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CROWN ASYMMETRIES OF TREES ON THE EDGES OF LOGGING GAPS IN A FOREST IN GUYANA

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Active foraging of tree branches for light and space can result in crown asymmetry. By opening canopy gaps, selective logging may increase the prevalence of trees with asymmetrical crowns and the extents of their asymmetries. Crown asymmetry is relevant to forestry insofar as it may stimulate bole curvature, decrease the range of angles over which trees can be directionally felled, increase rates of natural tree fall, and create dangerous conditions for forest workers. In a forest in Guyana that was selectively logged 23 years prior to our study, we evaluated the asymmetries of crowns of trees on the boundaries of mapped felling gaps. For 192 trees ≥ 20 cm diameter, we measured crown radii into and away from 56 canopy gaps. Assuming that tree crowns were symmetrical at the time of gap creation, we estimate the rate of lateral crown expansion into gaps as the difference between crown radii into and away from the canopy opening. We then compared apparent rates of lateral crown expansion into gaps by tree species, gap size, and stem diameter growth rates. We found that 83% of tree crowns were wider on the gap side than into the closed canopy forest, with crowns on average 2.1 m wider towards canopy gaps. Rates of gap-ward crown extension were faster among long-lived light-demanding pioneer species than in more shade tolerant climax species. Among trees ≥ 20 cm diameter at the time of gap creation, stem growth rates are positively but only weakly correlated with crown asymmetry.

Keywords: Selective logging, forest dynamics, canopy gaps, tropical silviculture, tree architecture

INTRODUCTION

The sizes and shapes of tree crowns respond to changes in the availability of light as well as mechanical interactions with neighbours (Putz et al. 1984, Fish et al. 2006), but also reflect intrinsic genetic, morphological, and higher-order phylogenetic characteristics (Hallé et al. 1978). The principal cause of changes in light availability in closed canopy forests is canopy gap creation by trees that die standing, fall, or are felled (e.g. Runkle 1982, Brokaw 1985, Denslow 1987, Elias & Dias 2009). Prior studies on canopy gaps mostly emphasised their effects on regeneration and tropical tree diversity (e.g. Hartshorn 1978, Rose 2000) with few studies that evaluate canopy tree responses to canopy gap creation (van der Meer 1995, Young & Hubbell 1991, Ruslandi et al. 2015). Here we study the crown response of canopy trees over a 23-year period after gap creation by selective logging in a tropical forest managed for timber.

In response to high light intensities and decreased crown abrasion, trees on the margins of canopy gaps typically extend their branches into canopy openings (e.g. Trimble & Tryon 1966, Hibbs 1982, Runkle & Yetter 1987). As these trees actively forage for light and space (Muth & Bazzaz 2002), their crowns become asymmetrical (Young & Hubbell 1991). The extent to which trees develop asymmetrical crowns varies with factors including growth rates, crown architecture, and biomechanical properties (Valladares & Niinemets 2008, Olivier et al. 2016, Lu et al. 2020).

Quantifying the rate of development of tree crown eccentricity in response to canopy gaps can provide insights into the dynamics of both natural forests and those managed for timber. This phenomenon is important because trees with crowns that are heavier towards gaps suffer increased likelihoods of toppling into the preexisting openings, thereby expanding the area of disturbed forest (Young & Hubbell 1991). Eccentric tree crowns may also pose challenges for forest managers where selective logging guidelines call for directional felling to reduce stand damage, protect future crop trees, promote worker safety, and facilitate timber yarding insofar as crown asymmetry limits the range of directions over which trees can be safely felled (Putro et al. 2015).

This study explores the crown characteristics of canopy trees on the edges of mapped gaps 23 years after the gaps were opened by selective logging of a forest in central Guyana. We hypothesised that logging gaps promote asymmetrical crown expansion and that this response varies among functional plant groups and increases with rates of stem diameter increment and gap size.

MATERIALS AND METHODS

Study area

The study was conducted in mixed lowland tropical forest at Pibiri Biological Research Station (5º 13‘ N, 58º 48‘ W) in central Guyana where the mean annual temperature is 26 ˚C and annual rainfall is approximately 2700 mm year^{-1} with rainier periods in May–August and December–February (Boot 1996, Rose 2000). The forest is diverse but with patches dominated by *Chlorocardium rodiei* (greenheart) (van der Hout 1999, Roopsind et al. 2018. Tree canopy height averages 30–40 m, with emergent trees reaching 50 m. Average stem density of trees ≥ 20 cm DBH (stem diameter at 1.3 m or above buttresses) is 180 stems ha^{-1} (van der Hout 1999). We assessed crown asymmetries in 2017 in permanent sample plots that were selectively logged in 1994. Immediately post-logging, felling gaps were mapped (van der Hout 1999) and measured using the modified centre point method of Brokaw (1982).

