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Measures of browse damage and indexes of ungulate abundance to quantify their impacts on aspen forest regeneration



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ABSTRACT

Ungulate communities are changing at a global scale, which is increasing the need for landscape scale quantification of ungulate impacts on plant communities. To achieve robust monitoring across variable landscapes, managers need quick and reliable indicators for assessing ungulate impacts. Our goal was to evaluate two direct (meristem removal, defoliation) and two indirect methods (fecal counts, camera counts) for evaluating ungulate activity on forest regeneration after fire. We examined the relationships between measures of browse activity (meristem removal, defoliation) of aspen with ungulate community estimates (fecal and camera counts) as a function of variation in physiographic conditions across the study sites. Measurements were made in belt transects at 28 sites across three fires that burned in National Forests in Utah in 2012. Aspen height was best predicted by a model with meristem removal, terrain ruggedness, aspect, and year. Mean aspen height was 5 cm lower for every 10% increase in meristem removal an effect that increased over time. We found moderate correlation between the year and percent defoliation interaction and aspen density. Percent defoliation was related to reduced aspen density in the 2nd and 3rd years but not in the 1st year. Results demonstrated that meristem removal is correlated closely with ocular estimates of defoliation ($r^2 = 0.83$), ungulate abundance using fecal counts ($r^2 = 0.65$) and camera counts ($r^2 = 0.63$). Fecal counts and camera counts also correlated well with each other ($r^2 = 0.74$). Estimates of meristem removal in our study suggest that 75% browse of apical meristems is an important threshold for successful aspen height growth and 50% defoliation for aspen regeneration density. Our study highlights the strengths of measurements of meristem removal and defoliation to predict ungulate effects on forest recruitment potential.

1. Introduction

Ungulate herbivory can have strong top-down effects on the abundance and composition of plant communities (Augustine and McNaughton, 1998; Carpio et al., 2015; Hobbs, 1996; Waller and Alverson, 1997). Ungulate communities and populations are changing drastically due to management of ungulate populations and introduction of non-native ungulates (Spear and Chown, 2009; Waller and Alverson, 1997). There is strong evidence that growing ungulate populations limits the regeneration of palatable tree species and reduces plant diversity (Augustine and Frelich, 1998; Edenius et al., 2011; Kaufmann et al., 2014; Rooney and Waller, 2003). As a result, there is increased interest in understanding how changing ungulate herbivory regimes are affecting forest recruitment at landscape scales (Frerker et al. 2013). However, accurate characterization of ungulate impacts on vegetation at large spatial scales is technically challenging due to the large degree of variation and complexity across landscapes (Frerker et al., 2013; Waller et al., 2009). Therefore, development and

comparison of indexes characterizing ungulate impact on ecologically important species is increasingly important under changing herbivory regimes.

Ungulate impacts on ecologically important pioneer plant species are well studied, yet often show conflicting patterns (Bartos et al., 1994; Barnett and Stohlgren, 2001; Kauffmann et al., 2010; Randall and Walters, 2011; Ripple et al., 2001). Differences in the methodologies used could contribute to the inconsistency in observed results (Waller et al., 2009). Studies that quantify the impact of ungulates on plant communities generally use two methodological approaches. The first method estimates ungulate population size to infer relative effect on plants across different study areas (Rooney and Waller, 2003; Waller et al., 2009). We refer to this first approach as “indirect” because it assumes that the number of ungulates is proportional to their impact on one or more plant species (Morellet et al., 2001). The second approach is to evaluate the ungulate herbivore damage on the focal plant by some measure of damage to plant tissue. We refer to this approach as “direct” given that the focal plant species is used directly to evaluate ungulate

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impact. Selecting optimal methods for estimating ungulate impacts on plant communities is crucial for effective management, yet few studies have explicitly compared the efficacy of multiple methods (Waller et al., 2009).

Indirect methods have been the basis of evaluating ungulate impacts for decades and generally estimate relative abundance through fecal counts, camera counts, or management derived population estimates (Barnett and Stohlgren, 2001; Randall and Walters, 2011; Rooney and Waller, 2003; Seager et al., 2013). Indirect methods have proven useful when compared to other estimates of ungulate habitat use (Loft and Kie, 1988), and can inform management decisions (Barnett and Stohlgren, 2001; Wan et al., 2014). Fecal counts have been successfully used since the 1940's to estimate relative abundance of ungulates (Bennett et al., 1940) and are often combined with assumptions about defecation rates to extrapolate population size (Neff, 1968; Royo et al., 2016). In recent years, camera-traps have been used for estimating animal abundance (Clare et al., 2015; Long et al., 2007), and ungulate behavior and forage patterns in plant communities (Faison et al., 2016a). Use of management derived population estimates have been used to estimate ungulate impact on plants (Seager et al., 2013). However, due to the wide variety of methods (Loft and Kie, 1988) and the known inaccuracies in estimating population sizes (Krebs, 1999; Waller et al., 2009) these methods may prove less useful at landscape scales (Frerker et al., 2013).

Indirect methods of quantifying ungulate impacts on vegetation have the advantage of identifying consumers when multiple herbivores are present (Rhodes et al. 2017a,b) but they generally have low model fit and predictability (Rhodes et al. 2017a; Rooney and Waller 2003; Stewart et al. 2009). This is likely due to confounding effects such as: changing forage availability, topography and climate across sites (Frerker et al. 2013; Rhodes et al. 2017a). Linking estimates of ungulate abundance directly to their impact on the plant community is challenging due to the high mobility of ungulates and inaccurate methods of estimating mobile animal populations (Krebs, 1999; Waller et al., 2009). For these reasons, there is increasing interest in using direct methods to assess ungulate impacts on focal plant species (Frerker et al., 2013).

