९९४

RANGELAND RESOURCES - MANAGEMENT AND UTILIZATION

PROCEEDINGS

THIRD INTERNATIONAL RANGELAND CONGRESS

New Delhi, 7-11 November, 1988

Editors

Panjab Singh
P.S. Pathak
Vinod Shankar
A.K. Srivastava

RANGE MANAGEMENT SOCIETY OF INDIA
INDIAN GRASSLAND AND FODDER RESEARCH INSTITUTE
JHANSI -284003, INDIA

PRIMARY PRODUCTIVITY AS AFFECTED BY INSECT HERBIVORES

TIMOTHY D. SCHOWALTER

Department of Entomolgy, Oregon state University
Corvallis, OR 97331 USA

Introduction

Rangelands have been valued primarily of for production of large biomasses of native and domesticated vertebrate grazers. Unfortunately, the primary productivity necessary to sustain livestock production often has been taken for granted, leading to excessive grazing and deterioration of the rangeland ecosystem. Forage species and vertebrate grazers have been the focus of rangeland management. Associated members of rangeland communities (such as non-forage vegetation and invertebrates) have received little attention at best or have been viewed as undesireable competitors or destructive agents, subject to control efforts. However, accumulatting evidence indicates that many of these associated species contribute to the maintenance of primary productivity and carrying capacity, hence to yields of forage and livestock biomass, in rangeland ecosystem.

The purpose of this paper is to consider the role of insect herbivores in rangeland ecosystems. The complex and potentially beneficial interactions between plants, Insects and vertebrate grazers reveal instricate balances among functional groups that may be critical to maintenance of rangeland productivity. I will discuss factors influencing level of herbivory, and consequences of varying levels of herbivory for primary productivity and carrying capacity in rangeland ecosystems.

Factors Influencing Herbivory

Insect herbivores typically are inconspicuous components of rangeland ecosystem because of their small size. Nevertheless, their biomass may exceed livestock biomass and contribute substantially to overall grazing pressure (Watts *et al.* 1982). Factors affecting herbivore populations determine effects on vegetation. The primary, and interrelated, factors affecting survival and reproduction of insect herbivores are weather patterns, host variables, interaction with other herbivores, and predation (Crawley 1983, Schowalter *et al.* 1986, Watts *et al.* 1982).

INSECT

ge biomasses of
ary productivity
inted, leading to
age species and
ociated members
ertebrates) have
e competitors or
latting evidence
maintenance of
ge and livestock

ores in rangeland
en plants. Insects
oups that may be
actors influencing
vory for primary

ngeland ecosystem
livestock biomass
al. 1982). Factors
The primary, and
bivores are weather
ion (Crawley 1983,

Weather patterns affect insect herbivores in several ways. Mortality can result from injury suffered during storms or form dessication or thermal stress (Watts and Everett 1976). Rainfall and relative humidity have a major effect on rangeland insects. Egg hatch of the range caterpillar *(Hemileuca oliviae)* is reduced by low relative humidity which prevents softening of the egg shell (Watts and Evertt 1976). On the other hand, low relative humidity reduces grasshoppoer mortality due to infection by the fungus, *Entomophthor grylli* (Fuxa 1987, Watts *et al.* 1982).

Insect herbivores respond strongly to vegetation factors. Primary vegetation factors are host condition, abundance and apparency (Courtney 1986, Crawely 1983, Schowalter et al. 1986).

Host condition is determined by metabolic processes as affected by environmental conditions. All plants allocate available resources to various metabolic pathways on a priority basis. Respiration, of course, occurs in all living cells, even though not contributing efficiently to plant productive processes. Foliage and root production and resource conversion processes are plant metabolic priorities because of their importance to plant survival. However , storage tissues, such as tubers and stem tissues, and chemical defenses, such as phenols, terpenes, and alkaloids, represent energy-expensive or luxury pathways maintained under optimal growing conditions. Under conditions of resource limitation or other environmental stress, resources in storage tissues or chemical defenses may be metabolized to meet plant survival needs (Bazzaz *et al.* 1987, Chapin *et al.* 1987). Drought stress, in particular, increases the soluble amino acid content of plant tissues and alters the balance of essential amino acid in ways that improve grass suitability for grasshopper feeding (Haglund 1980, Lewis 1979, Mattson and Haack 1987).

