

## AN ABSTRACT OF THE THESIS OF

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presented on May 30, 2003.

Title: The Effect of Diversity and Spatial Arrangement on Biomass of Agricultural Cultivars and Native Plant Species

Abstract approved:

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Species and cultivar combinations have been relatively well studied, though little is known about the influence of spatial arrangement on agricultural or native plant mixtures. The effect of spatial pattern on mixtures was explored in three experiments. In the first two, agricultural and native plants were planted in two-way mixtures that included combinations of cultivars, species, genera, or functional groups. Each combination was arranged as a random mixture within rows, alternating rows of different genotypes or species, and as alternating pairs of rows. Biomass was determined for each mixture component and compared to monoculture controls. In the third experiment, two wheat cultivars were planted in seven treatments in the 2000-2001 winter wheat season and three cultivars were planted in 18 treatments in the 2001-2002 season. One cultivar was always planted at full rate, and a second cultivar was added at  $\frac{1}{4}$  rate, either randomly mixed, or between rows of the other cultivar. Performance was measured in terms of seed yield. The specific species or cultivar combination had the most consistent influence on aboveground biomass or seed yield, while the effect of spatial arrangement was significant in few treatments.

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The Effect of Diversity and Spatial Arrangement on Biomass of Agricultural Cultivars  
and Native Plant Species

by  
Catherine Anne Worster

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# The Effect of Diversity and Spatial Arrangement on Biomass of Agricultural Cultivars and Native Plant Species

## Introduction

### *Diversity and productivity*

Most ecosystems are described as biologically diverse (Wilson, 1988), with diversity defined as the number of species in a community, and tend to become less so as they are transformed into industrial agro-ecosystems (Soule and Piper, 1992). Diversity loss can also be attributed to climate change, disturbances in complex food webs, spread of invasive species, and loss of key species such as pollinators (Moldenke, 1979). Many ecologists have asked if species loss leads to less productive ecosystems (Tilman, 1999; Adler and Bradford, 2002), with productivity defined as the rate of conversion of resources to biomass per unit area per unit time (Waide *et al.* 1999). Others have asked if species gain may create more productive agroecosystems (Soule and Piper, 1992). However, ecologists are still unable to make generalizations about the relationship of diversity to productivity (Kaiser, 2000; Loreau *et al.*, 2001). In fact, a comprehensive survey of ecological literature found 200 relationships between diversity and productivity, of which 30% were unimodal, 26% were positive linear, 12% were negative linear, and 32% were not significant (Waide *et al.*, 1999). In a study of grasslands, the ecosystem most closely the model this study, Tilman *et al.* (2001) found a positive link between biodiversity of plant species and productivity of the community.

Evidence suggests that diversity is most influential on productivity at the level of plant *functional groups*, representing the functional components of an ecosystem (Tilman *et al.*, 1997; Hector *et al.*, 1999; Loreau *et al.*, 2001; Tilman *et al.*, 2001). However, others have found that, rather than functional group, plant composition (the particular species present) explains more of the variation in production and nitrogen dynamics

(Hooper and Vitousek, 1997). Other studies have found that diversity is only important within structurally diverse ecosystems such as layered forests or those that experience seasonal or other infrequent extreme fluctuations (Grime, 1997). Even without extreme fluctuations, a model using the distribution of phenotypic traits showed that greater phenotypic variance, one measure of diversity, can lead to greater whole-system productivity for a community of individuals evolving in response to environmental change. This is because the rate at which traits can track environmental change is greater with increasing phenotypic variance (Norberg et al., 2001).

The functional groups of a prairie usually include graminoids ( $C_3$  and  $C_4$  grasses), nitrogen-fixing legumes, and forbs, though the groupings depend on the functions or processes under study (Hector et al., 1999). Most studies consider the functions of energy allocation, nitrogen fixation capability, and season of growth (Tilman et al., 1997); however, outside of whether a plant fixes or is simply a consumer of nitrogen, it is inconclusive whether the functions of each additional group are meaningful (Tilman et al., 1997; Hooper and Vitousek, 1997; Wardle et al., 2000). In addition, while the presence of certain functional groups, particularly  $C_4$  grasses and legumes, has been found to be significant, simply an increase in species number also seems to have a significant influence on productivity (Tilman et al., 2001).

Light interception and competition for nutrients in space and time have been shown to be significant factors determining diversity and productivity of agricultural species and cultivars. Light interception is shown to create competitive differences in cropping systems. In a study of a 4-meter tall sorghum cultivar intercropped with cowpea, the sorghum intercepted more than 60% of the incoming photosynthetically active radiation

(PAR) (Gilbert et al., 2003). Not only light, but nutrient and water availability, change competitive interactions (Wilson and Tilman, 1991; Oljaca et al., 2000; Cahill, 2002). Maize intercropped with beans can increase overall yield, especially when irrigated. However, when not irrigated, combinations do not tend to overyield and spatial arrangement patterns do not significantly affect leaf area index, or the size of leaf relative to unit ground surface area (Oljaca et al., 2000). Maturity date will also affect productivity of components in monoculture. If one component is harvested and the other allowed to grow and mature, it may follow the 'competition-recovery production principle' where the remaining cultivar, released from competition, increases its productivity (Zhang and Li, 2003). Likewise, if species or cultivars have similar timing of maximum resource capture, they will be more likely to compromise the full growth or reproductive potential of the other.

Theory and research indicate that the link between diversity and productivity is based on a mechanism that decreases competitive differences among species, thus preventing competitive exclusion (Aarsen, 1992). Four theories describe possible mechanisms that may prevent competitive exclusion. The lottery hypothesis suggests that differences in competitive ability are a consequence of stochastic differences in individual environmental experiences rather than deterministic genotype differences (Fägerstrom, 1988). The environmental heterogeneity hypothesis suggests that competitive ability is genetically variable, but coupled with environmental variability over space and time, confers no static advantage on one species (Steward and Levin, 1973; Chesson, 1986; Ellner, 1987). The circular networks hypothesis, studied primarily in corals, suggests competitive ability is genetically variable at the species level, but no species is superior to

all others (Connell, 1978; Karlson, 1985). The competitive combining ability hypothesis, also called complete equality hypothesis by Connell (1978), assumes not only that competitive ability differs at the species level, but also at the genotype level and that species coexist because they maintain similar competitive abilities as a consequence of ongoing coevolution (Aarsen, 1989, 1992).

The environmental heterogeneity model is the one most frequently used to explain diversity. In terms of space, this concept has also been called niche overlap (Vandermeer, 1989), habitat partitioning, or niche complementarity (Walker, 1992; Hector et al., 1999). Higher productivity at higher diversity can also lead to increased community stability, which over time and on average can be a more productive system than one with greater fluctuation in biomass (Lehman and Tilman, 2000). In other words, with higher diversity comes insurance that from year-to-year or season-to-season the most well adapted species for that environmental situation will maintain productivity at a high level.

Beyond avoiding competitive exclusion, one species may actually *benefit* from another species. While the actual frequency of positive interactions between plants is unknown, research suggests it is relatively uncommon. A review of literature found that, of about 50 papers on competition, 83% found negative interactions and 10% found positive impacts (Goldberg and Barton, 1992). This may suggest that one out of ten neighbor plant relationships is positive, resulting from complementarity (commensalism, mutualism), but that the majority are competing, and result in exclusion (causing a decrease in biodiversity), coexistence (escaping competitive exclusion), or an intermediate scenario (compromising their full growth potential). Agricultural

intercropping research suggests that belowground facilitation or complementary can be complex and specific. Research has found that maize improves iron nutrition in intercropped peanut, faba bean enhances nitrogen and phosphorous uptake by intercropped maize, and chickpea facilitates phosphorous uptake by associated wheat (Zhang and Li, 2003). Such combinations will often yield higher than their pure stands, suggesting improved utilization of resources (Hauggard-Nielsen et al., 2001).

One line of experimental support for positive competitive interactions is the demonstration of “overyielding”, where the total biomass or seed yield of a mixture of species exceeds that found in monoculture achieved by the highest yielding of the component species (Harper, 1977). However, some scientists have noted that comparing functional group mixtures to monocultures of the same components showed that, while there may be resource complementarity (demonstrated with measurements of nitrogen content in aboveground and overall biomass), overall productivity did not differ significantly from the mean of the yields of component one-group treatments (shown with biomass harvest) (Hooper, 1998). Hence, resource complementarity does not always result in overyielding.

If species are *redundant*, and not complementary, they potentially occupy identical resource depletion zones. Increasing species richness in this case can lead to no change in primary productivity (resource-use intensity independent of richness), or an increase in primary productivity (species added in increasing order of resource use intensity), or a decrease in primary productivity (species added in decreasing order of resource use intensity) (Loreau, 2000).

One common criticism of experiments with a positive diversity-productivity relationship is that they demonstrate a problem with sampling effect. Theoretically, this arises as species sampled tend to be those that are high yielding, and when included in a mixture, lead to plant communities with high productivity. As the number of species increases, more of these high yielding species are added, resulting in increasing productivity with increasing diversity (Aarssen, 1997; Huston, 1997; Tilman, 1997).

The inverse sampling effect, or negative selection effect, is based on the phenomenon that high diversity can lead to lower productivity. Loreau (2000) suggested that this is a possibility if competitive ability is correlated negatively with biomass production. Trade-offs between resource acquisition and interference competition, or between resource acquisition and resource-use efficiency, would lead to a negative correlation between resource-use intensity, and hence primary productivity, and biodiversity.

In small, relatively homogeneous study systems, the increase of productivity with an increase in diversity reaches an asymptote (Naeem et al., 1996; Garnier et al., 1997; Dukes, 2001). Dukes (2001) studied native and naturalized California grassland species grown in 0.2m diameter PVC pipes. Though there was great variation depending on species and availability of resources, an asymptote, or slow increase in productivity with an increase in diversity, was found at a relatively low number of species. Some research has found that a log-linear curve describes the productivity diversity relationship better. When communities of grasses and forbs, ranging from 32 to 1 species, were recreated at eight European grassland sites by removing plants and reestablishing them from seed, it was found that each halving of the number of plant species reduced productivity by approximately  $80 \text{ g m}^{-2}$  (Hector et al., 1999).

**I hypothesize that, if escaping competitive exclusion is a result of genetic variability, then a diversity of increasingly dissimilar individuals is more likely to be linked to higher productivity. Thus, a plant community with a diversity of function will be more productive than one with a diversity of species or genotypes within a functional group, which will be more productive than a monoculture.**

### *Spatial arrangements*

While in agriculture individuals are typically planted in rows of monoculture and amendments are added to equalize plant growing conditions, natural plant communities tend to reflect the environmental spatial heterogeneity found both in areas less than 1m<sup>2</sup> and on larger scales (Miller et al., 1995). Evidence from natural systems shows that species are often aggregated and segregated in plant communities (Rees et al., 1996) for reasons including growth form, as in cespitose grasses, uneven suitable soil conditions, uneven disturbance, escape from competition, and beneficial conditions facilitated by neighbors (Rice, 1984; Liebman, 1988; Thórhallsdóttir, 1990; Symstad et al., 2000). This means that some species may not compete with others in the same community (Silvertown et al., 1992). However, many plant competition models assume that species are well mixed (Schwinning and Parsons, 1996; Naeem et al., 1996).

