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# Through-growth by *Pseudotsuga menziesii*: A mechanism for change in forest composition without canopy gaps

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**Abstract.** The currently prevailing view is that saplings require gaps or larger disturbances in order to grow into the canopy. This study documents an exception. In California's *Pseudotsuga*-mixed hardwood forests, crowns of *Pseudotsuga menziesii* (Douglas fir) are within those of angiosperm trees (*Arbutus menziesii* and *Quercus* species). In the forests we examined, every *Pseudotsuga* was younger and all but one were growing more rapidly in girth than the *Arbutus* or *Quercus* whose crown it had penetrated. Furthermore, as saplings, the *Pseudotsuga* had grown at rates between those of suppressed saplings and canopy dominants. The recruitment of emergent *Pseudotsuga* substantially alters these canopies because of the large size *Pseudotsuga* attains. Given the density of *Pseudotsuga* growing in canopy crowns, such recruitment is likely. As a mechanism of recruitment, this through-growth differs from gap recruitment in that the turnover of canopy trees is determined by an understory species' growth rate rather than the overstory species' longevity, and community attributes may change rapidly by replacement of canopy dominants with a dissimilar species. *Pseudotsuga* could grow through the canopy because of its greater potential height (> 60 m vs. 20-40 m for the angiosperms), narrower crown and its branches suffering less mechanical damage than those of the angiosperms. In general, resource levels in the understory, canopy height, and interspecific differences in maximum height and crown architecture all influence the likelihood of through-growth. Therefore, for vegetation types whose dominants differ substantially in growth form, through-growth may be a mechanism for rapid ecosystem change.

**Keywords:** *Arbutus menziesii*; California Coast Range; Crown architecture; Douglas fir; Gap dynamics; *Quercus*; Stand dynamics; Succession.

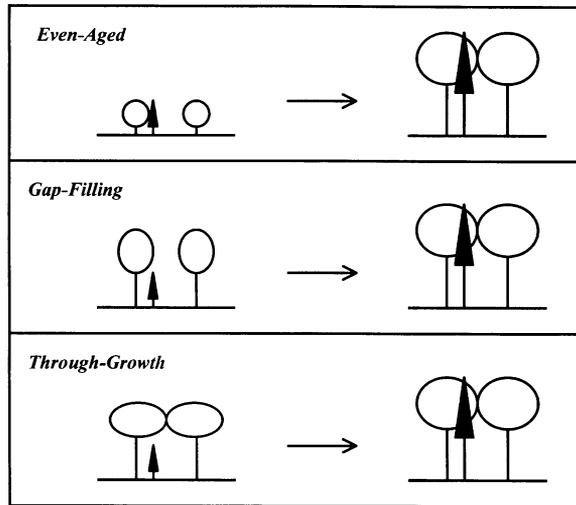
**Nomenclature:** Hickman (1993).

## Introduction

Over the last 20 years, a strong emphasis has been placed on the importance of canopy gaps for recruitment into canopies. In most understories, biomass gain is severely limited because canopy trees deplete resources to low levels, and even decades of growth may not allow an understory sapling to approach canopy height (e.g. Tappiener & McDonald 1984; Runkle 1985; Marks & Gardescu 1998). For this reason, it is generally believed that understory saplings cannot reach the canopy without benefiting from one or more gaps, and that recruitment into the canopy is therefore restricted to canopy gaps (e.g. Runkle 1985; Oliver & Larson 1990).

However, exceptions to this scenario probably exist. Many canopies are relatively open or are non-uniform in structure, and beneath them resource levels vary considerably (Smith et al. 1992; Baldocchi & Collineau 1994; Canham et al. 1994; Messier et al. 1998). Also, among tree species there is a wide range in growth form, e.g. in crown architecture, ratio of height increase to biomass gain and maximum height (Kohyama 1987; Küppers 1989; King 1994). Therefore, for some species, there are probably understory environments where, without the benefit of canopy gaps, saplings can increase in height substantially, reaching and perhaps even overtopping the canopy.

