Chlorophyll a fluorescence of *Bertholletia excelsa* Bonpl. plantations under thinning, liming, and phosphorus fertilization

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Abstract

Phosphorus (P) fertilization and liming can reduce negative effects caused by a sudden increase in light availability after thinning of forest plantations. In this study, immediately after thinning, photochemical performance (quantum yield of PSII and performance index) decreased, however, liming and P fertilization reduced the negative effects caused by thinning and accelerated the recovery of *Bertholletia excelsa* trees. After thinning, the remaining trees increased J-I phase with the formation of a positive K-band which occurred exclusively in unfertilized (no liming or no P) individuals. Additionally, enhanced effective dissipation (DI$_{0}$/RC) values (140%) were found in individuals without liming or P after thinning, while plants under liming and P increased DI$_{0}$/RC values by 47 and 79%, respectively. Photochemical performance of *B. excelsa* was positively correlated to iron, zinc, and manganese. Thus, P fertilization and liming are recommended for alleviating the stress caused by high irradiance after thinning in *B. excelsa* plantations.

Additional key words: Brazil nut tree; photosynthetic pigments; plant nutrition; silvicultural practices; stress physiology.

Introduction

Silvicultural practices are important for the management of planted forests and such treatments have been recommended for increasing plantation productivity (Forrester et al. 2013). In order to increase the primary production of planted forests, practices, which improve tree photosynthesis, are extremely useful since they increase carbon assimilation. But some forestry practices such as thinning may initially have negative effects and decrease biomass gain as observed in a boreal forest in which the leaf area index decreases from 8 to 6 (Vesala et al. 2005). In addition, recent study has shown that after thinning, the remaining trees may reduce their photochemical performance [quantum yield of PSII (F$_{V}$/F$_{M}$) and performance index (PI$_{ABS}$)] as a response to excess energy, thus enhancing photoinhibition, which may decrease the net photosynthetic rates ($\text{P}_{\text{n}}$) and consequently plantation productivity (Wu et al. 2018). So, some questions emerge, for example: Can other silvicultural practices mitigate or decrease the impact of thinning on photosynthesis?

Photosynthesis is determined by chlorophyll (Chl) content and the flux of energy in leaves. Plants should adjust Chl ($a+b$) content and Chl $a/b$ ratio to adapt to certain environmental conditions and optimize photosynthesis under high and low irradiance (Ma et al. 2015). Liming (material contains calcium and/or magnesium compounds capable of neutralizing soil acidity) and P fertilization treatments, just as in other silvicultural treatments, in turn, can reduce the high-light stress effects on chloroplast pigments and stimulate photosynthesis in high light plasticity plants (Filstrup and Downing 2017, Lopes et al. 2019) after thinning, due to the enhancement of the nutrient uptake of trees and the availability of nutrients in soil, mainly calcium (Ca), magnesium (Mg), and P. On the other hand, under conditions, where light is limited, liming can increase leaf Chl (due to the increase of Mg concentrations in leaves and P addition) in order to favor

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Abbreviations: Chl – chlorophyll; OJIP – fast chlorophyll fluorescence transients; DI$_{0}$/RC – dissipated energy flux per reaction center of PSII; ET$_{0}$/RC – electron transport of an active RC; TR$_{0}$/RC – maximum trapping rate per RC.

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increased light energy flux and use (Filstrup and Downing 2017).

When a Chl molecule absorbs light, approximately 80% of the absorbed light is used in photosynthesis, but under stress conditions, changes in the dynamics of energy flow in leaves may occur, which may alter the shape of the OJIP curve (Strasser et al. 2004). Plants in high light environments may increase initial fluorescence (F0) and reduce all the induction phases (O-J, J-I, and I-P), and show a much flatter curve (Kalaji et al. 2012), which may result in the formation of a positive K-band in O-J step, indicating more severe stress. The effects of P deficiency on OJIP curvature seem contradictory and nonspecific, but it was reported that under low P, the curvature of the OJIP transient is affected at around the I-step at 20 to 50 ms that gradually straightens and might be absent (Carstensen et al. 2018a).

