MODEL FOR CLASSIFYING AND MONITORING HACKBERRY (*CELTIS OCCIDENTALIS* L.)–SHRUB ECOLOGICAL TYPE IN SAND HILLS PRAIRIE ECOSYSTEM

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ABSTRACT

A classification and monitoring system for the hackberry-shrub ecological type was developed based on plant succession in the Sand Hills ecosystem in northern Nebraska and southern South Dakota. Seral stages are quantitatively derived groupings of vegetation composition based on the range of variability within the current ecological type. Multivariate statistical methods determined three key variables that best assign data (sites) to one of four seral stages within the contemporary hackberry-shrub ecological type and represent one of multiple possible stable states. Basal area of hackberry (*Celtis occidentalis* L.), combined canopy cover values of chokecherry (*Prunus virginiana* L.) and wild plum (*Prunus americana* Marsh.), and canopy cover of western snowberry (*Symphoricarpos occidentalis* Hook.) were the key plant variables required for classification and monitoring to determine succession or retrogression. Four seral stages (early to late) were quantitatively identified with an accuracy of 97%. Classification involves a single sample at a site where monitoring trends require multiple seral stage assignment at the same site over time. The assigned seral stages provide resource managers with a quantitative method to evaluate their management objectives by monitoring trend. We list all coefficients required to assign data to seral stage and calculate posterior probabilities, however details of methods for monitoring protocol, seral stage classification, calculation of seral stage probabilities can be viewed at the Forest Service web site http://www.fs.fed.us/rangelands/ecology/ecologicalclassification/index.shtml,

Keywords

Succession, seral stages, woodland, management, state and transition model

INTRODUCTION

Woodlands in the Northern Great Plains represent a very small portion of the area and are often confined to river channels, drainages, swales, or north facing slopes with higher soil moisture. Hackberry (*Celtis occidentalis* L.) trees represent less than 2-3% (measured by volume) of all tree species found in Nebraska (Meneguzzo et al. 2007). In the Sand Hills, the hackberry ecological type is limited to a small percentage of plant communities found in the Sand Hills prairie ecosystem (Bleed and Flowerday 1990), but are very important for wildlife habitat, biodiversity, livestock cover, and even carbon sequestration (Meneguzzo et al. 2007; Lesica and Cooper 1998; Schmidt 1986; Nudds 1977). Hackberry and the associated shrub species chokecherry (*Prunus virginiana* L.), wild plum (*Prunus americana* Marsh.), and snowberry (*Symphoricarpos occidentalis* Hook.) are all native to Nebraska (Kaul 1990). Hackberry (*Celtis*) fruit has been found in fossil sediment as early as Eocene (54-38 m.y ago) to present and common to abundant during the Miocene (26-7 m.y ago) in northern Nebraska and southern South Dakota (Retallack 1983; Gabel et al. 1998). Hackberry fruits were described as being common to abundant in 78% of the fossil floras (14-19 m.y. ago) investigated by Gabel et al. (1998). Hackberry trees are considered a mesic, shade tolerant, late successional tree species (Abrams and Knapp 1986). The hackberry-shrub community is not officially recognized as a terrestrial community in Nebraska, but all community classification systems are subjective, scale based, and possibly poorly studied in a large grassland ecosystem like the Sand Hills (Steinauer and Rolfsmeier 2003). This ecological type is partially contained within two communities in a more recent classification, the snowberry shrubland (early seral stages) and the chokecherry-plum thicket (mid-late seral stages) (Rolfsmeier and Steinauer 2010).

The hackberry-shrub community is one of the few tree-containing communities that are found in upland prairies of the Sand Hills and often found on sides and bottoms of north-facing slopes in areas less than an acre in size (Schmidt 1986) and low slopes, mesic swales, depressions, bottoms of ravines and floodplains (Rolfsmeier and Steinauer 2010). This community type may be currently more common since fire suppression has allowed trees and shrubs to become established in areas predominantly grasslands over the past century (Steinauer and Bragg 1987). Trees and shrubs were observed to increase by 34% in Kansas in the Flint Hills on unburned prairie sites, but soil texture, topography, and distance to seed source were also important (Bragg and Hulbert 1976; Ibanez and Schupp 2002).

Grassland and woodland ecological status undergoes changes over time, following natural and anthropogenic induced disturbances. Sandy soils are erodible and drain quickly and are therefore susceptible to vegetation disturbances like fire, drought, grazing, wind, and wildlife burrows (Loucks et al. 1985; Steuter et al. 1990). Changes to the vegetation condition result in different seral conditions within a community and throughout the landscape (Sousa 1984; Pickett and White 1985). These changes can be quantified using multivariate statistical models of plant succession (MacCracken et al. 1983; Uresk 1990; Benkobi et al. 2007). Plant succession has been used in classification studies for western forests and rangelands for many years (Sampson 1919; Humphrey 1947; Dyksterhuis 1985; Westoby et al. 1989; Uresk 1990). However, subjective interpretations make it difficult to obtain consistent measurements of vegetation trend. Multivariate quantitative models of plant succession allow resource managers to easily obtain quantitative measurements and relate current condition to management effects at one-time and over long-term on a repeatable basis.

