Provided for non-commercial research and education use. Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/authorsrights

Forest Ecology and Management 308 (2013) 90-100



Contents lists available at ScienceDirect

Forest Ecology and Management

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

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



Forest Ecology and Management

Miguel N. Bugalho^{a,*}, Inés Ibáñez^b, James S. Clark^c

^a Centre for Applied Ecology, School of Agriculture, Technical University of Lisbon, 1349-017 Lisbon, Portugal ^b School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI 48109-104, USA ^c Nicholas School of Environment, Duke University, Durham, NC 27708-90338, USA

ARTICLE INFO

Article history: Received 18 March 2013 Received in revised form 16 July 2013 Accepted 19 July 2013

Keywords: Forests Deer Plant diversity Global changes

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 to the species to be considered. The outcome of such interactions depends on seedling or sapling iffects 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.

© 2013 Elsevier B.V. All rights reserved.

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-

0378-1127/\$ - see front matter @ 2013 Elsevier B.V. All rights reserved. http://dx.doi.org/10.1016/j.foreco.2013.07.036 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-

 ^{*} Corresponding author. Tel.: +351 21 3653333; fax: +351 21 3653290.
E-mail address: migbugalho@isa.utl.pt (M.N. Bugalho).

Table 1

Soil nutrient content (mean ± 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 ± 0.261	3.774 ± 0.176	5.090 ± 0.194	3.561 ± 0.167	
Nitrate (mg Kg ⁻¹)	0.209 ± 0.014	0.199 ± 0.009	0.128 ± 0.008	0.095 ± 0.007	
Ammonium (mg Kg ⁻¹)	10.412 ± 0.476	5.792 ± 0.249	6.008 ± 0.247	4.053 ± 0.210	
Phosphate (mg Kg ⁻¹)	2.352 ± 0.176	0.480 ± 0.052	1.778 ± 0.129	0.201 ± 0.035	
Total carbon (%)	2.402 ± 0.112	0.735 ± 0.047	1.733 ± 0.086	0.557 ± 0.040	
Total nitrogen (%)	0.131 ± 0.007	0.044 ± 0.003	0.088 ± 0.004	0.034 ± 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 regrowth 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 particularly, 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 whitetailed 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 interannual 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/km² in 2005, as compared to historical deer densities of 3-4 deer/km² (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-

Author's personal copy

92

M.N. Bugalho et al. / Forest Ecology and Management 308 (2013) 90-100

Table 2

Effects of year, herbivory and forest type on the diversity, species richness and index of dominance of seedling and sapling communities. Numbers in bold indicate significant or marginally significant effects.

	Diversity			Species ricl	nness		Dominance		
	Wald	df	Р	Wald	df	Р	Wald	df	Р
Seedlings									
Year	11.07	3	0.011	8.16	3	0.043	19.61	3	< 0.001
Herbivory	0.00	1	0.998	0.82	1	0.366	0.48	1	0.489
Forest type	0.00	1	0.945	1.21	1	0.271	13.85	1	< 0.001
Year × herbivory	4.31	3	0.230	2.89	3	0.409	3.85	3	0.279
Year \times forest type	6.97	3	0.073	10.44	3	0.015	7.13	3	0.068
Hebivory \times forest type	0.72	1	0.398	0.01	1	0.910	1.44	1	0.230
Saplings									
Year	22.33	3	0.001	19.34	3	0.001	9.64	3	0.022
Herbivory	0.70	1	0.404	0.31	1	0.578	0.85	1	0.358
Forest type	2.07	1	0.15	1.65	1	0.199	11.16	1	0.001
Year \times herbivory	2.89	3	0.408	1.55	3	0.670	2.98	3	0.394
Year $ imes$ Forest type	16.30	3	0.001	11.70	3	0.008	4.92	3	0.178
Hebivory \times forest type	6.35	1	0.012	3.64	1	0.056	0.47	1	0.493



Fig. 1. Diversity, species richness and index of dominance of seedling communities in plots open (unfenced, dash line) and protected (fenced, solid line) from deer browsing, in two different forest types (hardwood and pine forest), between 2000 and 2003. Error bars represent the standard error of mean.

dress the effects of "presence" *versus* "absence" of herbivores rather than the effects of "gradients of grazing and browsing") although they also provide useful insights about the effects of herbivores on forest dynamics (Hester et al., 2000).

Tree seedlings (first year recruits) and saplings (recruits older line than one year and less than 50 cm in height) were identified, individually tagged, and counted during summer (June to August) of 2000–2003. Total vegetation ground cover was measured using a an

 $1 \text{ m} \times 1 \text{ m}$ size grid randomly placed between 4 and 6 times in each plot and by visually estimating cover of the plot. Cover was dominated by herb species and hereafter called herb cover.

