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16. ABSTRACT

We conducted a number of experiments to study the competitive interactions between herbaceous species used in erosion control seedings. We report results from an experiment designed to examine the potential suppressive effect of *Vulpia myuros* (Zorro fescue) on native grasses and resident weeds by testing the effects of varying densities of *V. myuros*. Because *V. myuros* significantly reduced the survival and performance of the mixture of perennial grasses and this effect increased with increasing *V. myuros* seeding density, including this exotic annual in native seeding mixtures is counterproductive. We also investigated whether species that use resources differently in space and time create more stable plant communities than species with more similar resource use patterns. The results of these experiments suggest that within an herbaceous plant community, species have the potential to partition their resources, which may allow them to coexist without competitively excluding one another. We found that mixtures including species with different spatial and temporal resource use patterns utilized soil water more completely and produced greater and more consistent above ground biomass than mixtures of species with more similar resource use patterns. More species rich mixtures used soil water more completely and produced more above ground biomass with more stable species composition than less diverse mixtures.

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NATIVE AND EXOTIC GRASSES
Final Report

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FINANCIAL DISCLOSURE STATEMENT

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IMPLEMENTATION STATEMENT

Information from this project will be disseminated through distribution of copies of this report, presentations at conferences and in courses, and published journal articles. Further details are included in the implementation section following the report conclusions and in the list of presentations in Appendix 1.

EXECUTIVE SUMMARY

We conducted a number of experiments to study the competitive interactions between herbaceous species used in erosion control seedings. In Chapter 1 we report results from an experiment designed to examine the potential suppressive effect of *Vulpia myuros* (Zorro fescue) on native grasses and resident weeds by testing the effects of varying densities of *V. myuros* on the growth and performance of a mixture of California native perennial grasses. Perennial grass seedling survival and aboveground biomass decreased and individuals became smaller with increasing *V. myuros* seeding densities. *Vulpia myuros* also significantly suppressed weed aboveground biomass and density. Weed densities appeared to be reduced more than native perennial grass densities, although biomass of native grasses and weeds were not differentially affected. Overall, because *V. myuros* significantly reduced the survival and performance of the mixture of perennial grasses and this effect increased with increasing *V. myuros* seeding density, we conclude that including this exotic annual in native seeding mixtures is counterproductive.

In a series of experiments reported in Chapters 2 and 3, we investigated whether mixtures of species that partition their resources in space and time create more stable plant communities than mixtures of species that have more similar resource use patterns. First, we conducted field and container studies to quantify plant growth and resource use characteristics in response to differences in soil textures and nitrogen levels. The selected species, which represented six species functional groups based on life history, taxon and

phenology, had different root distribution patterns indicating spatial differences in resource use patterns. Early-season annual grasses had the largest proportion of their roots in shallow soil layers. They utilized soil water only during the spring. Mid- and late-season perennial grasses and early-season legumes had the most evenly distributed roots. They continued to use soil water through the summer.

In the container experiment, there was little effect of soil texture on soil water depletion, but soil water was removed more evenly through the soil profile in the light texture soil and, for some species and depths at particular times in the growing season, the light texture soil was dryer than the heavy texture soil. In the field experiment, nitrogen fertilizer level did not effect root length distribution and soil water depletion patterns. The general spatial distribution of roots and spatial and temporal patterns of soil water depletion corresponded to species functional groups based on life history traits, taxonomic group and phenology.

The results of these experiments, reported in Chapter 2, suggest that within an herbaceous plant community, species have the potential to partition their resources in space and time, which may allow them to co-exist without competitively excluding each other. Furthermore, these patterns of resource use are characteristic of species functional groups, suggesting that functional group based assembly rules may be determinants of community structure in California Central Valley grasslands.

In an experiment reported in Chapter 3, we investigated whether plant community resource use, productivity and stability could be predicted *a priori* when mixtures of

varying species richness were constructed using species with known spatial and temporal resource use patterns. Overall, mixtures that included species with different spatial and temporal resource use patterns utilized soil water more completely, and produced greater and more consistent aboveground biomass than mixtures of species with more similar resource use patterns. More diverse mixtures used soil water more completely and produced more aboveground biomass with more stable species composition than less diverse mixtures. Despite some difficulties with size bias between compatibility treatments, our results indicate that diversity of resource use patterns was at least as important as diversity of species in producing the community functions measured and supports the hypotheses that diversity is positively related to resource use, biomass production and community stability.

To investigate the effects of community resource use patterns and species diversity on invasion by weeds, we studied the success of two invading plant species with different phenologies and rooting depths when planted into some of the species mixtures described above. These results are presented in Chapter 4. The early-season flowering annual grass (*Bromus hordeaceus*), and the late-season flowering annual forb (*Centaurea solstitialis*) were planted into mixtures with different species numbers (two- and five-species) and resource use patterns (compatible and incompatible). We found that the early-season, shallow rooted invader (*Bromus*) was least successful in mixtures composed of species with similar resource use patterns (incompatible mixtures). The late-season species (*Centaurea*) was least successful in the compatible mixtures, which were made up

of species with varied resource use patterns and included some species with resource use patterns similar to *Centaurea*. Overall, invaders were not as successful in plant communities composed of species that utilized resources similarly to the invader. Invaders were less successful in more diverse (greater species rich) mixtures and invader success was reduced by existing vegetation, no matter the resource use patterns of the established species. Invader populations showed the greatest potential for growth under more fertile conditions.

We also conducted a pilot study aimed at evaluating the success of erosion control plantings with native perennial grasses and comparing them with natural plant communities. In this study, reported in Chapter 5, we surveyed seven highway erosion control plantings and eight relict stands of native perennial grasses in Southern and Northern California. Environmental variables (longitude, latitude, elevation, potential annual solar radiation, soil drainage, soil extractable nitrate, extractable ammonium, mineralizable ammonium, total nitrogen and total carbon) and species composition data were evaluated. This allowed us to determine whether particular physical characteristics of the sites were strongly associated with the presence of native perennial grasses or other species or groups of species. We also compared the average levels for environmental variables and vegetation cover for revegetation and relict sites. We found that the environmental variables did not explain patterns in species composition well when revegetation and relict sites were considered together. However, this was a very small data set with too few sites to analyze revegetation sites separately from relict sites.

Annual precipitation was the most important environmental variable for explanation of species composition data. When the two types of sites were compared using parametric and non-parametric statistical tests, relict perennial grass stands had greater mineralizable and total nitrogen levels, higher perennial grass cover, and lower legume cover than revegetation sites.

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GENERAL INTRODUCTION

Perennial grasses have great potential for revegetation of newly constructed roadsides in order to control erosion. The use of perennial grasses has expanded in recent years due to their erosion control properties as well as potential to reduce weeds, maintenance costs, herbicide use and fire hazard and to improve environmental quality. In the long run, perennial grasses have the potential to more effectively control erosion than annual grasses. Extreme fluctuations in annual grass populations have been reported (Talbot et al. 1939). Long-lived perennial grasses are more consistent producers of biomass than annual grasses because of their life history and ability to tap deep soil water sources once established (Holmes and Ricc 1993, Brown 1998).

Not only are perennial grasses excellent for reducing erosion, but they can suppress weeds, which can in turn reduce maintenance costs and herbicide use. Some species of perennial grasses, e.g. Meadow barley, are very competitive against annual grasses during their first year of growth (Bugg et al. 1997). Once established, long-lived perennials are good competitors, persisting in plant communities for decades (White 1967). Although perennial grasses are generally slower growing than annual grasses (Chapin 1980), they can be helpful in controlling weeds (Northam and Callihan 1988). Once a stable perennial community has been established and is being properly managed, the need for herbicides to control weeds can be reduced (Bugg et al. 1997), decreasing costs for materials and labor.

Growth characteristics of perennial grasses can also reduce the need for mowing

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and decrease fire hazard. Some short statured species provide little biomass to serve as fuel or visual obstruction, eliminating the need for mowing (Bugg et al. 1997). In order to address concerns of fire hazard and visibility, taller species can be managed with a single annual mowing once they have become dormant (Anderson, personal communication).

In addition to reduced biomass production of some species, perennial grass longevity and timing of growth can result in reduced flammability compared to annual grasses. Many perennial species stay green longer into the summer and begin growth earlier in the fall than annuals (Laude 1953), while others grow actively throughout the summer. Green tissue has considerably higher water content than dry tissue and is less likely to burn, all else being equal.

Finally, an important advantage of using native perennial grasses and other native plants in roadside seedings is improved environmental quality. There is growing awareness of and concern for the conservation of California's native flora. Highway right-of-ways represent thousands of miles of potential habitat for native plants, including grasses and forbs. The complex nature of native plant communities proves more aesthetically pleasing than monocultures of starthistle or wild oat which often line our roadsides. Native prairie restoration on roadsides has been successfully implemented in other states such as Iowa (Integrated Roadside Vegetation Management, no date).

Although perennial grass species have tremendous potential for erosion control, and can decrease fire hazard, long term maintenance costs and herbicide use, and improve

environmental quality, there is growing concern that this potential has not been fully realized due to past recommendations (Kay 1972a, b, 1973, 1976, 1977, Kay et al. 1981, Adams et al. 1982) and current seeding practices (J. Haynes, personal communication). At present, very little is known about the interactions between annual and perennial species included in seed mixes. Seeding prescriptions have often been based on best guesses, past success and some knowledge of the species' ecology but not an understanding of how the species may interact (e.g. competition or facilitation) (J. Haynes, J. Anderson, personal communications). There are no native perennial grasses included in the most recent Caltrans Seeding Guide for California (Clary 1983), though many species have been used in recent revegetation prescriptions.

A great deal of research has been done investigating the mechanisms of coexistence of species in other plant communities (Aarssen 1983, Aarssen 1989, Pickett 1980, Taylor and Aarssen 1990). Aarssen (1983) identified factors necessary for species to exclude one another from a mixture of plants. In his view, if the species have sufficiently overlapping requirements for survival and one species is superior at reducing the availability of resources (e.g. light, nutrients and water) to a second species, the second species will be excluded from the mixture. The corollary to this is that all species in the mixture will persist if their basic requirements for survival do not overlap significantly and if they are relatively equal in their abilities to compete for resources.

Research suggests that some species are able to coexist by dividing mutually required resources in time or space, thus reducing competition (Gordon and Rice 1992,

Thorgeirsson and Richards unpublished data). A variety of growth characteristics that may facilitate resource partitioning have been shown to affect competitive relationships among plants. Hetrick et al. (1989) considered the division of resources in time between a cool season and warm season grass to be a possible mechanism for their coexistence in short grass prairie. Phenological characteristics of roots (e.g. germination time, initial root growth, rapid exploration of soil, dormancy and death) are important factors in competition between grasses (Harris 1977, Hetrick et al. 1989). Root morphology (e.g. branching pattern and rooting depth) can also affect competitive relationships between grass species (Harris 1967, Berendse 1979, 1982). Gordon and Rice (1992) found that the different rooting morphologies of two California annual prairie species, one having a tap root system and the other a fibrous root system, may contribute to their coexistence.

Rooting depth has also been shown to be a determinant of competitive outcome in grasses. Berendse (1979, 1982) found that plants with different rooting depths at least partially shared their resources. His theoretical evaluation led him to predict that because the root systems overlap in the upper region of the soil, the shallow rooting species must have a greater competitive ability in order to compensate for loss of nutrients to the deeper rooted species (Berendse 1979). This theoretical model approximately predicted results of experiments testing effects of rooting depth on competition in the field (Berendse 1982).

In addition to rooting characteristics, aboveground components of plant growth can affect the competitive relationships between plant species. The success of early

growing or tall statured plants through reducing light available to slower or lower growing species has long been recognized (Harper 1977, Grace and Tilman 1990, Barnes et al. 1988).

Physiological traits as well as morphological and phenological differences affect resource partitioning and competitive effects. Relative growth rates (Muller and Garnier 1990), tolerance of low water availability (Barbour et al. 1987), water use rates (Eissenstat and Caldwell 1988) and nutrient uptake rates (Chapin 1980) are all considered factors affecting competitive ability.

Finally, interaction with other organisms in the soil is also an important factor in competitive relationships between plant species. Mycorrhizal association has been shown to play a role in competitive interactions between grasses (Hetrick et al. 1989; Nelson and Allen 1991), sometimes reversing the suppressive effect of the weedy species on the non-weedy species (Fitter 1977). The mixture of grasses and legumes is a classic example of associated plants which are complementary (Fujita et al. 1992). Growing grasses in association with legumes often results in greater yields of the mixture than the sum of the yields for the species grown separately (de Wit 1966 cited in Harper 1977).

Not only is information upon which to base decisions about species for seed mixtures lacking, but little is known about the interactions between the species included in mixes and the fertilizer applied at the time of seeding. This may be a particularly important interaction when annual species are included with perennial species. In

California roadside seedings, the exotic annual Zorro fescue is often included with native perennials in seed mixes for quick cover (J. Haynes, personal communication).

Fertilizers are generally applied at the time of seeding. Although no longer in use (J. Haynes, personal communication), fertilizer rates from 250 to 500 lbs/acre of 16:20:0 (40-80 lbs nitrogen/acre) have been reported for Caltrans seedings (V. Claassen personal communication, Kay 1972a, b, 1973, 1976, 1977, Adams et al. 1982). There is concern that high nutrient availability may result in rapid growth of annuals, such as Zorro fescue, but that the slower growing perennial seedlings are not able to utilize abundant nutrients and are suppressed by the annuals (V. Claassen and J. Anderson personal communications). There is a good deal of evidence that annual species have generally faster growth rates than perennial species (Muller and Garnier 1990, Bishop 1995) and that species with faster growth rates have greater responses to changes in nutrient availability than species with slower growth rates (Chapin 1980, Garnier et al. 1989, Muller and Garnier 1990). This supports the argument that annual species will be better able to utilize abundant nutrients, increasing their biomass more than perennials. This will result in a distinct competitive advantage for the annuals over the perennials. Shading by the annuals could further reduce perennial growth. In addition, there is evidence that annual and perennial grasses reduce soil water availability to similar levels, but that the annuals reach the lowest level of water availability over two months earlier than the perennials (Rice and Holmes 1993). Competition with annual grasses could

leave perennial seedlings without water before they have become established and may result in increased mortality.

Based on the evidence of an advantage for annual grasses, fertilizer rate is an important factor in successful establishment of native perennial grasses. Research needs to be done to identify nutrient availability levels that are appropriate for simultaneously attaining short term (e.g. erosion control) and long term goals (e.g. perennial establishment). Nutrient availability levels that strike the balance between enhancing growth to obtain maximum soil coverage and low nutrient levels to allow maximum perennial success must be identified. Results from experiments to test this directly were included in a separate report submitted by one of us (V. Claassen).

Soil texture may also affect annual and perennial grass growth and their competitive relationships. Coarse soils generally are less able to retain nutrients and water and therefore are resource poor (Singer and Munns 1987). Perennial grasses may perform relatively better in competition with annuals in coarser, nutrient poor soils.

The five experiments executed during this project investigated the establishment of perennial grasses and their relationship to other herbaceous species in seeded plant communities. Each experiment was designed to answer different questions relevant to the success of native perennial grasses for roadside revegetation. In Chapter 1, we report the findings of an experiment studying the effects of the annual Zorro fescue (*Vulpia myuros*) on the establishment and growth of a mixture of native perennial grasses. The responses of annual and perennial grasses to soil nitrogen levels and soil texture were

studied in an experiment reported in the Chapter 2 of this report. In this study, we establish the possibility of applying the general principles of ecological combining ability to the selection of species for perennial grass seed mixtures.

By first gaining an understanding of the general above- and belowground morphology (shape of structures and growth habits), phenology (timing of growth and life stages) and physiology for species commonly used in revegetation projects, we made selections of species for mixtures that were tested in an experiment reported in Chapter 3 of this report. We expected the most suitable species to be those that had high ecological combining ability (i.e. they partition resources or utilize different resource niches) such that they would not competitively exclude one another from the mixture.

Mixtures of species that utilize resources most completely in space and time may be less prone to invasion by weeds than species that leave resources in the soil to be exploited by invaders. This hypothesis was tested in an experiment reported in Chapter 4 in which we introduced the cool season annual grass soft chess (*Bromus hordeaceus*) and the warm season annual forb yellow starthistle (*Centaurea solstitialis*) into selected mixtures of herbaceous species.

In choosing seeding mixes, it is of primary importance to know that the species included will minimally interfere with one another. Excessive interference results in the competitive exclusion of one or more species from the mixture. Species that are most likely to be compatible and will coexist can be posited from evaluation of natural populations that have existed for long periods of time (relict stands) and from attempted

revegetation projects. Results from a survey of selected existing relict stands has provided a better understanding of the ecological and environmental conditions conducive to the survival of these species. Information about the compatibility of species was also gained by evaluating the success of selected native perennial grass seedings made by Caltrans. Both vegetation and environmental variables were monitored at the relict and revegetation sites. From this survey, native grass seeding performance was evaluated and similarity to relict sites was evaluated. By conducting this survey, it was possible to compare the relict stands to the newly established populations, and identify commonalities between the two plant community types that may be important to the success of future seedings. The information gained from both surveys provided a strong background upon which to base the formal trials of species compatibility and competitive ability. Results from the survey are included in Chapter 5 of this report.

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Chapter 1

**The mark of Zorro: Effects of the Exotic Annual Grass
Vulpia myuros on a Mixture of California Native Perennial Grasses**

ABSTRACT

Native perennial grasses were once common in California prairies but these grasslands have become dominated by annual grasses introduced from Europe. Competition from these introduced species may be a principal impediment to re-establishment of native perennial grasses. In an attempt to reduce erosion during initial establishment, introduced annual grasses, such as *Vulpia myuros* (Zorro fescue), are often included with native perennial species in revegetation seed mixtures in California. In order to examine the potential suppressive effect of *V. myuros* on native grasses and resident weeds, we tested the effects of varying densities of *V. myuros* on the growth and performance of a mixture of California native perennial grasses. *Vulpia myuros* exhibited strong variability in size in response to plant density (i.e. plasticity), producing similar amounts of aboveground biomass at all seeding densities. Perennial grass seedling survival and aboveground biomass decreased and individuals became thinner with increasing *V. myuros* seeding densities. *Vulpia myuros* also significantly suppressed weed aboveground biomass and density. Weed densities were reduced relatively more than perennial grass densities, but the biomass of native grasses and weeds were not differentially affected. Overall, because *V. myuros* significantly reduced the survival and performance of the mixture of native perennial grasses and this effect increased with increasing *V. myuros* seeding density, we conclude that including this exotic annual in native seed mixtures may be counterproductive.

INTRODUCTION

Native perennial grasses were once a major component of the grasslands of California (Clements 1934, Beetle 1947, Burcham 1957, Heady 1988). With the introduction of annual grasses from the Mediterranean region, changes in disturbance patterns due to human activity (Heady 1988) and drought (Burcham 1957) these grasslands became dominated by non-native annual species. This change may have had serious effects on the California grassland ecosystem beyond altering its species composition including increased soil erosion.

Grasses have long been known to substantially reduce erosion and perennial grasses have been of special interest to soil conservationists (Bennett 1935, Fults 1944, Cornelius 1946, Siddoway 1970, Aase and Pikul 1989, 1995, Kemper et al. 1992, Magette et al. 1989, Dabney et al. 1995, Meyer et al. 1995, Daniels and Gilliam 1996, Dewald et al. 1996). Over the long term, perennial grasses can provide more consistent soil cover than annual grasses. Extreme fluctuations of annual grass populations (Talbot et al. 1939) reduce their effectiveness in erosion control. Long-lived perennial grasses may be more consistent producers of biomass than annual grasses because of their longevity, persistent root system, and ability to tap deep soil water sources once established (Holmes and Rice 1996).

In addition to soil erosion control benefits, California's native perennial grasses may be effective in suppressing weeds. Seedlings of some species of perennial grasses, e.g. meadow barley (*Hordeum brachyantherum* ssp. *brachyantherum* Barkworth), are

competitive with annual grasses during their first year of growth (Bugg et. al, unpublished data). Once established, long-lived perennials are good competitors, persisting in plant communities for decades (White 1967). Bugg et al. (1997) showed that perennial grasses can be established in the Sacramento Valley of California on roadsides where healthy stands of many species persisted into the fourth year after seeding. Although perennial grasses generally grow more slowly than annual grasses (Chapin 1980), they may be effective in controlling weeds dependent on residual summer soil moisture such as yellow starthistle (Northam and Callihan 1988; Larson and McInnis 1989; Roché et.al 1994).

Perennial grasses are good competitors once established, but evidence from both field and greenhouse studies indicate that native perennial grasses have difficulty competing with introduced annual plants as seedlings (Bartolome and Gemmill 1981, Dyer et al. 1996, Dyer and Rice 1997, Brown 1998). In California, seedlings of the perennial grass *Nassella pulchra* often do not survive the rapid spring growth period typical of the Mediterranean-type climate. In a study by Dyer et. al (1996) only 0.01% of *N. pulchra* seedlings that grew from seeds planted into an annual dominated grassland survived to the fourth year. The density of this species did not increase over a 20 year period at Hopland Field Station in northern California (Bartolome and Gemmill 1981), further evidence for poor seedling survival. Dyer and Rice (1997) showed that the growth of *N. pulchra* seedlings was reduced due to competition with annuals for light during spring, which resulted in a reduction in the ability of the perennial to utilize water

deep in the soil profile during the dry California summer. Container studies by Bartolme and Gemmill (1981) showed that both densities and growth of *N. pulchra* seedlings were reduced when they were grown with high densities of the introduced annual species *Bromus hordeaceus* and *Vulpia myuros*. These findings were supported by results from a container study by Dremann (1989).

There is strong evidence that introduced annual grasses interfere with establishment and growth of native perennial grasses, yet annuals are often included with perennials in seed mixtures for revegetation. One rationale for including annuals in such mixtures is that because annuals typically have faster emergence rates (Bartolome and Gemmill 1981) and higher relative growth rates (Chapin 1980, Jackson and Roy 1986, Muller and Garnier 1990, Garnier 1992), they are able to protect soil from erosion more quickly after seeding than perennial grasses. In addition, it has been suggested that the competitive nature of the annuals may help to reduce the growth of resident weed species without greatly suppressing perennial seeded species. Several studies have shown that some plant species can promote establishment of others by protecting seedlings from intense sun, heat, herbivores and frost (Muller 1953, Niering et al. 1963, Franco and Nobel 1989). It is possible that *V. myuros* may protect perennial grass seedlings similarly (i.e. it may serve as a nurse plant).

Vulpia myuros is one of the most common annual grasses used in mixtures with native perennial grasses in California. *Vulpia myuros* has been thought to exert minimal competitive pressure on other species within seed mixtures because it grows to only 30 to

50 cm tall and does not develop a dense canopy. However, the effects of *V. myuros* on native perennial grasses when included in seed mixtures has not been tested experimentally under field conditions. The purpose of this field experiment was to investigate the effects of *V. myuros* on the performance of a mixture of selected California native perennial grasses. We were interested in whether the presence of *V. myuros* positively or negatively affected native perennial grass aboveground biomass, density and seedling size. Increases in these performance measures would indicate that *V. myuros* acts as a nurse plant, promoting growth and establishment of the perennials; decreases would suggest competitive suppression of the perennials. We also evaluated the effects of *V. myuros* on the aboveground biomass and density of resident weeds (species that were not seeded), and assessed whether the native perennial grasses were affected relatively more strongly than weeds. This comparison allowed us to address the proposal that *V. myuros* might suppress weeds without negatively affecting the native perennial species.

METHODS

Experimental design, site preparation, and seeding

A randomized complete block experiment with four replicates was conducted in Yolo County, California in an agricultural field that had been planted in dryland wheat and then left fallow and untilled for several years before initiation of the experiment. The soil was predominantly Corning red gravelly loam (Typic Palexeralf). It is a well-

drained, terrace soil, of capability class IV, which is suitable for dryfarmed grain or pasture (Andrews 1990). The eastern end of the field included a Marvin silty clay loam (Aquic Haploxeralf). It is not as well-drained as the Corning soil and is capability class II, which is suitable for row crops (Andrews 1990). These soils are typical of revegetation sites where the experimental grasses may normally be used but are probably more fertile than roadside revegetation sites where hillsides have been cut away and top soil has not been replaced. The field was ripped to a depth of about 60 to 90 cm, laser levelled, disced, and cultivated. Beds 152 cm wide were created and the seed was planted on the top of the beds after harrowing. The native perennial grass seed mixture was planted at one density consistent with current standard practice (Table 1)(J. Haynes pers. com.)(nomenclature of Hickman 1993). The seed was mixed with equal proportions of rice hulls in order to achieve the desired final seeding density and to aid in even distribution. The mixture of native perennial grasses was planted using a wildflower broadcast seeder (Truax Company, Inc., 3609 Vera Cruz Avenue North, Minneapolis, Minnesota 55422) followed by a flexible chain harrow on November 21, 1993 (Table 1).

On November 24, 1993 the *V. myuros* seed was planted into plots 3 m wide (including 2 beds) and 6.1 m long that had been previously seeded with the native perennial grass mixture. *Vulpia myuros* seeding densities in these plots were 0.09, 0.46, 1.38 and 2.75 g m⁻² (Table 2) based on pure live seed. A treatment of the native grass seed mixture without *V. myuros* was included as a control. Plots were cultivated by hand

Table 1. Seeding densities for species included in the native perennial grass mixture. Seeding densities were based on pure live seed estimates, a revegetation standard for estimating seeding densities.

Perennial Grass		Seeding Density (live seed)			
Common Name	Scientific Name	Cultivar-Year Produced	lb/acre	g/m	seeds/m
Blue wildrye	<i>Elymus glaucus</i> Buckley	Anderson -1993	2.5	0.28	77
Meadow barley	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i> Barkworth	Cosumnes -1993	.86	0.10	24
California melic	<i>Melica californica</i> Scribner	Winters- 1993	2.25	0.25	145
Nodding needlegrass	<i>Nassella cernua</i> (Stebb. & Love) Barkworth	Benicia -1993	2.06	0.23	97
Purple needlegrass	<i>Nassella pulchra</i> (A. Hitchc.) Barkworth	unknown -1993	4.42	0.50	71
Pine bluegrass	<i>Poa secunda</i> ssp. <i>secunda</i> J.S. Presl	Fisk Creek -1993	0.58	0.07	48
		TOTAL	12.67	1.41	462

Table 2. *V. myuros* seeding densities based on pure live seed.

g m⁻²	lb acre⁻¹	seeds m⁻²	seeds ft⁻²
0.09	0.82	139	13
0.46	4.18	710	66
1.38	12.54	2129	198
2.75	25	4243	394

immediately after the *V. myuros* seed was broadcast to incorporate it in the top layer of soil.

Purity of seed was determined using methods of the Association of Official Seed Analysts (1989). Germination tests were conducted with 100 - 400 seeds of each species at room temperature. Seeds were placed in petri dishes or on germination slant boards on heavy germination paper and kept moist for at least 21 days. The germination tests were not conducted under ideal conditions so germination estimates may be low. These estimates were used to calculate the pure live seed percentage (P.L.S.), the standard used for determining seeding densities in the revegetation industry [percent P.L.S. = (proportion of pure seed in the seed lot) X (proportion of germinable seed) X 100].

The climate at the study site is Mediterranean; rain falls during the cool winter months with little or no precipitation during the hot summer months. The experiment received ambient rainfall with no supplemental watering. The thirty year average precipitation for Davis, California, about 71.3 km south east of the study site, for the

years 1961-90 is 46.05 cm (National Climatic Data Center 1992). Precipitation at Davis was 38.48 cm in 1994 and 77.24 cm in 1995 (National Oceanic and Atmospheric Association Reference Climatological Station, University of California, Davis). At the study site, 35.43 cm of precipitation were measured in 1994 and 78.28 cm in 1995. The distribution of rainfall events was similar to Davis. Precipitation during December and January was below average but rainfall events were fairly evenly distributed. Drought periods after the first germinating rains were 10 days in December, 14 days in January, and 12 days between January and February and are not expected to have negatively affected survival of seeded species (Brown, unpublished data). Although the annual precipitation during 1994 was lower than the thirty year average for the area, 3.17 cm of rain fell during May in Davis where the thirty year average for that month is 0.71 cm. This rain effectively lengthened the time that conditions were favorable for plant growth, i.e. temperatures were warm and water was available. In 1995 the annual rainfall was well above the thirty year average in Davis with 3.76 cm of rain falling during May and 1.80 cm during June. Thus, the precipitation pattern in 1995 made it an exceptionally wet year with an extended growing season.

Sampling methods

Plant density was estimated in each treatment plot by counting the number of individual plants that occurred within two randomly located 0.1 m² circular quadrats. Densities of *V. myuros* were estimated March 9 and April 12-19 in 1994. Native perennial grass densities were estimated March 9, April 12-19 and October 24 in 1994

and April 22 in 1995. Species that were not seeded were considered weeds. About 70% of the weed biomass was forbs with the remainder from the Juncaceae and Poaceae families. The most abundant dicotyledonous weeds were *Calandrinia ciliata* (Ruiz López & Pavón) DC. (Polygonaceae) (red maids), *Convolvulus arvensis* L. (Convolvulaceae) (field bindweed), *Centaurea solstitialis* L. (Asteraceae) (yellow starthistle), and a *Silene* species (Caryophyllaceae) (catchfly). The monocotyledonous weeds were predominantly *Avena fatua* L. (Poaceae) (wild oat) and *Juncus bufonius* L. (Juncaceae) (toad rush). Densities of weeds were estimated April 12-19, 1994.

Heights of *V. myuros* and native perennial grasses were estimated April 12-19, 1994 by measuring the extended height of one randomly selected plant of each type from each quadrat used for estimating density. Aboveground biomass samples of *V. myuros*, native perennial grasses, and weeds were taken May 3-10, 1994 by clipping the vegetation from a 0.1 m² circular quadrat placed within each treatment plot. Biomass samples were sorted, dried to constant weight at 65 °C and weighed. Biomass values were means of two randomly located subsamples taken in each treatment plot. Weed species composition was determined using the dried biomass samples. It was not always possible to determine the precise identity of the weed species.

Statistical analyses

Vulpia myuros seedling density and biomass data were log transformed and analyzed using simple linear regression. Perennial grass density data collected over the duration of the experiment were analyzed using repeated measures analysis of variance

(ANOVA) with time as the repeated measure. The hypothesis that the perennial grass data satisfied the assumption of sphericity (equal variance and independence) could not be rejected based on Mauchly's Criterion so results from the unadjusted ANOVA (i.e. degrees of freedom not reduced to compensate for dependence of residuals) were used (von Ende 1993). Linear contrasts were used to determine differences between the native grass mixture grown alone and grown in the presence of *V. myuros* at any density and between the effects of *V. myuros* seeded at 0.09 g/m² and the three higher densities.

One-way ANOVA was performed on variables that were measured once during the experiment when a linear regression model was judged inappropriate after visual inspection of the data. Square root transformed weed density and log transformed weed biomass were analyzed with ANOVA. Tukey's Studentized Range Test was used for *a posteriori* means comparisons in these cases. For native grass data, linear regression was performed on the log of biomass per square meter, the log of biomass per individual, and untransformed density and height data. Comparisons between weeds and native grasses were based on data taken during the April sampling period.

SAS for Windows (Release 6.10, 1994, SAS Institute Inc., Cary, NC) was used for repeated measures and one-way ANOVA. BMDP New System for Windows (Version 1.0, 1994, BMDP Statistical Software, Inc., Los Angeles, CA) was used for regressions and some one-way ANOVA. Further details and discussion of the methods and results of this experiment are contained in Brown (1998).

RESULTS AND DISCUSSION

Vulpia myuros density and biomass

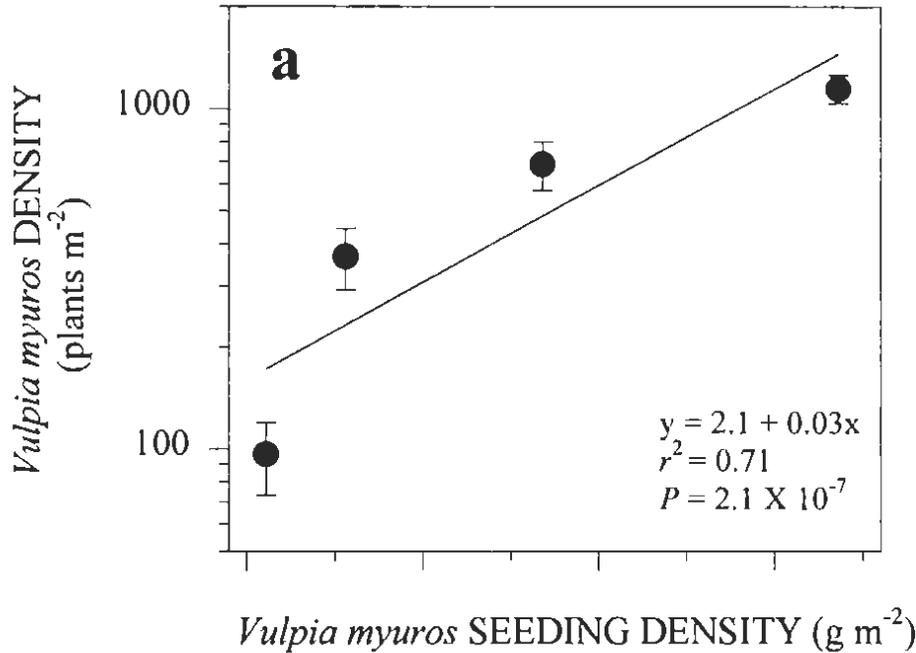
As expected, the number of *V. myuros* seedlings increased as seeding density increased (Fig. 1a, $P < 0.001$, $r^2 = 0.71$). Despite the increase in the number of seedlings per unit area shown in Fig. 1a, *V. myuros* biomass did not increase significantly with seeding densities (Fig. 1b). This was shown by an insignificant regression of *V. myuros* biomass against *V. myuros* seeding density ($P > 0.1$, $r^2 = 0.07$), which indicated that there was no relationship between the two variables. These two graphs show that there were few, large plants at low densities and many, small plants at high densities, demonstrating that the size of *V. myuros* individuals varied greatly in response to environmental conditions (i.e. it is a highly plastic species).

Perennial grass and weed density

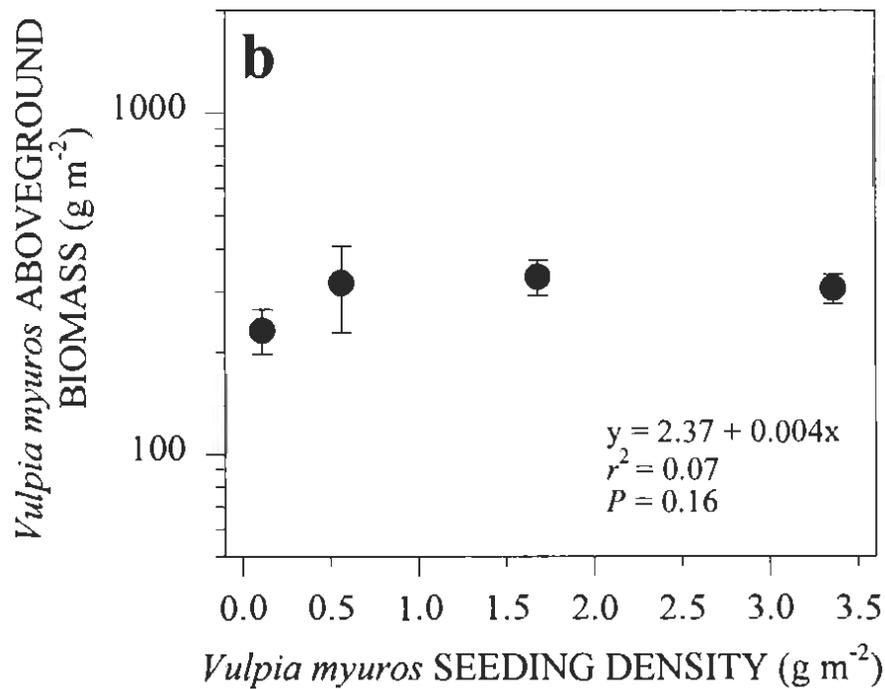
Native perennial grass and weed densities were reduced by *V. myuros*. Native perennial grass densities decreased over time with increasing *V. myuros* seeding rates ($P = 0.0017$) (Fig. 2). In analyses that included all sampling dates, perennial grass densities were higher for the native grass mixture grown alone compared to the mixture grown with *V. myuros* seeded at 0.09, 0.46, 1.38 and 2.75 gm^{-2} (linear contrast $P < 0.01$) (See photographs on page 38). Additional contrasts showed no significant difference between native grass densities in plots with the lowest seeding rate of *V. myuros* (0.09 gm^{-2}) and

Figure 1

Although the number of *V. myuros* plants increased with increasing seeding density, the amount of biomass did not change. There were few, large plants at low seeding densities and many, small plants at high seeding densities.

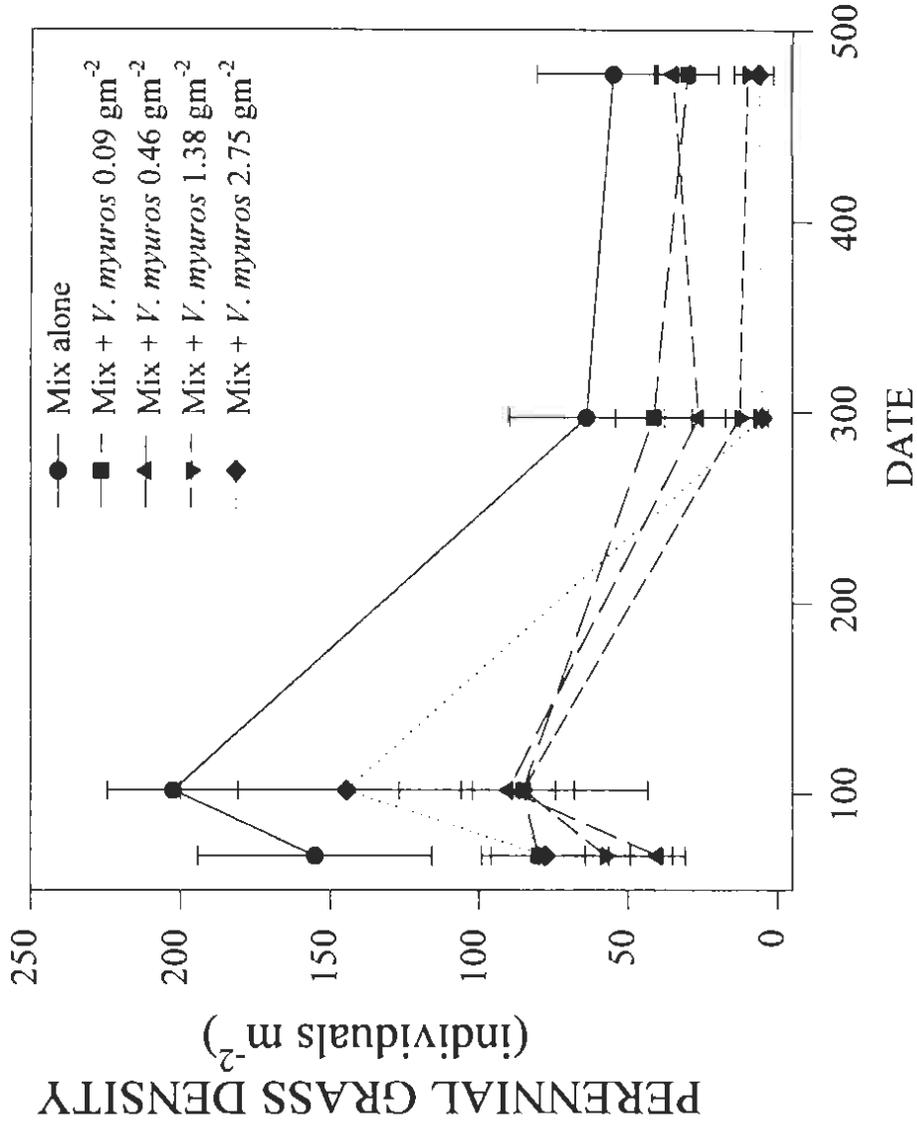


(a) *Vulpia myuros* plant densities measured on March 9, 1994 with respect to *V. myuros* seeding density. Values are means \pm 1 standard error of the mean, n = 4 for *V. myuros* seeding density of 0.46 gm⁻², n = 8 for other densities.



(b) *Vulpia myuros* biomass sampled May 3-10, 1994 with respect to *V. myuros* seeding density. Values are means \pm standard error of the mean, n = 4 for *V. myuros* seeding density of 0.46 gm⁻², n = 8 for other densities.

Figure 2
 Native perennial grass densities decreased over time at all seeding rates of *Vulpia myuros*.
 Densities of perennial grasses were reduced similarly by *V. myuros* at all treatment levels.



Changes in density of a mixture of California native perennial grass species when planted alone and with *V. myuros* at 0.09, 0.46, 1.38, and 2.75 gm⁻². Values are means ± 1 standard error of the mean, n = 4.

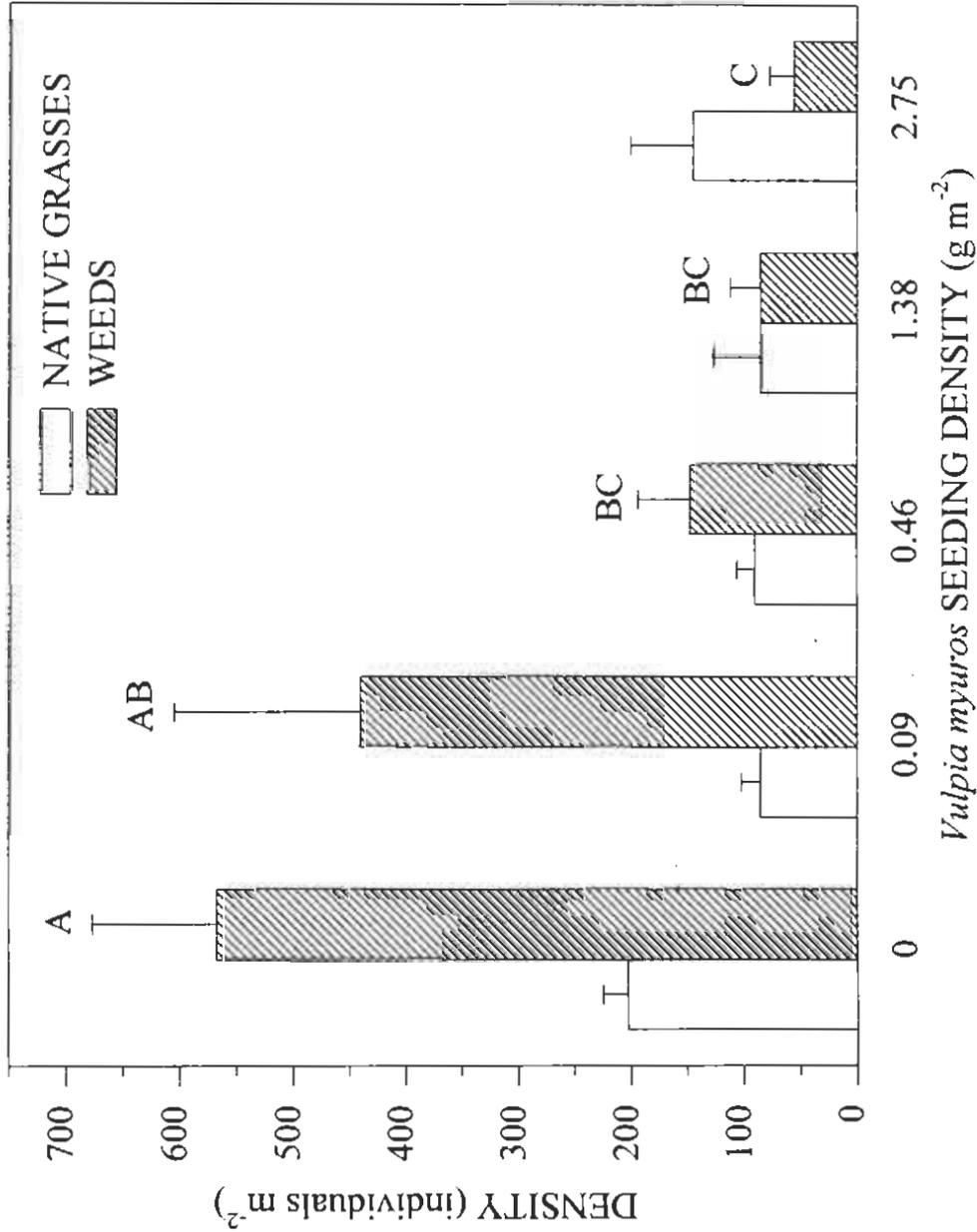
plots at higher *V. myuros* seeding rates (0.46, 1.38 and 2.75 gm⁻²). Maximum suppressive effects of *V. myuros* were observed at even the lowest seeding rates.

