

# Understanding Ungulate Herbivory-Episodic Disturbance Effects on Vegetation Dynamics: Knowledge Gaps and Management Needs

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## Abstract

*Herbivory by wild and domestic ungulates is a chronic disturbance that can have dramatic effects on vegetation dynamics. Herbivory effects, however, are not easily predicted under different combinations of episodic disturbance such as fire, timber harvest, drought, and insect defoliation. This lack of predictability poses a substantial obstacle to effective management of ungulate herbivory. Traditional models of vegetation transition in forested ecosystems have ignored the influences of ungulate herbivory, while research on effects of herbivory have typically excluded other disturbances. Of the 82 contemporary studies on ungulate herbivory we examined, only 15 (18%) considered the interactions of herbivory with episodic disturbances. Moreover, only 26 (32%) evaluated vegetation response to ungulate herbivory beyond the simplistic treatment levels of herbivory versus no herbivory. Only 31 (38%) used a repeated-measures design of sampling responses over 3 or more time periods. Finally, just 7 (9%) explicitly made inferences to large landscapes such as watersheds, which are often used for management planning. We contend that useful landscape research on herbivory must examine the interactions of ungulate grazing with other disturbance regimes at spatial extents of interest to forest and rangeland managers and under varying ungulate densities and species. We identify herbivory models that could accommodate such information for forested landscapes in western North America. Such models are essential for identifying knowledge gaps, designing future studies, and validating relations of ungulate herbivory on landscapes where episodic disturbances are common, such as those of western North America. (WILDLIFE SOCIETY BULLETIN 34(2):283-292; 2006)*

## Key words

*episodic disturbance, plant succession, state-and-transition models, succession, ungulate herbivory, ungulates, vegetation development, vegetation dynamics.*

Ungulate herbivory has profound effects on vegetation development and productivity in forest and rangeland ecosystems (Hobbs 1996, Healy et al. 1997, Augustine and McNaughton 1998, Weisburg and Bugmann 2003). When ungulates modify the structure and composition of vegetation, there is a potential cascading effect throughout the ecosystem. For example, suppression or elimination of nitrogen-fixing plants via herbivory reduces nitrogen accretion (Tiedemann and Berndt 1972, Bormann and Gordon 1989, Knops et al. 2000, Riggs et al. 2000). The outcome of decreased nutrient availability is a loss of forest productivity over time (Riggs et al. 2000) and a potential change in overstory composition (Hobbs 1996, Alverson and Waller 1997). As ungulates suppress or eliminate preferred plants in favor of unpreferred and less degradable plants, rates of nutrient cycling and energy flow change in space and time (Pastor and Cohen 1997, Schoenecker et al. 2004). A variety of above- and belowground ecological processes can be substantially altered by herbivory (Wardle 2002).

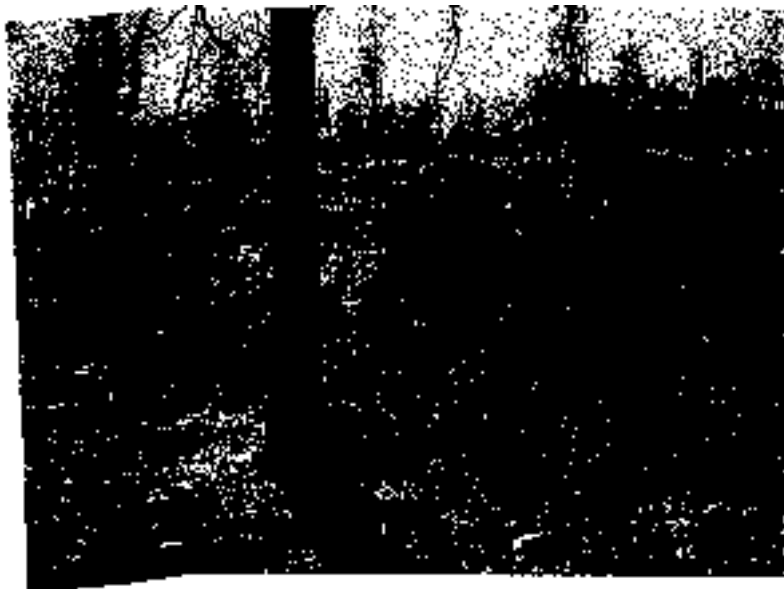
Ungulate herbivory also affects habitats for species. Herbivory-induced changes in vegetative structure can dramatically affect the associated vertebrate populations (deCalesta 1994, McShea and Rappole 2000, Cote et al. 2004). Individual plant species and entire plant communities may be at risk from some forms of

intensive ungulate herbivory (e.g., see Parks et al. 1998, Augustine and deCalesta 2003, Beschta 2005), while effects on other communities and species can be positive (Krausman 1996). Consequently, the role of herbivory in modifying floral and fauna communities suggests that ungulates can function as keystone species (i.e., species that exert a disproportionate, overriding effect on ecosystem structure or processes).

