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# PLANT DIVERSITY IN MANAGED FORESTS: UNDERSTORY RESPONSES TO THINNING AND FERTILIZATION

SEAN C. THOMAS,[1,3] CHARLES B. HALPERN,[1] DONALD A. FALK,[1,4] DENISE A. LIGUORI,[1] AND KELLY A. AUSTIN[2]

[1]*Division of Ecosystem Science, College of Forest Resources, Box 352100, University of Washington, Seattle, Washington 98195 USA*
[2]*Environmental Forestry Research, Weyerhaeuser Company, Tacoma, Washington 98422 USA*

*Abstract.* Although most temperate forests are actively managed for timber production, few data exist regarding the long-term effects of forest management on understory plant communities. We investigated the responses of understory communities to a factorial combination of silvicultural-thinning and nutrient-addition treatments maintained for 12–16 yr in a set of 21–27 yr old Douglas-fir (*Pseudotsuga menziesii*) plantations. The four thinning levels span those used operationally (final stem densities of 494–1680 trees/ha); the two fertilization levels included a control and N addition in the form of urea at ~60 kg $N \cdot ha^{-1} \cdot yr^{-1}$, about twice the dosage used operationally.

Understory vegetation cover showed significant effects of thinning, with the highest thinning level resulting in the highest observed cover values. However, in some cases low levels of thinning resulted in a reduction in understory cover compared to unthinned controls. Understory vegetation declined dramatically in response to urea fertilization, with up to a 10-fold drop in herb-layer cover in unthinned stands. Species richness showed a simpler response to treatments, increasing in response to thinning, but decreasing in response to fertilization. Examination of species–area relationships indicated that effects of thinning and fertilization on species richness were similar across the range of spatial scales examined. Tree canopy cover, assessed by means of hemispherical photograph analysis, increased with fertilization, and estimated understory light levels decreased with fertilization, but neither showed a significant response to thinning at the time of measurement (12–16 yr after tree removal). Thus, treatment effects on understory cover and species richness were not a simple function of canopy cover or estimated light availability. Rather, there was a weak positive relationship between estimated understory light flux and vascular plant cover and diversity in nonfertilized plots, and no such relationship in fertilized plots. The lack of correspondence between treatment effects on canopy cover and understory vegetation may be due to time lags in understory response to changes in canopy cover or to treatment effects not mediated by light availability, such as physical disturbance during thinning operations and toxicity responses following application of urea fertilizer.

Species-specific responses to treatments were in part predictable as a function of plant life-form and edaphic association: species affinity for high soil moisture was the best predictor of fertilization responses, while life-form was the best predictor of thinning responses, with ferns and graminoids showing the largest positive responses to thinning. The successional status and stature of understory plant species were not significantly related to treatment responses. In sum, our results indicate that silvicultural thinning and fertilization can have large effects on understory plant diversity and community composition. However, such effects were not a simple function of understory light levels, and conventional ''functional types'' were of only limited value in predicting species-specific responses to silvicultural treatments.

*Key words: disturbance; diversity; fertilization; forest management; forest understory; plant diversity in relation to forest management;* Pseudotsuga menziesii; *silvicultural thinning; species diversity in forest understory communities; temperate rain forest; understory responses to thinning and fertilization.*

## INTRODUCTION

In most north-temperate forest communities the vast majority of plant species are not canopy trees, but rather understory herbs, shrubs, and subshrubs (Raunkiaer 1934, Crawley 1986, Halpern and Spies 1995). In many regions, including the Pacific Northwest of the United States, most forests are managed for timber production. In such forests the fate of indigenous understory plant communities, and thus of plant diversity in general, is a function of silvicultural practices designed with the primary intent of maximizing the value of the dominant tree crop. Two management options that presently offer high economic returns, and accordingly are in wide use,

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[3] Present address: Faculty of Forestry, University of Toronto, Toronto, Ontario, M5S 3B3, Canada.

[4] Present address: Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA.

are thinning and the addition of nitrogen fertilizers (Bengtson 1979, O'Hara 1989, Chappell et al. 1992). The specific implementation of these practices, however, varies greatly within and among both private and public forest lands. A detailed understanding of the effects of silvicultural thinning and fertilization on understory vegetation is thus essential to manage forests effectively for biological diversity, as well as for sustained production of wood products.

What are the expected effects of forest thinning and fertilization on understory plant communities? One long-standing generalization in the ecological literature is that added resources generally act to exacerbate competitive interactions among species. At high resource levels this results in a decline in plant diversity as one or a few responsive species monopolize resources other than those added (Newman 1973, Huston 1979, Tilman 1984, 1993, Goldberg and Miller 1990, Wedin and Tilman 1992, Wilson and Tilman 1993). At the other extreme, relatively few species may be able to endure very low resource conditions. A unimodal (''humped'') relationship between plant-community productivity and diversity has therefore been predicted, and is commonly observed (Grime 1973*a*, *b*, Al-Mufti et al. 1977), although the mechanisms that account for this pattern remain an area of active debate (Rosenzweig and Abramsky 1993, Tilman and Pacala 1993, Abrams 1995). The contrasting effects of light and nutrient limitation figure centrally in many theoretical discussions of plant-community structure and diversity (Tilman 1988). However, experimental studies addressing these patterns have focused almost exclusively on grassland or old-field vegetation, and have manipulated levels of soil nutrients and/or water, but not light.

In forest communities, removal of canopy trees most immediately affects the understory by increasing light availability. It is widely appreciated that the overall cover and biomass of forest understory vegetation increases, often dramatically, with canopy openness (Ehrenreich and Crosby 1960, Halls and Schuster 1965, Blair 1967, Blair and Enghardt 1976, Ford and Newbould 1977, Malcolm 1994, Klinka et al. 1996, Stone and Wolfe 1996). Likewise, thinning may result in higher availability of water and mineral nutrients through formation of ''root gaps'' (e.g., Parsons et al. 1994). In contrast, forest fertilization commonly results in a gradual increase in tree leaf-area index and canopy cover (Gower et al. 1992). In theory, forest thinning, by increasing available resources, could allow a greater number of understory species to persist. Alternatively, thinning might result in increased dominance by one or a few understory species, and thus reduce understory diversity (Alaback and Herman 1988). As with thinning, nutrient additions could plausibly have either positive or negative effects on forest understory diversity. Through its effects on light levels, fertilization might act to decrease diversity by eliminating all but a few very shade-tolerant species. However, if competitive interactions among understory species are strong, fertilization might act to increase diversity by reducing dominance by one or a few species. Which of these outcomes is more likely will depend on initial stand structure, on the magnitude of changes in tree cover, on the forest understory community in question, and on the specific management practices imposed.

The composition of understory communities is also expected to change systematically in response to thinning and fertilization. First, to the degree that successional patterns are determined by changes in understory light regimes, thinning may be expected to favor early-successional and possibly exotic species (e.g., Collins et al. 1985). Likewise, fertilization may be expected to favor late-successional species by accelerating stand closure (Goldberg and Miller 1990). Second, competition for light may favor taller-statured understory species under high-light conditions, and lower-statured species under low light (Tilman 1984, Goldberg and Miller 1990). In particular, this prediction follows if tall-statured understory species are less shade tolerant than smaller-statured species (cf. Givnish 1982, Thomas 1996, Thomas and Bazzaz 1999). Third, many forest understory species are characterized by some degree of clonal growth (e.g., Bierzychudek 1982, Antos and Zobel 1984, Messier and Kimmins 1991, Tappeiner et al. 1991, Tappeiner and Zasada 1993), and it has been suggested that clonality may better enable species to persist under spatially variable resource conditions (Hartnett and Bazzaz 1983, Hutchings 1988). One might therefore predict that clonal species would be differentially favored by nitrogen additions, and non-clonal species by thinning. Alternatively, clonal species may be better able to proliferate rapidly in canopy openings, and so be differentially favored by thinning (e.g., Tappeiner et al. 1991, Tappeiner and Zasada 1993, Huffman et al. 1994, O'Dea et al. 1995). Finally, it has been hypothesized that species associated with nutrient-rich soils in natural communities may increase in relative abundance in fertilized stands (Kellner 1993).

