Forest Ecology and Management 364 (2016) 17–26

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Effects of disturbance on understory succession in upland and lowland boreal forests and implications for woodland caribou (*Rangifer tarandus caribou*)

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ARTICLE INFO

Article history:
Received 17 June 2015
Received in revised form 28 November 2015
Accepted 7 December 2015
Available online 8 January 2016

Keywords:
Boreal
Understory vegetation
Forage
Productivity
Disturbance
Drainage

ABSTRACT

Boreal forest development is influenced by both natural and anthropogenic disturbances that alter stand structure and nutrient cycling over decadal timescales. The effects of disturbance on boreal forests is likely to be modified by soil moisture, given that disturbance severity, vegetation structure and plant productivity vary between upland and lowland forest stands. Future changes in boreal vegetation dynamics are predicted to have consequences for a range of ecosystem services including climate feedbacks and wildlife management. Here, as part of a broader study on habitat use and forage of woodland caribou, we investigated the effects of soil drainage class (upland vs. lowland), disturbance (wildfire vs. timber harvest), and stand age on understory plant species richness, cover, biomass, productivity, and foliar C/N. Due to faster nutrient turnover rates in upland soils, we predicted that understory vegetation in uplands would be more productive, biodiverse and nutrient-rich than in lowlands. We also expected disturbance to lead to greater changes in understory vegetation in uplands, given that both fire and timber harvesting tend to be more severe in drier ecosystems. Our results showed that plant understory characteristics varied primarily between soil drainage classes, with few differences between stands recovering from wildfire or timber harvesting. Contrary to our predictions, lowland understory vegetation had greater total understory plant species richness, aboveground net primary productivity, and foliar C/N compared to upland understory vegetation. We also found no difference in total understory vegetation percent cover, productivity or foliar C/N between burned and harvested stands. Understory net primary productivity decreased with time following disturbance in uplands but increased nonlinearly with stand age in lowlands. Greater productivity in lowlands was attributed primarily to evergreen shrubs, though graminoids also were more productive in lowlands than in uplands. Our study has implications for the threatened woodland caribou with respect to the nutritional aspects of their habitat selection. Our results suggest that the commonly held assertion that, by selecting lowlands, caribou face a trade-off between lower predation risk and lower forage quality may be incorrect and requires further examination.

1. Introduction

In the boreal region, forests can be supported in ecosystems across a range of geomorphology and soil conditions (Baldwin and Sims, 1997; Taylor et al., 2000), which interact to govern soil moisture retention and soil drainage. Soil drainage is not straightforward to quantify, and commonly used classification schemes rely on a variety of indicators including soil depth, pore pattern, topographic position and characteristics of the soil profile such as mottling or gley horizons (Lee et al., 1998). Using a very simple soil drainage classification scheme, the boreal region of Ontario, Canada consists of roughly equal proportions of well-drained versus poorly-drained forested stands (Riley and Michaud, 1994). Upland forest communities tend to be dominated by conifer or mixedwood forests and only a small fraction of natural stands in this region are dominated by deciduous species (Sims et al., 1997; Taylor et al., 2000). Lowland boreal forest communities comprise of a range of ecosystem types, including treed bogs and fens, open bogs and fens, and poorly-drained conifer forests. Across all of these ecosystem types, soil moisture retention and slow rates of decomposition lead to the build-up of thick organic soil layers. The development of thick organic layers leads to an accumulation of nutrients such as nitrogen in unavailable organic forms, which

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http://dx.doi.org/10.1016/j.foreco.2015.12.001

contributes to a slow nutrient cycle and an exacerbation of nutrient limitation on plant productivity. Due in part to such slow nutrient cycles, plant communities in boreal lowland forests are thought to be less productive and diverse than in uplands.

Disturbance plays an important role in influencing vegetation structure and nutrient cycling both in upland and lowland forests. An important legacy of historical disturbance regimes is that vegetation in boreal forests is largely resilient to disturbance events (Rydgren et al., 2004; Thompson et al., 2009). Wildfires are the main stand-replacing natural disturbance in boreal North America. In Ontario, Canada, an estimated 230,000 ha of forests are affected by wildfires annually while approximately 100,000 ha are affected by timber harvesting each year (OMNR, 2011). Fire generally influences forest nutrient cycling by removing vegetation and soil material through combustion and leaching export (Boerner, 1982; Certini, 2005; Grier, 1975), altering vegetation community composition and productivity (Goulden et al., 2011; Reich et al., 2001; Thornley and Cannell, 2004), and increasing soil temperature (Kasischke and Johnstone, 2005). Combustion of aboveground fuels and post-fire mortality open the canopy, allowing more sunlight to reach the forest floor. Thus, burning tends to increase soil temperature and pH, lower C/N ratios and increase N mineralization (Harden et al., 2002; Hart and Chen, 2006; Smithwick et al., 2005; Turner et al., 2007). Yet despite these general effects of fire on ecosystem processes, some aspects of ecosystem recovery and vegetation succession following fire are likely to vary between upland and lowland stands. For example, some studies have suggested that upland forests have shorter fire return intervals than lowland forests or peatlands (Kurhy, 1994; Zoltai et al., 1998), though other studies have shown no difference in landscape patterns of fire activity (Turetsky et al., 2004). In relation to fire return interval, fewer studies have quantified variation in burn severity between upland and lowland forest stands. Moist soils or permafrost tends to limit deep burning fires in lowland forests, even under the same fire conditions that lead to extreme burning in adjacent upland forests (Turetsky et al., 2011). As a result, conifer forests with thick organic soil layers tend to be resistant to deep burning (Johnstone et al., 2010; Magnan et al., 2012; Turetsky et al., 2015).

Ontario's boreal forests also are influenced by human activities, including forestry, and hydroelectric and mining developments, among others. Over the past 40 years, modifications in technology have allowed large-scale logging to occur at much faster rates than those of natural disturbance (Bergeron et al., 2006). Timber harvesting in many types of boreal forest in Ontario is done by clear-cutting, distributed in a mosaic of cut-blocks that range in size from 50 ha to over 250 ha (McRae et al., 2001), with contiguous blocks that can be larger (up to several thousand ha). Current rates of landscape harvesting have reduced the amount of mature forest available to less than that expected under natural disturbances alone (Cyr et al., 2009). As a result of research into the issues associated with impacts, forest management practices now attempt to mimic the effects of fire at stand and landscape scales, to improve the rate of natural regeneration (Bergeron and Harvey, 1997; Harvey et al., 2002) and to help maintain forest resilience, ecosystem processes and biodiversity (Long, 2009). Many previous studies have focused on understanding the role of disturbance on tree species composition. While there is ample evidence that understory vegetation is important to stand succession and ecosystem nutrient cycling (c.f. Hart and Chen, 2006), fewer studies have focused on understory responses to either natural or anthropogenic disturbances.

The main goal of this study was to improve our current understanding of vegetation succession in boreal stands across disturbance types and drainage characteristics in Ontario forests. Our response variables included plant species diversity, species percent cover and aboveground biomass as measures of understory vegetation abundance and composition. We also quantified net aboveground productivity across vascular plant functional types. Finally, for both vascular and nonvascular plant functional types, we quantified foliar C/N as a general index of ecosystem productivity (LeBauer and Treseder, 2008) and to assess N content and relate it to forage quality for herbivores (Mattson, 1980). Our specific objectives were as follows: (1) quantify the effects of disturbance (fire vs. timber harvest) on understory plant species abundance and composition, (2) determine if patterns of post-disturbance succession vary between upland and lowland stands, and (3) examine the effects of disturbance type and drainage on the biomass, productivity, and foliar C/N of various plant functional groups. Due to both canopy closure and organic layer development, we predicted that total understory plant biomass would increase, whereas aboveground net primary productivity (ANPP) would decrease with time following disturbance in both uplands and lowlands. As a result of wetter conditions and slower rates of nutrient cycling in lowlands, we predicted that understory plant groups would have higher % cover, biomass and C/N but lower species richness and productivity in lowlands than in uplands. Finally, since fire can consume soil organic layers and expose mineral soil, whereas organic soil layers typically remain at least partially intact following timber harvest, we predicted that harvested stands would have fewer plant species and a less productive understory than burned stands.

