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ORIGINAL ARTICLE

Carbon allocation and tree diversity: shifts in autotrophic respiration in tree mixtures compared to monocultures

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Abstract

Mixed species forests are known to have a higher gross primary productivity (GPP) and net primary productivity (NPP) than forests containing only one single tree species. Trees growing in mixtures are characterized by higher autotrophic respiration (R_a), this results in a lower carbon use efficiency of mixed species forests compared to monocultures. The pathway responsible for the high quantities of carbon lost through respiratory pathways is still unclear. Here, we present the only existing measurements evaluating tree mixture effects based on stem CO_2 efflux (E_{stem}), scaled to woody respiration (R_w) on stand level. We conducted predawn E_{stem} measurements on five tree species in an experimental tree plantation in Central Panama. E_{stem} was scaled to the entire plot level woody respiration (R_w). Annual R_w was on average 0.25 ± 0.08 Mg C ha^{-1} in the monocultures and 0.28 ± 0.10 Mg C ha^{-1} in mixed species stands. In mixtures, annual R_a was more than three times higher than in monocultures. As mean R_w was almost constant across the mixture types and R_a varied largely, leads to the conclusion that mixed species plots allocate a higher amount of carbon toward respiratory processes in leaves and roots. This was supported by no significant differences in the mixture effects on the growth respiration relationship.

Keywords Ecosystem respiration · Forest productivity · Mixture effects · Sardinilla project · Stem respiration

Introduction

Forest ecosystem respiration can be divided into autotrophic and heterotrophic respiration. Autotrophic respiration is respiration by all organisms in a forest able to assimilate carbon in the process of photosynthesis, whereas heterotrophic respiration is by organisms not able to do photosynthesis. In forests, trees are responsible for most of the photosynthesis and most of the autotrophic respiration (e.g. Wofsy et al. 1993). The proportion of assimilated carbon allocated to respiratory processes varies largely between forest ecosystems and has been found to depend largely on forest age, disturbance, and species composition (DeLucia et al. 2007). Tropical forests are known to use assimilates less efficiently than most the other forest ecosystems worldwide (Malhi 2012; Fernández-Martínez et al. 2014). In very diverse tropical ecosystems, Kunert et al. (2019) showed that differences in carbon use efficiency, thus the allocation of assimilated carbon towards the growth of new biomass, are partly explained by tree diversity and complementarity mechanisms between different tree species. Such effects of tree species mixtures have been observed in many ecosystem processes (Piotto et al. 2004). For example, various studies found higher forest productivity of mixed species stands compared to monospecific stands (Forrester et al. 2004; Healy et al. 2008; Nelson et al. 2012). Further, a typical characteristic of mixed forests is better decomposition rates and nutrient retention (Scherer-Lorenzen et al. 2007; Oelmann et al. 2010; Zeugin et al. 2010). Mixing species had further positive effects on water cycling in forests, especially the water uptake and water use pattern of trees (Gebauer et al. 2012; Kunert et al. 2012; Schwendenmann et al. 2015; Forrester 2015). Whereas overall carbon cycling and carbon pool in mixed species have

Key message Predawn stem CO_2 efflux measurements in a tree diversity experiment revealed higher carbon allocation toward respiratory processes of leaves and roots than wood respiration.

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been previously studied (Potvin et al. 2011), little attention has been given to autotrophic respiratory processes and how they are affected by tree mixture effects.

CO_2 emitting out of tree organs comes from carbon the tree used to either grow or maintain living cells (Amthor 2000), tree autotrophic respiration is thus happening in leaves and all aboveground and belowground woody tissue. Besides other respiring tree organs, a great fraction of the autotrophic respiratory activity is happening in the tree stems, and accordingly CO_2 emitting out of the tree stems is an important compartment of the carbon budget of the forest (Jassal et al. 2007). In tropical forests, stem CO_2 efflux (E_{stem}) is making up to 20% of the carbon lost by trees through autotrophic respiration (Chambers et al. 2004; Malhi 2012). However, there have been certain concerns about the methodology of assessing E_{stem} on the ecosystem level in recent years due to possible stem-internal transport and re-fixation processes resulting in large dial variations of E_{stem} (Teskey et al. 2008; Trumbore et al. 2013; Hilman et al. 2019). It remains unclear to what portion of CO_2 emitting out of the tree stem at breast height originates locally by respiratory processes involving phloem-transported soluble sugars and storage reserves (Muhr et al. 2018), or to what portion it is imported with the xylem sap from other tree organs (Teskey and McGuire 2002; Aubrey and Teskey 2009; Bloemen et al. 2013b) have shown that a significant amount of dissolved CO_2 originating from the tree base gets recycled in aboveground tree organs. Accordingly, a significant amount might be re-fixated by corticular photosynthesis influencing the long-term efflux from tree stems (Bloemen et al. 2013a; Tarvainen et al. 2018). Constant values of E_{stem} in tropical trees have been reported from continuous measurements during early morning and before sunrise (Kunert and Mercado Cardenas 2012; Kunert 2018). For example, Kunert (2018) showed that the variation in predawn E_{stem} at the tree base and breast height was less than 5% over several hours. During this time, E_{stem} might come closest to actual stem respiration rate, as there is no significant transport with the transpiration stream and possibly only limited re-fixation through enzymatic pathways.

Besides the problem of assessing stem respiration rates, upscaling of E_{stem} to whole tree and plot level woody respiration is accompanied by certain difficulties. Various studies intended to scale E_{stem} from measurements at breast height to entire tree woody respiration (R_w) by using live tissue volume at the place of measurement and then estimate the total amount of woody respiration by calculating the total amount of living woody cells of a tree (see for example Ryan and Waring 1992; Ryan et al. 1997). Scaling living tissue from subsamples to the entire tree level carries some artifacts itself, e.g. due to variation of respiratory activity of different cells in different seasons (Sprugel 1990) and the challenge of estimating live sapwood and its activity in tropical trees (Aparecido et al. 2015, 2019). Other studies tried to upscale E_{stem} to R_w by using the stem surface area with relative general non-species-specific equations to estimate the bole surface (Chambers et al. 2004). However, species-specific allometric equations to calculate volume (or biomass) are available for many ecosystems and species. Instead of using a very unspecific equation for all species to calculate the surface, the volume could be used to upscale E_{stem}. The surface area and volume are strongly correlated parameters in biology and much better results should be achieved.

