Mixed-Density Designs for Evaluating Plant Interactions During Revegetation

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The purpose of revegetation is to provide a sustainable plant cover to protect soil, and to provide habitat and food for livestock and wildlife. Often, land identified for revegetation is currently occupied by competitive weeds. To increase the likelihood that desirable plants will establish after they are seeded, managers must reduce weeds before revegetating the land (Valentine 1989). Because weed reduction treatments rarely result in total elimination of weeds, revegetated desirable plants must compete with weeds. Recently, there has been an increased emphasis on using a diverse mixture of desirable plants in revegetation projects. This has led to some concern that the most competitive species in the mixture will dominate the revegetation project (Pyke 1996). In both cases above, revegetation scientists now have a technique to help them predict outcomes of such interactions.

Traditional approaches for evaluating mixtures of plant species have produced vast amounts of data from throughout the world. These approaches have added valuable knowledge to our understanding of how desirable species can coexist and how weedy competitors can affect desirable plants in various environments. However, most approaches evaluate only one total density (the number of plants in a unit of land area) for the mixture, not a realistic range of levels that can exist (Connolly 1986a, 1986b). For example, Figure 1 shows a typical mixture experiment where a constant total density of both species of 30 plants per foot^2. But in natural populations, the level may shift above and below this number from one year to the next. These fluctuations are rarely addressed in such studies. To compensate for this, studies of plant mixtures should include a wide range of total densities and of proportions of the species, such as these in Figure 2. This is particularly important when evaluating plants to use in a revegetation project, because we must often establish desirable plants into a background of undesirable plants or mix a diverse set of desirable plants. By incorporating a range of population levels into evaluations, we can determine: 1) which species compete directly and therefore are inherently incompatible; 2) which species may effectively divide the site's resources to minimize competition and therefore promote coexistence and diversity; and 3) which species may modify sites to aid in succession and establishment of additional species (Pyke and Archer 1991).

To investigate the feasibility of this approach, we conducted a seedling competition study in a greenhouse using three grasses that often interact on revegetated rangelands in the western U.S.A. (Pellant and Monson 1993). The goal was to compare a range of densities of two desirable perennials with that of a weedy annual during the seedling establishment phase. We used this approach to vary both the overall total density of the mixture (one desirable perennial with the weedy annual) and the proportions of the species to evaluate their abilities to compete with each other.

The Study

'Nordan' (*Agropyron desertorum* [Fish. ex Link] Shult.) and 'Hycrest' (a hybrid of 'Nordan' and 'Fairway' *A. cristatum* [L.] Gaertn.) crested wheatgrasses are important perennial species for revegetation in the Intermountain West. On many sites where these species are used, the weedy annual cheatgrass (*Bromus tectorum* L.), is commonly present. In our study, we compared the competitive ability of Nordan with cheatgrass to that of Hycrest with cheatgrass. In pots,

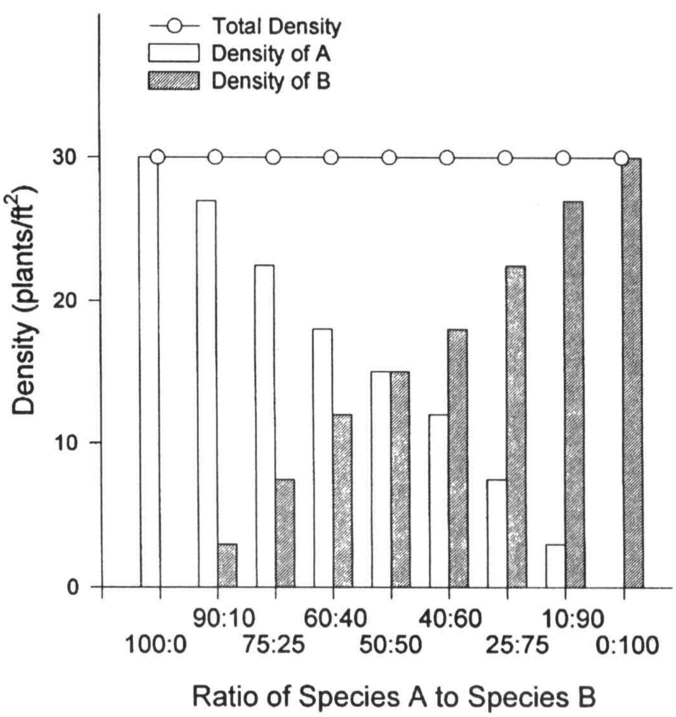

Fig. 1. *The density contribution of each species in a two-species mixture at varying ratios of the species while holding the total density constant.*

we sowed cheatgrass and one of the crested wheatgrasses using one of four population levels. Then we repeated this design with the other crested wheatgrass and cheatgrass. The recommended sowing rate for crested wheatgrass is approximately 24 seeds/ft ^{2} when no competitors are present. We evaluated population levels that ranged from one-half the recommended seeding rate (12 seeds/ft ^{2}) to twice the recommended rate (48 seeds/ft ^{2}). For the mixtures, we grew a range of proportions of the two species that were similar to Figure 2. Also, we grew each plant species by itself (monoculture) at each density. This gave us realistic combinations of the weed and the desirable plants.

