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RESEARCH ARTICLE

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Crop genotypic richness enhances biomass production and phosphorus acquisition in maize-mycorrhiza symbiosis

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Societal Impact Statement

Our study tests how soil and plant biodiversity can enhance sustainability of crop production in Kenya. We tested whether mixtures of maize varieties performed better than monocultures and tested their response to arbuscular mycorrhizal fungi. Mycorrhizal responsiveness differed significantly by maize variety, and genetic mixtures outperformed monocultures. These findings demonstrate the benefits of using naturally-occurring soil microorganisms in combination with genetic mixtures of crops to enhance food security.

Summary

- Plant genetic diversity is a key component of biodiversity but one that is often overlooked when considering the adoption of sustainable strategies to enhance crop production, such as inoculation with arbuscular mycorrhizal (AM) fungi. Here, we tested the hypothesis that the biomass of the most responsive maize genotypes to AM fungal inoculation when grown in genetic monoculture would be enhanced when grown in mixtures comprising a mix of genotypes (polyculture).
- In a first experiment, maize varieties were inoculated with *Rhizophagus irregularis* or *Funneliformis mosseae* or left uninoculated. We measured key growth parameters, AM fungal colonisation and phosphorus uptake and calculated mycorrhizal responsiveness. A second experiment evaluated the effect of crop genetic diversity on productivity by growing the four most responsive varieties as either monocultures or polyculture, with and without AM fungal inoculation.
- Mycorrhizal responsiveness differed significantly by maize variety, with some varieties demonstrating greater benefits from AM fungi. Polycultures outperformed monocultures in terms of AM fungal colonisation, biomass and phosphorus capture, which were driven by a combination of complementarity and facilitation effects resulting from biodiversity.
- Our findings demonstrate the critical role played by AM fungi in shaping crop genotype performance and the potential benefits of moving away from cropping systems that rely on genetic monocultures. The use of AM fungal inoculum in

combination with targeted locally adapted crop genotype mixtures maximises plant nutrient efficiency and productivity and provides a sustainable approach to maize production in sub-Saharan agroecological systems.

KEYWORDS
arbuscular mycorrhizal fungi, genetic diversity, Kenya, maize varieties, phosphorus, productivity, sub-Saharan Africa, symbiosis

1 | INTRODUCTION

The world's population faces multiple food insecurity challenges arising from the need to increase crop productivity and nutrition whilst minimising environmental impacts and using fewer resources. More than 70% of the world's food is produced by smallholder farmers who are excessively burdened by resource scarcity, poor soils and unreliable weather caused by climate change (Vanlauwe et al., 2015). This challenge is best illustrated in maize (*Zea mays* L.), a staple crop for millions of people, but farmers are finding it difficult to meet the rising demand (Shiferaw et al., 2011). Maize is globally cultivated due to its adaptation to different agro-ecological conditions (Hussain et al., 2021) and is a major source of calories and nutrition for many populations, but especially for African nations. In Africa, the crop is cultivated by smallholder farmers who struggle to maintain crop production because they lack resources and face compounding challenges of pests, disease and drought (Clora et al., 2021). Farm inputs such as fertilisers, pesticides and herbicides are expensive and unaffordable for many (Pasley et al., 2019). Besides, synthetic fertilisers and other farm inputs have been reported to pose potential pollution risks to the environment and have negative effects on animal and human health (Rashmi et al., 2020). Therefore, the increasing demand for food requires the adoption of innovative and sustainable solutions to increase agricultural production, especially for staple cereals like maize. One approach is to target locally adapted crop varieties which offer promise for increasing yield and resilience whilst requiring fewer resources (Shiferaw et al., 2011). In Kenya, 3-year randomised trials showed that locally adapted maize varieties led to increased productivity, for both for better-resourced farmers who used non-adapted hybrids and fertiliser prior to the intervention and less well-resourced farmers (Bird et al., 2022). But there remains uncertainty in identifying the mechanisms of such results, especially those related to resource capture from soils.

To increase crop productivity, enhancing soil fertility is crucial and in many regions of sub-Saharan Africa, phosphorus (P) is the principal nutrient limiting plant growth, primarily because tropical soils are highly weathered and P is tightly fixed to soil surfaces or bound with other elements to form insoluble forms (Magnone et al., 2022). Furthermore, the growing demand for P fertilisers has led to an increase in depletion of global supplies of rock phosphate, which is the primary source of P for fertiliser manufacture. Meeting global food security demands hinges significantly on P availability, with projections indicating a five-fold rise in elemental P application required by 2050 (Stewart et al., 2020). Therefore, the supply of P cannot be sustained, particularly because the supply of rock phosphate is expected to 'peak' in the next 30–300 years (Cordell & White, 2011; Cordell et al., 2009). This looming crisis highlights the critical need for tailored approaches for small-scale farming to efficiently address P deficiency.

One approach to address this issue is to use more affordable solutions such as biofertilisers (Bender et al., 2016) comprising beneficial microorganisms to enhance P accessibility in soil (Raimi et al., 2017). A key group of soil microorganisms are arbuscular mycorrhizal (AM) fungi, which are obligate symbionts that colonise the roots of most land plants, including the Poaceae (grasses) that contain all the major cereal crops, including maize (Chu et al., 2013). Mycorrhizal fungi often have wide-ranging benefits and can improve soil structure, nutrient uptake, growth and development of plants (Smith & Read, 2008). These effects are often seen both in natural communities of plants and in cultivated crop plants, of which many form AM fungal associations. For example, a recent meta-analysis found that inoculation of field-grown crops with AM fungi increased their biomass and yield in around 75% of studies (Zhang et al., 2019). Maize is generally considered to be one of the most mycorrhizal responsive cereal species, and several studies have shown AM fungi promote biomass, yield and nutrition (e.g. Chu et al., 2013, 2020). In addition, AM fungi have been found to increase the tolerance of maize to environmental stressors such as drought and salinity (Huang et al., 2020).

