Predicting intercrop competition, facilitation, and productivity from simple functional traits

Chloe MacLaren [a,b,*], Wycliffe Waswa [c], Kamaluddin Tijjani Aliyu [d], Lieven Claessens [e], Andrew Mead [f], Christian Schöb [g], Bernard Vanlauwe [c], Jonathan Storkey [a]

[a] *Protecting Crops and Environment, Rothamsted Research, West Common, Harpenden AL5 2JQ, UK*
[b] *Department of Crop Production Ecology, Swedish University of Agricultural Sciences, Almas Alle 8, Uppsala 750 07, Sweden*
[c] *International Institute of Tropical Agriculture (IITA), c/o ICIPE, Kasarani, Off Thika Highway, PO 30772, Nairobi 00100, Kenya*
[d] *International Institute of Tropical Agriculture (IITA), PMB 5320 Ibadan, Nigeria*
[e] *International Institute of Tropical Agriculture (IITA), P.O. Box 10, Duluti, Arusha, Tanzania*
[f] *Intelligent Data Ecosystems, Rothamsted Research, West Common, Harpenden AL5 2JQ, UK*
[g] *Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, calle Tulipán s/n, 28933 Móstoles, Spain*

ARTICLE INFO

ABSTRACT

Context: Recent meta-analyses demonstrate that intercropping can increase the land use efficiency of crop production by 20–30 % on average, indicating a strong potential contribution to sustainable intensification. However, there is substantial variability around this average: individual studies range from half to double the land productivity of monocrops. Legume-cereal intercrops and intercrops with high temporal niche separation tend to be more productive than the average, but these two combination types are not always suitable. There is a need to explore other possibilities to achieve productive intercrops.

Research question: We explored whether two simple functional traits involved in radiation use, plant vegetative height and specific leaf area (SLA), could be used to predict intercrop productivity. Height and SLA together are associated with key plant life-history and resource economy strategies determining competitiveness and tolerance of competition, especially with regard to light, and could therefore be expected to underpin overyielding in intercrops.

Methods: In the first year of our study, we grew crops as monocrops at one site in Kenya and measured their height and SLA. In the second year, we grew crops in monocrop, intercrop, and single plant treatments at two sites in Kenya and one site in Nigeria. Together, these treatments allowed us to identify whether each intercrop combination overyielded or underyielded, and whether any overyielding was driven by facilitation and/or differences in inter- vs intraspecific competition. We then related the strength of these interactions to the two traits.

Results: We found that intercrop grain yields varied in relation to the height and SLA of each species in the intercrop, but together these traits explained less than a third of variation in intercrop land equivalence ratios (LER). More variation could be explained by allowing for the effect of site, suggesting that the two traits interact with site conditions to determine yield. Biomass LERs responded differently to grain LERs, suggesting that plasticity in resource allocation in response to intercropping conditions may further influence yields.

Conclusions: Our study found some evidence that combining species with traits indicating contrasting responses to competition (an avoidant species with a tolerant species) could increase resource use complementarity and thus intercrop overyielding. However, it was clear that other factors (such as additional traits, or the trait by site interaction) are needed to refine our understanding of intercrop productivity.

Implications: A trait-based framework has potential to predict intercrop productivity, but simple measures of height and SLA alone are insufficient.

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* Corresponding author at: Department of Crop Production Ecology, Swedish University of Agricultural Sciences, Almas Alle 8, Uppsala 750 07, Sweden.
E-mail address: chloe.maclaren@slu.se (C. MacLaren).

1. Introduction

Intercropping has strong potential to sustainably intensify agriculture by increasing the land- and resource-use efficiency of crop production ((Martin-Guay et al., 2018, Tilman, 2020). Multiple recent meta-analyses have shown that intercrop productivity is on average 20–30 % higher than when the same crops are grown separately using the same land and/or inputs (Yu et al., 2016a, Yu et al., 2016b, Martin-Guay at al 2019, Daryanto et al., 2020, Li et al., 2020). This suggests a large proportion of future food demand (Hunter at al 2017) could be met by intercropping alone. However, intercropping is not globally widespread: it is rare in most industrialised farming systems (Bybee-Finley and Ryan, 2018), while smallholder farmers often utilise only a few crop combinations (MacLaren et al., 2021).

There are multiple barriers to overcome to make intercropping more feasible to farmers, such as labour use requirements and appropriate mechanisation (Brooker et al., 2015; Bybee-Finley and Ryan, 2018). An overarching challenge however is the need to increase the reliability of intercrop yield gains, to motivate innovation and adoption. A closer look at the recent meta-analyses reveals considerable variation around the mean land productivity gains in intercrops. For example, individual studies included in Martin-Guay et al. (2018) and Yu et al. (2016a) ranged from nearly a 50 % decrease in LER to more than a twofold increase. This variation presents a substantial risk to farmers and calls for a better understanding of the underlying processes responsible for yield gains and losses in intercropping. A systematic approach to selecting candidate intercrops would avoid the extensive field experimentation that is the basis of traditional empirical approaches to identify productive combinations. This would make it easier to assess the overyielding potential of a wider range of crops, such as the many underutilised (or "orphan") crops that have so far received limited research effort.

Productivity gains in intercropping occur when interspecific competition (in the intercrop) is lower than intraspecific competition (in the monocrops), leading to complementarity, and/or when interspecific facilitation is higher than intraspecific facilitation (Brooker et al., 2015; Stomph et al., 2020; Justes et al., 2021). In this paper, we use "productivity" to refer to increases in land productivity, i.e., gains in the combined crop yield when two crops are grown together as an intercrop, instead of separately as monocrops, on the same area of land. It is usually desirable to grow more than one crop for health or financial benefits (MacLaren et al., 2022; with some notable exceptions, Giller, 2020), so in this paper we explore how to get the most out of multiple crops through intercropping.

Previous studies have so far identified two key types of intercrop systems that utilise these interactions to consistently increase productivity, (1) cereal-legume combinations, where the legumes use complementary nitrogen resources to cereals (atmospheric rather than mineral), release nitrogen to cereals in subsequent years via decomposition, and may occasionally also facilitate the cereals via horizontal transfer of fixed nitrogen (Bedoussac et al., 2015; Daryanto et al., 2020), and (2) crop combinations with substantial temporal niche separation between species, where competition is minimised because the crops are actively growing at different points in the season (Yu et al., 2016a, Yu et al., 2016b, Li et al., 2020). Temporal niche separation is maximised in 'relay cropping' systems, where two crops are sown and harvested at different times in the same field so that their growing periods only partially overlap.

These two intercrop systems, cereal-legume combinations and relay intercropping, are useful starting points to guide farmers toward productive intercrops, but do not cover all eventualities: cereal-legume combinations are not always suitable, and in parts of the world with short growing seasons (such as the drier savannas of sub-Saharan Africa) it is difficult to achieve much temporal niche separation. For example, several previous studies have focused on 'doubled-up legumes' (e.g., Mwila et al., 2021), where two legumes are intercropped in a single season, with the aim of enhancing the services provided by a legume

phase in crop rotation (e.g., human dietary diversity, soil nitrogen fixation). In such circumstances, it may be possible to utilise a third type of intercropping system: one that exploits niche complementarity in space for improved resource use efficiency. In this study, we focus on this idea, drawing on ecological theory to identify functional traits that have the potential to predict overyielding of crops grown together over the same time period.

Overyielding in mixed plant communities compared to sole species can result from resource use complementarity and/or facilitation between species (Ammer, 2019; van der Plas, 2019). Complementarity occurs where niche partitioning reduces competition between species and leads to an overall greater capture of resources and thus productivity, while facilitation occurs when one species is adapted to take advantage of the conditions created by other species. Natural plant communities that are functionally diverse in ways that minimise competition and maximise facilitation tend to be more productive than those that are not.

1.1. Traits as indicators of potential competition, complementarity, and facilitation

Differences in plant resource economics and life history strategies may increase complementarity and/or facilitation. Grime's (1977) ruderal/stress-tolerant/competitive life history triangle and the 'fast-slow' plant resource economic spectrum (Wright et al., 2004; Reich, 2014) describe an inherent biological trade-off between resource acquisition and conservation. Plants can either grow quickly by capturing more resources while investing less in secondary metabolites and leaf defence, or follow a conservative strategy of slower growth rates and reduced nutrient loss from plant tissues via a longer leaf life span. Diverging plant resource economic strategies could allow for overyielding in intercrops, with "fast" species able to use easily available resources quickly to avoid competition, while 'slow' species may tolerate the lower resource levels induced by competition (for example in the shade of a taller neighbour) due to more efficient resource conservation. In contrast, combining two 'fast' species could intensify competition, while two "slow" species may be unable to capture the same total amount of resources to convert to yield. However, facilitation could add complexity; because 'fast' species tend to be less stress-tolerant, they may grow better if sheltered from weather extremes or insect pests by another vigorous partner.

Focusing on the plant functional traits that are indicative of contrasting ecological strategies could be a promising approach to screening potential candidate intercrop pairs. Two traits, vegetative plant height and specific leaf area (SLA), have been shown to describe a substantial proportion of the worldwide variation in plant resource economic and life-history strategies (Westoby, 1998, Garnier and Navas, 2012, Adler et al., 2014, Díaz et al., 2016). In annual plants, such as crops, a tall height and high SLA together are indicative of a "fast" or "competitive" strategy while a short height and low SLA are indicative of a "slow" or "stress-tolerant" strategy. To become relatively tall within the growing season, plants must grow relatively fast, while a high SLA is an indicator of investment in light capture rather than tissue conservation (Westoby, 1998). We hypothesise that a combination of these two extremes, a tall plant with a high SLA (indicating a 'fast' strategy) and a short plant with a low SLA (indicating a 'slow' strategy), would perform well when intercropped.