In the present study, we took advantage of existing long-term experiments originally designed to examine the growth responses of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) to thinning and fertilization. The experiments were implemented as a full-factorial design replicated over a large geographic area, thus greatly enhancing our scope of inference. We sampled understory vegetation within the experimental units, and quantified a variety of abiotic variables, with an emphasis on understory light conditions. We examined the following hypotheses: (1) Silvicultural thinning, by decreasing canopy cover and increasing understory light levels, will result in an increase in the overall cover of understory vegetation. (2) Conversely, fertilization, by increasing canopy cover and decreasing understory light levels, will result in decreased understory vegetation cover. (3) Where the overall cover of tall-statured shrubs and other understory dominants

TABLE 1. Characteristics of study sites in six Douglas-fir plantations in Washington State, USA, and history of treatment applications.

| Site location | Stand age (yr) | Elev. (m) | Slope (%) | Aspect | Soil pH† | Thinned at year: | Fertilization history: Fertilized at years: | Fert. dosages (kg N/ha) | Average rate (kg N·ha$^{-1}$·yr$^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|
| Bald Hills | 22 | 244 | 0–5 | Flat | 6.2 | 9 | 9, 11, 16, 21 | 448, 448, 224, 224 | 61.1 |
| Calligan Lake | 21 | 762 | 50–60 | SW | 5.3 | 9 | 9, 11, 16 | 448, 448, 224 | 53.3 |
| Griffin Creek | 24 | 305 | 5–10 | S | 5.8 | 8 | 8, 10, 13, 18, 23 | 448, 448, 112, 224, 224 | 60.7 |
| Greenwater‡ | 24 | 762 | 30–40 | NE | 5.1 | 11 | 11, 13, 18 | 448, 448, 224 | 46.7 |
| Lucas Creek‡ | 27 | 305 | 5–10 | W | 6.0 | 11 | 11, 13, 16, 21, 26 | 448, 164, 224, 224, 224 | 47.6 |
| Trestle Swamp‡ | 26 | 335 | 15 | S | 4.8 | 10 | 10, 12, 15, 20, 25 | 448, 448, 164, 224, 224 | 58.0 |

† Pretreatment measurements.
‡ Second-rotation stands; others are first-rotation (''second-growth'') stands.

remains relatively low, thinning will result in increased understory diversity, and fertilization in decreased diversity. (4) The more open canopy conditions associated with higher levels of thinning and lower levels of fertilization will result in a greater representation of early-successional species, tall-statured species, and clonal species. Fertilization will also result in an increased abundance of understory species associated with high nutrient levels in natural communities.

## METHODS

### *Study sites and experimental treatments*

The study was conducted in six Douglas-fir plantations managed by the Weyerhaeuser Company in western Washington State (USA). Stand ages ranged from 21 to 27 yr at the time of sampling, and included a range of elevations, slopes, and soil characteristics (Table 1). Understory vegetation was characteristic of the *Tsuga heterophylla* zone (Franklin and Dyrness 1973), with *Gaultheria shallon, Berberis nervosa, Polystichum munitum,* and *Acer circinatum* the most conspicuous species.

The stands were planted in the late 1960s and 1970s, and study plots established 8–11 yr later. All are part of a larger set of ''yield-forecasting installations'' designed to assess alternative silvicultural strategies. The plots selected include experimental manipulations of the longest duration available that incorporated a fully factorial design. Treated plots measure 35.4 m on a side (1250 m$^2$) and are separated by untreated buffer regions at least 53 m in width. A total of 48 plots were sampled: 1 plot/treatment × 8 treatments in each of six forecasting plot locations, giving a fully balanced design. All experimental stands were initially planted with 2-yr-old Douglas-fir stock at ~1680 trees/ha (~2200 trees/ha in two locations). ''Pre-commercial'' thinning treatments were conducted soon after stand closure, 8–11 yr after planting, by which time trees were ~6–10 cm in diameter at breast height (dbh) with dominant individuals reaching 5–7 m in height. Felled trees were systematically selected to yield relatively even tree spacing, and were then left in place. Treatments included a control (no thinning) and three levels of thinning, resulting in final stem densities of 1236 trees/ha (thin 1), 865 trees/ha (thin 2), and 494 trees/ha (thin 3). Thinned stems included both planted Douglas-firs and naturally regenerated conifers and hardwoods; sub-canopy individuals and understory shrubs were not cut.

Fertilized plots were initially treated with 448 kg/ha of N in the form of granular urea. The same rate of addition was repeated one or two additional times at 2–3 yr intervals, followed by additions of 224 kg N/ha at 5-yr intervals. The total amount of N added in fertilized plots thus varied from 1120 to 1512 kg, representing average rates of addition of 49–64 kg N·ha$^{-1}$·yr$^{-1}$ over the entire age of the stand (Table 1). Urea pellets were hand-broadcast to ensure an even coverage through the treated plots. Applications were made during the months of October to February to minimize urea losses through ammonia volatilization (cf. Nason et al. 1988). Plot surveys, treatment application, tree measurements, and other research activities involved some soil disturbance and trampling of understory vegetation. There may be some systematic differences in physical disturbance across treatments; thinned stands, in particular, were subject to soil disturbance, trampling, and the physical impacts of thinned stems.

### *Data collection*

Vegetation surveys and other measurements were conducted during periods of peak vegetation cover (June–August) in 1995 and 1996. Within each treated area a square 250-m$^2$ plot was centrally placed. Cover was visually estimated for all vascular plant species within the four 62.5 m$^2$ triangular quadrants (subplots) of each plot. Plants were assigned to the herb or shrub layer on the basis of plant height, not physiognomy: shrub-layer plants were defined as >1.3 m in height (measured to the highest apical meristem), and herb-layer plants as <1.3 m. (A given species could thus be assigned to both the herb and shrub layer.) Cover was defined as the vertically projected area of all aboveground plant parts. Estimated cover values <0.1% were scored as a ''trace,'' and were treated as 0.05% in statistical analyses. For all vascular plants, cover was estimated for each species, and the total cover for a plot

was calculated as the sum of species-specific cover values. Cover of bryophytes was pooled for all moss and liverwort species (including terricolous and lignicolous forms, but excluding epiphytes on lower tree trunks). The cover of coarse woody debris >10 cm in diameter (following Harmon and Sexton 1996) was visually estimated within each subplot. A tally was also made of all stems >1.3 m in height for tree species rooted within each sample plot (species defined as trees included *Abies amabilis, A. procera, Acer macrophyllum, Alnus rubra, Cornus nuttallii, Populus trichocarpa, Prunus emarginata, Pseudotsuga menziesii, Rhamnus purshiana, Salix scouleriana, Taxus brevifolia,* and *Tsuga heterophylla*). In addition, a systematic search of the entire forecasting plot (1250 $m^2$) was made for species not occurring within the central sample area. These whole-plot data are utilized only for examination of species–area relationships.

Point measurements of substrate and canopy characteristics were made at each of five points within a plot, corresponding to the plot center and the midpoint of the side of each sampled quadrant (5.6 m from the center point). Substrate measurements included the depth of the litter and organic soil layer. Canopy conditions were evaluated from hemispherical photographs obtained with a digital camera (Connectix QuickCam [Logitech, Fremont, California, USA]), affixed with an equalangular ''fisheye'' lens with a 135° field of view (wide-angle entry viewer, Number 7107, Safety 1st, Chestnut Hill, Massachusetts, USA). Photographs were taken under overcast sky conditions at a height of 1.3 m. Canopy cover estimates thus include tall shrubs in some instances. Greyscale images were processed using image-analysis software (Image, version 1.59 [W. Rasband, National Institutes of Health, Bethesda, Maryland, USA]) to obtain thresholds for canopy vs. sky, and analyzed using a solar arc tracing program (Solarcalc 6.05; modified from Chazdon and Field 1987). This program estimates the average total photosynthetic photon flux density (PPFD) at a given point. We assumed no seasonal changes in canopy cover, and uniform overcast conditions (Monsi and Saeki 1953) for the calculation of the diffuse radiation component. In addition, at each sampled point, the relative contribution to canopy cover of each tree species present in the hemispherical photo image was visually assessed.

To match point measurements of soil and canopy characteristics with understory vegetation characteristics for a given subplot (62.5 $m^2$), we calculated a weighted average of point measurements adjacent to each subplot. For this purpose the central point within each plot was weighted 1/2 relative to the points at the edge of each triangular quadrant. This weighting scheme was necessary to ensure that the average values for point measurements for the whole plot would equal the average of the four subplot values (i.e., all four quadrants border the central point, but each edge point is shared by only two subplots).

### *Species groupings according to habit and life history*

For the purposes of comparative analyses, plant species were divided into a priori categories describing aspects of life history, growth habit, and edaphic associations (Table 2). This information was gathered from local floras (Hitchcock and Cronquist 1973, Pojar and MacKinnon 1994), phytosociological studies (Klinka et al. 1989), and personal observations. The following life-form categories were used: ferns, forbs, graminoids (including grasses, sedges, and rushes), trees, and shrubs, the latter further divided into subshrubs, low shrubs, and tall shrubs. Plant stature was evaluated on a 1–6 scale based on the potential height of displayed leaves on mature individuals (1 = prostrate; 2 = 5–50 cm; 3 = >50–100 cm; 4 = >1–2 m; 5 = >2–5 m; 6 = >5 m). Successional status was divided into two broad categories: ''early successional'' and ''forest'' species, corresponding to ''invader'' and ''residual'' species, respectively, as described in studies of forest succession following logging (cf. Halpern 1989). Species were also evaluated as to production of woody stems (woody vs. non-woody), clonality (clonal vs. non-clonal), place of origin (native vs. exotic), and leafing habit (deciduous vs. evergreen). We used a broad definition of clonality, including species with short rhizomes or runners (such as caespitose graminoids), and those that characteristically layer (such as *Acer circinatum*; O'Dea et al. 1995). Edaphic characteristics describing species' associations with soil hydrology, nutrient status, and humus form were categorized using published phytosociological ''indicator values'' (Klinka et al. 1989). Species for which indicator values were not listed were excluded from a given analysis. Taxonomic nomenclature follows Hitchcock and Cronquist (1973).