In order to understand if an agricultural system would benefit from spatial heterogeneity, it is necessary to study the effect of spatial arrangements on productivity. Research in intercropping, or growing two complementary crop species together, has increased our understanding of agricultural plant communities (Francis, 1986). For example, the potential importance of spatial pattern on agricultural productivity can be seen with mixtures of rice cultivars. Earlier work showed that a tall, lower-yielding

cultivar mixed with a semidwarf, higher-yielding cultivar in a replacement approach reduced yield as compared to monoculture performance (Jennings and Aquino, 1968). This result is not surprising, as a taller, lower-yielding cultivar would be expected to shade a shorter, higher-yielding one. In contrast, more recent work in rice in which a reduced density of a tall, lower-yielding variety was added between every fourth row of the full monoculture density of a semidwarf, higher-yielding cultivar showed substantial increases in productivity as compared to the monocultures (Zhu et al., 2000). Though cultivar diversification reduced the severity of blast disease, the disease effects alone were insufficient to explain the large increases in productivity observed. However, the full yield effects can be explained if one assumes that the cultivars utilized different resources, which would increase productivity, and that planting in rows avoided the negative shading effects seen in earlier studies. Such spatial interactions would be expected to be both more complex and more beneficial in species mixtures (Hutchings and Discombe, 1986; Thórhallsdóttir, 1990)

**My second hypothesis is that plant communities will be most productive when a fortuitous spatial arrangement is achieved. The most productive combination and spatial arrangement will depend on minimizing competitive interactions (either intragenotypic/intraspecific or intergenotypic/interspecific) and creating combinations and spatial arrangements where complementarity exists.**

### *Willamette Valley prairie*

Grasslands once covered 40% of the contiguous United States (Carey, 2000). Of the 1.08 million acres of Willamette Valley prairie at the time of 1850s government land surveys, less than 1% remains. The remaining portion exists in very small isolated tracts

(Alverson, Willamette Valley Stewardship Ecologist, personal communication, 2001; Noss et al., 1995). For comparison, only about 0.2% remains of the Great Plains tallgrass prairie, with about 90 million acres lost to agriculture and development, which were well underway as early as the 1920s (Carey, 2000). Agricultural plants are now the dominant vegetation in the deep alluvial soils of the Willamette Valley. Their success and abundance contribute to an economic base that supports a relatively high and growing population of people in the Valley (Habeck, 1961). However, the management techniques of these species also contribute to watershed and river degradation. Agricultural runoff carrying both agri-chemicals and soil is an enormous problem in the Willamette Valley (Wentz et al., 1998). Receiving a great deal of attention is the harm this does to endangered salmon populations (Anderson et al., 1997), and more recently to amphibians (Hayes, 2002). In comparison to most large-scale agricultural systems, natural systems provide their own fertility, build and maintain soil, and when intact, are diverse enough to withstand native (and some non-native) pests (Piper and Soule, 1992).

The Willamette Valley upland prairie is a unique ecosystem, though it can also be compared to the largest expanse of prairie in North America, the Great Plains.<sup>1</sup> Large portions of the Willamette Valley prairie were burned one to two times per year by the first humans to live in this area, including 13 tribes collectively called the Kalapuya. European diseases and changes in land use decimated the Kalapuya and ended burning in the Valley in the early to mid-19<sup>th</sup> century (Johanesson et al., 1971; Boyd, 1986). Like the Great Plains, much of the Willamette Valley is now in agriculture. In the Valley this includes grass seed, wheat, corn, mint, trees, vineyards and orchards. With this change in

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<sup>1</sup> Habeck 1961 compares the ecological history of the Willamette Valley with that of southern Wisconsin.

the plant community has come the disappearance of several mammals from the Valley floor, such as the black-tailed jackrabbit (*Lepus californicus*) and North American black bear (*Ursus americanus*), the mountain beaver (*Aplodontia rufa*), chickaree (*Tamiasciurus douglasi*), and the Oregon vole (*Microtus oregoni*) (Maser, 1998).

Entomologists believe the ending of fire disturbance and introduction of agriculture is also linked to the loss of approximately 300 of the 400 native bee species believed to have pollinated flowering plants on the Westside of the Cascade Mountains in Oregon and Washington (Moldenke, 1976; Moldenke, 1979). Other insects, such as the Fender's blue butterfly (*Icaricia icarioides fenderi*) have also suffered losses with the loss of Willamette Valley grassland, habitat to this butterfly's host plant, Kincaid's lupine (*Lupinus sulphureus ssp kincaidii*) (Schultz and Dlugosch, 1999; Wilson et al., 2003).

Those who study the Willamette Valley prairie will contend that, beyond a few similarities, it is a dramatically different ecosystem than the Great Plains. The Valley soils were deposited between 15,000 and 13,000 years ago when a series of cataclysmic floods originating in the Clark Fork region of northern Idaho gushed down the Columbia Gorge and backed up in the Willamette Valley (Orr et al., 1992). Preceding the floods, volcanic activity and moving subterranean plates created the Coast and Cascade ranges to the west and east of the Valley, respectively, and are significant drivers of the Valley climate as we know it today. Moderate temperatures and almost exclusively winter rainfall are two of the most obvious characteristics that set the Willamette Valley apart from the Great Plains.

Of the original grassland vegetation of the Willamette Valley, most of it was upland prairie (70%) while the remainder was low, wet prairie (Habeck, 1961; Alverson,

Willamette Valley Stewardship Ecologist, personal communication, 2001). The height of the upland prairie plant community is generally around 0.2 m, with some grass flowering stalks reaching 150 cm (Wilson et al., 1998). It is a spatially heterogeneous mixture dominated by bunchgrasses with intervals either remaining bare or exploited by forbs that spread vegetatively (Wilson et al., 1998). The common grasses include Roemer's fescue (*Festuca roemeri*), California oatgrass (*Danthonia californica*), blue wild rye (*Elymus glaucus*), Lemmon's needlegrass (*Stipa lemmonii*), and junegrass (*Koeleria macrantha*) (Wilson et al., 1998). The wetland prairie is dominated by short, fine tufted hairgrass (*Deschampsia cespitosa*) and is generally shorter in stature (Wilson et al., 1998).

### ***Domestic and native species***

An agricultural system can mimic a natural system in several ways. Morphological mimicry involves the use of plants with shapes similar to that of native plants (Ewel, 1999). One can mimic spatial arrangements of the native plant community. In addition, genetically similar plants can be used, meaning either plants that are selected or bred by humans to contain genes similar to native plants, or simply using native plants grown in an agricultural context.

Terrestrial ecosystems vary widely in their relationship between biodiversity and productivity, with some deserts (particularly semi-desert at the scale of hectare) scoring high in biodiversity and low in biomass, arctic tundra falling on the low side of both, and tropical forests scoring high in both (Waide et al., 1999). Productivity and diversity of prairies is less well-understood. It has been generalized among ecologists as having productivity in the low to mid-range worldwide and high diversity, up in the range of

tropical rainforests, on the spatial scale of square meters. However, recent generalized data are lacking. Most of our grain agriculture is on land that was once prairie (Johannesson et al., 1971). Even though much of this agriculture is composed of grasses, it usually does not mimic the diversity found in prairie ecosystems. Modern agriculture also uses inputs to make these grasses grow in former prairie ecosystems, while grasslands cycle material produced from sunlight, water and soil nutrients. It is unclear whether particular spatial arrangements and levels of diversity will have similar effects in native plant communities as it does in agricultural plant communities. **However, I hypothesize that if niche complementarity plays a major role in overyielding, then spatial arrangement and species morphology will have more effect on productivity than whether a plant is a domestic or a native.**

Title:

**The Effect of Diversity and Spatial Arrangement on Biomass of Agricultural  
Cultivars and Native Plant Species**

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**Abstract**

Various spatial arrangements can be found within natural grassland plant populations and communities. In contrast, spatial arrangement diversity is typically not observed in agroecosystems. Little is known about the influence of spatial arrangement on the productivity and success of agricultural or native plants. Agricultural and native plants were planted in two-way mixtures that included combinations of cultivars, species, genera, or functional groups. Each combination was arranged as a random mixture within rows, alternating rows of the different genotypes or species, and as alternating pairs of rows. Aboveground biomass was determined for each mixture component and compared to monoculture controls. Though plot composition had the most consistent influence on aboveground biomass, spatial arrangement appeared to have some influence among agricultural cultivars. Whether native or agricultural, biomass generally increased with an increase in diversity.

**Keywords:** competition, complementarity, functional group, native species, spatial arrangement

**Introduction**

It has been suggested that natural ecosystems can be models for the development of sustainable agroecosystems (Soule and Piper, 1992). An agricultural system can be created to mimic a natural system in several ways. Morphological mimicry is the use of plants with shapes similar to that of native plants (Ewel, 1999). Spatial arrangement mimicry, then, is the use of spatial arrangements similar to those in the native plant community. Mimicry can be at the level of genes as well, meaning either that plants are

selected or bred by humans to contain genes similar to those in native plants, or that native plants are grown in an agricultural context.

Most of our grain agriculture is on land that was once prairie (Johannesson et al., 1971). The functional groups of a prairie usually include graminoids ( $C_3$  and  $C_4$  grasses), nitrogen-fixing legumes, and forbs (Hector et al., 1999). While the presence of certain functional groups, particularly  $C_4$  grasses and legumes, has been found to be significant to productivity (Hector et al., 1999; Loreau et al., 2001; Tilman et al., 1997; Tilman et al., 2001), simply an increase in species number also seems to have a significant influence on productivity (Tilman et al., 2001), with productivity defined as the rate of conversion of resources to biomass per unit area per unit time (Waide *et al.*, 1999). In a study of grasslands, the subject of this study, Tilman et al. (2001) found a positive link between biodiversity and productivity.

In agriculture, crops are typically maintained in rows of monoculture and amendments are added to equalize and embellish plant growing conditions. On the other hand, natural plant communities tend to reflect the abiotic and biotic spatial heterogeneity found both in areas less than  $1\text{m}^2$  and on larger scales (Miller et al., 1995). Evidence from natural systems shows that species are often aggregated and segregated in plant communities (Rees et al., 1996) for reasons including growth form, as in cespitose grasses, uneven suitable soil conditions, uneven disturbance, escape from competition, and beneficial conditions facilitated by neighbors (Rice, 1984; Liebman, 1988; Thórhallsdóttir, 1990; Symstad et al., 2000). This means that some species may not compete with others in the same community (Silvertown et al., 1992). However, many

plant competition models assume that species are well mixed (Schwinning and Parsons, 1996; Thornley et al., 1995).

It is unclear whether spatial arrangements and diversity can have similar effects in agricultural plant communities as they do in native plant communities. Thus, the purpose of this study was to determine the effect of plant spatial pattern on the productivity of native and agricultural species when grown in simple, two-way mixtures.

## **Materials and Methods**

### ***Field sites and experimental design***

In the growing season of 2001-2002, a series of agricultural species and cultivars and a series of species native to the Willamette Valley were planted in three different spatial arrangements and ten pair-wise combinations per series at two sites (Table 1). The two series were in a randomized split plot design with four replications (Fig. 1). The agricultural and native species were sown in separate experiments at each site. At each site, the four replicates of three spatial arrangements were planted—alternating rows, alternating pairs of rows, and randomly mixed within rows in a replacement design. Monoculture plots were planted as the controls. Each main plot (spatial arrangement) contained all monoculture and mixture treatments. The series of agricultural plants included three wheat (*Triticum aestivum*) cultivars, Gene, Foote, and Coda, and two species of clover, red clover (*Trifolium pratense*) and crimson clover (*Trifolium incarnatum*). The wheat cultivars had different panicle morphology, thus allowing them to be distinguished in mixture. The series of native Willamette Valley prairie plants included two grasses from the upland prairie, blue wildrye (*Elymus glaucus*) and

California or mountain brome (*Bromus carinatus*), and a third that grows in drier sites of the wetland prairie, tufted hairgrass (*Deschampsia cespitosa*) and two legumes, common vetch (*Vicia sativa*), found in upland prairie, and streamside lupine (*Lupinus rivularis*), found both in upland and wetland prairie. Seeds were collected and increased locally and donated by Pacific Northwest Natives in Albany, Oregon. *E. glaucus* was collected from a wild population along the Willamette River in North Albany, and is called Mid-Willamette Riverbottom blue wildrye. The seed was planted, and the second generation harvested, from a commercial seed field in 2000. The Eugene Bureau of Land Management (BLM) collected and increased seed of *B. carinatus* near Coburg, Oregon. The *D. cespitosa* population was collected by the Eugene BLM from West Eugene wetlands and the second generation seed was commercially produced near Brownsville, Oregon. Eugene BLM collected *L. rivularis* from West Eugene Wetlands and the second generation seed was grown in a commercial field near Coburg, Oregon. The seed identified as *V. americana* was collected and grown as that species, but has since been identified as common vetch, *V. sativa*, which is not native to the Willamette Valley. Original seed was collected in Western Oregon and was commercially produced in Albany, Oregon. *V. sativa* is native to Eurasia, though it may have been naturalized in the Pacific Northwest for at least 100 years as it is described as "introduced in waste places and cultivated" in Piper and Beattie (1915), and is also recorded from several localities in Washington state in Piper (1906).

