Strobilus production and growth of Pacific yew under a range of overstory conditions in western Oregon[1]

S.P. DiFazio, N.C. Vance, and M.V. Wilson

Abstract: Strobilus production, growth, and morphology of Pacific yew (*Taxus brevifolia* Nutt.) were examined at three sites in the Cascade Mountains and one site in the Willamette Valley of western Oregon. Strobilus production on branch segments was positively associated with overstory openness for male and female trees at all four sites over 2 years. Strobilus production was also associated with branch vigor, but not as consistently as with overstory. Other variables, including tree size and age, mass of branches, branch bifurcations, and potential radiation, failed to explain significant variation in strobilus production. Overstory openness was also correlated with 5-year growth increment for all trees and with mass of 1994 branch growth for female trees, suggesting that tree vigor increased with overstory openness. In addition, branch mass and the number of branch bifurcations were positively associated with overstory openness.

Résumé : La production de strobiles, la croissance et la morphologie de l'if de l'Ouest (*Taxus brevifolia* Nutt.) ont été examinées dans trois sites de la chaîne des Cascades et dans un site de la vallée Willamette de l'Ouest de l'Orégon. La production de strobiles sur des segments de branches était associée positivement avec l'ouverture de l'étage dominant chez les arbres mâles et femelles dans les quatre sites, au cours des deux années. La production de strobiles était aussi associée avec la vigueur des branches, mais pas de façon aussi régulière qu'avec l'étage dominant. D'autres variables, incluant la taille et l'âge des arbres, la masse des branches, leurs bifurcations et le rayonnement potentiel, n'ont pas réussi à expliquer les variations importantes dans la production de strobiles. L'ouverture de l'étage dominant était également corrélée avec l'augmentation de l'accroissement de cinq ans de tous les arbres, de même qu'avec l'accroissement en poids des branches de 1994 des arbres femelles, suggérant que la vigueur des arbres a augmenté avec l'ouverture de l'étage dominant. De plus, le poids des branches et le nombre de leurs bifurcations étaient associés positivement avec le degré d'ouverture de l'étage dominant.
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Introduction

Pacific yew (*Taxus brevifolia* Nutt.) is an understory conifer that grows primarily in late seral forests of the Pacific Northwest (McCune and Allen 1985; Busing et al. 1995). *Taxus brevifolia* has received much recent attention because its bark is the source of taxol, a potent anticancer compound (Wani et al. 1971). Hundreds of thousands of *T. brevifolia* trees have been harvested in the United States and Canada to provide raw material for taxol extraction, with unknown effects on the viability of *T. brevifolia* populations.

Taxus brevifolia is dioecious and wind pollinated. Male strobili are composed of 6–14 radially arranged peltate stamens. Mature female strobili consist of a single seed with a hard integument, surrounded by a bright red cuplike aril. Strobili are formed during the summer of the previous growing season,

S.P. DiFazio[2] and M.V. Wilson. Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331, U.S.A.
N.C. Vance. USDA Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331, U.S.A.

pollination occurs in early spring, and seeds mature from August to late October in western Oregon (DiFazio 1996).

Despite a strong association with late seral species (Busing et al. 1995), *T. brevifolia* is not an obligate understory tree, and it tolerates a broad range of overstory canopy coverage (Bolsinger and Jaramillo 1990; Busing et al. 1995). Crawford (1983) found that 2 years after a clearcut harvest of overstory trees in Idaho, *T. brevifolia* trees showed increased branching, increased epicormic shoots, shorter shoots and needles, increased needle deflection, and decreased seed production compared with control trees with no overstory canopy harvest. Bolsinger and Jaramillo (1990) reported increased growth of undamaged *T. brevifolia* following overstory removal in southwestern Oregon. Bailey and Liegel (1997) found that *T. brevifolia* showed increased diameter growth following partial overstory removal, compared with nearby control trees under relatively intact canopy. Kelsey and Vance (1992) found that *T. brevifolia* trees in a clearcut had a higher sapwood to heartwood ratio, thicker bark, lower specific leaf area (ratio of needle area to mass), and lower taxane concentrations in bark tissue than trees under intact canopy.

The first objective of the present study was to determine the relationship between overstory canopy openness and strobilus production of wild *T. brevifolia* populations in western Oregon. Second, to determine whether overstory removal resulted in reduced tree vigor, as had been reported previously (Crawford 1983; USDA Forest Service 1992), the relationship between overstory canopy openness and average 5-year growth increment

and the mass of new growth on branches was examined. Finally, to gain insight into modes of adaptation to changing light levels, the associations between overstory canopy openness, branch mass, and branch bifurcations were examined.

