



Assessing temporal response to biomass removal: A framework for investigating evolving constraints on boreal stand development

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ABSTRACT

Impacts of harvest intensity and soil disturbance on site productivity are likely to vary with stand development stage and interactive processes related to ecosystem function. On upland boreal sites, stand productivity may initially be constrained by microclimatic conditions. However, increasing nutrient demands and overstory light interception associated with canopy development may place progressively greater emphasis on nutrient availability, profile water storage capacity and asymmetric competition. We illustrate these effects using 20-yr post-harvest data from fourteen jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) BSP) Long-term Soil Productivity (LTSP) installations in northern Ontario.

Initial growth and ten-year survival were as great or greater without forest floors (NFF), but by year 15 dominant height increments were usually greater with intact forest floors (FF). Growing season frost occurrence and high vapor pressure deficits occurred more frequently with FF than NFF treatments during the initial stand establishment phase. Similarly, mean growing season soil temperatures were 2–5°C warmer with NFF during this phase, with stand Leaf Area Index (LAI) values < 0.5. During the following Accelerated Growth phase, treatment differences in microclimate dissipated as LAI increased. Foliar N concentrations and N:P ratios, and soil net N mineralization were usually greater from an early age with FF, and often declined as canopy closure approached. Likewise, modelled site-level constraints related to soil water availability increased with stand development, peaking at LAI values associated with the stem exclusion stage. Placing post-harvest response (i.e., impacts of harvest intensity) in the context of relationships among stand structural development, changes in microclimate, and resource supply and demand should provide greater insights into longer-term effects of establishment practices.

1. Introduction

Conceptual models of forest ecosystem development that incorporate stand dynamics and ecological processes provide a good basis for assessing temporal responses to stand-replacing disturbance. In particular, linking disturbance severity (Roberts, 2007) and pulse dynamics (Jentsch and White, 2019) with stages of stand structural development (Chen and Popadiouk, 2002; Franklin et al., 2002) and phases of ecosystem function that encompass variations in resource availability, energetics and ecosystem organization (Vitousek and Reiners, 1975; Switzer, 1978; Bormann and Likens, 1979; Holling, 1986) provides an integrative framework for evaluating forestry practices (Fig. 1). Harvest intensity and related regeneration treatments often have different impacts on seedling establishment and initial nutrient availability than on

longer-term growth, nutrient reserves and site productivity. Here we outline such a framework based on existing models and use it to explore temporal impacts of harvest-related organic matter removal on forest productivity over the first 20 years at fourteen boreal Long-term Soil Productivity (LTSP – Powers, 2006) installations in northern Ontario.

With even-aged forest management, temporal stages of stand development commonly include: i) Disturbance and Legacy Creation, ii) Stand Initiation, iii) Canopy Closure, iv) Stem Exclusion, and in some cases, v) Understory Re-initiation/Canopy Transition (Chen and Popadiouk, 2002; Franklin et al., 2002) (Fig. 1). The brief Disturbance and legacy Creation stage addresses the importance of previous stand conditions and disturbance severity on biological legacies associated with propagule abundance, carbon sources (e.g., forest floor mass, coarse woody debris (CWD) and logging residues) and nutrient retention

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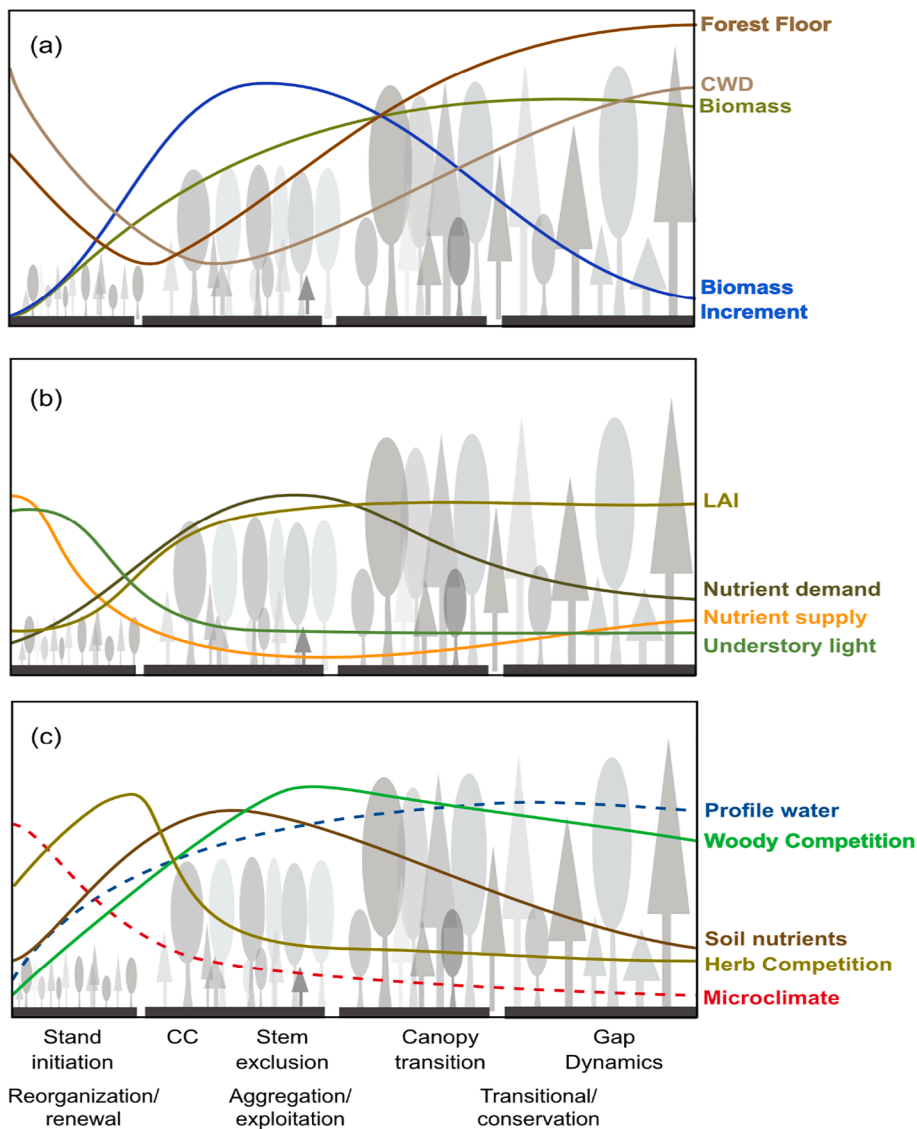


Fig. 1. Conceptual diagram depicting temporal patterns of relative stand-level a) above-ground biomass and biomass increment, forest floor mass and coarse wood debris (CWD); b) soil nutrient supply and tree nutrient demand, leaf area index (LAI) and understory light; and c) microclimate, soil nutrient and profile soil water limitations, together with woody and herbaceous competition. Also shown are associated stand development stages, including canopy closure (CC) (Chen and Popadiouk, 2002; Franklin et al., 2002), and ecosystem phases (Bormann and Likens, 1979; Holling, 1986).

(Roberts, 2007; Franklin et al., 2002). With clearcut harvesting, large quantities of carbon and nutrients bound in accumulated biomass become available. These resources are rapidly mobilized through decomposition and mineralization, and subsequently retained (to varying degrees) by soils, microbes and developing vegetation during the Stand Initiation stage which immediately follows. Together, these two stand development stages encompass the Reorganization phase of Bormann and Likens (1979) and the Renewal phase of Holling (1986).

The Stand Initiation stage consists of an Initial Establishment phase during which young seedlings are particularly susceptible to biotic and abiotic stresses (Johnson et al., 2011), followed by an Accelerated Growth (Free-to-Grow) phase where nutrient demands increase and intraspecific competition begins (Mason et al., 2012). Small planted seedlings initially have limited nutrient demands (Salifu and Timmer, 2003), while the post-disturbance “assart” flush often provides sizeable quantities of available nutrients through decomposition of litter, fine woody slash and roots, and dying understory vegetation (Fig. 1b) (Vitousek and Walker, 1987; Bradley et al., 2002). As stand establishment proceeds, nutrient demands increase while the post-disturbance nutrient flush is dissipating (Vitousek and Walker, 1987; Allen et al., 2001) and the developing canopy increasingly intercepts available energy (solar radiation). Thus treatment effects on microclimatic conditions and herbaceous competition may have large initial impacts, but

diminishing effects as crown closure approaches (Mason and Milne, 1999; Proe et al., 2001).

The Canopy Closure stage marks the transition from open- to closed forest conditions and the subsequent attainment of maximum LAI (Landsberg and Gower, 1997). At this point treatment-induced nutrient and understory light limitations are likely to peak (Miller, 1981, 1995) (Fig. 1c). The stages from Legacy Creation through to Canopy Closure, are often where disturbance-related impacts on ecosystem development exert their greatest influence (Allen et al., 1990; Miller, 1995).

The subsequent Stem Exclusion stage is characterized by rapid biomass accumulation, intense inter-tree competition, and density-related mortality as well as increasingly organized and tightly connected system components (e.g., the Aggregation or Exploitation phase of Bormann and Likens (1979) and Holling (1986), respectively). Stand nutrient demands are increasingly met through the recoupling of internal nutrient cycles, supposedly placing less demand on soil nutrient reserves (Switzer, 1978; Miller, 1995). This stage lasts through to maturity, or initiation of the Understory Re-initiation/Canopy Transition stage - the Transitional phase of Bormann and Likens (1979) and the Conservation phase of Holling (1986). At this point, canopy dominants start to senesce, reducing crown competition, and allowing shade-tolerant species to penetrate the overstory canopy (e.g., Chen and Popadiouk, 2002).

Table 1

General stand and soil characteristics of the study installations. Mineral soil depths exceeded 100 cm at all installations except Fensom 1–3 which had shallow soils over Precambrian bedrock).

Installation	Region/ Site Type ¹	Stand Age/Site index (m)	Stand Makeup ²	O horizon ³ / mineral soil depth (cm)	B horizon texture ⁴	C horizon texture	Water Holding Capacity ⁵ (mm)	Moisture Regime ⁶	Soil C Mg/ha O horizon/ mineral soil	Soil N kg/ha O horz/ min ⁶	Species/ soil group ⁷
Eddy1	NE jP-Si _{LH}	92/20.5	jP ₇ bS ₂ wB ₁	9/>100	23/72/5 SiL	LS	120.3	Moist	25/40		jP SiL _H
Eddy 2	NE jP-Si _{LH}	97/17.1	jP ₆ bS ₄	8/>100	20/75/5 SiL	LS	124.2	Mod. Moist	29/31		jP SiL _H
Eddy 3	NE jP-LS _L	71/15.9	jP ₁₀	6/>100	85/10/5 LS	mS-cS	72.0	Mod. Fresh	20/24	575/ 1637	jP LS _L
Eddy 4	NE jP-LS _L	71/17.3	jP ₉ tA ₁	6/>100	70/25/5 SiS	mS	85.7	Mod. Fresh	21/31	568/ 1392	jP LS _L
Nimitz ⁷	NE jP-Si _{SM}	68/18.8	jP ₉ bS ₁	9/>100	45/50/5 SiL	LS-mS	130.2	Mod. Fresh	25/25		jP SiS _M
Superior 1	Ne jP-Si _{SM}	65/17.4	jP ₇ bS ₃	6/>100	66/29/5 SiS	fS-mS	94.2	Mod. Fresh	27/32	773/ 1722	jP SiS _M
Superior 2	NE jP-Si _{SM}	75/16.9	jP ₁₀	5/>100	54/42/4 SiS	mS-cS	91.7	Mod. Fresh	24/27	570/ 1466	jP SiS _M
Superior 3	NE jP-Si _{SM}	82/18.5	jP ₉ bS ₁	3/>100	56/40/4 SiS	fS	110.4	Fresh	35/22	927/ 1969	jP Si
Wells	NE jP-Si _{SH}	57/20.7	jP ₈ wS ₁ rP ₁	6/>100	69/30/1 SiS	cS	65.2	Mod. Dry	23/37	591/ 1978	jP SiS _H
Geraldton	NW bS-LS _M	115/16.6	bS ₆ jP ₄	14/>100	90/5/5 fS	mS	61.9	Mod. Fresh	30/36	700/ 550	bS LS _M
Supawn1	NW bS- LS _M	123/14.1		11/>100	95/2/3 mS	cS	47.6	Mod. Dry	28/20	587/ 564	bS LS _M
Fensom 1	NW bS- Si _{Lsh}	105/18.3	bS ₇ jP ₃	7/20–30	42/46/12 SiL	NA	56.6	Mod. Fresh	30/26	624/ 975	bS SiL _{sh}
Fensom 2	NW bS- Si _{Lsh}	105/15.2	Sb ₇ Pj ₃	11/20–30	41/47/12 SiL	NA	74.1	Mod. Fresh	49/47	1142/ 1714	bS SiL _{sh}
Fensom 3	NW bS-Si _{Lsh}	105/15.3	bS ₁₀	11/20–30	48/42/10 L	NA	57.1	Mod. Fresh	40/31	813/ 1271	bS SiL _{sh}

¹ NE – northeastern Ontario, NW – northwestern Ontario, Group symbols indicate predominant species, followed by soil texture, with subscripts indicating relative stand productivity (H – high, M – medium, L – low), or mineral soil depth (sh – shallow (~30 cm): jP-Si_{LH} – jack pine silt loam, high productivity; jP-Si_{SH} – jack pine silty sand, high productivity; jP-Si_{SM} – jack pine silty sand, medium productivity; jP-LS_L – jack pine loamy sand, low productivity; bS-Si_{Lsh} – black spruce silt loam, shallow soil; bS-LS_M – black spruce loamy sand, medium productivity.

