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Effects of shade tree cover and diversity on root system structure and dynamics in cacao agroforests: The role of root competition and space partitioning

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Abstract

Background and Aims To increase yield, cacao is planted increasingly in unshaded monocultures, replacing a more traditional cultivation under shade. We investigated how shade tree cover and species diversity affect the root system and its dynamics.
Methods In a replicated study in Sulawesi (Indonesia), we studied the fine and coarse root system down to 3 m soil depth in three modern and more traditional cacao cultivation systems: unshaded cacao monoculture (Cacao-mono), cacao under either the legume *Gliricidia sepium* (Cacao-*Gliricidia*), or a diverse (> 6 species) shade tree cover (Cacao-multi). We analysed the vertical distribution of fine, large and coarse roots as well as fine root production, turnover and morphology on the species level.
Results Stand-level fine root biomass showed a doubling with increasing shade tree cover (from 206 to 432 g m^{-2}), but a tendency for a decrease in cacao fine root biomass. The presence of *Gliricidia* roots seemed to shift the cacao fine roots to a more shallow distribution, while the presence of shade tree roots in the Cacao-multi systems caused a biomass reduction and relative downward shift of the cacao roots. The turnover of cacao fine roots was much higher in the Cacao-multi stands than in the other two cultivation systems, although stand-level root production remained unchanged across the three systems. According to the stable isotope signature, *Gliricidia* extracted water from deeper soil layers than cacao, while no soil water partitioning was observed in the Cacao-multi stands.
Conclusions Our data suggest that the cacao trees altered their fine root distribution patterns in response to root competition. Both interspecific competition and root system segregation seem to play an important role in cacao agroforests with different shade tree cover.

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Introduction

Tropical rainforest conversion to agricultural land has proceeded at high rates in the last decades in many

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tropical regions (Achard et al. 2002; Hansen et al. 2013). In Indonesia, large-scale rainforest transformation into plantations of oil palm, rubber, cacao and other crops (Miettinen et al. 2011; Margono et al. 2014) has led to the highest rainforest loss rates worldwide in recent time (Lewis et al. 2015). On the Indonesian island of Sulawesi, where this study took place, rainforest conversion to cacao (*Theobroma cacao* (L.)) by smallholders is a main driver of deforestation. In the 1980s and 1990s, 50% of the newly established cacao plantations were established on cost of former tropical rainforest (Rice and Greenberg 2000). Increasing demand for chocolate on the world market (Rice and Greenberg 2000; Bisseleua et al. 2009) sets incentives for farmers to steadily increase the cacao cultivation area. As cacao is a neotropical understory rainforest species, it was initially planted in the shade of remaining forest trees (Rice and Greenberg 2000). In recent time, the cover by native forest tree species is increasingly replaced by planted non-native shade trees such as the nitrogen-fixing legume *Gliricidia sepium* (Jacq.). These shade trees are removed, when the cacao trees mature, because farmers fear yield losses due to competition between crop and shade trees (e.g. Rice and Greenberg 2000; Steffan-Dewenter et al. 2007; Bisseleua et al. 2009; Tscharntke et al. 2011).

Shade trees can have multiple effects on the crop, both negative and positive. While above- and belowground competition for light, water and nutrients may reduce resource availability with possible negative effects on yield (Beer 1987), shade trees can enhance nutrient supply by fixation of atmospheric nitrogen, as is the case with legumes, and they may enhance nutrient cycling by supplying additional leaf and root litter (e.g. Beer et al. 1998; Rice and Greenberg 2000; Bisseleua et al. 2009). Shading also does reduce the exposure of the cacao plants to excess light and elevated atmospheric saturation deficits for water vapor. While aboveground interactions between crop and shade trees have been studied in some detail (e.g. Ong et al. 1991; Beer et al. 1998; Rice and Greenberg 2000; Belsky and Siebert 2003; Bisseleua et al. 2009), less is known about root system structure and dynamics in shaded and non-shaded agroforestry systems and the effect of shade trees on the rooting patterns of the crop. Root system overlap could result in fierce belowground competition for water and nutrients, whereas in case of contrasting foraging strategies of crop and shade trees, or root system

segregation between competitors, root competition may be avoided (e.g. Defrenet et al. 2016). The latter was demonstrated for agroforestry systems by e.g. Schroth et al. (1996), Lehmann (2003), Ong et al. (2004), Ewel and Mazzarino (2008), Makumba et al. (2009), Moser et al. (2010), Schwendenmann et al. (2010) and Cardinael et al. (2015). One possible consequence of spatial root system segregation is the complementary use of soil water and nutrients, which may reduce interspecific root competition and maximize resource use efficiency in agroforestry systems (Livesley et al. 2000). The relatively small size of cacao trees compared to shade trees suggests that the latter should in principle root deeper in agroforestry systems than the crop. Indeed, several studies reported that the bulk of cacao fine root biomass was located in the uppermost soil layers (e.g. Kummerow et al. 1982; Nygren and Leblanc 2009; Moser et al. 2010; Nygren et al. 2013), but corresponding information about vertical rooting patterns of shade trees is scarce in the literature, as we poorly understand the subsoil rooting patterns of trees (Pierret et al. 2016).

The presence of shade trees results in higher stem densities and aboveground biomass, and it should increase root biomass over unshaded monocultures, thereby increasing competition intensity for light, water and nutrients. In apparent contradiction to this assumption, Abou Rajab et al. (2016) showed in an earlier investigation in the plots of this study in Sulawesi, that cacao bean yield was not negatively influenced by the presence of a diverse shade tree cover compared to unshaded cacao monoculture, even though above- and belowground biomass density increased with increasing shade tree cover and diversity. This seems to indicate that, in apparent conflict with the predictions of competition theory, the productivity of cacao in these agroforestry systems is not significantly limited by interspecific competition, or that positive effects of the shade trees are outweighing any competition effects. Comparative root system studies in agroforestry systems along a gradient of shade tree cover are needed for better understanding the mutual interaction between crop and shade tree root systems.

The aim of this study was to analyze the influence of shade trees on the vertical rooting patterns and fine root dynamics of cacao and shade trees in agroforestry systems differing in shade tree abundance and diversity. A comparative study with 3-fold replication at the plot level was carried out in the Kulawi valley in Central

Sulawesi, Indonesia, adjacent to a large forest national park (Lore Lindu National Park), where different cacao cultivation systems with variable degrees of shading from zero-shade to high shade tree cover are present under equal climatic and soil conditions. We investigated the standing biomass and vertical distribution of fine (<2 mm diameter), large (2–5 mm), and coarse roots (>5 mm) as well as fine root dynamics on the tree species level in (i) monospecific cacao agroforests, which are in many tropical regions the dominant cultivation system today, as compared to (ii) cacao agroforests with a single planted non-native shade tree species, the N-fixing legume *Gliricidia sepium*, and (iii) a more traditional cultivation system with a multitude of shade trees including former rainforest trees. We aimed to test the hypotheses that (1) standing fine root biomass increases with increasing shade tree abundance and diversity, and (2) increasing shade tree abundance and diversity results in higher stand-level fine root productivity, as predicted by functional biodiversity research. We further hypothesized that (3) the root systems of cacao and different shade tree species are vertically segregated, which results in complementary water uptake from different soil horizons. Finally, we expected (4) that fine root turnover is higher in the shaded systems due to a higher degree of soil resource depletion with higher overall root densities, despite complementarity in soil resource use.

Materials and methods

Study area and plot description

The study was conducted in the Kulawi valley southeast of Palu in the province of Central Sulawesi, Indonesia (1.5–1.7°S, 120°E, 387–571 m a.s.l.). The valley is situated in the western margin zone of a large remaining bloc of natural pre-montane to montane forest (Lore Lindu National Park). Mean annual air temperature is 25 °C and mean annual precipitation 2165 mm yr.$^{-1}$ (Köhler et al. 2014) with no distinct seasonality visible during the study period. Three different cacao cultivation systems of the following species composition were selected in order to investigate the effect of increasing cover and species diversity of shade trees on root system size, vertical rooting patterns and root dynamics: (i) monoculture of *Theobroma cacao* trees ('Cacao-mono') without shade trees, (ii) cacao growing with the N-fixing

legume tree *Gliricidia sepium* (Jacq.) ('Cacao-Gliricidia'), and (iii) cacao cultivated under different shade tree species ('Cacao-multi'). We selected three study plots of approx. 20 m × 20 m size per cultivation system type which all were located between the villages Marena and Lempelero in the southern part of the valley. The nine study plots were comparable in terms of topography (only slightly inclined and similar aspect), soil morphology (Cambic Umbrisols as soil type in all plots with only slightly different soil texture varying between sandy loam and silty-clay loam), and soil chemistry (Abou Rajab et al. 2016). This is reflected in similar pH values, cation exchange capacities, base cation concentrations, and C/N ratios in the nine plots (Supplementary Material SM1). The ages of the agroforestry plots were rather comparable: the year of the plantation establishment ranged from 1989 to 1997 (mean: 1992) in Cacao-mono plots, from 1993 to 1999 (mean 1996) in Cacao-*Gliricidia* plots, and from 1989 to 1999 (mean: 1993) in Cacao-multi plots. However, the precise age of the single Cacao trees as well as of the shade tree individuals cannot be provided.

