THE ROLE OF FIRE IN THE RECRUITMENT AND MORTALITY OF TREE SEEDLINGS WITHIN THE FOREST-SAVANNA BOUNDARY

Minor thesis
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ABSTRACT

At global scale, climate is thought to determine terrestrial vegetation. However, at local scale, vegetation patches with different tree densities can be found under the same climatic conditions. Artificial fire exclusion experiments followed by an invasion of forest tree species have led to the idea that forest and savanna represent alterable stable states mediated by fire vegetation feedbacks. Hence, two thresholds based on tree grass interactions have been proposed to explain the transition between these systems: the “fire-resistance threshold” and the “fire-suppression threshold”. These thresholds suggest that saplings should grow above the flame height and experience a fire free interval of sufficient duration to reach a fire resistance height, and that only forest tree species can suppress fire by closing canopy and reducing fuel loads in the ground layer. However, forest expands in areas where fire still occurs every year and the presence of vegetation types with structural characteristics of typical forest systems but at floristic level mainly composed with typical savanna tree species puts a big question mark in the fire-vegetation feedback. Therefore, this study tests the “fire-trap” hypothesis to understand to what extent is fire a key determinant of the mortality and recruitment of tree seedlings. We have found that seedling survival and precipitation started to decrease at the same time (September 2013). In a period of five months before the fire event (February 2014), seedling survival decreased by 50%. Therefore, based in our study, we suggest that fire is not the only factor to affect seedling survival. The effects of fire added to precipitation and induced drought stress due to a decline in precipitation significantly affects survival of the seedlings. Furthermore, area burnt was not affected by the type of fuel and fuel loads in the plots. This suggests that other factors such as fuel bed continuity may have a stronger effect on area burnt than fuel loads alone and should be taken into consideration to improve future research. With expected increases in temperature, likely associated with decreases in precipitation, forest and savanna distribution may change in a big extent. If precipitation reduces, it is expected to have an increase in extreme events such as droughts and fire. With more fire and less precipitation, a “die-back” of tropical forest may occur.
THE ROLE OF FIRE IN THE RECRUITMENT AND MORTALITY OF TREE SEEDLINGS WITHIN THE FOREST-SAVANNA BOUNDARY

INTRODUCTION

Forest and savanna dominate tropical landscapes, covering 15% and 20% of the land surface, and accounting for 33.5% and 25% of terrestrial gross primary production, respectively (Beer et al., 2010, Murphy and Bowman, 2012). However, global increases in temperature, likely associated with decreases in precipitation and increases in extreme events such as droughts (Sheffield and Wood, 2008), may cause a “die-back” of tropical forests (Malhi et al., 2009) and directly affect the stability of ecosystems and human welfare. For instance, changes in woody cover affect livestock production, wildlife conservation, predator-prey interactions, nutrient cycling, and carbon storage (Bond and Keeley, 2005, Scholes and Archer, 1997, Kimuyu et al., 2013). Hence it is important to understand the main factors that shape the distribution of forest and savanna.

Factors that underlie the distribution of forest and savanna remain poorly understood (Murphy and Bowman, 2012). It has been suggested that climate determines terrestrial vegetation (Polis, 1999) and influences tree cover at a global scale (Bond and Midgley, 2000, Sankaran et al., 2005, Staver et al., 2011b). However, at local scale, different modalities of canopy cover can be found under the same climatic conditions (Bond, 2008). Although the influence of factors such as water, nutrients, and soil structure in shaping vegetation structure at local scale have long being recognized (Sankaran et al., 2005, Bond, 2008, Hoffmann et al., 2009, Lehmann et al., 2011, Saiz et al., 2012), artificial fire exclusion experiments in savanna ecosystems followed by an invasion of forest tree species (Hopkins and Jenkin, 1962, Swaine et al., 1992, Bond et al., 2005) has led to the idea that forest and savanna represent alternable stable states generally mediated by fire vegetation feedbacks (Hoffmann et al., 2012, Murphy and Bowman, 2012, Staver et al., 2011a, Staver et al., 2011b). Global vegetation analyses have tried to find multiple stability in canopy cover (Hirotta et al., 2011, Staver et al., 2011a, Staver et al., 2011b). However, their findings may be due to statistical flaws in the methodology underlying the remote sensing tree-cover products used in the global vegetation analyses (Hansen et al., 2003) rather than a discontinuity in tree cover distribution in the real world (Hanan et al., 2014). Moreover, fire vegetation feedbacks have been questioned (Veenendaal et al., 2014, Medina, 2014).