Results of this research provide a multivariate statistical model that can be used by managers to determine seral stage classification within a contemporary tree-shrub ecological type and a method to determine succession and retrogression trends within and among seral stages. In addition, this model can be included in conceptual and working models of multiple stable states (state and transition) to describe vegetation dynamics common where a tree-shrub community can replace or retrogress to a grassland community demonstrating alternative stable states at a single site (Briske et al. 2005; Bestelmyer et al. 2003). State and transition models are conceptual models that can include vegetation change from fire, climate, management activities that include grazing and succession and also encompass threshold components like structural or functional changes at a single site. Our model consists of an interrelationship from a set of plant species (variables) that best characterizes the ecological type throughout the course of succession within a single stable state. The model also provides managers with quantitative site-specific data and statistically valid sample methodology which have been identified as important for assessment and monitoring (Pyke et al. 2002). The objectives of this study were to (1) develop an ecological classification and monitoring model for the Sand Hills prairie ecosystem hackberry – shrub community and (2) define seral stages.

STUDY AREA

The study was conducted on lands managed by the Nebraska National Forest and emphasized habitat that included woodland vegetation consisting of a hackberry-shrub plant community type in the Sand Hills region that extends into southern South Dakota. The specific study site is located in the north-central part of Nebraska on two areas of the National Forest. The north area is the Samuel R. McKelvie National Forest that encompasses 46,280 hectares (115,700 acres). The south area, the Bessey Ranger District of the Nebraska National Forest, has 36,183 hectares (90,456 acres), with about 24% of the area forested with planted ponderosa pine. The two areas are about 50 miles apart.

Climate is described as semi-arid (Burzlaf 1962). Long-term mean annual precipitation average compiled from three weather stations (Valentine, Halsey, and Nenzel) starting in 1903 was 53 cm (21 in). Annual precipitation for 1988 and 1989 were averaged from the Valentine and Halsey stations (HPRCC 2007). Precipitation is 41 cm (16 inches) in the western Sand Hills to near 61 cm (24 inches) in the southeast part (Farrar 1979). Seventy to 85% percent of the precipitation falls during the growing season (April-Sept.) from short duration intense thunderstorms (Perez et al. 1998). The average monthly temperature ranges between -45 °C (-48 °F) in the winter to 43 °C (110 °F) in the summer (Farrar 1979).

The Sand Hills flora has been described numerous times over the last century (Pool 1914; Weaver and Albertson 1956; Burzlaff 1962; Stubbendieck and Tunnell 2008). The descriptions are primarily concerned with grassland communities and production of vegetation in plant communities that represent considerable area. In contrast, the hackberry community occupies a very small area in the grasslands. Although trees are represented as small areas in the upland grassland ecosystem (Jakes and Smith 1982), they often are very important within the ecosystem for specific wildlife species or cover for livestock (Sisson 1970, 1976; Kauffman and Kruger 1984; Hodorff et al. 1988; Bleed 1990; Rumble and Gobeille 1998; Uresk et at. 2009).

METHODS

Data collection and analyses followed Uresk's (1990) procedures in addition to measuring diameter of all tree species within a 20 m x 40 m macroplot (800 m^2). The U.S. Forest Service Permanent Staff, familiar with the project area, selected study sites and collected all data. Sites were selected so that the existing full range of natural variability of the hackberry-shrub woodland type would be collected. All plant species names follow the nomenclature by NRCS Plants database (2010).

Data were collected on 39 macroplots during the summer of 1989. Each macroplot was randomly selected within one of three perceived seral stages (early, mid, late). At each macroplot, two 30 m parallel transects were set 20 m apart. Sampling of canopy cover for individual plant species, plant litter, and bare ground occurring within 0.1 m^2 (20 cm x 50 cm) microplots following the Daubenmire method (Daubenmire 1959) was completed at 1 m intervals along each transect. Tree diameters were measured with calipers at 4 feet (1.22 m) height in inches within each 800 m^2 macroplot. All macroplot data (60 microplots) for each site were averaged for individual plant species and for totals of plant cover, litter, and bare soil. Basal area of trees and stem numbers were also averaged for each site. Canopy cover was collected for the most common plant species.

Principal component analysis (Norusis/SPSS Inc. 1992) was used to identify plant variables that contributed various levels to the variation in the data. Additional variables like total grasses, total shrubs, and a combination of species at the genus level were also added to the data set to provide and identify the best variables to include for model selection. The combined basal area and canopy cover percentages of *Prunus* species, the diameter (inches) of all tree species, and combined shrub canopy cover were included in preliminary analyses. Data were then subjected to a non hierarchical cluster analysis, ISODATA, which grouped the 39 sites into 4 distinct cluster groups (seral stages) based on within group similarities and between group differences (Ball and Hall 1967; del Morel 1975; Hall and Khanna 1977).

The greatest possible variation among groups compared to within group variation will result with fewer errors of classification in discriminant analysis when applying discriminant functions (Afifi and Clark 1990). Therefore, a stepwise discriminant procedure was used to calculate discriminant function coefficients that simultaneously were used to analyze differences among variables for cluster groups (Klecka 1987). Information about numerous independent variables (plant species and basal area) is contained within a single index (SPSS 2003). Fischer classification coefficients (Klecka 1987) were calculated to provide a method to assign (classify) any unclassified case (marcoplot) into a group (seral stage) that it most closely resembled.

