

# Ungulate Ecology of Ponderosa Pine Ecosystems in the Northwest<sup>1</sup>

Martin Vavra<sup>2</sup>, Kenric Walburger<sup>3</sup> and Timothy DelCurto<sup>3</sup>

## Abstract

Ponderosa pine ecosystems provide important foraging habitats for both wild and domestic ungulates. Livestock typically graze ponderosa pine ecosystems from May through October. Mule deer and elk may utilize these habitats on a yearlong basis in some areas. Stand density has a significant effect on understory production. Competition for soil moisture and nitrogen limit understory production. Since these systems typically exist at lower elevations, south aspects and on rather shallow soils, soil moisture is usually unavailable to understory species by mid summer. Optimal forage quality, therefore, occurs from late spring through mid-summer. Livestock use for optimal production should occur during this time frame. Herbivory by both native and wild ungulates can influence the structure and composition of understory vegetation. Ungulates, through the act of selective foraging influence the competitive ability of understory plants utilized. Ungulates can be considered agents of change in ecosystems by three processes: the regulation of process rates, modification of spatial mosaics, and action as switches controlling transitions between alternative ecosystem states. These understory composition and structure changes may have important implications to such diverse attributes as nutrient cycling, energy flow, biodiversity, stand density, fire type and interval, forest productivity, and ungulate productivity. Key Words: habitat, deer, elk, herbivory, fire, and nutrition.

## Introduction

Ponderosa pine (*Pinus ponderosa* P.& C. Lawson) ecosystems are the most extensive and valuable grazed forestlands in North America (Skovlin and others 1976). In Oregon and Washington 4.5 million hectares (11 million acres) of ponderosa pine-bunchgrass type exists (Skovlin and others 1976), and in the four-state region of Colorado, New Mexico, Arizona and Utah there exists 10.5 million hectares (26 million acres) (Lowe and others 1978). These ecosystems additionally provide valuable habitat for wild ungulates (primarily mule deer and elk) (Skovlin and others 1976, Urness and others 1975). Specific habitat provided varies greatly with stand density, and may provide primarily foraging habitat at lower densities and security cover at higher densities. Habitat quality for both wild and domestic ungulates is often a function of past management practices such as logging and fire exclusion or natural disturbances such as fire and insect outbreaks. Herbivory, by both wild and domestic ungulates, can act as a chronic form of disturbance

---

<sup>1</sup>An abbreviated version of this paper was presented at the symposium on Ponderosa Pine: Issues, Trends, and Management, October 18-21, 2004, Klamath Falls, Oregon.

<sup>2</sup> Range Scientist, PNW Research Station, USDA, Forest Service, 1401 Gekeler Lane, La Grande, OR 97850 (mvavra@fs.fed.us)

<sup>3</sup> Graduate Research Assistant and Associate Professor and Superintendent, Eastern Oregon Agricultural Research Center, P.O. Box E, Union OR 97883 (walburgk@onid.orst.edu; Tim.DelCurto@oregonstate.edu)

interacting with periodic disturbances (logging, fire) to develop alternative steady states of understory succession, which, in turn, may confound restoration efforts (Riggs and others 2000). Weigand and others (1993) related that ungulate herbivory could have substantial impacts on site productivity when used in conjunction with prescribed fire, stocking control, and species selection.

## Habitat Characteristics

Ponderosa pine communities may be used by mule deer and elk on a year round basis (Skovlin and Vavra 1979), depending on elevation and snow conditions. Cattle use of these ranges is usually in summer and early fall (Skovlin and others 1976). Depending on stocking density, ponderosa pine communities have the potential to provide security cover and foraging habitat to ungulates. Certainly site specific variables such as aspect, soil depth, and annual precipitation have an influence on understory production of ponderosa pine communities. The principal variable, however, is probably stand density. Competition for nitrogen and water between the overstory and understory vegetation limits understory development (Riegel and others 1991).

Ponderosa pine stands in the western U. S. have long been recognized as overstocked and not at potential for producing forage for ungulates (McConnell and Smith 1970, Weaver 1951). However, with the passage of the Healthy Forest Restoration Act in 2003, increases in forage production can be expected (Germaine and others 2004). Germaine and others (2004) went on to caution that, if large treatment blocks are initiated, then use by mule deer could be precluded if all resource needs are not met within the treated area. The same can be hypothesized for elk. Manipulation of ponderosa pine communities has the potential to impact understory productivity and diversity, forage nutritional quality, and microhabitat characteristics. Post-manipulation management, e.g. road access, also has the potential to affect use of treated areas at least by wild ungulates.

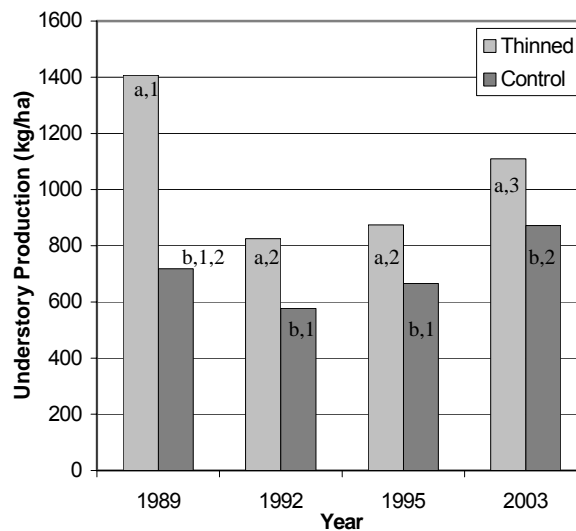
## Understory productivity

Of primary concern to domestic and wild ungulates is meeting nutritional needs. Herbivores commonly seek foraging areas that are high in understory production (DelCurto and others 2000). Understory productivity is controlled to a large extent by the density of the overstory (Riegel and others 1991). With fire exclusion and the resultant regeneration and ingrowth of trees (Germaine and others 2004), and the near cessation of public land timber harvest, ponderosa pine forests now provide much less forage than they did historically. Rehabilitation treatments will focus on reduction of basal area, overstory canopy cover, and stem density (Germaine and others 2004).