Two thresholds determined by grass-tree interactions have been proposed to explain transition between forest and savanna: ‘fire resistance threshold’ at individual tree level and ‘fire suppression threshold’ at ecosystem level (Hoffmann et al., 2012). In savanna, fire disturbance is high due to a continuous grass layer, fast regrowth (Bond, 2008) and a positive feedback between fuel load -grass biomass- and fire intensity (Van Langevelde et al., 2003). Fire disturbances prevent tree recruitment into adult sizes (Higgins et al., 2000) due to ‘topkill’ -complete loss of aerial biomass- (Bond and Midgley, 2000). Therefore, to avoid being susceptible to top-kill,
saplings have to grow above the flame height and should experience a fire-free interval of sufficient duration to reach the required height (Bond and Midgley, 2000). Hence, the height at which the tree surpasses this “fire trap” (Hoffmann et al., 2009) is denoted as ‘fire resistance threshold’. Moreover, at ecosystem level, canopy closure (> 40%) leads to a reduction of grass cover, light availability and an increase in moisture, which influence a decline in intensity and propagation of fires (Archibald et al., 2009, Cochrane, 2003, Hoffmann et al., 2009). Thus, the stage that marks the transition from highly flammable savanna to not or less flammable forest is denoted as ‘fire-suppression threshold’.

Hoffmann et al. (2012) suggest that whether a tree surpasses the “fire trap” or a canopy closes enough to suppress fuel loads in the ground layer generally depend on the functional traits of the tree species that compose those systems and on long fire-free intervals. For instance, forest tree species can only reach the fire resistance threshold if they experience a fire-free interval (Hoffmann et al., 2009) due to the lack of a protective thick bark, and savanna trees cannot reduce flammability of the ecosystem due to their open crowns, shade intolerance and low growth (Hoffmann et al., 2012, Hoffmann et al., 2003). However, some findings contrast with these ideas. For instance, it has been found that forest expands in areas where fire still burns every year (Mitchard et al., 2009), and vegetation types exist with structural characteristics typical of forest systems but at floristic level mainly composed with savanna tree species (Torello-Raventos et al., 2013, Medina, 2014). The establishment of trees under different fire regimes suggest that fire may not be the main factor in shaping the distribution of forest and savanna. Therefore, in order to understand the main role of fire and its effect on seedlings establishment and development, this study will test the “fire trap” hypothesis by assessing and quantifying mortality and recruitment of tree seedlings under fire disturbances.

The objective of this study is to test the “fire trap” hypothesis to understand to what extent is fire a key determinant of the mortality and recruitment of tree seedlings. In order to address the objective, research towards the following specific research questions is necessary: 1) What are the effects of different vegetation structures on area burnt within the forest-savanna boundary? It is expected that open plots will have higher fuel loads due to high light availability. Moreover, this high availability of fuel loads will have a positive effect on area burnt. 2) What is the effect of fire in the recruitment process and seedling mortality within the forest-savanna boundary? It is expected that fire will have a negative effect in mortality and recruitment of tree seedlings. Furthermore, to test the “fire-trap” hypothesis, manipulation of the standing biomass in 50% of the plots per vegetation type will be carried out. Standing biomass will be cut to ground level and therefore, fire effects will be reduced and with subsequent reduction in seedling mortality.
RESEARCH METHODS

Study site

The study was carried out in Kogyae Strict Nature Reserve, Ghana. The reserve is located in the north-eastern part of the Ashanti Region in Ghana, centred on 1°05'W /7°15'N in the Afram Plains (Figure 1). It has an extension of 386 km2, an altitude range of 120 - 230 m above sea level and average annual rainfall of 1364 mm (mean annual rainfall for the years 1961 to 1990 obtained from the nearest meteorological station at Ejura, 25 km north-west of the reserve) distributed in a double rainfall season between May and October with peaks in June and September. Kogyae was the only reserve designated as a Strict Nature Reserve and one of two reserves situated in the transitional vegetation zone between the Guinea savanna and forest regions of Ghana. The reserve was composed of a mosaic of vegetation including grassland, woodland savanna, transitional forest, riparian woodland and forest islands.

