

Gap-Based Silviculture in a Sierran Mixed-Conifer Forest: Effects of Gap Size on Early Survival and 7-year Seedling Growth¹

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Abstract

Experimental canopy gaps ranging in size from 0.1 to 1.0 ha (0.25 to 2.5 acres) were created in a mature mixed conifer forest at Blodgett Forest Research Station, California. Following gap creation, six species were planted in a wagon-wheel design and assessed for survival after two growing seasons. Study trees were measured after seven years to describe the effect of gap size on early growth of planted trees. Giant sequoia had the lowest mortality (2.4 – 5.0 percent), sugar pine, incense-cedar, ponderosa pine, and Douglas-fir all had comparable levels of mortality (5.8 - 18.9 percent), and white fir had the highest level of mortality (35.7 – 47.2 percent). To rank candidate models according to goodness of fit while penalizing for model complexity, we used an information-theoretic approach using Akaike Information Criteria. An asymptotic fit of height growth to gap size was most commonly selected as the best model among a set of feasible a priori candidate models, although there was some model parity. As gap size increased, height gains tended to diminish between 0.3 and 0.6 ha (0.75 to 1.5 acres). Shade tolerance classifications did not predict relative mortality levels or functional responses of height growth to gap size.

Introduction

Society places great demands on forests, managing them through the application of silviculture, to provide highly valued financial and conservation assets. As Kimmins (2002) notes, however, the rate of change in society's expectation of forests outpaces the scientific foundation to accommodate these new demands. For example, in the American West, social, political, and ecological concerns about single-cohort silvicultural systems have motivated demands for multi-cohort systems, which more closely approximate natural forest dynamics (O'Hara 2001), before methods for sound implementation have been developed, or their effects assessed.

Gap based silviculture, i.e., group selection, is one multi-cohort system in particular that has been proposed as a promising regeneration method, capable of achieving the multiple expectations of forest management. In theory, gap based silviculture mimics the structural diversity created by fine scale natural disturbances, resulting in canopy gaps (Smith et al. 1997). In practice, it is often perceived as a

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compromise approach for landowners aiming to avoid alleged environmental degradation associated with clearcuts and assumed limited productivity associated with single-tree selection (Bliss 2000). Management practices incorporating gap based silviculture have been proposed as a means for achieving a wide variety of objectives, including ecological restoration (Storer et al. 2001), maintenance of species diversity (Hamer et al. 2003, Lahde et al. 1999, Schutz 1999), and management of endangered species habitat (USDA Forest Service 1995). Gap based silviculture has recently been included in proposals for managing forests across regional scales for use within a wider framework of management, where the objective is maintaining fire-adapted forests (e.g. Herger-Feinstein 1998, USDA Forest Service 2003, USDA Forest Service 2002). However, scientific information to support the management decisions to implement these proposals is often limited.

A major source of uncertainty rests with the details of implementing a gap harvesting regime (Webster and Lorimer 2002). Of primary concern is the cost in terms of reduced growth productivity associated with the high edge-to-interior ratio of smaller openings (Bradshaw 1992, Dale et al. 1995, Laacke and Fiske 1983, Leak and Filip 1977). To address this concern, much of the research involving artificially created gaps has focused on the appropriate (often minimum) opening size that meets management objectives, particularly successful regeneration and growth of desired species within openings (Coates 2000, Gray and Spies 1996, Leak and Filip 1977, Malcolm et al. 2001, McDonald and Abbott 1994, McGuire et al. 2001, Van Der Meer et al. 1999, York et al. 2003, York et al. 2004). Still, the question of what is the “best” opening size, one that achieves the multiple promises of gap based silviculture, remains largely unanswered for even well-studied forest ecosystems.

To demonstrate an experimental approach for guiding local adaptive management decisions, and to provide specific insight into the capacity for gap-based silvicultural regimes to promote regeneration and growth in a western conifer forest, we established a manipulative experiment using artificial gaps and planted seedlings. Using treatments that remove competition between trees and from non-tree vegetation, we track the survival and early growth of planted trees, as it varies by species, within-gap position, and gap size. Here, we present results quantifying relative species performances in terms of seedling survival after two years and height growth through the first seven years after gap creation.

