Effects of organic matter removal, soil compaction, and vegetation control on 5-year seedling performance: a regional comparison of Long-Term Soil Productivity sites[1]

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Abstract: We examined fifth-year seedling response to soil disturbance and vegetation control at 42 experimental locations representing 25 replicated studies within the North American Long-Term Soil Productivity (LTSP) program. These studies share a common experimental design while encompassing a wide range of climate, site conditions, and forest types. Whole-tree harvest had limited effects on planted seedling performance compared with the effects of stem-only harvest (the control); slight increases in survival were usually offset by decreases in growth. Forest-floor removal improved seedling survival and increased growth in Mediterranean climates, but reduced growth on productive, nutrient-limited, warm–humid sites. Soil compaction with intact forest floors usually benefited conifer survival and growth, regardless of climate or species. Compaction combined with forest-floor removal generally increased survival, had limited effects on individual tree growth, and increased stand growth in Mediterranean climates. Vegetation control benefited seedling growth in all treatments, particularly on more productive sites, but did not affect survival or alter the relative impact of organic matter removal and compaction on growth. Organic matter removal increased aspen coppice densities and, as with compaction, reduced aspen growth.

Résumé : Les auteurs ont étudié la réaction des semis 5 ans après la perturbation du sol et le contrôle de la végétation dans 42 sites expérimentaux représentant 25 études répétées dans le cadre du projet nord-américain de productivité des sols à long terme. Ces études ont un plan expérimental commun mais couvrent une vaste gamme de climats, de conditions de station et de types de forêt. L'exploitation par arbres entiers a eu peu d'effet sur la performance des semis plantés comparativement à la récolte du fût seulement (témoin); une légère augmentation du taux de survie était habituellement compensée par une réduction de la croissance. L'enlèvement de la couverture morte a amélioré le taux de survie des

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semis et augmenté la croissance sous les climats méditerranéens mais a réduit la croissance dans les stations productives, chaudes et humides, où les nutriments sont un facteur limitant. La compaction du sol avec une couverture morte intacte a généralement favorisé la survie et la croissance des conifères, peu importe le climat ou l'espèce. La compaction du sol combinée à l'enlèvement de la couverture morte a généralement augmenté le taux de survie, a eu peu d'effet sur la croissance individuelle des arbres et a augmenté la croissance des peuplements sous les climats méditerranéens. La maîtrise de la végétation a favorisé la croissance des semis dans tous les traitements, particulièrement dans les stations les plus productives mais n'a pas affecté le taux de survie ou modifié l'impact relatif de l'enlèvement de la matière organique et de la compaction du sol sur la croissance. L'enlèvement de la matière organique a augmenté la densité des taillis de peuplier faux-tremble et, comme c'est le cas pour la compaction du sol, a diminué la croissance du peuplier faux-tremble.

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Introduction

Losses of soil organic matter (OM) and reductions in soil porosity are key factors associated with forest management activities that may affect long-term site productivity (Powers 1999). Soil OM is the primary source of many essential plant nutrients and also influences soil structure and water-holding capacity (Van Cleve and Powers 1995). Soil porosity governs various physical characteristics related to soil aeration, strength, and hydraulic properties (Greacen and Sands 1980).

There is wide variation in the extent of OM removal and soil compaction associated with different management activities. Furthermore, effects of given disturbance levels vary with site conditions and also over time (Egnell and Valinger 2003; Nilsson and Allen 2003). Plantation establishment is often enhanced by removing surface organic horizons (Morris and Lowery 1988; Örlander et al. 1990). While displacing nutrient capital, such treatments can increase soil temperatures, moderate surface temperatures, reduce competition, and enhance moisture and nutrient availability in mineral horizons (Burger and Pritchett 1984; Vitousek et al. 1992; Fleming et al. 1998). In contrast, benefits of OM retention in terms of nutrient supply (Henderson 1995; Jurgensen et al. 1997) may only become manifest as stands approach canopy closure and exert increased demands on site nutrient pools (Miller 1984).

Reductions in tree growth have commonly been reported following soil compaction (Wert and Thomas 1981; Froehlich et al. 1986), but effects vary greatly with soil texture, structure, and climate (Hatchell et al. 1970; Miller et al. 1996; Brais 2001). With finer textured soils, the resulting increases in soil strength and reductions in aeration porosity may restrict roots, reduce water-holding capacity, and limit gas exchange. With some coarser textured soils, however, compaction may increase water-holding capacity without unduly hampering soil aeration (Greacen and Sands 1980; Gomez et al. 2002*a*). On many sites, compaction also reduces the abundance of competing vegetation (Powers and Fiddler 1997; Brais 2001). Vegetation control usually enhances seedling growth and is often considered a requisite for rapid establishment (Brand 1991; Powers and Reynolds 1999; Nilsson and Allen 2003).

While many retrospective studies and nutrient budget analyses have identified putative productivity declines following harvest-related OM removal or compaction, results are often ambiguous, difficult to quantify, and (or) limited in scope (Morris and Miller 1994). To address these concerns, the USDA Forest Service's Long-Term Soil Productivity (LTSP) program developed a series of manipulative experiments that create gradients in soil porosity and site OM after harvest (Powers et al. 1990). Vegetation control treatments were often nested within the factorial designs to differentiate growth effects related to changes in site conditions from those due to partitioning of site resources. At present, over 60 such installations, each sharing similar experimental designs and measurement protocols, have been established. Here, we report 5-year seedling response from the oldest 42 installations representing 25 replicated experiments. Fifth-year treatment effects on soil carbon and nitrogen and soil porosity, moisture, and temperature are discussed in companion papers (Page-Dumroese et al. 2006; Sanchez et al. 2006).

Specific objectives of this paper are (1) to investigate seedling response to OM removal, soil compaction, and vegetation control for each of 25 replicated LTSP experiments and (2) to examine broad patterns of seedling response among treatments, climatic regions, soil textural classes, and species groups. From a climatic perspective, we expect seedling growth will benefit most from treatments that (1) enhance general resource partitioning to planted seedlings in warm–humid climates; (2) improve available water supply in Mediterranean climates; and (3) increase soil warming in cold, high-latitude climates. From a treatment perspective, we expect seedling performance will benefit more from (1) soil compaction on coarser than on finer textured soils; (2) vegetation control on treatments with unaltered surface organic horizons (i.e., intact soil seed and bud banks) than following compaction or forest-floor removal; and (3) forest-floor removal (i.e., amelioration of microclimatic extremes) than from vegetation control per se, in terms of survival.

Methods

Study areas and treatments

Sites, climatic regions in which they are situated, and species used are listed in Table A1. General site and pretreatment stand characteristics are presented in Powers (2006), while further references for individual sites are listed in Table A1. The LTSP standard installation is a factorial combination of three levels of OM removal (stem-only harvest (OM_0), whole-tree harvest (OM_1), and whole-tree harvest plus forest-floor removal (OM_2)), and three levels of soil compaction (none (C_0), moderate (C_1), and severe (C_2)) set out in large (minimum 0.4 ha) treatment plots (Powers et al. 1990). Page-Dumroese et al. (2006) specifically address application of compaction treatments at different sites and their effectiveness. Superimposed on this at some sites are split-plot treatments of vegetation control (V) and multiple species (Sp) plantings. With vegetation control, competing vegetation was eliminated chemically or mechanically on half of each treatment plot by the third year after harvest (VC) and left untreated on the other half (NVC). Plots were regenerated with native species, either as monocultures or as mixtures representing the natural forest type.

Most experiments were replicated two or three times per site or soil type. The jack pine sites included disk trenching in the OM_0 and OM_1 treatments, but only one compaction level (severe), applied after straight-blading (nominal OM_2: forest floor, stumps, and 5–10 cm of mineral soil removed). The black spruce study was replicated within sites and by soil type, but excluded compaction or vegetation control. Here, the OM_2 treatment consisted of straight-blading on upland sites and winter shear-blading to remove the frozen upper Of horizon on peatland sites. Aspen sites and conifer sites in British Columbia also did not have vegetation control.

Seedling measurements reported here include fifth-year survival (%) or, for aspen, stem density (stems/ha), diameter near ground level (cm), and stand volume index (stand basal area × mean height (m^3/ha)). At the Kiskatinaw installation only aspen heights and stem densities were measured. Survival data were arcsine transformed prior to analysis to improve normality.

Analysis of variance

We analyzed each replicated experiment separately using analysis of variance (ANOVA), changing the model to account for minor differences in designs between trials as required. Individual treatment differences were established using Tukey's multiple comparison test when $p < 0.10$. We selected this p level because we wanted to compare responses among different potential treatments (management alternatives), not to test underlying theory (Salsburg 1985). Actual p values or confidence intervals are also given for all ANOVAs and meta-analyses. Treatment differences in survival and diameter were displayed graphically when interactions were significant. ANOVAs were not performed for nonreplicated sites (Priest River, Challenge, and Wallace).

Meta-analysis

We used meta-analysis to provide a quantitative synthesis of the independent experiments and to give additional statistical power (Gurevitch et al. 2001). The suite of LTSP locations is particularly well suited to this technique because the similar experimental designs and common measurement protocols make treatment responses among studies readily comparable, whereas the broad distribution of locations provides an extensive range of climates, site conditions, and species to test results against. Publication bias was avoided by including results from all experiments, regardless of outcome.

We used the natural logarithm of the response ratio (ln$R$) as the effect-size metric. The response ratio (R, the ratio of mean outcome in a given treatment to that in the OM_0C_0 (the control)) quantifies the proportional treatment effect, and is well suited to situations like ours, where the magnitude of response may vary greatly among experiments. Taking the natural logarithm linearizes the metric and provides a more normal sampling distribution for small samples (Hedges et al. 1999). We conducted separate analyses of seedling diameter, survival or aspen stem density, and stand volume index.

For each OM–C treatment combination, R was calculated separately for the VC and NVC subplots. To simplify analyses, we considered only five OM–C combinations: OM_0C_0, OM_1C_0, OM_0C_2, OM_2C_0, and OM_2C_2 and designated OM_0C_0 the control. These represent the extremes in OM × C treatment application, but also include OM_1C_0, which is analogous to whole-tree logging. In a separate analysis, we evaluated vegetation control (VC) effects by comparing the response in VC versus NVC (the control) subplots for each OM–C treatment combination.

Weighted effect sizes were calculated from the means, standard deviations, and sample sizes (number of replicate plots) for each species × treatment (OM–C–V) combination per replicated experiment. Results from the nonreplicated Priest River, Challenge, and Wallace sites were included by assigning them conservative weights similar to those calculated for the Dome sites.

We carried out the meta-analysis using a weighted mixed-model procedure in MetaWin2 (Rosenberg et al. 2000). We used nonparametric weighted resampling methods (10 000 permutations) to calculate bias-corrected 90% confidence intervals (CIs) and test for homogeneity among groups (Adams et al. 1997). The between-group heterogeneity statistic Q_b was used to determine whether effect sizes differed significantly among groups for a given categorical variable. Groups whose weighted cumulative effect-size 90% CIs did not overlap were judged significantly different from each other, and they were judged significantly different from the control if their back-transformed 90% CIs did not overlap unity. All effect-size values and their CIs are presented following back transformation to unlogged R values (Hedges et al. 1999).