Figure 1. Location of Kogyae Strict Nature Reserve. The Geographic coordinate system is based on latitude and longitude.

Experimental design

For this study, 24 plots of 10x10 meters were established in June 2013. These plots were located in the northeast of the reserve in a mosaic of woodland savanna, transitional woodland and forest patches. The plots were selected to cover the maximum range of canopy cover. 8 plots were located in closed vegetation with structural and floristic characteristics of typical forest systems, 8 plots in open vegetation patches with structural and floristic characteristics of typical savanna systems and 8 plots in a mixed vegetation type with structural characteristics of forest systems but at floristic level composed by a mix of forest and savanna tree species (Figure 2).

Data collection

Fuel loads were estimated for standing biomass and litter separately. For standing biomass, a disc pasture meter was calibrated for grasses and herbs. For the calibration, settling height of 4 disc readings was collected over a square of 50x50 cm and the mean calculated. We measured 60 squares, 40 for grasses and 20 for herbs. The standing vegetation within each square was cut to ground level, wet weight determined, and one sub-sample per square collected. Wet mass of the sub-sample was measured, dried at 80°C for 48 h, and dry weight determined. Dry mass of total standing vegetation per square was estimated using the percentage of water loss obtained from the sub-samples. Then, a linear regression was made using the mean settling disc height per square as predictive variable and dry standing biomass per
For grasses, the obtained model was:

\[
\sqrt{\text{dry grass biomass (kg/ha)}} = 25.959 + 2.008 \text{ height (cm)}, \quad R^2=0.55.
\]

For herbs, the obtained model was:

\[
\sqrt{\text{dry herbs biomass (kg/ha)}} = 19.9551 + 0.8732 \text{ height (cm)}, \quad R^2=0.75.
\]

After the calibration, 3 random height measures were recorded in each plot and used in the models to estimate dry standing biomass per plot.

Litter was collected in 3 sub-plots of 30x30 cm in each plot, wet weight determined, and one sample collected. Wet mass of the sample was recorded, dried at 80°C for 48 h, and dry weight determined. Dry weight of each sub-plot was estimated using the percentage of water loss obtained from the samples. Furthermore, grass was manipulated on January 2014 by reducing standing biomass to ground level in 4 plots in each vegetation type.

Hemispheric pictures of the canopy were taken at each plot in January 2014 with a camera Nikon E4500 and a fisheye lens mounted on a tripod at 1.50 m height using a 180° angle. Canopy openness (%) was derived using the Gap Light Analyzer (GLA) imaging software (Frazer et al., 1999). Furthermore, area burnt of the plots was estimated visually four weeks after fire.

5 species typical from forest systems were selected for the experiment (table 1). These seedlings were planted in the first week of June 2013 and seedling survival was assessed by observation in the third week of June 2013, the second week of September 2013, the second week of January 2014, the first week of April 2014 and the second week of June 2014.

<table>
<thead>
<tr>
<th>Species</th>
<th>Functional group</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Terminalia superba</em></td>
<td>Forest²</td>
</tr>
<tr>
<td><em>Khaya ivorensis</em></td>
<td>Forest²</td>
</tr>
<tr>
<td><em>Nauclea diderrichii</em></td>
<td>Forest²</td>
</tr>
<tr>
<td><em>Triplochiton scleroxylon</em></td>
<td>Forest²</td>
</tr>
<tr>
<td><em>Bombax buonopozense</em></td>
<td>Forest³</td>
</tr>
</tbody>
</table>