We grew the grasses for 176 days from October to April 1989. Water and fertilizer were added throughout the growing season to maintain reasonable levels of these resources. At the end of the study, we measured growth (aboveground production and tiller counts) for each plant. Their growth was analyzed using a 'response function' approach (Connolly 1987) where equations relate the density of each species to the plant growth. From this, the competitive ability of each species can then be calculated. The 'substitution rate' is a numerical way of rating the competitiveness of interacting species based on their growth. The competitiveness of individuals of the same species is set to a standard level of one. The substitution rate is then compared to this standard, and is calculated for each species in the mixture. Specifically, the substitution rate represents the number of plants of the current species that would be necessary to substitute for the other species and still maintain the same level of growth. Thus, a substitution rate for Species A that is less than one indicates that for every individual of Species B in the mixture it will take less than one individual of Species A to have the same impact on growth of Species A. A substitution rate for Species A that is greater than one indicates that for every individual of Species B in the mixture it will take more than one individual of Species A to have the same impact on growth of Species A. Species B will also have a substitution rate that is calculated separately. It is not merely the reciprocal of Species A's rate.

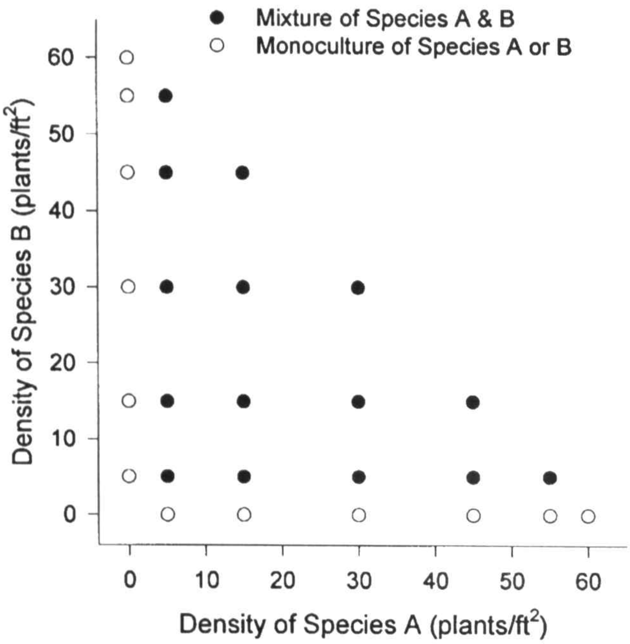

Fig. 2. *Representative densities for each species in a two-species mixture along with their monocultures illustrating a range of total densities (10 to 60 plants/ft ^{2}) and of ratios of the two species.*

As an illustration, let's take a mixture of two species with a total density of ten individuals. Species A has four and Species B has six individuals in this mixture. If Species A has a substitution rate of three, then Species B is more competitive than Species A. The value of three means that one individual of Species B has the same effect on an individual of Species A as substituting three individuals of Species A for each individual of Species B in the mixture.

The substitution rate for Species B in the mixture is not merely the inverse of the rate of Species A. In other words, we can not calculate Species B's substitution rate as merely being one-third. The reason this does not work is because each species may use different parts of the habitat, therefore both species may not have equal access and equal ability to obtain all of the available resources. Therefore, each species' substitution rate must be calculated separately. In our example, the substitution rate for Species B might be 0.7.

These substitution rates may change over seasons or years. This occurs because different species may have different periods of growth (phenologic stages) when they use more resources (seasonal changes). Alternatively, their resource needs may change as they get older or as they experience different weather events (year-to-year changes).

The point we want to make is that the competitive effect each species has on the other species is standardized for comparisons through using substitution rates. This information is valuable for evaluating many revegetation factors including seeding rates, long-term survivability, species compatibility, succession directions, and resource overlap among coexisting species.

Results and Discussion

In our study, cheatgrass was always the superior competitor when grown with first-year seedlings of either Hycrest or Nordan. For the two crested wheatgrasses, Hycrest exhibited a greater influence over cheatgrass than did Nordan (Francis and Pyke 1996). The study further indicated that lower densities of crested wheatgrass, particularly Hycrest, were better able to contend with cheatgrass as a competitor. The aboveground production of individual plants was the greatest for Hycrest and Nordan when their densities were low. However, as densities of cheatgrass or of either crested wheatgrass increased, there was a compounded effect of within and between species competition that led to cheatgrass becoming more competitive. Thus, the advantages of cheatgrass in crowded populations of mixed species allow it to exploit resources better than either crested wheatgrass.

