Available online at www.sciencedirect.com
ScienceDirect
ELSEVIER
Landscape and Urban Planning xxx (2006) xxx–xxx
LANDSCAPE AND URBAN PLANNING
This article is also available online at:
www.elsevier.com/locate/landurbplan

Modeling the effects of herbivores on the abundance of forest overstory states using a state-transition approach in the upper Grande Ronde River Basin, Oregon, USA

Marty Vavra [a,*], Miles A. Hemstrom [b], Michael Wisdom [a]

[a] *USDA Forest Service, Pacific Northwest Research Station, La Grande Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, USA*

[b] *USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, P.O. Box 3890, Portland, OR 97208-3890, USA*

Abstract

Herbivory by wild and domestic ungulates profoundly affects vegetation patterns and processes. We modeled changes in the abundance of different interior Pacific Northwest forest states in a large landscape over time, by using a simple state and transition model and assumptions regarding how the intensity of herbivory might influence conifer regeneration rates. We modeled hypothetical herbivory effects under three disturbance regimes: (1) a natural disturbance regime without fire suppression, (2) a natural disturbance regime with only fire suppression, and (3) an active fuels management regime in which forest management was used to reduce probabilities of severe wildfires and in which wildfires were suppressed. Herbivory effects were modeled as "high" or "low" to explore how the intensity of ungulate herbivory might influence overstory canopy structure and composition. Our simulations predicted that high herbivory influences the abundance of forest overstory structural classes over time in all three disturbance scenarios. Our results illustrate how landscape-level planning decisions affecting herbivore densities and grazing regimes might influence the structural attributes of forests over time under different disturbance regimes.

Keywords: Herbivory; Forest state dynamics; Disturbance; Landscapes

1. Introduction

Herbivory by wild and domestic ungulates has profound effects on ecosystem patterns and processes in a variety of forest settings (Augustine and McNaughton, 1998; Pastor and Naiman, 1992; Riggs et al., 2000). The implications of herbivory effects on landscape management decisions are of interest to land managers and planners and have legal and policy implications related to the Federal Endangered Species Act (1973) and National Forest Management Act (1976).

Hobbs (1996) made the case that native ungulates are critical agents of change in ecosystems via three processes: regulation of process rates, modification of spatial mosaics, and action as switches controlling transitions between alternative ecosystem states. Huntly (1991) identified the impact of herbivores on plant regeneration as a powerful yet little-studied mechanism of influence on vegetation composition, structure, and diversity. In the northwestern United States, both wild and domestic ungulates have been recognized as agents of chronic disturbance in forest landscapes, capable of influencing succession, nutrient cycles, and habitat characteristics to extents equal to episodic fire or timber harvest (Riggs et al., 2000).

Evidence is growing that succession can be controlled or altered dramatically by chronic herbivory (Augustine and McNaughton, 1998; Hobbs, 1996; Jenkins and Starkey, 1996; Peek et al., 1978; Schreiner et al., 1996). Variation in the herbivory regime (i.e., variation in the herbivore species, and timing, duration, or intensity of grazing) can vary the pattern and rate of successional change, and even vary the apparent endpoint of the succession. Thus, to predict landscape vegetation dynamics with confidence, one must understand how herbivory influences succession among both transient and stable vegetation states, and the herbivory thresholds that precipitate transitions among the various states.

An extensive review by Jones (2000) revealed that cover of grasses and shrubs as well as total vegetation biomass are

* Corresponding author. Tel.: +1 541 962 6561; fax: +1 541 962 6504.
E-mail addresses: mvavra@fs.fed.us (M. Vavra), mhemstrom@fs.fed.us (M.A. Hemstrom), mwisdom@fs.fed.us (M. Wisdom).

0169-2046/$ – see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.landurbplan.2006.10.005

often reduced by cattle grazing. Riggs et al. (2000) reported that understory biomass at seven grand fir (*Abies grandis*) and Douglas-fir (*Pseudotsuga menziesii*) exclosure sites averaged 2.1 times greater inside than outside and forest-floor biomass was 1.5 times greater inside than outside, largely the result of herbivory by wild ungulates. Shrub biomass was influenced more by ungulates than was grass or forb biomass. Augustine and McNaughton (1998) concluded that altered species composition of plant communities in response to selective foraging by ungulates is a general feature of plant-ungulate relations; ungulates alter competitive relations among plants, with specific plant species differing in tolerance to herbivory. Such effects are not limited to plant species growing in forest understories, but also include effects on overstory species as well (Augustine and McNaughton, 1998).

Woodward et al. (1994) and Schreiner et al. (1996) found that ungulates reduced understory standing crop, increased forb species richness, and determined the distribution, morphology, and reproductive performance of several shrub species. The extent to which herbivores can change ecosystem processes in forests likely depends on the scales of other disturbances (Woodward et al., 1994), and on the relationship between disturbance scale, herbivore density, and the rate of forest succession (Riggs et al., 2004). Effects of herbivores in interior forests may be more striking than in coastal forests because of the relatively slow rate at which succession proceeds in the drier interior environments (Riggs et al., 2004).

Herbivory-induced changes in plant composition have ramifications for plant and animal species. Changes in understory structure and litter accumulations may be important to bird and small mammal populations (DeCalesta, 1994; Fagerstone and Ramey, 1996). Persistence of some species of plants, and even plant communities may be at risk when subjected to prolonged intensive herbivory.

In interior landscapes, such as our study area, documented declines in aspen (*Populus tremuloides*), bitterbrush (*Purshia tridentata*), Pacific yew (*Taxus brevifolia*), and mountain mahogany (*Cercocarpus* spp.) (Parks et al., 1998) have implicated chronic herbivory. Negative effects on vertebrate species that depend on these plants (e.g., cavity nesters in aspen stands) have been implied as well (Wisdom et al., 2000). The role of herbivory interacts with the roles played by other disturbance agents such as fires, insect and disease outbreaks, and applied silviculture (Riggs et al., 2004). Thus, the combined effects of these disturbance events shape the structure and composition of forests and, ultimately, the biodiversity found there.

Management actions including prescribed burning and thinning may be used to reduce tree density and fuels as means of reducing fire risks. Concomitant with such management activities, however, will be the continuing risk of wildfires in areas yet to be treated, given the substantial portion of forest landscapes that may not receive management attention because of limitations of time, money, and practicality of application. Consequently, vast acreages have been and may continue to be altered by wildfire (Hemstrom et al., 2001, in this volume). For example, 17% of the Wallowa-Whitman National Forest has burned in the last 10 years. Such widespread disturbances set in motion secondary plant successions across broad fronts, which then are subject to modification by herbivores to varying extents.

Landscape management involves planning and modification of disturbance regimes that include chronic herbivory as well as episodic disturbance agents (e.g., wild and prescribed fire, fuels management, insects and disease) over long periods. Consequently, the design of landscape management scenarios should logically involve consideration of how these various disturbance agents can be expected to interact with one another over time. Thus far, with few exceptions, most research concerning herbivory influences on forest dynamics has not vigorously addressed the extent to which decisions concerning herbivore management might be expected to influence the outcome of management regimes for other disturbance agents. In this paper we explore how variation in herbivory by large herbivores might influence the temporal dynamism of transient and stable forest structures in interior Pacific Northwest forests under different disturbance regimes.

We use a simple state and transition model (STM) approach (e.g., Laycock, 1991; Westoby et al., 1989) to illustrate how variance in ungulate herbivory might be expected to influence forest structure over time in context with the regimes of other disturbance agents. Our modeling approach used both deterministic and probabilistic paths for vegetation change among stable states and transient states based on knowledge and assumptions regarding the influences of agents or conditions that induce transitions among states. The utility of the approach is dependent upon the reliability of knowledge and assumptions made by the model.

