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Competitive Interactions Between Two Closely Related Rhizomatous and Caespitose Perennial Grasses under Varying Conditions

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COMPETITIVE INTERACTIONS BETWEEN TWO CLOSELY RELATED RHIZOMATOUS AND CAESPITOSE PERENNIAL GRASSES UNDER VARYING CONDITIONS

by

L. David Humphrey

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of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

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Approved:

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ABSTRACT

Competitive Interactions Between Two Closely Related Rhizomatous and Caespitose Perennial Grasses under Varying Conditions

by

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Utah State University, 1995

Major Professor: Dr. David A. Pyke
Department: Rangeland Resources

Biomass, tiller numbers, flowering, and genet survival were accessed for the rhizomatous *Elymus lanceolatus* ssp. *lanceolatus* and caespitose *E. l.* ssp. *wawawaiensis* growing in mixtures with a range of densities of each taxon. Models of aboveground biomass of each taxon as a function of mixed densities were used to calculate competition indices. Tiller numbers and biomass of ssp. *lanceolatus* were higher than those of the caespitose taxon in the first year, but declined in the second year, while biomass and tiller numbers of ssp. *wawawaiensis* changed little. All tillers of ssp. *wawawaiensis* emerged in autumn; tillers of ssp. *lanceolatus* emerged from autumn through late spring. The rhizomatous taxon better exploited open resources in the first year; ssp. *wawawaiensis* had slower growth, but its production of many tillers early in the season may allow it to quickly exploit seasonally variable conditions of semiarid environments. Decline in flowering at higher densities and in the second year was more pronounced than that of biomass and tiller numbers. Genet survival was high and similar for both taxa. Substitution rates indicated ssp. _lanceolatus_ was the better competitor in both years. In the second year, the two taxa differed somewhat less in substitution rates. A greater overlap in resources used by the two taxa was indicated. Subspecies _lanceolatus_ experienced greater intensity of competition. Substitution rates and relative efficiency index indicated ssp. _lanceolatus_ was the greater competitor between early and late spring, when overlap in resource use was greater.

Another experiment addressed advantages of clonal foraging of ssp. _lanceolatus_ in exploiting soil nutrient patches. A foraging response was found in the rhizomatous taxon, with greater numbers of closely spaced tillers in high-nutrient patches adjacent to the main clone, but root biomass in these patches, and aboveground biomass of the clones, indicated that both taxa accessed nutrients in the patches, but ssp. _wawawaiensis_ used only root growth. The taxa were similar in their tolerance of low levels of soil nutrients. No difference among genets in degree of foraging response, and no relationship between degree of foraging response and fitness when nutrients are patchy were found. Subspecies lanceolatus did not show such a foraging response to high neighbor densities in mixed-density plots. Instead, rhizome lengths were reduced by higher neighbor densities and in the second year, by reduced resources overall.

(187 pages)

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CONTENTS

Page
ABSTRACT ii

ACKNOWLEDGMENTS v

LIST OF TABLES viii

LIST OF FIGURES x

CHAPTER

1. INTRODUCTION 1

    References 7

2. DEMOGRAPHIC AND GROWTH RESPONSES OF A CAESPITOSE AND A RHIZOMATOUS PERENNIAL GRASS IN COMPETITIVE MIXTURES 11

    Summary 11
    Introduction 12
    Methods 16

        Study Site...............................16
        Experimental Design and Planting Design.....16
        Data Collection 19
        Analyses 23

    Results 25

        Model Selection..........................25
        Tiller Numbers and Biomass...............27
        Proportion of Tillers Flowering..........32
        Survival of Target Individuals...........32

    Discussion 33
    References 39

3. COMPETITIVE INTERACTIONS BETWEEN TWO CLOSELY RELATED RHIZOMATOUS AND CAESPITOSE SEMIARID PERENNIAL GRASSES 61

    Abstract 61
    Introduction 62
    Methods 66
    Analyses 70
    Results 74

Competition Over Two Years 74
Competition Over Seasonal Intervals 78

Discussion...................................80
References 84

4. CLONAL FORAGING IN PERENNIAL WHEATGRASSES: A STRATEGY FOR EXPLOITING PATCHY SOIL NUTRIENTS....98

Summary 98
Introduction 99
Methods 103
Hypotheses and Data Analyses................106
Results 111

Soil Nutrients..............................111
Discrimination Between Low- and High-Nutrient Cells 112
Roots Exploiting High-Nutrient Cells 113
Total Aboveground Biomass 114
Biomass of Genets Differing in Foraging Ability 115

Discussion 115

Foraging Response...........................115
Benefits of Clonal Foraging Versus Root Proliferation 118
Growth Responses of Taxa to Nutrient Availability 120
Genetic Differences in and Advantages of Foraging 120

References 122

5. RAMET SPACING AND FORAGING RESPONSE IN THICKSPIKE WHEATGRASS IN RESPONSE TO NEIGHBOR DENSITY 138

Summary 138
Introduction 139
Methods 141
Results 145
Discussion 146
References 149

6. SYNTHESIS 155

References 169

CURRICULUM VITAE 172

LIST OF TABLES

Table Page

1 Monthly precipitation (cm) for the experiment (1990, 1991) from the North Logan, Utah weather station 2 km west of the site, along with the amounts of irrigation that were applied 47

2 Diagnostic information on the two model forms that provided the best fits in regressions of biomass (A) and tiller numbers (B) as functions of densities of thickspike and Snake River wheatgrass neighbors 48

3 Regression equations for biomass of thickspike and Snake River wheatgrasses, coefficients of determination (R^2), significance levels of parameters, and sample size (n), as a function of number of tillers (N) and mean height of the three tallest tillers (H), which were used to calculate predicted biomass values for the seasonal time periods 51

4 (A) Frequency of target plants in three classes of proportion (percent) of tillers flowering. (B) Equations where P is probability of producing no flowering tillers. (C) Equations where P is probability of having > 30 percent of tillers flowering 52

5 Models of end-of-season biomass as a function of mixed-densities of the two taxa obtained for each taxon in each year (Chapter 2), and approximate R^2's of the models 91

6 Models of biomass as a function of mixed-densities of the two taxa obtained for 1) the interval from the start of growth prior to the autumn sampling to early spring; and the intervals 2) early-late spring; and 3) late spring-summer 92

7 (A) Mean relative growth rates for the two taxa and relative efficiency index values based on those mean RGR's for the three time intervals. (B) Models of RGR for the early-late spring interval 93

8 Nutrient analysis of very fine sandy loam used as growing medium in the experiment, based on two replicate samples of *en situ* material 130

9 For the rhizomatous taxon, thickspike, relative contribution of root biomass from roots and rhizomes in destination cells. (A) Proportion of all roots that could be identified as to their source, using corrected total root biomass based on estimates of portion of root biomass not recovered by sieving. (B) Of those identified roots, the proportion that arose from rhizomes within the destination cell 131

10 Analysis of covariance of LN (spacing) of guerilla tillers as a function of densities of thickspike and Snake River neighbors and year 153

LIST OF FIGURES

Figure Page

1 Double-hexagon planting design with the target plant (from which data were collected) in the center (X) and an inner ring of six and an outer ring of 12 neighbor plants 53

2 Means over all mixed-densities (with standard errors) of (A) tiller numbers per plant and (B) biomass per plant of each taxon in each year 54

3 Nonlinear models of end-of-season tiller numbers per plant as a function of densities of the two taxa in mixtures for each taxon in each year 55

4 Nonlinear models of end-of-season biomass per plant as a function of densities of the two taxa in mixtures for each taxon in each year 56

5 Means over all mixed densities (with standard errors) of (A) tiller numbers per plant and (B) biomass per plant of each taxon at each seasonal sampling period in the 1990-1991 growing season 57

6 Nonlinear models of tiller numbers per plant as a function of densities of the two taxa in mixtures for each taxon in each of the three seasonal sampling periods, autumn, early spring and late spring 58

7 Nonlinear models of biomass per plant as a function of densities of the two taxa in mixtures for each taxon in each of the four seasonal sampling periods 59

8 Frequency distribution of target plants by proportion of tillers flowering for each taxon in each year 60

9 Substitution rates over the range of mixed densities for each taxon in each year 95

10 Substitution rates over the range of mixed densities for each taxon for the intervals beginning of growth-early spring, early-late spring and late spring-summer 96

11 Values of relative efficiency index (REI) over the range of mixed densities for the early-late spring interval 97

12 Means and standard errors (n = 8) of soil nutrients in samples taken over the course of the experiment 133

13 Means and standard errors for tiller counts and rhizome lengths in the destination cell. Values for low- (L) and high-nutrient (H) origin crossed with low- and high-nutrient destination are presented 134

14 Root biomass (means and standard errors) in the destination cell for each taxon for low- and high-nutrient origin cells crossed with low- and high-nutrient destination cells.................................136

15 Aboveground biomass (means and standard errors) for the entire plot in 1993. For each taxon, values for low- (L) and high-nutrient (H) destination crossed with low- and high-nutrient origin are presented 137

16 Spacing of guerilla tillers as a function of density of thickspike neighbors in each of the two growth periods (1989-1990 and 1990-1991)................154

CHAPTER 1

INTRODUCTION

Pronounced clonal growth is common in many perennial plants, including many herbaceous plants in temperate and boreal forests, aquatic environments, fire-prone environments, and at high latitudes and elevations (Cook 1983; Silvertown 1987). Advantages of clonal growth include the ability to invade other clones, resist invasion by seedlings, avoid extinction of the genet because the risk of death is shared among ramets (Cook 1983), and take advantage of patchy resources by extending ramets into areas that would not otherwise be accessible (Bell 1984). Lovett Doust (1981) used "phalanx strategy" to describe clonal species with modules or ramets closely spaced, resulting in an unbroken, slowly advancing front, and used "guerilla strategy" to describe species with ramets widely spaced that rapidly spread into new areas. Guerrilla species should have an advantage over phalanx species in exploiting open space (Lovett Doust 1981).

Clonal plants also may show a foraging response, effectively exploiting resource-rich patches by densely producing ramets in them and producing fewer ramets with longer rhizomes in resource-poor patches, thereby affording greater opportunity to encounter favorable sites with reduced investment in resource-poor patches (Salzman 1985; Slade & Hutchings 1987). Physiological integration among ramets allows clones to average habitat variability. Clonal plants can buffer ramets throughout the clone against localized extremes of a patchy environment by translocating water, minerals or photosynthate among ramets (Hartnett & Bazzaz 1983; Alpert & Mooney 1986).

Clonal growth along with a foraging response should be effective at exploiting resources that are distributed in patches, but high growth rates and overall resource levels high enough to support these growth rates are necessary for clonal foraging to be cost-effective (de Kroon & Schieving 1990). In the Intermountian West of the U.S.A., guerilla wheatgrasses are more abundant in moister areas and phalanx wheatgrasses more abundant in drier areas (Passey & Hugie 1963). However, rhizomatous grasses (e.g. western wheatgrass, _Pascopyron smithii_) and _Carex_ also exist in drier regions. de Kroon & Schieving (1990) concluded that rhizomatous growth with effective translocation of resources among parts of the clone, but without a foraging response, could be beneficial in resource-poor environments. In such environments, overall resources tend to be low with few rich patches. Instead of foraging for patches, the rhizome system serves to relatively uniformly occupy a large area and exploit resources from throughout the area.

Our experiment assessed competitive interactions between two closely related rhizomatous and caespitose taxa native to semiarid regions of the western U.S.A.: the rhizomatous thickspike wheatgrass, _Elymus lanceolatus_ ssp. _lanceolatus_

(Scribner & J. G. Smith) Gould (syn: *Agropyron* *dasystachyum* (Hooker) Scribner & J. G. Smith) and the caespitose Snake River wheatgrass proposed name, *E.* *lanceolatus* ssp. *wawawaiensis* (Scribner & Gould) J. R. Carlson & D. R. Dewey (Carlson et al. unpublished), which partially comprises *Agropyron* *spicatum* (Pursh) Scribner & Smith, and includes the commonly seeded cultivar 'Secar'. The revised genus *Elymus*, including all thickspike wheatgrasses, is tetraploid (2N = 28), containing two genomes designated the S and H genomes. Other grasses formerly *A.* *spicatum* are currently ascribed to *Pseudoroegneria* *spicata* (Pursh) A. Love (Barkworth & Dewey 1985), and contain only the S genome. *Elymus* *lanceolatus* ssp. *wawawaiensis*, most common along the Salmon, Snake and Columbia Rivers of Idaho and Washington (Carlson 1986), produces meiotically regular and fertile hybrids with *E.* *lanceolatus* ssp. *lanceolatus*, and the karyotype of *E.* *lanceolatus* ssp. *wawawaiensis* appears to be that of the SH genome (Carlson et al. unpublished). Other recent treatments (e.g. Melderis et al. 1980) have included all *A.* *dasystachyum* and *A.* *spicatum* in the same genus. Regardless of the taxonomic nominclature, the genomic relationships and presumably the phylogenetic relationships of these taxa are such that *E.* *l.* *wawawaiensis* is very closely related to *E.* *l.* *lanceolatus*, indeed more closely related than it is to other *Agropyron* *spicatum* that are designated *Pseudoroegneria* *spicata* by Barkworth & Dewey

(1985). Being so closely related, but with one taxon caespitose and the other rhizomatous, these taxa provide an excellent vehicle for addressing questions on the advantages of rhizomatous and caespitose growth forms.

Although the two taxa are sympatric, they are typical of different habitats. Snake River wheatgrass occurs only in eastern Washington and northern Idaho, while thickspike occurs throughout most of the Intermountain West. Snake River typically occurs on open sites with shallow, rocky soil, and is thought to be rather drought tolerant, while within the range of Snake River at least, thickspike usually occurs on deep sandy soils (Carlson et al. unpublished).

Our first experiment examined responses of biomass, tiller production, inflorescence production, and genet survival (Chapter 2) and assessed competitive interactions between the two subspecies of wheatgrasses (Chapter 3) in experimental mixtures of the two taxa. Our experimental design was an additive series design, with a range of relative frequencies of the two taxa crossed with a range of total densities. A nonlinear model of response per plant to mixed densities was used to describe responses of tiller numbers and of biomass. The model used to describe these responses was:

$$W_i = W_{imax} / (1 + d_i^{b_{i,i}} + d_j^{b_{i,j}})$$

where W_i is biomass per plant of species i, W_{imax} is the biomass of an isolated plant in the absence of competition, d_i and d_j are densities of the two species, $b_{i,i}$ is a coefficient describing the competitive effect of individuals of species i on species i, $b_{i,j}$ is a coefficient describing competitive effect of species j on species i (Law & Watkinson 1987; Firbank & Watkinson 1990).

Connolly (1987) described three indices designed to assess species interactions in mixtures based on models from additive series designs: (1) Relative Resource Total, reflecting resource capture in mixture relative to pure stands; (2) Substitution Rates (Maynard Smith 1974), indicating the influence of neighbors of another species relative to influence of neighbors of one's own species; and (3) Relative Efficiency Index, which is based on growth rate of one species relative to that of the other species. To describe competitive interactions, for each taxon, we fitted models of aboveground biomass as a function of densities of the two taxa in mixtures, and calculated values for these competition indices based on these models (Chapters 2 and 3). Models also were used to assess the intensity and importance of competition.

Since guerilla rhizomatous growth and foraging were proposed to be advantages in exploiting patchy resources, we used a second experimental design to compare abilities of the two taxa to exploit patches of soil nutrients on the scale of tens of centimeters (Chapter 4), a scale appropriately matched to the scale of rhizome growth (*sensu* Sutherland & Stillman 1988). We tested for the existence of a foraging response in thickspike, the guerilla wheatgrass, by comparing its placement of tillers in low- versus high-nutrient patches. We examined abilities of both taxa to exploit high-nutrient patches by root growth, and compared overall growth response (aboveground biomass) of the taxa under conditions of patchy soil nutrients. We also looked for fitness differences correlated with genetic differences in degree of foraging response, which would indicate that natural selection for foraging response was likely. This experiment also allowed comparison of the taxa as to the magnitude of their response to low soil nutrients to see if the two taxa differ in their abilities to tolerate low nutrient levels.

The field plots of the first experiment (Chapters 2 and 3) were used to test another hypothesis related to thickspike's clonal foraging for patchy soil nutrients, as addressed in the second experiment. Specifically, does thickspike exhibit a foraging response to neighbor densities as it does to patchy soil nutrients? We wished to determine if thickspike responds to greater genet densities (which result in reduced resource availability) with increased rhizome lengths, affording greater ability to search the habitat (Chapter 5).

In the final, synthesis chapter, it was proposed that because of thickspike's early fast growth and occcupancy of the site and because of Snake River's later ascendancy, the two species used together might be effective in revegetation projects. Since it was proposed that Snake River was adapted to temporal variability in soil resources, root-system traits related to spatial and temporal patchiness were also discussed. It was proposed that the aboveground traits beneficial under spatially patchy resources may co-occur with morphological plasticity of the root system (i.e. root proliferation in high-nutrient patches), whereas aboveground traits adapted to temporally patchy resources likely co-occur with large root systems with low morphological plasticity, but with plasticity in physiological nutrient uptake rates of the roots. Some suites of traits of clonal plants are described that emphasize that the interaction among traits, and the levels of overall resource availability, both temporally and spatially, are important.

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CHAPTER 2

DEMOGRAPHIC AND GROWTH RESPONSES OF A CAESPITOSE AND A RHIZOMATOUS PERENNIAL GRASS IN COMPETITIVE MIXTURES[1]

Summary

1 Biomass,tiller numbers, flowering, and genet survival of the rhizomatous Elymus lanceolatus ssp. lanceolatus and caespitose E. l. ssp. wawawaiensis were evaluated over two years in two-species mixtures over a range of densities of each taxon and under two levels of watering.

2 Tiller numbers and biomass of ssp. lanceolatus were higher than those of the caespitose taxon in the first year, but declined greatly in the second year, whereas ssp. wawawaiensis showed a slight decrease in biomass and a slight increase in tiller numbers in the second year. Biomass of ssp. lanceolatus remained greater than biomass of ssp. wawawaiensis. Tiller numbers were similar between taxa in the second year.

3 Both taxa reduced natality of tillers and avoided tiller self-thinning.

4 Taxa differed in phenology of tiller production. All tillers of ssp. wawawaiensis emerged in autumn, while tillers of ssp. lanceolatus emerged in autumn and into late spring.

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[1] Coauthored by L. David Humphrey and David A. Pyke

5 Flowering responded more strongly than biomass, decreasing greatly in both taxa at higher densities and in the second year.

6 Genet survival was high and similar for both taxa.

7 Subspecies lanceolatus more quickly exploited resources in the first year by faster growth and greater tiller production.

8 Subspecies wawawaiensis had slower growth, produced more tillers in later years, and delayed flowering until later years, but its production of large numbers of tillers early in the season may allow it to quickly exploit seasonally variable conditions, an important ability in semiarid environments.

Introduction

Most clonal plants are characterized by a clearly defined modular structure, with a genetic individual or genet consisting of numerous modules or ramets. Grasses are a typical example, with a genet consisting of numerous ramets (or tillers) arising separately from a basal crown or from rhizomes or stolons. Although modules are often physically and physiologically connected, dynamics of populations of ramets can be meaningfully studied. In fact, the dynamics of ramet numbers is an important trait shaping the growth of clonal plants and their interactions with other plants. Because of this modular structure, overall growth of the genet will depend heavily on number of ramets produced (Harper & Bell 1979). Ramet numbers and the spatial spread of ramets by means of rhizomes and stolons influence the interactions of clonal plants with other plants and their abiotic environment. Thus, patterns of ramet production should represent adaptations that have been shaped by evolutionary forces (Olson & Richards 1988).

Because clonal plants have two distinct levels of construction, the ramet and the genet, they can respond to competition and abiotic factors by altering genet size (number of ramets) or ramet size (de Kroon et al. 1992). A range of possible pairings of patterns of ramet production with patterns of ramet growth affords clonal plants the potential to adapt to many different environments by evolving patterns of ramet production and growth that constitute effective adaptive strategies under their particular environmental history. Some graminoids continuously produce ramets (e.g. de Kroon & Kwant 1991), whereas tiller production in some grasses is largely confined to seasonal periods. Examples include the caespitose wheatgrasses *Pseudoroegneria spicata* and *Agropyron desertorum*, late summer and fall (Mueller & Richards 1986); and *Schizachyrium scoparium*, October to March, a pattern which is similar to other grasses of temperate grasslands (Briske & Butler 1989). *Typha latifolia* displayed three pulses of tiller emergence (Dickerman & Wetzel 1985). Few studies have explicitly compared responses of tiller numbers and growth, with results differing among the studies (e.g. DiTommaso & Aarssen 1991; Hartnett 1993). Mueller & Richards (1986) found that two wheatgrass species, *Pseudoroegneria spicata* and *Agropyron desertorum*, differed in tiller production apparently because they had evolved different responses of tiller emergence from within the reservoir of available buds.

Our study addressed emergence of tillers and genet biomass in two closely related taxa of perennial wheatgrasses native to semiarid regions of the western United States: the rhizomatous *Elymus lanceolatus* ssp. *lanceolatus* (Scribner & J.G. Smith) Gould (thickspike wheatgrass) and the caespitose *Elymus lanceolatus* ssp. *wawawaiensis* (Scribner & Gould) J. R. Carlson & D. R. Dewey (Snake River wheatgrass). In the Intermountain West of the U.S.A., rhizomatous wheatgrasses are more abundant in moister areas and caespitose wheatgrasses more abundant in drier areas (Passey & Hugie 1963). Lovett Doust (1981) used phalanx strategy to describe clonal species with closely spaced ramets resulting in an unbroken advancing front and slow spread into new areas (such as caespitose grasses) and used guerrilla strategy to describe species (rhizomatous grasses) with widely spaced ramets that rapidly spread into new areas. Guerrilla species should have an advantage over phalanx species in exploiting open space (Lovett Doust 1981;

Schmid & Harper 1985), but most studies have compared taxa of different genera. Being so closely related, but with one taxon caespitose and the other rhizomatous, these wheatgrasses provide an excellent opportunity for addressing questions on the advantages of these two growth forms.

Plant reproduction can also be influenced by competition. Williams (1975) proposed that clonal reproduction is favored until density becomes high and survival of additional clonally produced individuals in the local area becomes unlikely. Then increased sexual reproduction and dispersal are favored. Newell & Tramer (1978) predicted that seed production should decline with increasing competition (density). Similarly, Loehle (1987) predicted that sexual repoduction should be favored with low density or favorable site conditions (when potential success of the progeny is higher and costs of sexual repoduction are reduced). According to r- and K-selection theory (MacArthur & Wilson 1967), species adapted for competitive ability are expected to invest relatively more in vegetative growth as density increases.

Our experiment examined responses of tiller numbers, genet biomass, flowering, and genet survival of these two subspecies of wheatgrass in mixtures of different relative frequencies of the two taxa and different total densities growing under two soil moisture levels. Responses of tiller numbers and biomass were assessed at the end of the growing season in two consecutive years and at intervals during the growing season to describe phenology of tiller production and growth of each taxon. To assess the effects on other components of plant fitness, proportion of tillers of each target plant that flowered and survival of target plants were assessed at the end of each of the two years.

Methods

STUDY SITE

This study was conducted at the Utah State University (USU) Ecology Center Complex near Green Canyon, 4 km northeast of the USU campus in Logan, Utah, U.S.A. The normal annual precipitation is 471 mm (18.38 in.), most of which comes in the winter as snow. Native vegetation is dominated by mountain big sagebrush (Artemisia tridentata ssp. vaseyana (Rydb.) Beetle) and perennial wheatgrasses (mainly Pseudoroegneria spicata (Pursh) A. Love). Plots were established by planting seedlings in native soil that was treated the previous year with methyl bromide to reduce viable seed banks, thoroughly plowed to remove existing vegetation (which was herbaceous), and raked to provide a smooth, uniform surface.