The response of plants to AM fungi is however complicated because the identity of the host plant and fungus, and their interaction with the environment, can substantially alter the resulting mycorrhizal phenotype, especially in terms of the key functional attribute of resource exchange (Johnson et al., 1997). Moreover, these outcomes are not just a product of the species involved, but also the genotype (Johnson et al., 2012). Indeed, individual AM fungus × plant genotype combinations have been shown to vary widely in a range of key traits including growth and nutrition of wheat lines (Thirkell et al., 2022). Screening how varieties of maize respond to AM inoculation confirms there is significant variation in the benefits incurred by the fungi (An et al., 2010), especially in terms of P uptake (Sawers et al., 2017). These findings, based largely on South American varieties of maize, provide rationale for testing how varieties relevant and available to sub-Saharan smallholder communities may also vary in their responsiveness to AM fungi.

A further strategy that can be used to enhance productivity is to manipulate biodiversity (Cappelli et al., 2022). Indeed, there is now a rich mechanistic and theoretical understanding of the importance of

biodiversity for regulating specific ecosystem functions including plant production and its resilience to climatic extremes (Isbell et al., 2015) and more recently as a driver of ecosystem multifunctionality (Allan et al., 2015; Maestre et al., 2012; Soliveres et al., 2016). Genotypic diversity is increasingly recognised as a key component of biodiversity that regulates numerous ecosystem processes in natural communities (Johnson et al., 2012), including resilience against climate change (Zhu et al., 2000) and pests (Tooker & Frank, 2012). A key consequence of genotypic diversity is variation in traits, and it is this variation that is likely to impact ecosystem processes, such as nutrient acquisition, and resilience (Jacott, 2017). Based on the observations of variation in genotype responses to AM fungi and environment, noted previously, there is emerging evidence that mixtures of crop cultivars may perform better than monocultures (Reiss & Drinkwater, 2018) and can have greater resilience to pests, diseases and other perturbations (Isbell et al., 2015; Tooker & Frank, 2012). Yet, the number of experiments that have manipulated intra-specific richness of crops remains limited (Reiss & Drinkwater, 2018; Tooker & Frank, 2012). Thus, it is now timely to test how crop genotypes interact in mixtures, especially where panels of locally-adapted crop varieties can be leveraged, as is the case for many small-holder farmers in sub-Saharan Africa. For example, mixture effects may be non-additive so that the use of 'sentinel' genotypes with low relative abundance may provide disproportionate positive effects on resilience or key ecosystem services, as seen in natural systems (Reiss & Drinkwater, 2018; Soliveres et al., 2016).

Here, we address these gaps in knowledge and focus on how maize varieties that are locally adapted to Kenya respond to AM fungal inoculation and how they performed in genetic monocultures and polycultures. We hypothesised that mycorrhizal responsiveness varies across maize genotypes and that this variation is underpinned by differences in P capture. We also hypothesised that using responsive genotypes in polycultures increases productivity and nutrient capture compared to monocultures due to a combination of selection and complementarity effects (Loreau & Hector, 2001).

2 | MATERIALS AND METHODS

2.1 | Soil sampling and physico-chemical analysis

Soil samples were collected from the Kenyatta University (KU) farm using a random sampling approach and then pooled together and homogenised. The sampling was carried out within a depth of 5–20 cm from the upper soil surface, which represents the active root zone for maize, where most nutrient uptake, particularly P, and microbial interactions occur. Soil pH was 6.75 and was measured in a 3:1 deionised water:soil slurry with a glass electrode. Subsequently, the soil samples were air-dried, pulverised and sieved (2 mm). Soil organic C was analysed by chromic acid titration (Walkley & Black, 1934), total N by Kjeldahl digestion (Bremner, 1960), Mg, K and Ca by atomic absorption spectroscopy following ammonium acetate extraction and Fe, Cu, Zn and Mn by atomic absorption spectroscopy following DTPA extraction. Soil phosphorus was extracted using a Mehlich 2 extraction (that contains acetic acid, ammonium chloride, hydrochloric acid, hydrofluoric acid and demineralised water) and analysed by calorimetric technique using the molybdenum blue method (Murphy & Riley, 1962). These analyses revealed 2.35% total organic C, 0.21% total N, 96.6 ppm P, 1.20% K, 1.0% Ca, 4.57% Mg, 39.1 ppm Fe, 1.76 ppm Cu, 27.0 ppm Zn and 0.63% Mn.

2.2 | AM fungal inoculum

Two AM fungal species, *Rhizophagus irregularis* and *Funneliformis mosseae*, were used in this study. These fungi were obtained from International Bank of Glomeromycota INRA, France, and multiplied at Kenyatta University greenhouse using Bermuda grass (*Cynodon dactylon*) as the host plant. A uniform mixture of the crude source of inoculum was created by severing the roots into small pieces and mixing with the soil while the shoots were cut off and discarded. The AM fungal inoculum was made up of small root segments, mycelium and 80–90 spores per kilogram of substrate as quantified using the wet sieving and sucrose density centrifugation method (Gerdemann & Nicolson, 1963).

2.3 | Maize varieties

Twenty varieties of maize seeds were obtained from farmers and established Kenyan seed distributors. The selection of these varieties was to ensure we captured a range of distinctive characteristics and to represent Kenya's various altitudinal growth zones (Table 1).

2.4 | Planting and maintenance of greenhouse bioassays

The maize seeds were surface sterilised before planting. The seeds were cleaned with soapy water and rinsed with distilled water and put in 70% ethanol for 30 s and immediately washed with sterile distilled water. The seeds were then exposed to 3% sodium hypochlorite for 2 min and rinsed three times with sterile distilled water.