Table 1.1

Treatments used to study the effect of plant spatial pattern on biomass of cultivar and species mixtures

Agricultural: Functional group	Cultivar or species					Cultivar or species	Native: Functional group
		Rows	Alternating single rows	Alternating pairs of rows	Random mixed in all rows		
Wheat	Gene	x				<i>Bromus carinatus</i>	Grass
	Foote	x				<i>Deschampsia cespitosa</i>	
	Coda	x				<i>Elymus glaucus</i>	
Legume	Red clover	x				<i>Vicia sativa</i>	Legume
	Crimson clover	x				<i>Lupinus rivularis</i>	
Wheat + Wheat	Gene + Foote		x	x	x	<i>B.carinatus</i> + <i>D. cespitosa</i>	Grass + Grass
	Gene + Coda		x	x	x	<i>B.carinatus</i> + <i>E.glaucus</i>	
	Foote + Coda		x	x	x	<i>D. cespitosa</i> + <i>E.glaucus</i>	
Legume + Legume	Red clover + Crimson clover		x	x	x	<i>V.sativa</i> + <i>L.rivularis</i>	Legume + Legume
Wheat + Legume	Gene + Red clover		x	x	x	<i>B.carinatus</i> + <i>V.sativa</i>	Grass + Legume
	Gene + Crimson clover		x	x	x	<i>B.carinatus</i> + <i>L.rivularis</i>	
	Foote + Red clover		x	x	x	<i>D. cespitosa</i> + <i>V.sativa</i>	
	Foote + Crimson clover		x	x	x	<i>D. cespitosa</i> + <i>L.rivularis</i>	
	Coda + Red clover		x	x	x	<i>E.glaucus</i> + <i>V.sativa</i>	
	Coda + Crimson clover		x	x	x	<i>E.glaucus</i> + <i>L.rivularis</i>	

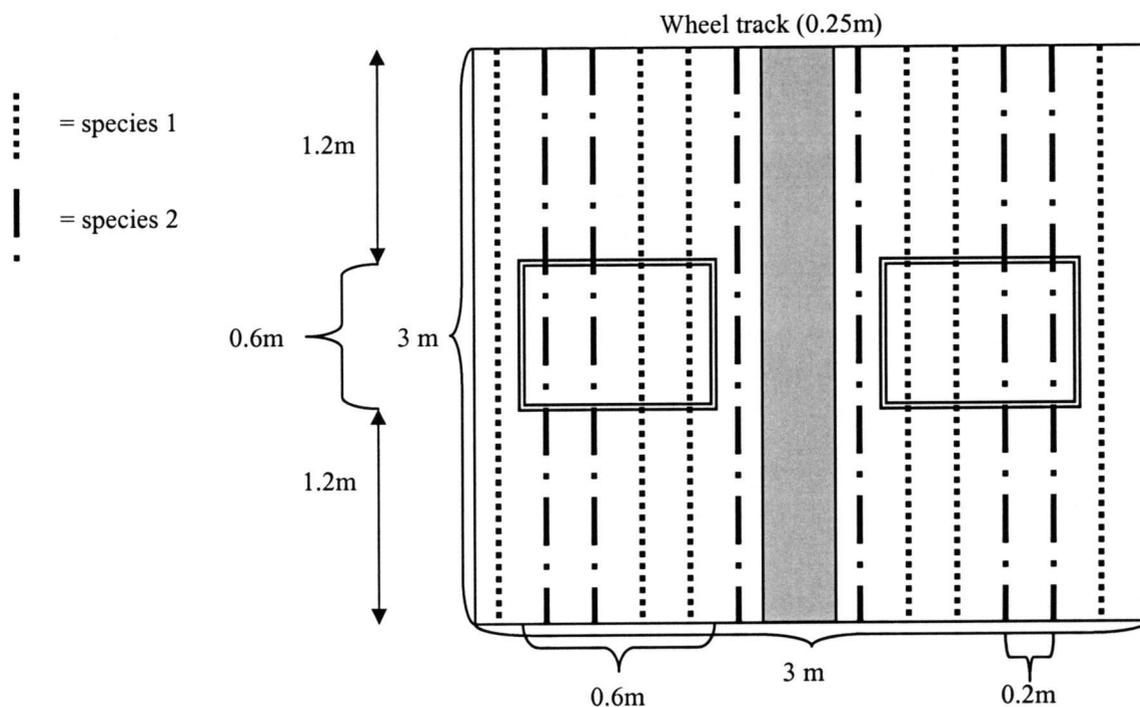


Fig. 1.1. Diagram of an individual subplot of paired rows planting and harvest scheme showing area harvested within box enclosed by double line.

*V. sativa*, is a common associate of *B. carinatus* and *E. glaucus*, (M.V. Wilson, Oregon State Univ., personal communication, 2003) and has naturalized primarily in upland prairie. The native or presettlement habitat of *L. rivularis* was primarily on open riverbanks and sand/gravel bars along major rivers that were occasionally flooded and thus kept open from woody succession, or were relatively newly formed from deposition of sediments. Of the three grasses, *E. glaucus* is the one that would be most likely to occur in this habitat (E. Alverson, Willamette Valley Stewardship Ecologist, personal communication, 2003).

The wheat cultivars were bred at either Oregon State University (Gene and Foote) or Washington State University (Coda). Though all three cultivars are grown extensively in both states, Coda is better adapted to and more commonly grown in the drier areas east of

the Cascade Mountains. Kenland red clover and crimson clover are grown widely in the Willamette Valley.

Each subplot was 3.0 x 3.0 m. The spatial arrangements included mixtures of cultivars or species planted mixed within rows, single species/cultivar in alternating single rows, and alternating pairs of rows, all with 0.2 m between each row (Fig. 1). These spatial arrangements were established for all possible two-way combinations among the native species and among the agricultural cultivars/species. A complete set of monoculture controls planted in 0.2 m rows was included in each main plot. The planting of both agricultural and native species was with two side-by-side passes of a 6-row drill, making 12 rows within each 3.0 m<sup>2</sup> plot (Fig. 1).

All species and cultivars were planted at two sites in the Willamette River floodplain. One site was sandy loam soil at the Oregon State University Botany and Plant Pathology Field Lab, located 1 km east of Corvallis, Oregon and the other site was silt loam soil at the Hyslop Field Lab, located 8 km north of Corvallis. Planting dates were 7 September 2002 at the Botany Farm and 10 September 2002 at Hyslop. Seeds were planted in a fine, firm seedbed with the drill at a depth of 0.5-1 cm. Irrigation the following day was to a depth of 2-5 cm, followed with about 1 cm of water every other day until the start of winter rains. No fertilizer was added, as extra fertilizer has been shown to alter competitive interactions (Wilson and Tilman, 1991; Cahill, 2002) and can make conditions more favorable for weeds rather than native species (Davis and Wilson, 2000; Blumenthal, 2003). In addition, research in cereals and legumes shows that higher levels of applied nitrogen confers an advantage on cereals, which then gains a competitive advantage over the legume (Davis et al., 1986).

Weeds were removed from within native plant subplots by hand or hoe, and between subplots with glyphosate herbicide. Only some hoeing and removal of very large weeds were performed as necessary in the agricultural subplots. Due to the magnitude of the weeds in the native plots, replicates were reduced to two at each site.

Rodent damage and lodging were noted throughout the growing season by an estimation of percent damage. No diseases were observed on the native species. Barley yellow dwarf virus symptoms were observed on the wheat cultivars and a rust was found on the clover. These were monitored, but not measured. Barley yellow dwarf virus is usually quantified through Elisa analysis of leaf samples, and is very difficult to measure visually in the field. The virus was prevalent at both sites, but was not specific to particular treatments. The rust was found primarily at Botany Farm and more common along one edge of the field; it was not specific to treatment.

On 3-9 June 2002, 0.6m of eight interior rows of each 12-row subplot were harvested. These were chosen within drill passes to avoid influence from neighboring plots and space created by tire tracks (Fig. 1). Aboveground biomass was separated by species or cultivar, dried in ovens at approximately 37 °C for 2-3 days, removed from ovens, allowed to equilibrate overnight, and weighed.

On 18 May and 22 May percent cover affected by rodents and percent cover affected by lodging were estimated for Botany Farm and Hyslop, respectively. Lodging may have been a result of the rodent damage and/or heavy winds. Shortly after measurement, rodenticide was successfully used in fields to prevent further damage to plants.

### *Statistical analyses*

To determine whether the two sites should be combined or analyzed separately, analysis of variance (ANOVA) using Splus (Mathsoft, Inc. 2000) was performed on total biomass per plot using a split plot design with site as a main effect. For both the native and agricultural experiments, site was significant ( $P < 0.01$ ). Thus, a separate split plot design ANOVA was conducted for each of the four experiments.

One replicate of the *D. cespitosa*, random arrangement, at Hyslop was omitted because it appeared to have been measured incorrectly. The missing value for Foote wheat + crimson clover in single rows at the Botany Farm is due to errors in planting of all replicates of this treatment. All spatial arrangements of this mixture were removed for the ANOVA.

Linear contrasts were used to make comparisons of mixtures with the mean of the corresponding monocultures (Table 3). A contrast was used to determine significance of each mixture compared to its corresponding monocultures weighted by frequency in mixture, assigning  $-1/2$  to each monoculture and  $+1$  to the mixture. Linear contrasts were also used to compare functional groups including a comparison of all grass mixtures versus all grass monocultures, with  $-1$  assigned to all three monocultures and  $+1$  assigned to all mixtures. A linear contrast between the legume mixtures versus the two legume monocultures was covered by the comparisons between the mixtures and monocultures described above. A contrast between all grass + legume mixtures versus all monocultures was performed by weighting the monocultures depending on their occurrence in mixtures. For example, agricultural cultivars at Hyslop had  $-1$  assigned to all wheat

cultivars, -1.5 assigned to clover species and +1 assigned to mixtures. Finally paired versus random and single versus random spatial arrangements were compared.

Because the experiment used a split plot design, contrasts of spatial arrangements used standard errors calculated using the Replicate \* Spatial Arrangement mean square, while contrasts of plot composition used standard errors calculated using the residual mean square (Table 4 and 5).

Though statistical analyses were always performed on biomass per plot, mixture biomass is shown as Relative Yield (RY) for ease of comparison with monoculture controls. Relative yield was calculated as  $RY_{AB} = Y_{AB}/0.5*(Y_A+Y_B)$ , where  $RY_{AB}$  is the relative yield of a 1:1 mixture of species A and B,  $Y_A$  is the yield of species A in monoculture, and  $Y_B$  is the yield of species B in monoculture. Thus, a mixture is said to be overyielding if the RY is greater than 1.0.

Components of each plot were compared to ½ of their corresponding monoculture using two-tailed t-tests.

## Results

For the natives, the main effect of spatial arrangement was significant neither at Botany Farm ( $P=0.40$ ), nor at Hyslop ( $P=0.430$ ) (Table 5). In the agricultural experiment, however, spatial arrangement was significant at both the Botany Farm ( $P=0.027$ ), and at Hyslop ( $P=0.018$ ). In mixtures, linear contrasts of random mixtures versus alternating single rows and versus alternating pairs of rows were significant for neither the agricultural nor the native experiment (Fig. 2, Tables 6 and 7). Among agricultural cultivars, there was a significant interaction of plot composition and spatial

arrangement at Botany Farm ( $P=0.037$ ), but not at Hyslop ( $P=0.800$ ). Among natives there was no significant interaction of plot composition and spatial arrangement (Table 4).

The composition in each plot had the most significant and consistent effect on biomass in both experiments at both sites ( $P<0.0001$ ).

The consistent outcome for pairwise mixtures was for one component to increase in biomass relative to its monoculture and for the other to decrease (Fig. 3). Overyielding at the community level was found more frequently among native species than among the agricultural species and cultivars (Fig. 4). For both the agricultural and native experiments, the biomass of all the grass + legume or wheat + clover mixtures had a higher total biomass than that of the corresponding weighted monocultures ( $P<0.05$ ). The *V. sativa* + *L. rivularis* mixture increased in biomass compared to monoculture at both sites, while the clover mixture decreased. These differences were not always significant, however (Tables 6 and 7). For the natives at both sites, the average of all the grass mixtures had a significantly greater total biomass than the corresponding weighted grass monocultures ( $P=0.05$  Botany Farm,  $P<0.001$  Hyslop), while the agricultural cultivars were not significant. Overall mixtures increased plot aboveground biomass, significantly among natives ( $P<0.01$ ) as well as among agricultural cultivars, though not significantly (Tables 6 and 7).

There were few individual mixture comparisons that were significant at both sites in either experiment, though many were marginally significant. Such mixtures always include wheat + clover (Table 6), or among natives, mixtures containing *V. sativa* (Table 7).