This may be the case for *Pseudotsuga menziesii* (Douglas fir, *Pinaceae*) in the mixed evergreen forests and oak woodlands of northern California, in which mature *Pseudotsuga* are emergent above an angiosperm canopy. Currently, in these vegetation types, understory saplings of *Pseudotsuga* approach canopy size and some have crowns within and surrounded by, or even partially overtopping, the crowns of canopy angiosperms, primarily *Arbutus menziesii* (madrone, *Ericaceae*) and oaks (*Quercus chrysolepis*, *Q. garryana*, *Q. kelloggii* and *Q. wislizenii*, *Fagaceae*; Hunter 1995; Barnhart et al. 1996). Fire kills *Pseudotsuga* saplings, and historical evidence suggests that these *Pseudotsuga* having established after fire suppression began in the 1920s and that they are



**Fig. 1.** Canopy dynamics resulting in intertwined crowns. Even-aged: trees fill vacant space by entering canopy simultaneously; Gap-filling: vacant space filled by lateral growth of canopy tree and upward growth of understory tree; Through-growth: understory tree enters canopy in absence of vacant space.

younger than the adjoining angiosperms (Johnson 1979; Reed & Sugihara 1987; Hunter 1995; Barnhart et al. 1996). This suggests that some *Pseudotsuga* saplings are growing up through and overtopping the crowns of canopy angiosperms.

However, there are three ways these trees could have become intertwined. They may have entered the canopy at the same time (even-aged recruitment, Fig. 1). Alternatively, crowns of canopy trees may have been entered by more recent recruits that: (1) reached the canopy in gaps filled by both their upward growth and the lateral growth of adjacent canopy trees (gap recruitment), or (2) grew from beneath the canopy up into the crowns of canopy trees ('through-growth'). The overlap of crowns during even-aged recruitment is well documented (Oliver 1980; Larson 1986; Oliver & Larson 1990), and crown overlap is consistent with the manner of tree growth into gaps (Büsgen & Münch 1931; Runkle & Yetter 1987; Young & Hubble 1991). Through-growth, in contrast, is little documented and considered a rare event (Oliver & Larson 1990). The purpose of our study was to determine whether the presence of *Pseudotsuga* saplings inside the crowns of canopy angiosperms indicates that species replacement by through-growth is occurring in these forests.

## Methods

### Sites

Three study sites were selected at the Angelo Reserve in California's North Coast Ranges (39° 35' N; 123° 37' W; 430-1290 m elevation). Soils are Inceptisols and Ultisols derived from sedimentary rocks (Gardner et al. 1964). Annual precipitation averages 2150 mm with almost all falling as rain between October and May. Though only 14 km from the ocean, the reserve receives little summer fog due to topographic barriers. Mixed evergreen forest covers most of this landscape. *Pseudotsuga*, *Arbutus*, and *Lithocarpus* (tanoak, *Fagaceae*) dominate north-facing slopes – *Pseudotsuga-Lithocarpus* forests. On other aspects, *Lithocarpus* is frequently absent and *Quercus* species are more abundant – *Pseudotsuga*-mixed hardwood forests.

Sites were selected on the basis of three criteria: (1) *Pseudotsuga* were growing within the crowns of canopy angiosperms; (2) canopy tree cover was > 95% in 1995 and on 1952 and 1987 aerial photographs; and (3) land use and fire history records existed for the site. The selected sites were all *Pseudotsuga*-mixed hardwood forests approximately 1 ha in area at 450-600 m elevation on southeast to west-facing slopes. Though none of the sites had been logged, they experienced fires every 5-40 yr until the imposition of fire suppression in 1924 (Johnson 1979; Rice 1985).