EXPERIMENTAL DESIGN AND PLANTING DESIGN

Plants used in this experiment were grown from seeds of ssp. lanceolatus (accession T-21076) obtained from the Soil Conservation Service (SCS) Plant Materials Center, Aberdeen, Idaho, and seeds of ssp. wawawaiensis (cultivar Secar) from the SCS Plant Materials Center, Pullman, Washington, hereafter referred to as thickspike and Snakeriver wheatgrasses, respectively. Plants were germinated outdoors in styrofoam seedling flats with 11 by 2.5 cm cylindrical cells, and were transplanted to plots during May and June 1989. Each transplant consisted of only one to five tillers when they were transplanted. Plots were watered during spring and summer 1989 to enhance establishment.

Our experimental design was based on the additive series design (Spitters 1983). The experimental design consisted of four levels of relative frequency (thickspike : Snake River) 1:5, 2:4, 4:2, 5:1 plus each taxon as the target plant in a monoculture of its own taxon crossed with four levels of total density, 12, 36, 58, 84 plants per m^2. This design was further crossed with the factor, taxon in two levels (i.e. it was repeated with each subspecies as the target plant), and two soil moisture levels in a split-plot design, with one half of each replicate receiving irrigation. There were three replications of the entire design.

The two water levels were actual precipitation and actual precipitation plus irrigation. In adding the supplemental water for the higher water level, an attempt was made to roughly mimic natural monthly precipitation patterns. Since most precipitation occurs November through March, irrigation was concentrated in spring to simulate higher soil moisture that would result from melting of increased snow, with smaller amounts of irrigation applied in the summer. Irrigation amounted to 34% of annual precipitation in 1990, but in 1991 precipitation was greater and irrigation was slightly less (Table 1).

The irrigation system consisted of a main manifold supplying water to a series of tubes spaced 35 cm apart (Laser Drip Tube®, Pep Co.). Tubes have slits 30 cm apart to provide drip irrigation. This system provided essentially uniform wetting when the equivalent of at least 25 to 30 mm of precipitation was applied. Water amounts were measured using 12 plastic containers per replicate. Each container was taped in place to collect the water from one drip hole in a tube. The amount of water applied at each of these collection points was calculated from the volume of water collected and the 35- by 30-cm area of soil surface corresponding to one drip hole (Table 1). The 12 collection points were approximately regularly distributed over the watered portion of each replicate (being restricted to spaces between plots or plot borders).

The planting design was based on neighbor plants arranged in two concentric hexagons around a central target plant such that all spacings between plants in a density treatment were equal (Fig. 1). This was a modification of a single-hexagon approach (e.g. Fasoulas 1973; Boffey &

Veevers 1977; Antonovics & Fowler 1985). Each plot contained seven observational units, each consisting of a pair of concentric hexagons of neighbors and a target plant. Each plot contained a single treatment combination (one relative frequency and total density and target plants all of the same taxon). Taxon positions around the hexagons are randomized in accordance with the specified relative frequency for that plot. Different levels of total density were achieved by using different-sized hexagon pairs.

Because early mortality of seedlings after transplanting substantially altered the original densities and relative frequencies on many plots, it was necessary to quantify densities of thickspike and Snake River neighbors in each observational unit, and to use these densities as two continuous variables in place of the relative frequency and total density levels of the original design. Because they represented too large a departure from the regular spacing design, observational units with $\geq$ 50% of the neighbors dead were omitted, as were observational units with dead target plants.

DATA COLLECTION

Tillers of target plants were counted and aboveground biomass was clipped at 8-cm height at the end of the growing season (summer senescence) in mid-July 1990 and late July 1991. Samples for each target plant were oven dried at 70° C for 24 hr before temporary storage at room temperature, then redried later at 70° C for 24 hr before weighing.

Plants were sampled at three time periods over the growth cycle for 1991, in addition to the end-of-season sampling period. Because much of the autumn growth overwinters and contributes to spring growth (as reported by Nowak & Caldwell (1984) for related species), the first of these counts was in October 1990. Sampling periods were (1) Autumn, collected 10-23 October 1990; (2) Early Spring, representing beginning-of-spring values, but actually collected 1-9 December 1990 and 8-21 April 1991 (persistent winter snow cover is common and winter survival of tillers is very high); (3) Late Spring, collected 3-11 June 1991; (4) Summer, collected 9-22 July 1991.

Because data were repeatedly collected on the same plants over one growing season, nondestructive measures related to biomass were collected. Multiple linear regressions indicated that two variables for which data could be quickly collected, mean height of the three tallest tillers (to collar of the uppermost leaf) and tiller number, were better than or as good as other variables tried (including leaf number and other height measures) as predictors of biomass, based on R^2, partial R^2's, and correlations among independent variables. Thus, these data were collected at the four sampling periods, and linear regressions were used to obtain predicted biomass values from these data.

Because the amount of growth in Autumn and Early Spring was similar, the same regression equation was used to calculate predicted biomass values from tiller number and height data from both time periods, but different equations were calculated for each taxon. To provide data to calculate these regression equations, on 20 plants of each taxon, systematically selected from among neighbors that formed the partial hexagons that filled corners of the plots, tiller number and height data were recorded, and aboveground biomass was clipped at 3-cm height (holding any decumbent leaves up) on 27 October 1990. This low clipping height was used because most tillers were very short. One regression for each taxon was also used to predict biomass from the nondestructive data collected in the Late Spring and Summer sampling periods. These regression equations were calculated from 24 plants of each taxon sampled on 17 and 18 June 1991 in the same manner, except plants were clipped at 5-cm height. Samples were oven-dried and weighed in the same manner as the end-of-season aboveground biomass samples. Predicted biomass values were used for the summer sampling period in the seasonal analysis, although clipped biomass data for July were available, to afford consistency of methodology among the four seasonal sampling periods.

Dead tillers were obviously few at any sampling period, with most tiller mortality occurring during summer senescence. The few dead tillers present at earlier periods were usually small, dried, and brittle and mixed with dead leaves and leaf sheaths, making reliable counts of dead tillers difficult. Therefore, although tiller number data consisted of numbers of live tillers present at each sampling time with turnover in the form of tiller births and deaths not accounted for, this turnover was a minor component. Because tillers were gradually dying over the Late Spring-Summer interval as summer senescence approached, no new tiller counts were done in July, and tiller numbers for the Summer sampling period were considered the same as June (Late Spring) counts, but height of the three tallest tillers was measured in July.

To provide data on proportion of tillers flowering, counts of number of tillers and number of flowering tillers were made on each target plant during early July 1990, and counts of flowering tillers were made in conjunction with collection of the tiller number and height data of the Summer sampling period in mid-July 1991.

For genet survival, a tally of surviving target plants taken in June 1990 served as the initial number of genetic individuals present. Survival of these genets over two time intervals, each consisting of one summer and the following winter, was censused in June 1991 and June 1992.

ANALYSES

For tiller numbers and biomass, there were four separate overall analyses: end-of-season tiller numbers in 1990 and 1991, end-of-season biomass in 1990 and 1991, and tiller numbers and biomass at seasonal time periods over one growth cycle. Regression models of biomass and of tiller numbers as a function of densities of the two taxa were constructed for each level of the classification variables, water, taxon, and years or seasons. Model forms for describing plant yield per individual as a function of densities of two species in mixtures that were tried included: multiple linear regression of biomass or tiller numbers as a function of density of thickspike and density of Snake River, with transformations of the dependent variable and quadratic terms of the density variables evaluated, and the reciprocal yield model (Ogawa 1961; Spitters 1983). A nonlinear parameterization of the reciprocal yield model with inverse of the right-hand (or x) side of the equation rather than reciprocal of yield (Shinozaki & Kira 1956) extended for densities of two species was also tried, as was a second nonlinear parameterization (Weiner 1982). A third nonlinear form tried (Law & Watkinson 1987; Firbank & Watkinson 1990) is related to the above nonlinear models, but fits power parameters to each of the two density variables. Linear mixed-density models were run in PROC REG, and nonlinear models were run in PROC NLIN (SAS 1988).

In nonlinear models, R^2 is not a meaningful criterion, because it is not sensitive to nonlinear instability (Ratkowsky 1983; Myers 1986). Similarly, significance levels of t-values may not be valid, because the least-squares estimators are not unbiased and normally distributed. Instead, relative magnitudes of t-values of parameters in different models for the same data set are good criteria for comparing different models, as is comparison of residual mean squares of the models (Ratkowsky 1983; Myers 1986). We used these two criteria in comparing nonlinear models. Linear models were compared on the basis of R^2 and Mallow's Cp. All models were evaluated on the basis of distributions of residuals, parsimony (related to Cp in linear models), biological interpretation, and theoretical basis.

Because nonlinear models were found to best describe density relationships, significant differences between levels of water, taxon, years, or seasons were determined by comparing mixed-density models for the two levels of the variable by the Extra Sum of Squares procedure (Mead 1970; *sensu* Ross 1985). This method tests the significance of the reduction in residual sums of squares obtained by fitting a separate parameter for each of the two treatment levels relative to the residual sums of squares obtained by fitting one common parameter for the two levels. This procedure was performed for each of the parameters in the mixed-density model.

Proportion of tillers of each target plant that flowered was analyzed by logistic regression, because the data had many zeros and the distribution of the data was nonnormal.

Values of proportion of tillers flowering were divided into three categories (no flowering tillers, 0-30%, and 30-100% of tillers flowering). Survival of target plants was also analyzed with logistic regression, with data consisting of a score of alive or dead for each target plant.

Results

MODEL SELECTION

Four model forms provided reasonable fits for both biomass and tiller number (based on end-of-season data for both taxa in both years): linear quadratic model, the "inverse x" model, Weiner's model, and the Law & Watkinson power-parameter model. For all models, best fits were obtained with square-root transformation of biomass or tiller numbers. Weiner's model (see model form in Table 2) was rejected, because it consistently had the lowest t-values of the four model forms, for both biomass and tiller numbers. The quadratic model was less parsimonious, and the response surface of the quadratic model showed a region where predicted biomass or tiller numbers decreased and then increased with increasing densities, a trend that did not match the data. Also, parameters of the nonlinear models are more biologically interpretable than the polynomial terms of the quadratic model (Keisling et al. 1984; Pantone & Baker 1991). Thus, the inverse-x model and the power-parameter model remained as acceptable models. In comparing models of biomass, the Law & Watkinson power-parameter model was best based on t-values of the model parameters, with consistently higher t-values for density parameters (Table 2A). Residual mean squares were similar for all four model forms. For tiller numbers, the inverse-x model's merit relative to that of the power-parameter model was greater: t-values of density parameters of the power-parameter model were again the highest, but t-values of W_{max} were clearly higher for the inverse-x model, and residual mean squares of the inverse-x model were somewhat lower than those of the power-parameter model (Table 2B). The predicted-value response surfaces of the power-parameter and inverse-x models differed somewhat, but results of extra sum of squares comparisons of mixed density models done with power-parameter models and with inverse-x models were similar, indicating no substantial differences between the two models. To be consistent, power-parameter models were used for tiller numbers as well as for biomass.

There are disadvantages to nonlinear regression models, but nonlinear models are more likely to have close-to-linear behavior with large sample sizes (Ratkowsky 1990). Our sample sizes (590 to 720 for each taxon in each time period with combined water levels) should result in reduced nonlinear bias.

TILLER NUMBERS AND BIOMASS

In interpreting the mixed-density models, the W_{max} parameter can be thought of as a y-intercept value representing maximum tiller numbers or biomass irrespective of effects of densities. The two density parameters describe how densities of neighbors of each taxon reduce yield below W_{max} (larger b_T or b_S indicate greater effects of density). However, the W_{max} parameters that were obtained are artificially high and cannot be taken as literal maximum values, because the data sets did not include densities low enough to represent the "leveling off" of the response of yield per plant to density that occurs when plants are too far apart to compete. Because of this, W_{max} was fit as if yield per individual continued to increase as densities approached zero. Still, relative comparisons of W_{max} parameters of models with the same ranges of densities are meaningful.

Although some differences among replicates existed for biomass in 1991, replicates were combined for analyzing water levels and taxa in each year and season. Replicate one was unsuitable for comparing the two water levels, because of higher mortality following planting that occurred on the lower-water-level portion of that replicate, resulting in differences in mean densities between the two water treatments. Therefore, comparisons of the two water levels were based on the other two replicates. Overall, biomass without competition (W_{max}) was larger for the higher water level for Snake River in 1990, based on extra sum of squares comparisons of W_{max} in the models for the two water levels for each taxon. Since no further differences among water levels were found for biomass and tiller numbers, comparisons of the two taxa and comparisons between time periods were made based on mixed-density models fitted to data sets for the combined water levels using all three replicates.

In the first year, tiller numbers of thickspike were generally higher than those of Snake River, especially at low densities of thickspike. However, by the second year tiller numbers of thickspike and Snake River became similar (Fig. 2, Fig. 3). For thickspike, tiller numbers without competion (R_{max}) did not differ between years, but as density effects increased in 1991, tiller numbers were decreased ($p < 0.001$ for both densities; Fig. 3). In contrast, Snake River tiller numbers without competition (R_{max}) were significantly higher in the second year ($p < 0.001$), but as with thickspike, effects of densities of both taxa significantly reduced tiller production (thickspike density $p < 0.002$; Snake River density $p < 0.005$), restricting substantial increases in tiller numbers to the lower densities only (Fig. 3). In the first year, thickspike tiller numbers without competition (R_{max}) were significantly higher than those of Snake River ($p < 0.001$), but by the second year this difference was eliminated. In both years, thickspike density affected thickspike tiller production more strongly than it did Snake River ($p < 0.02$). Snake

River density affected Snake River tiller production more strongly than it did thickspike ($p < 0.001$), and in fact, in the first year it had little effect on thickspike tiller numbers.

As with tiller numbers, biomass of thickspike without competition (W_{max}) did not differ between years, but effects of densities of both taxa were greater in the second year ($p < 0.001$ and $p < 0.003$ for densities of thickspike and Snake River), resulting in a reduction in biomass as the plants aged (Fig. 4). In contrast with tiller numbers, no parameters of the biomass models for Snake River differed between years. Although tiller numbers became equal by the second year, biomass of thickspike both with and without competition (W_{max}), remained greater than that of Snake River in both years ($p < 0.001$ in both years; Fig. 2, Fig. 4). In 1990, as with tiller numbers, effect of Snake River density was greater on Snake River than it was on thickspike ($p < 0.001$), but effects of density of thickspike were similar on each taxon. In the second year, however, effects of densities of both taxa were greater on thickspike biomass than on Snake River ($p < 0.001$ for thickspike density, $p < 0.01$ for Snake River density).

For both taxa, most tillers emerged by mid-October (Fig. 5A). Throughout the growing season, tiller numbers of Snake River were higher than those of thickspike (Figure 5A). Only in Early Spring was tiller number of Snake River without competition (R_{max}) significantly larger than that of thickspike ($p < 0.001$, Fig. 6). During this period, the density of Snake River caused a greater reduction on Snake River than it did on thickspike ($p < 0.001$). For thickspike, tiller production without competition (R_{max}) increased over the entire period from Autumn to Late Spring ($p < 0.005$), with no changes in the effects of densities (Fig. 6). For Snake River, however, tiller number without competition (R_{max}) increased from Autumn to Early Spring ($p < 0.001$), with the density of thickspike causing a greater reduction in tiller numbers ($p < 0.05$), but both parameters remained constant from Early to Late Spring. Both earlier and later, intrataxon densities had a greater impact on tiller numbers than intertaxon densities ($p < 0.001$ for all), but overall, tiller numbers of the two taxa were similar (Fig. 5A, Fig. 6).

In the regressions constructed to predict biomass values for the seasonal sampling periods, both tiller number and mean height of the three tallest tillers were highly significant ($p < 0.001$ in all cases, R^2's 0.91 or higher, Table 3). For both taxa, analysis of covariance indicated that the slopes of the regressions from October and from June were significantly different. Thus, these two separate regressions were used to generate predicted biomass values for the Autumn and Early Spring, and the Late Spring and Summer sampling periods.

In contrast to tiller numbers, biomass of thickspike was greater than that of Snake River over all periods, and most increases in biomass occurred later in the growing season (Fig. 5B). Biomass of thickspike without competition (W_{max}) was greater than that of Snake River without competition in all periods ($p < 0.001$). However, the density of thickspike reduced thickspike biomass more than it reduced Snake River in Autumn and Early Spring ($p < 0.001$). This difference diminished by Late Spring. Snake River density caused a similar degree of biomass reduction on both taxa through Late Spring, but by Summer the reduction to thickspike biomass was less than the reduction to Snake River biomass. Thickspike biomass models did not differ between seasonal periods that could be compared statistically (Autumn versus Early Spring; Late Spring versus Summer), but biomass for both taxa obviously increased greatly from Early to Late Spring. Snake River biomass without competition (W_{max}) also increased from Autumn to Early Spring ($p < 0.001$), coinciding with its early increase in tiller numbers, but thickspike density caused greater reductions in Snake River biomass ($p < 0.002$) from Autumn to Early Spring.

PROPORTION OF TILLERS FLOWERING

The probability of having no flowering tillers and of having > 30% of tillers flowering were significantly affected by density of each taxon, by taxon of the target plant, and by year (Table 4). Proportion of tillers flowering was reduced at higher densities of both taxa, and Snake River produced fewer flowering tillers than thickspike (Table 4). Most plants did not flower in the second year, in contrast to the first (Fig. 8). The impact of years on probability of producing no flowering tillers was greater for thickspike than for Snake River (Table 4).

SURVIVAL OF TARGET INDIVIDUALS

After the establishment phase of the experiment, mortality of target plants was less than 7% from June 1989 through June 1992. Logit models with probability of the target plant being dead versus alive (P) as the dependent variable indicated that the only significant variable was density of thickspike, which was positively related to the probability of being dead (chi-square > 11.89, $p < 0.001$). The regression equation was

$$LN(P/1-P) = -3.755 + 0.016\,D_T.$$

The small amount of mortality that occurred did not differ with taxa, years, soil moisture treatment, or Snake River density.

Discussion

Biomass of Snake River wheatgrass was significantly higher at the higher water level in 1990, but no differences between water levels occurred in 1991, and no differences in tiller numbers between water levels were found. Soil moisture differences between the two water levels may not have been great enough to result in significant differences in plant growth, especially in 1991, when differences were less than in the previous year (Table 1). The one difference that occurred is inconsistent with rhizomatous grasses doing better on moister sites. However, the difference was only in W_{max}; competitive effects did not change between water levels.

Productivity of the plots was lower in the second year than the first. Apparently, soil resources were depleted by abundant growth in 1989 and 1990. For the rhizomatous taxon, thickspike, the pronounced decline in tiller numbers and biomass from 1990 to 1991 indicated that reduced biomass largely involved reduced tiller numbers rather than reduced tiller growth. Similarly, Montero & Jones (1992) found that tiller numbers of thickspike were more affected by moisture stress than was tiller weight. Tiller numbers and biomass responses of thickspike are also similar to the responses to neighbor removals and changing nutrient levels seen in other rhizomatous perennial grasses (DiTommaso & Aarssen 1991; Hartnett 1993). Apparently, thickspike inherently produces large numbers of tillers in the first years after establishment, whereas Snake River delays production of larger numbers of tillers. Superimposed over these tendencies were increased effects of neighbor densities in

1991. When resources became more depleted, increases in tiller numbers of Snake River were restricted to the lower densities. Snake River appeared more tolerant of these conditions, since it maintained its growth at levels similar to 1990.

Ability to adjust tiller numbers by regulating tiller emergence should be an important advantage to clonal plants, because it avoids self-thinning, and thus is efficient with respect to utilization and redistribution of resources (Hutchings 1979; de Kroon & Kwant 1991). Negatively density-dependent ramet emergence has been seen in several clonal plants (e.g. Briske & Butler 1989; de Kroon & Kwant 1991; de Kroon 1993; and references therein).

Both taxa exhibited distinct periods of tiller emergence and few tillers died before summer senescence. The only decline in tiller numbers seen before summer senescence was a small and statistically insignificant decline in Snake River from March to Late Spring. Thus, density-dependent mortality of tillers, i.e. self-thinning, did not occur in these taxa. Lack of density-dependent mortality is seen in many clonal plants (Hutchings 1979; Pitelka 1984; de Kroon & Kwant 1991), along with distinct periods of tiller emergence and tiller death (e.g. Dickerman & Wetzel 1985; Briske & Butler 1989). However, density-dependent mortality of ramets has been reported in other clonal plants (e.g. Kays & Harper 1974; Weller 1987; de Kroon & Kalliola 1995).

The different patterns of tiller emergence of these two taxa may represent different adaptations to the environment. In these semiarid ecosystems of the Intermountain region of the western United States, high variability in rainfall and temperatures is common, and ability of plants to quickly exploit episodic occurrences of favorable conditions is important. With large numbers of tillers produced early, the likelihood of self-thinning in Snake River during unfavorable conditions is greater. With fewer tillers produced initially, thickspike is less subject to self-thinning, and can initiate new tillers in the advent of good conditions. However, already emerged tillers as in Snake River would have a photosynthetic advantage over newly emerging tillers of thickspike, which would experience some time lag before substantial amounts of photosynthetic surface were exposed. Limitations caused by time-lags in production of photosynthetic surface are an important factor for desert plants (Comstock & Ehleringer 1986). Thus, Snake River should be better adapted to favorable environmental conditions when they occur episodically in time (e.g. rainfall events). Such periods may account for much of the total resource availability in nutrient-poor habitats (Chapin 1980; Taylor et al. 1982; Crick & Grime 1987). In addition to producing larger numbers of tillers earlier in the year, Snake River had an earlier increase in biomass than thickspike. This earlier phenology could also be an advantage in this region, because growth is restricted to a few months during spring and autumn between cold winters and dry summers (Mack & Thompson 1982).

Snake River's pattern of all tillers emerging in fall is common to many grasses of temperate ecosystems (e.g. Mueller & Richards 1986; Briske & Butler 1989). The pattern exhibited by thickspike, with considerable tiller emergence continuing into late spring, is less typical of species of semiarid climates and more typical of moister climates or habitats (e.g. Lonsdale & Watkinson 1983; de Kroon & Kwant 1991). Mack & Thompson (1982) proposed that greater summer precipitation may promote rhizomatous grasses, and that rhizomatous growth is a major factor conferring grazing tolerance to Great Plains species, while early resumption of spring growth and elevation of meristems was a disadvantage under grazing. Thickspike, with tillers produced later in the season, is more tolerant of clipping than is Snake River wheatgrass (Jones & Nielson 1993). Thus, thickspike's rhizomatous growth habit and more extended period of tiller production are consistant with adaption to grazing pressure and greater summer precipitation. Snake River's early tiller emergence and growth are inconsistent with grazing tolerance, but better adapted to the seasonal conditions and climatic variability of the Intermountain region.

Both taxa decreased flowering when growing in higher densities and in the second year when resources were more depleted, consistent with responses of other species (Newell & Tramer 1978; Schmid & Harper 1985), and with Loehle's (1987) model. This is also consistent with species adapted for competitive ability, as described by r- and K-selection theory, (MacArthur & Wilson 1967). This is inconsistent with Williams' (1975) prediction that clonal plants should shift to sexual reproduction when density becomes high and survival probability of further ramets produced locally becomes low.

