Crop yields in intercropping: meta-analysis and virtual plant modelling

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Abstract

Intercropping, the cultivation of two or more crop species simultaneously in the same field, has been widely practiced by smallholder farmers in developing countries and is gaining increasing interest in developed countries. Intercropping can increase the yield per unit land compared to sole cropping. The yield advantage of intercropping is often assessed using the land equivalent ratio (LER). LER may be interpreted as the relative area required by sole crops to produce the same yields as achieved in a unit area of intercrop. LER>1 means intercropping is more efficient in land use than sole cropping. A large variation of LER has been found in the literature. However, few studies attempted to investigate reasons for this variation in LER. This thesis aims to reveal how temporal niche difference, crop type combination, and agronomic practices affect LER, productivity and interspecific interactions in annual intercrops.

LER increased with temporal niche differentiation according to our meta-analysis of literature data. This positive relationship was valid in mixtures of C3 and C4 species but not in C3/C3 mixtures. Application of N fertilizer in intercropping decreased LER when the intercropped species were sown and harvested simultaneously. However, reducing overlap in growing periods of the intercropped species mitigated the negative effect of N fertilizer on LER. A functional-structural plant (FSP) model was developed to investigate the interplay between temporal and spatial complementarity and plant traits in mixed plant systems. The results showed that complementarity of light use in time and space likely determine productivity of species mixtures. The early-sown plants benefited from later sowing of the late-sown plants due to the relaxed competition for light from the late-sown plants until a plateau when the growth durations of the intercropped species overlapped less than 50% of the total growth period of the intercrop. By contrast, the late-sown plants suffered a great reduction in biomass due to the competition for light from the early-sown plants especially at moderately delayed sowing time and when spatial arrangement of the intercrop allowed strong interspecific competition. The shading effect from the early-sown plants on the growth and productivity of the late-sown plants was smaller if the late-sown plants had the potential to grow tall and if it had a high maximum CO_2 assimilation rate. A meta-analysis of relative yields in cereal/legume intercrops was conducted to investigate the relationship between performance of intercropped species and management. Earlier sowing of one species increased its competitiveness towards the other species while later sowing decreased it. Application of N fertilizer enhanced the competitiveness of a cereal towards a legume,

resulting in overall low productivity of legumes in intercrops. However, sowing legumes earlier than cereals mitigated the negative effect of N on productivity of legumes.

Overall, this thesis shows that the complementary resource use resulting from plant traits diversity and temporal and spatial arrangements of plant mixtures is one of the key factors for high productivity of intercropping. This finding strengthens the basis for further research on the possible contribution of species diversity in agricultural systems to meeting the demand for food and other agricultural products while mitigating the environmental impacts of modern agriculture.

Contents

Chapter 1

General introduction

General introduction

What, where and why is intercropping?

Intercropping is defined as the cultivation of two or more crop species in the same field for the whole or part of their growing period (Willey, 1990; Hauggaard-Nielsen et al., 2008). Intercropping is an ancient agronomic practice and was applied worldwide. Before the 1940s, intercropping was commonly practiced in the United States and Europe (Andersen, 2005; Machado, 2009). It however has gradually disappeared in developed countries due to mechanization and the availability of cheap synthetic fertilizers and pesticides which make sole cropping an efficient way to go (Horwith, 1985; Machado, 2009). In developing countries in Asia, Africa and Latin America, where farmers have limited access to mechanization and agricultural chemicals, intercropping is still widely used (Machado, 2009; Lithourgidis et al., 2011). In Latin America, 70-90% of beans are intercropped with maize, potatoes and other crops (Lithourgidis et al., 2011). Vandermeer (1992) reported that almost all of the cowpeas grown in Africa were grown in intercrops.

It is clear from the ecological literature that ecological functioning and ecological services tend to increase with species richness (Tilman, 1999; Loreau et al., 2001). In this sense, intercropping is no exception (Cardinale et al., 2007) and intercropping has been shown to have clear advantages over sole crops in many aspects. For instance, intercropping may utilize land and other resources more efficiently than sole cropping (Reddy and Willey, 1981; Zhang and Li, 2003); intercropping may suppress pests and diseases (Andow, 1991; Trenbath, 1993), and weeds (Ayeni et al., 1984; Banik et al., 2006); and intercropping can increase stocks of organic soil carbon and nitrogen (Cong et al., 2015).

One of the challenges facing the world is to match the rapidly changing demand for food from an increasing population with limited land, using environmentally friendly agricultural methods (Godfray et al., 2010). Sustainable intensification of agriculture is one way to tackle the challenge (Tilman et al., 2011). Sustainable intensification is defined as a set of agricultural practices and technnologies that increase crop production and resource use efficiency on croplands, while reducing the environmental impact of agriculture. Given the advantages of intercrops, intercropping has the potential to contribute to sustainable intensification of modern agriculture (Bedoussac et al., 2015; Jensen et al., 2015). Therefore, intercropping is currently receiving renewed interest as an environmentally friendly agronomic practice in developed countries.

Land-use efficiency of intercrops

Land-use efficiency is one of the most widely studied aspects in intercropping research. Land-use efficiency of an intercrop may be compared to that of sole crops using the so-called land equivalent ratio (LER) (Mead and Willey, 1980). The LER is calculated as the sum of relative yields of component crops in an intercrop versus sole crops (Eq. 1).

$$\mathrm{LER} = \frac{Y_1}{M_1} + \frac{Y_2}{M_2} = \mathrm{PLER}_1 + \mathrm{PLER}_2 \tag{1}$$

where Y_1 and Y_2 are the yields (per unit of total area of the intercrop) of species 1 and 2 in the intercrop, and M_1 and M_2 are the yields of the species in sole crops (per unit area of the sole crops), and PLER_1 and PLER_2 are the partial land equivalent ratios of the intercropped species, i.e. the relative yields of the species.

If the relative yield of one species in a two species intercrop is 70% and the relative yield of the other species in the intercrop is 50%, the LER is 120%, or 1.2. LER indicates the relative land area required by sole crops to produce the same yield/biomass of component species as achieved on one unit area of intercrops (Mead and Willey, 1980; Reddy and Willey, 1981). LER > 1 means that, in order to produce the same component crop yield as in a unit area of intercrop, a greater land area of sole crops would be needed.

In addition to being the partial land equivalent ratios, PLER values are also a measure of competitiveness of the species within the system when comparing PLER of a species to its relative density (a ratio between density in intercrop to density in sole crop). If the PLER of a species is greater than its relative density, yield or biomass per plant in the intercrop is greater than in the sole crop indicating the species somehow experiences less competition in the intercrop as compared to sole crop situation. In contrast, if the PLER of a species is lower than its relative density, its productivity at plant level is decreased in the intercrop as compared to in its sole crop due to greater competition the species suffered in the intercrop.

Published studies show large variation in LER. Most intercropping studies reported values of LER well above one, but some reported values below one. Examples of high LER are 1.41 (maize/faba bean, Mei et al., 2012), 1.67-1.69 (maize/cowpea, Ofori and Stern, 1986; Ofori and Stern, 1987b) and 1.83 (sorghum/groundnut, Harris et al., 1987). Examples of low LER are 0.77 (wheat/pea, Naudin et al., 2010), 0.82 (wheat/soybean, Haymes and Lee, 1999) and 0.89 (maize/cowpea, Chang and Shibles, 1985). While a large number of intercropping studies have been conducted, few have attempted to generalize and quantitatively synthesize what factors contribute to variation in LER, and which species under what conditions contribute to a high LER. Such knowledge however could contribute important information needed in designing intercrops with a high LER. In this thesis, I aimed to synthesize and explore what factors affect LER and what factors influence the contribution of individual species to LER using meta-analysis and functional-structural plant modelling.

Meta-analysis

In this thesis, I use meta-analysis as the main research methodology (adopted in Chapters 2, 3 and 5). Meta-analysis is a set of statistical methods to quantitatively review and synthesize published information on a topic (Sileshi et al., 2008). Broadly, the goal of meta-analysis is to describe the distribution of the effect sizes associated with a set of experiments (Hedges et al., 1999). One of the advantages of meta-analysis is that effects that are not significant in a single study may become statistically significant when multiple studies are combined (Madden and Paul, 2011). Thus, the power to detect departures from a null hypothesis of "no effect" is enhanced. Furthermore, meta-analysis can be used to study the effect of co-variables on a measure of effect size (Viechtbauer, 2007). Meta-analysis has distinct advantages over the alternative so-called narrative review of research synthesis which is considered to be subjective, and not suitable for making quantitative predictions (Madden and Paul, 2011).

Possible mechanisms for high LER

Niche differentiation theory/complementary interactions

In ecology, niche theory has been developed to explain competition and coexistence of different species in natural communities (Vandermeer, 1972). According to niche theory, if the niches of two species are similar, the two species cannot coexist in the same community over years because of intense interspecific competition for resources (Vandermeer, 1992), while if their niches are different, the species in question can coexist and be productive due to complementary use of resources (Cardinale et al., 2011). Niche differentiation may be one of the mechanisms for high LER of intercrops (Vandermeer, 1992; Fukai, 1993; Lithourgidis et al., 2011), as species that occupy different niches when grown together in a crop or vegetation stand may together use growth resources more completely than when grown as mono-species stands, due to a complementary usage of the resources in time and/or space. This, in turn, results in higher production per unit area in intercrop than sole crops. According to

Lithourgidis et al. (2011), yield advantage of intercrops occurs when the component crops do not compete for the same ecological niches.

Under the niche differentiation hypothesis, niche differentiation in time, i.e. less overlap of resource usage in time, is one of the mechanisms for high production of species-rich plant communities (Vandermeer, 1992; Tilman, 1999; Loreau, 2000). Greater LER is expected with greater temporal niche differentiation because it may allow component species to realize a greater relative yield due to complementary use of resources in time (Li et al., 2013), and relaxed competition from the other species (Vandermeer, 1992; Keating and Carberry, 1993; Li et al., 2001a; Zhang et al., 2008). Effects of temporal niche differentiation on LER have been implied in many studies, but few studies analyzed it quantitatively. No indicators have been defined to quantify temporal niche differentiation in intercrops. In this thesis, I developed an index to quantify temporal niche differentiation in annual intercrops and quantitatively characterize the effect of temporal niche differentiation on LER using meta-analysis (Chapters 2 and 3).

Spatial niche differentiation, related to differences in plant stature or rooting depth, enabling intercrops to exploit available resources more completely than corresponding sole crops, may be another reason for high LER (Anten and Hirose, 1999; Li et al., 2006). Few studies reported information on plant stature, rooting depth etc., I am therefore not able to analyze the effect of spatial niche differentiation on LER using meta-analysis in this thesis. Instead, I investigated the effect of plant stature on intercropping productivity using an architectural plant modelling approach (Chapter 4).

Functional complementarity between intercropped species may improve resource capture and/or resource use efficiency in intercrops thus resulting in high LER. An example of this complementarity is mixing species with the C3 and C4 photosynthetic pathways. Plants with the C4 photosynthetic pathway have higher photosynthetic capacity than those with the C3 pathway, which means C4 plants have higher rates of photosynthesis than C3 plants at high light conditions (Connor et al., 2011), provided temperatures are conducive. By contrast, at low light, C3 plants might use light more efficiently than C4 plants (Anten and Hirose, 2003). Complementary effects of mixing C3 and C4 species may be correlated with other plant traits, e.g. plant stature. In mixtures of C3 and C4 species with similar plant stature one might expect no complementary capture of light but only intense competition for light. In this case, light use efficiency of the mixture might be low. In contrast, in C3/C4 mixtures with different plant stature, tall C4 plants might fully use light in the upper canopy layer where light intensity is high while short C3 plants could comparatively efficiently use light in the lower canopy layer where light intensity is low, resulting in an overall high light use efficiency for the canopy as a whole. Therefore, mixing short C3 and tall C4 species may be more effective in light use than combining C3 and C4 species of similar stature. This hypothesis is tested with functional-structural plant modelling.

Another example of functional complementarity is mixing legume and non-legume species since legumes can fix nitrogen from air through symbionts in addition to using soil N, while non-legume species acquire nitrogen only from the soil (Jensen, 1996; Hauggaard-Nielsen and Jensen, 2001; Chu et al., 2004; Corre-Hellou et al., 2006). In this thesis, I investigated whether species type combination (C3/C3 mixtures vs C3/C4 mixtures) affects LER (Chapters 2, 3 and 4). However, the effect of including legume species in intercrops was not assessed because I was not able to compare LER of legume/non-legume intercrops with non-legume/non-legume intercrops using information from the literature. The main body of the intercropping literature I used for the meta-analysis studies consists of papers about legume/non-legume intercrops while only few are related to non-legume/non-legume mixtures.

Facilitative effects in intercrop

Facilitative effects entail that one species is positively affected by the presence of another species, e.g. by directly or indirectly improving nutrient availability. An important example in relation to intercropping involves facilitative interactions between legumes and non-legumes that can contribute to higher nutrient uptake in intercrops as compared to sole crops, resulting in high LER (Zhang and Li, 2003). For instance, phosphorus uptake by maize was significantly higher in a maize/faba bean intercrop than in sole maize, because organic acids excreted by faba bean facilitate P uptake by maize in the intercrop (Li et al., 2003). Iron uptake by peanut was higher in an intercrop with maize than in sole peanut as the maize plants secrete siderophores that mobilize Fe (Inal et al., 2007). The contribution of facilitation of nutrient uptake can usually not be disentangled from that of niche complementarity, based on measurements of productivity and resource uptake (Loreau and Hector, 2001). Therefore, the effects of facilitation were not addressed specifically in this thesis.

Intercropping has often been reported to suppress pests, diseases, or weeds (Trenbath, 1993). Intercropping, on the one hand, may enhance the abundance of predators and parasites, which in turn prevent the build-up of pests. On the other hand, the environment and quality of host plants may be altered in intercropping, which affects the searching behavior and dispersal of pest insects and their population growth (Trenbath, 1993; Lithourgidis et al., 2011). A review of 209 studies containing 287 pest species showed that populations of pest insects in intercrops were lower compared with sole crop in 52% of studies, and higher in 15% of studies (Andow, 1991). Intercropping was often reported more successful in weed suppression than sole cropping which might be attributed to the improved competitive ability of crop stand towards weeds (Banik et al., 2006). In view of time constrains, I decided to exclude the effects of the biotic factors (pest, disease and weeds) on intercropping and limit the study to systems where biotic factors are managed to the point that system performance can be seen as essentially limited by abiotic factors and their interactions.

Agronomic practices influence intercrops

The stress gradient hypothesis (SGH) states that plant-plant interactions depend on environmental context, with competitive interactions dominating in favorable environments but facilitative interactions dominating in unfavorable environments (Brooker et al., 2008; He et al., 2013). In the context of intercropping, the hypothesis would for instance predict dominance of competitive interactions at high N input, but potentially greater importance of beneficial interactions at low N input, e.g. due to complementary N use strategies in mixtures of legume and non-legume crop species (Patra et al., 1986; Jensen, 1996). Therefore, application of nitrogen fertilizer might influence the interspecific interactions in intercrops and as such LER.

Sowing density of component species in intercrops is another key factor determining intra- and interspecific interactions (Vandermeer, 1992). Increasing density of one species in an intercrop might increase its productivity, while decreasing productivity of the associated species (De Wit, 1960; Braakhekke, 1980; Gardiner and Craker, 1981; Fawusi et al., 1982). As a result, LER as well as the contribution of individual species to LER might be changed by sowing density of component species in intercrops.

The way of mixing species may also affect species interactions in intercrops. There are roughly three main intercropping patterns, i.e. strip intercrop, row intercrop and fully mixed intercrop (Vandermeer, 1992). Mixed intercrops allow maximum interspecific interactions while strip intercrops minimize interspecific interactions.

In this thesis, the effects of agronomic practices on productivity (Chapters 2 and 3) and on relative contribution of individual species to productivity of intercrops (Chapter 5) have been analyzed using meta-analysis.

Statistical approach

Two statistical approaches are adopted in the meta-analysis chapters, i.e. mixed effects modeling (Chapters 2 and 5) and quantile regression (Chapter 3). I use mixed effects models to study the expected responses of dependent variables (LER or PLER) to independent variables (temporal niche differentiation, crop type combination and agronomic practices) based on data collected from intercropping publications. Random effects are included to account for the possibility of correlation between data originating from the same experiment and/or publication (Pinheiro and Bates, 2000; Zuur et al., 2009). Random effects associated with experiments and publications account for location, year, and study effects that are not accounted for by the independent variables.

Apart from the variation in LER related to the independent variables mentioned above, there is still a large unexplained variation in LER. Published studies often do not report environmental factors related to intercrop performance, such as weather conditions, soil fertility or other aspects of soil quality. Due to lack of measurements or reporting on these factors, their effects cannot be quantified and they end up in the scatter of the response variable. Mixed effects models can only estimate mean responses of dependent variables to independent variables, while the mean responses are only representative for average conditions of factors not included in the regression model, and are not necessarily valid for the entire distribution of the dependent variable. As a result, the sole use of mixed effects models will only give an incomplete picture of the relationships between dependent- and independent variables.

In order to get a more complete picture of the relationships between LER and the independent variables, I use quantile regression (Chapter 3) as a supplement to the analysis using mixed effects models (Chapter 2). Quantile regression (Koenker and Bassett, 1978) is a method that allows estimating functional relationships between a dependent variable and one or more independent variables for all portions (defined by quantiles) of a probability distribution. Quantile regression provides a more complete picture of possible spread in causal relationships between variables (Cade and Noon, 2003). The distribution of the regression curves fitted for different quantiles shows whether relationships between LER and independent variables depend on factors not included in the regression models.

Functional structural plant modelling

The effect of species type combination (C3/C3 vs C3/C4) on LER is studied using meta-analysis in Chapters 2 and 3 with data from the intercropping literature. However, in most of the cases reported in literature, C3/C3 intercrops are combinations of two species with a similar plant stature, while C3/C4 intercrops are usually short/tall combinations in which the C3 species is shorter than the C4 species. A combination of short/tall species may result in a complementary capture of light while a combination of species of different photosynthetic pathways (C3/C4) is a kind of functional complementarity resulting in more efficient use of captured light than in C3/C3 intercrops. Both complementarity in space and in plant function may contribute to the difference of LER between C3/C3 intercrops and C3/C4 intercrops. Nevertheless it is not possible to disentangle which plant traits (plant stature or photosynthetic pathway) contribute to the difference in LER between C3/C3 and C3/C4 intercrops using meta-analysis due to the confounding between plant stature and photosynthetic pathway in the literature. I hence use functional structural plant (FSP) modelling to investigate how the two plant traits and variation therein affect intercropping productivity and interspecific interactions (Chapter 4). FSP modelling is used since (i) it is a powerful tool for investigating plant-environment and plant-plant interactions (Evers et al., 2010; Bongers et al., 2014), (ii) it may be applied to explore how plant traits affect complementary use of light in intercrops (Zhu et al., 2015).

The C3 and C4 photosynthetic pathways differs in many aspects. For simplicity however , I do not include all differences in the process of photosynthesis that distinguish C3 and C4 photosynthetic pathways. Instead, I focus on a single key factor distinguishing C3 and C4 photosynthesis, maximum CO_2 assimilation rate (A_{max}) which is the photosynthesis rate of leaves at light saturation. In this modelling study (Chapter 4), I investigate the effect on LER of plant stature, A_{max}, and the interactions between these two and with temporal niche differentiation.

Outline of the thesis

In this thesis, I aimed to investigate how temporal niche differentiation, crop type combination as well as agronomic practices affect interspecific interactions and associated productivity and LER in intercrops. The thesis consists of six chapters: this general introduction (Chapter 1), four research chapters (Chapters 2 to 5), and a general discussion (Chapter 6).

In **Chapter 2**, I focus on temporal niche differentiation and LER in annual intercrops. Using mixed effects modeling, I evaluate the response of LER to temporal niche differentiation, demonstrating a positive relationship between LER and temporal niche differentiation in C3/C4 intercrops but not in C3/C3 intercrops.

In **Chapter 3**, I also study the effect of temporal niche differentiation on LER, but I use quantile regression to estimate the relationship for different quantiles of the distribution of LER. I demonstrate that the relationship between temporal niche differentiation and LER is robust for all quantiles of LER, indicating the relationship of LER and TND is not affected by the factors not included in the analysis.

In **Chapter 4**, I investigate how biomass production in species mixture is affected by maximum plant height and A_{max} as well as their interactions with each other and with temporal niche differentiation. I show how spatial and temporal complementarity in mixed cultivation systems is strongly determined by maximum plant height and A_{max} of the component species.

In **Chapter 5**, I examine the effects of agronomic practices on interspecific interactions between component species in cereal/legume intercrops, using meta-analysis. This study shows how competitive relationships between cereals and legumes are determined by the interplay between agronomic practices including relative sowing time, relative sowing density, and nitrogen fertilizer.

In **Chapter 6**, I integrate results of the research chapters and discuss the implications of the results for understanding mechanisms of high land use efficiency of intercrops, and deriving principles for the design of intercropping systems. Besides, I discuss some important aspects of intercropping including comparison between land use efficiency and productivity, contribution of intercropping to global food security and mechanization of intercropping.

Chapter 2

Temporal niche differentiation increases the land equivalent ratio of annual intercrops: A meta-analysis

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Abstract

Sustainable intensification of agriculture is needed to meet higher future food demands while mitigating agriculture's ecological footprint. Intercropping is a strategy for increasing agricultural productivity per unit land that is based on ecological mechanisms for improved resource capture. No quantitative synthesis has been made on the effect of intercrop system properties and species trait combinations on intercrop productivity. Here we use meta-analysis of the intercropping literature to study how the productivity of mixed systems is affected by intercrop system design and species traits. We focus on the effects of temporal niche differentiation between species, intercropping pattern, relative densities, the use of C3 and C4 species and the rate of nitrogen fertilizer. Land equivalent ratio (LER) is used as index for assessing the relative productivity of a mixed system as compared to sole crops. Average LER was 1.22 ± 0.02, and no differences in LER were found between the 50 most highly cited studies and a random sample from the literature, indicating that high LERs in highly cited papers are representative of the entire literature. Temporal niche differentiation contributed substantially to high LER in systems combining a C3 and C4 species, but not in systems based on C3 species mixtures. The amount of N fertilizer interacted positively with the effect of temporal niche differentiation on LER. The intercropping literature is dominated by studies on cereal/legume mixtures. However, the few studies on C3 cereal/C4 cereal mixtures indicate these mixtures have high LER.

Substantial improvements in land use efficiency in agriculture may be obtained by using mixtures, particularly C3/C4 mixtures. Thus, enhanced within-field crop diversity can make an important contribution to sustainable increases in food production.

Keywords: intercropping; land equivalent ratio; meta-analysis; nutrients; temporal niche differentiation

Introduction

Intercropping is the cultivation of two or more crop species simultaneously in the same field for the whole or a part of their growing period (Willey, 1990; Hauggaard-Nielsen et al., 2008). Intercrops may use land and other resources more efficiently than sole crops (Vandermeer, 1992; Zhang and Li, 2003; Lithourgidis et al., 2011) and could achieve food security with reduced anthropogenic inputs and lower environmental impacts (Brooker et al., 2015). Intercropping is a practical application of the principle of productivity increase by biodiversity (Cardinale et al., 2007). An important question is what system and species traits make intercropping productive. While there is a vast intercropping literature reporting yield advantages and other benefits of intercropping, little quantitative synthesis has been made. There is therefore insufficient guidance on how intercropping systems for the future might be designed.

The ecosystem service of food production in intercrops is often evaluated and compared to sole crops using the land equivalent ratio (LER). LER is calculated as the sum of the relative yields of component species in an intercrop as compared to their respective sole crops. LER may be interpreted as the area of sole crops that would be required to obtain the same yield or biomass of the component crops as a unit area of intercrop (Mead and Willey, 1980). LER is therefore not strictly an index for productivity but rather for the efficiency of land use. LER is useful to assess the benefits of intercropping for achieving sustainable yield increase in agriculture to meet future food demands.

Studies show large variation of LER, because of the wide variety of species combinations, management practices and environmental conditions. LERs range from well below one, e.g. 0.77 for wheat/pea (Naudin et al., 2010) to well above one, e.g. 1.83 for sorghum/groundnut (Harris et al., 1987). To date, no overarching quantitative analysis has been made of the causes of the variation of LER across systems. The large variability in LER is therefore unexplained. Insight in the factors responsible for variability of LER is necessary to select intercropping options for the future.

Here we use meta-analysis (Koricheva et al., 2013) to synthesize information from the literature, and determine the key system and plant traits affecting LER. In meta-analysis, the phenomenon of publication bias is well known (Koricheva et al., 2013). Publication bias occurs if published studies tend to report larger or more significant effect sizes (e.g. the effect of a treatment) than unpublished studies. Publication bias results in a biased sample of effect sizes in the literature, and affects the value of meta-analysis. By analogy, here, we hypothesized that there could also exist a citation bias in the intercropping literature. A citation bias could arise if authors preferentially cite studies reporting strong effects of intercropping. To detect such a citation bias, we made a comparative analysis of two datasets: a dataset with records of the most highly cited studies and an equally large dataset with a random sample of studies from the remaining intercropping literature. We use sensitivity analysis and bootstrapping to ascertain that our sample sizes are sufficient to draw robust and representative conclusions.

In ecological studies, it has been shown that primary production in natural ecosystems increases with species richness, in part through improved resource capture (Tilman et al., 1996; Yachi and Loreau, 2007; Cardinale et al., 2012). Greater LER is expected with greater temporal niche differentiation because it may allow component species to realize a greater relative yield due to complementary use of resource in time (Li et al., 2013), and relaxed competition from the other species (Vandermeer, 1992; Li et al., 2001a; Zhang et al., 2008). Here we study the role of temporal niche differentiation as a result of differences in growing period between species.

The stress gradient hypothesis (SGH) states that plant-plant interactions depend on environmental context, with competitive interactions dominating in favorable environments but facilitative interactions dominating in unfavorable environments (Brooker et al., 2008; He et al., 2013). In the context of intercropping, the hypothesis would predict dominance of competitive interactions at high N input, but potentially greater importance of facilitative interactions at low N input, e.g. due to complementary N use strategies of component crop species, e.g. a legume and non-legume (Jensen, 1996). Temporal niche differentiation, which relaxes competitive interactions, may therefore be especially relevant in highly productive situations, but less so in stressed environments, e.g. due to low nitrogen availability. However, it is equally possible that temporal niche differentiation would be important when resources are scarce, i.e. at low N input, to enable to access complementary resources in time. We therefore investigate the effect of N fertilization on LER and ask the questions whether the effect of temporal niche differentiation on LER is affected by N fertilizer amount.

Plant growth context in intercrops such as relative density compared to sole crops, intercropping patterns would also influence intra- and interspecific interactions in intercropping communities, consequently affecting LER and the effect of temporal niche differentiation on LER. Hence we study the effects of relative density and intercropping pattern on LER and the corresponding interactions with temporal niche differentiation.

Mixing C3 and C4 species, associated with combinations of different plant traits (growing season, plant height, photosynthetic mechanisms) is a form of functional complementarity that might enhance resource capture and LER in intercrops (Cong et al., 2014, 2015). We therefore study the effect of mixing C3 and C4 species.

In this study, we address three main questions 1) Does LER increase with temporal niche differentiation? 2) How do different factors influence effect of temporal niche differentiation on LER? 3) Are the results of highly cited studies consistent with those of a random sample of the intercropping literature?

Materials and methods

Data collection and extraction from the literature

A literature search was conducted on the Web of Science Core Collection (WoSCC) on 21st May 2013. We used as search terms: *intercrop** OR "*mixed crop**" OR "*crop mixture**" OR "*mixed cultivation**" OR *polyculture* in the title. The search yielded 3313 publications. Two samples from these 3313 publications were analyzed further: a top cited sample and a random sample (Appendix: Table A1 and Table A2). The top cited sample was made by first ranking the 3313 publications according to the citations received between 2003 and 2012 and then screening them one by one until 50 publications had been accumulated that met the inclusion criteria (Methods A1 and Fig. A1). A second sample of 50 publications was made by simple random sampling from the entire database, excluding the 50 publications already included in the top-cited sample (Methods A1 and Fig. A1).

Based on the number of experiments and relevant treatments within experiments in a publication, multiple data records were extracted from each publication. We coded the publication and each experiment in order to account for nested random effects during the data analysis. An experiment was defined by a unique combination of site and year. Treatments were defined by crop species, sowing dates, fertilizer amount, crop density and intercropping pattern within an experiment Information of each treatment and that of the corresponding experiment and publication were extracted (Table 1). Treatments not satisfying the inclusion criteria on control of disease, pest and weed were excluded. Besides, treatments in which the density in the intercrop was lower than that of the sole crops (see below, relative density total RDT<1) were excluded (Methods A2).

Table 1 Variables extracted from publications.

Variable	Definition	Unit
Title	Title of publication	-
Authors	Authors of publication	-
Continent	Continent where experiments were carried out	-
Country	Country where experiments were carried out	-
Latitude and longitude	Latitude and longitude of experimental site	Degree
Species	Latin name and common name of crop species	-
Sowing and harvest date	Sowing and harvest date of intercropped species or information on total period and overlap period of intercrops to calculate TND	-
C3/C4	Whether one or both crop species are C3 or C4 species (C3/C3, C3/C4, or C4/C4)	-
Legume/non-legume	Whether one or both crop species are legume or non-legume species (non-legume/non-legume, legume/non-legume, legume/legume)	-
Intercropping pattern	In which way the two species were intercropped. Strip intercropping: two species cultivated in alternative strips and at least one strip includes more than one row; Row intercropping: two species cultivated in alternate rows; Fully mixed intercropping: two species cultivated in the same field without any distinct row or strip pattern.	-
Density of crops	Density of each species in sole crops and in intercrop	plants/ha
Rate of N fertilization	Amount of N fertilizer was applied to sole crops and to intercrops	kg/ha
Yield	Grain yield or total biomass in the case of fodder crops	ton/ha

The sample of 50 top cited publications yielded 87 experiments and 345 data records. The random sample yielded 102 experiments and 401 data records. Initial analyses were conducted to compare the responses of LER to explanatory variables between the top cited sample and the random sample with mixed effects models given in Table 2. As initial analyses showed the two datasets gave very similar results, subsequent analyses were carried out on the combined sample of 100 publications, 189 experiments, and 746 data records. These publications appeared from 1978 to 2012.

Response variable

In all analyses, land equivalent ratio (LER) was taken as the response variable. LER is defined as:

$$\mathrm{LER} = \frac{Y_1}{M_1} + \frac{Y_2}{M_2} \tag{1}$$

where Y_1 and Y_2 are the yields (per unit of total area of the intercrop) of species 1 and 2 in the intercrop, and M_1 and M_2 are the yields of the species in sole crops (per unit area of the respective sole crop).

Explanatory variables

In the analyses, we use six explanatory variables, i.e. 1) continents, 2) crop type combinations (categorical with 2 levels: C3/C3 or C3/C4), 3) rate of N fertilization in intercrops (continuous), 4) intercropping patterns (categorical; 3 levels: mixed, row, strip), 5) relative density total (continuous; see eq. 2 below) and 6) TND (continuous; eq. 3 below). Values of the first four variables were directly extracted from publications, while relative density, relative density total and temporal niche differentiation were calculated.

Rate of N fertilization in intercrops may be different from that in sole crops. A categorical variable N_code with six levels (Table A4) was defined according to the amount of N fertilizer applied in an intercrop and the respective sole crops.

Three intercropping patterns are common: fully mixed intercropping, row intercropping and strip intercropping (Vandermeer, 1992). Mixed intercropping is growing two or more crops simultaneously with no distinct row arrangement or two crops growing in the same row; row intercropping is growing two or more crops simultaneously where at least

Table 2 Specification of the models fitted to the data. The indices *i*, *j* and *k* represent publication ID, experiment ID and treatment ID respectively. In all mixed effects models (model 1-12), a_i is a random publication effect. b_{ij} is a random experiment effect nested within the i^{th} publication. a_i and b_{ij} are assumed normally distributed with constant variances. ε_{ijk} is a residual random error assumed normally distributed with constant variance. The variance terms a_i, b_{ij} and ε_{ijk} were all assumed independent. Citation bias was analyzed using a linear model (model 13), relating the number of citations of a study to its average LER. In model 13, ε_i is a residual random error assumed normally distributed with constant variance.

Model	Equations
1	$\text{LER}_{ijk} = \beta_0 + \beta_1{*}\text{TND}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
2	$\text{LER}_{ijk} = \beta_0 + a_i + b_{ij} + \varepsilon_{ijk}$
3	$\text{LER}_{ijk} = \beta_0 + \beta_1{*}\text{Continent}_i^2 + \beta_2{*}\ \text{Continent}_i^3 + \beta_3{*}\ \text{Continent}_i^4 + \beta_4{*}\ \text{Continent}_i^5 + \beta_5{*}\ \text{Continent}_i^6 + a_i + b_{ij} + \varepsilon_{ijk}$
4	$\text{LER}_{ijk} = \beta_0 + \beta_1{*}\text{C3/C4}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
5	$\text{LER}_{ijk} = \beta_0 + \beta_1{*}\ \text{ICpattern}_{ijk}^2 + \beta_2{*}\ \text{ICpattern}_{ijk}^3 + a_i + b_{ij} + \varepsilon_{ijk}$
6	$\text{LER}_{ijk} = \beta_0 + \beta_1{*}\text{N}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
7	$\text{LER}_{ijk} = \beta_0 + \beta_1{*}\text{RDT}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
8	$\text{LER}_{ijk} = \beta_0 + \beta_1{*}\text{TND}_{ijk} + \beta_2{*}\ \text{C3/C4}_{ijk} + \beta_3{*}\text{TND}_{ijk}{*}\ \text{C3/C4}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
9	$\text{LER}_{ijk} = \beta_0 + \beta_1{*}\text{TND}_{ijk} + \beta_2{*}\ \text{ICpattern}_{ijk}^2 + \beta_3{*}\text{ICpattern}_{ijk}^3 + a_i + b_{ij} + \varepsilon_{ijk}$
10	$\text{LER}_{ijk} = \beta_0 + \beta_1{*}\text{TND}_{ijk} + \beta_2{*}\ \text{N}_{ijk} + \beta_3{*}\text{TND}_{ijk}{*}\ \text{N}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
11	$\text{LER}_{ijk} = \beta_0 + \beta_1{*}\text{TND}_{ijk} + \beta_2{*}\ \text{RDT}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
12	$\text{LER}_{ijk} = \beta_0 + \beta_1{*}\text{TND}_{ijk} + \beta_2{*}\ \text{N}_{ijk} + \beta_3{*}\text{N\_code\_2}_{ijk} + \beta_4{*}\text{N\_code\_4}_{ijk} + \beta_5{*}\text{TND}_{ijk}{*}\ \text{N}_{ijk} + \beta_6{*}\text{TND}_{ijk}{*}\text{N\_code\_2}_{ijk} + \beta_7{*}\text{TND}_{ijk}{*}\text{N\_code\_4}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
13	$\text{Citations}_i = \beta_0 + \beta_1{*}\ \text{LER}_i + \varepsilon_i$

one of the crops is planted in single rows bordered by the other species; strip intercropping is growing two or more crops simultaneously in different strips. Interactions with the other species are strongest in the fully mixed intercropping, while interactions with "same" are by comparison most prevalent in strip intercropping.

Relative density total (RDT) is calculated as the sum of relative densities of intercropped species as compared to respective sole crops:

$$\mathrm{RDT} = \frac{d_{1,\mathrm{ic}}}{d_{1,\mathrm{sc}}} + \frac{d_{2,\mathrm{ic}}}{d_{2,\mathrm{sc}}} \tag{2}$$

where $d_{1,\mathrm{ic}}$, $d_{2,\mathrm{ic}}$ are densities of species 1 and 2, respectively, in the intercrop, and $d_{1,\mathrm{sc}}$ and $d_{2,\mathrm{sc}}$ are densities of species 1 and 2, respectively, in sole crops. An RDT equal to 1 indicates replacement intercropping and a value of 2 indicates fully additive intercropping (density of the intercrop is the sum of densities of sole crops). A RDT between 1 and 2 is a partially additive intercropping system, for which we will use the term "augmentative", as overall density is augmented as compared to sole crops, but less than the full sum of sole crop densities. Intercrops with RDT < 1 were excluded from the database.

An index for temporal niche differentiation (TND) was calculated using sowing and harvesting dates of each species in the intercrop:

$$\mathrm{TND} = \frac{P_{\mathrm{system}} - P_{\mathrm{overlap}}}{P_{\mathrm{system}}} = 1 - \frac{P_{\mathrm{overlap}}}{P_{\mathrm{system}}} \tag{3}$$

where P_{overlap} represents the period of overlap of the growth period of the intercropped species, while P_{system} represents the duration of the whole intercrop (Fig. 1). This indicator quantifies the proportion of the total growing period of the intercrop that the two component species are growing as sole crops (i.e. before sowing or after harvest of the other species). In theory, TND is zero when both species are sown and harvested at the same time and TND would be one in the case of double cropping (i.e. the second species is sown after the first is harvested). Double cropping (i.e. a rotation within one year) is not included in our analysis.

