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Article

Response of tropical forest productivity to seasonal drought mediated by potassium and phosphorus availability

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Tropical forest productivity is increasingly reported to be nutrient limited, which may affect its response to seasonal droughts. Yet experimental evidence on nutrient limitation from Afrotropical forests remains rare. We conducted an ecosystem-scale, full factorial nitrogen (N)–phosphorus (P)–potassium (K) addition experiment in a moist forest in Uganda to investigate nutrient controls on fine litter production and foliar chemistry. The eight factorial treatments were replicated four times in 32 plots of 40 × 40 m each. During the three-year nutrient additions, we found K and P limitations on leaf litter production, exhibiting strong links to ecosystem responses to seasonal drought. Specifically, leaf litterfall consistently decreased in dry seasons with K additions, whereas P additions caused a reduction only during prolonged drought in the first year. Leaf litterfall was not significantly affected by N additions. Furthermore, K additions delayed the timing of leaf litterfall peak, underscoring the crucial role of K in regulating stomatal aperture and signalling during water-stress conditions and suggesting a prolonged leaf lifespan. Foliar N increased with N and P additions whereas K was the most resorbed nutrient. We conclude that the productivity and resilience of tropical forests, particularly under drier conditions, may depend on terrestrial K and P availability.

Tropical forests account for one-third of the world's biomass production and approximately half of the global forest carbon (C) sink[1]. However, the persistence of this C sink remains uncertain for reasons not yet fully reconciled, with increasing evidence suggesting a decline in C capture by tropical forests[2,3]. This uncertainty is partly caused by frequent changes in inter- and intra-annual hydroclimatic regimes[4], drought events[5,6] and increased seasonality, characterized by shorter wet seasons and longer, more intense dry seasons[4,7–9]. During dry seasons, the photosynthetic capacity of plants may stall or even decrease while leaf litterfall increases[10], primarily due to soil moisture deficits. Thus, rainfall remains a key driver of tropical ecosystem functioning[4] and is largely coupled with nutrient cycling and limitations in these ecosystems[11]. Moreover, nutrient limitations by N and P play an important regulatory role in plant growth, therein affecting ecosystem biomass allocation and specifically net primary productivity[12,13]. In line with the substrate-age hypothesis[14], productivity in central Amazonian lowland forests growing on highly weathered soils was reported to be P limited[15] due to strong substrate weathering and leaching losses

linked to high rainfalls[14]. Elsewhere, plant uptake of P and K diminished under drought conditions in a Mediterranean forest, leading to reduced biomass growth[16].

The physiological responses of tropical trees to seasonal drought (rainfall deficit over prolonged period, which in this study refers to the major dry seasons of ≤100 mm rainfall per month)[17,18], are confounded by soil nutrient availability, which influence their mortality risk[19], C assimilation[4,20] and causes shifts in C allocations[21]. Phosphorus is recognized for its drought-mitigating effects on plant growth through its role in anti-oxidative enzyme activities, osmolyte accumulation and lipid peroxidation levels[22,23]. Phosphorus and K are particularly recognized for improving water-use efficiency and drought resistance of various plant communities[16,22,24], and their limitation has been shown to induce nutritional stress in temperate forest trees during prolonged drought periods[25]. However, evidence of possible limitation of plant function by K is notably rare in tropical forests[12] and mostly overlooked in Earth system and global change models[26]. Despite predictions of drier future climates[9,27,28] and the higher vulnerability of drier tropical forests to climate change[29], the link between drought responses (that is, drought-induced physiological and biochemical changes) and nutrient limitation remains elusive, particularly in species-rich natural tropical ecosystems[30,31]. Thus, understanding processes that can potentially alter tropical forest C storage is crucial for predicting the impacts of climate change on these ecosystems.

The magnitude and identity of nutrient limitation vary widely across the tropics[12]. Different ecological processes (for example, photosynthesis, decomposition, growth, litterfall)[32], tree sizes, leaf habits[19] and compartments (for example, above- vs belowground allocations)[33] may differ in response to elevated nutrient input and the nutrient(s) that limit them[19,33]. This can warrant simultaneous multiple nutrients (co-)limitation[32,33] or shifts in nutrient limitations[34] along the vast and heterogeneous tropical biome. Understanding such shifts in nutrient limitations has become increasingly important as global change effects on tropical ecosystems intensify[6]. The current most-limiting nutrients to Afrotropical forest productivity and how they may change in the future remain open questions. Whereas P (co-)limitation is common in neotropical forests[12,15,35], experimental evidence of P-limited productivity in Afrotropical forests is yet to be reported. A recent meta-analysis involving 48 nutrient manipulation experiments (NME) in tropical forests[12] included neotropics (32), South-East Asia (8) and Hawaii (8), but not Afrotropical forests. This imposes a crucial biogeographic knowledge gap to understanding mechanisms of plant resilience and ecosystem responses to global change. Thus, the identity of limiting nutrients, mediating physical stressors and how nutrients control productivity in Afrotropical forests remain a notable knowledge gap. Furthermore, foliar nutrient ratios as 'rapid assessment tools[36]' vary among species over short timescales and have not always correctly predicted nutrient limitation as diagnosed by direct NMEs in lowland tropical forests[37]. Whether these shifts in foliar nutrient ratios represent changes in nutrient limitations is yet untested in Afrotropical forests. On a local–regional scale, these variations may represent environmental change effects such as drought, nutrient deposition or elevated CO_2, adaptation strategies and species plasticity[38].

In 2018, we established an ecosystem-scale full factorial (N–P–K) NME (Supplementary Fig. 1) in a moist semi-deciduous Afrotropical forest in Uganda. After two years, tree stem growth response to P additions was not significant, N additions increased stem growth of medium-sized trees (10 cm-30 cm diameter at breast height (DBH)) in the second year, whereas K additions enhanced stem growth (46%) of semi-deciduous trees, particularly following a strong and prolonged seasonal drought during the first year of the experiment[19]. The lack of stem growth response to P addition was attributed to the near-neutral soil pH of the site (Extended Data Table 1), for which P immobilization by Al and Fe hydroxides and consequent limitation are unlikely. Here we use the same experiment to investigate which (if any) and how

nutrient availability control fine litter production and foliar chemistry. Additionally, nutrient resorption efficiency (RE) was determined. We hypothesized that K and not N or P limitation affected the drought response of this Afrotropical forest, which has vital implications for ecosystem CO_2 assimilation, resilience and response to drier future climate.

Results

Leaf litterfall, which constituted 66% of fine litter production and ~50% of aboveground net primary productivity, was significantly reduced by K ($F_{1,24} = 5.45$, $P = 0.028$; Fig. 1c) and P additions ($F_{1,24} = 7.43$, $P = 0.012$; Fig. 1b), although total fine litter production was unaffected by nutrient additions. Whereas K addition effect on leaf litterfall was consistently evident, specifically in the dry seasons, throughout the experiment (K × season interaction; $F_{1,48} = 4.49$, $P = 0.039$; Fig. 1f), P addition effect was evident only in the first year (P × year interaction; $F_{2,48} = 5.78$, $P = 0.006$; Fig. 1b,e). Additionally, the timing of leaf litterfall peak experienced a four-week delay in the dry seasons with K addition relative to non-K treatments in the first year (Fig. 2c). During this first year, we observed a more intense and prolonged dry season with ~30% less rainfall than in the subsequent year (Fig. 2d and Extended Data Fig. 1). Reproductive litterfall (flowers and fruits; 10% of total litterfall), twigs (19%) and residue (barks, epiphytes and others; 5%) did not show treatment effect (Extended Data Tables 2 and 3). Leaf litterfall exhibited seasonality, reflective of the rainfall pattern (Fig. 2). Within the control plots, the bi-weekly leaf litterfall in the wet season (38 ± 2 g m^{-2}) approximately doubled in the dry season (December–February; 73 ± 7 g m^{-2}) when leaf senescence and abscission peaked.

Leaf litter chemistry was significantly affected by nutrient additions ~1.5 years into the experiment. N × P × K interaction effect increased leaf litter C content and C:N ratio ($F_{1,24} = 5.01$, 5.93 and $P = 0.034$, 0.023, respectively) and decreased Ca content ($F_{1,24} = 6.91$, $P = 0.015$) (Extended Data Tables 4 and 5). Leaf litter $\delta^{15}N$ increased by 10% with K addition ($F_{1,24} = 5.77$, $P = 0.024$; Extended Data Table 5). Leaf litter N, P, K contents and N:P ratio showed no treatment effect.

The response to nutrient addition of sunlit leaf chemistry, weighted by the importance value index of the sampled dominant tree species (Fig. 3), showed increased foliar N by 5% with N addition ($F_{1,24} = 9.26$, $P = 0.006$; Fig. 3a) and by 4% with P addition ($F_{1,24} = 5.86$, $P = 0.023$; Fig. 3b). Foliar $\delta^{15}N$ also increased with P addition (6%; $F_{1,24} = 8.05$, $P = 0.009$; Fig. 3b). For species-specific responses, N addition increased foliar N by 7% and foliar C by 5% in *Celtis mildbraedii* ($F_{1,15} = 5.53$, 6.05 and $P = 0.033$, 0.027, respectively) but decreased S content in *Funtumia elastica* ($F_{1,24} = 4.69$, $P = 0.040$) (Extended Data Tables 6 and 7). Phosphorus addition increased foliar P by 33%, $\delta^{15}N$ by 10% ($F_{1,20} = 7.0$, 9.2 and $P = 0.015$, 0.006, respectively) and decreased N:P ratio by 16% in *Celtis durandii* (Extended Data Table 7). The interaction effects of N × P enhanced foliar N in *Cynometra alexandri* (5%; $F_{1,22} = 5.34$, $P = 0.031$) and decreased foliar S in *Celtis mildbraedii* (3%; $F_{1,15} = 6.06$, $P = 0.026$). Potassium addition decreased foliar N by 5% ($F_{1,24} = 9.79$, $P = 0.005$), increased foliar Ca by 24% ($F_{1,24} = 9.15$, $P = 0.006$) and increased C:N ratio by 4% ($F_{1,24} = 4.91$, $P = 0.036$) in *Funtumia elastica* (Extended Data Table 7). Foliar K was unaffected by K addition and represented the third most abundant foliar nutrient (following N and Ca) (Extended Data Table 6). Across treatments, leaf nutrient RE was highest for K (23–43%), moderate for P (13–30%), low for N (6–25%) and negative for Ca (0–53%) (Extended Data Table 8).

