



# The effects of deer herbivory and forest type on tree recruitment vary with plant growth stage



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## ABSTRACT

Understanding the combined effects of land-use changes and expanding generalist herbivores on the recruitment of tree species is critical to predict forest community dynamics and for fulfilling conservation purposes. We assessed how deer herbivory and forest-type affected the diversity of seedlings and saplings of dominant tree species in a temperate forest of Eastern USA, during four consecutive years. Fenced and unfenced plots were established in hardwood and pine forests and tree seedlings and saplings identified and monitored annually. Tree recruitment patterns varied widely from year to year, particularly for seedlings. Sapling communities were richer in species, more diverse and with lower indexes of dominance than seedling communities. The diversity of seedlings and saplings was significantly affected by inter-annual variation of tree recruitment but not by deer herbivory or forest type. Herb cover was reduced for more than fourfold in unfenced hardwood plots. Results show that inter-annual variation of recruitment, herbivory and forest type can combine to shape the composition of tree seedlings and saplings. When assessing effects of deer on tree recruitment interactions between biotic (e.g. herbivory) and abiotic (e.g. forest type) factors need to be considered. The outcome of such interactions depends on seedling or sapling life stage.

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## 1. Introduction

Global changes, including climatic and land-use changes, are affecting forest ecosystems worldwide (Feeley et al., 2010). Increased inter-annual climatic variability alters the phenology, growth rates and survival of tree seedlings, and the consequent patterns of tree recruitment (Bertrand et al., 2011). Conversion between forest types, with associated changes in disturbance regimes (e.g. changed frequency of fire regimes or increased clear cutting practices) and site ecological conditions (e.g. nutrients, site productivity) constrains tree regeneration niches and the species composition of forests (Taverna et al., 2005; Turner, 2010; Edenius et al., 2011; Liira et al., 2011). Conversion between forest types and tree recruitment variability may further combine with deer herbivory and ultimately shape the species composition of adult forests.

Deer populations have been expanding, both in numbers and geographic range, across the temperate forests of the northern hemisphere. Such expansion is partly due to abandonment of farm-

ing land, increase of wooded areas and favorable habitat, and lack of predators (Fuller and Gill, 2001; Coté et al., 2004). Deer are keystone species in forest ecosystems as they affect the recruitment dynamics of tree species (Coté et al., 2004; Rooney and Waller, 2003; Hidding et al., 2012; Speed et al., 2013) and the overall diversity of forest ecosystems through their feeding activities (Allombert et al., 2005; Bugalho et al., 2011; Martin et al., 2011).

Deer feed selectively, that is, they preferentially consume the plants most palatable to them (Verheyden-Tixier et al., 2008). The main determinants of deer feeding selectivity are the availability and the nutritional quality of the plant food (van Soest, 1994). Plant availability, particularly woody seedlings in forests, vary with factors including inter-annual variation in tree recruitment and disturbance or legacy effects associated with different forest types, which restrict tree regeneration niches and the availability of propagules (Naaf and Wulf, 2007; Royo et al., 2010a; Royo et al., 2010b). Plant nutritional quality is mainly determined by the intrinsic biochemical properties of the plant, including the plant cell contents (e.g. nitrogen, cellulose or lignin) and the prevalence of chemical defences (e.g. secondary compounds) (van Soest, 1994). Site conditions, however, namely the nutrient content of soils prevailing under a particular forest type, may also affect the plant nutritional quality (Campo and Dirzo, 2003; Lindroth et al., 2007). Plant fertil-

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**Table 1**

Soil nutrient content (mean  $\pm$  standard error of mean) at hardwood and pinewood forest stands, at two 0–15 cm and 15–30 cm soil depths, in the study area (adapted from Parama, 2006).

Soil nutrient content	Hardwood		Pinewood	
	0–15 cm	15–30 cm	0–15 cm	15–30 cm
Organic Mater (%)	6.304 $\pm$ 0.261	3.774 $\pm$ 0.176	5.090 $\pm$ 0.194	3.561 $\pm$ 0.167
Nitrate (mg Kg <sup>-1</sup> )	0.209 $\pm$ 0.014	0.199 $\pm$ 0.009	0.128 $\pm$ 0.008	0.095 $\pm$ 0.007
Ammonium (mg Kg <sup>-1</sup> )	10.412 $\pm$ 0.476	5.792 $\pm$ 0.249	6.008 $\pm$ 0.247	4.053 $\pm$ 0.210
Phosphate (mg Kg <sup>-1</sup> )	2.352 $\pm$ 0.176	0.480 $\pm$ 0.052	1.778 $\pm$ 0.129	0.201 $\pm$ 0.035
Total carbon (%)	2.402 $\pm$ 0.112	0.735 $\pm$ 0.047	1.733 $\pm$ 0.086	0.557 $\pm$ 0.040
Total nitrogen (%)	0.131 $\pm$ 0.007	0.044 $\pm$ 0.003	0.088 $\pm$ 0.004	0.034 $\pm$ 0.002

ization in nurseries, for example, is known to change the leaf chemistry of nursery saplings (McArthur et al., 2003) making these saplings more attractive to feeding herbivores (Close et al., 2004; Hartley and Mitchell, 2005).