### *Statistical analysis*

Plot-level variables (e.g., canopy cover, litter depth, understory plant cover, and understory species richness) were analyzed using a mixed-model analysis of variance that included thinning and fertilization as main effect terms (fixed factor), a thinning × fertilization interaction, and a location term (random factor), correspoding to the six experimental sites (listed in Table 1). Averages of subplot values were computed prior to analysis, thus giving a sample size of six per treatment combination. Dependent variables examined were assessed for agreement with standard parametric statistical assumptions (normality and homoscedasticity of residuals). Agreement with these assumptions was considered sufficient, and transformation of these data was not deemed necessary. A posteriori contrasts employ the Scheffé method (e.g., Sokal and Rohlf 1981); reported correlations are the Pearson product-moment coefficient.

Species-specific responses were examined using a general linear-model analysis to calculate ''response

TABLE 2. Species-specific responses to thinning and fertilization treatments together with species characteristics. Species are listed in descending order of frequency, calculated with respect to occurrence within subplots.

| Species† | Species occurrence | | Treatment effect | | Growth form and life history | | | | | | | Edaphic characteristics§§ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Freq. (%) | Cover (%) | Thinning effect | Fertilization effect | LF‡ | Ht.§ | E/F‖ | W/H¶ | C/N# | N/E†† | D/E‡‡ | M | N | H |
| *Polystichum munitum* | 88.0 | 3.972 | +0.5102 | −0.0405 | Fe | 3 | F | H | C | N | E | ··· | 3 | 2 |
| *Berberis nervosa* | 70.8 | 4.363 | +0.2575 | −0.4103 | LS | 4 | F | W | C | N | E | 3 | 2 | ··· |
| *Rubus ursinus* | 55.7 | 0.223 | +0.3124 | −0.4032 | SS | 3 | F | H | C | N | D | 3 | 2 | ··· |
| *Vaccinium parvifolium* | 50.0 | 0.652 | +0.3031 | −0.7033 | TS | 4 | F | W | C | N | D | ··· | 1 | 1 |
| *Galium triflorum* | 49.0 | 0.028 | +0.1911 | −0.0654 | Fo | 1 | F | H | C | N | D | 4 | 3 | 2 |
| *Gaultheria shallon* | 45.3 | 5.906 | +0.2663 | −0.7501 | LS | 4 | F | W | C | N | E | ··· | 1 | 1 |
| *Trillium ovatum* | 41.1 | 0.039 | +0.0749 | −0.2131 | Fo | 2 | F | H | N | N | D | 4 | 3 | 2 |
| *Sambucus racemosa* | 38.5 | 0.253 | −0.3128 | +0.5638 | TS | 4 | F | W | N | N | D | 4 | 3 | 2 |
| *Trientalis latifolia* | 38.5 | 0.025 | +0.3577 | −0.3688 | Fo | 2 | F | H | C | N | D | 3 | 2 | ··· |
| *Athyrium filix-femina* | 38.0 | 0.607 | +0.7106 | +0.2761 | Fe | 3 | F | H | C | N | D | 5 | 3 | 2 |
| *Viola sempervirens* | 37.5 | 0.035 | +0.3219 | −0.3681 | Fo | 1 | F | H | C | N | E | 3 | 2 | ··· |
| *Montia sibirica* | 29.2 | 0.043 | −0.1110 | +0.5783 | Fo | 2 | F | H | N | N | D | ··· | ··· | ··· |
| *Acer circinatum* | 28.1 | 1.213 | +0.3963 | −0.7079 | TS | 5 | F | W | C | N | D | 4 | 3 | 2 |
| *Smilacina stellata* | 26.0 | 0.040 | +0.2707 | −0.7030 | Fo | 2 | F | H | C | N | D | ··· | 3 | 2 |
| *Alnus rubra* | 22.4 | 0.012 | −0.2124 | +0.0638 | Tr | 6 | F | W | N | N | D | ··· | 3 | 2 |
| *Tiarella trifoliata* | 21.9 | 0.054 | +0.8208 | +0.2632 | Fo | 2 | F | H | C | N | D | 4 | ··· | ··· |
| *Lactuca muralis* | 21.4 | 0.019 | +0.3139 | +0.0000 | Fo | 3 | F | H | N | E | D | ··· | ··· | ··· |
| *Linnaea borealis* | 20.3 | 0.381 | +0.0153 | −0.9711 | SS | 1 | F | W | C | N | E | 3 | ··· | ··· |
| *Rubus spectabilis* | 19.3 | 0.110 | −0.1952 | +0.6067 | TS | 4 | F | W | C | N | D | 5 | 3 | 2 |
| *Tsuga heterophylla* | 19.3 | 0.101 | +0.4372 | −0.5181 | Tr | 6 | F | W | N | N | E | ··· | ··· | 1 |
| *Blechnum spicant* | 18.2 | 0.112 | +0.7564 | −0.6845 | Fe | 1 | F | H | C | N | E | 4 | 1 | 1 |
| *Vancouveria hexandra* | 16.1 | 0.045 | +0.3862 | +0.7244 | Fo | 2 | F | H | C | N | E | ··· | ··· | ··· |
| *Clintonia uniflora* | 14.1 | 0.013 | +0.2108 | −0.6871 | Fo | 1 | F | H | C | N | E | 3 | 1 | 1 |
| *Pteridium aquilinum* | 14.1 | 0.241 | +0.9241 | −0.9460 | Fe | 3 | F | H | C | N | D | ··· | ··· | ··· |
| *Carex deweyana* | 13.5 | 0.009 | +0.4975 | +0.0303 | Gr | 3 | F | H | C | N | E | 4 | 3 | 2 |
| *Holodiscus discolor* | 13.0 | 1.056 | +0.3367 | −0.3903 | TS | 5 | F | W | N | N | D | 2 | 2 | ··· |
| *Bromus vulgaris* | 12.5 | 0.007 | +0.7181 | −0.3600 | Gr | 2 | F | H | N | N | D | ··· | 3 | 2 |
| *Hieracium albiflorum* | 12.0 | 0.009 | +0.2880 | −0.6107 | Fo | 3 | F | H | N | N | D | 3 | ··· | |
| *Luzula parviflora* | 11.5 | 0.006 | +0.6094 | −0.2174 | Gr | 1 | F | H | C | N | D | 4 | 2 | 3 |
| *Symphoricarpos mollis* | 11.5 | 0.045 | +0.0603 | −0.8953 | LS | 3 | F | W | C | N | D | ··· | ··· | ··· |
| *Maianthemum dilatatum* | 10.9 | 0.014 | +0.3695 | +0.2445 | Fo | 2 | F | H | C | N | D | 5 | 3 | 2 |
| *Prunus emarginata* | 10.9 | 0.035 | −0.8361 | −0.8361 | Tr | 6 | F | W | N | N | D | ··· | ··· | ··· |
| *Ribes lacustre* | 10.4 | 0.034 | +0.7226 | −0.3178 | TS | 4 | F | W | N | N | D | ··· | 3 | 2 |
| *Achlys triphylla* | 9.9 | 0.144 | +0.4029 | −0.8195 | Fo | 2 | F | H | C | N | D | ··· | 3 | 2 |
| *Rosa gymnocarpa* | 9.9 | 0.016 | +0.2550 | −0.4092 | TS | 4 | F | W | N | N | D | 2 | 2 | ··· |
| *Campanula scouleri* | 9.4 | 0.005 | +0.1778 | −0.4444 | Fo | 2 | F | H | C | N | D | 2 | 1 | 1 |
| *Dicentra formosa* | 9.4 | 0.015 | −0.0070 | +0.7899 | Fo | 2 | F | H | N | N | D | 4 | 3 | 2 |
| *Disporum smithii* | 9.4 | 0.028 | +0.4596 | +0.6293 | Fo | 2 | F | H | N | N | D | 4 | 3 | 2 |
| *Epilobium angustifolium* | 9.4 | 0.016 | +0.5328 | −0.7328 | Fo | 3 | E | H | C | N | D | ··· | 3 | ··· |
| *Fragaria vesca* | 8.9 | 0.004 | +0.0706 | −0.7624 | Fo | 1 | F | H | C | N | D | 3 | 2 | 3 |
| *Taxus brevifolia* | 8.9 | 0.013 | −0.3500 | −0.7080 | Tr | 6 | F | W | N | N | E | ··· | ··· | ··· |
| *Rubus parviflorus* | 8.3 | 0.180 | +0.4070 | −0.7623 | TS | 4 | F | W | C | N | D | ··· | 3 | 2 |
| *Chimaphila menziesii* | 7.8 | 0.004 | −0.0500 | −0.8760 | SS | 2 | F | W | C | N | E | 3 | 2 | ··· |
| *Dryopteris austriaca* | 7.8 | 0.011 | +0.2833 | +0.2195 | Fe | 2 | F | H | C | N | D | ··· | ··· | ··· |
| *Osmorhiza chilensis* | 7.8 | 0.004 | +0.3000 | +0.2500 | Fo | 3 | F | H | N | N | D | 4 | 3 | 2 |
| *Lathyrus polyphyllus* | 7.3 | 0.004 | +0.4000 | −0.7131 | Fo | 3 | E | H | C | N | D | ··· | ··· | ··· |
| *Veronica officinalis* | 7.3 | 0.004 | +0.0267 | −0.7360 | Fo | 2 | E | H | C | E | D | ··· | ··· | ··· |
| *Adenocaulon bicolor* | 6.8 | 0.003 | +0.3384 | −0.5385 | Fo | 2 | F | H | N | N | D | 3 | 3 | 2 |
| *Circaea alpina* | 5.7 | 0.042 | +0.8771 | +0.9254 | Fo | 2 | F | H | N | N | D | 4 | 2 | ··· |
| *Anaphalis margaritacea* | 5.2 | 0.004 | +0.4000 | −0.1250 | Fo | 3 | E | H | C | N | D | ··· | ··· | 3 |
| *Digitalis purpurea* | 5.2 | 0.009 | +0.9787 | −0.8347 | Fo | 3 | E | H | N | E | D | ··· | ··· | ··· |
| *Listera cordata* | 5.2 | 0.003 | +0.2400 | −0.4000 | Fo | 1 | F | H | N | N | D | ··· | 1 | 1 |
| *Oplopanax horridum* | 5.2 | 0.053 | +0.8565 | +0.6392 | TS | 4 | F | W | C | N | D | 5 | 3 | 2 |
| *Oxalis oregana* | 5.2 | 0.133 | +0.3953 | +0.9843 | Fo | 2 | F | H | C | N | D | ··· | ··· | ··· |

