

The influence of canopy cover on understorey development in forests of the western Cascade Range, Oregon, USA

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Abstract

Natural disturbances, especially fire and treefalls, influence tree canopy composition in the *Pseudotsuga menziesii* forests of the western Cascade Range, Oregon. The composition of tree, shrub, and herb assemblages in the understorey of stands with different canopy types, such as maturing *Pseudotsuga*, *Tsuga heterophylla*, or mixed species stands, also differs.

Differences in both canopy type and the prevalence of canopy openings correlated with different degrees of understorey development in stands of similar ages. This suggests that understorey assemblages also reflect disturbance history. Before understorey assemblages can be used to relate community samples to community or habitat types, the extent to which their composition reflects long term influences of stand history vs. differences in site potential must be determined.

Nomenclature: follows Hitchcock & Cronquist (1973), Flora of the Pacific Northwest, unless otherwise indicated.

Introduction

In previous work (Stewart 1986a, b) I showed that fire and other disturbances determine tree canopy composition and the prevalence of canopy openings in *Pseudotsuga* forests of the central western Cascade Range, Oregon, USA. The early establishment and dominance by a species on a site bared by fire was a determinant of subsequent regeneration. If *Pseudotsuga menziesii* dominated early, regeneration of *Tsuga heterophylla*, and often *Abies amabilis*, was rapid (Stewart 1986a). If however, *Tsuga heterophylla* established first, further regeneration of

other species was absent or minimal until canopy openings formed. In stands unaffected by fires for several centuries, regeneration was confined to tree-fall gaps or under *Pseudotsuga* canopies and rarely occurred under *Tsuga* (Stewart 1986b).

In the course of these earlier studies I observed that differences in the overstorey also affected understorey development. *Pseudotsuga* forests often had a lush herbaceous understorey while adjacent *Tsuga* or multilayered *Pseudotsuga-Tsuga* stands had only a trace of understorey development. In ten stands ca 100–400 yr old there was a significant negative correlation of understorey cover with per-

cent dominance of *Tsuga* in the canopy (Stewart 1985). In old-growth *Pseudotsuga* stands (>400–450 yr old) mean understorey cover under *Pseudotsuga* canopies or beneath canopy gaps was over twice that under *Tsuga* (Stewart 1986b). In southeast Alaska, Alaback (1982) also noted depauperate understoreys beneath *Tsuga heterophylla* and considered that they were a direct result of its high foliar biomass.

Because forest communities of the western Cascade Range are differentiated by the potential climax tree species and the cover of shrub and herb species I considered it important to determine the possible impacts of forest canopies on understorey development. In this paper I investigate the influence of canopy type and canopy openings on the composition and cover of understorey trees, shrubs, and herbs in *Pseudotsuga* forests of the central western Cascade range, Oregon.

Methods

Study sites

Two major forest zones are widespread in the central western Cascade Range; the *Tsuga heterophylla* zone (ca 300–1050 m elevation) and the *Abies amabilis*

zone (ca 1050–1550 m elevation). Between these zones there is a 'transition' zone where both *Tsuga* and *Abies* may assume a climax role (Franklin & Dyrness 1973). This study deals with forests of the 'transition' zone adjacent to Soapgrass Mountain in the Willamette National Forest, Linn County, Oregon.

The forest stands studied were: a mixed-canopy stand at lat. 44°26'N, 122°19'W (*Pseudotsuga menziesii*, *Abies procera*, *Tsuga heterophylla*, *Abies amabilis* – hereafter referred to as the 'mixed' stand); a *Pseudotsuga menziesii*-dominated stand (the '*Pseudotsuga*' stand), and an adjacent *Tsuga heterophylla*-dominated stand (the '*Tsuga*' stand) located approximately 2 miles southeast of the mixed stand (Table 1, Fig. 1). Canopy types in the mixed stand were identified as predominantly (1) *Tsuga heterophylla* (2) *Pseudotsuga menziesii*/*Abies procera* and (3) canopy gap (an opening in the forest canopy at least 3 m in diameter, as a vertical projection from the edges of the crowns to the forest floor). Canopy types in the other two stands were the dominant species, *Pseudotsuga* or *Tsuga*.

Canopy structure

Two indirect methods were used to assess differences

Table 1. Site variables and vegetation characteristics of each stand.