We used meta-analysis to determine whether relative responses varied quantitatively among treatments, climatic regions, soil textural classes (coarse (sands and sandy loams) vs. fine (finer loams and clays)), and species functional group (hard pines (loblolly, shortleaf, ponderosa, jack, and lodgepole pines) vs. other conifers) (Table A1). The oaks were included in the general analysis but not in the species groups. Aspen was analysed separately because its mode of reproduction (suckering) was quite different from that of the planted species.

Results

ANOVA of the primary studies

Southeastern loblolly pine

Loblolly pine survival was poorer in the OM_0 treatment at Croatan ($p = 0.051$) and Kisatchie ($p = 0.037$) and in the OM_2 treatment at Davy Crockett ($p = 0.001$) (Table 1) (Fig. 1*a*). Vegetation control (VC) reduced survival at DeSoto ($p = 0.026$) and interacted with OM and C at Davy Crockett (Fig. 1*b*). Forest-floor removal reduced diameter and stand volume at Davy Crockett ($p = 0.001$), and following VC, at Croatan and DeSoto (Table 1) (Fig. 1*c*, 1*d*). Diameters were larger ($p = 0.068$) with moderate compaction at Kisatchie, and at DeSoto, compaction increased seedling and stand growth following forest-floor removal (Fig. 1*f*). At Croatan, however, diameters in the VC–OM_2 treatment combination were reduced by compaction (Fig. 1*e*). VC had the most consistent effects on growth, increasing diameters and stand volumes at virtually all locations ($p = 0.001$).

Table 1. ANOVA *p* values for loblolly pine fifth-year survival (surv.), ground-level diameter (diam.), and stand volume index (vol.) at the Croatan, Kisatchie, DeSoto, and Davy Crockett sites (treatments include organic matter removal (OM), compaction (C), and vegetation control (V)).

Treatment	Surv.	Diam.	Vol.
Croatan			
OM	**0.051, $OM_1 > OM_0$**	**0.061**	**0.005**
C	0.806	0.720	0.763
OM × C	0.189	0.561	0.268
V	0.708	**0.001**	**0.001**
OM × V	0.216	**0.002**	**0.014**
C × V	0.834	0.365	0.792
OM × C × V	0.912	**0.061**	0.261
Kisatchie			
OM	**0.037, $OM_2 > OM_0$**	0.221	0.419
C	0.118	**0.068, $C_1 > C_0$**	0.145
OM × C	0.250	0.612	0.451
V	0.555	**0.001, VC > NVC**	**0.001, VC > NVC**
OM × V	0.565	0.794	0.921
C × V	0.429	0.549	0.812
OM × C × V	0.132	0.878	0.927
DeSoto			
OM	0.509	**0.001**	**0.001**
C	0.163	**0.011**	**0.015**
OM × C	0.892	**0.059**	**0.036**
V	**0.026, NVC > VC**	**0.001**	**0.001**
OM × V	0.899	**0.006**	**0.002**
C × V	0.793	0.315	**0.068**
OM × C × V	0.934	0.307	0.585
Davy Crockett			
OM	**0.001**	**0.001, $OM_0 > OM_1 > OM_2$**	**0.001, OM_0, $OM_1 > OM_2$**
C	0.374	0.208	0.427
OM × C	0.217	0.237	0.110
V	0.829	**0.001, VC > NVC**	0.209
OM × V	0.307	0.750	0.928
C × V	0.645	0.959	0.920
OM × C × V	**0.023**	0.975	0.561

Note: In the absence of interaction effects, significant differences among individual treatments are shown in bold for *p* values <0.10. Separate combined error terms were used to test for main treatment effects (OM, C) and interaction, and split-plot effect (V) and interactions. NVC, no vegetation control.

Missouri oaks and shortleaf pine

Shortleaf pine survival was much poorer ($p = 0.001$) than that of the oaks and was not affected by treatment ($p > 0.109$) (Table 2). Oak survival was improved ($p < 0.020$) by OM removal (Fig. 2*a*), and compaction improved white oak survival in the OM_0 treatment (Fig. 2*b*). OM removal did not affect seedling or stand growth ($p > 0.251$), but compaction increased pine diameter ($p = 0.035$) (Fig. 2*c*) and stand volume index ($p = 0.075$). VC increased diameter and stand volume for each species ($p = 0.001$), but particularly for shortleaf pine (Fig. 2*d*), which far outgrew the oaks ($p = 0.001$).

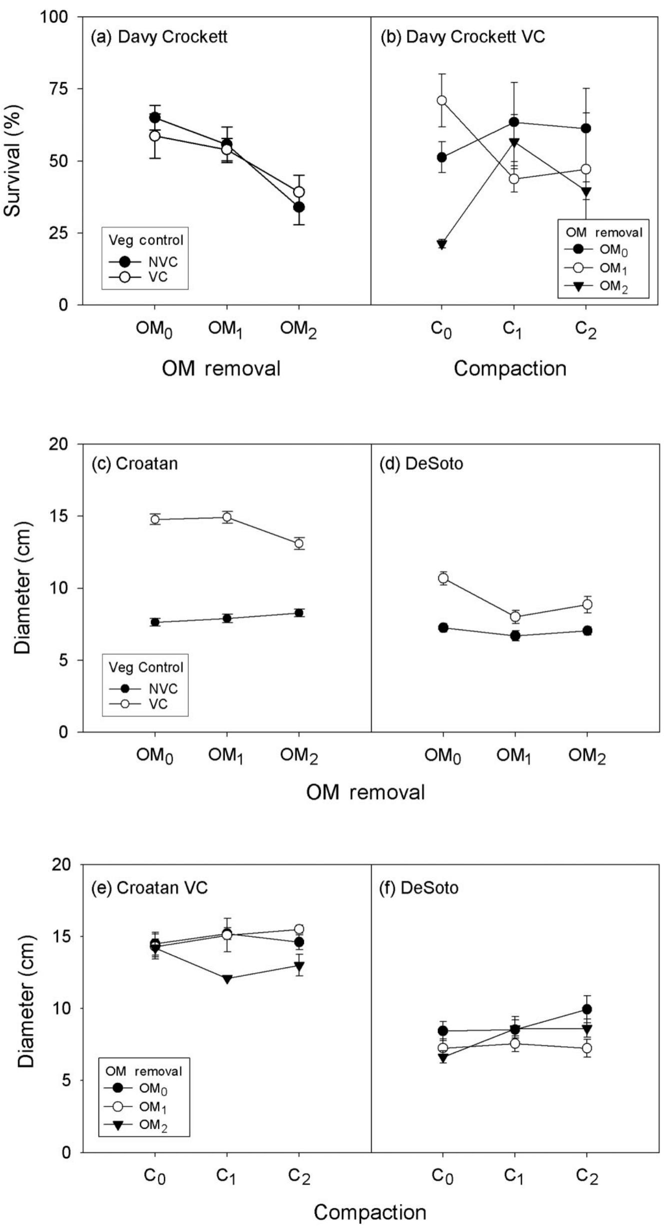
California conifers

Compaction of intact forest floors increased survival on both soils, but compaction following forest-floor removal had little impact (Table 3) (Fig. 3*a*, 3*b*). The C × Sp interaction ($p = 0.005$) for Cohasset reflected greater response to compaction by Douglas-fir than by other species. OM removal had no direct effects ($p > 0.10$) on growth, but forest-floor removal combined with VC increased stem diameters on Dome (Fig. 3*c*). For Cohasset, compaction increased both growth measures ($p < 0.073$) (Fig. 3*d*). VC increased tree and stand growth on both soil series, particularly for giant sequoia (Fig. 3*e*, 3*f*).

Cold, high-latitude conifers

Treatment responses were often less pronounced here than in other regions. Moderate compaction decreased survival slightly (94% vs. 90%) ($p = 0.046$) in central British Columbia, whereas forest-floor removal increased jack pine ($p = 0.001$) and black spruce ($p < 0.099$) survival on several sites (Table 4). Forest-floor removal increased jack pine growth ($p < 0.048$) at Tunnel Lake and black spruce growth on wet

Fig. 1. Treatment effects on loblolly pine 5-year seedling performance: (*a*) effects of organic matter (OM) removal and vegetation control (VC) on survival at Davy Crockett; (*b*) effects of compaction and organic matter removal, with vegetation control, on survival at Davy Crockett; (*c–d*) effects of organic matter removal and vegetation control on diameter at Croatan and DeSoto; and (*e–f*) effects of compaction and organic matter removal on diameter at Croatan (with vegetation control only) and DeSoto. Vertical bars represent standard errors of the mean.



mineral ($p \leq 0.088$), peatland ($p = 0.082$, diameter only), and one deep sandy site ($p = 0.044$, stand volume only). VC increased jack pine seedling and stand growth ($p < 0.003$) at Tunnel Lake but not at Superior 3.

Cold, high-latitude aspen

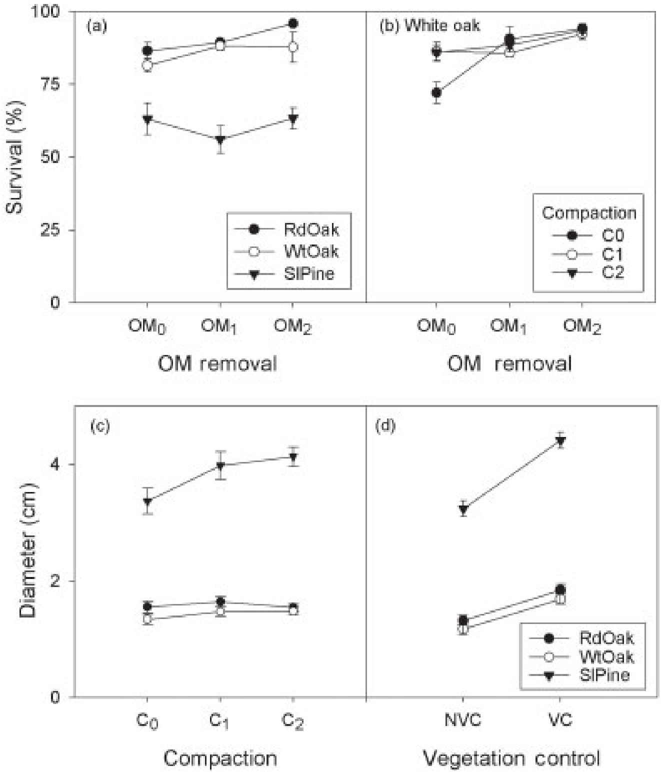
Forest-floor removal increased aspen densities on the three fine-textured locations ($p < 0.019$) (Table 5). Compaction

Table 2. ANOVA p values for fifth-year survival (surv.), ground-level diameter (diam.), and stand volume index (vol.) at Carr Creek, Missouri, for all species combined and for individual species (treatments include organic matter removal (OM), compaction (C), vegetation control (V), and species selection (Sp)).