*Notes:* Coefficients describing thinning and fertilization responses are based on a general linear-model analysis for each species (see *Methods*). Values for the coefficients correspond to the expected proportional change in cover given an increase in one ''unit'' of thinning (treatments scored on a 0–3 scale), or one ''unit'' of fertilization (treatments scored on a 0–1 scale).

† Species encountered within sampled plots, but occuring at frequencies of <5% include the following (in descending frequency): *Lonicera ciliosa, Smilacina racemosa, Pseudotsuga menziesii, Thuja plicata, Chimaphila umbellata, Chrysanthemum leucanthemum, Cornus canadensis, Elymus glaucus, Rhamnus purshiana, Rubus pedatus, Salix scouleriana, Actaea rubra, Anemone deltoidea, Corylus cornuta, Festuca occidentalis, Menziesia ferruginea, Prunella vulgaris, Streptopus streptopoides,*

coefficients'' to quantify treatment effects. The general linear model used was similar to that described above, but treated thinning and fertilization main effects as nominal continuous variables (with integer scores of 0–3 and 0–1, respectively), and omitted the thinning × fertilization term. To compare responses of species that differed greatly in absolute abundance on a comparable scale, the coefficients for thinning and fertilization effects were divided by the mean cover for each species, thus giving a scaled response coefficient corresponding to the expected proportional change in cover per ''unit'' change in the treatment. Thus, a thinning response coefficient of 0.5 indicates an average 50% increase in cover between adjacent thinning treatments (e.g., thin 0 vs. thin 1). These coefficients were then compared among species groups by ANOVA. Data on species-specific responses often included zero values, and thus frequently violated parametric statistical assumptions. We therefore do not report statistical test results for species-specific analyses, and used these coefficients only for the purpose of comparative analyses.

We evaluated plant diversity using two indices (Hill 1973): species richness, $N_0$, and species heterogeneity, $N_2$, calculated as the reciprocal of Simpson's index ($1/\Sigma\ p_i^2$), where $p_i$ is the proportional representation of each species in a sample, calculated on the basis of cover. Species heterogeneity shares the same units as species richness, and is commonly interpreted as the number of equally common species necessary to yield the same heterogeneity value as a given sample (see Magurran 1988).

To explore more fully relationships between canopy cover, edaphic characteristics, understory vegetation cover, and species diversity, we conducted two stepwise multiple-regression analyses. Independent variables used in estimating understory cover included estimated PPFD, coarse woody debris cover (continuous variables), and thinning and fertilization treatments (treated as nominal [dummy] variables as in the species-specific analyses). Independent variables used to predict species richness included this same set, and also total understory cover. All variables were calculated at the subplot level, to match local light, edaphic, and vegetation characteristics at the finest spatial scale available. We used an *F*-to-enter of 3.96, and an *F*-to-remove of 4.00 in these analyses (Sokal and Rohlf 1981).

## Results

### *Effects on canopy and edaphic characteristics*

There were no significant effects of thinning on tree canopy cover (Fig. 1a), or estimated understory light levels (Fig. 1b). In contrast, urea fertilizer additions resulted in significantly increased canopy cover (Fig. 1a), and generally in a corresponding decline in estimated understory light levels (Fig. 1b). This effect was relatively large: estimated PPFD (photosynthetic photon flux density) decreased by >40% with fertilization in unthinned stands. The proportion of canopy tree cover consisting of deciduous species was not significantly affected by either thinning or fertilization treatments, but qualitatively there was a trend toward decreasing deciduous tree cover in response to fertilization in thinned stands (Fig. 1c).

Significant treatment effects were also found for edaphic characteristics, including litter and organic horizon depth, and the cover of coarse woody debris (Fig. 1d–f). Litter depth was ~50% greater at the highest level of thinning than in unthinned plots (Fig. 1d), but fertilization did not significantly affect litter depth. Depth of the organic horizon showed a significant thinning × fertilization interaction, with the most marked effect being a decrease with fertilization in unthinned stands (Fig. 1e). The cover of coarse woody debris showed a marginally significant increase in response to fertilization (Fig. 1f), but no significant effect of thinning treatments.

The effects of resource additions on species diversity may potentially arise due to changes in the variance,

←

*Synthyris reniformis, Amelanchier alnifolia, Galium aparine, Ilex aquifolia, Ribes sanguineum, Rubus nivalis, Satureja douglasii, Senecio sylvaticus, Stellaria crispa, Abies amabilis, Acer macrophyllum, Asarum caudatum, Bromus sitchensis, Cirsium arvense, Cinna latifolia, Listera caurina, Lycopodium clavatum, Melica subulata, Oemleria cerasiformis, Polypodium glycyrrhiza, Populus trichocarpa, Taraxacum officinale,* and *Vaccinium ovalifolium.*

‡ LF = life-form categories: FE = fern; Fo = forb; Gr = graminoid (including grasses, sedges, and rushes); LS = low shrub; SS = subshrub; Tr = tree; TS = tall shrub.

§ Ht. = typical stature of displayed leaves on mature individuals: 1 = prostrate; 2 = 5–50 cm; 3 = > 50–100 cm; 4 = > 1–2 m; 5 = > 2–5 m; 6 = > 5 m.

‖ E/F: early-successional (E) vs. forest (F) species.

¶ W/H: woody (W) vs. herbaceous (H) species.

# C/N: clonal (C) vs. nonclonal (N) species.

†† N/E: native (N) vs. exotic (E) species.

‡‡ D/E: deciduous (D) vs. evergreen (E) species.

§§ The final three columns give indicator values for soil moisture (M), nutrient status (N), and humus form (H), respectively, as listed by Klinka et al. (1989). For M: 2 = moderate to very dry soils, 3 = dry to fresh soils, 4 = fresh to very moist soils, 5 = very moist to wet soils. For N: 1 = nitrogen-poor soils, 2 = nitrogen-medium soils, 3 = nitrogen-rich soils. For H (substrate): 1 = mor soils, 2 = moder and mull soils, 3 = mineral soil. Species with missing values (···) were not listed in Klinka et al. (1989).