	Mixed stand*	<i>Pseudotsuga</i> stand	<i>Tsuga</i> stand
Aspect	NW	SE	SE
Slope (°)	0–3	15	15
Elevation (m)	1250	1140	1140
Fire dates (AD) ^a	1230, 1410, 1540, 1870	1860	1410, 1840
Mean tree age (yr ± S.E.) ^a	101.6 ± 1.0 (n = 59)	108.5 ± 1.6 (n = 24)	128.7 ± 2.9 (n = 23)
Age of oldest tree (yr)	117	120	146
Basal area (m ² /ha)	100.3	96.5	115.2
Mean canopy height (m) ^a	30	40	30
% frequency canopy gaps ^a	11.9	9.3	1.3
Association ^b	Pacific silver fir/ coolworty foamflower	Pacific silver fir/ vine maple/cool- worty foamflower	Pacific silver fir/ dwarf Oregon grape

* = mixed stand (GM-2), *Pseudotsuga* stand (SM-1), and *Tsuga* stand (SM-2) in Stewart (1985).

^a = from Stewart (1985).

^b = from Hemstrom *et al.* (1982).

n = number of trees aged.

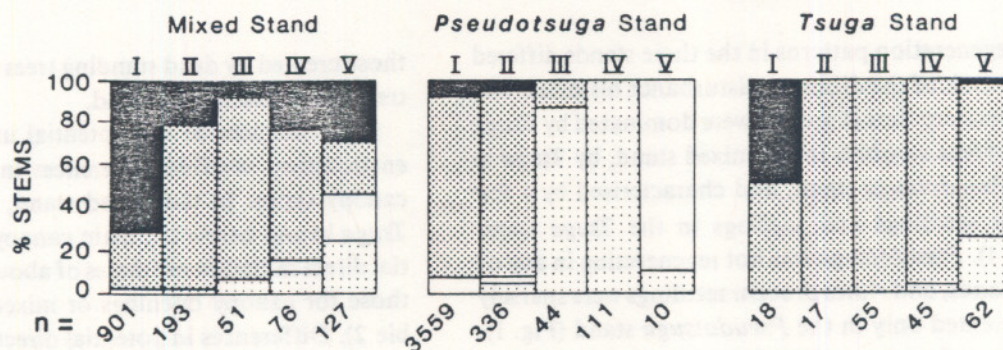


Fig. 1. Relative dominance of major tree species in each stand by relative height class (adapted from Stewart 1985).

□ = *Abies procera*, ▤ = *Pseudotsuga menziesii*, ▦ = *Tsuga heterophylla*, ■ = *Abies amabilis*.

Height classes are: I. seedlings (30–140 cm); II. overtopped; III. intermediate; IV. lower main canopy; and V. upper main canopy.

n = number of individuals in each relative height class.

in cover between canopy conditions within the mixed stand and between the *Pseudotsuga*- and *Tsuga*-canopied stands.

1. Canopy cover was estimated by assessing potential light conditions in each stand from hemispherical fish-eye photographs of the canopy. In the mixed stand, 11–13 photographs were taken at 1 m above ground level at random locations under each canopy type. In the *Pseudotsuga* and *Tsuga* stands, 8 and 11 photographs respectively were taken at 1 m above ground level at 10 m intervals along a transect bisecting each stand longitudinally. Percentages were calculated for potential total diffuse plus direct radiation ('total site factor') and potential direct radiation only ('direct site factor') for the growing season (May–September) (Anderson 1964a, b).
2. The frequency of canopy gaps was assessed for each stand from 3 × 3 m contiguous quadrats (Stewart 1985).

Understorey sampling

In each stand 50–100 quadrats (1 × 1 m) were sampled on a restricted-random basis beneath each specified canopy type. Each quadrat was located within 3 m of the trunk (*Tsuga* or *Pseudotsuga*/*Abies*) or within the canopy opening nearest to a randomly chosen point.

In each quadrat the presence of all vascular spe-

cies in the understorey was recorded, and total cover of each of the non-tree species was visually estimated in percentage cover classes of <1, 1–5, 6–25, 26–50, 51–75, and 76–100%. Tree seedlings were counted, height of the tallest individual of each species was measured, and the numbers rooted on fallen logs were recorded.

Results

Forest structure and stand development

Fire and other disturbances such as treefalls determined the composition of the forest canopies in all stands. In the mixed stand, *Pseudotsuga*, *Abies amabilis*, *Abies procera* and *Tsuga heterophylla* had all established as pioneers after a stand destroying fire in about 1870 (Table 1). A few remnant trees from older populations had scars from, or had established after, fires in about 1230, 1410, and 1540 AD. Recent treefalls of old *Pseudotsuga* snags had created small canopy openings (50–100 m²). The predominantly single species *Pseudotsuga* stand had established after a stand destroying fire in about 1860, and the *Tsuga* stand after an earlier less severe fire in about 1840 AD (Table 1). Several emergent old-growth *Pseudotsuga* that had established after a fire in about 1410, were a feature of the *Tsuga* stand. Both the *Pseudotsuga* and *Tsuga* stands were subsequently undisturbed by treefalls.