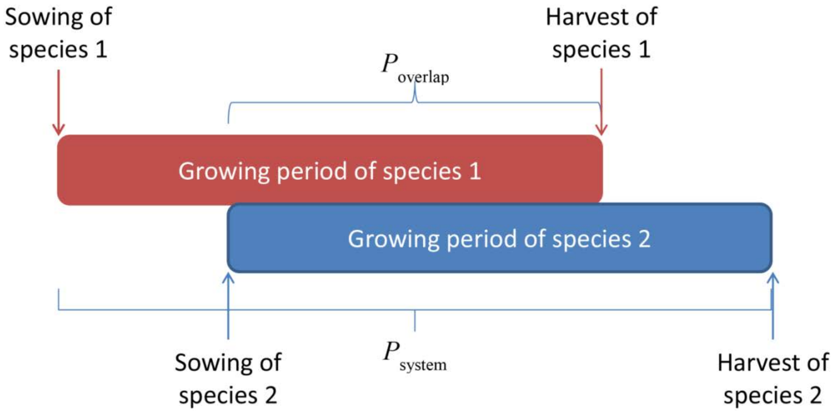

Fig. 1 Illustration of the quantitative characterization of temporal niche differentiation. The upper bar represents the growing period of the first sown species, and the lower bar represents the growing period of the second sown species. The index for temporal niche differentiation, TND, is defined as the proportion of the total system time (P_{system}) that component crops grow alone, i.e. don't overlap ($P_{\text{system}} - P_{\text{overlap}}$).

Statistical analysis

Relationships between LER and explanatory variables and the effect of interaction between TND and co-variables (i.e. C3/C4, intercropping pattern, rate of N fertilization and RDT) on LER were estimated via mixed effects modelling. Random effects were included to account for the possibility of correlation between data originating from the same experiment and/or publication (Pinheiro and Bates, 2000; Zuur et al., 2009). Random effects associated with experiments and publications account for effects of location, year, and study effects that are not accounted for by the explanatory variables (fixed effects). Eleven mixed effects models were fitted to the data of the two samples of publications (model 1-11 in Table 2). Data records with missing values of a variable were excluded from analyses which required that variable (Methods A3 and Table A3).

The interaction between TND and rate of N fertilizer might differ between intercrops that received the same amount of N as the sole crops and intercrops that received a different amount of N than the sole crops. An analysis was conducted to determine whether the interaction between TND and rate of N fertilizer is affected by the amount of fertilizer given to the sole crops. Practices on the comparative amounts of N given to mixed and sole crops were coded using a categorical variable "N_code" (Table A4 and Methods A4).

All analyses were conducted in R (R Core Team, 2013). Mixed effects models were fitted using the R function *lme* (R package *nlme*; (Pinheiro et al., 2013). Model selection was conducted using the R functions *AIC* and *anova* (R package *stats*; (R Core Team, 2013). The assumptions of normality and equal variance were checked by quantile plots and plotting model residuals against fitted values, respectively (Zuur et al., 2009). No violations of assumptions were found. Figures were made using R packages *plotrix* and *graphics* (Lemon, 2006; R Core Team, 2013). In meta-analysis, data are often weighed by their associated level of precision if standard errors are available. We did not do this because standard errors could not be estimated with sufficient confidence for many papers, due to lack of information.

Publication bias was evaluated using a funnel plot (Duval and Tweedie, 2000). A funnel plot is a scatterplot of effect sizes against some measure of their precision (e.g. sample size or standard error) (Richard, 1984; Koricheva et al., 2013). A symmetrical funnel shape indicates absence of publication bias (Peters et al., 2008). In this meta-analysis, a funnel plot of study size against LER of each publication was made to assess publication bias. For the funnel plot, we used average LER for each study, and we calculated a measure of accuracy, “study size”, by summing the number of experimental units (replicates) over experiments and treatments:

$$\text{StudySize}_i = \sum_{j,k} \text{N\_replicate}_{ijk}$$

where StudySize_i is the study size of publication *i*, N_replicate_{ijk} is the number of replicates of treatment *k* from experiment *j* in publication *i*.

Citation bias was studied in two ways. First, we analyzed the relationship between the number of citations of a publication and its average LER using an ordinary linear regression (model 13 in Table 2). Secondly, we compared the cumulative probability distribution of LER values from the top-cited sample with those from the random sample using the Kolmogorov-Smirnov test (Pearson and Hartley, 1954; Lilliefors, 1967).

The sufficiency of a sample size of 100 was evaluated by bootstrapping from the combined sample of 100 publications and the associated 746 data records and constructing 95% confidence intervals for the estimated parameters as a function of sample size (Methods A5).

Results

Comparison of the two samples from the literature

The frequency distributions of LER of the top cited and random samples of publications from the literature were similar (Fig. 2a&2b), and the estimated cumulative probability distributions were not significantly different according the Kolmogorov-Smirnov test ($D = 0.0675$, $P = 0.37$; Fig 2d). There were no differences between the top cited sample and the random sample in terms of relationships between LER and explanatory variables. The relationship between LER and TND, estimated with mixed effects model 1 (Table 2), is provided as a case in point (Fig. 3). Because of the similar patterns in the two samples, they were combined and only the results obtained with the combined sample of 100 publications are presented further.

Publication and citation bias, and sufficiency of sample sizes

There was a slight publication bias in our database since the funnel plot was somewhat asymmetrical, with missing values in the bottom left corner representing studies with low study size and low LER (Fig. 4a). No citation bias was observed in the meta-analysis. Firstly, distribution of LER was not different between the top-cited sample and the random sample (Fig. 2). Secondly, no relationship was found between the number of citations of a study and the average LER of the study (Fig. 4b). Results of the bootstrapping analysis (Fig. A2) showed that with increasing number of studies, the mean of the estimated β_1 changed only little, while the confidence interval became somewhat smaller. The confidence interval did not decrease much when sample size was increased beyond 100. This evidence supports the conclusion that the sample size is sufficient.

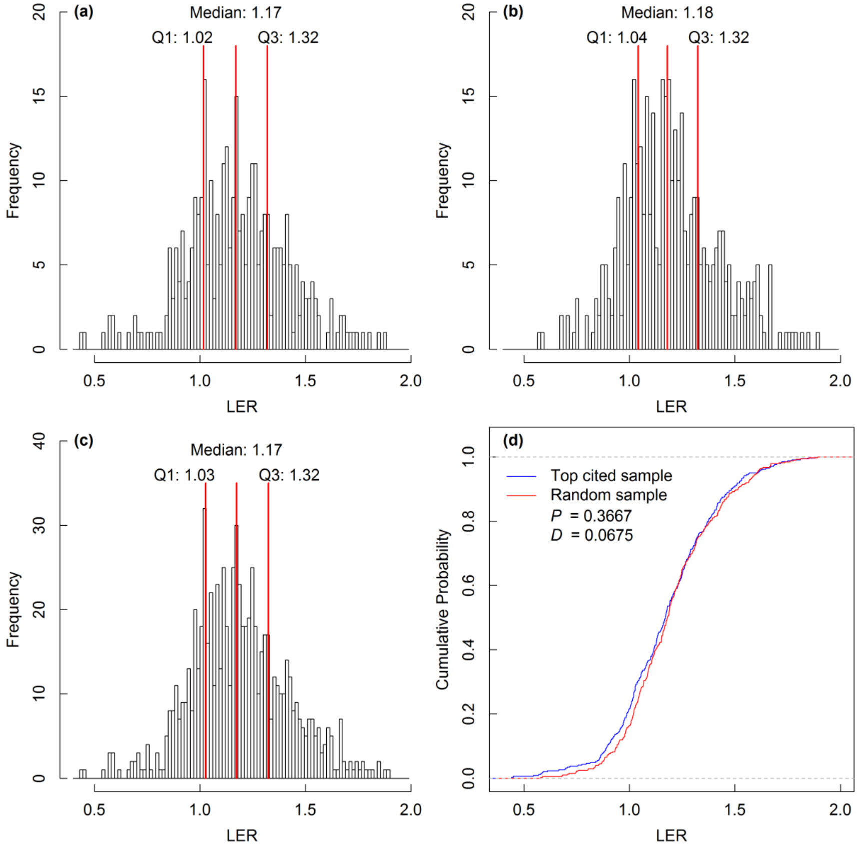

Fig. 2 Frequency distribution of LER for the top cited sample (a), the random sample (b) and the combined sample (c), and cumulative probability of LER for the top cited sample and the random sample (d). Vertical lines in panels of frequency distribution (a-c) indicate the first quartile (Q1), median and the third (Q3) quartile of LER. In panel d, *D* denotes the test statistic belonging to the Kolmogorov-Smirnov test. It represents the greatest difference of cumulative probability between the two samples. The *P* value indicates the probability of obtaining a value of *D* equal to or greater than the value found under the null hypothesis of no difference between the samples. The null hypothesis was not rejected.

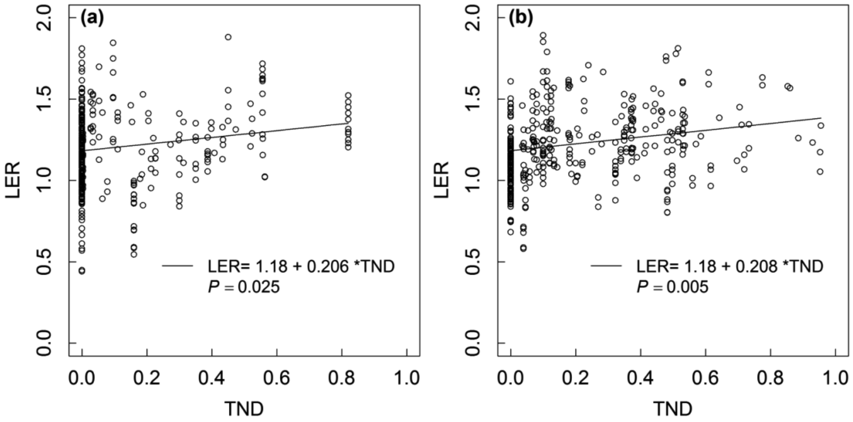

Fig. 3 Relationship between LER and TND estimated with a mixed effects model (model 1 in Table 2, i.e. $\mathrm{LER}_{ijk} = \beta_0 + \beta_1 * \mathrm{TND}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$) for the top cited sample (a) and the random sample (b). P-values relate to the slopes of the regressions.

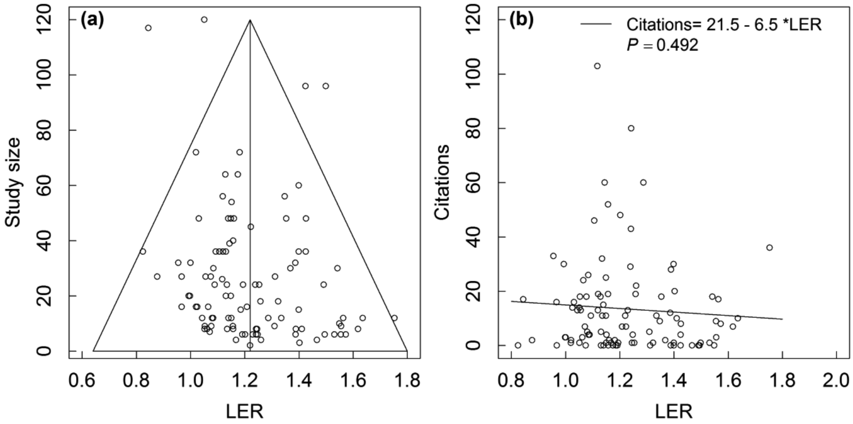

Fig. 4 Funnel plot of study size against LER (a) and plot of number of citations against LER (b). In panel a, the vertical line represents the estimated mean of LER via mixed effects model 2: $\mathrm{LER}_{ijk} = \beta_0 + a_i + b_{ij} + \varepsilon_{ijk}$. In panel b, the relationship between citations and LER is indicated by the dotted line, estimated by mixed effects model 13: $\mathrm{Citations}_i = \beta_0 + \beta_1 * \mathrm{LER}_i + \varepsilon_i$. No significant relationship was found ($\beta_1 = -6.5$; $P = 0.492$).

Descriptive analysis

The combined sample showed an uneven geographic distribution with 42 publications from Asia, 24 from Europe, 12 from Africa, 12 from North America, eight from Australia and two from Latin America (Fig. A3). The geographic distribution of publications was slightly different between the top cited sample and random sample. Publications in the top cited sample were mostly from Asia and Europe (15 and 18, respectively, out of 50) and five from Africa, six from North America and six from Australia. More than half of the publications in the random sample were from Asia (27 out of 50), while six were from Europe, seven from Africa, six from the North America, two from Australia and two from Latin America.

There was confounding between continents, species combination and intercropping pattern. For instance, intercrops in Asia were mostly strip-based, whereas intercrop systems in Europe were mostly mixed (Fig. 5a). This reflects a difference in purpose: most systems in Asia consist of two grain crops which are harvested separately for human or animal consumption, whereas in Europe, many of the tested systems are cereal/legume mixtures which are harvested as a mixture for animal feed. The frequency of strip, row and mixed systems in the other continents was intermediate between Asia and Europe. Overall, the dataset has 301 records on strip-based systems, 191 records on row-based systems and 205 records on mixed systems.

Usage of C4 species in intercrop systems also differed between continents. It was highly prevalent in Africa, the Americas and Oceania, less common in Asia, and rare in Europe (Fig. 5b). Overall, the combined dataset has 406 records on C3/C3 intercrops, 338 records on C3/C4 intercrops, and only two records on a C4/C4 intercrop. Intercrops of non-legume and legume species prevailed in the literature, as 625 out of 746 data records in the combined sample were non-legume/legume intercrops (Table A5). Out of the 406 C3/C3 records, 312 were a combination of a legume with a non-legume, 63 consisted of non-legumes only, and 31 records were mixtures of two legumes. Out of 338 records on C3/C4 mixtures, 313 had a legume as the C3 species, and 25 had a non-legume as the C3 species. The vast majority of C3/C3 intercrops with a single legume were cereal/legume combinations (239 out of 312). All C3/C4 intercrops with a legume were cereal/legume combinations (313 out of 313). A bias towards cereal-legume systems is true for all of the continents, except Asia, which has originated studies on a broad range of crop combinations, with cereals mixed with legumes, other cereals, or further crop species, as well as intercrops of legumes with non-cereals, e.g. vegetables or sesame (*Sesamum indicum* L.) (Fig. 5c). Regarding the use of replacement versus augmentative or fully additive designs, there is little difference between continents, with overall 301 records on replacement designs, 191 records on augmentative designs, and 295 records on fully additive designs (Fig. 5d).

The median LER in the whole data set was 1.17, the mean 1.22 ± 0.02 (Fig. 2c). Six hundred and five LER values (81%) were greater than one, indicating that a large majority of intercropping systems give higher land use efficiency than sole crops, but a substantial number of tested systems (19%) did not provide an advantage over sole crops.

As shown in Fig. 6a, LER was significantly higher in Asia than in Europe (model 3, β_1=-0.18, P<0.001), Africa (model 3, β_2=-0.12, P=0.03) or Latin America (model 3, β_3=-0.13, P=0.03). No significant difference of LER between any two other continents was observed.

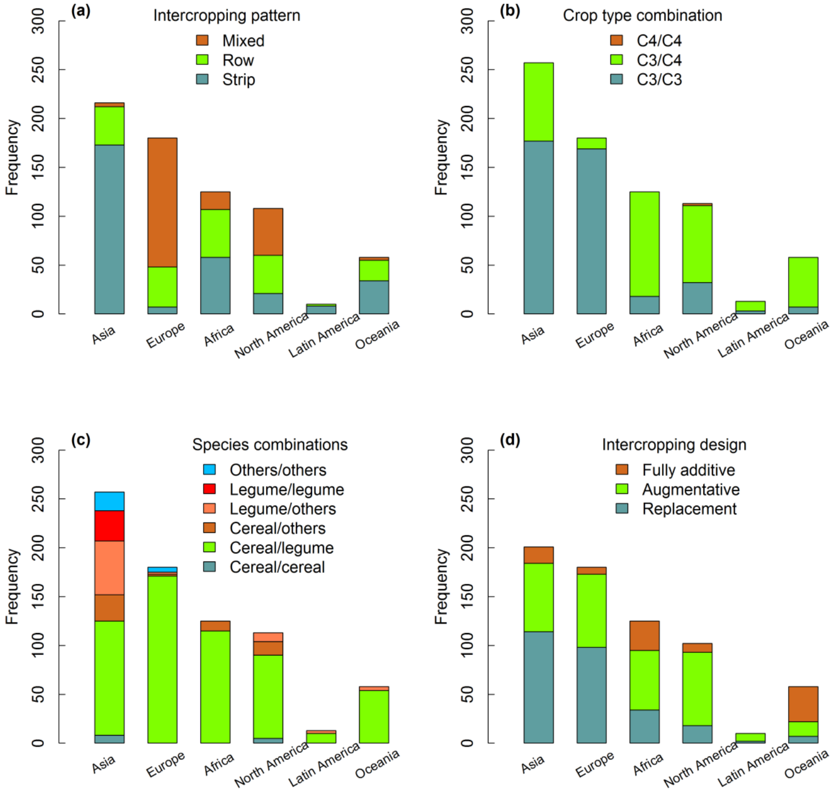

Fig. 5 Number of data records in the database related to traits of intercrop systems in different continents: intercropping patterns (a), usage of C3/C3, C3/C4 or C4/C4 combinations (b), species combinations in terms of cereals, legumes and other main groups (c) and intercropping designs (d).

LER of C3/C4 intercrops was significantly higher than of C3/C3 intercrops (model 4, β_1=0.12, P<0.001, Fig. 6b). LER of mixed intercrops was lower than of row and strip intercrops while the difference was only significant between mixed and strip intercrops (model 5, β_2=-0.10, *P*=0.001, Fig. 6c).

No response of LER to rate of N fertilization was found (model 6, β_1=0.000315, *P*=0.104, Fig. 7a). There was, however, a significantly positive relationship between LER and RDT, indicating that, overall, LER increases if densities are increased beyond replacement (model 7, β_1=0.162, *P*<0.001, Fig. 7b).

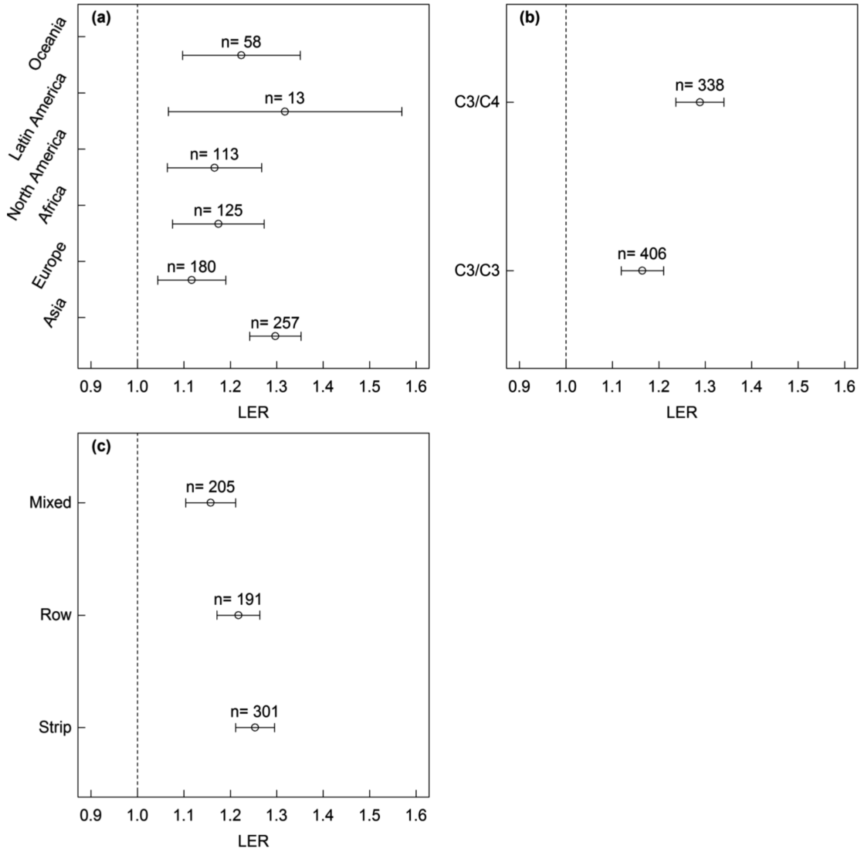

Fig. 6 Estimated means of LER across continents (a), crop type combinations (b) and intercropping patterns (c). The vertical dotted lines indicate LER equal to 1; the horizontal bars represent 95% confidence interval of estimations.

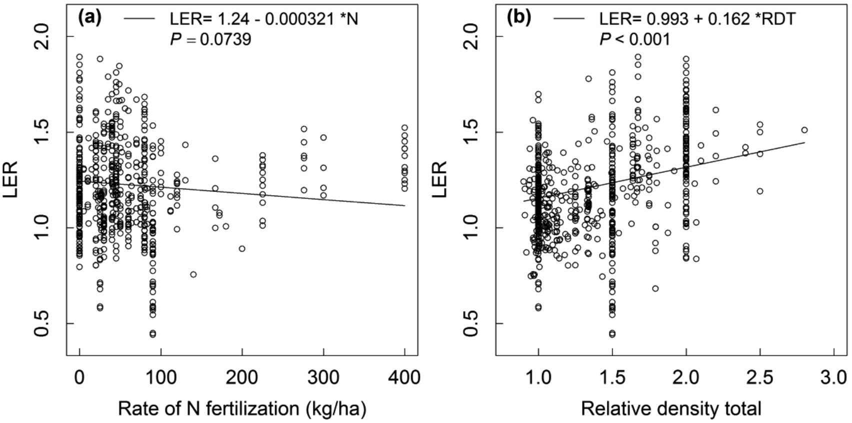

Fig. 7 Scatter plots of LER against rate of N fertilization (a) and relative density total (b). Relationships between LER and rate of N fertilization and relative density total were estimated by two mixed effects models; model 6: $LER_{ijk} = \beta_0 + \beta_1 * N_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$ and model 7: $LER_{ijk} = \beta_0 + \beta_1 * RDT_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$, respectively. Regression lines, estimated relationships and *P* values of β_1 are presented in each panel.

Effect of TND on LER

Overall effect of TND on LER

We had hypothesized a positive relationship between LER and temporal niche differentiation due to reduced competition between intercropped species with increased temporal niche differentiation. Our results indeed showed a positive relationship between LER and temporal niche differentiation. LER increased by 0.211 units per unit TND (model 1, β_1=0.211, $P <$ 0.001, Fig. 8a).

Interaction between effects of TND and other variables on LER

TND had a significant and positive effect on LER in intercrops mixing C3 and C4 species; LER increased with 0.274 units per unit increase in TND (model 8, $\beta_1 + \beta_3$=0.274, P= 0 .0019, Fig. 8b). On the contrary, for C3/C3 intercrops, TND had no significant effect on LER (model 8, β_1=0.095, P = 0.214, Fig. 8b).

The effect of TND was consistent across intercropping pattern (no significant interaction). A model with a common slope for different patterns (model 9, β_1=0.21, P<0.001), showed that LER was significantly lower in mixed intercrops than in strip intercrops (model 9, β_3=-0.08, P = 0.0092, Fig. 8c).

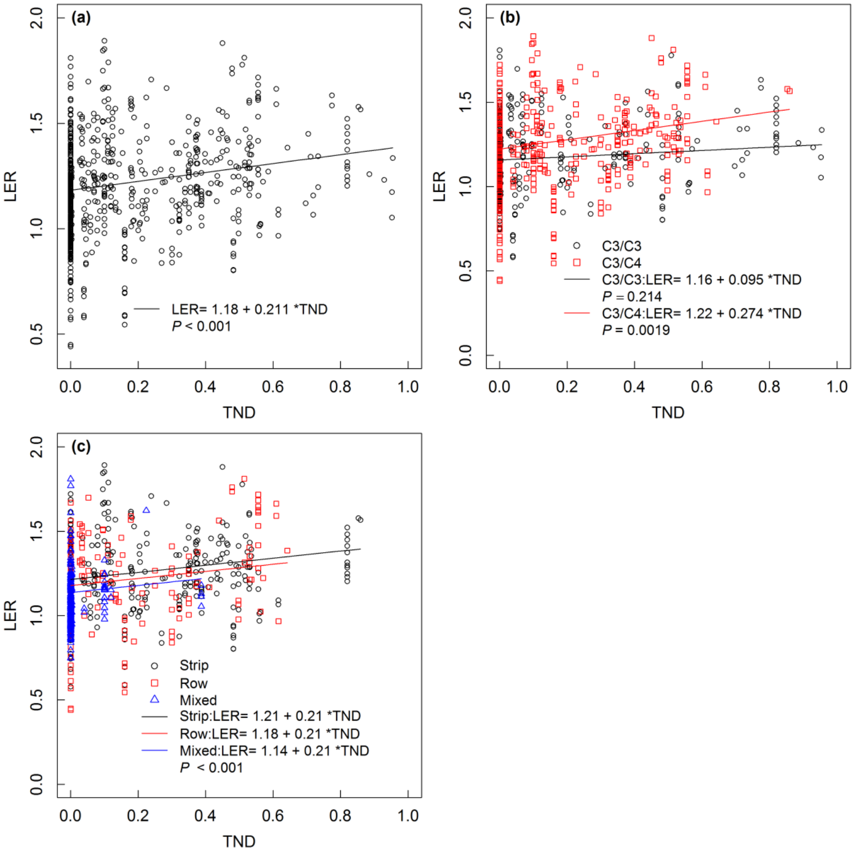

Fig. 8 Scatter plots and estimated regression lines relating LER to TND and two categorical co-variables, fitted by mixed effects models. Relationship between LER and TND was estimated by model 1: $LER_{ijk} = \beta_0 + \beta_1 * TND_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$ (a); relationship between LER and TND separately for C3/C4 and C3/C3 combinations was estimated by model 8: $LER_{ijk} = \beta_0 + \beta_1 * TND_{ijk} + \beta_2 * C3/C4_{ijk} + \beta_3 * TND_{ijk} * C3/C4_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$ (b); relationship between LER and TND separately for three intercropping patterns was estimated by model 9: $LER_{ijk} = \beta_0 + \beta_1 * TND_{ijk} + \beta_2 * ICpattern_{ijk}{}^2 + \beta_3 * ICpattern_{ijk}{}^3 + a_i + b_{ij} + \varepsilon_{ijk}$ (c). Regression lines, estimated relationships and *P* values of slopes are presented in each panel.

The interaction between the effects of TND and rate of N fertilization on LER did not depend on the relative amounts of fertilizer in the sole crops as compared to the intercrop (Fig. A4). There was a significant positive interaction between TND and the amount of N applied to the intercrop, indicating that niche complementarity between a short and a long season crop with relatively short period of overlap is more fully expressed when high levels of nutrients are provided. With a baseline effect of TND on LER of 0.227 unit increase of LER with one unit of TND, every application of 100 kg N/ha increased this effect of temporal niche differentiation on LER (i.e., the slope of the response of LER to TND) by 0.153 unit (model 10, β_3=0.153, P = 0.013, Fig. 9a). This interaction was mainly due to a decrease in the intercept value of LER at a TND of zero of 0.09 unit with every application of 100 kg N/ha (model 10, β_2=0.09, $P < 0.001$, Fig. 9a). In other words: to obtain the same LER at a higher rate of N fertilizer requires a greater TND. This result is in line with the stress gradient hypothesis.

No interaction between RDT and TND was found, but the effect of RDT on LER was significant, irrespective of TND; an increase of one unit of RDT increased LER by 0.16 unit (model 11, β_2=0.16, $P < 0.001$, Fig. 9b).

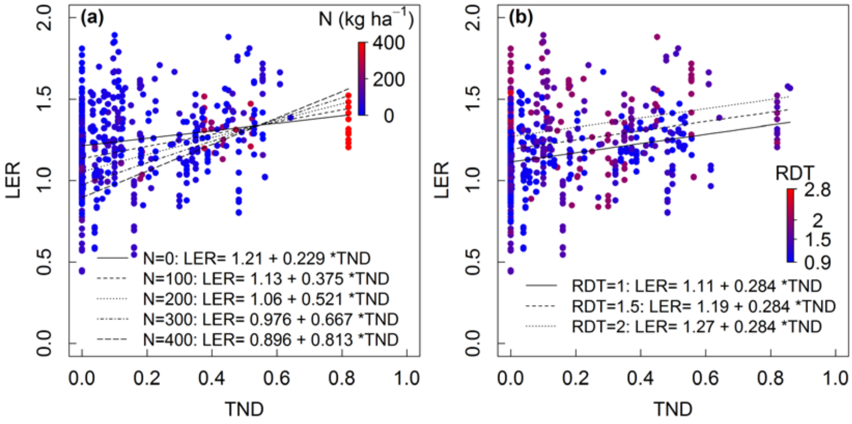

Fig. 9 Scatter plots and linear functions relating LER to TND and two continuous co-variables fitted by mixed effects models. Relationship between LER and TND and rate of N fertilization was estimated by model 10: $LER_{ijk} = \beta_0 + \beta_1{*}TND_{ijk} + \beta_2{*}\,N_{ijk} + \beta_3{*}TND_{ijk}{*}\,N_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$ (a); The relationship between LER and TND and relative density total was estimated by model 11: $LER_{ijk} = \beta_0 + \beta_1{*}TND_{ijk} + \beta_2{*}\,RDT_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$ (b). The intercepts of equations in panel a show the negative effect of N fertilizer on LER when TND is zero ($\beta_2{*}\,N_{ijk}$); slopes of equations show the combination of the main effect of TND ($\beta_1{*}TND_{ijk}$) and the interaction effect of TND with N fertilizer ($\beta_3{*}TND_{ijk}{*}\,N_{ijk}$). The regression lines in panel a cross at TND = 0.54, where the effect of N and the interaction of N and TND cancel out ($\beta_2{*}\,N_{ijk} + \beta_3{*}TND_{ijk}{*}\,N_{ijk}=0$, i.e. at TND = $-\beta_2/\beta_3$). The intercepts of equations in panel b show the positive effect of relative density total on LER ($\beta_2{*}\,RDT_{ijk}$).

Discussion

This is the first study showing that temporal niche differentiation is an important factor determining the land equivalent ratio in intercropping. This response of LER to TND only held when C3 and C4 species were combined. No significant response was found for C3/C3 combinations. Application of N fertilizer decreased LER when two intercropped species were sown and harvested simultaneously. Enhancing temporal niche differentiation alleviated the negative effect of N fertilization on LER. Furthermore, we found that LER increased with the relative density total, but there was no interaction between TND and relative density total. No interaction between TND and intercropping pattern was found.

Responses of intercrops to temporal niche differentiation

Intercrops of an early- and late-maturing species are adopted widely to exploit the length of the growing season (Lithourgidis et al., 2011) and increase light interception over time (Keating and Carberry, 1993; Zhang et al., 2008). Such relay intercropping (i.e. intercropping species with only partial overlap in growing periods) results in higher land use efficiency than can be achieved with sole crops, as these leave the soil uncovered during part of the growing. An alternative to relay intercropping would be sowing a second crop after harvest of the first. The theoretical maximum LER at a temporal niche differentiation approaching 1 would be 1.39 according to our analysis; therefore, if the temperature sum in a region is sufficient, double cropping would be a better alternative than relay intercropping. This is understandable as relay intercropping usually leaves part of the land bare during part of the growing season (e.g. Zhang et al., 2008). However, in many climates, growing a second crop for food is not possible due to limitations in length of the growing season.

Mechanistic reasons why C3/C4 intercrops respond more strongly to temporal niche differentiation than C3/C3 mixtures

Our statistical analysis shows that LER of C3/C4 intercrops increases with temporal niche differentiation, whereas the LER of C3/C3 does not respond significantly to TND. One explanatory factor might be the functional complementarity in terms of stature of the plants. In our dataset, C4 species are invariably tall cereals (including maize (*Zea mays* L.), millet (*Pennisetum glaucum* (L.) R.Br.), and sorghum (*Sorghum bicolor* (L.) Moench) while most C3 species are short by comparison, e.g. wheat (*Triticum aestivum* L.), soybean (*Glycine max* L.) and cowpea (*Vigna unguiculata* (L.) Walp). Therefore, C3/C3 intercropping is usually a short/short combination and C3/C4 intercropping is usually a short/tall combination, which could allow for better complementary light capture in a C3/C4 stand (Ghanbari et al., 2010). Functional structural plant modelling is a suitable method to explore the relative role in plant stature in shaping complementary light capture (Zhu et al., 2015). However, there is also a difference in photosynthesis mechanism and adaptation to higher temperatures as C4 species are better adapted to warm summer conditions whereas C3 species are better adapted to cool conditions in early spring (Ehleringer et al., 1997). Thus, the performance of C3/C4 mixtures may be explained by any combination of the factors stature, photosynthesis mechanism and temperature response. Our finding only partly confirms the hypothesis of complementary usage of growth resources in time since only C3/C4 intercrops responded significantly to temporal niche differentiation. Complementarity in other functional traits (plant stature and/or photosynthetic mechanism) between intercropped species might be involved in high land use efficiency in relay intercrop with high temporal niche differentiation.

Effect of intercropping patterns on LER

In the current study, we found that strip intercrops yielded higher LER than mixed intercrops. This is in part confounded with intercropping design: most strip intercrops in our dataset (179 out of 271) used an additive design, whereas only half of the mixed intercrops (92 out of 205) had an additive design. Intercrops with an additive design have a higher relative density total than intercrops with a replacement design and as a result a higher LER (Fig.7b). Hence, on average, LER of strip intercrops is expected to be higher than that of mixed intercrops.

Dominance of legumes in intercropping studies

The current dataset, based on combining a set of 50 most highly cited publications and a random sample of 50 publications was dominated by non-legume/legume intercrops (625 data records of non-legume/legume out of 726), both for C3/C3 and C3/C4 combinations. An extension of the database would be required to build a dataset allowing exploration of differences between legumes and non-legumes in the effects reported here for C3/C3 and C3/C4 intercrops. Based on the current database, the results largely represent systems with C3 legumes rather than C3 non-legumes.

Interactive effects of N fertilizer and temporal niche differentiation

Since our database mainly contains cereal/legume combinations due to their prevalence in the literature, our finding on response of LER to N fertilizer largely reflects the behavior of cereal/legume intercrops. It has been observed in both natural ecosystems (He et al., 2013) and intercropping systems (Li et al., 2013) that facilitative interactions between plants become less important as growth conditions improve, while competitive interactions become more important. Cereal/legume combinations are advantageous in low input agricultural systems, but LER could decrease with increasing application rate of N (Searle et al., 1981; Ofori and

Stern, 1986; Ofori and Stern, 1987b; Tobita et al., 1994). Our analysis shows a negative effect of N fertilization on LER when cereals and legumes are grown simultaneously (TND=0). At TND=0, an application of 100 kg N/ha decreases LER by 0.09 units. The negative effect of application of N on LER when TND equals zero could be due to the enhanced interspecific competition by application of N, and/or the loss of the advantage of nitrogen fixation from air by the legume. However, the negative effect of N fertilization on LER decreases as temporal niche differentiation between intercropped species increases. This finding is in agreement with the stress gradient hypothesis. When conditions are good (high N), competition is strong, and high LER is achieved by allowing temporal niche differentiation to mitigate strong competition. On the other hand, when nutrients are limiting (0 or low N), the effect of temporal niche differentiation on LER was not as strong as at high nutrient levels.

Learning from nature for future intercrop design

Results of this meta-analysis inform the design of intercropping systems that are adapted to future needs, with high productivity and high efficiency (Shen et al., 2013). Temporal niche differentiation is relevant in places where the growing season is too short for double cropping due to limitations of temperature but long enough for more than one crop, and with sufficient water. A C3/C4 intercrop with a large separation of growing period could then have high land use efficiency.

Other ecosystem services from intercropping

Intercropping can provide ecosystem services beyond food production including the suppression of pests and diseases (Andow, 1991; Trenbath, 1993), the suppression of weeds (Ayeni et al., 1984; Liebman and Dyck, 1993; Banik et al., 2006), and an increase in the retention of organic soil carbon and nitrogen (Cong et al., 2015). Intercropping as an agricultural strategy could therefore contribute to sustainable intensification of agriculture (Tilman et al., 2011; Bedoussac et al., 2015; Jensen et al., 2015).

Future research needs

We found that most intercropping research focusses on cereal/legume combinations; nevertheless, cereal/cereal intercropping systems tended to have higher land equivalent ratios than cereal/legume systems although not significantly (results not shown) probably due to lack of data on cereal/cereal combinations in our database (13 vs 552 data records for cereal/cereal and cereal/legume, respectively,). Only a couple of cereal/cereal intercropping systems have been studied in China and proved advantageous (Li et al., 2001a; Li et al., 2001b; Yang et al., 2011; Gao et al., 2014). Additional studies on cereal/cereal intercrops are needed to determine whether it can succeed in other places besides China. Such studies are of great importance because cereal production is one of the cornerstones of food security. If cereal/cereal intercrops prove more efficient in land use than sole crops in more ecological conditions around the world, it could greatly contribute to future food security, and provide important options for sustainable yield increase.

Appendix A

Methods A1 Inclusion criteria and procedure of paper selection and data extraction

Methods A2 Inclusion criteria for treatments of the 100 publications

Methods A3 Missing variables of data records in the random sample

Methods A4 Analysis of the interaction between TND and amount of N fertilization for three common strategies for supplying N in intercropping experiments

Methods A5 Bootstrapping strategy for testing sufficiency of a sample size of 100 publications

Methods A6 Reference list of the 100 publications used in this meta-analysis

Fig. A1 Paper selection procedure for the top cited publications and the random sample

Fig. A2 Bootstrap estimates and confidence intervals for β_1, estimated via mixed effects modelling

Fig. A3 World map with experimental sites

Fig. A4 Scatter plots and linear models relating LER to TND and N for three common strategies for supplying N in intercropping experiments

Table A1 List of the 50 publications in the top cited sample

Table A2 List of the 50 publications in the random sample

Table A3 Availability of information on selected variables in data sets of the random sample.

