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Vegetational changes under isolated Juniperus virginiana in an eastern Nebraska bluestem prairie.

Janet L. Gehring

VEGETATIONAL CHANGES UNDER ISOLATED *JUNIPERUS VIRGINIANA* IN AN EASTERN NEBRASKA BLUESTEM PRAIRIE

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Janet L. Gehring
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THESIS ACCEPTANCE

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Committee

Name	Department
David M. Sutherland	Biology
Larry J. Stephens	Math/CS

Thomas B. Bragg
Chairman

11 July 1983
Date

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ABSTRACT

Changes in species composition of a bluestem prairie were evaluated under isolated, 10-22 year old *Juniperus virginiana* (Eastern Red Cedar) in eastern Nebraska. Percent canopy cover was measured in full-canopy, canopy-edge, and open-canopy plots which were located along transects oriented to the cardinal compass directions. A total of 53 species were recorded. *Andropogon scoparius* and *A. gerardii* dominated open-canopy and canopy-edge plots; *Poa pratensis* and *A. scoparius* dominated full-canopy plots. Canopy cover of most prairie species decreased under full canopy but *Poa pratensis* and *Carex* spp. increased. There was a positive correlation between tree size and both the decrease of prairie species and the increase of *Poa pratensis* under a full-canopy. Similarly, aspect was significantly correlated to changes in species composition under a full-canopy. For those species with significant differences between cardinal directions, canopy cover was lowest on the north and east transects. The results of this study show that invasion of woody plants into native prairie rapidly affects the composition of native grassland species.

INTRODUCTION

Fire was a major environmental factor affecting the bluestem prairie (Küchler 1964) that once dominated much of the eastern portion of the North American grasslands. Extensive reviews of the effects of fire have been conducted by Daubenmire (1968) and Vogl (1974). Among the many effects noted is that fire inhibits woody plant invasion of prairie by directly killing or injuring many species of trees and shrubs (Kucera 1960, Blan 1970, Bragg and Hulbert 1976) and indirectly by reducing available soil moisture for seedlings (Hulbert 1969).

Grassland species can be divided into two main groups according to their mode of carbon fixation during photosynthesis: C_3, or cool-season and C_4, or warm-season (Williams 1974, Waller and Lewis 1979). C_4 species are thought to have a competitive advantage under conditions of high light, high temperature, and decreased moisture (Bjorkman 1971, Black 1971). Although C_3 and C_4 species often grow in the same habitat, most of the dominant species of bluestem prairies in eastern Nebraska possess the C_4 pathway (Waller and Lewis 1979). Moderation of the microenvironment by invading woody plants may cause the C_4 species to lose their advantage due to the effects of shading. Thus, under these modified conditions, species composition should reflect an increasing proportion of C_3

plants under the tree canopy. In addition, one of the major non-native invaders of bluestem prairie, Poa pratensis L. (Kentucky bluegrass) (Weaver 1965), is a C_3 species which may also be favored by the conditions created by invading woody plants. Changes in plant species composition under invading woody plants has been studied in other grassland ecosystems (Arnold 1964, Jameson 1966) as well as under trees in savanna ecosystems (Bray 1955, Parker and Muller 1982). No such studies, however, have been documented for the bluestem prairie of eastern Nebraska.

The objective of this study was (1) to document changes in species composition under invading trees and (2) to test the hypothesis that there is a correlation between the invasion of woody species and changes in species composition that reflect the effects of different photosynthetic pathways.

METHODS AND MATERIALS

Study Site:

The study was conducted on a native prairie located on bluffs adjacent to the Platte River Valley in southeastern Sarpy County, Nebraska (W1/2Sec34 T13N R10E). The bluffs are generally west-facing with 17 to 30 percent slopes. The loessal soils are Ida silt loams, low in organic matter and nitrogen, mildly to moderately alkaline, and well-drained (Bartlett 1975). Precipitation averages 71 cm annually with 78% of the precipitation falling during the growing season. Average temperatures range from -6 C in January to 24 C in July (U.S. Department of Commerce 1981).

The study area was chosen because (1) the prairie was mostly undisturbed and not presently or recently grazed, and (2) isolated _Juniperus virginiana_ L. (Eastern Red Cedar), a common early invader of tallgrass prairie, was found on the slopes and ridgetops.

Data Collection:

Six separate south- or southwest-facing slopes were selected as study sites, based on their having representative native prairie vegetation and an appropriate number and size of isolated trees. Trees were considered isolated if neighboring trees did not cast shadows on them during the majority of the day. Within each study area, six trees of approximately the same size were selected and marked with surveyor's flagging. An increment core was extracted near the base of each tree to provide an estimate of the time of its establishment and hence a measure of the length of time that microclimatic changes had affected plant composition. Ring counts were made on each core using standard techniques (Stokes and Smiley 1968). Other data recorded at each tree included tree canopy radius, the distance from the main tree stem to canopy edge, and percent slope.

