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# Responses of tree growth and biomass production to nutrient addition in a semi-deciduous tropical forest in Africa

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Abstract:

Experimental evidence of nutrient limitations on primary productivity in Afrotropical forests is rare and globally underrepresented, yet are crucial for understanding constraints to terrestrial carbon uptake. In an ecosystem-scale nutrient manipulation experiment, we assessed the early responses of tree growth rates among different tree sizes, taxonomic species and at a community level in a humid tropical forest in Uganda. Following a full factorial design, we established 32 (eight treatments × four replicates) experimental plots of 40 m × 40 m each. We added nitrogen (N), phosphorus (P), potassium (K), their combinations (NP, NK, PK, and NPK) and control at the rates of 125 kg N.ha$^{-1}$.yr$^{-1}$, 50 kg P.ha$^{-1}$.yr$^{-1}$ and 50 kg K.ha$^{-1}$.yr$^{-1}$, split into four equal applications, and measured stem growth of more than 15,000 trees with diameter at breast height (DBH) $\geq$ 1 cm. After two years, the response of tree stem growth to nutrient additions was dependent on tree sizes, species and leaf habit but not community-wide. First, tree stem growth increased under N additions, primarily among medium-sized trees (10−30 cm DBH), and in trees of *Lasiodiscus mildbraedii* in the second year of the experiment. Second, K limitation was evident in semi-deciduous trees, which increased stem growth by 46 % in +K than −K treatments, following a strong, prolonged dry season during the first year of the experiment. This highlights the key role of K in stomatal regulation and maintenance of water balance in trees, particularly under water-stressed conditions. Third, the role of P in promoting tree growth and carbon accumulation rates in this forest on highly weathered soils was rather not pronounced; nonetheless, mortality among saplings (1−5 cm DBH) was reduced by 30 % in +P than in −P treatments. Although stem growth responses to nutrient interaction effects were positive or negative (likely depending on nutrient combinations and climate variability), our results underscore the fact that, in a highly diverse forest ecosystem, multiple nutrients and not one single nutrient regulate tree

growth and aboveground carbon uptake due to varying nutrient requirements and acquisition strategies of different tree sizes, species and leaf habits.

## INTRODUCTION

Nutrient limitations play an important role in constraining plant growth and ecosystem productivity across all terrestrial biomes. Under increasing global atmospheric $CO_2$ concentrations, tropical forests remain one of the largest mitigants of climate change, storing nearly 55 % of the world's forest carbon stock and have the highest productivity compared to other biomes (Pan et al. 2011). The photosynthetic and carbon-fixation capacity of these forests relies largely on essential resources (light, water and nutrients) in sufficient quantities. It is therefore axiomatic that inadequate supply of any one or more resources will impose limits on the capacity of these forests to assimilate $CO_2$ efficiently and produce new plant biomass (Danger et al. 2008). Brienen et al. (2015) reported that the aboveground carbon sequestration rates of the Amazon rainforest decreased by about one-third between 2000 and 2010 in comparison to the 1990s. This potentially indicates that, among other adverse global changes, carbon saturation or nutrient limitations could be the constraining factor of the growth and productivity of these forests. How much carbon tropical forests will be able to store and sequester in the future remains uncertain particularly for underrepresented tropical regions

(Wieder et al. 2015). Moreover, many reviews and observations, thus far, have partly attributed these uncertainties to gaps in our knowledge of how nutrient availability control forest carbon assimilation and dynamics, which represents a major challenge for ecologists in modelling terrestrial ecosystem response to global changes (Oren et al. 2006, Hedin et al. 2009, Gerber et al. 2013).

Pathways of nutrient input in forest ecosystems (biological nitrogen fixation (BNF), rock weathering and atmospheric deposition) are variable as are nutrient requirements, acquisition and availability to different ecosystem processes (e.g. Hedin et al. 2009). Apart from N, all other nutrients primarily originate from the weathering of soil parent material and then cycled in the forest ecosystem (soil-biomass-litter-soil). In both direct and indirect observations, N and phosphorus (P) are commonly recognized to limit tree growth and other ecosystem processes in most terrestrial ecosystems (Elser et al. 2007). Soil age and climatic regimes are known large-scale controllers of nutrient limitations in tropical forests (Walker and Syers 1976, Cai et al. 2009). Young soils have a large supply of rock-derived nutrients, e.g. P and potassium (K), which diminishes as soils weather with age, whereas N accumulates as organic matter builds up with time (Walker and Syers 1976, Tanner et al. 1998, Fisher et al. 2013). In older, highly weathered soils under warm and humid climates, P and other rock-derived nutrients decrease as a result of excessive nutrient leaching (Veldkamp et al. 2020). In such soils, rock-derived nutrients may limit BNF and decomposition processes (Barron et al. 2009), which possibly down-regulates N availability (Hedin et al. 2009). On one hand, it is postulated that tropical lowland forests on highly weathered soils are P-limited but have high bioavailability of N due to the high abundance and diversity of N-fixing organisms (Hedin et al. 2009, Barron et al. 2011). Such postulation was, however, not supported by findings from a 15-year experiment of tropical

lowland forest in Panama (Wright et al. 2018). On the other hand, N limitation on plant productivity is more prevalent in tropical montane forests (Adamek et al. 2009, Wolf et al. 2011, Homeier et al. 2012) and become more pronounced with elevation (Tanner et al. 1998, Graefe et al. 2010). Notwithstanding, a more recent meta-analysis of 48 nutrient addition experiments showed that both N and P are equally likely to limit plant function in tropical forests regardless of elevation (Wright 2019).

In contrast to N and P, the role of K on ecosystem processes has largely been overlooked in tropical forests. To date, the only long-term, ecosystem-scale nutrient manipulation experiment in the lowland tropics that included a K treatment found that K is particularly limiting for the growth of young trees (Wright et al. 2011). Furthermore, indirect evidence has shown that K limitations likely affect ecosystem below- vs above-ground carbon allocations in the Congo basin (Doetterl et al. 2015). A meta-analysis of 38 K addition experiments, involving 26 different tree species revealed that many forest trees (in 69 % of the experiments) responded positively to increased K availability (Tripler et al. 2006). The spatial distributions of tree species at local scales has also been reported to be associated with K availability (John et al. 2007). It has therefore become imperative that the role of K on tree growth and development in highly diverse natural forest ecosystems is revisited.

