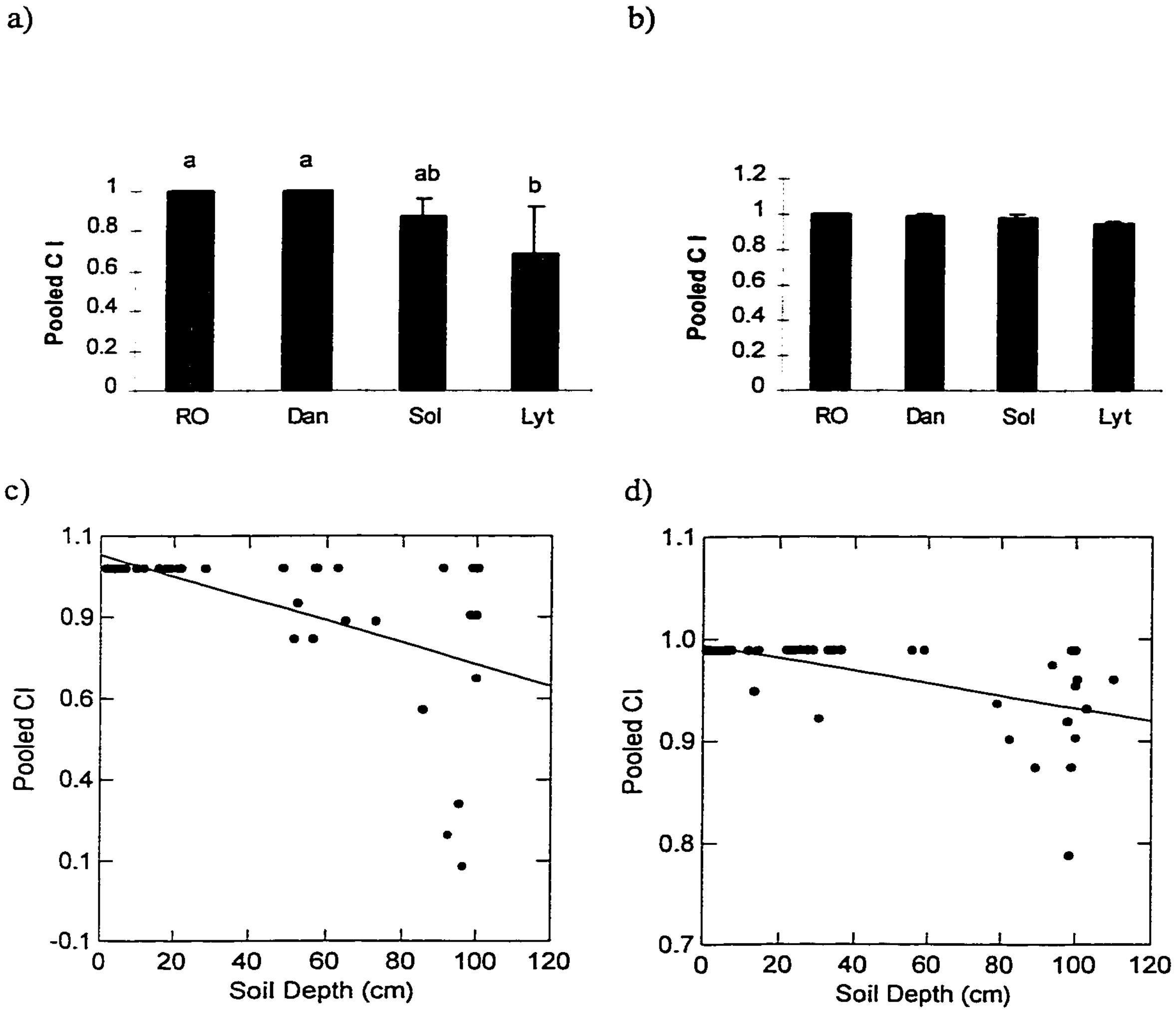

a)
b)
Pooled C I
a
a
ab
b
1
0.8
0.6
0.4
0.2
0
RO
Dan
Sol
Lyt
Pooled C I
1.2
1
0.8
0.6
0.4
0.2
0
RO
Dan
Sol
Lyt
c)
d)
Pooled CI
1.1
0.9
0.6
0.4
0.1
-0.1
0
20
40
60
80
100
120
Soil Depth (cm)
Pooled CI
1.1
1.0
0.9
0.8
0.7
0
20
40
60
80
100
120
Soil Depth (cm)

Figure 2.9 The relationship among herbivory in the four communities Rock Outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT) for a) *Liatris* (n=21, ANOVA, R^2=0.039, p=0.874), b) *Lythrum* (n=24, ANOVA, R^2=0.029, p=0.894). Also, between herbivory and soil depth again for c) *Liatris* (n=21, Spearman Rank Correlation, p>0.5) and d) *Lythrum* (n=24, Spearman Rank Correlation, p>0.5) and error bars are 95% confidence intervals.

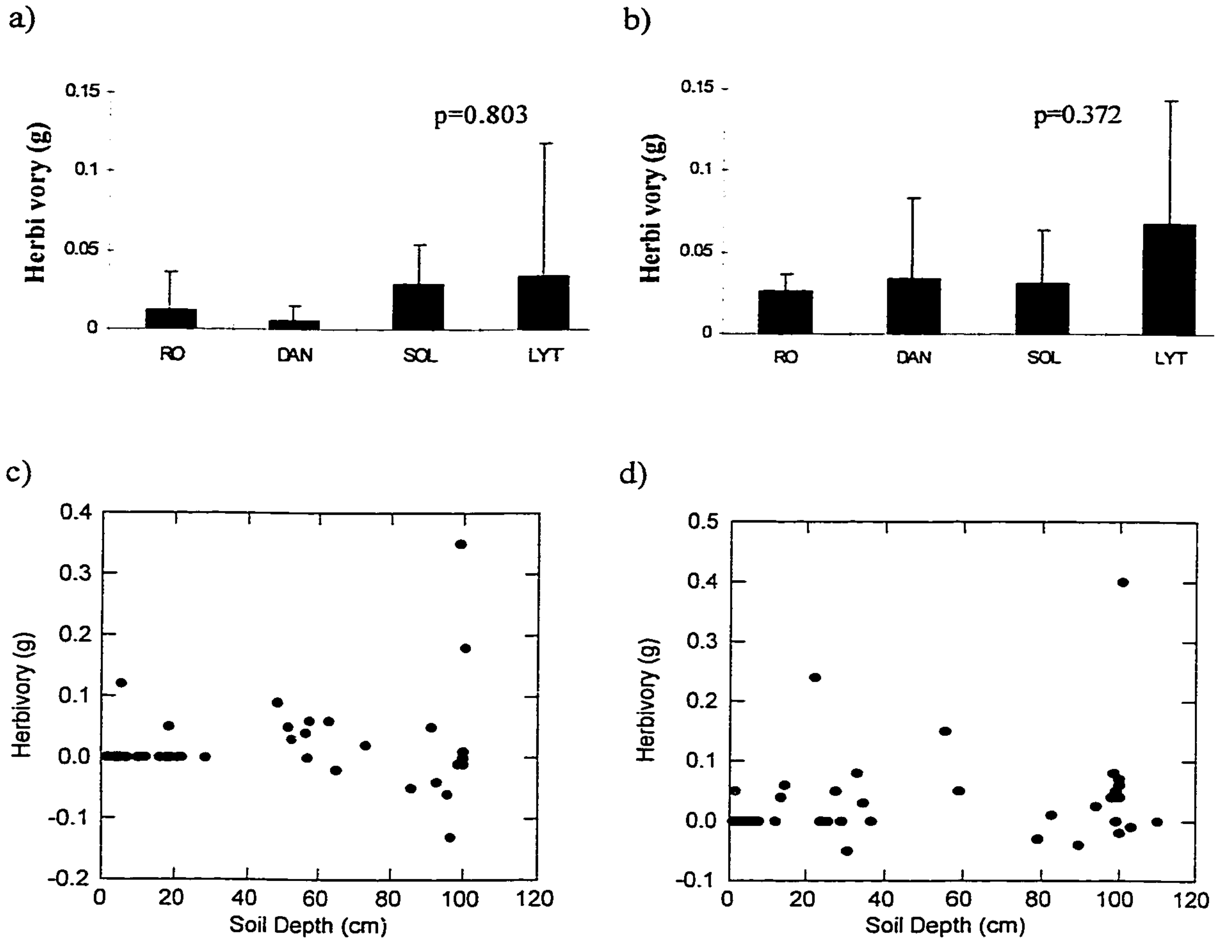

a)
Herbi vory (g)
0.15
0.1
0.05
0
p=0.803
RO
DAN
SOL
LYT
b)
Herbi vory (g)
0.15
0.1
0.05
0
p=0.372
RO
DAN
SOL
LYT
c)
Herbivory (g)
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
0
20
40
60
80
100
120
Soil Depth (cm)
d)
Herbivory (g)
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
0
20
40
60
80
100
120
Soil Depth (cm)

Figure 2.10 The relationship among stress in the four communities Rock Outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT) for a) *Liatris* (n=40, ANOVA, $R^2=0.595$, $p<0.001$), b) *Lythrum* (n=40, ANOVA, $R^2=0.235$, $p=0.021$). Also, between stress and soil depth again for c) *Liatris* (n=40, Spearman Rank Correlation, $p>0.5$) and d) *Lythrum* (n=40, Spearman Rank Correlation, $0.2<p>0.1$). Letters (a-b) are the result of Bonferroni post-hoc comparisons and error bars are 95% confidence intervals.

