Ecology of Pacific Yew (*Taxus brevifolia*) in Western Oregon and Washington

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Abstract: Taxus brevifolia, *a subcanopy tree or shrub in forests of the Pacific Northwest, has been harvested intensively in recent years. With management concerns as an impetus, we examined the distribution and population dynamics of* Taxus *based on data from the mountains of western Oregon and Washington. Surveys of natural forests, long-term studies of forest recovery following logging, and census data on marked trees in forest stands support the hypothesis that* Taxus *is a widespread but predominantly late-successional species. Sensitive to fire and slow to recover from disturbance on many sites,* Taxus *attains maximal basal area and adult stem density in old forests. Colonization of* Taxus *is often slow in potentially suitable habitats. Conservation of* Taxus *at the landscape level may require large, unmanaged reserves and maintenance of patches of old forest within managed forests. Long rotations (centuries) between harvest events will enhance the long-term viability of the species. Practices designed to accelerate the development of old-growth forest structure will not benefit* Taxus *and other species requiring long disturbance-free intervals for recovery.*

Ecologia del tejo del Pacífico (*Taxus brevifolia*) en el oeste de Oregon y Washington

Resumen: Taxus brevifolia, *un árbol o arbusto del sotobosque del Noroeste del Pacífico, ha sido cosechado intensamente en años recientes. Teniendo en cuenta una perspectiva de manejo, examinamos la distribución y dinámica de población de* Taxus, *en base a datos de las montañas del oeste de Oregon y Washington. Relevamientos de bosques naturales, estudios a largo plazo de recuperación del bosque después de la tala y datos de censos en árboles marcados en rodales de bosques sostienen la hipótesis de que Taxus es una especie de amplia distribución, pero es predominantemente una especie sucesional tardía. Siendo una especie sensible a los incendios y lenta para recuperarse de las perturbaciones en varios sitios,* Taxus *llega a su máxima área basal y densidad de tallos adultos en bosques de crecimiento antiguo. La colonizatión de* Taxus *es en general lenta en hábitats potencialmente adecuados. La conservación de* Taxus *a nivel del paisaje requeriría grandes, reservas sin manejo y el mantenimiento de parches de bosque antiguo dentro de bosques bajo manejo. Largas rotaciones (siglos) entre los eventos de cosecha aumentará la viabilidad a largo témino de las especies. Las prácticas designadas para acelerar el desarrollo de la estructura de bosques maduros no beneficiará a* Taxus *y otras especies que requieran largos intervalos libres de perturbaciones para recuperarse.*

Introduction

Taxus brevifolia, a small tree or shrub of the Pacific Northwest region of North America, has recently been harvested in large quantities for the pharmaceutical taxol (Anonymous 1992). Although recent advances in the production of synthetic taxol make it unlikely that wild populations will be heavily exploited for medicinal purposes, concerns about logging practices continue to focus attention on the conservation of *Taxus* (Anonymous 1993*a*). An underlying concern is that the area of old-growth forest, which harbors *Taxus* in substantial numbers (Spies 1991), has declined more than 50% in the last 50 years (Bolsinger & Waddell 1993).

In comparison with other coniferous tree species of

Paper submitted July 28, 1994; revised manuscript accepted November 8, 1994.

the Pacific Northwest, little is known about the distribution and population dynamics of *Taxus*. The species occurs in coniferous forests from northern California to southern Alaska as a widely scattered subcanopy tree or shrub (Bolsinger & Jaramillo 1990). It is tolerant of shade and grows slowly (Minore 1979; Bolsinger & Jaramillo 1990). Although it is known that this dioecious species can regenerate from seed, basal sprouts, or layering, the biotic and abiotic controls of its regeneration are poorly understood.

Forest-disturbance history is a major determinant of the distribution and abundance of *Taxus brevifolia* in some regions. McCune and Allen (1985) suggest that *Taxus brevifolia* populations in western Montana are decimated by fire. Crawford and Johnson (1985) reach the same conclusion for *Taxus brevifolia* populations in northern Idaho, where it is prevalent in stands that have not burned for at least 250 years. Thus, in the Rocky Mountains, fire is a major factor limiting *Taxus* distribution. Fire may play a similar role in western Oregon and Washington. Here, fire-return intervals are commonly less than 250 years, although some sites may experience fire-free periods of 750 years or more (Agee 1991, 1993). *Tsuga heterophylla*, a fire-sensitive species, is uncommon where fire-return intervals are less than 100 years (Huff 1984). If *Taxus* is sensitive to fire and slow to recover, it should be uncommon on such sites as well.

