Competitive Hierarchies Amongst Twelve Native Prairie Grasses

by

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A thesis presented to the University of Manitoba in partial fulfillment of the requirements
for the degree Master of Science in the Faculty of Graduate Studies

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A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University

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ABSTRACT

Two field experiments were established to determine the existence, form, and consistency of competitive hierarchies amongst 12 native prairie grass species: one at Carman, Manitoba in 1995; the other in Winnipeg, Manitoba in 1996. The 12 species were grown in a diallel replacement series experiment with 3 replicates in a randomized block design. In each 3.5 m x 1.25 m plot, above-ground biomass was harvested, dried, and massed after the first and second growing seasons. Competitive hierarchies were examined using relative yields, aggressivity indices, transitivity analysis, and ordination methods. At both sites, the strongest competitors were all highly productive C_3 species: *Elymus trachycaulus*, *Elymus canadensis*, *Pascopyrum smithii*, and *Elymus lanceolatus*. Weak competitors included *Schizachyrium scoparium*, *Bouteloua gracilis*, and *Sorghastrum nutans*, all low-productivity C_4 species. *S. comata*, a C_3 species of low productivity, was also a poor competitor. Intermediate competitors included *Panicum virgatum*, *Andropogon gerardii*, *Bouteloua curtipendula*, and *Nassella viridula*. These results indicate that in southern Manitoba, highly productive species are generally more competitive than less productive species, and C_3 species are generally more competitive than C_4 species. In 1996, a separate field experiment was sown in Carman, involving 8 native grass seed mixture sets, each consisting of a 'control' (i.e. non-adjusted) and 'adjusted' mixture, replicated 3 times using 1.25 m x 10 m plots. Mixtures were adjusted for differences in species establishment rates and competitive abilities based on the competitive hierarchies determined from Carman in 1995. There were no significant differences in species evenness between control and adjusted mixtures, with the exception of a mixture of strongly competitive C_3 and weakly competitive C_4 species. There were also no significant differences in effective species richness between control and adjusted mixtures, with the exception of a mixture of strong and weak C_3 competitors and a mixture of strongly competitive C_3 and weakly competitive C_4 species. Experimentally adjusted seed mixtures had significantly greater evenness and effective species richness than seed mixtures developed on a trial-and-error basis, although their final establishment densities were similar. Furthermore, experimentally adjusted seed mixtures consistently came closer to meeting the desired final mean establishment density.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction to the Prairies

1.1.1 Introduction

The question 'What is a prairie?' is not a simple one. In describing the prairie, a casual observer will likely draw attention not to its details but to the aesthetic sum of its parts. For the budding grassland ecologist, this view of the prairie is a familiar and comfortable perspective. However, after countless hours of studying taxonomy, anatomy, physiology, and ecological theory, the same budding ecologist realizes that in order to truly understand the prairie ecosystem, one must first carefully analyze and understand its component parts. And so, to the author's benefit, this chapter will begin with definitions. Next it will discuss grassland development and classification within North America as well as physiological differences between C_4 and C_3 plants. These topics will lead into a broader discussion of ecological concepts including competition, disturbance, and theories of coexistence and diversity.

1.1.2 Definitions

According to the Oxford Dictionary of Current English (Thompson 1993), a *prairie* is a "large area of treeless grassland"; a *grassland* is a "large open area covered with grass, esp. used for grazing"; a *meadow* is considered to be a "piece of grassland, esp. one used for hay."; and a *plain* is simply a "level tract of country". This being said, we know that these entities consist primarily of grasses, do not contain trees, are large, and perhaps flat. Interestingly, under these definitions, modern golf courses could qualify as prairies. However, regardless of this rather narrow definition of grasslands by the common literature, there are in fact different meanings to the words *prairie* and *grassland*.

For the purposes of this paper, *prairie* will refer specifically to the grassland biome of North America, including its more isolated patches outside of the Great Plains, as it existed prior to European settlement. The term *grassland*, will refer to all areas whose total plant biomass consists primarily of grasses, these areas generally lacking in significant tree

growth (Coupland 1992). This term encompasses all such landscapes around the world, and includes such entities as, for example, native North American *prairie*, the *steppes* of Ukraine and Russia, *pusztas* of Hungary, *velds* of southern Africa, and even agricultural hay meadows and croplands.

1.1.3 General Characteristics of Grasslands

Primary Productivity

Primary productivity and subsequent energy flow within ecosystems has long been of interest to ecologists wishing to compare the emergent properties of ecosystems around the world (see Van Dyne et al. 1976). In comparison with many other terrestrial ecosystems, temperate grasslands tend to have a somewhat intermediate level of above-ground annual productivity (McNaughton et al. 1991). This intermediate level of primary productivity has been attributed to large-scale ecosystem characteristics such as precipitation, photosynthetically active radiation, temperature, evapotranspiration rates, and other climatic variables -- characteristics which are themselves somewhat intermediate in nature for the temperate grassland region (McNaughton et al. 1991).

Energy Flow

Another emergent characteristic that is somewhat unique to temperate grasslands is the energy flow from primary to secondary producers (i.e. plants to herbivores). A survey of literature that has focused on assessing primary and secondary productivity simultaneously in various terrestrial ecosystems by McNaughton et al. (1991), has revealed that temperate grasslands have the greatest degree of energy transferred from primary to secondary production (i.e. they have amongst the highest secondary production:primary production ratios). According to McNaughton et al. (1991) differences in the efficiency of energy transfer can be attributed to differences in plant structure (i.e. trees vs. grasses), and herbivore type (i.e. invertebrates vs. vertebrates). Specifically, temperate grasslands tend to have a higher degree of palatable plant biomass than other forest ecosystems, and simultaneously have a relatively high degree of invertebrate herbivores, as opposed to, for example, a tropical grassland which tends to have more vertebrate herbivores (i.e. ungulates). Note that McNaughton et al. (1991) do not consider 'pulse' phenomena in the temperate grassland energy flow data -- such as outbreaks of grasshoppers, for example.

Such outbreaks would tend to increase the already relatively high ratio of secondary to primary production in temperate grasslands.

1.1.4 History of Prairie Development in North America

The North American Prairie began to develop in the Miocene and Pliocene epochs, with the rise of the Rocky Mountains and the subsequent climatic changes in central North America some 26-30 million years ago. (Risser et al. 1981; Collins and Glenn 1995). Specifically, the Rocky Mountains created a rain shadow in central North America which resulted in a relatively dry climate which exists to this day. This aridity combined with a periodically frost-free climate, grazing animals, fairly frequent fires, and a flat or rolling topography, helped to create the fairly extensive North American grassland biome between 7-5 million Y.B.P., within the Miocene-Pliocene transition era (Axelrod 1985).

More recent patterns of grassland development, on a smaller temporal scale, involved the roughly north-south expansion and retreat of glaciers, accompanied by subsequent shifts in temperatures and vegetation types. The most recent glacial retreat and subsequent recolonization of plants and animals in North America was that of the Wisconsinian glaciation, beginning approximately 18,000 Y.B.P. and ending around 3000 Y.B.P. At the time of the Wisconsinian ice sheet's furthest expansion south there existed a roughly north-south temperature gradient as well as a gradient of vegetation types, with tundra along the southern edge of the ice sheet, and boreal forests within the southern Great Plains.

Information about the development of North American grassland ecosystems has been reviewed by Axelrod (1985). The physical evidence primarily comes from fossilized pollen, plants, and animal remains. Conclusions were then drawn by making inferences on this data based on the ecology and natural history of similar plants and animals that exist today. Generally, as the Wisconsinian ice sheet began retreating north about 18,000 Y.B.P., so too did the associated cool climate vegetation types of the continent (Prentice et al. 1991), until grasslands reappeared in the southern Great Plains by 12,000 Y.B.P. At this point, the northern and eastern ecotone of the grassland consisted mostly of grasses and coniferous trees, with boreal forests dominating the landscape further northward and eastward.

This northern and eastern migration of boreal forest and grassland from the South continued steadily, until about 8000 Y.B.P. At this time, these ecotones began to gradually

shift back south and west, in response to a slight cooling trend in the later Holocene, until the vegetation types and their ecotones resembled those of the present day by about 3000 Y.B.P (Axelrod 1985). Prior to European settlement in North America, the entire grassland biome accounted for approximately 370 million ha of the total North American land area, forming the largest of all North American biomes (Sims 1988). Furthermore, the North American grassland is composed of approximately 7500 plant species, most of which are not endemic to the prairie (Axelrod 1985). Thus, despite the great size and species richness of the prairie, it is considered to be the youngest North American biome (Axelrod 1985).

1.2 Grassland Classification within the Great Plains

1.2.1 Introduction

Currently, despite many regional inconsistencies and arguments, there is some general agreement among grassland ecologists as to the broad scale classification of grassland types within North America. Sims (1988) divides the prairie into tallgrass, mixed-grass, shortgrass and palouse prairies, along with desert and California grasslands. Similarly, Risser et al. (1981) acknowledges tall, short, and mixed-grass prairie types, along with Californian annual grassland, a north-western bunchgrass steppe, and desert grassland. In Canada, Coupland (1950) has acknowledged four distinct prairie types -- tallgrass prairie, mixed-grass prairie, fescue prairie, and palouse prairie. Of these four prairie types, only fescue prairie is restricted to Canada. Although different grassland types are not delineated according to distinct measurable characteristics, we can describe several prairie types within the Northern Great Plains. These are the tallgrass, mixed-grass, and rough fescue prairies, classified according to their general geographic locations, climatological and edaphic differences, and species composition.

1.2.2 Tallgrass Prairie

Geographic Distribution

The tallgrass prairie (or 'true prairie') is the eastern-most prairie type in North America (Sims 1988). Prior to European settlement, it accounted for approximately 22% of the total land area (approx. 57.4 million ha) of the North American grassland biome (Küchler 1964). Within Canada, the tallgrass prairie's northern limit occurred within southern

Manitoba. From here, the tallgrass prairie stretched southward along the Red and Missouri rivers to reach its furthest southerly extent in eastern Oklahoma. The furthest westerly extent occurred as an 'outpocketing' of tallgrass prairie within Nebraska. Küchler (1964) refers to this Nebraska outpocket as the Nebraska Sandhills Prairie. Note that pockets of tallgrass prairie have been known to occur as far east as Long Island, New York, and as far south as Texas (Risser at al. 1981). Also, the tallgrass prairie forms ecotones with Aspen Parkland and Boreal Forests to the north, and deciduous forests to the south (Risser et al. 1981).

Climate and Soils

The tallgrass prairie is the most mesic grassland type within North America. Mean annual precipitation ranges from approximately 40 cm in the Northwest, to as much as 100 cm further south (Bragg 1995). Mean annual precipitation isoclines generally indicate an east-west gradient of decreasing precipitation. Temperature follows a north-south gradient, ranging from an average January temperature of -15 °C in the North to 15 °C in the South, and an average July temperature of 20°C in the North and 30°C to the South (Bragg 1995). Soils of the tallgrass prairie consist mostly of moist to wet udollic and aquollic mollisols, with mean annual soil temperatures exceeding 8 °C (Bragg 1995). In Canada, the tallgrass prairie soils are classified as chernozemic, with gleysols found closer towards the Red River (Clayton et al. 1977). An exception to these soil types occurs within the Nebraska Sandhills Prairie region, where the soils are classified as being within the dry and warm (i.e. mean annual soil temperature exceeds 8 °C) entisol order, and psamnent sub-order (Bragg 1995).

Species Composition

Of obvious importance to the species composition of any prairie type are the Gramineae. In fact, it is thought that grasses alone can account for 80-90% of tallgrass prairie biomass (Sims 1988). However, it is important to note that in terms of species richness, grasses account for only 25-33% of the total species richness -- the rest being forb species (Sims 1988). Of the grasses that are present, only a few species represent most of the biomass. For example, Weaver and Fitzpatrick (1932) found that only 10 grass species accounted for most of the tallgrass plant cover. Of these, *Andropogon gerardii* (big bluestem) and *Sorghastrum nutans* (indiangrass) together accounted for 70% of the total plant cover

(Weaver and Fitzpatrick 1932). According to Sims (1988) the average maximum grass height within the tallgrass prairie is approximately 0.5 m.

Sims (1988) recognized three common grass associations within the tallgrass prairie. The first (also known as 'true prairie') consists predominantly of *A. gerardii*, *S. nutans*, and *Panicum virgatum*. This association was the most mesic, or easternmost association within the tallgrass prairie. This same region is that referred to by Küchler (1964) as the Bluestem Prairie, to which he included *Schizachyrium scoparium* as a co-dominant. According to Küchler (1964), slightly further west occurred the *Agropyron*, *Andropogon*, and *Stipa* association. Finally, within the Nebraska Sandhills occurred the third association: the *Andropogon*, *Calamovilfa*, and *Stipa* association (Küchler 1964; Sims 1988). In all, the common element within these three associations is *A. gerardii* — not-surprisingly, a 'tall' grass (see Appendix I, II, and III for details on *A. gerardii* and other important prairie grasses).

1.2.3 Mixed-Grass Prairie

Geographic Distribution

As we move further west from the tallgrass prairie, there begins to be a gradual shift in the dominant grass type and in overall grass height. Specifically, the previously great abundance of *A. gerardii* and other tall-statured grasses gradually decreases as the abundance of the shorter-statured grasses increases. We would now be entering the mixed-grass prairie. The mixed-grass prairie accounts for approximately 21% of the total North American grassland by area, or 566,000 km^2 (Sims 1988). Within Canada, the mixed-grass prairie accounts for the majority of grassland area, by type. It occupies most of south-western Saskatchewan, and, in combination with fescue prairie, south-eastern Saskatchewan as well. It also occurs widely throughout southern Alberta and Manitoba. The mixed-grass prairie lies between the tallgrass prairie to the east, and the shorter grass fescue prairie to the west. Due in part to its geographic location, the mixed-grass prairie is considered by some to be an ecotone between the tallgrass and shorter grass prairies (Sims 1988).

Climate and Soils

Total mean annual precipitation within the mixed-grass prairie ranges from approximately 30 cm within eastern U.S., to about 60 cm in eastern Nebraska and South Dakota (Bragg 1995). Temperatures range quite drastically from a mean January temperature of between -10 to -20 °C, to a mean July temperature between 15 to 20 °C (Bryson and Hare 1974). Mixed-grass prairie soils are primarily mollisolic and entisolic (Bragg 1995). South Dakota and Nebraska soils tend to be dry and warm ustollic and xerollic mollisols. Further north, in a large portion of the Saskatchewan mixed-grass, moist and cool borollic soil is the predominant mollisol. In the more westerly areas of the mixed-grass prairie, dry and warm entisols of the orthentic sub-group are more common. Where the fescue prairie and mixed-grass prairies co-occur in Saskatchewan and Manitoba we find udollic and aquollic mollisols, similar to those found within most of the tallgrass prairie region. In smaller proportions, moist and warm alfisols occur within western South Dakota and northern Wyoming. Also, within a greater part of the Wyoming, dry and warm aridisols are common.

Species Composition

The mixed-grass prairie consists of a mixture of both tall and short statured species, ultimately depending on climatic and edaphic factors. Some species of particular importance to the mixed-grass prairie include *Bouteloua gracilis*, *Bouteloua curtipendula*, *S. scoparium*, *A. gerardii*, *Pascopyrum smithii*, *Buchloe dactyloides*, and *Sporobolus drumondii*. These species are considered to be dominants by Albertson (1937). Other grass and sedge genera of relative importance include *Carex*, *Aristida*, *Sitanion*, *Panicum*, *Elymus*, *Sorghastrum*, and *Poa*. Albertson (1937) considers these species to be 'principal species'.

Küchler (1964) has identified several principal mixed-grass associations according to vegetation characteristics. Within most of Montana and eastern Wyoming occurs the Grama-Needlegrass-Wheatgrass association, with *P. smithii*, *B. gracilis*, and *S. comata* being the three dominant species. Immediately to the east of this region is the Wheatgrass-Needlegrass association, occupying the western Dakotas. Here we find the same dominants as the previous association described, with the addition of *Nassella viridula*. Finally, just south of the Nebraska Sandhills region, and west of the tallgrass prairie we find the

Wheatgrass-Bluestem-Needlegrass association, which some authors consider to be part of the tallgrass prairie (e.g. Sims 1988). The three dominant grass species of this area are *P. smithii*, *A. gerardii*, and *S. spartea*. The dominant grasses that occur in all three of these mixed-grass associations are *Stipa* /*Nassella* spp. and *P. smithii*.

In Canada, the ecology of the mixed-grass prairie has been reviewed by Coupland (1950, 1961), who has divided mixed-grass prairie vegetation into five distinct types or 'facies'. These are as follows: the *Stipa-Agropyron*, *Stipa-Bouteloua-Agropyron*, *Stipa-Bouteloua*, *Bouteloua-Agropyron*, and *Agropyron-Koeleria* faciations (Coupland 1961). Among these five faciations, Coupland (1950) has named six species of primary importance to the mixed-grass prairie, based largely on their abundance. These are *Stipa comata*, *S. spartea*, *B. gracilis*, *Agropyron dasystachyum*, *P. smithii*, and *Koeleria cristata*, with a seventh species, *Muhlenbergia cuspidata*, also being important on eroded soils (Coupland 1950).

According to Coupland (1950, 1961), forb species do not tend to represent much in terms of biomass on the Canadian mixed-grass prairie -- they do, however, contribute greatly to the overall diversity. For example, in the *Stipa-Bouteloua* faciation, Coupland (1950) listed 19 grasses and sedges and 28 forbs as dominant, principal, or secondary species. When considering less frequent species, the number of forbs encountered rose to 40. Coupland's (1950) most commonly encountered forb species in the mixed-grass prairie was *Artemisia frigida*. Other present forbs included *Phlox hoodii*, *Malvastrum coccineum*, *Pulsatilla ludoviciana*, *Gutierrezia diversiflora*, *Solidago* spp., *Rosa* spp., *Sideranthus* spp., *Chrysopsis villosa*, *Potentilla* spp., *Artemisia* spp., and other legumes and composites (Coupland 1950).

1.2.4 Rough Fescue Prairie

Geographic Distribution

As mentioned previously, rough fescue prairie is the only prairie type that occurs solely in Canada. It is also the northern-most prairie type. Fescue grasslands occur within three distinct geographical locations in the northern Great Plains (Looman 1969). The largest fescue community occurs along the western and northern boundary of mixed-grass prairie in Alberta. From here, along the northern edge of the mixed-grass prairie, the fescue prairie extends eastward into mid-Saskatchewan. Another fescue prairie community occurs as an island within the mixed-grass prairie, in the Cypress Hills region of Alberta and

Saskatchewan. Finally, fescue prairie also co-occurs (i.e. alternates) with mixed-grass prairie in a band moving south-east from Saskatchewan to southern Manitoba, enclosing the boundaries of the Canadian tallgrass prairie on all sides (Looman 1969).

Climate and Soils

Mean annual precipitation within the fescue prairie region is approximately 45 cm. This is 5 cm greater than that within the Canadian mixed-grass prairie region, and approximately 5-10 cm less than that of the tallgrass prairie. Mean July temperatures remain similar to that of the Canadian mixed-grass prairie, at about 17°C (Bryson and Hare 1974). Soils within the fescue prairie regions are primarily moist and warm udollic and aquollic mollisols – similar to the soil type commonly found within the tallgrass prairie region (Bragg 1995). By the Canadian soil classification standards, this soil is considered to be mostly black to occasionally dark brown chernozemic. In the Cypress Hills fescue region, there occurs an island of black to dark brown chernozems, surrounded by brown chernozemic mixed-grass soils (Clayton et al. 1977).

Species Composition

Of obvious importance to the fescue prairie species composition is the graminoid genus *Festuca*. However, just what species of *Festuca* is a matter of some confusion due to the taxonomic complexity of the genus (Pavlick and Looman 1984). According to Pavlick and Looman (1984), the *Festuca* species that are most abundant in western Canada are *F. altaica, F. campestris*, and *F. hallii*, with only the latter two species occurring in the fescue prairie regions of central Canada. *F. campestris* is most likely found along the western border of the Alberta fescue region, and into interior British Columbia (Stout et al. 1981; Pavlick and Looman 1984). *F. hallii*, on the other hand is most likely found within the rest of the fescue prairie region, from central Alberta and Saskatchewan, to south-western Manitoba. Note that the fescue referred to by Coupland and Brayshaw (1953) as *F. scabrella*, and by Pylypec (1986) as *F. altaica*, is likely *F. hallii*, by Pavlick and Looman's (1984) classification. Meanwhile, the fescue of the Cypress Hills region could potentially be *F. hallii*, and/or *F. campestris* (Pavlick and Looman 1984).

In terms of species associations, fescue is usually the only dominant species within fescue prairie (Coupland and Brayshaw 1953). In the Cypress Hills region, for example,

44% of all species cover was composed of fescue, while 30% was composed of other grasses and sedges , 20% was composed of shrubs, and only 5% was composed of other forb species (Coupland and Brayshaw 1953). Other grasses of importance in the Cypress Hills include *Agropyron subsecundum, Danthonia intermedia, Helictotrichon hookeri*, and *Stipa spartea* (Coupland and Brayshaw 1953; Looman 1969) The dominant shrub species here are *Potentilla fruticosa*, while forbs include *Cerastium arvense, Achillea millefolium*, and *Galium boreale*.

In other portions of the fescue grassland, the landscape is dotted with bluffs of *Populus tremuloides* -- the actual grassland occurs around the periphery of these bluffs (Coupland and Brayshaw 1953). In this region, fescue is again the single dominant species (approx. 32% of composition), however it is commonly associated with the grasses *S. spartea, Koeleria cristata, Elymus trachycaulus, A. subsecundum, Helictotrichon hookeri, B. gracilis*, and *Muhlenbergia richardsonis*. Forbs of importance in the aspen-fescue prairie include many species of the Compositae family, including *Solidago glaberrima, C. arvense, A. millefolium*, and *Aster ericoides* (see Moss and Campbell [1947], Coupland and Brayshaw [1953], Looman [1969], Pylypec [1986], and Slogan [1997] for a more comprehensive listing of grasses, forbs, and shrubs present within the fescue prairie).

1.3 Grassland Ecophysiology: C_3 vs. C_4 Plants

1.3.1 Physiological Background

Physiological Differences Between C_3 and C_4 Species

The predominant method of carbon assimilation in plants occurs via the Calvin cycle, or the C_3 photosynthetic pathway. This method of carbon assimilation (occurring within bundle sheath cells) first combines CO_2 with ribulose-1,5-bis-phosphate (RuBP) via the ribulose bisphosphate carboxylase oxegynase (rubisco) enzyme, to form two 3-phosphoglyceric acid (3-PGA) molecules (Salisbury and Ross 1992). Another important carbon assimilation pathway (especially within grassland ecosystems) is known as the C_4 dicarboxylic acid pathway. This pathway acts as a sort of 'add on' to the mechanisms already used in C_3 photosynthesis. Here, before CO_2 molecules reach the bundle sheath cells, carbon is fixed within the mesophyll cells into either malate or aspartate, via the phosphoenolpyruvate (PEP) carboxylase enzyme and RuBP substrate. These 4-carbon

sugars are then transferred to the bundle sheath cells, where they are either stored or immediately decarboxylated back into CO_2 to be fed through the Calvin cycle (Black 1971). These physiological and anatomical differences between C_3 (cool-season) and C_4 (warm-season) species have further ecological ramifications, which will be discussed below.

Ecophysiological Traits

Overall, pre-packaging of CO_2 into malate or aspartate confers some photosynthetic advantages to C_4 plants, primarily by reducing the effects of photorespiration, the competitive fixation of O_2 by the rubisco/RuBP complex in the bundle sheath cells (Waller and Lewis 1979). In C_3 plants, high temperatures, drought, and high irradiance levels all contribute to an increase in the bundle sheath $[O_2]/[CO_2]$ ratio, resulting in decreased carbon fixation, increased O_2 fixation, and increased CO_2 production through photorespiration (Black 1971; Salisbury and Ross 1992). Since C_4 species maintain a low $[O_2]/[CO_2]$ ratio in bundle sheath cells, RuBP has relatively little O_2 to bind with. Furthermore, any CO_2 that is produced by photorespiration in C_4 plants may be intercepted within the mesophyll cells and fixed to malate or aspartate (Larcher 1991). Hence, we would expect C_4 plants to not only fix more CO_2, but to also produce less CO_2 through respiration than C_3 plants.

Furthermore, high temperatures decrease the solubility of CO_2 in bundle sheath chloroplast water. In C_3 species this decreases productivity, but in C_4 species, again because of their CO_2 concentrating ability, higher temperatures have less of an effect. Similarly, during periods of drought, C_3 species close their stomata, resulting in less CO_2 reaching the chloroplasts. C_4 species again have an advantage -- carbon assimilation can occur even with the stomata closed, using stored aspartate and malate molecules. Most loss of productivity in C_3 species occurs as a result of photooxidation or photorespiration. These processes result in the loss of already-fixed CO_2 in C_3 species. In C_4 species these processes do not occur, due to the concentration of CO_2 in the bundle sheath cell chloroplasts (Larcher 1991).

1.3.2 Ecological Patterns of Coexistence

Plant Competition

As discussed in greater detail in section 1.4, plants that are at a competitive advantage tend to have rapid growth rates, and other associated characteristics (i.e. large size, rapid CO_2 assimilation rates, and high photosynthetic capacities). In general, C_4 plants exhibit these favourable characteristics (Black 1971). However, where conditions favourable to C_4 growth do not occur, C_4 species may in fact loose their competitive advantage. Williams (1974) has determined that at 30°C, *Bouteloua gracilis* (a C_4 species) has a greater net photosynthetic rate than does *Pascopyrum smithii* (a C_3 species), but at 20°C, the reverse is true. Furthermore, transpiration rates were greater in *P. smithii* at 20°C, while at 30°C, transpiration rates were greater in *B. gracilis* (Williams 1974). In terms of maximum growth rates, *P. smithii* achieves its maximum rate between roughly 10-15°C daytime temperature, while *B. gracilis* achieves its maximum growth rate between 27-32°C (Williams and Markley 1973). In general then, C_4 species tend to grow best in hotter and drier conditions, while C_3 species tend to grow best in cooler and more moist conditions.

Niche Partitioning and Changes in Temperature

Potential differences in growth rates at different temperatures and moisture regimes can lead to an array of ecological and competitive phenomena. Williams and Markley (1973) have suggested that C_3 and C_4 temperature preferences have allowed for niche partitioning, and subsequent reduction in interspecific competition, since each type of species will grow at a different time of the year. This hypothesis is supported by phenological observations on shortgrass species by Dickinson and Dodd (1976), as well as by growth temperature observations on *B. gracilis* and *P. smithii* by Kemp and Williams (1980). Another ecological factor which affects C_3 and C_4 plants is water availability.

Although Kemp and Williams (1980) have shown that there is little difference in the response of C_3 and C_4 species to acute water stress, chronic drought may result in a shift in C_3 and C_4 abundance patterns. Specifically, Tilman (1996) has shown that the relative abundance of C_4 species significantly increased over a roughly three year drought period, only returning to the pre-drought abundance levels five years after the drought. Furthermore, although mean C_3 species abundance declined somewhat during the period of drought, the decline was not significant (Tilman 1996). A further observation made by Tilman (1996) was that nutrient addition within similar plots led to a gradual and significant increase in C_3 abundance, and decrease in C_4 abundance over time, even though overall species richness appeared to decrease. Finally, differences in soil texture, which in turn affect nutrient and water availability, have been shown to favour one type of C-assimilation strategy over another. By looking at relative abundance of C_3 and C_4 grasses at four grassland sites within the Great Plains, Epstein et al. (1997) have shown that the relative abundance of C_3 grasses decreases and C_4 grasses increases with increasing sand content and decreasing clay content.

Geographic Distribution of C_3 and C_4 Plants

Since there are clear patterns in relative abundance of C_3 and C_4 plants, based on temperature, and long-term water availability, we would likely expect to see a change in the relative abundance of these species with geographical changes in climatic conditions. In fact, a dramatic change in the relative abundance can be seen along a north-south gradient (Sims 1988; Epstein et al. 1997). According to Sims (1988), from 30° to 42° north latitude, C_4 species account for almost 100% of the grassland biomass. Further north a rapid increase in relative abundance of C_3 species occurs. For example, by 46° north latitude C_3 species account for almost 100% of the plant biomass (Sims 1988). Curiously, this data, as presented by Sims (1988), would indicate that the occurrence of C_4 species within the Canadian prairies would be extremely rare -- clearly this is not the case. Epstein et al. (1997) have shown that C_3 species will tend to be dominant in areas that have < 55 cm mean annual precipitation (MAP) and <9°C mean annual temperature (MAT). This area corresponds to all areas north of and including North Dakota (approx. 45° north latitude). However, zero C_4 production is not expected to occur until MAP drops at least below 25

cm and MAT drops at least below 10°C, well within the climatic ranges of many portions of the Canadian prairies (Epstein et al. 1997).

1.4 Competition and the Prairie

1.4.1 Definitions and General Mechanisms of Competition

Defining Competition

Competition is an important and frequent interaction amongst plants and animals (Schoener 1982, 1983; Connell 1983), and has been of great interest to plant ecologists. Newman (1992) has defined competition as an interaction where the following three criteria are met: a) the competitors in question share resources; b) at least one of the supplies of a shared resource is reduced for one competitor by the other; and c) this decreased supply of resources affects the growth, reproduction, and/or survival of the adjacent plant. This definition of competition is similar to that proposed by Begon et al. (1990), but Newman (1992) goes on to note that competition need not be a reciprocal interaction. In other words, species *A* may affect the growth of species *B*, but species *B* need not affect the growth of species *A*. Furthermore, Newman's (1992) definition of competition neither requires that a plant's growth, survival, or reproduction all be simultaneously affected, nor that they be decreased but simply 'affected'. Furthermore, although it may be implied, there is no direct inclusion of fitness (i.e. the degree to which an individual's genes are passed on to future generations) in this definition of competition.

Exploitation and Interference

In terms of general mechanisms of competition, two categories have generally been described in the literature. These categories, involving both above and below ground components, are exploitation competition and interference competition (Keddy 1989; Begon et al. 1990). Exploitation competition occurs when an individual is affected by the presence of a competitor due to the creation of a 'nutrient depletion zone' where both individuals' niches overlap. An example of exploitation competition includes local nutrient depletion in the soil surrounding the roots of two plants, as well as shading of a short-statured species by a tall-statured species. In contrast to this 'passive' type of competition is

interference competition. When a competitor actively suppresses the ability of another individual to obtain a resource, interference competition is said to be occurring. A commonly used example of this type of competition is allelopathy, in which one plant actively secretes substances which detrimentally affect a neighbouring plant's ability to grow, survive, or reproduce. Note, however, that allelopathy is neither a universally accepted phenomenon among plant ecologists nor a common one among plants (Newman 1992).

1.4.2 Dynamics of Competition

Individualistic Models

Although competition is said to occur via the two mechanisms described above, there are many forms that this competition may take. These forms or types have been summarized by Keddy (1989) as a) intraspecific competition, b) interspecific pairwise competition, c) competition intensity, and d) diffuse competition. Perhaps the first important distinction when defining competition is that between interspecific and intraspecific competition (Keddy 1989; Begon et al. 1990). Intraspecific competition is simply competition occurring between two or more members of the same species. It is usually measured by altering densities of plants, then subsequently measuring the change in an individual's growth, reproduction, or survival (Keddy 1989). This type of competitive interaction has utility within plant monocultures. Specifically, agriculturalists can measure intraspecific competition to help determine the maximum possible yield of a crop.

Interspecific pairwise competition is similar to intraspecific pairwise competition except that the competition is occurring between individuals of different species. This type of competition can be more useful to ecologists as it can be used to infer the effects of different species on each other in a more realistic plant community context, even though it is unlikely that an individual plant can distinguish these two types (Keddy 1989). Note that because this type of competition only considers species interactions between adjacent pairs of individuals, inferences on multi-species interactions must be made with caution.

Population and Community Models

The next two types of competitive interactions involve interactions between more than two adjacent individuals (i.e. greater than pairwise), taking competition effects beyond the

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sum of pairwise interactions. The first of these is competition intensity. This type of competition simply involves the combined effects of all neighbours in a population or individual species (Keddy 1989). Competition intensity is usually measured by 'removal' experiments, where neighbours are removed around a target species and the subsequent increase in target species biomass is compared to its 'controlled' biomass without neighbour removal (Keddy 1989; see Wilson and Shay 1990). Another method for measurement of competition intensity involves adding a 'phytometer' (i.e. an indicator plant) into an uncleared or cleared plot, and comparing the effects of neighbours vs. no neighbours, respectively, on growth and development (Keddy 1990). This type of competition measure is useful in that it can be observed and quantified in real communities involving several species. Its shortcoming is that it is difficult to determine which neighbours are having a greater or lesser effect on the target species.

The fourth measurable type of competition is diffuse competition. This type of competition is difficult to distinguish from competition intensity. Keddy (1989) considers diffuse competition as a case where competition intensity on a target species is evenly and equally diffused amongst all neighbour species. Mitchley (1987) notes two definitions of diffuse competition, used primarily within the zoological literature. The first is simply the additive effects of all pairwise competitive neighbours; the second is the competitive effects of all neighbours over and beyond the additive effects. Neither of these two definitions address the relative diffusion of the competitive effects across all neighbours (i.e. are they all equally competitive, or is competition caused mainly by one individual or species?).

1.4.3 Competition Intensity, Dominance, and Competitive Exclusion

Asymmetric Competition

The last point mentioned in the above paragraph deals with the question of relative intensities of competition. This is by no means a trivial issue, as competition is likely to be, at the very least, a bi-directional interaction. Just as species A may affect species B in a pairwise interaction, species B may affect species A. It follows that the intensity of competition need not be symmetrical (i.e. equal in both directions). In fact, intraspecific and interspecific competition are usually asymmetric (Keddy and Shipley 1989). Asymmetric competition is considered to be occurring when the effect of species A on species B is greater than that of species B on species A. A relatively conservative numerical definition has been used by Keddy and Shipley (1989): a pairwise competitive interaction

between species *A* and *B* is said to be asymmetric when the relative yield (i.e. a species yield in mixture/its yield in monoculture) of one species is >1, while the relative yield of the other species is <1. The species with the greatest suppressive effect in an asymmetric competitive interaction (i.e. the species with a relative yield of >1) is said to be the competitively dominant species, while the one with the lesser effect (relative yield <1) is said to be the competitive subordinate. Note, however, that Keddy's (1990) asymmetric interaction is based on reducing relative yield to a binary measure (i.e. a 1 [>1] or a 0 [<1]), in effect losing any information on the magnitude of the asymmetry. Furthermore, competitive dominance/subordinance based on relative monoculture performance (i.e. relative yields) need not imply competitive dominance/subordinance in mixtures (Connolly 1997).

The Competitive Exclusion Principle

If the magnitude of asymmetry between two competitors is great enough and the resistance of the subordinate is low enough, competitive exclusion is predicted to occur, at least in the absence of other factors such as disturbance (Keddy 1990). Observations of the 'competitive exclusion' phenomenon were first reported by Gause (1934) in experiments involving two species of yeast. Here, one 'dominant' species of yeast would suppress the growth of a 'subordinate' species when grown in mixture (Gause 1934). Keddy (1989) describes this type of competitive exclusion as occurring via a two loop positive feedback mechanism -- one loop is exploitation competition, while the other is interference competition. Furthermore, as a dominant species suppresses the growth of the subordinate via competition, it further enhances its competitive ability while simultaneously decreasing the subordinates competitive ability via induced stress on the subordinate. The competitive interaction thus becomes more asymmetric over time, until the subordinate is completely excluded from the community. Interestingly, Gause's (1934) 'dominant' yeast never did completely exclude the 'subordinate' from the population. Also, Gause's exclusion principle did not stress the importance of asymmetric competitive interactions *per se*, but stressed similarities in ecological and geographical niches and differences in reproductive rates (Hardin 1960).

1.4.4 Competitive Hierarchies

The Basic Model

Regardless of whether or not complete competitive exclusion will occur in practice, researchers have used the competitive exclusion principle, along with relative yields, in order to determine relative competitive abilities and competitive hierarchies amongst groups of plant species (Norrington-Davies 1967; Goldsmith 1978; Wilson and Keddy 1986a; Mitchley and Grubb 1986; Grace et al. 1992). The basis for experiments measuring competitive abilities lies in the diallel replacement series design (McGilchrist and Trenbath 1971), in which species are grown in all pairwise possible combinations and in monocultures. Species' yields in mixture are then compared to those in monoculture to form a matrix of relative yields, also known as a competition matrix, in which the relative yield of a species (the 'target' species) on the y-axis is displayed for each interaction with every other species (the 'neighbour' species) along the x-axis. From these matrices, one can determine competitive abilities amongst the group of plants, by using mean relative yields or other competitive ability measures derived from relative yields.

Mean Relative Yield as a Competitive Index: Target and Neighbour Scores

From logged mean yield values, the increase (or decrease) in relative biomass of a given 'target' species can be measured when grown in combination with any other 'neighbour' species by comparing its logged mean yield in mixture (Y_{ij}) with one-half of its logged mean yield in monoculture (Y_{ii}). This calculation is termed mean 'relative yield' or the species' mean yield in mixture relative to its mean yield in monoculture (Keddy and Shipley 1989). Symbolically this measure is denoted as X_{ij}, and is calculated as follows:

$$X_{ij} = Y_{ij} / Y_{ii}$$

Values of X_{ij} greater than 1 indicate that species i has a greater yield in mixture with species j than at equal density in monoculture. Wilson and Keddy (1986) term the mean relative yield across any one row its 'target score', or the mean relative yield of the target species over all neighbouring species. These scores can be used as an index of competitive ability. Species with higher target scores have greater competitive ability, since they tend to grow better in mixture than in monoculture. Similarly, relative yield means over the columns of the matrix represent 'neighbour scores', or the mean relative yield of the twelve neighbour

species when grown with a given target species. Those species with lower neighbour scores may also be considered to have higher potential competitive ability, since their neighbours tend to be suppressed.

Mean Aggressivity as a Competitive Index

The use of mean relative yields alone may be misleading as competitive indices since both the relative biomass of target and neighbour species have to be considered separately (Wilson and Keddy 1986). For example, a plant with a relative yield of 1.5 may appear to be a strong competitor within that mixture. However, if the neighbour species of that specific mixture also has a relative yield of 1.5, then we have a case of mutual enhancement, not competition. The competitive outcome of a mixture can perhaps be better determined when the relative yields of both species of a given mixture are considered simultaneously. This is done when the mean relative yield matrix is transformed into a matrix of 'aggressivity' values (McGilchrist and Trenbath 1971). Aggressivity (A_{ij}) is simply the difference between mean relative yield of a target species (X_{ij}) and its neighbour (X_{ji}):

$$A_{ij} = 0.5 \; (X_{ij} - X_{ji})$$

If the target species has a mean relative yield >1, and the neighbour has a mean relative yield <1 (i.e. is suppressed by the target species), then the target species will have a fairly high and positive aggressivity value for that specific mixture. Conversely, its neighbour's aggressivity will have the same magnitude but opposite sign (i.e. negative). Aggressivity is hence a composite measure of both a) the degree to which a target species fairs better or worse and b) the extent that it suppresses the growth of its neighbour. Thus species with high and positive mean aggressivity values are better competitors, since they grow well in mixture and suppress their neighbours. Those species with high but negative aggressivity values are poor competitors since they grow poorly in mixture and are less capable of suppressing their neighbours. As with relative yield values, the degree to which aggressivity predicts actual competitive exclusion is unknown (Connolly 1997).

Asymmetry as a Competitive Index

Another index that summarizes the interactions between species by using variables from both species is 'asymmetry', as defined by Shipley (1997). Asymmetry between a pair of

species (S_{ji}) is measured by the greater of X_{ji} and X_{ij} divided by the lesser. Note that because this is a ratio, asymmetry between species pairs with both relatively low X values will be fundamentally greater than that of species pairs in which both species have relatively high values, even though the absolute differences in X (i.e. aggressivity) may be equal. For example, 0.9/0.5 is greater than 2.9/2.5, even though their absolute differences (i.e. aggressivity values) are equal.

Binary Transformation: Dominance

In order to simplify data analysis, matrices of relative yields may be transformed into binary form. This has been done by assigning any relative yield > 1 a value of "1", and any relative yield < 1 a value of "0" (e.g. Shipley 1993). The species with the least amount of "1" 's across a row may be considered to be the least 'dominant' species, while that with the greatest amount of "1" 's the most 'dominant' species. Again, a "1" assigned to any species in a mixture may mistakenly confer a competitive advantage for that species, when in fact its neighbour species may also be assigned a "1". This scenario as an example, would be more consistent with mutual enhancement, not necessarily competition. Furthermore, a species assigned a "1" may fair better in mixture, but how much better remains lost with the conversion of a real number matrix to a simple binary matrix. In other words, the magnitude of asymmetry between the species is impossible to determine.

Relative Efficiency Indices

A competitive ability measure that completely does away with relative yield measurement is known as a 'Relative Efficiency Index' (REI). It was developed by Connolly (1987) and is calculates as follows:

$$REI_i = \ln\left(\frac{Y_{iT}}{Y_{io}}\right) \div \ln\left(\frac{Y_{jT}}{Y_{jo}}\right)$$

In the above equation, Y = yield (or some other measure of performance), i = the target species, j = the neighbour species, 0 = at onset of experiment, T = at time of harvest. As such, the above equation measures the growth rate of species i relative to that of species j. Grace et al. (1992) found that competitive hierarchies developed using REI indices were more consistent and less prone to size biases over a three year period than were hierarchies

constructed using relative yield indices alone. However, relative yield hierarchies became more correlated with REI hierarchies with time -- by the end of the third growing season, the R^2 value between these two types of hierarchies was 0.73 (p = 0.02). In experiments where transplants are not used, initial seed weights would have to be used as Y_0 values. In this case, Y_0 values would be extremely small relative to Y_T values, making this calculation unsuitable for experiments beginning from seed.

Transitivity

One of the central problems of using the above types of measures alone is that competitive hierarchies are constructed using values averaged across several species treatments. These averaged values may give the false impression of a consistent 'competitive ability' for any one plant, when competitive ability could potentially vary within any one species, depending on which species it is competing with. Keddy and Shipley (1989) and Shipley (1993) have thus developed a model which defines a completely transitive asymmetric competitive hierarchy. Using a FORTRAN program, Shipley (1993) scanned a binary competition matrix to extract all completely asymmetric and transitive competitive hierarchies from that matrix, involving any number of species from 2 to n. 'Asymmetry' in this context is used as described in sub-section 1.4.3, as defined by Keddy (1990). 'Transitivity', a mathematical term, is used to describe a case where if species *A* outcompetes species *B*, and species *B* outcompetes species *C*, then *A* must (by the principle of transitivity) outcompete *C*. These hierarchies were then counted and compared to the number expected given completely random interactions (i.e. a null model), as generated by a Monté Carlo simulation. From here, Shipley was able to determine if there was a trend towards hierarchical structure, or a trend towards random interactions. In examination of 10 published competition experiments, Shipley (1993) found "clear evidence of a general tendency for a hierarchical ordering of the competitive abilities of plant species".

Previous Diallel Competition Studies

Norrington-Davies (1967) performed a diallel competition experiment using five species of grasses, grown from seed within earthenware pots in a greenhouse. The entire set of treatments was only replicated once. Portions of the pots were harvested 136 days from sowing, while the rest were harvested 198 days from sowing. From this experiment, there appeared to be a clear tendency towards competitive asymmetry, or 'compensatory'

changes in mixture, meaning one species' relative yield would increase while the other's would decrease. Furthermore, total yields in mixture tended to exceed those in monoculture, due to the dominant species increasing in yield to a greater extent than the subordinate species would decrease its yield (Norrington-Davies 1967).

Goldsmith (1978) performed a similar experiment using eight perennial species of mature plants taken from relatively undisturbed cliff-sides, then transplanted into pots set within a greenhouse. The experiment, with only one replicate, was harvested once after 3 years of growth. The results from this experiment showed a tendency for the more competitive species to produce greater above-ground biomass than their subordinate counterparts. Furthermore, there existed a tendency for asymmetric competitive interactions to occur, as with the experiment described previously. Finally, Goldsmith (1978) notes that less competitive species appeared to survive by being 'fugitive species' or 'gap-fillers'.

Fowler (1982) performed two diallel competition experiments, each using five species of common lawn plants (two grasses and three forbs). This experiment, like those described above, was performed in a greenhouse using potted plants, although Fowler (1982) used five replicates of each treatment. Plants were grown from seed, and harvested after one growing season. All plants were clipped regularly to simulate regular mowing. Furthermore, plants were grown at two different densities, as well as in different proportions (i.e. 1:2 and 2:1 combinations) to test for density effects and effects of species proportions. In the second experiment, four moisture and nutrient treatments were also tested along with the diallel crosses (using two levels of water availability and two levels of soil fertility in a factorial design). The results from the density tests showed little difference in the relative competitive abilities of plants due to changes in overall sowing density. Of the three pairs of species tested for proportional effects, two showed no significant change in terms of their relative competitive abilities relative to their 1:1 mixtures. One pair did demonstrate 'negative frequency dependent' behaviour, meaning the species with the higher initial sowing density had the greater competitive ability in the end. Overall, environment was found to have a major effect on the intensity of competition as well as in the ranks of species within competitive hierarchies (Fowler 1982).

Three diallel competition experiments were performed by Moore and Williams (1983), all in pots within a greenhouse. In the first experiment, consisting of two replicates, seven 'weedy' species were sown from pre-germinated seeds, then thinned to appropriate densities. In the second experiment, consisting of four replicates, eight species were grown

from seed (four cool-season annuals, two grasses, and two cruciferous weeds) in replacement series at two levels of phosphorus, calcium, potassium, and nitrogen, in a factorial arrangement. The third experiment, replicated five times, used three closely related thistles grown from seed at three levels of calcium and nitrogen in a factorial arrangement. Moore and Williams (1983) observed a tendency for species with high monoculture productivity levels to have a competitive advantage under most, but not all, circumstances. Also, competitive abilities were found to vary according to nutritional status of the soil.

In an outdoor pot experiment, as well as a field experiment, Mitchley and Grubb (1986) tested the relative competitive abilities of chalk grassland species. In the pot experiment, fourteen species were grown from pre-germinated seed and tested relative to the performance of two 'phytometers' or indicator species. The pots were harvested after one and two growing seasons (18 and 70 weeks, respectively). In the field experiment, six species were grown from collected seed in a diallel replacement series arrangement, replicated three times. Data were collected over a six year period (1980-1985). Overall, above-ground competition appeared to be most significant after the first two years of growth, as competitive ability was correlated with the mean height of rosette leaves of each species. These short-term competitive trends were well correlated with the actual distributions and relative abundances of the species in their natural habitat. After two growing seasons, life-history traits including longevity, lateral spread, and seedling mortality, seemed to play more important roles in determining longer term competitive abilities.

Wilson and Keddy (1986a) grew seven shoreline species in an outdoor potted diallel experiment, replicated ten times. The species were grown from ramets of relatively similar size. The seven species naturally occur along the exposure gradient on the shoreline of Axe Lake, Ontario. Their relative abundances along this gradient were measured then compared to relative competitive abilities as determined by the diallel crosses. Overall, Wilson and Keddy (1986) observed that superior competitors tended to occur at the relatively benign end of the exposure gradient, where stress and disturbance were minimal. Where stress and disturbance increased, plants of relatively low competitive ability were found.

Grace et al. (1992) used a diallel competition experiment to evaluate the relative yield measure (RY) versus the 'size-independent' relative efficiency index (REI). Six wetland graminoids were grown in 1L pots from transplants collected in the field. Species performance was evaluated for the first two growing seasons using shoot length. For the

third and last growing season, species were harvested, dried, and massed. Species were much more prone to reversals in relative competitive ability from year to year when evaluated using RY's. When evaluated using REI's species were less prone to reversals in rank order. Also, RY's were dependent on initial transplant size, while REI' s were not. Note that the dependence of RY's on initial plant size decreased over time, such that by the third growing season RY's and REI's showed similar ranks in competitive ability (R^2 = 0.73, p = 0.02).

1.4.5 Shortcomings and Criticisms of Competitive Hierarchies

Despite the general consensus that competitive hierarchies do exist, the results of previous competition experiments and their general conclusions are subject to some debate (Joliffe et al. 1984; Firbank and Watkinson 1985; Connolly 1986, 1997; Silvertown and Dale 1991; Shipley 1994). The current shortcomings and criticisms of competitive hierarchy experiments can be broken down into three more or less unresolved issues: a) the degree to which competitive exclusion is actually predicted by competitive hierarchy models; b) how robust or consistent the competitive hierarchies are; and c) the importance of size bias in the interpretation of competitive hierarchy models.

Competitive Exclusion

Evidence for competitive hierarchies does not necessarily imply evidence for competitive exclusion (Connolly 1997). As of yet, there exists no information on how well competitive hierarchies actually predict competitive exclusion in the field.

Robustness of Competitive Hierarchies

It has yet to be determined to what extent competitive hierarchies amongst a group of plants remain true when grown under different climatic conditions, edaphic conditions, and disturbance regimes (Fowler 1982; Silvertown and Dale 1991). Most studies of competition indicate that changes in competitive ability are to be expected. For example, reversals in relative competitive ability have been observed along experimental nutrient gradients (Fowler 1982; Moore and Williams 1983; Tilman 1984, 1987; Wilson 1994), gradients of physiological drought (Kenkel et al. 1991), and gradients of stress and disturbance (Wilson and Keddy 1986a; Wilson and Tilman 1991, 1995).

