



Nutrient saturation of crop monocultures and agroforestry indicated by nutrient response efficiency

Marcus Schmidt · Marife D. Corre · Bomin Kim · Julia Morley · Leonie Göbel · Anuja S. I. Sharma · Sînziana Setriuc · Edzo Veldkamp

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Abstract Efficient use of nutrients is a key requisite for a sustainable intensification of agriculture in order to meet the increasing global crop demand while minimizing deleterious environmental impacts. Agroforestry systems exhibit tree–crop interactions, which potentially contribute to nutrient-efficient agroecosystems. Our goal was to determine whether the conversion from cropland monocultures to alley-cropping agroforestry increases nutrient response efficiency (NRE), the ability of plants to convert available nutrients into biomass. We found that crop yield, plant-available nutrients and NRE were comparable between agroforestry and monocultures, but the trees in agroforestry had high NRE, contributing to nutrient retention of the agroforestry systems as a whole. The unimodal relationship of the crops' NRE with plant-available nutrients suggests that NRE values were beyond optimum in both agroforestry and monoculture indicating nutrient saturation. This indicates that fertilizer inputs can be reduced (or

optimized) without sacrificing crop yield or profit. Based on the NRE curves, we assessed that a reduction of plant-available N by 50% would lead to a decrease in crop yield by 17% and a concomitant increase in N response efficiency by 67%, whereas a similar reduction of plant-available P would lead to a decrease in crop yield by 8% with an increase in P response efficiency by 83%. An optimized fertilization to achieve such lower levels of plant-available nutrients will have beneficial effects on nutrient retention and redistribution. Optimizing fertilizer input will make alley-cropping agroforestry a productive and profitable agro-ecosystem that contributes to an ecologically sustainable agriculture.

Keywords Environmentally sustainable agriculture · Alley-cropping agroforestry · Cropland monoculture · Soil nutrient stock · Soil organic carbon stock

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M. Schmidt (✉) · M. D. Corre · B. Kim · J. Morley · L. Göbel · A. S. I. Sharma · S. Setriuc · E. Veldkamp
Soil Science of Tropical and Subtropical Ecosystems,
University of Goettingen, Buesgenweg 2,
37077 Göttingen, Germany
e-mail: mschmidh@wdg.de

Introduction

Global food production has increased in the past decades, following the demands of a growing world population (Food and Agriculture Organization of the United Nations 2015). Concomitantly, fertilizer use has increased disproportionately with productivity, resulting in decreasing fertilizer use efficiency and

deleterious effects on the environment as a consequence of high loads of nitrogen and phosphorus (Tilman et al. 2002; Foley et al. 2005; Rockström et al. 2009). The dependency on pesticides and fertilizers common in conventional cropland monocultures is a major contributor to biodiversity loss (Geiger et al. 2010), groundwater pollution, global warming (Ward et al. 2014), N₂O-related ozone depletion (Ravishankara et al. 2009) and potential depletion of oxygen in the oceans (Handoh and Lenton 2003).

To meet the increasing global crop demand while minimizing environmental impacts, efficient use of nutrients is a key consideration, i.e. by maintaining or increasing yields on existing croplands while substantially lowering the use of fertilizers (Tilman et al. 2002, 2011; Foley et al. 2011). Improving the efficiency with which nutrients are converted into crop yield requires evaluation criteria of land-use systems that go beyond the traditional dose–response curves of fertilizer–yield relationships (Cerrato and Blackmer 1990). One important index is the nutrient response efficiency (NRE) = nutrient use efficiency (yield or biomass production per unit nutrient uptake) × nutrient uptake efficiency (nutrient uptake per unit available nutrient in the soil), or simply the ratio of yield or biomass production to plant-available nutrients in the soil (Bridgham et al. 1995). The NRE relationship with increasing nutrient availability depicts a unimodal curve (Electronic supplementary material Fig. 1). At low availability of a soil nutrient, NRE is also low, indicating nutrient limitation on productivity. As the nutrient availability increases, NRE increases towards an optimum, indicating high nutrient response with high productivity. When nutrient availability increases beyond this point, NRE declines and productivity levels off. A further increase in nutrient availability results in only minimal additional biomass gain and the ecosystem becomes nutrient-saturated (e.g. Pastor and Bridgham 1999; Hiremath and Ewel 2001; Schmidt et al. 2015). Maximizing productivity through chronic large fertilizer applications potentially leads to nutrient saturation and low NRE (e.g. Keuter et al. 2013) which, in turn, can decrease nutrient retention in biomass and in the soil, and ultimately increase nutrient losses and their negative environmental impacts (e.g. Hoefl et al. 2014).

Converting current monoculture-dominated agriculture into environmentally sustainable agriculture

will require not only a focus on productivity and profitability, but also on other ecosystem functions that enhance human well-being (Rockström et al. 2017). In many parts of the world, agroforestry systems are multifunctional systems, delivering important ecosystem functions (e.g. provision of fuel, water or soil fertility regulation, gas/climate regulation, organism habitat) that monocultures do not or minimally provide. These functions render services such as soil and water quality, water availability, and mitigation of climate change and biodiversity losses (Jose 2009; Tschardt et al. 2011). Crops produced in agroforestry are less affected by fungal pathogens and show similarly low mycotoxin concentrations in grains compared to those in monocultures (Beule et al. 2019). Additionally, modelling studies have suggested that across Europe, agroforestry has the potential to yield greater biomass than separate cultivation of crops and trees, especially where trees and crops were complementary in the use of light (Graves et al. 2007). Agroforestry systems can be equally or more profitable compared to cropland monocultures, depending on bio-economic factors such as subsidies and timber value (Graves et al. 2007). A recent pan-European analysis concluded that conversion towards multifunctional agroforestry systems would be favoured if their real value for society were reflected, e.g. through payments for ecosystem services (Kay et al. 2019).