The following woody species were identified in the plots: seedlings of Acer rubrum, Cercis canadensis, Cornus florida, Liquidambar styraciflua, Liriodendron tulipifera, Pinus spp.; and saplings of Acer rubrum, Acer saccharum, Carya spp., Cercis canadensis, Fraxinus americana, Liquidambar styraciflua, Liriodendron tulipifera, Quercus



Fig. 2. Diversity, species richness and index of dominance of sapling communities in plots open (unfenced, dash line) and protected (fenced, solid line) plots from deer browsing, in two different forest types (hardwood and pine forest), between 2000 and 2003. Error bars represent the standard error of mean.

alba, Quercus velutina, Ulmus spp. Representative species included shade-tolerant (e.g. A. Sacharum, C. canadensis), shade-intolerant (e.g. A. rubrum, L. tulipifera) and intermediate shade-tolerant (e.g. Q. alba, L. styraciflua) species.

Diversity of woody seedlings and saplings was estimated using the Shannon–Weaver index (Magurran, 1988); richness was considered as the number of different species in each plot; dominance was estimated using the Berger–Parker Index of Dominance, ID = CMax/C where CMax is the number of individuals of the highest abundance species and *C* is the total number of individuals in the plot (Berger and Parker, 1970). This index is commonly used to assess how most abundant species express in plant communities (Magurran, 1988; Caldeira et al., 2005).

Effects of exclusion of deer herbivory on community parameters (diversity, number of species, index of dominance), herb cover and proportional abundance of tree seedlings and saplings was assessed using Restricted Maximum Likelihood (REML) analysis of mixed models with repeated measures, using GenStat for Windows 6th (2002). REML was used to deal with unbalanced data (Patterson and Thompson, 1971) as there were plots that were unintentionally lost in 2002/2003 monitoring season (4 paired plots per each forest type in the last 2 years of monitoring) due to artificial creation of forest gaps conducted within a major research project being implemented in the study area (Dietze and Clark, 2008; Ibáñez et al., 2008). Herbivory, Year and Forest type were considered fixed factors, herb cover as a co-variate and plot (paired by the fence treatment) a random effect. Proportion of seedlings and saplings was angular transformed before analysis to normalize data distribution (Zar, 1996).

3. Results

3.1. Seedling and sapling communities

Sapling communities were richer in species than seedling communities, both in hardwood (mean ± s.e.m.: 4.3 ± 0.32 saplings/m² versus 2.2 ± 0.21 seedlings/m²; p < 0.001) and pine forest (4.6 ± 0.21 saplings/m² versus 2.4 ± 0.21 seedlings/m²; p < 0.001); more diverse, both in hardwood (Shannon–Weaver of saplings: 0.43 ± 0.03 versus Shannon–Weaver of seedlings: 0.25 ± 0.03 ; p < 0.001) and pine forest (0.46 ± 0.02 versus 0.22 ± 0.03 ; p < 0.001) and had lower index of dominance in hardwood (index of dominance of saplings: 0.44 ± 0.03 versus index of dominance of seedlings: 0.64 ± 0.03 ; p < 0.001) but not in pine forest (0.58 ± 0.02 versus 0.57 ± 0.03 ; p = 0.761).

The diversity (p = 0.073) and dominance (p = 0.068) of seedling communities responded marginally to year x forest type interaction whilst sapling richness responded marginally (p = 0.056) to herbivory × forest type interaction (Table 2). Diversity, richness (number of species) and index of dominance of seedlings varied significantly among years (Year fixed factor). Forest type (Forest type fixed factor) had significant effects on the community index of dominance which, in the pine stand plots, was higher in fenced as compared to unfenced plots (Table 2 and Fig. 1). Inter-annual variation in tree recruitment interacted with forest type to affect seedling richness, which was lower in fenced and hardwood plots, but there were no significant effects of herbivory (Herbivory fixed factor) on seedling richness or diversity (Table 2 and Fig. 1). Herb cover affected significantly the diversity of seedlings in 2000

