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Increase in Ponderosa Pine Density in the Nebraska Sandhills: Impacts on Grassland Plant Diversity and Productivity

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INCREASE IN PONDEROSA PINE DENSITY IN THE NEBRASKA SANDHILLS:

IMPACTS ON GRASSLAND PLANT DIVERSITY AND PRODUCTIVITY

by

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INCREASE IN PONDEROSA PINE DENSITY IN THE NEBRASKA SANDHILLS:
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Abstract

Increase in woody species encroachment into semi-arid grasslands and savannas has been of great concern at a global level. Temperature and precipitation are key factors determining vegetation cover; however other factors, such as fire regime and grazing may be at play in semi-arid ecosystems. Historically, in Nebraska's semi-arid grasslands, woody species have been controlled by periodic fires. Changes in social values and land use, fire suppression, overgrazing, increased N deposition, and climate change, have attributed to the observed shift from grasslands to shrublands or woodlands. The primary objectives of this study were to determine the impacts of Ponderosa pine (*Pinus ponderosa* P. & C. Lawson) expansion on grasslands productivity and species composition, and associated soil water content in the Nebraska Sandhills. Ten long-term vegetation plots, ranging from open grassland (basal area = 0 m^2ha^{-1}) to dense stands of ponderosa pine (basal area = 49.5 m^2ha^{-1}), were established in Nebraska National Forest (NNF) at Halsey, NE. Measurements at each site included basal area, LAI (leaf area index), understory species composition, biomass, and monthly soil water content. With increasing basal area, and thus, tree canopy cover, declines were reported in species composition, forage production, and volumetric soil water content, and cool-season (C_3) grasses began to replace warm-season (C_4) grasses before they both declined in dense canopy cover. The consequences of this shift from grassland to woodland are likely to include significant ecological, hydrological, and economical impacts.

Acknowledgements

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Table of Contents

List of Figures and Tables

Introduction

A major concern in many grassland ecosystems is vegetation cover change, especially the encroachment of woody plants, such as trees and shrubs (Archer 1995, Haugo and Halpern 2010). Temperature and precipitation are key factors in determining vegetation cover; however, other environmental and anthropogenic factors may be at play in determining vegetation cover and dynamics and therefore ecosystem services. Historically, woody species in semi-arid grasslands like the Nebraska Sandhills were controlled by periodic fires (Bond *et al.* 2005). Due to changes in social values and land use, fires have been, in large, suppressed, which facilitated the shift from grasses to shrublands or woodlands in such ecosystems. Ecosystem shifts in species composition and cover have also been attributed to over-grazing, elevated atmospheric CO_2 levels, atmospheric nitrogen deposition, human-enhanced dispersal, and landscape fragmentation (Scholes and Archer 1997, Briggs *et al.* 2007). The consequences of this shift from grasslands to woodlands are extensive and are likely to include significant ecological, biogeochemical, hydrological, and economical impacts (Hibbard *et al.* 2001, Huxman *et al.* 2005).

In the Great Plains, ecological concerns associated with shifts in vegetative land cover from native semi-arid warm-season (C_4) dominated grasslands to woodlands include changes in local site productivity, species richness and diversity, and, subsequently, ecosystem processes such as water availability and recharge and balances of nitrogen and carbon. Transpiration and evaporation in wooded communities have been found to be greater than in grassland communities (Bosch and Hewlett 1982, Jobbágy and Jackson 2004, Owens *et al.* 2006), which leads to drier soils and less groundwater recharge (Owens et al. 2006, Eggemeyer *et al.* 2009). Economically, land management practices may need to be reconsidered. Forage production

decreases as tree density increases, creating less pasture and feed for livestock dominated rangeland (Knap *et al.* 2008).

Changes in vegetation cover are being observed in grassland ecosystems throughout the Great Plains of North America (Van Auken 2000). Eastern redcedar (*Juniperus virginiana* L.) has expanded throughout tallgrass prairie in Kansas, the Loess Hills of eastern South Dakota, and the Nebraska Sandhills (Briggs *et al.* 2002, Spencer *et al.* 2009, Schmidt and Stubbendieck 1993). Honey mesquite (*Prosopis glandulosa* Torr.) has encroached upon grasslands throughout southern Texas and northern Mexico (Archer 1989, Hibbard *et al.* 2001). Ponderosa pine (*Pinus ponderosa* P. & C. Lawson) has advanced into tallgrass prairie of the western Great Plains of Nebraska, Wyoming, Colorado, and New Mexico (Kaye *et al*. 2010, Steinauer and Bragg 1987). Nebraska's Sandhills, once dominated by grasses, have seen a substantial increase in the expansion of woody species, especially in *P. ponderosa* (Schmidt and Stubbendieck 1993, Kaye *et al.* 2010).

Ponderosa pine is a major forest type in the western U.S. (Sala *et al.* 2005). Historically, ponderosa pine presence was scattered and widely dispersed in the savannas and grasslands of the western Great Plains (Wells 1970, Steinauer and Bragg 1987); however, it has been expanding into adjacent grasslands from historical grassland-woodland ecotones (Steinauer and Bragg 1987, Shinneman and Baker 1997). In the past, wildfire was a dominant factor in controlling woody species and maintaining an open landscape dominated by grasses and forbs. With the introduction of livestock grazing in the late 1800s (Truett 2003), grass fuels and competition for tree seedlings were reduced (Covington *et al.* 1997). As ponderosa pine exerts a more dominant presence in the Plains, major shifts will continue to be observed in species

composition, forage production and quality, and the balances of water, nitrogen, and carbon (Huxman *et al.* 2005).

As grasslands are replaced by woody species, ecological consequences will occur. Table 1 shows a summary of the effects of woody encroachment for eastern redcedar, a species that is increasing its presence in the Sandhills. Species richness and diversity of the herbaceous understory (Moore and Deiter 1992, Lett and Knapp 2005), and forage production (Moore and Deiter 1992, Scholes and Archer 1997) were found to decrease with an increase in eastern redcedar. Tree encroachment also causes shifts in plant functional groups. The once dominant C_4 grasses begin to disappear as C_3 grasses and shrubs take their place (Briggs et al. 2002, Lett and Knapp 2003). Combined, the ecological consequences of tree encroachment can have significant impacts on ecosystem functions, viability, and, consequently, services.

Table 2. Ecological Consequences of Eastern Redcedar (*J. virginiana*). This summary, compiled from various studies (Knapp *et al*. 2008, Ormsbee *et al*. 1976), shows the transformation from a warm-season (C4) grassland to a *Juniperus* forest.