Plant species vary in their composition of defensive compounds and essential nutrients. Individual plants also vary in their chemical composition as a result of responses to environmental conditions. Defensive compounds reduce energy- and resource-expensive enzymes to detoxify these plant compounds or to risk predation while searching for more palatable plants (Schowalter and Whitford 1979). Herbivores often are forced to accept resources that provide for less than optimal rates of development, survival and reproduction (Courtney 1986, Schowalter *et al.* 1977).

Resource abundance or density determines the distance, an herbivore must travel between acceptable resources. If host plants are sparse, herbivores expend limited energy (and often time) and attract attention from predators while seeking hosts acceptable for feeding or reproduction (Schowalter and Whitford 1979). Non-food resources also are important. Grasshoppers require dry, loose soil for oviposition; the range caterpillar shows higher reproductive rates when woody perennials or other persistent are available as oviposition sites (Watts and Evertt 1976).

Finally, host appearency influences the ease with which herbivores percrive resources. Herbivores often use cues indicating presence of acceptable resources to reduce search time. Cues may be visual, such as wavelengths of light (Prokopy and Owens 1983) or flower size (Courtney 1986), especially at long or short range. This orientation can be disrupted by confusion of host cues by non-host cues (Courtney 1986, Hunter and Arssen 1988, Visser 1986).

Although herbivores exploiting the same resources have been viewed as competitors, some herbivores can facilitate other herbivores. For example, Gordon (1988) found that cattle grazing in Scotland improved forage quality and quantity for deer. Plant feeding insects can induce plant biochemical responses that either facilitate or inhibit future herbivory by other species (Lewis 1979, Schowalter *et al.* 1986).

Interaction between vertebrate and invertebrate herbivores has rarely been examined. Overgrazing by livestock promotes grasshopper and termite populations, perhaps through increased aridity (Crawley 1983, Watts *et al.* 1982). Reproduction by the range caterpillar is promoted by the increased density of woody perennials resulting from overgrazing by cattle; in turn, the irritating spines of the larvae discourage further grazing by livestock (Huddleston *et al.* 1982). However, winter grazing by sheep can increase range caterpillar egg mortality due to ingestion and trampling (Bellows et al. 1982). Severe overgrazing by live stock could depress populations of insect herbivores by reducing food resources and increasing exposure to lethal extremes of temperature and moisture (Watts *et al.* 1982). Vegetation adapted to replace tissues lost to grazers could overproduce, relative to carrying capacity, in the absence of grazing (Sims *et al.* 1978). Resulting stress of resource-limited vegetation could trigger rapid population growth of insect herbivores, as discussed above.

Predation contributes to herbivore mortality. However, predation often may be a function of environmental factors providing weakned or conspicuous prey or adequate habitat for predators. Birds, small mammals, reptiles and amphibians, spiders, ants and wasps are major predators of insect herbivores (Watts *et al.* 1982). Many of these predtors require resources found only in diverse ecosytems (Perry 1988, Schowalter 1989). Birds, spiders and ants, for example, are generalist predators capable of preventing population outbreaks of insect herbivores, but often require alternate prey

tion; the
or other

percrive
ources to
kopy and
nge. This
(Courtney

iewed as
e, Gordon
uantity for
r facilitate
86).

arely been
opulations,
oduction by
ls resulting
discourage
grazing by
d trampling
pulations of
al extremes
place tissues
absence of
could trigger

en may be a
or adequate
ers, ants and
any of these
, Schowalter
s capable of
lternate prey

species to provide food throughout the period of residence (Hunter and Aarssen 1988, Schowalter 1989). Some birds and ants require nesting sites in woody vegetation (Campbell *et al.* 1983, Perry 1988).

Hence, a productive and driverse vegetation will normally maintain low to moderate levels of herbivory (Hunter and Aarssen 1988, wats *et al.* 1982). Healthy hosts limit herbivore feeding biochemically. A diverse assemblage of hosts and non-hosts maintains a high cost of searching for acceptable hosts. Similarly, landscape simiplification for management of regional commodities, e.g., planting of preferred forage species for vertebrate grazers, eliminates natural barriers to the spread of insect of herbivores and permits potentially destructive population growth.