In recent years, there are increasing evidence that different ecosystem or growth processes are limited by different nutrients, resulting in simultaneous multiple limitations on plant growth (Kaspari and Powers 2016). Nutrient addition experiments in lowland tropical forests reveal (co)limitations of N, P or K on tree growth of different size classes, components of net primary production (NPP) and succession groups (Wright et al. 2011, 2018). Most nutrient manipulation studies have been conducted on relatively young soils, and there is a serious

underrepresentation in regions with likely P- and K-depleted soils such as Ferralsols, Acrisols, Nitisols and Lixisols. To date, only one nutrient manipulation experiment of P (without N and K) has been conducted in tropical Africa (Newbery et al. 2002). In our present study, we established an ecosystem-scale nutrient manipulation experiment in a moist semi-deciduous tropical forest in Uganda, which exemplifies the underrepresented transition zone between African humid and dry tropical forests using a replicated full factorial experimental design. To our knowledge, this study represents the first ecosystem-scale nutrient manipulation experiment to be conducted on sandy soil (sand > 50 %), in contrast to nutrient addition studies that have been conducted on clay soils (Davidson et al. 2004, Siddique et al. 2010, Alvarez-Clare et al. 2013, Du et al. 2020). Our first objective was to investigate whether or not N, P and K or their interactions (co-) limit community forest growth. Here we hypothesize that there will be multiple nutrient co-limitations rather than a single nutrient limitation on community forest growth and biomass productivity, as this forest has a high species diversity (126 tree species), which will have many different nutrient acquisition strategies (Wright et al. 2011, Detto et al. 2018). Our second objective was to evaluate the response of tree diameter growth to nutrient additions by different tree size classes. Here, we predict that nutrient acquisition strategies will change over the life span of a tree, whereby small-sized trees that are still actively growing will require more nutrients than large canopy trees that have a low nutrient demand (Adamek et al. 2009, Alvarez-Clare et al. 2013). A small but important part of these trees may have a high demand for N or P (e.g. reproductive organs), which may surpass nutrient availability in the soil (Kaspari et al. 2008, Fortier and Wright 2021). We, therefore, expect that the alleviation of nutrient co-limitations will lead to a growth response of trees with small to medium stem diameters that had previously experienced high nutrient resource competition. The addition of K may alter biomass allocations (Wright et

al. 2011, Doetterl et al. 2015), stimulate processes responsible for tree growth as K plays an important regulatory role in the guard cells of leaves that control stomatal aperture and potentially limit $CO_2$ assimilation, particularly under drought stress conditions. Our last objective was to evaluate the response of stem diameter growth of different tree species, leaf habits (deciduous, semi-deciduous and evergreen) and functional traits (N-fixers and non-N fixers) to nutrient additions. We predict that N-fixing tree species will increase in stem diameter growth in response to P but not to N additions (Waring et al. 2019).

## METHODS

### *Site description*

This experiment was conducted in the Budongo Forest Reserve in northwestern Uganda (1°44'28.4"N, 31°32'11.0"E; elevation range: 1050−1070 m; Appendix S1: Fig. S1). The Budongo forest is a moist, semi-deciduous tropical rainforest situated on an uplifted Shield, specifically on a Precambrian gneissic-basaltic basement complex (van Straaten 1976). Annual precipitation and air temperature average $1670 \pm 50$ mm and $22.8 \pm 0.1$ °C, respectively (2000−2019; Budongo Conservation Field Station). The region experiences two dry seasons (< 100 mm per month) from December to February and in July. Annual nutrient depositions from rainfall are 8.5 kg $N.ha^{-1}.yr^{-1}$, 0.03 kg $P.ha^{-1}.yr^{-1}$ and 4.3 kg $K.ha^{-1}.yr^{-1}$. The soil is classified as Lixisol (IUSS Working Group WRB 2014), a well-drained (> 50 % sand), highly weathered soil commonly found in a transition zone between tropical forests and savannahs. Unlike other highly weathered soils, this Lixisol's high base saturation and pH (Appendix S1: Section S1, Tables S1 and S2) are contributed by depositions of aeolian dust and ashes from agricultural biomass

burning (Boy and Wilcke, 2008; Bauters et al., 2018) and by weathering of its parent material that consists of coarse-grained basaltic granulites with ~10 % CaO and 6−7 % MgO.

Vegetation at the site is composed of 126 tree species (Shannon-diversity index H':
2.53 ± 0.04 and canopy heights reaching up to 50 m). Among trees with diameter at breast height
(DBH) ≥ 10 cm, N-fixing trees (Family: Fabaceae or Leguminosae) constitute 6 % in stem
abundance (Appendix S1: Table S3) but account for 16 % of the forest's basal area and 25 % of
aboveground wood biomass (Table 1). Leaf area index averaged $3.3 ± 0.0$ $m^2/m^2$ (determined in
April 2018 and November 2019) in the control plots. The site was selectively logged in the
1950s (Appendix S1: Section S2) but has remained undisturbed for nearly 60 years (Plumptre
1996). As a result of the past logging, there is a higher abundance of some mid-stage succession
tree species (e.g. *Funtumia elastica*). The ten most dominant species together represent 78 % of
all trees ≥ 10 cm DBH in the experimental plots (Table 1, Appendix S1: Table S3). Larger trees
(> 30 cm DBH) contributed a large proportion (73 %) of the total wood biomass (395 ± 17
Mg/ha) and 66 % of carbon storage (annual wood biomass productivity of 5.04 ± 0.74 Mg
$C.ha^{-1}.yr^{-1}$). Out of 93 tree species ≥ 10 cm DBH (Appendix S1: Table S3), five species
(*Cynometra alexandri* (19 %), *Celtis durandii* (13 %), *Funtumia elastica* (8 %), *Celtis
mildbraedii* (8 %), and *Khaya anthoteca* (7 %)) could be considered biomass hyperdominant (i.e.
those tree species which collectively account for > 50 % of biomass; Fauset et al. 2015)  and just
eight tree species (listed in Table 1) were responsible for about half the total wood biomass
productivity (Table 1) at this site.

*Experimental design*

We established a full factorial NPK experiment with eight treatments: control, N, P, K, NP, NK, PK, and NPK (Appendix S1: Fig. S1). These treatments had four replicates and were randomly assigned to 32 plots, 40 m × 40 m each and separated by at least 40 m.  Within each 40 m × 40 m plot, we laid out sixteen 10 m × 10 m quadrats to facilitate fertilizer additions. Nitrogen was added as urea ($(NH_2)_2CO$) at a rate of 125 kg N.ha$^{-1}$.yr$^{-1}$, P as triple superphosphate ($Ca(H_2PO4)_2$) at a rate of 50 kg P.ha$^{-1}$.yr$^{-1}$ and K as muriate of potash (KCl) at a rate of 50 kg K.ha$^{-1}$.yr$^{-1}$. The experimental design and nutrient addition rates were consistent with Wright et al. (2011). Pre-packaged fertilizers for each 10 m × 10 m quadrat were mixed with soil directly adjacent to the plot (as filler material) and broadcasted by hand within each quadrat, walking forward and back and subsequently changing directions (north to south and east to west). We fertilized four times in a year in equal doses during the wet season (beginning from 17th May 2018, then August, November and March).

*Tree growth measurements and biomass productivity*

We conducted censuses of all trees ≥ 10 cm DBH in each 40 m × 40 m plot, and trees 1 cm ≤ DBH < 10 cm within an inner 30 m × 20 m subplot. All measured trees (3180 trees ≥ 10 cm DBH; 12,604 trees 1 cm ≤ DBH < 10 cm) were tagged with identification numbers and taxonomically identified to species level. Non-cylindrical stems at breast height due to buttresses or deformity were measured 50 cm above buttresses or deformity. All points of measurement were marked with spray paint to ensure that subsequent censuses were taken at the same point. We repeated censuses four times within the two-year experiment period, i.e. April 2018 (pre-

treatment), April 2019 (after 1 year), October 2019 (after 1.5 years) and April 2020 (after 2 years).