² jP – jack pine, bS – black spruce, tA – trembling aspen, rP – red pine, wS – white spruce. Subscript numbers refer to pre-harvest stand composition, by basal area, in 10% increments.

³ combined LFH horizons, following the Canadian System of Soil Classification.

⁴ L = loam, LS = loamy sand, Si = silt, SiL = silt loam, cS = coarse sand, fS = fine sand, mS = medium sand, SL = sandy loam. A horizons were usually < 5 cm thick.

⁵ Rawls et al. (2003), Saxton and Rawls (2006), Nemes et al. (2011) – 100 cm depth, except Fensom 1–3.

⁶ Ontario Centre for Soil Resource Evaluation (1993).

⁷ Not analyzed for foliar nutrition or dominant height because of missing year 5 measurements

The largest impacts of stand-replacing disturbance on forest ecosystem function often occur during the Renewal/Reorganization phase when system dynamics are open, and during the Aggregation/Exploitation phase when temporal trajectories are being established. During these two phases pulse dynamics, in terms of the magnitude, rate and duration of resource change, as well as their impacts on resource assimilation (Jentsch and White, 2019) are often most evident. With the onset of the Stem Exclusion stage, ecosystem resources and stand development trajectories are increasingly entrained (Holling, 1986; Newton, 2015), and harvest-related impacts on nutrient availability may abate with forest floor build-up and nutrient inputs from atmospheric deposition, nitrogen fixation and mineral weathering (Vitousek et al., 1998). Thus treatment effects on stand-level site productivity may diminish, while broader site-level constraints become increasingly important. Among the latter, climate, species composition, nutrient capital and cycling, and soil water storage capacity are commonly identified (Van Cleve et al., 1983; Augusto et al., 2015). However, treatment effects that include large changes in rates of resource accumulation, niche characteristics or species traits that may also become entrained, can lead to altered ecosystem trajectories (Payette and Delwaide, 2003; Royo and Carson, 2006; Turner, 2010).

These patterns and processes suggest that developing stands pass through different phases of primary resource constraints, reflecting both

changes in limiting conditions and in plant requirements. In boreal forest ecosystems, the forest floor often represents a substantial portion of the total site nutrient capital, and through microbial processes governing decomposition and mineralization, plays a key role in site productivity. However, thick O horizons also immobilize nutrients, alter microclimate conditions and impede natural regeneration (Weetman, 1980; Prescott et al., 2000). Thus stand establishment is often favored by removing logging debris and surface organic horizons (Örlander et al., 1990). Such treatments can increase growing season soil temperatures (Balisky and Burton, 1997; Ballard, 2000), mitigate air temperature extremes (Fleming et al., 1998; Proe et al., 2001), reduce competition (Thiffault et al., 2013), and stimulate microbial activity (decomposition and mineralization), thus increasing nutrient availability (Johansson, 1994; Prescott et al., 2000; Tan et al., 2005).

As the trees grow larger, stand leaf area index (LAI) builds, moderating near-surface microclimates while increasing soil nutrient demands for foliage production at a time when the nutrient assart flush is dissipating (Vitousek and Walker, 1987; Miller, 1995; Bradley et al., 2002). Thus with the approach of canopy closure and maximum LAI, treatment-induced nutrient limitations associated with forest floor removal may become increasingly evident (Miller, 1981; Jurgensen et al., 1997) and override the initial benefits provide by favourable microclimate conditions (Fig. 1c). Still longer-term benefits in terms of soil structure, water

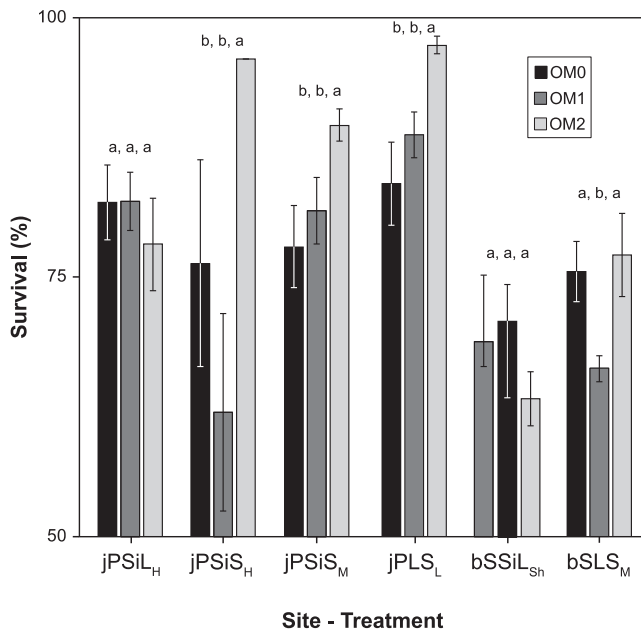


Fig. 2. Tenth year planted tree survival, by OM treatment, for six species - site type combinations covering a range of inherent productivity (_H - high, _M - medium, _L - low, _{Sh} - shallow soil over bedrock) (Table 1). Significant treatment differences ($p < 0.10$) for a given site type are indicated by different lower-case letters at the top of the diagram.

holding capacity, cation exchange and nutrient availability may accrue from the gradual decomposition of coarse woody debris (Fahey and Knight, 1986; Krankina et al., 1999; Brais et al., 2006; Wiebe et al., 2014) despite the fact that nutrient requirements are increasingly met by internal translocation (Miller, 1981).

Here we explore the utility of this conceptual framework in addressing impacts of biomass removal intensity using 20 years of post-harvest data from a range of boreal jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) BSP) LTSP installations. In particular, we examine whether:

1. Microclimate conditions were ameliorated with forest floor removal, with impacts attenuating as the new stands developed.
2. Forest floor removal initially benefited stand establishment but subsequently reduced stand growth;
3. There was evidence of changes in stand productivity related to harvest intensity as Canopy Closure approached.
4. Reductions in nutrient availability and foliar nutrition associated with increased biomass removal became increasingly apparent;
5. Soil N mineralization and foliar nutrition peaked within the first few post-harvest years and was consistently greater with intact forest floors.
6. Responses varied between species or among site types.

2. Materials and methods

2.1. Installation descriptions and experimental design

In 1993–1994 the Canadian Forest Service and the Ontario Ministry of Natural Resources established LTSP experiments on a variety of northern Ontario jack pine (Tenhagen et al., 1996) and black spruce (Duckert and Morris, 2001) site types. For this analysis, we are using data from fourteen installations, covering a range of site productivity and characteristic upland coarse-textured soils derived from Precambrian bedrock (Table 1). Many such site types are nitrogen-limited and considered “sensitive” to biomass removal because a high proportion of ecosystem nutrients reside in the vegetation and forest floor (Foster

et al., 1995; Morris, 1997). In this region, the climate is boreal, with growing seasons of 160–190 days, 1050–1500 growing degree days per year, and 700–1000 mm of annual precipitation, about half of which falls during the growing season (Mackey et al., 1996).

We examined three biomass removal treatments, each replicated three times per installation: 1) operational tree-length harvest followed by planting-spot preparation by boot-screefing (black spruce) or disc trenching (jack pine) (nominal OM0); 2) operational full tree harvest followed by similar planting-spot preparation (nominal OM1); and 3) full-tree harvest followed by forest floor and up to 5 cm of topsoil removal by blading (nominal OM2). In some previous papers (e.g., Fleming et al., 2014, 2018; Morris et al., 2019) these treatments have been referred to as SO, FT or WT, and FTB, respectively. Given similar treatment effects with the OM0 and OM1, we often refer to them together as FF (forest floor intact) in comparison with NFF (the OM2 treatment with no forest floor). Following harvest, all installations were planted with 1–0 containerized stock at 2×2 m spacing the following spring. The jack pine plots considered here were sprayed with herbicide (glyphosate at 5 L ha^{-1}) beginning at year 2, to remove competing vegetation either once (six installations) or, using a split-plot design, 3 times, beginning at year 2 (4 installations) (Table 1). No herbicide was applied at the black spruce installations but trees were manually released from overtopping woody species, and otherwise competition was not sufficient to have marked impacts on stand development.

2.2. Field sampling and laboratory analysis

2.2.1. Stand development

Fall assessments of tree survival and dominant height (H_D) were made at four to six year intervals at all installations from 1998 to 2013. H_D was calculated as the average height of the tallest quartile of planted trees in a given plot, and periodic dominant height increment (H_{Dinc}) was calculated on a normalized five-year basis. We chose H_D and H_{Dinc} as the stand productivity metrics because of their common usage as density-independent measures of site productivity (Burkhart and Tomé, 2012; Newton, 2015) and their applicability before full stocking/canopy closure is reached. We also used H_D rather than years since harvest as a temporal metric to graphically depict stand development stage because tree size and stand density rather than stand age largely govern tree physiological responses, stand structural development and ecosystem processes (Enquist, 2002; Steppe et al., 2011; Alexandrov and Golitsyn, 2015).

Finally, to account for inherent non-linear stand development trends we also calculated site-level differences in H_D time gain for the OM0 and OM1 vs. the OM2. In our case, the time gain refers to the difference in time (years) for the OM0 and OM1 to reach a similar size/development stage as the OM2 (South et al., 2006). For this, we first fit polynomial H_D equations to stand age for each treatment at a given installation, and rearranged the equations to predict age at a given H_D . We then inserted the parameters of the OM0 and OM1 age - H_D equations into the corresponding OM2 equations, and used the resulting values, together with the mean OM2 H_D values, to calculate the time gains at years 5, 10, 15 and 20. For illustrative purposes, we combined values for the OM0 and OM1 because they produced similar results.

2.2.2. Microclimate

At Nimitz we continuously measured 10 cm soil temperatures with copper-constantan thermocouples and 15 cm air temperatures with 0.013 cm fine-wire thermocouples at two locations per treatment replicate during the 1994–2001 growing seasons. At Wells, similar soil temperature measurements were made in one plot per treatment during the 1994–2006 growing seasons. At Fensom1, soil temperature was measured throughout the 1995–2008 growing seasons at four locations in one plot per treatment, using similar probes as above. One-sided plot-level leaf area index (LAI) was estimated using local dbh-based individual tree needle mass - leaf area allometric relationships.

Table 2

Mixed model ANOVAs of treatment and stand age effects on jack pine dominant height (H_D) and its five-year increment (H_{Dinc}), by site type. Shown are F values, numerator and denominator degrees of freedom (df - numerator/denominator) and p values. Treatment polynomial contrasts consisted of OMO, OM1 vs. OM2; and OM0 vs. OM1; stand age effects were evaluated using linear, quadratic and cubic polynomial contrasts. GLM ANOVA results of treatment effects at particular post-harvest years are also presented. P -values < 0.10 are shown in bold; NS (not significant); contrast p -value > 0.10.