Previous research on thinning and understory production effects provides an indication of the increases in forage that can be expected. McConnell and Smith (1970) thinned 48-year-old overstocked pine sapling stands to 625, 330, and 165 trees per hectare (253, 134, and 67 trees per acre) while maintaining control stands at 6,916 trees per hectare (2,800 trees per acre). The authors reported a 10 kilogram per hectare (9 pounds per acre) increase in grass yield and a 2.2 kilogram per hectare (2 pounds per acre) increase in shrub yield for each 30.8 cm (one foot) increase in pine spacing. Total understory production varied from 112 kilograms per hectare (100 pounds per acre) for controls to 384 kilograms per hectare (342 pounds per acre) for

the 165 trees per hectare (67 trees per acre) thinning. Gibbs and others (2004) working in South Dakota found that heavily thinned stands of ponderosa pine exhibited a standing biomass 2.9 times greater in shrubs, 6.1 times greater in graminoids, and 13.0 times greater in forbs than standing biomass of unthinned stands. Moderately thinned stands had a biomass 3.4 times greater in shrubs, 3.4 times greater in graminoids, and 4.9 times greater in forbs than did unthinned stands.

Walburger and others (2005) reported on a long term data set collected after a commercial thinning in ponderosa pine stands. Tree density was reduced from 346 to 148 trees per hectare (140 to 60 trees per acre) and canopy cover reduced from 61 to 29 percent. The study area was logged in 1985. Total understory production was twice as high in the thinned stands compared to controls in 1989 but the difference declined since this initial response (*fig. 1*). The site potential for understory production of ponderosa pine communities is excellently portrayed by these studies. Busse and others (2000), however, remarked that central Oregon ponderosa pine stands had six-fold lower understory production than did comparable stands in northeastern Oregon. Bennett and others (1987) found herbage yields similar among a gradient of soil types with dense canopy covers. However, with open canopies, soil production potentials were fully expressed with the more productive soils producing 3 times the herbage of the least productive at 10 percent canopy cover.



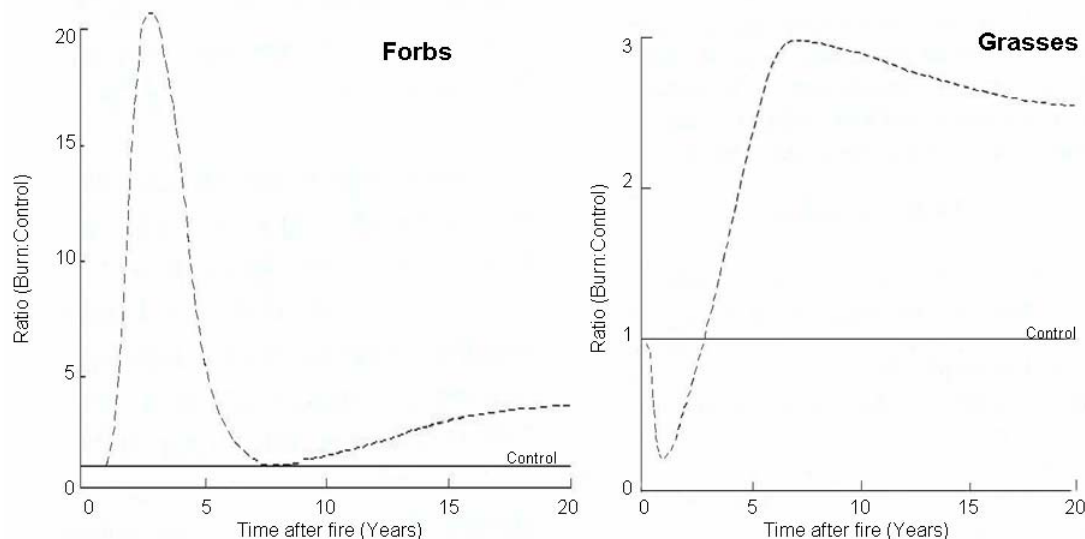
**Figure 1**— The effects of timber harvest through commercial thinning (Thinned) vs. no harvest (Control), on understory production (kg/ha) in a Ponderosa pine habitat type in northeastern Oregon. Bars with differing letters, within year, differ at  $\alpha = 0.05$ , and bars with differing numbers differ at  $\alpha = 0.05$ .

Fire may also have dramatic influences on forage production. Fire that reduces canopy cover may have the same stimulatory effect on understory production as overstory thinning. Busse and others (2000) provided citations of research that reported inconsistent understory response with application of low-severity understory burns. Their reasoning for lack of response was that low-severity fires did not reduce tree canopy and therefore competition for soil nitrogen and water remained nearly the same. Their research did not reveal any significant differences in grass or forb

productivity as a result of fire, but shrub cover (principally *Purshia tridentata*) was reduced 50 percent compared to controls.

Wildfires that are typically stand replacing in nature usually occur on areas where extensive fuels have built up over time. In this situation the suggested benefits of fire-reduced competition for soil resources, reduced litter, and increased nutrient availability (Busse and others 2000) may increase understory productivity. Lowe and others (1978) generalized expected responses of grasses and forbs to wildfire (fig. 2). The frequency of the principal shrub in their studies, *Ceanothus fendleri*, dropped to zero as a result of the fire then increased by three to four times the pre-fire condition. The initial response of the understory may be typical across the western U.S. Persistence of improved understory biomass is, however, dependent on the rapidity and increasing density of the regenerating overstory.

Understory productivity can be enhanced by a disturbance or management practice that reduces canopy cover. Fire treatments may lead to an increase or decrease in the shrub component over time depending on species composition. Low intensity fires that do not cause mortality in the overstory will probably provide an inconsistent response in understory vegetation.