Four transects were established at each tree, one for each of the cardinal compass headings. Cardinal direction was considered to be an important factor, not only because of solar angle, but also because of steep slopes at the study area. Three 20 x 50 cm plots were located along each transect with the long axis parallel to the canopy edge. One plot was located 70 cm from the main tree stem, one at the edge of the canopy, and one 70 cm outside of the canopy. These represent full-canopy, canopy-edge, and open-canopy plots respectively and, in combination, are termed successional plots. Open-canopy plots were considered to be the control. Each plot was evaluated once between July 24 and August 6, 1982. Data recorded for each plot included total vegetative cover, total grass cover, total forb cover, and total woody plant cover, as well as percent canopy cover by species. Canopy coverage categories were 0-5%, 5-25%, 50-75%, and 95-100% (Daubenmire 1959). Data were analyzed using mid-point values for each coverage category. Dominant species are defined as (1) the two species with the highest mean canopy cover for each group of successional plots and (2) any additional species within five percent canopy cover of these species.

Plant identifications were verified at the University of Nebraska at Omaha Herbarium (OMA). Common and scientific names are from Great Plains Flora Association (1977), and Sutherland (In press).

Data Analysis:

Vegetative diversity for each group of successional plots was calculated using the Shannon-Wiener Diversity Function (H') where H'=pi(logpi) and pi=the relative canopy coverage value of each species; high H' values indicate high diversity (Krebs 1978). Pearson's Correlation Coefficient, *r*, was used to determine the strength of linear relationships between two variables (Ott 1977). The Kruskal-Wallis test, a non-parametric procedure, was used for statistical analysis on canopy cover data of individual species because of unequal variance in the data (Ott 1977).

Transformation of the data was used to reduce variability and normalize canopy cover data. This involved dividing total grass cover by mean canopy cover of *Poa pratensis* and by the sum of mean values for all other grasses. Data from this manipulation are termed "transformed-percent-cover." Grasses that were combined included *Andropogon gerardii* Vitman (Big Bluestem), *A*.

scoparius Michx. (Little Bluestem), *Bouteloua curtipendula* (Michx.) Torr. (Side-oats Grama), *B. hirstua* Lag. (Hairy Grama), *Dichanthelium oligosanthes* var. *scribnerianum* (Nash.) Gould (Scribner Panicum), *D. wilcoxianum* (Vasey) Freckman (Wilcox Panicum), *Festuca octoflora* Walt. (Six-weeks Fescue), *Koeleria pyramidata* (Lam.) Beauv. (Junegrass), *Muhlenbergia cuspidata* (Torr. in Hook) Rydb. (Plains Muhly), *Paspalum setaceum* Michx., and *Sorghastrum nutans* (L.) Nash (Indian grass). *Poa pratensis* was analyzed separately because it was the only grass that increased significantly under the tree canopy. Transformed-percent-cover of *Poa pratensis* and of other combined grasses were tested using an Analysis of Variance (ANOVA) (Nie *et al.*, 1975). All statistical hypotheses were considered significant if $p \leq 0.05$.

RESULTS

A total of 53 species were recorded in 432 plots (Appendix Table I). Fourteen species averaged greater than 10% and 25 species averaged less than 1% frequency. *Andropogon scoparius* and *A. gerardii* dominated in open-canopy and canopy-edge plots; *Poa pratensis* and *Andropogon scoparius* dominated in full-canopy plots (Table 1). In addition, eight species of woody plant seedlings were recorded in the study plots: *Acer negundo* L. (Box Elder), *Cornus drummondii* Mey. (Rough-leaved Dogwood), *Fraxinus pennsylvanica* Marsh. (Green Ash), *Juniperus virginiana*, *Quercus macrocarpa* Michx. (Bur Oak), *Ribes missouriense* Nutt. (Missouri Gooseberry), *Symphoricarpos orbiculatus* Moench (Buckbrush), and *Ulmus* spp. (Elm).

Canopy cover of 16 species differed significantly between full-canopy, canopy-edge, and open-canopy plots. For 11 of these species, the lowest mean percent cover occurred in full-canopy plots; values averaged highest in full-canopy plots for *Poa pratensis*, *Carex* spp., and *Juniperus virginiana* (Table 1). Changes in *Andropogon scoparius*, a warm-season, C_4 grass, and *Poa pratensis*, a cool-season, C_3 grass, represent the major patterns observed (Fig. 1). *Dichanthelium oligosanthes* var. *scribnerianum*, also a C_3 species like *Poa pratensis*, decreased under the tree canopy. A regression of transformed-percent-cover of the full-canopy

Table 1. Mean percent canopy cover $\pm$ SE for species with significant differences ($p<0.05$) in distribution between successional plots based on Kruskal-Wallis Analysis of Variance: tr$\leq$0.5% cover. H'= Shannon-Wiener function for combined successional plots. Values represent combined data for all six study sites.