Table A4 Coding system for the strategy for N supply in intercropping experiments

Table A5 Contingency table for frequency of intercrops without a legume, or with one or two legumes in the case of C3/C3, C3/C4 and C4/C4 species combinations in the intercrop

Acknowledgements

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Chapter 3

Robust increases of land equivalent ratio with temporal niche differentiation: A meta-analysis with quantile regression

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Abstract

Intercropping has been proven more productive than sole crops in many studies, but large variation in land equivalent ratio (LER) among studies has been observed. Here we used quantile regression to estimate, for different parts of the LER distribution, the effect of temporal niche differentiation (TND) and its interaction with other key characteristics of intercropping systems, using data extracted from the intercropping literature. Quantile regression not only estimates the median response, but also other quantiles of the distribution of response. This method therefore gives a holistic view of the response.

LER increased with temporal niche differentiation and the effect of TND was significant for all tested quantiles. Response of LER to TND was significantly stronger for C3/C4 intercrops than for C3/C3 intercrops, but only at lower LER (quantiles below 20%). At higher quantiles of LER, no significant difference was found between C3/C3 and C3/C4 mixtures. There was a negative effect of N fertilizer on LER in the absence of temporal niche differentiation for all tested quantiles. At lower LER (corresponding to quantiles < 30%), this negative effect was alleviated by increasing temporal niche differentiation. There was a significant interaction between intercropping pattern (strip or row) and TND at higher LER only (quantile ≥ 65%). The analysis of interaction between intercropping pattern and TND did not include data of fully mixed intercrops, since most fully mixed intercrops had TND equal to zero (165 out of 205). The interaction between TND and relative density total was only significant at low to median LER (25% ≤ quantile ≤ 55%).

The results indicate that temporal niche differentiation has a robust positive effect on LER over a wide range of LER values, but the strength of this effect was influenced by intercrop characteristics, especially at low to median LER values.

Keywords: intercropping, land equivalent ratio, temporal niche differentiation, meta-analysis, quantile regression

Introduction

Intercropping is the cultivation of two or more crop species simultaneously in the same field (Ofori and Stern, 1987a; Vandermeer, 1992; Lithourgidis et al., 2011). It is an ancient agronomic practice which is still adopted by smallholder farmers in developing countries. Many advantages of intercrops have been reported, such as yield advantage (e.g. Ofori and Stern, 1986; Mei et al., 2012), suppression of pests and diseases (Trenbath, 1993), suppression of weeds (Ayeni et al., 1984) and retention of soil organic carbon and nitrogen (Cong et al., 2015). Intercropping has the potential for ecological and sustainable intensification of agriculture since intercropping is able to produce more food on limited arable land while exerting less impact on the environment than sole crops due to better exploitation of ecological mechanisms (Bedoussac et al., 2015; Jensen et al., 2015).

Yield advantage of intercrops is normally assessed by the land equivalent ratio (LER), defined as the sum of relative yields of the component crops. LER is interpreted as the relative land area required by sole crops to produce the same yields as achieved by a unit area of intercrop (Mead and Willey, 1980). Large variation of LER among studies has been observed (Yu et al., 2015). Many factors could contribute to the variation of LER, including crop species combination, fertilization, planting densities, etc. Yu et al. (2015) synthesized information from the literature and concluded that LER increases with temporal niche differentiation in intercrops that combine a C3 and a C4 species. LER was also found to increase with relative density total of intercrops. In general, there is no effect of N fertilization on LER (Pelzer et al., 2014) while a negative N effect is observed when intercropped species are sown and harvested simultaneously (Yu et al., 2015).

Apart from the variation of LER that can be related to the factors studied by Pelzer et al. (2014) and Yu et al. (2015), there is still large unexplained variation in LER. Environmental factors related to intercrop performance may not be reported, e.g. weather conditions, soil fertility or soil quality. As these factors are unmeasured, their effects on LER cannot be quantified and they end up in the scatter of the response variable. So far, the unexplained LER variability resulting from these unmeasured factors was not taken into account in published statistical analyses of LER data. Besides, statistical methods such as linear regression and mixed effects models were commonly used to estimate mean responses of LER to one or several explanatory variables (e.g. Yu et al., 2015). The mean responses fitted by these standard methods are only representative for average conditions of factors not included in the regression model, and are not necessarily valid for the entire distribution of the response variable. Responses of LER to explanatory variables might be modified by those factors not included in the regression models. It is well known in ecology that the relationship between a response variable and an explanatory variable could be stronger in the upper part of the response variable distribution and weaker in the lower part in case of interactions between the explanatory variable and one or several unmeasured factors (Cade, 1999; Cade and Noon, 2003). By focusing on the mean response, classic regression methods may give an incomplete picture of the relationships between LER and explanatory variables.

Quantile regression (Koenker and Bassett, 1978) is a method that allows estimating functional relationships between a response variable and one or more explanatory variables for all portions (defined by quantiles) of a probability distribution and provides a more complete picture of possible spread in causal relationships between variables (Cade and Noon, 2003). The distribution of the regression curves fitted for different quantiles indicates whether the relationship between the response variable and the explanatory variable depends on factors not included in the regression model. At a given value of an explanatory variable in a given regression model, the variability of the response variable across quantiles is due to these missing factors. Quantile regression has already been applied in ecology and agriculture to investigate relationships between variables for different conditional quantiles (Cade et al., 1999; Cade and Noon, 2003; Makowski et al., 2007; Casagrande et al., 2010; Hossard et al., 2014).

The objective of this paper is to further extend the meta-analysis of Yu et al. (2015) by studying the robustness of the relationship between LER and temporal niche differentiation and assess how the effect of temporal niche differentiation on LER is changed by crop type combination, rate of N fertilization, intercropping pattern and relative density total for different quantiles of the distribution of LER.

Materials and methods

Data collection and extraction from the literature

We use the dataset of 100 intercropping publications described in detail by Yu et al. (2015). Literature was searched from the Web of Science Core Collection (WoSCC) on 21 May 2013 with the intercropping related terms: *intercrop** OR "*mixed crop**" OR "*crop mixture**" OR "*mixed cultivation**" OR *polyculture* in the title. The 100 publications (Appendix Table B1 and A2) yielded 189 experiments and 746 data records. An experiment was defined by a unique combination of site and year. A data record consisted of identifiers for the publication and the experiment, and values specifying all relevant inputs, outputs and co-variables (Table B1). Not all data records did include all information on co-variables so there were some missing values for rate of N fertilization, intercropping patterns and relative density total (Table B2).

Response and explanatory variables

Land equivalent ratio (LER) was used as response variable. LER is defined as:

$$\mathrm{LER} = \frac{Y_1}{M_1} + \frac{Y_2}{M_2} \tag{1}$$

where Y_1 and Y_2 are the yields (per unit of total area of the intercrop) of species 1 and 2 in the intercrop, and M_1 and M_2 are the yields of the species in sole crops (per unit area of the respective sole crop).

We used five explanatory variables in the current study, i.c. crop type combination (categorical variable, two levels: C3/C3 or C3/C4), intercropping pattern (categorical variable, three levels: strip, row or mixed intercrops), rate of nitrogen fertilization (continuous variable, in kg ha^{-1}), relative density total (continuous variable; see eq. 2 below) and TND (continuous variable; see eq. 3 below).

The rate of N fertilizer in intercrops is not necessarily the same as in sole crops. Six experimental strategies of N fertilizer rate were distinguished. In strategy 1 (n = 339 data records), the fertilizer rate is the same in all treatments, both in the intercrop and the sole crops. In strategy 2 (n = 67), the fertilizer rate in the intercrop is intermediate between rates applied in the two sole crops, while N rate in the sole crops are different according to sole crop demand. In the remaining strategies, the N rate in the intercrops is (i) equal to the lowest of the sole crop fertilizer rate (strategy 3: n = 67), (ii) equal to the greatest of the sole crop fertilizer rate (strategy 4: n = 109), (iii) greater than the greatest of the sole crop fertilizer rate (strategy 5: n = 4) or (iv) smaller than the lowest of the sole crop fertilizer rate (strategy 6: n = 6).

Relative density total (RDT) is calculated as the sum of relative densities of intercropped species as compared to the sole crops:

$$\mathrm{RDT} = \frac{d_{1,\mathrm{ic}}}{d_{1,\mathrm{sc}}} + \frac{d_{2,\mathrm{ic}}}{d_{2,\mathrm{sc}}} \tag{2}$$

where $d_{1,\mathrm{ic}}$, and $d_{2,\mathrm{ic}}$ are densities of species 1 and 2, respectively, in the intercrop, and $d_{1,\mathrm{sc}}$ and $d_{2,\mathrm{sc}}$ are densities of species 1 and 2, respectively, in the sole crops.

An index for temporal niche differentiation (TND) was calculated using sowing and harvest dates of each species in the intercrop (Yu et al., 2015):

$$\mathrm{TND} = \frac{p_{\mathrm{system}} - p_{\mathrm{overlap}}}{p_{\mathrm{system}}} = 1 - \frac{p_{\mathrm{overlap}}}{p_{\mathrm{system}}} \tag{3}$$

where p_{overlap} represents the period of overlap of the growth period of the intercropped species, i.e. from sowing of the late sown species till harvest of the early sown species, while p_{system} represents the duration of the whole intercrop, i.e. from sowing of the early sown species till harvest of the late sown species. This indicator quantifies the proportion of the total growing period of the intercrop that the two component species are growing as sole crops (i.e. before sowing of the second sown species and after harvest of the first harvested species).

Statistical analysis

Quantile regression was used to determine the relationship between LER and TND for different quantiles (corresponding to probabilities ranging from 0.1 to 0.9 with increments of 0.05). The same approach was used to analyze the effects of interactions between TND and any of the other four explanatory variables (crop type combination, rate of N fertilization, intercropping pattern, and relative density total) on LER.

When only one explanatory variable is considered, say X, the τ^{th} quantile of Y is related to X by $Q_Y(\tau|X) = \beta_0(\tau) + \beta_1(\tau)*X$, where $\beta_0(\tau)$ and $\beta_1(\tau)$ are the regression parameters for the τ^{th} quantile. When two variables are included in the regression, $Q_Y(\tau|X) = \beta_0(\tau) + \beta_1(\tau)*X_1 + \beta_2(\tau)*X_2$, where $\beta_0(\tau)$, $\beta_1(\tau)$, and $\beta_2(\tau)$ are the regression parameters and X is now a vector of variables. The conditional quantile $Q_Y(\tau|X)$ is the inverse of the cumulative distribution function of the response variable LER (noted Y), and is defined such that $P[Y < Q_Y(\tau|X)] = \tau$, where τ is a probability ($\tau \in [0,1]$) (Cade et al., 1999). A range of conditional quantiles is defined here by selecting different values for τ (0.1, 0.15, 0.2, ..., 0.85, 0.9). For example, $Q_Y(\tau|X)$ represents the median if $\tau = 0.5$ and represents the 1st quartile if $\tau = 0.25$.

The estimates of quantile regression are semiparametric since no parametric distributional form is assumed for the random residual error of the model, while a parametric form is assumed for the deterministic part of the model (Cade and Noon, 2003). Five types of quantile regression models (Table 1) were fitted to data using the function `rq` of the package *quantreg* (Koenker, 2015) in R (R Core Team, 2013). We used 17 different values of τ (0.1, 0.15, …, 0.85, 0.9). Figures were made via R package *graphics* (R Core Team, 2013). A 95% confidence interval was computed for each parameter estimate using the R function `rq`.

The interaction between TND and rate of N fertilizer might depend on the strategy of N fertilization. We therefore analyzed the interaction between TND and rate of N fertilization using two different datasets, one dataset with all data records reporting the rate of N fertilizer, irrespective of the N fertilizer strategy, and a subset with only the data of N strategy 1 which is the main strategy in the dataset (Fig. B1).

The interaction between TND and intercropping patterns was analyzed using a subset of the dataset including strip and row intercrops but excluding mixed intercrops. As most mixed intercrops had TND equal to zero, the effect of TND on LER could not be estimated with sufficient accuracy for mixed intercrops.

Results

Effect of TND on LER (model 1)

LER increased with TND across all tested quantiles of LER (Fig. 1). The effect of TND on LER (parameter $\beta_1(\tau)$ of model 1) was always significant ($p < 0.05$) and varied from 0.2 to 0.3 units of LER per unit of TND across quantiles (Fig. 2b). The intercept of model 1, i.e. the LER at a TND of zero, increased with the quantile and became significantly greater than 1 when the quantile exceeded 0.3 (Fig. 2a).

Interaction between TND and the crop type combination (model 2)

LER increased with TND in both C3/C3 and C3/C4 intercrops (Fig. 3; Fig. 4b and d). The estimated slope of the effect of TND on LER ranged from 0.15 to 0.28 for C3/C3 intercrops (parameter $\beta_1(\tau)$ of model 2) and from 0.2 to 0.5 for C3/C4 intercrops ($\beta_1(\tau) + \beta_3(\tau)$) (Fig. 4b and d). The response of LER to TND was stronger for C3/C4 intercrops, especially at lower quantiles. At $\tau \leq 0.2$, the effect of TND on LER was significantly higher for C3/C4 than for C3/C3, while at higher quantiles no significant difference was found between C3/C3 and C3/C4 intercrops (Fig. 4b and d). Both crop type combinations led to similar estimates for $\beta_0(\tau)$, the value of LER at TND = 0, but the estimated values were slightly lower for C3/C4 mixtures at $\tau \leq 0.3$ and slightly higher for C3/C4 at $\tau > 0.3$ (Fig. 4a and c). In both crop type

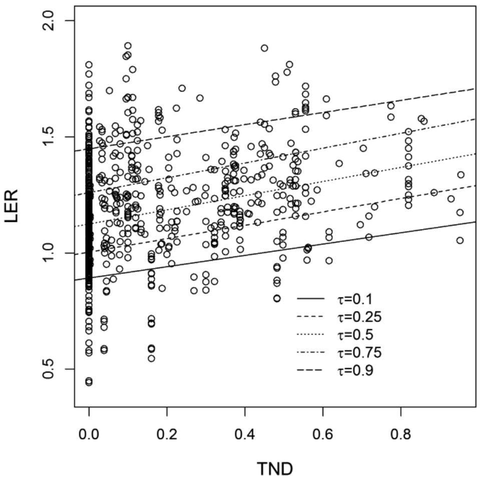

Fig. 1 Scatter plot of LER against TND (points) and linear functions relating LER to TND (lines) fitted by quantile regression with model 1: $Q_{LER}(\tau|TND) = \beta_0(\tau) + \beta_1(\tau)*TND_i$ for five quantiles (i.e. τ = 0.1, 0.25, 0.5, 0.75 and 0.9).

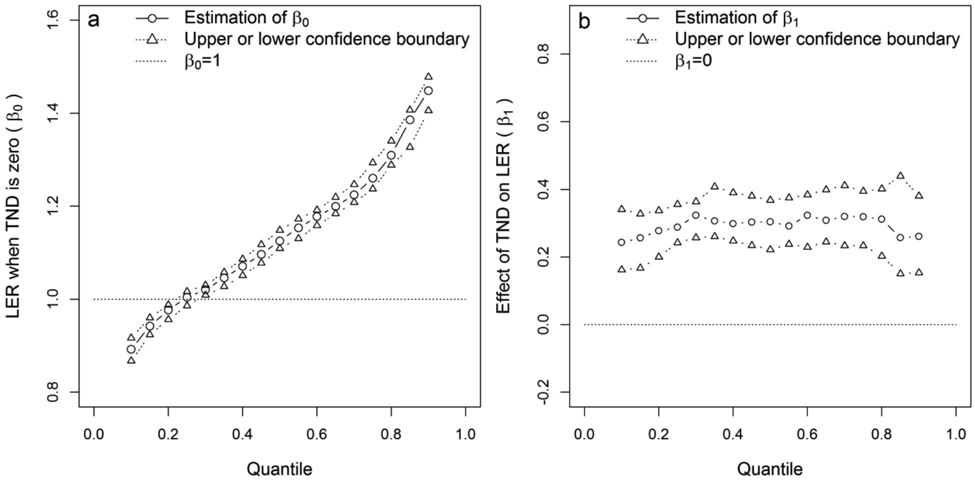

Fig. 2 Estimated values of the parameters of model 1: $Q_{LER}(\tau|TND) = \beta_0(\tau) + \beta_1(\tau)*TND_i$ for values of τ ranging from 0.1 to 0.9 with increment of 0.05. Circles represent estimates of β_0 (a) and β_1 (b) and triangles represent upper or lower boundary of 95% confidence intervals of estimated parameters. The horizontal line indicates 1 and 0 in panel (a) and (b) respectively.

combinations, LER was significantly above 1 at $\tau > 0.3$. These findings indicate that, in intercrops with LER at the lower end of the range (lower quantiles of LER), intercropping two C3 species would be better than mixing a C3 and C4 species as long as the two species are sown and harvested simultaneously. However, it would be better to mix a C3 and C4 species if there is a difference in growing period. In intercrops with comparatively high LER given the observed variables (higher quantiles of LER), intercrops of C3 and C4 species would be recommended irrespective of the degree of temporal niche differentiation.

Interaction between TND and N fertilization (model 3)

LER increased with TND when the rate of N fertilizer was zero; the estimated value of β_1 ranged from 0.11 to 0.45 from quantile 0.1 to quantile 0.9 (Fig. 5b). The effect of N fertilizer amount on LER (all quantiles) was negative when TND was zero (significant at most quantiles: $\tau = 0.1$, 0.15, 0.25, 0.4, 0.45, 0.7, 0.75, 0.85 and 0.9) (Fig. 5c). Interaction between TND and N fertilizer dose was positive at most of the tested quantiles, but was significant only at low quantiles values ($\tau < 0.3$) (Fig. 5d). This positive interaction shows that the negative effect of N fertilizer on LER was alleviated by reducing overlap of growing period between intercropped species. When both TND and rate of N fertilizer were zero, LER was significantly greater than one at most quantiles ($\tau > 0.2$) (Fig. 5a).

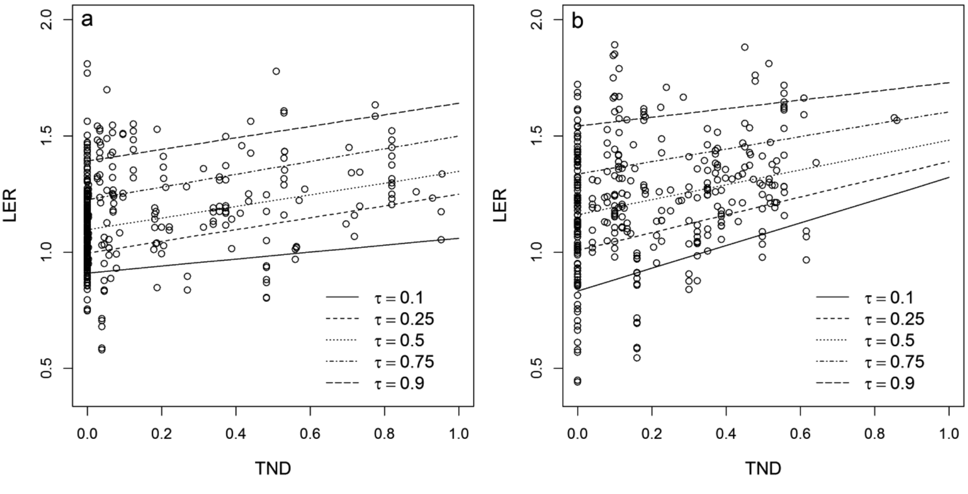

Fig. 3 Scatter plots of LER against TND (points) and linear functions (lines) relating LER to TND for C3/C3 (a) and C3/C4 intercrops (b) fitted by quantile regression with model 2: $Q_{LER}(\tau|\text{TND and C3/C4}) = \beta_0(\tau) + \beta_1(\tau)*\text{TND}_i + \beta_2(\tau)*\text{C3/C4}_i + \beta_3(\tau)*\text{TND}_i*\text{C3/C4}_i$ for five quantiles (i.e. $\tau = 0.1$, 0.25, 0.5, 0.75 and 0.9).

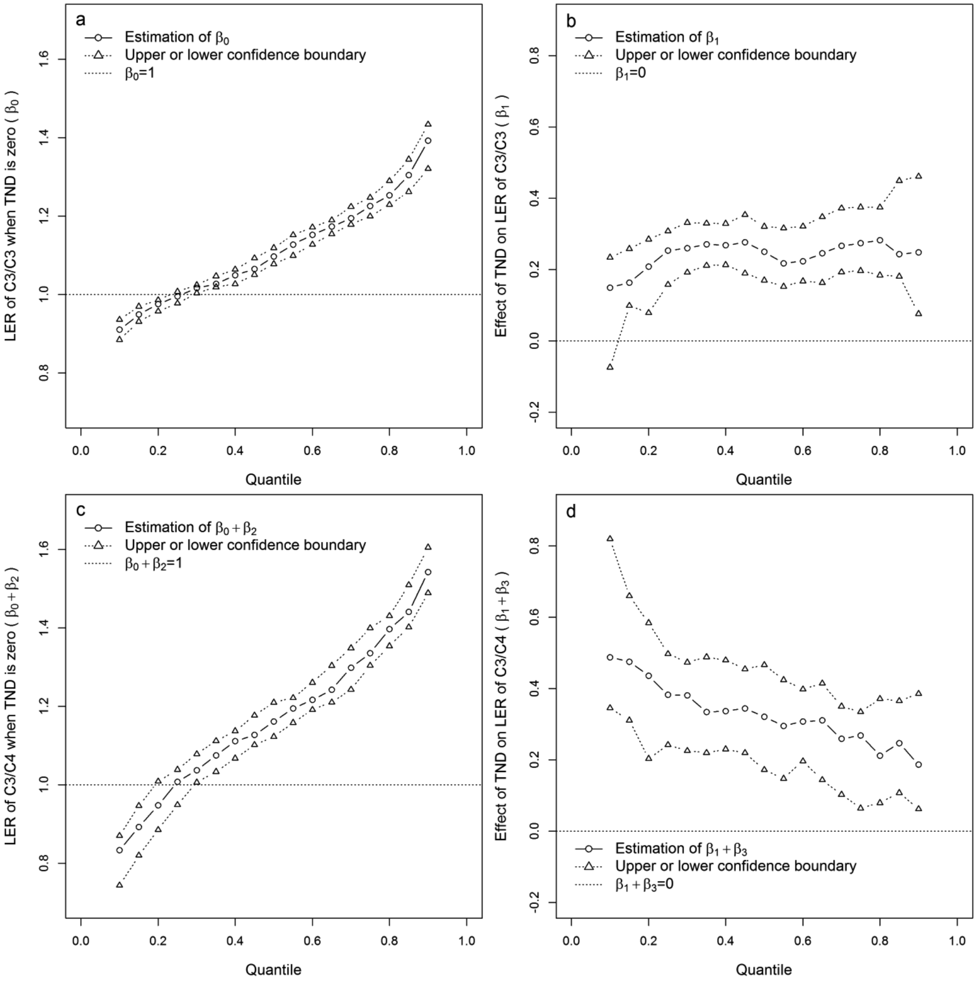

Fig. 4 Estimated values of parameters of model 2: $Q_{LER}(\tau|\text{TND and C3/C4}) = \beta_0(\tau) + \beta_1(\tau)*TND_i + \beta_2(\tau)*C3/C4_i + \beta_3(\tau)*TND_i*C3/C4_i$ for values of τ ranging from 0.1 to 0.9 with increment of 0.05. Circles represent estimates of β_0 (a), β_1 (b), $\beta_0 + \beta_2$ (c) and $\beta_1 + \beta_3$ (d) and triangles represent upper or lower boundary of 95% confidence intervals of estimated parameter values. The horizontal line indicates 1 in panel a and c, and 0 in panel b and d, respectively.

Interaction between TND and intercropping pattern (model 4)

TND had a positive effect on LER in both strip and row intercrops (Fig. 6b and d). In strip intercrops, the TND effect decreased with quantile, ranging from 0 to 0.25 units of LER per unit of TND (Fig. 6b). In row intercrops, the effect of TND was stronger at the higher quantiles of LER, ranging from 0.22 to 0.62 (Fig. 6d). The largest estimate of the TND effect ($\beta_1(\tau) + \beta_3(\tau)$) on LER was found at $\tau = 0.75$. Thus, the strength of the positive response of

LER to TND increased with quantile in row intercrops, but decreased with quantile in strip intercrops, indicating that other factors than TND that increase LER in row intercrops interact positively with TND, whereas factors that increase LER in strip intercrops interact negatively with TND.

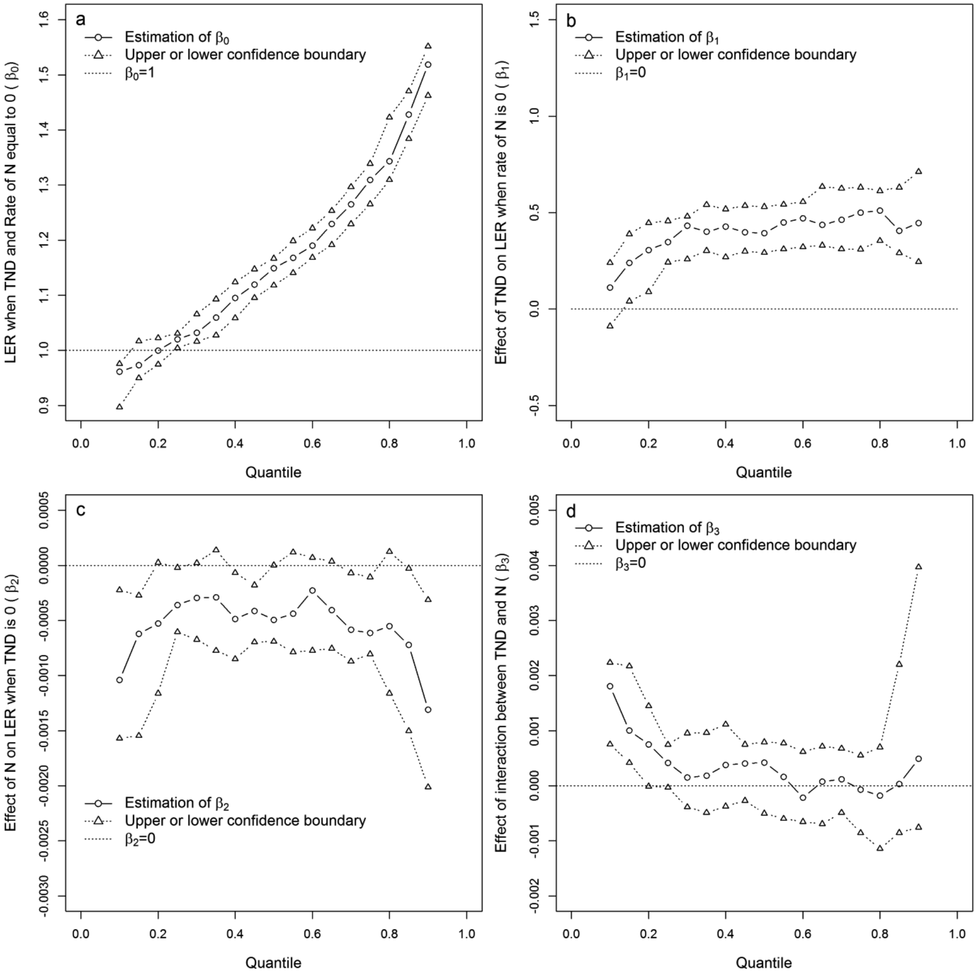

Fig. 5 Estimated values of parameters of model 3: $Q_{LER}(\tau|\text{TND and N}) = \beta_0(\tau) + \beta_1(\tau)*TND_i + \beta_2(\tau)*N_i + \beta_3(\tau)*TND_i*N_i$ for values of τ ranging from 0.1 to 0.9 with increment of 0.05. Circles represent estimates of β_0 (a), β_1 (b), β_2 (c) and β_3 (d) and triangles represent upper or lower boundary of 95% confidence intervals of estimated values. The horizontal line indicates 1 in panel a and c, and 0 in panel b and d, respectively.

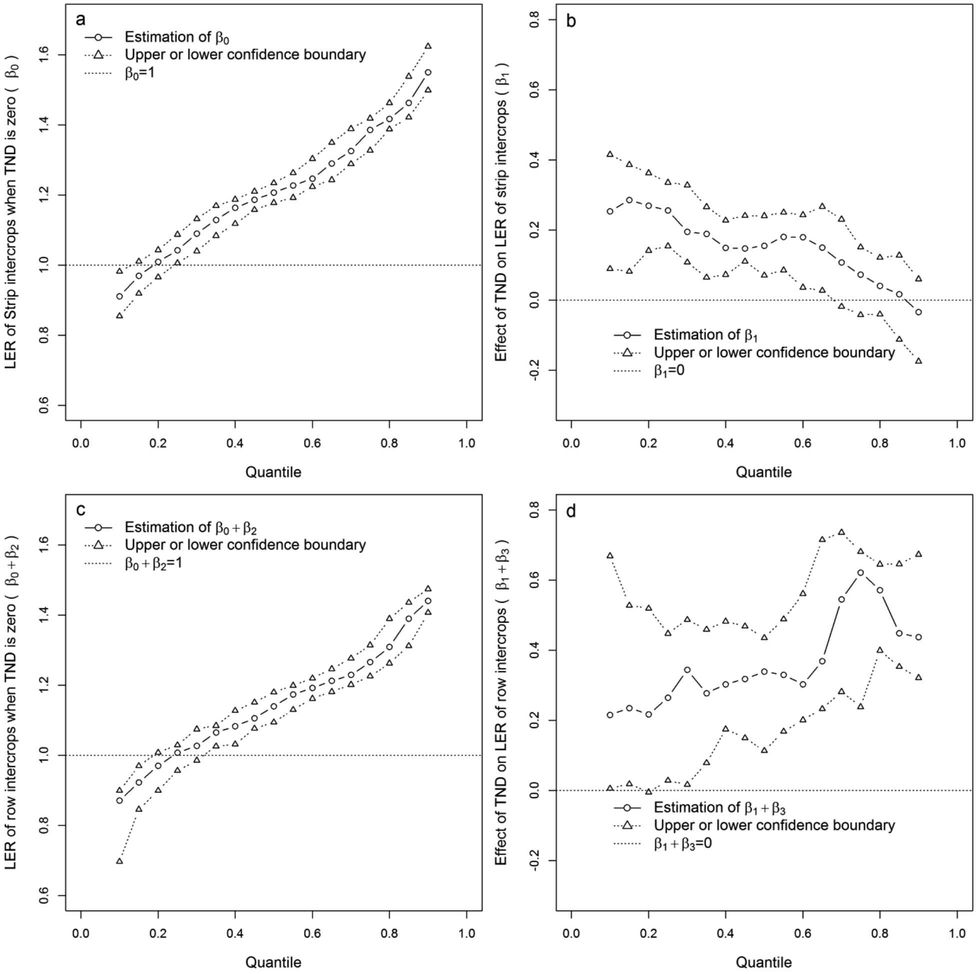

Fig. 6 Estimated values of parameters of model 4: $Q_{LER}(\tau|\text{TND and ICpattern}) = \beta_0(\tau) + \beta_1(\tau)*\text{TND}_i + \beta_2(\tau)*\text{ICpattern}_i^1 + \beta_3(\tau)*\text{TND}_i*\text{ICpattern}_i^1$ for values of τ ranging from 0.1 to 0.9 with increment of 0.05. Circles represent estimates of β_0 (a), β_1 (b), $\beta_0 + \beta_2$ (c) and $\beta_1 + \beta_3$ (d) and triangles represent upper or lower boundary of 95% confidence intervals of estimated values. The horizontal line indicates 1 in panel a and c, and 0 in panel b and d, respectively.

Interaction between TND and RDT (model 5)

LER increased with RDT when TND was zero at all tested quantiles, with only one exception ($\tau = 0.1$) (Fig. 7c). The value of β_2 increased from 0 to 0.26 with quantiles increasing from 0.1 to 0.35, and varied from 0.2 to 0.25 at quantiles between 0.4 and 0.8, increasing again with quantile to reach a maximum value of 0.31 at $\tau = 0.9$ (Fig. 7c). The interaction between TND and RDT was negative at almost all tested quantiles. However, this interaction was significant only at quantiles between 0.25 and 0.5 (Fig. 7d). These results indicate that LER increases with relative density, while the positive effect of TND on some quantiles of LER is smaller at high than at low relative density total.

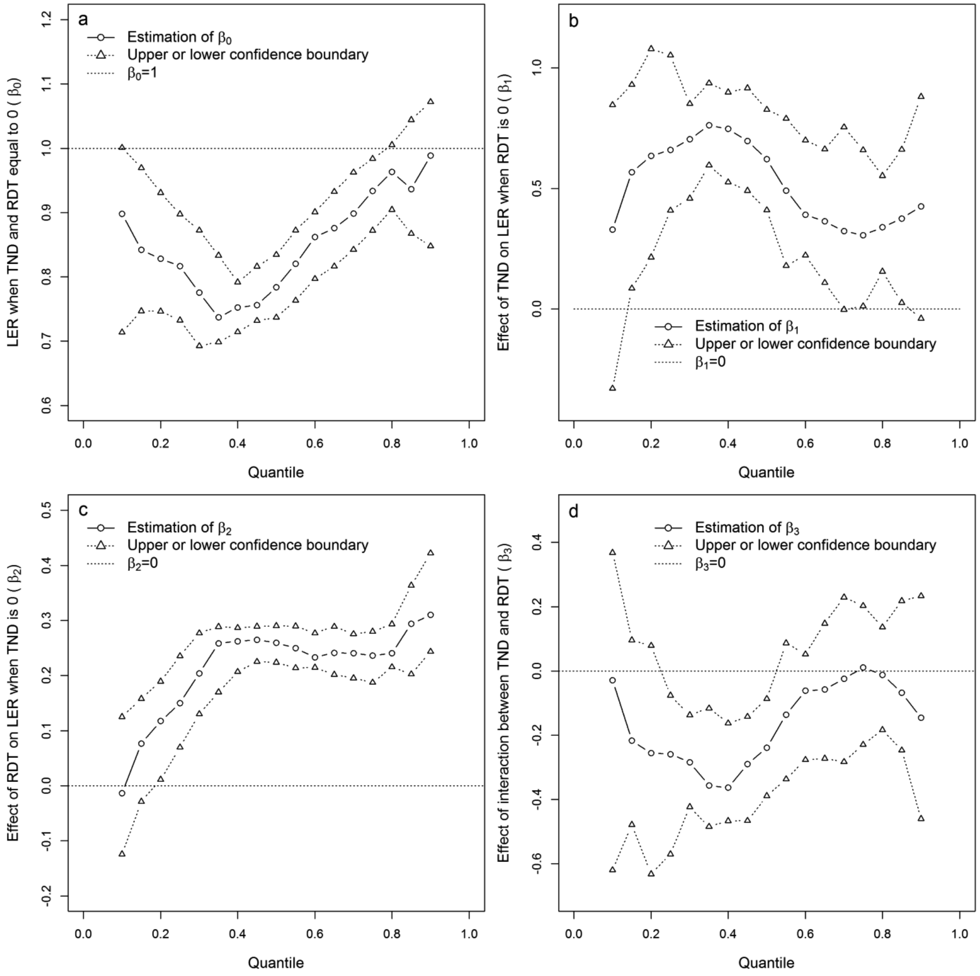

Fig. 7 Estimates values of parameters of model 5: $Q_{LER}(\tau|TND \text{ and } RDT) = \beta_0(\tau) + \beta_1(\tau)*TND_i + \beta_2(\tau)*RDT_i + \beta_3(\tau)*TND_i*RDT_i$ for values of τ ranging 0.1 to 0.9 with increment of 0.05. Circles represent estimates of β_0 (a), β_1 (b), β_2 (c) and β_3 (d) and triangles represent upper or lower boundary of 95% confidence intervals of parameter estimates. The horizontal line indicates 1 in panel a and c, and 0 in panel b and d, respectively.

Discussion

This study explored the effect of temporal niche differentiation on LER and its interaction with crop type combination, rate of N fertilization, intercropping pattern and relative density total at different quantiles of the LER distribution. The positive effect of temporal niche differentiation on LER held across all tested quantiles, but interactions with other variables modified the general picture. The response of LER to TND was stronger for C3/C4 as compared to C3/C3 intercrops only at low quantiles. Increasing the rate of N fertilizer decreased LER in the absence of temporal niche differentiation at all tested quantiles. This negative effect of N fertilization on LER was alleviated by increasing TND, but only at lower quantiles of LER ($\tau < 0.3$). Effects of TND on LER decreased with quantile in strip intercrops but increased with quantile in row intercrops. In other words, the positive effect of TND on LER in strip intercrops interacts negatively with factors that increase LER but are not included in the regression model. In contrast, in row intercrops, the response of LER to TND interacts positively with the factors not included in the model. Increasing relative density total reduced the positive effect of temporal niche differentiation on LER, especially in intercrops with a low to median LER.

Effect of TND on LER for C3/C3 and C3/C4

The current study gives a more complete picture of the interaction between TND and crop type combinations than the previous study by Yu et al. (2015). We show here that if LER of an intercrop would be low due to some unknown/unmeasured factors or factors not included in the regression model, the LER is greater in C3/C3 intercrops than in C3/C4 intercrops, if the two species are sown and harvested simultaneously. However, if LER is comparatively low (lower quantiles) while the growing season would allow temporal niche differentiation between the intercropped species, it would be better to combine a C3 and C4 species. However, in intercrops with high LER, we show that a C3/C4 intercrop is better in terms of land use efficiency than a C3/C3 intercrop, irrespective of temporal niche differentiation.

Effect of interaction between rate of N fertilization and TND on LER

A negative effect of N fertilizer on LER has been reported in many studies (e.g. Ofori and Stern, 1986; Ofori and Stern, 1987b; Tobita et al., 1994). Nevertheless, one recent meta-analysis by Pelzer et al. (2014) found no evidence for an effect of N fertilizer on LER, while another meta-analysis by Yu et al. (2015) found a negative effect of N fertilizer on LER when intercropped species are sown and harvested simultaneously. In the current study, we show that LER decreases with N fertilizer amount in the absence of temporal niche differentiation which is consistent with Yu et al. (2015). This negative effect could be alleviated by increasing temporal niche differentiation between intercropped species (Yu et al., 2015). The negative nitrogen effect thus only holds when there is little or no temporal niche differentiation. However, we also found that the positive interaction between TND and the rate of N fertilizer only holds at lower quantiles ($\tau \leq 0.25$). In other words, only for intercrops of low LER, e.g. conditions where competition between species dominates, the negative effect of N fertilization on LER can be alleviated by having temporal niche differentiation, while for intercrops with high LER, e.g. conditions where facilitative or complementary interactions dominate, the negative effect of N fertilization is little affected by temporal niche differentiation.

