Plant-plant interactions affecting plant establishment and persistence on revegetated rangeland

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Abstract

Restoration and revegetation of rangeland ecosystems is based on knowledge of abiotic and biotic interactions that affect plant establishment. Once plants become autotrophic, interactions within and between plant species may occur and these interactions may range from antagonistic to mutualistic. This full range of potential interactions needs to be considered to ensure successful revegetation. At the intraspecific level, we propose the development and use of density-yield diagrams for rangeland species. These diagrams would be based on the self-thinning principle, that aboveground biomass is related to plant density and to the dynamic process of density-dependent mortality. The proposed approach would be used to determine optimum seeding rates, and to predict future biomass of revegetated rangeland. At the interspecific level, competitive relationships of species used to reseed rangelands need to be identified to enhance the probability that species will coexist and thereby facilitate greater species diversity on the site. A diversity of species and growth forms may provide a more stable cover and productivity than a monoculture on sites characterized by environmental variability while potentially enhancing nutrient status for the site.

Key Words: competition, mutualism, resource partitioning, revegetation, self-thinning, species mixtures, stress tolerance

Revegetation may range from a total restoration of the original ecosystem, to rehabilitation (partial restoration), to natural reseeding, to a replacement of the original ecosystem with an alternative ecosystem (Bradshaw 1984). Regardless of the form of revegetation, our expectation of its outcome should be based on our knowledge of abiotic and biotic interactions that affect plant establishment. Unfortunately, our understanding of mechanisms regulating ecosystem processes is often limited. As a result, the applicability of several ecological paradigms has been rightfully questioned. For example, there is considerable debate as to what forces drive succession (Connell and Slatyer 1977, MacMahon 1981, Westoby et al. 1989) and as to the importance of competition in determining community composition (Schoener 1983, Connell 1983). No longer is the competitive exclusion principle (Gause 1934, Hardin 1960) accepted as the best explanation of species diversity and coexistence (Silvertown 1987). An array of alternative hypotheses have been proposed to explain spatial and temporal relationships of species in communities. These include the regeneration niche hypothesis (Grubb 1977), the resource ratio hypothesis (Tilman 1982), the aggregation hypothesis (Shmida and Ellner 1984), the gap-phase replacement hypothesis (Pickett and White 1985) and the storage effect hypothesis (Warner and Chesson 1985).

An understanding of biotic interactions and successional processes is central to revegetation, since strategies for rehabilitation and restoration typically center around augmenting, enhancing, or accelerating changes in species composition. The key to restoring native plant communities, in many cases, lies with identifying and overcoming factors that impede or restrict ecosystem development (Bradshaw 1987). Although descriptions of species composition through time provide valuable information regarding community change, they seldom provide insight as to why changes occurred. We must examine adaptations and processes that confer persistence and compatibility or incompatibility to understand why some species coexist while others do not.

Our purpose in this review is to focus on biotic interactions that are related to repairing rangeland ecosystems by revegetation. This is not an exhaustive review, but rather a synopsis of how plant-plant interactions determine success or failure of rangeland revegetation efforts. We recognize that animals also play a major role in the success of revegetation and we address their impacts in a companion paper (Archer and Pyke 1991). Throughout this paper, we relate the impact of these interactions to succession and landscape ecology and we suggest future research directions that will fill gaps in our current knowledge of rangeland revegetation and restoration.

Intraspecific Associations

Size, Biomass, and Density Relationships

Once plants become autotrophic, they begin to interact with both conspecific individuals and with plants of other species growing in the immediate vicinity. These interactions vary from being antagonistic (e.g., competitive) to being mutualistic (e.g., mycorrhizae-plant associations). A knowledge of mechanisms of plant interactions is required to transform range revegetation from a correlative science to a predictive science.

Ecological theory relating density-dependent plant interactions has been largely unexplored in rangeland revegetation research. The self-thinning principle, that aboveground plant biomass is related to initial plant density and to the dynamic process of density-dependent mortality over time, has been widely accepted in forest management (Drew and Flewelling 1977) and in plant ecology (White 1981, Westoby 1984). The principle has recently come under some scrutiny in plant ecology (Weller 1987) and may require carefully designed experiments to validate (Lonsdale 1990), but the original interpretation of the principle as an upper boundary for plant yield appears to remain valid for individual species (Osawa and Sugita 1989). This principle is conspicuously absent from range improvement (Vallentine 1989) and general range management texts (Stoddart et al. 1975, Holechek et al. 1989), although it is recognized in many fields of plant science.

