Gap colonization in grasslands of the Northern Great Plains
by Elibeth Mary Payson

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences
Montana State University

Abstract:
The effects of gap size on colonizer success was examined in two intermountain grasslands during two years. Eight species, four grasses and four forbs with a range of seed size and rooting systems was considered. Gaps ranging from 1 cm2 to 1 m2 were created in two sites. Measurements were taken on plant emergence, survival, biomass, and height on each plant. Environmental factors are examined to help explain the results.

Results indicate that gap size affects plant emergence, survival, biomass, and height. Emergence is little affected by gap size. Survival, especially in drier years, tends to increase with increasing gap size and significantly so when disturbances reach 1 m2. Biomass, an indicator of plant growth, tends to increase with gap size and this increase becomes significant with gap sizes of 1 m2. Another index of plant growth, height, shows similar behavior.

Survival and growth are affected by physical and biological factors. Thus, germination tended to be greater in a moister site. Available water plays an important role in both grasslands.

Key Words: gap colonization, competition, grassland

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ABSTRACT

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Results indicate that gap size affects plant emergence, survival, biomass, and height. Emergence is little affected by gap size. Survival , especially in drier years, tends to increase with increasing gap size and significantly so when disturbances reach 1 m^2. Biomass, an indicator of plant growth, tends to increase with gap size and this increase becomes significant with gap sizes of 1 m^2. Another index of plant growth, height, shows similar behavior.

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INTRODUCTION

Background

Due to intense competition, plants rarely establish in undisturbed vegetation. Disturbance creates gaps which allow change in grasslands through lateral growth of dominants or seeds from mobile natives, mobile exotics (both opportunists), or less mobile natives. We hypothesize that the likelihood of establishment of a plant from a seed increases as the size of disturbance increases, that is, as the probability of reinvasion by competing roots, stolons, or rhizomes diminishes.

Problem Statement

Natural disturbances in grasslands may range in size from worm holes (1 cm^2), hoof prints (10 cm^2), gopher mounds (100 to 1000 cm^2), and elk or bison wallows (1 m^2). The object of this paper was to compare the establishment success of diverse plants in these five hole sizes in two very different grasslands and two very different years. We tested four hypotheses: 1) Germination does not vary with gap size because the limiting resource, water, is abundant in the spring, 2) Establishment and growth is better in larger disturbance sizes. 3) Establishment and growth are better in moister grasslands and moister years, 4.) Forbs establish more easily than grasses in grasslands because their taproots compete less with the diffuse roots of grasses.

The study was conducted in two grasslands, one dry and one wet, over a dry year and a moist year. Success of plants representing varying seed size, rooting strategy, colonizing strategy, and growth form was compared. Our results shed light on community structure, illuminating the role that gaps play in natural community dynamics. We simultaneously show how weeds respond to natural disturbances.

Literature Review

Gaps are places in a plant community where either the shoot or root canopy have been disrupted. These disturbances are normal in grassland ecosystems, and provide space which plants may colonize. Tilman (1982) offers two ways to think of this space. The first is as an open space devoid of other organisms. The second, which he argues as the more pertinent, is as the sum of the resources which it offers. Lieberman and Leiberman (1989) echo this in their article "Forests are not just swiss cheese." Commonly gaps, or disturbances, are considered as a break in an otherwise continuous vegetative cover. Lieberman and Lieberman (1989) argue that this is the wrong supposition, and that to assess the effect of a disturbance, the entire community including gaps, must be included in a comparison of a particular gap to the fabric of a forest. It is beneficial, therefore, to compare grasslands of different densities, because they do not behave similarly. The importance of gaps and patchy landscapes have been emphasized by numerous authors (Tilman, 1982; Pickett and White, 1985a; McConnaughay and Bazzaz, 1987).

Gaps play a central role in community structure, diversity, development, and succession in grasslands. Once considered to be a stable community in which disturbance was infrequent (Clements and Shelford, 1939) researchers have come to recognize the importance of disturbances caused by animals, fire, and erosion (Arno and Gruel, 1983; Daubenmire 1978; Umbanhower, 1991). All three authors assert that the occurrence of fire in grasslands prevents encroachment by trees into the grassland. Disturbances caused by animals to plants or the soil are addressed by many authors as well. (McCaunnaghay and Bazzaz, 1990; Coffin and Lauenroth, 1989; Coffin and Lauenroth, 1990; Coffin and Lauenroth, 1994; Fenner 1980). The nonequilibrium approach, the idea that plant communities are constantly subjected to disturbances and different areas are in vaious stages of recovery, is clear (Reice, 1994). Small scale gaps influence succession by returning parts of a site to lower seral stages, and allowing for colonizer species to invade (Platt, 1975). This creates a mosaic of patches in various levels of succession, and increases diversity.