**Figure 2**— Time-trend response curves for basal area of forbs and grasses (Lowe and others 1978).

### Forage nutritional quality

Meeting nutritional needs is not just a case of adequate forage productivity; the animal must obtain forage of sufficient quality to satisfy physiological requirements (lactation, growth). Management manipulations and natural disturbances may improve the quantity of forage present but can in some cases result in a decline in forage quality compared to untreated stands (Svejcar and Vavra 1985).

The results of several studies are available that provide information on forage quality of individual plant species important to ungulates (Hickman 1975, Skovlin 1967) and quality of actual cattle diets, (Holechek and others 1981, Vavra and

Phillips 1979). Generally, in ponderosa pine ecosystems with summer drought, a decline in herbaceous forage quality occurs as plants mature and senesce, and nutrients are translocated into the roots. The rate of decline is affected by annual precipitation (Holechek and Vavra 1983).

Management manipulations that decrease canopy cover may accelerate the decline in nutritional quality of forage. Svejcar and Vavra (1985) speculated that decreasing canopy cover allows more sunlight to reach the soil surface which warms the soil more rapidly in the spring and dries it more rapidly in the summer, accelerating plant phenology. Low biomass productivity sites can also be expected to lose forage nutritional quality more rapidly as the summer progresses due to limited soil moisture and competition for that supply (Busse and others 2000). In northeastern Oregon, nutritional quality of ponderosa pine ranges deteriorates below required levels by mid- to late-August. Declining herbaceous forage quality can be mitigated in animal diets by the presence and consumption of palatable understory shrubs. It is generally accepted that mule deer and elk employ this dietary strategy (Ganskopp and others 1999). Typically on forested ranges, cattle will also increase their consumption of shrubs as herbaceous forage quality declines (Holechek and others 1982). Therefore management strategies that promote development of a diversity of understory species should provide adequate nutritional quality to ungulates later in the season. Problems of grazing distribution might, however, develop late in the grazing season in regard to concentration of animals around riparian areas. Typically, upland water dries up or has stagnated in late season, and upland forage is mature and dry. Both of these factors contribute to increased utilization of riparian vegetation.

## Cover

Much of today's ponderosa pine ecosystems are densely stocked, with closed canopies and provide no concern for lack of cover. With the implementation of the Healthy Forest Restoration Act, however, concern may develop if large blocks are uniformly treated. Additionally, silvicultural activities during restoration may disrupt mule deer and elk behavior (Edge and Marcum 1985, Ward 1976). Elk appear to be more affected by the act of timber harvest and concomitant activities like road building and resultant traffic (Leege 1976, Ward 1976, Wisdom and others 2004). From a review of the literature, Lyon and Christensen (2002) found elk could be displaced from habitats by as much as five miles. Most often, however, the distance moved appeared to be the minimum required to avoid contact with equipment and people. Continual timber harvest within an individual watershed for five consecutive years can impose learned behavior that delays return to previously used habitats (Lyon 1979). Edge and others (1985) did report that home ranges of individual animals were not altered when areas of extensive cover remained available within their home range. The authors speculated that where cover becomes limited, harvest activity may increase home-range size and reduce home-range fidelity.

If timber harvest activities decrease or increase human access to an area, elk distributions can be expected to shift, with elk avoiding areas with increased access, and selecting areas with little or no access (Wisdom and others 2004). Specifically, road density and traffic rates in areas open to vehicular travel negatively influence elk distribution; elk avoid habitats near roads open to traffic (Rowland and others 2000, Wisdom and others 2004). The influence is not demonstrably linear, however, with roads having no apparent influence at zero or very low traffic rates. Cole and others

(1997) found that road management areas where access was restricted to administrative uses reduced Roosevelt elk home range size. Additionally, Lyon (1976) found that elk used habitats with greater canopy closure in areas of higher road density.

Mule deer security cover and bed sites may be compromised (Germaine and others 2004) as a result of restoration activities. These authors found that, in a ponderosa pine landscape treated under a typical restoration prescription, mule deer day-bed (security) microhabitat was reduced 50-100 percent, while available foraging microhabitat was increased 30-60 percent compared to untreated forest. The authors went on to suggest that stands of saplings and pole-sized trees having greater than 40 percent midstory canopy closure should be retained in patches of at least 0.04 hectares (0.1 ac) during restoration efforts. Thomas and others (1979) suggested that an optimal landscape for mule deer and elk would be comprised of 40 percent cover and 60 percent foraging habitat. Clary (1972) prescribed timber basal areas of 9.1 to 18.3 square meters per hectare (40 to 80 square feet per acre) to improve big game habitats in ponderosa pine forests. Additionally, one pine sapling thicket per 40 hectares (100 acres) was recommended for big game bedding cover. Hillis and others (1991) defined a security area for elk as a 101 hectare (250 acre) block that was non-linear in shape and at least one-half mile from roads. Such areas should compose at least 30 percent of a watershed. Gibbs and others (2004) felt that unthinned stands that provide essential thermal and hiding cover could become more important where availability of these habitats is more limited.

In contrast to these conclusions, Wisdom and others (2004) noted changes in elk spatial distribution during timber harvest but found no loss of animal performance attributable to that change. During harvest activities elk traveled over areas twice as large as areas covered prior to harvest indicating disturbance to the animals (Edge and others 1985). After harvest animal spatial distribution decreased from the levels occurring during harvest but was still higher than pre-cut levels.