The principle is mathematically stated in 2 forms. One form relates individual plant biomass to density,

$$\log w = \log K - 1.5(\log d), \qquad \textbf{(eq. 1)}$$

where w is the mean plant biomass, d is the mean number of plants per unit area and K is a constant. The alternative form relates yield per unit area to density,

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$$\log b = \log C - 0.5(\log d), \qquad \text{(eq. 2)}$$

where b is mean aboveground biomass per unit area and C is a constant.

The outcome of these self-thinning relationships in revegetated rangeland is evident in studies that examine the effect of initial seeding rate on plant density (e.g., Hull and Holmgren 1964, Hull and Klomp 1967). However, it is difficult to demonstrate the principle with these studies since they rarely provide density (plants per unit area) and yield per unit area for the first 3 to 5 years after seeding. Foresters not only recognize the importance of self-thinning, but they use this principle to explain forest stand development and to guide management decisions. Drew and Flewelling (1977, 1979) describe 3 lines in a density-volume relationship (proportional to the density-mass relationship) (Fig. 1). Recent studies suggest that the slope of these lines may vary depending on the species (Weller 1987, Lonsdale 1990); however, we have used a slope of −0.5 for each line for explanatory purposes while recognizing that species-specific estimates of slope will need to be determined.

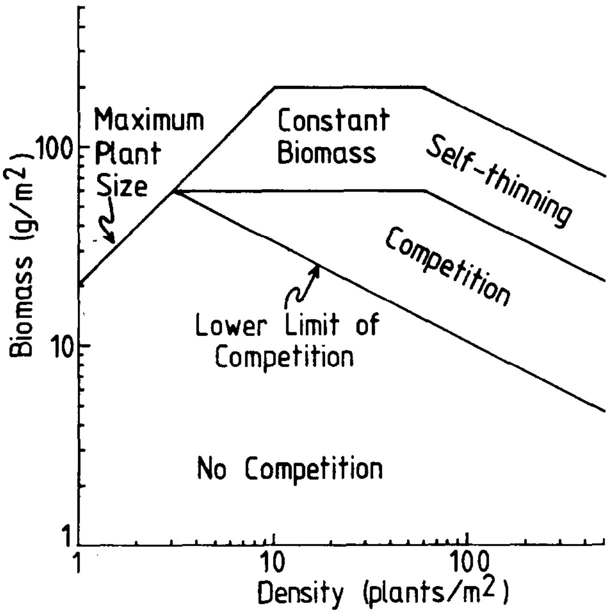

Fig. 1. Relationship between plant density and biomass for a hypothetical plant species (after Drew and Flewelling 1977).

The upper line describes the maximum size a stand of plants can attain at a given density and represents the upper morphological and physiological limit in size for a species grown without interspecific competitors. The next lower line describes the lower limit of the 'zone of imminent competition mortality' or a zone of sizes and densities where density-dependent mortality occurs. This zone is equivalent to the self-thinning band of Westoby (1984). The lowest line approximates the initiation of competition between plants. Between the competition line and the lower limit of density-dependent mortality is a zone of competition without density-dependent mortality. Density-dependent mortality will not occur in this zone although relative growth rates will decrease as resources become increasingly limiting. As a result, actual biomass at time t (b_t) will be less than the biomass which would have accumulated in the absence of competition (B_t) (Fig. 2).

Our hypothetical example also illustrates how the dynamic process of self-thinning and competition may reduce the density of a high-density population (300 plants/m²) to levels comparable to that of a medium density population (40 plants/m²) while maintaining production that is greater than or equal to the medium density population throughout the same time periods (Fig. 2). The high-density population at time t_1 has produced more biomass than the medium density population, but has entered the self-thinning zone. Plant density becomes reduced in this zone as individual survivors continue to increase in size. Both populations by t_3 have similar densities and both are in the zone of constant biomass where production losses resulting from plant mortality are compensated for by increased growth of remaining plants.

