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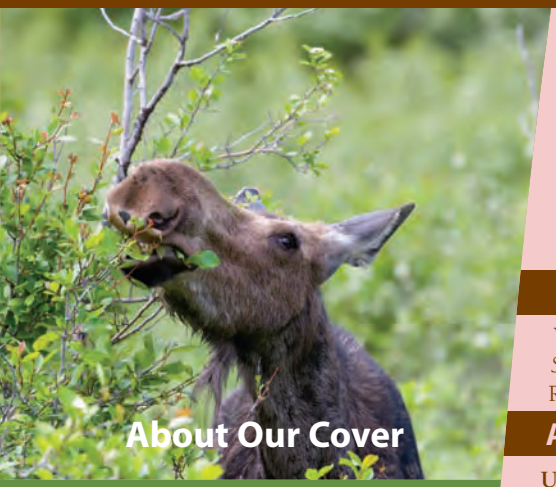


About Our Cover

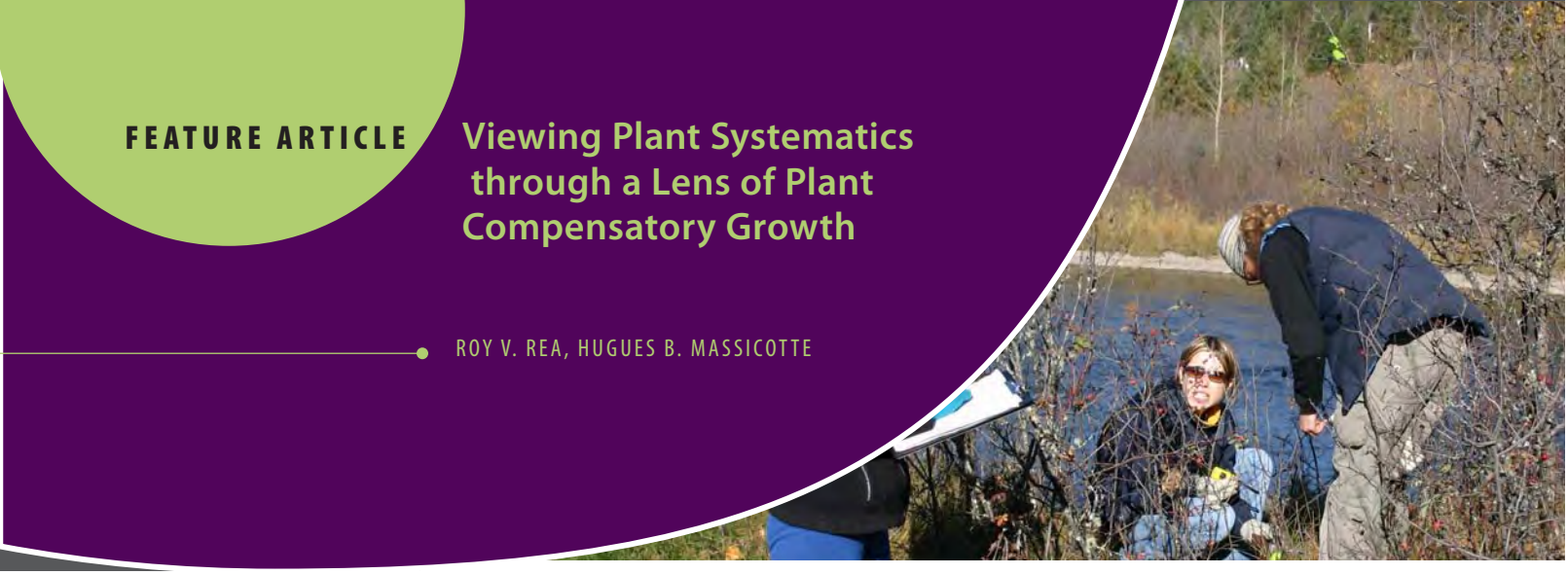
The moose (*Alces alces*) is the largest living member of the deer family. Bulls of the Tundra or Alaskan subspecies (A. a. gigas) are the largest (up to 1800 lbs), while the cows of the Shiras or Yellowstone moose (*A. a. shirasi*), such as the one pictured here, are the smallest (averaging 600–700 lbs) of the four North American subspecies. Moose have a circumpolar distribution from Alaska to Newfoundland in North America and throughout northern Eurasia from Norway to Manchuria. The name *moose* is derived from the Algonquian word *moos*, which means "he strips or bites off" or "twig biter" – making reference to the fact that bark and twigs make up a large portion of the moose diet. Moose consume up to 50 lbs of plant matter per day, often removing much of the above-ground biomass from individual shrubs and trees on which they browse. This "pruning" reduces the plant's number of growing points and results in more root resources being allocated to fewer shoots – which leads the plant to produce what is known as *compensatory growth*. Until root:shoot balance is reestablished, plants undergoing compensation are often characterized by large shoots, delayed leaf senescence, and a lack of flower and fruit production that can make them difficult to identify. Challenges faced by both biology teachers and their students and solutions to identifying plants undergoing compensatory growth as a result of moose browsing or other damage are the topic of an article in this issue of *ABT*. Roy Rea, a biology instructor at the University of Northern British Columbia in Prince George, BC, Canada, snapped this photo in Grand Teton National Park, near Jackson Hole, Wyoming, on 18 June 2009 with a Canon 5D using a Canon 300-mm f/2.8 lens.