To assess the effect of nutrient addition and seasonal pattern on individual tree stem growth to a finer temporal scale, we installed dendrometer bands (D1, UMS, Munich, Germany; with increment-sensitivity of 0.1 mm) on 20 selected trees $\geq$ 10 cm DBH in an inner 30 m $\times$ 30 m measurement zone of each plot. The selection of the 20 trees (which was ~ 40 % of the trees in this inner zone) was based on species composition and DBH distribution (Appendix S1: Section S3). The installed dendrometer bands were allowed to settle for a month before our first measurement (May 22, 2018), followed by two consecutive bi-monthly dendrometer measurements (July 22, September 22). Thereafter, all measurements were taken every month on the same date (22nd).

We calculated relative growth rate (RGR; Eq. (1)) (Hoffmann and Poorter 2002) as a metric for tree growth. We separately analyzed four DBH classes (1–5 cm, 5–10 cm, 10–30 cm and >30 cm) as these classes likely experience contrasting light availability and may accordingly differ in their response to nutrient additions (e.g. Wright et al. 2011, 2018). For all analyses of tree growth response to nutrient additions, we only included trees measured in the inner 30 m $\times$ 30 m zone in each plot to minimize edge effects.

$$RGR \left( cm.cm^{-1}.t^{-1} \right) = \left( \ln\left( DBH_f \right) - \ln\left( DBH_i \right) \right) / \Delta t \qquad (1)$$

where $f$ and $i$ represent final and initial measurement periods, respectively, and $\Delta t$ represents the change in time (year or month). For a specific DBH class, the RGR value for each plot was the mean RGR of trees belonging to that class. To assess community-level response to nutrient addition, we calculated community-level RGR (Eq. 2) for each plot by weighting the RGR of each DBH class with the corresponding number of trees (n) belonging to that size class.

$$\text{Community level RGR} = \frac{\left(\text{RGR}_{(1-5\text{cm})} \times n_1\right) + \left(\text{RGR}_{(5-10\text{cm})} \times n_2\right) + \left(\text{RGR}_{(10-30\text{cm})} \times n_3\right) + \left(\text{RGR}_{(>30\text{cm})} \times n_4\right)}{\left(n_1 + n_2 + n_3 + n_4\right)}$$

(2)

Furthermore, tree growth largely depends on biomass allocations to its various organs (roots, stem and leaves), which may differ among different species, functional groups (N fixers and non-N fixers) and different leaf habits (evergreen, semi-deciduous and deciduous) (Appendix S1: Table S3). For instance, deciduous tree species (which shed their leaves during the dry season) may have to resorb and reallocate nutrients in the leaf before shedding them, whereas evergreen species may not. Therefore, the RGR responses of these groups of species (Appendix S1: Table S3) under elevated nutrient supply may differ. Thus, we evaluated plot-level RGR responses of different tree species, leaf habits and functional groups to nutrient additions. For species-level analysis, we included five dominant tree species that were present in at least three replicate plots for each treatment.

We estimated the aboveground wood biomass (AWB; Eq. (3)) of each tree for the four census periods during the two years, using a pan-tropical allometric equation (Chave et al. 2014; Eq. 3),  $\text{AWB} = 0.0673 \times \left(\rho D^2 H\right)^{0.976}$           (3)

where $D$ refers to DBH (cm), $H$ is tree height (m) and $\rho$ represents wood density (g/cm$^3$). Heights of 783 trees (representing all species and at least 20 trees $\geq$ 10 cm DBH per plot) were measured using a Vertex III ultrasonic hypsometer and a T3 transponder (Haglöf, Sweden). The heights of all other trees $\geq$ 10 cm DBH were estimated using diameter-height allometry (Chave et al. 2005). Species-specific wood density was determined for 764 trees by driving an increment borer (Mora, Sweden) into the tree stem ~ 20 cm above the DBH measurement point. Wood

density was calculated by dividing the oven-dry mass (60 °C, 72 h) of the wood core by its fresh volume (Chave 2005). Wood biomass productivity for each tree was the change in AWB during 2018−2020, and summed for all the trees in each plot for each year; when expressed in terms of carbon, we assumed 50 % carbon in wood biomass (Chave et al. 2005, Lewis et al. 2009).

### *Statistical analyses*

We used a factorial analysis of variance (ANOVA) to test the effect of nutrient additions on community-level RGR as well as RGR of different DBH classes, species, leaf habits, and functional groups for each year of the experiment. We separately analysed for each year to isolate possible effects of climate variation or lag response of the RGR to nutrient additions. All parameters were first tested for normal distribution using Shapiro-Wilk's test and equality of variance using Levene's test. Logarithmic or square root transformation was applied when an assumption of the aforementioned tests is violated. For the monthly measured  RGR response to nutrient additions, linear mixed-effects (LME) models ('lme'-function in the nlme package) were used to test the fixed effects of treatments (N, P, K, each with two levels and their interactions). The spatial replication (for the plot-level RGR; n = 4 plots) and time (months) were included in the LME as random effects. A function ('weights') that allows different variances of the response variable per level of the fixed effect and/or a first-order temporal autoregressive process was included (e.g. Koehler et al. 2009, Corre et al. 2010, van Straaten et al. 2011), if this improved the relative goodness of the model fit based on Akaike Information Criterion (AIC). The significance of the fixed effect was evaluated using ANOVA (Crawley, 2009). The LME analyses were performed for the entire period of the experiment as well as for the first and second years separately. If residual plots revealed non-normal distribution or non-homogenous variance, we log-transformed the data and then repeated the analyses. To assess the short-term

influence of nutrient addition on tree mortality events among the different DBH classes, the proportion of dead stems per DBH class in each plot for the entire experimental period (2018−2020) were analyzed using logistic regression. Nutrient addition treatment (factorial N-P-K) was the predictor and the proportion of mortality events was the response variable. For all analyses, nutrient addition effects were considered significant at $P \leq 0.05$. All statistical analyses were conducted using the R statistical software version 3.6.2 (R Development Core Team 2018).

## RESULTS

We report results of both monthly dendrometer band monitoring of 20 selected individual trees per plot (Fig. 1) and growth rates based on annual censuses of all trees in each of the 32 plots (Fig. 2, 3 and 4). Data obtained from dendrometer measurements strongly correlates with the census data ($R^2 = 0.72$, $P < 0.001$; Appendix S1: Fig. S2). There were largely no differences in surface soil characteristics among treatment plots before nutrient additions (Appendix S1: Table S2) and accordingly, differences in tree growth rates can be attributed to nutrient addition treatments and not to inherent differences in soil biochemical characteristics. Overall, we found no treatment effects of nutrient additions on community-level RGR in either the first or second year of the experiment ($F_{1, 24} = 0.40$, 0.37 and $P = 0.892$, 0.909; Appendix S2: Fig. S1). Community-level RGR was, however, higher in the second year (0.046 ± 0.006 cm. cm$^{-1}$. yr$^{-1}$) than in the first year (0.025 ± 0.005 cm.cm$^{-1}$.yr$^{-1}$) in the control plots as well as in all other treatments ($t_{(31)} = 9.00$, $P < 0.0001$; Appendix S2: Fig. S1). In contrast to wood biomass productivity (Table 1), RGR tended to decrease with increasing DHB classes (Table 1).

