FATES OF TREES AND FORESTS IN BOLIVIA SUBJECTED TO SELECTIVE LOGGING, FIRE, AND CLIMATE CHANGE

By

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To my family, friends, and especially my wife who struggled alongside me
– we made it

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LIST OF ABBREVIATIONS

IBIF	Instituto Boliviano de Investigación Forestal
LTSRP	Long-term silvicultural research plot.
CWD	Climatological water deficit
MCWD	Maximum climatological water deficit
OLS	Ordinary least squares
RIL	Reduced-impact logging
DI	Distributional Drought Index. Index of tree species' drought tolerance derived from stem density ratios between a dry site and La Chonta.
SDI	Seedling Drought Index. Derived from a seedling drydown experiment (Poorter and Markesteijn 2008); the number of days it took for a seedling to die after watering stopped.
SMALL TREES	Refers to trees in regeneration transects. Always <10 cm DBH.
LARGE TREES	Refers to trees in the biennial censuses. Always >10 cm DBH.
VPD	Vapor pressure deficit

Abstract of Dissertation Presented to the Graduate School
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FATES OF TREES AND FORESTS IN BOLIVA SUBJECTED TO SELECTIVE LOGGING, FIRE, AND CLIMATE CHANGE

By

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Tropical forests are under siege, but more attention is paid to their total removal (i.e., deforestation) than to their degradation (i.e., loss of values without loss of forest). Here the focus in on forests degraded by logging and fires, coupled with the less obvious impacts of climate change. I evaluated the impacts of these factors and their interactions on tree mortality, growth, and species composition in a transitional tropical forest in Eastern Bolivia. To understand how this forest responds to the direct impacts of controlled selective logging, I evaluated the patterns and rates of stand recovery in logging gaps and the fates of trees damaged by timber harvests.

To understand the effects of logging on carbon dynamics, I surveyed 60 logging gaps 8-9 years after reduced-impact logging. I found that newly-recruited trees in large gaps are less likely to be liana-infested than those in small gaps, and that trees on gap borders grew 0.15 cm/year more rapidly in diameter and harbored fewer lianas than trees away from gaps. Also, new recruits contributed more biomass to the recovery of large than small gaps. Finally, tree biomass in gaps was not detectably related to the proximity of other gaps.

Logging, drought, and fire as well as their interactions all influenced tree species assembly and forest structure over a 7-year observation period. Models of tree mortality and growth in response to these forces revealed that logging shifts tree species composition into assemblages that should be more tolerant of future droughts. This shift was evident in the increased survival rates of seedlings of drought-tolerant tree species but might be counter-balanced by the observed higher mortality rates of trees >10 cm DBH of species characteristic of relatively dry forests. While species composition shifted towards drought tolerance, forest structure did not: large trees in this forest suffered disproportionally from droughts. Increased vulnerability to droughts was more closely related to crown exposure than to DBH.

Finally, to clarify one longer-term impact of selective logging, I tracked the fates of trees damaged during the harvest for up to 8 years afterwards. While damaged trees initially suffered elevated mortality rates, those that survived 8 years after being damaged then exhibited similar mortality rates to undamaged trees. Over that same period, trees with damaged roots suffered particularly high mortality rates and trees with damaged crowns grew very slowly.

Taken together, these studies illustrate that the while responses of tropical forests to disturbance and stress are complex, some factors stand out as particularly important. Large trees suffer disproportionally from drought and while logging may favor seedlings of drought-tolerant species, larger trees characteristic of dry forests may not endure droughts better than those from wetter forests. While mitigating climate change, improved forest management interventions such as liana cutting may enable forests to recoup carbon emissions from logging quickly.

CHAPTER 1

ABOVE-GROUND BIOMASS RECOVERY IN AND NEAR 9-YEAR-OLD LOGGING GAPS: EFFECTS OF GAP SIZE, GAP PROXIMITY, AND LIANA INFESTATIONS

Introduction

Although most of the tropical forests that contain globally important carbon stocks are disturbed, most knowledge of this carbon pool is based on research in areas selected to be as pristine as possible. Here we focus on carbon stocks and fluxes in a tropical forest subjected to planned selective logging by trained and supervised crews followed by silvicultural treatments. In particular, we investigate the effects of logging gaps and liana infestations on rates of carbon sequestration.

For at least several years after selective logging, tropical forests are known to grow more quickly than un-logged forests both in terms of overall basal area increments and individual tree growth rates (e.g. Toledo et al. 2010). Less is known about intra-stand variability in growth rates (but see Herault et al. 2010, Ruslandi et al. 2012), even though the effects of selective logging are known to be spatially variable (e.g., Medjibe et al. 2011, Medjibe et al. 2013). Here we examine the contributions to stand-level biomass stocks by above-ground biomass accumulation of trees growing within and adjacent to logging gaps.

Lianas are often abundant in treefall gaps where they benefit from increased light and decreased root competition (Putz 1984). Lianas also reportedly increase in abundance as gap size increases, as observed by Babweteera et al. (2000) in Uganda and Gerwing and Uhl (2002) in the Eastern Amazon. Although this trend was not significant in the study by Broadbent et al. (2006) in the same forest as this one, they found that liana coverage increased during the first 19 months after logging, especially in the area of the fallen crown. The fact that crown zones developed greater liana cover than the area near the fallen bole may be a function of increased light availability in the former. While increased light would also favor increased growth of trees liberated by their over-topping competitors and new recruits, even liberated trees are unlikely to vertically out-grow liana infestations.

We hypothesized that the proportion of liana-infested trees, the degree of infestation of those trees, and the portion of a gap's top canopy layer covered by lianas all increase with gap size. Because closely spaced gaps are expected to be similar to single large gaps, we also hypothesized that these relations will hold for spatially clustered gaps. A linked hypothesis is based on the observation that although recruitment of pioneer trees usually increases with gap size, we expect that this relationship will be weak or decrease in the extremely liana-dense forest in which we work. If liana infestation and coverage do increase with gap size, we predict that biomass contributions from newly-recruited trees will decrease with gap size and where gaps are clustered.

To assess the effects of felling gaps on rates of post-logging biomass recovery, we tracked the fates of new recruits and nearby trees as a function of gap size, distances to the closest gap, liana loads, and time up to 9-years post-logging (Figure 1 - 1). We used these data on growth, ingrowth, and mortality to estimate the portions of post-logging increases in growth attributable to growth of new recruits in felling gaps and trees on gap margins.

Trees on the borders of felling gaps may suffer from a number of growth-reducing conditions including higher rates and intensities of liana infestation (Putz 1984) as well as felling and skidding damage. On the other hand, they may benefit from release from both above- (light) and below-ground (water and nutrients) competition. These responses would influence the trajectory of biomass recovery in logging gaps. In a French Guianan forest with fewer lianas than ours, trees responded to gap-border conditions with increased growth rates (Herault et al. 2010). In biomass terms, if the benefits of bordering gaps outweigh the costs, then gap-border trees may initially contribute more to post-logging carbon stock recovery than new recruits, whereas new recruits and their successors may assume that role later in gap recovery.

Methods

Site Description

This study was conducted in the Long-Term Silvicultural Research Plots (LTSRPs) within the forestry concession of Agroindustria Forestal La Chonta, 30 km east of Ascención de Guarayos, Bolivia (15°47'S, 62°55'W; hereafter, La Chonta). This semi-deciduous forest receives an average of 1580 mm of precipitation annually with 4 months (May-September) that each receive <100 mm (Peña-Claros et al. 2008a). The soils of La Chonta are largely nutrient-rich inceptisols (Quintero, in prep). The concession's terrain is undulating with some granitic outcrops (i.e., inselbergs), none of which occur in the permanent sample plots. In terms of both climate and tree species composition, this forest is transitional between wet Amazonian forests to the north and dry Chiquitano forests to the south; it falls within WWF's Global 200 Southwestern Amazonian Moist Forest region and is located on the edge of the Amazon Basin. Approximately 30% of the tree species that grow to be >10 cm DBH (stem diameter at 1.4 m or above buttresses) are deciduous (Peña-Claros et al. 2008a). Another noteworthy feature of La Chonta is the abundance of lianas. In unlogged forest, 73% of trees >10 cm DBH reportedly carry at least one liana >2 cm DBH, infested trees carry

9.3 lianas on average, and 35% of tree crown areas are liana covered (Alvira et al. 2004).

The LTSRPs were established in 2000-2001 to investigate the effects of different methods and intensities of forest management. The permanent plots include three blocks of four 27 ha treatments: control (no logging); normal logging; improved logging; and, improved logging with intensive post-logging silvicultural treatments. The plots were logged in 2001-2002 and all trees >40 cm DBH in the entire plots and for trees >20 cm and >10 cm DBH in subplots were censused in one pre-logging census and then in 2002, 2003, 2005, 2007, and 2009 (Figure 3 - 1). Per good logging practice, lianas in felled trees were cut approximately 6 months prior to logging in all logged plots. That lianas were cut from felled trees has special importance for this research since many of our hypotheses either touch on or center on lianas. Some of our results in this regard may be specific to managed forests where liana cutting is performed.

Framework

To disaggregate the carbon dynamics of logging gaps (Figure 1 - 2), we classified each tree on the basis of its status, origin, and potential carbon contribution to carbon stock recovery as follows (Figure 1 - 1):

- Logged tree: Carbon losses due to biomass left in the forest (i.e., stumps and crowns), wood waste in the mill, and delayed emissions from wood products.
- Collateral mortality: Carbon loss due to mortality from collateral damage to trees in and around logging gaps.
- New recruits: Carbon gain via trees germinated from seed after logging and via competitive release of advanced regeneration.
- Remnant trees: Changes in carbon stocks of trees that survived, often with substantial damage, within felling gaps.

- Border trees: Changes in carbon stocks of trees adjacent to felling gaps. Reductions in above- and below-ground competition may stimulate increased growth but growth may decrease while mortality increases in response to increased liana loads and logging damage.

Field Surveys

Canopy gaps created by 60 felled trees were mapped 1-4 months after logging in 2001-2002 (Ohlson-Kiehn et al. 2003). In July 2010 (8-9 years post-logging) we re-surveyed these gaps and measured all trees > 10 cm DBH in an 8 m-wide strip plot along the long-axis of the gap (usually corresponding to the felling direction). We also estimated canopy cover (0%, 1-25%, 25-<50%, 50-75%, and 75-100%) for each life-form (trees, lianas, herbs, palms, and ferns) at 5-m height increments to the canopy top along 4 transects that crossed in the gap center and extended 5 m into the forest beyond the gap edge. To re-locate gap borders, we assumed that each felled tree left a circular gap above the stump that was one-half the radius of the remnants of the crown on the ground (or one-third the radius of crowns for tree species with especially large crowns; Figure 1 - 3).

We identified to species all trees > 10 cm DBH in the strip plots and measured their DBH, x/y location, liana infestation of their crown (0 = 0%, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = >75%), estimated height, and assigned a crown exposure or canopy position class (1-5, Clark and Clark 1992). We relied on the judgment of the primary author (A.S.) and two experienced field workers (Angel Wicho and Ricardo Mendez) to determine whether each tree was present but <10 cm at the time of logging, regenerated after logging (regeneration), or was already >10 cm DBH at the time of logging (remnant). We then identified all trees previously measured in the census (DBH

>10 cm, >20 cm or >40 cm depending upon the subplot where the gap occurred) that were rooted within 5 m of the gap edge, and classified these as border trees.

Data Analyses

Liana infestations on trees inside gaps (recruits and remnants) were analyzed in two ways. First, we used stepwise ordinary least squares (OLS) regression to estimate the effect of gap size, sqrt(gap size), gap size^2, and log(gap size) as potential additive factors on the proportion of trees in the gap with a given liana crown infection class or above (>0, >1, >2, >3 and >4). For this model our unit of analysis is a gap. The second approach employed maximum likelihood methods to fit a multinomial distribution of probabilities that a tree would be in a particular liana infestation class. We allowed these probabilities to vary linearly with gap size. The multinomial model was:

$$p_i = a_i + b_i \cdot \text{gap size},$$
$$\Pr(p_i) = C \cdot p_i^{x_i}, \text{ and}$$
$$i = 0, 1, 2, 3, 4,$$

where p_i indicates the probabilities of a tree within a gap having a liana class from 0 (tree free of lianas) to 4 (crown covered with lianas), a_i are the corresponding intercept parameters for each linear equation fit by the maximum likelihood algorithm, b_i are the corresponding slope parameters fit by the maximum likelihood algorithm, C is a constant, and x_i is a vector of i Bernoulli trials (0/1 with a binomial error distribution) where the ith element = 1 where i = liana class of that tree and 0 otherwise. $\Pr(p_i)$ is the probability of that particular set of p_i's being correct given the data. The maximum likelihood algorithm generates a $\Pr(p_i)$ value for each observation of k individual trees, and it then attempts to minimize the negative log likelihood, $-\log(\sum_{j=0}^{k} \Pr(p_i))$.

Border tree liana infestation rates were analyzed in R (R Core Team 2012) using the following mixed and maximum-likelihood models as implemented in the lme4 package (Bates et al. 2011): liana infection class of tree ~ Normal(canopy_position + dbh + species_group, σ^2), where "~" means "modeled as a function of" (Crawley 2012). We use species groups established by Blate (2005a) on the basis of their rates of growth, mortality, and recruitment, and their responses to competition. We included species groups and DBH to account for the possibility that some groups and size classes are more prevalent on gap borders than others, and to see if lianas infested some species groups more than others. All predictors were scaled to be centered on 0 with a standard deviation of 1. In the mixed models, each treatment was used as a random effect (for a total of 12 levels) because 3 blocks were too few to comprise a block random effect. Individual trees comprised another random effect to account for variation among individuals, and species comprised the final random effect since species groups were modeled. Categorical variables were scaled based on the number of categories, and continuous variables were scaled based on the population of values.

To address questions about spatial clusters of gaps, we developed a model to predict gap size because, while we needed to know the size of all gaps proximate to the focal gap, not all logging gaps were mapped soon after logging (Ohlson-Kiehn et al. 2003). We modeled gap size as a function of the DBH of the felled tree (Figure 1 - 9) based on data from 60 reconstructed gaps.

We analyzed the new-recruit biomass/gap-proximity relationship in two ways. First, we drew a 50 m-radius circle (7850 m^2) around the stump of each focal gap tree and added the areas of other gaps falling inside that circle to the "proximate gap area" of the focal gap (we included the focal gap area in the proximate gap area calculation). We added the focal gap area to the proximate gap areas in the calculation of total proximate area because we are interested in any additional explanatory power gap clustering may have for biomass recovery rates over-and-above the influence of the size of the focal gap itself. We then modeled biomass from new recruits versus total gap-proximate area with OLS regression.

The second approach to the analysis of new-recruit biomass versus proximate gap area recognizes that the influence of gaps on one another likely attenuates with distance. Therefore, this second model fits an exponential kernel function (Eq. 1 - 1) such that gaps further from the focal gap contribute less to the proximate-area predictor. The model is:

$$\frac{biomass}{area}_{focal\ gap} \sim N\left(\gamma + \alpha \cdot \sum_{g=1}^{G} \frac{area_g}{{dist_g}^{\beta}}, \sigma^2\right) \qquad (1 - 1)$$

where N is the normal distribution with variance σ^2, G is the total number of gaps sampled, and $\gamma, \alpha, \beta, \text{and } \sigma$ are parameters fit by the maximum likelihood algorithm. γ represents a linear relationship between new-recruit biomass and area of focal gap, $\propto$ represents the influence of the area nearby gaps on the focal gaps, and β is the kernel exponent. As the distance of each gap increases, its influence on the biomass/area relationship of the focal gap decreases by an exponential factor β.

The distance between the focal gap and itself is set to 1 so that the focal gap area is included without modification in the estimate of aggregated areas ($\sum_{g=1}^{G} \frac{area_g}{{dist_g}^{\beta}}$). If beta becomes large, this model simplifies to the OLS regression model above that uses only focal gap area to predict new-recruit biomass per gap area.

All statistical analyses were performed in R (R Core Team 2012), maximum likelihood fits were performed with the bbmle package (Bolker and R Development Core Team 2012), and spatial manipulation and calculations were performed with the spatstat package (Baddeley and Turner 2005).

Biomass Balance Analyses

In addition to the hypothesis-related analyses above, we need other information to track gap biomass over time since logging (Figure 1 - 2). One simple approach would be to survey trees in and around the felling gap before and after logging, but for this sort of analysis, data of more spatial precision than available is required. We therefore opted to verify tree locations and their proximity to gaps during our surveys and to analyze their growth. Our method has the disadvantage of not addressing mortality.

To describe the effects of gap creation on the growth of border trees, characteristics in addition to border status are needed; we used canopy position, DBH, liana load, and species group. Border status (i.e., whether a tree occurs within 5 m of a gap) can be represented as a direct effect on growth, but gap formation also affects the crown positions and liana loads of border trees. While a multilevel model such as this is may be addressed by a structural equation model, we used partial regression instead. We let border status, DBH, and species group explain as much of the variation in observed growth as possible, and then let residuals of canopy position and liana sub-models act as orthogonal predictors, to explain the remaining variation in the growth model. The models were fit with generalized linear models in R (R Core Team 2012) with treatments within blocks and individual trees as random effects. The first two models were fit and their residuals used in the final model:

cp model: $cp \sim N(dbh + border + species\ group)$
liana model: $liana\ class \sim N(dbh + border + species\ group)$
$RGR \sim N(dbh + border + residual(cp\ model) + residual(liana\ model), \sigma^2)$,

where cp is the canopy position index of the individual, border is a binary indicator of whether the individual occurs within 5 m of a gap border, and liana is the liana infestation index of the individual.

Results

Hypothesis 1 - Liana-infestion intensity of trees is positively correlated with gap size

Border trees

Overall, liana infestations of border trees increased with DBH and then leveled off when trees reached 70 – 80 cm (Figure 1 - 4). Gap border trees were more heavily infested with lianas than trees not on gap borders until 80 cm DBH for liana classes >1 and >2. For heavy infestation rates (liana class >3), border trees were more heavily infested for all DBH classes (Figure 1 - 4). Overall, we find that border trees were less infested with lianas (Figure 1 - 5, Border = -0.19, P <0.001, N = 43133; Likelihood Ratio Test value = 109.2, P < 0.001). Other than palms, short- and intermediate-lived pioneers were the least prone to be infested by lianas. Tree species characteristic of dry forests harbored the most lianas (Figure 1 - 5).

New recruits and remnant trees

Of the various functions of gap size tested, linear gap size and intercept-only were the best model fits. Hence, we use the linear gap size model. The proportion of trees with any class of liana infestation decreased with gap size (Figure 1 - 6). Trees in small gaps were more likely to be heavily liana infested (class 4) if infested at all (Figure 1 - 7). As gap size increased, the chance that a given tree in that gap was heavily liana infested (>50% crown coverage) declined, as did the chance that it was infested at all. The chance that such a tree was lightly or moderately infested (1 – 50%) rose slightly.

Hypothesis 2 – Biomass Contributions of New Recruits as a Function of Gap Size

The above-ground biomass of new recruits 8-9 years post-logging increased with gap size (Figure 1 - 8, linear regression, biomass (kg)/gap area (m^2) = 1.74 + 0.00280 · gap area, adjusted r^2 = 0.139, $P < 0.01$, N = 60).

Hypothesis 3 – Post-logging Biomass Recovery is Lower in Clustered than Isolated Gaps Due to Increased Liana Infestations in the Former

There was no relationship between proximate gap area and new-recruit biomass (Figure 1 - 10, new-recruit biomass/area = 2.90 + 0.000331 * gap proximity area, P = 0.35, N=60), and no relationship was apparent to the eye (Figure 1 - 11). A least-squares regression indicated a positive but non-significant relationship.

When we allow the influence of nearby gaps to attenuate with distance (the second gap-proximity method described above), the likelihood surface of the beta parameter (which controls how quickly that influence attenuates with distance) is essentially flat to the right. This result indicates that the model is driving the contributions to the area metric from proximate gaps to 0. When beta becomes large, the exponential kernel model converges on the model that includes just the area of the focal gap. Apparently there is little or no influence of nearby gaps on the regenerated biomass found in focal gaps. Because the optimization routines drive beta to a point that essentially excludes non-focal gap areas from the proximate gap area predictor, this model converges on the simple OLS regression model described above. Biomass predicted by this model does not increase with measured biomass.

Border tree growth

The effects of percent crown infestation of lianas on border tree growth rates were similar to those using liana categories, so here we present only the results with the continuous variable of cover. Overall, border trees grew an average of 0.15 cm/year more than forest interior trees after controlling for canopy position and liana loads ($P < 0.01$, $N = 54243$, 95% CI: 0.11 – 0.19). If those factors are included, the growth rate advantage of border trees was 0.066 cm/year.

Discussion

The effects of gap size on liana infestations and rates of post-logging biomass accumulation were opposite our predictions. Liana infestations were less common and less prolific in larger gaps and regenerated biomass increased with gap size. Liana proliferation may decline with gap size due to increased abundance of pioneer trees that avoid or shed lianas (Putz 1984). But further study is required to determine whether the decrease in liana infestations with gap size is due to the increasing abundance of pioneer trees as gap size increases, or for some other reason. Remnant trees may be particularly liana-prone if lianas take time to infest crowns from the ground or from other nearby crowns. Other factors may also play a role, such as pre-logging liana abundance, site history, and edaphic conditions.

The studies of Babweteera et al. (2000), Gerwing and Uhl (2002), and Broadbent et al. (2006) quantified liana abundance in different ways (the number infesting trees, sprouting in subplots, and covering ground area) and in gaps of different ages (6-25 months, 6 years, and <1 – 19 months, respectively), yet arrived at a consistently positive effect of gap size on liana density and cover. It is possible that, because of the time required for pioneer trees to recruit into the minimum DBH class for sampling and their ability to avoid infestation, the age of the gaps in this study (8-9 years) was an influential factor. Studies of liana infestation in older logging gaps in other sites may help clarify the relationship between liana abundance, logging gaps, and time since logging.

Contrary to the results of a study on natural forests in Panama (Putz 1984), border trees in our forest suffered less liana infestation than trees > 5 m from logging gaps. This difference may be the result of pre-logging cutting of lianas on trees to be harvested that was performed as part of the reduced-impact logging (RIL) guidelines followed by logging crews in these plots. Nevertheless, the precise mechanism that reduced liana infestations on border trees is not clear. Specifically, was it the reduction of on-the-ground re-sprouting lianas or the pre-cutting of lianas in to-be-felled trees (that may have grown into border tree crowns) that reduced border tree liana loads?

Lianas often abound in treefall gaps and on trees on their borders (Putz 1984), (Schnitzer and Carson 2001), but pre-felling liana cutting reportedly reduce their densities by 30 – 55% and basal area by 69 – 80% (Gerwing and Uhl 2002, Alvira et al. 2004). If the increased liana infestation on border trees reported in previous studies was due to fallen lianas that sprouted and re-climbed border trees via small-diameter trellis structures common on gap margins (Putz 1984), then a reduction of lianas inside logging gaps (on the ground, in tangles, and on remnant and newly-recruited trees) due to the silvicultural treatment would result in fewer border trees with lianas. Also, given that in the forest we studied an estimated 24% of lianas in a tree's crown emanate from the crowns of neighbors (Alvira et al. 2004), and given that felled trees are often larger and harbor more lianas than gap border trees, the cutting of lianas on trees to be felled would likely reduce the number of live lianas in nearby trees. It is unclear which of these mechanisms is responsible for the lower than expected liana infestations on gap border trees, but the finding helps explain the increased growth of these trees.

Liana abundance increases as precipitation decreases across tropical forests worldwide (Schnitzer and Bongers 2011). A number of mechanisms for this pattern have been proposed, but tree species architecture and other characteristics are not among them. Here we report that in a transitional forest composed of species characteristic of both wet Amazonian and dry Chiquitano forests, dry forest species harbored more lianas that wet forest species. Dry forest species may have architectural or other differences such as slow growth rates that allow lianas to climb and proliferate, or more dry forest species may be deciduous, thereby favoring the growth of evergreen lianas. Dry forest species may also preferentially occur in topographical and hydrological microenvironments within these plots that favor liana growth.

Adding proximate gap area to focal gap areas did not improve predictions of new-recruit tree biomass. Thus while new-recruit biomass increases with gap size, proximity to other gaps seems not to matter. Perhaps where logging results in more spatially clustered felling gaps, such as those resulting from logging long-lived pioneer species that recruit into large gaps and therefore occur in patches (e.g., *Swetenia macrophylla)*, inter-gap influences may be stronger.

In this logged forest, we observed coordinated forces on biomass accumulation that seem to favor quicker recovery per area in larger gaps. Larger gaps engendered lowered liana infestations of newly-recruited trees, and greater biomass of those new recruits. How border tree growth, remnant tree growth and initial biomass loss per area changes with gap size await further analyses, but our initial indications are that larger gaps favor faster recovery of biomass, and that nearby gaps do not seem to significantly impact this relationship.

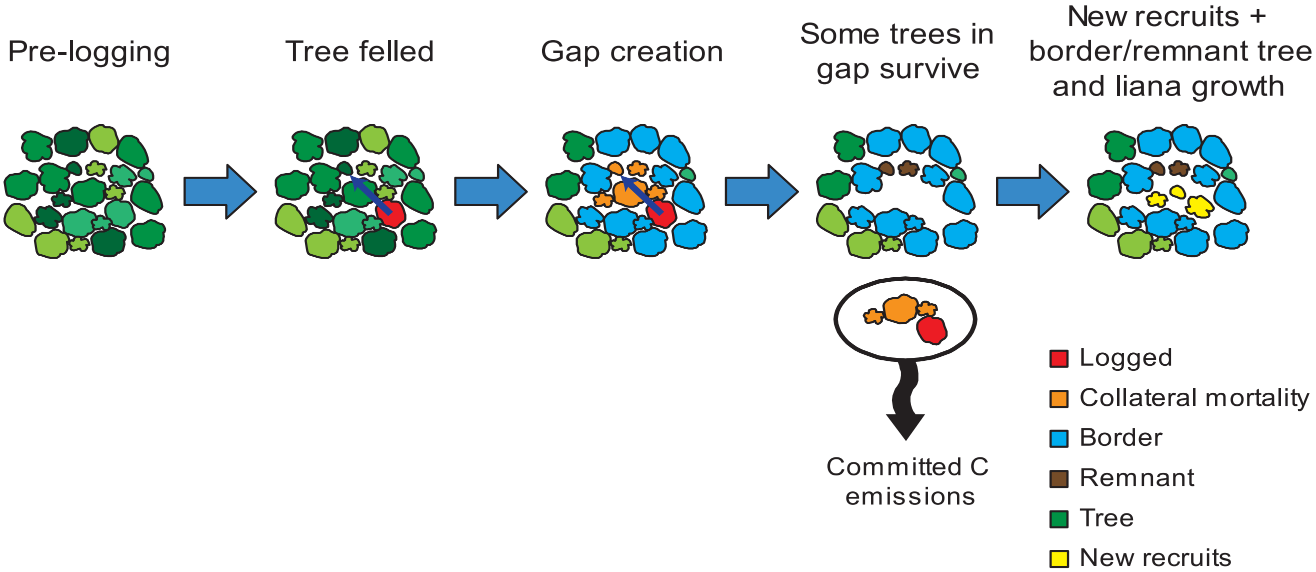


Figure 1 - 1. Classification of trees within and around a logging gap (crowns as if viewed from above canopy)

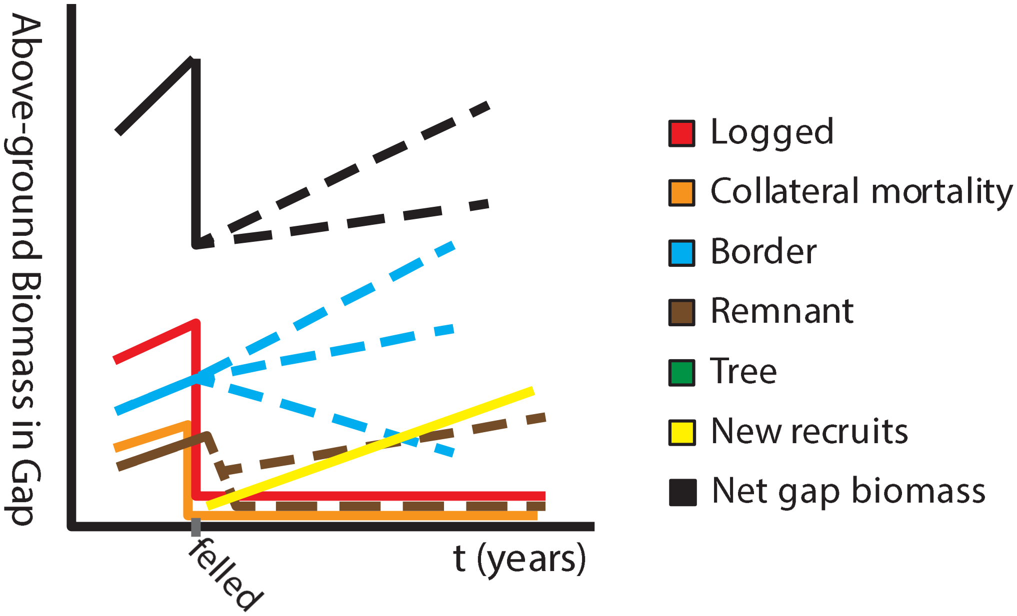


Figure 1 - 2. Hypothesized biomass trajectories of trees in and adjacent to canopy gaps opened by selective logging. Dashed lines indicate uncertain trajectories.

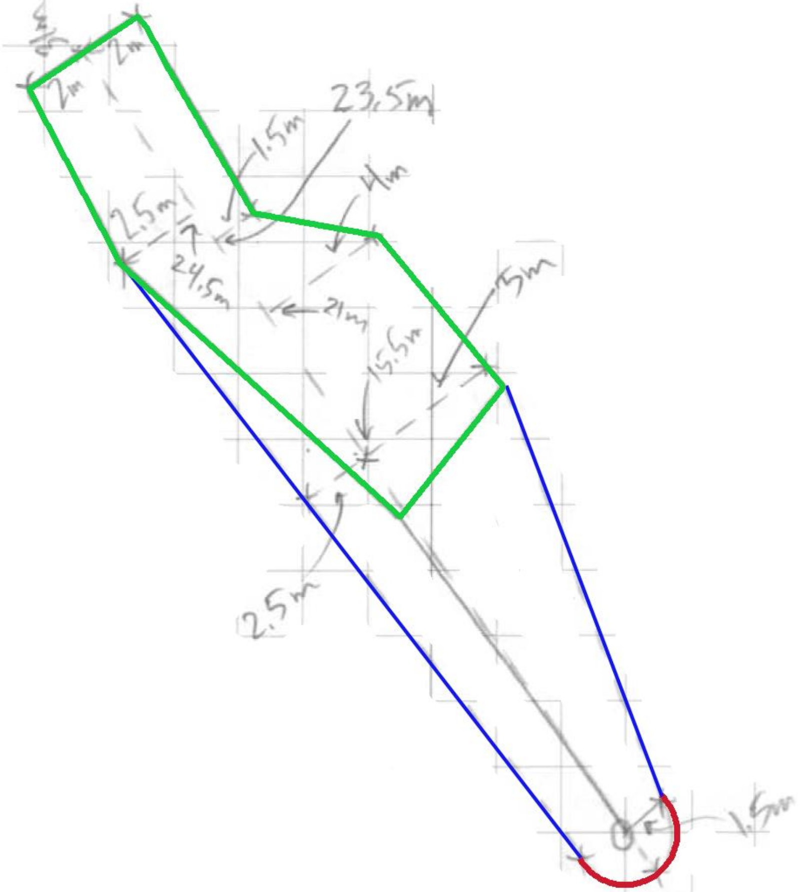
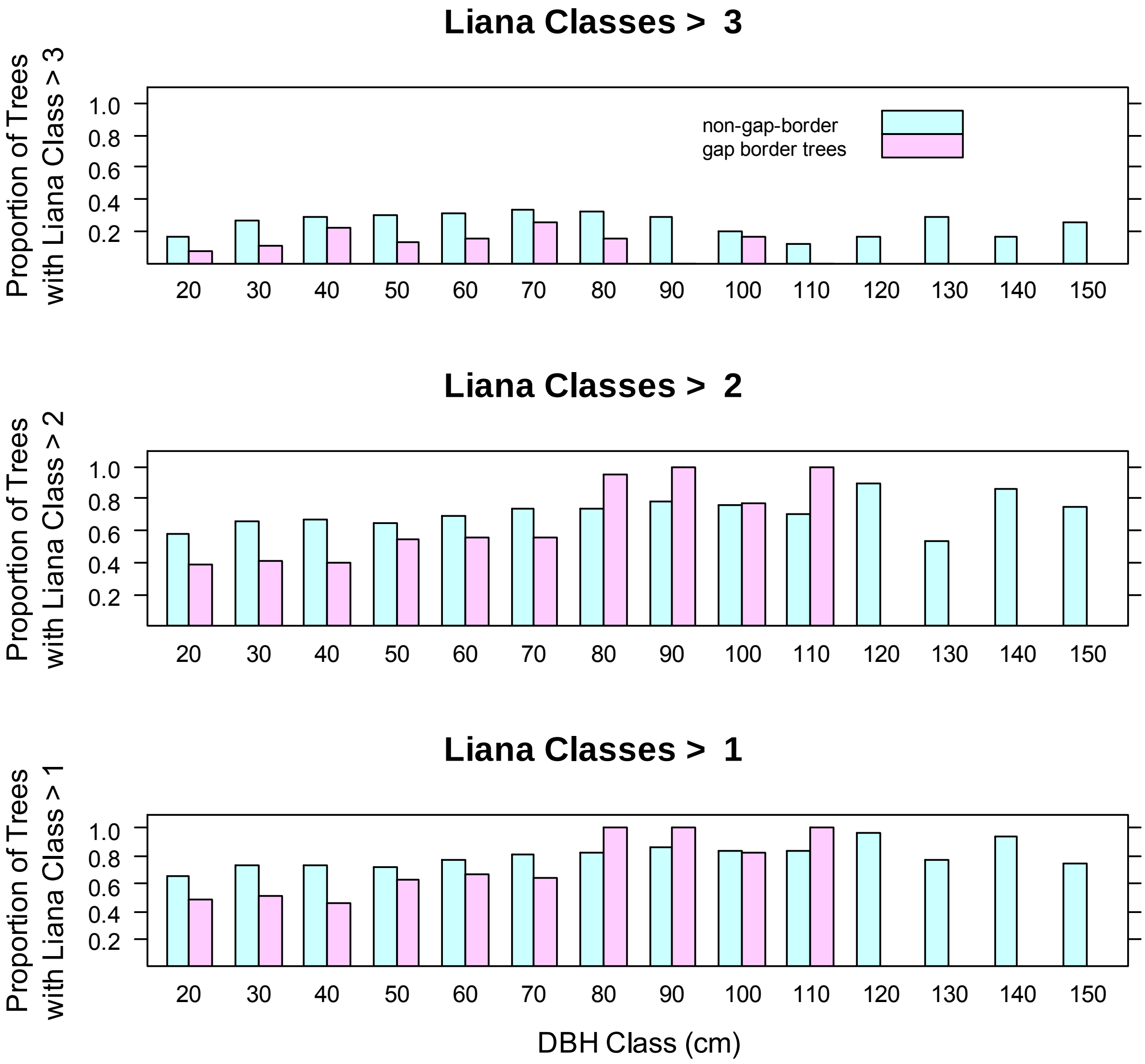


Figure 1 - 3. Diagram of a felling gap as reconstructed in the field. Green indicates the crown on the ground as surveyed after logging in 2001-2002, red indicates the assumed gap left by the original crown around the stump, and blue lines connect the circle around the stump and the crown area. The outline formed by the union of the colored lines constitutes the reconstructed gap.


Liana Classes > 3

Liana Classes > 2

Liana Classes > 1

Figure 1 - 4. Liana infestations of trees <5 m from felling gaps (border trees) and in the forest interior. Liana Class 1 = no lianas, Class 2 = lianas only on the trunk, Class 3 = lianas on trunk and in crown, Class 4 = entire crown covered by lianas.

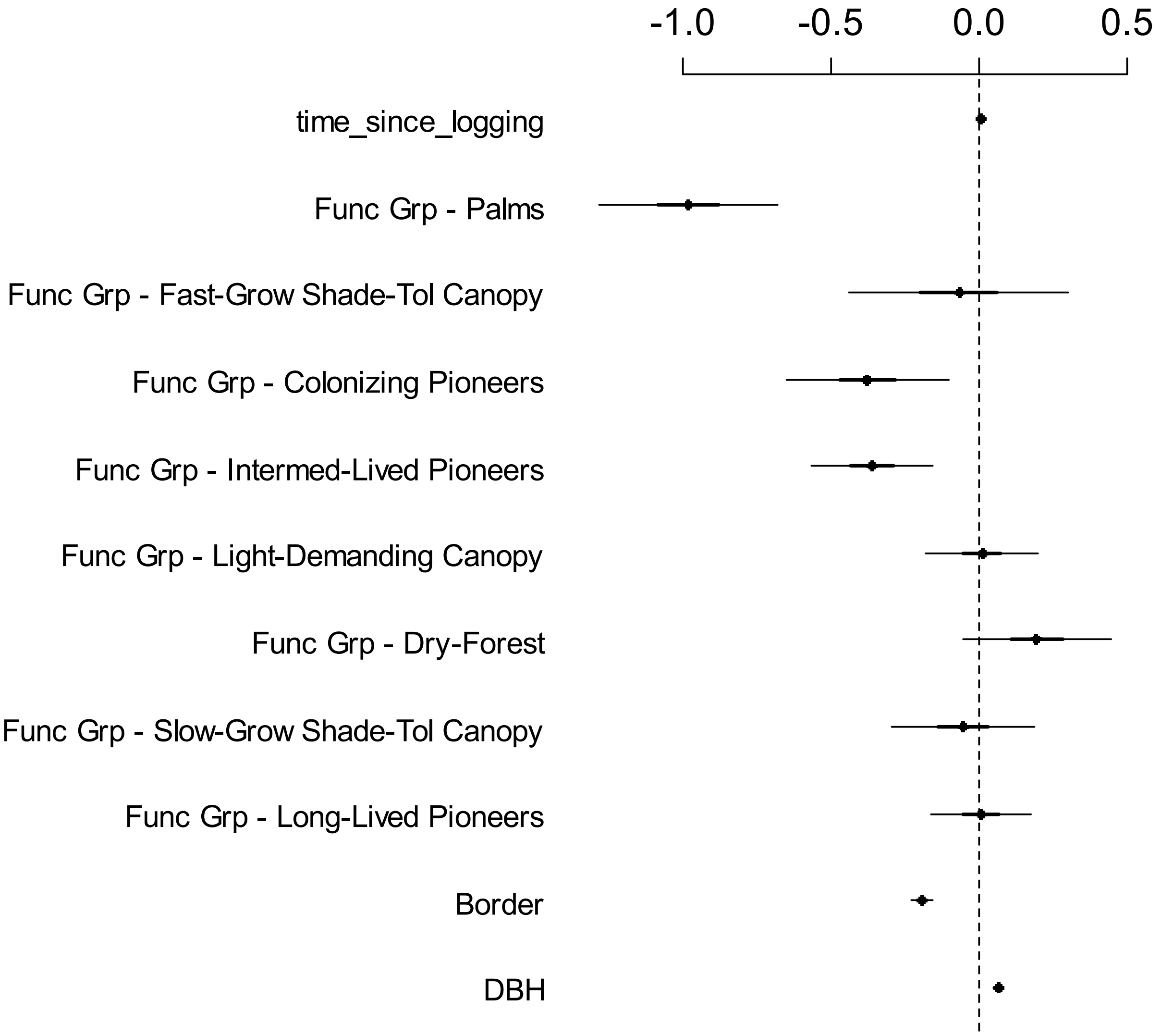


Figure 1 - 5. Coefficients for the model predicting liana infestation class based on DBH, gap border status, and species group. The residuals of this model are used in the model assessing the impact of border status on tree growth rates. Horizontal lines extend +/- 2 SE (or a total width of 4 SE).