Regeneration patterns in the three stands differed as a result of the different disturbance histories. The understorey tiers (I and II) were dominated by *Tsuga* and *Abies amabilis* in the mixed stand, by *Tsuga* in the *Pseudotsuga* stand, and characterised by a few *Tsuga* seedlings and saplings in the *Tsuga* stand (Fig. 1). *Pseudotsuga* was not regenerating in any of the stands, and *Abies procera* seedlings were sparsely represented only in the *Pseudotsuga* stand (Fig. 1).

The replacement of shade intolerant *Pseudotsuga* and *Abies procera* by the more shade tolerant *Tsuga* and/or *Abies amabilis* is apparently occurring at different rates, e.g., in the mixed stand *Abies amabilis* was present in all tiers indicating that it has been continuously regenerating since the last fire, whereas in the relatively undisturbed *Tsuga* stand *Abies amabilis* had only recently established as seedlings (Fig. 1).

Canopy cover

Canopy gaps were significantly more frequent in the mixed canopy and *Pseudotsuga* stands than in the *Tsuga* stand ($P < 0.001$, χ^2 test, Table 1). Although gaps were almost as frequent in the *Pseudotsuga* stand as in the mixed stand, they were generally small ($< 25 \text{ m}^2$) openings between the *Pseudotsuga* crowns, not distinct 'holes' in the canopy such as

those created by dead standing trees and snags or by treefalls in the mixed stand.

The estimates of the potential understorey light environment verified differences in cover between canopy types. In the mixed stand, dense-crowned *Tsuga* in and below the main canopy caused potential direct radiation estimates of about 50% less than those for canopy openings or mixed canopies (Table 2). Differences in potential direct radiation were even more substantial in the single species stands. The *Pseudotsuga* understorey received over twice the amount of radiation reaching the understorey in the *Tsuga* stand. Total potential radiation was not significantly different under the three canopy types in the mixed stand because of the strong influence of *Tsuga* in subcanopy tiers. Because of more even canopy cover, understoreys in the single species stands received lower total potential radiation than those in the mixed stand (Table 2).

Tree seedlings

Tsuga and *Abies amabilis* seedlings were rare or absent under *Tsuga* canopies in all stands (Tables 3, 4 and 5). Conversely, *Abies amabilis* seedlings were common under a *Pseudotsuga* or *Pseudotsuga/Abies procera* canopy. Seedlings were shortest beneath *Tsuga* canopies and tallest in canopy open-

Table 2. Mean light conditions (\pm S.E.) for different canopy types determined from hemispherical photographs.

Stand and canopy type	Nr photos	Percent total diffuse + direct radiation	Percent direct radiation
Mixed stand			
canopy gaps	11	43.6 ± 1.1	$9.6 \pm 0.6a$
<i>Tsuga heterophylla</i>	13	44.9 ± 1.6	$6.1 \pm 0.4b$
<i>Pseudotsuga/A. procera</i>	11	46.6 ± 1.9	$8.7 \pm 0.9a$
Pure stands			
<i>Pseudotsuga menziesii</i>	11	$36.6 \pm 0.7a$	$11.4 \pm 0.7a$
<i>Tsuga heterophylla</i>	8	$31.1 \pm 1.2b$	$4.8 \pm 0.5b$

Note: Percentages in each column followed by a different letter are significantly different according to a Kruskal-Wallis one-way analysis of variance by ranks test (3-way comparison, $P < 0.001$) or a Mann-Whitney U test (2-way comparison, $P < 0.005$). Only within area comparisons were made.

Table 3. Mean maximum height (cm, \pm S.E.) of tree seedlings in 1×1 m quadrats under different canopy types in the three stands. Percentages of seedlings on elevated surfaces also included.

Canopy type	Seedling species		% elevated	
	<i>Abies amabilis</i>	<i>Tsuga heterophylla</i>	<i>Abies amabilis</i>	<i>Tsuga heterophylla</i>
mixed stand				
<i>Tsuga heterophylla</i> (n = 100)*	11.3 \pm 6.3a	—	(0)	
<i>P. menziesii</i> / <i>A. procera</i> (n = 50)	20.0 \pm 3.2b	+ **	(22)	
canopy gaps (n = 50)	27.7 \pm 4.9c	37.5 \pm 2.5	(14)	(100)
pure stands				
<i>Tsuga heterophylla</i> (n = 100)	5.6 \pm 0.6a	—	(0)	
<i>Pseudotsuga menziesii</i> (n = 100)	23.6 \pm 6.6b	61.5 \pm 7.4	(42)	(86)

Note: Mean maximum heights for each species followed by a different letter are significantly different according to a one-way ANOVA and applying Duncan's new multiple-range test (3-way comparison, $P < 0.05$) or a t-test (2-way comparison, $P < 0.05$).