Methods

Study Site

Blodgett Forest Research Station (BFRS) is located on the western slope of the Sierra Nevada mountain range in California (38°52'N; 120°40'W). The study area lies within BFRS at an elevation between 1220 and 1310m. The climate is Mediterranean with dry, warm summers (14 to 17 °C) and mild winters (0 to 9 °C). Annual precipitation averages 166 cm, most of it coming from rainfall during fall and spring months, while snowfall typically occurs between December and March. The soil developed from granodiorite parent material and is highly productive for the region. Heights of codominant canopy trees typically reach 27 to 34m in 50 to 60 years (BFRS 2003). Olson and Helms (1996) provided a detailed description of BFRS, its management, and trends in forest growth and yield.

Vegetation at BFRS is dominated by a mixed conifer forest type, composed of variable proportions of five coniferous and one hardwood tree species (Laacke and

Fiske 1983, Tappeiner 1980). Native tree species include white fir (*Abies concolor* [Gord. & Glend.] Lindl. Ex Hildebr.), incense-cedar (*Calocedrus decurrens* Torr.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*), sugar pine (*Pinus lambertiana* Dougl.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), and California black oak (*Quercus kelloggii* Newb.). In harvested openings, BFRS also plants giant sequoia (*Sequoiadendron giganteum* [Lindl.] Buchholz), a species that is not present in the study area, but in the past had an expanded range that encompassed BFRS (Harvey 1985). Treatments for this study were all located on the same, north-facing slope (10-25 percent). Like much of the mixed conifer forests in the Sierra Nevada range (Beesley 1996), the study area was clearfell harvested for timber extraction in the early 1900's and allowed to regenerate from sparse residual trees. Nearly a century following this disturbance, young-growth stands at BFRS have developed to form a continuous mixed species canopy, averaging 35m in height and 83 m²/ha in basal area (BFRS 2003).

Experimental Design

Experimental treatments were designed to isolate the factor of opening size and the potential influence it may have on seedling growth within the openings, as well as on the mature forest (i.e. matrix) between the canopy openings over time. Care was taken to ensure a balanced design, so that each species was represented with the same density evenly throughout the gaps. The experiment involved a regeneration treatment (the harvest of the gaps and planting of seedlings), and a series of maintenance treatments designed to minimize confounding factors of non-tree and inter-tree competition. Clearing the harvested areas of debris and then planting seedlings reduced the degree of micro-site heterogeneity that could obscure gap size and position effects (Gray and Spies 1997). Four circular opening sizes (0.1, 0.3, 0.6, and 1.0 ha), each replicated three times, were harvested in 1996 and planted with an even mix of six species (Douglas-fir, giant sequoia, incense-cedar, ponderosa pine, sugar pine, and white fir). The ratios of gap diameters to the surrounding canopy heights for these sizes from smallest to largest are 1, 1.8, 2.6, and 3.2. Seedlings were planted along rows with a wagon wheel design, each species planted along “spokes” extending from the drip lines into the opening centers in cardinal and inter-cardinal directions. Douglas-fir, incense-cedar, white fir, and ponderosa pine were planted from bare root stock. Sugar pine and giant sequoia were from container stock. Seedling sizes were similar for all species at the time of planting. Non-tree vegetation was suppressed throughout the openings through the first three years after planting, and study trees were thinned from 3m spacing to an average of 4.5m spacing after the 7th growing season to avoid inter-tree competition. More information on findings of within-gap spatial variation in seedling growth, as well as further details of the treatments and layout design, were given by York et al. (2004).

Measurements

To assess the capacity for successful artificial regeneration within this gap regime, a mortality survey of all planted seedlings was conducted after the second growing season. For describing height growth responses to gap size, the experimental unit is each gap (n = 12). All study trees within the gaps were measured for height after the 7th growing season (n = 2440). In one of the 0.1 hectare gaps, Douglas-fir and white fir seedlings experienced high mortality where two seedling rows overlapped with a high water table near the edge of the gap. Typically, swampy areas like this would not be converted to gaps artificially and are therefore considered

unrepresentative of our intended study domain. Mean heights for Douglas-fir and white fir from this gap were therefore not included in the analysis.