### Data collection and analysis

The three study sites were located on aerial photographs from 1952 and 1987, and the percent of their area in canopy gaps was visually estimated. In 1997, a 0.1 ha plot (33 m × 33 m) was randomly located at each site and a general description of the vegetation recorded. The presence and area of canopy gaps was noted. We considered a gap to be any break in the canopy > 2 m in diameter below which vegetation was less than two-thirds the height of the adjacent canopy. Cover within the plots was estimated visually for each species in the understory shrub and sapling (1-12 m), canopy tree (12-40 m), and emergent (> 40 m) layers. For *Pseudotsuga*, density was recorded within each layer, as well as the number of trees with their crowns in the crown of a canopy angiosperm. *Pseudotsuga* crowns were counted as in the crown of canopy angiosperms if > 33% of their crown's height was within an angiosperm crown, and if in a horizontal projection all of their crown's perimeter was within the outline of an angiosperm's crown.

At each site, we numbered all pairs of a *Pseudotsuga* and an angiosperm with crowns intertwined of which we randomly selected six. For these pairs, dis-

tance between stems, trunk diameter (at 30 and 130 cm height), and crown diameter and height were recorded.

Both trees were cored at 30 cm height, and the cores used to age the trees and to reconstruct their growth history. These ages and growth histories were used to distinguish the three mechanisms by which *Pseudotsuga* and angiosperm crowns could have become intertwined in the canopy. Similarity of tree ages would distinguish even-aged recruitment from gap-filling and through-growth. Changes in growth indicating suppression and release would distinguish the gap-filling from through-growth.

Cores were sanded and rings were then counted. For cores missing the pith, the radius of curvature of the core's innermost rings was used to determine the distance to the center of the pith, and the average width of the three inner rings was used to estimate the number of missing rings (Applequist 1958). If cores did not pass within 2 cm of the pith, the tree was re-cored. Three of the angiosperms had trunks hollowed by fire. The incomplete cores taken from these trees were used to determine minimum ages, but not to reconstruct growth histories.

Annual increments were measured with a stage micrometer, and basal area and growth rates estimated for 5-yr intervals. Because there is a substantial size-related trend in the relationship between diameter and growth (Cook & Kairiukstis 1990), we based our growth rates on change in basal area, rather than diameter, to adjust for this trend. This was intended to aid comparisons of growth, particularly between *Pseudotsuga* and the angiosperms (trees of comparable height but quite different diameters). We assumed that percent of total core length approximated percent of 1997 tree radius, and calculated basal area (at 1.30 m height) as:

$$BA_t = 3.14 \left[ \left( \frac{L_t}{L_{97}} \right) R_{97} \right]^2 \quad (1)$$

where  $BA_t$  is basal area in year  $t$ ,  $L_t$  is core length in year  $t$ ,  $L_{97}$  is 1997 core length (= total length) and  $R_{97}$  is 1997 tree radius. For the 5-yr intervals, growth rates were calculated as:

$$r = [\ln(BA_t) - \ln(BA_i)]/t \quad (2)$$

where  $r$  is the estimated growth rate,  $BA_i$  is the initial basal area (at the beginning of the time interval),  $BA_t$  is the basal area after  $t$  years.

We interpreted substantial fluctuations in a tree's growth as periods of relative suppression or release (cf. Canham 1985; Lorimer et al. 1988; Frelich & Lorimer 1991). A > 50% decrease in the mean growth rate

between subsequent 5-yr intervals was considered suppression, and a > 50% increase was considered release. All *Pseudotsuga* were initially growing rapidly, and thus were considered 'released' until a period of suppression reduced their growth. Skeleton plots were used to coordinate core chronologies (Stokes & Smiley 1968; Cook & Kairiukstis 1990) before assigning dates to periods of relative suppression and release.