Crown measurements and analysis

We measured the crown radii of trees ≥ 20 cm DBH located on the margins of 56 logging gaps that ranged 107–2352 m^2 when created in 1994, 23 years prior to our study. We excluded gaps < 100 m^2 because once gaps are closed by lateral crown expansion, development of crown asymmetry should cease. We also excluded trees with crowns fully exposed to both vertical and lateral illumination on all sides (i.e. emergent trees) and those affected by natural tree falls that occurred after the gaps were mapped. We sampled 192 gap-edge trees of 44 species.

We used gap maps drawn in 1994 by van der Hout (1999) to estimate rates of crown expansion over the intervening 23 years as the difference in crown radius into the gap, and in the opposite direction into the closed canopy forest (Figure 1). We assumed that the crowns were symmetrical at the time of logging or at least that there was no overall tendency for them to be wider in the direction of closed canopy forest. Our estimates are conservative if edge trees suffered, for example, felling-induced branch losses, but we excluded trees that showed obvious signs of having suffered major crown loss. We used QGIS open-source software to calculate gap perimeter lengths and gap areas that we then used as covariates in our statistical analysis of crown expansion rates. We also classified tree species into functional groups (i.e. pioneers, long-lived pioneers, and climax species) based on tree specific wood density (g cm^{-3}), seed mass, and adult stature (Arets 2005).

For a subset of trees for which long-term data on DBH increments were available (N = 150 trees), we evaluated whether the extent of crown asymmetry 23 years post logging correlated with individual tree growth rates, functional group, and gap size (m^2). All models were fit using the brms package in R with default priors, four chains with 2000 iterations per chain, and a warm-up of 1000 iterations.

RESULTS

The crown radii of gap-edge trees (N = 172) averaged 6.2 m (standard error, SE = 1.63 m) into gaps compared to 4.1 m (SE = 0.14 m) into the adjacent closed canopy forest (Figure 2). Assuming crowns were symmetrical prior

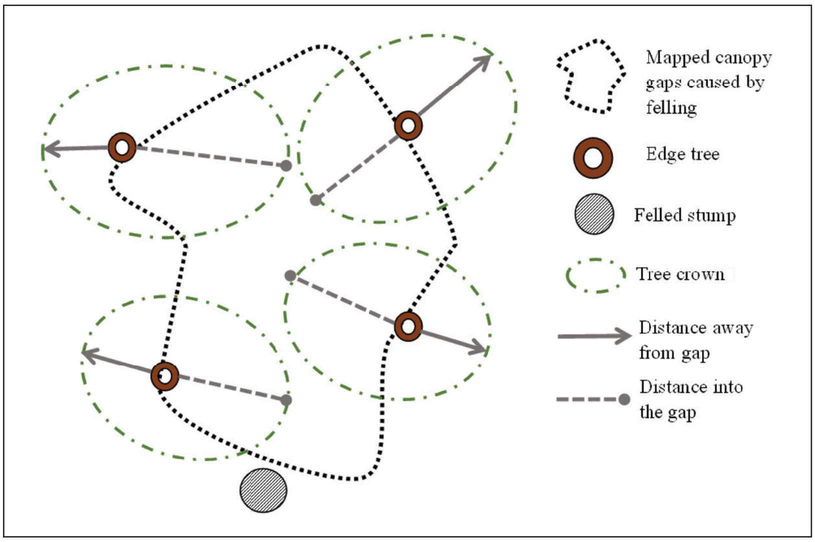

Figure 1 Illustration of the field method for assessment of tree crown width responses to a canopy gap created by selective logging in a closed canopy forest