Disturbance agents, however, rarely act alone (Weisburg and Bugmann 2003). Episodic disturbance agents, such as fire, drought, and insect defoliation, interact with ungulate herbivory across time and space. The nature of ungulate herbivory-episodic disturbance interactions is unknown but likely depends on ungulate species, ungulate densities, patch choices, landscape patterns, and the frequency and intensity of the specific episodic disturbances (Hobbs 1996).

Despite these uncertainties, ungulate herbivory is thought to have important interactions with episodic disturbances such as fire. The removal of fine fuels by ungulates may reduce the frequency of ground fires but can increase the opportunity for crown fires by enhancing the development of unpalatable ladder fuels (Hobbs 1996). Moreover, the combination of fire suppression and ungulate herbivory may favor a substantial increase in density of unpalatable conifers that provide ladder fuels for crown fires, thus repeating the cycle (Vavra et al. 2004). This pattern may partially explain the higher frequency of crown fire

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**Figure 1.** Recently burned forest that demonstrates the effects of herbivory by cattle, mule deer (*Odocoileus hemionus*), and elk (*Genius elaphus*) on vegetation development within summer range in eastern Oregon, USA. The area on the left was subjected to extant herbivory by the 3 ungulate species following the wildfire and is dominated by grass species of low palatability, such as pinegrass (*Calamagrostis rubescens*). The area on the right was dominated from ungulate herbivory after the fire and is dominated by highly palatable aspen (*Populus tremuloides*) and snowbrush ceanothus (*Ceanothus velutinus*). The photo was taken 4 years after the wildfire.

interior forests of the western United States today compared to conditions prior to European settlement (Hann et al. 1997, Hemstrom et al. 2001).

If variation in herbivory can modify the influence of episodic disturbances and resultant ecological processes, then the significance of ungulates as disturbance agents is a critical part of research and management of disturbance regimes (Hobbs 1996; Riggs et al. 2000, 2004). While scientists recognize the dramatic effects that ungulate herbivory can exert on vegetation development (Fig. 1), current policies of forest management in North America do not explicitly recognize herbivory as an ecological force (see reviews by Nevill et al. 1995, Aber 2000, Cote et al. 2004, Riggs et al. 2004, and Vavra et al. 2004). Moreover, the potential effects of ungulate herbivory on processes of vegetation development are generally known, but the magnitude of effects is neither recognized nor easily predicted under different combinations of episodic disturbance, particularly across large landscapes (Weisburg and Bugmann 2003). As an example, Turner et al. (1998) summarized the effects of episodic disturbance on forest landscapes but included only a brief discussion of ungulate herbivory and its potential interactions with other disturbances. This brief discussion appears to reflect the dearth of knowledge about herbivory interactions with episodic disturbance on forest landscapes.

A similar lack of knowledge appears to exist for rangelands in western North America. While the effects of herbivory by domestic ungulates have been studied extensively in these rangelands, experimental studies of vegetation response with proper controls are lacking and research on effects from wild ungulates is sparse (e.g., see summaries by Holechek et al. 1999,

2001, and The Wildlife Society Position Statement on livestock grazing, available online at <http://wildlife.org/policy/index.cfm?name=positionstatements>). Moreover, knowledge about the interactions of ungulate herbivory with episodic disturbance, as these interactions affect rangeland vegetation, is anecdotal (Hobbs 1996, Holechek et al. 2001). However, effects of ungulate herbivory and interactions with episodic disturbances often are considered in modeling rangeland ecosystems (e.g., Hemstrom et al. 2002, Briske et al. 2005).

The spatial extent (size and boundaries of an area) at which herbivory research is conducted also conflicts with the extent used for land-use planning (Weisburg and Bugmann 2003). For example, planning in western North America often considers expansive areas, such as an ecological province (millions of hectares), a subbasin (350,000 ha), or a watershed (20,000 ha; Hann et al. 1997, Raphael et al. 2001, Wisdom et al. 2002). Yet little is known about ecosystem-level impacts of herbivory or of related factors that may modify the effects of herbivory on landscapes (Russell et al. 2001). Instead, most studies of vegetation response to herbivory have focused on individual plants or single populations in small areas (Huntly 1991).