Several studies suggest that *Taxus brevifolia* is primarily an old-growth forest species (Habeck 1968; Alaback 1982; McCune & Allen 1985; Spies 1991), but it also occurs in some young forests (Spies 1991; Anonymous 1993*b*) and can be abundant following clearcutting (D. Minore, personal communication). We examined the extent to which *Taxus brevifolia* is associated with old-growth forests in Oregon and Washington. We analyzed several existing sets of forest data, including long-term observations of early and late-successional populations and a regional survey of populations across a range of sites with contrasting environmental conditions, disturbance histories, and species compositions. We pose the following questions: (1) Are *Taxus* basal area and density related to stand age? (2) Is *Taxus* strongly associated with late-successional dominants, such as *Tsuga heterophylla* and *Thuja plicata*; (3) Is *Taxus* regeneration abundant in old forest stands? (4) Does *Taxus* regeneration and recovery during forest-stand initiation vary with the severity of disturbance? (5) Are rates of *Taxus* growth and mortality comparable to those of late-successional tree species in montane areas of the region? Finally, we discuss the implications of our findings for conservation of the species.

Methods

We base our analyses on three sets of data from coniferous forests of western Oregon and Washington—forests dominated largely by *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata* (Franklin & Dyrness 1973; Franklin 1988). The data derive from (1) a vegetation survey of 216 stands spanning a wide range of ages and site conditions, (2) long-term, permanent plot observations following logging and burning of three experimental watersheds of the H. J. Andrews Experimental Forest of the central Oregon Cascade Range, and (3) repeated measurements of tree growth and survival in three sets of "reference" plots in mature and old-growth forests of the Oregon and Washington Cascade Ranges.

The first set of data includes measurements of vegetation and site characteristics from natural forests in three physiographic provinces—the southern Washington Cascade Range, the Oregon Cascade Range, and the southern half of the Oregon Coast Range (Spies 1991; Spies & Franklin 1991). Most stands were in the *Tsuga heterophylla* zone, the zone of transition to mixed conifer, or the lower *Abies amabilis* zone (Franklin & Dyrness 1973). All stands originated following stand-replacing wildfires and represent a wide range of overstory ages and site conditions. Sampling was conducted in 1983 and 1984 along two major gradients: stand age (40–900 years) and available moisture. Mature (80–194 years) and old-growth (≥195 years) stands (4–20 ha) comprised most of the samples ($n = 53$ and 119, respectively); the remaining samples were from young stands (<80 years, $n = 44$). Vegetation composition and structure were sampled with clusters of 0.1-ha plots spaced 100 to 150 m apart (3–5 circular plots per stand). Trees larger than 50 cm diameter at breast height (dbh; 1.37 m) were recorded by species and measured for diameter and height in each 0.1-ha circular plot; similar data were collected for trees 5 to 50 cm dbh in a nested 0.05-ha plot. Saplings (>1 m tall but <5 cm dbh) were tallied by height class and species in the 0.05-ha plot. Tree seedlings (<1 m tall) were tallied by species and height class in each of four 0.002-ha plots within each 0.1-ha plot. Mean overstory tree age (hereafter referred to as stand age) was estimated from ring counts on increment cores of dominant trees or stumps in adjacent clearcuts. Details of site selection, study-area attributes, sampling design, and field methods are described in Spies (1991) and Spies and Franklin (1991).

To examine the association of *Taxus* with other tree species and site factors, correlation analyses were conducted between measures of *Taxus* abundance (basal area, relative basal area, density, and relative density) and stand age or the abundance (basal area and relative basal area) of dominant tree species within the study area. The set of dominants included shade-intolerant, seral species such as *Pseudotsuga menziesii* and shade-tolerant, late-successional species such as *Tsuga heterophylla*.

To further investigate associations among woody species, forest stands were classified using two-way indicator species analysis (TWINSPAN; Hill 1979; Gauch 1982). This multivariate analysis, based on relative basal-area values of tree species, was used to examine the association of *Taxus* with certain other tree species and vegetation types.

The size-class structure of *Taxus* was analyzed by physiographic province and stand age groups. Three age groups—young (<80 years), mature (80–194 years), and old-growth (>194 years)—were recognized. Analyses were performed separately on stems smaller than 5 cm dbh and on stems 5 cm dbh and larger. In the former case, stems were tallied by height class; in the latter case, stems were tallied by diameter class.

