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How is the functioning of saplings limited by soil nutrients in tropical rainforests?

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Abstract. This study was conducted in an unmanaged tropical rainforest in French Guiana, in which either nitrogen (N), phosphorus (P) or a combination of N and P fertilisers were experimentally added to the soil. Here, we focused on the effects of fertilisation on photosynthetic capacity and growth of saplings in the understorey of the rainforest. We measured sapling photosynthesis and stem dimensions (height and diameter) after eight years of fertilisation, and compared these with pre-fertilisation data. In addition, we measured overstorey leaf area index, soil nutrients, foliar leaf nutrients, leaf morphology, total sapling leaf area and the leaf area/wood volume ratio. The results showed that an increase in available soil nutrients contributed to an increase in leaf area of tree canopies, reducing the light availability for saplings in the understorey, eliciting shade adaptations, such as an increase in specific leaf area and an increase in height increment. There was no fertilisation effect on the growth and photosynthesis of saplings that overrides the increase in light limitation. Nonetheless, the effect of fertiliser was significantly different among species, making it likely that fertilisation on the long-term will lead to a change in the composition of tropical rainforests.

1 Introduction

Tropical rainforests contain a wealth of biodiversity, drive the global water cycle and serve as an important buffer against global warming by absorbing about 40 billion tons of CO_2 annually (Hikosaka et al., 2005; Luyssaert et al., 2007; Beer et al., 2010; Hasegawa et al., 2016; Wright, 2019; Lugli et al., 2021; Ellsworth et al., 2022; Vallicrosa et al., 2023; Lugli et al., 2024). Tropical forests are, however, increasingly threatened by human impact; large rainforests areas are being cleared to make way for agriculture to feed the growing global population (Feng et al., 2021; Li et al., 2021; Tandalla et al., 2024). This agriculture is often over fertilised, with excess nutrients leaching out into tropical rainforests (Tandalla et al., 2024). Besides leaching, nutrients also enter these ecosystems via atmospheric deposition, with nutrients originating from upwind biomass burning and industry (Bauters et al., 2018; Li et al., 2021; Tandalla et al., 2024, Descals et al., in press). To date, little is known about how these nutrient inputs affect tropical rainforests, which is why several large-scale nutrient enrichment studies have been initiated (Holste et al., 2011; Pasquini and Santiago, 2012; Santiago et al., 2012; Magalhaes et al., 2014, Wright, 2019; Verryckt et al., 2020; Lugli et al., 2021; Vallicrosa et al., 2023).

If nutrient inputs affect the photosynthetic capacity of rainforests, it is important to know the effect thereof on the amount of CO_2 taken up from the atmosphere during photosynthesis, also known as gross primary production (GPP) (Beer et al., 2010). In most undisturbed tropical forests, trees accumulate carbon (C), albeit very little relative to the total ecosystem GPP (Luyssaert et al., 2007). Rainforest plants are C sinks during their growth and trees can accumulate large amounts of biomass (Körner, 2003; Baccini et al., 2017; Ellsworth et al., 2022; Lugli et al., 2024; Trugman and Anderegg, 2025), yet at least half of the stored C resides underground as undecomposed plant litter and soil organic matter (Luyssaert et al., 2007). Besides accumulation in biomass, about half of the GPP is used to produce energy via autotrophic respiration (like most other ecosystems) (Vicca et al., 2012). Finally, a large part of the GPP (15-20 %) is invested in mechanisms for nutrient uptake like maintaining the root system, maintaining symbiotic interactions with mycorrhiza, producing enzymes (such as phosphatases) or root exudation to chelate nutrients or to stimulate microbial activity (de Grandcourt et al., 2004; Hikosaka et al., 2005; Vicca et al., 2012; Hasegawa et al., 2016; Gargallo-Garriga et al., 2018; Lugli et al., 2021; Hildebrand et al., 2023; Lugli et al., 2024). In tropical forests, investment in nutrient acquisition is large because tropical soils are often deeply weathered and thus nutrient-poor, with most nutrients stored in living plants and the remainder locked up in soil organic matter or strongly bound to minerals (Hikosaka et al., 2005; Quesada et al., 2012; Lugli et al., 2021; Lugli et al., 2024). Due to this major investment in nutrient acquisition, on average only 42 % GPP can be invested in biomass production, in sharp contrast with forests growing on fertile soils that invest on average 58 % of GPP in biomass production (Vicca et al., 2012; Fernandez-Martinez et al., 2014). The photosynthetic capacity and the allocation of GPP to growth thus depends on availability of key nutrients, such as P or nitrogen (N) (Croft et al., 2017; Slot and Winter, 2018; Peng et al., 2021; Ellsworth et al., 2022). To protect rainforests from further degradation, it is important to properly understand soil and vegetation processes responsible for regeneration dynamics and investigate the impact of human activities (Tandalla et al., 2024).

A unique phenomenon in tropical rainforests is the dynamic relation between saplings and mature trees. Because dominant tall trees and the abundant lianas and epiphytes growing on branches develop a highly intricate canopy (that results in a large leaf area index: LAI), saplings receive extremely low photosynthetic photon flux densities (PPFD), on average less than two percent of the incoming PPFD (Montgomery and Chazdon, 2002; Verryckt et al., 2020). This is why light is often seen as the most limiting resource in rainforests understoreys (Pasquini and Santiago, 2012; Santiago et al., 2012). As such, rainforest saplings go through a huge bottleneck before reaching the canopy. Which saplings survive these dark conditions ultimately determines the species composition and diversity of the rainforest. This species-specific sapling survival and growth also depends on available resources, such as light and nutrients (Fahey et al., 1998; Kobe, 1999; Holste et al., 2011; Tandalla et al., 2024).

Due to the light-limited conditions, saplings can only achieve sufficient photosynthesis to sustain (faster) growth when a tree or a branch falls and more light reaches the forest floor through the newly formed canopy gap (Montgomery and Chazdon, 2002; Takahashi and Rustandi, 2006; Holste et al., 2011; Pasquini and Santiago, 2012; Santiago et al., 2012). With the exception of pioneer species, rainforest tree saplings are adapted to the low PPFD and manage to survive for a long time with low metabolic activity, until an opening appears in the canopy (Verryckt et al., 2020). Until this moment, saplings produce leaves with high specific leaf area (SLA): thin leaves with a large surface area with the aim of increasing light capture under shaded conditions with the lowest possible resources investment. In these thin leaves, the concentration of photosynthetic proteins is lower than in thicker leaves, which contributes to the slow growth of saplings in the understorey of a tropical rainforest (Anten and Hirose, 1998; Hikosaka et al., 2005; Bucci et al., 2006; Magalhaes et al., 2014).

Besides light availability, nutrient availability is also an important determinant of sapling growth (Hikosaka et al., 2005; Montagnini, 2000; Holste et al., 2011; Magalhaes et al., 2014; Chou et al., 2018; Wright et al., 2018). Not only in favourable light conditions, but even at low light availability, nutrient deficiency can cause limited photosynthesis and growth (Pasquini and Santiago, 2012; Santiago et al., 2012). As stated above, rainforests are usually characterised by nutrient deficient soils, although nutrient availability can vary greatly at microscale (Magalhaes et al., 2014; Wright, 2019; Van Langenhove et al., 2021; Ellsworth et al., 2022). Due to these nutrient-poor soils, saplings depend on litter fall from surrounding trees and decomposition for nutrient availability (Chou et al., 2018). While base cations such as potassium (K), magnesium (Mg) and especially calcium (Ca), have been reported to limit tropical tree growth (Holste et al., 2011; Magalhaes et al., 2014; Bauters et al., 2022), in general soil P is considered the most growth-limiting element in tropical ecosystems (Walker and Syers, 1976; Lambers et al., 2008; Quesada et al., 2009; Peñuelas et al., 2013; Dalling et al., 2016). Nitrogen is typically not the most limiting element due to the abundance of N-fixing heterotrophic- or root-associated microbes (Hedin et al., 2009; Domingues et al., 2010; Holste et al., 2011; Santiago et al., 2012; Hasegawa et al., 2016; Wright et al., 2018; Du et al., 2020; Lugli et al., 2021; Ellsworth et al., 2022; Vallicrosa et al., 2023; Lugli et al., 2024).

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Given the low soil P availability in tropical rainforests, plants have developed strategies to overcome P limitation (Hidaka and Kitayama, 2013; Wright et al., 2018; Van Langenhove et al., 2020; Urbina et al., 2021; Gargallo-Garriga et al., 2024). For example, tropical trees can use nutrients more efficiently, resorb more nutrients prior to leaf and root abscission, exude more chelating molecules and form associations with mycorrhiza to acquire nutrients more easily (Lambers et al., 2009; Magalhaes et al., 2014; Wright et al., 2018; Jiang et al., 2019; Urbina et al., 2021). While all supplying the least abundant element (P), these mechanisms come at a large C investment, explaining the low fraction of GPP that is invested in biomass growth in tropical forests (Vicca et al., 2012).

The amount of N present in leaves is often a good measure of photosynthetic capacity (Pasquini and Santiago, 2012). Much of this leaf N is invested in the enzyme rubisco (10-30 %) and other molecules important for photosynthesis, such as thylakoid membrane-bound proteins (Medlyn, 1996; Hikosaka et al., 2005; Pasquini and Santiago, 2012; Ellsworth et al., 2022). Exactly how much leaf N is invested in photosynthesis depends on the plant N strategy (Luo et al., 2021). At the global scale the link between photosynthetic capacity and foliar N concentration is stronger than the link with P (Jiang et al., 2019). However, in ecosystems where P is limited this relationship between photosynthesis and foliar N is less strong as the supply of electrons via ATP and NADPH generated in the light reactions is also a rate-limiting factor of photosynthesis (in addition to rubisco) and in tropical trees it depends on the concentration of leaf P (Ellsworth et al., 2022).