In this paper we quantify and discuss key knowledge gaps and management needs regarding the effects of ungulate herbivory, as such effects interact with those of episodic disturbance. Our specific objectives were to 1) document the degree to which past studies of ungulate herbivory have examined the interactions with other episodic disturbances, particularly across large landscapes, under multispecies grazing and varying ungulate densities, and with a repeated-measures sampling design; 2) present an example modeling approach that considers the effects of ungulate herbivory and potential interactions with episodic disturbances in forested ecosystems; and 3) describe information needed for effective management of ungulate herbivory with episodic disturbances.

## Methods

To frame our discussion, we searched for, obtained, and reviewed articles on ungulate herbivory that were available from the United States Department of Agriculture (USDA) National Agricultural Library (<http://www.nal.usda.gov/>). We also obtained articles using bibliographic software programs, such as Absearch (<http://absearch.com/>) and Current Contents- (<http://www.isinet.com/isil/products/eel>). We used a large and diverse number of keywords in our literature searches to maximize our chances of obtaining a broad spectrum of journal publications containing empirical data on the effects of ungulate herbivory.

Our literature searches were designed to acquire a representative set of journal publications containing empirical results about the ecological effects of ungulate herbivory, as opposed to an exhaustive search of all literature. For example, we did not search for "gray literature" such as that found in workshop proceedings, agency reports, or other nonjournal outlets. We also did not consider literature that contained empirical findings about livestock grazing but that did not focus on the ecological effects of such herbivory with the use of proper experimental controls such as exclosures that could adequately measure vegetation change under ungulate exclusion.

Based on results of these searches, we reviewed the literature

published since 1990 on ungulate herbivory to characterize the types of herbivory research conducted to date and to identify knowledge gaps associated with a lack of research on particular herbivory topics. We identified 82 articles that contained original research findings on the topic (Table 1). We then calculated the number and percentage of these studies by the following categories: 1) studies that included effects of episodic disturbance as a background agent-specifically, herbivory studies that were initiated <10 years after an episodic disturbance; 2) studies that examined the interactions of episodic disturbance with ungulate herbivory, such as those done under a factorial experiment or similar research design; 3) studies that included effects of multiple species of ungulates; 4) studies that addressed >3 densities of a given ungulate species, as opposed to studies that compared only extant herbivory with total exclusion; 5) studies that measured the same response variables repeatedly over time, encompassing >2 sampling periods over >2 years; and 6) studies that explicitly made inferences to a specified spatial extent, such as a watershed (20,000 ha; Hann et al. 1997) or other large areas typically used for management in western North America (Raphael et al. 2001, Wisdom et al. 2002).

## Results

Only 28 (34%) studies were conducted at locations that had some form of episodic disturbance that occurred just before herbivory research was initiated (Table 1). Sixty-six percent ( $n = 54$ ) of the herbivory studies were conducted at locations that did not report whether episodic disturbance was included as a background agent. By contrast, only 15 (18%) studies examined the interactions of herbivory with an episodic disturbance: that is, studies that evaluated both the single and joint effects of herbivory and episodic disturbance on vegetation development, such as would be done in a factorial experiment.

Most ( $n = 54$ ; 66%) studies evaluated effects of a single species of ungulate. Research conducted on wild ungulates accounted for 81% ( $n = 44$ ) of single-species studies. Of the 28 (34%) studies that reported multispecies effects, 16 (57%) focused on wild ungulates and just 10 (36%) evaluated both domestic and wild species.

Most ( $n = 56$ ; 68%) studies compared only extant herbivory by ungulates with total exclusion, thus not evaluating effects of >2 densities of ungulates. Moreover, the remaining 26 (32%) studies that evaluated multiple densities of ungulates involved only 1 species. Finally, of the 26 studies that examined effects of multiple densities of 1 ungulate species, only 4 (15%; DeGraaf et al. 1991, deCalesta 1994, Singer et al. 1994, White et al. 2003) evaluated the interactions with episodic disturbance.

A repeated-measures sampling design, in which response variables were estimated at multiple points in time, was not commonly used. Just 31 (38%) of the studies sampled response variables at >3 time periods, and 9 (11%) evaluated responses at 2 points in time.