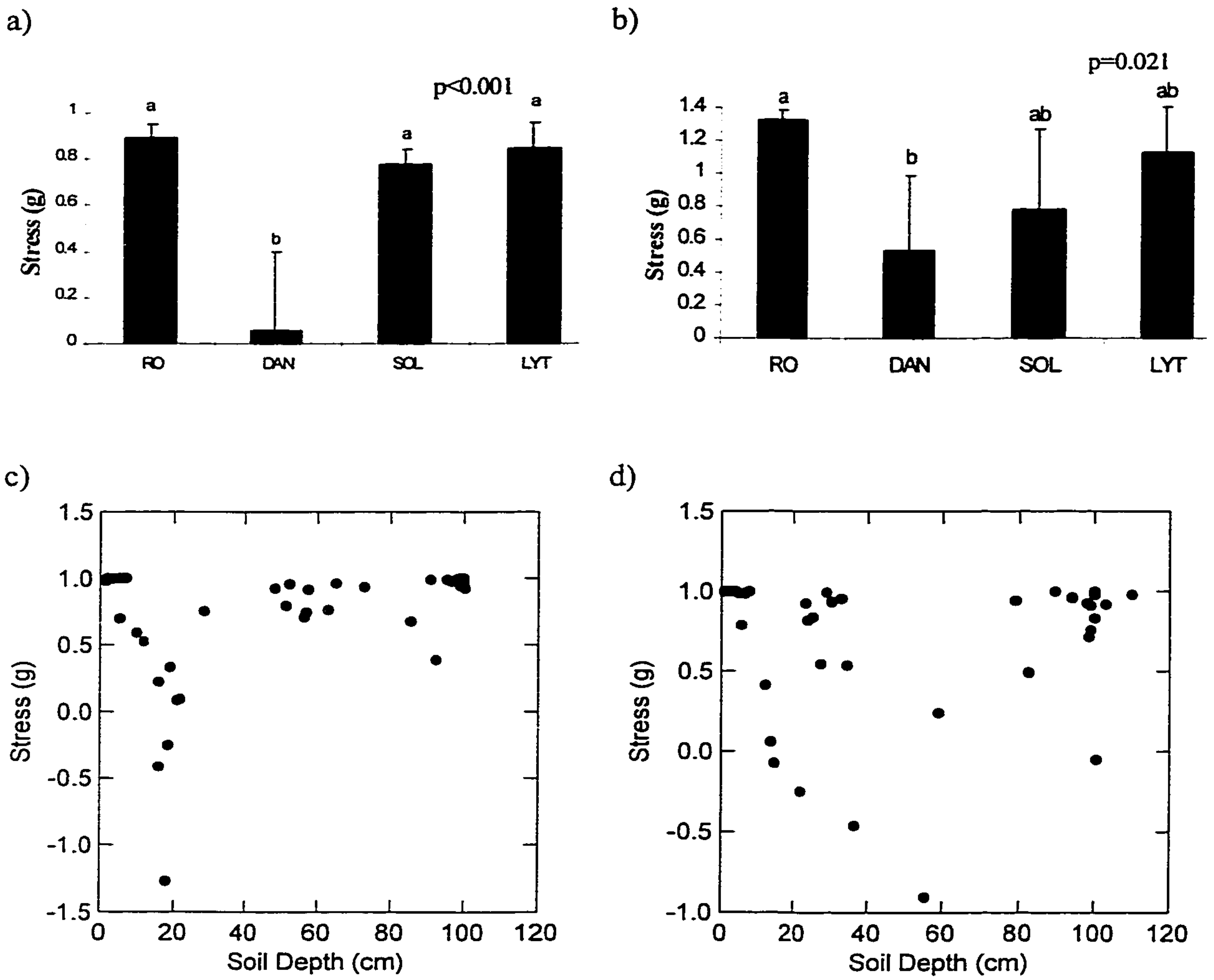

a)
p<0.001
Stress (g)
1
0.8
0.6
0.4
0.2
0
a
b
a
a
RO
DAN
SOL
LYT
b)
p=0.021
Stress (g)
1.4
1.2
1
0.8
0.6
0.4
0.2
0
a
b
ab
ab
RO
DAN
SOL
LYT
c)
Stress (g)
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
0
20
40
60
80
100
120
Soil Depth (cm)
d)
Stress (g)
1.5
1.0
0.5
0.0
-0.5
-1.0
0
20
40
60
80
100
120
Soil Depth (cm)

Figure 2.11 The relationship among soil characteristics for the four communities, Rock Outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT). For a) organic content (R^2=0.045), b) pH (R^2=0.614), c) nitrate (NO^{-3}, R^2=0.653), d) phosphorus (R^2=0.709), e) potassium (R^2=0.310) and f) magnesium (Mg, R^2=0.836) by one-way ANOVA (n=40).