In general, fertilisation (with N and P) in tropical rainforests stimulates P accumulation in tree biomass more than N accumulation, not only in leaves but also in stem, branch and root tissues (Ostertag et al., 2010; Pasquini and Santiago, 2012; Lugli et al., 2024). The P storage in the latter plant organs is even higher than the storage in the leaves, possibly to avoid increased risk of herbivory (Mao et al., 2021). The reason P accumulation is higher than N accumulation, is due to evolutionary pressures that increase survival rates in P-limited forests (Lambers and Shane, 2007). Because of this, plants take up available P even when they do not need it, to prevent surrounding plants from taking up this scarce resource (P) and eventually outcompete the neighbours. These plants have therefore evolved a high capacity to take up P as well as a large storage capacity (Lambers and Shane, 2007). Moreover, tropical rainforests tend to have an open N cycle, as evidenced by enriched N isotope compositions of soils and plant tissues and by high nitrification and denitrification rates (Amundson et al., 2003; Craine et al., 2015; Liao et al., 2021). Since sufficient N is already present, it is likely that plants' N storage is already saturated.

When fertilised, saplings experience higher nutrient availability, which will allow them to alter their C allocation by reducing C investments in nutrient acquisition (mycorrhizae, exo-enzymes, exudates) towards increased investment in light interception, photosynthesis and growth. These hypothesised adaptations highlight the interactions between light limitation and nutrient availability (Pasquini and Santiago, 2012; Sellan et al., 2025). Yet there is disagreement about the interaction

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between light and nutrient availability in the understorey of tropical rainforests (Pasquini and Santiago, 2012; Santiago et al., 2012; Magalhaes et al., 2014). Fertilisation experiments are therefore being conducted in various locations around the world to find out whether soil nutrient availability (besides light availability) has an effect on survival, growth and CO_2 assimilation capacity (Holste et al., 2011; Pasquini and Santiago, 2012; Santiago et al., 2012; Magalhaes et al., 2014; Wright, 2019; Vallicrosa et al., 2023).

Therefore, the goal of the study was to examine the effect of a combined N and P fertilisation on growth of saplings in a tropical rainforest. Nitrogen and P additions are expected to increase N and P availabilities in the soil, along a topographical gradient (valley bottoms, slopes and plateau ridges). The main hypothesis is that fertilisation leads to an increase in sapling growth, but that this increase is limited by the increase in overstorey LAI (and thus an increase in light limitation) as a result of this fertilisation. Figure 1 gives a schematic overview of the sub-hypotheses in this study and how they are linked to each other. As mentioned, we hypothesised that adding N and P leads to higher N and P availability in the soil (Hypothesis 1: H1). We expected that the increased nutrient availability in the soil will cause higher N and P concentration in the leaves of saplings (H2). We also hypothesised that the increased nutrient availability in the soil leads to higher overstorey LAI and thus lower light availability in the understorey (H3). Increased leaf nutrient concentrations are also expected to enhance photosynthetic capacity per unit leaf area (H4). However, we expected this positive effect to be counteracted by a negative impact of the increase in overstorey LAI (H5). An increase in photosynthetic capacity will probably contribute to an increase in sapling growth, although this effect may also be counteracted by the impact of the increase in overstorey LAI (H6). Finally, the growth of aboveground plant parts may also increase due to cheaper nutrient acquisition driving a C allocation shift towards growth of aboveground biomass (this direct impact could not be tested and is therefore not included statistically as hypothesis). The influence of different species and different topographical positions on these hypothesised effects is also investigated here.

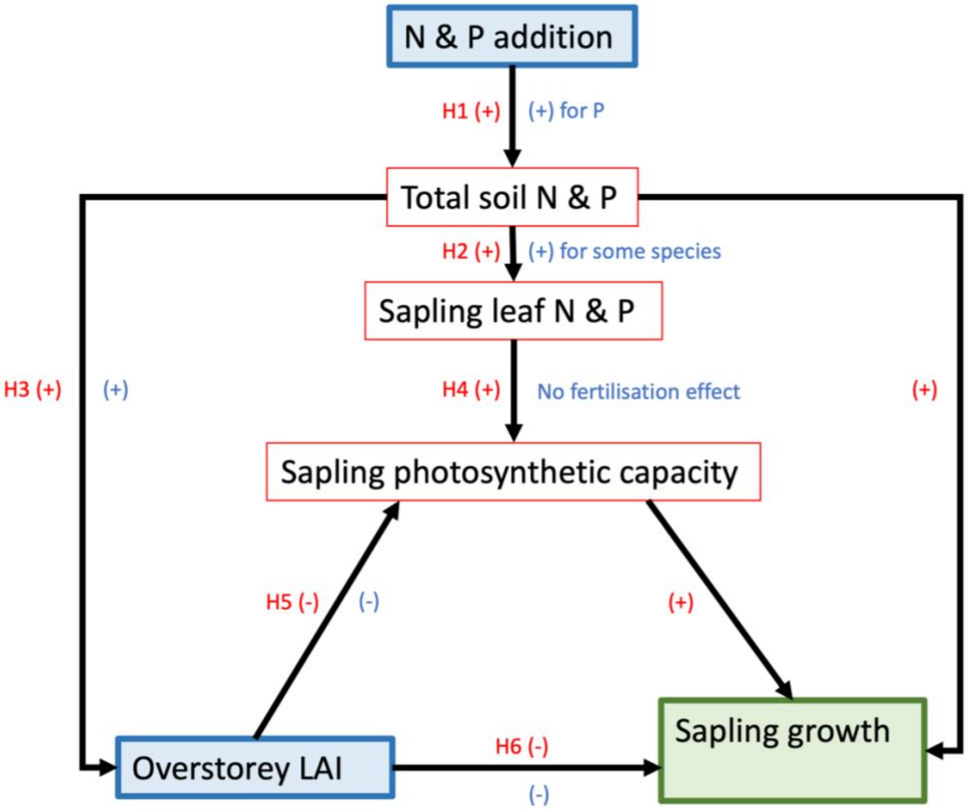

Figure 1: Overview of the hypotheses tested in this study in red. Each arrow represents an effect; whose hypothesised direction is represented by the sign. The results found in this study are shown in blue.

2 Materials and methods

2.1 Study area

Data was collected in a pristine rainforest in French Guiana, situated 5° north of the equator in South America. French Guiana has a tropical wet climate, with air temperature fairly constant around 26 °C throughout the year. Typical of the climate at this latitude is the alternation of a wet and a dry season (wet from December to July and dry from August to November). All data was collected during the dry season (August-September 2024) at the Paracou Research Station (5° 15′ N, 52° 55′ W). The average density of trees (with diameter > 10 cm) at the site is 587 trees per hectare and the average canopy height is 35 metres (Bonal et al., 2008; Van Langenhove et al., 2021; Llusià et al., 2022; Verryckt et al., 2022). The soil type at this research site is a nutrient-poor Acrisol, with very low P availability (Van Langenhove et al., 2021).

2.2 Plots and experimental set-up

Twelve plots were created in 2015, each measuring 50 by 50 metres. The plots were located at three different topographical positions: hill top, hill slope and valley bottom (Courtois et al., 2018; Van Langenhove et al., 2021; Llusià et al., 2022; Verryckt et al., 2022). The slope plots contain more clay than the bottom and top plots, therefore they retain more nutrients. Bottom plots are the most weathered and contain a higher proportion of quartz than the slope and top plots. The soil differences in texture and mineral composition are due to millennia of erosion and water dynamics in the different topographies (Van Langenhove et al., 2021). Since 2016, these plots have been part of a fertiliser addition experiment aimed at studying the long-term effects of fertilisation on forest functioning and biodiversity (e.g. Peguero et al., 2022; Verryckt et al., 2022; Sardans et al., 2023; Gargallo-Garriga et al., 2024). Through these plots there were four different fertilisation treatments: a treatment receiving only N, a treatment receiving only P, a treatment with N and P combined (NP) and a control treatment, where no fertilisation was carried out. Fertiliser was applied by hand twice a year between 2016 and 2019 (once during the wet season and once during the dry season), and once a year from 2020 onwards (during the dry season). We used commercial urea ($(NH_2)_2CO$; N) and triple superphosphate ($Ca(H_2PO_4)_2$; P) at rates of 125 kg N ha-1 yr-1 (N treatment), 50 kg P ha-1 yr-1 (P treatment) or 125 kg N ha-1 yr-1 and 50 kg P ha-1 yr-1 (NP treatment) as fertiliser.

This research focuses on the effects of fertiliser addition on saplings (defined as trees less than two metres in height). Our data was compared with the data before fertilisation started (following eight years of fertiliser addition). This study focuses on only six of these fertilisation plots, by comparing saplings in the NP combined treatment and in the control treatment at the three different topographic locations.

2.3 Tree selection

We selected four species that had been measured in 2016 in the NP and control plots: *Oxandra asbeckii* (Pulle) R.E.Fr., *Iryanthera hostmannii* (Benth.) Warb., *Licania alba* (Bernoulli) Cuatrec. and *Lecythis persistens* Sagot (Appendix A). In the fertilised bottom and slope plots, there was no 2016 data for the species *O. asbeckii* and *L. persistens* respectively. In these plots, therefore, no comparison could be made for these two species.

2.4 Data collection

2.4.1 Soil nutrient concentrations

In each plot, soil samples were taken at five locations (four at the corners of the plot and one centrally) in the topsoil (0–10 cm) using a soil corer. The samples were oven-dried at 40 °C for 72 hours. After drying, each sample was sifted with a 2-mm sieve to remove roots and coarse organic matter. After sieving, the dried samples were ground to fine powder using a ball mill MM 200 (Retsch GmbH, Haan, Germany). The ground samples were analysed for C and N concentration by dry combustion, based on the Dumas method using an elemental analyser FLASH 2000 (Interscience, Louvain-la-Neuve, Belgium). Total P analysis was done using a nitric acid digestion and samples were ultimately analysed with the spectrometer ICP-OES (iCAP 6300 Duo, Thermo Scientific).