No major changes in cattle spatial distribution during a timber harvest operation due to harvest activities are expected since cattle are domesticated animals, so are familiar with and tolerate human activity. After harvest, however, the physical changes in the grazing environment related to harvest may redistribute cattle. Harris (1954) reported that cattle seldom use dense overstory canopies except in conditions of extreme heat or intense insect harassment. Hedrick and others (1968) found it more difficult to obtain moderate or heavy utilization under dense overstory canopies than under low-density canopies. Following timber harvest and the concomitant decrease in overstory canopy a release of understory production usually occurs. This release may vary from two to eight times pre-harvest forage production (Svejcar and Vavra 1985) depending on intensity of the cut, site potential, and soil disturbance (Hedrick and others 1968). Miller and Krueger (1976) reported that 60 percent of the forage consumed in a given pasture by cattle was from areas logged and reseeded. Road construction to facilitate harvest also provides improved distribution of cattle by improving access (Hedrick and others 1968). Restoration efforts therefore, should provide new grazing areas for cattle.

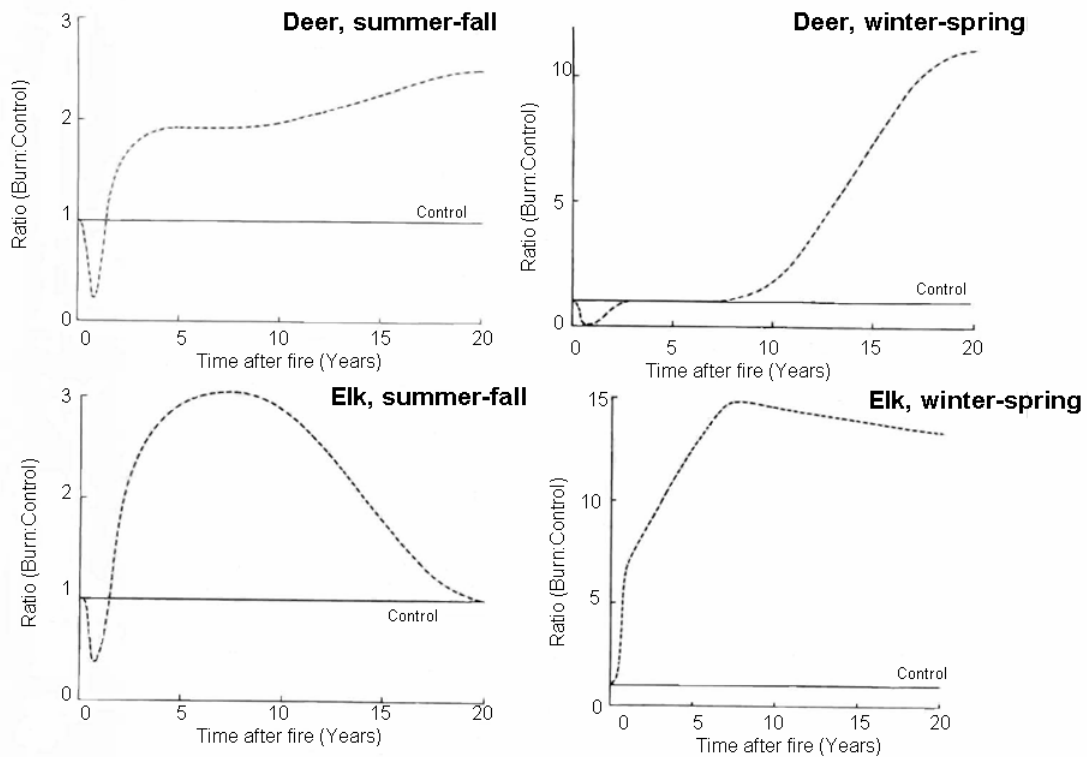
Stand replacement wildfires that are unusually intense due to long-term fire exclusion and unnaturally high stand densities create landscapes usually devoid of cover. In these cases effects on ungulates are similar to severe canopy reduction from timber harvest, so the same mitigating management options should be considered. Forage is not a limiting factor but cover may be. Increased vulnerability to hunting,

distribution alteration due to open roads, and increased vulnerability to predators are possible.

Ungulate use of large burns is usually a function of forage availability, but may be influenced by other factors like livestock grazing (Lowe and others 1978, *fig. 3*). For example, elk summer fall use declined after introduction of sheep grazing in summer on a 20-year burn (*fig. 3*).

### Herbivory Effects

Following disturbances like large fires or fuels reduction treatments, secondary succession of the understory and regeneration of conifers are initiated. These areas often become focal points of ungulate herbivory for two reasons: 1) vegetation developing after disturbance is often more palatable to ungulates relative to that available on undisturbed sites; and 2) surrounding untreated or unburned forest communities with dense canopies contain limited forage in the understory. Large herbivores are attracted to areas that are characterized by relatively high biomass of palatable food resources, and thus can be expected to focus foraging activity in recently disturbed areas.



**Figure 3** —Time-trend response curves for deer and elk use as a ratio of burn use to control use (Lowe and others 1978).

Only rudimentary data exist (Riggs and others 2000), but ungulate herbivory is strongly implicated as a significant agent in altering successional trajectories following disturbance (fire, logging, fuels reduction) in the Blue Mountains. Raedeke (1988) related that selective feeding of forest animals can result in complete changes in the structure, composition, and productivity of the forest. In general, plant communities within exclosures are more diverse than the surrounding forest community subjected to continual herbivory (Raedeke 1988). Recent literature reviews (Augustine and McNaughton 1998, Hobbs 1996) clearly indicate the important role of herbivory not only in modifying the composition of plant communities, but also of other biotic communities in the ecosystem. Ungulates are important agents of change in ecosystems by three processes: regulation of process rates, modification of spatial mosaics, and action as switches controlling transitions between alternative ecosystem states (Hobbs 1996). In the Blue Mountains herbivory has long been recognized to be a competitive factor in ungulate relationships (Cliff 1939, Pickford and Reid 1943) and in understory shrub suppression (Mitchell 1951). However, the role of herbivory is not well recognized in the predominant management paradigms, either in the Blue Mountains or any other forest ecosystem of the western U. S., and knowledge is more anecdotal than predictive (Riggs and others 2000).

