



Gap Characteristics and Vegetation Response in Coniferous Forests of the Pacific Northwest

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Reviewed work(s):

Source: *Ecology*, Vol. 70, No. 3 (Jun., 1989), pp. 543-545

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/1940198>

Accessed: 13/07/2012 12:14

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however, fire (both natural and human-set) is the large-scale disturbance most frequently responsible for the establishment of even-aged *N. dombeyi* stands (Veblen and Lorenz 1987, 1988).

CONCLUSIONS

The role of gaps of various sizes and origins in the regeneration of *Nothofagus dombeyi* varies markedly along the transandean gradient. This variation chiefly results from site-to-site differences in associated tree species and understory bamboos, as well as from differences in the abiotic environment. Other wide-ranging tree species, such as *Pseudotsuga menziesii* in the Pacific Northwest (Spies and Franklin 1989), are also known to respond differently to gaps in different forest types. In assessing the response of a given species to gaps, ecologists should consider that the response may vary geographically. Gap response may be predicated on the particular physical and biotic characteristics of

the study site and might well be different in other parts of the species range.

In South American *Nothofagus* forests, gap-creating disturbances of various types clearly have a major influence on forest structure and composition, and knowledge of disturbance regimes is essential to explaining vegetation patterns. Despite the striking influence of coarse-scale allogenic disturbance on the composition of these forests, the influence of fine-scale autogenic processes must also be considered. For example, microsite modification by both understory bamboos (Veblen 1982) and canopy trees (Veblen et al. 1979) may influence the response patterns of *Nothofagus* spp. to gaps. The recent emphasis in forest ecology on the pervasive influences of allogenic disturbance should not divert attention from autogenic processes, since most vegetation change reflects both types of processes.

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Ecology, 70(3), 1989, pp. 543–545
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GAP CHARACTERISTICS AND VEGETATION RESPONSE IN CONIFEROUS FORESTS OF THE PACIFIC NORTHWEST

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Gaps (*sensu* Watt 1947) in forest landscapes assume a wide range of sizes from the openings created by the death of single branches or trees to areas of hundreds or thousands of hectares created by catastrophic wildfire. Most "gap" studies have focused on the death and replacement of one to several canopy trees, excluding larger sized gap processes that occur in most landscapes. However, the importance of openings created by disturbance cannot be adequately addressed without considering both fine- and coarse-scale gap processes.

Opportunities for examining gap processes at a range of spatial and temporal scales are excellent in the Pacific Northwest where extensive, uncut forests still exist and stumps on many cutover areas retain a record of previous tree ages and fire scars. Canopy disturbances are of varied types and spatial and temporal scales, and intervals between stand-replacing disturbances poten-

tially exceed 1000 yr on many sites (Dale et al. 1986). In this essay we focus on coniferous forests dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Our objective is to contrast the roles and importance of fine- and coarse-scale disturbances, illustrating the importance of various disturbance characteristics and system context in controlling community dynamics.

COARSE-SCALE DYNAMICS

Wildfire, wind, and volcanic eruption are the primary agents that create canopy openings of 0.1 to > 100 000 ha. Wildfire has affected the largest area with the greatest frequency. The complex fire regime of the region cannot be characterized by a single estimate of rotation length or intensity. Estimates of fire rotation length in the Cascade Mountains range from 434 yr

for stand-replacing fires in central western Washington (Hemstrom and Franklin 1982) to 95 yr for low- and high-intensity fires in central western Oregon (Morrison and Swanson, *in press*).

After coarse-scale disturbance such as fire or clear-cutting, total plant species richness reaches maximum values within a few years (Dyrness 1973, Halpern 1987) and then declines as the forest canopy closes, 30–40 yr later (Long 1977). Tree species richness is also highest initially following formation of large openings. For example, of the 12 tree species found regenerating in two clearcuts (Halpern 1987), 8 occurred in adjacent old-growth forests (although only 5 were regenerating there); the remaining 4 species only occurred in nearby recent clearcuts. Douglas-fir, a shade-intolerant pioneer (*sensu* Whitmore 1975, 1982, 1989, Swaine and Whitmore 1988), typically dominates the regeneration producing nearly pure, closed stands following loss of early-colonizing, deciduous trees. More shade-tolerant species can dominate young stands, especially in coastal and northerly areas. Douglas-fir typically does not regenerate in small gaps in these stands, and shade-tolerants such as western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and Pacific silver fir (*Abies amabilis*) invade and eventually dominate the canopy.

The size of coarse-scale events may influence the development and composition of post-fire stands. For example, large fires ≈ 500 and 150 yr ago may have limited available seed sources of Douglas-fir and western redcedar sufficiently to delay full restocking of many stands for decades (Franklin and Hemstrom 1981, Klopsch 1985).

FINE-SCALE DYNAMICS

Fine-scale disturbances (<0.1 ha) break up the relatively uniform coarse-scale patches into a mosaic of openings and canopy areas dominated by narrow-crowned, tall (70+ m) Douglas-fir or by broader crowned, shorter (30–50 m) species such as hemlock and redcedar. In the Cascade Range, $>70\%$ of canopy Douglas-fir and western hemlock trees die standing or from stem breakage (T. A. Spies and J. F. Franklin, *personal observation*). Important causes of mortality are root pathogens, wind, and bark beetles (Gedney 1981, Franklin et al. 1984). Mortality rates of canopy trees range from 0.5 to 1.0% (Franklin et al. 1984). This translates into canopy-return intervals of 100–200 yr, which are about the same or shorter than coarse-scale events caused by fire.