Growth rates also were compared to standards for rapidly growing and suppressed *Pseudotsuga*. Because most similar locations are in Site Classes III and IV for *Pseudotsuga* (taller trees 30-50 m high after 100 yr of growth), we used average growth rates in these classes as a standard for rapid growth (McArdle et al. 1949; Gardner et al. 1964). Usually growth rates of understory saplings are used to calculate suppressed growth rates (Canham 1985; Lorimer et al. 1988), but because understory *Pseudotsuga* may not be fully suppressed in *Pseudotsuga*-mixed hardwood forests, we could not use their growth rates as the standard for suppression. Instead, we used growth rates of understory *Pseudotsuga* from three permanently marked plots in nearby *Pseudotsuga*-*Lithocarpus* forests. In these forests, understory *Pseudotsuga* suffer high mortality rates (> 5%/yr), are rarely recruited into the canopy, and their growth rates average < 2%/yr (Hunter 1997a, unpublished data). Statistical hypotheses were evaluated with the sign test (Zar 1999). Means are reported  $\pm$  one standard error.

## Results

On aerial photographs from 1952 and 1987, canopy gaps occupied < 5% of each site's area. In 1997, there were no canopy gaps within the plots, the canopy was multi-tiered, and tree cover exceeded 100% (Table 1). At each site, *Pseudotsuga* was an important component of both canopy and understory vegetation (Table 1). Some canopy *Pseudotsuga* were emergents, but most had crowns in the main canopy layer (Tables 1 and 2). Of *Pseudotsuga* in the main canopy layer ( $N = 37$ ), over 90% had part or all of their crown within the crown of a canopy angiosperm. These *Pseudotsuga* had crowns with 1-2 m radii (versus 2-4 m radii for canopy angiosperms), and their trunks were usually within 2 m of the trunks of canopy angiosperms (mean  $1.7 \pm 0.4$  m).

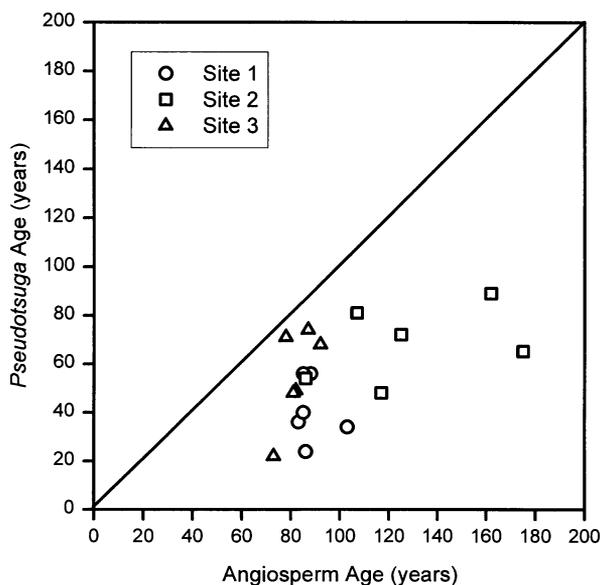
The *Pseudotsuga* were significantly younger than the angiosperms with which they were intertwined (Sign Test,  $P < 0.0001$ ,  $N = 18$ ). In every sampled pair, the *Pseudotsuga* (mean  $55 \pm 5$  yr) was younger than the angiosperm ( $100 \pm 7$  yr). Age differences ranged from 7 to 110 yr (mean  $45 \pm 6$  yr; Fig. 2).

Initially, the *Pseudotsuga* had relatively rapid in-

**Table 1.** Canopy composition (% cover) in the three 0.1 ha plots at the Angelo Reserve, Mendocino County California, visually estimated for understory (1-12 m), main canopy (12-40 m) and emergent layers (> 40 m).

	Site		
	1	2	3
<b>Emergent layer</b>			
<i>Pseudotsuga menziesii</i>	40	20	10
<b>Main canopy layer</b>			
<i>Arbutus menziesii</i>	60	-	15
<i>Pseudotsuga menziesii</i>	20	10	10
<i>Quercus chrysolepis</i>	5	-	20
<i>Quercus garryana</i>	-	70	-
<i>Quercus wislizenii</i>	15	20	55
<i>Umbellularia californica</i>	5	5	2
<b>Understory layers</b>			
<i>Arbutus menziesii</i>	5	-	1
<i>Pseudotsuga menziesii</i>	10	5	3
<i>Quercus chrysolepis</i>	5	1	2
<i>Quercus wislizenii</i>	5	1	1
<i>Rhamnus californica</i>	1	-	1
<i>Umbellularia californica</i>	10	-	2

creases in basal area (Fig. 3). These rates declined with increasing age (and size), much as they do for canopy *Pseudotsuga*. There were only three instances of suppression followed by release (Fig. 4). However, 44% of the *Pseudotsuga* have had their growth reduced without subsequent release. Despite being reduced, their