Some authors argue that replacement series methodology used to evaluate competitive hierarchies may be 'biased' towards larger plants (Firbank and Watkinson 1985; Connolly 1986, 1997; Grace et al. 1992). There are two premises to this argument. The first is that relative yields >1 indicate that a given species is either a) competing well with its neighbour in mixture, or b) is being released from intraspecific competition in monoculture. To what extent each effect is being expressed for a given species is unknown. The second premise is an assumption that large species have a greater propensity (i.e. a 'bias') towards the latter effect than smaller species (i.e. larger species are more likely to be 'released' from intraspecific competition) because their density is 'effectively' higher than that of smaller species. Hence, larger plants are more likely to have higher relative yields due to the greater probability of their being released from intraspecific competition, due to their higher 'effective' density (Connolly 1997).

One problem with this size bias argument is that the two 'separate' effects contained within the first premise are likely confounded. A species that is undergoing the former effect (i.e. is a strong competitor) is more likely to undergo the latter effect as well, since release from intraspecific competition by definition requires a species to be a strong intraspecific competitor. Furthermore, the assumption that larger plants are more likely to be released from intraspecific competition is itself a size bias. Specifically, larger plants are assumed to undergo stronger intraspecific competition than are smaller plants. In essence, this is arguing that relative yields are biased towards large plants because large plants are stronger competitors. Large plant size (i.e. above-ground biomass accumulation) may be a strategy used by certain plants to obtain and maintain dominance within an area. If this is true, then controlling for size in competition experiments would nullify a plant's predominant competitive strategy, and thus fail to detect the truly stronger competitor (Shipley 1994).

Regardless of the difficulties with the size bias argument, there are three conditions under which size bias is most critical:

(a) Although Wilson (1994) found little effect of different initial plant sizes on competitive responses, when there are strong differences in plant sizes and/or growth forms size bias will likely be more pronounced. This effect will likely not be as important when similarly-sized species of similar growth forms (e.g. all

graminoids) are grown from seed, since initial weights and final sizes are similar for all species.

(b) When competition experiments are grown in pots, the intensity of root competition may be artificially inflated relative to field conditions due to size constraints. Under these circumstances, large plants will be prone to even higher 'effective' density than in field conditions, thus exacerbating any potential size bias in pot experiments.

(c) Differences in sowing densities from experiment to experiment will have little effect on competitive responses of plants (Fowler 1982). When species are grown at exceedingly high densities however, size bias is expected to be exacerbated due to the greater occurrence of density effects in general.

1.4.6 Traits of Competitively Dominant Plants

Limiting Resources of Competing Plants

As mentioned previously, in order for competition to occur, plants must be limited by some shared resource. Since plants are sessile organisms with similar modes of energy acquisition (i.e. photosynthesis), the potential for sharing limiting resources is great. Among the most important of these resources are light, water, nutrients, pollinators, and carbon dioxide (Newman 1992). Ultimately, it is the lack of one of these resources in subordinate species that eventually suppresses their growth. Thus, it is believed that plants with the greatest and most efficient means of sequestering resources through both above-ground and below-ground mechanisms should be competitively dominant plants (Newman 1992).

The 'Holy Grail' of Competitive Ability Traits

If competitive hierarchies do in fact exist, and species do have measurable competitive abilities, then it follows that there exist traits that render a species more or less competitive. Aarssen (1983), in his classic paper on coexistence in systems of competition, has tabulated attributes of plants which could potentially make them more competitive, via either exploitation competition or interference competition. According to Aarssen (1983), in terms of exploitation competition, competitively dominant plants would have rapid growth

rates; tall plant heights; large leaf areas; extensive or deep root systems; large seed sizes; early arrival, germination and establishment; effective pollination and dispersal mechanisms; the ability to sequester resources from other species via rhizomes, stolons, or root graphs; and an ability to tolerate temporary extremes in the environment.

To be a good interference competitor, a plant would ideally carry pests or diseases harmful to other species, interfere with environmental triggers for other plants, produce large amounts of ground litter, be allelopathic, and interfere with another species' pollination mechanism (Aarssen 1983). Beyond Aarssen's (1983) predicted traits, Gaudet and Keddy (1988) have looked at a number of plant traits in an attempt to correlate these with competitive ability by growing 44 species of plants together with a 'phytometer' or indicator species. From this experiment, Gaudet and Keddy (1988) found that above-ground biomass was the single best predictor of competitive ability. In fact, when plant height, another relatively good measure of competitive ability, was combined with above-ground biomass, it only raised the correlation coefficient by 2%.

1.4.7 Positive Interactions: Beneficience

Introduction

Of growing interest to ecologists is the opposite of competition — beneficience (Hunter and Aarssen 1988; Wilson 1989; Bertness and Callaway 1994). Just as some plants may suppress each others' ability to sequester limiting resources, some plants will potentially increase each others' ability to sequester these same resources. Hunter and Aarssen (1988) cite several examples of conditions under which beneficience may be occurring, and how beneficience interacts with competition to affect community structure. These ideas will be discussed below.

Nutrient Transfer and Mycorrhizae

One example of beneficence, of potential importance in grassland ecosystems, is nutrient transfer via root grafts or mycorrhizal hyphae. Although root grafts appear to be relatively rare interspecifically, they may be important intraspecifically in allowing these species to transfer nutrients. Mycorrhizae have been demonstrated to be important plant components in the tallgrass prairie region, especially in C_4 species (Hartnett et al. 1994). Furthermore, mycorrhizae show very little host specificity in grasslands, and as such they may regularly

infect a vast array of different species. When considering the fact that in order to receive a mycorrhizal infection a plant must be infected by an existing fungal network, one can see the potential benefits that a species can reap by growing in association with other infected species (Hunter and Aarsen 1988).

The Nurse Plant Phenomenon and Other Examples

Beyond nutrient transfer, Hunter and Aarssen (1988) have also identified soil and microclimate modification as a possible scenario under which beneficience could and does occur. In terms of microclimate modifications, the phenomenon likely to be important in grassland ecosystems is the 'nurse plant' phenomenon. Here, an established 'nurse plant' will keep the soil beneath it relatively free from evaporative water loss. Consequently, a young seedling or ramet could develop within soil that has relatively high surface moisture relative to the surrounding area. Conversely, a nurse plant may lower the water table via a high transpiration rate, providing for better aerated soil in areas where this is a problem for seedlings. Other soil modifications include the addition of organic material and the fixation of nitrogen (especially in the Leguminosae), which effectively increase nutrient levels in the surrounding soil (Hunter and Aarsen 1988).

Bertness and Callaway (1994) have listed several stresses ameliorated by plants and other sessile organisms. Among these stresses are heat and desiccation in desert shrubs; low nutrients in terrestrial plants, seagrasses, and marsh grasses; osmotic and low oxygen stress in marsh grasses; soil moisture in terrestrial plants; and disturbance in marsh grasses and trees. Finally, beneficience could also occur through changes in the biotic environment. Under this category are plant defense guilds, an increase in rhizosphere microbes, and an attraction to pollinators and dispersal agents, all of which have been demonstrated to occur in a handful of experiments (see Hunter and Aarsen [1988] for examples).

The Competition/Beneficience Model

As a final note, Bertness and Callaway (1994) have brought forth a model which describes the occurrence of positive or negative interactions as a function of both increasing stress and increasing consumer pressure. This model predicts that beneficience will occur either under stressful physical conditions or high consumer pressure, the two of which are considered to be mutually exclusive. Under highly stressful physical conditions beneficience would occur via 'neighbourhood physical stress amelioration'; under

increased consumer pressure, beneficience would occur via 'associational defenses' such as, for example, palatable plants associating with less palatable plants to avoid disturbance. At intermediate levels of both physical stress and increasing consumer pressure, Bertness and Callaway's (1994) model predicts that interactions would tend to be more negative (i.e. more competitive). Although the model just described may have a few oversimplified assumptions (e.g. are physical stress and consumer pressure always mutually exclusive?), it is of interest in that it is the first attempt at integrating plant interactions rather than simply looking at competition and beneficience separately.

1.5 Disturbance and the Origins and Maintenance of the Prairie

1.5.1 Definitions and Types of Disturbance

Introduction

Disturbance is another important factor involved in the dynamics of grassland communities (Anderson 1982). Sousa (1984) has indicated that all plants are subject to local environmental changes whose effects range from mild to relatively severe. For example, a shift in temperature can be relatively mild in its effect on a given plant if it is a seasonal shift. Conversely, a sudden temperature change can be detrimental to the point of causing plant death, as for example, during a late spring frost. Thus, Sousa (1984) considers disturbance to be the extreme end of a range in environmental effects: "...a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies)..." (p.356). Sousa (1984) then goes on to include another dynamic component -- establishment of species that previously did not exist in that location. Specifically, a disturbance also, "...directly or indirectly creates an opportunity for new individuals (or colonies) to become established" (p.356). Collins (1990) (after Pickett et al. [1989]), noting that disturbance should neither be considered a positive nor negative factor, includes an element of community change in his definition of disturbance. Specifically, Collins (1990) defines disturbance as something that changes or disrupts a structured community.

Disturbance Types on the Prairie

Considering the above definitions, many forms of disturbance are possible and important in grassland ecosystems. Specifically, Collins and Barber (1985) have divided disturbance

in grassland ecosystems into three types: climatic, pyric, and biotic. Climatic disturbances on the prairie generally include drought (Knapp 1985), but may also include flooding. Pyric disturbance (i.e. fire) is another important disturbance type which usually interacts with biotic factors (such as grazing and the purposeful setting of fires by aboriginals) as well as climatic factors (such as precipitation, drought, and electrical storms). Finally, there is biotic disturbance. Biotic disturbance includes any disturbance caused directly by other organisms, most often herbivorous animals. Examples of this type of disturbance include rabbit scrapes (Burggraaf-van Nierop and van der Meijden 1984), bison grazing, bison wallows, and the construction of 'prairie dog towns' by prairie dogs. Note that although all of the above types of disturbances may act independently, they are also capable of acting in concert, as multiple disturbance regimes, in influencing species coexistence and diversity (see sub-section 1.6.4.).

1.5.2 Fire: the hottest topic in disturbance ecology

Can't start a fire without a spark...

The prairie, as was first seen by Spanish eyes in the 16th century, were the prairies that have for roughly 10,000 years (post glaciation) developed alongside Native Americans (Bragg 1995). Native Americans are thus considered to be as much a part of the prairie as are the plants and animals that compose it. One of the most important effects that these people had on the community structure of the prairie was the purposeful setting of grassland fires (Weaver 1954; Wells 1970; Axelrod 1985; Whelan 1995). Among the proposed reasons for prairie burning by Native, and later European, peoples were to drive herds of bison during a hunt (although doubtful in light of the fact that most large game are not afraid of fire), to keep snake populations low, to clear land and dense vegetation for travel and other purposes, to increase concentrations of bison, to remove cover of game animals, and to limit the threat of 'warfare fires' set by human enemies (Vogl 1974; Axelrod 1985). Thus, Native North Americans were the first wildlife managers of the prairie, primarily via the use of fire.

Apart from controlled fires being set by Natives, thunderstorms have also been implicated as potential sources of fire ignition, especially within the Great Plains. Looking at the frequency of lightning storms in North America, we see a concentration with its epicenter in the Gulf of Mexico. Here, along the Gulf coast, there are in excess of 70 thunder storms per year on average. This frequency drops off roughly linearly to approximately 50 storms

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per year in Kansas, 30 in North Dakota, and 15-20 in the Fescue Prairie region (Bryson and Hare 1974). Note that although there exists a correlation between thunderstorm frequency and lightning-induced ignition, fires caused by lightning tend to occur more frequently in drier times of the year and in locations where there is a relatively high accumulation of detritus (Komarek 1964). Hence the frequency of lightning-induced fires interacts with other climatic and biotic factors. Furthermore, although one may think that fires caused by lightning would be fairly rare due to the presence of rain, prior to rainfall lightning can ignite grassland fires that will burn despite the subsequent rainfall. Also, lightning can spark fires in grasslands after as little as a few hours of rain. Finally, the rolling topography, periodical and extensive drought, and high winds within the Great Plains have been cited as conducive to the vast spread of wild fires on the prairies (Vogl 1974; Anderson 1982; Axelrod 1985).

Short-term Effects of Fire

The most noted of fire's short-term effects on grasslands are changes in species composition, species diversity and total productivity. Wilson and Shay (1990) exposed Manitoba mixed-grass prairie plots at two different locations to treatments of burning, twice-burning, and nutrient addition. These plots were then harvested after a two year period. In terms of total productivity (as measured via biomass), both the once-burned and twice-burned plots tended to show decreased productivity relative to the control, although the twice-burned plots showed a greater decrease. Furthermore, the frequency of bare ground increased with burning. Nutrient addition had the opposite effect on productivity and frequency of bare ground. In terms of species composition, of the four most common graminoids (in descending order: *B. gracilis*, *Stipa spartea*, *Carex obtusata*, and *S. scoparium*), only *C. obtusata* showed a significant increase in frequency with burning, while the others showed no significant difference. Finally, species diversity and richness did not change significantly with burning but tended to decrease with nutrient addition. Note that all burning treatments for this study were applied in a significantly warmer than average month, under generally drier than average conditions (Wilson and Shay 1990). Collins and Barber (1985) reported a decrease in diversity and species richness in an Oklahoma mixed-grass prairie, following burning.

In the more mesic tallgrass prairie, Hulbert (1969) demonstrated that burning leads to an increase in productivity. Peet et al. (1975) also found increased post-burn productivity, which they attributed primarily to litter removal, and subsequent increases in spring soil

temperatures and decreases in soil moisture. Other effects of litter accumulation that are suggested include a decreased rate of mineral cycling, accumulation of soil toxins leached from the litter, and the formation of a physical barrier through which seedlings may not establish (Rice and Parenti 1978). Knapp (1985) also notes an increase in *A. gerardii* and *P. virgatum* after burning, but attributes it more to increases in these plants' efficiency in harvesting light, water, and nutrients after burning. Although most research indicates an increase in post-fire productivity in the tallgrass region, changes in species composition are actually quite minimal. When composition does change in the short term, usually the dominant grasses are favoured (Knapp 1985). Further, the specific response of tallgrass plants can vary according to other factors, such as moisture content and timing of the burn. For example, Glenn-Lewin et al. (1990) showed that *B. curtipendula* increased flowering by 600% following a late spring burn in a more mesic site, while simultaneously decreasing its flowering to 60% following an early spring burn at a more xeric site.

Long-term Effects of Fire

Although the short-term effects of fire have been discussed quite extensively in the literature, particularly in changes to productivity, more long-term changes in diversity and species composition have not (Collins and Gibson 1990). Collins and Gibson (1990) have reviewed the effects of fire on tallgrass and mixed-grass prairie diversity, evenness, species richness, and patch structure. Specifically, Collins and Glenn's review (1995) is based upon the established premise that prairies are often composed of a matrix of a few dominant species (such as *A. gerardii* in the tallgrass prairie and *S. scoparium* in the mixed-grass prairie). In between these matrix species occur the 'interstitial' species (mostly perennial or annual forbs) whose presence contribute most highly to biodiversity. In other words, a biologically diverse prairie will tend to have a relatively high proportion of interstitial species relative to the matrix species. So how does fire affect this dynamic? As indicated in the previous section, fire tends to increase productivity of dominants in the tallgrass prairie. As such, the proportion of interstitial species tends to decrease with fire as does diversity (Collins and Glenn 1995). In fact, on the Konza Prairie Research Natural Area in Kansas, species diversity was lowest just after burning, peaked approximately eight years after burning, then began to decrease at roughly the same rate as it previously increased (Gibson and Hulbert 1987). As such, fire plays a dual role -- decreasing biodiversity on the short term, while increasing biodiversity on the longer term.

Yet as we move further north, into the Alberta fescue prairie, we see a different trend. Here, according to Anderson and Bailey (1980), species richness tends to increase with annual spring burning. Why the discrepancy? According to Collins and Glenn (1995), fescue prairie increases in diversity because its matrix species are primarily C_3 species, which tend to die back as a result of fire, not increase as do the dominant C_4 matrix species in the tallgrass prairie region. These results from a more northern prairie region correspond to the results of Wilson and Shay (1990), described above, who generally found a decrease in productivity of the dominant C_3 species with burning. So overall, the relative proportion of C_3 to C_4 matrix species, and the types of interstitial species present, play a large role in determining the effects of fire, both long-term and short-term, on grassland community structure.

Fire, Acute Drought, and Woody Plant Removal

Despite differences in fire effects on established grasslands, there is one role which fire plays that seems to be fairly consistent in all North American Grasslands -- the reduction of tree, shrub, and annual species (Daubenmire 1968; Vogl 1974; Anderson 1982, 1990). Most perennial prairie graminoids and forbs are well adapted to the fire-prone prairies. For one, they tend to have underground meristems which are usually protected from the direct damaging effects of fire. Further, they tend to be relatively tolerant of the acute fire-induced spring drought conditions (Anderson 1990). Unlike the perennial grasses and forbs, however, prairie trees, shrubs, and annuals tend to be fire-susceptible. Hence within the tallgrass ecosystem, most of the extensively forested areas (consisting of fire-susceptible and mesic trees and shrubs such as *Ulmus*, *Fraxinus*, and *Acer*) occur only near fire-sheltered streams and waterways (Anderson 1990). Where fire is more frequent in occurrence, open forest areas or smaller patches of better-adapted trees and shrubs are more frequent. Specifically, the trees and shrubs tend to be more drought tolerant, shade intolerant, and fire resistant, such as *Pinus* spp. in the southeastern pine savannas and *Quercus* spp. along the eastern tallgrass-deciduous forest ecotone (Vogl 1974; Anderson 1990). In more mesic northern fescue prairies, regular burning has been found to inhibit the encroachment of *Populus tremuloides* (Anderson and Bailey 1980; Gerling et al. 1995). Thus, it seems that despite potential short-term decreases in diversity, fires and drought seem to be an important and necessary disturbance by preventing long-term invasion of trees, shrubs, and 'weedy' annuals.

The role of fire as an inhibitor of woody plant invasion is further strengthened by studies on the effects of drought (which tends to occur immediately after fire) and fire suppression on trees. Albertson and Weaver (1945) noted that the great and prolonged drought of the 1930's resulted in death, injury, and marked decreases in growth rates of many prairie trees within much of the Great Plains, except in relatively protected sites along waterways. Collins and Adams (1983) studied the change in Oklahoma tallgrass prairie species composition over 32 years of fire suppression. After approximately ten years of fire suppression (i.e. beginning in 1959) the relative percent cover of woody species began to dramatically increase, reaching levels of near 60% by 1981. Similar observations were made by Bragg and Hulbert (1976) in a Kansas tallgrass prairie site, left unburned for 32 years. The above observations imply that fire and the associated post-fire drought are key components in preventing the invasion of grassland areas by woody shrubs and tree species.

1.5.3 Grazing and Other Biotic Disturbances

Biotic Disturbances: Scale, Intensity, and Frequency

Among the more important variables shaping the community structure of the North American prairie are disturbances caused by other organisms, or biotic disturbances. These include primarily grazing, as well as other less studied but important disturbances such as bison wallows, and prairie-dog towns. In particular, grazing has probably received the greatest amount of attention, most likely due to its relationship to the effects of livestock on pasture quality. As a disturbance, grazing is in some ways similar to fire. Collins and Barber (1985) note that both fire and grazing are large scale disturbances (especially, if grazing is done by large ungulate herds), of light to moderate intensity. The difference between these two disturbances lies in their frequency. For example, whereas fire may pass through a tallgrass prairie region once every 5 years, grazing can occur every 2-3 months (Collins and Barber 1985). Less similar to fire and grazing are the disturbances of bison wallows and mound building or excavation (i.e. by mammals such as prairie dogs). Both of these are considered to be small scale disturbances. Further, the effects of bison wallows are severe, while mound building effects are moderate to severe in intensity. Finally, in terms of frequency, bison wallows are said to occur every 1-3 months, while mound building and excavation are continual processes (Collins and Barber 1985; Collins and Gibson 1990).

The effects of biotic disturbance on grasslands have been examined by several authors (Platt 1975; Bonham and Lerwick 1976; Bassett 1980; Bakker et al. 1984; Burggraaf-van Nierop and van der Meijden 1984; Polley and Collins 1984; Collins and Barber 1985; Campbell 1994). Collins and Barber (1985), looking at Oklahoma mixed-grass prairie exposed to varieties of burning, grazing, bison wallows, and prairie-dog towns, have found that grazing by ungulates tended to increase diversity by a factor of roughly 1.5 relative to the undisturbed control, while the presence of prairie dog towns increased diversity by a factor of 1.3. Further, while grazing increased species richness by a factor of 1.4, the prairie dog towns did not increase species richness substantially (Collins and Barber 1985). Bison have also been implicated in the historic suppression of *Populus tremuloides* in the aspen parkland region of western Canada (Campbell et al. 1994).

Coffin and Lauenroth (1988) examined the effects of cattle fecal pats, harvester ant mounds, and small animal burrows on the frequency and tiller production of *Bouteloua gracilis* in a northern Colorado shortgrass prairie. Here this species accounts for 85-90% of the basal plant cover. In all, grazing and cattle fecal pats had the greatest effect when the disturbance was 'heavy' and at drier upland sites. Sites on slopes or in lowlands did not seem to vary significantly in their cover of *B. gracilis* with a range of light to heavy grazing and fecal pat disturbance (Coffin and Lauenroth 1988), indicating that perhaps the topographic position of a community may be an important determining factor in the effects of biotic disturbance. Finally, the timing of the biotic disturbance could have an important role in determining its effect. For example, Silvertown et al. (1994), using a diallel competition experiment, found that differences in relative invasion rates amongst four perennial grasses depended on whether or not an area was grazed in the spring, and to what extent it was grazed in the summer.

1.6 Theories of Coexistence and Community Structure

1.6.1 Introduction

In G.E. Hutchinson's classic "Homage to Santa Rosalia" (1959), the question 'why are there so many animal species?' was posed, spearheading a movement in ecology which eventually led scientists to pose the question, 'how and why do plant species coexist?'. As

such it seems that much work has emphasized the complexity of interactions ongoing in ecosystems, and the difficulty involved in attempting to predict community dynamics and structure based on this complexity. So despite many studies of competition and disturbance in laboratories and in the field, very few authors have attempted to formulate summative theories regarding the evolution and maintenance of plant communities. This chapter attempts to summarize the theories and hypotheses posed by several authors who have embraced this complexity, in hopes of bringing us closer to solving the riddles posed by ecosystems. Further, the theories and hypotheses outlined in this chapter are not specific to grasslands, but potentially apply to all ecosystems.

1.6.2 Defining Diversity

Central to the novel and often controversial ideas surrounding species coexistence and community structure is the concept of diversity. In simple terms, plant diversity can be defined as the number of different individual species of plants growing within a single area. Traditionally, this definition of diversity is referred to as species richness (S). When considering grassland ecosystems and grasses in general, several ambiguities exist with this definition. For example, the 'individual' as it relates to diversity, is often ambiguous due to rampant clonal growth, hybridization, and introgression, -- especially amongst Triticeae grasses (which include *Elymus*, *Agropyron*, and *Hordeum* spp. among others; Dewey 1982). Further, the concept of area exists within varying temporal and spatial dimensions which are not considered by species richness alone. Finally, there exists the issue of relative importance of species, and how this contributes to diversity. Hence other alternative models of diversity were formulated, which attempt to take into consideration factors not included in species richness alone.

Shannon-Weiner Diversity, Simpson's Index, and Effective Species Richness

Perhaps the most common measures of diversity used in ecology are the Shannon-Weiner diversity function (H) and Simpson's Index (D). H is calculated as follows:

$$H = -\sum_{i=1}^{S} (p_i)(\ln p_i)$$

D is calculated as follows:

$$D = 1 - \sum_{i=1}^{S} \left(p_i \right)^2$$

S is the total number of species, while p_i is the proportion of species i's importance value (i.e. abundance, biomass, % cover, etc.) relative to the total. The utility of both these models lies in their consideration of both species richness and relative proportions of species (Goldsmith et al. 1986). For example, consider the hypothetical sites I and II, each with carrying capacities of 15 individuals. If each site contains 3 species, X, Y, and Z, species richness would be considered equal between these two sites. However, site I can have 5 individuals of each species, while site II can have 1 of X, 1 of Y, and 13 of Z. Clearly site I, with equal representation of all three species, should be considered more diverse than site II, which is dominated by species Z. Both of these indices would be able to make this distinction. The main difference between the Shannon-Weiner and Simpson's indices is that D has a theoretical maximum of 1, while H does not have a theoretical maximum. Furthermore, Simpson's index gives less weight to rare species than the Shannon-Weiner function. For most practical applications however, both of these indices will show similar trends (Goldsmith et al. 1986).

Using the Shannon-Weiner index, we can further analyze the species abundance data for *evenness*, or *equitability* – the relative distribution of individuals within a community. This measure is simply the ratio of actual diversity H to the theoretical maximum diversity, which is:

$$H_{\max} = \ln S$$

Also, the Shannon-Weiner Index is often transformed into an 'effective species richness' measure which is simply e^H. This transformation sets H_{max} to S instead of $\ln S$, allowing for a more biologically interpretable measurement.

One important and often cited diversity equation involves the concept of α, β, and δ diversity as proposed by Whittaker (1972). In this model, the total diversity (δ) is the product of α diversity, which is simply species richness (i.e. the number of species per unit total area), and β diversity, which is the number of species turnovers (i.e. total changes) among sub-samples of the total area in question. From this definition, other examples of more complex diversity models have arisen, most of which have not yet been sufficiently applied to resolve many of the taxonomic, temporal, and spatial problems inherent in measuring diversity (Schluter and Ricklefs 1993).

1.6.3 Evolutionary Theory in Diversity Models

Introduction

Theories that attempt to describe the causes of patterns in species diversity and coexistence often focus on a few unique, well-defined processes such as, for example, competition, stress tolerance, or disturbance. One very broad and long-term process that has been implicated by several authors as affecting diversity and coexistence is evolution (Huston 1979). For many ecosystems that exist today, and have been in existence for perhaps millions of years, it makes sense that we should look at evolutionary processes as affecting diversity — by definition, evolution is the ultimate driving force of diversity on a global scale. Despite the relatively young age of the North American prairie, many prairie species have already 'evolved' into ecotypes which are geographically limited in their distribution, despite wide-ranging distribution of their species as a whole. As such, evolution will be discussed below.

Limiting Similarity, Divergence, and Convergence

One hypothesis that attempts to look at the effects of evolution as a limit and mediator of diversity, based on the equations of Volterra (1926), is the 'limiting similarity, convergence, and divergence' hypothesis as proposed by MacArthur and Levins (1967). The 'limiting similarity' component of the above theory is reiterated by Grime's (1973) competitive exclusion principle. This principle states that if two species are identical, and

compete for the exact same resources, then eventually one species will competitively exclude the other, preventing the coexistence of both species -- hence two species can only be so much alike before one competitively excludes the other.

Following this limit to similarity, and hence diversity, there exists an evolutionary limit termed L. If two plants are more similar to each other than the distance L (i.e. along a 'similarity gradient'), then a third intermediate species will evolutionarily *converge* towards one of the two species, resulting in a failure to increase diversity. If the distance or similarity between two species is greater than L, then a third intermediate will evolutionarily *diverge* towards a unique intermediate species, with a unique niche, in effect increasing diversity (MacArthur and Levins 1967). Note that under the term 'niche', we include not just the habitat niche but the life-form (i.e. the above and below ground 'shape' of the plant), phenological, and regeneration niches as well (Grubb 1977). A caveat to the 'limiting similarity' theory, according to MacArthur and Levins (1967), is that diversity is proportional to the variability in the environment and inversely proportional to the niche breadth of the component species.

Coevolution and the Ghost of Competition Past

Another coexistence theory that is based upon evolution and competition is the 'ghost of competition past' theory, as described by Connell (1980). In simple terms, according to Connell (1980), many ecologists theorize that competition is (or was) an important causal factor in generating diversity. The mechanism behind many of these theories is based on the premise that two similar plants in competition for similar resources will evolve via divergent selection (rather than be excluded in the Gaussian sense), then coexist within their new and unique fundamental niches. Further, these same ecologists claim that the reason for not actually finding evidence of competition in some communities is due to the competition having occurred at some point in the past, before the evolutionary divergence occurred. So when one looks upon a diverse community, one is seeing the effects of past competition (i.e. the 'ghost'), and not the mechanism of competition in action (Connell 1980).

Connell's (1980) rejection of the ghost of competition past theory seems to be based largely on a lack of evidence in support of it, rather than evidence against it. Nonetheless, Connell (1980) believes that a more likely cause of species coexistence is niche differentiation, which evolved separately in different species, then manifest itself as

coexistence as these species later came into contact. Here, by rejecting the ghost of competition past theory, Connell (1980) assumes that competition had no role to play in this initial differentiation of niches — a somewhat unreasonable assumption. Regardless of many authors still believing that the ghost theory is plausible (e.g. Davic 1985; Maurer 1985), Connell's (1980) 'alternative' view might have some merit when considering characteristics of the North American prairie.

Most species within the prairie have initially evolved in ecosystems other than the prairie and are thus not endemic to it (Axelrod 1985). In all likelihood, these species did evolve under separate circumstances only to co-exist later in time. Further, having arisen from separate ecosystems, these species would have had little opportunity to compete and evolutionarily diverge prior to the development of the prairie biome. Hence, until it is known to what extent these species did co-occur before the rise of the prairie, and at what speed evolutionary changes can take place, it is possible that past coevolution and divergence via competition were not necessarily major factors in generating niche differentiation and hence prairie diversity today. In other words, there may not have been sufficient 'past competition' for there to exist a ghost of.

Ecological and Competitive Combining Ability

The above form of evolution as an ameliorator of competition is commonly called niche divergence or 'ecological combining ability', and it generally follows the axiom that competition avoidance, and hence evolutionary divergence, is always the best choice for a plant. According to Aarssen (1983), there exists an alternative path of evolution which could also generate coexistence: 'competitive combining ability'. Most models involving evolution and competition are based on the premise that if two species coexist, they must have sufficiently different fundamental niche requirements (following MacArthur and Levins' [1967] 'limiting similarity' hypothesis). Otherwise, if fundamental niches are the same, then one species will outcompete the other due to an imbalance in relative competitive ability. Aarssen (1983) believes that it is precisely this scenario under which selection may favour not niche divergence, but rather a balance in competitive abilities (i.e. selection for symmetric competition), making it possible for two species with the same fundamental niches to coexist. In other words, selection may favour competitive combining ability over ecological combining ability.

According to Aarssen (1983), there exist at least four conditions which may favour selection towards competitive combining ability over ecological combining ability, or vice versa. Firstly, there is the initial magnitude of competition. If a highly competitive species suddenly comes into contact with a much less competitive one with similar niche requirements, then exclusion is likely to occur, favouring selection towards ecological combining ability. This may be an important factor in the relatively young prairie biome, where species are relatively recently migrating from peripheral ecosystems and coming into contact. Further, this becomes important on the prairies when considering human introductions of highly competitive species from other ecosystems (e.g. *Bromus inermis*). Secondly, asexual or incrossing species will tend to evolve towards competitive combining ability due to their lowered capacity to adapt to new and different environments. This is an important consideration when considering that most plant reproduction on the prairies is in fact asexual (Weaver 1954; Glenn-Lewin et al. 1990). Thirdly, some species may be 'forced' to evolve towards competitive combining ability, as refuge from competition may be unavailable — not difficult to imagine in an undisturbed prairie, where unoccupied space may be a limited resource. Finally, if beneficience is occurring, selection might favour both competitive combining ability and ecological combining ability (Aarssen 1983).

1.6.4 Models Emphasizing Competition and Disturbance

The Intermediate Disturbance Hypothesis

Beyond the process of evolution being the driving force for species diversity and perhaps coexistence, many ecologists have looked at the effects of smaller scale processes in maintaining diversity. Two such processes are that of disturbance and competition. Although it has been demonstrated that competition does occur in the field, the role it plays in determining community composition is of some debate. Specifically, some authors argue that a periodic and intermediate level of disturbance, in addition to competitive interactions, is necessary in maintaining high diversity (Grime 1973; Connel 1975, 1978; Huston 1979; Tilman 1982). This hypothesis is termed the 'intermediate disturbance hypothesis', and because it assumes continuously fluctuating species compositions, it is considered to be a 'non-equilibrium' model of diversity (Connell 1978).

According to Grime (1973), under conditions of no disturbance, species with high competitive abilities can grow and exclude competitive subordinates with impunity. Conversely, at extremely high levels of disturbance, only species with high stress tolerance

can survive, to the exclusion of more stress-sensitive competitive dominants. Somewhere between these two extremes, at an intermediate level of disturbance, both extreme types of species plus all intermediate types can potentially coexist. Connell (1978) and Huston (1979) in describing the intermediate disturbance hypothesis, have focused more on the intervals between disturbance and its effect on succession. Specifically, without disturbance, a community is thought to go through a natural competitive succession (sensu Clements 1936) towards a low diversity community of competitively dominant species. Here, intermediate frequency of disturbance is thought of as increasing the frequency of seres in which both colonizing and climax species co-occur (Connell 1978; Huston 1979).

Intermediate Disturbance and Resource Competition

In agreement with the predictions of the above hypotheses, but not necessarily with the mechanisms, are the ideas of Tilman (1982). Specifically, while the previous views on intermediate disturbance assume decreased competition with intermediate disturbance, Tilman (1982) argues that competition for changing sets of resources is ongoing and important throughout the disturbance regime. Citing many instances in which diversity peaks at an intermediate level of disturbance (including a guild of prairie plants [Platt and Weis 1977]), Tilman (1982) believes that disturbance acts on diversity by mediating the supply of resources, such as light and nutrients. According to Tilman (1982), an intermediate degree of disturbance results in an intermediate supply of light and nutrients, ultimately allowing for a greater number of species to coexist. Furthermore, while the earlier views on intermediate disturbance predict 'strong competitors' to dominate only under a moderate to low intensity disturbance regime, in fact strong competitors may dominate at any point in the disturbance regime — they'll just be competing for different sets of limiting resources. For more information on resource competition, see sub-section 1.6.5. below.

Effects of Multiple Disturbance

Another set of experiments which agree with the predictions of the intermediate disturbance hypothesis, conducted on grassland species, are those of Collins and Barber (1985). In addition to the intermediate disturbance hypothesis, Collins and Barber (1985) have added the concept of multiple disturbance regimes and additive disturbance effects. Specifically, Collins and Barber (1985) noted that most grasslands are subject to a natural disturbance regime that includes many different types of disturbance (e.g. bison wallows,

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rabbit scrapes, prairie dog towns, etc.). In effect, and in agreement with Tilman's (1982) disturbance model, each different type of disturbance will affect the amounts and/or supply rates of different types of resources. When these multiple disturbances co-occur at intermediate intensities, the ultimate result is increased coexistence and diversity, to a level greater than that which would occur had any one of the disturbances been acting independently (Collins and Barber 1985).

1.6.5 Models Emphasizing Competition and Resource Gradients

The Resource Ratio Model

In the previous section, the concepts of resource competition in disturbance have been discussed relative to species diversity. This sub-section will further discuss the importance of resources, and competition for those resources, in the maintenance of species diversity. One model that looks into the mechanisms of resource competition and their resulting influence on species diversity is the resource ratio model as proposed by Tilman (1980). Underlying Tilman's (1980) relatively mechanistic and graphic model of competition and coexistence is the 'isocline approach' to modelling. This approach requires one to plot the 'growth isoclines' of species on an x-resource by y-resource graph. The isoclines simply represent the level at which a population's resource consumption will equal its minimum resource requirements for zero net growth (ZNGI). In other words, at resource levels below a species' ZNGI, a species will decrease in abundance; above the ZNGI, a species will increase in abundance (Tilman 1980, 1988).

Over this basic resource consumption and growth rate model, Tilman (1982, 1988, 1993) has layered phenomena of importance in community dynamics, such as disturbance, succession, multiple resource competition, resource supply rates, and species coexistence. It is this final phenomenon which is of particular interest here. According to the resource ratio hypothesis (Tilman 1982), there exist conditions in the supply and abundance of resources that allow for multiple species coexistence. Specifically, if species' ZNGI's overlap (i.e. species A requires less of resource I than species B for positive net growth, while species B requires less of resource II than species A for positive net growth), and the resource supply rate within a given area is heterogeneous, then on average, species can coexist, the degree to which is dependent on the overall resource availability, and the ratios of resource availability. In other words, diversity is predicted to be greatest at relatively low resource levels. As resource levels increase within the community, it is the ratio of these

resources that will determine which relatively small number of species will dominate (Tilman 1982).

The Tilman vs. Grime Debate

As reviewed by Grace (1990, 1991) there has been considerable debate on the validity and predictions of differing views on coexistence, specifically the resource based views of Tilman (1982, 1988), versus the life-history trait based views of Grime (1973). One of the debates is based around the question of how competitive superiority arises. According to Grime's model, the classic view of rapid resource uptake (i.e. high growth rates) as a competitively superior trait is defended. According to Tilman's model however, a species' low resource tolerance limit is stressed as being the most important trait in predicting competitive superiority (Tilman and Wedin 1991a). Another issue is whether or not a species can be a good competitor in general, as implied by Grime, or varies in its competitive ability according to varying environmental conditions, as implied by Tilman (Tilman and Wedin 1991b). Thirdly, the two models seem to differ in that Grime's model predicts decreased competition with lowered productivity, while Tilman's predicts equally intense competition under any degree of productivity. Finally, Grime views competitiveness as a trait that leads to dominance only in mid-successional habitats, whereas Tilman views competition as leading to dominance within all seres (Grace 1991).

Central to the debate surrounding the above issues are the differing definitions of competition (Grace 1991). Specifically, Tilman views competition as a general phenomenon, which factors in stress tolerance, disturbance, nutrient uptake, and resource competition. Any changes to a community's resource base ultimately affects the community composition via competition. On the other hand, Grime narrowly defines competition as a plant's ability to rapidly sequester resources -- other phenomena such as disturbance and stress tolerance are considered as separate life-history traits. When Grime's community undergoes resource changes, plants that, for example, are more 'stress-tolerant' than 'competitive' will prevail. Following the work of Grace (1991) and Bengtsson et al. (1994) the models of Grime and Tilman, when considering their respective definitions of competition, are not as conflicting as they initially seemed. In the words of Grace (1991), "The primary differences between theories are of perspective and emphasis". Furthermore, according to Bengtsson et al (1994), both the Tilman and Grime models fall within the same temporal and spatial scales: the ecological and the local (i.e. within communities), respectively.

On a somewhat larger spatial scale, encompassing processes among differing ecological communities, is the theory of centrifugal community organization (Bengtsson et al. 1994). Similar to the resource ratio model discussed above, this model incorporates resource gradients. Further, similar to Grime's model, the centrifugal model stresses the importance of life-history traits and assumes trade-offs between these traits (Keddy 1990; Wisheu and Keddy 1992). Inherent to the centrifugal model is the concept of 'nested modeling', or having models of smaller temporal and spatial dimension nested within models of greater temporal and spatial dimension (Keddy 1990).

At the smaller scale, the centrifugal model incorporates ideas of resource gradients, fundamental and realized niches, competitive hierarchies, and physiological tolerance limits. The model begins by stating that every species requires and tolerates a range of resources from which it can successfully develop and reproduce -- this is a plant's fundamental niche (Colwell and Fuentes 1975). This fundamental niche is thought to be determined largely by the available soil resources, thus playing an important role in determining on a broader scale where a plant will be geographically situated. Note that according to Keddy (1990), competition is not a truly important factor for species exclusion at this point, because competition for below ground resources tends to be relatively symmetric. Further, there exists the assumption that the majority of species within a community will 'prefer' (i.e. achieve maximum fitness at) the relatively benign end of a resource gradient (i.e. the end where the resource is in abundant supply; Wisheu and Keddy 1992).

Layered over the concept of fundamental niche is the concept of the realized niche. The realized niche is where a plant will be located along a resource gradient based on its fundamental niche requirements minus the effects of above ground competition for light (Keddy 1990; Wisheu and Keddy 1992). Here, exclusion is expected to occur due to the greater asymmetry inherent in above ground light competition. One important assumption of the realized niche is that trade-offs exist between a plant's ability to compete for light at the benign end of a resource gradient (a.k.a. 'core habitat'), and its ability to tolerate the stresses imposed on it at the opposite end of the resource gradient (a.k.a. the 'peripheral habitat'; Keddy 1990). In other words, the assumption follows the life-history trade-off model of Grime (1977), which groups plants according to their life-history strategies, into competitors, stress-tolerators, or ruderals. Now combining the concepts of fundamental

niches (as determined by resource tolerance limits), and realized niches (as determined largely by competition for light), we have what Keddy (1990) calls the competitive hierarchy model, which forms the basic unit from which the greater centrifugal model is built.

Given that competitive hierarchies exist, species are expected to partition themselves along resource/habitat gradients. At the benign end of the gradient or the core habitat, productivity is expected to be high, but diversity low, due to exclusion by competitively dominant species. At the peripheral end of the resource gradient, or the peripheral habitat, productivity is expected to be low, but diversity is expected to be high due to the occurrence of more symmetrical competition for nutrients and less competitive exclusion (Keddy 1990; Wisheu and Keddy 1992). Now to fully understand the concept of centrifugal organization, one needs to simply imagine the core habitat as being the hub of a wheel, from which radiate not one, but many 'resource' gradients, such as salinity, disturbance, nutrients, soil texture, etc. The overall model then consists of a low diversity core habitat, radiating into higher diversity peripheral habitats, along an array of differing resource gradients (Keddy 1990; Wisheu and Keddy 1992).

In their description of the centrifugal model, Wisheu and Keddy (1992) cite a wetland community as an example. Here, the core 'community' consists of a monodominant *Typha* population, with various other high-diversity communities (such as sandy lakeshores, gravel lakeshores, beaver ponds, etc.) radiating from it. Although there are no examples of grasslands *per se* following this model, it is not difficult to imagine similar circumstances in many grassland regions, where moisture gradients occur. In fact, it has often been observed that many grasslands communities change in species composition, according to smaller scale changes in elevation and/or water availability (e.g. Weaver 1954).

Resource Transport, Supply, and Coexistence

One assumption of the centrifugal model of community organization, and the competitive hierarchy model nested within it, is that competition in peripheral habitats is less intense (Keddy 1990) and more symmetric (*sensu* Weiner 1986). Unfortunately, neither Keddy's (1990) nor Wisheu and Keddy's (1992) description of the centrifugal model provides true mechanistic reasons for why competition should be less intense and more symmetric at peripheral habitats. This is especially troubling considering Tilman's (1982) model, which

considers competition to be equally important at all positions along a resource gradient. A discussion of resource supply and transport rates may provide some clarification.

Huston and DeAngelis (1994) have reevaluated the effects of resources (including nutrients and light) on competition by considering resources to be fundamentally similar in their effects -- what differs is their supply rate, or 'input flux' (I_o). Specifically, Huston and DeAngelis (1994) claim that when plants grow in a given location, they develop local nutrient depletion zones within proximity of their roots. If these depletion zones are very localized, and do not overlap into the rhizospheres of neighbouring plants, then competition intensity is predicted to be very low. Such would be the case if I_o was very high. On the other hand, if the depletion zones are highly overlapping, then competition intensity is predicted to be very high. Such would be the case if I_o was very low (Huston and DeAngelis 1994).

In turn, I_o is affected by the concentration of the resource, its rate of flow into the system, and its rate of flow out of the system. Thus, in a 'low nutrient' system, nutrients are either in low supply, or are quickly leached out of the rhizospheres. The overall result would be strongly overlapping depletion zones, a more homogeneous nutrient supply, intense but symmetric competition for nutrients, and hence relatively high diversity. For 'high nutrient' systems, nutrients are relatively high in availability relative to demand, and the resulting depletion zones are strongly localized, to the point where a plant will not have significant effect on its neighbour's nutrient supply. The overall result here is that competition intensity for nutrients is highly reduced. However, in this same 'high nutrient' system, another resource, likely not limiting under low nutrient availability, becomes increasingly important -- light.

Huston and DeAngelis (1994) factor in increasing competition for light as biomass increases. Light, in turn, has its own transport and supply properties relative to plants. Specifically, light is usually in high abundance, but is capable of being strongly depleted by rapidly growing species (Grace 1995). So while symmetric competition for nutrients is strongly reduced under high nutrient availability, asymmetric competition for light becomes increasingly intense, and thus diversity is predicted to be low under such conditions. Thus, the Huston and DeAngelis (1994) model predicts that competition is occurring along the entire resource spectrum, while simultaneously providing a mechanistic explanation for the implications of the centrifugal community model. Some recent evidence in support of this

model comes from Keddy et al. (1997) who demonstrated an increase in competitive asymmetry with increased levels of soil productivity.

1.6.6 The Diversity vs. Stability and Productivity Debates

Introduction

In light of the international symposium on biological diversity (Pineda 1990) and the relatively rapid species extinction rate ongoing within the biosphere (Wilson 1992), there has been much interest in the value of biodiversity in ecosystems (Bengtsson et al. 1997). Specifically, there seems to be an ongoing shift in perspective: from looking at the effects of different variables on biodiversity (see sub-sections 1.6.1 - 1.6.4), to looking at the effects of biodiversity on ecosystem stability and, more recently, ecosystem productivity. Robert May (1958) made the prediction that a decline in biodiversity would lead to decreased ecosystem stability. Almost 40 years later, Tilman (1996) and Tilman et al. (1996) have perhaps come the closest to closing (or perhaps reopening) the book on this issue. As seems common with ecological debates, much confusion and misunderstanding arises from a lack of proper definition (see Grace 1991).

Defining Stability

Overall, stability implies low temporal variation in species composition, richness, abundance, and average biomass, as well as resistance and resilience in the face of pertubations (Frank and McNaughton 1991; Tilman 1996). As with most emergent properties in ecology however, stability exists at various hierarchical levels. For example, at the level of the population, we would expect consistent abundance and biomass from year to year if the population was considered to be stable. At the level of the community, we would expect average biomass to remain relatively consistent, and so on. It is important to note that stability at one level of organization need not imply nor require stability at any other level. For example, a community may be relatively stable, but the populations within it need not be, as would be the case with high species turnover rates in a classic succession scenario (*sensu* Clements 1936).

Over a thirteen year period, Tilman (1996) found that year to year variability in community biomass decreased as diversity in natural and experimental grassland plots increased. Further, resistance to drought was significantly greater in more diverse plots, as was found in Frank and McNaughton's (1991) study of post-drought stability in species compositions within grasslands of Yellowstone National Park. At the level of the population, Tilman (1996) found that diversity did not confer stability, as some populations were prone to local extinction. However, at the community and ecosystem level, in diverse plots, when one species' abundance would be severely reduced, another species would increase in abundance in a compensatory manner (Tilman 1996). These results generally agree with previous studies on diversity and stability (e.g. Elton 1958; May 1973; DeAngelis 1975; Pimm 1979; King and Pimm 1983; Frank and McNaughton 1991; Tilman and Downing 1994).

Diversity and Productivity

Diversity is also related to ecosystem productivity, although these relationships often seem contradictory. The first relationship is a negative correlation between productivity and diversity, as is often observed in grassland and wetland ecosystems. Highly diverse plant communities are usually less productive than less diverse ones (McNaughton 1993), since highly productive plant habitats (i.e. nutrient rich habitats) favour competitive dominance by fast growing tall-statured species which preempt available light from competitive subordinates (see sub-section 1.6.5). A negative relationship between diversity and productivity also occurs under studies of controlled nutrient addition. Here, because of the same arguments used above, nutrient addition tends to increase productivity while simultaneously decreasing diversity (Tilman 1984, 1987).

The other relationship between diversity and productivity is a positive one. This relationship is observed when species diversity itself is controlled. In other words, within a habitat, plots sown with many species tend to be more productive than plots sown with fewer species (Tilman et al. 1996; Joliffe 1997). This version of the diversity-productivity hypothesis is based on the idea that as more species occupy an area, the available resources will be used more effectively by those species due to spatio-temporal niche differentiation. As more resources are utilized within an ecosystem, the greater the total ecosystem productivity will be (McNaughton 1993, Tilman et al. 1996). This effect is observed by

Tilman et al. (1996) on highly nutrient-deficient soils of the Cedar Creek Natural History Area in Minnesota. Hence, in practice, there appears to be a two-way relationship between diversity and productivity, depending largely on the nutritional status of the plant habitat. If more plants are added to nutrient poor habitats, productivity may increase. If nutrients are added to nutrient poor habitats, productivity will increase at the expense of diversity.

CHAPTER 2

POST-COLONIZATION DEVELOPMENTS AND ISSUES:
THE PRAIRIES IN THE 20TH CENTURY

2.1 Introduction

Within the last century, the human impacts on natural ecosystems have been devastating. Daily (1995) estimates that approximately 43% of the Earth's vegetated surface (i.e. approx. 5.0 billion ha) is in a generally degraded state. Soil degradation alone, since 1945, has occurred on approximately 17% (i.e. 2 billion ha) of the Earth's vegetated surface (Daily 1995). Soil degradation has been attributed primarily to human land use patterns such as overgrazing, deforestation, and other agricultural activities (Daily 1995), all common practices on the North American prairies. This type of insidious destruction of ecosystems and habitats is even more unsettling in light of 'extinction debt', or extinctions that occur generations after a habitat has been destroyed (Tilman et al. 1994). Hence, the more recent history of the North American prairie ecosystem, as described in this section, is one filled with human neglect, overuse, and ultimately destruction. Despite the often depressing facts laid out in front of us, there remains much hope in the more recent developments and research into grassland management and restoration, which will be described as well.