* number of quadrats sampled.

** + = absolute frequency < 5 .

ings (Table 3), indicating either different establishment times or different growing conditions under each canopy type.

Tsuga seedlings were most abundant on elevated woody substrates such as old *Pseudotsuga* logs and stumps (Table 3). These substrates were common beneath *Pseudotsuga*, mixed canopies and in canopy openings, but rare under *Tsuga*, again indicating different conditions under the different canopy types.

Shrub and herbaceous vegetation

In the mixed stand, most major understorey species were more frequent in canopy openings than beneath the other canopy types (Table 4). Many of these species were also frequent under a mixed canopy of *Pseudotsuga*/*Abies procera*, and were significantly more frequent here than beneath a *Tsuga* canopy (Table 4).

Differences in understorey cover for the different canopy types of the mixed stand were more marked than differences in frequency. All species had $< 2\%$

cover under a *Tsuga* canopy; most had $> 2\%$ cover under *Pseudotsuga*/*Abies procera* and in canopy openings (Table 4). Although several species (e.g., *Vaccinium alaskaense*) were present in many of the *Tsuga* plots, they contributed little cover as they were generally < 20 cm tall. Cover in canopy openings was significantly higher than under mixed canopies for most species (e.g., *Vaccinium*, *Clintonia*, *Smilacina*, and *Tiarella*).

Species richness was greater under mixed *Pseudotsuga*/*Abies procera* canopies and in canopy openings than under *Tsuga* (Table 4). No species grew exclusively under *Tsuga*, but several rare species were limited to one or both of the other canopy types (e.g., *Achlys triphylla*, *Listera borealis*, *Valeriana sitchensis*, *Campanula scouleri* and *Streptopus roseus*).

In the single species stands (Table 5) all species except *Abies amabilis* were significantly more frequent under *Pseudotsuga* than under *Tsuga*. Covers of most species were greater than 5% under *Pseudotsuga* but did not exceed 1% under *Tsuga*. Forty-four species were encountered under *Pseudotsuga*, but only 25 under *Tsuga*. Many species were exclusive to

Table 4. Frequency and cover of common species in 1 × 1 m quadrats under different canopy types in the 'mixed' stand. Only species with frequency >25% are listed.

Species	Canopy type					
	% frequency			% cover (± S.E.)		
	<i>Tsuga heterophylla</i> (n = 100) ^a	<i>P. menziesii</i> / <i>A. procera</i> (n = 50)	canopy openings (n = 50)	<i>Tsuga heterophylla</i> (n = 100)	<i>P. menziesii</i> / <i>A. procera</i> (n = 50)	canopy openings (n = 50)
Tree seedlings, shrubs						
<i>Abies amabilis</i>	3	38*	42*		not measured	
<i>Vaccinium alaskaense</i>	63	82*	92*	1.6 ± 0.3	22.3 ± 3.7	43.7 ± 4.5
<i>Rubus lasiococcus</i>	32	86*	88*	1.7 ± 0.5	16.9 ± 3.2	16.6 ± 2.7
Herbs, ferns						
<i>Clintonia uniflora</i>	21	38*	78*	+ ^b	4.5 ± 1.1	9.4 ± 1.5
<i>Cornus canadensis</i>	26	88*	84*	+	20.6 ± 2.9	26.9 ± 3.5
<i>Smilacina stellata</i>	9	12	50*	+	4.2 ± 2.3	13.0 ± 3.1
<i>Pteridium aquilinum</i>	9	34*	46*	+	5.2 ± 1.8	10.7 ± 2.9
<i>Tiarella unifoliata</i>	8	16	30*	+	+	4.4 ± 2.0
<i>Trillium ovatum</i>	21	46*	32*	+	1.8 ± 0.6	2.0 ± 0.9
<i>Viola</i> spp. ^c	41	88*	90*	+	5.3 ± 1.0	2.4 ± 0.5
<i>Coptis laciniata</i>	5	44*	54*	+	12.1 ± 3.1	11.2 ± 2.9
<i>Pedicularis racemosa</i>	4	12*	30*	+	1.6 ± 0.9	5.2 ± 1.8
All species ^d						
Total number of species	23	33*	27			
Total of absolute frequencies/n	2.6	7.3*	8.2*			

Note: Differences in percent frequency were subjected to a χ^2 test using the absolute frequencies and applying Yates' correction (Greig-Smith 1964). Pairwise comparisons were made between *Tsuga* and each of the other canopy types. Differences in cover were not statistically compared.