0.847 0.109 0.544 0.679 0.939 0.939

0.81 2.57 0.37 1.52 0.41 0.43

0.579 0.079 0.038 0.038 0.796 0.796 0.692 0.416

1.97 3.09 4.33 1.02 1.46

0.087 0.024 0.006 0.368 0.368 0.029 0.029

6.56 5.11 7.49 3.15 9.02 0.01

0.948 0.169 0.553 0.580 0.380 0.584 0.584 0.584

0.36 1.89 0.35 3.08 1.95 0.08

0.530 0.107 0.844 0.074 0.076 0.976

2.21 2.59 0.04 6.93 0.21 0.21

0.623 0.025 0.001 0.802 0.720 0.720

1.76 5.01 8.35 1.00 1.34 0.04

0.290 0.491 0.236 0.236 0.285 0.044

3.75 0.47 1.41 3.79 8.12

0.001 0.847 0.460 0.866 0.866 0.906 0.906

55.52 0.04 0.55 0.73 0.73 0.56 0.18

0.981 0.048 0.003 0.570 0.570 0.981 0.048

0.18 3.90 9.03 2.01 0.18 3.90

0.278 0.106 0.001 0.43 0.326 0.326 0.841

3.85 2.62 2.7.62 2.76 2.76 3.46 0.04

Year Herbivory Forest type Year × herbivory Hebivory \times forest type

Year \times forest type

(p < 0.010) but only marginally in 2001 (p = 0.079), 2002 (p = 0.060) and 2003 (p = 0.086). Species richness of seedlings was significantly affected by herb cover in 2000 (p < 0.010) and 2001 (p < 0.050), but not in 2002 (p = 0.149) or 2003 (p = 0.135). In the case of saplings, inter-annual variation of tree species recruitment (Year fixed factor) affected significantly the diversity, richness and index of dominance of the community while forest type (Forest type fixed factor) affected significantly the index of dominance of sapling communities which was higher in fenced pine plots (Fig. 2). Herbivory and forest type interactions affected significantly sapling diversity which increased consistently in hardwood unfenced plots (Fig. 2). There were no significant effects of herbivory (Herbivory fixed factor) on sapling diversity (Table 2). Herb cover did not significantly affect the diversity or species richness of saplings (p > 0.150) for all years).

3.2. Abundance of individual species

There were no consistent effects of deer herbivory on species abundances. Some species were more abundant in fenced plots whilst others were more abundant in unfenced plots by the end of the study. For example, the abundance of *C. canadensis* (0.26 *versus* 0.14 proportional abundance) and of *Q. alba* (0.13 *versus* 0.04) saplings were significantly higher in unfenced (deer browsed) hardwood plots. Also, the abundance of *A. rubrum* seedlings was significantly higher in unfenced pinewood plots (0.87 *versus* 0.66). Conversely, the abundance of *Q. velutina* saplings was marginally higher (0.02 *versus* 0.05) in fenced pine forest plots (Tables 3a and b, Figs. 3 and 4). Significant interactions herbivory × year for seedlings of *L. styraciflua* and saplings of *F. americana* (Tables 3a and b) suggest that deer herbivory affects the abundance of these species over time.

Some seedlings and saplings of the same species responded differently to protection from herbivory. For example, in pine forest, the abundance of *A.rubrum* seedlings (0.87 *versus* 0.66), but not of *A. rubrum* saplings (0.48 *versus* 0.39), was significantly higher in deer browsed plots by the end of the study. In hardwood, the abundance of *C. canadensis* saplings (0.26 *versus* 0.14), but not of seedlings, was significantly higher in unfenced plots (Tables 3a and b, Figs. 3 and 4).

Abundance of species varied with forest type. A.rubrum (seedlings and saplings) and Q. velutina (saplings) had significantly higher abundance in pine forest, while C. canadensis (seedlings and saplings) or Q. alba (seedlings) were significantly more abundant in hardwood (Tables 3a and b, Figs. 3 and 4). There were species responding to interactions between herbivory and forest type. Such was the case of saplings of A. sacharum and F. americana which had higher abundances in deer browsed pine forest plots (Table 3b, Fig. 4). There were also wide fluctuations in the annual recruitment of seedlings and saplings, although these fluctuations were significantly larger for a higher number of seedling than of sapling species (Tables 3a and b). There were five seedling species (A. rubrum, C. florida, L. styraciflua L. tulipifera and Pinus spp.) but only one sapling species (C. tomentosa) that varied significantly among years (Tables 3a and b). Conversely, herbivory and forest type affected mainly the abundance of saplings. Thus there were four species of saplings (Acer saccharum, Cercis canadensis, Quercus alba, Quercus velutina) but only one species of seedling (A.rubrum) responding significantly to herbivory and five species of saplings (Acer rubrum, Acer saccharum, Cercis canadensis, Quercus alba, Quercus velutina) but only two species of seedlings (A. rubrum and Cercis Canadensis) responding significantly to forest type (Table 3a and b). Most of the large seeded species, such as Carya spp., Quercus alba, and Quercus velutina were recorded only at the sapling stages and at a very low abundances (Figs. 3 and 4). (see also Supplementary annex Table 1).