It is important to evaluate the relative effects of *V. myuros* on weed and native grass densities in order to assess whether *V. myuros* might suppress weedy species without significantly reducing perennial grass establishment. These relative effects can be evaluated by examining differences between the effects of *V. myuros* on weeds and native perennial grasses shown in Figure 3. Weed densities, measured during only one sampling period (April 12-19), were reduced by more than an order of magnitude with increasing *V. myuros* seeding rates ($P = 0.0015$) (Fig. 3). Plots without *V. myuros* had significantly greater weed densities than plots with *V. myuros* seeded at 0.46, 1.38 and 2.75 gm⁻². Weed densities decreased incrementally as *V. myuros* seeding rates increased.

In contrast, perennial grass densities were not significantly reduced at any *V. myuros* seeding rates ($P = 0.11$) when only data collected on the April 12-19 sampling date were considered. For that sampling event, weed densities were reduced 90% and native grass densities were reduced 30% at the highest *V. myuros* seeding rates. Perennial grass densities were reduced by over 50% at the lowest *V. myuros* seeding rate. Weed densities were much greater than perennial grass densities at low *V. myuros* seeding rates and were similar to perennial grass densities at high *V. myuros* seeding rates.

In summary, weed densities were most affected by *V. myuros* when it was seeded at higher rates and perennial grasses were suppressed by even low densities of *V. myuros*. Weed densities were reduced relatively more than perennial grass densities and dropped

Figure 3
Increasing *Vulpia myuros* seeding rates reduced weed densities relatively more than perennial grass densities.



Density of native grasses and weeds at various *V. myuros* seeding rates on April 12-19, 1994. Values are means \pm 1 standard error, n = 4. Means with different letters are significantly different from one another according to Tukey's Studentized Range Test.

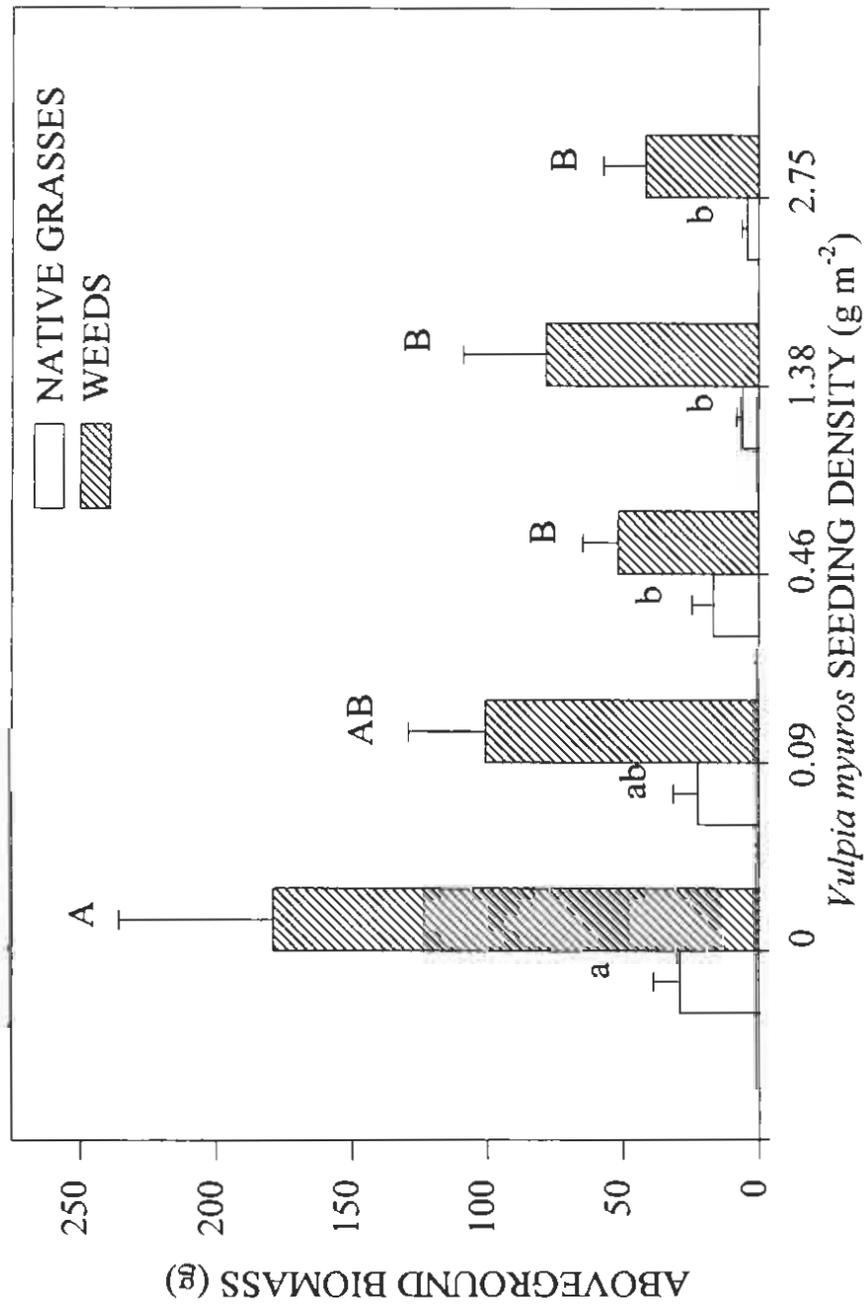
to levels similar to perennial grasses at high *V. myuros* seeding rates. Taken alone, these results suggest that *V. myuros* might be used effectively to suppress weeds without eliminating native perennial grass establishment.

Perennial grass and weed biomass

Because of plant plasticity (i.e. variability in plant size in response to environmental conditions) biomass production is often a more important determinant of plant success than plant density. Fast-growing, weedy species generally have greater plasticity than relatively slow-growing species like many native perennial grasses. At low densities, species with high plasticity are able to produce large amounts of biomass that can suppress slower growing plants through competition for light and soil resources. Under favorable growing conditions, highly plastic plants can also produce a great many seeds, so a few individuals can grow into a large population within a small number of generations.

Aboveground biomass of native perennial grasses and weeds decreased with increasing *V. myuros* seeding density ($P < 0.01$ and $P = 0.02$, respectively) (Fig. 4) (See photographs on page 38). For both native grasses and weeds, aboveground biomass was greater when no *V. myuros* was present than when *V. myuros* was seeded at densities of 0.46, 1.38 and 2.75 gm⁻². The relative effects of *V. myuros* on grass and weed aboveground biomass appeared to be similar. Weed and native perennial grass aboveground biomass were reduced by 77% and 86%, respectively. It is also important to note that weed aboveground biomass

Figure 4
 Increasing *Vulpia myuros* seeding rates reduced native perennial grass and weed aboveground biomass similarly. Aboveground biomass of weeds was much greater than that of perennial grasses in all treatments.



Aboveground biomass of native perennial grasses and weeds at various *V. myuros* seeding densities on May 3-10, 1994. Values are means \pm 1 standard error, n = 4. Means with different letters are significantly different from one another according to Tukey's Studentized Range T-test.

ranged from three to ten times that of perennial grasses depending on the treatment. This suggests much greater competitive and reproductive potential of weeds than perennial grasses at all *V. myuros* seeding rates.

Overall, aboveground biomass of both perennial grasses and weeds were reduced similarly on a relative basis. However, weed aboveground biomass was much greater than that of perennial grasses. Regardless of the effects of *V. myuros* on perennial grass and weed densities, our results indicate that it is ill-advised to use *V. myuros* in perennial grass seed mixtures to suppress weeds. The reduction of perennial grass biomass by *V. myuros* and the huge biomass advantage of weeds suggest that there will be no long-term advantage for either establishment of native perennial grasses or weed control through inclusion of *V. myuros* in revegetation seed mixtures.

Perennial grass height and biomass per individual

In addition to density and aboveground biomass, the relationship between the height and weight of individual plants is a good indicator of plant performance. Seedlings growing under low-light conditions become etiolated, growing pale, long, thin and spindly. We assessed whether perennial grass seedlings were experiencing low-light conditions by evaluating the heights and weights of individual perennial grass seedlings.

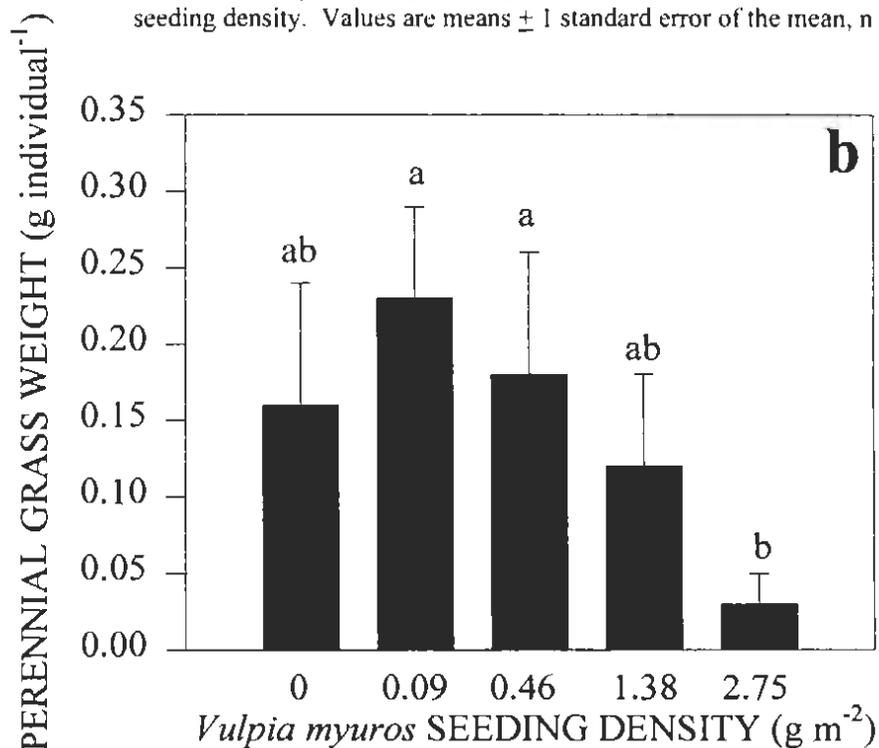
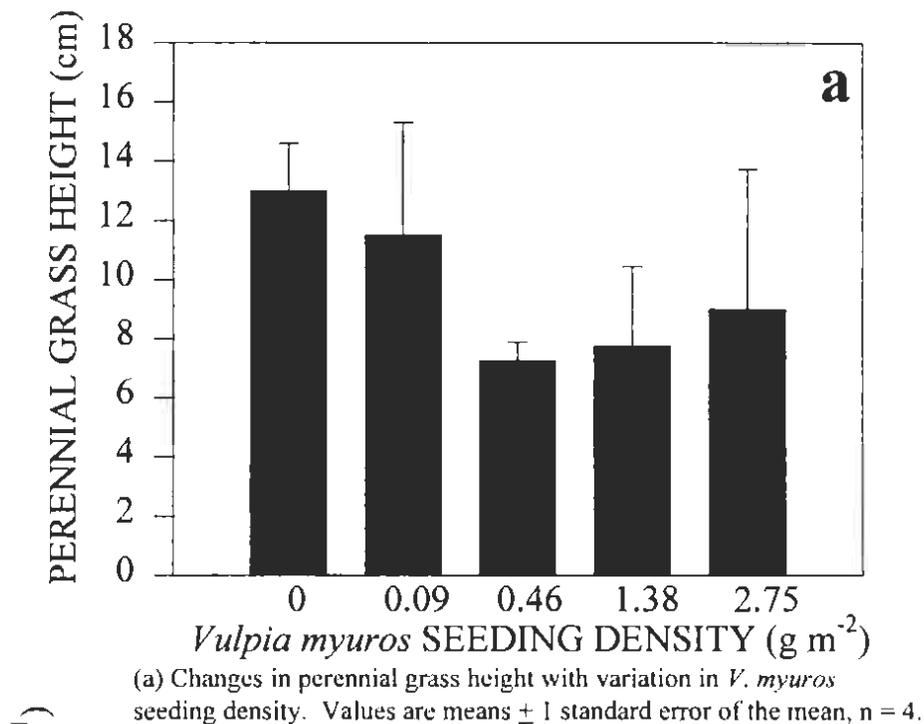
Perennial grass seedling heights and weights were measured once during the first growing season as an index of light limitation within the developing canopy of *V. myuros*. Perennial seedlings were of similar height but lighter weight at higher *V. myuros* seeding densities. Height did not differ statistically with changing *V. myuros* seeding

density (ANOVA $P > 0.5$) (Fig.5a). However, weights of individual perennial grass seedlings varied with *V. myuros* seeding density treatments ($P < 0.01$) (Fig. 5b) and tended to be lower at higher seeding rates.

These results indicate that perennial grass seedlings were suffering from reduced resources, one of which may have been light, when growing in the presence of *V. myuros*. Individuals were not taller in high *V. myuros* density treatments and did not appear to be strongly etiolated (blanched and spindly). However, seedlings weighed less at high *V. myuros* densities, suggesting that growth had been reduced. Seedlings in this weakened state may be less likely to survive than larger individuals (Harper 1977).

Figure 5

Perennial grass seedlings weighed less at higher *Vulpia myuros* seeding rates but height was not significantly affected.



CONCLUSIONS

Results of our experiment show that increasing seeding densities of *V. myuros* reduced aboveground biomass and densities of native perennial grasses and weeds. Native perennial grass and weed aboveground biomass were also suppressed, but weed aboveground biomass was from two to seven times as great as perennial grass aboveground biomass. Weed densities and not perennial grass densities were reduced by increased seeding rates of *V. myuros* when a single sampling event was examined. However, across all sampling events, perennial grass densities were reduced when *V. myuros* was present, even at the lowest seeding density.

The response of perennial grasses may be a reflection of the growth capacity of *V. myuros*. *Vulpia myuros* biomass at the lowest seed density was similar to the higher seed densities. This ability to produce similar amounts of biomass at different densities demonstrates the plasticity of *V. myuros*; at low seed density there were few large plants, while at high seed density there were many small plants. This pronounced plasticity may explain why low density stands of *V. myuros* suppressed native grasses almost as much as high density stands.

Our experiment showed that perennial grasses were suppressed by the presence of *V. myuros*. Although weeds were also reduced, their biomass was many times greater and their densities equal to, if not greater than, native perennial grasses. Therefore, we consider it unwise to include *V. myuros* in seed mixtures with California native perennial grasses. Emphasizing mechanical means of erosion control in the short term may be the

Zorro Trial



a. Emergence of perennial grass mixture with *F. myiuros* at 0.09 g m⁻²



b. Emergence of perennial grass mixture with *F. myiuros* at 2.75 g m⁻²



c. Perennial grass mixture without *F. myiuros* at end of first growing season



d. Perennial grass mixture with *F. myiuros* at 2.75 g m⁻²

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CHAPTER 2

Belowground Resource Use Patterns and Potential for Resource Partitioning

ABSTRACT

Differences in the spatial and temporal patterns of plant resource use may be an important mechanism determining the species composition of some plant communities. We conducted field and container studies in Yolo County, California to quantify plant growth and water resource use by plants in response to different soil textures and nitrogen levels. The selected species, which represented six functional groups defined by their life history, taxon and phenology, had varied root distribution patterns indicating spatial differences in belowground resource use. They also differed in timing of resource use during the year. Early-season annual grasses had the largest proportion of their roots in shallow soil layers, and utilized soil water only during the spring. Mid- and late-season perennial grasses and early-season legumes had the most evenly distributed roots. The perennial grasses continued to use soil water through the summer. In the container experiment, soil texture had little effect on soil water depletion, but soil water was removed more evenly through the soil profile in the light texture soil. In some cases, the light texture soil was dryer than the heavy texture soil. In the field experiment, nitrogen fertilizer level did not effect root length distribution and soil water depletion patterns. Each of the six species guilds had characteristic root distribution patterns and spatial and temporal patterns of soil water use. The results of these experiments suggest that within an herbaceous plant community, species have the potential to partition their resources in space and time in a manner that may allow them to coexist. Furthermore, these patterns

of resource use are characteristic of species functional groups and may play a role in determining which species occur together in prairie plant communities.

INTRODUCTION

At least since 1959 when G.E. Hutchinson wondered "why there are such an enormous number of animal species" (p 146), ecologists have been formally trying to answer questions about how species diversity is maintained in communities when available resources are limiting. If ecologists are baffled by the diversity of coexisting species in the animal kingdom, the stable coexistence of plant communities is even more difficult to understand (Harper et al. 1961, Aarssen 1983). The biological and physical requirements of a species for survival is considered a its ecological niche (Begon et al. 1996). A species' ecological niche without competition is called its fundamental niche (Begon et al. 1996). The competitive exclusion principle predicts that if the fundamental niches of two species overlap sufficiently, when the species are in competition with each other, the weakest competitor will be eliminated (Gause 1934). Because plants require essentially the same resources for survival and growth, it is difficult to envision how species of plants can have fundamental niches different enough to allow coexistence (Grubb 1977, Pickett 1980, Aarssen 1983, Bengtsson et al. 1994).

There is evidence that plants are capable of acquiring the resources they need in the presence of potential competitors through differences in resource use (i.e. niche separation). Direct competition may be avoided by using resources at different depths in the soil (spatial niche separation) or by using resources at different times (temporal niche separation). We performed a series of experiments investigating whether niche differentiation among selected herbaceous plant species and functional groups (i.e. groups

of species with similar traits) can determine which species coexist. This information may allow us to design mixtures of species that are compatible with each other to form stable plant communities for revegetation and erosion control.

In the experiments reported here, we tested whether belowground resource use differed spatially and temporally, thus suggesting niche separation, for up to seventeen species belonging to six functional groups from the California Central Valley grassland flora. In addition, we examined resource use by these species under different soil nitrogen levels and textures to assess the robustness of potential niche separation with variation in the physical environment.

METHODS

Container experiment

The container experiment was conducted in Davis, California, USA. The experiment was a randomized complete block design with six replicates the first year (1993-94) and three replicates the second year (1994-95). We examined patterns of belowground resource use of nine species of herbaceous California native or introduced prairie plants under two soil texture treatments. A control treatment with no plants was included to determine soil water levels without extraction by plants. Containers were polyvinylchloride (PR 100 PVC, approximately 4 mm thick), 15 cm in diameter and 1.3 meters deep. They were placed on end in a large excavated pit on top of a 30 cm layer of gravel covered with 5 cm of sand. The containers were surrounded with sand to within 5 cm of the rim to maintain realistic subterranean temperatures. Each container was filled with one of two textures of soil: either heavy texture (100% Corning gravelly loam, a Typic Palexeralf) or light texture mixture (50% Corning gravelly loam, 50% sand by volume). Before filling the containers, the soil was prepared by crushing clods, then passing the soil through a 1 cm mesh sieve to remove stones and remaining large clods. Soil was not sterilized in order to allow root association with naturally occurring mycorrhizal fungi.

Approximately fifty to one hundred seeds (enough to ensure survival of at least six plants) of a single species were planted into an 81 cm² area in the center of each container on November 16, 1993. We covered the seeds of *Bromus hordeaceus* L. (soft

chess), *Elymus glaucus* Buckley (blue wildrye), *Elymus multisetus* (J.G. Smith) Burt Davy (big squirreltail), *Lupinus succulentus* Koch (arroyo lupine), *Hordeum brachyantherum* ssp. *brachyantherum* Nevski (meadow barley) and *Nassella pulchra* (A. Hitchc.) Barkworth (purple needlegrass) with a 1.2 cm layer of sand (nomenclature is according to Hickman 1993). For the three species with smaller seeds, *Lupinus bicolor* Lindley (miniature lupine), *Poa secunda* ssp. *secunda* J.S. Presl (pine bluegrass) and *Vulpia microstachys* (Nutt.) Benth., we placed 0.6 cm of sand over the soil, sprinkled the seeds, and covered them with another 0.6 cm of sand. This shallower planting depth ensured that these smaller seeds were not buried too deeply to emerge effectively while keeping the sand layer the same depth in all containers. A 1.2 cm layer of sand with no seeds was added to one container of each soil type as a control treatment. Containers were kept moist until emergence. The species in the container experiment are listed in Table 1, organized according to their phenological, taxonomic and life history groups (i.e. functional groups).

The annuals *L. succulentus*, *L. bicolor*, *V. microstachys* and *B. hordeaceus* were replanted in the containers on November 8, 1994, before the second growing season. On January 7-12, 1994 six individuals within each container were randomly selected and the remaining seedlings removed. Due to poor germination in some containers seeded with *L. bicolor*, individuals of this species were transplanted from containers that had many seedlings so that there were at least three seedlings per container. January 26 and 31, 1995 *L. succulentus* and *L. bicolor* were thinned to three plants per container. *Bromus*

Table 1. List of species arranged in functional groups, with indication as to whether each is native or introduced to California, was included in the container or field experiments (+ = yes, - = no), and whether soil water potential data (Ψ) were collected in the container (C) or field (F) experiment. Taxonomic authors according to Hickman 1993.

GROUP	SPECIES	COMMON NAME	ORIGIN	CONTAINER	FIELD	Ψ
Early-season Perennial grasses	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i> Nevski	meadow barley	native	+	+	C
	<i>Poa secunda</i> ssp. <i>secunda</i> J.S. Presl	pine bluegrass	native	-	+	
Mid- and late-season Perennial grasses	<i>Elymus glaucus</i> (Buckley)	blue wildrye	native	+	+	C,F
	<i>Elymus multisetus</i> (J.G. Smith) Burt Davy	big squirreltail	native	+	+	C
	<i>Elymus trachycaulus</i> (Link) Shinn.	slender wheatgrass	native	-	+	
	<i>Hordeum brachyantherum</i> ssp. <i>californicum</i> (Covas & Stebb.) v. Bothmer, N. Jacobsen & O. Seberg	California barley	native	-	+	
	<i>Nassella pulchra</i> (A. Hitchc.) Barkworth	purple needlegrass	native	+	+	C

Table 1 continued

Early-season annual grasses	<i>Vulpia microstachys</i> (Nutt.) Benth.		native	+	+	C,F
	<i>Vulpia myuros</i> (L.) C. Gmelin	Zorro fescue	exotic	-	+	F
	<i>Bromus hordeaceus</i>	soft chess	exotic	+	+	
Early-season annual legumes	<i>Lupinus bicolor</i> Lindley	miniature lupine	native	+	+	
	<i>Lupinus microcarpus</i> ssp. <i>densiflorus</i> (Benth.) Jepson		native	-	+	
	<i>Lupinus succulentus</i> Koch	arroyo lupine	native	+	+	C,F
	<i>Trifolium gracilentum</i> Torrey & A. Gray		native	-	+	
Late-season annual legume	<i>Lotus purshianus</i> (Benth.) Clements & E.G. Clements	Spanish clover	native	-	+	
	<i>Centaurea solstitialis</i> (L.)	yellow starthistle	exotic	-	+	F
Late-season annual forbs	<i>Eremocarpus setigerus</i> (Hook) Benth.	turkey mullen	native	-	+	

hordeaceus seedlings were transplanted from containers with many seedlings to containers with few seedlings to reach a minimum of three seedlings per container. Fewer than three seedlings survived in one container each of *L. succulentus* and *B. hordeaceus*. On February 20, 1994 seedlings were transplanted into these containers from containers with excess seedlings to reach a minimum of three seedlings per container. No differences between transplanted seedlings and those that were not transplanted were observed.

In all other treatments, seedlings were removed at various times to leave three individuals per container during the growing season. One replicate of *E. multisetus* and all replicates of *H. brachyantherum* were eliminated from the second year of the experiment because the plants did not survive the summer drought period of 1994. Natural rainfall was supplemented by adding 1 liter of water to each container on March 12 and April 5, 1994. This was to delay soil moisture depletion within the containers because we were in the process of installing soil psychrometers and only 2 mm of precipitation fell between February 28 and April 9, 1994. We also added 250 ml of water to each container on February 20, 1995 in order to facilitate survival of seedlings that had just been transplanted.

Field experiment

The field experiment was conducted at Hedgerow Farms (Yolo County) near Winters, California USA in an agricultural field of predominantly Corning red gravelly loam, a fine, montomorillonitic, thermic Typic Palexeralf (Andrews 1990). It is class IV

capability unit, relatively well-drained, and of moderate fertility. The field had been planted in dryland wheat and then left fallow and untilled for several years before initiation of the experiment. The field was deep ripped to about 80 cm and disked.

The experiment was a split-plot design with five replicates. Nitrogen fertilizer levels, the main plot factor (two levels: moderate and none), were randomly assigned to one half of each of the replicates. Seventeen species treatments (Table 1) and a weeded control (the split-plot factor) were randomly assigned to plots within each fertilizer treatment level. Individual experimental units were 3 m by 3 m plots and were seeded with a single species.

We hand broadcast seed on November 8 and 9, 1993 at the densities listed in Table 2 and incorporated the seed into the top 2 cm of soil by hand cultivation. Target seed densities were 1,550 seeds m⁻² (1 seed in⁻²) to ensure dense stands of each species. However, some seeding densities deviated from this due to limited availability of seed (*Centaurea solstitialis*, *Eremocarpus setigerus*, *L. bicolor*, *L. microcarpus*, *L. succulentus* and *V. microstachys*) or errors in seed density calculations (*E. glaucus* and *Trifolium gracilentum*). Within one half of each 3 m by 3 m single species plot, a 1 m² area was kept weed free (i.e. a pure monospecific stand of the experimental species). Soil water potential measurements (Table 1) and root samples were collected from the weeded area. Entire 3 m by 3 m control plots were kept free from vegetation. Plots received natural rainfall without supplementation.

Table 2. Densities of viable seed for monoculture field experiment.

SPECIES	SEEDS/m ²	GERMINATION %	VIABLE SEEDS/m ²
<i>Elymus glaucus</i>	2,562	79	2,024
<i>Elymus multisetus</i>	1,550	87.5	1,356
<i>Elymus trachycaulus</i>	1,550	95	1,472
<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>	1,496	30	449
<i>Hordeum brachyantherum</i> ssp. <i>californicum</i>	1,550	85	1,317
<i>Nassella pulchra</i>	1,550	50*	775
<i>Poa secunda</i> ssp. <i>secunda</i>	1,550	43	666
<i>Vulpia microstachys</i>	258	96	248
<i>Vulpia myuros</i>	1,550	91	1,410
<i>Bromus hordeaceus</i>	1,550	96	1,488
<i>Lupinus bicolor</i>	366	93	340
<i>Lupinus microcarpus</i> ssp. <i>densiflorus</i>	592	92	545
<i>Lupinus succulentus</i>	366	96	351
<i>Trifolium gracilentum</i>	6,404	96	6,148
<i>Lotus purshianus</i>	1,550	69	1,069
<i>Centaurea solstitialis</i>	603	75	452
<i>Eremocarpus setigerus</i>	204	97	199

*Estimated from similar seed source under conditions similar to other species.

taken approximately bi-monthly during the growing season, and approximately monthly otherwise.

Container experiment.--- We placed psychrometers 40 and 100 cm below the soil surface in the containers of *N. pulchra*, *L. succulentus*, *H. brachyantherum*, *E. glaucus*, *V. microstachys* and *E. multisetus* (Table 1) by digging an access hole adjacent to the selected containers, inserting a psychrometer into the soil inside the container through a previously drilled hole and sealing the hole with plumber's putty. We installed psychrometers in four of the six replicates on March 14, 17 and 18, 1994. After allowing time for equilibration, we began taking soil water potential measurements on April 7, 1994. Three replicates were harvested in June 1994 leaving the psychrometers in three replicates for the remainder of the experiment.

Field experiment.---Psychrometers were installed in four replicates of seven species treatments (*E. glaucus*, *C. solstitialis*, *L. succulentus*, *N. pulchra*, *Vulpia myuros*, *V. microstachys* and the no plant control) at 30 and 70 cm below the soil surface. Psychrometers were installed by digging a 25 cm diameter, 90 cm deep hole immediately adjacent to selected plots using a power auger, and inserting the psychrometer into a 15 cm horizontal hole made with a power drill and right angle bit.

Root harvest

We harvested roots from three of the six replicates of the container experiment from May 31 through June 2, 1994 and the remaining three replicates from May 31 through June 6, 1995. At the time of harvest, soil samples for root length measurements

mm, (National Climatic Data Center 1992). Precipitation at Davis was 384.8 mm in 1994 and 772.4 mm in 1995 (National Oceanic and Atmospheric Association Reference Climatological Station, University of California, Davis). At the field study site, 354.3 mm of precipitation were measured in 1994 and 782.8 mm in 1995. The distribution of rainfall events was similar to Davis. Although the annual precipitation during 1994 was lower than the thirty year average for the area, 31.7 mm of rain fell during May in Davis, where the thirty year average for that month is 7.1 mm. This high rainfall during May effectively lengthened the time that conditions were favorable for plant growth because temperatures were warm and water was available. In 1995 the annual rainfall was well above the thirty year average in Davis. In addition, 37.5 mm of rain fell during May and 18.0 mm during June. The thirty year average precipitation for June in Davis is 3.8 mm. The precipitation pattern in 1995 made it an exceptionally wet year with an extended growing season.

Soil water

Calibrated screen-caged thermocouple psychrometers (J.D. Merrill Specialty Equipment, Logan, UT) were placed horizontally below the soil surface in both experiments to measure soil water potential. Microvolt output from the psychrometers was recorded with a CR-7 data logger (Campbell Scientific, Inc.) and converted to water potential in MPa (Brown and Bartos, 1982). Water potential is zero in wet soil and becomes increasingly negative as the soil dries. Psychrometers were individually calibrated according to the methods of Brown and Bartos (1982). Measurements were

Ammonium nitrate was applied to moderate nitrogen treatment plots on February 15, 1994 (23.5 kg N/ha). The fertilizer was dissolved by 13 mm of rain that fell two days later. Urea, rather than ammonium nitrate, was applied March 3, 1994 (40.4 kg N/ha) in order to reduce loss of nitrogen through volatilization before it was completely incorporated by rainfall. The next precipitation event was March 25, 1994 when 2 mm of rain fell. No fertilizer was applied to the low nitrogen treatments. Fertilizer was mistakenly applied to one of the low nitrogen treatment areas, so it was not included in the statistical analysis.

Seeds and germination tests

Seed for *E. setigerus*, *C. solstitialis*, and *V. microstachys* were collected from wild plants in the summer of 1993. Seed for the remaining species was obtained from commercial seed suppliers (Pacific Coast Seed, Livermore, CA; Hedgerow Farms, Winters, CA; Conservaseed, Rio Vista, CA). Seed germination tests were conducted using the methods of the Association of Official Seed Analysts (1986). Legumes were mechanically scarified and inoculated with appropriate rhizobia cultures (The Nitragin Company, Liphatec, Inc. Milwaukee, Wisconsin, USA).

Climate

The climate at the study sites is typically Mediterranean; rain falls during the cool winter months with little or no precipitation in the summer when warm temperatures are most conducive to plant growth. The thirty year average precipitation for Davis, California, (about 18.4 km southeast of the field study site) for the years 1961-90 is 460.5

were taken at 15-20, 55-60, and 105-110 cm depths. In the field experiment, we collected soil cores at 0-10, 20-30 and 50-60 cm depths between March 25 and April 19, 1994. Soil was hand-washed from the samples onto fine screens using a standard procedure to minimize loss of roots and root lengths were determined using a Comair Root Length Scanner (Hawker de Havilland Victoria Limited, Melbourne, Victoria, Australia).

Inherent soil fertility

Naturally occurring soil nutrient levels were low for both experiments. The Corning soil extractable nitrogen levels (Table 3) were comparable to those for soils of California annual grasslands (Gulmon 1979, Davidson et al. 1990), an unvegetated granitic road cut slope in Northern California (Claassen and Zasoski 1993), and a low nutrient grassland in Greece (Mamolos et al. 1995). According to soil analyses (A&L Laboratories, Fresno, California,) phosphorus levels were low for the 0-10 cm sample and high for the 20-30 cm sample with a minimum of 20 ppm recommended for average crop production. Potassium levels were low for the 1-10 cm sample and medium for the 20-30 cm sample. At the time of harvest, container extractable nitrogen levels were 0.57 ppm for light texture and 2.88 ppm for heavy texture soils in 1994; in 1995 they were 2.56 ppm and 5.15 for light and heavy texture soils, respectively. The available soil nutrient levels were, therefore, not abundant in the field experiment and deficient in the container experiment where rooting volume was restricted.

Table 3. Summary of soil nutrient analysis results. Soils were taken from the west end of the area used for the field experiment. The same soil was sieved and used for the heavy texture soil and mixed with equal parts of sand to create the light texture soil for the container experiment.

Sample	% Organic matter	Available ppm-P	ppm-K	ppm-Mg	ppm-Ca	ppm-Na	pH	C.E.C. meq/100g	ppm-NO ₃	ppm-S	ppm-Zn	ppm-Mn	ppm-Fe	ppm-Cu	ppm-B	Soluble salts mmhos/cm
0-10 cm	0.2	17	89	697	2600	89	7	20.9	2	3	0.6	11	11	1.1	1.6	0.5
20-30 cm	0.8	35	202	515	3220	35	7	21	9	8	2.2	17	24	0.9	2.2	0.2

Statistical analyses

Qualitative conclusions from statistical analyses with some discussion of specific statistical results have been presented in the Results and Discussion section. More technical discussion of the statistical analyses including univariate and multivariate analysis of variance tables can be found in Brown 1998. Descriptions of the statistical tests used follow.

Soil water potential.--- Univariate analysis of variance with repeated measures (ANOVA) and multivariate analysis of variance with repeated measures (MANOVA) with univariate and multivariate contrasts were conducted on soil water potential data. The assumption of sphericity was met marginally only by the 1994 spring container data (Mauchly's criterion $p=0.0522$), so the adjusted ANOVA (Greenhouse-Geisser [G-G]) and MANOVA (Wilks' lambda) results were reported (von Ende 1993). Using both univariate and multivariate results was suggested to be "a safe option" for repeated measures analyses (von Ende 1993).

In the 1994 container experiment, the soil water data collected between March and the June harvest of three replicates (spring data) were analyzed separately from those collected between June and September (summer data). In the 1994 field experiment data, 26 out of 768 (3.3%) measurements were missing values due to psychrometer malfunction. Missing values were estimated using a full factorial ANOVA model including all independent variables and the existing data set (Neil Willits personal communication). This procedure of estimating missing values allowed estimation of

means and orthogonal contrasts that would not have been possible otherwise and did not appreciably change the statistical results. Missing values were not estimated for the container experiment data for either year.

For the 1995 container experiment, results from adjusted repeated measures ANOVA and repeated measures MANOVA of soil water potential data from the container experiment agreed at the alpha level of 0.05 for twelve of the fifteen main effects and interactions of within-subject factors. In cases where they differed, trends ($P < 0.1$) indicated agreement. Results from both analyses are reported.

Root length density.---We plotted the log of root length density against depth for each species plot or container and then fit a line using simple linear regression to the data points (Appendix 1). The slope of the regression line was analyzed with ANOVA. The slope represents an integrated measure of rooting pattern; species that have a larger proportion of their roots in shallow soil layers will have greater slopes than species that have a larger proportion of their roots in deep soil layers. Due to lack of equality of variances in the data sets, the slopes were log transformed for the container 1994 data analysis and rank transformed for the field 1994 data analysis. Transformation was not necessary for the assumptions of ANOVA to be met by the container 1995 data.

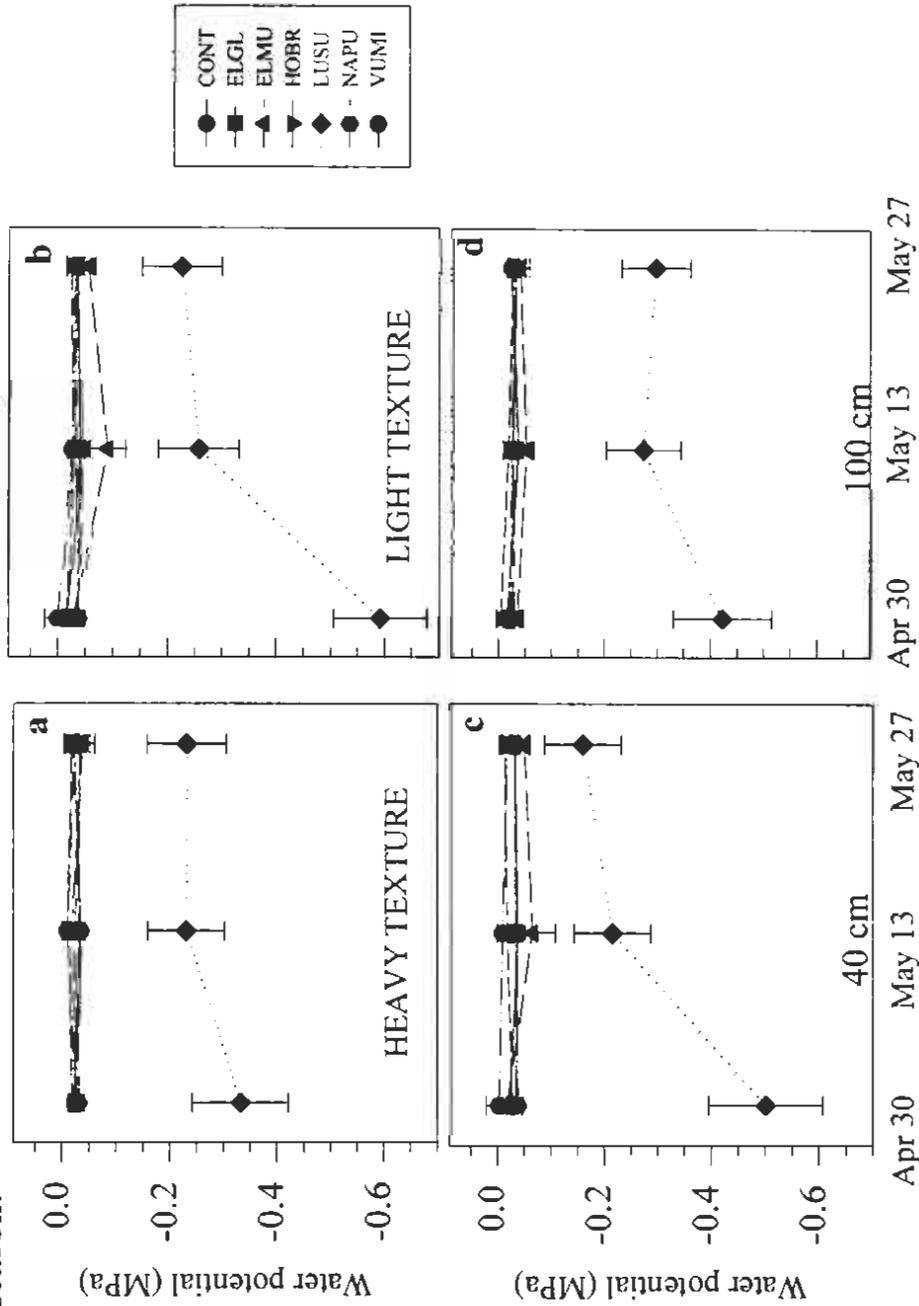
RESULTS AND DISCUSSION

Species and guild effects on soil water potential

Container 1994.---During the spring, differences between species in soil water use over time depended on soil texture treatment and soil depth. When measurements commenced, *L. succulentus* soil was drier (lower water potentials) within the light texture soil treatment than within the heavy texture soil treatment (Fig. 1a, b). By the second sampling date rainfall had restored the two soil texture treatment levels to the same water potential. The interaction between time, texture and species reflects this variation in response of *L. succulentus* ($P < 0.05$). The soil for other species and the no plant control remained moist (water potentials close to zero).

During the early part of the growing season, *L. succulentus* soil was about as dry at 40 cm as it was at 100 cm (between -0.45 and -0.50 MPa). When it rained in May, the soil became wetter at 40 cm (-0.15 MPa) than at 100 cm (-0.30 MPa) (Fig. 1c,d). Soil remained moist for other species and the no plant control (i.e. water potentials remained near zero) throughout the period. The response of *L. succulentus* resulted in a significant statistical interaction between time, depth and species during the early part of the growing season ($P < 0.05$). The response of *L. succulentus* also drove the observation that during spring, when species within functional groups were considered together, soil water use by early-season species differed from mid- and late-season species (Fig. 1c, d). For early-season species.

Figure 1. Data from the container study in spring 1994 showed that light texture soils with LUSU were drier than heavy texture soils and soils were drier at 40 cm than 100 cm. Soil water potentials in both textures and at both depths increased (became wetter) with late spring rains near the end of the LUSU growing season.