2.4.2 Leaf traits

For all collected leaves, leaf area was determined the same day in the lab, before leaf deformation occurred due to desiccation. Leaf area was measured with the leaf area meter LI-3100C (LI-COR, Lincoln, NE, USA). After this, leaves were labelled in paper bags and then put into the drying oven at 40 °C for at least 48 hours. These paper bags were then clustered by plot in a plastic bag and transported to Belgium. In the lab, leaves were dried for a further 48 hours at 40 °C to ensure the leaves did not reabsorb moisture. They were then cooled in a dessicator. After this, the dry mass of the leaves could be measured using the MC-1 AC210S Analytical Balance (Sartorius, Göttingen, Germany). From the previously measured leaf area and dry mass, SLA was calculated.

Finally, the dried leaves were ground to fine powder using a ball mill MM 200 (Retsch GmbH, Haan, Germany). The fine powder obtained was used for further chemical analysis, part of it was used for N content determination and part of it was used for P content determination. The same methods were used as in the determination for soil nutrient concentrations.

2.4.3 Overstorey leaf area index (LAI)

Above all saplings, the leaf area index (LAI; the surface area of leaves per unit soil surface area) of the forest canopy was measured with the LAI-2000 Plant Canopy Analyser (LI-COR, Lincoln, NE, USA) as an approximation of light availability. The overstorey LAI was determined by comparing the synchronous data from above the canopy with the data above a given sapling (light transmittance), assuming that light transmittance declines exponentially with the number of leaves the light encounters. The LAI-2000 sensors have a hemispherical lens divided into five concentric rings allowing the attenuation of diffuse sky radiation to be measured, the central zenith angles of these rings are: 7°, 23°, 38°, 53° and 68° (Li-Cor, 1992; Cutini et al., 1998; Garriques et al., 2008). After the measurements were made in the field, the collected data was transferred to the computer via the FV2000 software. Using this software, the number of rings was adjusted from five to two (7° and 23°), as the interest was on the incident light right above the sapling. Field LAI measurements require even skies, which is why measurements were taken just after sunrise (6 am-7 am LT) or just before sunset (5 pm-6 pm LT) each time.

2.4.4 Sapling photosynthesis

Leaf gas exchange of saplings was determined using a portable photosynthesis system (LI-6400XT, LI-COR, Lincoln, NE, USA). To enable comparisons with the 2016 data, the same settings were applied (Verryckt et al., 2022): the photosynthetic photon flux density (PPFD) was set at 500 µmol m^{-2} s^{-1}, the air flow rate was set at 500 µmol s^{-1}, the CO_2 concentration was

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kept at 400 ppm and the chamber block temperature was controlled at 30 °C. The area of the chamber was set at 6 cm^2 (2x3 cm), implying that of each sampled leaf photosynthesis was measured on a 6 cm^2 area, and the stomatal ratio was set at 0.5. From the change in CO_2 and H_2O concentrations, the air flow, temperature and the chamber surface area, photosynthesis and stomatal conductivity could be calculated. Measurements were made between 9am and 3pm and were all made on leaves still attached to the saplings (i.e. not on cut twigs).

Light-saturated photosynthesis (Asat) and stomatal conductance (g_s) were measured for five individuals per species per plot (sometimes an additional measurement was made), a total of at least 25 Asat measurements were thus made per plot. In the slope plots, no photosynthesis measurements had been made in 2016, so no comparison could be made for this topography type. Measurements were taken on one leaf per sapling, mature leaves were always selected with medium size and with as few traces of herbivory and epiphytes cover as possible. All leaves on which photosynthesis measurements were performed, were collected for further analysis (as described above).

2.4.5 Sapling growth

The height and stem diameter were measured of all selected saplings, with the aim of calculating the growth compared with the measurements made in 2016. In order to make this comparison, only saplings that showed undisturbed growth were used (i.e. saplings without broken branches or stem). Sapling height was measured with a tape measure, stem diameter was measured with a calliper, at 10 cm height and 50 cm height (same procedure as in 2016). The increment was then calculated by subtracting the 2016 measurements from the 2024 measurements. Besides height and diameter, the number of leaves of each sapling was counted. Calculation of stem volume was approximated using the cone formula (with the diameter measured at 10 cm height as the base of the cone).

2.5 Statistical analysis

All statistical analyses were performed using RStudio (version 2023.12.0+369), which draws on R (version 4.3.2 (2023-10-31); R Core Team, 2022). For the analysis, following packages in R were used: readxl (version 1.4.3), tidyverse (version 2.0.0), emmeans (version 1.11.0), car (version 3.1-3), gdata (version 3.0.1), minpack.lm (version 1.2.4). All graphs were made with the ggplot2 package (version 3.4.4) and put together with the patchwork package (version 1.3.0). Model assumptions like linearity, normality, homoscedasticity and the absence of high leverages or outliers were checked, using the diagnostic plots in combination with the Shapiro-Wilk normality test. All analyses were performed using p-values, based on the 95 % confidence interval. The main statistical model was an ANCOVA model, with treatment, species, topography and overstorey LAI as key explanatory variables (sometimes ANOVA, when overstorey LAI had no statistically significant effect).

3 Results

3.1 Soil nutrient concentrations

Eight years of P and N addition significantly increased soil P concentrations in the fertilised plots ($p = 0.0005$; Fig. 2c), whereas soil C and N concentrations did not (for C: $p = 0.2265$, Fig. 2a; for N: $p = 0.7442$; Fig. 2b) and even decreased. Soil N concentrations decreased in all plots, fertilised and unfertilised, proportional with the decreases in soil C concentration, suggesting a decline in soil organic matter between the 2015 and 2024 sampling.

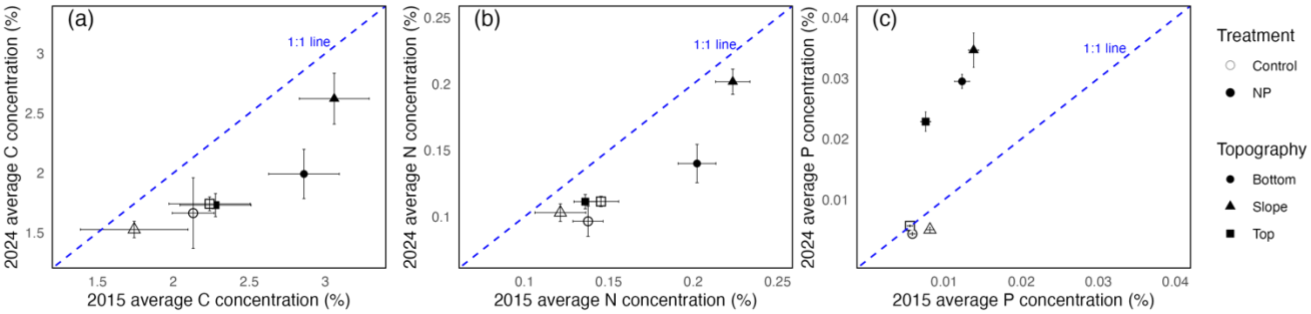

Figure 2: Average soil C concentrations measured in 2024 compared with measurements in 2015 in (a), where the blue dashed line indicates the 1:1 line (n=5). In (b), same is represented but this time for soil N concentrations. In (c) this is represented for soil P concentrations.

Increased or unaltered soil nutrient concentrations do not necessarily imply increased or unaltered nutrient availabilities. If the increased soil P would be strongly bound to the minerals, P availability would not be higher. If part of the added N fertiliser had already been taken up by the saplings at the time of the sampling, N availability was increased despite unaltered soil N concentrations. Therefore, it is also interesting to look at foliar leaf concentrations in order to gain a deeper understanding.

3.2 Foliar nutrient concentrations

With regard to foliar N concentration, despite the unaltered soil N concentrations at the time of sampling, there was a significant N concentration increase in the saplings growing in the fertilised plots for two of the four species (Fig. 3b). These species were *O. asbeckii* ($p < 0.0001$) and *I. hostmannii* ($p = 0.0025$). Although the other species exhibited no change in foliar N concentration, we can assume that soil N availability indeed increased upon fertilisation.

Foliar P concentrations increased significantly for three of the four sapling species in the fertilised plots, namely *L. persistens* ($p = 0.0008$), *O. asbeckii* ($p < 0.0001$) and *I. hostmannii* ($p < 0.0001$). The strongest increase in foliar P concentration was observed in *O. asbeckii* and *I. hostmannii*, the same species that also showed an increase in foliar N concentration in the fertilised plots (Fig. 3a). Figure 3c shows that for most saplings there was a stronger increase in foliar P concentrations compared to foliar N concentrations between 2016 and 2024.