Intercrop interactions can be mediated by belowground as well as aboveground processes, including competition for water and nutrients, and plant-microbe interactions (Duchene et al., 2017, Engbersen et al., 2021, Homulle et al., 2022). It might therefore seem simplistic to expect that height and SLA alone could explain much variance in intercrop productivity. However, many plant traits correlate with one another in relation to key life history trade-offs (Laughlin, 2014; Díaz et al., 2016), so it is possible that height and SLA may correlate with other traits determining belowground interactions. For example, height often
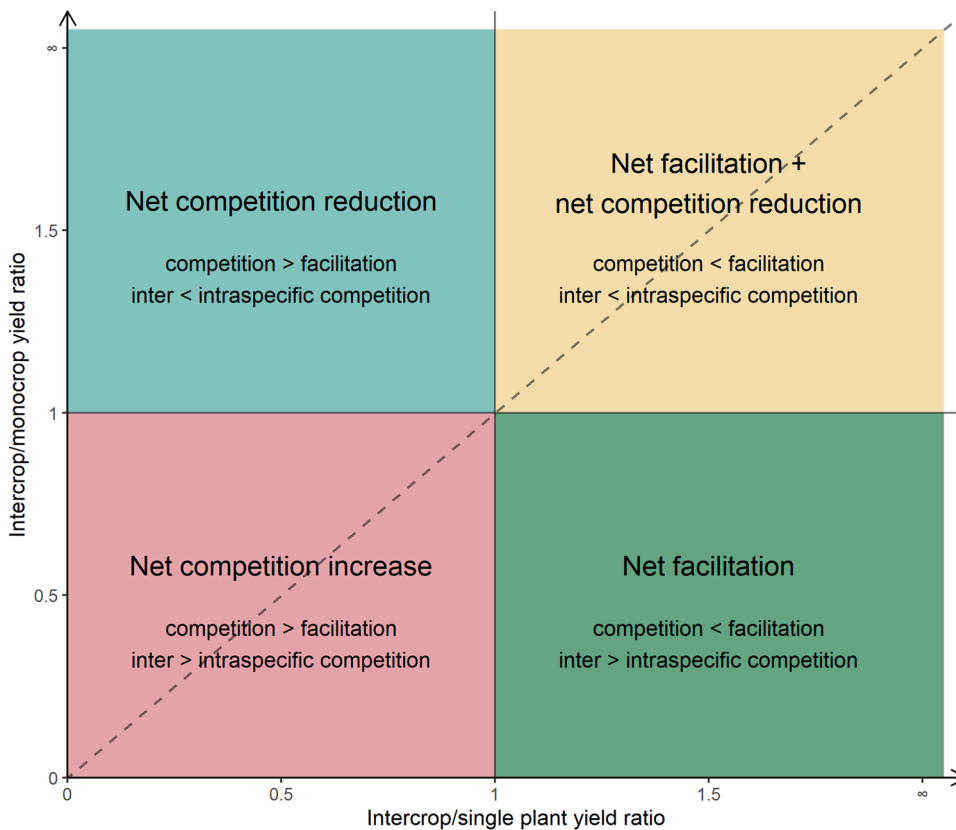
Fig. 1. A graphical representation of how different plant interactions can be separated using the ratio of a species' yield in intercrop over its yield when grown as a single free-standing plant (x axis) and the ratio of a species' yield in intercrop over its yield in monocrop (y axis). A yield ratio for an intercrop/single plant > 1 indicates the species had a higher yield in intercrop than as a single plant, and thus facilitative effects from the intercrop outweighed competition, leading to net facilitation. A yield ratio for an intercrop/monocrop > 1 indicates the species had a higher yield in intercrop than monocrop, indicating that interspecific competition was lower than intraspecific competition. Due to the relationship between relative gains in intercrop, monocrop and single plant yields, the dashed line (x = y) indicates where the single plant yield equals the monocrop yield, expressed on a per plant basis. Areas below that line (where intercrop/single > intercrop/monocrop) indicates that the monocrop outperformed the single plant (i.e. the species facilitated itself). The same species could appear in different locations on this figure if its yield in intercrop varied depending on the species it was intercropped with.

correlates with rooting depth (Garnier and Navas 2012), while SLA is an indicator of the 'fast-slow' whole plant resource economic trade-off and may thus also reflect root economic traits including root weight ratio (Reich, 2014). Thus, even if height and SLA are not the sole causal determinants of intercrop interactions, we hypothesise that they may represent sufficient variation in plant strategies to explain a useful proportion of variation in intercrop land productivity.

Height and SLA are attractive traits for assessing intercropping strategies, because they are often accessible from previous research and trait databases, or can be easily measured with simple equipment. They could thus feasibly be used by farmers, agronomists and/or extension officers for predicting the best combinations from a collection of crops suitable to a specific environment and farming system. If a farmer has 10 potential crops, there are 45 possible pairs of species, which is challenging to test in the field due to the large space and resource requirements to run such an experiment. In contrast, height simply requires a tape measure, and SLA can be measured by cutting portions of leaf with a known area, then drying and weighing them. If height and SLA can reliably predict intercrop productivity, they could make a crucial contribution to reducing the risk of adopting an intercropping strategy or of trying new crop combinations.

1.2. Distinguishing net plant interactions in an intercropping experiment

In this study, we explored the extent to which the mean height and SLA of each crop species could predict competition and facilitation in intercrops, and the overall productivity of an intercrop combination compared to the same crops grown as monocrops. Data for this study were collected from experiments undertaken in two stages over two years. In the first year (2019), we grew each species in monocrop at one site to measure their mean height and SLA. In the second year (2020), species were grown as single free-standing plants, in monocrop, and in different intercrop combinations across three sites. Biomass and yield measurements were taken in the second year.

The two-stage approach taken in this study allowed us to explore whether variation in height and SLA between crops grown as monocrops, measured in one field in one year, could predict intercrop productivity in the following year at multiple sites. Measuring traits once in monocrop at one site was intended to be representative of what might be feasible on-farm, while intercropping at multiple sites provided an assessment of how consistent the relationship between traits and productivity was under different conditions (as might be experienced on-farm in different locations or different years).

Growing species in monocrop, intercrop, and single plant treatments can be used to explore the dominant processes driving differences in intercrop productivity (Chen et al., 2021, Stefan et al., 2022a). In an intercrop, plants experience a combination of inter- and intra-species competition and/or facilitation, while in a monocrop, plants only experience intra-species competition and/or facilitation. Single plants, growing alone, experience neither competition nor facilitation from other plants. Thus, the yield ratios between these three treatments allowed us to quantify the extent to which each species in each combination experienced (1) ***net facilitation,*** where the beneficial effects of neighbouring individuals are greater than the competitive effects, indicated by higher yields for that species in intercrop than as single plants or monocrops, and (2) a ***net competition reduction,*** where a species experiences lower interspecific competition than intraspecific competition, indicated by higher yields for that species in intercrop than in monocrop. Net complementarity across the intercrop pair would arise where both species experience this net competition reduction, or where one experiences it to the extent that it compensates for any increased competition imposed on the other species (Justes et al., 2021). Where a species experiences higher interspecific competition than both intraspecific competition and any facilitative effects, plants experience (3) a ***net competition increase.*** The yield ratios of a species in intercrop compared to a single plant treatment, and in intercrop compared to a monocrop, can be plotted against one another to show whether a particular species in a particular intercrop experiences net facilitation or

Table 1
The species grown in this study, their monocrop sowing density, and the date at which traits were sampled in the 2019 Stage 1 experiment. The SLA and height columns show the mean of each trait estimated using an ANOVA of the 2019 Stage 1 experiment (with species and block as factors), with standard errors in brackets.

Common name	Code	Species name	Sowing density (plants/m^2)	DAP of trait sampling 2019	SLA	Height	Locations grown in 2020
Bambara nut	BB	*Vigna subterranea*	16	69	175.1 (21.0)	36.3 (5.01)	Kibos, Zaria
Greengram	GG	*Vigna radiata*	4	58	137.1 (21.0)	71.7 (5.01)	Kibos, Zaria
Finger millet	ml	*Eleusine coracana*	16	74	237.9 (22.3)	98.6 (5.27)	Mbita
Maize	MZ	*Zea mays*	4	70	69.4 (21.1)	259.3 (5.01)	Kibos, Mbita, Zaria
Groundnut/peanut	PN	*Arachis hypogaea*	16	60	111.4 (21.0)	42.5 (5.01)	Kibos, Mbita, Zaria
Pigeon pea	PP	*Cajanus cajan*	4	105	168.2 (16.6)	178.8 (3.97)	Kibos
Soybean	SB	*Glycine max*	16	66	173.1 (17.7)	90.5 (4.22)	Kibos, Mbita
Sesame/ simsim	SS	*Sesamum indicum*	16	68	197.0 (17.7)	136.0 (3.97)	Mbita, Zaria
Cowpea	CP	*Vigna unguiculata*	16	(not grown in 2019)	-	-	Zaria
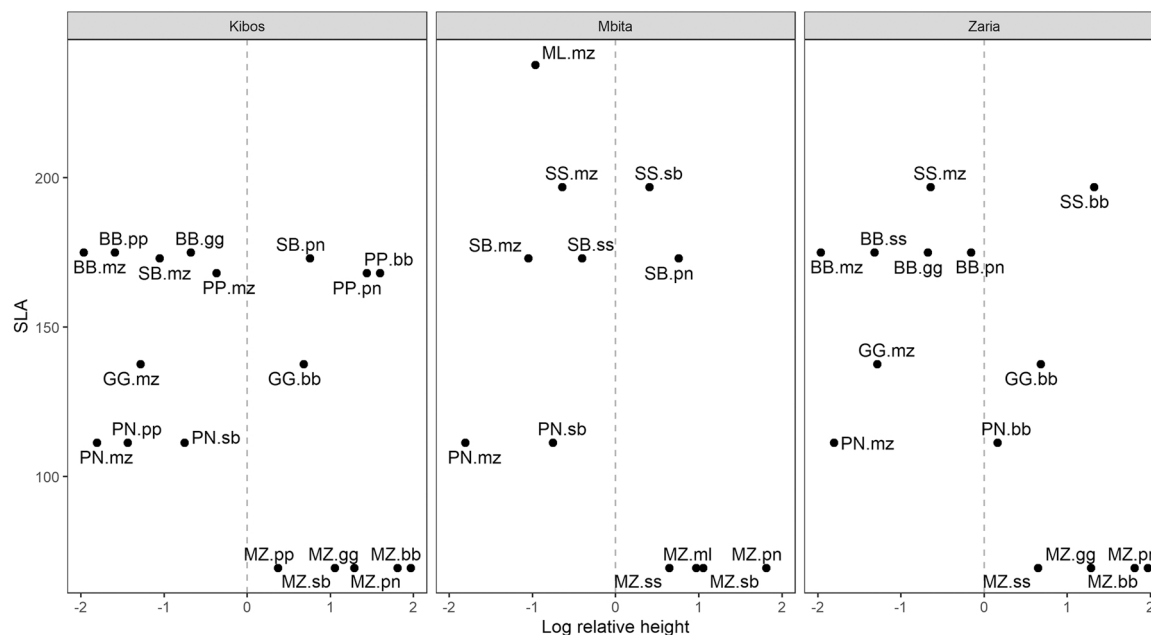
Fig. 2. Traits measured in monocultures for all species, plotted as absolute values for SLA and values relative to a companion crop used in the intercrop experiments for height; illustrating where a species was predicted to be the taller or shorter partner in a combination. The focal species is indicated in upper case letters and its pair in lowercase letters. Trait values for each species were measured in 2019 (Table 1). Species combinations were selected to maximise variance between species in traits. Species codes are shown in Table 1.

