

Gaps Designed to Tackle the Questions . . . 2
Chance and the Partitioning Hypothesis . . . 3
Survival of the Fittest in Gaps 3
Equal Gaps Below Ground 4
Seed Sources and Regeneration 4
Can Gap-Making Become a Management Tool? 5

Science

FINDINGS

“Science affects the way we think together.”

Lewis Thomas

CANOPY GAPS AND DEAD TREE DYNAMICS: POKING HOLES IN THE FOREST



Credit: A. Gray

A ground view of a one-half acre gap 7 years after gap creation. Douglas-fir, hemlock, and Pacific silver fir are visible.

“Commercial thinnings can now be guided by our knowledge of gap dynamics, especially as the emphasis moves from timber yield to complexity and biodiversity.”

Jim Mayo, silviculturist
Willamette National Forest

If a tree falls in the forest, will an ecologist be there to watch what happens next?

The concept of forests as mosaics, with shifting internal dynamics, the birth and

death of patches across the landscape, and continual change and interaction, has been in the scientific literature for more than half a century. But it took the high-intensity ecosystem studies and questioning of the 1980s and onward to bring “canopy gaps”—holes in the forest caused by trees dying and falling—into the forefront of research. Canopy gaps are now understood in the context of natural disturbance and diverse landscapes, and are raising important management questions.

“The characteristics and importance of small canopy gaps in coniferous forests have received far less attention than those in Eastern deciduous forests. In the West,

IN SUMMARY

When large trees die, individually or in clumps, gaps are opened in the forest canopy. A shifting mosaic of patches, from small single-tree gaps to very large gaps caused by wildfire, is a natural part of the development of composition and structure in mature forests. Gaps increase the diversity of forests across the landscape and present local environments that encourage the establishment and growth of new species.

The role, however, of small gaps is not yet well understood. A long-term study established in 1990 seeks to uncover the role of gaps in creating forest diversity, their different effects on multilayered old-growth forests and single-layer mature forests, and their effects on belowground ecosystem attributes such as root density, soil moisture, and nutrient cycling.

Management questions are numerous and important: Do gaps facilitate the development of late-successional forests? If so, what kinds of management treatments can mimic that process? Are gaps “hot spots” for biological diversity, nutrient cycling, and forest productivity?

The value of the long-term study lies in its efforts to continue tracking forest responses to gaps through time. As with so many other areas of forest research, changes through time tell a more complete story than does initial response.

research on forest dynamics has typically focused on large patches created by fire,” says Tom Spies. “Large fires are clearly an important regulator of patch patterns and dynamics in these landscapes; however, the importance of smaller canopy disturbances at stand and landscape scales is much less clear.”

Research questions abound. Do the rates of formation and the importance of gaps differ in different areas? Do gaps play a different role in younger single-layer Douglas-fir forests than in older, multi-layer Douglas-fir-hemlock forests? (Yes, on both counts.) Do aboveground gaps create an equivalent belowground gap, affecting root density, soil moisture, and decomposition?

“National forest managers are interested in whether gaps facilitate the development of late-successional forests and if so, what kinds of management treatments can mimic that process,” says Spies, a research forester with the PNW Research Station in Corvallis, Oregon. “Other managers and scientists would like to know whether gaps are ‘hot spots’ for biological diversity, nutrient cycling, and forest productivity.”

GAPS DESIGNED TO TACKLE THE QUESTIONS

Spies and Gray began a long-term study in 1990, with three sites at Wind River Experimental Forest in southern Washington, and one site at H.J. Andrews Experimental Forest in western Oregon. The objectives of the study centered on disturbance and succession. The researchers wanted to characterize above- and belowground responses of coniferous forests to gap size. They also wanted to contrast responses to gaps in single-layer and multilayer forests, and relate their findings to biodiversity issues.

Their study had a significant advantage over all gap studies that had come before it in the Pacific Northwest. Rather than studying existing natural gaps, without prior knowledge of pregap conditions, they created their own gaps, and thus were able to inventory forest conditions and choose similar areas before any trees were felled. They also tracked regeneration responses of three species at once: Douglas-fir, hemlock, and silver fir.

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KEY FINDINGS



- Douglas-fir and other conifer species can successfully regenerate and grow in a wide range of gap sizes and understory conditions in conifer forests. Light sensitivity of species is a key constraint, and niche specialization by different species is apparent.
- Reduced root density and increased soil moisture indicate that belowground gaps are created by all aboveground gaps, regardless of gap size. Combined with higher temperatures in gaps, increased moisture leads to increased decomposition and higher nutrient availability, boosting the productivity of the surrounding forest.
- Chance plays a major part in forest succession in gaps: gap size; within-gap position; differences in light, moisture, temperature; plant species survival; seed rain; and diversity of materials such as downed wood within the gap all play interacting roles in regeneration.
- Plant species diversity was higher in gaps than in closed-canopy areas. Some of this diversity results from weedy species invasion, but some comes from establishment and growth of native forest species.