Contents

FEATURE ARTICLE

Viewing Plant Systematics through a Lens of Plant Compensatory Growth

ROY V. REA, HUGUES B. MASSICOTTE



Abstract

Plant compensatory growth is a phenomenon of exaggerated vegetative growth that occurs in plants as a result of mechanical damage (e.g., cutting or browsing). Because shoots, leaves, and other plant parts grow larger on plants undergoing compensation, they typically fall outside of the normal ranges given in plant identification keys and confuse students who are attempting to classify them. Here, we describe the conundrum faced by students collecting compensatory materials and offer suggestions on how to help students identify their "plant-in-hand" and how to seize a teaching moment to examine and explain the underlying processes that lead to this fascinating plant response.

Key Words: *Dichotomous key; botany; systematic botany; plant identification; plant damage; plant response; field education.*

An important objective of most college and university plant systematics courses, and of thematic lesson units on plants in some high school science classes, is to teach students how to effectively use dichotomous keys for the purpose of identifying plants. The language of most keys is quantitatively descriptive and, as such, provides students the explanatory terms and measurements required to determine the fit of their "plant-in-hand" in the order, family, genus, and finally species to which it belongs.

Dichotomous keys are generally designed as a series or sequence of paired questions that, when answered, allow the student to move to the next set of paired questions. Answering questions in sequence ultimately enables students to identify the organism of interest. These questions are often framed in a way that requires students to determine answers and make decisions based on the presence or absence of structures or on some measurement (or range of measurements) for certain plant components, such as leaf blade length or width, thorn or petiole length, or plant height (e.g., Figure 1). Although dichotomous keys provide a useful range of measurements and attributes for each species in question, these measurements are often regional and derived from averages. They do not always account for the large plasticity exhibited by plants.

The term *plant compensatory growth* refers to exaggerated vegetative growth that results from mechanical damage to plants (e.g., cutting, animal browsing, or breakage from snow) as a physiological consequence of an increase in the root-to-shoot ratio following the loss of aboveground biomass (McNaughton, 1983). When aboveground tissues are damaged or removed, more root reserves are allocated to relatively fewer buds, which produce fewer but larger shoots and leaves (Millington, 1963; Danell et al., 1997).

Students who are attempting to use dichotomous keys are often confused when they encounter samples of exaggerated leaf and shoot growth.

All of the examples of plant compensatory growth that we have documented (see Figure 2) exceed (sometimes by one or two orders of magnitude) the size ranges described for the species in dichotomous keys. Consequently, it has been our experience that students who are attempting to use dichotomous keys are often confused when they encounter samples of exaggerated leaf and shoot growth; they may simply disregard these atypical forms or may confront the instructor, asking why their "plant-in-hand" does not fit the key. Seeking a simple explanation, instructors may answer that "Plants are variable and no keys are perfect" or "Botany is a science of exceptions to the rule," instead of proposing a response that helps students to understand why such variability can occur in nature. Here, we present several ideas for how instructors can turn these seeming conundrums into teachable moments.

At the University of Northern British Columbia (UNBC), we began to realize that our Plant Systems (Forestry 201) students were challenged each fall when attempting to key out plants during their laboratory exercises. Plants often came from areas such as river banks, where river-ice scouring sheared plants; ungulate winter ranges, where plants were heavily browsed by moose; road and trail sides, where plants were compensating from brush-cutting; and parks and city streets, where ornamental hardwoods are routinely pruned.