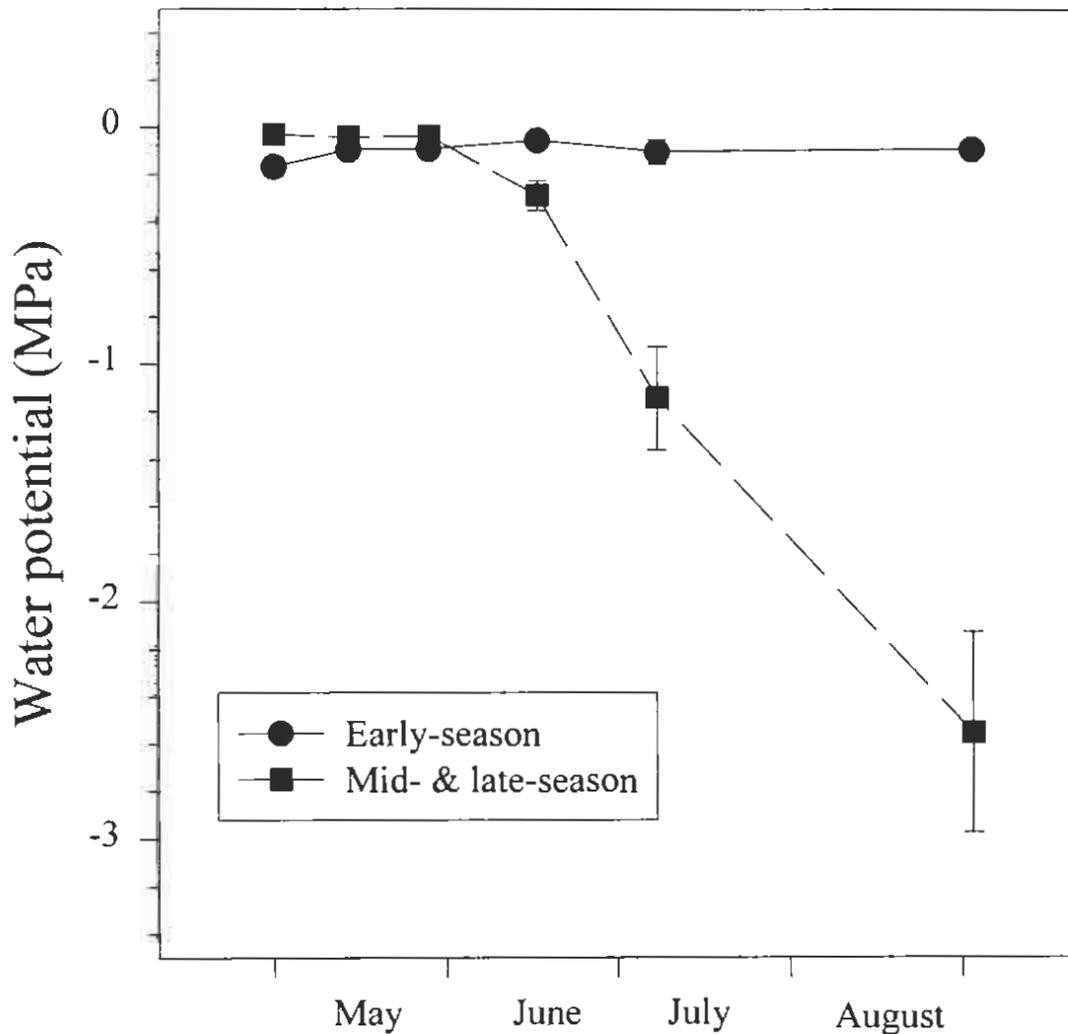
Soil water potential plot of the interactions between time, soil texture and species (a and b) and between time, depth and species (c and d) for the spring 1994 container experiment (means \pm standard error). CONT = no plant control, ELGL = *E. glaucus*, ELMU = *E. multisetus*, HOBR = *H. brachyantherum*, LUSU = *L. succulentus*, NAPU = *N. pulchra*, VUMI = *V. microstachys*. Wet soil = 0 MP; water potential becomes more negative as soil dries.

most notably *L. succulentus*, when it rained in the late spring, the soil became moist faster at 40 cm than at 100 cm. However, soil remained moist throughout the period for mid- and late-season species (water potentials near 0). Note differences in size between grasses and legumes in the photograph a on page 80.

By examining the response of species functional groups over time, without considering soil texture or depth, we can see how the groups differed in their water use patterns. Early-season and mid- and late-season species differed in timing and extent of soil water depletion during the spring and summer (Fig. 2). Early-season species completed growth in May. Since the plants were not removing water from the soil, late spring rainfall caused soil water potentials for early-season species (*H. brachyantherum*, *L. succulentus* and *V. microstachys*) to increase (i.e. the rain re-wet the soil). Mid- and late-season species did not begin growing quickly until May, so soil water potentials for mid- and late-season species (*E. glaucus*, *E. multisetus* and *N. pulchra*) remained relatively constant near zero (moist soil) during the early spring. Subsequently, during the summer, mid- and late-season species extracted soil water, decreasing soil water potentials (drying the soil). The soil in the containers of early-season species and the no plant control remained moist (i.e. water potentials were near zero). The statistical results demonstrating these effects were significant interactions between time and the linear contrast between early-season and mid- and late-season species for spring (Wilks' lambda $P = 0.003$, G-G $P = 0.0009$) and summer (Wilks' lambda $P = 0.0016$, G-G $P = 0.0002$).

Figure. 2 Early-season species used soil water (soil water potentials became more negative) during the spring. Mid- and late-season species dried soil during the summer.

Container 1994



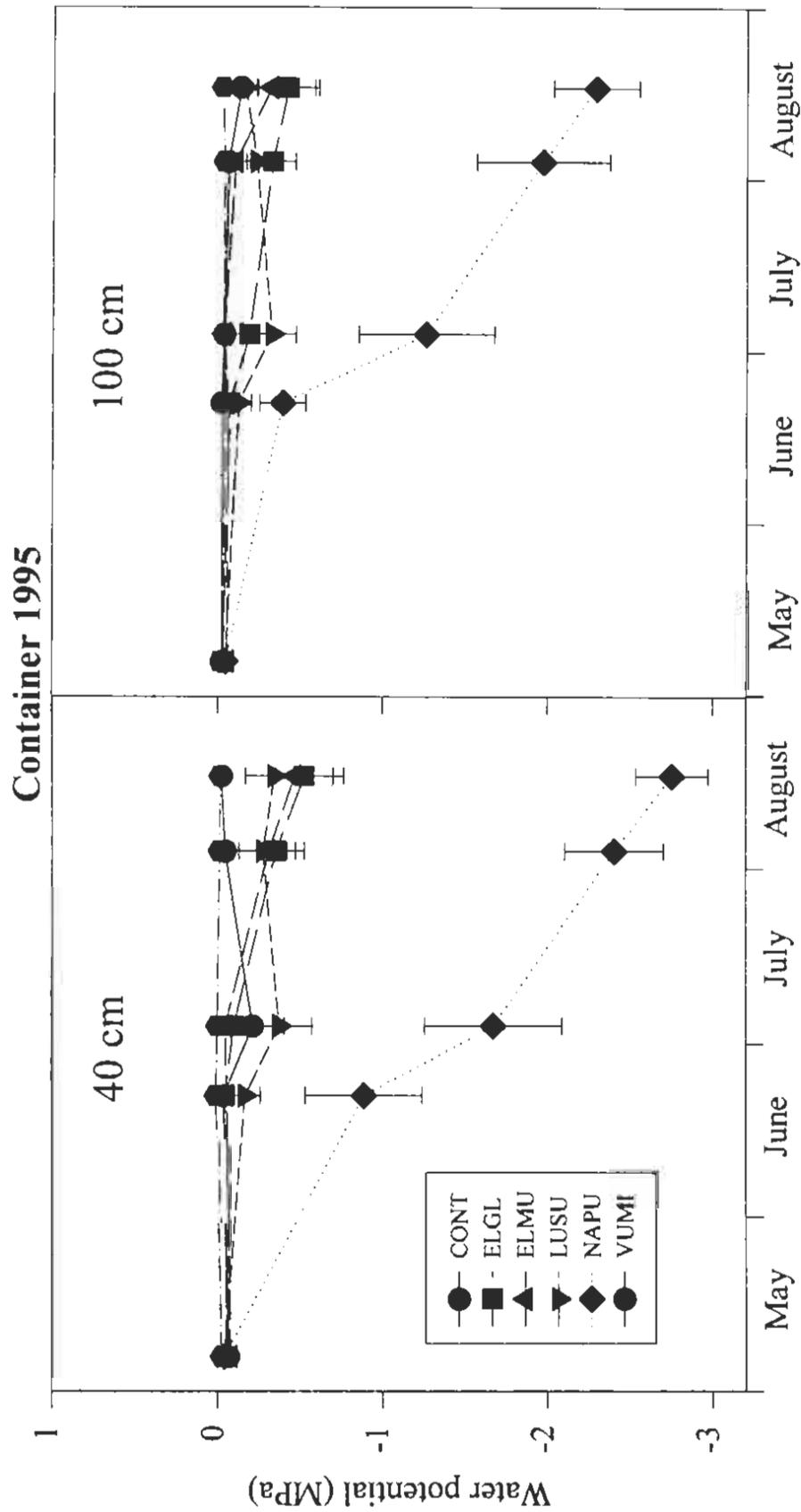
Soil water potential plot of the interaction between time and the contrast between mid- and late-season species (*E. glaucus*, *E. multisetus*, and *N. pulchra*) and early-season species (*H. brachyantherum* ssp. *brachyantherum*, *L. succulentus* and *V. microstachys*) for the 1994 container experiment (means \pm standard error of the mean). Error bars that appear to be missing are smaller than the point on the graph.

Container 1995.---Species differed in their patterns of soil water depletion with depth, time and soil texture in 1995. The mid- and late-season species, *E. glaucus*, *E. miltisetus* and *N. pulchra* reduced soil water more (i.e. more negative water potentials) than the early-season species *L. succulentus* and *V. microstachys* at both depths, but slightly more so at 40 cm than 100 cm (Fig. 3 and 4). The mid- and late-season perennial grasses depleted soil water up to the time of harvest in June in contrast to early-season annual species *L. succulentus* and *V. microstachys* that had water potentials near zero (i.e. moist soil) by June. Perennial grasses were more similar in size to legumes in the second growing season, as can be seen in photograph b on page 80.

The soil of the early-season native annual grass *V. microstachys* remained wet (i.e. water potential near zero) throughout the entire experiment, similar to the no plant control. This reflects the small size of plants growing under low soil nutrient levels. The differences between species in timing and extent of soil water use at 40 cm compared to 100 cm were indicated by the significance of the three-way interaction between depth, time and species (Wilks' lambda $P = 0.0004$, G-G $P = 0.0067$) and by the significance of the interaction between the contrast mid- and late-season vs. early-season species and the within-subject factors (repeated measures) of depth and time (Wilks' lambda $P = 0.0003$, G-G $P=0.053$)(Fig. 4).

Field 1994.---Field plots are pictured early (c) and late (d) in the growing season on page 80. Species differences in water use varied over time and between depths as indicated by significant statistical interactions between time, depth and species (Wilks'

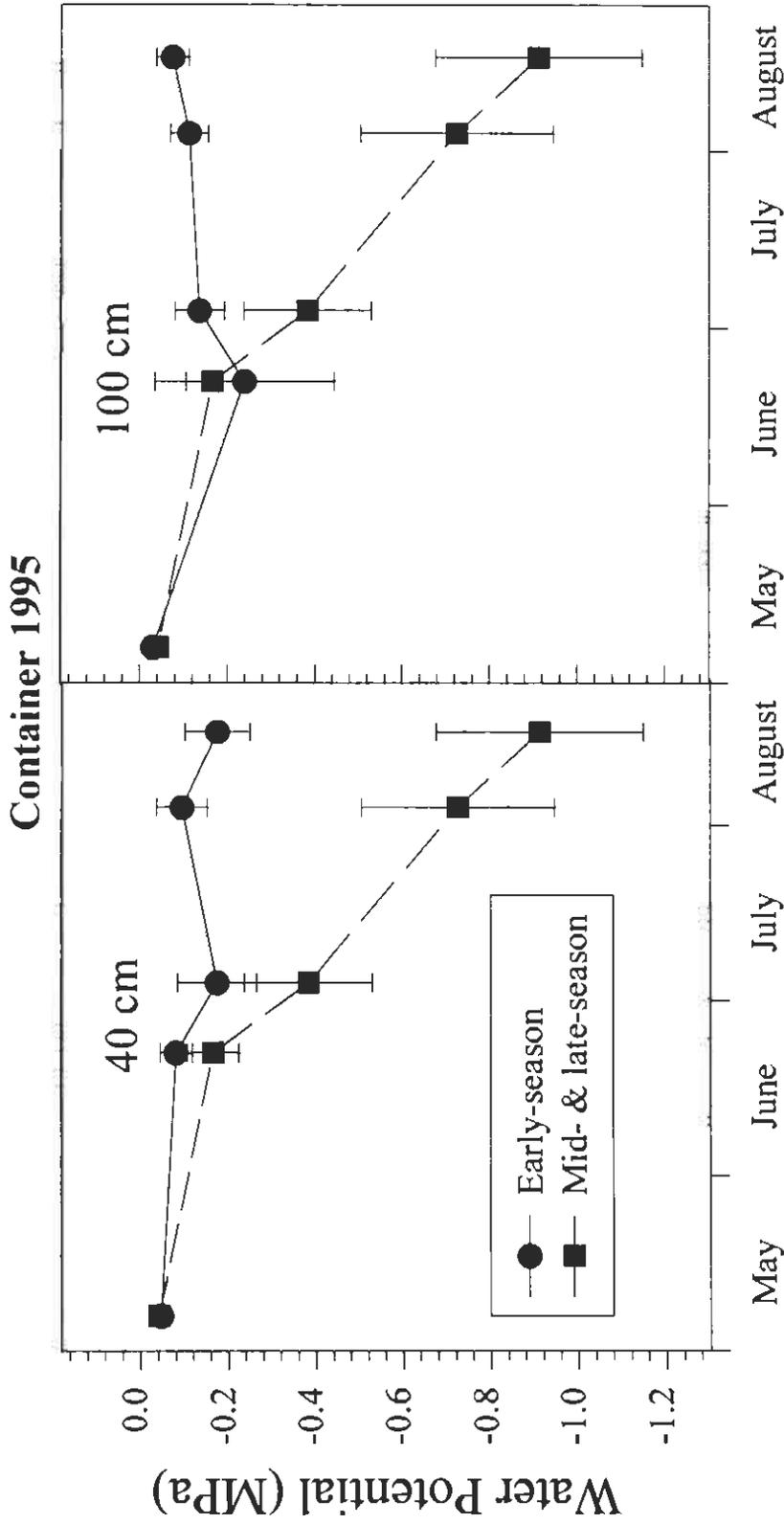
Figure. 3 The timing and extent of water use differed between species and depths.



Soil water potential plot of the interaction between time, depth and species for the 1995 container experiment (means \pm standard error of the mean). CONT = no plant control, ELGL = *E. glaucus*, ELMU = *E. multisetus*, LUSU =

L. succulentus, NAPU = *N. pulchra*, VUMI = *V. microstachys*.

Figure 4. Water use of mid- and late-season and early-season species differed in space and time. Mid- and late-season species reduced soil water (water potentials became more negative) throughout the summer at both depths, whereas, early-season species used soil water primarily during the spring at shallow depths.



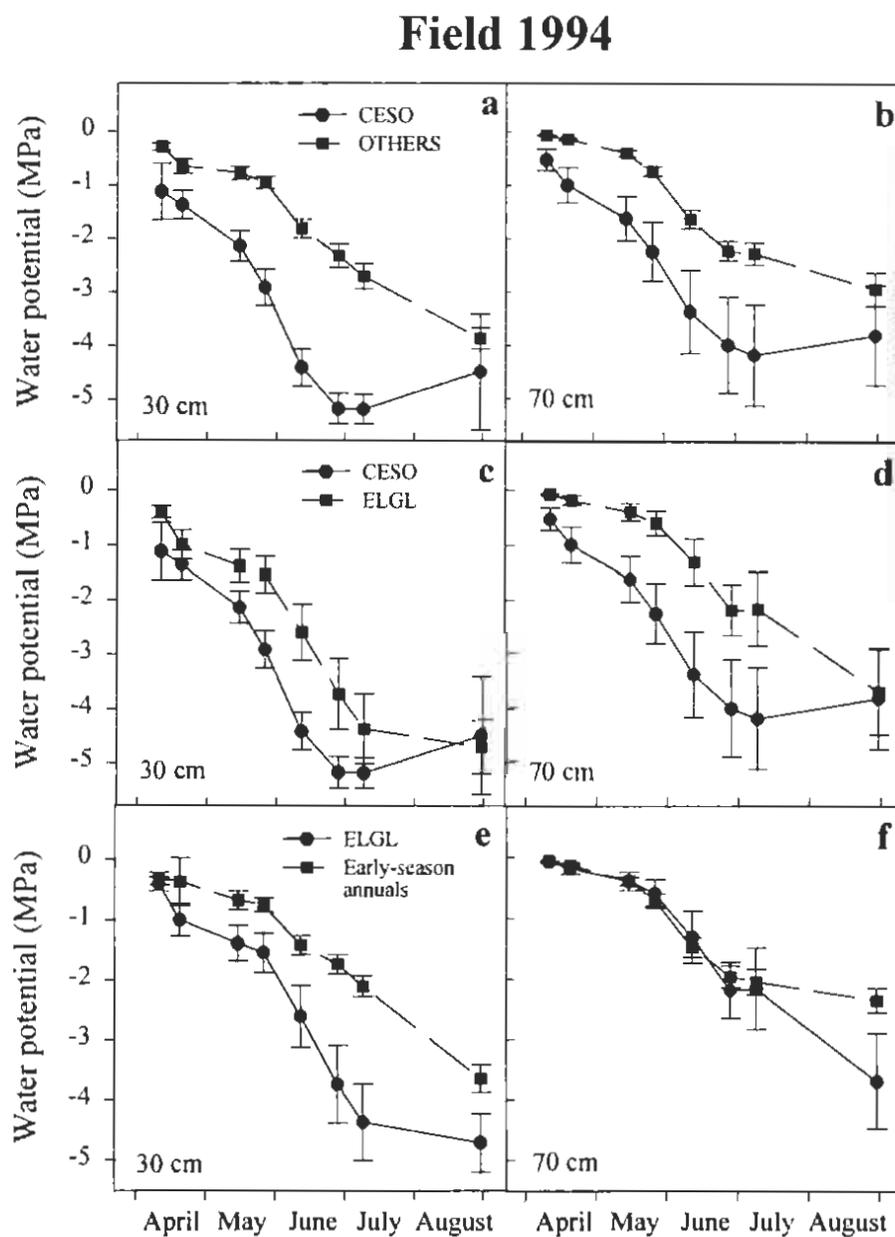
Soil water potential plot of the interaction between time, depth and the contrast between mid- and late-season species (*E. glaucus*, *E. multisetus*, and *N. pulchra*) and early-season species (*L. succulentus* and *V. microstachys*) for the 1995 container experiment (means \pm standard error of the mean).

lambda and G-G $P < 0.01$). *Centaurea solstitialis* dried soil to a much greater extent and more rapidly than the other species, resulting in very differently shaped depletion curves for *C. solstitialis* and other species at both depths (Fig. 5a, b). In addition, *C. solstitialis* dried soil to -5.0 MPa at 30 cm and about -4.0 MPa at 70 cm by July, whereas, other species did not deplete soil moisture to comparable levels until September.

Centaurea solstitialis removed water from soil more rapidly than *E. glaucus* at both depths (Fig. 5c, d). Soil water potentials in *C. solstitialis* plots were reduced to their lowest levels (driest) (approximately -5.0 MPa at 30 cm and -4.0 MPa at 70 cm) two months before *E. glaucus* plots. *Elymus glaucus* dried soil to a greater extent and more rapidly than the annual species at 30 cm, although water potentials at the final date of measurement were not greatly different (Fig. 5e, f). At 70 cm, *E. glaucus* appeared to have depleted soil water at the same rate as annuals through May. After that time, *E. glaucus* continued to use water at a similar rate while the annuals stopped taking up water when they completed their life cycles. Continued soil water use during the summer in early-season species plots may be due to summer weeds since roots were not excluded from the water potential sampling area (see *Field experiment limitations* section below).

Overall, plants from different functional groups exhibited spatial and temporal differences in soil water utilization. The differences described were based on statistical tests called orthogonal contrasts that compared the taxa (species or groups of species), water use by depth and water use over time. Statically significant differences ($P < 0.05$)

Figure 5. Individual species and groups of species with particular characteristics (functional groups) used soil water differently in space and time.



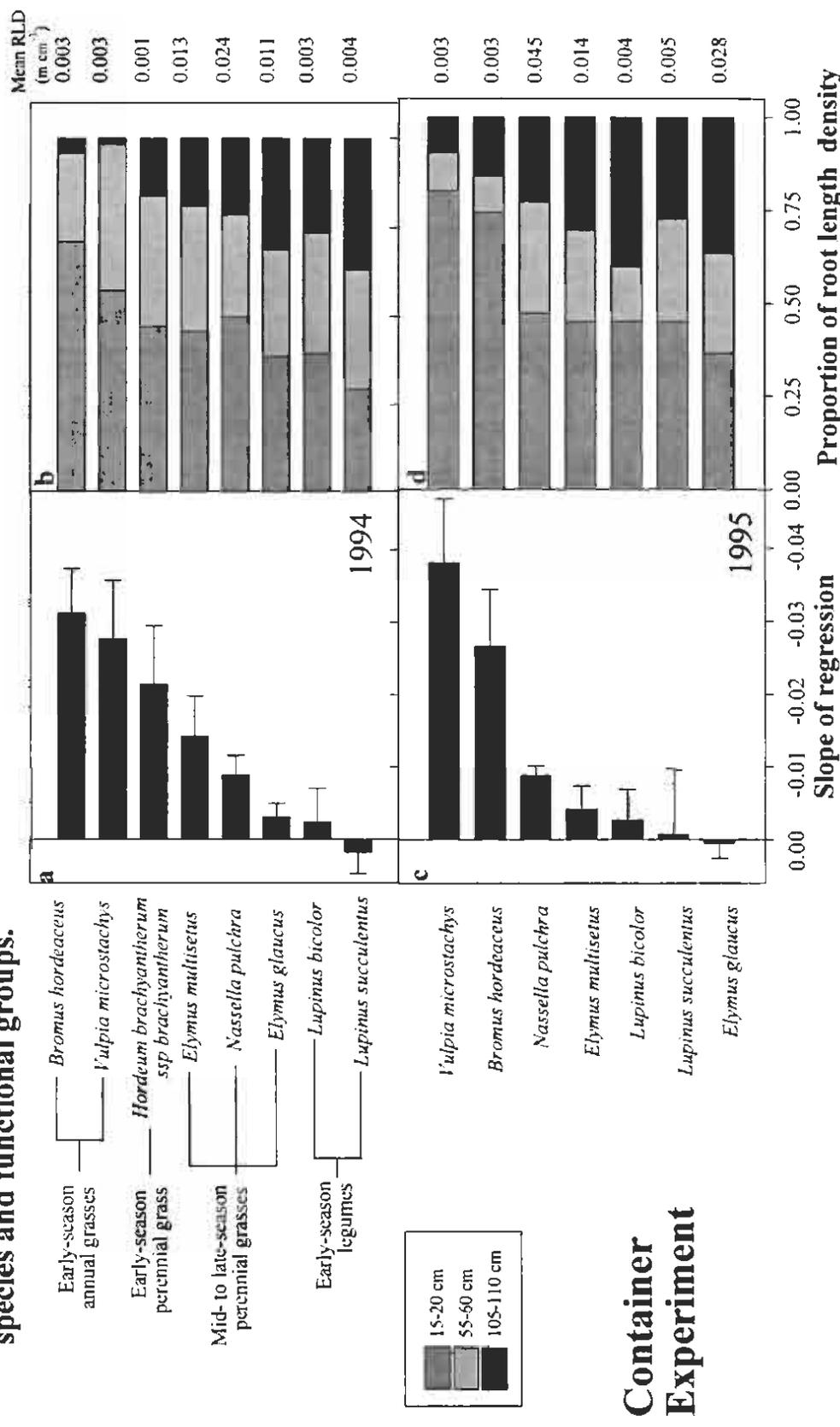
The plot of soil water potential over time at two depths shows the interactions between time, depth and the contrast between *C. solstitialis* (CESO) and the remaining species (a and b), between *C. solstitialis* (CESO) (c and d), and between *E. glaucus* (ELGL) and the early-season annual species (*L. succulentus*, *V. microstachys* and *V. myuros*)(e and f) for the 1994 field experiment (means \pm standard error).

were found between (1) *C. solstitialis* and other species, (2) *E. glaucus* and annual species and (3) *E. glaucus* and *C. solstitialis* as described above.

Species and functional group root length density

Container 1994 and 1995.---Mid- and late-season grasses and early-season legumes had more evenly distributed roots than early-season grasses in both years ($P < 0.001$). As described in the Methods section, the variable analyzed was the slope of the regression of root length density on depth for each species (see Chapter 2 Appendix 1 page 88). Steeper slopes indicated that a species had a high proportion of shallow roots. Less steep slopes indicated that a species had a higher proportion of deep roots. Early-season annual and perennial grasses had the steepest slopes (means ranged from -0.02 to -0.03 in 1994 and from -0.03 to -0.04 in 1995), i.e. they had relatively more roots in shallow layers of the soil than other species. The mid- and late-season perennial grasses and early-season legumes had less steep slopes (means ranged from 0.001 to -0.01 in 1994 and 0.0001 to -0.01 in 1995), i.e. more evenly distributed roots (Fig. 6a, c). These results were confirmed by significant linear contrasts comparing early-season species to mid- and late-season species ($P < 0.001$ in 1994, $P = 0.01$ in 1995). The proportion of root length densities at each depth are shown in Figs. 6b and 6d. The total root length densities are listed and show that in the first year of growth, for the depths measured, the perennial grasses had greater root length densities than the annual species (Figs. 6 b, d).

Figure 6. Root length distributions and slopes of regressions of root length distribution on depth for species and functional groups.



Container Experiment

The slope of the regression of root length density against depth for the container experiment in 1994 and 1995 means \pm standard error of the mean (a and c, respectively). The greater the slope, the greater the proportion of roots in shallow layers of soil. Species with smaller slopes have more evenly distributed roots. The proportion of roots at each depth are plotted for each species for the 1994 and 1995 container experiments (b and d, respectively). The species with the largest slopes for the regression of root length density against depth are at the top of these graphs.

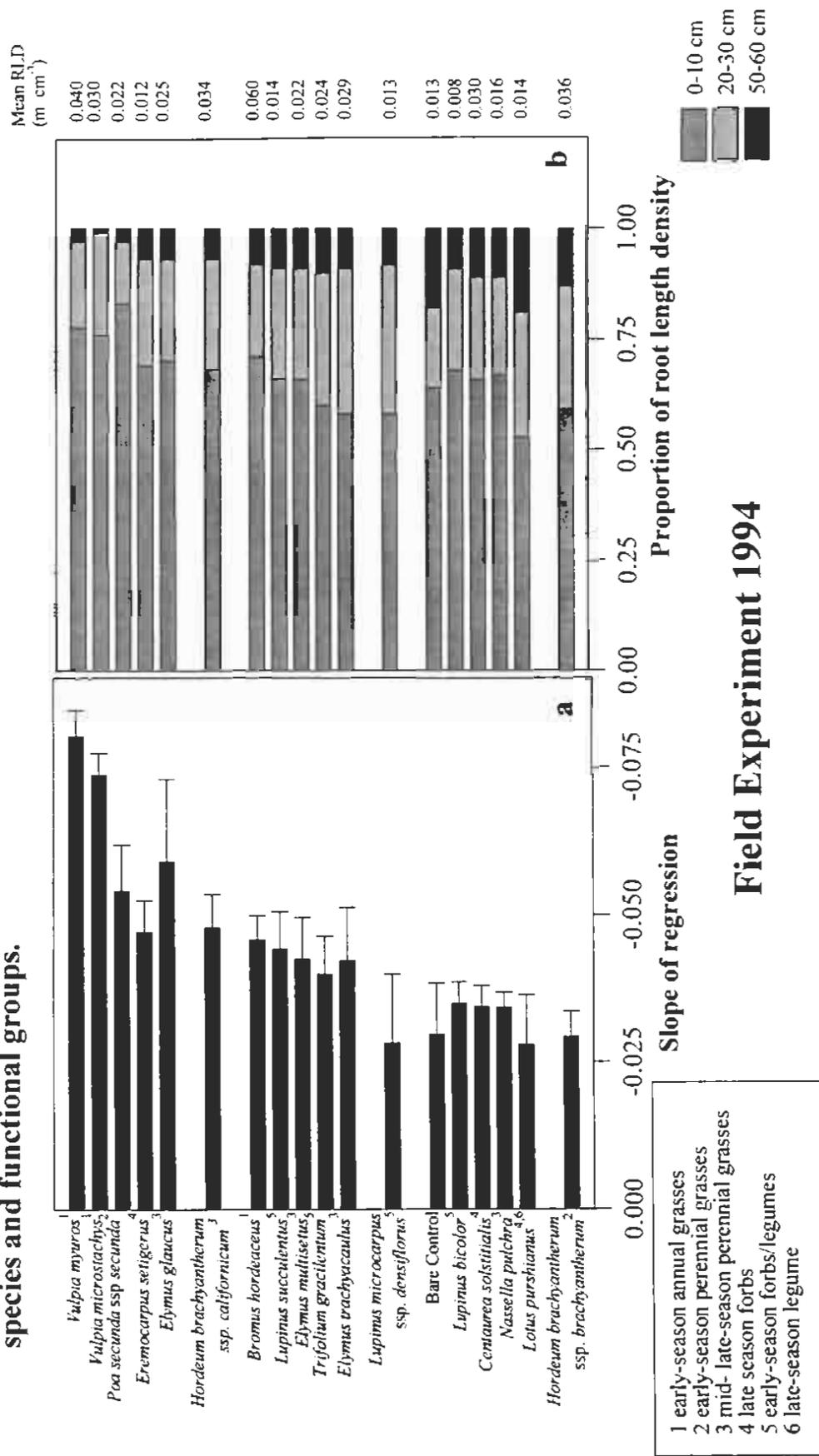
Not only did early-season species have relatively more shallow roots than mid- and late- season species, but annual grasses had a significantly higher proportion of their roots in shallow soil depths than perennial grasses. Linear contrasts detected significantly greater slopes of annual grasses compared to perennial grasses ($P < 0.001$ both years). These results show that annuals and early-season species had much higher proportions of roots in shallow soil layers and that perennials and mid- and late-season species had more evenly distributed roots.

Field 1994.---Similar to the container study, species differed from one another in their root length distributions in the field experiment ($P = 0.0001$)(Fig. 7a). Overall, mid- and late-season species had more evenly distributed roots than early-season species (linear contrast $P = 0.008$). Perennial grasses also had more evenly distributed roots than annual grasses, which concentrated their roots in shallow soil layers ($P = 0.0001$). Relative root length densities at each depth for each species illustrate that the root length distribution of species differed (Fig. 7b). Although no vegetation was allowed to grow above ground in the control treatment plots, measureable root length densities were found due to lateral root growth of plants adjacent to the cleared area. No effects of fertilizer treatment were detected.

Soil texture effects

The effects of soil texture on soil water was significant only in interaction with depth. When there were responses to soil texture, water potential of the light texture soil was usually reduced sooner and to a greater extent than the heavy texture soil. Most

Figure 7. Root length distributions and slopes of regressions of root length distribution on depth for species and functional groups.



(a) The slope of the regression of root length density against depth for the field experiment in 1994 (means \pm standard error of the mean). The greater the slope, the greater the proportion of roots in shallow layers of soil. Species with smaller slopes have more evenly distributed roots. (b) The proportions of roots at each depth are presented. The species with the largest slopes for the regression of root length density against depth are at the top of the graphs.

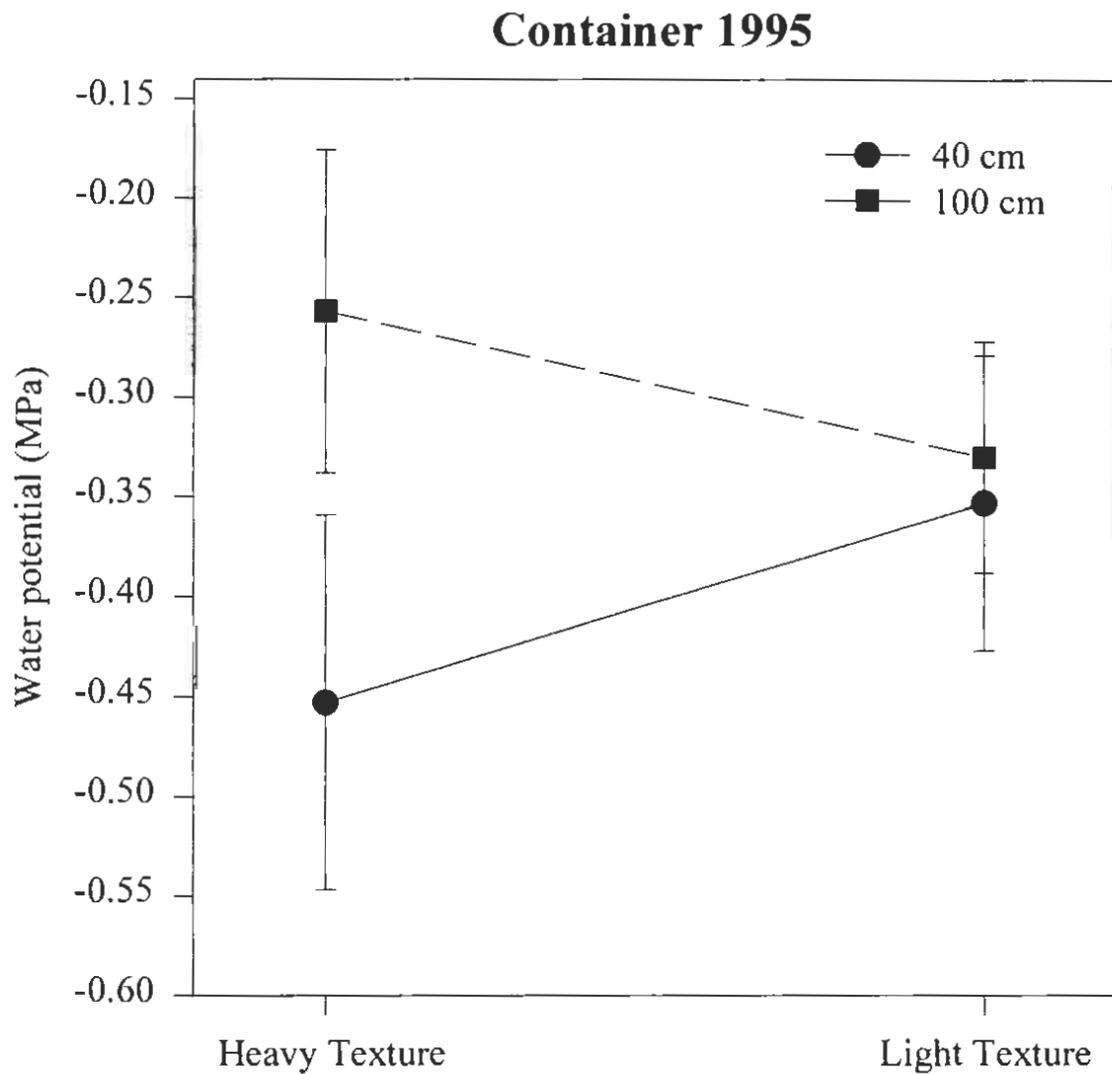
species reduced soil water potentials similarly at the two depths in the light texture soil treatment but depleted soil water more (lower water potentials) at the shallow depth than the deep depth in the heavy texture soil treatment. Soil water potential was lower (drier) at 40 cm than at 100 cm in the heavy texture soil treatment while the light texture soil treatment had similar water potentials at both depths. This resulted in a significant depth by texture interaction ($P = 0.02$) (Fig. 8). Overall, soil water was depleted from light texture soil more evenly across depths than the heavy texture soil. Also, soil water was depleted and recharged at 40 cm before 100 cm.

Soil texture affected root length density distribution only in 1994 when higher proportions of roots were found in shallow layers of heavy texture soil than light texture soil. Slopes of the regressions of log root length density on depth were greater in heavy texture soil than light texture soil ($P = 0.0118$). This response may have been due to the greater availability of nutrients and water at shallow depths of heavy texture soil relative to light texture soil that reduced the need for plants to explore deeper layers. Also, the heavy texture soil may have reduced root growth due to physical properties that increased impedance.

Soil nitrogen fertilizer effects

There were no detectable effects of soil nitrogen treatments on soil water use and root length densities. Although we could not see differences in aboveground growth between nitrogen treatments in 1994, when nitrogen fertilizer was applied again in 1995

Figure 8. Soil water potentials were lower at shallow depths in heavy texture soil while the light texture soil had similar water potentials at both depths.



Soil water potential plot of the interaction between soil texture and depth for the 1995 container experiment (means \pm standard error of the mean).

differences between the two treatments were obvious (Brown, personal observation). This suggests that we did not add enough fertilizer in 1994 to elicit responses from species that may have been readily apparent had the nitrogen fertilizer level been greater. However, it is possible that at higher nitrogen fertilizer levels, differences between species may have become less apparent as discussed below.

Effects of low inherent soil fertility

The low nutrient conditions, which were extreme in the container experiment, had significant effects on plant growth. In the field experiment, plant growth was not stunted. However, in the container experiment, there were large differences between species in response to low nutrient levels and individual annual grasses were extremely small in size. These annual species used very little water and their root systems were not fully developed. As a result, we probably were not able to characterize their patterns of soil water use and root distribution completely. In contrast, early-season annual legumes were large in size in the containers, which can be attributed to the ability of these species to fix atmospheric nitrogen, and thereby overcome the problem of limited soil nitrogen. Although the perennial grasses had much greater biomass than the annual grasses, they showed signs of nutrient deficiency including purple streaks on the leaves (P deficiency) and lack of reproduction in small individuals.

The low nutrient environments in our experiments prevent us from extrapolating to fertile sites and make it difficult to compare the extent of resource use between species. Undoubtedly individuals of all species would grow larger both above- and belowground

in higher nutrient conditions and soil water depletion would be more complete. Despite this, we observed important differences between the species and guilds in resource use that may not have been as apparent if nutrients had been more abundant. Greater resource availability sometimes results in decreased competition between species, although neither experimental evidence nor ecological theory agree whether competition is most severe when resources are abundant or limited (Tilman 1982, 1987, 1988, Welden and Slauson 1986, Campbell et al. 1991, Grime et al. 1991, Hardison 1991, Grace 1993, Grime 1993). Regardless of the disagreement, variation in the responses of species to competition often depend on the availability of resources and, in some cases, decrease as resources become abundant (Donald 1961, Inouye et al. 1980). Thus, niche separation may be reduced when resources are abundant.

Container experiment limitations

In the container experiment, harvests were made in June, well after annual species had senesced. The moist soil conditions and warm weather may have contributed to some decomposition of dead roots which, in turn, may have resulted in underestimation of absolute root length densities for these species. We expect decomposition to have been most rapid in the more aerated shallow soil layers, which would lead to an underestimation of root length density at that depth. If this were the case, our conclusions are conservative because slopes for the annuals are smaller than they would be without decomposition, making it more difficult to detect differences between the root distribution patterns of species.

Field experiment limitations

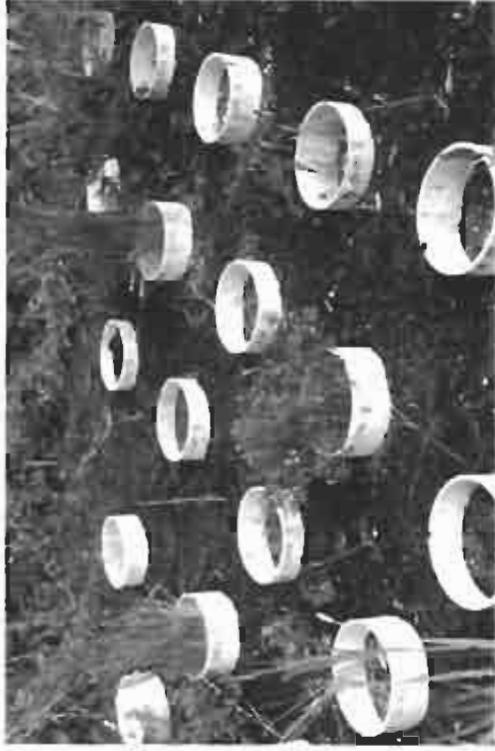
One of the limitations of our methods was that we sampled roots only once during the growing season which was the optimal time for characterizing the root systems of some species but not others. The field experiment sampling was conducted during March and April, which was very early in the growing season for the late-season species *C. solstitialis*, *E. setigerus* and *L. purshianus*. Although most *C. solstitialis* seedlings emerged in the late fall with the grasses, *L. purshianus* and *E. setigerus* did not emerge until late December and March, respectively (Brown, personal observation). Nonetheless, it is notable that even at such an early stage these species had root length densities comparable to other species.

The soil water potentials and slopes for the regression of root length density against depth for the plant-free control were not strongly different from the other species according to orthogonal contrasts ($P=0.06$ and 0.13 , respectively)(Also see Fig. 7 and Appendix 1). This was due to the fact that, even though we removed volunteer plants from the control plots, we did not exclude roots entering from adjacent plots. It is also possible that weeds affected the water potential values measured in species plots as well because only 1 m² around each psychrometer and root sampling sites was weeded. *Convolvulus arvensis* L. (field bindweed) was a particular problem because it was common and difficult to control. Its rhizomatous habit may have contributed to its ability to affect soil water potential readings and root length density measurements.

Monoculture Experiments



a. Container experiment April 30, 1994
Note relative size of legumes and grasses



b. Container experiment April 29, 1995
Note increase in size of perennial grasses relative to legumes



c. Field experiment February 2, 1994



d. Field experiment June 10, 1994

CONCLUSIONS

The grassland plant species we used in our experiments differed substantially in their spatial and temporal patterns of belowground resource use. Furthermore, particular patterns corresponded to species guilds (groups of species associated by phenological, taxonomic and life-history traits). The data suggest the possibility of niche separation and the potential for these guilds to partition belowground resources in space and time. Niche separation, as suggested Gause's competitive exclusion principle, may be a major force in reducing competition among species guilds and facilitating coexistence in California grasslands.

Niche separation may confer the ability to share resources rather than to compete directly for them. If niche separation can function as a mechanism of community assembly, species with divergent resource use patterns should form more stable plant communities, while species with similar resource use patterns should form less stable communities. If so, we should be able to predict the relative stability of mixtures *a priori*, as tested in experiments reported in the following chapter.

MANAGEMENT IMPLICATIONS

Including species with a variety of resource use patterns may lead to more successful revegetation for erosion control due to decreased competition for resources among species. In Table 4 the species included in this study have been ranked according to the percentage of root length density at the deepest depth measured and RLD slope, a

measure of relative distribution of root length density at different depths. These rankings may be used to select deep or shallow rooted species that will be able to partition their resources in space. Table 4 also indicates the phenological group for each species, which will allow designers to select species that may be able to partition their resources in time.

For erosion control applications, it is important to take into consideration the potential ability of different species to hold soil in place. The density of roots produced by a species is related to its ability to slow erosion; greater RLD will provide superior erosion control. As listed in Table 4, perennial grasses had slightly lower amounts of total RLD (sum of RLD at three depths) than annual grasses in the first year in the more fertile field experiment, but greater total RLD in the less fertile container experiment. In the second year perennial grasses had substantially greater total RLD than annual grasses. The ability of perennial grasses to accumulate root length density over time, especially in low nutrient conditions, is an important benefit of these species. Native perennial grasses should be included in erosion control seed mixtures to realize these long-term benefits.

Table 4. List of species according to functional groups including season of growth, whether each is native or introduced to California, percent root length density (RLD; length of root per volume of soil) at the deepest depth sampled (55-60 cm in container experiment and 105-110 cm in field experiment), slope of RLD and total RLD for the three depths sampled. Slope of RLD is a measure of the distribution of RLD across the three depths (See Chapter 2 Appendix 1, page 89). The closer the slope is to zero, the more evenly distributed the roots. Negative slopes indicate a greater proportion of roots are in shallower soil layers. Positive slopes indicate a greater proportion of roots are in deep soil layers (*L. succulentus* only).

Species are ranked by the percentage of roots at the deepest depth and the slope of RLD. The species with the highest RLD at the deepest depth measured and the smallest slope was assigned the rank of 1; the species with the lowest RLD at the deepest depth and the largest slope was assigned 7 for the container experiment and 14 for the field experiment. Ties were assigned the same rank.

Early-season species flower April through May. Mid-season species flower May through June. Late-season species flower June through August.