The second set of data is from long-term succession studies following logging of old forests on and adjacent to H. J. Andrews Experimental Forest, Cascade Range, Oregon (44°15′N, 122°10′W; Dyrness 1973; Gholz et al. 1985; Halpern 1988, 1989; Halpern & Franklin 1990; Halpern et al. 1992). On watersheds 1 and 3, 192 2 × 2 m vegetation plots were sampled in mature and old-growth forest of *Pseudotsuga menziesii* and *Tsuga heterophylla* that was subsequently clearcut and burned. Following burning, plots were assigned to one of the four classes representing a gradient of soil-disturbance intensity (Dyrness 1973): (1) undisturbed—little or no physical soil disturbance or burning; (2) disturbed-unburned—litter mixed with mineral soil, with little evidence of burning; (3) lightly burned—surface litter charred but not completely consumed, and (4) heavily burned—surface litter completely consumed by intense fire. *Taxus brevifolia* was a common subcanopy species on both watersheds prior to harvest (1962). Vegetation plots were sampled regularly between 1962 and 1987 using the methodology of Dyrness (1973) and Halpern (1988, 1989). Visual estimates of projected canopy cover of *Taxus* and other vascular plant species less than 6 meters tall were made at each sampling date. In a related study initiated in 1973 (watershed 10), 30 vegetation plots (each with 16 1 × 1 m subplots) were sampled in an old-growth forest that was subsequently harvested in 1975 (Hawk 1979; Gholz et al. 1985). Logs larger than 20 cm in diameter or 2.4 m in length were removed from the site, but the remaining debris was not broadcast burned. Vegetation plots were resampled regularly from 1976 to 1989.

The third set of data is from a series of permanent sample plots in old forests of the central Oregon Cascades and Mount Rainier National Park in the southern Washington Cascades. Established in the 1970s, these 1.0-ha "reference" stands have been sampled regularly to determine rates of growth and mortality of all woody stems larger than 5 cm dbh. Rates of *Taxus* growth and mortality in old forests were estimated from a sample of 1062 trees followed for at least 10 years. Plant nomenclature follows Hitchcock and Cronquist (1973).

Results and Discussion

Abundance of *Taxus* in Relation to Stand Age and Composition

The abundance of *Taxus* was positively correlated with stand age and with the abundance of three shade-tolerant, late-successional species: *Abies grandis*, *Thuja plicata*, and *Tsuga heterophylla* (Table 1). It was negatively correlated with the abundance of *Pseudotsuga menziesii*, a shade-intolerant, seral species. *Tsuga heterophylla* had the greatest number of positive correlations with *Taxus*. For stands less than 600 years old, density and basal area of *Taxus* increased with stand age (Fig. 1). *Taxus* was present at low levels, however, or was absent in stands of all ages.

Taxus occurred in each of the four broad forest classes produced by the first two divisions of the TWINSPAN classification (Fig. 2). It was always subdominant, with basal area consistently lower than that of the coocurring overstory species. Its distribution and abundance fit the description of a "rural" species: wide distribution but low dominance (Collins et al. 1993). Apparently, *Taxus* tolerates a wide range of site conditions but, because of its small stature, is never dominant in these tall coniferous forests.

Maximal relative basal area of *Taxus* was attained in *Pseudotsuga* forests codominated by *Tsuga heterophylla* (Fig. 2). Its basal area in these stands followed roughly the same pattern as that of *Tsuga heterophylla* (Fig. 2), although the abundance of *Taxus* was sometimes negligible in stands containing *Tsuga*. Conversely, *Taxus* was rarely important (by relative basal area) in

Table 1. Pearson coefficients of correlation between *Taxus brevifolia* abundance measures and parameters of stand age and species composition.

	Taxus brevifolia			
Species and Variable	*Basal Area*	*Relative Basal Area*	*Density*	*Relative Density*
Stand age	0.299*	0.273*	0.323*	0.358*
Abies grandis				
Basal area	0.129	0.118	0.028	0.001
Relative basal area	0.142**	0.143**	0.032	0.001
Pseudotsuga menziesii				
Basal area	−0.042	−0.130	−0.137**	−0.111
Relative basal area	−0.197*	−0.206*	−0.237*	−0.245*
Thuja plicata				
Basal area	0.151**	0.058	0.103	0.104
Relative basal area	0.170**	0.089	0.113	0.109
Tsuga heterophylla				
Basal area	0.102	0.107	0.103	0.207*
Relative basal area	0.105	0.153**	0.184*	0.242*

*$p < 0.01$.
**$p < 0.05$.