Table 1.2

Above ground biomass (g/plot) for monocultures of five wheat cultivars and two clover species at Botany Farm and Hyslop Field Lab

Botany Farm					
Spatial arrangement mainplot	Gene wheat	Footo wheat	Coda wheat	Crimson clover	Red clover
Random	2127	1345	2148	1402	1142
Single	1981	1238	1828	1329	1218
Paired	1820	1148	2004	1265	1246
Hyslop Field Lab					
Spatial arrangement mainplot	Gene wheat	Footo wheat	Coda wheat	Crimson clover	Red clover
Random	2376	1609	2064	1516	1028
Single	2118	1690	1800	1437	903
Paired	2178	1725	1711	1301	1061

Table 1.3

Above ground biomass (g/plot) for monocultures of five native species at Botany Farm and Hyslop Field Lab

Botany Farm					
Spatial arrangement mainplot	<i>B. carinatus</i>	<i>D. cespitosa</i>	<i>E. glaucus</i>	<i>V. sativa</i>	<i>L. rivularis</i>
Random	1454	312	847	2263	1426
Single	1379	218	1028	2289	1266
Paired	1293	201	702	2011	1272
Hyslop Field Lab					
Spatial arrangement mainplot	<i>B. carinatus</i>	<i>D. cespitosa</i>	<i>E. glaucus</i>	<i>V. sativa</i>	<i>L. rivularis</i>
Random	1433	22	348	1799	623
Single	1099	28	444	1883	566
Paired	1394	33	515	2072	744

Table 1.4

Analysis of variance for biomass of three wheat cultivars and two clover species when grown in all possible two-way mixtures and in three spatial patterns (randomly mixed within rows, single rows, paired rows) at Botany Farm and Hyslop Field Lab

Effect	Botany Farm			Hyslop Field Lab		
	df	Mean Square	P-value	df	Mean Square	P-value
Replicate	3	144672	0.0941	3	111257	0.3001
Spatial Arrangement <sup>a</sup>	2	247424	0.0272	2	372678	0.0184
Rep*Sp.arr.	6	97261	0.1954	6	143762	0.1543
Plot Composition	13	1815895	0.0000	14	1268114	0.0000
Plot Composition*Sp.arr.	26	111744	0.0366	28	68578	0.7955
Residuals	85	65805		117	90069	

<sup>a</sup>Tested with Rep\*Sp.arr. error

Table 1.5

Analysis of variance for biomass of five native Willamette Valley species, three grass species and two legume species, when grown in all possible two-way mixtures and in three spatial patterns (randomly mixed within rows, single rows, paired rows) at the Botany Farm and the Hyslop Field Lab

Effect	Botany Farm			Hyslop Field Lab		
	df	Mean Square	P-value	df	Mean Square	P-value
Replicate	1	62348	0.3743	1	641144	0.0005
Spatial Arrangement <sup>a</sup>	2	72501	0.3996	2	38794	0.4305
Rep*Sp.arr.	2	173139	0.1201	2	5421	0.8870
Plot Composition	14	1756188	0.0000	14	2833323	0.0000
Plot Composition*Sp.arr.	28	62334	0.7176	28	69705	0.1013
Residuals	37	77102		40	45065	

<sup>a</sup>Tested with Rep\*Sp.arr. error

Table 1.6

Linear contrasts performed on biomass in an agricultural experiment of three wheat cultivars and two clover species when grown in all possible two-way mixtures and in three spatial patterns (randomly mixed within rows=R, single rows=S, paired rows=P) at Botany Farm and Hyslop Field Lab (C=Coda wheat, F=Footo wheat, G=Gene wheat, Cr=crimson clover, Rc=red clover, mono=monoculture, mix=mixture)

Contrast Type	Contrast	Botany Farm		Hyslop Field Lab	
		Difference <sup>a</sup>	P-value	Difference <sup>a</sup>	P-value
Mixture	10 mix vs. 5 mono	936	0.1523	1045	0.1985
Mixture	CCr vs. mono	462	0.0042	220	0.2331
Mixture	CRc vs. mono	466	0.0039	254	0.1698
Mixture	FCr vs. mono <sup>b</sup>	N/A	N/A	126	0.4938
Mixture	FRc vs. mono	146	0.3553	306	0.0984
Mixture	GCr vs. mono	227	0.1518	85	0.6459
Mixture	GRc vs. mono	296	0.0628	382	0.0399
Mixture	FC vs. mono	-215	0.1742	-138	0.4539
Mixture	GF vs. mono	-130	0.4113	-96	0.6039
Mixture	GC vs. mono	-17	0.9121	18	0.9219
Mixture	CrRc vs. mono	-299	0.0604	-113	0.5416
Functional Group	All wheat mix vs. All wheat mono	-362	0.2521	-216	0.5586
Functional Group	All clover mix vs. All clover mono (same as mixture comparison)	-299	0.0604	-113	0.5416
Functional Group	All wheat + clover vs. all mono	1597	0.0002	1373	0.0142
Spatial Arrangement	R vs. S	106	0.7295	52	0.8791
Spatial Arrangement	R vs. P	149	0.6272	165	0.6329

<sup>a</sup>See text for description of weighting in contrasts

<sup>b</sup>Not included in series of contrasts at Botany Farm because all replicates of one spatial arrangement missing

Table 1.7

Linear contrasts performed on biomass in a native Willamette Valley experiment of three grass species and two legume species, when grown in all possible two-way mixtures and in three spatial patterns (randomly mixed within rows, single rows, paired rows) at Botany Farm and Hyslop Field Lab (B=*B.carinatus*, D=*D.cespitosa*, E=*E.glaucus*, V=*V.sativa*, L=*L.rivularis*, mono=monoculture, mix=mixture)

Contrast Type	Contrast	Botany Farm		Hyslop Field Lab	
		Difference <sup>a</sup>	P-value	Difference <sup>a</sup>	P-value
Mixture	10 mixtures vs. 5 monocultures	3557	0.0021	3439	0.0005
Mixture	BL vs. mono	23	0.9230	266	0.2022
Mixture	BV vs. mono	612	0.0152	283	0.1770
Mixture	DL vs. mono	-221	0.3636	168	0.3730
Mixture	DV vs. mono	1141	0.0000	830	0.0004
Mixture	EL vs. mono	-206	0.3983	119	0.5670
Mixture	EV vs. mono	892	0.0007	852	0.0002
Mixture	DE vs. mono	250	0.3060	-23	0.9108
Mixture	BD vs. mono	533	0.0328	175	0.3984
Mixture	BE vs. mono	187	0.4407	34	0.8708
Mixture	VL vs. mono	344	0.1607	734	0.0009
Functional Group	All grass mix vs. All grass mono	970	0.0509	186	0.0001
Functional Group	All legume mix vs. All legume mono	344	0.1607	734	0.0009
Functional Group	all grass + legume vs. all mono	2241	0.0036	2520	0.0002
Spatial Arrangement	R vs. S	-26	0.8956	-114	0.7126
Spatial Arrangement	R vs. P	207	0.3642	92	0.7637

<sup>a</sup>See text for description of weighting in contrasts

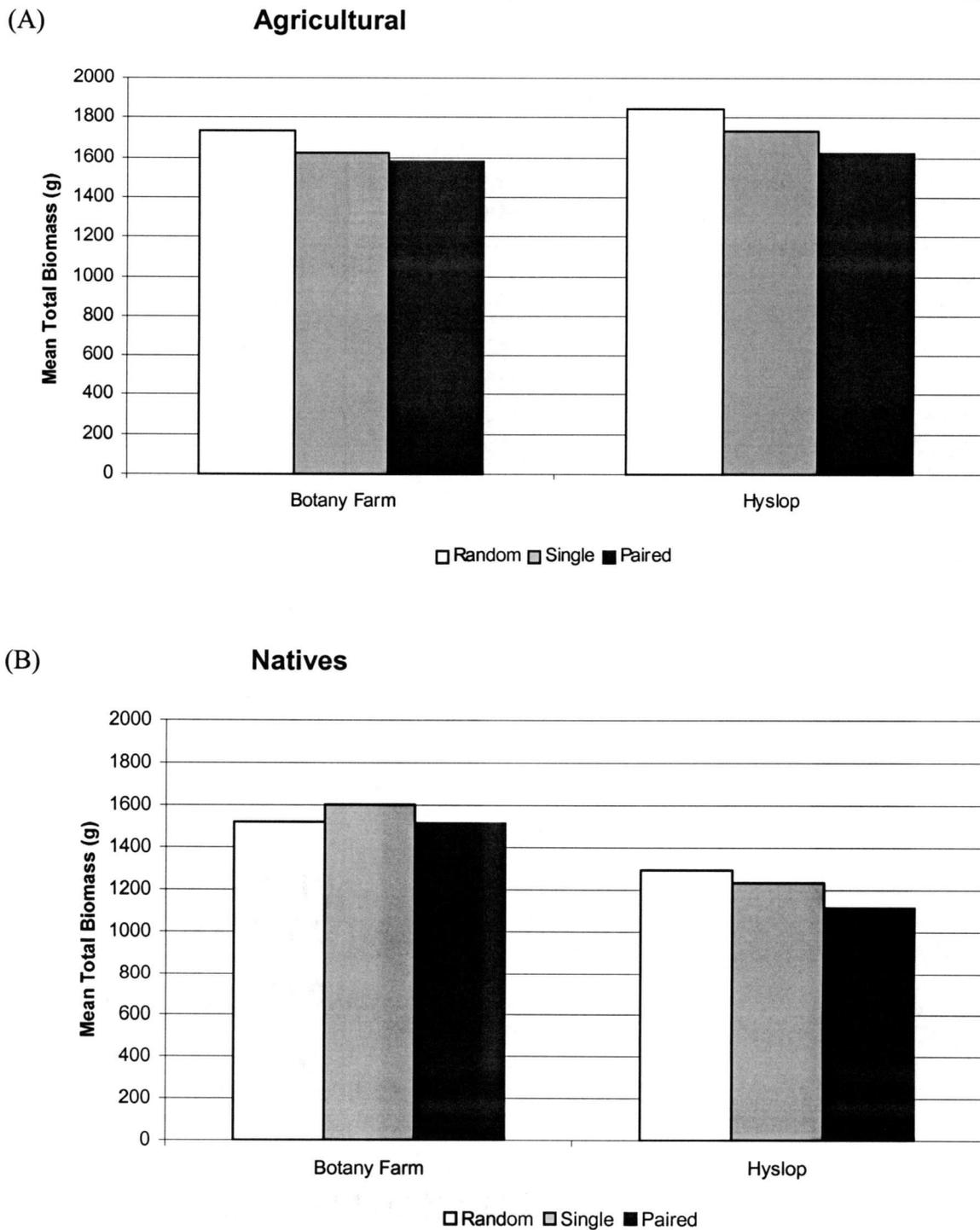


Fig. 1.2. Total above ground biomass of (A) three wheat cultivars and two clover species planted in 1:1 mixtures in three spatial arrangements at two sites, and (B) five native species planted in 1:1 mixtures in three spatial arrangements averaged over species or cultivar per plot. See Tables 6 and 7 for statistical analyses.