An inventory of aboveground stand structure was conducted in all plots at the beginning of the study in summer 2011, when canopy cover, tree and stem density, stand basal area, stem diameter, tree height as well as the diversity of the woody species (expressed with Shannon-Wiener's H′ index) were measured (Supplementary Material SM2). Accordingly, canopy cover (from 50 to 93%), overall stem density (from 1804 to 2909 ha^{-1}), stand basal area, mean stem diameter and mean tree height all increased in the sequence Cacao-mono – Cacao-*Gliricidia* – Cacao-multi (Supplementary Material SM2). In parallel, the species diversity of the woody plants rose from 1 (Cacao-mono) to >6 species per plot in the Cacao-multi system (equivalent to an increase in Shannon's H′ from 0 to 0.4). The shade trees from various species in the Cacao-multi system were much taller than the cacao trees and also than the *Gliricidia* shade trees, and had a much larger stem diameter. Despite their small number, these shade trees caused the stand basal area to be much higher in the Cacao-multi plots than in the other systems (Abou Rajab et al. 2016). The density of cacao trees was significantly higher in the shaded Cacao-*Gliricidia* and Cacao-multi plots than in the cacao monocultures, which seems to be a characteristic in the Kulawi valley, distinguishing the more traditional

shaded systems from the recently established unshaded systems. In contrast, the mean stem diameter of the cacao trees was significantly higher in the monocultures with lower stem density than when grown under *Gliricidia* shade tree cover, and it also tended to exceed the diameter of cacao in the Cacao-multi systems (difference not significant). Results of an earlier study in these plots (Abou Rajab et al. 2016) revealed that total above-ground biomass increased strongly with increasing shade tree cover and diversity from ca. 23 Mg ha^{-1} in the monocultures to >40 Mg ha^{-1} in the Cacao-*Gliricidia* plantations and to 124 Mg ha^{-1} in the Cacao-multi systems. Correspondingly, total aboveground net primary productivity increased in this sequence with the Cacao-*Gliricidia* plots having a nearly 30% higher aboveground NPP than the cacao monocultures (28 vs. 20 Mg ha^{-1} yr.$^{-1}$). The Cacao-multi stands exceeded the monocultures nearly twofold due to the high productivity of the shade trees (i.e. 38 Mg ha^{-1} yr.$^{-1}$) (Abou Rajab et al. 2016).

Standing fine root mass and vertical root distribution

For recording the standing fine root mass in the upper, densely rooted soil, twelve soil samples randomly distributed over the whole plot area were taken in every plot using a soil corer (3.5 cm in diameter) down to a depth of 60 cm. The cores were sliced into the four subsamples of 0–10, 10–20, 20–40, and 40–60 cm soil depth. The soil samples were transferred to plastic bags, transported to the laboratory of Tadulako University in Palu, and stored in the fridge at 4 °C until processing. In the laboratory, the root samples were soaked in water and cleaned of soil residues using a sieve with a mesh size of 0.25 mm. Large root fractions (>10 mm in length) were picked out manually and separated into fine roots (roots <2 mm in diameter), large roots (roots 2–5 mm in diameter), and coarse roots (roots >5 mm in diameter). Living and dead rootlets were distinguished under the stereomicroscope by color, root elasticity, and the degree of cohesion of cortex, periderm, and stele following the method established by Leuschner et al. (2001) and Hertel and Leuschner (2002). All root individuals were assigned to cacao or the shade tree species present in the respective study plots by means of morphological characteristics (see Supplementary Material SM5). Rootlets traced back to the

stem of the species, which occurred on or near the study plots, were studied and analyzed under the stereomicroscope prior to the main soil sampling campaign. The most frequent tree species in the plots were *Aleurites moluccana* (L.) Willd., *Ceiba pentandra* (L.) Gaertn., *Durio zibethinus* (L.), *Gliricidia sepium*, *Leucaena leucocephala* (Lam.) de Wit, *Pterocarpus indicus* Willd., and *Theobroma cacao L.* itself. In half of the samples, an additional detailed analysis of smallest fine root fragments (<10 mm in length) was conducted applying a method introduced by van Praag et al. (1988) and modified by Hertel and Leuschner (2002). The soil samples were cleaned using a finer sieve with a mesh size of 200 μm and after extraction of the large root fractions, the residue of the sample was evenly spread on a large sheet of filter paper (730 cm^2) with 36 squares marked on it. Six of the squares were randomly selected and analyzed under the stereomicroscope for even smallest fine root fragments. The mass of small rootlets was extrapolated to the entire sample by use of a regression equation, which relates the mass of small rootlets to that of large rootlets in the samples. All root material was dried at 70 °C for 48 h until constant weight.

In order to analyze the soil profile totals of fine, large and coarse root biomass and their vertical distribution pattern down to a soil depth of 300 cm, a few deep soil pits were excavated in every plot. In each of the Cacao-mono plots, two soil pits ca. 80 cm distant from randomly selected cacao trees were excavated; this is roughly half way between two neighboring stems. In case of the shaded cacao agroforests (Cacao-*Gliricidia* and Cacao-multi), two soil pits near cacao trees and another two near randomly selected shade trees were excavated in every plot. Root biomass was determined in soil monoliths of 30 cm × 30 cm × 20 cm (l x w x d) size down to 120 cm depth in the profile, and of 30 cm × 30 cm × 40 cm size from 120 to 300 cm depth, respectively. The soil monoliths were sieved (mesh size 2 mm) directly in the field and the root material transferred to plastic bags and transported to the laboratory of Tadulako University in Palu, where the root fragments were sorted by species and the different root diameter classes as described above. However, due to the necessity to sieve the soil material directly in the field with larger-mesh-size sieves it was not possible to extract finest dead root particles from the soil material in the laboratory as described above for the core samples taken

for the upper 60 cm soil. We therefore present fine root necromass numbers only for this upper soil profile.

Roots of grasses and herbs were easily distinguishable from tree fine roots by their smaller diameter, lighter color and the absence of a lignified periderm. Our root biomass data refer only to tree roots because the proportion of herb and grass root biomass was below 5% in all plots. In some plots, roots of tree species only growing outside the plots, or that were present only with dead tree stumps, were detected. In most cases, these fractions did not account for a larger percentage except of two Cacao-mono and one Cacao-*Gliricidia* plot with somewhat larger percentages (< 5%) of 'external' roots. In the calculation of standing fine root biomass, these root mass components were included.

Profile totals of standing fine, large, and coarse root biomass were calculated from both the root inventory data in the upper soil and the data from the deep soil pits in the study plots. An exception was one of the three Cacao-*Gliricidia* plots, where the soil pits could only be excavated to a depth of 100 cm due to water accumulation in the soil pits after continued rainfall during the field campaign. In this case, we used the mean root biomass values from 100 cm x 300 cm from the other two plots of that cultivation system to calculate the fine root biomass total of the entire soil profile in this plot. The data from the deep soil pits were not only used for analyzing the vertical root distribution patterns of the different species and the three cultivation systems, but served also for determining the mean and the absolute maximum extension of fine, large and coarse roots of the cacao trees and the common shade tree species. The mean maximum rooting depth of each species was derived by averaging over the pits of a species or cultivation system, whereas the deepest root penetration in all pits of a plot was taken as the absolute maximum rooting depth of a species. Furthermore, we analyzed the vertical change in fine and large root biomass per soil volume (i.e. fine root biomass density) individually for all more common shade tree species and cacao (Leuschner et al. 2006; Hertel et al. 2007) and expressed the steepness of the root density decrease with soil depth by the β value of the regression equation $y = 1\text{-}\beta^d$, with y being the cumulative root biomass fraction in g m^{-2} and d the soil depth in cm (Gale and Grigal 1987; Gaul et al. 2008). High β values indicate a large proportion of root biomass in deeper soil depths, whereas low

values stand for a large proportion of root mass near the soil surface. For example, $\beta = 0.930$, $\beta = 0.965$, $\beta = 0.979$, and $\beta = 0.987$ indicate that 90, 70, 50, and 30%, respectively, of the total fine root biomass of the 300 cm deep profile is located in the upper 60 cm of the soil.

Fine root morphology

For examining differences in fine root morphology between cultivation systems and species, one to two living fine root strands per tree species of each sample and soil depth collected during the fine root inventory were scanned and the images analyzed for mean root diameter, root surface area, and root length using the software WinRhizo 2002a (Régent, Quebec, Canada). Specific fine root surface area (SRA, in cm^2 g^{-1}) and specific root length (SRL, in m g^{-1}) were calculated from the dry weight of the respective root individuals.

Fine root production and turnover

Fine root production in the different cultivation systems was estimated by means of an ingrowth core experiment using local soil material according to the methodology described by Persson (1980), and Hertel and Leuschner (2002). At 10 randomly chosen locations in the nine plots, soil cores (3.5 cm in diameter) were taken from the upper 30 cm of the soil. All macroscopically visible living and dead root material was extracted manually directly in the field. The remaining soil material was replaced into the hole and marked precisely with plastic tubes for re-collection. Care was taken that the structure and density of the soil samples were conserved as much as possible. The sample locations were marked accurately with plastic markers to guarantee a precise re-sampling after the ingrowth period. The samples were re-collected with the same soil corer after 10 months and the extracted core sliced into the 0–10 and 10–30 cm layers. The relatively short length of this ingowth period was chosen to prevent bias by loss of (dead) fine root strands through rapid root litter decay under the warm and moist climate conditions in this tropical lower montane area. In the laboratory of Tadulako University in Palu, the root biomass was extracted as described above. Following Vogt et al. (1998) and Hertel and Leuschner (2002), we calculated fine root production

in the cores as the mass of living and dead roots (i.e. former living fine roots that had died during the study period) that were grown into the cores after the start of root recolonization (in our study one month after installation, see the study of Harteveld et al. 2007) until harvest after the 10-month ingrowth period. Fine root growth in the cores during the recolonization period was extrapolated to one year and expressed in g m^{-2} yr.$^{-1}$.

Fine root turnover (unit: year^{-1}) in the ingrowth cores was calculated as annual fine root growth divided by the standing fine root biomass in the corresponding soil volume (Aber et al. 1985; Aerts et al. 1992) by relating the fine root growth recorded in the ingrowth cores after a 1-year growth period to the fine root biomass detected in this horizon during the fine root inventory. We extrapolated the data to 60 cm soil depth by the standing fine root biomass data from 30 to 60 cm, assuming that the fine root turnover rate did not vary between 10–30 and 30–60 cm soil depth.