Effects of year, deer herbive Pinus undata, Acsa: Acer sac	ory and fores charum, Cato	st type on the Carya tomen	abundance of sf tosa, Carun: Car	oecies of (a) see	dlings and raxinus am	(b) saplings. Au ericana, Qual: (cru: Acer rubr Quercus alba, (um, Ceca: <i>Ce</i> Quve: Quercu	rcis canadensis, L Is velutina, Ulun:	ist: Liquidam : Ulmus spp.	tbar styraciflua, (Numbers in bolo	Cofl: <i>Cornus fl</i> 1 indicate sign	orida, Litu: <i>Liri</i> nificant or man	iodendrum tulij ginally signifi	<i>oifera</i> , Piun: ant effects.
(a) Seedlings															
		Acru		Ceca		Cofl		Coffres		List		Litu		Piun	
	df	Wald	Ρ	Wald	Р	Wald	Ρ	Wald	Ρ	Wald	Ρ	Wald	Р	Wald	Ρ
Year	с	20.15	<0.001	6.43	0.092	21.87	0.001	6.90	0.075	43.61	<0.001	12.66	0.005	12.68	0.005
Herbivory	1	4.77	0.029	1.50	0.220	0.07	0.786	4.83	0.028	2.16	0.142	0.67	0.411	0.18	0.668
Forest type	1	24.71	<0.001	7.59	0.006	1.31	0.252	1.63	0.201	2.33	0.127	2.13	0.144	0.06	0.812
Year $ imes$ herbivory	¢	1.68	0.640	0.17	0.983	0.11	0.991	8.06	0.045	17.08	<0.001	4.15	0.246	0.96	0.812
Year $ imes$ forest type	c	1.63	0.653	2.74	0.434	1.97	0.579	5.27	0.153	12.28	0.006	4.00	0.261	2.16	0.539
Hebivory \times forest type	1	0.06	0.807	0.45	0.500	0.13	0.715	4.93	0.026	0.07	0.795	0.13	0.721	2.68	0.102
(b) Saplings															
	Acri	n.	Acsa	Cato		Caun	Ceca		Fram	List	Qua	li I	Quve	Ulun	
	df Wai	Id P	Wald P	Wald	Ρ	Wald P	Wald	Ρ	Wald P	Wald	<i>P</i> Wai	d pi	Wald P	Wald	Ρ





Fig. 3. Abundances of seedlings, in hardwood and pine forest plots, unprotected (unfenced, dash line) and protected (fenced, solid line) from deer browsing, between 2000 and 2003. Error bars represent the standard error of mean.



Fig. 4. Abundances of saplings, in hardwood and pine forest plots, unprotected (unfenced, dash line) and protected (fenced, solid line) from deer browsing, between 2000 and 2003. Error bars represent the standard error of mean.

M.N. Bugalho et al./Forest Ecology and Management 308 (2013) 90-100



Table 4

Effects of year, herbivory and forest type on herb cover. Numbers in bold indicate significant effects.

	Herb cov	/er	
	df	Wald	Р
Year	3	2.69	0.442
Herbivory	1	18.03	<0.001
Forest type	1	13.41	<0.001
Year \times herbivory	3	6.31	0.097
Year \times forest type	3	0.20	0.978
Hebivory \times forest type	1	1.70	0.192

3.3. Herb cover

There was a significant effect of forest type on herb cover, with higher herb cover in hardwood as compared to pine forest plots. There were no differences in herb cover between fenced and unfenced plots at the beginning of the study either in hardwood (p = 0.264) or in pine forest (p = 0.427). By the end of the study, however, herb cover was significantly higher (p < 0.043) in hard-

97

wood fenced plots, where it was four fold higher than in hardwood unfenced plots (Fig. 5), with no significant differences between fenced and unfenced plots (p = 0.460) in pine forest. Overall, differences between fenced and unfenced plots increased over time, albeit only marginally (p < 0.097 for the interaction year × herbivory) (Table 4).

4. Discussion

Land-use changes, including conversion of primary to secondary forest types (e.g. hardwood to pine forest plantations) and expansion of generalist herbivores, such as deer, are among major drivers of global change affecting the dynamics and conservation of forest ecosystems. Here we show that deer herbivory, forest type and inter-annual variation of tree recruitment combine to affect the species composition of seedling and sapling communities of temperate forests and that these effects vary with plant growth stage. In particular, direct and indirect effects of deer selective browsing and grazing may favor the survival of some tree species and ultimately shape the species composition of adult forests.



Fig. 5. Herb cover (%) in hardwood and pine forest plots, unprotected (unfenced, dash line) or protected (fenced, solid line) from deer grazing, between 2000 and 2003. Error bars represent the standard error of mean.