We will compare growth of first year colonizers over an exponential range of gap sizes which has not been addressed in previous literature. Plants colonize disturbances ranging from less than 1cm^2 to whole agricultural fields. Past studies examining disturbances are summarized below. Umbanhower studied natural colonization of 7.5 dm artificially created mounds in northern prairies (1991) Heterogeneity has been examined at a scale of gaps less than 30 cm (Hook and Lauenroth, 1994a and 1994b; Hook, Burke, and Lauenroth, 1991; Reader, et al, 1994).. In the tall-grass prairie, Platts (1975) studied the effect of badger mounds on succession. The effect of size and frequency of disturbance has been examined by Campbell, Grime, and Mackey (1991), and Coffin and Lauenroth (1988). Monospecific interactions as well as interactions between two species have been examined extensively (Tilman, 1982, 1987; Ang, et al, 1995; Collins and Rhodes, 1994). Neighborhood interactions have received ample treatment (Harper, 1977; Aguilera and Lauenroth, 1993a and 1993b; Fowler, 1988). Patches have also been examined at the scale of landscape level succession (Tilman, 1988; Reice, 1994; Coffin and Lauenroth, 1990; Forman and Godron, 1981).

Colonizer species invade disturbances. Their success depends upon attributes which enable them to germinate, survive, and reproduce in a gap. Varying gap sizes select for different life histories of invading annuals (McConnaughay and Bazzaz, 1987). Several factors influence colonization success in grassland gaps. These are seed size, germination strategy, seedling growth, and regenerative and rooting strategy. The study of colonizer strategy must address individual life stages as success during each influences overall plant performance. Grime states that a plant's success depends upon a combination of these attributes, and that characteristics which are beneficial in one situation may not be beneficial in another (Grime 1979). Plants representing a range of these habits were chosen for this study.

Seed characteristics are important determinants of colonizer strategy. Fenner (1980) studied seed characteristics in relation to plant succession. He found that seed weight increases from early seral to late. He also found that light sensitivity was important in gap colonization. Fenner (1978) asserted that gap colonizers germinate when they detect wide fluctuations in temperature. Temperature extremes are greater in gaps than in canopies. Seeds can detect the presence of openings because of these temperature extremes. In comparing seedling emergence times, the earlier a seed germinated, the more successful a competitor it was (Fowler, 1988, Harper, 1977).

Early seedling growth is also important to colonization success. Large size, and the ability to dominate competitors bestow a great advantage to a plant (Grime 1979). One plant may dominate another by preempting soil resources such as nutrients or water, and intercepting light before it can reach a competitor. Harper (1977) described how the emergence date and growth rate enable a plant to overwhelm competitors by changing a site's physical and chemical characteristics. It is to a colonizing plant's advantage to have rapid seedling growth.

For all lifeforms, the ability to reproduce has been recognized since Darwin as the true measure of an individual's success. Regenerative strategy takes on a number of forms in colonizers. Annuals are common colonizers. They invest energy in rapid growth and seed production. The annual strategy is completely dependent on seed production within one growing season (Grime, 1979). Biennials allow themselves a season to accumulate resources before producing seed, and perennials rely on long term resource allocation and repeated seed production for success.

METHODS

Site Description

The effect of gap size on plant performance and conditions that may influence that success-- site conditions, yearly precipitation, and colonizer species-- were determined. Establishment was compared in two grassland communities. The first, was a *Festuca idahoensis/Agropyron spicatum* (Idaho fescue/ bluebunch wheatgrass) community, was a moist (89 cm/yr ppt.), densely populated grassland with productive soils (Mueggler and Stewart, 1980; Weaver, 1979). This site was located in a pristine field in Bozeman, MT (T2S, R6E, S 21, NE 1/4, NE 1/4). The second was in a *Stipa comata/ Bouteloua gracilis* (needle-and-thread grass/ blue grama) community; with drier (73 cm/yr ppt), finer, less productive soils (Mueggler and Stewart, 1980). This site is three miles west of Logan, MT, near Interstate 90 (T2N, R2E, S26, SE 1/4, SE 1/4). The Idaho fescue/ bluebunch wheatgrass site and the needle-and thread grass/ blue grama site will be referred to as the Idaho fescue (Feid) and blue grama (Bogr) sites respectively.

