Ungulate Browsing Behavior in Relation to Plant Mineral Nutrition



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'If I can keep my garden flourishing while more and more gaunt deer keep coming from the woods, since there's only so much room within a garden whether filled with people or with deer; some must make do within the woods where there can never be enough,'

Excerpt from "Deer at the Garden" by Robert Pack 2002



Ungulate Behavior

What drives behavior Mating Hunger/Thirst

What influences behavior Weather Landscape

People



Success of an individual is based on reproductive fitness

To maximize fitness:

- Minimize Energy Expenditures
- Maintain homeostasis (stable internal environment)
- Consume high quality food sources (forage)

Geist (1982)

Forage selection is based on sight, taste, and olfactory senses

Ungulates unfamiliar with an area and/or plants:

- 1. Taste for forage quality
- 2. Adverse digestion creates negative feedback
- 3. Build association with smell and/or sight



The Damage



http://www.nature.org/ourinitiatives/regions/northamerica/unitedstates/minnesota/howwework/oh-deer-the-mammal-that-ate-the-northwoods.xml

Damage on the Rise

Reasons

- Habitat is fragmented
- Decrease in natural predators
- Over abundance in ungulate populations

Problems

- Shifts in plant species composition
- Conflicts with domestic herbivores
- Impacts on Forest Regeneration

Impacts of Ungulates on Forest Regeneration

Forest regeneration sites promote animal browse due to enhanced forage quantity and quality.



Impacts of Ungulates on Forest Regeneration



Figure 1—Relation of forest stand condition (or seral stage) to deer and elk forage and cover areas (biomass curves adapted from Long 1976, Witmer and others 1985).

Typical browse preference for elk and deer:

grass > forbs > shrubs > trees

NOT a static selective process.

Conifer seedlings represent a crucial component of the diet during the WINTER.

Hardwoods generally have greater browse during summer (due to presence of foliage)

Ramsey and Krueger 1986; Nelson and Leege 1982; Mansson et al. 2009

Impacts of Ungulates on Forest Regeneration



DAMAGE:

- Terminal Shoot
- Lateral Shoot
- Entire Seedling (browsed or trampled)
- Pulled Seedling



Efforts to Mitigate Browse

THERE IS NO BLANKET PRESCRIPTION

- Fencing
- Hunting
- Chemical Repellents
- Physical Barriers (tubing, bud caps)
- Frightening Devices (air canons)
- Habitat Manipulation (multiple openings)
- Fertilization





Nutrients applied at the nursery and/or in the field

Controlled-release fertilizers have shown to promote early growth and development of seedlings

Advantage: - rapid growth above browse line
- recovery from browse due to nutrient reserve

Disadvantage: - higher browse probability?

Fertilization

Application Methods at Time of Planting

- Broadcast
- Dibbled
- Planting hole
- Incorporated into media



Why fertilization attracts herbivory?

Fertilization increases foliar nitrogen and thus foliar protein, the highest valued nutritional component of ungulate food sources

Why fertilization deters herbivory?

Production of toxic compounds (i.e., 2nd metabolites)

Measuring Browse

1. Bites or Plant Damage

- amount and/or severity over time
- terminal, lateral, whole plant

2. Animal Droppings

• abundance over time



Most evidence for relationships between fertilization and browse is outdated.

Year	Author(s)	Animal / Location	Impact	
1936	Mitchell and Hosley	Deer / NE USA	^ Fert = ^ Browse	
1956	Knott	Deer / NW USA	^ Fert = ^ Browse	
1961	Crouch et al.	Deer / NW USA	<pre>^ Fert = slight ^ Browse</pre>	
1970	Oh et al.	Elk Deer / NW USA	^ Fert = ^ Browse	
1973	Behrend	Deer / NE USA	^ Fert = ^ Browse	
1977	George and Powell	Deer / Central USA	^ Fert = ^ Browse	
1980	Laine et al.	Elk / Finland	<pre>^ Fert = ^ Browse</pre>	
1983	Anderson	Deer / NW USA	^ Fert = ^ Browse	

Ball et al. 2000 Moose Sweden



Fig. 5. The intensity of use (as indexed by pellet counts) by moose *Alces alces* of fertilized, close control and distant control. No differences existed before the experimental fertilizations, but moose used fertilized areas significantly more than controls during the summer following fertilization as well as during the following winter. Means \pm standard errors are given.

Sullivan et al. 2006

Mule Deer -----Canada



Månsson et al. 2009

Moose and Reindeer

Sweden



Fig. 5. Boxplot (median, quartiles (lower; upper) and whiskers showing 1.5 interquartile range) of number of summer bites in unfertilized and fertilized sites recorded in August. Sample sizes as in Table 1.