Changes in the curvature of OJIP transient reflect the alteration in the energy flux in leaves. Plants subjected to stressful conditions may increase effective dissipation (DI) of an active reaction center (RC) as a strategy to reduce excessive absorbed energy and enhance protective quenching of photosynthetic apparatus, thus they may also reduce other steps of the energy flux, such as absorption (ABS), trapped energy (TRs), and electron transport (ETs) (Strasser et al. 2004, dos Santos Junior et al. 2015). The increase in nonphotochemical dissipation, in general, results in the decrease of Fv/Fm and a decrease in PIus (Strasser et al. 2004, Kalaji et al. 2012, Stirbet and Govindjee 2012).

The effects of thinning, liming, and P fertilization on photochemical performance are associated with the photosynthetic capacity of plants, since it is a stress characteristic, and also demonstrates the species ability to acclimate to new environmental conditions. In this context, Bertholletia excelsa Bonpl. (Brazil nut tree) is a singular species and studies have indicated the capacity of this species to tolerate and recover from stress conditions (Ferreira et al. 2009, Lopes et al. 2019, Schimpl et al. 2019). But nowadays, it has been a common theme of discussion in the literature that fertilization can increase stress tolerance, and that plant’s ability to adapt to stressful environments can be detected and monitored using the Chl a fluorescence (Kalaji et al. 2017, Tariq et al. 2017).

B. excelsa is a highly valuable commercial Amazonian tree species that has occupied prominent position in the silvicultural scenario in this region (Scoles et al. 2011, 2014; Ferreira et al. 2015, Schrot et al. 2015). In a B. excelsa forest plantation for wood production, we evaluated the effects of thinning, liming, and P fertilization on photosynthetic pigments and Chl a fluorescence (ChIF). The two main hypotheses were: (1) thinning may affect photochemical efficiency of individuals and (2) liming and P fertilization may alleviate the effects of high light stress by causing enhanced light energy uptake and usage.

Materials and methods

Study site, thinning, and fertilization treatments: The Bertholletia excelsa Bonpl. (Brazil nut tree) plantation studied was located in Itacoatiara, Amazonas, Brazil (3°030.63"S, 58°50'1.50"E), which is 120 to 170 m a.s.l., has a mean annual temperature of 31.2°C, and an annual rainfall of 2,539.6 mm (INMET 2018). Two well-defined seasons exist; the rainy season with precipitation of > 300 mm from January to April and the dry season with precipitation of < 100 mm from August to September. The dominant soil type is ferrasol. The plantation was established in 2000, on an area of 2.69 hectares. Seven-month-old seedlings with 45 cm of height were used; the spacing between seedlings was 2.5 × 1.5 m, resulting in a stocking density of 2,666 trees per hectare. Seedlings were not fertilized.

A randomized complete block design was established in this study. The number of blocks was defined from the variable diameter (measured at 1.3 m above ground), obtained by a preliminary pilot inventory. We used the sample size for the infinite population equation in order to determine how many sample units were needed to have a degree of confidence of 95% and 10% precision. Thus, eight blocks (1,102.5 m²) were established and in each block, the six treatments were randomly applied: (1) control; (2) liming; (3) liming + phosphorus; (4) thinning; (5) thinning + liming; and (6) thinning + liming + phosphorus. The treatments plots were separated by a buffer zone of approximately 4 m. Thus, the measurements were performed in a plot of 12.5 m × 7.5 m (93.75 m²) with 25 trees per plot (a total of 1,200 trees).

Liming treatments were 0 and 2,000 kg ha⁻¹, applied to the soil in the high precipitation season (14 March to 1 April 2016), with applications of 824 g of limestone (relative power of total neutralization of 91%) per tree. Phosphorus treatments were 0 and 150 kg ha⁻¹ of triple superphosphate (46% of PO₄), applied 60 d after the liming was assigned, and when the soil pH increased to 5.5, then another 122 g per tree were applied. The estimate for the liming necessity was performed based on the methodology proposed by Batista (2014), while the requirement for P₂O₅ was extrapolated from suggestions for Eucalyptus spp. (CFSEMG 1999).