After establishment in 1989, death of genets was rare. Mortality was related only to density of thickspike, the taxon with the greater competitive effect, suggesting that once genets were established, effect of density on the survival component of fitness was minor. Low mortality after establishment for clonal plants appears common (Hartnett & Bazzaz 1985; Callaghan et al. 1990; de Kroon et al. 1992; Eriksson 1993). One factor reducing mortality relative to nonclonal plants may be that in clonal plants, lateral growth of the clone is more important than vertical growth. In two clonal graminoids, overtopping and light competition were of little importance, as demonstrated by lack of increase in size inequalities (de Kroon et al. 1992). Competition for light is inherently asymmetric: taller plants interfere with smaller plants but not vice versa (Silvertown 1991). Clonal plants escape this asymmetric competition by lateral clonal growth. Sharing risk of death among ramets also promotes genet survival (Cook 1979; de Steven 1989; de Kroon et al. 1992). In our experiment, the predominance of belowground competition may also reduce the mortality of genets due to competition. In contrast to competition for light, competition for belowground resources tends to be more symmetric and not to increase size inequalities (Weiner 1986). Thus, initial advantages of dominant plants are not amplified to the point that smaller plants are killed.

Thickspike wheatgrass, with guerrilla rhizomatous growth, high tiller numbers, rapid growth, and more flowering in the first year, was a better competitor than Snake River, at least in the first year, when space was available and resources were underutilized. These traits of thickspike are perhaps adaptations to high disturbance and/or high resource levels. de Kroon & Schieving (1990) proposed that exploiting patches in space by rhizomatous growth provided an advantage to guerrilla-rhizomatous plants only at relatively high resource levels, where higher growth rates could be maintained. The decline of thickspike in the second year is consistent with this. By producing large numbers of tillers early in the season, Snake River may effectively exploit resource patches in time, an adaptation to high climatic variability and low resource levels of semiarid environments. In this way, in later years, Snake River may gain some competitive advantage, or reduce the competitive advantage gained by thickspike.

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Table 1 Monthly precipitation (cm) for the experiment (1990, 1991) from the North Logan, Utah weather station 2 km west of the site, along with the amounts of irrigation that were applied. Means and standard deviations are reported for amounts of irrigation applied in each month, based on 36 samples

MONTH:	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	SUM
1990 Precip.	2.2	3.5	3.0	4.1	4.3	5.0	1.0	1.2	2.1	3.2	4.4	4.6	38.6
Mean Irrigation				4.4	3.1	2.9		2.6					13.1
Std. Deviation				0.70	0.64	0.52		0.55					
1991 Precip.	1.4	1.8	8.1	2.8	7.5	3.6	1.2	1.3	5.7	6.4	6.5	2.0	48.3
Mean Irrigation					5.3	5.7							11.0
Std. Deviation					1.21	0.87							

Table 2 Diagnostic information on the two model forms that provided the best fits in regressions of biomass (A) and tiller numbers (B) as functions of densities of thickspike and Snake River wheatgrass neighbors. W is biomass per plant and R = number of tillers (ramets) per plant. D_T and D_S are densities of thickspike (T) and Snake River (S); b_T and b_S are fitted parameters; a is the intercept, W_{max} or R_{max} is maximum biomass or tiller numbers without competition (and is equivalent to 1/a)

(A.) BIOMASS MODELS

(1.) Inverse-x $W^{0.5} = 1/(a + b_T D_T + b_S D_S)$

Thickspike, 1990:	$1/(0.106$	$+ 0.0060D_T$	$+ 0.0018D_S)$	Residual MS= 3.888
t-values:	22.89	15.83	6.26	
Snake River, 1990:	$1/(0.203$	$+ 0.0152D_T$	$+ 0.0050D_S)$	Residual MS= 1.336
t-values:	17.59	11.86	9.09	
Thickspike, 1991:	$1/(0.122$	$+ 0.0106D_T$	$+ 0.0063D_S)$	Residual MS= 1.474
t-values:	17.74	17.38	10.52	
Snake River, 1991:	$1/(0.215$	$+ 0.0145D_T$	$+ 0.0064D_S)$	Residual MS= 0.783
t-values:	20.47	13.18	11.34	

(2.) Power-parameter

$$W^{0.5} = W_{\max}/(1 + D_T^{b_T} + D_S^{b_S})$$

Thickspike, 1990: $35.41\ /(1 + D_T^{0.636} + D_S^{0.308})$ Residual MS= 3.996

t-values: 19.67 30.28 7.33

Snake River, 1990: $18.27\ /(1 + D_T^{0.621} + D_S^{0.495})$ Residual MS= 1.368

t-values: 16.49 18.41 18.74

Thickspike, 1991: $31.32\ /(1 + D_T^{0.740} + D_S^{0.565})$ Residual MS= 1.476

t-values: 21.11 35.01 18.01

Snake River, 1991: $17.65\ /(1 + D_T^{0.604} + D_S^{0.531})$ Residual MS= 0.793

t-values: 19.60 21.30 23.56

(B.) TILLER NUMBER MODELS

(1.) Inverse-x $R^{0.5} = 1/(a + b_T D_T + b_S D_S)$

Thickspike, 1990: $1/(0.079 + 0.0021D_T + 0.0006D_S)$ Residual MS= 7.351

t-values: 34.94 16.60 5.55

Snake River, 1990: $1/(0.111 + 0.0030D_T + 0.0012D_S)$ Residual MS= 4.418

t-values: 29.78 12.40 8.48

Thickspike, 1991: $1/(0.083 + 0.0033D_T + 0.0017D_S)$ Residual MS= 4.777

t-values: 29.48 17.90 9.41

Snake River, 1991: $1/(0.084 + 0.0037D_T + 0.0015D_S)$ Residual MS= 5.067

t-values: 28.41 14.85 11.58

(2.) Power-parameter

$$R^{0.5} = R_{\max}/(1 + D_T^{b_T} + D_S^{b_S})$$

Thickspike, 1990:	$45.33\ /(1 + D_T^{0.477} + D_S^{0.118})$	Residual MS= 7.569
t-values:	24.19 29.63 2.89	
Snake River, 1990:	$33.21\ /(1 + D_T^{0.385} + D_S^{0.378})$	Residual MS= 4.598
t-values:	22.10 13.24 19.56	
Thickspike, 1991:	$46.59\ /(1 + D_T^{0.579} + D_S^{0.349})$	Residual MS= 4.829
t-values:	25.21 34.90 11.83	
Snake River, 1991:	$45.72\ /(1 + D_T^{0.508} + D_S^{0.462})$	Residual MS= 5.295
t-values:	23.49 21.23 24.68	

Table 3 Regression equations for biomass of thickspike and Snake River wheatgrasses, coefficients of determination (R^2), significance levels of parameters, and sample size (n), as a function of number of tillers (N) and mean height of the three tallest tillers (H), which were used to calculate predicted biomass values for the seasonal time periods

Sampling Time	Regression Equation	R^2	Sig. levels of Parameters (p <)			n
Taxon			a	b_N	b_H	
Oct. 1990						
Thickspike	.239 + .0098N + .1156H	.95	.016	.0001	.0001	20
Oct. 1990						
Snake River	.607 + .0054N + .0568H	.91	.0001	.0001	.0009	20
June 1991						
Thickspike	.501 + .0199N + .0260H	.95	.003	.0001	.0001	24
June 1991						
Snake River	.183 + .0159N + .0309H	.96	.163	.0001	.0001	24

Table 4 (A) Frequency of target plants in three classes of proportion (percent) of tillers flowering. (B) Equations where P is probability of producing no flowering tillers. (C) Equations where P is probability of having > 30 percent of tillers flowering. In the logistic regression equations, P is either proportion of plants producing no flowering tillers (B), or proportion of plants with greater than 30 percent of their tillers flowering (C). D_T and D_S are densities of thickspike and Snake River, respectively, and Y is year. All factors were highly significant in all regressions ($p > 0.0001$)

A.

	Thickspike Proportion flowering			Snake River Proportion flowering		
Year	0	$0<q<0.3$	$q>0.3$	0	$0<q<0.3$	$q>0.3$
1990	65	132	508	250	165	196
1991	488	130	80	538	48	22

B.

Thickspike: $\mathrm{LN}(P/1-P) = -4.37 + 0.041D_T + 0.027D_S + 3.316Y$

Snake River: $\mathrm{LN}(P/1-P) = -2.13 + 0.056D_T + 0.021D_S + 2.595Y$

C.

Thickspike: $\mathrm{LN}(P/1-P) = 2.35 - 0.038D_T - 0.018D_S - 3.663Y$

Snake River: $\mathrm{LN}(P/1-P) = 0.54 - 0.060D_T - 0.020D_S - 3.635Y$

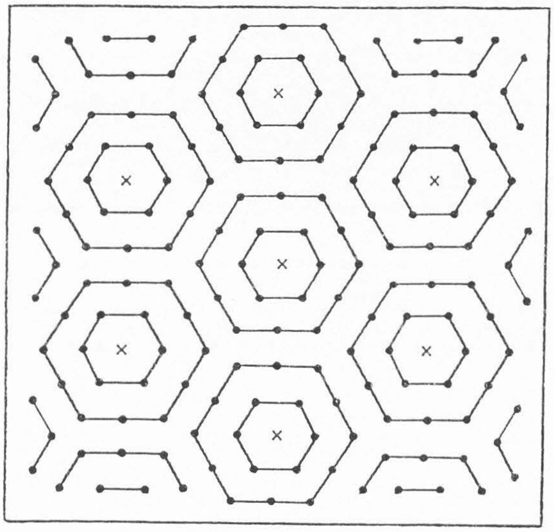


Fig. 1 Double-hexagon planting design with the target plant (from which data were collected) in the center (X) and an inner ring of six and an outer ring of 12 neighbor plants. Each plot contains seven concentric-hexagon pairs or observational units.

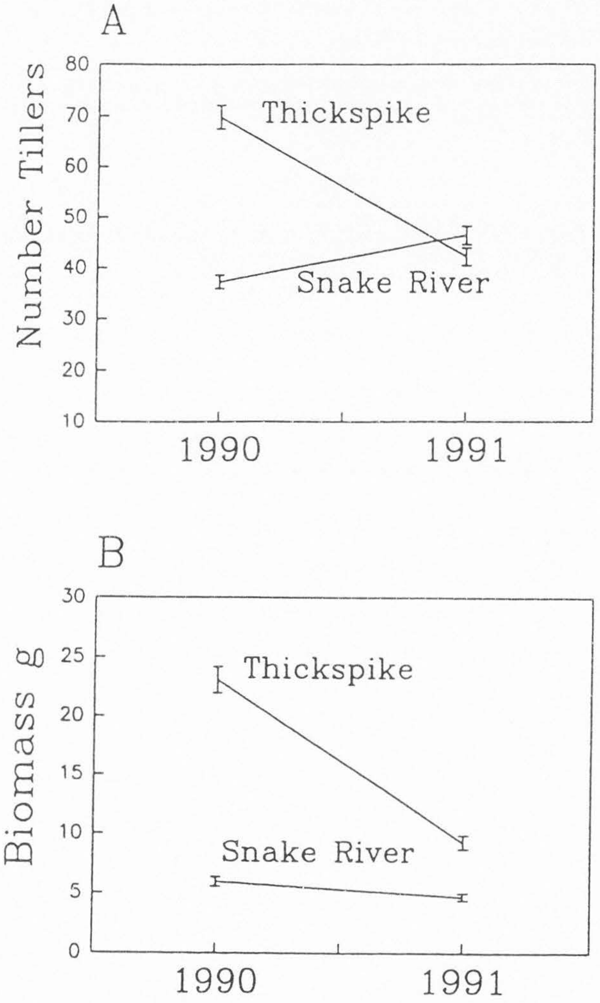
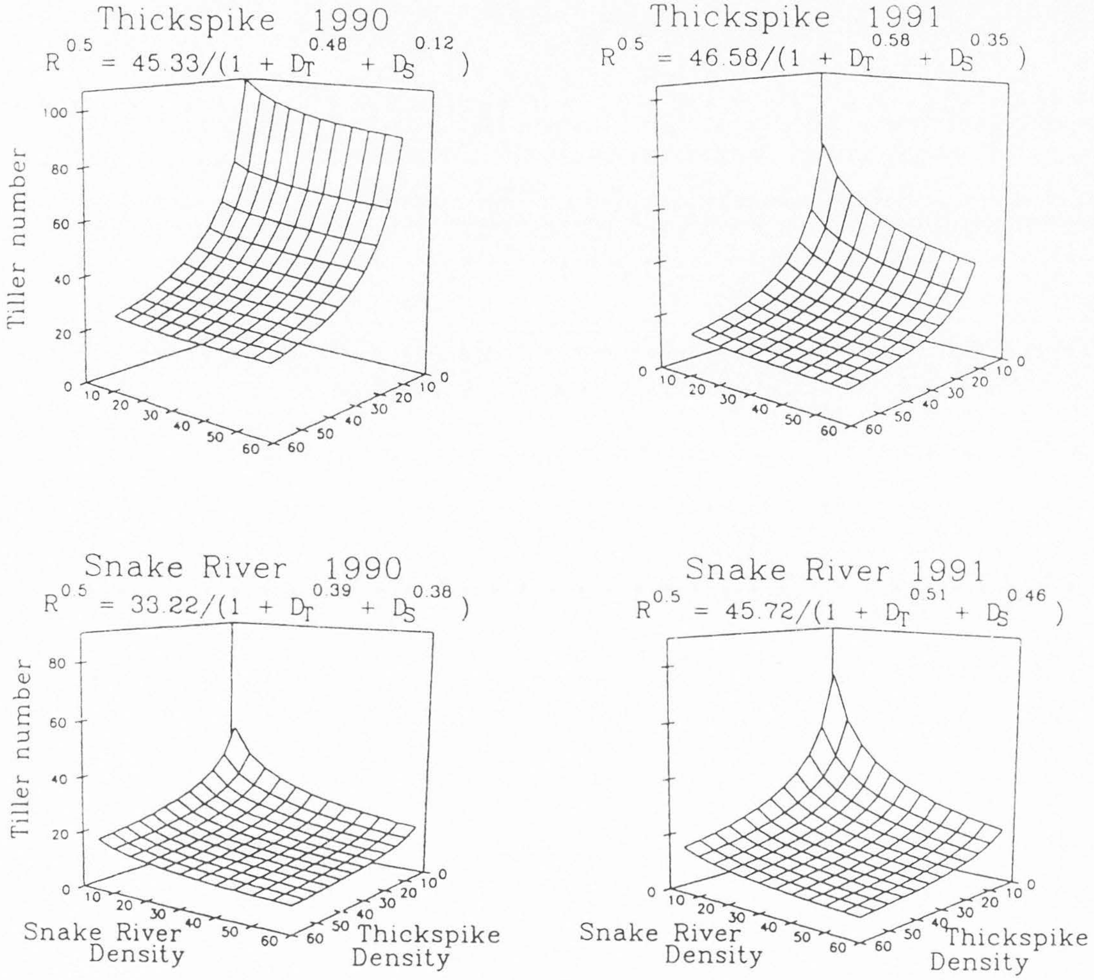


Fig. 2 Means over all mixed-densities (with standard errors) of (A) tiller numbers per plant and (B) biomass per plant of each taxon in each year.



Thickspike 1990

$R^{0.5} = 45.33/(1 + D_T^{0.48} + D_S^{0.12})$

Thickspike 1991

$R^{0.5} = 46.58/(1 + D_T^{0.58} + D_S^{0.35})$

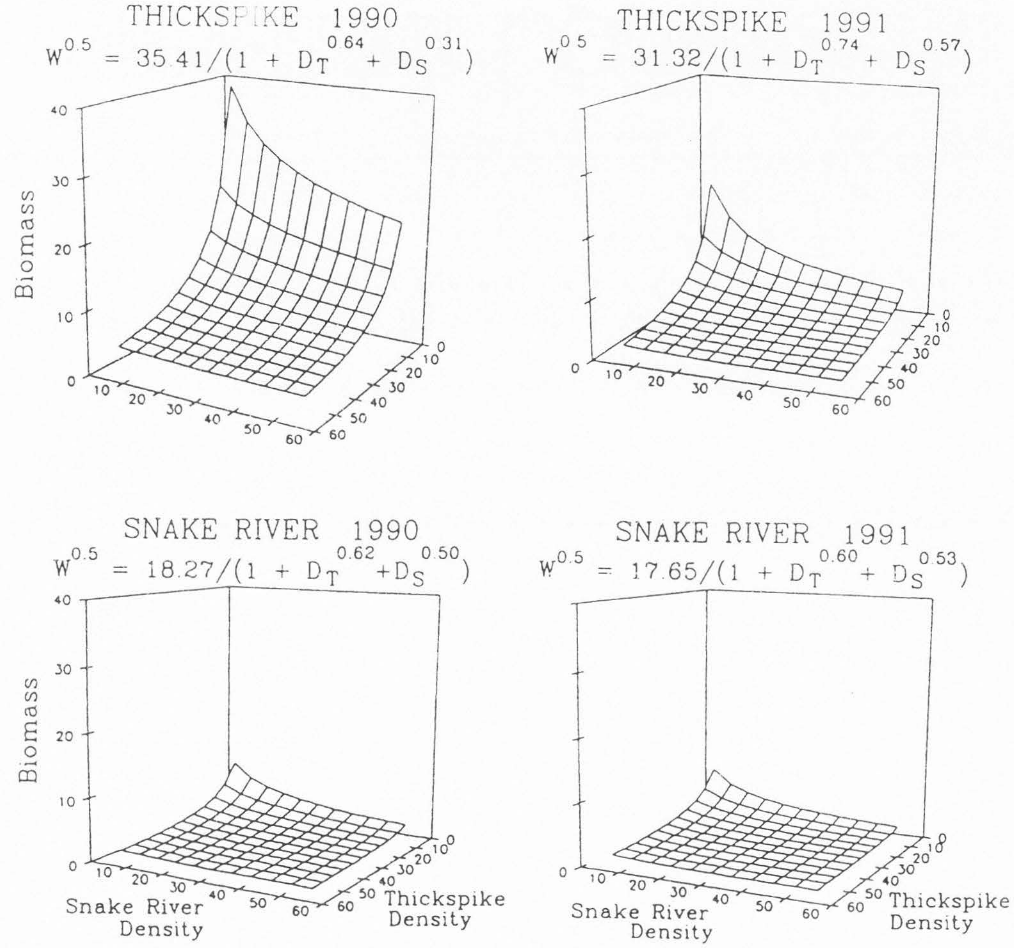
Snake River 1990

$R^{0.5} = 33.22/(1 + D_T^{0.39} + D_S^{0.38})$

Snake River 1991

$R^{0.5} = 45.72/(1 + D_T^{0.51} + D_S^{0.46})$

Fig. 3 Nonlinear models of end-of-season tiller numbers per plant as a function of densities of the two taxa in mixtures for each taxon in each year. D_T = density of thickspike, D_S = density of Snake River, R = number of tillers (ramets) per plant.



THICKSPIKE 1990

$W^{0.5} = 35.41/(1 + D_T^{0.64} + D_S^{0.31})$

THICKSPIKE 1991

$W^{0.5} = 31.32/(1 + D_T^{0.74} + D_S^{0.57})$

SNAKE RIVER 1990

$W^{0.5} = 18.27/(1 + D_T^{0.62} + D_S^{0.50})$

SNAKE RIVER 1991

$W^{0.5} = 17.65/(1 + D_T^{0.60} + D_S^{0.53})$

Fig. 4 Nonlinear models of end-of-season biomass per plant as a function of densities of the two taxa in mixtures for each taxon in each year. W = biomass per plant. See Fig. 3 for other model abbreviations.

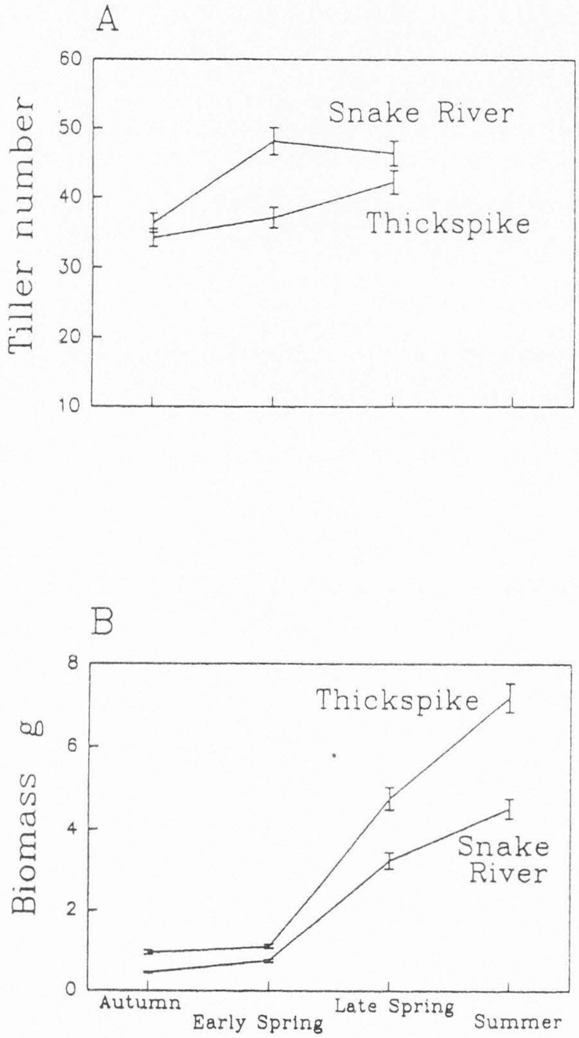


Fig. 5 Means over all mixed densities (with standard errors) of (A) tiller numbers per plant and (B) biomass per plant of each taxon at each seasonal sampling period in the 1990-1991 growing season.

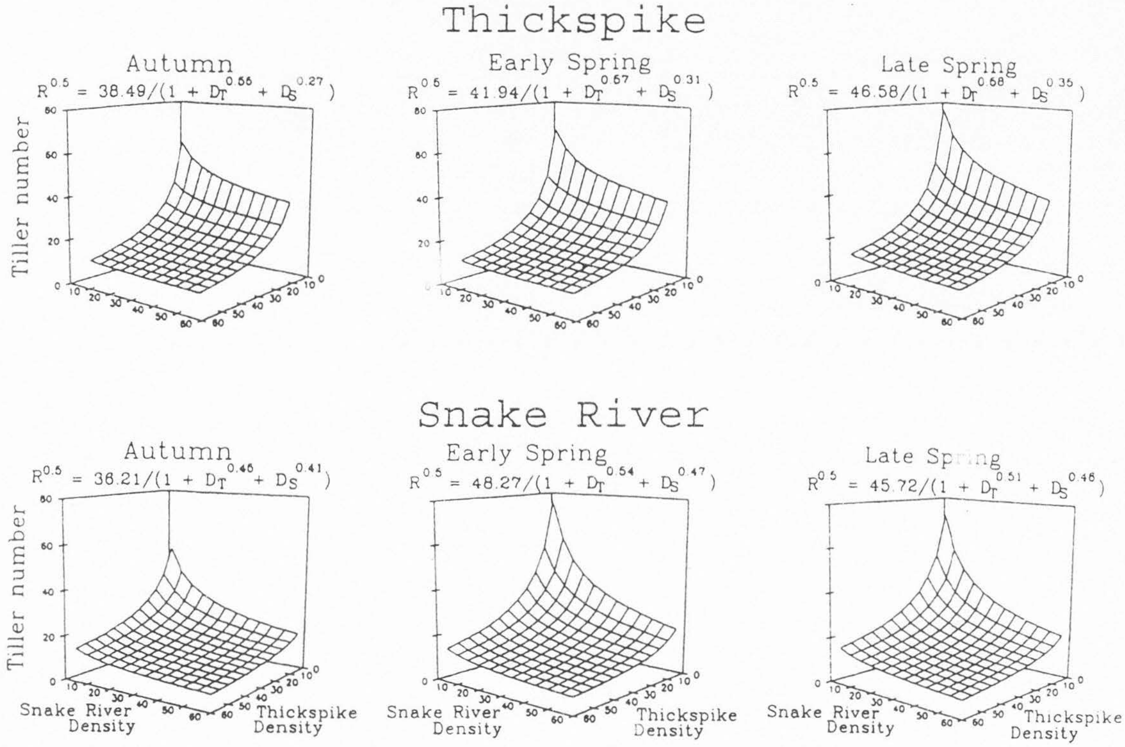


Fig. 6 Nonlinear models of tiller numbers per plant as a function of densities of the two taxa in mixtures for each taxon in each of the three seasonal sampling periods, autumn, early spring and late spring. See Fig. 3 and 4 captions for abbreviations and explanations.