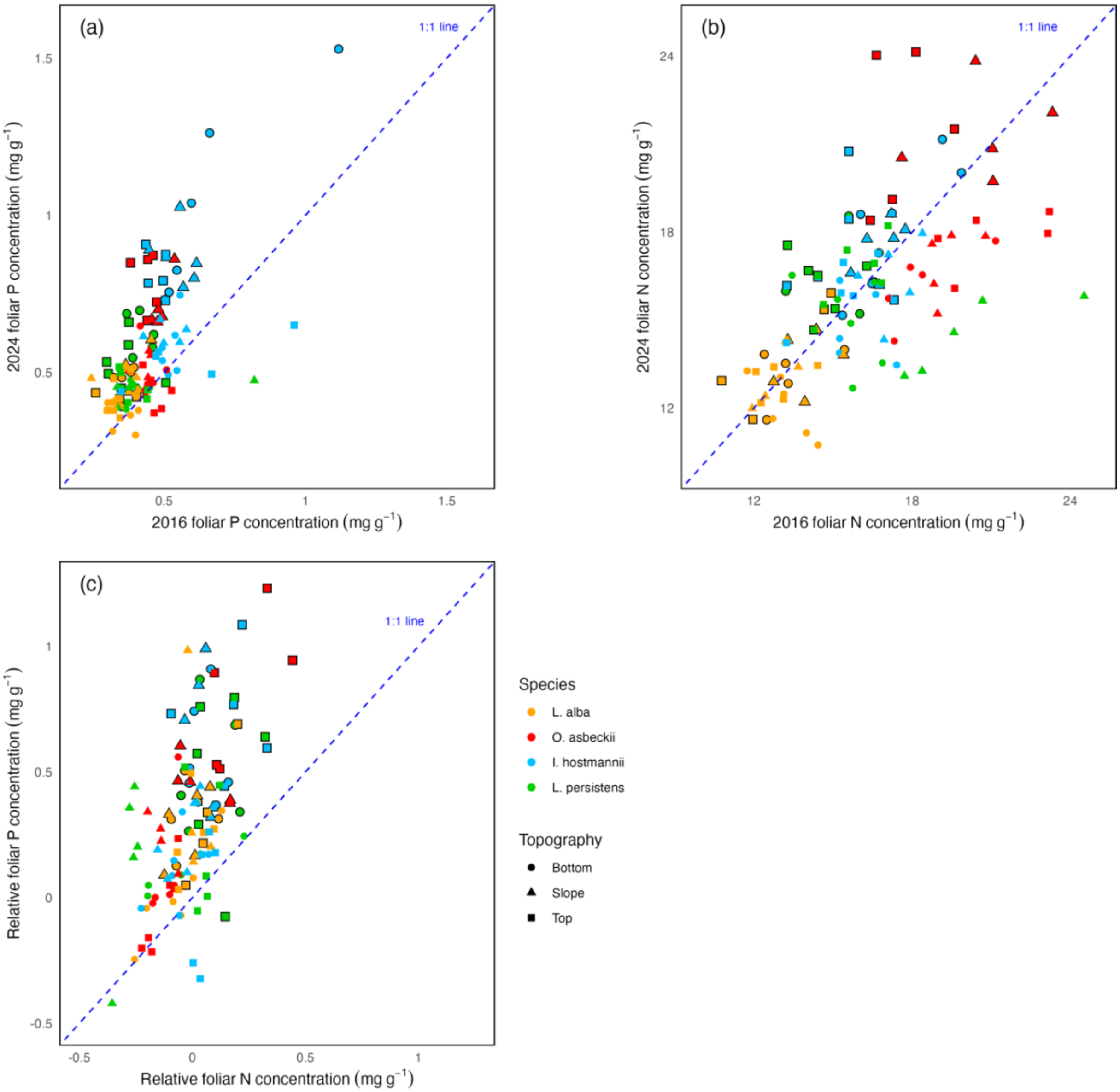

Figure 3: In (a) the foliar P concentration measured in 2024 is compared with the measurements made in 2016. The blue dashed line indicates the 1:1 line. Points above the line indicate an increase in foliar P concentration, points below the line indicate a decrease between 2016 and 2024. In (b) the foliar N concentration measured in 2024 is compared with the measurements made in 2016. The blue dashed line indicates the 1:1 line. Points above the line indicate an increase in foliar N concentration, points below the line indicate a decrease between 2016 and 2024. In (c) the relative change in foliar P concentration between 2016 and 2024 is compared with the relative change in foliar N concentration between 2016 and 2024, each time calculated as (2024 values - 2016 values) / 2016 values. The blue dashed line indicates the 1:1 line. Points above the line indicate a stronger increase in foliar P concentration, points below the line indicate stronger increase in foliar N concentration between 2016 and 2024. Points with a black edge represent measurements from saplings growing in the NP plots, points without black edge are saplings with control treatment.

3.3 Overstorey LAI

In support of the third hypothesis, fertilised plots exhibited an increase in overstorey LAI between 2016 and 2024. This increase was larger than in the control plots ($p < 0.0001$; Fig. 4). In fact, overstorey LAI in the control treatment bottom and top plots, decreased relatively to the 2016 measurements (Top: $p = 0.0002$; Bottom: $p = 0.0023$). The positive effect of fertilisation on overstorey LAI was significantly larger in the top plots than in the bottom plots ($p = 0.0015$; Fig. 4).

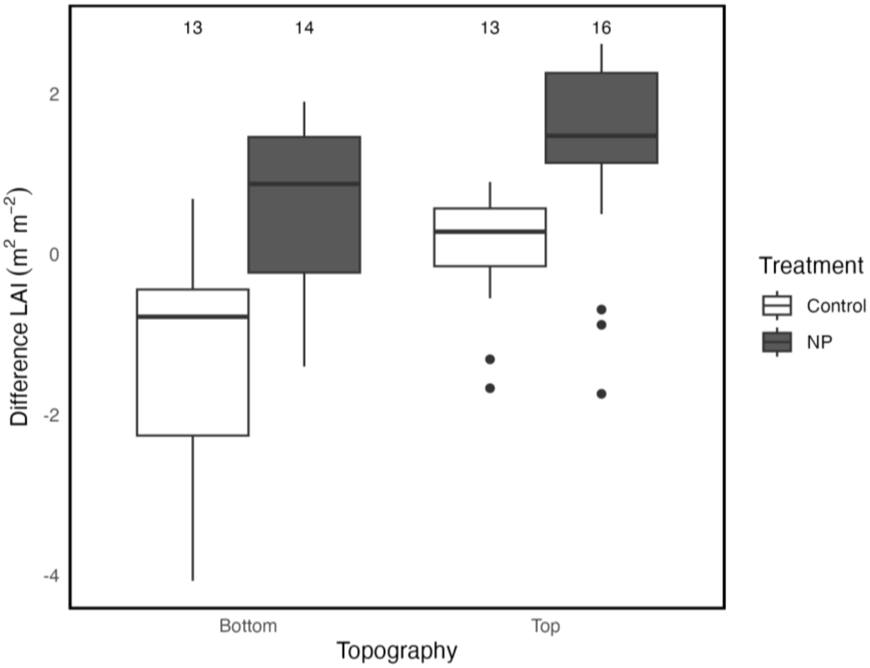

Figure 4: The fertilisation and topography differences in overstorey LAI between 2016 and 2024 are visualised in box plots. The box is formed by the lower quartile and upper quartile, the horizontal line in the box indicates the median. The vertical lines represent the fences, which are determined by the points in the dataset within 1.5 times the interquartile distance (above and below the box). Observations that fall out of the fences are represented by circles. The number of saplings used is indicated above each box plot.

3.4 Photosynthetic capacity

The hypothesis (H4 in Fig. 1) that photosynthetic capacity would increase in the fertilised plots could only be confirmed for the top plot ($p = 0.0054$; Fig.5). In the bottom plots, photosynthetic capacity tended to be lower for the fertilised plot than for the control plot (Fig. 5), albeit not significantly ($p = 0.2160$). The increase in photosynthetic capacity due to fertilisation was significantly higher in the species *I. hostmannii* ($p = 0.0445$) and *L. persistens* ($p = 0.0027$) compared to the species *L. alba* (Fig. 6).

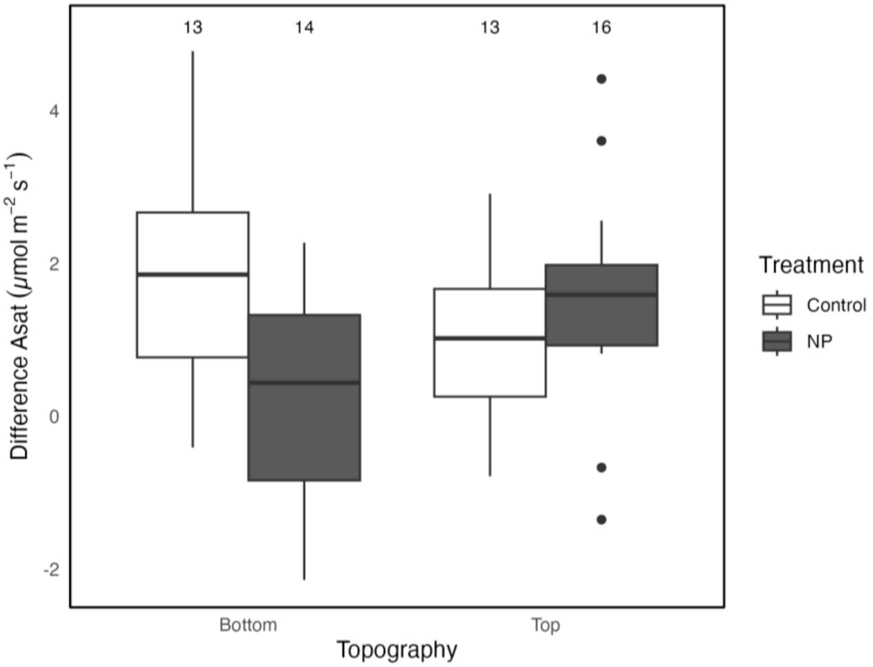

Figure 5: The fertilisation and topography differences in the change in photosynthetic capacity (Asat) between 2016 and 2024 are visualised in box plots. The box is formed by the lower quartile and upper quartile, the horizontal line in the box indicates the median. The vertical lines represent the fences, which are determined by the points in the dataset within 1.5 times the interquartile distance (above and below the box). Observations that fall out of the fences are represented by circles. The number of saplings used is indicated above each box plot.

As hypothesised (H5 in Fig. 1), there was a significant negative relationship between the change in overstorey LAI and that in photosynthetic capacity ($p < 0.0001$; Fig. 6), which means that the increase in sapling photosynthetic capacity decreased as light availability decreased.