Consequences of Herbivory

Reduction in plant mass often is a conspicuous result of herbivory, supporting the traditional view of herbivory as progressively detrimental (Dyer 1986). However, recent studies indicate that primary productivity; only excessive levels may lead to degradation of ecosystem carrying capacity and primary productivity (Dyer 1986, Schowalter 1981, Sims *et al.* 1978. Stimulation of primary productivity can occur as a result of herbivore-induced reduction in plant demand for resources or as a result of increased carrying capacity.

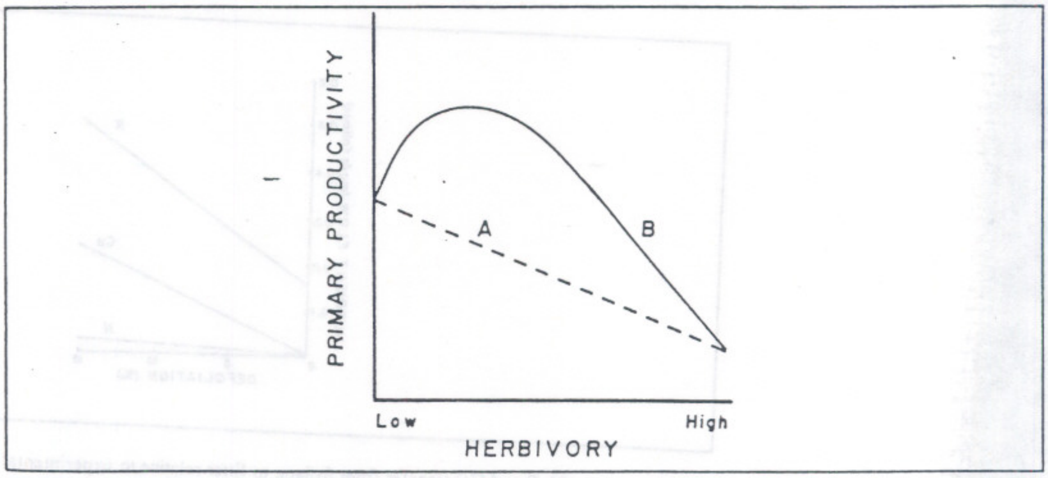


Fig I. Contrasting views of effect of herbivory on primary production : traditional view of progressive reduction in primary productivity with increasing herbivory (A) vs. emerging view of stimulation of primary productivity at low to moderate levels of herbivory.

Low to moderate levels of herbivory have essentially a pruning or thinning effect. Low value tissues, i.e., those contributing least to photosynthesis but representing a metabolic drain on plant resources, often show little investment in defensive chemicals. These tissues are the first targets of herbivores (Dirzo 1984) Selective removal of unproductive plant parts by small herbivores permits reallocation of resources to more productive tissues. At the vegetation level, thinning similarly makes resources relatively more available for vigorous production by surviving plants (Schowalter 1981, Wickman 1980).

In addition to the pruning effect, low to moderate levels of herbivory can increase rangeland carrying capacity through stimulation of nutrient cycling. Nutrients bound in plant mass, often in forms resistant to decomposition processes, are cycled via herbivory to litter as enriched throughfall leachate and more easily mineralized foliage fragments, feces, insect tissues, etc. (Schowalter *et al.* 1986, Seastedt and Crossley 1984). For example, Schowalter (unpubl. data) manipulated defoliation intensities from 0 to 15% of foliage standing crop in young Douglas-fir, *Pseudotsuga menziesii.* Nutrient transfer from foliage to litter as throughfall leaching and litterfall was significantly related to defoliation intensity (Figure 2). Decomposition rate can be stimulated by herbivore induced changes in the form and timing of litterfall, such as increased volume and nutrient content of throughfall (Seastedt and Crossley 1983).Nitrogen fixation and nitrification processes also can be stimulated by herbivore-induced opening of the canopy (Swank *et al.* 1981). Increased availablity of soil nutrients permits increased productivity.