2.2 Grazer Removal and Replacement with Livestock

2.2.1 Initial Impacts of Settlement

Although one would initially think that European stress on the prairie would be mostly due to tilling and grain agriculture, significant impacts were made long before this ever happened. Beginning in the 1780's, bison (*Bison bison*) were extensively hunted to provide food for settlers and later to provide coats to North Americans (Arthur 1984). This slaughter peaked within two significant periods of mass bison slaughter: from 1870-1873, and from 1880-1883. In addition to outright killing of bison, disease, thought to have been introduced to bison via domesticated cattle during the 1860's, may have played a significant role in decimating herds (Koucky 1983). One hundred years after this slaughter began, virtually all free roaming bison were eliminated from the prairies. With the loss of the

bison, hunting pressure dramatically reduced the abundances of other ungulates such as mule deer, pronghorn antelope, and elk (Mitchell, 1984; Government of Canada 1991). In addition to this, the abundance of prairie dogs (thought to be the most significant grazers on the prairie next to bison) is estimated to have declined by 98% since European settlement (Samson and Knopf 1994). Hence, by the turn of the 19th century, a major factor in maintaining the prairie ecosystem was already eliminated, namely the effects of grazing (see sub-section 1.5.3) by bison, other native ungulates, and prairie dogs.

2.2.2 Livestock Introduction to Historically Bison-free Grasslands

Since the removal of native grazers from the prairies, livestock grazing has been advocated as being of potential benefit to grasslands, much to the relief of ranchers and cattlemen. Although this idea seems logical at first, there are in fact many dangers in allowing livestock to graze on prairie. For example, many of the bunchgrass prairies that did not initially have large herds of bison present within their ranges are vulnerable to changes caused by livestock introduction. The dominant bunchgrass species of the bison-free inter-mountain grassland region were severely reduced following grazing by livestock (Mack and Thompson 1982). Similar effects were also found to occur under livestock grazing in historically bison-free American Southwest grasslands (Bock and Bock 1995). In Canadian fescue grasslands, where there exist both sod-forming and bunchgrass dominants, fescue decreased in abundance with the introduction of livestock grazing (Johnston et al. 1971). In Kansas, the relative proportion of bunchgrasses (such as *B. curtipendula*) increased with livestock removal (Tomanek and Alberston 1957). As such, it is obvious that livestock grazing is not necessarily beneficial or necessary in maintaining grassland ecosystem integrity, especially in areas that were historically bison-free.

2.2.3 Livestock Management on the Great Plains

In the Great Plains region where approximately 30 million bison once roamed (McHugh 1971), the use of livestock is potentially a better management tool than in other grassland areas. However, even in the Great Plains region, overgrazing by livestock has traditionally been a cause for concern. One of the largest discrepancies between the effects of bison and those of livestock are the rates of grazing. Bison were free-roaming herders, following nutrient-rich sources of fodder such as post-burn sites, leaving grazed sites with time to rehabilitate (McHugh 1971). Livestock, on the other hand, are traditionally enclosed within relatively small areas that inevitably become overgrazed. Hence, the rate and intensity of

livestock grazing tends to be severe relative to that of free-roaming bison. Coupled with the ever-present threat of exotic species invasion, overgrazing can severely damage native grasslands on both the short and long-term (Bock and Bock 1995).

From these traditional problems inherent with livestock grazing was born the practice of rotational grazing. Rotational grazing systems attempt to limit the degree of livestock disturbance by continuously moving herds to new locations, while simultaneously allowing other grazed areas to recuperate (Wallace and Dyer 1995). Several such grazing systems are currently practiced by livestock managers. They vary in the intensity and frequency of grazing, as well as in the amount of time that a grazed field is allowed to recuperate. Although these systems allow one to theoretically set the appropriate level of grazing disturbance to maximize diversity/productivity, factors such as climatic conditions, edaphic conditions, species composition, etc. lead to varying responses that are not yet easy to predict. Hence, the effects of current rotational grazing practices on the long-term sustainability of grassland ecosystems are not well understood (Wallace and Dyer 1995).

2.3 Agricultural Expansion and Urban Development

2.3.1 Expansion of Agriculture

One needs only to fly over the Great Plains to realize what humans' greatest use for the prairie today is -- agriculture. The mosaic of perfectly symmetrical 1 mile x 1 mile sections, each with a different hue, appear beautiful from 20,000 feet. From an ecological perspective, at ground zero, perhaps it is not quite as beautiful. What was once a diverse 'sea of grass' stretching from horizon to horizon, a wonderful mosaic of naturally occurring grassland species, is all but reduced to remnant patches of 'undisturbed' grasslands -- museum pieces. Today, largely due to agriculture, the prairie ecosystem is the most severely physically disturbed bioregions in all of North America. In 1991 it was estimated that only 24% of the mixed-grass prairie, 20-27% of the rough fescue prairie, 1-5% of the plains fescue prairie, and <1% of the tallgrass prairie in Canada remained in their 'undisturbed' state (Government of Canada 1991). The development of agriculture in the Canadian prairies began in 1811, in Selkirk, Manitoba. Initially, the rate of land disturbance was high, accounting for the cultivation of approximately 60% of the Canadian prairie by the year 1931 (Rowe and Coupland 1984). Agricultural expansion still continues at an alarming rate. For example, between 1971-1986, cropland area within the Canadian prairies increased by 22% (Government of Canada 1991). In Manitoba, the areas of

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historically tallgrass and mixed-grass prairie have both declined by 99.9% (Samson and Knopf 1994).

2.3.2 Increasing Human Population and Urban Sprawl

In addition to prairie disappearing to the plow, today it is also rapidly disappearing to the bulldozer and cement truck. Human population on the Canadian prairies has increased by 25% between 1971-1986, with the consequence that many rural areas have been converted to permanent urban areas. In Alberta, the most rapidly expanding prairie province in terms of human population, 17% of rural area has been converted to urban area between the years 1971-1986 (Government of Canada 1991). In addition to physically removing prairie vegetation from urbanized areas, expanding human populations have other effects on the prairie ecosystem. One effect is that of pollution. For example, irrigation, municipal effluents, industrial effluents, and flow regulation have all had major detrimental influence on river water quality within the Canadian prairie. Further, potential pollution problems stemming from the maintenance of urban landscaping include eutrophication caused by rapid runoff and excessive use of fertilizers, and the widespread use of herbicides (e.g. 2-4,D) and DDT-family pesticides such as lindane (Government of Canada 1991).

2.4 Exotic Species Invasion

2.4.1 Introduction: An Example of Successful Invasion

Beyond direct human disturbance of the prairie ecosystem, the indirect effects of non-native species invasions are also cause for concern. One example of such invasion, of significance to the Canadian prairies, is that of *Bromus inermis*. In the case of *B. inermis* and many other invading species, it is the characteristics that are valued by settlers and current agriculturalists (rapid growth, easy establishment, resistance to 'weed' invasions, etc.) that are causing problems for native plant communities (Romo et al. 1990). Further, when species were initially brought over from Europe, their natural parasites, pests, viruses, etc. did not come over with them, in effect releasing these plants from the competitively detrimental effects of disease (Romo et al. 1990). Hence, the principle danger of introduced species to the prairies is their strong ability to outcompete and supress growth of native species even in absence of disturbance. Looman (1969), Wilson (1989), and Wilson and Belcher (1989) have observed that *B. inermis* can competitively exclude native flora, and decrease overall diversity of native fescue grasslands. Oddly enough, despite the

general decline of the ecological integrity of the prairie ecosystem, cultivation of *B. inermis* and other invading species still occurs today for agricultural and economic purposes (Romo et al. 1990). Other introduced species that are invasive and persistent within Canadian prairies, and hence threaten its diversity and sustainability, include crested wheatgrass (*Agropyron cristatum*), leafy spurge (*Euphorbia esula*), timothy grass (*Phleum pratense*) and bluegrass (*Poa pratensis*) (Blood 1966; Trottier 1986; Culotta 1994; Goulet 1997).

2.4.2 Community Invasibility and Characteristics of Invasive Plants

As a result of the growing concern over introduced species invasions, research has been conducted to determine what community attributes lend themselves to successful invasion by exotic species, as well as what characteristics of species allow them to successfully invade native communities. Burke and Grime (1996) have looked at invasion of experimental plots by a variety of non-native species. The plots were subject to varying degrees of disturbance (i.e. gap formation and mowing) and fertility treatments. Plots that were fertile and highly disturbed were subject to the greatest magnitude of invasion. A similar observation was also made by Tilman (1990), who documented an invasion of *Poa pratensis* and *Agropyron repens* over a ten-year period in mildly fertilized (3 g N m^{-2} yr^{-1}) *Schizachyrium scoparium* prairie plots. Wedin (1992) predicts that the rate of exotic plant invasion has increased over the last few decades, and will continue to do so due to eutrophication of prairies via atmospheric N-deposition.

Characteristics associated with successful invaders are quite variable. Large-seeded invaders tend to be able to tolerate more prolonged periods of stress, and thus are capable of establishment within less disturbed or less fertile sites. Meanwhile, smaller seeded species are able to take advantage of temporary resource pulses via disturbance and fertilization, to grow and then reproduce fairly rapidly. Finally, the strength of an invading species also depends on geographical tolerance limits of the plant and its germination requirements (Burke and Grime 1996).

2.5 Native Grassland Restoration and Management

2.5.1 Introduction

With the division of the North American prairie into discreet units, to be used for either cropland or livestock grazing purposes, came the practice of range management. Early in its

conception, range management was used to keep levels of palatible grassland biomass relatively high, so that cattle production could yield continuously high profits per unit area of pasture. Today, in many disturbed grassland areas (usually considered to be 'marginal croplands'), management and restoration serves to prevent soil erosion and degradation, restore soil quality, prevent species extinctions, and generally maintain the long-term integrity and sustainability of the prairie (Bock and Bock 1995). In essence, grassland management and restoration attempts to reverse the damage caused by overgrazing, cultivation and exotic species, through the careful use of the land manager's tools: fertilization, bulldozing, root plowing, chaining, mowing, shredding, prescribed burning, contour furrowing, pesticide use, grazing systems, and reseeding of native vegetation (Bock and Bock 1995).

2.5.2 Classic Restoration Studies

Many attempts at grassland restoration have occurred in the past and continue to occur today. Among the earliest known restorations were undertaken by Aldo Leopold during the 1930-1940's, as 'educational samplers' (Harper-Lore 1992). Other restorations in North America and Europe have been traced as far back as the early 1800's (Hall 1997). Since these first restorations, ecologists, landscape architects, and other restorationists have propelled the field forward to the extent of creating the Society for Ecological Restoration (SER) in 1987. Prior to SER's establishment, few scientific investigations regarding the practice of restoration have been performed and widely published (Mlot 1990; Morgan 1992). The exceptions to this rule are studies emerging from the University of Wisconsin-Madison Arboretum (UWA; the site of Leopold's first restoration), and from the restoration (beginning in 1974) at the Fermi National Accelerator Laboratory (FNAL) in Batavia, Illinois.

From UWA emerged classic works from Curtis and Partch (1948, 1950) on the effects of fire on restored prairie. The results from these studies demonstrated that fire could be used every 2-3 years to control introduced species in favour of native species. Because of Curtis' extensive contributions to research at the UWA prairie, it was eventually named the Curtis Prairie. Other planned disturbances have since been documented as being of potential benefit to establishment of a diverse array of native species on restored sites. For example, O'Keefe (1995, 1997) observed that diversity of restored sights increased with frequency of mowing within the first two years after initial seeding. Towne and Knapp (1996) found increased diversity of tallgrass prairie legumes on restored sites that were

annually burned. At the FNAL prairie, Jastrow (1987) was able to demonstrate that restoring prairies had a positive effect on soil aggregation, and that after as little as 5-10 growing seasons, the size class frequencies of these aggregates resembled that of native undisturbed prairie.

2.5.3 Future Challenges for Grassland Restoration

Despite the relatively successful restorations described above, establishing and perpetuating biological diversity in the landscape remains a common challenge to restoration ecologists (Morgan 1992; Jacobsen et al. 1994). Many large scale grassland restoration programs currently depend upon the use of homogeneous mixtures of species. Establishment of many species from homogeneous mixtures is predicted to be very difficult due to differences in species germination, establishment, and competitive abilities (Grime 1973; Weiher and Keddy 1995). The rate of competitive exclusion is predicted to increase with increasing nutrient and moisture availability (Tilman 1988; Wilson and Shay 1990; Wilson and Tilman 1991; Keddy at al. 1997), increasing degrees of disturbance suppression (Collins and Barber 1985; Keddy 1990), and decreasing natural seed input from neighbouring areas, further impeding restoration efforts.

As for the success of previously attempted grassland restorations, complete restoration of a prairie site has not yet been observed. Cottam and Wilson (1966) have evaluated the restored portions of Curtis Prairie, one of the best examples of restored prairie, relative to native undisturbed prairie. They have determined that after 50 years of intensive management, a restored prairie may resemble a native prairie in terms of its species composition, but will not be undistinguishable from a native prairie for "many years" (Cottam and Wilson 1966: p.96). Because of the current difficulties in restoring prairies on the short term, and the lack of evidence for a 'completely restored' prairie after almost 70 years of restoration, the consensus is that it is much easier to conserve an existing prairie than to attempt to restore prairie after severe disturbance (Mlot 1990; Samson and Knopf 1990; Morgan et al. 1995).

CHAPTER 3

COMPETITIVE HIERARCHIES AND RESTORATION OF EASTERN CANADIAN NATIVE GRASSLANDS

3.1 Introduction

Many researchers believe that plant species can be organized into hierarchies of relative competitive abilities, or competitive hierarchies (Norrington-Davies 1967; Goldsmith 1978; Fowler 1982; Moore and Williams 1983; Wilson and Keddy 1986a; Mitchley and Grubb 1986; Grace et al. 1992; Shipley 1993, 1994). The existence of competitive hierarchies has many important implications for ecological theory (Keddy and Shipley 1989; Keddy 1990; Wisheu and Keddy 1992; Bengtsson et al. 1994). Despite the general consensus that competitive hierarchies do exist, the results of previous competition studies and their general conclusions are subject to some debate (Joliffe et al. 1984; Firbank and Watkinson 1985; Connolly 1986, 1997; Silvertown and Dale 1991; Shipley 1994). The primary objective of this study is to determine the existence and form of competitive hierarchies amongst twelve grass species native to North American grasslands. If these species are organized into competitive hierarchies, knowledge of plant traits that confer competitive superiority under a given set of climatic and edaphic conditions would allow one to potentially predict competitive outcomes amongst groups of other species. It is also of interest to know what the implications of competitive hierarchies are to ecological restoration efforts in North American grasslands.

3.1.1 Shortcomings and Criticisms of Competitive Hierarchies

The current shortcomings and criticisms of competitive hierarchy experiments can be broken down into three more or less unresolved issues: a) the degree to which competitive exclusion is actually predicted by competitive hierarchy models; b) how consistent the competitive hierarchies are; and c) size bias in the interpretation of competitive hierarchy models.

Exclusion of Competitive Subordinates

Most previously-published competitive hierarchy experiments predict or imply competitive exclusion of subordinate species based on their mixture performance relative to their monoculture performance (Keddy and Shipley 1989; Shipley 1993, 1994). To quote from Connolly (1997): "The evidence from the mixture itself provides no basis for any such conclusion". In other words, a species may indeed perform poorly in mixture relative to monoculture, but the proportions of the two species in mixture may very well be stable over time. As of yet, it is not known to what extent competitive hierarchies actually predict competitive exclusion in the field. One method used to determine this would to be to make observations on proportional yields (species yield/total plot yield) of species in mixtures over more than one growing season. Strong competitors will have increasing proportional yield in mixture over time, while the proportional yield of poor competitors will decline over time.

Consistency of Competitive Hierarchies

Reversals in relative competitive ability have been observed along experimental nutrient gradients (Fowler 1982; Moore and Williams 1983; Tilman 1984, 1987; Wilson 1994), gradients of physiological drought (Kenkel et al. 1991), and gradients of stress and disturbance (Wilson and Keddy 1986a; Wilson and Tilman 1991, 1995). As such, it has yet to be determined to what extent competitive hierarchies are consistent amongst a group of species when they are grown under different climatic and edaphic conditions, as well as under different disturbance regimes (Fowler 1982; Silvertown and Dale 1991).

The Size Bias Argument

Amongst the most contentious issues with competitive hierarchy research is the so-called 'size-bias' inherent with replacement series methodology (Firbank and Watkinson 1985; Connolly 1986, 1997; Grace et al. 1992). The first premise of the size bias argument is that a species with a relative yield >1 can be interpreted in two ways: a) it is competing well with its neighbour in mixture, or b) it is being released from intraspecific competition in monoculture. These two effects cannot be separated. The second premise is an assumption that large species have a greater propensity (i.e. a 'bias') towards the latter effect than smaller species (i.e. larger species are more likely to be 'released' from intraspecific competition) because their monoculture density is 'effectively' greater than that of smaller

species. Hence, larger plants are more likely to have higher relative yields due to the greater probability of their being released from intraspecific competition, due to their higher 'effective' density (Connolly 1997).

There are at least three difficulties with the size-bias argument. One difficulty is that the two 'separate' effects contained within the first premise are likely confounded. A species that is undergoing the former effect (i.e. is a strong competitor) is more likely to undergo the latter effect as well, since release from intraspecific competition by definition requires a species to be a strong intraspecific competitor. Second, the assumption that larger plants are more likely to be released from intraspecific competition presents a size bias in itself — larger plants are assumed to undergo stronger intraspecific competition than are smaller plants. In essence, this is arguing that relative yields are biased towards large plants because large plants are stronger competitors. Third, large plant size (i.e. above-ground biomass accumulation) may be a strategy used by certain plants to obtain and maintain dominance within an area. If this is true, then controlling for size in competition experiments would fail to detect the truly stronger competitor (Shipley 1994).

Three conditions under which size bias is potentially most critical have been avoided by the experiments described in this chapter. Although Wilson (1994) found little effect of different initial plant sizes on competitive responses, size bias will likely be more pronounced when there are great differences in plant sizes and/or growth forms. This effect will likely not be as important when similarly-sized species of similar growth forms (e.g. all graminoids) are grown from seed, since initial and final sizes are similar for all species. Second, when competition experiments are undertaken in small pots, the intensity of root competition may be artificially inflated relative to field conditions due to size constraints. Under these circumstances, large plants will be prone to even higher 'effective' density than in field conditions. Finally, when species are grown at exceedingly high densities, size bias is expected to be exacerbated due to the greater occurrence of density effects in general. Smaller differences in sowing densities from experiment to experiment have generally shown little effect on competitive responses of plants (Fowler 1982). Overall, experiments less prone to size bias should be undertaken in the field, at lower densities, using plants of similar size and growth form. These were the conditions under which the experiments described here were grown.

3.1.2 Features of Competitively Dominant Plants

For species to have measurable competitive abilities that are organized into competitive hierarchies, they must exhibit traits that make them more or less competitive. According to Aarssen (1983), in terms of exploitation competition, competitively dominant plants should have rapid growth rates; tall plant heights; large leaf areas; extensive or deep root systems; large seed sizes; early arrival, germination and establishment; effective pollination and dispersal mechanisms; the ability to sequester resources from other species via rhizomes, stolons, or root grafts; and an ability to tolerate temporary extremes in the environment. To be a good interference competitor, a plant should carry pests or diseases harmful to other species, interfere with environmental triggers for other plants, produce large amounts of ground litter, be allelopathic, or interfere with another species' pollination mechanism (Aarssen 1983).

Gaudet and Keddy (1988) have looked at a number of plant traits in an attempt to correlate these with competitive ability by growing 44 species of plants together with a 'phytometer' or indicator species. From this experiment, above-ground biomass was the single most effective predictor of competitive ability, as it was with several previously published diallel competition experiments (e.g. Goldsmith 1978; Moore and Williams 1983; Mitchley and Grubb 1986).

3.1.3 Competitive Hierarchies and Grassland Restoration

A common objective of restoration ecology is to establish and perpetuate biological diversity in the landscape (Jacobsen et al. 1994; Palmer et al. 1997). In the restoration of Canadian prairie grasslands, establishing and maintaining a diverse array of native species, even in the short term, has proven to be a considerable challenge (Morgan et al. 1995). It has been hypothesized that interspecific interactions occurring during the grassland establishment phase may lead to the exclusion of comparatively weak competitors, thereby reducing biodiversity. If this is true, and interspecific competition is hierarchical and strongly asymmetric, the maintenance of high species diversity will be compromised, especially if natural disturbances such as fire and grazing are suppressed (Collins and

Barber 1985; Keddy 1990). On the other hand, if competitive hierarchies do not exist, diverse grassland restoration will be easily achieved simply by increasing the number of species in seed mixtures. If competitive hierarchies are strong but predictable, then methods can be developed which compensate for relative species performance. An understanding of competitive hierarchies is therefore critical to the success of grassland restoration, particularly when the objective is to promote and maintain a diverse assemblage of native grasses.

3.2 Objectives

In this study, two field experiments were undertaken to examine interspecific competitive interactions among twelve native grass species in southern Manitoba. The objectives of this study are:

- To determine the magnitude and direction of competitive hierarchies among the twelve grass species after two growing seasons.

- To determine the consistency of competitive hierarchies in time and space by considering variation in species relative competitive abilities within and among two experimental locations.

- To create a conceptual model (*sensu* Jeffers 1988) that predicts changes in the direction of competitive hierarchies across the Great Plains. The model will be based on plant functional traits, and how these interact with climatic and edaphic conditions to make some species more competitive than others.

- To discuss the implications of competitive hierarchies to grassland revegetation and restoration efforts in North America.

3.3 Methods and Materials

3.3.1 Study Areas

Two field experiments were undertaken at the University of Manitoba: one at the Department of Plant Science Field Facility at Carman, Manitoba (49°26'N, 98°09'W); the other at The Point, a field research facility also run by the Department of Plant Science in Winnipeg, Manitoba (49°54'N, 97°06'W).

Pre-Glacial History of Southern Manitoba

Both Winnipeg and Carman are located within the physiographic region known as the Manitoba Lowlands. The grasslands within the southern portion of this region began to develop in the Miocene and Pliocene epochs, with the rise of the Rocky Mountains and the subsequent climatic changes in central North America some 26-30 million years ago. (Risser et al. 1981; Collins and Glenn 1995). Specifically, the Rocky Mountains created a rain shadow in central North America which resulted in a relatively dry continental climate which exists to this day. This aridity combined with a periodically frost-free climate, grazing animals, fairly frequent fires, and a relatively flat topography, helped to create fairly extensive grasslands in southern Manitoba within the Miocene-Pliocene transition era, between 7-5 million Y.B.P. (Axelrod 1985).

Post-Glacial History of Southern Manitoba

More recent patterns of grassland development, on a smaller temporal scale, involved the formation of glacial Lake Agassiz, the roughly north-south expansion and retreat of glaciers, and subsequent shifts in temperatures and vegetation types (Corkery 1996). The most recent glacial retreat and subsequent recolonization of plants and animals in North America was that of the Wisconsinian glaciation, beginning approximately 18,000 Y.B.P. and ending around 3000 Y.B.P. This ice sheet was responsible for forming glacial Lake Agassiz approximately 13,000 Y.B.P. by damming the northward drainage into Hudson's Bay. Sediments from the floor of this glacial lake are largely responsible for the flat land around Winnipeg and Carman -- relief is generally less than 8 m in these regions. These sedimentary deposits are composed primarily of fine sands, silts, and clays. At Winnipeg and Carman, underlying this thick layer of glacial deposits is bedrock material, composed

primarily of limestones, dolomites, and interbedded shales originating in the Paleozoic era, some 300-550 million Y.B.P. (Corkery 1996).

At the time of the Wisconsinian ice sheet's furthest expansion south there existed a roughly north-south temperature gradient as well as a gradient of vegetation types, with tundra along the southern edge of the ice sheet, and boreal forests within the southern Manitoba plains. As the Wisconsinian ice sheet began retreating north about 18,000 Y.B.P., so too did the associated cool climate vegetation types of the continent (Prentice et al. 1991), until grasslands reappeared in the southern Great Plains by 12,000 Y.B.P. At this point, the northern and eastern ecotone of the grassland consisted mostly of grasses and coniferous trees, with boreal forests dominating the landscape further northward and eastward. This northern and eastern migration of boreal forest and grassland from the south continued steadily, until about 8000 Y.B.P. At this time, these ecotones began to gradually shift back south and west, in response to a slight cooling trend in the later Holocene, until the vegetation types of Manitoba and their ecotones resembled those of the present day by about 3000 Y.B.P (Axelrod 1985).

Long-term Climatic Patterns

Being devoid of topographic landforms or water bodies large enough to affect macroclimate, southern Manitoba is characterized by a continental climate, with relatively high summer temperatures and low winter temperatures. Air masses from the Arctic, the North Pacific, the American Great Plains, and the Gulf of Mexico all flow unimpeded into this region (Blair 1996). The flow of air masses into Manitoba from all directions makes this region particularly susceptible to frontal weather phenomena such as thunderstorms. On average, this region is annually susceptible to between 28 - 30 days with thunderstorms (Blair 1996). Both Carman and Winnipeg receive between 500 - 525 mm of precipitation, most of which occurs in the summer months. In Winnipeg and Morris precipitation peaks in June, reaching approximately 84 mm and 83 mm, respectively (Government of Canada 1993).

Long-term (1938-1990) mean temperature in Winnipeg from May to August is 22.8°C with a mean monthly precipitation of 70 mm (Government of Canada 1993). The mean annual temperature in Winnipeg is 2.4°C, with mean monthly temperatures ranging from - 18.3°C in January to 19.8°C in July. Although long-term mean monthly maximum

temperatures are not available from Carman, from Morris (49°21'N, 97°22'W), a nearby town, the long-term (1883-1987) mean monthly maximum temperature from May to August is 23.9°C. The mean annual temperature in Morris is 2.8°C, with mean monthly temperatures ranging from -18.8°C in January to 20.1°C in July. The length of the snow free period at these latitudes is approximately seven months, beginning in April and ending in October. In Winnipeg and Morris, the number of monthly growing degree days (the number of Celsius degrees that the mean daily temperature is above 18 °C) reach their maximum in July at 73.1 and 77.8 gdd., respectively.

Climatic Conditions: Carman

Climatic data over the duration of the two field experiments is summarized in **Table 3.1.** Long-term climatic means (1964-1990) for Carman over the growing season (May-August) indicate a mean monthly precipitation of 65 mm (Government of Canada 1993). From May-August 1995, the mean monthly precipitation in Carman averaged 65.0 mm and the daily maximum temperatures averaged 24.2°C. From May-August 1996, the mean monthly precipitation in Carman averaged 72.1 mm and the daily maximum temperatures averaged 22.4°C.

Soils: Carman

Soils at the Carman site are well to moderately well-drained acidic (pH = 5.8) orthic black chernozems with a very fine sandy loam texture (Mills and Haluschak 1993). Total available nitrogen in the rooting zone (0-15 cm) is 2.54 g kg^{-1} (Mohr 1997).

Climatic Conditions: Winnipeg

From May-August 1996, the mean monthly precipitation in Winnipeg averaged 78.6 mm and the daily maximum temperatures averaged 23.9°C. From May-August 1997, the mean monthly precipitation in Winnipeg averaged 64.2 mm and the daily maximum temperatures averaged 23.5°C.

Table 3.1. Climate data for Carman, Manitoba and Winnipeg, Manitoba over the duration of two field experiments.

	Carman		Winnipeg	
	1995	1996	1996	1997
Growing Degree Days	2959	2734	2945	2924
Mean Max. Temperature (°C)				
May 1 - August 31	24.2	22.4	23.9	23.5
Mean Monthly PPT (mm)				
May	62.0	67.6	98.0	58.2
June	35.6	69.0	18.8	45.5
July	90.2	110.8	67.6	79.0
August	72.3	40.8	129.8	74.2
Total PPT (mm)				
May 1 - August 31	260.1	288.2	314.2	256.8

Soils at the Winnipeg site are slightly basic (pH = 7.6) cumulic regosols with a silty-clay texture -- more fine-textured than soils at Carman. Total available nitrogen in the rooting zone (0-15 cm) is 2.63 g kg^{-1} (Mohr 1997).

3.3.2 Experimental Design

The diallel replacement series competition experiment (de Wit 1960) forms the basis for evaluating competitive hierarchies in this study. Derived from diallel crosses in genetics studies (Williams 1962), this experimental design involves growing all the species of interest (i.e. "*n*" number of species) in monoculture, and in all possible pairwise combinations. Thus there are *n* monoculture plots and (*n*[*n*-1])/2 'mixture' plots (see Williams 1962; de Wit and van den Bergh 1965; Norrington-Davies 1967; Jacquard and Caputa 1970; Goldsmith 1978; Fowler 1982; Moore and Williams 1983; Mitchley and Grubb 1986; Wilson and Keddy 1986; and Grace et al. 1992 for examples). Since 12 species of native grasses were used in this experiment, with three replications of the entire replacement series, a total of 234 plots were sown per experiment (**Fig. 3.1**). Plot sizes were 3.5 m x 1.25 m, separated by 1.5 m wide lanes (**Fig. 3.2**). The initial sowing densities of all plots were kept constant to control for the effects of density on a given species' response.

At Carman, the diallel competition experiment was established in May, 1995 and harvested in September of 1995 and 1996. In Winnipeg, an identical experiment was established in May, 1996 and harvested in September in 1996 and 1997. Competitive hierarchies have thus been evaluated over time (i.e. from 1 year after planting to 2 years after planting), over space (i.e. under different edaphic conditions at the two experimental locations, Carman and Winnipeg), and under differing climatic regimes due to the two experiments being planted in different years.

3.3.3 Experimental Methods and Materials

Species Used

Competitive hierarchies were evaluated using 12 grass species native to the tallgrass and mixed-grass prairies of Canada and the United States (see Appendices I-III for more details
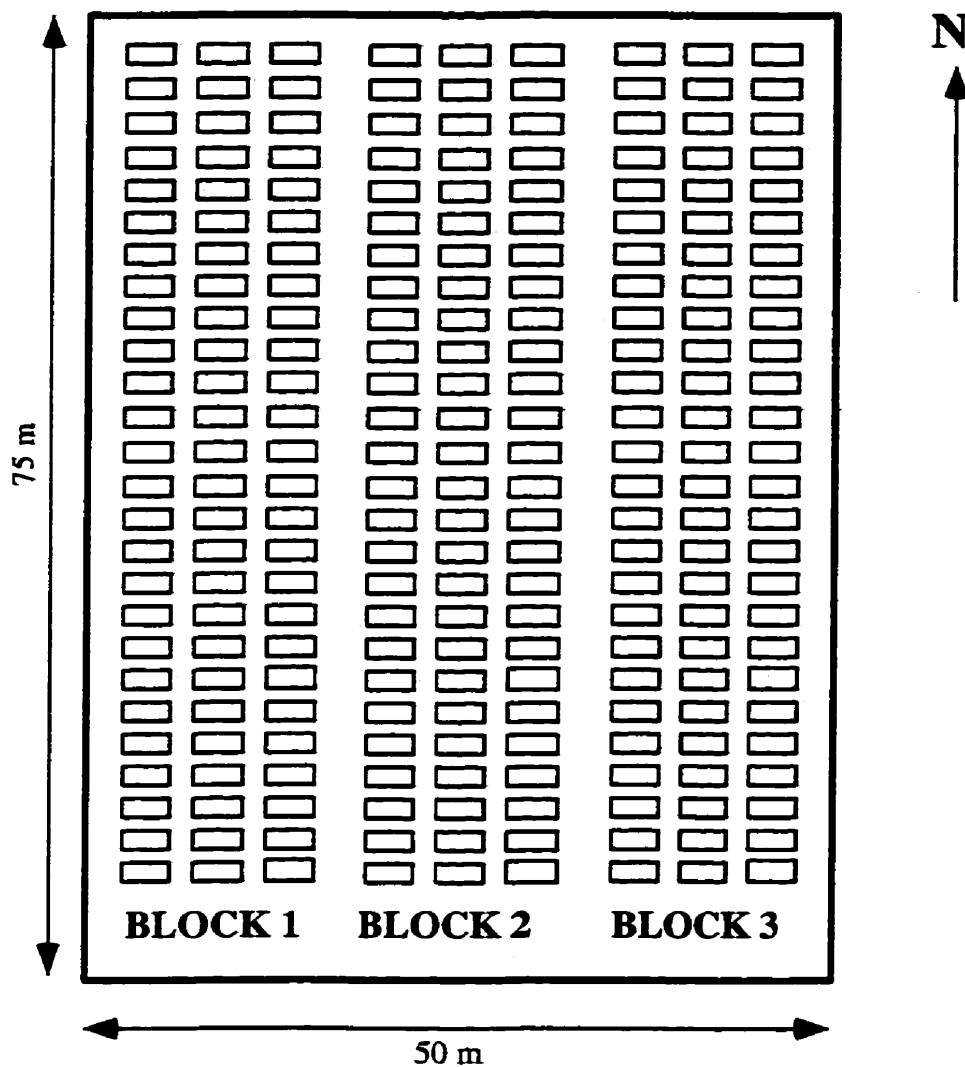
Figure 3.1. Experimental plot layout for diallel competition experiments planted in Carman and Winnipeg, Manitoba in 1995 and 1996, respectively. Each plot is 1.25 m wide and 3.5 m long. Lanes are 1.5 m wide. Treatments within blocks were randomized.
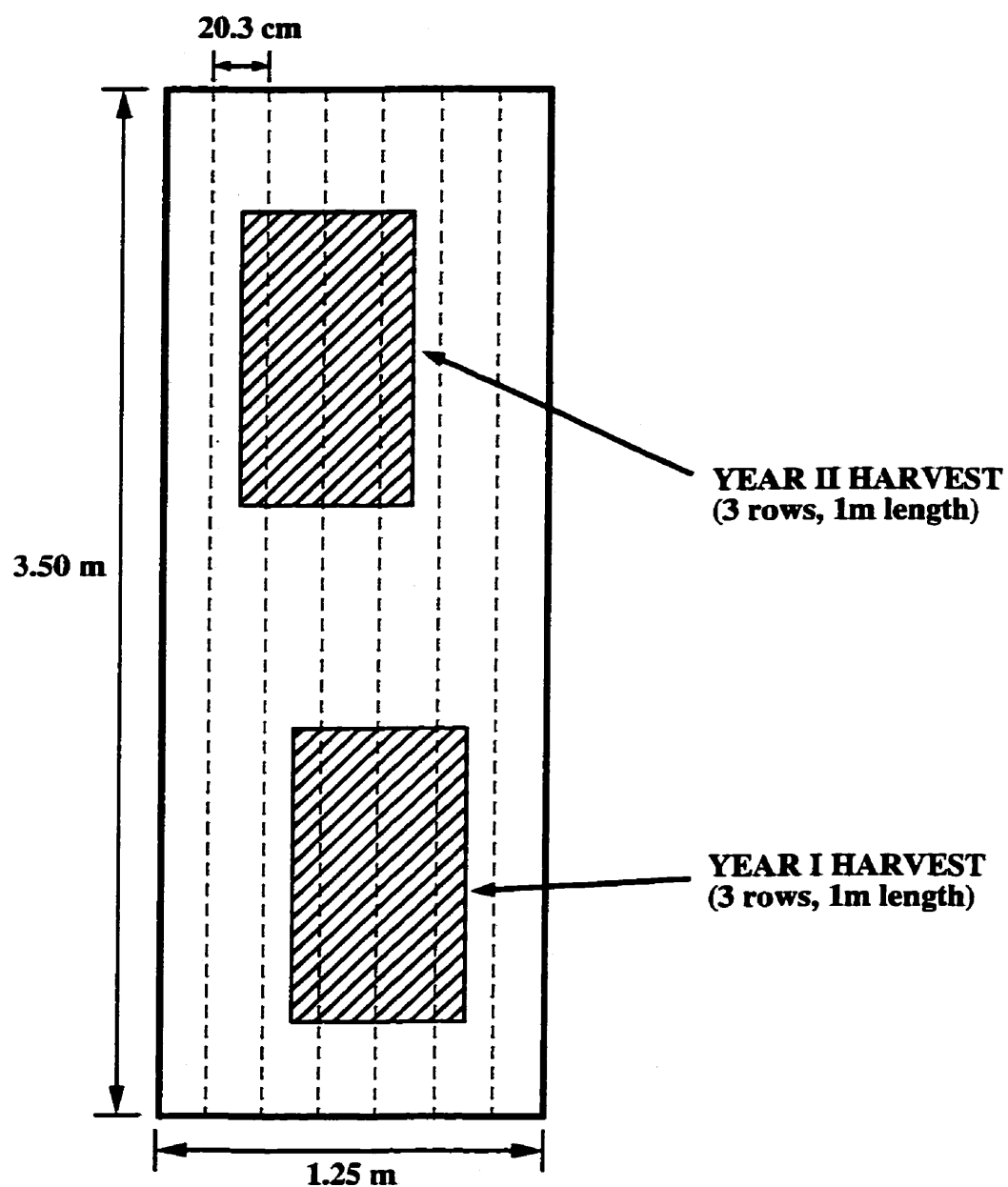
Figure 3.2. Diagram of a hypothetical experimental plot, showing six seeded rows (dashed lines) and two harvesting units (hatched boxes). Three seeded rows were harvested after the first and second growing seasons. Areas harvested between the two years were spaced at 50 cm from each other and from the two 1.25 m plot edges. Harvested areas did not include the two outer-most rows, or rows in which plants failed to establish.

on the autoecology of these twelve species). Six of the species used were cool-season (C_3) species, while the other six species used were warm-season (C_4) species (**Table 3.2**).

Pre-planting Laboratory Methods

Prior to planting, proportions of seed were weighed out in advance to help ensure a more consistent establishment density from species to species. To accomplish this, an estimate of the percentage of live seeds was used in conjunction with an estimate of the number of actual seeds present by mass. This estimate is commonly referred to as 'pure live seed' or PLS. The actual PLS value is the product of two other values: percent purity and percent germination, evaluated by several independent seed testing laboratories for each seed lot. Percent purity is simply the percentage of material, by mass, that is actually the species of seed that the lot claims to be. Percent germination is the percentage of those 'pure' seeds that are actually alive and capable of germination. This last figure is determined by tetrazolium hydrochloride (TZ) testing, or via an actual test of germination in moist petri dishes. The end result of using the PLS value for each seed lot is a measurement of seed, by mass, which should theoretically result in a known density of germinating seeds once planted. The theoretical density used for both experiments was 183 PLS seeds m^{-2} of seeded area (17 PLS ft^{-2}) for monoculture plots and two-species mixed plots.

Pre-planting Field Methods

Prior to any revegetation of an area with native grasses, it is often necessary to remove the existing vegetation, which is usually a mixture of exotic annual and/or perennial weeds. In both of the fields used in this study, the removal of unwanted vegetation was accomplished by the application of a glyphosate herbicide (Roundup™). Prior to planting the Carman experiment in 1995, there were several 'weedy' species beginning to establish within the field, including pygmyflower (*Androsace septentrionalis*), dandelions (*Taraxacum officinale*), and Canada thistle (*Cirsium arvense*). These species were effectively killed in mid-May using a single application of glyphosate at a rate of 880 g/ha. A similar complement of weeds was found to be establishing at Winnipeg in the spring of 1996. These too were effectively treated with the same application rate of glyphosate.

At Carman, approximately 1/3 of the field was covered by flax in the year preceding the first growing season of this experiment (i.e. in 1994). Although most of the above-ground

Table 3.2. Grass species used in diallel competition experiments at Carman and Winnipeg. Classification as C_3 or C_4 species follows Waller and Lewis (1979). Species nomenclature follows Kartesz (1994).

Species	Common Name
Cool-Season (C_3)	
Elymus canadensis L.	Canada Wild Rye
Elymus trachycaulus (Link) Gould *ex* Shinners	Slender Wheatgrass
Elymus lanceolatus (Scribn. & J.G. Sm.) Gould	Northern Wheatgrass
Nassella viridula (Trin.) Barkworth	Green Needlegrass
Pascopyrum smithii (Rydb.) A. Love	Western Wheatgrass
Stipa comata Trin. & Rupr.	Needle & Thread
Warm-Season (C_4)	
Andropogon gerardii Vitman	Big Bluestem
Panicum virgatum L.	Switchgrass
Sorghastrum nutans (L.) Nash	Indiangrass
Bouteloua curtipendula (Michx.) Torr.	Side-Oats Grama
Schizachyrium scoparium (Michx.) Nash	Little Bluestem
Bouteloua gracilis (Willd. ex Kunth) Lag. *ex* Griffiths	Blue Grama

flax biomass was removed in the fall of 1994, some straw did remain prior to planting. This remaining straw was hand-raked prior to seeding to further reduce the amount of existing flax straw on the field. Furthermore, the Carman experiment was established such that two blocks occurred within the flax-straw area while the third block remained completely within the non-flax-straw area. Prior to seeding, both fields were marked with 'scratch lines' using garden hoes and ropes, to facilitate proper placement of each of the 234 plots with the tractor and seeder in tow.

Planting Methods

Although many potential methods of sowing the plots were possible, mechanical seeding was used for two reasons. Firstly, this method best approximates the method used in large-scale revegetation programs. It is under these conditions that competitive hierarchies are of practical concern. Furthermore, this method places the grasses at a prescribed depth and density in parallel rows, assuring improved germination and establishment relative to hand-sowing. The tractor used for both experiments was a John Deere™ 950, and the seeder was a Fabro™ 6 row disk-type with the disks set ca. 20 cm apart and 2 cm deep (**Fig. 3.2**). The plots at Carman were seeded on May 29, 1995. Plots in Winnipeg were seeded on May 30, 1996.

Post-Sowing Management - 1995

After sowing, management of the experimental plots and the lanes between the plots was necessary to prevent invasion of the plots by undesirable native or introduced species. Weeding of the plots was first attempted by hand throughout the month of June, with the help of several volunteers. The major weed present, red-root pigweed (*Amaranthus retroflexus*), soon formed a carpet-like mat of seedlings throughout much of the experiment. Consequently, Buctril-M™, a broadleaf-specific herbicide, was applied over the plots in the first week of July at a rate of 1.00 L/ha using a 'bicycle' sprayer. As this application proved to be largely unsuccessful, Refine Extra™ was applied at 19.8 g/ha on July 14, with excellent results. The remaining weedy grasses, barnyard grass (*Echinochloa crusgalli*), and green foxtail (*Setaria viridis*), were effectively removed by hand throughout the remainder of the growing season.

Post-Sowing Management - 1996

Weeds present at Winnipeg after sowing were similar to those at Carman in 1995, and included lamb's-quarters (*Chenopodium album*), *E. crusgalli*, *S. viridis*, as well as Canada thistle (*Cirsium arvense*), wild buckwheat (*Polygonum convolvulus*), and wild mustard (*Brassica kaber* var. *pinnatifida*). The non-graminoid species amongst this group were eliminated using Refine Extra™, which was applied on June 13 at a rate of 19.8 g/ha. Following herbicide application, the graminoid weeds (and any other weeds that appeared over the summer) were successfully removed using simple hand tools and rotovation. Hand weeding within plots and rotovation of the lanes were the only weed management efforts required at Carman in 1996, since invasive weeds were less abundant.

Post-Sowing Management - 1997

At Winnipeg in 1997, hand weeding and rotovating of the lanes between plots were required on only two occasions. As with Carman in 1996, herbicide was not required to control invasive weeds within and around the experimental plots.

Harvesting and Data Collection

Due to the unreliability of measuring percent cover of dense grasses, species performance within each plot was determined by harvesting three rows (each 1 m in length) in which species had successfully established (**Fig. 3.2**). Harvesting took place in the first two weeks of September in all years. Harvests from year I and II within each plot were separated by at least 50 cm from one another to ensure the year I harvest had no effect on the year II results. The harvesting process involved digging up all of the plants, then sorting them by species into paper bags for drying. In 1995 and 1996, after all of the plots were harvested, individuals within the paper bags were separated and counted (**Appendix IV**). The number of individuals harvested from Winnipeg in 1997 were not counted. Root portions of all plants were removed prior to drying the above-ground phytomass at 80°C for 48 hours. Due to the large volume of phytomass harvested in 1996 and 1997, plants were dried in a plant-drying shed at the Fort Garry Campus of the University of Manitoba for a period of approximately 3 weeks. After drying, the plants were massed to the nearest 0.1 g using a Mettler™ digital balance (**Appendix V**).

3.4 Data Analysis

3.4.1 Logged Yield Matrices

Species yield (total dry above-ground biomass per unit area) is the base measurement from which most analyses of competition experiments begin. A matrix of mean yield values can be established in which any value (Y_{ij}) is simply the mean yield of species i or the 'target species' (species along the left, vertical axis) when grown in combination with species j or the 'neighbour species' (species along top, horizontal axis). This matrix thus represents the mean yields (over 3 replicates) of the 12 native grasses grown in all possible pairwise combinations, including monocultures (Y_{ii}). Because plants grow at an exponential rate, variances in plant yields can be quite high, and therefore problematic when running data analysis. Consequently, yields were log-transformed to decrease heteroscedasticity within the data (Jeffers 1988).

3.4.2 Mean Relative Yield as a Competitive Index: Target and Neighbour Scores

From logged mean yield values, the increase (or decrease) in relative biomass of a given 'target' species can be measured when grown in combination with any other 'neighbour' species by comparing its logged mean yield in mixture (Y_{ij}) with one-half of its logged mean yield in monoculture (Y_{ii}). This calculation is termed mean 'relative yield' or the species' mean yield in mixture relative to its mean yield in monoculture (Keddy and Shipley 1989). Symbolically this measure is denoted as X_{ij}, and is calculated as follows:

$$X_{ij} = Y_{ij} / Y_{ii}$$

Values of X_{ij} greater than 1 indicate that species i has a greater yield in mixture with species j than at equal density in monoculture. Wilson and Keddy (1986) term the mean relative yield across any one row its 'target score', or the mean relative yield of the target species averaged over all neighbour species. These scores can be used as an index of competitive ability. Species with higher target scores have greater competitive ability, since they tend to grow better in mixture than in monoculture. Similarly, relative yield means over the columns of the matrix represent 'neighbour scores', or the mean relative yield of the twelve neighbour species when grown with a given target species. Those species with lower neighbour scores may also be considered to have higher competitive ability, since their neighbours tend to be suppressed.

3.4.3 Mean Aggressivity as a Competitive Index

The use of mean relative yields alone may be misleading as competitive indices since both the relative biomass of target and neighbour species have to be considered separately (Wilson and Keddy 1986). For example, a plant with a relative yield of 1.5 may appear to be a strong competitor within that mixture. However, if the neighbour species of that specific mixture also has a relative yield of 1.5, then we have a case of mutual enhancement, not competition. The competitive outcome of a mixture can be better determined when the relative yields of both species of a given mixture are considered simultaneously. This is done by transforming the mean relative yield matrix into a matrix of 'aggressivity' values (McGilchrist and Trenbath 1971). Aggressivity (A_{ij}) is simply the difference between the mean relative yield of a target species (X_{ij}) and its neighbour (X_{ji}):

$$A_{ij} = 0.5 \ (X_{ij} - X_{ji})$$

If the target species has a mean relative yield >1, and the neighbour has a mean relative yield <1 (i.e. is suppressed by the target species), then the target species will have a fairly high and positive aggressivity value for that specific mixture. Conversely, its neighbour's aggressivity will have the same magnitude but opposite sign (i.e. negative). Aggressivity is hence a composite measure of both: a) the degree to which a target species fares better or worse and b) the extent that it suppresses the growth of its neighbour. Thus species with high and positive mean aggressivity values are better competitors, since they grow well in mixture and suppress their neighbours. Those species with high but negative aggressivity values are poor competitors, since they grow poorly in mixture and are less capable of suppressing their neighbours. As with relative yield values, the degree to which aggressivity predict actual competitive exclusion is unknown (Connolly 1997).

3.4.4 Graphical Analysis of a Binary Matrix

Competitive asymmetry has been defined by Shipley (1993) as occurring between any two species in which one's relative yield is > 1, while the other's is < 1. These interactions may be detected when the values within a relative yield matrix are renumbered as "1" (when R.Y. > 1) or "0" (when R.Y. < 1). In this binary matrix, asymmetric competition occurs when a target species' R.Y. is "1" and its neighbour's is "0". This matrix can be used to test for statistically significant transitive asymmetric competition (i.e. the presence of a competitive hierarchy), as described and developed by Keddy and Shipley (1989) and

Shipley (1993) for relative yields. This analysis also allows one to search a binary competition matrix (using the computer program "STRONG", by Shipley [1993]) for all fully transitive competitive hierarchies involving any n species.

Note that this method was originally designed for use with binary data from relative yield matrices (Shipley 1993). If the method is modified slightly to use binary aggressivity values (i.e. values $> 0 =$ "1"; values $< 0 =$ "0") rather than relative yields, one can establish transitive competitive hierarchies based on less restrictive criteria for competitive asymmetry. For example, with relative yields matrices, species pairs may exist in which both binary scores are 1, or both scores are 0. STRONG will essentially treat these species pairs as being symmetric and thus excluded from any possible transitive hierarchy. Using aggressivity values, all species pairs consist of a 1 and a 0 — there are no 1,1 or 0,0 pairs. Overall, this method of analysis measures the degree to which the data is organized into hierarchies, based on pairwise interactions and their resultant aggressivity values.