Soil depths with maximum water uptake

Soil water uptake patterns were analyzed through the assessment of stable isotope ratios (δ^2H and δ^{18}O) in plant and soil water (Ehleringer and Dawson 1992). Stem samples were taken in a Cacao-*Gliricidia* plot and a Cacao-multi plot from 16 trees using a stem corer (Haglöf, Långsele, Sweden) in October 2011. Soil samples were taken from 5 soil depth intervals (0–10, 10–20, 20–40, 40–60 and 60–100 cm) underneath the respective trees using a long steely soil corer (after Pürckhauer) and stored immediately in glass vials to prevent any change in the stable isotopic composition of the soil water. Due to the short sampling time requested for this method, soil areas below 100 cm depth could not be sampled for this method. Sampling was conducted after a period of eight rainless days with relatively high evaporative demand.

Soil and wood samples were immediately stored in 40 ml-glass bottles, closed with a teflon-coated lid, sealed with parafilm, and then kept frozen until water extraction (Ehleringer et al. 2000). Extraction of water from wood and soil samples was conducted via cryogenic vacuum extraction according to Ehleringer and Osmond (1989) with an extraction time of 70 min for soil and 90 min for wood samples (West et al. 2006). The extracted water samples were analyzed for δ^2H and δ^{18}O at the Center for Stable Isotope Research and Analysis (KOSI, Georg August Universität Göttingen, Germany). The analyses included a high temperature conversion elemental analyzer (TC/EA, Thermo Electron Corporation, Bremen, Germany) coupled via a Con-Flo III interface to a Delta V Plus isotope ratio mass spectrometer (Thermo Electron Corporation) (Gehre et al. 2004). Isotope ratios were expressed as per mill deviations to Vienna Standard Mean Ocean Water (VSMOW, $R_{Standard}$) with a measurement precision of ±2 ‰ for δ^2H.

Statistical analyses

All data were tested for Gaussian distribution using a Shapiro-Wilk test. The majority of the datasets showed non-Gaussian distribution and could not be transformed. Thus, differences between the cultivation systems and the tree species (or species groups) were analyzed for all variables with non-parametric analysis of variance (Kruskal-Wallis H test) and a subsequent Mann-Whitney two-sample test (Wilcoxon U test). These calculations as well as Pearson correlation analyses were done with the software package SAS 9.3 (version 9.3, SAS Institute, Cary, NC, USA). Regression analyses were conducted with the software package Xact7 (Sci Lab, Hamburg, Germany). For analyzing interrelations between tree species diversity, stand structure, plant biomass and productivity, we conducted a Principle Components Analysis (PCA) with the package CANOCO, version 5 (Biometris, Wageningen, The Netherlands).
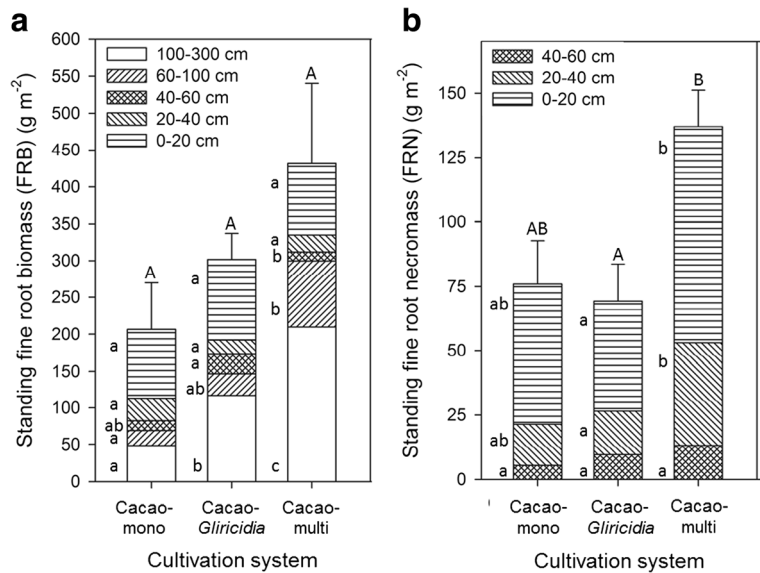
Results

Standing fine root biomass and necromass

Standing fine root biomass totals (0–300 cm soil depth; all trees combined) increased markedly with increasing shade tree cover, though only at marginal significance ($p < 0.10$, Fig. 1a). In the Cacao-mono plots, mean standing fine root biomass was 206.4 g m^{-2}, while it reached 301.4 g m^{-2} in the Cacao-*Gliricidia* and 431.8 g m^{-2} in the Cacao-multi plots, respectively. The shade tree fine roots contributed with 30 and 73% to the stand total fine root biomass in the Cacao-*Gliricidia* and Cacao-multi systems, respectively.

We detected significant differences between the three cultivation types also for the fine root abundance in the

Fig. 1 **a** Standing fine root biomass in the three cacao cultivation systems in the Kulawi valley for the profile to 300 cm depth, given separately for the five soil layers 0–20, 20–40, 40–60, 60–100 and 100–300 cm, and the total profile. **b** Standing fine root necromass in the same profiles to 60 cm depth, given separately for the 3 soil layers 0–20, 20–40, and 40–60 cm, and the total profile. Capital letters indicate statistically significant differences between the different cultivation systems; lower case Latin letters indicate significant differences for cacao or the shade tree species in a given soil depth between the cultivation systems

different soil depths (Fig. 1a) and with respect to the relative importance of deep-reaching roots. The deeper subsoil (100–300 cm) contained only ca. 25% of the fine root biomass total in the profile to 300 cm in the Cacao-mono plots, but roughly 40% in the Cacao-*Gliricidia* plots and about 50% in the Cacao-multi plots (Fig. 1a), demonstrating the increasing importance of deep roots with increasing shade tree cover.

Standing fine root necromass (0–60 cm soil depth; all trees combined) was markedly higher in the Cacao-multi systems with approx. 138 g m^{-2} than in the less diverse systems (65 and 62 g m^{-2} in the Cacao-mono and Cacao-*Gliricidia* plots, respectively; Fig. 1b); this was caused by high necromass amounts of the shade trees. The fine root necromass of the cacao trees (0–60 cm profile) slightly decreased with increasing shade tree diversity (difference not significant; see Supplementary Material SM3).

The live:dead ratio of fine root mass was highest in the Cacao-*Gliricidia* plots (2.2 for the 0–60 cm profile), intermediate in the Cacao-mono plots (1.8) and lowest in the Cacao-multi systems (1.0) (difference significant between the two shaded systems; Table 1). No consistent change in live:dead ratio was observed between topsoil and subsoil.

Comparison of the abundance of fine ($d < 2$ mm), large ($d = 2–5$ mm) and coarse ($d > 5$ mm) root biomass in the soil profile of the three cultivation systems showed that the three root diameter groups differed with respect to the vertical root density change in the profile (Table 2). A very large amount of fine root biomass of the cacao trees

was located in the uppermost 20 cm in all three cultivation systems or at least in the upper soil profile. The same was true for the large roots of cacao, but cacao coarse roots were more evenly distributed throughout the upper 100 cm of the profile in the Cacao-mono and Cacao-

Table 1 Ratio of fine root biomass (FRB) to fine root necromass (FRN) in the three different cacao cultivation systems ($n = 3$ per system) in the Kulawi valley (Sulawesi, Indonesia) in three soil layers and the profile to 60 cm depth

Depth (cm)	Cultivation system	Fine root mass live/dead ratio
0–20	Cacao-mono	1.7 ± 0.4 a
0–20	Cacao-*Gliricidia*	2.5 ± 0.2 b
0–20	Cacao-multi	1.2 ± 0.4 a
20–40	Cacao-mono	2.0 ± 0.8 a
20–40	Cacao-*Gliricidia*	1.2 ± 0.3 a
20–40	Cacao-multi	0.7 ± 0.2 a
40–60	Cacao-mono	2.2 ± 0.9 a
40–60	Cacao-*Gliricidia*	6.5 ± 4.4 a
40–60	Cacao-multi	1.4 ± 0.8 a
0–60	Cacao-mono	1.8 ± 0.4 AB
0–60	Cacao-*Gliricidia*	2.2 ± 0.2 A
0–60	Cacao-multi	1.0 ± 0.4 B

Capital letters indicate statistically significant ($p < 0.05$) differences of the total profile between the cultivation systems, lower case letters significant differences in a given depth between the cultivation systems

Gliricidia plots, while in the Cacao-multi systems, the largest biomass of cacao coarse roots was found in the deep soil (100–300 cm; Table 2). *Gliricidia* fine roots in the Cacao-*Gliricidia* plots were less abundant than those of cacao and increased in volume density with soil depth. The large roots of *Gliricidia* trees, in contrast, were concentrated more in the uppermost soil layers; the *Gliricidia* coarse roots revealed a similar vertical rooting pattern as the large roots in the soil profile 20–300 cm, but were not present in the uppermost soil (0–20 cm). In the Cacao-multi systems, shade tree fine root biomass was larger than cacao fine root biomass in all soil depths. Shade tree fine root biomass was highest in the uppermost soil, but was found in notable amounts in all layers of the soil profile. The same was true for the shade tree large roots in this cultivation system. In contrast to the cacao trees, the coarse root biomass of the shade trees was not only high in the uppermost layers, but in 60–300 cm as well (Table 2).