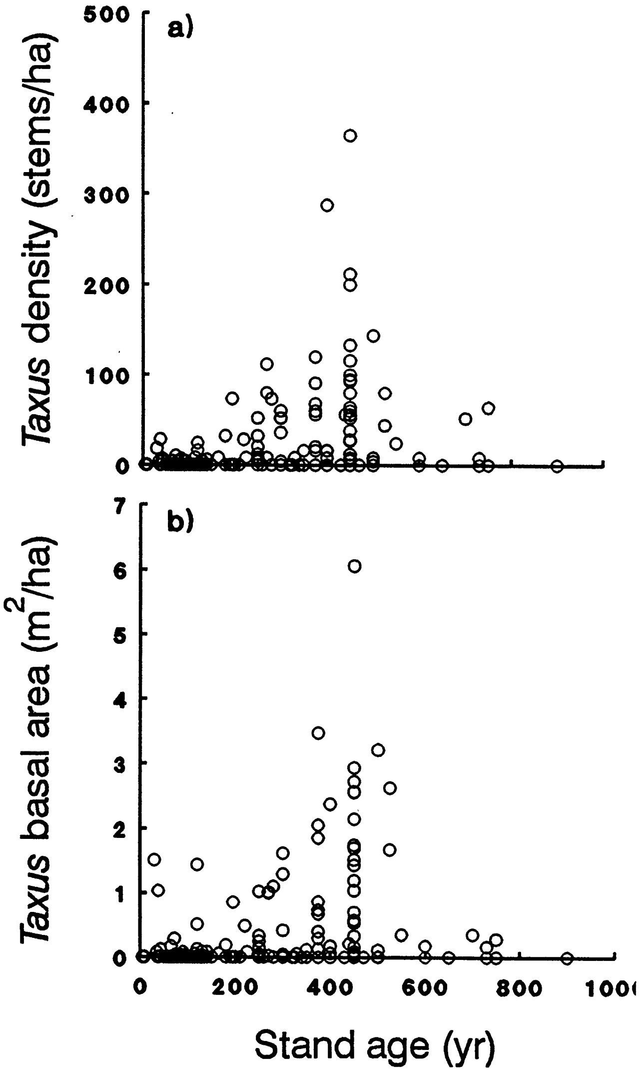

Figure 1. Taxus brevifolia *abundance as assessed by stem density (a) and basal area (b) versus stand age.*

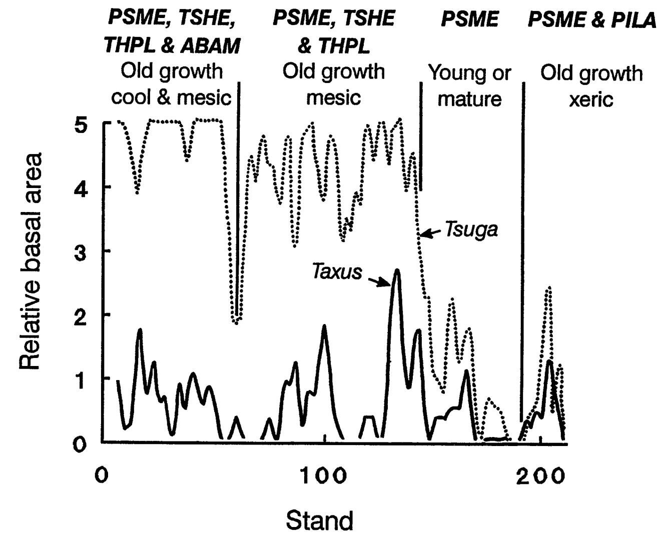

Figure 2. Classification diagram based on the two-way indicator species analysis. Tree stratum dominants and habitat characteristics are provided for four major classification units. Relative basal-area values of Tsuga heterophylla *and* Taxus brevifolia *are plotted for each stand. The sequence of stands along the bottom axis is such that similar samples are close together. Relative basal area classes are 1, 0–2%; 2, 2–5%; 3, 5–10%; 4, 10–20%; and 5, >20%. Species codes are as follows: ABAM,* Abies amabilis*; PILA,* Pinus lambertiana*; PSME,* Pseudotsuga menziesii*; THPL,* Thuja plicata*; and TSHE,* Tsuga heterophylla.

stands without high or moderate-to-high *Tsuga heterophylla* basal area. The association of *Taxus* with *Tsuga heterophylla* suggests that *Taxus*, like *Tsuga*, is sensitive to fire and drought. Both species are less abundant on xeric sites where fire and drought are more frequent. The fact that *Taxus* was absent or unimportant in some stands codominated by *Tsuga* suggests that *Taxus* is also limited by factors other than fire, such as seed dispersal or establishment.

Population Size Structure

The size-class structure of *Taxus* varied with stand age and geographic location (Fig. 3). Densities of mature stems were consistently higher in old-growth stands across all physiographic provinces (Fig. 3). Stems 5 to 15 cm dbh were generally most abundant in the old-growth stands (>195 years). Densities diminished rapidly with increasing stem size in these stands; stems larger than 50 cm dbh were uncommon. A notable contrast among populations of different provinces was the low abundance of *Taxus* in the Coast Range. This low abundance may reflect a distinctive disturbance regime in the Coast Range, where fire has been relatively frequent over the last 150 years (Martin et al. 1976; Juday 1977).

Seedling and sapling densities also varied with stand age and geographic location (Fig. 4). Densities were consistently highest in old-growth stands and generally lowest in the mature stands. Young stands in the Oregon Cascades had moderately high densities—several times greater than any of the density levels in the Coast Range, regardless of stand age.

In summary, high densities of *Taxus* seedlings, saplings, and small trees in old-growth stands throughout the study area indicate that regeneration in such stands is successful. Franklin and DeBell (1988) found substantial regeneration of *Taxus* over a 36-year period in an old-growth forest of the southern Washington Cascades. It appears that regeneration in old-growth forests is sufficient to maintain existing populations. Successful regeneration in some young forests of the Cascades shows that establishment can begin early in stand development.