a net change in competition (Fig. 1).

We investigated the extent to which the two traits, height and SLA, explained whether species experienced increased a net increase or reduction in competition, or net facilitation, in different intercrop combinations. Finally, we explored whether this understanding of the interactions experienced by each species could be used to predict the overall land-equivalent productivity (LER) of a species pair, based on the height and SLA of each species.

2. Materials and methods

2.1. Species

In the first year of the study (2019) we grew 11 different crop species: Bambara groundnut *(Vigna subterranea)*, chickpea *(Cicer arietinum)*, finger millet *(Eleusine coracana)*, french bean *(Phaseolus vulgaris)*, greengram *(Vigna radiata)*, peanut *(Arachis hypogaea)*, maize *(Zea mays)*, pigeon pea *(Cajanus cajan)*, sesame *(Sesamum indicum)*, soybean *(Glycine max)*, and sunflower *(Helianthus annuus)*. Of these, bambara groundnut, finger millet, french bean, and pigeon pea are considered underutilised or orphan crops by the African Orphan Crops Consortium (African Orphan Crops Consortium, 2022). In the second year (2020), we selected 14 pairs consisting of 8 species (Table 1) that had

established well in the first year (chickpeas, french beans and sunflower were excluded) and that spanned a range of height and SLA combinations (Fig. 2). These pairs were grown at three sites, two in western Kenya and one in northern Nigeria. An additional species, cowpea *(Vigna unguiculata),* was included at the site in northern Nigeria due to the local importance of this crop; however it later proved impossible to obtain appropriate trait data for this crop so we have excluded it from the analyses in this article.

It was not possible to test all 14 species pairs at every site in 2020 due to space and resource requirements, so we grew different sets of pairs at each site, with some pairs in common between sites. This approach increased our power to detect a consistent effect of traits across sites and species if there was one, but reduced our power to distinguish between site and species-specific effects within variation not explained by traits.

2.2. Stage 1 experiment, 2019: Trait measurements in monocrop

2.2.1. Location and layout

Crops were grown in monocrop in an experiment with a randomised complete block design with three replicates at the *icipe* Thomas Odhiambo campus, in Mbita, Kenya (−0.4298887, 34.2067662). Each crop was grown in monoculture in one plot per block (i.e., the "treatment" in this experiment was crop species). Each plot contained 105
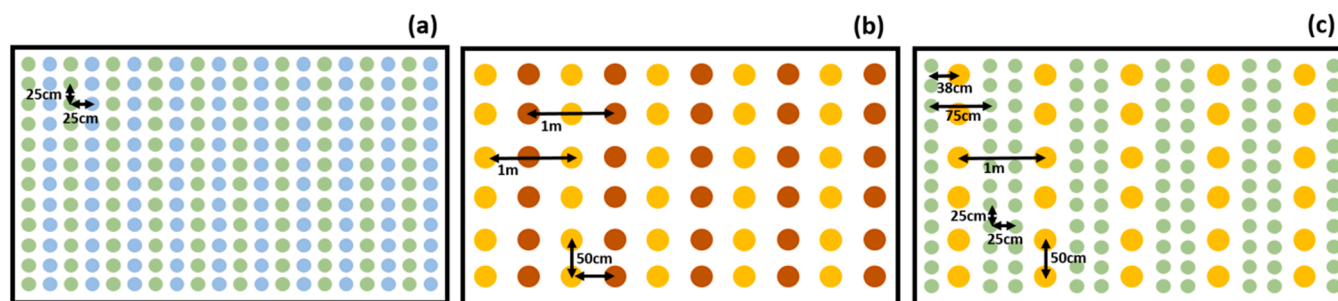
Fig. 3. Diagrams of the intercrop treatment layouts for (a) two species with a sowing density of 16 plants/m^2, (b) two species with a sowing density of 4 plants/m^2, and (c) one species with a sowing density of 16 plants/m^2 intercropped with another species with a sowing density of 4 plants/m^2. The exact number of plants and the plot sizes varied depending on the space available at each site (Supplementary Figs. S1 and S2).

plants, so the size of the plot depended on the sowing density of each species (Table 1). Crops were allocated to one of two sowing densities to facilitate intercrop layouts in the stage 2 experiments, either 4 plants/m^2 or 16 plants/m^2, depending on which was closest to locally used sowing densities. Plot sizes for crops sown at 16 plants/m^2 were 3.75 × 1.75 m, and plot sizes for crops sown at 4 plants/m^2 were 3.5 × 7.5. These plot layouts were designed to ensure that there was a guard row (not sampled) around the edge of the plot, and enough plants within the plot that adjacent plants would not be sampled at different times (to avoid allowing some plants to grow under reduced competition before sampling).

2.2.2. Crop sowing and management

Most crops were sown on 14th and 15th March 2019, coinciding with the beginning of the long rainy season in western Kenya (see Supplementary Table S1 for weather data). Greengram was sown on 25th March, due to a delay acquiring the seed. Crops were sown into a field that had not been cropped for three years, so the field was prepared first by clearing scrub and then by mouldboard plough. A disc harrow was used to create a fine seedbed. Seeds were planted according to local practice: a shallow hole was made with a hoe, seeds were placed in the hole and covered with soil. In most cases one seed was placed per hole but for some small-seeded species, multiple seeds were sown, and seedlings thinned following emergence.

No fertilisers were applied as the field was considered sufficiently fertile following three fallow years, in which time mixed woody shrubs, including legumes, had colonised the field (these were removing by cutting, and digging where necessary). Fallows are known to replenish soil nutrients in western Kenya (Sanchez and Jama, 2002), and we aimed for conditions representative of local farms rather than optimal fertilisation. Crops were irrigated using sprinklers on 17th and 22nd March and 14th April to ensure good establishment (quantities followed local judgement and could not be recorded due to technical limitations). All plots were weeded with hoes on 1st and 3rd April 2019, with subsequent hand-weeding undertaken when necessary (more often for the smaller, less competitive species such as bambara nuts and groundnuts, while taller species typically had very few weeds in the plots).

2.2.3. Trait measurements

Crop traits were sampled between 55 and 80 days after planting (DAP; Table 1), with sampling for each species coinciding with the point of maximum vegetative biomass just prior to the onset of seedset. Three plants were sampled in each plot, except in cases where plots had been affected by cane rats and too few plants remained to sample (a minimum of three plants from each of two blocks, or two plants from each of three blocks was sampled for each species). Vegetative height (henceforth just "height") was measured in the field, as the distance from the point where the stem met the soil to the highest vegetative part of the plant. SLA was measured for each plant using a representative sample of five leaves per plant. SLA is the area of a fresh leaf divided by the dry weight of the leaf,

and so for large-leaved crops (e.g., maize), portions of a known area were cut from each leaf, dried, and weighed. Two portions of 25 cm^2 were cut from each of the five leaves resulting in a known area of 250 cm^2. For small-leaved species, a photo of the five leaves was taken against a white background alongside a square of coloured paper of known area, and the image analysis software ImageJ was used to calculate the leaf area from the known area of the paper square. These leaves were then dried in drying ovens for 48 h at 80 °C and weighed.

Mean height and SLA values (and their standard errors) for each species were calculated using ANOVA, with the trait as the response, and species and block as explanatory factors. Mean trait estimates for each species across all blocks were extracted using the function *emmeans* in package *emmeans* (Lenth, 2020) in R (R Core Team, 2021) and are shown in Table 1.

We also initially considered growth rate (mean biomass gain per day) as an additional trait for this study. This was calculated by dividing the maximum biomass by the number of days after emergence of each species. However, growth rate correlated strongly with height (Pearson's R = 0.87, P = 0.005), so in this study, height can also be considered representative of growth rate. Height and SLA were not correlated (Pearson's R = 0.37, P = 0.369).

2.3. Stage 2 experiment, 2020: Intercrop, monocrop, and single plant performance

2.3.1. Location and layout

This experiment took place at three locations, the *icipe* Thomas Odhiambo campus in Mbita (Kenya; −0.42988, 34.20676), the KALRO Research Station in Kibos (Kenya; −0.06638, 34.81286), and the IITA research farm in Zaria (Nigeria; 11.20999, 7.59926). A different set of species were grown at each site (Table 1), in order to maximise the range of trait values present in the study (Fig. 2). Confounding of species effects with site effects was minimised by ensuring that most species were grown at least at two sites, and maize and peanuts at all three sites (and the effect of site was explored in the data analysis, see below).