Discussion

Nutrient-limited leaf litterfall linked to seasonal drought

Nutrient limitation is theorized to be evident when the additions of limiting nutrients lead to an increased response in the ecosystem process considered[13] and yet K addition in our experiment led to reduced leaf litterfall. The reduced leaf litterfall became evident approximately eight months after initial fertilization, during the strong and prolonged dry
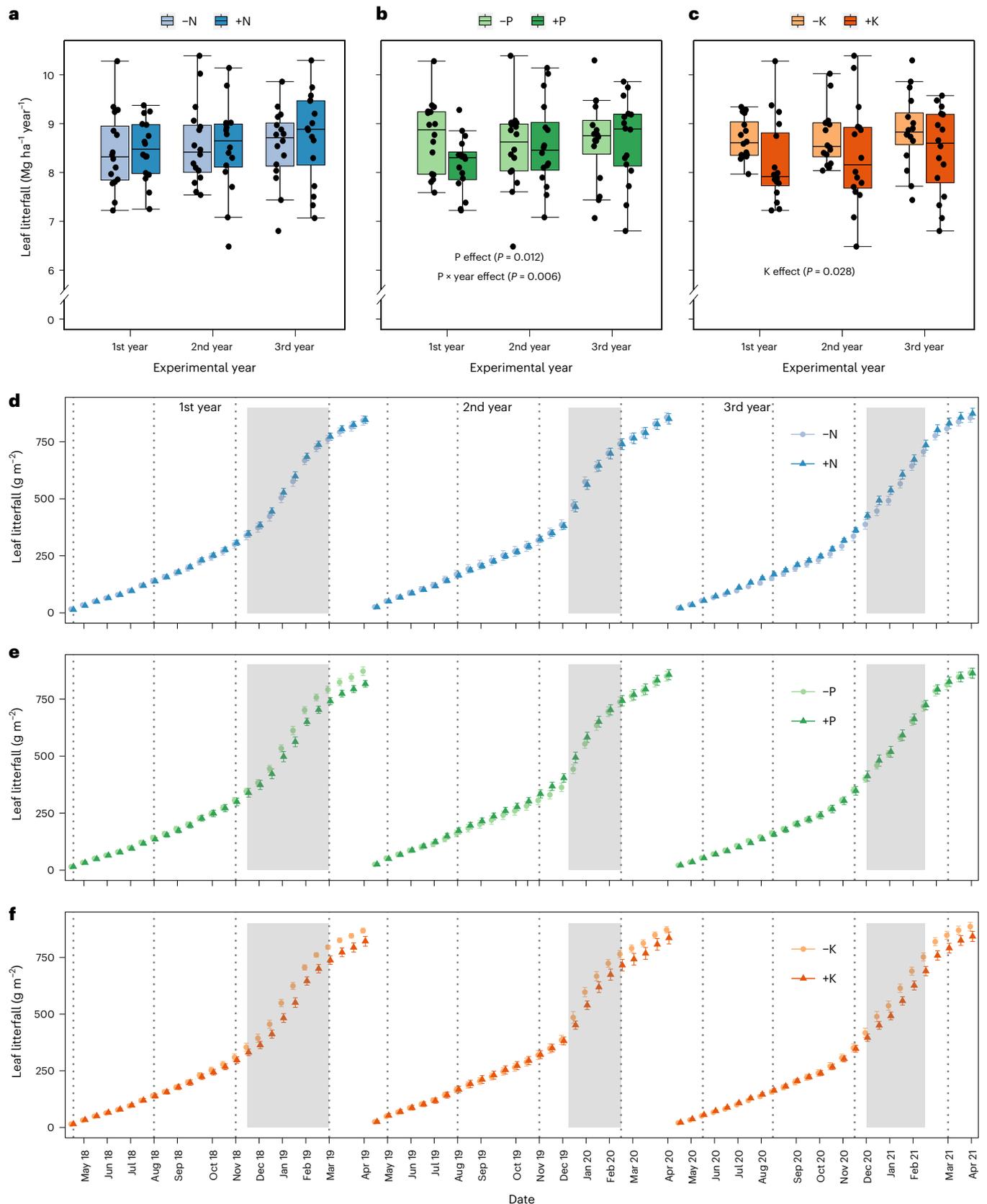
Fig. 1 | Nutrient addition effects on leaf litterfall in Budongo Forest Reserve, Uganda. a–f, Box plots (25th quartile, median and 75th quartile) and whiskers (1.5 × interquartile range) of annual leaf litter production (**a–c**; $n = 16$ plots) and cumulative leaf litterfall (**d–f**, mean ± standard error of the mean (SEM); $n = 16$ plots) measured bi-weekly from May 2018 to April 2021, pooled for plots with or without nitrogen (+N vs −N; **a,d**), phosphorus (+P vs −P; **b,e**) and potassium (+K vs −K; **c,f**). **b–c** and **e–f** show the reduction effects of P addition in the first year and of K addition in the three-year experimental period on leaf litterfall. The y-axis breaks in panels **a–c** represent the omitted range (1–5) of a continuous scale to improve the visualization of data points. Statistical analysis was based on a full factorial N–P–K experiment. Treatments +N (N, NP, NK, NPK) and −N (control, P, K, PK) are pooled in **a** and **d**. **b,c,e,f** follow a similar pooled approach. Grey shades represent the dry season (≤100 mm rainfall per month) whereas the vertical dashed lines indicate dates of fertilization.
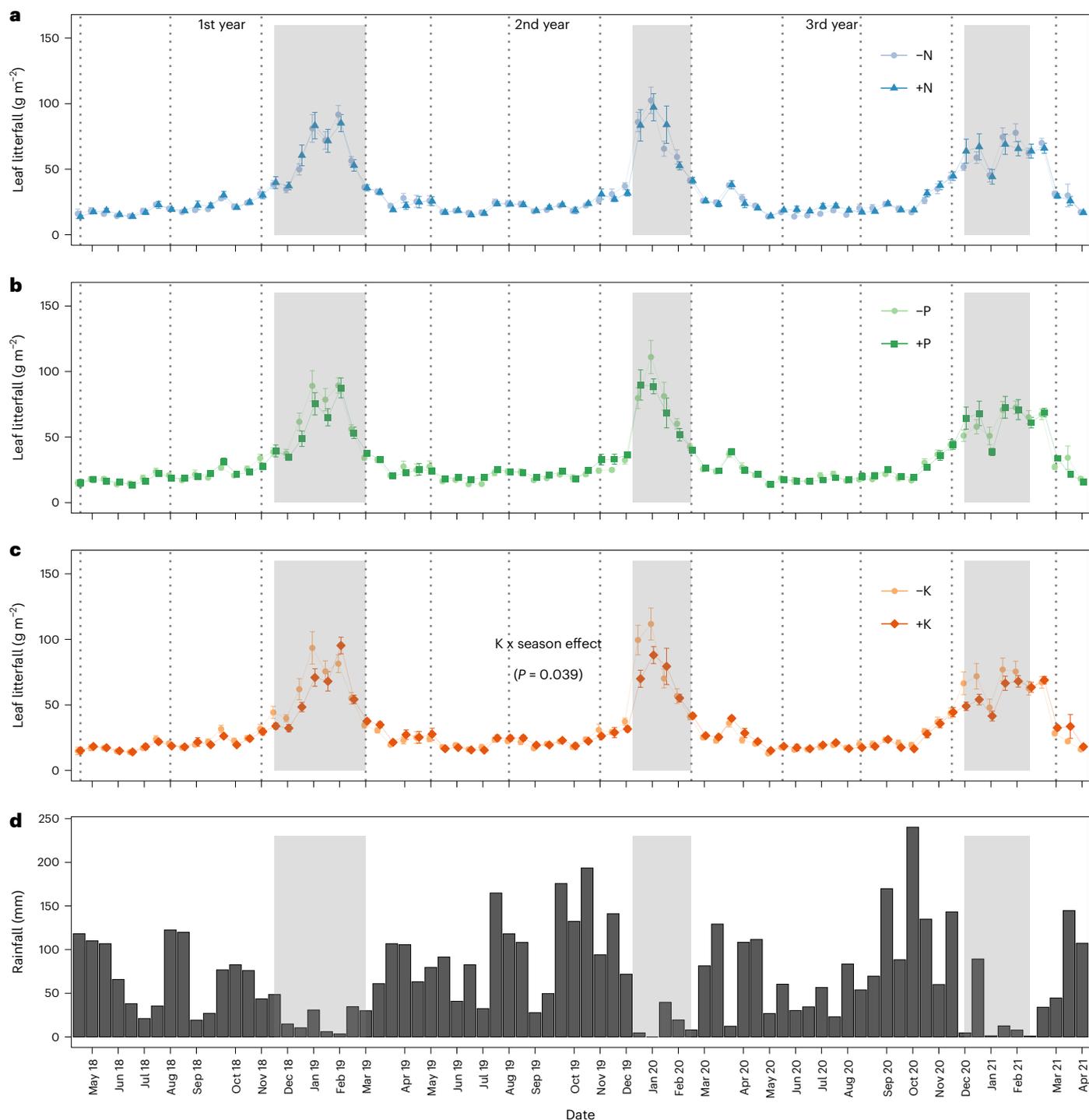
Fig. 2 | Temporal response of leaf litterfall to nutrient additions in Budongo Forest Reserve, Uganda. a–**c**, Bi-weekly leaf litter production (mean ± SEM, n = 16 plots) measured from May 2018 to April 2021, pooled for plots with or without nitrogen (+N vs −N; **a**), phosphorus (+P vs −P; **b**) and potassium (+K vs −K; **c**). **c**, The four-week delayed peak of leaf litterfall in +K treatments during the first year's prolonged dry season and lower leaf litterfall during the dry seasons of the three years compared to −K treatments (K × season interactions; $F_{1,48}$ = 4.49, P = 0.039). **d**, Bi-weekly rainfall corresponding to litter collection dates. Grey shades represent the dry season (≤100 mm rainfall per month), and vertical dashed lines indicate dates of fertilization.

