Forest Ecology and Management 329 (2014) 137–147

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Response of tree regeneration to experimental gap creation and deer herbivory in north temperate forests

Jodi A. Forrester *, Craig G. Lorimer, Jacob H. Dyer, Stith T. Gower, David J. Mladenoff

Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI 53706, USA

ARTICLE INFO

Article history:
Received 27 March 2014
Received in revised form 20 June 2014
Accepted 22 June 2014

Keywords:
Acer saccharum
Canopy gaps
Height growth
Northern hardwoods
Shade tolerance
Stump sprouts

ABSTRACT

Structural heterogeneity has become a goal of contemporary forest management, yet the effect of incorporating variable sized canopy openings characteristic of older forests on ecosystem services is still largely unknown. Single-tree selection silviculture reduces tree species diversity, and group-selection harvests often produce inconsistent results in maintaining the proportion of species with low or intermediate shade tolerance. It is unclear how much variability is related to inherent growth rate differences among shade tolerance classes, asymmetric competition, sprouting behavior, herbivory, and other factors. We conducted an experiment to control several of these factors. The northern hardwood study area in north-central Wisconsin included 15 replicates of each of 3 sizes of experimental gaps (50 m^2, 200 m^2, and 380 m^2). Ten main plots (80 × 80 m^2) were fenced to exclude deer. Vertical height growth of saplings and stump sprouts was monitored for two years pre-treatment and four years post-treatment.

Overstory gaps significantly increased height growth rates, but there was no significant difference between rates of the very shade-tolerant *Acer saccharum* and several midtolerant species in any gap size. Saplings dominated the regeneration layer in small gaps. Stump sprouts were more abundant and grew faster than saplings in large gaps, but after 4 years, *A. saccharum* advance regeneration still predominated in the upper height classes. Deer had limited effects on sapling development or species composition because tall advance regeneration was beyond their reach, but they severely affected the sprout layer. In unfenced plots, the unpalatable *Ostrya viriginiana* had the tallest sprouts. Overall, midtolerant species made up about 16% of the gap regeneration layer and appear to be increasing their proportion over time. Height growth rates of many saplings and sprouts exceeded 50 cm per year, suggesting that successful gap capture would be likely for both shade-tolerance groups under current environmental conditions. The non-significant difference in growth rates between shade-tolerant and midtolerant species across the light gradient could change as more time elapses since gap creation. However, our findings after four years are consistent with other studies in suggesting that there may be no consistent trends in the relative growth responses of shade-tolerant and midtolerant tree species to increased light and gap size.

1. Introduction

Forest harvest regimes must be continually assessed to ensure long-term ecosystem sustainability and a broad range of services under increasing demands for wood products. However, the impacts of forest management upon structural and functional characteristics that determine ecosystem sustainability and biodiversity are not fully understood. Diversity in structure provides greater functional diversity and contributes to a broader array of ecosystem services (Ishii et al., 2004; Hardiman et al., 2011; Keeton et al., 2011). Second-growth forests in the U.S. Lake States (Minnesota. Wisconsin, Michigan) region have lower diversity of structure, composition and microenvironments than old-growth counterparts that were not logged at the time of Euro-American settlement (Tyrrell and Crow, 1994; McGee et al., 1999; Crow et al., 2002; Goodburn and Lorimer, 1998; Scheller and Mladenoff, 2002).

Uneven-aged management has become increasingly popular on public forest lands to partly address these concerns through implementation of ecological forestry practices and to avoid controversies associated with clearcutting (Crow et al., 1994). However, single-tree selection can lead to a substantial loss of tree species diversity in managed forests because relatively few species are sufficiently shade tolerant to survive and prosper in small, single-tree gaps (Leak and Sendak, 2002; Schuler, 2004). In addition, the

* Corresponding author. Tel.: +1 (608) 265 6321; fax: +1 (608) 262 9922.
E-mail address: jforrester@wisc.edu (J.A. Forrester).

http://dx.doi.org/10.1016/j.foreco.2014.06.025
0378-1127/

presence of high white-tailed deer populations in the region can reduce the structural and species diversity of the understory vegetation (Rooney and Waller, 2003). To better understand the effects of structural heterogeneity on function and services, we conducted a large, replicated field experiment to add old-growth structural elements (gaps of various sizes and coarse woody debris (CWD)) and to control deer browsing in a second-growth northern hardwood forest (Dyer et al., 2010; Stoffel et al., 2010; Forrester et al., 2013). In this study, we compared the tree regeneration, diversity, and growth based on two years of pre-treatment and four-years of post-treatment data.

The ability to foster greater understory plant diversity in these forest ecosystems requires a quantitative understanding of minimum light requirements and opening sizes needed for species of lower shade tolerance. But survival and growth rates across a range of light environments are poorly known for most tree species. The traditional understanding is that shade tolerant species have a competitive growth advantage under low light, whereas intolerant species have a competitive advantage under high light (e.g., Horn, 1971; Givnish, 1988). These inferences have been based to a large extent on greenhouse studies or field studies of photosynthetic and respiration rates of small seedlings. As saplings become larger, factors such as mutual self-shading of leaves and greater respiration costs can alter the situation compared to small seedlings (Givnish, 1988). More recent studies of larger saplings in forest environments have reported a surprisingly wide range of outcomes, with the less tolerant species under a full canopy having greater (DeLucia et al., 1998; Janse-ten Klooster et al., 2007) lesser (Lin et al., 2002; Baltzer and Thomas, 2007), or equivalent growth rates (Gasser et al., 2010) to those of shade-tolerant species. While there is general agreement that the more tolerant species have higher survival rates under shade (Valladares and Niinemets, 2008), there is no strong consensus on the validity of the conventional hypothesis that shade-tolerant species have a competitive growth advantage under a closed canopy (Sack and Grubb, 2001; Baltzer and Thomas, 2007; Valladares and Niinemets, 2008).