Data Analysis

In accordance with our whole-gap level of inference, percent mortality was calculated for each gap ($n = 12$) for each of the six species. To explore gap size effects on mortality, standard linear regressions were used, with gap size as the independent variable, and percent mortality per gap as the dependent variable. Evidence of a gap size effect on mortality is confirmed by the probability of the regression line's slope differing from zero ($\alpha = 0.05$). To compare how overall survival differed between species, given the gap sizes used in this gap regime, mean percent mortality and 95 percent confidence intervals of the means are used for species comparisons. The gap size range used here represents the range used to define group selection regeneration method in the California Forest Practice Rules.

To assess the fine-scale relationship between opening size and within-gap tree height growth at year seven, we relied upon an information-theoretic approach to select an appropriate model of the data from a set of a priori candidate models. Candidate models (*table 1*) were selected to represent distinct and feasible biological realities. Their justifications are derived from either expectations generated by results from previous measurements or other studies, or from expected growth responses to the environmental gradients generated by the range of gap sizes, i.e., growth responses to changes in light and soil moisture availability. Candidate models were also both relatively parsimonious and had an implication for management. In other words, *bona fide* models (*sensu* Johnson and Omland 2004) had few parameters in order to maximize their application elsewhere, and they had realistic potential for guiding management decisions about appropriate opening sizes for meeting given objectives. Our inference, therefore, directly corresponds to the ranking of models and their associated strengths of evidence, given the data and set of models considered. Because of the small sample size ($n=12$), the number of candidate models was limited to four (Burnham and Anderson 2002).

We use the concept of shade tolerance to build a priori expectations for the model selections, and thereby assess the practical value of shade tolerance in predicting species' growth responses within gaps. The shade tolerance concept is widely used in categorizations of species into successional niches, but its significance has been criticized because the concept fails to incorporate drought tolerances that are usually not correlated with shade tolerances (Coomes and Grubb 2000). Those species considered to be highly responsive to varying magnitudes of light levels with respect to growth (giant sequoia and ponderosa pine [McDonald 1976, Schubert 1962]) are expected to conform to a power function, responding steeply and monotonically to the increased light levels across the range of gap sizes. The species less sensitive to light availability (white fir and incense-cedar [Minore 1988]) are expected to fit the more parsimonious models (power or asymptotic) with flat curves. The intermediate species (Douglas-fir and sugar pine [Oliver and Dolph 1992]) are expected to be relatively sensitive to gap size around a narrow range, corresponding to a logistic fit.

To rank the models according to goodness of fit, while penalizing for model complexity, we used a modified Akaike's information criterion (AIC), derived by Sugiura (1978). The modified AIC incorporates a bias-correction term to account for

small sample:parameter ratios among the alternatives. Our model alternatives have ratios of 12:2 for the asymptotic and power functions, and 12:3 for the quadratic

Table 1 - *A priori model alternatives and their implications for the relationship between mean tree height within openings and opening size.*

Model alternative	No. of parameters	Biological implication	Management implication
1. Asymptotic (Michaelis-Menten)	2	Heights increase with opening size and then level off above a certain opening size.	Above a threshold, increases in opening size return comparatively little in terms of increased height growth.
2. Quadratic	3	Heights increase with opening size and then decrease in the larger opening sizes.	Larger opening sizes can have a negative effect on height growth.
3. Logistic	3	Heights rapidly increase above an opening size threshold and then level off.	Height is very sensitive to opening size around a narrow range. Below a threshold, severe height suppression occurs.
4. Power	2	Heights increase monotonically, but the rate of increase diminishes across the range of opening sizes.	Seedling height is maximized in the largest opening size, although returns in height are diminishing.

and sigmoidal functions. The differences in AIC values are used to assess the level of empirical support, where differences of less than two are considered to have substantial support (Burnham and Anderson 2002). To evaluate candidate models in relation to the highest ranked model, the AIC values are transformed to Akaike weights and normalized to sum to one. The weights are interpreted as the likelihood that within the limits of the data and the set of alternatives, the given model is the most appropriate choice. The application of AIC for statistical inference in ecological studies is described in detail by Anderson et al. (2000) and Johnson and Omland (2004).