period of the first year and consistently recurred during dry periods of subsequent years (Fig. 1f and Extended Data Fig. 1). Furthermore, the delayed peaks of leaf litterfall associated with K addition during seasonal droughts (Fig. 2c,d) suggests that K availability affects the timing and peak of leaf litterfall by delaying leaf shedding and thereby enhancing leaf lifespan. Our results highlight the critical role of K in plant leaves through signalling, stomatal conductance and drought

tolerance[24,39] and suggest that K limits leaf litter production in this ecosystem (Fig. 1c,f). Trees will shed leaves upon the activation of reactive oxygen species when water-deficit conditions occur. However, increased availability of K mitigates the early formation of reactive oxygen species in leaves[24,39], which, in turn, delays senescence and abscission, thereby prolonging the leaves' lifespan. Moreover, K is recognized for regulating the stomatal openings of leaf guard cells under
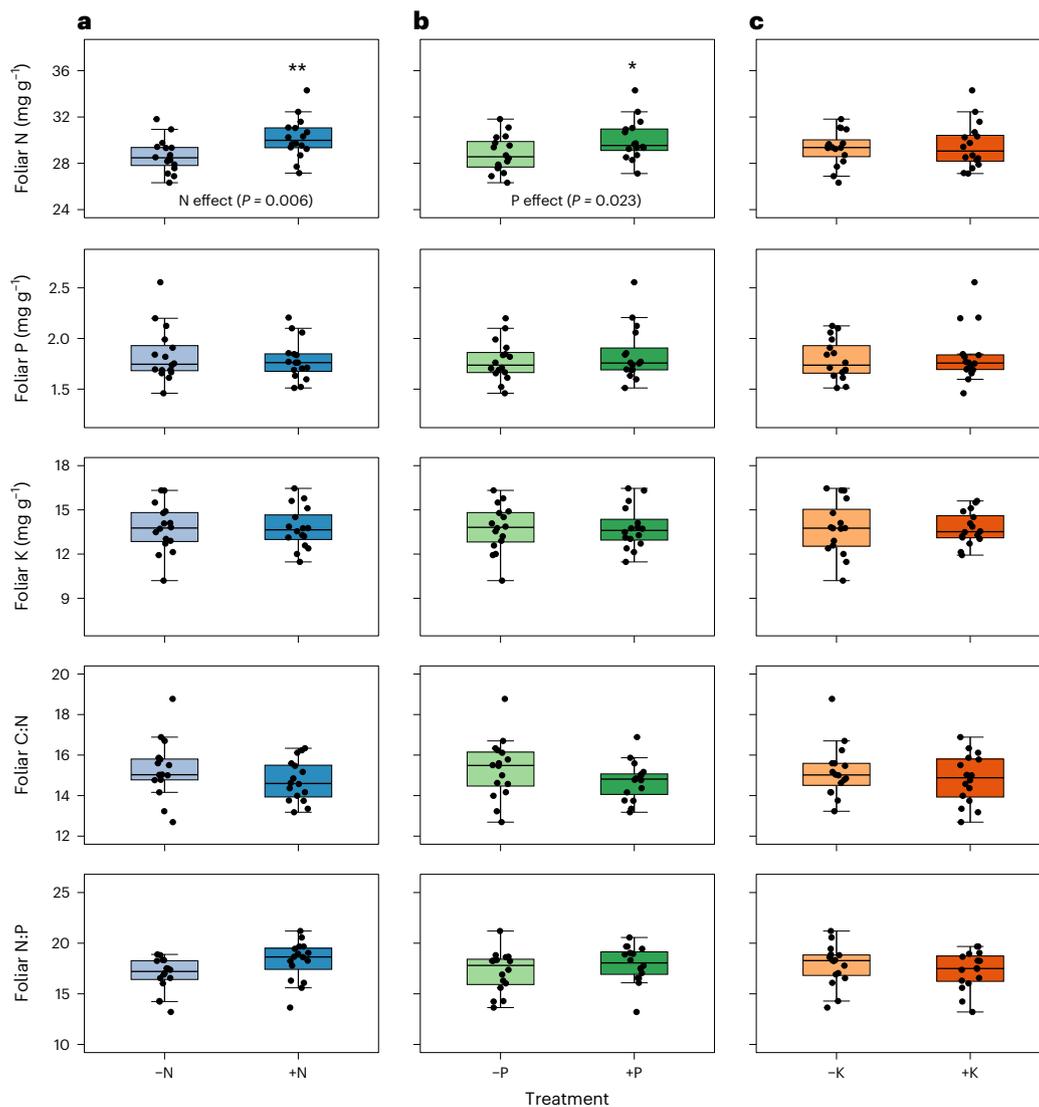
Fig. 3 | Nutrient addition effects on sunlit foliar chemistry, weighted by the importance value index of the sampled five dominant tree species in each replicate plot, at the nutrient addition experiment in Budongo Forest Reserve, Uganda. a–c, Box plots (25th quartile, median and 75th quartile) and whiskers (1.5 × interquartile range) of foliar chemistry (n = 16 plots) in treatments with or without nitrogen (+N vs −N), phosphorus (+P vs −P) and potassium (+K vs −K) after ~1.5 years of the nutrient addition experiment. Asterisks indicate the significant positive effects of N addition (**a**; $F_{1,24}$ = 9.26, P = 0.006**) and P addition (**b**; $F_{1,24}$ = 5.86, P = 0.023*) on foliar N content.

water-deficit conditions and thus maintaining stomatal conductance and photosynthesis[24,39]. These results support the increased stomatal conductance associated with P and K additions[40] and substantiate our earlier observation of increased tree stem growth with increased K availability during the drier first year of this experiment[19]. The observed K limitation in our site may be due to weathering over a long period[41], the soil's sandy texture (Extended Data Table 1) and the high mobility of rock-derived and easily dissolvable K^+ ions, which altogether may have potentially facilitated K^+ leaching.

Phosphorus addition resulted in decreased leaf litter production specifically during the intense and prolonged dry season in the first year (Fig. 1b,e and Extended Data Fig. 1). This response was surprising and in contrast to our hypothesis, considering that P limitation was originally perceived to be unlikely in this ecosystem. At near-neutral soil pH at our site (Extended Data Table 1), P will not be fixed by Al and Fe hydroxides, making P available for plant use[11]. Furthermore, total soil P at our site (Extended Data Table 1) was relatively higher than in most P-limited central Amazonia soils[15] and similar to sites in the Congo Basin with sandy texture, where plant function was not P limited[42,43]. Besides,

the addition of P increased soil (resin-extracted) P availability by ~80% compared with non-P treatment (R.M. and O.v.S., unpublished observations), suggesting that the bioavailability of P adequately meet plant demand. In our experiment, P additions did not increase stem growth of over 15,000 trees, indicating that P was not limiting ecosystem productivity[19]. We therefore attribute the observed reduction in leaf litterfall with P addition during the first year's prolonged dry season (Fig. 1b,e and Extended Data Fig. 1) to drought stress. Drought can decrease soil P availability, which, in turn, reduces P uptake by plants[16]. Addition of P may have counteracted this drought effect in the less-intense dry seasons of the succeeding two years (Fig. 1e). Phosphorus mitigates water-deficit conditions through its role in anti-oxidative enzyme activities, osmolyte accumulation and lipid peroxidation levels[22,23]. Additionally, P addition also significantly enhances the leaf relative water content (a common plant dehydration index) and net photosynthetic rate of drought-stressed seedlings[22,23]. This may be due to the improved ability of root water uptake or moisture conservation in the plant tissues[44], reducing moisture stress-induced leaf litterfall (Fig. 1e). This suggests that rainfall seasonality mediates the relative

importance of soil nutrients and their limitation to plant function and ecosystem processes.

The lack of treatment effects on total fine litter production may be due to the relatively short duration of this experiment (2018–2021) and the differential responses from the diverse tree species[19] or litter categories[32] to nutrient additions, which may have masked this ecosystem-level response. Indeed, in Venezuelan montane forest, it took four years to detect increased response to combined N + P fertilization, despite higher rates of nutrient additions (225 kg N ha^{-1} yr^{-1} and 75 kg P ha^{-1} yr^{-1}) (ref. [45]). Conversely, in lowland central Amazonian rainforest, litterfall increased after two years of P addition, but this was due to rapid leaf turnover and 10–20% decrease in leaf lifespan[15].

Foliar nutrient responses to nutrient additions

Foliar and leaf litter element concentrations (Fig. 3 and Extended Data Tables 4 and 6) were higher compared to those reported in Panama[46], Costa Rica and the Amazon forests[37]. Accordingly, the nutrient RE was lower (< 30%) in our site than in other tropical forests[47], supporting the leaf-economics theory that less nutrients are resorbed at high leaf nutrient concentrations and vice versa[48]. This is because nutrient resorption represents a nutrient conservation strategy, as soil nutrients can become vulnerable to leaching losses[14] or fixed in unavailable forms, and hence limit plant functions and ecosystem productivity. Although the resorptions of N and P have been widely studied[47], a dearth of data on important cations (for example, resorptions of K and Ca) persists. Consistent with the K-limited leaf litterfall and earlier global assessment[48], K was the most resorbed nutrient at our site underscoring its limitation to ecosystem function. Conversely, the negative Ca resorption suggests a down-regulation by plants due to the Ca-rich soil at our site (Extended Data Table 1). This result was consistent with other studies that indicate that Ca, as a structural element in plant cell walls, is usually less resorbed than other nutrients during senescence[48,49] due to its immobility within the plant[50]. The responses of foliar nutrients to nutrient additions were species-specific and considerably variable (Extended Data Table 6), posing a challenge to drawing meaningful conclusion on nutrient limitation status of the overall ecosystem, as espoused by others[36]. Generally, foliar N of pooled dominant species increased with N and P additions, similar to observations in French Guiana[35]. Nitrogen addition increased foliar N in *Celtis mildbraedii* whereas P addition increased foliar P in *Celtis durandii*, consistent with other studies[51,52], except for absence of K addition effect on foliar K. These highlight that leaf growth, biochemical traits and senescence of different species may be limited by different nutrients. Considering that our foliar samples were collected at the height of the rainy season (October), the lack of increased foliar K in response to K addition may be due to K$^+$ leaching from leaf apoplast[53] or its adaptive redistribution to other plant parts as K$^+$ ions are highly mobile in plant leaves[54].