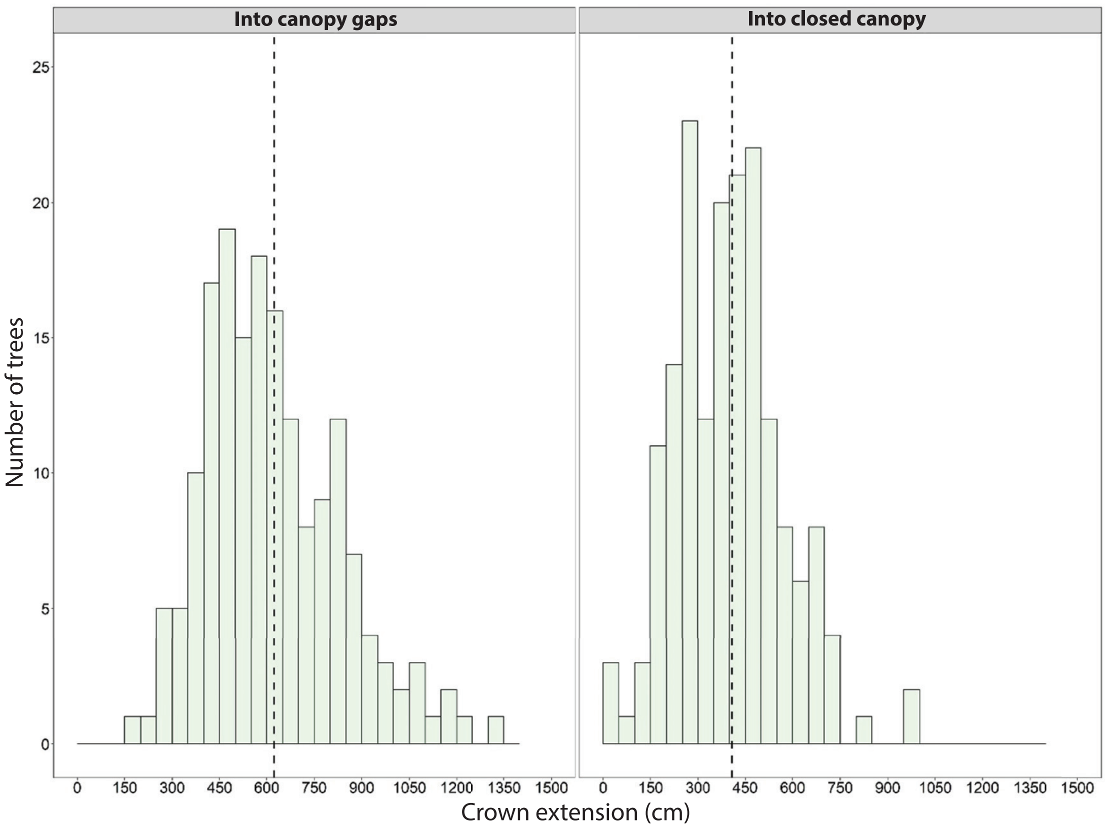

Figure 2 Crown extension of gap-edge trees (N = 172) into and away from canopy gaps 23 years after the gaps were created by selective logging of a closed-canopy forest in Guyana; dashed lines indicate average crown extension

to logging disturbance, crown extension into gaps was on average 9.3 cm year^{-1} faster than extension into the closed canopy forests.

Trees classified as climax species (N = 126 trees) and long-lived pioneers (N = 45 trees) showed gap-ward crown extension of 6.1 and 6.6 m relative to crown extensions of 4.2 and 3.6 m into the closed canopy forests respectively (Figure 3). Similarly, assuming that the crowns were initially symmetrical, the annual rates of crown extension into gaps of climax and long-lived pioneer species averaged 8.2 and 12.7 cm year^{-1} faster than into the closed canopy forest respectively. The best predictor of crown asymmetry was rate of stem diameter increment (Figure 4). Gap size was not related to the rate of development of asymmetrical crowns.

DISCUSSION

Twenty-three years after selective logging at our study site in Guyana, canopy gap-edge trees supported crowns that were on average 2.1 m wider towards the gap than into the adjacent forest. This response suggests active crown foraging for the light provided by the creation of canopy gaps (Muth & Bazzaz 2002). Similar results have been reported for both managed stands (Gillespie et al. 1994, Smith & Putz 2021, Forrester et al. 2013) and natural forests (Runkle & Yetter 1987). Lateral crown growth of gap-edge trees contributes to gap closure and affects tree regeneration (McCarthy 2001, Lu et al. 2015) with implications for future species composition and timber harvests.

In Guyana, tree crowns on the margins of canopy gaps expanded laterally 9.3 cm year^{-1} faster than they expanded in the opposite direction (i.e. into the forest). Since we measured differential and not absolute growth rates, our results are not directly comparable to other measures in the literature. This problem notwithstanding, the Guyana rates were slower than those reported for temperate hardwood forests by Trimble and Tryon (1966; 16–27 cm year^{-1}) and Runkle and Yetter (1987; 18 cm year^{-1}) but similar to the 6–14 cm year^{-1} reported by Hibbs (1982). One explanation for the apparently slow rate of crown expansion in our study site in Guyana is that trees on the Guiana Shield are notoriously slow growing due to extremely nutrient-poor soils (Roopsind et al. 2018).