At high population densities deer usually reduces the diversity of tree seedlings and saplings (Tilghman, 1989; Gill and Beardall, 2001). Prolonged and intensive deer browsing can lead to recruitment failure of most preferred species and dominance of less preferred species (Long et al., 2007; Kain et al., 2011; Salk et al., 2011) with concomitant loss of diversity. Deer population densities above 10 deer/km² are common in temperate forests (Coté et al., 2004) and in some areas of the United States of America deer population densities of 20-30 deer/km² have been recorded (Swihart et al., 1998). Historically, deer population density in the study area was relatively low (3-4 deer/km²) but almost doubled during a 14-year period, between 1985 and 1999 (North Carolina Wildlife Resources Commission, unpublished data), previously to the period of our study. A study longer than four years may be necessary for observing major changes in species composition of seedling and sapling communities. However, at our site, the relative moderate deer population densities (5–8 deer/km²) occurring during the period of the study may contribute to explain the lack of direct significant effects of deer herbivory on seedling and sapling diversity. At such population densities, deer rarely browse small seedlings feeding dominantly on the herb layer (Horsley and Marquis, 1983). The strong reduction of herb cover particularly in unfenced hardwood plots is likely to have affected seedling and sapling survival. Removal of herb cover through grazing, has been shown to benefit tree establishment (Virtanen et al., 2002; Vandenberghe et al., 2006) and reduction of forest understory by deer has been associated with an increase of tree seedling richness in temperate forests (Rogers et al., 2008; Taverna et al., 2005). In our site, herb cover interacted with seedling richness and diversity, which were higher in unfenced than fenced plots by the end of the experiment. These results imply that effectiveness of management practices promoting forest regeneration such as deer culling or establishment of forest enclosures (Gordon et al., 2004; Wright et al., 2012), may vary with forest type and alternative sources of food available at the understory level, namely herbs. In particular it is important to consider how ground cover vegetation, may vary among years. Moderate climate (e.g. warm winters with low snow cover) may result in higher availability and cover of herbs and potentially alleviate direct negative effects of deer on the survival of saplings. Similarly, in forest types where the availability of herbs is higher throughout the year, less negative effects on sapling survival could be expected. These factors need to be considered when implementing management practices such as culling, as reducing herbivore densities does not always imply recovery of tree regeneration (Wright et al., 2012). Moreover, in cases where herbs are competing with seedlings and saplings, mixed-feeders and grazers may positively affect tree recruitment (Riginos and Young, 2007; van Uytvanck et al., 2010) even if these are preferred species. For example, in our case, saplings of Quercus alba a species usually preferred by deer, had higher abundances in unfenced plots. Quercus alba usually benefits from increased light levels and reduced competition from the understory level (Stan et al., 2006). Q. alba occurred at very low abundances and may have been less apparent to direct browsing by deer as compared to other species available for deer to feed upon. Competition release from other sapling species and the herb cover, as well as potential increase of light at ground level as a consequence of herb cover reduction, may have benefited the survival of *Q.alba* in browsed plots. Survival of seedlings and saplings depends on an array of factors that include palatability, availability to herbivores, and the species response to competitors and microenvironment conditions (e.g. light). Such interacting factors may lead to positive responses of species in the presence of herbivores.

Forest type was itself a driver of tree recruitment. Seed availability, usually differs between forest types and is a main determinant of tree recruitment. While for some species in our plots variation in seed availability between forest types, could explain difference in species abundances, in other cases seed availability alone could not account for such differences. For example, Q. velutina and A. rubrum had higher abundances, but also higher seed rain, in pine forest during the period of study (averages for Q. velutina: 0.03 and 0 seeds/year m^{-2} in pine forest and hardwood, respectively; averages for A. rubrum: 20 and 8.1 seeds/year m⁻² in pine and hardwood forests [Ibáñez unpublished]). Conversely, C. canadensis and Q. alba, had higher abundances but also lower seed rains in hardwood (averages for C.canadensis: 0.42 and 0.30 seeds/year m⁻² in pine and hardwood forest, respectively; averages for Q. alba: 0.34 and 0.23 seeds/year m^{-2} in pine and hardwood forest, respectively [Ibáñez unpublished]). Other factors, including differences in soil nutrient contents between forest types, may contribute to explain differences in species abundances. For example, A. rubrum seedlings and saplings were significantly more abundant in the pine forest. A. rubrum is currently expanding across the United States of America (Fei and Steiner, 2007) and tends to dominate secondary forests, particularly pine plantations, which are usually low in organic matter, total carbon and extractable phosphorous in the upper soil horizons (Flinn and Marks, 2007), soil properties similar to those recorded in our pine forest plots (Table 1).

There were also large fluctuations in the annual recruitment of seedlings and saplings. Such fluctuations however tended to be larger and affected a higher number of species of seedlings than of saplings. The variable population patterns at the seedling stages are majorly determined by fluctuations in seed production which is primarily dependent on inter-annual climatic variability (Clark et al., 2004; Ibáñez et al., 2007). Observed trends also indicate more stable population patterns at the sapling stage with a high number of species within this age class responding significantly to herbivory and forest type. These results imply that abiotic (e.g. environmental conditions) and biotic (e.g. herbivory) factors affect the survival and abundance of juvenile trees differently, and that such effects can vary with tree life stage, seedling or sapling. Similar results were obtained for temperate forests in Europe where the early stages of tree regeneration were shown to be affected

by abiotic conditions and the later stages by deer herbivory (Kuijper et al., 2010).

The lower species richness and diversity (and higher indexes of dominance) of first year seedlings, as compared to that of saplings, reflect the dominance of particular species in favorable years (e.g. higher seed availability). In contrast, sapling communities, which result from accumulated years of recruitment, represent a larger pool of species and thus have higher richness and diversity. Additionally, saplings may be retained (not growing taller) because of browsing by deer in unfenced plots. Deer "browsing traps", in which saplings do not grow above 50 cm tall and cannot move to the higher tree canopy layer, have been observed in other temperate forests (e.g. Kuijper et al., 2010) and can contribute to maintain a high diversity of saplings. At the community level, the diversity, richness and dominance of tree seedlings and saplings, varied significantly among years confirming that inter-annual variation in tree recruitment is a primary factor affecting the diversity of young tree communities and needs to be accounted for, even when investigating the effects of herbivory or forest type, on forest diversity.