Attribute	C$_4$ Grassland	*Juniperus* Forest
Dominant Growth Form	Graminoid	Woody Tree
Photosynthetic Pathway	C$_4$	C$_3$
Leaf Phenology	Deciduous	Evergreen Conifer
Root	Fibrous, Shallow	Tap Root, Fibrous, Deep (up to 7m)
Sensitivity to Drought	More Sensitive	Drought Tolerant
Biomass Allocation	More Belowground	More Aboveground
Annual AG NPP	356 g m^{-2}	725-1044 g m^{-2}
Standing AG Biomass	850 g m^{-2}	14800 g m^{-2}
Response to Fire	Positive	Negative
Species Richness	High (21.4)	Low (1.2)

The primary objectives of this study are to determine the impacts of tree expansion (*i.e.* land-cover changes) on grassland productivity and species composition, and associated soil water content in the Nebraska Sandhills. The following hypotheses will be tested in this study: as tree canopy cover increases, 1) species composition and forage production decrease, 2) cool-season (C_3) grasses replace warm-season (C_4) dominants, and 3) soil water content decreases. Understanding the impacts of woody species encroachment is a concern, not only in the Sandhills, but also in other semi-arid grassland dominated regions around the world (Archer *et al.* 2001). Establishing the impacts is crucial in predicting and preparing for changes in the future landscape, species composition, and land-use availability of the Sandhills.

Materials and Methods

Site Description

This study was conducted at the Nebraska National Forest (NNF) Halsey, NE, U.S. (825 m altitude, $41^o51'45''$ N and $100^o22'6''$ W) (Fig. 1). The NNF is a 25,000 hectare ($\approx$55,000 acre) experimental forest located in the Nebraska Sandhills. It was established in 1902, predominantly planted with *P. ponderosa* in the 1930s and 1940s. Because of the forest's uniformity in stand age and soils, the site is a prime location to study woody expansion and thicketization with minimal variation.

The climate of the study site is semiarid continental with an average annual precipitation of 570 mm, with 75% falling during the growing season (April to September). The average annual temperature is 8.6°C. The average low temperature in January is –13°C and the average high temperature in July is 31°C. Soils are loose well-drained Valentine fine sand (Mixed, mesic Typic Ustipsamments).

Ten long-term vegetation plots were established. Plot density ranged from open grassland to dense stands of *P. ponderosa*. A fenced enclosure encompassing at least 400 m^2

4

surrounded each plot to prevent livestock grazing. All sites had similar slope and topographical features. The selected sites represent ponderosa pine stands with basal areas ranging from 0 m^2 ha^{-1} to 49.5 m^2 ha^{-1}. Data measured included tree cover, basal area, tree biomass, leaf area index (LAI), percent light penetration, and monthly soil moisture content (10 and 70 cm).

Composition and Yield

Relative understory composition was measured using the modified step-point method (Owensby 1973). In mid-June and mid-August, all standing vegetation was clipped to ground level in at least ten randomly placed 0.25 m^2 quadrats (31 x 80 cm) at each site. The herbage yields were then determined from the vegetation clippings. Herbage yield categorized by plant functional group (e.g., C$_3$ grasses and C$_4$ grasses) was estimated for each plot.

Tree Canopy Measurements

In July, hemispherical photographs were taken at the center of each clipping plot with a Nikon 995 digital camera and a Nikon fisheye lens, which was gimbal-mounted on a tripod. To exclude understory vegetation, photos were taken 60 cm above the forest floor. Gap Light Analyzer software (GLA 2.0) was used to estimate the leaf area index (LAI) integrated over the zenith angles 0-60° (LAI14) and 0-75° (LAI15) of the digital images (Frazer *et al.* 1999). The LAI15 algorithm used is identical to that of the LAI-2000 (LICOR, Inc. Lincoln, NE). LAI measurements were used to determine the amount of light penetrating through the canopy. These figures helped determine the impact of tree leaf density on light regime and understory plant yield.

Soil Water Content

A Trime TDR (Time Domain Reflectometry) soil moisture system was used to measure the soil wataer content. The TDR was inserted into the access tubes in the soil, which were

installed at each plot. The sensors measured volumetric soil water content at two depths, 10 cm and 70 cm.

Data Analysis

Data were analyzed using JMP® statistical package and Microsoft ® Excel. Basal area and LAI, the main drivers of afforestation, were the independent variables used as a measure of increased tree density.

Results

Environmental Conditions

Total precipitation received in 2005 was 491.9 mm, 14% below the long-term average of 573 mm (High Plains Regional Climate Center, University of Nebraska—Lincoln) (Fig. 2A). Air temperature was consistent with the 30-year average, with a maximum reached in July (40.5^{o}C, DOY 204) and a minimum reached in January (-17.23^{o}C, DOY 5) (Fig. 2B). Annual evapotranspiration (ET) was 1782.2 mm, while average daily ET was 4.88 mm, with a maximum reached in July (12.62 mm, DOY 197) and a minimum reached in January (0 mm, DOY 29) (Fig. 2C).

Canopy Cover and Biomass Production

LAI showed positive correlation with basal area (Fig. 3). The plots with a basal area of 0 m^{2}ha^{-1} had an LAI (leaf area index, a measure of light penetration through the canopy) of *P. ponderosa* of 0; whereas the plot with a basal area of 49.5 m^{2}ha^{-1} had an LAI of 1.87. Forage production and biomass decreased with increasing LAI.

Functional Group Density and Species Composition

Functional group density showed variability depending upon basal area. The overall species composition, except for grasslike plants and shrubs, decreased with increasing basal area