Despite, some existing studies intending to scale E_{stem} measurements to the ecosystem level, most studies used the described and very controversial method of daytime E_{stem} to scale to the individual or stand level (Chambers et al. 2004; Rowland et al. 2018). Here, we present some underpinning data to postulate that predawn measurements, instead of daytime measurements, could be used to assess E_{stem} if long-term continuous measurements are not possible. Further, we use this predawn approach and present a study on mixture effects on tree respiration. The study was conducted in an experimental forest plantation in Central Panama, which was designed to study the effects of tree mixtures on tree community performance (Scherer-Lorenzen et al. 2005). E_{stem} values were scaled on plot-level fluxes with an efflux-biomass relationship by using species-specific allometric equations and compared to existing literature values for autotrophic respiration on the plot level (Kunert et al. 2019).

Materials and methods

Study site

We conducted this study in a planted forest near the village of Sardinilla in Central Panama (9°19′N, 79°38′W) situated approximately 50 km to the North of Panama City. The elevation of the site is approximately 70 m above sea level. The climate is typical for a tropical moist lowland forest with 2300 mm of rainfall per year and a mean temperature of 26.2 °C (Kunert and Mercado Cardenas 2015). There is a distinct dry season from January to March. The surrounding of Sardinilla was clear-cut in the 1950s for extensive cattle farming (Scherer-Lorenzen et al. 2005). At the study site, six native species were planted in 45 × 45 m plots with 3-m spacings of varying tree species richness in 2001. The six selected species were characterized by different relative growth rates (RGR) observed in the 50 ha CTFS-ForestGEO plot on Barro Colorado Island (Scherer-Lorenzen et al. 2005). The fast-growing species were *Luehea seemannii* Triana & Planch (*Malvaceae*) and *Cordia alliodora* (Ruiz & Pav.) Oken (*Boraginaceae*) (RGR of 9.1% and 7.0% per year respectively). The intermediate fast-growing species were *Anacardium excelsum* (Bertero ex Kunth) Skeels

(*Anacardiaceae*) and *Hura crepitans* L. (*Euphorbiaceae*) (RGR of 5.9% and 4.0% per year, respectively). The slow-growing species were *Tabebuia rosea* (Bertol.) Bertero ex A.DC. (*Bignoniaceae*) and *Cedrela odorata* L. (*Meliaceae*) (RGR of 3.4% and 2.3% per year, respectively). Each species was planted in two monoculture plots; further, six plots were established with different species combinations of three different species per plot. All six species are combined in six 6-species plots (Table 1). There was a die-off event of all planted *Cordia alliodora* trees in the first year. For the analysis, we used the actual diversity in the plots at the time of the study. Accordingly, all three tree species were represented in a monoculture, and either one of the three 2-species mixtures or the three 3-species mixtures (in the following referred to as 2/3-species mixtures) and all surviving species in the 5-species mixtures.

Stem CO_2 efflux measurements

We measured *the* E_{stem} of 60 trees at breast height (1.3 m, either below or above the metal dendrobands depending on where we found a better suitable bark surface) during the early wet season in July 2011 on the same trees described in the study by Kunert et al. (2012), where each species was replicated four times in each mixture type. We conducted a second measurement campaign in late October 2011, which is during the peak-wet season. During the campaign in October 2011, we aimed to remeasure all 60 trees again, however, we could only measure 34 trees before the instrument broke on the third day during a sudden rain shower. Comparing the existing values from two measuring campaigns suggest that there was no large variation between the two dates (Fig. 1). The regression was close to the 1:1 line ($y = 1.05x$, $R^2 = 0.77$, $p < 0.001$) suggesting that E_{stem} was relatively stable on different days probably due to the low variation in mean daily temperatures throughout the year in the early morning hours. All trees were fully foliated during the measurements and had all souring neighbors of a given mixture type. Due to the very controversial discussion on the daily variation of E_{stem} due to internal transport processes, we tried to find a good time during the day to get representative measures of E_{stem}. We summarized values from various continuous measurements of E_{stem} on tropical trees and found that predawn values are highly correlated with daily mean values (Fig. 2). Hence, we decided to measure E_{stem} predawn when internal transport processes are low (Fig. 3) and assumed that those values are representative of daily mean E_{stem} and could easily be projected to annual values. The predawn measurements were carried out on four consecutive days, allowing to measure one tree individual per species and mixture type per day (15 trees per day). We measured E_{stem} with a closed dynamic chamber system with a similar setup described in Chambers et al. (2004) and applied the measuring protocol and calculations by Marthews et al. (2012). In brief, the system had an infrared gas analyzer (IRGA, LI 820, LiCor, Lincoln, Nebraska, USA) with the airstream controlled by a flow control unit allowing a constant flow rate of 0.5 L min^{-1}. The chamber to enclose and measure the rate of CO_2 emitting out of the tree stem was a semi-cylindrical, aluminum shielded polyvinylchloride (PVC) chamber with a volume of 250 mL. The chamber had a height of 15 cm and an inner diameter of 5.9 cm. For the measurement, the chamber was sealed to the tree stems with three tie-down straps on top of a frame of flexible closed porous foam for about two to three minutes. After each measurement, we tested if the chamber had any leaks. The output of the IRGA was recorded with a single-ended voltage recorder (TandD VR-71; T&D Corporation, Shimadachi Matsumoto City, Japan) every 5 s. E_{stem} was calculated from the voltage output by the methods described in Chambers et al. (2004). Briefly, E_{stem} (µmol $m^{-2\,s-1}$) was calculated as.

$$E_{stem} = \left(\frac{PV}{RTA}\right)\frac{dC}{dt'} \quad (1)$$

where P is the standard barometric pressure (Pa), V the volume of the chamber, R the universal gas constant, T the bark surface temperature of a tree (K), A refers to the projected area on the tree surface of the chamber and dC/dt' the increase of CO_2 inside the chamber in time over time. The temperature of the bark surface was measured after each measurement with an infrared thermometer (IR 260-8 S, Voltcraft, Conrad Electronic SE, Hirschau, Germany). The annual growth rate of the trees was assessed with homemade metal dendrometer bands.