5. Conclusions

Forest-type, deer herbivory and inter-annual variation in tree recruitment patterns combine to shape the abundance and diversity of juvenile trees, with effects varying with tree growth stage, seedling or sapling. Inter-annual variation of recruitment is larger for seedlings than for saplings, with saplings responding mainly to deer herbivory and forest type. Reduction of herb cover by deer is likely to play a role in determining the composition of juvenile tree communities with such effects varying with forest type. When managing deer populations for conservation purposes, or when modeling forest community dynamics, interactions between biotic (e.g. herbivory) and abiotic (e.g. forest type) factors need to be considered alongside plant growth stages. Such interactions may have opposite consequences on individuals or communities depending on the current life stage of such individuals.

Acknowledgements

MNB acknowledges the financial support of the Portuguese National Science Foundation (FCT) through Project POCI/AGR/63322/ 2004, Program "Ciência 2007" and Grant SFRH/BPD/90668/2012. We are grateful to M.C. Caldeira and two anonymous referees for their comments on a previous version of the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.07. 036.

References

- Allombert, S., Gaston, A.J., Martin, J.L., 2005. A natural experiment on the impact of overabundant deer on songbird populations. Biol. Conserv. 126, 1–13.
- Anderson, R.C., Katz, A.J., 1993. Recovery of browse sensitive tree-species following release from white-tailed deer *Odocoileus virginianus* Zimmerman browsing pressure. Biol. Conserv. 63, 203–208.
- Augustine, D.J., McNaughton, S.J., 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J. Wildlife Manage. 62, 1165–1183.
- Barrett, M.A., Stiling, P., 2006. Effects of key deer herbivory on forest communities in the lower Florida Keys. Biol. Conserv. 129, 100–108.
- Bee, J.N., Kunstler, G., Coomes, D.A., 2007. Resistance and resilience of New Zealand tree species to browsing. J. Ecol. 95, 1014–1026.
- Berger, W.H., Parker, F.L., 1970. Diversity of planktonic foraminifera in deep-sea sediments. Science 168, 1345–1347.