	All species combined			Northern red oak			White oak			Shortleaf pine		
Treatment	Surv.	Diam.	Vol.	Surv.	Diam.	Vol.	Surv.	Diam.	Vol.	Surv.	Diam.	Vol.
OM	**0.045, $OM_2 > OM_0$**	0.781	0.782	**0.018, $OM_2 > OM_1, OM_0$**	0.698	0.688	**0.001**	0.252	0.919	0.623	0.951	0.789
C	0.309	**0.081**	**0.087**	0.713	0.481	0.461	0.888	0.221	0.283	0.278	**0.035, $C_2 > C_0$**	**0.075, $C_2 > C_0$**
OM × C	0.147	0.858	0.738	0.587	0.560	0.520	**0.053**	0.900	0.949	0.572	0.735	0.697
V	**0.039, NVC > VC**	**0.001**	**0.001**	0.875	**0.001, VC > NVC**	**0.001, VC > NVC**	0.291	**0.001, VC > NVC**	**0.001, VC > NVC**	0.110	**0.001, VC > NVC**	**0.001, VC > NVC**
OM × V	0.686	0.576	0.475	0.133	0.833	0.659	0.659	0.828	0.479	0.923	0.461	0.593
C × V	0.695	0.179	0.840	0.492	0.436	0.298	0.532	0.430	0.766	0.900	0.121	0.861
OM × C × V	0.264	0.800	0.519	0.555	0.868	0.995	0.652	0.924	0.610	0.282	0.520	0.555
Sp	**0.001, RO, WO > SlP**	**0.001**	**0.001**									
OM × Sp	0.129	0.980	0.914									
C × Sp	0.546	**0.004**	**0.028**									
OM × C × Sp	0.957	0.630	0.778									
V × Sp	0.470	**0.001**	**0.001**									
OM × V × Sp	0.567	0.617	0.801									
C × V × Sp	0.794	0.138	0.944									
OM × C × V × Sp	0.528	0.399	0.679									

Note: In the absence of interaction effects, significant differences among individual treatments are shown in bold for p values <0.10. We used a factorial split-split-plot ANOVA design, with OM and C as main treatment effects, V as the split-plot effect, and Sp as the split-split-plot effect. NVC, no vegetation control. Species name abbreviations are listed in Table A1.

Fig. 2. Treatment effects on 5-year seedling performance at Carr Creek, Missouri: (*a*) effects of organic matter (OM) removal and species on survival; (*b*) effects of organic matter removal and compaction on white oak survival; (*c*) effects of compaction and species on diameter; and (*d*) effects of vegetation control (VC) and species on diameter. Vertical bars represent standard errors of the mean.



increased densities at Ottawa (p = 0.077) but reduced densities at Chippewa (p = 0.001), particularly in OM_2 (Fig. 4*a*). Forest-floor removal invariably reduced diameters (p < 0.040), but the OM_0 versus OM_1 treatment effects varied with location. Compaction reduced diameters at Ottawa (p = 0.056) and both growth measures at Chippewa (p = 0.001), particularly in the OM_0 treatment (Fig. 4*b*). At the coarse-textured Huron-Manistee, stand volume decreased with OM removal (p = 0.003) but increased with compaction (p = 0.074).

Intersite comparisons

General growth trends in the OM_0C_0 treatment

For comparative purposes and to provide context for subsequent response ratio analyses, we examined fifth-year survival, ground-level diameter, and stand volume index in the OM_0C_0 treatment across the range of experiments used for meta-analysis (Fig. 5). Trends in survival often bore little resemblance to those in growth. High survival, as well as growth, was achieved with loblolly pine, but British Columbia conifers and Ontario black spruce attained similar survival rates despite much poorer growth. Poor survival rates were found with shortleaf pine but not with oaks in Missouri, and with giant sequoia, Douglas-fir, white fir, and sugar pine, but not with ponderosa pine in California. VC seldom benefitted, and sometimes reduced, survival.

Table 3. ANOVA p values for mixed conifer fifth-year survival (surv.), ground-level diameter (diam.), and stand volume index (vol.) on the Cohasset and Dome soil series, for all species combined (treatments include organic matter removal (OM), compaction (C), vegetation control (V), and species selection (Sp)).

	Cohasset			Dome		
Treatment	Surv.	Diam.	Vol.	Surv.	Diam.	Vol.
OM	**0.082**	0.152	0.186	0.756	0.852	0.499
C	**0.001**	**0.027**	**0.072**	**0.093**	0.933	0.671
OM × C	**0.044**	0.512	0.918	**0.082**	0.169	0.201
V	0.641	**0.001**	**0.007**	0.206	**0.001**	**0.059**
OM × V	**0.017**	0.202	0.126	0.354	**0.020**	0.191
C × V	0.282	**0.060**	**0.086**	0.984	0.557	0.280
OM × C × V	0.357	0.187	0.331	0.516	0.217	0.233
Sp	**0.001**	**0.001**	**0.001**	**0.005**[a]	**0.001**	**0.014**
OM × Sp	0.220	0.588	0.711	0.561	0.403	0.697
C × Sp	**0.005**	0.456	0.544	0.892	0.117	0.429
OM × C × Sp	0.248	0.999	0.999	0.741	0.344	0.186
V × Sp	0.854	**0.014**	**0.001**	0.151	**0.001**	**0.036**
OM × V × Sp	0.428	0.388	0.175	0.245	0.178	0.312
C × V × Sp	0.464	0.194	**0.044**	0.539	**0.021**	0.194
OM × C × V × Sp	0.888	0.357	0.142	0.962	0.130	0.397

Note: In the absence of interaction effects, significant differences among individual treatments are shown in bold for p values <0.10. Separate combined error terms were used to test for main treatment effects (OM, C) and interaction, the split-plot effect (V) and interactions, and the split-split-plot effect (Sp) and interactions. For Dome, we only had replicated OM_0C_0, OM_0C_2, OM_2C_0, and OM_2C_2 treatments; for Cohasset, the Blodgett site was included only in analyses of ponderosa pine response.

[a]PP > WF, GS, SuP. Species name abbreviations are listed in Table A1.

The greatest individual tree growth and stand volume was achieved in the southeast, where loblolly pine reached 12 cm in diameter and 80 m^3/ha in stand volume index in 5 years. Giant sequoia in California ranked next in conifer growth. Ontario jack pine and California ponderosa pine showed a wide range in growth, with relatively high growth rates at some sites (Tunnel Lake, Challenge, Cohasset, Wallace) and reduced growth at others (Superior 3, Dome). Low growth rates were associated with Ontario black spruce, British Columbia hybrid spruce, and California sugar pine and white fir. While aspen stem diameters were relatively small, stand volume index values often rivaled those of the more productive conifers. Aspen had much higher stem densities as well as greater height/diameter ratios than the conifers. In Missouri, oak diameters were smaller than that of shortleaf pine.

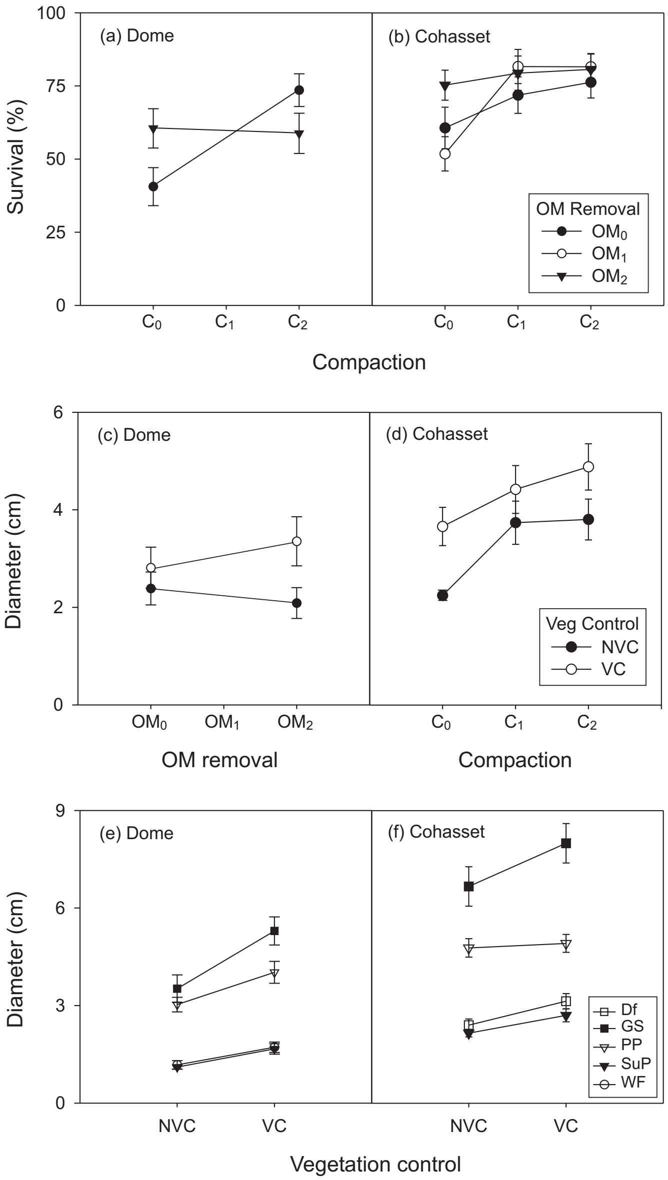
Trends in stand volume index generally followed those in diameter, with differences in seedling size generally having greater impact on stand volume than those in seedling survival. Notable exceptions were shortleaf pine, sugar pine, Douglas-fir, giant sequoia, and white fir; these species sometimes had poorer stand growth than expected because of low survival rates.

Meta-analysis

Survival

Main treatment effects on seedling survival varied significantly with OM–C treatment (p = 0.066), climate (p = 0.001) and species group (p = 0.001) (Table 6). Overall, survival was higher in all other main treatments than in the OM_0C_0 and higher following compaction than after whole-tree

Fig. 3. Treatment effects on 5-year seedling performance in California: (*a–b*) effects of compaction and organic matter (OM) removal on survival on the Dome and Cohasset series; (*c*) effects of organic matter removal and vegetation control (VC) on diameter on the Dome series; (*d*) effects of compaction and vegetation control on diameter on the Cohasset series; and (*e–f*) effects of vegetation control and species (Df, Douglas-fir; GS, giant sequoia; PP, ponderosa pine; SuP, sugar pine; WF, white fir) on diameter on the Dome and Cohasset series. Vertical bars represent standard errors of the mean.



harvest (Fig. 6*a*–6*d*). For a given treatment, and particularly those involving forest-floor removal, response ratios were usually highest for Mediterranean climates (Fig. 6*a*–6*h*). Survival, however, was not increased relative to the OM_0C_0 by intact forest floor treatments in cold, high-latitude climates, by forest-floor removal in warm–humid climates, and by whole-tree harvest for hard pines. In Mediterranean climates, other conifers showed greater survival response than did hard pines to compaction and forest-floor removal (Fig. 6*e*–6*h*).

VC effects on seedling survival varied slightly ($p = 0.095$) with OM–C treatment (Table 6), although VC had no significant effect on mean seedling survival for all OM–C treatments combined (Fig. 6*i*). Among climate regions, significant differences in OM–C treatment responses to VC were found only in Mediterranean climates ($p = 0.029$). There, VC had a negative effect on survival in the OM_0C_2 and a positive effect in the OM_2C_2 (Fig. 6*j*).