Metric; Site Type	Statistic	Treatment (T) ANOVA (<i>F</i> , df, <i>p</i>)	Stand Age (A) ANOVA (<i>F</i> , df, <i>p</i>)	T × A ANOVA (<i>F</i> , df, <i>p</i>)	Treatment Effects by Post-harvest Year			
		Orthogonal contrasts (<i>p</i> < 0.10)	<i>p</i> - linear-cubic contrasts		Year 5	Year 10	Year 15	Year 20
H _{Dinc} ; All Sites n = 9	ANOVA	12.68 2/14 0.001	23.56 3/21 < 0.001	5.13 6/42 < 0.001	0.20 0.849	0.61 0.557	12.55 0.001	8.82 0.003
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.861) > OM2 (<i>p</i> < 0.001)	< 0.001 , < 0.001 , 0.007 - cubic		NS	NS	OM0 = OM1 (<i>p</i> = 0.345) > OM2 (<i>p</i> < 0.001)	OM0 = OM1 (<i>p</i> = 0.761) > OM2 (<i>p</i> = 0.001)
H _D ; All Sites n = 9	ANOVA	6.73 2/14 0.009	820.4 3/21 < 0.001	13.8 6/42 < 0.001	0.20 0.849	0.55 0.588	6.61 0.010	12.68 0.001
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.864) > OM2 (<i>p</i> = 0.003)	< 0.001 , 0.854, 0.957 – linear		NS	NS	OM0 = OM1 (<i>p</i> = 0.674) > OM2 (<i>p</i> = 0.002)	OM0 = OM1 (<i>p</i> = 0.861) > OM2 (<i>p</i> < 0.001)
H _{Dinc} ; SiL _H n = 2	ANOVA	1.63 2/2 0.380	19.88 3/3 0.018	1.11 6/6 0.453	0.22 0.822	2.11 0.322	1.26 0.443	1.11 0.473
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.676) = OM2 (<i>p</i> = 0.224)	0.258, 0.005 , 0.306 – quadratic		NS	NS	NS	NS
H _D ; SiL _H n = 2	ANOVA	0.29 2/2 0.788	672.0 3/3 < 0.001	1.50 6/6 0.318	0.22 0.822	0.13 0.885	0.35 0.743	1.63 0.308
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.581) = OM2 (<i>p</i> = 0.740)	< 0.001 , 0.046 , 0.381 – quadratic		NS	NS	NS	NS
H _{Dinc} ; SiS _H n = 1	ANOVA	0.83 2/6 0.481	24.56 3/6 < 0.001	1.08 6/18 0.408	1.47 0.308	1.43 0.311	2.56 0.157	0.35 0.719
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.402) = OM2 (<i>p</i> = 0.395)	< 0.001 , < 0.001 , 0.024 – cubic		NS	NS	NS	NS
H _D ; SiS _H n = 1	ANOVA	0.34 2/6 0.728	1691 3/6 < 0.001	0.240	1.47 0.308	2.24 0.187	0.30 0.749	0.83 0.482
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.565) = OM2 (<i>p</i> = 0.604)	< 0.001 , 0.511, 0.922 – linear		NS	OM2 > OM0, OM1	NS	NS
H _{Dinc} ; SiS _M n = 3	ANOVA	38.71 2/4 0.002	14.88 3/6 0.003	2.11 6/12 0.128	3.19 0.149	10.92 0.024	10.21 0.027	8.52 0.036
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.650) > OM2 (<i>p</i> = 0.001)	0.003 , 0.010 , 0.036 - cubic		NS	OM0, OM1 > OM2	OM0, OM1 > OM2	OM0, OM1 > OM2
H _D ; SiS _M n = 3	ANOVA	28.6 2/4 0.004	722.0 3/6 < 0.001	25.9 6/12 < 0.001	3.19 0.149	10.22 0.027	22.47 0.007	38.7 0.002
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.502) > OM2 (<i>p</i> = 0.002).	< 0.001 , 0.742, 0.507 - linear		NS	OM0, OM1 > OM2	OM0, OM1 > OM2	OM0, OM1 > OM2
H _{Dinc} ; LS _L 2 = 2	ANOVA	1.71 2/2 0.369	6.47 3/3 0.080	1.70 6/6 0.267	1.41 0.415	0.07 0.933	21.38 0.045	0.91 0.524
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.947) = OM2 (<i>p</i> = 0.206)	0.303. 0.036 , 0.119 – quadratic		NS	NS	OM0, OM1 > OM2	NS
H _D ; LS _L n = 2	ANOVA	1.17 2/2 0.460	1144 3/3 < 0.001	2.42 6/6 0.154	1.41 0.415	0.17 0.851	2.31 0.302	1.71 0.369
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.775) = OM2 (<i>p</i> = 0.273)	< 0.001 , 0.079 , 0.710 – quadratic		NS	NS	NS	NS

2.2.3. Soil-surface CO₂ efflux

Measurements and calculated response functions for soil surface CO₂ efflux at Wells for post-harvest years 3–5 are reported in Fleming et al. (2006). We combined the resulting functions with daily soil temperature measurements and Drought Code values (Van Wagner, 1987) (a surrogate for soil moisture availability) to estimate post-harvest growing season trends in CO₂ efflux for each treatment. Given the similarity in soil surface CO₂ efflux response for the OM0 and OM1, these two treatments were pooled for analysis. The portion of soil surface CO₂ efflux attributable to seedling root respiration, and by subtraction, to heterotrophic respiration, in each treatment was estimated using local allometric relationships for coarse root biomass, fine root biomass estimates based on Steele et al. (1997), and the jack pine temperature-dependent fine and coarse root respiration response functions of Ryan et al. (1997).

2.2.4. Tree and soil nutrition

We concentrated on nitrogen nutrition because of it is widely considered the most common element limiting forest growth in northern ecosystems (Vitousek and Howarth, 1991). Fall current-year foliage was collected from the upper crowns of 9–15 dominant or codominant jack pine or black spruce trees per treatment replicate at years 4–5, 10, 15 and 20. Samples were bulked and needle weights were measured after drying at 70 °C for 24 h. N concentrations (N_{conc}) were determined using a nitrogen-carbon-sulphur combustion analyser (Vario EL III, Ekmentar Americas Inc., Mt. Laurel, NJ) for jack pine and a semi-micro Kjeldahl procedure (Tecator Kjeltac Auto 1030 Analyzer) for black spruce. P concentrations were determined by ICP following microwave digestion with Nitric Acid (Kalra and Maynard, 1991). We interpreted results in terms of general criteria for adequate N_{conc} : ≥ 10 g kg⁻¹ for black spruce and ≥ 1.2 g kg⁻¹ for jack pine (Weetman and Fournier, 1984; Thiffault et al., 2006), and an N:P ratio ($N:P$) ≥ 10 for both species (Knecht and Göransson, 2004).

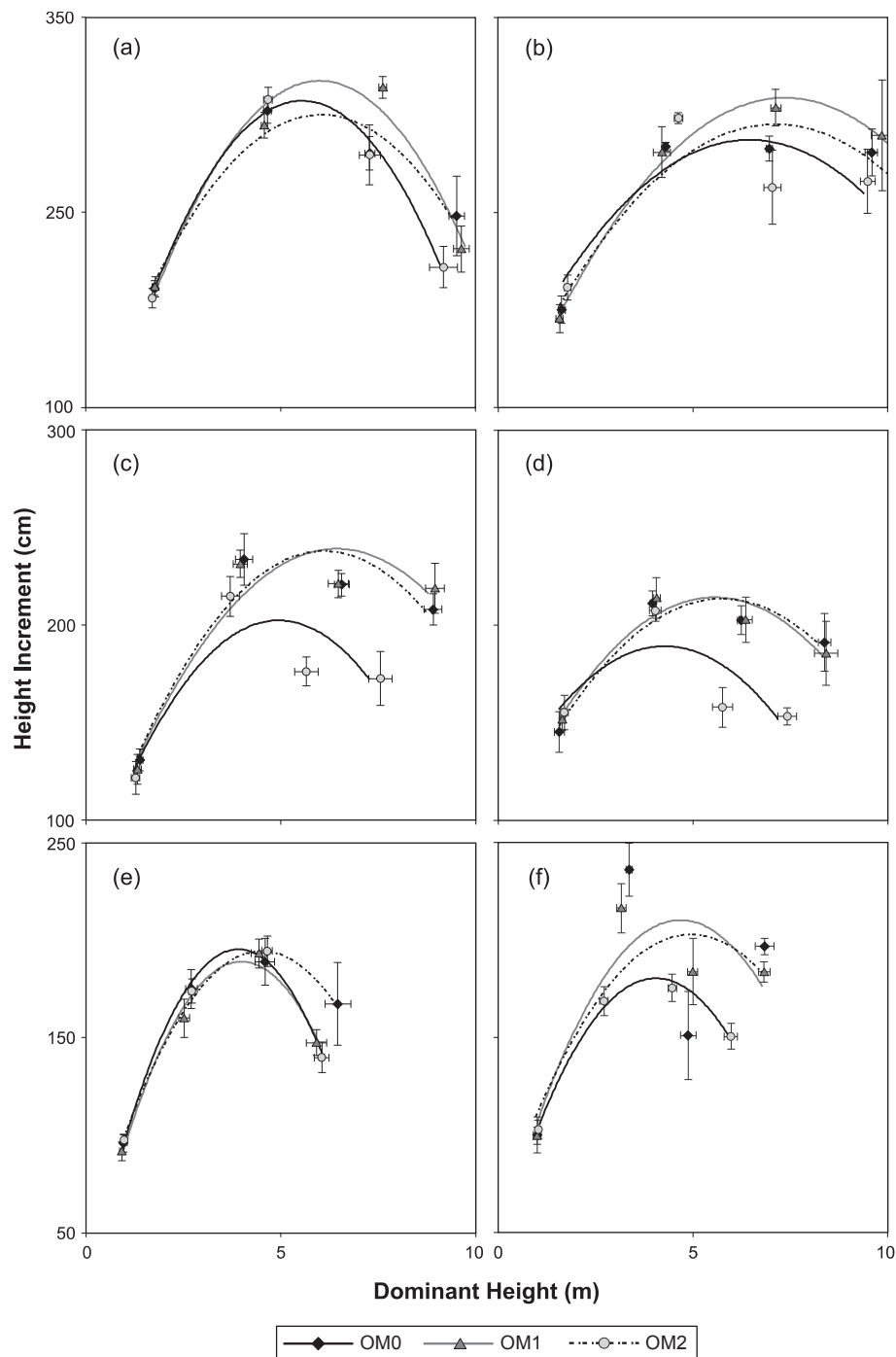


Fig. 3. Temporal trends in OM0, OM1 and OM2 dominant height increment (H_{Dinc}) as a function of biological age as depicted by dominant height (H_D). Shown are mean values (\pm standard errors) together with quadratic functions depicting general trends for the six species–site type combinations: a) jP-SiL_H, b) jP-SiS_H, c) jP-SiS_M, d) jP-LS_L, e) bS-SiL_S and f) bS-LS_M. Responses at post-harvest years 5, 10, 15 and 20 are discernable from treatment $\cdot H_D$ trajectories.

Aerobic net N mineralization was determined at Wells using 90-day *in situ* incubations with closed top cores following Raison et al. (1987), whereas anaerobic mineralizable N was measured at Fensom 1–3 using techniques outlined by Powers (1980). Both techniques are described in detail by Hazlett et al. (2021). At Wells in early June of post-harvest years 5, 10, 14 and 20, pairs of 30-cm-long, 5.1-cm-diameter PVC piping were driven into the soil at 7–10 locations per plot. One core of each pair was removed immediately for analysis, while the other was covered with a rubber stopper and left to incubate for 90 days. In the laboratory, core contents were separated into forest floor, 0–10 cm and 10–20 cm mineral soil layers, sieved and then homogenized. Moisture

contents were determined gravimetrically after heating at 110°C for 24 h, while separate subsamples were extracted using 1 N KCl. NH_4^+ -N, and NO_3^- -N were determined by Technicon autoanalyzer IIC. Accumulation or depletion of NO_3^- -N and NH_4^+ -N was calculated by subtracting initial from final concentrations. Profile net N mineralization was calculated as the product of plot level concentration change and soil mass for that depth.

For the black spruce installations, soil sampling for anaerobic laboratory incubations in post-harvest years 10, 17 and 20 involved nine forest floor and 0–20 cm mineral soil samples collected from each treatment replicate and bulked for analysis. In the laboratory, forest

Table 3

Mixed model ANOVAs of treatment and stand age effects on black spruce dominant height (H_D) and its five-year increment (H_{Dinc}), by site type. Shown are F values, numerator and denominator degrees of freedom (df - numerator/denominator) and p values. Treatment polynomial contrasts consisted of OMO, OM1 vs. OM2; and OM0 vs. OM1; stand age effects were evaluated using linear, quadratic and cubic polynomial contrasts. GLM ANOVA results of treatment effects at particular post-harvest years are also presented. P -values < 0.10 are shown in bold; NS (not significant); contrast p -value > 0.10.