While the data on aboveground production provided insights into the relationship between these species, the substitution rates for each species further illustrated how competition was occurring among them. Considering aboveground production in the mixture of Hycrest and cheatgrass, Hycrest substitution rates were always above one, even at the lowest densities, and remained below 4 (1 cheatgrass equaled the impact of 4 Hycrest plants) through the recommended seeding level. At the highest level of Hycrest densities, at twice the recommended seeding levels, the competitive effect was well above 10 (1 cheatgrass equaled 10 Hycrest). Therefore, adding more Hycrest to the population increased the competitive ability of cheatgrass in the mixture. In comparison, cheatgrass substitution rates when grown with Hycrest were all below 0.5 (1 Hycrest equaled less than one-half of a cheatgrass) indicating that cheatgrass individuals had more impact on cheatgrass production than Hycrest individuals had on cheatgrass.

Nordan was a weaker competitor with cheatgrass than Hycrest during the first year of growth. This became obvious when we attempted to find equations to explain Nordan and cheatgrass aboveground production based on the densities of the two species. Nordan's substitution rate in the cheatgrass mixtures was a constant 4.6 meaning that each cheatgrass individual had the same effect as 4.6 individuals of Nordan. Changes in the densities did not affect this rate. A cheatgrass substitution rate, however, did not exist in mixtures with Nordan because Nordan had no impact on cheatgrass growth.

Another aspect of the growth of grasses is the number of tillers (a tiller is roughly the same as a stem for a grass). When we examined the competitiveness of each species by using the number of tillers produced, the result contrasted with those of aboveground production. All substitution rates for tiller number per plant for each of the three species were below one. This means that tiller production is influenced more by individuals of the same species than by other species during this first year of growth.

Comparisons of our results with those of others reinforces the strength of cheatgrass as the dominant competitor. However, a problem in each of these previous studies was that few, if any, accounted for a range of population levels of each species in the mixtures. Our study accounts for this element, at least for the establishment phase in a desirable-undesirable plant mixture. Our results support the suggestion that lower densities of aggressive perennials may enable these perennials to better compete with invasive annuals such as cheatgrass (Buman et al. 1988, Pyke and Archer 1991). This premise relies on the fact that fewer individuals of the same species will require the identical resources, therefore, fewer individuals means less direct competition. This should allow greater growth as long as the overlap of resource requirements with other species is not too great. Indeed, our results indicate that Hycrest and Nordan appear to have a greater chance for exploiting resources in less crowded populations which should translate into greater growth with more tillers. However, what is not known is how many of these crested wheatgrass individuals will survive to the next year or how environmental inputs at field sites, i.e. soil types, precipitation regimes, microsites, etc., will affect their survival and competitive relationships with cheatgrass. Thus, additional research needs to investigate these relationships beyond one year and in natural field environments.

Conclusions

The ultimate goal of seeding competitive perennials on cheatgrass-dominated rangelands is to reduce cheatgrass abundance through the establishment and growth of desirable perennials. If lower seeding rates of crested wheatgrass will allow greater crested wheatgrass growth, then greater survival of crested wheatgrass individuals will likely occur over the first summer drought. If crested wheatgrass can increase its competitive ability in subsequent years, then cheatgrass densities may decline quicker than with currently recommended seeding rates. In a broader context, this approach emphasizes the need to know seed pool sizes of undesirable species so we can calculate appropriate seeding rates (densities) of desirable plants to optimize the establishment and growth of desirable species in subsequent years. By doing this, we hope to maintain and potentially increase the competitive edge against weeds.

This same approach and principle applies in mixtures of desirable plants where the goal is to establish a diverse set of species that are able to coexist. To achieve and sustain this goal, competition should be reduced to levels that allow for establishment and growth of all species. Ideally, we would want to determine the seeding rate of each species that would maintain a substitution rate near one after plants establish. The use of this kind of competition design allows many factors to be quantified and included in the planning process of revegetation.

Very little work has been done on determining combinations of species that lead to coexistence. Future work in this area should involve determining positive characteristics of potentially coexisting species (Aber 1987, Call and Roundy 1991), while simultaneously preparing for potential problems such as invasions of undesirable plants (Pyke and Archer 1991), changes in environmental stresses, or changes in the competitive regime over time. Regardless of the revegetation strategy, plant to plant interactions play a vital role in determining revegetation successes and failures. Nontraditional approaches, such as the one we have used for the design and quantification of these interactions, can provide information needed to help land managers produce stable and diverse plant communities on rangelands in the future.

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