Forty grams of the AM fungal inoculum was spread in the soil at a depth of 1 cm below the seeds in the +AM fungal treatments. The same quantity of autoclaved inoculum was applied in the non-mycorrhizal treatments. In order to reduce the variation in the soil microbial communities between the two treatments, 10 mL of a spore-free filtrate (0.22-μm filter) of the inoculum was added to the non-mycorrhizal treatment, and 10 mL of distilled water was added to the mycorrhizal treatment.

A first experiment was established to determine the responsiveness of the 20 Kenyan maize varieties to AM fungi and was conducted in a greenhouse at KU. The experiment was set up in a completely randomised design with four replicates per treatment resulting in a total of 240 pots (20 varieties × 3 treatments × 4

TABLE 1 Characteristics of Kenyan maize varieties and their predicted responsiveness (MR) to inoculation with arbuscular mycorrhizal (AM) fungi.

Altitude zone	Maize variety	Code	Variety type	Special attributes	MR	Source
Highland	KH 600-15A	V15	Hybrid	Good stand ability; double cobber	Neutral	East African seed company
	H6213	V13	Hybrid	High yielding; drought tolerant	Neutral	Kenya seed company
	H628	V6	Hybrid	Flint	Neutral	
	WH605	V11	Hybrid	Tolerant to MSV, GLS, and blight. Good tolerance to low nitrogen	+Ve	Western seed company
	N8	V17	Landrace	High yielding	Neutral	Farmer
	KSTP	V20	Landrace	Striga resistant	Neutral	
	CNL 216	V19	In-bred line	High quality protein	Neutral	
	144	V18	In-bred line	High quality protein	Neutral	
Medium altitude	H513	V16	Hybrid	Good stand ability; partially tolerant to MSV	Neutral	Kenya seed company
	H6506	V12	Hybrid	Short and resistant to lodging. Resistant to GLS.	Neutral	
	H624	V5	Hybrid	High yielding; tolerant to GLS, leaf blight, rust	Neutral	
	WH505	V10	Hybrid	Drought tolerant; tolerant to most leaf diseases	+Ve	Western seed company
	WH403	V9	Hybrid	Tolerant to leaf diseases; green stems at harvest	+Ve	
Mid to low altitude	Duma 43	V7	Hybrid	Very early maturing	+Ve	Seed co.
	Tosheka (MH-401)	V14	Hybrid	Early maturing; drought tolerant	Neutral	East African seed company
Dry low to mid altitude	DH04	V2	Hybrid	Drought tolerant; short stature; good husk cover	+Ve	Kenya seed company
	DH02	V1	Hybrid	Early maturing; stays green	Neutral	
Lowland	WH101	V8	Hybrid	Tolerant to drought, low nitrogen, MSV, GLS and blight	+Ve	Western seed company
	PH1	V3	Hybrid	Drought tolerant	+Ve	Kenya seed company
	PH4	V4	Hybrid	Heat tolerant; partial resistance to MSV	Neutral	

Note: +Ve = positive.
Abbreviations: GLS, grey leaf spot; MR, mycorrhizal responsiveness based on P response ratio; MSV, maize streak virus; N8, Namba nane.

replicates). The pots had a capacity of 3.5 L with a diameter of 16 cm, and had small holes drilled at the bottom to ensure adequate drainage. The pots were randomly arranged in the greenhouse and their positions rotated on a weekly basis. The maize seeds were planted in pots filled with autoclaved loam soil and sand mixed at a ratio of 4:1. The maize varieties were independently inoculated with two AM fungal species, *Rhizophagus irregularis* and *Funneliformis mosseae*, and the control pots were mock-inoculated with sterile AM fungal inoculum resulting in three treatments. During planting, four maize seeds were planted in each pot then thinned to two plants per pot after germination. The plants were watered with sterile water every 3 days. During the growth period, day temperature ranged from 20.7°C to 38°C while the night temperature ranged between 14°C and 18°C. The plants were monitored regularly for 7 weeks and thereafter harvested to determine the maize varieties with high mycorrhizal growth response (MGR). MGR was quantified by dividing the mean biomass of uninoculated plants (*NM*) by the biomass of inoculated plants (*AMF*) in individual pots and expressing it as a percentage (Veiga et al., 2011):

$$\mathrm{MGR}\% = 1 - ((NM/AMF) * 100)$$

A second experiment determined the effect of maize genetic diversity on productivity and nutrient uptake. Four maize varieties with the highest MGR measured in the first experiment were selected and used in monocultures and polycultures.

For the second experiment, two AM fungal species, *Rhizophagus irregularis* and *Funneliformis mosseae*, were mixed in a 1:1 ratio and inoculated to the maize planted as monocultures (four treatments comprising each selected maize variety) or polycultures (one treatment comprising a mixture of four varieties used in monocultures). Each pot contained four individual plants. The experiment was set up in a greenhouse at KU using a completely randomised design with each treatment replicated four times, resulting in a total of 40 pots (5 genotype treatments × 2 AM fungal treatments × 4 replicates). The controls were mock-inoculated. The maize plants were grown in pots containing autoclaved loam soil and sand mixed in a 4:1 ratio. We used clear plastic pots of 17 L capacity, with a diameter and height of 28 cm. The pots were perforated at the bottom to prevent

waterlogging. Wide-mouthed 10 L pots were used to provide enough space for the plants to grow. The plants were routinely watered and maintained in the greenhouse for 7 weeks, after which the maize plants were harvested and analysed for AM fungal root colonisation, shoot biomass and shoot P.