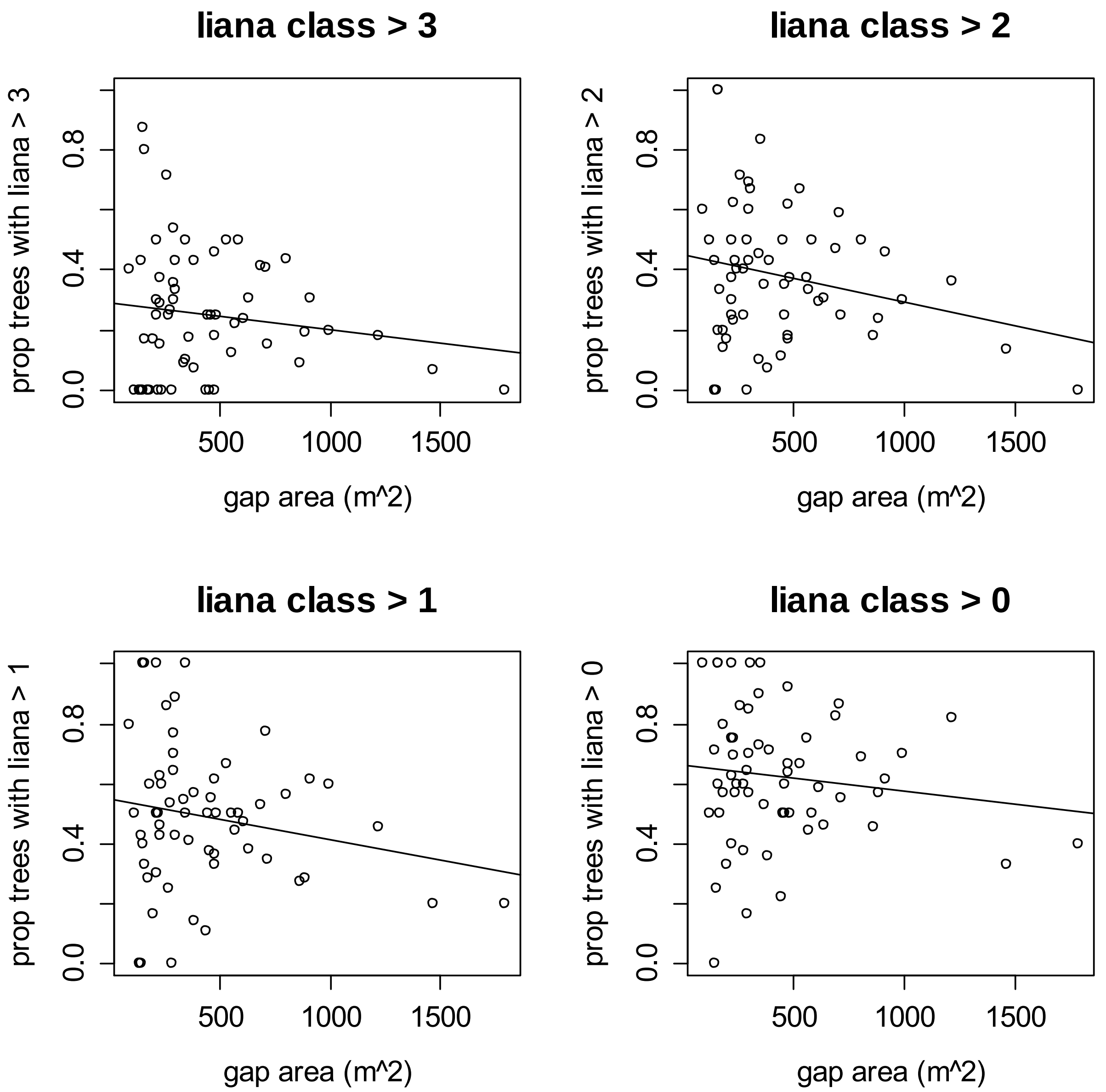


Figure 1 - 6. Proportions of trees in gaps with liana class > x versus gap area. All slopes are negative, suggesting that liana infestations decrease with gap size. Note that the largest gaps had very few trees with high liana loads. Lines indicate OLS regression fits.

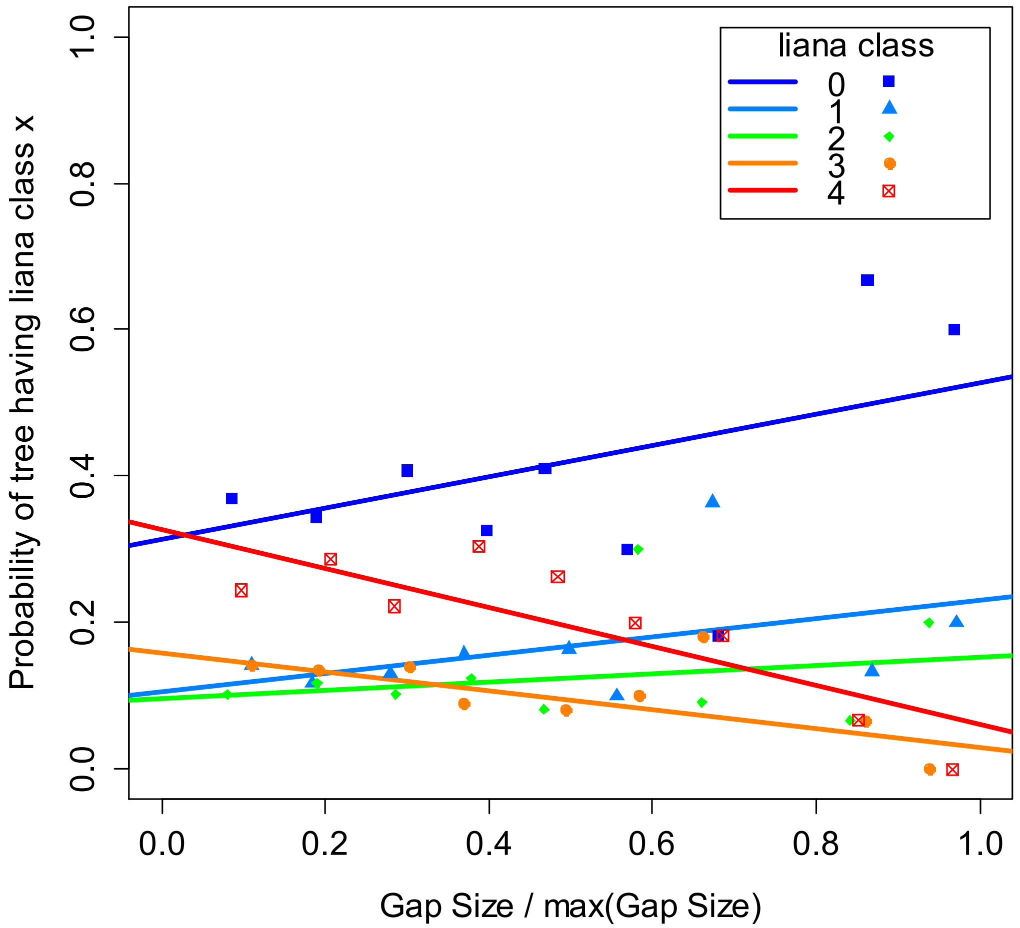


Figure 1 - 7. Multinomial model for the probabilities of liana infestations on trees in gaps (new recruit or remnant) as a function of gap size and degree of infestation. The model was fit using maximum likelihood methods and employed the additive log ratio transformation to insure that probabilities at each gap size add to 100% (Bolker 2008). Lines indicate model fits, points indicate data aggregated in 10 gap-size bins. The data has been jittered to see overlapping points.

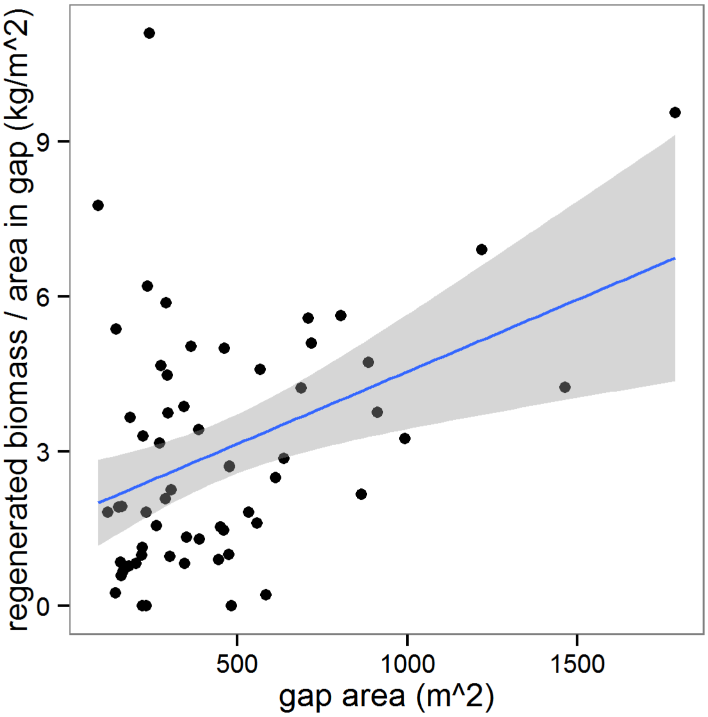


Figure 1 - 8. Above-ground biomass of newly recruited trees > 10 cm DBH in 9-year old logging gaps. Blue line indicates the OLS regression ofregenerated biomass per area = 1.74 + 0.00280 · gap area, $P < 0.01$, adjusted $r^2 = 0.139$. Grey envelope is the standard error, and each point indicates a sampled gap.

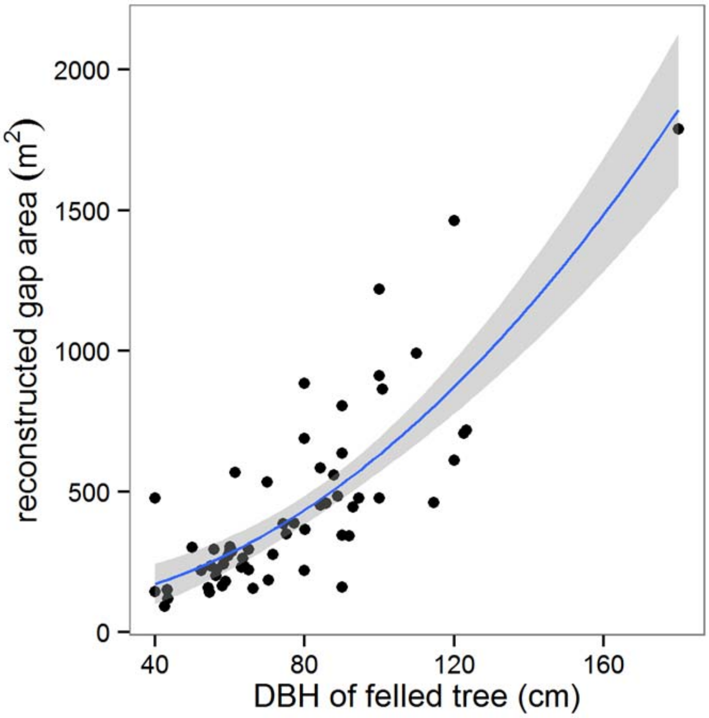


Figure 1 - 9. Gap size as a function of DBH of the felled tree. Blue line indicates the OLS regression ofgap area = 84.4 + 0.547 · DBH^2, adjusted $r^2 = 0.65$, $P < 0.001$, N=60. Grey envelope is the standard error, and each point indicates a sampled gap.

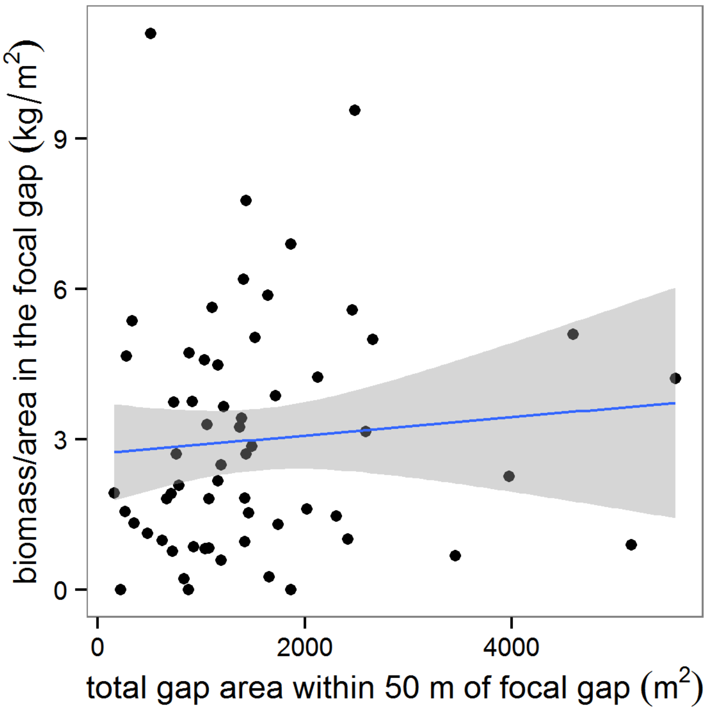


Figure 1 - 10. New-recruit biomass per area of the focal gap versus the sum of all gap areas within 50 m of the stump of the felled tree. Blue line indicates the OLS regression of biomass/area = 2.90 + 0.000331 · gap proximity area, P = 0.35. Grey envelope is the standard error, and each point indicates a sampled gap.

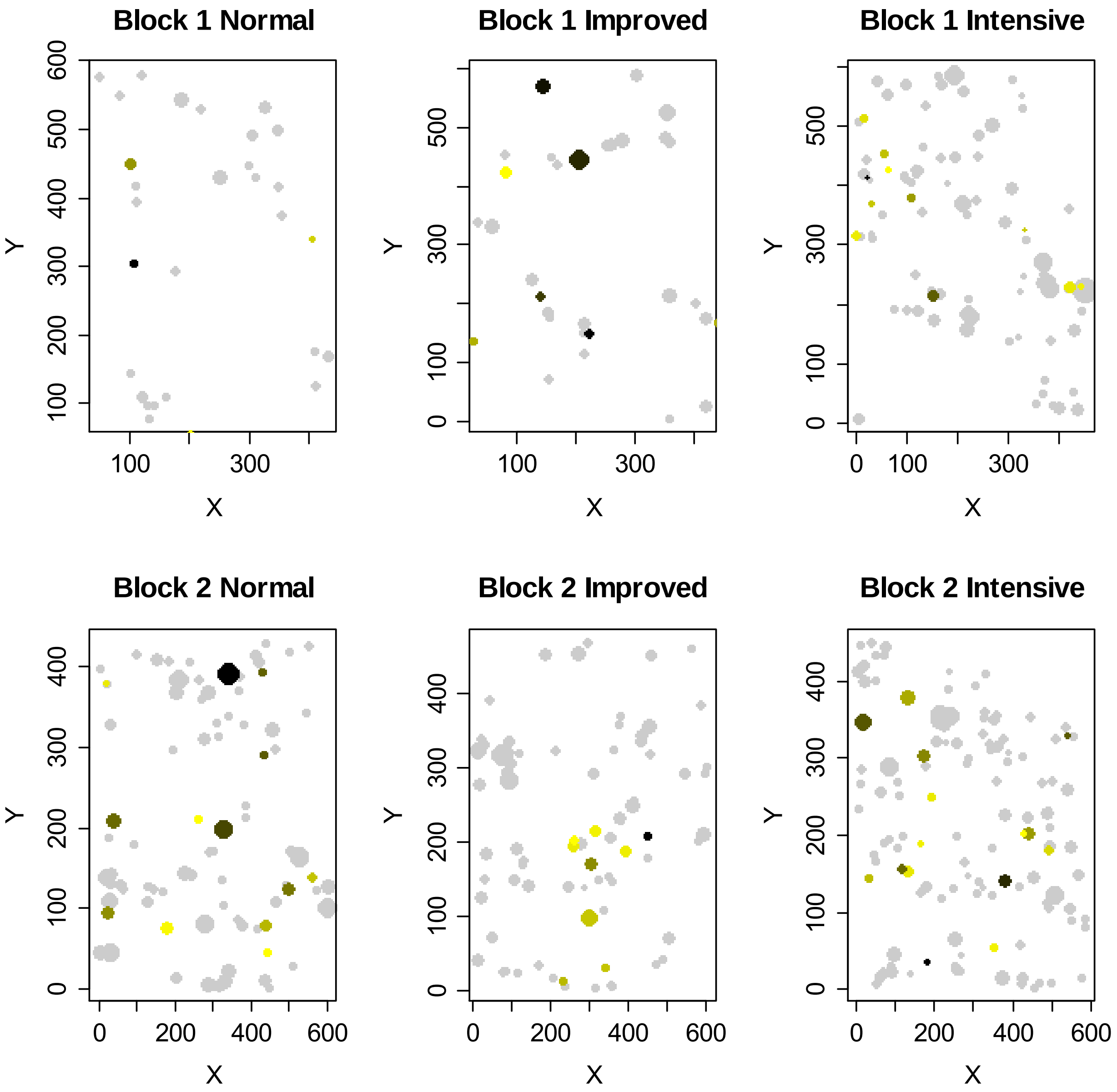


Figure 1 - 11. Spatial map of gap locations, sizes and new-recruit aboveground biomass. Axes are in meters. Size of circle correlates with predicted gap size. Darker colors indicate more biomass/m^2, and grey indicates a gap that was not surveyed.

Table 1 - 1. Coefficients from the maximum-likelihood model specified by Equation 1 - 1

	Estimate	Std. Error	z value	Pr(z)	Signif
alpha	0.00273	0.00086	3.19	1.44e-3	**
beta	2.47	0.0072	344	0	***
gamma	1.76	0.48	3.67	2.34e-4	***
sigma	2.16	0.20	11.0	5.74e-28	***

CHAPTER 2

INTERACTIVE EFFECTS OF DROUGHT, LOGGING, AND FIRE ON THE COMPOSITION, STRUCTURE, AND DYNAMICS OF A TROPICAL MOIST FOREST IN BOLIVIA

Introduction

Tropical forests may exhibit substantial resistance to climate change until pushed too far, for too long, or in too many ways (Malhi et al. 2009). Resistance and resilience of ecosystems to external forcings are often investigated in terms of one or two interactive drivers (e.g., Uhl and Kauffman 1990, Aragao and Shimabukuro 2010), but interactions among three or more forcing factors may determine the futures of tropical forests (Cochrane and Laurance 2008, Davidson et al. 2012). In an early study on this topic, Nepstad et al. (1999) suggested that logging, increased frequency and intensity of drought, and increased anthropogenic fires may work together to cause large-scale dieback of Amazonian forests. While the potential impacts of these interactive disturbances have garnered some attention (e.g., Nepstad et al. 2008, Silvério et al. in press, Brando et al. in review) the impacts of the critical three-way interaction between drought, logging, and fire are largely uninvestigated (but see Woods 1989).

We examine the effects of selective logging, fire, and drought on mortality rates of adults and seedlings of trees in a transitional Amazonian tropical forest in Eastern Bolivia. We consider each disturbance/stress to constitute an environmental filter for community assembly (sensu Keddy 1992) and assess the additivity of their effects (Figure 2 - 1). As tree communities pass through sets of environmental filters, altered forest structures develop that influence microenvironments and biotic interactions experienced by the trees and seedlings. Hence, while these filters may have immediate effects on tree mortality, growth, and recruitment, they can also have lasting effects by way of altered forest structure, microclimates, and biotic interactions.

Drought

Transitional forests with mean annual precipitation of 1,400 – 1,800 mm and dry seasons of 4 - 5 months reportedly show dry season declines in evapotranspiration, whereas wetter forests typically do not (da Rocha et al. 2009). Whether or not trees in transitional forests suffer or avoid dry season water stress, lack of water is likely an environmental filter for tree community assembly (Engelbrecht et al. 2007). The prediction that reductions in precipitation associated with climate change in Amazonian forests will be especially marked in our study area (Malhi et al. 2008) lends urgency to this study. It also suggests that the response of this transitional forest to increased drought will provide an early glimpse of how other neotropical forests will respond to climate change.

We expect drought to favor purportedly drought-tolerant tree species as forest communities assemble over time. We also expect that large trees suffer more from drought than small trees, as observed in various other tropical forests (Leighton and Wirawan 1986, Van Nieuwstadt and Sheil 2005, Nepstad et al. 2007, da Costa et al. 2010). While some studies suggest that tree stem diameter or height may be the cause of this vulnerability (Leighton and Wirawan 1986, Zhang et al. 2009), we hypothesize that the main cause of large tree vulnerability to drought is that their crowns are exposed to high light intensities and high vapor pressure deficits (VPDs), not due to their size *per se*.

Our expectation that drought impacts increase with tree size is based on the observation that competition among plants decreases soil water availability, which leads to reduced root, stem, and leaf water potentials. One common result of low plant water potentials is reduced photosynthesis, which can render trees susceptible to pests, pathogens, and other causes of mortality. The high VPDs experienced by trees with exposed crowns lead to high transpiration rates per unit of CO_2 fixed. Therefore, when soil water potential is low, trees with exposed crowns may fix less CO_2 (in the case of isohydry or facultative deciduousness) and/or suffer xylem cavitation (in the case of anisohydry).

Studies that identified tree size as the key cause of vulnerability to drought stressed the increase of water tension with tree height and concluded that xylem cavitation was the principal cause of mortality (Leighton and Wirawan 1986, Zhang et al. 2009). Leighton and Wirawan (1986) added that increased overall metabolic demands with increasing tree size may also play a role. They also reported that during a major drought in Borneo, large trees benefitted from low-intensity understory fires that killed many small trees, possibly due to reduced competition for water. If this competitive release is responsible for larger trees benefiting from fires during droughts, we might conclude that larger trees are hydraulically constrained. Soil water potential may constrain trees via reduced transpirational cooling and elevated leaf temperatures, reduced photosynthesis, xylem vessel cavitation, or other means. Trees with exposed crowns, regardless of their height, require more water for transpirational cooling and experience relatively high VPDs, and hence are particularly susceptible to drought-induced mortality. For this reason we hypothesize that canopy position is a better predictor of tree mortality than DBH or height. This hypothesis is supported at least indirectly by the finding of Nepstad et al. (2007) that tree species known to reach the canopy suffer from droughts more than those that typically remain in the mid- and understories. The question nevertheless remains whether there is something about the species themselves, tree size, or crown exposure that renders trees vulnerable to drought-induced mortality.

Logging

We expect selective logging to result in a lower-statured and more spatially heterogeneous forest with tree mortality rates that are elevated for a few years after the harvest but eventually settle back to pre-logging rates. Follow-on effects of logging may include increased mortality rates of trees damaged by felling and skidding, high mortality rates of trees on the edges of logging gaps due to rapidly increased exposure to insolation and wind, and increased densities of short-lived trees of pioneer species. Logging often results in increased mortality of smaller trees because skidder drivers tend to avoid large trees and because fellers try to direct the fall of trees to avoid hang-ups in other large trees.

Fire

Slow-moving surface fires are expected to increase in frequency in Amazonia as a result of a synergy between increasing droughts related to climate-change, forest fragmentation, selective logging, and increasing frequencies of ignition due to swidden agriculture and pasture management (Cochrane and Laurance 2008, Nepstad et al. 2008). Furthermore, burned forests are typically more flammable than unburned forests (Cochrane 1999, Cochrane and Schulze 1999).

The surface fires that move slowly through the understories of Amazonian forests change both forest structure and composition. By focusing on plant functional traits and how they relate to fire survival, we attempt to understand how these fires may change species compositions of future forests. Specifically, it has been shown that bark thickness, bark heat transfer rates, tree diameter, tree height, and wood density explain some of the variation in fire-induced tree mortality (Martin 1963, Pinard and Huffman 1997, Stephens and Finney 2002, Barlow et al. 2003a, Van Nieuwstadt and Sheil 2005, Brando et al. 2011). Bark thickness affects heat transfer rates and thus the temperature to which the cambium rises as flames heat the outer bark (Dickinson and Johnson 2001, Michaletz and Johnson 2008). In addition, taller trees may avoid crown damage from surface fires by being far away above the heat source. It may also be important that trees with dense wood may be better able to compartmentalize the pathogens and wood-rotting organisms that attack after fire-induced stem damage (Romero and Bolker 2008, but see Romero et al. 2009). Although our ability to detect a wood density effect on tree survival is limited by long time lags between the incidence of fire damage and pathogen-induced death (Barlow et al. 2003b), we nevertheless tested for this relationship. With these various mechanisms taken as a whole, we expect that fires in our study area favor large trees, especially those with thick bark and dense wood.

In most sections of this study we analyze data for both large (biennial censuses) and small trees (regeneration transects). However, while fires are likely to favor seedlings that have the ability to resprout after being top-killed, we lack data on this phenomenon and thus omit small tree responses to fire from our analysis.

Drought + Logging

If environmental filters are additive and if our hypotheses are correct, the combination of drought and logging should result in a forest of lower stature than that affected by drought or logging alone. Woods (1989) found that logging-damaged trees in Malaysia are vulnerable to subsequent drought and fire, and we expect to find the same in our plots (see chapter 3). Drought vulnerability due to logging damage may be caused by reduced stem flow due to sapwood damage. Another potential mechanism involves the interaction between drought and defense against pathogens (McDowell et al. 2011). If drought lowers a tree's ability to compartmentalize decay of sapwood damaged during timber harvest operations, then fungi may be able to invade and kill a tree that would otherwise have survived the drought or damage alone. This increased susceptibility to pathogens and wood-rotting organisms might also result in trees that survive but develop stem hollows, but this issue remains to be investigated.

Logging opens the forest canopy by creating felling gaps, skid trails, and log yards. In doing so, it exposes previously sheltered trees to more light and wind, which increase their transpirational demands. If release from below-ground competition does not fully compensate for this increased need for water, newly-exposed trees should be vulnerable to drought (Figure 2 - 2).

While soils under recent canopy gaps are generally wetter than in the surrounding forest due to reductions in both root length densities and transpiration, water availability in gap soils varies substantially in space and time (Vitousek and Denslow 1986, Becker et al. 1988, Denslow et al. 1998, Ostertag 1998, Poorter and Hayashida-Oliver 2000, Gray et al. 2002). Most studies on temporal trends in gap conditions report that as their canopies close over the course of 1-2 years, microclimate conditions come to resemble those in the understory (e.g., Blate 2005b). While temporary increases in soil moisture in gaps might favor drought-intolerant species, this benefit is reduced by the elevated VPDs and higher soil temperatures characteristic of gaps (Fetcher et al. 1985). In a study conducted in a semi-deciduous forest in Ghana with a rainfall regime similar to that of our study site, Veenendaal et al. (1996) found that as soils dried, seedlings of two light-demanding tree species suffered more drought stress in the understory than in gaps, as indicated by lower leaf water potentials and reduced stomatal conductances. This finding suggests that drought-intolerants may be favored in gaps due to increased soil moisture, despite the higher temperatures and VPD. Poorter and Hayashida-Oliver (2000) suggest that gaps allow seedlings to expand root systems in the wet season more than seedlings in the understory , thereby providing access to deeper water stores and a buffer against dry conditions. If such a root-investment strategy is advantageous in gaps, acquisitive species (Sterck et al. 2011) and/or species that invest relatively more in roots than in shoots may benefit from gaps, perhaps as long as there are no deep droughts that obviate the benefits of deep roots by drying deep soil layers. The root-investment strategy may also confer drought-tolerance by allowing plants to develop belowground carbohydrate and water storage structures (Poorter and Markesteijn 2008). While acquisitive species may benefit from being in gaps and tolerate droughts by rapidly expanding their root systems, they may be drought-intolerant due to large specific leaf areas and low wood densities.

Predictions about whether gaps favor seedlings of drought-tolerant or drought-intolerant tree species (as indicated by survival time in nursery dry-down experiments) become complicated by the mixture of influences discussed above. We expect that gaps favor drought-intolerant species because increased soil water availability more than compensates for increases in temperatures and VPD. Such a finding would suggest that logging may mal-adapt forests that with climate change will be subjected to more frequent and more intense droughts. If the opposite is found (i.e., that gaps favor drought-tolerant tree species), such a result would suggest that logging may "pre-assemble" forests to climate change-related drought via a drought-tolerance/drought-avoiding filter during the community assembly processes.

Gaps may draw moist, cool and CO_2-rich understory air horizontally from the forest understory and then vent it upwards through the canopy opening, thereby increasing VPD and air temperatures in the adjacent source areas (Miller et al. 2007, Bohrer et al. 2009). If understory VPDs rise as a result of proximity to the many canopy gaps opened by selective logging, understory seedlings, trees and shade leaves of canopy trees may experience lower leaf water potentials and more drought stress. To the extent that logging gaps favor drought-tolerant species in areas further into closed forests from gap edges, we expect logged stands to favor drought-tolerant species in gap-edge areas.

Logging may influence the water balances of trees that survive logging in a number of ways. Trees bordering logging gaps will experience similar countervailing forces to the small trees in gaps; increases in VPD, insolation, and leaf temperatures but also increases in plant available water. We expect that, just as for small trees in gaps, the greater transpirational demands of gap-border trees are more than compensated for by greater availability of water. Thus, we expected that drought-intolerant large trees are favored on the margins of gaps in logged plots.

Overall, we expect that due to decreased transpiration and consequently increased soil water availability, selective logging favors seedlings of drought-intolerant species. To the extent that this is true, logging may mal-adapt forests to future droughts. If the opposite holds – that is, seedlings of drought-tolerant species are favored by logging – then logging might “pre-adapt” forests to drought. If forests that are increasingly exposed to drought due to climate change must wait for large trees to die before recruiting drought-tolerant seedlings, logging may accelerate the assembly of that new community and hence pre-adapt forests to new climates.

Logging + Fire

Selective logging is likely to increase forest flammability (Uhl and Kauffman 1990, Holdsworth and Uhl 1997), though rapidly-closing logging gaps may render that increase short-lived (Blate 2005b). Areas that experience both logging and fire are expected to develop into medium-statured forests as logging removes large trees and fires kill small ones. We also expect logged areas to experience more intense fires due to increased fuel loads and understory drying, at least soon after logging. Even if fire intensities do not increase, fire-induced mortality may increase because logging-damaged trees are especially vulnerable to fire damage (Woods 1989).

Drought + Fire

Understory fires may reduce large-tree mortality in subsequent droughts due to release from below-ground competition (Leighton and Wirawan 1986). Canopy openness will likely increase post-fire, representing a release from above-ground competition as well (Figure 2 - 2). While greater canopy openness may result in higher understory VPDs that exacerbate water stress during droughts, the increased openness may also allow trees to store more non-structural carbohydrates that serve as a hedge against carbon starvation during droughts. Furthermore, fires can damage trees without killing them, resulting in increased sapwood resistance to water flow. While we expect that the two-way interaction between drought and fire will reduce forest stature overall, we also expect that fire-survivors will experience overall reduced drought-induced mortality for a period of time after the fire due to competitive release. Species with thick bark and large trees with crowns that are not exposed to high light intensities, VPDs, and wind speeds are expected to be favored.

Drought + Fire + Logging

The 3-way-interaction between drought, fire, and logging is expected to exhibit the largest impacts on forest structure due to deaths of both large and small trees. We expect the resulting community to be rich in drought-tolerant, thick-barked species that are capable of resprouting.

Methods

This study was conducted in the Long-Term Silvicultural Research Plots (LTSRPs) of the Instituto Boliviano de Investigación Forestal (IBIF) within the forestry concession held by Agroindustria Forestal La Chonta, 30 km east of Ascención de Guarayos, Bolivia (15°47'S, 62°55'W). This semi-deciduous forest (hereafter "La Chonta") receives an average of 1580 mm of precipitation annually with 4 months (May-September) that each receive <100 mm (Peña-Claros et al. 2008a). This forest is often referred to as being "transitional" between wet Amazonian lowland forests to the north and dry Chiquitano forests to the south and falls within WWF's Global 200 Southwestern Amazonian Moist Forest region. Located within but on the southern edge of the Amazon Basin, approximately 30% of the tree species that grow to be >10 cm DBH are deciduous and liana densities are very high (Peña-Claros et al. 2008a). Tree species from both wet and dry regions co-occur in this transitional forest. The soils of La Chonta are largely nutrient-rich inceptisols (Quintero, in prep). The concession's terrain is undulating with some granitic outcrops (i.e., inselbergs), none of which occur in the permanent sample plots.

The LTSRPs established in 2000/2001 include three blocks of four 27 ha treatments: control (no logging); normal logging; improved logging; and, improved logging with intensive silvicultural treatments (Peña-Claros et al. 2008a). All logging was selective, planned, and carried out by trained crews according to reduced-impact logging (RIL) guidelines. Pre-felling of lianas in to-be-felled trees was carried out approximately 6 months prior to logging, and lianas were cut from future crop trees in the improved and intensive treatments. Trees overtopping future crop trees were girdled in the improved and intensive plots, and the soil was scarified in gaps in the intensive plots to encourage pioneer tree establishment. Within each plot, all trees >40 cm DBH are censused semi-annually, with trees >20 cm and >10 cm DBH censused in half of the main plot and 4 1-ha plots, respectively. Regeneration of 25 canopy tree species is monitored in four transects in each plot with a nested design (Peña-Claros et al. 2008b) by measuring: pole-sized trees (>150 cm tall but <10 cm DBH) within a 4 m-wide strip; saplings (30-150 cm tall) in a 2-m wide strip; and, seedlings (<30 cm tall) in 1 m x 2 m sub-plots located every 10 m. The regeneration transects were established immediately post-logging and are remeasured on an irregular basis. This study refers to the trees >10 cm DBH and censused biennially as “large trees”, and those <10 cm DBH from the regeneration transects as “small trees.”

We estimate soil water deficits with the Maximum Climatological Water Deficit (MCWD), a simple “bucket” model that fills with precipitation and assumes evapotranspiration of 3.33 mm/day (Aragão et al. 2007, Malhi et al. 2009, Phillips et al. 2009). We start the calculation of the Climatological Water Deficit (CWD) from 1 January 1970 and run the calculation forward day-by-day, adding daily precipitation and subtracting 3.33 mm/day (Figure 2 - 3), and capping CWD at a maximum of 0 (saturated soil). For each census interval, MCWD is the most negative value of CWD observed (Figure 2 - 3 and Figure 2 - 11).

Statistical Models

Unless otherwise indicated, survival models were fit using generalized linear mixed model methods (Bates et al. 2011) in the R statistical environment (R Core Team 2012). Data were coded such that each survival or mortality event was associated with an individual census interval.

We fit complementary log-log models to the survival/mortality data for both small and large trees, fitting each survival and mortality event with a binomial error distribution. An “event” consists of one observation of one individual from one census to the next. For example, if an individual survives through all four census intervals, there will be four “survival events” for that tree.

We modeled survival of trees over census intervals that varied in length. When we found a previously-measured tree, we recorded a “1” for survival. If a previously-measured tree was not found or was found dead, we recorded a “0” for mortality.

The probability of a tree surviving any particular year is p, and the probability of it surviving n years is p^n. The probability that the tree dies sometime during those n years is therefore $1 - p^n$. If the probability of survival p is a function of a linear combination of factors x, then the probability of survival $p = f(x)$. In our survival models, $f(\,)$ is a complementary log-log function and we test various linear combinations of factors and their interactions for x.

For each census interval, the probability that a tree survives is $[\log(-\log(1-x))]^n$, and the probability that it dies is $1-[\log(-\log(1-x))]^n$. If a tree survives a census interval, the likelihood of the model being correct is $[\log(-\log(1-x))]^n$. If a tree dies during a census interval, the likelihood of the model being correct is $1-[\log(-\log(1-x))]^n$. Maximum likelihood methods attempt to minimize the model error by adjusting the coefficients of each factor to maximize the sum of the log of the likelihoods for all observations.

We include random effects in our models to account for block effects, repeated measures and, in some of our models, species effects. To account for block effects, we assign a random variable for all 12 plots since 4 treatments nested within 3 blocks would be too few levels. To account for repeated measures, we assign a random variable that estimates individual level variation. To account for species effects, we assigned a random variable that estimates species level variation.

In our analyses, we use "+" to indicate additive factors in a linear model, "*" to indicate a full interaction between factors including main effects and interactions, and ":" to indicate the interactive term without the main effects of the factor. Instead of repeating the model each time, we will refer to the linear combination of factors "x" as it appears in the equations above.

Independent variables were scaled and centered where appropriate to render outputs interpretable (Schielzeth 2010). Unless otherwise indicated, trees that died due to logging were removed, as were data for trees in areas that burned in 2004 except for analyses explicitly involving fire.

Small Tree Analyses

We tested models that predict small-tree survival as a function of a species drought index (SDI, Seedling Drought Index) derived from a seedling dry-down experiment (see Effects of Drought on Small Trees below, Poorter and Markesteijn 2008), MCWD, and if the tree occurred in a logging gap, gap edge, skid trail, or skid trail edge (gap; -1 = no, 1 = yes). Because logging gaps and skid trails close quickly, and because logging disturbances can be difficult to distinguish from natural disturbances after a few years, it was difficult to determine whether recruitment during census intervals >8 years after logging occurred in old logging gaps or on skid trails. Hence, small trees that recruited into the survey after the logging gaps were mapped were assigned to the habitat (gap/non-gap) of the nearest tree surveyed in the first post-logging census. If there was no first-census tree <5 m from the new recruit, the recruit was excluded from model sets that include the gap factor. We accounted for the large variation in census interval lengths of the regeneration transect data (1-6 years) by modeling annual survival probabilities (see Models above).

Effects of Drought on Small Trees

Droughts, fires, and logging may select for small trees of drought-tolerant tree species. To measure this effect, an *a priori* index of drought-tolerance is needed. We use two drought-tolerance indices for small trees in this study (we use a different index for large trees). Our first index borrows from Poorter and Markesteijn (2008) who, to explore how certain functional traits affect drought tolerance, grew tree seedlings in pots and measured the time it took each seedling to die after cessation of irrigation. We make use of their experimental days-to-death results as the “dry-down drought index” for each species (though we scale the variable to be centered on 0 with a standard deviation of 1). Of the 25 species in the regeneration census, 11 were included in their dry-down experiment. We excluded one of their species that was first included in the small tree census in 2009 (*Trema micrantha*) and another (*Spondias mombin*) with few individuals and an extreme drought tolerance estimate that substantially skewed the drought-tolerance scale. We therefore scored the drought tolerances of 9 species of small trees (*Cedrela fissilis, Swietenia macrophylla, Pseudolmedia laevis, Batocarpus amazonicus, Cariniana estrellensis, Cariniana ianeirensis, Gallesia integrifolia, Hymenaea courbaril*, and *Aspidosperma cylindrocarpon*). Our second index uses a "distributional drought index" (Markesteijn and Poorter 2009), defined by comparing species-specific stem densities of trees >10 cm DBH between a dry and a moist forest in Bolivia. The distributional drought index has the advantage that there are data for all species we studied, but the disadvantage that it is not a direct measure of drought-tolerance *per se*. We scaled the distributional drought index in the same way as we scaled the dry-down index.