The enriched foliar δ^{15}N associated with P and K additions may be indicative of a leaky soil N cycle in which light isotopic N were lost from the ecosystem during nitrification and denitrification in the soil, leaving behind isotopically enriched N for plant uptake[55]. Ecosystem C responses as expressed in leaf litter chemistry was mainly driven by N × P × K interaction effects, highlighting the innate complementary functions of these nutrients[32] in plant metabolism, physiology and biochemical adjustments to edaphic changes.

Implications of nutrient-limited drought responses

Increased duration and severity of droughts are expected in most parts of the world as a consequence of global climate change[9,27,28], with potentially adverse effects on ecosystem productivity. Current trends of tropical deforestation have been shown to cause large reductions in precipitation[9], shifts hydroclimatic regimes[7] and predicted to reduce precipitation in the Congo catchment by 8–10% in 2100[9]. Consistent with other studies[56], our results suggest that shifts in the intensity and intra-annual distribution of rainfall have profound consequences on

the relative demands or limitations of nutrients to plants in this ecosystem (Figs. 1 and 2). The prevailing concept of nutrient limitation is the assumption that mainly the nutrients added/tested and no other factors are limiting productivity[32,57,58]. We argue that under water-deficit conditions, the direction of productivity response to nutrient additions may change and therefore the mechanisms underpinning those responses should be included as basis of nutrient limitation assessment.

Unlike central Amazonia forests[15], P limitation in Afrotropical forests have not yet been reported[19,42,43] but that could change. Our results suggest that terrestrial P availability may limit productivity under extremely dry conditions, when low soil moisture hampers root nutrient uptake[16,22]. Experimentally, K limitations in tropical forests have been expressed in increased stem growth[19,33,59] and decreased fine root allocations[60]. Our results reveal that K availability controls the timing of leaf litterfall peak and leaf litter production, particularly under drier conditions, and hence is consistent with K modulation of vegetation structure and function[61]. Given that leaf CO$_2$ assimilation, litter and wood production are coupled with climate seasonality[19,20] and highly sensitive to rainfall threshold of <2,000 mm yr^{-1} (ref. [4]), K limitation may be more widespread in tropical forests than suspected. The C-sink potential and resilience of Afrotropical forests growing on heavily weathered soils, with strong dry seasons (Extended Data Fig. 2c), may depend on terrestrial K availability that is yet uncaptured in current models[26]. Global change models might therefore overestimate future CO$_2$ uptake while underrepresenting the impacts of nutrient limitation with shifts in rainfall seasonality[6–9]. This highlights the need to improve mechanistic representation of ecosystem response to drought stress to reduce uncertainties associated with tropical C-sink strength.

Whereas rock-derived P and K are recognized for enhancing plant water-use efficiency under drier conditions, torrential rains could increase their susceptibility to leaching losses[14,24]. Furthermore, plants with efficient K remobilization capacity will probably survive under K-limited and drier environments, thereby triggering shifts in species composition or colonization by alien species[24]. It remains to be evaluated if K input through deposition (4.3 kg K ha^{-1} yr^{-1}), litterfall (leaf; 77.4 kg K ha^{-1} yr^{-1}) and further weathering can offset the observed K limitations in this forest. However, K being the most resorbed macronutrient at this site implies that the trees employ a conservative K nutritional strategy. We, therefore, expect that K will continue to exert stronger controls on primary productivity in this forest and in other seasonally dry tropical forests.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41561-024-01448-8.

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Methods

Study site description

We conducted this research in the Budongo Forest Reserve in north-western Uganda (31° 32′ E, 1° 44′ N; mean elevation = 1,050 m above sea level). This moist semi-deciduous tropical rainforest is situated on an uplifted shield, east of the Albertine Rift, and underlain by Precambrian gneissic–granulitic rocks[62]. Soils at the study site are highly weathered, well drained (>50 % sand; Extended Data Table 1), and classified as lixi-sols[63], which are mostly found in transition zones between savannahs and tropical forests. Moreover, the soils at this site have a near-neutral pH, high base saturation and a calcium-dominated cation exchange capacity (Extended Data Table 1), attributed to parent material con-tent[19] and depositions of aeolian dust or ash from agricultural activities outside the forest[64]. The region has a bimodal rainfall pattern, with dry seasons (<100 mm per month) mostly occurring from December to February and in July. Annual air temperature and rainfall averaged $22.8 \pm 0.1\,°C$ and $1{,}670 \pm 50$ mm (2000–2019; Budongo Field Station). In the first year of our study, the region experienced an extended dry season lasting from December to March, resulting in ~30% lesser rain-fall than in the subsequent year[19]. Atmospheric nutrient depositions measured from rainfall were 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} (ref. [19]).

Although selectively logged in the 1950s, this forest site did not have any other anthropogenic disturbance in the past 60 years[65], resulting in a higher abundance of mid-stage succession species like *Funtumia elastica*. Vegetation characteristics of the site are typical for tropical forests with a high species diversity (126 tree species identified in the 32 study plots (~5.12 ha) and canopy heights reach-ing 50 m). Among trees ≥10 cm, there were cases, stem diameter growth rates were 0.011 ± 0.001 cm cm^{-1} yr^{-1} and C accumulation was 2.2 ± 0.4 Mg C ha^{-1} yr^{-1} (ref. [19]). Tree density classes with stem DBH: 1–5 cm was $5{,}938 \pm 269$; 5–10 cm was 627 ± 30; 10–30 cm was 514 ± 13; and >30 cm was 108 ± 5 trees ha^{-1} (ref. [19]). The ten most dominant tree species at the site are *Funtumia elastica* (24%), *Celtis mildbraedii* (15%), *Cynometra alexandri* (6%; N-fixing species), *Celtis durandii* (6%), *Celtis zenkeri* (6%), *Lasiodiscus mildbraedii* (6%), *Rinorea ardisiaeflora* (6%), *Trichilia rubescens* (4%), *Khaya anthoteca* (3%), *Tapura fischeri* (2%) and together constitute 78% of tree abundance (trees ≥10 cm DBH) (ref. [19]). Leaf area index (LAI) in the control plots averaged 3.3 m^2 m^{-2} (determined in April 2018–November 2019).

Experimental design and soil analysis

We established a full factorial N–P–K addition experiment consisting of eight treatments (that is, control, N, P, K, NP, NK, PK and NPK) with four replicates each, assigned randomly in 32 plots (40 m × 40 m each) positioned at least 40 m apart (Supplementary Fig. 1). Within each 40 m × 40 m plot, we laid out a 30 m × 30 m core area where all measure-ments were conducted to reduce edge effects. We added nitrogen as urea ($(NH_2)_2CO$) at a rate of 125 kg N ha^{-1} yr^{-1}, P as triple superphosphate ($Ca(H_2PO_4)_2$) at 50 kg P ha^{-1} yr^{-1} and K as potassium chloride (KCl) at 50 kg K ha^{-1} yr^{-1}, divided into four applications during the wet season in each year, similar to the fertilization method employed in the Gigante NME in Panama[33]. The Ca in the triple superphosphate was unlikely to be limiting productivity[15] at this site because the site's exchangeable cations were Ca dominated (Extended Data Table 1). For fertilizer appli-cation, we divided the 40 m × 40 m plot into 10 m × 10 m quadrats to facilitate uniform distribution of fertilizers. Within each 10 m × 10 m quadrat, pre-packaged fertilizers were mixed with small quantities of soil (taken directly adjacent to the plots as filler materials to facilitate complete and even fertilizer distribution) and broadcast by hand, walk-ing forward and backward and subsequently changing directions (east to west and north to south). Since May 2018, fertilizer was applied in four equal doses each year during the rainy seasons.

Before initial fertilization, we conducted baseline measurements of the litter and soil biochemical characteristics (Extended Data Table 1)

within the core area of each experimental plot. Soil samples were taken from ten randomly selected locations per plot at 0–0.1 m soil depth and five samples per plot for the lower soil depths (0.1–0.3 m and 0.3–0.5 m). Soil samples were air dried at room temperature, sieved (with 2-mm sieve) and sent to Goettingen University, Germany, for analyses. Soil organic carbon and total N were analysed on finely ground soils using a CN elemental analyser (VARIO EL Cube, Elementar Analysis Systems GmbH). Soil pH was analysed in 1:2.5 of soil-to-distilled water ratio. Soil ^{15}N natural abundance was analysed using isotope ratio mass spectrometry (IRMS; Delta Plus, Finnigan MAT). Exchangeable cations (Ca, Mg, K, Na, Al, Fe and Mn) were determined by percolating the soil samples with unbuffered 1 M NH$_4$Cl, and cation concentrations in per-colate were determined using the inductively coupled plasma-atomic emission spectrometer (ICP-AES; iCAP 6300 Duo VIEW ICP Spectrom-eter, Thermo Fischer Scientific GmbH)[66]. Soil total P was measured by digesting the soil samples in high pressure with 65% HNO$_3$ and the digests were analysed for P using ICP-AES[67]. For each plot, soil texture was determined from a composite sample using the pipette method after iron oxide and organic matter were removed[68]. Soil bulk density was measured by core method[69] at depths of 0.05 m, 0.2 m and 0.4 m from soil pits dug next to each plot.

Fine litter production and leaf litter chemistry

Fine litter production was measured bi-weekly for three consecutive years using four randomly placed 0.75 m × 0.75 m litter collectors per plot, similar to earlier studies[33]. These collectors were constructed from PVC pipe frames and 1-mm plastic mesh. Fine litter was collected bi-weekly and separated into seven categories: leaves, flowers, fruits, wood ≤2 cm diameter, epiphytes (Extended Data Table 2) and unclas-sified (others), following established methods[70]. Subsequently, the samples were oven dried at 60 °C until the constant mass was achieved usually 48–72 hours (season dependent) and then weighed. Due to labour shortage, only leaves were separated in the third year. We calcu-lated annual litter production as a sum of all litterfall for 12 consecutive months (from May to April of the next year). We also collected pooled samples of leaf litter per plot in May 2018 (pre-treatment) and ~1.5 years into the experiment for chemical analyses. Litter samples were finely ground, digested in high pressure with 65% HNO$_3$ and the digests analysed for P, K, Ca, Mg, S, Al and Fe concentrations using ICP-AES; C and N concentrations were determined on ground samples using a CN elemental analyser and ^{15}N natural abundance using IRMS, as mentioned above.