Methods

Study design and tree selection
This study was conducted on four sites in western Oregon (Table 1). The main criteria for site selection were the presence of at least 10 sexually mature *T. brevifolia* trees per hectare and a range of canopy cover above the *T. brevifolia* trees. All sexually mature *T. brevifolia* trees were mapped. To ensure an adequate range of overstory canopy cover, trees were selected by stratified random sampling. Trees were subjectively assigned to two groups: those growing under relatively open canopy (OPN) and those under canopy cover (CAN). An equal number of male and female trees were randomly selected from each canopy grouping, for a total of at least 28 trees per site.

Study sites
The Higher Cascade 1 site (HC1) was located in the Snow Creek drainage of the Willamette National Forest (44°23′N, 122°15′W). Overstory trees in the OPN plot were harvested in a 1990 clearcut. The CAN plot was located approximately 1 km upslope from the OPN plot.

The Higher Cascade 2 site (HC2) was located in the Hackleman Creek drainage of the Willamette National Forest (44°24′N, 122°02′W). Some overstory trees for the OPN plot were harvested in a 1978 salvage logging operation, and substantial windthrow of remaining trees had occurred since that time. The CAN plot was located approximately 1.5 km downslope from the OPN plot.

The Lower Cascade site (LC) was located in the McCrae Creek drainage of the H.J. Andrews Experimental Forest (44°15′N, 122°11′W). Canopy gaps in the OPN plot were created by a 1981 clearcut and construction of a road in the 1950s. The CAN plot was contiguous with the OPN plot.

The Willamette Valley site (VAL) was located in the west fork of the Oak Creek drainage of the McDonald Research Forest in the foothills of the Oregon Coast Range near Corvallis, Oregon (44°35′N, 123°35′W). Overstory trees in the OPN plot were harvested in a 1984 clearcut. The CAN plot was located approximately 2 km downslope from the OPN plot.

More detailed information about the study sites is provided in DiFazio (1996).

Male strobilus production and branch mass
In 1993, eight branch tips were selected from throughout the canopy of each tree by randomly selecting four branches each from the upper and lower canopy. Branches were flagged and strobili were counted 20 cm basipetally from the branch tip at the time of dehiscence. Estimates of strobilus production are based on subsampled branches. No attempt was made to estimate productivity of entire trees.

In April of 1994, branches were clipped at the 1993 flagging, or new branch apices were selected to compensate for mortality (approximately 1% of all branches). Each branch segment was transported to the laboratory in a separate paper bag. Branches were remeasured 20 cm basipetally from the apex, and strobili were counted as in 1993. Stems and foliage were weighed after drying at 65°C for 48 h.

Female strobilus production and branch characteristics
In 1993, eight branch apices were selected on female trees according to the protocol described for male trees; because female strobilus production was much lower than male strobilus production, branch segments of 30 cm instead of 20 cm were flagged (DiFazio 1996): these larger segments included more of the reproductive buds. The number of visible ovules was determined in May, June, and July. The maximum of the three counts was used as the estimate of female strobilus production.

The 1994 female strobilus production was measured as in 1993. In late September of 1994, all eight branches were clipped at the 1994 flagging. Branches were clipped in the fall rather than in the spring because seed development and attrition were followed for a related study (DiFazio 1996). All growth distal to 1994 bud scars was clipped and separated. All branch material was dried at 65°C for 48 h and stems, foliage, and 1994 growth were weighed separately. Bifurcations on each 30-cm length of branch were counted.

Explanatory variables
To determine ages and growth rates of the study trees, an increment core was extracted 30 cm above the base on the north face of each tree. Cores were analyzed under a stereomicroscope (30×) by counting the total number of increments and measuring the width of the first five full increments proximal to the cambium. In cases where some increments were obliterated by heartwood rot, age was estimated by extrapolation, based on the average increment width for that tree.

Tree size was estimated by measuring the height (h) of the stem up to a 1-cm-diameter top and the diameter at breast height, 1.37 m (DBH). Tree volume was estimated by $(DBH)^2 \cdot h$, which is linearly related to total aboveground biomass of *T. brevifolia* (Russell 1973).

Slope was measured at each tree with a clinometer. Aspect was measured with a compass pointed in the same direction as the clinometer. Annual potential solar radiation was determined for each tree by interpolating among values for slope, aspect, and latitude in the tables of Buffo et al. (1972). This is essentially an estimate of the cumulative amount of solar radiation (kilocalories per square centimetre per year) incident on the overstory. The amount actually reaching the *T. brevifolia* trees would be a function of overstory openness.

Overstory canopy openness above and to the south of each study tree was estimated with an LAI-2000 plant canopy analyzer (LI-COR, Lincoln, Nebr.). The value used in this study was Diffuse Noninterceptance (DIFN), which is based on the ratio of diffuse light measured beneath the canopy to diffuse light in the open. DIFN ranges from 0 (no sky visible) to 1 (completely open canopy) (Welles and Norman 1991).