FLORISTICS	SUCCESSIONAL PLOTS		
	Full-Canopy	Canopy-Edge	Open-Canopy
SPECIES DIVERSITY (H')	2.586	2.706	2.622
SPECIES:			
Andropogon scoparius (Little Bluestem)	10.3$\pm$1.42	38.4$\pm$2.31	43.7$\pm$2.34
Poa pratensis (Kentucky Bluegrass)	19.1$\pm$1.54	10.1$\pm$1.18	6.4$\pm$0.91
Aster ericoides (White Aster)	tr	3.6$\pm$0.49	5.0$\pm$0.62
Bouteloua curtipendula (Side-oats Grama)	3.9$\pm$0.84	8.6$\pm$1.24	5.6$\pm$0.91
Dichanthelium oligosanthes var. *scribnerianum* (Scribner Panicum)	0.8$\pm$0.16	2.8$\pm$0.37	2.6$\pm$0.48
Andropogon gerardii (Big Bluestem)	3.6$\pm$0.84	15.4$\pm$2.16	13.8$\pm$2.03
Ambrosia psilostachya (Western Ragweed)	tr	0.8$\pm$0.16	0.8$\pm$0.16
Carex spp. (Sedge)	1.2$\pm$0.27	tr	tr
Solidago spp. (Goldenrod)	tr	0.6$\pm$0.05	0.6$\pm$0.07
Bouteloua hirsuta (Hairy Grama)	tr	2.3$\pm$0.67	2.3$\pm$0.20
Linum rigidum (Flax)	tr	0.4$\pm$0.07	0.6$\pm$0.12
Lygodesmia juncea (Skeleton Weed)	tr	tr	0.8$\pm$0.19
Petalostemum purpureum (Purple Prairie Clover)	tr	0.6$\pm$0.19	1.1$\pm$0.30
Juniperus virginiana seedlings (Eastern Red Cedar)	0.8$\pm$0.21	tr	tr
Calylophus serrulatus (Yellow Evening Primrose)	tr	tr	tr
Hedeoma hispida (Rough Penneyroyale)	tr	tr	tr

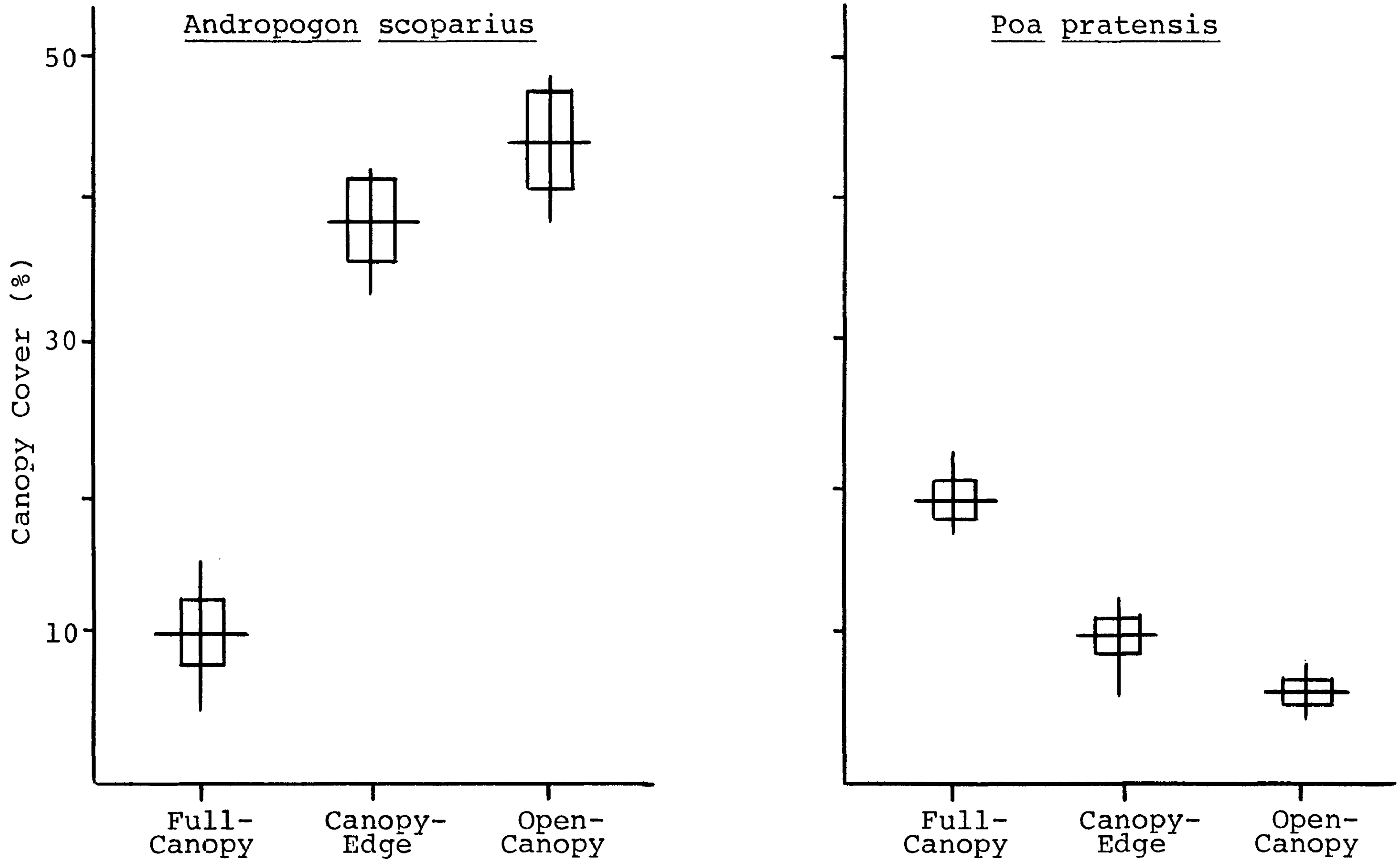

Figure 1. Mean percent canopy cover for *Andropogon scoparius* and *Poa pratensis*. Horizontal lines represent mean values, vertical lines connect maximum and minimum values, and vertical bars represent one standard error.

plots onto canopy radius, which reflects the length of time that full-canopy plots have been affected, further documents the sequential loss of prairie grasses (r=-.597, p=.005) and the increase of Poa pratensis (r=.555, p=.005) (Appendix Fig. 1-2). No correlation was observed for open-canopy and canopy-edge plots.