Gaps are indeed important in the natural development of composition and structure in forests of all ages, it seems. According to Spies and Andrew Gray, a research ecologist also with the Station in Corvallis, if a tree, or a group of trees,

falls in the forest, what happens next can affect the long-term future of the forest around it. Not only that, but much of that future-forming, or successional development, can depend on mere chance.

Four circular gap sizes with diameters of 0.2, 0.4, 0.6, and 1.0 times canopy height as well as controls were established (The largest gaps were about 150 feet in diameter or 0.5 acres in area.) Two stands were in old-growth forests dominated by Douglas-fir and hemlock, and two were in mature Douglas-fir forests.

In the four study areas, overstory trees in control areas and within 40 to 80 feet of gap edges were mapped and diameters measured before gap creation and again 7 years later. A subsample of trees were cored to quantify growth before and after gap creation. Overstory tree mortality was evaluated annually.

In order to capture the complex workings of above- and belowground forest dynamics, the researchers and their collaborators measured both overstory and understory vegetation (herb and shrub cover), light, temperature, soil moisture, tree regeneration, decomposition, root density, nutrient passage, and small mammal communities.

Purpose of PNW Science Findings

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CHANCE AND THE PARTITIONING HYPOTHESIS

A key hypothesis, known as the gap partitioning hypothesis, states that many species are adapted to certain sized gaps, and that species diversity in forests is maintained through ongoing gap dynamics.

“Most work in forest gaps tends to stress the role of single factors in controlling species composition, without showing the importance of interactions among them, or of their importance at different spatial scales,” Gray explains. “The gap partitioning hypothesis, which emphasizes gap size and within-gap position, may be too simple. It doesn’t account for the importance of diverse conditions on the ground and the different regeneration traits of individual species on the development of mature forest.”

Instead, it is becoming clear that species composition on a disturbed site can be influenced by a great number of factors—size and intensity of the disturbance, microclimate, presence or absence of nurse logs or other coarse woody debris, shading vegetation, existing seed banks, windthrow mounds, drought, and type of soil. And then there is the dynamic interaction of all these factors.

“In other words,” Spies points out, “complex interactions and chance play much greater roles in successional dynamics than was previously understood.”

Despite the reigning stereotype of the rainy Pacific Northwest, the fact is that the

SURVIVAL OF THE FITTEST IN GAPS

Seedling establishment was greater in gaps than in any closed-canopy areas, suggesting a response to the increased soil moisture and light. Seedling size increased with gap size and was greatest at gap centers. Each of the three species had a different relation to gap size: Douglas-fir growth was relatively low except in the largest gaps, hemlock growth increased dramatically with gap size, and silver fir growth responded least to gap size.

Solar radiation—both direct sunlight and diffuse radiation—generally increased with gap size, but the increase differed

 **LAND MANAGEMENT IMPLICATIONS** 

- Gaps can create structural complexity and provide sites for establishment and growth of tree species like western hemlock that can accelerate the development of late successional forest conditions.
- Gaps created by management may require underplanting for successful tree establishment.
- Understanding gap dynamics can provide guidelines for uneven-aged management on some sites. For example, uneven-aged management designed to maintain Douglas-fir in moist, hemlock-zone forests would have to rely on group selection and accommodate a mix of species.
- Even relatively small disturbances within mature forests can provide temporary sites for the invasion of non-native plant species. As gaps close, these species will likely disappear.
- When gaps are created in plantations to enhance ecological diversity, a range of gap sizes will provide greater diversity than use of a single size.

summer growing season is dry and warm. Gray explains that death of young tree seedlings is often associated with drought stress and high surface temperatures on soil bases exposed to direct sunlight.

“Shade from shrubs and logs may facilitate seedling establishment during the dry summers by providing moist or cool microsites,” he says. “In high-light environments, even the relatively shade-intolerant Douglas-fir may have its establishment helped along by shade from vegetation, woody debris, or live trees.” Douglas-fir is also sensitive to competition

from shrubs and to soil type.

The shade-tolerant hemlock, in contrast, is so sensitive to understory competition that in intact forests its seedlings are most commonly found on the surface of decayed Douglas-fir logs that are free of vegetation and litter. Silver fir commonly establishes on the forest floor in shady conditions, but still appears to be sensitive to canopy density of both understory and overstory.

How then do various gap sizes and conditions affect what happens after gap formation?

with positions within gaps. It is clear, though, that additional light was important: conifer seedling growth was 50 percent greater in the 0.2 gaps than in the controls, for example. Overstory tree growth also increased with gap size, suggesting that the trees surrounding gaps are benefiting from increased light and soil moisture. Growth rates appear to reach a threshold with increasing gap size and may decline for shade-tolerant hemlock and silver fir in the largest gaps, Spies says.