In contrast to cropland monocultures, agroforestry systems support several mechanisms that can contribute to efficient nutrient cycling. Both trees and crops can profit from nutrient redistribution, e.g. crops, because of the nutrients added via litterfall and turnover, and the trees, because they take up nutrients through their roots below the crop rooting zone (Jose et al. 2000a, 2008; Cardinael et al. 2015b). Such complementary use of nutrients, or facilitation, occurs in the transition zone where crops and trees interact. However, combining trees and crops will only be beneficial if the effects of complementary nutrient use exceed competitive effects (Cannell et al. 1996), such as competition for soil mineral N (Jose et al. 2000a), water (Jose et al. 2000b) and light (Pardon et al. 2018). Complementary use of nutrients has been shown in a Canadian poplar–barley agroforestry system as a result of different depths in nutrient acquisition between trees and crops (Thevathasan and Gordon 1997). Furthermore, trees planted on former

agricultural soil increased soil N, P and K contents as well as nutrient turnover rates (Tsonkova et al. 2012) possibly due to pumping effect of tree roots that take up nutrients from deep soil and return them to topsoil via litterfall. In agroforestry systems, trees are commonly not or less fertilized than crops (Jose et al. 2000a; Cardinael et al. 2015a), however, it is presently unknown whether agroforestry systems are more nutrient-efficient compared to monocultures (Cardinael et al. 2015b).

Alley-cropping agroforestry systems, consisting of alternating rows of crops and short rotation coppice, are relatively easy to establish on monoculture cropland and have the advantage that with an optimal row spacing, farming techniques similar to monocultures can be applied. For farmers engaged in monocultures, this makes alley-cropping agroforestry a potentially attractive alternative. Several experimental alley-cropping systems have been established in the last decade in Germany (e.g. Langenberg et al. 2018; Swieter et al. 2018). The present study was conducted at three of these sites with contrasting soil characteristics (Table 1). Each of these sites had a cropland monoculture and a converted alley-cropping agroforestry treatment, all owned and managed by farmers. The conversion from cropland monocultures to agroforestry systems occurred 6 to 9 years prior to this study. An economic analysis conducted at two of these three sites showed that alley-cropping agroforestry was a profitable alternative, because the reduced income from crop production, a result of the smaller area under cropping, was offset by income generated by wood (Langenberg et al. 2018).

Our first objective was to determine changes in nutrient availability, crop productivity, and NRE between monoculture and alley-cropping agroforestry systems, with consideration of various distances from the tree row. For this objective, we tested the hypothesis that plant-available nutrients in the soil will be higher in crop alleys than in monocultures, based on the expected complementary use of nutrients between tree and crop rows in the alley-cropping systems. Our second objective was to determine the NRE curves along gradients of plant-available N, P and K across sites as indicators of whether these agroecosystems are nutrient-limited, at optimum efficiency or display nutrient saturation. Such curves can be used to optimize nutrient inputs in agro-ecosystems. We hypothesized that in both cropland monoculture and

agroforestry systems, the NRE of the crops will fall in the nutrient saturation segment, as both crops in agroforestry and monocultures receive similar high fertilization rates and production practices, resulting in comparably high yield and low NRE for both crop rows and monoculture. Our study provides the first multi-site evaluation of alley-cropping agroforestry and cropland monocultures, using NRE as the main criterion, which can aid to improve strategies in optimizing nutrient acquisition efficiency in agroecosystems as well as in formulating policies geared towards more environmentally sustainable agricultural production.

Materials and methods

Site description and experimental design

Our study was conducted at three sites (Electronic supplementary material Fig. 2): Dornburg (11° 39' O, 51° 01' N Thuringia, Calcaric Phaeozem soil), Wendhausen (10° 38' O, 52° 20' N, Lower Saxony, Vertic Cambisol soil) and Forst (14° 38' O, 51° 47' N, Brandenburg, Gleyic Cambisol soil). Each site had an agroforestry system with an alley-cropping structure (i.e. alternating rows of crops and short rotation coppice; Electronic supplementary material Fig. 2) and an adjacent cropland monoculture. The agroforestry system was established by planting rows of fast-growing trees on the same area of monoculture such that at each site both the monoculture, being the reference land use, and the converted agroforestry area had the same management history. At all sites, the alley-cropping system consisted of 48-m wide fertilized rows of crops alternated with 12-m wide unfertilized rows of trees (Electronic supplementary material Fig. 2). Crop rotations included wheat (*Triticum aestivum*), barley (*Hordeum vulgare*) and rapeseed (*Brassica napus*) (Table 1). All agroforestry tree rows at the three sites consisted of poplar clone max 1 (*Populus nigra* × *Populus maximowiczii*), and were harvested 4 to 7 years after their establishment in the winter of 2013 or 2014 (Table 1). During our study years (2016 and 2017), tree age was between 2 and 4 years after their first cut and trees were 3 to 7-m high. The total annual atmospheric N deposition was 13–15 kg N ha⁻¹ yr⁻¹ for the agroforestry tree row

Table 1 Management practices and climatic characteristics at the three sites of cropland agroforestry and adjacent cropland monocultures in Germany in 2016 and 2017

Soil type (site)	Year of establishment of agroforestry system	First harvest of trees in agroforestry	Age of trees (year) since first harvest during study years 2016 and 2017	Crop rotation	Fertilizer application in 2016 (kg ha^{-1} yr $^{-1}$)	Fertilizer application in 2017 (kg ha^{-1} yr $^{-1}$)	Mean annual temperature ($^{\circ}\text{C}$)	Annual precipitation (mm)
Calcaric Phaeozem (Dornburg)	2007	Winter 2014	2–3	Summer barley (2016)	N: 45	N: 105	10.8 (2016)	531 (2016)
				Winter rapeseed (2017)	P: 19.8	P: 19.5	10.9 (2017)	648 (2017)
				Winter wheat Summer barley	K: 37.4	K: 97.2		
Vertic Cambisol (Wendhausen)	2008	Winter 2013	3–4	Winter rapeseed (2016)	N: 221	N: 162	10.3 (2016)	505 (2016)
				Winter wheat (2017)	P: 0	P: 0	10.3 (2017)	819 (2017)
				Winter barley	K: 0	K: 0		
Gleyic Cambisol (Forst)	2010	Winter 2014	2–3	Winter wheat (2016)	N: 122	N: 86.4	10.3 (2016)	593 (2016)
				Winter barley (2017)	P: 33.7	P: 15.1	10.3 (2017)	621 (2017)
				Corn	K: 51.6	K: 48.9		

The same fertilization rates were applied to both the agroforestry crop row and monoculture. Agroforestry tree rows were unfertilized. Management data were provided by farmers; meteorological data were taken from Deutscher Wetterdienst (German Meteorological Service 2020)

and 11–13 $\text{kg N ha}^{-1} \text{ yr}^{-1}$ for the agroforestry crop row and monoculture (Umweltbundesamt 2018).