2.5 | Maize plants harvesting and shoot P analysis

Three weeks after germination, maize chlorophyll content was assessed weekly using a Konica Minolta SPAD chlorophyll meter. At harvest (7 weeks), plant height was measured, and the shoots were cut off at a height of 0.5 cm above the soil to separate the roots from the shoots. A portion of the roots was immediately preserved at −20°C for subsequent analysis to assess AM fungal colonisation. The remaining roots and shoots were air-dried to obtain the plant dry weight. The shoot P concentration was determined using the acid digestion and photometric protocol described by Murphy and Riley (1962). A gridline intersect technique was used to quantify AM colonisation (Giovannetti & Mosse, 1980). Roots were first thawed then samples weighing 0.5 g were bleached using 10% (w/v) potassium hydroxide (KOH) and stained with 0.05% (w/v) trypan blue (Phillips & Hayman, 1970). The root samples were then examined under a Leica stereomicroscope at magnifications ranging from ×250 to ×400 to estimate the percentage of root sections containing hyphae, vesicles and arbuscules.

2.6 | Data analysis

All statistical analyses were conducted using R (version 4.3.1; R Core Team, 2003). Data visualisation and model diagnostics were performed to ensure the assumptions of statistical tests were met.

2.6.1 | Data exploration and normality testing

Prior to conducting inferential statistical analyses, we assessed the normality and homogeneity of variance of the following response variables: shoot biomass, root biomass, shoot phosphorus concentration, AM fungal colonisation, plant height and SPAD readings. We used a combination of graphical and statistical methods for this assessment: Histograms of each response variable were plotted using base R to visually inspect the distribution for deviations from normality (e.g., skewness, kurtosis). Levene's test for homogeneity of variance was performed using the leveneTest function in the *car* package (Fox & Weisberg, 2019). This test assesses whether the variances of the response variable are equal across groups (defined by AM fungal treatment, variety and/or planting treatment). A p-value < 0.05 was considered indicative of significant heterogeneity of variance. After fitting initial linear models (see below), we examined plots of residuals versus fitted values and normal Q-Q plots of the residuals to further assess normality and homogeneity of variance assumptions using base R.

2.6.2 | Experiment 1: Screening maize varieties for responsiveness to AM fungi

To analyse the effects of AM fungal inoculation and maize variety on the response variables in the first experiment, we initially fitted ordinary least squares (OLS) linear models. The general form of the model was: Response Variable ~ AM fungal Treatment × Variety. For response variables where the assumptions of normality and/or homogeneity of variance were violated (as determined by the tests described above), we employed generalised least squares (GLS) models using the gls function in the *nlme* package (Pinheiro et al., 2023). GLS models allow for the specification of different variance structures, accommodating heteroscedasticity. For each response variable where a GLS model was considered, we compared the GLS model to the corresponding OLS model using a likelihood ratio test (implemented via the anova function in R) and Akaike's Information Criterion (AIC). The GLS model was selected if it provided a significantly better fit to the data (likelihood ratio test $p < 0.05$) and had a lower AIC value ($\Delta AIC > 2$) compared to the OLS model. In all GLS models, we modelled the variance structure using the varIdent function within the weights argument of the gls function. This allows for different variances for each level of the interaction factors. This was chosen through diagnostic plots of model residuals vs. fitted values. Factors were assessed in the final models for significance using ANOVA tests.

2.6.3 | Experiment 2: Effect of genetic diversity (monocultures vs. polycultures)

For the second experiment, we used a similar approach, but the initial OLS models included an additional factor for planting treatment: Response Variable ~ AM fungal Treatment × Planting Treatment × Variety. We also included 'pot identity' as a random factor to consider data obtained from individuals from the same pot. This requirement was only relevant for the genetic mixture treatment, where pots comprised an individual of each of 4 maize varieties. The response data for the monocultures was combined to give a single value per pot. The same process of model diagnostics, GLS model consideration, variance structure, model selection (using likelihood ratio tests and AIC), and significance testing was followed as described for Experiment 1. To test whether these effects could be attributed to complementarity versus sampling effects, we applied the sample_to_population_partition function from the *partitionBEFsp* package (Clark et al., 2019). This function applies the net biodiversity effect equations provided by (Loreau & Hector, 2001).

2.6.4 | Post hoc comparisons

Following significant ANOVA results of predictor variables, we performed post hoc comparisons to determine which specific group means differed significantly. We used the *emmeans* package

(Lenth, 2023) to compute estimated marginal means (EMMs) and pairwise comparisons among levels of significant factors and interactions. We applied a multivariate t (mvt) correction to adjust *p*-values for multiple comparisons, controlling the family-wise error rate.

2.6.5 | Data visualisation

All figures were created using the *ggplot2* package in R. Final figure preparation and annotations were performed using Inkscape version 1.3. To simplify visualisation, response ratio was calculated by dividing the AM fungal treatment response by the average under uninoculated control conditions.

3 | RESULTS

3.1 | Interactions between maize genotype and AM fungal inoculation

None of the uninoculated plants contained mycorrhizal structures in their roots. There was a significant interaction between maize genotype and AM fungal inoculation to all measured plant variables ($p < 0.001$, Table 2, Figures 1 and S1–S3). The shoot biomass of most varieties had no significant response to AM fungal inoculation (Figure 1). However, there were plant genotypes that had a positive response to both AM fungal species (V10, V11, V9), a positive response to a single species and no response to the other (V7, V8, V2, V16), a negative response to a single species (V17, V20) or a negative response to both species (V15, Figure 1). Root biomass contrasted with these effects as all but one variety (V2) exhibited a positive response to AM fungal inoculation, although the amount root biomass increased relative to the control varied depending on the AM fungal species (Figure 1).

P concentrations did not increase in most varieties (Figure 1) in response to inoculation. Nevertheless, some genotypes demonstrated a positive increase in P concentration regardless of which fungal species was used for inoculation (V11, V10, V9, V3), while others demonstrated a positive response to a single AM fungal species (V7, V2). No AM fungal colonisation was observed in any uninoculated treatments, and colonisation varied across maize varieties (Figure 1). Overall, shoot P concentrations increased with AM fungal colonisation (Figure 2). However, the strength of this relationship varied significantly among maize varieties (Figure 2, $p < 0.001$). Some varieties showed a positive response to AM fungal colonisation (increased in P relative to uninoculated controls), while others showed no significant response.