Only 7 (9%) studies explicitly made inferences to specified spatial extents such as a watershed. Most (46 of 82; 56%) publications appeared to make inferences independent of spatial extent, implying that results were applicable to any size area and boundary type.

## Discussion

Results from our survey have obvious and important implications for research and management of ungulate herbivory. First, while many studies evaluated the effects of ungulate herbivory after episodic disturbance, only a small minority addressed the interactions of herbivory with such disturbances. Second, few studies examined the effects of multiple population densities of an ungulate species. That is, the majority of studies examined only 2 levels of herbivory: ungulate exclusion versus extant herbivory, with the latter often undefined. Third, studies on effects of multiple species of ungulates were less common than research on single species. Fourth, when effects of multiple species were examined, the typical comparison was that of complete exclusion with 1 background density. And finally, inferences from results of the herbivory studies were not explicitly made for any specified spatial extents, such as for extents typically used to make land-use decisions.

In most North American landscapes, with the exception of national parks, wild and domestic ungulates share common ranges. Typically, 2-6 species of wild and domestic ungulates share ranges during all or part of each year (Wisdom and Thomas 1996). Studies of ungulate herbivory obviously have not addressed the important question of how multiple species of wild and domestic ungulates affect extant plant communities or the development of new communities following disturbances like fire or timber harvest. Strikingly absent is research on multiple-ungulate systems under varying population densities of these different ungulates. Latham (1999) and Hester et al. (2000) concluded that thresholds of ungulate density exist, above which the interactions of multiple species of ungulates become important. Likewise, potential threshold effects of multiple ungulate species also appear to strongly influence the composition of existing plant communities or the successional trajectory of plant communities following disturbance (Riggs et al. 2000, 2004).

The absence of explicit inferences to any specific spatial extents also points to an obvious deficiency in past herbivory research. Because ecological patterns and processes are not independent of scale (Peterson and Parker 1998, Turner et al. 2001), the spatial and temporal extents of herbivory effects must be addressed explicitly, with scales adjusted to the appropriate biological context of the predictor and response variables of interest. For example, the effects of extensive wildfire and pervasive herbivory may operate as "top-down" processes over large landscapes but also may manifest in variable ways at local scales as "bottom-up" processes (Peterson and Parker 1998).

Top-down processes are those that dominate in a pervasive manner over long time periods or large areas (Gutzwiller 2002). Bottom-up processes are those that are unique to local areas or short time periods; that is, processes that are measured and that vary at fine scales of resolution (Turner et al. 2001). Our review of research on ungulate herbivory suggests that past studies have been implicitly designed to measure bottom-up processes, as indicated by the lack of explicit inferences to larger landscape scales and the absence of larger areas over which effects were measured (also see Weisburg and Bugmann 2003). Recent studies on the role of ungulate predators in changing the patterns of ungulate herbivory

**Table 1.** Literature on empirical studies since 1990 on ungulate herbivory that was reviewed as to whether the publication included episodic disturbance as a background agent, examined the interactions of episodic disturbance, evaluated effects of multiple (>2) species of ungulates, examined 3 or more densities of each ungulate species, and included a repeated-measures sampling design. Methods of literature review are described in the text.