### Data analysis

**Canopy openness and fuel loads**

One-way ANOVA was used to assess differences in canopy openness between plots. For multiple comparisons, the Tukey’s HSD test was used. If needed, the response variable was transformed to meet the requirements of the test. Moreover, a linear regression was used to assess the relationship between mean canopy openness (%) and total standing dry biomass (kg/ha) (only plots without standing biomass manipulation). To fulfil the conditions of linearity between variables, the response variable (dry standing biomass) was log transformed. To generate the standardized

\[
R^2 = 0.55
\]

\[
R^2 = 0.75
\]

\[
\sqrt{\text{dry grass biomass (kg/ha)}} = 25.959 + 2.008 \text{ height (cm)}, \quad R^2=0.55.
\]

\[
\sqrt{\text{dry herbs biomass (kg/ha)}} = 19.9551 + 0.8732 \text{ height (cm)}, \quad R^2=0.75.
\]

---

² Information obtained from: [http://www.worldagroforestry.org/](http://www.worldagroforestry.org/)

³ Information obtained from: [http://www.prota4u.info/](http://www.prota4u.info/) and [http://plants.jstor.org/](http://plants.jstor.org/)
parameter estimates, we used the ‘lm.beta’ function from the package QuantPsyc (Fletcher, 2012).

One-way ANOVA was used to assess differences in dry litter. To assess differences in dry standing biomass, Kruskal-Wallis test was used using the function ‘kruskal’ from the R package agricolae (Mendiburu, 2014). To assess differences between groups, the ‘kruskal’ function makes multiple comparisons using the Hochberg procedure as method to adjust p-values.

Fire characteristics and seedling survival

A Generalized linear model (GLM) using a negative binomial distribution was used to assess the effect of the type of vegetation, manipulation of the standing biomass, standing biomass and litter on area burnt. The response variable – proportion of area burnt-, was arcsine transformed using the function ‘transf.arcsin’ from the R package metafor (Viechtbauer, 2010). The function ‘glm.nb’ from the R package MASS (Venables and Ripley, 2002) was used to run the model. Moreover, Kruskal-Wallis test was used to assess differences in seedling survival between vegetation types in each of the 5 censuses and the Friedman test was used to assess differences in survival through time by using the function ‘friedman’ from the R package agricolae (Mendiburu, 2014). Furthermore, a GLM using a Poisson distribution was used to assess the effect of area burnt, vegetation type, manipulation of standing biomass, dry standing biomass and dry litter on seedling survival changes from January 2014 (before fire) to April 2014 (after fire).

RESULTS

Canopy openness and fuel loads

Canopy openness was significantly different between the 3 vegetation types (One-way Anova, F2,21=133.5, p<0.001). Canopy openness in savanna plots was significantly higher than mixed and forest plots. In mixed plots, canopy openness was significantly lower than savanna plots and higher than forest plots. Furthermore, forest plots had the lowest canopy openness (figure 3).
Mean canopy openness (%) explained 46% of the variance in dry standing biomass. It was found that canopy openness (%) significantly predicted log-dry standing biomass ($\beta=0.69$, $F_{1,34}=30.83$, $p<0.001$) (Figure 4).

Dry litter was significantly different between the plots (One-way Anova, $F_{2,69}=14.3$, $p<0.001$) (figure 5). Litter in savanna plots was significantly lower than in the mixed and forest plots. Furthermore, there is no significant difference between mixed and
forest plots (figure 5). Standing dry biomass was significantly different between the plots (Kruskal-Wallis, $X^2=48.16$, df=5, $p<0.001$) (figure 6). Dry standing biomass in savanna plots without manipulation was the highest. Savanna plots with manipulation was lower than savanna plots without manipulation and higher than mixed and forest plots with and without manipulation. Furthermore, there was no significant difference between mixed and forest plots with and without standing biomass manipulation.

**Figure 5.** Differences in dry litter between Forest, Mixed and Savanna plots. Letters represent significant differences. Error bar represent 95% confidence interval.

**Figure 6.** Differences in dry standing biomass between Forest, Mixed and Savanna plots with or without manipulation of the standing biomass. Letters represent significant differences. Error bar represent 95% confidence interval.
Fire characteristics

Fire occurred on Sunday, February 2, 2014 at 15:00 h. Wind speed was 1.13 m/s, air temperature 33.51°C and relative humidity was 11.76%. The different vegetation types, manipulation of the standing biomass, dry standing biomass and litter content did not have a significant effect on area burnt. To see the complete list of the model’s coefficients refer to the Appendix 1. There was no significant difference on area burnt between the different vegetation types (figure 7).