Upscaling of stem CO_2 efflux to plot level

To upscale E_{stem} from individual tree level measurements to plot level, we scaled first the chamber measurements to the entire circumference of the tree. Therefore, we calculated the total CO_2 efflux for a 15 cm high segment (E_{disc}) equal to the chamber height. We assumed that E_{stem} would be relatively equal all around the surface of the stem disc exposed to the atmosphere. E_{disc} was calculated as

$$E_{disc} = E_{stem}\left(\frac{DBH\pi}{W}\right) \quad (2)$$

where W is the width of the chamber. In the following, we compared E_{disc} to the tree's conductive sapwood area (Kunert et al. 2012 estimated the conductive xylem area of all trees by conducting sap flux profile measurements) and the carbon content of the stem segment (C_{disc}). We calculated C_{disc} by first multiplying the volume of the stem disc with the species-specific wood density and then calculating

Table 1 Summary of the data set from the experimental plantation in Panama

Plot No	Mixture	Species*	Mean DBH[1)] (cm)	Mean H[1)] (m)	Mean LAI[1)] $m^2\ m^{-2}$	Biomass stocks Mg C ha^{-1}	GPP[2)] Mg C ha^{-1}	NPP[2)] Mg C ha^{-1}	R_a[3)] Mg C ha^{-1}	R_w Mg C ha^{-1}	Uncertainty R_w %
LS1	monoculture	LS	16.3 ± 7.7	9.3 ± 1.7	3.22 ± 0.60	53.21 [A]	10.11 [A]	8.42	1.69 [A]	0.33 [A]	4.9
AE2	monoculture	AE	8.1 ± 4.8	5.8 ± 1.8	2.44 ± 0.65	13.27 [A]	3.02 [A]	2.20	0.82 [A]	0.25 [A]	8.5
HC1	monoculture	HC	5.4 ± 4.4	3.6 ± 1.7	1.79 ± 0.46	15.50 [A]	4.69 [A]	3.67	1.02 [A]	0.12 [A]	12.3
CO2	monoculture	CO	7.9 ± 3.8	9.2 ± 3.3	0.80 ± 0.60	17.28 [A]	2.31 [A]	1.98	0.33 [A]	0.25 [A]	6.2
TR1	monoculture	TR	10.4 ± 5.1	6.2 ± 1.7	1.28 ± 0.53	37.49 [A]	4.38 [A]	3.11	1.27 [A]	0.27 [A]	6.7
T1	2-species	CO;HC	11.4 ± 7.1	6.9 ± 3.8	1.91 ± 0.46	15.89 [A]	1.63 [A]	1.09	0.54 [A]	0.17 [A]	13.2
T2	3-species	TR;AE;LS	13.2 ± 8.6	9.2 ± 3.1	2.74 ± 0.58	48.92 [A]	10.33 [A]	8.81	1.52 [A]	0.12 [A]	6.8
T3	3-species	LS;CO,AE	11.8 ± 8.4	7.6 ± 3.4	2.90 ± 0.48	22.93 [A]	7.19 [A]	4.16	3.03 [A]	0.44 [A]	9.6
T4	3-species	LS,CO,HC	12.8 ± 7.3	9.3 ± 4.5	2.57 ± 1.13	36.09 [A]	6.89 [A]	2.14	4.75 [A]	0.20 [A]	5.7
T5	2-species	HC;TR	10.5 ± 5.0	6.7 ± 2.0	2.68 ± 0.54	23.80 [A]	3.52 [A]	2.50	1.02 [A]	0.22 [A]	9.1
T6	2-species	TR;AE	10.0 ± 6.3	5.0 ± 1.6	1.64 ± 0.59	15.57 [A]	3.14 [A]	2.70	0.44 [A]	0.30 [A]	10.0
A1	5-species	LS;AE;HC;CO;TR	11.0 ± 6.1	6.1 ± 6.1	2.30 ± 0.83	23.94 [A]	8.72 [A]	2.40	6.32[B]	0.39 [A]	9.5
A3	5-species	LS;AE;HC;CO;TR	14.3 ± 8.2	7.9 ± 3.1	2.95 ± 0.59	33.43 [A]	9.44 [A]	5.19	4.25 [B]	0.27 [A]	8.0
A4	5-species	LS;AE;HC;CO;TR	13.6 ± 8.4	8.8 ± 3.3	2.62 ± 0.99	37.30 [A]	9.32 [A]	5.14	4.18 [B]	0.29 [A]	7.7
A5	5-species	LS;AE;HC;CO;TR	10.7 ± 6.8	6.8 ± 7.1	2.14 ± 0.99	21.99 [A]	9.63 [A]	3.01	6.62 [B]	0.39 [A]	9.5

. Mean diameter at breast height (DBH), mean tree height (H) and mean leaf area index (LAI) are given with standard deviation. Values for biomass stocks, annual gross primary productivity (GPP), annual autotrophic respiration (R_a) and annual woody respiration (R_w) are absolute values

*LS: *Luehea seemannii*; AE: *Anacardium excelsum*; HC: *Hura creptitans*; CO: *Cedrela odorata*; TR: *Tabebuia rosea*

[1)] Literature value from Kunert et al. 2012

[2)] Literature value from Kunert et al. 2019

[3)] Calculated from literate values as R_a = GPP-NPP (Kunert et al. 2019)

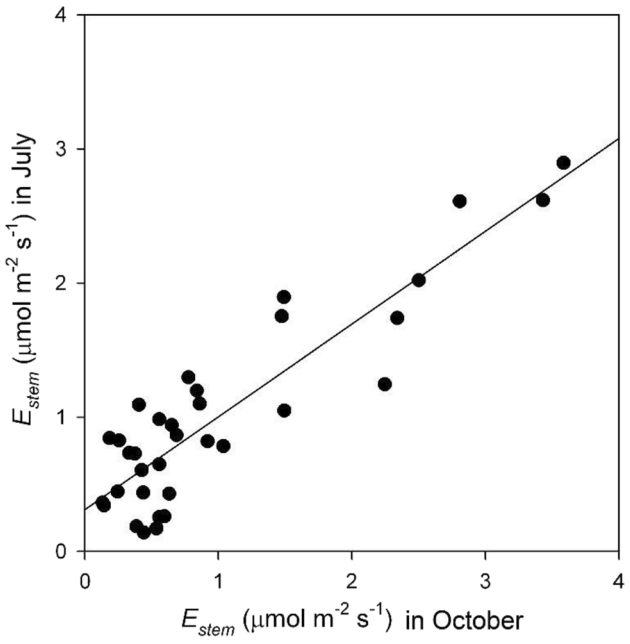

Fig. 1 Linear relationship between stem CO_2 efflux (E_{stem}) measured during the first field campaign in July 2011 and the second in October 2011. The slope between the regression line forced through the origin is 1.05 ($r^2 = 0.74$, $p < 0.001$)