Significant differences were found between sites for all successional plot groups indicating that plant species composition varied somewhat between study sites despite their topographic similarity.

The effect of plot direction from the main tree stem was analyzed in several different ways. Firstly, of the six most abundant species, the greatest number of significant, between-site variations was found for west aspect successional plots (Appendix Table II). Secondly, between-plot differences were separated by direction to assess the contribution of direction to between-plot differences for each species. West transects had the least number of significant differences (5), with increasing numbers of differences for south (8), north (11), and east (12). Thirdly, without transformation of data, Kruskal-Wallis analysis of variance resulted in relatively few significant between-aspect differences for each of the three plot groups for individual species. For those species, canopy cover was lowest on the north and east transects. Fourthly, after data transformation, aspect was found to be a significant factor for both *Poa pratensis* ($p=0.02$) and for other combined grasses ($p=0.005$). Interaction between plot and aspect was also significant for both groups (Appendix Table III).

The approximate age of trees chosen for the study ranged from 10-22 yr. Canopy radius increased with tree age ($r=0.523$, $p=.005$).

DISCUSSION

Grassland species are substantially affected by invading trees with the main effect occurring after complete coverage by the tree canopy. Two distinct patterns were found, one negative and one positive. All native prairie species decreased under full canopy with the exception of *Carex* spp. which increased. *Poa pratensis*, a non-native C_3 species, also increased as the tree canopy increased. This response has been reported to occur under other conditions such as drought and overgrazing where native prairie species decrease in abundance (Weaver 1965) thus supporting the idea that its increase may be a response to release from competition.

Tree size is an important factor particularly as it relates to time period of canopy influence. There is a sequential loss of native prairie species as they are covered by the canopy for longer periods of time. The largest trees had low vegetative cover under full-canopy, indicating that eventually no grassland species can grow under the environmental conditions that exist directly under the tree. As the tree canopy increases its influence, the area in which native prairie species are eliminated will increase.

Photosynthetic pathway was not an important predictive factor for negative or positive response under full-canopy. Of the two C_3 species that had sufficiently large populations to allow for statistical comparison, *Poa pratensis* increased under full-canopy whereas *Dichanthelium oligosanthes* var. *scribnerianum* decreased. One other native C_3 grass species, *Koeleria pyramidata* (Junegrass), was recorded in low abundance in canopy-edge and open-canopy plots and was absent under full-canopy. Other ecological factors may account for these different responses, of which some possible explanations include phytotoxity of *Juniperus virginiana* (Rice 1974), effects of tree litter (Jameson 1963, 1966, Rice 1974), and changes in water availability due to rainfall interception (Anderson *et al*. 1969). Any or all of these factors may act in conjunction with shading effects to cause the observed response to canopy closure. At least for some species these factors may mask the contribution of the type of photosynthetic pathway to declines in species cover.

The effects of aspect, or the cardinal direction from the main tree stem, were observed for a limited number of species due to high variation in the data. For those species with significant differences, canopy cover was lower on the north and east transects when compared to south and west transects, indicating solar angle was a factor. The combined data analysis of variance reinforced the importance of aspect.

The general results of this study show that, even when woody plant invasion is restricted to isolated trees, there is an effect on species composition of the prairie that is affected by aspect and increases as invasion continues. Further, the presence of woody plant seedlings in the study plots indicates that a single invader, such as *Juniperus virginiana*, provides a favorable environment for the establishment of other woody plants. In combination, the increase in woody plants and the decline in prairie species reaches a point where the one-time prairie will be irretrievably changed. Ecosystem managers need to be aware of these effects and the rate of changes in species composition so as to prevent excessive invasion and coincident loss of native species from areas intended to be maintained in their pristine state.

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APPENDIX

Appendix Table I. Floristics of study plots, 1 = full canopy, 2 = canopy edge, 3 = open canopy, N = north, S = south, E = east, W = west, TR=<0.1% for relative frequency.