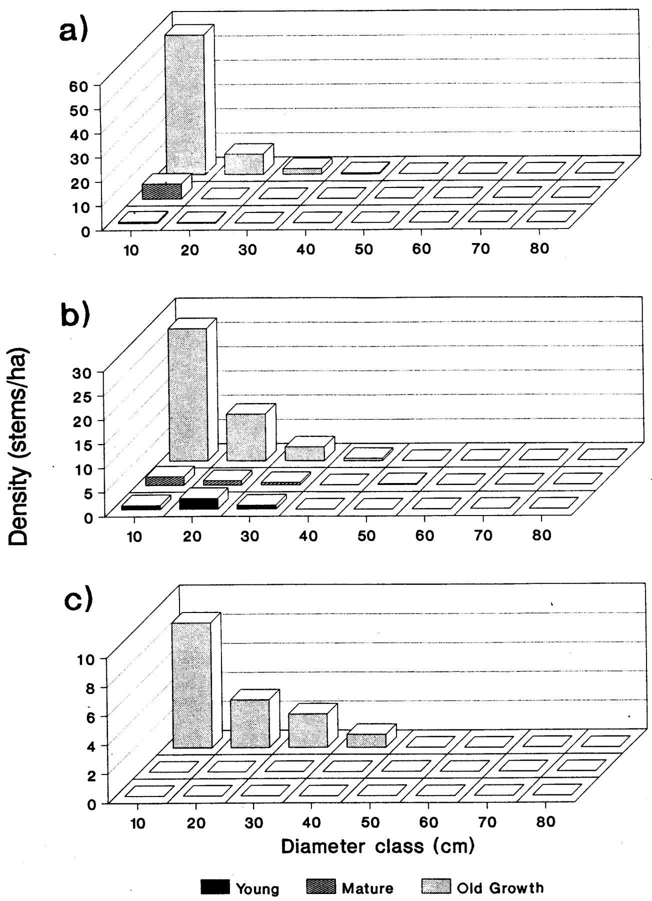

Figure 3. Density of Taxus brevifolia *by diameter class and overstory age in the Washington Cascades (a), Oregon Cascades (b), and Oregon Coast Range (c).*

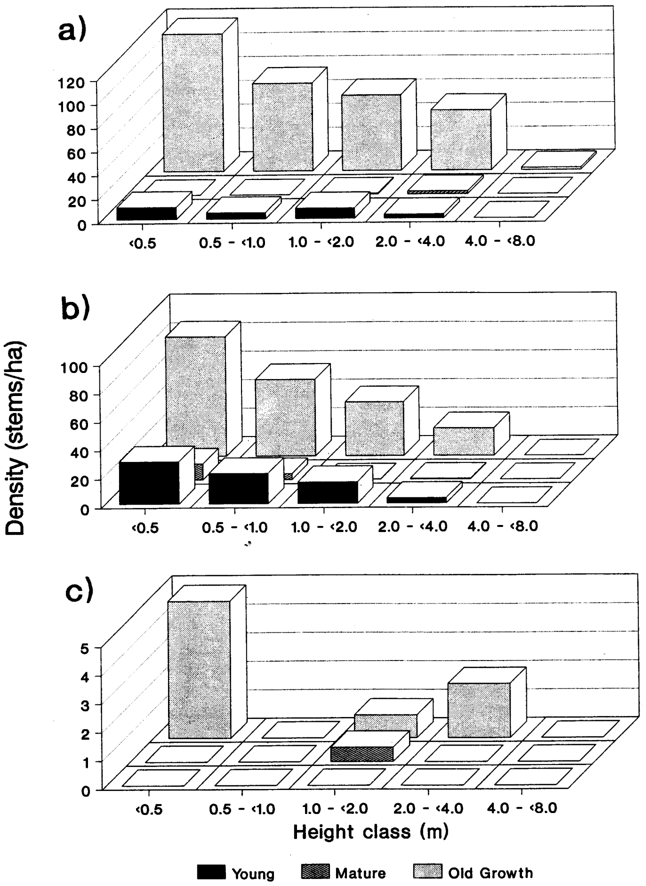

Figure 4. Density of Taxus brevifolia *regeneration by height class and overstory age in the Washington Cascades (a), Oregon Cascades (b), and Oregon Coast Range (c).*

Response to Disturbance

Survival and regrowth of *Taxus* following clearcut logging and broadcast burning on watersheds 1 and 3 were greatest on plots that experienced little physical soil disturbance or burning. Regrowth was primarily vegetative. Although pre-harvest constancy (frequency among plots) and cover varied among disturbance classes (Fig. 5), both were very low after logging and burning in all but the undisturbed plots (plots with little soil disturbance and no burning). In watershed 1, *Taxus* cover and constancy remained low in burned plots throughout the 25-year study period (Fig. 5a). In watershed 3 mean cover of *Taxus* exceeded 1% on undisturbed plots 5 years after burning and on disturbed-unburned sites (plots with soil disturbance) after 20 years (Fig. 5b). In contrast, *Taxus* cover remained low (<1%) on lightly burned sites and was rare or absent on heavily burned sites.