## (A) Agricultural

## Botany Farm

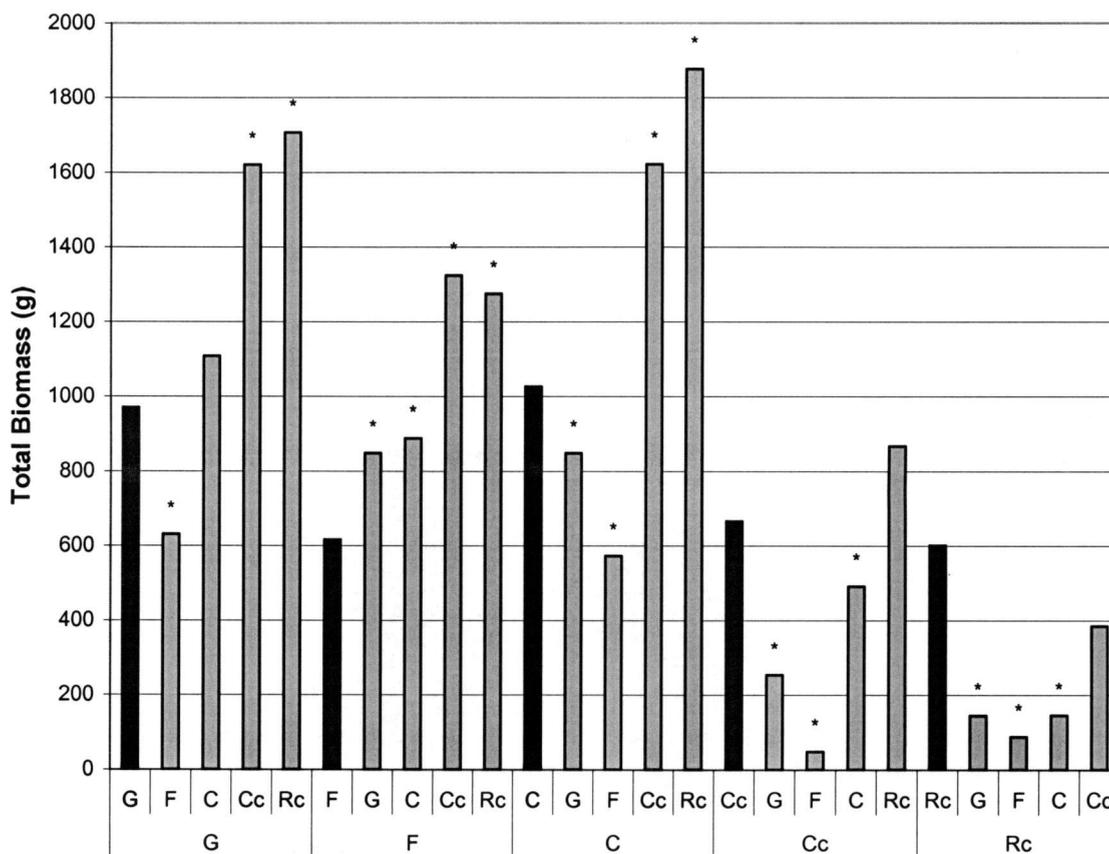


Fig. 1.3. Total aboveground biomass at two sites, Botany Farm and Hyslop Field Lab, of (A) five agricultural cultivars or species (G=Gene wheat, F=Footo wheat, C=Coda wheat, Cc=crimson clover, Rc=red clover) and (B) five native species (B=*B. carinatus*, D=*D. cespitosa*, E=*E. glaucus*, V=*V. sativa*, L=*L. rivularis*) planted in all possible 1:1 mixtures and averaged over spatial arrangement. Monocultures of each cultivar or species are shown in black and species or cultivars in mixtures are shown in gray. Monocultures are  $\frac{1}{2}$  total plot yield.

\* Component in mixture significantly greater than half of corresponding monoculture, two-tailed t-test (P=0.05)

Hyslop Field Lab

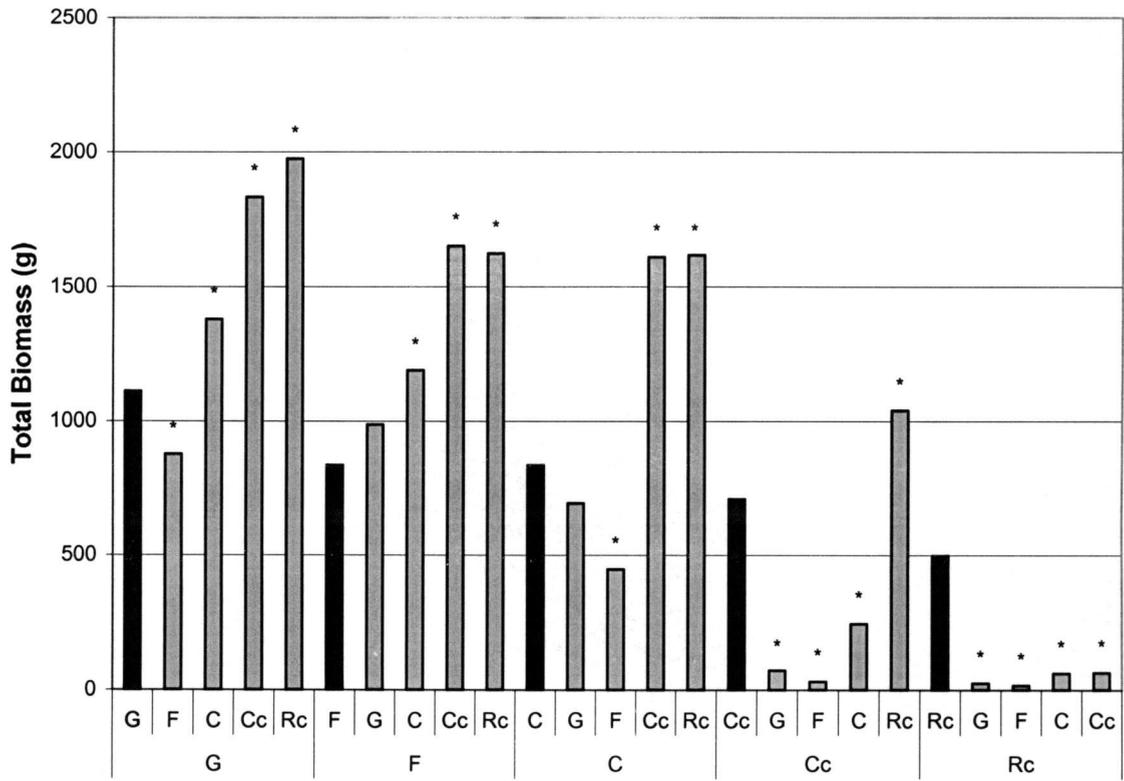


Fig. 1.3. (Continued)

(B)

Native

Botany Farm

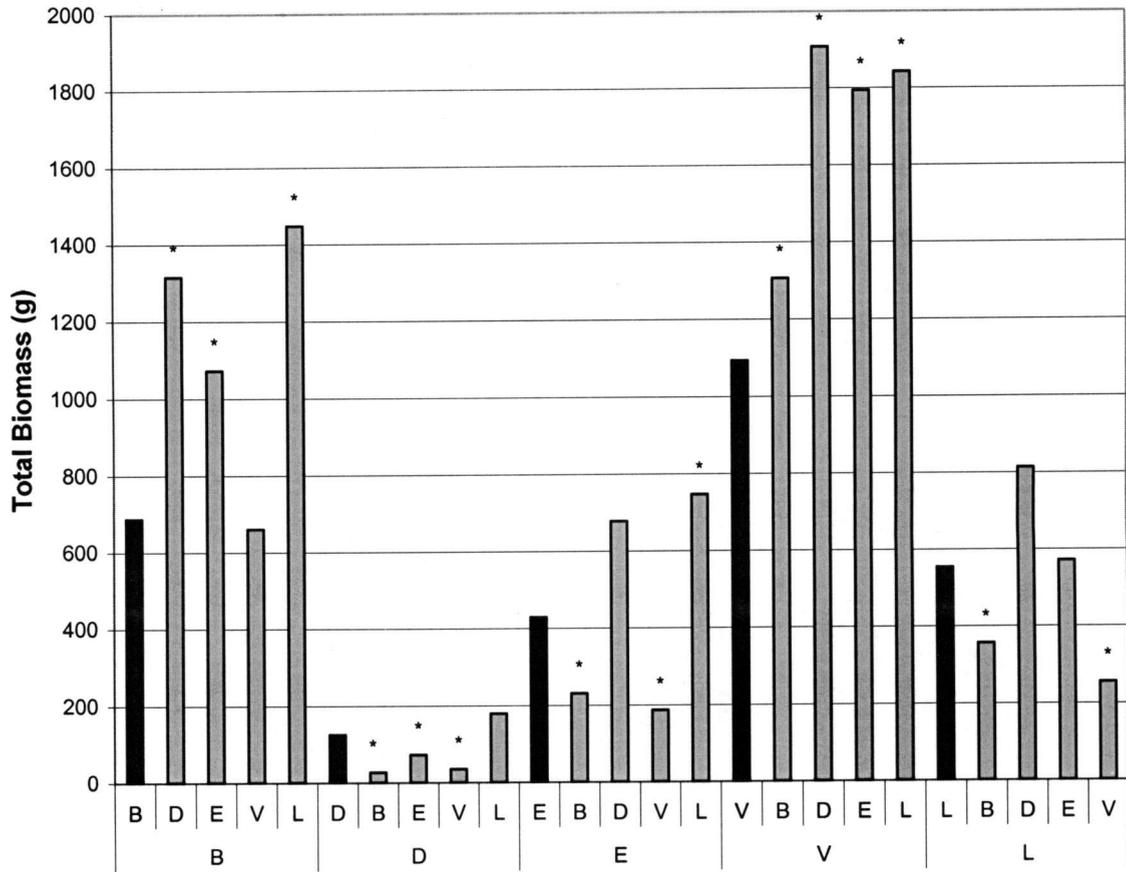


Fig. 1.3. (Continued)

Hyslop Field Lab

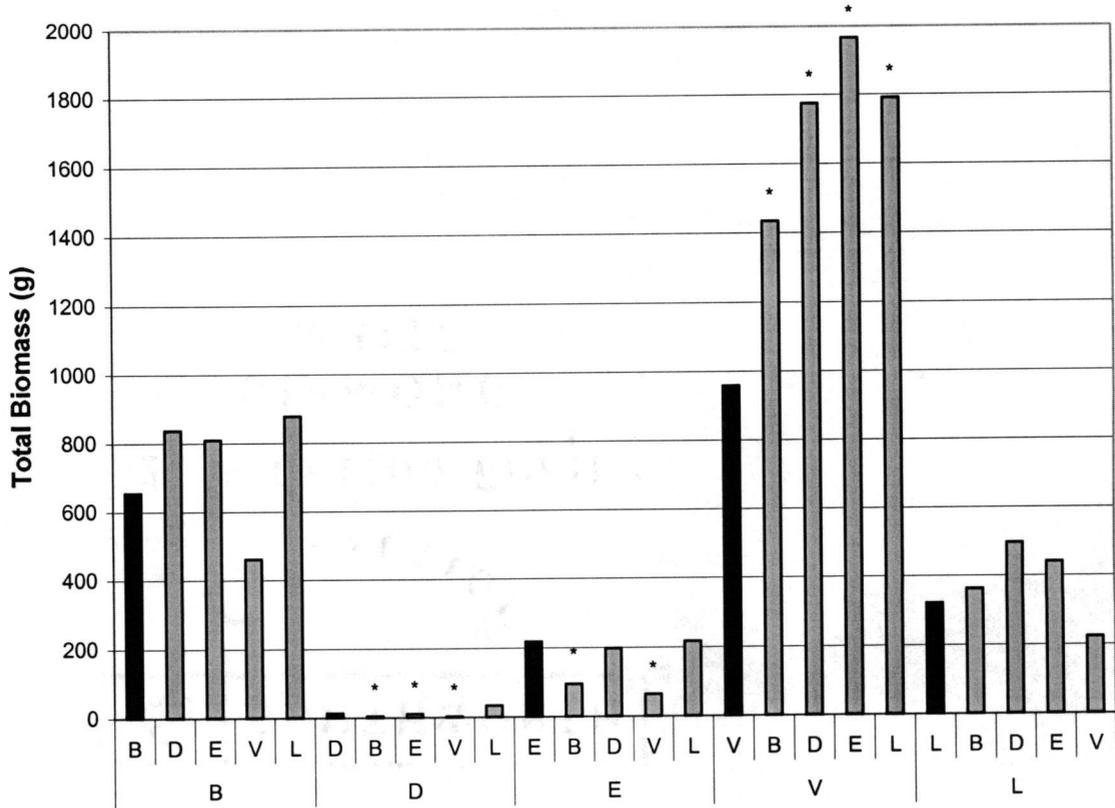


Fig. 1.3. (Continued)