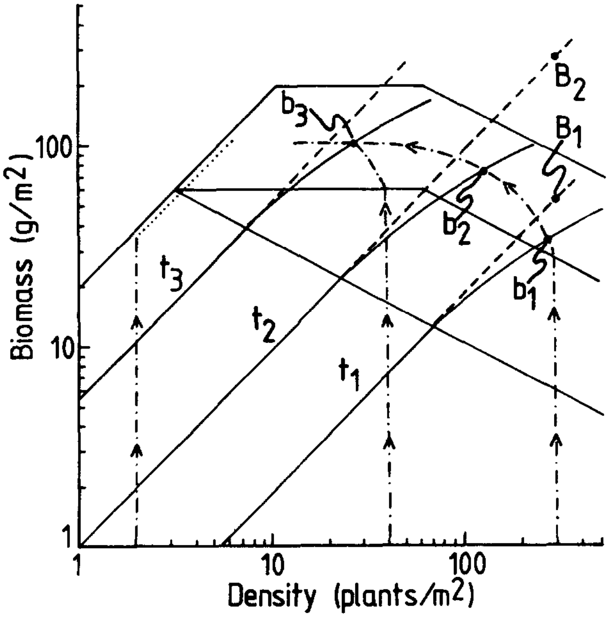

Fig. 2. Biomass of populations (b_t) harvested at times t_1 to t_3 for a range of densities of a hypothetical plant species. In the zones of competition and of density-dependent mortality (see Fig. 1) the dashed line indicates potential biomass (B_t). The dot-dashed lines represent the time trajectories of 3 densities. The dotted line associated with the low density population represents establishment of new individuals.

There are numerous aspects of revegetation that require experimental examination using this basic principle. If a density-yield diagram similar to Figure 2 was developed for a species, the predictions could be made of the time required to achieve an expected biomass from an initial density of plants. An economic analysis would be required to determine if the increased biomass and density of plants on the high-density site through t_3 was sufficient to warrant the cost of applying nearly 10 times more seed.

Recommended seeding rates are often set as the lowest seeding rate needed to achieve production comparable to that of stands receiving higher seeding rates, but at a rate that allows for density-independent mortality. That rate could be determined as a density slightly higher than the minimum competitive density using Figure 1. This would be the density that could theoretically achieve maximum production with the minimum number of plants. Populations sown at this density would not enter the competitive zone until they had completed density-independent mortality and had achieved their maximum plant size (Fig. 1). Plant densities below this level, for example the low-density population (2 plants/m²) in Figure 2, would result in yields per unit area that are less than their potential maximum even though the individual plants may achieve their maximum size. Any further increase in yield per unit area would only be achieved through the establishment of new individuals via seedlings or vegetative propagation (dotted line in Figure 2).

There are potential disadvantages of sowing at the minimum density that must be considered in any economic or ecological evaluation: (1) the probability of undesirable plants becoming established in areas between sown plants will be increased (e.g., McGinnies 1960, Cook et al. 1967, Hull and Klomp 1967); (2) soil stabilization and moisture infiltration may be reduced, while raindrop impact and surface runoff are increased at lower plant densities; (3) larger plants, characteristic of low-density stands, may be more susceptible to grazing than smaller plants characteristic of high-density stands (e.g., Westoby 1980). In addition, the probability of defoliation would be greater and would be spread over fewer individuals in low-density plantings; and (4) relative to high-density stands, low-density stands may produce plants with greater stem-to-leaf ratios making plants less palatable to grazing animals (Cook et al. 1967).

Sowing at densities that will generate early intraspecific competition has advantages and disadvantages. Early intraspecific competition may minimize establishment and seed production of undesirable species. Early competition, however, will also slow the growth of desirable plants and may contribute to mortality if individuals must achieve a minimum size to survive inclement conditions, such as summer drought or winter frost heaving. A tradeoff, therefore, exists between increasing early intraspecific plant density for the purpose of weed control and reducing intraspecific plant density for the purpose of optimizing individual plant size or stand production. Further research is needed to ascertain the optimum density required for maintenance of populations of desired plants while controlling undesirable species.

Interspecific Associations

Competitive Exclusion and Coexistence

Competition for limited resources may determine the presence, absence, or abundance of species in a community and determine their spatial arrangement. The importance of competition has been questioned, particularly for ecosystems with harsh environments (e.g., deserts and tundras). Abiotic stresses rather than competitive interactions may dictate community structure and function in these ecosystems (Grime 1977). Fowler (1986), however, conducted a thorough review of research investigating competition in arid and semiarid plant communities and concluded that competition does occur in these systems, that it involves many different species, and that it is an important determinant of community structure. One or more of the following factors may occur when plants compete for resources: (1) time to reproductive maturity may be increased; (2) growth rates of plants and the frequency and magnitude of viable seed production may be decreased; and (3) susceptibility to density-dependent and density-independent mortality factors may be increased.