2. Study area

The upper Grande Ronde River Basin study area is part of a fourth hydrologic unit code subbasin occupying approximately 178,000 ha of mixed forest and rangelands on the eastern flank of the Blue Mountains southwest of La Grande, Oregon (Fig. 1). Of this area 122,114 ha is managed by the USDA Forest Service. The remaining land is in mixed ownerships consisting of private (53,551 ha), tribal (1373 ha), and state (885 ha). The topography is highly varied and complex, with deeply dissected drainages feeding into the Grande Ronde River as it runs north through the center of the area. Vegetation ranges from dry bunchgrass-dominated communities at the lower, north end of the drainage, to high-elevation conifer-dominated forests at the southern end (Johnson and Clausnitzer, 1992). Elevations range from 360 m to over 2100 m. Lands managed by the USDA Forest Service (Forest Service) dominate the study area and include wilderness, riparian reserves, lynx habitat management areas, and general forest. Privately owned lands tend to be managed primarily for timber production and livestock forage, although this varies considerably by ownership.

The current disturbance regime includes occasional large wildfires and insect outbreaks, commercial timber management, and grazing by livestock and wild ungulates (Hemstrom et al., in this volume). The area has a long history of intensive grazing by horses, sheep, cattle, and wild ungulates. Intensive grazing probably began in the 1700s with Native American horses. Widespread impacts began in the 1870s with the expansion of

Please cite this article in press as: Vavra, M. et al., Modeling the effects of herbivores on the abundance of forest overstory states using a state-transition approach in the upper Grande Ronde River Basin, Oregon, USA, Landscape Urban Planning (2006), doi:10.1016/j.landurbplan.2006.10.005

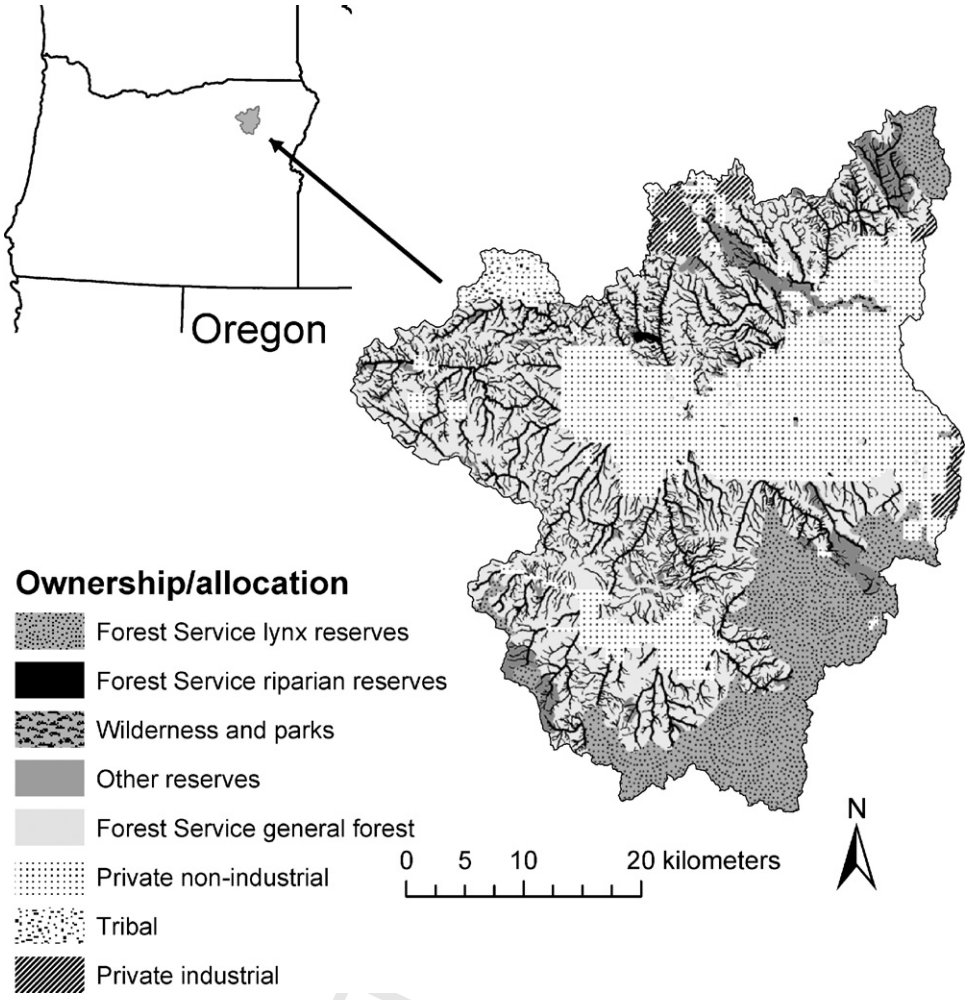

Fig. 1. The upper Grande Ronde River Basin, OR, USA.

cattle and sheep grazing, which then peaked by 1900 (Johnson and Swanson, 2005). Livestock numbers declined after 1906 as the Forest Service began to regulate grazing through the allotment system (Johnson and Swanson, 2005). In the last 30 years, livestock grazing has decreased slightly, but there has been a substantial increase in elk numbers with a decline in deer numbers (Wells et al., 2001) resulting in a net gain in animal unit months of herbivory.

Ecologists and managers in the Pacific Northwest routinely use potential vegetation classifications to reflect environment, disturbance regimes, and vegetation growth potential on forest sites (e.g., Johnson and Clausnitzer, 1992; Pfister and Arno, 1980; all adapted after Daubenmire, 1952), and for organizing matrices to support decision making (McGrath et al., 2003). Hemstrom et al. (in this volume) grouped potential natural vegetation described for the Blue Mountains (Johnson and Clausnitzer, 1992) into three major forest environments (cold, cool-moist, and warm-dry). Cold forest environments include potential vegetation in the subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and the highest elevation portions of the grand fir forest series. Engelmann spruce (*Picea engelmannii*) and subalpine fir dominate older forests in these environments. Cool-moist forest environments include potential vegetation in the grand fir and Douglas-fir series and occupy about 30% of the forest landscape in the study area. Mixed stands of grand fir and Douglas-fir dominate older cool-moist forests at middle elevations. Western larch (*Larix occidentalis*), lodgepole pine, and ponderosa pine occur in early seral stands in cool-moist environments, depending on local conditions. Warm-dry forests in the ponderosa pine and the driest portions of the grand fir and Douglas-fir series occupy about 42% of the forested land. Grand fir, Douglas-fir, and ponderosa pine are the major conifers in warm-dry forests. Ponderosa pine is especially drought tolerant and occurs on the warmest and driest sites capable of supporting forests. Hemstrom et al. (in this volume) used combinations of tree size class, canopy cover, canopy layering, non-forest vegetation life form, and potential vegetation classes to assign existing and projected future vegetation into 308 state classes that represent either transient or stable forest states that are included in their models.