*Seasonal pattern in tree growth rate*

Monthly RGR was highly seasonal and correlated strongly with monthly rainfall ($R^2 =$ 0.52, $P < 0.001$; Appendix S1: Fig. S3), with higher RGR recorded in the wet months than in the dry months (Fig. 1, Appendix S2: Fig. S2). In the first year (June 2018–May 2019) of the experiment, the region experienced a longer dry season (five dry months; annual rainfall = 1695 mm) than in the second year (three dry months; annual rainfall = 2168 mm) with ~ 30 % more rainfall recorded (Fig. 1d).

*Tree growth response to nutrient addition by different tree diameter classes*

The response of RGR to nutrient addition was dependent on tree diameter classes (Fig. 2). After separate analysis of different diameter classes (1–5 cm, 5–10 cm, 10–30 cm and > 30 cm DBH), no observable nutrient addition effect on the growth rates of young trees (1–10 cm DBH; Appendix S2: Table. S1) was found. There was, however, an increase in RGR of medium-sized trees (10–30 cm DBH) under N additions in the second year of the experiment ($F_{1, 24} =$ 4.76, $P = 0.039$; Fig. 2a; Appendix S2: Table S1), which was well corroborated by the temporal RGR response observed from the trees measured more intensively with dendrometer bands ($F_{1, 24} = 6.14$, $P = 0.021$; Fig. 1a). Additionally, there was a negative N × K interaction effect on tree growth, resulting in a decreased RGR among medium-sized trees in the second year ($F_{1, 24} =$ 4.71, $P = 0.040$; Fig 2b; Appendix S2: Table S1). Furthermore, while no single nutrient addition was associated with increased stem growth among larger trees (> 30 cm DBH), a positive N × P × K interaction effect on stem growth was found among these larger trees in the second year of the experiment ($F_{1, 24} = 5.56$, $P = 0.027$; Appendix S2: Table S2). Additions of P or K alone did not have any observable effects on stem growth (Fig. 1 and 2) in either the first or second year of

the experiment, although P additions reduced mortality among the smallest class of saplings (1–5 cm DBH; $P = 0.039$) and increased their survival by 30 %.

### *Tree growth response to nutrient addition by different species, leaf habits and functional groups*

Tree growth response to nutrient additions by different tree species was variable and time-dependent (Fig. 3). The RGR of *Lasiodiscus mildbraedii* increased significantly under N additions in the second year ($F_{1, 20} = 8.06$, $P = 0.010$) and under P × K interaction effect in both the first and second years of the experiment ($F_{1, 20} = 10.12$, $5.06$; $P = 0.005$, $036$) (Fig. 3e). All other species combined (apart from the five species presented in Fig. 3) also had a positive RGR response to P × K interaction effect in the first year ($F_{1, 24} = 5.12$, $P = 0.033$; Fig. 3f). In contrast, the RGR of *Funtumia elastica* declined in response to N × P interaction effect in the second year of nutrient additions ($F_{1, 24} = 5.45$, $P = 0.028$; Fig. 3a) as did the negative effect of K additions on the RGR of *Lasiodiscus mildbraedii* in the first and second years of the experiment ($F_{1, 20} = 5.68$, $13.03$; $P = 0.027$, $0.002$; Fig. 3e). Among different leaf habits, K additions were associated with increased RGR of semi-deciduous trees in the first year of the experiment when the site experienced a prolonged dry season (Fig. 1d). Specifically, we found that the RGR of this leaf habit increased under K additions and P × K interaction effect only in the first year ($F_{1, 24} = 7.48$, $4.80$ and $P = 0.012$, $0.042$; Fig. 4; Appendix S2: Table S2). Tree growth response to nutrient additions among N-fixers nor non-N-fixer were insignificant in both years of the experiment.

## DISCUSSION

### *Community-level tree growth and productivity response to nutrient additions*

The tree growth rate in this forest (trees $\geq$ 10 cm DBH in the control plots; $0.011 \pm 0.001$ cm.cm$^{-1}$.yr$^{-1}$) was comparable to those reported from humid tropical forests in Panama (Wright et al. 2011, 2018) but lower than those in Costa Rica (Alvarez-Clare et al. 2013, Waring et al. 2019). Carbon accumulation rate ($2.2 \pm 0.4$ Mg C.ha$^{-1}$.yr$^{-1}$) in this forest was also comparable to those measured in Panama (Adamek et al. 2009, Wright et al. 2011), Brazil, Colombia and Peru (Arağo et al. 2009, Malhi et al. 2009, 2011), but was lower than those reported from Costa Rica (Russell et al. 2010). The difference in tree growth and productivity with these other sites may be due to several factors related to species diversity and forest composition (Ammer, 2019), soil fertility (John et al. 2007), allocation of sequestered carbon between above- and below-ground tree components (Malhi et al. 2004) and climatic regimes (Toledo et al. 2011).

In this forest, as in other seasonal tropical forests, rainfall was the primary driver of tree growth (Toledo et al. 2011, Doughty et al. 2014, Wagner et al. 2014, Guan et al. 2015). This was evident in the close correlation between monthly tree growth and monthly rainfall ($P < 0.001$; Appendix S2: Fig. S3), where tree growth rates were slow during the dry season and increased in the wet season (Fig. 1, Appendix S2: Fig. S2). Moreover, relative growth rates were consistently higher in the second (wetter) year of the experiment where rainfall was $\sim$ 30 % more than the drier first year (Fig. 2−4; Appendix S2: Fig. S1).

The role of soil nutrients in regulating tree growth at this site was complex and heterogeneous as revealed in this field experiment. Overall, we did not detect a positive community-wide tree growth response to any of the nutrients added (Appendix S2: Fig. S1), which is consistent with other nutrient manipulation experiments conducted in tropical forests

(Alvarez-Clare et al. 2013, Jiang et al. 2018, Wright et al. 2018, Waring et al. 2019). The lack of a community-wide response can be explained by the diverse nature of the forest and varying nutrient acquisition strategies of (1) the many different species (126 species) that exist at the site (Turner et al., 2018); (2) the different tree sizes and phenological stages and (3) tree position in the canopy (shaded understory to large trees in the overstory; Zemunik et al. 2018). Moreover, tree species at this forest are adapted to the soil's nutrient supply and may accordingly have limited potential to increase stem growth rates in response to nutrient enrichment in the short term (Coley et al. 1985, Wright et al. 2018). Although this could mean a longer time is needed to observe significant community-wide tree growth responses to nutrient additions (Townsend et al. 2008, Vitousek et al. 2010, Wright et al. 2011, Alvarez-Clare et al. 2013), a longer experimental period does not guarantee tree growth responses, possibly due to confounding effects of climate patterns and/or pest susceptibility, as was the case for the nutrient manipulation experiment in Gigante, Panama (Wright et al. 2018), where they did not observe community-scale growth response despite 15 years of chronic nutrient additions.