Effects of Drought on Large Trees

In addition to the dry-down index for small trees (SDI) and the distributional drought index for both small and large trees, we use finer-scale geographical distribution data as a proxy for drought-tolerance. To this end, we make use of data from Toledo et al. (2012) to classify species as drought tolerant or intolerant. Toledo et al. (2012) surveyed 220 1-ha plots across lowland Bolivia and ordinated the data on four environmental axes (rainfall, temperature, soil texture, and soil fertility) to explain variation in abundance of each of 100 tree species. The positive rainfall axis indicates increasing abundance with increasing rainfall; the positive temperature axis indicates increasing abundance with increasing temperature; and the positive soil texture axis is associated with soils rich in clay and silt, whereas the negative direction is associated with sandier soils. The algorithm we used that is based on these data (henceforth referred to as the drought-tolerance algorithm) is as follows:

If rainfall PCA is significant, then:

If abundance increased with increasing rainfall: Not Tolerant

If abundance decreased with increasing rainfall: Tolerant

If rainfall PCA was insignificant, or its curve shape was flat or unimodal, then look at temperature (if PCA is significant):

If abundance increased with increasing temperature: Tolerant

If abundance decreased with increasing temperature: Not Tolerant

If drought tolerance was still not decided, then look at soil texture (if PCA is significant):

If abundance increased with increasing sandiness: Tolerant

If abundance decreased with increasing sandiness: Not Tolerant

If none of the three axes categorize the tree species, then determine its status based on geographical distributions in Killeen et al. (1993).

Once species were classified according to this algorithm, we ran our survival models with drought-tolerance as an independent variable: x = other variables + MCWD * drought tolerance.

These models classify species based on the ranges of their relative abundances with respect to environmental variables, and then fit survival models based on these classifications. If drought tolerance interacts significantly with MCWD, that indicates that mortality rates of plants classified as drought tolerant respond more or less than those classified as drought intolerant.

In addition to this drought-tolerance classification approach, we fit a second set of survival models using the directional tendency of each species with respect to these environmental axes. Thus, each species was assigned a rainfall, temperature, and soil texture “direction” (1 = increasing with the factor; -1 = decreasing with the factor; and, 0 = factor insignificant, unimodal, or flat). Instead of deciding *a priori* which environmental axes should be associated with drought-tolerance as in the model above, this approach lets the maximum likelihood algorithm fit the best coefficients for each environmental factor *a posteriori*. We ended up with the following model in its full and reduced forms where the “association factors” are the directions mentioned above: x = other variables + (rainfall_association + temperature_association + soil_texture_association) * MCWD.

We include the significant predictive factors from earlier models in the directional association model. As in the *a priori* drought classification model above, significant interactions with MCWD inform us about differential mortality responses of species to drying conditions.

Is Crown Exposure or DBH More Closely Linked to Death During Droughts?

To determine whether crown exposure or DBH was more associated with increased mortality during droughts, we fit a number of survival models that included either the crown position:MCWD interaction or the DBH:MCWD interaction. We compare the fit of these models to the data using AIC and likelihood ratio tests (LRTs).

To determine how logging changes the relationship between DBH, crown exposure, and drought, we tested four models that incorporate the most important predictors from the models described above, but substituted DBH and canopy position as the interactive factor (Model 1: x = DBH + canopy_position * MCWD * logged, Model

2: x = canopy_position + DBH * MCWD * logged, Model 3: x = DBH + canopy_position * MCWD, Model 4: x = canopy_position + DBH * MCWD).

Fire

Wildfires occurred in two of the 12 experimental plots (3 blocks of 4 treatments) late in November 2004 and January 2005. The affected areas included 4 ha of one “improved silviculture” plot and 15 ha of one control plot (C. Pinto, unpublished). The fourth census interval (October 2004-September/October 2006) included the fire event. In February 2005, researchers mapped the borders of burned areas (C. Pinto, unpublished). We digitized these maps and aligned the resulting spatial polygons of burned areas over tree locations to assign an in_burned_area True/False (later scaled as 1/-1) value to each tree.

Bark thickness was measured using the methods and some of the data from Pinard and Huffman (1997) and Poorter et al. (2013). Basically, bark thickness was measured using small squares of bark (c. 5 cm x 5 cm) removed from trees at 50 cm above the soil surface; stem diameters were measured at 50 cm and 130 cm. We regressed bark thickness on DBH for each species and used these relationships to assign an estimated bark thickness for each tree. Trees of species for which we did not have data were excluded.

Combined Effects of Drought, Fire, and Logging on Large Trees

We include the strongest factors from one- and two-way disturbance interaction models in our three-way interaction model (i.e., dbh, pc * mcwd, bark_t_predicted * in_burned_area, logged * in_burned_area, mcwd * in_burned_area). In addition, we test the three-way interaction between drought, fire, and logging with the following term: mcwd * logged * in_burned_area.

Results

Effects of Drought on Small Trees

The droughts of 2010 and 2011 in La Chonta were the deepest since at least 1970, according to our CWD calculations (Figure 2 - 4). While the large tree censuses (i.e., data for trees >10 cm DBH) did not cover this period, 4 of 48 small tree transects were included in that final measurement.

Survival models that used the drought index based on greenhouse dry-down experiments(SDI) fit the data better than those with the drought index based on stem count differences between a dry and wet site (“distributional drought index" or "DI", Poorter and Markesteijn 2008; models: x = DI * MCWD, & x = SDI * MCWD, delta-AIC = 142). Based on this finding, henceforth when we refer to the “drought index” of small trees, we refer to the dry-down drought index (SDI) and not the distributional drought index (DDI).

To understand what controls drought-induced mortality of small trees, we fit a variety of survival models that included SDI, MCWD, and tree height as predictors (Table 2 - 6, Table 2 - 7, and Figure 2 - 6). When we limited our models to those including SDI, MCWD, and their interaction, AIC and likelihood ratio tests indicate that the full model is the most parsimonious (Table 2 - 4 and Table 2 - 5). The SDI:MCWD interaction is positive, which counter-intuitively suggests that drought-tolerant species suffered greater increases in mortality during droughts than the purportedly drought-intolerant species.

Expanding the small-tree drought survival model to include tree height, the most parsimonious model includes that variable, the SDI*MCWD interaction the three-way interaction between tree height, MCWD, and SDI (Table 2 - 6). The two way interactions between height and SDI, and between height and MCWD, were not significant and the models including them were slightly less parsimonious according to AIC. Furthermore, the likelihood ratio test indicates that their inclusion does not significantly improve the model (Table 2 - 7). Likelihood profile plots show that the profiles of the independent variables are well-behaved (i.e., approximately quadratic).

Of note here is that, while in the simpler model the SDI:MCWD interaction was significant (SDI:MCWD = 0.049, $P < 0.05$), the inclusion of the three-way interaction increases the variance of the SDI:MCWD interaction and renders it insignificant (SDI:MCWD = 0.10, $P = 0.18$). Nonetheless, the magnitude of the estimate increases in the more complex model and it remains positive. A positive SDI:MCWD coefficient indicates the opposite of our expectation: the more drought-tolerant a species is according to Poorter and Markesteijn (2008), the more that species' mortality rate rises during dry periods.

Overall, small trees experienced lower annual survival probabilities during dry intervals than wet ones (Figure 2 - 5 and Figure 2 - 6). SDI exerts the largest influence on the model with a coefficient about 3 times larger than that for MCWD. Tree height was a strong predictor of survival, second only to SDI in importance. The SDI:MCWD interaction term is relatively weak, signifying that while there does seem to be a signal that mortality rates of drought tolerant species increase more during dry periods, other factors are more important.. While likelihood ratio tests do not support its inclusion in our models, the top 3 models according to AIC do include that term. The coefficient of the three way interaction between SDI, MCWD, and Tree Height was negative and included in the most parsimonious model, but the likelihood ratio test suggests it does not significantly improve the model.

Interactive Effects of Drought and Logging on Small Trees

The MCWD, SDI and the SDI:gap interaction were significant predictors of small tree survival in the most-parsimonious model (Figure 2 - 9), indicating that small-tree mortality increased with drying conditions and that while seedlings of purportedly drought-tolerant species suffered higher mortality rates overall, they suffered relatively less in gaps than did those of drought-intolerant species. Whether a small tree occurred in a logging gap or not is a marginally-significant predictor of its survival in the most-parsimonious model (Table 2 - 8). A likelihood ratio test (LRT) shows that models improve with the addition of SDI, MCWD, and the SDI:gap interaction. While the LRT indicates that the gap main effect does not significantly improve the model in this particular traverse of factors, AIC tests include the gap factor in the top 3 most-parsimonious models (Table 2 - 9).

When we include an independent variable that distinguishes between small trees in logged versus control plots (1 = occurs in logged plot, -1 = occurs in control [non-logged] plot), the SDI:MCWD (not shown) and SDI:logged interactions are significant and parsimonious additions to the model but the logged main effect is not (Table 2 - 11). The most parsimonious model tested is consistent across both AIC and Likelihood Ratio Tests (Table 2 - 10 and not shown): $P_{survival} = (\log(-\log(1 - (\mathrm{SDI} * \mathrm{MCWD} + \mathrm{SDI{:}gap} + \mathrm{SDI{:}logged})))^{n}$. The coefficients of the most parsimonious model with logging included are similar to those of the model with just the gap factor (Figure 2 - 9), with the positive SDI:logged interaction indicating that small trees of drought-tolerant species suffered lower increases in mortality rates than did those of drought-intolerant species (Figure 2 - 10).

Logging Effects on Large Trees

Mortality rates of large trees in logged plots were not significantly higher than those in control plots (logged = 0.024, P = 0.41 in model with x = dbh + canopy position * MCWD + predicted bark thickness * in burned area + MCWD * in logged area * in burned area, see Figure 2 - 33). In fact, while not significantly so, mortality rates tended to be lower in logged plots. Residual mortality of large trees due to logging is examined in more detail in Chapter 3.

Drought Effects on Large Trees

Large tree mortality rates increased during drier intervals in La Chonta (Figure 2 - 12). The significantly positive coefficient for the MCWD (MCWD becomes more negative as intervals become drier) term in all our large-tree survival models confirms this finding.

A priori drought-tolerant species classification algorithm model

Large trees of species expected to be drought-tolerant based on their abundances across three environmental axes (Toledo et al. 2012) suffered higher mortality rates during drier intervals than species expected to be drought-intolerant (Figure 2 - 13). Altering the algorithm for classifying tree species by considering that a flat distributional response to the factors (rainfall, temperature, and soil texture) used to predict drought-tolerance did not change the overall pattern.

We selected the most parsimonious large tree survival model indicated by AIC (Table 2 - 12 and Figure 2 - 14), but all models agreed on the sign of the factors in question and in the relative sizes of the coefficients. Consistent with Figure 2 - 13, the model indicated that trees classified as drought-tolerant by our algorithm based on Toledo et al. (2012) unexpectedly fared worse than drought-intolerants as census intervals became drier (MCWD:toledo_drought_tol = 0.043, $p < 0.001$).

A posteriori separate-environmental-axis association model

To understand how tree species respond differentially to drought, we look to predictor interactions with MCWD, since direct predictor-effects should reveal responses across all moisture conditions. Fits of the large-tree survival model that incorporate tree species associations with environmental axes across Bolivia (see Effects of Droughts on Large Trees in Methods above) result in marginally-significant interactions between the rainfall and soil texture gradients (rainfall_association:MCWD = 0.016, $p < 0.1$; soil_texture_association:MCWD = 0.020, $p < 0.1$) when all three environmental axes are included in the same model (Figure 2 - 15). When those same models were fit with just one environmental factor at a time, rainfall (rainfall_association:MCWD = 0.024, $p < 0.01$) and temperature (temperature_association:MCWD = -0.024, $p < 0.05$) interactions with MCWD were significant, whereas the soil texture association's interaction with MCWD (soil_texture_association:MCWD = 0.021, $p = 0.1$) was marginally so. Coefficient values in the full model are similar to those in the corresponding single-environmental-factor models.

Main effects of environmental association factors in the large tree survival model are significant, but they do not tell us about how tree species weather drought. Species that increase in abundance with increases in rainfall have lower overall (i.e., regardless of moisture conditions) survival rates (rainfall_association = -0.10, $p < 0.001$) according to the full model (Figure 2 - 15). Those that increase in abundance with increasing temperature (a hypothesized drought-tolerance indicator) have higher overall survival rates (temperature_association = 0.033, $p < 0.01$) whereas those that are more abundant in sites with coarser soils (a hypothesized drought-tolerance indicator) have lower overall survival rates (soil_texture_association = -0.073, $p < 0.001$).

While main effects of the directional association factors were significant in the full model of large tree survival, we expected but did not find them to interact strongly with MCWD. Putting aside the significance levels for the moment, we note that the signs of the coefficients for the environmental gradient associations are in mixed agreement with the counter-intuitive results found using our drought-tolerance classification algorithm based on tree species distribution data. That is, contrary to the findings of the model based on the distributional drought-tolerance classification algorithm but in accordance with what we expected, the positive interaction between the rainfall gradient association and MCWD indicates that species that increase in abundance as annual rainfall increases (species we expected to be drought-intolerant) suffered higher mortality rates as census intervals became drier. The sign of the temperature association:MCWD interaction, in agreement with the algorithm model (see *a priori* drought-tolerant species classification algorithm model above), suggests that while mortality rates of all species rise as census intervals become drier, mortality rates of species that increase in abundances as temperature increases (species we expected to be drought-tolerant) rise less than rates of species that do not. The same counter-intuitive relationship is implied by the direction of the soil texture gradient interaction. Temperature and texture are less direct indicators of plot dryness than rainfall, so we might conclude that the separate-environmental-axes models contradict the drought-tolerance-algorithm models above. Given that the relevant separate-environmental-axes model coefficients are only marginally significant, we consider the results of the distributional drought-tolerance classification algorithm to be stronger. We therefore conclude that species expected to be drought-tolerant suffer more during dry intervals than species expected to be drought-intolerant.

Are large trees in logged plots more susceptible to droughts than those in unlogged plots?

Large tree vulnerability to drought in logged versus unlogged plots was marginally elevated in some models (MCWD : in logged area = 0.09, $p<0.1$ in Figure 2 - 18), but not in others (Figure 2 - 17 and Figure 2 - 19). That is, mortality rates in the logged plots were still higher than in the control plots eight years after the harvest, and those rates varied marginally more with MCWD than those of the un-logged plots. Regardless of the level of significance, the interaction of logging and drought is consistently small when compared with the MCWD main effect.

Is crown exposure or DBH more associated with mortality during droughts?

Of the four models tested, AIC supports the one with the canopy position:MCWD interaction and without the logging factor (delta-AIC = 3.3, Table 2 - 13). Of the models without the logging factor, the crown position:MCWD effect was marginally significant (x = DBH + crown position:MCWD, crown position:MCWD = 0.0080, $p<0.1$, Figure 2 - 19) whereas the DBH:MCWD interaction was insignificant (x = crown position + DBH:MCWD, DBH:MCWD = 0.00060, $p=0.89$, Figure 2 - 18). Likelihood ratio tests indicate a significant model improvement when adding the canopy position:MCWD interaction to the model with x = DBH + canopy position ($p = 0.049$), but not when the DBH:MCWD interaction was added ($p = 0.44$). Adding the DBH:MCWD interaction to the model that already includes the canopy position:MCWD interaction does not improve the model ($p = 0.32$), whereas adding canopy position:MCWD to the model that already includes DBH:MCWD does improve it ($p = 0.039$).

Overall, large tree mortality rates increased more due to drought than rates for smaller trees (DBH:MCWD = 0.050, $p < 0.01$ in this model). Logging nearly counteracts the relationship between DBH and MCWD, whereas control plots experience twice the effect (MCWD : DBH : in logged area = -0.046, $p < 0.05$). Thus, large trees in logged plots tend not to respond more strongly to droughts than small trees, while large trees in control plots do. Logged plots experience lower total mortality increases as conditions dry than do control plots (MCWD : in logged area = -0.035, $p < 0.05$).

Fire

Large tree mortality in burned areas was higher than in non-burned areas (Figure 2 - 29). The full model of tree survival through fires included the linear combination of factors x = predicted bark_thickness * DBH * in burned area. In this model, DBH and the interaction between the “in burned area” factor and predicted bark thickness were significant (Figure 2 - 30) and strong predictors of survival. DBH was the strongest predictor of survival of any factor, followed by the bark thickness : in_burned area interaction. In fact, the interaction between bark thickness and in_burned_area was a stronger predictor of survival than the in_burned_area main effect, indicating that bark thickness played an important role in determining survival in burned areas.

The in_burned_area direct effect was marginally significant when interactions between it and the other variables were removed. Trees with thicker bark survived better than those with thinner bark in burned areas as indicated by a relatively large and signification bark thickness : in_burned_area interaction ((Figure 2 - 30, Figure 2 - 31 and Figure 2 - 32). Likelihood ratio tests confirm that adding the bark_thickness and DBH main effects improves the models (Table 2 - 14). Even though DBH and bark thickness are correlated, our models converged easily with the result that the DBH:in_burned_area interaction was always rendered insignificant when the bark thickness:in_burned_area interaction was included.

Interactive Effects of Fire and Logging

Our full model for large tree survival with logging included the factor combination x = modeled_bark_thickness * DBH * in_burned_area * logged, where logged equals 1 for logged plots and -1 for control plots. The fire only affected one logged plot and one control plot. The fire seems to have had an interactive effect with logging, increasing mortality more in logged than unlogged plots (in_burned_area:logged = 0.088, p<0.01 in model with x = in_burned_area*bark_t_predicted + in_burned_area*logged + dbh). This result should be treated with caution, however, since the fire was not replicated across blocks.

Drought + Fire + Logging – Large Trees

The three-way interaction between MCWD, logging, and fire (MCWD : logged : burned = 0.011, p = 0.66) is positive but weak and not significant as a predictor of large-tree survival (Figure 2 - 33). We would interpret a positive three-way interaction to mean that as census intervals become drier, areas that were both burned and logged exhibit steeper declines in tree survival rates over and above those attributed to logging alone (MCWD : logged = -0.024, p = 0.32) or burning alone (MCWD : burned = -0.017, p = 0.47).

Discussion

Tree mortality rates increased over the 9 years of the study for as yet unknown reasons. Tree mortality rates typically increase just after logging and then decrease thereafter (see Chapter 3), which renders this finding even more surprising. Given that our models show a strong relationship between MCWD and mortality (Figure 2 - 33), this strong trend might be related to decreasing MCWD over that same time period (Figure 2 - 11), , but investigations into other potential causes are warranted.

Drought Effect on Large Tree Survival

Large tree mortality rates increased as MCWD decreased, as expected, and the main effect of MCWD was by far the largest of all the explanatory variables we tested (Figure 2 - 14).

We hypothesized that species with abundances in plots scattered around Bolivia that increase with abiotic factors associated with drought-stress (less rainfall, higher temperatures, or coarser soil texture) would suffer less mortality during dry intervals than those whose abundances decreased along those same gradients. Our finding of the opposite – that species expected to be drought-tolerant suffered greater increases in mortality with drought – is puzzling. One possible explanation is that although species characteristic of dry forests may have the ability to withstand dry conditions, whether or not individual trees develop this capacity varies with the environmental conditions under which they develop. For example, trees of a typically drought-tolerant species growing under mesic conditions may fail to develop the deep roots and narrow xylem vessels that confer this tolerance. Another possible explanation is that whereas dry-forest species are often found on hilltops, wet-forest species tend to be found on slopes and in valleys (M. Peña-Claro pers. comm.). This topographic difference would mean that although a single MCWD value was assigned to the entire forest, dry-forest species would on average experience drier soil conditions than wet-forest species. Thus, dry-forest species may start from a drier baseline. While this topographic pattern is not enough to explain why mortality rates of dry-forest trees rose more quickly than those of wet-forest trees as MCWD became more negative, it offers a reasonable direction for further investigation.

Given that the drought-tolerance classification algorithm based on tree species distributions (Toledo et al. (2012) yielded unexpected predictors for drought-survival models, we expected but did not find that maximum likelihood models that included each environmental axis would substantially improve our drought-survival models . The failure of the maximum-likelihood models that fit each environmental axis individually to improve the algorithm-based model may indicate that variation in rainfall, temperature, and soil texture, or the response of species abundances to those factors are correlated enough to complicate fitting responses to all three axes simultaneously.

Drought Effect on Survival of Small trees

Small trees of species classified as drought-tolerant by a dry-down experiment (Poorter and Markesteijn 2008) suffered less mortality during dry intervals than drought-intolerant species (Figure 2 - 7). While drought-tolerant species generally suffered higher mortality rates overall, survival rates of the most drought-tolerant species increased during drier intervals whereas those of drought-intolerants decreased. These results indicate that dry periods may be driving the community assemblage of small trees towards more drought-tolerant species.

Logging Effects on Residual Mortality of Large Trees

Large tree mortality rates increased over the entire 2000-2009 period (Figure 2 - 20) in both logged and control plots (Figure 2 - 21). While residual mortality due to logging is generally expected to subside over time as damaged trees die off, mortality in La Chonta continued to rise after logging. This trend was also observed in the control (not logged) plots. As mentioned above, the rising mortality with time may be due to a general drying trend over the course of the decade, as evidenced by increasingly negative MCWD (Figure 2 - 11), a strong predictor of tree mortality (Figure 2 - 33).

Annual mortality rates of trees in the logged plots were elevated by approximately 0.25% 8 years after logging when viewed graphically (Figure 2 - 21), but our survival models do not show a significant effect of logging on post-logging mortality rates. These results should be viewed in the context of high and variable overall mortality rates. It is also noteworthy that these plots were logged with RIL techniques, and the most intensive treatment removed only 14.4 ± 1.6 m^3 ha^{-1} (Peña-Claros et al. 2008a).

Logging Effects on Mortality Across Crown Exposure and DBH Classes Overall mortality rates decreased with increased canopy exposure (Figure 2 - 22), especially in the logged plots but also to a lesser degree in the control plots (Figure 2 - 23). Understory trees in logged plots suffered especially high mortality rates (Figure 2 - 23). One possible explanation for this pattern is that logging quickly exposes the crowns of understory trees, which subsequently die due to water or heat stress. Based on the finding of Barlow et al. (2003b) that many large trees died 1-3 years after a drought, initially high post-logging-mortality rates of understory trees would likely taper off within a few years. Contrary to this expectation, high mortality rates of understory trees persisted and even increased over the 8-year post-logging period (Figure 2 - 25). Another possible explanation is that the high overall mortality rates were due to the deaths of trees that were damaged during logging but were not recorded as such because the damage was slight or hard to detect. Even if small trees usually suffered disproportionately from logging because skidder drivers and fellers avoided large trees, it does not explain why small trees also suffered high mortality rates in the control plots (Figure 2 - 23).

While trees with low crown exposure are vulnerable in logged plots, there is no evidence that small DBH trees suffer higher mortality in logged than control plots (Figure 2 - 24). Such a result is counter-intuitive given the high correlation between DBH and canopy position ($r_s = 0.59$, $p < 0.001$). One explanation for this unexpected pattern is that trees in logged plots are more likely to have highly-exposed crowns where smaller in DBH, and that those trees are more likely to survive than their shaded counterparts. Indeed, median DBH was consistently smaller in logged plots than in control plots for each canopy position (Figure 2 - 26). But this does not explain why trees whose crowns remained in the understory after logging were more prone to die than similar trees in the control plots.

The finding that tree mortality rates decreased with DBH (Figure 2 - 24) fits with the decreased mortality rates of trees in high canopy exposure-classes (Figure 2 - 23).

Our survival models show that tree survival rates declined as conditions became drier. They also show that trees with low crown exposure always suffered higher mortality rates than those with high exposure. However, as conditions dried, low-exposure trees suffered less than trees with high exposure. That is, mortality rates of understory trees increased less with dryness than did the rates for overstory-trees. Thus, while low-exposure, understory trees suffered higher mortality rates than high-exposure, overstory trees, that difference declined during dry periods (Figure 2 - 27).

Crown Exposure is More Associated with Mortality during Droughts than DBH

To test whether the exposure of tree crowns or DBH is better correlated with the observed pattern of drought-induced large-tree mortality, we fit a number of survival models. If trees with either exposed crowns or large diameter trunks experienced elevated mortality rates during dry census intervals, we would expect to see positive interaction terms between crown position and MCWD, or DBH and MCWD respectively. Our hypothesis that canopy exposure more than DBH increases a tree's risk of mortality during droughts predicts that the crown position:MCWD interaction will have a smaller standard error than the DBH:MCWD interaction, and that in two otherwise equal models, the one containing the crown position * MCWD interaction will be more likely than the one containing the DBH * MCWD interaction.

The DBH:MCWD terms were smaller and had more relative variance (DBH:MCWD = 0.00060; Figure 2 - 19) than the crown position:MCWD terms (crown position:MCWD = 0.0080; Figure 2 - 20). Although the DBH:MCWD interaction terms are not significant in our models, there are significant and positive crown position:MCWD terms. This means that mortality rates of trees with more exposed crowns increase more with drying conditions than trees in the understory. That is, while overall mortality decreases as tree crowns become more exposed, the slope of the mortality response of emergent trees to MCWD is steeper than the slope of the response of understory trees (Figure 2 - 27). Thus, consistent with other studies (Leighton and Wirawan 1986, Van Nieuwstadt and Sheil 2005, Nepstad et al. 2007), trees with exposed crowns experienced a greater increase in mortality as conditions dry.

Our hypothesis is confirmed, but it should not be overstated. While crown exposure better explains large tree responses to drought than DBH, the response to drought across all crown exposure classes is almost 50 times smaller (crown position:MCWD = 0.008) than the direct mortality response across all crown exposure classes to MCWD (MCWD = 0.385). While we find that crown exposure is the most important link between large-tree mortality and drought, DBH or height may be more important in different ecosystems. Zhang et al. (2009), for example, conducted their study in a savanna where many or most trees likely have highly-exposed crowns. In that case, variation in crown-exposure is unlikely to explain large-tree mortality.

Logging does not Change how Crown Exposure Affects Drought Response of Large Trees

Given that selective logging leads to increased crown exposures of small trees (Figure 2 - 26), logging is also expected to affect the relationships between crown exposure, DBH, and drought survival. This approach also represents a first step towards understanding the effects of the interaction between logging and drought on large tree survival.

The relationship between canopy position and drought response differs little between logged and unlogged plots, whereas the relationship between DBH and drought response in stronger in the latter. The models with canopy position interactions fit the data better than those with DBH interactions, so we once again conclude that drought response is better explained by crown exposure than by DBH. Logging had no detectable effect on the relationship between crown exposure and drought as evidence by an insignificant three-way interaction between crown position, MCWD, and logging. This finding is somewhat surprising, as we expected that by quickly exposing many trees to high VPDs and insolation, logging would render them vulnerable to drought-induced mortality. Apparently, exposing tree crowns through logging does not leave the stand appreciably more vulnerable to drought-induced mortality.

While the relationship between canopy position and drought did not detectably change with logging, logged plots had a marginally-significant overall reduced mortality response to drying conditions. This finding may indicate a reduced susceptibility to drought-induced mortality of trees in the logged plots, perhaps due to removal of some dominant treess, which reduces below-ground competition for waterand increases crown exposure of the restl. This effect may also be an artifact of the tendency for post-logging mortality rates to converge on pre-logging rates with time-since-logging because, in this study, MCWD was negatively correlated with time-since-logging (Figure 2 - 11).

Logging-Drought Interaction Effect on Small Tree Survival

While small trees of drought tolerant species suffered higher overall mortality rates, they benefitted more from gaps than drought-intolerant species. At the same time, drought tolerants suffered comparatively higher mortality rates in logged than in un-logged plots (Table 19). This unexpected result may be due to unrelated???? habitat differences across logged and unlogged plots, or perhaps drought tolerants suffered on gap-edges or other habitats associated with logging, but not in the gaps themselves.

These results indicate that logging affects drought tolerance of post-logging regeneration at the community level, but the effect is complex and difficult to tease apart. Overall, logging encourages a less drought tolerant community. The fact that gap conditions favored regeneration of drought tolerant species does not reveal the mechanism that causes this pattern.

Fire Effects on Large Trees

The hypothesis that tree survival through fires increases with bark thickness is supported by the positive interaction between bark thickness and in_burned_area variables, and by the fact that models that include the bark thickness:in_burned_area interaction fit the survival data better than those with the DBH:in_burned_area interaction (delta-AIC = 4.3, Table 2 - 15). Furthermore, when the bark thickness: in_burned_area interaction was included in models, the DBH:in_burned_area interaction was not significant. In contrast to some other studies (e.g., Brando et al. 2011), we did not find a strong effect of DBH on tree survival in the burned plots. If DBH was strongly correlated with survival in burned plots, the DBH:in_burned_area interaction would be positive. Hence, we conclude that bark thickness is important than DBH for fire survival in this forest. If DBH plays a role, it is small compared to that of bark thickness.

Fire – Logging Interaction Effects on Large Trees

We did not find a strong interactive effect of fire and logging on large tree mortality. Large trees in areas that were both burned and logged exhibited non-significant increases in mortality rates relative to areas that were just burned or just logged (in burned area : in logged area = 0.27, P = 0.34, Figure 2 - 33).

Logging-Drought-Fire Interaction Effect on Adult Tree Survival

Areas that were both burned and logged exhibited slight but non-significant increases in drought-associated mortality rates. The burned areas were not large and lacked replication, so it is possible that fire intensities were higher in logged than in burned control plots. If this was the case however, it is possible that logging led to these increased intensities.

Table 2 - 1. Likelihood Ratio Test (LRT) for nested models of large tree survival. cp represents canopy position. $\text{MCWD}_{\text{previous census}}$ is used to detect delayed mortality from drought. “+” indicates inclusion of main factors whereas “*” indicates that both main factors and their interaction were included. Significance codes are: 0 ‘***’, 0.001 ‘**’, 0.01 ‘*’, 0.05 ‘.’, 0.1 ‘ ’, 1. Terms up to “dbh + mcwd * canopy pos” continue to improve the model given this traverse of model possibilities. Adding DBH to the mcwd*canopy pos model significantly improves the fit, but adding a dbh * MCWD interaction does not.

	Df	AIC	logLik	deviance	Chisq	Chi Df	Pr(>Chisq)	Signif
MCWD	4	60732.6	-30362.3	60724.6				
cp + MCWD	5	60637.5	-30313.7	60627.5	97.1	1	6.5636e-23	***
cp * MCWD	6	60635.7	-30311.9	60623.7	3.8	1	0.052515	.
dbh + cp * MCWD	7	60624.0	-30305.0	60610.0	13.7	1	0.0002121	***
(dbh + cp) * MCWD	8	60625.0	-30304.5	60609.0	1.0	1	0.32224	
dbh * cp * MCWD	10	60623.2	-30301.6	60603.2	5.8	2	0.055372	.
dbh * cp * MCWD + (cp + dbh) * $\text{MCWD}_{\text{previous census}}$	13	58979.3	-29476.6	58953.3	1650.0	3	0	***

Table 2 - 2. Likelihood ratio test for nested models of large tree survival. Symbols as in Table 2 - 1. Results are the same as in Table 2 - 1 until the 4th model from the top (dbh + mcwd * canopy position). This LRT departs from that in Table 2 - 1 after the 4th model by adding the dbh * cp interaction instead of adding dbh * MCWD. In this LRT, model 5 (which adds the dbh * cp interaction) is significantly better than the dbh + mcwd * cp model, whereas adding the dbh * mcwd interaction in Table 2 - 1 did not result in a significant improvement.

	Df	AIC	logLik	deviance	Chisq	Chi Df	Pr(>Chisq)	Signif
MCWD	4	60732.6	-30362.3	60724.6				
cp + MCWD	5	60637.5	-30313.7	60627.5	97.1	1	6.5636e-23	***
cp * MCWD	6	60635.7	-30311.9	60623.7	3.8	1	0.052515	.
dbh + cp * MCWD	7	60624.0	-30305.0	60610.0	13.7	1	0.0002121	***
(dbh + MCWD) * cp	8	60621.5	-30302.8	60605.5	4.5	1	0.034328	*
dbh * cp * MCWD	10	60623.2	-30301.6	60603.2	2.3	2	0.3184	
dbh * cp * MCWD + (cp + dbh) * $\text{MCWD}_{\text{previous census}}$	13	58979.3	-29476.6	58953.3	1650.0	3	0	***

Table 2 - 3. Delta-AIC's for all mortality models for trees >10 cm DBH tested. Notation as in Table 2 - 1. The AIC confirms our findings in the LRT (Table 2 - 1). The most parsimonious model here was not tested in the LRT, but the best model in the LRT ranks above the other LRT models here.

	ΔAIC	df
dbh * cp * MCWD + (cp + dbh) * MCWD$_{\text{previous census}}$	0.0	13
cp * (MCWD + MCWD$_{\text{previous census}}$)	22.5	8
(dbh + MCWD) * cp	1642.2	8
dbh * cp * MCWD	1644.0	10
dbh + cp * MCWD	1644.7	7
(dbh + cp) * MCWD	1645.7	8
cp + dbh * MCWD	1648.0	7
cp * MCWD	1656.4	6
cp + MCWD	1658.2	5
dbh + MCWD	1679.7	5
dbh * MCWD	1684.3	6
MCWD	1753.3	4
(cp + dbh) * MCWDprevious census	6861.1	8
dbh	27286.4	4

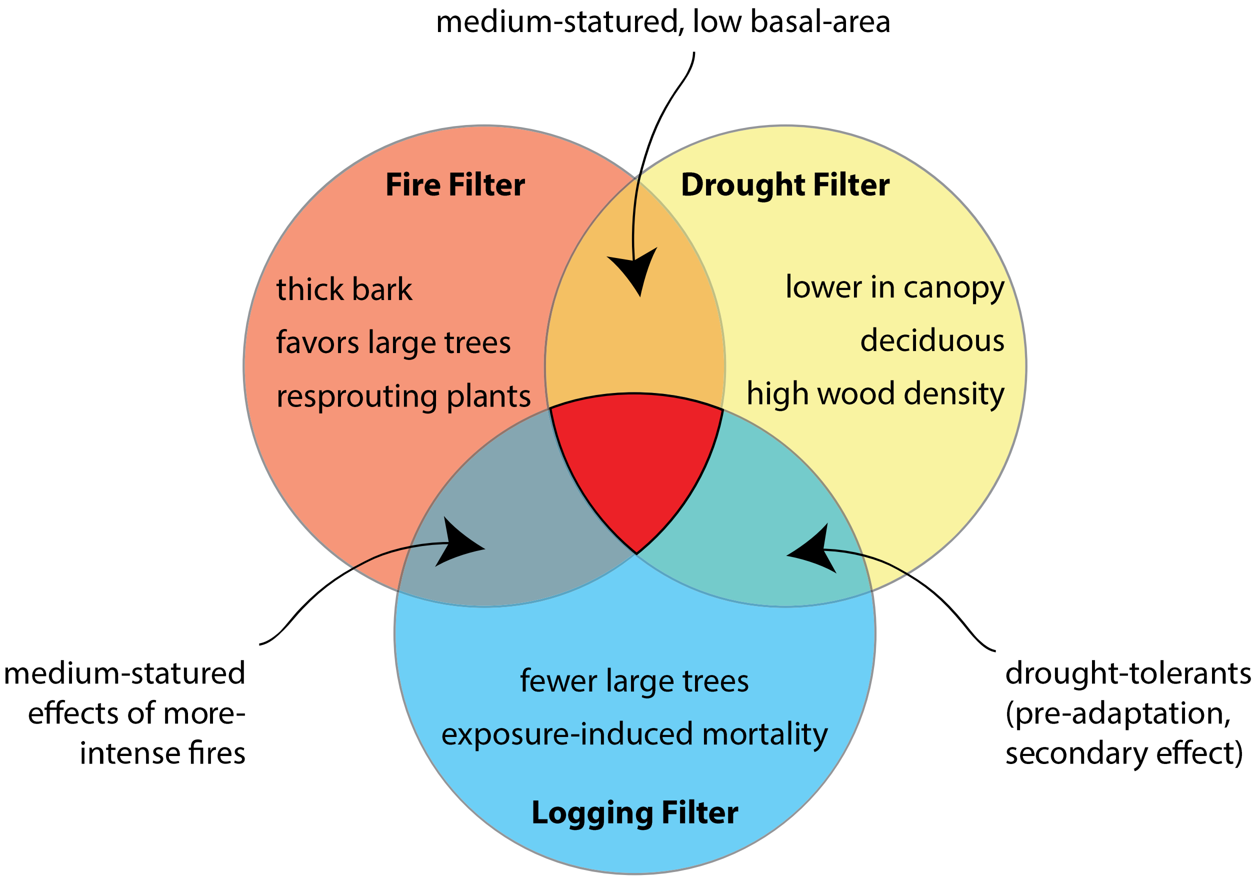


Figure 2 - 1. Gaant chart that depicts disturbances as filters. The tree community that results from passing through an intersection of the filters represents what would result from the effects of each filter alone (direct effects, additive) plus the interactions.