GROUP	SPECIES	ORIGIN	% RLD AT DEPTH		RLD SLOPE		DEEP ROOTED RANK		TOTAL RLD (m cm ⁻²)		
			cont	field	cont	field	cont	field	cont	field	
Early-season Perennial grasses	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>	native	16.0	13.0	-	-0.03	5	2	0.001	0.036	-
			-	3.0	-	-0.05	-	13	-	0.022	-
			33.8	7.0	-0.002	-0.06	2	11	0.011	0.025	0.028
Mid- and late-season Perennial grasses	<i>Elymus glaucus</i>	native	24.6	9.0	-0.0092	-0.04	4	7	0.013	0.022	0.014
			-	9.0	-	-0.04	-	6	-	0.029	-
			-	7.0	-	-0.05	-	10	-	0.034	-
	<i>Hordeum brachyantherum</i> ssp. <i>californicum</i>	native	-	-	-	-	-	-	-	-	
	<i>Nassella pulchra</i>	native	22.1	11.0	-0.009	-0.03	4	3	0.024	0.016	0.045

Table 4 continued

Early-season annual grasses	<i>Vulpia microstachys</i>	native	5.6	1.0	-0.033	-0.07	7	14	0.003	0.03	0.003
	<i>Vulpia myuros</i>	exotic	-	3.0	-	-0.08	-	14	-	0.04	-
	<i>Bromus hordeaceus</i>	exotic	10.1	8.0	-0.029	-0.04	6	9	0.003	0.06	0.003
Early-season annual legumes	<i>Lupinus bicolor</i>	native	-	33.0	-0.0025	-0.03	3	5	0.003	0.008	0.004
	<i>Lupinus microcarpus</i> ssp. <i>densiflorus</i>	native	-	8.0	-	-0.03	-	6	-	0.013	-
	<i>Lupinus succulentus</i>	native	-	37.1	-	0.0005	1	8	-	0.014	0.005
	<i>Trifolium gracilentum</i>	native	-	10.0	-	-0.04	-	6	-	0.024	-
Late-season annual legume	<i>Lotus purshianus</i> *	native	-	19.0	-	-0.03	-	1	-	0.014	-
	<i>Centaurea solstitialis</i> *	exotic	-	11.0	-	-0.03	-	4	-	0.03	-
Late-season annual forbs	<i>Eremocarpus setigerus</i> *	native	-	7.0	-	-0.05	-	12*	-	0.012	-

*Values are not representative of peak growing season for this species because samples were taken in the spring and this species grows primarily in the summer.

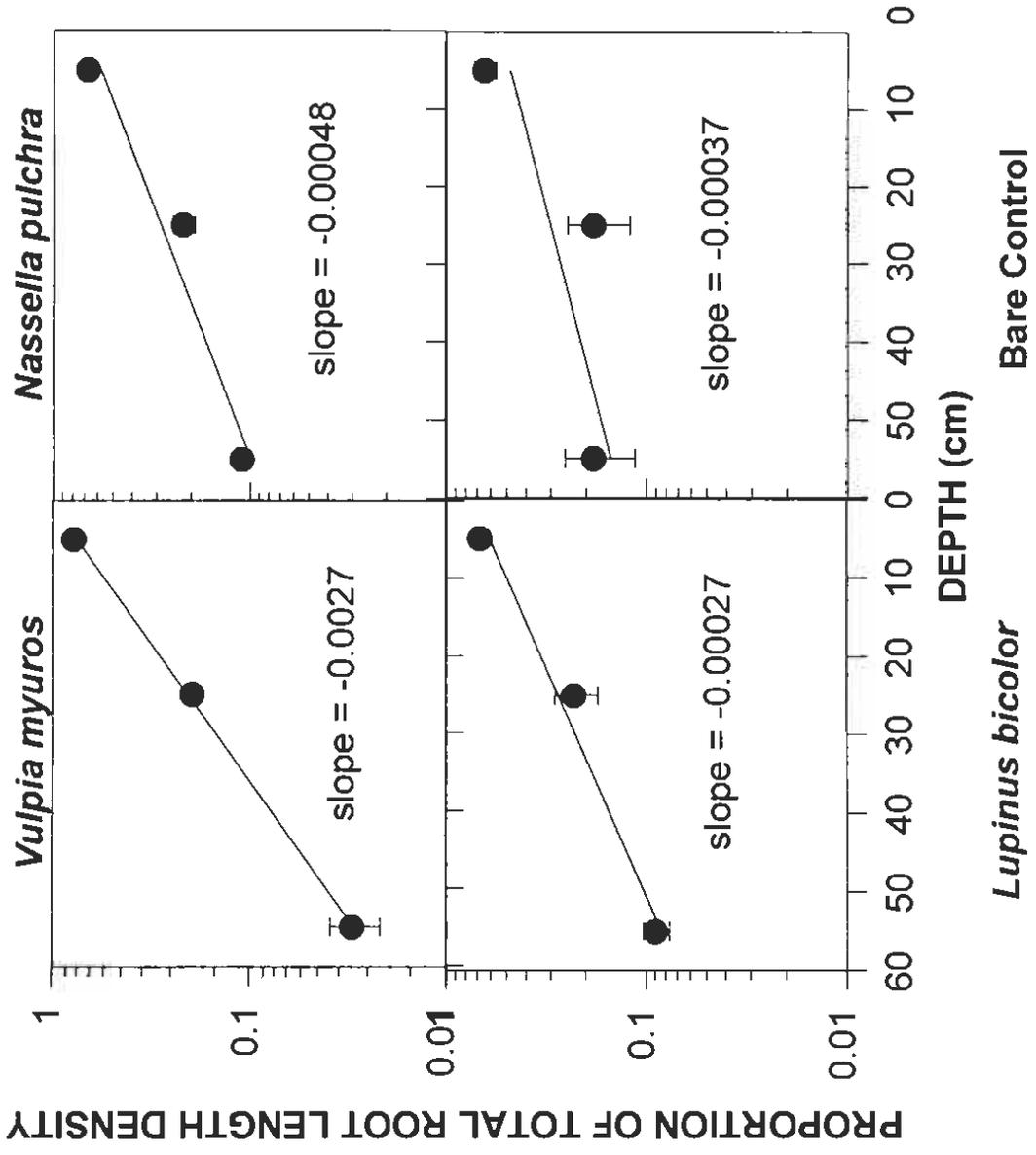
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**Appendix 1. EXAMPLES OF REGRESSIONS OF ROOT LENGTH DENSITY ON DEPTH
TO GENERATE SLOPES - FIELD EXPERIMENT 1994**



CHAPTER 3

**Effects of Resource Use Patterns and Species Diversity
on the Structure and Function of Constructed
Prairie Communities**

ABSTRACT

In mixtures of herbaceous plants selected from the prairie flora in California, we studied the effects of diversity of resource use patterns and species on plant community resource use, productivity, and stability. We investigated whether these plant community functions could be predicted *a priori* when mixtures of varying species richness were constructed using species with known spatial and temporal resource use patterns. Nine different species mixtures were planted at two densities and in two proportions. Five of the nine mixtures were designed to be compatible in the sense that they included species with differing resource use patterns determined by root distributions, phenologies, or mature plant height, or combinations of the three. Four of the mixtures were designed to be incompatible and included species with resource use patterns similar to each other. Five of the mixtures included two species, two included three species, and another two included five species. We detected both effects of compatibility across diversity treatments and effects of diversity across compatibility treatments. Overall, compatible mixtures utilized soil water more completely, and produced greater and more consistent aboveground biomass than incompatible mixtures, despite some changes in composition. Greater utilization of soil water and greater biomass production in compatible mixtures may have been in part due to larger size of species included in compatible mixtures. However, this absolute biomass size bias should not have greatly affected comparisons of stability between compatibility treatments based on relative changes in biomass composition. Regardless of compatibility, more diverse mixtures used soil water more

completely and produced more aboveground biomass with more stable species composition than less diverse mixtures. Despite some difficulties with interpreting biomass and resource use effects due to size bias between compatibility treatments, our results indicate that diversity of resource use patterns was at least as important as diversity of species in producing the effects on community functions observed and supports the hypotheses that diversity is positively related to resource use, biomass production and community stability.

INTRODUCTION

Ecologists continue to test new theories of controls on the composition (structure) and persistence of biological communities. One of the hypotheses developed within the last quarter century is the idea that biological community structure can be explained by 'assembly rules,' i.e. empirical patterns that result in the occurrence of only certain combinations of species and not others, due to some underlying mechanism other than individual species response to the physical environment (Wilson and Whittaker 1995). The term was first used by Diamond (1977) to describe the patterns he found for bird species associations in the islands of New Guinea. He evaluated these associations in search of evidence that the species combinations were based on complementarity of their basic requirements for survival and abundances. He believed that competition, or its avoidance, was the mechanism responsible for the patterns he observed. Based on the incidence of individual species on islands with different species numbers, he divided the birds of the archipelago into groups. He found that species were not randomly distributed between islands, that only certain combinations of species occurred together, and that these combinations followed empirical rules of assembly.

Diamond's claims stimulated much debate about (e.g. Connor and Simberloff 1979, Connell and Sousa 1983) and many tests for (e.g. Diamond 1986, Drake 1990, 1991) assembly rules in communities. Although Diamond worked with birds, he did not indicate that such rules should only exist for animals. In recent years, a great deal of effort has been spent testing the concept of assembly rules in plant communities. These

studies have generally been surveys of natural communities in which investigators looked for patterns indicating that associations of species or groups of species with particular characteristics (functional groups) are different than what would be expected if association of species were random (Wilson and Gitay 1995a, b, Wilson and Whittaker 1995, van der Maarel et al. 1995, Wilson et al. 1995a, b, Thórhallsdóttir 1990).

One of the ways that competition among species in plant communities may be reduced is through resource partitioning (a.k.a. niche separation). Resource partitioning has been reported to have important effects on plant coexistence and resource use. Parrish and Bazzaz (1976) found evidence for niche separation among successional herbaceous plants in terms of root distributions and timing of resource use. They suggested that niche separation facilitated plant coexistence in the plant community they studied. Results of McKane et al. (1990) also indicated that spatial (soil depth) and temporal (seasonal) niche separation in an old field plant community can promote coexistence between species. Gulmon et al. (1983) showed that phenology and rooting characteristics resulted in access to different soil water resources in three co-occurring grassland annuals. Others have also suggested that niche separation can lead to improved performance of species in mixtures. For example, Berendse (1979) presented data supporting the hypothesis that mixtures of plants can produce more biomass than monocultures if the species have different rooting depths and the shallow rooting species are better competitors for soil resources. Furthermore, the ability of some species to exhibit resource partitioning traits may depend on the competitive environment. Results

from Berendse (1982) suggested that *Plantago* was stimulated to use resources from deeper soil layers when grown in mixtures than when grown in monoculture.

The idea of assembly rules may or may not significantly advance our understanding, but the relative importance of ecological processes that determine plant community structure such as niche separation will continue to be debated. One of the most active areas of discussion and research concerns the importance of biodiversity for ecosystem function (e.g. Naeem et al. 1994, 1995, Weber and Schmid 1995) and, more narrowly, the effects of species diversity on plant community function (Tilman et al. 1996a,b, Tilman et al. 1997, Tilman 1996, 1997, Diemer et al. 1997). Several important recent studies indicate that species diversity can strongly affect community and ecosystem function. For example, Tilman and Downing (1994) argued that drought resistance in a grassland increased with species diversity. Tilman et al. (1996) asserted that more diverse grassland communities were more productive and utilized soil nitrogen more completely than less diverse communities. Based on an experiment using mesocosms, Naeem et al. (1994, 1995) reported that ecosystem processes were affected by species diversity.

In a critique of these and other recent experiments relating species diversity to ecosystem function, Huston (1997) pointed out that "hidden treatments" in experiments can limit the strength and validity of the conclusions regarding the importance of diversity. One of the problems occurs when biological or physical conditions are altered to create differences in species numbers (e.g. Tilman and Downing 1994, Tilman 1996),

thus confusing the effects of diversity with those of the altered environmental conditions. Other sources of difficulty arise in the selection of species. When a species has a large effect beyond that it is simply one more species in the community (e.g. the species is especially large), it is difficult or impossible to separate the effects of diversity from effects of individual species on ecosystem function. When species are randomly chosen, as species number increases there is an increased statistical probability of including species that will have a large effect (Aarssen 1997). As a result, effects attributed to diversity *per se* may in fact be caused by the productivity response or size of one or a few species. Despite their short-comings, these experiments have advanced our understanding of biodiversity and identified the need to conduct more manipulative experiments to further our knowledge of the effects and importance of biodiversity (Kareiva 1996).

Although many questions remain regarding community assembly and species diversity, even less is known about the importance of the interactions between them. Manipulative experiments testing hypotheses of mechanisms for community assembly (assembly rules) and effects of species diversity on community structure and function can begin to provide answers to remaining questions. In the experiment reported here we tested a number of hypotheses regarding whether resource use patterns, as a possible mechanism of community assembly (an assembly rule), and species diversity effect the structure (i.e species composition) and function (e.g. resource use and biomass production) of herbaceous plant communities. We hypothesized that mixtures of species

that are more diverse and those with species that utilize resources differently in space and time (1) use resources more completely, (2) produce more and less variable aboveground biomass, and (3) have more stable species composition than mixtures of species with more similar resource use patterns. We were also interested in addressing questions that would facilitate the successful restoration of disturbed land to prairie vegetation. We expected that low seeding density would result in lower biomass production and more variability in species composition of aboveground biomass than high seeding density. We also manipulated proportions of species included in the seed mixtures. Mixtures with higher proportions of less competitive species were expected to exhibit more stable species composition after the first growing season (i.e. after the establishment period), but more variable species composition during the first growing season due to higher mortality of less competitive species.

METHODS

The mixture experiment was conducted at three sites in Yolo County in the Sacramento Valley of California: (1) Hedgerow Farms near the intersection of County Road 27 and County Road 88 (hereafter Hedgerow Farms), (2) the Student Experimental Farm at U.C. Davis (hereafter Student Farm) and (3) in the clover-leaf of Richards Blvd-Interstate 80 freeway interchange in Davis, California (hereafter Freeway). Two replicates of the experiment were located at each of the three sites and are shown in photographs on page 134. The soils at the Student Farm site are Reiff fine sandy loam

and Yolo silt loam (Huntington 1981), and classified as coarse-loamy and fine-silty (respectively) mixed, nonacid, thermic Typic Xerothents (Andrews 1990). These are class I capability unit, well-drained, alluvial soils with moderately high to high fertility. The soils at the Hedgerow Farm site are predominantly Corning red gravelly loam, a fine, montmorillonitic, thermic Typic Palexeralf. This soil is class IV capability unit, found on terraces, relatively well-drained, and of moderate fertility. The soils at the Freeway site are of mixed texture, varying from silt loam to gravel, and include some imported soil and gravel used as fill. Soil compaction was variable at this site and quite severe in areas where a roadbed had been previously located.

Climate

The climate at the study sites is typically Mediterranean; rain falls during the cool winter months with little or no precipitation in the summer when warm temperatures are most conducive to plant growth. The climatological data station in Davis, California is located about 18.4 km south east of the Hedgerow Farms site, 3.4 km north west of the Freeway site and 1.1 km west of the Student Farm site. Precipitation at Hedgerow Farms, the site most remote to the climatological station, was found to be similar in amount and distribution to Davis (Brown and Rice, unpublished data). The thirty year average precipitation for Davis for the years 1961-90 is 460.5 mm (Owenby and Ezell 1992). Precipitation at Davis was 772.4 mm in 1995 and 693.7 mm in 1996 (National Oceanic and Atmospheric Association Reference Climatological Station, University of California, Davis). Not only was the 1995 annual rainfall well above the thirty year average in

Davis, but 37.5 mm of rain fell during May and 18.0 mm during June. This represents over five times the thirty year averages of 7.11 mm for May and 3.81 mm for June. The annual rainfall in 1996 was also well above the thirty year average and the potential growing season was extended by 61.5 mm of precipitation in May. The precipitation patterns in 1995 and 1996 made both years exceptionally wet with extended growing seasons due to late season rainfall.

Experimental design and set-up

This experiment was a randomized complete block design with nine plant species mixtures. Treatment plots (3 m by 4.5 m) were located on disked and harrowed 1.5 m beds at the Hedgerow Farm site, recently levelled soils at the Freeway site, and disked and harrowed soil at the Student Farm site.

Mixtures were designed to be either compatible or incompatible based on the spatial and temporal resource use patterns of their constituent species. We defined resource use characteristics for each species by its root length distribution with depth, phenology of growth and flowering and average height (see Brown 1998 for more background). The resource use patterns of individual species and species composition of mixtures are listed in Table 1. Nomenclature is according to Hickman (1993). The compatible mixtures (mixtures C^2_a , C^2_b , C^2_c , C^3 and C^5 , photographs shown on pages 137-140) were expected to have the most stable relative species composition and biomass production over time because they included species with differing resource use patterns. This would increase the likelihood that species would be able to partition the available

resources in space or time, or both, and coexist without competitively excluding one another. Conversely, incompatible mixtures (mixtures I^2_a , I^2_b , I^3 and I^5 , photographs shown on pages 137-140) included species with similar resource use patterns and were expected to have less stable species composition and biomass production over time.

As a factor crossed with the compatibility treatments, mixtures were constructed with different numbers of species to address questions about the effects of species diversity (i.e. species richness) on the stability of mixture composition and biomass production. Mixtures were made up of two species (mixtures C^2_a , I^2_a , C^2_b , I^2_b and C^2_c), three species (mixtures C^3 and I^3) or five species (mixtures C^5 and I^5). The species richness treatments were within the range of rapid increase of stability identified by Tilman and Downing (1994) in order to maximize the likelihood of detecting treatment effects.

We intended for each species to be represented in each compatibility and diversity treatment level. However, this approach was not possible due to logistical constraints of experiment size, the requirement of using species for which we had previously described resource use patterns (Chapter 2 of this report), and the need to maintain selected combinations of rooting depths, phenologies, and plant heights within mixture treatments. Most species were included in at least one of the compatibility treatment levels. However, *Lotus purshianus* (Benth.) Clements & E. G. Clements and *Eremocarpus setigerus* (Hook) Benth. occurred only in compatible mixtures and *Vulpia microstachys* (Nutt.) Benth., *Vulpia myuros* (L.) C. Gemlin and *Elymus multisetus* (J. G. Smith)

Table 1. Growth, phenology, origin and life history characteristics of species for mixture experiment.

MIXTURE	SPECIES	FLOWERING TIME	ROOTING DEPTH	HEIGHT	N-FIXING	ORIGIN	LIFE HISTORY	COMPATIBILITY
C ² _a	<i>Elymus trachycaulus</i> (Link) Shinn.	mid-late	intermediate	tall	no	native	perennial	compatible
	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i> Nevski	early	deep	intermediate	no	native	perennial	
I ² _a	<i>Elymus trachycaulus</i>	mid-late	intermediate	tall	no	native	perennial	incompatible
	<i>Nassella pulchra</i> (A. Hitchc.) Barkworth	mid-late	deep	intermediate-tall	no	native	perennial	
C ² _b	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>	early	deep	intermediate	no	native	perennial	compatible
	<i>Poa secunda</i> ssp. <i>secunda</i> J. S. Presl	early	shallow	short	no	native	perennial	
I ² _b	<i>Poa secunda</i> ssp. <i>secunda</i>	early	shallow	short	no	native	perennial	incompatible
	<i>Vulpia microstachys</i> (Nutt.) Benth.	early	shallow	short	no	native	annual	
C ² _c	<i>Lotus purshianus</i> (Benth.) Clements & E. G. Clements	late	deep	prostrate	yes	native	annual	compatible
	<i>Nassella pulchra</i>	mid-late	deep	intermediate-tall	no	native	perennial	

Table 1. continued

C ³	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>	early	deep	intermediate	no	native	perennial	compatible
	<i>Lotus purshianus</i>	late	deep	prostrate	yes	native	annual	
P ¹	<i>Poa secunda</i> ssp. <i>secunda</i>	early	shallow	short	no	native	perennial	incompatible
	<i>Poa secunda</i> ssp. <i>secunda</i>	early	shallow	short	no	native	perennial	
	<i>Vulpia microstachys</i>	early	shallow	short	no	native	annual	
	<i>Vulpia myuros</i> (L.) C. Gmelin	early	shallow	short	no	exotic	annual	
	<i>Eremocarpus setigerus</i> (Hook) Benth.	very late	intermediate	short	no	native	annual	
C ⁵	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>	early	deep	intermediate	no	native	perennial	compatible
	<i>Lotus purshianus</i>	late	deep	prostrate	yes	native	annual	
	<i>Nassella pulchra</i>	mid-late	deep	intermediate- tall	no	native	perennial	
	<i>Poa secunda</i> ssp. <i>secunda</i>	early	shallow	short	no	native	perennial	

Table 1. continued

1 ^s	<i>Elymus multisetus</i> (J. G. Smith)	mid-late	intermediate	intermediate- short	no	native	perennial	incompatible
	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>	early	deep	intermediate	no	native	perennial	
	<i>Poa secunda</i> ssp. <i>secunda</i>	early	shallow	short	no	native	perennial	
	<i>Vulpia microstachys</i>	early	shallow	short	no	native	annual	
	<i>Vulpia myuros</i>	early	shallow	short	no	exotic	annual	

occurred only in incompatible mixtures. Most species were included in at least one of each species richness treatment level. However, *E. setigerus* and *E. multisetus* occurred only in five-species mixtures, *Elymus trachycaulus* (Link) Shinn. occurred only in two-species mixtures, *Nassella pulchra* (A. Hitchc.) Barkworth occurred only in two- and five-species mixtures, and *V. myuros* occurred only in three- and five-species mixtures.

Each mixture was planted at high density (1076 seeds/m²) and low density (269 seeds/m²) and constructed in each of two proportions: (1) equal numbers of viable seeds of each species and (2) relatively more viable seeds of species characterized by small seed size, low vigor, slow growing seedlings, and small adult plant size. The method used to determine the relative amounts of species in proportion 2 treatments is described in Chapter 3 Appendix 1 (page 151). Each species mixture was thus planted in two proportions and at two densities for a total of 36 treatments within each of six blocks (Table 2). We planted the seeds by hand by evenly sprinkling pre-weighed seed mixed with wheat bran (to add bulk and aid in even distribution) over each plot, and cultivating the soil by hand to incorporate the seed. The Hedgerow Farm site was planted on November 22, 1994, the Freeway site was planted on December 8, 1994 and the Student Farm site was planted February 24, 1995. Seed was not incorporated by cultivation in the eastern-most replication at the Freeway site because the soil was saturated with water. Replicates at the Freeway site were covered with 4,485 kg ha⁻¹ of rice straw, a standard practice in erosion control plantings after road construction in California.

Table 2. Densities of viable seed and composition of mixtures.

MIXTURE	SPECIES	VIABLE SEEDS/m ²					
		PROPORTION 1			PROPORTION 2		
		LOW DENSITY 269 seeds/m ²	HIGH DENSITY 1076 seeds/m ²		LOW DENSITY 269 seeds/m ²	HIGH DENSITY 1076 seeds/m ²	
C ² _a	<i>Elymus trachycaulus</i>	135	538		135	538	
	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>	135	538		135	538	
I ² _a	<i>Elymus trachycaulus</i>	135	538		78	312	
	<i>Nassella pulchra</i>	135	538		191	764	
C ² _b	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>	135	538		32	129	
	<i>Poa secunda</i> ssp. <i>secunda</i>	135	538		237	947	
I ² _b	<i>Poa secunda</i> ssp. <i>secunda</i>	135	538		161	646	
	<i>Vulpia microstachys</i>	135	538		108	431	
C ² _c	<i>Lotus purshianus</i>	135	538		51	204	
	<i>Nassella pulchra</i>	135	538		218	872	

C ¹	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>	89	358	27	108
	<i>Lotus purshianus</i>	89	358	19	75
I ¹	<i>Poa secunda</i> ssp. <i>secunda</i>	89	358	223	893
	<i>Poa secunda</i> ssp. <i>secunda</i>	89	358	159	635
	<i>Vulpia microstachys</i>	89	358	105	420
	<i>Vulpia myuros</i>	89	358	5	21
	<i>Eremocarpus setigerus</i>	54	215	38	151
C ⁵	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>	54	215	19	75
	<i>Lotus purshianus</i>	54	215	11	43
	<i>Nassella pulchra</i>	54	215	48	194
	<i>Poa secunda</i> ssp. <i>secunda</i>	54	215	153	614
	<i>Elymus multisetus</i>	54	215	21	86
I ⁵	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>	54	215	16	65
	<i>Poa secunda</i> ssp. <i>secunda</i>	54	215	134	5381
	<i>Vulpia microstachys</i>	54	215	89	366
	<i>Vulpia myuros</i>	54	215	5	21

Because the Student Farm site was not planted until the end of February, this site was irrigated during the emergence and establishment periods. Impact sprinklers were used to apply approximately 0.71 cm of water on March 1 and April 24, and 1.4 cm of water on May 25. The last natural rainfall of 1995 at all sites was on June 14 and 15.

Seeds and germination tests.---Seed for most species was purchased from commercial seed suppliers (Pacific Coast Seed, Livermore, CA; Hedgerow Farms, Winters, CA; Conservaseed, Rio Vista, CA). Seed for *E. setigerus* was collected from wild plants near Davis, California during the summer of 1994. Seed germination tests of *E. setigerus* were conducted using the methods of the Association of Official Seed Analysts (Wiesner 1989). Germination rates of commercial sources of seed were determined by commercial seed laboratories. *L. purshianus* seed was inoculated with appropriate rhizobia culture (The Nitragin Company, Liphatec, Inc. Milwaukee, Wisconsin, USA).

Soil water

Soil water content was measured using a soil water capacitance probe (Sentry 200-AP Troxler Electronic Laboratories, Inc. Research Triangle Park, NC). The instrument records changes in the soil dielectric constant (D-values) that are positively correlated with changes in soil water content (i.e. water content increases as D-value increases) (Tomer and Anderson 1995). PVC access tubes extending 100 cm below and 10 cm above the soil surface were placed in high and low seeding densities and both proportional composition treatments of the mixtures 3, 4, 6, 7, 8, and 9. Measurements were taken 15, 35, 70 and 90 cm below the soil surface every two weeks during periods

of rapid plant growth and monthly otherwise. As a relative measure of soil water content, the proportion reduction in soil D-value during the growing season and drying cycle was calculated using the range between the highest and lowest D-values recorded during the measurement period (April - September in 1995, January - September 1996).

Aboveground biomass and density

Each treatment plot was divided equally into six sub-plots. Density estimates were made during the spring of 1995 and 1996 by placing a 0.1 m² quadrat in the center of two randomly selected sub-plots and counting the number of individuals of each species rooted in the quadrat. The two individuals of each species seeded in the plot closest to each of two fixed points on the quadrat were selected for biomass production estimates. Characteristics that could be non-destructively measured and correlated with total biomass for that species were measured on these two individuals. Biomass was predicted for each individual measured using a regression equation for the species at comparable age and phenological stage. Each species and stage specific regression was developed from plants grown and harvested near the experiment. Non-destructive measurements made on plants in the experiment were entered into the appropriate regression equation to generate an estimate of the biomass of the plants.

Measurements for making estimates of species composition and biomass were taken as close as possible to the time plants had reached peak standing biomass. However, the sampling period was protracted due to the length of time required to measure the entire experiment. By completing the sampling within each block (replicate)

within eight days, we minimized the effect that growth over time would have on our ability to detect treatment effects. In addition, although plants in different blocks were at slightly different stages when sampled, plants within each block were at similar stages. Density and biomass measurements were made for spring active species between April 8 and May 17, 1995 and between April 3 and May 28, 1996. Measurements for estimates of density and biomass were taken between August 9 and 24, 1995 and August 29 and 30, 1996 for *L. purshianus* and *E. setigerus*, the only species that actively grew during the summer.

Due to difficulty in distinguishing between *V. myuros* and *V. microstachys* under some conditions, biomass estimates for these two species were combined. Also, in mixture I² during 1996, some seedlings of the two species (*E. trachycaulus* and *N. pulchra*) were very difficult to differentiate, resulting in a number of individuals classified as unknown. If the unknown biomass or density estimates were greater than or equal to 5 % of the biomass or densities of known species, the sample was considered missing and not included in the analysis.

Weed control

Species not included in the originally seeded mixture of each plot were removed throughout the experiment using both chemical and mechanical methods. Before seed matured, inflorescences along plot edges were clipped to reduce dispersal of seeds into adjacent plots. At the Hedgerow Farm site, *Polygonum* sp. was extremely abundant and could not practically be removed by hand. The broadleaf-specific herbicide, triclopyr,

was applied to the mixtures that included only grasses on March 18, 1995 at a rate of 0.56 kg ha⁻¹. Because it began to rain within four hours after application, triclopyr was reapplied March 28 and 31 at a rate of 0.84 kg ha⁻¹. The broadleaf specific herbicide dicamba was applied to the grass mixtures on May 8 and 12, 1995 (1.4 kg ha⁻¹) and on March 15, 1996 (1.87 kg ha⁻¹). The furrows between beds were cultivated using a tractor on April 6, 1995. During 1995 and 1996, weeds were removed by hand from the treatments that had dicots included in the seed mixtures (mixtures 5C²_c, C³ and C⁵). Grass weeds and broadleaf weeds not controlled by herbicides were removed by hand from the mixtures containing only grasses. The majority of the hand weeding effort occurred during the months of March through June when growth was most rapid.

All mixtures at the Student Farm site were weeded by hand during both 1995 and 1996. At the Freeway site, weeds were removed by hand in all mixtures in 1995 and 1996 and dicamba was applied to mixtures containing only grasses on March 18, 1996 (1.37 kg ha⁻¹).

At the Hedgerow Farm site, successful removal of weeds became difficult due to drying of this well-drained soil. In order to facilitate weeding, the section of the experiment to be weeded was irrigated the previous evening. Plots received equal amounts of water applied with impact sprinklers between May 30 and June 18, 1995.

Statistical analyses

The general approaches taken to analyze the data are described below. More detailed information can be found in Brown (1998).

Soil water.---Relative changes in soil water content based on measurements of D-values taken at the beginning and end of the season were analyzed using repeated measures univariate and multivariate analysis of variance with depth as the repeated measure. Soil water measurements were made in mixtures C²_b, I²_b, C³, I³, C⁵ and I⁵. Soil moisture data from 1995 was analyzed separately from 1996 data because there were three replicates for 1995 and only two for 1996. Linear contrasts were conducted to test hypotheses about differences in soil moisture depletion in response to resource use patterns (i.e. compatible and incompatible mixtures) and in response to changes in species diversity (i.e. two- and five-species mixtures).

Total aboveground biomass production.---To evaluate the stability of total biomass production over time, the coefficient of variation ($CV = 100 * 1 \text{ S.D.} / \text{mean}$) for each plot was calculated for biomass estimates obtained during the growing seasons of 1995 and 1996. As noted by Tilman (1996) the CV serves as a measure of variation of biomass production relative to the mean. ANOVA was performed on ranks of CVs because the data were highly skewed and the variances were not equal (Conover and Iman 1981). Total biomass production responses were assessed with ANOVA of rank transformed 1995 data and log transformed 1996 data. Planned linear contrasts were performed to test for differences between response to resource use patterns (i.e. compatible and incompatible mixtures) and response to species richness (i.e. two- and five-species mixtures).

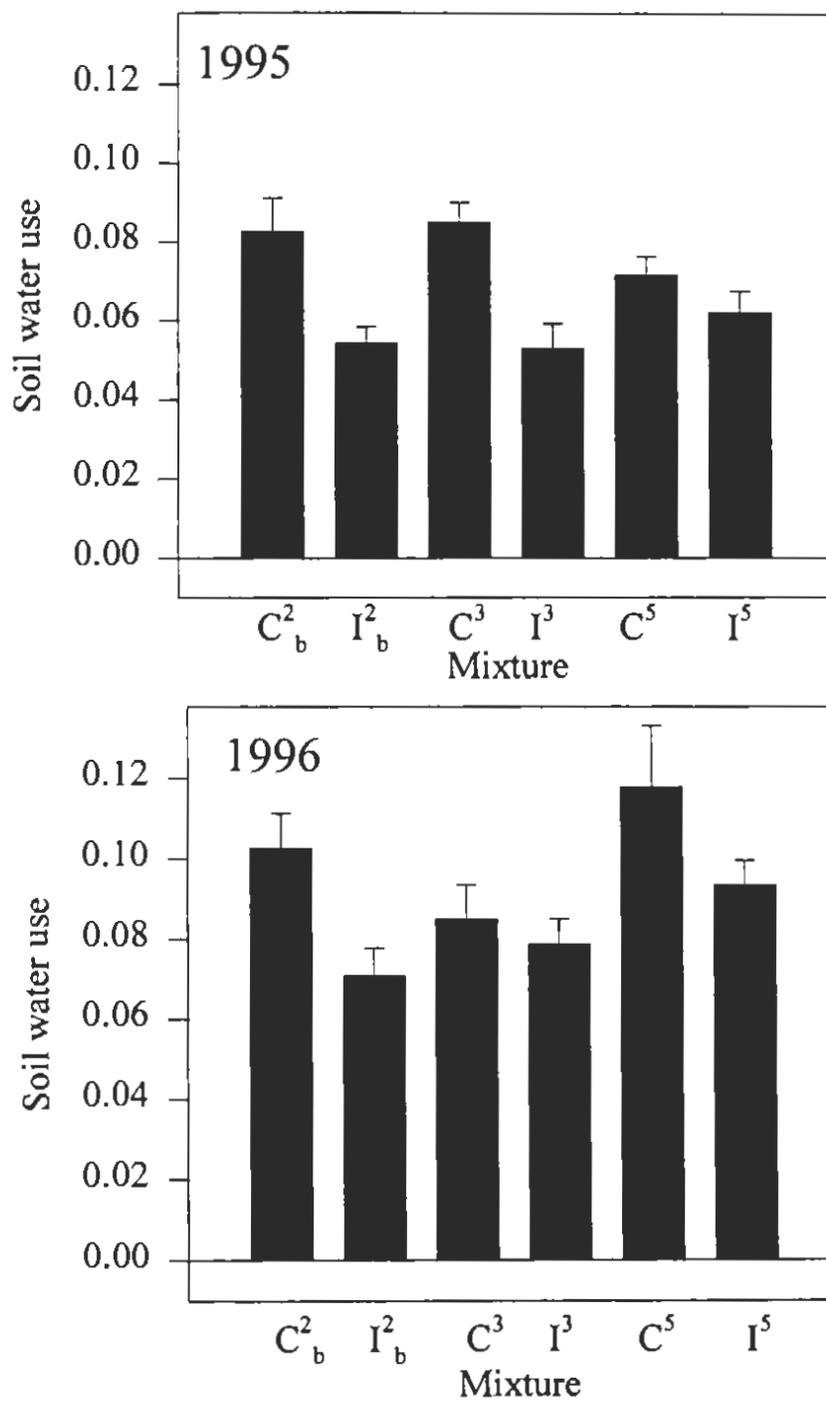
Stability of relative aboveground biomass and density.---The temporal stability of the species composition for each treatment combination was evaluated using proportional biomass estimates and a modified version of the chi square statistic. Reflecting instability of relative species composition over time, the index increases with increasing year-to-year variation in proportional representation by species within each treatment combination. The treatments that maintain relatively constant representation of their original species composition will have lower indices of instability than those with more variation in composition over time.

The ranks of the instability index data were then evaluated as the response variable in ANOVA. Ranks were used because the data were highly skewed and variances were not equal. Planned linear contrasts were conducted to test for differences between response to resource use patterns (i.e. compatible and incompatible mixtures) and response to species diversity treatments (i.e. two- and five-species mixtures). Rank means and their standard errors are reported because, given the skewed distribution of the data, mean and median of untransformed data were both poor measures of central tendency.

RESULTS

Outcomes of the experiment are described below with reference to statistical analyses. *P*- values less than 0.05 are considered statistically significant. More detailed discussion of statistical results including ANOVA tables can be found in Brown (1998).

Figure 1. Mixtures used different amounts of soil water.



Means \pm standard error of the mean for proportional reduction of water content measured as changes in soil dielectric constant (D-value) from beginning to end of season for mixtures for 1995 and 1996.

Soil water

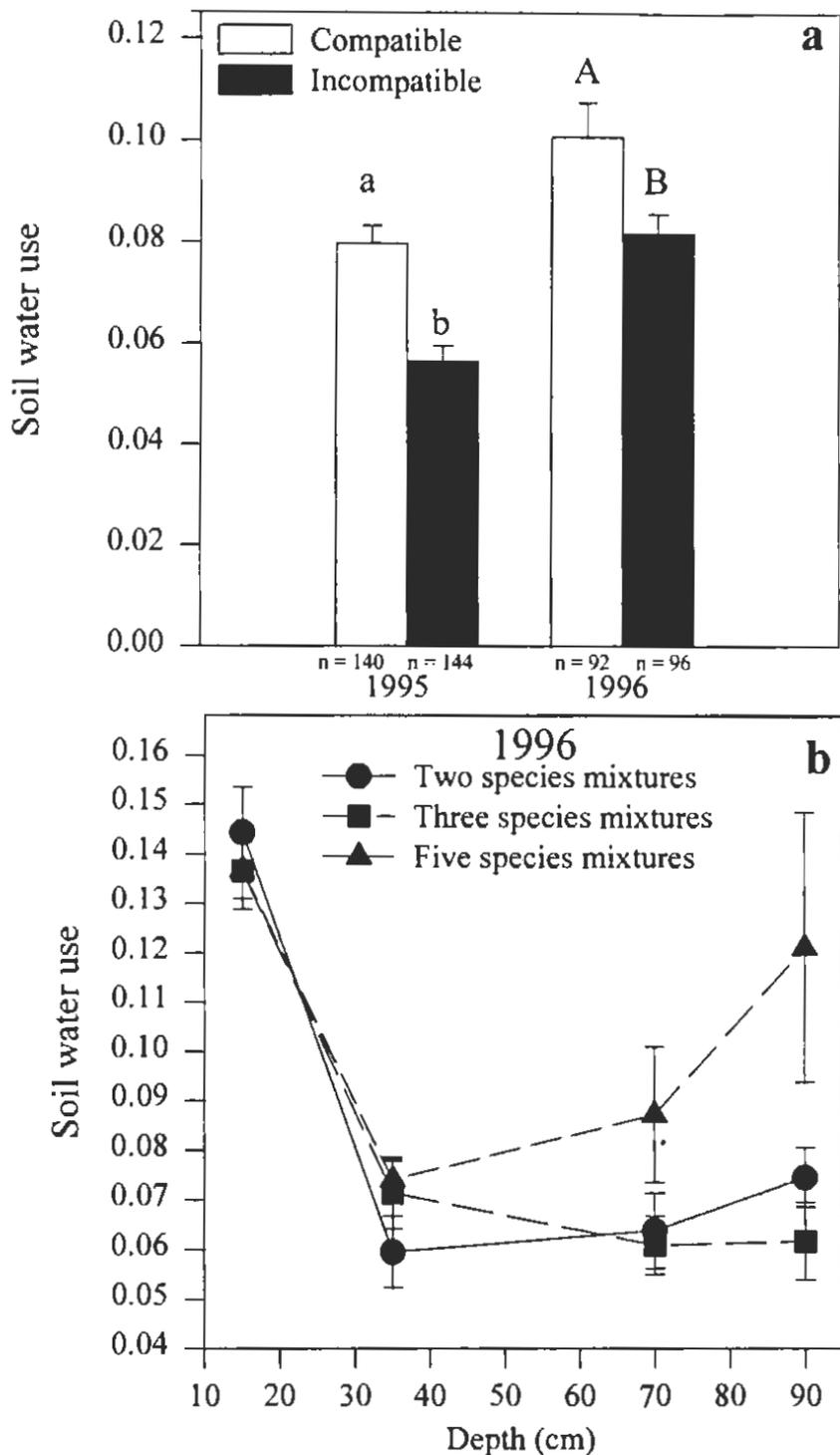
Mixtures differed significantly in the extent of soil water depletion across depths in 1996 ($P = 0.0012$) (Fig. 1a). The same trend was detected in 1995, although the effect was marginally insignificant ($P = 0.08$) (Fig. 1b). During both the establishment period (the first growing season after seeding, i.e. 1995) and the post-establishment period (the second growing season after seeding, i.e. 1996), compatible mixtures used more available soil water than incompatible mixtures ($P = 0.04$ and 0.0001 , respectively) as shown in Fig. 2a. After establishment (1996), five species mixtures tended to use lower proportions of soil water at 15 cm and higher proportions of soil water at 70 and 90 cm than two species mixtures ($P = 0.0781$) (Fig. 2b). The soil water depletion with depth for individual mixtures are presented in Fig. 3. The proportion of soil water used differed by depth in both years ($P = 0.0001$) with greater depletion in the shallow layer (15 cm) than in deeper layers (35, 70 and 90 cm).

Total aboveground biomass

Variability of aboveground biomass from the two growing seasons differed among mixtures based on coefficients of variation (CVs). Relative variability of biomass differed among mixtures during 1995 and 1996 ($P = 0.0001$). Variability of aboveground biomass was lower (lower CVs) in compatible mixtures than incompatible mixtures ($P = 0.0001$) (Fig. 4A). High seeding density plots had lower biomass variability (lower CVs) than low seeding density plots ($P = 0.008$) (Fig. 4B).

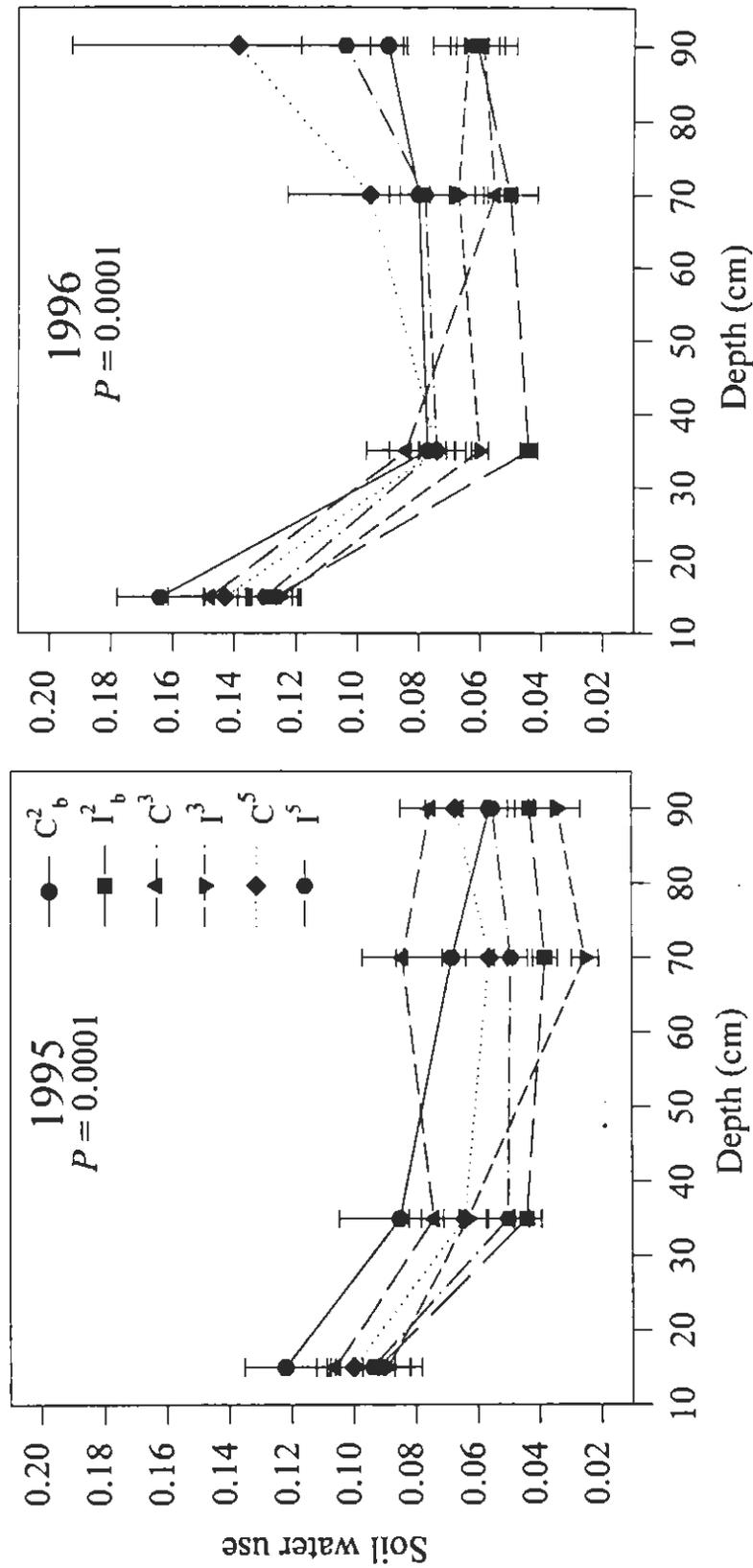
Total aboveground biomass differed among mixtures during both 1995 and 1996

Figure 2. Soil water use was greater in compatible mixtures than incompatible mixtures.