In the fall of 2015, we established four replicate plots at each site in both agroforestry and monoculture systems (Electronic supplementary material Fig. 2). Each replicate plot in the agroforestry spanned from the tree row into the crop row with four sampling locations: within the tree row (2.25 m from the crop

edge) and at 1 m, 4 m and 7 m from the tree row (i.e. 3 sites \times 4 replicate plots \times 4 sampling locations = 48 sampling locations), whereas each replicate plot in monoculture was sampled at the plot's center (i.e. 3 sites \times 4 replicates = 12 sampling locations) (Electronic supplementary material Fig. 2). Grain yield was additionally sampled at 24 m from the tree row (crop row center). Replicate plots were 30 m \times 30 m

(agroforestry) and 10 m × 10 m (monocultures), separated with a minimum distance of 30 m (agroforestry) and 10 m (monoculture).

General soil characteristic and plant-available nutrients

Soil bulk density, pH, organic C (SOC), total N, effective cation exchange capacity (ECEC) and base saturation were determined once during the growing season in 2016 for each sampling location. Bulk density was determined in the top 0.3 m using the core method (Blake and Hartge 1986). Soil samples for pH, SOC and ECEC were taken with an auger from the top 0.3 m, air-dried and sieved through a 2-mm sieve. Soil pH was measured in distilled water with a soil-to-water ratio of 1:4. The SOC and total N were measured using a CN analyser (Elementar Vario EL; Elementar Analysis Systems GmbH, Hanau, Germany). Soil samples with pH \geq 6.0 were acid-fumigated prior to SOC analysis to remove carbonates (Harris et al. 2001). The ECEC was determined by percolating the soils with unbuffered 1 mol L⁻¹ NH₄Cl and the percolates were analysed for exchangeable elements (Ca, Mg, K, Na, Mn, Al, and Fe) using an inductively coupled plasma-atomic emission spectrometer (ICP-AES, iCAP 6300 Duo View ICP Spectrometer, Thermo Fischer Scientific GmbH, Dreieich, Germany). Base saturation was determined as the percentage of base cations on the ECEC. The exchangeable K was used as an index of plant-available K (Schmidt et al. 2015; Waring et al. 2015). As ECEC, including exchangeable K, does not vary substantially in consecutive years, we present plant-available K for 2016 only. Stocks of SOC and N were calculated from their concentrations using the measured average bulk density of 1.19 Mg m⁻³ for Calcaric Phaeozem soil, 0.89 Mg m⁻³ for Vertic Cambisol soil, and 1.28 Mg m⁻³ for Gleyic Cambisol soil.

Our index of plant-available N in the top 0.05-m depth was assessed using net N mineralization rates (Hart et al. 1994) from in situ incubations of intact soil cores for 7 days. As N uptake by roots is excluded in the in situ-incubated soil cores, the difference in mineral N before (T0) and after incubation (T1) has been referred to as plant-available N (Hart et al. 1994). Net N mineralization was measured monthly at each sampling location during the growing seasons of 2016

and 2017. Soil cores were extracted in the field with prepared bottles of 0.5 mol L⁻¹ K₂SO₄. Concentrations of extracted NO₃⁻ and NH₄⁺ were measured with continuous flow injection colorimetry (SEAL Analytical AA3, SEAL Analytical GmbH, Norderstedt, Germany). Plant-available N for the entire growing season at each sampling location was calculated as the mean of monthly net N mineralization rates multiplied by the number of days of the growing season of the crops (from germination to harvest) or trees (whole year), added with the atmospheric N deposition and N fertilization rate (the latter only for the agroforestry crop row and monoculture; Table 1).

Plant-available P in the top 0.05-m depth was assessed as the sum of resin-exchangeable P and bicarbonate-extractable P (Tiessen and Moir 1993; Cross and Schlesinger 1995). These were determined monthly at each sampling location during the growing seasons of 2016 and 2017. Concentrations of resin-exchangeable and bicarbonate-extractable P were determined using the ICP-AES (see above). The index of plant-available P for the entire growing period at each sampling location was calculated as the mean of the monthly measurements during the crops' or trees' growing period.

The amount of plant-available nutrients (N, P and K) in the soil was converted from mass basis to area basis. In order to compare the same soil mass for both land uses at each site, and to avoid the interference of bulk density changes with land-use change, we used the average soil bulk density of the monoculture plots (as the reference land use), as mentioned above. All statistical analyses first considered all sampling locations of the agroforestry crop rows (see below). However, as we were also interested on the aggregated measure for the agroforestry crop row as a whole, the plant-available nutrients in each replicate plot at each site were weighted based on the various measured distances within the crop row. We first tested auxiliary data on plant-available nutrients between 7 m and 24 m distances from the tree row and found no difference between these distances. Hence, the weighting factors that we used for plant available-nutrients were: 2.5:24 for 1-m distance, 3:24 for 4-m distance, and 18.5:24 for 7 and 24-m distance. The weighting factors for grain yield were 2.5:24 for 1 m, 3:24 for 4 m, 6.5:24 for 7 m and 12:24 for 24 m. These weighting factors were derived from the widths within the crop row that were represented by the sampled

distances, e.g. 1 m crop row represented a width ranged from 0 m (edge of the tree row) to 2.5 m (distance to tree row), which was 2.5 m of the 24 m (or 2.5:24) covered by our sampling locations (Electronic supplementary material Fig. 2).