To help students understand ranges of variability in nature and concepts such as phenotypic plasticity (the ability of an organism to modify its morphology in response to a changing environment), and to prepare them for discrepancies between key descriptions and what they might observe in the field and in class, we now initiate discussions early in the semester on the concept (and consequences) of plant compensatory growth. We choose striking examples from the field that visually illustrate how imbalances in the root:shoot ratios can change plant morphology and phenology (e.g., how events such as bud burst or time of flowering are affected by climate). This approach allows us to discuss other related topics such as plant–animal interactions (e.g., moose browsing in our area can be significant), effects of sexual

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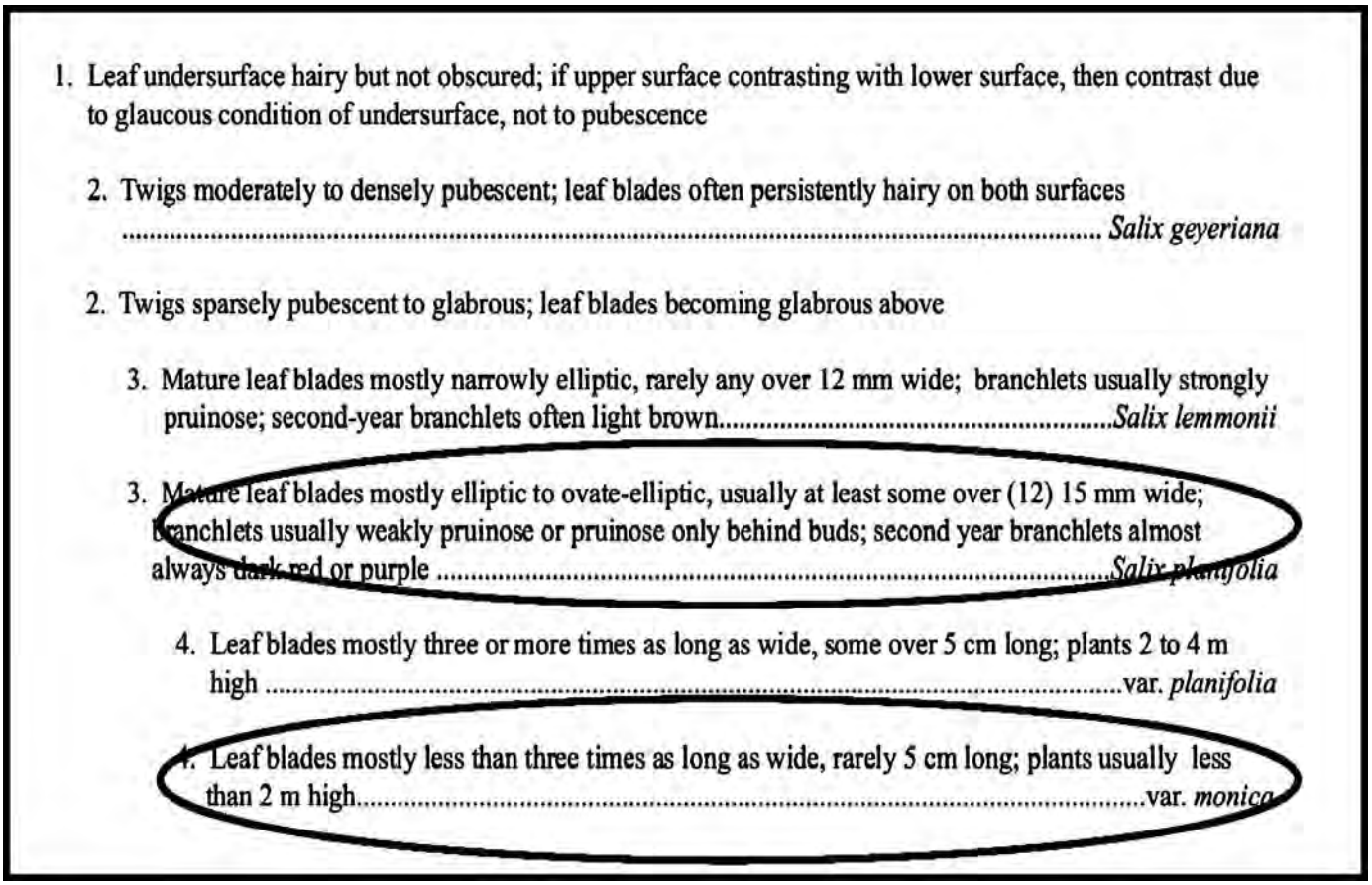

