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Transient nutritional peak in browse foliage after forest clearing advocates cohort management of ungulates

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Abstract

It is well established that forest clearing produces an intense upsurge of new plant material with assumingly improved nutrient availability to large herbivores. One aspect that is surprisingly unexplored is how the nutrient contents of plant tissue progress with time after clearing. We show that large-scale time-series of forest clearing and moose (*Alces alces* L.) fitness were positively related, with a temporal lag conforming to the nutritional peak in regrowth of birch (*Betula pubescens*). Foliage from 5-year-old clearcuts had higher contents of crude protein, and lower contents of indigestible lignin compared to 10- and 15-year-old clearcuts. Several mineral ratios also became less favourable with clearcut age, predominantly due to a rise in calcium content. The significant, but transient improvement of browse quality adds to the accumulating evidence emphasizing the need to consider the population ecology of large herbivores also in terms of cohorts. Furthermore, it underlines the applied importance of incorporating ungulate management into forestry planning.

Zusammenfassung

Es ist gut bekannt, dass Kahlschlag von Wäldern einen steilen Anstieg von neuem Pflanzenmaterial hervorbringt, wobei vermutlich die Nährstoffverfügbarkeit für große Herbivoren verbessert wird. Ein überraschend wenig untersuchter Aspekt ist, wie sich die Nährstoffgehalte in Pflanzengeweben in der Zeit nach dem Kahlschlag entwickeln. Wir zeigen, dass die langfristigen Zeitreihen zu Kahlschlägen und Fitness von Elchen (*Alces alces*) positiv miteinander korreliert waren, wobei es eine zeitliche Verzögerung gab, die mit dem maximalen Nährstoffgehalt der nachwachsenden Moorbirken (*Betula pubescens*) übereinstimmte. Das Laub von fünfjährigen Kahlschlagsflächen wies höhere Gehalte von Rohprotein und geringere Gehalte von unverdaulichem Lignin auf als das von zehn- und fünfzehnjährigen Kahlschlägen. Verschiedene Mineralkonzentrationen wurden ebenfalls mit zunehmendem Alter der Kahlschläge ungünstiger, besonders aufgrund einer Zunahme der Kalziumkonzentrationen. Die signifikante, aber vorübergehende, Verbesserung der Futterqualität trägt zu der wachsenden Zahl von Hinweisen bei, die auf die

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Notwendigkeit hinweisen, die Populationsökologie von großen Herbivoren als eine Ökologie von Kohorten zu betrachten. Sie unterstreicht desweiteren die angewandte Bedeutung der Berücksichtigung des Herbivorenmanagements für die Forstplanung.

Keywords: *Alces alces*; Assart effect; Body mass; Logging; Nutrition; Population ecology

Introduction

The nutrient content of plants plays a major functional role in practically all ecosystems, by directing the distribution of herbivory (Provenza et al. 2007), and by influencing the rate of decomposition (Aerts & Chapin 2000). It is well established that forest clearing produces an intense upsurge of new plant material with assumingly improved nutrient availability for large herbivores, i.e. an assart effect (Kimmins 2003). One aspect that is surprisingly unexplored, is how the nutrient contents in plants progress with time after clearing (but see, e.g., Bergquist & Örlander 1998; Palviainen, Finér, Mannerkoski, Piirainen, & Starr 2005).

Beneficial environmental conditions, such as improved forage availability, produce individuals with better health and, therefore, better reproductive opportunities (e.g., Pelletier, Moyes, Clutton-Brock, & Coulson 2012). Because areas of recently cleared forest add substantially to these conditions, it is important to determine the permanence of possibly improved abundance and nutritional value of plants on such sites. Several studies have documented an extensive increase in the browse abundance after forest clearing: up to 6–8 times is typical for boreal forests across the northern hemisphere (e.g., Tremblay, Huot, & Potvin 2006; Månsson 2009; Wam, Hjeljord, & Solberg 2010). Abundance increase is fairly proportional with time until trees start to grow out of reach of the herbivore. For the tallest herbivores having a browsing height up to about 3 metres this normally occurs within 10–15 years (Månsson 2007).

Although utilization of forage by large herbivores is partly governed by plant abundance, the nutritional quality of the forage is also important, in particular during summer (Hjeljord, Hövik, & Pedersen 1990). According to element turnover in boreal forests, the assumingly beneficial assart effect of logging on nutrient contents of foliage is expected to peak early after clearing (Odum 1969), but there is no empirical data giving a specific timeframe (see Spaeth, Bowyer, Stephenson, Barboza, & van Ballenberghe 2002 on twig quality). We are therefore lacking in our understanding of how a given forage type changes during early succession, how this may affect animal fitness, and what implications this may have for large herbivore management.

In this study we examined how nutrient contents of foliage from birch (*Betula pubescens* Ehrh.), vary with time after clearcutting. We focused on birch because the species dominates regrowth on clearcuts in much of the boreal forests (Renecker & Schwartz 1998) and is a staple forage for moose (*Alces alces* L.) in many areas (Wam & Hjeljord 2010), and because its growth and senescence is representative of most pioneer species (Kimmins 2003). We sampled foliage from pristine birch growing on 5-, 10- and 15-year-old clearcuts, and compared time series of forest clearing and moose body mass to test if body masses were higher when clearcuts peaked in assumed browse quality. High nutritional quality for large herbivores is commonly considered to constitute (but see discussion) (1) high levels of proteins, (2) low levels of structural carbohydrates, (3) balanced mineral ratios, and (4) low levels of herbivory defence metabolites. We predicted the browse quality to peak at 5 or 10 years based on the following hypotheses:

(1) Nutrient contents of forest plants are largely determined by availability of elements in the soil, along with water, light and temperature (Cole & Rapp 1980). In boreal forests, clearing leads to a flush of soil nitrate (NO_3^-) normally starting within one year (Kreutzweiser, Hazlett, & Gunn 2008), and suggested to last for 3–5 years (Prescott 2002). Because soil nitrate is the main source of nitrogen for most pioneer species (Min, Siddiqi, Guy, Glass, & Kronzucker 2000), the contents of crude protein should be higher in foliage from younger clearcuts. Total carbon in the foliage should not be much affected by forest clearing, because terrestrial plants assimilate more than 95% of their carbon from aerial CO_2 (Livingston & Beall 1934), and thus, carbon is rarely a limiting factor.
(2) While the total carbon may not change much, the allocation of carbon within the plant is likely to change with clearcut age (Friend, Coleman, & Isebrands 1994). Larger plants need a more vigorous physical support system, prioritizing structural carbon components. The content of cell-wall bound carbohydrates (neutral detergent fibre NDF, and in particular lignin) should therefore increase with clearcut age. Soluble carbohydrates (water soluble carbohydrates WSC in our study) act mainly as reservoirs for metabolism, becoming a source only in times of inadequate photo-assimilates (Kozlowski 1992). The contents of WSC may therefore decrease with clearcut age because these conditions is more likely to occur in more shaded environments.
(3) Calcium and magnesium, and to a lesser extent potassium, have been found to accumulate in new vegetation following forest clearing (e.g., Turner 1975). If so, this will also influence several mineral ratios, where even