Our observations suggest that even the shade-tolerant tree species require canopy gaps to reach the canopy in old-growth coniferous forests. *Tsuga*, the most shade tolerant of the group, can regenerate without canopy gaps (Stewart 1986) but may eventually require one or more small openings to survive and grow

into the overstory (T. A. Spies and J. F. Franklin, *personal observation*), as has been observed with some shade-tolerant species in eastern deciduous forests (Canham 1985, 1989). Small seedlings and very slow-growing saplings of several other shade-tolerant species can be found under intact canopies.

We hypothesize that the nature and role of fine-scale gaps changes over time following large-scale disruption. In young Douglas-fir stands with dense, closed canopies, gaps created by the normal thinning process and pathogens (Childs 1970) are generally small and ephemeral. Such gaps are closed primarily by lateral branch growth. Shade-tolerant species invading the deeply shaded understory of the stand during this time may have increased survivorship and growth rates in these small openings. As the Douglas-fir stand develops, canopy height increases, and understory light increases as numerous small openings form between crowns. Canopy gaps of one to several trees may be less important to invading shade-tolerant trees at this time because the general canopy transmits enough light for survival and growth. Eventually shade-tolerant species, such as hemlock and redcedar, dominate the canopy and transmittance of light through the canopy declines again. When this happens, canopy gaps of one to several trees may become more important in the survival and growth of understory seedlings of the shade-tolerant species.

Where minimum light levels occur in canopy gaps or under low-density canopies, seedling survivorship and growth is probably controlled by micro-scale gaps (<10 m²) in the herb/shrub, litter, and rooting zone layers of the forest. For example, western hemlock seedlings are almost exclusively found on rotten wood substrates that are elevated above the forest floor (Minore 1972, McKee et al. 1982). Christy (1986) found that trenching increased the growth of hemlock seedlings more than removal of foliage above seedlings. Harmon (1986) found that hemlock and Sitka spruce (*Picea sitchensis*) regeneration was inhibited on the forest floor by competition from mosses and herbs. Competition with shrubs and herbs and lack of suitable seedbeds may help explain why many gaps in old-growth Douglas-fir forests fill slowly, with many existing for >50 yr without development of tree saplings.

Douglas-fir, unlike shade-intolerant trees in other forest ecosystems (Brokaw 1985b, Runkle 1982), does not reach the canopy in gaps less than ≈ 700 –1000 m² in the Western Hemlock Zone (Franklin and Dyrness 1973). At least two mechanisms may be responsible for inhibiting regeneration and growth of Douglas-fir in most canopy gaps. First, light levels may be too low. The combined canopy strata of Douglas-fir and western hemlock typically reduces light in the understory beneath intact canopy to $<5\%$ of full sunlight. Hence,

unlike Eastern deciduous forests (see Poulson and Platt 1989), the additional light entering through gaps of even several trees may not be enough for regeneration of shade-intolerant species. Second, since most trees die standing or by top breakage, most canopy gap events do not form gaps in the lower strata of the forest or expose mineral soil which Douglas-fir germinants prefer to organic seedbeds (Minore 1979). Gaps with standing dead trees also transmit less light than gaps formed by fallen trees.

The importance of fine-scale gaps appears to differ locally and regionally among forest types. For example, Douglas-fir reproduces and reaches the canopy in small gaps on dry sites in the Western Hemlock Zone (Means 1982) and in the Mixed Conifer and Mixed Evergreen zones in southwestern Oregon (Franklin and Dyrness 1973). These forests have shorter canopies than Douglas-fir/western hemlock forests and lack the dense canopies of western hemlock. Consequently, light levels in gaps may be high enough for Douglas-fir regeneration. These forest types are also subjected to relatively frequent, patchy, low-intensity fires which would create gaps in the overstory and understory vegetation and expose mineral soil seedbeds favoring Douglas-fir regeneration.

CONCLUSIONS

In tall coniferous forests of the Pacific Northwest, as in temperate hardwood forests (see Lorimer 1989), species composition appears to be molded by gaps of a variety of sizes and types. Large, relatively uniform patches created at infrequent intervals by fire are converted to a mosaic of canopy and gap by smaller, more frequently occurring gap processes. In the Western Hemlock Zone, where fine-scale gaps are at least as common temporally and spatially as large gaps, most tree species can regenerate in the large, fire-created gaps, but less than half of the tree species regenerate in smaller gaps formed by other processes. This does

not match Denslow's prediction (1980*b*) that, in forests where small gaps were more common than large gaps, species able to regenerate in small gaps will be more common than species able to regenerate in large gaps.

The observed pattern of species composition in Northwestern coniferous forests probably results from most small gaps being formed by pests and wind breakage, whereas large gaps are typically fire-created. Small-gap processes typically create gaps only in the canopy layer and release relatively little above- and belowground resources, whereas large fires create gaps in nearly all layers of the forest, releasing more resources and creating a diversity of microsites. Shade-tolerant species are not restricted to small gaps because suitable regeneration sites are available in most large, fire-created openings. Clearly, predictive models of species composition based on gap dynamics must take into account disturbance type along with gap size.

While gap dynamics at the scale of one to several trees are important, finer scale processes at the level of the seedling microenvironment and coarser scale (landscape) processes also play important roles in community dynamics. Lower vegetational layers influence tree regeneration in Douglas-fir and *Nothofagus* forests (Veblen 1989). At a coarser scale, large disturbances may locally reduce seed sources of some species, affecting rates of succession and composition in the regenerating forest. At regional levels, variation in the response of Douglas-fir to small gaps illustrates the importance of community and environment in gap dynamics. Similar findings for *Nothofagus* in Chilean forests (Veblen 1989) suggest that geographic variation in species responses to gaps may be common in many forest regions.

ACKNOWLEDGMENTS

We thank A. McKee, M. Harmon, C. Halpern, B. Smith, D. Hibbs, and F. Swanson for their helpful comments on an earlier draft of this essay.

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