These are important factors determining the outcome of revegetation and restoration efforts. In formulating seed mixtures, information on overlap in plant resource requirements and acquisition strategies may help determine: (1) which species are likely to be in direct competition and are therefore inherently incompatible; (2) which species may effectively partition site resources to minimize competitive exclusion and therefore promote coexistence and diversity; and (3) which species may modify site characteristics to facilitate succession and establishment of additional species. It is important to keep in mind in addressing these issues that competition is probably not a continuous, uniform phenomenon in communities. The intensity, frequency, and periodicity of competitive interactions between plants may vary substantially on a seasonal and annual basis in accordance with the stage of life cycle, with patterns of physiological activity, and with resource availability (Connolly et al. 1990). Welden and Slauson (1986) present a theoretical comparison of the importance and the intensity of competition on plant growth.

Diversity and Primary Production

With the recent concern for maintenance of biological diversity, mixtures of species will likely be used for revegetation to a much greater extent than they have been in the past. Development of community diversity is also potentially important for stability of vegetation cover and productivity. Species in communities have different life-history strategies and adaptations. As a result, their patterns of growth and reproduction vary spatially and temporally and are limited by different combinations of resources or environmental factors. Most research to date has focused on plant responses and adaptations to single features of the environment, but plants in nature often encounter multiple stresses (Chapin et al. 1987). In addition, field experiments frequently indicate that 2 or more resources may simultaneously limit plant growth (Lauenroth et al. 1978, Chapin and Shaver 1985). Fluctuations in weather or resource availability may cause substantial annual variation in productivity of individual species. However, the productivity of the community may be much less variable, since years that are favorable for growth of some species reduce the growth of other species, because of direct plant responses and competitive interactions. Conversely, in stressful years, the productivity of some species may be less affected than that of others (Fig. 3).

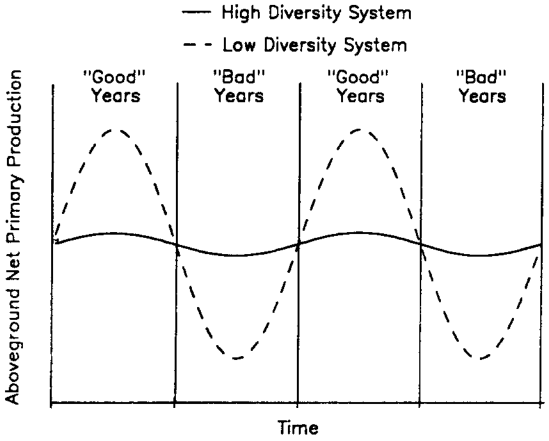

Fig. 3. Hypothetical relationship between species diversity and aboveground net primary production (ANPP) through time. Aboveground net primary production in the low diversity system will be high in years 'good' for species that dominate this system. Conversely, ANPP in the same system will be low in years 'bad' for these species. Fluctuations in productivity in this hypothetical community would therefore be substantial. In contrast, stability of ANPP might be enhanced on sites containing a diverse mixture of species which encompass an array of competitive and stress tolerance strategies. Aboveground net primary production of the high diversity system would not be as high as that of the low diversity system in certain years, but it would not drop as low in other years.

Changes in the relative growth rates and in the abundance of co-occurring species can therefore stabilize ecosystem processes such as primary production, relative to sites with low diversity, and can maximize resource utilization across heterogeneous landscapes over time (McNaughton 1977, Chapin and Shaver 1985, Collins et al. 1987). For example, C_3 plants are typically active early in spring or fall, whereas C_4 plants maintain growth during the warmest, driest portions of the growing season (Williams and Markley 1973, Ode et al. 1980, Sala et al. 1982). In addition, productivity and species composition of landscapes are regulated by edaphic heterogeneity and topography. Species with contrasting photosynthetic physiologies (or other characteristics) may be spatially distributed in accordance with variation in resource availability along gradients within the community (Barnes and Harrison 1982, Barnes et al. 1983, Archer 1984). As a result, a mixture of C_3 and C_4 species may give more stable and sustained annual productivity than a monoculture of either (Heitschmidt et al. 1986).