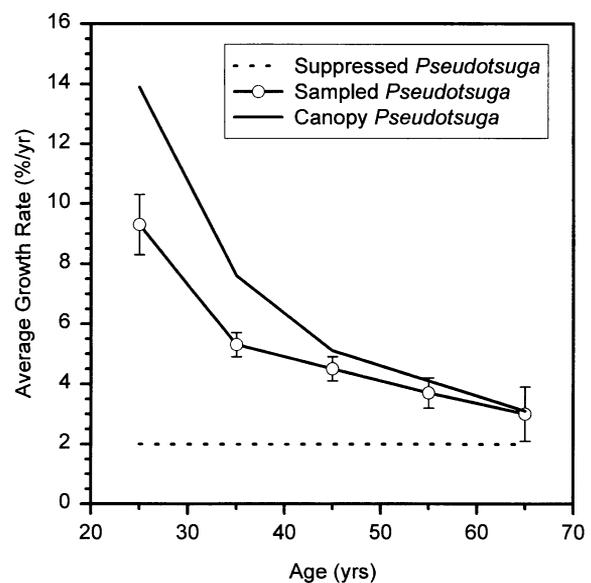
**Fig. 2.** Ages of intertwined trees. Each symbol represents the ages of a pair of intertwined trees ( $N = 18$  pairs). The diagonal line connects points where intertwined trees would be the same age.

**Table 2.** Density of *Pseudotsuga menziesii* (> 1 m height; trees/ha) in canopy layers of plots at Angelo Reserve, California. Emergent = entire crown above crowns of surrounding trees; Main Canopy = crown partially or completely at the same height as surrounding trees; Understory = crown entirely below surrounding trees.

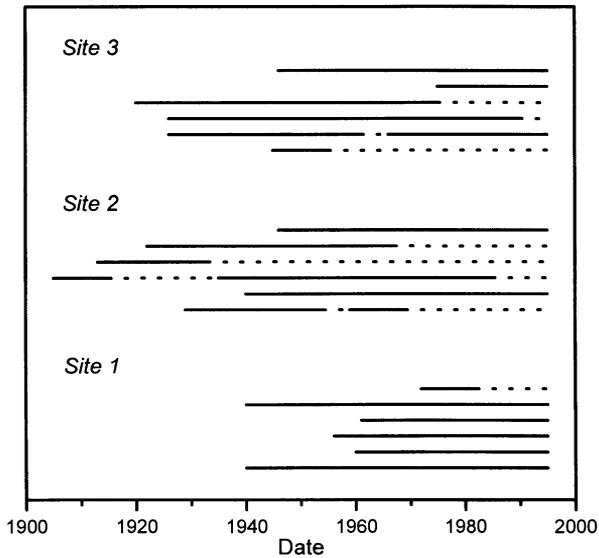
Canopy Layer	Site		
	1	2	3
Emergent	140	40	20
Main Canopy	210	90	70
Understory	670	90	50

diameter growth rates were still greater than those of highly suppressed saplings: *Pseudotsuga* classified as 'suppressed' in 1990-1995 averaged  $4.2 \pm 0.57\%$  annual growth which is significantly more rapid than the  $< 2\%/yr$  characteristic of highly suppressed saplings (Sign Test,  $P = 0.035$ ,  $N = 8$ ).