Vertical change in root density

All three cultivation systems showed by far the highest fine root densities (fine root biomass per volume) in the topsoil (0–20 cm) with no clear difference between shaded and unshaded systems. Below 60 cm, the Cacao-multi system exceeded the Cacao-mono system in fine root density by 50 to 100%, while the Cacao-*Gliricidia* system reached only slightly higher densities than the unshaded system (Fig. 2). On the species level, the density of cacao large roots decreased more rapidly with soil depth in the Cacao-mono and Cacao-*Gliricidia* systems (β values of 0.95 and 0.93 for the two systems, respectively) than that of cacao fine roots (β values of 0.98 in both systems), pointing to a more shallow distribution of the large roots of cacao (Fig. 3 and Table 3). The *Gliricidia* shade trees had smaller fine and large root densities in the uppermost soil layers than the cacao trees, but tended to have higher fine and large root densities than cacao in the mid and lowermost part of the soil profile in this system (β values of 0.99 for both root diameters, Fig. 3 and Table 3). In the Cacao-multi plots, cacao showed a more deeper-reaching distribution pattern of its fine and large roots than in the Cacao-mono and Cacao-*Gliricidia* systems (Fig. 3 and Table 3). This is also visible in the increasing contribution of the 100–300 cm layer to the fine root biomass profile total of cacao in Table 2 (24, 27 and 35% in the three systems). Despite these differences, the vertical

change in the fine root density of cacao was similar to that of the five co-occurring shade tree species investigated, with all six species showing notable fine root densities not only in the uppermost, but also in the middle and lowermost part of the profile. In the large root fraction, cacao and the shade trees were more different in their vertical distribution patterns. While *Durio zibethinus*, *Ceiba pentandra* and *Aleurites moluccana* showed a rather steep decrease in large root density with soil depth, *Pterocarpus indicus* and *Leucaena leucocephala* had notable peaks of large root density in middle and lower sections of the profile; the vertical pattern of change in cacao large roots was intermediate between these two groups of shade trees (Fig. 3 and Table 3).

Presence of 'deep roots'

In all three cultivation systems, single cacao fine roots were recorded to 300 cm depth in all plots (Table 4). The mean maximum rooting depth of cacao fine roots in the three plots of a cultivation system was high as well (260–280 cm) and tended to increase slightly with increasing shade tree cover and diversity. The mean maximum rooting depth of cacao large roots was not as large as in fine roots and differed not systematically between the three cultivation systems (ca. 130–170 cm). The mean maximum rooting depth of cacao coarse roots was much lower than that of fine and large roots: while it was 43 and 30 cm in the Cacao-mono and Cacao-*Gliricidia* plots, respectively, this diameter class reached a mean maximum rooting depth of 87 cm in the Cacao-multi plots (extremes were 80, 60 and 300 cm in the three systems, respectively; Table 4). In the Cacao-*Gliricidia* system, *Gliricidia* fine, large and coarse roots achieved a slightly higher mean maximum fine root depth (difference not significant) and a significantly higher mean maximum large root depth than the cacao trees. In the Cacao-multi plots, the mean maximum depth of shade tree fine roots was similar to that of cacao, while the shade tree large and coarse roots tended to penetrate deeper than those of cacao, but the difference was not significant.

Five of the six common shade tree species reached with their fine roots to 300 cm depth in certain plots (exception: *Ceiba pentandra*), while the large roots of four species penetrated maximally to 240–300 cm (*Aleurites moluccana* and *Ceiba petandra*: only to 120 cm). The coarse roots showed large species

Table 2 Biomass of fine roots ($d < 2$ mm), large roots ($d = 2$–5 mm) and coarse roots ($d > 5$ mm) of cacao trees and shade trees (in g m^{-2}) in the different soil depths of the three cacao agroforestry systems in the Kulawi valley

Depth (cm)	Cultivation system	Tree species	Fine root biomass ($d < 2$ mm) (g m^{-2})	Large root biomass ($d = 2$–5 mm) (g m^{-2})	Coarse root biomass ($d > 5$ mm) (g m^{-2})
0–20	Cacao-mono	Cacao	84.7 ± 35.6 (45.4) ab	294.3 ± 86.1 (64.7) a	884.2 ± 548.2 (17.7) a
0–20	Cacao-*Gliricidia*	Cacao	100.4 ± 26.4 (51.6) a α	235.9 ± 72.2 (81.6) a α	197.1 ± 192.8 (24.4) a α
0–20	Cacao-multi	Cacao	35.9 ± 13.2 (35.8) b α	157.9 ± 26.6 (51.9) a α	1.5 ± 1.5 (0.1) a α
0–20	Cacao-*Gliricidia*	*Gliricidia*	6.4 ± 1.5 (6.4) a β	40.4 ± 7.3 (27.4) a β	0.7 ± 0.7 (0.0) a α
0–20	Cacao-multi	Shade trees	60.9 ± 25.5 (21.9) b α	287.1 ± 83.2 (50.0) b α	364.0 ± 349.8 (10.0) a α
20–60	Cacao-mono	Cacao	38.7 ± 16.4 (20.8) a	137.8 ± 46.5 (30.3) a	2653.4 ± 554.1 (53.0) a
20–60	Cacao-*Gliricidia*	Cacao	28.8 ± 7.6 (14.8) a α	41.8 ± 22.4 (14.5) ab α	353.6 ± 225.5 (43.7) b α
20–60	Cacao-multi	Cacao	11.2 ± 4.4 (11.2) a α	43.6 ± 6.8 (14.4) b α	434.4 ± 217.2 (21.0) b α
20–60	Cacao-*Gliricidia*	*Gliricidia*	10.7 ± 2.3 (10.9) a β	36.5 ± 9.4 (24.7) a α	1005.7 ± 657.8 (49.9) a α
20–60	Cacao-multi	Shade trees	24.2 ± 3.2 (8.7) b α	78.7 ± 25.3 (13.7) a α	98.9 ± 93.1 (2.7) a α
60–100	Cacao-mono	Cacao	18.7 ± 7.5 (10.0) a	13.3 ± 5.8 (2.9) ab	1180.6 ± 481.2 (23.6) a
60–100	Cacao-*Gliricidia*	Cacao	12.8 ± 6.4 (6.6) a α	7.2 ± 3.6 (2.5) a α	230.0 ± 178.2 (28.5) a α
60–100	Cacao-multi	Cacao	18.3 ± 16.8 (18.3) a α	66.9 ± 33.6 (22.0) b α	457.1 ± 229.7 (22.1) a α
60–100	Cacao-*Gliricidia*	*Gliricidia*	17.2 ± 5.5 (17.4) a α	15.8 ± 7.6 (10.7) a α	268.1 ± 268.1 (13.3) a α
60–100	Cacao-multi	Shade trees	48.5 ± 8.9 (17.4) b α	57.1 ± 19.2 (10.0) b α	1331.7 ± 576.8 (36.4) a α
100–300	Cacao-mono	Cacao	44.5 ± 12.9 (23.8) a	9.6 ± 3.6 (2.1) a	285.0 ± 77.6 (5.7) a
100–300	Cacao-*Gliricidia*	Cacao	52.5 ± 0.1 (27.0) a α	4.1 ± 2.0 (1.4) a α	27.7 ± 27.7 (3.4) b α
100–300	Cacao-multi	Cacao	34.8 ± 33.2 (34.7) a α	35.6 ± 19.7 (11.7) a α	1176.4 ± 966.4 (56.8) ab α
100–300	Cacao-*Gliricidia*	*Gliricidia*	64.6 ± 5.6 (65.3) a β	54.8 ± 9.2 (37.1) a β	741.9 ± 479.9 (36.8) a α
100–300	Cacao-multi	Shade trees	144.6 ± 38.2 (52.0) b α	150.7 ± 83.5 (26.3) a α	1862.0 ± 1764.7 (50.9) a α
Profile	Cacao-mono	Cacao	186.5 ± 67.2 A	454.9 ± 61.2 A	5003.3 ± 538.2 A
Profile	Cacao-*Gliricidia*	Cacao	194.6 ± 33.1 A α	289.0 ± 98.3 A α	808.4 ± 404.1 B α
Profile	Cacao-multi	Cacao	100.2 ± 61.5 A α	304.0 ± 31.8 A α	2069.5 ± 846.4 B α
Profile	Cacao-*Gliricidia*	*Gliricidia*	98.8 ± 12.8 A β	147.5 ± 16.8 B β	2016.5 ± 829.4 A α
Profile	Cacao-multi	Shade trees	278.2 ± 69.2 B α	573.6 ± 178.0 B α	3656.5 ± 2043.2 A α

The relative contribution of a soil layer to the profile total (in %) is given in brackets. Different capital letters indicate statistically significant ($p < 0.05$) differences between the cultivation systems of comparing either the cacao or comparing the shade trees; lower case Latin letters indicate significant differences in a given soil depth between the cultivation systems of comparing either the cacao or comparing the shade trees; lower case Greek letters significant differences between cacao and shade trees within a cultivation system and a given soil depth

differences in maximum rooting depth (3 species to 280 cm, 1 species to 200 cm, 2 species only to 20–40 cm; Table 4).

Fine root production and turnover

Fine root production was surprisingly similar in the three cacao agroforestry systems with profile totals (0–60 cm) of 153 to 191 g m^{-2} yr.$^{-1}$, despite different stem densities (Fig. 4). The production of cacao fine roots decreased slightly from the Cacao-mono plots (167 g m^{-2} yr.$^{-1}$) to the more diverse systems (133 and 113 g

m^{-2} yr.$^{-1}$) despite increasing stem densities of cacao. The shade trees in both, the Cacao-*Gliricidia* and the Cacao-multi plots, had on average a significantly lower annual fine root production than the cacao trees (Fig. 4).