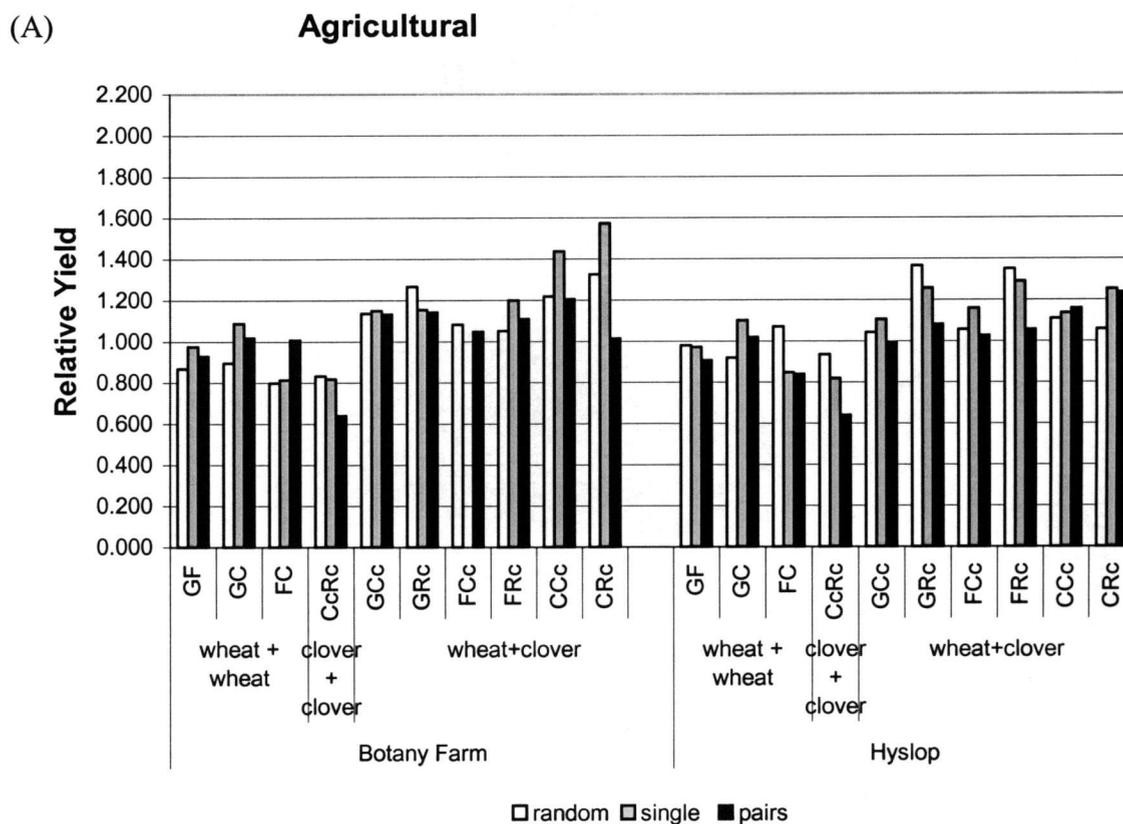


Fig. 1.4. Relative Yield of two-way mixtures in three spatial arrangements of (A) five agricultural species or cultivars (G = Gene wheat, F = Foote wheat, C = Coda wheat, Cc = crimson clover, Rc = red clover) and (B) five native species (B = *B. carinatus*, D = *D. cespitosa*, E = *E. glaucus*, V = *V. sativa*, L = *L. rivularis*) planted in every paired combination. See Tables 6 and 7 for statistical analyses.

(B)

## Native

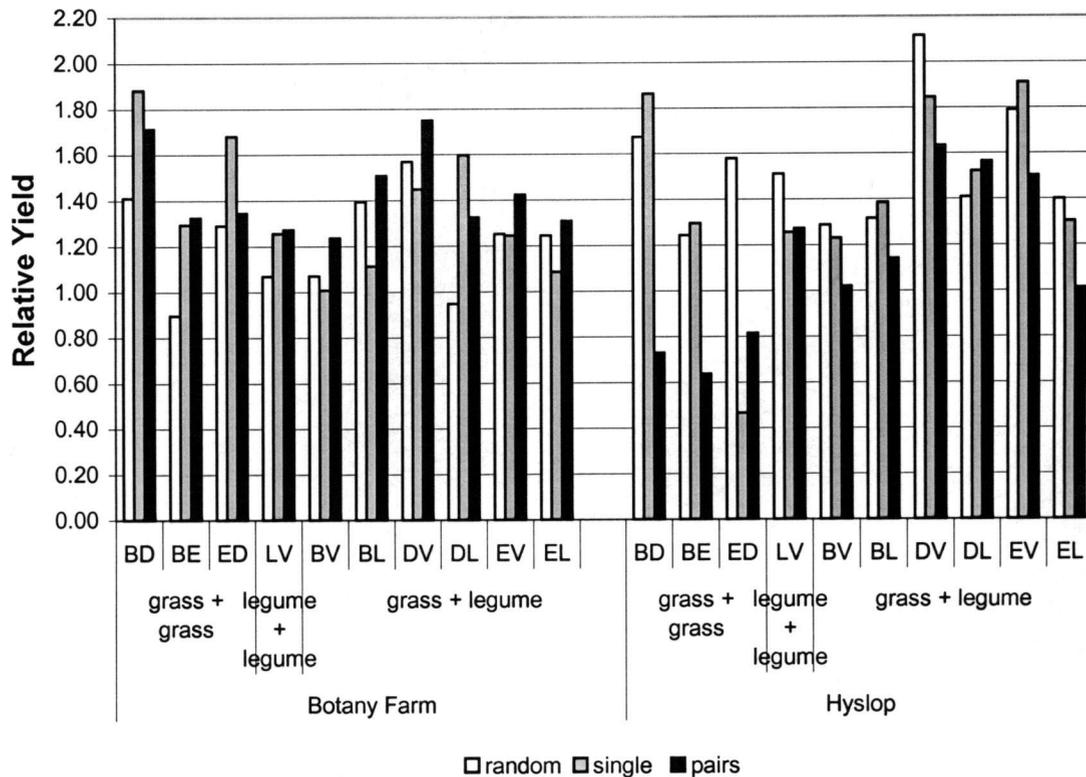


Fig. 1.4. (Continued)

## Discussion

Our results suggest that the species or cultivars grown in a plot have a greater impact on aboveground biomass production than does their spatial arrangement. One concern in this regard is lack of statistical power as there were only two replicates at each site for the native experiment. There was, however, sufficient power to identify significant plot composition effects at both sites. In most cases, there was clearly one species that was dominant in each plot. It is not surprising that the species or cultivar grown in a plot were important influences on biomass in both experiments, as these species and cultivars

varied widely in amount of vegetative growth. In addition, it is to be expected that particular planting combinations will vary in aboveground biomass based on varying competition for resources.

For the agricultural experiment, the main effect of spatial arrangement was significant at both sites, but the linear contrasts of random rows versus alternating single rows and versus alternating paired rows were significant at neither site. In addition, the significant main effect included the monocultures, which have no spatial patterns, while the linear contrasts excluded monocultures, but revealed no spatial arrangement effect. One explanation is that there was more statistical power for the main effect than for the single contrasts. An additional possibility is that the small number of replications and the randomness of soil differences combined such that main plots of different spatial arrangements were planted in areas of differing yield potential by chance. This possibility is supported by yields of monoculture controls for the three spatial pattern main plots (Table 2). In most cases, the monoculture yields were highest in the random main plots. With no significance in the linear contrasts for the mixtures, it is difficult to conclude an effect of spatial arrangement.

There are many potential explanations for the absence of substantial spatial pattern effects in this study. Natives are typically found in clumps due to differences in growth habit, soil conditions, and neighbors. However, the agricultural sites in this experiment are relatively uniform and minor variations were lost in averaging over replicate. The uniformity in soil is unlike typical native plant communities, which vary in plant composition, moisture availability, and neighbor competition. However, these experiments did have neighbor competition and possible variation in moisture availability

as a result of irrigation equipment. Further, interactions between species could have been different with the row arrangements used in our study, which do not necessarily reflect the clumping or random mixing spatial arrangements occurring in natural ecosystems. We used row arrangements for the native species because mechanical planting made it feasible to plant a large number of treatments.

Specific spatial arrangements may be required for optimum productivity, while ours were chosen based only on the available planting equipment. In native systems, productive spatial patterns may arise through natural selection. In agricultural systems, farmers often identify useful spatial patterns empirically. For example, a row mixture of rice cultivars that effectively controlled disease and increased yield was borrowed from a local farmer, potentially the result of years of trial and error (Zhu et al. 2000).

Intercropping of cereals with cereals and cereals with legumes takes a myriad of forms depending on the farmer's objectives and the local soil and climate conditions (Rao, 1986); hence, plantings vary each year and by region. Many intercropping systems have been developed over years. For example, in Colombia maize is added between every two to four rows of beans depending on conditions the year before and current prices of the two crops (Davis et al., 1986). Timing of planting of the two crops also varies (Connolly et al., 2001). In addition, to minimize competition between species, the spacing of the dominant cereal has to be sufficiently wide (Rao, 1986).

Patchiness in native communities often develops over time and, once it is established, communities that are patchy to begin with often remain or become increasingly patchy due to competitive asymmetry. Competitive asymmetry is defined as interspecific competition where individual plants of the dominating species perform better in the

mixed communities than in monoculture, and individuals of the subordinate species perform worse compared to monoculture (Shiple and Keddy, 1994). Competitive asymmetry is demonstrated by the deviation from equal performance of two species in mixture and monoculture as percentage mixing of species increases (Schippers and Kropff, 2001). Species in this experiment were on a gradient of increasing mixing with the spatial arrangements paired, in single rows, or randomly mixed within rows. If plants were allowed to grow for more than one season, we may have seen patchiness increase in the paired row treatments and perhaps this would be an arrangement under which certain combinations would thrive.

Agricultural breeding is typically done for high performance in isolation; however, natives are found in mixtures suggesting they have evolved strategies to coexist with each other and a variety of neighboring genotypes. Hence, it was expected that complementarity (overyielding) might be seen more commonly among natives. More combinations among native species than among the agricultural cultivars overyielded (approximately 68% of the native combinations in particular spatial arrangements overyielded compared to 41% of agricultural combinations) (Fig. 4). This is an inconclusive result, however, since the experiments with agricultural and native species were separate and statistical comparison is not possible. Further, a limited number of species was investigated and the native experiment incorporated different grass species, while the agricultural experiment utilized three different genotypes of the same grass species (wheat).

Our calculation of relative yield for the mixtures corresponds to the formula for weighting in linear contrasts, and is different from some Relative Yield Total (RYT)

calculations (McGilchrist and Trenbath, 1971; Williams and McCarthy, 2001) where the relative yield for each component is first calculated separately. RYT treats components with more specificity, while the method used here considers the per unit biomass of both mixture components to be of equal value, regardless of their monoculture yield.

Beneficial combinations of natives might seem to be predictable based on naturally occurring plant associations. *V. sativa* is a common associate of *B. carinatus* and *E. glaucus* (Wilson, personal communication, 2003), while *L. rivularis* was found in presettlement habitats also conducive to *E. glaucus* growth (Alverson, Willamette Valley Stewardship Ecologist, personal communication, 2003). However, these combinations did not overyield more than other combinations in our study nor was there a common spatial arrangement favored by these naturally associating plants. *B. carinatus* + *V. sativa* and *E. glaucus* + *L. rivularis* produced more total biomass in random and paired arrangements, while *E. glaucus* + *V. sativa* produced more total biomass in single rows.

There was a tendency for overyielding to occur more often for mixtures of a grass and a legume in both the agricultural and the native experiment. Grasses and legumes are the two most predominant functional groups of native prairies (Soule and Piper, 1992; Hector et al., 1999; Tilman et al., 1997; Tilman et al., 2001), and grass/legume mixtures are common in agriculture, particularly in intercropping (Connolly et al., 2001). The benefits of intercropping grass and legumes is widely known and practiced both in temperate climates (Steiner and Snelling, 1994; Bannon and Cooke, 1998) and throughout the tropical world (Rao, 1986; Kahurananga, 1991). In this experiment, the biomass of clover was much diminished when grown with wheat (Fig. 3A). This is reflected in other

such intercrops, where the benefit is usually to the more economically valuable cereal crop via the function of nitrogen fixation performed by legumes, or by the competitive superiority of the cereal. In a study with intercropped wheat (*Triticum durum*) and clover (*Trifolium quartinianum*), wheat yield increased when mixed with clover and clover yield decreased when mixed with wheat when compared to monocultures of each. Analyzing root yield versus shoot yield of the two species suggested that this asymmetric response may have been caused by changes in root morphology and that the intermingling of the roots decreased the ability of clover to fix nitrogen and perhaps increased available nitrogen to wheat (Dauro and Mohamed-Saleem, 1995). In a mixture of white clover and ryegrass, clover transferred 4.5 and 7.5 g/m<sup>2</sup> of N to ryegrass in the 1<sup>st</sup> and 2<sup>nd</sup> production year, respectively (Hogh-Jensen and Schjoerring, 2000). Research suggests that the mechanism of N transfer occurs with some plant (particularly root) death. For example, research in a tropical-legume mixture found that no significant direct belowground N transfer from legume to grass was observed during the lifetime of the legume. After the legume shoot was cut at ground level, however, the grass assimilated significant amounts of N derived from decaying legume roots (Trannin et al., 1999). Similar N transfer may have occurred in this experiment as both red and crimson clover had large amounts of dead plant matter beneath the living canopy, some of which had already decomposed. This may have resulted in the increase in wheat biomass. However, the presence of low canopy clover also meant that the wheat had less light competition in mixed plots.