Clearcut harvest without burning (watershed 10) also resulted in loss and slow recovery of *Taxus*. During the 14-year study period, the constancy of *Taxus* increased gradually (Fig. 6a), but mean cover remained low (<1%; Fig. 6b).

The combined results of these studies suggest that clearcut harvest of mature and old-growth forests is detrimental to *Taxus*. Although removal of forest overstories may induce mortality or partial die-back of individuals, to a greater extent, disturbances associated with site preparation (such as broadcast burning) determine longer-term patterns of recovery. Whereas scattered individuals may survive and resprout in protected or unburned microsites, recolonization of burned sites depends on regeneration by seed—generally a slower and less predictable process.

Growth and Mortality in Old Forests

In mature and old-growth stands *Taxus* diameter growth was slow (Table 2). Diameter growth at breast height typically ranged from less than 0.1 to 0.3 cm/year when averaged over a period of about 10 years. The average diameter-growth increment from a sample of 979 individuals larger than 5 cm dbh was 0.08 cm per year. Mortality

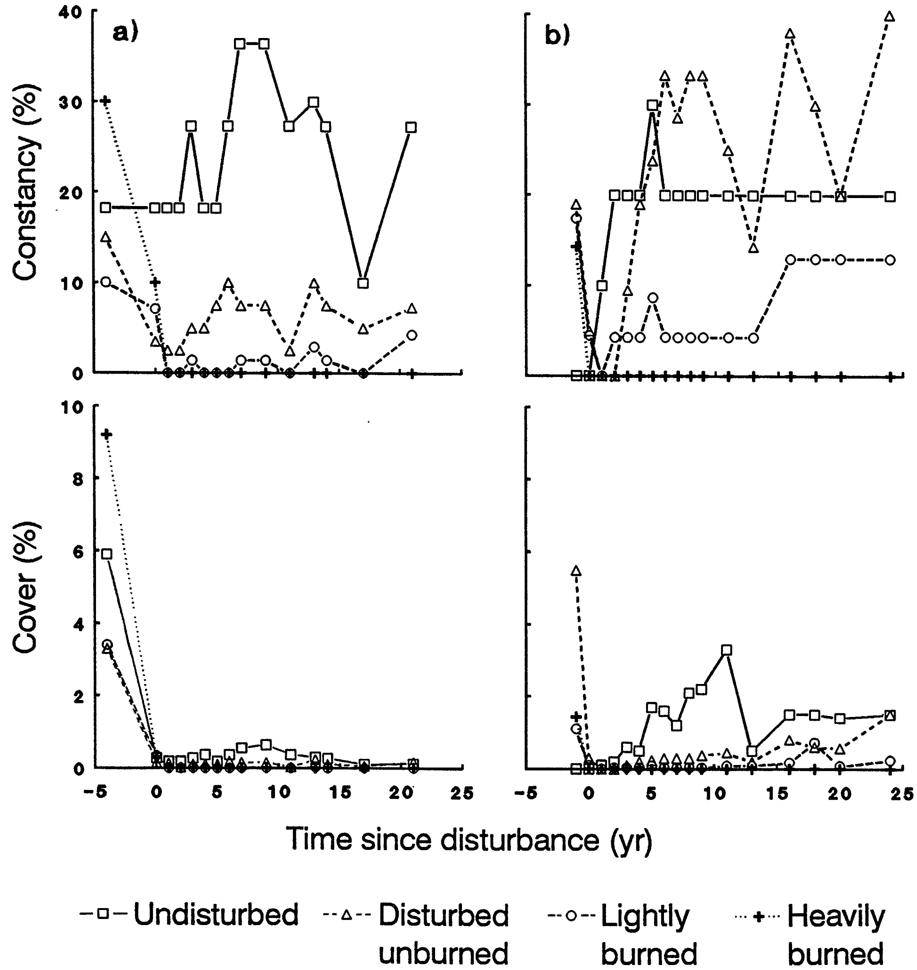

Figure 5. Constancy and mean cover of Taxus brevifolia *before and after clearcut logging and slash burning in watershed 1 (a), and watershed 3 (b) of H. J. Andrews Experimental Forest, Oregon.*

rates for the same populations were low (Table 2). The mean annual mortality rate for all stems larger than 5 cm dbh was 0.0083 of the total. Among the 68 cases of mortality observed, the common causes of natural mortality were suppression (29%), crushing by falling boles and limbs (26%), and windthrow (10%). A cause of mortality could not be determined for 28% of the observations. Franklin and DeBell (1988) obtained a similar overall estimate of *Taxus* mortality in a 36-year study of an old-growth forest in the southern Washington Cascade Range. Rates of mortality for *Taxus* are comparable to those of long-lived, shade-tolerant trees of the region (such as *Tsuga heterophylla* and *Thuja plicata*; Franklin & DeBell 1988; Spies et al. 1990).

