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Effects of organic matter removal, soil compaction and vegetation control on 10th year biomass and foliar nutrition: LTSP continent-wide comparisons

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ABSTRACT

We examined 10th year above-ground planted tree and total stand biomass, and planted tree foliar N and P concentrations across gradients in soil disturbance at 45 North American Long-Term Soil Productivity (LTSP) installations. While ranging across several climate regions, these installations all share a common experimental design with similar measurement protocols. Across all installations planted tree biomass with stem-only harvest (OM_0), no compaction (C_0) and chemical vegetation control (VC), ranged from 2 to 90 Mg ha^{-1}. When compared with the OM_0, full-tree harvest (OM_1) had little consistent effect on any response variable. Full-tree harvest plus forest floor removal (OM_2) also demonstrated few consistent effects on planted tree biomass, although Boreal – Great Lakes conifers showed some positive effects, reflecting high survival, but also negative effects on foliar nutrition. Compaction (C_2), regardless of OM treatment, increased planted tree stand biomass consistently in Warm Humid climates, and compaction with intact forest floors (OM_0C_2) did so across all regions. However, most installations had medium – or coarse-textured soils and compaction did not achieve theoretical growth-limiting bulk densities. Combining OM_2 with C_2 resulted in lesser gains in planted tree biomass. Planted tree biomass gains with the OM_0C_2 were attributed largely to changes in physical soil characteristics, not to vegetation control or nutrient availability. Total stand biomass (Mg ha^{-1}) was either unaffected or, with aspen, reduced by compaction. Vegetation control (VC) consistently enhanced planted tree biomass, regardless of climate, and also enhanced foliar nutrient concentrations on Warm Humid and Mediterranean sites. VC also increased total stand biomass on sites without abundant woody competitors, but decreased it on shrub-dominated Mediterranean sites. For many of the site types and species investigated, harvest-related organic matter removal and soil compaction (excepting aspen vegetative reproduction) have not resulted in large losses in stand biomass 10 year after harvest. Most stands, however, have not yet reached canopy closure, and treatment effects may continue to evolve.

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1. Introduction

The North American Long-Term Soil Productivity program (LTSP) addresses short- and long-term effects of harvest-related disturbance on fundamental soil productivity (i.e., the capacity to capture carbon and produce biomass). Manipulative treatments focus on site organic matter and soil porosity, two key properties affecting productive capacity which are influenced by harvesting and silvicultural activities (Powers, 2006). Additionally, vegetation control is considered because it influences both target tree and total biomass production (Wagner et al., 2006). This network of over 100 core and affiliate installations provides rigorous empirical evidence regarding short- and long-term treatment effects and their interactions, features lacking in most chronosequence, retrospective and modelling studies (Powers and Van Cleve, 1991; Morris and Miller, 1994).

Harvest and related regeneration treatments often have different impacts on seedling establishment than on longer-term growth. In particular, treatment effects on microclimatic conditions and competition from lesser vegetation may have large initial impacts, but diminishing effects following stand establishment (Mason and Milne, 1999; Proe et al., 2001). In contrast, increased post-harvest nutrient availability may provide adequate seedling nutrition, regardless of treatment (cf. Smethhurst and Nambiar, 1990; Vitousek et al., 1992; Sanchez et al., 2006). Subsequent reductions in nutrient availability, however, combined with increased nutrient demands as the newly-established stands build leaf area (Switzer and Nelson, 1972; Miller, 1995) may impose substantial productivity constraints related to organic matter removal (Proe et al., 1996; Egnell and Valinger, 2003; Mendham et al., 2003).

Impacts of harvest-related soil compaction often vary with soil conditions. For drier coarse-textured soils compaction can increase water holding capacity, root/soil contact and resource uptake whereas for moister, finer-textured soils compaction often restricts soil aeration, with soil strength and possible rooting restrictions increasing on many soil types (Greacen and Sands, 1980; Kozlowski, 1999). Further, the combined effects of these soil impacts may or may not affect stand productivity (Froehlich et al., 1986; Miller et al., 1996; Gomez et al., 2002a). Over time bulk densities and aeration porosities are likely to recover, but recovery rates can vary greatly, reflecting frost action, soil rock and water content, plant rooting, shrink-swell activity, and the action of soil fauna (Greacen and Sands, 1980; Corns, 1988; Powers et al., 2005; Eisenbies et al., 2007).

Effects of vegetation control on productivity are likely to vary with vegetation type, soil conditions, climate regime, and time (South et al., 2006). Further, results often depend on the productivity measure used (e.g., biomass production of crop trees vs. that of the entire plant community). Herbaceous competition is often severe initially but effects can diminish markedly with canopy closure and understory shading (Mason and Milne, 1999; Miller et al., 2003a,b). Larger woody competition often produces greater decreases in planted tree biomass as time proceeds, but effects on total stand biomass vary greatly, depending on site and time frame (Glover and Zutter, 1993; Miller et al., 1999, 2003a,b; Rose et al., 2006).

In earlier synthetic papers we addressed treatment effects on 5th year seedling establishment (Fleming et al., 2006), soil C and N (Sanchez et al., 2006) and soil physical properties (Page-Dumroese et al., 2006), and 10th year effects on soil C and nutrient availability, soil bulk density and stand biomass at 18 installations (Powers et al., 2005). Briefly, forest floor removal improved seedling establishment at Mediterranean (Medit) sites but reduced it at Warm Humid (WmHd) sites (Fleming et al., 2006). Overall, Powers et al. (2005) found 10th year total above-ground biomass (without vegetation control) was not significantly affected by organic matter removal. Compaction generally improved seedling establishment, particularly with intact forest floors (Fleming et al., 2006) whereas effects on 10th year total stand biomass (no forest floor only) varied with soil texture and were present (negative) only with vegetation control (Powers et al., 2005). Vegetation control benefited seedling establishment (Fleming et al., 2006), but general effects on subsequent biomass production were not assessed.

Here we analyze 10th year planted tree and total standing (above-ground) biomass across 45 installations, using additional analytic approaches, and consider both regional and transcontinental trends, as well as foliar N and P concentrations. In particular, we consider the following questions: (1) is there a consistent or regionally-based trend of decreased biomass production and/or foliar nutrition with increased organic matter removal?; (2) are compaction effects on biomass production or foliar nutrition evident at year 10, and if so, to what degree do such effects interact with vegetation control and forest floor removal?; and (3) what is the relative importance of vegetation control compared to other treatments in terms of planted-tree and total stand response?

2. Methods

2.1. Site location, forest description, experimental design

This paper draws on 10th year results from a broad spectrum of locations representing a range of climates, soil conditions and species, and organized into 29 replicated studies for most analyses (Table 1 and (Fig. 1). Studies and installations were assigned to four broad climate groupings based on principal components analysis of modeled climate variables (McKenney et al., 2006) (Table 1). We chose four groupings based on geographic location and general climate (e.g., Fig. 2): Warm Humid (WmHd) encompassing studies in the southeast U.S.; Mediterranean (Medit) for studies in California; Western Montane (WtMt) for studies in the higher-elevation western interior with cool temperate – boreal climates; and Boreal-Great Lakes for studies in northern cool temperate and boreal climates adjacent to the Great Lakes. The full LTSP factorial experimental design involves three organic matter removal levels (stem-only harvest (OM_0), full-tree harvest (OM_1) and full-tree harvest plus forest floor removal (OM_2)), and three soil compaction (Comp) levels (none (C_0), moderate (C_1), and severe (C_2)) (Table 2) (Powers et al., 1990). The organic matter removal levels encompass the extremes in removal levels apt to occur with clearcut harvesting and produce a step series in biomass and nutrient removal (see Powers et al., 2005, Table 1). For the C_0, large mechanized equipment was usually excluded from the plots, but in some cases (e.g., black spruce, jack pine and certain aspen installations (Stone, 2001; Stone and Kabzems, 2002)) dry-weather or winter harvesting was conducted with mechanized equipment crossing the plots. Compaction was accomplished with a variety of mechanical means when soils were near field capacity with the goal of the C_2 treatment to increase soil bulk density to 80% of that proposed by Daddow and Warrington (1983) as limiting root growth. In the event, however, both C_1 and C_2 compaction treatments increased root zone densities by similar amounts (averaging about 18% or 011 Mg m^{-3}) (Powers et al., 2005). As a result we only consider the C_0 and C_2 treatments in this paper. Greater increases in bulk densities were associated with lower initial bulk densities, but at all installations the C_2 treatment never achieved $\geqslant$80% of Daddow and Warrington's (1983) proposed growth-limiting values (Powers et al., 2005; Page-Dumroese et al., 2006).

Table 1
Location, site characteristics and species regenerated for the LTSP installations used in this paper. Ordered first by climate region (warmest to coldest) and then alphabetically by state/province and location.

State-province; location/soil family: study code	Installation – reps per installation	Climate region[a]; elevation (m)	Annual mean temp. (°C)	Growing degree days[b]	Precip, warmest quarter[b] (mm)	Site index (m at 50 yrs)	Soil texture[c]	Preharvest mean biomass: overstory/ forest floor (Mg ha^{-1})[d]	Species regenerated
Louisiana Kisatchee: LAKis	4 – 1 Glenmora, Malbis, Mayhew, Metcalf	WmHd 52–61	18.5	3759 – 3878	311–350	27	SL–CL	170/17.3	Loblolly pine (lobP) *Pinus taeda* L.
Missouri Carr Creek: MOCaC	1 – 3	WmHd 260	13.1	3176	281	24	SiL	184/5.8	Red oak (rO), white oak (wO), shortleaf pine (slP) *Quercus rubra* L., *Quercus alba* L., *Pinus echinata* Mill. (SlP)
Mississippi Freest: MSFre	3 – 1	WmHd 69	18.1	4160	364	28	L/CL	145/8.9	Loblolly pine
North Carolina Croatan: NCCro	2 – 1,2 Goldsboro, Lynchburg	WmHd 8	17.0	4076	469	27	LS	168/52.4	Loblolly pine
Texas Kurth: TXKur	3 – 1	WmHd 88	19.0	4200	253	26	SCL	223/14	Loblolly pine
California Dystroxerepts[e] CADys	3 – 1 Central, Owl, Vista	Medit 1560 – 1805	9.2	1573 – 1851	30 – 35	22	SL	457/75	Giant sequoia (gS), ponderosa pine (pP), sugar pine (suP), white fir (wF)[f] *Sequoiadendron gigantea* (Lindl.) Decne., *Pinus ponderosa* P. Laws. ex C. Laws., *Pinus lambertiana* Dougl., *Abies concolor* (Gord. & Glend.) Lindl.
California Haploxeralfs[e]: CAHap	3 – 1 Blodgett, Brandy, Lowell	Medit 1130 – 1320	11.2	2114 – 2295	51 – 55	28	L – SiC	382/76	Douglas-fir (DF), giant sequoia, ponderosa pine, sugar pine, white fir[f] *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco
California Palexerults[e]: CAPal	1 – 1 Challenge	Medit 790	13.0	2736	28	28	C	473/61	Douglas-fir, ponderosa pine, sugar pine, white fir[f]
California Xerumbrepts[e]: CAXer	2 – 1 Rogers, Wallace[l]	Medit 1200 – 1575	9.9	1830 – 1962	38 – 58	24	SL	472/97	Ponderosa pine, sugar pine, white fir, giant sequoia (Wallace), Douglas-fir (Rogers)[f]
British Columbia Sub Boreal Spruce: BCSBS	2 – 1 Log Lake, Topley	WtMt 785 – 1100	2.2	634 – 968	146 – 193	17	L	173/77	lodgepole pine (lpP), hybrid spruce (xS) *Pinus contorta* Dougl. Ex Loud. var *latifolia* Engelm, *Picea glauca* × *engelmannii*
British Columbia Kiskatinaw River: BCKiR	1 – 3	WtMt 720	1.0	956	210	18	SiL/SiC	520/55	trembling aspen (As) *Populus tremuloides* Michx.
Idaho Council: IDCou	1 – 3	WtMt 1575	3.9	931	100	28	SiCL	252/72	Douglas-fir, ponderosa pine, western larch (La), *Larix occidentalis* Nutt.
Idaho Priest River: IDPrR	1 – 1	WtMt 900	7.0	1564	119	25	SiL	191/68	Douglas-fir, western white pine (wwP) *Pinus monticola* Dougl. Ex D. Don
Michigan Huron Manistee: MIHuM	1 – 3	BorGL 245	6.2	1742	233	19	fS	98/48	bigtooth aspen (As), trembling aspen: *Populus grandidentata* Michx
Michigan Ottawa: MIOtt	1 – 3	BorGL 324	4.5	1566	272	18	C	106/128	Trembling aspen
Minnesota Chippewa: MNChi	1 – 3	BorGL 412	3.8	1705	286	24	SiCL	256/130	Trembling aspen
Ontario Eddy 3: ONEd3	1 – 3	BorGL 490	2.8	1333	242	13	vfS/mS	87/58	Jack pine (jP) *Pinus banksiana* Lamb.
Ontario Eddy 4: ONEd4	1 – 3	BorGL 490	2.8	1333	242	15	vfS/mS	113/60	Jack pine (jP)