3.4.5 Multivariate Analysis of Competitive Hierarchies

Virtually all of the analytical methods described above have problems associated with over-simplifying the information inherent in diallel competition experiments. Specifically, the use of mean competitive index values (e.g. target scores, mean aggressivity) results in the loss of finer-scale information regarding species by species interactions. Transitivity analysis (Shipley 1993) intricately pulls out transitive competitive hierarchies, but only after reducing values to binary form. Consequently, both of these methods 'force' the 12 species into clear linear additive hierarchies, which fail to illustrate the magnitudes of pairwise differences in species competitive abilities. Fortunately, a multivariate approach can be used ameliorate this problem.

Aggressivity values essentially give us 'distances' between pairs of species — competitive distances. The assumption presented here is that the greater these distances are, the more competitive asymmetry will occur between the species pair. When a linear competitive hierarchy is presented, these distances are represented as being equal and additive. For example, the top competitor A is one unit away from B, two units away from C, and so on until we get to the poorest competitor L which is 11 units away from A. Although this is possible, actual competition matrices will likely fail to demonstrate such clear patterns — they are prone to exceptions. For example, although the order of the competitive hierarchy may be completely transitive, species A may be 2 units of distance from B, 5 units from C

and 4 units of distance from L — a non-linear relationship. A more informative representation of the competitive hierarchy would be an ordination of the aggressivity matrix (converted to absolute values) using non-metric multidimensional scaling (NMDS). This method places each species in two-dimensional space such that all species are at distances as close to actual pairwise competitive distances (i.e. using absolute aggressivity values) as possible (Kenkel and Orloci 1986).

3.4.6 Changes in Competitive Hierarchies over Time and Space

Since it is ultimately the consistency of rank orders of species within hierarchies that are of interest, Spearman Rank correlations were performed on the aggressivity values from the four data sets collected (Carman 1995, 1996; Winnipeg 1996, 1997). This was done in order to evaluate the constancy of rank order over the two locations and time periods, as well as within each of the two locations over two years. Furthermore, in answer to Connolly's (1997) argument that relative yields do not necessarily reflect changes in raw mixture proportions over time, species proportional yields within sites were compared between years I to II. This evaluation, being independent of monoculture biomass, allows us to determine whether or not competitive exclusion will actually reflect the competitive hierarchies established from the relative yield, aggressivity, and transitivity analyses.

3.5 Results

3.5.1 Carman

Yields

Yields from Carman 1995 (Carman I) and 1996 (Carman II) are presented in **Table 3.3** and **Fig. 3.3**. The only evidence of complete exclusion is apparent within the plots in which *S. scoparius* was grown with *E. trachycaulus*. Here, *S. scoparius* averaged 4.1 g in Carman I, but was completely excluded by the second year. Other species that were almost excluded by *E. trachycaulus* included *S. nutans* and *S. comata* (**Table 3.3**). In Carman I, the four most productive species were *E. trachycaulus, P. virgatum, A. gerardii*, and *E. canadensis*. These remained the four highest biomass producers in the second year. *B. gracilis, S. scoparius, S. nutans*, and *S. comata* were the lowest overall producers in both years. Paired t-tests indicate that monoculture and mixture productivities significantly increased from year I to II (**Fig. 3.3**; $p \leq .0001$ for both mixtures and monocultures).

Table 3.3. Matrix of mean yields per m² for monocultures (bolded) and mixtures from Carman 1995 (a), and 1996 (b). Values are given for species in first column when grown in mixture with species in first row. Monoculture yields are halved. Codes: Ag = *Andropogon gerardii* , Bc = *Bouteloua curtipendula* , Bg = *Bouteloua gracilis* , Ec = *Elymus canadensis* , El = *Elymus lanceolatus* , Et = *Elymus trachycaulus* , Nv = *Nassella viridula* , Ps = *Pascopyrum smithii* , Pv = *Panicum virgatum* , Sc = *Stipa comata* , Sn = *Sorghastrum nutans* , Ss = *Schizachyrium scoparium* .

a)

	El	Ag	Bc	Bg	Ec	Et	Ps	Pv	Sc	Sn	Ss	Nv	Mean
El	**79.7**	59.0	68.2	84.2	83.2	32.2	51.4	59.0	89.2	60.6	52.6	48.8	62.6
Ag	408.6	**157.4**	261.4	280.8	218.0	136.2	283.6	341.0	236.6	321.2	271.8	314.2	279.4
Bc	56.4	95.2	**71.2**	144.8	112.4	59.2	79.8	84.8	167.8	139.0	133.4	202.4	115.9
Bg	51.6	76.8	40.8	**38.4**	29.6	15.4	22.4	24.2	81.4	19.6	42.6	37.2	40.1
Ec	207.6	252.8	249.4	229.0	**141.5**	120.4	288.4	213.4	319.6	261.8	208.4	235.6	235.1
Et	366.2	417.8	500.8	416.8	501.0	**304.0**	354.2	361.2	409.8	481.2	529.4	497.0	439.6
Ps	81.2	61.0	128.2	78.2	87.6	32.0	**114.0**	69.2	65.0	98.2	126.2	105.6	84.8
Pv	322.2	152.4	342.0	284.6	165.6	155.4	326.0	**249.0**	388.0	296.6	478.4	296.8	291.6
Sc	7.0	3.4	13.2	6.8	14.4	4.0	14.4	8.4	**12.6**	20.0	10.0	11.8	10.3
Sn	23.6	4.8	22.2	29.0	42.8	1.8	25.6	28.2	34.0	**23.6**	26.6	35.8	24.9
Ss	33.4	28.0	17.8	35.4	43.6	8.2	54.6	40.0	38.6	17.8	**60.7**	19.4	30.6
Nv	48.2	49.4	75.0	27.0	45.4	6.8	42.6	65.0	93.4	66.8	41.0	**66.2**	51.0

b)

	El	Ag	Bc	Bg	Ec	Et	Ps	Pv	Sc	Sn	Ss	Nv	Mean
El	**357.0**	490.4	764.8	1282.4	956.3	144.8	409.1	622.7	927.9	1123.8	1547.3	577.9	804.3
Ag	1115.9	**1038.3**	1722.5	2236.6	52.7	95.9	838.7	805.6	1473.1	1871.7	1779.5	1193.6	1198.7
Bc	494.5	147.7	**606.3**	881.2	63.1	9.9	225.9	296.7	809.8	1579.5	1339.0	706.9	595.8
Bg	66.5	56.1	88.9	**156.1**	5.5	6.1	45.1	27.4	560.7	333.3	463.2	64.9	156.2
Ec	2634.3	2288.9	3124.1	3388.0	**1573.1**	688.6	2595.5	3027.3	1932.1	3616.3	2820.2	4002.5	2738.0
Et	1436.0	2918.1	2274.3	2129.1	1837.0	**1238.5**	1541.7	1091.7	1951.6	2552.6	2550.7	1254.5	1957.9
Ps	1068.3	1158.9	751.3	1310.5	194.9	139.5	**593.7**	760.2	1203.1	1423.2	852.2	962.3	893.1
Pv	1210.5	1081.1	1106.3	2110.6	133.8	48.0	341.9	**1030.5**	1228.1	1049.7	2129.6	633.7	1006.7
Sc	121.8	62.3	148.4	201.3	5.3	0.2	61.2	133.5	**136.1**	108.2	167.9	93.4	100.3
Sn	168.0	2.5	164.4	125.9	11.9	0.2	19.2	20.8	627.2	**358.0**	292.7	188.4	147.4
Ss	182.7	67.7	294.2	811.7	26.7	0.0	63.7	59.4	1074.6	701.9	**516.0**	240.4	320.3
Nv	528.9	532.4	991.7	1052.6	86.7	4.9	472.3	414.7	1420.7	1692.8	902.5	**966.4**	736.4
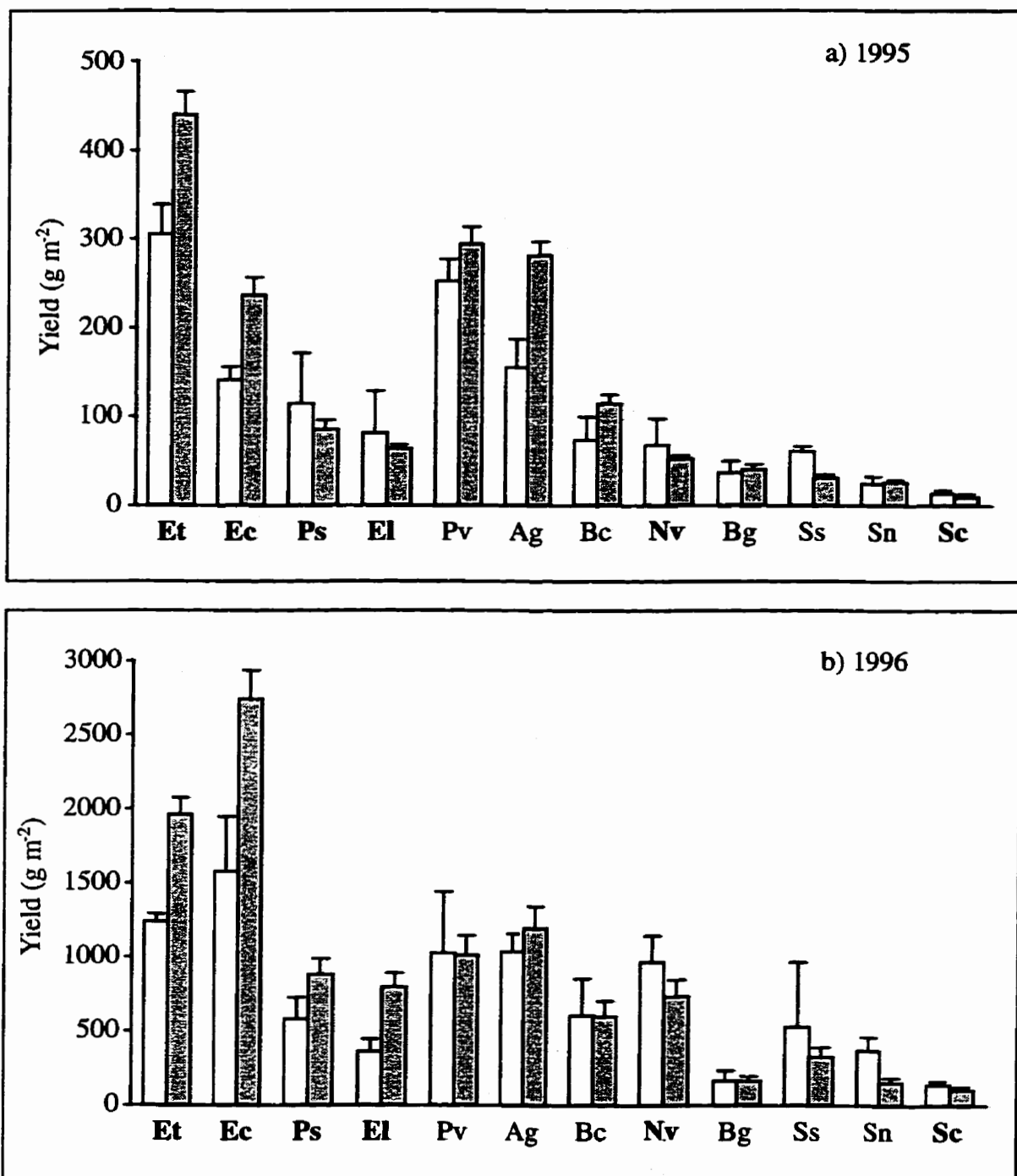
Figure 3.3. Mean above-ground dry biomass (+/- s.e.) of 12 native grasses grown at Carman in 1995 (a) and 1996 (b). Means were calculated from all pair-wise possible mixtures (shaded bars; n = 33) and monocultures (unshaded bars; n = 3). Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*. Species codes in bold represent C3 species; non-bolded codes represent C4 species. Species are ordered from strong (left) to weak (right) competitive ability, based on the 1996 STRONG hierarchy (Fig. 3.10).

Despite the relative consistencies in rank, some species did appear to increase into year II more than others. For example, *N. viridula* increased by a factor of 14.4, while *P. virgatum* only increased by a factor of 3.5 (**Table 3.4**). With the exception of *S. scoparium*, all of the six greatest increasers (i.e. C96/C95 $\geq$ 10) were C_3 species. Finally, two-sample t-tests indicate that mean mixture yields were significantly greater than mean monoculture yields in both Carman I (p = .0003) and II (p = .0111; **Fig. 3.4**).

Relative Yields

Results from relative yields can be described in terms of target scores (the mean relative yields across the rows of the matrix) and neighbour scores (the mean relative yields down the columns of the matrix). In Carman I, five species had mean relative yields > 1, while seven species have mean relative yields < 1 (**Table 3.5; Fig. 3.5**). The five strongest competitors in terms of target scores in Carman I were *A. gerardii, E. canadensis, B. curtipendula, E. trachycaulus,* and *P. virgatum. E. trachycaulus* was the only species to attain a neighbour score < 1 in 1995 (**Fig. 3.6**). By year II, the highest target scores (> 1) were attained by *E. lanceolatus, E. canadensis, E. trachycaulus* and *P. smithii,* all C_3 species. Neighbour scores were more variable in year II. Low neighbour scores (< 1) in Carman II were attained by six species: *E. trachycaulus, E. canadensis, P. smithii, E. lanceolatus, P. virgatum,* and *A. gerardii* (**Fig. 3.6**). Exclusion of *S. scoparium, S. nutans,* and *S. comata* by *E. trachycaulus* is evidenced by extremely low relative yield values for these species (**Table 3.5**). These same three species had the lowest mean relative yields in Carman II.

Species relative yields between Carman I and Carman II had a low rank-order correlation (ρ = 0.449, p = 0.09; **Fig. 3.7**). Species that remained at relatively constant positions in the ranked hierarchy (e.g. *S. scoparium, S. comata, E. trachycaulus, E. canadensis*) tended to be at the extreme ends of the relative yield scale. Those species that were above the 1:1 line in **Fig. 3.7** had increasing relative yields (and hence competitive abilities) in year II. These included all of the six C_3 species and one C_4 species, *S. scoparium* (which did not change dramatically from year I to II). All of the other C_4 species fell below the 1:1 line, indicating decreased competitive abilities from year I to II.

Table 3.4. Increase in mean biomass of 12 native grass species grown in all pairwise combinations and in monoculture. Increase is measured as the ratio between the mean yields for year 1 and 2.

Species	Increase	
	C96/C95	W97/W96
Nassella viridula	14.4	4.6
Elymus lanceolatus	12.9	3.4
Elymus canadensis	11.6	4.0
Pascopyrum smithii	10.5	9.4
Schizachyrium scoparium	10.5	4.6
Stipa comata	9.7	2.7
Sorghastrum nutans	5.9	3.6
Bouteloua curtipendula	5.1	2.5
Elymus trachycaulus	4.5	2.1
Andropogon gerardii	4.3	3.3
Bouteloua gracilis	3.9	2.9
Panicum virgatum	3.5	3.6
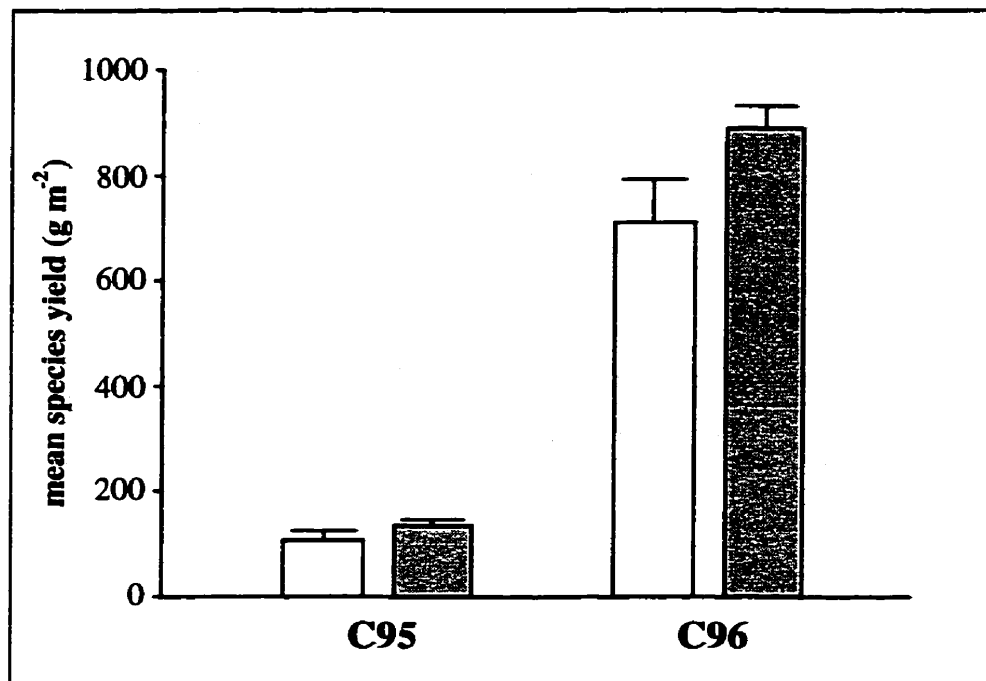
Figure 3.4. Mean total above-ground dry biomass (+/- s.e.) of 12 native grasses grown at Carman in 1995 (C95) and 1996 (C96). Unshaded bars represent species grown in monoculture; shaded bars represent species grown in all pairwise combinations.

Table 3.5. Matrix of relative yields from Carman 1995 (a), and 1996 (b). Values are given for species in first column when grown in mixture with species in first row. Codes: Ag = *Andropogon gerardii* , Bc = *Bouteloua curtipendula* , Bg = *Bouteloua gracilis* , Ec = *Elymus canadensis* , El = *Elymus lanceolatus* , Et = *Elymus trachycaulus* , Nv = *Nassella viridula* , Ps = *Pascopyrum smithii* , Pv = *Panicum virgatum* , Sc = *Stipa comata* , Sn = *Sorghastrum nutans* , Ss = *Schizachyrium scoparium* , t.s. = target scores, n.s. = neighbour scores.

a)

	El	Ag	Bc	Bg	Ec	Et	Ps	Pv	Sc	Sn	Ss	Nv	t.s.
El	-	0.92	0.96	1.01	1.01	0.77	0.89	0.92	1.03	0.93	0.89	0.87	0.93
Ag	1.22	-	1.11	1.13	1.07	0.97	1.13	1.18	1.09	1.16	1.12	1.16	1.12
Bc	0.94	1.08	-	1.19	1.12	0.95	1.03	1.05	1.23	1.18	1.17	1.29	1.11
Bg	1.09	1.22	1.02	-	0.92	0.72	0.83	0.86	1.24	0.79	1.03	0.99	0.97
Ec	1.09	1.13	1.13	1.11	-	0.96	1.17	1.10	1.19	1.14	1.09	1.12	1.11
Et	1.04	1.06	1.10	1.06	1.10	-	1.03	1.03	1.06	1.09	1.11	1.10	1.07
Ps	0.92	0.85	1.03	0.91	0.94	0.70	-	0.88	0.86	0.96	1.02	0.98	0.91
Pv	1.05	0.90	1.07	1.03	0.92	0.90	1.06	-	1.09	1.04	1.13	1.04	1.02
Sc	0.76	0.50	1.02	0.75	1.06	0.55	1.06	0.83	-	1.21	0.90	0.97	0.87
Sn	1.00	0.48	0.98	1.08	1.22	0.25	1.03	1.06	1.13	-	1.04	1.15	0.95
Ss	0.83	0.79	0.67	0.85	0.91	0.47	0.97	0.88	0.87	0.67	-	0.69	0.78
Nv	0.91	0.92	1.03	0.76	0.90	0.42	0.88	0.99	1.10	1.00	0.87	-	0.89
n.s.	0.99	0.90	1.01	0.99	1.01	0.70	1.01	0.98	1.08	1.02	1.04	1.03	x

b)

	El	Ag	Bc	Bg	Ec	Et	Ps	Pv	Sc	Sn	Ss	Nv	t.s.
El	-	1.06	1.15	1.25	1.19	0.83	1.03	1.11	1.18	1.22	1.28	1.09	1.13
Ag	1.01	-	1.08	1.12	0.53	0.62	0.97	0.96	1.06	1.09	1.09	1.02	0.96
Bc	0.96	0.75	-	1.07	0.61	0.31	0.83	0.88	1.05	1.17	1.14	1.03	0.89
Bg	0.81	0.77	0.87	-	0.30	0.32	0.72	0.62	1.29	1.17	1.25	0.80	0.81
Ec	1.08	1.06	1.10	1.11	-	0.88	1.08	1.10	1.03	1.12	1.09	1.14	1.07
Et	1.02	1.13	1.09	1.08	1.06	-	1.03	0.98	1.07	1.11	1.11	1.00	1.06
Ps	1.10	1.12	1.04	1.14	0.81	0.75	-	1.04	1.12	1.15	1.06	1.08	1.04
Pv	1.03	1.01	1.01	1.11	0.68	0.52	0.82	-	1.03	1.00	1.12	0.92	0.93
Sc	0.97	0.82	1.02	1.09	0.30	0.02	0.82	1.00	-	0.95	1.05	0.91	0.81
Sn	0.86	0.15	0.85	0.80	0.37	0.02	0.45	0.47	1.11	-	0.96	0.88	0.63
Ss	0.81	0.64	0.90	1.08	0.48	0.00	0.63	0.62	1.13	1.06	-	0.86	0.75
Nv	0.90	0.90	1.00	1.01	0.61	0.20	0.88	0.86	1.06	1.09	0.99	-	0.87
n.s.	0.96	0.86	1.01	1.08	0.63	0.41	0.84	0.87	1.10	1.10	1.10	0.98	x
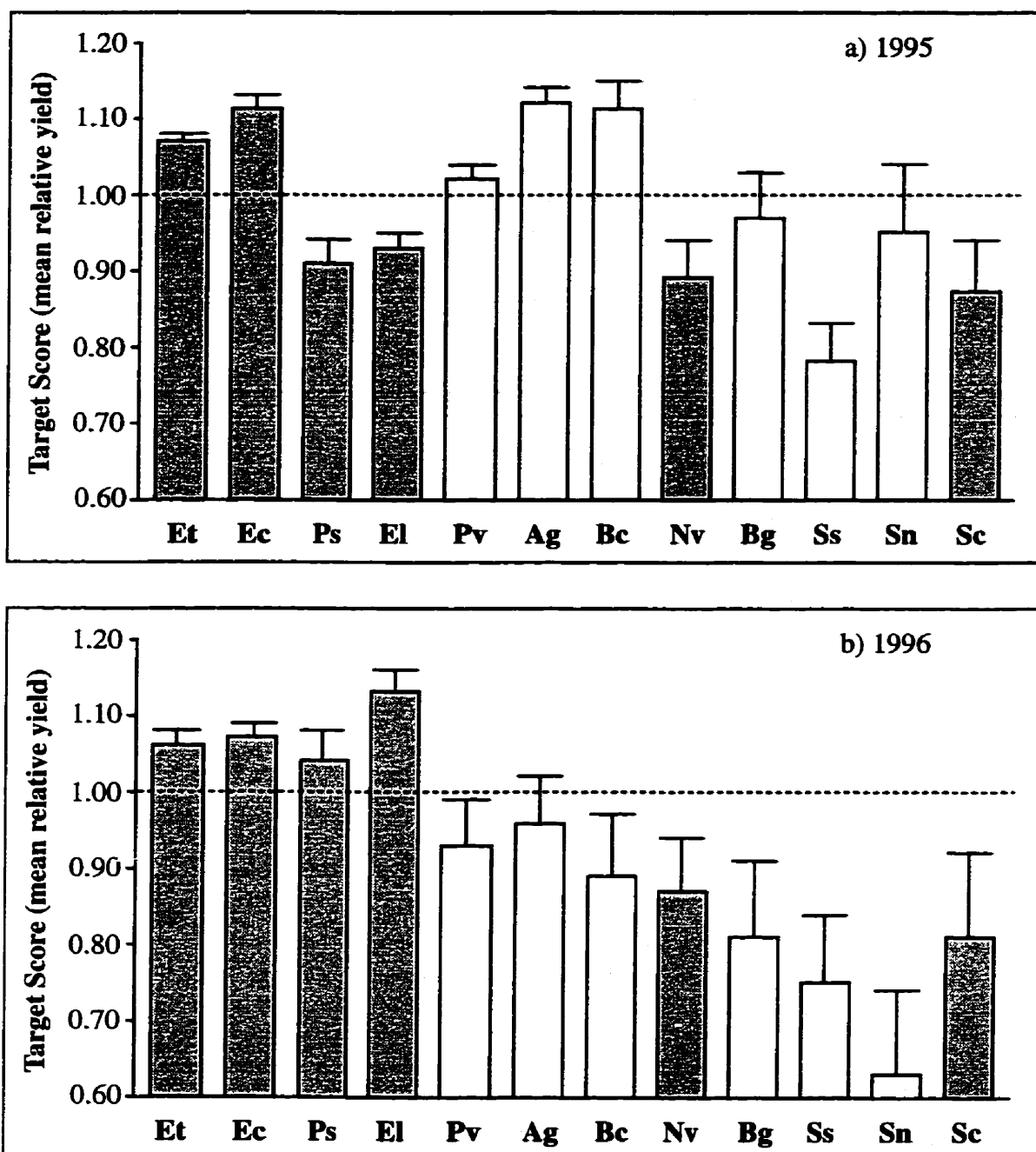
Figure 3.5. Target scores (+/- s.e.) of 12 native grasses grown at Carman in 1995 (a) and 1996 (b). Means for each species were calculated from 11 possible pair-wise mixtures. Species whose target scores exceed 1.00 (dotted line) tend to have higher yields in mixture than in monoculture; those below 1.00 tend to have higher yields in monoculture than in mixture. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*. Shaded bars represent C3 species; un-shaded bars represent C4 species. Species are ordered from strong (left) to weak (right) competitive ability, based on the 1996 STRONG hierarchy (Fig. 3.10).

Figure 3.6. Neighbour scores (+/- s.e.) of 12 native grasses grown at Carman in 1995 (a) and 1996 (b). Means for each species were calculated from 11 possible pair-wise mixtures. Species whose neighbour scores exceed 1.00 (dotted line) tend to have neighbour species with higher yields in mixture than in monoculture; those below 1.00 tend to have neighbour species with higher yields in monoculture than in mixture. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*. Shaded bars represent C3 species; un-shaded bars represent C4 species. Species are ordered from strong (left) to weak (right) competitive ability, based on the 1996 STRONG hierarchy (Fig. 3.10).

Figure 3.7. Mean relative yields (target scores) of 12 native grasses grown in all pairwise combinations at Carman in 1995 and 1996, ranked from lowest values (bottom, left) to greatest values (top, right). *rho* = 0.449, p < 0.10. Species with differences in mean relative yields < 0.005 were considered to be equal. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*. Black squares indicate C4 species; white squares indicate C3 species.

Aggressivity

Differences in competitive abilities between species pairs increase with increasing magnitude of aggressivity values. The magnitudes of aggressivity values in Carman I (**Table 3.6**) ranged from 0.00 (*B. curtipendula* with *E. canadensis*; and *B. curtipendula* with *P. smithii*) to 0.42 (*E. trachycaulus* with *S. nutans*). By Carman II (**Table 3.6**), values ranged from 0.01 (*B. curtipendula* with *N. viridula*) to 0.56 (*S. scoparius* w/ *E. trachycaulus*). Consistently strong competitors in year I and II were *E. trachycaulus*, *E. canadensis*, *A. gerardii*, and *P. virgatum* (**Fig. 3.8**). Consistently poor competitors from year I to II were *N. viridula*, *S. scoparium*, *S. nutans*, and *S. comata*.

The rank-order correlation between mean aggressivity values in years I and II (**Fig. 3.9**) was stronger than that of relative yields ($\rho = 0.575$; $p = 0.04$). As with relative yield values, the most consistently ranked species from years I to II are at the peripheral ends of the aggressivity gradient (e.g. *S. scoparium* and *S. comata* at the low end, and *E. canadensis* and *E. trachycaulus* at the high end). As with the relative yield values, aggressivities indicate that all of the C_3 species had greater competitive ability in year II, with *P. smithii* increasing to the greatest extent (**Fig. 3.9**). Species whose relative (ranked) competitive ability decreased by year II were all C_4 species, except for *S. scoparium* (**Fig. 3.9**). In Carman II, ranks of mean aggressivity values were correlated with species monoculture yields ($\rho = 0.664$; $p = 0.02$), indicating that more productive species tend to be more competitive than species of lower productivity.

Transitivity Analysis

Transitivity analysis based on aggressivity values indicated a high number of transitive hierarchies for both Carman I and II (**Table 3.7**). For Carman I, the largest completely transitive hierarchy found involved 9 species ($p < 0.0002$; **Fig. 3.10**). For Carman II, the 3 largest hierarchies found all involved 11 species ($p < 1.0 \times 10^{-7}$; **Fig. 3.11**). The lack of a completely transitive 12 species hierarchy in Carman II was attributable to a single intransitive loop involving *P. smithii*, *E. lanceolatus*, and *E. canadensis* within the second, third, and fourth positions of the hierarchy (**Fig. 3.11**). When these species were equated (i.e. all assigned 3rd place in the hierarchy), this hierarchy was correlated with species monoculture yields ($\rho = 0.641$; $p = 0.02$). Under the null hypothesis of random species

Table 3.6. Matrix of aggressivities from Carman 1995 (a), and 1996 (b). Values are given for species in first column when grown in mixture with species in first row. Codes: Ag = *Andropogon gerardii* , Bc = *Bouteloua curtipendula* , Bg = *Bouteloua gracilis* , Ec = *Elymus canadensis* , El = *Elymus lanceolatus* , Et = *Elymus trachycaulus* , Nv = *Nassella viridula* , Ps = *Pascopyrum smithii* , Pv = *Panicum virgatum* , Sc = *Stipa comata* , Sn = *Sorghastrum nutans* , Ss = *Schizachyrium scoparium* .

a)

	El	Ag	Bc	Bg	Ec	Et	Ps	Pv	Sc	Sn	Ss	Nv	mean
El	-	-0.15	0.01	-0.04	-0.04	-0.14	-0.02	-0.07	0.14	-0.04	0.03	-0.02	-0.03
Ag	0.15	-	0.02	-0.05	-0.03	-0.05	0.14	0.14	0.30	0.34	0.17	0.12	0.11
Bc	-0.01	-0.02	-	0.09	0.00	-0.07	0.00	-0.01	0.11	0.10	0.25	0.13	0.05
Bg	0.04	0.05	-0.09	-	-0.10	-0.17	-0.04	-0.09	0.25	-0.14	0.09	0.12	-0.01
Ec	0.04	0.03	0.00	0.10	-	-0.07	0.11	0.09	0.06	-0.04	0.09	0.11	0.05
Et	0.14	0.05	0.07	0.17	0.07	-	0.17	0.07	0.25	0.42	0.32	0.34	0.19
Ps	0.02	-0.14	0.00	0.04	-0.11	-0.17	-	-0.09	-0.10	-0.03	0.03	0.05	-0.05
Pv	0.07	-0.14	0.01	0.09	-0.09	-0.07	0.09	-	0.13	-0.01	0.13	0.02	0.02
Sc	-0.14	-0.30	-0.11	-0.25	-0.06	-0.25	0.10	-0.13	-	0.04	0.01	-0.06	-0.10
Sn	0.04	-0.34	-0.10	0.14	0.04	-0.42	0.03	0.01	-0.04	-	0.19	0.08	-0.03
Ss	-0.03	-0.17	-0.25	-0.09	-0.09	-0.32	-0.03	-0.13	-0.01	-0.19	-	-0.09	-0.13
Nv	0.02	-0.12	-0.13	-0.12	-0.11	-0.34	-0.05	-0.02	0.06	-0.08	0.09	-	-0.07

b)

	El	Ag	Bc	Bg	Ec	Et	Ps	Pv	Sc	Sn	Ss	Nv	mean
El	-	0.02	0.09	0.22	0.06	-0.10	-0.04	0.04	0.10	0.18	0.23	0.09	0.08
Ag	-0.02	-	0.16	0.18	-0.26	-0.26	-0.08	-0.02	0.12	0.47	0.22	0.06	0.05
Bc	-0.09	-0.16	-	0.10	-0.25	-0.39	-0.11	-0.07	0.02	0.16	0.12	0.01	-0.06
Bg	-0.22	-0.18	-0.10	-	-0.41	-0.38	-0.21	-0.25	0.10	0.19	0.08	-0.11	-0.13
Ec	-0.06	0.26	0.25	0.41	-	-0.09	0.13	0.21	0.36	0.38	0.30	0.26	0.22
Et	0.10	0.26	0.39	0.38	0.09	-	0.14	0.23	0.52	0.55	0.56	0.40	0.33
Ps	0.04	0.08	0.11	0.21	-0.13	-0.14	-	0.11	0.15	0.35	0.22	0.10	0.10
Pv	-0.04	0.02	0.07	0.25	-0.21	-0.23	-0.11	-	0.02	0.27	0.25	0.03	0.03
Sc	-0.10	-0.12	-0.02	-0.10	-0.36	-0.52	-0.15	-0.02	-	-0.08	-0.04	-0.07	-0.14
Sn	-0.18	-0.47	-0.16	-0.19	-0.38	-0.55	-0.35	-0.27	0.08	-	-0.05	-0.11	-0.24
Ss	-0.23	-0.22	-0.12	-0.08	-0.30	-0.56	-0.22	-0.25	0.04	0.05	-	-0.06	-0.18
Nv	-0.09	-0.06	-0.01	0.11	-0.26	-0.40	-0.10	-0.03	0.07	0.11	0.06	-	-0.06
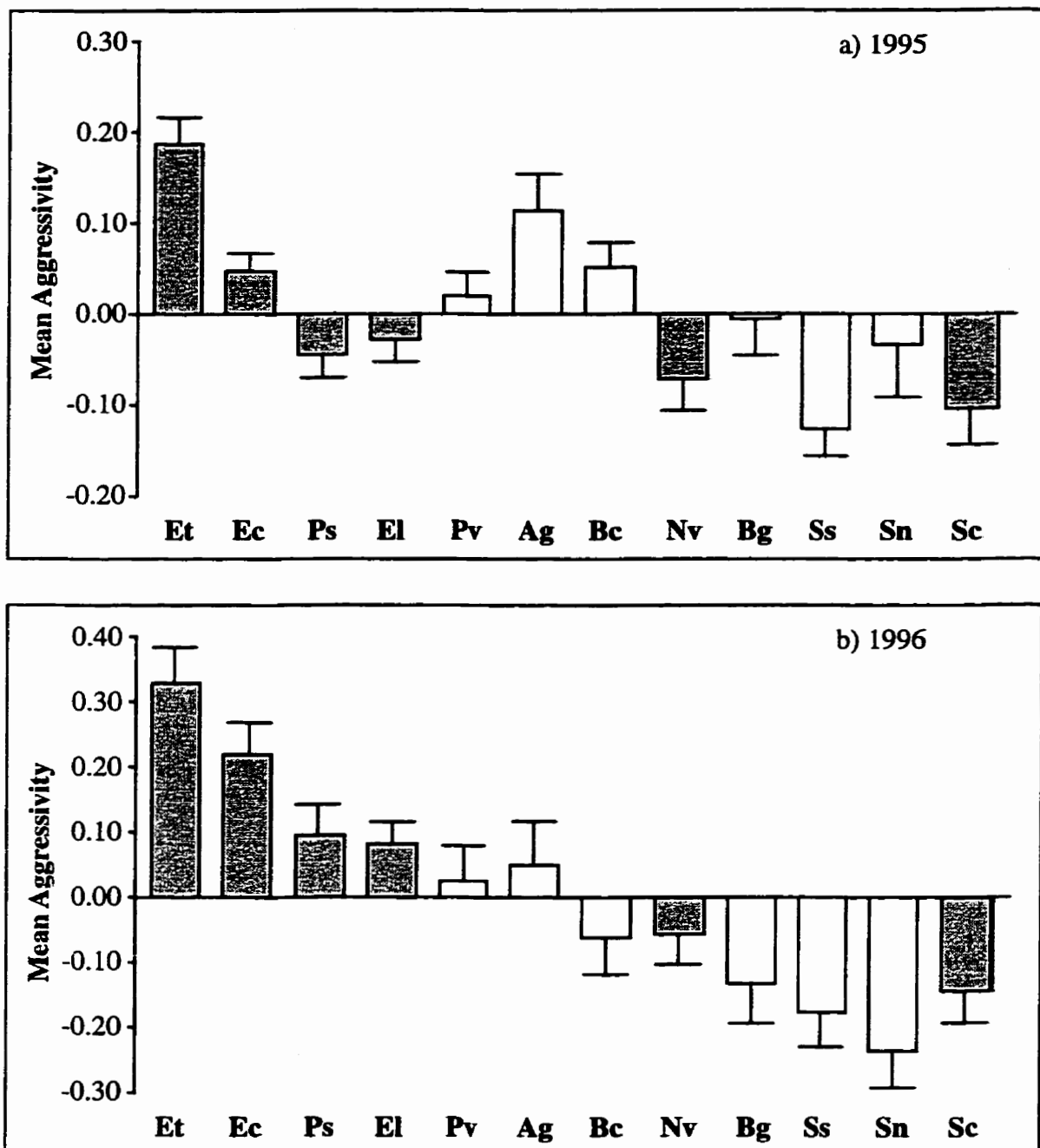
Figure 3.8. Mean aggressivity (+/- s.e.) of 12 native grasses grown at Carman in 1995 (a) and 1996 (b). Means for each species were calculated from 11 possible pair-wise mixtures. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*. Shaded bars represent C3 species; un-shaded bars represent C4 species. Species are ordered from strong (left) to weak (right) competitive ability, based on the 1996 STRONG hierarchy (Fig. 3.10).

Figure 3.9. Mean aggressivities of 12 native grasses grown in all pairwise combinations at Carman in 1995 and 1996, ranked from lowest values (bottom, left) to greatest values (top, right). *rho* = 0.575, p < 0.05. Species with differences in aggressivities < 0.005 were considered to be equal. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*. Black squares indicate C4 species; white squares indicate C3 species.

Table 3.7. Total number of completely transitive hierarchies found within pairwise aggressivity matrices from Carman 1995 (C95) 1996 (C96), and Winnipeg 1996 (W96) 1997 (W97). N = number of species within a transitive hierarchy. T = the total number of transitive hierarchies possible. E = the expected number of transitive hierarchies given random assignment of 1's and 0's within a given matrix. p(N) = the probability of species forming a single transitive path involving N species.

N	T	E	p(N)	C95	C96	W96	W97
2	66	66	1.00	66	66	66	66
3	220	165	0.75	201	219	203	220
4	495	186	0.38	365	486	385	495
5	792	93	0.12	407	756	477	792
6	924	20	0.02	276	840	396	924
7	792	2	0.002	107	666	218	792
8	495	0	< 0.001	20	369	75	495
9	220	0	< 0.001	1	136	14	220
10	66	0	< 0.001	0	30	1	66
11	12	0	< 0.001	0	3	0	12
12	1	0	< 0.001	0	0	0	1

STRONGEST ↑ Et

Sn

Ec

Pv

Ps

Bg

Nv

El

WEAKEST Ss
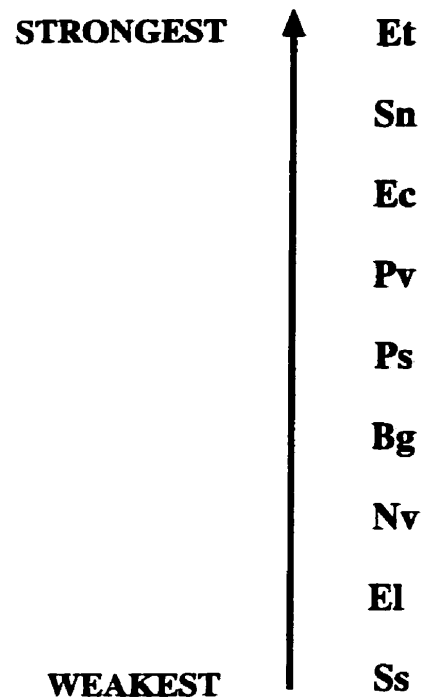
Figure 3.10. The largest completely transitive competitive hierarchy from the Carman 1995 pairwise matrix. Arrow points to the direction of the strongest competitor. Codes: Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*.

STRONGEST	Et	Et	Et
	Ps	Ec	El
	El	Ps	Ec
	Pv	Pv	Pv
	Ag	Ag	Ag
	Bc	Bc	Bc
	Nv	Nv	Nv
	Bg	Bg	Bg
	Ss	Ss	Ss
	Sn	Sn	Sn
WEAKEST	Sc	Sc	Sc
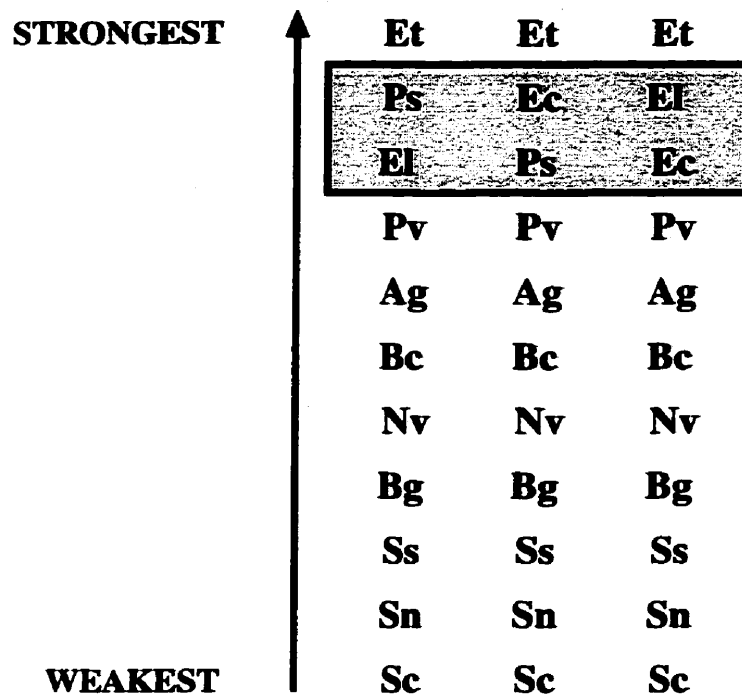
Figure 3.11. Three largest completely transitive competitive hierarchies from the Carman 1996 pairwise matrix. Arrow points to the direction of the strongest competitor. Species within greyed square are part of an intransitive loop. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*.

interactions, the largest transitive hierarchies expected would involve no more than 4 or 5 species (**Table 3.7**).

Non-metric Multidimensional Scaling

Non-metric multidimensional scaling (NMDS) ordination of the Carman II results was performed on the absolute values of aggressivity. Here, absolute aggressivity values are used as a measure of 'distance' (i.e. competitive distance) between species. The NMDS ordination diagram with the transitive hierarchy superimposed (**Fig. 3.12**) shows a non-linear/non-additive trend in pairwise aggressivity values, which is fairly representative of actual pairwise distances (stress $\approx$ 10.9%). Overall, the horizontal axis more or less corresponds to the transitive hierarchy (**Fig. 3.12**). The differences seen are attributed to the transitive hierarchy being based on qualitative binary data, whereas the ordination is based on actual aggressivity values (i.e. the pairwise distances are not converted to binary form). The intransitive loop involving *E. canadensis*, *A. dasystachyum*, and *P. smithii* appears as a triangle within the transitive path. Together, these three species are amongst the top four competitors; *E. trachycaulus* is the strongest competitor. On the other end of the ordination are the small-statured species, *S. comata*, *S. nutans*, *S. scoparium*, and *B. gracilis*, all of which are comparatively weak competitors.

Species Mixture Proportions

Changes in mean proportional yields in mixture from year I to II (**Fig. 3.13**) were generally reflective of the competitive hierarchy models developed using aggressivity values. Of the six strongest competitors based on year II aggressivity values, the four C_3 species (*E. trachycaulus*, *E. canadensis*, *P. smithii*, and *E. lanceolatus*) increased their mean proportional yields in mixture between years I and II. The two strong competitors that decreased in mean proportional yield (*P. virgatum*, and *A. gerardii*) are both C_4 species. Of the six poorest competitors based on year II aggressivity values, the four C_4 species decreased in mean proportional yield (*B. curtipendula*, *B. gracilis*, *S. scoparium*, and *S. nutans*). *N. viridula* and *S. comata*, both poorly competing C_3 species according to year II aggressivity values, increased in mean proportional yield between years I and II. Overall, the six species increasing in mean proportional yield were all C_3 species, while the six species decreasing in mean proportional yield were all C_4 species.
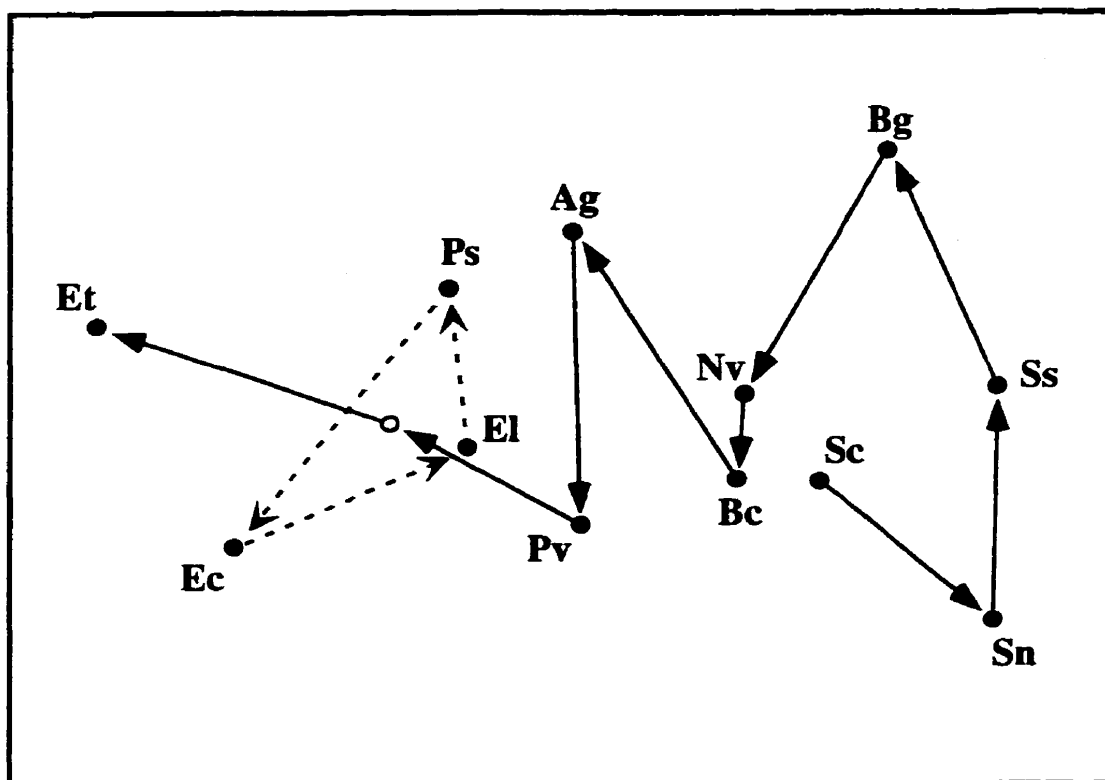
Figure 3.12. Non-metric multidimensional scaling ordination (stress = 10.9%) based on aggressivity values from Carman 1996 (Table 3.6). Species are connected according to the transitive competitive hierarchy developed from Carman 1996 aggressivity values (Fig. 3.11). The arrow points in the direction of increasing competitive ability. Dashed lines represent an intransitive loop (see Fig. 3.11). Codes: Ag = *Agropyron gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymuscanadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*.

