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Research

Soil geochemistry – and not topography – as a major driver of carbon allocation, stocks, and dynamics in forests and soils of African tropical montane ecosystems

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Summary

- The lack of field-based data in the tropics limits our mechanistic understanding of the drivers of net primary productivity (NPP) and allocation. Specifically, the role of local edaphic factors – such as soil parent material and topography controlling soil fertility as well as water and nutrient fluxes – remains unclear and introduces substantial uncertainty in understanding net ecosystem productivity and carbon (C) stocks.
- Using a combination of vegetation growth monitoring and soil geochemical properties, we found that soil fertility parameters reflecting the local parent material are the main drivers of NPP and C allocation patterns in tropical montane forests, resulting in significant differences in below- to aboveground biomass components across geochemical (soil) regions.
- Topography did not constrain the variability in C allocation and NPP. Soil organic C stocks showed no relation to C input in tropical forests. Instead, plant C input seemingly exceeded the maximum potential of these soils to stabilize C.
- We conclude that, even after many millennia of weathering and the presence of deeply developed soils, above- and belowground C allocation in tropical forests, as well as soil C stocks, vary substantially due to the geochemical properties that soils inherit from parent material.

Introduction

Tropical forests globally account for *c.* 50% of the terrestrial vegetation carbon (C) stock and one-third of the global net primary productivity (NPP) (Lewis *et al.*, 2015) and are, therefore, important components of the global terrestrial C cycle (Beer *et al.*, 2010). Nested within, montane forests represent *c.* 13% (*c.* 305×10^6 ha) of the total coverage of tropical and subtropical forests (Salinas *et al.*, 2021) with African montane forests recently highlighted as an important but greatly underestimated and understudied C store (Cuni-Sanchez *et al.*, 2021). The conservation of old-growth tropical forest is key in any effort to mitigate global climate change. African tropical forests constitute a major part of this biome, with the Congo Basin tropical forests being second only to the Amazonian forests in both C storage (Dargie *et al.*, 2017; Cuni-Sanchez *et al.*, 2021) and as an active yet declining C sink (Lewis *et al.*, 2009; Tchatchou *et al.*, 2015; Rammig & Lapola, 2021).

Research on identifying potential drivers for C dynamics in tropical forests has mostly focused on climatic parameters – that is, precipitation and temperature (Moore *et al.*, 2017; Tonin *et al.*, 2017; Hofhansl *et al.*, 2020), topographic patterns (de Castilho *et al.*, 2006; Malhi *et al.*, 2017; Jucker *et al.*, 2018) – or the effect of anthropogenic disturbance (Riutta *et al.*, 2018; Ross *et al.*, 2021). However, in many terrestrial ecosystems, soil parent material co-determines nutrient availability more so than other factors (Augusto *et al.*, 2017) with strong consequences for C cycling (Vitousek, 1984; Fernández-Martínez *et al.*, 2014; Wieder *et al.*, 2015). Owing to a lack of observational data, especially in Africa (Huang *et al.*, 2021), it is unknown whether parent material through influencing soil geochemical properties has a substantial effect on C cycling and nutrient availability in tropical forests, especially where long-term weathering has led to deeply developed, but often nutrient-depleted, soils (IUSS Working Group WRB, 2015). The complexity of the potential interplay of soil geochemistry and plant C allocation might be aggravated in tropical montane forests due to topographic controls on heterogeneity of forest landscapes (Werner & Homeier, 2015; Jucker *et al.*, 2018). Topographic features such as terrain relief, slope, and curvature strongly influence local-scale variation in soil chemistry, hydrology, and microclimate (Tiessen *et al.*, 1994; Chadwick & Asner, 2016; Xia *et al.*, 2016). As such, they directly constrain the conditions within which trees grow, driving environmental filtering, determining species habitat associations (Baltzer *et al.*, 2005; Russo *et al.*, 2008; Andersen *et al.*, 2014; Jucker *et al.*, 2018), and ultimately shaping the structure and composition of forest patches (Werner & Homeier, 2015). For instance, on ridges and steep slopes, strong competition for nutrients and water favors species with life-history traits geared towards maximizing survival (Paoli, 2006; Heineman *et al.*, 2011; Holdaway *et al.*, 2011). By contrast, forests in alluvial valleys are shaped by competition for light and generally develop taller, vertically stratified canopies (Paoli *et al.*, 2008; Banin *et al.*, 2012; Werner & Homeier, 2015), while also maintaining higher productivity and turnover rates (Aiba *et al.*, 2005; Stephenson & van Mantgem, 2005; Quesada *et al.*, 2012) Furthermore, erosional processes could potentially lead to a periodical 'rejuvenation' of soil surfaces, leading to the resurfacing of former subsoil or soil parent material that can be either more (Porder *et al.*, 2007) or less depleted in soil nutrients (Eger *et al.*, 2018; Doetterl *et al.*, 2021b).

To date, the connection between drivers of C allocation and its relationship to the controls responsible for the build-up of soil organic C (SOC) stocks in tropical forest have rarely been investigated, and never at the landscape scale from regions ($> 10\ 000\ \text{km}^2$) to catchments ($> 10\ \text{km}^2$) to local hillslopes ($< 1\ \text{km}^2$). To attenuate this crucial gap in our understanding of C cycling in tropical African forests it is necessary to collect combined vegetation and edaphic data across topographic and geochemical gradients. Owing to the wide extent of forest cover, difficult accessibility, limited field inventories, and lack of long-term monitoring sites, efforts to estimate the distribution of tropical forest biomass C stocks and associated fluxes often rely on remote-sensing techniques (Tyukavina *et al.*, 2013; Xu *et al.*, 2017). This is why it is common practice in large-scale modeling studies to use fixed ratios of shoot : root biomass/C allocation and apply allometric equations relating above- to belowground biomass to estimate ecosystem C budgets (Mokany *et al.*, 2006; Cleveland *et al.*, 2013; Gherardi & Sala, 2020). As such, the potential impact of local edaphic parameters, such as differences in soil geochemical properties and parent material, on NPP allocation in tropical forests has often been ignored or considered of secondary importance (Moser *et al.*, 2011; Moore *et al.*, 2017). In part, this is due to the assumption that nutrient cycling in deeply developed tropical soils should be largely decoupled from soil parent material (Augusto *et al.*, 2017; Doetterl *et al.*, 2021a,b) and that nutrients get recycled quickly in semi-closed systems with rapid turnover of organic litter by microbial decomposers and uptake into vegetation (Krishna & Mohan, 2017; Giweta, 2020).

However, there is reason to assume that differences in geochemical soil properties derived from parent material are likely to affect C dynamics in several ways. As such, the availability of rock-derived nutrients such as phosphorus (P), magnesium (Mg), calcium (Ca), or potassium (K) in soil depends on the concentration in the parent material source, the degree of weathering, and (potential) depletion or enrichment of certain elements in soil (Quesada *et al.*, 2010, 2020). Nutrient limitations that vary with parent material (Augusto *et al.*, 2017) may therefore drive the allocation strategies of tropical forests towards more efficient nutrient storage and uptake while minimizing leaching losses. Additionally, as a result of long periods of weathering, tropical soils are often enriched in iron (Fe) and aluminum (Al) oxyhydroxides compared with many (younger and less weathered) temperate soils (Khomo *et al.*, 2017). Fe- and Al-rich soils can typically form very stable (micro-)aggregates and complexes with organic matter (Bruun *et al.*, 2010; Torres-Sallan *et al.*, 2017). This provides a significant energetic barrier for microbial decomposers to overcome and can slow down organic matter turnover (Kleber *et al.*, 2021). Soil C stocks in tropical African forests have been shown to be determined predominantly by the potential of soils to stabilize C by these organo-mineral associations (Kirsten *et al.*, 2021; Reichenbach *et al.*, 2021). Recent studies from tropical African montane forests, for example, have demonstrated that geochemical soil properties related to the local parent material explain up to 75% of variability in SOC stocks (Reichenbach *et al.*, 2021) and were significant in explaining soil C turnover under stable, warm-humid atmospheric conditions (Bukombe *et al.*, 2021). Thus, drivers of NPP and the associated C fluxes in tropical forest systems remain unclear, as they crucially rely on the complex interplay of soil formation and nutrient availability, topography, climate, and biology (Yoo & Mudd, 2008). In this study, our objective was to improve our mechanistic understanding of NPP and C allocation strategies in tropical forests along geochemical and topographic gradients and how they link to soil properties. Here, we present the results of a 2-yr monitoring campaign on NPP components along topographic and geological gradients in African tropical montane forests. Specifically, this study is centered on the following questions:

(**1**) What is the role of soil geochemistry as a driver of NPP and C allocation in tropical montane forests? Do similarly developed forests exhibit plasticity in their root : shoot C allocation and NPP depending on soil geochemical properties? We hypothesize that above- and belowground NPP and C allocation in old-growth tropical forests are driven by soil chemical properties derived from its parent material that shape the availability of rock-derived nutrients for plant growth. Consequently, plant biomass and NPP should be higher in forest stands developed on fertile soils than on low-fertility soils. However, NPP allocation should react strongly to fertility differences in soil and we expect forests growing on poor soils to invest more in root biomass production to mine sufficient nutrients for plant growth.