Stress Tolerance vs. Competitive Ability

Plant attributes pertaining to stress tolerance and competitive ability (Grime 1979) should be considered when formulating seed mixtures. Distinctions between these 2 general categories of plants (Table 1) are based on the idea that there is an evolutionary relationship between intrinsic growth rate and resource availability. Natural selection in sites characterized by favorable environmental conditions and high resource (water, nutrients, light, etc.) availability should favor plants with rapid growth, because these would be most likely to capture resources and to subject slower-growing species to plant-induced stresses associated with shading and depletion of water and nutrients. However, in environmentally harsh sites and in sites where levels of resources are chronically low, conditions suitable for rapid plant growth may occur infrequently. Natural selection under these conditions would favor adaptations conferring tolerance to prevailing forms of abiotic stress and the ability to conserve resources that have been acquired. As a result, the most productive species or cultivars on sites when resources are plentiful may be the least persistent when resources become limiting (e.g., intermediate wheatgrass *Agropyron intermedium* (Host) Beauv.) is productive on mesic sites, but is susceptible to drought, whereas bulbous bluegrass (*Poa bulbosa* L.) is tolerant of drought, but has low yield potential) (Valentine 1989). Some species, however, combine favorable aspects of both categories, such as crested wheatgrass (*Agropyron desertorum* (Fisch. ex Link) (Shultz.), being tolerant of resource limitations while at the same time being highly competitive in semiarid regions.

Table 1. Characteristics of plants selected for competitive ability versus stress tolerance (from Grime 1979, Chapin 1980, Bryant et al. 1983, Gray and Schlesinger 1983).

Competitive plants	Parameter	Stress-tolerant plants
Competition	Primary Selection Pressure	Abiotic Stresses
High	Intrinsic Growth Rate	Low
High	Root and Leaf Turnover	Low
Low	Root:Shoot Ratio	High
Low	Association with Root Symbionts	High
No	Luxury Nutrient Consumption	Yes
High	Allocation Plasticity	Low
High	Susceptibility to Frost, Drought, and Heavy Metals	Low
Large	Belowground Carbon or Nutrient Reserves	Small
High	Capacity to Regenerate Following Defolition	Low
Low	Integrated Resource Use Efficiency	High
Low	Nutrient Retention in Foliage	High
High	Coupling of Nutrient Release and Uptake	Low

Considerations for Formulating Seed Mixtures

Most-seed mixture research on rangelands has taken a 'shotgun' approach; mix several species together and observe their establishment. Establishment and production of seed mixtures of native plants have been compared with that of introduced species in some instances (Doerr et al. 1983, Redente et al. 1984); however, the criteria for formulating multispecies mixtures is typically based on plant-soil and plant-climate relationships. Consideration of competitive relationships and of compatibility among plants in mixture and among desirable and undesirable species is rare.

Species sown in mixtures should be chosen based on sound ecological evidence that they can coexist. Unfortunately, research that provides this evidence is lacking and is needed in the future. Successful coexistence in many cases will depend on morphological or physiological attributes that enable various species at key stages in their life cycle to partition site resources effectively in space (vertical and horizontal, above- and belowground) and in time (seasonal or phenological). In other cases, coexistence can occur when a species exploits a resource more effectively when the resource is rare, while another enjoys the advantage when the resource is abundant (Armstrong and McGehee 1980). Oscillations in resource and species abundance may occur in these instances. Pattern and scale of spatial variability in resource abundance will also affect assessments of compatibility of potential competitors. If there is sufficient heterogeneity in resource abundance, species that would be competitors in more homogeneous environments may coexist via small-scale spatial segregation (Tilman 1980, 1982).

Seed mixtures that contain species with distinctly superior competitive and/or establishment abilities often produce stands with species abundances different from what would be predicted from the proportions of seed sown of each species (DePuit and Coenenberg 1979, Schuman et al. 1982, Redente et al. 1984). Increasing resource availability through fertilizer application or irrigation typically increases yield (Holechek et al. 1981), but may also reduce species diversity (DePuit et al. 1982, Stark and Redente 1985, Biondini and Redente 1986). This inverse relationship between production and diversity, known as the paradox of enrichment (Rosenzweig 1987), results because the competitive dominants are often better able to capitalize on increased resource availability and can therefore increase their biomass or density at the expense of other species (Huston 1979).