3.2 | Interactions between maize genotype, AM fungal inoculation and mono/polyculture planting

To assess the impact of polyculture planting on AM fungal inoculation, three top performing varieties (V9, V10, V11) and one poorer performing variety (V8) were used in a further greenhouse experiment. As expected, the varieties demonstrated similar responses to AM fungal inoculation (Table 1). Shoot root and shoot biomass were generally increased in response to inoculation, and there were increases in P concentration (Figure S3). There was no evidence of AM fungal colonisation in uninoculated controls.

There was a main effect of the planting treatment on every metric assessed (Table S1). These effects included a positive effect of polyculture planting on total biomass, shoot P concentration and AM fungal colonisation (Figure 3). These effects were found to be significantly attributed largely to a complementarity effect, with some metrics (shoot P concentrations and SPAD) also driven by a selection effect (Table 3). There were few interactive effects between mono/polyculture planting regime and AM inoculation (Table S2).

4 | DISCUSSION

A key finding from our work was that maize varieties grown in polycultures consistently outperformed monocultures, which supports our hypothesis. The improved performance of polycultures in terms of biomass, total P and AM fungal colonisation highlights the importance of genotypic diversity of populations in shaping biodiversity-ecosystem function relationships (Johnson et al., 2012; Reiss & Drinkwater, 2018) and also corroborates recent work using mixtures of maize cultivars in China (Su et al., 2024).

TABLE 2 Test statistics from ANOVA of plant response variables of different maize varieties to inoculation with either *R. irregularis* or *F. mosseae* and their interactions.

	AM fungal treatment		Variety		Interaction	
Variable	*F* value	*p* value	*F* value	*p* value	*F* value	*p* value
Shoot dry weight	26.13	<0.001	40.96	<0.001	6.20	<0.001
Root dry weight	244.4	<0.001	47.06	<0.001	2.32	<0.001
Shoot P concentration	41.83	<0.001	24.13	<0.001	1.70	<0.001
AM fungal colonisation	4285	<0.001	38.52	<0.001	15.57	<0.001
Height	65.17	<0.001	39.27	<0.001	2.04	0.001
Shoot density	13.52	<0.001	21.61	<0.001	2.49	<0.001
SPAD	14,560	<0.001	59.00	<0.001	10.10	<0.001

Abbreviations: AM, arbuscular mycorrhizal; SPAD, leaf chlorophyll.