### *Tree growth response to nutrient additions by different tree diameter classes*

The DBH-dependent response of stem growth to nutrient additions at our site was similar to those observed in other tropical forests (Adamek et al. 2009, Wright et al. 2011, Alvarez-Clare et al. 2013). Large trees, which have low relative growth rates yet accounted for a large portion of the forest's wood biomass productivity (Table 1), did not respond to individual nutrient additions (Fig. 2c). These large trees, however, did exhibit a significant response to the N × P × K interaction effect (Appendix S2: Table S1), which highlights the intrinsic complementary link among the functions of these nutrients in the production of new woody and reproductive tissues (flowers, fruits and seeds) (Rietra et al. 2017).

It was the medium-sized trees (10−30 cm DBH) that responded positively to N addition (Fig.1a and 2a), similar to the study of Adamek et al. (2009). This N limitation became evident approximately 1.25 years after the experiment began (August 2019), after which stem growth rates remained consistently higher for the duration of the experiment (Fig. 1a). We suspect that at the onset of the rainy season (April 2019) there was sufficient nutrient availability for tree growth in all treatments (Appendix S2: Fig. S2) as a result of the rapidly decomposing litter (Kagezi et al. 2016), most of which fell during the dry season (~ 50 % of annual litterfall). However, when nutrient release from decomposition subsided (leaf litter had decomposed after about 5 months, based on ancillary data) and the plant-available N decreased, tree growth limitations in N addition plots became pronounced (Fig. 1a; Appendix S2: Fig. S2). Considering it was still the rainy season, and these medium-sized trees have their leaves in the upper part of the canopy, tree growth would not have been constrained by either moisture or light, but mainly by N availability.

Surprisingly, the diameter increment of saplings and poles (1−10 cm DBH) did not respond to either N, P or K addition as others have observed (Appendix S2: Table S1; Alvarez-Clare et al. 2013, Wright et al. 2011). We did however find that P additions reduced tree mortality among the smallest trees sizes (1−5 cm DBH), a trend also observed by Alvarez-Clare et al. (2013). We suspect an intense competition in the dense understory (Table 1) for resources such as nutrients and light. Considering the relative importance of P for sapling survival (Alvarez-Clare et al. 2013), the growth of these small trees may be potentially co-limited by both P and light availability (Chou et al. 2018), which could explain why the addition of P alone did not increase growth.

***Tree growth response to nutrient additions by different species, leaf habits and functional trait***

The varied growth responses of different species to nutrient additions (Fig. 3) was similar to those reported for other species-rich tropical forests (Cárate-Tandalla et al. 2018, Turner et al. 2018). In this study, only two of the five most abundant tree species exhibited significant stem growth increases or decreases in response to nutrient addition (Fig 3). These two species (*Funtumia elastica and Lasiodiscus mildbraedii)* account for 30 % of the individuals analyzed. Such early responses by a few species are however not uncommon in highly species-diverse tropical forests (characterised by high abundance of a few species and many rare species), where different tree species have varying nutrient requirements, resource acquisition and adaptation strategies (Chou et al. 2018, Detto et al. 2018, Waring et al. 2019).

Nitrogen addition increased tree growth rates by 80 % in *Lasiodiscus mildbraedii*, which suggests that this species was N-limited. All individuals of this species were medium-sized; again, highlighting that even among different species N-limitation is predominantly evident in this tree size class.

Notably, in the drier first year, semi-deciduous tree species increased stem growth by 46 % (Fig. 4c) under +K compared to –K additions. This positive RGR response in the drier year (Fig. 4; Appendix S2: Table S2) indicate that these semi-deciduous tree species, which would normally have lost many leaves under the prolonged dry months, might have been able to delay leaf shedding (R. Manu, *unpublished data*), maintain photosynthesis during this period and enhance stem growth under elevated K availability (Hasanuzzaman et al. 2018, Wu et al. 2020). Furthermore, it is recognized that K, in particular, plays an important role in controlling cell signaling (e.g. activation of reactive oxygen species) and stomatal regulation in plants, particularly under water-deficit conditions, thereby alleviating drought stress (Detto et al. 2018, Hasanuzzaman et al. 2018, Wu et al. 2020).

In contrast to our hypothesis, that P would generally limit tree growth (Walker and Syers 1976, Vitousek et al. 2010) and specifically among N-fixing tree species (Waring et al. 2019), there was no positive response in stem growth as a result of P additions, as evident in the growth rates of any species (Figs. 1−3). This is not particularly surprising, however, considering that extractable P at this forest site was higher or comparable to other tropical forests (Allen et al. 2015, Newbery et al. 2002). The higher extractable P is attributed to the near-neutral soil pH at this site (Appendix S1: Table S1), which means that P is not fixed by hydrous oxides of Fe and Al, and hence sufficient P could be available for plant uptake. Therefore, in accordance with the recent review by Wright (2019), neither the prediction that P-limitation is widespread on old, highly weathered soils (Cárate-Tandalla et al. 2018, Turner et al. 2018, Vitousek et al. 2010, Walker and Syers 1976) nor a generalized P-limitation in N-fixing tree species (Waring et al. 2019) is supported.

### *Nutrient interaction effects on tree growth*

The rationale of nutrient additions in this experiment was to identify which nutrient(s) would cause a positive stem growth response and thereby reveal nutrient (co-)limitations on tree growth. However, while most observed growth responses to nutrient additions were positive, there were a few cases, in which reduced RGR were observed. This was the case in two tree species (*Funtumia elastica and Lasiodiscus mildbraedii)*) under different nutrient additions (Fig. 3). Although, decreased stem growth response to nutrient additions have been reported elsewhere (Báez and Homeier 2018, Braun et al. 2010, Pedas et al. 2011), it is not entirely clear what mechanisms could explain this observation at our site. We suspect that among other things, intense seasonal variability (prolonged dry period in the first year; Figs. 1; 3c−d; Appendix S2: Fig. 2) and nutrient interaction effects may have contributed to these observations. Nutrient

interaction effects may arise when the addition of one nutrient affects the availability, uptake, function and distribution of another nutrient. Specifically, the effect of N × K interactions resulted in decreased relative growth rates in the medium-sized trees (Fig 2b), where gains would normally have been made if N alone had been applied. A similar trend was also observed by Jiang et al. (2018), where tree stem growth rates in N + P plots were lower than those in either N or P addition plots. This could also be caused by nutrient antagonism (Rietra et al. 2017); nutritional imbalances (Boccuzzi et al. 2021) or an adjustment in biomass allocation to other organs other than for stem growth (leaves, roots or reproductive organs) (Wright et al. 2011, Alvarez-Clare et al. 2013).