Quantile regression

In standard linear regression and in mixed effects model, estimates of parameters in a regression model only represent the relationship between the mean of a response variable and the chosen explanatory variable(s). Such a regression represents the mean condition of factors that are not included in the regression model. However, the relationship between the response variable and explanatory variable(s) may interact with these factors not included in the regression model. Factors not included in the model cause variation of the response variable at given values of explanatory variables. Quantile regression provides us an opportunity to analyze relationship between variables for different portions of the response variable instead of only focusing on relationship between conditional means of the response and explanatory variables (Koenker and Bassett, 1978; Cade et al., 1999; Koenker and Hallock, 2001). In other words, quantile regression is capable of analyzing the interaction effect between factors included in a regression model and those not included in the structural part of the model but only in the distribution of the error.

This study is fundamentally different from the previous meta-analysis conducted by Yu et al. (2015). In the current study, we asked how the response of LER to temporal niche differentiation changes across different quantiles of the distribution of LER. We show that the effect of temporal niche differentiation on LER is robust and is valid for all quantiles, not only for the mean response.

A disadvantage of using the `rq` function to conduct quantile regression is that it does not account for nested error structures. In quantile regression, all data records are assumed to be independent. This is a simplification. As a result of this simplification, degrees of freedom are increased, which could lower p-values, while random errors associated with nesting are pooled into an overall error term, which could lower the power of the analysis. In the study by Yu et al. (2015), mixed effects models were used to analyze the causal relationships between LER and intercropping characteristics, considering correlations between data from the same experiment and study by taking experiment and study as random effects. Results of both methods are valuable. The study by Yu et al. (2015) showed us a general picture of relationships between LER and intercropping characteristics while the current study reveals a fuller picture of the causal relationships. The reader may focus on consistency and trends in significance in these two studies. Both of the studies show similar trends for the effect of temporal niche differentiation on LER, confirming that temporal niche differentiation is an important factor for increasing LER of annual intercrops. We found interactions between temporal niche differentiation and crop type combinations (C3/C3 vs C3/C4) or N rate in both studies, indicating crop type combination and N rate are two key factors modifying the effect of temporal niche differentiation on LER.

Appendix B

Fig. B1 Estimates of interactive effect between TND and rate of N fertilizer with two datasets: one dataset with all data reporting N rate, irrespective of N strategies and one subset with only the data of N strategy 1 which is the main N strategy in the database

Table B1 Variables extracted from publications

Table B2 Availability of information on selected variables in data set for this meta-analysis

Acknowledgements

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Chapter 4

Plant traits drive spatially and temporally complementary light capture, photosynthesis, and productivity in plant mixtures

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Abstract

Species richness tends to positively affect primary production in natural and agricultural ecosystems, an effect that is often strongly determined by spatial and temporal niche differentiation between species. Niche differentiation in turn is associated with variation in plant traits but the extent of this mediating effect has rarely been quantified.

Here, we use a functional-structural plant (FSP) model to explore the effect of temporal niche differences on biomass production of early- and late-emerging plants in an agricultural plant species mixture. This model contains the feedback between light absorption, photosynthesis, and the emergence of plant structure and biomass in species mixtures under different conditions of spatial and temporal arrangement. We quantify how the productivity of mixtures of an early-emerging tillering plant type with a late-emerging non-tillering plant type is affected by plant traits, i.c. the maximum plant height and rate of CO_2 assimilation (A_{max}), of the later emerging species, in an interplay with the spatial configuration of the mixture and the relative times of sowing of the two plant types.

Biomass of the early-emerging plants increased with later sowing of the late-emerging plants, reaching a plateau when the temporal overlap between the growth durations of the early- and late-emerging plants was less than 50% of the total growing period of the mixture. Productivity of the late-emerging plants suffered from competition for light with the early-emerging plants, especially at moderate delays in sowing time compared to the early-emerging plants and when the spatial configuration of the mixture allowed strong interaction. Maximum plant height of the late-emerging plants did not qualitatively affect its response to sowing time. The negative effect of the early-emerging plants on the late-emerging ones decreased when the A_{max} of the latter sown species was higher.

These results show how spatial and temporal complementarity (sowing pattern and sowing date) in mixed cultivation systems is strongly determined by the traits of the component species. FSP modelling is a useful tool to disentangle these interactions, and to help design productive intercrop systems that maximize complementarity and minimize the effects of competition.

Key words: temporal niche difference, plant height, maximum rate of CO_2 assimilate, FSP modelling, relative yield total, relative yield

Introduction

Species diversity positively affects productivity in grassland ecosystems, as shown in field experiments in the USA and Europe (Tilman et al., 1996; Loreau and Hector, 2001; Tilman et al., 2001; Van Ruijven and Berendse, 2003; Cardinale et al., 2007). One of the mechanisms to explain this effect of species richness on biomass production is the niche difference theory (Loreau et al., 2001; Tilman et al., 2001; Cardinale et al., 2007; Yachi and Loreau, 2007). This theory states that individual species in a mixture experience less niche overlap than in monocultures, resulting in complementary resource use in space and/or time and therefore higher biomass production.

One measure that indicates the productivity of mixtures is the sum of relative yields (RY) of the species in the mixtures, relative to that of the respective yields in the mono-stands i.e. relative yield total (RYT). RYT is calculated using eq. 1 (De Wit, 1960):

$$RYT = \sum RY_i = \sum \frac{Y_i}{M_i} \tag{1}$$

where Y_i is the yield of crop i in a crop mixture and M_i is yield of crop i in a monocrop. The definition of relative yield total (De Wit, 1960) is identical to the definition of land equivalent ratio (LER) (Mead and Willey, 1980):

$$LER = \sum PLER_i = \sum \frac{Y_i}{M_i} \tag{2}$$

where $PLER_i$ is the partial land equivalent ratio of crop i (equal to RY_i), LER is commonly interpreted as the area of land required to produce the same yield output as a unit area of the mixed crop (Mead and Willey, 1980). While the equations for calculation of RYT and LER are identical, the underlying philosophies of De Wit and Mead & Willey were different. The former was primarily interested in ecological relationships and required that in empirical trials the total relative density was kept at one, whereas Mead & Willey accepted the agronomic reality that farmers might increase relative density in the mixture above one to maximize total resource capture and yield.

In a meta-analysis of literature data on intercrops (crop mixtures, i.e. two or more crop species growing simultaneously in the same field), we found a positive relationship between LER and temporal niche differentiation, defined as the proportion of the total growth duration of a two-species mixture during which the species do not overlap in their growth (Yu et al., 2015). Temporal niche differentiation is attained if one species in an agricultural system is sown before the other or harvested later than the other. In both cases, one species would have all the resources to itself for part of the growing season, allowing an increase in its relative yield that would not directly go at the expense of the other species, as this species is not present at the same time. Under niche differentiation theory, complementary use of light has been suggested as one possible reason for the positive effect of species diversity on productivity of ecosystems (Naeem et al., 1994). However, it is not clear how performance of individual species would be affected by increasing temporal niche differentiation resulting in changed light conditions for the species in the mixtures in interaction with the species traits.

A positive effect of temporal niche differentiation on LER was found in mixtures with plants of C3 and C4 photosynthetic pathways (C3/C4 mixtures) but not in C3/C3 mixtures (Yu et al., 2015). C3/C3 mixtures were usually combinations of two short-stature species, while C3/C4 mixtures entailed combinations of a short C3 and a tall C4 species. In C3/C4 mixtures, it is very common that a C3 species is sown earlier than a C4 species. Normally, a late-sown tall C4 species is shaded by the early-sown short C3 species during its early growth, while it will overgrow the short C3 species at a later time (Fan et al., 2006; Zhu et al., 2014) and thereafter may recover from the early stress (Li et al., 2001a). Similar patterns can be observed in many natural grasslands where short C3 species dominate in spring and are gradually replaced by taller C4 grasses (Turner and Knapp, 1996; Anten and Hirose, 1999). A mixture of a C3 species (early and short) with a C4 species (late and tall) might have a better light capture as compared to short/short C3 mixtures (Anten and Hirose, 1999), as the early short species may dominate the light capture in early season while the late tall species would recover when it overgrows the short species and dominates in late season, achieving a complementary light capture in both time and space.

C4 species have higher maximum photosynthesis rates than C3 species (Connor et al., 2011) and this photosynthetic capacity, A_{max} is one of the key factors distinguishing C3 and C4 photosynthesis (Lövenstein et al., 1995; Lambers et al., 2008; Connor et al., 2011). A mixture of a C3 and a C4 species may have high light use efficiency especially if the species with the higher photosynthetic rate (C4) captures most of the light (high in the canopy), while the species with the lower rate of photosynthesis (C3) is better adapted to lower light conditions (Anten and Hirose, 2003). Such functional complementarity would further strengthen productivity increase arising from greater light capture due to differences in growth period (temporal complementarity).

However, to our knowledge few studies have quantitatively assessed the contribution of interspecific variation in individual traits to niche differentiation. Thus the question remains to what extent different responses of LER to temporal niche differentiation between C3/C3 and C3/C4 mixtures can be attributed to variation in maximum plant height and associated complementarity in light capture or variation in leaf photosynthesis and associated complementarity in light-use.

The current study has two objectives. Firstly we investigate how productivity of individual species in mixtures is affected by temporal niche differentiation. We expected that in a mixed cropping system, an early-sown species may profit from temporal niche differentiation because of the delayed sowing of the other species resulting in relaxed competition for light. Therefore, biomass production of the early-sown species is expected to increase with temporal niche differentiation, until a point at which sowing of the late-sown species has little effect on the early-sown one; after that point, biomass production of the early-sown species is not affected by further increasing temporal niche differentiation. Conversely, performance of the late-sown species is expected to decrease as its sowing is delayed and the competitiveness of the early-sown species increases. Therefore, biomass production of the late-sown species might decrease with temporal niche differentiation. However, from a certain time onward (the recovery point), later sowing of the late species which also implies that its growth duration extends beyond the harvesting time of the early species, will allow the late species to recover during its late growth and suffer less competitive impact from the early species.

Secondly, we assess the effect of the maximum plant height and photosynthesis rate (A_{max}) of the late-sown plant type on the temporally complementary use of light and the productivity of the mixture. A taller late-sown plant type may suffer less competition from the presence of early-sown plants because it can grow out of the shade more rapidly and reach the recovery point earlier. Therefore, we expect a smaller biomass reduction in a taller late-sown plant type than a shorter late-sown plant type. A taller late-sown plant type is furthermore likely to be a stronger competitor versus the early-sown plants than a shorter late-sown plant type. We hence expect that biomass production of the early-sown plants is lower in mixtures with the tall late-sown plant type than with the short late-sown plant type. We may expect that a late-sown plant type with a high A_{max} would suffer less growth reduction as a result of competition from the early plants than a plant type with a low A_{max} because of its greater photosynthesis, biomass accumulation and resulting length growth, which should allow it to grow out of the shade more rapidly. Thus, the recovery of a high A_{max} plant type is expected to be faster than that of a low A_{max} plant type.

To address our objectives, we use functional-structural plant (FSP) modelling, a 3D modelling approach which enables simulation of interactions between plant architecture and the physical and biological processes that drive plant growth and development (Vos et al., 2010; Evers, 2016). FSP models quantify light capture by individual species in mixtures (Zhu et al., 2015) and simulate the dynamic of interplay of plant growth, plant-plant interactions and light capture. In particular, these models account for the positive feedback loop between light capture, photosynthesis and growth in plants, and for the reciprocal effects of heterogeneous light environment in leaf canopies and the growth of individual competing plants within those canopies. We developed a generic FSP model which incorporates photosynthesis-driven organ growth of plants in a mixed setting, to quantify to what extent plant traits drive spatially and temporally complementary light capture, photosynthesis and productivity in plant mixtures.

Materials and methods

General description of model

The model used in this study simulates generic cereal crop plants using a FSP modelling approach (Vos et al., 2010; Evers, 2016). The model consists of several components: plant architectural development (i.e. production of new plant organs at certain rate with certain geometrical properties like orientation), assimilate production, and plant growth. Individual plants are arranged in a plot setup, allowing simulation of intercropping designs in which growing plants are competing with each other for light. Acquisition of belowground resources such as nutrients and water is not considered in the current approach, and is assumed to be optimal. The model was designed to simulate contrasting generic plant types in the simulation platform GroIMP (Hemmerling et al., 2008). Therefore, the choice of the mechanisms included and the calibration of the parameters was chosen such that the simulated plants represent the generalized phenotypes of interest (maximum plant height (potentially short/tall), tillering/non-tillering, high/low A_{max}, see below section ‘*Generic plant types*’).

Plant architecture

In the model, plant architecture is described as a repetition of elementary units called phytomers. Phytomers are sequentially placed at the top of the growth axis by the shoot apical meristem, and consist of a leaf, an internode and axillary meristem. In the tillering species, an axillary meristem develops into a bud and grows into a tiller only if the assimilate status of the plant is favorable. After having produced a fixed number of vegetative phytomers, the plant goes to its generative stage and the meristems produce an inflorescence after which no further new organs will be produced on the shoot. The inflorescence subsequently acts as a carbon sink. Individual grains are not considered. The root system architecture is not taken into account, but the root does act as a carbon sink (see below section '*Plant growth*').

Assimilate production

The light capture of the organs in the canopy (leaves, internodes) is calculated using the Monte Carlo pathtracer embedded in GroIMP; for details see Hemmerling et al. (2008). Light sources are set up in a hemispherical configuration providing both direct and diffuse light (Evers et al., 2010). Using reflectance and transmittance coefficients, the amount of photosynthetically active radiation (PAR) absorbed by each individual leaf is calculated. Subsequently, leaf photosynthesis rate is determined using a light response curve relating absorbed PAR to photosynthesis rate. Distribution of photosynthetic capacity in the canopy is approximated by making organ maximum CO_2 assimilate rate (A_{max}) dependent on the fraction of radiation absorbed by the organ using an established relationship between the two (Niinemets and Anten, 2009). The acquired assimilates by every organ are stored in a central carbon pool from which costs of respiration and growth are deducted each time step; the remainder is used for plant growth.

Plant growth

Sink strength of all organ types (leaf, internode, root system, inflorescence) in the model is defined as the potential capacity of the organ for biomass accumulation, and described by the beta growth function in relation to organ age (Yin et al., 2003). When assimilates are plentiful all organs have their demand satisfied, resulting in growth matching the sink strength. When assimilates are limiting they are distributed based on the relative sink strengths of the organs, i.e. the fraction of organ sink strength in the total plant sink strength (Heuvelink, 1996). This means that there is no hierarchy among organs for the allocation of assimilates under limiting conditions, and all organs are allocated the same percentage of demand. When the plant goes into the generative stage a large new sink emerges (the inflorescence), which strongly reduces the biomass allocation towards leaves and internodes, reducing their growth rate. Similarly, a change in sink strength of an internode through shade avoidance (see below section 'S*hade* *avoidance*') will affect plant growth by potentially lowering allocation to leaves and therefore reducing photosynthetic gain. The effects of source-sink dynamics on plant growth is the main driving mechanism in the model.

Shade avoidance

Shade avoidance in response to reductions in the red/far-red ratio (R:FR) of the light absorbed was added to make the plants respond plastically to the presence or absence or growth dynamics of a neighboring plant (Bongers et al., 2014). Plants generally absorb red light but scatter far-red light, and the change in R:FR is used to assess neighbor presence and perform shade avoidance responses such as increased stem elongation (Smith, 1982). The model uses separate reflectance and transmittance coefficients for red and far-red to calculate the absorption and scattering of light in both wavebands by the organs in the canopy. When the observed whole-plant R:FR (average R:FR values perceived by its organs) drops below a threshold (the same for all plant types used) the modelled plant initiates shade avoidance by increasing stem elongation (Franklin and Whitelam, 2005) in all plant types and by initiating tiller abortion (Sparkes et al., 2006; Evers et al., 2007) in the tillering plant type. Increased stem elongation is achieved by increasing internode sink strength, thereby increasing the demand for assimilates. Tiller abortion is performed during a juvenile stage only, before the start of stem extension of the main stem.

Generic plant types

Five generic plant types were defined. For the first-emerging (sown) plant, we use a short tillering and low A_{max} plant type (called "tillering type" from here on). This plant type broadly represents small grain cereal species which are commonly the first sown-species in relay-intercrops (but without attempting to represent any species in particular), and could be easily adapted to represent early season tillering grasses. The other four plant types do not tiller and are collectively called "non-tillering types". They are potentially either short or tall, and they have either a low or high maximum rate of photosynthesis. This plant type can represents a tall non-tillering cereal (e.g. maize or sorghum), again without the aim to represent any species in particular. The four types of the non-tillering species are: (1) short & low A_{max}, (2) short & high A_{max}, (3) tall & low A_{max}, and (4) tall and high A_{max}. The qualification of plant height as short or low reflects a potential because plant height is plastic. The maximum plant height was controlled by parameterization of the sink strength of the internodes. If their demand is always fully met, plant height will reach its maximum. If the demand is not fully met, due to competition, height will be less than the maximum. Tillering ability, maximum height and photosynthesis rate were the only plant traits that were varied in this study. Key parameters determining features of each plant type are listed in Table 1, and the expressions of features of plant types in monoculture are listed in Table 2.

In order to keep the analysis tangible, we fixed the traits of the early-emerging plants and only varied the type of the late-emerging plants, though noting that analysis could be extended in the future to include variation of plant traits in the early-emerging plants. The tillering plant type with low A_{max} was used as the early-emerging plants in the simulation studies, while the other four were used as the late-emerging plants to explore the plant height × A_{max} interaction with temporal niche differentiation and spatial configuration in the system as a whole.

Table 1 Key parameters determining features of each plant type. The parameter *Tiller* determines whether a plant is a tillering type or not. *A_{max}* determines the photosynthetic capacity of a plant type. *Sink strength of internode* determines the maximum height of a plant. *Growth period* indicate the total life cycle of a plant type.

Parameters	**Tillering**	**Short&low A_{max}**	**Short&high A_{max}**	**Tall&low A_{max}**	**Tall&high A_{max}**
Tiller	Yes	No	No	No	No
A_{max} (μmol/m^2/s)	25	25	57	25	57
Sink strength of internode(mg/internode)	150	3000	3000	6000	6000
Growth period (simulation days)	150	150	150	150	150

Table 2 The realized plant traits in mono-stand. *Biomass* represents the total aboveground biomass of a plant type at ‘harvest’ (simulation day 150). *Maximum height* is the maximum height a plant type can achieve. *Maximum leaf area index* is the leaf area per unit land area when the plant canopy is closed.

Features	**Tillering**	**Short&low A_{max}**	**Short&high A_{max}**	**Tall&low A_{max}**	**Tall&high A_{max}**
Biomass in monoculture (ton/ha)	~15	~20	~30	~18	~30
Maximum height (m)	~1.0	~1.0	~1.0	~1.8	~2.0
Maximum leaf area index	~5.0	~5.0	~5.0	~5.0	~5.0

Modelling assumptions

Our study focuses on the interaction between temporal niche differentiation and a set of plant functional traits, therefore we simplified the effects of abiotic conditions. Firstly, we did not implement a relationship between photosynthetic rate and temperature in our model. Therefore, leaf photosynthetic rate here was only a function of light absorption and the position of a leaf in the canopy. Second, a constant daily radiation was used (~18 MJ/m^2/day) throughout our simulations, and the seasonal variation of solar radiation and temperature was not considered. Third, we assume no constraint of water or nutrients on plant growth. In other words, light is the only limiting factor for plant growth.

Layout of the simulated scenes for monocultures and mixtures

All of the five plant types were simulated in both monocultures and mixtures. In plots of monoculture, the tillering plant type was sown at a density of 160 plants/m^2 with inter-plant and inter-row distances of 0.05 and 0.125 m, respectively, while the non-tillering plant type was sown at a density of 10.26 plants/m^2 and inter-plant and inter-row distances of 0.13 and 0.75 m, respectively. Species mixtures were designed based on the replacement principle (De Wit and van den Bergh, 1965) using a strip pattern, i.e. two species growing in alternative strips (Vandermeer, 1992; Zhang et al., 2007). There were four kinds of intercrop in this study, each with the early-emerging tillering plant type intercropped with one of the four late-emerging non-tillering plant types. Two configurations were adopted for every intercrop to vary the intimacy of the spatial species association in the intercrops and its effect on the strength of interaction: every six rows of the early crop intercropped with either one (Configuration I) row or two (Configuration II) rows of the late crop (Fig. 1). In Configuration I, a row of the late-emerging species is bordered on both sides by a row of the early-emerging species, while in Configuration II, a row of the late-emerging species is bordered on only one side by the first-emerging species. Thus, the opportunity for interspecific competition effects on the late-emerging species is greater in Configuration I. On the other hand, the opportunity for interspecific competition effects on the first plant type is somewhat diminished in Configuration I, because the six rows of this plant type are interacting with only one row of the late-emerging plant type on either side, versus 2 rows of the late-emerging plant type in Configuration II. In plots of the intercrop, the inter-plant and inter-row distances within a plant type were the same as in the monoculture, while the distance between strips of different plant types was set to 0.4375 m, i.e. equal to the mean

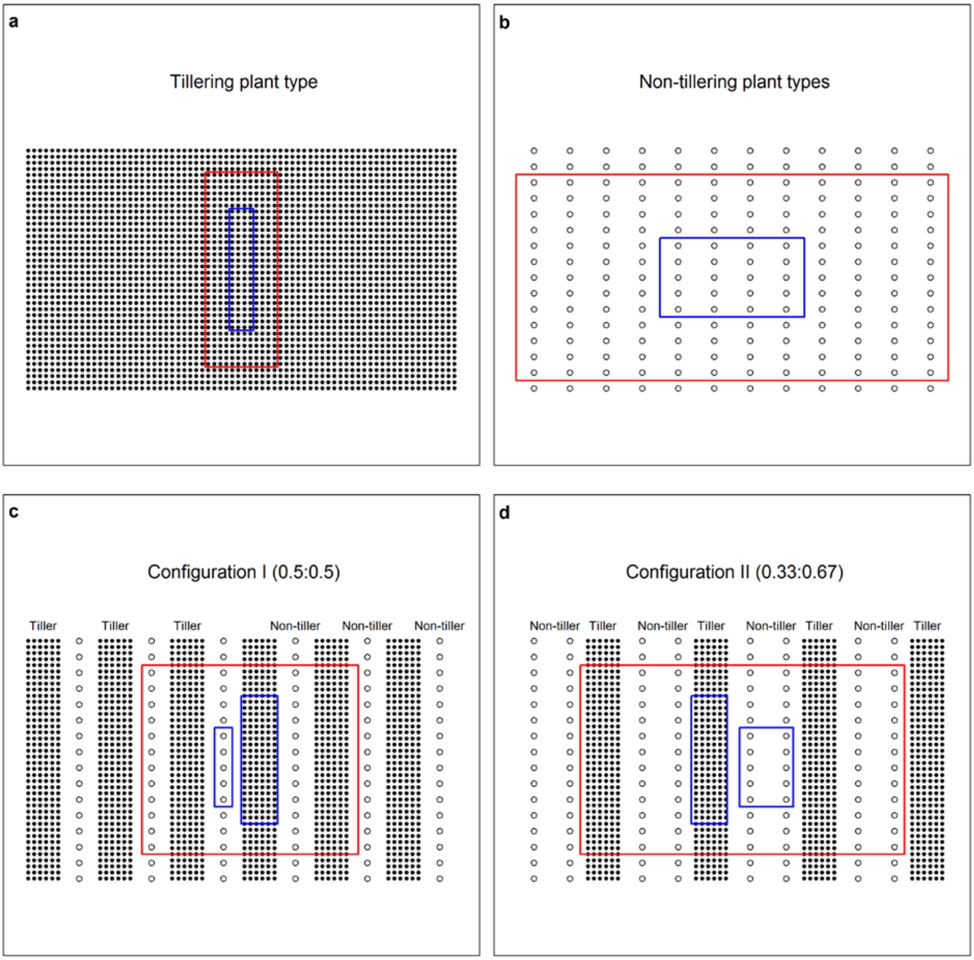

Fig. 1 Configurations of monocultures and mixtures. Monocultures of the tillering plant type (a) were simulated with inter-plant and inter-row distance of 0.05 and 0.125 m, respectively. Monoculture of the non-tillering plant types (b) were simulated with inter-plant and inter-row distance of 0.13 and 0.75 m, respetively. In Configuration I of mixtures, every 6 rows of the tillering plant type were mixed with 1 row of the non-tillering plant type (c), with a distance of 0.4375 m between strips of tillering and non-tillering plant types. The inter-plant and inter-row distance of each plant type was the same as the respective monocultures. In Configuration I, the relative density of the tillering and non-tillering plant types is 0.5, respectively. In Configuration II of mixtures, every 6 rows of the tillering plant type were mixed with 2 rows of the non-tillering plant type (d). The relative density of the tillering and non-tillering plant types is 0.33 and 0.67, respectively. Distances between plants, rows and strips in Configuration II were the same as in Configuration I. The red box indicates the number of plants simulated in each scence and the blue box indicates the number of plants used for data analyses.

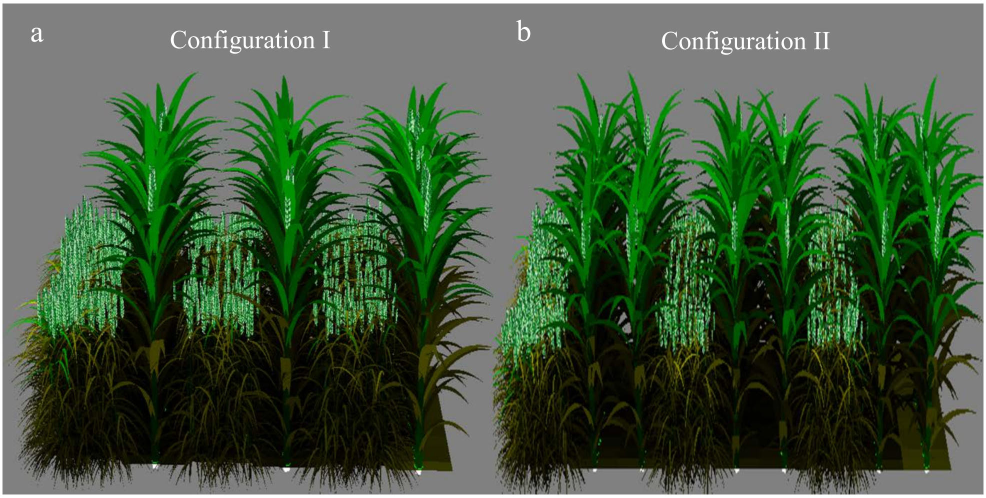

Fig. 2 Illustration of simulated intercrop scenes of Configuration I (a) and II (b). In both configurations, there are three strips of the tillering and non-tillering plant types, respectively. Each strip of the tillering plant type consists of 6 in both configurations. In Configuration I, strips of non-tillering plant types consist of 1 row, while in Configuration II, the strips of non-tillering plant types consist of 2 rows.

inter-row distance of the tillering and non-tillering plant types (Fig 1). Relative densities were 0.5 for both plant types in Configuration I, i.e. per unit area each plant type had half of the number of plants in the intercrop as compared to their monoculture, while they were 0.33 for the tillering plant type and 0.67 for the non-tillering plant type in Configuration II.

A simulated monoculture scene of the tillering plant type consists of 12 rows and 32 plants per row. A scene of the non-tillering plant type consists of 12 rows and 13 plants per row. A simulated intercrop scene consists of six strips, three for each plant type (Fig. 2a and b). To exclude edge effect and focus on effects of our treatments, plants on edges of a plot were excluded from the analysis. In monoculture scenes, data from 20 plants of tillering plant type or 5 plants of non-tillering plant types in each of 4 middle rows were used for analyses. In intercrop plots we used the data from 10 plants per row strip of the tillering plant type and 5 plants per row of non-tillering plant types, using all plant rows of the middle 2 strips.

Simulation scenarios

Temporal niche differentiation (TND) is an indicator quantifying the proportion of the total growing period of the mixture that two component species are growing as sole crops, i.e. before sowing or after harvesting of the other species (Yu et al., 2015):

$$\mathrm{TND} = \frac{P_{\mathrm{system}} - P_{\mathrm{overlap}}}{P_{\mathrm{system}}} = 1 - \frac{P_{\mathrm{overlap}}}{P_{\mathrm{system}}} \tag{3}$$

where P_{overlap} represents the period that two species grow simultaneously in the mixture, from sowing of a late-sown species till harvest of an early-sown species, and P_{system} represents the total period of the mixture, i.e. from sowing of the early-sown species until harvest of the late-sown species (Yu et al., 2015).

Eleven TND scenarios were simulated for each of the four intercrops, with TND ranging from 0 to 1 in steps of 0.1 (Table 3). All treatments, including monocultures and intercrops were replicated four times. There were thus in total 5 monoculture treatments (monocultures of 1 tillering and 4 non-tillering plant types), 44 mixtures of Configuration I, and 44 mixtures of Configuration II. These were all simulated in four replicates to account for variation in model output, due to stochastic variation in the initial orientation of plants, which affects light acquisition and growth in a positive feedback loop.

Relative biomass and relative biomass total

We used relative biomass to assess biomass production of individual plant types in the intercrop as compared to the monocultures. Relative biomass total, rather than relative yield total, was used to compare biomass production of an intercrop as a whole to monocultures. The calculation of relative biomass total is the same as relative yield total (eq.2), but using total biomass instead of grain biomass.

Results

Animation of simulations

Three example movies of our simulations are given in the Appendix (Movie C1, C2 and C3). In the first example, growth dynamics of plants was simulated in a Configuration I intercrop of the tillering plant type with a tall & high A_{max} plant type at TND = 0 (Movie C1). The simulation started at emergence of the two plant types and ended at day 150. Growth dynamics of the two plant types are presented. In the second example, the same combination and configuration of plant types was simulated at TND = 0.5 (Movie C2), i.e. with sowing of the late-emerging species 50 days after sowing of the early-emerging species, and harvest of the late-emerging species on day 200, 50 days after harvest of the early-emerging species on day 150. The third example shows the same plant type mixture at TND = 0.5 in Configuration II (Movie C3).

Relative biomass of early emerging plants (tillering plant type) in Configuration I

In Configuration I, relative density of the tillering plant type was 0.5, i.e. half of its density in monoculture, but relative biomass of the tillering plant type was in general above 0.5 (Fig. 3a), indicating that the early-emerging plants had an advantage in terms of biomass production in intercrops as compared to the monoculture. The maximum value of relative biomass (~0.8) was achieved at TND > 0.4. Thus, with half of the density of monoculture, the early-emerging plants in intercrops produced 80% of the biomass in monoculture, in line with our hypothesis that the relative biomass of the early-emerging plants would increase with TND till a point when later sowing of the late-emerging species would not further diminish its competitive effect on the early-emerging species.

The traits of the late-emerging plants had a clear effect on the biomass of the early-emerging plants at low TND (TND < 0.4) when interspecific competition is strong. The tall plant type with a high A_{max} had the greatest competitive effect on the biomass of the early-emerging plant among the four types tested as late-emerging plant (Fig. 3a). At low TND (0 or 0.1), tall stature was a more important competitive trait of the late-emerging plants, while at higher TND (0.2 or 0.3) high photosynthesis rate was more important, indicating that at low TND, light interception was a more important determinant of competitiveness of the late-emerging plants, while at somewhat higher TND, efficiency of light conversion into biomass was more influential. The early-emerging plants did not attain 100% of the monoculture yield, even with late sowing (TND > 0.4) of the late-emerging plants, reflecting incomplete light capture because of limitations in plasticity to fully cover the soil with leaves.

Relative biomass of late-emerging plants (non-tillering plant type) in Configuration I

The response of the late-emerging plants to TND was radically different from that of the early-emerging plants. While the early-emerging plants showed a saturating response, with the plateau being reached at TND > 0.4, the late-emerging plants showed a minimum response, with high relative biomass at low or high TND (up to approximately 0.8) and low relative biomass (approaching 0) at TND 0.3-0.6. Thus, the competitive effects of the first on the second-emerging plants were moderate to small at very low or high TND, but strong at intermediate TND, i.e. at moderate sowing delays of the second compared to the first plant types (Fig. 3b).

We had hypothesized that the relative biomass of the late-emerging plants would decrease with temporal niche differentiation up to a recovery point, beyond which relative biomass would again increase. The results support this hypothesis (Fig. 3b).

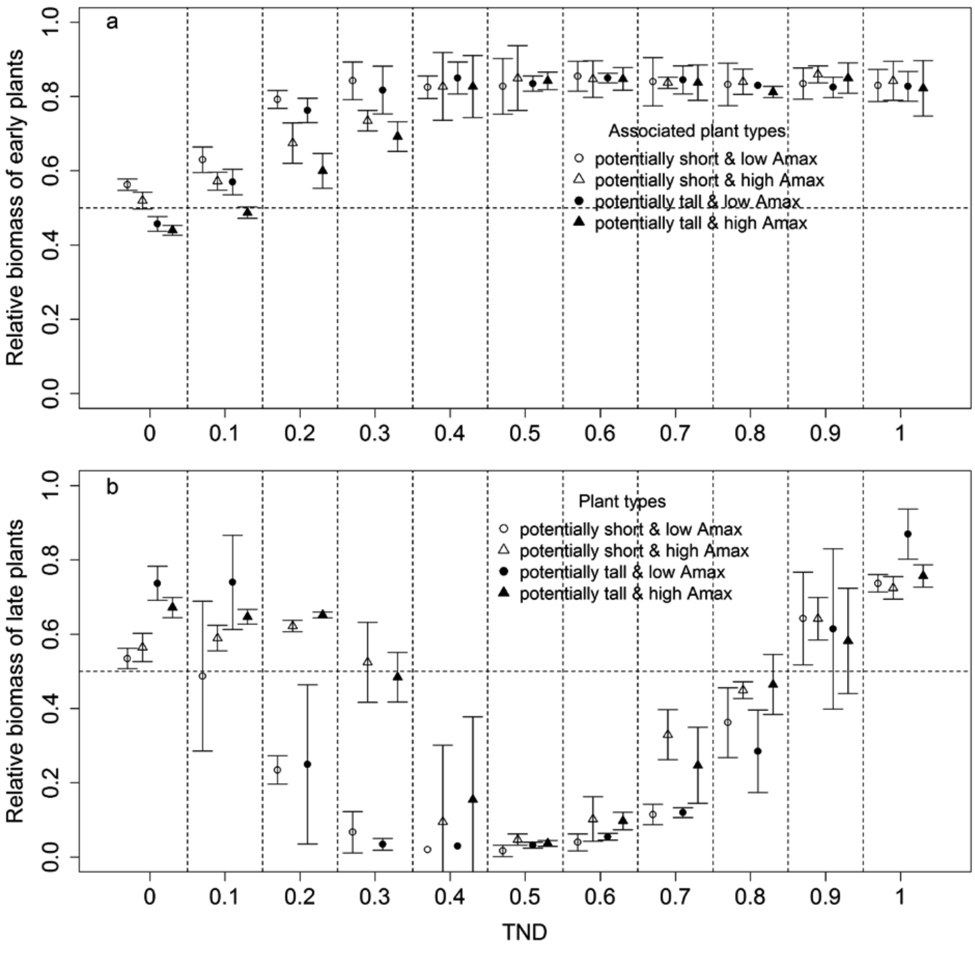

Fig. 3 Relative biomass of early-emerging plants (a) and late-emerging plants (b) at different TND categories for Configuration I, i.e. mixtures of six rows of early-emerging plants and one row of late-emerging plants. For Configuration I, relative density of each plant type is 0.5. The horizontal dashed line represents relative biomass equal to 0.5.

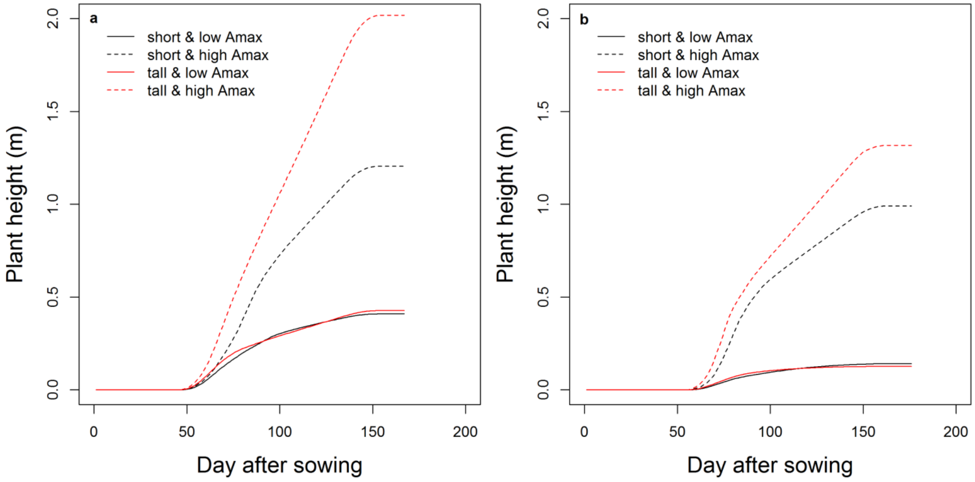

Fig. 4 Development of plant height of late-emerging plants in Configuration I at TND equal to 0.2 (a) and 0.3 (b). In Configuration I, mixtures consist of strips of six rows of the early-emerging plant type alternated with single rows of the late-emerging plant type. With TND = 0.2, the late-emerging plants emerged 17 simulation days after the early plants. With TND = 0.3, the late-emerging plants were delayed by 26 days as compared to the early-emerging plants. For both plant types, a growth duration of 150 days was simulated. This figure shows the positive interaction between the two plant traits maximum plant height and photosynthesis rate. A late-emerging type with a large maximum height will only realize its height growth potential if it photosynthesizes enough.