^a number of quadrats sampled.

^b + = <1% cover.

^c 3 species were recognised; *Viola glabella*, *V. sempervirens* and *V. orbiculata*.

^d includes 20 additional species which occurred in <25% of the quadrats under any canopy condition. The species are: *Tsuga heterophylla*, *Vaccinium membranaceum*, *Rosa gymnocarpa*, *Ribes lacustre*, *Chimaphila umbellata*, *Rubus ursinus*, *Anemone lyallii*, *Achlys triphylla*, *Vancouveria hexandra*, *Campanula scouleri*, *Xerophyllum tenax*, *Pyrola secunda*, *Listera borealis*, *Hieracium albiflorum*, *Valeriana sitchensis*, *Osmorhiza chilensis*, *Goodyera oblongifolia*, *Streptopus roseus*, *Linnaea borealis*, *Polystichum munitum*.

* indicates significant difference from *Tsuga* at $P < 0.05$.

the *Pseudotsuga* stand (e.g., *Acer circinatum*, *Anemone deltoidea*, *Pedicularis racemosa*, *Pyrola secunda*, and *Clintonia uniflora*). *Berberis nervosa* was the only species significantly more frequent under *Tsuga* than under *Pseudotsuga* (27% vs 3%).

Discussion

The three stands were following different successional pathways after fire (Stewart 1985). The replace-

ment of shade intolerant *Pseudotsuga* and *Abies procera* by the more shade tolerant *Tsuga* and/or *Abies amabilis* was occurring at different rates, e.g., in the mixed stand *Abies amabilis* was present in all height tiers and it had established intermittently over the last 120 yr (Stewart 1985). In contrast, in the relatively undisturbed *Tsuga* stand, *Abies amabilis* had only recently established as seedlings.

The differences in understorey composition documented in the present study indicate that understorey development was also occurring along differ-

Table 5. Frequency and cover of common species in 1 × 1 m quadrats under different canopy types in the 'pure' stands. Only species with frequency > 30% are listed.

Species	% frequency		% cover (± S.E.)	
	<i>Tsuga heterophylla</i> (n = 100) ^a	<i>Pseudotsuga menziesii</i> (n = 100)	<i>Tsuga heterophylla</i> (n = 100)	<i>Pseudotsuga menziesii</i> (n = 100)
Tree seedlings, shrubs				
<i>Abies amabilis</i>	8	13	not measured	
<i>Tsuga heterophylla</i>	-	23*	not measured	
<i>Vaccinium alaskaense</i>	16	45*	+ ^b	7.8 ± 1.6
<i>Vaccinium membranaceum</i>	18	44*	+	3.3 ± 0.8
<i>Chimaphila umbellata</i>	4	71*	+	12.5 ± 1.8
<i>Rubus ursinus</i>	7	93*	+	2.5 ± 0.3
<i>Rubus lasiococcus</i>	1	41*	+	3.2 ± 0.6
Herbs, ferns				
<i>Clintonia uniflora</i>	-	49*	-	8.0 ± 1.5
<i>Cornus canadensis</i>	7	52*	+	12.6 ± 2.0
<i>Smilacina stellata</i>	7	76*	+	25.1 ± 3.1
<i>Pteridium aquilinum</i>	2	52*	+	6.6 ± 1.3
<i>Viola</i> spp. ^c	8	67*	+	4.5 ± 0.7
<i>Linnaea borealis</i>	3	63*	+	6.5 ± 1.0
<i>Pyrola secunda</i>	-	32*	-	+
All species ^d				
Total number of species	25	44*		
Total of absolute frequencies/n	1.5	9.6*		

Note: Differences in percent frequency were subjected to a χ^2 test using the absolute frequencies and applying Yates' correction (Greig-Smith 1964). Differences in cover were not statistically compared.

^a number of quadrats sampled.

^b + = < 1% cover.

^c 3 species were recognised; *Viola glabella*, *V. sempervirens*, *V. orbiculata*.