Results

No effect of gap size on % mortality at the gap level was detected for any of the species. High variability in survival between the 12 gaps, however, caused power of detection to be low (<0.27). Despite gap-to-gap variability, there were clear differences in mean % mortality per gap between the species when comparing means and confidence intervals. Giant sequoia had the overall lowest mortality (CI95 percent = 2.4 - 5.0 percent). Sugar pine (CI95 percent = 6.6 - 12.4 percent), incense-cedar (5.8 - 14.2 percent), ponderosa pine (8.9 - 18.4 percent), and Douglas-fir (9.1 - 18.9 percent) all had comparable mortality levels. White fir had considerably higher mortality (35.7 - 47.2 percent).

For all species, height increased with gap size (*fig. 1*). An asymptotic fit was the highest ranked model for every species except Douglas-fir, which had the most

support for a power function and a low level of support for an asymptotic model (table 2). For four of the six species, there was parity among the candidate models

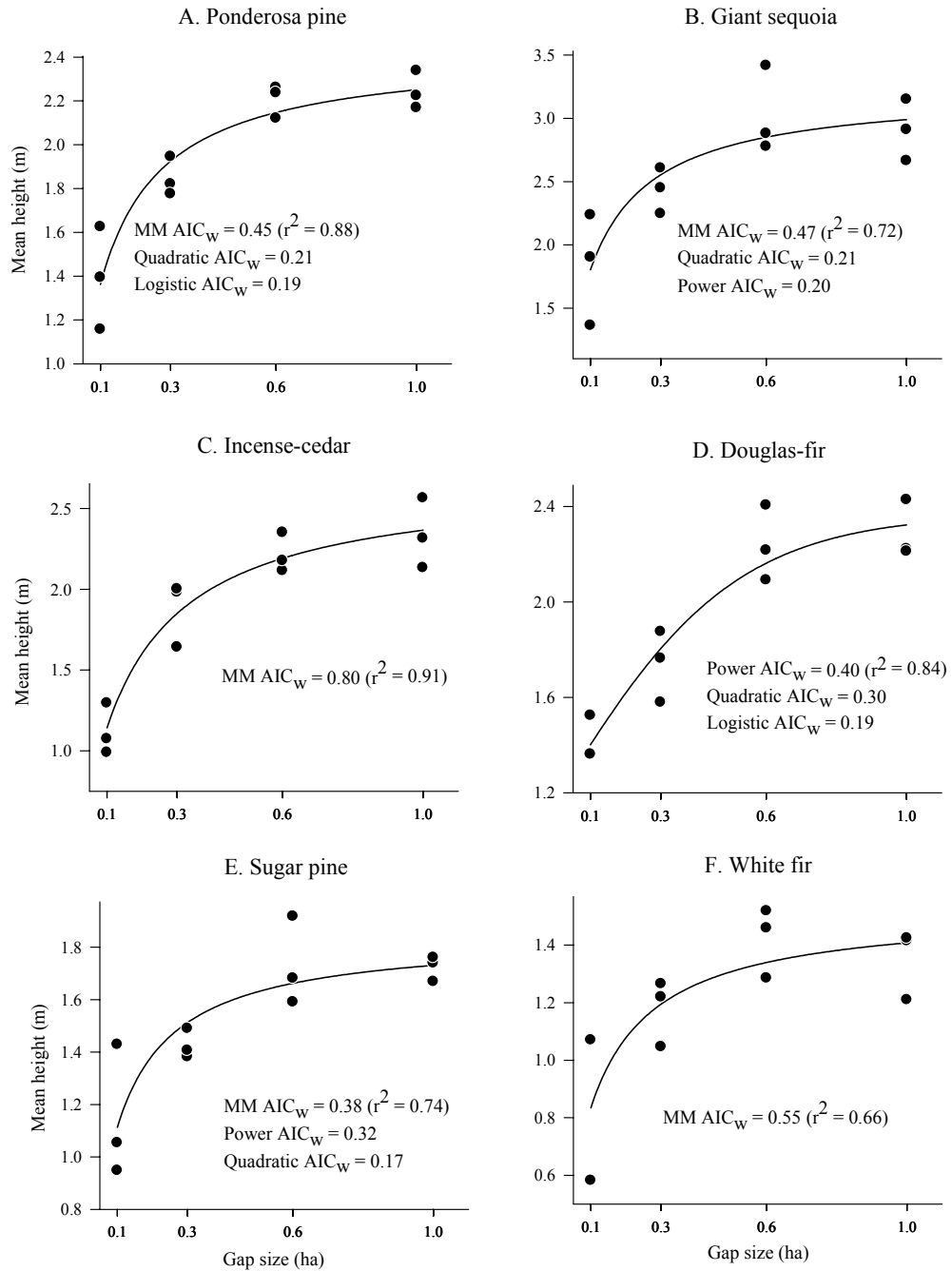


Figure 1 - Year 7 functional height responses to gap size in experimental gaps at Blodgett Forest, CA. Curves are shown for the highest ranked models. Akaike Information Criteria weights (AIC_w) are given for models with substantial empirical support (MM = Michaelis-Menton asymptotic curve). Y-axes are presented at different scales to display species-specific patterns.

for selecting a discriminating pattern of influence of gap size on growth, and no single model was consistently ruled out as a plausible alternative across all species. Douglas-fir, giant sequoia, ponderosa pine, and sugar pine growth patterns each had substantial support for three of the four models considered (table 2). Incense-cedar and white fir model selections had relatively strong support for an asymptotic fit.

Table 2--Model ranks using Akaike Information Criteria. K_i = number of parameters in model ranked i ; AIC_i = Akaike Information Criteria; Δ_i = absolute difference ($AIC_i - AIC_{i=1}$); w_i = Akaike weight (relative likelihood of model given the data and other candidate models.)

Model ranks	K_i	AIC_i	Δ_i	w_i	Ratio of ranks, w_1/w_i
Douglas-fir					