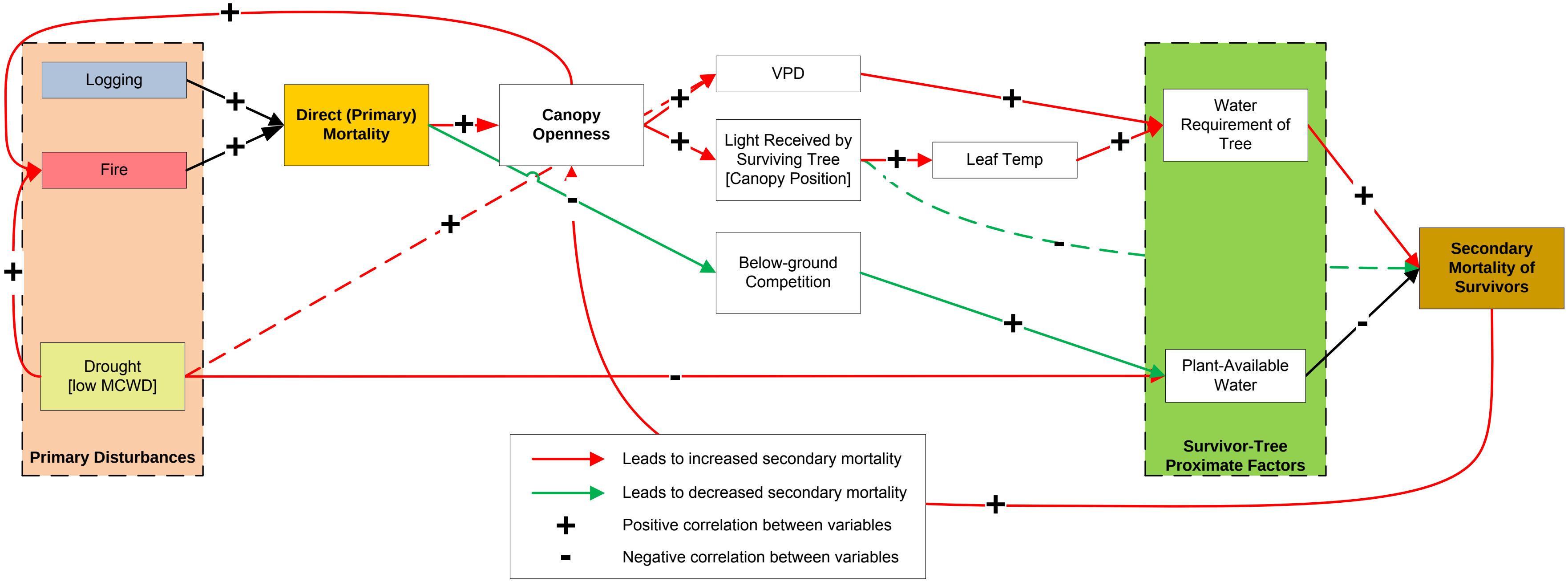


Figure 2 - 2. Logging and fire cause tree mortality that opens the canopy and affects the microclimates experienced by surviving trees that then may die due to these secondary effects

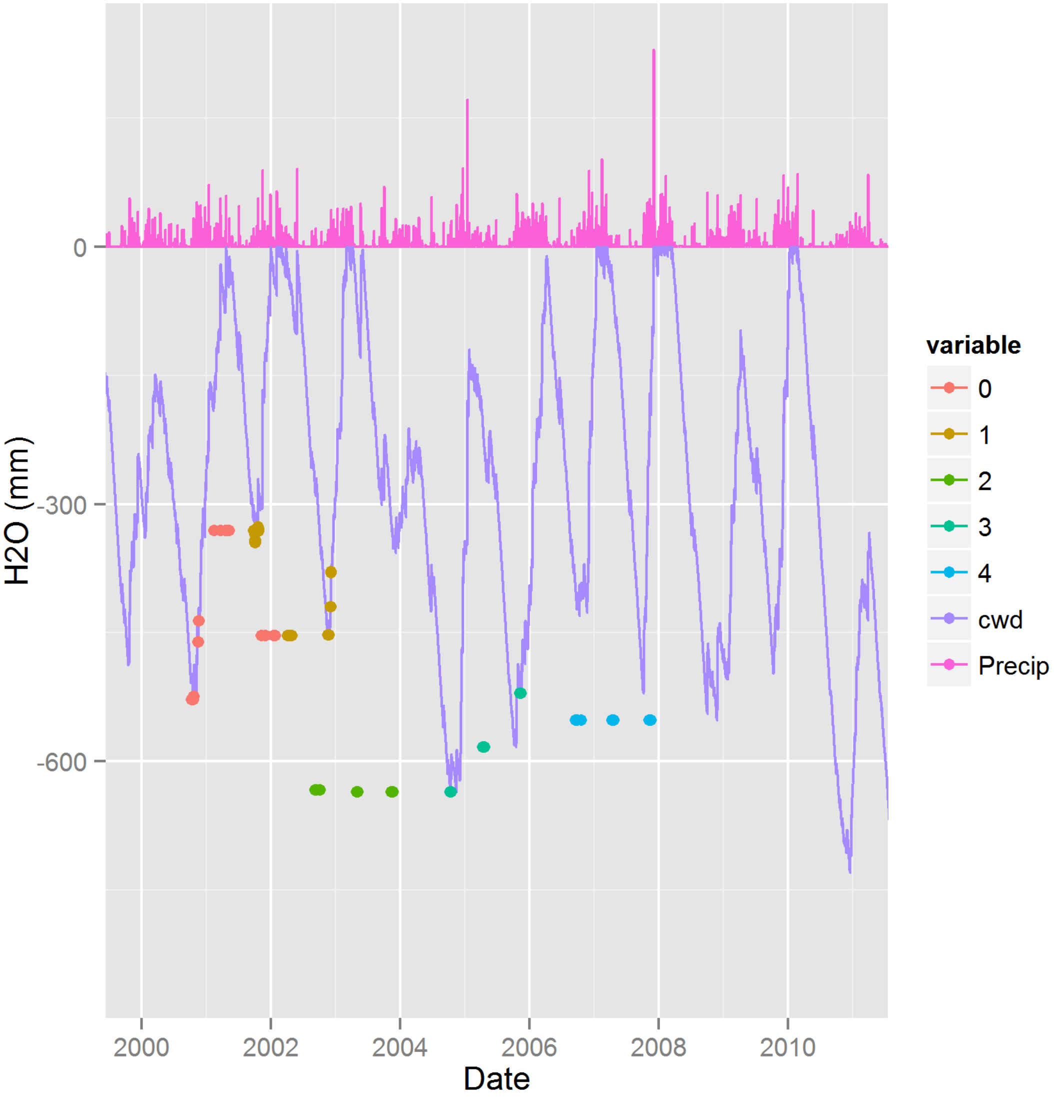


Figure 2 - 3. Precipitation (pink lines), Climatological Water Deficit (CWD, purple lines), and the MCWD experienced by censused trees during the interval between consecutive censuses (dots). Dot colors indicate different census numbers. The first census (a pre-logging census conducted between October 2000 and January 2002) is not shown because a prior interval is required to calculate a MCWD value.

Figure 2 - 4. As in Figure 2 - 3, but with an expanded date range to illustrate the historical context of soil moisture conditions.

Table 2 - 4. AIC test for survival models for small trees including SDI and MCWD as predictors. Data from burned areas were excluded.

	ΔAIC	df
SDI * MCWD	0.0	6
SDI + MCWD	2.1	5
SDI	71.4	4
MCWD	176.4	4
Intercept	252.2	3
SDI:MCWD	253.2	4

Table 2 - 5. Likelihood ratio tests for survival models for small trees. Data from burned areas were excluded.

	Df	AIC	logLik	deviance	Chisq	Chi Df	Pr(> Chisq)	Signif
Intercept	3	3737.9	-1866.0	3731.9				
MCWD	4	3662.2	-1827.1	3654.2	77.8	1	1.1542e-18	***
SDI + MCWD	5	3487.9	-1738.9	3477.9	176.3	1	3.137e-40	***
SDI * MCWD	6	3485.7	-1736.9	3473.7	4.1	1	0.041902	*

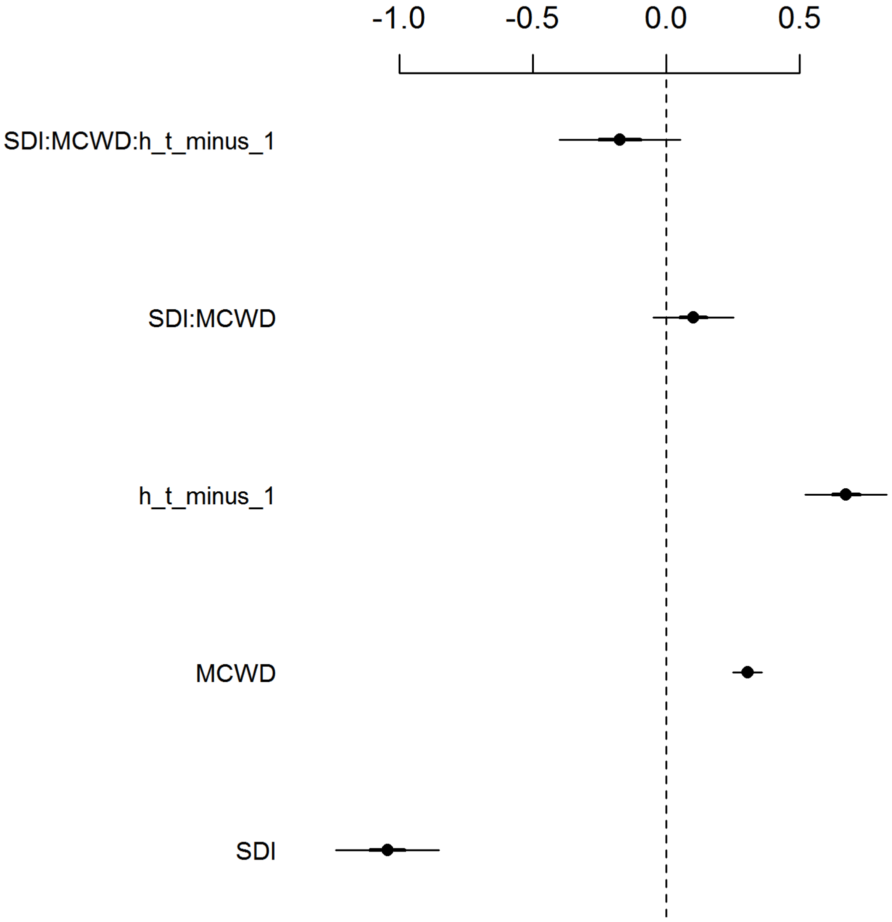


Figure 2 - 5. Coefficients from the best small-tree survival model including SDI and MCWD factors: $P_{survival} = [\log(-\log(1 - SDI * MCWD))]^{n})$. Points to the right of the dotted line indicate increasing survival rates as that factor increases, and vice versa. MCWD becomes more negative as conditions become drier, so a positive value for the MCWD coefficient indicates decreasing survival as conditions become drier. Data from burned areas were excluded.

Table 2 - 6. AIC test for small tree survival models including height (h_t_minus_1). The data for these models excludes trees for which height data were not available. The most parsimonious model includes the three-way interaction between SDI, MCWD and tree height, but excludes both two-way interactions involving height. Data from burned areas were excluded.

	ΔAIC	df
SDI * MCWD + h_t_minus_1 + SDI:MCWD:h_t_minus_1	0.0	8
SDI * MCWD + h_t_minus_1	0.9	7
SDI * MCWD * h_t_minus_1	1.2	10
SDI + MCWD + h_t_minus_1	2.0	6
SDI * MCWD	159.9	6
SDI	235.0	4
MCWD	296.7	4
SDI:MCWD	372.5	4
Intercept	374.2	3

Table 2 - 7. Likelihood ratio test for small tree survival models of the form $P_{survival} = [\log(-\log(1-x))]^n$, where n is census interval length, and x is a linear combination of the independent variables SDI, MCWD, and tree height. Data from burned areas were excluded.

	Df	AIC	logLik	deviance	Chisq	Chi Df	Pr(> Chisq)	Signif
Intercept	3	2689.6	-1341.8	2683.6				
MCWD	4	2612.0	-1302.0	2604.0	79.5	1	4.7176e-19	***
SDI * MCWD	6	2475.3	-1231.6	2463.3	140.7	2	2.7508e-31	***
SDI + MCWD + h_t_minus_1	6	2317.3	-1152.7	2305.3	158.0	0	0	***
SDI * MCWD + h_t_minus_1	7	2316.3	-1151.1	2302.3	3.0	1	0.082185	.
SDI * MCWD + h_t_minus_1 + SDI:MCWD:h_t_minus_1	8	2315.3	-1149.7	2299.3	2.9	1	0.086672	.
SDI * MCWD * h_t_minus_1	10	2316.6	-1148.3	2296.6	2.8	2	0.25234	

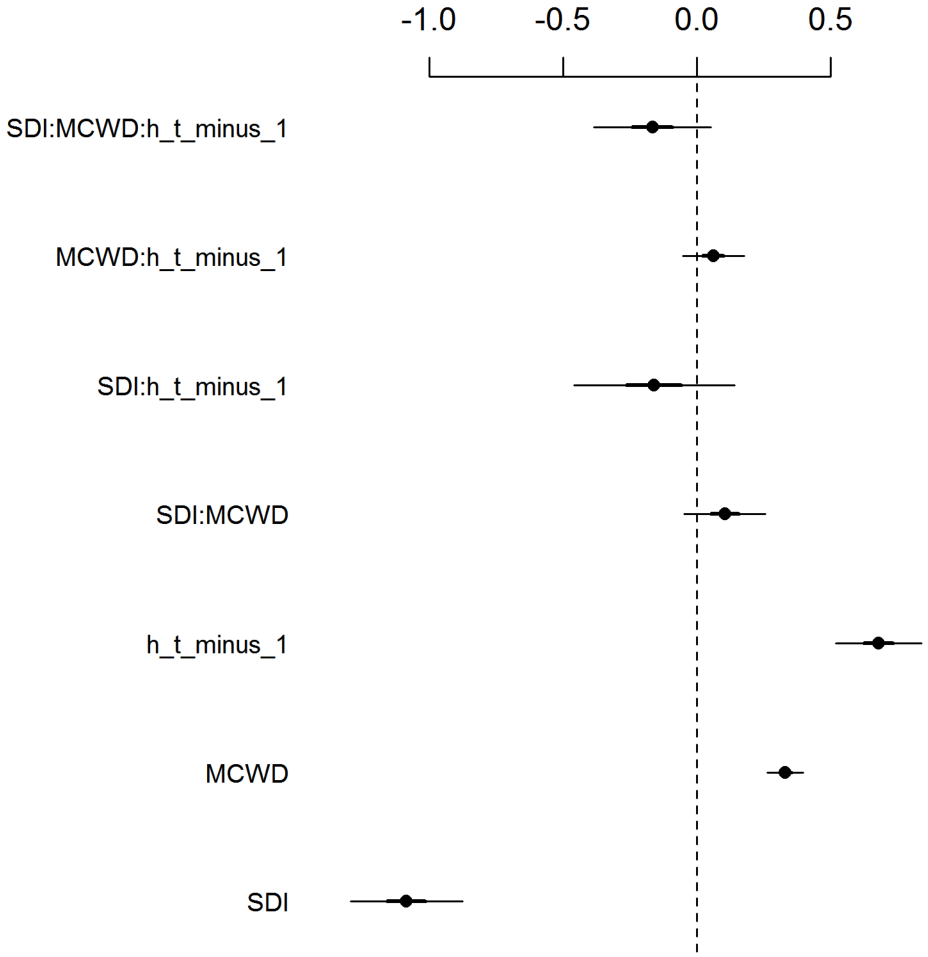


Figure 2 - 6. Coefficients for the full small tree survival model including SDI, MCWD and Tree Height (h_t_minus_1). Data from burned areas were excluded.

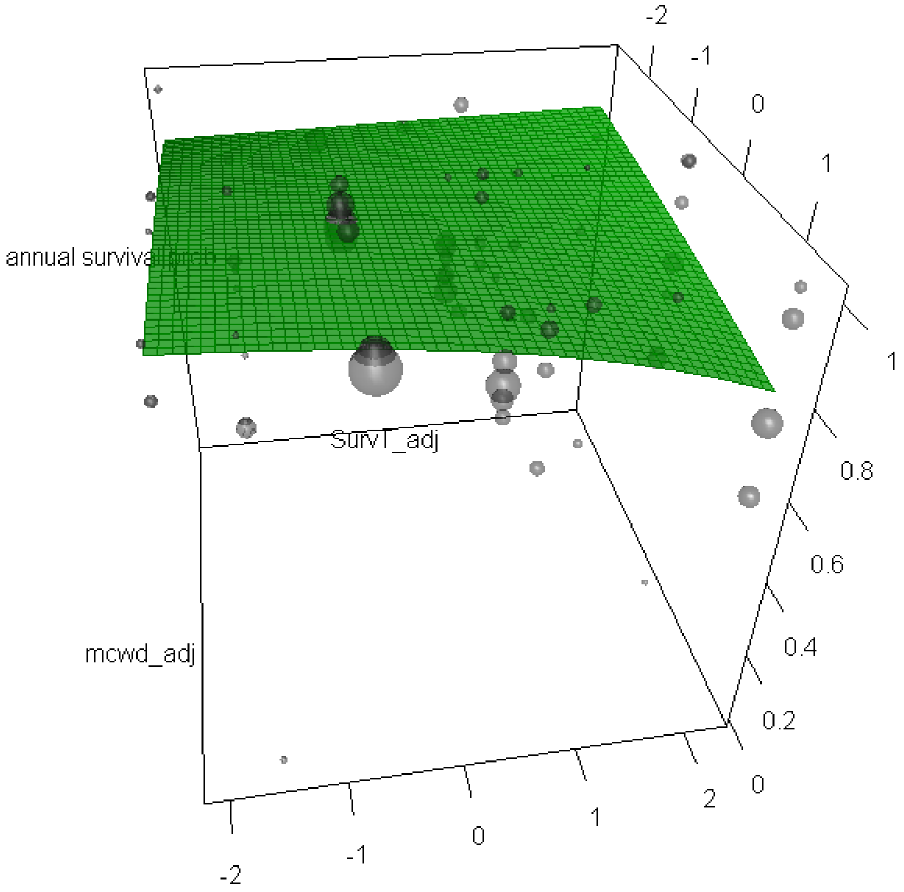


Figure 2 - 7. Annual survival probabilities of small trees as a function of MCWD and Drought Tolerance Index (SDI). Volumes of the grey spheres correspond to the number of observations at that combination of Drought Tolerance Index (SDI) and MCWD. The surface indicates the model fit to the data. While we only include the independent factors MCWD and SDI in this figure, their coefficients are taken from the most-parimonious model. Data from burned areas were excluded.

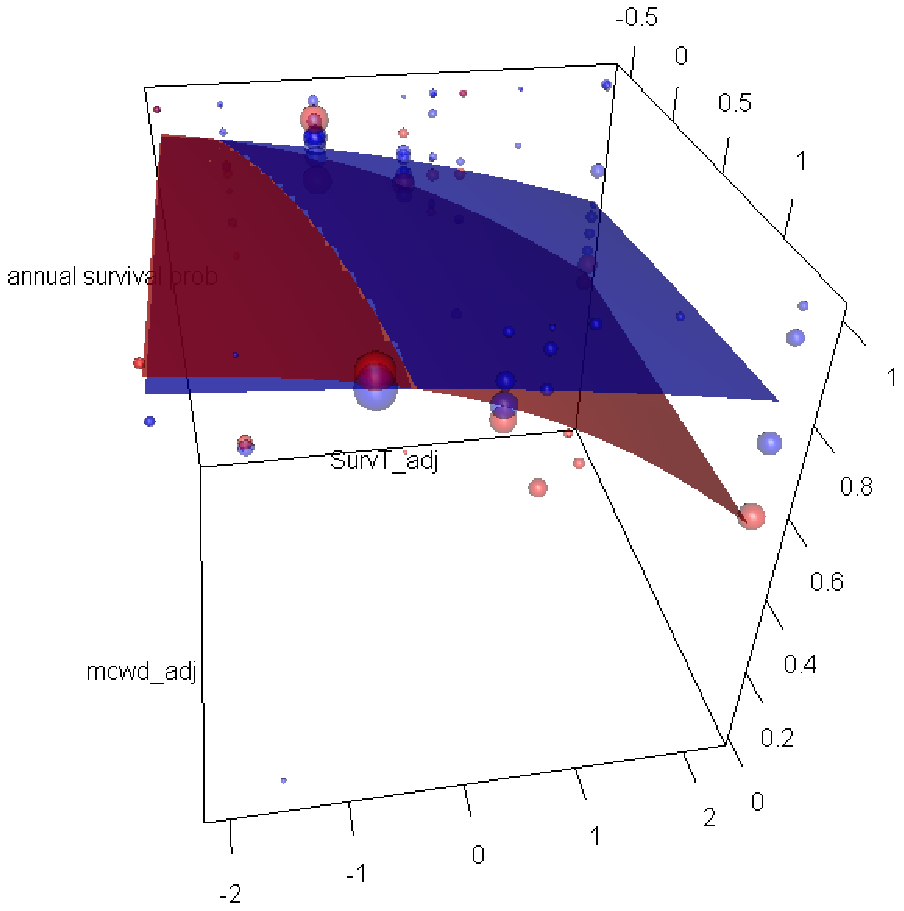


Figure 2 - 8. Survival of small trees versus Species Drought Tolerance Index (SDI) and dryness (MCWD). Surfaces are model predictions and spheres are data points. Blue surface and spheres represent logged plots whereas the red ones represent the control plots. Trees in burned areas were not included. Census data from 2009 and 2010 were removed because we had no unburned control measurements from that census. Thus, MCWD only reached -0.5 here (-635 mm un-normalized), whereas it reached -1 (-835mm un-normalized) in models that include the more recent censuses.

Table 2 - 8. AIC table for various models of small tree survival versus MCWD, drought index, and whether or not the tree occurs in a logging gap.

	ΔAIC	df
SDI * gap + MCWD * gap + SDI * MCWD	0.0	9
SDI * MCWD * gap	1.7	10
SDI * gap + MCWD	3.1	7
SDI + SDI:gap + MCWD	4.5	6
SDI * gap + MCWD * gap	4.9	8
MCWD * SDI	31.0	6
SDI + MCWD + gap	32.7	6
MCWD + SDI	33.5	5
MCWD * gap + SDI	34.4	7
SDI	100.3	4
MCWD	211.1	4
gap	283.4	4
Intercept	284.9	3

Table 2 - 9. Likelihood Ratio Test for models explaining small-tree survival as a function of MCWD, drought index, and occurrence in gap/non-gap areas. All models have binomial error structures, account for variation in census interval lengths, and were fit using maximum likelihood methods.

	Df	AIC	logLik	deviance	Chisq	Chi Df	Pr(> Chisq)	Signif
Intercept	3	3722.9	-1858.5	3716.9				
SDI	4	3538.3	-1765.2	3530.3	186.6	1	1.7721e-42	***
MCWD + SDI	5	3471.5	-1730.7	3461.5	68.9	1	1.0601e-16	***
SDI + SDI:gap + MCWD	6	3442.6	-1715.3	3430.6	30.9	1	2.6909e-08	***
SDI * gap + MCWD	7	3441.1	-1713.6	3427.1	3.4	1	0.063525	.
SDI * gap + MCWD * gap	8	3442.9	-1713.5	3426.9	0.2	1	0.65205	
SDI * gap + MCWD * gap + SDI * MCWD	9	3438.0	-1710.0	3420.0	6.9	1	0.0086841	**
SDI * MCWD * gap	10	3439.7	-1709.9	3419.7	0.3	1	0.58236	

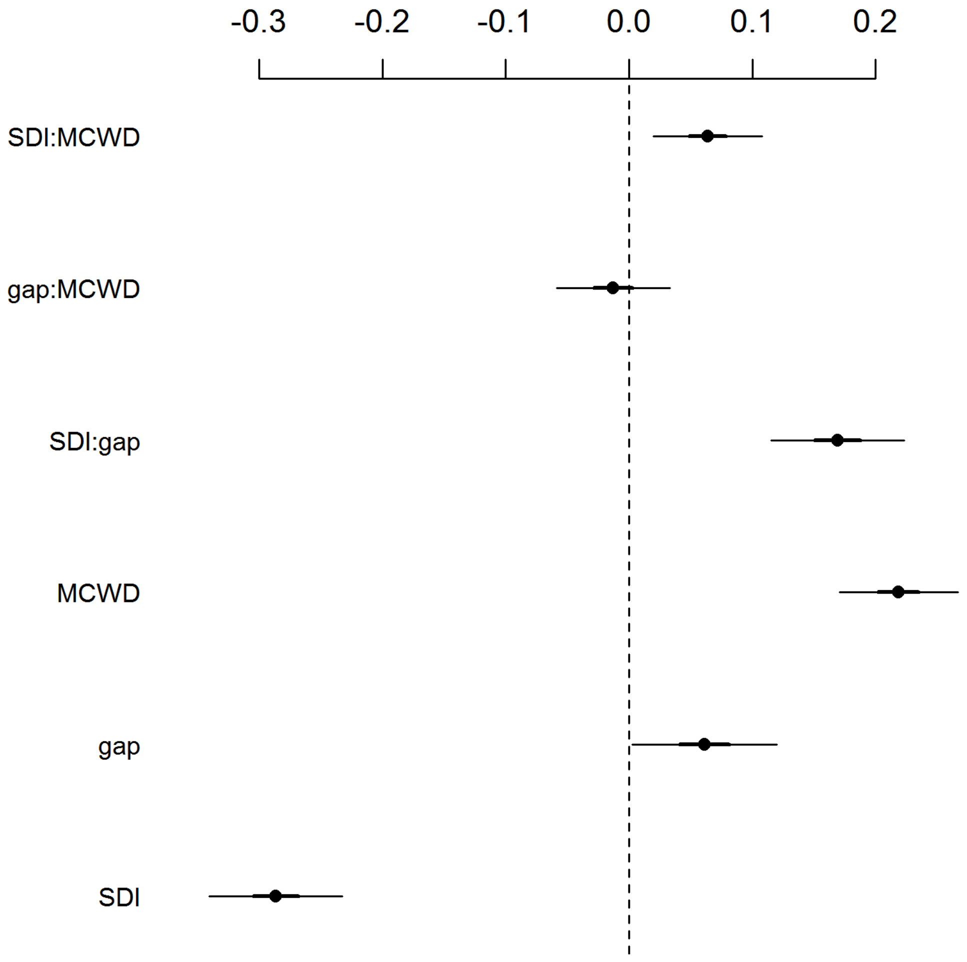


Figure 2 - 9. Coefficients of the most parsimonious small-tree survival model including SDI and MCWD factors, and whether or not the tree occurred in a logging gap

Table 2 - 10. AIC table for small-tree survival models including MCWD, Drought Index, gap, and logging factors

	ΔAIC	df
SDI * MCWD + SDI:gap + SDI:logged	0.0	8
SDI * gap + MCWD * gap + SDI * logged + MCWD * logged + SDI * MCWD	5.0	12
SDI * MCWD * (gap + logged)	6.0	14
SDI + SDI:gap + SDI:logged + MCWD	6.4	7
SDI:gap + SDI * logged + MCWD	6.8	8
SDI * gap + SDI:logged + MCWD	8.2	8
SDI * gap + SDI * logged + MCWD	8.7	9
SDI * gap + MCWD * gap + SDI * logged + MCWD * logged	11.3	11
SDI + SDI:gap + MCWD	17.9	6
MCWD * SDI	38.0	6
MCWD + SDI	43.9	5
SDI + MCWD + logged	44.7	6
SDI + MCWD + gap	45.7	6
MCWD * gap + SDI	46.3	7
SDI + MCWD + gap + logged	46.5	7
SDI	69.5	4
MCWD	182.2	4
Intercept	212.1	3
logged	212.7	4
gap	213.7	4

Table 2 - 11. Likelihood Ratio Test for small-tree survival models involving MCWD, drought index, gap, and logging factors

	Df	AIC	logLik	deviance	Chisq	Chi Df	Pr(> Chisq)	Signif
Intercept	3	3219.5	-1606.7	3213.5				
SDI	4	3076.9	-1534.5	3068.9	144.6	1	2.6779e-33	***
MCWD + SDI	5	3051.3	-1520.7	3041.3	27.6	1	1.4855e-07	***
SDI + SDI:gap + MCWD	6	3025.3	-1506.6	3013.3	28.0	1	1.1887e-07	***
SDI + SDI:gap + SDI:logged + MCWD	7	3013.8	-1499.9	2999.8	13.5	1	0.00023519	***
SDI:gap + SDI * logged + MCWD	8	3014.2	-1499.1	2998.2	1.5	1	0.21471	
SDI * gap + SDI * logged + MCWD	9	3016.1	-1499.1	2998.1	0.1	1	0.74907	
SDI * gap + MCWD * gap + SDI * logged + MCWD * logged	11	3018.7	-1498.4	2996.7	1.4	2	0.50046	
SDI * gap + MCWD * gap + SDI * logged + MCWD * logged + SDI * MCWD	12	3012.4	-1494.2	2988.4	8.4	1	0.0038471	**
SDI * MCWD * (gap + logged)	14	3013.4	-1492.7	2985.4	2.9	2	0.22933	

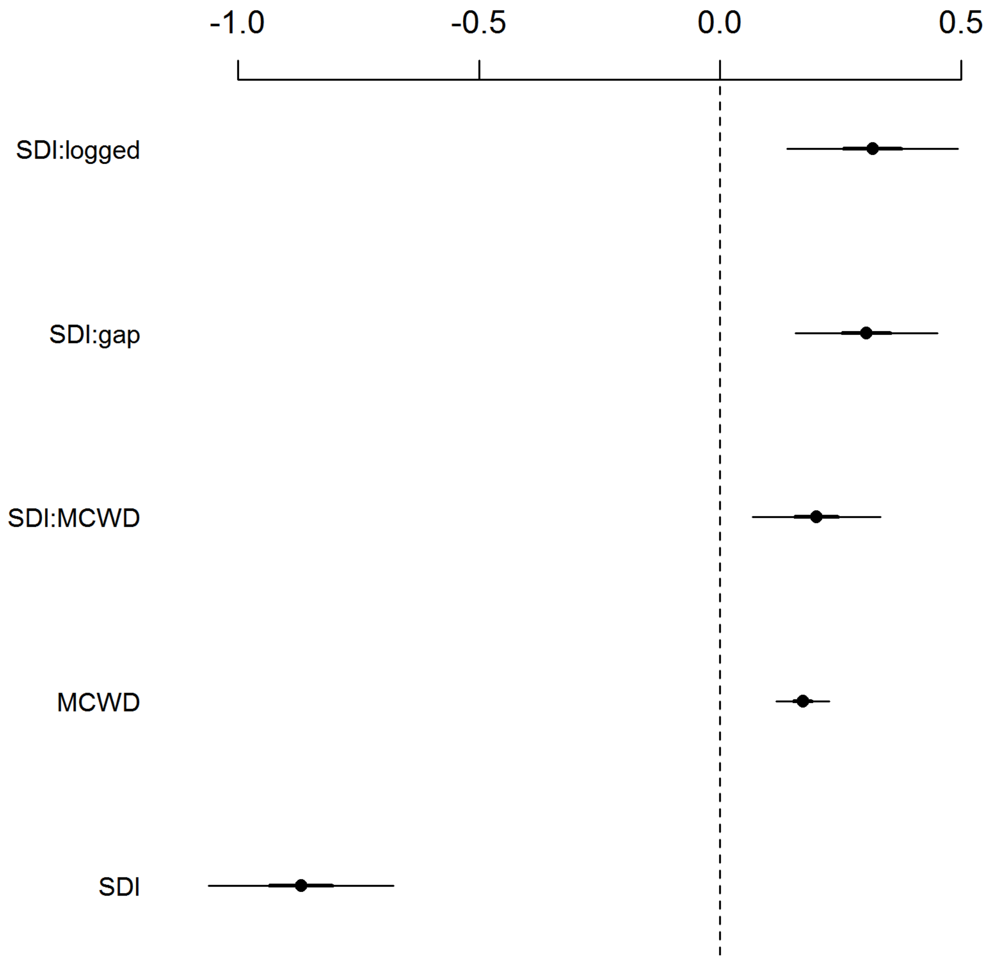


Figure 2 - 10. Coefficients for best small-tree survival model involving MCWD, drought index, gap, and logged factors

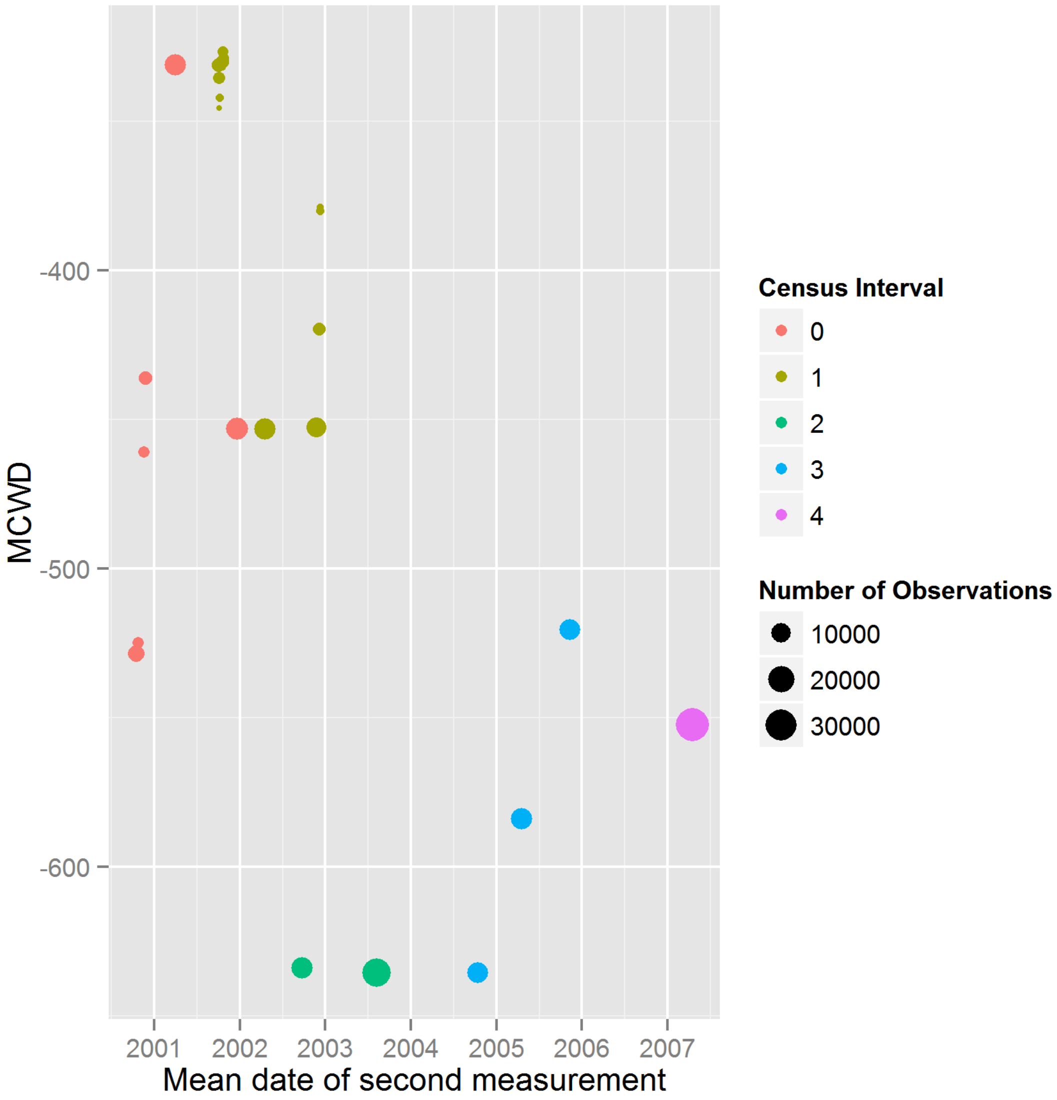


Figure 2 - 11. MCWD values over time; multiple MCWD values are provided for each census interval to reflect changes in conditions. Overall, MCWD increased over the course of the study.

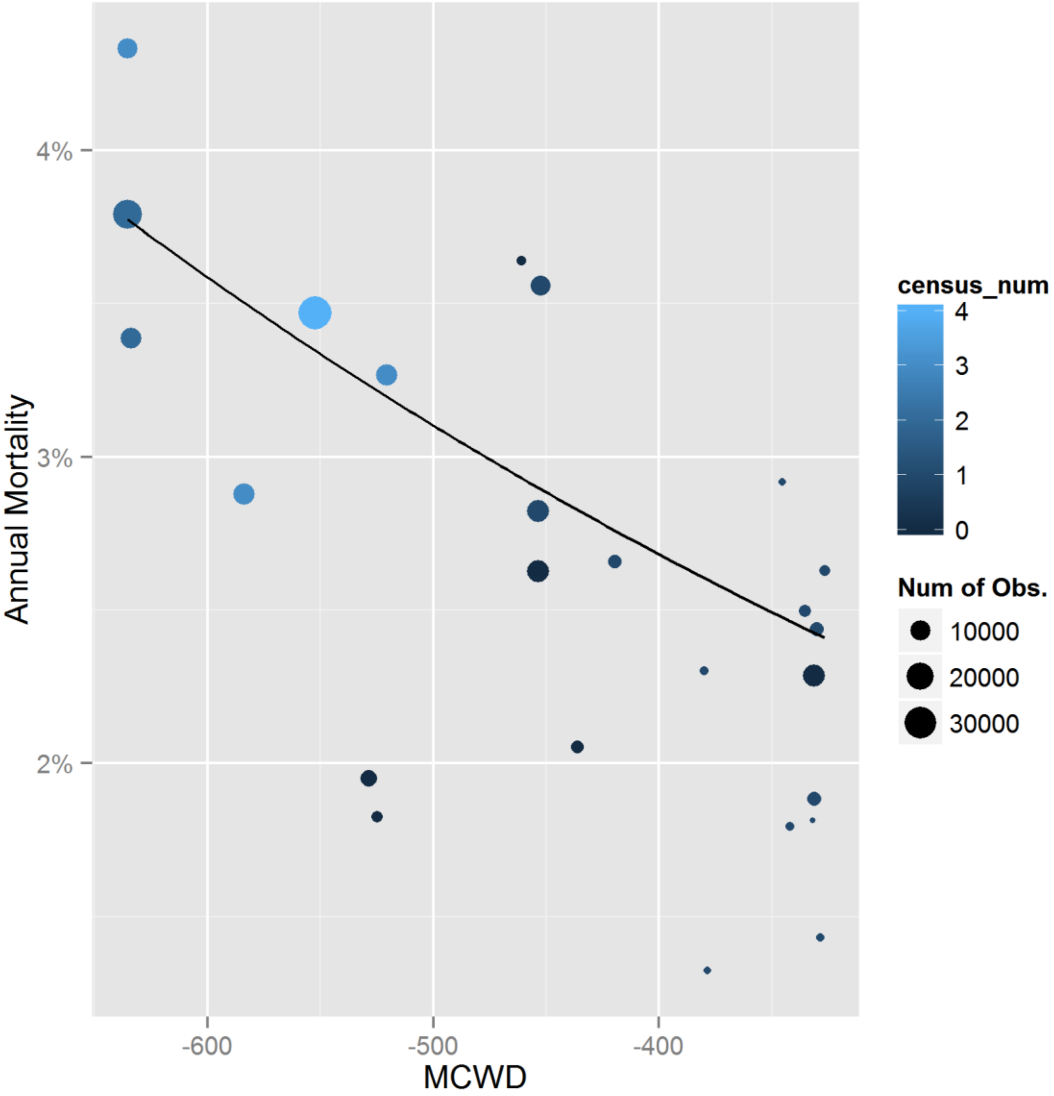


Figure 2 - 12. Large tree mortality rates as a function of MCWD. Trees that died due to felling, collateral logging damage, and silvicultural treatments were removed. Circle size indicates the number of survival and mortality events recorded during a census interval at that MCWD. Color indicates census number. Conditions go from dry to wet along the x-axis from left to right. The black line indicates a maximum likelihood fit of a logistic survival function to each survival and mortality event. The maximum-likelihood fit accounts for the census length of each individual survival and mortality event.

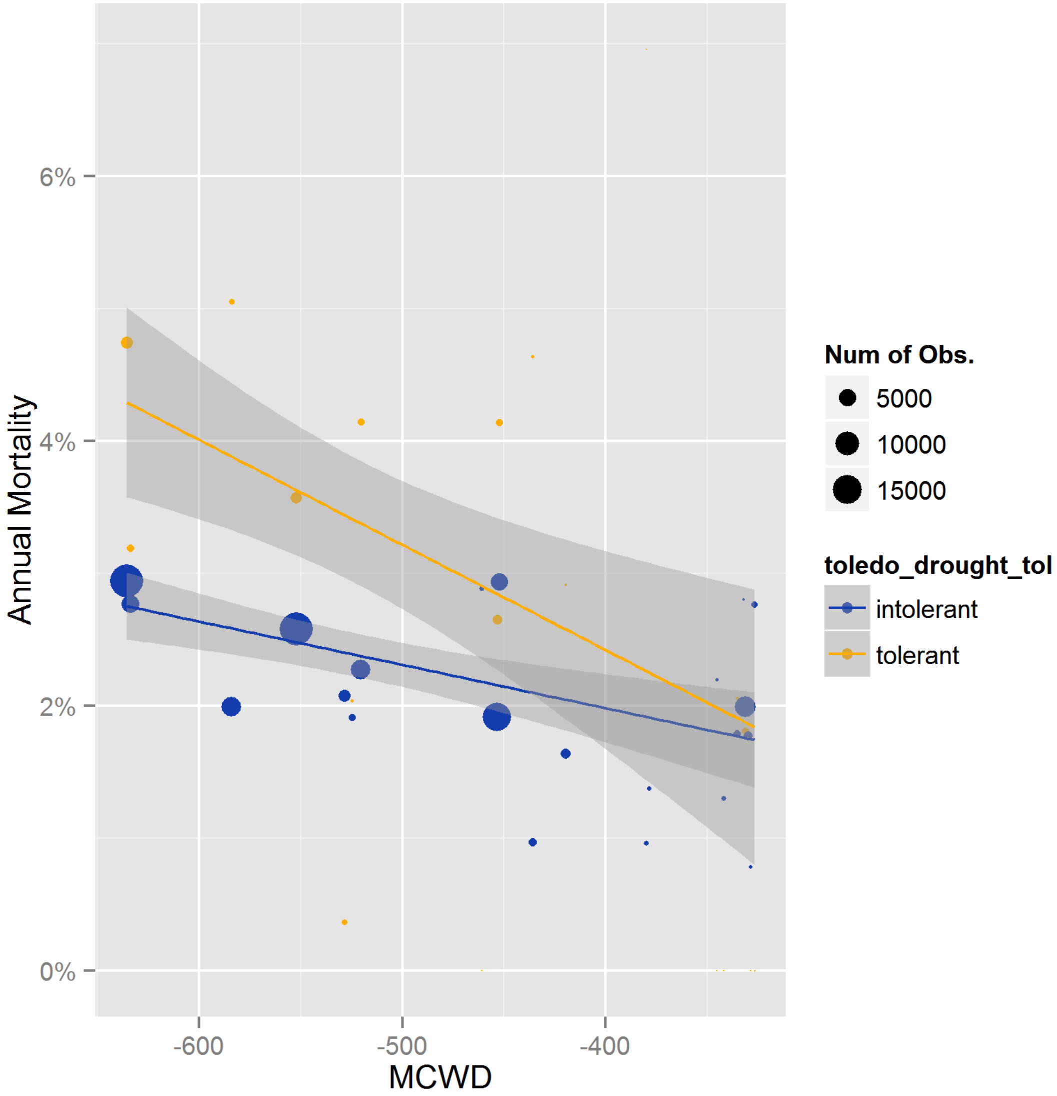


Figure 2 - 13. Annual mortality versus MCWD for all large trees (minus those killed by felling or silvicultural treatments and those in burned areas) grouped by their drought-tolerance as classified by our drought-tolerance algorithm based on Toledo et al. (2012). Conditions are drier to the left on the x-axis (more negative MCWD). Species aggregated in blue are expected to be drought-intolerant, whereas those in orange are expected to be drought-tolerant. Lines are linear regressions weighted by number of observations, and shaded areas are standard errors of the predicted means.