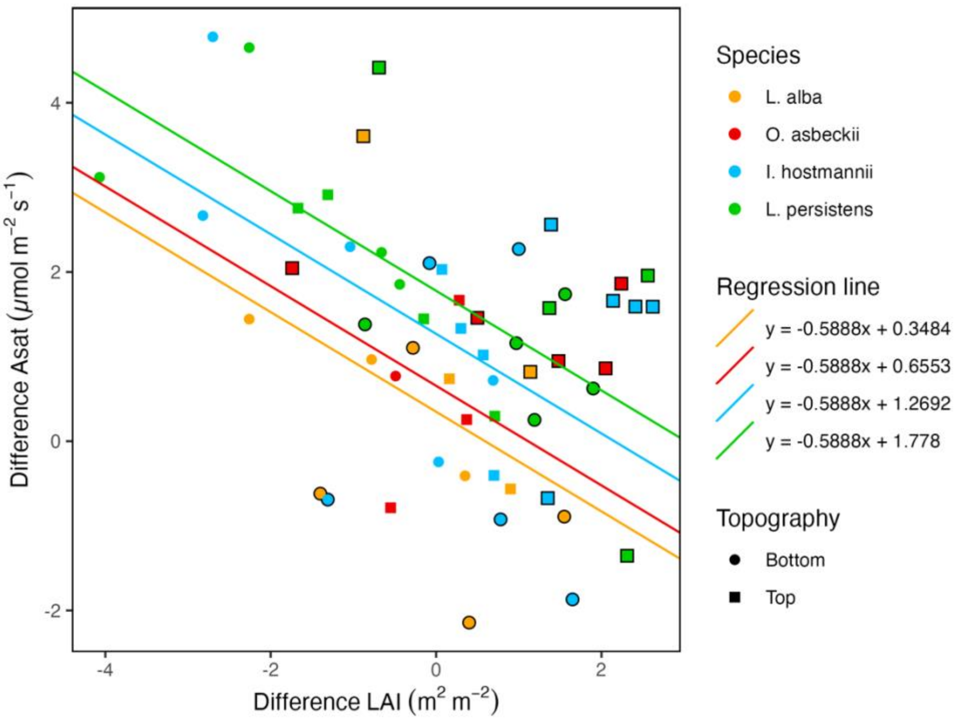

Figure 6: Difference in Asat between 2016 and 2024 is plotted against the difference in overstorey LAI between the same years. The different regression lines are shown by species, for reasons of clarity this is each time shown for the bottom topography with control treatment only. The function formulas for all regression lines can be found in Table E1, in Appendix E. Points with a black edge represent measurements from saplings growing in the NP plots, while points without black edge represent saplings growing in the control plots.

Sapling total leaf area and SLA were also examined. Unfortunately, there was no data available for total leaf area for 2016, so changes therein could not be evaluated. Treatment had a significant effect on the difference in SLA between 2016 and 2024, as fertilised saplings had on average a 11 cm^2 g^{-1} larger specific leaf area than saplings growing in the control plots ($p = 0.0422$) (Appendix B). The difference in SLA between 2016 and 2024 was positively correlated with the difference in overstorey LAI between 2016 and 2024 ($p = 0.0138$), providing evidence for dark adaptation of the fertilised saplings: leaves became larger and/or thinner when there was less light available.

3.5 Growth

3.5.1 Volume increment

With regard to stem volume increment, only saplings of *L. alba* grew significantly faster in the NP fertilised plots than in the control plots ($\beta_{alba:NP}$ = 44, t_{104} = 3.631, p = 0.0004; Fig. 7a). The other three species showed no significant fertilisation effect. The high average increase in stem volume of *L. alba* in the fertilised slope plot is based on only four saplings, that showed a huge increment compared to 2016 values. The fertilisation effect for this species may therefore possibly be overestimated.

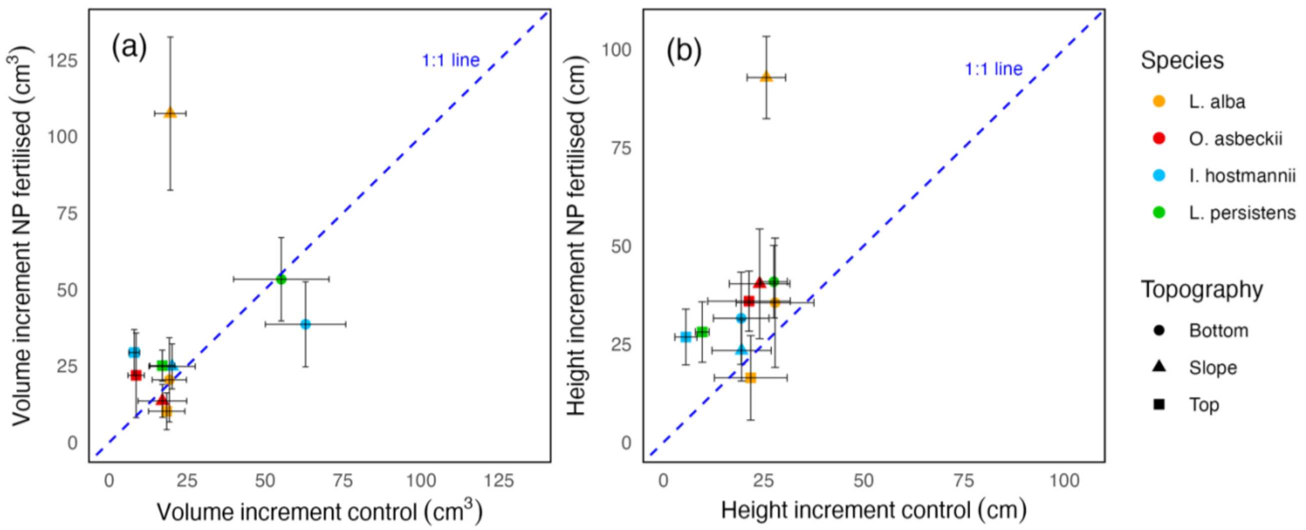

Figure 7: In (a) the average volume increment within a particular topography type and for a specific species is compared here between the fertilised plot and the control plot. In (b) the average height increment within a particular topography type and for a specific species is compared here between the fertilised plot and the control plot. The blue dashed line indicates the 1:1 line. Points above the line indicate higher increment in the fertilised plot than in the control plot. For the species *O. asbeckii* and *L. alba*, no comparison could be made between the bottom and slope plots respectively (which is why ten points are shown instead of twelve).

There was a significant negative association between volume growth and overstorey LAI (β_{LAI} = -8.6, t_{104} = -3.684, p = 0.0004; Fig. 8) and this relation did not differ between treatments, species and topographies. Volume increment decreased by 8.6 cm^3 per unit increase of overstorey LAI, supporting the hypothesis (H6 in Fig. 1) stating that sapling growth decreased when less light penetrated the canopy.

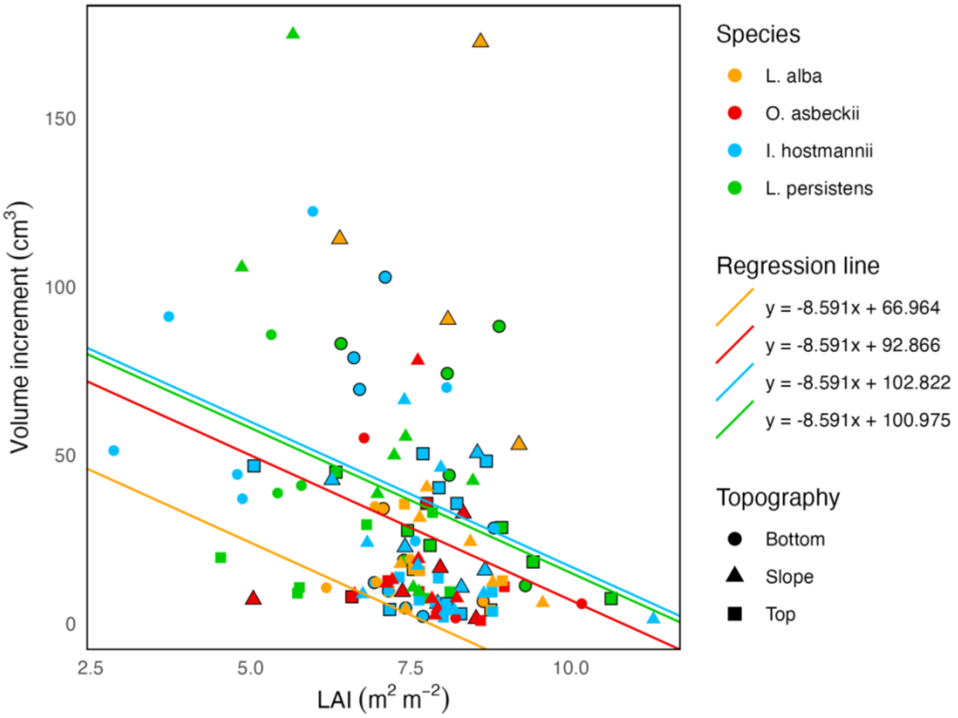

Figure 8: Volume increment is plotted against overstorey LAI (measured in 2024). The different regression lines are shown by species, for reasons of clarity this is each time shown for the bottom topography with control treatment only. The function formulas for all regression lines can be found in Table F1, in Appendix F. Points with a black edge represent measurements on saplings growing in the NP plots, points without black edge represent saplings growing in the control plots.

3.5.2 Height increment

Saplings in the fertilised plots grew on average 21 cm more in height than the saplings in the control plots ($p < 0.0001$; Fig. 7b). Saplings in the slope plots grew 13 cm taller in height than saplings in the bottom plots ($p = 0.0165$), whereas height growth in the top plots did not differ significantly from height growth in the bottom plots ($p = 0.4054$). Regarding the difference among species (Fig. 7.b), *I. hostmannii* grew significantly less in height than *L. alba* ($p = 0.0011$). The height growth of *L. persistens* and *O. asbeckii* did not differ significantly from *L. alba* (*L. persistens*: $p = 0.2152$; *O. asbeckii*: $p = 0.0515$).

In agreement with the volume growth observations, there was a significant negative association between height increment and overstorey LAI ($p = 0.0016$; Fig. 9). Height increment decreased by on average 5.3 cm per unit increase of overstorey LAI.