Metric; Site Type	Statistic	Treatment (T) ANOVA (<i>F</i> , df, <i>p</i>) Orthogonal contrasts (<i>p</i> < 0.10)	Stand Age (A) ANOVA (<i>F</i> , df, <i>p</i>) <i>p</i> - linear-cubic contrasts	T × A ANOVA (<i>F</i> , df, <i>p</i>)	Treatment Effects by Post-harvest Year			
					<i>F</i> , <i>p</i>	Year 5	Year 10	Year 15
H _{Dinc} ; All Sites n = 5	ANOVA	1.69 2/8 0.244	43.1 3/12 < 0.001	3.22 6/24 0.018	0.548 0.675	1.44 0.293	1.61 0.258	7.86 0.013
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.578) = OM2 (<i>p</i> = 0.118)	< 0.001 , < 0.001 , 0.099) - cubic		NS	NS	NS	OM0, OM1 > OM2
H _D ; All Sites n = 5	ANOVA	1.18 2/8 0.356	1546 3/12 < 0.001	3.50 6/24 0.013	0.29 0.755	0.78 0.489	0.32 0.734	3.33 0.089
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.421) = OM2 (<i>p</i> = 0.234)	< 0.001 , 0.130, 0.317 – linear		NS	NS	NS	OM0, OM1 > OM2
H _{Dinc} ; SiL _{Sh} n = 3	ANOVA	0.92 2/4 0.466	79.2 2/6 < 0.001	237 6/12 0.095	0.38 0.706	4.37 0.098	0.33 0.735	4.14 0.106
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.826) = OM2 (<i>p</i> = 0.251)	< 0.001 , < 0.001 , 0.475 – quadratic		NS	OM0 > OM1	NS	OM0, OM1 > OM2
H _D ; SiL _{Sh} n = 3	ANOVA	2.35 2/4 0.211	1625 3/6 < 0.001	2.47 6/12 0.086	0.38 0.706	1.87 0.267	0.85 0.492	6.10 0.061
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.105) = OM2 (<i>p</i> = 0.589)	< 0.001 , 0.205, 0.049 – cubic		NS	NS	NS	OM0 > OM1
H _{Dinc} ; LS _M n = 2	ANOVA	7.28 2/2 0.121	69.0 3/3 0.003	9.87 6/6 0.007	0.02 0.976	33.9 0.029	5.67 0.151	58.0 0.017
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.973) > OM2 (<i>p</i> = 0.062)	0.003 , 0.002 , 0.008 – cubic		NS	OM0, OM1 > OM2	OM0 < OM1	OM0 > OM1 > OM2
H _D ; LS _M n = 2	ANOVA	3.21 2/2 0.237	839 3/3 < 0.001	44.3 6/6 < 0.001	0.02 0.976	3.46 0.224	3.31 0.232	3.74 0.103
	Contrasts (<i>p</i> < 0.10)	OM0 = OM1 (<i>p</i> = 0.952) = OM2 (<i>p</i> = 0.126)	< 0.001 , 0.245, 0.571 – linear		NS	NS	NS	OM0, OM1 > OM2

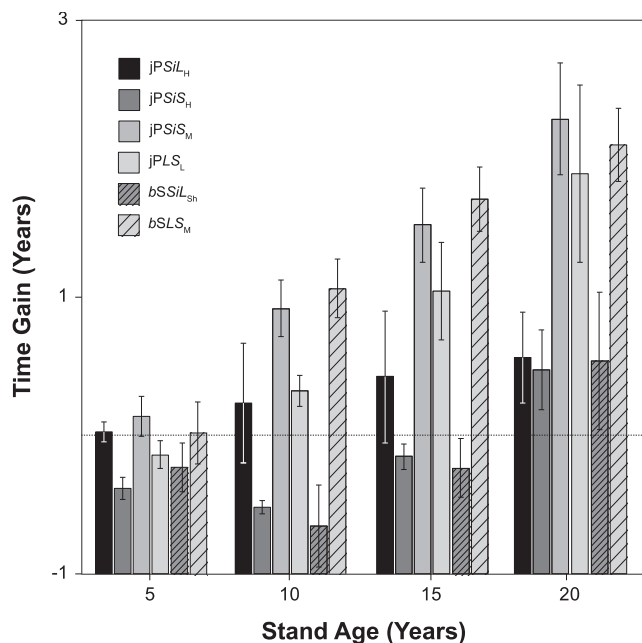


Fig. 4. Temporal trends in H_{Dinc} time gain for the OM0 and OM1 treatments combined, relative to the OM2, across the six species-site type combinations. Vertical bars represent standard errors of the mean. The horizontal line at zero on the vertical axis indicates no change in time gain among treatments.

floor and mineral soil samples were sieved, ground (forest floor only) and then homogenized. After adding de-ionized water, samples were incubated for 14 days at 30°. Following incubation, a 4 M KCL solution

Table 4

Mean monthly 10 cm soil temperatures in the OM1 and OM2 at Nimitz and Wells. Shown are mean values and standard errors for post-harvest years 3–5.

Installation	Treatment	Month				
		May	June	July	August	September
Nimitz	OM1	8.1 ± 1.29	13.3 ± 0.32	15.7 ± 0.43	15.9 ± 0.48	13.9 ± 0.31
	OM2	10.4 ± 1.64	16.4 ± 0.43	18.4 ± 0.78	17.8 ± 0.44	15.0 ± 0.26
Nimitz	OM2-OM1	2.3	3.1	2.7	1.9	1.1
Wells	OM1	10.0 ± 0.29	14.4 ± 0.23	16.3 ± 0.10	16.7 ± 0.14	14.2 ± 0.19
	OM2	13.2 ± 0.44	17.9 ± 0.27	20.3 ± 0.18	20.5 ± 0.18	15.9 ± 0.25
Wells	OM2-OM1	3.2	3.5	4.0	3.8	1.7

was added, and the extracted solutions were subsequently analyzed for NH_4^+ -N using the sodium nitroprusside method on a Technicor auto-analyzer IIC. The resulting concentrations were then combined with forest floor mass and mineral soil bulk density measurements to estimate potential available NH_4^+ -N pools.

2.3. Statistical analysis

Temporal trends in dominant height growth, foliar chemistry and net N mineralization were analyzed using Type III mixed-model repeated measures ANOVA with sites as random factors and year as repeated in a diagonal R matrix framework (NCSS 11 Statistical Software, 2016). Treatment and stand age sample distributions were assessed for normality (Shapiro-Wilk W test), equality of group variances (Levene's test) and equality of between-group covariance matrices (Bartlett's test).

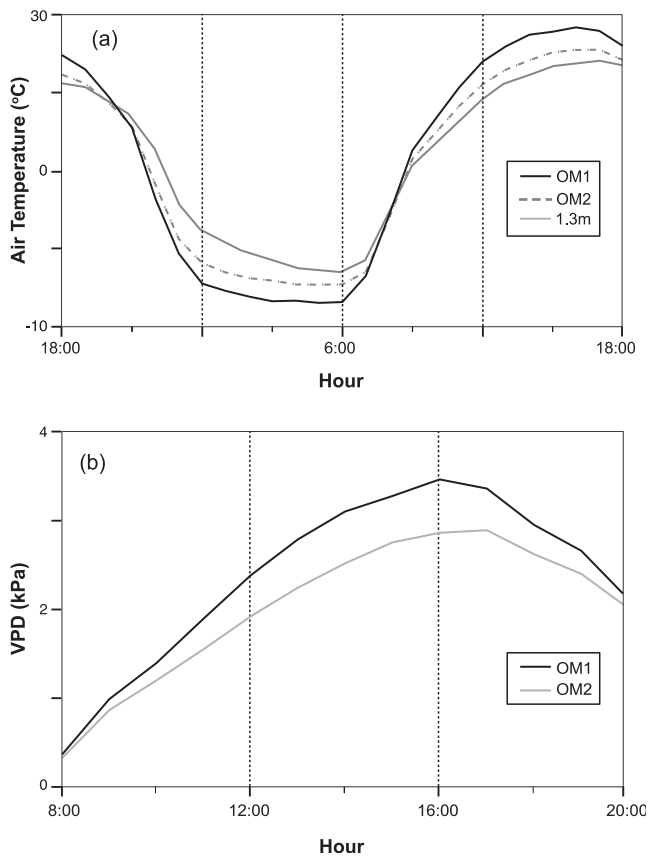


Fig. 5. Diurnal trends in OM1 and OM2; a) air temperature and b) vapor pressure deficit (VPD), 15 cm above ground on May 30–31, 1996 (year 3) at Nimitz. Also shown are air temperature trends at weather station height (1.3 m).

Following Log transformation of foliar N, assumptions were met in the vast majority of cases. For repeated measures, within-subject covariance matrix circularity was addressed using the Geisser-Greenhouse probability adjustment for F tests. Where treatment \times year interactions occurred, or to demonstrate treatment effects at a particular time, one-way GLM ANOVAs were performed for individual years. We did not analyze stand growth or foliar nutrition at the Nimitz installation because of missing year 5 measurements. We considered $p < 0.10$ as indicating statistical significance because our purpose was to compare alternative possibilities (Parkhurst, 2001), and because with few denominator degrees of freedom the chance of making Type II errors was reduced (Peterman, 1990). We also evaluated responses using orthogonal contrasts. For OM treatments we contrasted the OM2 with the OM0 and OM1, and then the OM0 with the OM1. For stand age trends, we used linear, quadratic and cubic contrasts.

2.4. Projecting drought constraints

We illustrated relationships between soil water storage capacity (SWSC), stand-level evapotranspiration (ET), and likely soil moisture-related reductions in stand productivity with a simplified dual-source ET model using 2018 growing season weather data from the Island Lake Biomass harvest experiment (Kwiaton et al., 2014). For dry days (precipitation (P) < 2 mm) daily canopy ET (ET_c) was calculated using the Simplified Penman-Monteith (SPM) model of Hogg (1997) together with the daily jack pine canopy conductance model of Bernier et al. (2006) ($G_c = g_l \cdot L$ where g_l is the average leaf-level stomatal conductance and L is the one-sided overstory leaf area index). This includes g_l modifiers for vapor pressure deficit and solar radiation. Understory/soil evaporation (ET_u) was calculated as one quarter of understory available

energy (Baldocchi et al., 2000), to a maximum of 1.5 mm d^{-1} , where understory available energy = $(Rn - G) \cdot \exp(0.5 \cdot L)$. Rn (net radiation) was estimated as $0.7552 \cdot \text{solar radiation}$, and G (soil heat flux) as $0.1 \cdot Rn$, with both estimates based on measurements at Nimitz 3–8 years post-harvest. For rainy days, (≥ 2 mm of precipitation), we assumed evaporation/canopy interception proceeded at the potential rate (i.e., using the Penman-Monteith equation with $G_c = 0$ and the aerodynamic conductance = 50 mm s^{-1} (e.g., Paul et al., 2003)) plus an additional interception carry-over of 3 mm (accounting for both canopy and forest floor surface wetting).

The relative extractable soil water content (REW in mm) was calculated as $(\theta - \theta_{\min})/(\theta_{\max} - \theta_{\min})$ where θ is the current calculated soil water storage (mm), θ_{\max} is the water storage at field capacity and θ_{\min} is the water storage at the wilting point. We based θ_{\max} and θ_{\min} on the mineral soil pedotransfer functions of Saxton and Rawls, (2006), and the forest floor pedotransfer functions of Laurén and Mannerkoski (2001). We assumed a bilinear relationship between REW and total ET (ET_{Tot}) (Spittlehouse and Black, 1981; Hogg et al., 2013), with a decrease in ET_{Tot} beginning at a critical REW of 0.4 (REW_c) (Kelliher et al., 1998; Granier et al., 1999). Below this, actual $ET = REW/REW_c \cdot ET_{\text{Tot}}$. Rainfall, ET and REW were calculated in mm and summed on a daily basis, with an upper REW limit of θ_{\max} (i.e., $\theta > \theta_{\max}$ was assumed lost to drainage).

3. Results

3.1. Survival and dominant height increment

Tenth year jack pine planted tree survival was greater with the OM2 than the OM0 or OM1 for the silty sand and loamy sand site types (Fig. 2) but not for the SIL installations ($p = 0.791$). With black spruce, 10th year survival was also greater with the OM2 than the OM1 on the loamy sand installations. However, while not statistically significant ($p = 0.338$), there was a trend of poorer survival on the OM2 than the OM1 and OM0 at the shallow-soiled black spruce (BS-SiL_{Sh}) installations.