Fine root turnover rates in the 0–60 cm profiles averaged over all tree species did not differ significantly between the cultivation systems with values ranging from 1.1 in the cacao monocultures to 1.3 in the Cacao-multi plots and 1.4 in the Cacao-*Gliricidia* plots (Table 5). On the species level, the cacao trees in the Cacao-multi systems had a more than two times higher fine root turnover than those in the Cacao-mono and the
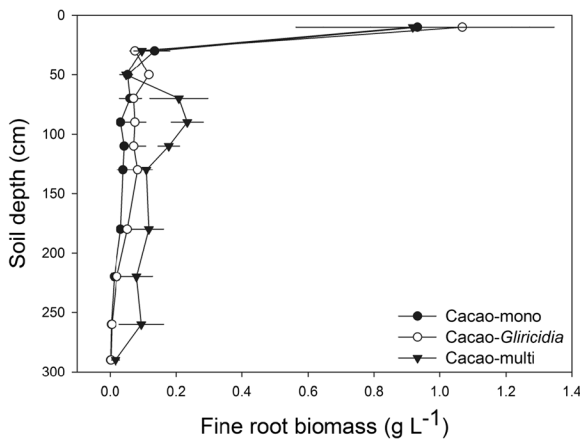
Fig. 2 Fine root biomass density (g L^{-1}) of all tree species per cultivation system in the soil profile from 0 to 300 cm

Cacao-*Gliricidia* systems (difference significant). While the fine root turnover of the cacao trees was almost invariant across the profile in the Cacao-mono plots, turnover was markedly higher in deeper layers of the Cacao-multi plots with abundance of shade tree roots (Table 5). The fine root turnover of the *Gliricidia* shade trees in this system was high particularly in the deeper soil layers and it significantly exceeded the turnover rate of the cacao trees. In contrast, the shade trees in the Cacao-multi plots had an only slow fine root turnover, which was significantly less than that of the cacao trees (Table 5).

Fine root morphology

The morphology of cacao fine roots differed with soil depth and also between the three cultivation systems. The mean fine root diameter of cacao trees did not change between topsoil and subsoil (0–300 cm) in Cacao-mono and Cacao-*Gliricidia* plots, but increased downwards from 0.41 to 0.70 mm in the Cacao-multi stands. Mean fine root diameter of cacao varied somewhat between the plots and soil layers, but showed no consistent difference between the three cultivation systems (Table 6). The shade trees had a markedly higher mean fine root diameter than the cacao trees in both shaded cultivation systems.

The specific root length and specific root area of cacao fine roots were markedly higher in 0–20 and 20–100 cm soil depth than in 100–300 cm in all three cultivation systems; the same was true for the shade trees (Table 6). The specific fine root length and area of the shade trees was of similar magnitude as the values

for cacao. However, the morphology of the different shade tree species in the Cacao-multi stands was highly variable (see Table SM4 in the supplementary information) with mean fine root diameter ranging from 0.1 to 1.3 mm, specific root length from 3.4 to 191.5 m g^{-1}, and specific root area from 91 to 1378 cm^2 g^{-1}.

Soil depths with highest water uptake

The isotopic composition of soil water extracted during the soil desiccation period in 2011 ranged from −25.7 to −75.9 ‰ (δ^2H) and −4.1 to −11.5 ‰ (δ^{18}O). The stable isotope ratios of water (δ^2H and δ^{18}O) were strongly correlated across our samples ($r^2 = 0.96$, $p < 0.001$; data not shown) and led to similar ecological interpretations concerning our research questions. We thus concentrate further descriptions on the hydrogen isotope ratio. In the soil, δ^2H values were less negative near the surface and decreased steadily down to 60–100 cm soil depth (Fig. 5). Water extracted from the xylem of the trees had an average δ^2H of −57.8 ‰.

The δ^2H patterns of soil and plant samples suggest complementary soil water use in case of the Cacao-*Gliricidia* cultivation system (Fig. 5a), with cacao trees extracting water mainly between 40 and 60 cm soil depth, while *Gliricidia* shade trees seem to take up water primarily from deeper soil depths. In the Cacao-multi system with presence of various shade tree species, a similar pattern of complementary soil water use of cacao and shade trees was not observed (Fig. 5b). In contrast to the Cacao-*Gliricidia* system, both cacao and shade tree species primarily obtained water from soil depths between 60 and 100 cm in the Cacao-multi system.

Interrelations between NPP, biomass, stand structure, and shade tree cover

A Principal Components Analysis (PCA) on the inter-relationships between above- and belowground net primary production and biomass (including fine root biomass and production), stand structural variables, and tree species diversity in the nine plots revealed a close association of the tested biomass and productivity variables with stand basal area, canopy cover, tree species diversity (H′) and fine root bio- and necromass in the 0–300 cm profile, but not with stem diameter, fine root biomass in 0–60 cm and fine root turnover and productivity in 0–60 cm
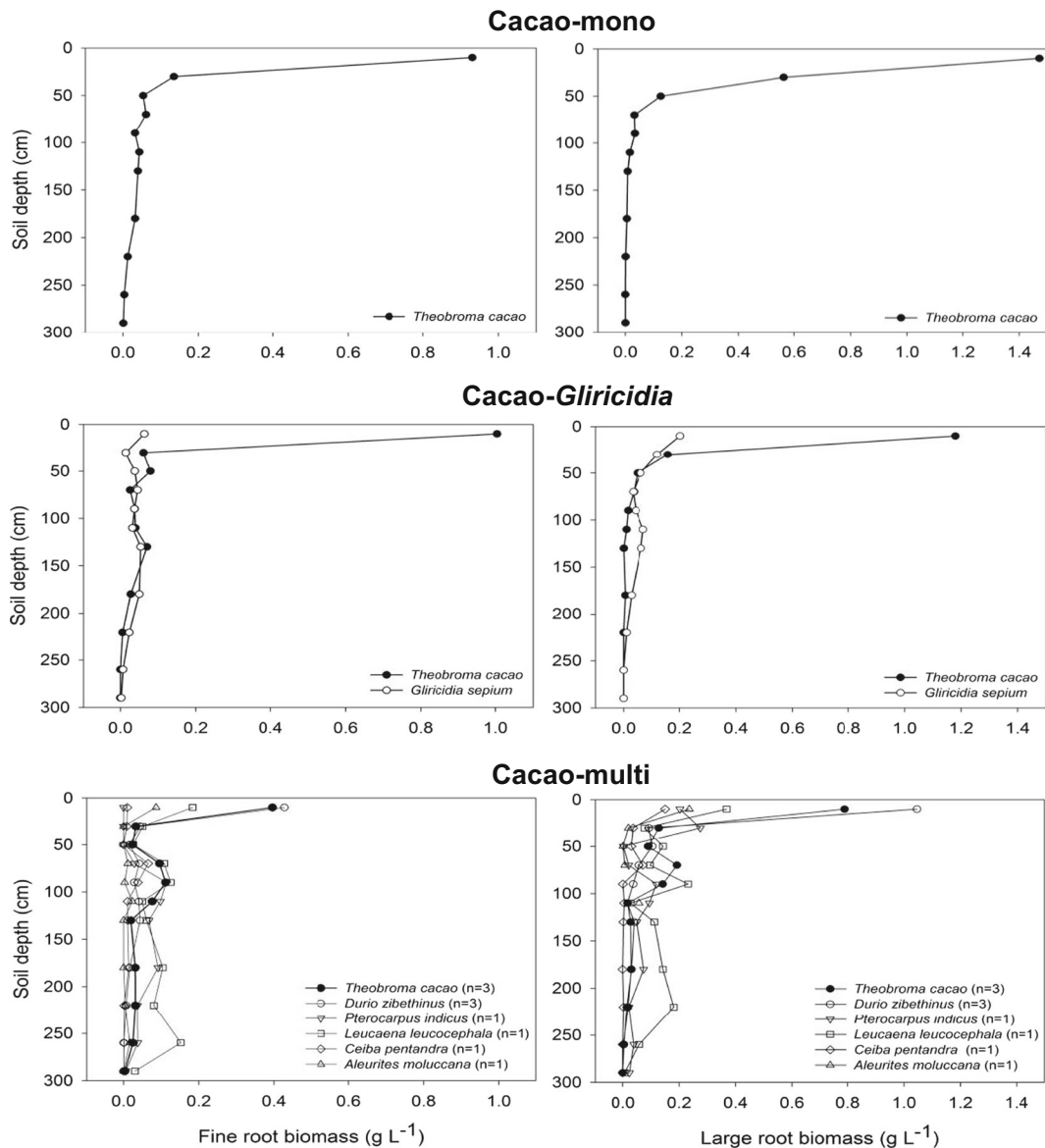
Fig. 3 Change with soil depth of the fine (< 2 mm) and large root (2–5 mm) biomass density (mass per soil volume) of cacao, *Gliricidia sepium* and five other common shade tree species in the three cacao cultivation systems (n = number of plots)

(Table 7). Fine root biomass and production in 0–60 cm depth showed a close (negative) association with axis 2 (EV: −0.859). Fine root turnover showed a close negative relation to axis 3 (EV: −0.630) as did tree density, suggesting that fine root turnover was positively related to stem density. Variables related to root biomass and productivity did not correlate with aboveground variables.

Bivariate Pearson correlation analyses did not show a consistent pattern of interrelations between fine root

biomass or production and various stand structural properties for cacao and shade trees (Table 8). The fine root biomass of the cacao trees seemed to be positively related to net primary production, fine root necromass as well as fine root turnover and production. Besides the close relationship between cacao fine root production and total belowground NPP (which is a consequence of the use of allometric equations: see Abou Rajab et al. 2016), cacao fine root production was negatively related to fine root biomass (0–300 cm depth), and positively to

Table 3 Vertical decrease in the biomass of fine and large roots down to 300 cm soil depth of cacao, *Gliricidia sepium* and five other common shade tree species in the three cacao cultivation systems expressed by the β value of the regression equation

$y = 1 - \beta^d$ (according to Gale and Grigal 1987), with y being the cumulative root biomass fraction in g m^{-2} and d the soil depth in cm

Cultivation system	Tree species	Fine roots (d < 2 mm)			Large roots (d = 2–5 mm)		
		β value	r	p	β value	r	p
Cacao-mono	*Theobroma cacao*	0.98	0.93	< 0.001	0.95	0.99	< 0.001
Cacao-*Gliricidia*	*Theobroma cacao*	0.98	0.91	< 0.001	0.93	0.99	< 0.001
	Gliricidia sepium	0.99	0.88	< 0.001	0.99	0.97	< 0.001
Cacao-multi	*Theobroma cacao*	0.99	0.97	< 0.001	0.98	0.97	< 0.001
	Durio zibethinus	0.99	0.95	< 0.001	0.97	0.89	< 0.001
	Pterocarpus indicus	1.00	0.77	< 0.001	0.99	0.96	< 0.001
	Leucaena leucocephala	1.00	0.84	< 0.001	0.99	0.95	< 0.001
	Ceiba pentandra	0.99	0.88	< 0.001	0.97	0.98	< 0.001
	Aleurites moluccana	0.99	0.91	< 0.001	0.97	0.89	< 0.001

High β values indicate a large proportion of root biomass in deeper soil depths, whereas low values stand for a large proportion of root mass near the soil surface, e.g. β = 0.930, β = 0.965, β = 0.979, and β = 0.987 indicate that 90, 70, 50, and 30%, respectively, of the total fine root biomass of the 300 cm deep profile is located in the upper 60 cm of the soil. Also given are the r and P values of the respective regression models. Please note that the number of observations (in maximum $n = 3$ per system in case of cacao and *Gliricidia*) differs across the different shade tree species, as not every shade shade tree species was present in all of the three Cacao-multi systems

fine root necromass (0–300 cm) and fine root biomass (0–60 cm) (Table 8). In contrast to the cacao trees, the shade trees showed a positive correlation of fine root biomass with above- and belowground, and total tree biomass. The fine root production of shade trees showed only weak and mostly non-significant correlations with tree biomass, NPP or stand structural variables. The only significant interrelationship was found in a negative (and weak) correlation with fine root turnover (Table 8).