(Fig. 4, Table 2). As basal area increased, the composition of C_3 and C_4 grasses decreased, with C_3 grasses beginning to replace C_4 grasses at basal areas greater than 5 m^2ha^{-1} (Fig. 5). The composition of C_4 grasses was greater than that of C_3 grasses when the basal area was between 0 and 5 m^2ha^{-1}. The greatest species composition of C_4 grasses (98 individuals $400m^{-2}$, or 2,450 individuals ha^{-1}) occurred at a basal area of 5 m^2ha^{-1}. However, when the basal area was greater than 5 m^2ha^{-1}, the composition of C_3 grasses was consistently greater than the C_4 grasses. The greatest species composition of C_3 grasses (91 individuals $400m^{-2}$, or 2,275 individuals ha^{-1}) occurred at a basal area of 17.34 m^2ha^{-1}. The percent cover of C_3 grasses was greatest (52%) at a basal area of 20.29 m^2ha^{-1} (Fig. 5). At a basal area of 49.5 m^2ha^{-1}, the percent cover of C_3 and C_4 grasses was 7.2% and 0%, respectively. *Poa pratensis*, a C_3 grass with high forage value, had the greatest density (66 individuals $400m^{-2}$, 1650 individuals ha^{-1}) at a basal area of 17.34 m^2ha^{-1}. Grasslike plant species composition was variable in relation to increasing basal area (Fig. 6). However, there was a general upward trend, with the exception of one outlier, which had the greatest composition (127 individuals $400m^{-2}$, or 3175 individuals ha^{-1}) at 5 m^2ha^{-1}. Both forb and shrub composition was found to be highly variable and showed little correlation to basal area (Fig. 6). Forb composition was lowest (4 individuals $400m^{-2}$, or 100 individuals ha^{-1}) at 0 m^2ha^{-1} and highest (63 individuals $400m^{-2}$, 1575 individuals ha^{-1}) at 17.3 m^2ha^{-1} basal areas. Shrub composition was both highest (16 individuals $400m^{-2}$, 400 individuals ha^{-1}) and absent in plots with a basal area of 0 m^2ha^{-1}.

Soil Water Content

Overall, volumetric soil water content decreased with increasing basal area (Fig. 7). Soil water averaged over the two measured depths (10 and 70 cm) was greatest in May (12.33%) and lowest in August (3.72%). The average daily weather calculations in May and August were

fairly similar (Fig. 2). In May, the average maximum temperature was 20.7°C, the average minimum temperature was 6.53°C, the average daily evapotranspiration was 6.41 mm, and the total precipitation was 74.9 mm. In August, the average maximum temperature was 29.3°C, the average minimum temperature was 15.3°C, the average daily evapotranspiration was 6.77 mm, and the total precipitation was 75.2 mm. Soil water content had greater variability at 10 cm than at 70 cm because of recent rainfall events and its closer proximity to the ground surface and thus, root systems.

Discussion

The results of this study were conclusive and confirmed the expected impacts of ponderosa pine encroachment in the Nebraska Sandhills. With increases in tree canopy cover and basal area, declines were reported in species composition, forage production, and volumetric soil water content, and cool-season (C_3) grasses began to replace warm-season (C_4) grasses before they both declined in areas of high tree basal area. Similar findings have been reported in other tree-grass interaction studies (Scholes and Archer 1997). Implications of this ecosystem shift from grasslands to woodlands are diverse and involve a wide array of ecological and socio-economical disciplines. Changes are likely to occur in livestock and land management, wildlife species diversity, and hydrology of the Sandhills.

The density and richness of understory plant species, including grasses and forbs, declined as the overstory canopy cover increased. This resulted in less diversity, and thus, changes in ecosystem services. These shifts in forage productivity and understory species diversity may have significant impacts for cattle production and management, an integral part of income and livelihood in the Sandhills. Volesky *et al*. (2007) found that 74% of cattle diet composition consisted of cool-season species, such as needle and thread (*Stipa comata),*

bluegrasses (*Poa* species), and sedges (*Carex* species). Both *Poa pratensis* and *S. comata* had

the greatest densities at a basal area of 17.34 m^2ha^{-1}, but greatly declined in abundance thereafter

with increasing basal area. These species are economically important to livestock managers as

cattle rely on them for a large part of their diet. Livestock managers will have to consider

alternate grazing and land management techniques as these key forage species, and other C_3 and

C_4 grass species decline. As land managers look at the effects of these changes and consider

land management techniques, they will also have to consider the cost-benefit analysis of human

interference on livestock production and ecological factors such as species composition and

diversity.

Changes in wildlife populations, especially grassland bird species, are likely to occur as

this ecosystem change develops. Because the Sandhills region is centrally located in North

America, hybridization of eastern and western species is common and allows for a diverse avian

community (Labedz 1998). Frost and Powell (2010) found that woody encroachment of eastern

redcedars decreased species richness and diversity of bird species. Open and mixed habitats,

similar to those found in the savanna ecosystem of the Sandhills, tended to be higher in species

richness.

Other ecological implications of this ecosystem shift include changes in water balance

and recharge. The vast water supply of the Sandhills is a defining feature and resource that

allows for great diversity and abundance in plant and animal species. The highly permeable soils

and subsurface deposits allow for superior infiltration and recharge to the groundwater supply

(Bleed 1998). However, woody encroachment may change the dynamics of hydrology in the

Sandhills. Throughout the study period, volumetric soil water content decreased, especially at a

depth of 70 cm, as basal area and tree canopy cover increased. Because most grass species roots

are often shallower (Weaver 1958), they rely on water from the upper soil profile (0.05-0.5 m) (Eggemeyer *et al.* 2009). Trees and shrubs have more plasticity in sources of water uptake because of their deeper, more extensive root system (Schenk and Jackson 2002). Eggemeyer *et al.* (2009) found that *P. ponderosa* in the Sandhills acquired most of its water from the 0.05-0.9 m soil profile and was capable of acquiring water from a depth of 0.9-7 m when soil water content declined in the upper soil profile. This plasticity and ability to acquire water from great depths may help woody species such as *P. ponderosa* to survive drought occurrences and increase their distribution in the future.

Conclusion

The primary objectives of this study were to determine the impacts of tree expansion on grasslands productivity and species composition, and associated soil water content in the Nebraska Sandhills. The results confirmed that the consequences of woody encroachment in the Sandhills were extensive and included ecological and hydrological impacts. We found as basal area increased 1) species composition and forage production decreased, 2) cool-season (C_3) grasses began to replace warm-season (C_4) dominants, and 4) soil water content decreased.

This decline in plant species diversity and grassland productivity will likely create changes in ecosystem services and functions. The Nebraska Sandhills are home to a diverse flora and fauna; however, its changing environment will provide different habitats for species to utilize. Understanding the effects of *P. ponderosa* expansion will enable land managers and ranchers to prepare for the changing environment and thus, consider appropriate management techniques, such as prescribed burning and thinning.

Future studies should include sampling a greater number of vegetation plots to understand threshold densities of canopy cover in relation to ecosystem shifts. Other studies

should also look at best land management practices for the changing environment of the

Nebraska Sandhills.

References

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? American Naturalist, 134:545-561.

Archer, S. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. Ecoscience, 2(1):83-89.