For the eight jack pine installations combined, H_D and H_{DInc} were greater in the OM0 and OM1 than the OM2 ($p = 0.007$ and < 0.001 , respectively) by year 15, and showed either linear (H_D) or cubic (H_{DInc}) trends with age (Table 2). However, there were also strong ($p < 0.001$) treatment \times age interactions. Neither of the two more productive jack pine site types (jP-Si_{LH} and jP-Si_{SH}) showed strong H_D or H_{DInc} treatment effects, although notably jP-Si_{SH} year 10 H_D was greater with OM2 than OM0 or OM1. H_D and H_{DInc} for the less productive jP-Si_{SM} installations showed significant treatment (OM0, OM1 $>$ OM2) and age effects, as well as treatment \times age ((jP-Si_{SM}) interactions). Together, the two low productivity jP-LS_L installations did not demonstrate statistically significant ($p < 0.10$) treatment effects. Considered separately, however, the Eddy 3 installation showed well-defined H_D and H_{DInc} treatment effects (OM1 $>$ OM0 $>$ OM2, $p \leq 0.007$), as well as stand age effects ($p < 0.001$), and for H_D , treatment \times age interactions ($p < 0.001$). On an individual year basis, there were no significant treatment impacts ($p < 0.10$) for either jP-Si_{SM} and jP-LS_L site types until year 10 when OM2 values began to fall below those of the OM0 and OM1. Temporal H_D trends were linear for all jack pine site types except jP-LS_L, which showed a slight quadratic decline with age. By comparison, H_{DInc} showed quadratic or cubic trends with age (e.g. Fig. 3). When considered in terms of biological age (i.e., H_D), the substantial and continued decline in OM2 H_{DInc} with stand development past the stand establishment phase at the two lower productivity jack pine site types was readily apparent (Fig. 3). Of particular note, whereas the ANOVA results for the LS_L site types were largely inconclusive, reflecting large treatment variation, the biological age effect sizes (Fig. 3 d) showed clear differentiation.

For the five upland black spruce installations combined, neither H_{DInc} nor H_D showed significant treatment effects overall, but there were strong treatment \times age interactions for both metrics as well as age

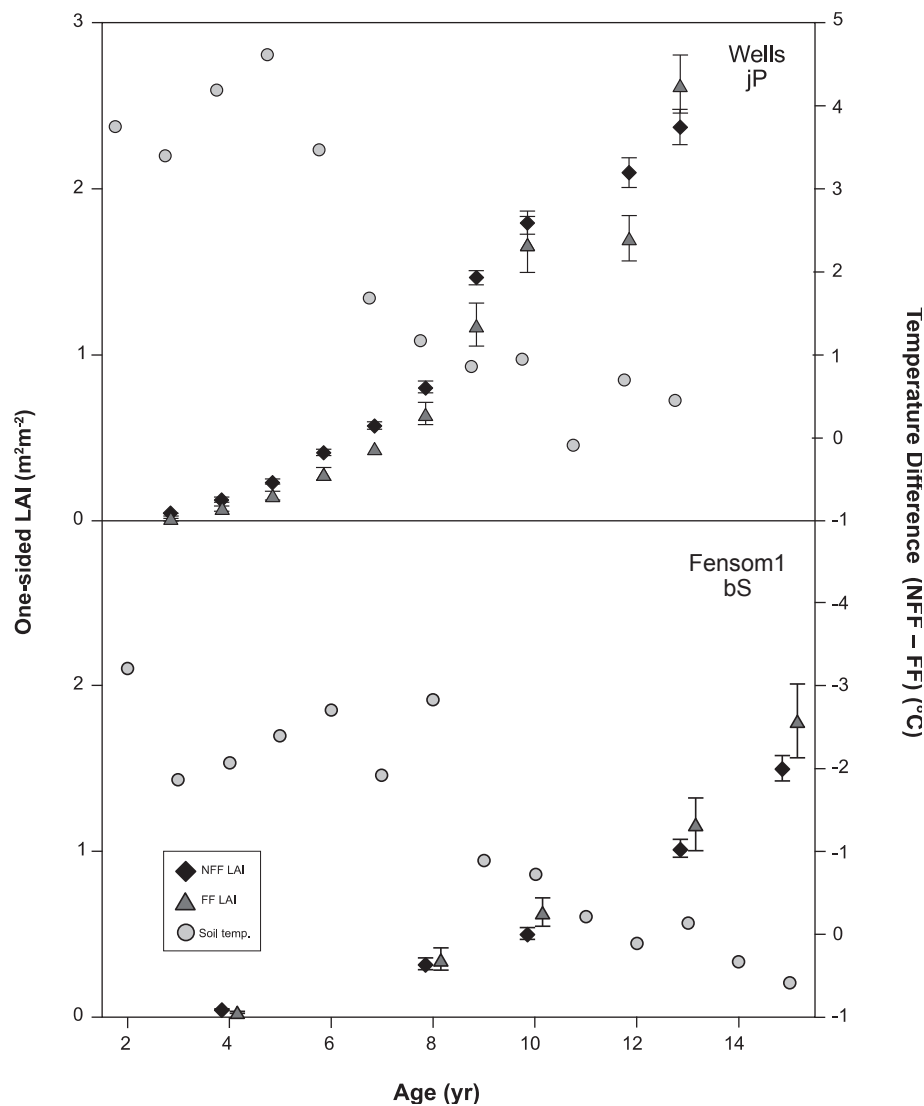


Fig. 6. Temporal trends in mean growing season (May 15–September 15) NFF–FF 10 cm soil temperature differences and stand one-sided leaf area index (LAI) at Wells and Fensom 1. FF represents treatments with forest floors left intact (OM0, OM1) while NFF represents treatments with forest floors removed (OM2). Vertical lines indicate LAI standard errors.

effects per-se (Table 3). When evaluated on an individual year basis with both site types combined, both H_{DInc} and H_D were significantly greater in the OM0 and OM1 compared to the OM2 at year 20. The bS-SiL_{Sh} site type did not show strong H_D or H_{DInc} OM treatment effects overall, but again there were strong treatment \times age interactions. This reflected greater H_{DInc} and H_D in the OM0 than the OM1 at years 10 and 20, respectively, and greater H_{DInc} in the OM0 and OM1 than OM2 at year 20. H_{DInc} for the bS-LS_M site type showed significant overall treatment (OM0, OM1 > OM2) as well as age effects, and treatment \times age interactions. On an individual year basis, significant bS-LS_M H_{DInc} treatment effects were evident by age 10, which were then manifest in H_D by year 20. Temporal H_D trends were linear for both black spruce site types whereas H_{DInc} peaked at year 15 for the bS-SiL_{Sh} compared to year 10 for the bS-LS_M. In terms of biological age (i.e., H_D), the marked decline in OM2 H_{DInc} at year 20 was particularly notable (Fig. 3).

Regarding temporal trends in time gain (Fig. 4), all species-site type groups had similar or lower values at year five for the OM0-OM1 treatments compared to the OM2. Conversely, by year 20 OM0-OM1 versus OM2 values were greater for all species-site type groups except the bS-SiL_{Sh}.

3.2. Microclimate

Near-surface microclimates showed the largest treatment-related differences during initial stages of stand establishment. Mean OM2 growing season 10 cm soil temperatures for post-harvest years 3–5 averaged 17.6 and 13.4 °C at Wells and Nimitz, respectively (Table 4). These values were about 3 °C greater than those for the OM1, with the largest differences occurring before mid-summer. During the stand establishment phase, the OM2 also reduced diurnal extremes in near-surface air temperature and vapor pressure deficit (VPD), particularly on clear days (Fig. 5). Notably, these near-surface diurnal extremes were considerably greater than at screen height (1.3 m) where most climatological data is collected. However, as the canopy developed and LAI increased, treatment differences in soil temperature as well as air temperature gradually attenuated (Fig. 6).

3.3. jP-SiS_H soil-surface soil surface CO₂ efflux

Projected growing season soil surface CO₂ efflux over post-harvest years 3–5 in the OM2 averaged only 2/3 of that in the OM0-OM1 and about 3/4 of that in the uncut forest, despite warmer soil temperatures (Fig. 7). Over this same period, projected heterotrophic respiration and

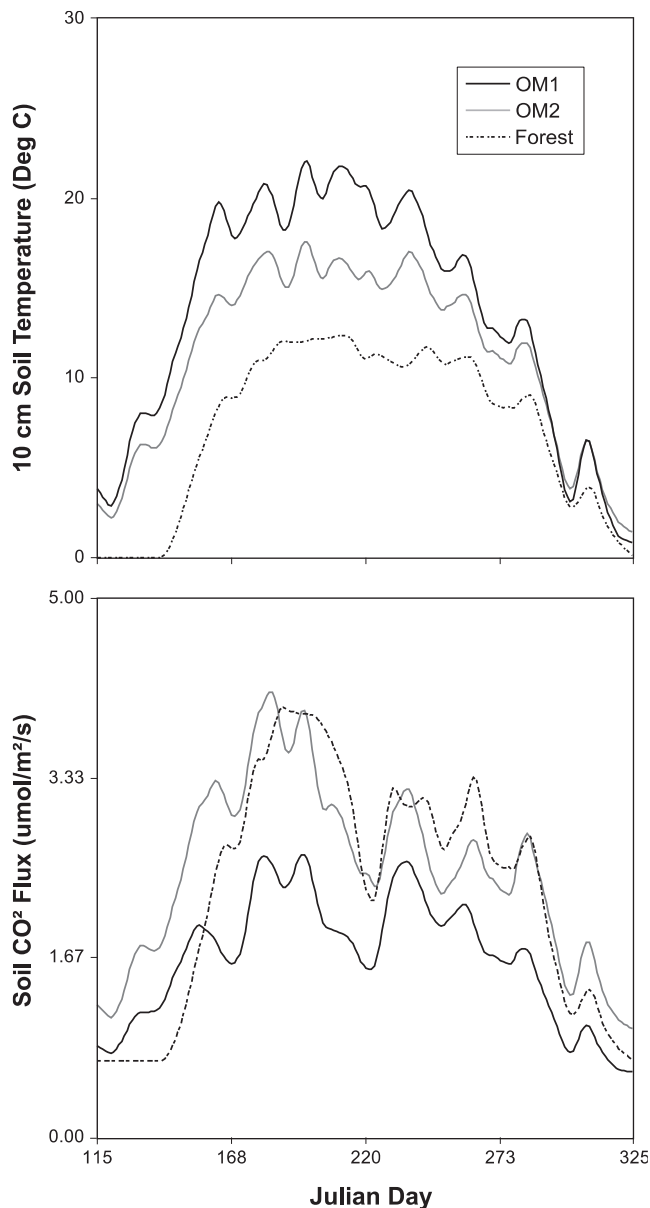


Fig. 7. Wells year four OM1, OM2 and uncut forest growing season trends in: a) 10 cm soil temperatures; and b) modelled soil surface CO_2 efflux (Fleming et al., 2006). Trends are shown using quadratic loess-smoothed lines based on 5% of the data range.

by inference, subsequent soil mineralization in the OM2 was also only 2/3 of that for the OM0-OM1, with the OM2 results strongly reflecting substrate limitations.

3.4. Foliar nutrition

Overall, jack pine N_{conc} and $N:P$, and black spruce N_{conc} were significantly greater with the OM0 and OM1 than the OM2 and declined with age, although significant treatment \times age interactions often marked both the overall and individual site type analyses (Tables 5 and 6). On an individual site-type basis, the jP-SiL_H showed no substantive treatment responses to either metric, whereas the other jack pine site types often had greater OM0 and OM1 than OM2 N_{conc} and $N:P$ values in various measurement years. The bS-LS_M installations had greater N_{conc} values in the OM0 and OM1 than in the OM2 across measurement years, but no significant differences in $N:P$ ratios in any year. The bS-SiL_S installations had significant treatment \times age interactions ($p \leq 0.006$) for

both nutrient metrics, with greater N_{conc} in the OM0 and OM1 than the OM2 only at year four, but with greater $N:P$ ratios in the OM2 than the other two treatments in all but year 20.

Both N_{conc} and $N:P$ showed distinct stand development trends for all site types; N_{conc} values were usually lowest at year 20 and often highest at year four or five, the most distinct exception being the peak in jP-SiL_H at year 15 (Figs. 8 and 9). We attribute the particularly low year five jP-SiL_H $N:P$ values to large foliar P rather than limited foliar N concentrations. Black spruce $N:P$ peaked at year four at both site types whereas peak jack pine $N:P$ ratios occurred between year 10 and 20, depending on site type (Fig. 9).

3.5. Net mineralization

Over the first 14 years, total (O (LFH) horizon + mineral soil) and mineral soil in-situ net N mineralization at Wells were greatest soon after harvest (yr 5) in all treatments (Fig. 10), and significantly greater ($p < 0.10$) in the OM0 and OM1 than in the OM2. Total net mineralization rates in the OM2 declined through year 14 and showed little subsequent recovery. In contrast, OM0 and OM1 mineral soil rates, and hence total values, were lowest at year 10 (with net immobilization occurring in the mineral soil), increased slightly at year 14, and demonstrated large increases in both O horizon and mineral soil mineralization rates in year 20. Across all years, temporal fluctuations in the FF treatments largely reflected changes in mineral soil rather than in O horizon N mineralization rates. A comparison of N net mineralization in subplots with and without vegetation control showed no significant effects of vegetation control on O horizon, mineral soil or total ($p = 0.456$) N mineralization in year 14. At year 20, somewhat larger O horizon and total (21.8 vs. 15.6, $p = 0.052$) net N mineralization values were found without than with vegetation control. There were no significant OM \times VegCtl interactions in either year ($p < 0.301$). Thus overall, results were generally similar with and without vegetation control.