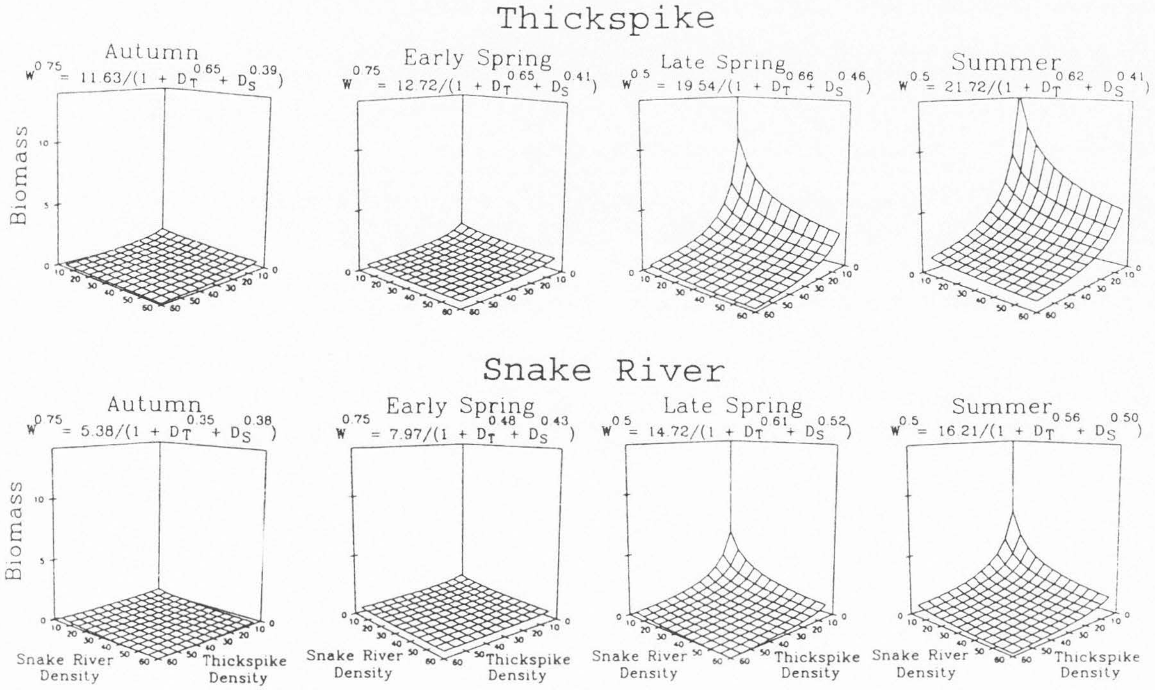


Fig. 7 Nonlinear models of biomass per plant as a function of densities of the two taxa in mixtures for each taxon in each of the four seasonal sampling periods.

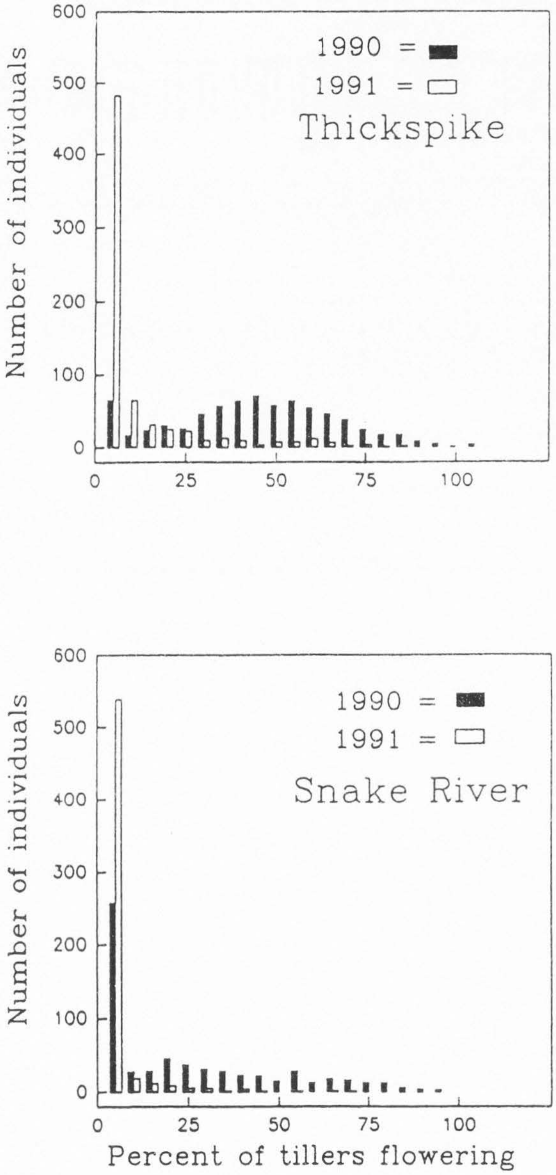


Fig. 8 Frequency distribution of target plants by proportion of tillers flowering for each taxon in each year.

CHAPTER 3

COMPETITIVE INTERACTIONS BETWEEN TWO CLOSELY RELATED RHIZOMATOUS AND CAESPITOSE SEMIARID PERENNIAL GRASSES[2]

Abstract. The competitive relationship between rhizomatous _Elymus_ _lanceolatus_ ssp. _lanceolatus_ and caespitose _E._ _l._ ssp. _wawawaiensis_ (thickspike and Snake River wheatgrasses) was examined in two-species mixtures with a range of densities of each taxon and two soil moisture levels. For two years and over seasonal intervals, models of aboveground biomass of each taxon as a function of mixed densities were used to calculate two competition indices, substitution rates and relative resource totals. Intensity and importance of competition were inferred from slopes and approximate R^2's of these models. Relative efficiency index was calculated from relative growth rates. In both years, thickspike was less affected by Snake River neighbors than by thickspike neighbors (substitution rate < one), and Snake River was more affected by thickspike neighbors than by neighbors of its own taxon (substitution rate largely > one). In the second year, thickspike showed minor increase and Snake River showed minor decrease in substitution rates, and thickspike experienced greater intensity of competition, whereas intensity for Snake River was unchanged, and products of substitution rates indicated greater overlap in

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[2] Coauthored by L. David Humphrey and David A. Pyke.

resources used by the two taxa. Importance of competition increased for both taxa in the second year. Substitution rates of Snake River were higher than those of thickspike in all seasonal intervals, but not significantly so in late spring-summer. During autumn-early spring and late spring-summer growing periods, relative growth rates of taxa were equivalent, but little growth occurred at these times. Most growth occurred between early and late spring when relative efficiency index indicated thickspike was the more efficient taxon, and when overlap in resource use was greater.

Introduction

Clonal plants are successful in a wide range of environments (Cook 1983; Silvertown 1987). General advantages of clonal spread include ability to invade other clones, resist invasion by seedlings, avoid extinction of the genet because the risk of death is shared among ramets (Cook 1983), and the ability to take advantage of patchy resources by extending ramets into areas that would not otherwise be accessible (Bell 1984). Lovett Doust (1981) used "phalanx strategy" to describe clonal species with modules or ramets closely spaced resulting in an unbroken, slowly advancing front and used "guerilla strategy" to describe species with ramets widely spaced that rapidly spread into new areas. Guerrilla species should have an advantage in exploiting open space (Lovett Doust 1981). Clonal plants may "forage" in that they selectively devote more resources to exploring resource-rich than resource-poor patches. Rhizomes grow longer and produce fewer ramets in unfavorable patches, quickly passing through these patches, whereas ramets are produced densely in favorable patches (Salzman 1985; Slade & Hutchings 1987). Physiological integration among ramets can allow clonal plants to buffer ramets throughout the clone against the localized extremes of a patchy environment through translocation of water, minerals, or photosynthate among ramets (Salzman & Parker 1985; Alpert & Mooney 1986).

Many studies have reported reversals in competitive superiority or changes in the competitive balance of species in communities when the environment differs (e.g. van der Maarel 1981; Austin et al. 1985; Rice & Menke 1985; Clay & Levin 1986). In the Intermountain West of the U.S.A., rhizomatous (guerilla) wheatgrasses are more abundant in moister areas and caespitose (phalanx) wheatgrasses more abundant in drier areas (Passey & Hugie 1963), indicating that advantages of the two growth forms may change along a moisture gradient.

The intensity of competition may increase (Grime 1977, 1987; Keddy 1989), or not change (Tilman 1982, 1988) with increasing productivity. Taylor et al. (1990) predicted that intensity of competition is not a function of productivity of the habitat, but is determined by the ratio of resource supply to demand, which is affected by disturbance. Thus, competition can be intense at almost any level of habitat productivity, if the vegetation is near carrying capacity, but competitive ability is conferred by different traits at different levels of habitat productivity. Ability of plants to tolerate low levels of resources and ability to quickly exploit resources (both components of Tilman's definition of competitive ability) are distinct traits that may differ independently of each other. Compared to plants adapted to high resource levels, plants adapted to stressful environments typically have low rates of resource uptake and poor ability to increase nutrient uptake when abundant nutrients become available, and have greater nutrient retention, resulting in greater tolerance of low soil nutrient levels (Chapin 1980; Berendse & Elberse 1990). DiTommaso & Aarssen (1991) found species responded individually to increasing nutrient levels, showing increases, decreases, or no change in the intensity of competition they experienced.

Our experiment assessed competitive interactions between two closely related rhizomatous and caespitose taxa native to semiarid regions of the western United States: the rhizomatous thickspike wheatgrass, Elymus lanceolatus ssp. lanceolatus (Scribner & J. G. Smith) Gould (syn: Agropyron dasystachyum (Hooker) Scribner & J. G. Smith) (Barkworth & Dewey 1985) and the caespitose Snake River wheatgrass, proposed name, E. lanceolatus ssp. wawawaiensis (Scribner &

Gould) J. R. Carlson & D. R. Dewey (Carlson, unpublished; which partially comprises Agropyron spicatum (Pursh) Scribner & Smith, including the cultivar 'Secar'). Being so closely related, but with one taxon caespitose and the other rhizomatous, these taxa provide an excellent vehicle for addressing questions on the advantages of rhizomatous and caespitose growth forms.

The additive series design is an improvement to the replacement series (de Wit 1960) in that it incorporates a range of relative frequencies of the species and a range of total densities (Spitters 1983). Replacement series experiments are inadequate when competitive interactions between the species differ with differences in overall density (Marshall & Jain 1969; Firbank & Watkinson 1985; Connolly 1986). There are also more general problems resulting from the nonorthogonality of densities of the two species in the design (Snaydon 1991; Sackville Hamilton 1994).

Connolly (1987) described three indices designed to assess interactions of species in mixtures based on response surface analysis of data from additive series designs: (1) Substitution Rates (Maynard Smith 1974), indicating the influence of neighbors of another species relative to influence of neighbors of one's own species, (2) Relative Resource Total, reflecting resource capture in mixture relative to pure stands, and (3) Relative Efficiency Index, reflecting growth rate of one species relative to that of the other species. We used models of aboveground biomass of each taxon as a function of mixed densities of the two taxa in an additive series design to calculate Substitution Rate and Relative Resource Total over a range of mixed densities, and calculated Relative Efficiency Index from relative growth rates of the two taxa. We further compared competitive interactions under two soil moisture levels, in two consecutive years, and at intervals through the growing season. Intensity and importance of competition were also evaluated using parameters from the mixed-density models.

Methods

This study was conducted at the Utah State University (USU) Ecology Center Complex near Green Canyon, 4 km northeast of the USU campus in Logan, Utah, U.S.A. The normal annual precipitation is 471 mm, most of which comes in the winter as snow. Native vegetation is dominated by _Artemisia_ _tridentata_ ssp. _vaseyana_ (Rydb.) Beetle (mountain big sagebrush) and perennial wheatgrasses, mainly _Pseudoroegneria_ _spicata_ (Pursh) A. Love (bluebunch wheatgrass). Plots were established on native soil that was throughly plowed and raked to provide a smooth, uniform surface. Seeds of thickspike wheatgrass (accession T-21076) obtained from Soil Conservation Service (SCS) Plant Materials Center, Aberdeen, Idaho and Snake River wheatgrass (cultivar 'Secar') from SCS Plant Materials Center, Pullman, Washington, were grown outdoors in partitioned styrofoam seedling flats, and transplanted to plots in May and June 1989. Each consisted of only 1-5 tillers when transplanted. Plots were watered during spring and summer of 1989 to enhance establishment.

The planting design was based on observational units which consist of 18 equidistant neighbor plants arranged in two concentric hexagons with a target plant (the plant on which data were obtained) in the center of the hexagons (Chapter 2). Our experimental design was an additive series, and a range of densities of monoculture plots of each taxon was included, to allow calculation of Relative Resource Total, as described by Connolly (1987). Four levels of relative frequency of the two taxa 1:5, 2:4, 4:2, 5:1 plus each taxon as the target plant in a monoculture of its own taxon were crossed with four levels of total density, 12, 36, 58, 84 plants m^{-2}. This design was further crossed with two taxa levels (i.e. it was repeated with each subspecies as the target plant), and two soil moisture levels, with three replications of the entire design. The two water levels were actual precipitation and actual precipitation plus irrigation, which was applied with a drip irrigation system (Laser Drip Tube®, Pep Co.) in a split-plot arrangement. To be roughly consistent with natural precipitation patterns, irrigation was applied mainly in spring to simulate augmented soil moisture that results from snow melt (see Chapter 2). Different levels of total density were achieved by using different sized observational units (hexagon-pairs). Density, relative frequency, and taxa were randomized. Each plot contained seven subsamples (i.e. seven observational units), all with the same relative frequency, total density and same taxon as the target plant. As a result of early mortality of seedlings after they were transplanted to the plots, densities and relative frequencies were altered to the extent that it was necessary to quantify densities of thickspike neighbors and Snake River neighbors in each observational unit and use the two continuous variables in place of the relative frequency and total density levels of the original design. Observational units with dead target plants or with $\geq$ 50% of neighbor plants dead were omitted.

End-of-season aboveground biomass data were obtained by clipping target plants at 8-cm height in mid-July 1990 and in late-July 1991. Samples for each target plant were oven-dried at 70°C for 24 hr in preparation for temporary storage, and later, again oven-dried at 70°C for 24 hr before weighing.

Plants were sampled at three times during the growth cycle for 1991, including the end-of-season sampling. Because autumn growth overwinters and contributes to spring growth (as reported by Nowak & Caldwell 1984 for related species), the first count, in early spring, mainly represented autumn growth.

Sampling periods and dates of data collection were (1) Early Spring, representing beginning-of-spring values, but actually collected December 1-9, 1990 and April 8-21, 1991 (persistent winter snow cover is common and winter survival of tillers is very high); (2) Late Spring, collected June 3-11, 1991; and (3) Summer, collected July 9-22, 1991.

Because data were repeatedly collected on the same plants over one growing season, we nondestructively estimated within-season biomass. Two measures were chosen as predictors of aboveground biomass, because data for them could be collected quickly, and because multiple linear regressions indicated these two variables were better than or as good as other variables tried (Chapter 2). Thus, these data, mean height of the three tallest tillers (measured to the collar of the uppermost leaf), and tiller number, were collected at each of the four sampling periods, and linear regressions were used to obtain predicted biomass. Because tillers were gradually dying over the Late Spring-Summer interval as summer senesence approached, no new tiller counts were done in July, and tiller numbers for July were considered to be the same as those in June, but height of the three tallest tillers was measured in July.

Analyses

The overall analysis consisted of two major parts. In the first part, the response, end-of-season aboveground biomass in 1990 and 1991, was analyzed over the experimental design. In the second part, predicted biomass was analyzed for the same experimental design for three seasonal intervals: Autumn-Early Spring, Early-Late Spring, and Late Spring-Summer.

Based on an earlier comparison (Chapter 2), a nonlinear model describing plant yield per individual as a function of densities of two species in mixtures (Law & Watkinson 1987; Firbank & Watkinson 1990) was chosen to describe the effects of densities of the two taxa on biomass. The model is:

$$W_i = W_{imax} / (1 + d_i^{b_{i,i}} + d_j^{b_{i,j}})$$

where W_i is **biomass per plant** of species i, W_{imax} is the biomass of an isolated plant in the absence of competition, d_i and d_j are densities of the two species, $b_{i,i}$ is a coefficient describing the competitive effect of individuals of species i on species i, $b_{,i,j}$ is a coefficient describing the competitive effect of species j on species i.

In work presented elsewhere (Chapter 2), the mixed-density models indicated differences in biomass between soil moisture levels in only one case, and no differences in effects of densities of the two taxa between soil moisture levels. Thus, the mixed-density models based on the two soil moisture levels and three replicates combined (fitted using PROC NLIN; SAS 1988) were used to calculate Substitution Rate and Relative Resource Total.

Substitution Rate indicates competitive effect of individuals of the other species relative to the effect of individuals of its own species. For each species, it is calculated as the partial derivative of the biomass-mixed density model for that species with respect to density of the other species divided by the partial derivative of the model with respect to density of its own species (Maynard Smith 1974). For the Law & Watkinson (1987) mixed-density model, substitution rate reduces to:

$$\begin{aligned} &Sub.\ Rate\ Taxon\ i = (b_{i,j}\, d_j^{(b_{i,j}-1)}) \ /\ (b_{i,i}\, d_i^{(b_{i,i}-1)}) \\ &Sub.\ Rate\ Taxon\ j = (b_{j,i}\, d_i^{(b_{j,i}-1)}) \ /\ (b_{j,j}\, d_j^{(b_{j,j}-1)}) \end{aligned}$$

Because substitution rates are a function of differences between the b_i and b_j parameters (which describe effects of densities of each taxon), tests of hypotheses concerning these parameters made using the common t-test procedure for testing hypotheses about regression parameters can be used as a crude surrogate statistical test for comparing substitution rates. (1) The first test is H_0: $b_{i,j} = b_{i,i}$, which is a test of whether the substitution rate of a taxon differs from one. (2) The second procedure tests whether substitution rates of the two taxa are different by testing whether the difference between b_i and b_j of the biomass model for one taxon differs significantly from the difference between b_i and b_j of the biomass model for the other taxon: H_0: $(b_{i,j} - b_{i,i}) = (b_{j,j} - b_{j,i})$. (3) The third test is a similar procedure, but tests whether substitution rates for a taxon differ in 1990 versus 1991: H_0: $(b_{90,j} - b_{90,i}) = (b_{91,j} - b_{91,i})$. To better identify appropriate standard error terms, these tests were conducted based on 95% confidence intervals of the parameters.

For each species in mixture, Relative Resource Total (RRT) relates yield per individual in the mixture to its yield in a monoculture. It is calculated as:

$$\mathrm{RRT} = d_i / d_{i,0} + d_j / d_{j,0}$$

where d_i and d_j are densities of species i and j in the mixture, and $d_{i,0}$ and $d_{j,0}$ are the densities of species i and j in monoculture that produce the same biomass per individual as that species in the mixture at a density of d_i or d_j, respectively, based on predicted biomass obtained from the mixed-density regression. An RRT > 1 indicates that more resources are being captured by the mixture than by a monoculture of either species. An RRT of 2 indicates that each species is unaffected by the presence of the other (i.e. $d_{i,0} = d_i$ and $d_{j,0} = d_j$). This index can indicate degree of niche overlap. Relative Resource Total addresses the total yield of the mixture rather than the yields of the individual species. The two components of RRT for yield of each taxon, $d_i/d_{i,0}$ and $d_j/d_{j,0}$ can change independently of each other, as well as one increasing as the other decreases. To assess species i and j components of RRT separately, the index, RRTsp (each taxon's contribution to RRT relative to its proportion in the mixture) was used.

$$\mathrm{RRTsp}_i = (d_i/d_{i,0})/(d_i/(d_i + d_j)) \text{ and}$$
$$\mathrm{RRTsp}_j = (d_j/d_{j,0})/(d_j/(d_i + d_j))$$

Like RRT, RRTsp = 1 indicates that growth response to individuals of the other species is the same as response to other individuals of its own species, RRTsp < 1 indicates a more negative response relative to members of its own species, and RRTsp > 1 indicates growth is less depressed by neighbors of the other species. RRTsp does not indicate relative competitive ability of the two species, because both species could be affected negatively or both positively in mixture.

Relative biomass over seasonal intervals was estimated biomass from tiller number and tiller height regressions for a sampling time minus the estimated biomass for the previous sampling time. By estimating biomass, we avoided problems associated with clipping different plots at different times (e.g. Connolly et al. 1990). For each taxon at each time interval, mixed-density models were fitted to the estimated biomass produced over that seasonal interval, and seasonal substitution rates and RRT were calculated based on these models.

A third index, Relative Efficiency Index, assessed seasonal changes in species interactions based on changes in relative growth rates. Relative growth rate (RGR) for each species can be expressed as the proportional change in yield over time RGR = w_t/w_{t+1} where w_t is biomass at time t and w_{t+1} is biomass at time t+1. Relative Efficiency Index (REI), the RGR of taxon i relative to that of taxon j, is: REI = RGR_i/RGR_j. When REI = 1, the taxa are equally efficient at converting resources to growth. Because this index is based on growth rate per unit biomass, efficiency is measured regardless of size differences. To calculate REI over the range of continuous mixed densities for each interval, models of RGR as a function of mixed densities were fitted for each species, and paired values of RGR_i and RGR_j, each for the same mixed density level, were predicted from the models (Connolly et al. 1990).

Results

Competition over two years

Biomass of thickspike was greater than that of Snake River overall. From the first to second year, there was substantial reduction in biomass of thickspike, but essentially no reduction in biomass of Snake River (Chapter 2). Substitution rates varied considerably over the range of mixed densities for both taxa (Fig. 9). In both years, thickspike was less affected by Snake River neighbors than by thickspike neighbors, as indicated by thickspike substitution rates generally less than one (significantly < one in both years based on surrogate t-test comparisons; Fig. 9). Substitution rates exceeded one only at lowest densities of Snake River (Fig. 9). In general, Snake River was more affected by thickspike neighbors than by neighbors of its own taxon. In both years, Snake River substitution rates were well above one at most mixed densities, but were below one at lower relative frequencies of Snake River (Fig. 9). In the first year, the substitution rate of Snake River was marginally significantly greater than one, indicating that it was more greatly affected by thickspike neighbors, but in the second year, the minor decrease in substitution rates of Snake River and minor increase in substitution rates of thickspike resulted in rates not significantly different from one. In both years, substitution rates of Snake River were significantly higher than those of thickspike, indicating that Snake River was affected more by interspecific competition than was thickspike in both years. The increase in thickspike substitution rates and the decrease in Snake River substitution rates from 1990 to 1991 was not significantly different for either taxon.