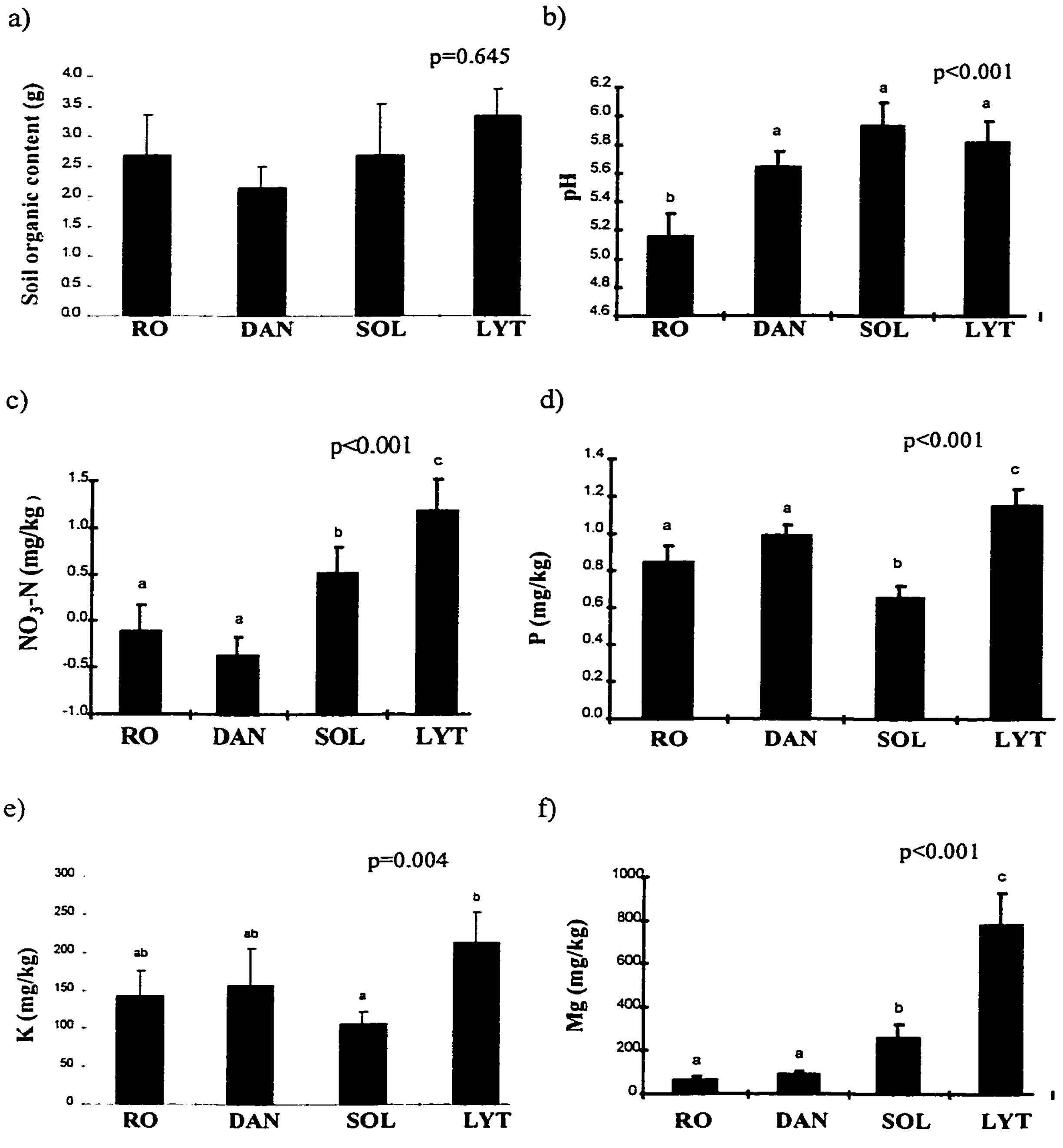
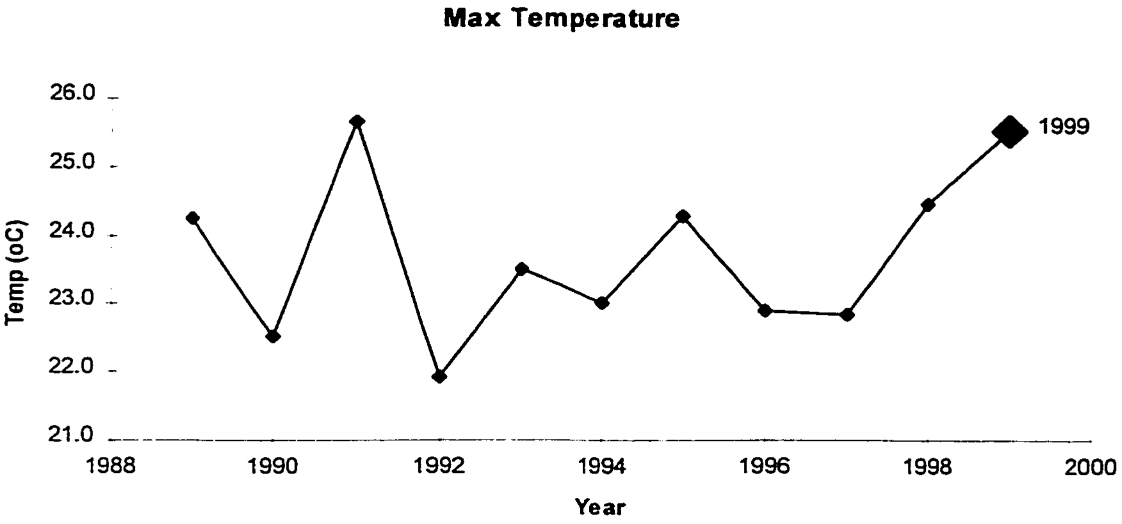
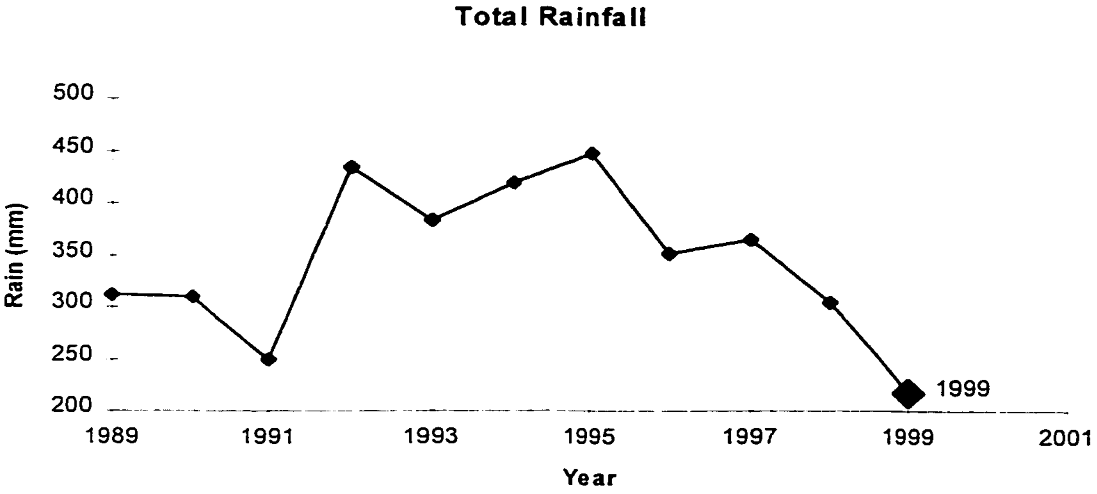

a)
p=0.645
Soil organic content (g)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
RO
DAN
SOL
LYT
b)
p<0.001
pH
6.2
6.0
5.8
5.6
5.4
5.2
5.0
4.8
4.6
b
a
a
a
RO
DAN
SOL
LYT
c)
p<0.001
NO_3-N (mg/kg)
1.5
1.0
0.5
0.0
-0.5
-1.0
a
a
b
c
RO
DAN
SOL
LYT
d)
p<0.001
P (mg/kg)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
a
a
b
c
RO
DAN
SOL
LYT
e)
p=0.004
K (mg/kg)
300
250
200
150
100
50
0
ab
ab
a
b
RO
DAN
SOL
LYT
f)
p<0.001
Mg (mg/kg)
1000
800
600
400
200
0
a
a
b
c
RO
DAN
SOL
LYT

Figure 2.12 Weather data from a weather station run by Environment Canada, near the study site. a) The average maximum daily temperature and b) average total daily rainfall for May, June, July and August 1999. Both a) and b) are compared to the previous ten summers using past Environment Canada data.

a)


Max Temperature
26.0
25.0
24.0
23.0
22.0
21.0
Temp (oC)
1999
1988
1990
1992
1994
1996
1998
2000
Year


Total Rainfall
500
450
400
350
300
250
200
Rain (mm)
1999
1989
1991
1993
1995
1997
1999
2001
Year

b)

Figure 2.13 A summary of the relationships between competition intensity, herbivory and stress along a soil depth gradient.

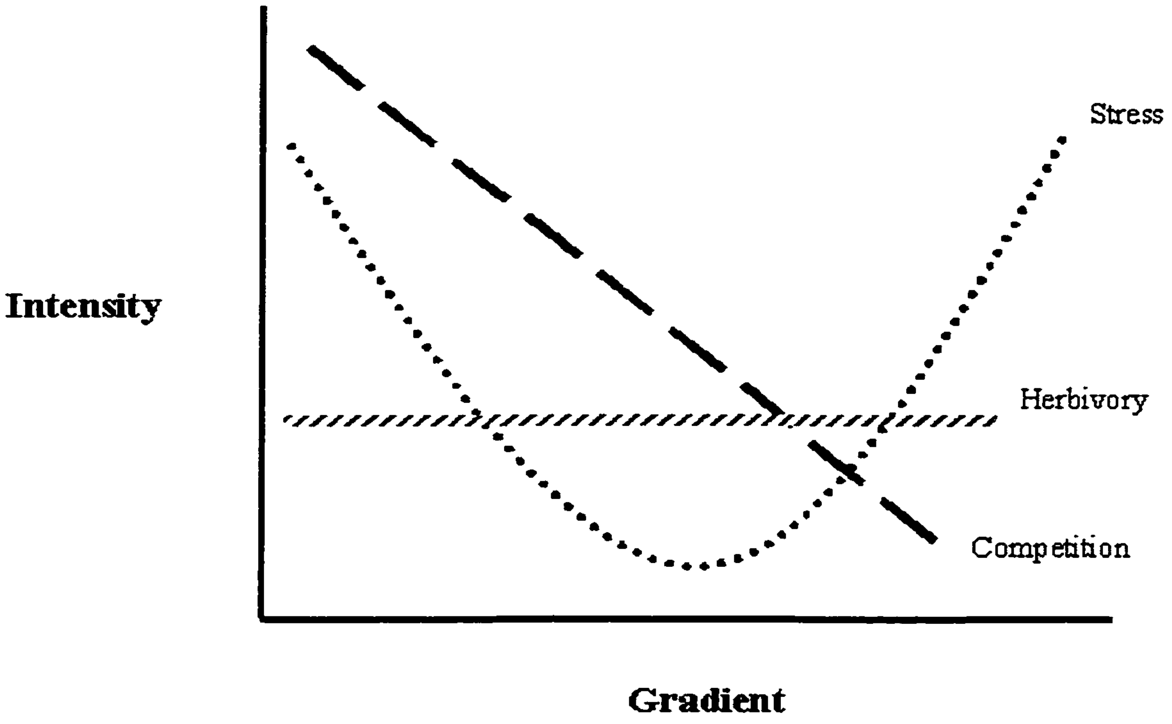
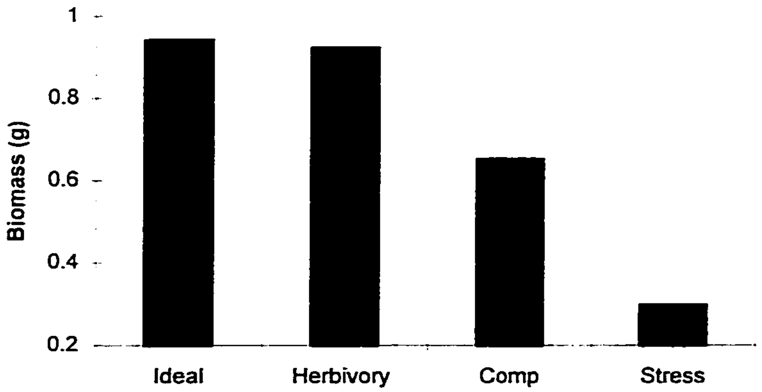