Total and O horizon (LFH) black spruce anaerobic N mineralization on loamy sands decreased with increasing biomass removal and from post-harvest year 10 to year 20 (Fig. 10). On silt loams, black spruce N mineralization increased from year 10 to year 15 but then decreased at year 20. O horizon but not mineral soil N mineralization was consistently greater with the OM0 and OM1 than the OM2.

3.6. Projecting drought constraints

Modelled year 2018 growing season trends in relative extractable soil water showed greater reductions with increasing LAI during drier periods as the growing season progressed, but with almost complete recovery, regardless of LAI, during periods of greater precipitation in late summer and fall (Fig. 11). Reductions below the critical relative extractable soil water content (0.4) were also generally greater, and extended for longer periods and across a wider range of LAI values, for soils with more limited soil water storage capacity.

The most accurate components of the model are likely regarding canopy transpiration since this was based on well-established relationships between canopy conductance and measured daily solar radiation, VPD and relative water content. Greater uncertainty is associated with estimates of understory/soil surface evaporation; theory suggests that soil surface evaporation would be more limited than the model projects (Novak et al., 2000; Brutsaert, 2014) whereas understory plants could substantially increase evapotranspiration (Black and Kelliher, 1989). Nevertheless, canopy (overstory) conductance is likely to dominate evapotranspiration and profile soil moisture availability as these stands approach canopy closure and beyond.

Table 5

Mixed model ANOVAs of treatment and stand age effects on current-year jack pine foliar N concentrations (g kg^{-1}) and N:P ratios, by site type. Shown are *F* values, numerator and denominator degrees of freedom (df - numerator/denominator) and *p* values. Treatment orthogonal contrasts consisted of OM0 and OM1 vs. OM2; and OM0 vs. OM1 whereas stand age effects were evaluated using linear, quadratic and cubic polynomial contrasts. GLM ANOVA results of treatment effects at particular post-harvest years are also presented. *P*-values < 0.10 are shown in bold; NS (not significant) = contrast *p*-value > 0.10.

Site Type	Statistic	Treatment (T) ANOVA (<i>F</i> , df, <i>p</i>) Orthogonal contrasts (<i>p</i> < 0.10)	Stand Age (A) ANOVA (<i>F</i> , df,, <i>p</i>) <i>p</i> - linear-cubic contrasts	T × A ANOVA (<i>F</i> , df, <i>p</i>)	Treatment Effects by Post-harvest Year			
					<i>F</i> , <i>p</i>	Year 5	Year 9	Year 15
Log N Concentration								
All Sites n = 8	ANOVA	6.38, 2/14, 0.011	8.63, 3/21, 0.001	0.29, 6/42, 0.940	0.88, 0.435	4.52, 0.031	7.56, 0.006	0.90, 0.427
	Contrasts	OM0 = OM1 (<i>p</i> = 0.801) > OM2 (<i>p</i> = 0.003)	< 0.001 , 0.123, 0.589 - linear		NS	OM0 = OM1 (<i>p</i> = 0.394) > OM2 (<i>p</i> = 0.012)	OM0 = OM1(<i>p</i> = 0.593) > OM2 (<i>p</i> = 0.002)	NS
SiL _H n = 2	ANOVA	0.23 2/2 0.812	4.40 3/3 0.129	9.62 6/6 0.007	3.55, 0.219	0.17, 0.852	3.15, 0.241	3.66, 0.215
	Contrasts	NS	0.089 , 0.075 , 0.572–quadratic		NS	NS	NS	NS
SiS _H n = 1	ANOVA	16.02 2/6 0.004	3.10 3/17 0.054	3.74 6/17 0.015	24.4, 0.003	2.66, 0.149	3.36, 0.105	3.33, 0.107
	Contrasts	OM0 = OM1 (<i>p</i> = 0.165) > OM2 (<i>p</i> = 0.001)	0.037 , 0.077 , 0.232 - quadratic		OM0 > OM1 > OM2	NS	OM0, OM1 > OM2	OM0, OM1 > OM2
SiS _M n = 3	ANOVA	3.38 2/4 0.138	28.503/6 0.001	0.58 6/12 0.739	0.36, 0.717	2.40, 0.206	2.91, 0.166	0.05, 0.950
	Contrasts	OM0 = OM1 (<i>p</i> = 0.360) > OM2 (<i>p</i> = 0.074)	< 0.001 , 0.091 , 0.004 -cubic		NS	OM0, OM1 > OM2	OM0, OM1 > OM2	NS
LS _L n = 2	ANOVA	3.41 2/2 0.227	4.47 3/3 0.125	0.90 6/6 0.548	4.86, 0.171	16.8, 0.006	0.50 0.667	1.07, 0.484
	Contrasts	NS	0.052 , 0.592, 0.169 - linear		OM0, OM1 > OM2	OM0, OM1 > OM2	NS	NS
N:P Ratio								
All Sites n = 8	ANOVA	12.30, 2/14, 0.001	3.35, 3/21, 0.039	2.99, 6/42, 0.016	0.45, 0.644	1.37, 0.287	14.67, < 0.001	9.78, 0.002
	Contrasts	OM0 = OM1 (<i>p</i> = 0.423) > OM2 (<i>p</i> < 0.001)	0.835 , 0.016 , 0.086 - cubic		NS	NS	OM0 = OM1(<i>p</i> = 0.698) > OM2 (<i>p</i> < 0.001)	OM0 = OM1 (<i>p</i> = 0.397) > OM2 (<i>p</i> = 0.001)
SiL _H n = 2	ANOVA	0.47 2/2 0.682	3.74 3/3 0.153	1.73 6/6 0.262	0.94, 0.515	0.59, 0.629	2.45, 0.290	2.58, 0.279
	Contrasts	NS	0.279 , 0.052 , 0.811 - quadratic		NS	NS	NS	NS
SiS _H n = 1	ANOVA	8.53 2/6 0.018	15.35 3/17 < 0.001	1.80 6/17 0.160	26.8, 0.002	0.001, 0.999	2.19, 0.193	3.30, 0.108
	Contrasts	OM0 = OM1 (<i>p</i> = 0.252) > OM2 (<i>p</i> = 0.007)	< 0.001 , 0.048 , 0.414 – quadratic		OM0 > OM1 > OM2	NS	OM0, OM1 > OM2	OM0, OM1 > OM2
SiS _M n = 3	ANOVA	7.91 2/4 0.040	2.92 3/6 0.123	1.97 6/12 0.150	6.01, 0.061	0.86, 0.489	5.40, 0.073	3.24, 0.146
	Contrasts	OM0 = OM1 (<i>p</i> = 0.542) > OM2 (<i>p</i> = 0.017)	0.223, 0.771, 0.039 - cubic		OM0 < OM1 < OM2	NS	OM0, OM1 > OM2	OM0, OM1 > OM2
LS _L n = 2	ANOVA	19.5 2/2 0.049	12.1 3/3 0.035	1.35 6/6 0.362	1.40, 0.417	9.47, 0.096	5.25, 0.160	2.78, 0.305
	Contrasts	OM0 = OM1 (<i>p</i> = 0.743) > OM2 (<i>p</i> = 0.025)	0.083 , 0.013 , 0.278 - quadratic		NS	OM0, OM1 > OM2	OM0, OM1 > OM2	NS

4. Discussion

4.1. Stand development

Equivalent or improved survival and planted conifer growth during the Stand Initiation stage, as found here with the OM2, are often associated with mineral soil exposure in northern forests (Örlander et al., 1990; Fleming et al., 1998; Périe and Munson, 2000). Compared with the OM1, and by inference, the OM0, the OM2 experienced increased growing season soil temperatures, moderated near-surface air temperatures and vapor pressure deficits, and reductions in night-time frost occurrence during this period. All of these factors contribute to enhanced seedling vigor (DeLucia and Smith, 1987; Grossnickle and Heikurinen, 1989; Lamontagne et al., 1998).

The relatively small OM treatment effects on H_{Dinc} at year 5 (Fig. 3) are juxtaposed by substantial treatment differences in foliar N nutrition

(Figs. 8 and 9) and N mineralization rates (Fig. 10) at this time. This likely reflects greater nutrient supply but not seedling demand at this stage of stand development with the OM0 and OM1 (Titus and Malcolm, 1999; Sikström, 2004), a dynamic which complicates causal interpretation of growth response (Proe et al., 1994, 2001). While latent nutrient supply limitations existed for the OM2 from an early age, their initial impact on growth was likely overridden by improved microclimatic conditions (Chapin, 1991; Johnson et al., 2011). By years 10–15, decreases in OM2 versus OM0 and OM1 H_{Dinc} at many installations were consistent with treatment-related declines in foliar nutrition and N mineralization and the diminishing treatment influence on near-surface microclimates.

The general lack of substantial OM0-OM1 differentiation in H_D and foliar nutrition across our various species - site type combinations are consistent with results from other northern LTSP studies (Curzon et al., 2014; Kranabetter et al., 2017) and Scandinavian Scots pine studies

Table 6

Mixed model ANOVAs of treatment and stand age effects on current-year black spruce foliar N concentrations (g kg^{-1}) and N:P ratios, by site type. Shown are *F* values, numerator and denominator degrees of freedom (df - numerator/denominator) and *p* values. Treatment orthogonal contrasts consisted of OMO, OM1 vs. OM2; and OMO vs. OM1 whereas stand age effects were evaluated using linear, quadratic and cubic polynomial contrasts. GLM ANOVA results of treatment effects at particular post-harvest years are also presented. *P*-values < 0.10 are shown in bold; NS (not significant) = contrast *p*-value > 0.10.

Site Type	Statistic	Treatment (T) ANOVA (<i>F</i> , df, <i>p</i>)	Stand Age (A) ANOVA (<i>F</i> , df,, <i>p</i>)	T × A ANOVA (<i>F</i> , df, <i>p</i>)	Treatment Effects by Post-harvest Year			
		Orthogonal contrasts (<i>p</i> < 0.10)	<i>p</i> - linear-cubic contrasts		<i>F</i> , <i>p</i>	Year 5	Year 10	Year 15
Log N Concentration (g kg⁻¹)								
All Sites n = 5	ANOVA	9.03 2/8 0.009	92.9 3/12 < 0.001	6.08 6/24 < 0.001	15.2 0.002	8.86 0.067	2.67 0.129	2.24 0.165
	Contrasts (p < 0.10)	OM0 = OM1 (<i>p</i> = 0.968 > OM2 (<i>p</i> = 0.005))	< 0.001 , 0.001 , < 0.001 - cubic		OM0 = OM1 (<i>p</i> = 0.612) > OM2 (<i>p</i> = 0.001)	OM0 = OM1 (<i>p</i> = 0.473) > OM2 (<i>p</i> = 0.028)	OM0 = OM1 (<i>p</i> = 0.394) > OM2 (<i>p</i> = 0.066)	OM0 = OM1 (<i>p</i> = 0.665) > OM2 (<i>p</i> = 0.069)
SiL _{Sh} n = 3	ANOVA	2.97 2/4 0.162	157.7 3/6 < 0.001	3.34 6/12 0.036	6.72 0.053	0.98 0.449	0.31 0.748	0.06 0.945
	Contrasts (p < 0.10)	OM0 = OM1 (<i>p</i> = 0.953) > OM2 (<i>p</i> = 0.071)	< 0.001 , 0.001 , < 0.001 -cubic		OM0, OM1 > OM2	NS	NS	NS
LS _M n = 2	ANOVA	17.95 2/2 0.053	40.99 3/3 0.006	1.66 6/6 0.277	6.32 0.137	11.18 0.082	7.47 0.118	22.29 0.043
	Contrasts (p < 0.10)	OM0 = OM1 (<i>p</i> = 0.979) > OM2 (<i>p</i> = 0.026)	0.003 , 0.013 , 0.036 - cubic		OM0, OM1 > OM2	OM0, OM1 > OM2	OM0, OM1 > OM2	OM0, OM1 > OM2
N:P Ratio								
All Sites n = 5	ANOVA	1.69 2/8 0.245	13.51 3/12 < 0.001	3.77 6/24 0.009	9.94 0.007	3.87 0.067	0.25 0.786	1.12 0.372
	Contrasts (p < 0.10)	NS	0.002 , 0.006 , 0.003 - cubic		OM0 = OM1 (<i>p</i> = 0.647) < OM2 (<i>p</i> = 0.002)	OM0 = OM1 (<i>p</i> = 0.680) < OM2 (<i>p</i> = 0.025)	OM0 = OM1 (<i>p</i> = 0.573) = OM2 (<i>p</i> = 0.708)	OM0 = OM1 (<i>p</i> = 0.677) = OM2 (<i>p</i> = 0.186)
SiL _{Sh} n = 3	ANOVA	4.40 2/4 0.098	45.4 3/6 < 0.001	5.42 6/12 0.006	5.86 0.065	5.48 0.072	5.08 0.080	0.14 0.874
	Contrasts (p < 0.10)	OM0 = OM1 (<i>p</i> = 0.572) < OM2 (<i>p</i> = 0.044)	0.001 , 0.001 , < 0.001 - cubic		OM0, OM1 < OM2	OM0, OM1 < OM2	OM0, OM1 < OM2	NS
LS _M n = 2	ANOVA	0.09 2/2 0.920	2.80 3/3 0.210	1.88 6/6 0.231	2.39 0.295	0.36 0.736	0.88 0.533	02.03 0.330
	Contrasts (p < 0.10)	NS	0.093 , 0.235, 0.741 - linear		NS	NS	NS	NS

(Saarsalmi et al., 2010; Egnell, 2017). However, they are in contrast with the reported OM1-related decreases in Scandinavian Norway spruce productivity (Egnell, 2017) and in some cases *Nconc* (Olsson et al., 2000). For our site types, we largely attribute the lack of such differentiation to the substantial carbon and nutrient reserves following the OM1 as well as the OMO treatments (Hazlett et al., 2014). This reflects both the operational nature of our treatments and the large biological nutrient legacies associated with harvesting these mature fire-origin stands (e.g., Franklin et al., 2002; Gaiser et al., 2020). We are now addressing the relative impacts of OM1 vs. OMO treatments in a younger second-growth forest with smaller biological legacies and a more intensive biomass harvest at our Island Lake Biomass Harvest experiment (Morris et al., 2020).