Figure 1. An example of plant descriptions and associated ranges of measurements from a dichotomous key for willows (from Fertig & Markow, 2001). Descriptions circled for emphasis indicate how plants are often identified according to a fairly rigid set of measurements.

versus vegetative reproduction, heterophylly (differences in leaf form on the same individual plant), delayed leaf senescence and winter hardening, and early spring leaf flush – all of which tend to occur especially in deciduous plants undergoing compensatory growth. Plant response to mechanical damage and the vigor with which this can happen also have important implications for research on vegetation management in forest plantations, for forest-fire-fuel load calculations, and for studies of animals' perception and use of plants that are undergoing plant compensatory growth. As an example, regrowth from plants that are cut during dormancy can be more palatable to moose than uncut plants or plants cut just after leaf flush; in turn, this may have implications for animal use of vegetation that is being managed along road and railway corridors (Rea et al., 2007). Such topics provide interesting and applied discussions on plant compensatory growth with our students.

Over several years, we have faced numerous plant-identification challenges for certain species; in-field and in-class discussions (Figure 3) on plant compensatory growth have generated a list of unexpected research questions and interesting ideas. Some of these find their way into lab discussions and reports, while others become the topics of independent study projects for our students. The following are some examples of questions and outcomes that have evolved from these ideas

1. *Do plants produce large compensatory shoots in response to browsing in order to grow taller so that new shoots can grow beyond the reach of terrestrial herbivores, or are they attempting to grow above interspecific competitors in order to secure more sunlight?* The answer to this question depends on the species of plant, soil nutrient regimes, and the life history of both the plant and the herbivore. A question similar to this served as a stimulus for one of our students to develop an undergraduate thesis on moose and aspen interactions from which he published two peer-reviewed papers (Carson et al., 2007, 2009).

2. *Is the total plant-leaf surface area comparable between undamaged plants with many small leaves and damaged (compensating) plants with fewer but larger leaves?* Although, to our knowledge, this question remains unanswered, such discussions reveal to students some of the possible implications of plant compensation and provide a platform from which to better understand how thoughtful questioning can lead to new research ideas.

3. *Do some species of plants demonstrate more compensatory growth than others?* A quick survey of plants along school trails reveals that fast-growing species such as willows and alders are quite adept at recovering from brush cutting, often demonstrating compensatory growth, while others such as conifers are less capable of rapid growth responses (Figure 4).

4. *Can beavers be considered "farmers/foresters" because they actively promote compensatory growth that they can then subsequently harvest and eat? The new growth originates from the stumps of trees that they initially cut down for dam and lodge building.* Concepts taken from this question have been used for a module that we teach at UNBC's Resource Management Field School; the course focuses on the impacts that beavers and their dam-building activities have on watersheds and forest succession.