(**2**) What is the role of topography as a driver of NPP and C allocation in tropical montane forests? Topography should have a modifying effect on biomass production based on established paradigms (Werner & Homeier, 2015; Chadwick & Asner, 2016; Malhi *et al.*, 2017; Jucker *et al.*, 2018). Based on this earlier work, we hypothesize that changes in water and nutrients along hillslopes should shift above- to belowground productivity, favoring slow-growing communities where water and nutrients become limited. Consequently, we expect higher NPP fine root and lower NPP litterfall and wood on slope positions. On plateaus and in valleys, a competition for light favors fast-growing communities. As a result, we expect at plateau and valley positions higher NPP litterfall and wood, and lower NPP fine root than on slopes.

(**3**) How closely are SOC stocks related to NPP and standing biomass C stocks in tropical forest soils? We hypothesize that SOC stocks are mainly controlled by the amount of C productivity and allocation to belowground biomass. Therefore, we expect that SOC stocks are higher in forest stands where root NPP and C allocation to root are high, compared with forest stands where plants invest more in aboveground NPP components. To answer these questions, we assessed C stocks and C allocation for both above- and belowground biomass and soil in old-growth forests across contrasting geochemical regions along the Albertine Rift in eastern Africa. Using linear and nonlinear models, we then determined the relationships of C allocation patterns among NPP components and C stocks to topography and soil (geo-)chemical properties.

Materials and Methods

Study regions

Study sites are located in the East African Rift Valley system in three forested (and highly protected) national parks along the Albertine Rift System at the borders between Uganda, Rwanda, and the Democratic Republic of the Congo (DRC), each situated in a distinct geochemical region: mafic magmatic rocks, felsic metamorphic rocks, and sedimentary/metamorphic rocks with a wider mixture of geochemical properties distinct from the mafic and felsic rocks (Fig. 1; Table S1) with strong topographic gradients (details later; Doetterl *et al.*, 2021a,c). The climate of the study region is classified as tropical humid with monsoonal dynamics (Köppen Af-Am). Vegetation cover in the study area is classified as closed-canopy evergreen montane forests. All forest sites (see Table S2) are similarly developed (Fig. S1; Table S3) and show the typical vegetation of tropical old-growth and primary forests (Imani *et al.*, 2017; Nyirambangutse *et al.*, 2017; Alexandra *et al.*, 2022). A recent global forest age dataset supports that all forest stands in our study area are > 300 yr old-growth forests (Besnard *et al.*, 2021). Hence, based on the available information, and although we cannot fully exclude historical disturbances, there is strong evidence that all forests investigated are in fact old growth.

Generally, soils differ in terms of nutrient content and key (biogeo-)chemical properties in the following way. The main rooting zone in mineral topsoil (0–30 cm) in the mafic region is characterized by high potential cation-exchange capacity (CEC_{pot}; 38.4 ± 5.5 cmol kg^{-1}; mean ± SD), high clay content (42.7 ± 11.1%), and high amounts of rock-derived nutrients such as P, K, Ca, and Mg. The potential of the mafic region soils to stabilize SOC with minerals is high due to a large presence of pedogenic oxyhydroxides and clay (Reichenbach *et al.*, 2021). In the felsic region, soils were characterized by low CEC_{pot} (17.6 ± 4.5 cmol kg^{-1}) and clay content (33.0 ± 5.5%) and moderate amounts of rock-derived nutrients. Soils in the felsic region were further characterized as low in pedogenic oxyhydroxides content (low potential to stabilize SOC with minerals). Soils in the sedimentary region are characterized by low soil-fertility indicators with low values in CEC_{pot} (15.3 ± 11.8 cmol kg^{-1}) and clay content (32.5 ± 13.9%) and were lower in rock-derived nutrients. Soils in the sedimentary region were further characterized by low to intermediate content of pedogenic oxyhydroxides. Topsoil SOC stocks were higher in the mafic region (145.3 ± 30.0 Mg C ha^{-1}), followed by the sedimentary region (130.0 ± 37.0 Mg C ha^{-1}) and lower in the felsic region (105.5 ± 27.0 Mg C ha^{-1}). Whereas soil C : N ratios for the mafic (10.3 ± 5.9) and felsic regions (12.5 ± 6.3) were comparably narrow, the sedimentary region was characterized by particularly wide ratios (56.4 ± 60.3). This is related to a specific feature of soils in the sedimentary region, which are rich of fossil, petrogenic organic C present in the parent material, characterized by wide C : N ratios (153.9 ± 68.5) and contributing up to 25% to total SOC (Reichenbach *et al.*, 2021). These attributes lead to generally poor-quality substrate for microbial communities that slows down organic matter turnover in soils together with the described poor fertility of the sedimentary region (Bukombe *et al.*, 2021).

Forest inventories and monitoring work along topographic and geochemical gradients

Twelve 40 m × 40 m plots under closed-canopy forest were established in March 2018 within each of the three geochemical regions, following an international, standardized protocol for C allocation and cycling assessments in tropical regions (Matthews *et al.*, 2012) and slightly modified where necessary due to local conditions. All plots are located in sloping mountainous landscapes. We classified the local topography into four topographic positions following a catena approach covering all main landforms in the area: flat plateaus/ridges (slope steepness 3–5%), upper slope (slope 9–15%), middle slope (slope 45–60%), and v-shaped valley/foot slope (slope 1–3%) (Doetterl *et al.*, 2021a). Within the plot setup, we carried out a detailed tree inventory, followed by a re-census after 2 yr. Furthermore, within this time frame, continuous NPP monitoring of litterfall and root growth was carried out in all study plots. Both inventory and NPP monitoring were done following established protocols (Malhi *et al.*, 2002; Matthews *et al.*, 2012) (for full protocol and further details to plot installation, see Methods S1 sections 'Forest inventory' and 'Biomass C stocks' and the various NPP calculations therein). NPP_{sum} in our study was calculated as the sum of components (wood growth, litterfall, and fine root production). Finally, the proportion of NPP_{sum} allocated into each component (x) was calculated using the following equation:

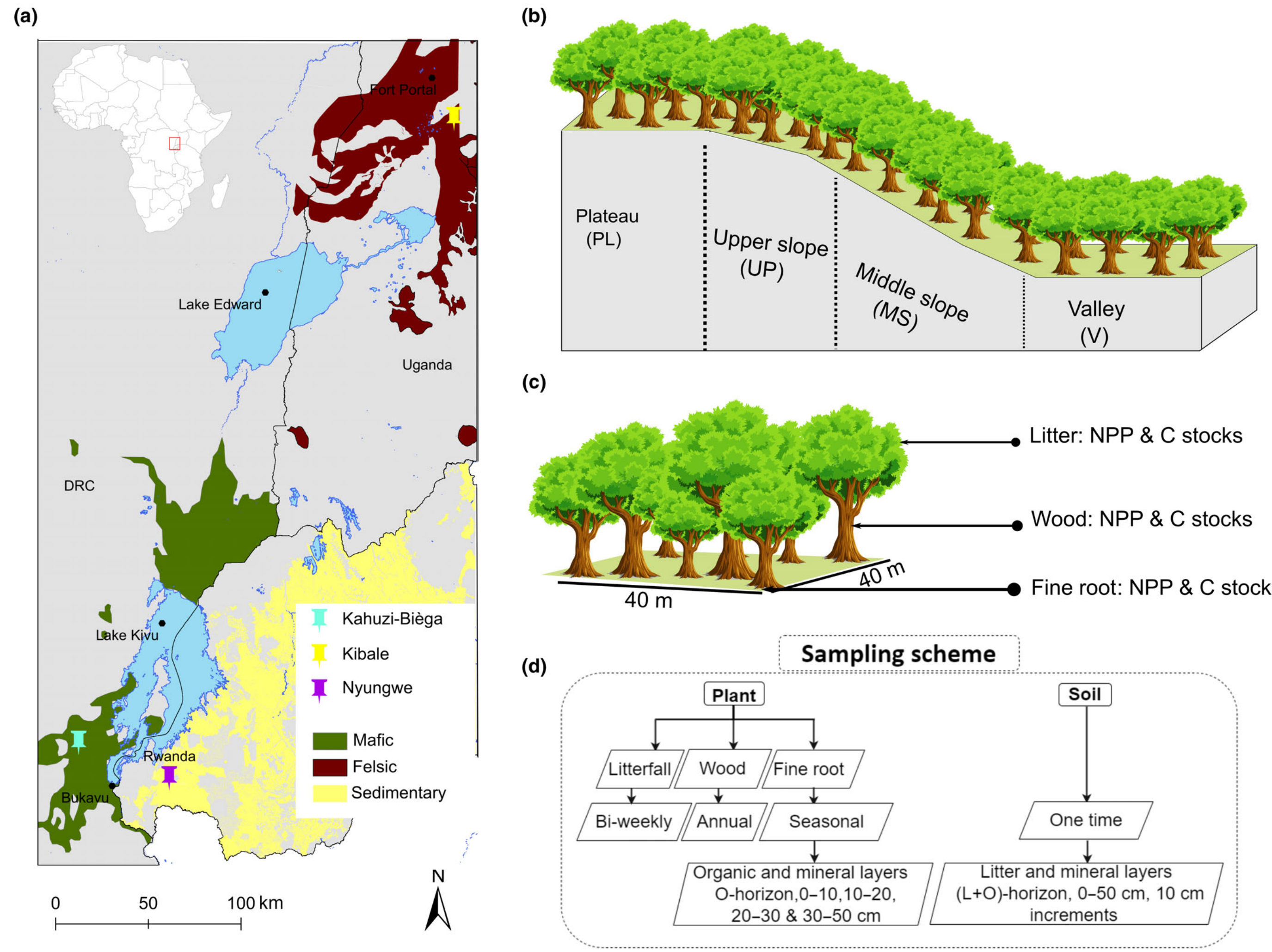


Fig. 1 Overview of the study region and location of the study sites in Central Africa with respect to the major factors investigated. (a) Geochemical regions and corresponding geology of soil parent material (i.e. mafic refers to mafic magmatic rocks, felsic refers to felsic metamorphic rocks, and sedimentary refers to sedimentary/metamorphic rocks). (b) Topographic positions following a catena approach with triplicates of topographic positions in each geochemical region. (c) Net primary productivity (NPP) and carbon (C) stocks' components investigated in this study. (d) Sampling scheme, type of collected plant biomass and soil samples, temporal resolution and soil/root sampling depth intervals.

$$\mathrm{Allocation}_x = \frac{\mathrm{NPP}_x}{\mathrm{NPP}_{\mathrm{sum}}} \times 100 \qquad \text{Eqn 1}$$

where Allocation$_x$ (%) is the NPP allocated to component x, NPP$_x$ is the absolute NPP value of a given component (litterfall, wood, or fine root), and NPP$_{\mathrm{sum}}$ (Mg C ha^{-1} yr^{-1}) is the sum of the three components. For practical reasons, we follow Poorter & Sack (2012), defining 'allocation' as the realized partitioning of C into litter, wood, and roots, noting that compounds allocated but 'lost' by processes such as volatile emission and exudation are excluded.

Assessed soil and topographic features

As part of an extensive sampling campaign (Doetterl *et al*., 2021a), organic soil litter (L and O horizons) and four 1 m soil cores were sampled across all forest plots. To assess relationships of potential soil controls on NPP components and their relative C allocation, we extracted plot-specific geochemical properties and topographic features from an existing database assembled in parallel to this study (Doetterl *et al*., 2021c). Included soil and topographic variables covered a wide range of predictors, such as soil fertility (CEC_pot, potential cation exchange capacity; ECEC_eff, effective cation exchange capacity; soil pH (pH$_{\mathrm{KCl}}$); Ca_ex, exchangeable calcium; K_ex, exchangeable potassium; Mg_ex, exchangeable magnesium; Base_ex, base saturation in CECpot; total_N, total nitrogen (N); NH$_4$, ammonium; NO$_3$, nitrate; Bio-P, bioavailable-P; total_Ca, total calcium; total_K, total K; total_Mg, total Mg; and total_P, total P), SOC stock, C : N ratio, clay, silt, and sand contents, TPI (topographic position index), TWI (topographic wetness index), SL-factor (slope length and steepness factor), slope inclination, SPI (stream power index), aspect (terrain aspect), and curvature. For further details on the assessed soil fertility indicators and topographic features, see Methods S1 ('Topography and plot installation, and C stocks of organic and mineral soil layers').

Statistical analysis

To assess species composition and similarities between the three geochemically regions, we performed a nonmetric multidimensional scaling (NMDS) on the inventory data of the plots, using the VEGAN package (Oksanen *et al*., 2013). The advantage of NMDS is that it does not rely on normally distributed data and NMDS does not use the absolute abundance of species but a rank orders approach. As such, this is a robust method for handling zero counts (i.e. where species are missing in a given plot) in a multidimensional analysis of tree diversity (Legendre *et al*., 2005). To assess differences in soil C stocks, aboveground biomass, NPP components (litterfall, wood, fine root), and the relative C allocation, across topographic positions and geochemical regions, we used the Kruskal–Wallis test available in the R package PGIRMESS (Giraudoux, 2021). For pairwise comparison of significant differences between topographic positions or geochemical regions, we used Dunn's test available in the RSTATIX package (Kassambara, 2021).

As multicollinearity between independent variables was expected due to the large number of variables and a relatively small number of aggregated observations, we conducted rotated principal component analysis (rPCA; Jolliffe, 1995) before regression analysis. Principal component analysis (PCA) linearly combines the explanatory variables, while successively maximizing the variability of the explanatory variables and representing it as a set of new orthogonal – uncorrelated – vectors. In addition to normal PCA, rPCA rotates the new axes using the 'varimax rotation method' in order to achieve simple and interpretable rotated components (RCs) (Kaiser, 1958). To map NPP components onto the RCs space, we used NPP and NPP allocation as qualitative supplementary variables. Supplementary variables, however, are not used for the determination of the principal components (Abdi & Williams, 2010). To assess the effects size and direction (positive or negative) of rotated principal components on different NPP compartments and their relative C allocations, we applied Bayesian multilevel linear mixed-effect models with intercepts set to zero to allow comparison of the effects size of rotated principal components between models for the different NPP compartments. All statistical analyses were carried out with R software (R Core Team, 2022). Further details on the parameterization and choice of our statistical analyses techniques and our quality assessments can be found in Methods S1 'Extended statistical analyses'.

Results

Patterns of aboveground biomass and soil carbon stocks across geochemical regions and topography

The three regions differ significantly in terms of dominant tree species composition and forest structure (Fig. S2; Notes S1). C stocks of the different biomass and soil components showed distinct patterns across geochemical regions (Fig. 2a). Wood C stocks were significantly higher in the sedimentary (206.4 ± 40.9 Mg C ha^{-1}) than in the felsic (117.9 ± 29.6 Mg C ha^{-1}) and mafic regions (99.1 ± 17.0 Mg C ha^{-1}) (Fig. 2a). The C stock of organic litter layers (sum of L and O horizons) in the sedimentary region (37.3 ± 5.4 Mg C ha^{-1}) was eight times that of the felsic (4.4 ± 0.9 Mg C ha^{-1}) and three times that of the mafic region (12.1 ± 3.0 Mg C ha^{-1}). Living fine-root C stocks (to 50 cm mineral soil depth) were higher in the sedimentary (4.4 ± 1.6 Mg C ha^{-1}) than in the felsic (1.7 ± 0.2 Mg C ha^{-1}) and mafic regions (1.6 ± 0.3 Mg C ha^{-1}), with a significant but small difference between the latter. Soil organic C stocks followed a different pattern than root C stocks. Soil organic C was significantly higher in the mafic (208.2 ± 22.6 Mg C ha^{-1}) than in the felsic (137.9 ± 25.3 Mg C ha^{-1}) or sedimentary regions (125.9 ± 36.7 Mg C ha^{-1}). No significant differences or consistent patterns in biomass C or SOC stocks were detectable related to the topographic position of plots in each geochemical region (Fig. 2b), following Kruskal–Wallis tests and pairwise comparison using Dunn's tests ($P < 0.05$).