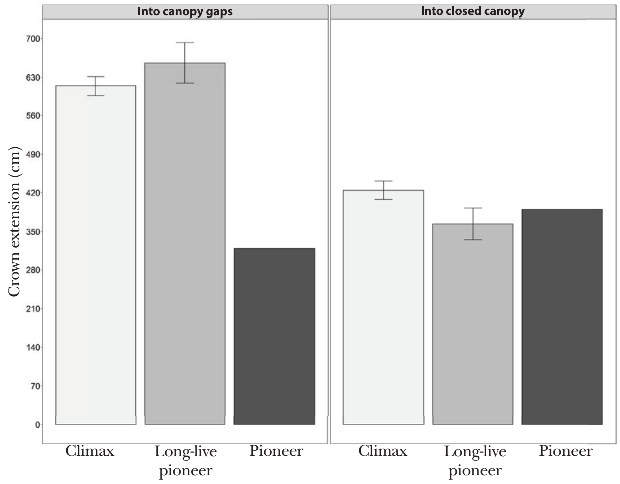

Figure 3 Lateral crown extension away from and into canopy gaps created by selective logging of trees classified into functional groups that include climax trees (N = 126), long-live pioneer trees (N = 45) and pioneer trees (N = 2); errors bars represent 1 standard error

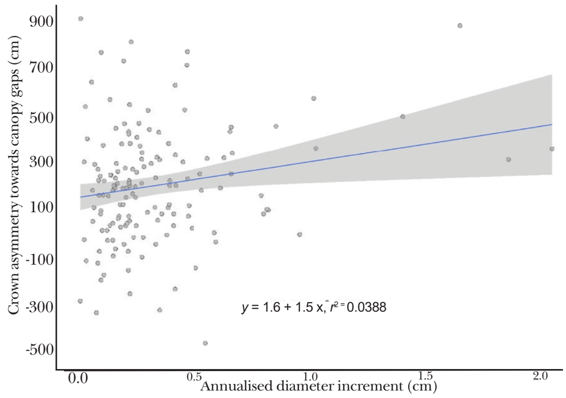

Figure 4 Relationship between annual rates of stem diameter growth (cm) and crown asymmetry for 150 trees 23 years after gap creation by selective logging; shaded bands are the 95% credible intervals

Lateral crown growth rate by functional groups, gap size and growth rates

Compared to shade tolerant climax tree species, long-lived pioneers species reportedly have large plastic response to increase light interception (Valladares & Niinemets 2008, Oliver et al. 2017). Our results support this contention insofar as the most common species in our study, *Chlorocardium rodiei* (N = 42) and *Lecythis confertiflora* (N = 27), both climax species, had average crown width differences of only 2.1 m compared to 3.1 m for the most common long-lived pioneer species (*Catostemma fragrans*, N = 16). Variation in rates of lateral crown growth among species and individuals indicate the inherent ontogeny, crown architecture and structure associated with different functional groups of canopy trees (Muth & Bazzaz 2002). For instance, pioneer species are rare along the edges of the gaps sampled as they tend to establish in areas with direct vertical light penetration (Boot 1996). As pioneer species tend to allocate resources for fast height growth to reach the canopy layer, they may invest less energy in horizontal crown expansion (Denslow 1987).

Although crown expansion rates in this forest did not increase with gap size, trees in other forests reportedly did (Runkle 1985, Cipollini et al. 1993, Bartemucci et al. 2002, Lu et al. 2015, Wenyan et al. 2022). While gap size and functional groups were not important predictors of crown expansion into gaps in Guyana, rates of stem diameter increment were positively but weakly correlated with rates of branch extension into gaps (Figure 4). We note that for every increase of 1 cm $year^{-1}$ in stem diameter over the 23-year observation period there was 1.47 m more crown expansion into gap than into the closed canopy forest, albeit with high variability (95% credible intervals: 0.21–2.69 m; Figure 4). Increased light availability in and around gaps most likely affected the growth of both stems and crowns with positive feedback as trees with larger crowns captured more sunlight.

Recognition of the crown asymmetry phenomenon is important for forest managers and ecologists as trees with unbalanced crowns are more likely to fall or drop branches in the direction of their heavy sides (Young & Hubbell 1991, Young & Perkocha 1994). Counterbalancing this tendency for gaps to expand (Lawton & Putz 1988) is the closure of gaps by the expansion of crowns of neighbhouring trees, as observed in this study.

CONCLUSION

The response of gap-edge tree crowns to increase availability of light and space was indicated by their development of asymmetrical crowns. While long-lived pioneer tree species seem especially capable of expanding their crowns into canopy openings, the weakness of the relationship between rates of stem diameter increments and crown expansion suggests that factors other than growth rates influence this phenomenon. These factors should be explored with remote sensing techniques for tree crown mapping.

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