Figure 3.13. Species mean proportional yield in mixture (+/- s.e) at Carman in 1995 (grey bars) and 1996 (white bars). Means were calculated from all pairwise combinations. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*. Bolded codes indicate C3 species. Species are ordered from strong (left) to weak (right) competitive ability, based on the 1996 STRONG hierarchy (Fig. 3.10).
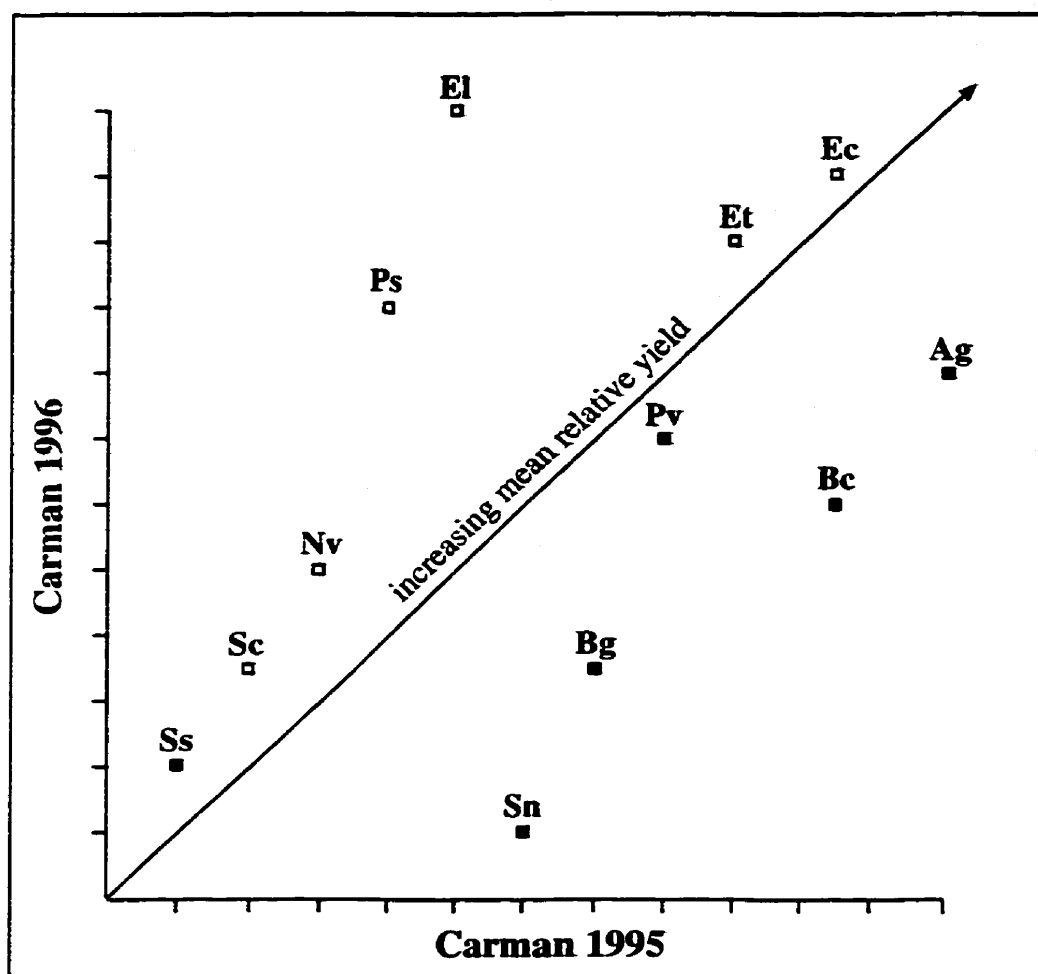
Summary

The ordering of species competitive abilities at Carman was relatively consistent using relative yield values, aggressivity values, and transitivity analyses. These three methods showed a consistent relationship between competitive ability, plant size and photosynthetic pathway types. Large-statured C_3 species (i.e. *E. canadensis*, *E. trachycaulus*, *E. lanceolatus*, and *P. smithii*) were consistently the strongest competitors, while small-statured C_4 species (i.e. *B. gracilis*, *S. scoparium*, and *S. nutans*) were consistently the poorest competitors. Larger-statured C_4 species (i.e. *A. gerardii*, *B. curtipendula*, *P. virgatum*) and smaller-statured C_3 species (i.e. *N. viridula*) were of intermediate competitive ability. An exception to this rule was *S. comata*, which is a C_3 species that performed poorly in both years likely due to its comparatively small size. Furthermore, in answer to Connolly's (1997) criticism of relative yields falsely inferring dominance and competitive exclusion, this same pattern of dominance and subordinance amongst the species is observed when looking at changes in species proportional yields over time, irrespective of monoculture values. Large C_3 species became more dominant by increasing their proportional yields over time, while smaller C_4 species became less dominant by decreasing their proportional yields over time.

3.5.2 Winnipeg

Yields

There is more evidence of complete exclusion apparent at Winnipeg compared to Carman (**Table 3.8; Fig. 3.14**). Species that were excluded by at least one other species at Winnipeg were *S. comata*, *B. gracilis*, and *S. scoparium*. These three species were excluded more often in year II than in to year I. Species responsible for exclusion in year I were *E. trachycaulus* and *B. curtipendula*. In year II, all species except *B. gracilis*, *S. comata*, *S. nutans*, and *S. scoparium* completely excluded at least one neighbouring species. The four largest species in both years were *E. trachycaulus*, *E. canadensis*, *A. gerardii* and *P. virgatum* (**Fig. 3.14**). These were also the four highest biomass producers at Carman II (**Fig. 3.3**). *P. smithii*, *S. scoparius*, *B. gracilis*, and *S. comata* were the lowest producers at Winnipeg I. This remained true into year II, with the exception of *S. nutans* replacing the position of *P. smithii*. As in Carman, paired t-tests indicate that species at Winnipeg had greater biomass on average in year II than in year I (**Fig. 3.15**; $p \leq$ 0.0001 for both monocultures and mixtures). Despite the relative consistencies in rank

Table 3.8. Matrix of mean yields per m² for monocultures (bolded) and mixtures fromWinnipeg 1996 (a), and 1997 (b). Values are given for species in first column when grown in mixture with species in first row. Monoculture yields are halved. Codes: Ag = *Andropogon gerardii* , Bc = *Bouteloua curtipendula* , Bg = *Bouteloua gracilis* , Ec = *Elymus canadensis* , El = *Elymus lanceolatus* , Et = *Elymus trachycaulus* , Nv = *Nassella viridula* , Ps = *Pascopyrum smithii* , Pv = *Panicum virgatum* , Sc = *Stipa comata* , Sn = *Sorghastrum nutans* , Ss = *Schizachyrium scoparium* .

a)

	El	Ag	Bc	Bg	Ec	Et	Ps	Pv	Sc	Sn	Ss	Nv	Mean
El	**177.8**	91.6	180.0	301.9	125.3	5.8	182.9	104.9	379.0	291.3	203.9	84.5	177.4
Ag	313.4	**402.4**	538.2	540.8	225.8	38.5	526.1	405.2	595.2	603.4	632.7	476.4	441.5
Bc	136.0	133.1	**210.1**	484.7	117.2	8.6	201.6	228.3	308.5	305.3	439.4	240.5	234.5
Bg	7.6	5.0	6.0	**14.6**	7.8	0.0	9.1	1.6	32.1	30.2	17.1	10.7	11.8
Ec	773.4	1016.0	634.9	434.9	**467.1**	249.2	848.7	796.2	820.0	964.8	445.5	342.3	649.4
Et	987.0	769.5	821.2	818.2	1116.6	**473.5**	877.0	1201.6	834.0	1166.3	1181.4	1044.3	940.9
Ps	61.8	41.9	66.3	132.6	7.8	5.5	**86.5**	48.5	126.1	186.4	111.7	93.6	80.7
Pv	162.9	265.6	446.9	469.7	253.3	35.3	204.5	**280.2**	530.4	345.9	364.1	538.5	324.8
Sc	0.4	8.9	0.0	54.9	1.1	0.1	0.6	1.7	**6.2**	3.1	1.5	9.3	7.3
Sn	93.5	24.1	82.5	51.9	9.1	1.8	122.1	70.8	150.1	**117.5**	87.0	268.9	89.9
Ss	16.7	2.8	15.0	108.2	9.1	0.0	4.7	28.9	55.3	96.0	**44.2**	12.7	32.8
Nv	37.1	62.9	99.9	156.7	3.2	3.6	215.3	421.0	181.3	165.2	76.9	**80.3**	125.3

b)

	El	Ag	Bc	Bg	Ec	Et	Ps	Pv	Sc	Sn	Ss	Nv	Mean
El	**596.2**	544.2	820.8	792.8	308.0	78.4	384.6	565.2	822.6	835.2	764.0	783.6	608.0
Ag	1345.6	**1380.5**	1579.4	2026.0	428.2	153.8	1151.8	1055.8	2739.8	1778.6	2573.0	1564.8	1481.4
Bc	380.6	302.6	**501.8**	1558.2	45.0	58.8	156.6	729.2	915.6	829.0	826.8	779.2	590.3
Bg	23.0	36.0	1.2	**44.8**	0.0	0.0	0.0	2.6	184.8	19.8	68.2	39.8	35.0
Ec	2187.8	2534.4	3405.0	4032.0	**1809.2**	789.2	2288.6	3077.8	2637.0	3176.2	2841.8	2426.6	2600.5
Et	2406.2	1586.8	2096.0	1982.4	1706.8	**1077.9**	1959.6	2068.4	2220.0	1914.4	2300.4	2123.6	1953.5
Ps	707.8	690.4	1086.0	1080.2	115.0	45.6	**480.6**	508.2	965.4	1006.4	883.8	1235.6	733.8
Pv	878.8	732.4	1467.4	2186.6	267.6	171.2	438.2	**1092.3**	2080.6	1282.6	1746.0	1663.6	1167.3
Sc	0.0	0.0	0.0	132.7	2.5	0.0	0.0	0.0	**10.0**	70.3	14.7	0.0	19.2
Sn	231.8	52.8	630.6	634.0	98.2	48.8	112.4	27.6	456.6	**712.8**	783.2	353.8	345.2
Ss	35.4	23.4	180.6	643.8	25.4	0.0	7.6	134.8	166.2	210.4	**409.6**	163.6	166.7
Nv	398.2	221.8	637.2	1375.4	245.6	147.8	221.2	484.8	1215.6	811.8	733.0	**559.7**	587.7
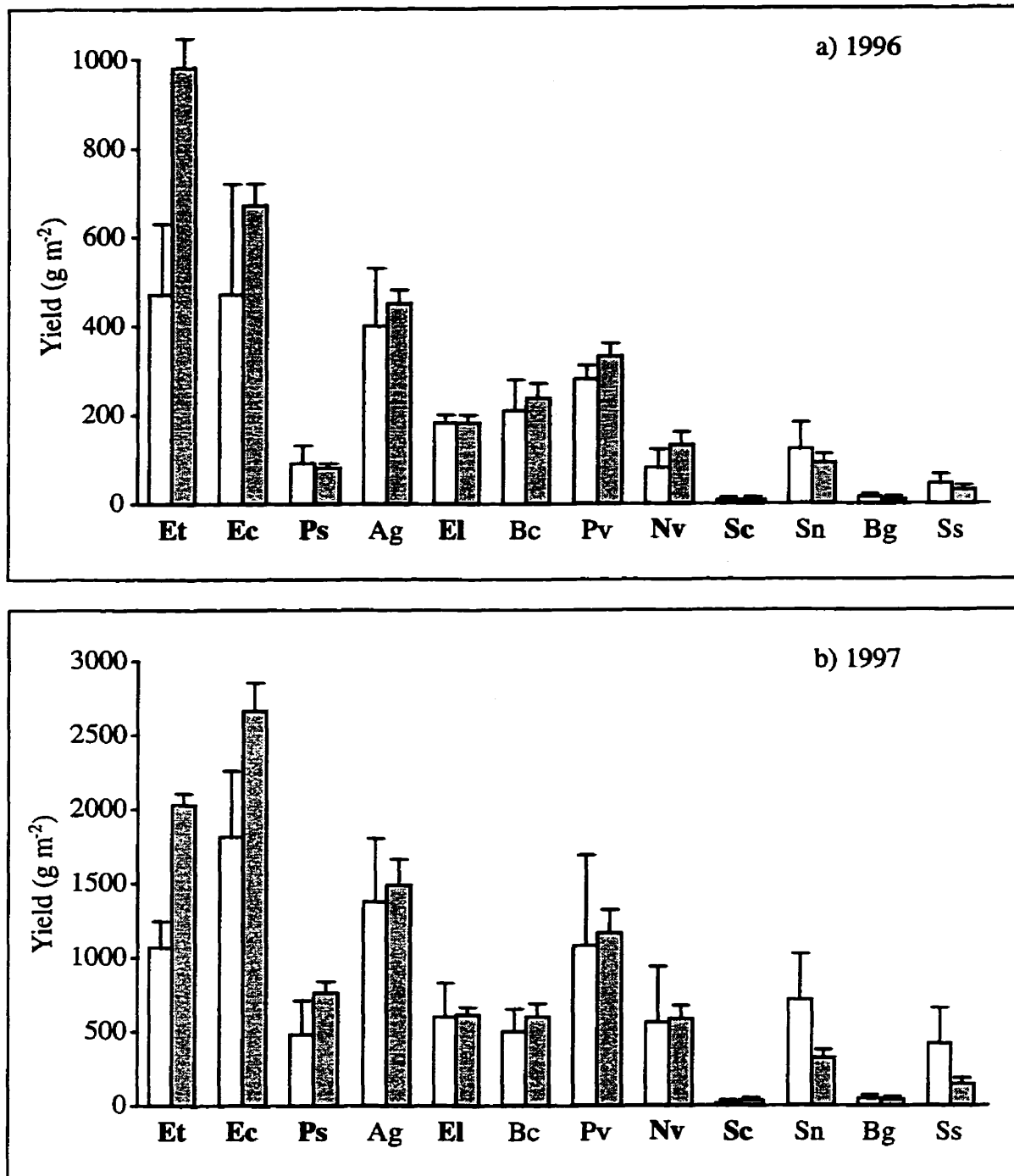
Figure 3.14. Mean above-ground dry biomass (+/- s.e.) of 12 native grasses grown in Winnipeg in 1996 (a) and 1997 (b). Means were calculated from all pair-wise possible mixtures (shaded bars; n = 33) and monocultures (unshaded bars; n = 3). Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*. Species codes in bold represent C3 species; non-bolded codes represent C4 species. Species are ordered from strong (left) to weak (right) competitive ability, based on the 1997 STRONG hierarchy (Fig. 3.21).
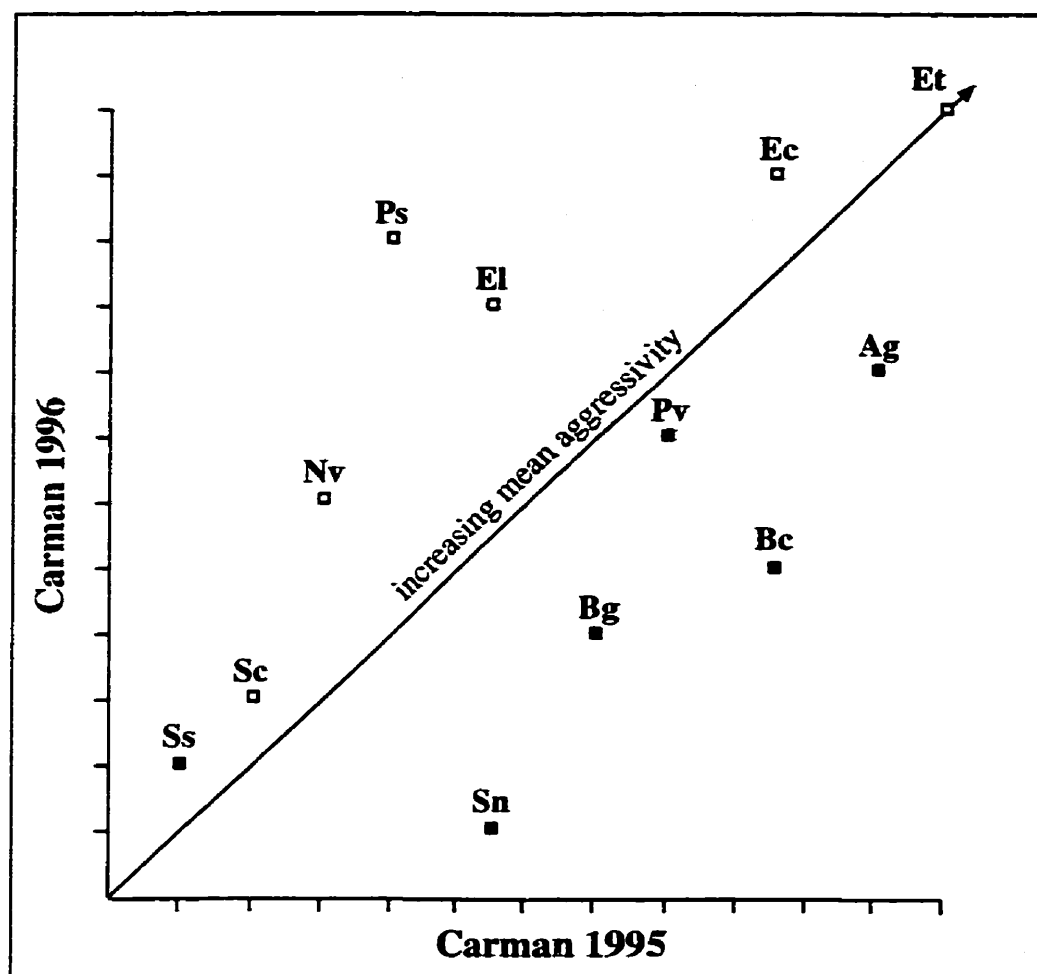
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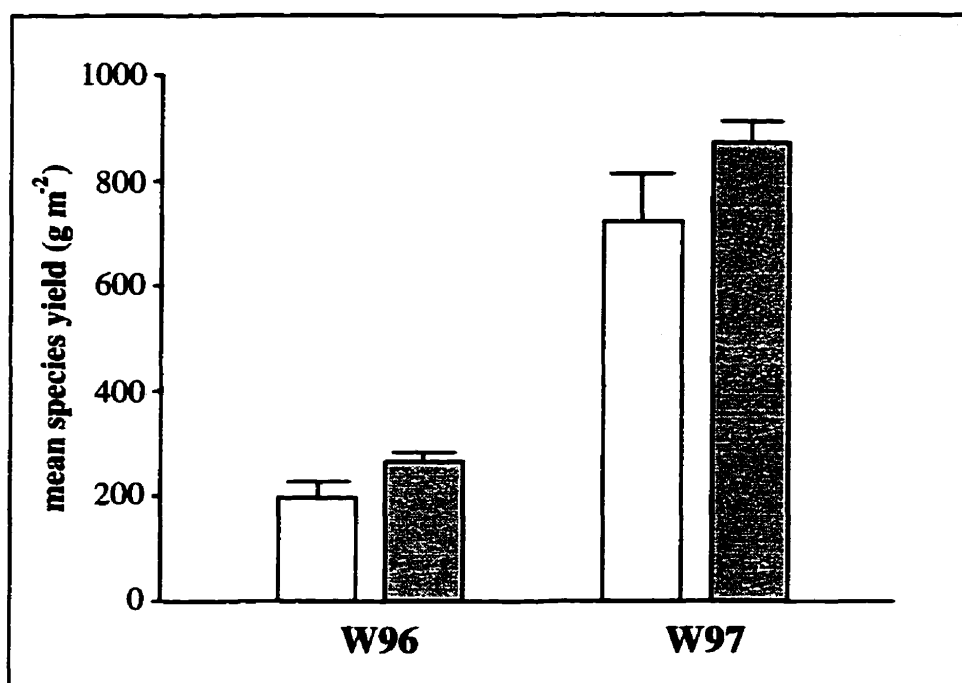
Figure 3.15. Mean total above-ground dry biomass (+/- s.e.) of 12 native grasses grown in Winnipeg in 1996 (W96) and 1997 (W97). Unshaded bars represent species grown in monoculture; shaded bars represent species grown in all pairwise combinations.

from year I to II, some species did appear to increase more than others (**Table 3.4**). *P. smithii* increased the greatest amount (year I mass/year II mass = 9.4), while *E. trachycaulus* increased by the least amount (year I mass/year II mass = 2.1). Finally, two-sample t-tests indicate that mean mixture yields were significantly greater than mean monoculture yields in both years I (p = .049) and II (p = .005; **Fig. 3.15**).

Relative Yields

Target scores in year I were greatest for *E. trachycaulus, E. canadensis, A. gerardii,* and *P. virgatum* (**Table 3.9**; **Fig. 3.16**). The lowest neighbour scores (i.e. the strongest 'suppressers' of other species) were attained by *E. trachycaulus* and *E. canadensis* (**Fig. 3.17**). In year II, the highest target scores were attained, in descending order, by *E. trachycaulus, E. canadensis, P. smithii,* and *E. lanceolatus* (**Table 3.9**; **Fig. 3.16**). The lowest neighbour scores in year II were again attained by *E. trachycaulus* and *E. canadensis,* and *P. smithii* (**Fig. 3.17**). Exclusion of *S. scoparium, S. comata,* and *B. gracilis* is again evidenced by low relative yield values for these species (**Table 3.9**). These same three species also had the lowest mean relative yields in years I and II. Rank orders of species relative yields between years I and II were highly correlated ($\rho = 0.861$; p < 0.001; **Fig. 3.18**). Species that remained at relatively constant positions tended to be at the ends of the relative yield scale. For example, *E. canadensis, E. trachycaulus, and A. gerardii* are amongst the strongest competitors based on relative yields; *S. scoparium, S. comata, B. gracilis,* and *S. nutans* are amongst the weakest competitors.

Aggressivity

The magnitude of aggressivity values from year I (**Table 3.10a**) ranged from 0.00 (*N. viridula* and *P. virgatum*) to 0.55 (*E. trachycaulus* with *B. gracilis*). In year II (**Table 3.10b**), values ranged from 0.01 (*P. virgatum* and *A. gerardii*) to 0.57 (*N. viridula* with *S. comata*). Mean aggressivity values for years I and II (**Fig. 3.19**) show that *E. trachycaulus* and *E. canadensis* were the strongest competitors in both years, while *S. scoparium* and *B. gracilis* were the poorest competitors. Rank correlation between mean aggressivity values between years I and II (**Fig. 3.20**) was strong and positive ($\rho = 0.908$; p < 0.001). As with relative yield values, the most consistent species from years I to II were at the peripheral ends of the aggressivity gradient (e.g. *N. viridula* to *S. comata* and *B. gracilis* at the low end, and *E. canadensis, E. trachycaulus* and *A. gerardii* at the high

Table 3.9. Matrix of relative yields from Winnipeg 1996 (a), and 1997 (b). Values are given for species in first column when grown in mixture with species in first row. Codes: Ag = *Andropogon gerardii* , Bc = *Bouteloua curtipendula* , Bg = *Bouteloua gracilis* , Ec = *Elymus canadensis* , El = *Elymus lanceolatus* , Et = *Elymus trachycaulus* , Nv = *Nassella viridula* , Ps = *Pascopyrum smithii* , Pv = *Panicum virgatum* , Sc = *Stipa comata* , Sn = *Sorghastrum nutans* , Ss = *Schizachyrium scoparium* , t.s. = target scores, n.s. = neighbour scores.

a)

	El	Ag	Bc	Bg	Ec	Et	Ps	Pv	Sc	Sn	Ss	Nv	t.s.
El	-	0.85	1.00	1.12	0.92	0.30	1.01	0.88	1.17	1.11	1.03	0.84	0.93
Ag	0.95	-	1.05	1.06	0.89	0.57	1.05	1.00	1.07	1.08	1.08	1.03	0.99
Bc	0.91	0.90	-	1.18	0.88	0.36	0.99	1.02	1.08	1.08	1.16	1.03	0.96
Bg	0.74	0.59	0.66	-	0.75	0.00	0.81	0.28	1.34	1.31	1.07	0.87	0.77
Ec	1.09	1.14	1.06	0.99	-	0.89	1.11	1.10	1.10	1.13	0.99	0.94	1.05
Et	1.13	1.09	1.10	1.10	1.16	-	1.11	1.17	1.10	1.16	1.17	1.14	1.13
Ps	0.91	0.82	0.93	1.11	0.42	0.35	-	0.85	1.10	1.20	1.07	1.02	0.89
Pv	0.89	0.99	1.09	1.10	0.98	0.59	0.94	-	1.13	1.04	1.05	1.13	0.99
Sc	0.13	1.20	0.00	2.37	0.32	0.02	0.19	0.44	-	0.66	0.40	1.22	0.63
Sn	0.95	0.63	0.92	0.81	0.42	0.16	1.01	0.88	1.06	-	0.93	1.20	0.81
Ss	0.71	0.28	0.68	1.28	0.55	0.00	0.39	0.87	1.07	1.24	-	0.64	0.70
Nv	0.80	0.94	1.06	1.18	0.26	0.28	1.26	1.44	1.22	1.19	0.99	-	0.96
n.s.	0.84	0.86	0.87	1.21	0.69	0.32	0.90	0.90	1.13	1.11	0.99	1.01	x

b)

	El	Ag	Bc	Bg	Ec	Et	Ps	Pv	Sc	Sn	Ss	Nv	t.s.
El	-	0.98	1.06	1.05	0.88	0.65	0.92	0.99	1.06	1.06	1.04	1.05	0.98
Ag	1.00	-	1.02	1.06	0.82	0.67	0.97	0.96	1.10	1.04	1.10	1.02	0.98
Bc	0.95	0.91	-	1.20	0.57	0.62	0.79	1.07	1.11	1.09	1.09	1.08	0.95
Bg	0.80	0.93	0.15	-	0.00	0.00	0.00	0.26	1.44	0.76	1.13	0.96	0.59
Ec	1.03	1.05	1.09	1.12	-	0.88	1.03	1.08	1.06	1.08	1.07	1.04	1.05
Et	1.13	1.06	1.11	1.10	1.07	-	1.09	1.10	1.11	1.09	1.12	1.11	1.10
Ps	1.07	1.07	1.15	1.15	0.74	0.58	-	1.01	1.13	1.13	1.11	1.17	1.03
Pv	0.97	0.94	1.05	1.11	0.78	0.71	0.86	-	1.10	1.03	1.07	1.07	0.97
Sc	0.00	0.00	0.00	2.35	0.46	0.00	0.00	0.00	-	2.00	1.19	0.00	0.54
Sn	0.81	0.56	0.98	0.98	0.67	0.55	0.69	0.46	0.92	-	1.02	0.88	0.77
Ss	0.55	0.48	0.85	1.08	0.49	0.00	0.29	0.79	0.83	0.88	-	0.83	0.64
Nv	0.94	0.84	1.02	1.16	0.85	0.77	0.84	0.97	1.14	1.07	1.05	-	0.97
n.s.	0.84	0.80	0.86	1.21	0.67	0.49	0.68	0.79	1.09	1.11	1.09	0.93	x
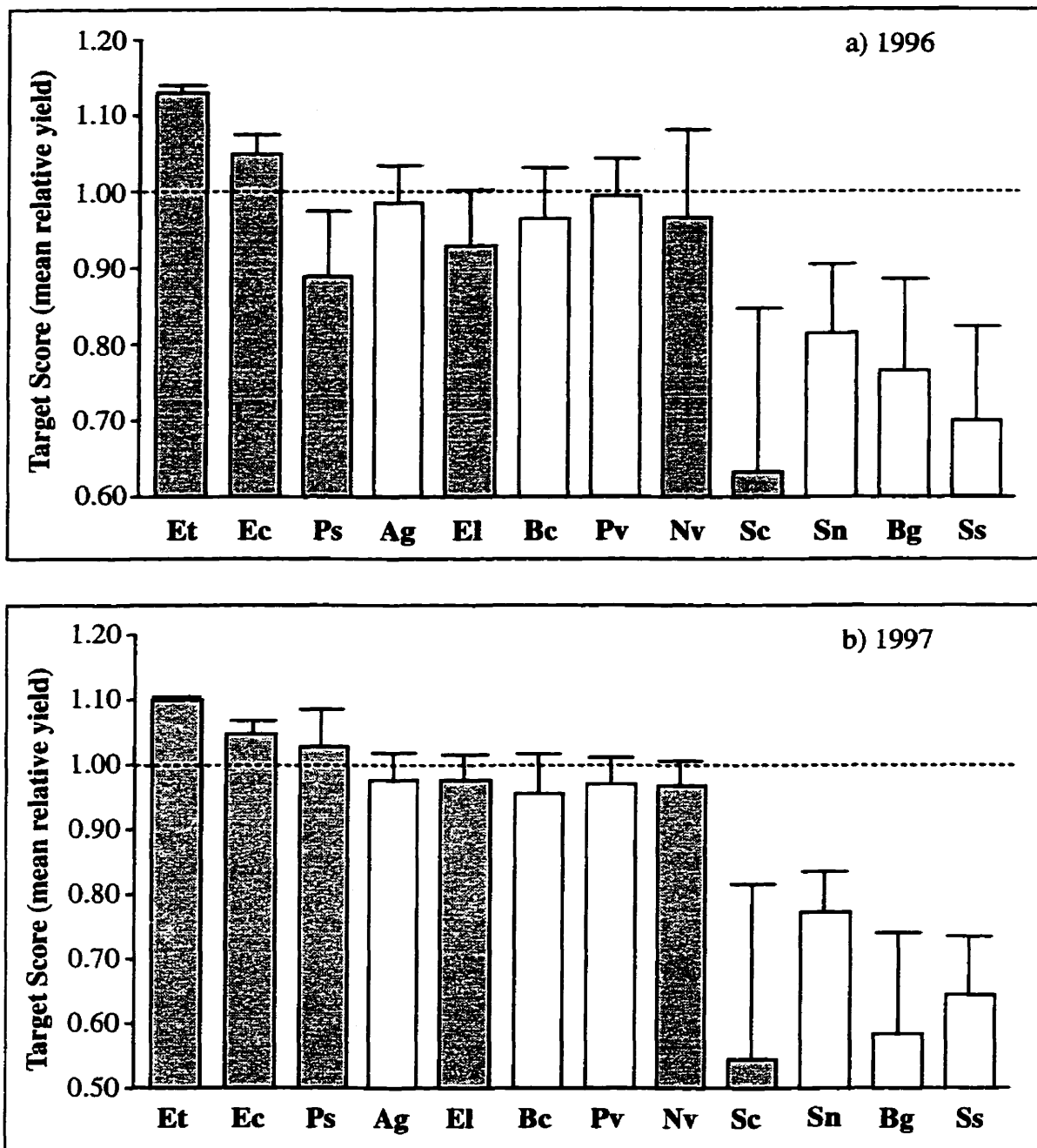
Figure 3.16. Target scores (+/- s.e.) of 12 native grasses grown in Winnipeg in 1996 (a) and 1997 (b). Means for each species were calculated from 11 possible pair-wise mixtures. Species whose target scores exceed 1.00 (dotted line) tend to have higher yields in mixture than in monoculture; those below 1.00 tend to have higher yields in monoculture than in mixture. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = 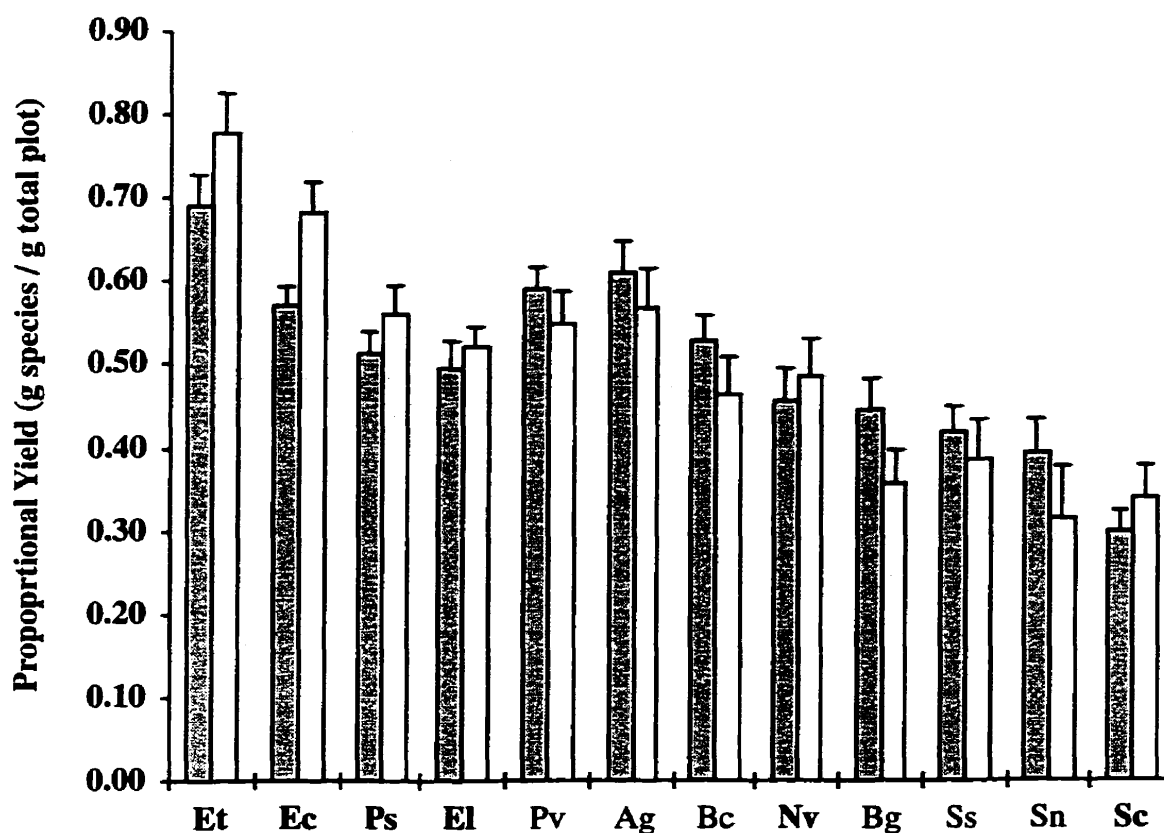*Sorghastrum nutans*, Ss = *Schizachyrium scoparium*. Shaded bars represent C3 species; un-shaded bars represent C4 species. Species are ordered from strong (left) to weak (right) competitive ability, based on the 1997 STRONG hierarchy (Fig. 3.21).

Figure 3.17. Neighbour scores (+/- s.e.) of 12 native grasses grown in Winnipeg in 1996 (a) and 1997 (b). Means for each species were calculated from 11 possible pair-wise mixtures. Species whose neighbour scores exceed 1.00 (dotted line) tend to have neighbour species with higher yields in mixture than in monoculture; those below 1.00 tend to have neighbour species with higher yields in monoculture than in mixture. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*. Shaded bars represent C3 species; un-shaded bars represent C4 species. Species are ordered from strong (left) to weak (right) competitive ability, based on the 1997 STRONG hierarchy (Fig. 3.21).

Figure 3.18. Mean relative yields (target scores) of 12 native grasses grown in all pairwise combinations in Winnipeg in 1996 and 1997, ranked from lowest values (bottom, left) to greatest values (top, right). *rho* = 0.861, p < 0.005. Species with differences in mean relative yields < 0.005 were considered to be equal. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*. Black squares indicate C4 species; white squares indicate C3 species.

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Table 3.10. Matrix of aggressivities from Winnipeg 1996 (a), and 1997 (b). Values are given for species in first column when grown in mixture with species in first row. Codes: Ag = *Andropogon gerardii* , Bc = *Bouteloua curtipendula* , Bg = *Bouteloua gracilis* , Ec = *Elymus canadensis* , El = *Elymus lanceolatus* , Et = *Elymus trachycaulus* , Nv = *Nassella viridula* , Ps = *Pascopyrum smithii* , Pv = *Panicum virgatum* , Sc = *Stipa comata* , Sn = *Sorghastrum nutans* , Ss = *Schizachyrium scoparium* .

a)

	El	Ag	Bc	Bg	Ec	Et	Ps	Pv	Sc	Sn	Ss	Nv	mean
El	-	-0.05	0.05	0.19	-0.08	-0.42	0.05	0.00	0.52	0.08	0.16	0.02	0.05
Ag	0.05	-	0.08	0.23	-0.13	-0.26	0.12	0.01	-0.06	0.22	0.40	0.05	0.06
Bc	-0.05	-0.08	-	0.26	-0.09	-0.37	0.03	-0.04	0.54	0.08	0.24	-0.01	0.05
Bg	-0.19	-0.23	-0.26	-	-0.12	-0.55	-0.15	-0.41	-0.51	0.25	-0.11	-0.15	-0.22
Ec	0.08	0.13	0.09	0.12	-	-0.14	0.34	0.06	0.39	0.36	0.22	0.34	0.18
Et	0.42	0.26	0.37	0.55	0.14	-	0.38	0.29	0.54	0.50	0.58	0.43	0.41
Ps	-0.05	-0.12	-0.03	0.15	-0.34	-0.38	-	-0.04	0.46	0.10	0.34	-0.12	0.00
Pv	0.00	-0.01	0.04	0.41	-0.06	-0.29	0.04	-	0.34	0.08	0.09	-0.15	0.05
Sc	-0.52	0.06	-0.54	0.51	-0.39	-0.54	-0.46	-0.34	-	-0.20	-0.33	0.00	-0.25
Sn	-0.08	-0.22	-0.08	-0.25	-0.36	-0.50	-0.10	-0.08	0.20	-	-0.16	0.00	-0.15
Ss	-0.16	-0.40	-0.24	0.11	-0.22	-0.58	-0.34	-0.09	0.33	0.16	-	-0.18	-0.15
Nv	-0.02	-0.05	0.01	0.15	-0.34	-0.43	0.12	0.15	0.00	0.00	0.18	-	-0.02

b)

	El	Ag	Bc	Bg	Ec	Et	Ps	Pv	Sc	Sn	Ss	Nv	mean
El	-	-0.01	0.05	0.12	-0.07	-0.24	-0.07	0.01	0.53	0.12	0.25	0.05	0.07
Ag	0.01	-	0.06	0.06	-0.11	-0.20	-0.05	0.01	0.55	0.24	0.31	0.09	0.09
Bc	-0.05	-0.06	-	0.53	-0.26	-0.24	-0.18	0.01	0.55	0.06	0.12	0.03	0.05
Bg	-0.12	-0.06	-0.53	-	-0.56	-0.55	-0.57	-0.42	-0.46	-0.11	0.02	-0.10	-0.31
Ec	0.07	0.11	0.26	0.56	-	-0.10	0.15	0.15	0.30	0.21	0.29	0.09	0.19
Et	0.24	0.20	0.24	0.55	0.10	-	0.26	0.20	0.56	0.27	0.56	0.17	0.30
Ps	0.07	0.05	0.18	0.57	-0.15	-0.26	-	0.08	0.56	0.22	0.41	0.17	0.17
Pv	-0.01	-0.01	-0.01	0.42	-0.15	-0.20	-0.08	-	0.55	0.28	0.14	0.05	0.09
Sc	-0.53	-0.55	-0.55	0.46	-0.30	-0.56	-0.56	-0.55	-	0.54	0.18	-0.57	-0.27
Sn	-0.12	-0.24	-0.06	0.11	-0.21	-0.27	-0.22	-0.28	-0.54	-	0.07	-0.09	-0.17
Ss	-0.25	-0.31	-0.12	-0.02	-0.29	-0.56	-0.41	-0.14	-0.18	-0.07	-	-0.11	-0.22
Nv	-0.05	-0.09	-0.03	0.10	-0.09	-0.17	-0.17	-0.05	0.57	0.09	0.11	-	0.02
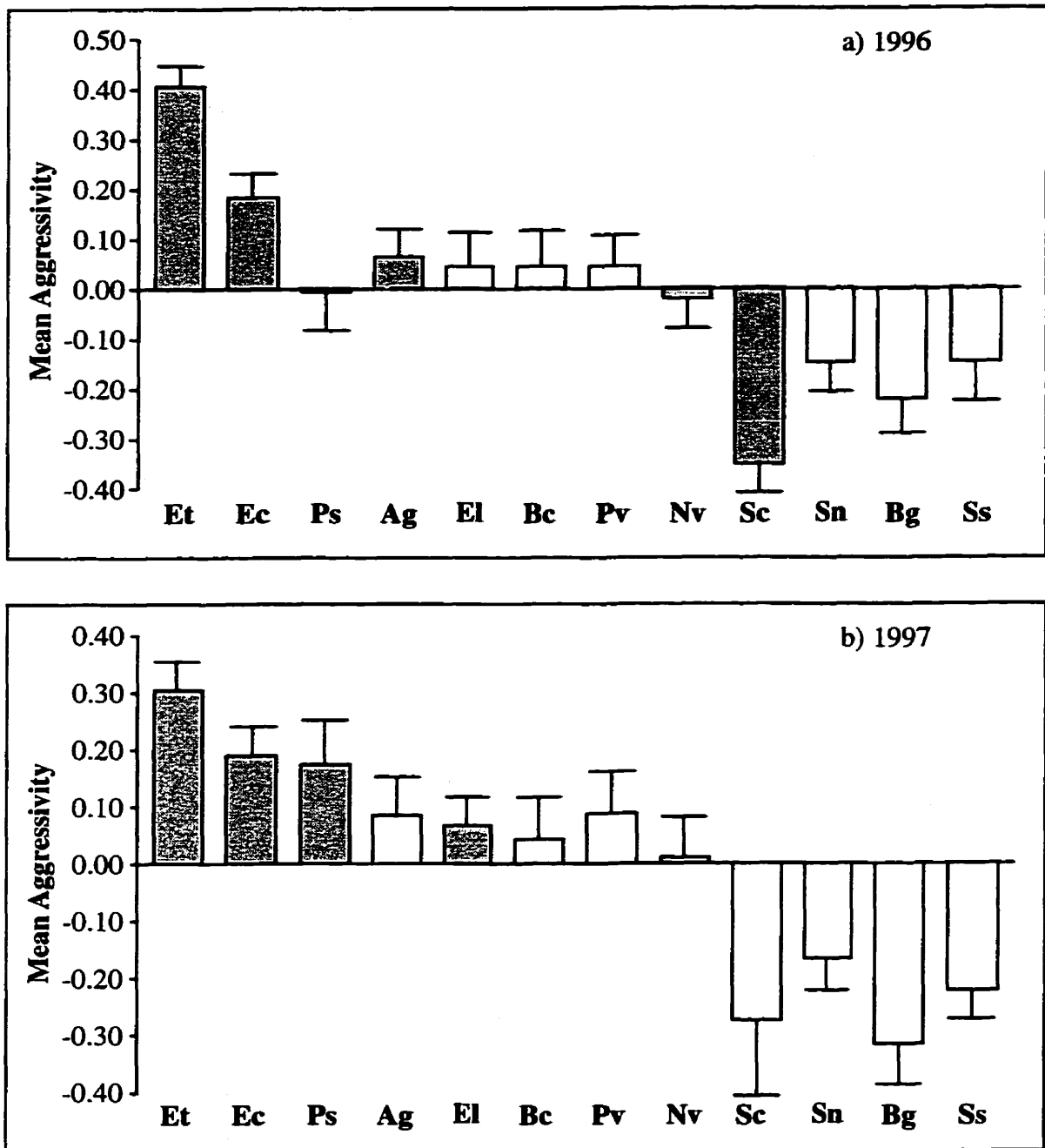
Figure 3.19. Mean aggressivity (+/- s.e.) of 12 native grasses grown in Winnipeg in 1996 (a) and 1997 (b). Means for each species were calculated from 11 possible pair-wise mixtures. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*. Shaded bars represent C3 species; un-shaded bars represent C4 species. Species are ordered from strong (left) to weak (right) competitive ability, based on the 1997 STRONG hierarchy (Fig. 3.21).

Figure 3.20. Mean aggressivities of 12 native grasses grown in all pairwise combinations in Winnipeg in 1996 and 1997, ranked from lowest values (bottom, left) to greatest values (top, right). *rho* = 0.908, p < 0.005. Species with differences in aggressivities < 0.005 were considered to be equal. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*. Black squares indicate C4 species; white squares indicate C3 species.

end). The greatest improvement in rank from year I to II was *P. smithii*, which increased from seventh place to third place. In year II, hierarchies of mean aggressivity were found to be highly positively correlated with species monoculture yields ($\rho = 0.734$; $p < 0.005$).

Transitivity Analysis

Transitivity analysis indicated a high number of transitive hierarchies within Winnipeg (**Table 3.7**). In year I, the largest completely transitive hierarchy found involved ten species ($p < 0.0001$; **Fig. 3.21**). By year II, a completely transitive hierarchy involving all twelve species was found ($p < 0.0001$; **Fig. 3.22**). This hierarchy was correlated with species monoculture yields ($\rho = 0.615$; $p = 0.025$). Under the null hypothesis of random species interactions, the largest transitive hierarchies expected (i.e. $p \geq 0.05$) would involve no more than six species (**Table 3.7**).

Non-metric Multidimensional Scaling

Non-metric multidimensional scaling ordination of the Winnipeg II aggressivity matrix, with the transitive hierarchy superimposed (**Fig. 3.23**) shows a non-linear/non-additive trend in pairwise aggressivity values, which is fairly representative of actual pairwise distances (stress $= 15.6\%$). *E. trachycaulus*, *E. canadensis*, and *P. smithii* co-occur at the 'strong' end of the competitive gradient. At the opposite end weak competitors such as *S. nutans*, *B. gracilis*, and *S. scoparium* occur. Intermediate competitors appear to be clustered towards the bottom and center of the ordination diagram. *S. comata* (the weakest competitor according to relative yields and aggressivity values) is an outlier, likely due to its relatively poor performance with stronger competitors, but relatively strong performance with weaker competitors such as *B. gracilis*, *S. nutans*, and *S. scoparium* (**Table 3.10**).