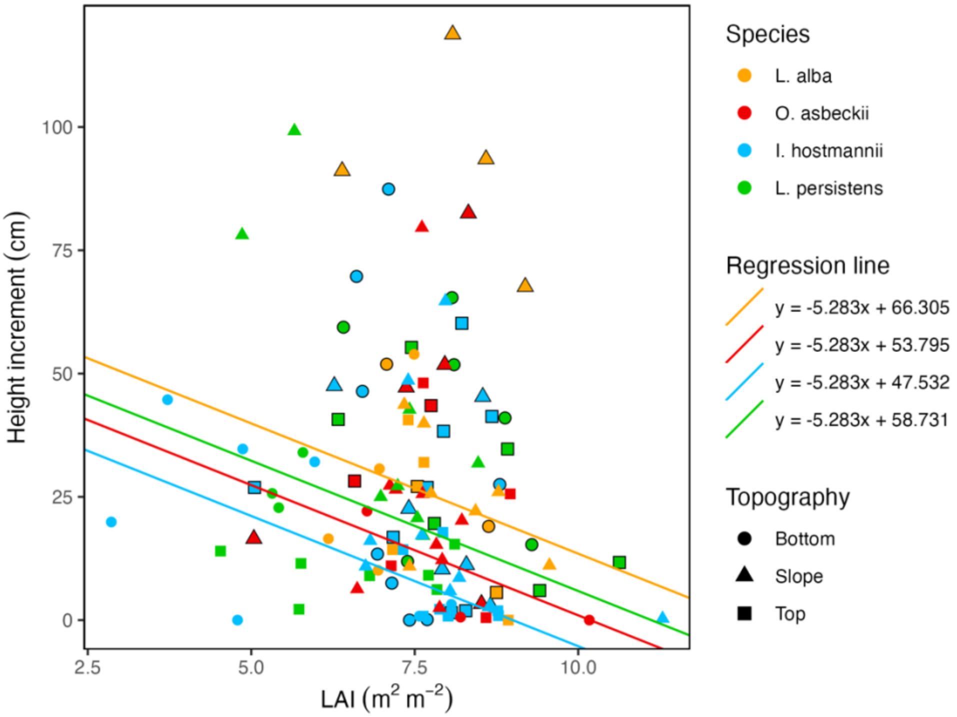

Figure 9: Height increment is plotted against overstorey LAI (measured in 2024). The different regression lines are shown by species, for reasons of clarity this is each time shown for the bottom topography with control treatment only. The function formulas for all regression lines can be found in Table G1, in Appendix G. Points with a black edge represent measurements on saplings growing in the NP plots, points without black edge represent saplings growing in the control plots.

4 Discussion

4.1 Impact of eight years of fertilisation on soil and foliar nutrient concentrations

Eight years of NP fertilisation led to higher P concentrations in the foliage and the soil compared to unfertilised control plots. Both the first and second hypotheses could be confirmed for P (increased soil nutrient availability and foliar concentrations). For N, however, soil concentrations were unaffected eight months after last fertilisers were added. Nonetheless, foliage N concentrations increased in two species and remained unchanged in the other two species, suggesting that there must have been, an albeit short-term increase in soil N availability, enabling these species to absorb extra N in their leaves. We therefore conclude that hypotheses 1 and 2 could not be rejected and that N and P addition increased the availability of these elements and subsequently also their foliar concentrations, at least for some species.

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The increased soil P concentration and availability as a result of fertilisation was to be expected given the P-limited nature of the soil caused by millions of years of weathering (Domingues et al., 2010; Holste et al., 2011; Santiago et al., 2012; Hasegawa et al., 2016; Wright et al., 2018; Du et al., 2020; Lugli et al., 2021; Ellsworth et al., 2022; Vallicrosa et al., 2023; Lugli et al., 2024). For soil N, although we had expected some increase given the huge fertiliser input, the absence of change is likely attributable to the open N cycle in tropical rainforests (Pajares and Bohannan, 2016; Elrys et al., 2023).

Despite the elevated nutrient availability, foliar nutrient concentrations only increased for two species in the case of N (*O. asbeckii* and *I. hostmannii*), and three species for P: *O. asbeckii* and *I. hostmannii*, and to a lesser extent also *L. persistens*. Consistent with biogeochemical niche theory, each niche of an organism is characterised by an optimal elementome, which is the content of bioelements (including N and P). The plasticity of the elementome varies between species; some species have a small elementome variation and are less able to adapt their elementome to environmental changes (such as fertilisation) than other species (Peñuelas et al., 2019; Sardans et al., 2021). Thus, *L. alba* and *L. persistens* may be less capable than *O. asbeckii* and *I. hostmannii* of adjusting their elementome composition to differences in P and N availability. It is possible that *L. alba* and *L. persistens* are not capable of absorbing more P and N than necessary, or that this species stores the extra P and N in plant tissues other than leaves. Those species that managed to absorb more nutrients (like *O. asbeckii* and *I. hostmannii*) may build up a competitive advantage compared to other species. Another possibility is that all saplings species absorb the extra nutrients, but they invest it differently. Saplings of canopy species (*L. alba* and *L. persistens*), in contrast to understorey and subcanopy species (such as *O. asbeckii* and *I. hostmannii*), invest the added nutrients directly in growth rather than stocking them in leaf tissues, as found by Sellan et al. 2025 in a Bornean white sand forest. This while understory and subcanopy species, would invest the extra nutrients to withstand life in the understorey, e.g. increasing leaf anti-herbivore compounds.

Due to these species-specific responses, fertilisation in the long term could alter the composition of tropical forests (Mayor et al., 2014; Yang, 2018; Mao et al., 2021). Reported responses of leaf N concentration to fertilisation include both increases and decreases. Increases in foliar N concentration after N fertilisation occurred predominantly in studies where either P was also added or where soils were P-rich (Vallicrosa et al., 2023; Yong et al., 2025). Vallicrosa et al. (2023) suggested that under these conditions, elemental limitation shifts from P to N, or N becomes co-limiting. An increase in foliar P concentration was observed in several other P-fertilisation studies conducted in tropical rainforests (Pasquini and Santiago, 2012; Yang, 2018; Mao et al., 2021; Yong et al., 2025). However, the response of saplings to P fertilisation was often species-specific (Yang, 2018; Yong et al., 2025), as was the case in this study.

4.2 Impact of eight years of fertilisation on overstorey LAI

Overstorey LAI increased significantly in the fertilised plots of this study, confirming the third hypothesis. Mature trees thus benefited from the enhanced nutrient availability, enabling them to build a denser canopy and indicating that low nutrient (N, but more likely P) availability was limiting tree productivity at the study site. Harrington et al. (2001) also showed that the LAI of a tropical rainforest increased when fertilised with a limiting nutrient (N or P, depending on the site). Besides fertilisation, also topography affected the difference in overstorey LAI between 2016 and 2024, with a significantly higher increase in overstorey LAI in top plots than in bottom plots. One possible explanation is that the plots in the valley bottom experience more disturbance from creek flooding, causing more tree fall (Ferry et al., 2010). This leads to a lower increase in overstorey LAI values and thus higher light availability for saplings in bottom than top plots.

4.3 Impact of eight years of fertilisation on sapling photosynthetic capacity

In this study, no consistent increases in sapling photosynthetic capacity at leaf level were observed. However, saplings may also increase photosynthetic capacity at tree level by enhancing total leaf area. Unfortunately, this cannot be confirmed in this study due to the lack of pre-treatment total leaf area data, but the 2024 total sapling leaf area data, as well as the ratio of total leaf area to above ground wood volume (Appendix C and D) were also not enhanced by the fertilisation. As such hypothesis 4 could be rejected.

In contrast to the lack of response of photosynthetic capacity to the fertilisation treatment, a clear negative correlation occurred between the change in photosynthetic capacity between 2016 and 2024 and the change in overstorey LAI between 2016 and 2024. This negative correlation has previously been observed in deeply shaded forest floors (Reich et al., 2003) and can be explained by the balance between costs and benefits of investments in photosynthetic capacity. When more light becomes available in the understorey (corresponding to a reduced overstorey LAI, e.g. after a tree fall), it is interesting for plants to invest energy and nutrients in the photosynthetic machinery needed for electron transport and carboxylation capacity to increase photosynthetic capacity and thereby photosynthesis. If in contrast, less light becomes available (e.g. because of increased overstorey LAI following fertilisation), photosynthesis would decline even if photosynthetic capacity is maintained. However, maintaining photosynthetic capacity comes at a great energy and nutrient cost, so under declining light conditions reduction of photosynthetic capacity is energetically beneficial (Reich et al., 2003). Under low light conditions, the best strategy for saplings to maximise photosynthesis is therefore not enhancing photosynthetic capacity per unit leaf, but increasing light capture by producing more and/or larger, thinner leaves (Valladares et al., 1997). The latter could be achieved by increasing SLA, which was indeed observed in our study and reflected in the negative relationship found between overstorey LAI and SLA (Appendix B).

The SLA of the fertilised saplings increased significantly between 2016 and 2024, suggesting that leaves became thinner and less costly to produce. Overall, there is no mechanistic reason for the saplings to produce thinner leaves when supplied with extra nutrients. Therefore, it can be postulated that the fertilisation effect on SLA reflects the indirect effect of fertilisation on overstorey LAI, eliciting deeper shade at the forest floor and thereby the expected increase in SLA (Reich et al., 2003). It is also possible that the extra nutrients leaded to thinner leaves with a higher turnover and therefore a shorter leaf lifespan (Yang et al., 2007), but this could not be confirmed in this study.