1. Power	2	63.7	0.0	0.40	
2. Quadratic	3	64.3	0.6	0.30	1.3
3. Logistic	3	65.2	1.5	0.19	2.1
4. Asymptotic	2	66.4	2.7	0.10	4.0
Giant sequoia					
1. Asymptotic	2	85.6	0.0	0.47	
2. Quadratic	3	87.2	1.6	0.21	2.2
3. Power	2	87.3	1.7	0.20	2.4
4. Logistic	3	88.3	2.7	0.12	3.9
Incense-cedar					
1. Asymptotic	2	70.0	0.0	0.80	
2. Logistic	3	73.7	3.7	0.13	6.2
3. Quadratic	3	76.0	6.0	0.04	20.0
4. Power	2	76.3	6.3	0.03	26.6
Ponderosa pine					
1. Asymptotic	2	65.6	0.0	0.45	
2. Quadratic	3	67.1	1.5	0.22	2.1
3. Logistic	3	67.4	1.8	0.19	2.4
4. Power	2	68.0	2.4	0.14	3.2
Sugar pine					
1. Asymptotic	2	68.7	0.0	0.38	
2. Power	2	69.0	0.3	0.32	1.2
3. Quadratic	3	70.2	1.5	0.17	2.2
4. Logistic	3	70.9	2.2	0.13	2.9
White fir					
1. Asymptotic	2	64.5	0.0	0.55	
2. Power	2	66.9	2.4	0.17	3.2
3. Quadratic	3	67.0	2.5	0.17	3.2
4. Logistic	3	67.7	3.2	0.11	5.0

Discussion

Ostensibly, gap based silviculture creates steep resource gradients within gaps that can successfully regenerate a wide variety of tree species. Reluctance by managers to accept this concept, however, arises mainly from uncertainty with the ability of shade intolerant species to survive in gaps that are partially shaded by the surrounding matrix forest. In this study, there was no alignment of overall survival with shade tolerance rankings. In fact, the shade-intolerant giant sequoia had the best survival, while shade tolerant white fir had the poorest survival. With some extra planting effort, we indeed successfully regenerated all six species. By planting two individuals at each planting spot, and by transplanting seedlings from nearby reserve

areas where both seedlings had died, nearly every planting spot (>95 percent) had a live individual by year three when the first measurements were taken.

The lack of detectable effect of gap size on mortality contrasts with the marked effect of gap size on growth. Shade tolerance rankings helped little in predicting survival by gap size. The mortality levels that we found in these gaps is similar to our observations in larger plantations at Blodgett Forest Research Station. Hence, planted seedling mortality appears to be a species-specific trait, rather than an effect of gap size in gaps above 0.1 ha in this study area.