RESULTS

Four seral stages (early to late) were defined in the hackberry – shrub ecological type. Seral stages were distinguished from one another by the distribution and abundance of three key plant species that help illustrate the dynamics of these species in the hackberry- shrub ecological type (Figure 1). Four distinct seral stages were identified based on the range of variability of the contemporary vegetation ranging from early to late succession. Results of stepwise discriminant analysis (Norusis/SPSS Inc. 1992) showed significant differences among these seral stages ($P < 0.05$). Basal area of hackberry, percent canopy cover of combined *Prunus* species and western snowberry are the best variables to be used in the classification and monitoring model (Table 1).

The late hackberry seral stage represents sites with greatest basal area of hackberry trees and other variables (Table 2). Late seral sites also had the greatest percent of bare soil and the lowest percent cover of litter, total grasses, and total shrubs compared to the other seral stages (Figures 1 and 2). These differences are partially explained by livestock use of the shaded habitat under the mature hackberry trees. Over time shading may also reduce understory development of shrubs, grasses, and forbs. The late-intermediate stage had the greatest canopy cover of the *Prunus* category (chokecherry + plum) and greater cover of shrubs compared to the other stages (Table 2).

This late-intermediate stage was similar in amount of litter and had twice the total grass canopy as the late seral stage. Some of the observed differences in the late and late-intermediate seral stages may be partially influenced by the low number of samples, 3 and 4 respectively, in each of these groups, compared with 21 and 11 samples in the early-intermediate and early seral stages. These two late seral stages had less percent cover of bluegrass (*Poa* spp.), little bluestem (*Schizachyrium scoparium*), and the forb starry false Solomon's seal (*Smilacina stellata*) compared to the earlier seral stages.

Tree numbers were the same in the late and early intermediate stage compared to the other stages, but diameters were much greater in the late sere. Percent canopy cover of litter was nearly double in the earlier two stages compared to the later two stages and bare ground decreased greatly from the late to late intermediate stage (Table 2, Figure 2).

The early seral stage represents the stage of this type where the transition from a grassland community to an early tree-shrub community has started. This state of the system has an increase of shrub cover, primarily western snowberry. Total

Table 1. Fisher's classification discriminant function coefficients used for classification of seral stages in Nebraska National Grasslands hackberry-shrub ecological type.

Species	**Late**	**Late intermediate**	**Early intermediate**	**Early**
Basal area *Celtis occidentalis*	0.8249947	-0.08342129	0.02235409	0.07811445
Canopy cover *Prunus* (*P. virginiana* + *P. americana*)	-0.02100902	0.5371982	0.1850731	0.07539636
Canopy cover *Symphoricarpos occidentalis*	0.1436558	-0.1181865	0.09415513	0.6525852
Constant	-22.97096	-18.64775	-3.968076	-12.87400

Table 2. Means and standard errors (in parentheses) of most common plant species or species characteristic (% canopy) among four seral stages in Nebraska National Grasslands hackberry-shrub ecological type.

Species (% cover) or variable	**Late**	**Late intermediate**	**Early intermediate**	**Early**
Basal area hackberry(ft•a^{-1}) *	51.1(4.8)	0.1(0.1)	3.4(1.3)	6.8(3.3)
Tree numbers	6.5(2.8)	2.0(2.0)	6.6(2.7)	3.8(2.8)
Prunus species combined	7.3(5.3)	64.3(10.3)	24.1(1.8)	17.2(4.3)
Wild plum				
Prunus americana	0.0(0.0)	0.0(0.0)	6.7(2.1)	3.8(1.4)
Chokecherry *Prunus virginiana*	7.3(5.3)	64.3(10.3)	17.0(3.0)	13.3(4.1)
Snowberry *Symphoricarpos occidentatlis*	8.2(3.3)	0.0(0.0)	6.6(1.4)	32.4(2.6)
Bluegrasses				
Poa species	0.0(0.0)	0.8(0.8)	6.9(3.7)	9.2(4.0)
Little bluestem *Schizachyrium scoparium*	0.8(0.8)	1.0(1.0)	4.0(1.7)	3.1(2.4)
Starry false Solomon's seal *Smilacina stellata*	0.1(0.1)	1.7(1.7)	1.3(1.0)	1.4(1.1)
Rose species *Rosa* species	0.3(0.2)	1.7(1.2)	2.5(0.8)	3.5(1.4)
Total Shrubs	21.4(6.2)	77.1(5.4)	56.9(4.1)	71.1(4.1)
Total Grasses	11.1(2.2)	24.7(14.5)	28.6(5.2)	42.4(3.1)
Total Forbs	16.8(5.4)	6.5(3.8)	14.1(2.4)	11.7(2.6)
Litter	30.2(4.4)	34.6(6.5)	66.5(5.8)	67.1(6.3)
Bare Ground	60.9(6.6)	13(8.1)	6.5(3.8)	0(0)

* To convert from ft^{2}•acre^{-1} to m^{2}•ha^{-1} multiply basal area by 0.229.