## Conclusion

The biomass of all species and cultivars studied was greatly impacted by being grown in mixture. However, we identified no spatial arrangement that consistently produced more above ground biomass either for the native species or for the agricultural cultivars.

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Title:

**The Effect of Varying Density and Spatial Arrangement on  
Three Cultivars of Wheat**

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**Abstract**

The effect of plant spatial pattern on the yield of wheat cultivar mixtures was studied. Two wheat cultivars were planted in seven treatments in the 2000-2001 winter wheat season and three cultivars were planted in 18 treatments in the 2001-2002 season. One cultivar was always planted at full rate, and a second cultivar was added at  $\frac{1}{4}$  rate, either randomly mixed, or between rows of the other cultivar. Spatial pattern had no effect on the overall yield of the mixtures, and mixtures rarely affected yield relative to monocultures. The contribution of each cultivar to mixture yield varied significantly among treatments, however, and was a result of cultivar competitive ability and planting density.

**Keywords:** cultivar mixtures, relative yield, random mixtures, row mixtures, winter wheat

**Introduction**

Substantial research has been conducted on the use of cultivar mixtures for disease control, and such mixtures have been used successfully in commercial agriculture (Finckh et al., 2000; Mundt, 2002a). Though cultivar mixtures often provide yield advantages even in the absence of disease, the yield performance of mixtures has varied substantially among studies (Smithson and Lenne, 1996). Less research exists on the effect that varying spatial arrangement will have on the desired results of low pathogen infection and high yield in mixtures. The effects of crop spatial pattern on resource allocation in intercrops have been substantial (Wilson and Tilman, 1991; Oljaca et al.,

2000; Hauggard-Nielsen et al., 2001; Cahill, 2002; Zhang and Li, 2003), and similar impacts may occur in cultivar mixtures.

The potential importance of spatial pattern on agricultural productivity can be seen with mixtures of rice cultivars. Earlier work showed that a tall, lower-yielding cultivar mixed with a semidwarf, higher yielding cultivar in a replacement approach reduced yield as compared to monoculture performance (Jennings and Aquino, 1968). This result is not surprising, as a taller, lower-yielding cultivar would be expected to shade a shorter, higher-yielding one. In contrast, more recent work in which a reduced density of a tall, lower-yielding variety was added between every fourth row of the full monoculture density of a semidwarf, higher-yielding cultivar showed substantial increases in productivity as compared to the monocultures (Zhu et al., 2000). Though cultivar diversification reduced the severity of blast disease, the disease effects alone were insufficient to explain the large increases in productivity observed. However, the full yield effects can be explained if one assumes that the cultivars utilized different resources, which would increase productivity, and that planting in rows avoided the negative shading effects seen in earlier studies.

Few studies have addressed the effect of spatial arrangement on yields of cultivar mixtures. In a study of four phenotypically contrasting spring barley cultivars grown in alternate row mixtures and in random mixtures, two random mixtures had a significant yield increase over the weighted mean of components grown in monoculture and four alternate row mixtures had one component that yielded significantly more than when grown in monoculture (Essah and Stoskopf, 2002). Overyielding of random mixtures of spring barley cultivars resulted from the combination of more dissimilar cultivars,

resulting in less direct competition. In alternating rows of different cultivars, the one component that overyielded compared to its monoculture was a tall, later maturing cultivar grown with a short, early maturing cultivar (Essah and Stoskopf, 2002).

Alternating swaths (4 rows) of two and three cultivars of wheat yielded higher than the same cultivars mixed randomly within rows, while alternating single row mixtures were not significantly different (Brophy and Mundt, 1991).

The above studies suggest that cultivar combinations and spatial arrangements interact in a specific and complex way. Therefore, the purpose of this study was to determine the effect of spatial pattern on the yield of three wheat cultivars when grown in varying spatial arrangements of two-way mixtures. We used an additive approach, by planting one cultivar at full rate and then adding a second cultivar at  $\frac{1}{4}$  rate in two spatial patterns, randomly mixed and alternating rows. Morphological markers allowed us to determine the yield of individual cultivars within mixtures.

## **Materials and Methods**

### ***Field sites and experimental design***

The cultivars were planted in bottomland sandy/loam soil of the Willamette River floodplain at the Oregon State University Botany and Plant Pathology Field Lab, located 1 km east of Corvallis, Oregon. Two wheat cultivars were planted in seven treatments in the 2000-2001 winter wheat season and three cultivars were planted in 18 treatments in the 2001-2002 season (Table 1 and Table 2). The two experiments were in a randomized complete block design with four replications. Wheat cultivars included Gene and Foote the first season, and a third cultivar, Coda, was added the second season. These cultivars

were chosen because their seed heads are distinct and allow for hand separation at harvest, and because they differ in height—Coda is tallest (110-122cm), Foote is mid-height (104-114cm), and Gene is shortest (78-104cm).

Each plot was 6.1x1.2m. Seeds were planted with one pass of a 6-row drill (Fig. 1). The approach was to plant each of the two or three cultivars in four rows at a full commercial seeding rate for the site (240 seeds/plot). In other treatments a  $\frac{1}{4}$  rate of a different cultivar was then added to this full rate, in different spatial patterns. The spatial arrangement and density variations (Table 1 and Table 2) included monocultures planted in six 20-cm rows; monocultures planted in four rows, keeping the 2<sup>nd</sup> and 5<sup>th</sup> rows empty; mixtures of cultivars planted mixed within all six rows; and single cultivars in separate rows (rows 1, 3, 4, and 6 in one cultivar and rows 2 and 5 in a second cultivar). The combinations of cultivars were always planted at full and  $\frac{1}{4}$  rate, though the arrangements varied. An exception was for the second year, when the random mixtures were accidentally planted at full plus  $\frac{1}{3}$  rate. Another variation was that, in the second year, while total density was 1 and  $\frac{1}{3}$  rate, the density per row differed from the first year. Rows 1,3,4, and 6, instead of being planted with a total of 2000 seeds, were planted with 1600, and rows 2 and 5, instead of being planted with a total of 1000 seeds were also planted with 1600 (Table 1 and Table 2).

Planting dates were 19 October 2000 and 15 October 2001. Preplant fertilizer was applied 12 September 2000 at 36 kg per ha each of N, P<sub>2</sub>O<sub>5</sub>, and K<sub>2</sub>O and 12 September 2001 at 43 kg per ha each of N, P<sub>2</sub>O<sub>5</sub>, K<sub>2</sub>O. Nitrogen was added at a rate of 100 kg per ha on 20 March 2000 and 20 and 21 March 2001.

Plots were mowed to 4.8 m in length in July of each year to facilitate harvest.

On 2-3 August 2001 and 5-8 August 2002 all plants in each plot were cut with a sickle bar mower. For those plots with two cultivars, cultivars were separated by hand. Each bundle of plants was then run through a stationary thresher and seed collected and weighed.

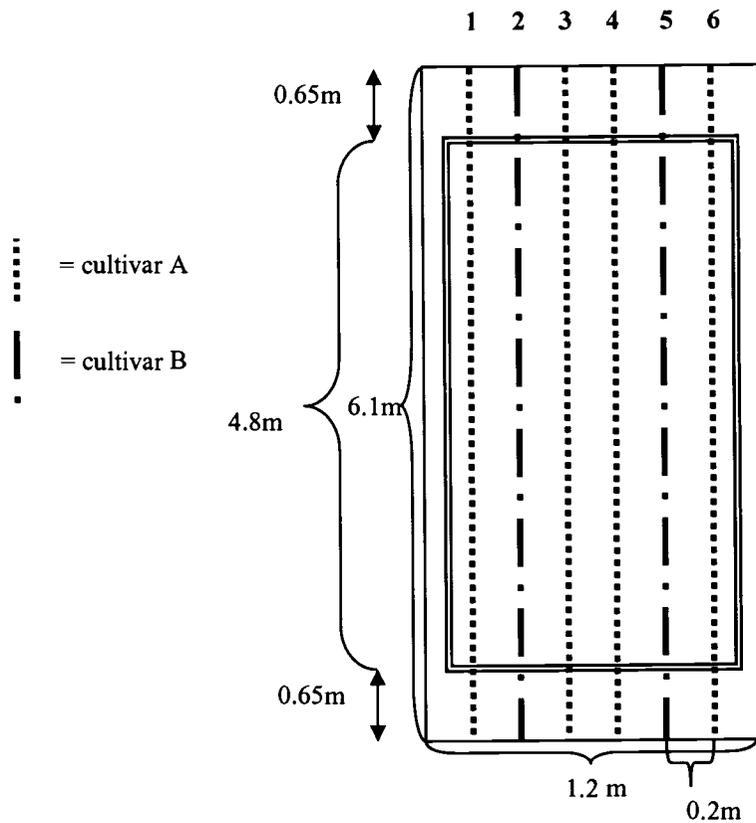


Fig. 2.1. Diagram of treatment with separate rows of two cultivars showing area harvested within box enclosed by double line and row numbers printed above plot.

Table 2.1

Yield and Relative Yield in Mixture (RYM) of wheat cultivars and cultivar mixtures sown at different rates and spatial arrangements in the field during the 2000-2001 winter wheat season<sup>a</sup>

Seeds per cultivar sown		Yield (kg/plot)	RYM <sup>b</sup>	P < F <sup>c</sup>
Rows 1, 3, 4 & 6	Rows 2 & 5			
2400 Gene		5.70		
2400 Gene	600 Gene	6.07		
2400 Foote		6.06		
2400 Foote	600 Foote	4.79		
2400 Gene	600 Foote	5.53	0.950	0.63
2400 Gene + 600 Foote		5.14	0.884	0.26
1600 Gene + 400 Foote	800 Gene + 200 Foote	5.17	0.889	0.28

<sup>a</sup>RYM is defined as  $(Y_{AB} + Y_{BA}) / (p_A Y_A + p_B Y_B)$ , where  $Y_{AB}$  is the relative yield of cultivar A when grown with B,  $Y_A$  = yield of cultivar A in monoculture;  $p_A$  = proportion of A in mixture

<sup>b</sup>Comparison with 6-row monocultures

<sup>c</sup>Significance for linear contrast of mixture versus weighted mean of pure stand

Table 2.2  
Yield and Relative Yield in Mixture (RYM) of wheat cultivars and cultivar mixtures sown at different rates and spatial arrangements in the field during the 2000-2001 winter wheat season<sup>a</sup>

Seeds per cultivar sown		Yield (kg/plot)	RYM <sup>b</sup>	P < F <sup>c</sup>
Rows 1, 3, 4 & 6	Rows 2 & 5			
2400 Gene		5.84		
2400 Gene	600 Gene	5.38		
2400 Gene	600 Foote	5.31	1.002	0.98
2400 Gene	600 Coda	5.22	1.013	0.87
1200 Gene + 400 Foote	1200 Gene + 400 Foote	5.21	0.987	0.67
1200 Gene + 400 Coda	1200 Gene + 400 Coda	5.17	1.014	0.67
2400 Foote		5.06		
2400 Foote	600 Foote	5.00		
2400 Foote	600 Gene	5.10	1.006	0.94
2400 Foote	600 Coda	5.08	1.047	0.58
1200 Foote + 400 Gene	1200 Foote + 400 Gene	4.9	0.963	0.25
1200 Foote + 400 Coda	1200 Foote + 400 Coda	4.98	1.034	0.32
2400 Coda		3.82		
2400 Coda	600 Coda	4.26		
2400 Coda	600 Gene	4.09	0.912	0.34
2400 Coda	600 Foote	3.95	0.898	0.28
1200 Coda + 400 Gene	1200 Coda + 400 Gene	4.34	0.957	0.25
1200 Coda + 400 Foote	1200 Coda + 400 Foote	4.09	0.921	0.04

<sup>a</sup>RYM is defined as  $(Y_{AB} + Y_{BA}) / (p_A Y_A + p_B Y_B)$ , where  $Y_{AB}$  is the relative yield of cultivar A when grown with B,  $Y_A$  = yield of cultivar A in monoculture;  $p_A$  = proportion of A in mixture

<sup>b</sup>Comparison with 6-row monocultures

<sup>c</sup>Significance for linear contrast of mixture versus weighted mean of pure stand

### Statistical analyses

All analyses were performed using Splus (Mathsoft, Inc. 2000). Two types of analyses were conducted: weight of seeds harvested per plot (“total plot yield”) and weight of seeds harvested divided by seeds planted per plot (“yield per seed”). While statistical analyses were done on total weight, total weight was also used to determine Relative Yield of Mixture (RYM) (Wilson, 1988; Williams and McCarthy, 2001): RYM

$= (Y_{AB} + Y_{BA}) / (p_A Y_A + p_B Y_B)$ , where  $Y_{AB}$  = relative yield of cultivar A when grown with B,  $Y_A$  = yield of cultivar A in monoculture;  $p_A$  = proportion of A in mixture (in this experiment, the value is either 1, 0.25 or 0.33 as cultivars were always planted either at full, 1/4 or 1/3 rate). Overyielding is indicated by a RYM greater than 1.0. For example, a RYM of 1.20 indicates that a mixture yielded 20% greater than the weighted means of its pure stand controls. Analyses of per seed yield were used to evaluate the performance of individual cultivars in mixtures as compared to their performance in pure stand.