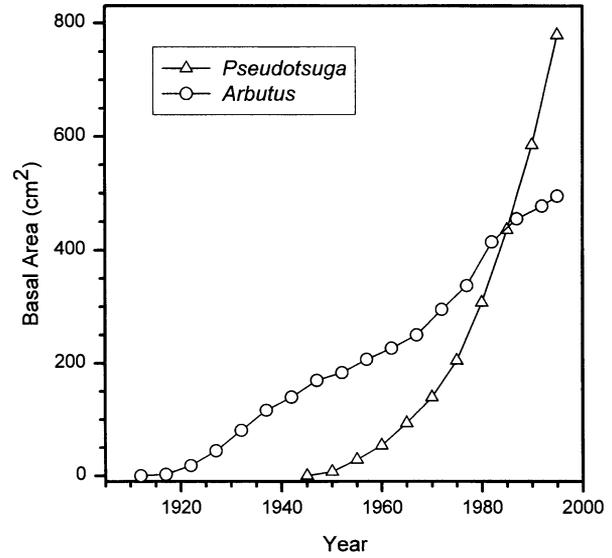
The *Pseudotsuga* currently have a significantly greater basal-area growth rate than the angiosperms they are growing through (Sign Test,  $P = 0.001$ ,  $N = 18$ ). The angiosperm canopy trees all exhibited initially rapid growth followed by a continual decline in growth rate. By 1990-1995, all were growing (mean  $0.9 \pm 0.14\%/yr$ ) at only 20% of the 1990-1995 growth rates of the *Pseudotsuga* trees ( $5.6 \pm 0.61\%/yr$ ). All but one *Pseudotsuga* had a higher growth rate than its



**Fig. 3.** Reconstructed growth rates of intertwined *Pseudotsuga* compared to rates for canopy and suppressed *Pseudotsuga*. Rates based on change in basal area during 10-yr intervals. Error bars = 1 standard error.



**Fig. 4.** *Pseudotsuga* growth histories. Each line represents one tree. Uninterrupted line = periods of rapid (released) growth; interrupted line = reduced (suppressed) growth.



**Fig. 5.** Growth of a representative angiosperm and intertwined *Pseudotsuga*. In 1997, approximately half of the *Pseudotsuga*'s crown was above the angiosperm crown.

associated angiosperm.

The *Pseudotsuga* growth rates have been intermediate between those of canopy and of highly suppressed *Pseudotsuga* (Fig. 3). For example, at 20-70 yr of age, their average rates were 70-100% of growth rates for canopy trees on similar sites and 150-450% of rates for highly suppressed saplings. These modest rates of growth have been sufficient for *Pseudotsuga* to enter the canopy, partly because of the relatively slower and declining growth rates of the canopy angiosperms (Fig. 5).

**Discussion**

In *Pseudotsuga*-mixed hardwood forests, *Pseudotsuga* are growing through the crowns of canopy angiosperms. At our study sites these *Pseudotsuga* were both widely varied in age and often substantially younger than the angiosperms they were growing through. Thus these stands were not the direct product of even-aged recruitment.

Also, it is unlikely that these *Pseudotsuga* reached the canopy by filling treefall gaps. First, their density is too high. In this study, 60-200 *Pseudotsuga* per ha were intertwined with canopy angiosperms. If each required a gap to reach the canopy, then gaps had to have formed and closed over most of the understory during the last 70 yr. That is inconsistent with the low cover of gaps (< 5%) in 1952 and 1987 aerial photographs, the absence of gaps in the plots, the ages of canopy trees, and the low

mortality rates of trees in similar stands nearby (Hunter 1995). Second, most of the *Pseudotsuga* have always maintained moderate to high growth rates, including those that are rooted near the center of the over-topping crown and thus unlikely to have ever been in a gap. Therefore, while gaps may have contributed to the growth of some saplings, *Pseudotsuga* is able to grow to canopy size while beneath a canopy of *Arbutus* or *Quercus*.

