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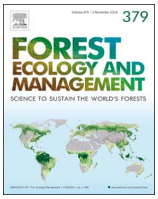

Species selection – A fundamental silvicultural tool to promote forest regeneration under high animal browsing pressure

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ABSTRACT

Heavily disturbed post-mining sites are often difficult to restore to forestland due to chemical and physical soil limitations, as well as frequent animal herbivory of planted tree seedlings. Forest tree species differ in how they allocate resources to defensive compounds or growth in order to resist abiotic and biotic stresses after outplanting. However, the influences of plant nutrition and secondary metabolite production on browse susceptibility and recovery are not well understood within and among species, especially for temperate deciduous forest trees. We investigated foliar tannin and nutrient responses under fenced (to exclude white-tailed deer, *Odocoileus virginianus*) and non-fenced environments on an abandoned mine land in southwestern Indiana, USA. Using field fertilization (15N-9P-10K controlled-release fertilizer at 0, 30 g, and 60 g per seedling), we also created a gradient of nutrient availability for planted black cherry (*Prunus serotina* Ehrh.), bur oak (*Quercus macrocarpa* Michx.), northern red oak (*Quercus rubra* L.), and white oak (*Quercus alba* L.) seedlings. Fencing improved growth relative to non-fenced seedlings; fertilization improved growth for all species except northern red oak, but only when combined with fencing. Fertilization reduced foliar tannin concentrations for black cherry and white oak, but did not change browsing preference or browse recovery for any species. Without fencing, browsing selection was solely driven by tree species, whereby black cherry had a higher likelihood of being browsed compared to all oak species. This response was likely associated with differences among species in resource allocation patterns; black cherry prioritizes structural growth and recovery, while oaks allocate resources to both growth and secondary metabolite production. As fencing is often considered cost-prohibitive for mine reclamation and other restoration efforts, species selection is perhaps the most fundamental silvicultural tool to promote forest regeneration success under conditions of high animal browsing pressure.

1. Introduction

Planting of forest trees to facilitate restoration of harsh sites, such as in post-mining reclamation, is often challenging (MacDonald et al., 2015). Major limitations to seedling establishment common to many degraded sites are low soil fertility (Vogel, 1980; Bussler et al., 1984; Showalter et al., 2007; Vega et al., 2013) and animal damage (Skousen et al. 2009), both of which impair basic physiological processes, such as CO_2 assimilation, respiration, translocation, and synthesis of sugars, proteins, and nucleic acids (Rook, 1991). These limitations may restrict the ability of seedlings to establish on a site and lead to slow growth and/or mortality. This may be of particular concern in the case of temperate deciduous hardwood species because they require high levels of nutrient availability following planting to achieve optimal growth (Wilson and Jacobs, 2006; Jacobs et al., 2005a, 2005b).

Fertilization at the time of planting may help to alleviate seedling nutrient deficiencies and promote early growth on post-mining sites (Auchmoody, 1982; Casselman et al., 2006; Sloan and Jacobs, 2013; Sloan et al., 2016). Rapid early seedling growth also supports development to a free-to-grow status above the browse line of ungulates, which may allow seedlings to escape animal damage. Additionally, increased levels of stored nutrients may aid seedlings in recovering from browse damage (Burney and Jacobs, 2011, 2012, 2013). High plant nutrient content may, however, make seedlings more susceptible to ruminant (e.g., deer, elk, and sheep) browsing (Crouch and Radwan, 1981; Anderson, 1981; Månsson et al., 2009; Burney and Jacobs, 2013). In conifers, palatability appears to be at least as dependent on production of plant chemical defenses, particularly monoterpenes, as plant nutrient content (Burney and Jacobs, 2011, 2013). Interactions among foliar nutrient concentration, plant chemical defenses, and animal

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browsing damage are complex, however, and have been studied sparsely, particularly for temperate deciduous hardwood trees.

Phenolic compounds are the most common secondary metabolite found in plants. They have a variety of roles, which includes the production of lignin to support structural growth, and tannins, compounds that defend against damaging agents such as pathogens, herbivores, and environmental stresses (Haslam, 1998; Pereira et al., 2009; Bhattacharya et al., 2009). Tannins are naturally occurring plant compounds that bind and precipitate proteins and other macromolecules (Haslam, 1998). Located mainly in the vacuoles or surface wax of plant tissue, tannins are found in plant buds, leaves, stems, roots, and seeds. Tannins are common to both gymnosperms and angiosperms, including oaks (*Quercus* spp.), pines (*Pinus* spp.), maples (*Acer* spp.), and birches (*Betula* spp.) (Talbot and Finzi, 2008).

Forest tree seedlings that contain high concentrations of tannins tend to be less palatable, more difficult to digest, and even toxic to most herbivores (Robbins et al., 1987; Kimball and Nolte, 2005). However, deer and other ungulates have developed a counter-defense mechanism that allows them to tolerate higher levels of tannins in their diet. Through the production of glycoproteins (proline, glycine, and glutamate/glutamineproline) in saliva, deer are able to bind tannin compounds to theses proteins, thereby minimizing absorption and reducing toxicity of high tannin consumption (Austin et al., 1989; Barry and McNabb, 1999). Regardless of the use of detoxifying salivary compounds, ruminants have shown preference for lower concentrations of tannins possibly to minimize overloading detoxification pathways (Bergvall et al., 2006; Kimball and Nolte, 2005; Jones et al., 2010). In an effort to maintain adequate energy and protein intake, ruminants will balance their diets with a combination of both nutritional plants and forage containing toxic chemical compounds (Jenkins and Starkey, 1993; Provenza et al., 2003; Burney and Jacobs, 2013).