Analysis of variance was performed on total yield per plot for each year, with spatial arrangement and cultivar combination as treatments. Linear contrasts with weighted means were then made to compare cultivar components per plot to the corresponding pure stands. A series of comparisons was made to the 6-row pure stands. For example, when comparing the mixture of Gene (full rate) + Foote (1/4 rate) to its weighted pure stands, the coefficients were -4 for 6-row Gene monoculture and -1 for 6-row Foote monoculture and 5 for the Gene (full) + Foote (1/4) mixture treatment (Table 1 and Table 2).

The following additional linear contrasts were performed the first and second seasons: all mixtures to all 4-row monocultures, all row mixtures to all random mixtures, all 4-row random mixtures to all 6-row random mixtures, all 4-row monocultures to all 6-row monocultures, and all 6-row monocultures to all 6-row random mixtures and row mixtures.

One ANOVA was conducted for the per seed yield of each cultivar in all treatments in which it was present. In this case coefficients were 1 and -1 and a direct contrast was made of per seed yield of a cultivar in mixture to the per seed yield of the same cultivar

in 6-row monoculture. An additional linear contrast was made to compare the per seed yield of the 6-row monoculture to the 4-row monoculture.

## Results

The overall treatment effect in the ANOVA for total plot yield was significant in 2001-2002 ( $P < 0.0001$ ) but not in 2000-2001 ( $P = 0.36$ ). The 4-row and 6-row monocultures were not significantly different ( $P > 0.28$ ) in either year. There was also no evidence for an effect of spatial arrangement of mixtures on yield. Linear contrasts of total yield between all random and all row mixtures were insignificant in both seasons ( $P = 0.47$  and  $P = 0.91$ ). In the second season, one Coda/Foote mixture was the only mixture that yielded significantly different than the weighted means of the pure stands and this was a yield reduction (Table 2). No mixture yielded significantly differently from its component pure stands in the first season (Table 1). None of the additional linear contrasts described in the Materials and Methods were significant ( $P > 0.14$ ).

Overall treatment effects were significant for separate ANOVAs of per seed yield of each cultivar in both seasons ( $P < 0.01$ ). As expected, the per seed yield of all monocultures declined with increased seeding rate, though not all were significant (Table 3 and Table 4). In mixtures, the per seed yield changes were a result of cultivar competitive ability and of cultivar dominance (major or minor component) in a plot. In all cases, Foote was the strongest competitor, followed by Gene and then, Coda, in both seasons, and regardless of spatial arrangement. The per seed yield of Foote, as the minor component, significantly increased with both Gene and Coda ( $P < 0.05$ ). As the dominant component, Foote was not affected by the presence of either cultivar. Gene, as

the minor component, significantly increased with Coda ( $P < 0.05$ ), and significantly decreased with Foote ( $P < 0.001$ ). As the dominant component, Gene decreased significantly when randomly mixed with Foote, but was not affected by Coda ( $P < 0.001$ ). And, Coda, as the minor component, significantly declined with both cultivars, especially Foote ( $P < 0.001$ ), except when in row mixtures with Gene, where it was not affected. As the major component, it declined with Foote ( $P < 0.05$ ), but was not significantly affected by Gene.

Table 2.3

Yield per seed sown for wheat cultivars sown in pure stand and mixtures at different rates and spatial arrangements and comparisons of yield per seed sown in mixture versus 6-row monocultures, 2000-2001 season

Seeds per cultivar sown		Gene		Foote	
Rows 1, 3, 4 & 6	Rows 2 & 5	Yield (g/seed)	P < F <sup>a</sup>	Yield (g/seed)	P < F <sup>a</sup>
2400 Gene		2.37			
2400 Gene	600 Gene	2.02	(0.22) <sup>b</sup>		
2400 Foote				2.52	
2400 Foote	600 Foote			1.60	(0.00) <sup>b</sup>
2400 Gene	600 Foote	1.44	0.05	3.45	0.00
2400 Gene + 600 Foote		1.29	0.02	3.39	0.00
1600 Gene + 400 Foote	800 Gene + 200 Foote	1.28	0.02	3.49	0.00

<sup>a</sup> Significance for linear contrast of mixture versus 6-row monoculture

<sup>b</sup> Significance for linear contrast of 6-row monoculture versus 4-row monoculture in parentheses

Table 2.4  
Yield per seed sown for wheat cultivars sown in pure stand and mixtures at different rates and spatial arrangements and comparisons of yield per seed sown in mixture versus 6-row monocultures, 2001-2002 season

Seeds per cultivar sown		Gene		Foote		Coda	
Rows 1, 3, 4 & 6	Rows 2 & 5	Yield (g/seed)	P < F <sup>a</sup>	Yield (g/seed)	P < F <sup>a</sup>	Yield (g/seed)	P < F <sup>a</sup>
2400 Gene		2.43					
2400 Gene	600 Gene	1.79	(0.00) <sup>b</sup>				
2400 Gene	600 Foote	1.55	0.24	2.63	0.01		
2400 Gene	600 Coda	1.86	0.75			1.28	0.49
1200 Gene + 400 Foote	1200 Gene + 400 Foote	1.18	0.00	2.96	0.00		
1200 Gene + 400 Coda	1200 Gene + 400 Coda	1.71	0.67			1.34	0.00
2400 Foote				2.11			
2400 Foote	600 Foote			1.67	(0.21) <sup>b</sup>		
2400 Foote	600 Gene	0.94	0.00	1.89	0.52		
2400 Foote	600 Coda			1.97	0.39	0.58	0.00
1200 Foote + 400 Gene	1200 Foote + 400 Gene	0.94	0.00	1.73	0.86		
1200 Foote + 400 Coda	1200 Foote + 400 Coda			1.91	0.49	0.49	0.00
2400 Coda						1.59	
2400 Coda	600 Coda					1.42	(0.41) <sup>b</sup>
2400 Coda	600 Gene	2.24	0.03			1.42	0.99
2400 Coda	600 Foote			3.11	0.00	0.87	0.01
1200 Coda + 400 Gene	1200 Coda + 400 Gene	2.11	0.13			1.11	0.14
1200 Coda + 400 Foote	1200 Coda + 400 Foote			2.49	0.03	0.88	0.01

<sup>a</sup>Significance for linear contrast of mixture versus 6-row monoculture

<sup>b</sup>Significance for linear contrast of 6-row monoculture versus 4-row monoculture in parentheses

## Discussion

There was no effect of spatial arrangement on the yield of cultivar mixtures in this study. Identification of useful spatial patterns may require substantial empirical knowledge or testing. For example, a row mixture of rice cultivars that effectively controlled disease and increased yield was borrowed from a local farmer, potentially the result of years of trial and error (Zhu et al. 2000). Intercropping of cereals with cereals and cereals with legumes takes a myriad of forms depending on the farmer's objectives and the local soil and climate conditions (Rao, 1986); hence, plantings vary each year and by region. Timing of planting of two crops also varies (Connolly et al., 2001). In addition, to minimize competition between species, the spacing of the dominant cereal has to be sufficiently wide (Rao, 1986).

In an experiment with wheat, alternating four-row swaths of three cultivars showed a significant yield advantage, but a random mixture and alternating rows of the three cultivars did not (Brophy and Mundt, 1991). These results suggest that it is not until cultivars are in four-row swaths that a difference can be distinguished between randomly mixing cultivars and keeping them in separate rows because an individual has a large area of competitive influence. Thus, we may not have tested spatial patterns that were sufficiently coarse to provide a benefit in our study.

Total yields of plots revealed no significant advantage of cultivar mixtures over monoculture. Random mixtures of barley cultivars with varying heights or with complementary abiotic and biotic stress tolerances showed some advantage over monocultures, though the lack ofoveryielding of the highest yielding monoculture was explained by a lack of complementarity in resource capture strategies (Jedel et al., 1998;

Juskiw et al., 2001). Similar results have been found in random mixtures of fall-sown hard red spring wheat (Jackson and Wennig, 1997). The overlap of maturity date may sometimes explain the direct competition, or complementarity, between cultivars in timing of resource capture. In a rice study demonstrating substantial yield benefits to mixing (Zhu et al., 2000), one cultivar was later maturing than its companion (Mundt, unpublished). There is some variation in heading date among the wheat cultivars that we studied, but the cultivars tend to mature at the same time.

Cultivar mixtures are often used to reduce disease (Mundt 2002b). In this experiment, even *Septoria tritici* blotch, which is often severe in the Willamette Valley, was not a significant factor. The lack of advantage mixtures have under disease pressure could potentially explain the absence of a significant benefit to yield of mixtures in this study. In addition, it has been suggested that yield benefits of cultivar mixtures are greater in stressful and/or variable environments (Frey and Mulonado, 1967; Mundt, unpublished). In contrast, the Willamette Valley is a near optimum environment for wheat.

While some research has found an effect of height on performance in mixtures (Gilbert et al., 2003; Essah and Stoskopf, 2000), the cultivars used in this study were probably affected by other aspects of competitive ability. Based on the height differences of the three cultivars, it was expected that Coda, the tallest, would intercept more light and be more competitive, but its yield decreased significantly when grown with the shorter cultivar, Foote. Gene, the shortest, significantly increased relative to monoculture when planted with Coda as the minor component.

There were clearly differences in competitive ability among the three cultivars in this study. Foote was the most competitive, followed by Gene, and then Coda. In general, Foote per seed yield increased with both Gene and Coda when grown as the minor component and, when grown as the dominant component resulted in a significant decrease in per seed yield of the companion. In contrast, Coda decreased significantly as the minor component with Foote and Gene, but was also compromised when grown as the dominant component with Foote. Likewise, Gene significantly decreased as the minor or major component with Foote, but was either not affected or increased with Coda.

It has often been shown that increasing planting density has little effect on yield (e.g. Darwinkle, 1978). In this experiment, yield did not significantly increase with an increase in seeding rate, suggesting that yield was maximized at 4-row monocultures and that the plots had attained their "constant final yield". Thus, effects of adding a second cultivar to the full seeding rate were likely due to factors such as competition and resource complementarity.

Comparisons were made with random mixtures in the second year, despite the mistake in the overall planting density and the change in seeds per row from the first season. The mistake in planting density represents only a 6% error (1.25 to 1.33 total rate), and comparisons of per seed yield made between random mixtures and 4-row monocultures (not shown) were very similar in most cases to the comparisons of per seed yield between random mixtures and 6-row monocultures. In terms of the variation in row density, the RYM of the random mixture of Gene and Foote obtained for the first and second season were similar (0.889 and 0.987, respectively). Likewise, yield and RYM

obtained for the row mixtures and random mixtures in the second year were similar. In addition, a linear contrast on plot yield between random mixtures and row mixtures in the second season revealed an insignificant difference ( $P = 0.47$ ). Finally, yield per seed was similar between random mixtures and row mixtures in the second year (Table 4). Thus, although the planting errors were unfortunate, they do help to confirm the general conclusion that planting pattern had little effect on mixture performance.

### **Conclusion**

The yield of cultivars was greatly impacted by the companion in mixtures. However, there was no yield advantage of mixtures, nor a yield difference between row and random mixtures. This research suggests that cultivars interact over a large distance and that to detect an effect of spatial arrangement, planting patterns need to be sufficiently coarse.

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## **Conclusion**

Within this range of spatial patterns, there is no effect of spatial arrangement on productivity, measured in terms of above ground biomass or seed yield. However, species and cultivar combinations clearly result in variations in productivity. It is proposed that these variations are caused by competitive interactions involving capture of sunlight, water and nutrients over space and time. Species and cultivar interactions are specific and complex and, between individuals, seem to occur over large areas. For this reason, I believe that spatial arrangements may need to be more coarse for detectable effects to arise.

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