Sunlit leaves, leaf area index and nutrient resorption efficiency

As is typical in most tropical forest, there is a high abundance of only a few species and rarity of many identified species[19], making it logisti-cally challenging to sample fresh leaves for all species within each plot. Thus, we collected 160 sunlit leaf samples (5 tree species × 32 plots) (ref. [71]) from the five most dominant species per replicate plot. This dominance is based on their importance value index (IVI)[72], which is the sum of relative density, relative frequency and relative basal area, all expressed as a percentage. There were cases where a species of interest was not found in a given replicate plot; thus, the leaves of a substitute species (which is next in the IVI ranking) was sampled, resulting in a total of seven species (*Celtis durandii, Celtis mildbraedii, Celtis zenkeri, Cynometra alexandri, Funtumia elastica, Khaya anthoteca, Lasiodiscus mildbraedii*) across the plots, which together represented ~67% of the site's tree abundance (≥10 cm DBH). The selection of an individual tree to represent a given species within each plot was done randomly. The foliar element concentration (mass basis) of the tree species within each replicate plot was dominance-weighted[73] to obtain plot-level values.

For the purpose of species-specific foliar nutrient response to nutrient addition, we selected only four of the seven dominant tree

species (*Funtumia elastica, Celtis mildbraedii, Celtis durandii, Cynometra alexandrii*), as these species were present in at least three replicate plots enabling sound statistical testing. Together, these four species accounted for ~51% of tree stem abundance[19]. We then determined their element concentrations and δ^{15}N natural abundance (same analytical method as the leaf litter samples). The stoichiometry (that is, N:P ratios) in leaves can indicate nutrient limitations[36], whereas the δ^{15}N natural abundance in sunlit leaves and leaf litter can indirectly indicate increases in N losses[74]. With tree canopy heights reaching up to 50 m at this site, sampling sunlit leaves was challenging. We used a big throw bag slingshot (Notch SET1025) as a throw-line launcher; the line was equipped with a throw weight and a portable chainsaw for cutting down small tree branches. Sampling of sunlit leaves was done after ~1.5 years (October 2019) of the nutrient addition experiment.

In April 2018 (before the start of the experiment) and in October 2019 (~1.5 years of the nutrient addition experiment), we measured LAI using an automated fisheye lens camera (Solariscope, Behling SOL300). This device calculates LAI by analysing hemispherical photographs[75], taken under sky-overcast conditions between 12.00 p.m. to 2.00 p.m. at 1 m above the ground facing skyward, from the centre of each of the 16 quadrats (10 m × 10 m each) per plot.

Additionally, we estimated nutrient resorption efficiency, which is the proportional withdrawal of nutrients during leaf senescence in plants, based on the nutrient concentrations (mass basis) of sunlit leaves and leaf litter (sampling described above) as: (sunlit leaf (mg g^{-1}) − leaf litter (mg g^{-1})) / sunlit leaf (mg g^{-1}) × 100 (ref. 76). For nutrient resorption efficiency, we used all sunlit leaf samples collected from the five dominant tree species per plot (totalling to the 160 leaf samples), as these were likely to mirror the species composition of leaf litter within the litter traps at the plot level.

Statistical analysis

For annually estimated parameters (total fine litterfall, leaf litterfall, twigs, barks, reproductive litter), linear mixed-effect (LME) model (*lme* function in the 'nlme' package) was used to test the effects of nutrient treatments and experimental years in the full factorial N–P–K design. In the LME, nutrient treatment, experimental year or seasons (to test for effects of nutrient treatments seasonally) were considered as fixed factors whereas replicate plots were random effect. The significance of the fixed effect was evaluated using analysis of variance (ANOVA)[77]. If residual plots revealed non-normal distribution or non-homogeneous variance, we log-transformed the data (that is, flowers, fruits and litter residues) and then repeated the analyses. Parameters measured only once (leaf litter chemistry, sunlit leaf chemistry) and baseline measurements (soil characteristics before the start of experimental treatments) were analysed using full factorial ANOVA ('lm-function'). In cases where no significant interaction effects were detected between the different fertilization nutrients and by reason of simplified graphical visualization, results are shown as plots with a specific nutrient not added (for example, −N; n = 16 plots) against plots where that nutrient was added (for example +N; n = 16 plots)[60]. In all tests, statistical significance was set at P ≤ 0.05. All statistical analyses were performed using the statistical package R version 3.6.2[78].

Data availability
Data are available from Göttingen Research Online at https://doi.org/10.25625/SB1I57 (ref. 79).

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Author contributions

O.v.S., M.D.C. and E.V. conceived the project. R.M., O.v.S., A.A. and M.G.M. conducted the experiment and collected data. R.M. analysed the data (with contributed ideas from E.V., M.D.C., O.v.S. and N.A.-A.I.) and wrote the manuscript with contributions from all authors.

Competing interests

The authors declare no competing interests.

Additional information

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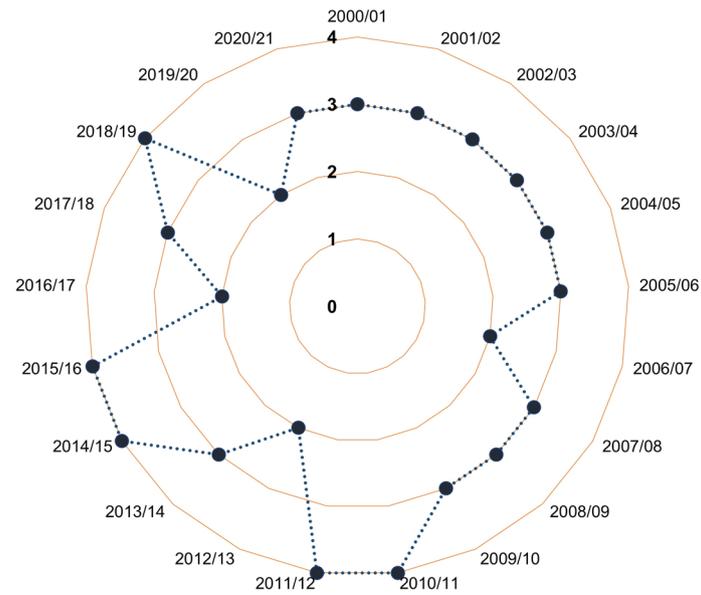
Extended Data Fig. 1 | Dry season lengths (number of months with precipitation < 100 mm month⁻¹) at the Budongo Forest Reserve, Uganda. Data extends from 2000 to 2021 measured at the Budongo Conservation Field Station. Nutrient addition experimental period was from 2018 to 2021; the prolonged dry season of the first year of the experiment lasted four consecutive months (2018/19), second year had only two dry months (2019/20), and the third year had three dry months (2020/21).
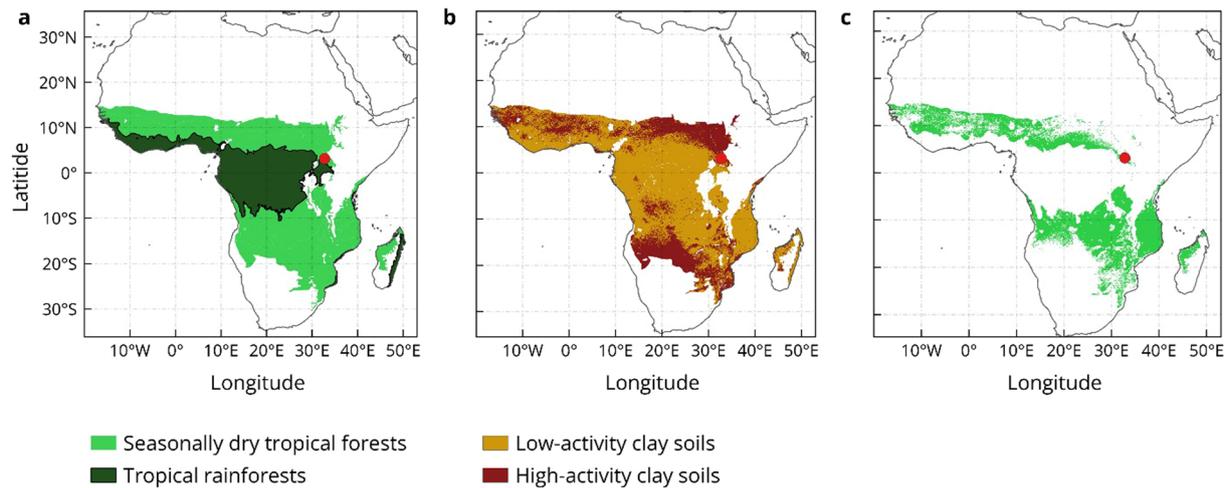
Extended Data Fig. 2 | Extent of seasonally dry Afrotropical forests on heavily weathered soils, showing study location in Uganda (red dot).
a-c, Afrotropical forests cover distinguished between rainforests and seasonally dry tropical forests (moist deciduous forests and seasonally dry forests) based on the Global Forest Resources Assessment[80] **(a)**. Heavily weathered soils dominated by low activity clays (Ferralsols, Acrisols, Lixisols, Nitisols) and less weathered soils dominated by high activity clays (Cambisols, Luvisols, Vertisols, Planosols,

Alisols) in the African tropics using the 250 m SOILGRID dataset[81] classified according to FAO World Reference Base for soil resource[63] **(b)**. Only seasonally dry forests (that is, experience dry seasons (precipitation < 100 mm month^{-1}) of three or more consecutive months) on heavily weathered soils dominated by low activity clays and likely to exhibit nutrient limitation with increasing drought conditions **(c)**.