2. Methods

2.1. Study site description

Our study was conducted near Nakina, Ontario, located 275 km northeast of Thunder Bay. Monthly mean temperature is −19.2 °C in January and 16.9 °C in July (Environment Canada, 1971–2000 climate data, Geraldton station). Our landscape was chosen for its comprehensive silviculture data from the past 70 years and extensive network of roads, which allowed for site access. The majority of stands in this region are conifer-dominated, with a small percentage of deciduous forests (<10%). We initially selected stands based on Forest Resource Inventory (FRI) data from aerial photographs that had the following primary conditions: (1) conifer- or mixedwood-dominance (deciduous-dominant stands were excluded), (2) type of disturbance (post-wildfire vs. post-timber harvest), (3) stand age class reflecting time following most recent disturbance, and (4) site access from primary roads. Stands were considered separate sites if they were at least 0.5 km apart. We then verified the FRI data using empirical measurements of the depth of the organic soil layer to classify stands as either an upland or a lowland, and to verify stand age by using dendrochronology (see methods below). We used these criteria to arbitrarily populate a factorial design of drainage class (upland versus lowland) × disturbance type (post-fire versus post-timber harvesting) × age class (young: 0–30 yrs; intermediate: 31–70 yrs; mature: >71 yrs). We aimed for three replicates in each combination of these main effects, but this was not always possible. For example, mature harvested stands were not included in this study as there were no records of harvesting >80 years ago in the study area. Upland stands were dominated by black spruce (*Picea mariana* Miller), jack pine (*Pinus banksiana* Lamb.) and balsam fir (*Abies balsamea* (L.) Miller) with some deciduous trees including poplars (*Populus* spp.) and white birch (*Betula papyrifera*). Lowland stands were dominated by black spruce, eastern white cedar (*Thuja occideantalis* L.), and tamarack (*Larix laricina* (Du Roi) K. Koch). Upland organic layer depths were typically less than 20 cm, whereas lowland organic layer depths exceeded 40 cm (Table 1).

Table 1
Stand characteristics for each stand in the stand matrix including stand type, successional stage, stand age (yrs), disturbance origin, average depth of the organics (cm), average tree density (stems m^{-2}), average diameter at breast height (DBH) (cm) and tree density (stems m^{-2}). Tree density includes trees >3 cm diameter at DBH of 1.2 m. Data are means ± 1 SE.

Stand name	Drainage class	Age class	Stand age (yrs)	Disturbance type	Depth of organics (cm)	Tree density (stems m^{-2})	DBH (cm)
AY11	UP	Young	14	Fire	0.7 ± 0.2	0.01	3.7 ± 0.2
AY12	UP	Young	13	Fire	2.0 ± 0.6	0.04	3.0 ± 0.0
AY02	UP	Young	15	Harvest	3.7 ± 1.2	0.03	6.7 ± 2.7
AC35	UP	Young	16	Fire	5.6 ± 1.0	0.79	8.3 ± 0.2
AC32	UP	Young	17	Harvest	13.0 ± 3.5	0.45	4.9 ± 0.4
AY05	UP	Young	25	Harvest	1.3 ± 0.9	0.08	6.8 ± 0.7
AC04	UP	Int.	33	Harvest	5 ± 0.0	0.43	14.3 ± 1.1
AC16	UP	Int.	34	Harvest	6.8 ± 2.1	0.14	16.3 ± 1.8
AC20	UP	Int.	38	Fire	5.9 ± 0.4	0.15	8.3 ± 0.7
AC14	UP	Int.	52	Harvest	9.3 ± 1.9	0.24	12.3 ± 1.5
AC23	UP	Int.	55	Fire	7.0 ± 2.5	0.13	14.0 ± 0.6
AC13	UP	Int.	60	Harvest	5.7 ± 2.4	0.22	18.4 ± 2.2
AC29	UP	Mature	72	Fire	10.8 ± 2.1	0.35	15.0 ± 0
AC30	UP	Mature	77	Fire	5.0 ± 1.2	0.19	16.2 ± 1.3
AC28	UP	Mature	81	Fire	9.3 ± 0.9	0.47	10.0 ± 0.6
AY16	LOW	Young	11	Fire	38.7 ± 10.1	0.07	4.7 ± 0.2
AY01	LOW	Young	21	Harvest	>120	0.06	4.8 ± 0.4
AL01	LOW	Young	22	Harvest	>120	0.15	12.5 ± 1.6
AL02	LOW	Young	26	Harvest	>120	[a]	[a]
AL22	LOW	Int.	31	Fire	>120	0.04	11.7 ± 1.6
AL18	LOW	Int.	35	Harvest	>120	0.15	12.8 ± 0.8
AL15	LOW	Int.	57	Harvest	>120	0.16	12.8 ± 0.6
AL13	LOW	Int.	60	Harvest	54.3 ± 2.0	0.19	12.3 ± 0.3
AL20	LOW	Int.	70	Fire	>120	0.14	11.0 ± 0.0
AL29	LOW	Mature	128	Fire	>120	0.22	15.0 ± 0.0
AL25	LOW	Mature	149	Fire	>120	0.13	23.7 ± 0.9
AL26	LOW	Mature	151	Fire	76.7 ± 6.7	0.37	13.0 ± 0.6

[a] Data not collected.

In each stand, we determined a 50 m buffer from the stand edges to avoid sampling across ecotones. We then created a main plot by walking 25 m past the buffer in the direction of the middle of the stand to establish the center of a 25 × 25 m (625 m^2) plot. This main plot was used to measure tree species densities and determine community composition. At the center of each main plot, we established one 5.64 m radius (100 m^2) tree density plot, six randomly placed 1 m^2 understory plots, each with one 25 × 25 cm (625 cm^2) biomass subplot placed inside. Understory vegetation layer was defined as live plants <1 m in height while overstory vegetation layer was defined as live plants $\geqslant$1 m in height.

2.2. Soil organic layer, stand age and percent cover

Depth of the organic soil layer (up to 120 cm) was measured with a soil auger at three points within each 25 × 25 m main plot. The effective texture of the mineral soil, when present, was recorded along with the slope and aspect at each soil auger point. We used these data to corroborate the FRI-based designations of upland versus lowland sites, given that lowland stands should have thicker organic layers (>40 cm) due to saturation and slow decomposition rates.

Tree height was visually estimated in one 100 m^2 tree density plot in each stand. We also recorded the diameter at breast height (DBH) of each individual with a meter stick in each plot (Table 1). Tree density was quantified by counting stems of all tree species in the tree density plot that were >1.5 m tall with a DBH >3 cm (Table 1). As mentioned above, our initial stand age assessments were based on FRI data, which provides information on the timing of last disturbance. We corroborated these FRI stand ages using mean tree age derived from tree rings. We selected three trees from the dominant cohort, and used an increment borer to obtain tree cores at DBH (Lecomte et al., 2007) (Table 1). To estimate stand age, tree rings in all cores were counted and recorded in the field.

Post-hoc rarefaction indicated that six 1 m^2 understory plots were sufficient to adequately represent 80% of the understory species composition in all stands. The percent cover of each species in each plot was visually estimated. We estimated percent cover of understory species in the following classes: <1%, 1–5% and then by 5% increments up to 100%. Species were then grouped by plant functional type, including deciduous shrub, evergreen shrub, forb, graminoid, pteridophyte, true/feather moss, *Sphagnum* moss, and terrestrial lichen. Estimates of percent cover were averaged across the six understory plots to obtain mean plant functional type cover. We then summed percent cover estimates to estimate total understory vegetation cover at each site.

2.3. Aboveground biomass and net primary productivity

In all stands, live understory aboveground biomass was collected from the six randomly placed understory plots used to estimate percent cover (six subplots × 27 stands, $n = 162$). Within each understory plot, we then randomly established one 25 × 25 cm subplot for destructive harvest of plant biomass. Sampling occurred during peak biomass (mid-July). Only vegetation in the understory layer (<1 m) was harvested. Before harvesting biomass, we visually estimated the percent cover of each species in the subplot to allow for scaling of biomass and % cover to a per m^2 basis. All vascular plant material was clipped at the root collar and sorted in the field. For ground layer species, living *Sphagnum*, feather and true mosses were clipped 10 cm from the tip of the plant. Lichens were clipped from the soil/stem interface and separated from moss as required.

Current year's growth was used to estimate shrub aboveground net primary productivity (ANPP), which was estimated from terminal growth (fresh twigs and leaves and fruits). Radial stem growth, was not estimated because of the complex measurement required

Table 2
Total understory and plant functional type richness averaged by drainage class (upland/lowland) × age class (young, intermediate and mature). Data are means ± 1 SE.