Liming and P were applied at a distance of 50 cm from the stem base and 20-cm depth from the soil surface, forming a circle around the plant (soil amendment circle). The distance from stem base, depth of liming, and P application was defined according to studies regarding root distribution, which showed that 70% of the total root biomass of adult trees are in 0–20 cm depth from the soil surface and 61% are at a distance of 50 cm from the stem base (Sudmeyer et al. 2004). Thus, all liming and P treatments were applied within the influence of the root absorption zones.

After the P fertilizer was applied, a low level thinning of high intensity was performed, where 50% of the basal area was removed from the stand and suppressed, tortuous, and forked trees were eliminated. The thinning intensity was defined using the recommendations made by Costa (2015).

After application of the treatments, thinning increased the light availability from 51 to 423 µmol(photon) m⁻² s⁻¹ and, from rainy to dry season, the daily PAR in unthinned
plots increased by 70%, while in thinned plots the increase was 200% (Fig. 1A). However, the treatments applied did not change the availability of water in the soil, but we observed a progressive reduction of soil moisture from rainy to dry season (Fig. 1B). Sixty days after lime application, the soil pH increased from 4.3 to 5.8, and 30 d after P application, the P in soil increased from 2.1 to 88.2 mg g\(^{-1}\) (Fig. 1C,D). Values of pH and P remained greater in these plots throughout the experimental period (Fig. 1C,D).

**Data collection and tree sampling:** Data collection was performed between 2016–2017, during historical peaks of high precipitation (precipitation > 300 mm) and low precipitation (precipitation < 100 mm), as well as in the transition between these seasons (Fig. 2). Due to the impossibility of taking measurements from all the trees of the experiment (1,200 trees in total), three sample trees were selected in each plot for data collection. The criteria for selected trees were representativeness in diameter, height, and crown form in each plot.

**Nutrients:** Five healthy and fully expanded leaves were taken from the middle third of the sample trees. The leaf samples were dried in an oven at 65°C for mass constant evaluation. The total N was determined by the Kjeldahl method (Bremner and Mulvaney 1982). Macronutrients (Ca, Mg, P, and K) and micronutrients (Fe, Zn, Cu, and Mn) were extracted with a 3:1 nitric-perchloric solution, the concentrations of these nutrients were determined by atomic absorption spectrometry (Perkin-Elmer 1100B, Uberlingen, Germany) and P was determined by spectrophotometry (UV/VIS spectrophotometer Ultrospec 2100 pro, Amersham Biosciences) at 725 nm (Miyazawa et al. 1999).

**Photosynthetic pigments:** Chl contents were estimated from samples with 0.1 g of healthy and fully expanded leaves (fresh material) collected between 7:00–9:00 h and taken from the middle third of the sample trees. The pigments were extracted with 10 ml of 80% (v/v) acetone and 0.5% (w/v) magnesium carbonate (MgCO\(_3\)). The suspension was filtered (filter Quanty JP42) and the absorbance was determined using a spectrophotometer (Ultrospec 2100 pro, Armersham Biosciences) with wavelengths set at 663 nm (Chl a), 645 nm (Chl b), and...
total chlorophyll $\text{Chl}_{\text{total}} = \text{Chl} (a+b)$ (Arnon 1949). The calculations for the mass (µmol g$^{-1}$) of Chl pigments were obtained using the equations of Hendry and Price (1993).

**Chl a fluorescence and JIP-test:** The Chl a fluorescence induction curve was measured using a Handy-PEA fluorimeter (Hansatech Instruments Ltd., UK). The data were collected between 9:00–12:00 h in healthy and fully expanded leaves that were taken from the middle third of the sample trees. The selected leaves were subjected to a 30-min period of adaptation to darkness. Immediately after the dark-adaptation period, the leaves were exposed to a pulse of saturated light at an intensity of 3,000 µmol(photon) m$^{-2}$ s$^{-1}$ (peak at 650 nm) for 1 s, thus, fast fluorescence transients were obtained and were analyzed by the so-called ‘JIP-test’ (Strasser et al. 2004).

**Data analysis:** A linear mixed model was performed to evaluate the effects of treatments and seasonality on leaf pigment content and Chl a fluorescence. Block and plots were included in the models as nested random effects in order to control potential spatial autocorrelation. Pearson’s product-moment correlations were used to assess the influences of nutrients (mass basis) on Chl a fluorescence.