Extended Data Table 1 | Soil physical and chemical characteristics (mean±SE; n=32 plots) measured before the start of the nutrient addition experiment

Site characteristics		Soil depth			Depth-weighted means or element stocks (0−50 cm) [a]	
		0−10 cm	10−30 cm	30−50 cm		
Bulk density	$g\ cm^{-3}$	1.23 ± 0.03	1.53 ± 0.03	1.38 ± 0.03		1.41 ± 0.02
Texture: Sand	%	54.8 ± 1.6	55.3 ± 1.6	48.7 ± 1.4		51.94 ± 1.50
Silt	%	27.0 ± 1.7	21.3 ± 1.2	13.7 ± 0.9		19.24 ± 0.92
Clay	%	18.2 ± 0.8	23.4 ± 1.1	37.6 ± 1.3		27.57 ± 1.01
Soil pH (1:2.5 H_2O)		6.43 ± 0.04	6.08 ± 0.09	5.90 ± 0.10		6.08 ± 0.09
Soil organic carbon	$g\ C\ kg^{-1}$	33.17 ± 1.15	10.24 ± 0.56	6.03 ± 0.33	$Kg\ C\ m^{-2}$	12.70 ± 0.41
Total nitrogen	$g\ N\ kg^{-1}$	3.45 ± 0.12	1.27 ± 0.07	0.82 ± 0.04	$Kg\ N\ m^{-2}$	1.55 ± 0.05
Total phosphorus	$mg\ P\ kg^{-1}$	660 ± 104	506 ± 124	327 ± 26	$Kg\ P\ m^{-2}$	0.33 ± 0.04
C:N ratio		9.54 ± 0.10	7.99 ± 0.08	7.22 ± 0.11		7.99 ± 0.07
^{15}N natural abundance	‰	7.79 ± 0.06	9.22 ± 0.13	9.51 ± 0.16		9.09 ± 0.12
ECEC [b]	$mmol^+\ kg^{-1}$	149.2 ± 8.3	63.0 ± 4.1	51.9 ± 2.6		75.80 ± 3.20
Base saturation	%	98.2 ± 0.2	97.5 ± 1.0	97.2 ±1.3		97.51 ± 0.88
Aluminum	$mg\ Al\ kg\ soil^{-1}$	1.5 ± 0.9	21.8 ± 17.3	58.6 ± 43.2	$g\ Al\ m^{-2}$	2.31 ± 1.73
Calcium	$mg\ Ca\ kg\ soil^{-1}$	6254 ± 362	5205 ± 180	1945 ± 128	$g\ Ca\ m^{-2}$	202.5 ± 11.0
Iron	$mg\ Fe\ kg\ soil^{-1}$	0.003 ± 0.003	0.82 ± 0.36	0.33 ± 0.13	$g\ Fe\ m^{-2}$	0.03 ± 0.02
Potassium	$mg\ K\ kg\ soil^{-1}$	119.6 ± 6.1	52.0 ± 6.5	46.0 ± 5.8	$g\ K\ m^{-2}$	4.24 ± 0.26
Magnesium	$mg\ Mg\ kg\ soil^{-1}$	1410 ± 87	787 ± 83	811 ± 88	$g\ Mg\ m^{-2}$	62.58 ± 4.43
Manganese	$mg\ Mn\ kg\ soil^{-1}$	68.0 ± 5.8	36.5 ± 5.7	25.5 ± 4.3	$g\ Mn\ m^{-2}$	2.59 ± 0.24
Sodium	$mg\ Na\ kg\ soil^{-1}$	6.2 ± 1.0	1.4 ± 0.6	0.6 ± 0.4	$g\ Na\ m^{-2}$	0.13 ± 0.02

[a]Values represent depth-weighted (0–10cm, 10–30cm, 30–50cm) averages of the soil characteristics, except for element stocks, which represent the sum of the entire 50cm soil depth.
[b] Effective cation exchange capacity (ECEC); base saturation is the sum of exchangeable bases (Ca, Mg, K and Na)÷ECEC×100.

Extended Data Table 2 | Annual fine litter production (Mg ha^{-1} year^{-1}; mean±SE, N=4 plots) in full factorial N-P-K experiment in the Budongo Forest Reserved, Uganda

Treatment	Total fine litterfall	Leaves	Twigs ≤2 cm	Barks	Flowers	Fruits	Epiphytes	Others
Control	12.9 ± 0.8	8.5 ± 0.3	2.5 ± 0.3	0.3 ± 0.1	0.36 ± 0.16	0.9 ± 0.1	0.02 ± 0.01	0.3 ± 0.06
N	14.9 ± 0.9	9.1 ± 0.1	2.7 ± 0.1	1.2 ± 0.7	0.53 ± 0.11	1.0 ± 0.2	0.01 ± 0.00	0.4 ± 0.04
P	13.8 ± 1.1	8.8 ± 0.2	2.4 ± 0.1	0.5 ± 0.2	0.34 ± 0.11	1.3 ± 0.6	0.02 ± 0.01	0.4 ± 0.05
K	14.0 ± 1.2	8.7 ± 0.5	2.4 ± 0.2	0.4 ± 0.1	0.45 ± 0.11	1.6 ± 0.6	0.06 ± 0.04	0.4 ± 0.03
NP	13.4 ± 0.7	8.7 ± 0.2	2.5 ± 0.1	0.7 ± 0.2	0.38 ± 0.13	0.7 ± 0.2	0.02 ± 0.01	0.4 ± 0.06
NK	12.3 ± 1.1	8.2 ± 0.5	2.1 ± 0.3	0.3 ± 0.1	0.33 ± 0.14	0.9 ± 0.3	0.06 ± 0.05	0.3 ± 0.07
PK	11.8 ± 0.7	8.1 ± 0.4	2.2 ± 0.3	0.4 ± 0.2	0.18 ± 0.04	0.5 ± 0.1	0.01 ± 0.00	0.3 ± 0.05
NPK	12.4 ± 0.5	8.4 ± 0.5	2.4 ± 0.3	0.3 ± 0.2	0.22 ± 0.04	0.7 ± 0.3	0.01 ± 0.01	0.4 ± 0.08

Bi-weekly litter production was summed for 12 consecutive months, and annual values were averaged for the three-year experimental period (May 2018–April 2021), and the remaining categories (twigs, barks, fruits, flowers, epiphytes and 'others') were averaged for the first two years.

Extended Data Table 3 | The *F* statistics of full factorial N-P-K experiment with linear mixed-effect models, testing treatment effects on fine litter production (within columns, bolded *F* values indicate significant effects at *P*<0.05) in the Budongo Forest Reserve, Uganda

Treatment	*numDF, denDF*	Total fine litterfall	Leaves	*numDF, denDF*	Twigs ≤2 cm	Barks	Flowers	Fruits	Epiphytes	Others
N	*1, 24*	0.002	0.248	*1, 24*	0.042	1.276	0.010	1.084	0.007	1.973
P	*1, 24*	1.004	**7.427**	*1, 24*	0.851	0.134	0.153	2.245	2.169	0.002
K	*1, 24*	2.032	**5.449**	*1, 24*	1.876	2.074	0.858	0.344	1.635	0.210
N × P	*1, 24*	0.005	0.028	*1, 24*	3.007	1.142	0.085	0.014	0.030	0.379
N × K	*1, 24*	1.252	0.006	*1, 24*	0.655	1.812	2.141	0.002	0.160	1.332
P × K	*1, 24*	0.185	2.023	*1, 24*	1.933	0.164	0.151	0.893	3.135	0.142
N × P × K	*1, 24*	2.522	3.144	*1, 24*	1.036	0.937	1.180	0.694	0.003	0.196
Year	*2, 48*	1.917	1.112	*1, 24*	**39.69**	1.991	**7.156**	0.827	2.158	**221.5**
N × Year	*2, 48*	0.135	0.330	*1, 24*	0.439	0.769	0.123	0.627	0.049	0.004
P × Year	*2, 48*	0.786	**5.779**	*1, 24*	2.839	1.543	1.361	0.189	2.609	0.895
K × Year	*2, 48*	0.920	0.161	*1, 24*	0.285	1.439	0.092	0.782	2.773	0.911
N × P × Year	*2, 48*	2.017	0.119	*1, 24*	0.383	1.714	0.027	0.651	0.027	2.190
N × K × Year	*2, 48*	1.173	1.217	*1, 24*	4.802	0.816	1.689	0.398	0.267	0.261
P × K × Year	*2, 48*	0.373	1.956	*1, 24*	2.898	0.662	0.602	0.101	0.026	2.601
N × P × K × Year	*2, 48*	0.074	0.074	*1, 24*	0.001	1.429	0.488	0.108	0.026	2.501

Extended Data Table 4 | Leaf litter chemistry (mean±SE, n=4 plots) after ~1.5 years of the full factorial N-P-K experiment in the Budongo Forest Reserved, Uganda

Treatment	C	N	P	K	Ca	Mg	S	Al	Fe	δ^{15}N	C:N	N:P
	mg g^{-1}	mg g^{-1}	mg g^{-1}	mg g^{-1}	mg g^{-1}	mg g^{-1}	mg g^{-1}	mg g^{-1}	mg g^{-1}	‰		
Control	422 ± 5	26.5 ± 1.1	1.55 ± 0.05	9.5 ± 0.7	36.9 ± 4.5	3.3 ± 0.3	1.97 ± 0.32	0.28 ± 0.02	0.31 ± 0.02	6.19 ± 0.27	16.0 ± 0.8	17.1 ± 1.0
N	431 ± 9	23.2 ± 1.3	1.23 ± 0.07	8.2 ± 1.1	30.2 ± 4.0	2.8 ± 0.2	1.57 ± 0.07	0.33 ± 0.05	0.37 ± 0.05	5.77 ± 0.41	18.8 ± 1.0	18.9 ± 0.8
P	430 ± 10	24.0 ± 1.4	1.26 ± 0.12	8.3 ± 0.8	26.4 ± 2.8	3.1 ± 0.3	2.17 ± 0.26	0.30 ± 0.04	0.34 ± 0.05	6.24 ± 0.32	18.1 ± 1.1	19.3 ± 1.2
K	436 ± 6	24.5 ± 2.0	1.35 ± 0.09	8.3 ± 0.6	25.1 ± 5.1	2.5 ± 0.3	1.82 ± 0.10	0.32 ± 0.05	0.36 ± 0.03	6.65 ± 0.14	18.2 ± 1.5	18.2 ± 0.4
NP	430 ± 13	27.2 ± 1.1	1.48 ± 0.15	8.5 ± 0.5	32.9 ± 5.3	3.3 ± 0.1	1.99 ± 0.12	0.42 ± 0.07	0.49 ± 0.09	6.23 ± 0.55	15.9 ± 1.1	19.0 ± 1.9
NK	412 ± 7	24.3 ± 1.5	1.44 ± 0.13	9.1 ± 1.2	34.6 ± 2.2	2.9 ± 0.3	1.84 ± 0.06	0.34 ± 0.05	0.40 ± 0.04	6.43 ± 0.32	17.2 ± 1.0	17.3 ± 2.3
PK	413 ± 13	25.5 ± 1.7	1.43 ± 0.17	9.8 ± 1.1	33.5 ± 5.9	3.1 ± 0.2	2.01 ± 0.06	0.38 ± 0.10	0.40 ± 0.07	7.50 ± 0.42	16.5 ± 1.4	18.3 ± 1.7
NPK	437 ± 4	24.3 ± 0.6	1.42 ± 0.08	8.0 ± 0.6	25.4 ± 1.2	2.7 ± 0.2	1.86 ± 0.18	0.49 ± 0.16	0.37 ± 0.13	6.24 ± 0.22	18.0 ± 0.4	17.2 ± 0.8