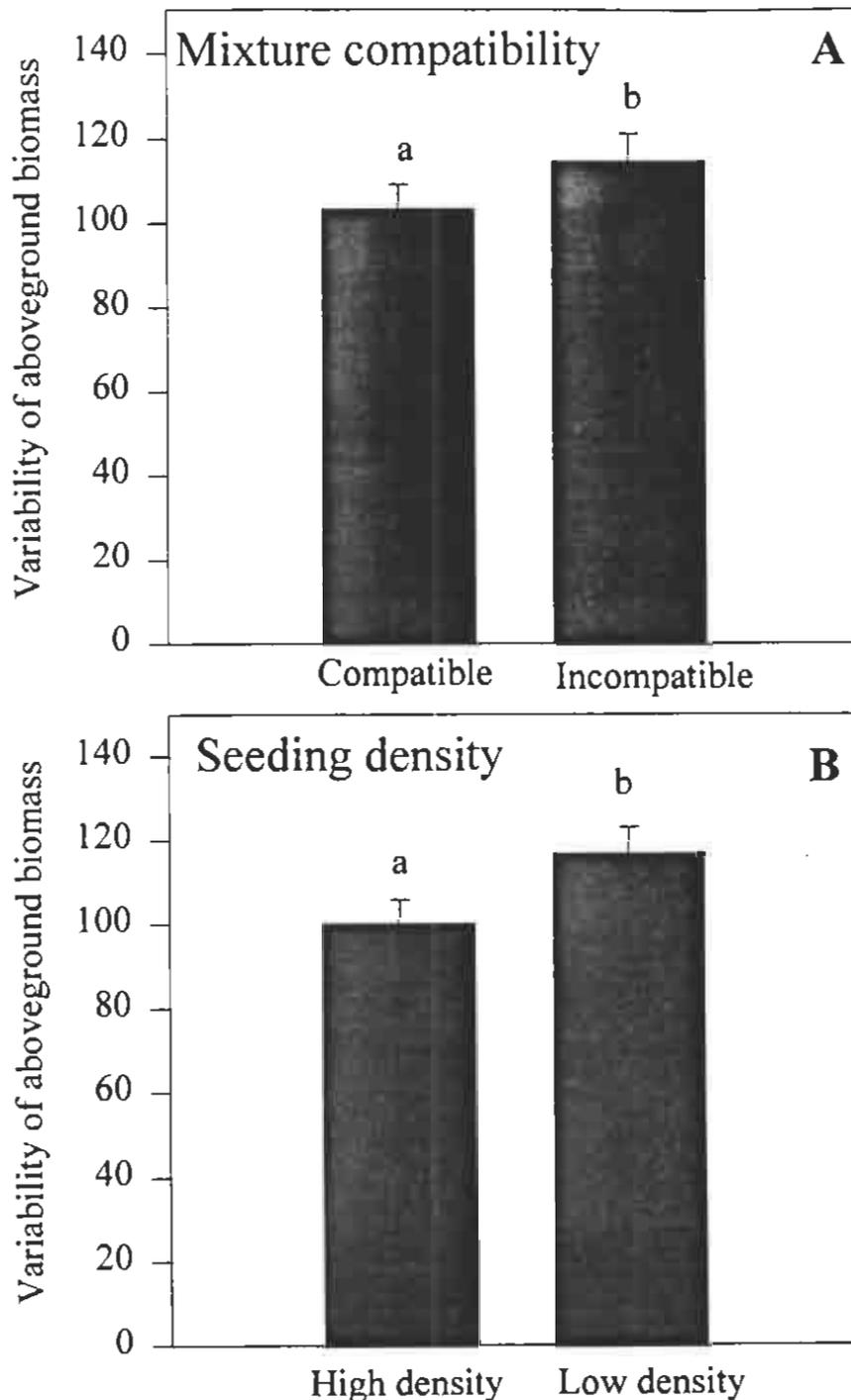
Means \pm standard error of the mean for a) proportional reduction of water content measured as changes in soil dielectric constant (D-value) from beginning to end of season for compatible mixtures (C^2_b , C_3 and C_5) ($n = 3, 4, 4$, respectively) and incompatible mixtures (I_2_b , I_3 and I_5) ($n = 4$ for all) for 1995 and 1996 and for b) two- ($n = 16$), three- ($n = 15$) and five-species ($n = 16$) mixtures in 1996.

Figure 3. Mixtures used more water at shallow depths than at deep depths.



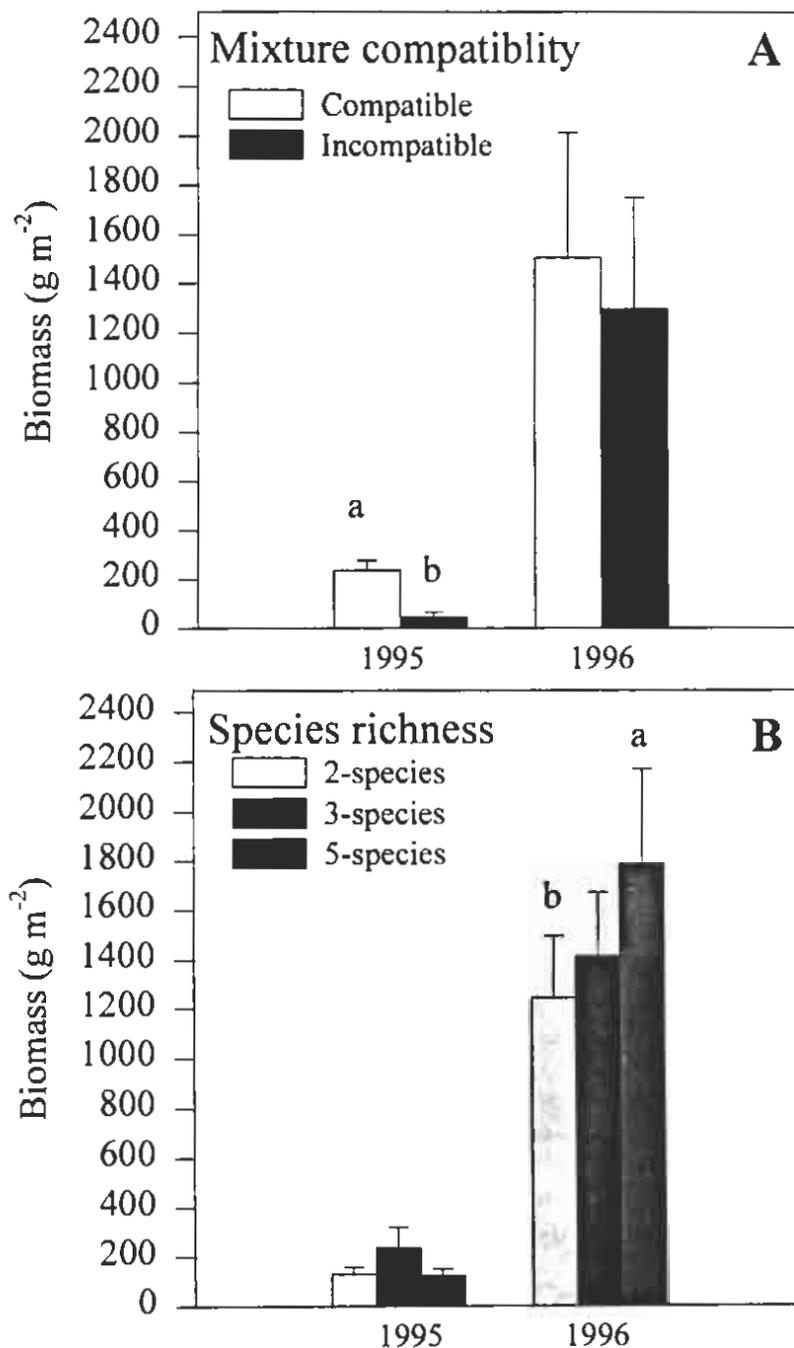
Means ± standard error of proportional reduction of soil water content measured as changes in soil dielectric constant (D-value) from beginning to end of season for mixtures.

Figure 4. There was more variation in biomass production in 116
A) incompatible mixtures than compatible mixtures and in B) the
low density seeding treatment than the high density seeding treatment.



a) Means \pm standard errors of the mean for the CVs of ranks of compatible mixtures ($n = 120$) and incompatible mixtures ($n = 96$). Means are significantly different according to linear contrasts performed on rank transformed data ($P = 0.0001$). b) Means \pm standard errors for the ranks of CVs of high seeding density and low seeding density treatment levels. Means are significantly different based on ANOVA of rank transformed data ($P = 0.008$) ($n = 108$).

Figure 5. More aboveground biomass was produced by A) compatible than incompatible mixtures and by B) 5-species than 2-species mixtures.



A) Means \pm standard error of the mean for aboveground biomass estimates of compatible mixtures ($n = 120$) and incompatible mixtures ($n = 96$). Means are significantly different according to linear contrasts performed on rank transformed data ($P = 0.0001$).
 B) Means \pm standard error of the mean for aboveground biomass estimates for two- ($n = 120$), three- ($m=48$) and five-species ($n=48$) mixtures. Means with different letters are significantly different based on linear contrasts ($P=0.0001$).

($P = 0.0001$). Aboveground biomass was greater in compatible mixtures than in incompatible mixtures in 1995 ($P = 0.0001$) (Fig. 5A). Five-species mixtures had greater aboveground biomass than two-species mixtures in 1996 ($P = 0.0001$) with a similar, but marginally insignificant, trend in 1995 ($P = 0.06$) (Fig. 5B). The average maximum plant size for species included in the mixtures (Table 3) are based on destructive harvests of plants growing at or near the experimental sites. Species included in compatible mixtures were on average larger than those included in incompatible mixtures; species included in two-species mixtures were the same size or larger than those included in three- and five-species mixtures.

In 1995, high density mixtures had greater biomass than low density mixtures ($P = 0.0001$) and the trend was similar in 1996 ($P = 0.07$) (Fig. 6A). Proportion 1 (equal numbers of viable propagules of each species) had greater biomass than proportion 2 (higher proportion of seeds of the small seeded, slow growing, short stature species) in 1995 and 1996 ($P = 0.004$ and 0.03 , respectively) (Fig. 6B). In 1995, biomass was much higher in proportion 1 than proportion 2 for high density treatments and essentially equal in low density treatments (Fig. 7) resulting in a significant density by proportion interaction ($P = 0.03$).

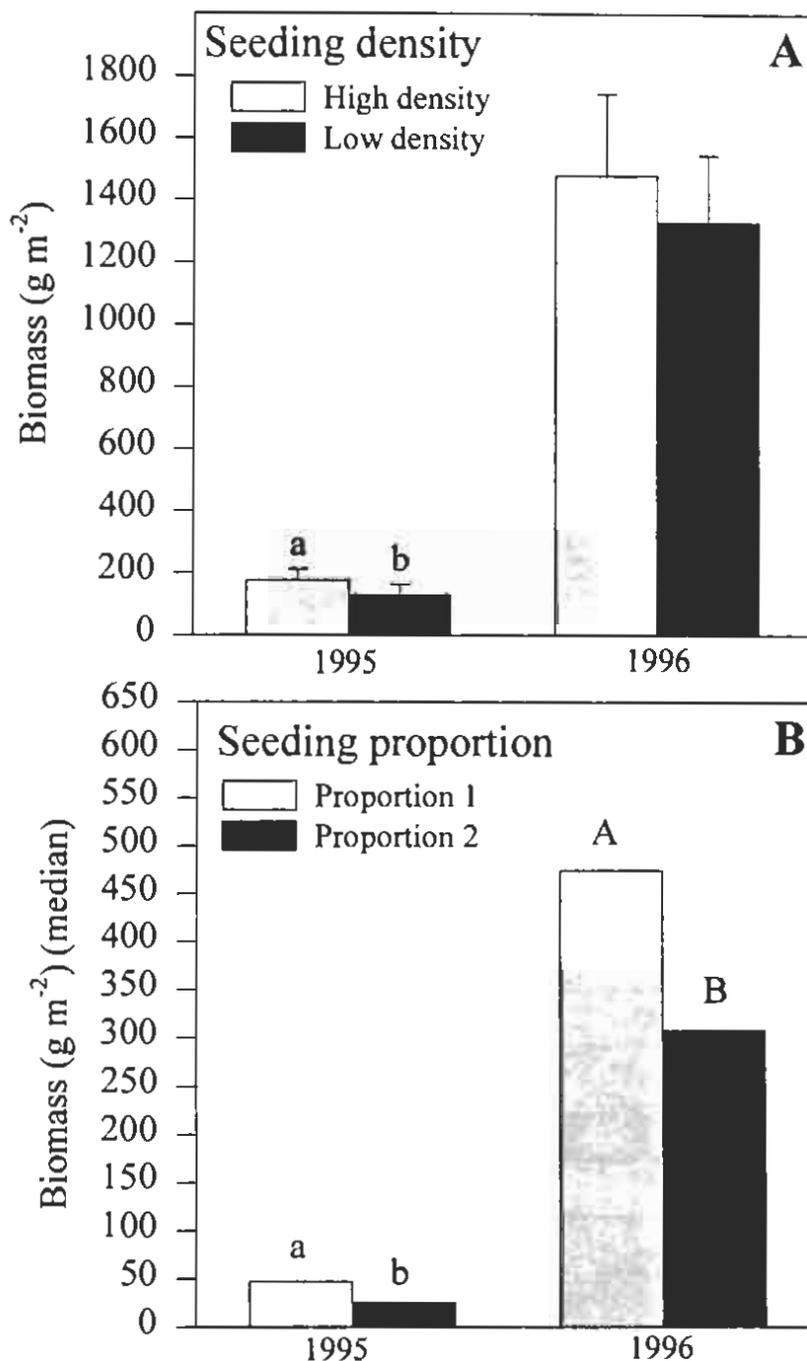
Relative aboveground biomass stability

The stability of the species mixtures differed in all three year combinations (1994-95, 1994-96 and 1995-96) ($P = 0.0001$). Compatible mixtures were more stable than incompatible mixtures overall (1994-96) ($P = 0.0001$), but less stable during the post-

Table 3. Biomass for largest individual of each species included in the mixtures and means \pm standard error of biomass for the largest individuals of the species included in each mixture, compatibility and diversity treatment.

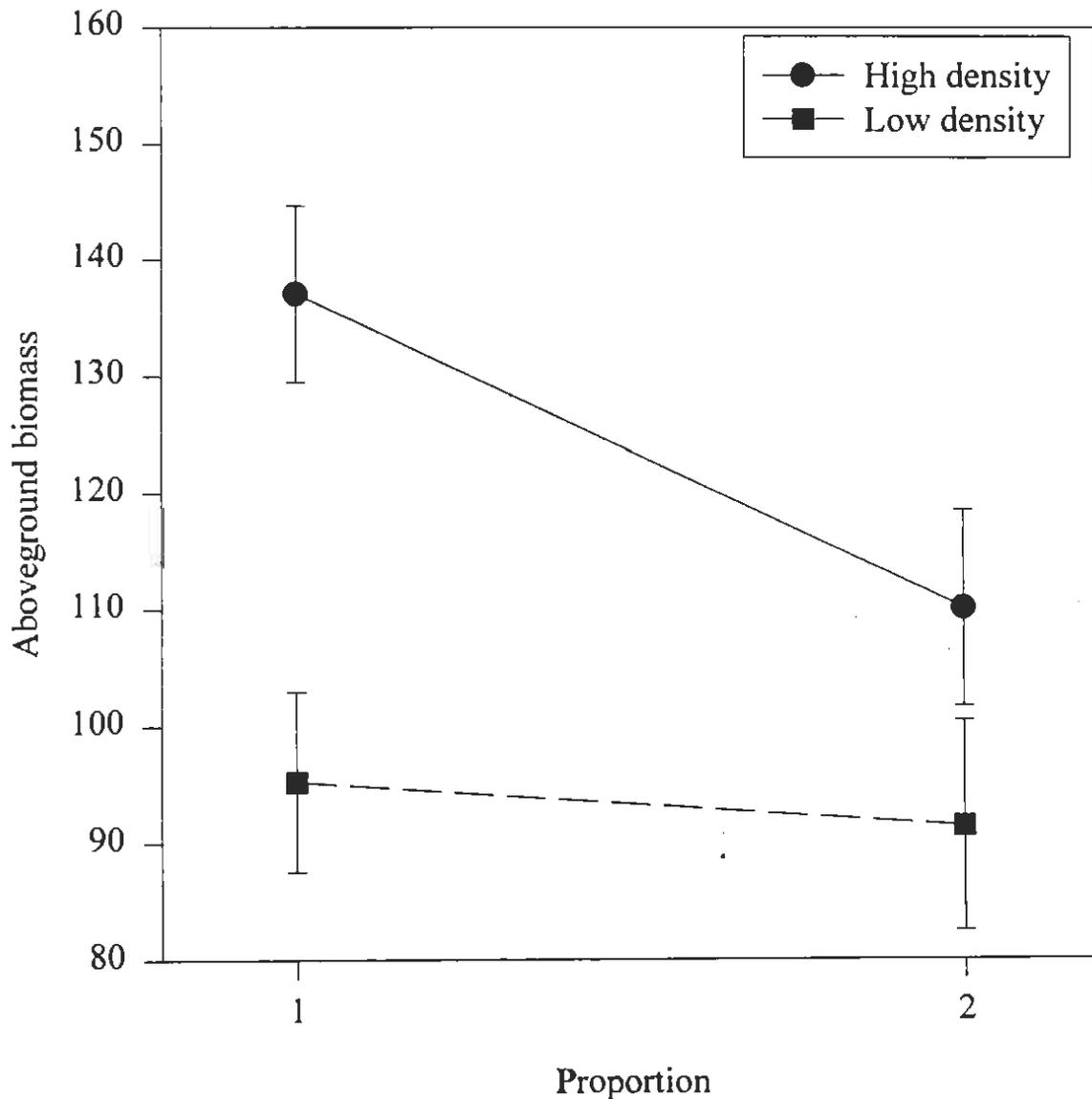
SPECIES	BIOMASS (g)
<i>Elymus multisetus</i>	72.5
<i>Elymus trachycaulus</i>	172.8
<i>Eremocarpus setigerus</i>	140.6
<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>	63.0
<i>Lotus purshianus</i>	308.1
<i>Poa secunda</i> ssp <i>secunda</i>	6.4
<i>Nassella pulchra</i>	138.6
<i>Vulpia microstachys</i>	0.7
<i>Vulpia myuros</i>	0.44
Mix 1 (two-species compatible)	117.9 \pm 54.9
Mix 2 (two-species incompatible)	155.7 \pm 17.1
Mix 3 (two-species compatible)	34.7 \pm 28.3
Mix 4 (two-species incompatible)	3.6 \pm 2.8
Mix 5 (two-species compatible)	223.3 \pm 119.8
Mix 6 (three-species compatible)	125.8 \pm 92.6
Mix 7 (three-species incompatible)	3.5 \pm 2.9
Mix 8 (five-species compatible)	131.3 \pm 50.8
Mix 9 (five-species incompatible)	35.6 \pm 18.7
Compatible mixtures	126.6 \pm 29.9
Incompatible mixtures	49.6 \pm 36.1
Two-species mixtures	107.0 \pm 40.0
Three-species mixtures	64.6 \pm 61.2
Five-species mixtures	83.5 \pm 47.8

Figure 6. A) More biomass was produced by high density mixtures than low density mixtures in the first year only. B) More biomass was produced by mixtures with equal numbers of seeds of each species.



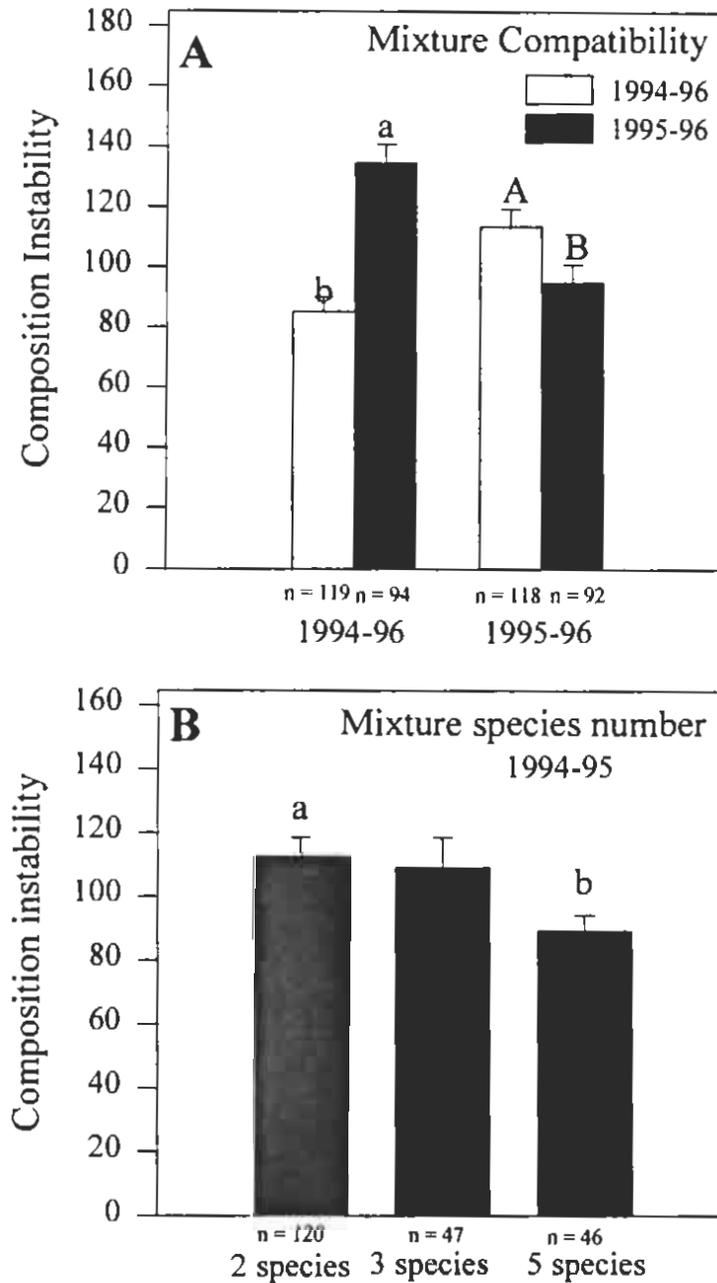
A) Means \pm standard errors of the mean of aboveground biomass of high seeding density and low seeding density treatment levels in 1995 and 1996. Means with different letters are significantly different ($a > b$) based on ANOVA of rank transformed data ($P = 0.0001$) ($n = 108$ except for low density 1996 where $n = 107$). B) Medians of aboveground biomass for proportion 1 and proportion 2 in 1995 and 1996. Medians with different letters are significantly different from each other based on ANOVA of ranked 1995 data ($P = 0.004$) and log transformed 1996 data ($P = 0.03$).

Figure 7. Proportion 1 treatments produced more biomass than proportion 2 treatments at high seeding rates but the two proportion treatments produced similar amounts of biomass at low seeding rates in 1995.



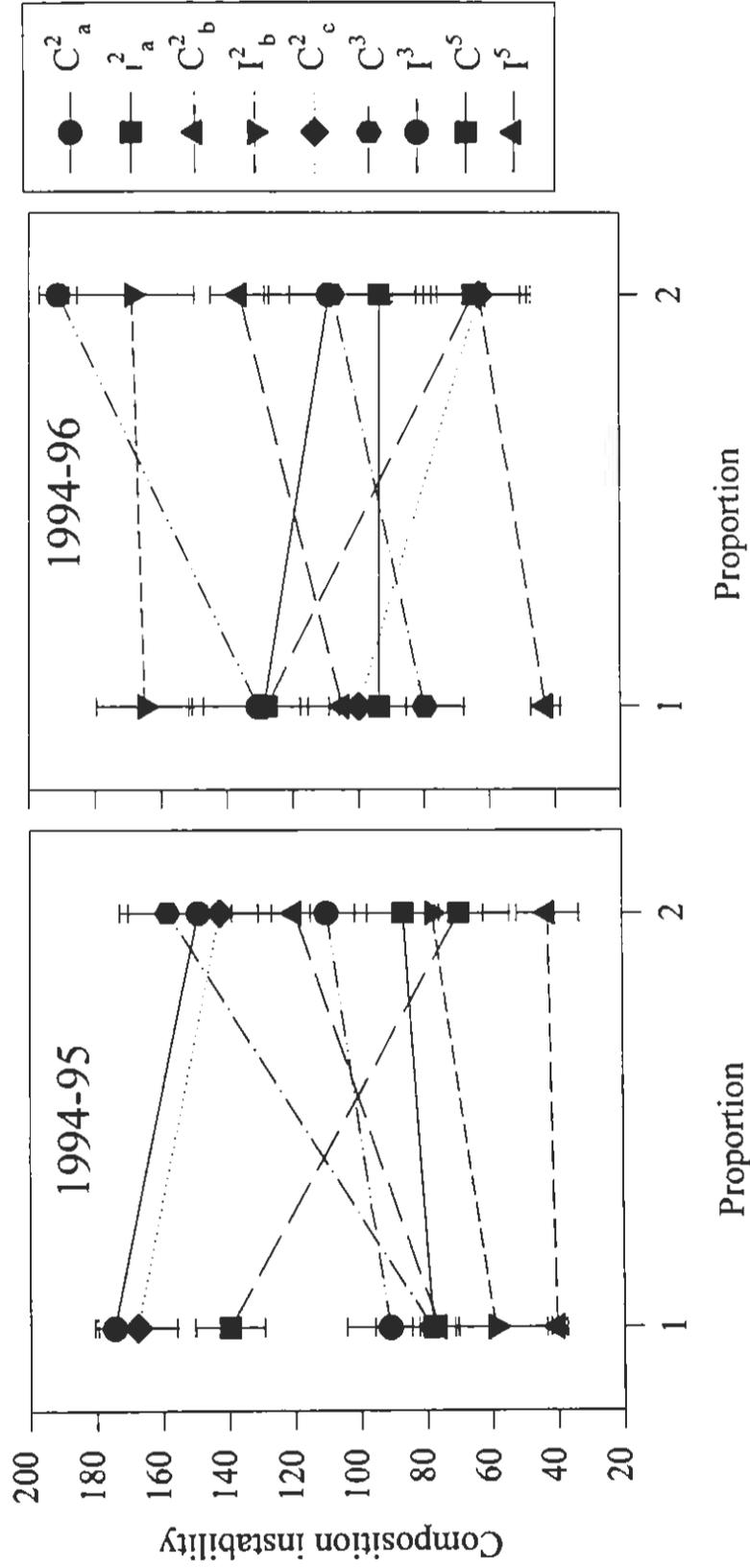
Means \pm standard errors of the mean for ranks of aboveground biomass for high and low density seeding rates and two levels of proportions ($n = 54$). Proportion 1 had equal numbers of seeds of each species. Proportion 2 had higher proportions of small seeded, slow growing, short stature species than other species. The interaction between density and proportion was significant ($P = 0.03$).

Figure 8. A) Compatible mixtures had more stable species composition over the duration of the experiment but incompatible mixtures had more stable composition during the post-establishment period. B) 5-species mixtures had more stable composition during establishment.



A) Means \pm standard errors of the mean for ranks of chi square measures of instability for compatible and incompatible mixtures. Means with different letters are significantly different based on linear contrasts ($P < 0.001$ 1994-96, $P = 0.02$ 1995-96). B) Means \pm standard errors of the mean for ranks of chi square measures of instability for 2-, 3-, and 5-species mixtures. Means with different letters are significantly different based on linear contrasts ($P = 0.004$).

Figure 9. Stability of species composition depended on both the mixture and the proportion treatment. Mixtures that included *P. secunda* were less stable in proportion 2 than proportion 1.



Means \pm standard errors of the mean for ranks of chi square measures of instability for species mixtures at two seeding proportions. Proportion 1 had equal numbers of seeds of each species. Proportion 2 had higher proportions of small seeded, slow growing, short stature species. The interaction between density and proportion was significant ($P < 0.001$).

establishment period alone (1995-96) ($P = 0.015$) (Fig. 8A). Two-species mixtures were less stable than five-species mixtures during the establishment period (1994-95) ($P = 0.004$) (Fig. 8B). For intervals that included the establishment period (1994-95 and 1994-96), stability differed between proportion treatments (Fig. 9). This was indicated by a significant statistical interaction between mixture and seeding proportion for both 1994-95 and 1994-96 data ($P = 0.0001$ and 0.0005 , respectively). Patterns are explained in the Discussion.

DISCUSSION

Some of the phenological and biomass production differences between mixtures are demonstrated in photographs on pages 141-143.

Effects of mixture compatibility on community structure and function

Resource depletion... We found that soil resources were used more completely in the compatible mixtures (mixtures C²_b, C³ and C⁵) than in the incompatible mixtures (mixtures I²_b, I³ and I⁵) in both 1995 and 1996. This result suggests that because species in the compatible mixtures had different phenologies, rooting depths, and plant heights (Brown 1998) they utilized soil resources more completely than incompatible mixtures.

However, the ability to partition resources is not the only possible explanation for these results. A species with strong characteristics, such as high resource uptake, is more likely to be included in mixtures with more species simply due to chance. Huston (1997) suggested that increased resource use in diverse plant communities could be due to this

probabilistic phenomena and the identity of the species included, not simply due to the presence of more species. Conceivably, the effects of a species with high resource use included in one compatibility treatment and not in the other might have resulted in differences in soil moisture depletion between compatible and incompatible treatments. In other words, the increased resource use detected in compatible mixtures may have been due to the effects of a species found in only one of the compatibility treatments, not due to the ability of species in compatible mixtures to partition resources. A careful review of the species included in the mixtures suggests that this was unlikely (see Brown 1998 for details).

Although no particular species dominated and caused compatible mixtures to have greater soil resource use than incompatible mixtures, greater water uptake in compatible mixtures may reflect greater biomass production of these mixtures in the field (Fig. 5A). The question arises whether plants in compatible mixtures had the potential to become larger than plants in incompatible mixtures. To evaluate this, we examined the maximum size that an individual plant of a particular species could attain under the best conditions in the experiment (i.e. potential biomass). We then calculated the average potential size for species included in each treatment (Table 3). The average potential biomass of the species included in compatible mixtures was two and a half times as great as those included in the incompatible mixtures. This indicates that if they achieved their potential size, the species in the compatible mixtures could have reduced resources more than those in incompatible mixtures simply because they were larger.

Despite the potential size differences between species included in compatible and incompatible mixtures, there was not a statistically significant difference between biomass production of the two groups after establishment (1996)(Fig. 5A). Therefore, larger plant size is less likely to explain the observed difference in soil water depletion between compatible and incompatible mixtures in the post-establishment year (Fig. 2a). Overall, although increased soil water depletion by compatible mixtures might be explained by differing resource use patterns of species in these mixtures, we cannot rule out the possibility that the larger size of the species within compatible mixtures might also explain, in part, the greater depletion of soil moisture, especially during the establishment period.

Aboveground biomass production-... We predicted that mixtures of species with differing resource use patterns, regardless of species number, would also have more consistent aboveground biomass production than mixtures with more overlapping resource use patterns. We proposed that this would be possible through more complete use of resources due to morphological and phenological differences that allow resource partitioning (McNaughton 1993, Swift and Anderson 1993, Naeem et al. 1994, Naeem 1995, Tilman et al. 1996). In other words, because species with differing resource use patterns compete less directly in space and time, they should have relatively greater access to resources than species that compete more directly. As a result, mixtures of species with differing resource use patterns may be capable of greater and more constant biomass production than mixtures of species with more overlapping resource use patterns.

These hypotheses are supported by our finding that compatible mixtures had less variable biomass production (lower CVs) than incompatible mixtures. Responses of individual species were not likely to have been responsible for the effect. *Lotus purshianus*, the most variable species of significant size that had the potential to create large variability in total biomass, occurred only in the compatible mixtures. The largest individual of this species was nearly twice the weight of the next largest species in the mixtures, its biomass dropped ten fold from 1996 to 1995, and it was included in three of the five compatible mixtures. Such huge fluctuations of a large and abundant species would be expected to result in increased biomass variation. Instead, the variability of biomass production of compatible mixtures was lower than incompatible mixtures, which had no comparable dominant species fluctuations. Apparently, when *L. purshianus* populations were reduced by herbivory in the second year, other species in the compatible mixtures compensated for the loss by increasing growth.

Many authors have attributed stability of communities to compensation by species that are differentially damaged by disturbance (Mellinger and McNaughton 1975, McNaughton 1977, Tilman 1996). McNaughton (1977) found that in a Serengeti grassland, grazing released understory species from competition and resulted in 83% regrowth in the more diverse community and only 9% regrowth in the less diverse community, and that the stability effect could be traced to the response of a single species to competitive release. He found similar mechanisms were responsible for increased stability of more diverse plant communities in response to variable rainfall and

concluded that biomass production was stabilized by the presence of species with different environmental optima.

If species in compatible mixtures were able to more fully exploit belowground resources in our experiment, we would expect the compatible mixtures to have greater absolute biomass than incompatible mixtures. Although this expected trend was especially evident in 1995 (Fig. 5A), the response might be attributed to factors other than resource partitioning. Most importantly, the primary criteria for selecting species for the incompatible mixtures were that they be shallow-rooted, early-season and of short-stature, while species selected for the compatible mixtures were not under such selection restrictions. As described for soil water reduction, the largest individuals of the species included in the incompatible mixtures were on average smaller than the largest plants of the species included in the compatible mixtures (Table 3). Higher biomass production of compatible mixtures compared to incompatible mixtures supports our hypothesis that mixtures with a greater range of resource use patterns will be more productive due to more complete utilization of resources in space and time, but greater size of species included in compatible mixtures was at least partly responsible for the observed effect.

Aboveground biomass composition stability-... Mixtures of species with more varied resource use patterns (compatible mixtures) were expected to be more stable, i.e. have more constant proportional abundance of constituent species, by virtue of being able to exploit resources in different spatial and temporal niches. This appeared to be true during both establishment and post-establishment growth (1994-96) because compatible

mixtures had greater stability than incompatible mixtures during this period. However, the hypothesis that compatible mixtures would be more stable than incompatible mixtures was not supported by data from post-establishment growth (1995-96) when stability in compatible mixtures was lower than incompatible mixtures. This might be explained by the response of a single species, *L. purshianus*, which suffered a population crash in 1996, as described above. Its proportional biomass increased greatly in 1995 (47%) compared to 1994 seed mass proportion (18%), then decreased to very low levels in 1996 (12%). Because of the high biomass proportion of *L. purshianus* in 1995, the differences between the 1995 and 1996 levels were much greater than between 1994 and 1996 levels. Since *L. purshianus* was present only in compatible mixtures, the fluctuations resulted in decreased stability compared to incompatible mixtures. This is an example of how one species with a strong response to something other than an applied treatment, in this case herbivory (i.e. grazing by voles), can dominate and obscure possible effects of an intended treatment, as suggested by Huston (1997).

In our experiment, we were able to construct plant communities with predictable structural and functional properties according to a resource use based strategy that may function as an assembly rule. Although the strength of our conclusions is somewhat limited by a size bias effect (i.e. larger species were included in compatible mixtures) and the response of a single species to factors other than resource use (i.e. herbivory), compatible mixtures used more soil resources, produced more and less variable biomass, and had more stable biomass composition during establishment (when herbivory was not

a major factor) than incompatible mixtures. The simple assembly rule that species with different resource use patterns will form more stable plant communities may be an important determinant of community structure (i.e. composition) and function (i.e. performance).

Effects of species richness on community structure and function

Resource depletion-... In the second year of growth, increased species richness was associated with increased soil water depletion at depth. Although two-species mixtures (mixtures C²_b and I²_b) and five-species mixtures (mixtures C⁵ and I⁵) reduced soil water similarly in shallow soil layers, five-species mixtures depleted soil water to a greater extent than two-species mixtures at 70 and 90 cm (Fig. 2b). The increase in soil water depletion at depth by five-species mixtures compared to two-species mixtures supports the hypothesis that more diverse mixtures will utilize soil resources more completely than less diverse mixtures (Ewel et al. 1991, Vitousek and Hooper 1993, Swift and Anderson 1993, Tilman et al. 1996).

We compared the resource use patterns of mixtures containing species with high resource use potential to the resource use patterns of mixtures not containing such species, to determine whether the responses of individual species were likely to be responsible for the diversity effects detected. There were three species (*N. pulchra*, *E. multisetus*, *L. purshianus*) that occurred in one of the five-species mixtures but not in the two-species mixtures and, therefore, had the potential to cause the observed species richness effect. After careful consideration (Brown 1998), we determined that observed

effects were unlikely to have been due to effects of these individual species and can be attributed to species number (richness).

Although, no single species response dominated the depletion of soil moisture within mixtures, we need to address the possibility that the increased use of soil water by more diverse mixtures might be due to greater potential to produce biomass. To do this, we examined the average potential biomass for the species in each of the diversity treatments (Table 3). If the average potential biomass for the species included in five-species mixtures was greater than that for two-species mixtures, then greater plant size may have caused the increased resource use observed in more diverse mixtures. On the contrary, our analysis indicated that average potential biomass for two-species mixtures was greater than five-species mixtures (Table 3), eliminating the possibility that larger plant size in five-species mixtures was the cause for their increased resource use.

Aboveground biomass production-... Consistent with the results of Tilman (1996), more diverse mixtures, regardless of compatibility, produced more biomass than less diverse mixtures. It is unlikely that this effect was solely due to the responses of individual species because all of the large biomass producing species included in five-species mixtures were also included in at least one of the two-species mixtures. In addition, the mean maximum individual biomass of the species included in the five-species mixtures was smaller than that of the species included in the two-species mixtures. As a result, if any effect were predicted by plant size, it would be that the two-species mixtures had the potential to produce more biomass than the five-species

mixtures. This evidence suggests that five-species mixtures produced more biomass than two-species mixtures because of diversity effects and not because of the responses of individual species or greater average plant size.

Aboveground biomass composition stability-... We expected that more diverse mixtures would be more stable in terms of biomass composition due to resource partitioning. We found this to be true only in the establishment year (1994-95). This indicates that during the stages of germination, emergence and seedling growth, the changes in proportional representation within mixtures were smaller in two-species than five-species mixtures. We were unable to detect differences in stability between five-species and two-species mixtures after the establishment period.

Our results generally support those of authors who have found that resource utilization (Tilman et al. 1996, Tilman et al. 1997b), aboveground biomass (Tilman 1996), and community stability (Tilman 1996) increase with species richness. Because the effect were detected regardless of mixture compatibility, we consider this to be robust evidence that diversity can facilitate these plant community functions. The effects of individual species added to a plant community in order to increase diversity did not have overwhelming effects, but were an integral part of the effects of diversity.

Seeding density effects

*Aboveground biomass production-...*Low seeding density plots had more variable aboveground biomass production (higher CVs) than high seeding density plots (Fig. 4B). This high variability was probably due to recruitment of new seedlings and growth of

established perennials after the establishment period in low seeding density plots. It also suggests that density dependent processes (e.g. competition) were limiting increases in biomass in the high density treatment. Aboveground biomass of low seeding density plots was less than high seeding density plots in 1995 and similar to high seeding density plots in 1996 (Fig. 6A). This supports the notion that greater initial variability of biomass production in low seeding density plots was caused by population and individual growth that was less restricted by density effects compared to high seeding density plots.

Seed mixture proportion effects

Aboveground biomass production-... Due to their differences in composition, we expected that mixtures with equal numbers of seeds of each species (proportion 1) would have higher biomass than mixtures with higher proportions of small seeded, slow growing, short stature species (proportion 2) during the establishment period. We expected this difference to be reduced over time as the more competitive species began to dominate after establishment. This prediction was supported by the results because the average biomass of proportion 1 mixtures was greater than proportion 2 mixtures in 1995 and the effect decreased in 1996 (Fig. 6B).

At high seeding density, reduced biomass in proportion 2 compared to proportion 1 was probably due to differential competitive effects on the smaller seeded, slower growing species (Fig. 7). Because higher proportions of seeds of species with small seedlings were included in proportion 2, proportion 1 had relatively more of the species with larger seedlings, resulting in greater biomass of the proportion 1 treatments

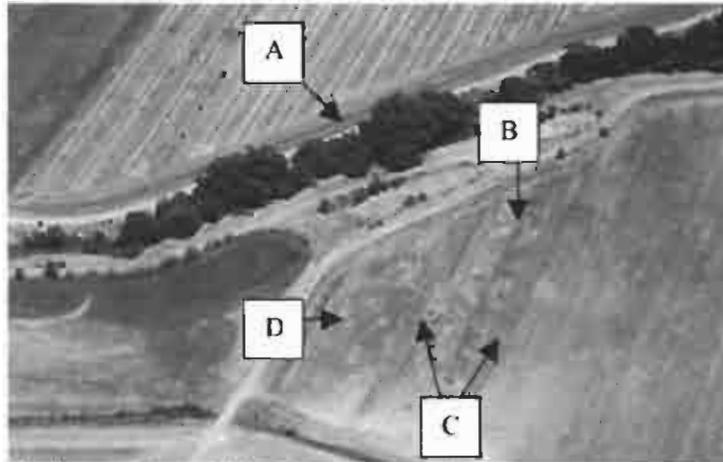
compared to proportion 2 treatments in the first year of growth (Fig. 6B). The significant interaction between proportion and seeding density (biomass of proportion 1 was much greater than proportion 2 at high and not low seeding density) suggests that density dependent processes were at work in the high seeding density treatment (Fig. 7). All species were probably able to perform relatively better in both proportion treatments in the low seeding density treatment compared to the high seeding density treatment because of reduced competition. As a result, at low seeding density total biomass for both proportion treatments was similar.

Aboveground biomass composition stability... We included the two proportion treatment levels in the experiment to determine whether species that are less competitive, especially as seedlings, can be maintained in mixtures by including a higher proportion of their seeds initially. Given their lower competitive ability, we expected the proportional biomass of these species to decrease in the first year. As a result, we expected greater fluctuations in the relative species biomass during the establishment period for proportion 2 plots than proportion 1 plots since proportion 2 plots were seeded with relatively more of the less competitive species. If the pattern continued beyond establishment, it would suggest that these less competitive species continued to be eliminated from the mixtures over time. If there were not differences between the stability of proportional biomass for the two proportion treatments at any stage, it would suggest that neither means of constructing seed mixes resulted in more stable plant mixtures.

In our experiment, some species mixtures were more stable in proportion 1 and

others more stable in proportion 2 (Fig. 9). All of the mixtures that contained the species *Poa secunda* ssp. *secunda* were less stable in proportion 2 than proportion 1 treatments. This may be explained by the population dynamics of this poor competitor when it represented a higher percentage of the initial seed mass in proportion 2 than proportion 1. Low establishment and small adult size usually resulted in biomass for this species near zero by the end of the establishment period (1995) or post establishment period (1996) in both proportion treatments. The difference between initial biomass percentages (1994) and the 1995 and 1996 biomass percentages was greater for proportion 2 than 1, resulting in greater instability measures for proportion 2. Because there was no difference between the two proportion treatment levels during post-establishment growth (1995-96), it seems that the effect was related to sorting of species abundances during establishment. By 1995-96 stability between the two proportion treatment levels was not different, but *P. secunda* had been all but eliminated from most mixtures. In this case, including higher proportions of this less competitive species did not facilitate its persistence in the plant mixtures.