the carbon content with the known species-specific carbon content estimated for the plantation by Elias and Potvin (2003). We received a very good fit of a linear model for the conductive xylem (Fig. 4a), but even a better fit when comparing E_{disc} with the C_{disc}. As we had carbon biomass stocks of all plots available (Potvin et al. 2011), we opted to scale respiratory fluxes (R_w) from E_{disc} using C_{disc}. Accordingly, R_w was calculated as

$$R_w = E_{disc}\left(\frac{C_{tree}}{C_{disc}}\right) \quad (3)$$

where C_{tree} is the total carbon content of a tree calculated after (Potvin et al. 2011) established specific-specific allometric equations to estimate tree biomass on the plantation in 2007. We combined the inventory data from 2008 and the stem-efflux data from 2011 to budget the tree respiratory processes on the plot level. Whole plot autotrophic respiration (R_a) was therefore calculated by subtracting NPP from GPP given in the study by Kunert et al. (2019). Plot-level GPP values in Kunert et al. (2019) were derived by following the approach by (Tang et al. 2006; Tatarinov et al. 2017). Briefly, the approach assumes that xylem sap flux measurements can predict photosynthesis by adapting the strong relationship between water use efficiency (WUE) and vapor pressure deficit (D). The main factors controlling WUE, calculated out of canopy transpiration (E_c) from xylem sap flux measurements and GPP from the eddy flux measurements, is accordingly D. The correction is used to model the GPP of certain trees or forest stands that are contributing to the initial canopy transpiration (Kunert et al. 2019). For calculating leaf respiration (R_l) and root respiration (R_r) we assumed a fixed proportion (62% and 38%, respectively) of the remaining carbon ($R_a - R_w$) to be allocated to the leaves and roots (we assumed the ratio from a review by Malhi 2012).

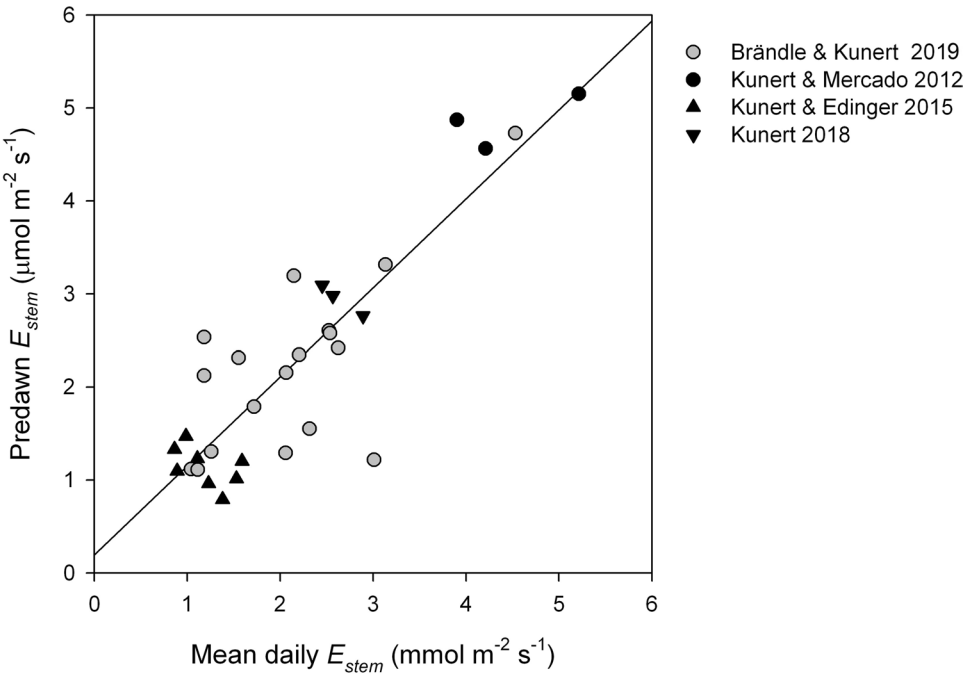

Fig. 2 Relationship between stem CO_2 efflux (Predawn E_{stem}) measured predawn and daily mean CO_2 efflux (Mean daily E_{stem}) derived from continues measurements conducted on a variety of tree species growing in tropical moist climates ($y = 0.96 + 0.19$, $r^2 = 0.75$, $p < 0.001$). Data compiled from different tropical studies measuring continuously E_{stem} over various days. (Brändle and Kunert 2019) used an automated closed dynamic chamber system with industrial CO_2 sensors. Kunert and Mercado Cardenas (2012) used a open chamber system based on a LI-6252 with flow control unit. Kunert and Edinger (2015) and Kunert (2018) used the same Licor system as in this study, manually repeating measurements in certain time intervals