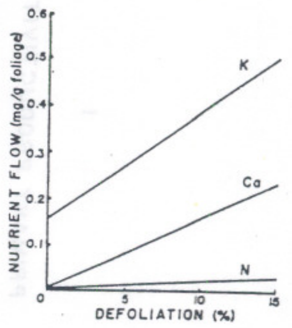
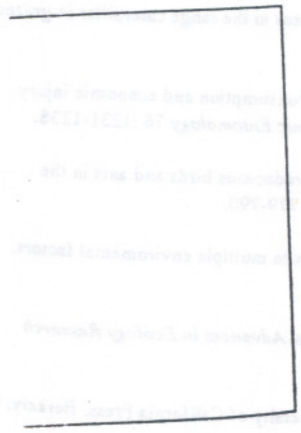


Fig 2. Nutrient (N, P and Ca) transfer from foliage to litter relative to experimental level of herbivory on yong Douglas-fir (*Pseudotsuga menziesii)* in western Oregon. All regression lines are significant at $P < 0.05$ and have $R > {}^{2}0.2$.

ıg or thinning effect.
.s but representing a
ıdefensive chemicals.
Selective removal of
of resources to more
ıly makes resources
ıts (Schowalter 1981,

erbivory can increase
g. Nutrients bound in
sses, are cycled via
ly mineralized foliage
Seastedt and Crossley
iation intensities from
ʻeudotsuga menziesii.
ıg and litterfall was
ıposition rate can be
ɩ of litterfall, such as
ıstedt and Crossley
ın be stimulated by
ıcreased availablity of



ıl of herbivory on yong Douglas-
.0.05 and have R > ^{2}0.2.

The net effect of pruning and nutrient mobilization processes is increased carrying capacity coupled with plant allocation of resources to more productive tissues. Tree and shrub responses to increased carrying capacity may be slower and less dramatic than grass and forb responses. Nutrients made available as a result of herbivore feeding on trees or shrubs can benefit forage species growing under the canopy (Schowalter *et al.* 1986).

At high levels of herbivory, excessive removal of, or damage to, plant parts may cause plant stress and mortality. Reduction in vegetation cover cause plant soil deccication and loss severe than vertebrate herbivory with regard to trampling and soil erosion. Hence, insect outbreaks triggered by vertebrate over grazing could be beneficial, from an ecosystem standpoint, if they discourage continued overgrazing and rangeland degradation. Further more, because insect herbivory usually is concentrated on particular plant taxa, out breaks typically occur when hosts become abundant, apparent and/or suitable, often through stress associated with resource limitation, as discussed above. Herbivory under these conditions may appear destructive in the short term, especially from a commodity standpoint, but may contribute to long-term stability by promoting nutrient cycling and vegetation diversity.

For example, grasshoppers responding in a predatory manner to unproductive, drought-stressed grasses provide openings which are suitable sites for germination of legumes and other plant species. These plant species often contribute to the carrying capacity of rangeland ecosystem by providing symbiotically- fixed nitrogen and by retaining other nutrients; this role may be hindered by increasing competition for space and non-host plants and the increased primary productivity assosiated with reduced vegetation demand for limiting resources returns grasshopper populations to normal, mutualistic levels (Figure 3). Primary productivity should be higher and more stable in the post-outbreak community than in the pre-outbreak community because of the greater niche utilization of the more diverse vegetation (Schowalter 1981, Wickman 1980). Models used to determine economic thresholds for rangeland insects have not addressed these potentially beneficial effects (Bellows *et al.* 1983).