Experiments at all sites followed randomised complete block designs with three replicates. Each species was present in each block in single plant and monocrop treatments, and in one or more intercrop treatments. Plots (and blocks) were separated by at least one metre. Species were grown in monocrop using the same sowing densities as in the 2019 Stage 1 experiment (Table 1). Intercrop treatments followed a replacement design: where two species with the same sowing density were planted together, species were planted in alternating rows with the same distance between all plants. Where two species with different sowing densities were planted together, one row of the species at the lower density (4 plants/m^2) was alternated with two rows of the species at the higher density (16 plants/m^2) (Fig. 3). Plot sizes differed between sites. In Mbita, each plot was 3 × 5 m, except for monocrops of densely spaced plants that were 3 × 2 m (this smaller size contained enough plants to sample and thus made efficient use of space) (Supplementary Fig. S1). In

Kibos and Zaria, all plots were 5 × 6 m (Supplementary Fig. S2).

In the single plant plots, all plants were 1 m apart (Supplementary Figs. S1 and S2, with photos provided in Supplementary Fig. S3). This spacing meant that the plants were free of competition for most of their growth, although some shading may have occurred later in the season for plants with tall neighbours. To minimise any overall neighbour effect, species were allocated to random positions in single plant plots. Land availability for the experiments was not sufficient to have larger spacings between single plants. To ensure that enough single plants were available for sampling, multiple plots per block were allocated to single plants (5 plots at Kibos and Zaria, 3 plots at Mbita). Each single plant plot contained a minimum number of each species, and where the number of single plants in each plot was not divisible by the number of species, then the remainder were randomly allocated among species.

2.3.2. Crop sowing and management

Crops were sown on 4th April 2020 at Kibos and 9th April 2020 at Mbita, coinciding with the beginning of the long rains in Kenya. In Zaria, crops were planted within their best planting window: maize and sesame on 22nd June, bambara nut, greengram, and peanut on 16th July, and cowpea on 13th August. At Mbita, crops were sown in the same field as used in 2019, and at Kibos and Zaria into fields that had been uniformly cropped the previous year. The soil was prepared using a mouldboard plough followed by a disc harrow. Crops were sown manually as described for Stage 1.

Crops at Kibos and Zaria received fertiliser shortly after planting to ensure all plants had sufficient nutrients to grow well, and to avoid facilitation occurring simply as a result of legumes providing nitrogen (N) to non-legumes (an already well-known phenomenon that we did not intend to investigate here). At Mbita, the field had good fertility status following a 12 month natural fallow, so fertilisers were not applied. At Kibos and Zaria, fertiliser applications in intercrop and single treatments were targeted to individual crops, i.e. applied per row or plant. At Kibos, maize received 120 kg N ha^{-1}, 60 kg P_2O_5 ha^{-1} and 60 kg K_2O ha^{-1}. N was applied in 2 doses: one third during planting, and two thirds at 4 weeks after planting (WAP). All legumes received 40 kg P_2O_5 ha^{-1} at planting. At Zaria, fertiliser rates were tailored to the crop (maize received 120 kg N ha^{-1}, 50 kg P_2O_5 ha^{-1} and 50 kg K_2O ha^{-1}, with N applied in three doses at 1, 4 and 6 WAP, and all P and K applied at 1 WAP; sesame received 60 kg N ha^{-1}, 30 kg P_2O_5 ha^{-1} and 30 kg K_2O ha^{-1}, with the N split between 1 and 4 WAP, and all P and K applied at 1 WAP; all legumes received 40 kg P_2O_5 ha^{-1} at 1 WAP).

Insect pests were controlled where necessary with pesticide applications based on local expertise of the active ingredients needed to protect each crop. At Zaria, Ampligo 150 ZC was applied to maize at 4 and 7 WAP at a rate of 200 ml/ha, while in cowpea, Imiforce 22 SL GL was applied at 150 ml/ha at 3 WAP and Kartodim 315EC at 0.8 ml/ha at 6 WAP. At Mbita and Kibos, Lufeneron at a rate of 50 g/L was used to control stemborers in maize, and Imadocloprid at 200 g/L for aphids in soybean. Insect pests tend to be species specific, and pest pressure on other crops was observed to be low (presumably because these crops were not grown so widely in the landscapes around each research farm) so no pesticides were used. Pesticides were applied to each specified crop in all treatments, with applications in intercrop and single treatments targeted to the crop, i.e. applied per row or plant.

Plots were manually weeded (using hoes) as necessary to prevent competition between weeds and crops. No irrigation was required at any site in 2020. The Kibos site was affected by flooding (standing water in some plots) following heavy downpours during the early growth phase, which appeared to reduce growth rates across the experiment. Weather data for each site is reported in Supplementary Table S1.

2.3.3. Biomass and grain yield measurements

Biomass was sampled when each species reached maximum biomass, around the onset of seed filling. For monocrops and intercrops, one row of plants per plot were sampled for each species (avoiding guard rows at the edges of plots). The length of row depended on the plot size, which differed between sites (Supplementary Figs. S1 and S2). The row length sampled and the number of plants in the sample were recorded (to calculate average biomass per plant and per m^2). For single plants, a random selection of plants were sampled, distributed evenly across plots and blocks. Exact numbers of single plants also differed between sites due to different plot sizes (Supplementary Figs. S1 and S2).

Sampled plants were cut at ground level and fresh weights recorded. Two plants were subsampled from each plot, dried, and weighed again to obtain a fresh:dry weight ratio. This ratio was used to obtain an average biomass per plant and per m^2 from the total fresh weight of the samples. At Mbita and Kibos, plants were dried in drying ovens for 48 h at 80 °C. In Zaria, due to a fire incapacitating the drying ovens, plants were sun-dried for 3 weeks in a glasshouse.

Plants were sampled for grain yields when each species was ready to harvest, so early maturing species (e.g. greengrams) were harvested earlier than late-maturing species (e.g. pigeon peas). The same total area of each plot was sampled for monocrops and intercrops, equal to either six rows of densely spaced species (16 plants/m^2) or four rows of widely spaced species (4 plants/m^2). In monocrop plots, all rows were the same species, while in intercrop plots, half the rows were from each species in the plot (Supplementary Figs. S1 and S2). Row length depended on the plot size at each site, and again guard rows were avoided. Number of rows, row length, and number of plants in the harvest area was recorded.

All ears/pods from sampled plants were harvested and weighed fresh. A subsample of approx. 250 g was taken (or two ears of maize) and the grain separated from the pod/ear material. This subsample was weighed fresh, dried, and weighed again. The ratio of dry grain weight to fresh whole ear/pod weight could then be used to calculate average dry grain weight per plant and per m^2. Within each plot, two plants were also cut at ground level and the vegetative biomass and grain separated. These were dried and weighed to obtain the harvest index.

For single plants, grain from all remaining plants was harvested. Ears/pods were weighed fresh for all plants. One plant was cut at ground level and separated into leaf/stem biomass, ear/pod material, and grain. These parts were weighed separately fresh and dry to calculate the harvest index and the ratio of fresh ears/pods to dry grain.

2.4. Data analysis

First, we calculated the relative productivity (measured as grain yield or maximum biomass) of each species in intercrop compared to monocrops and single plants. This allowed us to identify the extent to which each species experienced complementarity and facilitation in each intercrop combination. We then used regression models to explore the relationships between each of the traits (height and SLA) and the extent to which each species experienced competition or facilitation. Finally, we modified our models describing the response of each species to intercropping into models that used the trait values of both species to predict the land equivalent ratio (LER) for each intercrop combination based on biomass or yield. All analysis was undertaken in R version 4.1.2 (R Core Team, 2021).

2.4.1. Estimating treatment means and identifying net interactions

A separate model for biomass and grain yield was created for each site, containing treatment nested within species, and block, as explanatory factors. The treatment variable described whether the yields were measured for a single plant, a monocrop, or in an intercrop with a specific partner (i.e the levels for this variable were single plant, monocrop, intercropped-with-peanuts, intercropped-with-maize, intercropped-with… etc). These models were used to estimate the mean biomass and grain yields per plant for each species in each site, and the variances associated with those means. The results of these models are not reported because we were not using these models to test the effect of treatment and species on productivity, but simply to acquire the estimated means and variances.

To calculate the relative productivity of each species in each intercrop combination compared with the monocrop and single plant treatments at each site, ratios between mean yield estimates from our models were obtained via pairwise comparisons using the *pairs* function in package *emmeans* (Lenth, 2020). The pairwise comparisons were implemented on the log scale in order to obtain standard errors; given that differences of logs are logs of ratios, back-transformation of pairwise comparisons of means provides ratios of means and standard errors for those ratios.

As shown in Fig. 1, these ratios can be used to identify the net interaction experienced by each species in each intercrop. If the yield of the species in intercrop is higher than the single plant treatment (ratio > 1), we can infer that benefits of having neighbours (facilitation) outweigh the costs (competition). Likewise, if the yield of the species in intercrop is higher than in monocrop, this indicates that interspecific competition is weaker than intraspecific competition within that species. Although we define the net interaction categorically, based on certain thresholds (i.e., intercrop/monocrop = 1 and intercrop/single plant = 1), it is important to note that each ratio is a continuous variable. A value of 1 indicates no net advantage nor disadvantage of either treatment, while values close to 0 indicate a strong net disadvantage of being intercropped, and values above 1 indicate a net advantage.

2.4.2. Traits associated with intercrop interactions

To explore the association between species traits and species performance in intercrop, we created separate regression models for four response variables: the intercrop/monocrop yield ratio and the intercrop/single plant yield ratio for each of biomass yield and grain yield. These ratios were estimated for each species in each site (see above) averaged across multiple plots, each ratio had an associated standard error. To account for this, we used weighted regression models, with the weight for each data point calculated as the reciprocal of the standard error of that ratio.

Our models included the two traits and their interaction (product) as explanatory variables. Height was included in the models as the *relative height of each species compared to its partner,* because it is relative heights rather than absolute heights that determine competition for light. In contrast, we included the *SLA as an absolute value for each species,* because SLA is related to how a plant uses the resources available to it, rather than how it affects the resources available to another species. In so doing, we aimed to quantify the power to predict whether a species was more likely to experience increased competition, reduced competition, or facilitation when grown in combination with another species on the basis of its leaf morphology and its relative position in the canopy.