Drainage class	Uplands $n = 15$			Lowlands $n = 12$		
Age class	Young $n = 6$	Intermediate $n = 6$	Mature $n = 3$	Young $n = 5$	Intermediate $n = 4$	Mature $n = 3$
Total	36.8 ± 3.0	32.7 ± 3.0	22.6 ± 0.3	40.6 ± 1.8	42.5 ± 2.7	32.3 ± 1.5
Deciduous tree	2.0 ± 0.6	0.8 ± 0.3	0.3 ± 0.3	0.8 ± 0.4	0	0.7 ± 0.7
Coniferous tree	2.3 ± 0.4	2.3 ± 0.3	2.0 ± 0.6	2.0 ± 0.4	2.3 ± 0.3	1.7 ± 0.3
Arboreal lichen	1.5 ± 0.6	3.0 ± 0.0	3.0 ± 0.0	2.6 ± 0.6	3.0 ± 0.0	3.0 ± 0.0
Deciduous shrub	7.8 ± 0.3	5.1 ± 0.9	5.0 ± 0.0	6.8 ± 0.4	7.5 ± 0.9	5.3 ± 0.3
Evergreen shrub	1.3 ± 0.4	2.8 ± 0.8	2.3 ± 0.3	5.8 ± 0.7	5.0 ± 0.7	6.0 ± 0.0
Forb	14.8 ± 2.3	9.6 ± 2.6	4.7 ± 0.7	12.8 ± 2.9	13.8 ± 1.4	6.0 ± 0.6
Graminoid	1.7 ± 0.7	0.8 ± 0.3	0	3.4 ± 0.2	4.8 ± 0.9	1.7 ± 1.2
Pteridophyte	1.5 ± 0.6	1.5 ± 0.3	0	0.8 ± 0.4	0.8 ± 0.3	0.7 ± 0.3
Lichen	2.5 ± 0.8	3.8 ± 0.7	2.0 ± 0.0	3.2 ± 0.7	1.5 ± 1.2	4.0 ± 0.5
Feather/true moss[a]	2.8 ± 0.3	3.8 ± 0.4	4.0 ± 0.0	1.6 ± 0.6	3.0 ± 0.9	2.3 ± 0.7
Sphagnum moss[a]	0	0.3 ± 0.2	0	0.8 ± 0.2	1.0 ± 0.0	1.0 ± 0.0

[a] Species richness is based on genera.

Table 3
F-values from an analysis of variance (ANOVA) analyzing the effects of stand drainage class (upland/lowland), disturbance type (fire/harvest), and stand age class (young, intermediate and mature) on understory vegetation % cover, biomass (g m^{-2}), and aboveground net primary productivity (g m^{-2} yr^{-1}). Productivity was only measured on vascular plants (NA).

Variable	Total $F_{(\text{num,den df})}$	Deciduous shrub $F_{(\text{num,den df})}$	Evergreen shrub $F_{(\text{num,den df})}$	Forb $F_{(\text{num,den df})}$	Graminoid $F_{(\text{num,den df})}$	Pteridophyte $F_{(\text{num,den df})}$	Terrestrial lichen $F_{(\text{num,den df})}$	Feather/true moss $F_{(\text{num,den df})}$	*Sphagnum* moss $F_{(\text{num,den df})}$
Understory % cover									
Drainage	$0.01_{(1,26)}$	$0.11_{(1,26)}$	$15.25_{(1,26)}^{***}$	$9.46_{(1,26)}^{**}$	$10.24_{(1,26)}^{**}$	$0.11_{(1,26)}$	$0.58_{(1,26)}$	$12.98_{(1,26)}^{**}$	$17.79_{(1,26)}^{***}$
Disturbance	$0.21_{(1,26)}$	$4.45_{(1,26)}^{*}$	$1.36_{(1,26)}$	$0.18_{(1,26)}$	$1.11_{(1,26)}$	$0.09_{(1,26)}$	$2.67_{(1,26)}$	$0.52_{(1,26)}$	$0.49_{(1,26)}$
Age class	$8.52_{(2,26)}^{**}$	$1.92_{(2,26)}$	$3.53_{(2,26)}^{*}$	$2.89_{(2,26)}$	$1.64_{(2,26)}$	$1.64_{(2,26)}$	$1.00_{(2,26)}$	$4.83_{(2,26)}^{*}$	$1.19_{(2,26)}$
Dist. × Drain	$0.39_{(1,26)}$	$0.40_{(1,26)}$	$0.2_{(1,26)}$	$0.35_{(1,26)}$	$0.53_{(1,26)}$	$0.45_{(1,26)}$	$0.54_{(1,26)}$	$0.62_{(1,26)}$	$0.02_{(1,26)}$
Age × Drain.	$0.15_{(2,26)}$	$0.74_{(2,26)}$	$0.12_{(2,26)}$	$1.36_{(2,26)}$	$0.74_{(2,26)}$	$0.14_{(2,26)}$	$0.68_{(2,26)}$	$2.08_{(2,26)}$	$0.84_{(2,26)}$
Understory biomass									
Drainage	$10.95_{(1,26)}^{**}$	$8.44_{(1,26)}^{**}$	$57.98_{(1,26)}^{***}$	$0.28_{(1,26)}$	$6.34_{(1,26)}^{*}$	$1.98_{(1,26)}$	$0.26_{(1,26)}$	$6.95_{(1,26)}^{*}$	$11.58_{(1,26)}^{**}$
Disturbance	$0.29_{(1,26)}$	$0.99_{(1,26)}$	$1.71_{(1,26)}$	$3.94_{(1,26)}$	$5.58_{(1,26)}^{*}$	$0.79_{(1,26)}$	$0.65_{(1,26)}$	$0.38_{(1,26)}$	$0.00_{(1,26)}$
Age class	$2.74_{(2,26)}$	$9.18_{(2,26)}^{**}$	$5.04_{(2,26)}^{*}$	$4.94_{(2,26)}^{*}$	$2.15_{(2,26)}$	$0.16_{(2,26)}$	$0.20_{(2,26)}$	$3.58_{(2,26)}^{*}$	$2.40_{(2,26)}$
Dist. × Drain.	$0.00_{(1,26)}$	$0.00_{(1,26)}$	$2.51_{(1,26)}$	$1.49_{(1,26)}$	$1.67_{(1,26)}$	$0.89_{(1,26)}$	$0.01_{(1,26)}$	$0.64_{(1,26)}$	$0.24_{(1,26)}$
Age × Drain.	$4.66_{(2,26)}^{*}$	$3.74_{(2,26)}^{*}$	$6.33_{(2,26)}^{**}$	$0.28_{(2,26)}$	$0.98_{(2,26)}$	$0.15_{(2,26)}$	$1.20_{(2,26)}$	$3.81_{(2,26)}^{*}$	$2.00_{(2,26)}$
Understory ANPP									
Drainage	$19.22_{(1,26)}^{**}$	$2.85_{(1,26)}$	$43.91_{(1,26)}^{***}$	$0.28_{(1,26)}$	$6.34_{(1,26)}^{*}$	$1.98_{(1,26)}$	NA	NA	NA
Disturbance	$1.29_{(1,26)}$	$1.03_{(1,26)}$	$0.29_{(1,26)}$	$3.94_{(1,26)}$	$5.58_{(1,26)}^{*}$	$0.79_{(1,26)}$	NA	NA	NA
Age class	$15.75_{(2,26)}^{***}$	$9.17_{(2,26)}^{*}$	$2.09_{(2,26)}$	$4.94_{(2,26)}^{*}$	$2.15_{(2,26)}$	$0.16_{(2,26)}$	NA	NA	NA
Dist. × Drain.	$2.87_{(1,26)}$	$0.05_{(1,26)}$	$0.45_{(1,26)}$	$1.49_{(1,26)}$	$1.67_{(1,26)}$	$0.89_{(1,26)}$	NA	NA	NA
Age × Drain.	$1.07_{(2,26)}$	$0.77_{(2,26)}$	$1.89_{(2,26)}$	$0.28_{(2,26)}$	$0.98_{(2,26)}$	$0.15_{(2,26)}$	NA	NA	NA

[*] $p < 0.05$.
[**] $p < 0.01$.
[***] $p < 0.001$.

(c.f. Bond-Lamberty et al., 2004). All live herbaceous vegetation (e.g., forb and graminoid) was quantified as current year ANPP.

All biomass was dried at 60 °C to a constant mass in a drying oven and weighed to the nearest 0.01 g. Biomass values were averaged by stand and scaled to g m^{-2} for analysis.

2.4. Foliar C/N and %N

In each stand, we collected up to 5 g of live foliage for each species with ⩾10% cover. Plant samples were separated by species but analysis was based on species averages by plant functional type. For forbs and graminoids, we collected the entire live plant, whereas mosses and lichens were collected following our biomass methods. For vascular woody species, we collected green biomass from the current year. We stored all samples in paper bags to air dry before they were ground and homogenized for analysis. Final particle size post-grinding was approximately 1 mm. Samples were then dried for 3–4 h at 60 °C in a drying oven. We used an Elementar CNS Analyzer to analyze %C and %N, using an external alfalfa standard. 10% of the samples were run as duplicates to quantify analytical error (SE ± 0.6% for C and 0.9% for N).

2.5. Data analysis

Data were scaled to a m^2 basis for all statistical analyses. Significance was determined using an alpha value of 0.05 and data are presented as mean ± standard error.

Mean understory species richness, percent cover, understory biomass, C/N ratio, and net primary productivity were analyzed using general linear models (PROC GLM, SAS v9.2, SAS Institute Inc., Cary, NC, USA). These models explored the effects of drainage class (uplands vs. lowlands), disturbance type (wildfire vs. timber harvest), stand age class, and interactions among these variables as fixed effects. Our matrix of sites was imbalanced as mature post-harvest stands were not present on the landscape. Thus, we did not test for the interaction between stand age × disturbance type. Finally, we examined whether responses to drainage class, disturbance type, and stand age effects were consistent among different plant functional types.