Patterns of carbon allocation in net primary productivity across geochemical regions and topography

Similar to C stocks, we found differences in NPP related to the geochemical region of the respective study site (Fig. 3a). For wood, NPP_{wood} was higher in the mafic region (6.2 ± 1.8 Mg C ha^{-1} yr^{-1}), followed by the felsic (5.01 ± 1.2 Mg C ha^{-1} yr^{-1}) and then the sedimentary region (3.4 ± 1.1 Mg C ha^{-1} yr^{-1}). For leaves, $NPP_{litterfall}$ was higher in the sedimentary region (5.3 ± 0.8 Mg C ha^{-1} yr^{-1}), followed by the mafic (4.5 ± 0.6 Mg C ha^{-1} yr^{-1}) and then the felsic region (3.3 ± 0.5 Mg C ha^{-1} yr^{-1}). For fine root (in the O horizon and top 50 cm of mineral soil), NPP_{roots} was more than twofold higher in the sedimentary region (5.5 ± 2.0 Mg C ha^{-1} yr^{-1}) than in the felsic region (2.0 ± 0.5 Mg C ha^{-1} yr^{-1}), and fourfold higher than in the mafic region (1.1 ± 0.8 Mg C ha^{-1}- yr^{-1}). No significant difference or consistent pattern in NPP was detectable related to the topographic position of plots in each geochemical region (Fig. S3). NPP_{sum} was higher in the sedimentary region (14.2 ± 4.0 Mg C ha^{-1} yr^{-1}), followed by the felsic region (11.9 ± 3.0 Mg C ha^{-1} yr^{-1}) and then the mafic region (10.4 ± 2.3 Mg C ha^{-1} yr^{-1}). Based on Pearson's correlation coefficients ($P < 0.05$), NPP_{sum} was strongly positively correlated with NPP_{roots} and $NPP_{litterfall}$, but there was no relationship between NPP_{sum} and NPP_{wood} (Fig. S4). Instead, NPP_{wood} was negatively correlated with NPP_{roots} (Fig. S4). Relative NPP C allocation into wood was significantly lower in the sedimentary region (24 ± 6% of total NPP C) than in the felsic (48 ± 5%) or mafic (52 ± 6%) regions, with a nonsignificant difference between the latter (Fig. 3b). NPP C allocation into leaves was lower in the felsic (32 ± 2%) than in the sedimentary (38 ± 5%) or mafic (39 ± 3%) regions. By contrast, relative NPP C allocation to fine root was significantly different across the geochemical regions and differed by a factor of four, with higher values observed in the sedimentary region (38 ± 8%), followed by the felsic region (20 ± 4%) and then the mafic region (10 ± 4%). No significant difference or consistent pattern in

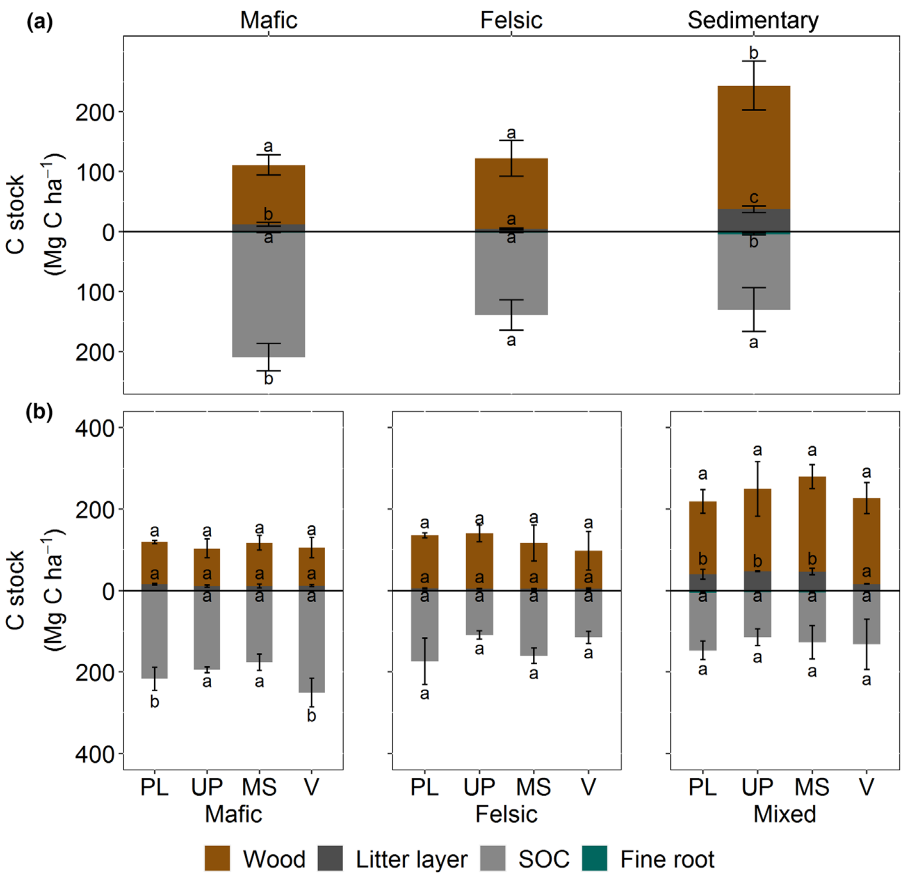


Fig. 2 (a) Carbon (C) stocks of aboveground woody biomass, organic litter layers (L + O horizon), living fine root and mineral soil organic C (SOC) across the felsic, mafic, and sedimentary geochemical regions (mean ± SD; for wood, $n = 12$ per region), for litter layer and fine root ($n = 8$, 12, and 12 for mafic, felsic, and sedimentary regions, respectively). SOC stocks were determined for the top 50 cm of the soil profile. (b) C stocks for aboveground coarse woody, litter layers (L and O horizons), living fine root, and SOC across the three geochemical regions and along topographic positions (PL, plateau; UP, upper slope; MS, middle slope; V, valley) (mean ± SD). For both panels, y-axis zero value divides aboveground from belowground stocks. Different letters on top of bars indicate significant differences between geochemical regions or topographic positions separately for each C stock component (NPP_{wood}, $n = 12$ per region; $NPP_{litterfall}$ and NPP_{roots}, $n = 8$, 12, and 12 for mafic, felsic, and sedimentary regions, respectively), following Kruskal–Wallis tests and pairwise comparison using Dunn's test ($P < 0.05$). NPP, net primary productivity.

relative NPP C allocation was detectable in relation to the topographic position of plots in each geochemical region (Fig. S3), following Kruskal–Wallis tests and pairwise comparison using Dunn's test ($P < 0.05$).

Mineral soil controls on net primary productivity and relative carbon allocation among components

The rPCA yielded four significant RCs based on chemical properties of the mineral soil layers in the main rooting zone that all together explained 84.1% of the cumulative variance of the dataset (Fig. 4; Table S4). From these components, RC1 and RC2 explained *c.* 54% of the entire variance in the dataset. RC1 was interpreted as being related to soil exchangeable base cations and predictors for RC2 related to reserve of total base cations in soil. Hence, we interpreted those RCs as 'soil exchangeable cations' (RC1) and 'soil base cation stocks' (RC2). RC3 and RC4 explained *c.* 30.1% of the variance within the dataset with varying loading of independent predictors that relate to 'soil CNP stocks and NP availability' (RC3) and 'soil texture' (RC4).

When using RCs to predict the various NPP components investigated and their distribution, we found that RC1–RC2, broadly representing various aspects of soil nutrient status and general soil fertility, together with soil texture (RC4) can explain significant amounts of variability and patterns observed in NPP and C allocation to litterfall, wood, and fine root (Fig. 5a–f). Interpreting R^2, RMSE, and ratio of performance to deviation, all models show a high to moderate performance in explaining the various components. We found that, in general, soil properties explain the patterns of relative C allocation similarly well to how they explain the absolute NPP. Additionally, we found higher explanatory power of the RCs for NPP and relative C allocation to fine root compared with leaf litterfall or wood components.

For $NPP_{litterfall}$, the selected RCs explained 52% of the observed variability and 45% of the variability in the relative C allocation to litterfall (Fig. 5a,d). Predictions of $NPP_{litterfall}$ were mainly driven by a combination of negative correlation to soil exchangeable base cations and soil texture, and a positive correlation to CNP stocks and NP availability (Fig. 5a). C allocation to litterfall was driven mostly by a negative correlation to soil textural coarseness (Fig. 5d). For NPP_{wood}, the selected RCs explained 49% of the observed variability (Fig. 5b) and 58% of the variability in the relative C allocation to wood (Fig. 5e). Predictions of NPP_{wood} and C allocation to wood were mainly driven by positive correlations to soil exchangeable base cations stocks and availability, CNP stocks and NP availability, and soil texture (Fig. 5b,e). For NPP_{roots}, the selected RCs explained 65% of the observed variability (Fig. 5c) and 64% of the variability in the relative C allocation to fine root (Fig. 5f). Predictions of NPP_{roots} and C allocation to fine root were strongly and negatively correlated to soil exchangeable base cations and soil texture (Fig. 5c,f).