![Figure 7. Differences in area burnt between Forest, Mixed and Savanna plots with and without standing biomass manipulation. Letters represent significant differences.](image)

Seedling survival

Seedling survival was not significantly different between vegetation types in June 2013, September 2013, January 2014 and June 2014 (figure 8A, B, C and E, respectively). However, seedling survival was significantly different between forest, mixed and savanna plots 8 weeks after fire, April 2014 (figure 8D). In April 2014, seedling survival in forest was significantly lower than mixed and savanna plots. However, there was no significant difference between mixed and savanna plots.
Survival of the seedlings changed since June 2013 to June 2014 (Friedman, X2 =10.93, df=4, p<0.05). Between June and September 2013, survival was not significantly different (Figure 10). Furthermore, survival in January 2014 decreased by 50%. Fire arrived in February 2014. Survival after fire, April 2014, reduced to around 10% and was not significantly different than June 2014.
Precipitation, area burnt and standing biomass content had a significant effect on seedling survival. However, the type of vegetation, litter content and manipulation of the standing biomass did not have a significant effect on seedling survival (Appendix 2). Furthermore, some significant interactions between variables were found. For savanna, litter content had a significant effect on survival. For mixed and forest, litter content had no effect on survival. Furthermore, for mixed type of vegetation, standing biomass and manipulation of the standing biomass had a significant effect on survival. For savanna and forest, standing biomass and manipulation had no effect.

Figure 10 shows changes in precipitation. From the figure can be observed that precipitation started to decrease in September 2013, from 180 mm to 12 mm in December 2013. From December 2013 to January 2014, precipitation was almost null. Furthermore, a low increase can be seen in February 2014.
DISCUSSION

Fire has been suggested to be the main factor that shapes vegetation distribution in the forest-savanna ecotone (Hoffmann et al., 2012, Murphy and Bowman, 2012, Staver et al., 2011a, Staver et al., 2011b). Furthermore, a fire-vegetation feedback underlined by two thresholds had been proposed to explain the distribution of forest and savanna at local scale (Hoffmann et al., 2012), the “fire-resistance threshold” and the “fire-suppression threshold”. These thresholds suggest that saplings should grow above the flame height and experience a fire free interval of sufficient duration to reach a fire resistance height, and that only forest tree species can suppress fire by closing canopy and reducing fuel loads in the ground layer. However, some findings challenge these ideas. For instance, forest expands in areas where fire still occurs every year (Mitchard et al., 2009), and the presence of vegetation types with structural characteristics of typical forest systems but at floristic level mainly composed with typical savanna tree species (Torello-Raventos et al., 2013, Medina, 2014). Therefore, this study provides empirical evidence to test the fire-vegetation feedback by assessing to what extent is fire a key determinant of the mortality and recruitment of tree seedlings.

Vegetation structure and fire characteristics

Three vegetation structures were found in the forest savanna ecotone: forest, mixed and savanna. Forest and mixed plots had canopy openness values lower than 30% (figure 3). However, canopy openness in savanna plots was significantly higher, 55%. Other studies have found in the forest-savanna transition zone a vegetation type with structural characteristics typical of forest systems but at floristic level, mainly composed with typical savanna tree species (Torello-Raventos et al., 2013, Medina, 2014). These results agree with our study. Although we did not carry out a species inventory of the plots, we observed that the floristic composition between mixed and forest plots was different (see Medina, 2014). We observed that mixed plots had a higher amount of typical savanna tree species, relative to typical savanna plots. These findings suggest that typical savanna trees can adopt a forest-like nature in the forest-savanna transition zone. Hence, the presence of this vegetation type challenges the idea of fire as the main driver of canopy openness and that savanna trees cannot adopt a forest like nature due to their open crowns (Hoffmann et al., 2012).