3. Methods

We modeled the abundance of transient and stable forest states by using a simple state-transition approach similar to those developed for rangeland ecosystems (Laycock, 1991; Westoby

Please cite this article in press as: Vavra, M. et al., Modeling the effects of herbivores on the abundance of forest overstory states using a state-transition approach in the upper Grande Ronde River Basin, Oregon, USA, Landscape Urban Planning (2006), doi:10.1016/j.landurbplan.2006.10.005

et al., 1989). These models may include one or more state classes that are relatively stable over a long period (hundreds of years or more), transient states that are not stable over such long periods and which may have their ultimate potential altered by events that occur during their lifespan, and transitions among states that are precipitated by explicit conditions or disturbance events. In northwestern forests, the stable states in such models are appropriately defined by late seral or climax plant associations (e.g., Johnson and Clausnitzer, 1992) that have been described based on polyclimax ecological theory (Riggs et al., 2004). In polyclimax theory, more than one plant association may develop on any given site depending on the disturbance agents that control the succession and maintain the climax. We chose to aggregate some of the polyclimax forms into various warm-dry, cool-moist, and cold forest types.

In our simulations, transient states are represented by the various seral, or structural stages of forest overstory development, and herbivory is integrated into the model as one of the agents capable of precipitating transitions within sequences of transient and stable states (e.g., Cattelino et al., 1979; Hann et al., 1997; Horn, 1975; Laycock, 1991; Noble and Slayter, 1980; Westoby et al., 1989). For example, a grass/forb-closed herbland might become dominated by small trees, grasses, forbs, and shrubs after a period in the absence of significant disturbance, or might remain as a grass/forb community indefinitely under a regime of recurrent wildfire. In the first disturbance regime, the herbland is a transient state, but under the second it is a fire climax. As Hemstrom et al. (in this volume) apply the concept, state change along the successional, time-dependent path is generally deterministic, and, without disturbance or management, all the vegetation would ultimately accumulate in one long-term stable state (a climatic, edaphic, or physiographic climax, after Tansley, 1935). However, disturbances or management activities can change the course of vegetative development at any point, and recurrent disturbances may under some circumstances be responsible for the maintenance of long-term stable, facilitated equilibria (fire or grazing climax, after Tansley, 1935). Depending on disturbance probabilities and consequences, very little or no vegetation may actually accumulate in the long-term stable state at the endpoint of succession. Our models include several alternative stable states in each forest environment. We define these as stable states if the state class cycled back to itself either through the passage of time with no disturbance or through a natural disturbance agent operating in the background disturbance regime (see below). Stable states included two conditions in each forest environment: (1) large tree, single-story, open structure dominated by a fire-tolerant species (maintained by frequent under-burning); and (2) large tree, multi-story, open structure dominated by shade-tolerant species (in the absence of disturbance). All other state classes were transitory, although some could persist for long periods owing to infrequent disturbance.

The basis for our herbivory-mediated transitions was the analysis of ungulate herbivory effects in the Blue Mountains from long-term ungulate exclosures in the area and the implications Riggs et al. (2000) made about the density of conifer regeneration inside and outside grazing exclosures. In general, Riggs et al. (2000) results showed that competing vegetation (grasses, forbs, and shrubs) was much more abundant inside ungulate exclosures, where small conifers were not abundant, than outside exclosures, where small conifers were generally abundant. The abundance of conifer regeneration outside exclosures compared to inside exclosures is, we suggest, due to a combination of reduced vegetative competition and more mineral soil seed bed outside exclosures.

We adapted the STM developed by Hemstrom et al. (in this volume) and used their existing and potential vegetation classes in our STM. They used vegetation data from aerial photograph interpretation and field stand examinations developed by the Wallowa-Whitman and Umatilla National Forests. These data are typical of the kind used by the local national forests and other land managers in the Blue Mountains and elsewhere in the northwest. Hemstrom et al. (in this volume) defined forest structure classes based on dominant lifeform (trees, shrubs, grass/forb), diameter breast height (dbh) of dominant trees, tree canopy cover, and tree canopy layering. The forest structure classes accommodated modeling of a variety of forest products, wildlife habitat, available vegetation (aerial photograph interpretation and stand examinations), and disturbance effects (e.g., wildfire, fuels treatments, etc.). Their classification was not specifically designed for modeling herbivory effects, but was useful for our purposes. Vegetation size class was divided into six categories based the presence of trees and average dbh for dominant trees: (1) grass/forb dominated, (2) shrub dominated, (3) seedlings/saplings (dominant trees <12.5 cm dbh), (4) small trees (dominant trees 12.5 to <40 cm dbh), (5) medium trees (dominant trees 40 to <52.5 cm dbh), and (6) large trees (dominant trees ≥52.5 cm dbh). Stands dominated by trees were further divided into three canopy cover classes: (1) tree canopy ≤10% cover was classified as grass/forb or shrub dominated, (2) tree canopy 10% to <40% (warm-dry forests) or 10 to <60% (cool-moist and cold forests) was open forest, and (3) tree canopy ≥40% (warm-dry forest) or ≥60% (cool-moist and cold forest) was dense forest. Finally, tree-dominated stands were divided into those with one, two, or multiple canopy layers. For the most part, we combined structures into simple one versus multiple layers and open versus dense canopy cover.

In sum, our STM included combinations of structure class (tree size, canopy cover, canopy layering), overstory species, disturbance history, and potential vegetation for a total of 308 state classes (Hemstrom et al., in this volume). We did not include lands that do not potentially support forests in our models owing to lack of information about their fire and disturbance regimes.

3.1. Assumptions

Based on information from Riggs et al. (2000), similar studies in other comparable ecosystems (Schreiner et al., 1996; Woodward et al., 1994) summarized knowledge of ungulate/vegetation relationships (Augustine and McNaughton, 1998; Hobbs, 1996), and our own observations about ungulate behavior in the study area, we made several important assumptions in building our STM. Our assumptions have two major themes: (1) ungulate grazing mediates the development of vegetation that competes with conifer seedlings and thereby affects

Please cite this article in press as: Vavra, M. et al., Modeling the effects of herbivores on the abundance of forest overstory states using a state-transition approach in the upper Grande Ronde River Basin, Oregon, USA, Landscape Urban Planning (2006), doi:10.1016/j.landurbplan.2006.10.005

the rate of seedling establishment, and (2) natural conifer regeneration occurs as probabilistic events conditioned by seed year frequency, local climate, seed availability, and competing vegetation. In the following Sections 3.1.1–3.1.4 we illustrate our assumptions by highlighting their implications to grazing effects in the dry Douglas-fir/grand fir plant association group, which is part of our warm, dry environment. We utilized transition probabilities populated by expert opinion because we lacked sufficient data from long-term exclosures in a wide variety of habitat types. In addition, most studies of succession and descriptions of habitat types include the confounding influence of extant herbivory so the potential vegetation community composition in the absence of herbivory is not really known. However, except for our assumption that heavy herbivory is currently pervasive in our study area, we tried to use conservative estimates about the rates and pathways of herbivory effects.

3.1.1. High herbivory definition

We assume that "high" ungulate herbivory could occur across 90% of the study area, limited only by the relatively few areas of very steep slopes or topography otherwise inaccessible to wild ungulates and domestic livestock. In normally shrub-dominated seres, we define high ungulate herbivory as any combination of type, density, or distribution of herbivores sufficient to cause a transition between model state classes when continued for 5 years. Riggs et al. (2000) reported that shrubs were more strongly affected than herbs by herbivory, and that striking herbivore-induced changes in species composition could be observed within as little as 4 years following episodic disturbance. For seres normally dominated by native grasses, we define the time threshold for a state change owing to high herbivory as 20 years. This timeframe was difficult to estimate owing to the complex defoliation aspects for grasses. The removal of current year's growth from a shrub has lasting impacts owing to the persistent nature of the stems, so that the timing of defoliation is less important than in grasses. Defoliation of grasses after senescence has little impact on the physiological well being of the plant as most above-ground material is standing dead at that time. Mack and Thompson (1982) estimated that native grasses in the intermountain region could be replaced in less than 40 years owing to herbivory effects. Milchunas and Lauenroth (1993) performed multiple regression analyses on a world-wide grassland data set and found that changes in dominant grass species leveled off after approximately 30 years of grazing. We chose 20 years based on our interpretation of Riggs et al. (2000) and local experience.