4.4 Impact of eight years of fertilisation on sapling growth

With increased nutrient availability, less C and energy are needed underground for nutrient acquisition, shifting C allocation to above-ground plant parts (Bucci et al., 2006; Santiago et al., 2012). Indeed, Vicca et al. (2012) showed that nutrient availability is an important determinant of biomass production efficiency. When more nutrients are readily available, a larger fraction of GPP can be invested in woody biomass production because less C needs to be invested in nutrient uptake mechanisms such as root exudation, symbiotic N and P uptake, or fine root turnover (de Grandcourt et al, 2004; Hikosaka et al., 2005; Vicca et al., 2012; Hasegawa et al., 2016; Gargallo-Garriga et al., 2018; Lugli et al., 2021; Hildebrand et al., 2023; Lugli et al., 2024). However, this study revealed no overall fertilisation effect on stem volume increment. According to the results of this study, only the canopy species *L. alba* showed a significant increase in volume increment, although this would need to be confirmed in a follow-up study with more sapling data.

In contrast to the absence of a general fertilisation impact on stem volume increment, there was a statistically significant positive effect on stem height increment. This response was probably a consequence of the lower light availability due to the increase in overstorey LAI, causing the saplings to grow taller in search of light. Indeed, the hypothesised (H6) negative relation between overstorey LAI and sapling growth (volume- and height increment) was confirmed. Higher overstorey LAI reduces light availability, probably the key growth-limiting resource for saplings growing in tropical rainforests (Pasquini and Santiago, 2012; Santiago et al., 2012; Wagner et al., 2016). It is likely that the hypothesised positive fertilisation effect on growth is offset by the negative shading effect caused by the increase in overstorey LAI, resulting in no net fertilisation effect.

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5 Conclusions

In conclusion, our results highlight the impact of nutrient addition on tropical rainforest saplings. This study confirms that certainly P availability in the soil increased after eight years of NP fertilisation. For some sapling species, this increased availability led to higher leaf nutrient concentrations (both P and N). Despite this increase in leaf nutrients for some species, there was no fertilisation effect on photosynthetic capacity.

The increased P availability probably also led to a lower investment in underground mechanisms for nutrient uptake, allowing more GPP to be invested in the production of above-ground biomass. Nevertheless, there was no overall increase in sapling volume increment, which was due to the decrease in light availability caused by the increased overstorey LAI in the fertilised plots. The combination of extra nutrient availability and decreased light availability in the understorey as a result of this fertilisation led to a strong increase in height increment and an increase in SLA as shade adaptations.

This study highlights the importance of the two most limiting resources in the understorey of tropical rainforests, namely nutrients and light, and how they interact with each other. We did not observe immediate mortality or growth divergence strong enough to shift composition within this eight-year window, but differences in nutrient uptake suggest potential long-term competitive shifts.

6 Appendices

Appendix A: Species characteristics

Table A1: Overview of specific characteristics of the four tropical rainforest species studied: I. hostmannii, L. persistens, L. alba and O. asbeckii. The specific characteristics include information on family, genus, shade tolerance, type of mature tree form, the habitat they grow in, maximum measured diameter at breast height (DBH) and whether the species symbiotises with N-fixing bacteria. Information was taken from the following sources: Mori et al., 1996; Vincent et al., 2011; Hogan et al., 2018; Molino et al., 2022.

Family	Genus	Species	Shade tolerance	Form	Habitat	Max DBH (cm)	N-fixing
Myristicaceae	*Iryanthera*	*hostmannii*	Strong	Subcanopy tree	Seasonally flooded forest	46.2	No
Lecythidaceae	*Lecythis*	*persistens*	Medium	Canopy tree	Non-flooded forest	65.6	No
Chrysobalanaceae	*Licania*	*alba*	Medium	Canopy tree (to 35m)	Non-flooded forest	96.5	No
Annonaceae	*Oxandra*	*asbeckii*	Strong	Small tree (7-14m)	Non-flooded forest	59.8	No

Appendix B: Specific leaf area (SLA)

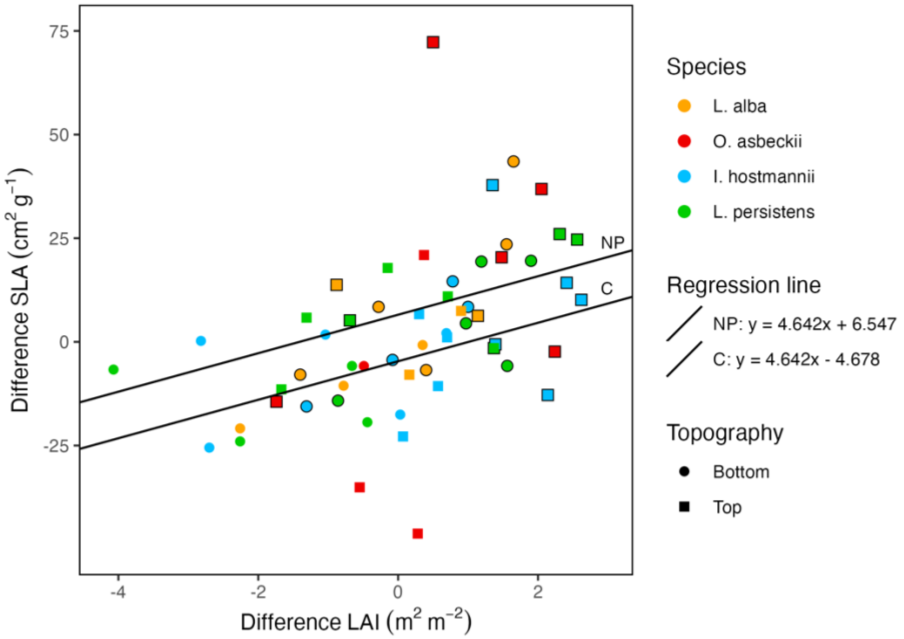

Figure B1: The difference in specific leaf area (SLA) is plotted against the difference in overstorey LAI between 2016 and 2024, with NP the regression line for the fertilised saplings and C the regression line for the saplings growing in the control treatment. Points with a black edge represent measurements on saplings growing in the NP plots, points without black edge represent saplings growing in the control plots.

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Appendix C: Sapling total leaf area

As no 2016 data was available for the total leaf area, the treatment effect is assessed here using only the 2024 data. Treatment had no significant effect on the total leaf area per sapling ($F_{1,119} = 0.9184$, $p = 0.3398$) and neither did overstorey LAI ($F_{1,119} = 1.2852$, $p = 0.2592$), contrary to what was expected with regard to shade adaptations due to lower light availability in the understorey. A post hoc Tukey test showed that saplings in the top plots had a significantly lower total leaf area than saplings in the bottom plots ($\beta_{\text{top-bottom}} = -0.2$, $p = 0.0217$; Fig. C1). Species also differed (Fig. C1), e.g. the species *O. asbeckii* had a significantly lower total leaf area than the species *I. hostmannii* ($\beta_{\text{hostmannii-asbeckii}} = 0.2$, $p = 0.0240$).

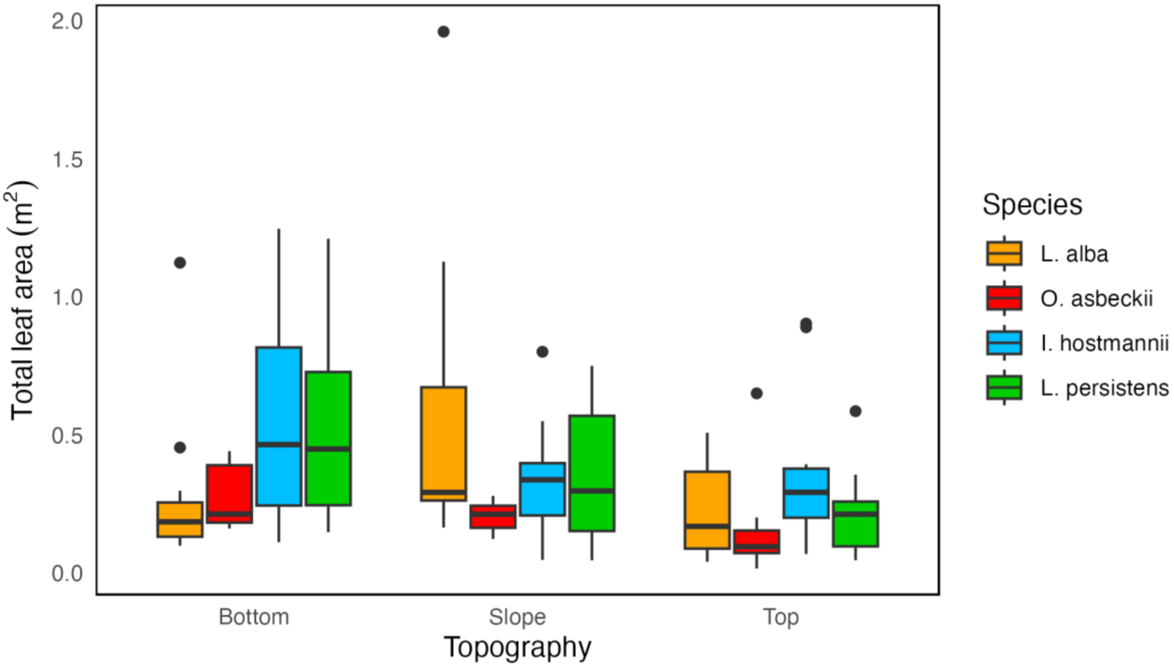

Figure C1: Total leaf area measured in 2024, visualised with boxplots for different species per topography type. The box is formed by the lower quartile and upper quartile, the horizontal line in the box indicates the median. The vertical lines represent the fences, which are determined by the points in the dataset within 1.5 times the interquartile distance (above and below the box). Observations that fall out of the fences are represented by circles.

Appendix D: Sapling ratio total leaf area / wood volume

As no 2016 data was available for the total leaf area, the treatment effect is evaluated here using only the 2024 data. Treatment had a significant effect on the ratio total leaf area/wood volume only for species *O. asbeckii* ($\beta_{asbeckii:NP} = 53$, $t_{109} = 4.207$, $p < 0.0001$; Fig. D1). In addition, the interaction between topography and species was also significant ($F_{6,109} = 3.6108$, $p = 0.0026$), with *O. asbeckii* saplings exhibiting a significantly lower ratio total leaf area/wood volume in the top and slope plots compared to the bottom plots (for slope plots: $\beta_{asbeckii:Slope} = -67$, $t_{109} = -4.288$, $p < 0.0001$; for top plots: $\beta_{asbeckii:Top} = -56$, $t_{136} = -3.573$, $p = 0.0005$). Overstorey LAI did not affect the ratio total leaf area/wood volume significantly ($F_{1,109} = 0.4871$, $p = 0.4867$).