**Results**

Phosphorus and liming did not change the Chl and Chl a/b ratio in leaves of unthinned trees in the plots (Fig. 3, but thinning decreased the Chl in leaves. P and liming minimized these reductions and significant differences were not observed for the Chl and Chl a/b ratio between trees from thinned plots that received liming and Chl, when compared to the trees from unthinned plots (Fig. 3A). Accentedual differences in Chl and Chl a/b ratio between treatments were observed during the rainy–dry transition (July 2017) (Fig. 3). In this period, the trees in unthinned plots showed the Chl content 60% higher and the Chl a/b ratio 25% lower than that in trees of thinned plots, regardless of liming or P fertilization (Fig. 3).

Liming and P fertilization did not influence the $F_{v}/F_{m}$ ratio and $PI_{ABS}$ of *B. excelsa* trees of unthinned plots (Fig. 4). However, immediately after thinning, the $F_{v}/F_{m}$ and $PI_{ABS}$ decreased; liming and P fertilization helped minimize the stress caused by thinning and accelerated the recuperation (Fig. 4). After thinning, the reductions of $F_{v}/F_{m}$ in trees under thinning + liming treatments were 3% and thinning + P was 7%, while, in trees without liming or P, the reductions were in the order of 12% (Fig. 4A). Seasonality only influenced trees under thinning without liming or P fertilization. In these trees, we found a decrease in $F_{v}/F_{m}$ from 0.82 to 0.80 (for rainy and dry season, respectively) (Fig. 4A).

In order to understand factors associated with stress and recuperation of *B. excelsa* after thinning, the OJIP transients were measured during the most severe stress stage (June 2016) and after the complete recovery from stress in all treatment regimes (April 2017). During the period of the most severe stress, we observed a decrease in the I-P phase in all trees under thinning, irrespective of P. The increase in the J-I phase and positive K-band formation was also observed, but only in trees under thinning without liming or P (Fig. 5A,B). After recuperation from stress, no differences were found between treatments for OJIP transients and the formation of positive K-band for treatments was not observed (Fig. 5C,D).

Additionally, we found that during stress conditions, after thinning, there was an increase of 140% in photo-chemical dissipation (DIL/RC) in trees without liming or P, though the increase for trees under liming was only 47% and under liming + P it was only 79% (Table 1). We also found that stress conditions caused by thinning increased the absorption flux per PSII reaction center (ABS/RC), trapped energy flux per PSII reaction center (TR/RC), nonphotochemical dissipation per PSII reaction center (DIL/ABS), but no differences were found for electron transport flux from Q$_{a}$ to Q$_{b}$ per PSII (ET/RC).

During investigation of the effects of nutrients on photochemical performance of *B. excelsa*, we found positive effects for Fe and Zn micronutrients, on mass basis, on $F_{v}/F_{m}$ and $PI_{ABS}$ (Fig. 6). Macronutrients (N, P,
K, Ca) were not significantly correlated to \( F_v/F_m \), but N and P positively influenced P\( _{I_{ABS}} \) (Fig. 6).

**Discussion**

We found that thinning decreased Chl and the Chl a/b ratio, but application of P and liming minimized these reductions. The reduction of Chl concentrations in plants after thinning probably occurred due to high incident light on thinned trees. The degradation of Chl under these conditions is due to the formation of reactive oxygen species (ROS) which are responsible for a faster degradation of Chl (Croft and Chen 2017). In addition, the reduction of Chl content suggests a reduction in the light-harvesting complex, which may prevent the absorption of excessive light energy and thus avoid oxidative damage.

Chl b is mainly present in the light-harvesting complexes of PSI and PSII, however, Chl a is present in both the light-harvesting complexes and also in the reaction centers of the photosystems. Leaves under high irradiance tend to degrade the light-harvesting complexes in order to avoid damage to the photosynthetic apparatus due to the excess irradiance and tend to increase the number of PSII in order to increase the photosynthetic capacity of the plants (Živčák et al. 2014). The increase in ABS/RC values immediately after thinning indicates an increasing amount of the absorbing Chl a molecules per active RC. In this case, this response of ABS/RC after thinning may reflect a strategy that *B. excelsa* possesses for increasing the use of available energy.