Above-ground biomass production and nutrient response efficiency

Harvested grain yield was measured in July or August of 2016 and 2017, using a small harvester (plot combine), within an area of 17.5 m² at each sampling location. Tree leaf litter was measured bi-weekly from September to November of 2016 and 2017 at all sampling locations of the agroforestry sites using collection baskets with 0.14-m² area. To determine the tree woody biomass at all tree rows of the agroforestry sites, a site- and year-specific allometric equation [*woody dry mass* = $a \times \text{stem diameter}^b$, with a and b as constants derived from the relationship between woody dry mass and stem diameter, Verwijst and Telenius (1999)] was fitted to the stem diameter and biomass of 25 trees, sampled to cover the diameter range found at each site. Annual woody biomass production of trees in 2016 and 2017 was calculated as the difference between standing woody biomass between two consecutive years. The above-ground biomass production for the tree row was the sum of wood and leaf litter production. For the agroforestry crop row and monoculture, grain yield (excluding crops' straw) was used for the NRE calculation as yield is the parameter of farmers' interest. The grain yield of the sampling locations within the agroforestry crop row was also weighted (as explained above) to get a value for the whole crop row in each replicate plot at each site.

The NRE is calculated as grain yield (for crops) or above-ground biomass production (for trees) \div plant-available nutrients in the soil (Bridgham et al. 1995). To assess an index for plant-available nutrients, we measured a consistent depth interval across land uses or management systems. Measuring plant-available nutrients for the entire soil profile is neither necessary nor practical (Hiremath and Ewel 2001; Keuter et al. 2013; Schmidt et al. 2015; Waring et al. 2015). Similarly, NRE does not constitute a nutrient budget but serves as an indicator of the status of an agroecosystem, allowing assessment of whether it is nutrient limited, at optimum efficiency or nutrient

saturated (Bridgham et al. 1995). We used the crops' NRE to assess whether the resource efficiency in the agroforestry crop row was comparable, larger (prevailing tree–crop complementarity) or lower (suggesting tree–crop competition) than in the monoculture at each site. The agroforestry tree row, having inherently different productivity than the crops, were not statistically compared with the crops. Additionally, we assessed the relationships of the crops' NRE with gradients of plant-available nutrients across sites (see “Statistical analysis” section below), where sites represented a soil fertility gradient (i.e. total N, SOC, ECEC, texture, Table 2) and different crop management (e.g. fertilization rates, Table 1).

Leaf-litter nutrient input and root density

Input of nutrients from leaf litter at all sampling locations of the agroforestry sites (i.e. within the tree row and at various distances from the tree rows) was calculated as the mass of leaf litter per area multiplied by the nutrient concentrations, analyzed from the collected leaf litter. Total N concentration in leaf litter was measured after drying and grinding of samples, using the CN analyzer mentioned above. Total P and K concentrations of the leaf litter samples were measured using the ICP-AES (see above) after pressure digestion in concentrated HNO₃.

For root quantification, we took soil cores of 0.6-m length and 65-mm in diameter with three subsamples per sampling location at the sites with Calcaric Phaeozem and Vertic Cambisol soils during the growing season of 2017. The soil cores were divided into depth intervals of 0–0.1 m, 0.1–0.2 m, 0.2–0.4 m and 0.4–0.6 m. The soils were washed carefully and all roots \geq 10-mm length were collected and dried at 70 °C for 3 days. Dry root mass was expressed per unit area for the top 0.3-m depth and the subsoil of 0.3–0.6 m.

Statistical analysis

For comparison of plant-available nutrients, NRE and productivity at each site, we first tested whether there was a difference in soil texture among sampling locations; texture is a management- or land use-independent indicator to ascertain comparability of soil conditions between agroforestry and monoculture plots at each site (e.g. de Blécourt et al. 2013; Schmidt

Table 2 Soil biochemical and physical properties, measured within 0–0.3-m depth in 2016, at the three sites of cropland agroforestry (AF) and adjacent cropland monocultures in Germany

Soil type (site)	pH (1:4 soil–H ₂ O-ratio)	Total N (kg m ⁻²)	Organic C (kg m ⁻²)	C:N ratio	Effective cation exchange capacity (mmol _c kg ⁻¹)	Ca saturation (%)	K saturation (%)	Mg saturation (%)	Na saturation (%)	Base saturation (%)	Texture (% sand/silt/clay)
Calcaric Phaeozem (Dornburg)											
AF tree row	6.5 ± 0.1c	0.64 ± 0.03a	6.18 ± 0.48a	9.6 ± 0.3a	152 ± 5b	84.5 ± 0.6b	5.7 ± 0.5b	8.6 ± 0.3a	0.4 ± 0.1a	99.2 ± 0.1a	4b/76a/20b
AF crop row	6.7 ± 0.0b	0.59 ± 0.01a	5.13 ± 0.12a	8.7 ± 0.1b	160 ± 2b	85.8 ± 0.5b	5.1 ± 0.2b	8.1 ± 0.1a	0.4 ± 0.0a	99.3 ± 0.3a	4b/71a/25b
Monoculture	7.9 ± 0.1a	0.56 ± 0.07a	4.64 ± 0.73a	8.1 ± 0.4b	590 ± 101a	92.6 ± 1.5a	1.9 ± 0.4a	5.4 ± 1.1a	0.1 ± 0.0a	100.0 ± 0.0a	11a/51b/38a
Vertic Cambisol (Wendhausen)											
AF tree row	7.1 ± 0.3a	0.71 ± 0.03a	6.82 ± 0.33a	9.7 ± 0.1a	363 ± 77a	92.7 ± 1.5a	2.2 ± 0.3a	4.8 ± 1.1a	0.2 ± 0.1a	99.9 ± 0.0a	18ab/47a/35a
AF crop row	7.4 ± 0.1a	0.70 ± 0.01a	6.58 ± 0.08a	9.5 ± 0.1ab	386 ± 45a	93.4 ± 0.7a	2.1 ± 0.2a	4.2 ± 0.5a	0.2 ± 0.0a	99.9 ± 0.0a	18b/44a/38a
Monoculture	7.4 ± 0.0a	0.72 ± 0.05a	6.16 ± 0.10a	8.7 ± 0.5b	316 ± 8a	91.5 ± 0.6a	2.5 ± 0.3a	5.7 ± 0.4a	0.2 ± 0.1a	99.9 ± 0.0a	27a/29b/44a
Gleyic Cambisol (Forst)											
AF tree row	7.1 ± 0.1a	0.47 ± 0.01a	4.12 ± 0.27ab	8.8 ± 0.7a	57.9 ± 7.1a	80.0 ± 2.0a	2.5 ± 0.6a	16.5 ± 1.4ab	0.5 ± 0.1a	99.4 ± 0.2a	61a/32a/7a
AF crop row	7.0 ± 0.0a	0.45 ± 0.01a	4.18 ± 0.12a	9.3 ± 0.2a	57.0 ± 3.4a	81.2 ± 0.9a	2.3 ± 0.3a	15.2 ± 0.8b	0.7 ± 0.2a	99.4 ± 0.0a	67a/24a/9a
Monoculture	7.1 ± 0.0a	0.41 ± 0.02a	3.48 ± 0.20b	8.5 ± 0.2a	54.3 ± 6.5a	77.1 ± 2.2a	1.2 ± 0.1a	20.4 ± 2.2a	0.6 ± 0.2a	99.4 ± 0.1a	67a/24a/9a

