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Woody regeneration in and around aging southern bottomland hardwood forest gaps: Effects of herbivory and gap size

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Abstract

We examined long-term impacts of mammalian herbivores and canopy gap characteristics on woody plant establishment and growth within six size classes of canopy gaps created in 1994 in a southern bottomland hardwood forest. Woody stem composition (1996, 2004) and height (2004) were assessed in and out of white-tailed deer (*Odocoileus virginianus*) and swamp rabbit (*Sylvilagus aquaticus aquaticus*) exclosures in gap centers, and in additional plots in gap centers, edges, and beneath adjacent forest canopy. Herbivory did not influence vegetation patterns. Composition was more homogenous in 1996 than in 2004, both in gap centers, and along the gap center—forest understory gradient. Composition differed among gap sizes (oaks were more prevalent in larger gaps) and with distance from gap centers (wind-dispersed trees, wind- and animal-dispersed trees, and oaks typified gap centers, gap edges, and forest understory, respectively). Seedlings and saplings were tallest in the smallest gaps and gap centers, intermediate on gap edges, and shortest in the forest. Maintaining low deer densities could continue to minimize mammalian herbivore effects on woody regeneration in this bottomland hardwood forest system. In addition, management for canopy openings in a variety of sizes could promote woody vegetation heterogeneity and regeneration of desirable tree species.

Keywords: Bottomland hardwoods; Canopy gaps; Gap partitioning; Herbivory; Natural regeneration; Oak regeneration; Seedling establishment and dynamics

1. Introduction

In eastern North America, herbivory by white-tailed deer (*Odocoileus virginianus*) and other mammals can impact regeneration of forest trees and influence the composition and dynamics of forested communities. Most notably, deer can increase seedling mortality, and repeated browsing can decrease tree seedling and sapling growth rates (Hough, 1965; Ross et al., 1970; Anderson and Loucks, 1979; Marquis, 1981; Tilghman, 1989; Pedersen and Wallis, 2004; Rossell et al., 2005). Deer and other mammalian herbivores also can impact woody seedling survival and growth indirectly by increasing susceptibility to drought (Peterson and Pickett, 1995) or changing the herb layer composition (Castleberry et al., 2000; Gitzen and West, 2002). In areas with unnaturally high concentrations of herbivores, preferential browsing on certain species could lead to increased growth rates or decreased mortality of less-browsed species, and thus result in unexpected vegetation and successional patterns (Tilghman, 1989; Healy, 1997; Stromayer and Warren, 1997).

Treefall gaps and a number of their associated characteristics (e.g. location within and near treefall gaps, gap size, and gap age) also are known to have important effects on natural regeneration in forests of eastern North America. An extension of the gap/non-gap paradigm of forest regeneration incorporates ‘‘gap partitioning’’ (sensu Denslow, 1980), or the notion that tree species display distinct distributions over gap size, age, and center—closed canopy gradients. Specifically, seedlings of shade-tolerant species can establish in smaller gaps, while seedlings of shade-intolerant species may be restricted to larger or more open gaps (Runkle, 1985, and many others). In addition, seedling establishment and growth rates may be greatest in the short-term in gap centers (Phillips and Shure, 1990; Battaglia et al., 2004a), where light levels are highest and there is low influence from gap edges in all of the gap sizes.

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Group selection timber harvests, which involve the removal of groups of trees to create canopy gaps (usually <2 ha) for tree regeneration, provide an opportunity to investigate the interactive effects of canopy opening characteristics and mammalian herbivory on seedling establishment. Few studies have examined this interaction. Much of the tree regeneration research conducted on group selection harvesting has centered on its utility compared to other silvicultural techniques (Miller et al., 1995; Jenkins and Parker, 1998; Battles et al., 2001) or the effects of gap size and location within openings (McDonald and Reynolds, 1999; York et al., 2003, 2004) on seedling establishment.

In 1994, 36 canopy gaps, with six replicates of six size classes (7, 10, 14, 20, 29, and 40 m radius) were created by group selection harvest in a southern bottomland hardwood forest to examine effects of mammalian herbivory (white-tailed deer (*O. virginianus*) and swamp rabbit (*Sylvilagus aquaticus aquaticus*)) and canopy opening characteristics on composition of woody regeneration. Short-term results from this research suggest that although browsing likely has little immediate effect on the seedling establishment of most tree species (Castleberry et al., 1999, 2000), gap size appears to have a short-term effect on woody species (Castleberry et al., 2000), and herbivory interacts with gap size. More specifically, for some species, recruits in smaller gaps are more susceptible to herbivory than those in larger gaps, possibly due to deer preferentially browsing in less open areas (Castleberry et al., 1999). We conducted follow-up research (1996, 2003–2004) to examine long-term herbivore effects and gap partitioning on woody plant establishment and height growth within the aging (9–10-year-old at the time of our study) gaps (Castleberry et al., 1999, 2000). We asked if herbivory, location within and around gaps, or gap size has influenced establishment patterns over time, and whether management that incorporates gaps of various sizes can increase vegetation heterogeneity and successful establishment of desired tree species.