The main aim of this study was to investigate whether a useful amount of the variation in intercrop productivity across species and sites can be explained using plant trait values for each species that were measured in monocrops once at one site. Therefore, the models presented in the main text do not include site as an explanatory variable, and any differences between sites contribute to unexplained residual variation. However, we also fitted models that did include site to gain an understanding of the amount of variation explained by site and the interactions between site and plant traits (allowing separate relationships with plant traits for each site). The results of these models are noted where relevant in the main text and are fully presented in the Supplementary materials.

To explore the relationship between intercrop productivity and relative height, SLA, and the interaction between (i.e. product of) relative height and SLA, we first created a full model (ratio ~ relative_height + SLA + relative_height:SLA) and then ran a backwards selection process where variables were removed if they improved the AIC (using function *step* in R's default *stats* package; R Core Team, 2021). The model selection process respected the marginality of terms and thus only removed the main effect if the combined term had already been removed. The aim of this process was to identify a simple model that fitted the data well. For the models including the site effect, the full model included both traits and site and all combined terms (ratio ~ relative_height + SLA + site + relative_height:SLA + relative_height:site + SLA:site + relative_height:SLA:site) and the same selection procedure was used. The variation explained by each variable in the final model and its significance was explored using Type III F-tests, which test the marginal effect of each term when all other variables and combined terms are included.

Species identity was not included as an explanatory variable in our models because we aimed to explore the extent to which traits alone predict intercrop performance, so that traits could be used in the future to predict the performance of novel intercrops that have not previously been tested and for which no species-specific intercropping performance information is available. However, we were concerned that species with extreme trait values may have biased the results if other characteristics of those species also played a strong role in determining intercropping performance. Maize may be problematic here (Fig. 2), so we also ran all models on a dataset excluding the observations for maize. We found no change in the variables included in the final models chosen via the backward selection procedure, nor any change in the direction of the effect estimates, so we conclude that maize was not unduly contributing to the results. Thus, we only present results from the models including all species.

2.4.3. Predicting overall LER per m² from individual species traits in monoculture

In this step, we wanted to know how well height and SLA could predict the overall performance of an intercrop combination, in terms of the total productivity of both species relative to their productivity if grown in monoculture on the same area of land, i.e. the land equivalence ratio (LER). The LER for a given intercrop combination is calculated as:

LER = (yield of species X per m^2 intercrop/yield of species X per m^2 monocrop) + (yield of species Y per m^2 intercrop/yield of species Y per m^2 monocrop).

To calculate the LER for each combination, we first estimated the mean yield per m^2 for each species in each treatment using a model for each site, with treatment nested within species and block as explanatory factors. We then calculated the LER, according to the above equation, and the standard error of the LER for each combination from these mean estimates using the function *deltaMethod* in package *car* in R (Fox and Weisberg 2019). This function accepts means with standard errors into an equation (such as the LER equation), solves the equation using the mean values, and estimates the standard error of the solution using the delta method.

To predict LERs for different intercrop combinations, we took the final models from the previous section and rearranged them to include the trait values of both species. Height was still included as a ratio to indicate the difference in height between the species (representing the extent to which competition for light is asymmetric between species), and was always expressed as the height of the shorter species in the combination divided by the taller species. The SLAs of both species were included as absolute values. Interactions between (products of) height and the SLA of each species were included, but interactions between (products of) the SLA of both species was not, because SLA affects how a plant uses the light it receives but has less influence on the environment experienced by other plants in the intercrop. The response variable in this model was the LER of each intercrop combination, leading to a full model with the formula:

LER ~ relative_height + SLA_species1 + SLA_species2 + relative_height: SLA_species1 + relative_height:SLA_species2

We also fitted a model including the site effect and the interactions of site with each of the traits, with results presented fully in the Supplementary materials.

We assessed whether the models predicting the LER of species combinations made useful *qualitative* predictions of the LERs of each
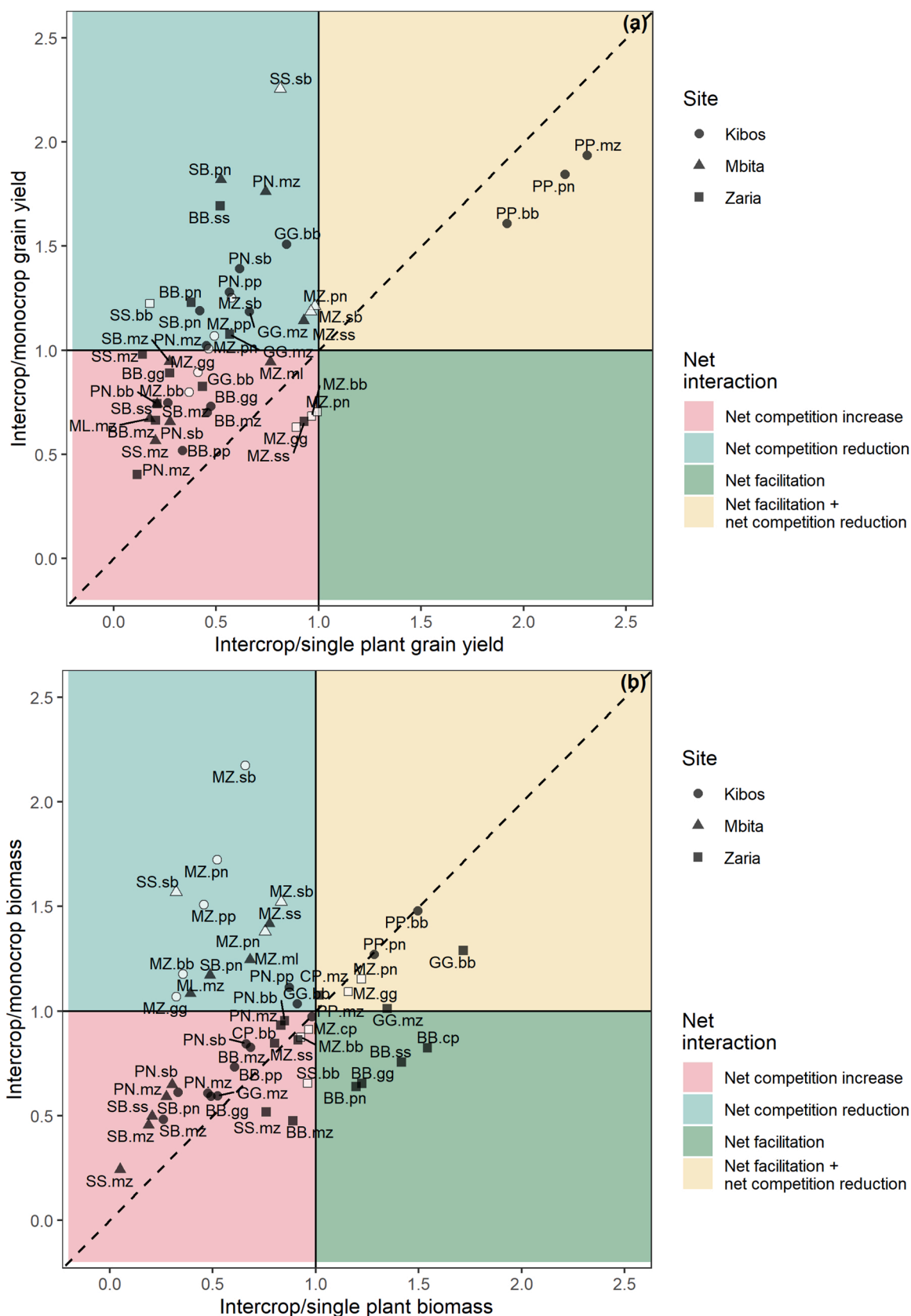
Fig. 4. The ratio of (a) grain yield and (b) biomass yield in intercrop compared to a monocrop (y axis) plotted against the ratio of yield in intercrop compared to a single plant (x axis). Ratios were calculated using a pairwise comparison function of mean yields in each treatment (see Materials and Methods). Each species in each combination is shown, with upper case letters indicating the focal species and lower case letters indicating its intercropped partner. Points with white centres indicate non-legumes paired with legumes. Background colours show where the ratios indicate whether net facilitation or a net increase or decrease in competition occurred (see Fig. 1).

Table 2

Type III sums of squares, F-values, P-values, and total variance explained (R^2) for the final models describing how relative height and SLA influence the intercrop/monocrop and intercrop/single plant yield ratios for grain and biomass.

Model	R^2	Model parameters	d.f.	Sum Sq	F-value	P-value
Grain yield ratio for intercrop/ monocrop (competition)	0.26	intercept	1	10.290	22.565	< 0.001
		log(relative height)	1	2.236	4.904	0.033
		SLA	1	1.058	2.321	0.136
		log(relative height):SLA	1	4.585	10.055	0.003
		residual	40	*18.240*		
Grain yield ratio for intercrop/ single plant (facilitation)	0.23	intercept	1	70.431	109.972	< 0.001
		log(relative height)	1	7.992	12.478	0.001
		residual	42	*26.899*		
Biomass yield ratio for intercrop/ monocrop (competition)	0.42	intercept	1	28.313	74.934	< 0.001
		log(relative height)	1	2.577	6.819	0.013
		SLA	1	4.266	11.290	0.002
		residual	41	*15.492*		
Biomass yield ratio for intercrop/ single plant (facilitation)	0.16	intercept	1	30.728	30.453	< 0.001
		SLA	1	9.125	9.028	0.004
		residual	42	*42.453*		

combination. Compared to the models in the previous section, these models had half the effective sample size (intercrop combinations as opposed to each species in each combination) and double the variance associated with each point (the LER is calculated from the intercrop/monocrop ratios for two species, each with their own site-level variance). Thus, we did not expect these models to have much power to detect significant effects of traits on LERs. Nonetheless, the overall R^2 values of the models provide an indication of how much variation is explained by the combined set of terms included in the model. We also used a Spearman's rank correlation test to explore whether the models predicted a similar rank order of LERs as we observed in our experiments.