(*continued on next page*)

Table 1 (*continued*)

State-province; location/soil family: study code	Installation – reps per installation	Climate region[a]; elevation (m)	Annual mean temp. (°C)	Growing degree days[b]	Precip, warmest quarter[b] (mm)	Site index (m at 50 yrs)	Soil texture[c]	Preharvest mean biomass: overstory/ forest floor (Mg ha^{-1})[d]	Species regenerated
Ontario Fensom 1: ONFe1	1 – 3	BorGL 450	0.4	1095	266	9	SiL	137/42	Black spruce (bS) *Picea mariana* (Mill.) BSP
Ontario Fensom 2: ONFe2:	1 – 3	BorGL 450	0.4	1095	266	9	SiL	166/63	Black spruce
Ontario Fensom 3: ONFe3	3–3	BorGL 450	0.4	1095	266	9	SiL	145/64	Black spruce
Ontario Geraldton: ONGer	1 – 3	BorGL 350	−0.4	1022	267	12	fS–cS	175/91	Black spruce
Ontario Nemagos Lake ONNeL	1 – 3	BorGL 457	1.6	1168	255	17	SiL/LmS	167/84	Jack pine
Ontario Rd 620: ONR62	1 – 3	BorGL 435	−0.1	1107	266	6	Organic peatland	65/277	Black spruce
Ontario Supawn 1: ONSn1	1 – 3	BorGL 277	−0.4	1081	249	10	fS–cS	177/45	Black spruce
Ontario Supawn 2: ONSn2	1 – 3	BorGL 274	−0.1	1082	249	6	Organic peatland	83/254	Black spruce
Ontario Superior 1: ONSu1	1 – 3	BorGL 458	1.7	1200	249	18	SiS–SiL/mS	101/93	Jack pine
Ontario Superior 2: ONSu2	1 – 3	BorGL 461	1.7	1199	250	17	SiS–SiL/mS	122/69	Jack pine
Ontario Tunnel Lake: ONTuL	1 – 3	BorGL 228	4.4	1533	232	18	SiS/cS	175/68	Jack pine
Ontario Whitefin 1: ONWh1	1 – 3	BorGL 480	0.3	1073	270	9	LfS–SiL	108/247	Black spruce
Ontario Whitefin 2: ONWh2	1 – 3	BorGL 480	0.3	1073	270	12	LfS–SiL	122/111	Black spruce

WmHd = Warm Humid; Medit = Mediterranean; WtMt = Western Montane; BorGL = Boreal – Great Lakes. See Powers (2006) for latitude, longitude, annual precipitation and pre-harvest forest conditions.

[a] Based on multivariate analysis of modeled climate variables (McKenney et al., 2006), including mean annual temperature and precipitation, warmest quarter mean temperature and precipitation, precipitation seasonality, growing season length, summer vapor pressure deficit (Ung et al., 2001), potential evaporation (Pereira and de Camargo, 1989 and aridity index (Thornthwaite, 1948).

[b] Cumulative annual growing degree days, base temperature = 5 °C.

[c] Soil texture: C = clay, SiC = silty clay, CL = clay loam, SiCL = silty clay loam, SCL = sandy clay loam, L = loam, SL = sandy loam, SiL = silt loam, Si = silt, SiS = silty sand, LS = loamy sand, vfS = very fine sand, fS = fine sand, mS = medium sand, cS = coarse sand.

[d] Powers, 2006.

[e] California soil groupings (by soil Family): Mesic Typic Dystroxerepts; Mesic Ultic Haploxeralfs; Mesic Typic Palexerults; and Mesic Pachic or Andic Xerumbrepts.

[f] Together referred to as California mixed conifers (CAMxC).

Superimposed at many installations were split-plot treatments of vegetation control (VgCtl) and/or multiple species (Sp) plantings. With vegetation control, competing vegetation was eliminated on half of each plot (VC) with regular applications of herbicide suitable for controlling the predominant competing vegetation, and left untreated on the other half (NVC). All installations were planted to native species except aspen sites, which were left for natural regeneration. Site selection criteria targeted forest types, age classes and soil conditions suitable for active forest management. Thus fully-stocked even-aged stands on mesic sites were often chosen, although in some cases (e.g., Ontario jack pine and black spruce and some California mixed conifer sites) selection criteria also involved nutrient-poor site types considered particularly susceptible to productivity declines associated with harvest removals (Tenhagen et al., 1996; Duckert and Morris, 2001; Powers, 2006). Powers et al. (1990) describe the overall rationale and experimental design, with further information on site conditions, stand characteristics and immediate treatment effects provided by Powers (2006), Fleming et al. (2006), Page-Dumroese et al. (2006) and Sanchez et al. (2006).

The jack pine installations included disc trenching (Sutherland and Foreman, 1995) in the OM_0 and OM_1, one additional compaction treatment (C_2) at four installations, applied after straight-blading (nominal OM_2 – forest floor, stumps and 5–10 cm of mineral soil removed), and vegetation control treatments at three installations. The black spruce installations did not have compaction or VC, and the OM_2 consisted of straight-blading on uplands and winter shear blading of the upper Of horizon on peatlands. Aspen and B.C. conifer installations also did not have VC.

2.2. Measurements

Tenth year plot biomass was obtained by summing individual tree diameter (and sometimes height) – based values, calculated using local (Powers et al., 2005) or previously-published regional biomass equations (cf. Ter-Mikaelian and Korzukhin, 1997; Jenkins et al., 2004). At BCKiR only heights and densities were measured and therefore aspen biomass was estimated from these two measures using regressions developed with the Lake States MI-HuM, MIOtt and MNChi data sets. Woody biomass of non-crop trees was estimated in similar fashion or, together with herbaceous vegetation, as outlined in Powers et al. (1990). Foliar nutrient samples were fall-collected from current or one-year-old upper crown foliage of dominant or codominant conifers (Linder, 1995; Fisher

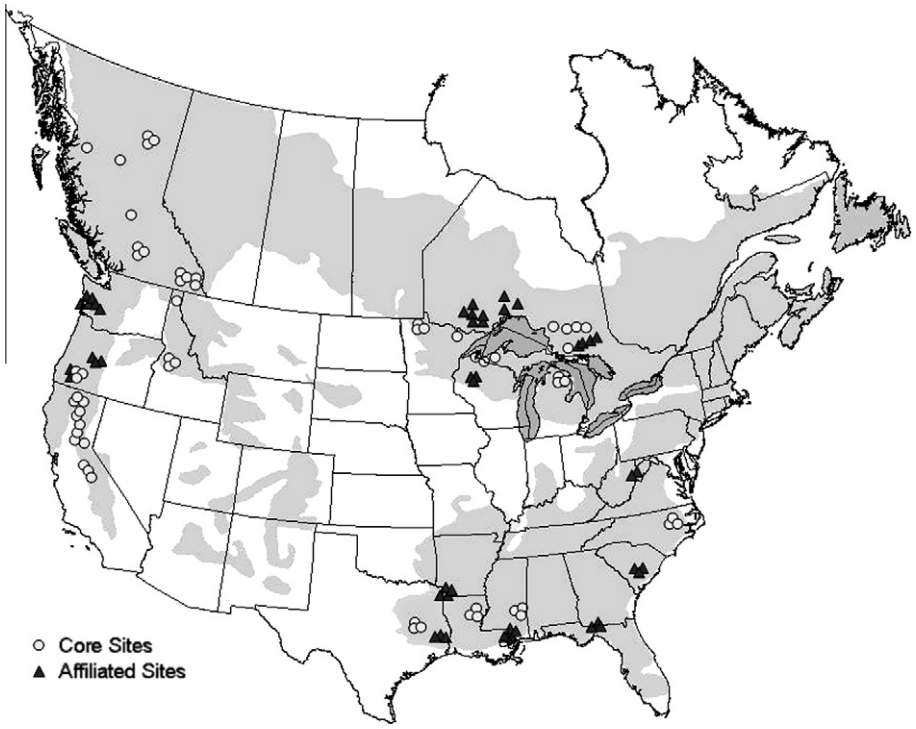

Fig. 1. Geographic locations of North American Long-Term Soil Productivity (LTSP) core and affiliated installations. The shaded portion represents areas of commercially exploitable forest.

and Binkley, 2000), and summer-collected in similar fashion from oaks. Methods of foliar N and P analysis varied somewhat among studies but all investigators followed standard procedures and implemented quality assurance methods including use of standard and reference samples.

2.3. Statistical analyses

We examined response in terms of year 10 planted tree and total woody stand-level above-ground biomass (Mg ha^{-1}), and year 5 or 10 foliar N and P concentrations. We considered five OM-Comp combinations: OM_0C_0, OM_0C_2, OM_1C_0, OM_2C_0, and OM_2C_2, but also used the OM_1C_2 to balance regional factorial ANOVAs. These five represent the OM-C treatment extremes but also include OM_1C_0 which is analogous to full-tree logging with no or limited physical ground impact (depending on installation). To address differences in regional growth rates and hence stages of stand development and nutrient availability (e.g., Oliver and Larson, 1996) we used 5th year foliar analyses for WmHd and Medit studies, and 10th year foliar analyses for Boreal – Great Lakes (BorGL) and Western Montane (WtMt) studies. Spearman rank correlations between 5th and 10th year N and P foliar nutrient concentrations usually ranged from 0.40 to 0.70 and from 0.55 to 0.75, respectively.

We first assessed treatment response across studies on a species-specific regional basis using mixed-model factorial ANOVA (Greenwood, 1994). Given significant treatment/study interactions, individual study treatment (t) differences were assessed as:

$$t = (x_1 - x_2)/(\mathrm{sqrt}(\mathrm{MSE}(1/n_1 + 1/n_2)) \quad (1)$$

where, x_i and n_i represent treatment means and sample sizes, and MSE is the error mean square from the ANOVA. Where treatments/species were not replicated across studies, we analyzed individual studies using standard mixed model ANOVA. OM treatment differences were established using Tukey's multiple comparison test. We selected $p < 0.10$ as the cutoff for statistical significance, but also report actual p values.

We then used meta-analysis to provide an inter-regional quantitative synthesis of biomass response (Gurevitch et al., 2001). We chose the natural logarithm of the response ratio (lnR_0) as the effect-size metric, where R_0 is the ratio of biomass in a given treatment to that in the OM_0C_0 for a particular study. This ratio quantifies the proportional treatment effect and is well suited for situations where the magnitude of response varies considerably among installations (e.g., across climatic regions). Taking the logarithm linearizes the metric and improves sampling distribution normality (Hedges et al., 1999). Weighted effect sizes were calculated from the means, standard deviations and sample sizes (number of replicate plots) for each species – treatment (OM-Comp-VgCtl) combination per replicated study or installation. Observations from the two non-replicated studies (CAPal and IDPrR) were included by assigning them weights similar to those calculated for nearby studies (CADys and IDCou, respectively). The mixed-model factorial ANOVA allowed us to examine site and treatment interactions in detail whereas meta-analysis provided a quantitatively rigorous method with good statistical power for identifying overall trends.

We carried out the meta-analysis using a weighted mixed-model procedure (Rosenberg et al., 2000), and used non-parametric weighted resampling methods (10,000 permutations) to calculate bias-corrected bootstrap 90% confidence intervals (CIs). Groups whose weighted cumulative effect size 90% CIs did not overlap were judged significantly different, and significantly different from the control if their 90% CIs did not overlap zero. All effect-sizes and their CIs are presented following back-transformation to unlogged R values. Aspen studies were analyzed separately because the regeneration mode (suckering) and hence potential treatment effects differed from that of the planted species.