Species:	% Rel. Freq.	Mean percent canopy cover ± SE											
		1-N	2-N	3-N	1-S	2-S	3-S	1-E	2-E	3-E	1-W	2-W	3-W
Andropogon scoparius	82	5.1 ±1.63	39.8 ±5.16	45.2 ±4.65	13.9 ±3.26	35.6 ±4.39	45.8 ±4.86	7.0 ±2.45	40.9 ±4.58	45.5 ±4.87	15.3 ±3.42	37.4 ±4.42	38.5 ±4.37
Poa pratensis	74	19.2 ±2.90	11.6 ±2.11	6.58 ±1.64	18.7 ±3.06	6.5 ±2.25	3.9 ±1.29	19.7 ±2.99	9.4 ±2.01	7.56 ±2.20	18.9 ±3.47	12.9 ±2.93	7.5 ±2.02
Aster ericoides	56	.3 ± .12	2.9 ± .74	4.3 ±1.31	.8 ± .17	4.6 ±1.02	4.6 ± .95	.3 ± .12	3.7 ±1.24	6.0 ±1.40	.6 ± .16	3.1 ± .82	5.0 ±1.32
Bouteloua curtipendula	55	1.7 ± .69	2.3 ± .78	5.6 ±1.29	7.4 ±2.75	14.3 ±3.47	6.2 ±2.05	1.4 ± .58	8.5 ±2.04	4.6 ±1.57	5.1 ±1.58	9.5 ±2.52	7.8 ±2.25
Dichanthelium oligosanthes var. *scribnerianum*	51	.5 ± .15	2.1 ± .55	2.7 ± .95	.6 ± .15	3.4 ± .89	2.1 ± .68	1.1 ± .43	2.9 ± .74	3.8 ±1.23	1.1 ± .43	2.6 ± .76	1.78 ± .57
Andropogon gerardii	33	3.6 ±1.18	19.7 ±4.49	13.2 ±3.43	4.7 ±2.25	9.5 ±3.34	8.4 ±2.9	2.2 ± .87	17.2 ±4.62	16.5 ±4.56	5.2 ±2.04	15.2 ±4.73	16.9 ±5.00
Ambrosia psilostachya	26	.2 ± .09	.8 ± .13	.8 ± .15	.2 ± .11	1.0 ± .43	.8 ± .43	.3 ± .12	1.2 ± .43	1.1 ± .43	.3 ± .13	.7 ± .16	.7 ± .16
Carex spp.	23	2.1 ± .78	1.0 ± .43	.5 ± .12	1.3 ± .58	.2 ± .11	.3 ± .13	.9 ± .43	.3 ± .12	.4 ± .14	.6 ± .16	.6 ± .15	1.2 ± .58
Solidago spp.	20	.1 ± .08	.28 ± .12	.6 ± .16	.4 ± .13	2.8 ± .43	.5 ± .15	0.0 ± .00	.9 ± .43	.6 ± .15	.2 ± .11	.6 ± .15	.5 ± .15

Appendix Table I. Floristics of study plots (continued). Mean percent canopy cover ± SE, and relative frequency.

Species:	% Rel. Freq.	Mean percent canopy cover ± SE 1-N	2-N	3-N	1-S	2-S	3-S	1-E	2-E	3-E	1-W	2-W	3-W
Bouteloua hirsuta	17	1.0 ±1.06	0.4 ± .42	2.3 ± .87	0.4 ± .42	7.0 ±2.41	4.1 ±1.33	0.5 ± .42	0.5 ± .42	0.6 ± .42	0.1 ± .06	1.2 ± .58	2.4 ± .86
Linum rigidum	16	0.0 ± .00	0.1 ± .06	0.4 ± .14	0.0 ± .00	.6 ± .16	1.1 ± .43	0.0 ± .00	0.2 ± .11	0.5 ± .15	0.1 ± .06	0.9 ± .17	0.3 ± .13
Lygodesmia juncea	15	0.0 ± .00	0.3 ± .12	0.6 ± .16	0.2 ± .09	0.8 ± .43	0.9 ± .43	0.1 ± .06	0.3 ± .12	0.8 ± .43	0.1 ± .08	0.3 ± .13	0.8 ± .43
Petalostemum purpureum	12	0.0 ± .00	0.1 ± .08	1.8 ± .79	0.1 ± .06	1.2 ± .58	1.1 ± .58	0.0 ± .00	0.7 ± .43	0.9 ± .58	0.1 ± .06	0.3 ± .13	0.5 ± .42
Juniperus virginiana	11	1.4 ± .58	0.3 ± .12	0.1 ± .08	0.3 ± .12	0.0 ± .00	0.0 ± .00	1.2 ± .58	0.1 ± .08	0.1 ± .08	0.3 ± .13	0.2 ± .09	0.1 ± .06
Echinacea angustifolia	9	0.0 ± .00	0.2 ± .11	0.3 ± .12	0.1 ± .08	0.1 ± .06	0.2 ± .11	0.1 ± .08	0.2 ± .09	0.2 ± .11	0.2 ± .09	0.3 ± .13	0.17 ± .09
Muhlenbergia cuspidata	6	0.0 ± .00	1.1 ±1.06	1.7 ±1.72	0.4 ± .42	0.4 ± .42	0.4 ± .42	0.0 ± .00	0.4 ± .42	0.5 ± .42	1.1 ±1.06	0.1 ± .06	0.0 ± .00
Anemone cylindrica	5	0.2 ± .09	0.2 ± .09	0.1 ± .06	0.2 ± .11	0.1 ± .06	0.0 ± .00	0.6 ± .42	0.1 ± .06	0.1 ± .08	0.1 ± .06	0.1 ± .06	0.1 ± .08
Erigeron strigosus	5	0.1 ± .06	0.1 ± .06	0.0 ± .00	0.1 ± .06	0.1 ± .06	0.1 ± .08	0.1 ± .06	0.2 ± .09	0.2 ± .11	0.0 ± .00	0.1 ± .08	0.2 ± .11

Appendix Table I. Floristics of study plots (continued). Mean percent canopy cover ± SE, and relative frequency.