3. Results

3.1. Competition and facilitation

The ratios of grain yield in intercrop to grain yield in monocrop, expressed on a per plant basis, indicated that some species combinations included in our experiment resulted in increased competition and others in decreased competition, but only pigeon pea experienced facilitation for grain yield (Fig. 4a). In contrast, ratios for biomass yield indicated that several species experienced facilitation at Zaria, including maize, greengrams, bambara nuts, and pigeon peas (Fig. 4b).

Because the plots were fertilised, we did not expect to see a benefit to the non-legumes of biological nitrogen fixation by legumes, and pairing non-legumes with legumes did not appear to increase facilitation for either grain yield or biomass (Figs. 4a and 4b). It is possible that non-legumes paired with legumes experienced a competition reduction in terms of biomass production (Fig. 4b), but as most of these pairs included maize as the non-legume, it is not clear if this is an effect of the legumes or a result of maize typically producing more biomass in intercrop. Maize also performed relatively better when paired with non-legumes, including millet and sesame.

3.2. Effect of traits on competition and facilitation

Relative height and/or SLA were observed to explain some variation in competition (the ratio of yield in intercrop over yield in monocrop) and/or facilitation (the ratio of yield in intercrop over yield as a single plant) for both grain and biomass yields, with at least one trait having a statistically significant effect in each final model (Table 2). R^2 values for the four models ranged from 0.16 to 0.42, suggesting that our two traits have some predictive power in intercrop facilitation and competition, but much variation remains unexplained.

The interaction between relative height and SLA also impacted on the intercrop/monocrop ratio of grain yields, indicating that species tended to produce more grain in intercrop than monocrop either if they were shorter than their partner and had a low SLA, or if they were taller than their partner and had a high SLA (Fig. 5a). The intercrop/single plant grain yield ratio was best predicted simply by height (Table 2, Fig. 5b), with relatively taller species more likely to experience net facilitation than relatively shorter species. The final model for the intercrop/monocrop biomass yield ratio indicated an additive effect of height and SLA (Table 2), so that relatively taller species were more likely to produce more biomass in intercrop, but especially if they also had a low SLA (Fig. 6a). SLA also had a negative relationship with biomass production in intercrop compared to single plants (Fig. 6b).

When site and interactions between site and both relative height and SLA were included in the models (Supplementary Table S2), R^2 values rose to 0.54 for the intercrop/monocrop grain yield ratio, 0.56 for the intercrop/single plant grain yield ratio, 0.52 for the intercrop/monocrop biomass yield ratio, and 0.75 for the intercrop/single plant biomass yield ratio respectively. In these models, site did not typically have a significant main effect (intercept parameter), but was involved in significant interactions with relative height and SLA (Supplementary Table S2), suggesting that the responses to the traits varied with the conditions at each site to determine intercrop productivity.

Our models describe different relationships between traits and grain and biomass yields in intercrop combinations (Table 2, Fig. 5 and 6). Differences in whether species experience increased or reduced competition and/or facilitation in intercrop combinations in terms of either grain or biomass yields are also visible by comparing Figs. 4a and 4b. Fig. 7 directly visualises these differences by showing relative grain yield in intercrop to monoculture against relative biomass yield in intercrop compared to monoculture. Although there is a general trend that relative intercrop grain yields increase as relative intercrop biomass yields increase, it is also notable that species with a low SLA tended to increase biomass production relative to grain production in intercrop combinations compared to species with a high SLA. This trend was stronger for short species with a low SLA, and for tall species with a high SLA. The differences in the model output for grain yield and biomass are indicative of variation between species in partitioning of resources between vegetative and reproductive parts of the plant in monoculture and intercrops; the plasticity in resource partitioning appears to be related to the ecological strategies associated with SLA and height.

3.3. Using traits to predict intercrop LERs

Respecifying the models described in Table 2 to include the two traits for both species in an intercrop pair explained 28 % of the variation in relative intercrop grain LERs across our experiment ($R^2 = 0.28$) and 15 % of the variation in intercrop biomass yield LER ($R^2 = 0.15$; Supplementary Table S3). Fig. 8 shows the relationship between the observed LERs and the LERs predicted by our models. The overall trend in grain yield LERs (Fig. 8a) was described well by the model, although there was substantial uncertainty associated with both the observed mean and the predicted LERs (indicated by the error bars) leading to a lack of statistical significance.

Overall, our models suggested that intercrop grain yield LER is maximised where one species is much shorter than the other, particularly with the taller species having a high SLA and the shorter species having a low SLA (Supplementary Fig S4). The biomass yield LER was more likely to be greater where the two species are similar in height, and both species have a low SLA (Supplementary Fig. S5). Photos of some intercrops and single plant treatments with species differing in their trait
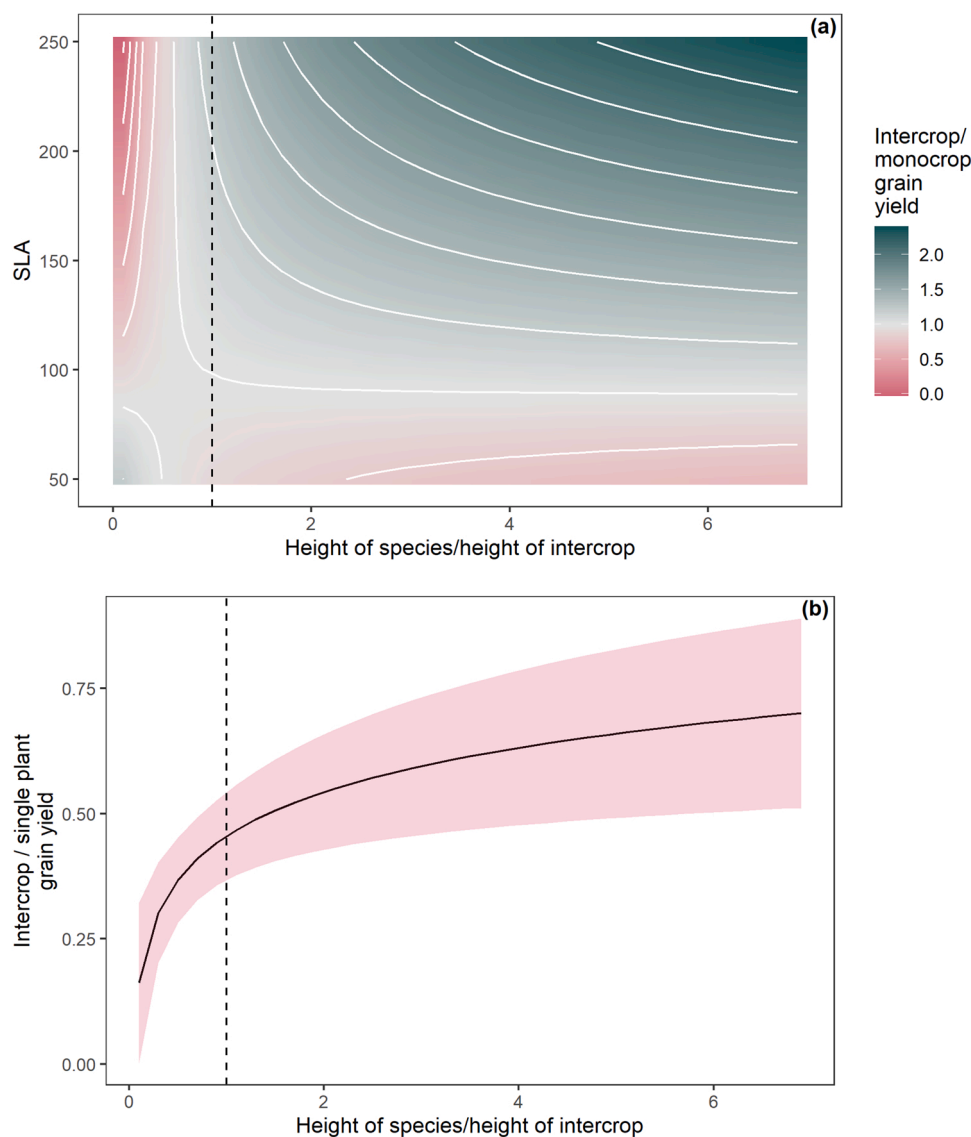
Fig. 5. The final model predictions for (a) the ratio of grain yield in intercrop to monocrop given SLA and relative height of a species, and (b) the ratio of grain yield in intercrop to a single plant given the relative height of a species. SLA was not included in the final model for (a) (Table 2).

combinations are given in the Supplementary materials (Figs. S6 and S7). The effects of height and SLA are not statistically significant in either model, but this was expected given the relatively low number of intercrop combinations (compared with individual species tested in the previous models) and the variance associated with relative yields of two species contributing to the LER (Supplementary Table S3).

A Spearman's rank correlation test comparing whether the predicted grain LERs followed a similar rank order to observed grain yield LERs indicated a reasonable correlation (Spearman's R = 0.67, P = 0.007), with better predictions made for Kibos (Spearman's R for combinations tested at Kibos only = 0.83, P = 0.008) than for Mbita (R = 0.60, P = 0.563) and Zaria (R = 0.5, P = 0.267). In contrast, only a weak correlation was found between observed and predicted biomass LERs (Fig. 8b, R = 0.42, P = 0.048), with better predictions for Zaria (R = 0.79, P = 0.048) but poor prediction for Kibos (R = 0.37, P = 0.336), and Mbita (R = −0.26, P = 0.658).

These results indicate that site-specific differences may influence the effect of traits on intercrop productivity, and indeed, we also found that predicting LERs using models that allowed for differences between sites (using the terms from the models in Supplementary Table S2) explained higher amounts of variation. The model for grain yield LERs had an R^2 of

0.87, and for biomass yield LER the R^2 was 0.39 (Supplementary Table S4).