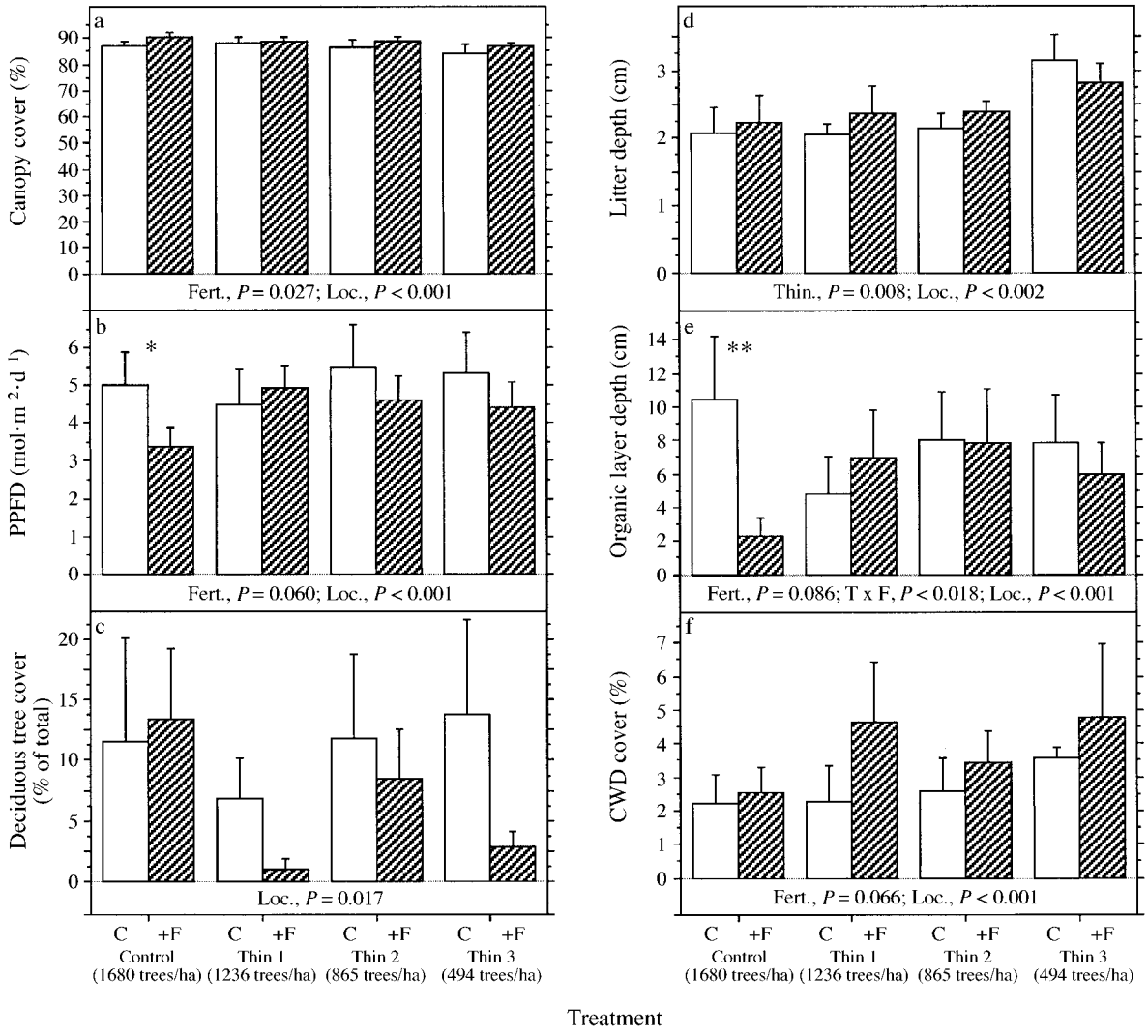


FIG. 1. Responses (means and 1 SE) of overstory canopy and edaphic characteristics to thinning and fertilization in 21–27 yr old Douglas-fir plantations. Hatched bars indicate stands repeatedly fertilized with urea (see Table 1 for details of addition rates). Asterisks indicate significance of a posteriori contrasts between control (C) vs. fertilization (+F) treatments within a given thinning level: * $P < 0.05$, ** $P < 0.01$. Probability values are listed for significance of thinning (Thin.), fertilization (Fert.), location (Loc.), and thinning × fertilization interaction (T × F) terms for each variable.

rather than the mean, of relevant environmental characteristics. To examine treatment effects on microenvironmental variability, we calculated the coefficient of variation for the five measurements within each plot for the following variables: litter depth, organic-horizon depth, canopy cover, and estimated PPFD. Analysis of variance for these parameters indicated no significant effect of thinning or fertilization on variability in litter depth or canopy cover. However, there was a significant positive effect of fertilization on variability in O-horizon depth (CV = 1.01 ± 0.12 in fertilized vs. 0.67 ± 0.10 in control plots, pooled across thinning treatments: $P = 0.033$; ANOVA $F$ test). In addition, a marginally significant increase in estimated variability in PPFD was detected in response to thinning ($P = 0.059$; ANOVA $F$ test).

### *Understory plant cover*

There were large effects of thinning and fertilization on understory plant cover (Fig. 2). Vegetation cover was consistently higher under the most intense thinning treatment (thin 3) than in unthinned control plots. However, in unfertilized plots there is an indication of a non-monotonic response to thinning for both herb- and shrub-layer cover, with values observed in thinning treatments 1 and/or 2 lower than those in unthinned plots. This pattern is statistically significant only for herb-layer cover, for which the thin 1 treatment was significantly lower than other treatments (a posteriori, contrast: $P < 0.05$). Bryophyte cover was, in contrast, somewhat higher at intermediate thinning levels (in unfertilized plots), although bryophyte cover was also

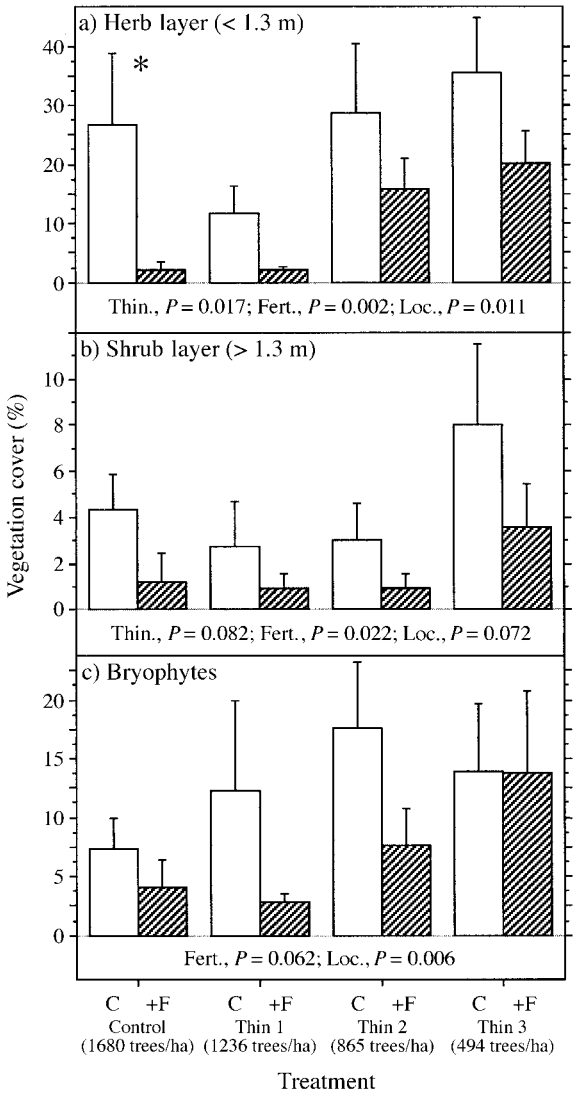


FIG. 2. Responses (means and 1 SE) of understory vegetation cover to thinning and fertilization treatments. Herb-layer vegetation included individuals of all species reaching a maximal height of <1.3 m within sampled quadrats. Shrub-layer vegetation included all species attaining heights >1.3 m. Bryophytes include all species of mosses and liverworts inhabiting soil, litter, or woody debris substrates but exclude epiphytes. Asterisks indicate significance of a posteriori contrasts between control (C) vs. fertilization (+F) treatments: * $P < 0.05$. Probability values are listed for significance of thinning (Thin.), fertilization (Fert.), location (Loc.), and thinning × fertilization interactions (T × F) terms for each variable.

highly variable among plots, and thinning treatment effects were not significant.

Urea fertilization resulted in large declines in vegetation cover. This trend was especially pronounced in unthinned stands, where we observed nearly an order-of-magnitude decline in herb cover in response to fertilization (27 vs. 3%: Fig. 2a). In some cases these dramatic fertilization effects were visible in the field as straight-line boundaries between treated and untreated areas (S. C. Thomas, *personal observation*). Treatment effects on bryophytes were less pronounced than those for vascular plants, with no response to fertilizer addition observed in the highest level of thinning (Fig. 2c). A similar analysis for total vascular-plant cover (herb- plus shrub-layer cover) indicated highly significant thinning and fertilization effects ($P < 0.001$ and $P = 0.006$, respectively), as did an analysis for cover summed across all three vegetation layers ($P < 0.001$ and $P = 0.004$, respectively). Thinning × fertilization interactions were not statistically significant in any of these analyses.

### *Species-specific responses*

The most common species encountered, and those that largely account for the observed trends in total herb and shrub cover, included *Gaultheria shallon*, *Berberis nervosa*, *Polystichum munitum*, and *Acer circinatum* (Table 2). The first two species showed particularly dramatic responses to fertilization: both were almost completely eliminated from unthinned, fertilized plots. Among these common species, *Polystichum munitum* showed the greatest positive response to thinning, and the least negative response to fertilization.

The effects of both thinning and fertilization treatments were remarkably consistent among the species censused. Qualitatively, 46 of 54 species (85%) found in >5% of subplots showed positive effects of thinning on average cover (Table 2). Likewise, 38 of 54 species (70%) exhibited a trend toward decreased cover in fertilized plots. On average, species showed a 31 ± 5% (mean ± 1 SE) increase in cover per thinning level. The average species-specific decline in response to fertilizer addition was 26 ± 8%. However, for a number of species cover increased markedly in response to fertilization. Examples of the latter response include both shrubs (*Sambucus racemosa* and *Rubus spectabilis*), and herbaceous plants (*Montia sibirica* and *Vancouveria hexandra*).