Analyses
The data were analyzed by using the multiple linear regression procedure of SAS (SAS Institute Inc. 1987). Explanatory variables included DIFN, age and volume of trees, and mass, bifurcations, ratio of foliage to branch mass, and 1994 growth of sampled branches. Separate analyses were performed for male and female strobilus production, growth, and morphology response variables. Variables were transformed where appropriate to correct for heteroscedasticity. Best fit regression equations were obtained by forward and backward selection techniques (Neter and Wasserman 1974).

Several explanatory variables exhibited collinearity, including DIFN, mass, bifurcations, and 1994 growth of sampled branches. To account for this, each analysis was performed in three phases. The first phase was a backward selection procedure with DIFN and all variables that showed weak collinearity as explanatory variables, including interactions with site indicator variables (with separate regression lines allowed for each site). All variables that caused a significant ($\alpha = 0.05$) drop in the regression sum of squares were retained in the model. The second phase was a forward selection procedure with the final model from phase one as a starting point. Variables that showed collinearity with DIFN were tested individually in this phase. Sites were again treated separately by including interaction terms with site indicator variables. In the final phase, regression lines for different sites were tested for equality to assess the generality of the relationships and the impact of site differences on those relationships.

Table 1. Mean values for variables measured at the four sites.

Site[a]	Elev. (m)	Precip. (mm)[b]	Canopy group[c]	N[d]	Overstory openness (DIFN)	Potential radiation (kcal·cm⁻²·year⁻¹)	Age (years)	Vol. (m³)	5-year increment (mm)	Male trees			Female trees				1994 growth (g)
										1993 strobili	1994 strobili	Branch mass (g)	1993 strobili	1994 strobili	Branch mass (g)	Branch bifurcations	
HC1	1150	2560	OPN	14	0.87	178.14	91	0.10	8.09	68.96	74.11	3.42	32.42	19.91	10.99	29.62	1.52
					(0.01)	(6.42)	(12)	(0.03)	(0.94)	(9.45)	(15.70)	(0.34)	(2.99)	(2.02)	(0.89)	(4.91)	(0.28)
			CAN	14	0.19	224.49	119	0.13	4.35	28.98	20.52	1.47	21.32	16.21	4.96	14.57	0.55
					(0.02)	(2.70)	(12)	(0.03)	(0.62)	(5.48)	(4.01)	(0.11)	(4.59)	(4.90)	(0.31)	(0.81)	(0.10)
HC2	1092	2143	OPN	16	0.37	157.77	151	0.41	4.45	57.14	60.23	2.89	22.33	18.31	8.16	19.55	0.87
					(0.06)	(2.27)	(11)	(0.08)	(0.53)	(10.88)	(13.39)	(0.27)	(4.14)	(4.31)	(0.85)	(2.66)	(0.11)
			CAN	14	0.11	168.64	146	0.10	2.14	17.68	12.63	1.52	10.53	7.79	6.10	11.79	0.77
					(0.02)	(2.13)	(11)	(0.03)	(0.29)	(2.93)	(2.99)	(0.16)	(2.92)	(3.75)	(0.55)	(1.31)	(0.10)
LC	850	2098	OPN	14	0.50	198.92	148	0.28	4.77	23.11	38.16	2.40	16.11	12.64	6.02	17.57	0.76
					(0.05)	(3.83)	(14)	(0.05)	(0.71)	(7.32)	(16.44)	(0.65)	(7.48)	(5.16)	(0.71)	(2.44)	(0.14)
			CAN	14	0.14	198.10	141	0.16	3.08	6.61	8.23	1.23	4.52	2.94	4.40	12.00	0.48
					(0.02)	(1.70)	(9)	(0.04)	(0.55)	(1.82)	(2.85)	(0.05)	(0.77)	(0.75)	(0.51)	(1.89)	(0.09)
VAL	250	1094	OPN	14	0.83	203.81	91	0.58	10.29	53.98	73.43	4.59	22.45	19.89	8.64	23.34	1.99
					(0.02)	(5.87)	(6)	(0.13)	(0.82)	(7.09)	(12.21)	(0.38)	(7.30)	(4.05)	(1.06)	(3.31)	(0.28)
			CAN	14	0.14	164.48	78	0.26	3.08	4.46	9.86	1.52	1.71	1.89	3.15	10.87	0.39
					(0.03)	(5.97)	(4)	(0.06)	(0.48)	(0.99)	(2.46)	(0.14)	(0.24)	(0.86)	(0.36)	(1.43)	(0.07)

Note: Values in parentheses are 1 SE. See text for a description of methods.

[a]HC1, Higher Cascade 1; HC2, Higher Cascade 2; LC, Lower Cascade; VAL, Willamette Valley.

[b]Average annual precipitation values derived from interpolations of 10-year averages from nearby climate stations, based on the PRISM climate model (Daly et al. 1994).

[c]OPN, populations occurring in clearcuts; CAN, populations occurring under overstory canopy.

[d]N, number of trees per canopy group. There are equal numbers of males and females per group.

[e]DIFN, Diffuse Noninterceptance.