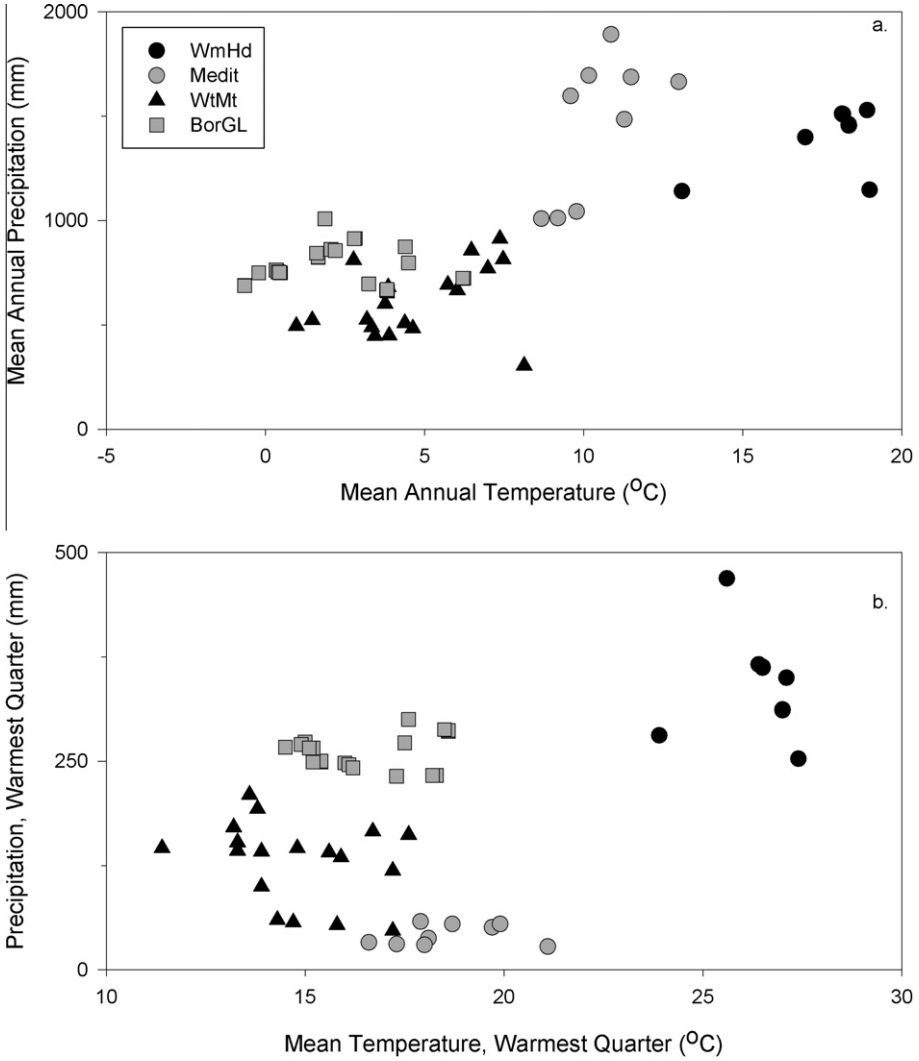

Fig. 2. Climatic groupings of the LTSP installations as illustrated for relationships between modeled: (a) mean annual precipitation and mean annual temperature and (b) mean warmest quarter precipitation and mean warmest quarter temperature. Climate variables for all installations were modeled following McKenney et al., 2006.

We also used agglomerative hierarchical cluster analysis to examine continent-wide similarities in treatment response, providing support for the meta-analysis results and a graphical depiction of overall treatment effects. We employed Ward's minimum variance linkage with relative Euclidean distance and a general distance cut-off value of 1.2 (Hintze, 2007). To explicitly include the OM_0C_0, we used R_{avg}, the ratio of biomass in a given treatment combination to the average value for all treatment combinations for that installation.

To further investigate compaction effects on planted tree biomass, we combine meta-analysis with a modification of Markham and Chanway's (1996) relative neighbour effect to apportion response due to compaction per se, competition influences, and soil disturbance effects as represented by forest floor removal:

$$RE_0 = (R_{0(OM_2C_2)} - R_{0(OM_0C2)})/R_{0max} \quad (2)$$

$$RE_{OM} = (R_{(xOM_2C_2)} - R_{xOM_0C_2})/R_{xOMmax} \quad (3)$$

$$RE_{VgCtl} = (R_{xVC} - R_{xNVC})/R_{xVgCtlmax} \quad (4)$$

Here $R_{0(OM_2C_2)}$ and $R_{0(OM_0C_2)}$ are the response ratios for a given OM-C treatment combination, calculated separately for VC and NVC, based on the OM_0C_0 treatment (i.e., $R_{0(OM_2C_2)} = OM_2C_2/OM_0C_0$; $R_{0(OM_0C_2)} = OM_0C_2/OM_0C_0$), and R_{0max} = maximum $\{R_{0(OM_2C_2)}, R_{0(OM_0C_2)}\}$. Likewise, $R_{x(OM_2C_2)}$ and $R_{x(OM_0C_2)}$ are the response ratios for the C_2 treatment, calculated separately for VC and NVC, where x represents a given OM treatment (i.e., $R_{x(OM_2C_2)} = OM_2C_2/OM_2C_0$ and $R_{x(OM_0C_2)} = OM_0C_2/OM_0C_0$), and R_{xOmax} = maximum $\{R_{x(OM_2C_2)}, R_{x(OM_0C_2)}\}$. Finally, R_{xVC} and R_{xNVC} are the response ratios for VC and NVC, respectively, for the C_2 treatment of a given OM treatment (e.g., $R_{xVC(OM_2C_2)} = OM_2C_2VC/OM_2C_0VC$ and $R_{xNVC(OM_2C_2)} = OM_2C_2NVC/OM_2C_0NVC$), and $R_{xVgCtlmax}$ = maximum $\{R_{xVC}, R_{xNVC}\}$. *RE* values represent the proportional change in response ratios of the first vs. the second variable within brackets. For validation, we compared these results with those obtained with factorial ANOVAs of each study by looking for OM (OM_0, OM_2) × Comp (C_0, C_2) and Comp × VgCtl interaction effects.

3. Results

3.1. Biomass

3.1.1. ANOVA of intra-regional response

Tenth year planted tree biomass showed no consistent OM response in any region. Where present, study differences within a given region were idiosyncratic (Table 3), and with black spruce, attributable to differences in survival. Compaction generally increased planted tree biomass across WmHd studies, but effects

Table 2
Treatment Abbreviations (Powers, 2006).

Treatment type	Symbol	Description
Modify site organic matter (OM)	OM_0	Tree boles removed. Crowns, branches, woody and herbaceous understory and forest floor retained
	OM_1	Boles, crowns and branches removed. Woody and herbaceous understory and forest floor retained
	OM_2	All aboveground biomass, including forest floor, removed
Modify soil porosity through compaction (Comp)	C_0	No soil compaction
	C_2	Soils substantially compacted
Modify non-crop tree vegetation through vegetation control (VgCtl)	VC	Vegetation control – non-crop tree vegetation removed
	NVC	No vegetation control – all vegetation develops unhindered
Apportioning compaction response based on proportional change in response ratios (*RE*) (see Eqs. (2)–(4))	$R_{0(OM_xC_2)}$	Response ratio for a given OM_x-C_2-VgCtl treatment calculated as OM_xC_2/OM_0C_0 for the same VgCtl treatment, where *x* represents a given OM treatment (OM_0 or OM_2). Relative response ratios (RE_0) are based on differences between OM_xC_2 and OM_0C_0 response ratios for a given VgCtl treatment
	$R_{x(OM_xC_2)}$	Response ratio for a given OM_x-C_2-VgCtl treatment calculated as OM_xC_2/OM_xC_0 for the same VgCtl treatment. Relative response ratios (RE_{OM}) are based on differences between OM_2C_2 and OM_0C_2 response ratios for a given VgCtl treatment
	$R_{x(VgCtl)}$	Calculated similarly to $R_{x(OMxC2)}$ above but where subsequent relative response ratios (RE_{VgCtl}) are based on differences between VgCtl treatment response ratios for a given OM_xC_2/OM_xC_0 treatment combination
	R_{0max}, R_{xOMmax}, $R_{xVgCtlmax}$	Larger of the two contrasting response ratios for a given comparison

were not significant for California (Medit) studies or for central BC (BCSBS). In contrast, VC increased planted tree biomass in almost all locations where it was applied (e.g., Fig. 3a).

Total stand biomass also showed no consistent response to OM treatment (Table 4). Where OM × study interactions occurred, however, OM_2 treatments often had the lowest biomass. Compaction generally increased WmHd total stand biomass, but had a negative effect on total stand biomass of aspen installations with finer-textured soils. While Medit studies showed no significant OM-Comp responses, overall stand biomass was consistently greater with NVC (Fig. 3b). In contrast, total stand biomass was greater with VC for several WmHd loblolly pine studies, and at BorGL jack pine installations having vegetation control comparisons.

3.1.2. General trends in biomass accumulation – OM_0C_0 cross-region comparisons

To provide context in terms of stand development and response ratio comparisons, we plotted OM_0C_0 above-ground biomass across the range of studies and species, using VC values for planted trees to express maximum growth, but average values (NVC and VC) for total stand biomass because vegetation control effects on this variable were inconsistent. The largest planted tree biomass was found in WmHd climates where loblolly and shortleaf pine attained 46–90 Mg ha^{-1}(Fig. 4a). Medit mixed conifer values ranged from 12 to 35 Mg ha^{-1}, while those of BorGL jack pine and WtMt conifers in Idaho ranged from 8 to 20 Mg ha^{-1} and from 12 to 28 Mg ha^{-1}, respectively. In contrast, BorGL black spruce and WtMt BCSBS conifer values (although generally with NVC) were almost always <7 Mg ha^{-1}. Substantial differences between fast-growing conifers (larch and hard pines) and other species were noted with multiple species plantings at IDCou and MOCaC.

Tenth year total stand biomass generally followed similar trends, except for Medit studies (Fig. 4b). On Medit installations large amounts of shrubby biomass resulted in values often approaching those on WmHd sites. Total biomass for aspen stands ranged from 5 to 35 Mg ha^{-1} among the four installations.

3.1.3. Meta-analysis of treatment response ratios – regional treatment comparisons

Overall, planted tree biomass was greater in the OM_0C_2 than in the OM_0C_0 and OM_2C_0, with that in the OM_1C_0 slightly exceeding the OM_0C_0 (Fig. 5a). The OM_2C_0 generally increased BorGL but not WtMt planted conifer biomass over the OM_0C_0. In comparison, the OM_1C_0 increased WtMt and BorGL black spruce but not BorGL jack pine planted tree biomass.

Planted tree response in Medit and WmHd climates varied with vegetation control (Fig 5b): in Medit climates OM_0C_2 values were distinctly greater than those of the OM_0C_0 with VC, whereas with NVC the most notable trend was the low OM_1C_0 values. In WmHd climates planted conifer biomass in the OM_0C_2, and in the OM_2C_2 with NVC, exceeded that in the OM_0C_0, whereas with VC that in the OM_2C_0 was the lowest.

Total stand biomass with NVC[3], for all planted tree studies combined, showed no significant OM-C effects. Response among individual species groups, however, varied considerably (Fig. 5c). WmHd loblolly pine OM_1C_0 and OM_2C_0 values were lower than those in the OM_0C_0 and the OM_0C_2. In contrast, OM_0C_0 values for Medit mixed conifers were the lowest of any treatment and significantly lower than those in the OM_1C_0 and OM_2C_0. In more limited treatment combinations, BorGL black spruce OM_1C_0 values exceeded those in the OM_0C_0, whereas jack pine OM_2C_0 and OM_2C_2 values fell below those for the OM_0C_0. With aspen, values were highest in the OM_1C_0, and distinctly lower with compaction (OM_0C_2 and OM_2C_2).

Overall, the proportional effect of forest floor removal, in addition to compaction, when compared with the OM_0C_0, was to reduce the relative advantage of compaction (RE_0) by 11.1% ($p = 0.089$) (Fig. 6a), with fairly similar trends across VgCtl and climate groups. With either NVC or VC, the relative impact of compaction with vs. without forest floor removal (i.e., RE_{OM}) was not significant overall ($p = 0.469$–0.607) (Fig. 6b and c), but for VC was greater with the OM_0C_2 by 39.6% in Medit climates ($p = 0.099$). Proportional growth attributable to compaction effects on competition (i.e., RE_{VgCtl} for a given R_x(OM-Comp)) was not significant overall for the OM_0C_2 ($p = 0.792$) or OM_2C_2 ($p = 0.199$) (Fig. 6d and e), although with the latter the RE_{VgCtl} value of 20.1% was equivalent to 75.3% of the compaction-related treatment gain over the OM_2C_0.