A_{max} of the late-emerging plants influenced the response to TND. Late-emerging plants with low A_{max} suffered a greater reduction in biomass with increasing TND than plant types with a high A_{max} (Fig. 3b). The greater robustness of plant types with high A_{max} to competition was related to their greater length growth. For example, at TND equal to 0.2 and 0.3 the plant type with high A_{max} exhibited greater height increment as compared to the type of low A_{max} (Fig. 4). Therefore, in turn, more light could be intercepted by the crop of high A_{max} due to its better development in plant height, resulting in a positive feedback. Indeed, maintaining high rates of photosynthesis under shade conditions appears to be a key trait for species to perform in an intercrop if sown at a growth delay compared to a companion crop.

Maximum plant height of the late-emerging plants also affected the response of its relative biomass to TND but only at very low TND (TND < 0.2) and less strongly than A_{max}. Relative biomass of a potentially tall late-emerging plant-type was greater than of a potentially short late-emerging plant-type at TND < 0.2 (Fig. 3b).

Relative biomass of early-emerging plants in Configuration II

Configuration II, with a relative density of 0.33 for the first-emerging plants and 0.67 for the second-emerging plants, showed responses of relative biomass to TND and plant traits that were similar in shape but not as strong as the pattern observed for Configuration I. The less intimate association with the early plant type allowed the late plant type to perform relatively better in this configuration than in Configuration I. The early-emerging plants showed a high relative biomass in Configuration II when compared to relative density (0.33), ranging from a minimum value of 0.4 at TND = 0 to almost 0.6 at TND > 0.4 (Fig. 5a), but not as high as in Configuration I, due to low relative density (0.33 in Configuration II, compared to 0.5 in Configuration I). The effects of traits of the late-emerging plants on relative biomass of the early-emerging plants were similar in shape as those in Configuration I.

Relative biomass of late-emerging plants in Configuration II

The competitive effects of the first-emerging plants on the second-emerging plants were markedly less in Configuration II (Fig. 5b) than in Configuration I (Fig. 3b). This is because each row of the second-emerging plant in Configuration II interacted with both a row of the same plant type and a row of another plant type, whereas in Configuration I, between-row interactions of the second-emerging plants were exclusively with rows of the first emerging plant type, which aggravated competitive effects of the first-emerging plants on the second-emerging plants up to TND of 0.8. Relative biomass of the late-emerging plants did not decrease as much with increasing TND as in Configuration I, and relative biomass had a minimum slightly above 0.4, at values of TND from 0.3 to 0.5. The recovery point was not changed compared to Configuration I, and the highest relative biomass was about 0.8, similar to Configuration I. High A_{max} resulted in greater competitiveness of the second-emerging plants, and a higher value for the biomass at TND = 0.4 (Fig. 5b). As in Configuration I, height of the late-emerging plants had a minor effect on relative biomass at TND < 0.4 and no effect at higher TND. Conversely, high A_{max} contributed noticeably to relative biomass at TND values from 0.2 to 0.4, indicating importance of photosynthesis response of the later emerging plants for its productivity in a situation in which it is overshadowed by earlier emerging plants (Fig. 5b).

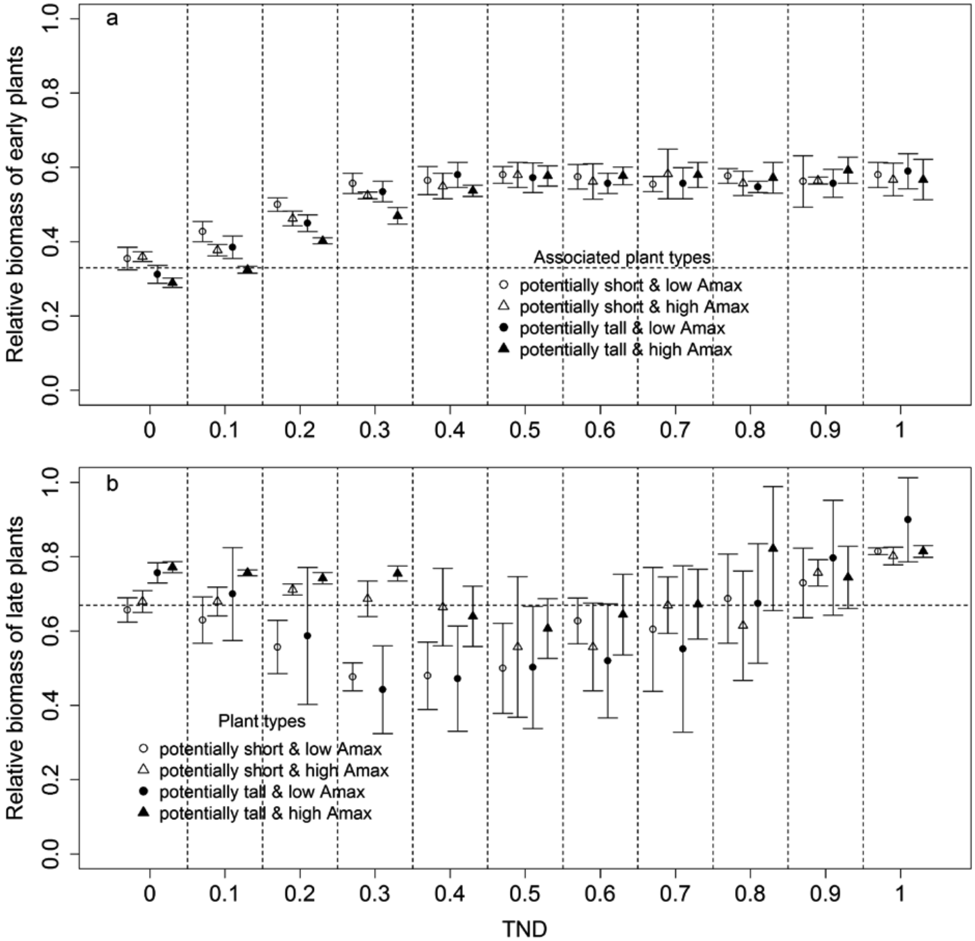

Fig. 5 Relative biomass of early-emerging plants (a) and late-emerging plants (b) at different TND categories for Configuration II, i.e. mixtures consisting of strips of six rows of early-emerging plants alternated with strips of 2 rows of late-emerging plant types. For Configuration II, relative density of early-emerging plants and late-emerging plants is 0.33 and 0.67, respectively. The horizontal line represents relative biomass equal to 0.33 in panel a and 0.67 in panel b.

Effect of TND and plant type combinations on relative biomass total in species mixtures

The sum of relative biomasses of the two components in a mixture showed different responses to TND in the two configurations. In Configuration I, with a strong competitive effect of the first-emerging plants on the second-emerging plants, the decrease in relative biomass of the second-emerging plants at intermediate TND (0.4-0.6) was greater than the increase (already

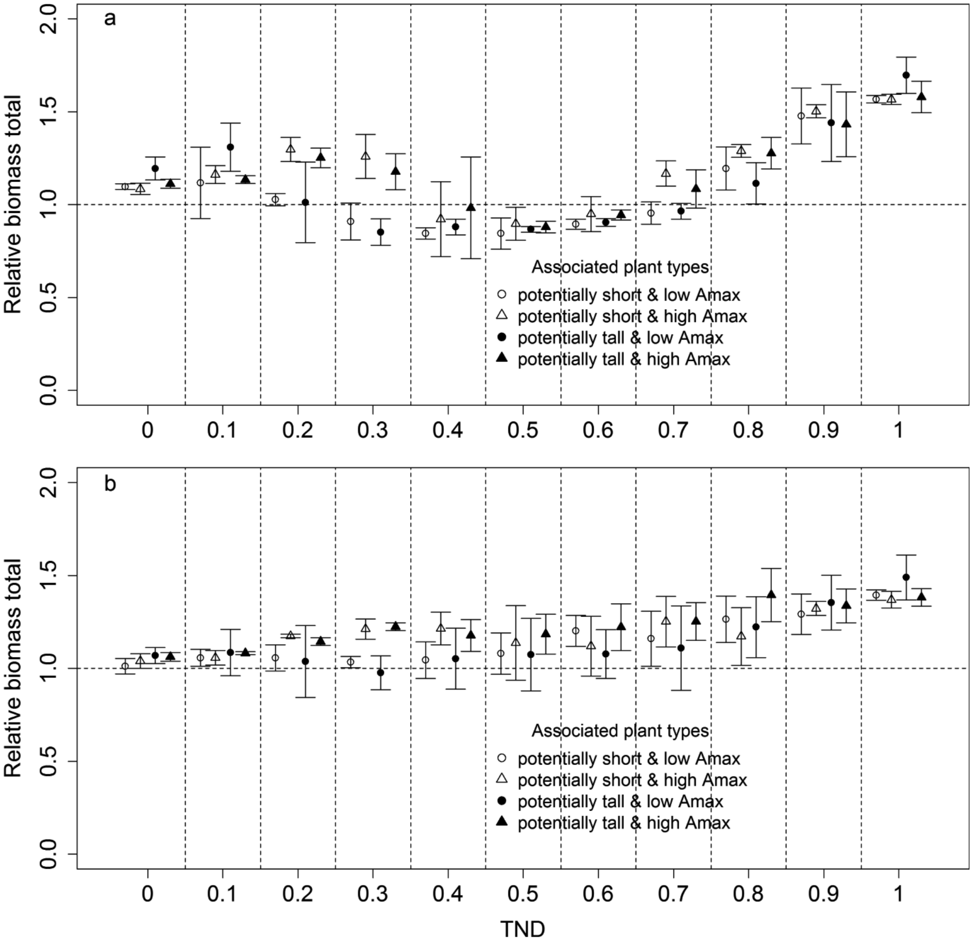

Fig. 6 Relative biomass total of different mixtures at different categories of TND for Configuration I (a) and Configuration II (b). In Configuration I, every six rows of the early-emerging plant type are grown with one row of either of the late-emerging plant types; in Configuration II, every six rows of early-emerging plants are grown with two rows of either of the late-emerging plant types. The horizontal line represents LER equal to 1.

at plateau) of relative biomass of the first-emerging plants and at TND = 0.3 for low A_{max}. Thus, the relative biomass total in Configuration I had a minimum at TND 0.3 to 0.6. This asymmetry in intercropped components response to TND was not clearly expressed in Configuration II. In this case, with less strong competitive effects on the second-emerging plants, the overall system performance was more robust (high relative biomass total) than in Configuration I. However, the highest relative biomass total was attained at high TND in Configuration I, when both the first- and second-emerging plants profited maximally from the temporal niche differentiation, and the later sown plants were more evenly distributed reducing intra-specific competition.

Discussion

To our knowledge, this is the first functional structural plant modelling study addressing mechanistically the interactions between plant growth and photosynthesis and the reciprocal effects between the light environment and plant photosynthesis and growth in mixtures. In this modelling study, we found that the early-emerging plants benefited from later sowing of the late-emerging plants due to the relaxed competition for light from the late-emerging plants, while this positive relationship levelled off when the temporal overlap between the growth durations of plant types was less than 50% of the total growing period of the mixture. The late-emerging plants suffered a great reduction in biomass due to the competition for light from the early-emerging plants especially at moderately delayed sowing time and when spatial arrangement of the mixture allowed strong interspecific interactions (i.c. Configuration I). High A_{max} or potential plant height reduced the negative effect of competition from an early-emerging plant type if the later species was sown with a relatively short delay after the first species.

Model choices

In our model, we assumed a constant daily incoming solar radiation (~18MJ/m^2/day), allowing us to investigate the effect of temporal niche differentiation on performance of species mixtures without confounding effects of the course of seasonal radiation intensity. This enabled us to also analyze extreme TND scenarios (TND = 1) in which total growing time was 300 days.

The maximum assimilation rate of CO_2, i.e. A_{max}, is one of the key factors distinguishing the photosynthetic pathways for C3 and C4 species (Connor et al., 2011). C4 species normally have higher A_{max} than C3 species (Goudriaan and Van Laar, 1994; Lambers et al., 2008). According to Lövenstein et al. (1995), A_{max} of C3 species ranges from 12 to 32 µmol /m^2/s depending on plant species and growth environment, while A_{max} of C4 species in general varies between 30 and 50 µmol/m^2/s. In some extreme cases, A_{max} of C4 species could be even higher, for instance Evans et al. (2000) reported a value of A_{max} for maize approximating 60 µmol/m^2/s. In this modelling study, we used an A_{max} of 25 µmol /m^2/s for plant types with C3 photosynthesis and 57 µmol /m^2/s for plant types with C4 photosynthesis.

We chose a rather extreme value for the 'high A_{max}' plant type to be able to identify significant effects. However, under real field conditions, the actual difference in photosynthesis between C3 and C4 plants depends strongly on the abiotic environment, e.g. nutrient and water availability. Hence, the effects of differences in photosynthetic capacity between species in different environments needs to be further explored.

We distinguished C3 and C4 photosynthetic pathways using A_{max} only because the difference in respiration rate between C3 and C4 photosynthetic pathways is much smaller than the difference in their A_{max} (Yin et al., 2011). Nevertheless, plant species with a high A_{max} may also have a high respiration rate (Anten and Hirose, 2003) both in monoculture and mixed stands. It is difficult to assess whether taking this difference into account would increase or decrease the potential benefit of mixtures. This issues also deserves further study.

Interactive effect between niche differentiation and plant traits

In this study, we explored answers to the question: which species traits contribute to the difference in response of LER to TND between C3/C3 and C3/C4 mixtures. In a meta-analysis of published empirical experiments, Yu et al. (2015) found that LER of C3/C4 mixtures responded more strongly to increasing TND than C3/C3 mixtures. It has also been argued that temporal niche differentiation between early short C3 species and later taller C4 species may contribute to high productivity in tall-grass prairies (a wide spread ecosystem in the North America) (Turner and Knapp, 1996; Anten and Hirose, 2003). Yet, the relative contributions of variation in plant height and photosynthesis rate to the difference in response to TND in these systems is unclear. The results presented here indicate that in intercropping systems the high rate of photosynthesis of C4 plants as compared to C3 plants is likely to be a key factor underlying the different response, while variation in maximum plant height may also have an effect but possibly not as large as photosynthesis rate.

A factor that is also likely involved in the stronger response of C3/C4 mixtures to temporal complementarity, but was not studied here, is the difference between C3 and C4 species in temperature response. Temperature is one of the key factors influencing plant photosynthesis (Sage and Kubien, 2007; Yin and Struik, 2009). C4 plants have on average higher temperature optima for photosynthesis and growth than C3 species (Connor et al., 2011). There is a divergence between C3 and C4 plants in their response to temperature, which could also underlie strong complementarity when grown in different parts of the growing season in a particular region. In our modelling framework, we assumed that the growth and photosynthesis of the C3 and C4 species was not constrained by temperature. This simplification was intentionally made to allow focusing on complementarity mechanisms for light capture, in relation to plant traits and spatial and temporal configuration of the system. Effectively, therefore, we did not consider the cultivation of a C4 species during the early season, because this assumption would in many situations not be biologically realistic. In future work, the temperature responses for real species should be built into the modelling framework to further explore the comparative importance of temperature in shaping the complementarity between C3 and C4 plants in mixed plant communities. In real systems, the scope for increasing TND may be constrained by the available length of growing season with sufficiently high temperatures. This might particularly apply to C4 species which require higher temperatures than C3 species to fully realize high rates of photosynthesis and growth.

Temporal and spatial complementarity

Yachi and Loreau (2007) distinguished two possible species relationships in light competition in mixtures: competitive relaxation (complementarity) and competitive imbalance (dominance). Competitive relaxation refers to the relaxed competition for resources - in our case light - between mixed species due to niche differences while competitive imbalance means unequal access to light since one of the mixed species is dominant. The current study showed that the extent to which competitive relaxation is accomplished depends on interactions between temporal niche differentiation and configuration. At low (TND < 0.4) and high (TND ≥0.8) temporal niche difference, most species combinations exhibit competitive relaxation in both tested configurations. At medium TND (0.4 ≤ TND ≤ 0.7), all species in Configuration I experienced competitive imbalance, i.e. the early-emerging plants dominates the mixture while no competitive imbalance was observed in Configuration II. The competitive imbalance was strongest in the second species in Configuration I, in which it was growing in a single row, neighboring at both sides to the first species which was dominant. At high TND, the late-emerging plants experienced greater competitive relaxation in Configuration I than Configuration II. The difference in competitive relaxation is not so much related to the interspecific competition, but rather due to less intraspecific competition between the late-emerging plants in Configuration I, as the late-emerging plants are more evenly spaced in Configuration I than in Configuration II. This finding shows that spatial effects that enhance competitive imbalance (narrow rows) may be mitigated by increasing temporal complementarity, and vice versa. Likewise, in a situation with competitive relaxation (high TND), the effects are stronger if the spatial arrangement allows reduced intraspecific competition (Configuration I).

Effect of TND on relative biomass total

In the meta-analysis by Yu et al. (2015), a positive relationship between LER and TND was found using a linear model: LER = $\beta_0+\beta_1$*TND, with β_0 the LER at TND = 0 and β_1 the effect of TND on LER. The estimations of β_0 and β_1 equal to 1.18 and 0.21, which means TND increasing from 0 to 1 results in an increase of LER from 1.18 to 1.39. In the current modelling study, our simulations show that at TND = 1, relative biomass total (equal to LER) are greater than 1.39 in all species mixtures and all configurations, especially in Configuration I, in which relative biomass total are all greater than 1.5. The difference of LER at extreme TND are likely due to the difference of limiting factors between the modelling study and the meta-analysis. In the modelling study, light is the only abiotic factor affecting plant growth and interactions. In the modelling framework, under condition of extreme TND, both species in the mixtures could maximize the use of captured light without limitation on growth from the other abiotic factors, e.g. nutrients and water. On the contrary, in the meta-analysis framework, apart from light, other abiotic factors could also limit plant growth, therefore the benefit of light use in species mixtures at extreme TND might be limited by e.g. nutrient or water limitation, as well as by seasonal trends in temperature and light.

Conclusion

In this study, an FSP model incorporating photosynthesis-driven growth of plant organs was developed to investigate the interplay of temporal and spatial complementarity and plant traits in mixed plant systems. We have shown that complementarity of light use in time (sowing time) and space (row arrangement) likely determine productivity of species mixtures. This spatial and temporal complementarity is affected by plant traits of component species in the mixtures, i.e. maximum plant height and photosynthetic capacity. These findings help us to identify species trait combinations and spatial and temporal configurations of species with different traits to maximize the complementary effect, minimize competitive unbalance, and achieve sustainably high yield output.

Appendix C

Movie C1[*] Simulation of plant growth in a mixture of tillering species with tall&high Amax species in configuration I (every 6 rows of tillering species mixed with 1 row of non-tillering species) at TND=0, i.e. simultaneously sown and harvested. The total simulation time is 150 simulation days.

Movie C2 Simulation of plant growth in a mixture of tillering species with tall&high Amax species in configuration I (every 6 rows of tillering species mixed with 1 row of non-tillering species) at TND=0.5. TND equal to 0.5 means the tillering species is sown first and harvested at simulation day of 150 while the non-tillering species is sown 50 simulation days later than sowing of the tillering species and harvested at simulation day of 200. The total simulation time is 200 simulation days.

Movie C3 Simulation of plant growth in a mixture of tillering species with tall&high Amax species in configuration II (every 6 rows of tillering species mixed with 2 rows of non-tillering species) at TND=0.5. TND equal to 0.5 means the tillering species is sown first and harvested at simulation day of 150 while the non-tillering species is sown 50 simulation days later than sowing of the tillering species and harvested at simulation day of 200. The total simulation time is 200 simulation days.

* In Appendix C, no movies but links for these movies are presented. These movies can be watched on YouTube through the links.

Acknowledgements

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Chapter 5

A meta-analysis of relative crop yields in cereal/legume mixtures suggests options for management

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Abstract

Intercrops of cereals and legumes are grown worldwide, both in smallholder agriculture in developing countries and in organic farming systems in developed countries. The competitive balance between species is a key factor determining productivity in mixtures. Management factors, e.g. sowing time, sowing density and rate of N fertilizer, affect the relative competitiveness and performance of intercropped species. There is a need for an overarching analysis to elucidate general principles governing the relative performance of legumes and cereals in mixtures. We therefore conducted a meta-analysis of published studies to explore how the relative yield of legumes and cereals in mixtures responds to relative sowing time, relative density and nitrogen fertilizer.

An index for relative sowing time, RST, was developed to quantify the relative difference in sowing time between the intercropped species. RST is defined as the amount of time that a species is sown earlier or later than its companion species, relative to the length of its own growing period. RST is greater than zero if a species is sown earlier than its companion species and smaller than zero if it is sown later. Relative performance of a species was characterized by its relative yield (or partial land equivalent ratio, PLER) in the intercrop compared to the yield in the sole crop.

In 409 out of 552 cases, the cereal had a greater relative yield than the legume. Sowing a species earlier than its companion increased its relative yield, and vice versa. An increase in density of a species increased its relative yield and decreased the relative yield of the companion species. The relative yield of cereals increased and that of legumes decreased with the amount of N fertilizer,. The negative effect of N on the relative yield of legumes was mitigated if the legume was sown before the cereal.

The study shows how the performance of cereals and legumes in an intercrop is affected by sowing densities, relative sowing times, and nitrogen fertilizer. Growers can exploit these relationships to manage competition between cereals and legumes in mixtures and enhance species complementarity, total productivity and economic profit.

Keywords: intercrops, competition, PLER, cereal, legume, relative density, relative sowing time, nitrogen fertilizer, meta-analysis

Introduction

Intercropping (i.e. the mixed cultivation of crop species) is a traditional agronomic practice that is widely used by smallholder farmers in Asia, Africa and Latin America (Vandermeer, 1992; Lithourgidis et al., 2011). Intercropping is also drawing increasing interest as a strategy for increasing productivity and sustainability of mechanized western crop production systems, e.g. through incorporation of legumes in cereal production systems (e.g. Dhima et al., 2007; Lithourgidis et al., 2007; Bedoussac and Justes, 2010; Pelzer et al., 2012). There are many types of intercrops, including mixtures of two cereals, mixtures of two legumes, as well as mixtures of a cereal and a legume or non-legume (Li et al., 2013; Yu et al., 2015). Mixtures of a cereal and a legume are by far the most common type of intercrop (Rao et al., 1987).

Cereals and legumes are complementary in their acquisition of nitrogen because legumes can fix nitrogen from air through symbionts in addition to using soil N, while cereals acquire nitrogen only from the soil (Jensen, 1996; Hauggaard-Nielsen and Jensen, 2001; Chu et al., 2004; Corre-Hellou et al., 2006). Nitrogen fixation from air is critical if there is little N available from the soil. Acquisition of soil N by the cereals may reduce the availability to the legumes and trigger the legumes to fix more N from the air (Lambers et al. 2008). Nitrogen fixation from the air is also seen as a step in making agriculture more sustainable because it circumvents the need for industrial nitrogen fixation based on fossil energy (Courty et al., 2015; Duc et al., 2015).

The different N acquisition strategies of the cereals and the legumes offer opportunity for complementarity, which could result in a high relative yield for each species (little reduction from competition), and a high relative yield total of the mixture. The relative yield of each species is considered a useful index for the extent to which each species has realized its potential growth, given the conditions and the competition from the other species, while the relative yield total is a useful index for the total niche realized in mixture (Vandermeer, 1992). The extent to which this relative yield total exceeds one is an indicator for complementarity.

The land equivalent ratio (LER) is widely used to characterize the land use efficiency in intercropping. LER is calculated as the sum of the relative yields of intercropped species in an intercrop, as compared to their sole crops (Mead and Willey, 1980). The value of LER may be interpreted as the land area required to produce the same yields in sole crops as obtained from a unit area of intercrop. An LER greater than one implies that intercropping makes a more efficient use of the land than sole cropping. The partial land equivalent ratio (PLER) is the relative yield of an intercropped species compared to its yield in a sole crop (Ofori and Stern, 1987a). PLER can be interpreted as a measure for the contribution of each species to the efficiency of land use by the system as a whole.

In older literature (e.g. Mead and Riley, 1981), a distinction is made between relative yield (total) and (partial) land equivalent ratio. The premise is that relative yield total should be measured in experimental settings with replacement designs in which the relative density total is one (e.g. De Wit's replacement series; De Wit, 1960), whereas land equivalent ratios are measured in experimental settings with a much wider set of designs, including additive designs with a relative density total of two, and augmentative designs that have a relative density total between one and two. Relative yield (RY) is calculated in the same way as partial land equivalent ratio, while the relative yield total (RYT) is calculated in the same way as the land equivalent ratio. Therefore the distinction between RY and PLER, and between RYT and LER is nowadays seldom made, and we consider it unnecessary and obsolete.

According to the stress gradient hypothesis (SGH) (Brooker et al., 2008), plant-plant interactions depend on the environmental context with negative interactions (competition) dominating under favorable conditions, and positive interactions (facilitation) prevailing under unfavorable conditions. The SGH predicts that at high doses of nitrogen fertilizer, interspecific competition would be dominant in intercrops, whereas at low nutrient inputs, complementary use of N would be dominant. In cereal/legume intercropping, under low nitrogen input conditions, the complementary acquisition of nitrogen from different sources would be dominant (Jensen, 1996) while at high nitrogen input, interspecific competition would lead to a dominance of cereals in the mixture due to the stronger competitiveness of cereals as compared to the companion legumes (Ofori and Stern, 1987a).

The competitiveness of individual species in mixtures might be affected by differences in sowing date. The first-sown species will get a competitive advantage while the second-sown species is likely to have a competitive disadvantage. However, if the sowing delay of the second species is very large, such that its growth period is to a large extent after the growth period of the first species (as in relay intercropping), the suppression on the second species might be minor or transient (Zhang and Li, 2003). The strength of interspecific competition could also be determined by relative plant densities of the mixed species (Ofori and Stern, 1987a; Vandermeer, 1992). Increased density of one intercropped species is likely to increase its competitiveness in the intercrop, and suppress the performance of the associated species (De Wit, 1960; Braakhekke, 1980; Gardiner and Craker, 1981; Fawusi et al., 1982). Although the effects of these agronomic practices (rate of N fertilizer, sowing time and sowing density of intercropped components) on competitiveness of the species in mixtures have been reported, there is a large variation in these effects across studies. There is a lack of quantitative assessment across studies of the extent to which these agronomic practices can influence the performance of individual species in mixtures. Besides, it is not clear how species performance in mixtures is affected by the interplay between these factors.

In this study we conduct a meta-analysis to investigate how performance of cereals and legumes is affected by sowing time, sowing density, rate of N fertilizer and the interactions between these factors in cereal/legume intercrops. PLER is taken as a measure of performance of intercropped species. As PLER is the ratio of yield of one species in an intercrop over yield in the respective sole crop, low yields in sole crops might result in high PLERs. We therefore also explore whether high PLERs are associated with low yields of the sole crops.

Materials and methods

Paper and data selection

Data on yields in cereal/legume intercrops used here are a subset of records from a database built by Yu et al. (2015). From the original database, 552 data records of cereal/legume intercrops were extracted, representing data from 144 experiments out of 77 publications. Each data record provides the PLER of both the cereal and the legume. An experiment was defined as a unique combination of site and year. Within experiments, data records were defined by treatment, including crop species combination, sowing dates, rate of fertilizer application and crop densities. Data were entered into the database using identifiers for the publications, and the experiments, and listing all relevant inputs and outputs (Appendix: Table D1). Not all data records reported all variables mentioned in Table D1. There were some missing values for density of crops (5 out of 552 records) and rate of N fertilizer (92 out of 552 records; Table D1). Data records with missing values of a variable were excluded only from those analyses that required that variable.

Response and explanatory variables

In all analyses, partial land equivalent ratio (PLER), was taken as response variable. PLER is defined as:

$$\text{PLER} = \frac{Y}{M} \qquad (1)$$

where *Y* and *M* represent yield of a species in intercrop and sole crop respectively.

In this meta-analysis, we used four explanatory variables, i.e. (i) relative sowing time (RST, continuous, see Eq. 2 below), (ii) relative density (RD, continuous, see Eq. 3 below), (iii) rate of N fertilizer application in the intercrop (N, continuous), and (iv) Crop type (0 for cereal or 1 for legume). Rates of N fertilizer application and crop type were extracted from the publications while relative sowing time and relative density were calculated.

In many studies, rates of N fertilizer are different between intercrops and sole crops. A categorical variable "**N strategy**" with four levels was defined according to the comparative amounts of N applied in intercrops and sole crops. In strategy 1, all treatments receive the same amount of N fertilizer (n = 243). In strategy 2, the rate of N fertilizer in the intercrop is intermediate between that in the two respective sole crops (n = 43), while in strategy 3, the N rate in the intercrop is equal to the lowest N rate in sole crops (n = 67), and in strategy 4, the N rate in intercrop is equal to the highest N rate used in sole crops (n = 107). For N strategies 2-4, sole cropped cereals usually received more N fertilizer than sole cropped legumes (215 cases out of 217).

Relative sowing time of a species is calculated as the ratio of the difference of sowing time of that species and its companion species divided by its own growing period:

$$\text{RST}_\text{a} = \frac{S_b - S_a}{H_a - S_a} \qquad (2)$$

where RST_a represents relative sowing time of species *a* with respect to species *b*. In the analysis, *a* can represent either the cereal or the legume, while *b* represents the companion species. S_a and S_b represent sowing times of species *a* and *b* in Julian day number, respectively. H_a represents harvesting time of species *a* in Julian day number (Fig. 1). The magnitude of RST_a is the ratio of the difference in sowing time between species *a* and the species it is intercropped with to the growing period of species *a*. For the earlier sown species RST > 0, while for the later sown species RST < 0. RST measures the time, relative to the total growing period, that a species is growing before (after), and therefore without (with) competition from, the companion species. This index is expected to be a useful predictor of the relative yield in the intercrop.

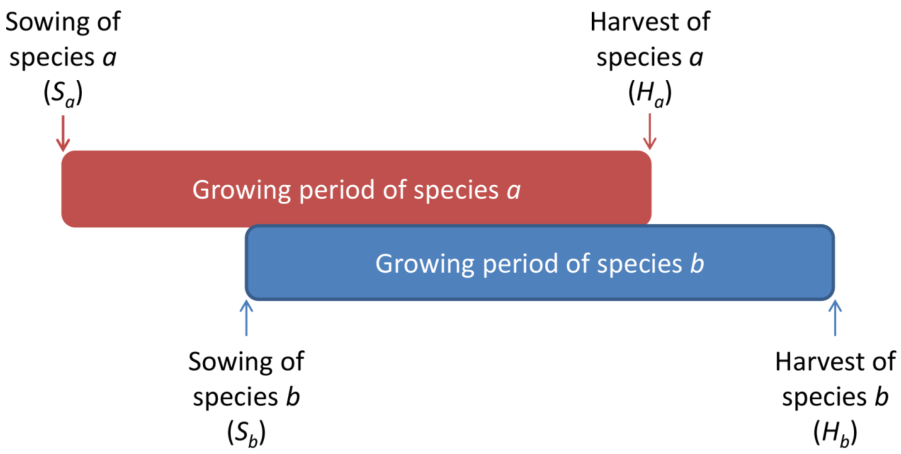

Fig. 1 Illustration of calculation of relative sowing time. The upper bar represents the growing period of the first-sown species (species ***a***) and the lower bar represents the growing period of the second-sown species (species ***b***). The arrows represent sowing and harvesting time of each species in days after sowing of the first sown species. Relative sowing time is calculated as: $RST_a = (S_b-S_a)/(H_a-S_a)$. $RST_a > 0$ means species ***a*** is sown earlier than species ***b***, and vice versa. In the analysis, ***a*** can represent either the cereal or the legume, while ***b*** represents the companion species.

Relative density of a species is calculated as the ratio between the density of that species in intercrop and in its sole crop:

$$\mathrm{RD}_{\mathrm{a}} = \frac{d_{\mathrm{ic,a}}}{d_{\mathrm{sc,a}}} \tag{3}$$

where $d_{\mathrm{ic,a}}$, and $d_{\mathrm{sc,a}}$ are densities of species *a* in the intercrop and sole crop, respectively. Density of a species in intercrop is defined as number of plants of a species per land area of the intercrop. Relative density of an analyzed species is denoted by RD, relative density of the companion species is denoted by $\mathrm{RD}_{\mathrm{associated}}$.

Statistical analysis

Relationships between PLER and explanatory variables, i.c. relative sowing time, relative density and rate of N fertilizer, were estimated for cereals and legumes using mixed effects modelling to account for correlation between data belonging to the same experiment and/or publication (Pinheiro and Bates, 2000; Zuur et al., 2009). Six mixed effects models were formulated (Table 1, models 2-7). All these six models were fitted to the dataset of 1104 (i.e. 2 * 552) PLER records. All analyses were conducted in R (R Core Team, 2013). Mixed effects models were fitted using R function *lme* from R package *nlme* (Pinheiro et al., 2015). Mixed effects models were also used to estimate the relationships between PLERs of cereals and the associated legumes (Table 1, model 1) and between PLER and yield of the corresponding sole crop (Table 1, model 8). The assumption of equal variance for mixed effects models was checked by analyses of quantile plots and plots of residuals against fitted values (Zuur et al., 2009). No violations of assumptions were observed. Figures were made using R packages *plotrix* and *graphics* (Lemon, 2006; R Core Team, 2013).

The PLERs of the cereal and the legume from the same data record might be correlated and have a negative correlation due to the interspecific competition. Therefore, a negative correlation structure of data between the cereal and the legume from the same data record was added in the mixed effects models to account for the correlation using R function *corCompSymm* for the argument of *correlation* in *lme* (Pinheiro and Bates, 2000).

A mixed effects model (Table 1, model 9) was fitted to the data to detect whether the effect of N fertilizer on PLER differed between N strategies. The relationship between PLER of the cereals and PLER of the legumes might be non-linear, and PLER of the cereal should be one when PLER of the legume is zero (i.e. sole crop of cereal) and *vice versa*. Therefore, a non-linear model which could reveal this feature of the relationship between PLER of the cereals and PLER of the legumes (Table 1, model 10) was fitted to the data using R function *gnls* (Pinheiro et al., 2015). The non-linear model is

$$PLER_{\text{cereal},ijk} = \frac{q(1-PLER_{\text{legume},jk})}{1+(q-1)(1-PLER_{\text{legume},ijk})} + \varepsilon_{ijk} \tag{4}$$

A comparison of goodness of fit between the linear mixed effects model (model 1) and the non-linear model (model 10) was conducted with Akaike information criterion (Zuur et al., 2009). In this meta-analysis, we did not use the inverse variance of LER as a weight since there were too few publications reporting measures of variance of yields.

Table 1 List of models fitted to data. The indices *i*, *j* and *k* represent publication, experiment and treatment respectively. In all mixed effects models (models 1-9), a_i is a random publication effect. b_{ij} is a random experiment effect nested within the *i*th publication. a_i and b_{ij} are assumed normally distributed with constant variances. ε_{ijk} is a residual error associated with the *k*th observation in the *j*th experiment in the *i*th publication, assumed normally distributed with constant variance. The variances of a_i, b_{ij} and ε_{ijk} are all assumed independent. The relationship between PLER of the cereal and PLER of the legume was also analyzed using a simple non-linear model (model 10). In the non-linear model, ε_{ijk} is a residual error assumed normally distributed with constant variance.