3.1.2. Understory succession

We assume that the normal condition after a stand-replacement event (especially wildfire) is initially a native grass/shrub community (Table 1). We also assume that native grasses and forbs would be replaced by exotic-dominated grasses and forbs following 20 years of high grazing. If not grazed or otherwise disturbed for 20 years, however, native grass/forb communities succeed to a state dominated by palatable shrubs. In the dry Douglas-fir/grand fir plant association group, for example, several palatable shrubs may become dominant after a stand-replacing disturbance, including snowberry (*Symphoricarpos albus*), spirea (*Spirea betulifolia* var. *lucida*), ninebark (*Physocarpus malvaceus*), and *Ceanothus* spp. (Johnson, 1998). We assume that communities dominated by palatable shrubs, native grasses and forbs, and scattered conifers may persist for decades in the absence of stand-replacing disturbance or heavy grazing.

3.1.3. Initial conifer regeneration

Relatively infrequent conifer regeneration events may produce an open stand of conifers with dense shrub/grass/forb understories (Table 1). We assume these regeneration events are substantially hindered by the dense understory, taking an average of over 50 years to occur in the dry Douglas-fir/grand fir environment.

Heavy grazing, however, favors development of exotic grasses and forbs with unpalatable shrubs. We assume that heavy grazing reduces the competitive abilities of this understory, compared to that in an ungrazed condition, and that a transition to a dense conifer stand may develop in less than 20 years as a consequence of conifer regeneration events and succession (Table 1).

3.1.4. Regeneration under a canopy

We assumed, above, that heavy grazing increased rates and densities of conifer regeneration early in stand development. We also assumed that heavy grazing affects the establishment and development of small trees under an existing conifer canopy (Table 1). A stand that has developed under heavy grazing often develops dense canopy cover and high tree numbers early in succession. Tree growth may produce larger trees under such conditions, but we assume that inter-tree competition often makes this a slow process. For example, we assumed that it takes 50 years for a small tree, one-layer, dense stand to reach a medium tree, one-layer, dense stand in the absence of disturbance. This allows for a condition often called "stagnation" to occur where trees in densely crowded stands grow slowly.

Our models allow some, albeit a small, portion of our landscape under a heavy grazing regime to escape grazing on a stochastic basis. These stands develop into more open conditions with relatively more dense understories of palatable shrubs and native grasses and forbs. However, these lightly grazed or ungrazed stands may begin to experience heavy grazing and, as a consequence of reduced understory competition, develop layers of small conifers (Table 1). Over time, these stands become dense and follow the development of other heavily grazed conditions. We assume conifer regeneration under an open tree canopy following the onset of heavy grazing proceeds more slowly than it would after stand-replacing disturbance because the existing larger trees produce shade that hinders seedling establishment. Shade also tends to favor regeneration of the more shade-tolerant conifer species.

Our models generally allow several alternative development paths from a given class owing to within-class variation. For example, a medium tree, one-layer, open ponderosa pine stand may be sparsely stocked and contain a dense shrub layer that inhibits regeneration. In the absence of heavy grazing, trees grow into large tree size so that the stand becomes large tree, one-layer, open structure. The same stand may have been more densely

Please cite this article in press as: Vavra, M. et al., Modeling the effects of herbivores on the abundance of forest overstory states using a state-transition approach in the upper Grande Ronde River Basin, Oregon, USA, Landscape Urban Planning (2006), doi:10.1016/j.landurbplan.2006.10.005

Table 1
Assumed grazing, succession, and growth transitions of conifer-dominated structures in the ponderosa pine cover type in a warm, dry Douglas-fir/grand fir environment

From-class	Agent[a]	To-class	Begin years	Transition years
Native grass/forb	Succession	Palatable shrub	1	20
	Regen PP	PP—seedling/sapling open	1	53
	Graze	Exotic grass/forb	1	22
Palatable shrub	Succession	Palatable shrub	100	1
	Regen PP	PP—seedling/sapling open	1	107
	Graze	Unpalatable shrub	1	6
Exotic grass/forb	Succession	Unpalatable shrub	20	1
	Regen PP + graze	PP—seedling/sapling dense	1	27
	Regen DF/GF + graze	DF/GF—seedling/sapling dense	1	159
Unpalatable shrub	Succession	PP—seedling/sapling dense	20	1
	Regen PP + graze	PP—seedling/sapling dense	1	53
	Regen DF/GF + graze	DF/GF—seedling/sapling dense	1	312
PP—seedling/sapling open	Tree growth	PP—small tree one layer open	32	1
	Tree growth	PP—seedling/sapling dense	25	10
	Graze	PP—seedling/sapling dense	1	74
PP—seedling/sapling dense	Tree growth	PP—small tree one layer dense	32	1
PP—small tree one layer open	Tree growth	PP—medium tree one layer open	50	1
	Tree growth	PP—small tree one layer dense	40	20
	Regen PP	PP—small tree two layer open	40	40
	Regen DF/GF	DF/GF-small tree two layer open	40	40
	Regen PP + graze	PP—small tree two layers open	1	74
PP—small tree one layer dense	Tree growth	PP—medium tree one layer dense	50	1
	Regen DF/GF	DF/GF—small tree one layer dense	1	3
PP—small tree two layer open	Tree growth	PP—medium tree two layer open	50	1
	Tree growth	PP—small tree two layer dense	40	13
	regen DF/GF	DF/GF—small tree two layer open	40	40
	Regen PP + graze	PP—small tree two layer dense	1	74
PP—small tree two layer dense	Tree growth	PP—medium tree two layer dense	50	1
	Regen DF/GF	DF/GF—small tree one layer dense	40	100
PP—medium tree one layer open	Tree growth	PP—large tree one layer open	55	1
	Tree growth	PP—medium tree one layer dense	40	20
	Regen PP	PP—medium tree two layer open	40	20
	Regen PP + graze	PP—medium tree two layers open	1	74
PP—medium tree one layer dense	Tree growth	PP—large tree one layer dense	55	1
	Regen DF/GF	DF/GF—medium tree one layer dense	40	100
PP—medium tree two layer open	Tree growth	PP—large tree multi-layer open	55	1
	Tree growth	PP—medium tree two layer dense	40	10
	Regen PP + graze	PP—medium tree multi-layer dense	1	74
PP—medium tree two layer dense	Tree growth	PP—large tree multi-layer dense	55	1
PP—medium tree multi-layer open	Tree growth	PP—large tree multi-layer open	55	1
	Tree growth	PP—medium tree multi-layer dense	40	10
	Regen PP + graze	PP—medium tree multi-layer dense	1	74
PP—medium tree multi-layer closed	Tree growth	PP—large tree multi-layer dense	55	1
PP—large tree one layer open	Tree growth	PP—large tree one layer open	363	1
	Tree growth	PP—large tree one layer dense	40	20
	Regen DF/GF	DF/GF—large tree multi-layer open	40	20
	Regen PP + graze	PP—large tree multi-layer open	1	111
PP—large tree one layer closed	Tree growth	PP—large tree multi-layer dense	34	1
	Regen DF/GF	DF/GF—large tree single layer open	40	100
PP—large tree multi-layer open	Tree growth	PP—large tree multi-layer open	363	1
	Tree growth	PP—large tree multi-layer dense	40	10
	Regen PP + graze	PP—large tree multi-layer dense	1	74
PP—large tree multi-layer closed	Tree growth	PP—large tree multi-layer dense	363	1
	Regen DF/GF	DF/GF—large tree multi-layer dense	40	100

Begin time is the years a modeling unit (area of vegetation in the from-class) must spend before the agent begins to occur. Transition time is the average time taken for a modeling unit to make the transition once the agent begins to occur. The same agent may cause more than one transition based on the variability within the from-box.