Table 2. Regression equations for strobilus production versus overstory openness (DIFN) and FOLBR.

Model	df[a]	R^2
Males		
$\ln(\text{♂STROB93}^b) = -1.55{\cdot}X_{12} - 2.66{\cdot}X_3 - 2.75{\cdot}X_4 + 1.94{\cdot}\text{DIFN}^c{\cdot}X_{123} + 3.14{\cdot}\text{DIFN}{\cdot}X_4 + 6.39{\cdot}\text{FOLBR}^d$	67	0.81
$\quad\quad\quad(0.07)\quad\quad(0.002)\quad(0.001)\quad\quad\quad(0.0001)\quad\quad\quad\quad(0.0001)\quad\quad\quad(0.0001)$		
$\ln(\text{VIAB93}^e) = -1.58{\cdot}X_{12} - 2.75{\cdot}X_3 - 2.84{\cdot}X_4 + 1.89{\cdot}\text{DIFN}{\cdot}X_{123} + 3.23{\cdot}\text{DIFN}{\cdot}X_4 + 6.34{\cdot}\text{FOLBR}$	67	0.81
$\quad\quad\quad(0.07)\quad\quad(0.002)\quad(0.001)\quad\quad\quad(0.0001)\quad\quad\quad\quad(0.0001)\quad\quad\quad(0.0001)$		
$\ln(\text{♂STROB94}) = 2.38{\cdot}X_{12} + 1.79{\cdot}X_{34} + 2.57{\cdot}\text{DIFN}$	65	0.64
$\quad\quad\quad(0.0001)\quad(0.0001)\quad\quad(0.0001)$		
$\ln(\text{VIAB94}) = 2.24{\cdot}X_1 + 1.93{\cdot}X_2 + 0.75{\cdot}X_{34} + 0.84{\cdot}\text{DIFN}{\cdot}X_1 + 3.18{\cdot}\text{DIFN}{\cdot}X_{234}$	65	0.65
$\quad\quad\quad(0.0001)\quad(0.0001)\quad(0.0001)\quad\quad\quad(0.15)\quad\quad\quad\quad(0.0001)$		
Females		
$\ln(\text{♀STROB93}^f) = 2.54{\cdot}X_{12} + 0.99{\cdot}X_{34} + 1.04{\cdot}\text{DIFN}{\cdot}X_{12} + 2.46{\cdot}\text{DIFN}{\cdot}X_{34}$	50	0.60
$\quad\quad\quad(0.0001)\quad(0.0001)\quad\quad\quad(0.0035)\quad\quad\quad\quad(0.0001)$		
$\ln(\text{♀STROB94}) = 2.11{\cdot}X_{12} + 0.70{\cdot}X_{34} + 1.11{\cdot}\text{DIFN}{\cdot}X_{12} + 2.75{\cdot}\text{DIFN}{\cdot}X_{34}$	50	0.50
$\quad\quad\quad(0.0001)\quad(0.009)\quad\quad\quad(0.0079)\quad\quad\quad\quad(0.0001)$		
Alternative models		
$\ln(\text{♀STROB93}) = 2.59{\cdot}X_1 + 1.61{\cdot}X_2 + 0.73{\cdot}X_{34} + 0.37{\cdot}\text{DIFN}{\cdot}X_1 + 2.67{\cdot}\text{DIFN}{\cdot}X_{234}$	50	0.55
$\quad\quad\quad(0.0001)\quad(0.0001)\quad(0.0018)\quad\quad\quad(0.46)\quad\quad\quad\quad(0.0001)$		
$\ln(\text{♀STROB94}) = 2.91{\cdot}X_1 + 2.12{\cdot}X_2 + 1.08{\cdot}X_{34} + 0.55{\cdot}\text{DIFN}{\cdot}X_1 + 2.26{\cdot}\text{DIFN}{\cdot}X_{234}$	50	0.60
$\quad\quad\quad(0.0001)\quad(0.0001)\quad(0.0001)\quad\quad\quad(0.21)\quad\quad\quad\quad(0.0001)$		

Note: Averages were based on eight branch samples per tree. X_i, indicator variable for site i: 1 = Higher Cascade 1, 2 = Higher Cascade 2, 3 = Lower Cascade, and 4 = Willamette Valley. If more than one subscript appears for an indicator variable, the parameter estimates were not significantly different for those sites ($\alpha \le 0.05$) P-values for regression coefficients are in parentheses below each estimate.

[a]df, total degrees of freedom.

[b]♂STROB, average number of male strobili per 20-cm branch segment.

[c]DIFN, overstory canopy openness.

[d]FOLBR, ratio of mass of foliage to total branch mass (BRMS).

[e]VIAB, average number of viable male strobili produced per 20 cm.

[f]♀STROB, average number of ovules per 30-cm branch segment.