Archer S., T.W. Boutton, and K.A. Hibbard. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Schulze E.A., S.P. Harrison, M. Heimann, E.A. Holland, J. Lloyd, I.C. Prentice, and D.S. Schimel (eds.). Global Biogeochemical Cycles and their Interrelationship with Climate. Academic Press, Durham, NC, 115-138.

Bleed, A.S. 1998. Pages 67-92 in A.S. Bleed and C.A. Flowerday, editors. An atlas of the Sandhills. Conservation and Survey Division, Institute of Agriculture and Natural Resources, University of Nebraska, Lincoln.

Bond, W.J., F.I. Woodward, and G.F. Midgley. 2005. The global distribution of ecosystems in a world without fire. New Phytologist, 165(2):525-538.

Bosch, J.M. and J.D. Hewlett. 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. Journal of Hydrology, 55:3-23.

Briggs, J.M., G.A. Hoch, and L.C. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems, 5(6):578-586.

Briggs, J.M., H. Schaafsma, and D. Trenkov. 2007. Woody vegetation expansion in a desert grassland: Prehistoric human impact. Journal of Arid Environments, 69(3): 458–472.

Covington, W.W., P.Z. Fule, M.M. Moore, S.C. Hart, and T.E. Kolb. 1997. Restoring ecosystem

health in ponderosa pine forests of the southwest. Journal of Forestry, 95(4):23-29.

Eggemeyer, K.D., T. Awada, F.E. Harvey, D.A. Wedin, X. Zhou, and C.W. Zanner. 2009. Seasonal changes in depth of water uptake for encroaching trees *Juniperus virginiana* and *Pinus ponderosa* and two dominant C_4 grasses in a semiarid grassland. Tree Physiology, 29:157-169.

Frazer, G.W., C.D. Canham, and K.P. Lertzman. 1999. Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.

Haugo, R.D. and C.B. Halpren. 2010. Tree age and tree species shape positive and negative interactions in a montane meadow. Botany, 88(5):488-499.

Hibbard, K.A., S. Archer, D.S. Schimel, and D.W. Valentine. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. Ecology, 82(7):1999-2011.

Huxman, T.E., B.P. Wilcox, D.D. Breshears, R.L. Scott, K.A. Snyder, E.E. Small, K. Hultine, W.T. Pockman and R.B. Jackson. 2005. Ecohydrological implications of woody plant encroachment. Ecology, 86(2):308–319.

Jobbágy, E.G. and R.B. Jackson. 2004. Groundwater use and salinization with grassland afforestation. Global Change Biology, 10(8):1299-1312.

Kaye, M.W., C.A. Woodhouse, and S.T. Jackson. 2010. Persistence and expansion of ponderosa pine woodlands in the west-central Great Plains during the past two centuries. Journal of Biogeography, 37(9):1668-1683.

Knapp, A.K., J.K. McCarron, A.M. Silletti, G.A. Hoch, J.C. Heisler, M.S. Lett, J.M. Blair, J.M. Briggs, and M.D. Smith. 2008. Ecological consequences of the replacement of native grassland by *Juniperus virginiana* and other woody plants. In Western North American *Juniperus* Communities, 196(2):156-169.

Labedz, T.E. 1998. Pages 173-192 in A.S. Bleed, and C.A. Flowerday, editors. An atlas of the Sandhills. Conservation and Survey Division, Institute of Agriculture and Natural Resources, University of Nebraska, Lincoln.

Lett, M.S. and A.K. Knapp. 2003. Consequences of shrub expansion in mesic grassland: resource alterations and graminoid responses. Journal of Vegetation Science, 14(4):487-496.

Lett, M.S. and A.K. Knapp. 2005. Woody plant encroachment and removal in mesic grassland: production and composition responses of herbaceous vegetation. American Midland Naturalist, 153(2):217-231.

Moore, M.M. and D.A. Deiter. 1992. Stand density index as a predictor of forage production in Northern Arizona pine forests. Journal of Range Management, 45:267-271.

Ormsbee, P., F.A. Bazzaz, and W.R. Boggess. 1976. Physiological ecology of *Juniperus virginiana* in Oldfields. Oecologia, 23(1):75-82.

Owens, M.K., R.K. Lyons, and C.L. Alejandro. 2006. Rainfall partitioning within semiarid juniper communities: effects of event size and canopy cover. Hydrological Processes, 20:3179-3189.

Owensby, C.E. 1973. Modified step-point system for botanical composition and basal cover estimates. Journal of Range Management, 26(4):302-303.

Sala, A., G.D. Peters, L.R. McIntyre, and M.G. Harrington. 2005. Physiological responses of

ponderosa pine in western Montana to thinning, prescribed fire and burning season. Tree Physiology, 25:339-348.

Schenk, H.J. and R.B. Jackson. 2002. Rooting depths, lateral root spreads and below-ground/ above-ground allometries of plants in water-limited ecosystems. Journal of Ecology, 90: 480-494.

Schmidt, T.L. and J. Stubbendieck. 1993. Factors influencing eastern redcedar seedling survival on rangeland. Journal of Range Management, 46(5):448-451.

Scholes, R.J. and S.R. Archer. 1997. Tree-grass interactions in savannas. Annual Review of Ecology & Systematics, 28:517-544.

Shinneman, D.J. and W.L. Baker. 1997. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the Black Hills. Conservation Biology, 11:1276-1288.

Spencer, C.N., S.L. Matzner, J. Smallery, M. Bukrey, J. Onberg, M. Chapman, and M. Steck. 2009. Forest expansion and soil carbon changes in the Loess Hills of eastern South Dakota. American Midland Naturalist, 161(2):273-285.

Steinauer, E.M. and T.B. Bragg. 1987. Ponderosa pine (*Pinus ponderosa*) invasion of Nebraska Sandhills prairie. American Midland Naturalist, 118:358-365.

Truett, J.C. 2003. Migrations of grassland communities and grazing philosophies in the Great Plains: a review and implications for management. Great Plains Research: A Journal of Natural and Social Sciences, Paper 646. http://digitalcommons.unl.edu/ greatplainsresearch/646

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics, 31:197-215.

Volesky, J.D., W.H. Schacht, P.E. Reece, and T.J. Vaughn. 2007. Diet composition of cattle

grazing Sandhills range during spring. Rangeland Ecology and Management, 60(1):65-

70.

Weaver, J.E. 1958. Summary and interpretation of underground development in natural

grassland communities. Ecological Monographs, 28:55-78.