[a] Succession, replacement of species without disturbance. Regen, a regeneration event. Graze, heavy grazing. Tree growth, increase in tree diameter or canopy cover over time. PP, ponderosa pine, DF, Douglas-fir.

Please cite this article in press as: Vavra, M. et al., Modeling the effects of herbivores on the abundance of forest overstory states using a state-transition approach in the upper Grande Ronde River Basin, Oregon, USA, Landscape Urban Planning (2006), doi:10.1016/j.landurbplan.2006.10.005

stocked initially while still meeting our criteria for small tree, one-layer, open structure. In the absence of heavy grazing, the trees grow into large tree size and the canopies converge so that the stand becomes large tree one-layer dense structure. However, if high grazing begins, herbivory reduces competing vegetation cover, allows conifer regeneration, and the stand becomes a medium tree, multi-layer, dense structure. Note that when the model is run with heavy grazing these disturbances are additive. The tree growth that occurs without heavy grazing occurs with heavy grazing, but stands can also take an additional path leading to dense forest condition. In sum, heavy grazing increases the rate at which forests can become dense by adding pathways or increasing transition rates.

3.2. Disturbance scenarios

We modeled vegetation state-dynamics and disturbance conditions that might result from two management scenarios and one natural disturbance scenario as described by Hemstrom et al. (in this volume). The scenarios represent likely combinations of management activities and natural disturbances. Our model formulation allows the user to adjust the probabilities of disturbances or management activities or, in fact, turn entire suites of disturbances or activities on or off by using a set of multipliers to form a "scenario." A scenario includes the set of allowed disturbances and activities as well as the scaling of their probabilities to mimic a particular management strategy or disturbance regime for each land ownership and allocation category. Because multiple disturbances lead to and from each state class and because the model revisits each state class and its associated disturbances in each annual time step, the model has many potential feed-back loops. For example, high ungulate herbivory can produce abundant dense forest structures that have high probabilities for stand-replacing wildfire. Stand-replacing wildfire followed by high ungulate herbivory once again produces abundant dense forest structure. The strength of the feed-back loop and resulting simulation results depend on the entire combination of transitions and probabilities in the model. To simulate the potential effects of high ungulate herbivory, we added transitions and probabilities representing our assumed herbivory effects to the models developed by Hemstrom et al. (in this volume) and turned those herbivory effects "on" or "off" for each of the following scenarios.

3.2.1. Background natural disturbance scenario

The background natural disturbance scenario did not include management activities and was intended to represent the likely conditions under current climate in the absence of modern management activities. Fire, insects, disease, and other natural disturbances were modeled at what Hemstrom et al. (in this volume) assumed to be the rates and probabilities that would apply under the current climate without human intervention. This scenario was modeled with the same natural disturbance probabilities across all ownerships and land allocations.

The background natural disturbance scenario is generally similar to disturbance conditions assumed in various analyses of the "historical range of variability" (Agee, 2003; Hann et al., 1997; Wimberly et al., 2000) but does not assume that model projections actually represent some set of past or historical conditions (Hemstrom et al., in this volume). Rather, the scenario estimates the effects of the disturbance regimes described in the fire history literature (e.g., Heyerdahl et al., 2001) and from expert opinion on the vegetation as it might occur at present. Projections from this scenario represent potential conditions given current climatic conditions and natural disturbance probabilities as inferred from fire history studies.

3.2.2. Fire suppression only scenario

The fire suppression only scenario developed by Hemstrom et al. (in this volume) assumed no management activities on publicly-owned lands other than fire suppression, salvage following stand-replacement disturbances, and tree planting following salvage. However, the scenario assumed active management, mostly for timber production, on privately-owned forest lands. This assumes that current management (e.g., as modeled in the active fuel treatment approach below) would continue on privately-owned lands even if a fire suppression only approach was undertaken on publicly-owned lands.

3.2.3. Active fuel treatment scenario

An active fuels treatment scenario included levels and kinds of management activities on publicly-owned lands designed to: (1) actively treat canopy and surface fuels to reduce wildfire risks in general forest lands within the first decade and (2) to maintain relatively low levels of canopy and surface fuels across the landscape after the first decade. We did not adjust the management regime on privately-owned lands in this scenario because management on privately owned industrial forest land (the bulk of privately-owned forest land in the study area) already had a management regime that actively thinned stands and treated fuels. The probabilities of all activities were adjusted to reflect differences in ownership and land allocation (see Hemstrom et al., in this volume). On public lands, for example, precommercial thinning is not used in lynx habitat areas, and silvicultural management is very limited in riparian areas. Wildfire suppression continued at current levels. Natural disturbance probabilities other than those for wildfire remained at current levels.

3.3. Model projections

We ran the model for 200 years with an annual time step for each scenario. Input for each model run was the current vegetation conditions and the multiplier file that adjusted transitions and probabilities for disturbance and management by ownership as appropriate for the three scenarios. Output from each simulation was a database of the proportional distribution of each state class and proportion of the landscape affected by each disturbance or management activity for each simulation year.

4. Results and discussion

4.1. Background natural disturbance scenario

High herbivory in the background natural disturbance scenario produced abundant seedling/sapling and small tree

Please cite this article in press as: Vavra, M. et al., Modeling the effects of herbivores on the abundance of forest overstory states using a state-transition approach in the upper Grande Ronde River Basin, Oregon, USA, Landscape Urban Planning (2006), doi:10.1016/j.landurbplan.2006.10.005

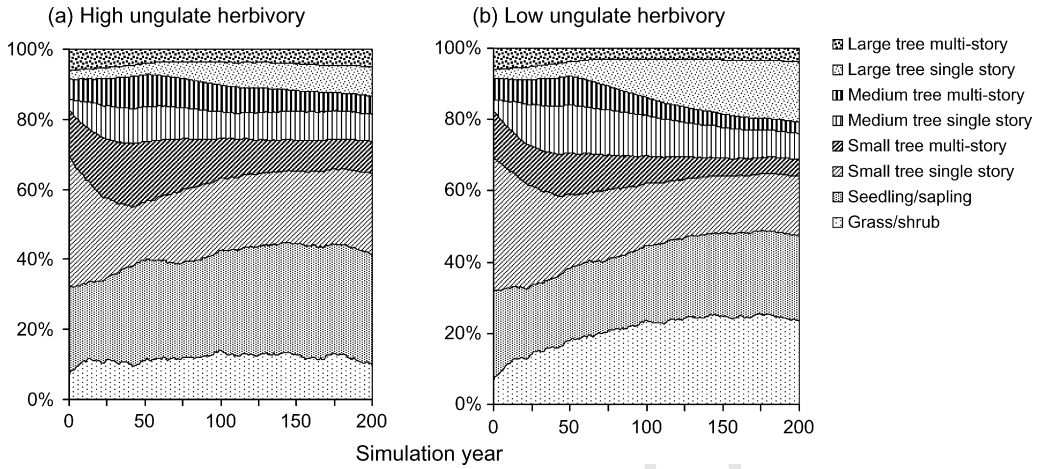

Fig. 2. Proportion of landscape in different forest structure classes under background natural disturbances with (a) high levels of ungulate herbivory and (b) low levels of ungulate herbivory in the upper Grande Ronde River Basin, OR, USA.