Table 2 - 12. AIC table for survival models that include drought tolerance classes based on tree species distributions from Toledo et al. (2012)

	ΔAIC	df
dbh + MCWD * crown_pos + toledo_drought_tol * MCWD	0.0	10
dbh + MCWD * crown_pos + MCWD * toledo_drought_tol + crown_pos * toledo_drought_tol	2.0	11
dbh + MCWD * crown_pos * toledo_drought_tol	3.9	12
toledo_drought_tol * MCWD	53.3	7
MCWD * crown_pos + toledo_drought_tol * MCWD	55.7	9
MCWD * crown_pos + MCWD * toledo_drought_tol + crown_pos * toledo_drought_tol	57.7	10

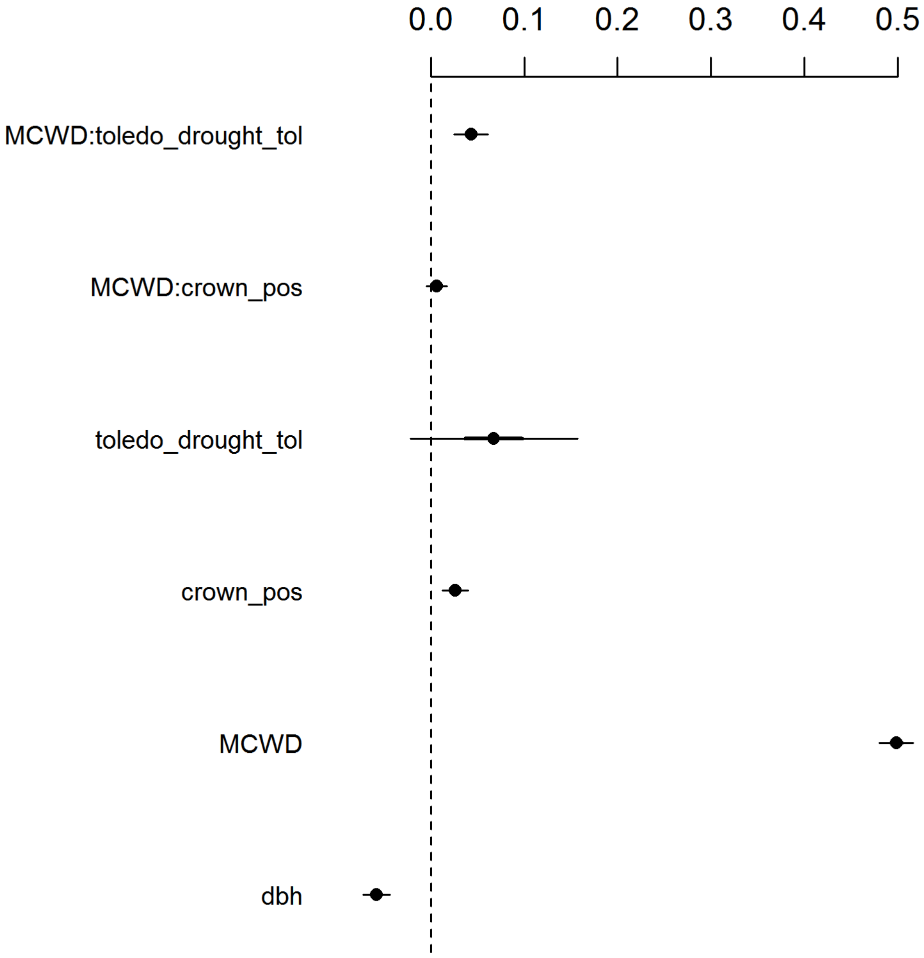


Figure 2 - 14. Coefficients for the best large-tree survival model according to AIC (Table 2 - 12) including drought tolerance classification based on tree species distributions from Toledo et al. (2012)

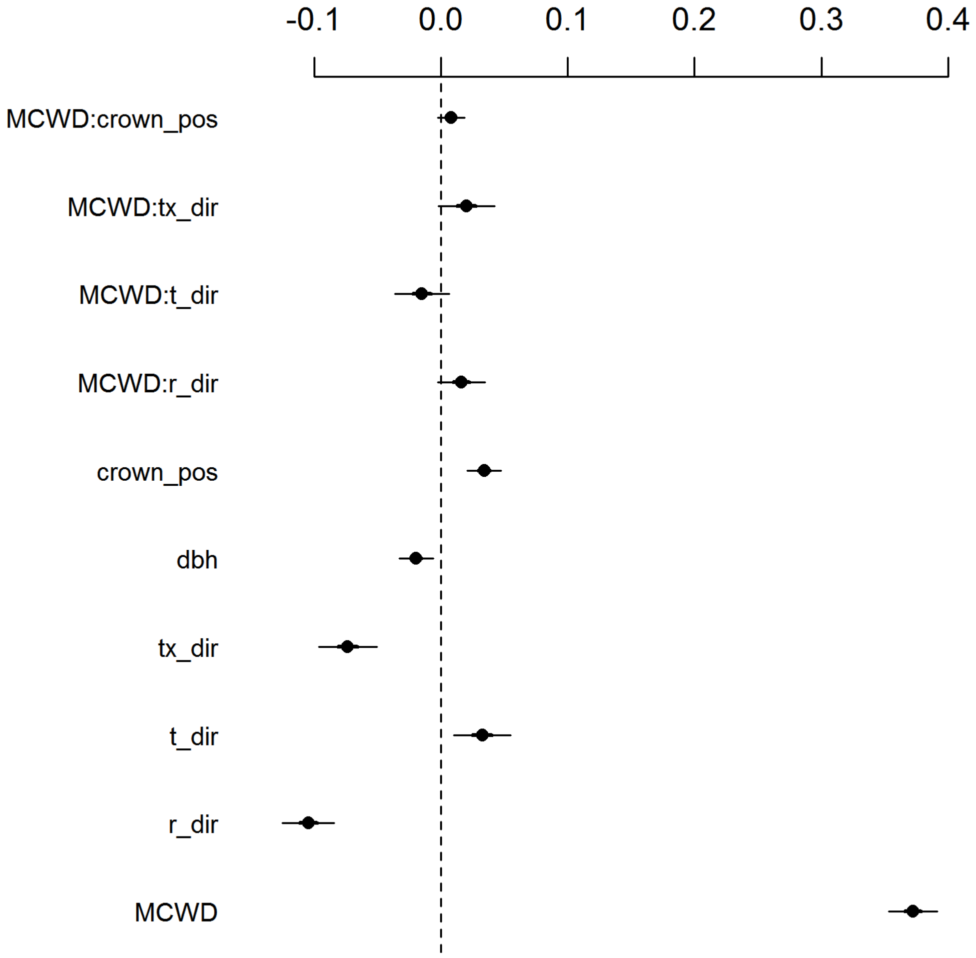


Figure 2 - 15. Coefficients from the survival model including species' directional associations with environmental gradients (rainfall_association = rainfall, temperature_association = temperature, soil_texture_association = soil texture). Note that while the main effects of the environmental gradient associations were significant, their interactions with MCWD were only either marginally (rainfall association, MCWD:r_dir and soil texture association, MCWD:tx_dir) or not significant (temperature association, MCWD:t_dir).

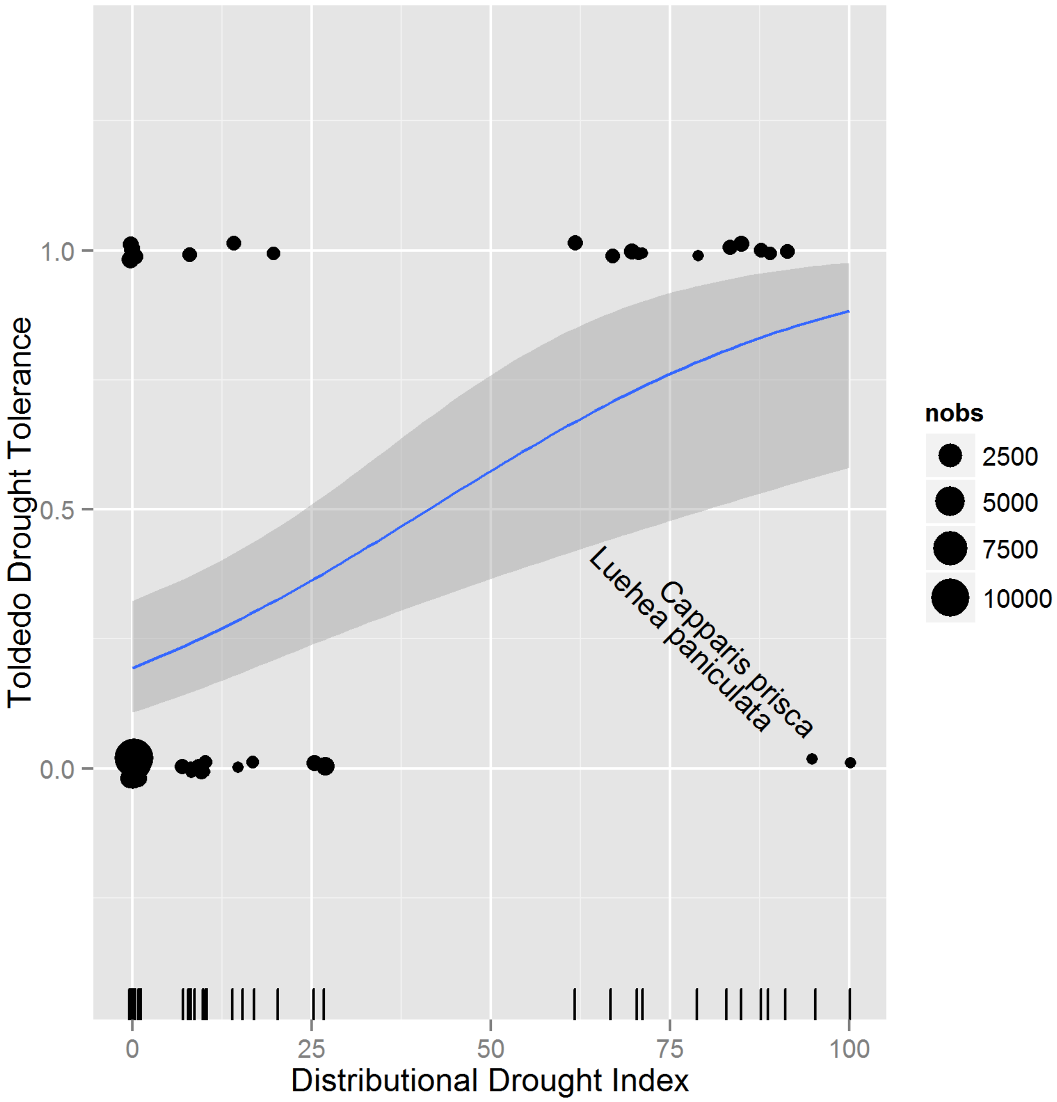


Figure 2 - 16. The relationship between the continuous Distributional Drought Index based on stem densities between a moist (La Chonta) and dry (INPA) site (y-axis), and the discrete Toledo Drought Index (x-axis) based on increasing or decreasing stem abundance in more widely distributed plots related to three environmental factors (Toledo et al. 2012). The blue line is a GAM fit with a binomial error distribution.

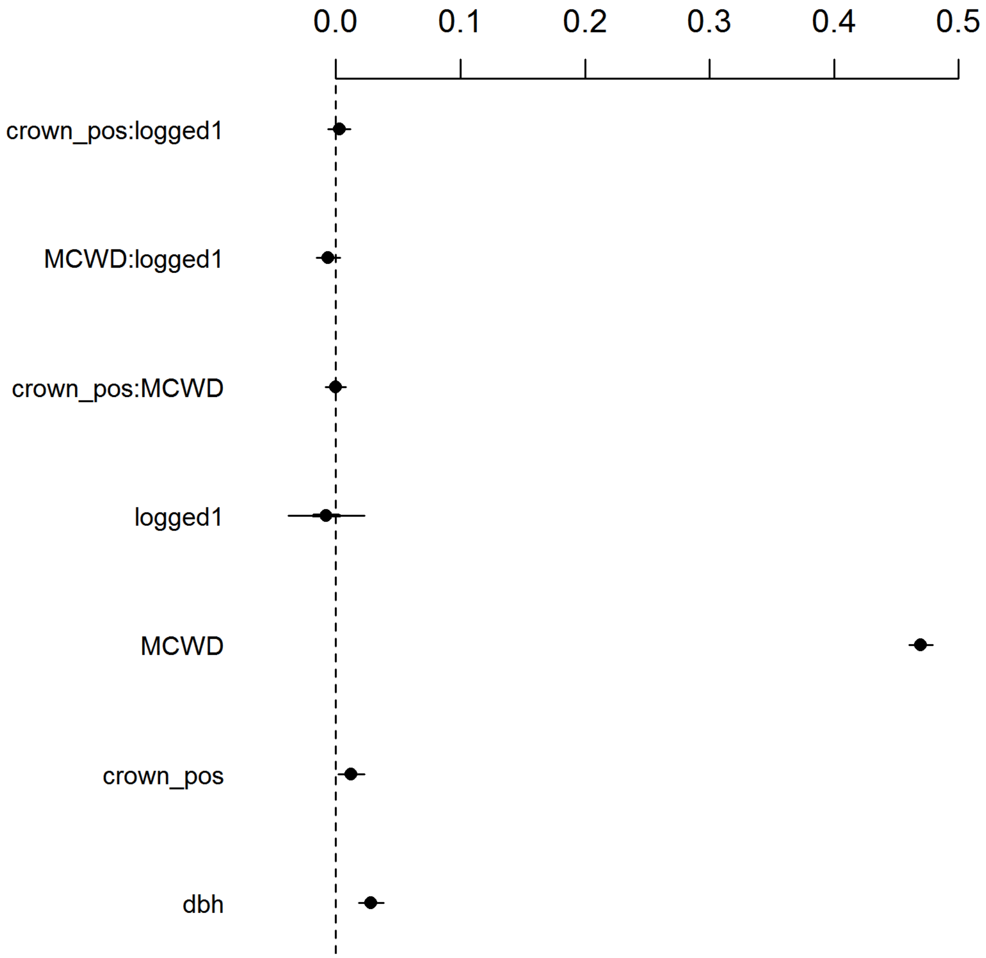


Figure 2 - 17. Survival model for large trees including the strongest predictive factors from the large tree models above and interacts them with the logged predictor (survival ~ dbh + pc*mcwd + logged*mcwd + pc*logged).

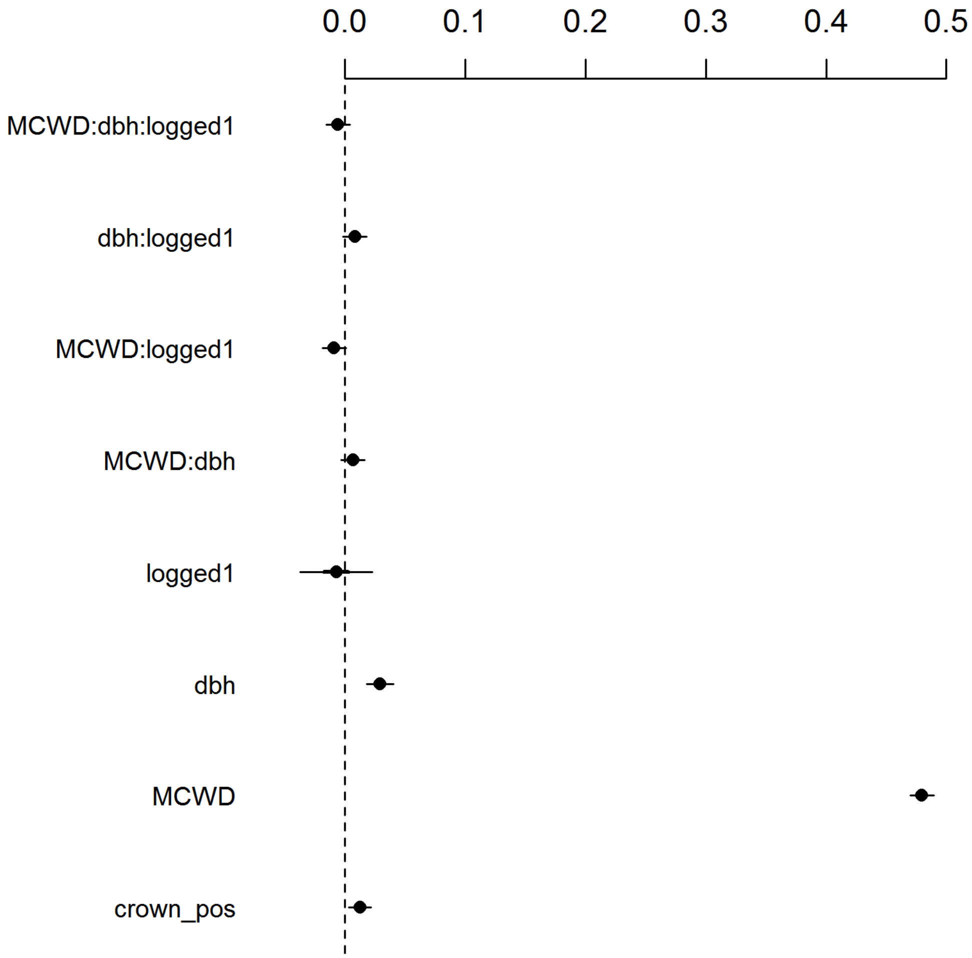


Figure 2 - 18. Large-tree survival model coefficients including interactions with DBH (x = crown_position + MCWD * DBH * logged).

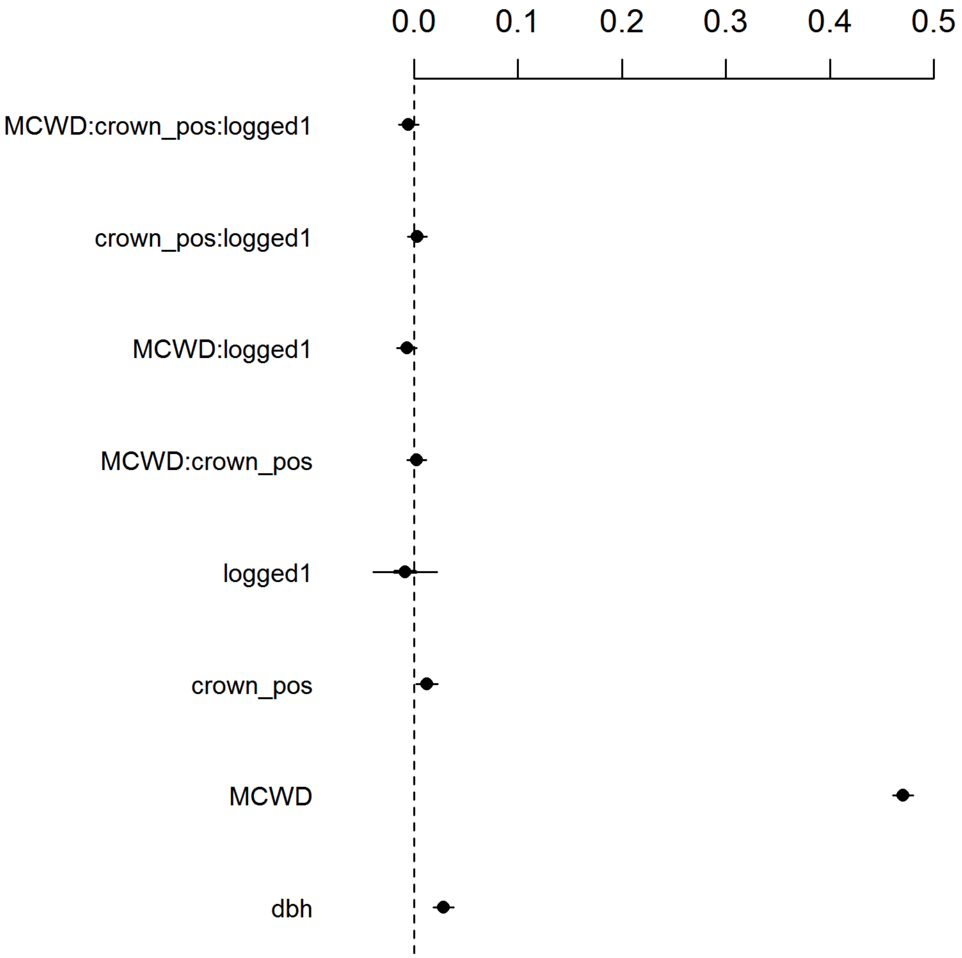


Figure 2 - 19. Large-tree survival model coefficients including interactions with canopy position (x = DBH + MCWD * crown_position * logged).

Table 2 - 13. AIC test of large tree survival models involving various interactions of DBH and crown position with MCWD. The crown position:MCWD interaction is a better predictor of tree survival than the DBH:MCWD interaction.

	ΔAIC	df
dbh + crown_pos * MCWD	0.0	7
crown_pos + dbh * MCWD	3.3	7
dbh + MCWD * crown_pos * logged	13201.8	11
crown_pos + MCWD * dbh * logged	13204.0	11

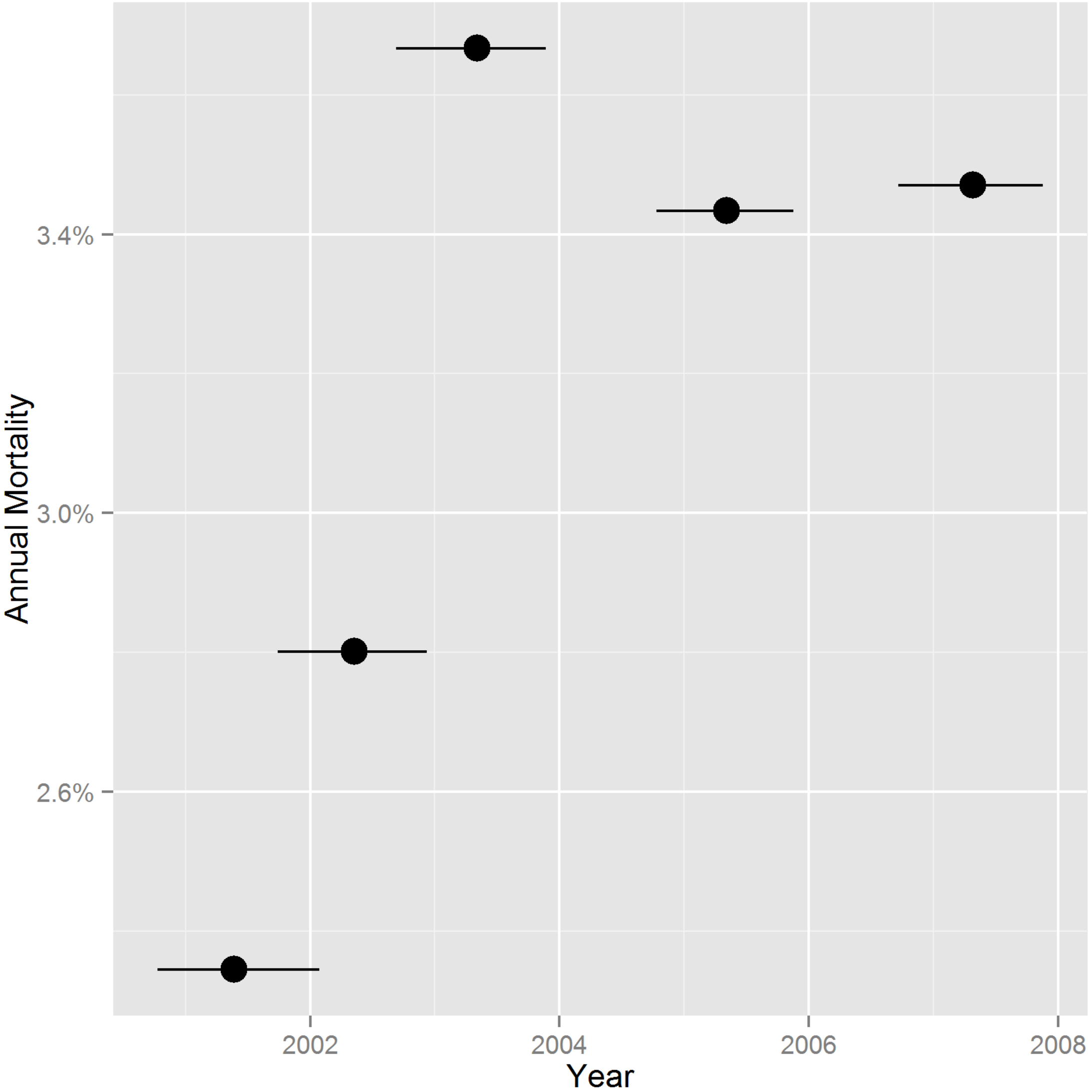


Figure 2 - 20. Large tree mortality rates for each census interval. Tree deaths due to logging and silviculture as well as all trees in burned areas were removed. Horizontal lines indicate the time periods over which each census was conducted.

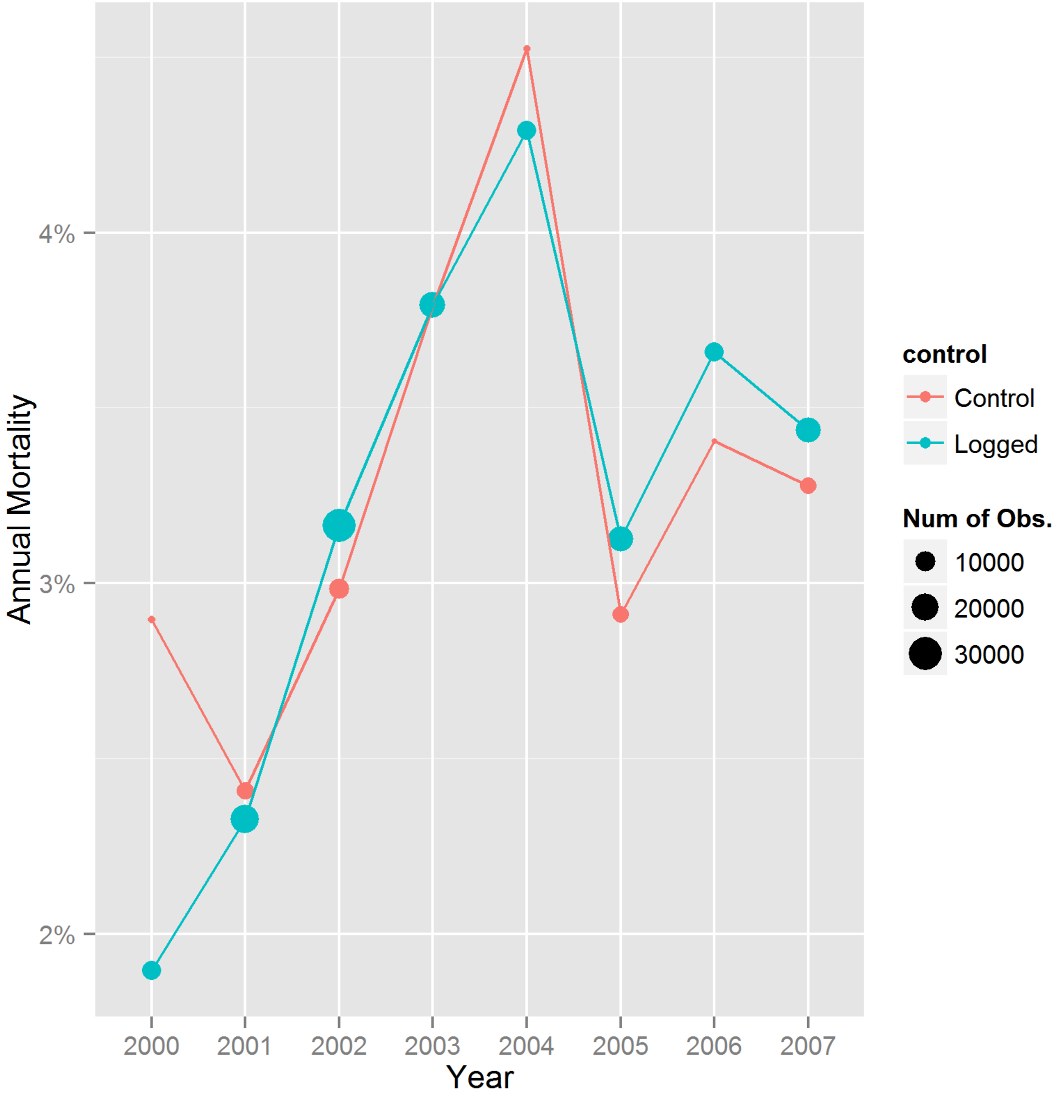


Figure 2 - 21. Mortality rates of trees >10 cm DBH versus year of the census. Tree directly killed by logging and silviculture treatments as well as all trees in burned areas were removed. Dot size represents number of survival and mortality events observed.

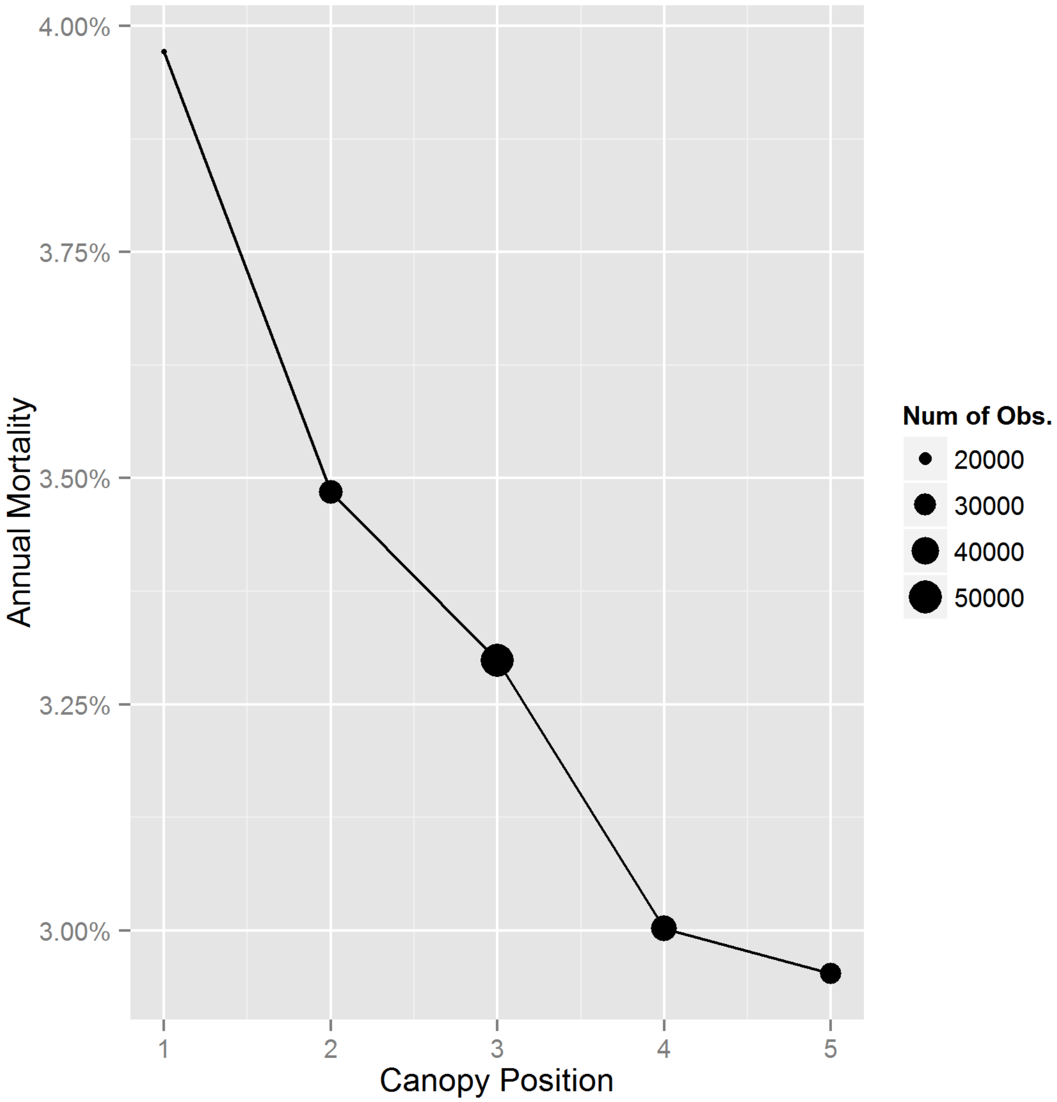


Figure 2 - 22. Adult mortality per crown class (canopy position; Clark and Clark 1992). Tree deaths due to logging and silviculture as well as all trees in burned areas were removed. Dot size represents number of survival and mortality events observed.

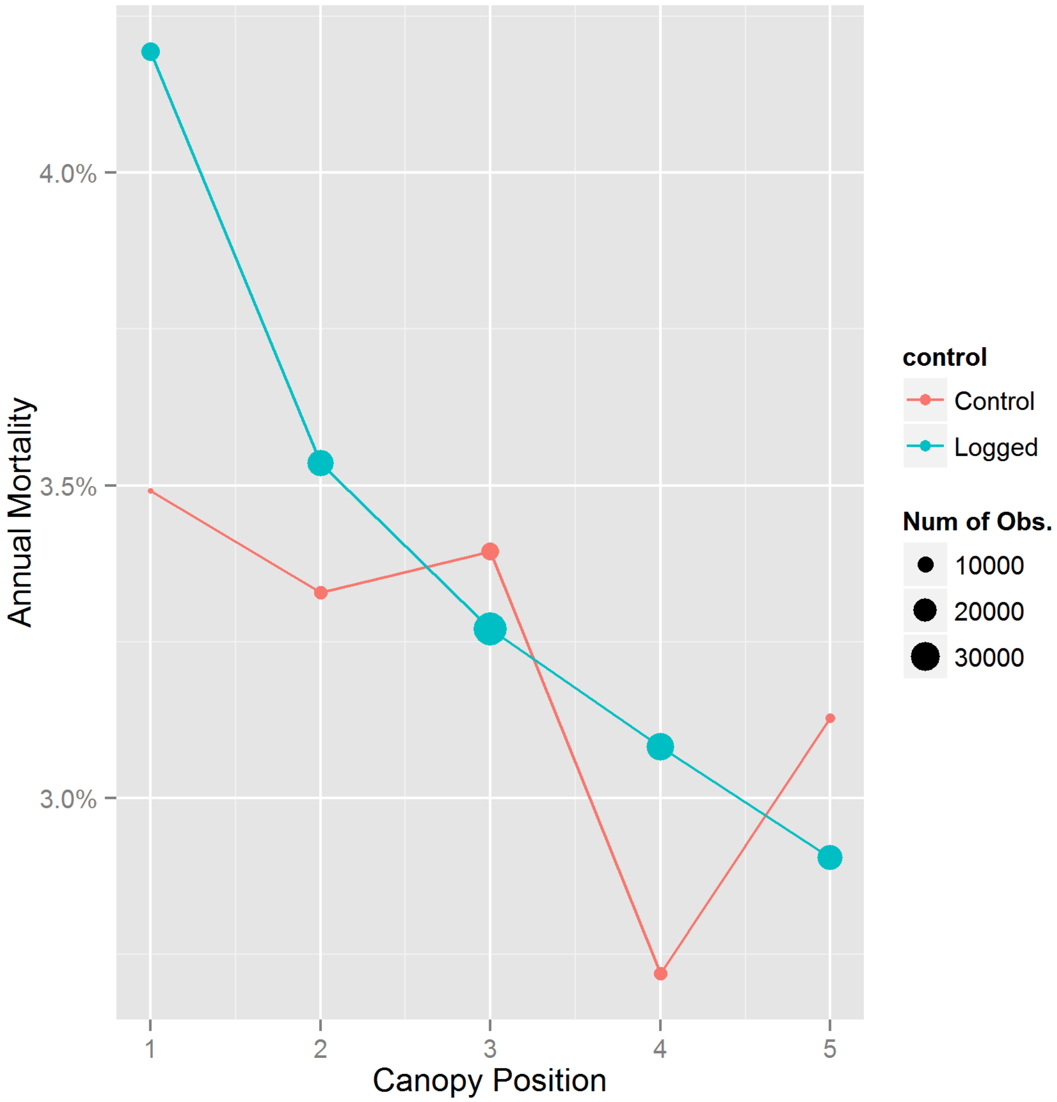


Figure 2 - 23. Adult mortality per crown exposure class for logged and control plots. Tree deaths due to logging and silviculture as well as all trees in burned areas were removed. Dot size represents number of survival and mortality events observed.