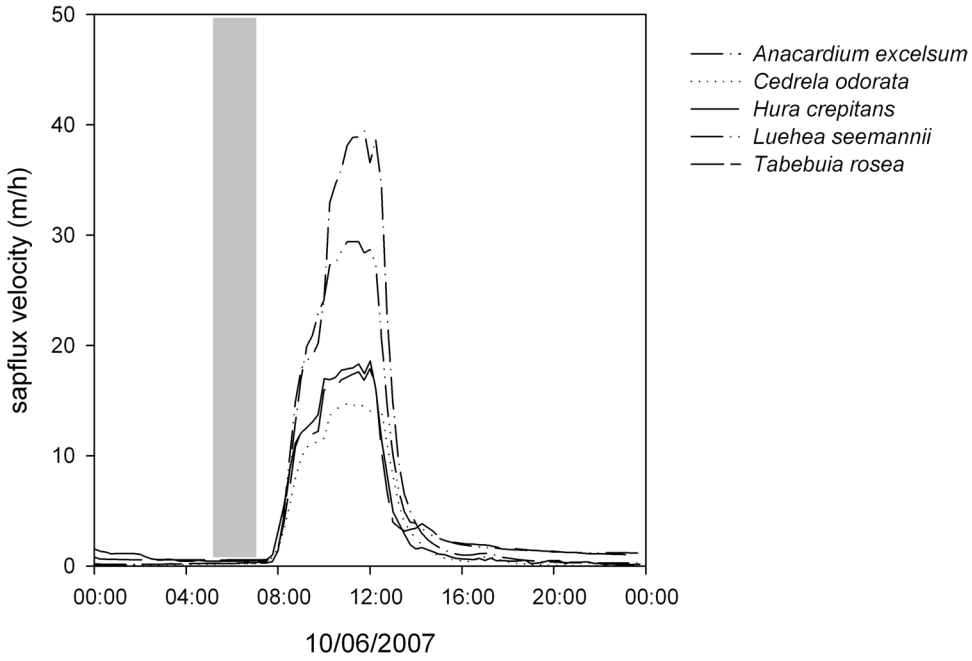

Fig. 3 Example for the diurnal course of xylem sap velocity of the five species measured with Granier type thermal dissipation probes (for more details see Kunert et al. 2010). The time of the predawn measurements is highlighter in grey

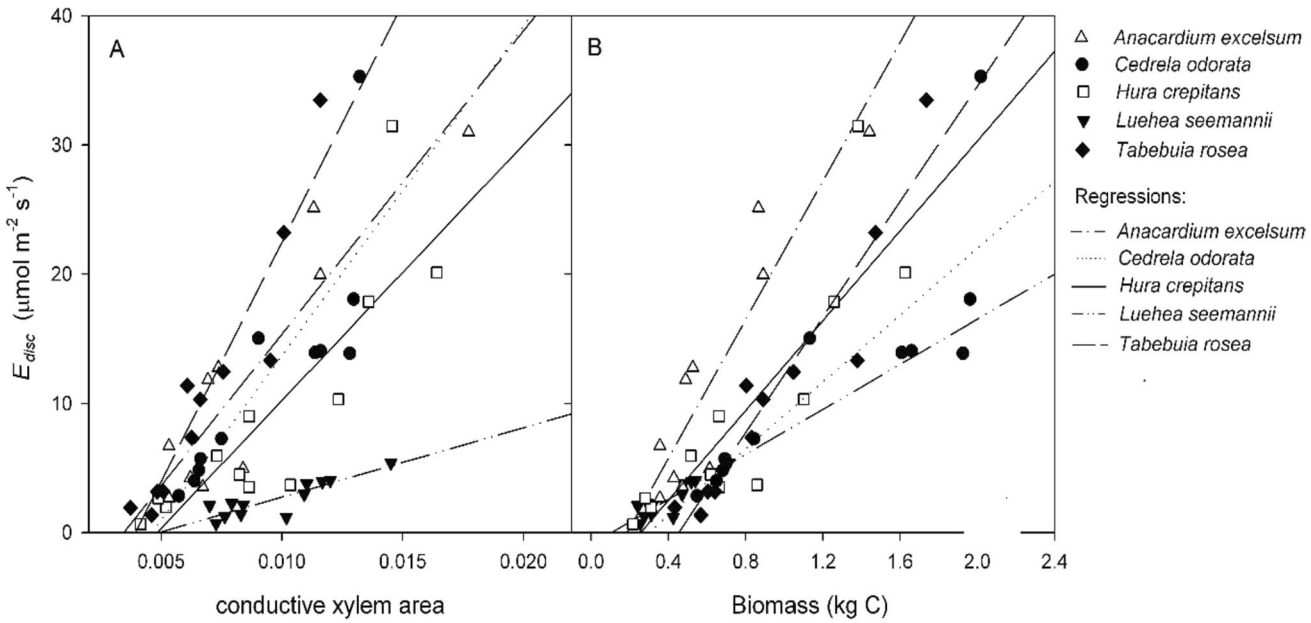

Fig. 4 Linear relationships between (**A**) E_{disc} and conductive xylem area, (**B**) E_{disc} and biomass for the 5 tree species. E_{disc} is given as the E_{disc} from the chamber measurements extrapolated on the entire circumference of the tree. The biomass is given for the stem segment (15 cm high segment) where the E_{stem} was measured. Regression equations for A: *Anacardium excelsum* ($y = 2345.9x - 8.1$.; $r^2 = 0.82$; $p < 0.001$), *Cedrela odorata* ($y = 2546.5x - 11.8$; $r^2 = 0.67$: $p < 0.001$), *Hura crepitans* ($y = 1979.2x - 9.6$; $r^2 = 0.72$; $p < 0.001$), *Luehea seemannii* ($y = 537.3\ x\ -2.6$; $r^2 = 0.77$; $p < 0.001$) and *Tabebuia rosea* ($y = 3689x - 14.5$; $r^2 = 0.89$; $p < 0.001$). Regression equations for B: *Anacardium excelsum* ($y = 26.8x\ -5.0$; $r^2 = 0.83$; $p < 0.001$), *Cedrela odorata* ($y = 12.9x - 3.8$; $r^2 = 0.68$: $p < 0.001$), *Hura crepitans* ($y = 17.4x - 4.5$; $r^2 = 0.74$; $p < 0.001$), *Luehea seemannii* ($y = 8.71x - 0.91$.; $r^2 = 0.77$; $p < 0.001$) and *Tabebuia rosea* ($y = 22.3x\ -10.1$; $r^2 = 0.90$; $p < 0.001$)

Statistical analysis and estimation of uncertainties

An essential question of our work was the uncertainty of the results caused by the upscaling process. Therefore, we performed a Monte Carlo simulation to estimate the uncertainty of R_w using the standard error of the coefficients of the equation used to scale on plot level from E_{stem} and biomass (Fig. 4). We assumed a normal distribution of the averages. Random individual trees were sampled from the distribution and the woody respiration for each tree in the different

plots was calculated 1000 times. In the following, we used the standard error of the distribution of the averages as an estimate of the uncertainty of R_w in the different plots. Differences in biomass stocks, gross primary productivity, autotrophic respiration, and woody respiration among mixtures were assessed by applying an analysis of variance (ANOVA, followed by a post hoc Tukey HSD test). Statistical analysis was performed in Excel (Office 2016, Microsoft Corporation, USA) with the Analysis ToolPak (Version 2016, Microsoft Corporation, USA).