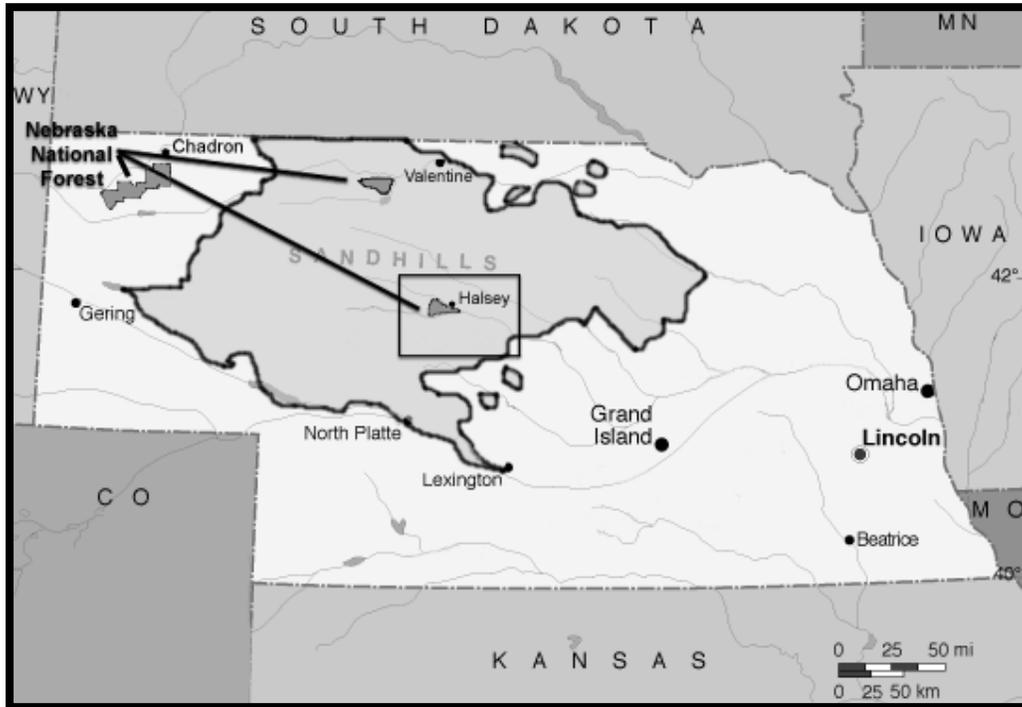Wells, P.V. 1970. Postglacial vegetational history of the Great Plains. Science, 167:1574-1582.