^d includes 28 additional species which occurred in < 30% of the quadrats under either canopy condition. The species are: *Abies procera*, *Pseudotsuga menziesii*, *Vaccinium parvifolium*, *Acer circinatum*, *Berberis nervosa*, *Rubus nivalis*, *Rosa gymnocarpa*, *Chimaphila menziesii*, *Spiraea* sp. (probably *S. betulifolia*), *Symphoricarpos mollis*, *Pyrola picta*, *Galium oreganum*, *Listera borealis*, *Polystichum munitum*, *Tiarella unifoliata*, *Vancouveria hexandra*, *Xerophyllum tenax*, *Hieracium albiflorum*, *Oxalis oregana*, *Streptopus roseus*, *Campanula scouleri*, *Corallorhiza mertensiana*, *Anemone deltoidea*, *Achlys triphylla*, *Trillium ovatum*, *Pedicularis racemosa*, *Goodyera oblongifolia*, *Coptis laciniata*.

* indicates significant difference from *Tsuga* at $P < 0.05$.

ent trajectories. Canopy type has a marked influence on the degree of understorey development once trees dominate a site (cf. Zamora 1982). In the mixed stand the degree of understorey development depended on the canopy type, with gaps > *Pseudotsuga/Abies procera* canopies > *Tsuga* canopies. In the *Pseudotsuga* stand the understorey was well developed after 120 yr, whereas in the dense-canopied *Tsuga* stand after ca 150 yr it was still minimal (Tables 1 and 5). As the canopies of the

Pseudotsuga and *Tsuga* stands open up it is unlikely that their understoreys will become like those of the mixed stand.

Differences in understorey composition between canopy types may have been related to the potential light environment in which the understorey developed. Potential direct radiation was low beneath *Tsuga* canopies where tree seedlings were rare and understorey development was minimal (Table 2, 4 and 5). Potential direct radiation beneath the other

canopy types, however, was significantly higher, and *Abies amabilis* and/or *Tsuga heterophylla* were able to regenerate and maintain height growth. The percent frequency, cover, and species richness of most understorey shrubs and herbs were also significantly higher beneath the other canopy types than beneath *Tsuga*.

However, differences in canopy type will also determine other variables not measured in this study, such as available soil moisture (e.g., Voigt 1960), a factor critical for understorey development (Christy 1982; Daubenmire 1930). In addition, canopy type influences the type of substrates available for seedling regeneration. For example, *Tsuga* seedlings may have been rare in the *Tsuga* stand because most log substrates available for their establishment were fallen *Tsuga* stems, not old *Pseudotsuga* logs or stumps, their favoured establishment sites (Christy & Mack 1984).

Similar overstorey-understorey relationships have been observed for *Tsuga canadensis* (L.) Carr. (eastern hemlock) in Indiana (Daubenmire 1930, 1936), central New York (Lewin 1974), hemlocks northern range (Rogers 1980), and in the Great Smoky Mountains (Hicks 1981). It has been suggested that many understorey species common to non-hemlock forests are apparently unable to reproduce or even survive under hemlock canopies due to a combination of deep evergreen shade, leached coarse-textured soil, and persistent, probably antibiotic, litter (Daubenmire 1930; Lewin 1974; Rogers 1980).

Woods & Whittaker (1981) and Woods (1984) found that total sapling density was significantly lower in the hemlock-northern hardwood forests in areas with high hemlock dominance and that seedling and sapling establishment or mortality were related to the species of nearby canopy trees. Furthermore, maintenance of spatial heterogeneity in forest floor resources by the presence of different species of canopy trees may be important in the maintenance of diversity in understorey herb communities (Crozier & Boerner 1984). The lack of understorey species under eastern hemlock led Glenn-Lewin (1977) to suggest that conifer species have a strong negative effect on temperate-zone plant diversity in North America.

The extent to which vegetation layers are correlat-

ed has significant implications for classification (McCune & Antos 1981), e.g., in boreal forests the poor correspondence between tree canopy types and their understoreys led the Finnish (Cajander 1926) to develop a system of classification based primarily on the understorey vegetation (although sole reliance on the understorey has now been questioned – see Lahti & Vaisanen 1987). Similarly, in the western United States the view that the forest overstorey and understorey occupied their areas independently, responding more directly to abiotic than to biotic influences, led to the development of the habitat type classification (Daubenmire 1952).

Forest classification systems based on the habitat type concept (Layser 1974) require recognition of the potential climax (*sensu* Daubenmire 1952) tree species and understorey assemblages in a stand (Daubenmire & Daubenmire 1968). Potential climax trees can be identified by evaluating the stand structure and relative shade tolerance of the tree species since the most shade tolerant are the most likely to become dominant (Daubenmire & Daubenmire 1968; Pfister & Arno 1980). Once the canopy closes, sun-requiring herbs and shrubs are eliminated, leaving shade tolerant species to persist indefinitely.