Assessing Competition

The competitive balance between species is influenced by the density and the proportion of the competing species. The experimental design most used for evaluating plant mixtures is that of the replacement series (de Wit 1960); however, this approach has recently come under considerable criticism (Mead 1979, Inouye and Schaffer 1981, Jolliffe et al. 1984, Firbank and Watkinson 1985, Connolly 1986, Taylor and Aarssen 1989). In additive-replacement series experiments, with their associated techniques of numerical analysis (Law and Watkinson 1987, Connolly 1987, 1988), changes in both density and the proportion of the competing species are evaluated and these experiments are currently the standard for evaluating most species interactions (Silvertown 1987). Research using this experimental design has been conducted in glasshouses (Law and Watkinson 1987, Roush et al. 1989), but field experiments are critical for understanding which plants can be successfully grown together.

Mixture experiments also allow the development of zero growth isoclines for populations (Law and Watkinson 1987). These isoclines predict the trajectories of various populations over time. In some mixtures, 1 or more species may be driven to extinction (Fig. 4a), whereas other mixtures may develop a dynamic equilibrium (Fig. 4b). Niche differentiation and differential competitive abilities combine to establish distinct positive and negative associations between species as revegetated rangelands develop through time. Aarssen and Turkington (1985) demonstrate this on pastures of differing ages, initially seeded with similar mixtures (Fig. 5). We should expect species that are positively associated over time to coexist when sown in a common seed mixture.

Facilitation, Coexistence, and Resource Partitioning

Seed mixtures of plants having contrasting patterns of above- and belowground growth enhance partitioning of resources in the community and enhance species diversity. Opportunities exist

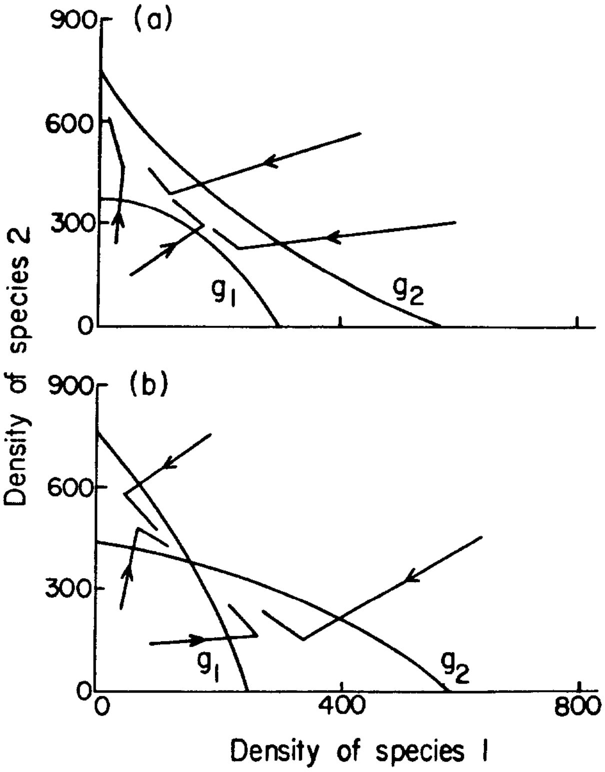

Fig. 4. Zero-growth isoclines for a mixture of 2 hypothetical plant species (g_i) illustrating (a) extinction of species 1 and (b) a dynamic equilibrium between the 2 species. Arrows illustrate several possible time-trajectories for species abundances of the 2 populations (adapted from Law and Watkinson 1987).

within herbaceous growth forms to enhance stratification in reconstructed communities. Mixtures of tall-, mid-, and short-height species with C_3 versus C_4 photosynthetic pathways offer an array of combinations that have potential for enhancing productivity, diversity, and coexistence via vertical and temporal stratification of resources.