Diagnostic plots on models that included biomass, productivity and C/N data indicated that residuals were approximately normally distributed and there were no signs of heteroscedasticity or observations with undue influence. We determined relationships between stand age and biomass/ANPP using a series of regression models. We used a correlation analysis (PROC CORR; SAS 9.2) to examine relationships between mean biomass and productivity and their relationship with mean foliar %N. Finally, we used a one tailed *t*-test to compare mean foliar %N among plant functional types in uplands and lowlands.

3. Results

3.1. General stand characteristics

Across upland stands, organic soil layer depth averaged 6.3 ± 0.6 cm. The mean depth of the organic layer in uplands tended to increase with time following disturbance (young: 4.4 ± 1.2 cm, intermediate: 6.6 ± 0.6 cm; mature: 8.8 ± 1.2 cm) although there were no significant differences among these age classes (Table 1). Mean organic layer depth did not vary between burned and harvested stands (5.7 ± 0.7 cm and 6.4 ± 1.1 cm, respectively) (Table 1). Organic layer depth was clearly much greater in lowlands than in uplands, and the magnitude of the true difference could be even greater than that recorded in our study because 75% of our lowland soil depth measurements exceeded the length of our 120 cm auger.

Tree density was greater in upland than in lowland stands, averaging 2700 ± 600 stems/ha in uplands and 1500 ± 30 stems/ha in lowlands. In both uplands and lowlands, young stands had, on average, fewer stems m^{-2} than intermediate and mature class stands (Table 1). Mean tree DBH was similar between upland and lowland stands (10.5 ± 1.3 cm and 12.2 ± 1.5 cm, respectively). Across all stands, mean DBH increased with stand age and was significantly greater in intermediate and mature stands compared to young stands (young 6.1 ± 0.2 cm, intermediate: 13.1 ± 0.8 cm and mature 15.5 ± 1.9 cm).

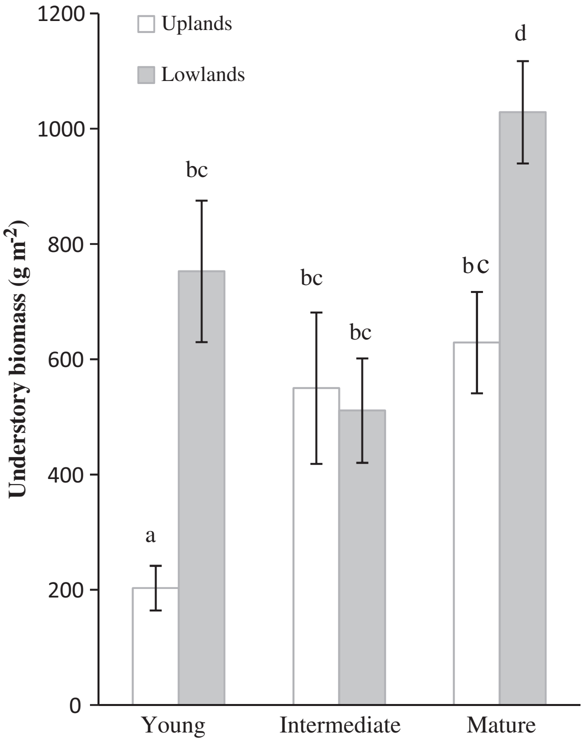

Fig. 1. Total understory vegetation biomass (g m^{-2}) across stand age class. Same letter superscripts denote non-significant differences according to post hoc comparison of means tests.

3.2. Understory vegetation % cover, biomass, and productivity

On average, upland stands had lower understory species richness than lowlands (32 ± 2 vs. 39 ± 2 species, respectively) (Table 2). Uplands and lowlands had similar forb species richness, whereas lowlands had more evergreen shrub and graminoid species than uplands (Table 2). In both uplands and lowlands, total understory species richness decreased with time following disturbance. Total understory plant species richness was lower in burned uplands than in harvested uplands (burned: 27 ± 3; harvested: 37 ± 3 species) (Table 2), again mostly due to differences in forb species between disturbance types. Though not as prominent, the same trend was present in lowlands (burned: 37 ± 2, harvested: 41 ± 2 species) (Table 2).

Total understory % cover varied with time following disturbance and the highest overall plant abundance was found in mature sites, largely due to bryophyte abundance. Percent cover was also

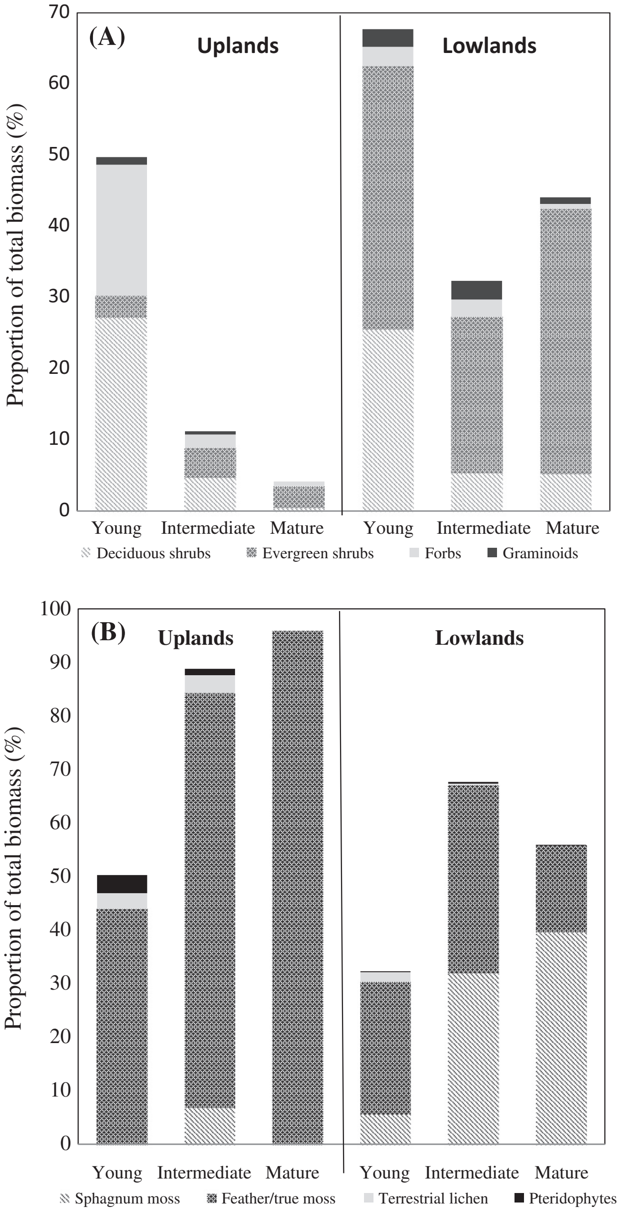

Fig. 2. Effects of drainage and stand age class on the proportion of plant functional type biomass to total biomass in (A) deciduous shrubs, evergreen shrubs, forbs and graminoids and (B) *Sphagnum* moss, feather/true moss, terrestrial lichen and pteridophytes.

affected by drainage in many plant groups and this effect was most significant in evergreen shrubs and *Sphagnum* mosses, which both had greater cover in lowlands than uplands (Table 3). On average, lichen contributed little to total understory cover, comprising <0.3% and <1.1% of the mean understory vegetation across lowlands and uplands, respectively.

We found that total biomass also varied between drainage classes, with greater total biomass in lowlands than uplands. However, the effect of drainage class on the biomass of individual plant functional groups was more variable in both drainage classes (Table 3). For example, we found that feather moss on average had greater biomass in uplands than lowlands, whereas deciduous and evergreen shrubs, graminoids and *Sphagnum* moss showed the opposite trend (Table 3, Fig. 2). Deciduous shrub cover was the only plant function type that varied by disturbance type, and was greater in harvested stands than burned stands (13.56 ± 2.75% and 6.94 ± 1.21%).

There was a significant interaction between drainage class and stand age on total aboveground understory biomass, but with no effect of disturbance type (Table 3). Understory biomass in both uplands and lowlands increased with stand age though this was only significant in uplands (Fig. 3A). Total understory biomass in lowlands was greater, or comparable to, biomass in upland stands, regardless of age class (Fig. 1). Drainage class and disturbance type had significant effects on graminoid biomass (Table 3). Lowlands had greater graminoid biomass than uplands (14.20 ± 4.96 g m^{-2} and 1.87 ± 1.28 g m^{-2}), respectively). Burned stands had greater graminoid biomass than harvested stands (10.06 ± 2.51 g m^{-2} and 4.41 ± 2.12 g m^{-2}, respectively). In uplands, deciduous shrubs and forbs dominated understory vascular plant biomass in young and intermediate stands, whereas evergreen shrubs dominated understory vascular plant biomass in mature stands (Fig. 2A, Table 3). In lowlands, evergreen shrubs dominated total biomass regardless of disturbance type or stand age (Fig. 2A). Although some upland stands had relatively high lichen biomass (e.g., up to 75.45 g m^{-2}), mean terrestrial lichen biomass did not differ significantly between uplands and lowlands (9.62 ± 5.12 g m^{-2} versus 4.96 ± 2.83 g m^{-2}, respectively). Lichen biomass was highest in intermediate uplands stands where it comprised 3% of the total understory biomass (Fig. 2B).