Besides the differences in structural and floristic characteristics between vegetation types, differences in fuel loads were observed. Dry standing biomass (figure 6) in mixed and forest plots was significantly lower than savanna plots, the opposite for litter (figure 5). Furthermore, no significant effect of fuel loads was found on area burnt. This can be explained by the lack of continuity of the fuel bed. As other studies suggest, the continuity of the fuel bed controls area burnt (Archibald et al., 2009). Although we did not assess fuel bed continuity, we observed patches with low or without fuel and patches with high fuel content in every plot.
We expected to find a significant effect of manipulation of the standing biomass on area burnt and a significant interaction between manipulation of the standing biomass and standing biomass on area burnt. However, we did not find any significance (Appendix 2). As mentioned above, this may be also explained by a discontinuity of the fuel bed (Archibald et al., 2009). For instance, manipulation of the standing biomass was only applied to reduce fuel loads, not to increase continuity of the fuel bed. Therefore, fuel bed discontinuity was maintained and this may be a reason of why manipulation of the standing biomass did not have an effect on area burnt.

**Seedling survival**

Survival of the seedlings did change through time (figure 9). However, this change was not only mediated by fire. Figure 9 shows that seedling survival was 50% on January 2014, 1 month before fire. This suggests that other factors, besides fire, may affect survival. For instance, figure 10 shows that, besides seedling survival, precipitation also started to decrease on September 2013. This change in precipitation significantly affected survival of the seedlings (Appendix 2), probably due to drought stress. This suggestion is supported by other studies. For instance, it has been found that drought stress is the main factor of seedling mortality (Engelbrecht and Kursar, 2003, Engelbrecht et al., 2005). Nevertheless, it has been generally accepted that only fire shapes vegetation distribution in the forest-savanna boundary due to top-kill of the tree seedlings (Hoffmann et al., 2012, Murphy and Bowman, 2012, Staver et al., 2011a, Staver et al., 2011b).

From the 5 censuses, only April 2014 (8 weeks after fire) showed significant differences on seedling survival between vegetation types. Figure 8D shows that survival in forest plots was significantly lower than mixed and savanna plots. Although the amount of litter was not significant to predict survival of the seedlings (Appendix 2) and moisture content of the fuel loads was not available, we consider that fire residence time in forest plots was higher than mixed and savanna plots due to high loads of litter and assumed higher moisture content than grasses (Burrows, 2001). Hence, fire residence time may be an important factor to predict seedling survival. Other studies suggest that fire induced tree mortality is determined by bark thickness and fire residence time (Cochrane et al., 1999). However, bark traits have been considered as the main factors to affect tree mortality (Hoffmann et al., 2003, Hoffmann et al., 2012, Brando et al., 2012).

It has been suggested that global increases in temperature, likely associated with decreases in precipitation and increases in extreme events such as droughts (Sheffield and Wood, 2008), may cause a “die-back” of tropical forests (Malhi et al., 2009). We have found that seedling survival was significantly affected by precipitation and area burnt. Therefore, with a decrease in precipitation and an increase in droughts and fire events, a die-back of tropical forest may occur.
CONCLUSIONS

Our study suggest that area burnt was not affected by fuel loads, manipulation or by the type of vegetation where the plots were established. However, we can infer by observation and other studies, that fuel continuity may have a significant effect on area burnt. Therefore, in order to understand and predict area burnt, assessment of the continuity of the fuel bed is strongly recommended.

The fire-trap hypothesis suggest that seedlings in order to avoid being susceptible to top-kill should experience a fire free interval of sufficient duration to acquire a fire resistance size. However, from our study we conclude that other factors such as precipitation have a strong effect on seedling survival. Hence, low precipitation and an increase in drought stress and fire, decrease survival probability of the seedlings.
BIBLIOGRAPHY


APPENDIX

Appendix 1. Results of the Generalized linear model using area burnt as dependent variable, and vegetation type (Veg type), standing biomass manipulation (Manipulation), standing biomass (Stand Biomass) and litter (Litter) as independent variable. “::” represents interaction.

GLM Model coefficients

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>Std. Error</th>
<th>Z val.</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-2.0780</td>
<td>5.7615</td>
<td>-0.36</td>
<td>0.72</td>
</tr>
<tr>
<td>VegType &quot;M&quot;</td>
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<td>0.75</td>
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<tr>
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<td>6.0223</td>
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<tr>
<td>Stand biomass</td>
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<td>0.0108</td>
<td>0.05</td>
<td>0.96</td>
</tr>
<tr>
<td>Manipulation</td>
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<td>5.2650</td>
<td>-0.05</td>
<td>0.96</td>
</tr>
<tr>
<td>Litter</td>
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<td>0.0004</td>
<td>1.07</td>
<td>0.28</td>
</tr>
<tr>
<td>VegType &quot;M&quot;:StandBiomass</td>
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<td>VegType &quot;S&quot;:StandBiomass</td>
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<tr>
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<td>0.11</td>
<td>0.91</td>
</tr>
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</table>

Appendix 2. Results of the Generalized linear model using seedling survival as dependent variable, and precipitation, area burnt, vegetation type (Veg type), litter, standing biomass and manipulation as independent variable. “::” represents interaction. “***” represents significant effects.