Seedling diameter

Main treatment effects on seedling diameter varied significantly only with OM–C treatment ($p = 0.011$) (Table 6). In comparison with the OM_0C_0, overall seedling diameters were larger following compaction of intact forest floors and smaller following whole-tree harvest (Fig. 7*a*–7*d*). Response to OM–C treatments also varied with climate (Fig. 7*a*–7*h*). Compaction of intact forest floors in warm–humid and particularly Mediterranean climates elicited positive growth responses in all species combined and in hard pines. At high latitudes, however, seedling diameters in this treatment were similar to those in the OM_0C_0. Effects of whole-tree harvest did not vary significantly among climate regions for either species grouping, but growth of hard pines in cold, high-latitude climates and of all species combined in Mediterranean and warm–humid climates was slightly poorer than in the OM_0C_0. Forest-floor removal decreased hard pine growth in warm–humid climates but increased it in Mediterranean climates. Forest-floor removal plus compaction had no significant effect on seedling growth for all species combined in any climatic region, but increased hard pine growth in Mediterranean climates. In Mediterranean climates, hard pines and other conifers had fairly similar diameter responses with intact forest floors, but hard pines reacted more favorably to forest-floor removal treatments (Fig. 7*e*–7*h*). VC effects on seedling diameters varied significantly with climate ($p = 0.003$) and soil texture ($p = 0.023$), but not with OM–C treatment (Fig. 7*i*) or species group (Table 6). Overall, VC resulted in a 27% increase in diameter growth, with response most pronounced in warm–humid climates, and least pronounced in cold, high-latitude climates (Fig. 7*j*). VC also produced greater diameter responses on finer than on coarser textured soils (Fig. 7*k*).

Stand volume index

Main treatment effects on stand volume index varied significantly with OM–C treatment ($p = 0.019$) and climate ($p = 0.001$) (Table 6). Compared with the OM_0C_0, overall stand volume index was larger with both forest-floor removal and compaction (Fig. 8*a*–8*d*). Although response to a given OM–C treatment varied with climate, responses were similar for all species combined and for hard pines (Fig. 8*a*–8*h*). Compaction of intact forest floors elicited positive responses in all climatic regions and greater response in Mediterranean than in warm–humid climates. Whole-tree harvest effects did not vary significantly among climate regions or in comparison with the OM_0C_0. Forest-floor removal increased stand volume index considerably in Mediterranean climates, but decreased stand growth in warm–humid climates. Forest-floor removal plus compaction increased stand growth relative to the OM_0C_0 only in Mediterranean climates. Soil texture effects were significant only in the OM_2C_2 treatments with-

Table 4. ANOVA *p* values for fifth-year survival (surv.), ground-level diameter (diam.), and stand volume index (vol.) for (*a*) lodgepole class in northwestern Ontario.

(*a*) Lodgepole pine and hybrid spruce.

Treatment[a]	Surv.	Diam.	Vol.
OM	0.761	0.482	0.357
C	**0.046, $C_0 > C_1$**	0.197	0.504
OM × C	0.870	0.581	0.562
Sp	**0.003, LpP > HS**	**0.001, LpP > HS**	**0.001, LpP > HS**
OM × Sp	0.567	0.974	0.801
C × Sp	0.697	0.660	0.855
OM × C × Sp	0.591	0.917	0.952

(*b*) Jack pine.

	Superior 1–2			Nemagos Lake		
Treatment[b]	Surv.	Diam.	Vol.	Surv.	Diam.	Vol.
OM–C	**0.001, $0M_2C_0$, OM_2C_2 > OM_1C_0, OM_0C_0**	0.667	0.660	0.636	0.366	0.491
V	na	na	na	na	na	na
OM–C × V	na	na	na	na	na	na

(*c*) Black spruce.

	Soil textural class					
	Shallow coarse loamy (*n* = 3)			Deep sandy (*n* = 2)		
Treatment	Surv.	Diam.	Vol.	Surv.	Diam.	Vol.
Loc	0.224	0.775	0.897	0.365	0.045	0.552
OM	0.262	0.867	0.890	**0.006, $OM_2 > OM_1 > OM_0$**	0.978	0.921
Loc × OM	0.447	0.446	0.328	0.955	**0.033**	**0.014**
Loc1 OM	na	na	na	na	0.213	0.298
Loc2 OM	na	na	na	na	0.158	**0.044, $OM_2 > OM_1$, OM_0**

Note: Species name abbreviations are listed in Table A1. na, not applicable. In the absence of interaction effects, significant differences among
[a]Treatments include organic matter removal (OM), compaction (C), and species (Sp). Separate combined error terms were used to test for main treatment
[b]Treatments are organic matter removal – compaction (OM–C) combinations for Superior 1–2 and Nemagos Lake, and OM–C combinations and vegetation. (Superior 1–2 and Nemagos Lake), or split-plot ANOVA with the OM–C treatment combinations as the main effect, and V as the split-plot effect (Superior 3
[c]Treatments are organic matter removal (OM), without compaction (C_0). Where significant ($p < 0.10$) location (Loc) × OM interactions occur, individual effect and OM treatment as the fixed effect.

out VC in Mediterranean climates; in this situation treatment effects were greater on finer than on coarser soil textures ($p = 0.009$).

Overall, VC increased mean stand volume index by 73%, although treatment effects varied directly only with climate ($p = 0.093$) (Table 6). While response did not vary significantly among OM–C treatments overall (Fig. 8*i*), on finer textured soils stand volume index responded more favorably to VC in some treatments with noncompacted (OM_1C_0, OM_2C_0) than compacted forest floors (Fig. 8*j*). VC increased stand volume index in all climates, but effect sizes were largest in warm–humid climates and smallest in cold, high-latitude climates (Fig. 8*k*).

Cold, high-latitude aspen

Without compaction, aspen stand densities increased with increasing levels of OM removal (Fig. 9*a*). Both OM removal and compaction reduced aspen stem diameters, and both diameter and stand volume index were greater with noncompacted, intact forest floors than following forest-floor removal plus compaction (Fig. 9*b*–9*c*). With compaction, treatment effects on all three performance measures varied greatly among locations.

Discussion

Main treatment effects

Whole-tree harvest

Overall, whole-tree harvest slightly increased survival and reduced seedling diameters compared with stem-only harvest, but had no significant effect on stand volume index. The relatively minor effects of this treatment on seedling performance may relate to better planting conditions, warmer soil temperatures, and greater turbulent mixing with debris removal versus provision of partial shade, greater frost protection, and site nutrient retention with logging debris. Other studies have similarly noted only limited differences in whole-tree versus stem-only harvesting effects on seedling establishment (e.g., Smethurst and Nambiar 1990; Zabowski et al. 2000). Differences in stand development resulting from these two treatments are often not evident until after canopy closure (Smith et al. 2000; Egnell and Valinger 2003). The notable increase in survival with whole-tree harvest in Mediterranean climates may reflect the influence of air pockets in the OM_0C_0 planting holes. Air pockets created by undecomposed litter and woody debris become a lethal artifact pine and hybrid spruce in central British Columbia, (*b*) jack pine by site in northeastern Ontario, and (*c*) black spruce by soil textural

Superior 3			Tunnel Lake		
Surv.	Diam.	Vol.	Surv.	Diam.	Vol.
0.901	0.155	0.225	**0.001, OM_2C_0, OM_2C_2 > OM_0C_0, OM_1C_0**	**0.047, OM_2C_2, OM_2C_0 > OM_1C_0**	**0.023, OM_2C_0, OM_2C_2 > OM_1C_0**
0.421	0.622	0.541	0.160	**0.001, VC > NVC**	**0.002, VC > NVC**
0.334	0.687	0.752	0.530	0.409	0.389

Wet mineral, peaty phase (n = 2)			Peatland (n = 2)		
Surv.	Diam.	Vol.	Surv.	Diam.	Vol.
0.811	0.051	0.009	0.251	0.005	0.024
0.098, OM_2 > OM_0	**0.087, OM_2 > OM_0**	0.182	0.331	**0.082, OM_2 > OM_1**	0.122
0.853	0.130	**0.008**	0.537	0.607	0.529
na	na	**0.014, OM_2 > OM_1,OM_0**	na	na	na
na	na	**0.002, OM_2 > OM_1, OM_0**	na	na	na

individual treatments are shown in bold for p values <0.10.
effects (OM, C) and interaction, and split-plot effect (Sp) and interactions.
control (V) at Superior 3 and Tunnel Lake. These experiments were analysed using either one-way ANOVA for the OM–C treatment combinations and Tunnel Lake).
one-way ANOVA results are presented for each location. These experiments were analysed using mixed-model ANOVA with soil type as the random

when planting through fresh logging slash in summer-dry climates.

Forest-floor removal

Forest-floor removal increased survival in cold, high-latitude climates, and especially in Mediterranean climates. In Mediterranean climates, this treatment increased the survival of more drought- and heat-sensitive species such as Douglas-fir, giant sequoia, and sugar pine to a greater degree than it did ponderosa pine. Similar results were found in Missouri, where oak but not shortleaf pine survival was improved in the OM_2C_0. Warmer soil temperatures and moderated near-surface air temperatures associated with our OM_2 (Fleming et al. 1999; Kranabetter and Chapman 1999; Li et al. 2003; Page-Dumroese et al. 2006), as well as better root–soil contact, aid survival by improving root growth, water uptake, and seedling water status and by reducing heat and frost damage (Grossnickle and Heikurinen 1989; Helgerson 1990). In general, however, much less is known about causal factors and interactions affecting survival than those affecting growth.

While forest-floor removal had no significant overall effects on seedling diameter, the large positive response of ponderosa pine contrasts with the negative response of hard pines in warm–humid climates. We attribute this to different resource limitations. For warm–humid locations, rapid growth increased demands for available soil nutrients, while nutrient supply (e.g., phosphorus) was reduced by forest removal (Tuttle et al. 1985). Scott et al. (2004) demonstrated a strong correlation between growth and extractable soil phosphorus for warm–humid LTSP locations. For Mediterranean locations, moisture limitations, and their interaction with soil strength and nutrient availability, are of primary importance (Powers and Reynolds 1999; Gomez et al. 2002*b*, 2002*c*); here, growth is promoted by increased spring temperatures when moisture is plentiful and by improved soil water supply in dry summer conditions (Kurpius et al. 2003). Forest-floor removal increases soil heat flux and evaporative losses because energy receipt and convective transfer at the mineral soil surface are increased (Cochran 1969; Bussière and Cellier 1994). As a result, this treatment should promote early-season growth by increasing soil temperatures, yet suppress summer growth by reducing soil water content and increasing soil strength in upper mineral horizons. This may explain positive OM_2 effects on growth at Dome with VC (i.e., reduced soil water loss), but negative effects without

Table 5. ANOVA *p* values for aspen fifth-year stand density (stems/ha), ground-level diameter (diam.), and stand volume index (vol.) at the Ottawa, Chippewa, Huron-Manistee and Kiskatinaw River (treatments include organic matter removal (OM) and compaction (C)).

	Ottawa			Chippewa			Huron-Manistee			Kiskatinaw River
Treatment	Stems/ha	Diam.	Vol.	Stems/ha	Diam.	Vol.	Stems/ha	Diam.	Vol.	Stems/ha
OM	**0.018, OM_2 > OM_1, OM_0**	**0.038, OM_1 > OM_2**	0.262	**0.007**	**0.001**	0.311	0.495	**0.001, OM_0 > OM_1, OM_2**	**0.003, OM_0 > OM_1, OM_2**	**0.001, OM_2 > OM_0**
C	**0.077, C_1 > C_0**	**0.056, C_0 > C_1**	0.614	**0.001**	**0.001**	**0.001, C_0 > C_1, C_2**	0.179	0.528	**0.074 C_2 > C_0**	0.849
OM × C	0.727	0.557	0.430	**0.040**	**0.002**	0.438	0.974	0.484	0.167	0.945

Note: In the absence of interaction effects, significant differences among individual treatments are shown in bold for *p* values <0.10. Because of data limitations we analysed two levels of compaction (C_0 and C_1) for the Ottawa site and two levels of organic matter removal (OM_0 and OM_2) for the Kiskatinaw River. Seedling diameters were not measured at the Kiskatinaw River. A combined error term was specified to test treatment effects and interactions (OM, C, and OM × C).