Results

Strobilus production

General patterns
In both years of study, overstory openness was the variable most consistently associated with male and female strobilus production by yews. Even when the effects of size and age of trees were taken into account, overstory openness explained a significant amount of the variation in male and female strobilus production. Also, the variables DIFN^2, average branch mass, branch bifurcations, potential radiation, and dry mass of 1994 branch growth did not account for significant variation in male strobilus and female strobilus production beyond that explained by DIFN.

Male strobilus production
The 1993 male strobilus production significantly increased with DIFN and the ratio of foliage to branch mass (Table 2; Fig. 1A). The relationship was nearly identical for viable strobili (Table 2; Fig. 1C). The relationships for the two high-elevation sites were not significantly different from each other ($P = 0.58$) but differed from those for LC and VAL ($P < 0.0001$) (Table 2; Fig. 1A and 1C).

The 1994 strobilus production also was significantly associated with DIFN, but none of the other explanatory variables accounted for significant additional variation. The relationships were not significantly different among the four

sites ($P = 0.62$), although the high-elevation sites had higher strobilus production than the lower elevation sites, as in 1993 ($P < 0.09$) (Table 2; Fig. 1B). When nonviable strobili were excluded from the analysis, there was no longer a significant relationship between 1994 strobilus production and DIFN at HC1 (Table 2; Fig. 1D).

Female strobilus production
Female strobilus production was significantly and positively associated with DIFN in 1993 at all sites. None of the other site or morphology variables tested accounted for significant variation in female strobilus production ($P > 0.37$). The relationships for the higher Cascade sites were significantly different from those for LC and VAL ($P < 0.02$), and female strobilus production was greater on average for the higher Cascade sites than for the two lower sites (Table 2; Fig. 1E). In 1994, female strobilus production was also positively associated with DIFN at all sites (Table 2; Fig. 1F). Again, the higher Cascade sites had higher average strobilus production than LC and VAL ($P < 0.001$).

An alternative regression model was nearly as well supported as those described above for 1993 and 1994 strobilus production. The primary difference between the alternative models and the "best fit" models was that the residuals were not normally distributed for the alternative models. In both of the alternative models, female strobilus production was positively associated with DIFN at HC2, LC, and VAL, but not at HC1 (Table 2).

Fig. 1. Regressions of strobilus production on DIFN. Each point is an average from a single tree. (A) 1993 male strobilus production: components effects plot with the effects of FOLBR removed. (B) 1994 male strobilus production per 20-cm branch segment. (C) 1993 viable male strobilus production: components effects plot with the effects of FOLBR removed. (D) 1994 viable male strobilus production per 20-cm branch segment. (E) 1993 female strobilus production per 30-cm branch segment. (F) 1994 female strobilus production per 30-cm branch segment. The broken line has a slope that is not significantly different from 0. Regression equations and R^2 values are provided in Table 2.
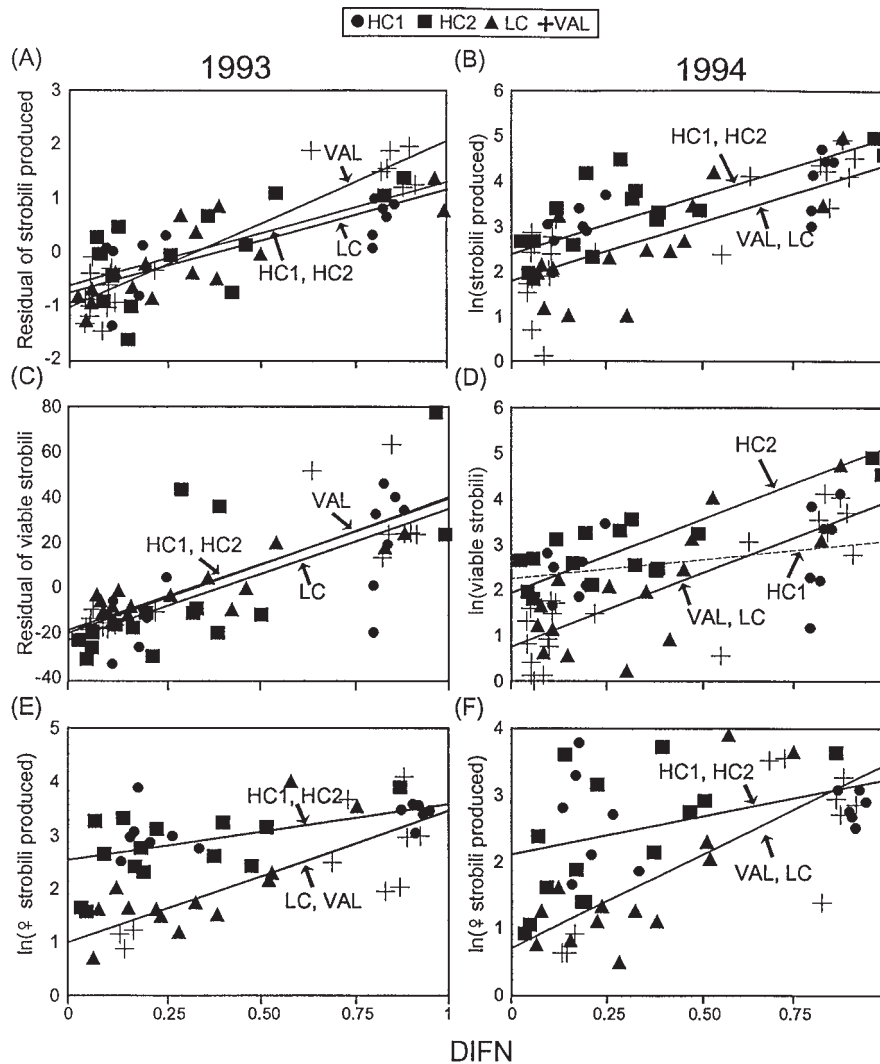
Growth