Jones (2000) reviewed the effects of cattle grazing and reported that cover of grasses and shrubs, as well as total vegetation biomass often was reduced. Riggs and others (2000) reported that, in the Blue and Wallowa Mountains of eastern Oregon, understory biomass in ungulate exclosures was 2.1 times greater inside than outside exclosures, and forest-floor biomass was 1.5 times greater inside than outside. Shrub biomass was influenced more by ungulates than was grass or forb biomass. Mazancourt and Loreau (2000) stated that herbivory, in general, could lead to species replacement in plant communities. Augustine and McNaughton (1998), stated that species composition of plants can be dramatically altered by selective foraging of ungulates and that this phenomenon is a trademark of plant-ungulate relations. The authors noted that by altering the competitive relations among plants, differential defoliation tolerances to grazing of co-occurring plant species appear to be important determinants of how woody and herbaceous plant communities respond to herbivory.

Augustine and McNaughton (1998) went on to include effects on overstory species as well, and listed several species of coniferous and deciduous trees that were reported as herbivory intolerant. Healy (1997) found that white-tailed deer interrupted the sequence of stand development and simplified understories in eastern oak forests. Likewise, Alverson and Waller (1997) found that white-tailed deer abundance reduced the size and number of hemlock seedlings and explained the widespread regenerative failure of eastern hemlock. The literature review of Alverson and Waller (1997) also indicated that white-tailed deer substantially altered tree, shrub and herbaceous components of plant communities.

Ungulate herbivory shapes vegetation pattern in coniferous forests of the Northwestern U.S. (Schreiner and others 1996, Woodward and others 1994). Research by these authors indicated that ungulates maintained a reduced standing crop, increased species richness of forbs, and determined the distribution, morphology, and reproductive performance of several species of shrubs. Woodward and others (1994) stated that the extent to which herbivores can change forest ecosystem processes might depend on the scale and magnitude of other disturbances. All of the observations are consistent with available information in interior forests.



With ungulates, attraction to and therefore selectivity for areas of lower canopy cover and greater forage production may create a chronic disturbance effect after timber harvest. Walburger and others (2005) reported that timber harvest had a greater effect on understory vegetation than did herbivory, but many species were affected by the interaction of timber harvest and herbivory (*fig. 4*). Plant production was measured as peak standing crop in the absence of cattle grazing the year measured. However, herbivory affected production and presence of grasses, forbs and shrubs. Total understory production was 124 kilograms per hectare (110 pounds per acre) lower in cattle grazed pastures than in exclosures. Production of pinegrass and elk sedge was also reduced by cattle grazing; whereas, Kentucky bluegrass and other perennial grass production was not affected by grazing. The total production of forbs was not affected by herbivory; however, there were varying species effects.

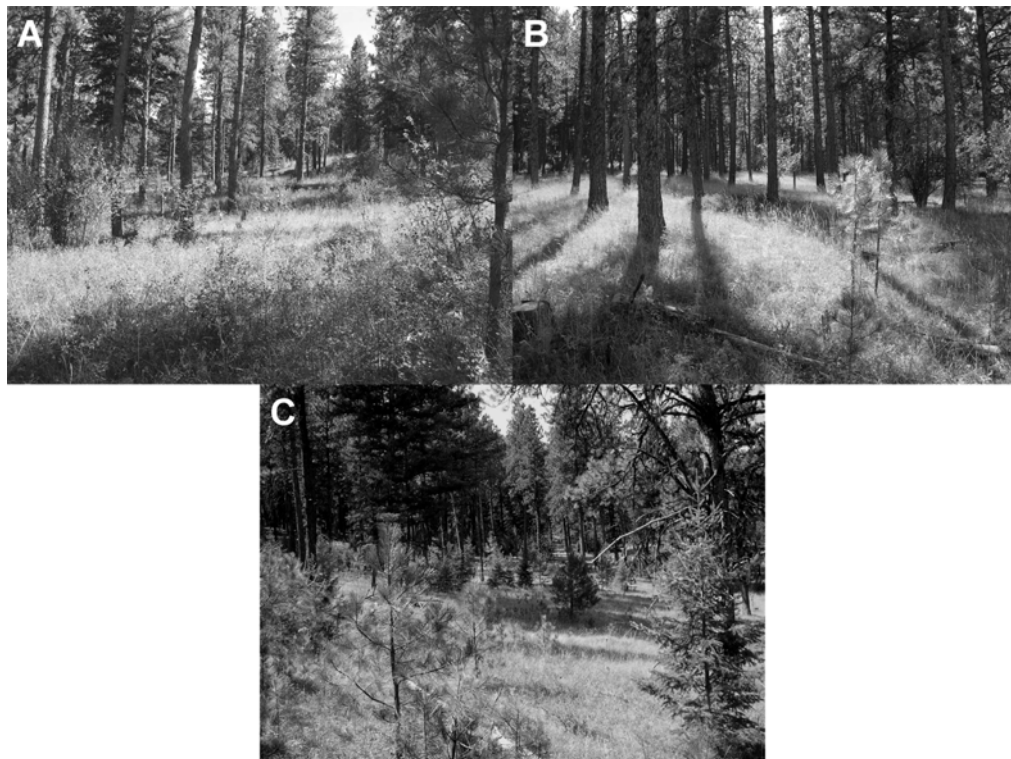
Walburger and others (2005) also reported that shrub production was moderately affected by herbivory and that species diversity was not affected by either timber harvest or herbivory. This lack of response of species diversity and shrub production to herbivory may be due to years of fire exclusion or to prior management.

Forest succession is a function of edaphic factors, the density and viability of seed and sprouting rootstocks, episodic disturbance regimes, and herbivores (Riggs and others 2000). Herbivory alters the utilization profile of a plant community (palatable versus unpalatable plants) and thus can alter its successional trajectory. Herbivores influence growth, recruitment, and mortality rates of plants and may do so in ways correlated with plant density, frequency, or other neighborhood traits, or with competitive abilities (Huntly 1991). Moreover, herbivory may increase, offset, or generate reciprocal negative interactions among plants (Huntly 1991). Herbivory is highly variable in space and in time, and these spatial and temporal patterns of herbivory can generate heterogeneity in plant population structure, the existence of which strongly influences community dynamics.