GLM Model coefficients

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>Std. Error</th>
<th>Z val.</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
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<td>0.4727</td>
<td>-0.60</td>
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</tr>
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<td>Precipitation *</td>
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<td>0.0066</td>
<td>-2.73</td>
<td>0.006</td>
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<td>Area burnt *</td>
<td>-0.0260</td>
<td>0.0109</td>
<td>-2.38</td>
<td>0.017</td>
</tr>
<tr>
<td>Veg type &quot;M&quot;</td>
<td>0.1984</td>
<td>0.1158</td>
<td>1.71</td>
<td>0.087</td>
</tr>
<tr>
<td>Veg type &quot;S&quot;</td>
<td>-0.5272</td>
<td>0.3119</td>
<td>-1.69</td>
<td>0.091</td>
</tr>
<tr>
<td>Litter</td>
<td>4.4E-05</td>
<td>4.7E-05</td>
<td>0.94</td>
<td>0.346</td>
</tr>
<tr>
<td>Stand Biomass *</td>
<td>0.0002</td>
<td>5.1E-05</td>
<td>4.01</td>
<td>5.9E-05</td>
</tr>
<tr>
<td>Manipulation</td>
<td>-0.0973</td>
<td>0.2330</td>
<td>-0.42</td>
<td>0.676</td>
</tr>
<tr>
<td>Manipulation: StandBiomass</td>
<td>0.0006</td>
<td>0.0003</td>
<td>1.78</td>
<td>0.076</td>
</tr>
<tr>
<td>Area burnt:Veg type &quot;F&quot;:Litter</td>
<td>-1.1E-05</td>
<td>8.9E-06</td>
<td>-1.20</td>
<td>0.229</td>
</tr>
<tr>
<td>Area burnt:Veg type &quot;M&quot;:Litter</td>
<td>-4.6E-06</td>
<td>3.7E-06</td>
<td>-1.25</td>
<td>0.212</td>
</tr>
<tr>
<td>Area burnt:Veg type &quot;S&quot;:Litter</td>
<td>9.1E-06</td>
<td>4.0E-06</td>
<td>2.26</td>
<td>0.024</td>
</tr>
<tr>
<td>Area burnt:Veg type &quot;F&quot;:Manipulation 0:StandBiomass</td>
<td>9.2E-05</td>
<td>9.0E-05</td>
<td>1.02</td>
<td>0.306</td>
</tr>
<tr>
<td>Area burnt:Veg type &quot;M&quot;:Manipulation 0:StandBiomass</td>
<td>6.1E-05</td>
<td>2.7E-05</td>
<td>2.27</td>
<td>0.023</td>
</tr>
<tr>
<td>Area burnt:Veg type &quot;S&quot;:Manipulation 0:StandBiomass</td>
<td>4.7E-07</td>
<td>1.6E-06</td>
<td>0.29</td>
<td>0.770</td>
</tr>
<tr>
<td>Area burnt:Veg type &quot;F&quot;:Manipulation 1:StandBiomass</td>
<td>7.3E-05</td>
<td>5.8E-05</td>
<td>1.26</td>
<td>0.209</td>
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<tr>
<td>Area burnt:Veg type &quot;M&quot;:Manipulation 1:StandBiomass*</td>
<td>5.6E-05</td>
<td>2.7E-05</td>
<td>2.09</td>
<td>0.037</td>
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<tr>
<td>Area burnt:Veg type &quot;S&quot;:Manipulation 1:StandBiomass</td>
<td>-1.1E-05</td>
<td>1.1E-05</td>
<td>-1.00</td>
<td>0.319</td>
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