Synthesis

Our analyses suggest that the response to disturbance and the population dynamics of *Taxus brevifolia* west of the Cascade crest in Oregon and Washington are similar to those of populations in the Rocky Mountains of Montana and Idaho. In both regions, *Taxus* is predominantly a fire-sensitive, late-successional species. Its shade tolerance and abundant regeneration in old-growth stands allow populations to persist in the understory of dense coniferous forests. Although suppression is a source of mortality, individuals are lost at rates no higher than those of late-successional forest dominants (Franklin & DeBell 1988; Spies et al. 1990).

It is important to note that, despite its greatest development in old-growth forest, *Taxus* is not restricted to old growth. In general, vascular plants attaining maximal abundance in older forests of the Pacific Northwest are not obligate old-growth species (Spies 1991; Halpern & Spies 1995); strong associations with old-growth habitat

Table 2. *Taxus brevifolia* growth and mortality in mature and old-growth forests of the Cascade Range of Oregon and Washington.

Size Class (cm dbh)	*Initial Number of Live Stems*	*Mean Annual Mortality (%)*	*Mean Annual Growth and SD (cm dbh)*
5–15	787 (715)	0.74	0.074 ± 0.084
> 15–25	212 (201)	1.39	0.102 ± 0.109
> 25	63	0.00	0.105 ± 0.101
Total ≥ 5	1062 (979)	0.83	0.082 ± 0.092

**Sample sizes for the calculation of growth rates are provided in parentheses when unequal to the initial number of live stems.*

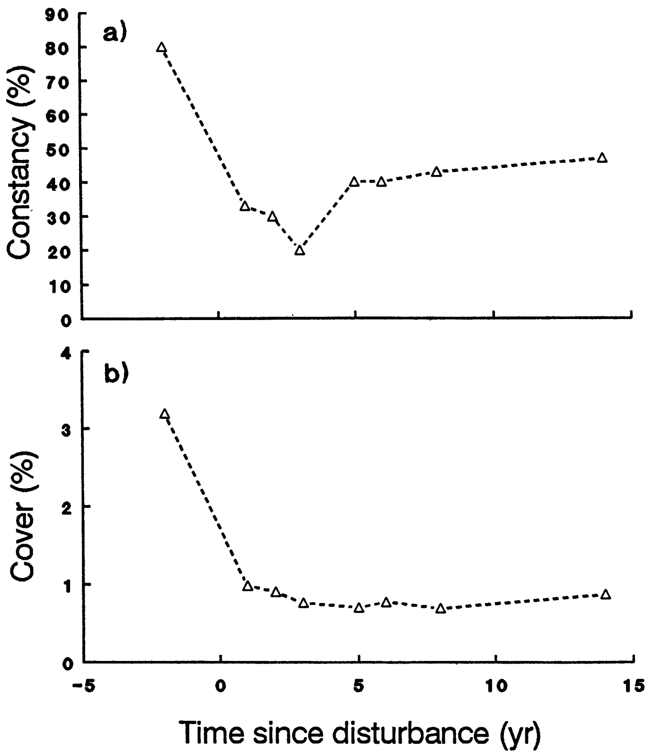

Figure 6. Constancy (a) and mean cover (b) of Taxus brevifolia *before and after clearcut logging of watershed 10 near H. J. Andrews Experimental Forest, Oregon.*

are more common among forest animals (Ruggiero et al. 1991). If we apply the concept of habitat selection to *Taxus*, we see little evidence of narrow habitat choice or habitat specialization (Bazzaz 1991). The species colonizes some early successional sites and occurs over a wide range of physical habitats and vegetation types. We suggest that it is abundant in old-growth forests largely because of its slow recovery from major disturbance.

Further evidence for the pivotal role of disturbance in the distribution and abundance of *Taxus* stems from the association of *Taxus* with the fire-sensitive species *Tsuga heterophylla*. In our natural forest sites *Taxus brevifolia* was uncommon in stands lacking *Tsuga heterophylla*, a late-successional dominant. Although their cooccurrence may reflect similar ecophysiological traits—shade tolerance and a capacity for slow, continuous growth in the forest understory—similar responses to disturbance may also produce the observed pattern of association. Both species are susceptible to fire and tend to recover slowly. Most forests of the region are eventually invaded by *Tsuga heterophylla*, but *Taxus* is not ubiquitous in old forest. Its rarity or absence in some stands with well-developed populations of *Tsuga* may reflect contrasts in seed production and dispersal. Whereas *Tsuga* commonly has prolific, wind-dispersed seed, seed production in *Taxus* is probably limited and dispersal is likely to depend on vertebrate vectors (based on fruit morphology; Willson 1993). Our uncertainty about the temporal and spatial nature of reproduction and dispersal in *Taxus* underscores the need for further autoecological research on this and other understory plants associated with old growth.