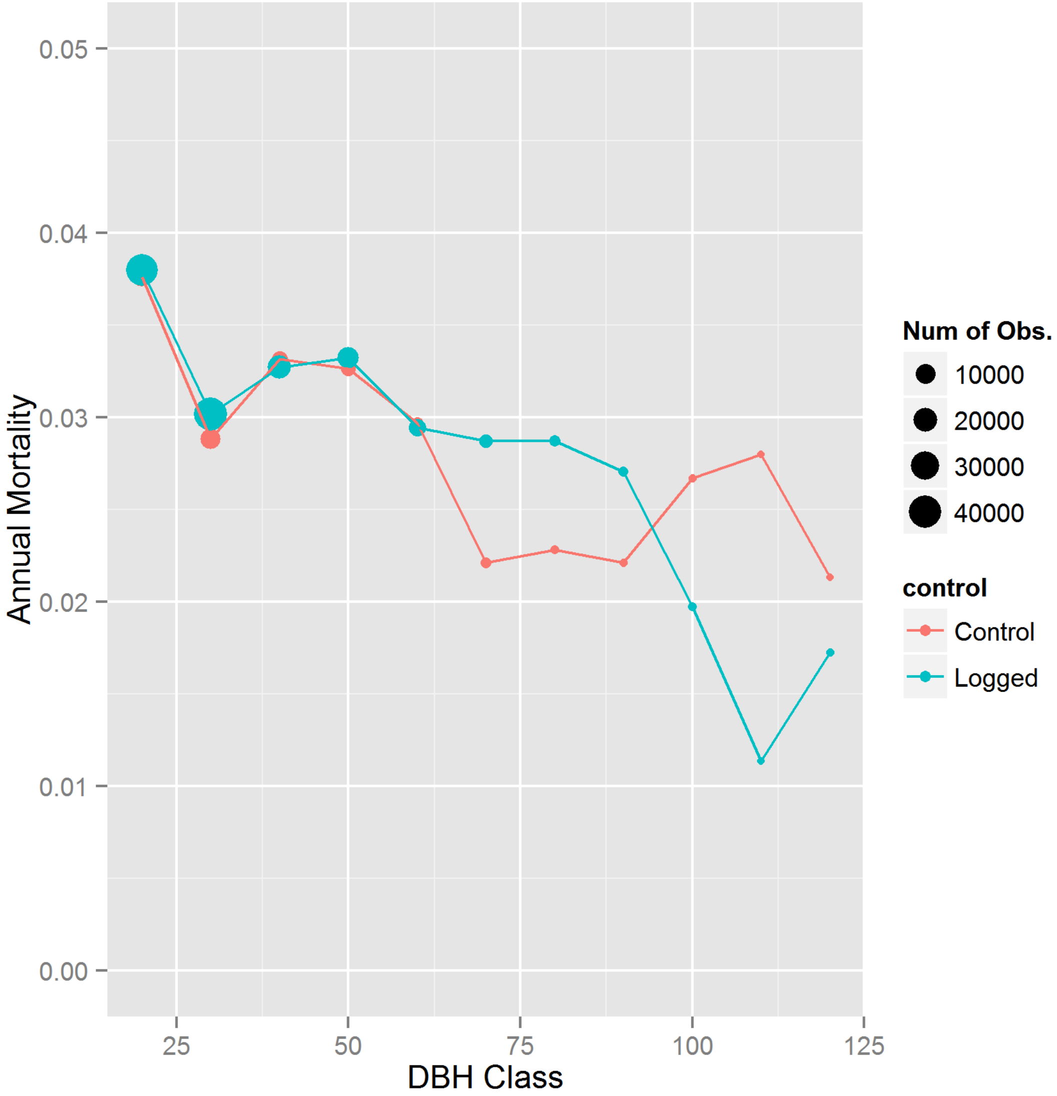


Figure 2 - 24. Adult mortality per DBH class for logged and un-logged plots. Tree deaths due to logging and silviculture as well as all trees in burned areas were removed. Dot size represents number of survival and mortality events observed.

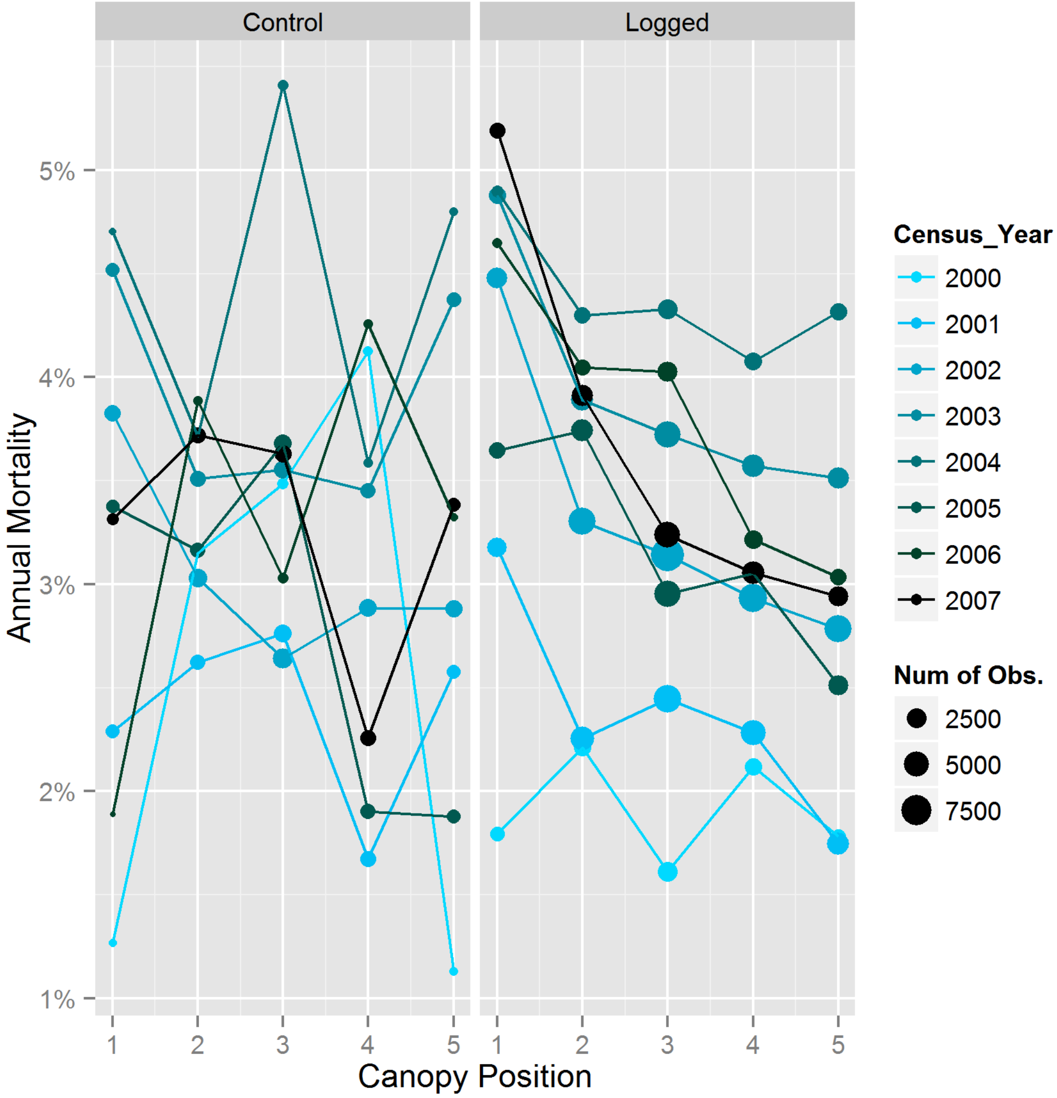


Figure 2 - 25. Adult mortality per crown class for logged and control treatments. Tree deaths due to logging and silviculture as well as all trees in burned areas were removed. Dot size represents number of survival and mortality events observed. Each line represents a different years' census.

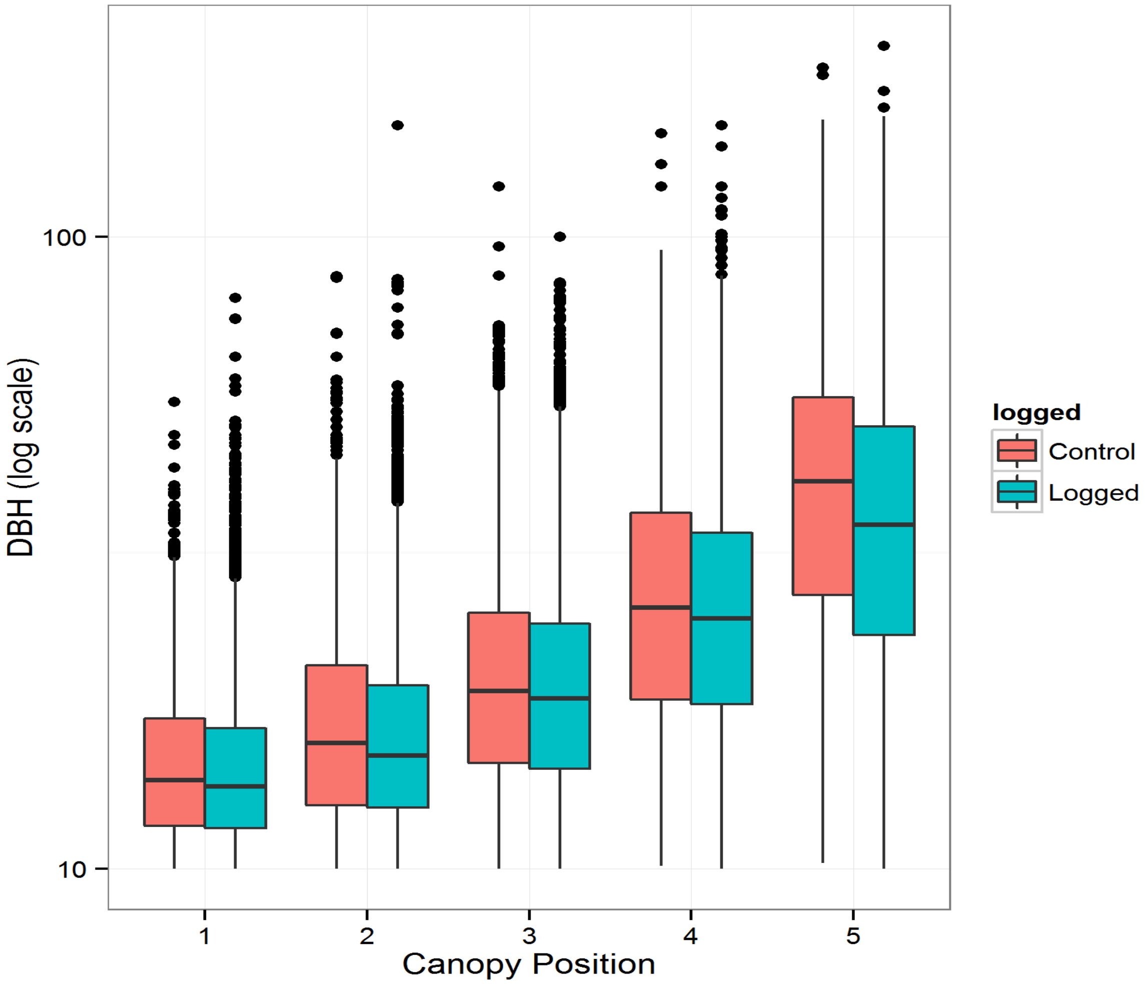


Figure 2 - 26. Box plot of DBH vs. Canopy Position for all subplots that measured trees >10 cm DBH over all post-logging censuses

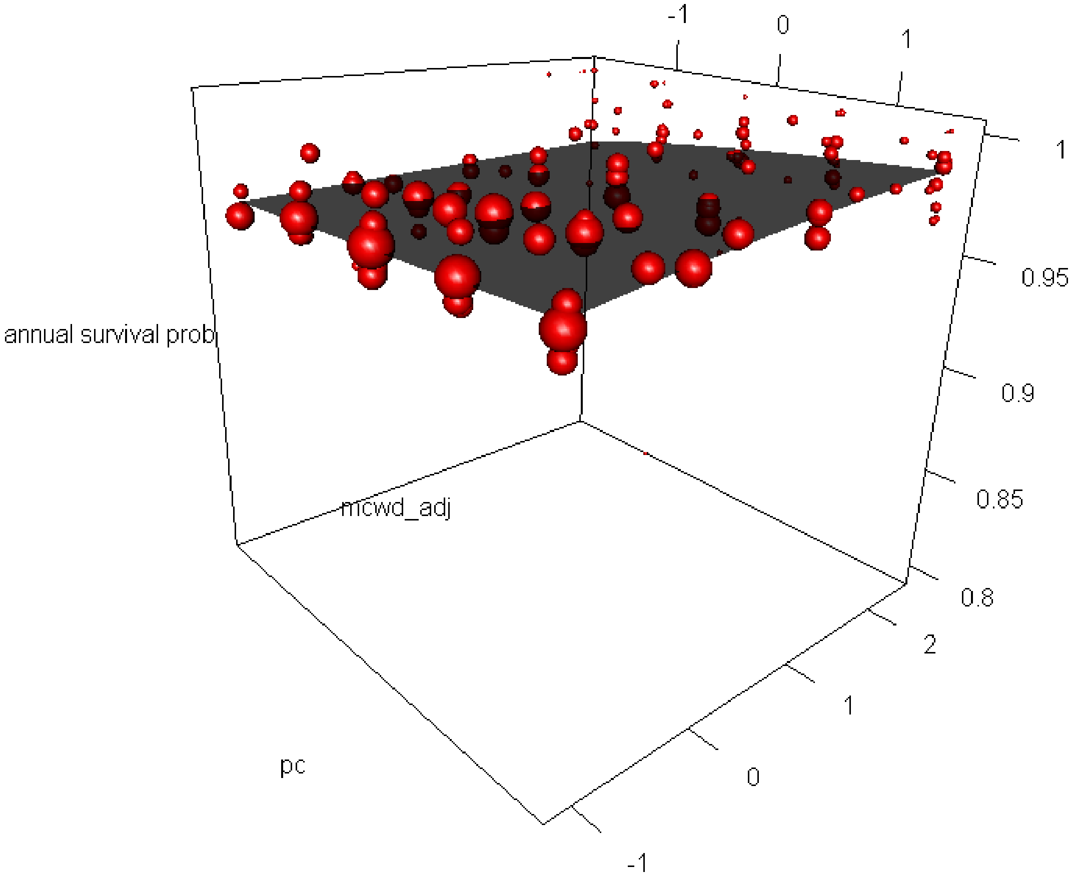


Figure 2 - 27. 3-D plot of large tree survival versus MCWD and Crown Position (pc). Tree deaths due to logging and silviculture as well as all trees in burned areas were removed. Note that the z-axis represents survival rate. MCWD is scaled from -1 (dry) to 2 (wet). Crown position is also scaled from -1 (no direct overhead or lateral light) to 2 (crown fully exposed to vertical and lateral light; emergent). Volumes of the red spheres correspond to the number of survival and mortality events observed at that combination of canopy position and MCWD. The surface indicates the maximum-likelihood fit to the data. Model specification: survival ~ canopy_position * MCWD.

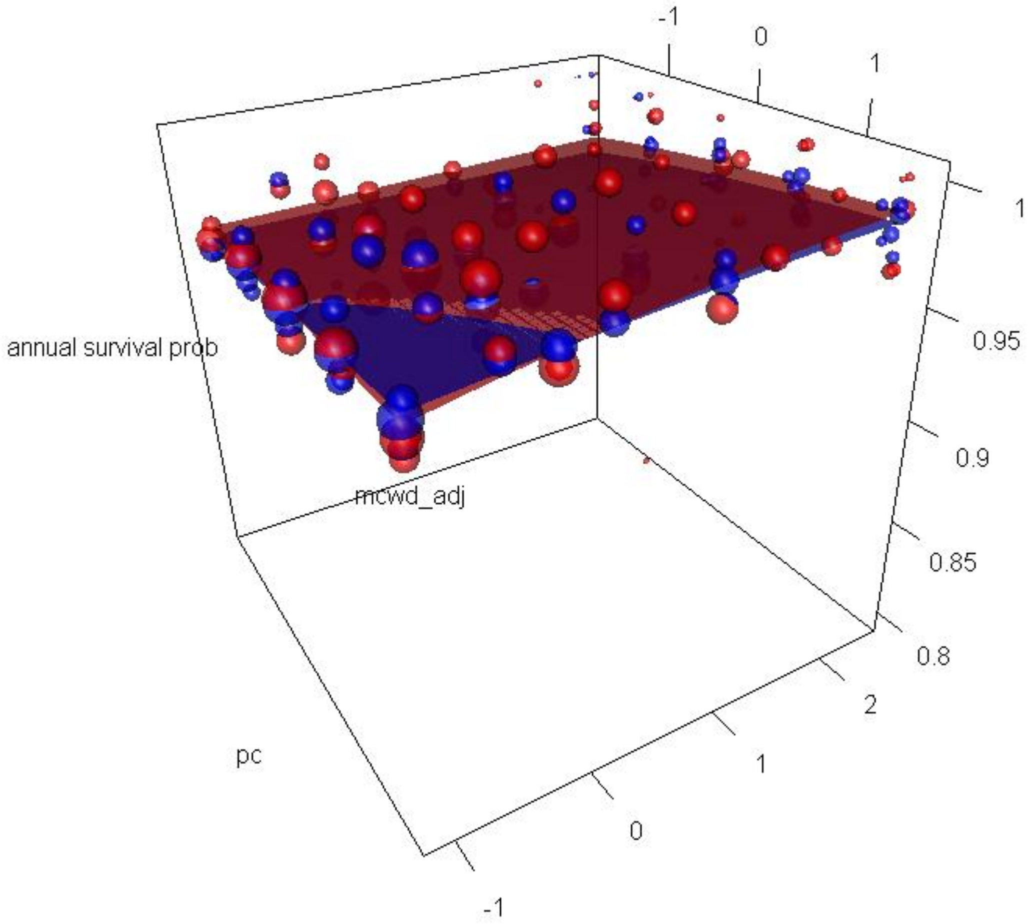


Figure 2 - 28. Large tree survival as a function of canopy position (pc) and MCWD. Tree deaths due to logging and silviculture as well as all trees in burned areas were removed. The red surface and the red dots represent, respectively, the model and data from the control plots. The blue surface and blue dots represent the logged plots. Axes as in Figure 2 - 27.

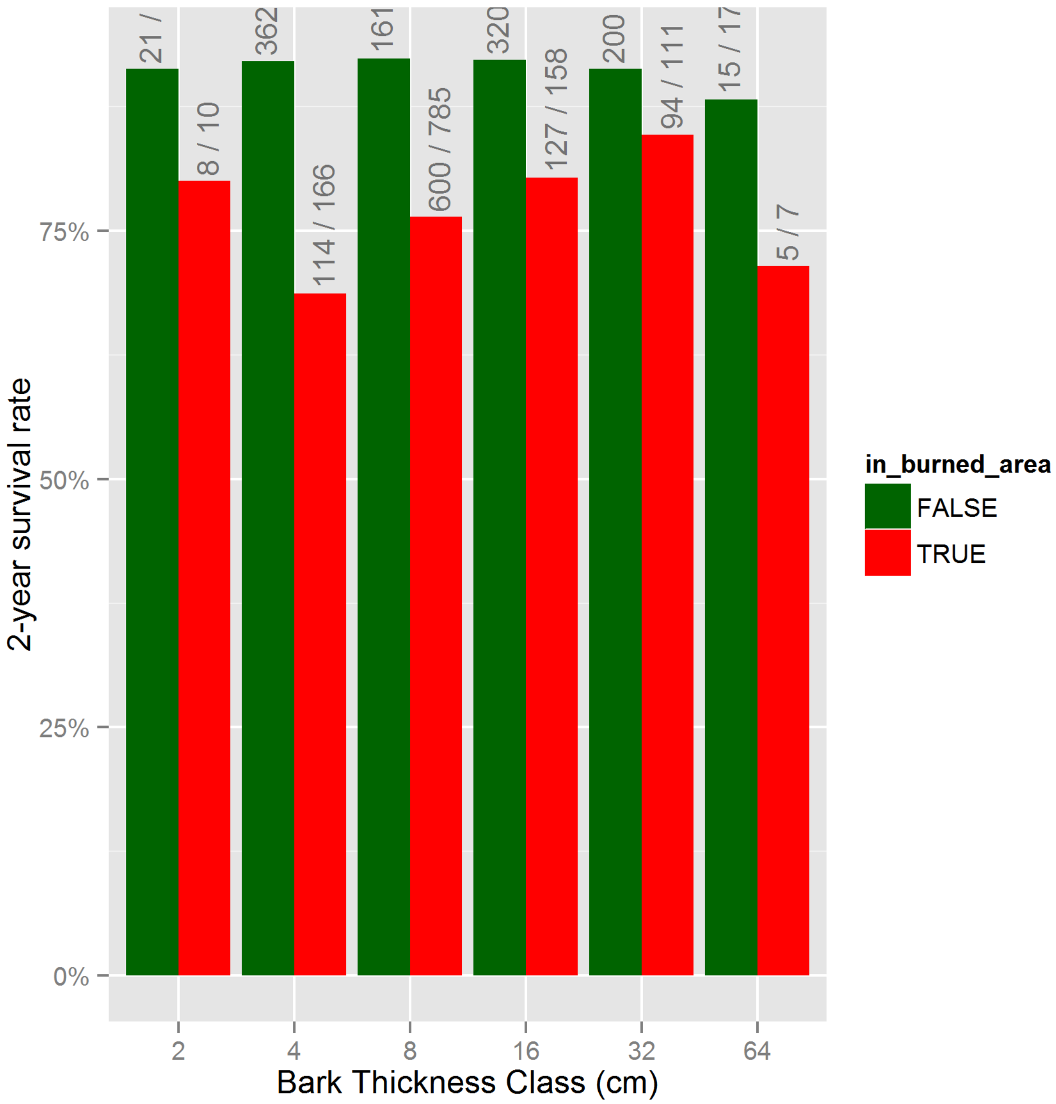


Figure 2 - 29. 2-year survival rates for large trees (>10 cm DBH) in burned vs unburned areas. Data only includes the census interval within which the fire occurred and the species for which we have bark thickness measurements. Bark thickness was determined by species-specific bark-thickness regression models.

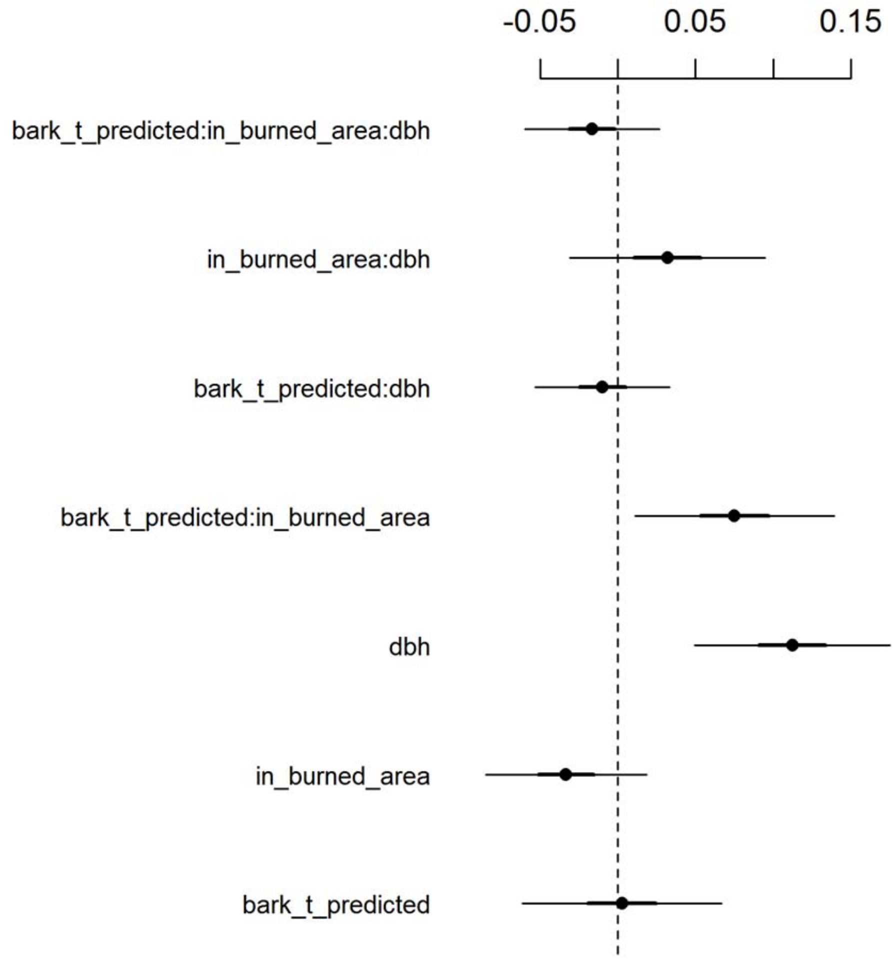


Figure 2 - 30. Coefficients for the full model of adult survival during the interval in which the fire occurred (November 2004 - January 2005) with predictor variables x = modeled_bark_thickness * DBH * in_burned_area

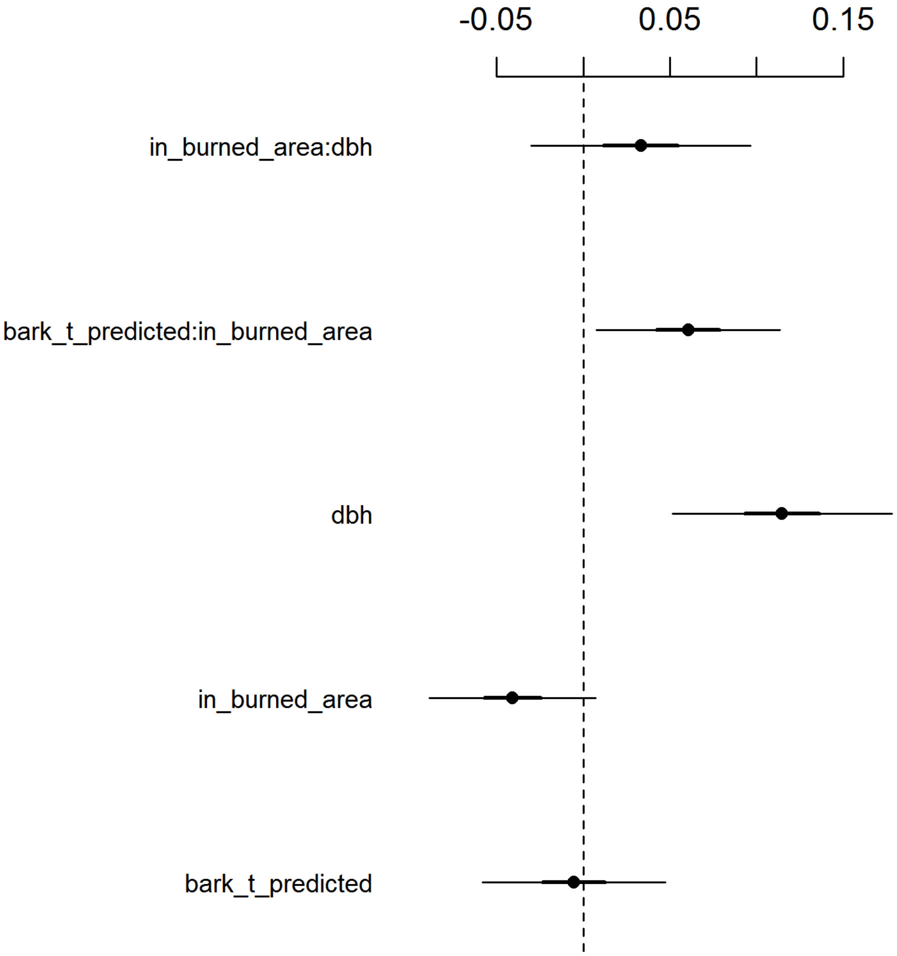


Figure 2 - 31. Coefficients for model of adult survival during the interval in which the fire occurred (November 2004 - January 2005) with predictor variables x = modeled_bark_thickness * in_burned_area + DBH * in_burned_area

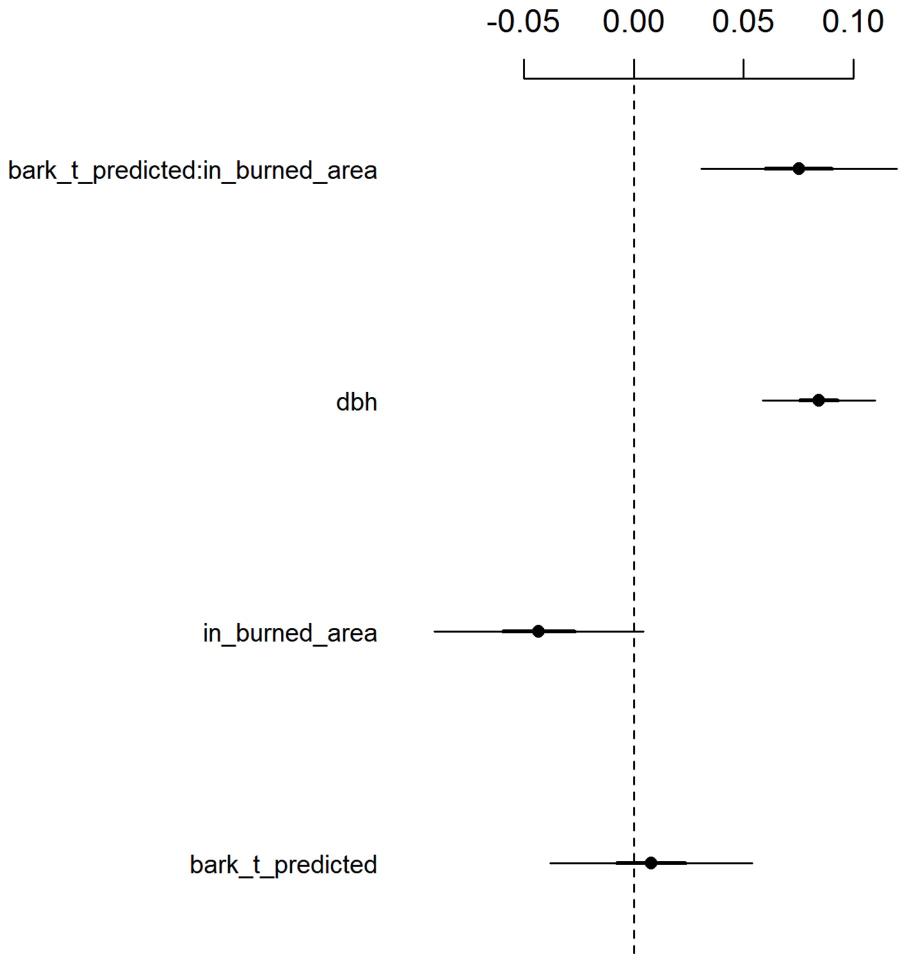


Figure 2 - 32. Coefficients for reduced model of large-tree survival during the interval in which the fire occurred (November 2004 - January 2005) with predictor variables x = modeled_bark_thickness * in_burned_area + DBH.

Table 2 - 14. Likelihood Ratio Tests for adult fire survival models. Bark_t represents the predicted bark thickness for an individual tree, and burned_area indicates whether that individual occurred in the area burned in 2004 or not.

	Df	AIC	logLik	deviance	Chisq	Chi Df	Pr(> Chisq)	Signif
Intercept	3	9952.1	-4973.1	9946.1				
bark_t:burned_area	4	9943.3	-4967.6	9935.3	10.9	1	0.00098565	***
bark_t * burned_area	6	9938.7	-4963.3	9926.7	8.6	2	0.013662	.
bark_t * burned_area + dbh	7	9894.9	-4940.4	9880.9	45.8	1	1.2875e-11	***
bark_t * burned_area + dbh * burned_area	8	9895.7	-4939.9	9879.7	1.1	1	0.28895	
bark_t * burned_area * dbh	10	9898.8	-4939.4	9878.8	0.9	2	0.62266	

Table 2 - 15. AICs for large tree fire survival models. The top model includes the bark_t : burned_area interaction, whereas the bottom model includes the DBH : burned_area interaction.

	ΔAIC	df
bark_t * burned_area + dbh	0.0	7
dbh * burned_area + bark_t	4.3	7

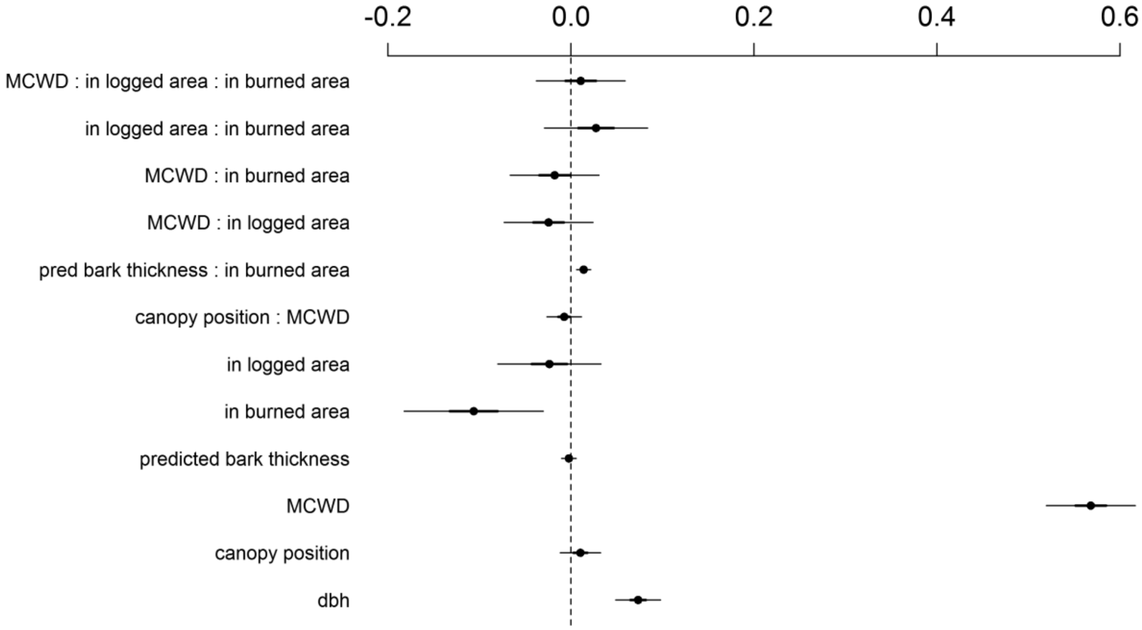


Figure 2 - 33. Model coefficients for large-tree survival model including the 3-way interaction between drought, logging, and fire for all census periods. Categorial variables (such as logged and in_burned_area) were coded as -1/1 so that the treatment levels sum to zero. All continuous variables were scaled such that the population average is zero and the standard deviation = 1 (Schielzeth 2010). Trees in burned areas were included in this model.

CHAPTER 3
FATES OF TREES DAMAGED BY LOGGING

Introduction

While several studies on collateral damage due to selective logging in tropical forests report the incidence of damage and trees immediately killed, data on the long-term fates of damaged trees are less available (but see Sist and Nguyen-Thé 2002, Mazzei et al. 2010, Werger 2011). Such data are needed to inform silvicultural decisions and to predict future yields. Damaged trees may suffer elevated mortality rates for years or decades after logging, survive but grow slowly and develop heartrots and stem hollows, or largely recover. In the absence of data, most stand projection models assume that overall tree mortality rates are elevated for the first 8-10 years after logging and then decline back to pre-logging rates. In fact, heavy logging can engender elevated mortality rates that persist for 18 years or more post-logging, while rates in lightly logged areas are sometimes indistinguishable from those in unlogged areas (e.g., Kasenene and Murphy 1991, Mazzei et al. 2010). Without the benefit of data on logging damage, Hawthorne et al. (2012) found that mortality rates of trees near felling gaps and skid trails in Ghana returned to background rates after 22 years, whereas areas within logged stands but away from skid trails or gaps did so after only 15 years. Here we report on the growth and mortality rates of damaged trees over the first 9 years after selective logging of a tropical moist forest in Bolivia.

Damaged trees are expected to grow slowly and suffer elevated risks of mortality due to a number of potential processes. Most prominently, damaged stems, branches, and roots are susceptible to infection by pathogens and wood-rotting organisms that, if not successfully compartmentalized, may kill the trees outright or render them prone to break. Various structural traits of trees influence their susceptibility to mechanical damage (e.g., thick bark or flexible branches), but here the focus is on the fates of damaged trees and on the traits that influence those fates. For example, the capacities of trees to compartmentalize decay and close bark wounds vary with wood density, production of resin and latex, and bark traits (Romero and Bolker 2008, but see Romero et al. 2009). In regards to the effects of mechanical damage on subsequent growth rates, large reductions are expected from crown loss both due to the initial loss of photosynthetic surface coupled with the physiological costs of branch replacement. Similarly, root damage reduces tree access to water and nutrients while it compromises structural integrity. These initially non-lethal injuries are also expected to render trees especially vulnerable to the subsequent effects of drought, pathogens, and herbivores (Franklin et al. 1987).

While trees damaged by logging are likely to suffer due to the reasons mentioned above, they may also recover quickly due to their likely proximity to the above and below-ground gaps opened by logging. Damaged trees that survive the disturbance may enjoy reduced competition for light, water, and nutrients.

To inform predictions of future yields, forest structures, and composition, we here tested the following hypotheses. (1) Mortality rates of damaged trees spike initially and then settle to a rate similar to that of undamaged trees. (2) Trees that snapped but then resprout suffer high mortality rates both initially due to physiological and structural stress and over the longer term due to the effects of pathogens. (3) Root damage is associated with increased mortality rates whereas crown damage is associated with decreased growth rates. (4) Tolerance of damage increases with tree size because larger trees have more stored reserves from which to draw. (5) Trees with high wood density suffer lower mortality rates after damage due to their ability to compartmentalize decay and their biomechanical resistance to breakage. Finally, (6) we expect damaged trees to suffer higher increases in mortality rates during droughts than undamaged trees.

Methods

This study was conducted in the Long-Term Silvicultural Research Plots managed by the Instituto Boliviano de Investigacion Forestal in the La Chonta Forest Concession (see chapters 1 and 2 for a description of the site and experimental design; hereafter “La Chonta”). One pre-logging census was conducted 0-4 mo prior to selective logging, and the post-logging census in which damage was recorded was completed 3 – 6 mo after logging finished (Figure 3 - 1). All trees >40 cm DBH (stem diameter at 1.4 m or above buttresses) in approximately 300 ha of permanent sample plots were located and measured, with all trees >20 cm DBH measured in half the area and all trees >10 cm DBH in 4 1-ha subplots within each treatment (i.e., 36 ha of logged forests for trees >10 cm DBH).

During the first post-logging census, crown, bole, and root damage were recorded separately as follows (variable names noted parenthetically): bark damage (small =< 20 x 20 cm, (>20 x 20 cm; whether that damage was just to the bark or penetrated down to the wood (bark damage depth); superficial root damage, or root breakage (root damage); crown damage (0%, 1-25%, 26-50%, 51-75%, 76-99%, and 100% of the crown lost); and, whether the bole was straight, leaning, split and leaning, or toppled (stem status; see Mostacedo et al. (2006) for more detailed descriptions of the methods). We removed toppled trees from the analysis because they assumed dead and we also removed all trees (damaged or not) that died before the first post-logging census because we are interested in the fates of damaged trees that survived logging (for immediate collateral damage see Jackson et al. 2002, Mostacedo et al. 2006). We also excluded all new recruits, trees in the 4 ha that burned in 2004, and trees with damage that was first noted after the initial survey. To account for the drying of our study site over the 2000-2010 period, as indicated by the Minimum Climatological Water Deficit (MCWD), we included MCWD as a term in the model whenever we also included time since logging to account for this potentially confounding factor (MCWD – time since logging; Pearson correlation = -0.59).

To simplify some analyses we classified trees into 4 groups: no damage, minor damage (small bark damage, superficial root damage, 1 – 50% crown damage, a leaning stem, or a combination thereof), resprouted (100% crown loss), or other major damage (large bark damage, root breakage, 51 – 99% crown loss, leaning and split stem, or a combination thereof). Growth rates were quantified as: $(DBH_{t2} - DBH_{t1}) / (time_2 - time_1)$..

Growth models were fit using maximum likelihood methods as linear mixed models on repeated measures of trees over time and their associated growth rates. When the effect of damage types were included as fixed effects, orthogonal polynomial categorical coding was used because damage classes were ordinal or ratios . Two types of generalized linear mixed survival and mortality models were employed. The first fit survival and mortality events to repeatedly-measured individuals during each census period up to 8 years after logging, and included individual and treatments across blocks (4 treatments across 3 blocks yielded 12 random effect levels). The second type of mortality model employed the same framework, but fit total mortality after 8 years (i.e. no repeated measures) to simplify interpretation of model results. We use the term “survival model” to mean a model in which positive coefficients have a positive relationship with survival rates, whereas “mortality model” indicates a negative relationship between coefficients and survival rates. A complementary log-log link function transformed the binary survival probability to an infinite continuous scale. Analyses were performed using the lme4 package (Bates et al. 2011) in the R statistical environment (R Core Team 2012).