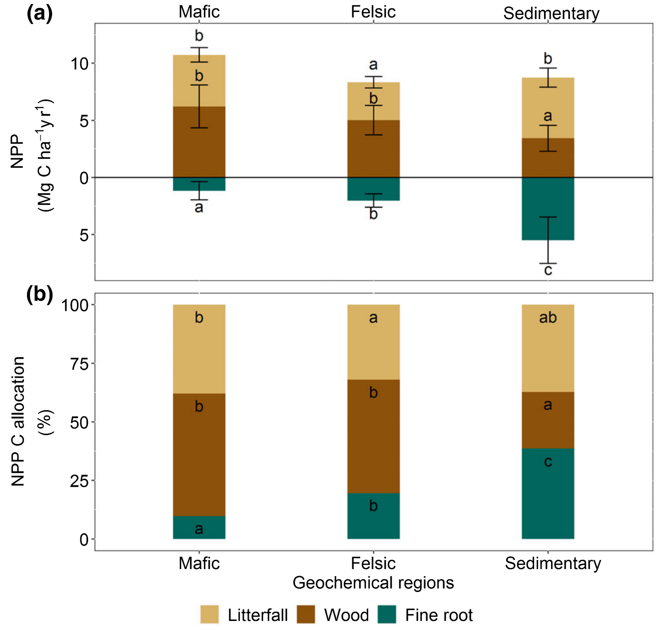


Fig. 3 (a) Net primary productivity (NPP) of biomass carbon (C) for leaf litterfall, wood, and fine root (≤ 2 mm) across the felsic, mafic, and sedimentary geochemical regions (mean ± SD). y-axis zero value divides aboveground from belowground NPP. (b) Relative NPP C allocation for leaf litterfall, wood, and fine root (as a proportion of $\mathrm{NPP_{sum}}$) tested separately for each NPP component across the three geochemical regions. For both panels, different letters on top of bars indicate significant differences between geochemical regions within each NPP component ($\mathrm{NPP_{wood}}$, $n = 12$ per region; $\mathrm{NPP_{litterfall}}$ and $\mathrm{NPP_{roots}}$, $n = 8$, 12, and 12 for mafic, felsic, and sedimentary regions, respectively), following Kruskal–Wallis tests and pairwise comparison using Dunn's test ($P < 0.05$).

Discussion

Soil parent material drives tropical forest net primary productivity and net primary productivity allocation

Across the three regions of tropical central Africa investigated, forest stands in the mafic and felsic regions (more fertile soils) showed a much higher investment in aboveground biomass (Figs 3a,b, S3a,b) than their counterparts in the sedimentary region (less fertile soil), where soils were characterized by wider C : N ratios, low bioavailable-P, and low base-cation content (Ca, Mg, and K) as well as low potential and effective CEC. Note that though $\mathrm{NPP_{wood}}$ and C allocation in wood was lower in the sedimentary region (Fig. 3a), aboveground wood C stocks and $\mathrm{NPP_{sum}}$ were higher (Fig. 2a). The contrast between $\mathrm{NPP_{wood}}$ and wood C stocks can be explained largely by how plants respond to changes in nutrient and soil fertility status. Consistent with literature (King *et al.*, 2006; Doughty *et al.*, 2018; Phillips *et al.*, 2019), we found that trees with high wood C stocks tend to grow more slowly, resulting in lower wood productivity (Figs 3a, 6c) while still accumulating considerable biomass (Fig. 2a). Indeed, our data suggest that forests dominated by trees with high wood density and slow growth rates allocate less of their annual C uptake into wood biomass but slowly accumulate and maintain high wood C stocks (Fig. 6a–c), in accordance with findings of King *et al.* (2006). Consistent with our findings, a strong relationship between trees with low wood density and higher wood productivity has also been reported in other tropical regions (Malhi *et al.*, 2004). Note that none of the study sites have been disturbed for at least the last five decades and that the forests studied are considered at their respective climax state with respect to species composition. Therefore, we argue that the trends observed (Fig. 6) are not resulting from variation in forest age but driven by edaphic factors. Furthermore, we acknowledge that differences in climatic parameters may influence NPP and C dynamics in tropical montane forest ecosystems. However, the available observational data on mean annual precipitation and mean annual temperature variability do not show a clear effect on NPP and plant growth across our study plots. This illustrates that local geochemical and edaphic differences between sites are likely more important for explaining our observations on NPP and plant growth than climatic differences are. Furthermore, recent work on tropical Afro-montane forests (Cuni-Sanchez *et al.*, 2021) and sub-Saharan African soil systems (von Fromm *et al.*, 2021) have shown a secondary and rather minor influence of climatic over (bio)geochemical controls on biomass C as well as on soil C. Contrastingly, patterns of fine-root NPP and root C allocation strongly followed the exact opposite of those trends for wood along our soil fertility gradient (Fig. 7; Table S1), with high $\mathrm{NPP_{roots}}$ on nutrient-poor soils such as those found in the sedimentary region. Contrarily, low $\mathrm{NPP_{roots}}$ was observed for nutrient-rich soils, whereby soil fertility was strongly related to geochemical regions (Fig. 3a,b). This finding is remarkable, as the forests investigated grow on soils that developed over millennia under a (at least currently) similar tropical climate and in systems where weathering has strongly altered the chemical composition of soil compared with its parent material (Doetterl *et al.*, 2021a,b).

It has been shown that tree species can alter topsoil chemical properties in tropical forest ecosystems (Bauters *et al.*, 2017). However, background information (Doetterl *et al.*, 2021a) on the geological parent material of these soils reveals that the geochemical differences between soils of the three regions investigated remain consistent with what to expect from soil formation in terms of soil chemical alteration. In addition, in deep subsoil and below the main rooting zone of plants (> 70 cm soil depth) a similar range of geochemical variability is found across the study sites as for topsoil layers. Thus, it is most likely that plant communities co-evolved with soil geochemical properties in the area and that these communities are likely to influence topsoil chemical properties in agreement with ecological theory. However, our data give a clear indication that plant community structure and the observed patterns of NPP and their relation to SOC across our sites are the result of soil (geochemical) properties that are distinct across the geological parent material due to soil formation. First, the negative correlation of C allocation to wood with standing wood biomass stocks (Fig. 6a) suggests that, in low-fertility systems (soils of the sedimentary region), forests establish communities that grow slow but can result in high (aboveground) biomass (Figs 2, 4). A closer analysis of the relationship of wood components (standing wood biomass,

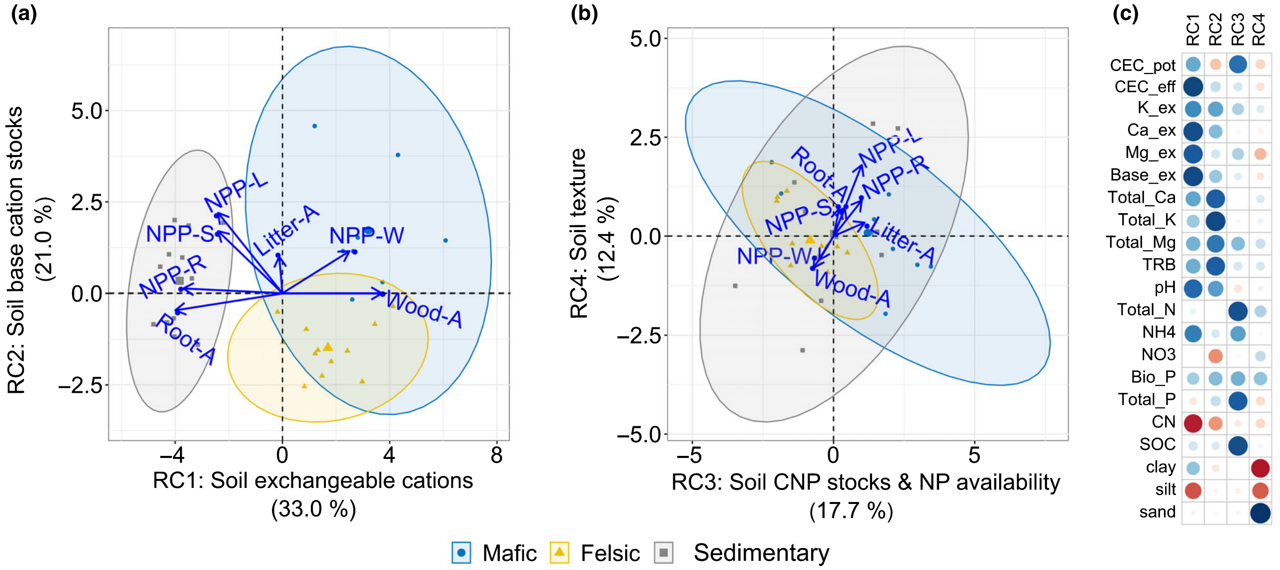


Fig. 4 Rotated principal component analysis (rPCA) of soil properties and their relation to net primary productivity (NPP) components. (a, b) The four rotated components (RCs) included, their mechanistic interpretation (on axes), and the score vectors that show the coordinate of projection of the NPP compartments and carbon (C) allocation onto the RCs plane. Note that absolute NPP and relative NPP C allocation vectors (in blue) were not included in the rPCA and are displayed here only for the purpose of visualizing their alignment with the RC space. NPP-W, NPP$_{\text{wood}}$; NPP-L, NPP$_{\text{littterfall}}$; NPP-R, NPP$_{\text{roots}}$; NPP-S, NPP$_{\text{sum}}$; Wood-A, NPP C allocation to wood; Litter-A, NPP C allocation to leaves; Root-A, NPP C allocation to root. Points and colored ellipses indicate observations within each geochemical region. The positions of the various NPP components within the panels (absolute NPP biomass C and relative NPP C allocation) indicate correlation to RC. The distance between a variable and the center indicates the quality of the variable representation on the RC map, with greater distance indicating stronger representation of a variable by the RC. CNP, carbon–nitrogen–phosphorus; NP, nitrogen–phosphorus. (c) The loading of the variables included related to soil fertility, SOC properties, and texture as soil predictors to the four RCs (for details, see Table S4).