Data Collection

We tested the effect of gap size on colonization success. To do this, we made gaps in two grasslands over two growing seasons. Study blocks in each grassland were chosen for uniform terrain and visual homogeneity. Small plots ranging in size from 1 cm^2 through 10, 100, 1000, to 10,000 cm^2 were disturbed. In each disturbance size, soil was removed to a depth of 10 cm, sieved with a 1 cm mesh screen and mixed in a central location, and returned to the disturbance. Roots, rhizomes and rocks were removed in the sieve. Uniformity was insured by the use of 1 cm^2 and 10 cm^2 cores for the smaller holes, and careful measurement and excavation with trowels and shovels for larger holes. Soil was removed from all holes, mixed, and returned to insure homogeneity in soil texture, nutrients, and treatment.

Many replications were used to support statistical tests. In 1993, each replication included five 1 cm^2, three 10 cm^2, one 100 cm^2, and one 1000 cm^2 gap. Also, one 10,000 cm^2 disturbance was created for each plant. Five replications were made for each plant at each site. Thus a total of twenty-five 1 cm^2, fifteen 10 cm^2, five 100 cm^2, five 1000 cm^2 and one 10,000 cm^2 disturbances were studied at each site. In the second year more 100 and 1000 cm^2 holes were created. The 10,000 cm^2 disturbances were divided into quarters, and one plant was grown in each quarter. This was done to minimize damage to the site, and create replications at the largest disturbance size. In 1994, five 1 cm^2, three 10 cm^2, two 100 cm^2, and two 1000 cm^2 gaps were created. Again, five replications were planted for each species. Thus, establishment was observed in twenty-five 1 cm^2, fifteen 10 cm^2, ten 100 cm^2, and ten 1000 cm^2 gaps, and four replications of the 1 m^2 gap for each plant in 1994.

Growth was observed between May and August. In 1993, the Idaho fescue sites were planted on 22 May, and the blue grama site was planted on 29 May. Emergence and height measurements were recorded every two weeks. Plants were harvested on 13 August at the Idaho fescue site, and 20 August at the blue grama site. Plant height and weight were documented at harvest. In 1994, seeds were planted earlier to take advantage of early season precipitation. Seeds for most plants were planted at the blue grama site on 7 April and at the Idaho fescue site on 14 April. Corn and sunflower were planted on 10 May at both sites. Emergence, height, stem diameter, and volume were recorded every two weeks throughout the summer. Plants were harvested at the blue grama site on 12 August, and at the Idaho fescue site on 23 August. When harvested, plant height, canopy width, stem diameter, and weight were measured.

Eight species were studied. In 1993 knapweed (*Centaurea maculosa*) and wheat (*Triticum aestivum* cultivar Winridge) were planted. In 1994, we wanted to contrast performance of a greater variety of plant species. We planted four grasses: wheat (*Triticum aestivum* cultivar Winridge), cheatgrass (*Bromus tectorum*), crested wheatgrass (*Agropyron cristatum*), and corn (*Zea mays* cultivar Silver bullet), and four forbs: spotted knapweed (*Centaurea maculosa*), yellow sweet clover (*Melilotus officinalis*), shepherd's purse (*Capsella bursa-pastoris*), and sunflower (*Helianthus annuus* cultivar Giant Greystripe). Nomenclature follows Hitchcock and Cronquist (1973) and Gould and Shaw (1983). These plants were chosen for their range of seed size, rooting strategy, lifeform, and colonization strategy. Table 1 summarizes the species' characteristics.

Grasshoppers destroyed many plants during the 1993 field season. To minimize this, we treated the sites with Sevin insecticide on bran bait every two weeks in 1993. Control was inadequate, so in 1994, sites were treated each week.