Intensity
Stress
Herbivory
Competition
Gradient

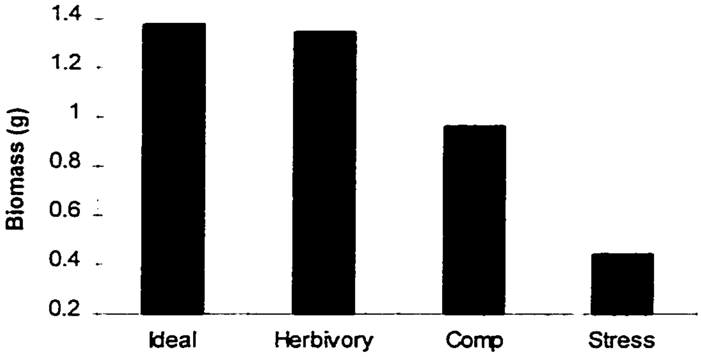
Figure 2.14 The change in performance of a) *Liatris* and b) *Lythrum* phytometers due to competition intensity, herbivory and stress.

a)



Biomass (g)
1
0.8
0.6
0.4
0.2
Ideal
Herbivory
Comp
Stress

b)



Biomass (g)
1.4
1.2
1
0.8
0.6
0.4
0.2
Ideal
Herbivory
Comp
Stress

General Conclusions

An old field was chosen as the location for this study for a couple of reasons. First and foremost, the field has undulating gneiss bedrock overlaid with clay which results in a natural soil depth gradient. This gave an opportunity to explore how various factors could change along this natural gradient. Second, the native flora of the old field is associated with the granite barrens to the west (Catling and Brownell 1999) and alvars to the east (Belcher *et al.* 1992). And third, abandoned farmland is an abundant and important habitat in North America, with old fields having the greatest species richness of abundant herbs (Keddy *et al.* in prep.).

Soil depth appears to affect the number of species that can grow, the height a plant can reach, the amount of biomass, the limiting resource and the percentage of native species, all resulting in four distinct communities. It seems reasonable to conclude that the soil depth gradient is the main factor controlling the distribution and abundance of vegetation.

Total competition intensity decreased as soil depth increased along the gradient. This was mostly due to the decrease in below ground competition. Above ground competition was not really detected in the field and below ground competition was also found to decrease along the gradient. Both of the phytometer species used, *Liatris spicata* and *Lythrum salicaria*, gave similar results. These results are apparently inconsistent with the published literature in the field. However, Goldberg *et al.*'s (1999) meta-analysis indicates that when the data from many of these studies are combined a decreasing trend is found. Herbivory was not found to vary significantly along the gradient and stress only varied significantly among the communities.

Though this study gave fairly convincing evidence of a decrease in competition intensity, this question is still not fully resolved. Several better designed studies, looking at natural gradients, that measure both above and below ground competition are needed to resolve this debate that has plagued plant ecology for over fifteen years. I hope this thesis offers a significant step towards resolution.

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Appendix 1 The soil depth, biomass, canopy height and number of species in each 50 cm^2 quadrat for the four communities within the old field. The communities are Rock Outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT) and soil depth was measured to a maximum of 50 cm during the first season due to difficulties of using the soil auger.

Community	Replicate	Soil Depth* (cm)	Biomass (g)	Canopy Height (cm)	Species (#)
RO	1	5.0	52.86	18.0	5
RO	2	3.0	24.32	15.5	7
RO	3	6.0	28.27	19.0	5
RO	4	7.0	102.89	14.0	6
RO	5	6.0	37.50	13.0	10
RO	6	1.5	0.42	7.0	1
RO	7	4.0	20.34	19.0	5
RO	8	3.0	43.38	21.0	5
RO	9	6.0	32.90	24.0	9
RO	10	5.0	31.57	14.0	5
DAN	1	11.0	114.79	19.0	18
DAN	2	12.0	116.02	27.0	15
DAN	3	12.0	126.90	29.0	13
DAN	4	12.0	131.41	23.0	13
DAN	5	14.0	122.96	16.0	6
DAN	6	13.0	115.72	31.0	10
DAN	7	15.5	103.45	31.0	9
DAN	8	22.0	126.94	35.0	13
DAN	9	9.0	97.56	26.0	5
DAN	10	8.0	108.00	22.0	7
SOL	1	43.0	186.30	73.0	13
SOL	2	34.0	163.31	91.5	15
SOL	3	38.0	281.02	52.0	12
SOL	4	36.0	134.52	78.0	11
SOL	5	50.0	114.53	50.0	12
SOL	6	34.0	170.80	68.0	14
SOL	7	50.0	107.27	48.0	13
SOL	8	50.0	170.87	54.0	13
SOL	9	38.0	148.33	67.0	17
SOL	10	50.0	133.93	58.0	11
LYT	1	50.0	219.19	74.0	8
LYT	2	50.0	136.22	57.0	10
LYT	3	50.0	103.49	62.5	8
LYT	4	50.0	163.96	56.0	6
LYT	5	50.0	162.89	68.0	8
LYT	6	50.0	243.38	70.0	5
LYT	7	50.0	98.76	51.0	8
LYT	8	50.0	152.56	61.0	7
LYT	9	50.0	187.06	73.0	7
LYT	10	50.0	129.70	63.0	9

Appendix 2 The list of species found in the forty sample quadrats within the field with the number of occurrences (n) and the average Braun-Blanquet (BB) abundance score.

Species[1,2,3]	**n**	**BB (average)**
Achillea millefolium	4	1.3
Agrostis gigantea	3	1.3
Elymus repens	3	2.0
Asclepias syriaca	7	1.4
Aster ciliolatus	3	1.3
Aster lanceolatus	2	1.0
Aster novae-angliae	7	1.9
Carex crawfordii	5	1.6
Carex gracillima	21	2.0
Carex pallescens	2	1.0
Chysanthemum leucanthemum	13	1.3
Dactylis glomerata	6	1.8
Danthonia spicata	25	2.7
Echium vulgare	8	1.3
Erigeron strigosus	10	1.1
Fragaria virginiania	21	1.8
Fraxinus nigra	2	1.0
Geum macrophyllum	10	1.3
Hieracium pilosella	25	2.6
Hieracium caespitosum	9	1.1
Hypericum perforatum	7	1.0
Linaria vulgaris	14	1.1
Lycopus americanus	3	1.0
Lythrum salicaria	10	3.7
Oenothera perennis	10	1.1
Oxalis stricta	11	1.0
Panicum implicatum	2	1.0
Phleum pratense	16	1.3
Plantago lanceolata	7	2.0
Poa compressa	26	1.8
Potentilla argentea	9	1.7
Potentilla recta	8	1.3
Prunella vulgaris	2	1.0
Ranunculus acris	3	1.0
Rumex acetosella	8	1.1
Setaria viridis	2	2.0
Sisyrinchium montanum	3	1.0
Solidago canadensis	10	3.1
Euthamia graminifolia	3	1.0
Solidago nemoralis	10	1.5
Spiraea alba	3	1.0
Taraxacum officinale	7	1.0
Tragopogon pratensis	8	1.4
Trifolium pratense	8	1.3
Trifolium agrarium	9	1.4
Trifolium repens	4	2.0
Vicia cracca	20	1.2

[1] In addition, these herbaceous species were present on one occasion: *Agrimonia gryposepala* (BB=2.0), *Anemone canadensis* (BB=2.0), *Carex crawfordii* (BB=2.0), *Cerastium vulgatum* (BB=1.0), *Eupatorium perfoliatum* (BB=3.0), *Poa pratense* (BB=1), *Polygonum persicaria* (BB=1.0), *Satureja vulgaris* (BB=1.0), *Scirpus atrovirens* (BB=1.0), *Sedum telephium* (BB=1.0), *Solidago rugosa* (BB=2.0), and *Verbascum thapsus* (BB=1.0).