## Management Implications

Ponderosa pine ecosystems have been modified by fire exclusion for most of the twentieth century. Consequently, ungulate habitat provided by these ecosystems has changed dramatically. In the coming years, resources will be directed to the rehabilitation of these ecosystems to restore some target structure and functionality. If ungulate habitat is a priority then certain considerations are in order for improving effectiveness of rehabilitation treatments and follow-up management.

In order to persist in an environment, wild ungulates, must utilize food that results in a given level of fitness, allowing persistence or growth of their population in that environment (Belovsky and others 1999). Likewise, utilization of that food must occur with minimum risk to the individuals (predation avoidance). Therefore, in the management of ungulates, forage resources and cover are considerations. The current condition of most ponderosa pine ecosystems is such that cover is not limiting. As fuel reduction treatments are implemented, however, cover may become a limiting factor. Uncut or unburned cover patches should be considered where treatment patches are large. Topography plays a mitigating role, so that in landscapes with irregular topography, cover patches can be fewer and strategically placed. Cover provides for predator avoidance, both human and animal.



**Figure 4** — Influence of herbivory, A) big game (elk and deer) and cattle exclosure, B) grazed by big game and cattle and C) grazed by big game only, on a commercially thinned Ponderosa pine site in northeastern Oregon.

Once areas have been treated, the roads developed to gain entry also allow easy access for hunters, increasing animal vulnerability to harvest. Open roads that provide both easy access and decreased tree density after thinning may result in animal harvests above desired levels. Road closures not only limit hunter access, but in the case of elk, prevent compression of available habitats because of their aversion to road traffic.

With a reduction in overstory canopy cover, increased forage production is possible. The degree to which it occurs will be dependent on site factors and the remaining tree density. Late summer forage nutritional quality, however, may be impacted by the fuels reduction/thinning process because maturation and senescence of herbaceous plants may occur earlier in the summer in thinned areas (Svejcar and Vavra 1985). Livestock should, where possible, utilize ponderosa pine communities early in the summer to optimize the capture of plant nutritional value (Vavra 1983). Problems of over-utilization of riparian vegetation likely will occur in late summer.

The development of prescribed fire intervals for ponderosa pine ecosystems poses questions for ungulate nutritional ecology. Frequent return interval prescribed burning may result in decreased productivity of forbs and shrubs (Tiedemann and others 2000). These two forage components are important in optimizing quality of ungulate diets. Shrubs play a particularly important role in late summer and fall when grasses have senesced and declined in nutritional quality (Vavra 1983). Tiedemann and others (2000) note that the issue was not whether to burn, but rather, defining the minimum interval to burn without unacceptable risks to productivity.

Herbivory by wild and domestic ungulates has the potential to impact vegetation dynamics following rehabilitation efforts on ponderosa pine ecosystems. In ponderosa pine stands Walburger and others (2004) did not note the large differences due to herbivory on grand fir associations observed by Riggs and others (2000). Changes to productivity and structure may be the most pronounced herbivory effects on ponderosa pine ecosystems. Within a given watershed, size and number of rehabilitation units, as well as anticipated ungulate (wild and domestic) utilization are important considerations if management goals include specific levels of understory plant community productivity, diversity and structure.

Ponderosa pine ecosystems are important to ungulates throughout the western U.S. These diverse and wide-spread ecosystems have been recognized to be undergoing alterations attributable to fire exclusion for more than half a century (Weaver 1951). Also, unregulated historic livestock grazing has played a role in the alteration process (Belsky and Blumenthal 1997). Rehabilitation efforts in the next few years will begin to drastically change the composition and structure of these ecosystems. Ungulate habitat will continue to be a critical product of these ecosystems, although specific use at a given location may change (security cover converted to foraging habitat).

## References

- Alverson, W.S.; Waller, D.M. 1997. **The white tailed deer: a keystone herbivore.** Wildlife Society Bulletin 25:217-226.
- Augustine, David J.; McNaughton, S.J. 1998. **Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance.** Journal of Wildlife Management 62(4):1165-1183.
- Belovsky, G.E.; Fryxell, J.; Schmitz, O.J. 1999. **Natural selection and herbivore nutrition: Optimal foraging theory and what it tells us about the structure of ecological communities.** In: Jung, Hans-Joachim G.; Fahey, George C; (eds.) Nutritional ecology of herbivores. American Society of Animal Science, Savoy, IL; 1-70.
- Belsky, A.J.; Blumenthal, D.M. 1997. **Effects of livestock grazing on stand dynamics and soils in upland forests of the interior West.** Conservation Biology 11:315-327.
- Bennett, D.L.; Lemme, G.D.; Evenson, P.D. 1987. **Understory herbage production of major soils within the Black Hills of South Dakota.** Journal of Range Management; 40(2):166-169.
- Busse, Matt D.; Simon, Steven A.; Riegel, Gregg M. 2000. **Tree-growth and understory responses to low-severity prescribed burning in thinned *Pinus ponderosa* forests of Central Oregon.** Forest Science 46(2):258-268.
- Clary, Warren P. 1972. **A treatment prescription for improving big game habitat in ponderosa pine forests.** In: Proceedings of the 16<sup>th</sup> Annual Arizona Watershed Symposium, Sept. 20, 1972; Phoenix, AZ: Arizona Water Commission Report 2:25-28.
- Cliff, Edward P. 1939. **Relationship between elk and mule deer in the Blue Mountains of Oregon.** In: Proceedings of the Fourth North American Wildlife Conference. Portland, OR: USDA Forest Service, 560-569.
- Cole, E.K.; Pope, M.D.; Anthony, R.G. 1997. **Effects of road management on movement and survival of Roosevelt elk.** Journal of Wildlife Management 61(4):1115-1126.
- DelCurto, T.; Johnson, B.K.; Vavra, M.; Ager, A.A.; Coe, P.K. 2000. **The Influence of season on distribution patterns relative to water and resource use by cattle grazing**