Results

The largest variation in E_{stem} was observed between species. The lowest mean E_{stem} among all mixtures was found in *Luehea seemannii* (0.40 ± 0.16 µmol m^{-2} s^{-1}) and the highest in *Anacardium excelsum* (1.89 ± 1.15 µmol m^{-2} s^{-1}). Mean E_{stem} among all *Hura crepitans* trees were 0.71 ± 0.45 µmol m^{-2} s^{-1}, among all C*edrela odorata* trees 1.41 ± 0.80 µmol m^{-2} s^{-1}, and among all *Tabebuia rosea* trees 1.68 ± 1.19 µmol m^{-2} s^{-1} (Fig. 5). Even if there seemed to be a tendency that E_{stem} scaled with annual growth (Fig. 6), there was only a significant increase in E_{stem} with higher growth rates in *Cedrela odorata* ($p = 0.017$). There was a stronger relationship of E_{stem} scaled to E_{disc} with conductive xylem area and biomass, however, those values might be autocorrelated as all measures include a tree diameter in their estimation. E_{stem} did only differ significantly between mixture types for *Anacardium excelum*, E_{stem} rates of all other species were not significantly different among mixtures.

Annual R_w was not significantly higher in the mixtures compared to the monocultures. For example (Fig. 7), R_w in the monocultures was on average 0.25 ± 0.08 Mg C ha^{-1} whereas R_w averaged 0.28 ± 0.10 Mg C ha^{-1} overall mixed species stands (0.24 ± 0.11 Mg C ha^{-1} in 2/3-species mixtures; 0.33 ± 0.07 Mg C ha^{-1} in 5-species mixtures, mean ± SD across plots). On contrary, annual R_a was on average more than three times higher in the mixtures (3.27 ± 2.31 Mg C ha^{-1} per year, mean ± SD across plots) (compare Table 1) than in monocultures (1.03 ± 0.51 Mg C ha^{-1} per year, mean ± SD across plots) (Fig. 7). In the monocultures, estimates for R_l and R_r were on average 0.49 ± 0.27 Mg C ha^{-1} and 0.29 ± 0.16 Mg C ha^{-1}, respectively (Fig. 7). In the mixtures, the estimates for R_l were on average 1.86 ± 1.37 Mg C ha^{-1} and R_r was on average 1.13 ± 0.8 Mg C ha^{-1}.

Discussion

Our study shows, that predawn E_{stem} does not vary between monospecific stands and mixed species stands. We found a strong dependency of predawn E_{stem} rates on conductive xylem area and biomass, whereas the E_{stem}-growth relationship was only significant for one species. Species differences in E_{stem} were more pronounced than mixture effects. The estimated R_a was higher in the mixed species plots indicating significant mixture effects on R_a. With R_w not being affected by mixture effects but strong effects on R_a, we suspect that there are mixture effects of carbon allocation pattern. Mixtures allocate more carbon to leaf and root respiration which could potentially support process enhancing species complementary and niche facilitation in the forest canopy and the belowground root niche separation.

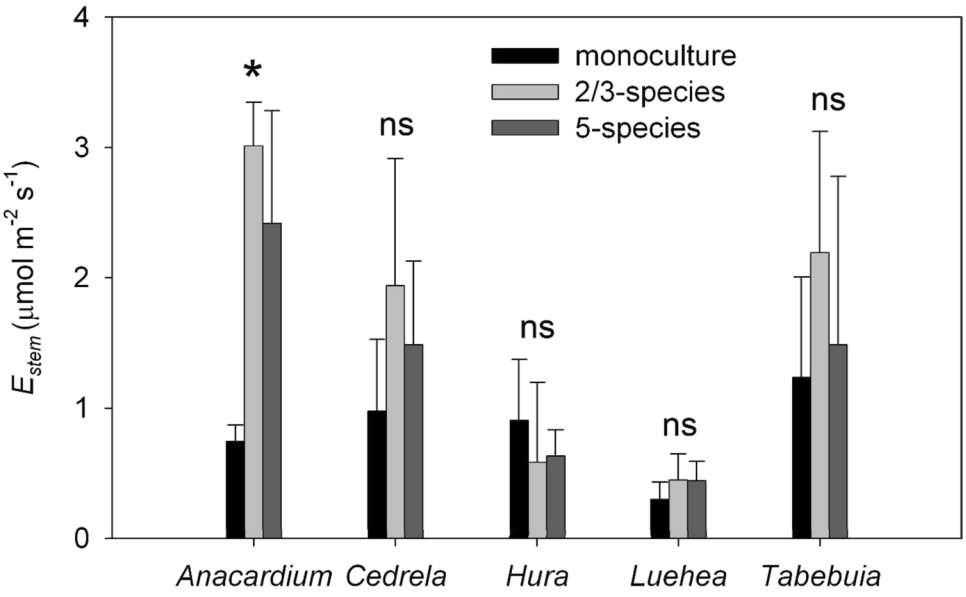

Fig. 5 Mean stem CO_2 efflux (E_{stem}) of trees in different mixtures (n = 4 trees per species and mixture, error bars represent the standard deviation) end of July 2011 at the Biodiversity Plantation in Sardinilla, Panama. Differences in means between mixtures was tested with a One-way ANOVA. Ns $P > 0.05$* $P \leq 0.05$ ** $P \leq 0.01$ ***$P \leq 0.00$