Species:	% Rel. Freq.	Mean percent canopy cover ± SE											
		1-N	2-N	3-N	1-S	2-S	3-S	1-E	2-E	3-E	1-W	2-W	3-W
Strophostyles leiosperma	4	0.0 ± .00	0.1 ± .08	0.1 ± .06	0.1 ± .08	0.2 ± .09	0.1 ± .08	0.1 ± .06	0.0 ± .00	0.0 ± .00	0.1 ± .06	0.2 ± .09	0.2 ± .11
Dichanthelium wilcoxianum	4	0.0 ± .00	0.0 ± .00	0.1 ± .06	0.1 ± .08	0.5 ± .42	0.0 ± .00	0.0 ± .00	0.1 ± .06	0.0 ± .00	0.1 ± .06	0.2 ± .09	0.9 ± .58
Antennaria neglecta	3	.9 ± .58	0.0 ± .00	.2 ± .09	.1 ± .06	.1 ± .06	.1 ± .06	1.1 ±1.06	.5 ± .42	.1 ± .06	.1 ± .06	0.0 ± .00	0.0 ± .00
Verbena stricta	3	.1 ± .06	0.0 ± .00	.1 ± .06	0.0 ± .00	.1 ± .06	.1 ± .06	.1 ± .06	.2 ± .11	0.0 ± .06	0.0 ± .00	.1 ± .06	.1 ± .06
Calylophus serrulatus	2	0.0 ± .00	.1 ± .08	.1 ± .08	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00	.1 ± .06	.1 ± .08	0.0 ± .00	0.0 ± .00	.2 ± .09
Hedeoma hispida	2	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.2 ± .09	.7 ± .56	0.0 ± .00	.1 ± .08	0.0 ± .00	0.0 ± .00	.1 ± .08	.1 ± .06
Euphorbia marginata	2	0.0 ± .00	0.0 ± .00	.1 ± .06	.1 ± .08	0.0 ± .00	.1 ± .06	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00	.1 ± .08	.1 ± .06
Cornus drummondii	2	.1 ± .06	0.1 ± .06	.4 ± .42	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ±. 08	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00
Gaura coccinea	1	0.0 ± .00	0.0 ± .00	.1 ± .06	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	.1 ± .06	.1 ± .06	.1 ± .06	0.0 ± .00

Appendix Table I. Floristics of study plots (continued). Mean percent canopy cover ± SE, and relative frequency.

Species:	% Rel. Freq.	Mean percent canopy cover ± SE 1-N	2-N	3-N	1-S	2-S	3-S	1-E	2-E	3-E	1-W	2-W	3-W
Sisyrinchium campestre	1	0.0 ± .00	.1 ± .06	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .08	0.0 ± .00	.1 ± .06
Physalis seedling	1	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	0.0 ± .00	.1 ± .00	.1 ± .06	0.0 ± .00	.1 ± .06
Opuntia compressa	1	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	0.0 ± .00	.1 ± .06	0.0 ± .00	.1 ± .06	0.0 ± .00
Ulmus spp.	1	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	.1 ± .06	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00
Toxicodendron radicans	1	.1 ± .06	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00
Amorpha canescens	1	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.4 ± .42	1.7 ±1.72
Rosa arkansana	1	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	.1 ± .06
Aster oblongifolia	1	0.0 ± .00	1.1 ±1.06	1.1 ±1.06	1.1 ±1.06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00
Mirabilis hirsuta	1	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	.1 ± .06

Appendix Table I. Floristics of study plots (continued). Mean percent canopy cover ± SE, and relative frequency.

Species:	% Rel. Freq.	Mean percent canopy cover ± SE 1-N	2-N	3-N	1-S	2-S	3-S	1-E	2-E	3-E	1-W	2-W	3-W
Koeleria pyramidata	tr	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00
Aster sagittifolia	tr	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00
Quercus macrocarpa	tr	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.5 ± .42	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00
Ribes missouriense	tr	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .08	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00
Acer negundo	1	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00
Fraxinus pennsylvanica	tr	.1 ± .08	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00
Parthenocissus seedling	tr	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00
Sorghastrum nutans	tr	0.0 ± .00	1.7 ±1.72	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	1.1 ±1.06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00
Oxalis spp.	tr	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00

Appendix Table I. Floristics of study plots (continued). Mean percent canopy cover ± SE, and relative frequency.