## CONCLUSIONS

The response of tree growth and wood biomass productivity to nutrient additions offers many important insights into understanding the magnitude and direction of nutrient limitations in this Afrotropical forest with implications on previous widely adopted hypotheses. First, our results strongly suggest that, in addition to rainfall, tree growth in this semi-deciduous forest was dominantly controlled by N availability, occasionally by K availability (climate-dependent), but not P availability. While the concept of multiple nutrient limitation was supported, neither the prediction that P-limitation is widespread on old, highly weathered soils nor P-limitation on N-fixing tree species was supported in this diverse forest ecosystem. Second, the response of tree growth to nutrient additions was dependent on tree sizes, in which neither small nor large trees but medium-sized trees positively responded to N additions suggesting that these medium-sized trees, under conditions of sufficient rainfall and light, were indeed N limited. Third, tree growth response to nutrient addition at our site was species-dependent and not community-wide. Our data suggest that rainfall and leaf habits mediate tree growth responses to nutrient additions and

that seasonal and inter-annual changes in rainfall may regulate the relative importance of nutrients and their requirement by forest plants. Finally, considering that to our knowledge, this study is the first in tropical Africa and the second worldwide to include N, P and K in a factorial large-scale ecosystem nutrient manipulation experiment, additional studies are crucial to advance our understanding of the mechanisms of nutrient control on carbon assimilation.

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**Table 1**. Vegetation characteristics of the experimental site (mean ± SE; n = 32 plots for DBH classes and 27−32 plots for tree species). Percentages in parentheses represent the contribution of individual species to the total aboveground wood biomass productivity of the forest.

| DBH classes; Species | Tree density (trees/ha) | Mean height (m) | Basal area (m$^2$/ha) | AWB † (Mg/ha) | Rel. growth rate †† (cm.cm$^{-1}$.yr$^{-1}$) | Wood biomass Productivity †† (Mg C.ha$^{-1}$.yr$^{-1}$) |
|---|---|---|---|---|---|---|
| DBH classes | | | | | | |
| 1−5 cm | 5938 ± 269 | − | 2.4 ± 0.1 | 6.1 ± 0.3 | 0.042 ± 0.007 | 0.32 ± 0.09 |
| 5−10 cm | 627 ± 30 | − | 2.3 ± 0.1 | 10.4 ± 0.5 | 0.020 ± 0.005 | 0.33 ± 0.04 |
| 10−30 cm | 514 ± 13 | 16.3 ± 0.1 | 11.8 ± 0.3 | 90.8 ± 3.1 | 0.012 ± 0.001 | 1.04 ± 0.05 |
| > 30 cm | 108 ± 5 | 30.0 ± 0.4 | 22.0 ± 1.0 | 287 ± 17 | 0.011 ± 0.000 | 3.35 ± 0.89 |
| Tree species§ | | | | | | |
| *Funtumia elastica* | 150 ± 13 | 17.6 ± 0.2 | 4.2 ± 0.4 | 29.2 ± 3.1 | 0.011 ± 0.001 | 0.41 ± 0.10 (9.3%) |
| *Celtis mildbraedii* | 92 ± 10 | 15.2 ± 0.4 | 2.7 ± 0.4 | 29.6 ± 5.2 | 0.007 ± 0.003 | 0.12 ± 0.07 (2.8%) |
| *Rinorea ardisiaeflora* | 42 ± 8 | 13.2 ± 0.3 | 0.9 ± 0.3 | 8.8 ± 4.4 | 0.017 | 0.06 (1.4%) |
| *Cynometra alexandri* | 39 ± 4 | 21.3 ± 1.2 | 4.2 ± 0.7 | 70 ± 12.9 | 0.021 ± 0.003 | 0.27 ± 0.16 (6.1%) |
| *Celtis zenkeri* | 39 ± 4 | 18.0 ± 0.6 | 1.4 ± 0.2 | 14.1 ± 2.1 | 0.008 ± 0.002 | 0.14 ± 0.06 (3.3%) |
| *Celtis durandii* | 37 ± 4 | 28.4 ± 0.6 | 4.3 ± 0.4 | 51.0 ± 5.5 | 0.004 ± 0.002 | 0.36 ± 0.13 (8.1%) |
| *Lasiodiscus mildbraedii* | 36 ± 6 | 14.5 ± 0.5 | 0.8 ± 0.2 | 8.1 ± 1.9 | 0.009 ± 0.004 | 0.06 ± 0.04 (1.5%) |
| *Trichilia rubescens* | 28 ± 5 | 15.5 ± 0.5 | 0.7 ± 0.1 | 5.0 ± 1.2 | 0.026 ± 0.015 | 0.04 ± 0.01 (0.9%) |
| *Khaya anthoteca* | 20 ± 2 | 22.8 ± 1.4 | 2.4 ± 0.4 | 28.0 ± 2.5 | 0.021 ± 0.004 | 0.86 ± 0.31 (19.6%) |
| *Trichilia prieuriana* | 15 ± 2 | 19.1 ± 0.5 | 0.6 ± 0.1 | 5.5 ± 1.1 | 0.033 ± 0.010 | 0.10 ± 0.04 (2.4%) |

†AWB: aboveground woody biomass, measured in all plots in April 2018 before nutrient addition.

††Measured from the control plots (n = 4) during the 2018−2020 measurement period.

§Tree species listed here includes only trees ≥ 10 cm DBH and are the most dominant species in the experimental site (Appendix S1: Table S3).

**List of Figures:**

**Figure 1.** Relative growth rate (RGR) responses of trees 10–30 cm diameter at breast height (82 % of 656 trees on which dendrometer bands were installed) to nitrogen (N), phosphorus (P) and potassium (K) additions. Presented are pooled +N (N, N + P, N + K and N + P + K) and −N (control, K, P and P + K) in panel (a), +P (P, N + P, P + K, and N + P + K) and −P (control, N, K and N + K) in panel (b), +K (K, P + K, N + K and N + P + K) and −K (control, N, P and N + P) in panel (c), and monthly precipitation (d). Error bars are standard errors of the mean for each treatment aggregation, n = 16 plots. Statistical analysis was based on the eight treatments in the full factorial NPK design where the main effect of N additions was found in the second year (linear mixed-effects model; $F_{1, 24} = 6.14$, $P = 0.021$). Dotted vertical lines correspond to dates of nutrient additions; grey shades represent dry months (< 100 mm mo$^{-1}$ precipitation, shown by the horizontal dotted line in panel d).

**Figure 2**. Relative growth rate (RGR; mean ± SE) responses of different tree size classes to nutrient additions for trees ≥ 10 cm diameter at breast height (DBH). Census intervals for 2018−2019 and 2019−2020 are reported as first and second years of growth, respectively. Panel (a) presents RGR of trees 10−30 cm DBH, where we found a positive RGR response to N additions in the second year ($F_{1, 24} = 4.76$, $P = 0.039$; n = 4 plots with full factorial ANOVA). Panel (b) illustrates a negative N × K interaction (for trees 10−30 cm DBH in the second year) with RGR enhanced in the +N treatment but not in the +NK treatment ($F_{1, 24} = 4.71$, $P = 0.040$; n = 8 plots; full factorial ANOVA). In panel (c), a positive response to N × P × K interaction for trees ≥ 30 cm DBH was found in the second year ($F_{1, 24} = 5.56$, $P = 0.027$; n = 4 plots with full factorial ANOVA).