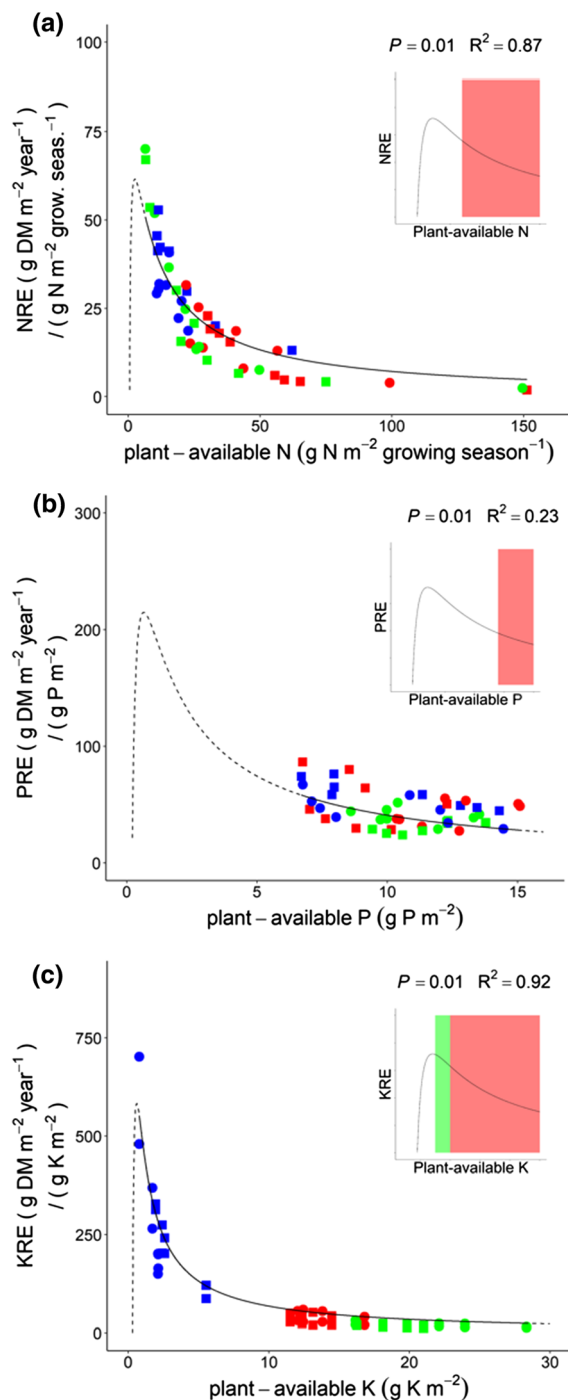
At each site, mean ± SE (n = 4) with different letters indicate significant differences between AF tree and crop rows and monoculture (one-way ANOVA with Tukey HSD test at P ≤ 0.05)

et al. 2015). If there was no difference, further analysis was done without a covariate; if otherwise, clay content was used as a covariate, as in the case of the Calcaric Phaeozem soil (Table 1). Using clay content as a covariate results in the exclusion of confounding effects caused by textural differences, which affect other soil parameters such as ECEC (e.g. Schmidt et al. 2015). Each parameter was first tested for equality of variances with a Levene test and for normal distribution with a Shapiro–Wilk test. If these two conditions were met, differences between groups (i.e. sampling locations or land uses) were tested with a one-way ANOVA followed by Tukey HSD test. If normal distribution was not met, a Kruskal–Wallis test with multiple comparison extension was used. If equality of variances was not met, a one-way T test pairwise comparison with a Holm-correction was used. For the site with Calcaric Phaeozem soil, we used ANCOVA with clay content as a covariate, and checked for normality and homogeneity of variance of the model residuals using diagnostic plots. If normality and variance homogeneity of residuals were not met, we used the Generalized Linear Model (GLM) with a Gamma distribution. If still the GLM residuals did not show normality and variance homogeneity, the model (either ANCOVA or GLM Gamma) with the diagnostic plot closely approximating these conditions was chosen. We accepted statistical differences as significant at P values ≤ 0.05 . We refrained from comparing NRE between crops and trees due to their inherent productivity differences, but reported the trees' NRE for its added value in the agroforestry system.