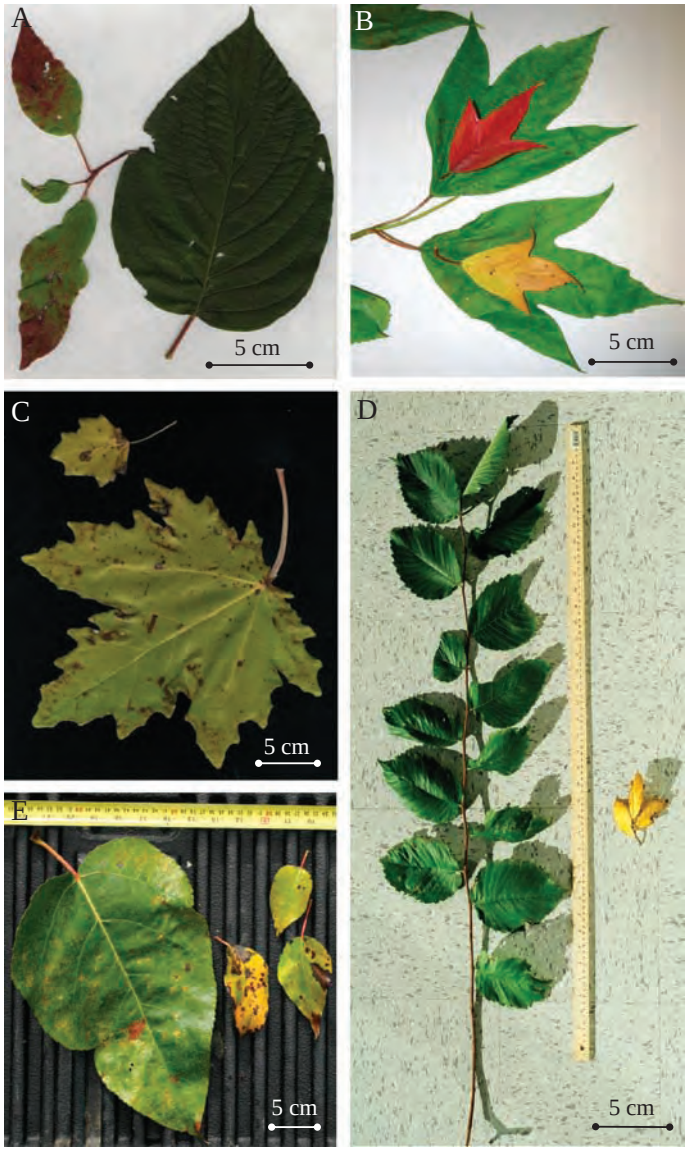

Figure 2. Examples of exaggerated leaf growth due to various forms of plant mechanical damage. Plants undergoing compensatory growth were collected in or near Prince George, British Columbia, Canada, between 2001 and 2009. **(A)** Compensatory (right) and noncompensatory (left, lighter green with red tips) leaves of dogwood (*Cornus stolonifera Michx.*). Increased growth is due to heavy winter browsing by moose. **(B)** Compensatory leaves of *Viburnum opulus* L. following damage from cutting (note: smaller, noncompensatory leaves on top are orange-red and yellow). **(C)** A large leaf (bottom) from a compensatory branch of white poplar (*Populus alba* L.) that was damaged during an ice storm. **(D)** A regenerating annual shoot showing large leaves (left) of elm (*Ulmus americana* L.) in the year after autumn pruning; on the right is a small shoot with yellow leaves from an unpruned elm growing in the vicinity. **(E)** A large compensatory leaf (left) from a shoot growing from a cottonwood (*Populus balsamifera* L.) tree stump after clearcut logging; smaller leaves from a nearby uncut cottonwood show noncompensatory growth.

Field excursions allow students to collect data on how beavers use resprouts, and to form their own conclusions on whether or not beavers "farm" these products. Discussions can also include

The Challenge

Students respond positively when we challenge them to seek out and harvest examples of plant compensatory growth for their assigned plant collections, especially through persuading them to explore locations that they may not have previously considered. To add a little "detective work" to their collecting, we encourage them to try to determine the causal agent of the compensatory reaction. Upon discovering such examples, students will illustrate their findings and add descriptions in lab reports, or make additional comments in the "Notes" section of their herbarium labels - which otherwise are often left blank!

Figure 3. Instructors can encourage students to think about plant compensatory growth by helping them approach collecting as exploration and detective work.

Which Plants Compensate?

Although compensatory growth is known to occur in many plant species, including conifers (Edenius et al., 1993), it is more obvious and easier to detect in hardwood shrubs and trees such as the Salicaceae (poplars and willows), Ulmaceae (elms), and Betulaceae (birches, alders, and hazels) – all of which we use for demonstration purposes in our class.

Figure 4. Plant species respond differently to damage and, as such, vary in the degree to which they can be used to illustrate the effects of plant compensatory growth in the classroom.

Figure 5. Students assess the response of Douglas hawthorn shoots to clipping and cutting by measuring current annual shoot lengths as well as thorn lengths (October 2005).

other related research findings such as those described by Dyer (1980), who found that saliva left on shoots by some herbivores contains growth-promoting hormones that allow plants to recover quickly following damage. Such insights allow students to consider animals as more than passive consumers of plant materials.

5. *How is the architecture of plant arming (e.g., thorns) altered during plant compensatory growth?* Uncomplicated surveys conducted by some of our students (Figure 5) have compared the thorns from branches of hawthorn (*Crataegus douglasii* Lindl.) plants that are undamaged to those that have been cut or browsed, revealing that thorns as well as branch length can be altered after mechanical damage. Considering how plant resources dedicated to branches and arming may change during compensatory growth has led to interesting discussions and new questions.
6. *Can compensation by plants extend into later autumn the period of leaf availability for herbivores, or are late-season green leaves made less palatable by plant-inducible defense systems that are initiated by compensation?* An independent study project by one student

addressed this question. Inquiry led to the discovery that plants cut later in the year retained green leaves long into the fall and that this presumably altered the forage value of leaves for herbivores.