Aerial Photographs of Mixture Experiment - July 6, 1995 - First growing season



Hedgerow Farms Yolo County near Winters

(A) Union School Slough, (B) Monoculture Field Experiment, (C) *Vulpia myuros* Experiment, (D) Mixture Experiment



Richards Boulevard exit off East-bound Interstate 80 at Davis



Student Farm, University of California, Davis

Hedgcrow Farms May 14, 1997
Third Growing Season



C^2_a Two-species compatible



I^2_a Two-species incompatible



C^2_b Two-species compatible



I^2_a Two-species incompatible



C^2_c Two-species compatible

Hedgerow Farms May 14, 1997
Third Growing Season



C³ Three-species compatible



I³ Three-species incompatible



C⁵ Five-species compatible



I⁵ Five-species incompatible

Richards Boulevard May 5, 1995
First Growing Season



C^2_a Two-species compatible



I^2_a



I^2_a Two-species incompatible – same mixture in different replicates of same site



C^2_b Two-species compatible



I^2_b Two-species incompatible

Richards Boulevard May 5, 1995



C^2_c Two-species compatible



C^3 Three-species compatible



I^3 Three-species incompatible



C^5 Five-species compatible



I^5 Five-species incompatible

Student Farm, University of California

Selected plots from Replicate 1. 2-species incompatible in foreground and background. Notice contrast in biomass production.

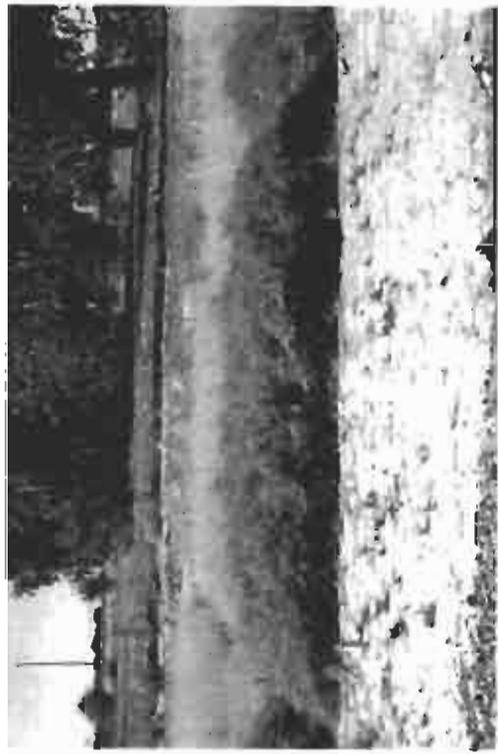


October 13, 1995



March 20, 1996

Selected plots from Replicate 2. Incompatible 2-species in foreground; compatible 2-species in background. Notice phenological differences and *L. otus* thatch.



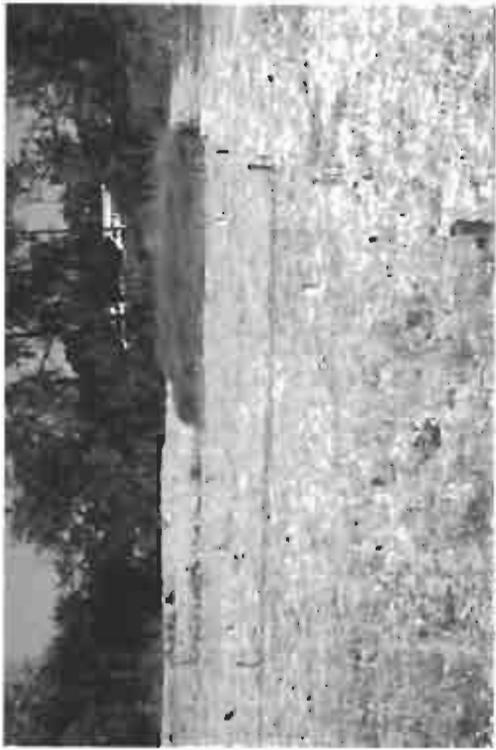
October 13, 1995



March 20, 1996

Richards Boulevard, East bound Interstate 80 exit

Selected plots from Replicate 3. Plots in foreground is 5-species incompatible; second plot is 2-species compatible. Notice low biomass of this replicate.



October 13, 1995



March 20, 1996

Selected plots from Replicate 4. Plot in foreground is 5-species compatible; second plot is 5-species incompatible.



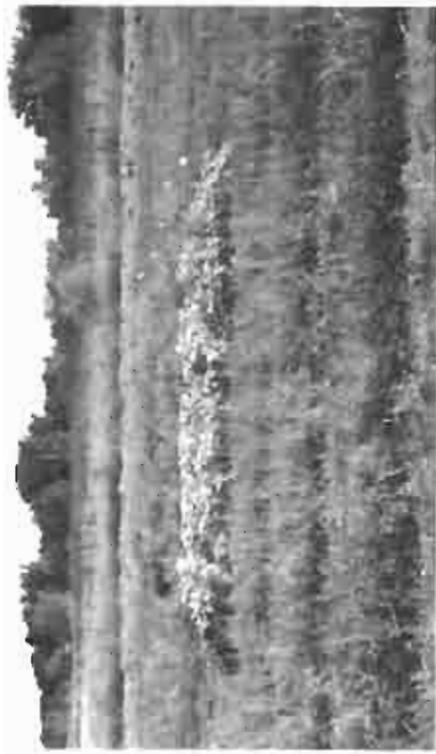
October 13, 1995



March 20, 1996

Hedgerow Farms, Yolo County, Roads 27 and 88

Selected plots from Replicate 5. 2 plots in foreground (between first 4 visible furrows) are 2-species incompatible. 3rd plot is 5-species compatible.

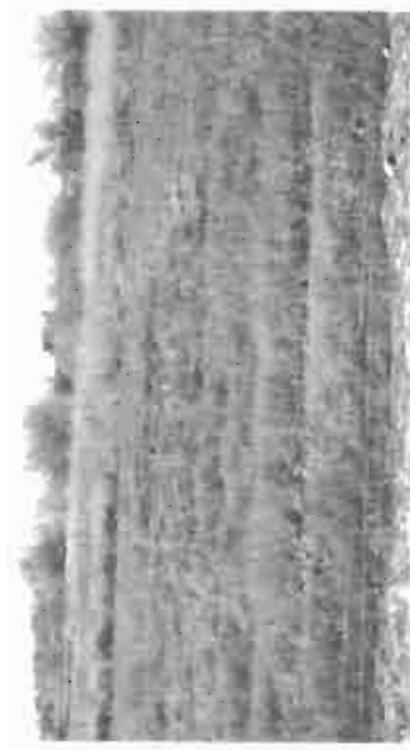


July 14, 1995

Selected plots from Replicate 6.



July 14, 1995



March 24, 1996



March 24, 1996

CONCLUSIONS

We hypothesized the existence of assembly rules based on resource use patterns that lead to partitioning of resources and found that they may be operative in our constructed communities under some, but not all conditions. As Drake (1990) asserted, we consider the assembly rule to be "the mechanism behind the variation" of community structure observed. In our experiment, we were able to show that an assembly rule based on belowground resource use can, in part, explain community structure and function, although the strength of our conclusions is limited by size bias (i.e. larger species were included in compatible mixtures) and factors other than resource use (i.e. herbivory). We found that mixtures of species with complementary resource use reduced soil water to a greater extent, produced more and less variable biomass, and had more stable biomass composition during establishment (without herbivory) than mixtures of species with more similar resource use patterns. Although the resource use and total biomass results may have been influenced by the larger average size of species included in compatible mixtures, this was less problematic for the composition stability results because stability was a measure of relative change in species composition.

Species richness of mixtures also had important implications for community functional characteristics. Regardless of compatibility, more diverse mixtures utilized soil water more completely and produced more aboveground biomass with more stable species composition during establishment than less diverse mixtures. These diversity effects were not due to dominance of individual species or because of size bias of species

included in diversity treatments. Overall, we were able to determine that there were effects of compatibility treatments on soil water use and aboveground biomass production and stability, regardless of species diversity. In addition, regardless of compatibility treatment, there were effects of species diversity on soil water use, aboveground biomass production, and biomass composition stability.

In summary, resource partitioning appears possible within these herbaceous plant communities. This was predictable through *a priori* knowledge of the belowground resource use patterns of species grown separately. Diversity of species guilds within the communities (i.e. compatibility), regardless of species number, produced many of the community functions associated with greater species diversity. Thus, we suggest that complementarity of spatial and temporal belowground resource use serves as a mechanism of community assembly, an assembly rule, for these herbaceous plant communities. Species diversity *per se* was not necessary to produce the observed community functions, but in its absence, diversity of species functional groups was.

MANAGEMENT IMPLICATIONS

Based on the findings of this experiment, we make a number of suggestions to erosion control practitioners. Construction of mixtures with multiple species that have different resource use patterns (e.g. shallow and deep rooting, early and late flowering) can lead to more stable plant communities, providing superior erosion control. Also, we found that increasing the proportion of seed of species that have small seeds, slow

growing seedlings, and small plant size did not improve the stability of plant communities. Equal numbers of seeds of each species was a satisfactory approach to constructing the seeding mixtures.

Seeding at high density (1076 seeds m⁻²) resulted in higher biomass, representing greater protection of soil from erosion, than the low seeding density (269 seeds m⁻²). However, under experimental conditions where weeds were removed, the low density mixtures produced similar biomass to the high density mixtures by the second year of growth. There appeared to be no advantage to higher seeding densities after the first growing season in terms of aboveground biomass amount or variability when weeds were controlled. We recommend using the high seeding rate when economically feasible and the potential for competition from weeds is high (e.g. when seed banks are present and the possibility for weed control is limited). If weeds can be controlled, the low seeding rate may be sufficient.

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Chapter 3 Appendix 1

The proportion 2 seeding treatment included a higher proportion of small seeded, slow growing, low vigor species. The size of the increase was determined by a formula arrived at through discussions with prairie restorationists experienced with native and introduced species in California including John H. Anderson (Hedgerow Farms, Winters, CA), David Gilpin (Pacific Coast Seeds, Livermore, CA), John Haynes (Caltrans), Paul Kephart (Circle M Ranch, Big Sur, CA) and Scott Stewart (Conservaseed, Rio Vista, CA). Each species was assigned a species factor used in calculating its proportion within each mixture.

Species factor = $1 / (\text{seed size factor})(\text{plant size factor})(\text{growth factor})$

Proportions of species included in mixtures were determined by dividing each individual species factor by the sum of the species factors for the species in the mixture.

Seed size factor:

Seeds/kg	Seed size factor
> 2,200,000	0.25
1,100,000 - 2,200,000	0.5
550,000 - 1,100,000	0.75
275,000 - 550,000	1
137,500 - 275,000	1.5
< 137,500	2

Plant size factor = height factor + area factor (rating for area covered by canopy of average mature plant including vegetative propagules, e.g. tillers and rhizomes):

Height class	Height factor	Area class	Area factor
< 30 cm	0.5	0 - 30	1
30 - 70 cm	1	30 - 60	2
> 70 cm	2	> 60	3

Plasticity/growth rate/vigor factor:

Type of plants	Growth factor	Species
Small seeded, slow growing, low vigor seedlings	0.5	<i>Eremocarpus setigerus</i> <i>Poa secunda</i> ssp. <i>secunda</i> <i>Nassella pulchra</i> <i>Vulpia microstachys</i>
	0.6	
	0.7	<i>Elymus multisetus</i>
	0.8	
	0.9	
Large seeded, slow growing, low vigor seedlings	1.0	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i> <i>Elymus trachycaulus</i>
	1.25	
Fast growing perennial grasses, legumes	1.5	<i>Lotus purshianus</i>
	1.75	
	2	
Aggressive annuals	3	
	4	<i>Vulpia myuros</i>
	5	
	6	
	7	
	8	

Species	Seed size factor	Plant size factor	Growth factor	1/Species factor	Species factor
<i>Elymus multisetus</i>	1	1	0.75	0.75	1.33
<i>Elymus trachycaulus</i>	1	1	1	1	1
<i>Eremocarpus setigerus</i>	2	0.5	0.5	0.5	2
<i>Hordeum brachyantherum</i> <i>ssp. brachyantherum</i>	1	1	1	1	1
<i>Lotus purshianus</i>	0.75	1.5	1.5	1.69	0.59
<i>Nassella pulchra</i>	1	0.8	0.5	0.4	2.5
<i>Poa secunda</i> ssp. <i>secunda</i>	0.5	0.5	0.5	0.125	8
<i>Vulpia microstachys</i>	0.75	0.5	0.5	0.19	5.3
<i>Vulpia myuros</i>	0.5	2	4	4	0.25

CHAPTER 4

Effects of Plant Community Resource Use Patterns and Species Diversity on Success of the Invaders *Bromus hordeaceus* (soft chess) and *Centaurea solstitialis* (yellow starthistle)

ABSTRACT

I studied the success of two invading plant species with different phenologies and rooting depths when planted into established herbaceous plant communities. One of the invaders was an early-season flowering annual grass (*Bromus hordeaceus*), the other a late-season flowering annual forb (*Centaurea solstitialis*). Two two-species and two-five species mixtures, each seeded at two densities, were included in the experiment. One of the two-species mixtures and one of the five-species mixtures were composed of species with varying rooting depths and phenologies (compatible mixtures). The other two-species and five-species mixtures were composed of species that had shallow rooting depths and early-season flowering times (incompatible mixtures). A control treatment with no background vegetation was included in one of the two years of the experiment. Two replicates of the experiment were located at each of two sites with different fertility levels.

I found that the early-season, shallow rooted invader (*Bromus*) was most successful in mixtures of species with varied resource use patterns (compatible mixtures); *Bromus* was least successful in mixtures composed of species with resource use patterns most similar to each other and to *Bromus* (incompatible mixtures). The late-season species (*Centaurea*) was most successful in the incompatible mixtures made up of early-season, shallow rooting species; *Centaurea* was least successful in the compatible mixtures that included some species with resource use patterns similar to itself. Overall, invaders were not as successful in plant communities composed of species that utilized

resources similarly to the invader. Invaders were less successful in more diverse (greater species rich) mixtures and invader success was reduced by existing vegetation, no matter the resource use patterns of the established species. Invader populations showed the greatest potential for growth under more fertile conditions.

In summary, species diversity, the presence of existing vegetation, and limited fertility reduced invader success. The community resource use patterns associated with the ability to reduce invader success depended on the resource use patterns of the invader. There was no indication that invasion could be prevented with established herbaceous vegetation. However, revegetation specialists should be aware that (1) establishing a desirable plant community, (2) planting a variety of species that compete directly with invaders for resources, and (3) avoiding the increase of readily available nutrients will reduce invader success.

INTRODUCTION

Maintaining desirable vegetation and reducing invasion of weedy species on roadsides is a costly undertaking that conventionally includes mowing, the use of herbicides, and blading. All of these practices require labor, equipment and materials. Developing plant materials and techniques that reduce the need for the disturbance based management practices mentioned above, is one way to reduce maintenance costs and herbicide use.

Grassland communities on roadsides are especially prone to invasion. Disturbance is common and propagules of alien species are abundant near roads due to human activity. A previous study found that alien species decreased with increasing distance from roadways (Frankel 1977 cited in Mooney and Drake 1986).

Since early this century, scientists have been investigating the characteristics of invading species and plant communities in search of mechanisms that promote species invasions. Although a suite of characteristics associated with invasive plants have been identified, there are no universal rules that reliably identify which species will become pests. G.H. Orians (1986) lists the characteristics of invasive species as having high population growth rates, short life cycles, high allocation to reproduction, good dispersal, and flexible utilization of a variety of environmental resources. However, Roy (1990), in a review of the characteristics of plant invaders, could find no physiological or genetic attributes common to all invaders. He emphasized that the ecological and evolutionary features of both habitats and introduced species were important determinants of invasion

success. The observation that invading species perform best in habitats with climates and disturbance patterns similar to their place of origin (Crosby 1986) is an example of this.

Certain characteristics of plant communities predispose them to invasion. There is widespread agreement that disturbance can facilitate the establishment of invading species (Elton 1958, Crosby 1986, Mooney and Drake 1986). Plant communities with closed canopies that limit light at the soil surface (such as forests) appear to be resistant to invasion while grasslands, among other communities, are easily invaded (Frankel 1997 cited in Mooney and Drake 1986). In the same text, H.G. Baker (1986) indicated that grasslands are prone to invasion because of patchy disturbance that provides footholds for invasive species. It has also been hypothesized that decreased species diversity in plant communities can encourage the establishment of invasive species. Elton (1958) stated that invasive plants are found most often in habitats that have been disturbed and simplified (i.e. species numbers have been reduced) by human activity.

In this study, I experimentally test two of the early ideas about the mechanisms of invasion. First, I investigate the hypothesis that plant communities that utilize resources most completely, leaving little for invaders, are less susceptible to invasion. This view indicates that plant communities including species with varied resource use patterns (e.g. early- and late-season, shallow and deep rooting) may more completely utilize resources in space and time, reducing invasibility. Second, I address the hypothesis that more diverse plant communities are less prone to invasion than simpler communities. Plant communities with many species may be more likely to include species that will compete

directly with invading species for the essential resources water, light and nutrients, reducing invader success. I conducted an experiment to investigate how the number of species included in a plant community and their patterns of belowground resource use affect the establishment, growth and reproduction of two weedy species with different growth forms and phenologies.

METHODS

In the fall of 1996, the weed invaders *Bromus hordeaceus* (soft chess, hereafter *Bromus*) and *Centaurea solstitialis* (yellow starthistle, hereafter *Centaurea*) were planted into existing mixtures of herbaceous prairie plants. In the fall of 1997, the experiment was repeated with *Centaurea*. The mixtures had been seeded in the fall of 1994 and winter of 1995 as described in Chapter 3 of this report. Two replicates were located at the Student Farm site and two replicates at the Hedgerow Farms site.

Invaders were planted into four mixtures; two of the mixtures included two species and two included five species (Table 1). One of the two-species and one of the five-species mixtures were composed of species with different resource use patterns (i.e. compatible mixtures). In the two-species compatible mixture (2-C), one species had shallow roots and the other had deep roots (*per* Chapter 2 of this report). In the five-species compatible mixtures (5-C), species had a variety of rooting depths (shallow and deep) and flowering times (early-, mid-, and late-season). One of the species in this mixture was also a nitrogen fixing legume.

Table 1. Densities of viable seed and composition of mixtures. 2-C = two-species compatible, 2-I = two-species incompatible, 5-C = five-species compatible, 5-I = five-species incompatible.

MIXTURE	SPECIES	VIABLE SEEDS/m ²	
		LOW DENSITY 269 seeds/m ²	HIGH DENSITY 1076 seeds/m ²
2-C	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>	135	538
	<i>Poa secunda</i> ssp. <i>secunda</i>	135	538
2-I	<i>Poa secunda</i> ssp. <i>secunda</i>	135	538
	<i>Vulpia microstachys</i>	135	538
5-C	<i>Eremocarpus setigerus</i>	54	215
	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>	54	215
	<i>Lotus purshianus</i>	54	215
	<i>Nassella pulchra</i>	54	215
	<i>Poa secunda</i> ssp. <i>secunda</i>	54	215
5-I	<i>Elymus multisetus</i>	54	215
	<i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>	54	215
	<i>Poa secunda</i> ssp. <i>secunda</i>	54	215
	<i>Vulpia microstachys</i>	54	215
	<i>Vulpia myuros</i>	54	215

The two remaining mixtures were composed of plants with similar resource use patterns (i.e. incompatible mixtures). In the two-species incompatible mixture (2-I), both species had shallow roots and flowered early in the season. The species included in the five species incompatible mixtures (5-I) were early-season or shallow rooting, or both.

Low and high density mixtures of established prairie plants (Table 1) were included in the invader experiment. Equal numbers of seeds of the species in the mixtures were planted to reach the final seeding densities of 269 seeds m^{-2} (low density) and 1076 seeds m^{-2} (high density). The plots were 3 m by 4.5 m and were divided into six subplots that were 1.5 m on each side. Invader species treatments were randomly assigned to subplots. Each invader species was planted at two densities. The high density treatment was 36 seeds planted equidistant from each other in a 0.063 m^2 grid (25 cm by 25 cm, 5 cm between seeds). The low density treatment was 36 seeds planted equidistant from each other in a 1.0 m^2 grid (1 m by 1 m, 20 cm between seeds). Seeds were planted at a depth of 0.5 to 1.0 cm by making a small impression in the soil with a rod, dropping a seed into the impression through a tube, then passing the rod through the tube and pressing the seed into the surface of the impression. In 1997, three seeds of *Centaurea* were planted at each of the 36 locations within the 0.063 m^2 and 1.0 m^2 grids (108 seeds/grid) as described above but no impressions were made and the final step of pressing the seed into the soil surface with a rod was omitted.

In addition to planting invaders in established mixtures of prairie plants in 1997, both species were also planted similarly at low and high densities into bare ground as a

control. All species that were not planted were removed from these controls throughout the experiment. Results from this control represent invader performance without interspecific (between species) competition and with minimal intraspecific (within species) competition. In 1998, seeds were planted into the same control plots used in 1997 where a seedbank of *Centaurea* had been established. Species other than *Centaurea* were removed from these plots throughout the 1998 growing season. Results from this control represent *Centaurea* performance with intraspecific competition. We were unable to distinguish between *Centaurea* plants that had grown from seeds we planted and seeds that were present in the seed bank. Consequently, we were not able to evaluate population level responses and the meaning of individual responses was not completely clear. The controls were omitted from the analyses because the data were not comparable to the other treatments.

For the first year of the experiment, replicates at the Student Farm site were planted October 28 through October 31, 1996 and those at Hedgerow Farms were planted November 2 and 3, 1996. For the second year, the Student Farm site was planted September 16 and 17, 1997 and the Hedgerow Farms site was planted on September 11 and 15, 1997.

The mixtures at the Student Farm were watered with furrow and sprinkler irrigation from October 23 through November 5, 1997. *Centaurea* emergence was noted on November 3, 1997. Natural rainfall began on November 10, 1997.

Seed germination rates

Centaurea seed planted in both 1996 and 1997 was collected from wild plants near Davis, California in August of 1996.

Bromus seed was obtained from Albright Seed Company (Camarillo, California) in 1989. Germination of seed was tested using modified methods described in the Official Seed Testing Handbook (Wiesner 1989). *Centaurea* germination was 72.5 ± 3.35 % and *Bromus* germination was 86.0 ± 3.0 % (both are the mean percentage of 300 seeds that germinated \pm standard error of the mean).

Climate 1996-1997

The total precipitation in Davis for 1997 was 467.36 mm, near the thirty year average of 460.05 mm (Owenby and Ezell 1992). Despite this, the pattern of rainfall was unusual. In January 219.96 mm of precipitation fell, 220% of the thirty year average. Precipitation in February, March and April was a fraction of normal with 0.9%, 16% and 11% of the thirty year average falling. In May and June rainfall was about 30% higher than the thirty year average which extended water availability.

The wet season for 1998 began in the fall of 1997 with 111.0 mm of rain falling in November, about 150% of the thirty year average. Rainfall for December 1997 and January 1998 were close to the average, but precipitation was well above average for February (297.94 mm, 410% of the thirty year average) and May (59.44 mm, 835% of the thirty year average). Precipitation was below average for March (47.24 mm, 70% of the thirty year average). Overall during 1998, 565.15 mm of rain fell, 123% of the thirty year

average. This year was an above normal rainfall year and water availability was extended due to considerable rainfall late in the season.

Centaurea solstitialis

In 1997, we evaluated seedling emergence of *Centaurea* February 16 through 28 and found it to be extremely low. In the hope of increasing the number of established plants surviving to the end of the experiment, four *Centaurea* seedlings were transplanted into each of the subplots of prairie mixtures assigned to this treatment. The transplants were grown from seeds planted on January 23, 1997 in 105 ml (13.6 cm deep) containers filled with standard potting soil. Seedlings were transplanted February 23 and 24, 1997 into replicates at the Hedgerow Farms site and Student Farm site, respectively. The seedlings had no true leaves at the time of transplanting and their roots reached the bottom of the containers. Transplants were positioned at the corners of a square 50 cm on a side located in the middle of each subplot. To transplant the seedlings, holes were created in the soil using a rod, the transplant roots were separated from potting soil and dipped in water. The roots were placed in the hole, moist soil was pressed into to hole to surround the roots, and 50 ml of water was added. On February 27 and 28, 27 ml of water was sprayed on each transplant at the Student Farm and Hedgerow Farms sites, respectively. *Centaurea* seedlings that had grown from the original seed were removed from the plots.

Centaurea transplant survival, biomass production and reproductive potential (i.e. number of seeds, whether filled or unfilled) were evaluated from the surviving plants

harvested July 29 through 31, 1997. The surviving transplants were counted and clipped at ground level. The flower heads were counted and 15 to 20 flower heads (or all of the flowerheads on the plant if less than 15) were selected from each individual for reproductive potential estimation. The selected flower heads used to estimate reproductive potential had completely faded flower petals (corollas), had not dropped any seeds, and the bracts at the base of the flower head were green or dry. Selected flower heads and remaining biomass were dried separately at 100 ° C for one hour, then 60 ° C to constant weight (24 hours). The diameters of the selected flower heads were measured after drying and number of ovules (filled or unfilled seeds) was counted.

The reproductive potential of each plant was estimated by multiplying the individual's average number of ovules per flower head (the mean of up to 20 selected flower heads) by the plant's total number of flower heads. All dried plant parts were weighed to determine total biomass.

In 1998, we counted the number of *Centaurea* plants within the subplots and selected four plants to measure and harvest. We chose two plants closest to the center of the subplot and two plants closest to two arbitrarily selected diagonal corners of the subplot. The flower heads (mature and immature) on each plant were counted and the diameters of 30 flowerheads that were in full bloom (corollas bright yellow to faded, bracts at base of flower head green) were measured. Biomass samples were dried at 55 ° C to constant weight (24 hours) and weighed.

There was a significant positive relationship between flower head wet diameter and ovule number (ovules/flower head = $11.56 + 5.58$ (flower head wet diameter), $P = 1.08 \times 10^{-6}$, $r^2 = 0.62$). This was determined by performing a simple linear regression of the average number of ovules per flower head against the average wet flower head diameter for individuals harvested in 1997 (BMDP New System for Windows, Version 1.0, BMDP Statistical Software, Inc., Los Angeles, California). This relationship was used to estimate the reproductive potential of individual plants harvested in 1998. Average wet flower head diameters measured in 1998 were entered into the above regression equation to generate estimates of the number of ovules in each flower head. The estimate of ovules per flower head was multiplied by the number of flower heads to estimate the reproductive potential of each plant (i.e. the number of ovules produced).

Bromus hordeaceus

We did not evaluate initial emergence of this invader species because it was impossible to distinguish its seedlings from those of other grasses in the prairie mixtures. *Bromus* densities (plants surviving to flowering) were determined and biomass and reproductive potential harvests were made April 23 through 25, 1997. We counted the number of *Bromus* plants within the area where seed was originally planted. We then harvested the three individual plants closest to the center of the subplot. The vegetative parts of the plant were dried at 100 ° C for an hour then 60-65 ° C to constant weight (24 hours).

The spikelets in each inflorescence were counted. The florets in a subsample of the spikelets were counted in order to estimate the average number of florets per spikelet. In a sample of thirty plants, the mean number of florets per spikelet estimated with our subsampling method was not significantly different from the actual mean number of florets per spikelet (t-test $p = 0.78$, i.e. we cannot say that the two means were different; there is a 78 % chance of being wrong if we say that the means are not equal when they are in fact equal). By knowing the total number of spikelets and the average number of florets per spikelet, we were able to estimate the number of florets produced by each plant, i.e. its reproductive potential.

After counting, inflorescences were dried at 60-65 ° C to constant weight (24 hours). We were unable to estimate reproductive potential for plants that had lost florets and had no intact spikelets so these were considered missing data. Vegetative parts and inflorescences were weighed to determine total plant biomass, whether or not florets had been lost.

Statistical analysis

Statistical significance was set at the 0.05 probability level. Probability estimates lower than 0.05 were considered statistically significant results indicating that the probability the means could be different due to chance alone and not a real treatment effect were less than 5%.

Statistical tests that do not rely on the distributional properties of the data (in particular, data are not required to be normally distributed or have equal variances) were

employed in the analyses. Percent emergence of *Centaurea* and all *Bromus* variables were analyzed with analysis of variance of ranked data. Differences between treatments were determined using planned linear contrasts. Significant linear contrasts are reported in the Results section when ANOVA probability levels (i.e. *P* values) for the relevant treatment effect was less than 0.05, unless otherwise stated. Means of *Centaurea* transplant treatments were compared using the Mann-Whitney independent rank sum test.

RESULTS

Centaurea solstitialis

In 1997, percent emergence of *Centaurea* was greater in the control treatments with no background vegetation (mean \pm standard error of the mean: 34.03 ± 5.42 %) than in species mixture treatments (6.33 ± 1.27 %)(linear contrast $P = 0.0001$). None of the *Centaurea* seedlings transplanted into the mixtures survived to flowering that year, but 84.37 % survived to flowering in the controls (no background vegetation). The plants in the control plots produced more biomass (142.26 ± 86.33 g) and had greater reproductive potentials ($23,084.38 \pm 13,576.26$ g) than those planted into the mixtures (0 g) ($P = 3.56 \times 10^{-9}$).

In 1998, we could not detect an effect of compatibility treatments on *Centaurea* emergence or density. However, individual *Centaurea* plants tended to have higher reproductive potentials (more ovules) in incompatible mixtures than compatible mixtures, though the result was not statistically significant (linear contrast $P = 0.052$). Populations

of *Centaurea* had greater reproductive potential in incompatible mixtures than compatible mixtures (linear contrast $P = 0.04$). Individual plants produced more biomass (linear contrast $P = 0.04$) in incompatible mixtures than compatible mixtures. Populations of *Centaurea* produced more biomass in the incompatible treatments compared to compatible mixtures (linear contrast $P = 0.03$)(Table 2). Photographs of these treatments can be found on pages 176 and 177.

Table 2. Performance of *Centaurea solstitialis* seeds planted into compatible mixtures (species with differing resource use patterns) and incompatible mixtures (species with similar resource use patterns) (108 seeds planted in each plot) in 1998. Values are mean \pm standard error of the mean for survival, biomass production and reproductive potential (the number of ovules produced). Means followed by symbols are significantly different at the following probability levels: + $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

COMPATIBILITY	SURVIVAL TO FLOWERING (%)	BIOMASS (g)		REPRODUCTIVE POTENTIAL (ovule number)	
		Individual	Population	Individual	Population
Compatible	6.74 \pm 1.03	92.61 \pm 21.35*	888.01 \pm 256.81*	14,686 \pm 3,336+	142,346 \pm 40,748+
Incompatible	9.20 \pm 1.50	215.78 \pm 47.15	2,334.17 \pm 565.30	32,492 \pm 7,495	354,970 \pm 77,209

In 1997, percent emergence of *Centaurea* was greater in two-species mixtures (8.51 \pm 2.21) than five-species mixtures (3.93 \pm 0.95 %)($P = 0.03$). No difference in emergence or percent survival to flowering could be detected between two- and five-species mixtures in 1998. Reproductive potentials of *Centaurea* individuals tended to be greater in two-species mixtures than five-species mixtures (ANOVA $P = 0.07$, linear

contrast $P = 0.0004$) (Table 3). The reproductive potentials of *Centaurea* populations were greater in two-species mixtures than five-species mixtures (linear contrast $P = 0.0003$) (Table 3). Biomass production of individual plants was greater in two-species mixtures than five-species mixtures (linear contrast $P = 0.0001$). Biomass production by *Centaurea* populations was greater in two-species mixtures than five-species mixtures (linear contrast $P = 0.0002$) (Table 3). Photographs of these effects can be found on pages 176 and 177.

Table 3. Performance of *Centaurea solstitialis* seeds planted into two-species mixtures and five-species mixtures (108 seeds planted in each plot) in 1998. Values are the mean \pm standard error of the mean for survival, biomass production and reproductive potential (the number of ovules produced). Means followed by symbols are significantly different at the following probability levels: + $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

MIXTURE SPECIES NUMBER	SURVIVAL TO FLOWERING (%)	BIOMASS (g)		REPRODUCTIVE POTENTIAL (ovule number)	
		Individual	Population	Individual	Population
Two-species	9.55 \pm 1.20	233.54 \pm 44.86 ***	2,467.60 \pm 559.36 ***	34,607 \pm 7,227 ***	364,658 \pm 75,362 ***
Five-species	6.40 \pm 1.35	74.85 \pm 22.48	754.58 \pm 242.97	12,570 \pm 3,516	132,659 \pm 42,464

In 1997, percent emergence of *Centaurea* was greater at the less fertile Hedgerow Farm site (14.44 \pm 2.4 %) than at the more fertile Student Farm site (4.49 \pm 1.98 %) (linear contrast $P = 0.0001$). In 1998, there were no detectable differences between *Centaurea* emergence or percent survival to flowering at the two sites. Individual and population reproductive potentials and individual plant biomass were greater at the

Student Farm site than at the Hedgerow Farm site (linear contrast $P = 0.002, 0.008, 0.006$, respectively) (Table 4). Biomass of *Centaurea* populations tended to be greater at the Student Farm site (ANOVA $P = 0.07$, linear contrast $P = 0.01$) (Table 4).

Table 4. Performance of *Centaurea solstitialis* seeds planted at the Student Farm and Hedgerow Farms sites (108 seeds planted in each plot). Values are mean \pm standard error of the mean for survival, biomass production and reproductive potential (the number of ovules produced). Means followed by symbols are significantly different at the following probability levels: + $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

SITE	SURVIVAL TO FLOWERING (%)	BIOMASS (g)		REPRODUCTIVE POTENTIAL (ovule number)	
		Individual	Population	Individual	Population
Student Farm	7.29 \pm 1.57	229.22 \pm 61.21 **	2,188.89 \pm 691.96 +	35,578 \pm 9,643 **	418,982 \pm 103,237 **
Hedgerow Farms	8.65 \pm 1.88	49.28 \pm 11.98	1,143.92 \pm 482.98	6,923 \pm 1,634	85,602 \pm 24,422

Bromus hordeaceus

Bromus was more successful in control treatments than other mixture treatments based on percent survival to flowering, individual plant and population (i.e. the plants established from the original 36 seeds planted) biomass and reproductive potential (number of florets, i.e. potential seeds). A greater percentage of *Bromus* seeds planted reached the flowering stage in the control treatment (no background vegetation) than in the plant mixture treatments (linear contrast $P = 0.0001$) (Table 5). Individual plants were larger and produced more florets (linear contrast $P = 0.0001$ and 0.0001 , respectively), and population biomass and reproductive potentials were greater (linear

contrast $P = 0.0001$ and 0.0001 , respectively) in the control with no background vegetation than in the mixture treatments (Table 5).

Table 5. Performance of *Bromus hordeaceus* seeds planted into the control treatment with no background vegetation and the species mixture treatments (36 seeds planted in each plot) in 1997. Values are the mean \pm standard error of the mean for survival, biomass production and reproductive potential (the number of florets produced). Means followed by symbols are significantly different at the following probability levels: + $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

BACKGROUND VEGETATION	SURVIVAL TO FLOWERING (%)	BIOMASS (g)		REPRODUCTIVE POTENTIAL (floret number)	
		Individual	Population	Individual	Population
None	61.46 \pm 6.93	9.43 \pm 2.25 ***	229.89 \pm 75.23 ***	3,342.43 \pm 643.25 ***	80,432.27 \pm 22,564.23 ***
Species Mixtures	14.37 \pm 2.29	0.28 \pm 0.07	3.01 \pm 1.16	166.48 \pm 40.91	1,268.30 \pm 495.72

Bromus survival, growth and reproduction were greater in compatible mixtures than incompatible mixtures. More of the seeds planted into compatible mixtures reached flowering stage than those planted into incompatible mixtures (linear contrast $P = 0.0001$) (Table 6). Individual *Bromus* plants growing in compatible mixtures produced similar amounts of biomass as those growing in incompatible mixtures, but plants tended to be larger in compatible mixtures (linear contrast $P = 0.08$). *Bromus* individuals growing in compatible mixtures tended to produce more florets than those growing in incompatible mixtures (linear contrast $P = 0.07$) (Table 6). Populations of *Bromus* produced more

biomass had higher reproductive potentials when growing in compatible mixtures than when growing in incompatible mixtures (linear contrast $P = 0.003$ for both) (Table 6).

Table 6. Performance of *Bromus hordeaceus* seeds planted into compatible mixtures (species with differing resource use patterns) and incompatible mixtures (species with similar resource use patterns) (36 seeds planted in each plot) in 1997. Values are the mean \pm standard error of the mean for survival, biomass production and reproductive potential (the number of individual flowers produced). Means followed by symbols are significantly different at the following probability levels: + $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

COMPATIBILITY	SURVIVAL TO FLOWERING (%)	BIOMASS (g)		REPRODUCTIVE POTENTIAL (florete number)	
		Individual	Population	Individual	Population
Compatible	22.22 \pm 3.92	0.37 \pm 0.13 *	5.24 \pm 2.24 ***	197.88 \pm 68.47 +	2,147.01 \pm 920.00 **
Incompatible	6.51 \pm 1.41	0.18 \pm 0.06	0.78 \pm 0.31	122.88 \pm 26.88	298.67 \pm 98.12

Bromus had greater survival, biomass production and reproductive potential when planted into two-species mixtures compared to five-species mixtures. More of the seeds planted into two-species mixtures reached flowering than those planted into five-species mixtures (linear contrast $P = 0.007$) (Table 7). Plants growing in two-species mixtures were larger and produced more florets than those growing in the five-species mixtures (linear contrast $P = 0.007$ for both) (Table 7). Populations of *Bromus* growing in two-species mixtures produced greater biomass and had greater reproductive potentials than those growing in five-species mixtures ($P = 0.007$ for both).

Table 7. Performance of *Bromus hordeaceus* seeds planted into two-species mixtures and five-species mixtures (36 seeds planted in each plot) in 1997. Values are the mean \pm standard error of the mean for survival, biomass production and reproductive potential (the number of florets produced). A means followed by symbols are significantly different from the second mean in the same column at the following probability levels: + $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

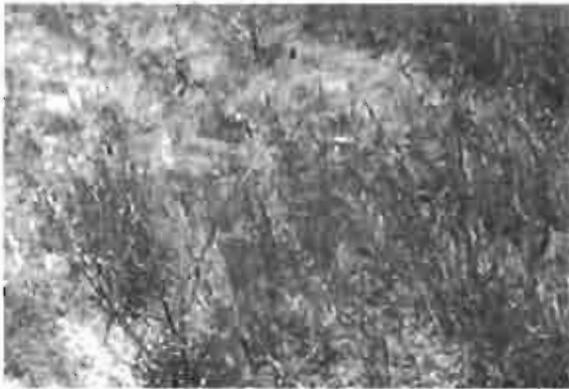
MIXTURE SPECIES NUMBER	SURVIVAL TO FLOWERING (%)	BIOMASS (g)		REPRODUCTIVE POTENTIAL (foret number)	
		Individual	Population	Individual	Population
Two-species	17.22 \pm 3.44 **	0.40 \pm 0.13 **	5.21 \pm 2.25 **	201.13 \pm 66.85 **	2,139.10 \pm 950.54 **
Five-species	11.46 \pm 3.01	0.15 \pm 0.05	0.81 \pm 0.25	113.49 \pm 28.50	368.46 \pm 114.18

A higher percentage of *Bromus* individuals reached maturity at the less fertile Hedgerow Farms site than at the more fertile Student Farm site (linear contrast $P = 0.0001$) (Table 8). However, individual plants were larger (linear contrast $P = 0.0021$) and produced more seed (linear contrast $P = 0.0001$) under more fertile than less fertile conditions (Table 8). The biomass and seed produced by *Bromus* populations were greater at the more fertile site than the less fertile site (linear contrast $P = 0.002$ and 0.0001 , respectively) (Table 8).

Table 8. Performance of *Bromus hordeaceus* seeds planted at the Student Farm and Hedgerow Farms sites (36 seeds planted in each plot) in 1997. Values are the mean \pm standard error of the mean for survival, biomass production and reproductive potential (the number of florets produced). A mean followed by symbols is significantly different from the second mean in the same column at the following probability levels: + $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

SITE	SURVIVAL TO FLOWERING (%)	BIOMASS (g)		REPRODUCTIVE POTENTIAL (floret number)	
		Individual	Population	Individual	Population
Student Farm	11.81 \pm 3.35 ***	1.38 \pm 0.72 **	33.76 \pm 20.42 **	796.08 \pm 369.77 ***	12,312.29 \pm 7,008.60 ***
Hedgerow Farms	27.39 \pm 4.10	1.20 \pm 0.44	22.68 \pm 11.30	564.98 \pm 193.68	8,736.63 \pm 4,144.49

Hedgerow Farms Replicate 5



Low density *C. solstitialis* in two-species compatible mixture



High density *C. solstitialis* in two-species compatible mixture



Low (foreground) and high (background) density *C. solstitialis* in two-species incompatible mixture



C. solstitialis control plot without competition from other plants

Hedgerow Farms Replicate 6



Low density *C. solstitialis* in five-species compatible mixture



High density *C. solstitialis* in five-species compatible mixture



Low density (right background) and high density (left foreground) *C. solstitialis* in five-species incompatible mixture



Low density (left foreground) and high density (right background) *C. solstitialis* control (1997) without competition from other plants

DISCUSSION

Invading species performed better without competition from existing vegetation. This was true for both the early-season annual grass *Bromus hordeaceus* and the late-season annual forb *Centaurea solstitialis*. This result indicates that the presence of a desirable plant community is better at preventing invader success than not having vegetation present. The control with no background vegetation is analogous to the bare, scraped condition of roadsides after blading or herbicide use (after soil residual activity has disappeared), both regular roadside management practices. Management treatments that create this kind of disturbance are prone to the establishment of weedy plants. Given that roadways are sources of propagules of invasive species, creating disturbance through management increases their chances for success greatly.

The resource use patterns of existing vegetation was an important determinant of invader success. However, invader performance depended upon the resource use patterns of the particular invader and the species present in the established plant community, supporting the view that the interaction between invader and community characteristics determine invader success (Roy 1990). The early season annual grass, *Bromus*, performed better in the compatible mixtures (those composed of species with resource use patterns that varied in space and time) than incompatible mixtures (those composed of species with similar resource use patterns, i.e. early season, short stature, shallow rooting). This result may indicate that in the incompatible mixtures *Bromus* always had to compete directly with plants that had similar resource use patterns to itself; neighbors

were always early season, short stature and shallow rooting, just as it is. In incompatible mixtures, at least some of the time, the nearest *Bromus* neighbors would be species with later phenologies or deeper roots; these species made demands on water and nutrients at different times and different parts of the soil profile than *Bromus*, making more resources available to *Bromus* when it needed them.

Conversely, *Centaurea* performed better in the incompatible mixtures than the compatible mixtures. This late season, deep rooted species was probably more likely to encounter species that competed directly with it for soil water and nutrients in the compatible mixtures than the incompatible mixtures resulting in reductions in biomass production and reproductive potential in compatible mixtures.

The response of *Centaurea* was consistent with our original hypothesis that mixtures with more different resource use patterns will be less easily invaded, however, the response of *Bromus* does not support the hypothesis. It appears that the particular resource use patterns of an invader and the species existing in the plant community are more important determinants of invasibility. When the plant community includes species that can compete directly with the invader for resources, the invader is likely to be less successful.