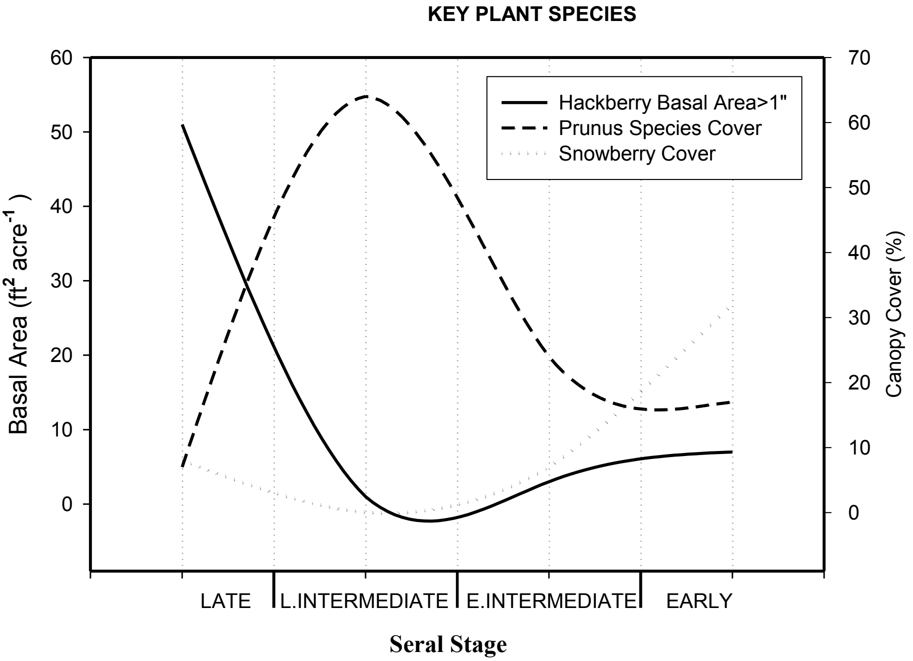

Figure 1. Means of 3 key plant species variables through four stages of succession in a hackberry-shrub ecological type. Smoothed lines connect the means of each key variable at each stage and provide an approximate representation of the mixture of key species at each seral stage. To convert from ft^2•acre^{-1} to m^2•ha^{-1} multiply basal area by 0.229.

grass canopy decreases from about 40% in the early stage to near 10% in the late stage. The changes in canopy cover, basal area of hackberry, and bare ground and litter can be seen in Figures 1 and 2.

An examination of the magnitude of the canonical discriminant function coefficients (Klecka 1987) indicated the relative importance that 3 key variables had among groups within each function (Table 3). Basal area of hackberry was most important in function 1 and explained 54% of the total variation. Cover of western snowberry was important in function 2, followed by hackberry basal area, and this function explained 40% of the total variation. Function 3 explained 6% of the total variation, and the combined cover of *Prunus* species (chokecherry + wild plum) was the most important variable in the final function (Table 3).

Each key variable is weighted as a separate function that reflected the biotic contribution of each key plant variable in characterizing vegetation dynamics within this ecological type, and the magnitude of the Fisher's classification function coefficients indicated the contribution that each variable had among seral stages (Table 1). Mean values of each variable can be viewed graphically in Figure 1. Fisher's classification discriminant function coefficients represent the equations that are easily calculated to define seral stages only (Table 1) (see Benkobi and Uresk 1996 for an example of the calculation). Posterior probabilities, calculated from the unstandardized canonical coefficients, group centroids, and Fisher's classification function coefficients, indicate not only the most likely seral

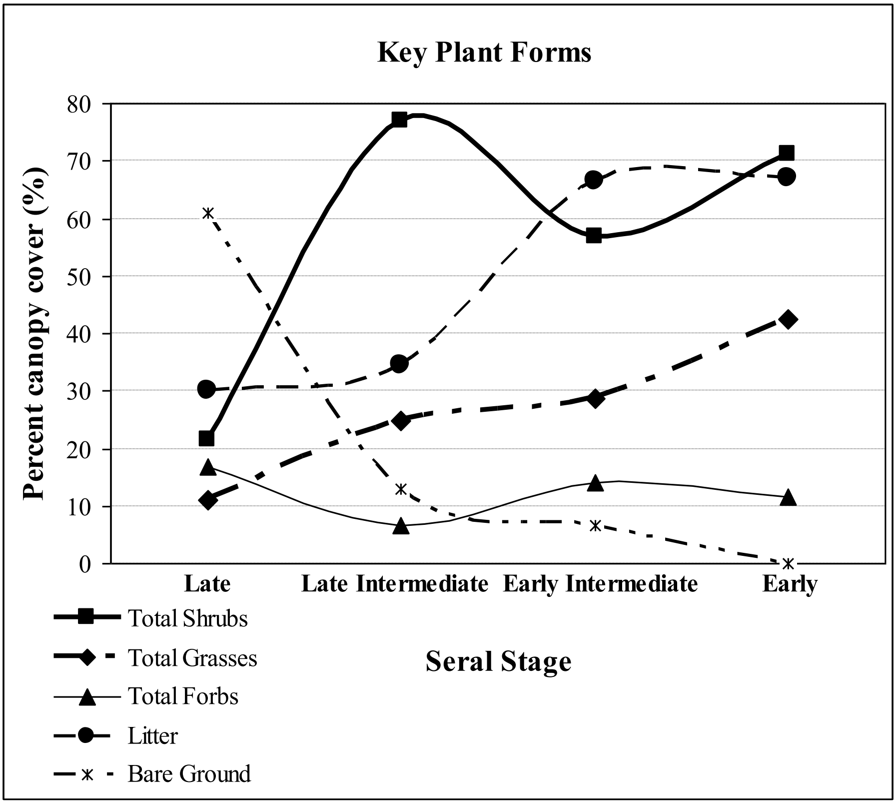

Figure 2: Means (% cover) of life forms, litter, and bare ground through four stages of succession in a hackberry-shrub ecological type. Smoothed lines connect the means of each key variable at each stage and provide an approximate representation of the mixture of life forms, litter and bare ground at each seral stage.

stage, but also the location of a sample site within a seral stage. The magnitude of the posterior probabilities (between 0 and 1) calculated for any combination of key variable values is used to determine if a site is at a seral stage center or between two seral stages. The result of the discriminant analysis model presented in this paper (Tables 1 and 3) defines seral stages and provides quantitative information about successional trend within and among seral stages. This model can be used easily to assign sites to seral stages. Excel based spreadsheets can be downloaded from the Forest Service web site (www.fs.fed.us/rangelands/ecology/ecologicalclassification/index.shtml) and used as both data sheet and a tool to provide all required calculations. All coefficients required to assign data to seral stage and calculate posterior probabilities are listed in Tables 1 and 3.