Delayed leaf senescence in plants undergoing compensation, as referred to above (example 6), is an important topic and benefit of compensatory growth. The duration of persistent leaves depends on the time of the year that plants are damaged (Rea et al., 2007); most plants that are damaged grow new shoots and leafy materials long after undamaged plants have dropped their leaves and hardened off for the winter. Plants undergoing compensatory growth often take on a more juvenile form (i.e., put energy into vegetative rather than sexual reproduction and growth) and may not produce flowers in the first few years after damage (Bryant et al., 1985). To reflect this variability in growth in our lab exercises, we combine compensatory with noncompensatory shoots in a montage of plant materials that we collect for our students to identify, press, and study during the semester. In some years, when fall arrives early, we rely heavily on plant compensatory growth in plants such as hawthorn and hazelnut (*Corylus cornuta* Marsh.) to provide fresh plant materials for the laboratory.

Students have responded with openness and interest to our discussions on plant compensatory growth. In chance meetings with students after they have taken our class, they often comment on how the concept of compensation has remained with them and how they see examples of it wherever they go. Some also comment on how these discussions helped them realize that plants are not just static, predictable organisms covering the landscape but are part of a dynamic habitat to which they respond in a myriad of interesting ways, serving as animal food and cover as well as resource materials for humans.

As instructors, we have also benefited from integrating plant compensatory growth into our curriculum. Each year, we discover different examples of plant damage (e.g., ice storms and insect galling) that can lead to new ways in which plants respond to that damage through compensation. Compensatory growth has provided us with opportunities to enrich our fall field collections and herbarium specimens, as well as to integrate plant and wildlife topics into the teaching curriculum of natural resources. More importantly perhaps, it has allowed us to discuss with our students why some things in nature cannot always be easily assigned to predetermined categories (such as dichotomous keys or textbook descriptions) and how using average measurements to describe plants will sometimes fail.

Exploring concepts of plant compensatory growth encourages students to think outside the box, to critically analyze source materials when sampling, to collect from several individuals, to take good field notes, and to do some problem solving. Teaching students to integrate concepts of plant compensatory growth and to understand why growth varies in some plant parts reinforces the value of dichotomous keys and strengthens the students' ability to successfully use these aids for meaningful identification. Whether in university or grade 6, the value of critical inquiry and exploration allows students to realize that much of nature still remains to be better understood.

○ Acknowledgments

We are grateful to Linda Tackaberry for a critical review of the text. We also thank all of our Plant Systems students who, over the years, have contributed to many exciting discussions about plant compensatory growth as it relates to systematics. We are grateful to four anonymous reviewers for their comments on an earlier draft of the manuscript.

References

Bryant, J.P., Wieland, G.D., Clausen, T. & Kuropat, P. (1985). Interactions of snowshoe hare and feltleaf willow in Alaska. *Ecology*, *66*, 1564–1573.

Carson, A.W., Rea, R.V. & Fredeen, A.L. (2007). Extent of stem dieback in trembling aspen (*Populus tremuloides*) as an indicator of time since simulated browsing. *Rangeland Ecology and Management, 60,* 543–547.

Carson, A.W., Rea, R.V. & Fredeen, A.L. (2009). Compensatory shoot growth in trembling aspen (*Populus tremuloides* Michx.) in response to simulated browsing. *Alces*, *45*, 101–108.

Danell, K., Haukioja, E. & Huss-Danell, K. (1997). Morphological and chemical responses of mountain birch leaves and shoots to winter browsing along a gradient of plant productivity. *Ecoscience, 4,* 296–303.

Dyer, M.I. (1980). Mammalian epidermal growth factor promotes plant growth. *Proceedings of the National Academy of Sciences, 77,* 4836–4837.

Edenius, L., Danell, K. & Bergström, R. (1993). Impact of herbivory and competition on compensatory growth in woody plants: winter browsing by moose on Scots pine. *Oikos, 66,* 286–292.

Fertig, W. & Markow, S. (2001). Guide to the willows of Shoshone National Forest. US Department of Agriculture, Forest Service General Technical Report RMRS-GTR-83.

McNaughton, S.J. (1983). Compensatory plant growth as a response to herbivory. *Oikos, 40,* 329–336.

Millington, W.F. (1963). Shoot tip abortion in *Ulmus americana. American Journal of Botany, 50*, 371–378.

Rea, R.V., Child, K.N., Spata, D.P. & MacDonald, D. (2007). Influence of cutting time on brush response: implications for herbivory in linear (transportation) corridors. *Environmental Management, 40,* 219–230.

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