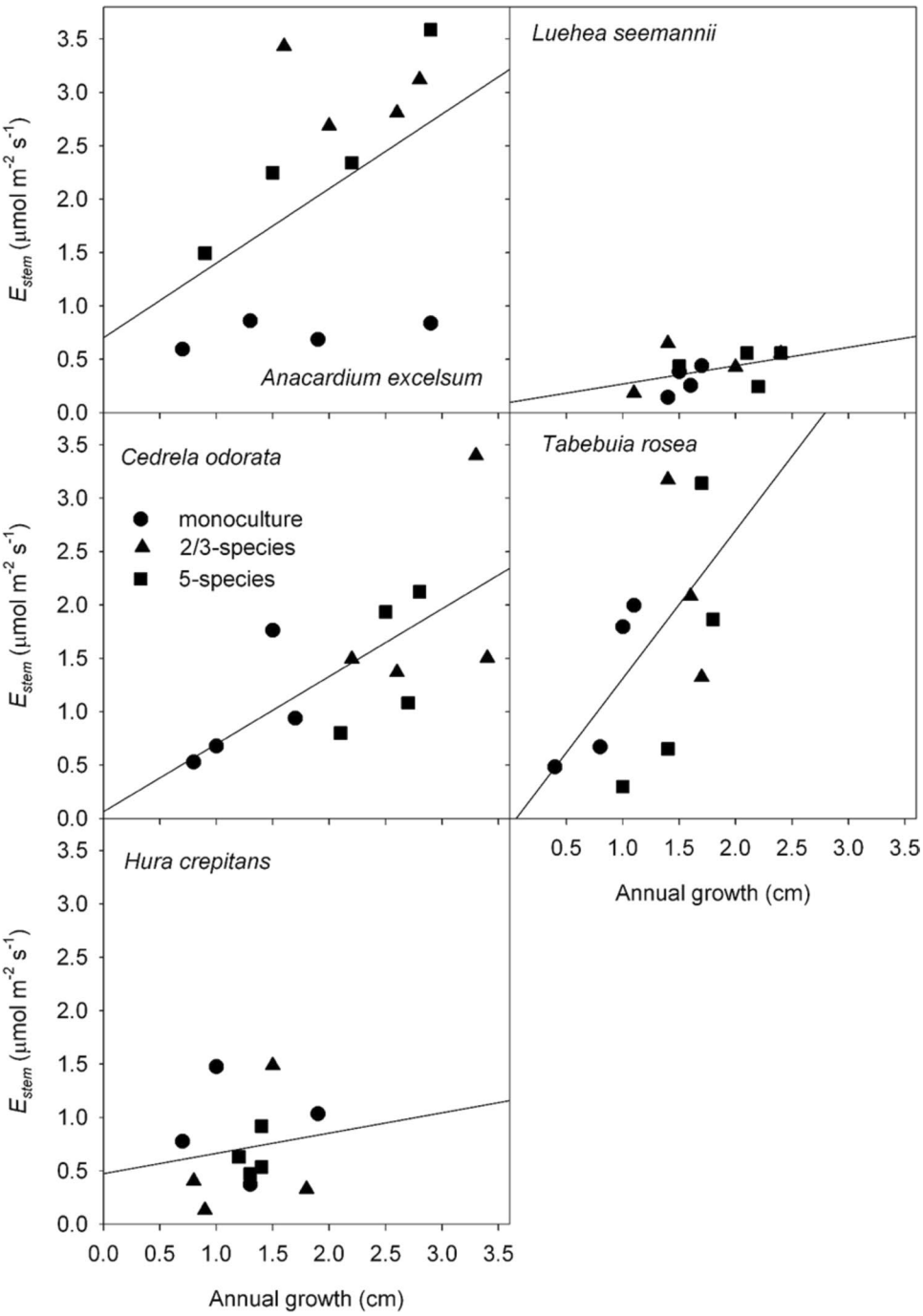

Fig. 6 Linear relationship between stem CO_2 efflux (E_{stem}) and annual growth rate measured on *Anacardium excelsum* ($y = 0.70x + 0.70$; $r^2 = 0.23$; $p = 0.115$), *Cedrela odorata* ($y = 0.63x + 0.06$; $r^2 = 0.44$: $p = 0.017$), *Hura crepitans* ($y = 0.19x + 0.47$; $r^2 = 0.02$; $p = 0.617$), *Luehea seemannii* ($y = 0.17x + 0.10$; $r^2 = 0.20$; $p = 0.142$) and *Tabebuia rosea* ($y = 1.39x - 0.07$; $r^2 = 0.26$; $p = 0.106$) in the different mixtures. An ANCOVA showed significant difference between mixtures only for *Anacardium excelsum* ($p < 0.001$)

Respiratory processes on the plot level

In our study, R_w was on average constant among the different mixtures (Fig. 7) and no significant mixture effect could be detected among the different species mixtures (Table 1). To our knowledge, there is no literature existing on mixture effects so far. Studies were either conducted in very species-rich forests such as the more recent studies by Stahl et al. (2011) or Rowland et al. (2018) or species-poor forest stands (Ryan and Waring 1992). Comparative studies do not exist, and we needed to take a more speculative approach to interpret the results. From an earlier study on carbon fluxes in the plantation, we knew that all mixed species plots had on average 30% more assimilated carbon available (Fig. 7) (Kunert et al. 2019). Further, the estimated mean R_a from the mentioned study was significantly higher in mixtures than in monocultures. We would have expected that this 'extra' carbon would have been allocated to the different tree organs (leaves, aboveground woody tissue, and roots) in proportionally equal parts. Consequently, we would expect a higher

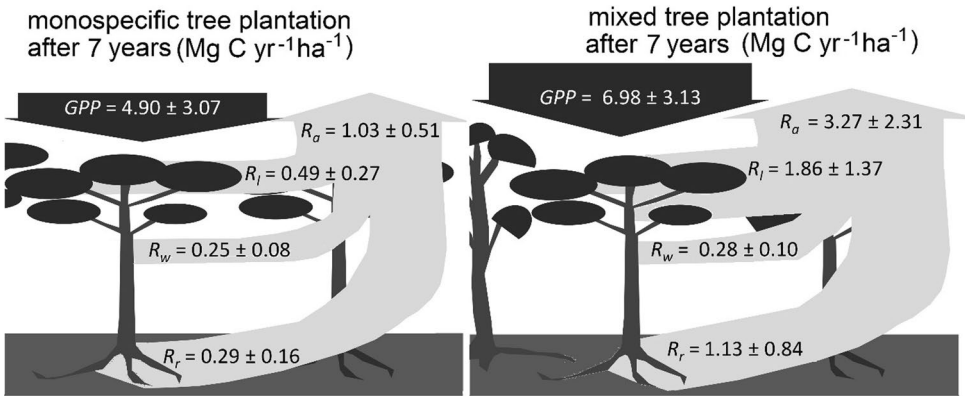

Fig. 7 Budget of the ecosystem carbon uptake and autotrophic respiration in monospecific tree stands and mixed tree stands (values are given with standard deviation). For calculating R_l and R_r we assumed a fixed proportion (62% and 38%, respectively) of the carbon been allocate to the leaves and roots according to Malhi (2012)