Publication	Episodic disturbance		Herbivory regime			Repeated measures	
	Background agent	Interaction with herbivory	Multiple (>2) ungulate densities	Multiple (>2) ungulate species	Type of ungulate species	Yes or No	Frequency
Allredge et al. 2001	Yes	No	No	Yes	Wild	No	
Anderson and Briske 1995	No	No	No	Yes	Wild	Yes	2 periods
Augustine and deCalesta 2003	No	No	Yes	No	Wild	No	
Augustine and Frank 2001	No	No	No	Yes	Wild	No	
Augustine and Jordan 1998	No	No	Yes	No	Wild	No	
Augustine et al. 1998	No	No	Yes	No	Wild	Yes	>3 periods
Belsky 1992	Yes	Yes	No	Yes	Wild	Yes	>3 periods
Berger et al. 2001	No	No	Yes	No	Wild	No	
Beschta 2005	No	No	No	No	Wild	Yes	>3 periods
Bock and Bock 1.999	No	No	No	No	Domestic	Yes	2 periods
Castleberry et al. 2000	Yes	Yes	No	No	Wild	Yes	>3 periods
Collins et al. 1998	Yes	Yes	No	No	Wild	Yes	2 periods
Coughenour 1991	No	No	No	No	Wild	Yes	2 periods
deCalesta 1994	Yes	Yes	Yes	No	Wild	No	
DeGraaf et al. 1991	Yes	Yes	Yes	No	Wild	No	
Didier and Porter 2003	No	No	Yes	No	Wild	No	
Donald et al. 1998	No	No	No	No	Wild	No	
Edenius et al. 1993	No	No	Yes	No	Wild	Yes	>3 periods
Ericsson et al. 2001	No	No	Yes	No	Wild	No	
Fabricius 1994	No	No	Yes	No	Wild	No	
Fletcher et al. 2001	No	No	No	No	Wild	No	
Fuhlendorf and Smeins 1997	No	No	Yes	Yes	Wild-domestic	Yes	>3 periods
Fuhlendorf and Smeins 1998	No	No	Yes	Yes	Wild-domestic	Yes	>3 periods
Goheen et al. 2004	No	No	No	Yes	Wild-domestic	No	
Gomez 2005	No	No	No	Yes	Wild	Yes	>3 periods
Harmer 2001	Yes	No	No	No	Wild	Yes	>3 periods
Heroldova et al. 2003	No	No	No	No	Wild	No	
Hobbs et al. 1996	No	No	Yes	Yes	Wild-domestic	Yes	>3 periods
Homolka and Heroldova 2003	Yes	No	No	Yes	Wild	Yes	>3 periods
Hunt 2001	No	No	No	No	Domestic	Yes	>3 periods
Huntsinger 1996	Yes	No	No	No	Domestic	Yes	>3 periods
Husheer et al. 2003	No	No	No	No	Wild	Yes	2 periods
Kay and Bartos 2000	No	No	No	Yes	Wild-domestic	No	
Knops et al. 2000	Yes	Yes	No	No	Wild	Yes	>3 periods
Kraft et al. 2004	Yes	Yes	No	No	Wild	No	
Kuiters and Slim 2003	No	No	No	No	Domestic	No	
Kupferschmid and Bugmann 2005	Yes	Yes	No	Yes	Wild	Yes	2 periods
Liang and Seagle 2002	No	No	No	No	Wild	Yes	>3 periods
Manseau et al. 1996	No	No	No	No	Wild	No	
Matlack et al. 2001	Yes	No	No	Yes	Wild-domestic	No	
McInnis et al. 1992	No	No	No	No	Wild	No	
McIntyre et al. 1995	No	No	Yes	Yes	Domestic	No	
McLaren 1996	No	No	No	No	Wild	Yes	2 periods
McShea and Rappole 2000	No	No	No	No	Wild	Yes	>3 periods
Merrill et al. 2003	Yes	No	No	No	Wild	Yes	>3 periods
Molvar et al. 1993	No	No	Yes	No	Wild	No	
Moore et al. 2000	Yes	No	No	No	Wild	Yes	2 periods
Moser and Witmer 2000	No	No	No	Yes	Wild-domestic	No	
Motta 2003	Yes	No	No	Yes	Wild	No	
Opperman and Merenlender 2000	No	No	No	No	Wild	No	
Paige 1992	No	No	No	Yes	Wild	Yes	>3 periods
Paige 1999	No	No	No	Yes	Wild	No	
Parks et al. 1998	No	No	No	Yes	Wild	No	
Pastor et al. 1993	Yes	No	Yes	No	Wild	No	
Patel and Rapport 2000	Yes	No	Yes	No	Wild	No	
Puerto et al. 1990	Yes	No	No	No	Domestic	No	
Rambo and Faeth 1999	No	No	No	Yes	Wild-domestic	No	
Reed and Clokie 2000	No	No	Yes	Yes	Domestic	No	
Reimoser and Gossow 1996	Yes	Yes	No	No	Wild	No	
Renaud et al. 2003	No	No	No	No	Wild	No	
Riggs et al. 2000	Yes	Yes	No	Yes	Wild-domestic	Yes	>3 periods
Ripple and Larsen 2000	No	No	No	No	Wild	Yes	>3 periods