The width of 5-year increment was positively associated with overstory openness and negatively associated with age (Table 3). The relationships for HC1, HC2, and LC were significantly different from that for VAL ($P < 0.047$) (Table 3; Fig. 2A). The equation accounts for nearly half of the observed variation in increment growth ($R^2 = 0.46$) (Table 3).

Dry mass of 1994 growth on female branches was positively associated with DIFN at HC1 and VAL, but not at HC2 and LC. The lowest growth under shaded conditions was found at VAL, as was the highest growth under open conditions (Table 3; Fig. 2B). HC1 was second lowest in the shade and second highest in the sun. Overstory openness accounted for more than half of the variation in dry mass of 1994 branch growth ($R^2 = 0.56$) (Table 3).

Tree size, potential radiation, the ratio of foliage to branch mass, and DIFN^2 failed to significantly improve the 5-year increment and branch growth models.

Morphology

The dry mass of sampled branches was significantly and positively associated with DIFN for male and female trees. For male trees, the relationship did not differ among sites ($P = 0.62$), except that average branch mass was higher at HC2 and VAL than at HC1 and LC (Table 3; Fig. 3A). The relationship between female branch mass and DIFN also did not differ among sites, although branch mass was higher at HC2 than at the other three sites ($P < 0.037$) (Table 3; Fig. 3B). The regression equations accounted for a relatively small proportion of the total variation in branch dry mass for male ($R^2 = 0.28$) and female ($R^2 = 0.31$) trees (Table 3). The average number of bifurcations per branch on female trees was positively associated with DIFN

Table 3. Regression equations for growth and morphological characteristics versus overstory openness and other variables with significant associations.

Model	df	R^2
$\ln(5\text{YRINCR}^a) = 1.32 \cdot X_{123} + 1.58 \cdot X_4 + 1.11 \cdot \text{DIFN} \cdot X_{123} + 2.47 \cdot \text{DIFN} \cdot X_4 - 0.0035 \cdot \text{AGE}^b \cdot X_{123} - 0.014 \cdot \text{AGE} \cdot X_4$ $\quad$ (0.0001) $\quad$ (0.0001) $\quad$ (0.0003) $\quad\quad$ (0.0001) $\quad\quad\quad$ (0.023) $\quad\quad\quad$ (0.0048)	112	0.46
$\ln(94\text{GRTH}^c) = -0.97 \cdot X_1 - 0.414 \cdot X_2 - 0.81 \cdot X_3 - 1.27 \cdot X_4 + 1.40 \cdot \text{DIFN} \cdot X_1 + 0.63 \cdot \text{DIFN} \cdot X_{23} + 2.22 \cdot \text{DIFN} \cdot X_4$ $\quad$ (0.0002) $\quad$ (0.015) $\quad$ (0.0001) (0.0001) $\quad\quad$ (0.0003) $\quad\quad\quad$ (0.14) $\quad\quad\quad$ (0.0001)	56	0.56
$\ln(\male\text{BRMS}^d) = 0.13 \cdot X_{13} + 0.35 \cdot X_{24} + 1.26 \cdot \text{DIFN}$ $\quad$ (0.026) $\quad$ (0001) $\quad$ (0.0001)	67	0.28
$\ln(\female\text{BRMS}) = 1.29 \cdot X_{13} + 1.63 \cdot X_2 + 1.07 \cdot X_4 + 1.13 \cdot \text{DIFN}$ $\quad$ (0.0001) $\quad$ (0.0001) $\quad$ (0.0001) $\quad$ (0.0001)	56	0.31
$\ln(\text{BIFUR}^e) = 2.35 + 0.98 \cdot \text{DIFN}$ $\quad$ (0.0001) $\quad$ (0.0001)	57	0.43

Note: Abbreviations are as described for Table 2, except as indicated below.
[a]5YRINCR, width (mm) of 5-year increment.
[b]AGE, age of yew tree.
[c]94GRTH, dry mass (g) of stem and foliage growth distal to 1994 bud scars.
[d]BRMS, average dry mass (g) of branch samples (20 cm for males, 30 cm for females).
[e]BIFUR, average number of bifurcations per 30-cm branch segment.