Factorial ANOVAS of the studies used in the above *RE* analyses usually did not show significant ($p < 0.10$) OM × Comp (for VC and NVC separately) or Comp × VgCtl (for OM_0 and OM_2

[3] With VC, total stand and planted tree biomass with VC were usually very similar.

Table 3
Effects of study, organic matter removal (OM), compaction (Comp) and vegetation control (VgCtl) on intra-region planted tree biomass (Mg ha^{-1}). Significant differences ($p < 0.10$) are shown in bold, with individual treatment differences noted below. *N* is the number of individually replicated studies for a given region. All *p* values for Comp interactions, except for WtMt OM × Comp were >0.10 (not shown). See Table 1 for climate region, study and species codes.

Region/species	Planted tree biomass (kg ha^{-1})						
	Study	OM	Study × OM	Comp	VgCtl	Study × VgCtl	OM × VgCtl
WmHd lobP[a]	**<0.001** *N* = 4	0.217	0.161	**0.004** $C_2 > C_0$	0.182	**<0.001** LA, MS, NC : VC > NVC	0.351
WmHd rO[a,b]	MOCaC	0.425	n/a	0.851	**0.001** VC > NVC	n/a	0.438
WmHd wO[a,b]	MOCaC	0.587	n/a	**0.020** $C_2 > C_0$	**<0.001** VC > NVC	n/a	0.634
WmHd slP[a,b]	MOCaC	0.963	n/a	**0.014** $C_2 > C_0$	**<0.001** VC > NVC	n/a	0.484
Medit. CAMxC[a]	**0.018** *N* = 3	0.670	0.739	0.361	**0.070**	**0.001** All studies: VC > NVC	0.388
WtMt La[b]	IDCou	0.951	n/a	0.338	**<0.001** VC > NVC	n/a	0.298
WtMt pP, C_0 [a,b,c]	IDCou	0.341	n/a	n/a	**0.046** VC > NVC	n/a	**0.050** OM_2: VC > NVC; VC: $OM_2 > OM_1$
WtMt pP, C_2 [a,b,c]	IDCou	**0.005** OM_2, $OM_0 > 0M_1$	n/a	n/a	**0.032** VC > NVC	n/a	0.882
WtMt DF, C_0 [a,b,c]	IDCou	0.145	n/a	n/a	0.159	n/a	0.367
WtMt DF, C_2 [a,b,c]	IDCou	**0.048** OM_0, $OM_1 > OM_2$	n/a	n/a	0.806	0.396	n/a
WtMt lpP[b]	BCSBS	0.882	n/a	0.935	n/a	n/a	n/a
WtMt xS[b]	BCSBS	0.627	n/a	0.868	n/a	n/a	n/a
BorGL jP[d]	**<0.001** *N* = 6	0.686	0.342	n/a	n/a	n/a	n/a
BorGL jP[e]	**<0.001** *N* = 3	0.662	**0.006** ONNeL: $OM_1 > OM_2$; ONTuL: $OM_2 > 0M_1$	n/a	**0.099**	**0.004** All Studies: VC > NVC	**0.096** OM_1C_0: VC > NVC
BorGL bS Upland[d,f]	**<0.001** ***N*** = 5	**0.051** OM_1, $OM_2 > 0M_0$	0.214	n/a	n/a	n/a	n/a
BorGL bS Lowland[d,f]	**<0.087** *N* = 4	0.985	0.0.148	n/a	n/a	n/a	n/a

[a] OM – Comp 3 × 2 factorial, with nested VgCtl treatments.
[b] Species was a significant ($p = 0.001$) nested factor.
[c] OM × Comp was a significant interaction term ($p < 0.10$).
[d] OM treatments only, jack pine with VC, black spruce with NVC. With jack pine there was no significant difference ($p = 0.736$) between the OM_2C_0 and OM_2C_2 ($N = 4$).
[e] Jack pine comparisons for studies with VgCtl treatments.
[f] Upland black spruce studies include dry sandy (ONGer and ONSn1)and shallow-to-bedrock coarse loamy soils (ONFe1-3); lowland black spruce studies include wet mineral (ONWh1-2) and peatland soils (ONR62 and ONSn2).

separately) interactions, supporting the general independence of OM, Comp and VgCtl effects. In particular, there were no such interactions for any of the four WmHd studies or for two of the three Medit studies, with the only occurrence a Comp × VgCtl (OM_0 only) interaction ($p = 0.077$) for CAHap, resulting from larger C_2 values with VC than with NVC (i.e., the opposite effect expected if compaction also reduced competition). For IDCou, no significant interactions occurred with western larch or ponderosa pine, whereas significant Douglas-fir OM × Comp interactions, both with VC ($p = 0.037$) and NVC ($p = 0.078$), resulted from $OM_0C_2 > OM_0C_0$ but $OM_2C_2 < OM_2C_0$. The decrease in OM_2 biomass with compaction was rarely found elsewhere.

3.1.4. Relative treatment response across regions

Cluster analysis of both 10th year planted tree and total stand biomass R_{avg} values across studies with all five primary OM-Comp combinations showed close linkages between the OM_0C_2 and OM_2C_2, and between the OM_0C_0 and OM_1C_0 (Fig. 7a and b). The OM_2C_0, however, showed closer affiliation with compaction treatments for planted tree response, and with non-compacted treatments for total biomass response. When VgCtl was also considered, the closest linkages for planted tree response invariably occurred first between vegetation control treatments within a given OM-Comp treatment, and then among OM-Comp treatments (Fig. 7c).

3.2. Foliar nutrition

3.2.1. ANOVA of intra-regional response

Regional trends indicated relatively low conifer P concentrations and high N/P ratios for WmHd studies whereas spruce N concentrations and N/P ratios in particular were often lower in more northern regions (Fig. 8). Foliar N/P ratios in the OM_0C_0 averaged 15.9 ± 0.6 for loblolly pine, 11.7 ± 0.2 for jack pine and 6.6 ± 0.2 for black spruce. For a given region, however, there were often strong inter-study variations (Table 5). OM-Comp treatments had little effect on loblolly pine foliar nutrition, although compaction when combined with VC, increased N/P ratios. At MOCaC, red oak foliar nutrition did not respond significantly to treatment, whereas white oak N/P ratios were greater in the OM_0 than in the OM_1 or OM_2. Shortleaf pine had greater P concentrations and lower N/P ratios (14.7 vs. 16.6) with C_2 than with C_0.

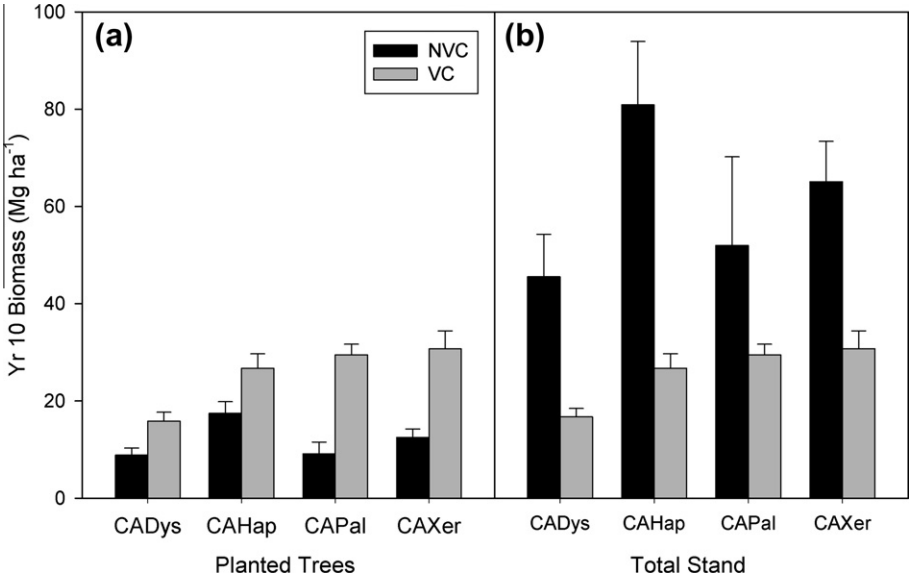

Fig. 3. Mean 10th year response (±standard errors) to vegetation control (all OM-Comp treatments combined) for Mediterranean (California) studies in terms of mixed conifer: (a) planted tree biomass and (b) total stand biomass. See Table 1 for study codes.

Table 4
Effects of study, organic matter removal (OM), compaction (Comp) and vegetation control (VgCtl) on intra-region total stand biomass (Mg ha^{-1}). Significant differences ($p < 0.10$) are shown in bold, with individual treatment differences noted below. *N* is the number of individually replicated studies. All *p* values for VgCtl interactions, except Study × VgCtl, were >0.10 (not shown). See Table 1 for climate region, study and species codes.

Region/species	Total biomass (Mg ha^{-1})							
	Study	OM	Study × OM	Comp	Study × Comp	OM × Comp	VgCtl	Study × VgCtl
WmHd lobP[a]	**<0.001** *N* = 4	0.294	**0.099** MSFre: $OM_0 > OM_1, OM_2$; TXKur: $OM_0 > OM_2$	**0.080** $C_2 > C_0$	0.485	0.870	0.105	**<0.001** LA, MS, NC : VC > NVC
Medit. CAMxC[a]	**0.048** *N* = 3	0.887	0.857	0.772	0.388	0.345	**0.035** NVC > VC	0.302
BorGL/WtMt As[b]	**<0.001** *N* = 4	0.470	0.414	0.318	**<0.001** MNChi: $C_0 > C_2$	0.271	n/a	n/a
BorGL jP[c],	**<0.001** *N* = 6	**0.065**	**0.076** ONSu1, ONSu2: $OM_0 > OM_2$	n/a	n/a	n/a	n/a	n/a
BorGL bS Upland[d]	**<0.001** *N* = 5	**0.084** $OM_1, OM_2 > OM_0$	0.186	n/a	n/a	n/a	n/a	n/a
BorGL bS Lowland[d]	**<0.001** *N* = 4	0.048	**0.037** ONWh1, ONWh2:OM_0, $OM_1 > OM_2$	n/a	n/a	n/a	n/a	n/a

[a] OM – Comp 3 × 2 factorial design with nested VgCtl treatments.
[b] OM – Comp 3 × 2 factorial design, no vegetation control. Included in this analysis are BCKiR, MNChi, MIHuM and MIOtt.
[c] OM treatments only, VC. There was no significant difference ($p = 0.290$) between OM_2C_0 and OM_2C_2 ($N = 4$), whereas for studies with OM – VgCtl treatments ($N = 3$), total biomass was significantly greater ($p < 0.061$) with VC.
[d] OM treatments only, NVC: upland sites include ONFen1-3, ONGer and ONSn1; lowland sites include ONWh1-2, ONR62 and ONSn2.

For BorGL but not WtMt studies, foliar nutrient concentrations were usually lower with the OM_2. Compaction had no significant effect on western white pine or jack pine OM_2 foliar nutrition, but increased Douglas-fir N concentrations at IDPrR. Limited data from Medit sites showed no significant response in ponderosa pine N concentration to OM-Comp treatments at two installations (Challenge and Rogers), with greater N concentrations in OM_2 than OM_0 at a third (Blodgett) (Gomez et al., 2002b). At Wallace, mean mixed conifer N concentrations were somewhat greater ($p = 0.050$) in the OM_2 than in the OM_0.

In contrast, vegetation control often affected foliar nutrition (Fig. 9). With WmHd loblolly pine, VC increased N but decreased P concentrations for all four studies, and increased N/P ratios at three of these. In California, both Wallace ($p = 0.039$) and Central ($p = 0.012$) showed increased N concentrations with VC. However, at more northern locations (e.g., Ontario jack pine and Idaho mixed conifers) vegetation control had no significant effects.