DISCUSSION

The ability to identify seral stages and relate them to prescribed management activities is essential for resource managers to achieve a desired seral stage

Table 3. Unstandardized canonical discriminant function coefficients and constant with variables listed in order of entrance into the discriminant analysis. The size of the coefficient (absolute value) is an indication of the importance the variable has within a function. Bottom part of table lists the seral stage mean canonical coefficients for the Nebraska National Grasslands hackberry-shrub ecological type.

Species	**Function 1**	**Function 2**	**Function 3**
Basal area *Celtis occidentalis*	0.09334948	-0.0766484	0.04247468
Canopy cover *Prunus* (*P. virginiana* + *P. americana*)	-0.05533517	-0.0127679	0.07205255
Canopy cover *Symphoricarpos occidentalis*	0.07191538	0.1176954	0.04650303
Constant	-0.5116958	-0.6596175	-2.708885
Percent of variation explained	54	40	6
Seral stage mean canonical coefficients (group centroids)			
Late	4.44154	-3.68304	0.37231
Late intermediate	-4.06130	-1.32605	1.92567
Early intermediate	-1.05214	-0.39519	-0.51764
Early	1.50116	2.45539	0.32765

(Dyksterhuis 1985; Uresk 1990). The developed statistical model related to the hackberry-shrub succession, which was based on ecological concepts of plant succession (Clements 1916; Dyksterhuis 1949; Daubenmire 1968), allows the determination of seral stages, thus providing a useful tool for resource managers with field measurements of only a few key variables (Table 1). The current model was developed using data collected from a contemporary ecological type and thus can be used to determine seral stages regardless of hypothetical past or future climax vegetation. It is more realistic to monitor existing ecological types based on key plant species currently present for grazing and wildlife management purposes than attempt to predict hypothetical past or future climax vegetation. Therefore, a range of seral stages (early to late) and dominant plant species collected during sampling were used in a sequence of multivariate statistical analyses to determine the key plant species that best characterizes the seral stages of the hackberry – shrub ecological type.

Monthly precipitation was above average the year before data collection (1988) and much below compared to the long-term average of the region in 1989 during data collection. Average monthly precipitation for the Nebraska locations compared to long-term monthly data for 1988 show above average precipitation (106-380% greater) in all but four months. Monthly precipitation for 1989 represented 12% - 92% below the long-term average for all months except January and February of 1989, which were 35% greater and equal, respectively (HPRCC 2007). This probably had some effect on annuals and herbaceous vegetation, but less measurable impacts on the trees and shrub species selected as key variables for the model.

State and transition models of plant succession have received much attention as a method to describe ecological processes and transitions from multiple possible stable states at a single site (Briske et al. 2005). The hackberry–shrub multivariate statistical model provides a quantitative process and method to assign seral stages at a given site over time within a contemporary ecological type to measure succession. Natural processes (drought, wildfire, wildlife burrows and others) and management activities (livestock grazing, prescribed burns, fire suppression and others) as they impact vegetation at a site can be monitored using the model and defined seral stages. This type of plant community succession model fits well into the state and transition conceptual model.

The greater canopy cover of western snowberry in the early stage of this ecological type may be the results of fire suppression or other environmental change and/or management prescription. Once snowberry or other shrubs become established and begin to increase, then the site condition has crossed or begins to cross a structural threshold and begins to change from grassland site to shrub-woodland site. Depending on site conditions and management, the site progresses toward woodland, remains static as a snowberry shrubland, or reverts back to grassland. The establishment of snowberry or other shrubs alters the succession process by altering the grassland microclimate and enables the growth and establishment of *Prunus* species and hackberry saplings. Snowberry canopy in the early seral stage can triple the amount of aboveground biomass and increase the mass of large roots at a site (Bai et al. 2009). The shrub canopy increases, and high levels of litter in the early seral stages may inhibit or enhance emergence survival of some tree and shrub species (Ibanez and Schupp 2002). The establishment of shrubs and the greater litter cover in the early seral stages can change the chemical and physical condition of the microhabitat (Carson and Peterson 1990; Paez and Marco 2000). These changes may include an increase in mineral and nutrient availability from greater mycorrhizal fungus activity, an increase in available soil moisture and decreases in soil temperature, light levels, evaporation, and evapotranspriation at a site. All of this can affect seedling germination and survival (Facelli and Pickett 1991a, 1991b; Ibanez and Schupp 2002).