Figure 1. Location of the Nebraska Sandhills in relation to the study site, Halsey National Forest. (http://nematode.unl.edu/halseyNEmap.htm)
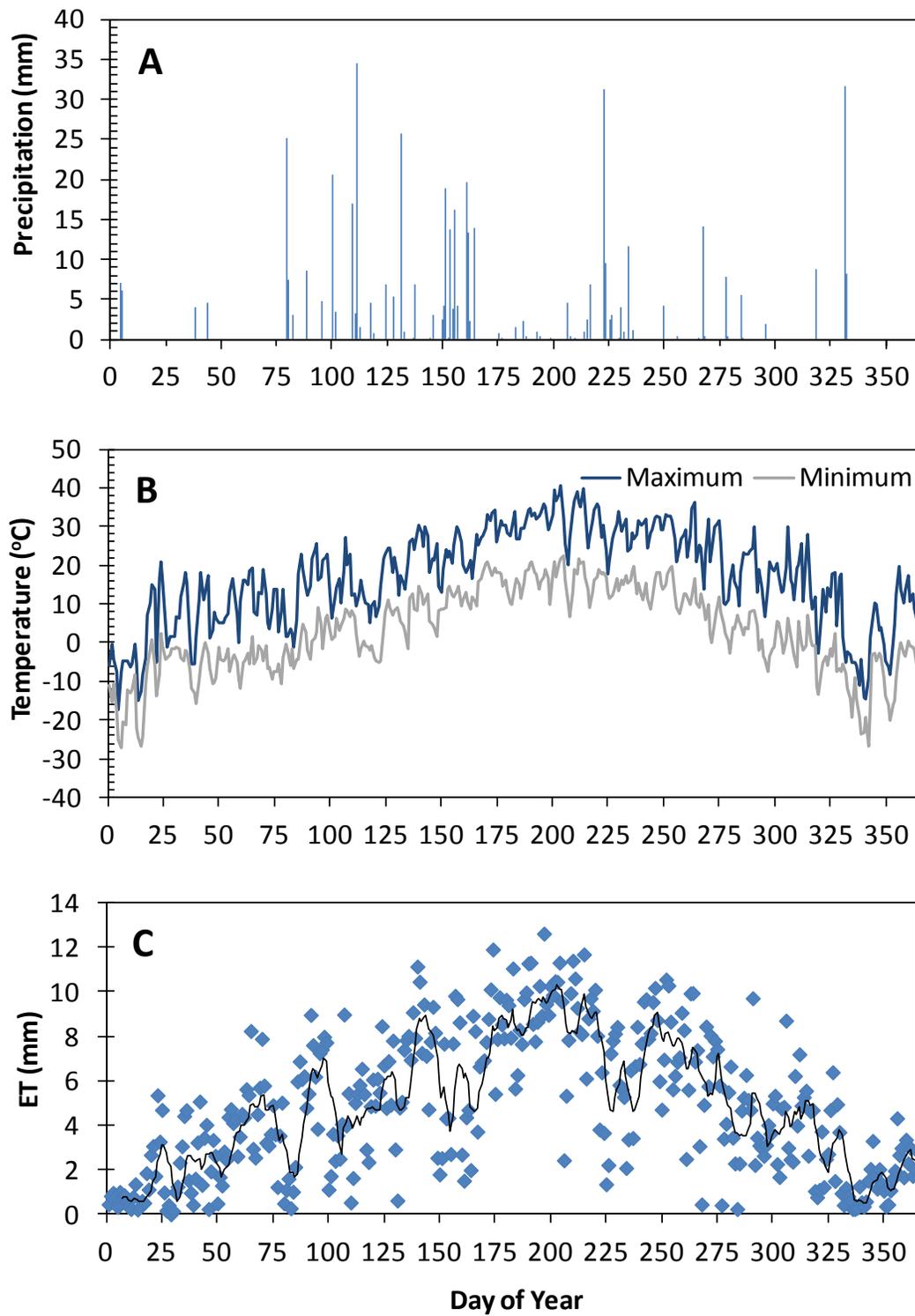
Figure 2. Seasonal dynamics in a) precipitation (mm), b) temperature (°C), and c) evapotranspiration (mm).
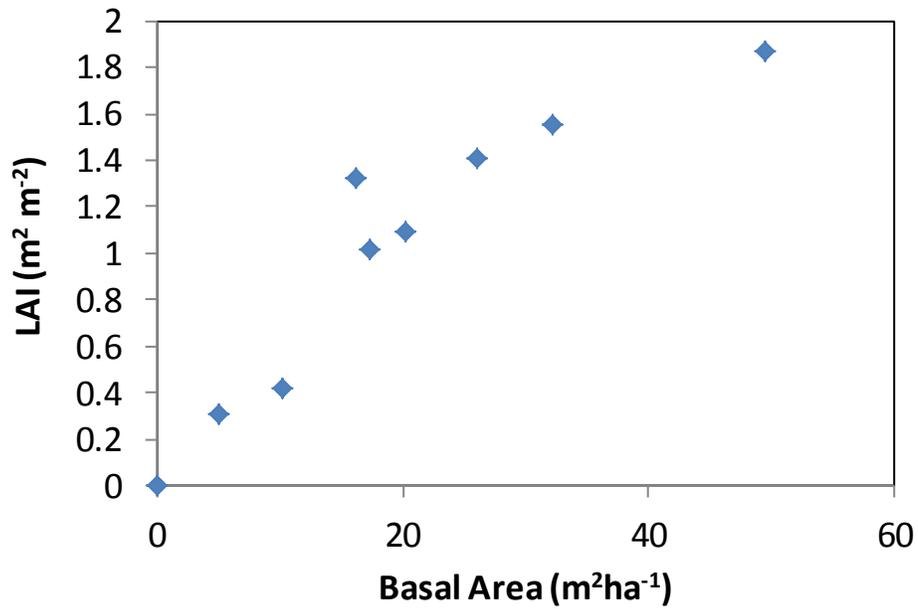
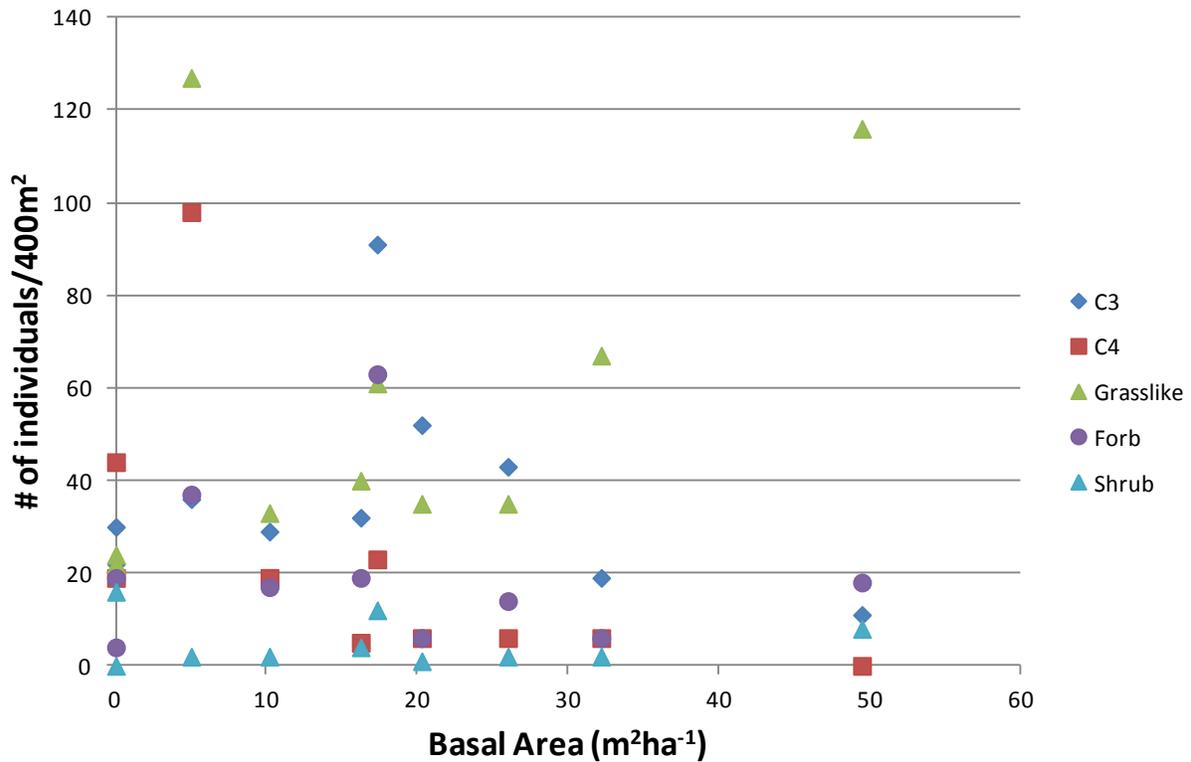Figure 3. Site LAI (leaf area index) as a function of basal area (m^2ha^{-1}).

Figure 4. Functional group density (# of individuals/400m^2) of C_3 grasses, C_4 grasses, grasslike plants, forbs, and shrubs as a function of basal area (m^2ha^{-1}).