4.2. Soil and foliar N

As found here (Fig. 10), net N mineralization rates are often highest within a few years of clearcutting (Bradley et al., 2002; Kranabetter et al., 2006), and with substantial reductions in N availability in OM2 compared with OMO and OM1 treatments (Ross et al., 1995; Munson and Timmer, 1995). Our estimates of year 3–5 heterotrophic respiration at Wells (Fig. 7 and Fleming et al., 2006) are consistent with the 5th year N mineralization rates of the respective treatments. Greater OMO than OM1 *bS*-LS_M N mineralization at years 10–15 may reflect greater absolute differences between the two treatments in woody slash and hence post-harvest C and N pools (Morris et al., 2019). Whereas needles may release half of their N content within 6–8 years, substantially longer periods are often needed for similar percentages to be released from twigs and branches (Hyvönen et al., 2000; Wiebe et al., 2014).

The substantial *jP*-SiS_H OMO and OM1 net mineralization values compared to negligible OM2 values out to year 20, together with the widespread reductions in jack pine *Nconc* and N:P at this time, indicates

that forest floor removal is resulting in continued reductions in N availability. In contrast, the *bS*-SiL_{Sh} and *bS*-LS_M N mineralization rates, as well as foliar N indices, for the three treatments converged to some extent by year 20. This suggests that either the OM2 soil N status is recovering or, given the low *Nconc* and N:P for all three treatments, that the individual treatments are reaching their own equilibrium, balancing nutrient supply and demand. The latter would be consistent with phase 2 of Rastetter et al. (2020) whereby the individual treatments are converging on a quasi-steady state in which vegetation and soil microbial processes are in balance. This would coincide with the end of the Reorganization/Renewal phases (Fig. 1). The increasing OM0 and OM1 *H_D* time gains (in comparison with the OM2) from year 15 to year 20 across virtually all site types (Fig. 4) supports this contention.

4.3. Species response

Treatment impacts on stand development (*H_D* and *H_{Dmc}*) and foliar nutrition varied to a much greater extent across site types than between species. For both species, richer site-types appear less affected by the OM2 than coarser soiled, more nutrient-poor site-types. Nevertheless, there were distinct species, as well as site-related, differences in survival, *H_D* and N nutrition. The positive OM2 impact on jack pine survival at three site types, together with the earlier onset of declines in *Nconc* with black spruce, highlights the importance of species autecological characteristics (Munson and Timmer, 1995; Kranabetter et al., 2003, 2017; Houle et al., 2014). With jack pine, there was little evidence of reduced *Nconc* in the OM2 compared with the OMO and OM1 until post-harvest years 10–15, and negligible site-related N limitations (i.e., *Nconc* < 12 g kg^{-1}) until year 20, despite reduced N mineralization at *jP*-SiS_H by year five. With black spruce, OM2-related reductions in *Nconc* and N mineralization were more evident at younger ages; by year 15 these were restricted to the *bS*-LS_M, whereas site-related foliar N limitations

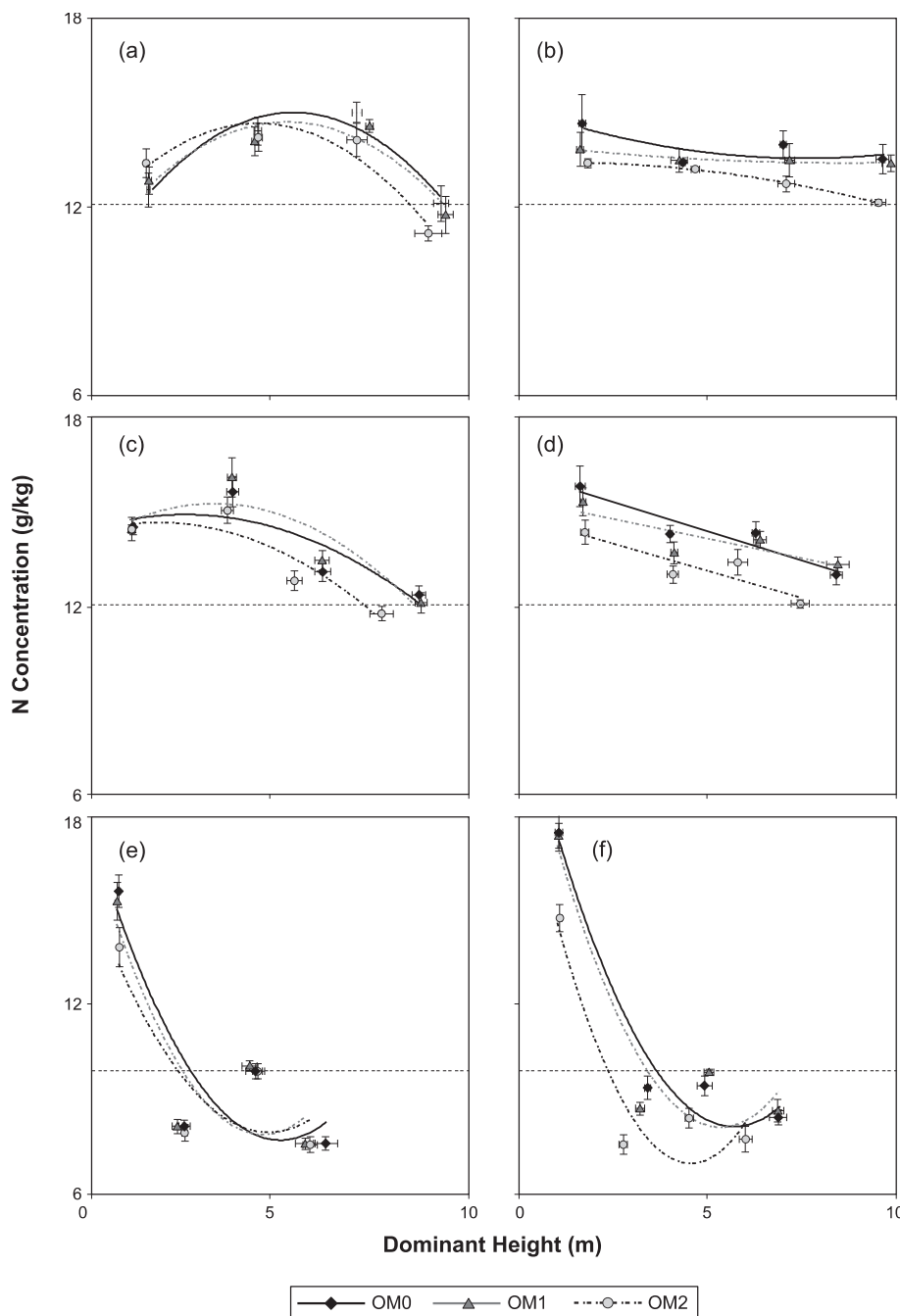


Fig. 8. Temporal trends in OM0, OM1 and OM2 current-year foliar N concentrations as a function of biological age (dominant height). Shown are mean values (\pm standard errors), together with quadratic functions depicting general trends for the six species-site type combinations: a) jP-SiL_H b) jP-SiS_H, c) jP-SiS_M, d) jP-LS_L, e) bS-SiL_{Sh} and f) bS-LS_M. Responses at post-harvest years 4–5, 9–10, 15 and 20 are discernable from treatment - H_D trajectories. The horizontal line at 12 g kg⁻¹ for jack pine and 10 g kg⁻¹ indicate N concentrations below which foliar N deficiencies commonly occur.

were apparent at both black spruce site types from age 10 onward.

Foliar $N:P$ ratios also point towards species-related differences in the progression of N limitation; with jack pine, $N:P$ values generally suggest greater potential for N limitations (i.e., $N:P < 10$ (Knecht and Göransson, 2004)) during the Initial Establishment phase and as Canopy Closure approaches, whereas with black spruce, $N:P$ values indicate N limitations may be small initially, but increase substantially during the Accelerated Growth phase, and with some recovery as Canopy Closure approaches. Notably, while the OM2 markedly reduced total root zone soil nitrogen reserves (Hazlett et al., 2014), there were no discernable

treatment-related temporal changes in total reserves across soil types over the 20 year period (Morris et al., 2019). Similar contrasting results in temporal dynamics of foliar N versus total soil N reserves were reported by Bond-Lamberty et al. (2006b) for a post-wildfire black spruce chronosequence.

We suspect similar evolving constraints may occur in other regions with harsh climates and coarse soils (e.g., Sloan and Ryker, 1986; Gomez et al., 2002). With finer-textured soils and wetter moisture regimes, however, forest floor removal increases susceptibility to frost heaving (de Chantal et al., 2007), puddling and watering-up, all of which can

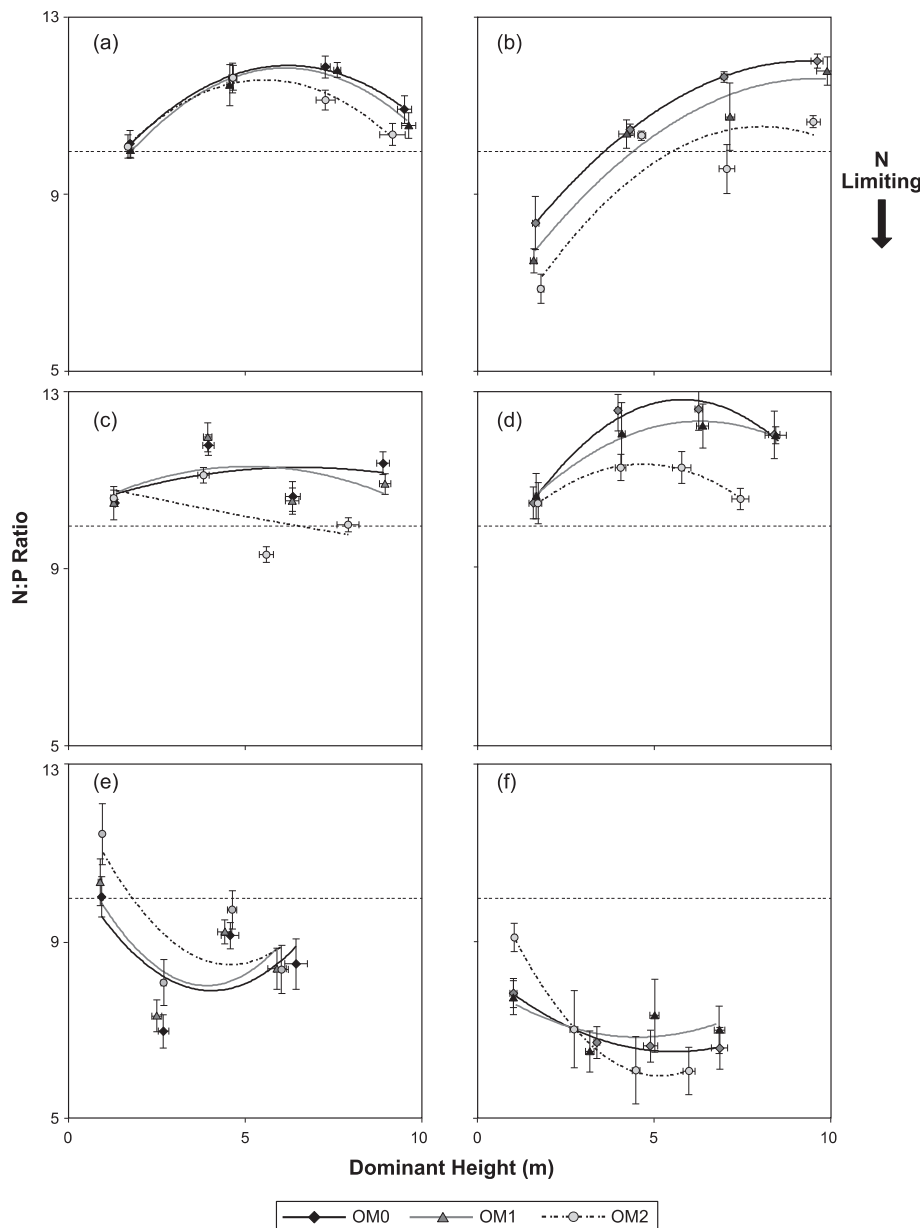


Fig. 9. Temporal trends in OM0, OM1 and OM2 current-year foliar N/P ratios as a function of biological age (dominant height). Shown are mean values (\pm standard errors) together with quadratic functions depicting general trends for the six species–site type combinations: a) jP-SiL_H, b) jP-SiS_H, c) jP-SiS_M, d) jP-LS_L, e) bS-SiL_{Sh} and f) bS-LS_M. Responses at post-harvest years 4–5, 9–10, 15 and 20 are discernable from treatment - H_0 trajectories. The horizontal line at an N:P ratio of 10 marks the ratio below which conifer N deficiencies commonly occurs (Knecht and Göransson, 2004).