Height growth responses to gap size consistently diminished as gap size increased, typically leveling off or decreasing in rate beyond a size range from 0.3 to 0.5 ha. Early height growth suppressions could have therefore been avoided in this case with a gap regime consisting of gap sizes above this size range. Because the absolute differences in AIC values were not large (*table 2*), the choice of models can generally be judged to be appropriate. Burnham and Anderson (2002) subjectively suggest an absolute difference of less than two as providing “substantial” empirical evidence for an appropriate model. Using this threshold, every model was appropriate at least twice across the six species. At the same time, the near-unanimity of the asymptotic fit as the selected model (when testing the models against each other and the ruling out of other models in incense-cedar and white fir) give support to the primacy of the asymptotic pattern. Despite testing of the asymptotic fit against “better” models compared to the year-5 analysis, the asymptotic fit continues to be an appropriate quantitative description of the effect of gap size on tree growth.

The resulting model rankings and their strengths of evidence run largely counter to expectations derived solely from tolerance rankings. Primacy of the asymptotic fit over other candidate models was evident for both white fir and incense-cedar. Some ambivalence between quadratic and asymptotic models was expressed after the fifth year for white fir (York et al. 2004), but a resolution of pattern appears to be occurring by the seventh year. Although the asymptotic fits were expected according to their shade tolerance classifications, both species were surprisingly sensitive to gap size in terms of absolute growth. White fir and incense-cedar were the most sensitive to gap size in terms of relative change in stature between the smallest and largest gap sizes. In other words, the functional role of gap size (suppression in small gap sizes, followed by a saturating effect in larger sizes) was consistent with expectations for shade tolerant species. But the magnitudes of the observed pattern’s parameters (steep slope and large asymptote compared to y-intercept) were not expected for the shade tolerant species.

For giant sequoia, there was twice as much strength of evidence for an asymptotic model than the next closest model (quadratic). Nevertheless, the quadratic and power models had enough strength of evidence to make it difficult to rule out their plausibility in contributing to the observed pattern, especially in the larger gap sizes. Whether the 0.6 ha size is a leveling-off point (asymptotic), maximum (quadratic), or mid-point (power) would be more clear with incorporation of larger gap sizes. Competition from surrounding gap border trees is certainly an influence on overall giant sequoia height, as its sensitivity to reductions in both soil moisture and direct light availability effectively reduce a large portion of the gap area where maximum growth occurs (York et al. 2003). Within-gap edge zones reduce giant sequoia growth on both pole-facing (light and water limiting) and equator facing (water limiting) edges. This co-limitation in giant sequoia is in contrast to ponderosa pine, which tends to partition growth along a single light gradient. The area where

rapid growth occurs for ponderosa pine is expanded closer to equator-facing edges of gaps where direct light tends to be relatively abundant in small gaps of temperate forests (Canham et al. 1990, Minkler et al. 1973).

The power function, predicted to fit well for ponderosa pine because of rapid increases in growth responding to higher levels of light, was instead the lowest ranked model. The predicted model for sugar pine, a logistic fit, was likewise ranked last. Given the data, and because of the high degree of plausibility of each candidate model, a best model could not easily be distinguished for the two pine species. Functionally, however, they are similar in terms of biological and management implications. For both species, height growth diminishes considerably near 0.3 ha and does not increase monotonically. Unlike the other species, the least amount of support was given to an asymptotic fit for Douglas-fir. Height increased sharply between 0.3 and 0.6 ha, dividing the gap sizes into two classes and most clearly defining a size threshold where significant height suppression can be avoided. However, more data from smaller gap sizes is necessary to test whether the threshold is distinct enough to result in a logistic fit as an appropriate model.

Many considerations besides maximization of growth will contribute to the decision of gap size and density in a gap-based silvicultural regime. A diversity of practice in gap size creation should indeed be central in achieving the purpose of structural diversity across forests. The patterns that we found are expected to vary by latitude, gap shape, matrix disturbance history, and time since gap creation. Tracking growth in this study over time and implementing similar studies elsewhere that incorporate both seedling and matrix growth may help in describing commonalities and differences in patterns across various forest types.

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