On impoverished sites with poorly developed nitrogen cycles, legumes may be sown as early colonizers and as a 'nurse crop'. Once a viable nitrogen cycle has been established and conditions are altered so that other species can establish, the importance of these legumes may diminish and they may be outcompeted by the plants whose establishment they facilitated. In other instances, maintenance or addition of leguminous plants in established stands of highly competitive grasses is a management goal, because they improve forage production and forage quality for animals. Legume survival is often temporary in these situations (Rumbaugh and Pederson 1979, McGinnies and Townsend 1983). Persistence of legumes in stands of grass can depend on levels of both nitrogen and phosphorus and can therefore be influenced by fertilization regimes (Barnhisel 1988). However, over the long-term, when competitive abilities of plants are severely unbalanced and when species overlap in resource needs, then the less competitive population is often driven to extinction. Since the potential exists for species to undergo natural selection for either niche differentiation or for balanced competitive ability (Aarssen 1985), it is likely that plant breeders may be able to improve the coexistence of legumes and grasses. This could be achieved by selecting for traits that balance their competitive abilities or for traits that facilitate their partitioning of limiting resources, thus reducing the need for fertilization.

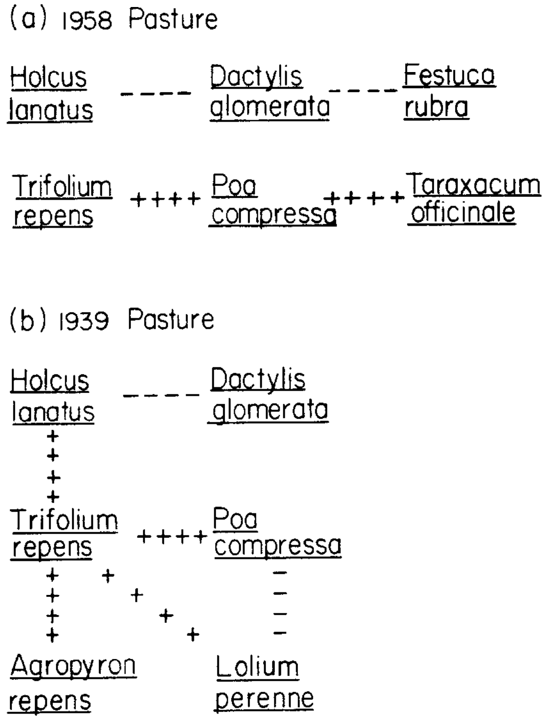

Fig. 5. Species that were positively (++++) and negatively (----) associated with each other in (a) a pasture sown in 1958, and (b) a pasture sown in 1939 (from Aarssen and Turkington 1985).

Shrubs and trees encompass an array of morphological and physiological traits that can contribute to vertical stratification of resources with grasses and forbs. These lifeforms are often considered undesirable on rangelands because they are presumed to reduce herbaceous production or because their presence increases the difficulty of livestock manipulation. Yet, in many regions or landscapes within a region, woody plants are well adapted to prevailing biotic and abiotic conditions. They play a key role in primary production and nutrient cycling while stabilizing soils, creating islands of fertility (Garner and Steinberger 1989), and providing habitat for wildlife (McKell 1989). The negative connotation associated with woody plants may reflect the fact that woody species with desirable characteristics may have been eliminated or reduced in abundance by excessive utilization or by nonselective brush removal and may have been replaced by less desirable species (Fulbright and Beasom 1987, Welch 1989). Selective inclusion of woody plants in restoration plans offers several potential advantages, including:

(1) enhanced herbaceous production (Frischknecht 1963 with rubber rabbitbrush (*Chrysothamnus nauseosus* (Pallas) Britt.); Christie 1975 with poplar box (*Eucalyptus populnea* F. Muell.); Barth and Klemmedson 1978 with algarrobo (*Prosopis juliflora* (Sw.) DC.); Scifres et al. 1982 with huisache (*Acacia farnesiana* (L.) Willd.); Belsky et al. 1989, Weltzin and Coughenour 1990 with umbrella thorn (*Acacia tortilis* (Forsk.) Hayne);

(2) enhanced diversity and seasonal productivity of herbaceous vegetation (Ludwig et al. 1988) by creating microclimates suitable for C_3 grasses in areas otherwise dominated by C_4 grasses (Heitschmidt et al. 1986);

(3) reduced grazing pressure on grasses by providing a refuge for heavily utilized herbaceous species (Welsh and Beck 1976, Davis and Bonham 1979, Jaksic and Fuentes 1980);

(4) enhanced soil nutrient status (Tiedemann and Klemmedson 1973, Charley and West 1975, Kellman 1979), mineralization (Charley and West 1977), water infiltration (Pressland 1973, Brock et al. 1982), snow accumulation (West and Caldwell

1983) and vertical distribution of moisture through hydraulic lift (Richards and Caldwell 1987);

(5) improved habitat for wildlife (Parmenter et al. 1985) and soil microbes (Allen 1988, Urness 1989).