3.2.2. Foliar nutrition – biomass relationships: intra-regional comparisons

Loblolly pine foliar N and P concentrations and N/P ratios showed relatively strong negative correlations overall with 10th year planted tree and total stand biomass across studies (Table 6). For individual studies, however, correlations were usually not significant ($p > 0.10$). At MOCaC, white oak showed no significant correlations but shortleaf pine foliar N (+ve) and N/P ratios (−ve) of both red oak and shortleaf pine with VC were significantly correlated with 10th year biomass. IDPrR western white pine and BCSBS lodgepole pine foliar nutrition was not correlated ($p > 0.10$) with 10th year planted tree biomass, but there were positive correla-

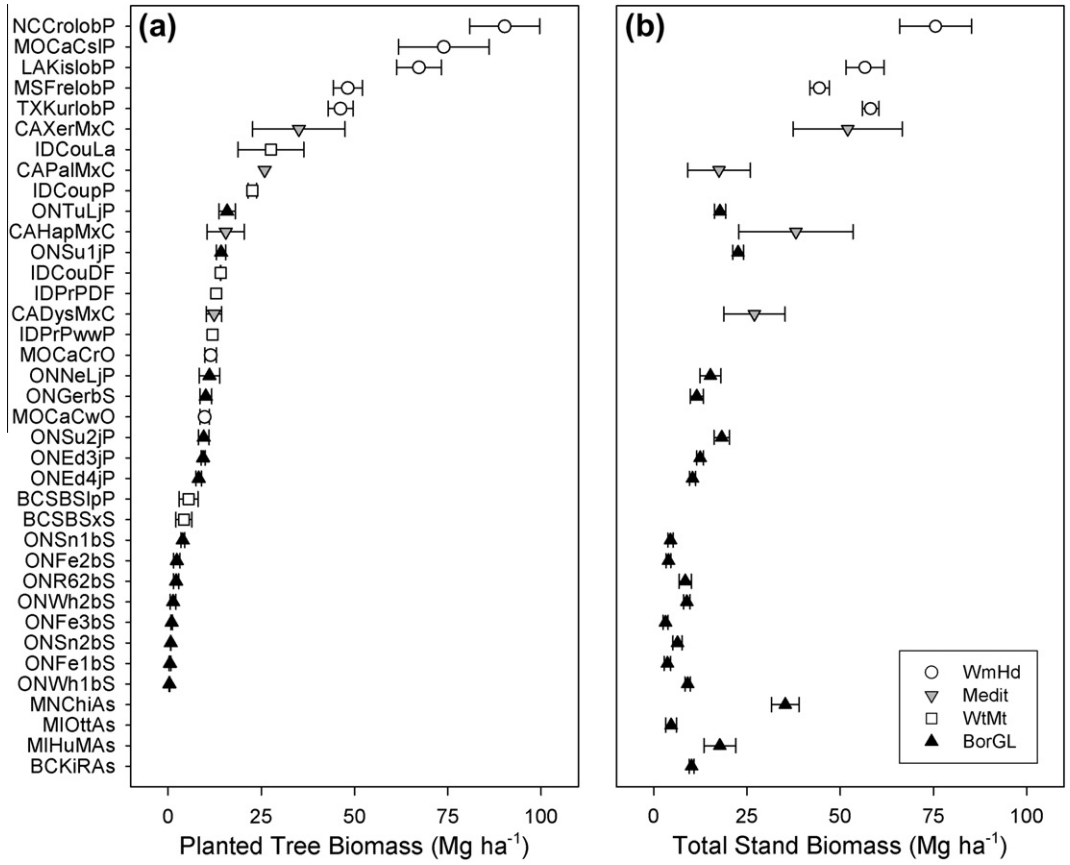

Fig. 4. Mean OM_0C_0 10th year biomass for various study – species combinations: (a) planted tree biomass, with vegetation control where present and (b) total stand biomass, NVC and VC combined. Horizontal bars indicate standard errors of the mean. See Table 1 for study and species codes.

tions between foliar nutrients and biomass production for IDPrR Douglas-fir (N concentration) and BCSBS hybrid spruce (P concentration). Across most BORGL jack pine and black spruce studies (e.g., excluding peatland black spruce and ONTuL jack pine), foliar N and P concentrations were positively correlated with 10th year planted tree biomass and, excluding black spruce foliar N concentration, with total stand biomass (although to a lesser degree). Jack pine total stand biomass was also positively, although weakly ($\tau = 0.218$) correlated with N/P ratio. At a finer scale, while positive correlations were also found with some installation groupings (e.g., black spruce wet mineral (ONWh1-2) and shallow loamy (ONFe1-3), and jack pine ONSu1-2 and ONEd3-4), these were often not as strong as those reported overall. The exception to this was several positive correlations of planted tree biomass (black spruce ONFe1-3, jack pine ONTuL) or total stand biomass (jack pine ONSu1-2 and ONEd3-4) with N/P ratios.

4. Discussion

4.1. Organic matter removal

The absence of consistent planted tree and total stand biomass responses to OM treatments highlights the site- and region-specific nature of treatment response. Nevertheless, the overall lack of differentiation of OM_0 vs. OM_1 treatments, in terms of both biomass and foliar nutrition, is notable. Studies by Olsson et al. (2000) showed lower OM_1 foliar N concentrations on N-deficient sites relative to OM_0 8–10 years after planting, consistent with subsequent growth declines (Egnell and Valinger, 2003). Other studies (Proe and Dutch, 1994; Smith et al., 2008) have demonstrated sizeable growth declines with OM_1 vs. OM_0 treatments despite limited foliar nutrient response. Possible contributing factors to the lack of response in our studies include: (1) most LTSP installations were established on deep, relatively productive soils where nutrient limitations are less likely because of greater quantities and proportions of nutrients left on-site (Malkonen, 1976; Weetman and Algar, 1983; Gordon, 1983; Mendham et al., 2003); (2) the operational nature of OM_1 (full-tree logging) treatments on the less productive jack pine and black spruce sites whereby substantial quantities of fine and coarse woody material were left on-site (Duckert and Morris, 2001; Hazlett, unpublished data); (3) mounting evidence that soil microorganisms may play important roles in enhancing tree nutrition by utilizing otherwise inaccessible organic and/or mineral nutrient reserves (Kranabetter et al., 2006; Paul et al., 2007; Ouahmane et al., 2009), and (4) that despite overall trends, there are instances of significant reductions in OM_1 vs. OM_0 biomass for some individual installations (e.g., MSFre (Scott et al., 2007) and CAPal (Powers and Fiddler, 1997).

Further, while site fertility may prove sufficient regardless (Johnson and Todd, 1998; Briggs et al., 2000; Walmsley et al., 2009), considerable potential for declines still exists since most installations have not reached full canopy closure and hence maximum leaf area and peak soil nutrient demand (Switzer and Nelson, 1972; Miller, 1995, see Du Toit et al., 2008; Mason et al., 2012). For instance, results from similar research in a broad network of fast-growing tropical and subtropical plantations show dominant height (a productivity index) responses to harvest residue treatments were seldom manifest until heights reached 10–12 m (i.e., full canopy closure)(Saint-André et al., 2008). The majority of our

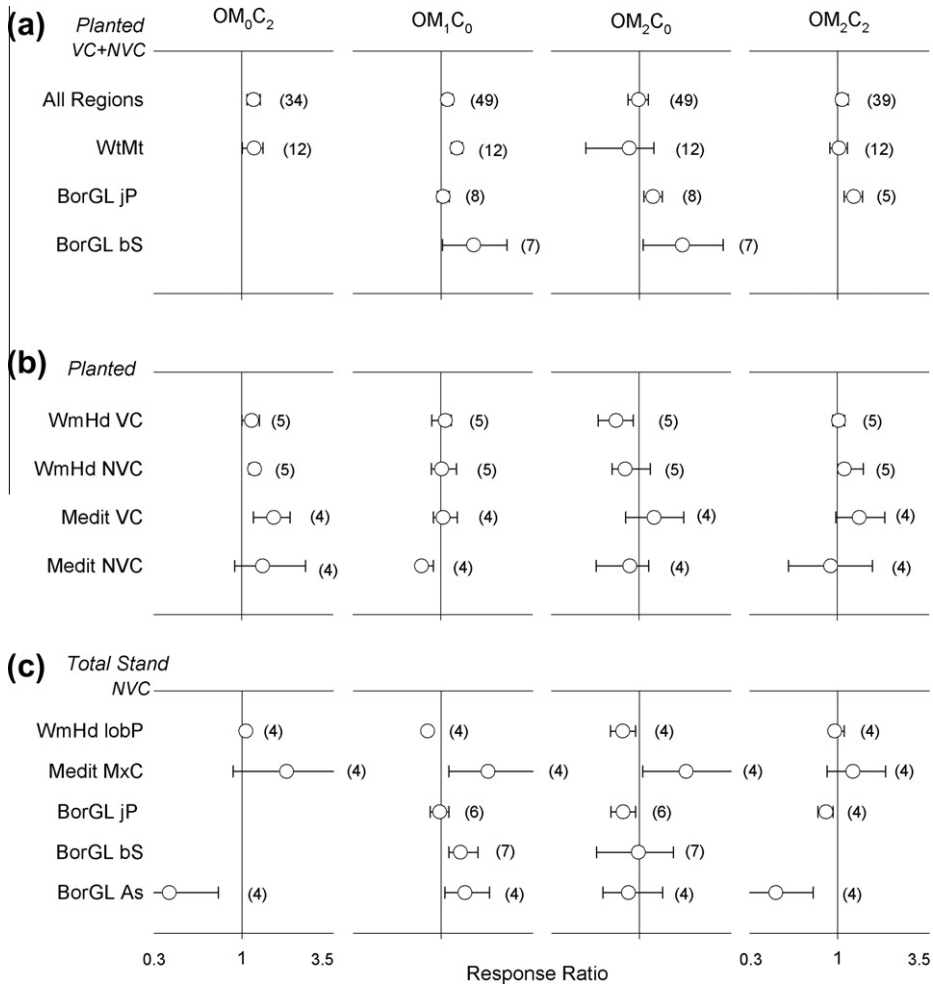

Fig. 5. Tenth year biomass (Mg ha^{-1}) response ratios by OM-Comp treatment relative to the OM_0C_0: (a) planted tree ratios, overall and by climate region, VC and NVC combined; (b) planted tree ratios for Medit and WmHd studies, calculated separately for VC and NVC; and (c) total stand ratios by species grouping (NVC only). Horizontal bars represent bias-corrected bootstrap 90% confidence intervals. Values in parentheses are the number of studies per category. See Table 1 for climate region and species codes. Note: total stand and planted tree values with VC were usually very similar.

sites have yet to reach this stage. Using a larger database which incorporated Gulf States LTSP installations, Scott and Dean (2006) found that on average the OM_1 reduced loblolly pine biomass accumulation by 18% compared with the OM_0 7–10 years after harvest. The greatest declines were associated with poorer quality P-limited sites (Scott and Dean, 2006). Since these stands were comparatively well-advanced in terms of tree size, development stage (cf. Oliver and Larson, 1996) and thus soil nutrient demand, these results may be a precursor for nutrient-poor sites in other regions. In this regard, however, these Coastal Plain soils are notoriously low in mineral soil P with nutrient reserves residing almost exclusively in surface organic layers (Pritchett, 1979), and thus more susceptible to P deficiencies from factors which disrupt organic P cycling (e.g., enhanced biomass removals) than most other North American soils.

Differing responses among regions to the OM_2C_0 were still evident at year 10, although biomass responses were often not as marked as at year 5 (Fleming et al., 2006). WmHd pines continued to show reduced OM_2C_0 total stand biomass overall, particularly at TXKur and MSFre. Hence the lack of OM effects on planted tree foliar nutrition on these nutrient-deficient soils (Allen, 1987) is noteworthy. While these results are consistent with a lack of treatment effects on 10th year total soil N, 10th year extractable soil P was reduced with increasing OM removal at both LAKis and NCCro (Sanchez et al., 2006). Further, both overall foliar P concentrations <0.9 g kg^{-1} (Fisher and Binkley, 2000) and N/P ratios $\geqslant$15 (Güsewell, 2004; Ågren, 2008) suggest P deficiencies. Finally, the negative cross-study correlations we found between foliar N/P ratios and loblolly pine biomass with VC are consistent with the positive relationships between pre-harvest soil P availability and relative OM_1/OM_0 response reported by Scott and Dean (2006).

Greater nutrient demands by larger trees, together with dilution effects through increased fascicle growth, may account for the negative overall correlations between planted loblolly pine biomass and foliar N and P concentrations (c.f., Zutter et al., 1999), whereas the lack of significant OM treatment effects on planted tree foliar nutrition and biomass at the study level is consistent with much greater variation in soil nutrient availability between sites than among treatments at a given site (e.g., Li et al., 2003; Kranabetter and Chapman, 2004).