Model	Explanatory variables	Equation
1	$\text{PLER}_{\text{legume}}$	$\text{PLER}_{\text{cereal},\,ijk} = \beta_0 + \beta_1 * \text{PLER}_{\text{legume},\,ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
2	RST, Crop type	$\text{PLER}_{ijk} = \beta_0 + \beta_1 * \text{RST}_{ijk} + \beta_2 * \text{Crop type}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
3	RD, RDassociated, Crop type	$\text{PLER}_{ijk} = \beta_0 + \beta_1 * \text{RD}_{ijk} + \beta_2 * \text{RDassociated}_{ijk} + \beta_3 * \text{Crop type}_{ijk} + \beta_4 * \text{RD}_{ijk} * \text{RDassociated}_{ijk} + \beta_5 * \text{RD}_{ijk} * \text{Crop type}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
4	N, Crop type	$\text{PLER}_{ijk} = \beta_0 + \beta_1 * \text{N}_{ijk} + \beta_2 * \text{Crop type}_{ijk} + \beta_3 * \text{N}_{ijk} * \text{Crop type}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
5	RD, RST, Crop type	$\text{PLER}_{ijk} = \beta_0 + \beta_1 * \text{RD}_{ijk} + \beta_2 * \text{RST}_{ijk} + \beta_3 * \text{Crop type}_{ijk} + \beta_4 * \text{RD}_{ijk} * \text{Crop type}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
6	RST, N, Crop type	$\text{PLER}_{ijk} = \beta_0 + \beta_1 * \text{N}_{ijk} + \beta_2 * \text{RST}_{ijk} + \beta_3 * \text{Crop type}_{ijk} + \beta_4 * \text{RST}_{ijk} * \text{N}_{ijk} + \beta_5 * \text{N}_{ijk} * \text{Crop type}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
7	RD, N, Crop type	$\text{PLER}_{ijk} = \beta_0 + \beta_1 * \text{N}_{ijk} + \beta_2 * \text{RD}_{ijk} + \beta_3 * \text{Type}^1_{ijk} + \beta_4 * \text{RD}_{ijk} * \text{Type}^1_{ijk} + \beta_5 * \text{N}_{ijk} * \text{Type}^1_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
8	Yield_sc, Crop type	$\text{PLER}_{ijk} = \beta_0 + \beta_1 * \text{Yield\_sc}_{ijk} + \beta_2 * \text{Crop type}_{ijk} + \beta_3\ \text{Crop type}_{ijk} * \text{Yield\_sc}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
9	N, N strategy*, Crop type	$\text{PLER}_{ijk} = \beta_0 + \beta_1 * \text{N}_{ijk} + \beta_2 * \text{N strategy}^2_{ijk} + \beta_3 * \text{N strategy}^3_{ijk} + \beta_4 * \text{N strategy}^4_{ijk} + \beta_5 * \text{Crop type}_{ijk} + \beta_6 * \text{N}_{ijk} * \text{N strategy}^2_{ijk} + \beta_7 * \text{N}_{ijk} * \text{N strategy}^3_{ijk} + \beta_8 * \text{N}_{ijk} * \text{N strategy}^4_{ijk} + \beta_9 * \text{N}_{ijk} * \text{Crop type}_{ijk} + \beta_{10} * \text{N strategy}^2_{ijkl} * \text{Crop type}_{ijk} + \beta_{11} * \text{N strategy}^3_{ijk} * \text{Crop type}_{ijk} + \beta_{12} * \text{N strategy}^4_{ijk} * \text{Crop type}_{ijk} + \beta_{13} * \text{N}_{ijk} * \text{N strategy}^2_{ijk} * \text{Crop type}_{ijk} + \beta_{14} * \text{N}_{ijk} * \text{N strategy}^3_{ijk} * \text{Crop type}_{ijk} + \beta_{15} * \text{N}_{ijk} * \text{N strategy}^4_{ijk} * \text{Crop type}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$
10	$\text{PLER}_{\text{legume}}$	$\text{PLER}_{\text{cereal},\,ijk} = q*(1 - \text{PLER}_{\text{legume},\,ijk})/(1+(q-1)*(1 - \text{PLER}_{\text{legume},\,ijk})) + \varepsilon_{ijk}$

* N strategy is a categorical variable with four levels. N strategy 1: intercrop and both sole crops receive the same amount of N fertilizer, N strategy 2: the rate of N fertilizer in the intercrop is intermediate between that in the two respective sole crops, N strategy 3: the N rate in the intercrop is equal to the lowest N rate in sole crops, N strategy 4: the N rate in intercrop is equal to the highest N rate in sole crops. The superscript of N strategy in model 10 distinguishes the estimates of parameters for each level of N strategy.

Results

Characteristics of cereal-legume intercrops

On average, intercrops were more efficient in land use than the corresponding sole crops, with 434 out of 552 calculated LER values larger than 1 (Fig. 2a). The median LER was 1.16 (Fig. 2b), the mean 1.17 and the standard deviation 0.24, indicating substantial variation of LER over treatments, experiments and publications. More than 90 percent of the intercrops in the database received less than 100 kg/ha N fertilizer (Fig. 3a) and about 80 percent of the intercrops were sown simultaneously, i.e. RST equal to zero (436 out of 552 cases, Fig. 3b, c). Each data record provides yield and relative yield of both cereal and legume. Among the 116 cases with an RST not equal to zero, the cereals were sown earlier than the legumes in 71 cases, and in 45 cases the cereals were sown later than the legumes (Fig. 3b, c).

Competitiveness of individual species in cereal/legume intercrops

PLER of the cereals was greater than that of the legumes in ~75% of the cases (409 out of 552 cases) indicating that the competitiveness of cereals is normally higher than that of legumes in a mixture. A high PLER of the cereal corresponded with a low PLER of the legume and *vice versa* (Fig. 4). We chose a linear model to represent the

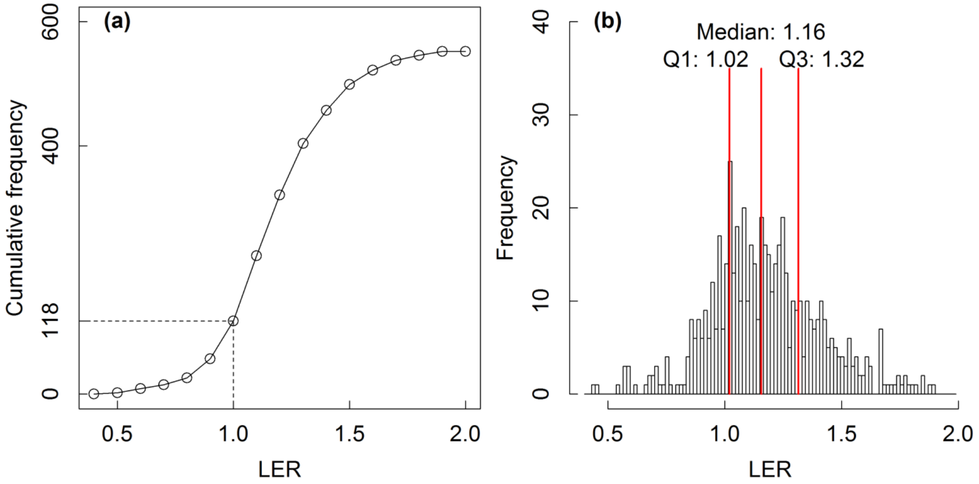

Fig. 2 Cumulative frequency (a) and frequency distribution (b) of land equivalent ratios (LER) for cereal/legume mixtures.

relationship between PLER of the cereal and the legume since the goodness of fit of the linear model (model 1) was better than that of the non-linear model (model 10) according to Akaike's information criterion. One unit increase of PLER of the legume resulted in 0.605 unit decrease of PLER of the cereal (model 1, β_1=0.605, SE=0.035, P<0.001, Fig. 4).

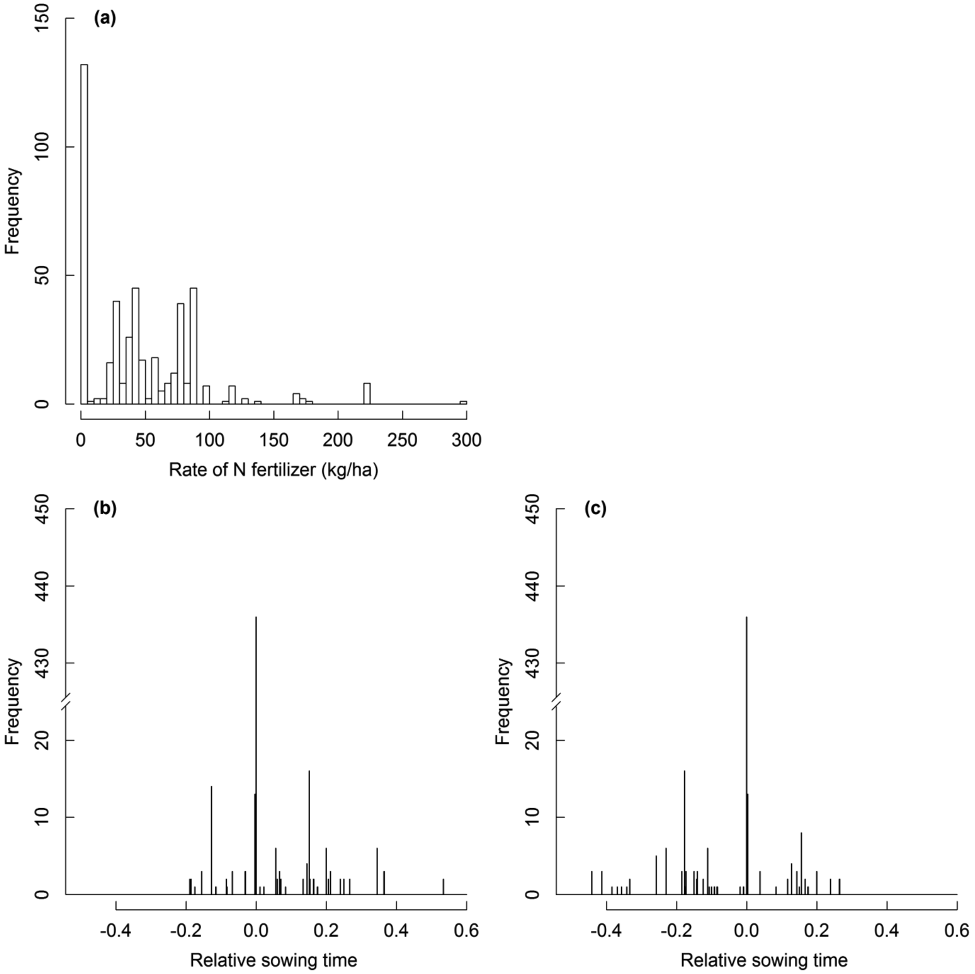

Fig. 3 Frequency distribution of the rate of N fertilizer on intercropping (a) and relative sowing time of the cereal (b) and the legume (c) in intercrops. (Note the broken y-axis.)

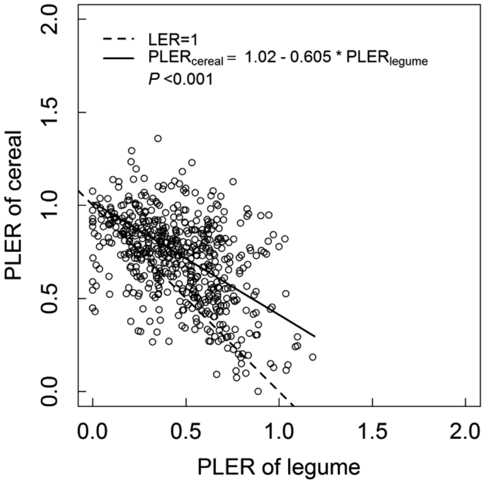

Fig. 4 Scatter plot of partial land equivalent ratio (PLER) of the cereal against PLER of the legume in analyzed intercrops. The broken line represents a theoretical negative relationship with a slope of 1 between the two PLERs, the solid line represents the observed relationship between $PLER_{cereal}$ and $PLER_{legume}$ as fitted by mixed effects model 1: $PLER_{cereal,ijk} = \beta_0 + \beta_1 *PLER_{legume,ijk} + a_i + b_{ij} + \varepsilon_{ijk}$.

Effect of relative sowing time on PLER

Earlier sowing as compared to the companion species increased PLER for both the cereals and the legumes (Fig. 5). The effect of relative sowing time on PLER was not significantly different between the cereals and the legumes. Therefore, a model with a common slope for cereals and legumes (model 2) was fitted to the data. Increase of one unit in relative sowing time resulted in an increase of 0.7 unit of PLER (model 2, $\beta_1 = 0.7$, SE = 0.15, $P < 0.001$) for both cereals and legumes.

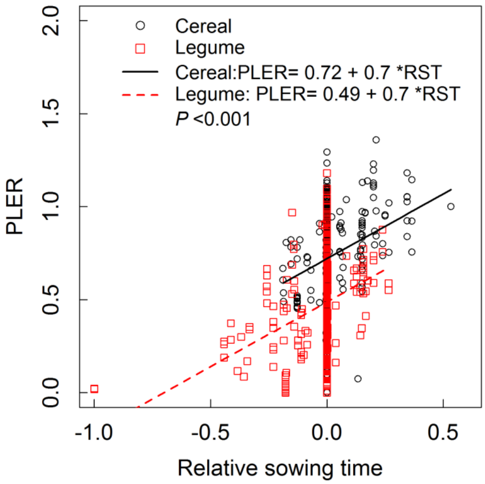

Fig. 5 Effect of relative sowing time (RST) on partial land equivalent ratio (PLER) of cereals (black circles) and legumes (red squares). The solid and broken line respectively represent relationships between PLERs of cereals and legumes and their relative sowing time fitted by mixed effects model 2: $\text{PLER}_{ijk} = \beta_0 + \beta_1 {*}\text{RST}_{ijk} + \beta_2 {*}\text{Crop type}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$.

Effect of relative density on PLER

A significant positive effect of relative density on PLER was observed for both cereals (model 3, $\beta_1 = 0.35$, SE = 0.06, $P < 0.001$) and legumes (model 3, $\beta_1 + \beta_5 = 0.22$, SE = 0.06, $P < 0.001$). The effect of relative density on PLER was stronger in cereals than in legumes (model 3, $\beta_5 = 0.13$, SE = 0.04, $P = 0.002$). On the other hand, there was a negative relationship between PLER of a species and the relative density of the associated species in both cereals and legumes (model 3, $\beta_2 = -0.36$, SE = 0.06, $P < 0.001$, Fig. 6), i.e. increasing relative density of one species decreased PLER of the associated species. There was no difference in this negative effect between cereals and legumes. This result supports the hypothesis that increasing density of one species in a mixture increases its relative yield while decreasing the relative yield of the associated species.

There was a significant positive interaction between the relative density of an analyzed species and the relative density of the associated species on PLER of the analyzed species (model 3, $\beta_4 = 0.16$, SE = 0.07, $P = 0.03$). This positive interaction indicates that the negative effect of relative density of the associated species on PLER of the analyzed species is mitigated by increased relative density of the analyzed species.

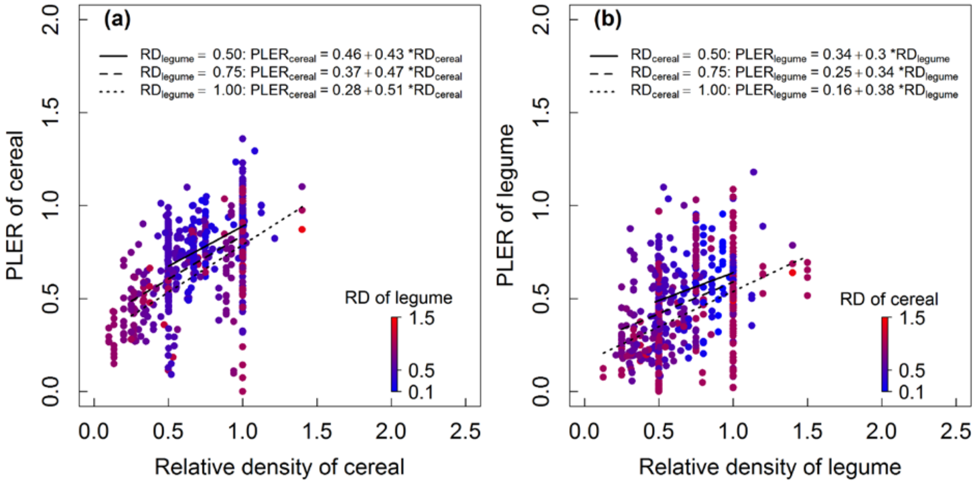

Fig. 6 Linear functions relating partial land equivalent ratio (PLER) of cereals (a) and legumes (b) to relative densities of both cereals and legumes fitted by mixed effects model 3: $PLER_{ijk} = \beta_0 + \beta_1{*}RD_{ijk} + \beta_2{*}RDassociated_{ijk} + \beta_3{*}Crop\ type_{ijk} + \beta_4{*}RD_{ijk}{*}RDassociated_{ijk} + \beta_5{*}RD_{ijk}{*}Crop\ type_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$. The colors of dots represent relative density of the companion species, i.e. either legume (a) or cereal (b), from low (blue) to high (red).

Effect of N fertilizer applicate on PLER

We found a significant negative effect of N fertilizer application rate on PLER of legumes (model 4, $\beta_1 + \beta_3 = -0.0013$, SE = 0.0002, $P < 0.001$, Fig. 7). PLER of legumes decreased 0.13 unit when the rate of N fertilizer application was increased with 100 kg/ha. PLER of cereals increased slightly with N fertilizer (model 4, $\beta_1 = 0.00058$, SE = 0.00023, $P = 0.01$, Fig. 7). This finding is in line with the hypothesis that increasing the rate of N fertilizer leads to an increase in the relative performance of the cereals but a decrease for the legumes.

The effect of N was not expected to be different between different N strategies. However, the results showed some pattern in cereals (Fig. D1a). There was a slight positive effect of N on PLER of the cereals for strategies 1 (equal rate of N in intercrop and sole crops) and 2 (N in intercrop intermediate between sole crops). However, for strategy 3 (N in intercrop equal to lowest level in sole crops), there was a strong positive effect of N fertilizer on PLER while there was a strong negative effect of N fertilizer on PLER with strategy 4 (N in intercrop equal to the highest level in sole crops) (Fig. D1a). This pattern is mainly due to confounding between the rate of N and the relative density of cereals in strategies 3 and 4. For strategy 3, low N plots of the cereals were also those with low relative density, that the apparent N effect was therefore driven by the relative density. The reverse held for strategy 4 where a low rate of N was associated with a higher relative density of the cereals compared to the treatments receiving higher rate of N. The effect of N fertilizer on PLER of the legumes was consistently negative (Fig. D1b).

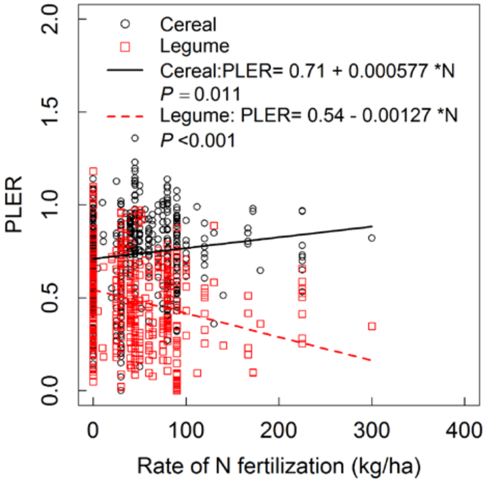

Fig. 7 Effect of N fertilizer application on partial land equivalent ratios (PLER) of cereals (circles) and legumes (squares). The solid and broken lines respectively represent relationships between PLER and rate of N fertilizer application for cereals and legumes fitted by mixed effects model 4: $PLER_{ijk} = \beta_0 + \beta_1{*}N_{ijk} + \beta_2{*}\text{Crop type}_{ijk} + \beta_3{*}N_{ijk}{*}\text{Crop type}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$.

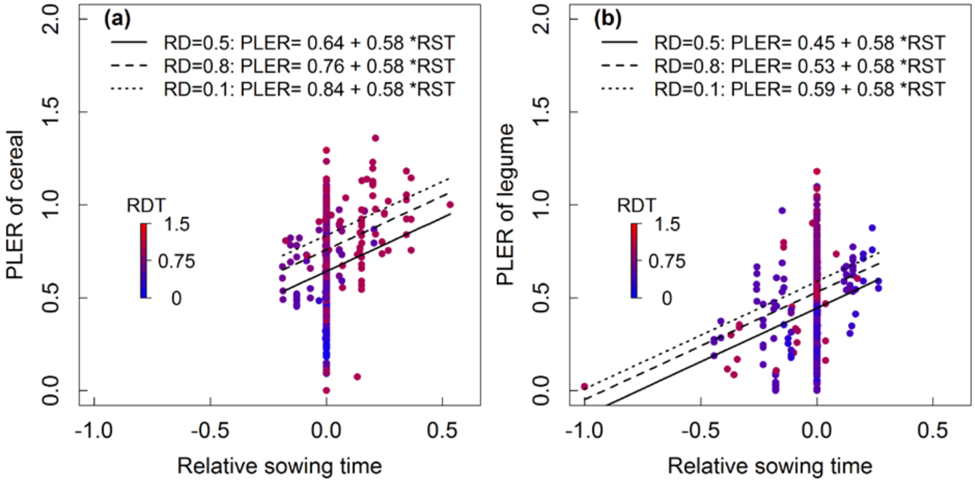

Fig. 8 Linear functions relating the partial land equivalent ratio (PLER) to the relative sowing time and relative density for cereals (a) and legumes (b) fitted by a mixed effects model 5: $PLER_{ijk} = \beta_0 + \beta_1{*}RD_{ijk} + \beta_2{*}RST_{ijk} + \beta_3{*}\text{Crop type}_{ijk} + \beta_4{*}RD_{ijk}{*}\text{Crop type}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$. The colors of dots represent relative densities from low (blue) to high (red).

Interactions between factors

No interaction between RST and RD was found for either cereals or legumes. A model with RST and RD but without interaction was therefore fitted to the dataset (model 5). For cereals (Fig. 8a) and legumes (Fig. 8b), both the effects of RD ($\beta_1 = 0.39$, SE = 0.03, $P < 0.001$ and $\beta_1 + \beta_4 = 0.29$, SE = 0.03, $P < 0.001$ respectively) and of RST ($\beta_2 = 0.58$, SE = 0.07, $P < 0.001$) were positive and significant. These results indicate that relative sowing time and relative density of the species in mixtures may be adjusted to achieve desired PLERs of the cereals and the legumes according to production aims.

A positive interaction effect of N rate and relative sowing time on PLERs of cereals and legumes was expected. In other words, we expected that the positive effect of N fertilizer on competitiveness of cereals would be enhanced by sowing cereals earlier than legumes while the negative effect of N on competitiveness of legumes would be alleviated by sowing legumes earlier than cereals. Indeed, a positive interaction between the relative sowing time and the rate of N fertilizer was found in both the cereals and the legumes (model 6, $\beta_4 = 0.0051$, SE = 0.0021, $P = 0.017$, Fig. 9). For the cereals, there was a slight positive effect of N fertilizer on PLER when the two intercropped species were sown simultaneously, i.e. RST = 0 (model 6, $\beta_1 = 0.00064$, SE = 0.00022, $P = 0.003$). The positive interaction between RST and the rate of N fertilizer for the cereals indicates that sowing legumes later than the cereals enhances the positive effect of N fertilizer on PLER of cereals. For legume species, there was a negative effect of N fertilizer on PLER when the legumes were sown simultaneously with the cereals (model 6, $\beta_1 + \beta_5 = -0.0014$, SE = 0. 00022, $P < 0.001$). However, this negative effect was alleviated by sowing the cereals later than the legumes.

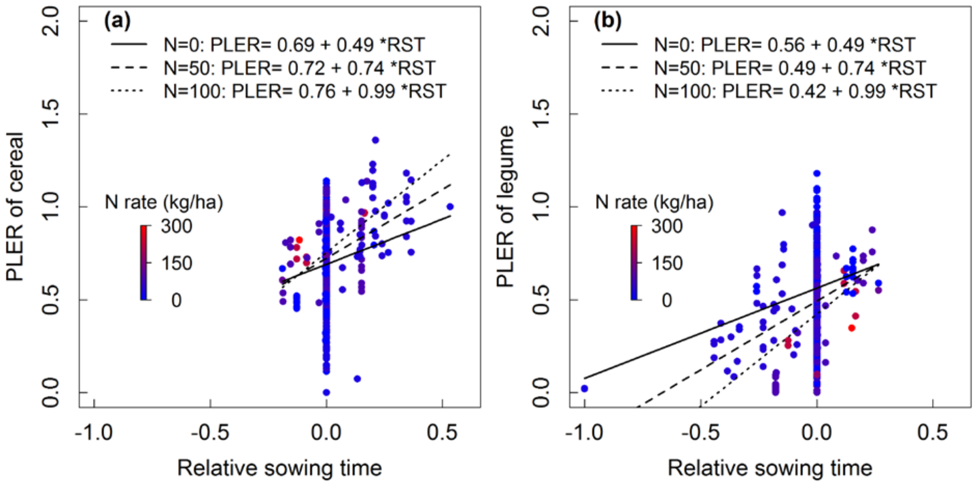

Fig. 9 Relationships of partial land equivalent ratio (PLER) to relative sowing time and rate of N fertilizer application for cereals (a) and legumes (b). Relationships were analyzed by fitting mixed effects model 6: $PLER_{ijk} = \beta_0 + \beta_1{*}N_{ijk} + \beta_2{*}RST_{ijk} + \beta_3{*}\text{Crop type}_{ijk} + \beta_4{*}RST_{ijk}{*}N_{ijk} + \beta_5{*}N_{ijk}{*}\text{Crop type}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$. The colors of dots represent N fertilizer rates from low (blue) to high (red).

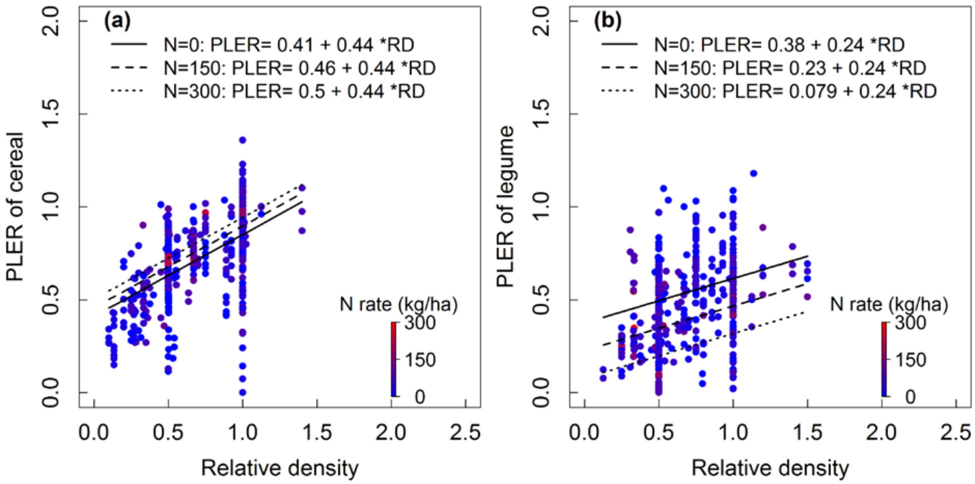

Fig. 10 Relationships of partial land equivalent ratio (PLER) with relative density and rate of N fertilizer for cereals (a) and legumes (b). Relationships were analyzed by fitting mixed effects model 7: $PLER_{ijk} = \beta_0 + \beta_1{*}N_{ijk} + \beta_2{*}RD_{ijk} + \beta_3{*}\text{Crop type}_{ijk} + \beta_4{*}RD_{ijk}{*}\text{Crop type}_{ijk} + \beta_5{*}N_{ijk}{*}\text{Crop type}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$. The colors of dots represent N fertilizer rates from low (blue) to high (red).

We expected that increasing N fertilizer in intercrops would enhance the positive effect of relative density on relative performance of the cereals but decrease the density effect for the legumes. However, the results showed no interaction between relative density and rate of N on PLER for either the cereals or the legumes (model 7, Fig. 10).

Relationship between PLER and yield of corresponding sole crops

A negative relationship between PLERs of both the cereals and the legumes and yields in sole crops was hypothesized, as low yields of sole crops would result in high PLERs. For the cereal species, indeed, a slight negative effect of sole crop yield on its PLER was observed (model 8, $\beta_1 = -0.007$, SE = 0.0024, $P = 0.04$, Fig. 11a) however this did not seem to be related to a high PLER at low sole crop yields, but rather to a low PLER with some extremely high sole crop yields of C4 fodder cereals e.g. maize or millet, harvested as whole plants. For the legume species there was no effect of sole crop yield on PLER (model 8, $\beta_1+\beta_3 = 0.0023$, SE = 0.0029, $P = 0.44$, Fig. 11b). Our results indicate therefore that in the sampled intercropping literature, PLER was not biased by low yield of sole crops.

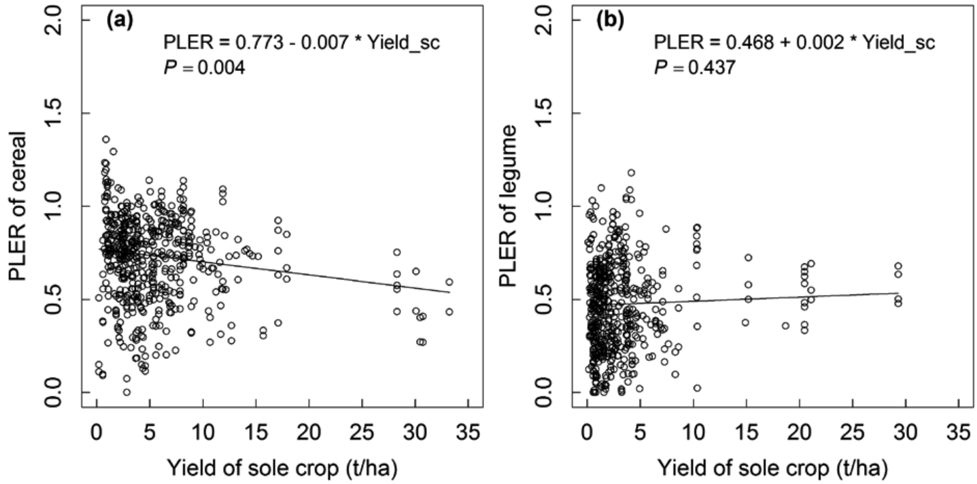

Fig. 11 Relationships between partial land equivalent ratio (PLER) of cereals (a) or legumes (b) and yield of their respective sole crops. The lines represent relationships between PLER and sole crop yields fitted by mixed effects model 8: $\text{PLER}_{ijk} = \beta_0 + \beta_1 * \text{Yield\_sc}_{ijk} + \beta_2 * \text{Crop type}_{ijk} + \beta_3 * \text{Crop type}_{ijk} * \text{Yield\_sc}_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$.

Discussion and conclusion

This is the first meta-analysis to quantitatively assess the effects of agronomic management levers (sowing date, density, N fertilizer) on the relative performance of the cereals and legumes in mixtures. We showed that sowing time is a key factor determining species competitiveness. Sowing one species earlier increases its competitiveness and decreases the competitiveness of the later sown species. Besides, we confirmed the hypothesis that increasing relative density of a species increases its performance while decreasing the performance of the associated species in a mixture. Furthermore, we showed that application of N in cereal/legume intercrops increases the competitiveness of the cereals but decreases that of the legumes. A positive interaction between relative sowing time and rate of N fertilizer was found for both the cereal and the legume. For the cereals, the positive interaction means that sowing the cereals earlier enhances the positive effect of N fertilizer, while for the legumes the positive interaction means that sowing the legumes earlier mitigates the negative effect of N fertilizer. Finally, we showed that partial land equivalent ratio values were not biased by low yields of sole crops.

Competitive balance in species mixtures

In species mixtures, competition between species is always present as the plants require the same growth resources, e.g. water, nutrient and light. While nutrients and water may be supplied at a level that they are no longer limiting, competition for them being negligible, the same is not true for light, because the interception of light by one species in a closed stand goes inevitably at the expense of light interception by another species. The strength of competition depends on the similarity of the patterns of resource acquisition in time and space between the species in the mixture. The species of similar spatial and/or temporal niche tend to compete intensively, which in turn, would result in reduced biomass and seed production of the relatively weaker species. In natural systems this could lead to extinction of the weaker species (Vandermeer, 1992), while in agricultural systems this could mean failure of one of the two crops. The competitive balance, i.e. equal/similar competitiveness of the mixed species plays an important role in maintaining high productivity of the community (Yachi and Loreau, 2007) and LER values greater than one in intercrops. Therefore, understanding how the competitiveness of the mixed species changes with the environment is important for achieving a high productivity in a mixture.

In this study, we showed that in general, the cereals achieve higher relative yields than the legumes in cereal/legume intercrops. This balance depends on the sowing times of the species relative to one another (relative sowing time, RST). We showed that separating the growing period of the cereals and the legumes results in a stronger competitiveness of the early sown species and a weaker competitiveness of the late sown one as compared to the corresponding species in an intercrop in which two species are sown simultaneously. Therefore, to maintain the competitive balance in cereal/legume intercrops, sowing the legumes earlier than the cereals would be one option, though other agro-ecological demands of the species (e.g. a difference in optimal growth temperature in relation to the spring-summer sequence) should obviously also be considered.

Many studies have shown that application of N fertilizer in cereal/legume intercrops would increase the competitiveness of the cereals, very likely leading to a competitive imbalance and a failure of legumes in mixtures (Ofori and Stern, 1986; Ofori and Stern, 1987b; Cowell et al., 1989; Tobita et al., 1994; Pelzer et al., 2014). This meta-analysis confirmed the negative effect of N fertilizer on competitiveness of the legumes. The negative effect of N fertilizer on the legumes might be one of the reasons that researchers state that intercropping is mainly important in low-input agriculture (e.g. Brooker et al., 2015). However, we show there are options to combine higher N rates with maintained production gains of intercropping because of the positive interaction between relative sowing time and N fertilizer. This interaction indicates that the negative effect of N fertilizer on the legumes can be alleviated by sowing the legumes before the cereals. This finding may be used to further integrate legumes in modern high-input agricultural systems.

Implications for the design of productive intercrops

This study shows how an increase in competitiveness of one species results in a decrease in competitiveness of the companion species. To increase productivity of intercrops, it is important to achieve a greater increase in performance of one species associated with a smaller decrease in performance of the companion species resulting overall in complementarity within the system. The results of this study suggest possibilities for achieving higher intercropping productivity by manipulating the agronomic practices including sowing time, sowing density and rate of N fertilizer in cereal/legume intercrops.

In this study, we showed an identical effect of relative sowing time on PLER for cereals and legumes. The positive effect of sowing one species earlier on its relative yield is canceled out by the negative effect of delayed sowing of the companion species, which results in an overall null effect on productivity of the system as a whole. However, this is only true when the span of growing periods of intercropped species are identical. For instance, in a cereal/legume intercrop, the growth period of both the cereal and the legume is 150 days. Sowing the legume 50 days earlier than the cereal results in a relative sowing time of 0.33 (50/150) for the legume and -0.33 for the cereal. According to the estimated relationship between RST and PLER (model 2, Fig. 5), PLER of the legume increases 0.23 while PLER of the cereal decreases 0.23 with RST, which would suggest no effect on the total productivity (LER). However, if a species with a short growing period is grown together with a species with a longer growing period, sowing the former before the latter would result in an increase in the total productivity of the intercrop due to the greater positive RST for the species with the short growing period as compared to the negative RST for the species with the longer growing period.

It has been shown that application of N in cereal/legume intercrops decreases total productivity of the intercrop when the cereals and the legumes are sown simultaneously (Yu et al., 2015), because the legumes suffer more from the competition with cereals. The finding of a positive interaction between relative sowing time and N rate indicates that combining an early sown short growing period legume with a later sown longer growing period cereal is an option for high-input cropping systems.

Our results show that the relative yield of a species is increased by increasing its density, but at the expense of the relative yield of the companion species. On average, the positive effect of increasing the relative density of the cereal on its relative yield was stronger than the negative effect on the companion legume. The findings altogether imply that increasing density of the cereal species in a cereal/legume intercrop would not only increases the productivity of the cereal but also increase the productivity of the intercrop as a whole.

Conclusion

In this study, we quantitatively assessed how the performance of each species in cereal/legume intercrops is affected by agronomic practices including sowing time, sowing density and rate of N fertilizer as well as the interplay between these factors. These three factors play important roles in determining the relative performance of individual species in cereal/legume intercrops and overall system performance. These findings can be used to design cereal/legume intercrops by fitting the competitive balance with production aims that farmers have related to intercrop productivity. Such aims are related to prices of inputs and outputs and the uses farmers may have for the two products. A next step would be to translate our findings to decision support tools rather than to set rules simply to optimize total yield.

Appendix D

Table D1 List of Variables extracted from publications

Fig. D1 Estimates of relationship between PLER and rate of N fertilizer application for different N application strategies.

Acknowledgements

We thank staff from the crop systems analysis and plant production systems groups of Wageningen University for suggestion how to improve this study. The financial support by China Scholarship Council (CSC) and Key Sino-Dutch Joint Research Project of NSFC (grant number: 31210103906) are gratefully acknowledged.

Chapter 6

General discussion

General discussion

It has been shown that species richness tends to increase primary production in plant communities (Loreau and Hector, 2001; Van Ruijven and Berendse, 2003). In crop production systems, the cultivation of two or more species simultaneously in the same field, i.e. intercropping, has also been observed to be more productive than monoculture (Zhang and Li, 2003; Li et al., 2013). The yield advantage of intercropping is very often evaluated using the land equivalent ratio (LER). LER is calculated as the sum of the relative yield of the intercropped species compared to the respective sole crop. LER thus can be seen as the relative land area required by sole cropping to produce the same yields as achieved in intercropping (Mead and Willey, 1980). Values of LER above one mean intercropping is more efficient in land use than sole cropping and values below one mean intercropping is less efficient. While advantage in efficiency of land use in intercrops has been documented in many studies (e.g. Zhang et al., 2007; Lithourgidis et al., 2011) the pattern and direction in which this increased efficiency is affected by variation in environmental factors, species identity and crop management is still poorly understood. In this thesis, I therefore investigated how temporal niche difference, plant traits, agronomic practices and their interactions affect LER and interspecific interactions between intercropped species in annual intercrops using both meta-analysis (Chapters 2, 3, and 5) and functional-structural plant (FSP) modelling (Chapter 4). According to my knowledge, this is the first thesis combining meta-analysis and FSP modelling to analyze the factors that affect yield advantage in intercropping. This chapter will place the findings of this thesis in a broader context and discuss how the findings can improve our understanding of intercropping.

Does intercropping have advantages over sole cropping?

Many studies have indicated that intercropping is advantageous over sole cropping, having benefits such as higher land and/or resource use efficiency (Reddy and Willey, 1981; Lithourgidis et al., 2011). Intercropping may also suppress pests, diseases and weeds (Ayeni et al., 1984; Trenbath, 1993) as compared to sole cropping. However, reported effects of intercropping vary widely and some studies have found negative effects whereby intercropping performed less well in terms of land use efficiency. While a large number of studies reported LER > 1, e.g. 1.41 in a maize/faba bean (Mei et al., 2012) and 1.36 in a barley/faba bean intercrop (Agegnehu et al., 2006), there are also a couple of studies reporting LER < 1, e.g. 0.77 (wheat/pea, Naudin et al., 2010) , 0.82 (wheat/soybean, Haymes and Lee, 1999), 0.89 (maize/cowpea, Chang and Shibles, 1985). These latter results show that intercropping is not always more efficient in land use than sole cropping. Similar variable results have been obtained for other performance measures. For instance, Marshall and Willey (1983) reported that in a millet/groundnut intercropping, light capture of the whole system was not increased while light conversion efficiency (i.e., growth per unit of absorbed light) of groundnut was enhanced. By contrast, in a wheat/cotton intercropping system, high productivity of intercropping was only attributed to increased light capture while light conversion efficiency was not changed in intercropping (Zhang et al., 2008). The findings illustrate that both the benefits of intercropping and the processes underlying these benefits can vary considerably. To date however, very little systematic research has been done to determine under what conditions intercropping is advantageous over sole cropping or what factors make intercropping advantageous.