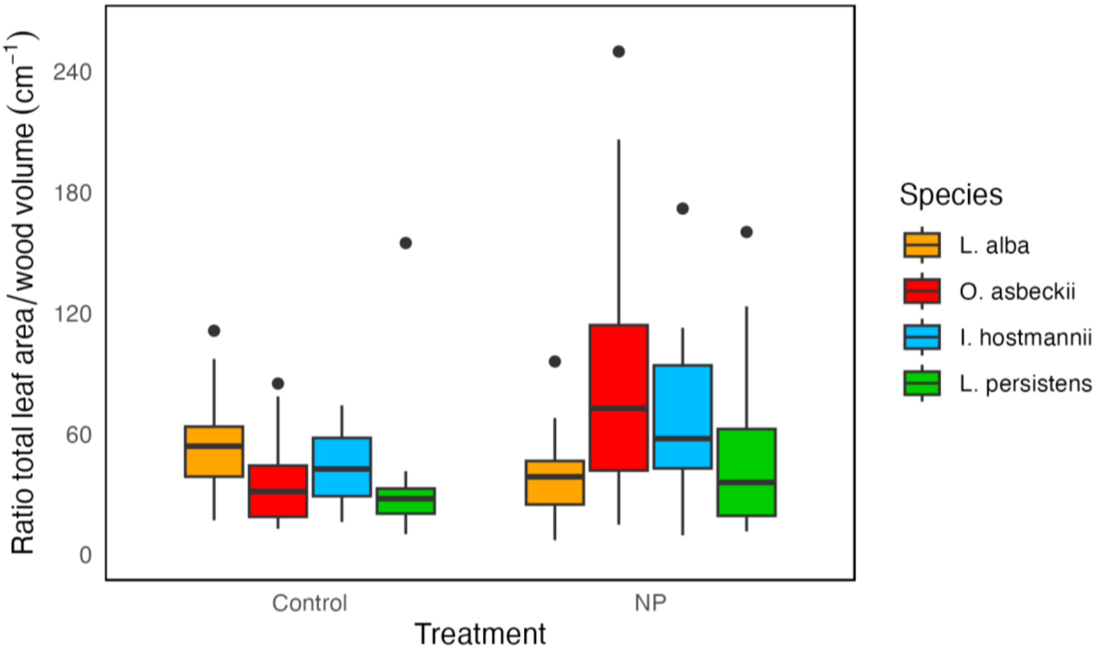

Figure D1: Ratio total leaf area/wood volume measured in 2024, visualised with boxplots for different species per treatment. The box is formed by the lower quartile and upper quartile, the horizontal line in the box indicates the median. The vertical lines represent the fences, which are determined by the points in the dataset within 1.5 times the interquartile distance (above and below the box). Observations that fall out of the fences are represented by circles.

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Appendix E: Overview of all function formulas of the regression lines in Fig. 6

Table E1: Overview of all function formulas of the regression lines in Fig. 6, which for reasons of clarity are not all shown. The sapling code shows the topographical position and fertilisation type: B stands for bottom, T for top, 2 for NP fertilisation and 4 for control treatment, AL for *L. alba*, OX for *O. asbeckii*, IH for *I. hostmannii* and LP for *L. persistens*. The function formulas of the regression lines that are shown in the graph are shown in red. Significant p-values are shown in bold.

Sapling	Function formula	R^2-value	p-value
B2-AL	y= -0.59x - 0.3	0.49	< **0.0001**
B2-OX	y= -0.59x	0.49	< **0.0001**
B2-IH	y= -0.59x + 0.6	0.49	< **0.0001**
B2-LP	y= -0.59x + 1.1	0.49	< **0.0001**
B4-AL	y= -0.59x + 0.3	0.49	< **0.0001**
B4-OX	y= -0.59x + 0.7	0.49	< **0.0001**
B4-IH	y= -0.59x + 1.3	0.49	< **0.0001**
B4-LP	y= -0.59x + 1.8	0.49	< **0.0001**
T2-AL	y= -0.59x + 1.6	0.49	< **0.0001**
T2-OX	y= -0.59x + 1.9	0.49	< **0.0001**
T2-IH	y= -0.59x + 2.5	0.49	< **0.0001**
T2-LP	y= -0.59x + 3.0	0.49	< **0.0001**
T4-AL	y= -0.59x + 0.2	0.49	< **0.0001**
T4-OX	y= -0.59x + 0.5	0.49	< **0.0001**
T4-IH	y= -0.59x + 1.1	0.49	< **0.0001**
T4-LP	y= -0.59x + 1.6	0.49	< **0.0001**

Appendix F: Overview of all function formulas of the regression lines in Fig. 8

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Table F1: Overview of all function formulas of the regression lines in Fig. 8, which for reasons of clarity are not all shown. The sapling code shows the topographical position, fertilisation type and species: B stands for bottom, S for slope, T for top, 2 for NP fertilisation, 4 for control treatment, AL for *L. alba*, OX for *O. asbeckii*, IH for *I. hostmannii* and LP for *L. persistens*. B2-OX and S2-LP are missing because there was no 2016 data for them. The function formulas of the regression lines that are shown in the graph are shown in red. Significant p-values are shown in bold. 595

Saplings	Function formula	R^2-value	p-value
B2-AL	y= -8.6x + 111	0.41	**0.0004**
B2-IH	y= -8.6x + 107	0.41	**0.0004**
B2-LP	y= -8.6x + 123	0.41	**0.0004**
B4-AL	y= -8.6x + 67	0.41	**0.0004**
B4-OX	y= -8.6x + 93	0.41	**0.0004**
B4-IH	y= -8.6x + 103	0.41	**0.0004**
B4-LP	y= -8.6x + 101	0.41	**0.0004**
S2-AL	y= -8.6x + 149	0.41	**0.0004**
S2-OX	y= -8.6x + 79	0.41	**0.0004**
S2-IH	y= -8.6x + 93	0.41	**0.0004**
S4-AL	y= -8.6x + 105	0.41	**0.0004**
S4-OX	y= -8.6x + 81	0.41	**0.0004**
S4-IH	y= -8.6x + 89	0.41	**0.0004**
S4-LP	y= -8.6x + 121	0.41	**0.0004**
T2-AL	y= -8.6x + 113	0.41	**0.0004**
T2-OX	y= -8.6x + 79	0.41	**0.0004**
T2-IH	y= -8.6x + 89	0.41	**0.0004**
T2-LP	y= -8.6x + 97	0.41	**0.0004**
T4-AL	y= -8.6x + 69	0.41	**0.0004**
T4-OX	y= -8.6x + 80	0.41	**0.0004**
T4-IH	y= -8.6x + 84	0.41	**0.0004**
T4-LP	y= -8.6x + 75	0.41	**0.0004**

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Appendix G: Overview of all function formulas of the regression lines in Fig. 9

Table G1: Overview of all function formulas of the regression lines in Fig. 9, which for reasons of clarity are not all shown. The sapling code shows the topographical position, fertilisation type and species: B stands for bottom, S for slope, T for top, 2 for NP fertilisation, 4 for control treatment, AL for *L. alba*, OX for O. *asbeckii*, IH for *I. hostmannii* and LP for *L. persistens*. B2-OX and S2-LP are missing because there was no 2016 data for them. The function formulas of the regression lines that are shown in the graph are shown in red. Significant p-values are shown in bold.

Saplings	Function formula	R^2-value	p-value
B2-AL	y= -5.3x + 87	0.30	**0.0016**
B2-IH	y= -5.3x + 68	0.30	**0.0016**
B2-LP	y= -5.3x + 79	0.30	**0.0016**
B4-AL	y= -5.3x + 66	0.30	**0.0016**
B4-OX	y= -5.3x + 54	0.30	**0.0016**
B4-IH	y= -5.3x + 48	0.30	**0.0016**
B4-LP	y= -5.3x + 59	0.30	**0.0016**
S2-AL	y= -5.3x + 100	0.30	**0.0016**
S2-OX	y= -5.3x + 87	0.30	**0.0016**
S2-IH	y= -5.3x + 81	0.30	**0.0016**
S4-AL	y= -5.3x + 79	0.30	**0.0016**
S4-OX	y= -5.3x + 66	0.30	**0.0016**
S4-IH	y= -5.3x + 60	0.30	**0.0016**
S4-LP	y= -5.3x + 71	0.30	**0.0016**
T2-AL	y= -5.3x + 83	0.30	**0.0016**
T2-OX	y= -5.3x + 70	0.30	**0.0016**
T2-IH	y= -5.3x + 64	0.30	**0.0016**
T2-LP	y= -5.3x + 75	0.30	**0.0016**
T4-AL	y= -5.3x + 62	0.30	**0.0016**
T4-OX	y= -5.3x + 49	0.30	**0.0016**
T4-IH	y= -5.3x + 43	0.30	**0.0016**
T4-LP	y= -5.3x + 54	0.30	**0.0016**

Data availability

The 2024 data used in this paper is available at https://doi.org/10.5281/zenodo.18469254 (van Poecke, 2026). The 2015 and 2016 data used in this paper are available at https://doi.org/10.5281/zenodo.5638236 (Verryckt, 2021).

Author contributions

ALVP, LB, CS, GS, GH, BB contributed to the field work and collected the data in 2024. The 2015 soil data was collected by LVL and the 2016 sapling data was collected by LTV. JS, JP, LB and IAJ provided the project funding. The manuscript was drafted by ALVP and IAJ and all co-authors contributed to the writing.

Competing interests

The authors declare that they have no conflict of interest.

Disclaimer

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Review statement

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