In general, total understory ANPP was governed by drainage class and stand age, but not disturbance type nor any interactions (Table 3). Total understory ANPP declined with stand age as did forb ANPP (Fig. 3B). Averaged across stand age, mean understory ANPP was greater in lowlands (114.83 ± 16.39 g m^{-2} yr^{-1}) than in uplands (43.23 ± 12.61 g m^{-2} yr^{-1}), due primarily to greater shrub productivity in lowlands. Lowlands also had greater graminoid ANPP than uplands (14.10 ± 4.57 g m^{-2} yr^{-1} and 1.09 ± 1.08 g m^{-2} yr^{-1}, respectively), though forbs contributed less than shrubs to total understory productivity. Although total understory productivity did not differ between disturbance types (Table 3), graminoid ANPP was greater in burned stands than in harvested stands (10.06 ± 4.51 g m^{-2} yr^{-1} and 4.44 ± 2.12 g m^{-2} yr^{-1}, respectively).

The slope of the total understory biomass plotted against ANPP was steeper in uplands than lowlands, indicating that for similar levels of understory biomass, productivity was greater in upland than in lowland stands (Fig. 4A). We also examined relationships between ANPP and biomass among plant functional groups. Deciduous shrub, forb and pteridophyte functional groups tended to have higher ANPP/biomass ratios in uplands whereas evergreen shrubs and graminoids had higher ratios in lowlands (Fig. 4B).

3.3. Understory vegetation foliar C/N and %N

Mean C/N ratio of understory foliage differed by age class and plant functional type with no other main effects or interaction terms. Mature stands had greater foliar C/N ratios than young or intermediate stands (mature: 67.43 ± 6.46, intermediate: 45.72 ± 2.57, young: 58.86 ± 4.66, $F_{2,194} = 3.34$, $p < 0.0199$). There were few differences among plant functional types. On average, C/N ratios of lichen tended to be greater than that of other plant

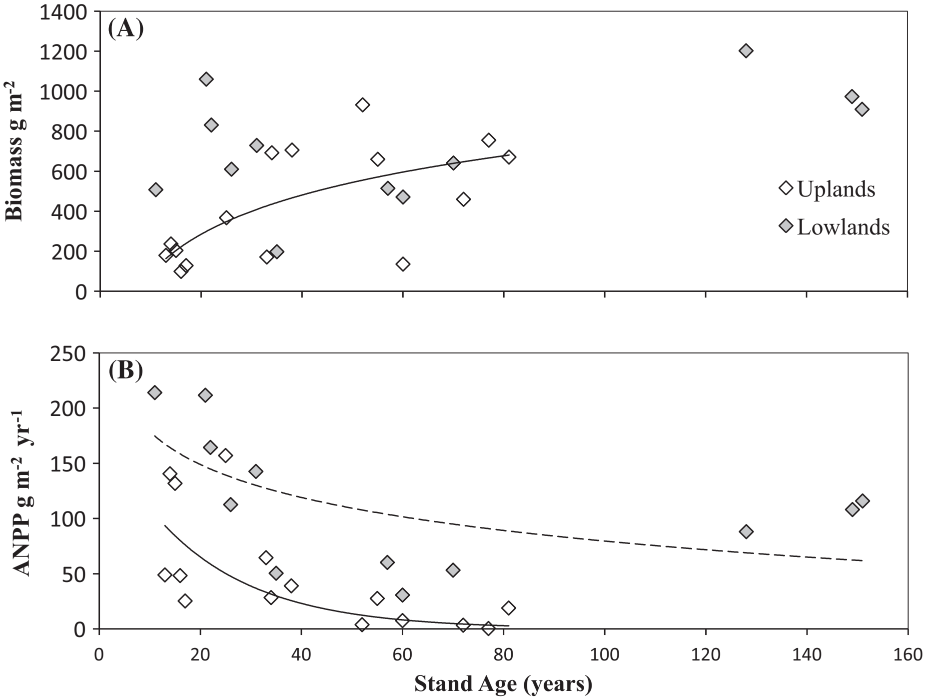

Fig. 3. (A) Understory biomass increased logistically with stand age in uplands (solid line) but not in lowlands (no relationship). (B) Aboveground net productivity declined exponentially with stand age in uplands ($r = 0.84$, $p < 0.001$, $F_{1,88} = 218.61$, $R^2 = 69.0$; solid line), whereas lowland productivity declined logarithmically with stand age ($r = 0.73$, $p < 0.001$, $F_{1,70} = 79.00$, $R^2 = 53.0$; dashed line). *ANPP was not quantified for the lichen and moss plant groups.

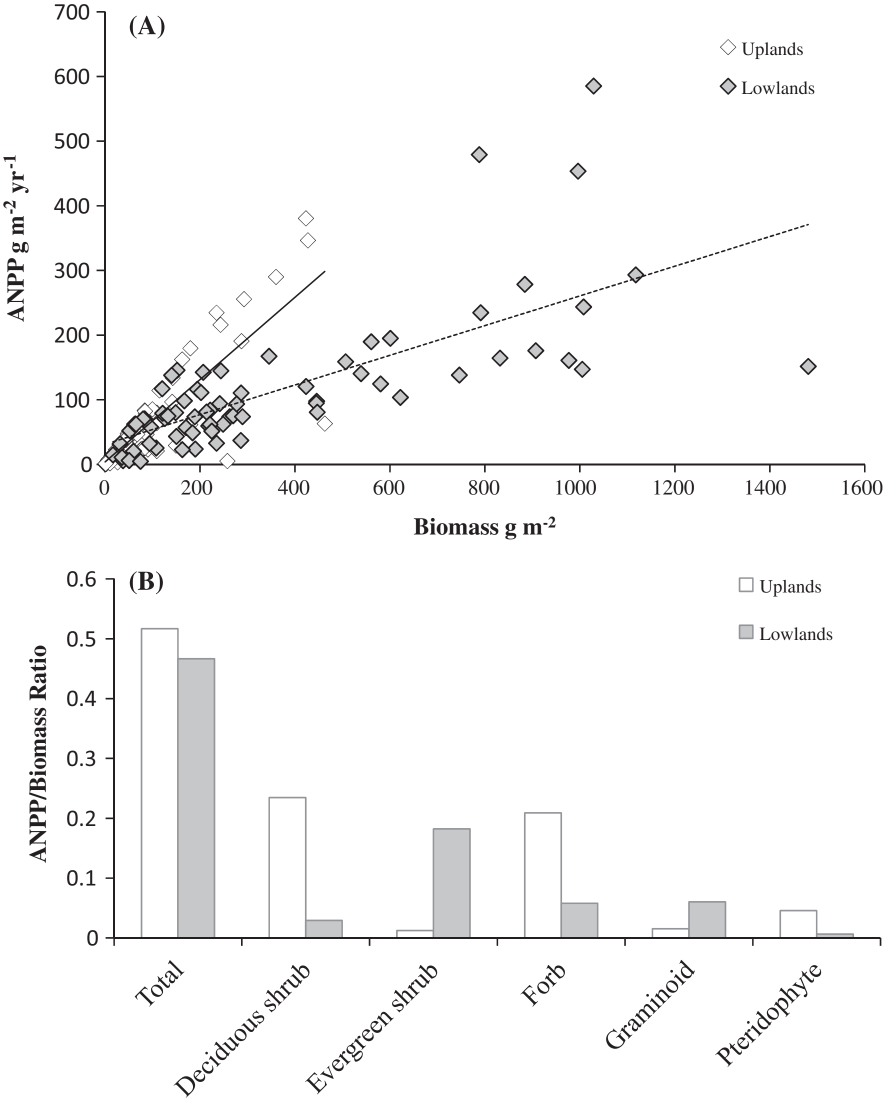

Fig. 4. (A) Relationships between total understory biomass and total understory aboveground net primary productivity in uplands and lowland stands (uplands: $r = 0.84$, $p < 0.001$, $F_{1,88} = 218.61$, $R^2 = 69.0$ and lowlands: $r = 0.73$, $p < 0.001$, $F_{1,70} = 79.00$, $R^2 = 53.0$, respectively). Solid and broken lines denote upland and lowland models respectively. (B) Total ANPP/Biomass ratio of total understory vegetation and by plant functional type. *Lichen and mosses are absent from these data as ANPP was not determined for these plant groups.

types (lichen: 106.01 ± 5.18; other: 38.33 ± 1.16, $F_{1,194} = 6.55$, $p < 0.0001$).