R_w in the mixtures than in monocultures, but on the contrary, we estimated that quantities of carbon were allocated to woody respiration. We suspect a change in the carbon allocation pattern in mixed stands. The 'extra' carbon that we would have expected to be respired as wood respiration must have been allocated to other tree organs - like leaves and roots. This would make sense under the aspect that the mixed stands in the plantation in Sardinilla are known to have developed differences in leaf area, canopy structure, crown shading pattern, and belowground niche separation (Sapijanskas et al. 2012, 2014; Kunert and Zailaa 2019). This is supporting the idea that trees in mixtures develop denser and multilayered tree crowns and have higher living biomass with the need to respire comparably higher amounts of carbon than monocultures. Studies on belowground root development in relationship to mixtures effect in other tree mixture experiments have shown a clear positive response of fine root productivity (Brassard et al. 2011; Lei et al. 2012; Liu et al. 2014) and niche differentiation (Kelty 2006) to tree species mixture effects. Further, it has been speculated that part of the carbon is even allocated to the roots and the surrounding soil environment to maintain a diverse mycorrhiza (Kunert et al. 2019) helping the tree to better retain nutrients from the soil or decompositional processes (Read 1991). In summary, either higher carbon investment in leaves or fine roots could give a possible explanation for higher R_a in mixtures at stable R_w. Most likely, it might be a combination of higher investment in both tree organs.

The uncertainty of the upscaling process

Our estimates for the upscaling of E_{stem} to R_w assumed that predawn measurements are giving a representative value for the mean daily values of the E_{stem}. However, the standard error of the estimate was 0.56, indicating the high reliability of our assumption. The main source of error in estimating stand level fluxes is probably the scaling fluxes from chamber measurements to tree level carbon fluxes (Damesin et al. 2002; Maier 2001). The uncertainty for the plot level estimates of R_w did not show any patterns among the different plots and ranged between 4.9 and 13.2% across all plots (in the monospecific plot LS1 and the 2-species mixture T1, respectively – Table 1). Another possible error in our final value could come from the fact that we sampled only two times during the wet season. However, the difference between the two sampling dates was very low (Fig. 1). Seasonal assessments of changes in E_{stem} suggest that there are large seasonal differences. Most of those studies are from temperate areas where also large fluctuations in temperature occur (Maier 2001; Damesin et al. 2002; Kuptz et al. 2011). In contrast, the mean annual temperature at our study site in Panama is very stable throughout the entire year (Kunert et al. 2010). The probably only concise study on the seasonal effect on E_{stem} in a tropical moist lowland forest ecosystem gives a variation of 20% between seasons (Stahl et al. 2011). In the mentioned study, E_{stem} increased during transition periods from wet to dry season and wet to dry season for about 20% compared to the wet season average. However, during the dry season, E_{stem} was 20% lower than during the wet season. At our study site in Panama, a relatively long transition occurs. During the study, the dry season lasted 90 days and the transition from wet season to dry season and from dry season to wet season lasted altogether 76 days (Kunert et al. 2010). We can, therefore, assume that there would have been an increase of E_{stem} of the same magnitude as there might have been a decrease.

Stem CO_2 efflux on tree level

The observed E_{stem} values are within the range observed for tropical trees during predawn and growing in similar relatively open environments, like tree plantations or orchards in tropical moist areas (Kunert and Mercado Cardenas 2012). *Anacardium excelsum* growing in mixtures had a four to seven times higher E_{stem} per unit growth compared to *Anacardium excelsum* trees growing in monoculture characterized. In general, this species was the species with the most pronounced physiological responses to biodiversity effects

in other studies (Kunert et al. 2012; Schwendenmann et al. 2015), probably due to its evergreen leaf phenology (Kunert and Zailaa 2019). *Hura crepitans* was the species with the highest E_{stem} observed in the monoculture opposite to their mixed-species counterpart (Fig. 5). Differences in growth rates between mixtures were minimal for this species (Fig. 6), resulting in a point cloud of E_{stem} around a low range of growth rates (Fig. 6). In all other species, E_{stem} increased linearly with higher growth rates. The growth of tree individuals of *Cedrela odorata*, *Luehea seemannii*, and *Tabebuia rosea* was faster in the mixed species plots. Accordingly, those tree individuals emitted more CO_2 per unit stem surface than trees in monocultures did. We conclude that the respiration rate reflects a relative fixed amount of carbon that needs to be invested to grow a certain volume of woody tissue. A tree accumulating more biomass in less time has thus a higher respiration rate than a slow-growing tree independent from the tree community in which the tree is growing. Trees in mixtures have a higher gross primary productivity probably due to the development of more highly photosynthesizing leaves (Kunert and Zailaa 2019) and better-stratified tree canopies (Sapijanskas et al. 2014), they can invest more into the last two mention tree compartments.

Conclusions

In conclusion, at the stem level, there were no detectable differences in internal metabolisms indicated by higher or lower CO_2 emissions out of the stem that could be attributed to mixture effects. However, the overall autotrophic respiration of mixed species stands is higher, such as the woody respiration mainly due to higher respiring biomass. According to our analysis of previous studies, more carbon might be allocated to processes in leaves and roots in mixtures compared to mono-specific stands. This is supporting the hypothesis, that especially canopy/leaf plasticity and belowground development of roots into different niches promote tree species complementarity and overyielding in mixtures. We are fully aware, that the measurements present only a snapshot from the early wet season and that seasonal differences in wood respiration might change the observed pattern. Further, we would like to advocate predawn measurements as being a good way to avoid other tree-internal physiological processes affecting the E_{stem} measurements if long-term efflux measurement systems cannot be applied.

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Author contribution NK designed the study and conducted the field in Panama. JB contributed data to underline the basic assumption of the representativeness of predawn measurements. NK wrote the manuscript. TEM gave significant advice in statistical analysis. All authors contributed to the revision final version of the manuscript.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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