### *Species diversity*

There were consistent increases in species richness in response to thinning, but large decreases in response to urea fertilization (Figs. 3 and 4). Species–area relationships indicate that these responses were qualitatively similar across the range of spatial scales examined, with the same rank order among treatments observed at each spatial scale (Fig. 4). At the sampling-plot level (250 $m^2$), mean species richness increased from 20 species/plot in nonthinned plots to 26 species/plot at the highest level of thinning (in unfertilized plots). Species richness declined from 21 to 13 species/plot in response to fertilizer addition in unthinned plots (Fig. 4). The observed trends for the subset of ''forest'' plant species are nearly identical to those for all plant species combined (Fig. 3b). Species heterogeneity ($N_2$) showed no significant effects of either fertilization or

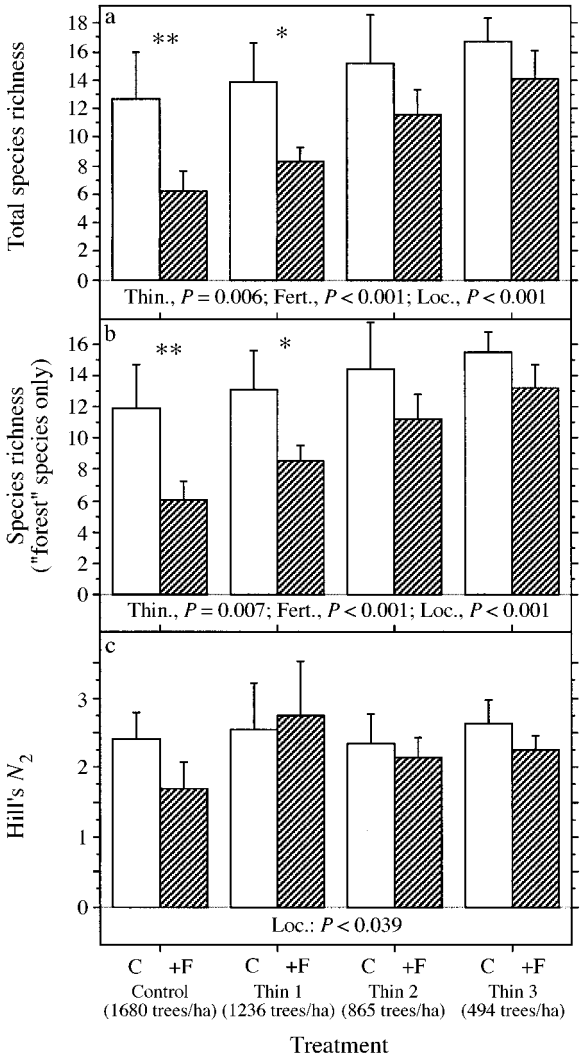


FIG. 3. Effects (means and 1 SE) of thinning and fertilization treatments on vascular-plant diversity quantified as (a) total number of species within sampled 62.5-m$^2$ subplots; (b) total number of "forest" species within sampled 62.5-m$^2$ subplots; (c) Hill's $N_2$ diversity index (all species), calculated as $1/\Sigma\ (p_i^2)$, where $p_i$ is the proportional cover of species $i$ in the sample unit (Hill 1973). Asterisks indicate significance of a posteriori contrasts between control (C) vs. fertilization treatments (+F): * $P < 0.05$; ** $P < 0.01$. Probability values are listed for significance of thinning (Thin.), fertilization (Fert.), location (Loc.), and thinning × fertilization interactions (T × F) terms for each variable.

thinning (Fig. 3c). The lack of response in $N_2$, in conjunction with the observed increase in species richness, indicates that the equitability of species' abundances declined in response to thinning (Hill 1973, Magurran 1988).

### *Differential responses of "functional types"*

We used the response indices presented in Table 2 to test for potential differences among species grouped by aspects of growth form and life history (Table 3). No statistically significant differences in thinning responses were found for the following comparisons: early-successional vs. forest species, clonal vs. nonclonal species, native vs. exotic species, evergreen vs. deciduous species, or for comparisons among edaphic indicator values ($P > 0.05$ in all cases). However, species with woody stems showed significantly smaller responses to thinning than did herbaceous species. Likewise, thinning responses differed significantly among plant size categories and plant life-forms (Table 3). Specifically, fern and graminoid species showed large positive responses to thinning, while tree species (represented as seedlings and saplings) showed a negative response on average (Fig. 5a). Life-form explained 41% of the variance in thinning-response coefficients, considerably more than did the other variables considered (0–27%).

No significant differences in average responses to fertilization were found among plant life-forms or most other morphological criteria (Fig. 5b). Clonal species did show significantly lower negative responses to fertilization than did nonclonal species. However, differences among groups defined by indicator values based on natural edaphic associations (Klinka et al. 1989) were more striking. Species associated with nitrogen-poor soils tended to show a stronger response (i.e., a larger negative response coefficient) than did species associated with nitrogen-rich soils, with nitrogen-medium species being intermediate (Fig. 6b); however, this pattern was not statistically significant. Ground surface (humus form) indicator values were a signifi-

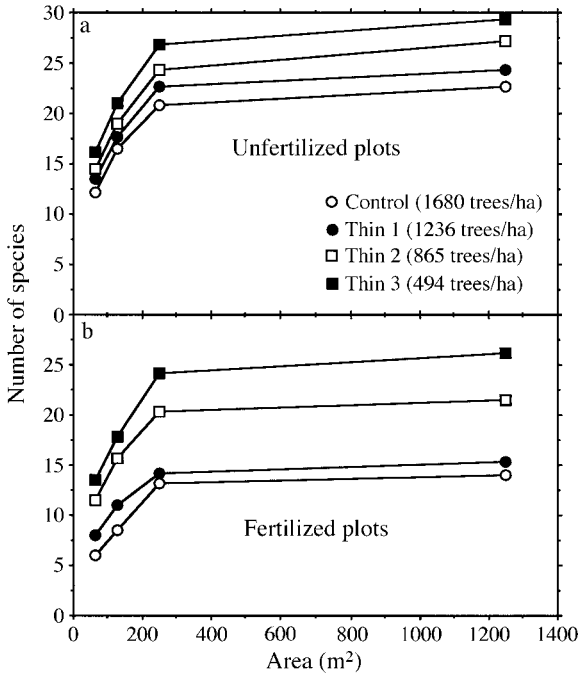


FIG. 4. Species–area curves within each thinning and fertilization treatment combination. Each curve represents the mean across six study locations within a given treatment.

TABLE 3. Tests for differences in average responses of species groups to thinning and fertilization treatments, using one-way ANOVA. Dependent variables are response coefficients listed in Table 2. See *Methods: Species groupings . . .* for details regarding category definitions.

| Variable | No. of categories | Thinning response | | Fertilization response | |
|---|---|---|---|---|---|
| | | *F* | *P* | *F* | *P* |
| Successional status | 2 | 0.0366 | 0.8491 | 2.3996 | 0.1281 |
| Life-form (Fig. 5) | 7 | 4.8324 | 0.0008*** | 1.0849 | 0.3870 |
| Plant size (1–6) | 6 | 3.1613 | 0.0162* | 1.3492 | 0.2623 |
| Woody vs. herbaceous | 2 | 10.6180 | 0.0021** | 3.7937 | 0.0574 |
| Clonal vs. nonclonal | 2 | 2.6584 | 0.1097 | 5.0757 | 0.0290* |
| Native vs. exotic | 2 | 0.2346 | 0.6304 | 0.0624 | 0.8038 |
| Deciduous vs. evergreen | 2 | 0.0199 | 0.8884 | 1.5197 | 0.2238 |
| Soil moisture indicators (Fig. 6) | 4 | 0.6916 | 0.5661 | 8.6347 | 0.0005*** |
| Soil nutrient indicators (Fig. 6) | 3 | 0.0453 | 0.9558 | 3.0461 | 0.0615 |
| Humus form indicators (Fig. 6) | 3 | 0.3045 | 0.7403 | 4.9351 | 0.0160* |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

cant predictor of species responses to N additions (Fig. 6c). Species associated with moder and mull humus forms showed a less negative response than did species associated with mor humus or exposed mineral soil. Indicator values for soil moisture were by far the best predictor of species-specific responses to fertilizer addition, explaining 38% of the variance in fertilization response (Table 3; Fig. 6a). Species of very moist to wet soils (an indicator value of 5) showed positive responses on average to fertilizer additions, while species of drier soils showed average relative declines of ~50% (Fig. 6a).

### *Relations between understory cover, diversity, and estimated light levels*

A statistically significant but weak relationship was found among estimated light levels (PPFD in mols per square meter per day, estimated as the daily average through the annual cycle), and both the cover and diversity of understory vascular plants (Fig. 7). In both cases this relationship holds only for the unfertilized plots (understory cover vs. PPFD: $r = 0.539$; $P < 0.001$; species richness vs. PPFD: $r = 0.262$; $P = 0.010$), with the estimated slope for fertilized plots not significantly different from zero. ANCOVA results for understory cover vs. PPFD indicate a significant light level × fertilization interaction ($P < 0.001$ for the heterogeneity of slope term). There was also a significant correlation between species richness and total vascular-plant cover in both fertilization treatments (pooled data: $r = 0.538$; $P < 0.001$).