Table 4 Mean and absolute maximum rooting depth of fine roots (diameter < 2 mm), large roots (diameter 2–5 mm), and coarse roots (diameter > 5 mm) of cacao and six shade tree species in 300 cm-deep soil profiles of the three cacao cultivation systems

Cultivation system	Tree species	Mean maximum rooting depth (cm)[a]		
		Fine roots (d < 2 mm)	Large roots (d = 2–5 mm)	Coarse roots (d > 5 mm)
Cacao-mono	*Theobroma cacao*	257 ± 23 (300) a	173 ± 41 (300) a	43 ± 9 (80) a
Cacao-*Gliricidia*	*Theobroma cacao*	265 ± 3 (300) a α	130 ± 17 (200) a α	30 ± 6 (60) a α
Cacao-multi	*Theobroma cacao*	280 ± 10 (300) a α	147 ± 47 (280) a α	87 ± 52 (300) a α
Cacao-*Gliricidia*	*Gliricidia sepium*	290 ± 0 (300) a β	220 ± 0 (240) a β	45 ± 14 (120) a α
Cacao-multi	All shade trees	280 ± 15 (300) a α	230 ± 36 (300) a α	210 ± 35 (280) a α
Cacao-multi	*Aleurites moluccana*	n.a. (300)	n.a. (120)	n.a. (20)
	Ceiba pentandra	n.a. (200)	n.a. (120)	n.a. (200)
	Durio zibethinus	293 ± 7 (300)	227 ± 27 (280)	167 ± 64 (280)
	Gliricidia sepium	n.a. (300)	n.a. (240)	n.a. (40)

Given are means and standard errors of 2 soil profiles per species and 3 plots per cultivation system ($n = 3$ in total per system). Different lower case Latin letters indicate statistically significant ($p < 0.05$) differences between the cacao plants or the shade tree species between the different cultivation systems; lower case Greek letters indicate significant differences between cacao and shade trees within a cultivation system

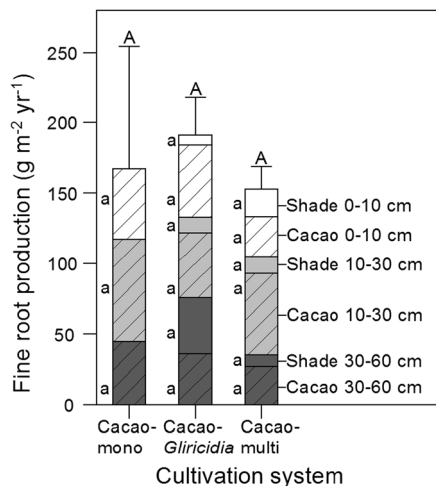[a] peak value (maximum) of rooting depth in brackets

Fig. 4 Fine root production in three different soil depths (0–10 cm, 10–30 cm and 30–60 cm) and in the total profile (0–60 cm) of the three cacao cultivation systems, given separately for cacao and shade trees. Capital letters indicate statistically significant differences between the different agroforestry systems; lower case Latin letters indicate significant differences for cacao or the shade trees in a given soil depth between the cultivation systems. Shade = shade trees

Discussion

The root system in shaded and non-shaded cacao agroforests

In support of our first hypothesis, standing fine root biomass increased by c. 50% from the unshaded cacao monocultures to the Cacao-*Gliricidia* system and by about 100% to the Cacao-multi system, reflecting the increase in stem density, stand basal area and canopy cover in this sequence of agroforestry systems. Interestingly, the increase in fine root biomass totals matches the doubling in aboveground NPP from the Cacao-mono to the Cacao-multi systems (from 17 to 34 Mg ha^{-1} yr.$^{-1}$), but the increase is much weaker than that of standing aboveground biomass (about 6fold). Synchronous increases in fine root biomass and aboveground NPP are plausible in the light of belowground resource acquisition, assuming constant rates of water and nutrient absorption per unit fine root biomass. Roots of larger diameters, especially the coarse root fraction (>5 mm in diameter) with mainly transport and storage function, did not mirror the fine root biomass increase from the unshaded mono to the shaded multi system (5003 vs. 5726 g biomass m^{-2} in the 0–300 cm profile). The fine root biomass increase is partly a consequence of deeper

fine root soil penetration with increasing shade tree cover, but it does also result from higher fine root densities in the profile at 60–300 cm depth in the shaded cacao agroforests. Higher root densities should result in greater resource depletion and thus higher competition intensity in both shaded systems as compared to the Cacao-mono stands. As the shade tree fine roots contributed with 30 and 73% to the stand total fine root biomass in the Cacao-*Gliricidia* and Cacao-multi systems, respectively, we expect that interspecific root competition between cacao and shade trees must have been more important in the systems with diverse shade tree cover than in the *Gliricidia* systems. This is supported by the cacao tree fine root biomass data when expressed on a tree individual basis (as tree and stem density per plot varied largely across the plots: see Table SM2): they decreased from 0.21 g m^{-2} per cacao tree (profile to 3 m) in the Cacao-mono systems to 0.09 g m^{-2} in the Cacao-*Gliricidia* systems and to 0.07 g m^{-2} in the Cacao-multi systems. Thus, the cacao trees in the shaded cultivation systems maintained much smaller fine root systems than the trees in the unshaded cacao monocultures. However, since the cacao tree density increased from the Cacao-mono to the Cacao-*Gliricidia* and the Cacao-multi system by ca. 17% and ca. 55%, respectively, this suggests that asymmetric root competition by the shade trees might be responsible for the relatively low fine root biomass amounts per cacao tree in the shaded systems.

Our root biomass inventory to 3 m depth should have covered the bulk of fine, large and coarse root biomass in the three agroforestry systems (see for comparison e.g. Defrenet et al. 2016). Other root inventories in cacao agroforests investigated only the upper profile to 50 or 100 cm depth, but yielded fine root biomass totals well comparable to our figures for these soil layers (c. 130–150 g m^{-2} in 0–60 cm depth in all three cultivation systems) (e.g. Kummerow et al. 1982; Muñoz and Beer 2001; Harteveld et al. 2007; Leuschner et al. 2009, 2013). This is only about 30% of the total fine root biomass determined in a nearby primary rainforest (c. 400 g m^{-2} in 0–50 cm; Leuschner et al. 2006) representing the natural vegetation at the sites. Even the Cacao-multi stands with >93% canopy cover had a much smaller fine root biomass than a nearby rainforest with larger canopy gaps due to selective logging (ca. 230 g m^{-2} in 0–50 cm; Leuschner et al. 2006). This suggests that cacao plantations repl0acing natural forest in Sulawesi always develop a much smaller fine root

Table 5 Mean turnover of fine root biomass (< 2 mm; in yr.$^{-1}$) in 0–10 and 10–30 cm depth, and in the 0–60 cm profile of the cacao and shade trees of the three cacao cultivation systems. Given are means and standard errors (n = 3 plots) of 12 replicate samples

Depth (cm)	Cultivation system	Tree species	Fine root turnover (yr^{-1})
0–10	Cacao-mono	Cacao	1.2 ± 0.3 a
	Cacao-*Gliricidia*		0.7 ± 0.1 a α
	Cacao-multi		2.0 ± 1.0 a α
	Cacao-*Gliricidia*	*Gliricidia*	1.7 ± 0.3 a β
	Cacao-multi	Shade trees	0.5 ± 0.1 b β
10–30	Cacao-mono	Cacao	1.1 ± 0.4 a
	Cacao-*Gliricidia*		1.7 ± 0.6 a α
	Cacao-multi		3.8 ± 0.4 b α
	Cacao-*Gliricidia*	*Gliricidia*	2.7 ± 1.7 a α
	Cacao-multi	Shade trees	0.5 ± 0.2 a β
Total profile 0–60	Cacao-mono	All trees	1.1 ± 0.2 A
	Cacao-*Gliricidia*		1.4 ± 0.3 A
	Cacao-multi		1.3 ± 0.2 A
	Cacao-mono	Cacao	1.1 ± 0.2 a
	Cacao-*Gliricidia*		1.2 ± 0.3 a α
	Cacao-multi		2.8 ± 0.6 b α
	Cacao-*Gliricidia*	*Gliricidia*	2.4 ± 1.4 a β
	Cacao-multi	Shade trees	0.5 ± 0.1 b β

Capital letters indicate statistically significant differences between the cultivation systems for all tree species together and the data summed over the 0–60 cm profile; lower case Latin letters indicate significant differences in a given soil depth between the cacao plants or the shade tree species between the different cultivation systems; lower case Greek letters indicate significant differences between cacao and shade trees within a cultivation system

system than a natural forest, irrespective of shade tree cover presence.