Quantifying direct ungulate impacts on plants by measuring browse damage, accurately measures the impact but identifying the ungulate species responsible can be challenging (Frelich and Lorimer 1985; Rooney and Waller 2003; Waller et al. 2009). Direct measurements of ungulate impact on plants include removal of meristems (McInnes et al. 1992; Wan et al. 2014), removal of leaf tissue or indices that use a single plant species as indicators of ungulate impact (Balgooyen and Waller 1995; Frelich and Lorimer 1985; Mason et al. 2010; Rooney and Waller 2003). Ocular estimations of removal of leaf tissue could be analogous to percent cover. Ocular cover estimates, while often considered highly subjective, can be similar to and more efficient than more complex methodologies (Vales and Bunnell 1988). Direct methods sometimes allow differentiation between vastly different herbivores (hares vs. moose, McInnes et al. 1992), but distinguishing between ungulates can be difficult (Faison et al. 2016b).

Aspen (*Populus tremuloides* Michx.) forests are model systems for understanding plant-herbivore interactions because they provide habitat and forage for many herbivore species and their defense chemistry is well characterized (Lindroth and St. Clair, 2013). There is concern that heavy browsing of aspen by ungulate in some areas may contribute to aspen decline (Lindroth and St. Clair, 2013; Seager et al., 2013). In the Intermountain West, fire is a major driver of aspen regeneration and retention across the landscape (Romme et al., 2005; Smith et al., 2011a). Aspen is particularly susceptible to ungulate herbivory as root suckering occurs after fire (Seager et al., 2013). However, there is considerable controversy over the magnitude of the impact of ungulates on aspen recruitment (Kauffmann et al., 2010; Rhodes et al., 2017a; Ripple et al., 2001; Romme et al., 2005). Vertical escape through height growth is an important aspen defense strategy against ungulate herbivory, and sufficient density is needed for stand replacement after fire

(Bartos et al., 1994; Rhodes et al., 2017b; Seager et al., 2013). Monitoring of aspen regeneration has shown acute failure of aspen regeneration after fire in some areas (Bartos et al., 1994; Ripple et al., 2001) and stable regeneration despite high ungulate densities in other locations (Barnett and Stohlgren, 2001; Romme et al., 2005). Aspen regeneration success can vary depending on climate, topography and stand composition (Rhodes et al., 2017a; Smith et al., 2011a), which can confound our understanding of the direct effect that ungulates have on aspen regeneration success. Further, quantifying ungulate impacts on plants is inherently complex given the diversity and complexity of ungulate behavior and diet (Beck and Peek, 2005; Long et al., 2014).

Exploring the advantages and disadvantages of various methods for quantifying ungulate impacts on aspen regeneration and recruitment is vital to managing for resilience and sustainability of forest ecosystems. Our central research question was: which measures of ungulate impact are best for predicting aspen establishment and recruitment in post-fire environments across large landscapes? The objective of this study was to compare the efficacy of common methods for estimating ungulate impact on aspen. We measured the height and density of aspen regeneration for three years post-fire. We then compared the relative performance of four methodologies (two indirect and two direct) for estimating ungulate impact on aspen regeneration. Secondly, we used physiographic features to account for variation in the impact of ungulate species on aspen regeneration due to topography. We predicted that aspect, terrain ruggedness, and elevation would influence aspen vertical growth and density. We hypothesized that aspen height would be better estimated by direct methods given that loss of plant tissue can translate into reduction of height. Finally, we predicted that aspen density would be better estimated by indirect methods of estimating ungulate impact because removal or death of aspen through herbivory is likely related to total ungulate number.

2. Materials and methods

2.1. Study area

This study was conducted in post-fire environments in mixed aspen-conifer forests across three National Forests of central and southern Utah. Our study consisted of 28 sites across three fires that burned in summer 2012 that demonstrated aspen suckering in the fall of 2012 (Fig. 1). Fire sizes ranged from 900 to 19,400 hectares. Site elevations ranged from 2500–3030 m and slope ranged from 1 to 28 degrees. Thirty year mean annual precipitation ranged from 380 to 800 mm. Dominant tree species in the Seeley and Box Creek fires included: Aspen, Subalpine Fir (*Abies lasiocarpa* (Hooker) Nuttall) and White Fir (*Abies concolor* (Gordon) Lindley ex Hildebrand). While the dominant conifer component of Harris Flat fire is Ponderosa Pine (*Pinus ponderosa* Douglas ex C. Lawson). Cattle (*Bos taurus*), Mule deer (*Odocoileus hemionus*), and American elk (*Cervus canadensis*) were the most abundant ungulates herbivores at the study sites.

2.2. Sampling design

Eight sites were established in 2012 and the remaining 20 were established in May 2013. At each site we established one 50 × 2 meter belt transect for characterizing aspen regeneration density, height, damage to aspen and fecal counts. The first samples were taken in September 2013. In total, there were 15 sites in the Seeley fire, 8 sites at the Box Creek fire, and 5 sites at the Harris Flat fire. We randomly selected the direction of each belt transect and marked both end points with u-posts and GPS waypoints. In September of 2013, 2014, and 2015 we surveyed aspen sucker regeneration responses and herbivory patterns along these transect lines. We defined an aspen sucker as emerging independently from the ground (unbranched above ground level) within transects.

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