Results

Of the 25734 surveyed trees that survived logging, 2.5% suffered minor damage, 1.6% major damage, and the stems of 1.4% snapped and resprouted. 2327 trees were reported as dead or missing in the census immediately following logging approximately one year later, not including logged trees and trees killed due to silvicultural treatments. Resprouted trees suffered the highest cumulative mortality, followed by those with other major damage, and finally those with minor damage (Figure 3 - 14). Annual mortality rates for all damage groups were highest in the first post-logging census and then remained more-or-less level until the final census in year 8 when the mortality rates approach those of undamaged trees (Figure 3 - 16). Mean mortality rates of undamaged trees fall within the 95% confidence interval of rates for trees with minor damage by the fourth year after logging, while other groups remain significantly higher than the undamaged trees until year 8.

Root damage, crown damage, damage size and especially stem inclination were all associated with substantial increases in tree mortality (Figure 3 - 2). Total mortality was higher in trees that sustained major damage and in those with snapped and resprouted stems than in those with just minor damage (Figure 3 - 3). While mortality of trees with minor damage was initially higher than that of undamaged trees (Figure 3 - 15), models that included DBH did not detect elevated mortality rates of trees with minor damage 8-years after logging (Figure 3 - 3).

Trees that suffered crown damage suffered the most notable reductions in growth rates, with snapped trees growing 0.33 cm less in diameter per year than not-snapped trees (Figure 3 - 4 and Figure 3 - 5). Recorded root damage was associated with reductions in growth up to 0.15 cm / year, though there was substantial variation in this relationship (Figure 3 - 4 and Figure 3 - 6). Like mortality, the size of stem damage did not seem to affect growth rates substantially (Figure 3 - 4, Figure 3 - 7, and Figure 3 - 8). Unlike mortality, stem inclination apparently did not affect growth. Trees with major (-0.05 cm/year; 95% CI 0.12 to -0.02) and minor (-0.06 cm/year; 95% CI 0.13 to 0.00) damage grew more slowly than undamaged trees, but these effects were only marginally significant (Figure 3 - 9).

To elucidate the role tree size plays in response to mechanical damage, we examine the interactions between DBH and various types and classes of damage. While larger DBH trees suffered lower mortality rates than smaller DBH trees overall as expected (Figure 3 - 2), likelihood ratio tests show that the interactive terms do not differ from zero (Table 3 - 3). Still, of all the interactions tested, tree size most noticeably reduced mortality attributed to the size of bark damage. That is, larger trees could tolerate larger damage to the bark than smaller trees could (Figure 3 - 2). Tree size also did not mollify mortality responses to damage between damage groups except in the case of resprouted trees (Figure 3 - 11). This marginally-significant result suggests that mortality rates increased more for larger than for smaller trees that snapped and resprouted, after accounting for overall effects of DBH on mortality rates.

Contrary to our expectations, higher wood density only marginally reduced mortality of all groups combined (Figure 3 - 12). Likelihood ratio tests are equivocal because, while addition of the damaged:wood_density interaction did not improve the model, further addition of the wood_density direct effect did (Table 3 - 4). We interpret this to mean that while high wood density is related to lower mortality rates for trees overall, it is not important in protecting trees against logging damage-induced mortality. AIC tests with all permutations of these terms (not shown here) result in all models being within 2.3 AIC units of each other (the simplest model containing just DBH and damaged/not damaged, and excluding wood density terms, is slightly more parsimonious by 1.9 AIC points).

In models that considered other factors but reduced damage to a yes/no variable, drought, time since logging, and whether a tree was damaged or not had the largest influence on mortality rates (Figure 3 - 13). Mortality rates of undamaged trees increased more as a result of drier conditions than those of damaged trees. This unexpected result could be due to the correlation between MCWD and time since logging as mentioned above, and it bears further investigation. It might also relate to the proximity of damaged trees to below-ground gaps where soil water might be more available. The nested model without the damaged:MCWD term is better than that without the damaged:time since logging term. Regardless, the full model with both interactions explains the data better than either of the nested models (Table 3 - 5). While mortality rates did not decline linearly with time since logging (Figure 3 - 16), the drought model does not consider the first pre-logging observation, and thus does not have to fit the non-linear mortality peak in the first post-logging census. Hence, the assumption of a linear relationship between mortality rates and time since logging is not unreasonable. We conclude that both time since logging and interval dryness affect the mortality rates of damaged trees.

Discussion

Mortality rates of damaged trees were initially high after logging but then nearly converged on those of undamaged trees 8 years later; for trees with only minor damage, convergence took only 3 years (Figure 3 - 16). These results suggest that if a damaged tree manages to survive for 8 years after logging, it is likely to have a lifespan similar to an undamaged tree; longer-term data are needed to confirm this conclusion.

Root and crown damage had similar effects on mortality and growth but crown damage was associated with slight increases in mortality and substantial influences on growth. Given the correlated nature of damage data (e.g., an inclined tree is likely to have suffered root damage), disentangling the individual effects of each type of damage remains a challenge. When we remove all other damage factors except root and crown damage, root damage is a stronger predictor of mortality than crown damage (coefficients of 0.39 and 0.32 for root and crown damage, respectively, with both $p<0.001$), whereas crown damage has a stronger influence on growth than root damage (coefficients of -0.090 ($p < 0.05$) and -0.104 ($p < 0.001$) for root and crown damage, respectively). This finding does not provide support for our hypothesis that root damage is of more consequence for tree mortality whereas the effects of crown damage are mostly on growth rates, but it does support the perspective that while crown damage is more important overall than root damage, root damage has more influence on mortality than growth.

The lack of correspondence between growth (Figure 3 - 9) and mortality rates (Figure 3 - 3) of trees with minor damage, major damage, and resprouts is puzzling. While resprouted trees suffered both high mortality and low growth rates, trees with other major damage suffered increased mortality but not much diminution in growth. In contrast, trees with minor damage suffered only small increases in mortality but reductions in growth rates that were not detectably different from the effects of major damage. This pattern might be understood if the weaker trees with major damage are more likely to die, and those that do survive are more likely to thrive. If trees with minor damage are not very likely to die, then even trees that were disadvantaged prior to receiving damage may persist but grow even more slowly.

DBH had an unexpectedly-small influence on the mortality rates of damaged trees. While it is possible that our sample sizes were too small to detect an effect in a model with 7 – 9 terms, the DBH : damaged term is still insignificant when simplifying the model to 3 terms: damaged/not-damaged, DBH, and their interaction. If DBH does influence damage-induced mortality, the effect is noisy and difficult to discern (Figure 3-5).

Contrary to our expectation, the mortality rates of damaged trees did not decrease with increasing wood density. While wood density coefficients were not significant in the mortality model (Figure 3 - 12), they were on the edge of significance. Adding wood density terms to the survival models did not improve them in terms of AIC, but neither did they degrade them. Thus, while wood density seems to have some explanatory power for mortality of damaged trees, it is apparently not a strong factor.

Finally, we found that the effect of drought on damaged tree survival was opposite what we expected. That is, under drought conditions, mortality rates of damaged trees increased less than those of undamaged trees. This result bears further investigation, but one possible explanation is that damaged trees are likely to be near logging gaps and skid trails where they suffer less below-ground competition for water, which allows them to weather droughts better than other trees.

Overall, we find that types and severity of logging damage to trees have strong effects on their subsequent growth and survival. While the functional and ontogenetic traits we tested had only minor effects on the fates of damaged trees for reasons we do not yet understand, the overall patterns of mortality rates amongst damage groups were clear. Further research into the unexpected response of damaged trees to drought could prove fruitful, as could investigation into the apparent inelasticity of damaged tree response to functional and ontogenetic traits. Finally, it remains important to determine the proportions of damaged trees that end up with stem hollows and other defects that render them unsuitable for timber.

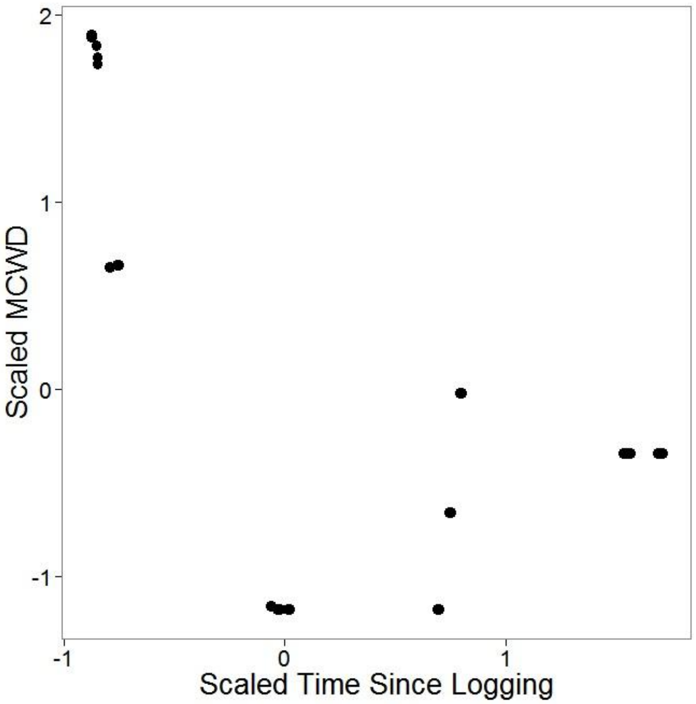


Figure 3 - 1. Illustration of the correlation between MCWD and time since logging. Dots represent observations of trees in this study.

Table 3 - 1. Logging and census dates.

Block	Census 1	Logging	Census 2	Census 3	Census 4	Census 5	Census 6
1	Feb – May 2001	Sep – Nov 2001	Apr – May 2002	Apr – May 2003	Apr 2005	Apr 2007	Apr 2009
2	Oct – Nov 2000	Feb – Jul 2001	Sep – Oct 2001	Oct – Nov 2002	Oct 2004	Sep – Oct 2006	Apr – May 2009
3	Nov 2001 – Jan 2002	Jan – Jul 2002	Nov – Dec 2002	Nov 2003	Nov 2005	Nov 2007	Oct – Nov 2009

Table 3 - 2. Number of trees damaged by logging per category. Trees found dead in the first post-logging census are not included.

		Root Dam	none			superficial			breakage		
		Bark Dam	none	sm	large	none	sm	large	none	sm	large
Stem Status	Crown Damage										
Straight	0%		21161	125	57	0	45	44	0	1	8
	1 - 25%		0	76	9	0	4	2	0	0	0
	26 - 50%		0	59	20	0	4	2	0	0	1
	51 - 75%		0	23	34	0	0	2	0	1	0
	76 - 99%		0	21	65	0	2	5	0	0	1
	100%		0	47	255	0	2	5	0	0	1
Leaning	0%		0	6	5	0	12	5	0	3	5
	1 - 25%		0	2	6	0	1	2	0	0	0
	26 - 50%		0	7	1	0	0	3	0	0	1
	51 - 75%		0	4	2	0	0	1	0	0	0
	76 - 99%		0	1	5	0	0	0	0	0	0
	100%		0	1	3	0	0	1	0	0	1
Split	0%		0	0	0	0	0	0	0	0	0
	1 - 25%		0	0	0	0	0	0	0	0	0
	26 - 50%		0	0	0	0	0	0	0	0	0
	51 - 75%		0	0	0	0	0	0	0	0	0
	76 - 99%		0	0	0	0	0	0	0	0	0
	100%		0	0	0	0	0	0	0	0	0
Toppled	0%		0	1	5	0	0	0	0	0	11
	1 - 25%		0	0	0	0	0	1	0	0	1
	26 - 50%		0	0	0	0	0	0	0	0	1
	51 - 75%		0	0	0	0	0	0	0	0	0
	76 - 99%		0	0	2	0	0	0	0	0	2
	100%		0	0	10	0	0	1	0	0	8

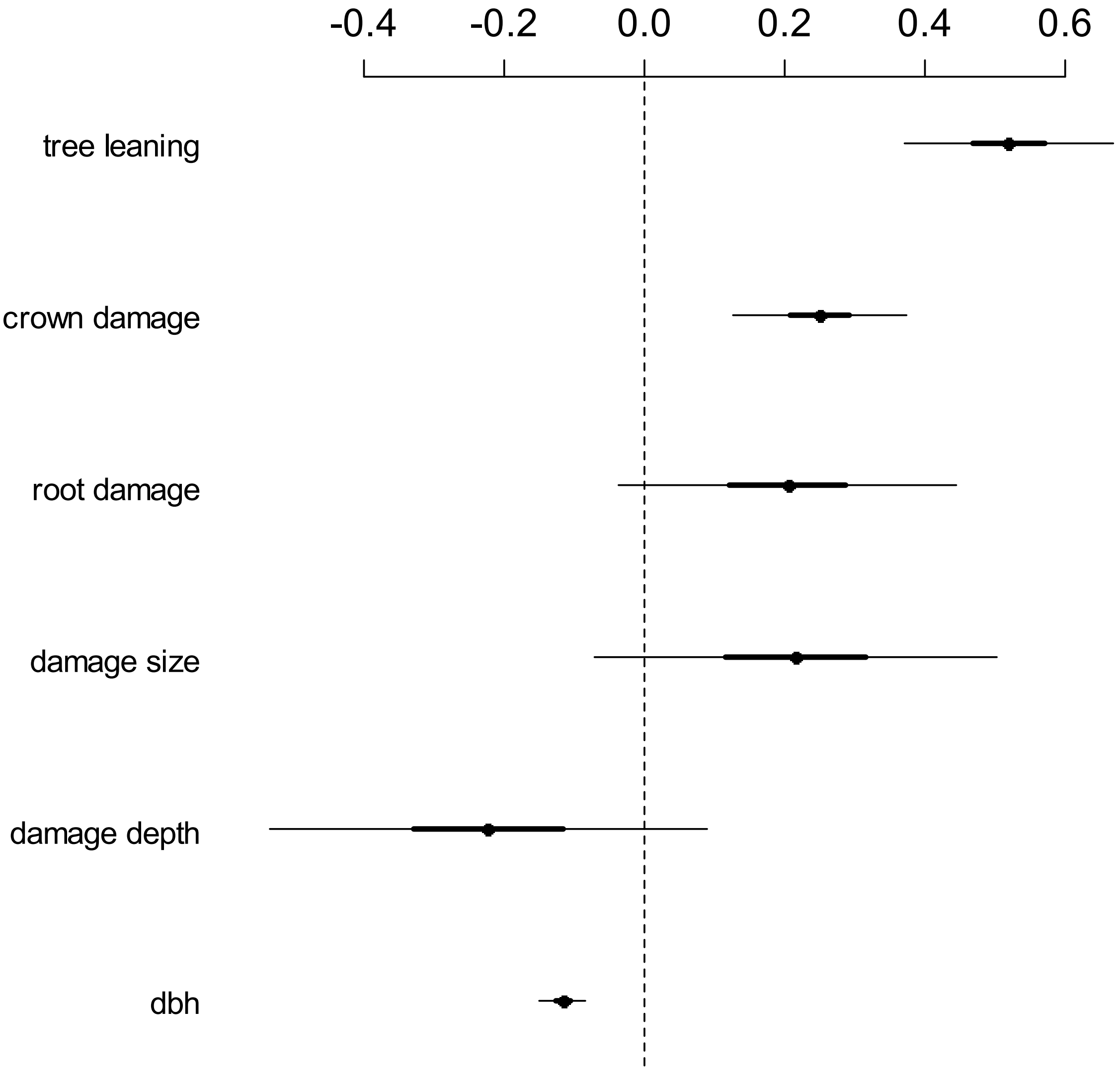


Figure 3 - 2. Coefficient values of fixed effects for a mixed model of mortality 8 years after logging of the cohort of trees present pre-logging. Individual trees and treatments crossed with blocks comprised the random effects (not shown). Damage classes were coded as numeric predictors, scaled to a standard deviation of 1, and centered around 0. A positive estimate indicates that higher values of that predictor correspond to higher mortality rates.

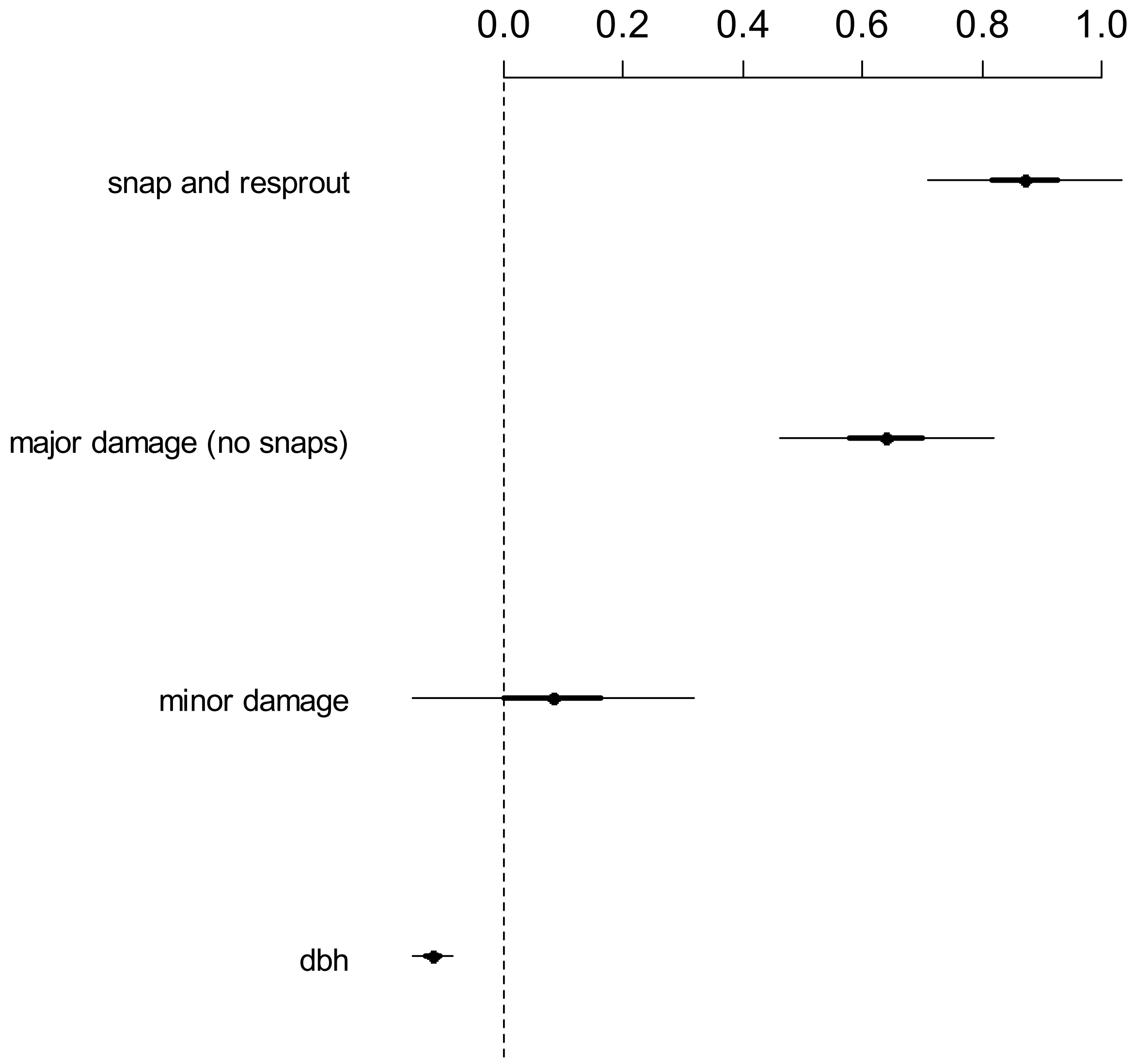


Figure 3 - 3. Coefficients of model predicting total mortality in the 8 year post-logging interval as a function of damage severity. Data and methods as in Figure 3 - 2.

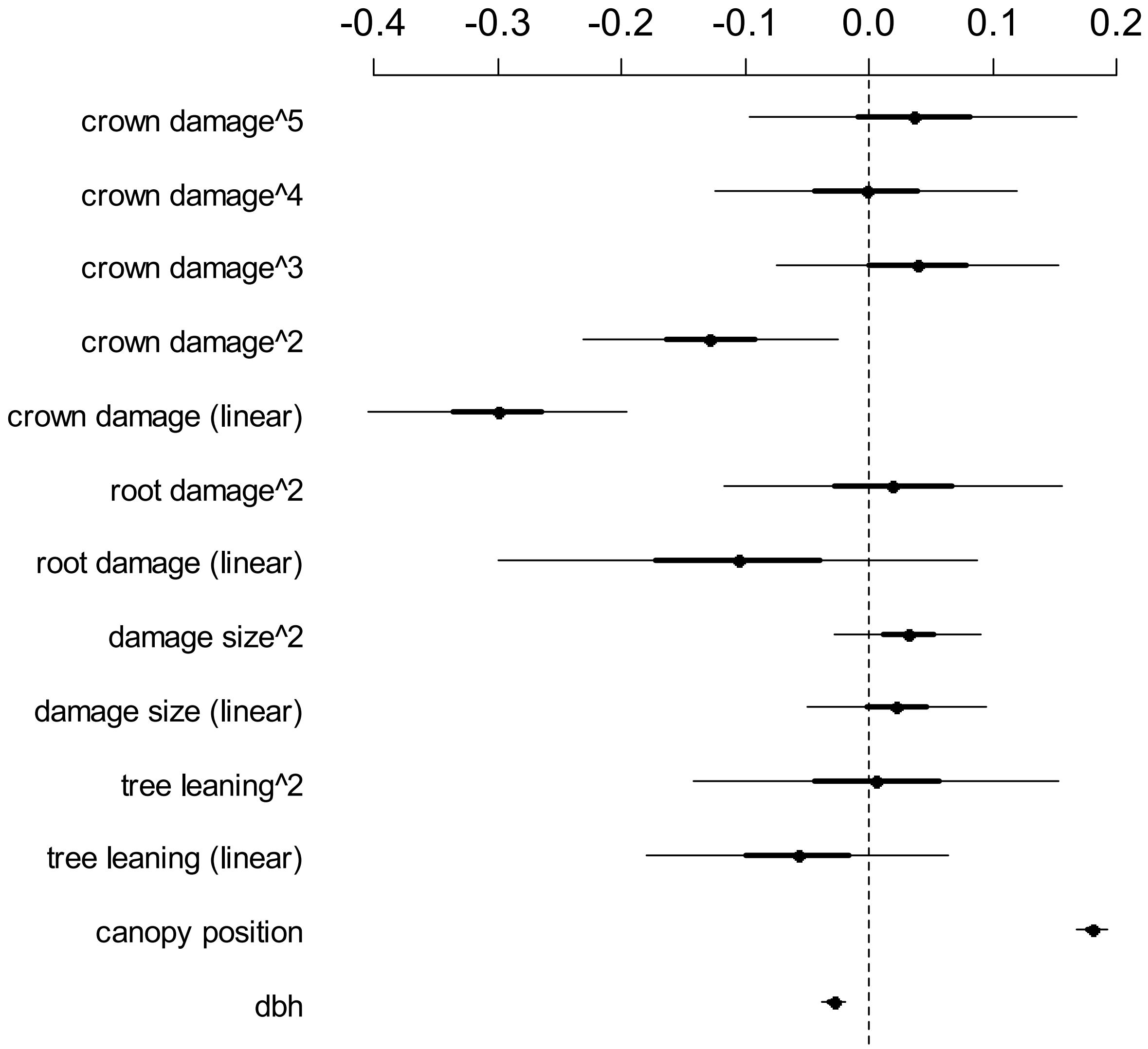


Figure 3 - 4. Orthogonal polynomial coefficients for model of stem diameter growth rates as a function of different types of damage, crown position, and dbh.

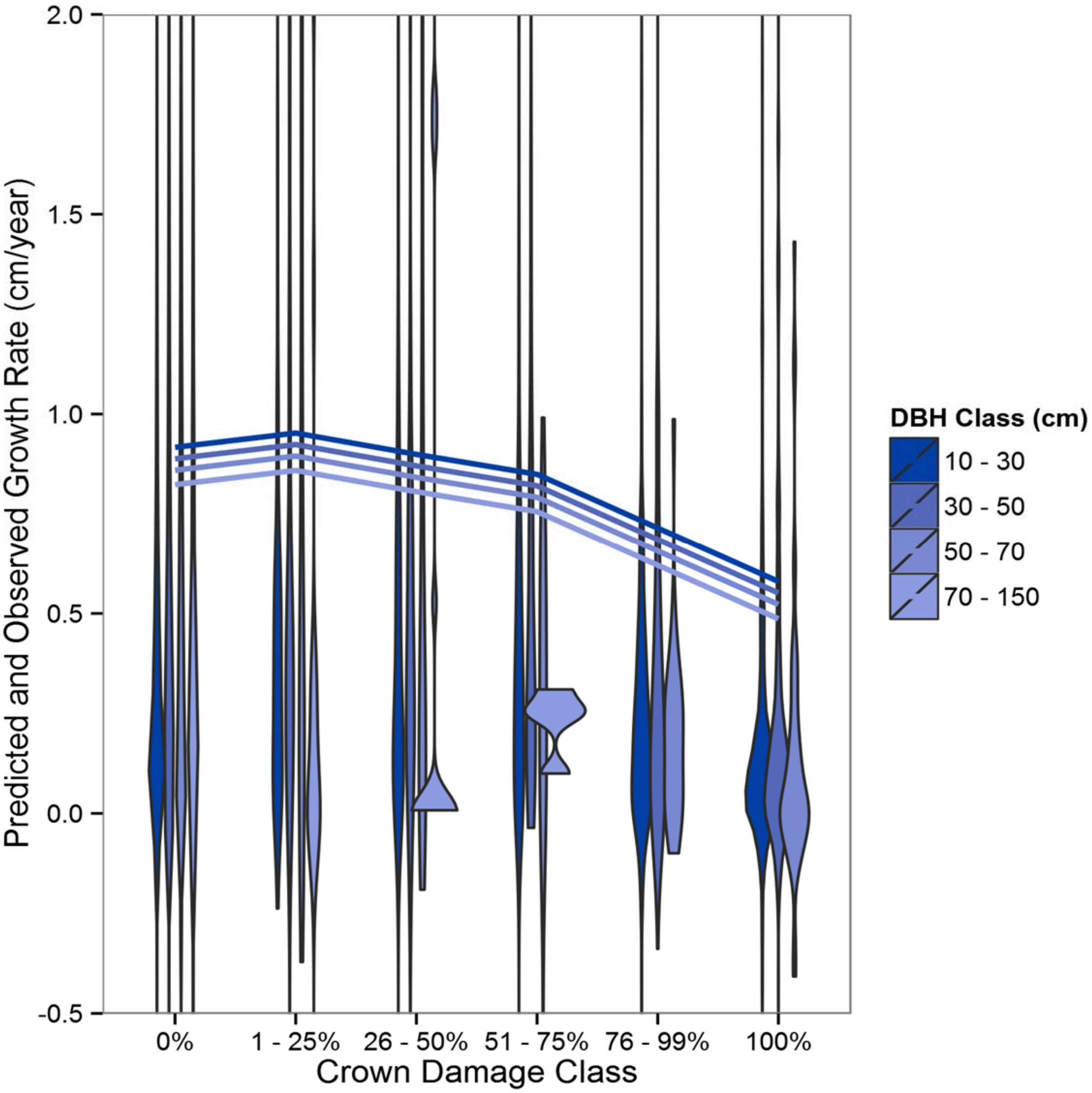


Figure 3 - 5. Measured (violin/forest plot) and predicted (lines) annual growth rates of trees per DBH class. Widths of violin shapes relate to the number of trees observed with that growth rate for that combination of crown damage and DBH class. All individual shapes have the same total areas. Predictions based on the following model: $\frac{\mathrm{DBH}_2-\mathrm{DBH}_1}{t_2-t_1} \sim \mathrm{N}(\mathrm{DBH} + \mathrm{canopy\_position} + \mathrm{crown\_damage} + \mathrm{root\_damage} + \mathrm{damage\_depth} + \mathrm{damage\_size} + \mathrm{tree\_leaning}, \sigma^2)$, including individuals, and treatment crossed with block as random effects. Plot truncated at -0.5 and 2 cm/year. There were no trees >50 cm DBH with crown damage classes 4 or 5. Measurements are not balanced with respect to canopy position of trees, and predictions are balanced means of canopy positions crossed with diameters, with the random

effect of individual set to Individual #1 and averaged across block and treatment random effects.

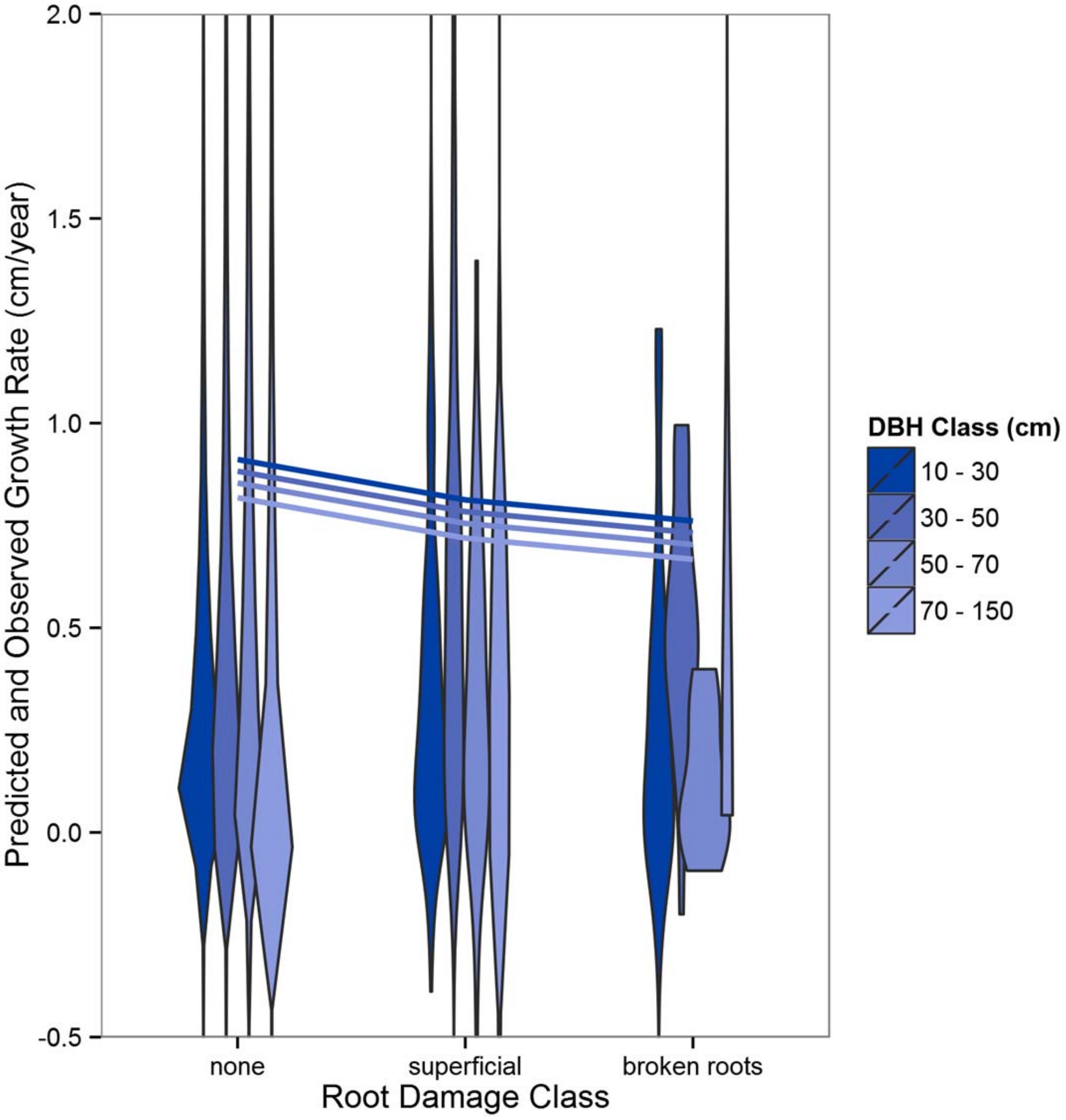


Figure 3 - 6. As in Figure 3 - 5 but for root damage classes

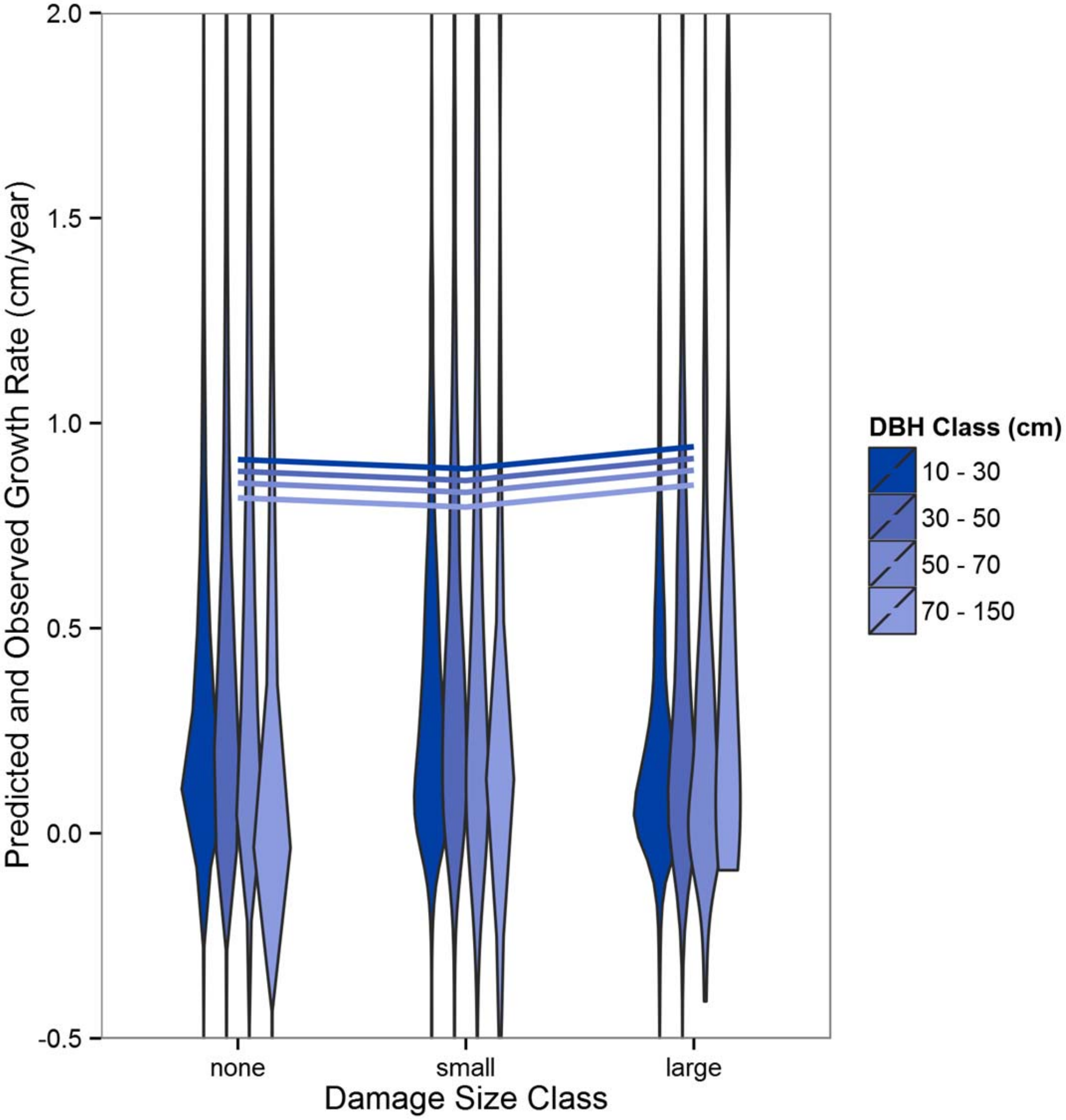


Figure 3 - 7. As in Figure 3 - 5 but for bark damage size classes

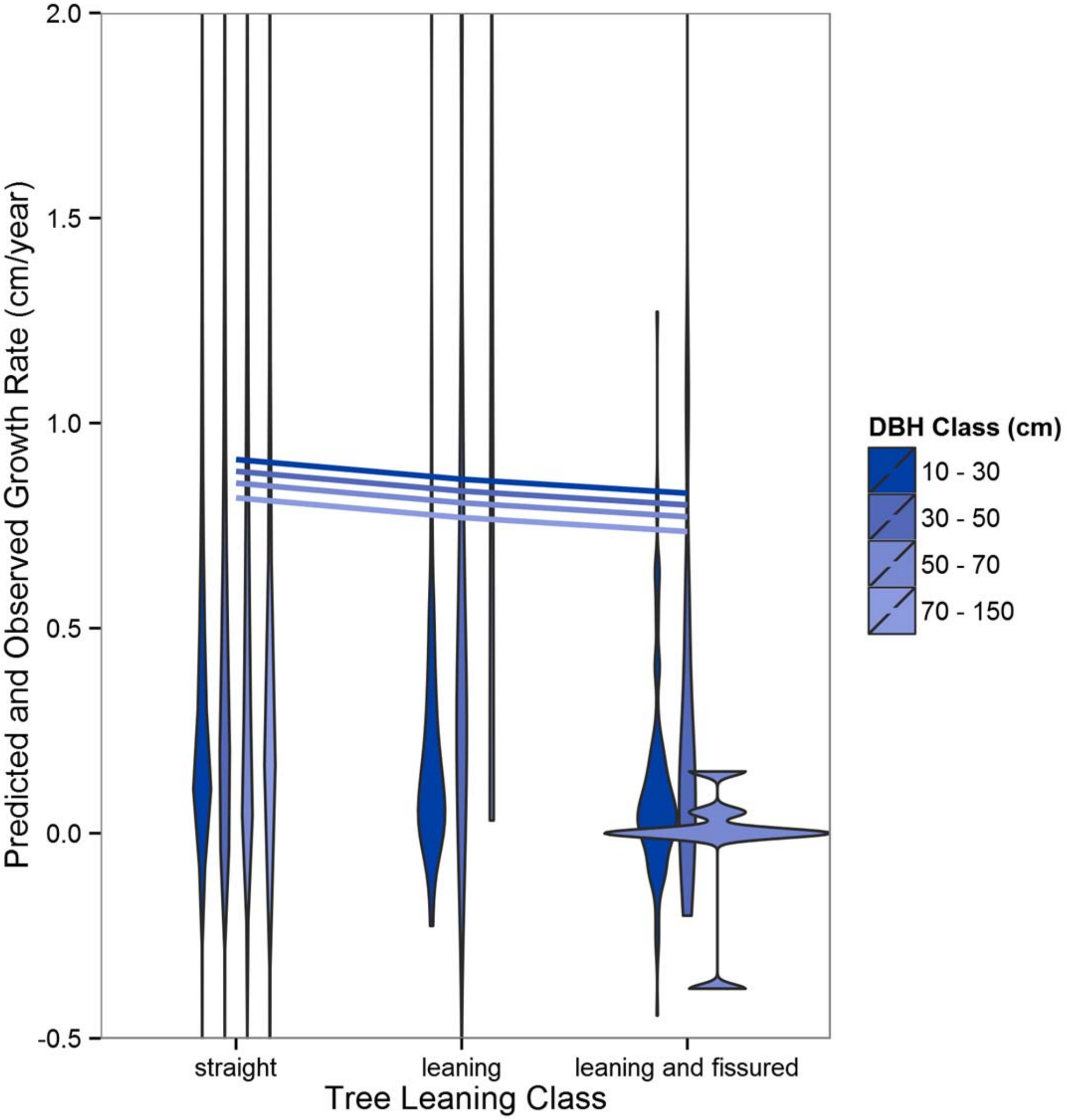


Figure 3 - 8. As in Figure 3 - 5 but for tree lean damage classes

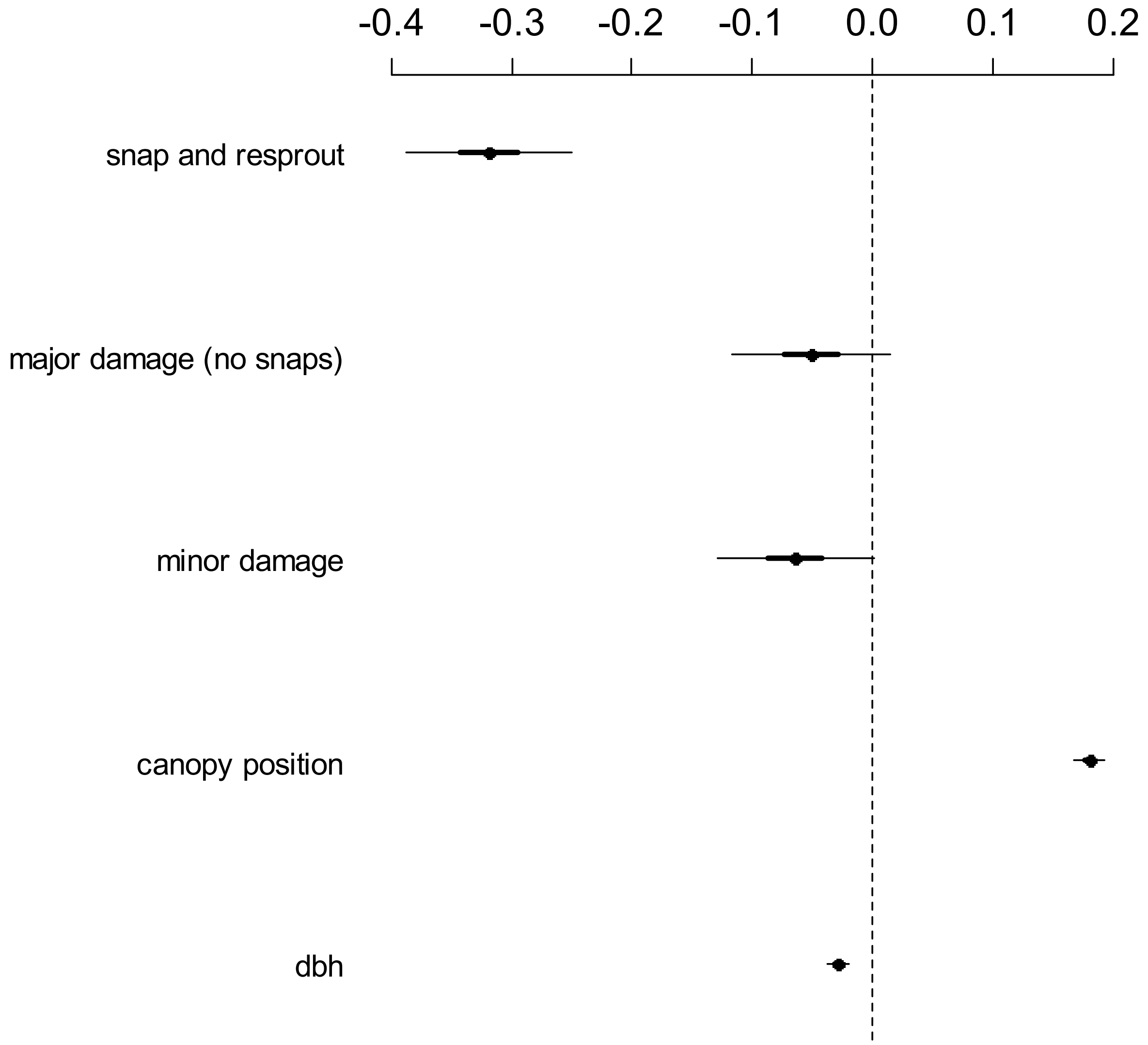


Figure 3 - 9. Growth rates (DBH increments) modeled as a function of damage groups, canopy position, and dbh.