NPP$_{\text{wood}}$, and wood C allocation) and soil properties using Kruskal–Wallis tests ($P < 0.05$) is further supportive of this interpretation, showing that wood biomass is higher where soil exchangeable bases and total base cation stocks are lower (Fig. 2a; Table S1). By contrast, according to Pearson correlation analysis ($P < 0.05$), wood growth and C allocation to wood are higher where soil exchangeable bases and total base cation stocks are higher (Fig. 7; Table S1). Similarly, our data on the chemical composition (C : N ratios) of living canopy leaves (Fig. S5) and the findings of Bukombe *et al.* (2021) provide further support for the notion that nutrient-limited systems tend to develop plant traits that are typically signs of resource conservation strategies (Grau *et al.*, 2017; Urbina *et al.*, 2021) while accumulating comparably thick litter layers (Fig. 2a,b) and thick O-horizons (Fig. S6). Second, research on plant physiology has shown that nutrient-poor soils force plants to invest more in nutrient acquisition by spending more of their energy and C resources in the nutrient uptake process, by growing more roots, fuel root exudation, and C delivered to mycorrhiza to enhance the availability of nutrients and therefore, reducing resources available for the growth of aboveground plant components (Hartmann *et al.*, 2020; Epihov *et al.*, 2021). This is consistent with evidence highlighting strong shifts in plant C allocation towards more belowground components (Fig. 2a,b) as soil nutrients become increasingly limiting (Fernández-Martínez *et al.*, 2014; Werner & Homeier, 2015). Additionally, the lower the nutrient availability in mineral soil the more the roots grew in the nutrient-rich organic litter horizons where remaining nutrients are recycled back into living biomass. In more nutrient-rich mineral soil layers, roots tended to grow more strongly in deeper soil layers (Fig. S6). Our results suggest that NPP$_{\text{roots}}$ and C allocation to root were primarily driven by exchangeable base cation availability and total cation stocks and only secondarily by N and P content (Figs 4c, 5c,d). Noteworthy is that NPP$_{\text{litterfall}}$ remained fairly constant across geochemical regions, relative to the shifts in absolute NPP$_{\text{roots}}$ and NPP$_{\text{wood}}$ (Fig. 3) and showed little to no correlation to the soil and topographic variables investigated (Fig. 7). The reasons behind this lack of responsiveness of NPP litterfall are unknown and the subject of future investigation.

In summary, our data suggest that soil geochemistry impacts tropical montane forest functioning through ecological processes. First, our data suggest that fertility constraints have a major effect on shoot : root C allocation strategies in tropical montane forests that relate predominantly to variation in the soil chemical properties, which in turn are inherited from its parent material. Indeed, a recent study conducted at the global scale has shown that rock-derived nutrient limitations are mainly driven by soil parent material (Augusto *et al.*, 2017). But the fact that these patterns hold for deeply weathered tropical soils where nutrients are recycled rather than actively acquired through weathering is unexpected and surprising (Cleveland *et al.*, 2013). When established on nutrient-poor soils, tropical forests invest significantly more C belowground biomass (Figs 4, 7).

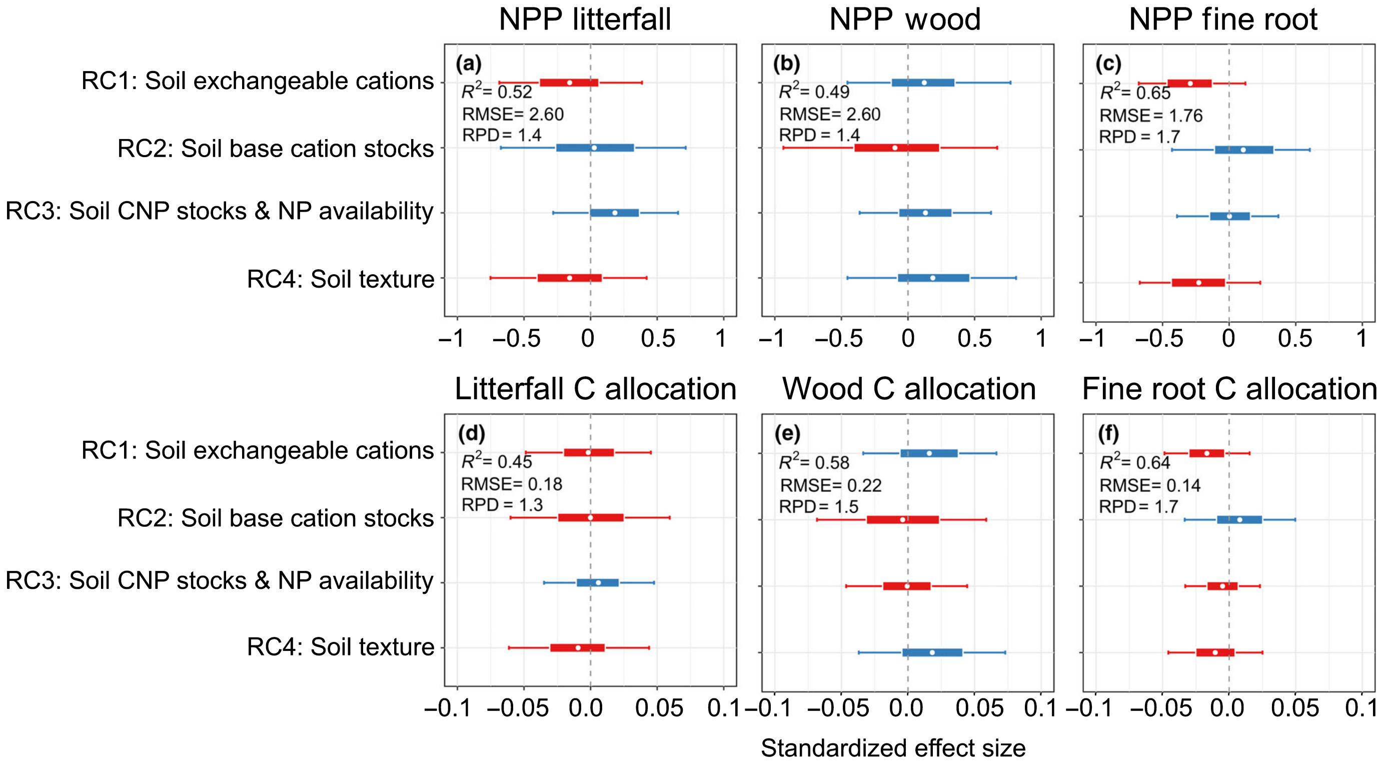


Fig. 5 Standardized effect size of the rotated principal components (RCs) as explanatory factors on net primary productivity (NPP): (a) $\text{NPP}_{\text{litterfall}}$, (b) NPP_{wood}, (c) $\text{NPP}_{\text{roots}}$, and (d–f) relative C allocation into each of these components (as proportion of $\text{NPP}_{\text{total}}$). Points in the middle of boxplots indicate mean effects size, and error bars indicate the 95% confidence intervals. The color codes indicate the direction of the effect, with blue indicating a positive effect and red indicating a negative effect on the response variable. Displayed for assessing model performance are marginal R^2 values (i.e. only fixed effects considered), RMSE, and ratio of performance to deviation (RPD). Note that *x*-axes on panels a–c and d–f are scaled differently. CNP, carbon–nitrogen–phosphorus; NP, nitrogen–phosphorus.

Second, consistent with our findings, strong relationships between nutrients and ecosystem properties, such as C-use efficiency and aboveground wood productivity, have been reported at regional to global scales (Malhi *et al.*, 2004; Fernández-Martínez *et al.*, 2014). For example, pan-tropical analyses showed that soil P can explain a significant proportion of the variation observed in NPP_{wood} (Cleveland *et al.*, 2011). However, our results (estimated effect sizes and Pearson correlation coefficients) indicate that the availability of rock-derived cations, in particular total and exchangeable Ca, Mg, and K, is an overlooked factor governing NPP and biomass allocation (Figs 5, 7).