The mathematical relationships of NRE along the range of plant-available nutrients across sites were fitted using a least-squares approach on the Michaelis–Menten equation (Bridgham et al. 1995).

$$NRE = \frac{(Nutrient_{av} - Nutrient_{min})Production(P)_{max}}{(Nutrient_{av} - Nutrient_{min}) + Nutrient_{at\ 0.5\ P_{max}}} / Nutrient_{av}. \quad (1)$$

$Nutrient_{av}$ is the availability of an essential nutrient, $Nutrient_{min}$ is the nutrient availability at zero production and $Nutrient_{at\ 0.5\ P_{max}}$ is the nutrient requirement at half of the maximum production P_{max} . This relationship depicts the change of productivity or NRE along a gradient of nutrient availability (Electronic supplementary material Fig. 1). We used the best fit curves of Eq. 1 across sites (Fig. 1) to assess



potential changes in crop yield as well as N and P response efficiencies when plant-available N and P are reduced by 50%. For this, we set the plant-available nutrient to $\frac{1}{2}$ of its observed mean. We then calculated the corresponding NRE according to the estimated

◀ **Fig. 1** Relationships of nutrient response efficiencies of crops with gradients of plant-available N (NRE), P (PRE) and K (KRE) at three sites, which indices were measured in the top 0.05-m depth during the growing seasons of 2016 and 2017. The inset shows the range of the actual observations within the NRE conceptual model in Electronic supplementary material Fig. 1, with the green area at the optimum level and the red area at nutrient saturation. For the data points, squares = agroforestry crop rows, circles = cropland monocultures, green = Calcaric Phaeozem soil (Dornburg), red = Vertic Cambisol soil (Wendhausen), and blue = Gleyic Cambisol soil (Forst). As the NRE did not differ between crops in monoculture and in agroforestry systems (Table 4), we present one combined curve for both systems. The functions for the presented curves are: $y = (x - 0.5) * 770 / (x - 0.5 + 8) / x$ (for N); $y = (x - 0.2) * 450 / (x - 0.2 + 1) / x$ (for P); and $y = (x - 0.3) * 700 / (x - 0.3 + 0.3) / x$ (for K). (Color figure online)

equations presented in the caption of Fig. 1. We did not do this for K since its availability strongly differs with sites (Fig. 1c). All analyses were conducted using R version 3.5.1.

Results

Plant-available nutrients and nutrient response efficiency

Tree-mediated nutrient redistribution reached far into the crop rows, illustrated by nutrient inputs from tree leaf litter and roots that were measurable even at 7-m distance from the tree row (Electronic supplementary material Fig. 3). In the crop rows of the agroforestry systems, N, P and K inputs from tree leaf litter decreased with increasing distance to the tree rows (Electronic supplementary material Fig. 3a, b, c). In addition, tree root mass within the top plow layer (0–0.3 m, Electronic supplementary material Fig. 3d) and subsoil (0.3–0.6 m, Electronic supplementary material Fig. 3e) decreased with distance from the tree row to the crop row.

Plant-available N, P and K under crops at different distances from the tree row were not different, with the exception of lower plant-available N at the 1 or 4 m distance compared to the 7 m distance (Calcaric Phaeozem or Vertic Cambisol in 2017; Electronic supplementary material Table 1; $P = 0.01$). Crops in the agroforestry crop row (weighted by sampled distances) and monoculture did not differ in plant-

available N, P or K (Table 3), except for plant-available P in Vertic Cambisol soil in 2016 and 2017; $P \leq 0.03$).

The crops' NRE did not differ between agroforestry crop row (weighted by sampled distances) and monoculture with the exception of a higher N response efficiency in the agroforestry crop row at the Gleyic Cambisol soil in 2017 (Table 4; $P = 0.01$). These comparable NREs of crops in the two systems were a result of the similar grain yields between agroforestry crop row and monoculture treatments (with only slightly diminished yield at 1 m crop row; Electronic supplementary material Table 2) as well as their analogous soil nutrient availability, described above. The agroforestry tree rows displayed large NRE, caused by their high biomass productivity (Electronic supplementary material Table 2) with generally comparable levels of nutrient availability as those in the agroforestry crop row (Table 3 and Electronic supplementary material Table 1).

The best-fit curves for NRE of agroforestry crop row and monoculture along the ranges of plant-available nutrients across sites showed a monotonous decrease with increases in plant-available nutrients ($P \leq 0.01$ for N, P and K; Fig. 1a, b, c). This corresponded to a condition where plant-available nutrients in the soil are higher than optimum efficiency (Electronic supplementary material Fig. 1)—nutrient saturation was strongest for plant-available P (Fig. 1b). We assessed that a reduction in plant-available N by 50% would lead to a decrease in crop yield by 17% and an increase in N response efficiency by 67%, whereas a similar reduction of plant-available P would lead to a decrease in crop yield by 8% and an increase in P response efficiency by 83%.

Soil characteristics

With the exception of the higher SOC in the agroforestry crop row compared to the monoculture at the site with Gleyic Cambisol soil ($P = 0.04$), the general soil characteristics did not differ between the agroforestry tree or crop rows and monocultures ($P > 0.05$ – 0.91 ; Table 2). Furthermore, at the site with Calcaric Phaeozem soil, the higher soil C:N ratio, lower pH and lower ECEC of the agroforestry tree or crop rows compared to the monoculture ($P = 0.01$ – 0.04) were associated with lower clay contents at the agroforestry system ($P = 0.01$)

Table 3 Plant-available N, P and K measured within the top 0.05-m soil depth at the three sites of cropland agroforestry (AF) and adjacent cropland monocultures in Germany during the growing season of 2016 and 2017