reduce planted seedling survival and initial growth as well as longer-term stand development in OM2-related treatments (Boateng et al., 2006). In warmer, humid climates, OM2-related nutrient limitations may appear earlier, and without preceding gains in initial growth resulting from microclimate amelioration (Scott et al., 2004; Laclau et al., 2010). This may reflect the early onset of phosphorous deficiencies in these older, more weathered soils (e.g., Albaugh et al., 2018). In contrast, nutrient levels in more fertile soils may be sufficiently high to maintain good OM2 growth rates (Piatek et al., 2003; Ponder et al., 2012).

4.4. Longer-term limitations

Nitrogen availability is often cited as the principle limitation to stand

productivity and related ecosystem functions in boreal regions (Weetman and Fournier, 1984; Höglberg et al., 2017). However, there are strong linkages between canopy conductance, transpiration, photosynthesis, and stand productivity, with proximal effects of both foliar nutrition (through maximum conductance) and water availability (Baldocchi et al., 1997; Reich, 2012). Hogg (1997), Bond-Lamberty et al. (2006a) and Grant et al. (2007) have all identified direct constraints of root zone extractable water on boreal forest productivity. Our water balance calculations suggest that profile soil moisture availability will increasingly limit stand transpiration and hence productivity as stand LAI increases through Canopy Closure to the Stem Exclusion stage. Further, such limitations are likely to occur at earlier stand development stages (biological ages) for stands with more limited soil water storage capacities (e.g., coarser-textured or shallower soils).

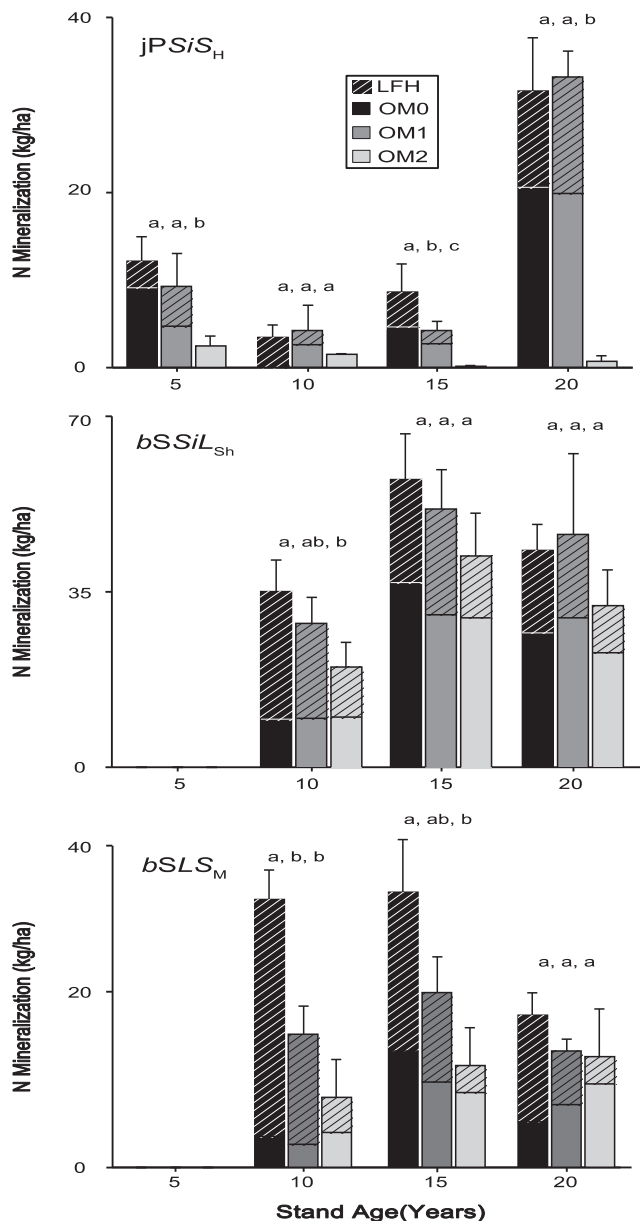


Fig. 10. Temporal trends in N availability in the OM0, OM1 and OM2 for: a) jP-SiS_H net N mineralization; and potentially mineralizable N for b) bS-SiL_{Sh}; and c) bS-LS_M. Values are given for the O horizon (LFH - hatched areas) and 0–20 cm mineral soil depth. Vertical lines represent standard errors of the mean for total values.

Thus a broader view suggests the interactive effects of soil nitrogen and water availability, as influenced by regional climate, topoposition, soil texture and pH can increasingly constrain boreal stand productivity during later stages of stand development, particularly on coarse-textured soils with limited soil water storage capacity and low nutrient reserves (Weetman et al., 1980; Morrison and Foster, 1990; Bond-Lamberty et al., 2006a; Grant et al., 2007; Blaško et al., 2015). Additionally, while we have focused on N, potassium (Duchesne and Houle, 2008; Quimet et al., 2013) as well as phosphorus availability (Goswami et al., 2018), may also constrain boreal stand productivity,

particularly on droughty soils (Tripler et al., 2006).

Finally, our results highlight potential pitfalls associated with projecting short-term results from the Stand Establishment phase through subsequent stand development stages (e.g. Cortini et al., 2010). Unfortunately few manipulative studies have been specifically designed for long-term assessment or followed long enough to address temporal changes in resource supply and biomass increment across stand development stages for specific regions, species and site types (Powers, 1999, but see Egnell, 2011, 2016; Brandtberg and Olsson, 2012). In our case, we currently have little information after canopy closure. To what extent and for how long will stand development and soil processes begin (OM0 vs. OM1) or continue (OM2) to diverge, and likewise what will be the timing and extent of any subsequent recovery? Contrasting hypotheses regarding the importance of coarse woody debris (Fahey, 1983; Laiho and Prescott, 2004; Wiebe et al., 2014), temporal patterns of soil nutrient supply and demand (Fahey and Knight, 1986; Miller, 1995; Foster et al., 1995; Olsson et al., 2000; Hazlett et al., 2007), and both trends in and processes driving later forest floor and stand development (Ryan et al., 1997; Prescott et al., 2000) highlight the importance of continued measurement of manipulative experiments such as these through subsequent development stages.

5. Concluding remarks

To date, our studies are congruent with a multi-stage model of stand development on these drier, nutrient-poor coarser-textured boreal site types: The Stand Initiation stage consisted of an Initial Establishment phase largely governed by microclimatic conditions reflecting surface energy exchange, followed by an Accelerated Growth phase associated with crown development reflecting increased nutrient demand, reduced nutrient availability, and moderated microclimate controls. We found this conceptual framework particularly useful for exploring the impacts of species and site conditions as well as biomass removal intensity, as stand development progressed through to the Canopy Closure stage. For natural regeneration, an initial phase could be added addressing propagule sources and substrate availability (Roberts, 2007), whereas different constraints including nutrient availability and profile water storage are likely to limit stand growth and ecosystem function at later stages. While not considered here, this framework would also be useful for investigating effects of harvest intensity and vegetation control on species functional traits, soil microbial and mesofaunal communities, and interactive feedbacks related to soil productivity.

CRediT authorship contribution statement

Robert L. Fleming: Conceptualization, Investigation, Methodology, Resources, Validation, Data curation, Writing – original draft, Writing – review & editing. **Dave M. Morris:** Investigation, Methodology, Resources, Validation, Data curation, Writing – review & editing. **Paul W. Hazlett:** Investigation, Methodology, Resources, Validation, Data curation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

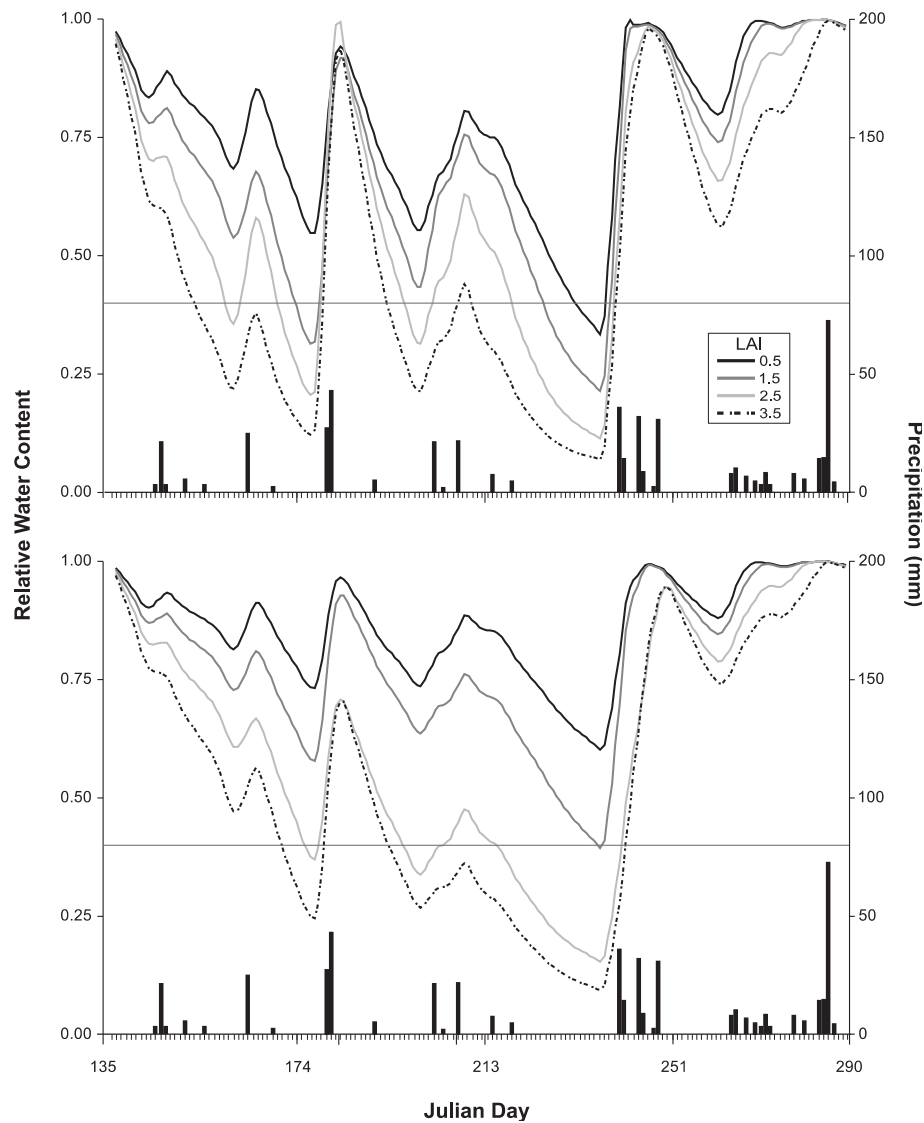


Fig. 11. Modelled growing season trends in relative water content as a function of stand leaf area index for a) a soil water storage capacity of 72 mm, and b) a soil water storage capacity of 122 mm. Projections are based on 2018 daily clearcut weather conditions near Chapleau, Ontario. Trends are shown using quadratic loess-smoothed lines based on 5% of the data range. The horizontal line at 0.4 indicates the onset of soil water limitations to evapotranspiration.

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