[2] This woody species was present as a seedling: *Ulmus americana* (BB=1.0).

[3] These species occurred in the field but not in the sample quadrats: *Agrimonia striata, Anaphalis margaritacea, Antennaria neglecta, Apocynum cannabinum, Berteroa incana, Bromus inermus, Carex flava, Carex lupulina, Carex tenera, Carex tuckermanii, Carex vulpinoidea, Cirsium vulgare, Daucus carota, Dianthus armeria, Elymus repens, Erigeron annus Eupatorium maculatum, Euphorbia supina, Galium boreale, Galium verum, Hieracium aurantiacum, Juniperus communis, Lepidium campestre, Medicago lupulina, Meliotus alba, Oxalis stricta, Phalaris arundinacea, Poa palustris, Portulaca oleracea, Rosa* sp., *Rudbeckia hirta, Scirpus lineatus, Sedum telephium,* and *Silene cucubalus*.

Appendix 3 The biomass of 30 cm^2 quadrats in each community subjected to three different treatments in order to determine the limiting resource. The communities are Rock Outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT).

Community	Treatment	Replicate	Biomass
RO	Watered	1	2.98
		2	7.07
		3	6.19
		4	7.51
		5	1.45
RO	Fertilized	1	12.99
		2	10.27
		3	16.10
		4	34.26
		5	11.82
RO	Control	1	4.04
		2	1.08
		3	3.03
		4	3.05
		5	8.57
DAN	Watered	1	48.56
		2	41.60
		3	65.54
		4	49.33
		5	75.30
DAN	Fertilized	1	72.91
		2	83.40
		3	57.29
		4	86.97
		5	51.53
DAN	Control	1	47.73
		2	39.94
		3	42.51
		4	45.65
		5	34.77
SOL	Watered	1	71.13
		2	27.50
		3	38.67
		4	33.01
		5	43.31
SOL	Fertilized	1	225.77
		2	45.44
		3	155.91
		4	61.85
		5	117.23
SOL	Control	1	88.35
		2	41.65
		3	18.86
		4	37.08
		5	17.12
LYT	Watered	1	73.77
		2	52.82
		3	81.45

Community	Treatment	Replicate	Biomass
		4	65.93
		5	24.95
LYT	Fertilized	1	37.76
		2	13.63
		3	35.30
		4	23.26
		5	16.73
LYT	Control	1	79.15
		2	24.16
		3	22.27
		4	20.34
		5	33.89

Appendix 4 The final weight (weight f) of each phytometer at the end of the growing season. All zeros indicate a mortality. The communities are Rock Outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT) and the treatments are total competition (T), no neighbours (NC), no herbivory (CA) and below ground competition only (BG).

Community	Plot	Phytometer	Treatment	Weight f (g)
RO	1	*Liatris*	T	0.00
			NC	0.00
			CA	0.00
			BG	0.00
RO	2	*Liatris*	BG	0.00
			T	0.00
			NC	0.28
			CA	0.00
RO	3	*Liatris*	CA	0.00
			NC	0.00
			BG	0.00
			T	0.00
RO	4	*Liatris*	NC	0.00
			T	0.00
			CA	0.00
			BG	0.00
RO	5	*Liatris*	BG	0.00
			NC	0.00
			CA	0.00
			T	0.00
RO	6	*Liatris*	T	0.00
			NC	0.00
			BG	0.00
			CA	0.00
RO	7	*Liatris*	NC	0.02
			BG	0.00
			CA	0.00
			T	0.00
RO	8	*Liatris*	NC	0.00
			CA	0.12
			T	0.00
			BG	0.00
RO	9	*Liatris*	BG	0.00
			CA	0.00
			NC	0.01
			T	0.00
RO	10	*Liatris*	NC	0.00
			BG	0.00
			CA	0.00
			T	0.00
Dan	1	*Liatris*	NC	0.44
			CA	0.00
			BG	0.00
			T	0.00
Dan	2	*Liatris*	BG	0.00
			NC	0.72
			T	0.00
			CA	0.00

Community	Plot	Phytometer	Treatment	Weight f (g)
Dan	3	*Liatris*	CA	0.05
			NC	1.16
			BG	0.00
			T	0.00
Dan	4	*Liatris*	CA	0.00
			T	0.00
			BG	0.00
			NC	0.85
Dan	5	*Liatris*	NC	0.84
			BG	0.00
			CA	0.00
			T	0.00
Dan	6	*Liatris*	BG	0.00
			NC	0.23
			CA	0.00
			T	0.00
Dan	7	*Liatris*	NC	0.38
			CA	0.00
			T	0.00
			BG	0.00
Dan	8	*Liatris*	T	0.00
			BG	0.00
			NC	0.62
			CA	0.00
Dan	9	*Liatris*	CA	0.00
			BG	0.00
			NC	2.10
			T	0.00
Dan	10	*Liatris*	CA	0.00
			BG	0.00
			T	0.00
			NC	1.31
Sol	1	*Liatris*	CA	0.06
			T	0.00
			BG	0.01
			NC	0.22
Sol	2	*Liatris*	T	0.00
			NC	0.08
			BG	0.02
			CA	0.06
Sol	3	*Liatris*	CA	0.05
			BG	0.01
			T	0.02
			NC	0.04
Sol	4	*Liatris*	CA	0.01
			BG	0.08
			T	0.03
			NC	0.04
Sol	5	*Liatris*	NC	0.06

Community	**Plot**	**Phytometer**	**Treatment**	**Weight f (g)**
			T	0.03
			CA	0.05
			BG	0.00
Sol	6	*Liatris*	NC	0.19
			T	0.04
			CA	0.09
			BG	0.00
Sol	7	*Liatris*	CA	0.09
			NC	0.07
			BG	0.04
			T	0.00
Sol	8	*Liatris*	CA	0.00
			T	0.00
			BG	0.02
			NC	0.24
Sol	9	*Liatris*	CA	0.03
			NC	0.30
			BG	0.03
			T	0.08
Sol	10	*Liatris*	T	0.04
			NC	0.27
			BG	0.02
			CA	0.08
Lyt	1	*Liatris*	T	0.15
			BG	0.14
			NC	0.01
			CA	0.09
Lyt	2	*Liatris*	NC	0.00
			T	0.00
			CA	0.01
			BG	0.01
Lyt	3	*Liatris*	CA	0.02
			T	0.03
			BG	0.08
			NC	0.00
Lyt	4	*Liatris*	NC	0.01
			BG	0.10
			CA	0.05
			T	0.00
Lyt	5	*Liatris*	CA	0.35
			NC	0.05
			BG	0.64
			T	0.00
Lyt	6	*Liatris*	BG	0.07
			T	0.00
			NC	0.09
			CA	0.18
Lyt	7	*Liatris*	NC	0.00
			CA	0.06

Community	Plot	Phytometer	Treatment	Weight f (g)
			BG	0.13
			T	0.07
Lyt	8	*Liatris*	CA	0.13
			NC	0.57
			BG	0.04
			T	0.17
Lyt	9	*Liatris*	CA	0.03
			BG	0.14
			T	0.03
			NC	0.04
Lyt	10	*Liatris*	BG	0.06
			CA	0.06
			T	0.19
			NC	0.02
RO	1	*Lythrum*	T	0.00
			CA	0.00
			BG	0.03
			NC	0.00
RO	2	*Lythrum*	BG	0.00
			CA	0.00
			T	0.00
			NC	0.00
RO	3	*Lythrum*	BG	0.00
			NC	0.29
			CA	0.00
			T	0.00
RO	4	*Lythrum*	BG	0.00
			NC	0.00
			T	0.00
			CA	0.00
RO	5	*Lythrum*	BG	0.00
			T	0.00
			CA	0.00
			NC	0.00
RO	6	*Lythrum*	T	0.00
			CA	0.00
			BG	0.00
			NC	0.02
RO	7	*Lythrum*	BG	0.00
			NC	0.00
			T	0.00
			CA	0.05
RO	8	*Lythrum*	CA	0.00
			NC	0.00
			T	0.00
			BG	0.00
RO	9	*Lythrum*	T	0.00
			BG	0.00
			CA	0.00