Another key finding relates to the effects of gap side—north or south. Light, temperature, moisture, and plant species survival

and growth differed substantially between north and south sides of large gaps. Scorching of seedlings, even the shade-intolerant Douglas-fir, is not uncommon in the hot, direct sunlight of the Pacific Northwest summer.

“The relatively cool, moist, diffuse light areas in the southern portions of large gaps were areas of abundant regeneration and growth of a wide range of plant species,” Gray says. “Shade-tolerant hemlock, in particular, appears to benefit from increased diffuse sunlight and moderate amounts of direct sunlight.”

WRITERS' PROFILE

Sally Duncan is a science communications planner and writer specializing in forest resource issues. She lives in Corvallis, Oregon.

Seedling establishment and growth differed among the four stands, further reinforcing the idea of the importance of microsites and the vulnerability of every site to chance factors. Although Douglas-fir, hemlock, and silver fir were able to establish in most gap sizes, the researchers believe that the three species showed signs of “niche specializing” or strategies for success based on localized conditions. Douglas-fir tended toward more success in gaps larger than one-third of an acre, thriving in the northern portions affording more sunlight. Hemlock and silver fir appear to

be more opportunistic, with higher growth rates in smaller gaps and in shadier portions of large gaps.

In stark contrast to rapid gap closure in tropical and temperate deciduous forests, Pacific Northwest forest gaps can remain devoid of tree saplings for as much as 50 years after formation. Tree regeneration and growth can be quite slow in the most common natural gap size, that created by the death of individual large trees.

“It is unclear whether filling of gaps in the Pacific Northwest is limited by low light

levels in narrow gaps surrounded by tall, deep tree crowns, or by lack of suitable microsites for tree establishment because of minimal disturbance to the forest floor and understory vegetation in most gaps,” says Gray.

Findings from the long-term study may clarify such questions over time, but for the moment are throwing their light on other aspects of gap dynamics. What happens below ground in forest gaps, for example, is just as significant.

EQUAL GAPS BELOW GROUND

Plants must make fundamental tradeoffs in allocating plant growth to capture both above-ground and belowground resources (for example, leaves for light and roots for water), and no single species is able to maximize both compared to other species, Gray explains. So the effects of gaps on such elements as soil moisture are crucial to how well tree seedlings and other vegetation can regenerate.

“While many aboveground gap effects are relatively obvious, like increased light, belowground effects are less known,” says Spies. “We found that belowground growing space is created regardless of the size of the gap above, as indicated by reduced root density and increased soil moisture

with the dead tree or trees no longer drawing on it. Intermediate-sized gaps about 80 feet in diameter (about one-tenth acre) had the highest available moisture.”

Combined with higher temperatures in larger gaps, increased moisture led to increased decomposition and greater nutrient availability, he notes. Soil moisture in gaps varies with distance from gap edge and orientation. Gap centers are usually wetter than gap edges, which are usually wetter at least initially, than surrounding forest.

“Soil moisture was more abundant in gaps than in controls, was most abundant in intermediate-sized gaps, and tended to decline during the growing season in

single-tree gaps and on the north edges of large gaps,” Gray says. “However, there was substantial variation in moisture availability within individual gaps, primarily related to the variety of organic matter—like decayed logs—present. Moisture in gaps declined over multiple years, likely caused by encroachment of vegetation within and around gaps.”

Both decomposition and nutrient cycling rates increased in large gaps compared to intact forest because of higher temperatures and soil moisture levels. Several years after gaps were created, these higher cycling rates resulted in gaps having fewer mycorrhizal mats, thinner litter layers, less microbial activity, and lower soil respiration rates.

SEED SOURCES AND REGENERATION

With seed fall as a known constraining factor of regeneration, Gray conducted a seeding experiment to determine whether natural regeneration was consistently successful in revegetating gaps.

“Since none of the principal tree species in the Pacific Northwest has seed banks in the soil, the timing of seed production can be important,” he notes. Hemlock sheds some seed every year, an advantage for early arrival in suitable microsites. Douglas-fir and silver fir, on the other hand, only shed seed abundantly every 3 to 5 years, although the larger seed of these species confers an advantage on less-than-ideal microsites.

“Low abundance of suitable microsites may not be critical, however, if large seed

crops ensure that at least some seed disperses to suitable microsites. Thus,” he concludes, “seed size and the abundance and timing of seed dispersal could greatly influence species composition in gaps.” A lack of seed was seen to be the cause in some areas of low regeneration in otherwise suitable gaps. Chance factors such as seed rain can therefore strongly influence response to gaps.