Extended Data Table 5 | The *F* statistics of the full factorial N-P-K experiment, testing treatment effects on leaf litter chemistry (within columns, bolded *F* values indicate significant effects at P<0.05) in the Budongo Forest Reserved, Uganda

Treatment	numDF, denDF	C mg g⁻¹	N mg g⁻¹	P mg g⁻¹	K mg g⁻¹	Ca mg g⁻¹	Mg mg g⁻¹	S mg g⁻¹	Al mg g⁻¹	Fe mg g⁻¹	δ¹⁵N ‰	C:N	N:P
N	1, 24	0.129	0.178	0.004	0.760	0.010	0.215	2.277	2.023	1.306	3.642	0.146	0.016
P	1, 24	0.160	0.460	0.008	0.017	0.533	0.750	3.607	2.099	0.702	1.383	0.277	0.321
K	1, 24	0.304	0.347	0.143	0.089	0.425	3.201	0.024	0.722	0.016	**5.773**	0.110	0.709
N × P	1, 24	2.294	2.017	1.864	0.079	0.139	0.070	0.004	0.422	0.012	0.398	0.578	0.407
N × K	1, 24	0.147	0.128	0.373	0.003	0.022	0.074	0.719	0.131	1.092	1.116	0.001	0.760
P × K	1, 24	0.045	0.024	0.099	0.257	0.357	0.071	1.103	0.009	0.615	0.018	0.000	0.330
N × P × K	1, 24	**5.006**	3.684	4.069	3.210	**6.906**	4.044	0.966	0.005	0.600	2.142	**5.927**	0.236

Extended Data Table 6 | Foliar chemistry (mean±SE, n=3 or 4 plots) of the four dominant tree species after ~1.5 years of the full factorial N-P-K experiment in the Budongo Forest Reserved, Uganda

Treatment	C mg g⁻¹	N mg g⁻¹	P mg g⁻¹	K mg g⁻¹	Ca mg g⁻¹	Mg mg g⁻¹	S mg g⁻¹	Al mg g⁻¹	Fe mg g⁻¹	15N ‰	C:N ratio	N:P ratio
Celtis durandii (6%; Semi-deciduous species)												
Control	384 ± 17	27.5 ± 4.0	1.87 ± 0.32	10.2 ± 1.7	27.4 ± 2.6	3.08 ± 0.43	1.71 ± 0.29	0.4 ± 0.09	0.37 ± 0.11	7.4 ± 1.0	15.57 ± 3.78	15.07 ± 1.05
N	380 ± 9	30.9 ± 1.3	2.16 ± 0.29	12.7 ± 1.5	29.3 ± 0.6	3.36 ± 0.29	1.56 ± 0.13	0.33 ± 0.09	0.22 ± 0.05	9.1 ± 0.3	12.32 ± 0.37	15.14 ± 2.18
P	383 ± 12	31.9 ± 1.3	2.46 ± 0.07	15.1 ± 2.6	29.3 ± 4.0	3.65 ± 0.40	1.57 ± 0.08	0.39 ± 0.18	0.41 ± 0.21	8.8 ± 0.4	12.07 ± 0.43	13.03 ± 0.86
K	384 ± 6	31.3 ± 1.4	2.06 ± 0.21	12.8 ± 1.1	26.9 ± 1.6	4.20 ± 0.96	1.52 ± 0.13	0.24 ± 0.04	0.23 ± 0.03	8.7 ± 0.2	12.31 ± 0.57	15.46 ± 1.53
NP	376 ± 4	34.3 ± 0.5	2.99 ± 0.41	16.3 ± 0.9	33.1 ± 1.6	3.45 ± 0.44	1.71 ± 0.05	0.26 ± 0.05	0.25 ± 0.04	8.8 ± 0.2	10.98 ± 0.23	11.91 ± 1.58
NK	371 ± 6	32.4 ± 0.9	2.36 ± 0.18	15.6 ± 2.0	36.2 ± 5.4	3.38 ± 0.25	1.55 ± 0.04	0.37 ± 0.07	0.38 ± 0.09	8.4 ± 0.6	11.48 ± 0.37	13.99 ± 1.19
PK	387 ± 9	30.7 ± 0.8	2.47 ± 0.33	12.7 ± 1.7	27.9 ± 2.6	3.29 ± 0.35	1.42 ± 0.08	0.25 ± 0.00	0.19 ± 0.07	9.7 ± 0.3	12.64 ± 0.17	12.92 ± 1.87
NPK	401 ± 16	40.0 ± 6.3	3.55 ± 1.05	19.5 ± 5.0	26.1 ± 6.9	3.66 ± 0.42	2.41 ± 0.69	0.29 ± 0.03	0.33 ± 0.05	9.4 ± 0.3	10.37 ± 1.09	12.12 ± 1.45
Celtis mildbraedii (15%; Semi-deciduous species)												
Control	362 ± 19	31.6 ± 1.6	1.17 ± 0.15	11.1 ± 1.5	45.2 ± 6.3	3.38 ± 0.38	1.70 ± 0.07	0.45 ± 0.08	0.45 ± 0.07	7.8 ± 1.2	11.45 ± 0.23	27.76 ± 2.63
N	389 ± 1	33.1 ± 0.1	1.14 ± 0.02	12.7 ± 2.2	37.9 ± 3.1	2.26 ± 0.37	1.51 ± 0.08	0.42 ± 0.11	0.39 ± 0.07	8.5 ± 0.2	11.73 ± 0.07	28.99 ± 0.50
P	373 ± 7	29.9 ± 1.4	1.08 ± 0.04	9.0 ± 1.2	40.4 ± 4.6	2.65 ± 0.06	1.36 ± 0.11	0.43 ± 0.08	0.31 ± 0.12	8.7 ± 0.3	12.50 ± 0.46	27.57 ± 0.39
K	366 ± 0	29.9 ± 0.0	1.03 ± 0.0	11.4 ± 0.0	52.6 ± 0.0	3.45 ± 0.00	1.43 ± 0.00	0.30 ± 0.00	0.33 ± 0.00	9.3 ± 0.0	12.22 ± 0.00	29.04 ± 0.00
NP	383 ± 4	32.8 ± 0.2	1.23 ± 0.10	10.4 ± 0.8	42.1 ± 2.4	2.88 ± 0.28	1.56 ± 0.06	0.33 ± 0.05	0.30 ± 0.03	8.4 ± 0.3	11.71 ± 0.12	27.03 ± 1.80
NK	388 ± 11	34.0 ± 2.2	1.46 ± 0.19	10.7 ± 2.3	37.8 ± 6.6	3.33 ± 0.39	1.50 ± 0.09	0.34 ± 0.04	0.30 ± 0.02	8.0 ± 0.4	11.47 ± 0.43	23.80 ± 1.77
PK	382 ± 5	31.1 ± 0.6	1.28 ± 0.04	12.4 ± 1.0	39.6 ± 3.0	3.00 ± 0.19	1.54 ± 0.06	0.25 ± 0.02	0.29 ± 0.03	9.0 ± 0.8	12.29 ± 0.38	24.32 ± 0.37
NPK	390 ± 6	31.8 ± 0.8	1.17 ± 0.03	10.1 ± 1.1	32.8 ± 3.5	2.89 ± 0.27	1.59 ± 0.03	0.39 ± 0.08	0.35 ± 0.06	9.0 ± 0.7	12.29 ± 0.48	27.30 ± 0.77
Cynometra alexandri (6%; Evergreen species)												
Control	451 ± 4	25.6 ± 0.6	1.62 ± 0.12	9.9 ± 0.5	15.7 ± 1.5	1.60 ± 0.15	1.49 ± 0.06	0.16 ± 0.02	0.18 ± 0.02	7.5 ± 0.5	17.67 ± 0.28	16.10 ± 1.40
N	449 ± 5	24.7 ± 0.9	1.65 ± 0.16	10.6 ± 1.4	13.2 ± 1.3	1.50 ± 0.13	1.53 ± 0.08	0.18 ± 0.03	0.17 ± 0.02	7.8 ± 0.8	18.27 ± 0.76	15.33 ± 1.42
P	450 ± 6	24.5 ± 1.1	1.53 ± 0.19	8.9 ± 0.9	16.3 ± 2.5	1.44 ± 0.08	1.40 ± 0.03	0.17 ± 0.02	0.17 ± 0.01	7.7 ± 0.3	18.45 ± 1.01	16.54 ± 2.37
K	456 ± 3	26.5 ± 0.8	1.7 ± 0.18	9.0 ± 1.1	14.0 ± 2.2	1.27 ± 0.16	1.55 ± 0.08	0.20 ± 0.04	0.19 ± 0.03	8.1 ± 0.4	17.24 ± 0.47	15.95 ± 1.05
NP	450 ± 6	27.1 ± 0.8	1.7 ± 0.15	9.2 ± 0.9	12.6 ± 1.0	1.38 ± 0.08	1.49 ± 0.07	0.14 ± 0.02	0.16 ± 0.02	6.8 ± 0.2	16.68 ± 0.46	16.35 ± 1.66
NK	457 ± 5	25.6 ± 0.7	1.6 ± 0.13	10.0 ± 1.3	12.6 ± 0.5	1.34 ± 0.06	1.56 ± 0.08	0.25 ± 0.04	0.23 ± 0.03	7.6 ± 0.5	17.96 ± 0.67	16.39 ± 1.72
PK	457 ± 8	24.9 ± 1.1	1.75 ± 0.06	10.6 ± 0.7	10.1 ± 1.7	1.57 ± 0.21	1.70 ± 0.17	0.13 ± 0.04	0.14 ± 0.03	8.1 ± 0.4	18.50 ± 0.94	14.21 ± 0.70
NPK	457 ± 15	26.1 ± 1.0	1.58 ± 0.08	9.6 ± 0.2	16.5 ± 3.6	1.45 ± 0.18	1.36 ± 0.06	0.17 ± 0.04	0.19 ± 0.03	7.5 ± 0.1	17.61 ± 1.25	16.55 ± 0.66
Funtumia elastica (24%; Evergreen species)												
Control	462 ± 6	31.1 ± 0.1	2.39 ± 0.16	20.2 ± 2.4	17.0 ± 1.4	7.72 ± 0.64	2.83 ± 0.09	0.34 ± 0.06	0.32 ± 0.05	5.8 ± 0.5	14.86 ± 0.22	13.15 ± 0.84
N	467 ± 4	30.7 ± 0.9	2.09 ± 0.18	16.7 ± 1.2	19.1 ± 2.2	7.16 ± 0.55	2.40 ± 0.15	0.36 ± 0.03	0.34 ± 0.05	7.1 ± 0.4	15.26 ± 0.46	15.02 ± 1.25
P	465 ± 3	30.3 ± 0.9	2.24 ± 0.27	19.8 ± 0.8	16.4 ± 0.9	7.33 ± 0.40	2.68 ± 0.10	0.30 ± 0.01	0.31 ± 0.02	5.9 ± 0.4	15.39± 0.36	13.92 ± 1.16
K	462 ± 6	28.8 ± 1.0	2.14 ± 0.20	17.5 ± 1.7	21.6 ± 2.8	7.27 ± 0.58	2.70 ± 0.16	0.34 ± 0.05	0.32 ± 0.04	5.5 ± 0.4	16.10 ± 0.42	13.77 ± 1.28
NP	463 ± 7	30.7 ± 0.8	1.85 ± 0.14	18.3 ± 2.9	16.5 ± 1.0	6.69 ± 0.75	2.17 ± 0.24	0.33 ± 0.05	0.25 ± 0.08	6.2 ± 0.6	15.13 ± 0.60	16.91 ± 1.39
NK	451 ± 6	28.3 ± 0.6	1.87 ± 0.18	17.2 ± 1.7	23.5 ± 2.8	7.53 ± 0.94	2.20 ± 0.07	0.33 ± 0.03	0.28 ± 0.03	6.1 ± 0.4	15.96 ± 0.30	15.45 ± 1.17
PK	456 ± 10	28.7 ± 0.6	2.22 ± 0.61	13.5 ± 1.7	21.0 ± 2.1	5.58 ± 1.24	2.12 ± 0.37	0.29 ± 0.07	0.23 ± 0.09	6.5± 0.6	15.89 ± 0.18	15.23 ± 2.89
NPK	459 ± 2	30.6 ± 0.4	1.84 ± 0.07	16.8 ± 1.0	19.5 ± 1.2	7.26 ± 0.15	2.42 ± 0.13	0.36 ± 0.02	0.34 ± 0.03	6.6 ± 0.1	15.01 ± 0.24	16.68 ± 0.57