Root system segregation and complementary water use of cacao and shade trees

In the Cacao-*Gliricidia* system, we found clear indications of vertical root system segregation between cacao and the shade tree species, supporting our third hypothesis and confirming results of a review of rooting patterns in tree-based cropping systems (Lehmann 2003). Cacao displayed a shallower root system with by far highest fine root density in the upper 20 cm of the soil, whereas *Gliricidia* showed a more even vertical fine root distribution and a higher proportion of fine root biomass in the subsoil layers below 100 cm. This species difference in vertical root distribution is also visible in the large root fraction (d = 2 - 5 mm). Several other studies have confirmed the existence of root segregation in tropical agroforestry systems (e.g. Schroth and Zech

1995; Akinnifesi et al. 2004). Makumba et al. (2009) observed vertical root system segregation between *Gliricidia* and maize plants with *Gliricidia* having highest root length densities in the subsoil at 40–100 cm, which was associated with nutrient pumping from deeper soil layers.

In the Cacao-*Gliricidia* system, this rooting pattern corresponds to convincing evidence of complementary soil water extraction by cacao and *Gliricidia* as displayed by the isotopic composition of plant water, which was simultaneously extracted from stem wood tissue of the two species. Accordingly, cacao trees extracted water mainly between 40 and 60 cm soil depth, while *Gliricidia* primarily took up water from deeper soil layers. This result confirms earlier investigations in similar cacao agroforest stands of our study region that also showed a clear vertical segregation of the water extracting root zone of cacao and *Gliricidia* shade trees (Moser et al. 2010; Schwendenmann et al. 2010). Complementary water use seems to be one of the causes of

Table 6 Three fine root morphological traits of cacao and the shade trees as determined in different soil depths of pits dug to 300 cm depth in the three different cultivation systems

Depth (cm)	Cultivation System	Tree species	Fine root diameter (mm)	Specific root length (m g^{-1})	Specific root area (cm^2 g^{-1})
0–20	Cacao-mono	Cacao	0.55 ± 0.02 a	32.7 ± 2.2 a	309 ± 15 a
	Cacao-*Gliricidia*		0.52 ± 0.04 a α	25.0 ± 2.3 b α	287 ± 27 a α
	Cacao-multi		.41 ± 0.02 b α	58.1 ± 5.1 c α	487 ± 19 b α
	Cacao-*Gliricidia*	*Gliricidia*	0.70 ± 0.05 a β	54.2 ± 15.8 a β	674 ± 142 a β
	Cacao-multi	shade trees	0.88 ± 0.06 a β	46.5 ± 16.6 a α	456 ± 107 a α
20–100	Cacao-mono	Cacao	0.61 ± 0.08 a	39.1 ± 11.8 a	362 ± 82 a
	Cacao-*Gliricidia*		0.55 ± 0.02 a α	41.5 ± 9.0 a α	02 ± 56 a α
	Cacao-multi		0.67 ± 0.07 a α	48.1 ± 6.1 a α	440 ± 87 a α
	Cacao-*Gliricidia*	*Gliricidia*	0.77 ± 0.01 a β	29.9 ± 6.8 a α	530 ± 91 a α
	Cacao-multi	shade trees	1.04 ± 0.04 a β	16.5 ± 2.6 a β	247 ± 2 b β
100–300	Cacao-mono	Cacao	0.49 ± 0.03 a	19.0 ± 3.1 a	217 ± 21 a
	Cacao-*Gliricidia*		0.54 ± 0.11 ab α	16.2 ± 2.0 a α	214 ± 5 a α
	Cacao-multi		0.70 ± 0.09 b α	8.7 ± 1.2 b α	144 ± 14 b α
	Cacao-*Gliricidia*	*Gliricidia*	0.86 ± 0.08 a α	15.9 ± 1.5 a α	361 ± 21 a β
	Cacao-multi	shade trees	1.02 ± 0.13 b β	0.3 ± 3.7 a α	232 ± 40 b α

Given are means and standard errors of 12 samples per plot and 3 plots per cultivation system ($n = 3$ in total per system). Different lower case Latin letters indicate significant differences ($p < 0.05$) for cacao or the shade trees in a given soil depth between the different cultivation systems; lower case Greek letters indicate significant differences between cacao and shade trees within a cultivation system

the observed higher water consumption of the Cacao-*Gliricidia* system compared to the cacao monoculture (Köhler et al. 2014).

The results from the Cacao-multi stands suggest that the vertical root segregation observed for cacao and *Gliricidia* shade trees cannot be generalized. Other tree species and differently structured shade tree layers may

be associated with different rooting patterns, and complementary water use might be of marginal importance. An important influencing factor is tree size, which has been found to affect the soil depth of preferential water uptake in tree species mixtures (Meinzer et al. 1999; Meißner et al. 2012), with smaller trees sometimes tapping at deeper sources of water than larger ones.

Fig. 5 δ^2H signature of soil water in five soil depths (markers and solid line) and in wood tissue of the stem (dashed bars) of cacao, *Gliricidia*, and various other shade trees species in a Cacao-*Gliricidia* and a Cacao-multi shade tree-plot in the Kulawi valley. Given are means and standard deviation ($n = 4$). Shaded areas indicate the soil depths, in which the isotopic signature of soil water was similar to the signature of the water in stem wood tissue
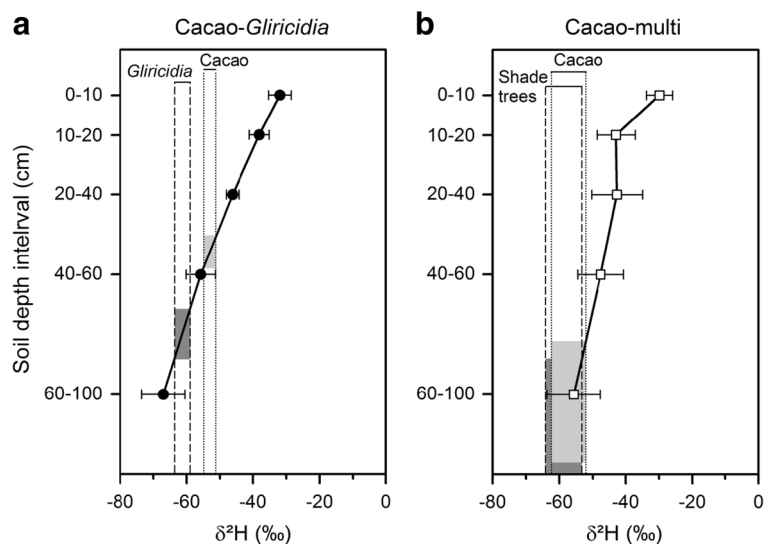
Table 7 Results of a principal components analysis based on plot-level data of above- and belowground net primary production, biomass, structure and tree species diversity (Shannon Index) for the three studied cacao cultivation systems

Variables	Axis 1 (EV 0.5681)	Axis 2 (EV 0.1465)	Axis 3 (EV 0.1025)	Axis 4 (EV 0.0755)
Aboveground NPP	**−0.884 (0.78)**	−0.096 (0.79)	0.149 (0.81)	0.163 (0.84)
Belowground NPP	**−0.809 (0.65)**	−0.416 (0.83)	−0.351 (0.95)	−0.117 (0.96)
Total NPP	**−0.902 (0.81)**	−0.161 (0.84)	0.082 (0.85)	0.125 (0.86)
Aboveground biomass	**−0.935 (0.87)**	0.209 (0.92)	0.1854(0.95)	−0.050 (0.95)
Belowground biomass	**−0.973 (0.95)**	0.073 (0.95)	0.136 (0.97)	−0.022 (0.97)
Total biomass	**−0.945 (0.89)**	0.179 (0.93)	0.175 (0.96)	−0.046 (0.96)
Tree density	**−0.612 (0.37)**	0.416 (0.55)	**−0.618 (0.93)**	0.204 (0.97)
Stand basal area	**−0.892 (0.80)**	0.325 (0.90)	0.049 (0.90)	−0.201 (0.94)
Stem diameter	−0.454 (0.21)	0.086 (0.21)	**0.637 (0.62)**	**−0.576 (0.95)**
Canopy cover	**−0.641 (0.41)**	0.378 (0.55)	−0.257 (0.62)	0.142 (0.64)
Shannon Index	**−0.769 (0.59)**	0.236 (0.65)	−0.226 (0.70)	0.261 (0.77)
Fine root biomass (0–300 cm)	**−0.859 (0.74)**	−0.407 (0.90)	0.137 (0.92)	0.123 (0.94)
Fine root necromass (0–300 cm)	**−0.784 (0.61)**	0.244 (0.67)	0.060 (0.68)	−0.060 (0.68)
Fine root biomass (0–60 cm)	−0.377 (0.14)	**−0.794 (0.77)**	0.162 (0.80)	0.329 (0.91)
Fine root turnover (0–60 cm)	−0.207 (0.04)	−0.193 (0.08)	**−0.630 (0.48)**	**−0.707 (0.98)**
Fine root production (0–60 cm)	−0.459 (0.21)	**−0.822 (0.89)**	−0.227 (0.94)	−0.136 (0.96)

Given are the eigenvalues (EV) of the four main axes and the loading of sixteen parameters on these. The values in brackets give the cumulative fraction of variance explained by the variable. The most important factors on each axis are printed bold. The data of aboveground biomass and NPP (see Table SM2) were obtained from Abou Rajab et al. 2016

Isaac et al. (2014) could prove a difference in the water acquisition zone of cacao growing either in monoculture or in mixture.