The nature of potential climaxes can therefore be inferred from population analyses of the trees and the shade-tolerant shrubs and herbs present in the understoreys of old-stable stands (Daubenmire & Daubenmire 1968; Daubenmire 1980), in maturing seral stands often as young as 50–100 y (Hemstrom *et al.* 1982; Pfister & Arno 1980; Brockway *et al.* 1982), or in 'stable-state' stands (Hall 1980).

Because in the forests of the western Cascade Range many species are widely distributed, communities are usually differentiated by the cover, rather than the presence, of shrub and herb species (Dyrness *et al.* 1974; Hemstrom *et al.* 1982; Brockway *et al.* 1983). This classification system is similar to the habitat type concept except that the habitat type includes the climax plant communities *and* the land area they occupy. Communities are composed of different plant associations, or 'more or less discrete, recurring collections of plant species which maintain stable populations over a long time period' (Hemstrom *et al.* 1982). Inherent in this definition is a rapid (50–100 y) stabilisation in understorey

composition and a long, disturbance-free period; only those plants which can grow and reproduce in competition with their neighbours remain.

However, extensive areas of forest in the central portion of the western Cascade Range have been affected by recurrent fires and treefalls (see Introduction). In these stands succession from shade intolerant pioneers to climax shade tolerant species can follow different pathways and occur at different rates, e.g., *Pseudotsuga menziesii* and/or *Abies procera* may be replaced by *Tsuga heterophylla* and/or *Abies amabilis* but any or all of these species may behave as pioneers immediately after fire (Franklin & Hemstrom 1981; Stewart 1986a). Therefore, although potential climax tree species in these forests can be easily recognised in stands undisturbed by fire (Franklin & Dyrness 1973), their recognition in most stands depends on a knowledge of the historical factors influencing successional development (cf. Alaback 1982). My results also suggest that although relatively long fire-free periods may occur the understorey may not stabilise for several centuries because of the influences of canopy composition and small-scale canopy openings.

Recently, White *et al.* (1985) contrasted various predictions of stand composition as a way of examining the assumptions of the overstorey/understorey comparison. They found that traditional methods for prediction of future forest composition result in divergent predictions depending on the kind of data and assumptions that are used. In particular the traditional methods do not account for canopy/understorey interactions, differential survivorship among species, longevity of canopy species and fail to adequately predict the importance of species which exploit canopy gaps. In my study both the composition and cover of understorey species varied greatly between canopy types (Tables 4 and 5). This suggests that differences in understorey species cover must be interpreted cautiously before community samples can be related to community or habitat types.

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References

- Alaback, P. B. 1982. Dynamics of understorey biomass in Sitka spruce – western hemlock forests of southeast Alaska. *Ecology* 63: 1932–1948.
- Anderson, M. C. 1964a. Studies on the woodland light climate. I. The photographic computation of light conditions. *J. Ecol.* 52: 27–41.
- Anderson, M. C. 1964b. Studies on the woodland light climate. II. Seasonal variation in the light climate. *J. Ecol.* 52: 643–663.
- Brockway, D. G., Topik, C., Hemstrom, M. A. & Emmingham, W. H. 1983. Plant association and management guide for the Pacific silver fir zone, Gifford Pinchot National Forest. U.S. D.A. For. Serv., Pacific Northwest Region R6-Ecol. 130a.
- Cajander, A. K. 1926. The theory of forest types. *Acta. Forest. Fenn.* 29: 1–108.
- Christy, E. J. 1982. Population dynamics of understorey *Tsuga heterophylla*, western hemlock, in the Cascade Mountains, Oregon. Ph.D. thesis, Washington State University, Pullman, Washington.
- Christy, E. J. & Mack, R. N. 1984. Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. *J. Ecol.* 72: 75–91.
- Crozier, C. R. & Boerner, E. J. 1984. Correlations of understorey herb distribution patterns with microhabitats under different tree species in a mixed mesophytic forest. *Oecologia* 62: 337–343.
- Daubenmire, R. F. 1930. The relation of certain ecological factors to the inhibition of forest floor herbs under hemlock. *Butler Univ. Bot. Stud.* 1: 61–76.
- Daubenmire, R. F. 1936. The 'Big Woods' of Minnesota: its structure, and relation to climate, fire, and soils. *Ecol. Monogr.* 6: 233–268.
- Daubenmire, R. F. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. *Ecol. Monogr.* 22: 301–330.
- Daubenmire, R. F. 1980. The scientific basis for a classification in land-use allocation. In: *The scientific and technical basis for land classification*, pp. 7–10. Society of American Foresters, Technical session, Spokane Convention, October 7, 1980.
- Daubenmire, R. F. & Daubenmire, J. B. 1968. Forest vegetation of eastern Washington and northern Idaho. *Wash. Exp. Sta., Tech. Bull.* 60.
- Dyrness, C. T., Franklin, J. F. & Moir, W. H. 1974. A preliminary classification of forest communities in the central portion of the western Cascades in Oregon. *U.S. Int. Biol. Prog., Ecosys-*