This growth of *Pseudotsuga* beneath *Quercus* and *Arbutus* contrasts strongly with the suppression of *Pseudotsuga* beneath canopies dominated by *Lithocarpus densiflorus* (tanoak, *Fagaceae*) or by conifer species (Franklin & Hemstrom 1981; Hunter 1997a). Greater availability of both light and nutrients is probably contributing to *Pseudotsuga*'s growth. Beneath *Quercus* and *Arbutus*, light levels are higher than beneath *Lithocarpus* and conifers (Waring & Major 1964; Minore 1986; Hunter et al. 1999). Additionally, shared mycorrhizal associates may contribute to *Pseudotsuga*'s growth beneath *Arbutus* (Perry et al. 1992).

Due to differences in form, *Pseudotsuga*'s growth results in it reaching and passing through the crowns of canopy *Arbutus* and *Quercus*. *Quercus* species and *Arbutus* have broad and often discontinuous crowns. Within their crowns, spaces with little or no foliage (often 0.1-1 m<sup>2</sup> in area) may function as 'mini-gaps' that enhance resource levels in the understory. These broad-crowned species reach heights of only 20-40 m and their rate of height increase slows substantially before reaching 20 m (Porter 1965; Stein 1990). In contrast, the narrow-crowned *Pseudotsuga* can exceed 60 m in height,

and its rate of upward growth does not drop off until reaching 30-40 m (McArdle et al. 1949). Also, *Pseudotsuga* suffers little mechanical damage in growing through another crown. The branches of *Arbutus* and the *Quercus* individuals seem to be more brittle and to suffer most of the damage where abrasion does occur (Hunter, pers. obs. during storms).

In addition to height and crown width, several aspects of growth form are integral to through-growth. Understory light environments are largely a product of the crown attributes of canopy trees (Baldocchi & Collineau 1994; Canham et al. 1994; Messier et al. 1998). The ability of saplings to grow in the understory is largely due to their own crown attributes (Küppers 1985; Kohyama 1987; Popma & Bongers 1988; King 1994; Hunter 1997b). A high ratio of height increase to increase in crown mass is probably necessary if an understory sapling is to reach canopy height. Recruitment by through-growth results from specific combinations of these canopy and understory species' attributes.

Because the canopy dominants are being replaced by a dissimilar species, community attributes are altered. *Pseudotsuga* attains such a great height and diameter that through-growth of its stems substantially alters vegetation physiognomy. This change in canopy structure alters wildlife habitat values (Ruggiero et al. 1991), and the replacement of basally sprouting angiosperms with a non-sprouting gymnosperm alters vegetation response to fire (Kauffman 1990). By through-growth, this ecosystem turnover can replace an angiosperm canopy within only 5-10 decades of its initial formation. For these ecosystems, this is a rapid change because the angiosperm species could reside in the canopy far longer than 5-10 decades. In other words, the duration of angiosperms in the canopy is being determined not by their longevity but by the rate of *Pseudotsuga* growth beneath them.

Through-growth may occur in other types of woody vegetation. In forests with tall and closed canopies, such as the *Fagus-Acer* forests of northeastern North America, through-growth would be exceedingly unlikely because of low resource levels in the understory, the great distance to the canopy, and only modest interspecific differences in maximum height. In shrublands, through-growth would be much more likely due to the short distance to the canopy and potentially large interspecific differences in maximum height and crown architecture. In fact, trees often grow through the crowns of shrubs (Callaway 1992; Callaway & Walker 1997) and, in some shrub-dominated habitats, succession seemingly involves through-growth (Chapin et al. 1994; Richardson et al. 1994; Hill et al. 1995). In some other types of woody vegetation, interspecific differences in growth form are comparable to those between *Pseudotsuga* and

the angiosperms in this study, particularly in Mediterranean regions with their structurally varied mosaics of shrubland, woodland and forest. And indeed, in these regions, the dynamics of several woody vegetation types seem to involve through-growth (Johannessen et al. 1971; McBride 1974; McDonald & Littrell 1976; Stein 1990; Callaway 1992; Burns 1993; Richardson et al. 1994; Barnhart et al. 1996).

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