Calculation of RRT was problematic, because many equivalent monoculture densities for Snake River ($d_{j,0}$) greatly exceeded the range of density values used to obtain the biomass-mixed-density model, making accuracy of these predicted biomass and corresponding monoculture densities suspect. For this reason, RRT was calculated only up to a total density of 70 rather than 85 plants per m^2; still, many $d_{j,0}$ values were high. Any values above twice the maximum density in the data sets were replaced with the twice-maximum-density value (16 observations in 1990, 10 in 1991, and fewer for seasonal intervals). Connolly et al. (1990) also commented on this problem with RRT. Values for RRT were similar for both years, and consistently below one (0.89-0.71 in 1990; 0.87-0.67 in 1991; lower at lower total densities in both years), indicating not only great overlap in resources used by the two taxa, but antagonistic effects of one or both taxa on the other.

For thickspike, values for RRTsp ranged from 3.0-0.8 in the first year with most values near 1.0-1.5, and ranged from 1.9-0.8 in the second year with most values near 1.0; RRTsp of Snake River was generally below 0.5 (0.56-0.30 in 1990, 0.63-0.41 in 1991). This indicates the low RRT values are mainly a result of reduced contribution of Snake River to the RRT value, while the contribution of thickspike overall, was proportional to its relative frequency (or slightly above in 1990).

A near-inverse relationship between substitution rates of two taxa indicates competition was largely for the same resources, and products of substitution rates of the two taxa near one indicate such an inverse relationship (Menchaca & Connolly 1990). Because of problems with obtaining equivalent monoculture densities for RRT, we used products of substitution rates as an additional indicator of overlap in resource use. Products of substitution rates indicated greater dependence on the same resources (greater interspecific competition) in the second than in the first year. None of the values of products of substitution rates were very close to one, which would indicate complete reciprocity (0.6-0.8 for the second year and during the Early-Late Spring period which were highest). The extent of overlap in resources used, indicated by RRT, is greater than indicated by products of substitution rates. Unlike products of substitution rates, RRT varied little among times.

Welden & Slauson (1986) used linear regression of plant size as a function of distance separating neighboring plants to describe competition, and considered the slope of the regression to represent the intensity of competition (effects of competition independent of effects of other factors) and the R^2 to represent the importance of competition (magnitude of effects of competition relative to magnitude of effects of other factors). We used our biomass mixed-density models similarly, treating both the thickspike and the Snake River density parameters as the slope. Since these were nonlinear models, approximate R^2 (Lindquist et al. 1994) was used. Increases in the effects of densities of both taxa on thickspike in 1991 (Table 5) indicated an increase in the intensity of competition in the second year, but for Snake River, the density parameters for models in both years were similar (Table 5), indicating no change in intensity of competition. Approximate R^2 (Table 5) indicated that competition became more important for both taxa in the second year.

Competition over seasonal intervals

Mixed density models for thickspike and for Snake River for each seasonal interval are listed in Table 6. For all three intervals, surrogate t-test comparisons of density parameters of the mixed-density models indicated that thickspike substitution rates were significantly less than one (Fig. 10), indicating that intraspecific competition had a significantly greater impact than interspecific competition. Snake River substitution rates were not significantly different from one, indicating similar impacts of intra- and interspecific competition on growth of Snake River. Minor changes in substitution rates over time (Fig. 10) were not significant for either taxon. However, one important change over time was noted. In the initial interval, and in Early-Late Spring, substitution rates of thickspike were significantly lower than those of Snake River, but in Late Spring-Summer, substitution rates did not differ between taxa.

As with the end-of-season analysis, problems with reliable calculation of RRT occurred. Also, RRT and RRTsp for all three seasonal intervals were similar to yearly RRT and RRTsp. Therefore, these data are not presented.

Intensity and importance of competition were not addressed for seasonal intervals, because transformations applied to biomass in the mixed-density models differed among intervals.

Nonlinear Law & Watkinson mixed-density models with relative growth rate as the response variable were fit to the Early-Late Spring interval (Table 7B). Predicted values from these models were used to calculate Relative Efficiency Index over the range of mixed densities. For the other two intervals, Autumn-Early Spring where the amount of growth was very small (as stated previously), and Late Spring-Summer, models of RGR as a function of mixed-densities were not obtainable. For these two intervals, one mean REI value for the range of mixed densities was calculated from the mean RGR's of the two taxa over the range of mixed densities. These mean RGR's were low for both taxa in both periods, and mean REI values were near one (Table 7A). The mean REI value for Early-Late Spring calculated in the same way was 0.78, indicating lower efficiency of Snake River relative to thickspike. The Early-Late Spring REI, based on the RGR mixed-density models, varied mainly with total density, exceeding one at the lowest total densities (Fig. 11).

Discussion

The increase in effect of Snake River on thickspike and the decrease in effect of thickspike on Snake River from 1990 to 1991 as indicated by substitution rates was rather minor, but other analyses provided futher indications of changes in competitive relationships. Products of substitution rates indicated greater overlap of resource use between the two taxa in the second year. Increase in the intensity of competition experienced by thickspike (although it was still the superior competitor), but no change in the intensity experienced by Snake River indicated that this increase in overlap largely consisted of thickspike being more affected by competition in the second year, when space above- and belowground was more fully occupied, and resources were apparently more depleted.

DiTommaso & Aarssen (1991) concluded that intensity of competition experienced by a species may increase or decrease depending on the adaptations the species (and its neighbors) possess in regard to high or low resource levels. Thickspike experienced increased intensity of competition in 1991 under conditions to which it was apparently less well adapted, while Snake River experienced no change in intensity. Reduced importance of competition, but similar intensities with increased stressfulness of the habitat (Campbell & Grime 1992), and no changes in intensity of competition with changes in nutrient level (Wilson & Shay 1990; Wilson & Tilman 1991) have been found. Reports of increased intensity of competition with reduced productivity are the most rare. However, increased density-dependent regulation of growth has occurred in grasses in drought years (i.e. increased stress; Briske & Butler 1989; Fowler 1986), consistent with the increased intensity of competition for thickspike in 1991. The increase in importance of competition to Snake River while intensity was unchanged indicated intensity and importance of competition can vary independently of each other, consistent with conclusions of Welden & Slauson (1986).

The competitive advantage of thickspike appeared to decline in late spring and summer of the second year, in that substitution rates of the two taxa were no longer significantly different. Also, REI (mean over mixed densities) was near one, indicating that growth rates of the two species were equivalent in Late Spring-Summer. However, the perceived importance of this shift should be tempered. Relative Growth Rates over this interval were very low (Table 7). This change in competitive effects could be largely due to differences in phenology, with thickspike entering summer senescence somewhat earlier than Snake

River. Relative Efficiency Index was also near one in Autumn-Early Spring, but again, little growth occurred over this interval. Still, relative competitive abilities in autumn could be important, because any initial size advantages achieved during that time could substantially affect competitive interactions during later growth in spring. In the Early-Late Spring interval when most growth occurred, RGR of Snake River was substantially less than that of thickspike. Products of substitution rates indicated the two taxa depended on the same resources more during the Early-Late Spring interval than at any other time of the year. In autumn, dependence of the two taxa on the same resources was lower perhaps because resource demand was lower. In late spring and summer, phenological differences may reduce demands made by thickspike on resources used by Snake River, as discussed above.

In this semiarid environment, it is reasonable to assume that competition occurs primarily belowground (*sensu* Tilman 1988). Competitive ability may be based on a plant's ability to quickly draw down resources to low levels, and to tolerate low resource levels (Tilman 1982, 1988), but different traits may be important in conferring competitive ability at different levels of site productivity (Taylor et al. 1990). Because of reduced nutrient loss, plants adapted to low nutrient levels can have a lower relative nutrient requirement, i.e. more growth per amount of nutrient taken up (Berendse & Elberse 1990; but see Aerts & de Caluwe 1994). It appears that thickspike has greater ability to quickly draw down resources, as indicated by its abundant growth in the first year. Relative to Snake River, it grew much larger in the first year and reached reproductive maturity sooner (Chapter 2). Rhizomatous spread and higher growth rates may have allowed it to exploit large unoccupied resource patches in 1990 better than Snake River, but a related experiment (Chapter 4) indicated both taxa equally exploited large resource patches. The shift in competitive abilities in the second year was also apparantly not a result of greater ability of Snake River to tolerate reduced nutrients: Data from a related experiment (Chapter 4) indicated the two taxa responded similarly to greatly reduced soil nutrients, indicating similar relative nutrient requirements. Following the concept of scale versus precision of foraging (Campbell et al. 1991), plants adapted to conditions of more depleted resources might be better able to exploit smaller more infrequent patches of soil resources that remain under these conditions, but no information is available on abilties of thickspike and Snake River to exploit patches of soil resources on a small scale.

Perhaps thickspike's competitive advantage was due mainly to its quicker growth as a young plant relative to Snake River; it preempted a large share of resources as plants were first becoming established on plots. Thus, at later stages, it had the advantage of being larger. Since competition is belowground and therefore less of a positive-feedback process, and since the two taxa responded similarly to reduced soil nutrients, the competitive advantage of thickspike might be expected not to increase in the second year. Apparently, the shift in competitive abilities toward Snake River, and greater intensity of competition experienced by thickspike occurred in the second year, because Snake River possess some unidentified traits that made it a better competitor under the conditions in 1991, and/or traits of thickspike (other than its early growth) that conferred competitive advantage in 1990 were less effective under the conditions of 1991. Schmid & Harper (1985) reported a competitive reversal between a phalanx and a guerrilla species. The ability of the guerrilla species to exploit open space was an advantage only at low densities. The phalanx species was superior at high densities apparantly because it was better able to persist on a site. Our shifts in competitive abilities between years appeared consistent with their results over low and high densities.

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Table 5 Models of end-of-season biomass as a function of mixed-densities of the two taxa obtained for each taxon in each year (Chapter 2), and approximate R^2's of the models. D_T = density of thickspike, D_S = density of Snake River, W = biomass.

Taxon, Year	Model	Approximate R^2
Thickspike, 1990:	$W^{0.5} = 35.41 / (1 + D_T^{0.64} + D_S^{0.31})$	0.30
Snake River, 1990:	$W^{0.5} = 18.27 / (1 + D_T^{0.62} + D_S^{0.50})$	0.42
Thickspike, 1991:	$W^{0.5} = 31.32 / (1 + D_T^{0.74} + D_S^{0.57})$	0.40
Snake River, 1991:	$W^{0.5} = 17.65 / (1 + D_T^{0.60} + D_S^{0.53})$	0.51

Table 6 Models of biomass as a function of mixed-densities of the two taxa obtained for 1) the interval from the start of growth prior to the autumn sampling to early spring; and the intervals 2) early-late spring; and 3) late spring-summer. D_T = density of thickspike, D_S = density of Snake River, W= biomass. T-values of each of the three parameters are listed below each equation. Transformations of biomass used are listed

Interval, Start of growth-Early Spring

Thickspike: $W^{0.75} = 12.72 /(1 + D_T^{0.65} + D_S^{0.41})$

t-values: 19.8 30.5 11.2

Snake River: $W^{0.75} = 7.97 /(1 + D_T^{0.48} + D_S^{0.43})$

t-values: 21.8 18.6 21.5

Interval, Early-Late Spring

Thickspike: $W^{0.5} = 16.71 /(1 + D_T^{0.64} + D_S^{0.46})$

t-values: 23.1 34.46 15.56

Snake River: $W^{0.5} = 13.53 /(1 + D_T^{0.62} + D_S^{0.53})$

t-values: 19.47 21.4 23.2

Interval, Late-Spring Summer

Thickspike: $W^{0.75} = 18.36 /(1 + D_T^{0.60} + S_S^{0.40})$

t-values: 17.9 25.3 10.4

Snake River: $W^{0.75} = 8.79 /(1 + D_T^{0.37} + D_S^{0.41})$

t-values: 19.64 12.33 18.37

Table 7 (A) Mean relative growth rates for the two taxa (averaged over all mixed densities) and relative efficiency index values based on those mean RGR's for the three time intervals. (B) Models of RGR for the early-late spring interval. Models of RGR as a function of mixed densities were not obtainable for the other two intervals. T-values of the three parameters are listed below each equation. The model form is:

$$G = G_{\max} / (1 + D_T^{b_T} + D_S^{b_S})$$

where G is RGR, $G_{\max}$ is maximum RGR without competition, D_T = density of thickspike, D_S = density of Snake River, and b_T and b_S are fitted parameters

(A)

INTERVAL	Mean RGR, Thickspike	Mean RGR, Snake River	Mean REI (RGR_S/RGR_T)
Autumn-Early Spring	1.35	1.48	1.094
Early-Late Spring	3.62	2.84	0.784
Late Spring-Summer	1.70	1.81	1.062

(B)

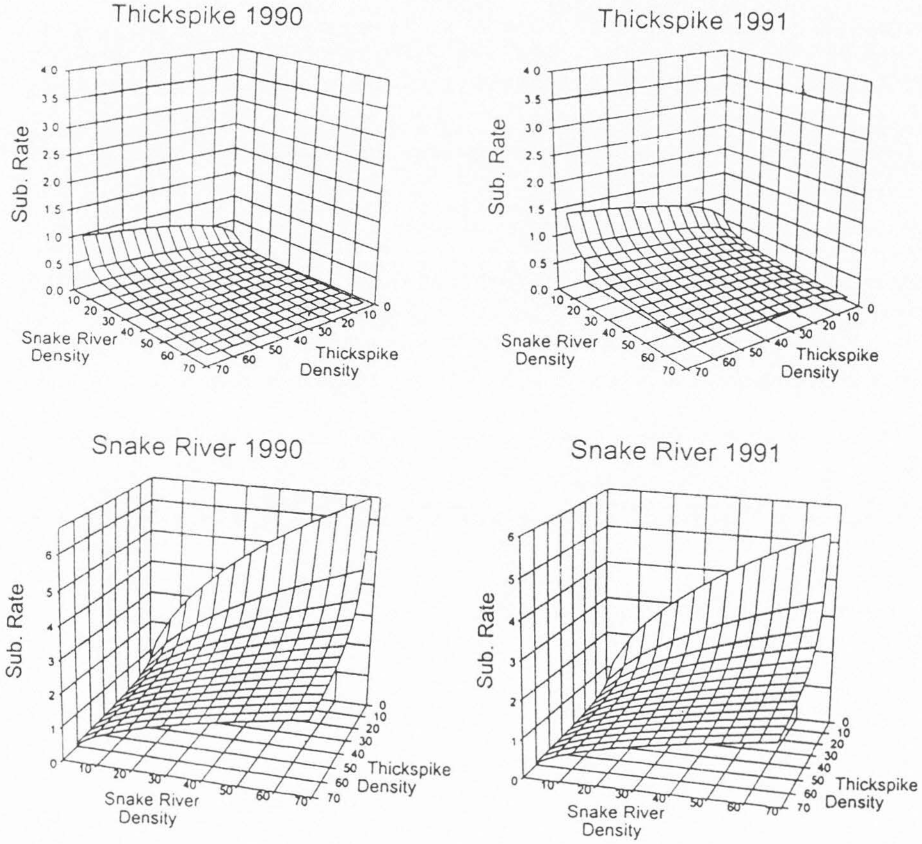
RGR-Mixed Density Models for the Early-Late Spring Interval:

Thickspike: $17.34 / (1 + D_T^{0.34} + D_S^{0.18})$

t-values: 15.34 12.41 3.65

Snake River: $22.97 / (1 + D_T^{0.50} + D_S^{0.49})$

t-values: 13.83 11.91 15.41



Thickspike 1990

Thickspike 1991

Snake River 1990

Snake River 1991

Fig. 9 Substitution rates over the range of mixed densities for each taxon in each year.

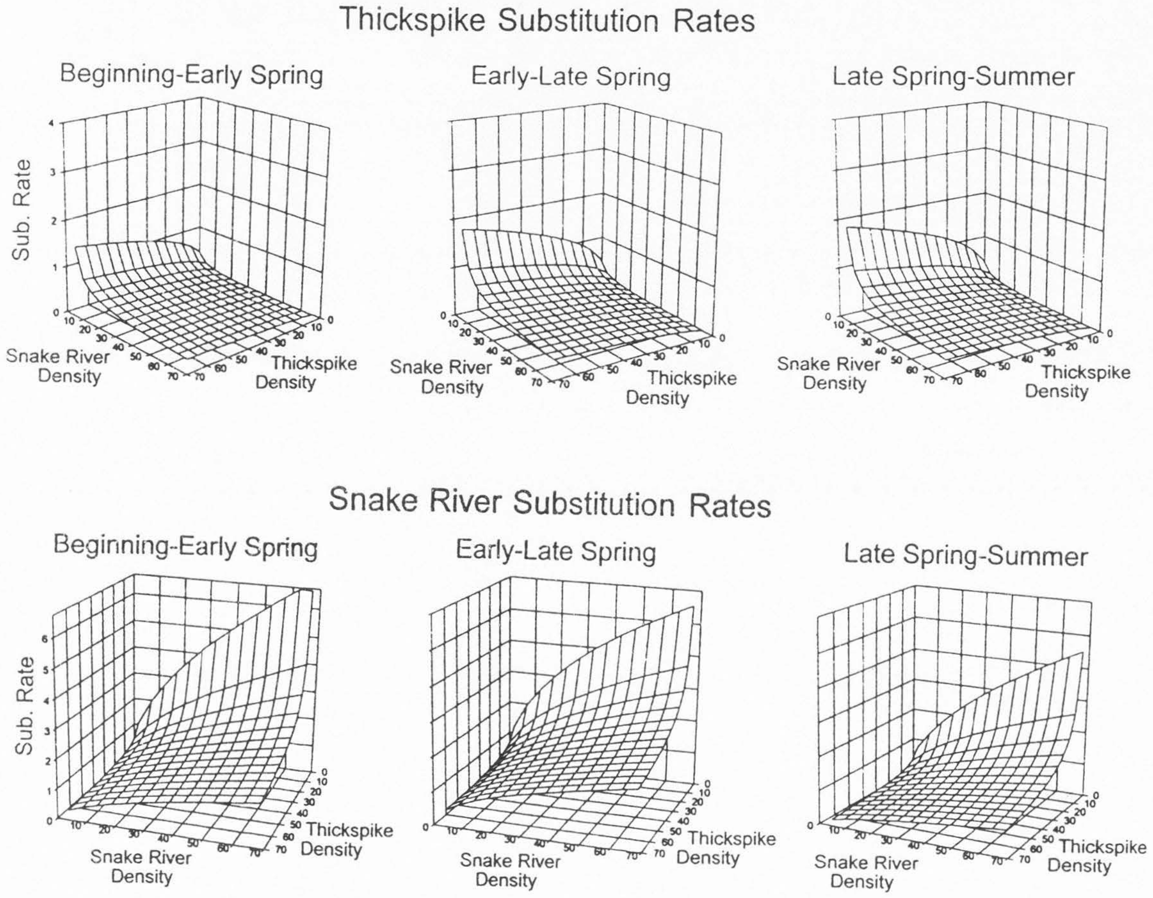


Fig. 10 Substitution rates over the range of mixed densities for each taxon for the intervals beginning of growth-early spring, early-late spring and late spring-summer.

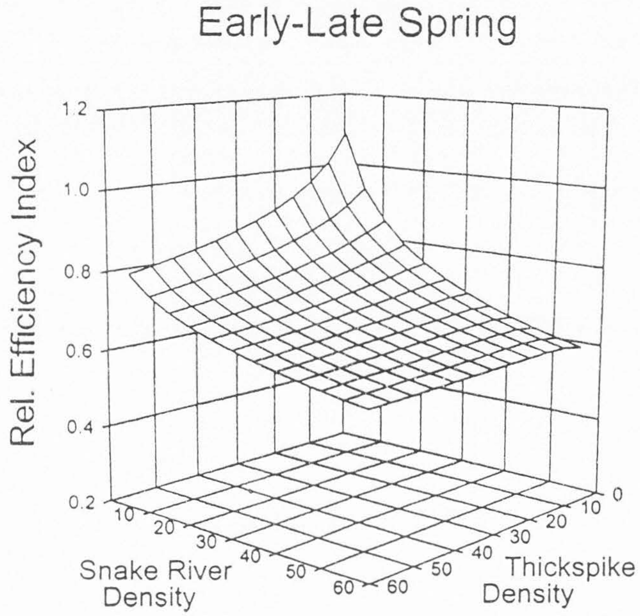


Fig. 11 Values of relative efficiency index (REI) over the range of mixed densities for the early-late spring interval.

CHAPTER 4

CLONAL FORAGING IN PERENNIAL WHEATGRASSES: A STRATEGY FOR EXPLOITING PATCHY SOIL NUTRIENTS[3]

Summary

1 Clonal foraging response to low- and high-nutrient patches was examined in the rhizomatous wheatgrass, _Elymus lanceolatus_ ssp. _lanceolatus_, and its ability to exploit soil nutrient patches was compared to that of the closely related bunchgrass, _E. lanceolatus_ ssp. _wawawaiensis_.

2 Clones of 14 genets of each taxon were planted in boxes consisting of two cells: the origin cell where clones were planted, and the adjacent destination cell, with each cell having either low or high levels of nutrients.

3 A foraging response was found in the rhizomatous taxon, with more tillers and preferential production of closely spaced tillers in high-nutrient destination cells; nutrient status of the origin cell also affected the response.

4 Roots of both taxa accessed nutrients in destination cells (the bunchgrass by root growth only), and aboveground biomass of both taxa increased similarly with high-nutrient destination cells. Under these experimental conditions, root growth was as important as clonal foraging response in exploiting nutrients in destination cells.

5 The taxa appeared similar in their tolerance of low levels of soil nutrients.

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[3] Coauthored by L. David Humphrey and David A. Pyke.

6 No difference among genets in degree of foraging response, and no relationship between degree of foraging response and fitness (biomass of the clone) when high-nutrient destination cells were present were found.

Introduction

Species with clonal spread should have an advantage over caespitose species in exploiting patchy resources (Harper 1977). Bell (1984) described clonal species as "foraging" for resources by extending ramets into other parts of their surroundings that would not otherwise be accessible. Foraging responses for plants or animals have been defined as responses that: (1) occur before resource uptake; (2) modify the degree of uptake; and (3) can be varied by the foraging organism (Kelly 1990). Some clonal plants meet at least the last two of these three requirements by exhibiting morphological plasticity in ramet placement in response to resource patches; ramets are produced densely within resource-rich patches and sparsely within resource-poor patches, allowing the plant to effectively exploit the rich patches and pass through the poor patches to continue foraging with a minimal investment of biomass within poor patches. The plasticity involved in the foraging response can be achieved by decreased spacing between parent and daughter ramets or increased rhizome branching within resource-rich patches (Salzman 1985; Slade & Hutchings 1987; Sutherland & Stillman 1988; de Kroon & Knops 1990).

Mechanisms of plastic responses of internode length and rhizome branching to soil nutrient levels likely include regulation by auxins and cytokinins, levels of which can be modified by availability of soil resources (Hillman 1984; Salisbury & Marinos 1985; Hutchings & Mogie 1990; Hutchings & de Kroon 1994). This provides a link between morphological responses involved in the foraging response and patch quality. Thus, the foraging response to patchy soil nutrients involves a hormonally mediated response to resource uptake, once patches are encountered.

Plasticity has been suggested as an important adaptation to variable or unpredictable environments, such as patchy environments (Bradshaw 1965; Jain 1978; Hume & Cavers 1982). Phenotypic plasticity can be described as the norm of reaction, i.e. array of phenotypic responses produced by a single genotype over a range of environmental conditions, (Schlichting 1986; Scheiner 1993). Genetic differences among individuals in degree of plasticity of various traits have been found for many plant species (e.g. Bradshaw 1965; Jain 1978; Brown 1983; Taylor & Aarssen 1988; Thompson et al. 1991). Degree of plasticity can be subject to natural selection (Bradshaw 1965; Schlichting 1986), and plasticity of a trait can evolve independently of the mean of that trait (Schlichting 1986; Schlichting & Levin 1986; MacDonald & Chinnappa 1989; Thompson 1991). However, high phenotypic variability can also make genetic variation "invisible" to natural selection, limiting the effect of selection (Bradshaw 1965; Schlichting 1986; Sultan 1987).