VC. Infiltration may also be increased during lighter rains in the absence of slash and forest-floor interception.

During droughts, the most pronounced drying of finer textured bare mineral soils (those with higher vapor diffusion resistances) occurs near the surface (Gardner and Gardner 1969), and substantially higher water contents may occur at depth (Fleming et al. 1998). Poorer growth in the OM_2 on coarse-textured (Davy Crockett, Rodgers; Gomez et al. 2002*b*) but not medium- or fine-textured soils at locations with drier climates is consistent with this, but also with nutrient reductions on inherently nutrient-poor sites.

At high latitudes, hard pine growth response to increased soil temperatures following forest-floor removal was likely tempered by losses of soil nutrients, species adaptations to resource-poor environments (Munson and Timmer 1995) and, for jack pine, by the removal of the upper nutrient-rich 5–10 cm of mineral soil in the OM_2C_0 and OM_2C_2. Fifth-year jack pine foliar nitrogen concentrations were often lower in the OM_2C_0 than in the OM_0C_0 (Table A2). As well, disk trenching (in the OM_0C_0 and OM_1C_0) often improves survival and growth at high latitudes (Weber et al. 1995; Burton et al. 2000) and may have masked positive jack pine treatment responses in the OM_2C_0 and OM_2C_2. Beneficial effects of forest-floor removal on black spruce growth on peatland and wet mineral but not coarse loamy or deep sandy sites likely reflects a balance between improved soil warming, moderated temperature extremes, decreased competition, and reduced nutrient availability. The forest floor is an important nutrient source for this species, which roots intensively near the mineral soil – humus interface on upland sites (Lamhamedi and Bernier 1994).

Soil compaction

Adverse effects of compaction on plant growth have long been known and are associated with poor root development, limited nutrient supply, and insufficient aeration (Unger and Kaspar 1994; Lipiec and Stepniewski 1995). There is growing recognition, however, that compaction is not always detrimental to seedling performance (Powers 1999). In our studies, compaction of soils with intact forest floors generally improved both survival and growth, even where adverse effects on aeration, and hence nutrient availability (warm–humid climates; Kelting et al. 2000), or on soil strength and water availability (Mediterranean climates; Gomez et al. 2002*a*) could dominate. Compaction reduced competition and increased moisture availability at several LTSP locations (Powers and Fiddler 1997; Gomez et al. 2002*a*; Li et al. 2003; Page-Dumroese et al. 2006) and at times interacted positively with other treatments to improve survival (OM_0: Carr Creek, Dome) or growth (OM_2: DeSoto). However, the general (but not universal; see Gomez et al. 2002*b*) effectiveness of compaction in promoting seedling establishment, regardless of soil texture or VC, suggests that other mechanisms are also important.

Compaction can increase thermal diffusivities and unsaturated hydraulic conductivities, improve root–soil contact, and enhance ion uptake by mass flow and diffusion (Sikora et al. 1990; Arvidsson 1999). We found compaction increased growing-season soil temperatures at many of our LTSP locations (Fleming et al. 1999; Kranabetter and Chapman 1999; Li et al. 2003; Page-Dumroese et al. 2006). At two

Fig. 4. Effects of organic matter (OM) removal and compaction on fifth-year (*a*) stem densities and (*b*) stem diameters for aspen at Chippewa. Vertical bars represent standard errors of the mean.

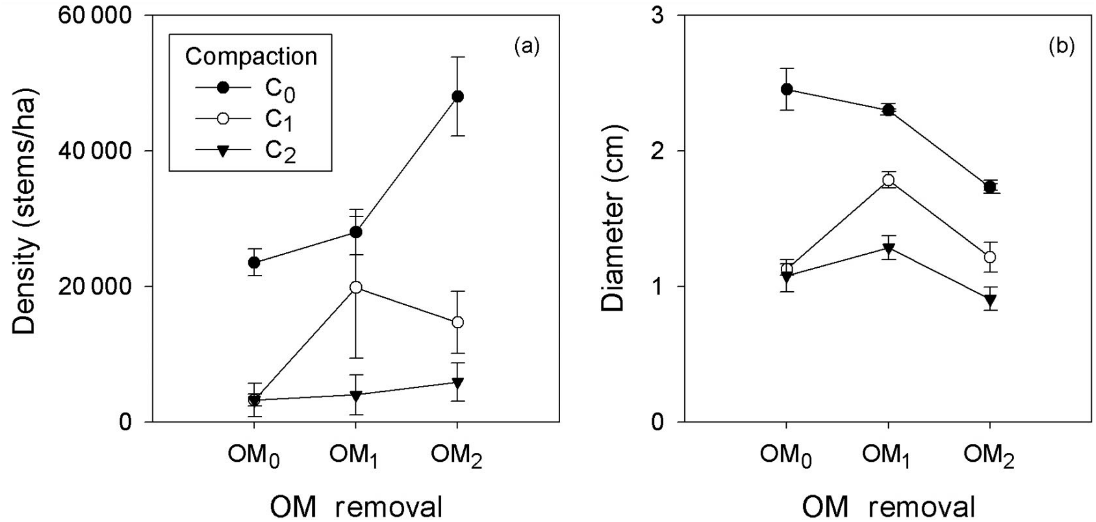


Fig. 5. Mean fifth-year seedling survival, ground-level diameter, and stand volume index in the OM_0C_0 treatment, with and without vegetation control, for the various species in replicated experiments (see Table A1 for codes). Horizontal bars indicate standard deviations. Entries are identified by state or province (first two letters), location or soil series (three letters), and species (last two or three letters). Species–site combinations are ranked in decreasing order by diameter. Stand volume index is plotted on a semilogarithmic scale to improve visual interpretation.

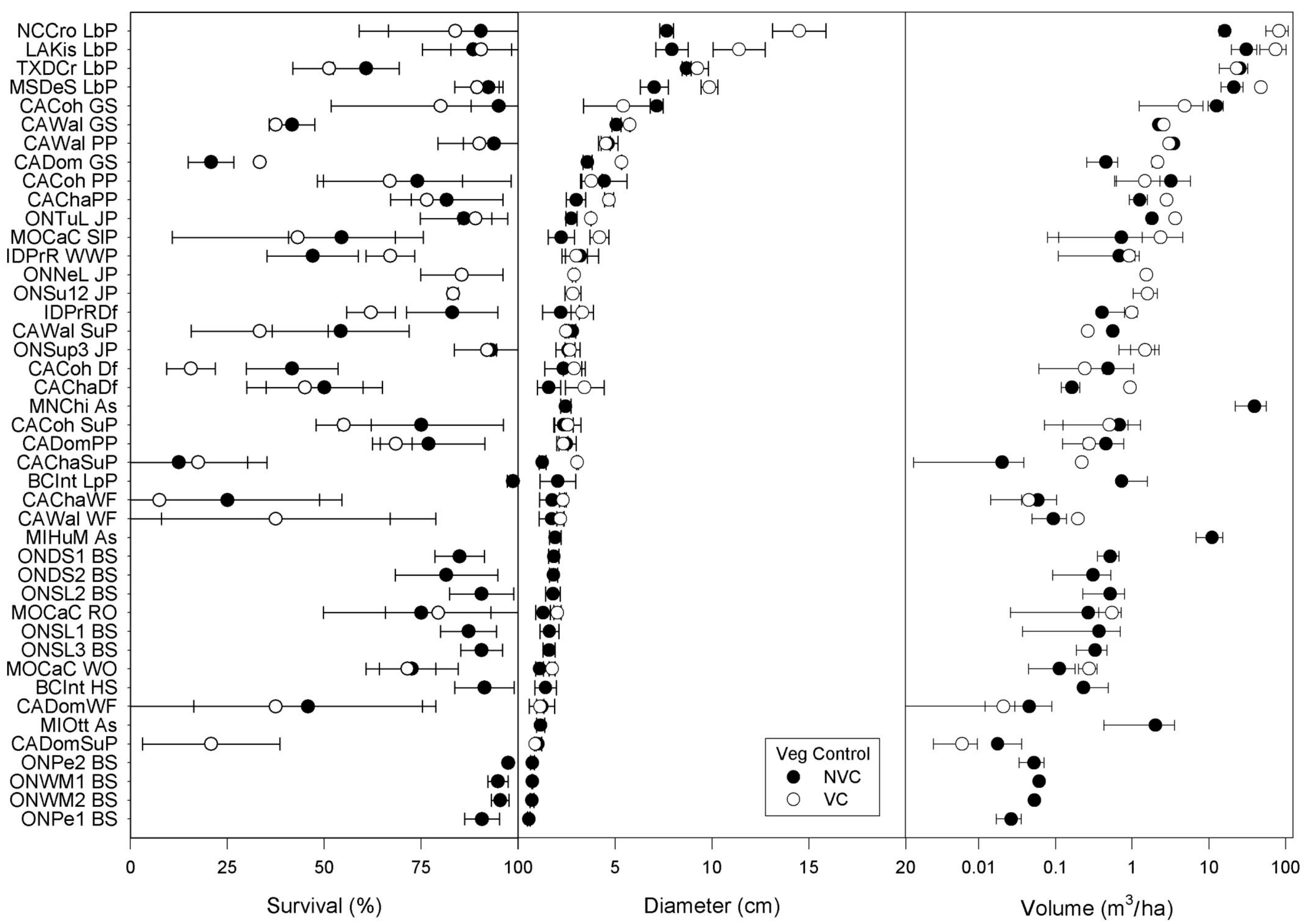


Fig. 6. Five-year survival response ratios of main treatment (OM–C) effects relative to the OM_0C_0 treatment (*a–h*) or vegetation control effects relative to no vegetation control (*i–j*): (*a–d*) main treatment response ratios by climate region, all species combined; (*e–h*) main treatment response ratios by climate region for hard pines (HPine) and for other Mediterranean conifers (MOCon); and (*i–j*) vegetation control response ratios by OM–C treatment for all climates and Mediterranean climates, all species combined. Horizontal bars represent 90% confidence intervals. Values in parentheses are the number of experiments per category.