In the Cacao-multi system of the present study, the stable isotope signatures indicate that cacao and the shade trees used the same soil layers (60–100 cm) for water uptake, in contrast to the Cacao-*Gliricidia* system. The presence of various shade tree species in the Cacao-multi stands seems to have altered the vertical distribution of cacao fine roots toward deeper rooting relative to the monospecific stands, while this apparent displacement effect was less obvious in the Cacao-*Gliricidia* system. The greater mean maximum rooting depth of the fine, large and coarse roots of cacao in the Cacao-multi stands compared to the other systems is in line with this picture. These rooting patterns suggest that the cacao fine roots were forced to grow into deeper soil layers than in the Cacao-mono and Cacao-*Gliricidia* stands, despite the presence of relatively high amounts of shade tree fine root biomass in the subsoil below 100 cm. The apparent consequence for cacao and shade trees was root foraging in the same soil horizons instead of water uptake in different layers.

There are a number of studies which show alteration of root system size or root distribution patterns in the profile in response to the presence of allospecific competitors (Schenk 2006), but the observed effects differ in direction. Lehmann (2003) reported shallower rooting of crops like cacao when grown with shade trees (see also Nygren et al. 2013), while Schroth (1995) observed deeper rooting. Shifts in root distribution were also observed in larger root diameters: Isaac et al. (2014) observed shallower coarse root distribution in cacao monocultures than when grown with different shade trees. Our results demonstrate that the response of the target species depends largely on competitor identity and most likely also on tree size. While both neighborhood constellations (*Gliricidia* vs. multiple tree species) apparently caused a reduction in cacao fine root biomass, the frequent occurrence of *Gliricidia* roots below 60 cm seems to have pushed the cacao fine roots both upwards (to the 0–20 cm layer) and downwards, while the high density of shade tree roots in the Cacao-multi

Table 8 Pearson correlation coefficients of linear regressions between the parameters fine root biomass (0–300 cm soil depth), fine root biomass (0–60 cm soil depth), and fine root production (0–60 cm soil depth), and 14 different variables characterizing above- and belowground net primary production, above- and belowground biomass and stand structure of the cacao (all three systems) and the shade trees (two shade systems (* $p < 0.1$; ** $p < 0.05$; *** $p < 0.001$)

Variable / Source	Fine root biomass (0–300 cm)		Fine root biomass (0–60 cm)		Fine root production (0–60 cm)	
	Cacao	Shade trees	Cacao	Shade trees	Cacao	Shade trees
Aboveground NPP	0.59 *	0.67	0.64 *	0.65	0.23	−0.04
Belowground NPP	0.64 *	0.19	0.75 **	0.14	0.94 ***	0.65
Total NPP	0.66 **	0.65	0.72 **	0.62	0.36	0.03
Aboveground biomass	−0.25	0.87 **	−0.16	0.78 *	−0.04	−0.32
Belowground biomass	−0.26	0.84 **	−0.15	0.75 *	−0.06	−0.30
Total biomass	−0.25	0.87 **	−0.16	0.78 *	−0.04	−0.32
Tree density	−0.31	−0.37	−0.10	−0.18	0.00	−0.41
Stand basal area	−0.25	0.72	−0.16	0.64	−0.04	−0.34
Stem diameter	−0.24	0.80 **	−0.34	0.68	−0.15	−0.39
Fine root necromass (0–300 cm)	0.77 **	0.50	0.86 **	0.48	0.77 **	−0.24
Fine root biomass (0–300 cm)	–	–	0.88 ***	0.95 **	−0.60 *	−0.40
Fine root biomass (0–60 cm)	0.88 ***	0.95 **	–	–	0.78 **	−0.14 **
Fine root turnover (0–60 cm)	−0.60 *	−0.40	−0.61 *	−0.48	−0.20	0.88
Fine root production (0–60 cm)	0.72 **	−0.15	0.78 **	−0.14	–	–

Please note that the source variable 'belowground NPP' is different from the variable 'fine root production', as it was obtained from allometric equation models and also includes the production of large and coarse roots as well as the root stump. The data for aboveground biomass and NPP (see Table SM2) were obtained from Abou Rajab et al. 2016

systems has led to a biomass reduction and relative downward shift of the cacao roots. Both patterns indicate that root competition is largely asymmetric in terms of biomass production with superior performance of the shade trees. A likely cause of asymmetry is the height difference observed between cacao and shade trees (Freckleton and Watkinson 2001), which was more pronounced in the Cacao-multi system.

Fine root dynamics of cacao and shade trees

According to the ingrowth core data, fine root turnover rates differed between cacao and shade trees in the shaded systems, and between the cacao trees in the three cultivation systems, indicating species differences in mean fine root longevity and possible effects of root competition on root lifespan. While the fine roots of *Gliricidia* were on average turned over twice as fast as the cacao roots in the Cacao-*Gliricidia* system, the turnover of the shade trees in the Cacao-multi system was by a factor of five slower than that of the cacao trees. These differences may in part be caused by the higher mean fine root diameter of the shade tree roots in

the Cacao-multi systems, but must have other causes in case of the Cacao-*Gliricidia* system. Possible influencing factors could be species differences in fine root N content and tissue density, or differences in carbohydrate supply and resistance to pathogen attack. The much shorter mean lifespan of the *Gliricidia* fine roots as compared to the cacao fine roots in the Cacao-*Gliricidia* system suggests that the former should be physiologically more active, which could partly compensate for the lower standing fine root biomass of *Gliricidia* in this system. In turn, the much higher turnover of the cacao fine roots than the shade tree roots in the Cacao-multi system may partly have outweighed the disadvantage of cacao in terms of fine root biomass and active root surface area.

The two to threefold faster fine root turnover of cacao in the Cacao-multi system with high abundance of shade tree roots compared to the Cacao-mono and Cacao-*Gliricidia* systems is interesting, as it points to a negative effect of the presence of shade tree roots on the lifespan of cacao roots (see also our discussion on the over-proportionally smaller cacao fine root biomass per cacao tree individual in the shaded systems). A possible

explanation of the reduced cacao root longevity in the Cacao-multi system is that the shade tree fine roots, which contributed ca. 65% of the total fine root biomass in 0–60 cm and pushed the root density in the soil to relatively high values, have reduced soil resource levels, which may have been experienced as stress by the cacao roots. Such a response was expected by us (hypothesis 4) and it would match the apparent competition-induced reduction in cacao fine root biomass in this system, in that high competition pressure increased the mortality of cacao fine roots. In turn, more short-lived fine roots should have higher per mass resource uptake rates than longer-living fine roots, which could also represent a strategy of cacao to cope with reduced resource levels, albeit at the cost of higher C investment in root turnover (e.g. Eissenstat et al. 2000). This would support the assumption of a root economics spectrum in perennial plant communities (Prieto et al. 2015). In the Cacao-*Gliricidia* system with smaller overall fine root density, cacao neither decreased its fine root biomass on the stand level, nor increased fine root turnover in response to the presence of shade tree roots.

Even though stand-level fine root biomass doubled from the Cacao-mono to the Cacao-multi system, we found no increase in fine root productivity in this sequence, which is mainly a result of the low fine root productivity of the shade trees in the latter system. This result from the belowground compartment conflicts with the prediction of functional biodiversity research that more diverse communities of woody plants are generally more productive (e.g. Gamfeldt et al. 2013; Liang et al. 2016) and therefore, our second hypothesis has to be rejected. Our results indicate a doubling of aboveground NPP, but no significant change in belowground NPP from the monospecific unshaded cacao stands to the shaded stands with 6–7 species. A possible explanation is that the shaded systems were able to use light in a complementary way, while complementary soil resource use occurred only in the two-species system. Apparently, the presence of additional species triggered a stress response in the fine root system of cacao, and complementary resource capture between cacao and the shade trees seemed to be of minor importance. Across our nine plots, fine root production was not related to any aboveground structural variable, which demonstrates that belowground NPP is controlled by other factors than aboveground NPP. This could be another cause why root production did not increase with tree species diversity in our study.

Our fine root production figures (153–191 g m^{-2} $yr.^{-1}$ in the 0–60 cm profile, cacao and shade trees combined) are relatively low compared to other numbers obtained with the ingrowth core method in cacao agroforests under natural shade trees (Steffan-Dewenter et al. 2007; Leuschner et al. 2009). A possible explanation is the relatively high age of c. 20 years of the investigated plantations in the Kulawi valley, as fine root productivity may decline with age (John et al. 2001). Despite increasing tree density, the fine root production of cacao tended to decrease in the sequence Cacao-mono - Cacao-*Gliricidia* - Cacao-multi system, in a similar manner as did the aboveground productivity of the cacao trees (Abou Rajab et al. 2016). It should also be kept in mind that fine root production estimates with the ingrowth core technique often are lower than results obtained with other methods (e.g. Hertel and Leuschner 2002). Since we used the fine root turnover rate from 10 to 30 cm soil depth to extrapolate the fine root production estimate to the 0–60 cm profile, ignoring a likely activity decrease with soil depth, our numbers should overestimate rather than underestimate fine root productivity in the profile. Consequently, these production figures can serve for comparing different stands, but the absolute root production values must be interpreted with care.

Conclusions

Our detailed investigation of root system structure and functioning in three different cacao agroforestry systems demonstrates marked tree species differences in fine, large and coarse root system size, root dynamics, and also root morphology, which shape the belowground interaction between the crop and shade trees. Root productivity was largely independent of aboveground structure and productivity, and no tree species diversity effect on root productivity was detected. We found hints for both asymmetric root competition and spatial root system segregation with complementary water use in the shaded systems. Another likely response is increased fine root mortality in cacao as an outcome of higher competition intensity, which increases the cost of root system maintenance, but may also increase water and nutrient uptake capacity. Still unidentified root system properties of the tree species and tree size likely control these processes. Our data and those of Abou Rajab et al. (2016) on aboveground NPP show that competition by

shade trees does reduce above- and belowground productivity of cacao as expected, but cacao bean yield remained unchanged in our plots despite increasing shading. This is partly caused by the higher density of cacao trees in our shaded systems, but it may also reflect a C allocation shift from leaf and fine root to fruit production under shading, which is beneficial for the farmer. Our results confirm the importance of belowground interactions for understanding the performance and yield of tree-based cropping systems.

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