structures (Fig. 2a). The largest differences between high and low grazing model results were in the relative abundances of grass/shrub and large tree, single-story, open forests. Grass/shrub conditions occupied nearly 25% of the landscape area at the end of 200 years under low grazing, but only 10% under high grazing (Fig. 2a and b). Likewise, large tree, single-story stands occupied about 17% of the landscape under low grazing, but only 8% under high grazing. All the other structural classes increased slightly under high grazing compared to low grazing. High grazing caused a decrease in both old, single-story forests open forests and grass/shrub conditions by increasing the rate of conifer invasion, as one might expect given assumptions built into the models. High grazing also increased the proportion of the area dominated by trees in the small and medium size classes, both open and dense, by increasing the overall potential for stands to become dense. Because dense stands have a higher probability of experiencing stand-replacement wildfire in our background disturbance regime, wildfire recycled forests back through early seral conditions (small and medium tree size classes) more frequently under high grazing than low grazing. Our models and underlying assumptions suggest that high ungulate herbivory might reduce accumulation of vegetation in the large tree, single-story stable state under natural conditions by enhancing the effects of stand-replacing disturbances.

Our projections of background disturbance conditions raise some interesting questions about how land managers, scientists, and others might think about "historic range of variability". Mack and Thompson (1982) argued that most ecological systems in our portion of the interior west did not evolve with high populations of large ungulates. If our model and assumptions were reasonable and Mack and Thompson (1982) were correct, historical fire regimes in our study area would have been constrained by relatively small ungulate grazing effects, whereas we consider current grazing levels to be high in our study area.

4.2. Fire suppression only scenario

High ungulate herbivory in the fire suppression only scenario produced the lowest total area of large tree forest of any of our simulations (Fig. 3a). This result is a straight-forward result of the combined effects of grazing (increases stand density) and stand-replacement disturbances (more frequent in dense stands).

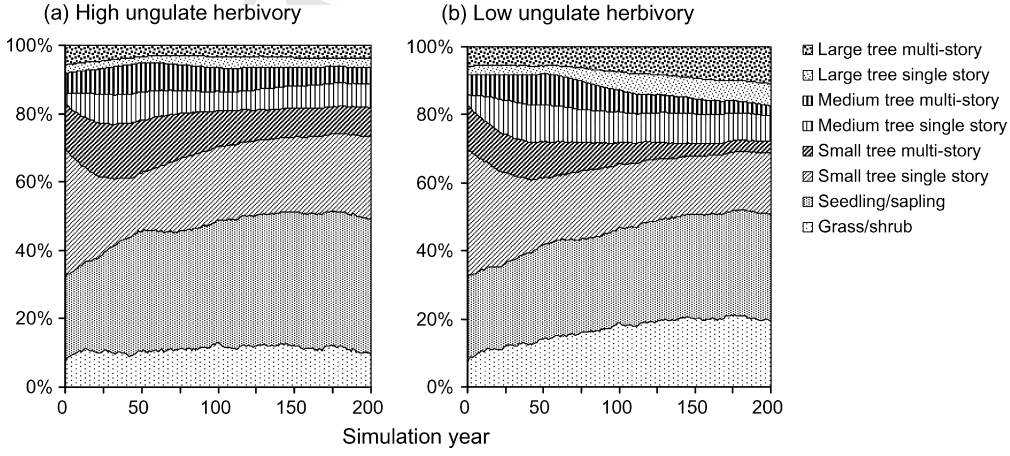

Fig. 3. Proportion of landscape in different forest structure classes under a fire suppression only management scenario with (a) high levels of ungulate herbivory and (b) low levels of ungulate herbivory in the upper Grande Ronde River Basin, OR, USA.

Please cite this article in press as: Vavra, M. et al., Modeling the effects of herbivores on the abundance of forest overstory states using a state-transition approach in the upper Grande Ronde River Basin, Oregon, USA, Landscape Urban Planning (2006), doi:10.1016/j.landurbplan.2006.10.005

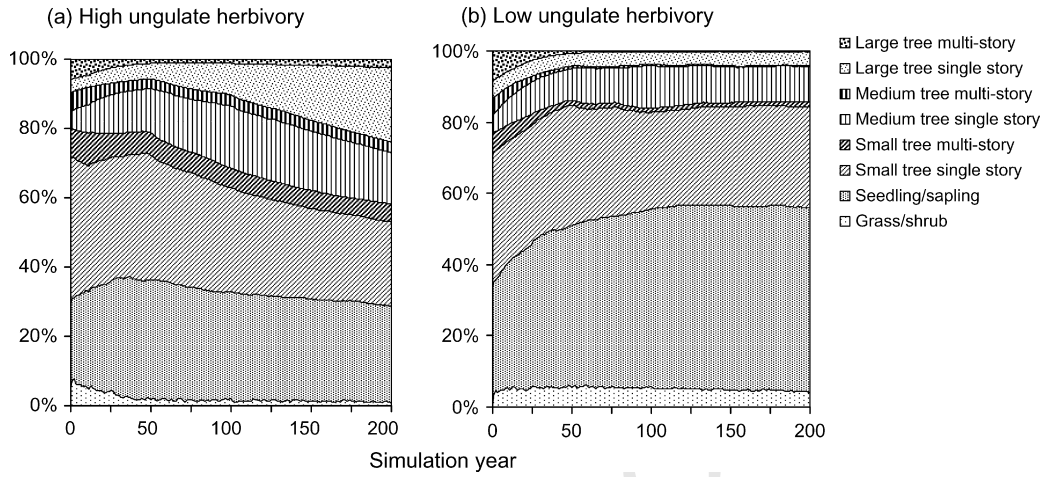

Fig. 4. Proportion of landscape in different forest structure classes under an active fuel treatment management with (a) high levels of ungulate herbivory and (b) low levels of ungulate herbivory in the upper Grande Ronde River Basin, OR, USA.

The combination of wildfire suppression, lack of fuel treatment on publicly-owned land, and high ungulate grazing resulted in lower area in large tree forests than currently exists. Interestingly, the combination of fire suppression only and high grazing produced results that most closely resemble the current condition. Somewhat conversely, the combination of fire suppression only and low herbivory produced the highest amount of large tree, multi-story forest of any simulation we ran (Fig. 3b). These results suggest that the long-term effects of grazing may have important implications for many wildlife species dependent on large tree forests (Wales et al., in this volume).

4.3. Active fuel treatment scenario

The active fuel treatment scenario with high grazing illustrates the effects of two opposing disturbances: fuels treatment is aimed at keeping fuels and, consequently, stand densities relatively low but, high ungulate grazing allows quick conifer regeneration (Fig. 4a) and, hence, pushes the system toward dense forest structures that are more prone to wildfire. However, reducing fuels and production of single-story large tree stands was a primary objective of active fuel treatments. The interaction of both influences generates rapid conversion of multi-story forests to single-story condition through treatment, whereas rapid regeneration reduces grass/shrub components. This synergy produced the greatest amounts of medium and large tree single-story forests of any we tested. It also produced very little grass/shrub and medium to large multi-story forests.