The hackberry-shrub type provides a food source for many mammal and bird species, provides nesting cover for many prairie bird species, and provides shade and protective winter cover for wildlife and livestock (Martin et al. 1961; Severson and Boldt 1978; Uresk 1982; Kauffman and Krueger 1984; Lesica and Cooper 1998). The different structural stages of this type may offer various thermal regimes and the ability to intercept and alter snow accumulation. The vertical structure is also important for numerous wildlife species, like deer for bedding, or forage areas (Nudds 1977; Rumble and Gobeille 1995; Rumble and Gobeille 1998) for birds (Hodorff et al. 1988; Bleed 1990; Fritcher et al. 2004; Uresk et al. 2009).

Sharptail grouse are an important ground nesting game bird in the Nebraska Sand Hills ecosystem and prefer dense cover of shrubs, grasses and forbs (Hillman and Jackson 1973; Sisson 1970; Prose 1987; Meints et al. 1992) and depend on grass-dominated habitats intermixed with patches of trees and shrub cover year round (Connelly et al. 1998). Patches of tree and shrub cover provide sharp-tailed grouse food and protective winter cover (Sisson, 1976; Oedekoven 1985; Meints 1991; Giesen and Connelly 1993). McDonald (1998) in eastern Washington found litter cover and visual obstruction were greater at nest sites and bare ground was less at nest sites compared to random sites. Litter cover at successful nest sites was greater than 80% compared with near 70% observed in the early seral stages of the hackberry-shrub type. Therefore, maintaining different seral stages within the habitat type and providing some hackberry-shrub ecological type throughout the landscape are important for managers in order to provide year round habitat for multiple species.

This model was specifically developed on National Forest System lands within boundaries of the Nebraska National Forest and limited to the hackberry – shrub ecological type. It is important that the same ecological type be present when collecting data. Verification testing of this model should be completed when using this model beyond National Forest System lands.

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LITERATURE CITED

Abrams, M.D. and A.K. Knapp. 1996. Seasonal water relations of three gallery forest hardwood species in northeast Kansas. Forest Sci. 32(3):687-696.

Afifi, A.A. and V. Clark. 1990. Computer-aided multivariate analysis. 2nd Ed. Van Nostrand Reinhold Company, New York.

Bai, Y., T. Colberg, J.T. Romo, B. McConkey, D. Pennock, and R. Farrell. 2009. Does expansion of western snowberry enhance ecosystem carbon sequestration and storage in Canadian prairies? Agric. Ecosystems, and Environ. 134(3-4): 269-276.

Ball, G.H.,and D.J. Hall.1967. A clustering technique for summarizing multivariate data. Behavioral Sci. 12: 153-155.

Benkobi, L., and D. W. Uresk. 1996. Seral stage classification and monitoring model for big sagebrush/western wheatgrass/blue grama. In: J. R. Barrow; M.E. Durant, R.E. Sosebe, R.J. Tausch, Ed. Shrubland ecosystem dynamics in a changing environment; Proceedings of the symposium; 1995 May 23-25; Las Cruces, NM. Gen. Tech. Rep. INT-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Benkobi, L., D.W. Uresk, and R.D. Child. 2007. Ecological Classification and monitoring model for the Wyoming big sagebrush shrubsteppe habitat type of northeastern Wyoming. W. N. American Nat. 67(3): 347-358.

Bestelmyer, B.T., J. R. Brown, K.M. Havstad, R. Alexander, G. Chavez, and J. E. Herrick. 2003. Development and use of state-and-transition models for rangelands. J. Range Manage. 56: 114-126.

Bleed, A., and C. Flowerday. 1990. An atlas of the Sand Hills. A. Bleed and C. Flowerday, Eds. Conservation and Survey Div., Univ. of Nebraska, Lincoln, NE. 265 pp.

Bleed, A. 1990. Introduction to plants and animals. Pp. 123-126. In: An atlas of the Sand Hills, A. Bleed and C. Flowerday, Eds. Conservation and Survey Div., Univ. of Nebraska, Lincoln, NE.

Bragg, T.B. and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. J. Range Manage. 29(1):19-24.

Briske, D.D., S.D. Fuhlendorf, and F.E. Smeins. 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. J. Range Manage. 58: 1-10.

Burzlaff, D.F. 1962. A soil and vegetation inventory and analysis of three Nebraska sandhills range sites. Nebraska Agr. Exp. Sta. Res. Bull. 206. Lincoln, NE.

Carson, W.P., and C.J. Peterson. 1990. The role of litter in an old field community: impact of litter quantity in different seasons on plant species richness and abundance. Oecologia 85: 8-13.

Clements. F.E. 1916. Plant succession: An analysis of the development of vegetation. Carnegie Inst. Publ. 242.

Connelly, J.W., M.W. Gratson, and K.P. Reese. 1998. Sharp-tailed grouse (*Tympanuchus pahianellus*). No. 354 in A. Poole and F.Gill, Ed. The birds of North America. Acad Nat. Sci. and Amer. Ornith. Union. Philadelphia, PA.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33(1): 43-64.

Daubenmire, R. 1968. Plant communities: a textbook of plant synecology. Evanston and London: Harper & Row. New York, 300 pp.

del Morel, R. 1975. Vegetation Clustering by Means of ISODATA: Revision by Multiple Discriminant Analysis. Vegetatio 29: 179-190.

Dyksterhuis, E.J. 1949. Condition and management of rangeland based on quantitative ecology. Journal of Range Management. 2(1): 104-115.

Dyksterhuis, E.J. 1985. Follow-up on range sites and condition classes as based on quantitative ecology. Rangelands. 7(4): 172-173.