Invading species always performed better in the less species rich communities. This is consistent with our original hypothesis and support the view of Elton (1958). Although there are alternative explanations, invaders may be less successful in less divers

mixtures because the more species there are, the higher the probability that one of them will compete directly with the invader for resources.

MANAGEMENT RECOMMENDATIONS

Based on these results, we suggest that the best mixtures for reducing weed success in roadside revegetation will be those with five or more species that have phenologies and rooting depths that will reduce the resources available to invading species. If specific weeds are expected to be a problem, then constructing the seed mixture to include species that will compete directly with those invaders will reduce their success. As an example, in our experiment the presence of established, late-season perennial grasses was associated with decreased success of *Centaurea*. If general resistance to invasion is desired, I suggest constructing mixtures of five or more species that have varied resource use patterns (i.e. early- and late-season flowering times and shallow and deep rooting depths) and life history traits (i.e. annuals and perennials). It should be noted that year-to-year variation in climate can change the patterns of resource availability and the interaction of this variation with the invading species and constructed plant community should be considered.

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CHAPTER 5

Comparison of Species Composition and Environmental and Soil Nutrient Characteristics for California Native Perennial Grass Relict Stands and Highway Revegetation Sites

ABSTRACT

Native perennial grasses are being specified for erosion control seedings in California with increasing frequency, but the soil protection provided by perennial grass plantings and their approximation to plant community and environmental characteristics of native stands has not been systematically evaluated. In this study we began to address the need for information about the success of past revegetation attempts by evaluating California Department of Transportation projects. We monitored seven highway erosion control plantings in southern and northern California and compared them to eight relict stands of native perennial grasses. We estimated canopy cover by species and vegetation type (i.e. annual grasses, perennial grasses, legumes, non-legume forbs, shrubs and trees). Environmental variables including longitude, latitude, elevation, potential annual solar radiation, soil drainage, soil extractable nitrate, extractable ammonium, mineralizable ammonium, total nitrogen and total carbon, were also measured at both revegetation and relict sites. Canonical correspondence analysis was used for ordination of the sites based on both species composition and environmental variables. This type of data analysis can provide a valuable integrated evaluation of real field ecosystems as opposed to simple lab or greenhouse experiments. However, to be most useful, the data set should be larger with more intensive sampling of the most important variables than in this preliminary study. Differences between means of vegetation cover and environmental variables were determined using parametric and non-parametric tests.

Canonical correspondence analysis ordination axes explained only a little over a third of the variation in the species composition data. Annual precipitation was the most

important environmental variable for explanation of species composition data; the geographic variables, longitude and latitude, were also important. Relict perennial grass stands had greater mineralizable and total nitrogen levels, higher perennial grass cover, and lower legume cover than revegetation sites. Based on this small data set, we cannot make strong claims about the importance of particular environmental variables for the establishment of California native perennial grasses. However, soils at sites that supported natural populations of perennial grasses appeared to be at later developmental stages than revegetation sites.

INTRODUCTION

Re-establishing vegetation on disturbed land remains a challenge, despite years of systematic study and trial and error. In recent years, interest in returning roadside rights-of-way to native vegetation has increased (Bugg et al., 1997). In California, native perennial grasses are being specified for erosion control seed mixtures with increasing frequency. However, there is concern that the success of these species has been poor due to limited understanding of the conditions necessary for their establishment (Haynes, pers. com.), which results in increased erosion and revegetation costs.

Many biotic and abiotic factors contribute to the successful establishment and growth of plants on disturbed land. Physical characteristics of a site such as its longitude and latitude, elevation, slope and aspect determine the range of temperatures, precipitation and solar radiation plants growing at the site will experience and, consequently, the probability that a particular species will perform well at a site. Geographic ranges of species correspond to their environmental adaptations. Interacting with these environmental factors are the soil characteristics such as mineral composition, texture, structure and organic matter content that determine the suitability for plant growth. In addition to these physical characteristics, the species composition at a site can be affected by biological factors including effects of other plant species, microbial and mycorrhizal activity, and grazing by vertebrates and invertebrates. The frequency and intensity of disturbance other than grazing such as trampling, snow melt, and soil movement also help to determine which species will persist at a site. Although some of these factors cannot be controlled, knowing which factors are most important

determinants of plant community species composition can result in improved success of revegetation of disturbed land.

The purpose of this study was to compare species composition, soil nutrient levels, and other environmental characteristics of relict native perennial grass stands and highway right-of-way revegetation sites. This comparison allows evaluation of whether current seeding practices have been successful in establishing perennial grass cover and identification of environmental differences between the two types of sites that may be contributing to differences in species composition.

METHODS

Site descriptions

Fifteen sites were surveyed in northern and southern California (Table 1). Eight of the sites were natural grassland or grassland/shrub communities that included populations of California native perennial grasses. The remaining seven sites were California Department of Transportation (Caltrans) erosion control revegetation sites that included at least one species of California native perennial grass in the seed mixture (Table 2). The actual dates of seeding are not known but the date for opening of bids for contractors and date of sampling are listed in Table 3.

Sampling

A standardized sampling method was applied at each site to characterize the plant community and environmental variables of the site. Two transects were sampled at each

Table 1. Native perennial grass relict stand and revegetation site information.

SITE NAME	TYPE	LATITUDE (degrees)	LONGITUDE (degrees)	SLOPE (degrees)	ASPECT	DRAINAGE
Dye Creek	relict	122.03	40.30	12	S	well
China Mountain	relict	122.63	41.43	18	WSW	very well
Yreka	revegetation	122.55	41.72	14	SW	well
McCloud	revegetation	122.00	41.25	0	none	well
Cottonwood	revegetation	122.28	40.37	34	E	well
Atascadero	revegetation	120.68	35.45	0	none	well
Fontana	revegetation	117.48	34.07	0	none	very well
Escondido	revegetation	117.17	33.40	8	NW	well
Santa Rosa Plateau	relict	117.25	33.53	10	SW	well
Gaviota State Beach	relict	120.23	34.47	30	SE	well
Elwood Mesa	relict	119.88	34.42	3	E	well
La Jolla Valley	relict	119.03	34.10	16	W	well
Carrizo Plain Natural Area	relict	119.78	35.10	28	NE	well
Jesusita Trail	relict	117.53	34.47	17	SW	well
Cucamonga	revegetation	117.53	34.00	23	NW	very well

Table 2. Seeding specifications for erosion control sites. Values listed are lb acre⁻¹/minimum % purity/minimum % germination.

GROUP	SPECIES	Yreka	McCloud	Cottonwood	Atascadero	Fontana	Escondido	Cucamonga
Perennial Grasses	<i>Bromus arizonicus</i>	0	0	0	0	11/95/80	0	10/95/80
	<i>Bromus carinatus</i>	0	0	0	20/95/85	0	0	0
	<i>Festuca idahoensis</i>	25/95/80	25/95/80	0	0	0	0	0
	<i>Festuca rubra</i>	20/90/80		5/95/80	0	0	0	0
	<i>Festuca ovina</i>	15/95/80	15/90/70	5/90/70	0	0	0	0
	<i>Melica californica</i>	0	0	0	0	0	0	2/90/60
	<i>Nassella cernua</i>	0	0	0	0	16/70/60	0	15/70/60
	<i>Nassella pulchra</i>	0	0	0	0	0	2/70/60	0
	<i>Vulpia myuros</i>	10/90/80	10/90/80	5/90/80	15/85/80	0	0	0
Annual Grass	<i>Escholtzia californica</i>	3/90/70	3/90/70	3/90/70	0	5/90/70	1/95/75	2/70/90
	<i>Chrysanthemum leucanthemum</i>	0	5/80/90	0	0	0	0	0
Non-legume Forbs	<i>Plantago insularis</i>	0	0	0	0	0	20/95/75	0

Shrubs and Sub-shrubs	<i>Artemisia Californica</i>	0	0	0	0	0	0	0	0	5/15/50	0
	<i>Eriogonum fasciculatum</i>	0	0	0	0	0	0	0	0	10/10/65	0
	<i>Salvia mellifera</i>	0	0	0	0	0	0	0	0	3/70/50	0
Legumes	<i>Trifolium hirtum</i>	0	0	0	20/95/85	15/95/85	41/95/85	20/95/85	40/95/85		
	<i>Trifolium incarnatum</i>	0	0	0	15/95/85	0	0	0	0		
	<i>Lupinus albicaulis</i>	0	0	0	2/90/75	0	0	0	0		
	<i>Lupinus succulentus</i>	0	0	0	0	10/95/85	0	0	0	4/95/85	0
	<i>Lotus scoparius</i>	0	0	0	0	0	0	0	0	8/90/60	0

Table 3. Erosion control materials and amounts for revegetation sites. Materials were applied in the order indicated by numbers in parentheses.

Material	Yreka SIS-3- 51.6/51.9	McCloud SIS-89-15.4	Cottonwood TEH-5- 39.8/41.5	Atascadero SLO-41- 13.4/16.0	Fontana SBD-10-13.2	Escondido SD-15-53.9	Cucamonga SBD-15-5.5
Date bids open	4/6/93	3/31/92	3/23/93	8/11/92	2/4/93	3/19/93	2/25/93
Date sampled	6/28/94	6/28/94	6/27/94	5/16/94	5/19/94	5/19/94	5/19/94
Legume seed (lb acre ⁻¹)	0	0	(1) 37	(1) 25	(1) 41	(1) 32	(2) 40
Fiber (lb acre ⁻¹)	0	0	(2) 500 (4) 400	(2) 1600 (3) 400	0	(2) 1500 (4) 300	(2) 500 (3) 1500
Non-legume seed (lb acre ⁻¹)	(1) 48	(1) 58	(2) 23	(2) 41	(2) 38	(2) 41	(1) 2 (2) 27
Straw (tons acre ⁻¹)	0	0	(3) 2	0	0	(3) 2	0
Commercial fertilizer (lb acre ⁻¹ , %N:%P:%K)	(1) 400	(1) 400	(4) 350	(2) 350	(2) 19	(4) 350, 0:36:0	(3) 200
Stabilizing emulsion (solids) (lb acre ⁻¹)	0	0	(4) 100	(3) 100	0	(4) 150	0
Erosion control blanket	0	0	0	0	(3) Wood excelsior mats	0	0

site, unless the plant community could be fully characterized by a single transect. Transects were located in areas that were judged to be representative of the plant community at the site and were oriented in a randomly selected compass direction. Transects were either 15 or 20 meters long and vegetation samples were taken at ten random locations along each linear transect. The plant canopy cover of each species (relative cover) was estimated using slightly modified methods of Daubenmire (1959). At some sites, the smallest cover class was 12.5% instead of 5% in the conventional Daubenmire method. Percent bare ground and rock were also determined. Soil samples were taken at regular intervals at five of the ten vegetation sampling locations on one of the two transects.

Soil nutrient samples were collected from five of the ten randomly selected vegetation sampling locations on one transect at each site. The organic matter layer on the soil surface was removed, then soil was collected from 0 to 10 cm deep using a coring device that was approximately 6.5 cm interior diameter. Soils were sieved and the fraction < 2 mm was collected for nutrient analyses.

Soil nutrient analyses

Nutrient analyses included total carbon and nitrogen (dry combustion, gas chromatography/ thermal conductivity detection; Dumas 1831)(Carlo Erba NA1500) and extractable and mineralizable nitrogen (one week, anaerobic, 40 °C incubation, 2 M KCl extraction; Keeney 1982). Solution nitrogen was determined by reduction of nitrate to ammonium in a continuous flow copper coated zinc column followed by conductimetric measurement of ammonium (Carlson 1978, 1986). Extractable nitrogen is an estimate of

the soil solution nitrogen available to plants. Mineralizable nitrogen is an estimate of the nitrogen that will become available in a growing season (Keeney 1982).

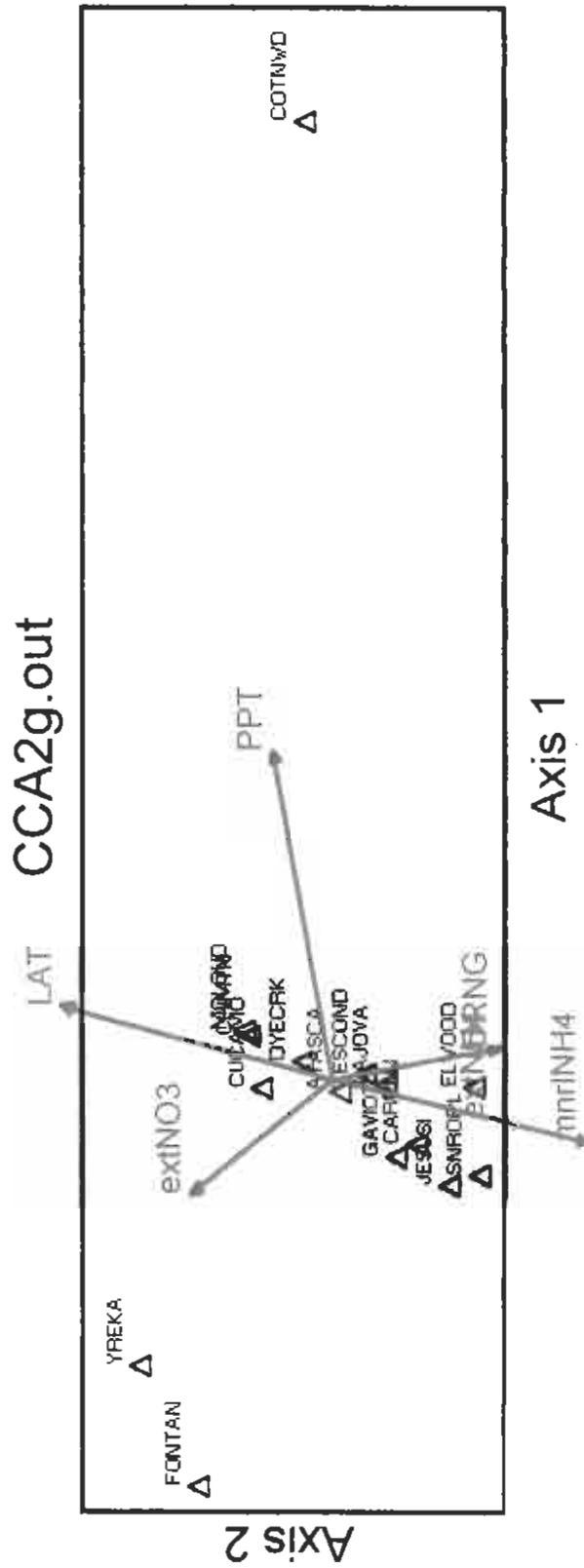
Statistical analyses

Canonical Correspondence Analysis-... Canonical correspondence analysis is a method of analyzing vegetation data from different locations (sites) that allows the sites to be organized simultaneously according to their similarity in both species composition and environmental variables (e.g. elevation, precipitation, soil nitrogen, etc.). Two data sets are required for the analysis, one data set that includes the abundance of each species at each of the sites and a second data set that includes the values for environmental variables at each of the sites. Based on these two data sets, this ordination method identifies the location of each site with respect to axes that are linear combinations of the species composition and environmental variables. The first axis is the multiple regression that simultaneously minimizes the variation in species (vegetation) composition and environmental variable data. The second axis is independent of the first axis and again minimizes the variation between species composition and environmental variables at the sites. Additional axes are obtained similarly. As many axes as there are environmental variables can be extracted but usually only the first two or three are of importance.

The output of the analysis includes coordinates that place each site, defined by its species composition and environmental variables, with respect to these ordination axes. The points can be included in a diagram as shown in Fig. 1. Sites and species are represented by points and the environmental variables by arrows. Each site point is

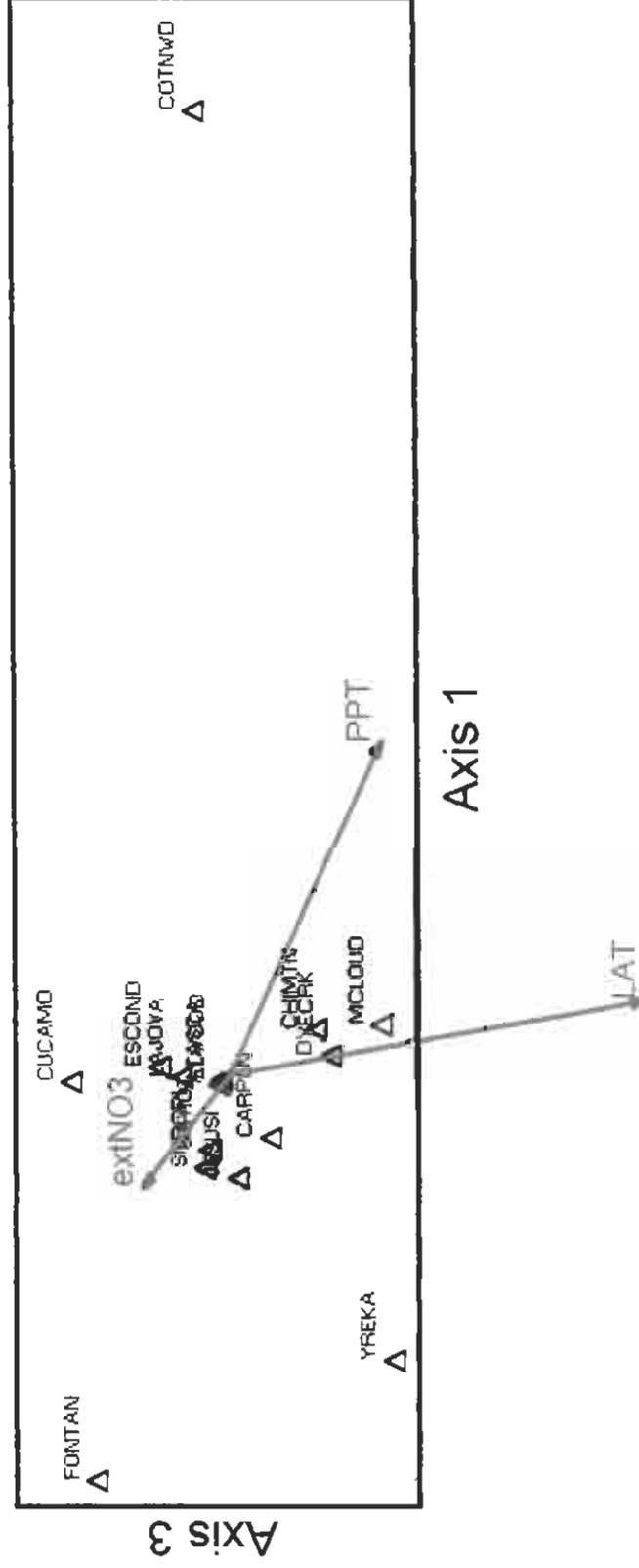
Figure 1. Graphs of canonical correspondence analysis ordination of eight native perennial grass relict stands and seven revegetation sites. Sites are indicated by triangles; relict sites are yellow (LAMOVA = La Jolla Valley, GAVIOT = Gaviota, SNROPL = Santa Rosa Plateau, ELWOOD = Elwood Mesa, JESUSI = Jesusita Trail, CARPLN = Carrizo Plain, DYECRK = Dye Creek, CHIMTN = China Mountain), revegetation sites are not colored (ATASCA = Atascadero, CONTNWD = Cottonwood, CUCAMO = Cucamonga, ESCOND = Escondido, FONTAN = Fontana, MCLOUD = McCloud, YREKA = Yreka). The three axes are linear combinations of the environmental variables. Sites are plotted with respect to the first and second ordination axes in (a), the first and third ordination axes in (b), and the second and third ordination axes in (c). The environmental variables are indicated by red arrows. The environmental variable gradients extend in both directions from the point where the red arrows meet, and increase in value in the direction that the arrow is pointing. The relative lengths of the environmental lines indicate the relative importance of the environmental variables in explaining patterns in vegetation data. The approximate level of an environmental variable for a site can be estimated by extending a perpendicular line from the site symbol to the environmental variable arrow. The environmental variables in (a) and (c) are latitude (LAT), mineralizable ammonium (mnrNH4), drainage (DRNG), extractable nitrate (extNO3), extractable ammonium (extNH4), and precipitation (PPT). The environmental variables in (b) are latitude, precipitation, and extractable nitrate.

(a)

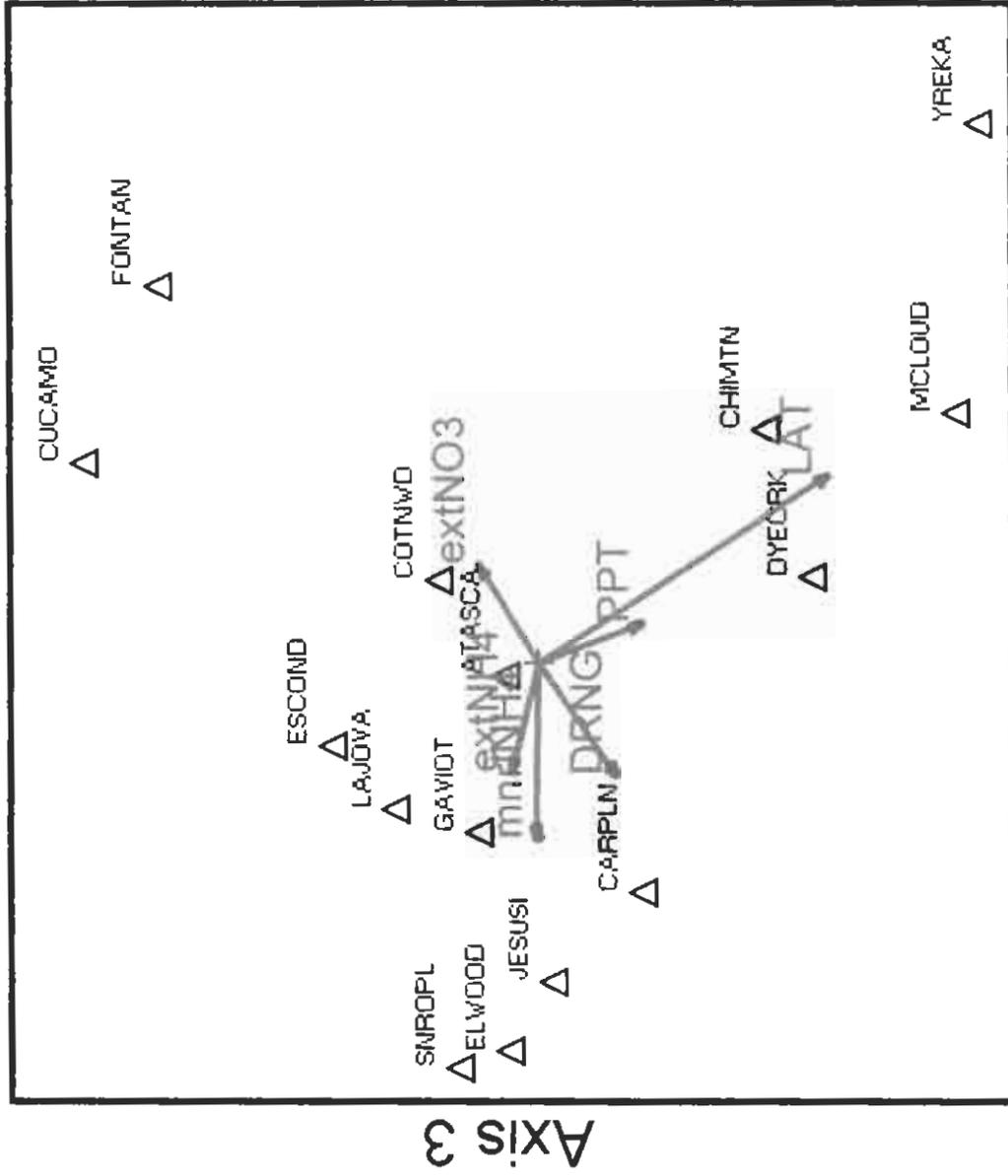


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(b)



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(c)

Axis 2

located at the centroid (roughly, a weighted mean) of the species that occur at that site. The species points indicate the optimum for each species in relation to the environmental axes. Abundance of a species decreases with distance from its location in the diagram. By drawing a perpendicular line from a species or site point to an environmental variable arrow, one may infer the approximate level of the environmental variable at which the site and species occurred.

Twelve environmental variables were initially evaluated (Table 4). Annual potential solar radiation was estimated for each site based on latitude, slope (degrees) and aspect (e.g. N, NNE, NE)(Buffo et al. 1972). Annual precipitation was based on rainfall data collected at stations located as near to the site as possible (University of California Integrated Pest Management Home Page 1996). The software used to perform the ordination was PC-ORD (version 3.14, MjM Software Design, PO Box 129, Gleneden Beach, OR 97388, USA) and CANOCO (Ter Braak, 1986). Both software programs were used to take advantage of unique features of each. PC-ORD produces graphs that CANOCO does not and CANOCO allows the inclusion of covariates in the analysis that PC-ORD does not.

Highly correlated environmental variables ($P < 0.1$; probability that they are independent < 0.1) were eliminated from the PC-ORD ordination of the data for two reasons. First, including as many or more variables than there are sites in an ordination can lead to results that indicate strong relationships between the environmental variables and sites or species when no real relationship exists. Also, including environmental variables that are highly correlated with each other can lead to inaccurate results. Since it

Table 4. CORRELATIONS BETWEEN ENVIRONMENTAL VARIABLES. Values in this table are simple correlation coefficients, a measure of the strength of association between two variables. In this case, the correlation coefficient for a pair of variables is located in the cell at the intersection of the row for the first variable and the column for the second variable. For example, the correlation coefficient for variables elevation and solar radiation is -0.29. The greater the magnitude of the correlation coefficient, the more the value of one variable will be dependent on the value of the other. If a correlation coefficient is negative, the two variables are negatively associated (i.e. one decreases when the other increases). If the two variables have a positive correlation coefficient, they are positively associated (i.e. the variables increase and decrease simultaneously). Significance levels (p values) are indicated as follows: $P < 0.1 = +$, $P < 0.05 = *$, $P < 0.01 = **$, $P < 0.001 = ***$. P values indicate the probability that two variables could be associated at the level indicated by the correlation coefficient by chance alone and are actually unrelated (i.e. their real correlation coefficient is 0)(Zar 1996).

	LONGITUDE	LATITUDE	SOLAR RADIATION	PRECIPITATION	DRAINAGE	ELEVATION	extractable NO ₃ , ug/g	extractable NH ₄ , ug/g	mineralizable N	% N	% C
LONGITUDE	1	0.89***	-0.05	0.82***	0.21	0.25	-0.34	-0.16	-0.30	-0.11	-0.18
LATITUDE	0.89***	1	-0.13	0.78***	0.01	0.40	-0.13	-0.44	-0.38	-0.23	-0.29
SOLAR RADIATION	-0.05	-0.13	1	0.04	0.23	-0.29	0.04	0.13	0.31	0.41	0.47+
PRECIPITATION	0.82***	0.78***	0.04	1	0.15	0.02	-0.24	-0.21	-0.26	-0.14	-0.25
DRAINAGE	0.21	0.01	0.23	0.15	1	-0.40	-0.48+	-0.14	0.10	-0.01	0.04
ELEVATION	0.25	0.40	-0.29	0.02	-0.40	1	-0.22	-0.04	-0.15	0.10	0.05
extractable NO ₃ , ug/g	-0.39	-0.13	0.04	-0.24	-0.48+	-0.22	1	0.03	0.21	0.17	0.25
extractable NH ₄ , ug/g	-0.16	-0.44	0.13	-0.21	-0.14	-0.04	0.03	1	0.55*	0.62*	0.49+
mineralizable N	-0.30	-0.38	0.31	-0.26	0.10	-0.15	0.21	0.55*	1	0.87***	0.71**
% N	-0.11	-0.23	0.41	-0.14	-0.01	0.10	0.17	0.62*	0.87***	1	0.86***
% C	-0.18	-0.29	0.47	-0.25	0.04	0.05	0.25	0.49+	0.71**	0.86***	1

is not possible to include such correlated variables as covariates in PC-ORD, they were eliminated from the analysis. We used eight of the twelve possible environmental variables in the analysis. These eight variables were least correlated with each other but explained the greatest amount of the variation in the data. They included latitude, annual potential solar radiation, annual precipitation, drainage, elevation, extractable nitrate, extractable ammonium, and mineralizable nitrogen (indicated in bold type in Table 4).

In the CANOCO ordination, all twelve environmental variables were included. We systematically explored the data by executing the analysis with different combinations of environmental variables as covariates. Covariates are variables that are related to the environmental variables being analyzed; they can add noise, reducing the ability to detect the effect of environmental variables of interest. The covariate procedure allowed us to evaluate how much of the variation in the data could be explained by the environmental variables when the variability due to the covariates was removed. The vegetation data were analyzed using (1) individual species identities and abundance data and (2) species grouped according to plant types (annual grasses, perennial grasses, non-legume forbs, legume forbs, shrubs/sub-shrubs and trees).

For both software procedures, statistical tests were generated using randomization methods called Monte Carlo tests. In these tests, the environmental data are assigned randomly to the sites and the ordination procedure was executed again. This is repeated many times (at least 100 times in my analyses). Each time, the amount of variation in vegetation data explained by the ordination axes (called the eigenvalues) and the correlation between the species and environmental data (called the species-environment

correlation) were evaluated. The proportion of times the eigenvalue or species-environment correlation is greater for the randomized data sets than the real data set indicates the probability that the real data set could also have such a high value by chance alone. For instance, say that the eigenvalue for a particular axis were 0.82. If the Monte Carlo tests result in a *P*-value (probability) of 0.01 for the eigenvalue of that first ordination axis, there was a 1 in 100 probability that an eigenvalue as high as 0.82 could be purely due to chance association of environmental variable values with sites, not due to meaningful structure in the data set. *P*-values less than 0.05 were considered significant in these analyses.

*Parametric and non-parametric tests-...*Differences in environmental and vegetation characteristics between revegetation and relict sites were evaluated using *t*-tests when data met the assumptions of parametric statistics and Wilcoxon rank sums two-sample tests when the assumptions were not met. Parametric statistics are based on the assumption that the data are randomly selected from a population is normally distributed. Non-parametric statistics are not based on this assumption and are generally more conservative tests (i.e. less likely to detect a true difference). The vegetation data were analyzed using (1) individual species identities and abundance data or (2) species data grouped into plant types (annual grasses, perennial grasses, non-legume forbs, legume forbs, shrubs/sub-shrubs and trees), or both.

RESULTS

Photographs of the study sites can be found within the Discussion section.

Ordination using canonical correspondence analysis

*PC-ORD results-...*Very little of the variation in species data was explained by the ordination axes. Only 14.4 % of the variation was explained by the first axis, 12.0 % by the second and 10.3 % by the third (Table 5), resulting in only a little over a third of the total variation being explained by the three axes. An eigenvalue is a measure of the amount of variation explained by a particular axis. There was a small probability ($P < 0.05$) that eigenvalues as high as those for axes 1 and 3 could have been obtained due to chance alone (Table 5). Therefore, the ordination relationships are accepted as being real. However, each ordination combination had a small effect on the plant species data due to the influences of multiple factors, which resulted in the low explanatory power of the axes as described above.

The most important environmental variables in explaining the species composition data were (axis 1) precipitation, latitude, and potential annual solar radiation and (axis 2) mineralizable nitrogen, drainage, and latitude and (axis 3) latitude, drainage, and extractable nitrate (Fig. 1a, b, and c).

CANOCO results-...

1) *The importance of geographical data (longitude and latitude)*

When longitude and latitude were included as covariables to control for geographical effects (i.e. variation due to their association with the environmental

Table 5. Selected results from PC-ORD ordination on survey of native perennial grass relict stands and revegetation sites. Eigenvalues are a measure of the amount of variation explained by each axis. Pearson correlations indicate the strength of the association between the species cover estimates and the environmental variables. *P*-values generated through Monte Carlo tests (see text for explanation) are in parentheses.

Result	Axis 1	Axis 2	Axis 3
Eigenvalue (variance in the species matrix that is attributed to a particular axis)	0.98 (0.01)	0.82 (0.14)	0.71 (0.04)
% of variance in species matrix that is explained by each axis (eigenvalue/total variance*100)	14.4	12	10.3

variables in the analysis was removed), a very low percentage of the variability in the vegetation and environmental data was explained by the first ordination axis (Monte Carlo test $P = 0.88$) and the overall ordination (Monte Carlo test $P = 0.62$). When longitude and latitude were used as the environmental variables and the remaining environmental variables were used as covariables (i.e. error due to association of environmental variables other than longitude and latitude was removed with these geographical variables was removed), neither the first axis nor the overall ordination were significant (Monte Carlo $P = 1.0$ and 0.73 , respectively). When longitude and latitude were used as the only environmental variables, the first axis was nearly significant (Monte Carlo test $P = 0.08$) and the overall ordination was significant (Monte Carlo test $P = 0.01$). When all environmental variables except for longitude and latitude were included in the analysis, neither the first axis nor the overall ordination were significant ($P = 0.66$ and 0.1 , respectively).

These results indicate that geographical information specifying site location explained a great deal of the variation in vegetation, more than all of the other environmental variables combined. Combining species into groups (i.e. annual grasses, perennial grasses, legumes, etc.) gave similar results except that geographic data alone did not explain variation in species composition data. This approach did not provide additional understanding of the relationship between environmental variables and species composition.

2) *The importance of climatic data (solar radiation and precipitation)*

Solar radiation and precipitation explained the patterns in the vegetation data very well (Monte Carlo $P = 0.01$ for the first axis). The addition of the environmental variables drainage and total N did not explain more variation in the vegetation data than solar radiation and precipitation alone. Results were similar for species groups.

3) *The importance of solar radiation and precipitation*

Precipitation was the most important environmental variable according to these analyses. When precipitation was used as the only environmental variable and solar radiation was used as a covariable, the first ordination axis was significant (Monte Carlo $P = 0.01$). When solar radiation was used as the only environmental variable and precipitation was used as a covariable, the first ordination axis was not significant (Monte Carlo $P = 0.54$). Results were similar for species groups (for first axis, Monte Carlo $P = 0.80$).

4) *Is precipitation the only important factor?*

Precipitation was the most important environmental variable for explaining the

species composition data, but geographical data were also important. When precipitation was used as the only environmental variable and longitude and latitude were used as covariables, the first axis was nearly significant (Monte Carlo $P = 0.05$). When longitude and latitude were used as the environmental variables and precipitation was included as a covariable, the first ordination axis was not significant (Monte Carlo $P = 0.09$). This suggests that longitude and latitude included some information useful in explaining the vegetation data that precipitation contained, but not all of it.

Parametric and non-parametric test results: Comparison of relict stands and revegetation sites

Relict and revegetation sites had similar cover of shrubs, trees, non-legume forbs, annual grasses, rock and bare ground. However, revegetation sites had higher cover of legumes than relict stands ($P < 0.05$)(Table 6). Relict native grass sites had higher cover of perennial grasses than revegetation sites ($P < 0.05$)(Table 6).

The environmental variables were similar for revegetation sites and relict stands with the exception of extractable and mineralizable ammonium and percent nitrogen (Table 7). These environmental factors were higher for relict stands than for revegetation sites. Percent carbon tended to be higher in relict site soils, but this was not statistically significant ($P = 0.09$)(Table 7).

Table 6. Comparison between cover estimates for perennial grass relict sites and revegetation sites. *P*-values are for t-tests, except if + present when *P*-values are approximated for t-tests from non-parametric statistical tests for the difference between two means (Wilcoxon two-sample test). Means with *p*-values less than 0.05 are significantly different from each other and are indicated in bold.

Species group	Relict mean cover \pm S.E.	Revegetation mean cover \pm S.E.	<i>p</i> -value
Shrub	10.16 \pm 7.60	1.06 \pm 0.55	0.29
Tree	0.0 \pm 0.0	0.70 \pm 0.70	+ 0.28
Legume	0.42 \pm 0.90	16.81 \pm 10.77	+ 0.048
Non-legume forb	8.60 \pm 3.84	10.11 \pm 4.29	0.80
Annual grasses	26.87 \pm 7.74	12.19 \pm 5.40	0.15
Perennial grasses	1.18 \pm 0.19	0.50 \pm 0.21	0.03
Rock	0.09 \pm 0.09	0.0 \pm 0.0	+ 0.44
Bare ground	2.51 \pm 1.33	14.30 \pm 6.81	+ 0.34

Table 7. Comparison between environmental variables for perennial grass relict sites and revegetation sites. *P*-values are for t-tests, except if + present when *P*-values are approximated for t-tests from non-parametric statistical tests for the difference between two means (Wilcoxon two-sample test). Means with *p*-values less than 0.05 are significantly different from each other and are indicated in bold.

Environmental Variable	Relict mean \pm S.E.	Revegetation mean \pm S.E.	<i>p</i> -value
Longitude (degrees)	119.70 \pm 0.54	120.29 \pm 0.87	+ 1.0
Latitude (degrees)	35.20 \pm 0.87	37.71 \pm 1.34	+ 0.86
Elevation (meters)	298.71 \pm 101.59	543.75 \pm 179.30	0.27
Solar radiation (cal cm ⁻² year ⁻¹)	215327.90 \pm 10813.39	202114.20 \pm 6439.72	0.30
Precipitation (mm)	3717.14 \pm 461.89	4307 \pm 681.93	0.50
Drainage	1 \pm 0.0	0.62 \pm 0.18	+ 0.52
extractable NO ₃ (ug g ⁻¹ soil)	3.61 \pm 1.78	4.86 \pm 2.55	0.70
extractable NH ₄ (ug g ⁻¹ soil)	4.41 \pm 0.83	1.89 \pm 0.58	0.02
mineralizable NH ₄ (ug g ⁻¹ soil)	55.32 \pm 6.36	11.37 \pm 4.64	0.000097
Percent N	0.167 \pm 0.01	0.067 \pm 0.02	0.001
Percent C	1.87 \pm 0.18	1.04 \pm 0.27	+ 0.09

DISCUSSION

Across the sites sampled, relict native perennial grass stands and highway revegetation sites showed differences in legume cover, perennial grass cover and soil nitrogen levels despite having similar ranges of geographic location, elevation, annual potential solar radiation, annual precipitation and soil drainage. Native perennial grass stands had higher mineralizable ammonium indicating greater nitrogen availability over a time scale of months (Keeney 1982). They also had higher percent nitrogen levels and nearly higher carbon levels, which can be attributed to higher organic matter contents.

A number of issues should be considered in making conclusions based on these data. First, the dates of seeding of revegetation sites are not known. Differences in species composition between the two types of sites may be due to differences in the amount of time the perennial grasses had to become established since seeding. Based on the dates that bids opened for the revegetation projects, only the Atascadero site could have been in its second growing season; the rest were in their first growing season.

In addition, it is recognized that over time, plant cover at revegetation sites often decreases as nutrients are removed from the soils through leaching or incorporation into plants, litter, and microbial biomass (Claassen and Hogan 1998). This may result in a divergence of species composition and cover for the two types of sites as plants respond to long term soil nutrient availability.

Seeding mix composition may have caused some differences between the two site types in species composition. Legumes are often included in seeding mixtures, which may explain the higher cover of legumes at the revegetation sites. However, legumes

Northern California



Dye Creek Reserve – Relict Stand



China Mountain – Relict Stand



Yreka – Revegetation Site
SIS-3-51.6/51.9



McCloud – Revegetation Site
SIS-89-15.4



Cottonwood – Revegetation Site
TEH-5-39.8/41.5

Southern California



La Jolla Valley - Relict Stand



Carrizo Plain Natural Area - Relict Stand



Santa Rosa Plateau - Relict Stand



Jesusita Trail - Relict Stand



Elwood Mesa - Relict Stand



Gaviota State Beach – Relict Stand



Cucamonga – Revegetation Site
SBD-15-5.5



Atascadero – Revegetation Site
SLO-41-13.4/16.0



Atascadero – Revegetation Site
SLO-41-13.4/16.0



Fontana – Revegetation Site
SBD-10-13.2



Escondido – Revegetation Site
SD-15-53.9

perform relatively better than other species in low nitrogen soils (Brown, 1998), which would have contributed to their increased relative abundance at revegetation sites.

Based on canonical correlation analysis, the one environmental variable that best indicated the species composition of the sites was annual precipitation; longitude and latitude were also important. Horticulturalists will not be surprised by this result. However, it is surprising that none of the other environmental variables were important indicators of species composition and that when all of the environmental variables measured were considered together (including precipitation, longitude and latitude), they explained only a little over a third of the variation in the vegetation data. There may be a number of reasons for this, not the least of which is that this was a very small data set for this type of analysis and the sites were highly variable. In addition, the environmental variables measured may not have been those that were most important in determining species composition. For example, historical factors not measured may have influenced which species arrived and the stage of development of each plant community. Also, soil depth has been identified as an important factor in success of revegetation seedings (Claassen and Hogan 1998) but was not measured. Furthermore, in order for canonical correspondence analysis to accurately detect patterns the data must exhibit particular characteristics. The species must have a single peak in abundance across the environmental gradients measured and the environmental variables must have a linear relationship with the ordination axes. These criteria may not have been met.

In order to draw strong conclusions, more sites should be sampled, and more information about the revegetation sites (e.g. the actual date of seeding) is necessary. It is

also important to know whether the soils at the revegetation sites were native soil or imported fill. It would also be beneficial to measure the soil depth in order to estimate effective rooting depth. The application of short lived, soluble fertilizers on these recently constructed sites may have resulted in plant growth that is not reflected in soil fertility tests. This can be expected to cloud the relationship between plants and soil fertility pools (Claassen and Hogan 1998).

CONCLUSIONS

We can make no strong claims about the importance of site characteristics to success of native perennial grass seeding due to a small data set and apparent inability of the environmental variables to explain the species composition patterns. Despite this, the results can provide some guidance for revegetation. First, precipitation, longitude and latitude were the environmental variables that most strongly predicted species composition. This indicates the importance of selecting species that are adapted to each revegetation site when developing erosion control seed mixture specifications. We also found that relict stands of native grasses had higher mineralizable soil nitrogen (available to plants over months) and total nitrogen levels compared to the revegetation sites and that annual precipitation was an important determinant of species composition. This result suggests that perennial grasses flourish in soils with increased levels of nitrogen that becomes available to plants on the order of months.

MANAGEMENT IMPLICATIONS

Management activities that promote development of conditions similar to relict sites should be practiced. Addition of organic matter and non-labile nitrogen sources when planting perennial grasses may promote these later successional conditions. In addition, species that are locally adapted or naturalized to target revegetation sites should be selected for seed mixtures because they have the best chance for success.

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IMPLEMENTATION

Implementation of the results of this project within the California Department of Transportation will be accomplished by sending a copy of the final report to the District Deputy Directors of Project Development, District Landscape Architects and Environmental Offices. Additional copies of the final report will be made available from the Caltrans Publication Unit. The availability of the report will be advertised in professional and trade journals.

The findings of this project have been presented in a number of technical posters and lectures, detailed in Appendix 1. Manuscripts are also in preparation to be submitted to peer reviewed journals for publication (Appendix 1).

Information generated by this project has resulted in significant changes in erosion control specifications for species and fertilizers. The annual grass Zorro fescue (*Vulpia myuros*) is no longer included as a nurse plant in mixtures with native perennial grass seed. Also, fertilizers that result in high levels of easily available nitrogen are no longer applied when seeding native perennial grasses. Highly labile nitrogen fertilizers have been replaced by compost, which provides a slow release, long term nitrogen source for establishing plants.