Conversely, active fuel treatment combined with low herbivory produced relatively little large tree single-story forest but abundant seedling/sapling and small tree forests (Fig. 4b). Active fuel treatment converted much of the currently available multi-story forest to single-story structure. Stand-replacing disturbances, although generally lower than in some other scenarios, cycled some medium and large tree forests back to early seral stands, most of which were planted with conifers. Rapid re-planting of burned areas coupled with low herbivory favored abundant grass/shrub competition in relatively open stands of small trees. The landscape became dominated by open stands of seedling/sapling and small tree stands, a component of medium and large tree single-story stands, and little else.

4.4. Knowledge limitations

Many factors define the herbivory regime on any particular forest site (Riggs et al., 2004), and site-specific regimes vary across landscapes as a function of how the types of herbivores (e.g., cattle, wild herbivores) differ in terms of distribution and density (Coe et al., 2001). Because each landscape is unique, and because the combinations of animal type, density, and distribution are many, the development of predictive models is at the same time both important and difficult. Important variables for the development of realistic models include vegetation types and condition, animal distribution as it relates to vegetation preferences and factors that mediate those preferences such as physical features of the landscape (slope, aspect, and topography), water distribution, and factors that modify use of preferred vegetations such as traffic on roads, or the presence of other herbivore species. We largely ignore these spatial factors in this paper, choosing instead to focus on how large differences in the intensity of herbivory might be expected to influence forests over time without respect to spatially-explicit variation.

Rupp et al. (2000a,b) and Starfield et al. (1993) explored the likely influences of climate change on disturbance probabilities and resultant state transitions with more detailed process-based STM. We recognize that climate change could have a strong influence on disturbance probabilities and vegetative trajectories in our area as well (Riggs et al., 2004), but did not include climate change in our models. Most of our model projections reached relatively stable levels after 200 years; a somewhat shorter time than observed in studies that have incorporated climate change (see Rupp et al., 2000a,b; Starfield et al., 1993).

Ungulate herbivory, as we modeled it, modified forest succession through alteration of conifer regeneration rates as a function of impacts on competing grass/shrub canopy cover and forest floor conditions. We assumed that a high level of herbivory

Please cite this article in press as: Vavra, M. et al., Modeling the effects of herbivores on the abundance of forest overstory states using a state-transition approach in the upper Grande Ronde River Basin, Oregon, USA, Landscape Urban Planning (2006), doi:10.1016/j.landurbplan.2006.10.005

would substantially reduce the canopy cover of competing vegetation and expose more mineral soil, thereby facilitating conifer establishment. Dense, multi-story forests did not necessarily become more abundant under high grazing, however, because of interactions among grazing and other natural disturbance and management effects produced mixed results in this regard (Figs. 2–4). In addition, our models projected herbivore-induced differences in the abundance of both transient and stable states in all three scenarios.

4.5. Model limitations

STM require explicit statement of assumed relations among factors that shape forest structure across large landscapes. A weakness in this approach is that many of the critical relations between herbivory, competing vegetation, and conifer regeneration are not well understood and are not documented in the literature. We relied on the sparse existing literature, our interpretations of the literature, and the knowledge of local experts. This approach, does, however, point to important gaps in scientific understanding of herbivory and conifer regeneration. Hemstrom et al. (in this volume) discuss the more general strengths and weaknesses of the STM approach. They suggest that STMs have several particularly useful aspects: (1) they are relatively easy to build and understand, (2) they can incorporate information of differing types (including the literature, expert opinion, and other models), and (3) they integrate and subsume complex ecological interactions in a box and arrow conceptual understanding that allows exploration, projection, and hypothesis testing. This approach has weaknesses, often as counterpoints to its strengths. In particular, collapsing complex ecological relations and variable sources of information make it difficult to understand the potential impacts of varying data reliability and the details of complex interactions.

Further examination of our models and assumptions presented might be best accomplished with parallel work by using models that are more closely linked to ecosystem processes (e.g., Coughenour, 1993; Rupp et al., 2000a,b; Weisburg et al., 2002). In particular, such models might operate at finer spatial and temporal scales and consider the influences of unequal herbivore distribution and range of densities. Developing process-based models would provide opportunity to adjust probabilities of herbivory effects on stable and transient state transitions and provide a second, independent source of estimates for transition paths, rates, and probabilities. However, modeling spatially-explicit forage removal by multiple species of ungulates across large landscapes is a complex problem (Weisburg et al., 2002). The most difficult challenge would be modeling the long-term response of plant population densities to herbivory.

5. Conclusions

It is important to consider ungulate herbivory, and indeed any disturbance, in light of synergistic interactions with other disturbances and management activities. Our models integrated ungulate herbivory, natural disturbances, and management activities. The models contain many inter-dependencies and feed-back loops that generated complex interactions among disturbances. We also explicitly included both conifer regeneration and ungulate grazing as disturbances, which allowed us to consider interactions between herbivory, competing vegetation, and conifer regeneration.

Varying the level of ungulate herbivory had substantial effects on the abundance of some forest structures over time. The direct effects of high ungulate herbivory were increased conifer density and decreased levels of grass/shrub conditions. The ultimate effects of herbivory, however, depended to a large degree on interactions with other disturbances and management activities.

Our hypotheses about the interactions of ungulate herbivory and long-term forest structure imply that large herbivores might have substantial influences on conifer density, amounts of various forest structural classes, and disturbance regimes in a large landscape. Although our model predictions are uncertain, they do suggest that high levels of herbivory might tend to make forests denser and increase fuels, counter to the intentions of managers trying to reduce fuels and fire risks.

Acknowledgements

The authors would like to acknowledge support from the USDA Forest Service, Pacific Northwest Research Station Focused Science Delivery and Managing Disturbance Regimes Programs, the USDA Forest Service National Fire Plan for project funding, and the La Grande Ranger District of the Wallowa-Whitman National Forest for assistance in building and calibrating models and supplying vegetation data.

References

Agee, J.K., 2003. Historical range of variability in eastern Cascades forests, Washington USA. Landscape Ecol. 18, 725–740.

Augustine, D.J., McNaughton, S.J., 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J. Wildl. Manage. 62, 1165–1183.

Cattelino, P.M., Noble, I.R., Slayter, R.O., Kessell, S.R., 1979. Predicting the multiple pathways of plant succession. Environ. Manage. 3, 41–50.

Coe, P.K., Johnson, B.K., Kern, J.W., Findholt, S.L., Kie, J.G., Wisdom, M.J., 2001. Responses of elk and mule deer to cattle in summer. J. Range Manage. 54, A51–A76.

Coughenour, M.B., 1993. The SAVANNA Landscape Model-Documentation and User's Guide. Natural Resources Ecology Laboratory, Colorado State University, Fort Collins, CO.

Daubenmire, R.F., 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecol. Monogr. 22, 301–330.

DeCalesta, D.S., 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. J. Wildl. Manage. 58, 711–718.

Endangered Species Act [ESA], 1973. 16 U.S.C. 1531–1536, 1538–1540.

Fagerstone, K.A., Ramey, C.A., 1996. Rodents and lagomorphs. In: Krausman, P.R. (Ed.), Rangeland Wildlife. The Society for Range Management, Denver, CO, pp. 83–132.

Hann, W.J., Jones, J.L., Karl, M.G., Hessburg, P.F., Keane, R.E., Long, D.G., Menakis, J.P., McNicoll, C.H., Leonard, S.G., Gravenmier, R.A., Smith, B.G., 1997. Landscape dynamics of the basin. In: Quigley, T.M., Arbelbide, S.J. (Tech. Eds.), An Assessment of Ecosystem Components in the Interior Columbia Basin and Portions of the Klamath and Great Basins: Volume 2. Gen. Tech. Rep. PNW-GTR-405. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, pp. 337–1055.