Initial beneficial effects of OM_2C_0 on planted BorGL black spruce and jack pine biomass (Fleming et al., 2006), while still evident because of enhanced survival, were dissipating, and for total stand biomass, reversing in some cases (e.g., ONWh1, ONWh2, ONSu1, and ONSu2). We suspect these reversals reflect both changes in resource limitations from primarily microclimatic to nutrient-driven with stand development, as well as the impact of continued ingress of naturals in the OM_0 and OM_1 on total stand biomass. Reduced jack pine and black spruce nutrient concentrations and N/P ratios in the OM_2 are consistent with soil nutrient limitations in similar

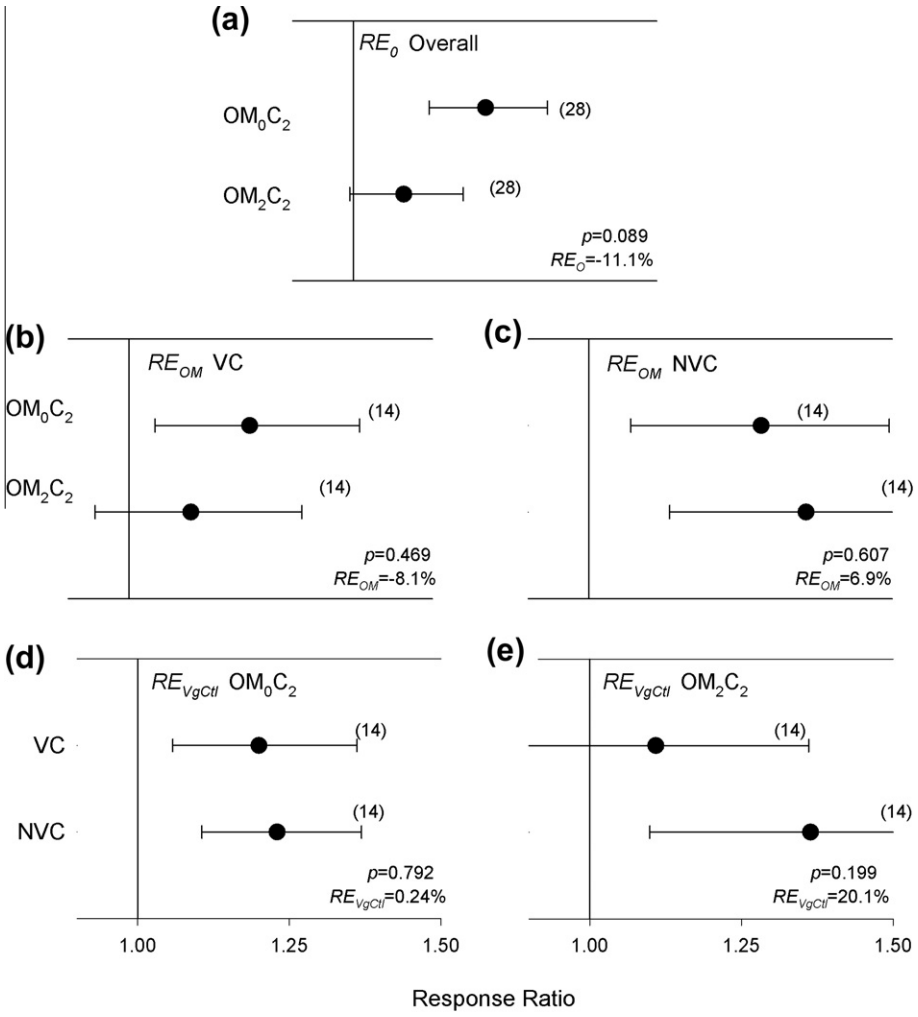

Fig. 6. Tenth year planted conifer biomass (Mg ha^{-1}) response ratios for compaction treatments: (a) RE_0 – OM_0C_2/OM_0C_0 and OM_2C_2/OM_0C_0 ratios, VC and NVC combined; (b and c) RE_{OM} – OM_0C_2/OM_0C_0 and OM_2C_2/OM_2C_0 ratios, compared separately for VC and NVC, respectively, and (d and e) RE_{VgCtl} – OM_0C_2/OM_0C_0 and OM_2C_2/OM_2C_0 ratios, VC vs. NVC, respectively. Horizontal bars represent bias-corrected bootstrap 90% confidence intervals. Values in parentheses are the number of studies per category.

treatments (Munson and Timmer, 1995) and with N limitations in recently glaciated (e.g., boreal) soils (Tamm, 1991; Vitousek et al., 1993).

While not evident with multi-study ANOVA, meta-analysis indicated the OM_1C_0 increased 10th year total stand biomass in aspen stands relative to the OM_0C_0. Other studies have also noted enhanced initial aspen stand growth, often reflecting increased aspen densities, with full-tree versus stem-only logging (Bella, 1986; Shepperd, 1996; Kabzems and Haeussler, 2005). Slash removal may stimulate stand growth by increasing soil temperatures and reducing physical obstructions to sucker emergence (Maini and Horton, 1966; Frey et al., 2003). Lack of 10th year OM_2C_0 vs. OM_0C_0 differences are consistent with the relative lack of longer-term effects of mechanical site preparation on aspen production (Fraser et al., 2006). By combining all relevant studies and more heavily weighting those with lower variances, meta-analysis provides greater power in detecting overall trends (e.g., OM_1C_0 vs. OM_0C_0). Interaction effects, however, were not considered; thus with our meta-analysis the positive effects of the OM_2C_0 on total stand biomass on clay loams at MIOtt offset negative effects on lighter soils at MIHuM and MNChi (Voldseth et al., 2011), and both went undetected.

For Medit studies and with BCSBS spruce the OM_2C_0 did not significantly affect planted tree biomass. However the OM_2C_0 enhanced foliar N concentrations at some of these installations despite N mineralization rates as low as or lower than the OM_0C_0 (Gomez et al., 2002b; Kranabetter et al., 2006). Both vector and critical concentration analyses of year 5 foliar nutrition suggest that N is not a major growth-limiting factor for our Medit sites (Gomez et al., 2002b), but 10th year hybrid spruce foliar N concentrations indicated severe deficiency.

Finally, results from the CIFOR (Centre for International Forestry Research) network examining residue retention effects in fast-growing Eucalypt plantations provide important contrasts. There half of the 10 study sites showed some improvement in late-rotation dominant height with increased slash retention, although substantial reductions in OM_2 vs. OM_0 – type treatments were only evident in two cases (Saint-André et al., 2008). Across the entire 16-site CIFOR network (which includes other fast-growing species) positive stand productivity responses to increased residue retention (especially double slash treatments) (Nambiar and Kallio, 2008) were usually associated with more nutrient-poor sites (e.g., Deleporte et al., 2008; Mendham et al., 2008; Gonçalves et al., 2008).

4.2. Soil compaction

Perhaps the most notable result to date is the marked positive planted conifer growth response to compaction. While many studies have identified negative compaction-related effects (Froehlich

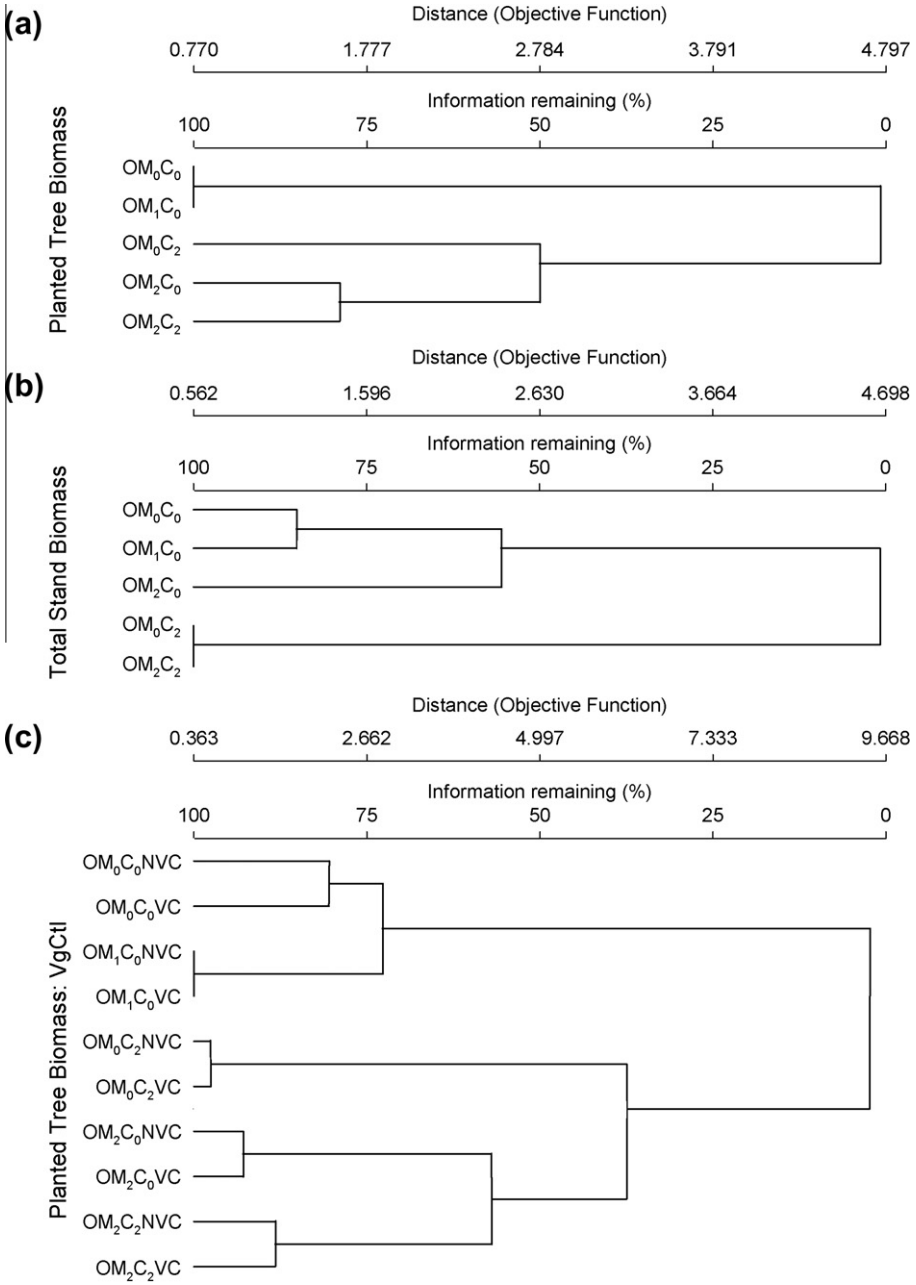

Fig. 7. Cluster analysis of 10th year R_{avg} values for the five primary OM-C treatment combinations: (a) planted tree biomass, VC and NVC combined; (b) total stand biomass, VC and NVC combined, and (c) planted conifer biomass, calculated separately for VC and NVC.

and McNabb, 1984; Froehlich et al., 1986; Kozlowski, 1999), positive effects on stand productivity, particularly on better-drained soils with coarser textures, high carbon contents and/or low bulk densities, are increasingly being recognized (Brais, 2001; Gomez et al., 2002a; Aries et al., 2005). Factors include increased soil moisture and temperature regimes (Sikora et al., 1990; Gomez et al., 2002a,b; Aries et al., 2005), and nutrient availability and uptake rates (Arvidsson, 1999; Li et al., 2003), as well as indirect effects through vegetation control (Brais, 2001; Godefroid and Koedam, 2004; Ponder, 2009).

Sixty percent of the locations reported here have sandy to coarse loamy soils, with another 30% having clay loam soils, and the large majority being relatively well-drained. Thus wetter and clay-dominated sites, where negative compaction effects on soil aeration, root development and nutrient supply are often identified (Greacen and Sands, 1980; Kozlowski, 1999; Kelting et al., 2000), were distinctly under-represented. While compaction did increase bulk densities, increases were smallest at installations with the highest initial bulk densities (i.e., >1.4 Mg m^{-3}) (Powers et al., 2005), and always remained above the growth-limiting values proposed by Daddow and Warrington (1983). Negative effects of compaction on biomass production were limited to a few finer-textured soils (e.g., MNChi aspen and CACha ponderosa pine).