Species contribution to stem abundance of trees ≥ 10 cm diameter at breast height and the leaf habit of the tree species are shown in parenthesis.

Extended Data Table 7 | The *F* statistics of the full factorial N-P-K experiment, testing treatment effects on foliar chemistry of the four most dominant tree species (within columns, bolded F values indicate significant effects at P<0.05) in the Budongo Forest Reserve, Uganda

Treatment	numDF, denDF[1]	C mg g⁻¹	N mg g⁻¹	P mg g⁻¹	K mg g⁻¹	Ca mg g⁻¹	Mg mg g⁻¹	S mg g⁻¹	Al mg g⁻¹	Fe mg g⁻¹	¹⁵N ‰	C:N	N:P
Celtis durandii													
N	*1, 20*	0.187	3.963	2.937	3.529	1.711	0.059	1.758	0.001	0.1386	0.705	3.126	0.361
P	*1, 20*	0.837	4.010	**7.005**	4.026	0.092	0.032	1.139	0.492	0.186	**5.155**	2.016	**5.023**
K	*1, 20*	0.222	1.450	0.635	0.948	0.000	0.564	0.022	0.392	0.038	1.842	0.845	0.042
N × P	*1, 20*	0.547	0.397	0.768	0.095	0.748	0.147	3.383	0.201	0.474	1.208	0.007	0.019
N × K	*1, 20*	0.045	0.112	0.201	0.834	0.131	0.197	1.758	1.841	**5.254**	2.469	0.010	0.109
P × K	*1, 20*	1.404	0.086	0.028	0.512	1.944	0.988	0.658	0.025	0.452	0.669	0.702	0.039
N × P × K	*1, 20*	0.829	1.383	0.225	0.642	1.481	1.655	0.772	0.058	0.000	1.111	0.594	0.185
Celtis mildbraedii													
N	*1, 15*	**6.049**	**5.535**	1.581	0.015	2.823	0.818	0.204	0.085	0.157	0.013	0.816	0.043
P	*1, 15*	0.424	1.570	0.221	1.117	0.827	0.637	0.441	0.311	1.264	1.338	4.277	0.048
K	*1, 15*	0.592	0.005	1.357	0.019	0.727	2.372	0.004	1.201	0.400	0.561	0.644	2.879
N × P	*1, 15*	1.108	0.076	0.617	0.077	0.852	2.516	**6.060**	0.034	0.844	0.024	0.398	0.971
N × K	*1, 15*	0.046	0.013	0.006	1.717	1.243	0.211	0.010	1.933	0.210	0.370	0.012	0.054
P × K	*1, 15*	0.208	0.007	0.419	0.843	1.708	1.553	2.796	0.450	1.632	0.059	0.130	0.700
N × P × K	*1, 15*	0.003	1.542	4.458	0.073	0.006	1.788	3.039	0.517	0.038	1.236	2.536	4.113
Cynometra alexandri													
N	*1, 22*	0.018	0.423	0.057	0.092	0.060	0.3367	0.545	0.866	0.761	1.672	0.332	0.226
P	*1, 22*	0.000	0.020	0.016	0.128	0.071	0.116	0.251	3.558	2.864	0.449	0.000	0.014
K	*1, 22*	2.060	0.157	0.094	0.043	0.987	0.616	1.255	1.690	1.159	1.438	0.037	0.081
N × P	*1, 22*	0.002	**5.341**	0.019	0.825	1.651	0.224	1.311	0.284	0.017	0.992	3.889	0.437
N × K	*1, 22*	0.029	0.284	1.280	0.105	4.208	0.099	2.768	1.022	1.954	0.241	0.201	0.786
P × K	*1, 22*	0.001	0.971	0.029	1.647	0.000	2.760	0.080	1.741	0.776	0.228	0.677	0.543
N × P × K	*1, 22*	0.047	0.240	0.271	0.362	3.090	0.333	2.317	0.085	0.003	0.643	0.130	0.104
Funtumia elastica													
N	*1, 24*	0.069	0.511	2.894	0.158	0.223	0.134	**4.694**	0.733	0.033	3.585	0.693	3.690
P	*1, 24*	0.002	0.511	0.578	0.380	2.036	1.900	1.891	0.461	0.761	0.294	0.542	1652
K	*1, 24*	2.914	**9.791**	0.895	3.788	**9.153**	0.377	1.440	0.013	0.136	0.031	**4.908**	0.262
N × P	*1, 24*	0.130	2.409	0.000	1.186	0.970	0.427	1.807	0.348	0.150	1.588	1.781	0.046
N × K	*1, 24*	0.412	0.511	0.082	2.452	0.116	2.350	1.969	0.000	0.589	0.713	1.234	0.171
P × K	*1, 24*	0.038	2.259	0.217	1.231	0.066	0.284	0.000	0.104	0.217	3.171	2.207	0.000
N × P × K	1, 24	1.631	0.583	0.057	0.091	0.047	0.539	2.723	0.327	2.044	0.094	0.005	0.106

Extended Data Table 8 | Nutrient resorption efficiency (mean±SE, n=4 plots) after ~1.5 years of the full factorial N-P-K experiment in the Budongo Forest Reserved, Uganda

Treatment	C	N	P	K	Ca	Mg	S
	%	%	%	%	%	%	%
Control	0.8 ± 0.4	6.2 ± 4.0	12.7 ± 5.1	27.8 ± 9.1	-56.3 ± 26.4	23 ± 11	8 ± 15
N	-0.1 ± 2.3	21.4 ± 3.8	30.0 ± 6.0	38.4 ± 9.9	-27.0 ± 15.9	28.9 ± 8	20 ± 6
P	-1.7 ± 2.9	18.6 ± 5.4	31.3 ± 5.5	42.4 ± 7.0	-6.1 ± 11.0	29.7 ± 5.5	-15 ± 14
K	-3.9 ± 3.9	13.9 ± 5.7	23.9 ± 3.9	41.2 ± 4.1	-11.9 ± 30.1	42.2 ± 6.7	8 ± 4
NP	-0.3 ± 2.8	9.0 ± 3.3	15.8 ± 8.1	36.2 ± 5.1	-36.4 ± 18.2	14.9 ± 7.6	-12 ± 13
NK	3.1 ± 2.7	16.9 ± 3.2	18.4 ± 7.0	33.9 ± 8.1	-43.8 ± 22.3	28.8 ± 14.8	-4 ± 6
PK	3.8 ± 3.0	10.0 ± 5.6	23.1 ± 13.2	23.1 ± 9.8	-46.5 ± 25.7	6.9 ± 18.4	-11 ± 6
NPK	-2.7 ± 0.8	24.6 ± 2.8	22.1 ± 2.3	43.4 ± 5.3	-0.3 ± 10.5	37.5 ± 4.2	3 ± 11

Note: Nutrient resorption efficiency (%)=(element concentrations in sunlit leaf [a] − element concentrations in leaf litter) ÷ element concentrations in sunlit leaf × 100%[76]. [a] Values of sunlit leaves representing each replicate plot were weighted by the importance value index (IVI)[72] of the tree species sampled in that plot (that is, the sum of the products of a species' nutrient content and its IVI divided by the sum of their IVIs). Trees measured comprise seven species (*Celtis durandii, Celtis mildbraedii, Celtis zenkeri, Cynometra alexandri, Funtumia elastica, Khaya anthoteca, Lasiodiscus mildbraedii;* altogether, these species contribute 67% of the entire study site's tree abundance[19]).