CONCLUSIONS AND RECOMMENDATIONS

The presence of *V. myuros* reduced the performance of native perennial grass seedlings. Perennial grass seedling survival and aboveground biomass decreased with increasing *V. myuros* seeding densities. *Vulpia myuros* also significantly suppressed weed

aboveground biomass and density. Weed densities may have been suppressed more than native perennial grass densities, although biomass of native grasses and weeds were not differentially affected. Weeds produced from two to seven times as much biomass per unit area as perennial grasses. Overall, because *V. myuros* significantly reduced the survival and performance of the mixture of perennial grasses and this effect increased with increasing *V. myuros* seeding density, we conclude that including this exotic annual in native seeding mixtures is counterproductive.

As a result of these findings, *V. myuros* is no longer specified in erosion control seed mixtures as a nurse crop. Additional research is needed in order to determine the competitive effects of other species of erosion control cover crops on native perennial grass species. We suggest that the use of non-biological means of erosion control (e.g. straw mulch, mats or wetting agents) with native perennial grasses may be preferable to including fast growing species. Physical erosion control methods in combination with planting perennial grasses, forbs and shrubs, may optimize erosion control by shielding the soil from impacts of rain and run-off in the short term and establishing stable plant communities with dense and deep root systems for long term soil protection.

In further experiments, we found that selected species, which represented six species guilds (functional groups) based on life history, taxon and phenology, had different root distribution patterns indicating spatial differences in resource use patterns. Early-season annual grasses had the largest proportion of their roots in shallow soil layers. They utilized soil water only during the spring. Mid- and late-season perennial grasses and early-season

legumes had the most evenly distributed roots. The mid- and late-season species continued to use soil water through the summer.

In a container experiment, there was little effect of soil texture on soil water depletion, but soil water was removed more evenly through the soil profile in the light texture soil and, for some species and depths at particular times in the growing season, the light texture soil was dryer than the heavy texture soil. In the field experiment, nitrogen fertilizer level did not affect root length distribution and soil water depletion patterns. The general spatial distribution of roots and spatial and temporal patterns of soil water depletion corresponded to species functional groups based on life history traits, taxonomic group and phenology.

The results of these experiments suggest that within an herbaceous plant community, species have the potential to partition their resources in space and time, which may allow them to co-exist without competitively excluding one another. Furthermore, these patterns of resource use are characteristic of species functional groups, suggesting that functional group based assembly rules may partly determine which species occur together (i.e. community structure) in California Central Valley grasslands.

We found that plant community resource use, productivity and stability could be predicted *a priori* when mixtures of varying species richness were constructed using species with known spatial and temporal resource use patterns. Overall, mixtures that included species with different spatial and temporal resource use patterns (compatible mixtures) utilized soil water more completely, and produced greater and more consistent aboveground biomass than mixtures of species with more similar resource use patterns (incompatible

mixtures). More diverse mixtures used soil water more completely and produced more aboveground biomass with more stable species composition than less diverse mixtures. Our results indicate that diversity of resource use patterns was at least as important as diversity of species in producing the community functions measured and supports the hypotheses that diversity is positively related to resource use, biomass production and community stability.

We investigated the effects of community resource use patterns and species diversity on invasion by weeds by introducing two invading plant species with different phenologies and rooting depths into some of the species mixtures described above. The early-season flowering annual grass (*Bromus hordeaceus*), and the late-season flowering annual forb (*Centaurea solstitialis*) were planted into mixtures with different species numbers (two- and five-species) and resource use patterns (compatible and incompatible).

We found that the early-season, shallow rooted invader (*Bromus*) was least successful in mixtures composed of species with similar resource use patterns (incompatible mixtures). The late-season species (*Centaurea*) was least successful in the compatible mixtures made up of species with varied resource use patterns that included some species with resource use patterns similar to *Centaurea*. Overall, invaders were not as successful in plant communities composed of species that utilized resources similarly to the invader. Invaders were less successful in more diverse (greater species rich) mixtures and invader success was reduced by existing vegetation, no matter the resource use patterns of the established species. Invader populations showed the greatest potential for growth under more fertile conditions.

These mixture studies have important implications for erosion control. In order to

establish stable plant communities, we suggest including several species of herbaceous plants that have differing rooting depths and phenologies in seed mixtures. If particular species of weeds are known to be problematic at a site, then revegetation species that have resource use patterns similar to the weeds should be included. Following these guidelines will result in maximizing stability of soil cover while minimizing proliferation of weedy species.

In a pilot study which surveyed seven highway erosion control plantings and eight relict stands of native perennial grasses in Southern and Northern California we assessed which environmental variables were related to perennial grass success. Environmental variables (longitude, latitude, elevation, potential annual solar radiation, soil drainage, soil extractable nitrate, extractable ammonium, mineralizable ammonium, total nitrogen and total carbon) and species composition data were evaluated. This allowed us to determine whether particular physical characteristics of the sites were strongly associated with the presence of native perennial grasses or other species or groups of species. We also compared the average levels for environmental variables and vegetation cover for revegetation and relict sites. We found that the environmental variables did not explain patterns in species composition well when revegetation and relict sites were considered together. However, this was a very small data set with too few sites to analyze revegetation sites separately from relict sites. Annual precipitation was the most important environmental variable for explanation of species composition data; the geographic variables longitude and latitude were also important. When the two types of sites were compared, relict perennial grass stands had greater mineralizable

and total nitrogen levels, higher perennial grass cover, and lower legume cover than revegetation sites.

A more extensive study of revegetation sites with perennial grasses and relict stands is needed in order to more completely understand what controls success of these species in erosion control seedings. Many additional relict perennial grass stands and revegetation sites in all parts of the state should be studied. Revegetation sites should be from two to at least five years old and information about actual seeding date should be included in the analysis. Although we cannot draw strong conclusions from the current study due to its small size, some results are important indicators. The strong association of precipitation and geographic location with species composition indicates the importance of basic principles of ecology in selecting species for revegetation seedings. The first concern should be whether a species is locally adapted to the conditions at the target site; species that are native or naturalized have the greatest chance of success.

Stable perennial grass communities occurred on soils with relatively high nitrogen in a form that will become available over months and is associated with soil microbial communities. These soils also had substantial organic matter content. We recommend the addition of nitrogen and carbon to soils in a form such as compost that results in the slow release of nitrogen that is available to plants. This practice will encourage the development of healthy below-ground ecosystems similar to the relict sites we studied and promote the establishment of stable perennial grass communities.

APPENDIX 1: DISSEMINATION OF INFORMATION GENERATED FROM THIS PROJECT-LIST OF PRESENTATIONS AND PUBLICATIONS

Technical posters and presentations

- C.S. Brown and K.J. Rice. Effects of species diversity and resource partitioning on plant mixture productivity and stability. Annual Meeting of the Ecological Society of America, August 5-9, 1998.
- C.S. Brown and K.J. Rice. Using ecological combining ability as a predictor of herbaceous plant community stability. Annual Meeting of the Ecological Society of America, August 10-14, 1997. Abstract published in Supplement to the Bulletin of the Ecological Society of America, 78:60.
- C.S. Brown and K.J. Rice. Suppressive effects of the exotic annual grass *Vulpia myuros* on a mixture of California native perennial grasses. Annual Meeting of the Soil and Water Conservation Society, March 13, 1997. Abstract published in Journal of Soil and Water Conservation, July 1998.
- C.S. Brown and K.J. Rice. Competitive effects of the exotic annual grass *Vulpia myuros* on a mixture of California native perennial grasses. Annual Meeting of the Ecological Society of America, August 10-14, 1996. Abstract published in Supplement to the Bulletin of the Ecological Society of America, 77:55.
- C.S. Brown, K.J. Rice and J.H. Anderson. Soil nitrogen and texture effects on below ground growth characteristics of herbaceous plant species: implications for resource partitioning in mixtures. Annual Meeting, Ecological Society of America, July 30-August 3, 1995. Abstract published in Supplement to the Bulletin of the Ecological Society of America, 76: 32.

Invited lectures

- Effects of resource use patterns and species diversity on the structure and function of constructed herbaceous plant communities. Merton Love Award for the best dissertation in Evolution and Ecology in 1998. June 4, 1998, University of California, Davis, California.
- Resource use and partitioning in grassland species. Ecology 230, Grassland Ecosystems, December 2, 1997. University of California, Davis.

The value of using native perennial grasses for roadside revegetation and benefits of taking an experimental approach in revegetation. Landscape Architecture 183, Landscape Architecture Studio, February 26, 1997. University of California, Davis.

The value, establishment, and maintenance of native perennial grasses for roadsides. Environmental Horticulture 133, Woody Plants. February 19, 1997. University of California, Davis.

Experimental approaches to studying species compatibility in mixtures for roadside revegetation. California Native Grass Association Field Day, May 13, 1995. Hedgerow Farms, Yolo County, California.

Investigating the compatibility of plant species in mixtures. Conservation Biology Seminar, May 2, 1995. University of California, Davis.

Publications

C.S. Brown and K.J. Rice. Suppressive effects of Zorro fescue (*Vulpia myuros*) on California native perennial grasses. Summary of results published in Grasslands, 6: 1-2 (1996).

Cynthia S. Brown and K.J. Rice. The mark of Zorro: effects of the exotic annual grass *Vulpia myuros* on a mixture of California native perennial grasses (In press Restoration Ecology).

Cynthia S. Brown, K.J. Rice and J. Connolly. Effects of species diversity and resource use patterns on plant community stability, productivity and resource use (In prep. for Ecology).

Cynthia S. Brown and K.J. Rice. Belowground resource use patterns of selected herbaceous species indicate potential for resource partitioning in mixtures (In prep. for Ecology).

Cynthia S. Brown. Effects of plant community resource use patterns and species diversity on establishment of the invaders *Bromus hordeaceus* and *Centaurea solstitialis* (In prep. for Ecological Applications).

Cynthia S. Brown. Comparison of some biotic and abiotic characteristics of highway revegetation sites and natural communities of California native perennial grasses (In prep. for Restoration Ecology).

Cynthia S. Brown. The role of resource use patterns in stability of assembled herbaceous plant communities (In prep. for Ecology).

OOKSHIRE, ELAN N.,* and J. B. KAUFFMAN. Oregon State University, Corvallis, OR 97333 USA. Aboveground biomass and allochthonous coarse particulate organic matter input in forest and meadow reaches of headwater streams.

Land-use degradation of headwater streams and riparian areas of eastern Oregon have contributed to the extinction or decline of several resident and anadromous fish species. Studies have established the importance of riparian vegetation to the organic matter budgets of forested streams and the invertebrate food base of fish but few have measured inputs into open meadow streams in which material enters primarily during annual high-flow events. We quantified allochthonous coarse particulate organic matter (CPOM) inputs and associated C, N, P, and S contents in relatively unaltered coniferous forest and unconstrained meadow reaches of two headwater tributaries of the Upper Grande Ronde River, OR. Total aboveground biomass (TAGB) averaged 203 and 222 Mg/ha in forest reaches. Potential CPOM within high-flow channel margins averaged 249 and 303 g/m² in forest reaches and 574 and 866 g/m² in meadow reaches.

TOWN, CYNTHIA S.,* and KEVIN J. RICE. University of California, Davis, CA 95616 USA. Effects of species diversity and resource partitioning on plant mixture productivity and stability.

We investigated the importance of spatial and temporal resource use patterns in determining the coexistence of herbaceous California prairie plant species. We addressed the questions of how resource partitioning and species diversity affected soil water use, biomass production and ability of mixture composition. The constituents of the compatible mixtures had differing resource use patterns that conferred the potential to partition resources in space or time, or both. The incompatible mixtures were composed of species that had similar resource use patterns promoting more direct competition for resources than in the compatible mixtures. Results from this field experiment showed that compatible mixtures used higher proportions of soil water, exhibited higher and less variable post-establishment biomass production, and had more stable composition than incompatible mixtures. More diverse mixtures used more soil water at depth, produced more aboveground biomass after establishment, and had more stable composition during establishment than less diverse mixtures. We conclude that not only species number, but spatial and temporal resource use patterns of species, should be considered when evaluating effects of diversity on ecosystem function.

RUGAM, RICHARD B.,* and PATRICIA SWAIN.² ¹Southern Illinois University, Edwardsville, IL 62026 USA; ²Massachusetts Division of Fisheries and Wildlife, Westborough, MA 01581 USA. Peatland development in central Minnesota.

Pollen and diatom analysis was performed on a sediment core from Bogongia Bog, a peatland located in the Big Woods region of Minnesota. During the mid-postglacial warm period (8800 to 3820 years BP), the watershed supported a mosaic of oak woodlands and prairie. Between 3820 and 400 years BP, oak forest expanded at the site. At 400 years BP Big Woods species increased. Diatom analysis shows that during the mid-postglacial period, species indicating high acid neutralizing capacity dominated. At 2200 years BP, these were replaced by peatland-indicating species. A weighted averaging analysis of surface samples shows that this change is associated with a large decline in acid neutralizing capacity which was probably caused by peatland growth in the basin. Terrestrial plants of peatlands only appear in the pollen after 400 years BP.

Annual Meeting of the Ecological Society of America, August 5-9, 1998.

BUCKLEY, DAVID S.,*¹ THOMAS R. CROW,¹ ELIZABETH A. NAUERTZ,¹ and ANGELA M. LUETKENHAUS.² ¹USDA Forest Service, North Central Forest Experiment Station, Rhinelander, WI 54501 USA; ²McKendree College, Lebanon, IL 62254 USA. Effects of timber management on the diversity of understory plants in northern hardwood forests.

To test the hypothesis that altered disturbance regimes in forests managed for timber affect understory plant species diversity, we compared species composition and cover in replicated northern hardwood stands representing uneven-aged management, even-aged management, unmanaged old growth, and unmanaged second growth. Species richness and the proportion of introduced species were consistently greater in managed than in unmanaged stands, with maximum richness in stands under uneven-aged management. Although introduced species were a factor, greater richness in managed stands was primarily due to the addition of native species adapted to open conditions and forest floor disturbance. These native and introduced species were concentrated in logging roads within managed stands, and declined sharply from road edges to the interior of forest patches between roads. These results suggest that disturbance related to timber harvesting can increase species richness, and that logging roads are a particularly important factor. Most of the introduced species sampled appeared to have a limited ability to invade forest patches between logging roads, but the area occupied by logging road networks in managed forests is often substantial.

BUTLER, MARK J.,*¹ and ALISTAIR MACDIARMID.² ¹Old Dominion University, Norfolk, VA 23529 USA; ²National Institute of Water and Atmospheric Research, Wellington, New Zealand. Sperm limitation in exploited populations of spiny lobsters.

Changes in the population structure of marine species that are exploited by humans can have large effects on mating, and therefore reproductive success. For spiny lobsters, the reproductive output of females increases exponentially with female size, so a shift toward smaller females in exploited areas has clear implications for reproductive success. Less clear is the effect of reduced male size on reproductive dynamics, especially in spiny lobsters where male size declines more precipitously than female size when subject to exploitation. We conducted surveys of two species of spiny lobster in marine reserves and exploited areas in the Caribbean and New Zealand to compare population structure and mating patterns in the field. We also conducted laboratory experiments on both species to determine the effect of male size on reproductive success. Our results provide convincing evidence for sperm limitation and strong male size effects on the reproductive success of both species.

BYERS, JAMES E. University of California, Santa Barbara, CA 93106 USA. Mechanisms of competition in two estuarine snails: implications for an exotic species invasion.

Understanding mechanisms that lead to the success of exotic species will provide predictive power for future invasions and insight for management of presently invaded systems. Most studies to date have emphasized the instrumental role that freedom from natural enemies plays in enabling exotic invasion. However, the most basic requirement for any species, including exotics, is suitable habitat. Since suitable habitat within a community is most often utilized, its presence is likely to correlate strongly with the presence of similar native species. Competitive superiority, therefore, may be a fundamental, if not essential, trait for success of exotic species. I quantified consumer-resource interactions of two size classes of a native estuarine snail (*Cerithidea californica*) and an introduced snail (*Batillaria attramentaria*) and their shared food resource (diatoms). I mathematically combined the resulting consumer-resource interaction equations to generate predictions of the exploitative competitive effect of each snail on its heterospecific. These prediction values corresponded extremely well to independent field tests of each snail's effect on the other, thus corroborating the hypothesis that exploitative competition is a predominant mechanism of interaction between the snails. In addition to demonstrating predictive success, quantification of consumer-resource interactions exposed at least one mechanism, superior resource conversion, which contributes to *Batillaria's* success as an invading species.

BRODY, A. K.,* and M. ZIMMERMAN. University of Vermont, Burlington, VT 05405 and University of Wisconsin, Oshkosh, WI 54901 USA. Oviposition behavior in a pre-dispersal seed predator: suboptimal host plant choice?

A lack of correspondence between oviposition choices and offspring performance has been frequently observed for herbivorous insects. To fully understand why there is a lack of such a correspondence, one needs to know how females go about choosing oviposition sites. A dipteran, pre-dispersal seed predator, *Hylemya* sp. (Anthomyiidae), is common at our study site where it regularly oviposits on two Rocky Mountain herbs in the Polemoniaceae, *Lpomopsis aggregata* and *Polemonium foliosissimum*. We examined the importance of flower morphology in determining which flowers *Hylemya* sp. females oviposit on and the success of their eggs on those flowers. *Lpomopsis aggregata* sepals are narrower than *P. foliosissimum*'s and eggs were more likely to be exposed on them than on *P. foliosissimum* ($\chi^2 = 33.21$, $P < 0.0001$). Egg mortality was greater for exposed vs. unexposed eggs ($\chi^2 = 4.95$, $P < 0.025$). We manipulated flower size for potted plants placed in arrays in the field to test whether females use flower morphology in determining where to lay their eggs. However, we found no correlation between flower size and propensity to receive eggs (paired $t = 1.29$, $P > 0.05$). The traits determining egg laying remain unclear, and oviposition on *L. aggregata* may represent suboptimal host plant choice.

BROOKS, VANESSA, and CHRISTOPHER POTTER.* NASA Ames Research Center, Moffett Field, CA 94035 USA. Global analysis of empirical relationships between annual climate and seasonality of NDVI.

This paper describes the use of satellite data to calibrate a new climate-vegetation greenness function for global change studies. We examined statistical relationships between annual climate indexes (temperature, precipitation, and surface radiation) and seasonal attributes of the AVHRR Normalized Difference Vegetation Index (NDVI) time series for the mid-1980s in order to refine our empirical understanding of intra-annual patterns and global abiotic controls on natural vegetation dynamics. Multiple linear regression results using global 1° gridded data sets suggest that three climate indexes: growing degree days, annual precipitation total, and an annual moisture index together can account to 70-80% of the variation in the NDVI seasonal extremes (maximum and minimum values) for the calibration year 1984. Inclusion of the same climate index values from the previous year explained no significant additional portion of the global scale variation in NDVI seasonal extremes. The monthly timing of NDVI extremes was closely associated with seasonal patterns in maximum and minimum temperature and rainfall, with lag times of 1 to 2 months. We separated well-drained areas from 1° grid cells mapped as greater than 25% inundated coverage for estimation of both the magnitude and timing of seasonal NDVI maximum values. Predicted monthly NDVI, derived from our climate-based regression equations and Fourier smoothing algorithms, shows good agreement with observed NDVI at a series of ecosystem test locations from around the globe. Regions in which NDVI seasonal extremes were not accurately predicted are mainly high latitude ecosystems and other remote locations where climate station data are sparse.

Annual Meeting of the Ecological Society of America, August 10-14, 1997
Supplement to the Bulletin of the Ecological Society of America 78:60.

BROOKSHIRE, BRIAN L.,* JOHN M. KABRICK,² DAVID R. LARSEN,² and STEPHEN R. SHIFLEY.³ ¹Missouri Department of Conservation, Jefferson City, MO 65109 USA; ²University of Missouri-Columbia, Columbia, MO 65211 USA; ³North Central Forest Experiment Station, Columbia, MO 65211 USA. Soil, geology, landform and vegetation interactions in the eastern Ozarks.

The Missouri Ozark Forest Ecosystem Project (MOFEP) is a 100-year study to investigate forest management impacts on multiple ecosystem attributes. MOFEP also provides opportunities to investigate interrelationships between biotic and abiotic components of the forest ecosystem in the eastern Ozarks. We analyzed relationships among soils, geology, landform position and woody vegetation. Information collected from two land-type associations (Current-Eleven Point River Hills and Current-Black River Breaks) and six geolandforms with accompanying soil descriptions was used to identify if there were differences in woody vegetation composition. The Current-Eleven Point River Hills land-type association (Hills LTA) has broader and longer slopes, comprised of fewer geological strata and has a greater proportion of weathered soils compared to the Current-Black River Breaks land-type association (Breaks LTA). We found significantly less white oak ($P < 0.001$) and more scarlet oak ($P < 0.001$) in the Hills LTA compared to the Breaks LTA. Changes in species composition from the summit to lower backslope positions were similar between LTA s but were different in magnitudes of change. The Breaks LTA had greater site indices than the Hills LTA and there were greater site index differences among geolandforms within the Breaks LTA. This research is resulting in a better understanding of oak-pine and oak-hickory ecosystems in the eastern Ozarks and is providing a framework for implementing an ecological approach to natural resource management.

BROSOFKSKE, KIMBERLEY D.,¹ JIQUAN CHEN,¹ THOMAS R. CROW,² and SARI C. SAUNDERS.¹ ¹Michigan Technological University, Houghton, MI 49931 USA; ²North Central Experiment Station, Rhinelander, WI 54501 USA. Plant diversity at multiple scales across a northern Wisconsin pine barrens landscape.

Increasing awareness of interrelationships between landscape structure and processes and concern about biodiversity loss has promoted efforts to understand biodiversity at multiple scales. We examined patterns of plant species diversity and relationships to landscape structure across scales in a managed landscape. We recorded overstory patch type and species coverage in 1 x 1 m plots every 5 m along a 3580-m transect. A total of 114 herbaceous and 42 woody species were encountered. Most had relatively low coverage per plot and low occurrence frequency. DCA and TWINSPLAN techniques identified four large species groups, seemingly distributed along disturbance and successional gradients. Wavelet analysis revealed scale-dependent patterns of diversity (richness, Shannon-Weiner, Simpson's, and heterogeneity measures) and associations with landscape structure across resolutions of 5-1500 m. Strong correspondence between overstory patch type and diversity was found for several patches at certain scales, but not for others at any scale. Effects of small features (i.e., roads, clearings) were apparent in the wavelet transforms at resolutions of 5-250 m. Disturbance (i.e., fire) effects on diversity were observable over all resolutions. These results emphasize the changing influences of landscape structure and disturbance on plant species distribution over differing scales.

BROWN, CYNTHIA S.,* and KEVIN J. RICE. University of California, Davis, CA 95616 USA. Using ecological combining ability as a predictor of herbaceous plant community stability.

We conducted a series of experiments to investigate whether the resource use patterns of individual species can be used to predict, a priori, the relative stability of a constructed herbaceous plant community. We first evaluated individual species growing alone in field and container experiments to characterize their above- and belowground resource use in space and time. Selections were made for two, three, and five species mixtures based on the time of most rapid growth for a species, its relative root length distribution, and its height. Mixtures were designed to be more or less stable by including plants expected to have high or low degrees of ecological combining ability, respectively. Mixtures of species that had the potential to partition above- and belowground resources were expected to be more stable than those with more similar resource use patterns. A novel analytical method was applied to evaluate the stability of the constructed communities over two growing seasons. Patterns of resource use explained many of the changes in species composition observed in this experiment. However, resource supply and herbivory were also important ecological factors influencing community stability.

We will summarize the results of six years of field assessments of a wide range of cover crops under condition of high winter rainfall, poor soil structure, and waterfowl grazing. The sustainability of the local farm community and the wildlife habitat it provides is threatened by soil degradation and the socioeconomic stresses associated with farming in an urbanized region and in an ecosystem with intensive overwinter waterfowl utilization. Effectiveness of cover crops depended on species, seeding date, soil conditions, and grazing intensity. Successful overwinter cover crops provided soil protection and/or forage for migratory waterfowl. Allowed to grow until late April, cover crops such as winter wheat, fall rye, and annual ryegrass, were capable of adding large amounts of green manure and conserved nitrogen to the soil. Increased soil polysaccharide content, earthworm numbers, aggregate stability, and infiltrability are indicators of improved soil quality and ecosystem function. Costs to farmers of cover cropping must be kept low and shared by the nonfarm community when this practice improves habitat for populations of migratory birds such as widgeon, mallard, pintail, snowgeese, and swans. The Delta Farmland and Wildlife Trust is a community based organization which organizes, monitors, and shares the costs of overwinter cover cropping and other conservation programs.

Demonstrating the potential of annual legumes in the northern Great Plains

Paul Finnicum, NRCS, Calbertson, MT

The objective is to show substituting annual legumes for mechanical, season long summerfallow, can reduce the potential for erosion, break weed and disease cycles, provide nutrients for subsequent crops, provide high quality forage for livestock, and reduce potential groundwater contamination by pesticides and fertilizers.

This region of the northern Great Plains receives 12 to 14 inches of precipitation in a normal year and is predominantly in a crop/fallow cropping system.

For the past three years, a dielectric moisture probe has been used to demonstrate the annual legumes, grown for 60 days, can use less soil moisture than what is lost through conventional summerfallow. Up to 2,500 lbs. of forage has been produced losing no more soil moisture than summerfallow, receiving less than three inches of precipitation during the growing season.

Local producers are adopting this information and converting strip cropped acres into larger management units utilizing idled land for annual legume grazing. All legume growth is terminated at 60 days regardless of planting date. The producers vary the planting date to provide the high quality feed at a time of the year when native forage has diminished nutritional value. This also provides rest for native pastures.

The blocks are in grain crop or legume further reducing the potential for erosion. Sixty-day termination prevents weeds from going to seed.

Cattle graze the legumes which also reduces the need for mechanical manure spreading.

The legume residue and manure are then incorporated into the soil the following spring prior to planting.

Small grain cover crops in Hawaii for erosion and weed control

Carl I. Evensen, Samir A. El-Swafy, University of Hawaii; Robert V. Osgood, Hawaii Agriculture Research Center

Objective: This paper presents findings from five years of research on the use of small grain cover crops for erosion and weed control in plantation agriculture in Hawaii. Initial studies indicated that tall spring oats, interplanted between sugarcane rows, provided rapid soil cover and good weed control, but competed with the sugarcane. In a subsequent series of trials conducted on the islands of Hawaii, Molokai, and Lanai, 51 cultivators of oat, barley, wheat, ryegrass, and rye grain were compared and several cultivators of each species were selected for vigorous growth, rapid soil cover, weed suppression, low plant height, and lack of flowering. A large scale planting was then established on the island of Oahu to demonstrate 10-acre blocks of selected oat and rye grain varieties intercropped with sugarcane. The results of this work has shown that small grain cover crops can be effective in both erosion and weed control in sugarcane and has been designated by the Natural Resources Conservation Service as an alternative conservation practice. Information from these studies has been used in ongoing cover cropping work in pineapple, coffee, and tropical fruit tree orchards.

Cover crops in potatoes to recover nitrogen and reduce fertilizer use

J.L. Brunty, W.L. Pan, R.A. Boydston, M.R. Moneymaker, R. Stevens; Washington State University

Winter cover crops can recapture leachable nitrate and when used as green manures, can supply N to subsequent crops, reducing the need for inorganic fertilizers. Rapeseed and white mustard cover crops were planted in the fall of 1995. The white mustard frose-killed in November while the rapeseed overwintered. The respective desiccated residues and fresh vegetation were disked in one week prior to planting. Cover crops reduced soil nitrate prior to spring plowdown. All plots were fertilized with 112 kg ha⁻¹ preplant nitrogen. Nitrate was lowest in rapeseed plots prior to planting but increased rapidly as mineralization occurred. Nitrogen levels peaked at 530 kg ha⁻¹ in rapeseed plots, compared to 300 kg ha⁻¹ fallow plots. Yields of larger potatoes were increased in the low fertilizer rate rapeseed treatment. Overwintering cover crops can reduce nitrate leaching and fertilizer requirement.

Effects of cover crops on nitrate dynamics under maize continuous crop

Marco Mazzoncini, University of Pisa-Centro E. Avon; Lorella Ciugharini, Stefano Meuni, Enrico Bonari, Rosalba Risaliti

Objective: Evaluate the effect of different cover crops, tillage techniques, and nitrogen rates on nitrate content under maize continuous crop.

The effects of two tillage techniques (30-35 cm plowing and no-tillage), two nitrogen rates (0 to 300 kg ha), and three cover crops (*Secale cereale*, *Trifolium incarnatum*, and *Trifolium subterraneum*, in comparison to maize residues) on N-NO₃ of soil content were evaluated. Soil samples were collected at different depths (0 to 20 cm, 20 to 40 cm, and 40 to 60 cm) in different periods of the year in a long-term experiment, started in 1993 on a silty-loam soil at Research Centre "E. Avanzi" of the University of Pisa, Italy.

Suppressive effects of the exotic annual grass *Vulpia myuros* on a mixture of California native perennial grasses and exotic weeds

Cynthia S. Brown and K.J. Rice, Dept of Agronomy and Range Science, University of California, Davis

Annual grasses are usually included with native perennial grasses in revegetation and erosion control seed mixtures in California. *Vulpia myuros* (*Zorro fescue*) is one of the most common annual species used in these mixes. This experiment tested the effects of varying densities of *Vulpia* on a mixture of California native perennial grasses. Results showed that perennial grass seedlings did not appear to be light stressed. *Vulpia* also had a significant suppressive effect on weed density and above-ground biomass within the experimental plots. Weed densities were more negatively affected by *Vulpia* than perennial grass densities were. However, above-ground biomass of weeds and perennial grasses were equally reduced by increases in *Vulpia* densities. Overall effects of *Vulpia* on native perennial grass survival and growth were negative and weed suppression benefits were not sufficient to outweigh these effects.

Nitrogen uptake and yield in dryland wheat/fallow and wheat/green manure rotations

A.M. McGuire, Graduate student, University of California, Davis

Objective: In this study a winter legume green manure crop was substituted for fallow in a two year wheat rotation to determine if the short term effects of a green manure are due solely to nitrogen and water differences.

Erosion and decreased soil fertility have been attributed to the long term use of fallow in dryland wheat production systems. In this study a winter legume green manure crop was substituted for fallow in a two year wheat rotation to determine if the short term effects of a green manure are due solely to nitrogen and water differences. Soil moisture, inorganic soil nitrogen, and wheat yields were compared in both fertil-

BROOKE, ANNE P. Department of Marine and Wildlife Resources, Pago Pago, American Samoa 96799, USA. Factors influencing the apparent population size of the Samoan flying fox.

The Samoan flying fox, *Pteropus samoensis*, is endemic to the Samoan archipelago and Fiji islands. This species one of several Pteropodid bat species that are active diurnally on South Pacific Islands. Samoan flying foxes roost in mature forest either singly or in pairs. Populations in American Samoa declined dramatically during the 1980's from commercial hunting and the early 1990's after two severe hurricanes. In 1992, an estimated 200-400 individuals remained in American Samoa, an estimate that now appears inaccurate. Monthly surveys have been conducted since 1992 to monitor population size. It has been assumed that since bats are active during the day, counts of day-flying individuals are a realistic method for assessing the population size. Approximately 1000 individuals are now present on AS, an increase impossible from reproduction alone. Immigration of bats from other islands in large numbers is unlikely. In this study I investigate both diurnal and nocturnal activity patterns. The importance of diurnally flowering plants and increased population pressure are examined as factors that alter the perceived population size.

BROOKS, CHRISTOPHER P. and LAURA J. HECHTEL. Kennesaw State College, Kennesaw GA 30144. The effects of land disturbance on amphibian metapopulation dynamics.

Amphibian populations in Cherokee County, GA were examined to determine the effects of habitat fragmentation and disturbance on metapopulation dynamics. Amphibian metapopulations, which consisted of varying numbers of breeding sites varied in level of disturbance and size. Driftence-pitfall traps and mark recapture methods were used to estimate breeding population sizes and degree of migration between breeding sites. Egg mass counts were used as an estimate of reproductive effort for the population. Abiotic and biotic components of the breeding sites were also examined. Migration between sites decreased with increased breeding site size and increased population sizes. Small breeding sites had smaller populations of amphibians and probably could not replace themselves if isolated. Breeding sites separated by roads prevented migration of salamanders and lowered that of frog populations. Breeding sites adjacent to recently cleared patches of forests showed lower survival and population sizes when compared to undisturbed breeding sites. Breeding success was positively correlated with percent cover and persistence of breeding sites.

BROWN, CATHY, G.A. BRADSHAW and DEDE OLSON. PNW Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331, USA. Cascade frog (*Rana cascadae*) population response to environmental variability: assessing heterogeneity across scales.

Theoretical models have demonstrated the importance of spatial structure (e.g. landscape connectivity and patchiness) on population dynamics. This study examines the extent to which environmental spatial heterogeneity is reflected in the distribution of populations of the montane frog, *Rana cascadae*, in the central Cascade Range, Oregon. Habitat variability was measured in terms of habitat quality (e.g. resistance to desiccation, vegetation) and connectivity (e.g. density and distribution of suitable breeding sites, topography relief among sites, and distribution of connecting creeks). Potential breeding sites within three watersheds were identified from aerial photos and field verified. Sites were surveyed for eggs, tadpoles, and adults to assess occupancy relative to site quality and connectivity. The integration of digitized aerial photo, field, and topographic data in a geographic information system provided an effective means for across scale analysis. Only a proportion of breeding sites were occupied; occupancy appeared to have a stronger association with local site quality than with intra-watershed connectivity. This study provides insights for conservation strategies such as the importance of maintaining linkages among populations, identification of potential corridors, and the importance of "source" populations.

BROWN, CYNTHIA S. and K.J. RICE. University of California, Davis CA 95616, USA. Competitive effects of the exotic annual grass *Vulpia myuros* on a mixture of California native perennial grasses.

Competition from introduced annual grasses can be a principal impediment to establishment of native perennial grasses in California prairies. Furthermore, introduced annual grasses are usually included with native perennial species in revegetation seed mixtures in California. *Vulpia myuros* (Zorro fescue) is one of the most common species used in such seed mixes. This experiment tested the effects of varying densities of *Vulpia* on a mixture of California native perennial grasses. *Vulpia* exhibited a strong plastic response to plant density; similar amounts of phytomass (above-ground dry weight) were produced at both low and high plant densities. Results showed that perennial grass seedling survival and phytomass decreased with increasing *Vulpia* seeding densities but seedlings did not appear to be light stressed. *Vulpia* also suppressed weeds. At low *Vulpia* seeding densities, weed phytomass was decreased to a larger degree than perennial grass seedling phytomass but this differential effect disappeared at higher seeding densities. Observations of *Vulpia* densities in subsequent years suggest that any weed control benefits seen in the initial year after seeding will be eliminated over time and that *Vulpia* has a net negative effect on native perennial grass establishment.

BROWN, CYNTHIA S., KEVIN J. RICE and JOHN H. ANDERSON. University of California, Davis, CA 95616 USA. Soil nitrogen and texture effects on below ground growth characteristics of herbaceous plant species: implications for resource partitioning in mixtures

Field and container studies quantified growth and resource acquisition characteristics of California grassland species in response to differences in soil texture and nitrogen levels. Results indicated that species vary in root distribution patterns and specific root lengths. Grasses had greater root length densities and specific root lengths than non-grasses. Soil water potential data demonstrated differences between species in the extent of soil water reduction as well as variation in timing of depletion. Soil nitrogen and texture treatments did not affect specific root length, root length density, or soil water depletion levels. Taking into consideration root growth and water acquisition patterns, species were selected for an ongoing experiment investigating resource partitioning in mixtures.

BROWN, D. GORDON and ARTHUR E. WEIS. College of St. Benedict, Collegeville, MN 56321 USA and University of California, Irvine, CA 92717 USA. Ambient herbivore density and plant genotype influence infestation and defoliation of goldenrod by a specialist leaf beetle

We examined how ambient herbivore density and plant genotype affected infestation and defoliation of goldenrod (*Solidago altissima*) by a specialist herbivore (*Trirhabda* spp.) in field experiments during 1993 and 1994. In 1993 we planted 10 plots with 5 replicates of 35 goldenrod genotypes and randomly assigned plots to one of five mean *Trirhabda* densities (0, 1.25, 2.5, 5, or 10/stem). We released *Trirhabda* adults systematically within each plot and estimated infestation and defoliation visually. In 1993 infestation and defoliation were significantly affected by ambient *Trirhabda* density, goldenrod genotype, and density x genotype interaction. In 1994 we re-randomized the assignment of treatments to plots and found similar results. In addition, we observed a positive genotypic correlation between 1993 and 1994 infestation levels. Infestation was positively correlated with *Trirhabda* density, and defoliation was positively correlated with infestation. The density x genotype interaction arose because some clones had fairly flat infestation reaction norms across densities, while others had increasing reaction norms. However, density-dependent departure from experimental plots resulted in a sigmoid shape for most reaction norms. These results suggest that plant genotype had a consistent impact upon herbivore densities over two successive seasons.

BROWN, JAMES H. and DOUGLAS A. KELT. University of New Mexico, Albuquerque, NM 87131 USA. Community structure and assembly rules: confronting conceptual and statistical issues with data on desert rodents.

Patterns of community structure presumably reflect underlying processes of species assembly, but demonstration of pattern and inferences about processes are complicated by several conceptual and statistical issues. Distinguishing deterministic patterns from null hypotheses of random assembly requires us to make decisions about: how to define the community, what kind of structure to expect on the basis of theory or empirical induction, how to deal with redundancy (the recurrence of the same species and combinations of species in multiple assemblages), whether and how to designate an appropriate species pool, whether to use standard statistics or randomization techniques, how to deal with correlated variables, and so on. We illustrate these issues with analyses of assembly of community of desert rodents, a system where we know a good deal about both the patterns of community structure and the processes that affect the dynamics of coexisting species.

BROWN, SHANNON E. and GEORGE R. PARKER. Purdue University, West Lafayette, IN 47907 USA. Response of forest communities to white-tailed deer herbivory.

The white-tailed deer (*Odocoileus virginianus*) is considered to be a keystone species which can significantly influence the structure of forest ecosystems throughout the eastern United States. This research was initiated to examine the effects of this species on the plant communities within state parks in Indiana which have been closed to hunting for several decades. Sites, stratified by physiographic position, were sampled within Brown County State Park and adjacent state and national forest lands (open to public hunting) during 1993 and 1994. Results showed a definite decline in percent cover and plant height inside the parks as opposed to the external sites subject to hunting pressure. Species richness was also lower within the park. Regeneration of most woody species within the park was significantly reduced and current forest structure indicates that this has been occurring for many years. This, along with the damage occurring in the herbaceous layer, suggests that the sustainability and structure of the forests within the park may ultimately be affected.

BRUGAM, R.B., BETH OWEN and KATHLEEN MCKEEVER. Dept. of Biological Sciences Southern Illinois University, Edwardsville 62026. Lake and Bog Development at Glimmerglass Lake in the Sylvania Wilderness Area, Michigan.

We used pollen and diatom analysis to reconstruct post-glacial development of Glimmerglass Lake and its adjacent *Sphagnum* peatland using transects of cores. Glimmerglass lake has existed since late-glacial times with little or no change in water levels. In contrast the peatland began growing as a floating mat in a pond that was separated from the main lake by a spit of land. Over time, the floating mat became grounded in the pond but continued growing to cover an adjacent low area that had never been underwater. The peatland continues to grow



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Suppressive effects of Zorro fescue (*Vulpia myuros*) on California native perennial grasses

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Many involved in revegetation projects wonder about the effects of introduced annual grasses, such as Zorro fescue, on native perennial grasses when they are combined in seed mixtures. The rationale for including annual grasses in reseeding mixtures seems to be that the quick ground cover and erosion control provided by annuals outweigh any negative effects they have on the native perennial grass species. The evidence which has accumulated over years clearly indicates that native perennial grasses are negatively affected by annual grasses (Heady 1989; Harris 1967; Harris and Ison 1970). In California, results from field studies by Dyer (unpublished data) and Dyer et al. (1996) at Jepson Prairie, a container study by Craig Dremann (1989), and field and container studies by Bartolome and Gemmill (1981) all show that annuals have a strong negative effect on the survival and performance of the California native perennial grass Purple needlegrass (*Nassella pulchra*). Results from the experiment we conducted continue to strengthen the case that annual grasses significantly interfere with the success of native perennial grasses.

We conducted an experiment in Yolo County between 1993 and 1995 to specifically address the question of how the annual grass Zorro fescue (*Vulpia myuros*) affects native grasses when both are planted in erosion control seedings. Preliminary results of this experiment were presented at the 1994 CNGA Annual Meeting. Zorro fescue was selected as the annual competitor primarily because it has been, and continues to be, included in revegetation seed mixtures throughout California. Based on its height and the density of its canopy, the impact of Zorro fescue on native grasses would seem to be minimal compared to other, more robust introduced annual grasses such as Soft chess, Italian ryegrass, and gut brome. Some have hypothesized that Zorro fescue might act as a nurse plant by suppressing weeds, providing protection from herbivores, and reducing water stress through shading in hot, dry summer months.

We assessed the effects of varying densities of Zorro fescue on a mixture of California native perennial grasses. The perennial grass mixture included the following: Blue wildrye (*Elymus glaucus*) 1 lb/acre, Meadow barley (*Hordeum californicum* ssp. *richyantherum*) 3 lb/acre, California melic (*Melica californica*) 3 lb/acre, Nodding needlegrass (*Nassella cernua*) 3 lb/acre, Purple needlegrass (*Nassella pulchra*) 6 lb/acre, Pine bluegrass (*Poa secunda* ssp. *secunda*) 1.5 lb/acre. The total seeding density for the perennial mixture was 19.5 lb/acre. At the time of the study, this was considered a state-of-the-art erosion control seed mixture. The mixture was planted first using a Truax wildflower seeder. The Zorro fescue was broadcast over the mixture in small plots (10 ft by 1 ft) and raked in by hand. Zorro fescue seeding densities were 1, 15 and 30 lb/acre. The native perennial mixture was also grown in as a control.

The results of our experiment show that increasing seeding densities of Zorro fescue produced both lower above ground biomass and densities of native perennial grasses and weeds. Native perennial grass and weed above ground biomass were suppressed to the same degree. However, perennial grass densities were not

reduced as much as weed densities were by increased seeding densities of Zorro fescue. There was no detectable difference in height of native grass seedlings but biomass per plant decreased with increasing Zorro fescue seeding densities. These results suggest that reduced light levels under the Zorro fescue canopy inhibited growth.

The differential effect of Zorro fescue on native perennial grasses and weeds (i.e. weed densities were more negatively affected than perennial grass densities), might seem to warrant including Zorro fescue in mixtures with native perennial grasses to control weeds. However, before coming to this conclusion it is important to consider the absolute amounts of weeds compared to native grasses and the goals of the reseeding effort. In our experiment, the weed densities and above ground biomass were many times greater than those of perennial grasses. Because weeds are generally prolific seed producers, it is doubtful that reductions in their densities in the first year after seeding would be sufficient to prevent growth of the weed population.

Vegetation establishment and erosion control are two common objectives of reseeding projects. With regard to establishing native perennial grasses, our results clearly show that fewer, smaller native grasses survived when Zorro fescue was present than when it was not. Zorro fescue did not act as a nurse plant for native perennial grasses in this case. When erosion control is of primary concern, one should consider that the amount of protection provided by quick germinating and fast growing annual grasses depends a great deal on the rainfall pattern after seeding. If a rainy season begins with torrential storms, even the annuals may not reduce erosion significantly. Because the absolute amount of weeds did not appear to be reduced enough to be biologically meaningful, perennial grasses were suppressed by the presence of Zorro fescue, and the protection provided by annual grasses against erosion is contingent on weather patterns, it appears unwise to include Zorro fescue in seed mixes with California native perennial grasses. Emphasizing mechanical means of erosion control in the short term may be the best use of resources in order to reach long term vegetation establishment and erosion control goals.

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