Many studies relating harvest traffic intensity to subsequent stand growth did not separate compaction effects per se from related soil disturbances including organic matter displacement, vegetation removal, changes in soil structure and microtopographic alteration (Powers, 1999; Aries et al., 2005). Our OM-Comp-VgCtl treatment combinations provide increased clarity in this regard. Overall, the positive effects of compaction on planted conifer biomass were reduced by 11% when combined with forest floor removal. Better overall planted tree growth with the OM_0C_2 than

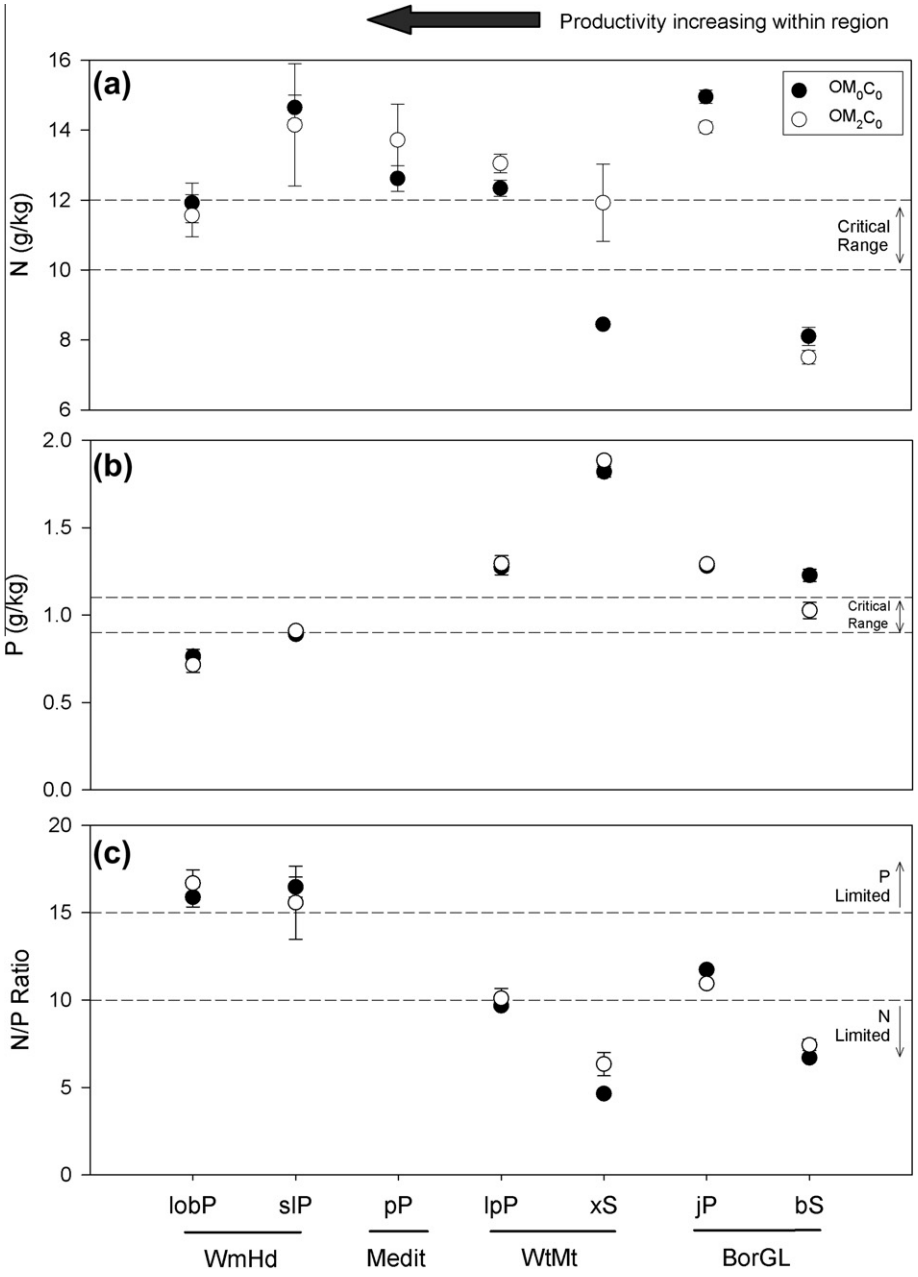

Fig. 8. Mean upland conifer OM_0C_0 and OM_2C_0 foliar nutrient concentrations ± standard errors, VC and NVC combined for (a) N, (b) P, and (c) N/P ratios, by climate region and species (see Table 1 for codes). Dashed lines indicate common ranges of critical N and P concentrations for many conifers (Fisher and Binkley, 2000). N/P ratios <10 or >15 are often considered indicative of N and P limitations, respectively (Güsewell, 2004).

the OM_2C_2 or the OM_0C_0 indicates that negative effects associated with vehicle traffic on similar sites may be more reflective of general soil disturbance including organic matter loss.

In comparison, compaction effects attributable to vegetation control (RE_{VgCtl} values) accounted for only 2.4% of the planted tree biomass or 13.0% of the overall advantage of the OM_0C_2 over the OM_0C_0, but 20.1% and 75.3%, respectively, of the advantage of the OM_2C_2 over the OM_2C_0. Thus vegetation control influences did not contribute substantively to the positive effects of compaction per se (OM_0C_2) on planted conifer growth. In contrast, despite less benefit to conifer growth overall (i.e., vs. the OM_0C_0), a substantial portion of the OM_2C_2 advantage over the OM_2C_0 was associated with vegetation control. While compaction can alter plant community composition and abundance (Powers and Fiddler, 1997; Haeussler and Kabzems, 2005; Scott et al., 2007; Ponder, 2009; Voldseth et al., 2011), this largely involves impacts on shoots and bud banks, and hence vegetative regrowth. Forest floor removal reduces buried seed banks, as well as shoot and bud banks, while simultaneously enhancing seedbed receptivity for many species. Subsequent compaction may alter seedbed receptivity and destroy newly-established germinates. Thus compaction effects on planted tree growth and understory abundance may or may not be strongly linked, depending on the type and degree of forest floor disturbance.

It is noteworthy that other traffic-related soil impacts such as soil mixing and displacement, loss of aggregation, surface crusting, soil dispersion and surface waterlogging (Herbauts et al., 1996; Startsev and McNabb, 2001) were not directly invoked by our compaction treatments. Our treatments also did not substantially alter microbial communities (Busse et al., 2006), but did improve soil water availability in several instances (Gomez et al., 2002a; Aries et al., 2005).

Table 5
Effect of study, organic matter removal (OM), compaction (Comp) and vegetation control (VgCtl) on intra-region foliar nutrition. Significant differences ($p < 0.10$) are shown in bold, with treatment differences noted below. *N* is the number of replicated studies for a given region. Year 5 values are used for WmHd and Medit regions, whereas year 10 values are used for WtMt and BorGL regions to more closely match stage of stand development.

Region/species	Foliar nutrition								
	Factor	Study	OM	Study × OM	Comp	OM × Comp	VgCtl	Study × VgCtl	Comp × VgCtl
WmHd[a] lobP	N conc.	**<0.001** *N* = 4	0.974	**0.076** NCCro: OM_0, $OM_2 > OM_1$	0.351	0.959	**0.059**	**<0.001** All studies: VC > NVC	0.405
	P conc.	**<0.001** *N* = 4	0.393	0.372	0.782	0.675	**0.021**	**0.001** All studies: NVC > VC	**0.015** Comp – ns
	N/P ratio	**<0.001** *N* = 4	0.710	**<0.001** NCCro: OM_0, $OM_2 > OM_1$	0.390	0.593	**0.050**	**<0.001** All studies: VC > NVC	**0.028** VC: $C_2 > C_0$
WmHd [b] wO	N/P ratio	MOCaC	**0.015** $OM_0 > OM_1$, OM_2	n/a	0.831	n/a	0.826	n/a	n/a
WmHd[b] slP	N conc.	MOCaC	0.879	n/a	0.608	n/a	**<0.001** VC > NVC	n/a	n/a
	P conc.	MOCaC	0.757	n/a	**0.026** $C_2 > C_0$	n/a	0.647	n/a	n/a
	N/P ratio	MOCaC	0.925	n/a	**0.080** $C_0 > C_2$	n/a	0.146	n/a	n/a
Medit.[c] pP[d]	N conc.	Blodgett	**0.01** $OM_2 > OM_0$	n/a	n.s.	n/a	n/a	n/a	n/a
Medit[c] CAMxC	N conc.	Central	0.177	n/a	0.420	n/a	**0.012** VC > NVC	n/a	n/a
Medit[c] CAMxC	N conc.	Wallace	**0.050** $OM_2 > OM_0$	n/a	0.571	n/a	**0.039** VC > NVC	n/a	n/a
WtMt xS[e]	N conc.	BCSBS	0.253	n/a	0.300	**0.024** C_0: $OM_2 > OM_0$,OM_1	n/a	n/a	n/a
WtMt DF[f]	N conc.	IDPrR	0.141	n/a	**0.059** $C_2 > C_0$	n/a	0.243	n/a	n/a
BorGL jP[g]	N conc.	**<0.001** *N* = 6	**0.009** $0M_0$,$OM_1 > OM_2$	**0.073**	n/a	n/a	n/a	n/a	n/a
	P conc.	**<0.001** *N* = 6	0.676	0.989	n/a	n/a	n/a	n/a	n/a
	N/P ratio	**<0.001** *N* = 6	**0.012** OM_0,$OM_1 > OM_2$	0.370	n/a	n/a	n/a	n/a	n/a
BorGL bS[g]	N conc.	**<0.001** *N* = 7	**0.050** OM_0,$OM_1 > OM_2$	0.223	n/a	n/a	n/a	n/a	n/a
	P conc.	**0.036** *N* = 7	**>0.001** OM_0,$OM_1 > OM_2$	0.606	n/a	n/a	n/a	n/a	n/a
	N/P ratio	**<0.001** *N* = 7	**0.017** $OM_2 > OM_1$, OM_0	0.530	n/a	n/a	n/a	n/a	n/a

All *p* values for Loc × Comp and OM × VgCtl interactions were > 0.10 (not shown). See Table 1 for climate region, study and species codes.

[a] OM – Comp 3 × 2 factorial with nested VgCtl.

[b] At MOCaC, ANOVA with species as a nested factor showed species treatment effects or interactions ($p < 0.10$) for all three variables. Individual species ANOVAs showed no significant effects ($p > 0.10$) with red oak for all three variables, and with white oak for N or P concentrations (not shown).

[c] Only N concentrations were measured at Medit (California) installations. Also, values listed are for individual installations since measurements were not available for other installations within a given soil type. Treatment effect *p* values for Central and Wallace were determined using values for individual species as replicates.

[d] Values from Gomez et al. (2002b) for OM_0, OM_2, C_0, C_2; VC only. There were no significant differences ($p > 0.10$) between OM or Comp treatments in foliar N concentration at Challenge (8-year–old seedlings) or Rogers (3-year-old seedlings).

[e] ANOVA with species (LpP, xS) as a nested factor showed species effects or interactions ($p < 0.10$) for all three variables. Individual species ANOVAs showed no significant treatment effects ($p > 0.10$) for any lodgepole pine variable and for hybrid spruce P concentration and N/P ratios (not shown).

[f] ANOVA with species (wwP, DF) as a nested factor showed species effects or interactions ($p < 0.10$) for all three variables. Individual species ANOVAs showed no significant treatment effects ($p > 0.10$) for any western white pine variable and for Douglas-fir P concentration and N/P ratios (not shown).

[g] OM treatments only, jack pine with VC, black spruce with NVC and excluding peatland installations. With jack pine, there was no significant difference ($p \geqslant 0.358$) between OM_2C_0 and OM_2 C_2 ($N = 4$) (plots with VC) for any variable. For three jack pine studies with OM × VgCtl, VgCtl had no significant effects ($p \geqslant 0.132$) on any variable.