4. Discussion

4.1. Using height and SLA to predict competition, facilitation, and productivity in intercrops

Our aim was to develop a trait-based approach to screening potential species combinations for overyielding in intercrops using two easily measured functional traits that are indicative of plant ecological strategies. The results of this study indicate that the two traits, relative height and SLA, can be used to predict some of the variation in relative intercrop competition, facilitation, and overall productivity across 8 species grown in 14 different combinations at three sites, suggesting that there is promise in the approach.

Although we found that relative height and SLA only explained a modest proportion of the variation in intercrop productivity (<0.5), the trends we observed for grain yields matched predictions from ecological theory. We found that competition was more likely to decrease for both species in an intercrop when a taller species with a high SLA (indicative
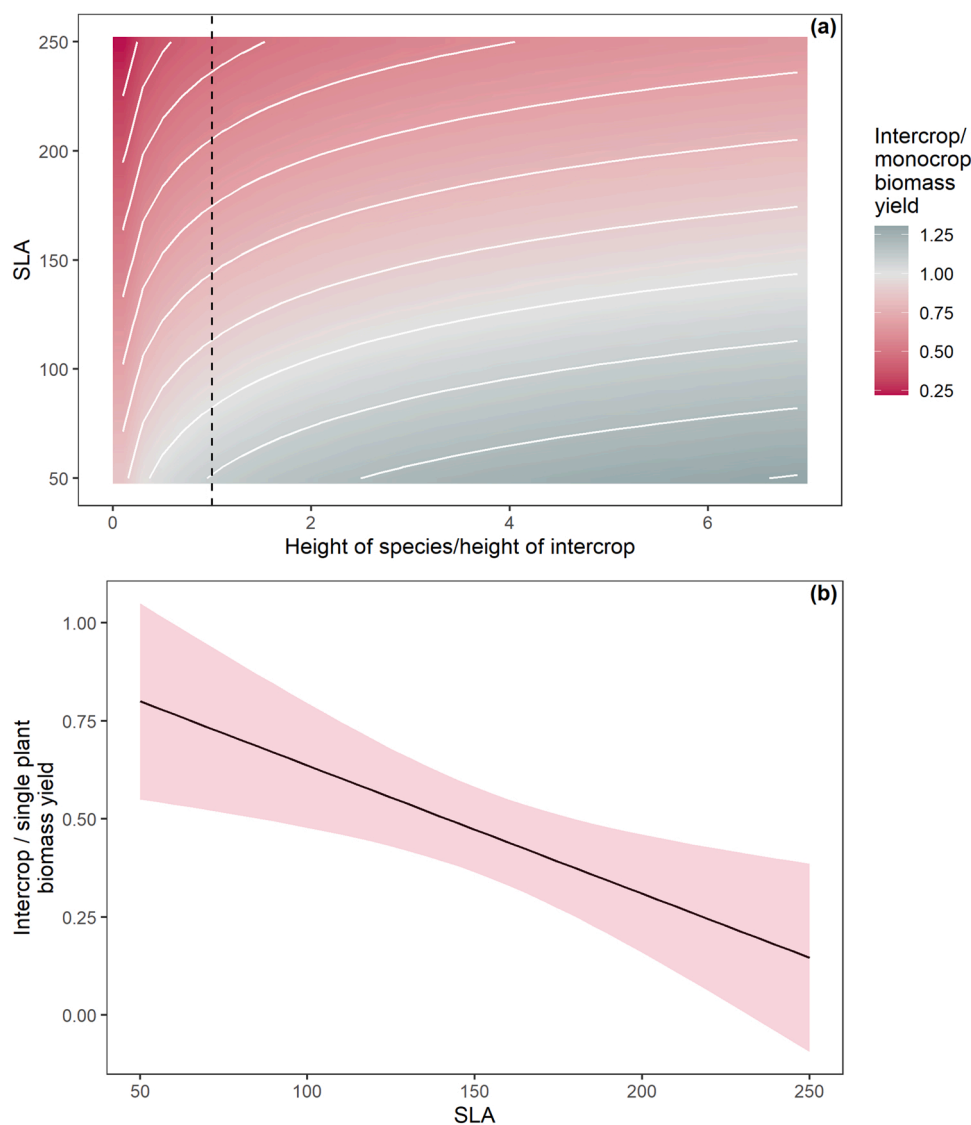
Fig. 6. b The final model predictions for (a) for the ratio of biomass yield in intercrop to monocrop given the SLA and relative height of a species, and **(b)** the ratio of biomass yield in intercrop to single plant given the SLA of a species. Relative height was not included in the final model for (b) (Table 2).

of a 'fast' plant resource economic strategy) was paired with a shorter species with a low SLA (indicative of a "slow" plant resource economic strategy). 'Fast' species tend to do better in high resource availability scenarios (Westoby, 1998; Wright et al., 2004; Reich, 2014), and intercropping these species with less competitive short species thus allows them to access more resources, grow larger, and produce more seed. In contrast, "slow" species are more economically conservative, stress-tolerant, and better at accessing limiting resources, and are thus more able to thrive despite competition imposed by a "fast" partner. Our results suggest that greater complementarity and consequently a more productive intercrop can be achieved by combining one species that can capitalise on additional resource capture with a second species that tolerates competition. In contrast, if both species are 'fast' then the less dominant species is likely to react poorly to competition, and if both are "slow" then neither can take advantage of additional resources.

We did not however find the same pattern for biomass, indicating that different species respond to intercropping by altering their partitioning between vegetative biomass and grain in different ways. Notably, we observed that tall species with a lower SLA tended to produce relatively more biomass than grain when intercropped, while short species with a high SLA tended to produce more grain than biomass in intercropping. There are many potential reasons for this pattern,

including trait-based constraints (perhaps tall species with a lower SLA require more vegetative biomass to increase their grain yield) and adaptive responses to different conditions (perhaps short species with a high SLA allocate more resources to grain sooner, resulting in an overall lower yield but higher harvest index than a short species with a low SLA). However, given the low R^2 of the model for the biomass LER (0.15), we suggest further work is required to confirm this pattern before too much attention is paid to possible mechanisms.

The proportion of the variation explained by relative height and SLA for grain or biomass yield ratios from intercrop combinations relative to monocrops or single plants was always less than 0.5. This suggests that although these two traits may play a role in determining intercrop interactions, much more work remains to be done to understand the remaining variation before this knowledge can be used to reliably predict relative intercrop productivity. Possible explanations for the lack of predictive power and opportunities to improve this approach to intercrop research are discussed below: (1) the importance of site characteristics (environmental context) in determining competitive interactions, (2) contribution of additional traits, and (3) trait plasticity.
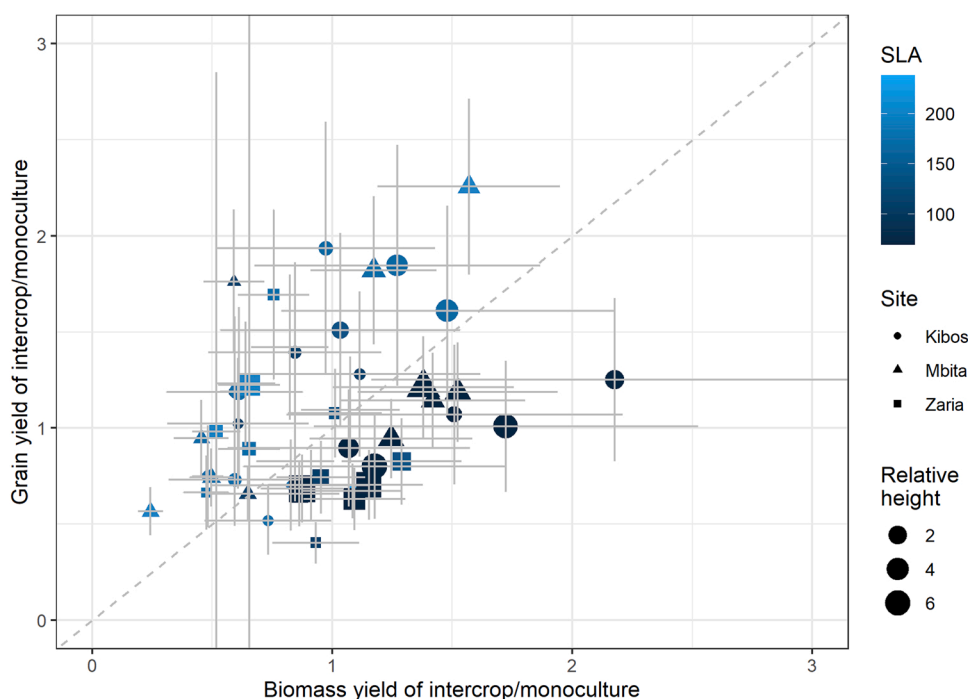
Fig. 7. The relative grain yield of each species at each site in intercrop compared to monoculture plotted against the relative biomass of that species in intercrop compared to monoculture. Point sizes indicate relative height and point colours indicate SLA to highlight that differences in relative grain yield compared to relative biomass yield are associated with differences in these traits. Vertical grey lines indicate 95% confidence intervals for relative grain yield and horizontal grey lines indicate 95% confidence intervals for relative biomass.

4.2. Possible additional sources of variation in intercrop performance

Interactions between traits and site characteristics (different effects of traits under different site conditions) seem particularly worthy of further investigation, given that allowing for an effect of site substantially increased the proportion of the variation explained in relative grain and biomass yields. We could not investigate the cause of site differences in this study because three sites are insufficient to account for the multiple differences in weather conditions and soil characteristics between sites, but other research suggests that trait effects interact with resource availability and physiological stress to determine pairwise interactions between plants. For example, Soliveres et al. (2015) review multiple studies showing that plants are more likely to experience direct facilitation from other plants in stressful or resource-limited environments, and Blonder et al. (2018) emphasise that facilitation depends on interactions between the effects of plant functional traits and specific types of stresses. Copeland and Harrison (2017) show that while productivity is more likely to benefit from facilitation in stressful environments, complementarity is more important in resource-rich, non-stressful environments. The relative importance of facilitation or complementarity under different conditions may thus influence the effects of plant traits on intercrop productivity. The direct effects of the traits themselves on yields may also differ depending on conditions. For example, a high SLA may confer shade tolerance in otherwise resource-rich environments (Bourgeois et al., 2019), so for short plants, either a high or a low SLA may be optimal depending on nutrient and moisture availability.