- mixed forested rangelands.** In: Proceedings of the Western Section American Society of Animal Science; June 21-22, 2000; Davis, CA; 51:171-175.
- Edge, W.D.; Marcum, C.L. 1985. **Movements of elk in relation to logging disturbances.** Journal of Wildlife Management 49(4):1115-1126.
- Edge, W.D.; Marcum, C.L.; Olson, S.L. 1985. **Effects of logging activities on home-range fidelity of elk.** Journal of Wildlife Management. 49(3):741-744.
- Ganskopp, Dave; Svejcar, Tony; Taylor, Fred; Farstvedt, J.; Paintner, K. 1999. **Seasonal cattle management in 3 to 5 year old bitterbrush stands.** Journal of Range Management 52:166-173.
- Germaine, Stephen S.; Germaine, Heather L.; Boe, Susan R. 2004. **Characteristics of mule deer day-bed and forage sites in current-condition and restoration-treated ponderosa pine forest.** Wildlife Society Bulletin 32 (2):554-564.
- Gibbs, Mary C.; Jenks, Jonathan A.; Deperno, Christopher S.; Sowell, Bok F.; Jenkins, Kurt J. 2004. **Cervid forage utilization in noncommercially thinned ponderosa pine forests.** Journal of Range Management 57:435-441.
- Harris, Robert W. 1954. **Fluctuations in forage utilization on ponderosa pine ranges in eastern Oregon.** Journal of Range Management 7(6):250-255.
- Healy, W.M. 1997. **Influence of deer on the structure and composition of oak forests in central Massachusetts.** In: McShea, W.J.; Underwood, H.B.; Rappole, J.H. (eds); The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington D.C.; 249-266.
- Hedrick, D.W.; Young, J.A.; McArthur, J.A.B.; Kenistor, R.F. 1968. **Effects of forest and grazing practices on mixed coniferous forests in northeastern Oregon.** Technical Bulletin 103; Corvallis, OR: Agricultural Experiment Station; Oregon State University; 1-24.
- Hickman, O.E. 1975. **Seasonal trends in the nutritive content of important range forage species near Silver Lake, Oregon.** Res. Paper PNW-RP-187. Portland, OR: Pacific Northwest Forest and Range Experiment Station, USDA Forest Service; 33 p.
- Hillis, J.M.; Thompson, M.J.; Canfield, J.E.; Lyon, L.J.; Marcum, C.L.; Dolan, P.M.; McCleery, D.W. 1991. **Defining elk security: the Hillis paradigm.** In: Christensen, A.G.; Lyon, L.J.; Lonner, T.N.; compilers. In: Proceedings, elk vulnerability symposium. Bozeman, MT: Montana State University; p. 38-43.
- Hobbs, N.T. 1996. **Modification of ecosystems by ungulates.** Journal of Wildlife Management 60(4):695-713.
- Holechek, J.L.; Vavra, M.; Skovlin, J. 1981. **Diet quality and performance of cattle on forest and grassland range.** Journal of Animal Science 53:291-298.
- Holechek, J.L.; Vavra, M.; Skovlin, J.; Krueger, W.C. 1982. **Cattle diets in the Blue Mountains of Oregon II: Forests.** Journal of Range Management 35(2):239-242.
- Holechek, J.L.; Vavra, M. 1983. **Drought effects on diet and weight gains of yearling heifers in northeastern Oregon.** Journal of Range Management 36(2):227-231.
- Huntly, N. 1991. **Herbivores and the dynamics of communities and ecosystems.** Annual Review of Ecological Systems 22:477-503.
- Jones, A. 2000. **Effects of cattle grazing on North American arid ecosystems: a quantitative review.** Western North American Naturalist 60(2):155-164.
- Leege, T.A. 1976. **Relationship of logging to decline of Pete King elk herd.** In: Proceedings of the Elk-Logging-Roads Symposium; Moscow, ID: University of Idaho; 6-10.