This thesis in part fills this knowledge gap as I investigated land use efficiency in intercropping, using LER and tried to generalize which factors determine LER in annual intercrops. Though a large variation in LER was observed in the literature (ranging from ~0.5 to ~2), the estimated mean of LER was 1.22±0.02 which is significantly greater than 1 (Chapter 2). This finding indicates that on average intercropping is 22% more efficient in land use than sole cropping. Many factors however, may be involved in determining the large variation in LER that was observed.

Temporal niche difference drives productivity of species mixtures

Temporal niche difference has been proposed as one of the factors driving the positive effect of species richness on productivity in vegetation stands (Vandermeer, 1992; Tilman, 1999; Loreau, 2000). Temporal niche difference refers to asynchronous life cycle of the species in a mixture resulting in a distinct demand for resources in time (Loreau, 2000), which may allow for temporal complementary use of resources by these species. For example, a species with a short growth cycle mixed with a species with a long growth cycle might complementarily capture the resources e.g. light or nutrients, due to the asynchrony of resource demand, which in turn, would result in a high productivity of the mixture (Zhang et al., 2008). Though the term temporal niche difference is not often used in agricultural research, in practice several cropping systems exist that benefit from this mechanism. Relay intercropping is an exemplary application of the principle of temporal niche difference. In relay intercropping, two or more species grow simultaneously during part of the life cycle of each (Vandermeer, 1992), For instance, in the case of wheat/maize intercrops, wheat is sown in strips in spring and gaps between wheat strips are kept for the late-sown maize; maize is sown in the gaps in summer when the wheat is approaching maturity (Zhang and Li, 2003; Zhu et al., 2014). Such relay intercropping could better exploit the length of the growing season (Lithourgidis et al., 2011) and intercept more light over the whole growing season (Keating and Carberry, 1993; Zhang et al., 2008) than sole crops. Relay intercropping has been widely applied in China. In Northwest China, the area of wheat/maize strip intercropping has been estimated at ~275,000 ha (Li et al., 2001b). More than 65% of cotton was cultivated as a relay intercrop in the Yellow River valley; the total area of wheat/cotton relay intercropping in China has been estimated at ~1.4 million ha (Zhang et al., 2007).

While the potential for temporal niche difference to contribute to productivity of intercrops has been documented there was still little known about the magnitude of this effect and how this in turn was affected by growth conditions and species traits. In this thesis a new index TND was developed to quantify the temporal niche complementarity in annual intercrops, calculated as:

$$TND = \frac{P_{system} - P_{overlap}}{P_{system}} = 1 - \frac{P_{overlap}}{P_{system}} \tag{1}$$

where P_{system} represents the total growing period of the intercrop and P_{overlap} represents the overlap in growing period of the intercropped species. TND quantifies the proportion of the total growing period that the two intercrop species grow as sole crops, i.e. before sowing of the later-sown species or after harvest of the first-harvested species. TND equal to 0 means the two intercropped species are sown and harvested simultaneously, while TND equal to 1 means there is no overlap of growing period between intercropped species.

I found that LER increased by 0.21 unit per unit increase in TND (Chapter 2) and the positive relationship between TND and LER was robust and was not influenced by the factors not included in the analysis, e.g. soil and climate conditions (Chapter 3). This positive effect indicates that relay intercropping results in higher land use efficiency than can be achieved in sole crops and this effect increases with further separation of growing period of intercropped species. Double cropping/sequential cropping in which a second crop is sown after harvest of the first crop is an alternative to relay intercropping when season length allows it. Double cropping is similar to relay intercropping with TND equal to one in terms of sowing sequence, as in both cases two species are grown sequentially on the same field without overlap. However double cropping is different from relay intercropping because two sole crops are sequentially sown full field in double cropping systems while in relay intercropping space is left between the first sown plants for the sowing of the second plants. A maximum theoretical value of LER at a TND approaching 1 was estimated to be 1.39 (Chapter 2), while an LER of 2 can be achieved by double cropping. Higher land use efficiency of double cropping is reasonable since it keeps the land fully covered throughout the growing season but a relay intercrop usually leaves part of the land bare during part of the growing season. Therefore, if climatic conditions such as temperature sum and solar radiation is favorable, double cropping is definitely more efficient in terms of land use than relay intercropping. However, in many climates, the length of the growing season is not sufficient for a second crop. In such a situation, relay intercropping may be the best option to increase land use efficiency for agricultural production.

Functional complementarity matters in species mixtures

Functional complementarity might be another driver for high productivity in mixed cultivation (Cong et al., 2014; Cong et al., 2015). Mixing species with C3 and C4 pathways is an example of functional complementarity increasing plant productivity (Tilman et al., 1997). In most cases C3/C4 mixtures are combinations of a short C3 species and a tall C4 species as C4 species tend to be taller than most C3 species. A mixture of short C3 and tall C4 species might increase light use efficiency resulting from complementary use of light, since the taller C4 species can express its higher photosynthetic capacity associated with its C4 pathway at high light (upper layer of the canopy) while C3 species may perform relatively better at low light (lower canopy layer) (Anten and Hirose, 2003). In this thesis I indeed observed that mixtures of C3 and C4 species have greater LER than C3/C3 combinations (Chapter 2). Furthermore, in the meta-analysis studies (Chapter 2 and 3), I found that C3/C4 intercrops have a stronger response of LER to temporal niche difference than C3/C3 intercrops. Contrary to C3/C4 mixtures, C3/C3 mixtures normally are combinations of two short-stature species. In agricultural systems C3/C4 mixtures most often entail an early-sown C3 species mixed with a late-sown C4 species in which the late-sown tall C4 species is shaded by the early-sown short C3 species during its early growth (Fan et al., 2006; Zhu et al., 2014). A mixture of a C3 (short and early) and a C4 (tall and late) species might achieve better light acquisition than short/short C3 mixtures (Anten and Hirose, 1999) since the early short species may dominate the light capture in early season while the late tall species would recover once overgrowing the short species and dominate in late season, resulting in complementary light acquisition over time. Therefore both the spatial complementarity in light acquisition resulting from combinations of short/tall species and functional complementarity in light use from combining species with C3 and C4 photosynthetic pathways might contribute to the difference in response of LER to temporal niche difference between C3/C3 and C3/C4 mixtures. In a modelling study (Chapter 4), I showed for the first time that both types of complementarity can drive the effect of temporal niche differentiation on productivity in species mixtures but that the effect of functional complementarity is stronger than that of spatial complementarity. These findings help us to design intercrops of species with different traits and temporal arrangement to maximize the complementary effect and minimize the competitiveness, in order to achieve high yield output.

Mixing a legume with a non-legume species is another example of functional complementarity. Such mixtures tend to have greater plant productivity than mixtures that include only legume or non-legume species (Hector et al., 1999). Mixtures of legume and non-legume species might be complementary in acquisition of nitrogen as legumes can capture nitrogen from the air through symbionts in addition to using soil nitrogen, while non-legume species acquire nitrogen only from the soil (Jensen, 1996; Hauggaard-Nielsen and Jensen, 2001). Legume species fix more nitrogen from the air when soil N is limited. In legume/non-legume mixtures, the non-legume species may be a stronger competitor for soil nitrogen than the legume species and may capture most of the soil nitrogen, stimulating the nitrogen fixation of the legume from the air (Jensen, 1996) which would increase nitrogen in the system as a whole. However, according to the stress gradient hypothesis (SGH), plant-plant interactions depend on environmental context with negative interactions, e.g. competition dominating in favorable environments while positive interactions, e.g. complementarity dominate in unfavorable conditions (Brooker et al., 2008; He et al., 2013). In the intercropping context, the SGH would predict dominance of interspecific competition under high N input but greater interspecific complementarity at low N input, e.g. complementary N use strategies in legume/non-legume mixtures. Temporal niche difference which relaxes interspecific competition therefore might work well in a high N input environment but less so in low N input conditions. Nevertheless, it could also be that temporal niche difference would play a role when N is scarce, as it may enable complementary acquisition of N over time. In the meta-analysis studies on LER (Chapter 2 and 3) and PLER (Chapter 5) with data mainly consisting of cereal/legume intercrops, I found that there is a negative effect of N fertilization on LER which is due to the decrease of PLER of legumes when two species were sown and harvested simultaneously (TND = 0), while this negative effect is alleviated by separating the growth period of the mixed species, i.e. increasing temporal niche difference. These results are in line with the stress gradient hypothesis: when growing conditions are favorable (high N input), interspecific competition dominates and high LER can be achieved by having temporal niche difference. On the contrary, when resources are limited (low N input), complementary interactions dominate while increasing temporal niche difference reduces this complementary effect. This finding to some extent contributes to the debate about relevance of complementarity with respect to N uptake in agricultural and natural systems. In agricultural or other ecosystems in which soil is rich in N, the complementary acquisition of N by mixing legume and non-legume species may not have a large positive effect on production. But when temporal niche difference is involved, e.g. when species with asynchronous life cycles are combined, productivity of the mixtures could be increased. By contrast, under conditions where soil N availability is low (e.g. in low input agriculture or in many natural systems), growing legume with non-legume species simultaneously may increase total productivity.

Does a high land equivalent ratio mean high productivity?

Productivity is defined by yield or useful product per unit land area (Connor et al., 2011). A key question is therefore whether intercropping can increase total production per unit area. A “transgressive” overyielding of a mixture is defined as that the total yield in the mixture is greater than the highest yield among the sole crops (Schmid et al., 2008). Indeed transgressive overyielding has been found. For instance, Corre-Hellou et al. (2006) reported that a pea/barley intercrop had greater total yield (6.6 ton/ha) than either sole pea (3.6 ton/ha) or sole barley (5.3 ton/ha), so an overyielding by about 25% as compared to the highest yielding sole crop (i.e., (6.6 – 5.3)/5.3 = 1.245) . On the other hand, as noted above, the land equivalent ratio (LER) is a more widely used index for assessing land use efficiency of intercropping. An LER > 1 means more land area is needed for sole crops to produce the same yield as in intercrop. In the example of Corre-Hellou et al. (2006), the yield of pea in the intercrop was 2.1 ton/ha, and the yield of barley was 4.5 ton/ha. The LER was therefore 1.43 (2.1/3.6+4.5/5.3). A value of 1.43 means that 1.43 ha of land would be needed to produce the same yield as achieved on 1 ha of intercrop when growing pea and barley as sole crops: 2.1 ton pea (0.58 ha) and 4.5 ton barley (0.85 ha).

The question is: does an LER > 1 always imply a transgressive overyielding? That is not always the case. In the database I used for the meta-analysis of LER (Chapter 2 and 3), there were 746 sole- vs intercrop comparisons and in most of the cases (605), LER was greater than 1, while only 292 out of these 605 cases represented transgressive overyielding. However the reverse statement, i.e. transgressive overyielding indicates LER > 1, is always true. Here I define a transgressive overyielding index (TOI) to demonstrate why transgressive overyielding leads to LER > 1. The transgressive overyielding index is calculated as the ratio of total intercropping yield over the maximum sole crop yield:

$$\mathrm{TOI} = \frac{Y_1 + Y_2}{\mathrm{Max}(M_1, M_2)} = \frac{Y_1}{\mathrm{Max}(M_1, M_2)} + \frac{Y_2}{\mathrm{Max}(M_1, M_2)} \tag{2}$$

where Y_1 and Y_2 represent yield of species 1 and 2 in intercrop, and M_1 and M_2 represent the respective yields in sole crop. TOI>1 means that an intercrop is more productive than either of the sole crops (transgressive overyielding). LER is calculated as:

$$\mathrm{LER} = \frac{Y_1}{M_1} + \frac{Y_2}{M_2} \tag{3}$$

$$\text{Given, } \frac{Y_1}{M_1} \geq \frac{Y_1}{\mathrm{Max}(M_1, M_2)} \text{ and } \frac{Y_2}{M_2} \geq \frac{Y_2}{\mathrm{Max}(M_1, M_2)} \tag{4}$$

$$\text{Therefore, } \mathrm{LER} \geq \mathrm{TOI} \tag{5}$$

According to the Eqs 2-5, LER is always greater or equal to TOI. Therefore, when there is transgressive overyielding (TOI > 1), LER must be greater than 1, but if LER > 1, TOI can be smaller than 1.

Species combinations involving the principle of complementarity would probably achieve higher land use efficiency than sole crops. However, such complementarity may not guarantee transgressive overyielding, because of differences in yield potential between species, e.g. in relation to their growth duration. Transgressive overyielding depends on species composition. Mixtures of species with a similar yield are more likely to achieve transgressive overyielding than mixtures of species with different yield levels. Or, from the other perspective, if one of the species in the mixture has much greater yield than the other, transgressive overyielding is not easily achieved. For example, Chu et al. (2004) reported transgressive overyielding from a rice/peanut intercrop, where the sole crop yields of rice and peanut ranged from ~2.5 to 4.5 ton/ha. In such an intercrop, yield of each species in the intercrop is lower than in the respective sole crop due to relative densities (density of one species in intercrop compared to in the sole crop) below 1. However, the yield loss of the species in intercrop due to lower density could well be compensated by yield of the other species if there is complementary resource use in the mixture, resulting in a greater total yield in intercropping than sole cropping. On the other hand, the loss of yield of a high yielding species in an intercrop would not be easily compensated by yield of the lower yielding species in the mixture, even if resource acquisition was complementary, and relative yield total well above one.

Here I used the data for the meta-analysis of LER (Chapter 2 and 3) to link TOI and yield ratio of sole crops, further illustrating the relationship between transgressive overyielding and yield levels of the sole crops. The yield ratio is defined as the ratio of sole crop yields of the highest yielding to the lowest yielding species, when grown as sole crops. The yield ratio is per definition at least one (i.e. if the sole crop yields are the same). A yield ratio equal to 1 means equal sole crop yields of the intercropped species, and a larger yield ratio means a greater difference of yield between the sole crops. The results showed TOI > 1 mainly occurred at yield ratios smaller than 5 (Fig. 1a), indicating that transgressive overyielding can be hardly achieved if sole crop yield of one species is more than four times greater than of the other species.

Transgressive overyielding may be more common in fully additive intercropping (simply adding the two species together without reducing their density in the mixture compared to the sole crops) than in replacement intercropping. For instance, Haymes and Lee (1999) reported transgressive overyielding in wheat/bean intercropping, when plant density in the intercrop was higher than in replacement intercropping. Based on the database for the meta-analysis of LER (Chapter 2 and 3), a mixed effects model ($TOI = \beta_0 + \beta_1 * RDT + a_i + b_{ij} + \varepsilon_{ijk}$) was used to analyze the relationship between transgressive overyielding index (TOI) and relative density total (RDT, the sum of relative densities of intercropped species compared to their respective sole crops). Here a_i is the random effect of publication, b_{ij} is the random effect of experiment, nested in the ith publication, and ε_{ijk} is the residual random error. TOI increased 0.102 unit per unit increase of relative density total ($P < 0.001$, Fig. 1b). This finding indicates that increasing plant density in intercrop may increase its total productivity, enhancing the chance of transgressive overyielding. However, there is still a large unexplained variation in the transgressive overyielding index (Fig. 1b), illustrating the need for further work to investigate what factors determine total productivity in intercropping.

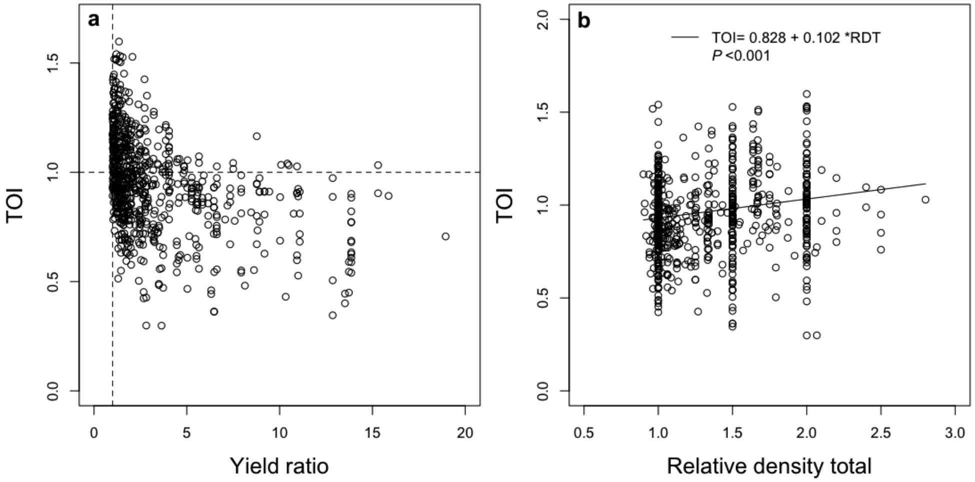

Fig. 1 Scatter plot of transgressive overyielding index (TOI) against the yield ratio of the sole crops (a) and relative density total (b). The yield ratio is defined as the ratio of sole crop yields of the highest yielding to the lowest yielding species, when grown as sole crops. The vertical line in panel a indicate yield ratio equal to 1. The yield ratio is per definition at least one (i.e. if the sole crop yields are the same). Yield ratio equal to 1 means the yields of sole crops are equal and a larger yield ratio indicates a greater difference of yield between the sole crops. The transgressive overyielding index is calculated as the ratio of the total yield in intercropping over the maximum yield in the corresponding sole crops (cf. eq. 2). The horizontal line in panel a indicate TOI equal to 1. TO I> 1 means intercropping is more productive than both of the sole crops. Relative density total equal to 1 means intercropping has the same density as sole crops (replacement intercropping) and greater relative density total indicates a higher plant density in intercropping than in sole cropping. Fully additive intercropping means a relative density of 2. The regression line in panel b is fitted using a mixed effects model: $TOI = \beta_0 + \beta_1 * RDT + a_i + b_{ij} + \varepsilon_{ijk}$. $P < 0.001$ means β_1 is significantly greater than 0.

How can intercropping contribute to modern agriculture?

One of the challenges for modern agriculture is to feed the increasing population with limited arable land while alleviating the environmental impacts of modern agriculture (Tilman et al., 2011). It has been projected that the world's population will reach ~9.15 billion by 2050. Together with shifts in diets (e.g. more meat consumption) and increases in biofuel production, this entails that overall agricultural production will need to increase by an estimated 60 percent between 2005-07 and 2050 (Alexandratos and Bruinsma, 2012). Intercropping has the potential to increase crop production with limited area of cropland as it is in general more efficient in land use than sole cropping. However, the issue is not only about how to feed the increasing population but also related to how to reduce the environmental impact of agriculture. Modern agriculture already imposes major strains on the environment including biodiversity loss due to expansion of agriculture (Dirzo and Raven, 2003), global climate change (Foley et al., 2005) and pollution.

Ecological intensification entailing environmentally friendly replacement of anthropogenic input and/or enhancement of crop productivity is suggested as a means to tackle the issue (Bommarco et al., 2013; Jensen et al., 2015). Intercropping based on ecological mechanisms for increasing resources use may contribute to the ecological intensification of modern agriculture and may reduce anthropogenic inputs and lower environmental impacts without decreasing productivity (Brooker et al., 2015). For instance intercropping is capable of suppressing pests, diseases and weeds, and reducing the corresponding damages to crop production (Trenbath, 1993; Smith and McSorley, 2000; Banik et al., 2006), which in turn leads to a lower need for chemical inputs and the associated environmental impacts compared to sole crops (Lithourgidis et al., 2011). Given the symbiotic nitrogen fixation by legumes, intercropping a non-legume with a legume species is an option to reduce the use of synthetic nitrogen fertilizer and the associated fossil energy consumption and environmental impacts (Lithourgidis et al., 2011). These legume/non-legume intercrops are currently mainly used in organic farming systems which do not allow the use of agricultural chemicals (Bedoussac et al., 2015). All in all, intercropping can play a crucial role in meeting the challenge of global food security by increasing/maintaining crop production with reduced environmental impact. As depicted in the next section however, this potential can only be realized if intercropping is compatible with modern mechanization.

Might intercropping disappear due to lack of mechanization? If so how to reverse the trend?

Intercropping was widely used across the globe until the 1940s (Andersen, 2005; Machado, 2009), likely because of the earlier-mentioned advantages over sole cropping. With the onset of modern mechanization and the increased availability of synthetic inputs for agriculture, this situation changed and growing only one crop in a field became an economically more attractive option (Horwith, 1985). As a result, intercropping gradually disappeared in developed countries (Machado, 2009). By contrast, in developing countries, where access to mechanization and synthetic fertilizer and pesticides is limited for farmers, intercropping is still widely used (Machado, 2009; Lithourgidis et al., 2011). Nevertheless, along with economic development in developing countries, the accessibility to mechanization and agricultural chemicals increases as well, which in turn may drive the farmers to shift from intercropping to sole cropping.

Such a shift has been observed in China. Around one-third of the arable land was used for intercropping in the early 1990s (Zhang and Li, 2003), while the figure strongly decreased in the last two decades. For instance, in the North China Plain, one of the major agricultural regions in China, only five percent of arable land was cultivated by intercropping in 2010 (Feike et al., 2012). The decrease in cultivated area of intercropping can be partly attributed to the migration of labor from agriculture to non-agricultural sectors which is more profitable than agriculture. Due to lack of labor, farm households switch from intercropping to sole cropping which can be more easily mechanized and managed and requires less labor input than intercropping.

Interestingly, interest in intercropping in Europe seems to be reemerging, particularly as the pressure to reduce agricultural inputs, and environmental impact of agriculture is increasing (Bedoussac and Justes, 2010; Pelzer et al., 2012). Even so the eventual adoption of intercropping by farmers depends on the compatibility with modern agricultural practices, particularly mechanization. In the mixtures of cereals and legumes for silage production (Dhima et al., 2007), in which cereals and legumes are fully mixed, sown and harvested simultaneously and where there is no need for post-harvest separation of seeds, mechanization of sowing and harvest using current machinery is not a problem. In more complicated intercropping such as strip or row intercropping in which component species are cultivated in alternative strips or rows, current machines would not work. In this case, there are two possible pathways to adapt intercropping to future demands: either intercropping has to be innovated in a way that at least part of the management practices can be accomplished by existing machinery, or new machinery has to be developed that enables the mechanization of existing systems (Feike et al., 2012). Both pathways require that firstly we find out which species combinations we want to mechanize, e.g. cereal/legume, cereal/cereal, cereal/vegetable, or some other species combinations. The choice of species combinations is determined by the purpose of crop production and the demand of farmers. The second issue involves planting designs and particularly strip width. Generally, wider strips would facilitate mechanized planting and harvesting of crops but they reduce interspecific interactions and thus the potential benefits of niche differentiation and complementarity. The challenge thus lies in finding optimal designs that meet both demands. The selection of intercropping patterns needs efforts from both agronomists and engineers, since agronomists can research what intercropping patterns are most productive while engineers are able to analyze what innovations are needed for which pattern and so which patterns can be mechanized relatively easily.

Some last remarks

Citation bias analysis

One of the novel aspects of this thesis is the analysis of citation bias. I determined whether publications reporting high LERs were cited more often than publications reporting low LERs. If this was the case, a positive relationship would result between the number of citations of a publication and its reported LER. The results show that there is no relationship between number of citations and LER in our dataset, indicating no citation bias in intercropping research (Chapter 2). Researchers do not only cite publications reporting high LERs but also publications reporting low LERs in their studies. Analysis of citation bias is novel and interesting and might be applied to other research areas. If citation bias is detected in certain research topics, then researchers should make their new hypotheses not only based on the findings from publications receiving high citations but also considering the publications with low citations. In this case, an analysis of all publications on the topic is necessary before making new hypotheses, for instance using meta-analysis.

Analysis on temporal niche difference and relative sowing time

In this thesis I analyzed the effect of temporal niche difference on land equivalent ratios (LER) (Chapter 2) and the effect of relative sowing time on partial land equivalent ratios (PLER) of individual species (Chapter 5). There are important differences between these analyses. LER is an index characterizing the land use efficiency of an intercropping system as a whole compared with the respective sole crops. Temporal niche difference (TND) is the factor representing the extent to which the growing periods of intercropped species are asynchronous. The greater the temporal niche difference, the more asynchronous the growing periods of intercropped species are, and consequently the greater the scope for complementarity in resource use. Both LER and TND are indicators for the system as a whole and do not allow a zooming in at the performance of individual species. On the other hand, PLER (relative yield of a species in an intercrop compared to the respective sole crop) can be used to assess the performance of the species within an intercrop. Thereby it allows assessment of the distribution among species of advantages and disadvantages of growing in competition with a different species as neighbor compared to growing with conspecific competitors. Relative sowing time is an index for the proportion of the growth duration of one species that it is sown earlier or later than the companion species in an intercrop. This index is defined with reference to the growth duration of each species separately, not with reference to the aggregate growing period of the two species, as is the case with TND. There are therefore subtle but important differences in the mathematical formulation and ecological interpretation of the metrics and indices that are used in the Chapters 2 and 5. While Chapter 2 focuses on system level performance, Chapter 5 focuses on the species level.

It is important to understand what factors would contribute to high productivity of intercrops. The study of the effect of temporal niche difference on LER (Chapter 2 and 3) investigated how the productivity of an intercropping system as a whole is influenced by temporal niche difference resulting in a complementary use of resources in time. However, the same species combination with the same productivity may end up with different composition of output due to the variable competitiveness of the intercropped species in different environments or when the order of sowing is inversed. It is important to understand the variation in competitiveness of intercropped species for optimizing designs of intercrops according to our demand for different products. The study on competitiveness of intercropped species (Chapter 5) showed that the competitiveness of individual species increases if the species in question is sown earlier than the companion species.

Combination of meta-analysis with FSPM

Meta-analysis is a way of quantitative research synthesis (Koricheva et al., 2013). Meta-analysis is applied to test hypotheses using data from publications with potentially large variation in results. For instance, due to the debate of whether organic agriculture has lower productivity than conventional farming system, meta-analyses were conducted and showed that organic agriculture indeed has lower productivity than conventional agriculture (de Ponti et al., 2012; Seufert et al., 2012). Using meta-analysis, hypotheses can be tested while also new hypotheses may arise. In Chapters 2 and 3, I confirmed the hypothesis that LER responds to temporal niche difference stronger in short C3/tall C4 than in short C3/short C3 intercrops using meta-analysis, but the underlying mechanisms were not clear. In agricultural systems, the short C3 species are normally sown earlier than the tall C4 species. I hypothesized that a combination of a C3 species (short and early) with a C4 species (tall and late) either (i) realizes complementary light acquisition in time due to the height differences (cf. section Functional complementarity matters in species mixtures), or (ii) realizes complementary light use by combing an early C3 (short) with a late C4 (tall) species that is able to use the light in a more efficient way after harvest of the early species or when it outgrows the early C3.

Crop modelling is an effective tool to test the plausibility of new ideas before conducting new experiments based on these new ideas. A concept model can be built to assess possible performance of plants in different environmental settings based on our current knowledge about plant physiology, plant architecture development, plant-plant interactions, and plant-environment interactions. Functional-structural plant (FSP) modelling is a 3D modelling approach which enables simulation of the interplay of plant architecture and the physical and biological processes that drive plant development (Vos et al., 2010; Evers, 2016). FSP models are able to quantify light capture by individual species in mixtures (Zhu et al., 2015) and simulate the dynamic interplay between plant growth, plant-plant interactions and light capture. Though less developed in this regard they can do the same with respect to belowground interactions and soil resources (e.g. Postma and Lynch, 2012; Lobet et al., 2014). In this thesis, an innovative generic FSP model was developed, that incorporates photosynthesis-driven organ growth of plants in a mixed setting, to quantify to what extent plant traits drive spatially and temporally complementary light capture, photosynthesis and productivity in plant mixtures. Using this model, I explored the plausibility of ideas developed from the meta-analysis studies (Chapter 2 and 3). This thesis showed that the combination of meta-analysis and modelling approach is a powerful tool to extend our knowledge, to find patterns among seemingly controversial observations and to understand the underlying mechanisms. Such a powerful combination of methods may not only be applied in intercropping research, but may be adopted more widely in plant ecological research.

Conclusion

Many studies have been conducted on intercropping and have reported a large variation in performance of intercropping systems in terms of productivity, land use efficiency, interspecific interactions etc. There exist a number of possible mechanisms formulated in the ecological literature that would influence performance of species mixtures that seem relevant also for intercropping, e.g. niche differentiation theory entailing complementary use of resources in space and/or time, and stress gradient hypothesis which states plant-plant interactions depend on environmental conditions. However, there was a lack of quantitative synthesis of information from intercropping studies and a need to generalize what factors related to these mechanisms influence the performance of intercropping . As far as I know this is the first thesis using the combination of meta-analysis and FSP modelling to quantify the effects of plant traits, temporal niche difference, and other agronomic practices and their respective interplays on productivity and the interspecific interaction in annual intercrops. I hope that the analyses and datasets assembled in this thesis provide a useful basis for further work demonstrating how diversification of our production systems can help to meet the demand for food and other crop production while moderating environmental impacts of agriculture.

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Appendix A

Temporal niche differentiation increases the land equivalent ratio of annual intercrops: a meta-analysis

Methods A1 Inclusion criteria, and procedure of paper selection and data extraction for the top cited sample and random sample.

Inclusion criteria of publications for the top cited sample are: (1) peer reviewed English language publication, i.e. excluding conference proceedings, (2) reporting primary data, i.e. excluding reviews (3) reporting field data on annual intercrops, thus excluding publications on systems with perennials, (4) reporting yield data on both intercrops and sole crops, (5) reporting treatments in which pests, diseases and weeds had been adequately controlled, (6) intercropping design was either replacement or additive, (7) reporting of sowing and harvesting dates or reporting total duration and overlapping period of intercrops to allow estimating temporal niche differentiation, (8) reporting consistent results, i.e. excluding publications with discrepancies between reported LER and yield data, or inconsistencies between data in different figures and tables. In the case of the top cited sample we selected only those publications that reported information on all key explanatory variables: temporal niche differentiation, rate of N fertilizer, intercropping pattern and plant densities for intercrops and sole crops. The criterion of completeness of data was not applied to the random sample because only few randomly sampled publications reported information on all explanatory variables. This resulted in a lower number of records for some analysis for which records with missing data had to be excluded (see below, Methods A3).

To find the 50 publications for the top cited sample, 420 publications were reviewed and screened according to our criteria for paper selection (Fig. A1). Among these 420 publications, 13 publications were excluded because they were not journal publications in English, 36 publications were excluded because they lacked primary research data, 21 were excluded because they reported results of non-field experiments, 110 were excluded because they only reported on systems with perennial species, and 8 were excluded because the intercrops consisted of more than two species. A large number of publications were excluded (168 publications) due to lack of information on yield. Two publications without disease control and 11 publications having no information on sowing and harvesting date of intercrops were excluded. One publication lacked information on the rate of N fertilizer, intercropping pattern and relative densities. In all remaining 50 publications results were reported consistently.

Similarly, 499 randomly selected publications were reviewed to obtain a random sample (Fig. A1). In this 499 publications, 49 were excluded because they were not journal publications, in English, 3 publications were excluded because they did not report primary research data, 39 were excluded because they reported results of non-field experiments, 61 were excluded because they only reported on systems with perennial species, 3 were excluded because they only reported on intercrops with more than two species, 172 were excluded because of lacking of yield information, 23 publications were excluded because of inadequate control of diseases, pest or weeds, and 98 were excluded because of lack of information to calculate TND. One publication was excluded because results were not consistent. For this second set of publications, selection criteria were less stringent, and papers lacking information on rate of N fertilizer, intercropping pattern or relative densities were not excluded.

A total of 746 data records out of 100 publications published between 1978 and 2012 were used in the meta-analysis.

Methods A2 Inclusion criteria for treatments of the 100 publications.

Inclusion criteria needed to be met at the treatment level; otherwise a treatment would not be included, even if other treatments from the same publication did meet the criteria and were included.

Methods A3 Missing variables of data records in the random sample.

In the random sample, there were 401 data records, while not all of these data records reported all variables of interest. There were records with missing values for rate of N fertilizer, intercropping pattern and relative density total in the random sample (Table A3). Data records with missing values of a variable were excluded only from those analyses that required that variable.

Methods A4 Analysis of the interaction between TND and amount of N fertilizer for three common strategies for supplying N in intercropping experiments.

The interaction between TND and rate of N fertilizer might be different between intercrops that received the same amount of N as the sole crops and intercrops that received a different amount of N than the sole crops. An analysis was conducted to detect whether interaction between TND and rate of N fertilization is different for different N situations using a mixed effects model (model 12 in Table 2): $LER_{ijk} = \beta_0 + \beta_1 * TND_{ijk} + \beta_2 * N_{ijk} + \beta_3 * N\_code\_2_{ijk} + \beta_4 * N\_code\_4_{ijk} + \beta_5 * TND_{ijk} * N_{ijk} + \beta_6 * TND_{ijk} * N\_code\_2_{ijk} + \beta_7 * TND_{ijk} * N\_code\_4_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$. This model was fitted to a subset consisting of three of N_code groups (1, 2 and 4, Table A4). The other three N_code groups were excluded from this analysis, either because the range of TND in the group was too limited for a meaningful analysis (N_code group 3) or because of low number of observations (N_code groups 5 and 6).

Methods A5 Bootstrapping strategy for testing sufficiency of a sample size of 100 publications.

In the bootstrapping strategy, the effect of temporal niche differentiation on LER (parameter β_1) was estimated via a mixed effects model (model 1 in Table 2):

$LER_{ijk} = \beta_0 + \beta_1 * TND_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$

where β_0 is the intercept, β_1 is the slope, a_i is a random study effect, b_{ij} is a random experiment effect and ε_{ijk} is the within study error in LER. Bootstrapping was conducted by sampling with replacement 50, 100, 150, 200, 250 or 300 publications out of the population of 100 publications. The sampling from the 100 publications was replicated 100 times at each bootstrap sample size (50, 100, ..., 300), and the parameter β_1 was estimated 100 times at each sample size. Mean and confidence intervals of the resulting sets of estimated values of β_1 were then plotted against bootstrap sample size and compared to the value of β_1 estimated with the full sample (Fig. A2a).

The same bootstrapping method was applied to models 3-11 in Table 2. Parameters for other main effects and interactions were very little affected by sample size, demonstrating that the sample from the literature was sufficient to obtain robust results (Fig. A2b,c).

Methods A6 Reference list of the 100 publications used in this meta-analysis.

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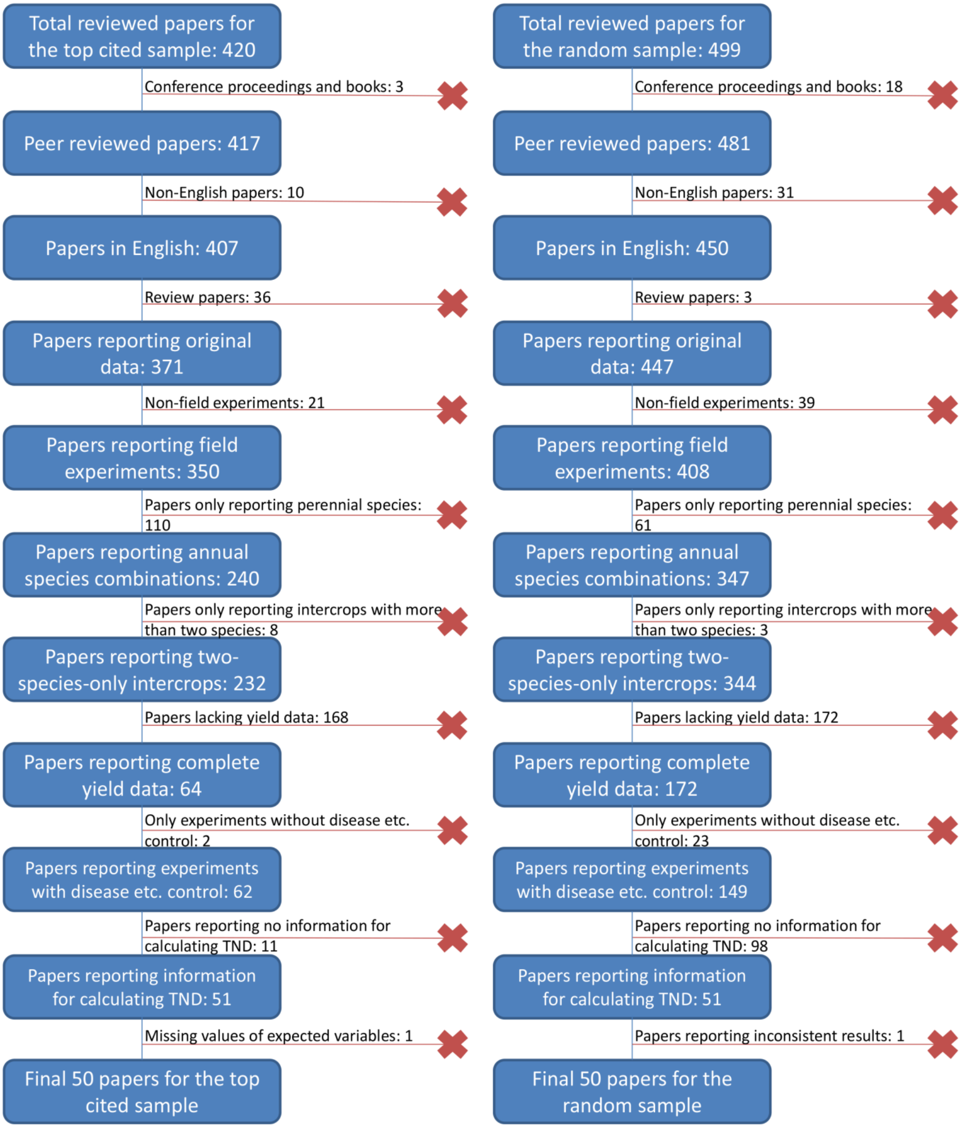

Fig. A1 Paper selection procedure for the top cited publications (left) and the random sample (right).