Soil type (site)	Plant-available N (g N m ⁻² growing season ⁻¹)		Plant-available P (g P m ⁻²)		Plant-available or exchangeable K (g K m ⁻²) 2016
	2016	2017	2016	2017	
Calcaric Phaeozem (Dornburg)					
AF tree row	9.6 ± 3.6a	9.0 ± 1.2a	12.6 ± 0.9a	10.4 ± 0.6a	20.3 ± 2.2a
AF crop row	14.5 ± 4.3a	41.7 ± 12.0a	12.7 ± 0.4a	10.3 ± 0.4a	18.8 ± 1.0a
Monoculture	13.4 ± 3.3a	63.0 ± 29.4a	11.8 ± 0.9a	10.1 ± 0.7a	22.6 ± 2.5a
Vertic Cambisol (Wendhausen)					
AF tree row	3.2 ± 0.3b	5.9 ± 1.6b	7.7 ± 0.5b	9.7 ± 0.8b	12.4 ± 0.2a
AF crop row	82.9 ± 22.9a	33.6 ± 1.9a	8.4 ± 0.7b	9.2 ± 1.2b	12.9 ± 0.6a
Monoculture	48.6 ± 17.4ab	36.5 ± 7.8ab	11.2 ± 0.6a	13.8 ± 0.7a	13.8 ± 1.1a
Gleyic Cambisol (Forst)					
AF tree row	3.8 ± 0.8b	4.7 ± 0.8b	14.1 ± 1.1a	7.9 ± 0.8a	3.6 ± 1.1a
AF crop row	33.3 ± 10.3a	11.4 ± 0.3a	13.0 ± 0.6a	7.6 ± 0.3a	3.1 ± 0.8a
Monoculture	19.3 ± 1.5ab	12.1 ± 0.8a	12.4 ± 0.7a	7.3 ± 0.3a	1.7 ± 0.3a

Values for agroforestry crop row are weighted with the measured distances within the crop row. At each site, mean ± SE (n = 4) with different small letters indicates significant differences between AF tree and crop rows and monoculture (one-way ANOVA with Tukey HSD test at $P \leq 0.05$)

Table 4 Nutrient response efficiency (NRE) at the three sites of cropland agroforestry (AF) and adjacent cropland monocultures in Germany during the growing season of 2016 and 2017

Soil type (site)	N response efficiency (g DM m ⁻² yr ⁻¹ /g N m ⁻² growing season ⁻¹)		P response efficiency (g DM m ⁻² yr ⁻¹ /g P m ⁻²)		K response efficiency (g DM m ⁻² yr ⁻¹ /g K m ⁻²)	
	2016	2017	2016	2017	2016	2017
Calcaric Phaeozem (Dornburg)						
AF tree row	169.6 ± 45.86	175.4 ± 14.8	91.5 ± 13.3	149.5 ± 18.3	56.7 ± 7.2	77.7 ± 8.2
AF crop row	42.9 ± 10.6a	9.2 ± 2.5a	35.0 ± 0.6a	26.4 ± 1.1a	23.9 ± 2.0a	14.7 ± 1.6a
Monoculture	45.9 ± 9.8a	9.4 ± 2.8a	44.4 ± 2.8a	37.0 ± 3.1a	24.0 ± 3.3a	16.8 ± 1.8a
Vertic Cambisol (Wendhausen)						
AF tree row	590.3 ± 86.1	473.4 ± 152.6	239.2 ± 29.5	223.3 ± 22.0	146.5 ± 12.3	171.5 ± 7.5
AF crop row	4.2 ± 0.9a	18.9 ± 1.5a	35.5 ± 4.1a	70.4 ± 8.1a	22.9 ± 1.9a	48.3 ± 1.9a
Monoculture	10.2 ± 2.6a	22.2 ± 4.1a	33.5 ± 2.5a	52.1 ± 1.5a	27.5 ± 2.4a	52.9 ± 3.9a
Gleyic Cambisol (Forst)						
AF tree row	NA	283.4 ± 39.6	NA	162.9 ± 19.0	NA	415.9 ± 79.0
AF crop row	26.1 ± 6.1a	45.5 ± 2.6a	50.0 ± 3.0a	68.5 ± 4.1a	241.3 ± 43.9a	201.2 ± 46.2a
Monoculture	27.3 ± 4.9a	30.8 ± 0.6b	41.8 ± 6.4a	51.6 ± 5.9a	368.1 ± 118.2a	265.0 ± 76.1a

Values for agroforestry crop row are weighted with the measured distances within the crop row. At each site, mean ± SE (n = 4) with different small letters indicates significant differences between agroforestry crop row and monoculture ($P \leq 0.05$); AF tree row, being functionally different from the crops, was not statistically compared with the crops' NRE but evidently showed large NRE at all sites. NA—data on woody biomass production was not available

(Table 2). We accounted for this variation in soil texture by including clay content as a covariate in all further statistical analyses of the Calcaric Phaeozem site.

Discussion

No effects of agroforestry on soil fertility in young systems

The potential of agroforestry systems to increase SOC and nutrient stocks have been reported in other studies (Tsonkova et al. 2012; Cardinael et al. 2015a; Pardon et al. 2017). In contrast to these studies, SOC and N stocks as well as base saturation in our alley-cropping agroforestry systems remained generally comparable with the cropland monocultures (Table 2). Most studies reporting increases in SOC and nutrient stocks have been conducted on relatively mature systems (Pardon et al. 2017), while the agroforestry systems that we studied were established 6 to 9 years prior to our study. Furthermore, systems from which increases in SOC and nutrient stocks were reported often had an inherently lower soil fertility (e.g. post-mining sites; Tsonkova et al. 2012), and with that a high potential for improvement, compared to the relatively fertile soils at our sites (with high ECEC and > 99% base saturation; Table 2). Our findings were in line with earlier observations that only agroforestry systems with a tree component older than 15 years display significant increases in SOC and nutrient stocks (Pardon et al. 2017). Nonetheless, at our relatively young agroforestry systems, we observed considerable tree–crop row interactions, such as tree litter-nutrient inputs and tree roots at the crop rows (Electronic supplementary material Fig. 3). These are critical prerequisites for possible increases in SOC and nutrient stocks with age of agroforestry systems (e.g. Dhillon and Van Rees 2017).