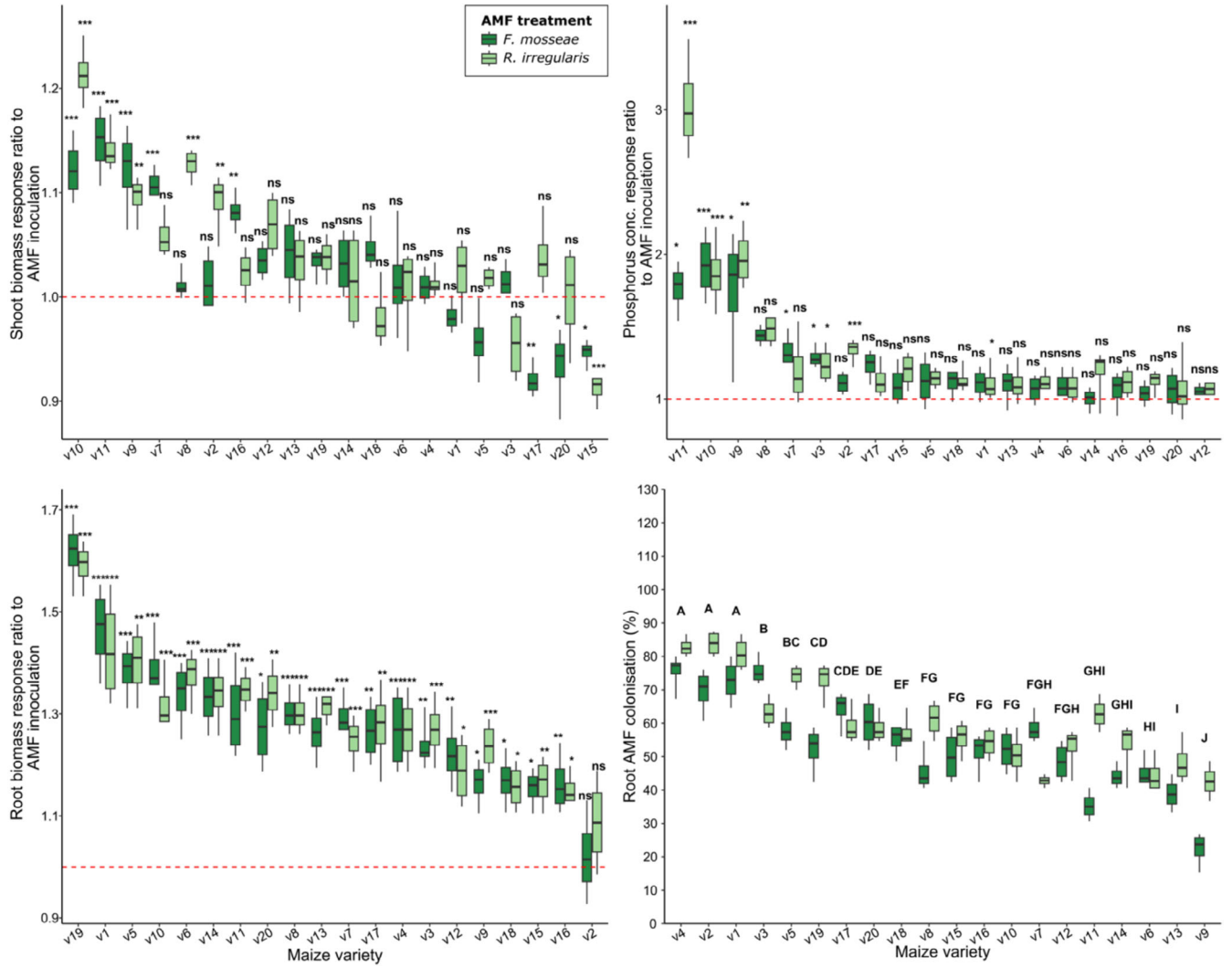

FIGURE 1 Shoot and root biomass and P concentration response ratios and arbuscular mycorrhizal fungal (AMF) colonisation in different varieties of maize in response to two AM fungal species. Red horizontal lines represent a response ratio of 1 (equal to the mean of the control). Horizontal lines represent median values, boxes represent the interquartile range, and vertical lines represent the data range. For shoot and root biomass and phosphorus concentration, asterisks represent whether the AM fungal treatment is significantly different to the uninoculated control according to post hoc analysis (*** < 0.001, ** < 0.01, * < 0.05, ns = non-significant). For AM fungal colonisation, letters represent varieties that significantly differ according to post hoc analysis.

In polycultures, we found the outcomes of interactions of maize varieties were shaped by both selection and complementarity effects. Selection occurs when high performing genotypes that dominate production are present in a mixture, resulting in an overall increase in productivity (Loreau & Hector, 2001). The polycultures exhibiting a superior performance in the study probably included a genotype with optimal resource utilisation efficiency, competitive capability and mycorrhizal responsiveness that generally improves biomass accumulation. Complementarity often results from resource partitioning, and thus, the responses we observed may be driven by genotypes having preference for different forms of nutrients, notably P (Ahmad-Ramli et al., 2013), thus minimising intraspecific competition and maximising resource use through different root structures or nutrient uptake strategies (Loreau & Hector, 2001; Maestre et al., 2012). However, facilitation among varieties may also be occurring where some varieties ameliorate the growth conditions of others, for example, by altering root secretions or microbial associations (Brooker et al., 2021). In our system, where root systems and their associated AM fungi could interact, complementarity may also be driven by formation of common mycorrhizal networks that can generate a range of potential benefits (Alaux et al., 2021; Babikova et al., 2014) even if the hyphae do not form continuous connections (Rillig et al., 2024). Other mechanisms explaining complementarity effects may arise from production of signalling molecules in root exudates that have been shown to regulate competition in grassland (Semchenko et al., 2019; Semchenko et al., 2021).

Besides biomass production, polyculture systems can provide multiple benefits including increased resistance to diseases, enhanced

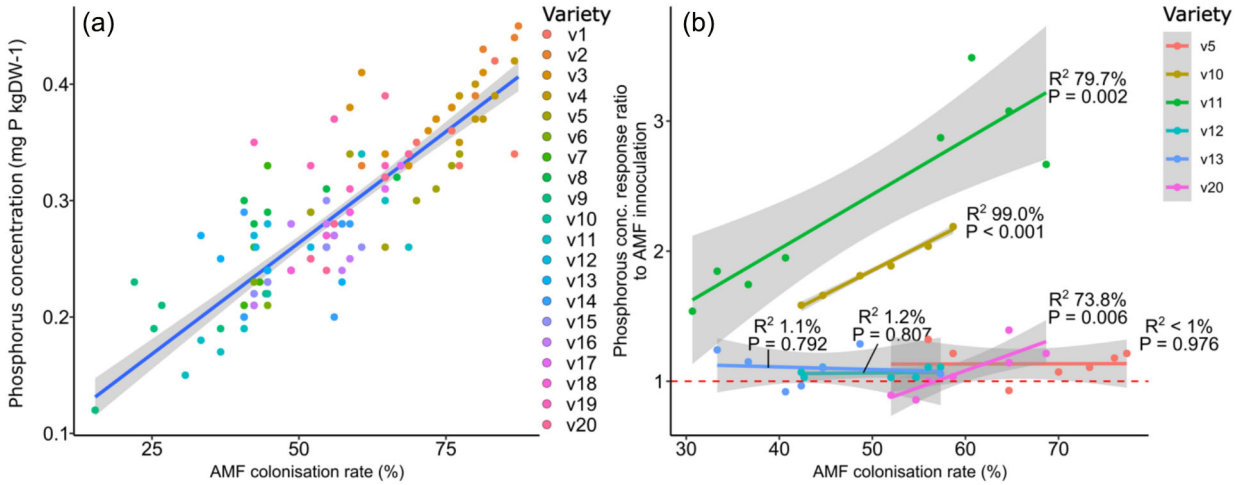

FIGURE 2 Relationship between arbuscular mycorrhizal (AM) fungal colonisation of different maize varieties and (a) shoot P concentration and (b) shoot P concentration response ratio of six varieties that had the three highest and three lowest regression slopes. Shaded areas represent 95% confidence intervals.