Table 1. Continued

Publication	Episodic disturbance		Herbivory regime			Repeated measures	
	Background agent	Interaction with herbivory	Multiple (>2) ungulate densities	Multiple (>2) ungulate species	Type of ungulate species	Yes or No	Frequency
Ripple et al. 2001	Yes	No	No	No	Wild	No	
Rosenstock 1996	No	No	No	No	Domestic	No	
Schoenecker et al. 2004	No	No	No	No	Wild	Yes	>3 periods
Schreiner et al. 1996	No	No	No	Yes	Wild	No	
Schutz et al. 2003	No	No	Yes	No	Wild	Yes	>3 periods
Scott et al. 2000	No	No	Yes	No	Wild	Yes	>3 periods
Sharrow et al. 1992	Yes	No	No	No	Domestic	Yes	>3 periods
Singer 1995	No	No	No	Yes	Wild	No	
Singer and Harter 1996	Yes	Yes	No	No	Wild	Yes	2 periods
Singer and Renkin 1995	No	No	Yes	Yes	Wild	Yes	>3 periods
Singer and Schoenecker 2003	No	No	No	No	Wild	Yes	>3 periods
Singer et al. 1994	Yes	Yes	Yes	Yes	Wild	Yes	>3 periods
Smit and Kooijman 2001	No	No	Yes	No	Domestic	Yes	>3 periods
Steen et al. 2005	No	No	Yes	No	Domestic	Yes	>3 periods
Stein et al. 1992	Yes	Yes	No	No	Wild	No	
Stohlgren et al. 1999	No	No	Yes	Yes	Wild-domestic	No	
Tracy and McNaughton 1997	Yes	Yes	No	No	Wild	No	
White et al. 2003	Yes	Yes	Yes	No	Wild	No	
Woodward et al. 1994	No	No	No	Yes	Wild	Yes	>3 periods
Zaady et al. 2001	No	No	No	No	Domestic	Yes	>3 periods

(Beschta 2005, Fortin et al. 2005) suggest that top-down processes also deserve attention in research and management.

### New Paradigms Needed

The knowledge gaps documented from our survey suggest that new paradigms and conceptual models are needed to spark new research and management thinking about the joint effects of ungulate herbivory and episodic disturbances. We contend that useful models of herbivory must examine the interactions of ungulate grazing with other disturbance regimes at spatial extents of interest to land managers and under varying ungulate densities, both wild and domestic. Moreover, we suggest that desirable models of ungulate herbivory consider multiple steady states of vegetation development, including potential threshold effects from herbivory. We also propose that herbivory models address the joint effects of grazing on understory and overstory development of vegetation. Finally, we assert that such models need to accommodate both top-down and bottom-up ecological processes.

Recent models of forest development, as applied to landscapes of the interior northwestern United States (Hann et al. 1997; Hemstrom et al. 2001, 2002), contain many of the above characteristics, including multiple steady states, threshold effects, overstory dynamics in relation to episodic disturbances, and landscape scales of application (Fig. 2). These vegetation-disturbance models were designed as state-and-transition models, which identify distinct vegetative conditions that exist for a given area at a given point in time (states), and that describe the potential ways in which each state can change (transition) to another state over time. The concepts and structure of these models were originally developed for vegetation in arid rangelands (Westoby et al. 1989, Laycock 1991), where various disturbances can cause dramatic transitions from one vegetative state to another, and where certain transitions are difficult or impossible to reverse because of thresholds (Hemstrom et al. 2002).

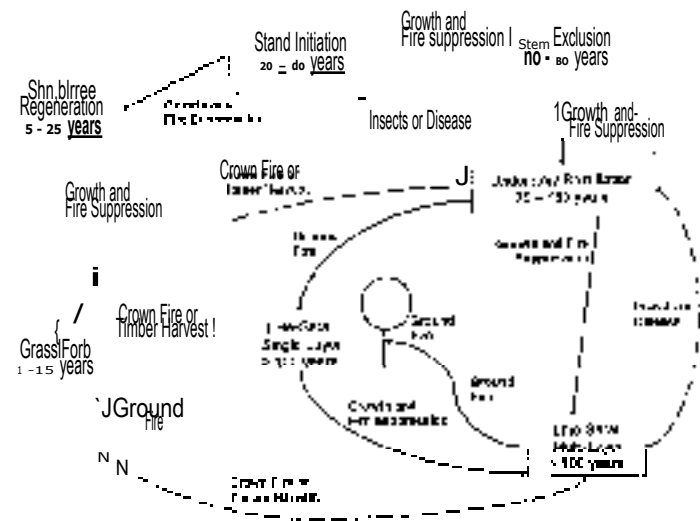
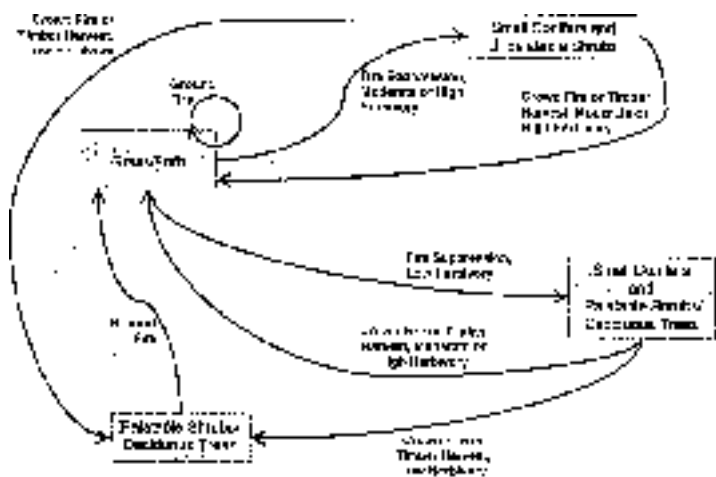