Mean foliar %N showed positive relationships with understory biomass (Fig. 5A) and understory ANPP (Fig. 5B). Shrubs, mosses and lichens did not differ in mean foliar %N whereas forbs, graminoids and pteridophytes had greater %N in lowlands than uplands (Fig. 6).

4. Discussion

4.1. Effects of disturbance on upland and lowland forest vegetation

The primary goal of this study was to quantify trends in vegetation succession between drainage classes and disturbance types in forested stands in boreal Ontario. Our factorial design of drainage classes (uplands vs. lowlands) and disturbance types (wildfire vs. timber harvest) allowed us to examine basic ecological patterns of understory recovery following natural and anthropogenic disturbance. As previously noted, the influence of disturbance on boreal vegetation has been documented more in upland stands (Hart and Chen, 2008; Lecomte et al., 2006; Shrestha and Chen, 2010) than in poorly-drained lowlands. Studies that have examined successional trends in lowlands have tended to focus on ecosystem recovery following wildfire (Turetsky et al., 2010; Bond-Lamberty et al., 2006, 2004; Mack et al., 2008) and have not examined trends following timber harvesting. We predicted that understory biomass and productivity would be greater in uplands than in lowlands, but our results showed that biomass and productivity were greater in lowlands than in uplands across all stand age classes. Despite wetter soil conditions and thicker organic soil layers, lowland stands had a more productive understory, with greater biomass than uplands of similar age and disturbance origin. Our lowland sites tended to have more shrub biomass than uplands, likely as a result of low canopy density and greater light availability for understory species. These results are similar to Bond-Lamberty et al. (2002), who found higher leaf area indices (indicative of productivity) in mesic forested stands compared to well-drained stands.

We also predicted that foliar material from vegetation in poorly-drained systems would have higher C/N ratios, reflecting lower relative N availability relative to upland stands (Côté et al.,

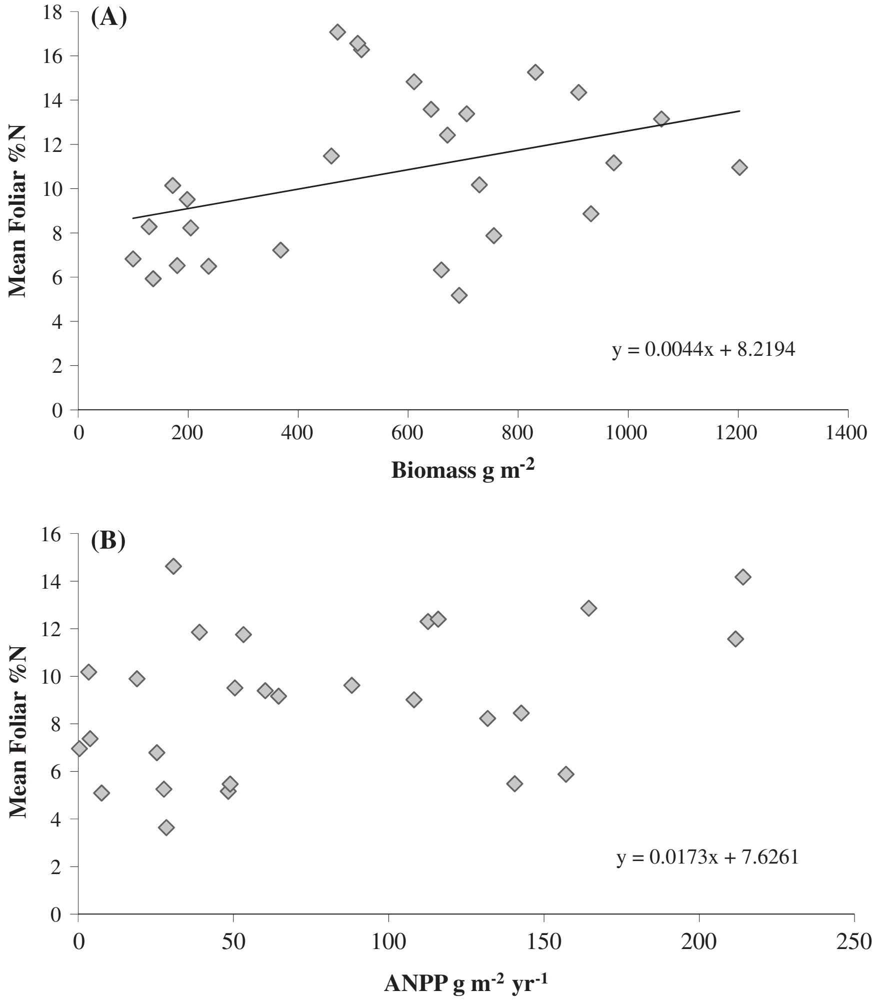

Fig. 5. (A) Relationship between understory biomass and mean foliar %N, which did not vary among drainage classes ($r = 0.83$, $p < 0.0489$, $F_{1,25} = 4.29$). (B) Relationship between understory net primary productivity and mean foliar %N ($r = 0.36$, $p < 0.0643$, $F_{1,25} = 3.75$).

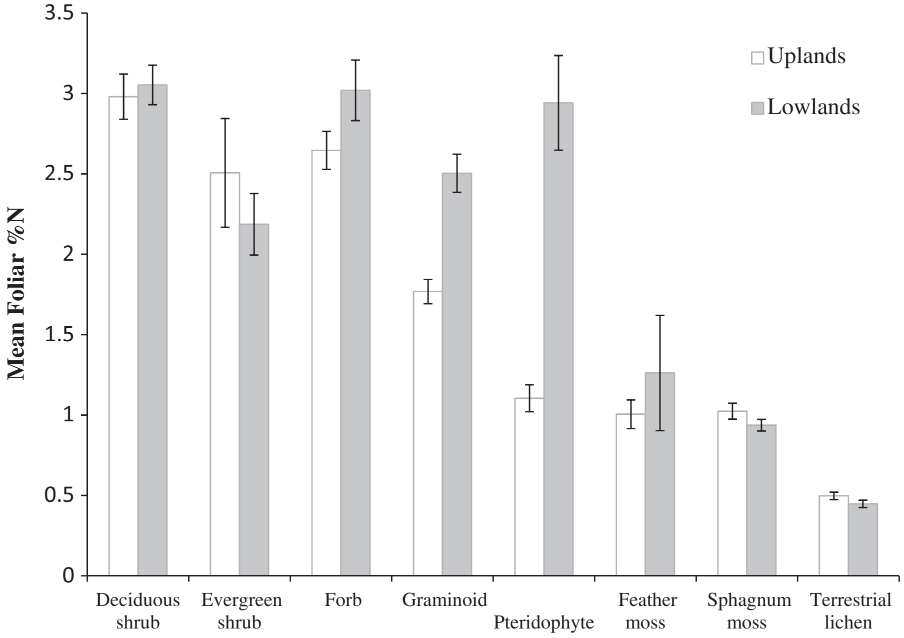

Fig. 6. Mean foliar %N by plant functional type collected in uplands and lowlands. There were no significant difference in %N by drainage class in shrubs, mosses or lichens but forbs, graminoids and pteridophytes had significantly greater %N in lowlands than uplands ($p = 0.039$, $p = 0.006$ and $p = 0.0013$, respectively).

2000). Lowland soils tend to have lower soil N availability relative to uplands due to higher water tables, cooler soils, and slower litter decomposition rates (Moore and Basiliko, 2006). Bond-Lamberty et al. (2006) found that understory N differed significantly among plant tissues (wood, old foliage and new foliage) but they found no difference between well-drained and poorly-drained forest stands, suggesting that vascular plant allocation of N occurs independently of coarse differences in soil moisture. This is consistent with our findings for woody species, as shrubs in both uplands and lowlands had similar mean foliar C/N. However, lowland herbaceous understory vegetation had higher %N than upland understory vegetation, suggesting that N allocation in these plant groups may be more sensitive to soil moisture.

In our study, both upland and lowland stands followed similar successional trends post-disturbance, with decreases in understory species richness, increases in total understory biomass (vascular and non-vascular), and declines in productivity with time following disturbance. Previous studies have found maximum understory ANPP early in succession (10–35 years) (Bond-Lamberty et al., 2002; Mack et al., 2008). Our results are similar, with peaks in understory ANPP between 10 and 25 years following disturbance in both uplands and lowlands.

We predicted higher % cover and productivity and lower C/N in burned vs. harvested stands but our results showed that total understory composition, abundance or productivity did not vary significantly between burned and harvested sites. We also found no evidence of disturbance type driving variation in productivity or C/N among plant functional types. The only difference among disturbance types was greater deciduous shrub cover in harvested stands and greater graminoid productivity in burned stands. Following either disturbance type, the understory showed declines in vascular cover and productivity, and increases in bryophyte and lichen biomass with time (stand age). Thus, our findings support previous research suggesting there is a convergence in ecosystem succession on decadal scales after wildfire and timber harvest (Harper et al., 2002; Hart and Chen, 2008; Lecomte et al., 2006; McRae et al., 2001; Shrestha and Chen, 2010; Simard et al., 2001).