Community	Plot	Phytometer	Treatment	Weight f (g)
			NC	0.02
RO	10	*Lythrum*	BG	0.00
			CA	0.00
			T	0.00
			NC	0.00
Dan	1	*Lythrum*	NC	1.70
			CA	0.24
			T	0.00
			BG	0.00
Dan	2	*Lythrum*	NC	0.80
			T	0.00
			BG	0.00
			CA	0.00
Dan	3	*Lythrum*	CA	0.06
			NC	1.46
			T	0.00
			BG	0.07
Dan	4	*Lythrum*	T	0.05
			NC	0.09
			CA	0.00
			BG	0.00
Dan	5	*Lythrum*	T	0.03
			BG	0.02
			CA	0.07
			NC	1.28
Dan	6	*Lythrum*	CA	0.05
			BG	0.00
			NC	0.62
			T	0.00
Dan	7	*Lythrum*	CA	0.00
			NC	0.01
			BG	0.00
			T	0.00
Dan	8	*Lythrum*	CA	0.00
			NC	0.10
			BG	0.00
			T	0.00
Dan	9	*Lythrum*	T	0.00
			BG	0.00
			NC	0.22
			CA	0.00
Dan	10	*Lythrum*	T	0.00
			BG	0.00
			CA	0.00
			NC	1.99
Sol	1	*Lythrum*	NC	1.03
			BG	0.06
			CA	0.05
			T	0.00

Community	Plot	Phytometer	Treatment	Weight f (g)
Sol	2	*Lythrum*	BG	0.00
			T	0.05
			NC	0.69
			CA	0.06
Sol	3	*Lythrum*	BG	0.00
			CA	0.00
			NC	0.08
			T	0.03
Sol	4	*Lythrum*	NC	0.23
			CA	0.00
			T	0.02
			BG	0.00
Sol	5	*Lythrum*	CA	0.00
			BG	0.00
			NC	0.12
			T	0.00
Sol	6	*Lythrum*	CA	0.08
			NC	0.10
			T	0.04
			BG	0.01
Sol	7	*Lythrum*	T	0.00
			BG	0.00
			CA	0.03
			NC	0.63
Sol	8	*Lythrum*	CA	0.08
			BG	0.00
			T	0.00
			NC	0.06
Sol	9	*Lythrum*	CA	0.15
			T	0.00
			NC	2.59
			BG	0.00
Sol	10	*Lythrum*	NC	0.25
			CA	0.00
			BG	0.00
			T	0.00
Lyt	1	*Lythrum*	BG	0.00
			CA	0.07
			NC	0.00
			T	0.00
Lyt	2	*Lythrum*	BG	0.03
			CA	0.15
			T	0.07
			NC	0.39
Lyt	3	*Lythrum*	NC	0.03
			CA	0.01
			BG	0.05
			T	0.01
Lyt	4	*Lythrum*	T	0.00

Community	Plot	Phytometer	Treatment	Weight f (g)
			CA	0.06
			BG	0.02
			NC	0.03
Lyt	5	*Lythrum*	BG	0.04
			T	0.04
			CA	0.09
			NC	0.33
Lyt	6	*Lythrum*	NC	0.11
			T	0.02
			BG	0.03
			CA	0.01
Lyt	7	*Lythrum*	BG	0.00
			NC	0.00
			T	0.04
			CA	0.00
Lyt	8	*Lythrum*	CA	0.07
			NC	0.00
			BG	0.00
			T	0.03
Lyt	9	*Lythrum*	BG	0.14
			CA	0.03
			T	0.01
			NC	0.05
Lyt	10	*Lythrum*	CA	0.41
			T	0.01
			NC	1.43
			BG	0.16

Appendix 5 A summary of all the data for the *Liatris spicata* phytometer obtained in the field. N/a denotes that the variable could not be calculated due to a mortality that resulted in a zero denominator and the communities are Rock Outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT). Community (Comm.), the plot, soil depth, competition intensity (CI), herbivory and stress are reported.

Comm.	**Plot**	**Soil Depth (cm)**	**Total CI**	**Below CI**	**Above CI**	**Pooled CI**	**Herbivory (g)**	**Stress (g)**
RO	1	2.00	n/a	n/a	n/a	1.00	n/a	0.93
	2	5.50	1.00	1.00	0.00	1.00	n/a	0.65
	3	3.50	n/a	n/a	n/a	1.00	n/a	0.93
	4	7.00	n/a	n/a	n/a	1.00	n/a	0.93
	5	7.00	n/a	n/a	n/a	1.00	n/a	0.93
	6	2.00	n/a	n/a	n/a	1.00	n/a	0.93
	7	1.50	1.00	1.00	0.00	1.00	n/a	0.91
	8	5.50	n/a	n/a	n/a	1.00	0.12	0.93
	9	1.50	1.00	1.00	0.00	1.00	n/a	0.92
	10	4.50	n/a	n/a	n/a	1.00	n/a	0.93
DAN	1	12.00	1.00	1.00	0.00	1.00	n/a	0.49
	2	16.00	1.00	1.00	0.00	1.00	n/a	0.21
	3	18.50	1.00	1.00	0.00	1.00	0.05	-0.24
	4	21.00	1.00	1.00	0.00	1.00	n/a	0.08
	5	22.00	1.00	1.00	0.00	1.00	n/a	0.09
	6	28.50	1.00	1.00	0.00	1.00	n/a	0.70
	7	10.00	1.00	1.00	0.00	1.00	n/a	0.55
	8	19.00	1.00	1.00	0.00	1.00	n/a	0.31
	9	18.00	1.00	1.00	0.00	1.00	n/a	-1.18
	10	16.00	1.00	1.00	0.00	1.00	n/a	-0.39
SOL	1	63.00	1.00	0.95	0.05	1.00	0.06	0.71
	2	57.50	1.00	0.75	0.25	1.00	0.06	0.85
	3	52.50	0.50	0.75	-0.25	0.89	0.03	0.89
	4	65.00	0.14	-1.29	1.43	0.84	-0.02	0.89
	5	73.00	0.50	1.00	-0.50	0.84	0.02	0.87
	6	51.50	0.79	1.00	-0.21	0.78	0.05	0.74
	7	48.50	1.00	0.43	0.57	1.00	0.09	0.86
	8	57.00	1.00	0.92	0.08	1.00	n/a	0.69
	9	85.50	0.73	0.90	-0.17	0.57	-0.05	0.63
	10	56.50	0.85	0.93	-0.07	0.78	0.04	0.66
LYT	1	95.50	-14.00	-13.00	-1.00	0.28	-0.06	0.92
	2	100.00	n/a	n/a	n/a	1.00	0.01	0.93
	3	98.50	n/a	n/a	n/a	0.86	-0.01	0.93
	4	91.00	1.00	-9.00	10.00	1.00	0.05	0.92
	5	99.00	1.00	-11.80	12.80	1.00	0.35	0.88
	6	100.50	1.00	0.22	0.78	1.00	0.18	0.86
	7	100.00	n/a	n/a	n/a	0.66	-0.01	0.93
	8	92.50	0.70	0.93	-0.23	0.18	-0.04	0.36
	9	100.00	0.14	-3.00	3.14	0.86	0.00	0.89
	10	96.50	-8.50	-2.00	-6.50	0.08	-0.13	0.91

Appendix 6 A summary of all the data for the *Lythrum salicaria* phytometer obtained in the field. N/a denotes that the variable could not be calculated due to a mortality that resulted in a zero denominator and the communities are Rock Outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT). Community (Comm.), the plot, soil depth, competition intensity (CI), herbivory and stress are reported.