Although several studies have demonstrated a genetic component to phenotypic plasticity, few have addressed effects of a plastic foraging response on fitness. Demonstrated fitness differences correlated with genetic differences in plasticity would indicate that natural selection for plasticity is likely.

We investigated the existence of and advantages to the genet of clonal foraging response, i.e. discrimination between habitats in ramet placement under conditions of patchy soil nutrients for a rhizomatous perennial wheatgrass native to the western United States, <u>Elymus</u> <u>lanceolatus</u> ssp. <u>lanceolatus</u> (Scribner & J. G. Smith) Gould (thickspike wheatgrass). Its ability to exploit patchy soil nutrients was compared to that of a closely related native grass, proposed name, <u>E.</u> <u>lanceolatus</u> ssp. <u>wawawaiensis</u> (Scribner & Gould) J. R. Carlson & D. R. Dewey (Snake River wheatgrass), that is caespitose and therefore cannot exhibit a clonal foraging response. However, rapid root proliferation into nutrient-rich patches has been demonstrated for other species (Crick & Grime 1987; Eissenstat & Caldwell 1988; Jackson & Caldwell 1989) and is likely an important mechanism for accessing patchy soil nutrients (Tilman 1988). Therefore, it is possible that the caespitose subspecies Snake River, as well as the rhizomatous subspecies thickspike, may be able to exploit the nutrient rich patches, but by alternative mechanisms.

Different clonal species may possess different growth strategies. Foraging is a component of only one strategy (de Kroon & Schieving 1990). Because high growth rates are necessary to forage effectively, clonal plants with a foraging strategy should have high growth rates and adaptations to higher levels of soil resources (de Kroon & Schieving 1990). The caespitose grass may be adapted to lower overall resource levels at which foraging is not effective. Low-nutrient adaptations often include reduced nutrient loss, resulting in more growth per unit nutrient taken up and less reduction in biomass in response to lower soil nutrients (Berendse & Elberse 1990; but see Aerts & de Caluwe 1994). In addition to assessing ability to exploit patchy resources, this experiment also compared responses of the two taxa to reduced soil nutrients.

We addressed hypotheses concerning: (1) degree of foraging response exhibited by the rhizomatous taxon; (2) ability of roots of both taxa to access patchy soil nutrients; (3) total genet aboveground biomass of the rhizomatous taxon, thickspike compared to the caespitose taxon, Snake River under patchy soil-nutrient conditions; and (4) effects of differences among genets in degree of foraging response on total genet biomass.

Methods

Plants were grown in contrasting patchy nutrient environments consisting of two levels each of two factors: (1) nutrient status (high or low) of the soil cell where the plant originates; and (2) nutrient status of the additional or "destination" cell, into which the plant can grow. The overall experimental design was a factorial analysis of variance with the factors origin and destination, each with two nutrient levels, taxon (two levels, thickspike and Snake River), and genet, in two replications. The factor genet was nested within taxon. Origin, destination and taxon were fixed variables; genet was a random variable. There were 14 levels of genet: each of 14 genets of the two taxa were divided into 8 clones of essentially equal size and morphology. This design allowed testing for genetic variation in the responses measured (as defined by Schlichting 1986 & Thompson 1991).

Plots for addressing this design consisted of two cells, the origin cell and the destination cell. Each cell was 30 cm by 30 cm by 60 cm deep. Paired cells were constructed of plywood sharing a continuous bottom. Removable walls dividing paired cells consisted of 6-mm (0.25 inch) thick plywood fit into slots on the interior of the walls.

Boxes filled with soil were located at the Utah State University Ecology Center Complex 4 km northeast of campus in Logan, Utah, U.S.A. in October 1991. Soil settled over winter, before treatments were begun. Soil was very fine sandy loam from a deposit of pluvial Lake Bonneville shoreline sediments excavated from a pit 4.5 km south of Logan, Utah. It was chosen because nitrogen and phosphorus contents were low. However, potassium, other cations, and pH were high (Table 8). Low-nutrient cells received no additional nutrients. High-nutrient cells received 3.88 g per 30 cm^2 (surface area of the cell) of K_2HPO_4 and 1.93 g per 30 cm^2 NH_4NO_3 (applied in 500 ml of aqueous solution per cell). To extend the time when nitrogen was available in the high-nutrient patch, sulfur-coated urea, a slow-release nitrogen fertilizer (consisting of 33% soluble nitrogen), was applied on the surface of high-nutrient cells at a rate of 3.27 g per 30 cm^2.

Genets were divided and clones were planted into origin cells on March 19-20, 1992. Nutrient solution was added April 27-30, and sulfur-coated urea was added May 5-6, 1992. During the establishment phase of the experiment, cell divider walls remained in place between cell pairs. Cells with plants were watered in amounts sufficient to promote rapid establishment of the plants.

Dividers were removed on May 23-25, 1992. To limit diffusion of nutrients between high- and low-nutrient cells, and thus preserve the patchy nutrient conditions, surface watering was limited, and plots were sheltered from rain by a temporary structure covered with clear polyethylene film with ventilation openings along the base and top. Water was added using a PVC pipe that was inserted into the side of each cell 5 cm from the bottom and with its opening in the center of the cell. This bottom watering provided water to the plants while causing less diffusion of soil nutrients, which were primarily in the upper portion of the soil. At about 5-week intervels starting after shelter construction, plots were watered with 2 liters per cell, except the first interval which received 1 liter. Also, plots were watered aboveground with 500 ml per cell at 2- to 3-week intervals. Effectiveness of this belowground watering was variable, therefore a shift was made to greater reliance on aboveground watering for August through November. Belowground watering of 1.5 liter per cell was applied about every 4 weeks, and 750 ml per plot was applied aboveground every 1 to 2 weeks.

After establishment in spring, the experiment continued through the remainder of the 1992 and 1993 growing seasons until summer senescence in July 1993. In February 1993, the shelter excluding precipitation was removed, resulting in greater soil moisture and greater plant growth than in 1992. This was done because the conditions of the experiment in 1992 substantially limited plant growth, although dissolution of the nutrient patches was more rapid under the conditions of 1993.

Soil samples (about 200 cm^3) were taken throughout the course of the experiment (June 2, July 17, and September 23, 1992, and January 21, and July 20, 1993) to monitor nutrient depletion in the high-nutrient cells and any diffusion of nutrients into the low-nutrient cells. These samples were taken from the top 10 cm at three locations in the low-nutrient cell 10 cm and 5 cm from the border between the two cells, and in the high-nutrient cell 5 cm from the border. In each sample period, eight plots were randomly chosen, without replacement, from among those paired cells that had one low-nutrient and one high-nutrient cell. Samples were analyzed for available nitrogen and available phosphorus by the Utah State University Soil Testing Lab.

Hypotheses and data analyses

Analysis of variance (ANOVA) is a powerful way of comparing plastic responses of a series of genotypes over a series of environments. A significant "environment" response indicates that some genotypes respond differently to different environments. A significant "genotype by environment" interaction indicates that genotypes differ in the plasticity they display. It also represents the heritable component of phenotypic plasticity (Schlichting 1986; Thompson 1991; Bell & Lechowicz 1994).

The following is a description of each of the four hypotheses that were tested, the data gathered, and the factors of interest. Hypotheses were tested using either a factorial analysis of variance, or with linear regressions

(Proc GLM or Proc REG, SAS 1988).

The first hypothesis tested for plasticity in tiller placement in response to soil nutrient patches (i.e. foraging response), and for genetic differences in foraging response in the rhizomatous thickspike wheatgrass. This hypothesis is not applicable to the caespitose grass, Snake River. More tillers in the destination cell can simply be a direct result of greater growth when more nutrients are available, but decreased rhizome lengths between parent and daughter ramets in high-nutrient patches is evidence of a mechanism promoting effective exploitation of nutrient patches (Hutchings & de Kroon 1994; Cain 1994). Therefore (adapting terms of Lovett Doust 1981), tillers in the destination cell were divided into (1) phalanx tillers--intravaginal tillers, and those arising from short rhizomes (≤ 3 cm) and thus forming bunchgrass-like clumps, and (2) guerilla tillers--those with longer rhizomes. Number of phalanx tillers and of guerilla tillers were analyzed separately. A foraging response occurs when more phalanx tillers are produced in high-nutrient patches, but numbers of guerilla tillers are unaffected. Related proportional responses, including proportion of tillers that were phalanx tillers, number of tillers per rhizome entering the destination cell, and number of tillers per rhizome length, were not amenable to statistical analysis because missing observations resulted in zeros in either the numerator or the denominator. Total length of all rhizomes in the destination cell, and number of rhizomes entering the destination cell, should depend on nutrient status of the origin cell rather than the destination cell.

Tiller and rhizome counts in the destination cells were obtained from destructive harvests of above- and belowground biomass in 1993. A significant difference between low- and high-nutrient destination cells demonstrates a clonal foraging response with respect to soil nutrient patches. The effects of nutrient status of the origin cell and the origin-by-destination cell interaction indicate how current nutrient status affects a plant's search for and exploitation of nutrient patches. A significant genet-by-destination cell interaction indicates genetic differences in the foraging response.

The second hypothesis addressed whether roots of Snake River effectively exploited nutrient-rich patches even though ramets do not invade those patches. The null hypothesis stated that root biomass in the destination cell does not differ between taxa, destination or origin cell nutrient status, or among genets nested in taxon. If roots of the two taxa are equally able to invade high-nutrient destination cells, and they respond similarly to nutrient status of those cells, taxon-by-destination interactions should not be significant.

Root biomass for each destination cell was obtained by sieving roots from soil (3 mm mesh) at the end of the experiment. Only 10 of the 14 genets were used in analysis of root biomass, because of dead plants or compromised soil conditions. In the thickspike plots, to the extent possible, roots were separated into those arising from rhizomes that entered the destination cell and those arising from roots in the origin cell that grew into the destination cell. Roots were oven dried at 70°C and weighed.

Sieving in this way is not a rigorous method of obtaining root biomass (Bohm 1979; Caldwell & Virginia 1989), but it should be acceptable for making relative comparisons of root biomass among plots. To obtain an estimate of root biomass not recovered, subsamples of sieved soil from six plots (22% of the total sample) were processed through a hydropnuematic elutriation system (Smucker et al. 1982).

The third hypothesis tested whether total aboveground biomass of the clone differed with nutrient status of the origin and destination cells, taxon, or genets nested in taxon. This tested if the rhizomatous or caespitose taxon had a growth advantage when grown where nutrients are patchy. A growth advantage should exist, if either taxon was better able to exploit patchy soil-nutrient conditions. A significant taxon-by-destination interaction indicates differences in growth between taxa due to differences in ability to exploit patchy soil nutrients. A taxon-by-origin interaction indicates differences in aboveground biomass between taxa were due to different soil nutrient levels. Aboveground biomass was clipped at 5-cm height in July 1993 (summer senescence), oven-dried at 70°C for 48 hours, and weighed.

The fourth hypothesis, applying only to the rhizomatous taxon, addressed the question, does a foraging response result in a fitness advantage in patchy environments, suggesting greater foraging response could be favored by natural selection in patchy environments? The null hypothesis stated that total aboveground biomass of the genet does not differ with degree of foraging response of the genet when high-nutrient patches are available. The hypothesis was tested with a linear regression of total aboveground biomass in the destination high-nutrient plot as a function of discrimination by that genet between high- and low-nutrient cells (foraging). The degree of foraging response (F) was calculated using:

$$F = N_H/(N_H + N_L)$$

where N is one of three measures of tiller production (number of tillers, number of phalanx tillers, or number of tillers per rhizome enterng the destination cell, in the destination cell) in high- or low-nutrient (H or L) destination cells. Missing values for F were often found in plots with low-nutrient origin cells. Thus, only plots with high-nutrient origin were used to develop these regressions. In any of these three regressions no more than two of the 14 genets were omitted as a result of missing values.

Results

SOIL NUTRIENTS

Amounts of nitrogen and phosphorus in low-nutrient cells were low enough to limit plant growth throughout the course of the experiment, although a small increase in nitrogen occurred in September and in winter (Fig. 12). Nutrient levels in high-nutrient cells were usually an order of magnitude higher than the low-nutrient cells (Fig. 12). By the end of the experiment in July 1993, phosphorous was reduced by one-half in the high-nutrient plots, and nitrogen was depleted in both high- and low-nutrient cells (Fig. 12). This nitrogen depletion occurred during spring when abundant plant growth occurred; thus, plant responses measured can be assumed to be responses to patches of low and high nitrogen and phosphorus.

In plots with one cell low-nutrient and the other high-nutrient, potential existed for nutrients to diffuse into the low-nutrient cell more than they would if the adjacent cells had the same nutrient status. Comparisons in September 1992 and again in July 1993 of eight randomly chosen low-nutrient cells attached to low-nutrient cells and eight low-nutrient cells attached to high-nutrient cells indicated no significant differences in levels of nitrogen or phosphorus between low-nutrient cells attached to low- and high-nutrient cells.

DISCRIMINATION BETWEEN LOW- AND HIGH-NUTRIENT CELLS

Nutrient status of both the origin and destination cells was highly significant in determining number of tillers in the destination cell; their interaction was not significant (Fig. 13A). Tiller numbers in the destination cell did not differ when one cell was high-nutrient whether the high-nutrient cell was the origin or the destination cell (Fig. 13A). Total tiller numbers were highest when both cells were high-nutrient and were lowest when both cells were low-nutrient. Number of tillers did not differ significantly among genets in the destination cell, regardless of the nutrient status of the cells.

Number of phalanx tillers was lower in low- as compared to high-nutrient destination cells even when origin was high-nutrient (Fig. 13B), in contrast to the response of guerilla tillers.

The number of guerilla tillers in the destination cell was more strongly influenced by nutrient status of the origin cell than of the destination cell. A significant interaction between the origin and destination nutrient status revealed that destination was an important factor for determining number of guerilla tillers in destination cells only when the origin cell was low-nutrient (Fig. 13C).

Total rhizome length was greatest whenever high amounts of nutrients were available in either the origin or the destination cell. Total length of rhizomes in the destination cell was high when origin cells had high nutrient status regardless of the status of the destination, whereas nutrient status of the destination cell significantly affected rhizome lengths when origin cells were low-nutrient (Fig. 13D). Unlike the measures described above, rhizome length did differ significantly among genets ($p < 0.05$).

The number of rhizomes entering the destination cell was primarily a function of nutrient status of the origin cell. However, a significant interaction between origin and destination indicated that number of rhizomes entering a destination cell differed with nutrient level of that cell when origin cells were low-nutrient (Fig. 13E).

ROOTS EXPLOITING HIGH-NUTRIENT CELLS

Snake River, the caespitose grass, had slightly higher root biomass in destination cells than thickspike, regardless of nutrient status of origin and destination cells (Fig. 14). Roots of both taxa invaded high-nutrient destination cells regardless of nutrient status of the origin, but few roots invaded low-nutrient destination cells if their origin cell was low-nutrient (Fig. 14). Origin-by-taxon and destination-by-taxon interactions were not significant, indicating effects of origin and destination on each taxon were similar. Root biomass of genets also did not differ significantly.

For the rhizomatous grass, an attempt was made to identify the relative contributions of roots arising from rhizomes and of roots arising from the origin cell to the root biomass in the destination cells. Only about 35% of the root biomass in destination cells was identified as being from roots or from rhizomes (Table 9A). Considering the large portion of roots that were not identified as to source, data on proportion of roots from rhizomes can be considered only crude estimates. Large portions of the roots were from rhizomes whenever the origin or the destination cell was high-nutrient (Table 9B), but since these proportions were only near 50%, roots in the destination cell that arose from roots in the origin cell were equally important.

TOTAL ABOVEGROUND BIOMASS

Thickspike consistently produced about 25% more biomass than Snake River in all nutrient status combinations. High-nutrient status in the origin cell resulted in greater biomass regradless of the nutrient status of the destination cell and of the taxon. Nutrient status of the destination cell became more important when origin cells were low-nutrient (Fig. 15). Genet-level variation in aboveground biomass was found within each taxon ($p < 0.05$).

Aboveground biomass was also clipped in 1992, the year the plots were established. Biomass was lower overall in that year, and the effect of nutrient status of the destination cell was minor, indicating the plants had largely not yet accessed the destination cells.

BIOMASS OF GENETS DIFFERING IN FORAGING ABILITY

Although genet-level variation in aboveground biomass was shown, such variation is not directly related to the foraging response. No relationship was found between degree of foraging response and total aboveground biomass when high-nutrient destination cells were available.

Discussion

FORAGING RESPONSE

Rhizomatous spread in thickspike wheatgrass follows a two-phase search-occupy strategy (*sensu* Carlsson & Callaghan 1990). A genet sends out rhizomes frequently 20 to 50 cm long that produce guerilla tillers (pers. obs.). Later, numerous tillers arising from shorter rhizomes branching from the initial rhizome and also intravaginal tillers are often produced.

A foraging response was indicated by the greater resources invested in high-nutrient than in low-nutrient destination cells. The response involved a decrease in the number of phalanx tillers in low-nutrient destination cells, even when resources for their production were available from the origin cell. Phalanx tillers proliferated in high-nutrient destination cells, whereas production of guerilla tillers was favored over production of phalanx tillers in low-nutrient destination cells. Number of guerilla (exploratory) tillers produced was essentially a function of whether sufficient resources for rhizome production were available to the plant. Nutrient status of the origin cell was more important in determining number of guerilla tillers in the destination cells than was nutrient status of destination, with number of guerilla tillers responding to nutrient status of destination only when the origin cell was low in nutrients. The responses of phalanx tillers versus guerilla tillers clearly demonstrate a foraging response, rather than merely a difference in amounts of growth, because the response of phalanx tillers represents differences in morphology in response to nutrient patches, which promote more effective exploitation of patchy soil resources (*sensu* Hutchings & de Kroon 1994; Cain 1994).

Although numbers of tillers and numbers of phalanx tillers in the destination cell responded to nutrient status of the destination cell, nutrient status of the origin cell was equally important. High growth rate in terms of biomass and ramet numbers is needed to forage effectively, because it enables plants to access and acquire resources in favorable patches before the patch quality declines (Lovell

& Lovell 1985; Hutchings 1988; de Kroon & Schieving 1990). Therefore, resource availability in favorable patches should be high enough to support high growth rates for foraging to be adaptive (de Kroon & Schieving 1990). Connection to ramets in favorable patches resulted in greater magnitude of response to unfavorable patches in Hydrocotyle (greater petiole length, Evans 1992) and Trifolium repens (greater stolon length, Turkington & Klein 1991). The large effect of nutrient status of the origin cell on investment of resources in the destination cell is consistent with this, in that it indicates expression of foraging response is to a large degree, dependent on the resources available to the plant overall.

Total length of all rhizomes in the destination cell also emphasized the importance of nutrient status of the whole clone. Although this is a measure that reflects both lengths and numbers of rhizomes collectively, it indicated that rhizome numbers and lengths largely depend on resources available to the whole plant and are high even in low-nutrient patches, if nutrients are available to the plant elsewhere.

As expected, the number of rhizomes entering the destination cell was mainly a function of nutrient status of the origin cell. Plants with more resources produced more rhizomes, and thus more entered the destination cell. However, when plants originated in low-nutrient cells, more rhizomes entered high-nutrient destination cells than low-nutrient ones, suggesting rhizomes may have detected the existence of high-nutrient destination cells before they actually encountered them. Soil analysis indicated that enrichment of low-nutrient cells by diffusion of nutrients from high-nutrient cells was minimal. One explanation for this response could be that roots accessed high-nutrient destination cells before rhizomes. Roots could then provide the plant with nutrients necessary to grow more rhizomes, some of which grew into the destination cell. It is reasonable to suspect that root invasion occurred first, because direct growth of roots into destination cells appeared to be at least as important a mechanism for accessing soil nutrients in destination cells as was invasion by rhizomes, especially when origin cells had low amounts of nutrients (Table 9).

BENEFITS OF CLONAL FORAGING VERSUS ROOT PROLIFERATION

A foraging response in tiller placement existed, and the benefits of devoting more resources to resource-rich patches and simply passing through resource-poor patches are evident, but the importance of the rhizomatous foraging response was overshadowed by root foraging. Not only was root invasion an important second mechanism of accessing patches in the rhizomatous grass, the bunchgrass also accessed patches as effectively by root invasion alone, resulting in similar aboveground biomass responses of the two taxa to high-nutrient destination cells. Exploitation of nutrient patches by root proliferation is effective in increasing whole-plant growth in other species as well (Drew & Saker 1975; Birch & Hutchings 1994).

Yet for both taxa, root biomass in the destination cell did not show the same type of discrimination between high- and low-nutrient patches as did tiller placement. Unlike number of tillers and number of phalanx tillers, root biomass was not reduced in low-nutrient destination cells, when origin cells were high-nutrient. The response of root proliferation in high-nutrient soil patches is typically described as increased root production in high-nutrient patches with no reference to root growth patterns that result in avoiding low-nutrient patches (e.g. Eissenstat & Caldwell 1988).

Although foraging with respect to tiller placement was less important to the plant in this system, it may be more important in species where the spatial/temporal scale of rhizome growth and root growth causes rhizomes to access patches that roots cannot (e.g. Evans 1991; McIntyre 1967; Lovett Doust 1987). Sutherland & Stillman (1988) concluded that patch size and rhizome length (between ramets) should be of similar magnitudes for foraging responses to result in most ramets occurring in high-quality patches. Perhaps the scales of rhizomatous growth and of alternative mechanisms of accessing patches should be considered in relation to the scale (or scales) of resource patches. It is plausible that a greater advantage of foraging in thickspike wheatgrass could be demonstrated by investigating at larger spatial or temporal scales.

GROWTH RESPONSES OF TAXA TO NUTRIENT AVAILABILITY

Since clonal growth and foraging are associated with higher growth rates (de Kroon & Scheiving 1990), the bunchgrass might be adapted to relatively lower levels of soil resources. Such adaptations often include greater nutrient retention, resulting in more growth per unit nutrient taken up (i.e. lower relative nutrient requirement; Berendse & Elberse 1990). If Snake River had lower relative nutrient requirement than thickspike, it should show less reduction in biomass under reduced levels of soil nutrients, but aboveground biomass of both taxa responded similarly to high and low levels of soil nutrients.

GENETIC DIFFERENCES IN AND ADVANTAGES OF FORAGING

Finding no significant relationship between biomass and genetic differences in clonal foraging is to be expected considering the diminished importance to biomass of clonal foraging relative to root growth. Also, no differences among genets in foraging response were revealed. The role of phenotypic variation in obscuring genetic variation from natural selection is well known (Bradshaw 1965; Schlichting 1986). Much inherent variation in plant morphology is not plastic in response to environmental conditions (de Kroon et al. 1994). This inherent variability may be much larger than the plastic response to environmenmental conditions, and may obscure the plastic response, so that differences in plastic response are not only difficult to detect statistically, but are also likely to have little effect on fitness as well. The variation in foraging response (tiller numbers, number of phalanx tillers) in this experiment was considerable.