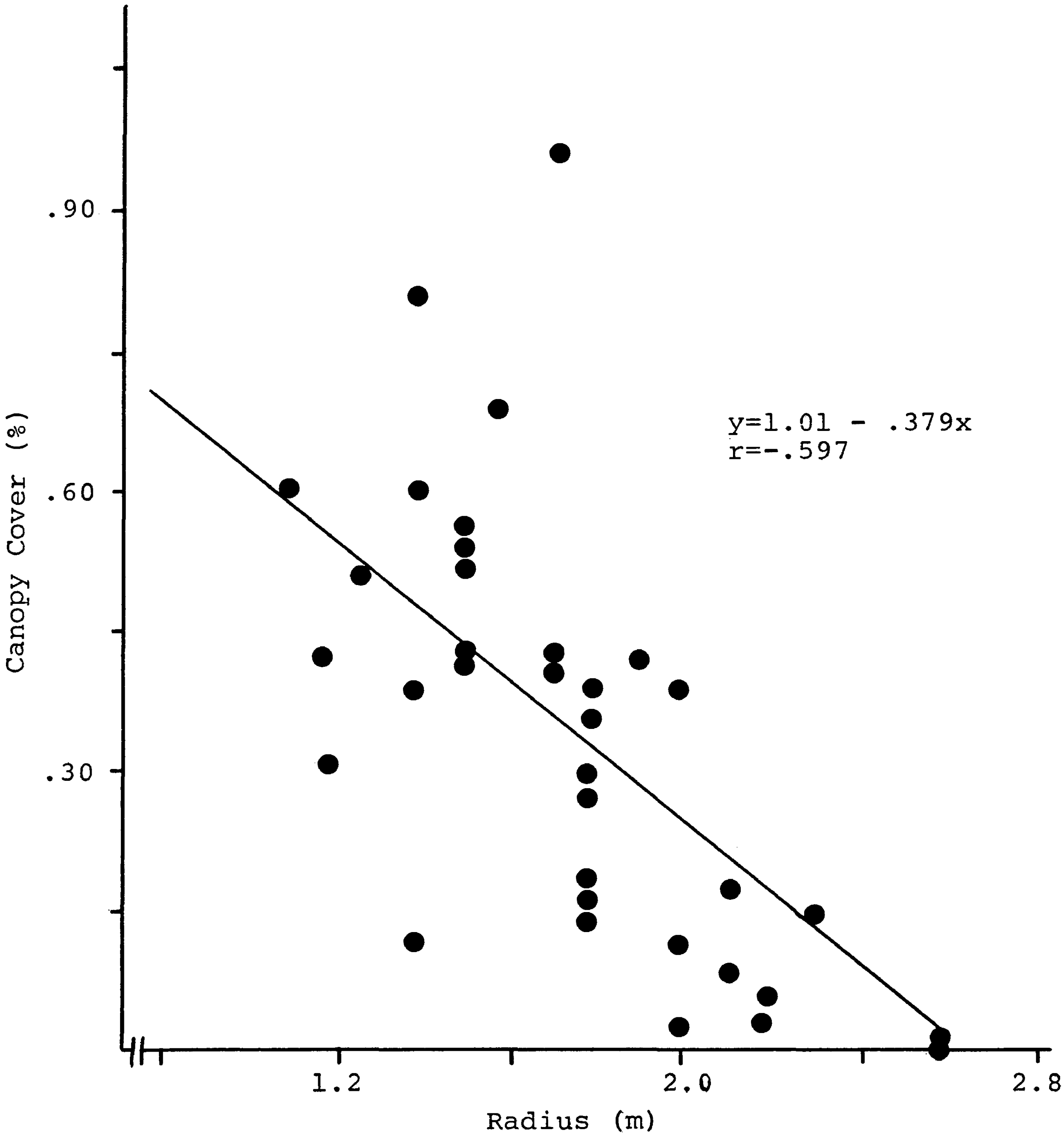
Species:	% Rel. Freq.	Mean percent canopy cover ± SE											
		1-N	2-N	3-N	1-S	2-S	3-S	1-E	2-E	3-E	1-W	2-W	3-W
Kuhnia spp.	tr	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.4 ± .42	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00
Ribes spp.	tr	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00
Symphoricarpos orbiculatus	tr	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06
Apocynum seedling	tr	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00
Paspulum setaceum	tr	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00
Oxytropis lambertii	tr	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00
Achillea millefolium	tr	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00
Festuca octoflora	tr	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	0.0 ± .00	.1 ± .06	.0 ± .00

Appendix Table II. Significant differences between sites, separated by plot and aspect. Significance is based on Kruskal-Wallis AOV ($P \leq .05$). 1=full-canopy, 2=canopy-edge, 3=open-canopy.