**Figure 3.** Relative growth rate (RGR; mean ± SE) response of different tree species (a−e; representing 57 % of tree abundance and all other species combined (f)) to nutrient additions, for trees ≥ 10 cm diameter at breast height (DBH). Census intervals for 2018−2019 and 2019−2020 are reported as first and second years of growth. All panels present the eight treatments of the full factorial NPK design. Bars represent the RGR of at least three replicate plots per treatment. For *Funtumia elastica* in the second year, the N × P interaction was significantly negative with greater growth in the +N, +P, +NK and +PK treatments and lower growth in the +NP and +NPK treatments (panel a; $F_{1, 24}$ = 5.45, $P$ = 0.028). For *Lasiodiscus mildbraedii* (panel e), N addition increased RGR significantly in the second year ($F_{1, 20}$ = 8.06, $P$ = 0.010) and K addition reduced RGR in both years ($F_{1, 20}$ = 5.68, 13.03; $P$ = 0.027, 0.002); however, the P × K interaction was also significant and positive in both years with greater RGR in the +PK and +NPK treatments ($F_{1, 20}$ = 10.12, 5.06; $P$ = 0.005, 0.036). For all other species, the P × K interaction was significant and positive in the first year, with greater RGR in the +PK and +NPK treatments and lower RGR in the +P, +K, +NP and +NK treatments (panel f; $F_{1, 24}$ = 5.12, $P$ = 0.033).

**Figure 4.** Relative growth rate (RGR; mean ± SE) responses of semi-deciduous trees (≥ 10 cm diameter at breast height) to nutrient additions. Census intervals for 2018−2019 and 2019−2020 are reported as first and second years of growth. Panel (a) presents the eight treatments of the full factorial NPK design. To the right are the four treatments with K additions, illustrating the positive effect of K additions on RGR in the first year ($F_{1, 24}$ = 7.48, $P$ = 0.012). Panel (b) presents a significant, positive P × K interaction effect in the first year ($F_{1, 24}$ = 4.80, $P$ = 0.042). Sample size is eight plots for each bar: Control (control, +P), P (+P, +NP), K (K, +NK) and PK (+PK, +NPK)). Panel (c) presents the significant effect of K additions for the first year. Treatments without added

K (control, +N, +P, +NP) are pooled (denoted −K on the horizontal axis) with the appropriate