We found no benefit of clonal foraging, largely because the benefit of root growth in exploiting the patches was predominant. Clonal foraging may be more important under other conditions, such as other spatial or temporal scales of resource patchiness, or in foraging for other resources, such as light patches. On the other hand, plastic responses such as foraging may exist, yet not be associated with a demonstrable fitness advantage in any current context. Dong (1993) found foraging response in Lamiastrum galeobdolon, but no significant differences in biomass in response to light regimes, and a study of Lemna minor (Vasseur & Aarssen 1992) suggested that existing plasticity often may not be associated with current fitness advantages. Even if benefits of a clonal foraging response cannot be demonstrated in other specific contexts, there still may be an explanation for it being maintained by natural selection. Plastic responses of roots and shoots are often more common and may be more advantageous than clonal foraging responses (de Kroon & Hutchings 1995), and plants may often possess these mechanisms along with clonal foraging. Based on simulation models of clonal growth, the benefit of any one mechanism of ramet placement alone was usually very limited (Oborny 1994). Clonal foraging may be of benefit mainly in concert with other mechanisms, such as plastic root and shoot responses. Thus, its benefit may be manifested mainly in its interaction with these other mechanisms and not strictly with patchy nutrient environments.

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Table 8 Nutrient analysis of very fine sandy loam used as growing medium in the experiment, based on two replicate samples of *en situ* material (pH 7.9).

	-----(mg /kg)------				--(mg / l H_2O solution)--			
	NO_3 - N	P	K	Percent Organic C	Ca	Mg	Na	K
Sample								
No.1	2.0	3.3	170	0.20	21.10	11.28	51.68	14
No.2	5.8	2.6	132	0.22	52.48	35.39	110.90	18

Table 9 For the rhizomatous taxon, thickspike, relative contribution of root biomass from roots and rhizomes in destination cells. (A) Proportion of all roots that could be identified as to their source (from rhizomes or from roots outside the destination cell), using corrected total root biomass based on estimates of portion of root biomass not recovered by sieving. (B) Of those identified roots, the proportion that arose from rhizomes within the destination cell. For both A and B, means and standard errors (across genets and replicates) for each combination of origin and destination are presented.

(A) PROPORTION OF ROOTS IDENTIFIED		
	MEAN	STANDARD ERROR
Origin Low - Destination Low	0.26	0.05
Origin Low - Destination High	0.35	0.03
Origin High - Destination Low	0.40	0.02
Origin High - Destination High	0.40	0.02
ALL PLOTS	0.35	0.02

(B) PROPORTION OF ROOTS THAT AROSE FROM RHIZOMES

	MEAN	STANDARD ERROR
Origin Low - Destination Low	0.14	0.11
Origin Low - Destination High	0.40	0.11
Origin High - Destination Low	0.46	0.11
Origin High - Destination High	0.66	0.10

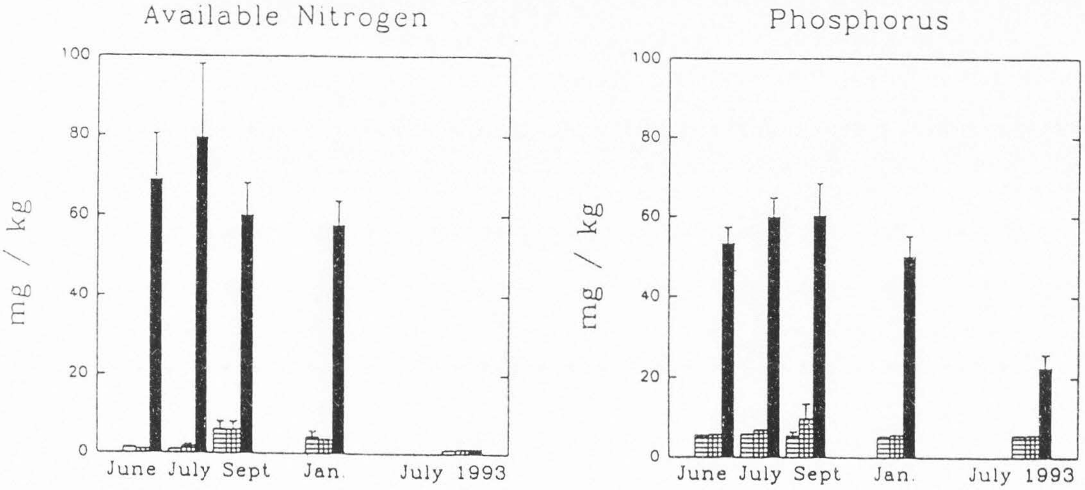
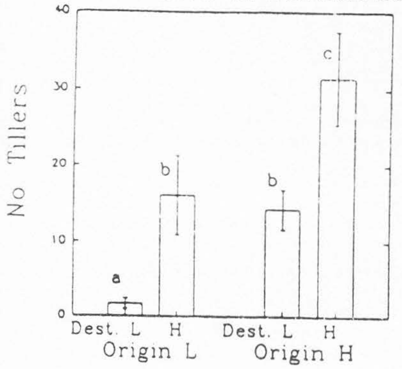


Fig. 12 **Means and standard errors** (n = 8) **of soil nutrients** in samples taken over the course of the experiment. Samples were taken 2 June 1992, 17 July 1992, 23 September 1992, 21 January 1993, and 20 July 1993. Hatched bars are 10 cm into low-nutrient cells from the border between cells, cross-hatched bars are 5 cm into low-nutrient cells from the border, and solid bars represent 5 cm into high-nutrient cells from the border.

Fig. 13 Means and standard errors for tiller counts and rhizome lengths in the destination cell. Values for low- (L) and high-nutrient (H) origin crossed with low- and high-nutrient destination are presented. Origin and destination were the only significant factors for Number of Tillers (A; $p < 0.0001$, $p < 0.001$ respectively) and for Number of Phalanx Tillers (B; $p < 0.001$ for both factors). For Number of Guerilla Tillers (C), Total Length of Rhizomes (D) and number of rhizomes entering the destination cell (E), A significant origin by destination interaction occurred ($p < 0.04$, $p < 0.005$, $p < 0.003$, respectively). Means with the same letter above them are not significantly different.

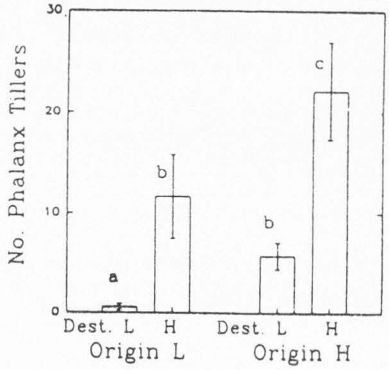
A

Number of Tillers in Destination Cell



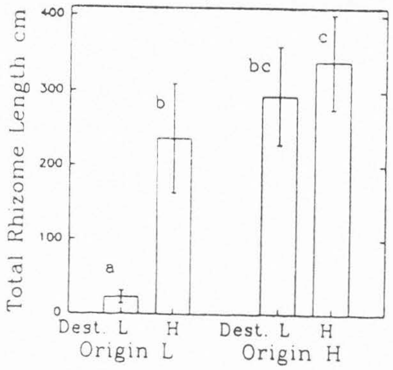
B

Phalanx Tillers in Destination Cell



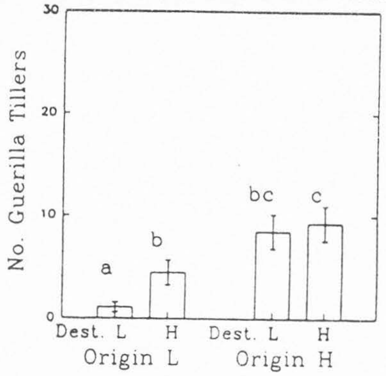
D

Total Rhizome Length in Destination Cell



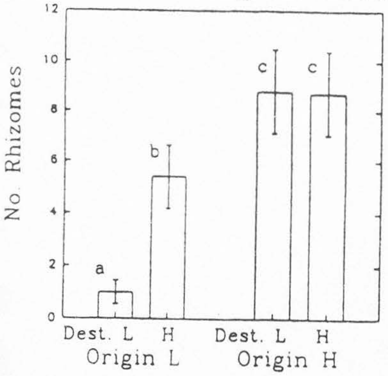
C

Guerilla Tillers in Destination Cell



E

Rhizomes Entering Destination Cell



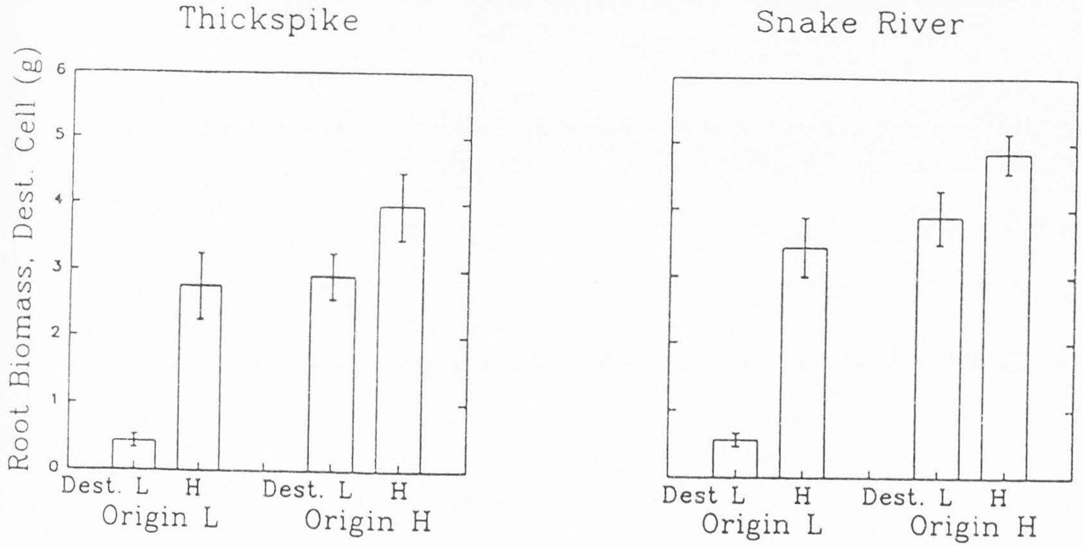


Fig. 14 Root biomass (means and standard errors) in the destination cell for each taxon for low- and high-nutrient origin cells crossed with low- and high-nutrient destination cells. Origin, destination and their interaction were highly significant ($p < 0.0001$), and taxa also differed ($p < 0.05$).

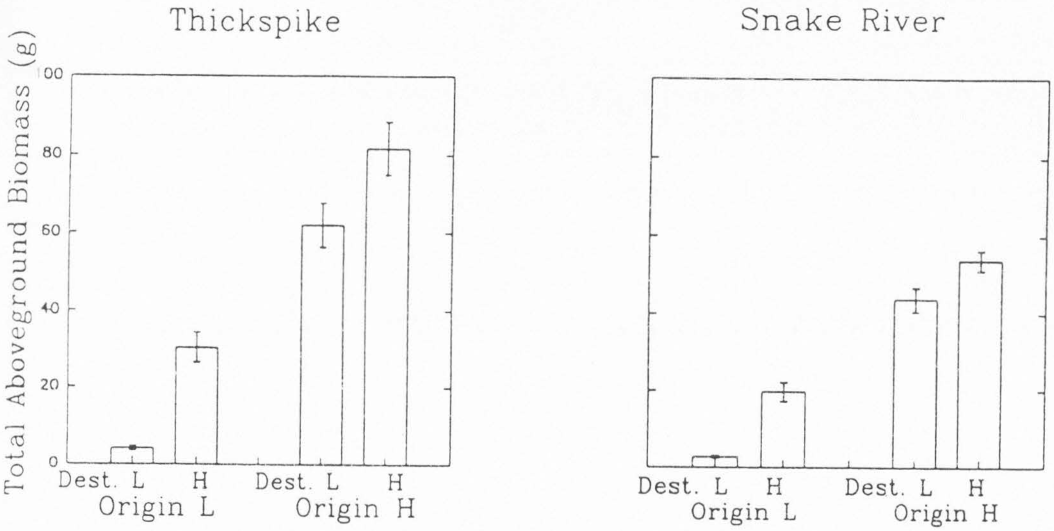


Fig. 15 Aboveground biomass (means and standard errors) for the entire plot in 1993. For each taxon, values for low- (L) and high-nutrient (H) destination crossed with low- and high-nutrient origin are presented. The origin by destination interaction was highly significant ($p < 0.0001$). Taxon and genet were also significant ($p < 0.04$, $p < 0.05$).

CHAPTER 5

RAMET SPACING AND FORAGING OF THICKSPIKE WHEATGRASS IN RESPONSE TO NEIGHBOR DENSITY

Summary

1 Plots of a grass competition experiment with varying total densities and relative frequencies of the rhizomatous Elymus lanceolatus ssp. lanceolatus and the caespitose Elymus lanceolatus ssp. wawawaiensis were used to identify a foraging response in E. l. lanceolatus to neighbor densities.

2 Rather than an increase in spacing of guerilla tillers at high densities, as expected with a foraging response, there was a slight decrease in spacing and in the number of target plants producing guerilla tillers in response to increased densities of ssp. lanceolatus, but no relationship to ssp. wawawaiensis densities.

3 Less rhizome spread was seen also in the second season of growth when soil resources were more depleted overall.

4 Elymus lanceolatus ssp. lanceolatus is known to show a foraging response to patchy soil nutrients. Long, costly rhizomes were not produced at higher densities and in the second year perhaps because sufficient resources to do so were not available from other parts of the genet.

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[4] Coauthored by L. David Humphrey and David A. Pyke.

Introduction

Patches of contrasting resource availability over short distances are common: e.g. "islands of fertility" created by shrubs in desert ecosystems (Garcia-Moya & McKell 1970); patches of light and other resources created by tree-fall gaps (Canham & Marks 1985); localized soil disturbances created by animals in grasslands (Platt 1975; Loucks et al. 1985; Inouye et al. 1987); and complex patterns of soil nutrient and moisture availability due to microtopography, presence of individual plants, and to other factors (Pigott & Taylor 1964; Robertson et al. 1988; Reader & Best 1989). Many clonal plants have foraging responses that allow them to effectively exploit resource-rich patches. Ramets are produced densely in resource-rich patches and sparsely with long rhizomes in resource-poor patches, so that ramets pass through these areas, affording greater opportunity to encounter favorable sites (Salzman 1985; Hartnett & Bazzaz 1983; Slade & Hutchings 1987). This response is usually achieved by decreased spacing between parent and daughter ramets and/or increased rhizome branching in resource-rich patches (Sutherland & Stillman 1988).

Conditions of intense competition or high densities of neighbor plants are usually characterized by low availability of resources, because neighboring plants preempt soil nutrients and/or light. Although most studies of foraging response to patchy resources have been concerned with resource patchiness in contexts not involving competition or neighbor densities, some studies have investigated whether clonal plants display a foraging response to variations in neighbor densities. Hieracium pilosella produced more ramets in lower neighbor densities (Bishop & Davy 1985), thereby devoting more resources to low-density sites. Trifolium repens (Harper 1983) and Prunella vulgaris (Schmid 1986) increased branching and decreased stolon length in the absence of competing grasses. Stolons and petioles of Glechoma hederacea were longer when grown with competitors (Birch & Hutchings 1994). Solidago canadensis produced fewer and longer rhizomes under higher densities (Hartnett & Bazzaz 1985). In contrast, Aster lanceolatus and three Solidago species produced more, but shorter rhizomes in the presence of competitors with high rooting densities (Schmid & Bazzaz 1992).

The rhizomatous perennial wheatgrass Elymus lanceolatus ssp. lanceolatus thickspike wheatgrass showed a foraging response to patchy soil nutrients, producing ramets sparsely in low-nutrient patches and densely in high-nutrient patches (Chapter 4). The present experiment investigated whether thickspike wheatgrass showed a similar foraging response to a gradient of neighbor densities. The approach taken was to examine the spacing from parent to daughter tillers for those tillers located around the periphery of the genet. These outermost tillers were assumed to be the exploratory (or guerilla) tillers of the genet. A foraging response to density should result in greater spacing of these tillers (greater rhizome lengths) under higher densities.

Methods

This experiment was conducted using a portion of the plots established for a related experiment investigating competition between thickspike wheatgrass and a bunchgrass Elymus lanceolatus ssp. wawawaiensis (Snake River wheatgrass; Chapter 2). Seedlings of thickspike wheatgrass (accession T21076) and Snake River wheatgrass (cultivar 'Secar') were grown outdoors in partitioned styrofoam seedling flats and transplanted to the plots at the Utah State University, Ecology Center's Green Canyon Complex 4 km northwest of the campus in Logan, Utah, U.S.A., in May and June 1989.

Each observational unit consisted of 18 equidistant neighbor plants arranged in two concentric hexagons with a target plant (the plant on which data were obtained) in the center of the hexagons (Chapter 2). In the portion of the experimental design relavent to the present experiment, four levels of relative frequency of the two taxa (1:5 2:4 4:2 5:1) were crossed with four levels of total density (12, 36, 58, 84 plants per m^2) with thickspike as the target plant. Different levels of total density were achieved by using different-sized hexagons that adjusted the spacings between neighbors. In each of six replicates, seven subsamples of each treatment-level combination (seven concentric hexagon-target observational units) were planted. As a result of early mortality of seedlings after planting, densities and relative frequencies were altered to the extent that it was necessary to quantify densities of thickspike and Snake River neighbors in each observational unit and use these densities in place of the relative frequency and total density levels of the original design (see Chapter 2).

In investigating spacing of exploratory tillers, we only used plots of the two intended relative frequencies with lower proportions of thickspike neighbors (1:5 and 2:4, thickspike:Snake River) to avoid uncertainty as to whether tillers were from the target plant or from thickspike neighbors. Some observational units were omitted because of early mortality of seedlings. Observational units were also omitted if it was impossible to reliably distinguish guerilla tillers of the target plant from tillers of neighbors. Thus, 250 observational units were used.

Plants produce seeds and senese in July. Growth and tiller production resume in late summer or autumn. Autumn tillers overwinter and resume growth in spring. Data were collected for two summer-to-summer growth cycles. In June 1990, any tillers that had emerged beyond the main clump were marked with colored wires. Distance from these tillers to the nearest tiller of the main clump represented spacing of guerilla tillers (*sensu* Lovett Doust 1981) produced from establishment of plots in May and June 1989 until June 1990. In July 1991, spacing from parent to daughter tillers was measured for tillers arising from tillers marked in June 1989 and for any tillers arising from the main clump after tillers were marked in 1989. Of those target plants that produced guerilla tillers, most (83%) produced only one guerilla tiller over either sample period. When more than one guerilla tiller per target plant existed, the mean spacing of the tillers was used.

Spacing of guerilla tillers was analyzed as a response to densities of neighbors and to year (the 1989-1990 and 1990-1991 growth cycles). Density of thickspike and density of Snake River were treated as separate variables, because the two taxa were found to differ in their competitive effects (Chapter 3). Because total densities varied considerably (from 12 to 84 plants per m^2), and relative frequency varied little (usually near the 1:5 and 2:4), density of one taxon was positively correlated with density of the other taxon. Therefore, the two density variables were orthogonalized before proceeding with analyses, using an approach based on regression of one independent variable as a function of the other (Box & Draper 1986).

Orthogonalization of the two density variables was based on a linear regression of density of Snake River (D_S) as a function of density of thickspike (D_T). Density variables were orthogonalized separately for (1) the larger data set which included target plants without guerilla tillers and (2) the data set with only target plants for which guerilla tillers were measured, but results for the smaller and larger data sets were similar. For the larger data set,

$$D_S = 12.298 + 1.508\ D_T\ , \quad R^2 = 0.43$$

for the smaller data set,

$$D_S = 10.925 + 1.570\ D_T\ , \quad R^2 = 0.48$$

To orthogonalize the two density variables, in the analyses, the explanatory variable, density-Snake River, was replaced with orthogonalized density-Snake River ($D_{S,O}$), where (for the larger data set, for example)

$$D_{S,O} = D_S - (12.298 + 1.508\ D_T)$$

leaving only the orthogonal component of D_S as the variable.

Most target plants did not produce guerilla tillers during each year (63% in 1989-1990, 82% in 1990-1991). A two-step approach was used in analyzing these data. In the first step, the effect of densities on the binary response, producing guerilla tillers or not, was analyzed by logistic regression using the model:

$$LN(P/1 - P) = a + b_T D_T + b_S D_S + b_Y Y$$

where LN is natural log, P is probability of a target plant producing guerilla tillers, D_T and D_S are the densities of thickspike and Snake River, Y is the year, a is intercept, and b's are coefficients for each variable. In the second step, using only those target plants for which guerilla tillers were recorded, analysis of covariance was used to analyze spacing of guerilla tillers as affected by densities in the two years.

Results

Logistic regression indicated that probability of producing guerilla tillers (P) was significantly less with greater densities of thickspike and was less in the second year (D_T: chi-square > 4.79, $p < 0.03$; Y: chi-square > 11.14, $p < 0.001$). Density of Snake River was not significant. In individual logistic regression equations for each year, density of neither taxon was significant in the first year, with density of thickspike affecting probability of producing guerilla tillers only in the second year. The regression equation for the second year was

$$LN(P/1-P) = -0.49 - 0.12 D_T$$

In the analysis of covariance of tiller spacing, natural log-transformed spacing was the best transformation, based on R^2 and distributions of residuals. Density of thickspike was significant, but not density of Snake River (Table 10). Tiller spacing was less at higher densities of thickspike and less in 1991 than in 1990. Although the model was significant, R^2 was low (Table 10), indicating that factors tested explained a small portion of the variation in spacing of guerilla tillers. Since the two years differed in the analysis of covariance, individual regressions of spacing as a function of neighbor densities for each year were calculated. As in the analysis of covariance, Snake River density was not significant in individual regressions for each year, and thus the regressions for each year described responses to the density of thickspike neighbors (Fig. 16).

Discussion

In thickspike wheatgrass, like several other clonal plants, a foraging response to patchy soil resources has been seen (Chapter 4), but that response was not related to density. Although stoloniferous (Bishop & Davy 1985; Harper 1983; Schmid 1986; Birch & Hutchings 1994) and rhizomatous (Hartnett & Bazzaz 1985) plants have shown a foraging response to neighbor densities similar to that shown to patchy resources, the response of spacing of guerilla tillers in thickspike wheatgrass to density of thickspike neighbors was opposite to that expected as part of a foraging response. The greater effect of neighbors of thickspike than of Snake River is consistent with results of a related experiment, which indicated greater competitive effect of thickspike neighbors than of Snake River neighbors on thickspike (Chapter 3). There was only a weak response of reduced spacing of guerilla tillers at higher densities, in those target plants that produced guerilla tillers, but consistent with this reduced spacing, fewer target plants produced guerilla tillers at higher densities, although again, the effect of density was significant but not large.

In 1991, space in the plots was more fully occupied by plants, but overall biomass declined relative to 1990, indicating that soil resources were depleted. Thus, the reduced spacing of guerilla tillers and reduced numbers of target plants producing guerilla tillers in 1990-1991 relative to 1989-1990 can be considered a response to reduced levels of soil resources overall. As with higher neighbor densities, greater rhizomal "searching" was expected under these conditions rather than reduced tiller spacing.

Some clonal plants have shown reduced rhizome or stolon growth at higher neighbor densities. Schmid & Bazzaz (1992) proposed that some forbs that showed reduced rhizome lengths with higher neighbor densities of grasses did so because of mechanical resistance to rhizome growth from the dense mat of grass roots. <u>Trifolium</u> <u>repens</u> reduced stolon growth rate in response to proximity of neighbor ramets (Bülow-Olsen et al. 1984). The apparent strategy is to grow into open space when it is available, but reduce growth when neighbors are encountered. de Kroon & Schieving (1990) have described a similar response. The strategy of reducing stolon growth in response to crowding would be more beneficial in plants with a high degree of physiological integration, because resources used for growth in one patch could be efficiently transferred and used for growth in a favorable patch elsewhere. Results indicating physiological integration in thickspike were seen (Chapter 4). However, the existence of mechanical resistance to rhizome growth from roots, or of responses that reduce rhizome growth from ramets that are in crowded conditions, appears unlikely in thickspike, because guerilla tillers were sometimes observed that had grown into clumps of tillers of neighbor plants.