- Bertrand, R., Lenoir, J., Piedallu, C., Riofrio-Dillon, G., Ruffray, P., Vidal, C., Pierrat, J.C., Gegout, J.C., 2011. Changes in plant community composition lag behind climate warming in lowland forests. Nature 479, 517–520.
- Boege, K., Marquis, R.J., 2005. Facing herbivory as you grow up: the ontogeny of resistance in plants. Trends Ecol. Evolut. 20, 441–448.
- Bugalho, M.N., Lecomte, X., Goncalves, M., Caldeira, M.C., Branco, M., 2011. Establishing grazing and grazing-excluded patches increases plant and invertebrate diversity in a Mediterranean oak woodland. Forest Ecol. Manag. 261, 2133–2139.
- Caldeira, M.C., Hector, A., Loreau, M., Pereira, J.S., 2005. Species richness, temporal variability and resistance of biomass production in a Mediterranean grassland. Oikos 110, 115–123.
- Campo, J., Dirzo, R., 2003. Leaf quality and herbivory responses to soil nutrient addition in secondary tropical dry forests of Yucatan. Mexico. J. Trop. Ecol. 19, 525–530.
- Clark, J.S., LaDeau, S., Ibáñez, I., 2004. Fecundity of trees and the colonizationcompetition hypothesis. Ecol. Monogr 74, 415–442.
- Close, D.C., McArthur, C., Pietrzykowski, E., Fitzgerald, H., Paterson, S., 2004. Evaluating effects of nursery and post-planting nutrient regimes on leaf chemistry and browsing of eucalypt seedlings in plantations. Forest Ecol. Manag. 200, 101–112.
- Coté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Syst. 35, 113–147.
- Dietze, M.C., Clark, J.S., 2008. Changing the gap dynamics paradigm: vegetative regeneration control on forest response to disturbance. Ecol. Monogr. 78, 331– 347.
- Edenius, L., Ericsson, G., Kempe, G., Bergström, R., Danell, K., 2011. The effects of changing land use and browsing on aspen abundance and regeneration: a 50year perspective from Sweden. J. Appl. Ecol. 48, 301–309.
- Fei, S.L., Steiner, K.C., 2007. Evidence for increasing red maple abundance in the eastern United States. Forest Sci. 53, 473–477.
- Feeley, K.J., Davies, S.J., Perez, R., Hubbell, S.P., Foster, R.B., 2010. Directional changes in the species composition of a tropical forest. Ecology 92, 871–882.
- Flinn, K.M., Marks, P.L., 2007. Agricultural legacies in forest environments: Tree communities, soil properties, and light availability. Ecol. Appl. 17, 452–463.
- Fuller, R.J., Gill, R.M.A., 2001. Ecological impacts of deer in woodland. Forestry 74, 189–192.
- GenStat for Windows 6th, 2002. Lawes Agricultural Trust. Rothamsted Experimental Station. Rothamsted, UK.
- Gill, R.M.A., Beardall, V., 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry 74, 209–218.
- Gordon, I.J., Hester, A.J., Festa-Bianchet, M., 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. J. Appl. Ecol. 41, 1021–1031.
- Harper, J.L., 1977. Population Biology of Plants. Academic Press, London.
- Hartley, S.E., Mitchell, R.J., 2005. Manipulation of nutrients and grazing levels on heather moorland: changes in *Calluna* dominance and consequences for community composition. J. Ecol. 93, 990–1004.
- Hester, A.J., Edenius, L., Buttenschon, R.M., Kuiters, A.T., 2000. Interactions between forests and herbivores: the role of controlled grazing experiments. Forestry 73, 381–391.
- Hidding, B., Tremblay, J.P., Cote, S.D., 2012. Survival and growth of balsam fir seedlings and saplings under multiple controlled ungulate densities. Forest Ecol. Manage. 276, 96–103.
- Hoffman, R.R., 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78, 443–457.
- Horsley, S.B., Marquis, D.A., 1983. Interference by deer and weeds with Allegheny hardwood reproduction. Can. J. Forest Res. 13, 61–69.
- Horsley, S.B., Stout, S.L., DeCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol. Appl. 13, 98–118.
- Hulme, P.E., 1996. Herbivory, plant regeneration, and species coexistence. J. Ecol. 84, 609–615.
- Husheer, S.W., Coomes, D.A., Robertson, A.W., 2003. Long-term influences of introduced deer on the composition and structure of New Zealand Nothofagus forests. For. Ecol. Manag. 181, 99–117.
- Ibáñez, I., Clark, J.S., LaDeau, S., HilleRisLambers, J., 2007. Exploiting temporal variability to understand tree recruitment response to climate change. Ecol. Monogr. 77, 163–177.
- Ibáñez, I., Clark, J.S., Dietze, M.C., 2008. Evaluating the sources of potential migrant species: implications under climate change. Ecol. Appl. 18, 1664–1678.
- Ibáñez, I., Clark, J.S., Dietze, M., 2009. Estimating performance of potential migrant species. Global Change Biol. 15, 1173–1188.
- Kain, M., Battaglia, L., Royo, A., Carson, W.P., 2011. Over-browsing in Pennsylvania creates a depauperate forest dominated by an understory tree: Results from a 60-year-old deer exclosure. J. Torrey Bot. Soc. 138, 322–326.
- Kuijper, D.P.J., Cromsigt, J., Jedrzejewska, B., Miscicki, S., Churski, M., Jedrzejewski, W., Kweczlich, I., 2010. Bottom-up versus top-down control of tree regeneration in the Bialowieza Primeval Forest. Poland. J. Ecol. 98, 888–899.
- Lindroth, R.L., Donaldson, J.R., Stevens, M.T., Gusse, A.C., 2007. Browse quality in quaking aspen (*Populus tremuloides*): effects of genotype, nutrients, defoliation, and coppicing. J. Chem. Ecol. 33, 1049–1064.
- Liira, J., Sepp, T., Kohv, K., 2011. The ecology of tree regeneration in mature and old forests: combined knowledge for sustainable forest management. J. Forest Res. 16, 184–193.