4.2. Implications for woodland caribou (Rangifer tarandus caribou)

Our study on vegetation recovery following disturbance was conducted as part of a broader study on woodland caribou habitat selection in the boreal forests of Ontario (Avgar et al., 2015; McGreer et al., 2015; Newmaster et al., 2013; Thompson et al., 2015). Woodland caribou in Ontario are protected under the Endangered Species Act (OMNR, 2010). Over the last century, caribou have been declining in abundance and have experienced range retraction throughout large parts of Ontario and Canada (Schaefer, 2003; Vors et al., 2007), likely a result of anthropogenic landscape alteration and increased predation (Stuart-Smith et al., 1997; Rettie and Messier, 1998; Wittmer et al., 2007), which are not mutually exclusive. Several studies have suggested that caribou may select lowlands as a spatial separation strategy to minimize predation by wolves (Hins et al., 2009; James et al., 2004; Latombe et al., 2014; Rettie and Messier, 2000). Due to their dense and spongy understories, lowlands are not easily accessible to wolves, allowing caribou to distance themselves and reduce their encounter rates with these predators (James et al., 2004). Additionally, alternate prey species, such as moose, prefer well-drained uplands to gain access to suitable deciduous shrub browse (Crête, 1989) and thus are more heavily preyed on by wolves than are caribou in these environments (McCutchen, 2007). Despite a much higher predation risk in uplands than in lowlands, caribou continue to use upland habitats at various times of the year (i.e., to access more abundant and/or higher quality vegetation) despite a greater risk of encountering predators (McLoughlin et al., 2005). This suggests that caribou face a trade-off between energy intake and predation risk through their selection of lowlands.

In our study region, Thompson et al. (2015) found that the majority of forage selected by caribou in summer and winter is comprised of terrestrial lichens. Our study indicated that upland and lowland stands had similar amounts of terrestrial lichen biomass and that lichen cover across all of our sites was surprisingly low, with the highest mean value estimated in one upland stand at 7% of total understory percent cover (4% of total understory biomass). We also found no evidence of differences in lichen N concentrations across upland and lowland stands, and this was consistent across stand age classes.

To a lesser extent, caribou in our study region also select forbs and graminoids in summer (Thompson et al., 2015). Similar to lichens, we found no difference in forb biomass, productivity, or foliar N content in upland versus lowland stands. However, opposite to our predictions, graminoids were more productive, diverse, and had greater %N in lowlands than in uplands. Taken together, our results do not support the hypothesis that caribou face diminished forage quality or quantity when selecting lowlands to minimize predation risk. Instead, we found that lowland understory communities provide equal lichen and forb biomass and greater graminoid biomass than uplands. Likewise, we found no evidence of lower quality of caribou forage in lowlands compared to upland stands, at least as evidenced by foliar N content, suggesting that the costs of lowland use by caribou may be lower than expected from a nutrient/forage quality perspective. This conclusion assumes that caribou choose forage independently of any other external factors such as predation risk or species competition, which seems reasonable based on studies examining forage selection for elk, sheep, and moose (Ganguli et al., 2010; Larter and Gates, 1991; Van Beest et al., 2010; Van Dyke and Darragh, 2007). Despite this assumption, our results may help to explain why, in addition to seeking refuge from predators, caribou are shown to frequently select lowland environments.

Acknowledgements

We would like to thank staff at the Center for Northern Forest Ecosystem Research (CNFER) for their guidance, support and resources. This project was made possible by the Canadian Forest Service and Ontario Ministry of Natural Resources and the Forest Ecosystem Science Co-operative Inc. We would also like to thank Marco Raponi and research assistants Steve Hart, Eric McNeill and Tyler Blauel for their hard work in helping to collect the data.

References

Avgar, T., Baker, J.A., Brown, G.S., Hagens, J., Kittle, A.M., Mallon, E.E., Mosser, A., Newmaster, S.G., Patterson, B.R., Shuter, J., Street, G.M., Thompson, I., Turetsky, M., Wiebe, P.A., Fryxell, J.M., 2015. Space-use behavior of woodland caribou based on a cognitive movement model. J. Anim. Ecol. 84, 1059–1070.

Baldwin, K.A., Sims, R.A., 1997. Field guide to the common forest plants of northwestern Ontario. Ontario Ministry of Natural Resources, NWST, Thunder Bay Ont. FG-04. pp. 359.

Bergeron, Y., Cyr, D., Drever, C.R., Flannigan, M., Gauthier, S., Kneeshaw, D., Lauzon, È., Leduc, A., Goff, H. Le, Lesieur, D., 2006. Past, current, and future fire frequencies in Quebec's commercial forests: implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. Can. J. For. Res. 36, 2737–2744.

Bergeron, Y., Harvey, B.D., 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manage. 92, 235–242.

Boerner, R.E.J., 1982. Fire and nutrient cycling in temperate ecosystems. Am. Inst. Biol. Sci. 32, 187–192.

Bond-Lamberty, B., Gower, S.T., Wang, C., Cyr, P., Veldhuis, H., 2006. Nitrogen dynamics of a boreal black spruce wildfire chronosequence. Biogeochemistry 81, 1–16.

Bond-Lamberty, B., Wang, C., Gower, S.T., 2004. Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. Glob. Change Biol. 10, 473–487.

Bond-Lamberty, B., Wang, C., Gower, S.T., Norman, J., 2002. Leaf area dynamics of a boreal black spruce fire chronosequence. Tree Physiol. 22, 993–1001.

Certini, G., 2005. Effects of fire on properties of forest soils: a review. Oecologia 143, 1–10.

Côté, L., Brown, S., Paré, D., Fyles, J., Bauhus, J., 2000. Dynamics of carbon and nitrogen mineralization in relation to stand type, stand age and soil texture in the boreal mixedwood. Soil Biol. Biochem. 32, 1079–1090.

Crête, M., 1989. Approximation of K carrying capacity for moose in eastern Quebec. Can. J. Zool. 67, 373–380.

Cyr, D., Gauthier, S., Bergeron, Y., Carcaillet, C., 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. Front. Ecol. Environ. 7, 519–524.

Ganguli, A.C., Hale, M.B., Launchbaugh, K.L., 2010. Seasonal change in nutrient composition of spotted knapweed and preference by sheep. Small Rumin. Res. 89, 47–50.

Goulden, M.L., Mcmillan, A.M.S., Winston, G.C., Rocha, A.V., Manies, K.L., Harden, J. W., Bond-Lamberty, B.P., 2011. Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. Glob. Change Biol. 17, 855–871.

Grier, C.C., 1975. Wildfire effects on nutrient distribution and leaching in a coniferous ecosystem. Can. J. Bot. 5, 599–608.

Harden, J.W., Mack, M., Veldhuis, H., Gower, S.T., 2002. Fire dynamics and implications for nitrogen cycling in boreal forests. J. Geophys. Res. 107, 8223.

Harper, K.A., Macdonald, S.E., Karen, A., Ellen, S., 2002. Structure and composition of edges next to regenerating clear-cuts in mixed- wood boreal forest. J. Veg. Sci. 13, 535–546.

Hart, S.A., Chen, H.Y.H., 2006. Understory vegetation dynamics of North American boreal forests. Crit. Rev. Plant Sci. 25, 381–397.

Hart, S.A., Chen, H.Y.H., 2008. Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. Ecol. Monogr. 78, 123–140.

Harvey, B.D., Leduc, A., Gauthier, S., Bergeron, Y., 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. For. Ecol. Manage. 155, 369–385.

Hins, C., Ouellet, J., Dussault, C., St-Laurent, M., 2009. Habitat selection by forest-dwelling caribou in managed boreal forest of eastern Canada: evidence of a landscape configuration effect. For. Ecol. Manage. 257, 636–643.

James, A.R.C., Boutin, S., Hebert, D.M., Rippin, B., 2004. Spatial separation of caribou from moose and its relation to predation by wolves. J. Wildlife Manage. 68, 799–809.

Johnstone, J.F., Chapin, F.S., Hollingsworth, T.N., Mack, M.C., Romanovsky, V., Turetsky, M., 2010. Fire, climate change, and forest resilience in interior Alaska. Can. J. For. Res. 40, 1302–1312.

Kasischke, E.S., Johnstone, J.F., 2005. Variation in groundlayer surface fuel consumption and its effects on site characteristics in a Picea mariana forest complex in Interior Alaska. Can. J. For. Res. 35, 2164–2177.

Kurhy, P., 1994. The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada. J. Ecol. 82, 899–910.

Larter, C., Gates, C., 1991. Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. Can. J. Zool. 69, 2677–2685.

Latombe, G., Fortin, D., Parrott, L., 2014. Spatio-temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. J. Anim. Ecol. 83, 185–198.