Fig. 2. Regressions of growth on DIFN. (A) Width of 5-year increments: components effects plot with the effect of age removed. (B) Dry mass of 1994 growth on female branches. Regression equations and R^2 values are provided in Table 3. The broken lines have slopes that are not significantly different from 0.
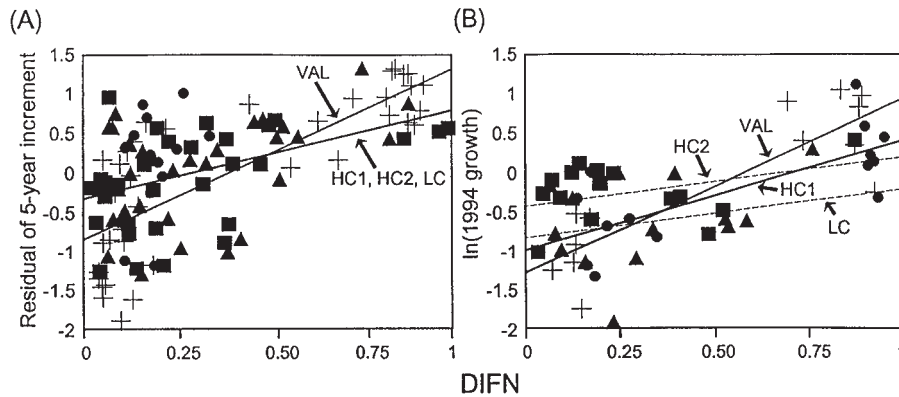
$(R^2 = 0.42)$ (Table 3; Fig. 3C). No differences in relationships were detected among the four sites.
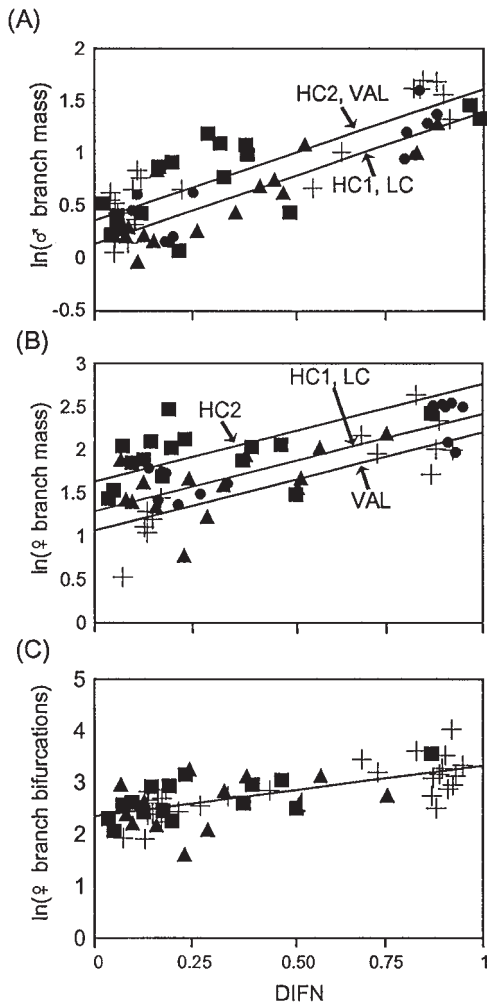
Discussion

Strobilus production

Strobilus production of branch segments on *T. brevifolia* trees was strongly related to overstory openness. The positive relationship between strobilus production and DIFN was consistent at four different sites over two growing seasons. Also, with the exception of the ratio of foliage to branch dry mass for 1993 male strobilus production, no other variables significantly improved the fit of the regressions. However, the regression equations did not account for all of the variation in branch strobilus production, as illustrated by the coefficients of variation (R^2 ranged from 0.54 to 0.81) (Table 2). The regression lines always differed among sites, suggesting that environmental factors other than those measured also influenced strobilus production (e.g., precipitation varied markedly among sites) (Table 1).

The major exception to the positive relationship between DIFN and branch strobilus production was production of viable male strobili and female strobili at HC1 (Table 2; Fig. 1D). Part of the reason for this lack of correlation may have been the stressful conditions on the clearcut at HC1 during the winter of 1994, when morphological evidence showed frost damage to male strobili (personal observation). Frost also may have destroyed female strobili prior to anthesis, in which case the ovules would not have been detected.

The only variable that accounted for significant variation in strobilus production after the effects of DIFN were taken into account was the ratio of foliage to branch dry mass (FOLBR) for 1993 male strobilus production (Table 2). FOLBR was measured in the spring of 1994 for male trees. This variable may have acted as an indicator of branch vigor at the time of strobilus formation. Perhaps FOLBR was associated exclusively with 1993 strobilus production because conditions in 1992, at the time of 1993 strobilus formation, were severe, causing foliage abscission and inhibiting strobilus production. In fact, 1992 was the driest year of the study (Oregon Climate Service, unpublished data).