Species Mixture Productivity Trajectories

Species mean proportional yields at Winnipeg (**Fig. 3.24**) were generally reflective of the competitive hierarchy models developed using aggressivity values, although not as consistently as in Carman. At Winnipeg, three of the six poorest competitors, based on year II aggressivity values, decreased in mean proportional yield from year I to year II. Of the six strongest competitors, *P. smithii*, *P. virgatum*, and *E. lanceolatus* increased in mean proportional yield from year I to year II. Although the other strong competitors decreased

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STRONGEST ↑ Et

Ec

Ag

Pv

El

Bc

Ps

Ss

Bg

WEAKEST Sn
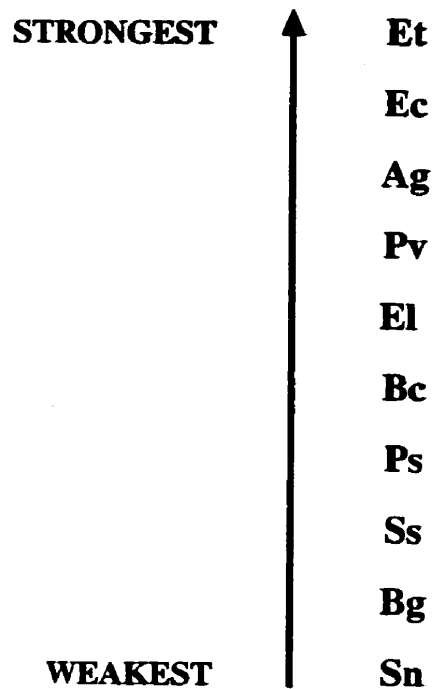
Figure 3.21. The largest completely transitive competitive hierarchy from the Winnipeg
1996 binary aggressivity matrix. Arrow points to the direction of the strongest
competitor. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg =
Bouteloua gracilis, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus
trachycaulus*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sn = *Sorghastrum
nutans*, Ss = *Schizachyrium scoparium.*

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STRONGEST   ↑   **Et**

Ec

Ps

Ag

El

Bc

Pv

Nv

Sc

Sn

Bg

WEAKEST   **Ss**
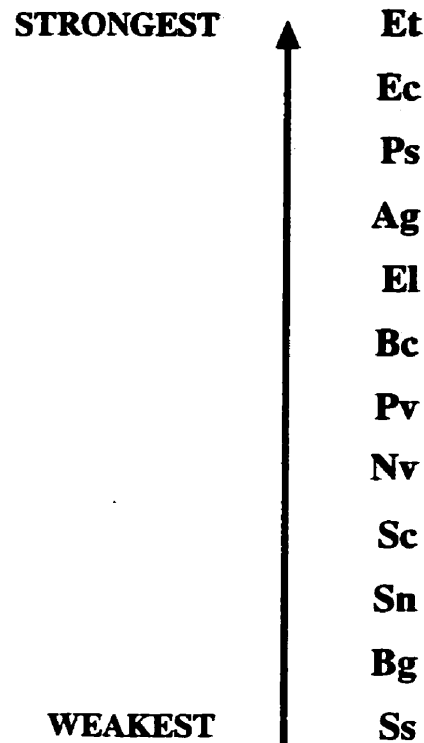
Figure 3.22. The completely transitive competitive hierarchy from the binary aggressivity matrix of Winnipeg 1997. Direction of arrow indicates increasing competitive ability. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*.
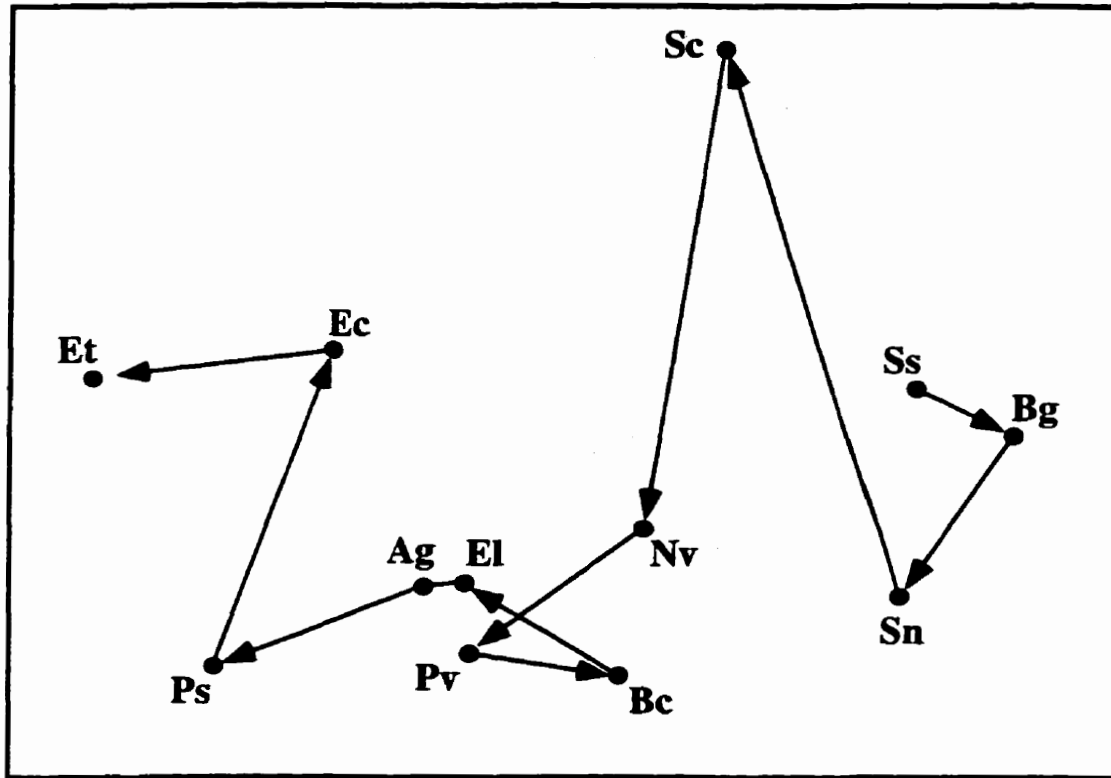
Figure 3.23. Non-metric multidimensional scaling ordination (stress = 15.6%) of aggressivity values from Winnipeg 1997 (Table 3.10). Species are connected according to the transitive competitive hierarchy developed from aggressivity values from The Point 1997 (Fig. 3.22). The arrow points in the direction of increasing competitive ability. Codes: Ag = *Agropyron gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymuscanadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*.
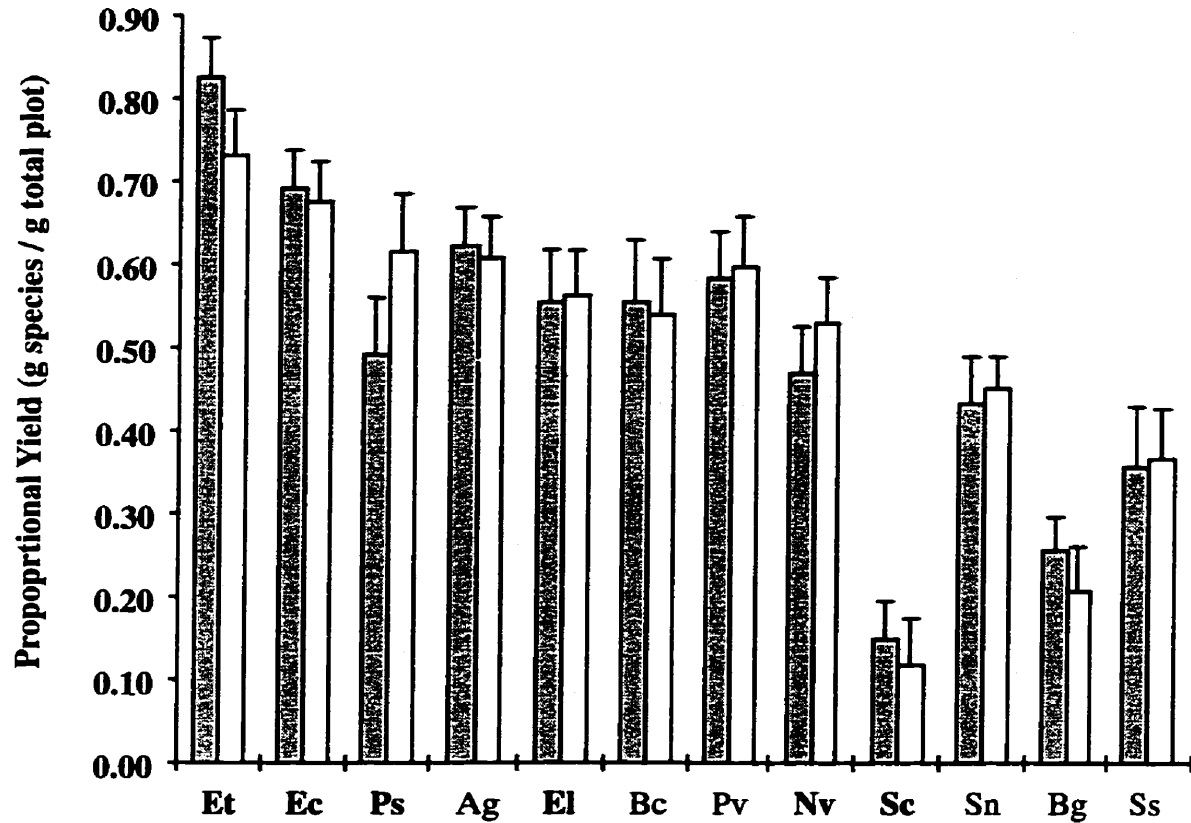
Figure 3.24. Species mean proportional yield in mixture (+/- s.e) in Winnipeg in 1996 (grey bars) and 1997 (white bars). Means were calculated from all pairwise combinations. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*. Bolded codes indicate C3 species. Species are ordered from strong (left) to weak (right) competitive ability, based on the 1997 STRONG hierarchy (Fig. 3.21).

somewhat, these decreases are far less significant than similar decreases seen in species having low proportional yields in year I (e.g. a drop from 97% to 92% is prop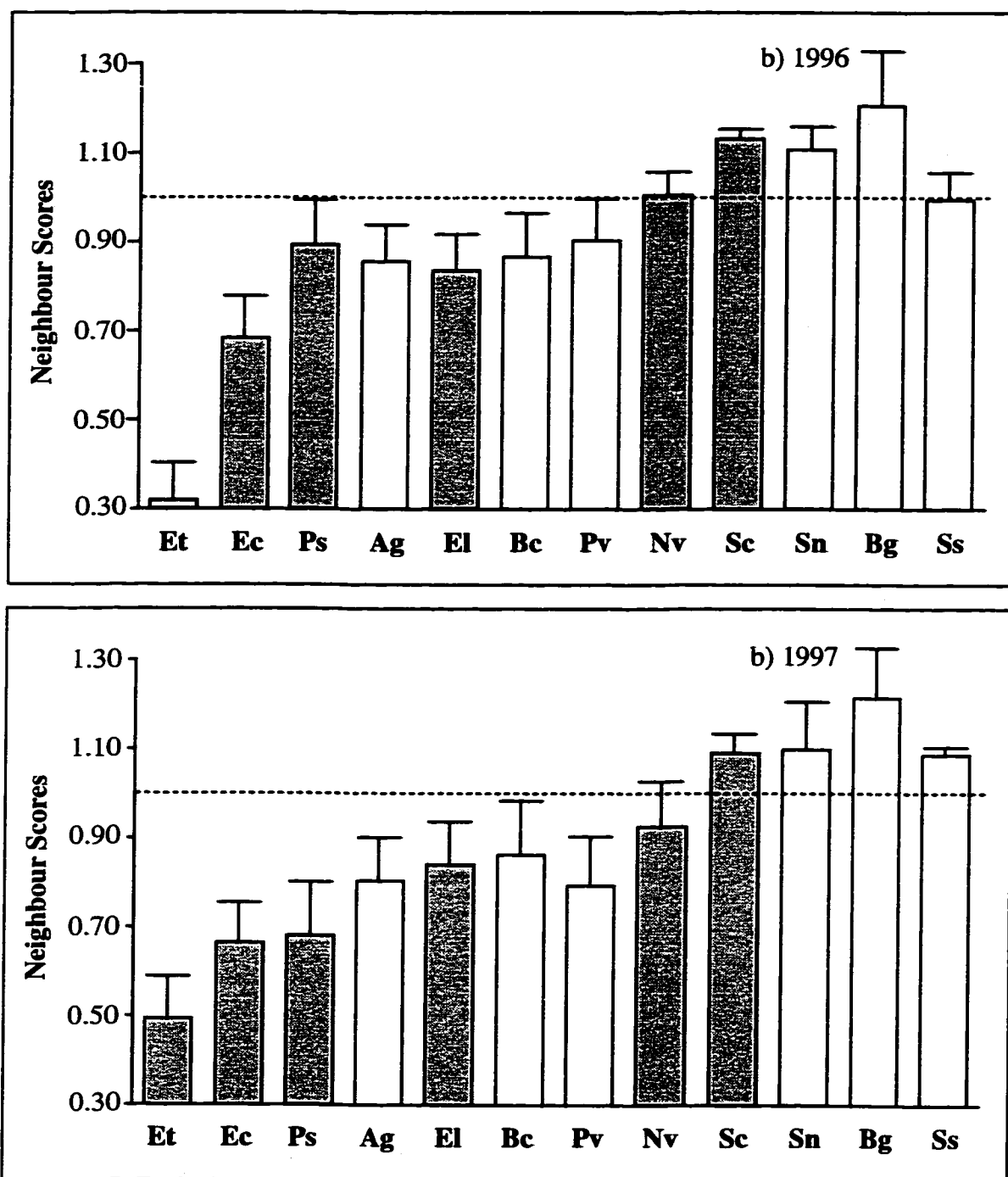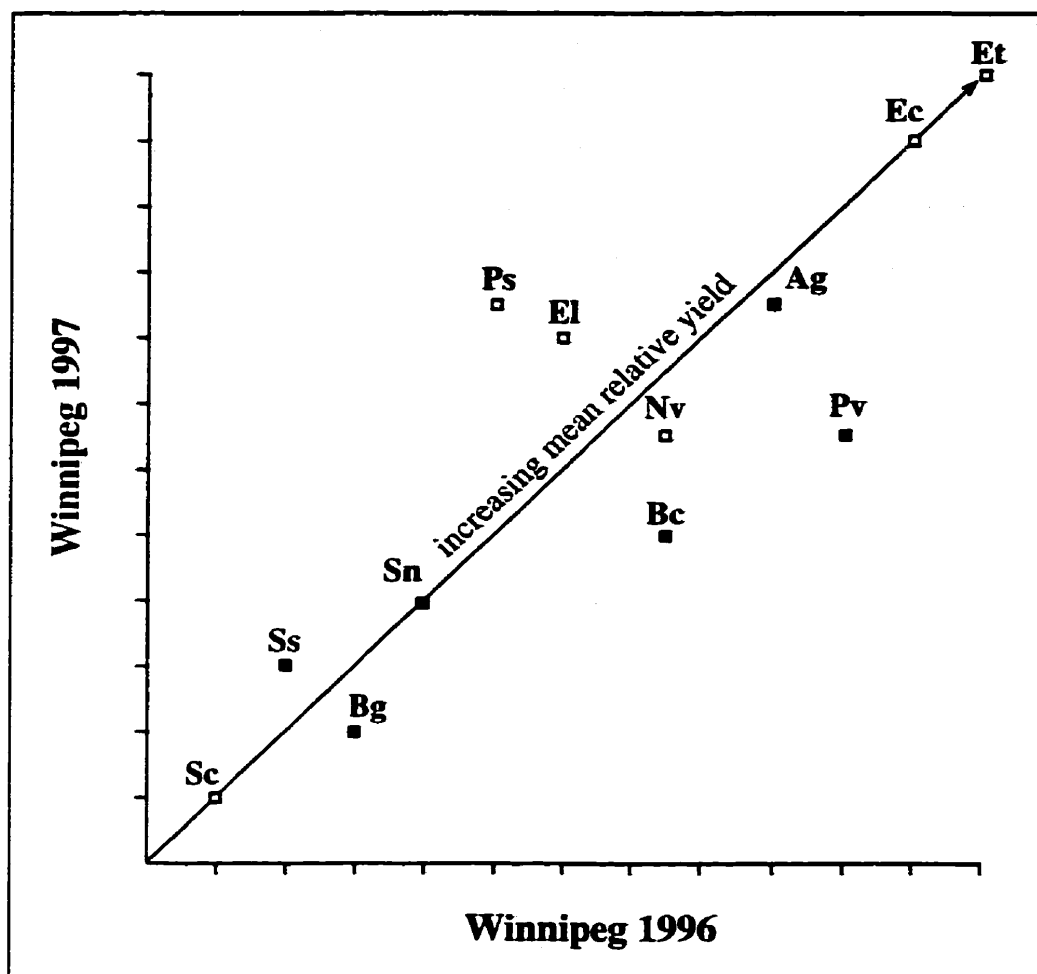ortionately less of a drop than from 10% to 5%, even though the magnitude of change is the same). Species that consistently increased in proportion between years I and II at both Winnipeg and Carman included *P. smithii*, *E. lanceolatus*, and *N. viridula*, all C_3 species. Species that consistently decreased in proportion were *A. gerardii*, *B. curtipendula*, and *B. gracilis*, all of which are C_4 species. Species that were inconsistent in their year to year trends within sites included *E. trachycaulus*, *E. canadensis*, *P. virgatum*, *S. nutans*, *S. scoparium*, and *S. comata*.

Summary

The ordering of species competitive abilities at Winnipeg was relatively consistent using relative yield values, aggressivity values, or transitivity analyses. The competitive relations between years were more consistent at Winnipeg relative to Carman. As in Carman, the three approaches in determining competitive hierarchies showed a consistent relationship between competitive ability, plant size and photosynthetic pathway types. Large-statured C_3 species (i.e. *E. canadensis*, *E. trachycaulus*, *E. lanceolatus*, and *P. smithii*) were consistently the strongest competitors, while small-statured C_4 species (i.e. *B. gracilis*, *S. scoparium*, and *S. nutans*) consistently appear to be the poorest competitors. Larger-statured C_4 species (i.e. *A. gerardii*, *B. curtipendula*, *P. virgatum*) and smaller-statured C_3 species (i.e. *N. viridula*) are of intermediate competitive ability. As in Carman, the exception to this rule is *S. comata*, which is a C_3 species that performs poorly in both years likely due to its comparatively small size.

In answer to Connolly's (1997) criticism of relative yields falsely inferring dominance and competitive exclusion, the same pattern of dominance and subordinance observed using relative yields, aggressivity values, and transitivity analysis was observed (although not as strongly as in Carman) in changes in species proportional yields over time, irrespective of monoculture values. Large species such as *P. smithii*, *E. lanceolatus*, and *P. virgatum* became more dominant by increasing their proportional yields over time. Species that decreased in proportional yield over time included *A. gerardii*, *B. curtipendula*, and *B. gracilis*, all of which are C_4 species. *S. comata*, a poor C_3 competitor based on relative yields and aggressivity values, also decreased its proportional yield from year I to II, likely due to its comparatively small size. The two strongest competitors based on relative yields, aggressivity values, and transitivity analysis (*E. trachycaulus* and *E. canadensis*) actually

decreased their proportional yields in mixture over time, indicating that perhaps the performance of initially strong C_3 competitors may decrease over time.

3.5.3 Robustness of Competitive Hierarchies

Productivity

Total productivity values at Carman and Winnipeg are presented in **Fig. 3.25**. In year I, Carman had roughly 50% of the productivity of Winnipeg (9.8 kg vs. 18.7 kg). In year II, biomass harvested from both sites differed by only 1.2 kg (1.9%), with Carman having slightly more biomass than Winnipeg.

Aggressivity and Transitivity

The transitive hierarchies based on year II aggressivity values are strongly and positively correlated between Carman and Winnipeg (**Fig. 3.26**; $\rho = 0.887$, $p < 0.001$), indicating consistency in rank orders despite differences in climatic and edaphic conditions. Generally, species can be divided into three groups (strong, intermediate, and weak competitors) based on relative competitive abilities. Strong competitors included *E. trachycaulus*, *E. canadensis*, *P. smithii*, and *E. lanceolatus* -- all highly productive C_3 species (**Figs. 3.3, 3.14**). Weak competitors included *S. scoparium*, *B. gracilis*, *S. nutans*, and *S. comata*, all small-statured C_4 species, except *S. comata*. *S. comata* is likely amongst the poorest competitors because of its low productivity -- it is the lowest-productivity species (in monoculture) of the all species in this study (**Figs. 3.3, 3.14**). Intermediate competitors included *P. virgatum*, *A. gerardii*, *B. curtipendula*, and *N. viridula*, the later being the only C_3 species in this group. Species within this group are of intermediate to high productivity in monoculture (**Fig.'s 3.3, 3.14**).

Asymmetry

Mean asymmetry values at both sites increased from year I to year II (**Fig. 3.27**). These differences were significant at Carman ($p = 0.0023$), but not at Winnipeg ($p = 0.4628$). Asymmetry values at Carman I were roughly half those of Winnipeg I ($p \leq 0.0001$), while those of Carman II were three quarters those of Winnipeg II ($p = 0.063$), indicating that
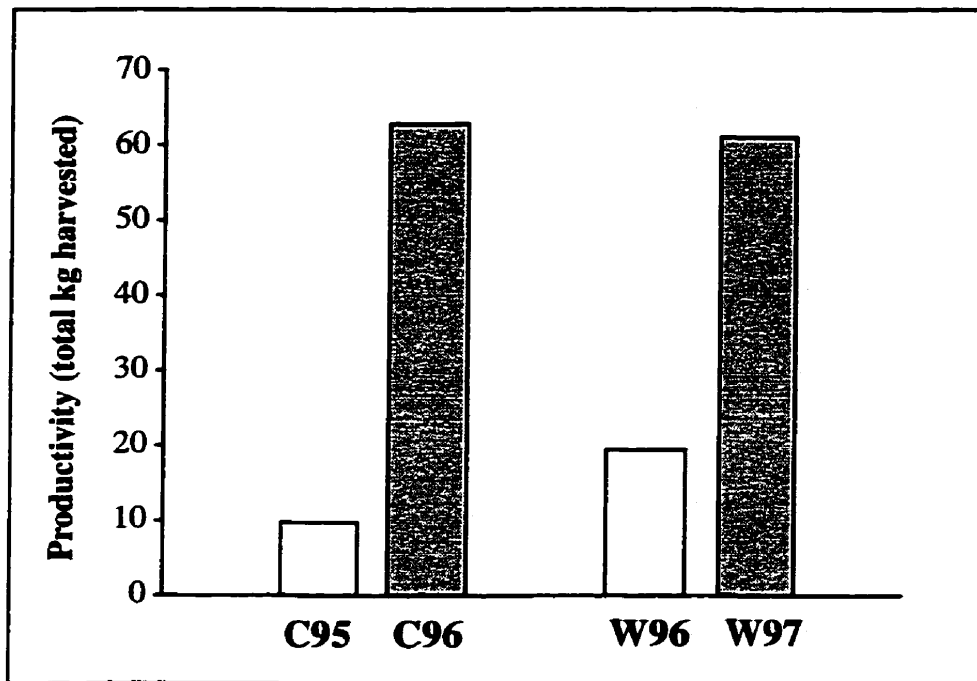
Figure 3.25. Total productivity, measured as the total harvested above-ground dry weight, of 12 native grasses within two diallel competition experiments. Plants were harvested at Carman in 1995 (C95) and 1996 (C96), and in Winnipeg in 1996 (W96) and 1997 (W97).
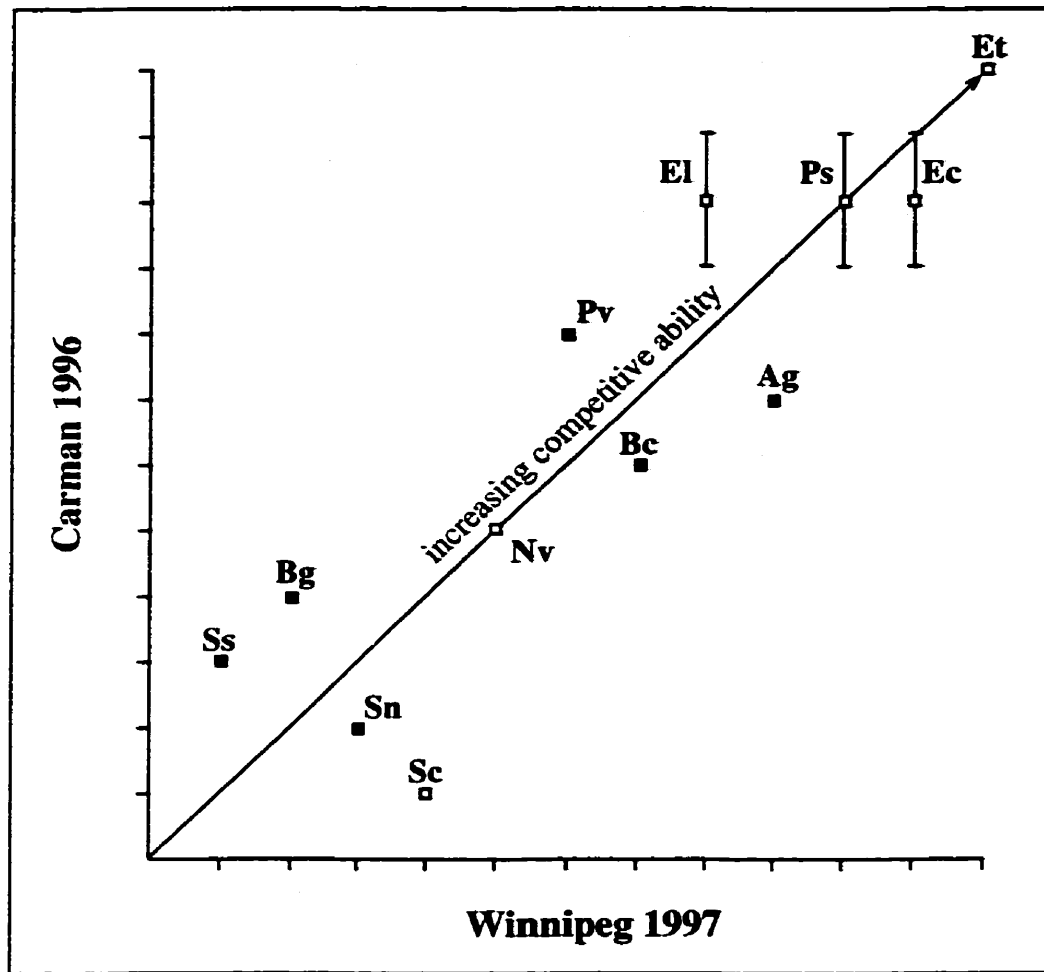
Figure 3.26. Rank correlation between the STRONG hierarchies from Winnipeg in 1997 and Carman 1996. *rho* = 0.887, p < .005. Ranks increase upwards and to the right. Codes: Ag = *Andropogon gerardii*, Bc = *Bouteloua curtipendula*, Bg = *Bouteloua gracilis*, Ec = *Elymus canadensis*, El = *Elymus lanceolatus*, Et = *Elymus trachycaulus*, Nv = *Nassella viridula*, Ps = *Pascopyrum smithii*, Pv = *Panicum virgatum*, Sc = *Stipa comata*, Sn = *Sorghastrum nutans*, Ss = *Schizachyrium scoparium*. Black boxes indicate C4 species; white boxes indicate C3 species. Species with 'error bars' are part of an intransitive loop along the Carman 1996 axis.
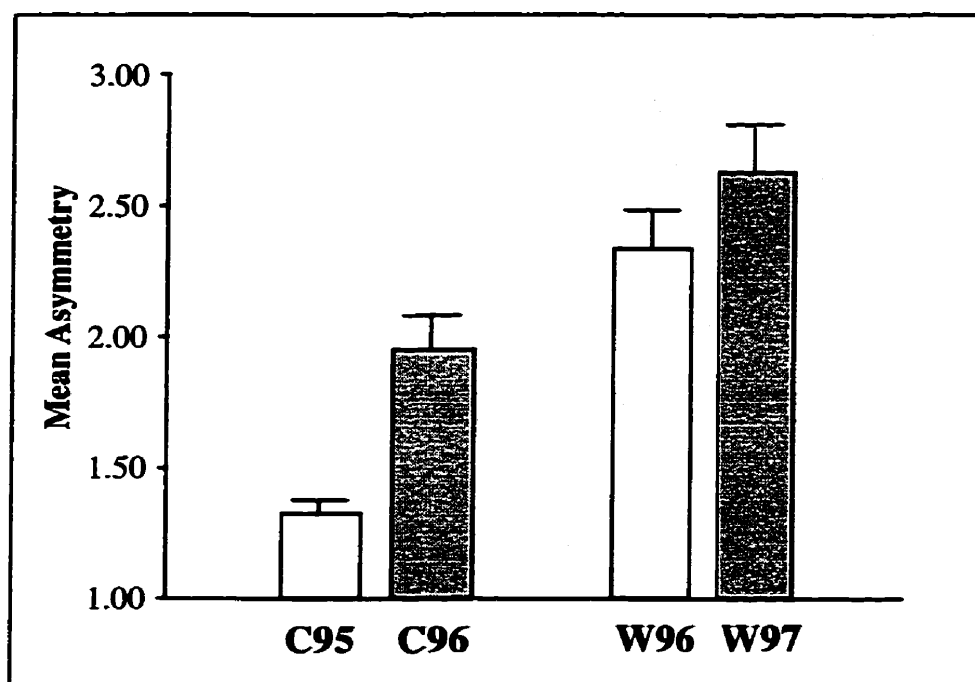
Figure 3.27. Mean competitive asymmetry (+/- s.e.) between 12 native grasses grown in pair-wise mixtures within two diallel competition experiments. Plants were harvested at Carman in 1995 (C95) and 1996 (C96), and in Winnipeg in 1996 (W96) and 1997 (W97).

asymmetry values tended to be initially greater at Winnipeg than at Carman in year I, but less so in year II.

3.6 Discussion

This study has demonstrated that for the twelve grasses studied, competitive hierarchies are present and are relatively consistent in both time and space. Despite these consistencies, three critical questions must be examined in more detail:

(1) What factors contribute to the spatial and temporal variability of competitive hierarchies?

(2) What traits render some species more competitive than others?

(3) What are the implications of these results for grassland restoration and management?

3.6.1 Spatial and Temporal Variability of Competitive Hierarchies

Variability in Time: Year 1 vs. Year 2

Within-site variability (i.e. from year 1 to 2) will likely be caused by changes in climatic conditions and/or changes in species interactive effects over time. At Carman, mean monthly precipitation from May to August increased slightly in year II (from 65.0 mm to 72.1 mm). The mean temperature over the same period decreased from 23.9 to 22.4°C. Cooler and wetter conditions at Carman in year II would result in greater soil moisture availability in the second year. One effect of these changing conditions may have been a shift from below-ground competition for moisture, to greater above-ground competition for light (Tilman 1984; Wisheu and Keddy 1992; Huston and DeAngelis 1994; Keddy et al. 1997). This shift would inevitably favour those species that could preempt the greatest amount of light from other species (i.e. species with high allocation to aboveground tissue production; Wedin and Tilman 1993). This is consistent with the high correlation between monoculture productivity and ranks in the competitive hierarchies of Carman in year II. Another potential effect of the changing climatic conditions towards cooler and wetter conditions at Carman is a favouring of C_3 species over C_4 species. This also was evidenced

in Carman: in year I, two of the four top competitors were C_4 species; in year II, all top four competitors were C_3 species. Furthermore, all of the species that improved in performance in year II were C_3 species (**Figs. 3.7, 3.9, 3.13**) Hence differences in competitive ranks from year 1 to 2 at Carman seem to be in agreement with the predicted effects of increasingly cooler and wetter climatic conditions.

At Winnipeg, a different story emerges. Mean monthly precipitation from May to August decreased from 78.6 mm in year I to 64.2 mm in year II, but daily maximum temperatures decreased only slightly from 23.9°C to 23.5°C. The predominant climatic effect at Winnipeg from year I to II was therefore decreased precipitation, and hence increased below-ground competition for moisture. Species allocating more energy to below-ground production would therefore be expected to be more competitive. However, high above-ground producers still managed to be the most competitive species at Winnipeg in year II. Furthermore, much like at Carman, C_3 species were more successful in year II at Winnipeg (although not to the same extent as in Carman), but this was *not* attributable to a drop in temperature. These results force us to question whether or not the degree of yearly variability in precipitation and temperatures seen at Carman and Winnipeg would be sufficient to account for the consistent shifts in competitive ability seen from year I to II at both sites.

The other potential cause of rank shifts in competitive hierarchies is changes in species interactions over time. Keddy (1989) hypothesized that competitive exclusion will likely occurs via a positive feed-back mechanism of increasing productivity for the dominant species coupled with decreasing productivity of the subordinate species. The implication of this feedback loop is that competitive asymmetry increases over time until the subordinate species are completely excluded. This hypothesis implies a consistent competitive ability, (and therefore a consistent competitive hierarchy) throughout the development of the community. Contrary to this hypothesis, Grace et al. (1992) found inconsistencies in competitive ranks of species over a three year period, although these changes were attributed to the use of relative yields in data analysis rather than to any changes in species performance over the experimental test period. Yet from observations made in the field, and our knowledge of community succession, should we not expect species competitive ability to change over time?

One example from this study that suggests we should is *P. smithii*. The yield of this species increased considerably in the second year, and it had the greatest shift in mean aggressivity rank between years at Winnipeg. In effect, the strong competitive ability of this species was not detected in year I. *P. smithii* appeared to invest much of its energy into below-ground production in year I. After this initial year of 'anchorage', when overall aboveground productivity (and hence light preemption by other species) was relatively low, it would have a solid foundation from which to launch its year II competitive 'assault'. Thus the competitive abilities of certain species, and the hierarchies of which they are a part, may change as the community develops. The observation that Carman's year II aggressivity hierarchy is more highly correlated with Winnipeg's year II hierarchy ($\rho = 0.895$; $p < 0.05$) than it is with its own hierarchy from year I ($\rho = 0.575$; $p < 0.05$) is consistent with this hypothesis, while simultaneously indicating that consistency of competitive hierarchies develops over time.

Variability in Space: Carman vs. Winnipeg

Between site variability (i.e. differences between Carman and Winnipeg) in competitive hierarchies will likely occur due to differences in climatic and edaphic conditions. One potentially significant difference in competitive hierarchies is the greater degree of consistency in species rank orders from year I to II at Winnipeg. Furthermore, there appears to be greater overall asymmetry at Winnipeg than at Carman. This was likely due to more rapid growth/establishment of all species in year I at Winnipeg, as evidenced by greater productivity at Winnipeg in year I as compared to Carman in year I. One factor that is known to increase competitive asymmetry is competition for light, mediated by the availability of below-ground resources -- as soil productivity increases, competition for light increases and becomes more asymmetric (Tilman 1984; Wisheu and Keddy 1992; Wedin and Tilman 1993; Keddy et al. 1997). In other words, there was a more rapid development of the competitive hierarchy in year I at Winnipeg, than in year I at Carman.

Several climatic and edaphic factors may have contributed to the more rapid development of the competitive hierarchy at Winnipeg. Mean monthly precipitation from May to August at Winnipeg in year I (1996) was substantially greater than that at Carman in year I (1995), 78.6 mm and 65.0 mm, respectively, and mean daily maximum temperature was lower at Winnipeg than at Carman in year I. These factors would result in greater relative moisture availability at Winnipeg I. Furthermore, the sandy loam soil at Carman is better drained

than the silty clays of Winnipeg, further increasing moisture availability at Winnipeg. With more rapid drainage at Carman, nutrient availability is also expected to be lower. This is in fact the case with Carman having 2.54 g kg^{-1} of available N in the rooting zone, and Winnipeg having 2.63 g kg^{-1}. Although this is not a large difference in fertility, relatively acidic soils at Carman (pH = 5.8) will further reduce effective N availability relative to Winnipeg (pH = 7.6). Overall, these differences in climatic and edaphic conditions could have resulted in increased symmetric competition for below-ground resources at Carman, and asymmetric competition for light at Winnipeg, resulting in the greater competitive asymmetry observed at Winnipeg.

Despite the temporal and spatial differences seen in the competitive hierarchies, the rankings of species within all four data sets are still positively correlated. From this information alone, it could be argued that competitive hierarchies within the geographic range of southern Manitoba are fairly consistent from year to year and from site to site. However, given that changes in competitive rank are likely to occur over larger temporal and spatial scales, it is useful to consider in some detail the role of plant traits and climatic/edaphic variables in predicting competitive outcomes.

3.6.2 Plant Traits, Site Conditions, and Competitive Hierarchies

The highly transitive competitive hierarchies found in both experiments after the second growing season appear to be a reflection of two important plant functional traits: above-ground productivity (monoculture yield), and the photosynthetic pathway type (C$_4$ vs. C$_3$). The results of the experiments examined here indicate that highly productive species tend to be more competitive than less productive ones. This is in agreement with results from previous investigations (e.g. Aarsen 1983, Weiner 1985, Gaudet and Keddy 1988, Newman 1992). The other indication is that C$_4$ species are generally less competitive than C$_3$ species. In both experiments, the weakest competitors were C$_4$ species of low above-ground productivity. These experimental results are broadly applicable to the mesic, dark soils of the north-eastern prairie. However, it is unreasonable to assume that these competitive hierarchies will hold true in all North American grasslands. Rather, species competitive hierarchies at a given site are likely dependent on two factors: the relative availability of resources, and the number of growing-degree days.

As discussed previously, competition for light becomes increasingly important as soil resource (nutrients and/or water) supply rates increase (Wisheu and Keddy 1992; Peltzer et

al. 1998). As the availability of soil resources increases, taller and more highly productive species will preempt available light to the detriment and eventual exclusion of less productive species (Wedin and Tilman 1993). This shift from below-ground, symmetric competition to above-ground, asymmetric light competition as soil resource supply rates increase has been widely documented (e.g. Tilman 1984; Wisheu and Keddy 1992; Wedin and Tilman 1993; Huston and DeAngelis 1994; Keddy et al. 1997). In the North American prairie, soil resource availability (water and nutrients) generally increases from west to east, reflecting a gradient of increasing annual precipitation (Bryson and Hare 1974). Tall, highly productive species, such as A. gerardii and P. virgatum, are therefore favoured in the eastern 'tall-grass' prairie (Sala et al. 1988).

Relative competitive abilities of C_3 and C_4 grasses are dependent on the number of growing-degree days (Williams 1974; Ehleringer 1978; Zangerl and Bazzaz 1984). In the northern prairie, cooler summer temperatures and a shorter growing season favour grasses with the C_3 photosynthetic pathway, as it has lower inherent energetic costs and higher quantum yields at lower temperatures (Ehleringer 1978). However, quantum yields for C_3 species decrease to levels below those of C_4 species as temperature increases (Black 1971; Kemp and Williams 1980). It has been shown that shaded C_4 plants (for example, those grown under a 'canopy' of C_3 plants) have light saturation levels similar to those of C_3 species, thereby reducing any inherent advantages of the C_4 pathway (Williams and Markley 1973). Phenological niche differentiation occurs in grasslands where cool-season and warm-season grasses co-occur, with warm-season species delaying their period of maximum growth until later in the growing season when temperatures are higher (Kemp and Williams 1980). In more northern latitudes, the early onset of cooler autumn temperatures is unfavourable to warm-season species. Reduction in the relative competitive abilities of warm-season grasses in cooler climates is reflected in the decreased relative abundance of C_4 grasses along a south-north gradient in the North American prairie (Epstein et al. 1997).

Dependence of species competitive abilities on both soil resource supply rates and number of growing-degree days suggests a conceptual model for predicting variation in competitive hierarchies in North American prairie (**Fig. 3.28**). The prevailing environmental conditions in the experiments described here (north-eastern prairie: adequate soil resource supply rates, and a short growing season) generally favour highly productive, C_3 grasses over short-statured, C_4 ones. Conversely, lower water and/or nutrient supply rates in the north-western prairie favour short-statured, C_3 grasses with well-developed

Above-Ground Productivity

Low   **High**

Photosynthetic Pathway

C-3

C-4

northwest (cool, dry)

northeast (cool, moist)

southwest (warm, dry)

southeast (warm, moist)
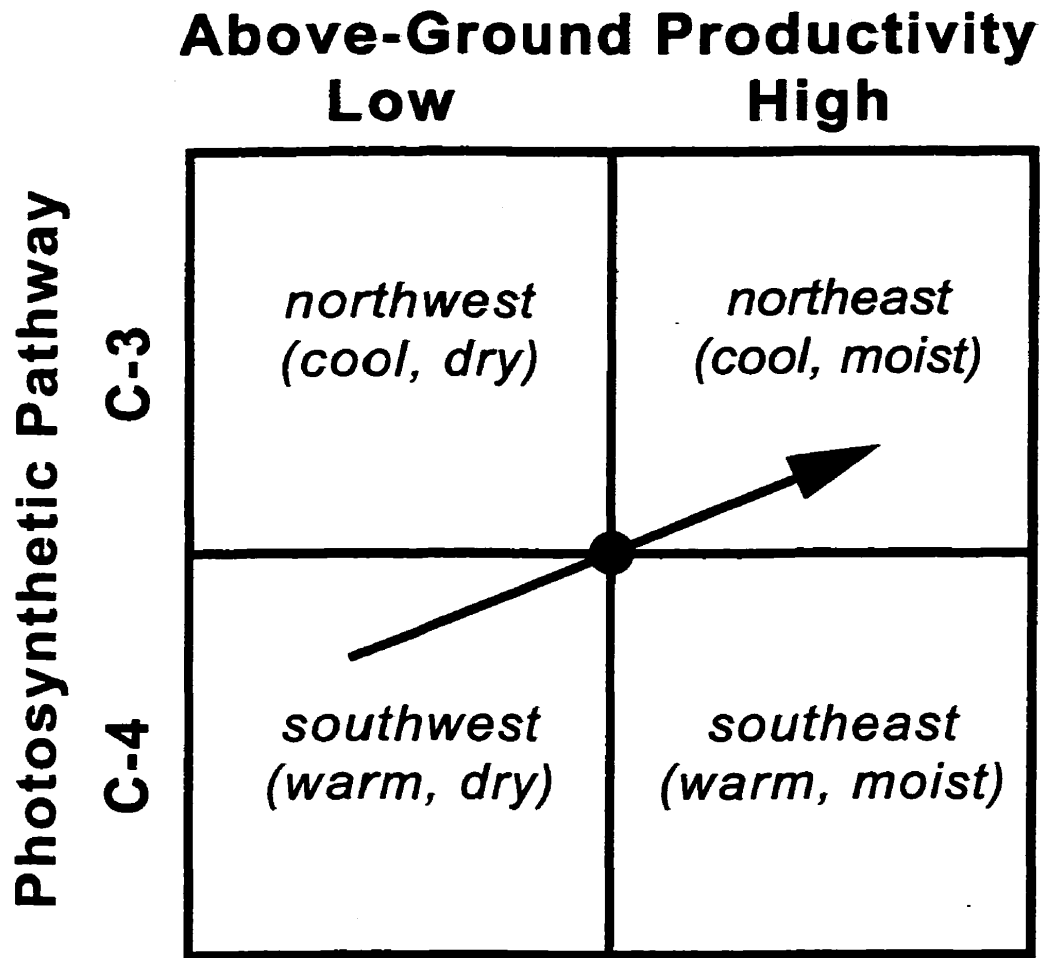
Figure 3.28. Model illustrating direction of competitive hierarchies based on species photosynthetic pathway and above-ground productivity. The pointer indicates the direction of the competitive hierarchies in our experiment, from weakest competitors (low productivity C4 species) to strongest competitors (high productivity C3 species). The direction of the arrow points towards the location (italics) of the species within the Great Plains or the prevailing conditions (italics and brackets) at a given site. For example, in the southwestern Great Plains (or in an otherwise warm and dry climate) the arrow would point in the opposite direction.

root systems (Coupland 1950). C_4 grasses are increasingly favoured as one moves south and the number of growing-degree days increases (Epstein et al. 1997). In southern prairies, productive tall-statured C_4 grasses are generally favoured in the moist nutrient rich eastern prairie, whereas short-statured, less productive C_4 grasses dominate the drier and more nutrient depleted western prairie (Sala et al. 1988).

It should be noted that the large-scale geographic patterns illustrated in the model (**Fig. 3.28**) could potentially be substituted with finer-scale topographic features that affect resource supply rates. For example, the species competitive hierarchy that develops on relatively steep, north-facing slopes in south-eastern prairie is expected to be more typical of north-west prairie, due to lower levels of soil moisture and insolation. Studies on species distributions in native North American prairie generally support this hypothesis. In North Dakota, species of high above-ground productivity (*E. trachycaulus*, *S. nutans*, *A. gerardii*) dominate mesic habitats, whereas smaller-statured species such as *Bouteloua gracilis*, *Nassella viridula* and *Pascopyrum smithii* dominate less mesic sites (Dix and Smiens 1966). Similar results have been obtained in Saskatchewan prairie (Baines 1973; Hulett et al. 1966). In the mixed-grass prairie of Kansas, warm-season grasses dominate but vary in abundance along a soil moisture gradient (Albertson 1937). In xeric uplands, short-statured grasses such as *Buchloe dactyloides* and *B. gracilis* dominate, whereas medium-statured bunchgrasses such as *Aristida purpurea* and *S. scoparium* are more abundant in less xeric sites. The most mesic sites are generally dominated by tall-statured, productive species such as *A. gerardii*, *B. curtipendula*, and *Sporobolus drumondii*, as well as *P. smithii*, a C_3 species.

3.6.3 Implications for Grassland Restoration

Adjusting Seed-mixtures

Many large-scale grassland restoration and revegetation programs currently depend upon the use of seed mixtures composed of a variety of species. In this approach, the hope is to increase biodiversity simply by increasing the number of species planted simultaneously into the ground (Morgan et al. 1995). Artificially generating plant diversity in this way is predicted to be very difficult, due to factors including differential germination and establishment, as well as competitive exclusion of subordinate species (Grime 1973; Weiher and Keddy 1995). Furthermore, the rate of competitive exclusion is predicted to increase with increasing nutrient and moisture availability (Tilman 1988; Wilson and Shay

1990; Wilson and Tilman 1991; Keddy at al. 1997). The results of the experiments described here agree with these observations and predictions. One potential mechanism used to circumvent this problem has been the alteration of proportions of species in seed mixtures based on competitive abilities (see Chapter 4). This involves decreasing the proportions of strong competitors in seed mixtures while increasing the proportions of weak competitors. Once planted, strong competitors are still expected to outcompete weaker competitors, but the time required to completely exclude other species is expected to be greater since the dominants now cover a lower proportion of the total area of the restored field. This time period may be sufficient to at least give subordinate species time to establish and survive until other management measures to promote diversity (e.g. prescribed burning, grazing, etc.) are undertaken.

Adjusting Sowing Patterns

Beyond adjusting for competitive ability by altering frequency of species in mixture, adjustments could be made spatially. Spatial pattern has been shown to affect the competitive responses and the long-term persistence of species (e.g. van Andel and Nelisson 1981; van Andel and Dueck 1982; Thorhallsdottir 1990). Silvertown et al. (1992) have modelled community responses to revegetation based on data from a replacement series competition experiment involving six species. Competitive exclusion was found to occur most rapidly when species were initially arranged in a random mixed pattern (i.e. similar to the sowing methods currently used in grassland restoration). When species were arranged in bands of monocultures, competitive exclusion was delayed. Furthermore, different arrangements of species bands had different outcomes. Long-term coexistence was maximized when species were arranged such that invasiveness between neighbouring bands was minimized (Silvertown et al. 1992).

In restoration and revegetation programs, this could be implemented by minimizing total aggressivity values between all paired bands of planted monocultures (e.g. *E. trachycaulus* would never be placed adjacent to *S. scoparium*). The only method currently used for adjusting for spatial pattern of revegetation programs has been described by Jacobsen et al. (1994). This method, known as 'sculptured seeding', involves using different seed mixtures according to the topographical variation of the site. Although this method likely does promote greater diversity at the level of the landscape, it fails to account for competitive interactions occurring within a given seed mixture.

Adjusting Timing of Species Introductions

In addition to proportionally adjusting seed mixtures and implementing spatial patterning in plantings, adjustments could also be made on a temporal scale. Specifically, one could adjust the timing of species introductions into a system rather than planting all species simultaneously. This approach to prairie restoration, still in its infancy, has been termed 'assembly-based restoration' by Lockwood (1997). This method of restoration is based on computer simulation research on assembly rules in ecological communities (e.g. Diamond 1975; Post and Pimm 1983; Law and Morton 1993; Luh and Pimm 1993; Morton et al. 1996). Assembly rule models throw a pool of species together, from various trophic levels, and allow these species to interact based on Lotka-Volterra models. Over many iterations, observations are made on the dynamics and final outcome(s) of these interactions (Lockwood et al. 1997).

Although these models do not take into account competitive interactions between plants *per se*, the general conclusion is that ecological communities assemble themselves towards multiple persistent and invasion-resistant states. The final species composition of these 'climax' communities is often dependent on the stochastic introduction of other 'nexus' species earlier on in the assembly process (Robinson and Edgemon 1988; Drake 1990, 1991; Wilson 1992; Drake et al. 1993; Law and Morton 1996; Lockwood et al. 1997). The suggestion here for restoration ecologists is that a final 'climax' community may only be attainable if specific species interactions occur within the field at an earlier time. In other words, rather than planting a mixture of seed and letting interactions occur somewhat randomly, restorationists should guide a restoration through time by carefully adding appropriate species at various key moments in time (Lockwood 1997). Competitive hierarchies become important here, in that they allow us to model the potential alternative states of plant communities undergoing competition.

Assessing Unfamiliar Sites and Untested Seed-Mixtures

This study indicates that competitive hierarchies are relatively consistent from year to year and from site to site, over a relatively large geographical range (i.e. southern Manitoba). Therefore determining a competitive hierarchy could potentially benefit restorationists in two respects. First, restoration efforts in unique areas or in regions where restoration work is in its infancy (e.g. northern fescue prairies, grasslands beyond the Great Plains) could benefit from such an approach since restorationists would be able to predict how species

will interact once planted. Second, restorationists can use competitive hierarchy experiments in familiar settings where the introduction of a new species into a seed mixture may affect competitive outcomes. In this case, perhaps an entire replication of a competition experiment would not even be required. Rather, a smaller number of 'benchmark' species or 'phytometers' (who's competitive ability against other species has already been tested) could be used to assess a new species' relative competitive ability. Under both of these scenarios, competitive hierarchy experiments can be used as relatively efficient and low-investment tools to evaluate new locations and/or seed mixtures for restoration.

CHAPTER 4

RESTORING GRASSLAND COMMUNITIES USING SEED MIXTURES ADJUSTED FOR GERMINATION, ESTABLISHMENT, AND COMPETITIVE ABILITY

4.1 Introduction

Many large-scale grassland restoration and revegetation programs currently depend upon the use of seed mixtures composed of a variety of species (Jacobsen et al. 1994; Morgan et al. 1995). In this approach, the hope is to increase biodiversity simply by increasing the number of species planted simultaneously into the ground. Artificially generating plant diversity in this way is predicted to be very difficult, due to factors such as differential germination and establishment, as well as the potential competitive exclusion of subordinate species (Grime 1973; Weiher and Keddy 1995). The rate of competitive exclusion is predicted to increase with increasing nutrient and moisture availability (Tilman 1988; Wilson and Shay 1990; Wilson and Tilman 1991; Keddy et al. 1997). These observations and predictions are in general agreement with the experimental results described in chapter 3.

One potential strategy to circumvent this problem is to alter the proportions of species in seed mixtures, based on their relative competitive abilities. Such an approach would involve decreasing the proportions of strong competitors in seed mixtures, while increasing the proportions of weak competitors. Once planted, strong competitors are still expected to dominate if left alone for several years, but the time required to exclude subordinate species is expected to be greater since the dominants initially cover a much lower proportion of the total area of the restored field. This additional time may be sufficient to at least give subordinate species time to establish and survive until other management measures used to promote diversity (e.g. prescribed burning, grazing, etc.) are implemented.

During the summer of 1995, twelve native grass species (six C_4, and six C_3) were grown in all pair-wise combinations and monocultures in order to determine a hierarchy of relative competitive abilities amongst these species (see Chapter 3). This experiment was carried out at the University of Manitoba, Faculty of Agriculture Research Station at Carman, Manitoba. From the first-year results of this experiment, seed mixtures were developed to

promote multiple species coexistence, by accounting for differences in establishment rates and competitive abilities. The objective of this study is to determine how mixtures with these compensatory measures compare to control mixtures and a mixture currently used by Ducks Unlimited Canada in their revegetation programs, after one growing season.

4.2 Methods and Materials Used

4.2.1 Experimental Design

Species Composition of Mixtures

In all, eight mixture sets were developed and planted at the University of Manitoba Department of Plant Science Field Facility at Carman, Manitoba during the 1996 field season (see sub-section 3.3.1 for a description of the study area). Each of seven mixture sets consisted of a 'control' mixture and an 'adjusted' mixture, each replicated three times. The control mixtures assumed no differences in establishment and competitive ability, while the adjusted mixtures were adjusted for differences in species establishment and competitive ability. Overall, the theoretical final plant density of all plots was the same: 64.6 plants m^{-2} (6 plants ft^{-2}). This is the species density indicative of a 'successful' planting, according to Ducks Unlimited Canada (DUC).

Determining the final species compositions for each of the mixtures involved dividing the twelve species into four three-species groups based on mean aggressivity values: a) most competitive C_3's; b) least competitive C_3's; c) most competitive C_4's; and d) least competitive C_4's. Each of these four species groups (a-d) were used in the following combinations:

1) a+b+c+d
2) c+d
3) a+b
4) a+c
5) b+d
6) a+d
7) b+c

Note that in mixtures 2 through 7, only six species were sown, while in mixture 1, all twelve species were sown.

In addition to the seven mixtures sets above, an additional mixture set (#8) was included in the experimental trial after consultation with DUC. This eighth mixture consisted of ten species which DUC currently uses at designated sandy loam restoration sites. In this mixture set, there were both 'control' and 'adjusted' mixtures (determined exactly as above) plus an additional mixture at DUC's normal sowing densities.

In all, since there were eight mixture sets, each replicated three times with two types of plots (i.e. control vs. experimental; plus mixture #8 with a third type), 51 plots were sown and evaluated after one growing season. Plots were 1.5 m x 10.0 m, with 1.5 m lanes between them.

4.2.2 Determining Seed Mixture Species Proportions

The numbers used for calculating sowing densities are shown in **Appendix VI**. Sowing densities were determined using two different methods (i.e. 'control' and 'adjusted' mixtures), each with a total establishment rate of 64.6 plants m^{-2} (6 plants ft^{-2}) set as a theoretical 'goal'. Note that control seed mixtures had the exact same species compositions as adjusted mixtures. The only difference between these mixtures was the relative sowing densities of the component species. Several factors were taken into consideration when determining species sowing densities: percent purity, germination, and establishment, as well as relative competitive ability. Control mixtures were adjusted for percent purity and germination only (i.e. pure live seed [PLS] values), while adjusted mixtures were also adjusted for percent establishment and relative competitive ability.