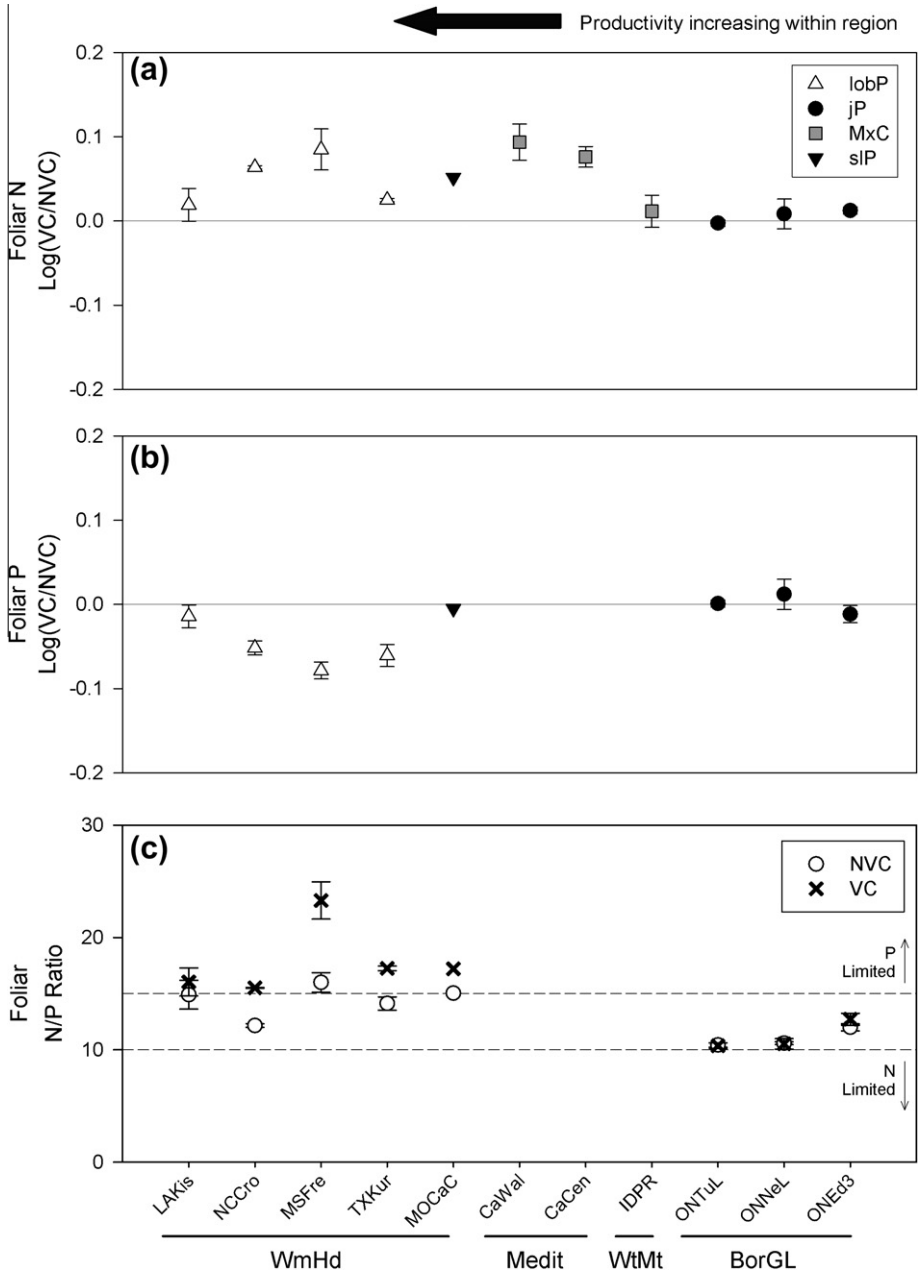

Fig. 9. Mean planted conifer vegetation control foliar nutrient response ratios (± standard errors) and N/P ratios, by climate region and study (see Table 1 for codes): (a) N concentration, (b) P concentration, and (c) N/P ratios. N/P ratios <10 or >15 are often considered indicative of N and P limitations, respectively (Güsewell, 2004). VC = vegetation control, NVC = no vegetation control.

In contrast to planted tree response, compaction did not generally increase total stand biomass (without vegetation control) because of reductions in non-crop vegetation. With aspen stands, equally low $R_0OM_0C_2$ and $R_0OM_2C_2$ values suggest compaction effects per se rather than combined effects with forest floor removal, largely accounts for the low standing biomass in these treatments. These effects may include loss of vigour reflecting root damage and fragmentation (Zahner and DeByle, 1965; Shepperd, 1993), decreased soil aeration (Bates et al., 1993), and for the MNChi installation, compaction after sucker emergence (Stone and Kabzems, 2002). In addition, where compaction increased the abundance of herbaceous species, competitive interactions (e.g., *Calmagrostis canadensis* L.) could be involved (Kabzems and Haeussler, 2005).

The cluster analysis of cross-continental R_{avg} values provides further evidence regarding underlying causes of compaction effects. Overall, planted tree productivity in the OM_2C_2 was more similar to that in the OM_2C_0 than in the OM_0C_2 (i.e., OM removal dominated planted conifer OM_2C_2 response). In contrast, among the five OM-Comp treatments, total stand biomass was most similar in the OM_0C_2 and OM_2C_2, suggesting decided compaction effects on other vegetation and hence on plant community productivity (Powers et al., 2005).

In contrast with biomass accumulation, compaction had limited effects on foliar nutrition (cf. Gomez et al., 2002b; Choi et al., 2005; Kranabetter et al., 2006; Aries et al., 2007). In the two instances with significant direct effects (IDPrR Douglas-fir and MOCaC shortleaf pine) compaction increased nutrient concentrations. Reported effects of compaction on soil nutrients are varied. Compaction may have no significant effect (Sanchez et al., 2006; Krzic et al., 2009) or increase (Tan et al., 2005) total soil N and P contents, but also may

Table 6
Spearman correlations between 10th year planted tree and/or total biomass (Mg ha^{-1}) and foliar nutrition, by species, study, and vegetation control. n.s., $p \geqslant 0.10$; $^{*}p = 0.050$–0.099; $^{**}p = 0.010$–0.049; $^{***}p < 0.010$. No significant ($p > 0.10$) correlations were found for MOCaC white oak, IDPrR white pine or BCSBS lodgepole pine. See Table 1 for climate region, study and species codes.

Species	Study	Biomass component	*N*	Foliar N (g kg^{-1})	Foliar P (g kg^{-1})	Foliar N/P ratio
Loblolly pine	LAKis, MSFre, NCCro, TXKur	Planted VC	76	−0.791***	−0.474***	−0.460***
		Planted all	152	n.s.	−0.194**	n.s.
		Total	152	−0.475***	−0.305***	−0.244***
Red oak[a]	MOCaC	Planted VC	6	n.s.	n.s.	−0.943***
Shortleaf pine	MOCaC	Planted VC	6	n.s.	n.s.	−0.771*
		Planted all	12	0.697**	n.s.	n.s.
Douglas-fir[b]	IDPrR	Planted all	12	0.601**	n/a	n/a
Hybrid spruce[c]	BCSBS	Planted	12	n.s.	0.596**	−0.587**
Jack pine[d]	ONEd3,4, ONSu1,2; ONNeL	Planted VC	60	n.s.	0.320**	n.s.
		Planted all	75	0.300***	0.402***	n.s.
		Total	63	0.482***	0.426***	0.218*
Black spruce[e]	ONFe1-3;ONWh1-2; ONGer, ONSn1	Planted	61	0.534***	0.380***	n.s.
		Total	61	n.s.	0.226*	n.s.

[a] No significant correlations ($p > 0.10$) for all planted trees (VC and NVC combined).
[b] No significant correlations ($p > 0.10$) for planted trees, VC only.
[c] Initial manual vegetation control around individual seedlings only.
[d] Most biomass (>90%) consists of planted trees plus jack pine naturals; the most southern installation (ONTuL) was excluded because the associated large biomass values weakened relationships.
[e] No vegetation control applied; peatland sites (ONR62, ONSn2) excluded.

(Li et al., 2003) or may not (Tan et al., 2005; Blumfield et al., 2005; Kranabetter et al., 2006) reduce mineralization rates. Kranabetter and Chapman (2004) showed limited OM-Comp effects on yr 5 litter nitrogen dynamics. Overall, compaction effects on productivity appear more closely related to soil physical properties and competition effects, than to soil nutrient availability.

4.3. Vegetation control

Vegetation control increased 10th year planted conifer biomass fairly consistently across OM-Comp treatments in most studies. Herbaceous and woody competition reduces early conifer growth in many ecosystems, although the magnitude and duration often varies (Walstad and Kuch, 1987; Wagner et al., 2006). With herbaceous competition, large initial but transitory growth increases are expected (Type 1 response – Mason and Milne, 1999; South et al., 2006) whereas with larger woody species, competition and hence planted tree response may not be as great initially, but of longer-lasting duration (Glover and Zutter, 1993). Thus continued gains with VC in ecosystems with predominantly herbaceous competitors (e.g., loblolly pine, Fall River Douglas-fir) are unlikely past canopy closure (Haywood and Tiarks, 1990; Aries et al., 2007)

Total stand biomass was also greatest with vegetation control for jack pine, and for loblolly pine at most locations, as well as in the 5th year at the Fall River LTSP affiliate installation (Aries et al., 2007). Natural pine regeneration, which was largely unaffected by vegetation control, dominated non-planted biomass at all jack pine and the NCCro loblolly pine installations, whereas woody non-crop vegetation was limited at the LAKis, MSFre and Fall River installations. At Medit installations, however, strong and persistent shrubby competition (e.g., *Arctostaphylos* and *Ceanothus* spp.), together with more limited tree productivity, resulted in greater stand biomass without vegetation control.

Vegetation control consistently increased planted conifer foliar N concentrations in WmHd and Medit regions but not with BorGL jack pine, at IDPrR, or at the Fall River installation (Aries et al., 2007). In the latter cases, foliar nutrient concentrations were well above critical levels. Further, Munson and Timmer (1995) showed vegetation control can greatly increase soil nutrient availability and jack pine growth without measurably affecting nutrient concentrations. At WmHd locations, paradoxical reductions in foliar P concentrations and increased N/P ratios with VC may reflect increased demand by larger trees and foliar dilution effects, as outlined earlier. At the NCCro, VC increased 5th year soil N mineralization rates (Li et al., 2003) and 10th yr total soil N and extractable P contents, but had limited effects on the latter at LAKis (Sanchez et al., 2006).

4.4. Species comparisons

There were often species × treatment interactions for studies with multiple species plantings, and results were sometimes unexpected. At MOCaC the positive white oak response to compaction resembled that of shortleaf pine, not red oak. In Idaho, western larch showed little response to OM-C treatments, whereas ponderosa pine and Douglas-fir showed significant OM-Comp interactions, with opposing responses to OM treatments with C_2. Further, unlike the other two species, Douglas- fir did not respond significantly to vegetation control. Species responses are likely to vary with their silvical characteristics, including rooting patterns, growth rates, nutritional demands, drought tolerance, heat and frost sensitivity, and mycorrhizal associations (Kamaluddin et al., 2005; Kranabetter et al., 2006). While microclimate-related differences in species response should moderate as canopy closure approaches, differences in shade tolerance and nutrient requirements will likely result in continued species-specific treatment responses. Thus harvest impacts are likely to be species- as well as site-specific.

5. Conclusions

Organic matter removal had no consistent study-wide impacts on 10th year planted tree or total above-ground biomass. Nevertheless, OM_2 growth reductions in WmHd climates, where stand development was most advanced, together with evolving OM_2 reductions in soil nutrient availability at Medit installations (Powers et al., 2005) and foliar nutrition at BorGL installations suggest broader effects on stand productivity may appear as more stands approach canopy closure and place greater demands on soil nutrients for canopy development. From a broader perspective, many LTSP installations are situated on mesic sites, on recently glaciated soils with relatively high nutrient contents, and/or replaced natural forests with substantial nutrient legacies in the forest floor. On older, less fertile and more nutrient depleted soils, and those with fewer nutrient reserves in the forest floor, organic matter removal may have a substantially greater impact on stand productivity,

particularly over multiple rotations with fast-growing species (Nambiar and Kallio, 2008).

Soil compaction per se generally increased planted tree biomass on these predominantly coarser-textured soils, particularly in the absence of forest floor removal (i.e., OM_0C_2). Overall, this positive OM_0C_2 response was more strongly associated with amelioration of the physical environment rather than nutritional effects or reduced vegetative competition. Conversely, smaller benefits of the OM_2C_2 on stand productivity were more closely associated with reduced competition.

Vegetation control increased 10th yr planted tree biomass and in many cases, foliar N concentrations, with positive responses usually occurring consistently across organic matter removal and compaction treatments. Vegetation control also increased total stand biomass at installations with abundant conifer ingress (e.g., BorGL jack pine) which was not affected by control measures (herbicides), and at installations with primarily herbaceous competition which was being shaded out with canopy development (e.g., WmHd loblolly pine). At installations with abundant shrubby competitors (e.g., Medit sites), however, total stand biomass was reduced by vegetation control.

To date the suite of LTSP study installations have been of great value in addressing the short-term consequences of harvest-related site and soil disturbances to fundamental site productivity across broad ecological gradients. However, their greatest value will only be realized if measurement schedules can be followed to address treatment impacts on the longer-term productive capacity of the sites. Undoubtedly impacts will change with stand age and development stage, reflecting both evolving environmental constraints, plant community development and recovery from treatment.

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