The greater availability of light associated to the increase of ABS/RC and TR\(_{o}/RC\), did not change ET\(_{o}/RC\). The increase in TR\(_{o}/RC\) and the consistency in ET\(_{o}/RC\) indicate that the electron transport from pheophytin (Pheo) to Q\(_{A}\) (reduction of Q\(_{A}\) to Q\(_{A}^-\)) during photosynthesis in the leaves of *B. excelsa* increased, while the rates for transporting electrons were minimally affected by the sudden increase in light availability. The increase in TR\(_{o}/RC\) values immediately after thinning indicates an increasing amount of the absorbing Chl a molecules per active RC.

![Graph](image1.png)

**Fig. 4.** Seasonal variation of quantum yield of PSII (\( F_v/F_m \)) (A) and performance index (P\( _{I_{ABS}} \)) (B) of *Bertholletia excelsa* plantations under thinning, liming, and phosphorus fertilization. Values are means ± SE, \( n \) = 8.

![Graph](image2.png)

**Fig. 5.** OJIP transient and K-band performance under stress after thinning (A,B) and after recuperation (C,D) of *Bertholletia excelsa* under thinning, liming, and phosphorus fertilization.
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Table 1. Specific flux of energy per reaction center (RC) in leaves of *Bertholletia excelsa* plantations under thinning, liming, and phosphorus fertilization. Initial fluorescence (F₀), maximum fluorescence (Fₘ), effective antenna size expressed as absorbance per reaction center (ABS/RC), amount of energy dissipated per active reaction center (DI₀/RC), electron transport per reaction center (ET₀/RC), trapping efficiency per reaction center (TR₀/RC), and performance index (PIABS).

<table>
<thead>
<tr>
<th>Fluorescence parameters</th>
<th>Liming</th>
<th>Liming + P</th>
<th>Thinning</th>
<th>Thinning + liming</th>
<th>Thinning + liming + P</th>
<th>R²</th>
<th>p</th>
</tr>
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<tbody>
<tr>
<td>F₀</td>
<td>Stress</td>
<td>6.45</td>
<td>-0.57</td>
<td>36.56</td>
<td>7.56</td>
<td>10.75</td>
<td>0.22</td>
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<td></td>
<td>Recupered</td>
<td>-3.47</td>
<td>-1.09</td>
<td>1.46</td>
<td>-5.49</td>
<td>-5.22</td>
<td>0.01</td>
</tr>
<tr>
<td>Fₘ</td>
<td>Stress</td>
<td>8.11</td>
<td>1.32</td>
<td>-9.13</td>
<td>-4.49</td>
<td>-14.3</td>
<td>0.26</td>
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<tr>
<td></td>
<td>Recupered</td>
<td>-1.79</td>
<td>1.16</td>
<td>-5.23</td>
<td>-10.74</td>
<td>-5.21</td>
<td>0.09</td>
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<tr>
<td>ABS/RC</td>
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<td>-5.16</td>
<td>10.64</td>
<td>39.66</td>
<td>22.74</td>
<td>28.9</td>
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<td></td>
<td>Recupered</td>
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<td>-0.82</td>
<td>1.84</td>
<td>-0.86</td>
<td>-5.51</td>
<td>0.05</td>
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<td>DI₀/RC</td>
<td>Stress</td>
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<td>140.65</td>
<td>47.11</td>
<td>78.57</td>
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<tr>
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<td>-2.11</td>
<td>10.97</td>
<td>5.61</td>
<td>-4.22</td>
<td>0.01</td>
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<td>TR₀/RC</td>
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<td>17.66</td>
<td>18.51</td>
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<tr>
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<td>Recupered</td>
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<td>-1.99</td>
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<td>ET₀/RC</td>
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<td>0.95</td>
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<td>Recupered</td>
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<td>-8.08</td>
<td>-11.77</td>
<td>-19.77</td>
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</tr>
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</table>