Fig. 3. Regressions of branch characteristics on DIFN.
(A) Average mass of 20-cm branch segment, male trees.
(B) Average mass of 30-cm branch segment, female trees.
(C) Number of bifurcations per 30-cm branch segment, female trees. Regression equations and R^2 values are provided in Table 3.

study had been exposed 3–15 years before measurements were taken. An alternative explanation is that female strobilus production of the Idaho trees was actually higher in the clearcut than in the control population, but that ovule attrition was higher for the clearcut. This would agree more closely with the pattern observed in the present study, where female strobilus production was elevated under open conditions but attrition was higher, as described elsewhere (S.P. DiFazio et al., unpublished manuscript).

Growth
Overstory openness was positively associated with tree growth, as indexed by 5-year increment measured for all trees and 1994 branch growth measured on female trees. The 5-year increment also was negatively associated with tree age. This association is not simply an allometric relationship because basal diameter did not significantly improve the regression of 5-year increment on DIFN ($F = 1.08$; $P = 0.37$).

The results of this study are in agreement with a retrospective study of *T. brevifolia* (Bailey and Liegel 1997) that showed that 10-year increments were significantly larger after overstory removal than before the disturbance event. These findings contradict the supposition that abrupt exposure to full sunlight causes reduced vigor or mortality of *Taxus* species (Crawford 1983; USDA Forest Service 1992).

Morphology
It appears that *T. brevifolia* has sufficient phenotypic plasticity to adapt and even thrive under the drastic changes in microclimate that overstory removal entails. The photosynthetic rates of many shade-tolerant trees show limited plasticity in response to increased light levels (Strauss-Debenedetti and Bazzaz 1991). However, morphological changes that increase the quantity of photosynthetic tissues or establish a multilayered branch arrangement can compensate for this lack of plasticity (O'Connell and Kelty 1994). Intensity of branching of *T. brevifolia* (as indicated by the number of bifurcations and mass of branch samples) was positively associated with overstory openness. This increased branching resulted in a tendency for open-grown trees to have more multilayered branches and irregular branching patterns than those growing under shaded conditions, which have relatively planar branches with herringbone-type branching patterns (personal observation). This pattern is in agreement with the response of other shade-tolerant species to overstory removal (Horn 1971; Steingraeber et al. 1979; Veres and Pickett 1982; Tucker et al. 1987; O'Connell and Kelty 1994).

The increased branching observed under open conditions could have accounted in part for the positive relationship between strobilus production and DIFN. However, neither branch mass nor branch bifurcations significantly improved the model for 1994 female strobilus production ($P > 0.37$). Furthermore, DIFN did significantly improve female strobilus production models containing branch mass and branch bifurcations as explanatory variables ($P < 0.0004$). Therefore, strobilus production was much more strongly associated with overstory openness than with branch mass or branch bifurcations.

Conclusions

The increased strobilus production and growth seen in yew

The results of this study contrast somewhat with those of related studies. Allison (1991) found that for Canada yew (*Taxus canadensis* Marsh.) shrubs growing in a gap, female strobilus production was higher than for nearby plants under full canopy, but male strobilus production was unchanged. A possible explanation for this discrepancy is that the monoecious habit of *T. canadensis* allows competition between male and female strobili for resources, and female strobili are a stronger sink for photosynthates than male strobili. Other studies also have demonstrated a stronger response to light for female than for male reproductive structures (Silen 1973; Niesenbaum 1992). In contrast, the relationship between overstory canopy openness and strobilus production was strongly positive for both male and female trees in the present study.

Taxus brevifolia trees in Idaho showed lower seed production 2 years after overstory removal than control trees under intact overstory (Crawford 1983). It is possible that the trees were still suffering stress from increased radiation and temperature extremes. *Taxus brevifolia* may require several years to equilibrate following overstory removal; trees in the present

trees under open canopy may be directly attributable to elevated light levels. There is ample evidence that shading limits flowering and seed production in other species (Silen 1973; Owens and Blake 1985; Schutte Dahlem and Boerner 1987; Devlin 1988; Dale and Causton 1992; Niesenbaum 1993). However, light may not have been the major factor controlling strobilus production in the present study; removal of the overstory drastically changes the microenvironment of the tree in many ways besides increasing light levels (Horn 1971).

It is important to note that strobilus production was measured on subsampled branches only, and no attempt was made to extrapolate results to whole trees. Nevertheless, it is likely that whole-tree strobilus production would have followed the same qualitative trends as subsampled branches: intensity of branching increased with DIFN, and trees were larger on average under open conditions on three of four sites (Table 1). Therefore, overstory removal resulted in increased vigor of *T. brevifolia* trees, as indicated by increased strobilus production and growth at these sites.

Acknowledgments

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