We conclude that in the Pacific Northwest *Taxus brevifolia* has a broad environmental distribution and is associated with a variety of tree species. Fire appears to be an important factor in its distribution and rate of recovery. It is most abundant in old forests, probably as a consequence of time since major disturbance rather than environmental constraints.

Implications for Management and Conservation

Prior to recent interest in *Taxus* as a source of taxol, the effects of forest management practices on the species were not considered. Recent concerns over the loss or fragmentation of natural populations and communities have focused attention on the consequences of forest management practices for species such as *Taxus* (Anonymous 1993*a*; Halpern & Spies 1995). The traditional forest practices of clearcutting and slash-burning on short rotations have undoubtedly reduced the abundance and potential viability of *Taxus* populations at local, if not regional, scales.

Since the publication of an interim conservation guide for *Taxus* populations subject to harvest for taxol (Anonymous 1992), a comprehensive forest-ecosystem management plan has been developed for the Pacific Northwest (Anonymous 1993*a*). Cornerstones of the recommended plan for ecosystem management are (1) a network of late-successional reserves (>20,000 ha each) and riparian reserves that meet many of the genetic, population, and ecosystem-level objectives expressed in the interim guide, and (2) a set of guidelines for management practices inside and outside the reserves. Most forest harvesting will take place in the "matrix" lands between reserves and will be subject to guidelines that limit selective harvest of *Taxus* and enhance its chances for survival within and adjacent to patches of retained forest.

Our findings support many of the assumptions that underlie the interim guide for *Taxus* (Anonymous 1992) and the forest ecosystem management plan (Anonymous 1993*a*). In particular, *Taxus* is more abundant in old-growth forests, and it tends to recover slowly from major disturbance. Given the lag between disturbance and recolonization, conservation and management strategies should include the maintenance of existing populations across the landscape. Patches of late-successional forest large enough to minimize the direct and indirect effects of edges (such as increased herbivory, disturbance, and climatic variation) may sustain *Taxus* in cut-over areas. Although the proposed ecosystem management plan advocates the use of retained forest patches, the critical size and dispersion of such patches necessary to maintain viable populations of *Taxus* remains unclear. These uncertainties stress the need for further research on the autoecology and reproductive biology of the species. Revision and refinement of ecosystem- and species-level strategies for the conservation of *Taxus* hinge on a better understanding of the factors controlling its distribution, reproduction, and growth.

The tendency for some understory plant species to be most abundant in old growth is common in forest ecosystems (Habeck 1968; Alaback 1982; Peterken & Game 1984; Whitney & Foster 1988; Anonymous 1993*a*; Peterken 1993). The foremost requirement of many of these plants may be a long disturbance-free interval rather than the particular environmental conditions of old-growth forests. It is essential that this requirement be considered in the development of strategies for their conservation (Duffy & Meier 1992). For *Taxus* and many other understory species, it is likely that population growth rates at landscape scales are limited primarily by rates of recolonization and growth after fire. This leads us to two major recommendations for the conservation and management of *Taxus* and similar plant species. First, current population centers will be important sources for recolonization of disturbed areas within surrounding landscapes. Source populations should be maintained. Second, additional landscape units with disturbance-free intervals long enough to allow natural establishment and growth to maturity would enhance population viability. Silvicultural manipulation of stand structure intended to accelerate the development of old-growth forest habitat (Anonymous 1993*a*) may not benefit plant species with slow rates of colonization and growth. Where colonization is prevented by inadequate dispersal, artificial seeding or planting may be beneficial, but artificial establishment of a large number of species over large areas would be difficult. If we consider that the reproductive biology of many of these species is poorly understood and that establishment may be only one of several rate-limiting steps, it becomes clear that artificial establishment is not always feasible or effective. Thus, in landscapes dominated by active forest management, the establishment of reserves comparatively free of pervasive disturbance and the use of long rotations on harvested lands may serve to maintain species that are sensitive to severe disturbance and that have slow rates of recovery.

Acknowledgments

We thank Don Minore and two anonymous reviewers for comments on earlier drafts of the manuscript. Funding was provided by Bristol Myers-Squibb, the U.S. Forest Service Program on Old-Growth Wildlife Habitat, and the National Science Foundation through the Long-Term Ecological Research Program at H. J. Andrews Experimental Forest (NSF BSR-90-11663).

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