Kimball et al. 2011

Elk and Deer

Oregon, USA

NO BROWSE RESPONSE TO FERTILIZATION



FIGURE 1: Block layout: three replicate blocks located at seven sites in Western Oregon were employed for the field experiment. Four treatment plots (whole plot) contained four species (split-plot) of conifers planted in rows of ten seedlings (D: Douglas-fir; G: grand fir; H: western hemlock; R: western redcedar).

Burney and Jacobs 2011



Douglas-fir Logistic Regression – Odds Ratio

Contrast	2007	2008
0 vs 40g	-1.5	-4.0

Example:

2008 - Control treatment is 4 times less likely to be browsed compared to the 40 gram treatment

Burney et al. 2011



Western red-cedar Logistic Regression – Odds Ratio

Contrast	2007	2008
0 vs 40g	3.6	3.8

Example:

2008 - Control treatment is 3.8 times more likely to be browsed compared to the 40 gram treatment

WHY ARE THERE DIFFERENCES IN BROWSE PREFERENCE ?

'The effect of fertilization upon browsing resistance may be a consequence of the effect of plant carbon-nutrient balance upon secondary metabolite production.'

Bryant et al. 1983

Plants develop complex array of 2nd metabolites

- many functions in plants including chemical defenses (e.g., toxins)
- 3 Types of 2nd metabolites
 - Alkaloids (i.e., caffeine)
 - Phenylpropanoids (i.e., tannins)
 - Terpenoids (i.e., terpenes scents, oils)

Carbon / Nutrient Balance Hypothesis

Increase in nutrient availability = Increase in plant growth = Decrease in production of 2nd metabolites

However, this is not static. Allocation of resources are:

- Fixed = no influence from environmental resources
 and/or
 Flexible = influence from environmental resources
- **Based on species**, phenological stage, individual plant genetics, and age (Lerdau et al. 1995)

Allocation of Resources – Terpenoid Production

Species	Year	Fertilizer Rate			
		0g	20g	40g	60g
Western red-cedar	Fall 2007	1.3ab	1.7bc	2.0c	2.6d
Douglas-fir	Fall 2007	0.5	0.6	0.7	0.5
Western hemlock	Fall 2007	0.5	0.3	0.4	0.5

mg g⁻¹[foliar dry weight]

Over 60% of the total monoterpenes for western red-cedar were oxygenated monoterpenes alpha and beta-thujone, known to inhibit rumen activity

Burney and Jacobs 2011

Allocation of Resources

Variable

Height Diameter Foliar Nitrogen **Douglas-fir Browse Douglas-fir Terpene** Western Hemlock Browse Western Hemlock Terpene Western Red-cedar Browse Western Red-cedar Terpene

Supplemental Nutrition

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Allocation of Resources / Ungulate Reactions



Why do ungulates ingest phytotoxins?

With lower forage quality and quantity (i.e., winter), ungulates balance diet with some level of toxicity to maintain adequate energy and protein inputs.

How?

- binding the compound,
- metabolizing the compound,
- tolerating the compound

(Provenza et al. 1992)

OVERALL CONCLUSIONS

INCREASED PLANT NUTRITION

- Increase growth of regenerating stand
- Increase quality of forage
- Increase production of toxic 2nd metabolites, thus decrease palatability
- Allow recovery to browse due to stored carbohydrates

Allocation of supplemental nutrients vary by species and individual plants.

OVERALL CONCLUSIONS

Regardless of plant mineral nutrition and defensive chemical composition, the dynamic behavior of ungulates has a powerful influence in the fate of forest regeneration.

QUESTIONS?



Terpenes



What are Terpenes?

- Secondary metabolites found in most plants (>25,000 known compounds with few having been studied)
- Broken into groups based on size: mono-, sesqui-, di-, ...
- Formed by repetitive fusion of isoprene unit making: floral scents, carotenoids, plant hormones, natural rubber
- Plants produce for chemical resistance and defense against: fungi, bacteria, and animal herbivory
- Smaller terpene compounds are extremely volatile and can be sensed by ungulates (taste and odor)
- Specific terpenes inhibit rumen activity in ungulates

Terrain



Field Site at Planting



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The impacts of browsing on young tree seedlings are well-known and have been documented in the scientific literature for decades. Elevated deer populations intensify these impacts. More than 17,000 peer-reviewed articles have been published on the topic since the early 1990s.

- The Nature Conservancy

Impacts of Ungulates on Forest Regeneration

Google Scholar Search 1990–2012

"browse, seedling, elk, deer"
= 2,530

" 'fertilization', browse, seedling, elk, deer"

= 748, HOWEVER FEW ABOUT THIS RELATIONSHIP