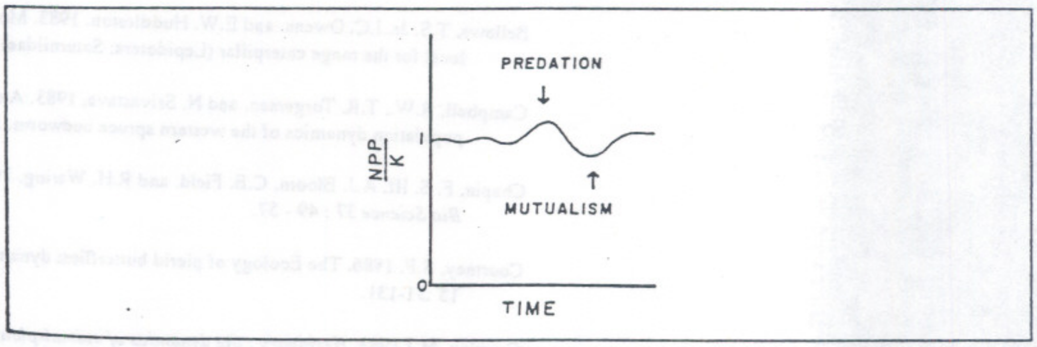


Fig 3. Hypothetical balance between rangeland carrying capacity and primary productivity as affected by herbivory. Low to moderate levels of herbivory in vigrous, diverse vegetation (NPP/K < 1) affect plants in a mutualistic way, increasing carrying capacity and primary productivity (through puming and nutrient cycling); high levels affect plants in a predatory manner, reducing productivity of stressed vegetation exceeding carrying capacity for limiting resources (NPP/K > 1).

Conclusions

Insect herbivores are maintained at low to moderate population levels by healthy, diverse vegetation. At these levels, herbivory contributes to nutrient cycling and stabilization of carrying capacity and primary productivity. However, changes in environmental conditions, including overgrazing, can trigger outbreaks of insect herbivores.

Livestock production depends on sustainability of rangeland primary productivity. Management of rangeland ecosystems must protect non-commerical species and interactions which promote carrying capacity and primary productivity if sustainable yield of rangeland resources is to be achieved. Maintenance of vegetation diversity and low to moderate levels of total herbivory will tend to optimize the balance between carrying capacity, primary productivity and herbivory necessary to accomplish this management goal.

Acknowledgements

This paper was supported by the National Science Foundation (Grant BSR 8306490), the Oregon Agricultural Experiment Station and the Forest Researc Laboratory at Oregon State University. C.S. Schowalter reviewed the manuscript.

References

Bazzaz, F.A.,N.R. Chiariello, P.D. Coley, and L.F. Pitelk. 1987. Allocating resources to reproduction and defense. *Bioscience* 37 : 58-67.

Bellows, T.S. Jr., J.C Owens and E.W. Huddlestion. 1982. Persistence of egg masses to the range caterpillar in grazed and ungrazed rangeland. *Journal of Economic Entomolgy* 75 : 574-576.

Bellows, T.S. Jr.,J.C. Owens, and E.W. Huddleston. 1983. Model for simulating consumption and economic injury level for the range caterpillar (Lepidotera: Saturniidae). *Journal of Economic Entomology* 76 :1231-1238.

Campbell, R.W., T.R. Torgersen, and N. Srivastava. 1983. A suggested role for predaceous birds and ants in the population dynamics of the western spruce budworm. *Forest Science* 29 : 779-790.

Chapin, F. S. III, A.J. Bloom, C.B. Field, and R.H. Waring. 1987. Plant responses to multiple enviromental factors. *Bio Science* 37 : 49 - 57.

Courtney, S.P. 1986. The Ecology of pierid butterflies: dynamics and interactions. *Advances in Ecology Research* 15 :51-131.

Crawley, M.J.1983. *Herbivory : the dynamics of animal-plant interactions.* University of California Press, Berkely, C

evels by healthy, ient cycling and ever, changes in breaks of insect

nary productivity. rical species and vity if sustainable ation diversity and balance between o accomplish this

lation (Grant BSR e Forest Research manuscript.

oduction and defense.

range caterpillar in grazed

on and economic injury
76 :1231-1238.

birds and ants in the

ple enviromental factors.

es in Ecology Research

California Press, Berkely, CA.

Dirzo, R. 1984. Herbivory: a Phytocentric overview. pp.141-165, In: R. Dirzo and J.Sarukhan, eds., *Perspectives on plant population ecology*, Sinuer Assoc., Inc., Sunderland, MA.

Dyer, M.I. 1986. The role of herbivores in forest ecosystems: the case for Biosphere Reserves. pp. 97-102, In : Yang. H., Z. Wang, J.N.R. Jeffers and P.A. Ward, eds., *The temperate forest ecosystem*. Institute of Terrestrial Ecology, Cumbria, U.K.