Establishment and growth differences across gap size might be due to differences in light, temperature, or resource (water and nutrient) availability. These characteristics were therefore measured across gap sizes. Light intensity was compared across gap sizes using the Friend (1961) method. Twenty-five sheets of blueprint paper, 2.5 cm x 2.5 cm, were assembled into booklets and wrapped in black construction paper envelopes. A 0.4 cm hole was punched in the envelope with a hole punch, so light could penetrate only in this spot. These envelopes were placed in 4 cm petri dish to exclude rainfall. Five of these were placed in each disturbance size for 24 hours. After removal, the papers were kept together in their black construction paper envelopes and developed with ammonium hydroxide fumes for 15 minutes. Light exposed areas become yellow and unexposed areas are blue. The number of exposed sheets were counted as an index of light intensity. The light levels in the different disturbance sizes were compared with analysis of variance.

Soil moisture was measured on three dates throughout the 1994 field season (Idaho fescue site: 5/15/94, 7/22/94, and 9/8/94; blue grama site: 5/24/94, 7/15/94, and 9/8/94). Samples were collected to a depth of 10 cm from each gap size and placed in a lined paper bag. Three bags were taken from each gap size on each date, except June 15, in Bozeman, when only two bags per gap were collected. Moist weights were recorded, then samples were dried in an oven at 60 C for 2 weeks, then dry weights were taken. Soil moisture % was calculated as grams of water divided by grams of soil. Temperature was measured in each gap size onfour dates. We do not present this data because effects of time of day confounded effects of gap size.

Analysis

Each year's data were analyzed separately. In addition a pooled analysis of knapweed and wheat over both years was performed. The 1993 analysis shows how wheat and knapweed respond to a wet year, 1994 data show how they respond to a dry year, and simultaneous analysis illuminates the difference between an exceptionally wet and a dry summer. 1994 analysis of other plants permits comparison of gap size effects on different species of plants in a dry year. Effect of disturbance size, grassland type, and lifeform was determined for individual species and for all plants together.

Data sets were first tested for normal distributions and equal variance using the Wilks-Shapiro test (Winer, 1962) and Hartley's test respectively (Neter, Wasserman, and Kutner, 1990). Additionally, residuals were graphed against normal scores, gap size, and fitted values to visually confirm normality and equal variance.

Emergence was related to gap size, emergence date, and species on plant emergence percentages using Kruskall-Wallace (Neter, Wasserman, and Kutner, 1990) and Mann-Whitney tests (Neter, Wasserman, and Kutner, 1990). Differences in emergence across disturbance size, dates, and species were analyzed as categorical variables using Kruskall-Wallace analysis of variance on ranks and Dunn's test for multiple pairwise comparisons (Winer, 1962). This non-parametric test was used because these data were not normally distributed. Since there was no reason to believe that a trend would exist between disturbance sizes, dates, or species, analysis of variance was appropriate. Dunn's test for pairwise comparisons was used for all Kruskall Wallace tests, since it can be used with non-parametric tests and on unequal sample sizes. Mann-Whitney tests (Neter, Wasserman, and Kutner, 1990) were used to compare plant treatments, years, and sites in 1993.

Plant survival was related to gap size, site, year, and species using analysis of variance and Tukey's pairwise comparisons (Neter, Wasserman, and Kutner, 1990). All possible combinations of factors and their interactions were tried, and this was the best model. This test was conducted on 1993 and 1994 data separately, and on the 1993-1994 knapweed and wheat data together with the addition of the year factor included.

Height and weight responses to gap size, site, species, and year were treated as categorical variables using analysis of variance and Tukey's pairwise comparisons. The Box-Cox procedure was used to find the best transformation of the data for analysis of variance (Neter, Wasserman, and Kutner, 1990). Based on this, the log transformation was used for anovas. The appropriate Anova model used the response variable, log (weight or height), and the factors site, gap size, species, and year. Before analysis, the mean of responses for each species at each gap size was calculated and used in anova. This created equal sample sizes, one of the assumptions for Tukey's pairwise comparisons.

Differences in biomass and height across gap size, site, year, species, and habit were also treated as continuous variables to which regression analysis was applied. Single species weights and heights were regressed against site, log(gap size), and log(gap size)^2 for the 1993 and 1994 data separately. To compare wheat and knapweed growth in the two years, each plant's weight and height were regressed against site, year, log(gap size), and log(gap size)^2. Examination of residual distribution indicated that these same factors provided the best fit line for most other species. In some cases, the best fit line did not include all of these factors (year was only used in comparing knapweed and wheat responses both years), or the log of plant height or weight yielded a better expression of the data (less the 50% of height data are log transformed). This is indicated in the results.