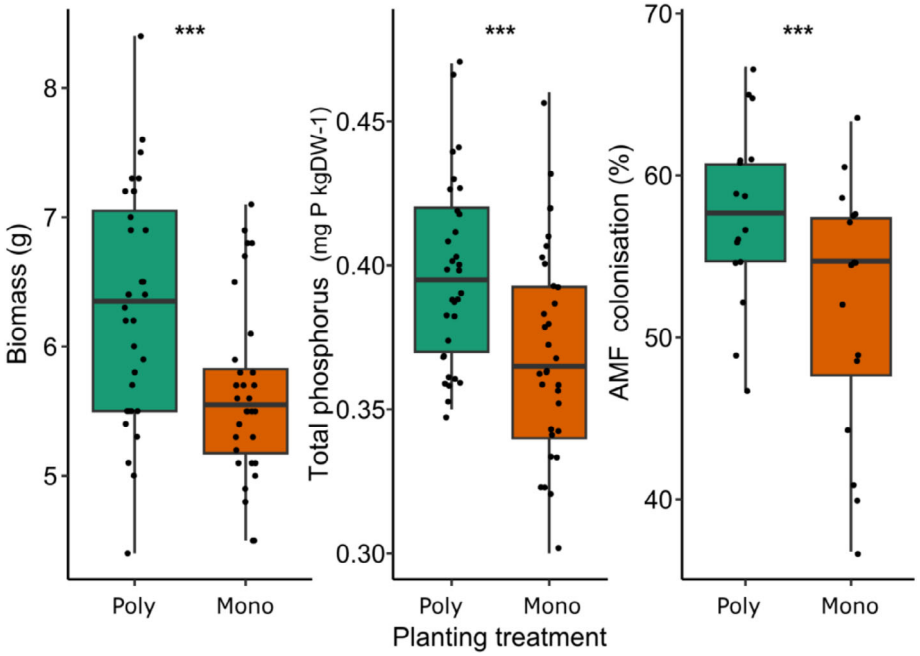

FIGURE 3 Plant biomass, total shoot P concentration and arbuscular mycorrhizal fungal (AMF) colonisation in mixtures (poly) or monocultures (mono) of maize varieties. Horizontal lines represent median values, boxes represent the interquartile range and vertical lines represent the data range. Overlaid dots represent individual data points. ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

	Sampling effect			Complementarity effect		
	Mean	Std dev	*p* value	Mean	Std dev	*p* value
Shoot dry weight	0.01	0.02	0.337	14.87	0.66	**<0.001**
Root dry weight	0.02	0.05	0.458	6.86	0.91	**<0.001**
Shoot P concentration	<−0.01	<0.01	**0.001**	1.27	0.04	**0.012**
Height	−0.98	0.69	0.063	378	6.27	**<0.001**
Shoot density	<−0.01	<0.01	0.048	0.12	0.01	**<0.001**
SPAD	<0.01	<0.01	**0.011**	0.13	<0.01	**<0.001**

TABLE 3 The mean effect attributable sampling and complementarity effects on key plant response variables underpinning net diversity effects of polycultures of maize varieties.

Abbreviation: SPAD = leaf chlorophyll.
Note: Bold indicates significant values.

resilience to climatic stresses and improved resource use efficiency (Zhu et al., 2000). Mixing genotypes promotes functional diversity, thereby cushioning plants against environmental fluctuations and curbing pathogen attacks (Stewart et al., 2020). However, there are implementation hurdles relating to optimising plant designs and harmonising growth cycles to ensure maximum return (Hussain et al., 2021). Plant differences in maturity rates, competition for resources and harvesting logistics must be put into consideration for polyculture systems to succeed in smallholder and industrial agriculture. In addition, our study was conducted under controlled conditions, but the results align to result field trials with mixtures of maize genotypes (Su et al., 2024). Furthermore, there remains a need to explore the mechanistic drivers in natural environments where variability in soil properties, competition and more complex microbiomes may alter these interactions. For example, under more realistic growth conditions, it has been shown that genetically diverse mixtures of grassland communities can select for a less diverse pool of AM fungal species compared to communities with little genetic diversity (Johnson et al., 2010). Determining whether our current results are reproducible under field conditions will be crucial in selecting genotypic combinations for sustainable agriculture. Finally, we measured biomass production after just 7 weeks, which is about half the time required to reach maturity and flowering. While maize yield can be accurately predicted from early growth rates (Liu et al., 2020), clearly more refined analyses are needed to confirm the impacts of polyculture on grain yield.

The results from our work are consistent with previous findings (Chen et al., 2017; Huang et al., 2020; Smith et al., 2011) that AM fungi significantly improve maize growth, particularly in terms of biomass production and P uptake. A well-known regulator of mycorrhizal responsiveness, including for maize, is soil P availability (Chu et al., 2020). Our soils contained 96 ppm of Mehlich 2 extractable phosphate, which is modest for sub-Sahran African soils (Hengl et al., 2017). Enhancing P uptake is important since this is an essential macronutrient for plant growth, which is required for photosynthesis, ATP production, nucleic acid synthesis and root development (Chen et al., 2017). However, P shortage is an impediment to maize production as P is often fixed in the soil, limiting its availability, particularly in the P-deficient environments of sub-Saharan Africa (Pasley et al., 2019; Stewart et al., 2020; Wang et al., 2020). The correlation between AM fungi and P concentration in plant tissues is well known, as mycorrhiza fungi promote P solubilisation and transport to host plants (Sawers et al., 2018). However, in support of our hypothesis, our study highlights that not all maize varieties used had an increase in P concentration when inoculated with AM fungi, suggesting a variety-specific response in terms of nutrient acquisition capacities (based on the P concentration 'response ratio'; Figure 2). Irrespective of AM fungi colonisation, some varieties had intrinsically greater total P concentrations, suggesting that these cultivars have higher inherent capability for P acquisition through direct root uptake pathways (Chu et al., 2013). This finding is consistent with studies demonstrating that certain maize varieties may obtain P independently of AM fungi due to extensive root systems, higher exudation rates or more effective phosphate transporter genes (Guo et al., 2022).