Fuxa, J.R. 1987. Ecological considerations for the use of entomopathogens in IPM. *Annual Review of Entomolgy*. 32 : 225-251.

Gordon, I.J. 1988. Facilitation of red deer grazing by cattle and its impact on red deer grazing performance. *Journal of Applied Ecology*. 25 : 1-10.

Haglund, B.M. 1980. Proline and valine-- cues which stimulate grass hopper herbivorey during drought stress. *Nature* 288 :697-698.

Helgerson, O.T., J.C. Gordon and D.A. Perry. 1984. N_2 fixation by red alder *(Alnus rubra)* and scotch broom *(Cytisues scoparius)* planted under precommercially thinned Douglas-fir *(Pseudotsuga menziesii)*. *Plant and Soil* 78 : 221-233.

Huddleston, E.W. , E.M. Dressel and J.G. Watts. 1976. Economic threshold for range caterpillar larve on blue grama pasture in northeastern Lincoln Country, New Mexico, In 1975. New Mexico Agricultural Experiment Station *Resrarch Report* 314. Las Cruces,NM.

Hunter, A.F. and L.W. Aarssen. 1988. Plants helping plants. *BioScience*. 38 : 34-40.

Lewis, A.C. 1979. Feeding preference for diseased and wilted sunflower in the grasshopper, *Melanoplus differentialis*. *Entomologia Experimentalis and applicata* 26 : 202-207.

Mattson, W.J. and R.A. Haack. 1987. The role of drought in outbreaksof plant-eating insects. *BioScience* 37 : 110-118.

Perry, D.A. 1988. Landscape pattern and forest pests. *Northwest Environmental Journal* 4 : 213-228.

Prokopy, R.J. and E.D. Owens. 1983. Visual detection of plants by herbivorous insects. *Annual Review of Entomology* 28: 337-364.

Schowalter, T.D. 1981. Insect herbivore relationship to the state of the host plant: regulation of ecosystem nutrient cycling throught ecological succession. *Oikos* 37 : 126-130.

Schowalter, T.D. 1989. Canopy arthropod cummunity structure and herbivory in old-growth and regenerating forest in western Oregon. *Canadian Journal of Forest Research* (in press).

Schowalter, T.D. and W.G. Whitford. 1979. Territorial behavior of *Bootettix argentatus* Bruner (Orthoptera: Acrididae). *American Midland Naturalist* 102 : 182-184.

Schowalter, T.D., W.G. Whitford and R.B. Turner. 1977. Bioenergetics of the range caterpillar, *Hemileuca oliviae* (Ckll.). Oecologia (Berl.) 28 : 153-161.

Schowalter, T.D., W.W. Hargrove and D.A. Grossley, Jr. 1986. Herbivory in forested ecosystem. *Annual Review of Entomology* 31 : 177- 196.

Seastedt, T.R. and D.A Crossley, Jr. 1983. Nutrients in forest litter treated with naphthalene and simulated throughfall: a field microcosm study. *Soil Biology and Biochemistry* 15: 159-165.

Seastedt, T.R. and D.A. Crossley, Jr. 1984. The influence of arthropods on ecosystems. *Bioscience* 34 : 157-161.

Sims, P.L. and J.S. Singh. 1978. The structure and function of ten western North American grasslands. III. Net primary production, turnover and efficiencies of energy capture and water use. *Journal of Ecology* 66 : 573-592.

Sims, P.L., J.S. Singh and W.K. Lauenorth.1978. The structure and function of ten Western North American grasslands. I. Abiotic and vegetational characteristics. *Journal of Ecology* 66 : 251-285.

Visser, J.H. 1986. Host odor perception in phytophagous insects. *Annual Review of Entomology* 31 : 121-144.

Watts, J.G. and T.D. Everett. 1976. Biology and behaviour of the range caterpillar. New Mexico Agricultural Experiment Station *Bulletin* 646, Las Cruces, NM.

Watts, J.G., E.W. Huddleston, and J.C. Owens. 1982. Rangeland entomolgy. *Annual Review of Entomology* 27 : 283-311.

Wickman, B.E. 1980. Increased growth of white fir after a Douglas-fir tussock moth outbreak. *Journal of Forestry* 78 : 31-33.