Stepwise multiple regression yielded a final accepted model for understory cover that included terms for thin-

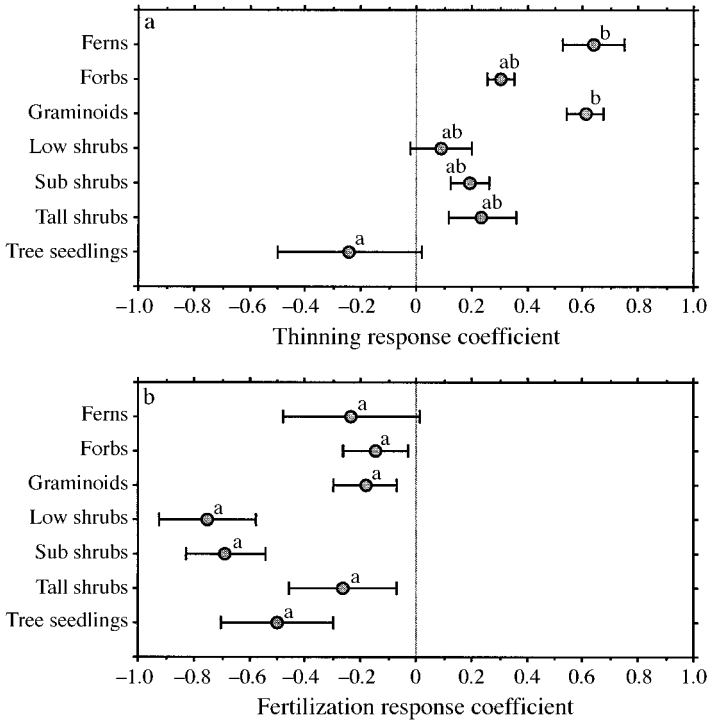


FIG. 5. Differential responses (means ± 1 SE) of plant life-forms to thinning and fertilization. Coefficients give the expected proportional change in cover given an increase in one ''unit'' of thinning or fertilization (see *Methods: Statistical analysis*). Means with the same lowercase letter are not significantly different at $P < 0.05$ using a posteriori contrasts between groups.

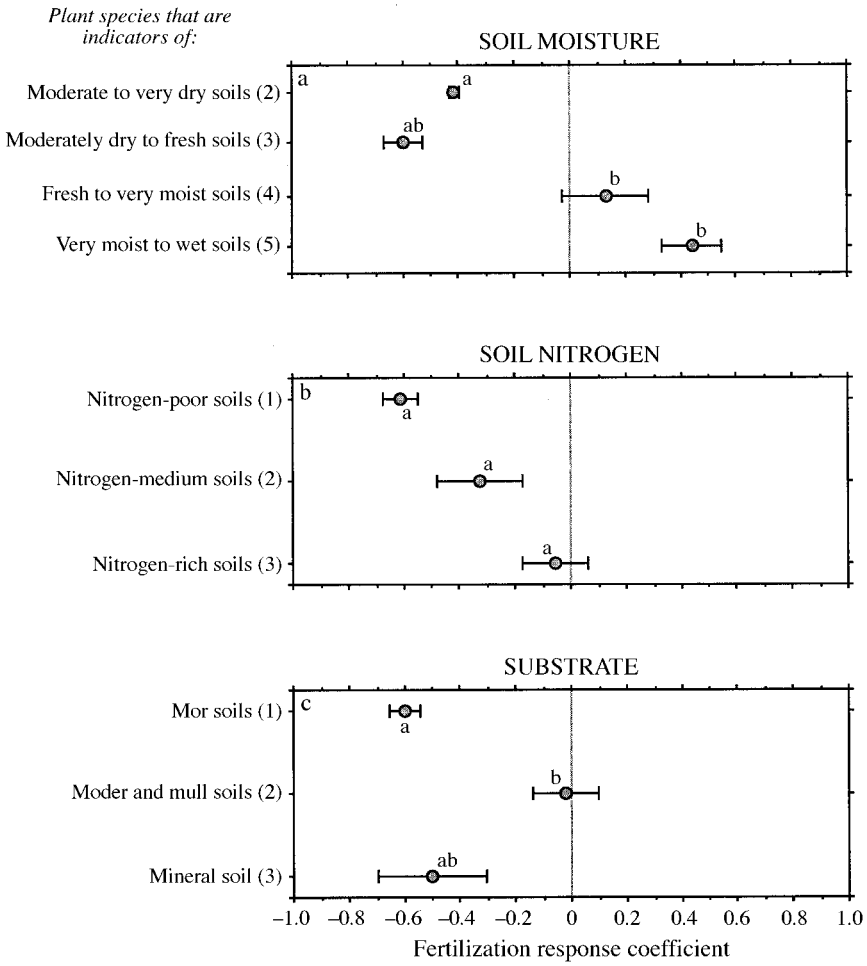


FIG. 6. Differential responses (means ± 1 SE) of species groups based on soil indicator values given by Klinka et al. (1989). Coefficients give the expected proportional change in cover given an increase in one ''unit'' of thinning or fertilization (see *Methods: Statistical analysis*). Means with the same lowercase letter are not significantly different at $P < 0.05$ using a posteriori contrasts between groups.

ning (positive), fertilization (negative), and PPFD (positive). Partial coefficients of determination for these variables were 0.051, 0.078, and 0.087, respectively, with the model explaining 27.0% of the total variance. The final accepted model for species richness included terms for thinning (positive), fertilization (negative), coarse woody debris (positive), and vascular-plant cover (positive). Partial coefficients of determination for these variables were 0.039, 0.045, 0.065, and 0.142, respectively, with the model explaining 43.4% of the total variance.

## DISCUSSION

Thinning of canopy trees and repeated additions of urea fertilizer each had dramatic, long-term consequences to understory vegetation cover, diversity, and community composition in Douglas-fir plantations. As expected, understory cover values were highest in the most intense thinning treatment; however, the lowest thinning level showed a trend toward decreased cover in comparison to unthinned control stands. Thinning effects on overstory canopy cover and understory light availability were small and not statistically significant at the time of measurement, 12–16 yr following tree removal. There was, however, a marginally significant trend toward higher spatial variability in understory light levels in thinned stands. Pooling all treatments, the overall relationship between estimated light levels and understory vegetation cover was very weak. This result contrasts with a number of previous studies that have found relatively tight relationships between canopy openness and understory vegetation cover (Halls and Schuster 1965, Malcolm 1994, Klinka et al. 1996, Stone and Wolfe 1996).

We suggest two potential reasons for a lack of correspondence between thinning effects on understory vegetation and canopy characteristics, namely, time lags in vegetation response to understory light conditions, and the effects of physical disturbance during thinning operations. Large effects on canopy cover and

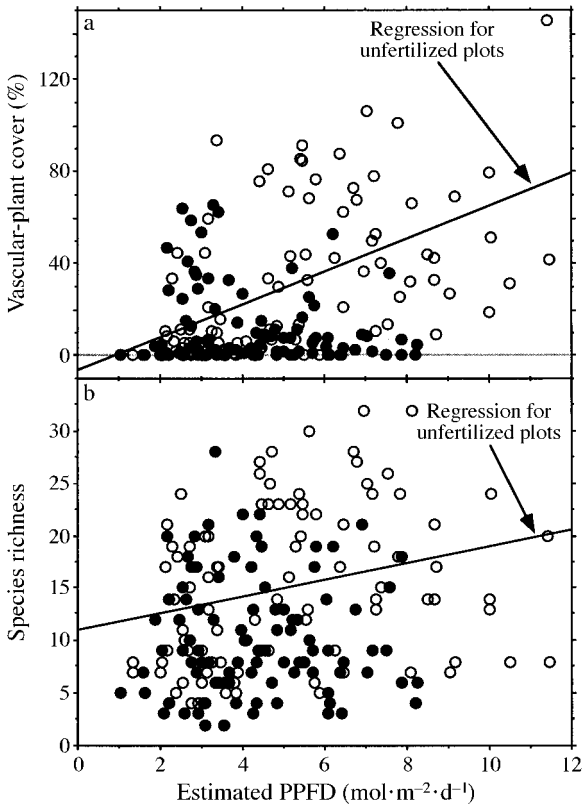


FIG. 7. Relationships between understory light levels (estimated as the annual mean of daily photon flux, using hemispherical photograph analysis) and (a) understory vegetation cover (herb plus shrub layers) and (b) vascular-plant species richness. Solid symbols are fertilized plots; open symbols are unfertilized plots.

understory light levels would almost certainly be seen immediately following tree removal. Growth responses of understory vegetation to increased light must accumulate over time, and thus effects on understory cover are likely to be greatest during the first several years following thinning. Thereafter, thinning effects on understory vegetation are expected to decline as stands develop and treatments converge in leaf-area index. In the present study we observed substantial effects of thinning treatments on understory vegetation cover 12–16 yr after tree removal. This suggests that the positive response of the understory to thinning diminishes quite slowly as canopy cover increases (see also Alaback and Herman 1988), and that the early effects of thinning on understory vegetation may persist long after effects on canopy structure have essentially disappeared (see also Milchunas and Lauenroth 1995). We speculate that the apparent reduction in herb-layer cover at low thinning intensities relative to controls may be due to physical disturbance during thinning operations. Understory vegetation in thinned stands is subject to trampling and smothering by cut trees, and this may often result in a reduction in cover immediately after thinning (e.g., Reader et al. 1991). Increased resource availability is expected to compensate over time for this disturbance effect, but at very low thinning intensities the initial disturbance may potentially outweigh any increase in resource availability. Studies that examine the detailed time course of vegetation responses to thinning are necessary to better evaluate both time lags and disturbance effects.