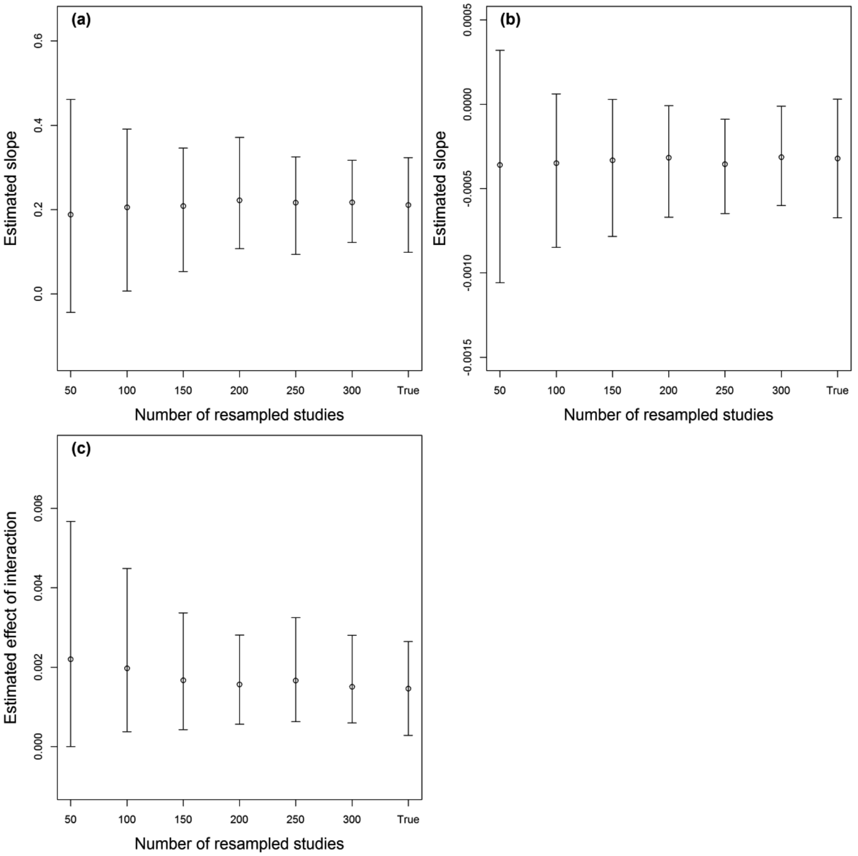

Fig. A2 Bootstrap estimates and confidence intervals for parameters, estimated via a mixed effects models with sample size of 50, 100, 150, 200, 250 and 300 publications sampled with replacement out of the population of 100 publications. Estimate of β_1 of model 1: $LER_{ijk} = \beta_0 + \beta_1 * TND_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$ (a). Estimate of β_1 of model 6: $LER_{ijk} = \beta_0 + \beta_1 * N_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$ (b). Estimate of β_3 of model 10: $LER_{ijk} = \beta_0 + \beta_1 * TND_{ijk} + \beta_2 * N_{ijk} + \beta_3 TND_{ijk} * N_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$ (c). X-axis indicates number of publications used for the estimates of parameters. The label “True” on the X-axis represents the estimates of parameters with the actual samples size of 100 publications. Y-axis represents the value of estimates. For each sample size along the X-axis, resampling was carried out 100 times, thus mean and confidence interval of estimates of parameters were calculated with 100 estimates. Circles represent means of estimates of parameters and error bars represent 95% confidence intervals.

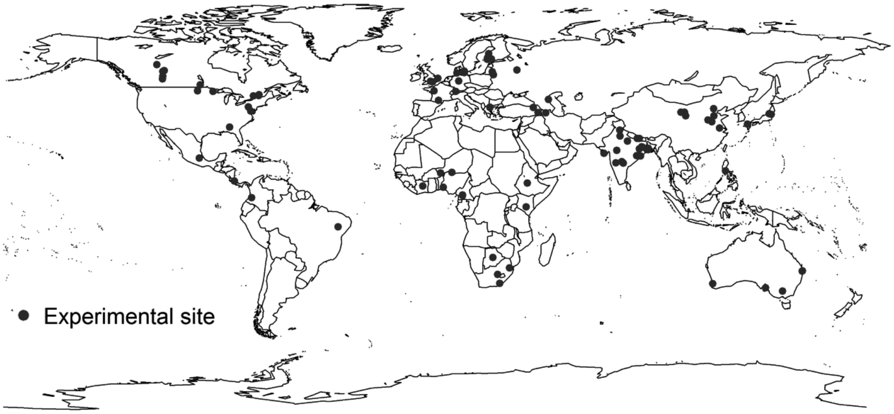

Fig. A3 World map with experimental sites.

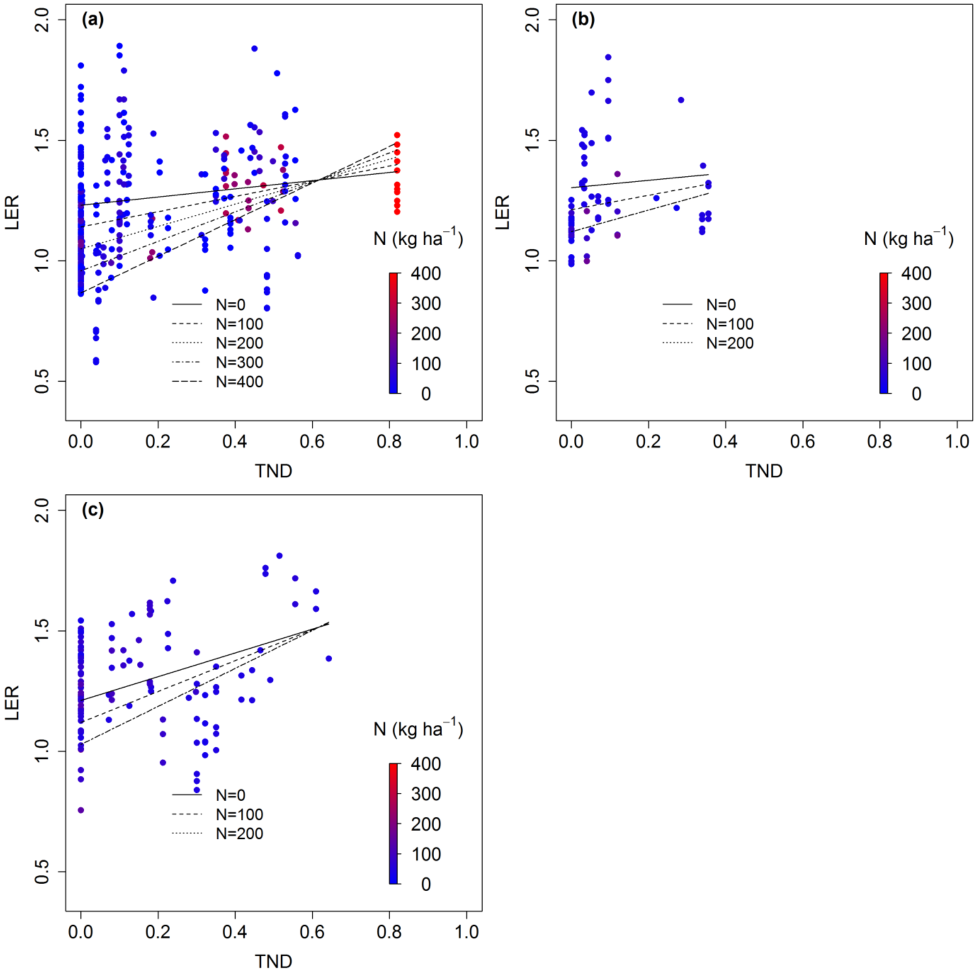

Fig. A4 Scatter plots and linear models relating LER to TND and N for three common strategies for supplying N in intercropping experiments: N_code group 1 (a), group 2 (b) and group 4 (c). Relationship between LER and TND and rate of N fertilization was estimated by model: $LER_{ijk} = \beta_0 + \beta_1 * TND_{ijk} + \beta_2 * N_{ijk} + \beta_3 * N\_code\_2_{ijk} + \beta_4 * N\_code\_4_{ijk} + \beta_5 * TND_{ijk} * N_{ijk} + \beta_6 * TND_{ijk} * N\_code\_2_{ijk} + \beta_7 * TND_{ijk} * N\_code\_4_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$. Regression lines for different rates of N fertilization are presented in each panel.

Table A1 List of the 50 publications in the top cited sample. The column Citations indicates the 10 years citations received between 2003 and 2012 of respective publication.

Reference	Citations	Country	Crop combination
Jensen, 1996	103	Denmark	Barley/Pea
Hauggaard-Nielsen et al., 2001	80	Denmark	Barley/Pea
Bulson et al., 1997	60	England	Bean/Wheat
Li et al., 2001	60	China	Wheat /Soybean and Wheat /Maize
Li et al., 1999	52	China	Pea/Faba bean and Faba bean/Maize
Hauggaard-Nielsen et al., 2003	48	Denmark	Barley/Pea
Hauggaard-Nielsen and Jensen, 2001	46	Denmark	Barley/Pea
Li et al., 2006	43	China	Faba bean/Maize and Wheat /Maize
Ghosh, 2004	36	India	Pearl millet/Groundnut, Sorghum/Groundnut and Maize/Groundnut
Dhima et al., 2007	33	Greece	Oat/Common vetch, Barley/Common vetch, Triticale/Common vetch and Wheat /Common vetch
Andersen et al., 2005	32	Denmark	Barley/Rape, Rape /Pea and Barley/Pea
Baumann et al., 2001	30	Switzerland	Leek/Celery and Leek/Celeriac
Banik et al., 2006	30	India	Wheat /Chickpea
Corre-Hellou et al., 2006	29	France	Barley/Pea
Chu et al., 2004	28	China	Rice/Peanut
Fan et al., 2006	26	China	Faba bean/Wheat and Faba bean/Maize
Agegnehu et al., 2006	25	Ethiopia	Barley/Faba bean
Hauggaard-Nielsen et al., 2006	24	Denmark	Barley/Pea
Reddy and Willey, 1981	22	India	Millet/Groundnut
Awal et al., 2006	20	Japan	Maize/Peanut
Waterer et al., 1994	19	Canada	Pea/Mustard
Song et al., 2007	19	China	Faba bean/Maize, Wheat /Faba bean and Wheat /Maize
Banik et al., 2000	19	India	Mustard/Gram, Mustard/Lentil and Mustard/Pea
Watiki et al., 1993	18	Australia	Cowpea/Maize
Olasantan et al., 1994	18	Nigeria	Maize/Cassava
Zhang et al., 2007	18	China	Wheat /Cotton

Haymes and Lee, 1999	18	UK	Wheat /Field bean
Ghaley et al., 2005	18	Denmark	Wheat /Field bean
Tobita et al., 1994	17	India	Sorghum/Pigeon pea
Carruthers et al., 2000	17	Canada	Maize/Lupin and Maize/Soybean
Lithourgidis et al., 2007	16	Greece	Barley/Vetch and Wheat /Vetch
Knudsen et al., 2004	16	Denmark	Barley/Lupin, Barley/Faba bean and Barley/Pea
Chabi-Olaye et al., 2005	15	Cameroon	Soybean/Maize and Cowpea/Maize
Helenius and Jokinen, 1994	14	Finland	Oat/Faba bean
Carr et al., 1995	14	USA	Wheat /Lentil
Martin et al., 1990	13	Canada	Corn/Corn and Corn/Soybean
Bedoussac and Justes, 2010	13	France	Durum wheat /Winter pea
Jahansooz et al., 2007	13	Australia	Wheat /Chickpea
Gunes et al., 2007	13	Turkey	Wheat /Chickpea
Ofori and Stern, 1986	12	Australia	Maize/Cowpea
Willey and Reddy, 1981	11	India	Pearl millet/Groundnut
Ntare, 1990	11	Niger	Pearl millet/Cowpea
Chowdhury and Rosario, 1994	11	Philippines	Maize/Mungbean
Schmidtke et al., 2004	11	Germany	Barley/Lentil
Akanvou et al., 2002	11	Ivory Coast	Rice/Carribean stylo and Rice/Pigeon pea
Moynihan et al., 1996	10	USA	Barley/Medic
Reynolds et al., 1994	10	Mexico	Wheat /Common vetch and Wheat /Berseem clover
Ofori et al., 1987	9	Australia	Maize/Cowpea
Ofori and Stern, 1987b	9	Australia	Maize/Cowpea
Ofori and Stern, 1987a	8	Australia	Maize/Cowpea

* Publications are listed in order of number of respective citations.

Table A2 List of the 50 publications in the random sample. The column *Citations* indicates the 10 years citations received between 2003 and 2012 of respective publication.

Reference	Citations	Country	Crop combination
Agegnehu et al., 2008	5	Ethiopia	Wheat/Faba bean
Aggarwal et al., 1992	7	Philippines	Rice/Mungbean
Ahmed et al., 2000	0	Japan	Maize/Mungbean
Allen and Obura, 1983	7	USA	Corn/Soybean
Arlauskiene et al., 2011	1	Lithuanian	Triticale/Pea, Oat/Pea, Barley/Pea and Wheat/Pea
Asl et al., 2009	1	Iran	Potato/Pinto bean
Behera et al., 2002	0	India	Rice/Radish and Rice/Okra
Cenpukdee and Fukai, 1992	1	Australia	Cassava/Pigeonpea
Chang and Shibles, 1985	4	USA	Maize/Cowpea
Ciftci and Ulker, 2005	0	Turkey	Barley/Lentil and Wheat/Lentil
Clément et al., 1992	1	Nepal	Maize/Soybean
Das et al., 1991	0	India	Groundnut/Pigeonpea
Dua et al., 2005	1	India	Potato/French bean
Fisher, 1979	2	Kenya	Maize/Beans
Gao et al., 2009	8	China	Wheat/Maize
Gao et al., 2010	4	China	Maize/Soybean
Giri, 1990	1	India	Groundnut/Pigeonpea
Guvenc and Yildirim, 2006	7	Turkey	Cabbage/Cos lettuce, Cabbage/Beans, Cabbage/Onion, Cabbage/Radish and Cabbage/Leaf lettuce
Hummel et al., 2009	3	Canada	Canola/Wheat
Kontturi et al., 2011	2	Finland	Oat/Pea
Kumar and Prasad, 2003	0	India	Maize/Cowpea
Lei et al., 2005	0	China	Corn/Alfalfa and Corn/Rye
Lithourgidis et al., 2011	4	Greece	Triticale/Pea, Rye/Pea and Wheat/Pea
Mandal and Mahapatra, 1990	5	India	Barley/Flax and Barley/Lentil
Mason et al., 1986	3	Australia	Maize/Lablab bean and Maize/Soybean
Mason and Pritchard, 1987	3	Colombia	Cassava/Peanut and Cassava/Cowpea

Mei et al., 2012	0	China	Faba bean/Maize
Miyazawa et al., 2010	5	Japan	Sorghum/Sunflower, Crotalaria/Sunflower and Sorghum/Crotalaria
Mohapatra and Pradhan, 1993	0	India	Maize/Ricebean and Maize/Cowpea
Mondal et al., 2004	0	India	Sesame/Soya bean
Morgado and Willey, 2003	0	UK	Maize/Beans
Morgado and Willey, 2008	4	Brazil	Maize/Beans
Mutsaers, 1978	0	Cameroon	Maize/Groundnut
Nelson et al., 2012	0	Canada	Wheat/Pea, Wheat/Canola and Wheat/Barley
Neumann et al., 2009	0	Germany	Oat/Pea
Ogbuehi and Orzolek, 1987	2	USA	Carrot/Maize
Ong et al., 1991	1	India	Millet/Groundnut
Ossom and Thwala, 2005	0	Switzerland	Maize/Groundnut and Maize/Sugar bean
Prasad and Srivastava, 1991	0	India	Soybean/Pigeonpea
Reddy et al., 1990	4	Nigeria	Millet/Cowpea
Rees, 1986	2	Botswana	Sorghum/Cowpea
Sarkar and Sanyal, 2000	2	India	Sesame/Sunflower, Sesame/Groundnut, Sesame/Blackgram and Sesame/Greengram
Silwana et al., 2007	0	South Africa	Maize/Beans
Singh and Rathi, 2003	3	India	Chickpea/Mustard
Subedi, 1998	0	Nepal	Barley/Peas
Subramanian and Rao, 1988	1	India	Sorghum/Mungbean and Sorghum/Pigeonpea
Teasdale and Deahl, 1987	1	USA	Potato/Snap bean
Tomar et al., 1987	1	India	Pigeon pea/Soybean
Tsubo and Walker, 2004	7	South Africa	Maize/Beans
Vyas et al., 2006	1	India	Pigeon pea/Soybean

* Publications are listed alphabetically according to authors.

Table A3 Availability of information on selected variables in the data set of the random sample.

Variable	Number of publications	Number of experiments	Number of data records
Title	50	102	401
Authors	50	102	401
Continent	50	102	401
Country	50	102	401
Latitude and longitude	50	102	401
Species	50	102	401
Sowing and harvest date	50	102	401
C3/C4	50	102	401
Legume/non-legume	50	102	401
Intercropping pattern	45	88	352
Density of crops	41	80	331
Amount of N fertilizer	30	56	247
Yield	50	102	401

* In the top cited sample, 345 data records with all variables mentioned above were extracted from 87 experiments out of the 50 publications.

Table A4 Coding system for the strategy for supplying N in intercropping experiments. N_{ic} represent amount of N applied in intercrops, $N_{sc,1}$ and $N_{sc,2}$ represent the amount of N applied in sole crops.

N_Code	N in intercrops and sole crops	No. of data records
1	$N_{ic}=N_{sc,1}=N_{sc,2}$	339
2	$\min(N_{sc,1},N_{sc,2}) < N_{ic} < \max(N_{sc,1},N_{sc,2})$	67
3	$N_{ic} = \min(N_{sc,1},N_{sc,2})$	67
4	$N_{ic} = \max(N_{sc,1},N_{sc,2})$	109
5	$N_{ic} > \max(N_{sc,1},N_{sc,2})$	4
6	$N_{ic} < \min(N_{sc,1},N_{sc,2})$	6

Table A5 Contingency table for frequency of intercrops without a legume, or with one or two legumes in the case of C3/C3, C3/C4 and C4/C4 species combinations in the intercrop.

	No legume	**1 legume species**	**2 legume species**	**Total**
C3/C3	63	312	31	406
C3/C4	25	313	0	338
C4/C4	2	0	0	2
Total	90	625	31	746

Appendix B

Robust increases of land equivalent ratio with temporal niche differentiation: A meta-analysis with quantile regression

Fig. B1 Estimates of interactive effect between TND and rate of N fertilizer with two datasets: one dataset with all data reporting N rate, irrespective of N strategies and one subset with only the data of N strategy 1 which is the main N strategy in the database.

Table B1 Variables extracted from publications.

Table B2 Availability of information on selected variables in data set for this meta-analysis.

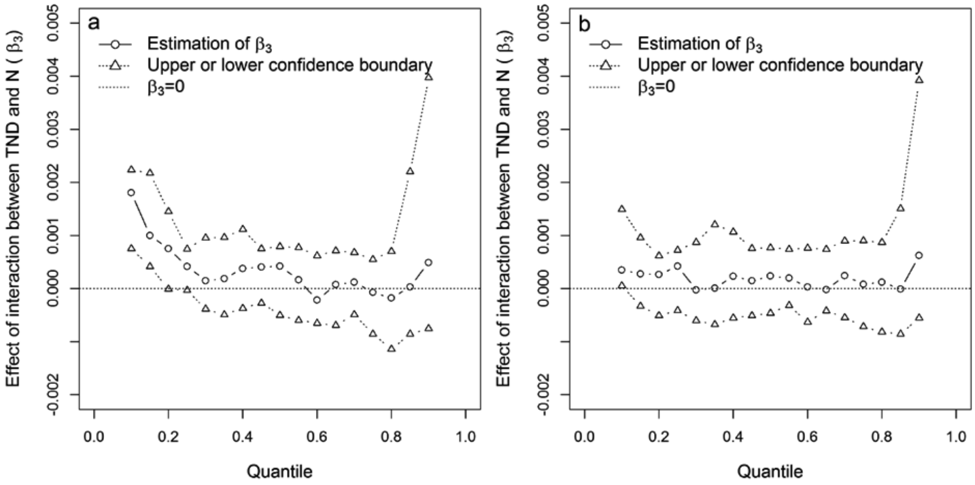

Fig. B1 Estimates of interactive effect between TND and rate of N fertilizer using model 3: $Q_{LER}(\tau|TND, N) = \beta_0(\tau) + \beta 1(\tau)*TND_i + \beta_2(\tau)*N_i + \beta_3(\tau)*TND_i*N_i$, for values of τ ranging from 0.1 to 0.9 with increment of 0.05 with two datasets. Estimates with a dataset including all data reporting rate of N (a). Estimates with a subset only consisting of N Strategy 1 (b), i.e. equal amount of N fertilizer was received in intercrops and sole crops. Circles represent estimates of β_3 and triangles represent upper or lower boundary of 95% confidence intervals of estimated values. The horizontal line indicates 0. There was no difference of trend for interactive effect between TND and rate of N fertilizer with quantiles between datasets.

Table B1 Variables extracted from publications.

Variable	Definition	Unit
Title	Title of publication	-
Authors	Authors of publication	-
Continent	In which continent experiments were carried out	-
Country	In which country experiments were carried out	-
Latitude and longitude	Latitude and longitude of experimental site	Degree
Year	Year in which experiments were carried out	-
Species	Latin name and common name of crop species	-
Sowing and harvest date	Sowing and harvest date of intercropped species or related information for calculating TND	-
C3/C4	Whether one or both crops are C3 or C4 species	-
Legume/non-legume	Whether one or both crops are legume or non-legume species	-
Intercropping pattern	In which way the two species were intercropped. Strip intercropping: two species cultivated in alternative strips and at least one strip includes more than one row; Row intercropping: two species cultivated in alternative rows; Fully mixed intercropping: two species cultivated in the same field without any pattern.	-
Density of crops	Density of each species in sole crops and in intercrop	Plants/ha
Rate of N fertilization	How much N fertilizer was applied to sole crops and to intercrops	kg/ha
Yield	Grain yield or total biomass if fodder crops	ton/ha

Table B2 Availability of information on selected variables in the dataset for this meta-analysis.

Variable	**Number of publications**	**Number of experiments**	**Number of data records**
Title	100	189	746
Authors	100	189	746
Continent	100	189	746
Country	100	189	746
Latitude and longitude	100	189	746
Species	100	189	746
Sowing and harvest date	100	189	746
C3/C4	100	189	746
Legume/non-legume	100	189	746
Intercropping pattern	95	175	697
Density of crops	91	167	676
Amount of N fertilizer	80	143	592
Yield	100	189	746

Appendix C

Plant traits drive spatially and temporally complementary light capture, photosynthesis, and productivity in plant mixtures

Movie C1 Simulation of plant growth in a mixture of tillering species with tall&high Amax species in configuration I (every 6 rows of tillering species mixed with 1 row of non-tillering species) at TND=0, i.e. simultaneously sown and harvested. The total simulation time is 150 simulation days.

Link: https://youtu.be/2NT-mFxW0Rk

Movie C2 Simulation of plant growth in a mixture of tillering species with tall&high Amax species in configuration I (every 6 rows of tillering species mixed with 1 row of non-tillering species) at TND=0.5. TND equal to 0.5 means the tillering species is sown first and harvested at simulation day of 150 while the non-tillering species is sown 50 simulation days later than sowing of the tillering species and harvested at simulation day of 200. The total simulation time is 200 simulation days.

Link: https://youtu.be/8c-iLZrZRPc

Movie C3 Simulation of plant growth in a mixture of tillering species with tall&high Amax species in configuration II (every 6 rows of tillering species mixed with 2 rows of non-tillering species) at TND=0.5. TND equal to 0.5 means the tillering species is sown first and harvested at simulation day of 150 while the non-tillering species is sown 50 simulation days later than sowing of the tillering species and harvested at simulation day of 200. The total simulation time is 200 simulation days.

Link: https://youtu.be/YF4YzsyxzXE

Appendix D

A meta-analysis of relative crop yields in cereal/legume mixtures suggests options for management

Table D1 List of Variables extracted from publications and availability of information.

Fig. D1 Estimates of relationship between PLER and rate of N fertilizer application for different N application strategies.

Table D1 List of variables extracted from publications and availability of information on selected variables

Variable	**Definition**	**Unit/Data type**	**No. publications**	**No. experiments**	**No. data records**
Title	Title of publication	Text	77	144	552
Authors	Authors of publication	Text	77	144	552
Species	Latin name and common name of crop species	Text	77	144	552
Sowing and harvest date	Sowing and harvesting date of intercropped species	Date	77	144	552
Crop type	Whether one crop is legume or cereal species	Categorical	77	144	552
Density of crops	Density of each species in sole crops and in intercrop	Plants/ha	77	143	547
Rate of N fertilization	How much N fertilizer was applied to sole crops and to intercrops	kg/ha	66	117	460
Yield	Grain yield or total biomass if fodder crops	ton/ha	77	144	552

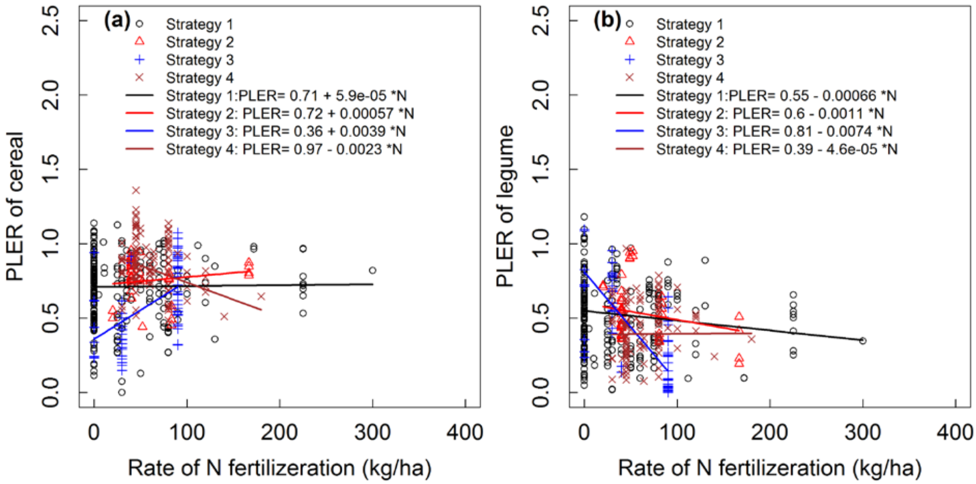

Fig. D1 Estimates of relationship between PLER and rate of N fertilizer application for different N application strategies, for cereals (a) and legumes (b), using a mixed effects model: $PLER_{ijk}=\beta_0+\beta_1{*}N_{ijk}+\beta_2{*}N\_strategy^1_{ijk}+\beta_3{*}N\_strategy^2_{ijk}+\beta_4{*}N\_strategy^3_{ijk}+\beta_5{*}Type^1_{ijk}+\beta_6{*}N_{ijk}{*}N\_strategy^1_{ijk}+\beta_7{*}N_{ijk}{*}N\_strategy^2_{ijk}+\beta_8{*}N_{ijk}{*}N\_strategy^3_{ijk}+\beta_9{*}N_{ijk}{*}Type^1_{ijk}+\beta_{10}{*}N\_strategy^1_{ijkI}{*}Type^1_{ijk}+\beta_{11}{*}N\_strategy^2_{ijk}{*}Type^1_{ijk}+\beta_{12}{*}N\_strategy^3_{ijk}{*}Type^1_{ijk}+\beta_{13}{*}N_{ijk}{*}N\_strategy^1_{ijk}{*}Type^1_{ijk}+\beta_{14}{*}N_{ijk}{*}N\_strategy^2_{ijk}{*}Type^1_{ijk}+\beta_{15}{*}N_{ijk}{*}N\_strategy^3_{ijk}{*}Type^1_{ijk}+a_i+b_{ij}+\varepsilon_{ijk}$. For explanation of the different N application strategies see the materials and methods section.

Summary

One of the major global challenges is to produce enough food for an increasing and more affluent population with reduced environmental impacts. Ecological intensification of modern agriculture, i.e. using ecological means to increase or at least maintain crop production while simultaneously mitigating the footprint of agriculture on the environment is one way to go. Intercropping, i.e. the growing of more than one species simultaneously on a field, is an application of ecological intensification in agriculture. As compared to sole cropping (i.e., growing only one species), intercropping may increase productivity and resource use efficiency. The ecological mechanisms that drive these benefits include: niche complementarity and facilitation. The yield advantage of intercropping is often assessed using the land equivalent ratio (LER). LER is calculated as the sum of relative yield of intercropped species as compared to the respective sole crops. LER can be interpreted as the relative area required by sole crops to produce the same yields as achieved in intercrop. LER>1 means intercropping is more efficient in land use than sole cropping and LER<1 implies intercropping is less efficient. A large variation in LER is found in the literature. Many factors could contribute to this variation, including temporal arrangement of mixed species, crop management and species identity. Knowing the relative contributions of these factors would provide important clues to improve intercropping systems. However, so far, few studies have attempted to quantitatively analyze how these factors affect LER. In this thesis, I therefore investigated how temporal niche difference, crop type combination as well as agronomic practices affect LER, productivity and the interspecific interactions in annual intercrops.

In Chapter 2, I investigated how LER is affected by species traits and designs of intercropping systems using meta-analysis, based on data collected from publications on intercrop productivity around the globe. I focused on the effects of temporal niche difference between the intercropped species, intercropping pattern, relative density total (sum of the relative densities of intercropped species as compared to the respective sole crops), the use of C3 and C4 species and the rate of N fertilizer. Statistical mixed effects models were used to evaluate the relationships. Random effects were included to account for factors that influence crop performance, but could not be analyzed in detail due to lack of consistent and sufficiently detailed reporting in the literature, e.g. weather variables, soil factors, pest, diseases, and weeds. Random effects associated with experiments and publications account for the effects associated with location, year and study which are not accounted by the independent variables. The analysis showed that LER increases with temporal niche

differentiation. The positive relationship between LER and the temporal niche difference is stronger in C3/C4 mixtures than in C3/C3 mixtures (only two cases about C4/C4 mixtures occur in the data set, therefore not analyzed). Application of nitrogen fertilizer decreases LER when there is no temporal niche difference between intercropped species (i.e. sown and harvested simultaneously) while the negative effect of N on LER is alleviated when the temporal niche difference increases. These findings indicate that temporal niche difference is a key factor determining land use efficiency of intercropping but this effect can be modified by species traits and agronomic practices.

Apart from the variation in LER related to temporal niche difference, crop type combination and agronomic practices, there is still large unexplained variation in LER that is likely associated with variation in environmental factors, e.g. weather conditions, soil qualities which are not often measured in intercropping studies. In Chapter 3, quantile regression is used to test whether relationships between LER and explanatory variables, e.g. temporal niche difference depend on these unmeasured factors. The results showed that the effect of temporal niche difference on LER is not changed with quantiles, indicating that the relationships found in Chapter 2 are robust and are not changed qualitatively or quantitatively by the factors not included in the analyses.

In Chapter 4, a functional-structural plant (FSP) model was developed to investigate how interspecific interactions and productivity of individual species in strip intercropping are affected by the interplay between temporal and spatial complementarity and plant traits of the late-sown species, i.c. variation in maximum plant height and CO_2 assimilation rate (Amax). The analysis showed that temporal niche difference increases productivity of early-sown species until a plateau when the temporal overlap between the growth duration of the early- and late-sown species becomes less than 50% of the total growing period. By contrast, productivity of the late-sown species suffered from competition for light with the early-sown species, especially at moderate delays in sowing time compared to the early-sown species and when the spatial configuration of the mixture allowed strong interspecific interactions. The negative effect of shading by the early-sown species on growth and productivity of the late-sown species was smaller if the later-sown species had a high genetic potential for length growth and a high Amax. The competition mitigating effect of a high Amax in the later-sown species was greater than that of its tallness. The analysis shows that the spatial and temporal complementarity in species mixtures (sowing pattern and sowing time) can be strongly affected by plant traits of the component species.

In Chapter 5, I investigated how competitiveness of individual species in cereal/legume intercrop is affected by agronomic management practices, i.c. sowing time, sowing density and rate of N fertilizer. The analysis shows that cereals are overall more competitive than legumes. Earlier sowing of one species increases its competitiveness towards the other species while later sowing decreases it. A high density of a species in the intercrop compared to its density in the respective sole crop had a positive effect on its competitiveness. Application of N fertilizer enhanced the competitiveness of a cereal towards a legume, resulting in overall low productivity of legumes in intercrops. However, sowing legumes a bit earlier than cereals mitigates the negative effect of N on productivity of the legume. These findings help us understand how competitiveness of intercropped species are influenced by agronomic practices and can be used to optimize designs of intercropping systems according to our demands.

In conclusion, many studies have been conducted on intercropping and have reported a large variation in performance of intercropping in terms of land use efficiency, productivity and interspecific interactions. There was a lack of quantitative synthesis of information from the large body of intercropping studies and a need to generalize what factors influence the performance of intercropping. In this thesis, I quantitatively showed that complementarity of resource use resulting from plant traits diversity and temporal and spatial arrangements of the mixtures is one of the key mechanisms for high productivity of intercropping. This thesis only focused on elaborating complementary use of light and nitrogen in species mixtures. More research is needed to explore how other mechanisms drive intercropping productivity, e.g. complementary nutrient acquisition below-ground due to asynchronous distribution of plant roots and effects of pests and diseases. I hope that the analyses and datasets assembled in this thesis provide a useful basis for further analyses demonstrating how diversification of agricultural systems can help to meet the demand for food and other crop produce while moderating agriculture's environmental impacts.

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This thesis is not complete without expressing my sincere gratitude to people who helped me during my PhD study.

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Publication list

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Yu, Y., Makowski, D., Stomph, T.J., van der Werf, W. Robust increase of land equivalent ratio with temporal niche differentiation: A meta-analysis with quantile regression. (In preparation)

Yu, Y., de Vries, J., Stomph, T.J., Evers, J.B., Anten, N.P.R., Zhang, L.Z., van der Werf, W. Plant traits drive spatially and temporally complementary light capture, photosynthesis, and productivity in plant mixtures. (In preparation)

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PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)

- Resource use efficiency in intercrop systems

Writing of project proposal (4.5 ECTS)

- Resource use efficiency in intercrop systems: from empirical analysis to process-based modelling (2013)

Post-graduate courses (6.3 ECTS)

- Introduction to R for statistical analysis; PE&RC (2012)
- Meta-analysis; PE&RC (2012)
- Mixed linear models; PE&RC (2013)
- Zero inflated models and GLMM with R; PE&RC (2014)
- Meta-analysis; PE&RC (2014)
- Bayesian statistics; PE&RC (2014)

Laboratory training and working visits (2.4 ECTS)

- Discussion on techniques of meta-analysis; INRA, Grignon, France (2013)
- Study techniques of meta-analysis; INRA, Grignon, France (2013)

Invited review of (unpublished) journal manuscript (1 ECTS)

- Organic Agriculture: intercropping of maize and pulse: an evaluation of organic systems

Deficiency, refresh, brush-up courses (18 ECTS)

- Systems analysis, simulation and systems management (2011)
- Advanced statistics (2011)
- Ecological models and data in R (2012)

Competence strengthening / skills courses (2.7 ECTS)

- Information literacy PhD including EndNote introduction; Wageningen UR Library (2012)
- Project and time management; Wageningen Graduate Schools (2013)
- Interpersonal communication for PhD candidates; Wageningen Graduate Schools (2013)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.5 ECTS)

- PE&RC Weekend (2011)
- PE&RC Weekend (2014)

Discussion groups / local seminars / other scientific meetings (5.5 ECTS)

- Plant production system seminars (2012-2014)
- R Using meeting (2014)
- Sustainable intensification of agriculture systems (2014)

International symposia, workshops and conferences (8.8 ECTS)

- International intercropping workshop; oral presentation; China (2013)
- European Society of Agronomy Congress; poster and oral presentation; Hungry (2014)
- Netherlands Annual Ecology Meeting; oral presentation; the Netherlands (2014)
- International intercropping workshop; oral presentation; China (2015)

Lecturing / supervision of practical's / tutorials (3.6 ECTS)

- Plant and soil interaction (2013-2014)
- Population and systems ecology (2014)

Curriculum vitae

Yang Yu was born on 31st July, 1986 and grew up in Dandong, Liaoning Province, China. In 2005, he graduated from high school and began a four year BSc study at Agro-meteorology group, China Agricultural University (CAU). He received his BSc degree in 2009 and started a two year MSc study at Agro-meteorology group, CAU. During his MSc study, he focused the effect of intercropping on mitigating the soil wind erosion in Inner Mongolia, China. In 2011, he received his MSc degree and got a scholarship from China Scholarship Council supporting him to start his PhD research in Wageningen University in Centre for Crop Systems Analysis group. During his PhD study, he focused on productivity and land use efficiency in intercropping, under the supervision of promoter Prof. dr. Niels Anten and co-promoters dr. Wopke van der Werf and dr. Tjeerd Jan Stomph. Details of his PhD research are presented in this thesis.

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