Although the browse content of deer diets varies among species, deer are generally categorized as intermediate feeders (sensu Hoffman, 1989) as they feed both on herb (grazing) or woody (browsing) plant communities (Horsley et al., 2003). The survival of tree seedlings can thus be affected by direct browsing (e.g. Tilghman, 1989) or indirectly by changes in plant competition interactions, induced by selective browsing, that favor the survival of “unpalatable” shrubs or trees species (Skarpe and Hester, 2008). Additionally, through effects on herb cover, grazing may indirectly mediate the survival and establishment of tree seedlings (Horsley and Marquis, 1983; Gill and Beardall, 2001; van der Waal et al., 2009).

The diversity of seedling and sapling communities can thus change as a direct or indirect response to deer herbivory. Usually the abundance of preferred plant species in the community decreases and that of less preferred species increases (Augustine and McNaughton, 1998; Barrett and Stiling, 2006). More seldom, if preferred species are browse-tolerant (they have a high re-growth capacity after consumption) their abundance may also increase (Anderson and Katz, 1993; Bee et al., 2007). Nevertheless, consumption of the whole plant, or plant parts, by herbivores usually impairs plant competitive capacity and decreases plant ability to persist in the community (Harper, 1977; Hulme, 1996). Moreover, the susceptibility of juvenile trees to herbivory can vary between the seedling and sapling stages, even within species, as plant nutritional quality and efficiency of chemical and structural defences (e.g. spines, trichomes) may differ between juvenile and older plant growth stages (Boege and Marquis, 2005).

Although there is an abundant literature on the effects of deer on tree regeneration and diversity (Coté et al., 2004; Fuller and Gill, 2001; Husheer et al., 2003; Rooney and Waller, 2003; Takatsuki, 2009) fewer studies have focused on the interactions between forest type, tree recruitment patterns and deer herbivory (but see Horsley et al., 2003; Edenius et al., 2011) and, in particular, on how different tree growth stages may respond to these interactions. Here we assess how the species richness and diversity of tree seedlings and saplings respond to the combined effects of deer herbivory, forest type and inter-annual variation of tree recruitment in a temperate forest of USA. We assessed the effects of deer herbivory on the species composition of tree seedlings and saplings in two adjacent hardwood and pine forest sites during a four year period. More specifically we asked:

- (1) Which are the effects of the interactions between white-tailed deer (*Odocoileus virginianus*) herbivory, forest-type and inter-annual variation of tree recruitment on the abundance of individual species and on the overall diversity of seedling and sapling communities?

- (2) Do different plant growth stages, seedlings and saplings, respond differently to herbivory, forest-type and inter-annual variation of tree recruitment?
- (3) How does variation in herb cover between grazed and ungrazed plots interact with forest-type and affect the coexistence of seedlings and saplings?

## 2. Methods

The study area was located in Duke Forest (35°58' N and 79°06' W), North Carolina, USA. The area is characterized by a warm temperate climate with temperatures varying, on average, between 0 °C and 11 °C in January, the coldest month, and 20 °C and 31 °C in July, the hottest month. Rainfall varies between 1000 mm and 1250 mm annually with July and August being the wettest and October to November the driest months (Peet and Christensen, 1980). Duke forest is a 2860 ha forest area located in the eastern edge of North Carolina Piedmont Plateau used mainly for teaching and research purposes. Duke forest is characterized by uneven aged stands of mature deciduous hardwood (mainly oaks *Quercus* spp., hickory *Carya* spp. and Ash *Acer* spp.) that resulted from secondary forest growth after abandonment of farming fields, and eighty to one hundred years old, uneven-aged pine stands, namely loblolly pine (*Pinus taeda*) plantations established since 1931. Canopy cover is heterogeneous with percent light reaching the soil varying between 1.4% and 53.9% (Ibáñez et al., 2009). These conditions allow light-demanding and shade-tolerant species to regenerate. White-tailed deer (*Odocoileus virginianus*) is a common and widespread species throughout Duke Forest. Deer population densities in the study area increased steadily during the period of study and were recorded at 6–8 deer/km<sup>2</sup> in 2005, as compared to historical deer densities of 3–4 deer/km<sup>2</sup> (North Carolina Wildlife Resource Commission, unpublished). More detailed description on the study area can be obtained at <<http://www.dukeforest.duke.edu>>.

Paired fenced (to exclude grazing and browsing by white-tailed deer) and unfenced plots were established in May of 2000, adjacent to each other (distance between fenced and unfenced plots varied between 2 and 3 m), in the middle of an hardwood and a pine forest stand (an 80 year old loblolly pine plantation). Fences were 1.80 m height with a squared mesh size of 5 cm by 5 cm. Hardwood and pine forest stands were representative of the forest cover in the study area and were only separated by a track road. Soil properties differed between hardwood and pine forest (for detailed information on soil properties see Parama, 2006) (Table 1). We established sixteen paired plots (16 fenced and 16 unfenced), with a rectangular shape and size of 6 m  $\times$  3 m, in hardwood forest and sixteen paired plots in pine forest. We used a 50 cm of distance buffer zone relatively to where measurements were conducted within the plots.

Manipulative experiments based on the total exclusion of grazing and browsing have limitations (for example, results of such experiments are usually limited by the size of fenced plots and ad-

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