Complications also arise when relying upon shade-tolerance theory to predict response of saplings to harvest regimes such as single-tree and group selection. A number of studies of forest saplings across a light gradient have shown that some species with limited shade tolerance may actually grow faster than shade-tolerant species in small as well as large gaps (Beaudet and Messier, 1998; Gasser et al., 2010). Given the documented tendency of single-tree gaps to foster dominance by shade-tolerant species, this suggests that the effective minimum opening size for successful gap capture by the less tolerant species is influenced by several other aspects of forest dynamics. For example, tall advance regeneration of shade-tolerant species may induce initial competitive inequities that may be difficult for less tolerant species to overcome (Webb and Scanga, 2001; Povak et al., 2008; Bolton and D'Amato, 2011). Likewise, vegetative sprouting from mature rootstocks is often a dominant regeneration pathway in deciduous forests, and sprouts may have a strong competitive advantage over existing sapling advance regeneration (Dietze and Clark, 2008). Small and medium gaps are also susceptible to lateral closure by crown expansion of mature gap-border trees (Runkle and Yetter, 1987; Webster and Lorimer, 2005). Furthermore, shorter saplings and sprouts are vulnerable to herbivory that may vary among species. Thus, even if shade-tolerance theory predicts a competitive growth advantage for less tolerant species for a given sapling height and opening size, the species may still commonly fail to capture the gap for a host of other reasons.

These issues are sufficiently complex, and involve such a long time frame for analysis, that a satisfactory resolution will likely require multiple approaches with several independent lines of evidence, including replicated experiments, retrospective studies, chronosequences, and simulations. In this paper, we present preliminary results from a replicated, long-term experiment in which sapling and sprout growth were monitored in gaps of three size classes and uncut control plots in an even-aged, second-growth northern hardwood forest. A disadvantage of the experimental approach is that decades of observation are required before the outcome of gap capture can be determined. But advantages of the experimental approach include documentation of pre-treatment conditions, periodic monitoring of changes over time, documentation of trees that died at various intervals (and which would not survive to be sampled in retrospective studies), and experimental control over factors such as deer browsing.

Our main objective of this study was to evaluate how the survival and growth of saplings and sprouts of shade-tolerant and midtolerant species in northern hardwood forests are affected by gap size, as well as the presence or absence of moderately high levels of deer browsing. Specific questions include: (1) do shade-tolerant species have a competitive survival and growth-rate advantage in small gaps, and midtolerant species in large gaps, as predicted by traditional shade-tolerance theory? (2) does this response change with time since disturbance? (3) how does the growth response of vegetative sprouts compare with sapling response? (4) how strongly do deer modify the species composition and growth rates of gap regeneration under the moderately high deer densities typical of this region?

2. Methods

2.1. Study area

This study is a part of a larger project that was initiated to quantify the effects of canopy gap formation and coarse woody debris on ecosystem processes in northern hardwood forests. The 280-ha study area (45° 37.4′N, 90° 47.8′W) is located in the Flambeau River State Forest, Rusk County, north-central Wisconsin, USA. The field site is representative of the Great Lakes forest landscape with maturing, even-aged, second-growth hardwood stands originating after clearcutting between 1925 and 1927, based on a sample of stem cross-sections taken about 30 cm above ground. Most of the stems originated between 1920 and 1940, with a few originating before 1900 that were advance regeneration released by the clearcut. While the very shade-tolerant sugar maple (*Acer saccharum*) is the principal overstory tree species (56% of stand basal area), 42% of the basal area is comprised of species that are either intermediate in shade tolerance (hereafter 'midtolerant'; Niinemets and Valladares, 2006) or tend to have sparse regeneration beneath a sugar maple canopy and appear to require canopy gaps for successful recruitment. Midtolerant species include white ash, (*Fraxinus americiana*, 12% of basal area), bitternut hickory (*Carya cordiformis*, 4%), black ash (*Fraxinus nigra*, 4%), northern red oak (*Quercus rubra*, 2%), and yellow birch (*Betula alleghaniensis*, 2%). Other species often dependent on sizable gaps in these forests include basswood (*Tilia americana*, 16%) and red maple (*Acer rubrum*, 1%). Sugar maple, white ash, bitternut hickory and hophornbeam (*Ostrya virginiana*) are the most common species in the sapling layer and sugar maple dominates the seedling layer. The site averages 444 trees per hectare and 29 $m^2\ ha^{-1}$ basal area for trees $\geqslant$10 cm diameter breast height (dbh, 1.37 m) (Burton et al., 2011).

The site is generally mesic with level to gently sloping topography. Soils are deep silt loams (Aquic or Oxyaquic Glossudalfs) of the Magnor, Ossmer, and Freeon series overlaying dense till (David Hvizdak, USDA, NRCS). Soils range from moderately well drained (Freeon) to somewhat poorly drained (Magnor and Ossmer), but all are subject to seasonally perched or high water tables. Mean