The response of growing longer rhizomes in low-resource plots may have been inhibited, because sufficient resources to do so were not available. High growth rates are needed for plants to forage effectively. Thus, resource availability in favorable patches must be high enough to support high growth rates for foraging to be effective (de Kroon & Schieving 1990). Greater provision of resources from other parts of the genet can increase the magnitude of the response of increased stolon lengths in unfavorable patches (Turkington & Klein 1991; Evans 1992). The production of guerilla rhizomes in thickspike was limited by nutrient availability to the genet as a whole (Chapter 4).

Rhizomes are structurally expensive, do not photosynthesize, and in thickspike, do not produce roots except where tillers are produced. Less spread by guerilla rhizomes at high neighbor densities and in the second year may have been the result of decreased allocation of resources to this costly activity when few resources were available. Thompson (1993) found differing morphological responses of Trifolium repens to different levels of shading. The greatest increase in stolon internode lengths was seen with mild shading; with deep shade, there was little growth and short internodes. Thickspike's longer rhizomes in low-nutrient patches, when high- and low-nutrient patches were available (Chapter 4), and the mild reduction in rhizome spacing in response to increased densities and in the second year may constitute a similar nonlinear response of thickspike's rhizome lengths over a range of nutrient availability.

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Table 10 Analysis of covariance of LN (spacing) of guerilla tillers as a function of densities of thickspike and Snake River neighbors and year (the 1989-1990 and 1990-1991 growth cycles). D_T = density of thickspike neighbors, $D_{S,O}$ = orthogonalized density of Snake River. Nonsignificant interactions were omitted. (LSmeans for years: 1990 = 1.81, 1991 = 1.61).

Overall ANOVA: $F_{3,134} = 9.89$ $p < 0.0001$ $R^2 = 0.181$

Factor	Parameter Estimate	P <
Intercept	1.844	0.0001
D_T	-0.024	0.0001
$D_{S,O}$	-0.004	0.1192
Year	+0.199*	0.0132

*when year 1989-1990 = 1, and year 1990-1991 = 0

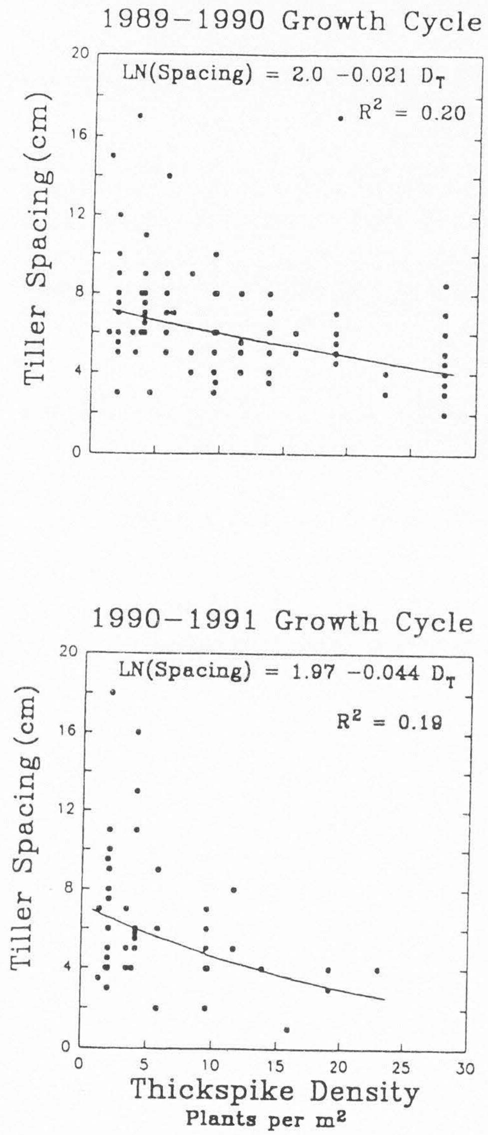

Fig. 16 Spacing of guerilla tillers as a function of density of thickspike neighbors in each of the two growth periods (1989-1990 and 1990-1991). Both regressions were significant: $p < 0.0001$ and $p < 0.011$ respectively. Significance levels of densities were: in 1989-1990, density thickspike (D_T) $p < 0.0001$ and orthogonalized density Snake River $p < 0.098$; in 1990-1991, $p < 0.003$, and $p < 0.710$ respectively.

CHAPTER 6

SYNTHESIS

The performance of the rhizomatous thickspike wheatgrass and the bunchgrass, Snake River wheatgrass, growing in mixtures over two years was examined in the first experiment. Biomass, tiller production, flowering, and genet survival for the two taxa were compared (Chapter 2), and competition indices based on biomass described competitive interactions (Chapter 3). In the second experiment (Chapter 4), an attempt was made to identify the importance of rhizomatous growth and clonal foraging in thickspike wheatgrass. These traits potentially provided an advantage for the rhizomatous taxon when spatial patches of unoccupied soil resources were available. Data from this experiment were also used to determine if the bunchgrass, Snake River, is less affected by low levels of soil nutrients, as might be expected of a plant adapted to low resource levels. Plots from the first experiment were used to determine if thickspike exhibited a foraging response to higher neighbor densities as it did to patchy soil nutreints (Chapter 5).

In the first year, the rhizomatous thickspike was characterized by large biomass, rapid growth, large numbers of tillers, and high competitive ability. It appeared aggressive and efficient at quickly occupying sites when resources were available. Its greater flowering in the first year is a beneficial trait for a disturbance-adapted species, affording ability to quickly produce seeds to further exploit the site, or to produce and disperse seeds before being displaced. The caespitose Snake River wheatgrass had slower growth, fewer tillers in the first year, and poorer competitive ability than thickspike. Tiller numbers indicated that it typically increases in size with age, and its flowering was delayed until later years. Thickspike declined in biomass, tiller numbers, and competitive ability in the second year, when resources were apparently depleted overall. Traits that allowed it to effectively exploit resources and successfully compete in the first year were apparently less useful in the second year, when sites were occupied and resource levels were low.

Thickspike exhibited a clonal foraging response to patchy soil nutrients, proliferating closely spaced tillers in high-nutrient patches, while producing fewer tillers with longer rhizomes in low-nutrient patches. However, in the competition plots, it did not exhibit such a response to higher neighbor densities (which reduced resource availability) or to the generally reduced resource levels of the second year. Instead of increased rhizome lengths under these low-resource conditions, which would afford greater searching of the habitat, shorter rhizome lengths occurred. Apparently, when resources were low overall, they were not allocated to the construction of long rhizomes.

Thickspike's high growth rate and foraging response are likely associated with higher levels of soil resources (de Kroon & Schieving 1990). Snake River, the slower growing bunchgrass, might be expected to be adapted to lower levels of soil resources. One such adaptation is greater growth per unit of acquired nutrient (i.e. lower relative nutrient requirement; Berendse & Elberse 1990). However, in the second experiment, aboveground biomass of the two taxa declined similarly in response to low soil nutrients, suggesting no advantage of Snake River over thickspike in relative nutrient requirement.

The seasonal tiller phenology of Snake River may be an advantage in low-resource environments with temporally patchy resource availability, such as semiarid habitats. Because rapid production of a photosynthetic surface when conditions are favorable is important in such habitats (Comstock & Ehleringer 1986), early production of large numbers of tillers may allow Snake River to effectively exploit pulses of resources in time, whereas thickspike is more effective at exploiting patchy resources in space.

Although the pattern of Snake River tiller production on the scale of years, its slower growth, and later flowering suggest a stress-tolerant (*sensu* Grime 1977) life history strategy, the seasonal pattern of tiller production may confer ability to quickly exploit high-resource conditions that occur episodically in time. The yearly and seasonal tiller dynamics of Snake River can be described as comprising two temporal hierarchical levels (*sensu* O'Neill et al. 1986). There may be selection for stress-tolerant traits on a yearly scale. Plants with slow growth rates and other traits beneficial under conditions of resource stress or low productivity (*sensu* Chapin 1980) may survive low-resource years better in a temporally variable semiarid environment. At a seasonal scale, selection may favor quickly exploiting episodically occurring periods of high resource availability.

Although thickspike wheatgrass showed a foraging response to high- and low-nutrient soil patches, preferentially placing tillers in high-nutrient patches, this foraging response was relatively unimportant to the plant, because root growth was an effective means of accessing patches for both the bunchgrass and the rhizomatous grass. Clonal foraging may be more advantageous to thickspike in contexts other than those tested in our patchy nutrient experiment. Perhaps the foraging response is more important when competition is primarily for light, such as when gaps are created through soil disturbance by rodents or through death of neighbor plants. The foraging response may also be more important when patches exist at larger spatial scales than those we tested.

If both the clonal forager, thickspike, and the bunchgrass were able to access patchy resources, other traits of thickspike, its higher growth rate and faster life history, may have been the main factors responsible for its success over Snake River, rather than clonal foraging. Much of the competitive advantage of thickspike seen in 1990 and 1991 may have been the result of preempting a greater share of resources from Snake River in 1989 and 1990, when the plots were planted. Clonal foraging was not shown to be uneffective at exploiting patchy resources in Chapter 2, only no more effective than root proliferation. Both taxa exploited patchy resources, but by different mechanisms. Plants typically possess a suite of traits that are adapted to their particular environments. Co-occurrence of clonal foraging and high growth rates have already been pointed out. Plastic responses of shoots as well as roots and ramets are often important mechanisms of exploiting patchy resources (de Kroon & Hutchings 1995). The benefit of any one mechanism alone may be limited (Oborny 1994). The benefit of clonal foraging may be expressed mainly in its functioning as a member of a suite of traits.

The contrast between thickspike and Snake River in yearly patterns of tiller production, biomass, and flowering might have management implications. In revegetation projects intended to establish perennial grasses, early competition from aggressive annuals, such as Bromus tectorum, is a factor limiting establishment. On some semiarid sites, thickspike, with its ability to produce more biomass in early years and quickly exploit resources, might be a perennial grass that is effective at establishing in the presence of an aggessive annual competitor. But it may be less effective at maintaining dominance later, as indicated by its decline in the second year in our competition study. If only a small portion of Snake River plants established on the site at or after the time of thickspike establishment, it might be possible for Snake River to increase in prominence on the site as thickspike declines, thereby maintaining stands of perennial grasses on the site.

The problems with Relative Resource Total, that equivalent monoculture densities fell well beyond the range of densities used in the experimental design, will occur any time one species is a substantially better competitor than the other. To solve this problem, higher densities of the less competitive species must be planted to provide predicted monoculture biomass values for obtaining equivalent monoculture densities. RRT values would be calculated only for a subset of the total range of densities in the experimental design, excluding the added higher density plots. Thus, this solution would use a substantially larger number of plots, and would require some prior knowledge of competitive relationship between the species. The number of plots could be minimized by including only higher-density monoculture plots, and by calculating separate monoculture-density regressions to provide predicted monoculture biomass values for obtaining equivalent monoculture densities. This, however, departs from the fundamental approach used to calculate RRT values for additive series designs (e.g. Connolly 1987). Also, predicting values at monoculture densities may be problematic with at least some mixed-density models (alluded to by Law & Watkinson 1987). RRT is pertinent when the primary interest is on yield, and it is easily interpretable. For example, RRT would be useful in evaluating mixtures of forage grasses for livestock or for evaluating interseeding of crops. But substitution rates, along with products of substitution rates, convey much of the ecologically important information RRT is intended to represent, and are free of the problem involving monoculture densities. One major disadvantage of substitution rate is the difficulty associated with its calculation or interpretion when it is calculated from some complex models (e.g. Connolly et al. 1990), but generaly, it may be preferable to use substitution rates and products of substitution rates in place of RRT.

We pointed out that traits such as clonal foraging typically exist as components of a suite of traits adapted to some environment. We proposed that thickspike's quicker life history, higher growth rate, guerilla growth form, and foraging ability were traits adapted to exploiting spatially patchy resources or disturbed areas, while Snake River's slower growth and seasonal pattern of tiller production were adaptations to low resource levels and temporally patchy resources. It might be important to attempt to determine if these two species possess other traits adapted to these two respective environments. Our second experiment compared the abilities of the two taxa to exploit spatially patchy resources. It might also be important to compare their abilities to exploit temporally patchy resources. Because the role of roots appeared important relative to that of rhizomes (Chapter 4), attention might best be focused on roots.

A species adapted to high nutrients, _Agrostis stolonifera_, showed a pronounced root proliferation in high-nutrient patches, and great plasticity in amount of root biomass, while the low-nutrient-adapted _Scirpus sylvaticus_ did not show root proliferation in high-nutrient patches, and maintained a large, but constant root biomass (though shoot biomass was plastic; Crick & Grime 1987). They proposed that this large, unvarying root mass was more effective in low-nutrient environments where temporal pulses of nutrient availability were important. Plants can also effectively exploit nutrient patches by increasing the physiological nutrient uptake capacity of roots in the patch (Robinson & Rorison 1983; Jackson et al. 1990). The experiments just cited focused on spatial patches, but there was a temporal component to the nutrient patches as well, and the physiological response was rapid (a few days or less). Pseudoroegneria spicata (which is similar to Snake River wheatgrass) did not proliferate roots in high-nutrient patches, like Scirpus, while another wheatgrass, Agropyron desertorum, did (Jackson & Caldwell 1989). But both of these wheatgrasses showed increased physiological uptake rates in high-nutrient patches (Jackson et al. 1990). Increased physiolocical uptake rates, but not the plastic morphological response of root proliferation, may be important in effectively exploiting resources that episodically occur in time. It might seem reasonable to list a large root system, low morphological plasticity of the root system, high plasticity of physiological nutrient uptake capacity, early production of large numbers of tillers, and high plasticity of shoot biomass as adaptations to low-resource, temporally variable environments, and to list plastic allocation of root biomass, root proliferation in high-nutrient patches, high growth rates, and (often) rhizomatous growth with clonal foraging as adaptations for acquiring resources that are patchy in space. Plasticity in physiological uptake capacity may be important in exploiting both spatial and temporal patchiness; further, a resource pulse may often have important spatial and temporal components. The effective uptake of temporal nutrient pulses, coupled with tiller production patterns that are effective at quickly producing photohsynthetic surface when these nutrients are available (Comstock & Ehleringer 1986), should be advantageous in low-resource, temporally variable environments. It would be interesting to know if this proposed suite of traits in fact occurs in Snake River.

We emphasized the importance of considering a trait as part of a suite of traits, and proposed suites of traits related to spatial and temporal patchiness of resource availibility for thickspike and Snake River wheatgrasses. Patterns of resource availibility appear to shape traits of a wide range of clonal plant species. There are many potential patterns of resource availability, and the suites proposed for thickspike and Snake River are only two possible suites of adaptations. Many clonal plants do not possess a ramet-foraging response, but exhibit other clonal growth strategies. For example, Carex flacca, which grows in nutrient-poor grasslands, produces an extensive rhizome system with widely spaced ramets, but shows no foraging response with respect to rhizome length or branching (de Kroon & Knops 1990).

de Kroon and Schieving (1990) described three strategies of plant clonal growth, foraging strategy, conservative strategy, and consolidation strategy, each beneficial in different types of environments. The following expansion of their three strategies, drawing on our research on thickspike and Snake River wheatgrasses and on other research discussed above, describes four suites of traits and their proposed benefit under certain habitat conditions.

The foraging strategy is beneficial in habitats with resource levels that are at least moderately high overall and spatially patchy. These plants have high growth rates, and exhibit shorter rhizomes and greater rhizome branching in high-resource patches. Root proliferation in high-nutrient patches, with plastic allocation of root biomass, and perhaps also plastic shoot growth responses (Thompson 1993; de Kroon & Hutchings 1995) can be added as subsets of this strategy.

de Kroon & Schieving (1990) described one conservative strategy, but I describe two. The conservative-integrated strategy is beneficial in habitats with resource levels low overall, with temporal patchiness of great importance but spatial patchiness also important. Traits include slow growth rate, slow turnover of plant parts, efficient nutrient resorption from senescensing parts, and extensive clonal systems with a high degree of physiological integration. de Kroon & Schieving (1990) concluded that rhizomatous growth with effective translocation of resources among parts of the clone, but without a foraging response, could be beneficial in resource-poor environments with few rich patches. Instead of foraging for patches, the rhizome system serves to relatively uniformly occupy a large area. When temporal pulses of resource availability occur, the clone can acquire these resources from a larger area, transporting them to localized areas where they are needed. In the understory herb Lamiastrum vulgaris, a high level of between-ramet resource sharing, and little morphological difference between ramets in different light conditions, appeared to best exploit temporally brief and spatially patchy sun flecks for the benefit of the whole clone (Dong 1995), consistent with the conservative-integrated strategy. Carex flacca (de Kroon & Knops 1990) is also consistent with this strategy.

The conservative-temporal strategy is also beneficial when resources are low overall and importance of temporal patchiness is great, but here spatial variability is of little or no importance. Traits include a large root system with low morphological plasticity of the root system, and little rhizomal spread. Like the rhizome system of the conservative-integrated strategy, this root system continuously occupies a large soil space, allowing it to effectively exploit temporal resource patches when they occur. Traits also include high plasticity of physiological nutrient uptake rates, early (or eposodically rapid) production of large numbers of ramets, and high plasticity of shoot biomass, though slow long-term growth rates. Since ramets are less dispersed and spatial patchiness is unimportant, physiological integration among ramets is less important. This is the strategy proposed for Snake River.

The consolidation strategy is beneficial for occupying sites and maintaining dominance under high and relatively uniform resource levels. Most rhizomes are short. There is considerable variation in rhizome lengths, but it is unrelated to resource variability. Shorter rhizomes serve to fully occupy space, while longer rhizomes extend the clone beyond its perimeter. Typha latifolia is an example of the consolidation strategy.

These four strategies can be mapped onto a three-dimensional space with the axes: overall resource level, degree of temporal patchiness, and degree of spatial patchiness of the resources. This illustrates differences in expression or in function of traits in combination with other traits or in different environments, as well as illustrating the importance of these three habitat axes.

The consolidation strategy, with highest growth rates, occupies high overall resource levels, when spatial and temporal variability are low. With increasing importance of spatial variability, which would tend to involve at least somewhat lower overall resource levels, the foraging strategy would become more beneficial, with the epicenter of the foraging strategy being intermediate overall resource levels with high spatial variability. At these intermediate overall resource levels, as temporal variability increased, plasticity of physiological uptake rates and plasticity in aboveground biomass production (conservative-temporal traits) would increase in importance, but these plants would probably also need rather high growth rates to be competitive. The conservative-temporal strategy would be more important as overall resource levels became lower and temporal variability remained high. Species with the foraging strategy would decline in abundance, or cease to display foraging, as these lower resource levels were approached, even if there is substantial spatial variability. As lower overall resource levels are approached, conservative-integrated strategists could have an advantage over conservative-temporal species, when spatial patchiness is also important.

A fourth habitat attribute, scale of patchiness, might also come into play here, in that the conservative-integrated strategy, with the integrated clone encompassing a large area, might have a greater advantage over conservative-temporal strategists, when the habitat consists of a low-resource matrix containing widely spaced high-resource patches. This describes the habitat of Hydrocotyle bonariensis (Evans 1991). Rhizomatous growth may also be suited to a specific attribute of this species' habitat, i.e. shifting sand. Scale of patchiness could also be the axis on which the ramet-foraging "substrategy" is separated from root-proliferation foragers. Similarly, scale of light patches might separate species with ramet placement foraging response from those with plastic petiole or leaf response.

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Dissertation, Utah State University: Competitive interactions between two closely related rhizomatous and caespitose semiarid perennial grasses under varying conditions.
Thesis, Idaho State University: Patterns and mechanisms of plant succession after fire on sagebrush-grass sites in southeastern Idaho.
Undergraduate Independent Study, University of Georgia: Effects of *Nitella* on structure and production of the epiphytic algae community.

MEMBERSHIPS:

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Research Assistant:

Department of Rangeland Resources and the Ecology Center, Utah State University, Logan, UT 84322-5230. (Phone 801 797-2475). July 1994 - present part time.

Duties and Responsibilities: Developed a planting design for a rangeland seeding experiment. Established plots and collected population monitoring data on seedlings, and supervised assistants in this work. Analyzed data and prepared an annual report.

Contract Biologist:

The Nature Conservancy, Great Basin Field Office, P.O. Box 11486, Salt Lake City, UT 84147-0486. (Phone 801 531-0999). July 1 1993 - Aug. 31 1993 part time.

Duties and Responsibilities: Established population monitoring plots for the endangered plant species, *Astragalus desereticus*, and prepared instructions for conducting continued monitoring. Defined life stage classes, described population structure and compared populations on different sites. Described spatial characteristics of populations.

Graduate Research Assistant:
Department of Range Science and the Ecology Center, Utah State University, Logan, UT 84322-5230. (Dr. D. A. Pyke's current phone: 503 750-7334). Jan. 1988 - Aug. 1993 part time.

Duties and Responsibilities: Developed a planting design for studying plant competition in two-species mixtures, and developed plot design for a second project asessing the resopnse of plants to patchy soil nutrients. Established plots and collected data, and supervised assistants in this work. Developed the statistical designs for these projects and analyzed data.

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Duties and Responsibilities: Assisted with field trips in which students (senior level class) were taught to employ several vegetation sampling methods. Prepared lab handouts on analysis of vegetation data. Instructed students in computerized data analysis and answered questions in lab. Reviewed students' lab reports.

Contract Biologist:
General Refractories Company, U.S. Refractories Division, 600 Grant Street, Room 3000, Pittsburgh, PA 15219. (Phone: 412 562-6020, Glenn Jones, Mining & Properties). Sept. 1989 part time.

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Biological Technician:
Georgia Department of Natural Resources, Game and Fish Division, Protected Plant Program, Route 2, Box 119-D, Social Circle, GA 30279. (Phone: 404 557-2514). March 31 1986 - Sept. 30 1987 full time.

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Stewardship Intern:
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North Carolina Nature Conservancy, P.O. Box 805, Chapel Hill, NC 27514. (Phone: 919 967-7007). October 1985 part time.

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PRESENTATIONS:

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Poster presentation: David Humphrey and David A. Pyke. August 1993. Competitive interactions of caespitose and rhizomatous perennial grasses. At Ecological Society of America meeting.

Poster presentation: David Humphrey and David A. Pyke. August 1991. Competitive interactions between two closely related rhizomatous and caespitose semiarid perennial grasses under varying conditions. At Botanical Society of America meeting.

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Humphrey, L. D., 1989. Life history traits of *Tsuga caroliniana* Engelm. (Carolina hemlock) and its role in community dynamics. *Castanea* 54: 172-190.

Humphrey, L. D., 1985. Use of biomass predicted by regression from cover estimates to compare vegetational similarity of sagebrush-grass sites. *Great Basin Naturalist* 45:94-98.

Humphrey, L. D., 1984. Patterns and mechanisms of plant succession after fire on *Artemisia*-grass sites in southeastern Idaho. *Vegetatio* 57:91-101.

UNRELATED EMPLOYMENT:

Intermittent employment in house building and remodeling:
Nov. 1981 - May 1985.

Food Service:
Wendy's Hamburgers of Athens, Athens, GA 30601. Jan. - March 1977 part time.

Carpenter's Helper:
Humphrey and Bryant Builders, Holiday Rd., Buford, GA 30518. Aug. - Sept. 1976, March - Sept. 1975, Summers 1971 - 1974.

INTERESTS:

Hiking, fishing, cross-country skiing, water skiing.

Member: The Nature Conservancy, National Wildlife Federation, Natural Resources Defense Council.

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