Comm.	Plot	Soil Depth (cm)	Total CI	Below CI	Above CI	Pooled CI	Herbivory (g)	Stress (g)
RO	1	1.00	n/a	n/a	n/a	1.00	n/a	1.36
	2	7.50	n/a	n/a	n/a	1.00	n/a	1.36
	3	5.50	1.00	1.00	0.00	1.00	n/a	1.07
	4	4.00	n/a	n/a	n/a	1.00	n/a	1.36
	5	3.00	n/a	n/a	n/a	1.00	n/a	1.36
	6	6.50	1.00	1.00	0.00	1.00	n/a	1.34
	7	1.50	n/a	n/a	n/a	1.00	0.05	1.36
	8	2.50	n/a	n/a	n/a	1.00	n/a	1.36
	9	5.00	1.00	1.00	0.00	1.00	n/a	1.34
	10	1.00	n/a	n/a	n/a	1.00	n/a	1.36
DAN	1	22.00	1.00	1.00	0.00	1.00	0.24	-0.34
	2	12.00	1.00	1.00	0.00	1.00	n/a	0.56
	3	14.50	1.00	0.95	0.05	1.00	0.00	-0.10
	4	30.50	0.44	1.00	-0.56	0.94	0.06	1.27
	5	13.50	0.98	0.98	-0.01	0.96	-0.05	0.08
	6	27.50	1.00	1.00	0.00	1.00	0.04	0.74
	7	29.00	1.00	1.00	0.00	1.00	n/a	1.35
	8	23.50	1.00	1.00	0.00	1.00	n/a	1.26
	9	25.50	1.00	1.00	0.00	1.00	n/a	1.14
	10	36.50	1.00	1.00	0.00	1.00	n/a	-0.63
SOL	1	59.00	1.00	0.94	0.06	1.00	0.05	0.33
	2	82.50	0.93	1.00	-0.07	0.92	0.05	0.67
	3	79.00	0.63	1.00	-0.38	0.95	0.01	1.28
	4	100.00	0.91	1.00	-0.09	0.97	-0.03	1.13
	5	99.00	1.00	1.00	0.00	1.00	-0.02	1.24
	6	98.00	0.60	0.90	-0.30	0.94	0.04	1.26
	7	34.50	1.00	1.00	0.00	1.00	0.03	0.73
	8	33.00	1.00	1.00	0.00	1.00	0.08	1.30
	9	55.50	1.00	1.00	0.00	1.00	0.15	-1.23
	10	24.00	1.00	1.00	0.00	1.00	n/a	1.11
LYT	1	100.00	n/a	n/a	n/a	1.00	0.07	1.36
	2	98.50	0.82	0.92	-0.10	0.82	0.08	0.97
	3	110.00	0.67	-0.67	1.33	0.97	0.00	1.33
	4	100.00	1.00	0.33	0.67	1.00	0.06	1.33
	5	99.00	0.88	0.88	0.00	0.90	0.05	1.03
	6	103.00	0.82	0.73	0.09	0.95	-0.01	1.25
	7	89.50	n/a	n/a	n/a	0.90	-0.04	1.36
	8	100.00	n/a	n/a	n/a	0.92	0.04	1.36
	9	94.00	0.90	-1.80	2.70	0.99	0.03	1.31
	10	100.50	0.99	0.89	0.10	0.97	0.40	-0.07

Appendix 7 The final weight of plants grown in the greenhouse to test for effects of the cages and nets used in the field experiment. The cages were used in the no herbivory treatment and the nets were used in the below ground competition only treatment.

Species	**Treatment**	**Replicate**	**Weight (g)**
Lythrum	Cage	1	0.05
Lythrum	Cage	2	0.13
Lythrum	Cage	3	0.08
Lythrum	Cage	4	0.01
Lythrum	Cage	5	0.01
Lythrum	Net	1	0.04
Lythrum	Net	2	0.04
Lythrum	Net	3	0.04
Lythrum	Net	4	0.11
Lythrum	Net	5	0.10
Lythrum	Control	1	0.12
Lythrum	Control	2	0.09
Lythrum	Control	3	0.15
Lythrum	Control	4	0.03
Lythrum	Control	5	0.04
Liatris	Cage	1	0.25
Liatris	Cage	2	0.26
Liatris	Cage	3	0.12
Liatris	Cage	4	0.26
Liatris	Cage	5	0.34
Liatris	Net	1	0.31
Liatris	Net	2	0.36
Liatris	Net	3	0.09
Liatris	Net	4	0.12
Liatris	Net	5	0.13
Liatris	Control	1	0.28
Liatris	Control	2	0.19
Liatris	Control	3	0.48
Liatris	Control	4	0.28
Liatris	Control	5	0.15

Appendix 8. The native and exotic species found in the study site, including species outside the quadrats used in the analysis. These designations were obtained from Gleason (1952), Peterson and McKenny (1968) and Gleason and Cronquist (1991).

Native	**Exotic**
Agrimonia gryposepala	*Achillea millefolium*
Agrimonia striata	*Agrostis gigantea*
Anaphalis margaritacea	*Berteroa incana*
Anemone canadensis	*Bromus inermus*
Antennaria neglecta	*Cerastium vulgatum*
Apocynum cannabinum	*Chysanthemum leucanthemum*
Asclepias syriaca	*Cirsium vulgare*
Aster ciliolatus	*Dactylis glomerata*
Aster lanceolatus	*Daucus carota*
Aster novae-angliae	*Dianthus armeria*
Carex crawfordii	*Echium vulgare*
Carex gracillima	*Elymus repens*
Carex lupulina	*Galium verum*
Carex pallescens	*Hieracium aurantiacum*
Carex tenera	*Hieracium caespitosum*
Carex tuckermanii	*Hieracium pilosella*
Carex vulpinoidea	*Hypericum perforatum*
Danthonia spicata	*Lepidium campestre*
Erigeron annus	*Linaria vulgaris*
Erigeron strigosus	*Lythrum salicaria*
Eupatrium maculatum	*Medicago lupulina*
Eupatorium perfoliatum	*Meliotus alba*
Euphorbia supina	*Phleum pratense*
Euthamia graminifolia	*Plantago lanceolata*
Fragaria virginiania	*Poa compressa*
Fraxinus nigra	*Polygonum persicaria*
Galium boreale	*Portulaca oleracea*
Geum macrophyllum	*Potentilla argentea*
Juniperus communis	*Potentilla recta*
Lycopus americanus	*Prunella vulgaris*
Oenothera perennis	*Ranunculus acris*
Oxalis stricta	*Rumex acetosella*
Panicum implicatum	*Satureja vulgaris*
Phalaris arundinacea	*Sedum telephium*
Poa palustris	*Setaria viridis*
Poa pratense	*Silene cucubalus*
Rudbeckia hirta	*Taraxacum officinale*
Scirpus atrovirens	*Tragopogon pratensis*
Scirpus lineatus	*Trifolium pratense*
Sisyrinchium montanum	*Trifolium agrarium*
Solidago canadensis	*Trifolium repens*
Solidago nemoralis	*Verbascum thapsus*
Solidago rugosa	*Vicia cracca*
Spiraea alba	
Ulmus americana	

Appendix 9 A summary of the concentration of various nutrients, the pH and the organic content of the soil samples from each community. The nutrients are abbreviated as nitrate (NO_3-N), phosphorus (P), potassium (K) and magnesium (MG), while the samples refer to the communities, Rock Outcrop (RO), *Danthonia* (DAN), *Solidago* (SOL) and *Lythrum* (LYT).

Sample	**NO_3-N (mg/kg)**	**P (mg/kg)**	**K (mg/kg)**	**Mg (mg/kg)**	**pH**	**Organic content (g)**
1 RO	4.88	5.77	237.07	79.27	5.4	73.87
2 RO	0.58	9.79	118.21	29.76	4.9	24.86
3 RO	1.29	5.38	96.70	43.62	5.3	38.32
4 RO	0.77	5.84	104.75	57.85	5.3	52.55
5 RO	0.28	12.71	75.68	52.27	5.0	47.27
6 RO	2.70	4.03	168.49	104.59	5.7	98.89
7 RO	0.19	7.50	96.49	54.26	5.0	49.26
8 RO	0.37	8.40	122.31	77.35	5.1	72.25
9 RO	1.49	8.08	190.54	70.62	4.8	65.82
10 RO	0.30	6.38	204.23	65.22	5.0	60.22
1 DAN	2.14	9.81	158.48	78.13	6.0	72.13
2 DAN	0.55	9.58	99.63	103.23	5.8	97.43
3 DAN	0.59	10.14	85.85	64.63	5.7	58.93
4 DAN	0.27	9.35	62.67	56.45	5.6	50.85
5 DAN	0.29	9.08	171.40	55.81	5.4	50.41
6 DAN	0.19	9.37	293.66	108.21	5.5	102.71
7 DAN	0.24	9.04	238.04	133.62	5.7	127.92
8 DAN	0.25	8.69	100.22	89.69	5.5	84.19
9 DAN	1.00	16.91	251.69	115.94	5.7	110.24
10 DAN	0.32	7.22	96.05	84.88	5.5	79.38
1 SOL	2.48	4.89	93.75	337.50	5.7	331.80
2 SOL	8.60	6.85	89.88	375.61	5.6	370.01
3 SOL	1.60	5.18	102.55	229.59	5.8	223.79
4 SOL	0.85	4.35	161.65	154.98	5.9	149.08
5 SOL	1.09	3.70	87.50	133.70	5.7	128.00
6 SOL	7.75	3.59	109.27	303.37	6.1	297.27
7 SOL	20.68	3.87	131.74	415.73	6.5	409.23
8 SOL	6.13	6.27	97.30	266.22	6.1	260.12
9 SOL	1.79	3.63	113.32	217.34	6.0	211.34
10 SOL	2.36	3.63	79.57	131.28	5.9	125.38
1 LYT	0.51	6.45	230.12	1237.58	6.1	1231.48
2 LYT	21.23	18.50	164.52	967.74	5.9	961.84
3 LYT	22.70	14.59	180.25	919.75	5.9	913.85
4 LYT	30.65	13.66	200.76	881.10	6.2	874.90
5 LYT	20.00	13.01	169.08	918.64	6.1	912.54
6 LYT	24.35	11.92	132.39	538.18	5.7	532.48
7 LYT	7.89	13.11	190.39	601.32	5.6	595.72
8 LYT	16.11	16.22	282.70	635.17	5.6	629.57
9 LYT	38.31	22.10	353.35	589.79	5.6	584.19
10 LYT	32.41	18.52	216.38	464.69	5.4	459.29