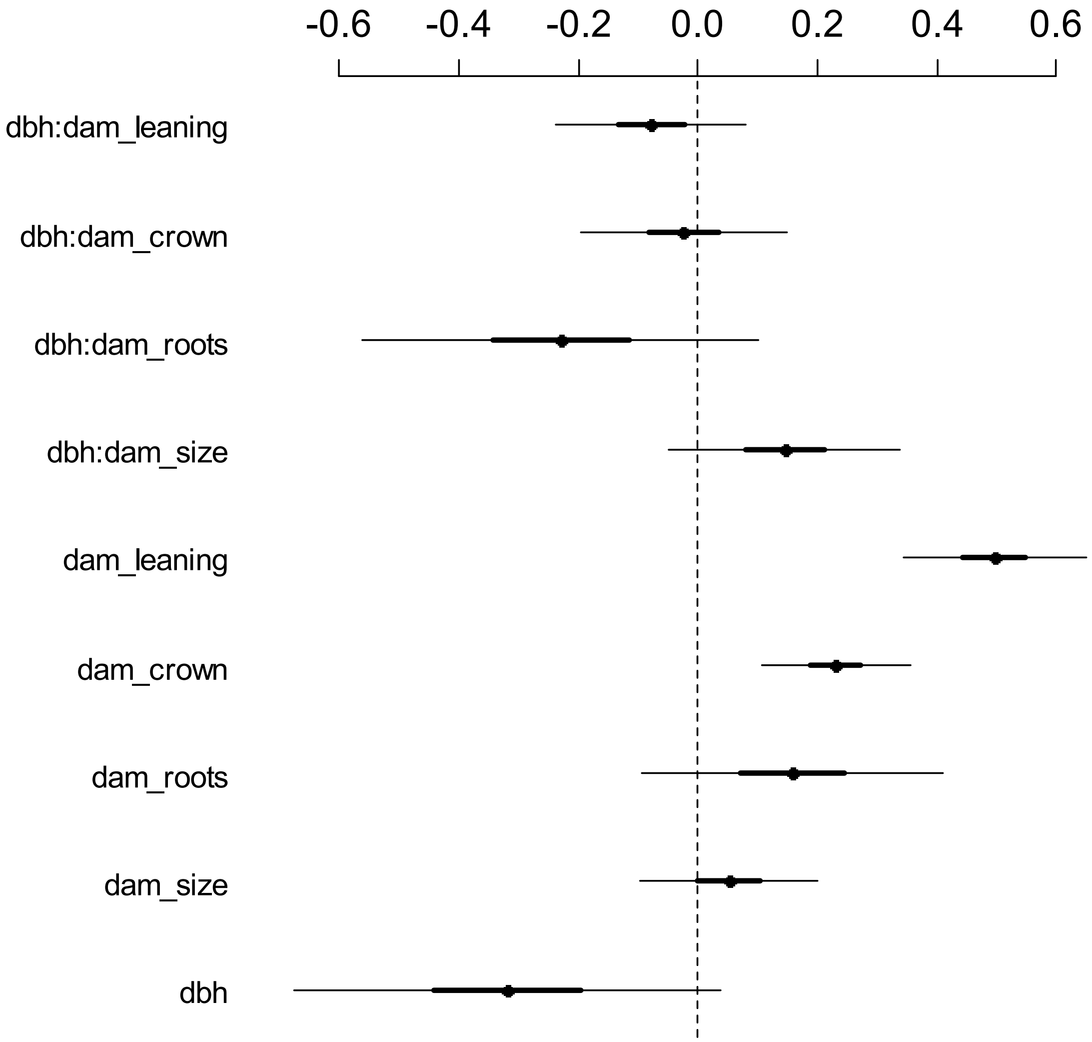


Figure 3 - 10. Coefficients of mortality model 8 years after logging as in Figure 3 - 2, with interactions between DBH and damage types

Table 3 - 3. Likelihood ratio tests for interactive terms in the mortality model of Figure 3 - 10.

	ΔAIC	LRT	Pr(> Chisq)
dbh : dam_size	0	1.98116	0.1593
dbh : dam_roots	0	1.91388	0.1665
dbh : dam_crown	2	0.06166	0.8039
dbh : dam_leaning	1	1.07693	0.2994

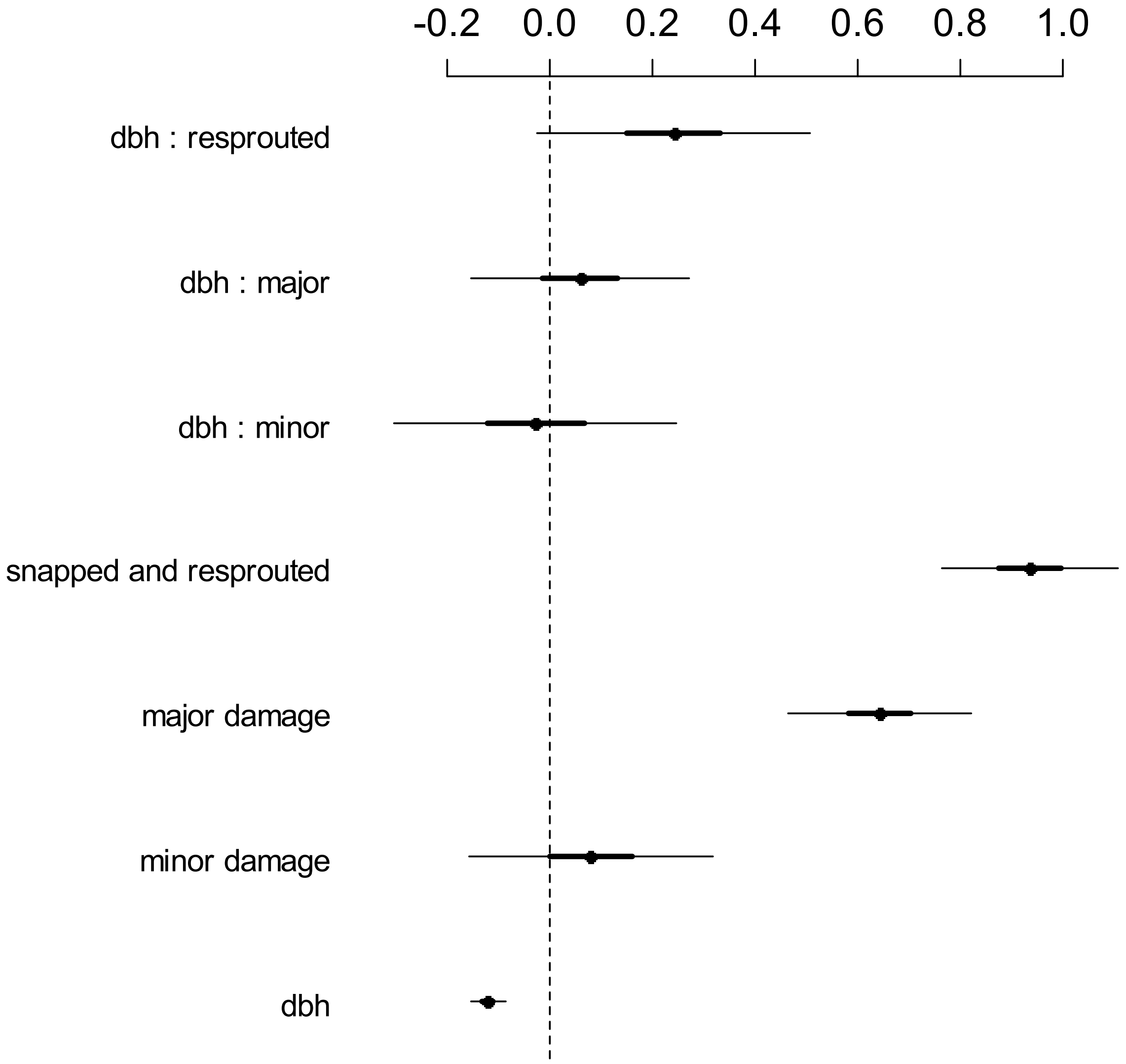


Figure 3 - 11. Mortality model as in Figure 3 - 2, with interactions between DBH and damage groups and DBH.

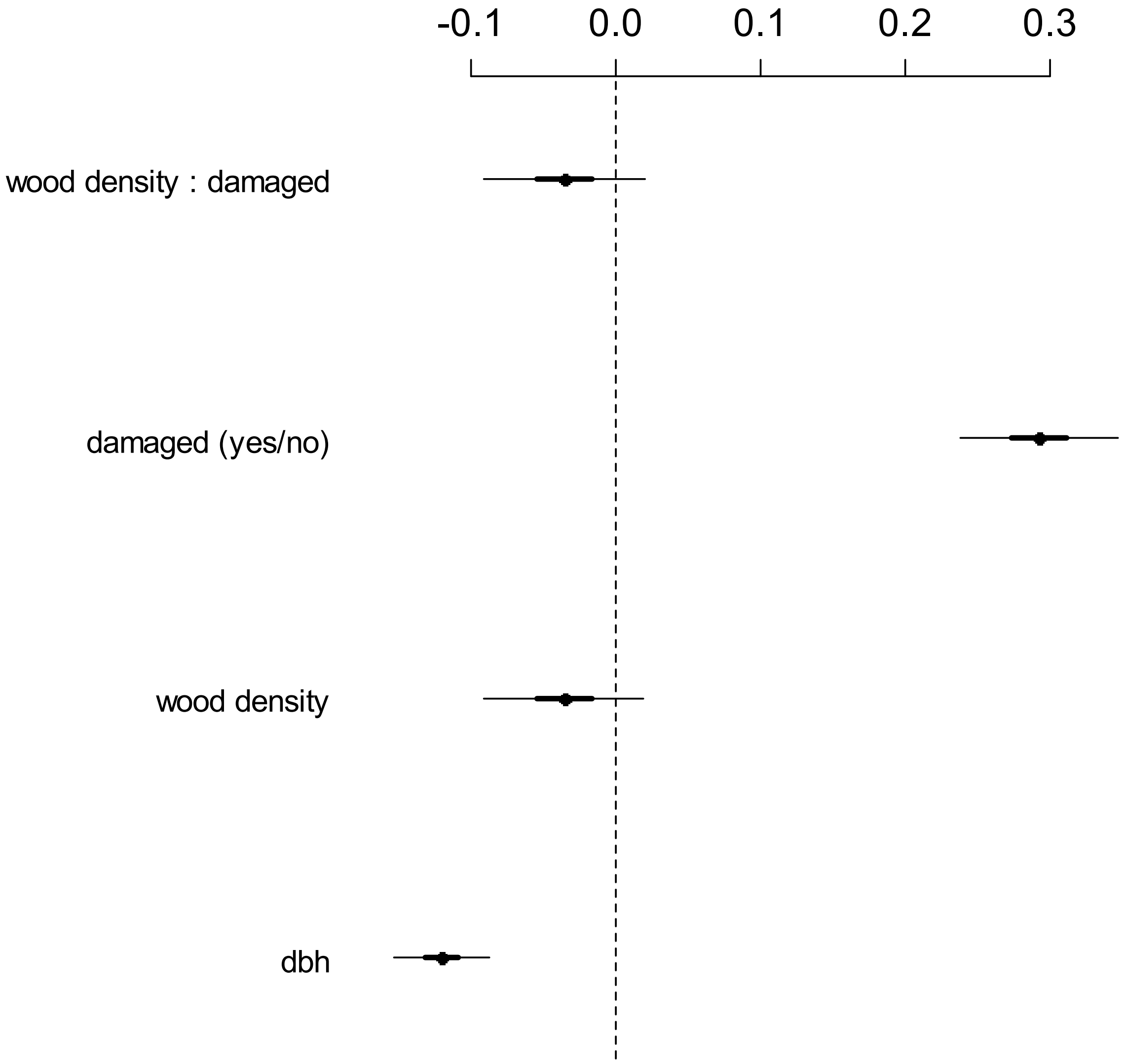


Figure 3 - 12. Mortality model including wood density as a predictor. Data and methods as in Figure 3 - 2.

Table 3 - 4. Likelihood ratio test for the model fit in Figure 3 - 12 with the direct effect of wood density (WD, model 2) and its interaction with the damaged category (dam, model 3) removed.

	Df	AIC	logLik	deviance	Chi sq	Chi Df	Pr(> Chisq)	Signif
dbh.0 + dam	5	22597.9	-11294.0	22587.9				
dbh.0 + dam + dam:WD	7	22600.2	-11293.1	22586.2	1.7	2	0.421	
dbh.0 + WD * dam	7	22600.2	-11293.1	22586.2	0.0	0	0	***

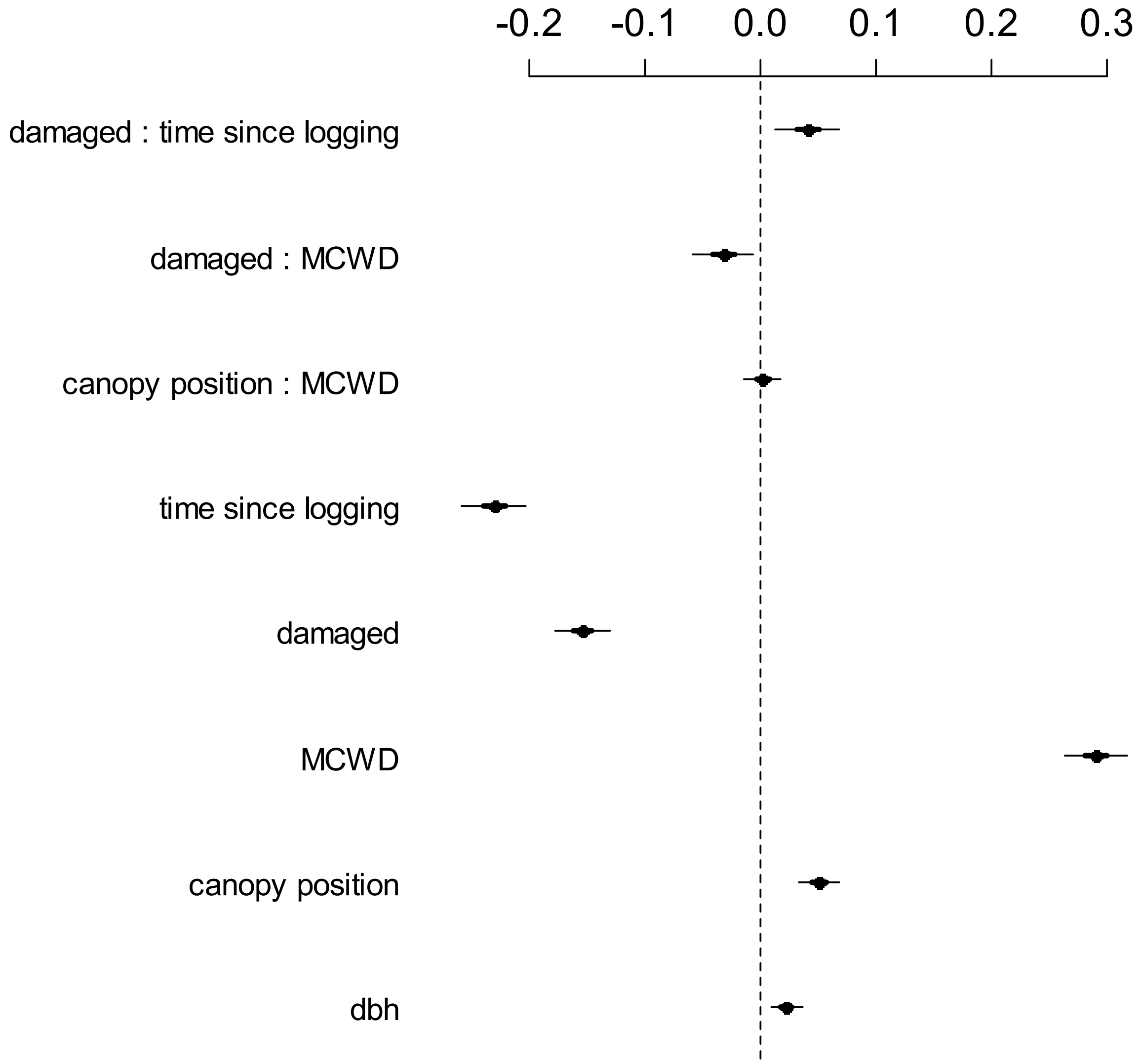


Figure 3 - 13. Repeated-measures survival model including all terms and corrected for variable census lengths. A positive estimate indicates that the term is associated with higher survival rates. This survival model fits survival (coded as 1) and mortality (coded as 0) events of individual trees as repeated measures over each census interval. Random effects include a term for individual trees and a term for treatment crossed with block.

Table 3 - 5. AIC of survival model with all terms (Figure 3 - 13 and model 1), the full model with the damaged : MCWD interaction removed (model 2), and the full model with the damaged : t_since_logging term removed (model 3). cp represents canopy position.

	ΔAIC	df
dbh + cp * MCWD + damaged * MCWD + damaged * t_since_logging	0.0	11
dbh + cp * MCWD + damaged * t_since_logging	3.2	10
dbh + cp * MCWD + damaged * MCWD	1675.2	9

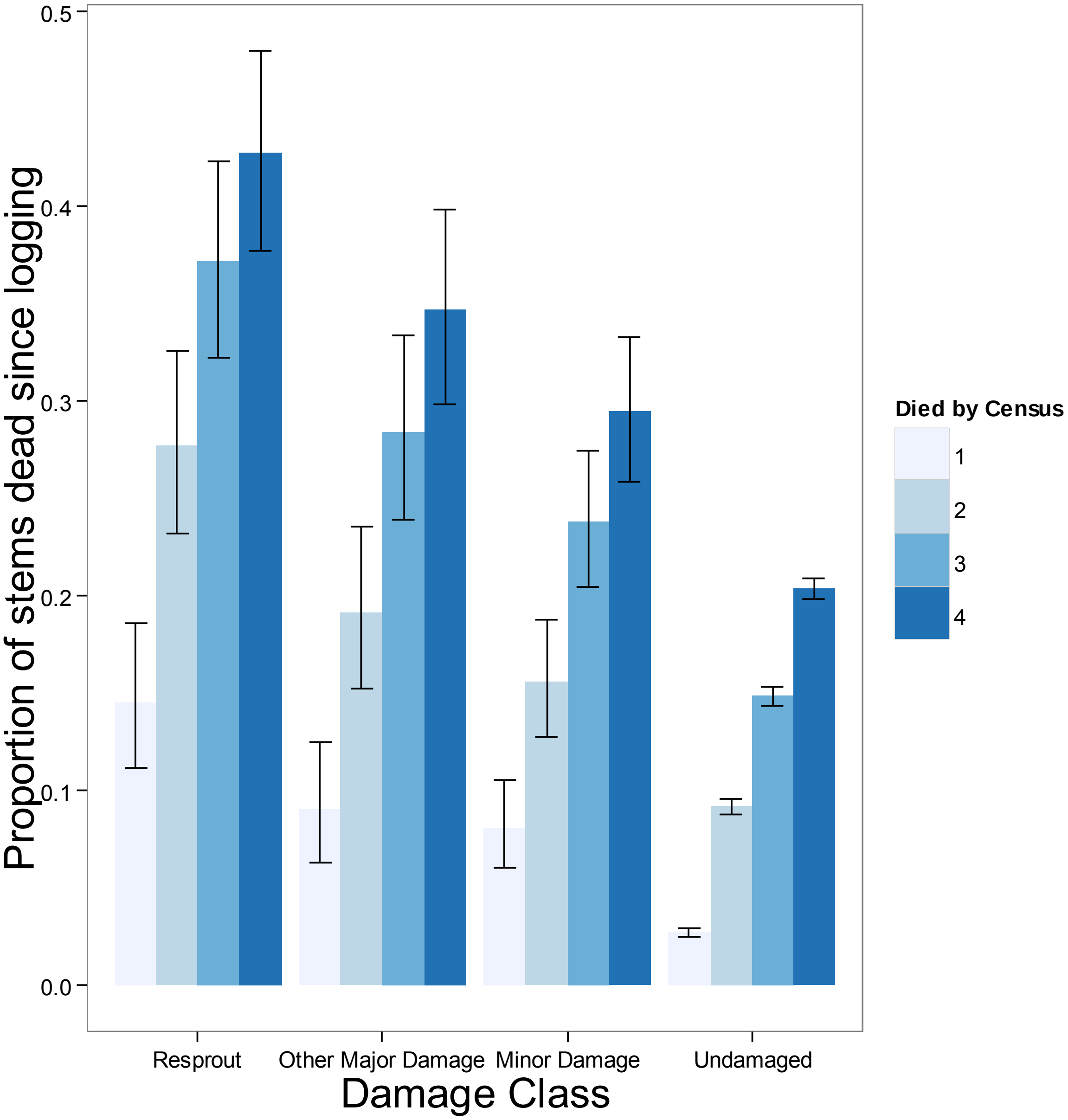


Figure 3 - 14. Fates of trees that survived the immediate effects of logging. Error bars indicate 95% Pearson-Klopper binomial confidence intervals. See Table 3 - 1 for the dates of the censuses.

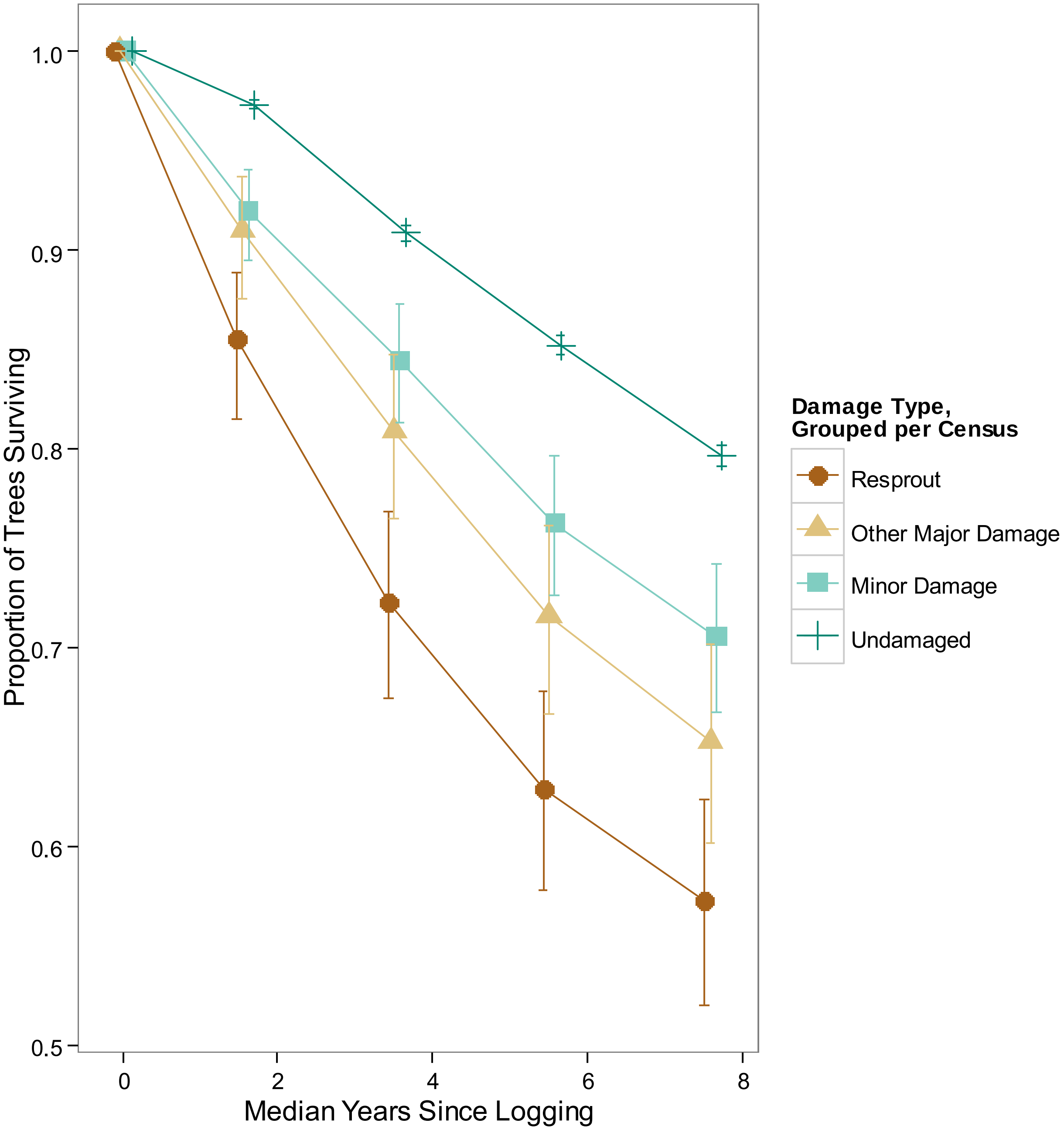


Figure 3 - 15. Tree survivorship as a function of time since logging and damage severity. Data and error bars as in Figure 3 - 14

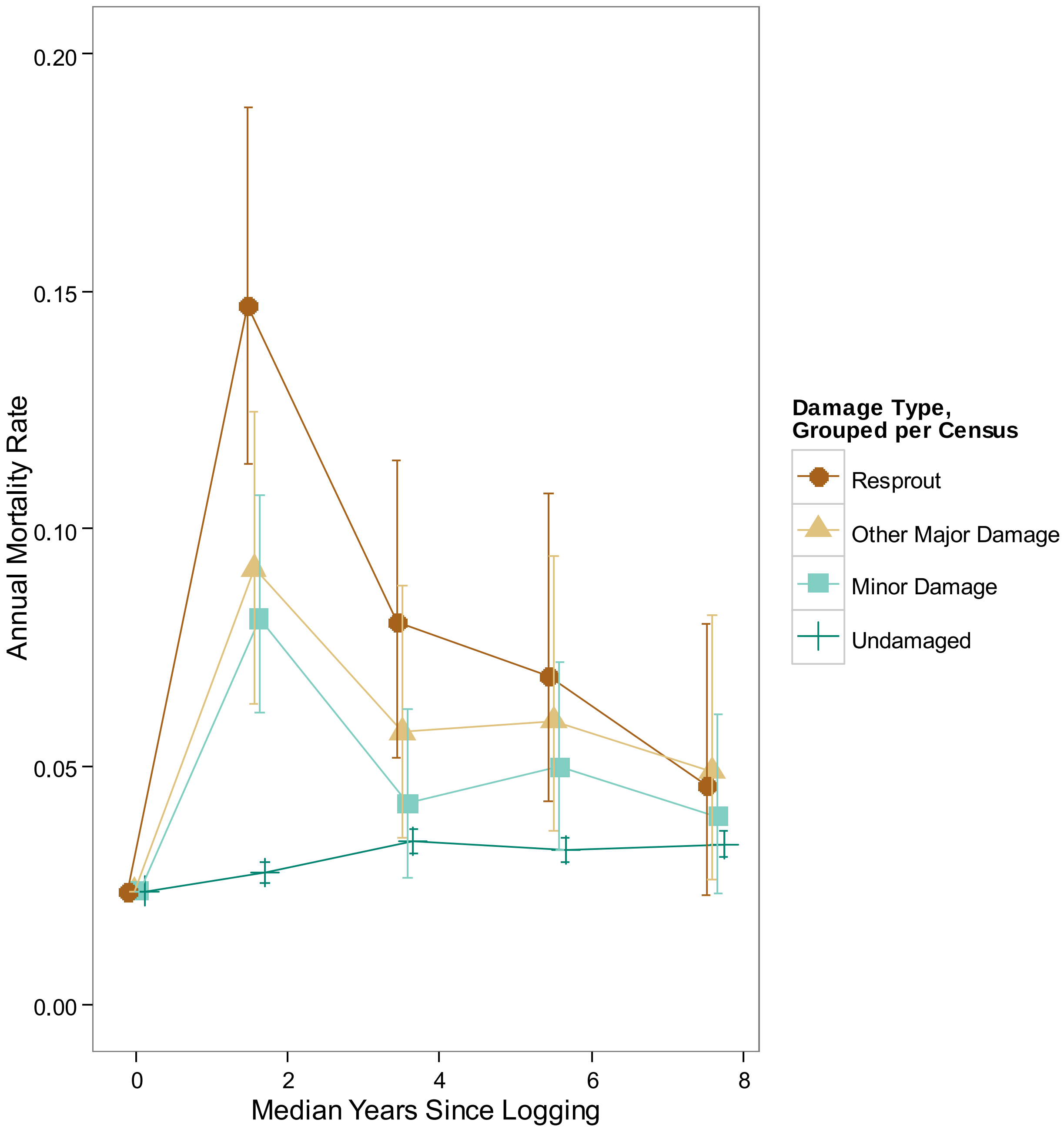


Figure 3 - 16. Mortality rate as a function of time since logging and damage severity. Mortality rate at 0 years since logging set to the mortality rate of the control plots during the first census interval. Data and error bars as in Figure 3 - 14.

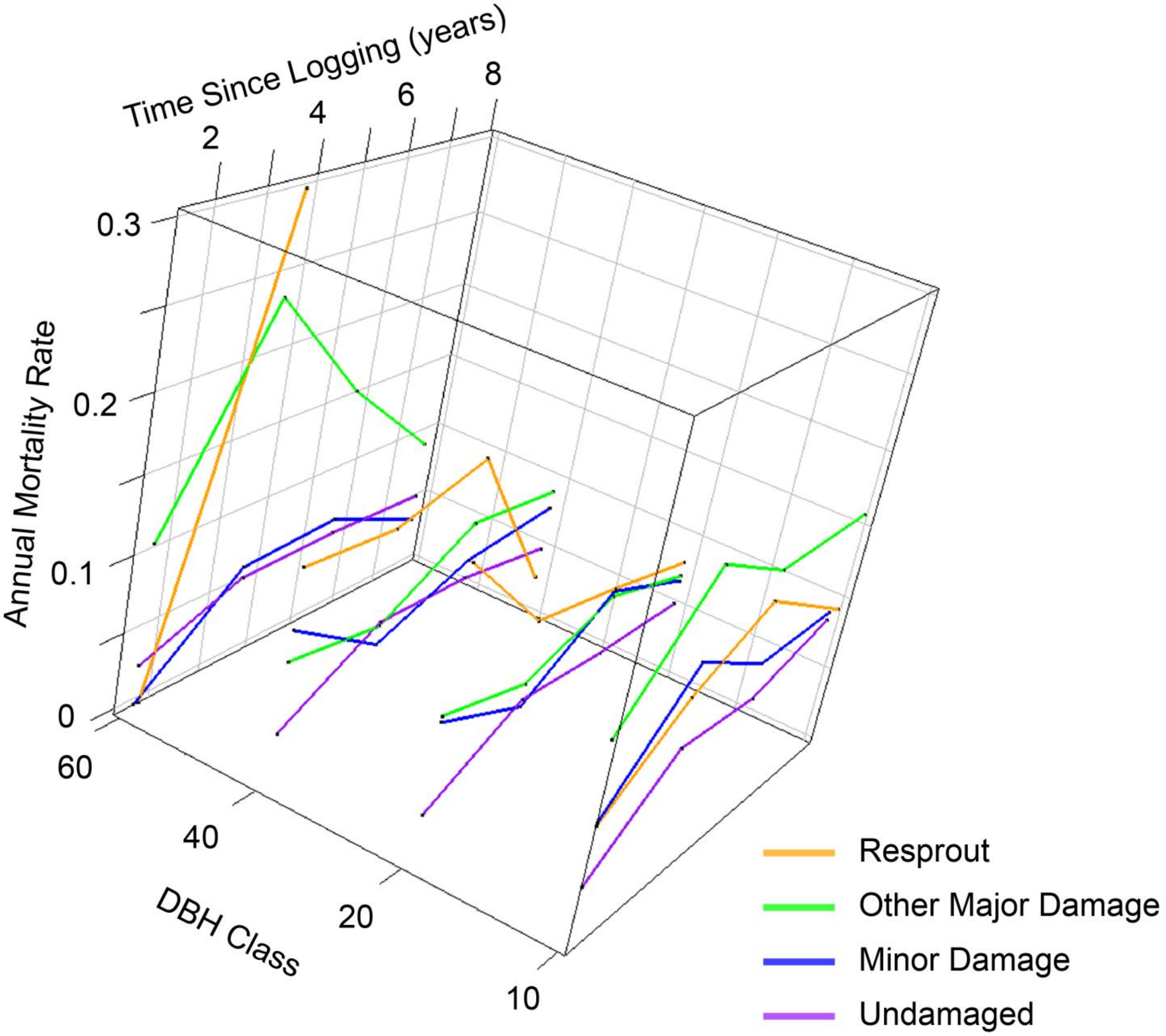


Figure 3 - 17. As in Figure 3 - 16, but with trees separated according to DBH class and without an estimate of pre-logging mortality rates at year 0. Extreme variation in the high DBH classes is related to the low sample sizes. Mortality rates of snapped and resprouted trees were >0.3 but were truncated here for display purposes.

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BIOGRAPHICAL SKETCH

Alexander “Allie” Shenkin was born in Berkeley, California and largely educated in local public schools. His affinity for math and science led him to graduate in 1994 from the University of California at San Diego with a degree in Engineering Physics. Despite his interest in non-human primates, after graduation he worked as an engineer and therefore missed the opportunity to volunteer at the Orangutan Foundation International’s Camp Leakey in Kalimantan. After designing and building prototype high-speed satellite communication subsystems for a number of years as a Research and Design Engineer at Lockheed Martin in Silicon Valley, Allie joined the “dot-com revolution” that was changing the world from a few miles north in San Francisco. As a consultant, he continued with hardware development but also designed and implemented backend software systems for internet-based services such as Microsoft LinkExchange and JC Whitney.

Allie knew that he wanted a post-graduate education, so he decided to attend the University of Colorado’s School of Engineering. With a merit scholarship from the department and a fellowship from the Colorado Space Grant Consortium to support work on the Citizen Explorer Satellite, he graduated in 2000 with a master’s degree in Electrical Engineering. Perhaps more important than graduation, that summer he finally took the opportunity to spend time in Camp Leakey. The loss of habitat from illegal logging and the complexity of the underlying problems confronting the Camp’s area in Kalimantan, Indonesia, motivated him to take some conservation and ecology courses after his return to the USA. Following up on his growing interests in conservation, he moved to Washington D.C. to intern with the Environmental Literacy Council, the Nature Conservancy, and Conservation International. He soon realized the need for more education if he was to contribute substantially to conservation, so he earned a second master's degree from Yale's School of Forestry and Environmental Studies. He performed his thesis work at the Smithsonian Tropical Research Institute in Panama on the role of climate, soil fertility, and soil biotic communities on tree growth differences between two reforestation sites. While conducting his field work he met his future wife in Panama's Casco Viejo.

Allie then embarked on a Ph.D. program at the University of Florida. He was initially geared towards an interdisciplinary project and spent his first two years working on socio-ecological resilience of roadside communities and forests in the MAP (Madre de Dios, Peru, Acre, Brazil, and Pando, Bolivia) region. While he found it intellectually rewarding to think about governance, decision-making, and economics from an ecological anthropology viewpoint, he decided that a more focused approach was appropriate for his Ph.D. research. He thus shifted his attention to a forest concession in transitional forest in Santa Cruz, Bolivia, where he studied the dynamics of a forest subjected to selective logging, wildfires, and climate change related droughts.

Immediately upon completion of his Ph.D., Allie commenced a post-doctoral position with Oxford University. His field research and modeling efforts focus on forest canopies and photosynthesis in 3-D space along an elevation gradient in Peru using hyperspectral, LiDAR, and field data. He hopes to steer his career in a direction that allows him to address questions of import to society with innovative tools and techniques, to collaborate in addressing those question with people from research institutions, governments, and communities, and to bring to bear his skills in engineering, forest ecology, and human ecology in ways that benefit from their synergies.