Adjusting for Purity and Germination

A PLS value is the product of a species percent purity and germination, evaluated by several independent seed testing laboratories for each seed lot. Percent purity is simply the proportion of seed that is actually of the species that the lot claims to be, and not other 'undesirable' species (such as *A. repens*, for example). Percent germination is the percentage of those 'pure' seeds that are actually viable and capable of germination. This last figure is determined by tetrazolium hydrochloride (TZ) testing, or by actual germination tests in moist petri dishes, by several independent seed testing laboratories for each seed lot.

Adjusting for Differences in Establishment

By counting the number of individual plants actually established in monoculture in 1995 (**Appendix IV**), it was clear that different species had different degrees of establishment success. For example, *S. nutans* established at a density of 11.2 plants m^{-2}, while *E. canadensis* established at 108.6 plants m^{-2}. These values were used to determine percent establishment of pure live seed for each species. In order to compensate sowing rates for purity, germination and establishment, a PGE (purity, germination, and establishment) factor was calculated, which is the inverse of the product of percent purity, germination and establishment for that species. For the control mixtures, percent establishment was assumed to be 100%, and species were assumed to have equal competitive abilities. For adjusted mixtures, sowing densities were adjusted by incorporating actual 1995 establishment rates into the PGE factor.

Adjusting for Differences in Competitive Abilities

Post-establishment competitive ability adjustments were made using reciprocal target scores (see sub-section 3.4.1 for definition of target scores). Competition adjustment factors (COMP factors), the inverse of a species target score, were calculated for each species within a mixture. In adjusted plots, these factors were multiplied by PGE factors to account for differences in competitive abilities. At this point, however, COMP factors did not average out to 1.0. This problem was alleviated by standardizing the relative yields so that they averaged out to 1.0 across all of the species in a mixture, thus restoring the total theoretical plant establishment density back to 64.6 plants per m^2. Final sowing densities of all species are shown in **Table 4.1**.

Sample Calculation

As an example, I will refer to *E. canadensis* in mixture #1 (see **Appendix VI**). Since mixture #1 consists of 12 species, and our establishment goal is 64.6 plants m^{-2}, 5.38 individuals of each species must establish per m^2. Percent purity and germination for the *E. canadensis* seed lot was found to be 93.62% and 80.00%, respectively. For the control mixture, percent establishment is assumed to be 100%. The PGE factor is calculated as follows:

Table 4.1. Sowing densities (PLS m⁻²) of species in experimental seed-mixtures. Treatment codes: a = adjusted for establishment and competitive ability; c = sown at equal PLS rates (see text for details on how sowing densities were adjusted); du = species were sown at DUC mixture densities. Species codes: Ag = *Andropogon gerardii* , Bc = *Bouteloua curtipendula* , Bg = *Bouteloua gracilis* , Ec = *Elymus canadensis* , El = *Elymus lanceolatus* , Et = *Elymus trachycaulus* , Nv = *Nassella viridula* , Ps = *Pascopyrum smithii* , Pv = *Panicum virgatum* , Sc = *Stipa comata* , Sn = *Sorghastrum nutans* , Ss = *Schizachyrium scoparium* .

Mixture	Ec	El	Et	Nv	Ps	Sc	Ag	Bc	Pv	Bg	Sn	Ss	TOTAL
1a	19.2	36.8	29.6	70.0	33.7	76.6	19.5	12.9	52.6	42.1	216.2	33.0	642.3
1c	5.4	5.4	5.4	5.4	5.4	5.4	5.4	5.4	5.4	5.4	5.4	5.4	64.6
2a	-	-	-	-	-	-	38.9	25.6	105.3	84.5	447.7	68.0	770.0
2c	-	-	-	-	-	-	10.8	10.8	10.8	10.8	10.8	10.8	64.6
3a	37.5	72.5	57.7	143.4	67.9	147.4	-	-	-	-	-	-	526.4
3c	10.8	10.8	10.8	10.8	10.8	10.8	-	-	-	-	-	-	64.6
4a	41.8	78.9	62.9	-	-	-	41.8	29.5	117.3	-	-	-	372.2
4c	10.8	10.8	10.8	-	-	-	10.8	10.8	10.8	-	-	-	64.6
5a	-	-	-	132.2	63.6	134.0	-	-	-	82.1	368.9	62.4	843.2
5c	-	-	-	10.8	10.8	10.8	-	-	-	10.8	10.8	10.8	64.6
6a	110.7	64.2	119.1	-	-	-	-	-	-	46.2	30.0	137.9	507.9
6c	10.8	10.8	10.8	-	-	-	-	-	-	10.8	10.8	10.8	64.6
7a	-	-	-	131.2	69.5	158.6	40.1	26.2	108.1	-	-	-	533.7
7c	-	-	-	10.8	10.8	10.8	10.8	10.8	10.8	-	-	-	64.6
8a	23.2	45.1	35.3	84.5	40.1	-	23.3	15.8	63.5	-	268.6	40.5	639.9
8c	6.5	6.5	6.5	6.5	6.5	-	6.5	6.5	6.5	-	6.5	6.5	64.6
8du	50.6	35.5	47.4	9.7	10.8	-	19.4	14.0	4.3	-	8.6	89.3	289.5

$$\text{PGE factor} = \frac{1,000,000}{\%\text{purity} \times \%\text{germination} \times \%\text{establishment}}$$

$$\text{PGE factor} = \frac{1,000,000}{93.62 \times 80.00 \times 100}$$

$$\text{PGE factor} = 1.34$$

Since competitive abilities are assumed to be equal amongst the 12 species, competition adjustment factors (COMP factors) all equal 1.00. The actual number of seeds to be planted (S) is calculated as follows:

$$S = \text{number of individuals desired} \times \text{PGE factor} \times \text{COMP factor}$$

$$S = 5.38 \times 1.34 \times 1.00$$

$$S = 7.17$$

Therefore, in the control plot, 7.17 seeds from the *E. canadensis* seed lot must be sown per m^2 in order to achieve our goal establishment density. For the adjusted plot, a similar calculation is made, except that the establishment rate is now set at 24.35% (as determined from actual species establishment rates at Carman in 1995) instead of 100%. Hence the PGE factor is as follows:

$$\text{PGE factor} = \frac{1,000,000}{\%\text{purity} \times \%\text{germination} \times \%\text{establishment}}$$

$$\text{PGE factor} = \frac{1,000,000}{93.62 \times 80.00 \times 24.35}$$

$$\text{PGE factor} = 5.48$$

Meanwhile, since competitive abilities were found to differ in the field, COMP factors vary for each species. For *E. canadensis* the COMP factor = 0.87 (values < 1.00 are indicative of strong competitors -- there proportions must be reduced). Hence S for *E. canadensis* in the adjusted plot is:

$$S = \text{number of individuals desired} \times \text{PGE factor} \times \text{COMP factor}$$

$$S = 5.38 \times 5.48 \times 0.87$$

$$S = 25.65$$

Therefore, in the adjusted plot, 25.65 seeds from the *E. canadensis* seed lot must be sown per m^2 in order to achieve our goal establishment density of 5.38 individuals per m^2.

4.2.3 Sowing, Management, and Harvesting Techniques

Site Preparation

Prior to seeding, the weed *Agropyron repens* was spot-treated using glyphosate (Roundup™) herbicide applied with a hand-held sprayer. Plots were delineated using spikes, ropes, and hoes. No other preparatory measures were taken since the soil was of appropriate firmness for planting.

Planting Methods

Although many potential methods of sowing the plots were possible, mechanical seeding was used for two reasons. Firstly, this method best approximates the method used in large-scale revegetation programs. It is under these conditions that competitive hierarchies are of practical concern. Furthermore, this method places the grasses at a prescribed depth and density in parallel rows, assuring improved germination and establishment relative to hand-sowing. Also, this was the exact sowing method used in the previous year to determine establishment rates and relative competitive abilities. The tractor used for both experiments was a John Deere™ 950, and the seeder was a Fabro™ 6 row disk-type with the disks set ca. 20 cm apart and 2 cm deep. The plots were seeded at Carman on May 31, 1996. Proper depth and seed placement was verified immediately after planting.

Post-Planting Management

Hand weeding and rotovating between plots were required on only two occasions. Weeds present included lamb's-quarters (*Chenopodium album*), Canada thistle (*Cirsium*

arvense), and wild mustard (*Brassica kaber* var. *pinnatifida*). Herbicide was not required to control invasive weeds within and around the experimental plots.

Harvesting Technique

Harvesting of plots was undertaken during the third week of September, 1996. Since the plots were 10 m in length, they were divided into four possible 2 m length sub-plots (excluding 1 m on either end). One sub-plot was randomly sampled from each plot. In each of the 51 sub-plots the number of individuals of each species were counted. Obvious 'runs' of a rhizomatous species (e.g. *P. smithii*), were counted as a single individual. When it was not clear whether or not plants were connected by underground rhizomes, they were considered to be separate individuals.

4.3 Data Analysis

Since the primary objective of this study was to determine the feasibility of experimentally adjusting seed mixtures so that maximum diversity is attained, the primary analysis tools utilized were diversity indices. The Shannon-Weiner diversity function (*H*) is a commonly used diversity index. *H* is calculated as follows:

$$H = -\sum_{i=1}^{S} p_i \ \ln p_i$$

S is the total number of species, and p_i is the proportion of species *i* in the harvested plot. 'Effective' species richness (Hill 1973) is simply e^H. As such, its theoretical maximum value is *S*, making interpretation somewhat easier.

Diversity indices incorporate both species richness and relative proportions of species in a single calculation (Goldsmith et al. 1986). For example, consider the hypothetical sites I and II, each with carrying capacities of 15 individuals. If each site contains 3 species, A, B, and C, species richness would be equal between the two sites. However, site I can have 5 individuals of each species, while site II can have 1 of A, 1 of B, and 13 of C. Clearly site I, with equal representation of all 3 species, should be considered more diverse than site II, which is dominated by species C. Both of these indices would be able to make this distinction. Simpson's index gives less weight to rare species than the Shannon-Weiner

function. Using the Shannon-Weiner index, we can further analyze the species abundance data for *evenness* — the relative distribution of individuals within a community. This measure is simply the ratio of actual diversity H to the theoretical maximum diversity, which is:

$$H_{max} = \ln S$$

4.4 Results and Discussion

Sowing Densities

Differences in sowing densities between control and adjusted plots were large (**Table 4.1**), reflecting increases in mean PGE values in adjusted plots (by a factor of 9.4) relative to control plots. The mean PGE adjustment factor for all adjusted plots was 13.8, ranging from 5.1 (*B. curtipendula*) to 64.0 (*S. nutans*). The mean competitive ability adjustment factor (i.e. COMP factor) was 1.00, ranging from 0.85 to 1.27. Therefore, changes in overall sowing densities are largely attributable to differences in establishment rates rather than differences in competitive ability.

Final Establishment Densities

Mean densities at the end of the first growing season were consistently greater in adjusted mixture plots compared to control mixture plots, although these values were not always significant between mixtures of the same set (**Table 4.2**; **Fig. 4.1**). The average increase in density between adjusted and control plots was 240%, ranging from 140% (mixture set #6) to 470% (mixture set #3). There was no significant difference in species density between mixture set #8 plots adjusted for establishment and competitive ability, and mixture set #8 plots sown at DUC's standard densities. The mixtures that came closest to meeting the 64.6 individuals m^{-2} goal were the adjusted mixtures from sets #1 and #8, as well as the DUC mixture of set #8 (**Fig. 4.1**). Note, however that none of these mixtures exceeded 50 individuals m^{-2}.

Table 4.2. Mean number of individuals of species per m² from experimental seed-mixture trials. Treatment codes: a = adjusted for establishment and competitive ability; c = sown at equal PLS rates (see text for details on how sowing densities were adjusted); du = species were sown at DUC mixture densities. Species codes: Ag = *Andropogon gerardii* , Bc = *Bouteloua curtipendula* , Bg = *Bouteloua gracilis* , Ec = *Elymus canadensis* , El = *Elymus lanceolatus* , Et = *Elymus trachycaulus* , Nv = *Nassella viridula* , Ps = *Pascopyrum smithii* , Pv = *Panicum virgatum* , Sc = *Stipa comata* , Sn = *Sorghastrum nutans* , Ss = *Schizachyrium scoparium* .

Mixture	Ec	El	Et	Nv	Ps	Sc	Ag	Bc	Pv	Bg	Sn	Ss	TOTAL
1a	2.2	2.7	5.3	2.5	2.7	0.5	2.8	2.5	7.3	5.3	6.9	2.3	40.8
1c	0.5	0.8	0.3	1.2	1.8	0.2	1.2	0.8	1.3	0.5	2.5	0.8	11.2
2a	-	-	-	-	-	-	3.0	3.8	7.0	8.0	10.3	1.0	32.1
2c	-	-	-	-	-	-	4.5	3.0	5.8	1.8	3.5	1.5	18.7
3a	6.2	5.5	8.7	5.0	9.3	4.2	-	-	-	-	-	-	38.8
3c	0.3	1.7	0.8	1.5	3.5	0.5	-	-	-	-	-	-	8.3
4a	2.7	2.7	8.2	-	-	-	4.5	3.8	9.0	-	-	-	30.8
4c	4.0	1.5	4.5	-	-	-	4.0	2.0	4.2	-	-	-	20.2
5a	-	-	-	5.0	5.3	2.2	-	-	-	7.0	9.1	6.5	28.6
5c	-	-	-	2.7	6.2	1.3	-	-	-	1.2	3.7	1.2	15.0
6a	5.5	3.5	5.4	-	-	-	-	-	-	4.9	6.3	4.0	25.7
6c	1.0	1.8	3.7	-	-	-	-	-	-	4.7	7.8	4.0	19.0
7a	-	-	-	9.2	3.5	3.2	2.3	5.2	6.2	-	-	-	29.5
7c	-	-	-	3.8	2.3	1.2	3.7	3.3	4.7	-	-	-	19.0
8a	2.5	2.7	7.5	5.0	3.2	-	2.2	4.8	5.7	-	8.0	1.7	41.5
8c	1.3	3.5	1.8	0.5	2.0	-	2.0	0.8	2.2	-	2.0	2.0	16.2
8du	1.0	5.2	1.5	9.0	2.8	-	12.0	8.0	3.2	-	2.3	1.5	45.0
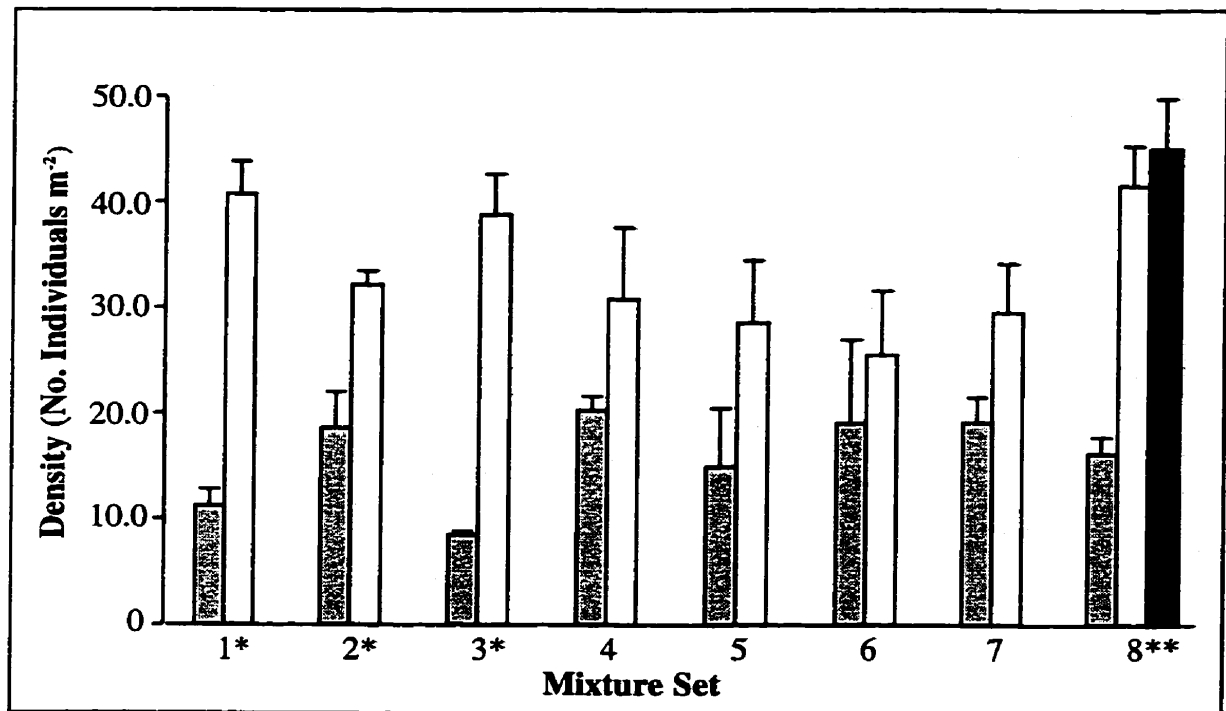
Figure 4.1. Species establishment density (+/- s.e.) for 17 experimental mixtures grown at Carman in 1996. Theoretical target density was 65 individuals per square meter. Unshaded bars represent mixtures adjusted for establishment and competitive ability. Shaded bars represent control mixtures. Black bar represents proportions used by DUC for that mixture. *p < 0.05 between control and adjusted mixtures. **p < 0.05 between adjusted and control mixture, as well as between DUC and control mixture, but not between adjusted and DUC mixture.

Diversity and Evenness

Evenness values generally failed to show any trends between adjusted and control plots except in mixture #6 where evenness was significantly greater in adjusted plots (p = 0.02; **Fig. 4.2**). Also, in mixture #8, evenness was significantly greater for adjusted plots compared to plots sown at DUC's suggested densities (p = 0.02). Effective species richness (i.e. diversity) was significantly greater only for the adjusted mixtures of sets #3 and #6 (**Table 4.3; Fig. 4.3**). Mixtures with the greatest effective species richness were the adjusted mixtures of sets #1 and #8, since a greater number of species were present within these plots.

Overall Success

In terms of planting success, the adjusted seed mixtures clearly came closer to meeting the initial objectives of 64.6 established plants m^{-2}. Using PLS values alone as a predictor of final first year establishment rates (i.e. as was done with the control mixtures) is therefore not reliable. Competitive ability adjustments were quite low relative to establishment rate adjustments and were thus also less important in terms of affecting the final outcome of the adjusted mixtures. In other words, the differences in final plant densities were largely attributable to the adjustments made based on monoculture establishment rates rather than competitive ability adjustments.

Experimental vs. Trial-and-Error Adjustments: Mixture Set #8

In terms of mixture set #8, there were no significant differences in density between the adjusted mixture and the mixture sown at DUC's densities (**Fig. 4.1**). However, both of these mixtures had significantly higher density at establishment than the control mixture. In the DUC mixture, the species with the highest final density was *A. gerardii*, with 24.0 individuals per sample. In the adjusted mixture, the most dominant species was *S. nutans*, which established at a rate of 16.0 individuals per sample. *S. nutans* had the highest PGE adjustment factor for the adjusted mixture (63.9). The adjusted mixture did have significantly greater evenness and effective species richness than the DUC mixture (**Figs. 4.2** and **4.3**). Experimentally adjusting mixtures for species establishment rates and relative competitive abilities can therefore ensure good density of species at establishment, as well as greater diversity than mixtures developed from years of 'trial-and-error' adjustments based on informal field observations (as in the DUC mixture).
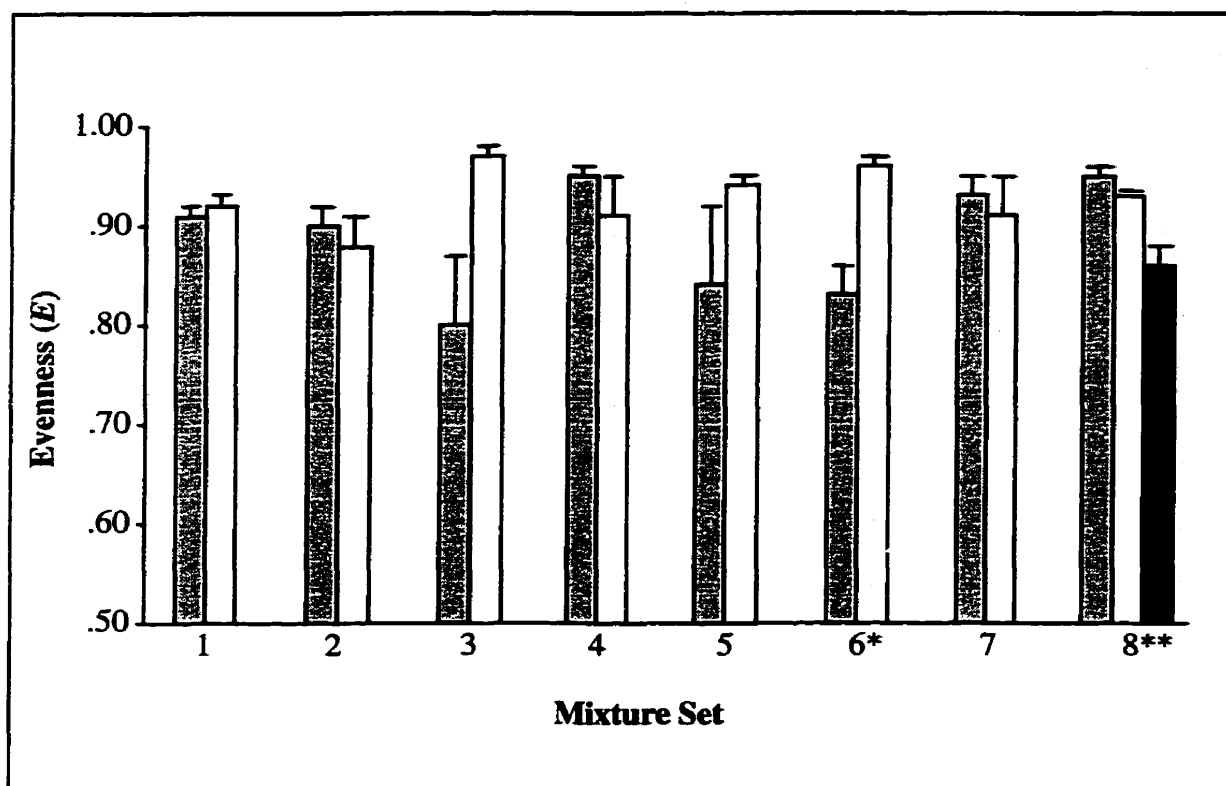
Figure 4.2. Evenness (+/- s.e.) of 17 experimental mixtures grown at Carman in 1996. Shaded bars represent control mixtures. Unshaded bars represent mixtures adjusted for establishment and competitive ability. Black bar represents mixture #8 with species proportions as set by DUC. * p < 0.05 between control and adjusted mixtures. ** p < 0.05 between control and DUC mixtures, as well as between adjusted and DUC mixtures, but not between adjusted and control mixtures.

Table 4.3. Measures of density and diversity for experimental seed-mixtures after one growing season at Carman in 1996. Treatment codes: a = adjusted for establishment and competitive ability; c = sown at equal PLS rates (see text for details on how sowing densities were adjusted); du = species were sown at DUC mixture densities. Codes: E.S.R. = Effective Species Richness; E = Evenness; s.e. = Standard Error. See Table 4.1 for list of species present in mixtures.

Mixture	Plants/m^2	s.e.	E.S.R.	s.e.	E	s.e.
1a	40.8	3.1	9.82	0.35	0.92	0.01
1c	11.2	1.7	9.51	0.29	0.91	0.01
2a	32.1	1.3	4.85	0.27	0.88	0.03
2c	18.7	3.3	4.99	0.24	0.90	0.03
3a	38.8	3.5	5.66	0.17	0.97	0.02
3c	8.3	0.2	4.26	0.47	0.80	0.07
4a	30.8	6.6	5.12	0.39	0.91	0.04
4c	20.2	1.6	5.52	0.03	0.95	0.00
5a	28.6	5.8	5.37	0.10	0.94	0.01
5c	15.0	5.5	4.58	0.67	0.84	0.09
6a	25.7	5.8	5.56	0.14	0.96	0.01
6c	19.0	8.0	4.46	0.25	0.83	0.03
7a	29.5	4.6	5.16	0.32	0.91	0.03
7c	19.0	2.6	5.26	0.26	0.93	0.03
8a	41.5	3.8	8.53	0.07	0.93	0.00
8c	16.2	1.7	8.85	0.24	0.95	0.01
8du	45.0	4.9	7.31	0.28	0.86	0.02
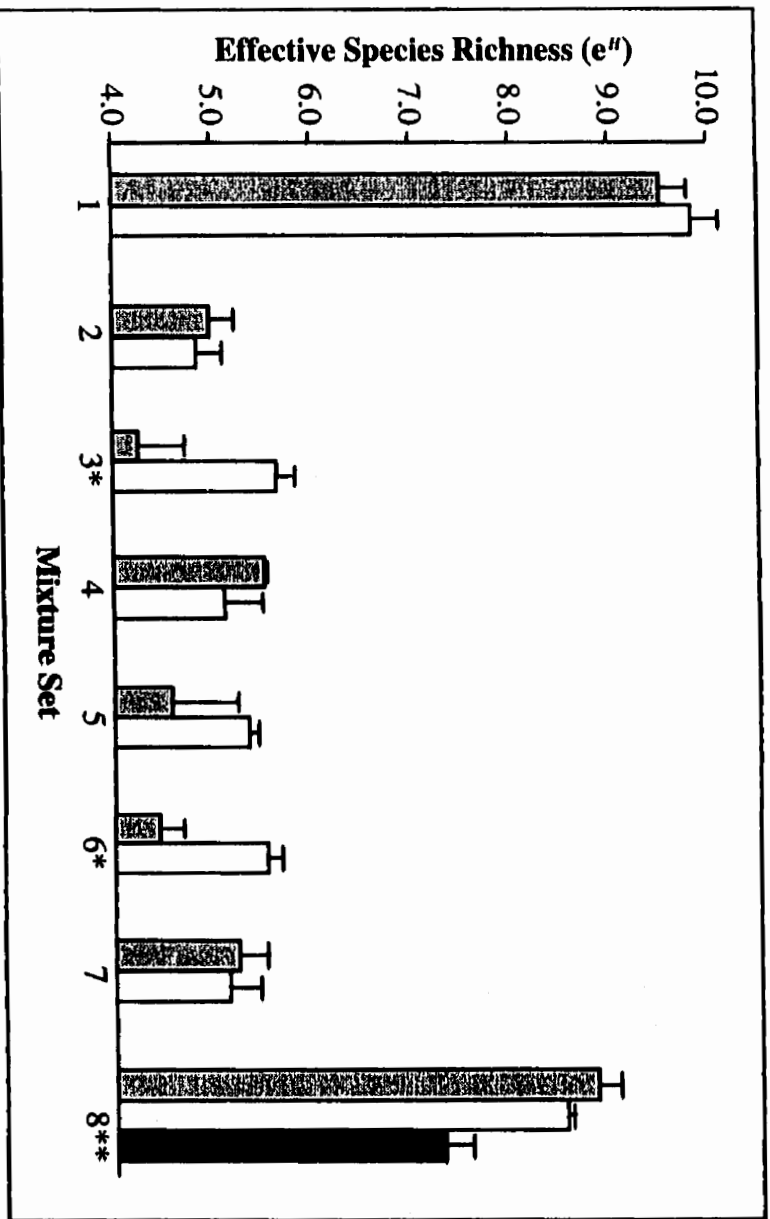
Figure 4.3. Effective species richness (+/- s.e.) of 17 experimental mixtures grown at Carman in 1996. Shaded bars represent control mixtures. Unshaded bars represent mixtures adjusted for establishment and competitive ability. Black bar represents mixture #8 with species proportions as set by DUC. * $p < 0.05$ between control and adjusted mixtures. ** $p < 0.05$ between control and DUC mixtures, as well as between adjusted and DUC mixtures, but not between adjusted and control mixtures.

Summary

Most differences in establishment rates and evenness between control and adjusted plots can be attributed to establishment adjustments made to the adjusted seed mixtures — competitive ability adjustments were relatively minor. In general, seed mixtures adjusted for establishment and competitive ability failed to have greater evenness by the end of the first growing season than control seed mixtures designed using percent purity and germination values alone. However, experimentally adjusted seed mixtures will likely come closer to meeting the desired final density than control seed mixtures designed using percent purity and germination values alone. Experimentally adjusted seed mixtures may also result in greater evenness than seed mixtures developed on a trial-and-error basis, even though their final overall densities may be similar.

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APPENDIX I

Characteristics of 12 Common Native Grass Species

Pascopyrum smithii (Rydb.) A. Love -- Western Wheatgrass

• **Sources**

Weaver and Fitzpatrick (1934); Weaver and Albertson (1956); Quinnild and Cosby (1958); Coupland and Johnson (1965); Ahlenslager (1986b).

• **Synonyms**

Agropyron smithii Rydb.

• **Physical Attributes**

A long-lived C_3 perennial. Height is 30-75 cm. Highly rhizomatous. Main roots are 1.5-2 mm thick, with profusely branched laterals. Depth of roots is generally between 5-7', but can reach as deep as 11.8'. Rhizomes lie 1.3-5 cm below surface. An endomycorrhizal grass.

• **Reproductive Characteristics**

Generally reproduces via rhizomes.

• **Growth Characteristics**

Most growth occurs during the spring. Relatively dormant during summer. Perennating buds are located below ground.

• **Successional Status**

Facultative seral species. Common in many climax communities. Increases in abundance during secondary succession.

• **Common Associations and Interactions**

Associated with *B. gracilis*, *B. curtipendula*, *Sporobolus airoides*, *Buchloe dactyloides*, and *Stipa* spp. Tends to exclude other species due to dense sod formation.

Elymus trachycaulus (Link) Gould *ex* Shinners -- Slender Wheatgrass

• **Sources**

Weaver and Fitzpatrick (1934); Howard (1992)

• **Synonyms**

Agropyron caninum (L.) Beauv.

Agropyron pauciforum (Schwcinitz) A. Hitchc.

Agropyron tenerum Vaset

Agropyron trachycaulum (Link) Malte ex H.F. Lewis

Agropyron subsecundum (Link) A. Hitchc.

Agropyron violaceum (Hornem.) Lange

• **Physical Attributes**

A short-lived C_3 perennial. Height is 8-120 cm. Dense root system with coarse and fibrous roots, extending >30 cm depth. May have short rhizomes. A tufted bunchgrass.

• **Reproductive Characteristics**

Generally reproduces by seed, although tillering may be more common amongst northern ecotypes. Abundant seed producer.

• **Growth Characteristics**

Perennating buds are located close to ground level. Growth occurs primarily in early spring, following snowmelt.

• **Successional Status**

Obligate initial community species. Dominant in early seral grassland communities. Decreases dramatically with succession, but may remain as a minor component of climax communities.

• **Common Associations and Interactions**

Extensive hybridization and introgression occurs between all members of the Triticaceae tribe (incl. *Elymus, Agropyron, Pascopyrum*). Because of its wide distribution and many ecotypes, it potentially interacts with many other species.

Elymus lanceolatus (Scribn. & J.G. Sm.) Gould -- Northern Wheatgrass

• **Sources**

Ahlenslager (1986a)

• **Synonyms**

Agropyron dasystachyum

Agropyron albicans

Agropyron elmeri

Agropyron griffthsii

Agropyron psammophilus

Agropyron riparium

• **Physical Attributes**

A native, long-lived, C₃, long-lived, perennial, sod-forming grass. Height ranges between 0.4-0.8 m. Usually rhizomatous. Roots extent 1.5-3.6 m in depth. A highly drought tolerant species.

• **Reproductive Characteristics**

Vegetative reproduction via branched rhizomes and wind-dispersed seed is common.

• **Growth Characteristics**

Perennating buds are located below ground. Rarely form pure stands over large area, but may dominate smaller patches.

• **Successional Status**

Generally associated with climax grassland communities.

• **Common Associations and Interactions**

Commonly associated species of dry sagebrush-grassland communities, including *Oryzopsis hymenoides*, *Sporobolus cryptandrus*, *Artemesia tridentata*, *Calamovilfa longifolia*, *Pseudoroegernia spicata*, *Festuca idahoensis*, and *Stipa/Nassella* spp.

Andropogon gerardii **Vitman var.** *gerardii* -- **Big Bluestem**

- **Sources**

Weaver and Fitzpatrick (1934); Uchytil (1988)

- **Synonyms**

Andropogon gerardii Vitman

- **Physical Attributes**

A native, long-lived, C_4, perennial, sod-forming grass. Height ranges between 0.9-3.6 m. Usually rhizomatous. Coarse and highly branched rhizomes are usually 1-4" in depth. Roots extent from 6-10'. Can occur as a bunchgrass on drier sites.

- **Reproductive Characteristics**

Vegetative reproduction via rhizomes and tillers is most common. Seed reproduction is limited, and occurs generally after fire, or in highly moist years/sites.

- **Growth Characteristics**

Perennating buds are located below ground. Begins very rapid growth in mid to late spring. Leaves can grow as rapid as 2 cm per day.

- **Successional Status**

Commonly occurs in climax grassland communities. Usually dominates where present.

- **Common Associations and Interactions**

Commonly associated with *B. curtipendula*, *Sporobolus* spp., *P. virgatum*, *S. nutans*, *E. canadensis*, and *S. scoparium*. Dominant in well-aerated lowlands, but gives way to *P. virgatum* on less well-drained sites. Together with *S. scoparium*, comprise 70% or more of the tallgrass prairie vegetation. Roots are deeper and coarser than those of *S. scoparium*, and thus require more soil moisture. Freely hybridizes with *Andropogon halii* Hack. at dune-meadow interfaces.

Schizachyrium scoparium (Michx.) Nash -- Little Bluestem

⚫ Sources

Weaver and Fitzpatrick (1934); Uchytil (1989)

• Synonyms

Andropogon divergens (Hack) Anderss. ex A.S. Hitchc.

Andropogon littorale Nash

Andropogon scoparium Michx

⚫ Physical Attributes

A native, C4, perennial, long-lived, sod-forming and bunchgrass species. Bunches are 10-25 cm in diameter. Can reach heights of 0.5-1.5 m. Roots are very fine (0.1-1.0 mm), and extend to 1.3-1.8 m depth, spreading usually 1.5 ft laterally.

• Reproductive Characteristics

Reproduces by seed and short rhizomes. Usually requires 2 growing seasons to flower.

⚫ Growth Characteristics

Perennating buds are generally located at ground level, although some variation does exist. Growth occurs in late spring, after growth of cool-season species. May have 100-300 tillers per 4" diameter individual.

⚫ Successional Status

Facultative seral species. Occurs as a climax species in many xeric grasslands in western US. Further east, it occurs in many seral stages, and can even be an early successional plant along cattle trails, road cuts, and deciduous or pine-deciduous forests.

⚫ Common Associations and Interactions

Associates include *A. gerardii, S. nutans, B. curtipendula, Stipa spartea, Sporobolus heterolepsis, B. gracilis, S. comata, Oryzopsis hymenoides, A. halii,* and prairie sandreed. Roots are finer than those of *A. gerardii,* and so does better on drier sites, yet is adversely affected by drought (Bragg 1995). Considered a true prairie upland species. Exceeds the abundance of all other upland species combined. Can compose 50-90% of the vegetation within its range.

Nassella viridula (Trin.) Barkworth. -- Green Needlegrass

- **Sources**

Weaver and Fitzpatrick (1934); Kartesz (1994); Tirmenstein (1987d)

- **Synonyms**

Stipa parviflora Nutt.

Stipa viridula Trin.

- **Physical Attributes**

A long-lived, C_3, native, perennial bunchgrass. Height is usually between 45-110 cm. Has an extensive fibrous root system. Roots extent between 60-90 cm deep, and spread up to 20 cm laterally.

- **Reproductive Characteristics**

Reproduces primarily by seed. Seeds exhibit strong mechanical and physiological dormancy. Considered by some to be a therophyte.

- **Growth Characteristics**

Perennating buds are located near the ground surface. Seedlings are usually slow to establish, often reaching full maturity during the third growing season. Growth usually begins in early spring, following snowmelt.

- **Successional Status**

Can be a climax species in several grassland communities, but is also known to colonize abandoned fields and disturbed sites.

- **Common Associations and Interactions**

Associated with *Artemisia cana*, *P. smithii*, *B. gracilis*, and *S. comata*.

Stipa comata Trin. & Rupr. -- Needle & Thread Grass

• **Sources**

Weaver and Fitzpatrick (1934); Tirmenstein (1987c)

• **Synonyms**

• **Physical Attributes**

A native, C_3, long-lived, perennial bunchgrass. Height is 30-60 cm. Fibrous roots mostly occur in the first 0.5-1.0 m of soil, but can extent up to 1.5 m depth. Roots spread up to 90 cm in diameter.

• **Reproductive Characteristics**

Regeneration is primarily by seed. Tillering can occur, but not usually in great abundance.

• **Growth Characteristics**

Perennating buds occur at the soil surface. Growth begins in early spring.

• **Successional Status**

A facultative seral species. Occurs as a climax species in many mixed-grass communities, but can also occur in early seral communities. Can regenerate fairly well on disturbed sites.

• **Common Associations and Interactions**

Associated with *P. smithii*, *B. gracilis*, and *S. comata*.

Elymus canadensis **L. Barkworth -- Canada Wild Rye**

- **Sources**

Weaver and Fitzpatrick (1934); McMurray (1987)

- **Synonyms**

- **Physical Attributes**

A short-lived, C_3, native, perennial bunchgrass. Culms range from 80-200 cm in height. Has a coarse and shallow root system, with rhizomes.

- **Reproductive Characteristics**

Reproduction can occur by seed or by rhizomes and tillers, but seed regeneration is most common.

- **Growth Characteristics**

Perennating buds occur at soil surface. Growth begins in early spring, approximately 2-3 weeks sooner than associated C_4 species. Growth often occurs throughout the summer. Rarely forms pure stands, but does clump. Tillering occurs 4-5 weeks after germination.

- **Successional Status**

Plants favour disturbance, and are considered generally to be weak competitors. Often a secondary species on tallgrass or lowland grasslands.

- **Common Associations and Interactions**

Tends to occur between *A. gerardii* and prairie cord grass, along a moisture gradient. Other species associations include *P. virgatum*. Increases in abundance in more northern prairie communities.

Bouteloua gracilis (H.B.K.) Lag. ex Steud. -- Blue Grama

- **Sources**

Weaver and Fitzpatrick (1934); Tirmenstein (1987b)

- **Synonyms**

Chondrosium gracile	*Atheropogon oligostachyus*
Actinochloa gracilis	*Eutriana oligostachya*
Eutriana gracilis	*Chondrosium oligostachyum*
Atheropogon gracilis	*Bouteloua oligostachya*

- **Physical Attributes**

A native, C_4, sod-forming perennial. Can reach heights from 30-77 cm. Not much is known about the longevity of this species, but generally appears to be short-lived. Fine, fibrous roots occur mostly within 35-75 cm of soil, but can extend as deep as 1.8 m. Has short rhizomes. Lateral spread of roots is 30-45 cm.

- **Reproductive Characteristics**

Reproduction occurs via seed, rhizomes, or tillers. Seedling are proficient drought avoiders.

- **Growth Characteristics**

Perennating buds are located either at or below the soil surface. Growth begins in late spring, and is rapid under favourable conditions. Can enter temporary dormancy during temporary periods of drought. Plants mature in 60-70 days. High root-shoot ratio. Roots may reach 30-60 cm in first year of growth.

- **Successional Status**

Dominant in climax shortgrass prairies.

- **Common Associations and Interactions**

Often associated with *Stipa comata*. Does well on overgrazed prairies, where taller species are more heavily disturbed.

Bouteloua curtipendula (Michx.) A. Gray -- Side-Oats Grama

• **Sources**

Weaver and Fitzpatrick (1934); Tirmenstein (1987a)

• **Synonyms**

Chloris curtipendula	*Andropogon curtipendulum*
Dineba curtipendula	*Melica curtipendula*
Eutriana curtipendula	*Heterostegon curtipendulus*
Cynodon curtipendula	*Atheropogon curtipendulus*

• **Physical Attributes**

A perennial, C_4 grass. Can reach heights of 20-100 cm. Scaly rhizomes reach 5-13 cm in length. Coarse, fibrous roots can grow to 60-120 cm deep, spreading approximately 30-50 cm laterally. Most roots occur in the top 5-10 cm of soil. A relatively short-lived plant.

• **Reproductive Characteristics**

Reproduction occurs via seed, rhizomes, or tillers. Reproduction by seed is most common when adequate moisture is available.

• **Growth Characteristics**

Perennating buds occur either at or below soil surface. Rapid growth generally begins early in spring. Both rhizomatous and non-rhizomatous varieties of *B. curtipendula* occur. The rhizomatous variety reproduces primarily by rhizomes. Grows in tufts or small bunches.

• **Successional Status**

Obligate climax species. Found on drier, eroding slopes and disturbed (drought and grazing) areas.

• **Common Associations and Interactions**

Commonly associated with *A. gerardii, S. scoparium, B. gracilis, Festuca* spp., *E. trachycaulus, Carex filifolia,* and prairie junegrass.

Sorghastrum nutans (L.) Nash -- Indiangrass

-- Sources

Weaver and Fitzpatrick (1934); Walkup (1991)

-- Synonyms

Sorghastrum avenaceum (Michx.) Nash

- Physical Attributes

A native, C_4 perennial. Reaches heights of 1-2 m. Roots and scaly rhizomes can extent up to 6 ft. deep. Roots are of intermediate coarseness and depth between the *A. gerardii* and *S. scoparium.*

- Reproductive Characteristics

Seed regeneration is common under favourable conditions. Rhizomatous reproduction also occurs, but tillering is limited by severe competition.

- Growth Characteristics

Perennating buds are located below the soil surface. Begins growth in mid spring, from short rhizomes. Tends to mature from September to November.

- Successional Status

Facultative seral species. Occurs as a climax species in many tallgrass prairies, especially where moisture is high. Invades disturbed areas well.

- Common Associations and Interactions

Commonly associated with *A. gerardii*, *S. scoparium*, and *P. virgatum*. Usually occurs at abundances of 1-5%. Lands of occasional flooding and burning favour this species.

Panicum virgatum L. -- **Switchgrass**

● **Sources**

Weaver and Fitzpatrick (1934); Uchytil (1993)

● **Synonyms**

● **Physical Attributes**

A C_4, native perennial. Has both sod-forming (lowland), and bunchgrass (upland) ecotypes. Can reach heights of 0.9-3.0 m. Coarse roots extend from 3-4 m depth. Rhizomes occur between 5-12 cm depth.

● **Reproductive Characteristics**

Both asexual and sexual reproduction is common. Rhizomes can extend from 30-60 cm, or only a few centimeters, depending on ecotype. Seed production is usually fairly abundant.

● **Growth Characteristics**

Perennating buds are located below the ground. Rapid growth is initiated by warmer soil temperatures in mid to late spring. Usually growth begins about 1 week after that of associated C_4 species. Tillering occurs between. 5-7 weeks, unless under strong competition.

● **Successional Status**

A climax species of the tallgrass prairie. Requires relatively high fertility for growth, and thus is a poor colonizer of abandoned farmlands.

● **Common Associations and Interactions**

Commonly associated with other climax tallgrass species. Prefers slightly less well drained sites than *A. gerardii*. Rarely ever found as an extensive monoculture. Almost always a transitional species between the drier *A. gerardii* and wetter prairie cord grass (*Spartina pectinata*).

APPENDIX II: Climatic and edaphic preferences of 12 grass species native to the northern Great Plains (from Wark et al. 1995)

Species	Photosynthetic Strategy	Min. PPT/year (cm)	Soil Texture	Soil Drainage/Water Table	Soil pH	Fertility Req.	Salt Tolerance (mmhos/cm)	Flood Tolerance	Drought Tolerance
Elymus cinereus	cool season	25	coarse to moderately fine	moderate-well drained 15-90cm	N-weakly B	low	>1	moderate	moderate
Elymus lanceolatus	cool season	25	moderately coarse to fine	Well drained 15-90cm	weakly A-moderately B low	low	>8	good	excellent
Elymus trachycaulus	cool season	35	moderately coarse to moderately fine	Well drained 15-90cm	weakly A-strongly B	low	<16	good	moderate
Nassella viridula	cool season	35	medium to moderately fine	moderate-well drained >90cm	N-weakly B	moderate	<6	fair	moderate
Pascopyrum smithii	cool season	35	moderately coarse to very fine	Poorly drained 0-40cm	N-strongly B	low	<16	good/50-60	good
Stipa comata	cool season	25	moderately coarse to moderately fine	well-drained/moderately drained >90cm	N-weakly B	low	>1	poor	excellent
Andropogon gerardii	warm season	50	moderately coarse to moderately fine	Well drained >90cm	N-weakly basic	high	>1	moderate	moderate-full
Bouteloua curtipendula	warm season	30	moderately coarse to moderately fine	well-poorly drained >90cm	N-weakly B	moderate-low	>1	poor	good
Bouteloua gracilis	warm season	25	moderately coarse to moderately fine	Well-poorly drained >90cm	N-weakly B	low	>1	poor	excellent
Panicum virgatum	warm season	45	medium to fine	well-poorly drained 15-90cm	N-moderately B	moderate-high	<16	good	poor
Schizachyrium scoparium	warm season	25	moderately coarse to moderately fine	Well drained >90cm	N-weakly basic	moderate	>1	fair-poor	good
Sorghastrum nutans	warm season	50	moderately coarse to moderately fine	medium-well drained 15-90cm	N-slightly B	moderate	>1	good	moderate

APPENDIX III: Range of flowering times of native grass species in Manitoba (from Morgan et al. 1995). Manitoba phenology data is unavailable for *Bouteloua curtipendula*, and *Pascopyrum smithii*.
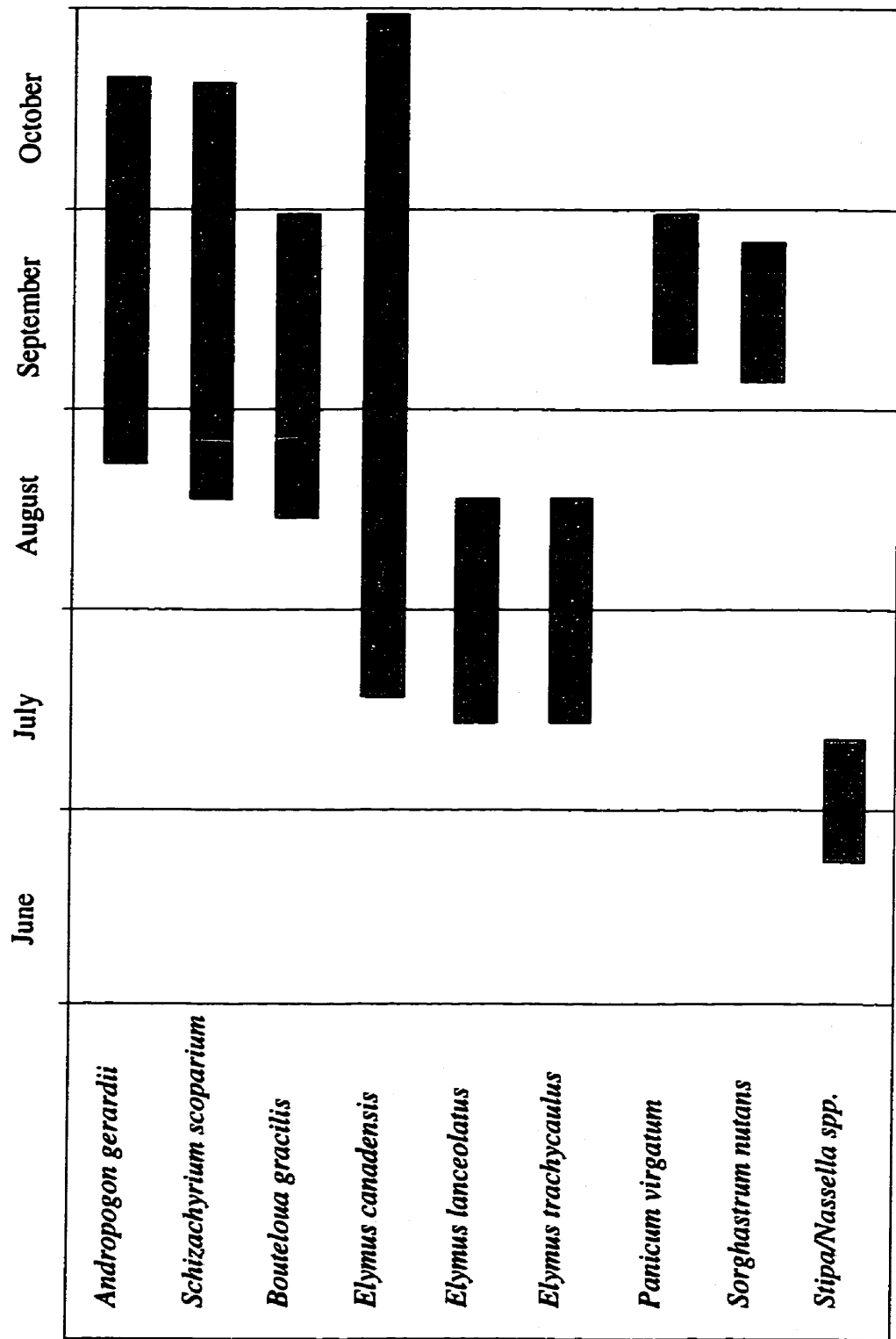
APPENDIX IV. Monoculture densities (no. individuals m^{-2}) of twelve native grass species grown in a diallel competition experiment at Carman and Winnipeg in 1995 and 1996.