Figure 2. An example vegetation-disturbance model for montane forests of western North America, considering the effects of episodic disturbances (adapted from Hemstrom et al. 2001). The model is based on concepts of vegetation states and transitions, including multiple steady states, potential threshold effects, and abrupt transitions caused by episodic disturbances. Gray boxes are vegetation states; arrows are transitions between states, with the associated disturbance agents of fire, insects, disease, and timber harvest that cause transitions. States shown here were originally defined as structural stages by Oliver and Larson (1990) and Hann et al. (1997). Notably absent are transitions caused by ungulate herbivory, alone or in combination with episodic disturbances. Also absent are details about understory composition of vegetation for many of the vegetative states and the potential transitions brought about by the interactions between understory and overstory development of vegetation. We hypothesize that the dashed arrows represent transitions and resulting states that are more likely to occur under moderate or high levels of ungulate herbivory. For such transitions, forest managers typically assume that such effects are brought about solely by disturbances of fire, insect, disease, or timber harvest.



**Figure 3.** Conceptual model of understory plant development and dominance in montane forests of western North America, as influenced by varying densities of wild or domestic ungulates, interacting with episodic disturbance regimes of fire and timber harvest. Gray boxes are vegetation states, arrows are transitions between states, with the associated disturbance agents of herbivory, fire, and timber harvest that cause transition to the vegetation states. Dominant life forms of plants in each understory state are given.

The dynamics of vegetation change in state-and-transition models differ from the processes of plant succession traditionally assumed to progress and regress predictably to and from climax plant associations, based on traditional succession theory of Clements (1936). Instead, state-and-transition models allow for the possibility that vegetation development operates as a set of nonlinear states and transitions, with potential thresholds, some of which may be difficult to reverse. The thresholds are caused by disturbance agents that act as catalysts for the transitions, as well as impediments to further transitions once a threshold is reached.

Briske et al. (2003) and Riggs et al. (2004) recently made compelling arguments that traditional, "Clementsian" models of succession also can account for these same characteristics of nonlinear vegetation changes, threshold effects, and multiple disturbance agents. Consequently, the manner in which a model accounts for these desired characteristics is of primary interest as opposed to debating the model form. Moreover, notably absent from both the traditional models of succession and the more recent vegetation-disturbance models are the effects of ungulate herbivory. The combination of ungulate herbivory and episodic disturbances may manifest in many plausible ways, and whatever model form is used must account for such possibilities.

To illustrate some of these possibilities, we built a conceptual model of understory development for montane forests in western North America that considers the combined effects of herbivory and episodic disturbances (Fig. 3). This model contrasts strongly with models of forest development that typically focus on overstory dynamics (Fig. 2). Different combinations of herbivory and episodic disturbance are treated as transitions that affect potential understory states dominated by grasses and forbs, shrubs, deciduous trees, small conifers, or a combination of shrubs and small conifers (Fig. 3). In turn, the type of understory that dominates a forest environment presumably affects the states of overstory development (dashed arrows in Fig. 2), which requires

consideration of the interactions of processes shown separately in Figs. 2 and 3.

Our conceptual model of understory development (Fig. 3) is intended to complement the vegetation-disturbance regime dynamics outlined in Fig. 2 for large forest landscapes. This type of conceptual, state-and-transition model for forest understories could be used as a starting point to develop hypotheses for empirical testing under new research designs that address some of the key knowledge gaps that we have documented.