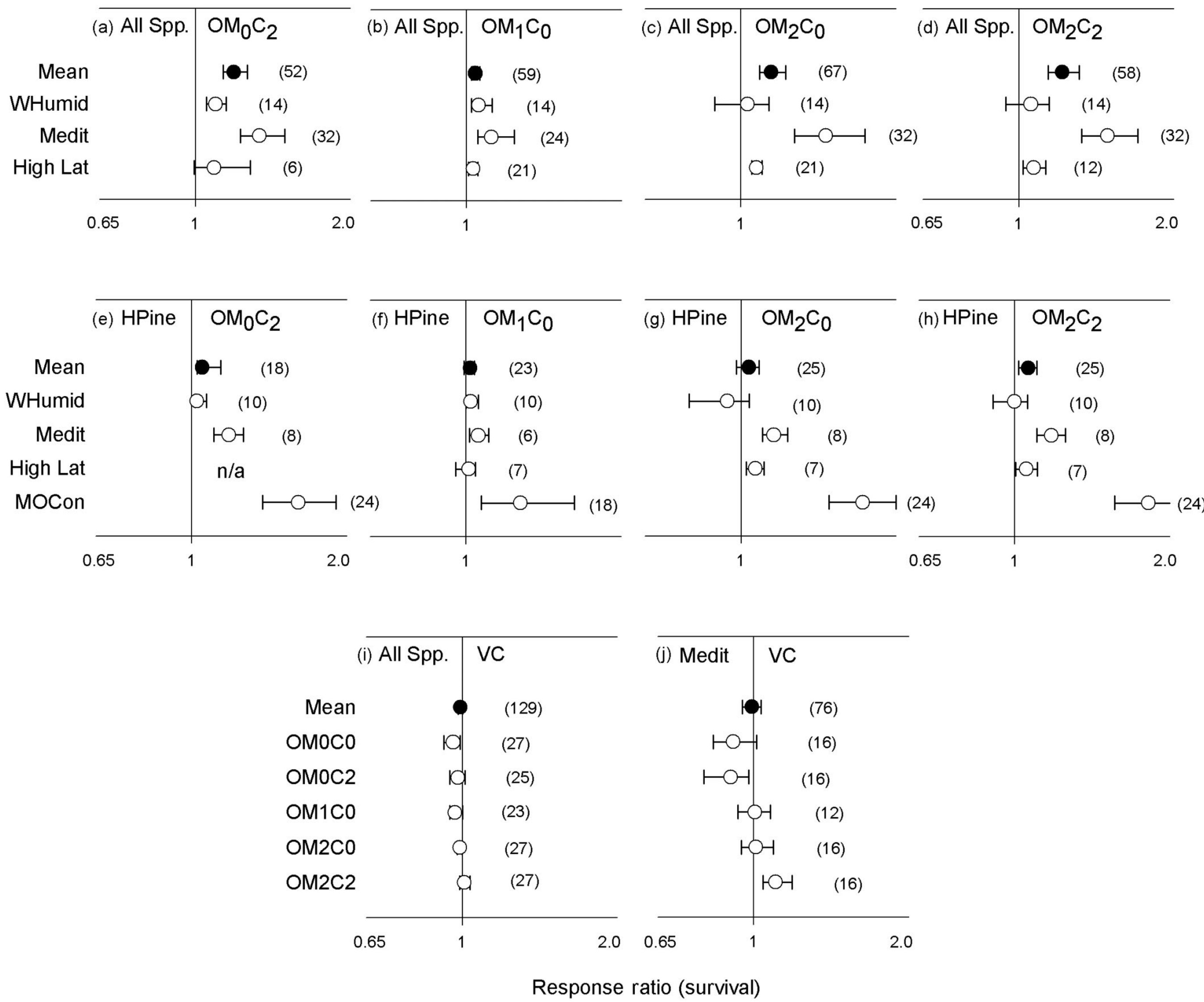
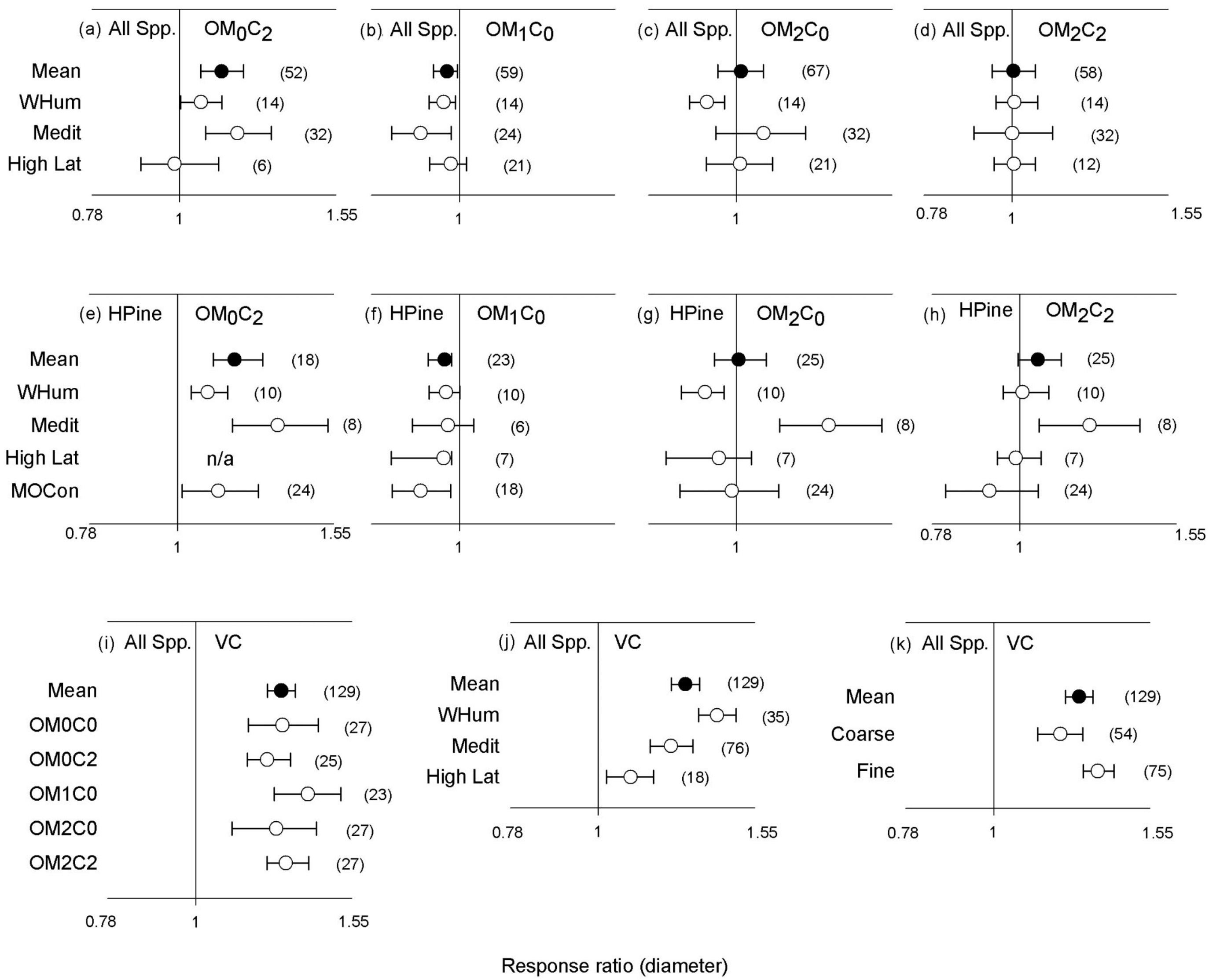


Table 6. Significance (*p* values) of between-group heterogeneity (Q_b) of weighted main treatment (main; OM–C) and vegetation control (VC) effect sizes across four categorical variables.

	Categorical variable							
Response variable	OM–C treatment	*k*	Climate	*k*	Species group	*k*	Soil texture	*k*
Survival, main	**0.066**	236	**0.001**	236	**0.001**	220	0.224	232
Survival, VC	**0.095**	129	0.644	129	0.618	119	0.672	129
Diameter, main	**0.011**	236	0.166	236	0.214	220	0.148	232
Diameter, VC	0.773	129	**0.003**	129	0.919	119	**0.023**	129
Volume, main	**0.019**	236	**0.001**	236	0.857	220	0.101	232
Volume, VC	0.226	129	**0.093**	129	0.722	119	0.123	129

Note: Responses for percent survival, ground-level diameter, and stand volume index are shown. Species groups include hard pines and other conifers. Aspen was omitted from all analyses and evaluated separately. Each response variable – categorical variable combination was represented by *k* response ratio comparisons.

Fig. 7. Fifth-year diameter response ratios of main treatment (OM–C) effects relative to the OM_0C_0 treatment (*a–h*) or vegetation control effects relative to no vegetation control (*i–k*): (*a–d*) main treatment response ratios by climate region, all species combined; (*e–h*) main treatment response ratios by climate region for hard pines (HPine) and for other Mediterranean conifers (MOCon); and (*i–k*) vegetation control response ratios by OM–C treatment, by climate region, and by soil textural class, all species combined. Horizontal bars represent 90% confidence intervals. Values in parentheses are the number of experiments per category.



California LTSP sites, Gomez et al. (2002*b*) reported greater potential mineralization and increased nitrogen uptake by ponderosa pine seedlings in OM_0C_2 plots. Most of our sites are well to imperfectly drained with loamy surface textures and had adequate aeration for aerobic microbes, soil fauna, and plant growth following compaction (Conlin and van den Driessche 2000; Jordan et al. 2000). As well, our compaction treatments rarely increased bulk densities to levels considered sufficient to reduce root growth, and near-surface densities often showed partial recovery within 5 years (Conlin and van den Driessche 2000; Page-Dumroese et al. 2006). Negative effects of the OM_0C_2 on soil strength may also have been moderated by higher soil water contents resulting from reduced competition and limited evaporation through the intact forest floor. Finally, compaction also commonly increases soil CO_2 levels (Conlin and van den Driessche 2000) and shoot/root partitioning (Heilman 1981; Corns 1988), and thus the measured increases in shoot growth we report may overestimate whole-plant response. Conlin and van den Driessche (1996) demonstrated this in a greenhouse study pertaining to the Skulow Lake LTSP site.

Our results, together with those of Miller et al. (1996) and Brais (2001), suggest that some soil compaction may actually promote seedling performance on many sites. Compaction effects may also change with time. Corns (1988) speculated that negative effects may appear over time as growing trees place greater demands on water and nutrient uptake and tree rooting is restricted by high bulk densities. Conversely, as soils gradually revert to precompaction levels, growth effects may subside. The LTSP experiments provide an

Fig. 8. Fifth-year stand volume index response ratios of main treatment (OM–C) effects relative to the OM_0C_0 treatment (*a–h*) or vegetation control effects relative to no vegetation control (*i–k*): (*a–d*) main treatment response ratios by climatic region, all species combined; (*e–h*) main treatment response ratios by climate region for hard pines (HPine); (*i–j*) vegetation control response ratios by OM–C treatment and by OM–C treatment for finer textured soils, all species combined; and (*k*) vegetation control response ratios by climatic region, all species combined. Horizontal bars represent 90% confidence intervals. Values in parentheses are the number of experiments per category.