By contrast, some varieties captured more total P in response to AM fungal inoculation. These varieties are likely dependent on P uptake mediated by AM fungi because they lack efficient or alternative P acquisition strategies. In particular, drought tolerant varieties (V2, V3, V8, V10) demonstrated a substantial increase in total P when colonised by AM fungi indicating that under limiting factors, these varieties may be dependent on AM fungi for nutrient acquisition (Figure 1.). Similarly, varieties tolerant to low nitrogen (V8, V11) exhibited increased P uptake under AM fungal inoculation, reinforcing the contribution of AM fungi in nutrient-deficient soils. However, disease tolerant varieties displayed diverse responses with some exhibiting strong positive responses (V11, V9, V10, V8), while others (V5, V12, V20) demonstrated neutral or marginal responses. Early maturing varieties exhibited moderate responses to AM fungal inoculation, probably attributable to shorter growth cycles restricting extended interactions with AM fungi. This outcome suggests that AM fungal benefits may be contextual and determined by the interactions between, for example, host crop, pathogen and AM fungi. Bender et al. (2016) and Sawers et al. (2018) argue that the differentiation between P efficient and P dependent varieties implies that AM fungal response for P acquisition can be used as a selection basis for breeding programs especially when targeting nutrient deficient environments where plant-fungal symbiosis is essential for nutrient uptake.

Furthermore, maize varieties differed significantly in their response to inoculation by particular AM fungal species. Some maize varieties (V10, V11, V9) exhibited positive responses to both species, whilst others demonstrated negative or species-specific responses. These differences indicate that the efficiency of AM fungal inoculation depends on the variety's inherent capacity to support and profit from mycorrhizal associations (Sawers et al., 2018). This variety-specific responsiveness lends credence to the hypothesis that genetic factors significantly influence the efficiency of AM fungal associations (Guo et al., 2022), as suggested by the dissociation between colonisation and plant response. The effectiveness of AM fungal symbioses hinges on factors such as the efficiency of nutrient capture, functional characteristics of AM fungi and the plant metabolic cost of sustaining the association (Klironomos, 2003; Smith & Read, 2008). While varieties from low nutrient environments benefit from AM fungal symbiosis, those adapted to nutrient-rich soils may have less reliance on the fungi (van der Heijden & Horton, 2009). The variety-specific characteristic of the maize responses to AM fungal inoculation emphasises the need for customised inoculation approaches that consider both the mycorrhizal species and maize genotype. Such precision strategies could improve productivity and resource use efficiency in various agroecological settings Chialva et al. (2024).

Although more work is needed to understand the mechanisms underpinning our findings, we suggest that the variety specific responses may be best explained by carbon allocation from hosts to the fungi, which can be considerable (Johnson, Leake, Ostle, et al., 2002; Johnson, Leake, & Read, 2002). The fungal symbiont supplies nutrients (P and N) in exchange for the photosynthetic carbon

produced by the host plants. However, plants differ in how they allocate carbon to the AM fungi, with some restricting carbon flow to the fungal partner, particularly if they have alternative nutrient acquisition mechanisms, while others prioritise mycorrhizal colonisation and nutrient trade (Johnson et al., 1997; Kiers et al., 2011). More responsive cultivars may supply more carbon to AM species that yield higher nutrient returns, whereas less responsive cultivars may limit this flow, resulting in weakened or detrimental responses to colonisation (Kiers et al., 2011). We found that the root biomass mycorrhizal response ratio was mainly positive across the varieties, indicating greater below-ground energy allocation to promote AM fungal colonisation. The interaction between plants and AM fungi can enhance root growth as more carbon is allocated to root structures to feed the fungal partner in exchange for increased nutrient uptake, especially P (Smith & Read, 2008).

Our findings indicate that the use of AM fungi as a biofertiliser is a promising practice in Kenya and sub-Saharan Africa since maize production in these regions mainly occurs in low-input, smallholder systems where yields are constrained by P deficit and decreasing soil fertility (Kiboi et al., 2019; Mutuku et al., 2020; Stewart et al., 2020). Nevertheless, our results demonstrate that maize responses to mycorrhizal inoculation are variety specific, with some exhibiting strong positive responses while others had negative or weak responses to AM fungi colonisation. Although we have not made formal comparisons, maize in North America, Europe, and some parts of South America is cultivated in high-input agricultural systems which rely on chemical inputs, hence reducing the reliance on AM fungi (Sawers et al., 2018). However, in intensive agricultural systems in Asia and Brazil, the use of AM fungal inoculants is gaining momentum in order to reduce fertiliser application while maintaining crop production (Pasley et al., 2019; Wang et al., 2020), suggesting a sustainable alternative for farmers in sub-Saharan Africa who have constrained access to fertiliser. AM fungi could be particularly useful in Kenya's semi-arid areas since they improve the resilience of maize crops to erratic climate by enhancing root development and soil water retention in addition to nutrient acquisition (Hussain et al., 2021; Mumo et al., 2021; Ochieng et al., 2017). In order to optimise the benefits from AM fungi, breeding programs in sub-Saharan Africa should focus on choosing maize genotypes with high AM fungal mediated P acquisition efficiency.

Overall, our findings demonstrate that locally adapted maize varieties in combination with AM fungi can provide significant agronomic and ecological benefits in low-input agricultural systems that support the view that locally adapted varieties possess a higher stress tolerance, resource-use efficiency and resistance to local pathogens (Mumo et al., 2021; Stewart et al., 2020). A key finding was that combinations of individual varieties that were the most responsive to AM fungi over-yielded compared to monocultures, and these effects were driven by both complementarity and selection effects. Therefore, careful exploitation of maize genetic diversity and movement away from the use of genetic monocultures may therefore provide a way of enhancing food security in smallholder agricultural systems in Kenya.

AUTHOR CONTRIBUTIONS

Grace Ng'endo Kanyita, Ezekiel Mugendi Njeru and David Johnson conceived and designed the study. Grace Ng'endo Kanyita conducted the experiments, collected the data and drafted the manuscript. Henry Birt conducted all the analysis and designed the figures. Ezekiel Mugendi Njeru and David Johnson reviewed the manuscript. All the authors read and approved the manuscript for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted without any commercial or financial relationship that would be considered for declaration of a potential conflict of interest.

DATA AVAILABILITY STATEMENT

Data supporting the findings of this study are available from the corresponding author upon reasonable request. All data were collected and processed in compliance with relevant ethical guidelines.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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