Please cite this article in press as: Vavra, M. et al., Modeling the effects of herbivores on the abundance of forest overstory states using a state-transition approach in the upper Grande Ronde River Basin, Oregon, USA, Landscape Urban Planning (2006), doi:10.1016/j.landurbplan.2006.10.005

Hemstrom, M.A., Korol, J.J., Hann, W.J., 2001. Trends in terrestrial plant communities and landscape health indicate the effects of alternative management strategies in the interior Columbia River Basin. Forest Ecol. Manage. 153, 106–126.

Hemstrom, M.A., Merzenich, J., Reger, A., Wales, B. Integrated analysis of landscape management scenarios using state and transition models in the upper Grande Ronde River Basin, Oregon, USA. Landscape Urban Plan., in this volume.

Heyerdahl, E., Brubaker, L.B., Agee, J.K., 2001. Factors controlling spatial variation in historical fire regimes: a multiscale example from the interior west, USA. Ecology 82, 660–678.

Hobbs, N.T., 1996. Modification of ecosystems by ungulates. J. Wildl. Manage. 60, 695–713.

Horn, H.S., 1975. Markovian properties of forest succession. In: Cody, M.L., Diamond, J.M. (Eds.), Ecology and Evolution of Communities. Harvard University Press, Cambridge, MA, pp. 196–211.

Huntly, N., 1991. Herbivores and the dynamics of communities and ecosystems. Annu. Rev. Ecol. Syst. 22, 477–503.

Jenkins, K., Starkey, E., 1996. Simulating secondary succession of elk forage values in a managed forest landscape, western Washington. Environ. Manage. 20, 715–724.

Johnson, C.G., Jr. 1998. Vegetation response after wildfires in National Forests of northeastern Oregon. R6-NR-ECOL-TP-06-98. U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Portland, OR, 128 pp.

Johnson, C.G., Clausnitzer, R.R., 1992. Plant associations of the Blue and Ochoco Mountains. R6-ERW-TP-036-92. U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Portland, OR, 164 pp.

Johnson, C.G., Swanson, D.K., 2005. Bunchgrass plant communities of the Blue and Ochoco Mountains: A guide for managers. PNW-GTR-641. Pacific Northwest Research Station, U.S. Department of Agriculture, Forest Service, Portland, OR, 119 pp.

Jones, A., 2000. Effects of cattle grazing on North American arid ecosystems: a quantitative review. West. N. Am. Nat. 60, 155–164.

Laycock, W.A., 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. J. Range Manage. 44, 427–434.

Mack, R., Thompson, J., 1982. Evolution in steppe with few large, hooved mammals. Am. Nat. 119, 757–773.

McGrath, M.T., DeStefano, S., Riggs, R.A., Irwin, L.L., Roloff, G.J., 2003. Spatially explicit influences on northern goshawk nesting habitat in the interior Pacific Northwest. Wildl. Monogr. No. 154, 63.

Milchunas, D.G., Lauenroth, W.K., 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol. Monogr. 63, 327–366.

National Forest Management Act [NFMA], 1976. Act of October 22, 1976. 16 U.S.C. 1600.

Noble, I.R., Slayter, R.O., 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43, 5–21.

Pastor, J., Naiman, R.J., 1992. Selective foraging and ecosystem processes in boreal forests. Am. Nat. 139, 691–705.

Parks, C.G., Bednar, L., Tiedemann, A.R., 1998. Browsing ungulates—an important consideration in dieback and mortality of Pacific Yew (*Taxus brevifolia*) in a northeastern Oregon stand. Northwest Sci. 72, 190–197.

Peek, J.M., Johnson, F.D., Pence, N.N., 1978. Successional trends in a ponderosa pine/bitterbush community related to grazing by livestock, wildlife, and to fire. J. Range Manage. 31, 49–53.

Pfister, R.D., Arno, S.F., 1980. Classifying forest habitat types based on potential climax vegetation. Forest Sci. 26, 52–70.

Riggs, R., Tiedemann, A.R., Cook, J.G., Ballard, T.M., Edgerton, P.J., Vavra, M., Krueger, W.C., Hall, F.C., Bryant, L.D., Irwin, L.L., DelCurto, T., 2000. Modification of mixed-conifer forests by ruminant herbivores in the Blue Mountains Ecological Province. Res. Pap. PNW-RP-527. U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, La Grande, OR, 77 pp.

Riggs, R.A., Cook, J.G., Irwin, L.L., 2004. Management implications of ungulate herbivory in Northwest forest ecosystems. March 20, 2004. Trans. N. Am. Wildl. Nat. Res. Conf. 69, 767–772.

Rupp, T.S., Starfield, A.M., Chapin III, F.S., 2000a. A frame-based spatially explicit model of sub-arctic vegetation response to climatic change: a comparison point model. Landscape Ecol. 15, 383–400.

Rupp, T.S., Starfield, A.M., Chapin III, F.S., 2000b. Response of sub-arctic vegetation to transient climate change on the Seward Peninsula in north-west Alaska. Global Change Biol. 6, 5431–5555.

Schreiner, E.G., Krueger, K.A., Happe, P.J., Houston, D.B., 1996. Understory patch dynamics and ungulate herbivory in old-growth forests of Olympic National Park, Washington. Can. J. For. Res. 26, 255–265.

Starfield, A.M., Cummings, D.H.M., Taylor, R.D., Quadling, M.S., 1993. A frame-based paradigm for dynamic ecosystem models. Artif. Intell. Appl. 7, 1–13.

Tansley, A.G., 1935. The use and abuse of vegetational concepts and terms. Ecology 16, 284–307.

Wales, B., Suring, L. Hemstrom, M. Effect of landscape management alternatives on habitat for species of conservation concern in the Blue Mountains, northeastern Oregon, USA. Landscape Urban Plan., in this volume.

Weisburg, P.J., Hobbs, N.T., Ellis, J.E., Cougenhour, M.B., 2002. An ecosystem approach to population management of ungulates. J. Environ. Manage. 65, 181–197.

Westoby, M., Walker, B., Noy-Meir, I., 1989. Opportunistic management for rangelands not at equilibrium. J. Range Manage. 42, 266–276.

Wells, M., Healy, J., Vavra, M., 2001. A history of livestock and native ungulate grazing in the Wallowa-Whitman National Forest. Final Report Submitted to Pacific Northwest Research Station, Portland, OR, CD-ROM.

Wisdom, M.J., Holthausen, R.S., Wales, B.C., Hargis, C.D., Saab, V.A., Lee, D.C., Hann, W.J., Rich, T.D., Rowland, M.M., Murphy, W.J., Eames, M.R., 2000. Source habitats for terrestrial vertebrates of focus in the interior Columbia Basin: broad scale trends and management implications. Gen. Tech. Rep. PNW-GTR-485. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 529 pp.

Wimberly, M.C., Spies, T.A., Long, C.J., Whitlock, C., 2000. Simulating historical variability in the amount of old forests in the Oregon coast range. Conserv. Biol. 14, 167–180.

Woodward, A., Schreiner, E.G., Houston, D.B., Moorhead, B.B., 1994. Ungulate-forest relationships in Olympic National Park: Retrospective exclosure studies. Northwest Sci. 68, 97–110.

Please cite this article in press as: Vavra, M. et al., Modeling the effects of herbivores on the abundance of forest overstory states using a state-transition approach in the upper Grande Ronde River Basin, Oregon, USA, Landscape Urban Planning (2006), doi:10.1016/j.landurbplan.2006.10.005