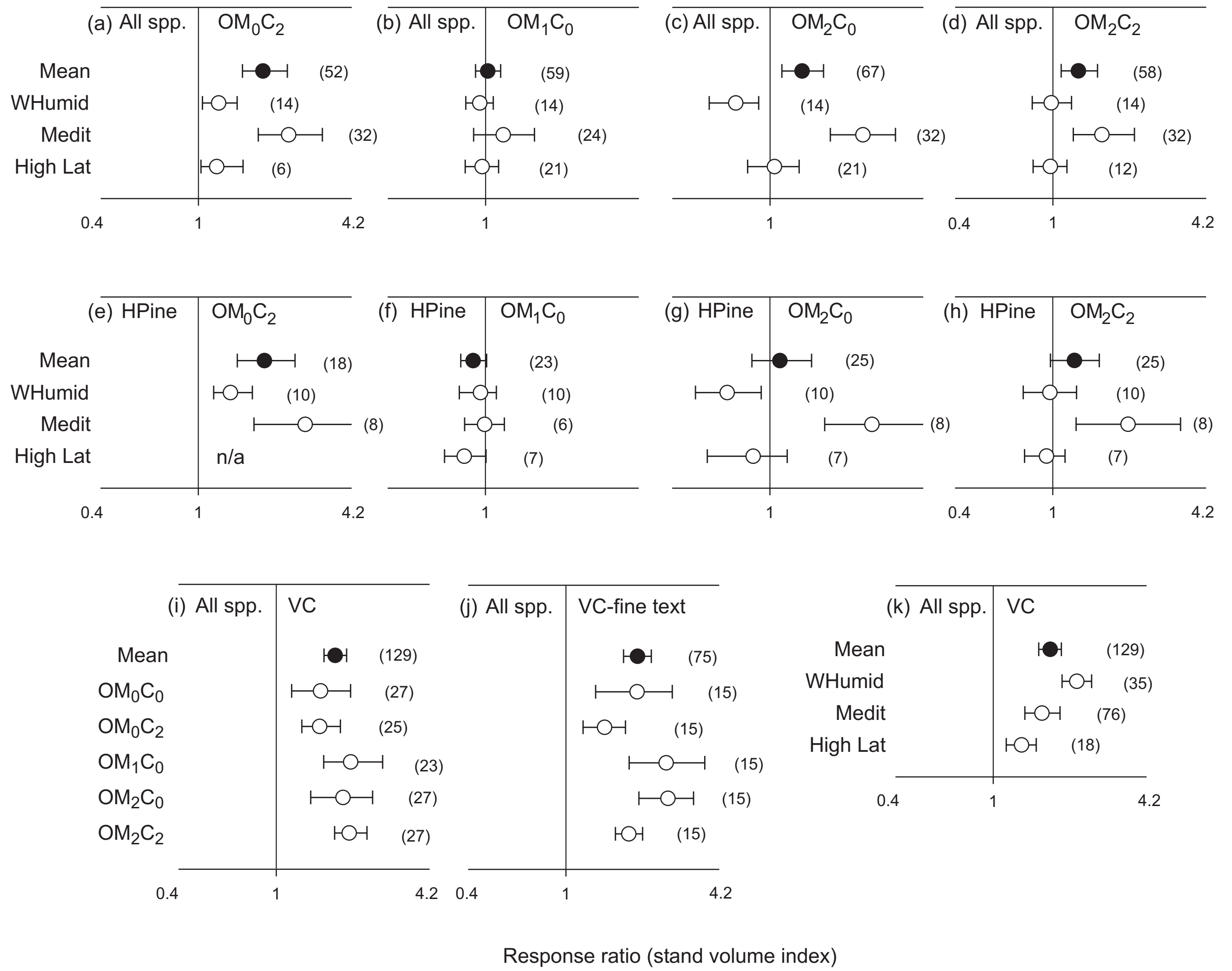
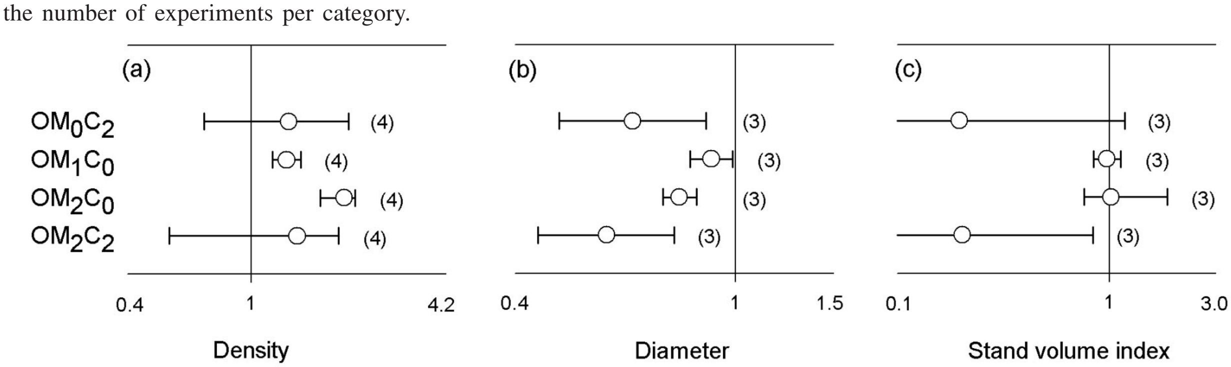


Fig. 9. Fifth-year aspen response ratios of main treatment (OM–C) effects relative to the OM_0C_0 treatment: (*a*) stand density (stems/ha), (*b*) stem diameter, and (*c*) stand volume index. Horizontal bars represent 90% confidence intervals. Values in parentheses are the number of experiments per category.



excellent opportunity to examine how compaction effects on soil conditions and plant growth change with time across a broad spectrum of sites.

Forest-floor removal and compaction

There was a notable lack of additivity in seedling response to forest-floor removal plus compaction; while both compaction and forest-floor removal often increased survival and growth, combining these two treatments rarely provided additional benefits and sometimes reduced growth in comparison with the OM_0C_2 treatment. OM_2C_2 growth responses generally showed greater similarities to those commonly found on landings and skid trails (Hatchell et al. 1970; Helms and Hipkin 1986; Brais 2001) than did responses following compaction alone. Thus, the combined effects of soil disturbance, rather than compaction per se, may account for most seedling growth reductions on harvest traffic areas.

For some higher porosity soils, compaction following forest-floor removal may improve root/soil contact, available water-holding capacity, thermal regimes, and (or) nutrient uptake. In other cases (e.g., some finer textured soils) the combination of increased surface drying (forest-floor removal) and reduced porosity and water-holding capacity (compaction) can produce excessive soil strength earlier in the growing season, particularly in drier climates (Gomez et al. 2002*a*). The resulting combination of smaller rooting volumes and limited water and nutrient availability may restrict nutrient uptake (Gomez et al. 2002*b*). In wetter climates, the formation of surface crusts on bare mineral surfaces, combined with reductions in macropore volume with compaction, may limit oxygen diffusion and microbial activity. We attribute reduced seedling growth in the OM_2C_1 and OM_2C_2 at the poorly drained Croatan site to restricted aeration and consequent limitations to phosphorus mineralization and uptake (Li et al. 2003).

Aspen OM–C response

The consistent increase in aspen stem densities with OM removal parallels findings from many studies (Frey et al. 2003) and likely reflects the influence of increased soil temperatures (Maini and Horton 1966) and greater root fragmentation (Shepperd 1996). While compaction effects on aspen densities were inconsistent, we attribute density reductions and inordinately poor OM_2 growth response on compacted plots at Chippewa to treatment application after sucker emergence (Stone and Kabzems 2002). The decrease in stem diameter with forest-floor removal may reflect nutritional limitations or greater interclonal competition at higher densities (Stone 2001; Frey et al. 2003), while decreases with compaction may reflect greater root fragmentation or reduced soil aeration (Bates et al. 1993). Effects of compaction on aspen densities, stem diameters, and particularly stand growth varied greatly among sites, suggesting that site conditions and treatment timing have a substantial influence on aspen response (Stone 2001).

Vegetation control

VC had similar effects on seedling performance across the different OM–C combinations; survival was unaffected, while, for a given region, diameter and stand volume index were increased proportionately in each OM–C treatment. The absence of VC effects on seedling survival, regardless of OM–C treatment, was not unexpected. Similar results have been reported for various species and locations (Lanini and Radosevich 1986; Brand 1991; Jokela et al. 2000). Exceptions occurred in Mediterranean climates, where VC resulted in significant declines in white fir (R = 0.766) and to a lesser extent, sugar pine (R = 0.908) survival. White fir is frost and heat sensitive and prefers sheltered environments.

Since VC usually elicited similar relative growth responses across the different OM–C treatments, beneficial effects of compaction and forest-floor removal appear largely unrelated to any purported ability of these treatments to reduce competition. The magnitude of treatment growth response, however, varied with climate. VC provided the greatest relative growth increases in warm–humid climates, where productivity is highest, and the smallest increases in cold, high-latitude climates, where productivity is lowest. Nevertheless, for high-latitude conifers as well as loblolly pine and oaks, VC produced larger and more consistent positive effects on individual tree and stand growth than did any OM–C treatment.

There is general agreement that competing vegetation, through its influence on water, nutrient, and light availability, strongly influences seedling growth in many regions (Stransky 1961; Johnson et al. 1989; Brand 1991; Sword et al. 1998; Powers and Reynolds 1999). Consistent with this, VC increased soil moisture (Page-Dumroese et al. 2006) and foliar nutrient concentrations (Table A2) at many LTSP locations, particularly in warm–humid and Mediterranean climates. Poorer growth following forest-floor removal in VC but not NVC subplots at Croatan underscores the importance of interactions between nutrient supply and competition on nutrient availability to seedlings.

Other metadata relationships

Climate

The greatest individual tree and stand growth rates were associated with warm–humid climates characterized by long growing seasons and plentiful moisture. These were also the only sites that showed consistent evidence of growth reductions associated with OM removal. While substantially lower than in warm–humid climates, individual tree and stand growth varied widely among sites in Mediterranean and cold, high-latitude climates. The greatest stand growth response ratios to both forest-floor removal and compaction were found in Mediterranean climates. There, stand volume index responses for ponderosa pine and other conifers were similar, but primarily reflected improvements in seedling growth for ponderosa pine and survival for other conifers. Hard pines often demonstrate greater response than other conifers to improved growing conditions resulting from site preparation (Grossnickle and Heikurinen 1989; Lopushinsky and Max 1990; Fleming et al. 1996). At high latitudes, the lack of significant OM–C responses in central British Columbia was unexpected but not unparalleled (Thompson and McMinn 1989; Bedford et al. 2000), and growth in all treatments was slow. Conversely, black spruce responses to OM removal were evident, despite slow growth.

Soil texture

The most notable soil texture effects were greater diameter response to VC on finer than on coarser textured soils and greater stand volume response on finer textured soils to

VC on noncompacted versus on compacted treatments. Assuming compaction reduces the proliferation of competing species (Brais 2001; Small and McCarthy 2002), results are consistent with increases in competition generally associated with fine loamy versus sandy soils. In warm–humid climates, survival was higher on finer than on coarser textured soils, primarily reflecting poor survival following forest-floor removal at Davy Crockett, the most drought-prone of the Coastal Plain sites. Undoubtedly soil properties play a greater role in defining OM–C response than we have shown here using only two categories of one particular property (cf. Gomez et al. 2002*a*, 2002*b*, 2002*c*).

Species

Seedling morphological and physiological attributes are important considerations when evaluating treatment impacts on productivity. We found that treatment response at a given location often varied among species in magnitude and sometimes direction. For instance, in California, giant sequoia, followed by ponderosa pine, had the greatest growth, ponderosa pine the highest survival, and white fir the greatest inter-treatment variation in response ratios. Ponderosa pine roots deeply, has greater stomatal control of water loss, begins growth earlier in spring, and has greater growth response to increased soil temperature than most associated conifers. In contrast, white fir initiates growth quite late, encountering proportionately longer periods of water deficit, shows less control of water loss, and is quite heat sensitive (Lopushinsky and Klock 1974; Lopushinsky and Max 1990).

In Missouri, shortleaf pine had higher growth rates, lower survival, and greater relative growth responses to compaction and VC than the two oaks. Planted oaks often have good initial survival but limited stem growth response, reflecting their episodic shoot growth habit, high root/shoot allocation, and propensity for stem dieback (McGee and Loftis 1986; Kolb et al. 1990). With aspen, treatment effects on reproductive processes and intraspecific competition, as well as on resource availability, may have been important. Thus, species choice is an important consideration when assessing impacts on productivity. Intersite comparisons and broad-based evaluations of harvest impacts are strengthened both by using common species or functional groups and by using contrasting species or functional groups representing different physiological attributes.