The mode of vegetative regeneration of plants sown as a mixture of species may influence the outcome of species interactions. Clonal propagation is ecologically important for several reasons (Jackson et al. 1985): (1) it enables plants in harsh environments to persist until suitable conditions for viable seed production or seedling establishment are encountered; (2) it enables plants to survive shoot damage resulting from grazing, fire, freezing, or drought stress; and (3) the mode of vegetative growth determines how plants exploit space and resource heterogeneity.

Two primary vegetative growth forms of herbaceous plants are caespitose (e.g., bunchgrasses or tussock grasses) and rhizomatous or stoloniferous (e.g., sod-forming grasses). Lovett Doust (1981) has described these contrasting growth form strategies using the terms 'phalanx' and 'guerilla', respectively. 'Phalanx' species are tightly packed advancing fronts of ramets or tillers that restrict other plants from entering their clonal territory. 'Guerilla' species have either long rhizomes or stolons that allow plants to range over large areas of their habitat. Sutherland and Stillman (1988), using foraging theory, have predicted how patterns of plant growth are affected by the environment that is sampled by 'guerilla' species: (1) the probability of branching will be higher in better environments; (2) branch angles will not change in varying environments; and (3) internode length of stolons or rhizomes will decrease with decreasing quality of the environment. Research supports predictions (1) and (2), and in some cases prediction (3).

Plants with caespitose and rhizomatous growth forms are commonly sown together in seed mixtures (Hull 1971, Schuman et al. 1982, Redente et al. 1984, Biondini et al. 1984/85), yet little is known of their interactions. On a given site, will 'guerilla' species spread more rapidly, capture the greatest space, and exploit small-scale variability in resource abundance better than 'phalanx' species? Or will 'phalax' species more effectively and efficiently garner soil resources than 'guerilla' species? To what extent are these contrasting growth forms compatible and under what conditions?

Species interactions are potential driving forces for successional change. Connell and Slatyer (1977) have proposed 3 models of succession based on species interactions: facilitation, tolerance, and inhibition. In the facilitation model, the entry of new species into a habitat is made possible by other species altering conditions or resource availability. This is particulary true for seed germination and for early seedling survival and is exemplified by the 'nurse plant' phenomenon, whereby established plants protect seedlings of other species from stresses such as grazing, trampling, high temperatures, freezing, and desiccation (Fowler 1986, McAuliffe 1988). Inanimate objects can be used to perform the same functions (Turner et al. 1966, 1969; Steenberg and Lowe 1969). The tolerance model suggests that a predictable sequence of species is produced in a habitat because different species have different strategies for exploiting resources. Species that appear later in succession can tolerate lower resource levels and can grow and reproduce in the presence of earlier species, eventually outcompeting them. Inhibition occurs when a species prevents establishment of other species. Later species gradually accumulate by replacing early individuals when they die.

The above models illustrate that the rate and direction of succession can vary in accordance to the characteristics of the species that inhabit a site. Knowledge of the extent to which certain species may facilitate the ingress or establishment of other species (Yarranton and Morrison 1974; Vasek and Lund 1980; McAuliffe 1984, 1986; Yeaton and Manzanares 1986; Archer et al. 1989; Vitousek and Walker 1989) would be valuable in formulating assembly rules for ordering the introduction of species into a site. Selective use of species that may behave as inhibitors would produce communities resistant to change. Conversely, selective avoidance of the use of such species in restoration would enable succession to proceed more rapidly.

Conclusion

The rangeland revegetation specialists of the future must become the physicians of the land, broadly trained in the biological sciences with an understanding of the mechanisms that drive ecosystems so that they may prescribe the appropriate treatments for a recovery. We should not depend upon a single species as the cure for degraded rangelands any more than a physician would prescibe the same antibiotic to a single patient for all infections. Revegetation requires that we examine the rangeland as a physician would examine an ill patient, then prescribe an appropriate treatment for recovery, while at the same time preparing for potential secondary problems (i.e., invasions of weedy species) that may arise in the future. Part of the examination process is recognizing the interactions that take place among plants and between plants and animals (Archer and Pyke 1991) so that an effective prescription can be applied to degraded rangelands.

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