Facelli, J.M., and S.T.A. Pickett. 1991a. Indirect effects of litter on woody seedling subject to herb competition. Oikos 62: 126-138.

Facelli, J.M., and S.T.A. Pickett. 1991b. Plant litter: its dynamics and effects on plant community structure. Bot. Rev. 57: 1-32.

Farrar, J. 1979. The Nebraska Sandhills. North Central States Student Wildlife Conclave, Lincoln, NE, March 17, 1979.

Fritcher, S.C., M.A. Rumble, and L.D. Flake. 2004. Grassland bird densities in seral stages of mixed-grass prairie. J. Range Manage. 57: 351-357.

Gabel, M.L., D.C. Backlund, and J. Haffner. 1998. The Miocene flora of the Ogallala Group, northern Nebraska and southern South Dakota. J. Paleont. 72(2): 386-397.

Giesen, K.M., and J.W. Connelly. 1993. Guidelines for management of Columbian sharp-tailed grouse habitats. Wildlife Soc. Bull. 21: 325-333.

Hall, D.J., and D. Khanna. 1977. The ISODATA Method of computation for relative perceptions of similarities and differences of complex and real data. In: Statistical Methods for Digital Computers, K. Enslein, A. Ralston, and H.W. Wilf (Editors). John Wiley and Sons, New York, Vol. 1, pp.340-373.

Hillman, C.N., and W.W. Jackson. 1973. The sharp-tailed grouse in South Dakota. No. 3, G125730001, SD Dept. Game, Fish, and Parks, Pierre, SD.

Hodorff, R.A., C.H. Sieg and R.L. Linder. 1988. Wildlife responses to stand structure of deciduous woodlands. J. Wildl. Manage. 52: 667-673.

HPRCC-High Plains Regional Climate Center. 2007. High Plains Regional Climate Center website (http://www.hprcc.unl.edu/products/home.htm, specifically at http://www.hprcc.unl.edu/products/home.htm, specifically http://www.hprcc.unl.edu/cgi-bin/cli_perl_lib/cliMONtpre.pl?ne8755 (/cliMONtpre.pl?ne3540 and /cliRECtM.pl?ne5860 respectively). Long-term monthly totals for Valentine (June 1948 – October 2006) and Halsey (February 1903 – December 1989) Nebraska were summarized for long-term mean. Data accessed April 28, 2007.

Humphrey, R.R. 1947. Range forage evaluation by the range condition method. J. Forest. 45(1): 10-14.

Ibanez, I., and E.W. Schupp. 2002. Effects of litter, soil surface conditions, and microhabitat on *Cercocarpos ledifolius* Nutt. seedling emergence and establishment. J. Arid Environ. 52: 209-221.

Jakes, P.J., and W.B. Smith. 1982. A second look at North Dakota's timber land. U.S. Dep. Agric. For. Serv. Bull. NC-58.

Kaul, R. 1990. Plants. in: An atlas of the Sand Hills. A. Bleed and C. Flowerday, Eds. Conservation and Survey Div., Univ. of Nebraska, Lincoln, NE, pp. 127-142.

Klecka, W.R. 1987. Discriminant Analysis. Sage University paper Series Quantitative Applications in the Social Sciences, Series No. 07-019. Sage Publ. Beverly Hills, CA.

Kauffman, J.B., and W.C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications-a review. J. Range Manage. 37: 430-438.

Lesica, P., and S.V. Cooper. 1998. Succession and disturbance in Sandhills vegetation: constructing models for managing biological diversity. Cons. Biol. 13: 293-302.

Loucks, O.L., M.L. Plumb-Mentjes, and D. Rogers. 1985. Gap processes and large-scale disturbances in sand prairie. In: S.T.A. Pickett and P.S. White, Eds. The ecology of natural disturbance and patch dynamics. Acad. Press, Orlando, FL, pp. 72-85.

MacCracken, J.G., D.W. Uresk, and R.M. Hanson. 1983. Plant community variability on a small area in southeastern Montana. Great Basin Nat. 43(4): 660-668.

Martin, A.C., H.S. Zim and A.L. Nelson. 1961. American wildlife and plants, a guide to wildlife food habits. Dover Pub. Inc. New York. 500 pp.

McDonald, M.W. 1998. Ecology of the sharp-tailed grouse in eastern Washington. Thesis. Univ. Idaho, Moscow, ID.

Meints, D. R. 1991. Seasonal movement, habitat uses, and productivity of Columbian sharp-tailed grouse in southeastern Idaho. Thesis. Univ. Idaho, Moscow. ID.

Meints, D.R., J.W. Connelly, K.P. Reese, A.R. Sands and T.P. Hemker. 1992. Habitat suitability index procedures for Columbian sharp-tailed grouse. Idaho Forest, Wildlife and Range Exp. Station, Bull. 55.

Meneguzzo, D.M., G.J. Brand, and W.R. Lovett. 2007. Nebraska's forest resources in 2005. Resour. Bull. NRS-16. Newton Square, PA: USDA. Forest Service Northern Research Station. 21p.

Norusis, M.J./SPSS Inc. 1992. SPSS/PC+ professional statistics version 5.0. Chicago, IL.

Nudds, T.D. 1977. Quantifying the vegetative structure of wildlife cover. Wildlife Soc. Bull. 5(3): 1313-117.