Conclusions

In evaluating our initial hypotheses, we found the following: (1) In warm–humid climates, VC provided consistent, substantive increases in seedling growth in all treatments; main-treatment OM–C growth responses were more limited and significant only for compaction (positive) and forest-floor removal (negative). (2) In Mediterranean climates, diameter response varied with species; ponderosa pine responded positively to compaction, forest-floor removal, and their combination, while other conifers responded positively to compaction but negatively to whole-tree harvest. Stand volume response, however, was similar for both species groups and followed the trends in ponderosa pine diameter response outlined above. VC increased mean diameter and stand volume increment for both species groups. (3) In cold, high-latitude climates, there was no significant difference in overall response among OM–C treatments and hence little evidence (excepting black spruce) that direct increases in soil warming (i.e., OM_2 treatments) increased seedling growth. VC produced significant increases in seedling diameters that were of similar magnitude in the different OM–C treatments. (4) Overall, compaction effects on seedling establishment did not vary greatly with soil texture. With aspen, however, compaction had a positive effect on stand growth on coarse- but not on fine-textured soils. (5) Effects of VC on seedling survival and growth were similar for all OM–C treatments. (6) Overall, forest-floor removal was more beneficial than was VC to seedling survival.

Treatment responses varied with climate, species, and to some degree, location; nevertheless, some consistent trends were evident. Whole-tree harvest often provided limited but concomitant reductions in individual tree growth and increases in survival. Soil compaction combined with intact forest floors usually benefitted both growth and survival of planted trees, but decreased aspen growth. Forest-floor removal increased conifer survival in Mediterranean and cold, high-latitude climates and increased aspen stem densities. This treatment also increased stand growth in Mediterranean climates, but reduced aspen stem diameters and both individual tree and stand growth in warm–humid climates. Soil compaction following forest-floor removal increased survival and stand growth in Mediterranean climates and survival to a slight degree in cold, high-latitude climates. For warm–humid and cold, high-latitude climates, however, individual tree and stand growth of planted trees in this treatment differed little from those following stem-only harvest, while aspen growth was reduced. VC had little effect on survival but benefitted growth in all treatments and climates. Overall, survival rates generally showed little relationship to individual tree growth, suggesting that different factors govern these two aspects of seedling establishment. Intersite comparisons across climatic regions were strengthened by using species common to particular physiologically based functional groups (e.g., hard pines).

Results to date suggest that early seedling performance is often dominated by microclimate- and competition-related effects on resource availability and physiological stress. In many cases, multiple impacts on resource availability could be invoked, suggesting that treatment effects are often complex, cumulative, and vary with site and climate. As stand development proceeds and the expanding canopies place greater demands on nutritional reserves while moderating microclimatic conditions, productivity limitations associated with OM removal may become increasingly evident.

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Appendix A

Appendix appears on the following page.

Table A1. Site characteristics and species planted (common names, short forms, and scientific names) for the Long-Term Soil Productivity locations considered in this paper, including nine affiliate black spruce locations in northwestern Ontario.

Name	State or province	Code	Installations	No. replicated experiments	No. replications per site	Species	Climate region	Soil texture	References
Carr Creek	Missouri	MOCaC	1	1	3	Red oak (RO; *Quercus rubra* L.), white oak (WO; *Quercus alba* L.), shortleaf pine (SlP; *Pinus echinata* Mill.)	Warm–humid	Fine	Ponder and Mikkelson 1995
Central British Columbia	British Columbia	BCInt	Log Lake, Topley, Skulow Lake	1	1	Lodgepole pine (LpP; *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), hybrid spruce (HS; *Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm)	Cold, high latitude	Fine	Holcomb 1996
Challenge[a]	California	CACha	1	Not replicated	1	Douglas-fir (DF; *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), ponderosa pine (PP; *Pinus ponderosa* Dougl. ex P. & C. Laws.), sugar pine (SuP; *Pinus lambertiana* Dougl.), white fir (WF; *Abies concolor* (Gord. & Glend.) Lindl.)	Mediterranean	Fine	Powers and Fiddler 1997
Chippewa[a]	Minnesota	MNChi	1	1	3	Trembling aspen (As; *Populus tremuloides* Michx.)	Cold, high latitude	Fine	Stone 2001
Cohasset[b]	California	CACoh	Blodgett, Brandy, Lowell	1	1	Douglas-fir, giant sequoia (GS; *Sequoiadendron giganteum* (Lindl.) Buchh.), ponderosa pine, sugar pine	Mediterranean	Fine	Powers and Fiddler 1997
Croatan[a]	North Carolina	NCCro	Goldsboro, Lynchburg	1	2, 1	Loblolly pine (LbP; *Pinus taeda* L.)	Warm–humid	Coarse	Tiarks et al. 1992, Scott et al. 2004
Davy Crockett[a]	Texas	TXDCr	Kurth 1–3	1	1	Loblolly pine	Warm–humid	Coarse	Tiarks et al. 1992, Scott et al. 2004
DeSoto[a]	Mississippi	MSDeS	Freest 1–3	1	1	Loblolly pine	Warm–humid	Fine	Tiarks et al. 1992, Scott et al. 2004
Dome[b]	California	CADom	Central, Vista	1	1	Giant sequoia, ponderosa pine, sugar pine, white fir	Mediterranean	Coarse	Powers and Fiddler 1997
Huron[a]	Michigan	MIHuM	1	1	3	Bigtooth aspen (As; *Populus grandidentata* Michx.), trembling aspen	Cold, high latitude	Coarse	Stone 2001
Kisatchee[a]	Louisiana	LAKis	Lousiana 1–4	1	1	Loblolly pine	Warm–humid	Fine	Tiarks et al. 1992, Scott et al. 2004
Kiskatinaw	British Columbia	BCKiR	1	1	2	Trembling aspen	Cold, high latitude	Fine	Holcomb 1996
NW coarse loamy[c]	Ontario	ONSL1-3	3	3	3	Black spruce (BS; *Picea mariana* (Mill.) BSP)	Cold, high latitude	Fine	Gordon et al. 1993
NW sandy[c]	Ontario	ONDS1-2	2	2	3	Black spruce	Cold, high latitude	Coarse	Gordon et al. 1993
NW wet mineral[c]	Ontario	ONWM1-2	2	2	3	Black spruce	Cold, high latitude	Coarse	Gordon et al. 1993

Table A1 (*concluded*).

Name	State or province	Code	Installations	No. replicated experiments	No. replications per site	Species	Climate region	Soil texture	References
NW peatland[c]	Ontario	ONPe1-2	2	2	3	Black spruce	Cold, high latitude	n/a	Gordon et al. 1993
Nemagos Lake	Ontario	ONNeL	1	1	3	Jack pine (*Pinus banksiana* Lamb.)	Cold, high latitude	Fine	Tenhagen et al. 1996
Ottawa[a]	Michigan	MIOtt	1	1	3	Trembling aspen	Cold, high latitude	Fine	Stone (2001)
Priest River[a]	Idaho	IDPrR	1	Not replicated	1	Douglas-fir, western white pine (WWP; *Pinus monticola* Dougl. ex D. Don)	Cold, high latitude	Fine	Tiarks et al. (1992)
Superior 1–2	Ontario	ONSup12	Superior 1–2	1	5	Jack pine	Cold, high latitude	Coarse	Tenhagen et al. 1996
Superior 3	Ontario	ONSup3	1	1	3	Jack pine	Cold, high latitude	Coarse	Tenhagen et al. 1996
Tunnel Lake	Ontario	ONTuL	1	1	3	Jack pine	Cold, high latitude	Coarse	Tenhagen et al. 1996
Wallace[a]	California	CAWal	1	Not replicated	1	Giant sequoia, ponderosa pine, sugar pine, white fir	Mediterranean	Coarse	Powers and Fiddler 1997

[a]National forest.
[b]Soil series.
[c]Site type.

Table A2. Nitrogen (N) and phosphorus (P) concentrations in current-year foliage of 5-year-old seedlings from selected Long-Term Soil Productivity installations.

Location	Species	Element (g/kg)	Treatment					
			OM_0	OM_2	C_0	C_2	VC	NVC
IDPrR	Douglas-fir	N	21.3	22.2	20.0	23.6	23.7	21.2
IDPrR	Western white pine	N	15.1	14.6	15.8	14.1	14.4	15.2
BCInt	Lodgepole pine	N	12.8	13.8	14.1	12.7	na	na
BCInt	Hybrid spruce	N	12.6	11.3	13.7	11.3	na	na
LAKis, MSDeS	Loblolly pine	N	12.5	12.0	12.3	12.2	13.2	11.9
NCCro	Loblolly pine	N	8.9	9.2	8.8	9.2	13.2	9.4
MOCaC	Shortleaf pine	N	14.7	14.4	14.5	14.9	15.3	13.9
MOCaC	Red oak	N	20.2	20.1	20.9	19.5	22.3	18.1
MOCaC	White oak	N	18.4	18.5	18.6	18.3	19.1	17.9
MI	Aspen	N	na	na	19.7	19.0	na	na
CA	Ponderosa pine	N	11.7	13.5	12.1	13	14.1	11.1
CA	Sugar pine	N	12.3	13.8	13.2	12.9	13.6	12.5
CA	White fir	N	14.7	17.7	16.1	16.3	18.8	13.6
CA	Giant sequioa	N	11	11.4	12.7	9.8	12.4	10.0
CARog	Ponderosa pine	N	13.8	11.5	13.7	11.6	13.3	12.0
CARog	Sugar pine	N	13.6	13.7	14.1	13.1	15.2	12.0
CARog	White fir	N	14.0	10.4	11.0	12.5	13.0	11.0
CARog	Giant sequioa	N	11.0	10.7	11.5	10.2	11.9	9.8
CABlo[a]	Ponderosa pine	N	13.3	16.5	15.2	14.7	na	na
CACha[a]	Ponderosa pine	N	11.7	12.9	12.5	1.21	na	na
CARog[a]	Ponderosa pine	N	11.8	13.3	13.0	12.1	na	na
ONEd3	Jack pine	N	16.7	15.1	na	na	16.4	15.3
ONNeL	Jack pine	N	16.1	14.9	15.5	15.3	15.6	15.2
ONTuL	Jack pine	N	15.8	12.0	12.0	10.5	12.6	1.29
BCInt	Lodgepole pine	P	1.28	1.48	1.37	1.33	na	na
BCInt	Hybrid spruce	P	1.57	1.66	1.63	1.78	na	na
LAKis, MSDeS	Loblolly pine	P	0.75	0.74	0.83	0.76	0.70	0.77
NCCro	Loblolly pine	P	0.74	0.86	0.78	0.81	0.70	0.78
MOCaC	Shortleaf pine	P	0.92	0.98	0.88	1.02	0.96	0.95
MOCaC	Red oak	P	1.22	1.20	1.24	1.05	1.24	1.06
MOCaC	White oak	P	1.12	1.12	1.00	1.13	1.13	1.07

Note: Sampling and analyses were done following standard procedures outlined in individual study plans on file at study location offices. CARog is a coarse-textured California LTSP site with a Mediterranean climate (Gomez et al. 2002*b*). ONEd3 is a coarse-textured Ontario LTSP site with a cold, high-latitude climate.

[a]From Gomez et al. (2002*b*), for VC only; na, value not available.