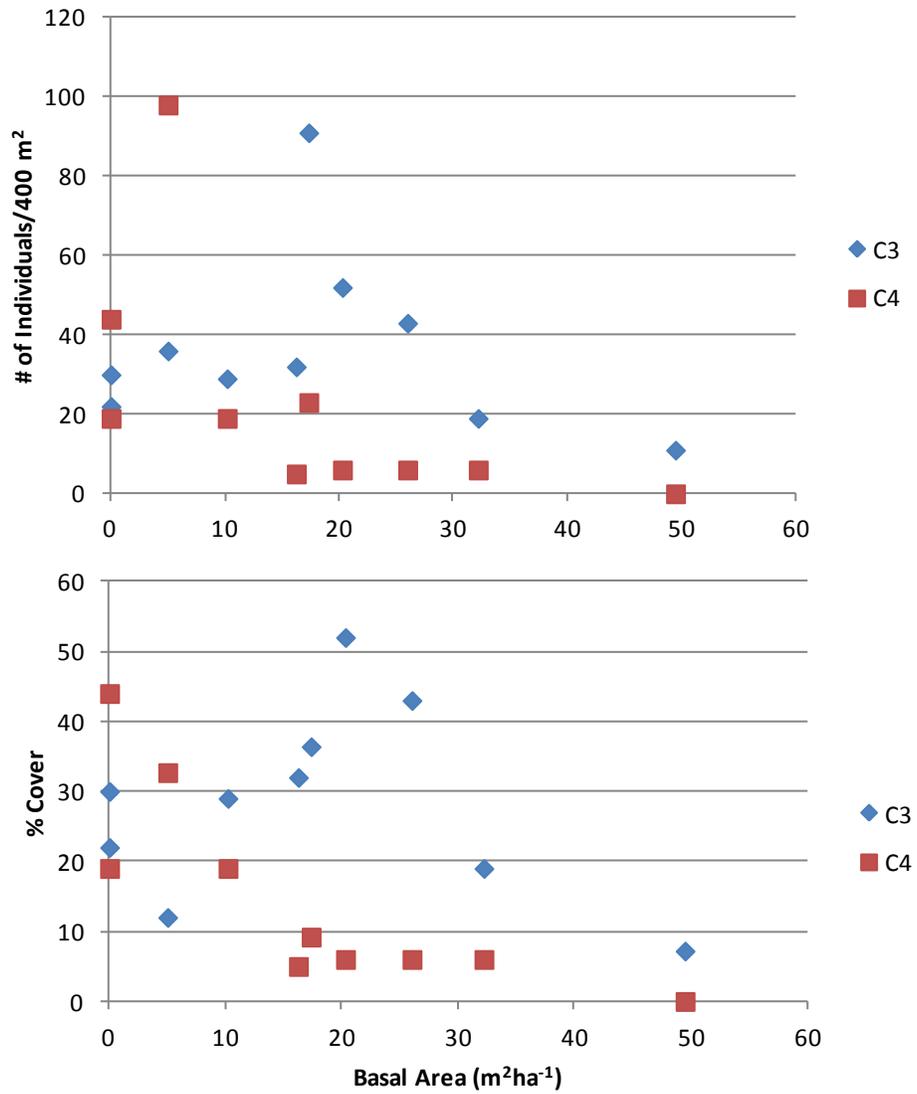Figure 5. Density (# of individuals/400m^2) and percent cover (%) of C$_3$ and C$_4$ grasses as a function of basal area (m^{2}ha^{-1}).
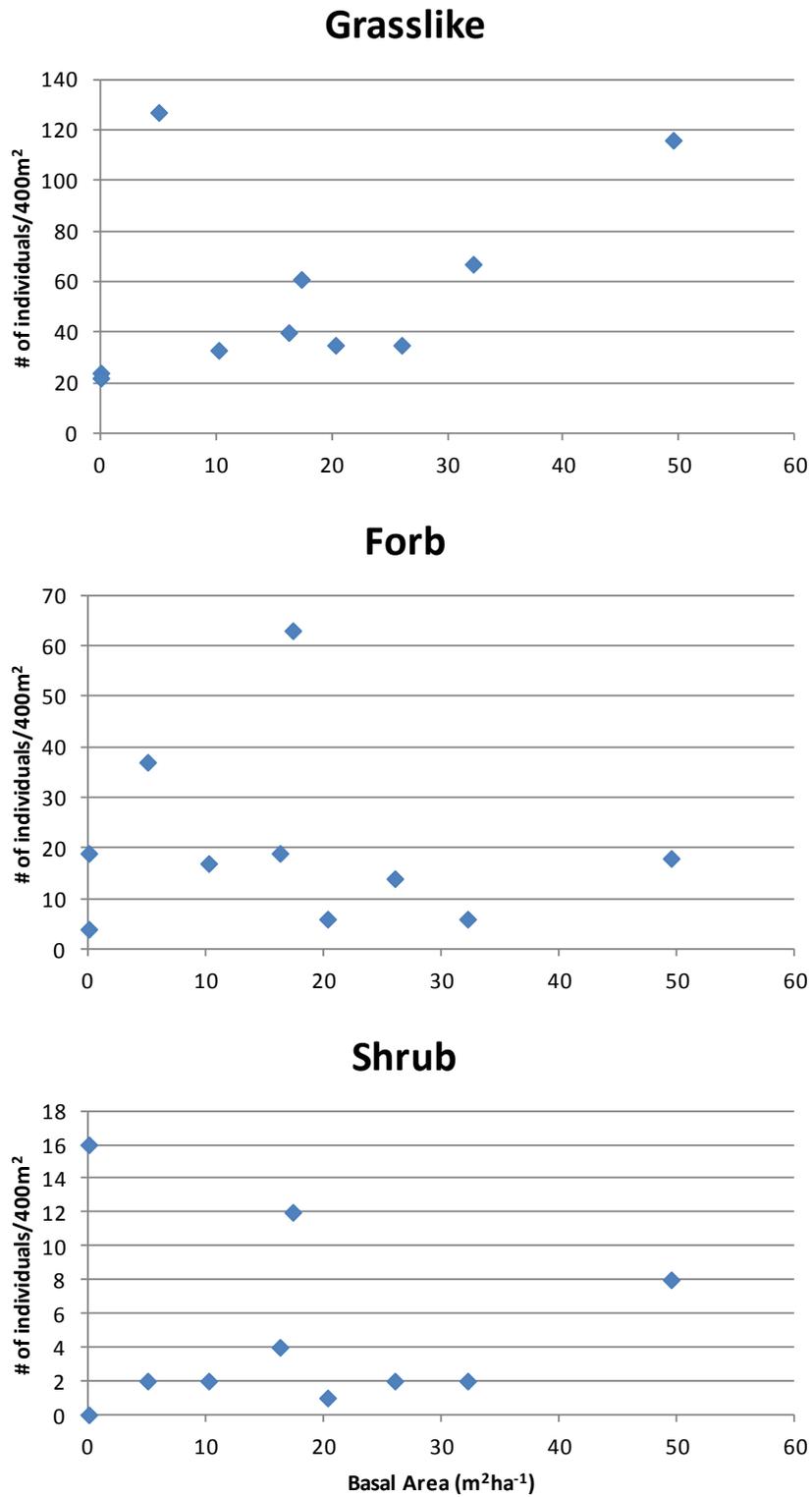
Figure 6. Density (# of individuals/400m^2) of grasslike plants, forbs, and shrubs as a function of basal area (m^{2}ha^{-1}).
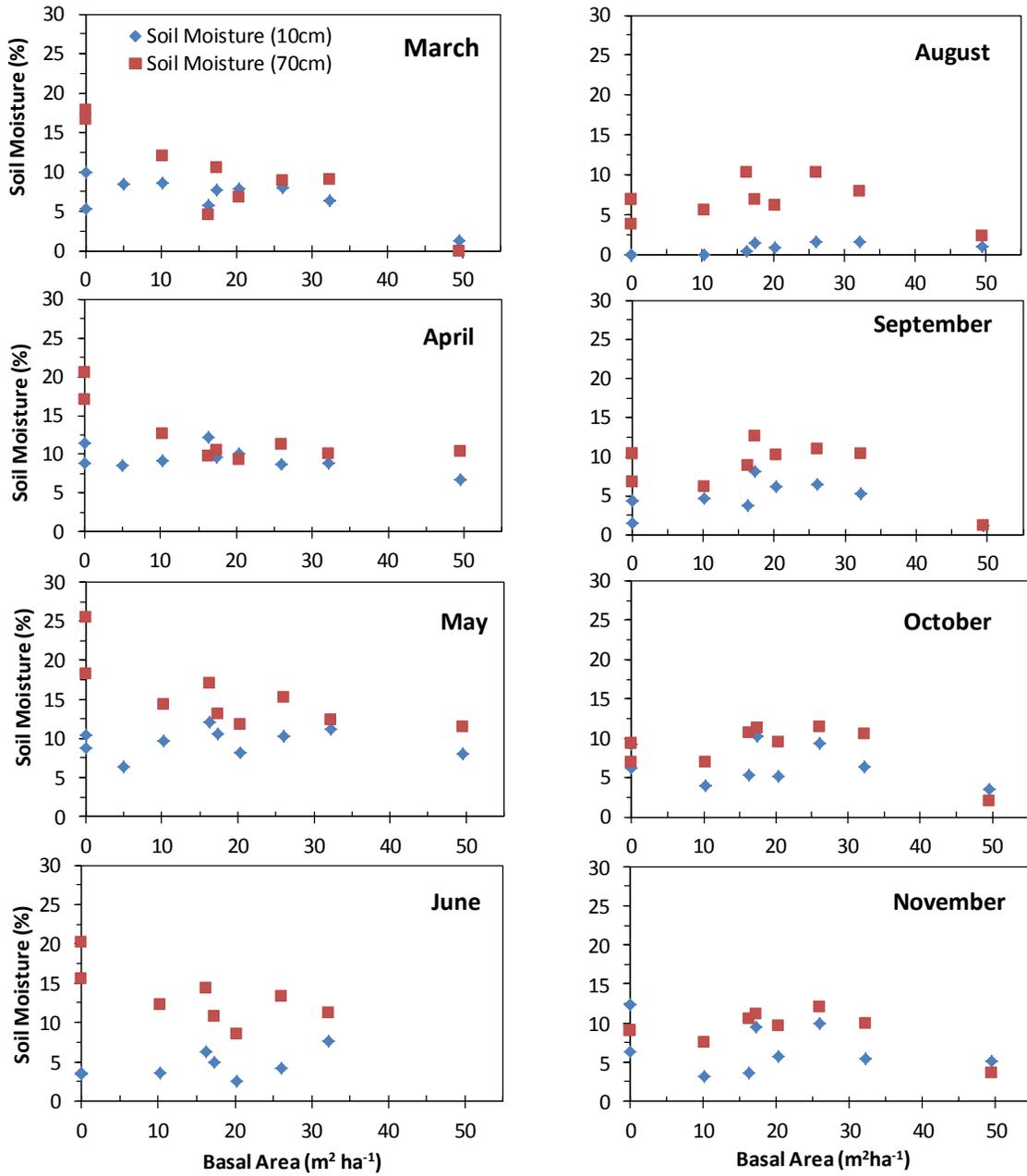
Figure 7. Monthly dynamics (March 2005 to November 2005; excluding July 2005) in soil moisture (%) and corresponding basal area ($m^2 ha^{-1}$).