The Durbin-Watson test was used to test for autocorrelation (Neter, Wasseman, and Kutner, 1990)

Performance of grasses and forbs was also contrasted with regression; Partial F tests were used to compare the performance of grasses versus forbs. This analysis was conducted on the 1994 height and weight data only. The log of plant weight or height was regressed against the log of gap size, log of disturbance size squared, a code of 1 or 0 for forb or grass respectively, and an interaction term for this code and hole size. An F statistic comparing the ratio of (the sum of squared error attributed to the interaction of hole size and plant habit divided by its degree of freedom) to (the sum of square error for the model divided by its degrees of freedom) to test for differences between the lifeforms.

Individual species height and weight responses to gap size and site for both years were analyzed using one way anovas. Transformations were applied where appropriate. Some species were left untransformed, some were transformed with the log transformation, and for those which the log transformation did not normalize distributions or equalize the variance, non- parametric Kruskall Wallace tests were used (Neter, Wasserman, and Kutner, 1990). To make pairwise comparisons, Dunn's test, which can be employed on unequal sample sizes and non-parametric tests Mann-Whitney tests were used (Neter, Wasserman, and Kutner, 1990).

The light intensity data were analyzed with analysis of variance and Bonferroni's multiple pairwise comparisons. Data were normally distributed.

Soil moisture was analyzed with Kruskall Wallace anova on ranked data, except for the blue grama June moisture which was normally distributed. Dunn's test was used for Kruskall-Wallace tests and a Bonferroni's test was used for the parametric anova.

The effect of grasshopper control was analyzed in 1994 using the signed rank sum test for difference in means (Neter, Wasserman, and Kutner, 1990).

SAS (1995) was used for the Box-Cox procedures and for the multi-species ANOVAs, and Sigma Stat (1994) was used for single species ANOVA's and Kruskall Wallace tests. Regressions and the corresponding analysis of residual normality were run in Minitab (1994). Soil moisture and light intensity were analyzed in SigmaStat (1994).

RESULTS

Introduction

The effects of gap size, site, year, and species on the emergence, survival, biomass, and height of colonizers were measured. These are presented in the first section of the results. Environmental conditions of the sites, including precipitation, light intensity in the gaps, and grasshopper herbivory, which may have contributed to the establishment differences among gap size, site, and year, were also measured. These are presented in the second section of the results.

Plant Performance

Emergence Response to Gap Size, Site, Species, and Year

In 1993, gap size was a significant predictor of emergence (p=0.006, Table 2). Emergence in 1cm^2 disturbances was significantly lower than in 100 cm^2 and 1m^2 gaps (p=0.05, Table 2). All other comparisons showed response to disturbances was similar. In 1993, there was no difference in emergence at the two sites (p=0.649, Table 2). Emergence within single sites could not be analyzed in 1993 because there were only two responses for each site. There was no statistically significant difference between knapweed and wheat emergence (p=0.956). The dates on which observed emergence was greatest were 6/4/93 and 6/11/93 (Table 3). Emergence was significantly greater on these dates than on later dates (p=0.05, Table 3), when no plants emerged.

In 1994, disturbance size had no significant effect on emergence (Table 2). Emergence at the Idaho fescue site was significantly higher than at the blue grama site in 1994 (Table 2 footnote). Shepherd's purse emergence, both total and surviving, were the only percentages significantly different from other species (Table 4). Emergence was higher in 1993 than 1994 (p=0.001, Table 4 footnote). Emergence differed among dates as in 1993. That is, significantly more plants emerged between 5/26/94 and 6/4/94 than on other dates sampled (Table 3). Survival of cohorts from these germination dates was also significantly higher than on other dates.

Survival Response to Gap, Site, Species, and Year

In moist 1993, the Anova model relating plant survival to disturbance, species, and site as factors was not significant (p=0.13, Table 5) Although the overall model was not significant, site had some predictive power at (p=0.04, Table 6). Neither disturbance size (p=0.18) nor species (p=0.89) was significant in the model.

In dry 1994, analysis of variance on percentages of plants which survived showed that disturbance size, site, and species all influenced plant survival at p=0.0001 (Table 7). Survival was highest in the 1 m^2 disturbances and second highest for 1 and 10 cm^2 disturbances, and the lowest was in the 1000 cm^2 gaps (Table 8). Survival was greater at the Idaho fescue site than the blue grama (p=0.05). In 1994, seven of the eight species seeded survived (Table 8); no shepard's purse survived at either site.

To determine whether survival of grasses and forbs differed, an analysis of