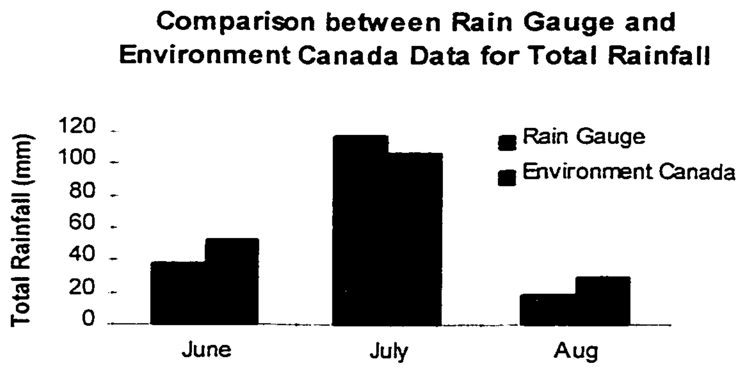
Appendix 10 The maximum temperature and total daily rainfall for the summer of 1999.

The temperature data and the rain data was from a nearby Environment Canada (EC) weather station and the rain gauge was directly in the field. The rain gauge was only set up at the beginning of June, therefore the data for May is not applicable (n/a). Tr in the rain data from EC denotes a trace amount of rainfall, i.e. less than 0.1mm and nm in the rain gauge indicates that a measurement was not read on that date. The figure compares the accuracy of the rain gauge to the Environment Canada data.

Month	Day	Temperature Max (°C) EC	Rain (mm) EC	Rain Gauge (mm)
May	1	24.5	0.0	n/a
	2	26.0	0.0	n/a
	3	26.5	0.0	n/a
	4	27.0	0.0	n/a
	5	26.0	0.0	n/a
	6	26.0	0.0	n/a
	7	23.5	2.2	n/a
	8	20.0	7.2	n/a
	9	18.0	2.6	n/a
	10	12.5	0.0	n/a
	11	15.0	0.0	n/a
	12	14.0	0.0	n/a
	13	17.0	0.0	n/a
	14	22.0	0.0	n/a
	15	24.5	0.0	n/a
	16	23.5	0.0	n/a
	17	24.0	0.0	n/a
	18	26.5	0.0	n/a
	19	20.0	Tr	n/a
	20	18.0	0.0	n/a
	21	22.5	0.0	n/a
	22	22.0	0.0	n/a
	23	23.0	0.0	n/a
	24	18.0	14.0	n/a
	25	13.5	2.2	n/a
	26	17.0	0.0	n/a
	27	21.0	0.0	n/a
	28	26.0	0.0	n/a
	29	29.5	0.0	n/a
	30	32.5	0.0	n/a
	31	30.5	0.4	n/a
June	1	20.5	4.0	2.0
	2	26.5	23.6	12.8
	3	19.5	0.0	0.0
	4	22.0	0.0	nm
	5	25.0	0.0	nm
	6	30.0	0.0	nm
	7	34.0	0.0	0.0
	8	28.5	0.0	0.0
	9	21.0	1.0	nm
	10	26.5	0.2	nm
	11	30.0	0.0	nm
	12	30.5	0.0	nm
	13	31.0	0.0	nm
	14	26.5	3.6	2.5
	15	15.5	0.6	nm
	16	19.5	0.0	0.0
	17	21.0	1.0	nm
	18	21.5	5.2	nm
	19	26.0	0.0	nm
	20	28.5	0.2	nm
	21	29.0	0.0	8.6

Month	Day	Temperature Max (°C) EC	Rain (mm) EC	Rain Gauge (mm)
	22	31.0	0.0	0.0
	23	31.5	0.0	0.0
	24	32.0	2.6	nm
	25	30.0	3.0	nm
	26	32.5	0.0	nm
	27	33.5	5.4	nm
	28	28.0	Tr	0.0
	29	27.5	2.2	nm
	30	25.0	0.0	12.3
July	1	29.5	0.0	0.0
	2	26.5	17.2	nm
	3	29.5	0.0	nm
	4	31.5	4.0	nm
	5	32.0	0.0	50.0
	6	30.5	7.8	nm
	7	25.5	0.0	nm
	8	22.5	4.0	0.8
	9	18.0	8.0	nm
	10	20.0	14.8	nm
	11	24.5	0.0	nm
	12	27.0	0.0	22.5
	13	28.0	0.0	0.0
	14	28.5	0.0	nm
	15	30.0	0.0	0.0
	16	33.5	0.0	nm
	17	34.5	0.0	nm
	18	28.5	7.8	nm
	19	25.0	0.0	nm
	20	26.0	1.2	5.8
	21	29.0	0.0	0.0
	22	31.5	0.0	0.0
	23	29.5	18.0	nm
	24	28.0	16.0	nm
	25	27.5	8.2	nm
	26	27.5	0.0	38.0
	27	29.5	0.0	nm
	28	28.0	0.0	0.0
	29	29.5	0.0	0.2
	30	31.5	0.0	nm
	31	28.0	0.0	nm
Aug	1	26.0	0.0	nm
	2	22.0	0.0	0.0
	3	25.5	0.0	0.0
	4	22.0	2.6	nm
	5	24.0	0.0	nm
	6	19.5	2.2	nm
	7	22.5	Tr	nm
	8	19.5	13.8	nm
	9	19.0	0.0	11.5
	10	22.0	0.0	0.0
	11	21.0	0.0	0.0
	12	27.5	0.0	nm
	13	22.5	4.4	nm

Month	Day	Temperature Max (°C) EC	Rain (mm) EC	Rain Gauge (mm)
	14	20.5	1.2	nm
	15	25.5	0.0	nm
	16	24.5	Tr	nm
	17	28.0	5.2	nm
	18	24.0	Tr	7.0
	19	27.0	0.0	0.0
	20	24.0	0.0	nm
	21	25.5	Tr	nm
	22	28.0	0.0	nm
	23	30.0	0.0	0.0
	24	31.5	0.0	0.0
	25	30.0	0.0	nm
	26	29.5	0.0	0.0
	27	30.5	0.0	nm
	28	32.5	0.0	nm
	29	19.0	0.0	nm
	30	21.5	0.0	0.0
	31	26.5	0.0	0.0



Appendix 11 The maximum temperature and total daily rainfall for the summers of 1989 to 1998. This data was all obtained from a nearby Environment Canada weather station.

	May	June	July	Aug
1989				
Temp Max (°C)	19.4	24.0	28.4	25.2
Total Rainfall (mm)	111.0	59.2	86.3	54.2
1990				
Temp Max (°C)	17.6	23.7	missing	26.3
Total Rainfall (mm)	96.0	43.4	110.6	58.6
1991				
Temp Max (°C)	22.1	25.9	27.8	26.8
Total Rainfall (mm)	83.4	24.0	73.0	69.6
1992				
Temp Max (°C)	19.8	22.8	missing	23.2
Total Rainfall (mm)	79.4	68.6	139.0	146.8
1993				
Temp Max (°C)	18.5	22.5	26.6	26.4
Total Rainfall (mm)	67.2	125.6	108.4	81.6
1994				
Temp Max (°C)	17.8	24.4	26.5	23.4
Total Rainfall (mm)	103.2	121.8	96.8	97.2
1995				
Temp Max (°C)	18.7	26.0	26.9	25.5
Total Rainfall (mm)	44.6	114.0	121.2	167.8
1996				
Temp Max (°C)	17.1	23.2	24.9	26.4
Total Rainfall (mm)	66.4	47.2	189.4	48.6
1997				
Temp Max (°C)	15.4	26.4	26.1	23.4
Total Rainfall (mm)	62.4	70.8	174.6	55.8
1998				
Temp Max (°C)	23.0	23.4	25.9	25.5
Total Rainfall (mm)	33.8	105.2	112.2	53.0