- Lowe, P.; Ffolliott, P.F.; Dieterich, J.H.; Patton, D.R. 1978. **Determining potential wildlife benefits from wildlife in Arizona ponderosa pine forests.** Gen. Tech. Rep. RM-52. Ft. Collins, CO: Rocky Mountain Forest and Range Experiment Station, USDA Forest Service; 1-12.
- Lyon, L.J. 1976. **Elk use as related to characteristics of clearcuts in western Montana.** In: Proceedings of the Elk-Logging-Roads Symposium; Moscow, ID: University of Idaho; 69-72.
- Lyon, L.J. 1979. **Influences of logging and weather on elk distribution in western Montana.** Res. Paper INT-RP-236. Ogden, UT: Intermountain Forest and Range Experiment Station, USDA Forest Service; 12 p.
- Lyon, L.J.; Christensen, A.G. 2002. **Elk and land management.** In: Toweill, D.E.; Thomas, J.W.; (eds). North American Elk Ecology and Management; Smithsonian Institution Press, WA; 557-582.
- Mazancourt, C.; Loreau, M. 2000. **Effect of herbivory and plant species replacement on primary production.** American Naturalist 155:735-754.
- McConnell, Burt R.; Smith, Justin G. 1970. **Response of understory vegetation to ponderosa pine thinning in eastern Washington.** Journal of Range Management 23(3):208-212.
- Miller, R.; Krueger, W. 1976. **Cattle use on summer foothill rangelands in northeastern Oregon.** Journal of Range Management 29:367-371.
- Mitchell, G.E. 1951. **Status of browse on ranges of eastern Oregon and eastern Washington.** Journal of Range Management 4:249-253.
- Pickford, G.; Reid, E. 1943. **Competition of elk and domestic livestock for summer range forage.** Journal of Wildlife Management 7:328-332.
- Raedeke, K.J. 1988. **Forest management and wildlife in the pacific northwest.** Journal of Northwest Environments 4:263-278.
- Riegel, Gregg M.; Miller, Richard, F.; Krueger, William. C. 1991. **Understory vegetation response to increasing water and nitrogen levels in a *Pinus ponderosa* forest in northeastern Oregon.** Northwest Science 65(1):10-15.
- Riggs, Robert A.; Tiedemann, Arthur R.; Cook, John G.; Ballard, Teena M.; Edgerton, Paul J.; Vavra, Martin; Krueger, William C.; Hall, Frederick C.; Bryant, Larry D.; Irwin, Larry L; DelCurto, Timothy. 2000. **Modification of mixed-conifer forests by ruminant herbivores in the Blue Mountains ecological province.** Res. Pap. PNW-RP-527. Portland, OR: Pacific Northwest Forest and Range Experiment Station, USDA Forest Service; 77 p.
- Rowland, M.M.; Wisdom, M.J.; Johnson, B.K.; Kie, J.G. 2000. **Elk distribution and modeling in relation to roads.** Journal of Wildlife Management 64(3):672-684.
- 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.** Canadian Journal of Forest Research 26:255-265.
- Skovlin, J. M. 1967. **Fluctuations in forage quality on summer range in the Blue Mountains.** Res. Paper PNW-44. Portland, OR: Pacific Northwest Forest and Range Experiment Station, USDA Forest Service; 20 p.
- Skovlin, J.M.; Harris, R.W.; Strickler, G.S.; Garrison, G.A. 1976. **Effects of cattle grazing methods on ponderosa pine-bunchgrass range in the Pacific Northwest.** Technical Bulletin No. 1531. Portland, OR: Pacific Northwest Forest and Range Experiment Station, USDA Forest Service; 44 p.

- Skovlin, Jon; Vavra, Martin. 1979. **Winter diets of elk and deer in the Blue Mountains, Oregon.** Res. Paper PNW-RP-260. Portland, OR: Pacific Northwest Forest and Range Experiment Station, USDA Forest Service; 23 p.
- Svejcar, Tony; Vavra, Martin. 1985. **The influence of several range improvements on estimated carrying capacity and potential beef production.** Journal of Range Management 38(5):395-399.
- Thomas, J.W.; Black, H., Jr.; Scherzinger, R.J.; Pedersen, R.J. 1979. **Deer and elk.** In: Wildlife habitats in managed forests--the Blue Mountains of Oregon and Washington. Handbook No. 553. Portland, OR: Pacific Northwest Forest and Range Experiment Station, USDA Forest Service; 124-137.
- Tiedemann, Arthur R.; Klemmedson, James O.; Bull, Evelyn L. 2000. **Solution of forest health problems with prescribed fire: are forest productivity and wildlife at risk?** Forest Ecology and Management 127:1-18.
- Urness, P.J.; Neff, D.J.; Watkins, R.K. 1975. **Nutritive value of mule deer forages on ponderosa pine summer range in Arizona.** Res. Note RM-304. Ft. Collins, CO: Rocky Mountain Forest and Range Experiment Station, USDA Forest Service; 6 p.
- Vavra, Martin. 1983. **Managing grazing animal response to forestland vegetation.** In: Ben F. Roche, Jr. and David M. Baumgartner (eds); Forestland grazing proceedings of a symposium held Spokane, WA: Feb. 23-25, 1983; 43-51.
- Vavra, M.; Phillips, R.L. 1979. **Diet quality and cattle performance on forested rangeland in Northeastern Oregon.** In: Proceedings of the Western Section American Society of Animal Science; July 28-Aug. 1, 1979; Tucson, AZ. Vol. 30:170-173.
- Walburger, K.J.; DelCurto, T.; Vavra, M. 2005. **The effects of domestic and wild ungulate herbivory and timber harvest on the understory vegetation structure and composition in a Ponderosa pine (*Pinus ponderosa*) habitat in northeastern Oregon** [abstract]. In: Abstracts for the 58th Annual Meeting of the Society for Range Management; Ft. Worth, TX: Feb. 5-11, 2005.
- Walburger, Kenric; DelCurto, Tim; Vavra, Martin. 2004. **The effects of cattle and big game herbivory and logging on the understory vegetation structure and composition in a grand fir (*Abies grandis*) habitat in northeastern Oregon** [abstract]. In: Abstracts for the 57th Annual Meeting of the Society for Range Management; Salt Lake City, Utah: January 24-30 2004; #379.
- Ward, A.L. 1976. **Elk behavior in relation to timber harvest operations and traffic on the Medicine Bow Range in South-Central Wyoming.** In: Proceedings of the Elk-Logging-Roads Symposium; Moscow, ID: University of Idaho; 32-43.
- Weaver, H. 1951. **Fire as an ecological factor in the southwestern ponderosa pine forests.** Journal of Forestry 49:93-98.
- Weigand, James F.; Haynes, Richard W.; Tiedemann, Art R.; Riggs, Robert A.; Quigley, Thomas M. 1993. **Economic assessment of ungulate herbivory in commercial forests of eastern Oregon and Washington, USA.** Forest Ecology and Management 61:137-155.
- Wisdom, Michael J.; Johnson, Bruce K.; Vavra, Martin; Boyd, Jennifer M.; Coe, Priscilla K.; Kie, John G.; Ager, Alan A.; Cimon, Norman J. 2004. **Cattle and elk response to intensive timber harvest.** In: Transactions of the North American wildlife and natural resources conference. March 20, 2004; Spokane, WA; 727-758.
- Woodward, A.; Schreiner, E.G.; Houston, D.B.; Moorhead, B.B. 1994. **Ungulate-forest relationships in Olympic National Park: Retrospective enclosure studies.** Northwest Science 68(2):97-110.