Author's personal copy

100

M.N. Bugalho et al. / Forest Ecology and Management 308 (2013) 90-100

- Long, Z.T., Pendergast, T.H., Carson, W.P., 2007. The impact of deer on relationships between tree growth and mortality in an old-growth beech-maple forest. For. Ecol. Manag. 252, 230–238. Magurran, A.E., 1988. Ecological Diversity and its Measurement. Cambridge
- University Press, Cambridge, UK.
- Martin, T.G., Arcese, P., Scheerder, N., 2011. Browsing down our natural heritage: deer impacts on vegetation structure and songbird populations across an island archipelago. Biol. Conserv. 144, 459–469.
- McArthur, C., Marsh, N.R., Close, D.C., Walsh, A., Paterson, S., Fitzgerald, H., Davies, N.W., 2003. Nursery conditions affect seedling chemistry, morphology and herbivore preferences for Eucalyptus nitens. For. Ecol. Manag. 176, 585-594.
- Naaf, T., Wulf, M., 2007. Effects of gap size, light and herbivory on the herb layer vegetation in European beech forest gaps. For. Ecol. Manag. 244, 141-149.
- Patterson, H.D., Thompson, R., 1971. Recovery of inter-block information when block sizes are unequal. Biometrika 58, 545–554.
- Parama, R., 2006. Heterogeneidad especial de nutrients del suelo en ecosistemas terrestres. PhD Thesis. Universidad de Vigo. Vigo. Spain.
- Peet, R.K., Christensen, N.L., 1980. Hardwood forest vegetation of the North Carolina piedmont. Veröff. Geobot. Inst. ETH Stiftung Rübel. 69, 14-39.
- Riginos, C., Young, T.P., 2007. Positive and negative effects of grass, cattle, and wild herbivores on Acacia saplings in an East African savanna. Oecologia 153, 985-995
- Rogers, D.A., Rooney, T.P., Olson, D., Waller, D.M., 2008. Shifts in southern Wisconsin forest canopy and understory richness, composition, and heterogeneity. Ecology 89. 2482-2492.
- Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. For. Ecol. Manag. 181, 165-176.
- Royo, A.A., Collins, R., Adams, M.B., Kirschbaum, C., Carson, W.P., 2010a. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. Ecology 91, 93-105.
- Royo, A.A., Stout S.L., deCalesta, D.S., Pierson, T.G., 2010b. Restoring forest herb communities through landscape-level deer herd reductions: is recovery limited by legacy effects. Biol. Conserv. 143, 2425–2434. Salk, T.T., Frelich, L.E., Sugita, S., Calcote, R., Ferrari, J.B., Montgomery, R.A., 2011.
- Poor recruitment is changing the structure and species composition of an oldgrowth hemlock-hardwood forest. For. Ecol. Manag. 261, 1998-2006.
- Skarpe, C., Hester, A.J., 2008. Plant traits, browsing and grazing herbivores and vegetation dynamics. In: Gordon, I.J., Prins, H. (Eds.), The Ecology of Browsing and Grazing. Ecological Studies 195. Springer, Netherlands, pp. 217-261.

- Speed, J.D.M., Austrheim, G., Hester, A.J., Solberg, E.J., Tremblay, J.P., 2013. Regionalscale impacts alteration of moose browsing on the regeneration of clear-cut forests by moose browsing. Forest Ecol. Manag. 289, 289–299. Stan, A.B., Rigg, L.S., Jones, L.S., 2006. Dynamics of a managed oak woodland in
- northeastern Illinois. Nat. Area J. 26, 187-197.
- Swihart, R.K., Weeks, H.P., Easter-Pilcher, A.L., DeNicola, A.J., 1998. Nutritional condition and fertility of white-tailed deer (*Odocoileus virginianus*) from areas with contrasting histories of hunting. Can. J. Zool. 76, 1932–1941.
 Taverna, K., Peet, R.K., Phillips, L., 2005. Long-term change in ground-layer vegetation of deciduous forests of the North Carolina Piedmont. USA J. Ecol.
- 93, 202-213.
- Tilghman, N.G., 1989. Impacts of White tailed deer on forest regeneration in Northwestern Pennsylvania. J. Wildl. Manage. 53, 524-532.
- Takatsuki, S., 2009. Effects of sika deer on vegetation in Japan: a review. Biol. Conserv. 142, 1922-1929.
- Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. Ecology 91, 2833-2849.
- Vandenberghe, C., Frelechoux, F., Gadallah, F., Buttler, A., 2006. Competitive effects of herbaceous vegetation on tree seedling emergence, growth and survival: does gap size matter? J. Veg. Sci. 17, 481-488.
- van der Waal, C., de Kroon, H., de Boer, W.F., Heitkonig, I.M.A., Skidmore, A.K., de Knegt, H.J., van Langevelde, F., van Wieren, S.E., Grant, R.C., Page, B.R., Slotow, R., Kohi, E.M., Mwakiwa, E., Prins, H.H.T., 2009. Water and nutrients alter herbaceous competitive effects on tree seedlings in a semi-arid savanna. J. Ecol. 97, 430-439.
- van Soest, P.J., 1994. The Nutritional Ecology of the Ruminant, 2nd edition. Cornell University Press, Cornell, USA
- van Uytvanck, J., Milotic, T., Hoffmann, M., 2010. Interaction between large herbivore activities, vegetation structure, and flooding affects tree seedling emergence. Plant Ecol. 206, 173-184.
- Verheyden-Tixier, H., Renaud, P.C., Morellet, N., Jamot, J., Besle, J.M., Dumont, B., 2008. Selection for nutrients by red deer hinds feeding on a mixed forest edge. Oecologia 156, 715-726.
- Virtanen, R., Edwards, G.R., Crawley, M.J., 2002. Red deer management and vegetation on the Isle of Rum. J. Appl. Ecol. 39, 572–583. Wright, D.M., Tanentzap, A.J., Flores, O., Husheer, S.W., Duncan, R.P., Wiser, S.K.,
- Coomes, D.A., 2012. Impacts of culling and exclusion of browsers on vegetation recovery across New Zealand forests. Biol. Conserv. 153, 64-71.
- Zar, J.H., 1996. Biostatistical analysis. Prentice Hall International, Inc., New Jersey, USA.