As predicted, nitrogen additions resulted in increased overstory canopy cover, decreased understory light levels, and decreased understory vegetation cover. The decline in the total amount of understory vegetation also corresponded to a substantial decrease in species diversity. This is consistent with the widely observed pattern of declining plant diversity with increased site productivity (e.g., Tilman 1984, 1993). The most widely invoked explanation for this decline is increased intensity of competition for light (Newman 1973, Goldberg and Miller 1990). Under this scenario, fertilization should result in declining plant diversity as understory species that are not extremely shade tolerant are eliminated. We directly tested this hypothesis by comparing differences in fertilization responses between successional groups, but did not find evidence for any consistent differences. However, we separated only one group of extreme early-successional species (e.g., *Epilobium angustifolium*, *Digitalis purpurea*, and *Anaphalis margaritacea*,) from a very broad class of ''forest'' understory species. A finer distinction based on shade tolerance and physiological capacity for dark acclimation could possibly account for the observed variability within this latter group (e.g., Collins et al. 1985). Detailed studies of the physiological ecology of understory plant species may thus be necessary to fully understand and predict their distribution and abundance in intensively managed forests.

Relationships between understory light levels and both the cover and species richness of understory vegetation differed strongly between fertilization treatments (Fig. 7). This suggests that reductions in understory cover and richness in fertilized stands were not simply due to canopy closure, but rather involved some other mechanism(s). One possibility is toxicity. After application, urea is commonly hydrolyzed by urease enzymes present in soil microbes to form ammonia, which can then volatilize from the soil surface. This process is particularly pronounced under relatively dry soil conditions (Nason et al. 1988), and there is strong evidence for toxic effects of volatilized ammonia following urea applications in agricultural systems (Bremner 1995). In addition, biochemical detoxification of ammonia is energetically expensive, and the capacity for detoxification may be particularly limited under low-light conditions (Van der Eerden 1982). Thus, forest understory plants may be particularly sensitive to the effects of ammonia volatilization due to a limited capacity for detoxification. Toxicity responses are also consistent with our observations in some replicate plots of straight-line boundaries in the presence of under-

story plants between fertilized and unfertilized areas. Other possible explanations for the reduction in plant cover and diversity include effects of urea or its chemical products on mycorrhizae or other soil microorganisms, or enhanced root competition between understory vegetation and crop trees following fertilizer additions. Regardless of the specific mechanism, it seems likely that additions of N in the form of urea should not be viewed simply as a ''resource'' that has positive effects on plant performance under all environmental conditions.

In addition to effects on canopy cover, thinning and fertilization also resulted in changes in edaphic conditions (Fig. 1). Thinning consistently resulted in increased litter depth. This effect is likely due to increased litter inputs as a direct consequence of ''precommercial'' thinning operations, in which stems and litter input from branches of thinned trees are left on site. There is also some evidence for a positive effect of fertilization on coarse woody debris cover. We suggest that this may have been due to an accelerated rate of growth and self-thinning in fertilized stands (e.g., Weiner and Thomas 1986, Morris and Myerscough 1991). It is also possible that downed stems of plantation trees could positively affect the abundance of plant species strongly associated with woody debris (such as *Vaccinium parvifolium, Dryopteris austriaca,* and *Cornus canadensis*). Although we did not directly examine species' rooting substrates in this study, woody debris cover as a whole emerged as a significant correlate of species richness in our stepwise regression analysis.

With respect to comparisons of responses among ''functional types,'' few of our a priori hypotheses were supported. Tall-statured species did not show a disproportionate positive response to thinning or a negative response to fertilization; in fact, tree saplings as a group showed negative responses to thinning, while relatively small-statured ferns and grasses showed the largest positive responses to thinning (Fig. 5). Surprisingly, no differences were detected in thinning responses of early-successional vs. ''forest'' species, or of clonal vs. nonclonal species. On average, clonal species tended to show a more negative average response to fertilization than did nonclonal species. Quantitative information on rooting morphology and capacity for clonal spread in understory species may facilitate a better understanding of species-specific responses to both thinning and fertilization (e.g., Antos and Zobel 1984, Antos and Halpern 1997).

Similar to a pattern reported in Scandinavia (Kellner 1993), we detected a trend toward increased relative abundance of understory species associated with high nutrient levels in fertilized treatments. Species associated with high soil nutrients also tend to be those associated with wetter sites (Klinka et al. 1989). This pattern may partially account for the observed association between soil moisture indicators and fertilization responses. However, species-specific responses to fertilization were actually better predicted by indicator values for soil moisture than by those for soil nitrogen levels. One possible explanation is that ammonia volatilization following urea additions is less pronounced in moister sites (Nason et al. 1988). If toxicity thresholds are similar among plants differing in their association with soil moisture, then lower rates of volatilization in moist sites would result in an association between soil moisture indicator values and fertilization responses similar to that observed.

Previous studies documenting negative effects of fertilizer additions on forest species have emphasized impacts on Ericaceous shrubs (Prescott et al. 1993, 1995) and mosses (e.g., Kellner 1993). In the present study we found no marked differences in fertilizer responses among taxonomic groups (i.e., plant families). For example, large negative responses to fertilizer occurred in many common species of the Liliaceae, Rosaceae, and Berberidaceae, in addition to the Ericaceae. Forest-floor mosses, dominated by the ubiquitous *Eurynchium oreganum,* did not show particularly strong negative responses to fertilization compared to the vascular flora.

### *Management implications*

The observed declines in understory cover and diversity in response to fertilization are of obvious concern from a management perspective. However, it should be noted that fertilizer dosages used in this study (47–61 kg $N \cdot ha^{-1} \cdot yr^{-1}$) were considerably higher than dosages used operationally, which generally do not exceed 30 kg $N \cdot ha^{-1} \cdot yr^{-1}$. Single-application dosages were also high, particularly early in the study (Table 1), and may have been above toxicity thresholds for particular dominant species, such as *Gaultheria shallon* (Prescott et al. 1993). Thus, it is not clear that current operational fertilizer dosages are having large negative effects on understory vegetation. Nevertheless, any decline in plant cover and diversity is of concern, particularly in a broader ecological context. For example, shrub cover has been found to be a strong correlate of the abundance of small mammal species in Pacific Northwest forests (Carey 1995, Carey and Johnson 1995). A direct examination of potential fertilizer effects at operational dosages should therefore be a high priority.

The generalization has previously been made that understory species diversity increases with light or moderate thinning, but decreases under heavy thinning (e.g., Alaback and Herman 1988; see also Reader et al. 1991). However, existing data are inconclusive on this point. Studies cited in support of this idea provide quantitative data on total plant cover or that of dominant species rather than direct measures of diversity (McConnell and Smith 1970, Stanek et al. 1979, Alaback and Tappeiner 1991), or report qualitative patterns but present no direct statistical support (Alaback

1984, Alaback and Herman 1988). Here we found that plant species richness increased monotonically with the level of thinning over the range of thinning intensities employed (Fig. 3a). This trend, combined with a lack of response in Hill's (1973) $N_2$ index to thinning (Fig. 3c), indicates that the equitability of species' abundances declined at high thinning levels. Thus, while there was increased dominance of a few species in thinned stands, this did not result in any decline in species diversity. However, densities of remaining trees did not approach the ''extreme'' thinning treatments included in some previous studies (e.g., Alaback and Herman 1988). It should also be emphasized that the diversity of our class of ''forest'' species may be maximized at some intermediate level of thinning, although evidently at a higher level than that employed in the present study. More work on the community consequences of very high thinning intensities is needed, and would be of direct relevance to ''new forestry'' methods such as green-tree retention (e.g., DeBell and Curtis 1993, North et al. 1996, Tappeiner et al. 1997, Halpern et al. 1999).

We conclude that the effects of both silvicultural thinning and fertilization on forest understory communities can be very large. We observed changes in species richness of up to 30–50% between treatments. This equals or even exceeds the magnitude of successional differences in plant diversity recorded between young stands (<60 yr) and old-growth (>300 yr) documented in chronosequence studies in the region (Spies 1991, Halpern and Spies 1995). However, despite the magnitude of these effects, few conventional ecological expectations regarding the community consequences of silvicultural treatments were borne out. Most notably, we did not find a simple relationship between overstory canopy openness and the amount or diversity of understory vegetation, nor any evidence that early-successional species were favored at high thinning levels. The situation is more complex. We suggest that a comprehensive understanding of silvicultural impacts on understory plant communities will need to consider time lags in vegetation response, non-resource-based mechanisms such as physical disturbance and toxicity effects, and relatively subtle differences in species-specific resource and edaphic requirements.

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