Local topography does not control patterns of net primary productivity, carbon allocation or carbon stocks in tropical forests

Throughout the three geochemical regions of tropical African montane forests investigated, local topographic position along hillslopes did not emerge as a strong driver of NPP, C allocation, or C stocks. Though we observed smaller (nonsignificant) differences in NPP components with topography within each region, these were not consistent across components (Figs 2b, S3a–f). Based on Pearson correlation analysis ($P < 0.05$), major topographic indices representing hydrological processes and material fluxes along hillslopes did not correlate with NPP or C allocation for all components investigated (Fig. 7). However, we found weak – and not significant – negative correlations between soil erosivity indices (LS-factor and SPI) and litterfall NPP and litter C allocation (Fig. 7), suggesting a slight decrease in litter productivity with slope length and steepness. Nevertheless, the fact that all NPP and C stocks' compartments were comparable along topographic positions within each geochemical region (Figs 2, S3) suggests that productivity is likely driven by mechanisms other than topography in these old-growth intact tropical forests. Consistent with our findings, similar results have been reported in other tropical regions. An assessment of the effect of slope gradients (ranging from 0.5° to 27°) on aboveground biomass in Amazonia revealed that slope gradients did not have a detectable effect on aboveground biomass (de Castilho *et al.*, 2006). Similar to NPP, studies on SOC stocks and soil C turnover have shown that the effect of topography in our investigation sites is rather limited to differences related to hydrological conditions between valley and nonvalley positions of the local hillslopes (Bukombe *et al.*, 2021; Reichenbach *et al.*, 2021). Although it has been shown that topography can influence tropical forest structure as well as water and nutrient availability (Jucker *et al.*, 2018), our findings provide evidence that topographic features at the hillslope scale, in the absence of severe waterlogging, are not driving plant NPP and C allocation strategies in our study system. Additionally, our findings suggest that the lack of strong effects of

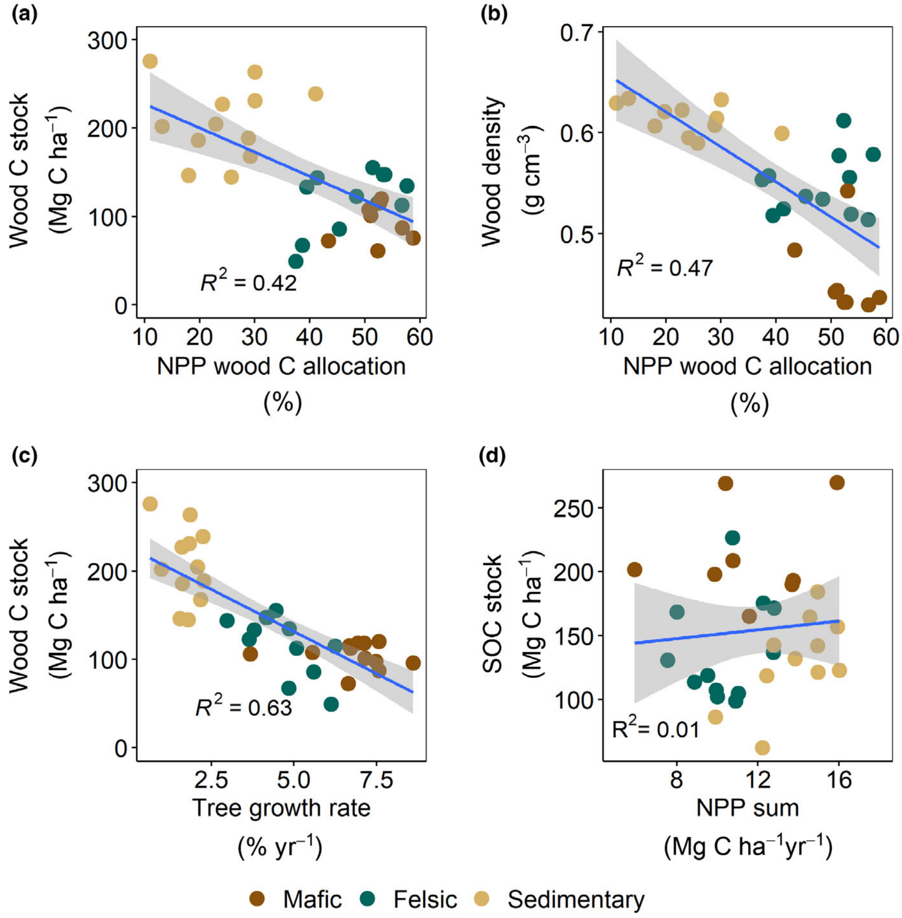
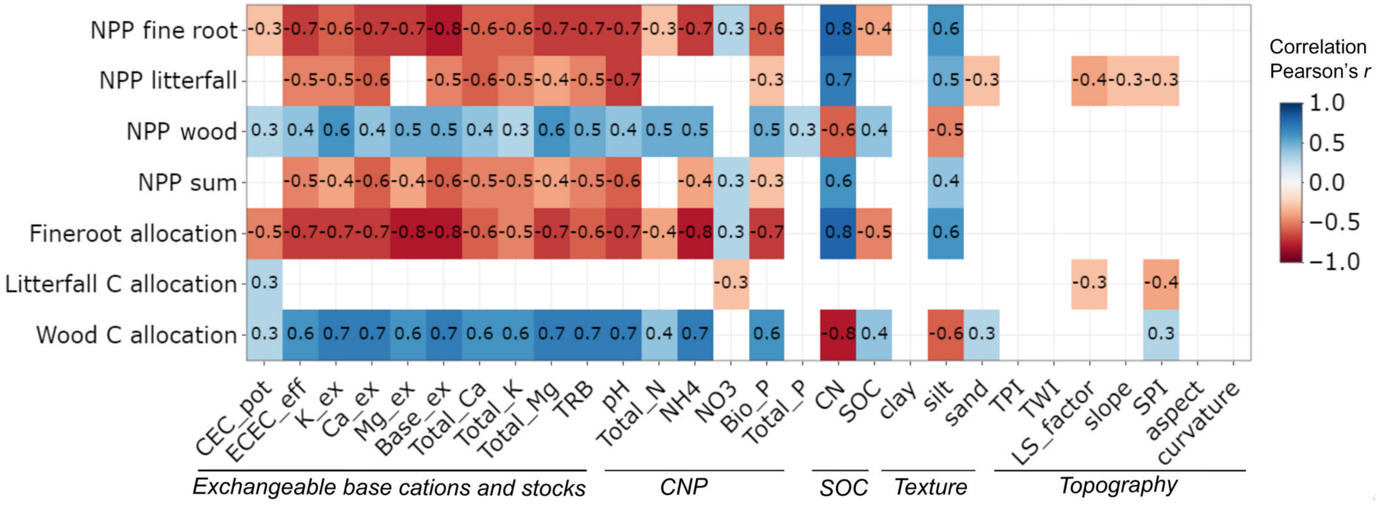


Fig. 6 (a) Relationship between wood carbon (C) stocks and wood net primary productivity (NPP_{wood}) C allocation; (b) relationship between wood density and NPP_{wood} C allocation; (c) relationship between tree growth rate and wood C stocks; (d) relationship between soil organic C (SOC) stocks and NPP_{total} for the three geochemical regions investigated. The points represent average values per plot (n = 8, 12, and 12 for mafic, felsic, and sedimentary regions, respectively). The blue line indicates ordinary least square regression function, and the gray shaded area indicates the 95% confidence interval ($P < 0.05$).