- tem Analysis Studies, Coniferous Forest Biome, Bull. 4.
- Franklin, J. F. & Dyrness, C. T. 1973. Natural vegetation of Oregon and Washington. U.S. D.A. For. Serv., Gen. Tech. Rep. PNW-8.
- Franklin, J. F. & Hemstrom, M. A. 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. In: West, D. C., Shugart, H. H. & Botkin, D. B. (eds), Forest succession, pp. 212–229. Springer-Verlag, New York.
- Glenn-Lewin, D. C. 1977. Species diversity in North American temperate forests. *Vegetatio* 33: 153–162.
- Greig-Smith, P. 1964. Quantitative plant ecology. 2nd ed. Butterworth & Co., Kent, U.K.
- Hall, F. C. 1980. Application of a classification system based on community types (associations) with special reference to wildlife, range and timber management. In: The scientific and technical basis for land classification, pp. 11–17. Society of American Foresters, Technical session, Spokane Convention, October 7, 1980.
- Hemstrom, M. A., Emmingham, W. H., Halverson, N. M., Logan, S. E. & Topik, C. 1982. Plant association and management guide for the Pacific silver fir zone, Mt. Hood and Willamette National Forests. U.S. D.A. For. Serv., Pacific Northwest Region R6-Ecol. 100.
- Hicks, D. J. 1981. Intrastrand distribution patterns of southern Appalachian Cove Forest herbaceous species. *Am. Midland Nat.* 104: 209–223.
- Lahti, T. & Vaisanen, R. A. 1987. Ecological gradients of boreal forests in South Finland: an ordination test of Cajander's forest site type theory. *Vegetatio* 68: 145–156.
- Layser, E. F. 1974. Vegetative classification: its application to forestry in the northern Rocky Mountains. *J. For.* 72: 354–357.
- Lewin, D. C. 1974. The vegetation of the ravines of the southern Finger Lakes, New York region. *Am. Midland Nat.* 91: 315–342.
- McCune, B. & Antos, J. A. 1981. Correlations between forest layers in the Swan Valley, Montana. *Ecology* 62: 1196–1204.
- Pfister, R. D. & Arno, S. F. 1980. Classifying forest habitat types based on potential climax vegetation. *For. Sci.* 26: 52–70.
- Rogers, R. S. 1980. Hemlock stands from Wisconsin to Nova Scotia: transitions in understorey composition along a floristic gradient. *Ecology* 61: 168–193.
- Stewart, G. H. 1985. Forest structure and regeneration in the *Tsuga heterophylla*-*Abies amabilis* transition zone, central western Cascades, Oregon. Ph.D. thesis, Oregon State University, Corvallis, Oregon.
- Stewart, G. H. 1986a. Population dynamics of a montane conifer forest, western Cascade Range, Oregon, U.S.A. *Ecology* 67: 534–544.
- Stewart, G. H. 1986b. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade Range, Oregon. *Can. J. For. Res.* 16: 558–568.
- Voigt, G. K. 1960. Distribution of rainfall under forest stands. *For. Sci.* 6: 2–10.
- White, P. S., MacKenzie, M. D. & Busing, R. T. 1985. A critique of overstorey/understorey comparisons based on transition probability analysis of an old growth spruce-fir stand in the Appalachians. *Vegetatio* 64: 37–45.
- Woods, K. D. & Whittaker, R. H. 1981. Canopy-understorey interaction and the internal dynamics of mature hardwood and hemlock-hardwood forests. In: West, D. C., Shugart, H. H. & Botkin, D. B. (eds), Forest succession, pp. 305–323. Springer-Verlag, New York.
- Woods, K. D. 1984. Patterns of tree replacement: canopy effects on understorey pattern in hemlock-northern hardwood forests. *Vegetatio* 56: 87–107.
- Zamora, B. J. 1982. Understorey development in forest succession: an example from the inland Northwest. In: Means, J. E. (ed.), Forest succession and stand development research in the Northwest, pp. 63–69. Forest Research Laboratory, Oregon State University, Corvallis, Oregon.

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