Species	Rep. No.	Carman 1995	Mean	Carman 1996	Mean	Winnipeg 1996	Mean
Elymus	1	46	68.0	16	15.3	18	18.0
lanceolatus	2	88		12		12	
	3	70		18		24	
Andropogon	1	136	106.0	34	26.0	22	18.7
gerardii	2	78		22		10	
	3	104		22		24	
Bouteloua	1	356	162.0	0	16.7	30	26.0
curtipendula	2	104		40		26	
	3	26		10		22	
Bouteloua	1	68	56.7	0	7.3	10	9.3
gracilis	2	100		14		10	
	3	2		8		8	
Elymus	1	68	50.7	18	27.3	48	32.7
canadensis	2	58		34		16	
	3	26		30		34	
Elymus	1	28	29.3	30	34.0	20	34.7
trachycaulus	2	46		42		34	
	3	14		30		50	
Pascopyrum	1	62	75.3	20	25.3	20	15.3
smithii	2	92		32		20	
	3	72		24		6	
Panicum	1	44	43.3	30	22.0	10	14.0
virgatum	2	64		18		20	
	3	22		18		12	
Stipa	1	64	37.3	32	15.3	2	3.3
comata	2	40		14		4	
	3	8		0		4	
Sorghastrum	1	8	11.3	12	12.7	12	12.7
nutans	2	22		22		8	
	3	4		4		18	
Schizachyrium	1	90	90.0	20	17.3	8	15.3
scoparium	2	120		20		14	
	3	60		12		24	
Stipa	1	46	34.7	28	23.3	18	18.0
viridula	2	50		18		16	
	3	8		24		20	

APPENDIX V. Dry above-ground biomass (g per sample) of 12 species grown in two replacement series diallel competition experiments at Carman and Winnipeg, over two growing seasons. Codes: Ag = *Andropogon gerardii* , Bc = *Bouteloua curtipendula* , Bg = *Bouteloua gracilis* , Ec = *Elymus canadensis* , El = *Elymus lanceolatus* , Et = *Elymus trachycaulus* , Nv = *Nassella viridula* , Ps = *Pascopyrum smithii* , Pv = *Panicum virgatum* , Sc = *Stipa comata* , Sn = *Sorghastrum nutans* , Ss = *Schizachyrium scoparium* .

Monoculture Yields

Species	Neighbour	Rep. No.	Carman				Winnipeg			
			1995	Mean/2	1996	Mean/2	1996	Mean/2	1997	Mean/2
El	None	1	51.8	39.8	287.8	178.5	155.2	88.9	367.7	298.1
El		2	58.3		350.7		185.6		738.3	
El		3	128.9		432.4		192.6		682.6	
Ag	None	1	180.9	78.7	1064.2	519.2	479.3	201.2	1177.0	690.3
Ag		2	129.8		1131.6		273.1		1167.5	
Ag		3	161.6		919.1		454.7		1797.0	
Bc	None	1	71.2	35.6	596.3	303.2	153.5	105.1	471.0	250.9
Bc		2	96.5		826.3		200.1		642.3	
Bc		3	45.9		396.4		276.8		392.0	
Bg	None	1	40.8	19.2	182.4	78.0	18.4	7.3	37.4	22.4
Bg		2	46.3		197.1		16.7		56.3	
Bg		3	28.2		88.7		8.7		40.7	
Ec	None	1	157.2	70.7	1618.3	786.6	703.5	233.6	1476.6	904.6
Ec		2	131.4		1863.2		270.0		1706.4	
Ec		3	135.8		1237.9		427.8		2244.6	
Et	None	1	300.3	152.0	1276.9	619.3	473.2	236.8	1241.8	539.0
Et		2	275.5		1192.7		332.7		1026.4	
Et		3	336.3		1245.9		614.7		965.6	
Ps	None	1	78.3	57.0	721.7	296.8	79.4	43.2	704.7	240.3
Ps		2	94.1		543.9		123.7		412.2	
Ps		3	169.7		515.4		56.3		325.0	
Pv	None	1	273.0	124.5	937.8	515.3	298.4	140.1	1657.5	546.1
Pv		2	229.7		731.0		252.0		630.7	
Pv		3	244.2		1422.7		290.3		988.6	
Sc	None	1	16.0	6.3	120.4	68.0	8.0	3.1	12.3	5.0
Sc		2	9.1		151.7		8.6		13.6	
Sc		3	12.6		136.1		2.1		4.1	
Sn	None	1	18.9	11.8	291.8	179.0	128.1	58.8	590.5	356.4
Sn		2	31.9		460.6		56.6		532.6	
Sn		3	20.1		321.6		167.9		1015.3	
Ss	None	1	59.1	30.4	956.4	258.0	64.9	22.1	436.5	204.8
Ss		2	65.1		360.4		38.4		614.7	
Ss		3	57.9		231.1		29.2		177.7	
Nv	None	1	52.2	33.1	982.2	483.2	116.9	40.1	503.0	279.8
Nv		2	97.9		1114.1		60.0		268.2	
Nv		3	48.5		803.0		63.9		907.8	

Elymus lanceolatus

			Carman				Winnipeg			
Species	Neighbour	Rep. No.	1995	Mean	1996	Mean	1996	Mean	1997	Mean
El	Ps	1	31.6	25.7	215.5	204.5	80.5	91.5	330.0	192.3
El		2	18.0		276.5		137.1		123.1	
El		3	27.6		121.6		56.8		123.8	
El	Et	1	12.8	16.1	21.3	72.4	1.2	2.9	34.0	39.2
El		2	20.8		72.3		1.6		18.0	
El		3	14.7		123.6		5.9		65.7	
El	Ec	1	36.9	41.6	135.9	478.1	40.6	62.6	130.3	154.0
El		2	42.3		549.2		60.0		239.1	
El		3	45.5		749.3		87.3		92.6	
El	Sc	1	62.8	44.6	332.3	464.0	289.2	189.5	330.6	411.3
El		2	34.3		367.6		155.9		525.6	
El		3	36.6		692.0		123.4		377.8	
El	Nv	1	35.3	24.4	187.9	289.0	32.5	42.3	223.8	391.8
El		2	24.6		377.7		50.3		358.9	
El		3	13.3		301.3		44.0		592.8	
El	Ag	1	21.3	29.5	304.7	245.2	36.6	45.8	77.3	272.1
El		2	40.0		177.8		76.8		361.2	
El		3	27.3		253.1		24.0		377.7	
El	Ss	1	28.1	26.3	847.9	773.6	49.5	102.0	234.9	382.0
El		2	30.7		717.5		168.9		521.3	
El		3	20.2		755.5		87.5		389.8	
El	Bc	1	20.6	34.1	415.9	382.4	80.5	90.0	432.7	410.4
El		2	36.7		398.9		120.5		412.3	
El		3	44.9		332.4		69.0		386.2	
El	Bg	1	53.5	42.1	755.2	641.2	121.1	151.0	311.3	396.4
El		2	34.2		434.4		202.4		407.5	
El		3	38.7		734.0		129.4		470.5	
El	Pv	1	24.1	29.5	509.3	311.4	37.4	52.5	173.1	282.6
El		2	23.1		238.8		37.1		329.8	
El		3	41.3		186.0		82.9		344.8	
El	Sn	1	33.3	30.3	472.9	561.9	119.8	145.6	456.4	417.6
El		2	28.8		565.1		98.3		520.3	
El		3	28.9		647.7		218.8		276.0	

Andropogon gerardii

Species	Neighbour	Rep. No.	Carman				Winnipeg			
			1995	Mean	1996	Mean	1996	Mean	1997	Mean
Ag	Ss	1	63.3	135.9	332.5	889.7	283.4	316.3	1382.4	1286.5
Ag		2	147.3		1088.4		405.6		1160.9	
Ag		3	197.1		1248.3		260.0		1316.1	
Ag	Bc	1	170.6	130.7	731.8	861.3	269.1	269.1	636.3	789.7
Ag		2	118.4		855.4		284.5		916.9	
Ag		3	103.2		996.6		253.7		815.9	
Ag	Bg	1	82.0	140.4	1568.8	1118.3	238.1	270.4	1434.7	1013.0
Ag		2	154.0		1244.1		329.7		1063.2	
Ag		3	185.3		542.0		243.4		541.1	
Ag	Pv	1	155.9	170.5	454.5	402.8	199.3	202.6	834.5	527.9
Ag		2	208.2		545.0		308.9		605.8	
Ag		3	147.5		208.9		99.6		143.5	
Ag	Sn	1	176.2	160.6	1028.2	935.8	382.0	301.7	1379.0	889.3
Ag		2	136.4		689.7		339.0		543.1	
Ag		3	169.3		1089.6		184.1		745.7	
Ag	Ps	1	161.1	141.8	522.8	419.3	260.1	263.0	414.6	575.9
Ag		2	170.4		317.9		252.6		673.5	
Ag		3	93.9		417.3		276.4		639.7	
Ag	El	1	223.5	204.3	736.3	557.9	156.7	156.7	1035.1	672.8
Ag		2	228.7		616.0		191.1		714.9	
Ag		3	160.7		321.5		122.3		268.4	
Ag	Et	1	70.6	68.1	32.2	47.9	17.3	19.2	42.5	76.9
Ag		2	91.0		45.3		22.1		87.9	
Ag		3	42.8		66.3		18.3		100.3	
Ag	Ec	1	116.0	109.0	14.8	26.3	120.1	112.9	138.2	214.1
Ag		2	140.8		26.3		155.1		323.6	
Ag		3	70.1		37.9		63.5		180.5	
Ag	Sc	1	76.3	118.3	599.5	736.5	441.2	297.6	2065.4	1369.9
Ag		2	204.3		916.4		173.0		981.0	
Ag		3	74.4		693.7		278.6		1063.4	
Ag	Nv	1	174.9	157.1	570.3	596.8	294.0	238.2	1162.6	782.4
Ag		2	157.4		453.0		223.7		527.9	
Ag		3	139.1		767.0		196.9		656.8	

Bouteloua curtipendula

Species	Neighbour	Rep. No.	Carman				Winnipeg			
			1995	Mean	1996	Mean	1996	Mean	1997	Mean
Bc	Ag	1	45.7	47.6	96.0	73.8	92.9	66.6	107.2	151.3
Bc		2	20.1		84.5		71.6		164.5	
Bc		3	76.9		41.0		35.2		182.3	
Bc	Ss	1	55.2	66.7	894.7	669.5	253.7	219.7	414.3	413.4
Bc		2	57.7		394.2		129.0		588.4	
Bc		3	87.2		719.6		276.4		237.6	
Bc	Bg	1	83.6	72.4	260.3	440.6	409.4	242.3	481.6	779.1
Bc		2	101.3		831.1		255.4		1341.1	
Bc		3	32.2		230.4		62.2		514.7	
Bc	Pv	1	46.2	42.4	238.3	148.3	74.6	114.2	422.4	364.6
Bc		2	58.2		102.7		85.0		373.2	
Bc		3	22.9		104.0		182.9		298.2	
Bc	Sn	1	77.3	69.5	651.7	789.7	163.7	152.6	330.0	414.5
Bc		2	93.2		898.2		170.3		438.6	
Bc		3	38.1		819.3		123.9		475.0	
Bc	Ps	1	54.6	39.9	71.5	113.0	107.3	100.8	48.5	78.3
Bc		2	23.5		167.8		94.3		68.4	
Bc		3	41.7		99.6		100.8		117.9	
Bc	El	1	44.0	28.2	109.2	247.2	117.8	68.0	318.8	190.3
Bc		2	17.7		221.6		44.1		136.4	
Bc		3	22.9		410.9		42.1		115.6	
Bc	Et	1	25.6	29.6	0.1	4.9	4.2	4.3	12.6	29.4
Bc		2	32.6		0.0		6.7		70.9	
Bc		3	30.7		14.7		2.1		4.6	
Bc	Ec	1	63.3	56.2	1.5	31.6	32.4	58.6	10.1	22.5
Bc		2	79.5		25.2		95.6		43.6	
Bc		3	25.7		68.0		47.8		13.8	
Bc	Sc	1	92.9	83.9	653.1	404.9	126.9	154.3	689.0	457.8
Bc		2	114.0		397.8		186.6		300.7	
Bc		3	44.8		163.8		149.3		383.7	
Bc	Nv	1	105.1	101.2	295.8	353.5	178.7	120.3	292.1	389.6
Bc		2	89.1		537.7		130.5		683.7	
Bc		3	109.3		226.9		51.6		193.1	

Bouteloua gracilis

Species	Neighbour	Rep. No.	Carman				Winnipeg			
			1995	Mean	1996	Mean	1996	Mean	1997	Mean
Bg	Ag	1	21.5	38.4	26.3	28.1	0.0	2.5	0.0	18.0
Bg		2	84.4		57.9		0.0		0.0	
Bg		3	9.2		0.0		7.5		54.0	
Bg	Ss	1	23.0	21.3	114.2	231.6	13.1	8.6	77.8	34.1
Bg		2	24.8		257.2		2.2		0.6	
Bg		3	16.0		323.4		10.4		24.0	
Bg	Bc	1	20.1	20.4	11.2	44.5	2.9	3.0	0.0	0.6
Bg		2	14.5		58.4		6.1		1.8	
Bg		3	26.7		63.8		0.0		0.0	
Bg	Pv	1	11.9	12.1	35.5	13.7	0.8	0.8	0.0	1.3
Bg		2	21.0		5.6		0.9		0.0	
Bg		3	3.5		0.0		0.6		3.8	
Bg	Sn	1	8.0	9.8	72.3	166.6	24.8	15.1	0.0	9.9
Bg		2	19.0		325.2		1.9		0.0	
Bg		3	2.5		102.4		18.6		29.6	
Bg	El	1	24.1	25.8	43.3	33.2	1.5	3.8	3.9	11.5
Bg		2	40.8		5.1		0.0		0.0	
Bg		3	12.6		51.3		9.9		30.5	
Bg	Sc	1	43.1	40.7	228.0	280.3	4.3	16.0	59.9	92.4
Bg		2	44.2		334.3		25.8		142.8	
Bg		3	34.8		278.7		18.0		74.6	
Bg	Nv	1	18.8	18.6	55.4	32.5	7.3	5.4	16.9	19.9
Bg		2	36.6		15.2		6.5		27.7	
Bg		3	0.5		26.8		2.3		15.2	
Bg	Ec	1	16.7	14.8	6.4	2.8	6.6	3.9	0.0	0.0
Bg		2	6.0		1.9		3.2		0.0	
Bg		3	21.8		0.0		1.9		0.0	
Bg	Et	1	5.5	7.7	2.0	3.0	0.0	0.0	0.0	0.0
Bg		2	5.4		7.1		0.0		0.0	
Bg		3	12.3		0.0		0.0		0.0	
Bg	Ps	1	24.3	11.2	15.9	22.6	7.4	4.6	0.0	0.0
Bg		2	4.6		9.6		5.7		0.0	
Bg		3	4.8		42.2		0.6		0.0	

Elymus canadensis

Species	Neighbour	Rep. No.	Carman				Winnipeg			
			1995	Mean	1996	Mean	1996	Mean	1997	Mean
Ec	Ps	1	133.1	144.2	1612.1	1297.7	430.0	424.3	600.4	1144.3
Ec		2	111.1		1218.3		502.1		1394.4	
Ec		3	188.4		1062.8		340.9		1438.0	
Ec	El	1	64.7	103.8	1465.7	1317.2	472.0	386.7	1426.8	1093.9
Ec		2	63.6		1252.2		257.9		698.0	
Ec		3	183.2		1233.6		430.2		1157.0	
Ec	Et	1	33.1	60.2	196.5	344.3	102.9	124.6	495.1	394.6
Ec		2	29.9		168.3		110.4		143.4	
Ec		3	117.7		668.1		160.5		545.2	
Ec	Sc	1	93.7	159.8	412.4	966.1	443.5	410.0	1456.8	1318.5
Ec		2	225.6		1690.0		432.4		1205.9	
Ec		3	160.2		795.8		354.1		1292.8	
Ec	Nv	1	66.8	117.8	1978.3	2001.3	415.7	171.2	1307.5	1213.3
Ec		2	140.4		2149.4		48.4		728.7	
Ec		3	146.2		1876.1		49.4		1603.6	
Ec	Ag	1	85.8	126.4	605.2	1144.5	628.7	508.0	1238.9	1267.2
Ec		2	86.6		1378.4		508.0		1140.1	
Ec		3	206.9		1449.8		387.3		1422.6	
Ec	Ss	1	124.5	104.2	2053.3	1410.1	114.3	222.8	761.5	1420.9
Ec		2	66.2		1095.5		166.4		1857.2	
Ec		3	121.8		1081.5		387.6		1643.9	
Ec	Bc	1	128.2	124.7	1977.9	1562.0	120.9	317.4	1762.2	1702.5
Ec		2	101.7		1317.2		289.3		1678.3	
Ec		3	144.2		1391.0		542.1		1666.9	
Ec	Bg	1	16.2	114.5	1161.4	1694.0	156.5	217.5	1146.4	2016.0
Ec		2	139.1		1657.0		244.8		2758.4	
Ec		3	188.2		2263.6		251.1		2143.2	
Ec	Pv	1	31.7	106.7	961.5	1513.7	301.9	398.1	1872.2	1538.9
Ec		2	96.9		1463.2		375.4		1156.6	
Ec		3	191.4		2116.3		517.0		1587.9	
Ec	Sn	1	85.3	130.9	2653.0	1808.2	576.5	482.4	1272.2	1588.1
Ec		2	153.4		1414.4		527.7		1658.0	
Ec		3	154.0		1357.1		343.0		1834.0	

Elymus trachycaulus

Species	Neighbour	Rep. No.	Carman				Winnipeg			
			1995	Mean	1996	Mean	1996	Mean	1997	Mean
Et	Ps	1	163.4	177.1	720.3	770.8	438.5	438.5	1078.4	979.8
Et		2	155.0		783.4		420.3		1233.2	
Et		3	212.8		808.8		456.7		627.9	
Et	El	1	105.8	183.1	582.6	718.0	472.6	493.5	1153.7	1203.1
Et		2	169.4		903.6		469.7		1075.3	
Et		3	274.0		667.8		538.2		1380.4	
Et	Ec	1	114.0	250.5	815.6	918.5	870.4	558.3	672.0	853.4
Et		2	248.9		769.1		546.1		1131.9	
Et		3	388.5		1170.8		258.4		756.2	
Et	Sc	1	234.2	204.9	1199.4	975.8	573.3	417.0	981.9	1110.0
Et		2	193.1		984.7		259.1		1193.1	
Et		3	187.5		743.3		418.6		1155.1	
Et	Nv	1	250.7	248.5	477.8	627.2	203.3	522.2	1145.3	1061.8
Et		2	244.2		541.4		845.1		1118.0	
Et		3	250.6		862.5		518.1		922.1	
Et	Ag	1	169.6	208.9	1611.7	1459.0	278.3	384.7	710.3	793.4
Et		2	137.0		1091.3		366.8		928.6	
Et		3	320.0		1674.1		509.1		741.3	
Et	Ss	1	199.9	264.7	1327.9	1275.3	760.1	590.7	1153.9	1150.2
Et		2	171.0		890.5		590.5		1244.4	
Et		3	423.1		1607.6		421.5		1052.3	
Et	Bc	1	227.5	250.4	1030.1	1137.2	434.8	410.6	983.1	1048.0
Et		2	225.1		815.9		336.6		975.2	
Et		3	298.5		1565.5		460.4		1185.6	
Et	Bg	1	206.9	208.4	708.8	1064.5	365.6	409.1	610.7	991.2
Et		2	163.6		1245.0		479.5		932.9	
Et		3	254.8		1239.8		382.2		1429.9	
Et	Pv	1	164.8	180.6	360.5	545.9	1002.6	600.8	1158.6	1034.2
Et		2	108.4		734.1		601.3		1036.4	
Et		3	268.5		543.0		198.5		907.5	
Et	Sn	1	252.7	240.6	1366.6	1276.3	480.8	583.2	928.9	957.2
Et		2	189.9		1221.4		551.2		559.3	
Et		3	279.1		1240.9		717.5		1383.3	

Pascopyrum smithii

Species	Neighbour	Rep. No.	Carman				Winnipeg			
			1995	Mean	1996	Mean	1996	Mean	1997	Mean
Ps	El	1	31.5	40.6	433.4	534.2	29.7	30.9	121.6	353.9
Ps		2	44.6		428.6		19.8		483.7	
Ps		3	45.7		740.5		43.2		456.3	
Ps	Et	1	21.6	16.0	57.2	69.7	1.4	2.7	9.5	22.8
Ps		2	13.8		52.6		5.9		14.2	
Ps		3	12.6		99.4		0.9		44.6	
Ps	Ec	1	43.4	43.8	6.1	97.5	3.8	3.9	108.5	57.5
Ps		2	42.3		181.0		5.5		17.5	
Ps		3	45.8		105.3		2.5		46.5	
Ps	Sc	1	19.5	32.5	648.9	601.6	39.9	63.1	327.1	482.7
Ps		2	23.5		466.2		53.1		811.6	
Ps		3	54.6		689.6		96.2		309.4	
Ps	Nv	1	26.9	52.8	613.2	481.2	26.0	46.8	982.9	617.8
Ps		2	55.0		203.4		24.4		406.6	
Ps		3	76.4		626.9		90.0		463.8	
Ps	Ag	1	32.3	30.5	310.4	579.5	11.8	21.0	327.6	345.2
Ps		2	15.6		522.0		24.8		548.0	
Ps		3	43.6		906.0		26.3		160.1	
Ps	Ss	1	45.5	63.1	238.3	426.1	54.7	55.9	459.7	441.9
Ps		2	42.3		418.8		85.2		565.6	
Ps		3	101.5		621.2		27.7		300.3	
Ps	Bc	1	24.8	64.1	304.5	375.7	51.6	33.2	541.9	543.0
Ps		2	57.3		252.2		40.6		555.8	
Ps		3	110.1		570.3		7.3		531.4	
Ps	Bg	1	18.5	39.1	332.9	655.2	125.1	66.3	603.5	540.1
Ps		2	38.7		1018.0		32.9		714.9	
Ps		3	60.0		614.8		40.9		301.9	
Ps	Pv	1	33.9	34.6	483.6	380.1	42.4	24.2	123.0	254.1
Ps		2	27.9		320.6		21.4		338.8	
Ps		3	42.0		336.1		8.9		300.4	
Ps	Sn	1	39.1	49.1	631.8	711.6	81.4	93.2	529.5	503.2
Ps		2	78.1		727.0		110.8		457.0	
Ps		3	30.1		776.0		87.4		523.2	

Panicum virgatum

Species	Neighbour	Rep. No.	1995	Mean	1996	Mean	1996	Mean	1997	Mean
					Carman			**Winnipeg**		
Pv	Ag	1	72.4	76.2	499.9	540.5	122.6	132.8	575.0	366.2
Pv		2	124.8		503.9		167.7		389.7	
Pv		3	31.3		617.8		108.1		134.0	
Pv	Ss	1	268.6	239.2	1103.4	1064.8	95.8	182.1	975.4	873.0
Pv		2	157.4		1025.5		203.4		934.0	
Pv		3	291.6		1065.5		247.0		709.5	
Pv	Bc	1	76.7	171.0	101.3	553.1	169.6	223.5	946.5	733.7
Pv		2	167.2		589.1		288.3		584.0	
Pv		3	269.0		969.0		212.5		670.6	
Pv	Bg	1	124.4	142.3	893.6	1055.3	234.9	234.9	1132.4	1093.3
Pv		2	171.8		1106.7		352.3		1445.6	
Pv		3	130.8		1165.6		117.4		701.8	
Pv	Sn	1	145.9	148.3	223.9	524.9	255.3	172.9	572.3	641.3
Pv		2	137.8		738.0		114.4		684.0	
Pv		3	161.1		612.7		149.1		667.7	
Pv	Ps	1	186.5	163.0	366.4	171.0	180.9	102.3	188.6	219.1
Pv		2	125.2		69.2		94.8		69.1	
Pv		3	177.3		77.3		31.1		399.7	
Pv	El	1	202.2	161.1	866.4	605.3	112.7	81.5	568.2	439.4
Pv		2	130.3		368.8		81.5		432.7	
Pv		3	150.9		580.6		50.2		317.3	
Pv	Et	1	80.3	77.7	53.4	24.0	31.3	17.6	109.9	85.6
Pv		2	87.6		18.6		10.3		117.0	
Pv		3	65.2		0.0		11.3		29.9	
Pv	Ec	1	13.9	82.8	11.3	66.9	140.2	126.6	55.8	133.8
Pv		2	185.7		163.3		143.2		234.1	
Pv		3	48.7		26.1		96.5		111.6	
Pv	Sc	1	192.4	194.0	336.3	614.1	205.9	265.2	622.0	1040.3
Pv		2	241.4		817.4		290.9		912.4	
Pv		3	148.3		688.5		298.8		1586.5	
Pv	Nv	1	221.1	148.4	430.2	316.9	313.6	269.3	536.4	831.8
Pv		2	132.7		172.7		249.1		1251.7	
Pv		3	91.3		347.7		245.1		707.4	

Stipa comata

Species	Neighbour	Rep. No.	Carman				Winnipeg			
			1995	Mean	1996	Mean	1996	Mean	1997	Mean
Sc	Et	1	1.4	2.0	0.0	0.1	0.1	0.0	0.0	0.0
Sc		2	0.5		0.3		0.0		0.0	
Sc		3	4.2		0.0		0.0		0.0	
Sc	Ec	1	6.8	7.2	2.8	2.6	1.2	0.6	0.0	1.3
Sc		2	14.8		5.1		0.0		0.0	
Sc		3	0.0		0.0		0.5		3.8	
Sc	Ss	1	2.3	5.0	102.5	84.0	0.8	0.8	5.6	7.4
Sc		2	5.1		117.7		0.9		4.2	
Sc		3	7.6		31.7		0.6		12.3	
Sc	Bg	1	3.6	3.4	91.3	100.6	51.2	27.4	62.8	66.3
Sc		2	5.6		96.4		23.2		83.3	
Sc		3	1.1		114.2		7.9		52.9	
Sc	Sn	1	9.1	10.0	34.3	54.1	1.0	1.5	23.6	35.2
Sc		2	6.7		47.0		1.6		18.6	
Sc		3	14.1		81.0		2.0		63.3	
Sc	Bc	1	5.2	6.6	111.2	74.2	0.0	0.0	0.0	0.0
Sc		2	10.5		43.8		0.0		0.0	
Sc		3	4.1		67.6		0.0		0.0	
Sc	Pv	1	3.6	4.2	19.1	66.7	0.4	0.9	0.0	0.0
Sc		2	4.7		27.9		1.7		0.0	
Sc		3	4.4		153.2		0.5		0.0	
Sc	Ps	1	10.0	7.2	56.1	30.6	0.9	0.3	0.0	0.0
Sc		2	7.5		21.0		0.0		0.0	
Sc		3	4.0		14.7		0.0		0.0	
Sc	Nv	1	1.8	5.9	18.2	46.7	3.4	4.6	0.0	0.0
Sc		2	3.3		22.1		8.7		0.0	
Sc		3	12.7		99.8		1.8		0.0	
Sc	El	1	5.4	3.5	58.9	60.9	0.0	0.2	0.0	0.0
Sc		2	3.5		54.3		0.6		0.0	
Sc		3	1.5		69.5		0.0		0.0	
Sc	Ag	1	1.3	1.7	39.4	31.1	3.7	4.5	0.0	0.0
Sc		2	1.7		38.5		0.0		0.0	
Sc		3	2.1		15.5		9.7		0.0	

Sorghastrum nutans

Species	Neighbour	Rep. No.	Carman				Winnipeg			
			1995	Mean	1996	Mean	1996	Mean	1997	Mean
Sn	Ag	1	3.1	2.4	0.0	1.2	23.6	12.1	64.1	26.4
Sn		2	2.7		3.7		7.4		2.6	
Sn		3	1.3		0.0		5.2		12.5	
Sn	Ss	1	3.9	13.3	38.7	146.4	82.2	43.5	202.1	391.6
Sn		2	2.9		140.3		29.4		441.0	
Sn		3	33.1		260.1		18.9		531.7	
Sn	Bc	1	8.7	11.1	21.7	82.2	44.7	41.3	507.4	315.3
Sn		2	20.8		164.0		29.3		261.0	
Sn		3	3.7		60.9		49.8		177.5	
Sn	Bg	1	18.8	14.5	42.9	62.9	23.2	25.9	254.0	317.0
Sn		2	23.8		122.5		9.9		85.0	
Sn		3	1.0		23.4		44.7		612.1	
Sn	Pv	1	21.1	14.1	23.3	10.4	46.6	35.4	0.0	13.8
Sn		2	12.9		7.9		12.6		25.7	
Sn		3	8.3		0.0		47.0		15.7	
Sn	Ps	1	18.5	12.8	21.9	9.6	23.7	61.0	13.7	56.2
Sn		2	13.4		0.0		95.8		32.5	
Sn		3	6.6		6.9		63.6		122.3	
Sn	El	1	12.6	11.8	70.3	84.0	28.0	46.7	150.7	115.9
Sn		2	12.5		116.5		81.1		92.3	
Sn		3	10.4		65.2		31.1		104.7	
Sn	Et	1	0.0	0.9	0.0	0.1	1.2	0.9	48.3	24.4
Sn		2	2.0		0.0		0.6		10.2	
Sn		3	0.8		0.2		0.8		14.8	
Sn	Ec	1	6.2	21.4	4.0	5.9	3.0	4.5	54.9	49.1
Sn		2	31.6		13.8		3.8		65.9	
Sn		3	26.4		0.0		6.8		26.5	
Sn	Sc	1	14.0	17.0	504.5	313.6	41.7	75.0	206.9	228.3
Sn		2	25.1		288.7		76.7		183.9	
Sn		3	12.0		147.6		106.7		294.0	
Sn	Nv	1	14.5	17.9	77.0	94.2	23.5	134.4	156.6	176.9
Sn		2	13.8		125.5		290.6		202.2	
Sn		3	25.5		80.1		89.2		172.0	

Schizachyrium scoparium

			Carman				Winnipeg			
Species	Neighbour	Rep. No.	1995	Mean	1996	Mean	1996	Mean	1997	Mean
Ss	Ag	1	20.8	14.0	101.5	33.8	0.4	1.4	16.8	11.7
Ss		2	10.8		0.0		1.9		8.6	
Ss		3	10.5		0.0		1.9		9.8	
Ss	Bc	1	7.0	8.9	128.9	147.1	6.2	7.5	130.7	90.3
Ss		2	7.7		216.8		3.9		101.6	
Ss		3	12.0		95.6		12.4		38.7	
Ss	Bg	1	14.8	17.7	119.1	405.8	73.7	54.1	195.8	321.9
Ss		2	15.1		517.3		31.5		229.1	
Ss		3	23.3		581.1		57.1		540.7	
Ss	Pv	1	12.4	20.0	16.8	29.7	21.2	14.4	41.8	67.4
Ss		2	21.7		28.0		5.1		87.0	
Ss		3	25.8		44.3		17.0		73.4	
Ss	Sn	1	7.5	8.9	431.9	350.9	46.9	48.0	114.1	105.2
Ss		2	7.6		241.3		19.0		82.6	
Ss		3	11.5		379.6		78.1		118.8	
Ss	Ps	1	7.5	27.3	15.2	31.9	5.9	2.4	0.0	3.8
Ss		2	34.1		80.4		0.7		1.0	
Ss		3	40.2		0.0		0.5		10.3	
Ss	El	1	12.6	16.7	99.3	91.4	13.0	8.3	28.9	17.7
Ss		2	25.5		109.4		11.5		14.0	
Ss		3	11.9		65.4		0.5		10.1	
Ss	Ec	1	11.7	21.8	22.5	13.4	4.9	4.6	8.9	12.7
Ss		2	29.6		17.6		6.7		7.5	
Ss		3	24.0		0.0		2.1		21.7	
Ss	Sc	1	3.6	19.3	312.1	537.3	54.6	27.7	94.6	83.1
Ss		2	32.8		682.5		13.1		55.3	
Ss		3	21.6		617.3		15.3		99.4	
Ss	Nv	1	12.3	9.7	78.3	120.2	5.4	6.4	136.1	81.8
Ss		2	11.5		130.5		10.3		51.2	
Ss		3	5.2		151.8		3.4		58.1	
Ss	Et	1	3.1	4.1	0.0	0.0	0.0	0.0	0.0	0.0
Ss		2	8.3		0.0		0.0		0.0	
Ss		3	1.0		0.0		0.0		0.0	

Nassella viridula

Species	Neighbour	Rep. No.	Carman				Winnipeg			
			1995	Mean	1996	Mean	1996	Mean	1997	Mean
Nv	Ps	1	13.2	21.3	353.8	236.1	61.7	107.7	49.9	110.6
Nv		2	35.9		210.3		66.2		217.8	
Nv		3	14.8		144.3		195.1		64.0	
Nv	El	1	27.0	24.1	237.3	264.4	9.4	18.6	75.0	199.1
Nv		2	26.8		137.2		25.3		396.6	
Nv		3	18.5		418.8		21.0		125.8	
Nv	Et	1	0.9	3.4	7.3	2.4	1.2	1.8	30.6	73.9
Nv		2	5.8		0.0		1.8		82.4	
Nv		3	3.4		0.0		2.3		108.8	
Nv	Ec	1	21.5	22.7	52.8	43.3	0.4	1.6	53.4	122.8
Nv		2	36.2		15.3		2.8		129.0	
Nv		3	10.4		61.9		1.7		185.9	
Nv	Sc	1	44.0	46.7	306.8	710.3	112.4	90.6	642.7	607.8
Nv		2	48.2		1148.7		88.6		829.1	
Nv		3	47.9		675.5		70.9		351.5	
Nv	Ag	1	8.2	24.7	117.8	266.2	68.4	31.4	108.7	110.9
Nv		2	41.9		166.6		13.5		106.3	
Nv		3	23.9		514.2		12.4		117.7	
Nv	Ss	1	15.9	20.5	318.7	451.2	15.2	38.4	73.5	366.5
Nv		2	30.1		407.8		70.8		478.9	
Nv		3	15.4		627.2		29.3		547.1	
Nv	Bc	1	21.0	37.5	511.1	495.8	18.5	50.0	120.7	318.6
Nv		2	55.1		685.2		91.9		632.1	
Nv		3	36.4		291.2		39.5		202.9	
Nv	Bg	1	13.0	13.5	766.8	526.3	30.3	78.4	242.8	687.7
Nv		2	17.3		375.7		68.3		705.6	
Nv		3	10.3		436.4		136.5		1114.6	
Nv	Pv	1	26.7	32.5	184.7	207.4	496.2	210.5	253.9	242.4
Nv		2	41.9		132.6		108.9		365.5	
Nv		3	28.9		304.8		26.4		107.7	
Nv	Sn	1	33.4	33.4	616.8	846.4	61.4	82.6	130.6	405.9
Nv		2	39.1		789.8		150.5		451.9	
Nv		3	27.7		1132.6		35.9		635.1	

APPENDIX VI. Contents and proportions of species used in eight experimental seed mixture sets. Codes: %Pure =% purity; %Germ = % germination; %Estab = % monoculture establishment from Carman 1995 data; PLS factor = factor correcting for %Pure and %Germ; COMP factor = factor correcting for competitive abilities observed at Carman in 1995 competitive differences observed at Carman 1995; Plants/ft² = theoretical establishment density of species; PLS/m² = number of PLS seeds sown per m².

MIXTURE SET # 1 (control)

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
E. canadensis	3596	93.62	80.00	100.00	1.34	1.00	0.50	5.38
E. lanceolatus	W-14-05-1050	97.40	97.00	100.00	1.06	1.00	0.50	5.38
E. trachycaulus	89-8-95308	96.62	97.00	100.00	1.07	1.00	0.50	5.38
N. viridula	NG-95-001	98.87	86.00	100.00	1.18	1.00	0.50	5.38
P. smithii	west5226	95.94	99.00	100.00	1.05	1.00	0.50	5.38
S. comata	5CW 95-1	88.40	84.00	100.00	1.35	1.00	0.50	5.38
A. gerardii	3584	89.68	91.00	100.00	1.23	1.00	0.50	5.38
B. curtipendula	#5-95	82.25	66.00	100.00	1.84	1.00	0.50	5.38
P. virgatum	7545	99.04	73.00	100.00	1.38	1.00	0.50	5.38
B. gracilis	#2-95	67.27	57.00	100.00	2.61	1.00	0.50	5.38
S. nutans	#5-95	82.10	75.00	100.00	1.62	1.00	0.50	5.38
S. scoparius	#4-95	68.32	72.00	100.00	2.03	1.00	0.50	5.38

MIXTURE SET # 1 (adjusted)

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
E. canadensis	3596	93.62	80.00	24.35	5.48	0.87	0.44	19.23
E. lanceolatus	W-14-05-1050	97.40	97.00	15.24	6.95	1.04	0.52	36.84
E. trachycaulus	89-8-95308	96.62	97.00	16.44	6.49	0.90	0.45	29.58
N. viridula	NG-95-001	98.87	86.00	8.37	14.06	1.09	0.54	69.96
P. smithii	west5226	95.94	99.00	16.88	6.24	1.06	0.53	33.74
S. comata	5CW 95-1	88.40	84.00	7.77	17.33	1.11	0.55	76.64
A. gerardii	3584	89.68	91.00	23.76	5.16	0.86	0.43	19.53
B. curtipendula	#5-95	82.25	66.00	36.31	5.07	0.87	0.43	12.89
P. virgatum	7545	99.04	73.00	9.71	14.24	0.95	0.47	52.56
B. gracilis	#2-95	67.27	57.00	12.70	20.54	0.99	0.50	42.08
S. nutans	#5-95	82.10	75.00	2.54	63.94	1.02	0.51	216.19
S. scoparius	#4-95	68.32	72.00	20.17	10.08	1.24	0.62	33.02

MIXTURE SET # 2 (control)
SPECIES: ALL C₄ SPECIES

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
A. gerardii	3584	89.68	91.00	100.00	1.23	1.00	1.00	10.76
B. curtipendula	#5-95	82.25	66.00	100.00	1.84	1.00	1.00	10.76
P. virgatum	7545	99.04	73.00	100.00	1.38	1.00	1.00	10.76
B. gracilis	#2-95	67.27	57.00	100.00	2.61	1.00	1.00	10.76
S. nutans	#5-95	82.10	75.00	100.00	1.62	1.00	1.00	10.76
S. scoparius	#4-95	68.32	72.00	100.00	2.03	1.00	1.00	10.76

MIXTURE SET # 2 (adjusted)
SPECIES: ALL C₄ SPECIES

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
A. gerardii	3584	89.68	91.00	23.76	5.16	0.86	0.86	38.94
B. curtipendula	#5-95	82.25	66.00	36.31	5.07	0.86	0.86	25.63
P. virgatum	7545	99.04	73.00	9.71	14.24	0.95	0.95	105.27
B. gracilis	#2-95	67.27	57.00	12.70	20.54	1.00	1.00	84.46
S. nutans	#5-95	82.10	75.00	2.54	63.94	1.06	1.06	447.70
S. scoparius	#4-95	68.32	72.00	20.17	10.08	1.27	1.27	67.95

MIXTURE SET # 3 (control)
SPECIES: ALL C₃ SPECIES

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
E. canadensis	3596	93.62	80.00	100.00	1.34	1.00	1.00	10.76
E. lanceolatus	W-14-05-1050	97.40	97.00	100.00	1.06	1.00	1.00	10.76
E. trachycaulus	89-8-95308	96.62	97.00	100.00	1.07	1.00	1.00	10.76
N. viridula	NG-95-001	98.87	86.00	100.00	1.18	1.00	1.00	10.76
P. smithii	west5226	95.94	99.00	100.00	1.05	1.00	1.00	10.76
S. comata	SCW 95-1	88.40	84.00	100.00	1.35	1.00	1.00	10.76

MIXTURE SET # 3 (adjusted)
SPECIES: ALL C₃ SPECIES

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
E. canadensis	3596	93.62	80.00	24.35	5.48	0.85	0.85	37.50
E. lanceolatus	W-14-05-1050	97.40	97.00	15.24	6.95	1.03	1.03	72.53
E. trachycaulus	89-8-95308	96.62	97.00	16.44	6.49	0.88	0.88	57.67
N. viridula	NG-95-001	98.87	86.00	8.37	14.06	1.11	1.11	143.40
P. smithii	west5226	95.94	99.00	16.88	6.24	1.07	1.07	67.93
S. comata	SCW 95-1	88.40	84.00	7.77	17.33	1.06	1.06	147.39

MIXTURE SET # 4 (control)
SPECIES: 3 BEST C₃ X 3 BEST C₄

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
E. canadensis	3596	93.62	80.00	100.00	1.34	1.00	1.00	10.76
E. lanceolatus	W-14-05-1050	97.40	97.00	100.00	1.06	1.00	1.00	10.76
E. trachycaulus	89-8-95308	96.62	97.00	100.00	1.07	1.00	1.00	10.76
A. gerardii	3584	89.68	91.00	100.00	1.23	1.00	1.00	10.76
B. curtipendula	#5-95	82.25	66.00	100.00	1.84	1.00	1.00	10.76
P. virgatum	7545	99.04	73.00	100.00	1.38	1.00	1.00	10.76

MIXTURE SET # 4 (adjusted)
SPECIES: 3 BEST C₃ X 3 BEST C₄

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
E. canadensis	3596	93.62	80.00	24.35	5.48	0.95	0.95	41.79
E. lanceolatus	W-14-05-1050	97.40	97.00	15.24	6.95	1.12	1.12	78.95
E. trachycaulus	89-8-95308	96.62	97.00	16.44	6.49	0.96	0.96	62.87
A. gerardii	3584	89.68	91.00	23.76	5.16	0.92	0.92	41.80
B. curtipendula	#5-95	82.25	66.00	36.31	5.07	1.00	1.00	29.53
P. virgatum	7545	99.04	73.00	9.71	14.24	1.06	1.06	117.26

MIXTURE SET # 5 (control)
SPECIES: 3 WORST C₃ X 3 WORST C₄

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
N. viridula	NG-95-001	98.87	86.00	100.00	1.18	1.00	1.00	10.76
P. smithii	west5226	95.94	99.00	100.00	1.05	1.00	1.00	10.76
S. comata	SCW 95-1	88.40	84.00	100.00	1.35	1.00	1.00	10.76
B. gracilis	#2-95	67.27	57.00	100.00	2.61	1.00	1.00	10.76
S. nutans	#5-95	82.10	75.00	100.00	1.62	1.00	1.00	10.76
S. scoparium	#4-95	68.32	72.00	100.00	2.03	1.00	1.00	10.76

MIXTURE SET # 5 (adjusted)
SPECIES: 3 WORST C, X 3 WORST C.

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
N. viridula	NG-95-001	98.87	86.00	8.37	14.06	1.03	1.03	132.20
P. smithii	west5226	95.94	99.00	16.88	6.24	1.00	1.00	63.58
S. comata	5CW 95-1	88.40	84.00	7.77	17.33	0.97	0.97	134.01
B. gracilis	#2-95	67.27	57.00	12.70	20.54	0.97	0.97	82.06
S. nutans	#5-95	82.10	75.00	2.54	63.94	0.87	0.87	368.94
S. scoparium	#4-95	68.32	72.00	20.17	10.08	1.17	1.17	62.38

MIXTURE SET # 6 (control)
SPECIES: 3 BEST C, X 3 WORST C.

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
E. canadensis	3596	93.62	80.00	100.00	1.34	1.00	1.00	10.76
E. lanceolatus	W-14-05-1050	97.40	97.00	100.00	1.06	1.00	1.00	10.76
E. trachycaulus	89-8-95308	96.62	97.00	100.00	1.07	1.00	1.00	10.76
B. gracilis	#2-95	67.27	57.00	100.00	2.61	1.00	1.00	10.76
S. nutans	#5-95	82.10	75.00	100.00	1.62	1.00	1.00	10.76
S. scoparium	#4-95	68.32	72.00	100.00	2.03	1.00	1.00	10.76

MIXTURE SET # 6 (adjusted)
SPECIES: 3 BEST C, X 3 WORST C.

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
E. canadensis	3596	93.62	80.00	8.37	15.96	0.86	0.86	110.65
E. lanceolatus	W-14-05-1050	97.40	97.00	16.88	6.27	1.01	1.01	64.16
E. trachycaulus	89-8-95308	96.62	97.00	7.77	13.73	0.86	0.86	119.09
B. gracilis	#2-95	67.27	57.00	23.76	10.98	1.02	1.02	46.16
S. nutans	#5-95	82.10	75.00	36.31	4.47	1.01	1.01	29.97
S. scoparium	#4-95	68.32	72.00	9.71	20.93	1.24	1.24	137.89

MIXTURE SET # 7 (control)
SPECIES: 3 WORST C, X 3 BEST C.

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
N. viridula	NG-95-001	98.87	86.00	100.00	1.18	1.00	1.00	10.76
P. smithii	west5226	95.94	99.00	100.00	1.05	1.00	1.00	10.76
S. comata	5CW 95-1	88.40	84.00	100.00	1.35	1.00	1.00	10.76
A. gerardii	3584	89.68	91.00	100.00	1.23	1.00	1.00	10.76
B. curtipendula	#5-95	82.25	66.00	100.00	1.84	1.00	1.00	10.76
P. virgatum	7545	99.04	73.00	100.00	1.38	1.00	1.00	10.76

MIXTURE SET # 7 (adjusted)
SPECIES: 3 WORST C, X 3 BEST C.

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
N. viridula	NG-95-001	98.87	86.00	8.37	14.06	1.02	1.02	131.18
P. smithii	west5226	95.94	99.00	16.88	6.24	1.09	1.09	69.52
S. comata	5CW 95-1	88.40	84.00	7.77	17.33	1.14	1.14	158.56
A. gerardii	3584	89.68	91.00	23.76	5.16	0.89	0.89	40.11
B. curtipendula	#5-95	82.25	66.00	36.31	5.07	0.88	0.88	26.23
P. virgatum	7545	99.04	73.00	9.71	14.24	0.98	0.98	108.11

MIXTURE SET # 8 (control)

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
E. canadensis	3596	93.62	80.00	100.00	1.34	1.00	0.60	6.46
E. lanceolatus	W-14-05-1050	97.40	97.00	100.00	1.06	1.00	0.60	6.46
E. trachycaulus	89-8-95308	96.62	97.00	100.00	1.07	1.00	0.60	6.46
N. viridula	NG-95-001	98.87	86.00	100.00	1.18	1.00	0.60	6.46
P. smithii	west5226	95.94	99.00	100.00	1.05	1.00	0.60	6.46
A. gerardii	3584	89.68	91.00	100.00	1.23	1.00	0.60	6.46
B. curtipendula	#5-95	82.25	66.00	100.00	1.84	1.00	0.60	6.46
P. virgatum	7545	99.04	73.00	100.00	1.38	1.00	0.60	6.46
S. nutans	#5-95	82.10	75.00	100.00	1.62	1.00	0.60	6.46
S. scoparium	#4-95	68.32	72.00	100.00	2.03	1.00	0.60	6.46

MIXTURE SET # 8 (adjusted)

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
E. canadensis	3596	93.62	80.00	24.35	5.48	0.87	0.52	23.20
E. lanceolatus	W-14-05-1050	97.40	97.00	15.24	6.95	1.06	0.64	45.12
E. trachycaulus	89-8-95308	96.62	97.00	16.44	6.49	0.90	0.54	35.33
N. viridula	NG-95-001	98.87	86.00	8.37	14.06	1.10	0.66	84.52
P. smithii	west5226	95.94	99.00	16.88	6.24	1.05	0.63	40.12
A. gerardii	3584	89.68	91.00	23.76	5.16	0.86	0.51	23.32
B. curtipendula	#5-95	82.25	66.00	36.31	5.07	0.89	0.53	15.75
P. virgatum	7545	99.04	73.00	9.71	14.24	0.95	0.57	63.47
S. nutans	#5-95	82.10	75.00	2.54	63.94	1.06	0.63	268.62
S. scoparium	#4-95	68.32	72.00	20.17	10.08	1.26	0.76	40.45

MIXTURE SET # 8 (DUC proportions)

Species	Lot #	%Pure	%Germ	%Estab	PGE factor	COMP factor	Plants/ft²	PLS/m²
E. canadensis	3596	93.62	80.00	100.00	1.34	1.00	4.70	50.59
E. lanceolatus	W-14-05-1050	97.40	97.00	100.00	1.06	1.00	3.30	35.52
E. trachycaulus	89-8-95308	96.62	97.00	100.00	1.07	1.00	4.40	47.36
N. viridula	NG-95-001	98.87	86.00	100.00	1.18	1.00	0.90	9.69
P. smithii	west5226	95.94	99.00	100.00	1.05	1.00	1.00	10.76
A. gerardii	3584	89.68	91.00	100.00	1.23	1.00	1.80	19.38
B. curtipendula	#5-95	82.25	66.00	100.00	1.84	1.00	1.30	13.99
P. virgatum	7545	99.04	73.00	100.00	1.38	1.00	0.40	4.31
S. nutans	#5-95	82.10	75.00	100.00	1.62	1.00	0.80	8.61
S. scoparium	#4-95	68.32	72.00	100.00	2.03	1.00	8.30	89.34