2. Materials and methods

2.1. Study site

This research was conducted on the 780 km^2 Savannah River Site (SRS), a National Environmental Research Park (NERP) in west-central South Carolina, U.S.A., in the Upper Coastal Plain physiographic province. The SRS has been maintained by the U.S. Department of Energy since 1950. Approximately 700 km^2 of the site is forested; forested areas include stands of planted pine (mainly *Pinus taeda* and *Pinus palustris*), upland hardwoods, bottomland hardwoods, and swamp forests (Whipple et al., 1981; Workman and McLeod, 1990).

The study area was a 120 ha, 70-year-old, bottomland hardwood stand located 1.5 km east of the Savannah River (UTM 437,168.91E; 3,667,701.39N). Common overstory species were swamp chestnut oak (*Quercus michauxii*), laurel oak (*Quercus laurifolia*), cherrybark oak (*Quercus pagoda*), loblolly pine (*P. taeda*), and sweetgum (*Liquidambar styraciflua*) at a basal area of 33 m^2/ha (Pauley et al., 1996). The Society of American Foresters forest classification was Type 91, swamp chestnut oak–cherrybark oak (Shropshire, 1980). Primary mammalian herbivores in bottomland hardwood habitats at the SRS include white-tailed deer and swamp rabbits. Conservative study site density estimates for white-tailed deer, which are harvested at the SRS, are approximately 7 deer/km^2 (Leberg and Smith, 1993); although such densities are less than those in other forested systems in the eastern U.S., they are consistent with densities documented as having effects on forest regeneration (Alverson et al., 1988; Tilghman, 1989). Estimates of fewer than one swamp rabbit per hectare are based on those obtained by Lowe (1958) in Georgia bottomland hardwood systems; despite their low densities and limited short-term impact on vegetation dynamics at our study site (Castleberry et al., 2000), rabbits are known to cause shifts in plant species composition (Hjältén, 1991), and their potential long-term impacts need to be determined (Castleberry et al., 2005).

2.2. Procedures

In 1994, 36 gaps in the forest canopy were created by a group selection timber harvest. The gaps were located in areas with mature oaks that could serve as seed trees after harvest. Trees were felled with mechanized harvesting equipment and grapple skidded to loading decks. The only additional site preparation involved manual felling of undersized stems before the first growing season (Castleberry et al., 2000). The 36 gaps included six replicates of six sizes (7, 10, 14, 20, 29, and 40 m radius).

Three types of fenced herbivore exclosures (6.5 m × 3.5 m) were constructed in the center of each gap (Castleberry et al., 2000). Exclosures were designed to exclude deer, swamp rabbits (*S. aquaticus*), or both deer and rabbits, and one exclosure of each type was established in the center of each gap. Unfenced controls were established adjacent to the exclosures. The exclosures were constructed using welded wire fencing and 2.4 m metal posts. The deer exclosures were built with 1.5 m high fencing, but raised 20 cm to allow free movement of swamp rabbits underneath. Rabbit exclosures were 20 cm high, and the deer/rabbit exclosures were 1.5 m high and not raised.

Our research focused on three replicate gaps of each of the six (7, 10, 14, 20, 29, and 40 m) gap sizes. These gaps ($N = 18$), or half of the original 36 gaps, were selected for ground layer vegetation studies in 1994 (Pauley et al., 1996; Collins, 2003). In each gap, three replicate 0.5 m × 1 m unmanipulated plots (hereafter, 'exclosure plots') were established in 1994 as part of a series of ground layer treatment plots (Pauley et al., 1996; Collins, 2003) within each exclosure type (deer, rabbit, deer + rabbit, unfenced controls; Fig. 1a). In addition, 0.5 m × 1 m unmanipulated plots were established as part of a series of ground layer treatment plots along two parallel north–south transects spanning the east and west portions of each gap (Fig. 1a). There was one of these unfenced plots (hereafter, 'sideplots') along each transect in gap center, edge, and forest (1 × gap diameter into the forest beneath the canopy) locations (Collins, 2003). The identity and number of naturally