All our experiments were fertilised, irrigated, and weeded where necessary, and plants were protected from key pests. These management actions are likely to have created more comparable conditions between sites but also would have created resource-rich and low stress environments, limiting the amount of facilitation that occurred within intercrop combinations. On one hand, this was useful to rule out facilitation of non-legumes by legumes so that we could focus on other traits, but on the other hand, our results may not be representative of the potential for facilitation within intercrop combinations in stressful or resource-limiting conditions. However, given that we did observe some variation in responses between sites, it is possible that other site

characteristics such as temperatures and soil type meant that different levels of stress were experienced by plants at different sites, and/or that different amounts of different resources were available at different sites.

The site effect in our study may also have been partially confounded with species effects, given that we grew different sets of species in the different locations (though with some species in common between locations). A species effect in addition to the effects of height and SLA would suggest that other traits are also important. Other studies have highlighted the importance of phenological traits in competitive interactions (Yu et al., 2016a, Engbersen et al., 2021), which we were not able to capture in this study given our single biomass and single grain samples. We could roughly estimate growth rates from the date of our biomass sample (in terms of biomass accumulation per day) but could not consider changes in growth rates throughout the season. Our growth rate estimates correlated strongly and positively with plant height, and so the fact that pigeon pea and maize were more likely to experience both net facilitation and a net competition reduction in this study (Fig. 4a and b) may relate to their growth rate as much as their height. However, a study by Engbersen et al. (2021) indicates that whether growth is concentrated earlier or later in the growing season is key to explaining overyielding, suggesting a more detailed exploration of phenology is required than we could achieve in this study.

Belowground traits are also likely to be important (Homulle et al., 2022). For example, in previous research Engbersen et al. (2021) found that competition for belowground nutrients interacted with aboveground competition for light to determine intercropping outcomes, while Duchene et al. (2017) highlight that plant-microbe interactions can mediate competitive and facilitative effects between plants. Stomph et al. (2020) note that acid-adapted plants can increase nutrient availability to alkaline-adapted plants in acid soils, and vice versa, thus contributing to overall increased productivity. Although we speculated in the introduction of this paper that belowground and aboveground traits may be sufficiently correlated to predict intercrop productivity from aboveground traits alone, the fact that even our models allowing for a site effect typically only explained half the variation in relative yield responses suggests that a wider range of traits should be considered in future research.

Further variation in intercrop productivity may also be explained by
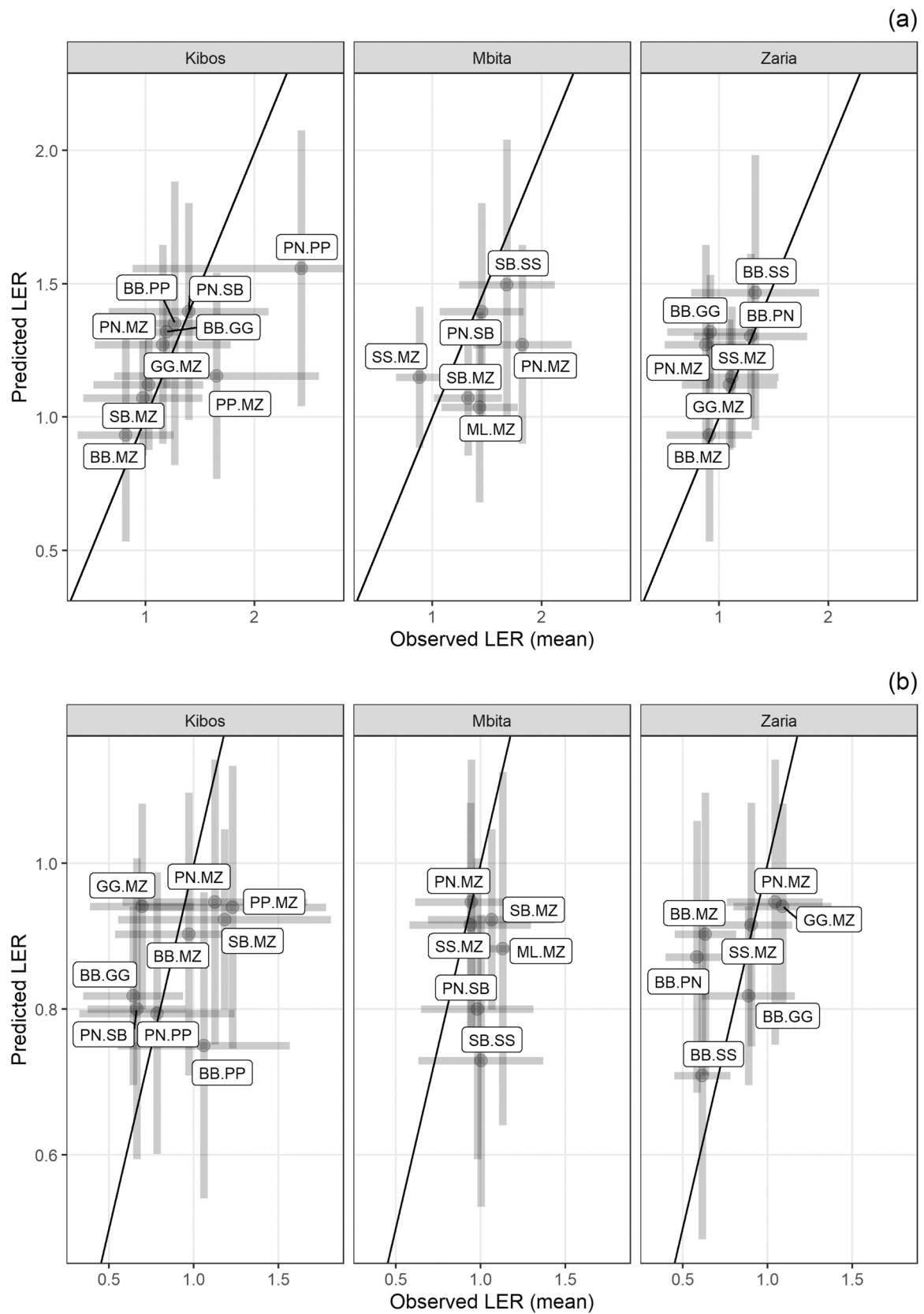
Fig. 8. Predicted LERs against observed LERs for each site, for **(a)** grain yield and **(b)** biomass yield. The diagonal line is a 1:1 line indicating where predicted LERs were better or worse than the observed LERs.

trait plasticity within species. Plants can alter the expression of their traits in response to different conditions, such as when experiencing increased or reduced competition in an intercropping context. The extent to which plants can adapt their traits to these conditions may explain why some species are relatively more productive in intercrop combinations than others. We found some evidence for trait plasticity in this study, in terms of differential allocation of resources to either vegetative biomass or grain depending on whether a plant was grown as a monocrop or in an intercrop combination (Fig. 7). In terms of the two traits used in our models, our measurement of traits had three limitations that meant phenotypic plasticity may have played a role in reducing the explanatory power of the models. Firstly, the traits were only measured at a single site, not accounting for varietal differences or local adaptation. Secondly, SLA was only measured at a single point in the season but is known to be related to developmental stage and, finally, both height and SLA may differ if measured in an intercrop compared to a monocrop. Previous research by Engbersen et al., 2022a found that species that grow relatively taller and have a higher SLA in intercrop than monocrop typically yield more in intercrop compared with species that grow relatively shorter with a lower SLA, while Chen et al. (2021) found that species that grew relatively taller in intercrop tended to have a higher harvest index and species that increased their SLA in intercrop typically had a lower harvest index. Engbersen et al., 2022b also observed that complementarity between intercropped species increases over time, suggesting that plants continue to adapt to their conditions throughout their lifetime, while Stefan et al. (2022a) found generational trait shifts as plant populations adapted to intercropping. Future studies should attempt to quantify species differences in phenotypic plasticity (which is, itself, a trait of interest; Brooker et al., 2022) and the trade-offs between direct measurements of traits and the use of single database values or measurements taken at a single site.

In future research it would also be useful to explore whether our findings regarding optimal traits for intercrop combinations hold across different intercropping arrangements and layouts, which are known to influence yield benefits (Stefan et al., 2022b). In this study we used a simple alternate row replacement design, but it is also common for farmers to use additive designs (where the sowing density of one crop is not reduced to create space for the other). Some farmers will also mix the seed when sowing so that both species emerge within each row, while in some systems, strip intercropping is preferred where several rows of the same species are planted together before alternating with two or more rows of another species. Such arrangements have been shown to increase yields compared with alternate row intercropping (Mucheru-Muna et al., 2010; Rusinamhodzi et al., 2012), and could be explored for their potential to optimise complementary or facilitative relationships between intercropped species.

4.3. Conclusion

This study found support for the idea that differences in plant traits can be exploited to optimise intercrop combinations to increase yields, beyond established effects such as temporal niche separation and cereal-legume combinations. Two simple functional traits indicative of "fast" vs "slow" plant resource economic strategies, relative height and SLA, explained some variation in intercrop land productivity. Our results suggested that intercropping two species with divergent resource economic strategies could increase complementarity, and thus increase land productivity. However, these two traits explained less than 50 % of the variation and cannot consistently predict land productivity. Much more research is required before a trait-based framework could be reliably used by farmers or others to identify optimal intercrop combinations. In particular, we recommend that future research further explores (1) interactions between the effects of traits and site conditions (resource availability and stress), (2) additional traits beyond height and SLA, and (3) trait plasticity in response to intercropping. We hope this article inspires other researchers to contribute to developing a trait-based

understanding of intercrop productivity that could be used to help realise the potential of intercropping.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2023.108926.

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