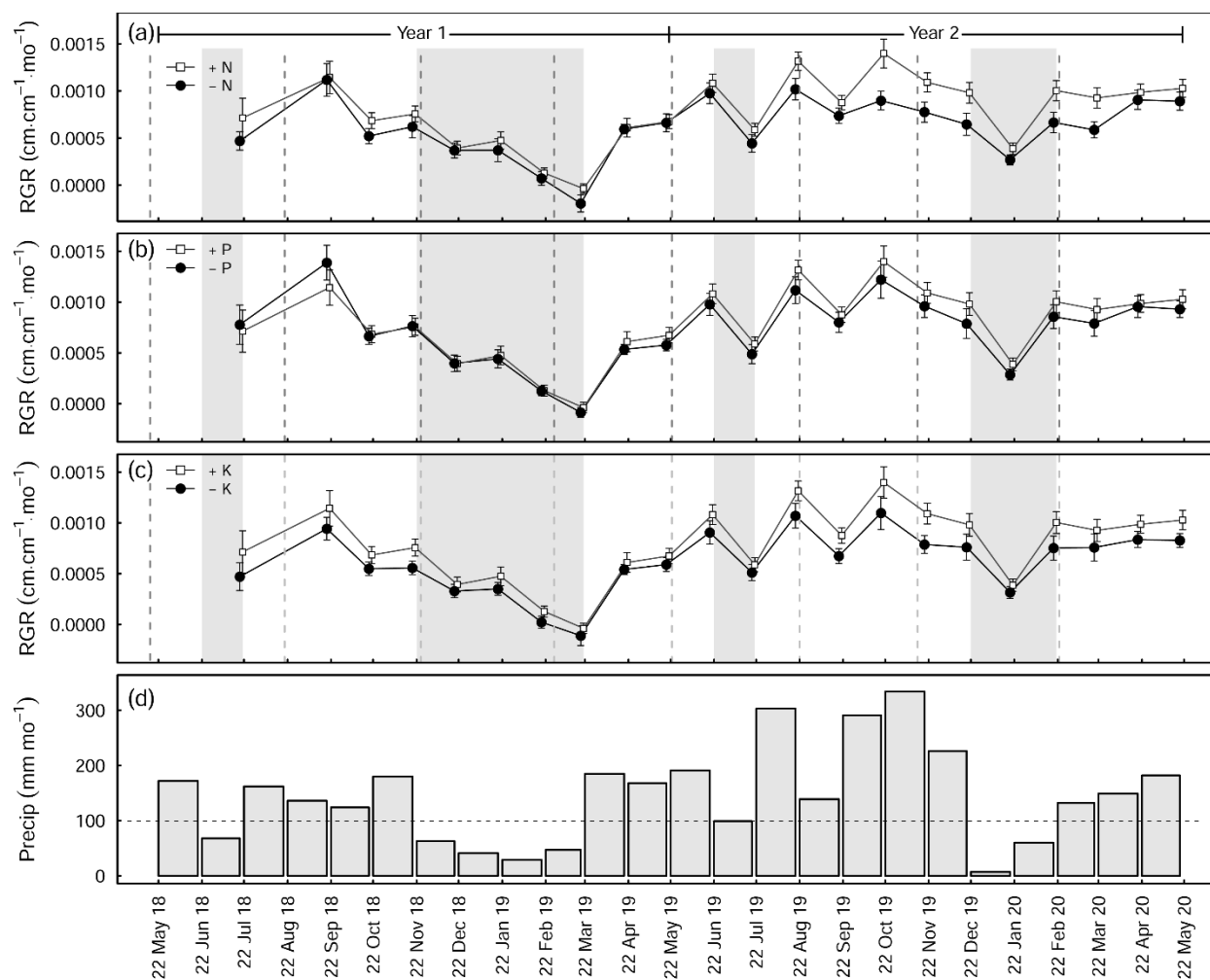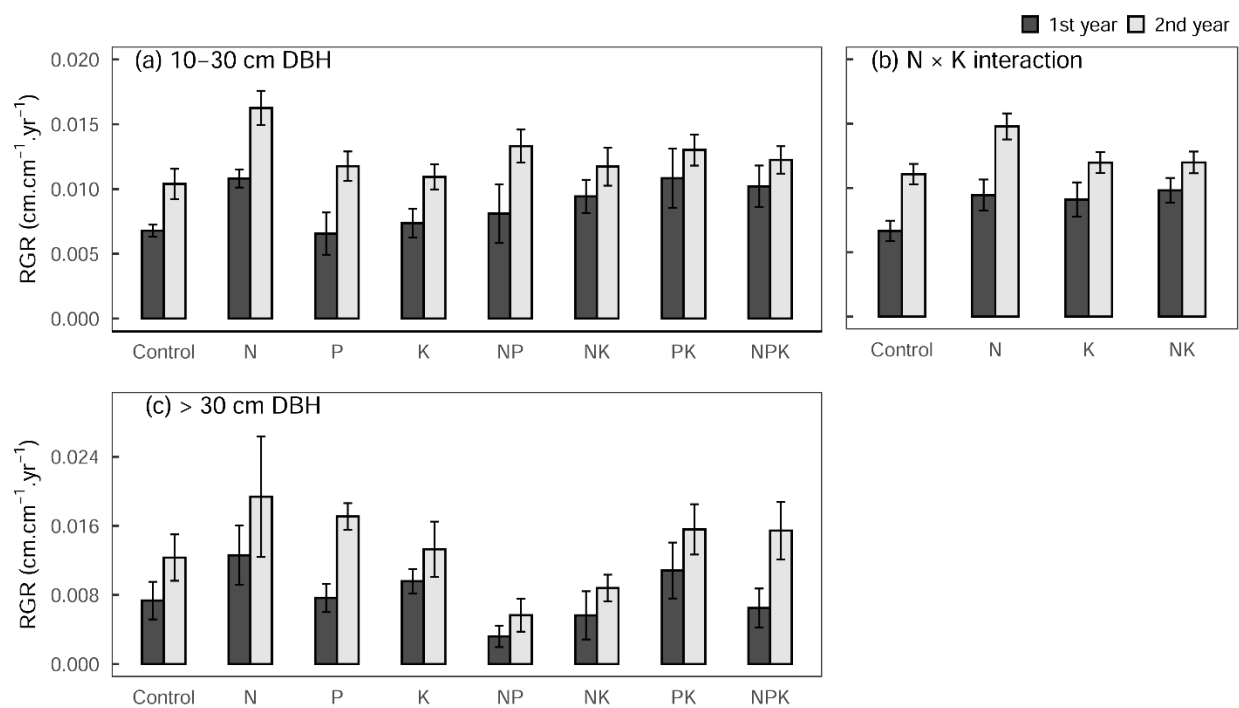treatments with K (+K, +NK, +PK, +NPK); thus, the sample size is 16 plots for each bar.
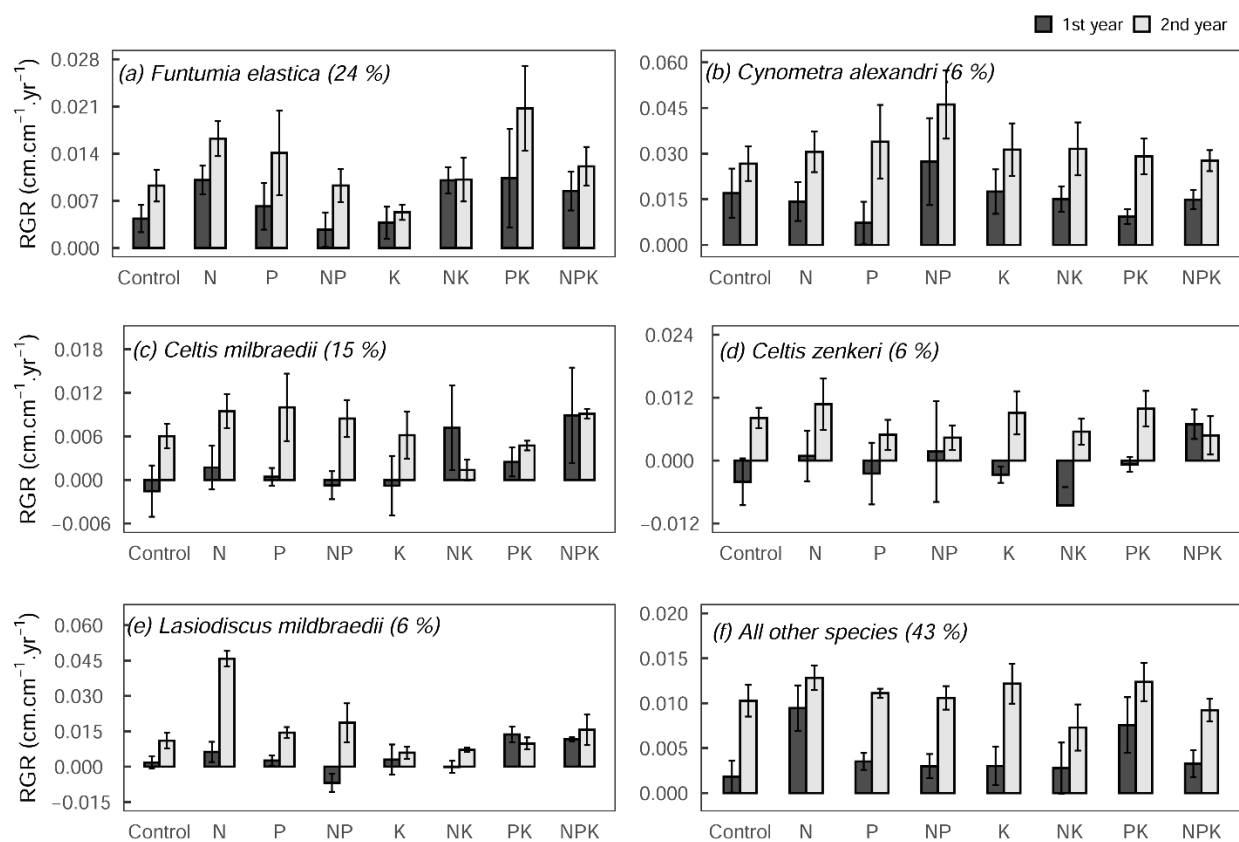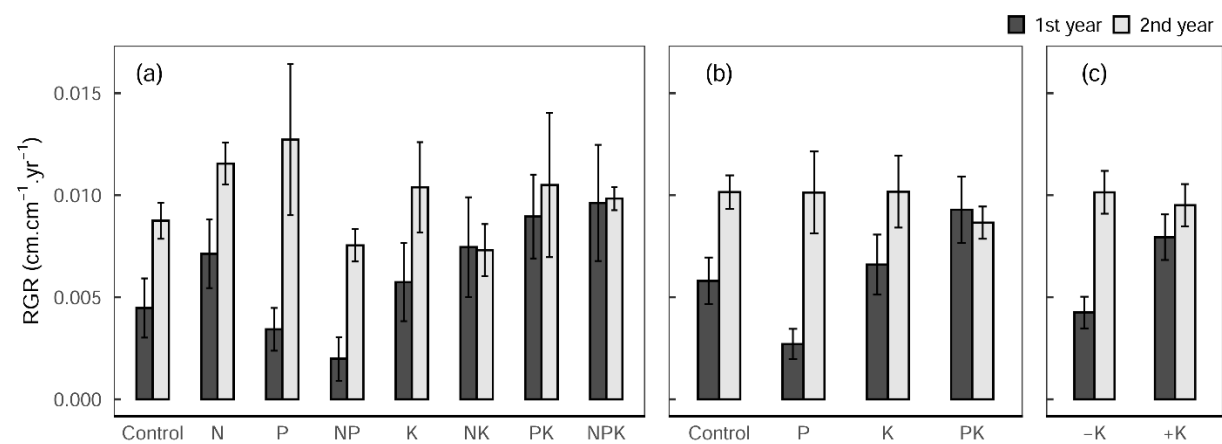
**Figure 1.**

(a) 10–30 cm DBH

(b) N × K interaction

(c) > 30 cm DBH

Figure 3.

**Figure 4.**