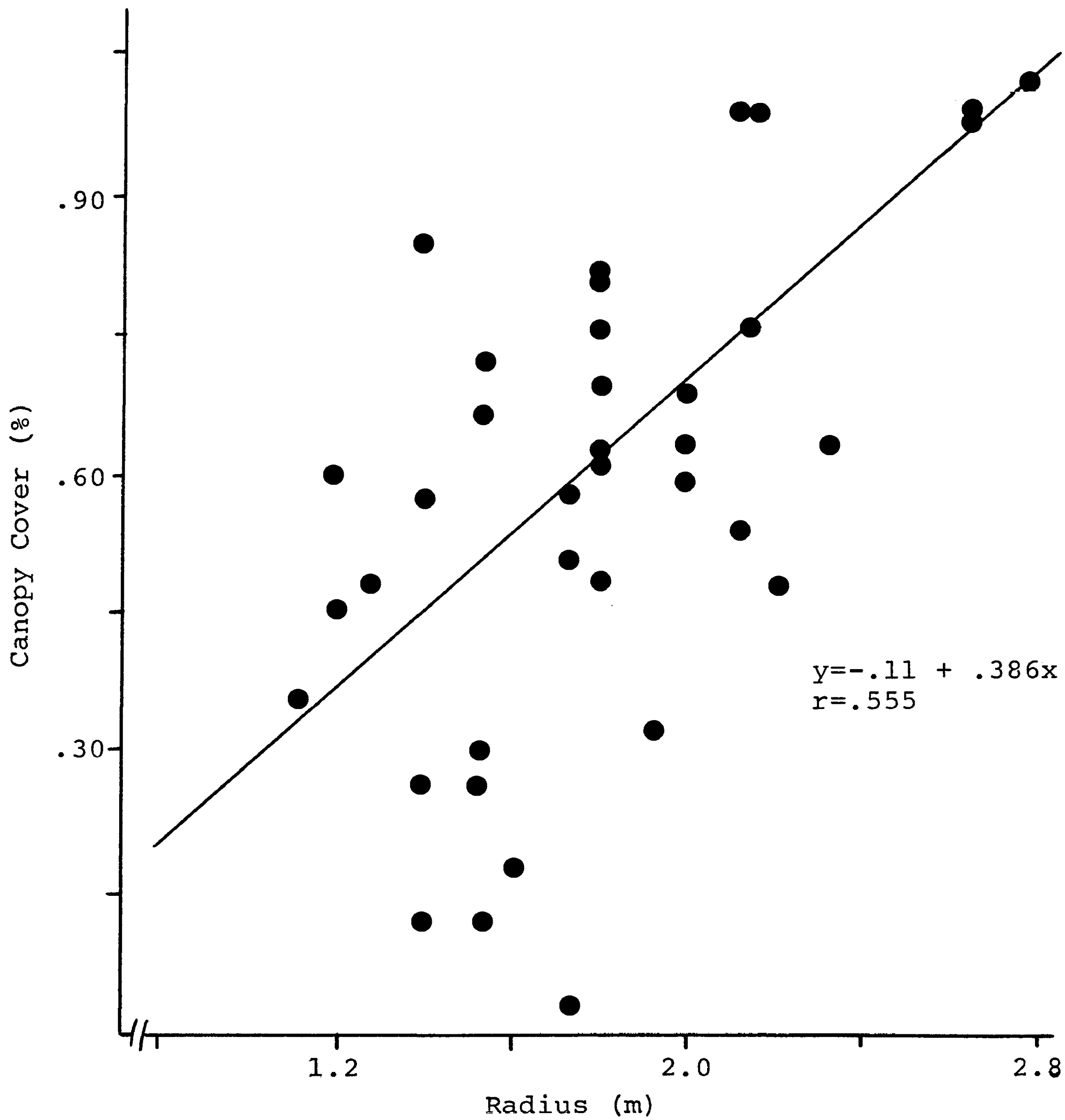
Species	SUCCESSIONAL PLOTS
Andropogon scoparius	1-North, 1-West
Poa pratensis	2-South, 2-East, 2-West, 3-North 3-West
Bouteloua curtipendula	2-West
Dichanthelium oligosanthes var. *scribnerianum*	2-South, 3-East
Andropogon gerardii	1-West, 2-West, 3-East

Appendix Table III. Analysis of variance on transformed-percent-cover for *Poa pratensis* and other combined grasses.

Source of Variation	Sum of Squares	Df	Mean Square	F	P
POA PRATENSIS					
Main Effects	24.226	10	2.423	40.458	0.000
Plot	20.589	2	10.295	171.922	0.000
Aspect	0.596	3	0.199	3.319	0.020
Site	3.012	5	0.602	10.061	0.000
Interactions	2.756	31	0.089	1.485	0.049
Plot and Aspect	0.819	6	0.136	2.279	0.036
Plot and Site	0.610	10	0.061	1.020	0.426
Aspect and Site	1.330	15	0.089	1.481	0.109
Explained	26.982	41	0.658	10.990	0.000
Residual	23.293	389	0.060		
Total	50.275	430	0.117		
OTHER COMBINED GRASSES					
Main Effects	27.562	10	2.756	44.959	0.000
Plot	25.190	2	12.595	205.448	0.000
Aspect	0.795	3	0.265	4.320	0.005
Site	1.553	5	0.311	5.068	0.000
Interactions	3.349	31	0.108	1.762	0.008
Plot and Aspect	1.025	6	0.171	2.787	0.011
Plot and Site	0.950	10	0.095	1.550	0.120
Aspect and Site	1.370	15	0.091	1.490	0.105
Explained	30.911	41	0.754	12.298	0.000
Residual	23.848	389	0.061		
Total	54.759	430	0.127		



Appendix Figure 1. Regression of transformed-percent-cover of combined other grasses in full-canopy plots onto canopy radius.



Appendix Figure 2. Regression of transformed-percent-cover of *Poa pratensis* in full-canopy plots onto canopy radius.