High fertilizer inputs override potentially beneficial tree–crop interactions

Despite the observed complementary interactions between tree and crop rows, we did not observe differences in plant-available N, P and K in the soil between the monoculture and various distances within the crop rows (Electronic supplementary material

Table 1). This is in contrast to the expectation of higher plant-available nutrients in the crop row. This seemed puzzling at first, especially as changes in available nutrients occur more rapidly than changes in total nutrient stocks (Jose et al. 2000a; Pardon et al. 2017). However, a comparison of the quantities of nutrients redistributed by tree litterfall within the first few meters of the crop rows (Electronic supplementary material Fig. 3a, b, c) with the amounts of nutrients added by fertilizers (Table 1) illustrated that the high levels of fertilizer application in the agroforestry crop row probably overrode any potential facilitation effect. Other competitive tree–crop row interactions were more obvious. The reduction in the crop’s grain yield at 1-m distance compared to the farther distances from the tree rows (Electronic supplementary material Table 2) was probably caused by competition between trees and crops for resources other than nutrients, such as light (Pardon et al. 2018) or water (Jose et al. 2000b). However, this decrease in the crop’s grain yield close to the trees was compensated by the higher production of crops at greater distances from the tree rows (Swieter et al. 2018) (Electronic supplementary material Table 2).

The large NRE of the tree rows (Table 4) indicate that agroforestry systems have an overall advantage in NRE compared to cropland monocultures, particularly in fertile soils where the tree component is productive. The large NRE of trees indicated high nutrient retention and, given the complementary interactions of the tree and crop rows (Electronic supplementary material Fig. 3), will foster redistribution of nutrients within the system. For agroforestry systems with a tree component managed as a short rotation coppice, woody biomass production will be moderated during the first years following establishment or the first year following harvest. We expect that during such earlier periods of tree (re-)growth, the overall NRE of agroforestry systems may not be higher than the cropland monocultures. However, considering that the trees in our alley-cropping systems are being harvested every 4 to 7 years (Table 1) and that their NRE were already substantial after 2 to 4 years from cutting (Table 4), the overall NRE of these agroforestry systems for the tree growing cycle of 4 to 7 years may surpass the NRE of cropland monocultures. Our field-based assessment of NRE is crucial for developing policies geared towards optimizing the use of

fertilizer and improving ecosystem services (Kay et al. 2019).

Reduced fertilization largely increases NRE with only small reduction in crop yield

The monotonous decrease in NRE of agroforestry crops and monocultures with increasing ranges in plant-available N, P and K levels across sites (Fig. 1a, b, c) illustrated that the levels of these nutrients in the soil mostly exceeded optimal values in both monocultures and alley-cropping systems (Pastor and Bridgman 1999; Fig. 1 with Electronic supplementary material Fig. 1 as insets). This supports our hypothesis that the NRE of the crops in both agroforestry and monocultures display nutrient saturation. These results were in stark contrast to unmanaged, mixed deciduous forest stands in central Germany, wherein the P and K response efficiencies were at the optimal level (Schmidt et al. 2015). However, the available P and K levels within the same 0.05-m depth of that forest site were much lower than in our present fertilized agroforestry crop rows and monocultures (Table 1). Our results provide enticing indications that plant-available nutrients, especially N and P, can be reduced in both agroforestry crop rows and monocultures with only small reductions in crop yield. The obvious way to reduce plant-available N, P and K in these agroforestry and monoculture systems is by reducing fertilization rates. Based on inherent mechanisms that contribute to a more efficient acquisition and recycling of nutrients in agroforestry systems compared to monocultures (i.e. tree leaf litter-nutrient input and a permanent deep root system of the trees; Electronic supplementary material Fig. 3), we anticipate that agroforestry systems will perform better than cropland monocultures under reduced fertilizer application. This emphasizes the need for an ecosystem level index of resource efficiency such as NRE that, unlike fertilizer use efficiency, takes into account the inherent provision of nutrients by the soil under adapted management, e.g. agroforestry. A reduced fertilization regime may also enhance the microbial cycling and retention processes of N, via mineralization (Carpenter-Boggs et al. 2000) and N immobilization (Hoeft et al. 2014). Earlier studies (Jose et al. 2000a; Cardinael et al. 2015a) have speculated, based on observed increases in SOC and nutrient concentrations, that a reduction of the fertilization regime to

crops in agroforestry systems is promising. Although nutrient redistribution via tree litterfall in agroforestry systems varied spatially (Electronic supplementary material Fig. 3) and temporally, as it is controlled by productivity of and distance to the tree rows (Pardon et al. 2017), precision farming techniques can be implemented to compensate for tree row-induced nutrient gradients (Cardinael et al. 2015a). Reducing the costs of fertilizer inputs may further increase the profitability of agroforestry systems (Langenberg et al. 2018) compared to monocultures, particularly when crop yield is maintained (i.e. at optimum NRE). Optimization of the already high NRE in agroforestry systems (Table 4) through a reduced fertilization regime (e.g. for N, Fig. 1a) will reduce the risk of N losses (Tilman et al. 2002) and improve ecosystem services (Hoeft et al. 2014; Rockström et al. 2017).

Conclusions

Our study demonstrated that the concept of NRE is useful to evaluate the nutrient status of agricultural systems across locations. NRE curves further allowed to detect potentials for optimizing fertilization rates and thus a more sustainable nutrient management. The shape of NRE curves depends on factors such as crop demand, the ability of the soil to mineralize and retain nutrients and, in the case of agroforestry, the amount of nutrients released from litterfall from the tree row. Alley-cropping agroforestry, aside from being a productive and profitable agro-ecosystem, may have additional ecosystem functions through redistribution of nutrients via leaf litterfall and tree roots (e.g. soil fertility regulation, water filtration, and gas/climate regulation), which can contribute to environmentally sustainable agricultural production. Future investigation should focus on economic valuation of these ecosystem functions as well as quantification of nutrient leaching losses and soil greenhouse gas fluxes for a holistic assessment of ecosystem functions of cropland agroforestry versus monocultures.

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Author's contribution MS, MDC and EV designed the experiment and wrote the manuscript. MS, BK, JM, LG, AS and SS carried out the field and laboratory works. MS conducted the data analysis.

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Availability of data and materials All compiled data in this study are published in figures and tables. Detailed primary data are stored and published in the BonaRes DataCentre and available via the BonaRes Repository at <https://doi.org/10.20387/bonares-q82e-t008>.

Code availability Data analysis has been conducted using the free software R as described in the “Statistical analysis” section.

Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

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