Availability of seed becomes an issue in management if the objective is to move a forest more rapidly along the successional path; if no seed is available for natural regeneration of late-successional species, planting becomes a necessity, Gray notes.

Seed banks for invasive species, on the other hand, were frequently the cause of

significant increases in plant diversity; fireweed, thistle, blackberry, and groundsel thrived more readily in even the smallest gaps than they did in closed-canopy settings.

“We were surprised by the initial response of alien herb species in gaps,” Spies says. “While we’re not sure of the exact mechanism, wholesale landscape changes seem to leave these seed banks available for regeneration. What it indicates is how widely we have altered the landscape, how invasive species have spewed out seeds that can carpet the forest, even in intact old-growth forest.” These invasive species typically die out within a few years, he adds, but researchers are monitoring them to see how long they do persist.

CAN GAP-MAKING BECOME A MANAGEMENT TOOL?

The management questions coming from national forest managers seeking to move reserve forests along the successional spectrum concern methods of mimicking small and large gap formation in young plantations. “The frequency of large disturbances probably controls the importance of small canopy gaps,” Spies says. “Where large disturbances are frequent, small gaps may be relatively unimportant in forest dynamics.”

Furthermore, in old-growth forests in the Pacific Northwest, gap formation is infrequent, possibly as a result of low rates of mortality of such long-lived trees as Douglas-fir, or to the infrequency of high winds in the area, or to the multistoried nature of the stands, where an overarching Douglas-fir can die without creating a gap in the dense canopy of the lower hemlock layer.

Nonetheless, gaps can create structural complexity and provide sites for establishment and growth of tree species like western hemlock that can accelerate the development of late-successional forest conditions, the researchers believe.

“Our results provide scientific support for nonuniform and patchy thinning practices,” Spies says. “Many national forest managers are incorporating gaps as part of thinning prescriptions designed to diversify dense plantations and accelerate development of late-successional conditions. Research studies with the same objectives are incorporating gaps in treatments in a wide range of stand ages.” Jim Mayo, silviculturist with the Willamette National Forest, notes that this gap study is one of

the few sources of information on gap dynamics and has greatly helped managers as the emphasis has shifted from commercial thinnings to increase timber yields to methods for increasing complexity and diversity.

Uneven-aged management techniques can be improved by information from the gap studies; for example, uneven-aged management designed to maintain Douglas-fir in moist hemlock-zone forests would have to rely on group selection and accommodate a mix of species, Gray explains. Availability of seed sources and suitable microsites will remain critical constraints to successful tree establishment; however, gaps created by management may require underplanting for successful tree establishment.

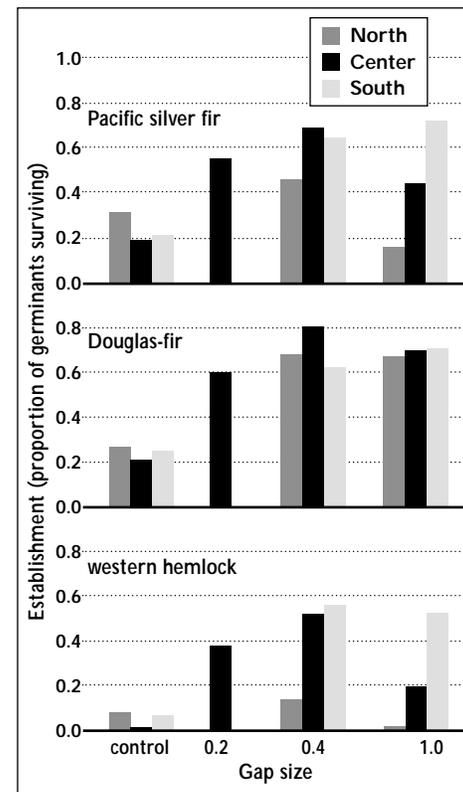
The pervasive nature of weedy species is also highlighted. Even relatively small disturbances within mature forests can provide temporary footholds for invasive species, Spies says. If they are to be controlled, the effects of canopy gaps on their spread cannot be ignored.

The results of gap research were used in the Northwest Forest Plan to show that gaps formed by natural disturbances are an integral part of the forest and should not be viewed as something detrimental to the dynamics of the forest ecosystem, he adds.

Thus, the tree falling in the forest—for ecologists—no longer raises the question of whether it makes a noise. Rather, it is a question of how big a hole it pokes in the forest and how lasting an impact it might have.

FOR FURTHER READING

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▲ Seedling establishment after two growing seasons for three species by gap size and within-gap position.

STATION LAUNCHES NEW PUBLICATION

Science Update, a 12-page color publication, offers scientific knowledge for pressing decisions about controversial natural resource and environmental issues. The first issue, published in May 2002, can be found online at the PNW Research Station Website at www.fs.fed.us/pnw.



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