	CEC_pot	ECEC_eff	K_ex	Ca_ex	Mg_ex	Base_ex	Total_Ca	Total_K	Total_Mg	TRB	pH	Total_N	NH4	NO3	Bio_P	Total_P	CN	SOC	clay	silt	sand	TPI	TWI	LS_factor	slope	SPI	aspect	curvature
NPP fine root	-0.3	-0.7	-0.6	-0.7	-0.7	-0.8	-0.6	-0.6	-0.7	-0.7	-0.7	-0.3	-0.7	0.3	-0.6		0.8	-0.4		0.6								
NPP litterfall		-0.5	-0.5	-0.6		-0.5	-0.6	-0.5	-0.4	-0.5	-0.7				-0.3		0.7			0.5	-0.3			-0.4	-0.3	-0.3		
NPP wood	0.3	0.4	0.6	0.4	0.5	0.5	0.4	0.3	0.6	0.5	0.4	0.5	0.5		0.5	0.3	-0.6	0.4		-0.5								
NPP sum		-0.5	-0.4	-0.6	-0.4	-0.6	-0.5	-0.5	-0.4	-0.5	-0.6		-0.4	0.3	-0.3		0.6			0.4								
Fineroot allocation	-0.5	-0.7	-0.7	-0.7	-0.8	-0.8	-0.6	-0.5	-0.7	-0.6	-0.7	-0.4	-0.8	0.3	-0.7		0.8	-0.5		0.6								
Litterfall C allocation	0.3													-0.3										-0.3		-0.4		
Wood C allocation	0.3	0.6	0.7	0.7	0.6	0.7	0.6	0.6	0.7	0.7	0.7	0.4	0.7		0.6		-0.8	0.4		-0.6	0.3					0.3		

Fig. 7 Pearson correlations between geochemical soil properties used in our analysis as explanatory variables for net primary productivity (NPP) (fine root, litterfall, wood) and the corresponding relative NPP carbon (C) allocation as response variables. Blank cells indicate nonsignificant correlations, $P \leq 0.05$. Note (1) the absence of strong correlations between litterfall C allocation and soil variables, and (2) the absence of strong correlations between soil organic C (SOC) stocks and NPP litterfall or C allocation.

topography on NPP, C allocation, or C stocks is an indicator that lateral fluxes of soil and water in our study sites do not significantly influence soil nutrient dynamics (Reichenbach *et al.*, 2021; Wilken *et al.*, 2021). Though erosional processes have been shown to be significant for tropical montane landscape denudation at geological timescales (Montgomery, 2007; Flores *et al.*, 2020), there is no indication that erosion has altered the soil landscapes in our study systems under intact tropical forest cover

(Wilken *et al.*, 2021). For the same area, Doetterl *et al.* (2021a) reported several meters of deeply weathered soils along slope transects. It is therefore astonishing that, in deeply developed soils, (bio)geochemical variables retain a strong explanatory power for NPP and C dynamics. We argue that the explanatory power of soil chemistry, especially for wood and root growth (Figs 3, 5), suggests that NPP patterns are driven by soil properties that relate much more to the regional parent material than to topography.

No relationship between net primary productivity carbon input and soil organic carbon stocks in weathered tropical forest soils

Global land-surface models generally simulate an increase of SOC stocks with plant NPP (Todd-Brown *et al.*, 2013; IPCC, 2019). Root C input in particular is presumed to be strongly linked and correlated to SOC stocks (Dijkstra *et al.*, 2021), a relationship that is also implemented this way in many assessments of tropical belowground C stocks (Saatchi *et al.*, 2011; Spawn *et al.*, 2020). However, in the three Afro-tropical montane forests investigated, SOC stocks did not reflect or relate to either below- or aboveground NPP and biomass C stocks (Figs 2a, 3a) or to $\mathrm{NPP}_{\mathrm{sum}}$ of the systems investigated (Fig. 6d). Instead, SOC stocks were higher where root C NPP and stocks were lower (Figs 2a, 3a). These results suggest that, although soil nutrients and fertility emerged as the main drivers of plant NPP and C allocation strategies, C storage and its persistence in soil are likely driven by mechanisms other than C input. Namely, the potential of soils to stabilize SOC through various mineral-related stabilization mechanisms that are present or lacking in a given geochemical context (Khomo *et al.*, 2017; Rasmussen *et al.*, 2018; Traoré *et al.*, 2020; von Fromm *et al.*, 2021). Indeed, data for the top 50 cm reported for our study sites shows that the sum of organically complexed, amorphous and crystalline Al and Fe (hydro-)oxides were high in soils developed on mafic compared with their counterparts in the felsic and sedimentary regions (Doetterl *et al.*, 2021a). Recent studies suggest that high amounts of pedogenic Fe and Al (hydro-)oxides in the mafic region are responsible for the efficient stabilization of C inputs through formation of organo-mineral complexes that represent an additional barrier for microbial decomposers to overcome (Reichenbach *et al.*, 2021; von Fromm *et al.*, 2021). In addition, pedogenic, secondary Fe- or Al-oxides, which are often dominating in highly weathered tropical soils such as the ones investigated in our study sites, can improve the stability of aggregates and ultimately increase soil C storage potential (Quesada *et al.*, 2020; Kirsten *et al.*, 2021). In line with this assessment, a recent study on laboratory-based specific heterotrophic soil CO_2 respiration of the soils investigated showed that CO_2 respiration was generally lowest in mafic soils of our study region (Bukombe *et al.*, 2021; Reichenbach *et al.*, 2021). In combination with the results of our current study (Fig. 2), these findings suggest that soil C input of tropical forests generally exceeds the C stabilization potential of deeply weathered tropical soils given the high annual C input (Lewis *et al.*, 2009; Sayer *et al.*, 2011) and high turnover rates (Raich & Schlesinger, 1992). This finding has potentially large implications in the way belowground C stocks and dynamics have to be assessed in the future. Our data show that relationships between NPP, biomass, and SOC stocks in tropical forests are more soil property driven than what is currently shown in large-scale assessments (Del Grosso *et al.*, 2008; Todd-Brown *et al.*, 2014; Sha *et al.*, 2022) or represented by inland surface models (Baartman *et al.*, 2018; Thum *et al.*, 2020) (Figs 2, 3). Our findings point at the necessity of measuring SOC stocks directly, instead of deriving them from aboveground biomass proxy data.

There are still severe limitations and challenges in conducting field experiments in complex tropical forests that aim to understand soil–plant interaction. For example, the long time (decades) needed to develop mature forest plantations in tropical systems makes it difficult to establish a realistic experimental setup to further disentangle the role of soil geochemistry on forest NPP following long-term manipulations. Likewise, nutrient addition experiments can be greatly informative, but are difficult to implement, and the response time of species composition and forest structure to changes in soil geochemistry are well beyond the time frame of most research funding cycles (Sullivan *et al.*, 2014). Hence, new approaches will be needed to explore the mechanistic linkages between rock-derived nutrients varying with the weathering status of soil and soil parent material as well as their potential control on C dynamics in low-fertility systems. These approaches should include a combination of field experiments and detailed long-term observational setups with full NPP monitoring across spatial scales making it possible to integrate soil geochemical changes occurring at longer timescales to short-term responses of the biosphere to environmental change.

Conclusions

Our findings suggest a strong control of local edaphic factors on tropical forest C stocks and dynamics. This adds substantial and previously unknown complexity that needs to be unraveled to better understand plant–soil interactions and their consequences for biogeochemical cycles in the tropical ecosystems investigated. We found that differences in soil fertility as a result of soils developing from varying parent material – and not topography – have a significant effect on NPP and the root : shoot C allocation in old-growth African tropical montane forest ecosystems. Despite many millennia of weathering under warm, humid conditions, soil fertility indicators varied systematically across geochemical regions and were identified as important factors driving NPP and C allocation. Afro-montane tropical forests growing on more fertile soils allocated less NPP to root and more to wood than their counterparts in less fertile soils. Though the effect of geochemistry on NPP and C allocation across the study sites was clearly distinct, local topography did not influence the variability in NPP and C allocation. Importantly, SOC stocks were not related to vegetation C input and biomass C stocks, with soils seemingly exceeding their maximum potential to stabilize C despite high input.

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Author contributions

SD led the project; SD, MB and PF designed the research; SD, PF, MB, BR and BB designed the field experiments; BB, LKK, DIM and LNC established experimental plots, conducted the sampling campaigns and monitoring; BB compiled and analyzed the data, PB, MC, IM and KV assisted in the assessment of forest community structure and characteristics. All authors interpreted the data, BB, MB and SD led the writing of the manuscript, and all authors contributed to the writing of the paper.

Competing interests

None declared.

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Data availability

All data used for the analyses of this study are publicly available and are published in an open-access project-specific database with a separate DOI at https://doi.org/10.5880/fidgeo.2021.009 as part of Doetterl *et al.* (2021a,c).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Contribution of each diameter class to the total number of trees per unit area.

Fig. S2 Species composition and similarities across geochemical regions.

Fig. S3 Net primary productivity (NPP) and NPP allocation for three components across geochemical regions and along topographic positions.

Fig. S4 Correlations between net primary productivity (NPP) and NPP allocation.

Fig. S5 Carbon : nitrogen ratio of living leaves and litter layer for the three geochemical regions.

Fig. S6 Relative root biomass along soil depth for the three geochemical regions.

Methods S1 Detailed descriptions of study sites, existing data, protocols, and assessment methods.

Notes S1 Results of forest structure and species composition.

Table S1 Mineral soil properties of the three geochemical regions.

Table S2 General plot information.

Table S3 Forest stands' characteristics across the three geochemical regions investigated.

Table S4 Rotated principal components and their mechanistic interpretation.