Our conceptual model of understory development in montane forests of western North America is based on the following assumptions:

1. Intensive herbivory by domestic cattle, elk, and mule deer favors selective and rapid removal of highly palatable deciduous trees and shrubs (Riggs et al. 2000). In turn, selective removal of these highly palatable deciduous trees and shrubs confers competitive advantage to establishment and growth of non-palatable shrubs and less palatable grasses and forbs (Riggs et al. 2000) or nonpalatable conifers (Hobbs 1996, Belsky and Blumenthal 1997).
2. Fire suppression in these forests favors understory development of shade-tolerant conifers (Agee 1993, McIver and Starr 2001). In turn, the combination of high levels of ungulate herbivory and fire suppression magnify conifer ingrowth (Belsky and Blumenthal 1997). The combination of low levels of herbivory and chronic fire suppression, however, favors codominance of unpalatable conifers and palatable shrubs in the understory.
3. Crown fires or timber harvest substantially reduce or eliminate the conifer understory, and, if combined with a high level of herbivory, favor a postdisturbance dominance of grasses and forbs. Crown fire or timber harvest, in combination with a low level of herbivory, favor dominance of highly palatable shrubs and deciduous trees after disturbance.
4. Ground fires, regardless of the level of herbivory, eliminate understory conifers, substantially reduce shrubs, and favor understory dominance by grasses and forbs.

Notably, the above assumptions regarding the univariate effects of either herbivory or episodic disturbances have a clear empirical basis. By contrast, the combined effects of such disturbances lack empirical basis, despite the fact that most forest landscapes in western North America during the past century have been dominated by a combination of fire suppression (Agee 1993) and high levels of ungulate herbivory (Hobbs 1996). This dearth of knowledge regarding disturbance interactions again points to obvious knowledge gaps, demonstrates the need for building the types of models shown in Fig. 3, and begs for validation with new research.

The a priori construction of such models is fundamental to the credible design of future studies of ungulate herbivory on large landscapes where episodic disturbances are common, such as those of western North America. Moreover, the a priori construction of such models is important for ensuring that the models have management utility. That is, the models can be built and evaluated for management utility at the same time that validation research addresses their ecological utility.

## Management and Research Needs

New conceptual models can help change thinking about ways in which ungulate herbivory interacts with fire, insects, disease, and drought to affect vegetation dynamics. While changes in conceptual thinking are needed, the ultimate requirement for improved management is new knowledge about ungulate herbivory that addresses the following issues: 1) effects of wild versus domestic ungulates; 2) effects of varying densities of each ungulate species, such that potential threshold effects can be identified; and 3) the interactions of issues 1 and 2 with episodic disturbances such as fire and timber harvest. Experimental treatments that address cause-effect relations of multiple ungulate densities, ungulate species, and disturbance interactions on vegetation dynamics are essential if management is to gain sufficient knowledge to effect desired changes in land management. However, large spatial extents are required for research on ungulate herbivory to maximize inference space.

The need for research at landscape scales versus the need for controlled, manipulative experiments is a challenge that cannot be fully resolved. It is logistically infeasible, perhaps impossible, to implement controlled experiments, with multiple treatment levels of ungulate species, grazing intensity, and episodic disturbances, and also apply these experiments over large areas and with sufficient replication. Consequently, we propose that researchers address cause-effect relations of ungulate herbivory and vegetation dynamics through the use of manipulative experiments, with proper controls and replication, at the feasible, smaller spatial extents. We further suggest that inferences to larger spatial extents then be evaluated with methods of adaptive management (Walters 1986, Lancia et al. 1996). Under adaptive management, ungulate densities could be reduced on targeted landscapes specifically to

test results and model predictions from the controlled experiments, per methods detailed by Walters (1986).

The combination of new experimental research and adaptive management needed to understand ungulate herbivory-episodic disturbance relations on vegetation dynamics will be costly, time-consuming, and operationally challenging. Such research would cost millions of dollars, take >10 years to complete, involve a large number of tractable ungulates that demand care and attention, and require a variety of research sites needed for adequate replication. We suggest that researchers begin to design and propose such research, perhaps first taking on smaller design components, implemented over shorter time periods, as a pilot effort to test the efficacy of implementing the long-term designs. One example of such new research is underway in northeastern Oregon, where controlled grazing trials using low, moderate, and high densities of elk and cattle are being implemented as treatment levels to evaluate effects on vegetation development, in contrast to complete exclusion of ungulates (Vavra et al. 2004).

Without such a transition to more rigorous studies, the knowledge needed for effective management of ungulate herbivory and interactions with episodic disturbances will continue to be anecdotal and uncertain. Given the ecological stakes, more reliable knowledge on the subject remains a compelling management need.

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