Fertilization has been shown to decrease condensed tannin production in a variety of oak species, including *Quercus rubra* L. and *Quercus prinus* L. (Forkner and Hunter, 2000) and *Quercus laevis* Walt. (Cornelissen and Stiling, 2006). Reduced tannin production may be the result of a shift in the allocation of plant resources from defense mechanisms to growth under nutrient-rich conditions (Stamp, 2003; Blanch et al., 2007; Burney and Jacobs, 2012). The combination of increased foliar nutrition and decreased tannin production implies that field fertilized seedlings may initially be more susceptible to animal browsing. A potential tradeoff, however, is that fertilization may promote the ability of seedlings to achieve a free-to-grow status through rapid growth prior to browse damage, and/or to recover from incurred browse damage faster than non-fertilized seedlings.

We studied relationships between soil nutrient availability gradients (achieved via field fertilization) and production of plant tannins, as well as susceptibility and recovery from animal browse for four temperate deciduous hardwood species planted on an abandoned mine site in southwestern Indiana, USA. Browse damage due to white-tailed deer (*Odocoileus virginianus*) has been identified as a major limiting factor to forestry plantation success in this region (Jacobs et al. 2004). Treatments consisted of fertilization at three levels (including an unfertilized control) and fencing to exclude white-tailed deer vs. no fencing. Specific study objectives were to: (i) examine species differences in seedling performance and likelihood of browsing; (ii) assess the effect of fertilization on seedling performance and the relationship to browsing among species; and (iii) evaluate the susceptibility of planted seedlings to animal browse in relation to foliar concentrations of nutrients and tannins as affected by fertilization treatments.

2. Methods

2.1. Plant material

Bareroot (1 + 0) seedlings of black cherry (*Prunus serotina* Ehrh.), bur oak (*Quercus macrocarpa* Michx.), northern red oak, and white oak (*Quercus alba* L.) were grown from seed germinated in spring of 2007 at Vallonia State Nursery (38°85′N, 86°10′W) in Indiana, USA. As per operational nursery protocols detailed in Jacobs (2003), seed was collected from sources local to the nursery and all standard cultural practices for seedling production were followed. Seedlings were mechanically lifted in December of 2007 and processed for over-winter storage in coolers (3 °C) at Purdue University (40°25′N, 86°55′W) in West Lafayette, Indiana, USA. Plants were removed from storage in May 2008; randomly collected samples of 5 seedlings per species were divided into root and shoot components and processed for initial nutrient sampling as described below. Planting was conducted using a machine planter (i.e., tractor-hauled coulter with trencher and packing wheels) with a crew of two to three people.

2.2. Experimental site

This experiment was established at the Indiana Department of Natural Resources Division of Reclamation Dugger Unit (39°4′N, 87°15′W), an 870-ha abandoned mine reclamation site within the Greene-Sullivan State Forest located near Dugger, IN, USA. The property was owned and operated by Peabody Coal Company until 1985. After mining, the site was graded to the original contour of the land and the topsoil was replaced to a depth of about 45 cm and compacted. The site was reclaimed in accordance with regulations associated with the Surface Mining Control and Reclamation Act (SMCRA; MacDonald et al., 2015); it was completed in 1988. The soils vary between clay loam and silt loam with clay, shale, and sandstone, intermixed with large rocks, beneath the soil layer. Vegetation was mechanically removed by mowers in early spring 2008 prior to planting. As a release treatment, competing vegetation was controlled using 0.04 kg ai ha^{-1} metsulfuron methyl (Escort® XP, Dupont, Wilmington, DE, USA). Dominant vegetation that persisted on the site during the experiment included goldenrod (*Solidago virgaurea* L.), sericea lespedeza (*Lespedeza cuneata* [Dum. –Cours.] G. Don), red clover (*Trifolium pretense* L.), ragweed (Ambrosia artemisiifolia L.), and foxtail barley (*Hordeum jubatum* L.).

2.3. Experimental design and treatments

A randomized block design with split-split plots and three blocks was used in this study (Fig. 1). The whole plot treatments were browsing control (fence or non-fenced). The subplot treatments included four hardwood tree species, and the sub-subplot treatments were the three fertilizer application rates, which were completely randomized within each species subplot. Three 2.3-m plastic mesh fences were erected for each of the deer exclusion fenced treatments within a block. These fences did not protect again rodent activity, including rabbits (*Sylvilagus floridanus*). The three fertilization rates were 0 g, 30 g, and 60 g of Osmocote Exact Lo-Start 15N-9P-10K plus minors with 14–16-month release duration (Marysville, OH, USA) applied at the time of planting. The fertilizer was applied immediately after planting by dibbling the prescribed amount into a hole at 15 cm depth in the soil 5–7 cm upslope from the target seedling, an effective method of fertilizer delivery in past trials with hardwoods (Jacobs et al., 2005a, 2005b) and conifers (Sloan and Jacobs, 2013; Sloan et al., 2016). The size of each whole plot was 40.6 m × 36.6 m, and each subplot was 20.3 m × 18.3 m. In each subplot, 90 seedlings of each species were planted 1.2 m apart within rows and 4.5 m apart between rows (Fig. 1). In total, 2160 seedlings were planted for the experiment.

2.4. Measurements

Field measurements for survival, shoot height (cm), and ground line diameter (mm) were conducted at the time of planting (May 2008), October 2008, April 2009, and March 2010. Type of browse damage (deer or rabbit) was evaluated at each sampling period, excluding