Table 2. Understory species composition on site in relation to basal area (m^2ha^{-1}).

Species	Basal Area (m^2ha^{-1})									
C₃ Grasses:	**0**	**0**	**5.00**	**10.19**	**16.24**	**17.34**	**20.29**	**26.01**	**32.20**	**49.50**
Bromus japonicus				X	X		X	X	X	
Bromus tectorum			X		X		X	X	X	
Dichanthelium oligosanthes	X		X	X	X	X	X	X	X	X
Dichanthelium wilcoxianum								X		
Elymus canadensis										X
Hesperostipa spartea	X		X			X	X			
Koeleria macrantha				X						
Poa pratensis	X	X	X	X	X	X	X	X		
Poa secunda		X								
Stipa comata	X	X	X	X		X	X	X	X	
Vulpia octoflora	X		X			X		X		
C₄ Grasses:										
Andropogon hallii		X	X	X						
Bouteloua gracilis		X	X					X		
Bouteloua hirsuta			X	X						
Calomovilfa longifolia	X		X	X	X	X	X	X	X	
Eragrostis curvula	X		X			X			X	
Panicum virgatum	X	X	X			X		X		
Schizachyrium scoparium	X	X	X	X			X			
Sporobolus cryptandrus	X		X	X	X	X	X	X	X	
Grasslike:										
Carex inops heliophilia	X	X	X	X	X	X	X	X	X	X
sedge	X	X	X	X	X	X	X	X	X	X
Forb:										
Ambrosia psilostachya	X	X	X	X	X	X	X	X	X	
Antennaria neglecta	X		X			X				
Artemisia ludoviciana	X		X	X	X	X	X		X	
Asclepias arenaria									X	
Chenopodium album	X									
Conyza canadensis	X	X	X							
Helianthus annuus				X						
Lepidium densiflorum	X							X		
Lithospermum canescens			X							
Maianthemum racemosum										X
Physalis heterophylla						X		X		X
Plantago patagonica	X		X	X	X			X		
Solidago missouriensis									X	
Taraxacum officinale										X
Toxicodendron radicans						X				X
Tradescantia occidentalis						X		X		X
Tragopogon dubius					X	X			X	
annual mint	X			X		X	X	X		
unknown forb	X	X	X	X	X	X			X	X
Shrub:										
Amorpha canescens	X				X	X			X	
Juniperus virginiana						X				X
Opuntia polyacantha								X		X
Pinus ponderosa					X			X	X	X
Prunus virginiana										X
Rosa arkansana	X		X			X	X			
Rosa woodsii				X		X				