LeBauer, D.S., Treseder, K.K., 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89, 371–379.

Lecomte, N., Simard, M., Asselin, H., Nappi, A., Noël, J., Bergeron, Y., 2006. Similarities and differences between harvesting- and wildfire-induced disturbances in fire-mediated Canadian landscapes. Tech. Bull. No. 924. Res. Triangle Park. N.C. Natl. Counc. Air Stream Improv. Inc.

Lecomte, N., Simard, M., Fenton, N., Bergeron, Y., 2007. Fire severity and long-term ecosystem biomass dynamics in coniferous boreal forests of eastern Canada. Ecosystems 9, 1215–1230.

Lee, H., Backowsky, W., Riley, J., Bowles, J., Puddister, M., Uhlig, P., McMurry, S., 1998. Ecological Land Classification for Southern Ontario: First Approximation and its Application. Ontario Ministry of Natural Resources, Southcentral Science Development and Transfer Branch. SCSS Field Guide FG-02.

Long, J.N., 2009. Emulating natural disturbance regimes as a basis for forest management: a North American view. For. Ecol. Manage. 257, 1868–1873.

Mack, M.C., Treseder, K.K., Manies, K.L., Harden, J.W., Schuur, E.A.G., Vogel, J.G., Randerson, J.T., Chapin, F.S., 2008. Recovery of aboveground plant biomass and productivity after fire in mesic and dry black spruce forests of interior Alaska. Ecosystems 11, 209–225.

Magnan, G., Lavoie, M., Payette, S., 2012. Impact of fire on long-term vegetation dynamics of ombrotrophic peatlands in northwestern Québec, Canada. Quat. Res. 77, 110–121.

Mattson, W.J., 1980. Herbivory in relation to plant nitrogen content. Annu. Rev. Ecol. Syst. 11, 119–161.

McCutchen, N.A., 2007. Factors Affecting Caribou Survival in Northern Alberta: The Role of Wolves, Moose, and Linear Features. University of Alberta.

McGreer, M., Mallon, E.E., Vander Vennen, L.M., Wiebe, P.A., Baker, J.A., Brown, G.S., Avgar, T., Hagens, J., Kittle, A.M., Mosser, A., Street, G.M., Reid, D.E.B., Rodgers, A. R., Shuter, J., Thompson, I.D., Turetsky, M.R., Newmaster, S.G., Patterson, B.R., Fryxell, J.M., 2015. Selection for forage and avoidance of risk by woodland caribou (*Rangifer tarandus caribou*) at coarse and local scales. Ecosphere 6, 288.

McLoughlin, P.D., Dunford, J.S., Boutin, S., 2005. Relating predation mortality to broad-scale habitat selection. J. Anim. Ecol. 74, 701–707.

McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J., Woodley, S., 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. Environ. Rev. 9, 223–260.

Moore, T.R., Basiliko, N., 2006. Decomposition in boreal peatlands. In: Wieder, R.K., Vitt, D.H. (Eds.), Boreal Peatland Ecosystems. Springer Verlag, Berlin, pp. 125–143.

Newmaster, S.G., Thompson, I.D., Steeves, R.A.D., Rodgers, A.R., Fazekas, A.J., Maloles, J.R., Mcmullin, R.T., Fryxell, J.M., 2013. Examination of two new technologies to assess the diet of woodland caribou: video recorders attached to collars and DNA barcoding. Can. J. For. Res. 43, 897–900.

OMNR, 2010. Ontario's woodland caribou conservation plan [WWW Document]. Gov. Ontario. <http://files.ontario.ca/environment-and-energy/species-at-risk/277783.pdf> (accessed 1.6.15).

OMNR, 2011. Harvesting in the boreal forest [WWW Document]. Gov. Ontario. <http://www.pellet.org/images/Harvesting_in_the_Boreal_Forest.pdf> (accessed 1.6.15).

Reich, P.B., Bakken, P., Carlson, D., Frelich, L.E., Friedman, S.K., Grigal, D.F., 2001. Influence of logging, fire, and forest type on biodiversity and productivity in southern boreal forests. Ecology 82, 2731–2748.

Rettie, W.J., Messier, F., 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. Can. J. Zool. 76, 251–259.

Rettie, W.J., Messier, F., 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography (Cop.) 23, 466–478.

Riley, J.L., Michaud, L., 1994. Ontario Peatland Inventory: Field-Work Methods. Ontario Geol. Surv. Misc. Pap. 155, pp. 62.

Rydgren, K., Økland, R.H., Hestmark, G., 2004. Disturbance severity and community resilience in a boreal forest. Ecology 85, 1906–1915.

SAS Institute Inc., 2008. SAS Version 9.2. SAS Institute, Cary, North Carolina, USA.

Schaefer, J.A., 2003. Long-term range recession and the persistence of caribou in the taiga. Conserv. Biol. 17, 1435–1439.

Shrestha, B.M., Chen, H.Y.H., 2010. Effects of stand age, wildfire and clearcut harvesting on forest floor in boreal mixedwood forests. Plant Soil 336, 267–277.

Simard, D.G., Fyles, J.W., Paré, D., Nguyen, T., 2001. Impacts of clearcut harvesting and wildfire on soil nutrient status in the Quebec boreal forest. Can. J. Soil Sci. 81, 229–237.

Sims, R.A., Towill, W., Baldwin, K.A., Uhlig, P., Wickware, G.M., 1997. Field guide to the forested ecosystem classification for northwestern Ontario. Ontario Ministy of Natural Resources, Northwest Sci. and Technol., Thunder Bay.

Smithwick, E.a.H., Turner, M.G., Mack, M.C., Chapin, F.S., 2005. Postfire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. Ecosystems 8, 163–181.

Stuart-Smith, A.K., Bradshaw, C.J.A., Boutin, S., Hebert, D.M., Rippin, B., 1997. Woodland caribou relative to landscape patterns in northeastern Alberta. J. Wildlife Manage. 61, 622–633.

Taylor, K.C., Arnup, R.W., Merchant, B.G., Parton, W.J., Nieppola, J., 2000. Field Guide to the Forest Ecosytems of Northeastern Ontario, second ed. Ontario Ministy of Natural Resources, Northwest Sci. and Technol., Thunder Bay.

Thompson, I., Mackey, B., McNulty, S., Mosseler, A., 2009. Forest Resilience, Biodiversity, and Climate Change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems. Secretariat of the Convention on Biological Diversity, Montreal. Technical Series no. 43, 67 pages.

Thompson, I.D., Wiebe, P., Mallon, E., Rodgers, A.R., Fryxell, J.M., Baker, J., Reid, D., 2015. Factors influencing the seasonal diet selection by woodland caribou in boreal forests in Ontario. Can. J. Zool. 98, 87–98.

Thornley, J.H.M., Cannell, M.G.R., 2004. Long-term effects of fire frequency on carbon storage and productivity of boreal forests: a modeling study. Tree Physiol. 24, 765–773.

Turetsky, M.R., Amiro, B.D., Bosch, E., Bhatti, J.S., 2004. Historical burn area in western Canadian peatlands and its relationship to fire weather indices. Global Biogeochem. Cycles 18.

Turetsky, M.R., Benscoter, B., Page, S., Rein, Guillermo, van der Werf, Guido R., Watts, A., 2015. Global vulnerability of peatlands to fire and carbon loss. Nat. Geosci. 8, 11–14. http://dx.doi.org/10.1038/ngeo2325.

Turetsky, M.R., Kane, E.S., Harden, J.W., Ottmar, R.D., Manies, K.L., Hoy, E., Kasichke, E.S., 2011. Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. Nat. Geosci. 4, 27–31.

Turetsky, M.R., Mack, M.C., Hollingsworth, T.N., Harden, J.W., 2010. The role of mosses in ecosystem succession and function in Alaska's boreal forest. Can. J. For. Res. 40, 1237–1264.

Turner, M.G., Smithwick, E.A.H., Metzger, K.L., Tinker, D.B., Romme, W.H., 2007. Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone ecosystem. Proc. Natl. Acad. Sci. USA 104, 4782–4789.

Van Beest, F.M., Mysterud, A., Loe, L.E., Milner, J.M., 2010. Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. J. Anim. Ecol. 79, 910–922.

Van Dyke, F., Darragh, J.A., 2007. Response of elk to changes in plant production and nutrition following prescribed burning. J. Wildlife Manage. 71, 23–29.

Vors, L.S., Schaefer, J.A., Pond, B.A., Rodgers, A.R., Patterson, B.R., 2007. Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. J. Wildlife Manage. 71, 1249–1256.

Wittmer, H.U., McLellan, B.N., Serrouya, R., Apps, C.D., 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. J. Anim. Ecol. 76, 568–579.

Zoltai, S.C., Morrissey, L.A., Livingston, G.P., De Groot, W.J., 1998. Effects of fires on carbon cycling in North American boreal peatlands. Environ. Rev. 6, 13–24.