Oedekoven, O.O. 1985. Columbian sharp-tailed grouse population distribution and habitat use in south central Wyoming. Thesis, Univ. Wyoming, Larimie, WY.

Pickett, S.T.A., and P.S. White. 1985. The ecology of natural disturbance and patch dynamics. Acad. Press. Orlando, FL.

Paez, S.A., and D.E. Marco. 2000. Seedling habitat structure in dry Chaco forest (Argentina). J. Arid Environ. 46: 57-68.

Pool, R.J. 1914. A study of the vegetation of the Sand Hills of Nebraska: Univ. Minnesota Bot. Studies 4, pp. 189-312.

Prose, B.L. 1987. Habitat suitability index models – plains sharptailed grouse. USFWS Biol. Rep. 82(10.142) 31 pp.

Pyke, D.A., J.E. Herrick, P. Shaver and M. Pellant. 2002. Rangeland health attributes and indicators for qualitative assessment. J. Range Manage. 55: 584-597.

Retallack, G.J. 1983. A paleopedological approach to the interpretation of the terrestrial sedimentary rocks: the mid-Tertiary fossil soils of Badlands National Park South Dakota. Geolog. Soc. of America Bull. 94: 823-840.

Rolfsmeier, S., and G. Steinauer. 2010. Terrestrial ecological systems and natural communities of Nebraska. Version IV-March 9. Nebraska Natural Heritage Program and Nebraska Game and Parks Comm. Lincoln, NE. 223 pp. Accessed online June 29, 2010 at:http://www.prairienebraska.org/NE%20terr%20comm%20complete%20final%20doc%20in%20word%20_Mar%202,%202010_.pdf.

Rumble, M.A., and J.E. Gobeille. 1995. Wildlife associations in Rocky Mountain juniper in the Northern Great Plains, South Dakota. In: D.W. Shaw; E.F. Aldon; C. LoSapio, Ed. Desired future conditions for piñon-juniper ecosystems; proceedings of the symposium; 1994 August 8-12; Flagstaff, AZ. Gen. Tech. Rep. RM-258. Fort Collins, CO: U.S. Dept. Agric., Forest Service, Rocky Mountain Forest and Range Experiment Station. pp. 80-90.

Rumble, M.A., and J.E. Gobeille. 1998. Bird community relationships to succession in green as (*Fraxinus pennslyvanica*) woodland. Am. Midl. Nat. 140: 372-381.

Sampson, A.W. 1919. Plant succession in relation to range management. U.S. Dept. Agric. Bull. No. 791. 76 pp.

Severson, K.E., and C.E. Boldt. 1978. Cattle, wildlife, and riparian habitats in western Dakota. In: Management and use of northern Plains rangeland (J.C. Shaver, ed.) Regional Rangeland Symposium, Bismark, ND. North Dakota State University, Fargo, ND.

Schmidt, T.L. 1986. Forestland resources of the Nebraska Sandhills. T.D. Wardle, Ed. U. Neb. Lincoln, Dept. Forestries, Fisheries, and Wildlife, Neb. For. Serv. 86p.

Sisson, L.H. 1970. Vegetational and topographic characteristics of sharp-tailed grouse habitat in Nebraska. Project W-38-R-3, Nebraska Game and Parks Commission, Lincoln, NE.

Sisson, L.H. 1976. The sharp-tailed grouse in Nebraska. Nebraska Game and Parks Commission, Lincoln, NE.

Sousa, W.P. 1984. The role of disturbance in natural communities. Annual review of ecology and systematics. 15: 353-391.

SPSS Inc. 2003. SPSS Base 12 for Windows User Guide. SPSS Inc., Chicago, IL.

Steinauer, E.M., and T.B. Bragg. 1987. Ponderosa pine (*Pinus ponderosa*) invasion of Nebraska Sandhills Prairie. Am. Midl. Nat. 118: 358-365.

Steinauer, G., and S. Rolfsmeier. 2003. Terrestrial natural communities of Nebraska. Version III-June 30. Nebraska Natural Heritage Program and Nebraska Game and Parks Comm. Lincoln, NE. 162 pp.

Steuter, A.A., C.E. Grygiel, and M.E. Biondini. 1990. A synthesis approach to research and management planning: the conceptual development and implementation. Nat. Areas J. 10: 61-68.

Stubbendieck, J., and S.J. Tunnell. 2008. Seventy-eight years of dynamics in a Sandhills grassland. Nat. Areas J. 28: 58-65.

Uresk, D.W. 1990. Using multivariate techniques to quantitatively estimate ecological stages in a mixed-grass prairie. J. Range Manage. 43: 282-285.

Uresk, D.W., J.J. Javersak, and D.E. Mergen. 2009. Tree sapling and shrub heights after 25 years of livestock grazing in green ash draws in western North Dakota. Proc. SD Academy Sci. 88: 99-108.

Uresk, D.W. 1982. Importance of woodlands to wildlife and livestock use on the Northern High Plains. In: Proceedings of the Great Plains Agricultural Council, North Platte, NE. pp. 7-12.

USDA, NRCS. 2010. The PLANTS Database (http://plants.usda.gov. 22 November 2010). National Plant Data Center, Baton Rouge, LA 70874-4490. USA.

Weaver, J.E., and F.W. Albertson. 1956. Grasslands of the Great Plains: their nature and use. Lincoln, NE: Johnson Publishing Company. 395 pp.

Westoby, M., B.Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. J. Range Manage. 42: 266-274.