Fig. 6. Correlations between nutrients on mass basis and specific flux of energy per reaction center (RC) of *Bertholletia excelsa* plantations under thinning, liming, and phosphorus fertilization. Values highlighted in gray are significant correlations. Initial fluorescence (F₀), maximum fluorescence (Fₘ), quantum yield of PSII (Fᵥ/Fₘ), effective antenna size expressed as absorbance per reaction center (ABS/RC), trapping efficiency per reaction center (TR₀/RC), electron transport per reaction center (ET₀/RC), amount of energy dissipated per active reaction center (DI₀/RC), flux reduction of end-electron acceptors (RE/RC), and performance index (PIABS).

and maintenance of ET₀/RC in trees of *B. excelsa* seems to be associated with the Fe concentration in leaves. Typically, approximately 80% of Fe is found in photosynthetic apparatus, where it is essential for the biosynthesis of cytochromes and other heme molecules, including Chl, the electron transport system, and the construction of Fe-S clusters. It is also an active cofactor of many enzymes that are necessary for synthesis of plant hormones (Rout and Sahoo 2015).

The increase in light availability after thinning also resulted in an enhancement in effective dissipation of an active RC (DI₀/RC). The increase in DI₀/RC values in
plants submitted to high-light environments is common and usually represents a photoprotective mechanism of the photosynthetic apparatus to counter photooxidative damage (Derks et al. 2015, Gurrurani et al. 2015). Thus, the increase in DIb/RC after thinning may be the main factor that led the remaining trees to reduce Fv/Fm ratio from 0.83 to 0.72 and the PIABS from 1.7 to 0.8. This association between DIb/RC and photochemical efficiency (Fv/Fm and PIABS) has been previously demonstrated by Boisvert et al. (2006) and Souza et al. (2010). However, our results indicate that liming and P fertilization alleviate the effects of high light stress after thinning.

Pi deficiency renders the light income excessive for their actual capacity to process it, thereby leading to photooxidation. ATP production is affected under Pi deficiency. The photophosphorylation of ADP is impaired under Pi limitation due to low availability of Pi in the stroma, therefore causing limited ribulose 1,5-bisphosphate (RuBP) regeneration. Furthermore, decreased utilization of NADPH and reduced ferredoxin due to decreased activity of the Calvin cycle, together with enhanced acidification of the lumen pH due to restrained ATP synthesis, lead to the accumulation of reduced electron transporters such as plastoquinone or ferredoxin. As a consequence of the feedback inhibition in photosynthesis, Pi deficiency causes Chl loss and a decrease in Fv/Fm, which are symptoms of photooxidative stress (Hernández and Munné-Bosch 2015).

In addition, we found increases in the J-I phase and positive K-band formation only in trees under thinning without liming or P. Increases in the J-I phase and positive K-band formation are considered indicative of stress in plants (Frydenv Pang et al. 2015, Luo et al. 2016). Changes in the J-I phase have been associated with responses of plants under low phosphorus availability, and K-band formation is normally observed in plants subjected to stress factors such as increased temperature (Sengupta et al. 2013, Carstensen et al. 2018a,b). However, plants under other stress factors, such as high irradiance, water and nutrient limitation, are also associated with alteration of the shape of the J-I phase and positive K-band formation (Cendrero-Mateo et al. 2015).

The increase in the J-I phase can occur due to the reduction of ATP synthase and therefore accumulate protons in the thylakoid lumen which causes acidification, and this can decrease the oxidation of the plastoquinone pool (PQ) at the cytochrome b f complex in the electron transport chain. The decreased oxidation changes the flow of electrons towards PSI, which is reflected by the shape of the J-I phase (Carstensen et al. 2018a,b). The presence of the positive K-band, in turn, indicates an imbalance between the donation of electrons from the oxygen-evolving complex (OEC) to the oxidized PSII reaction center chlorophyll (Pauw) and the reoxidation of reduced PSII acceptors (Qa). This is usually due to the impaired OEC, which is very sensitive to suboptimal conditions (Strasser 1997).

**Conclusions:** Thinning reduces the photochemical efficiency of *B. excelsa*, but liming and phosphate fertilization alleviate the effects of high irradiance stress and accelerate tree recovery. Thus, phosphorus fertilization and liming are recommended for attenuating the stress caused by high irradiance after thinning in *B. excelsa* trees because they increase plant tolerance to stress in this species when established on plantation conditions in central Amazonia.

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