

# HOW MULTISPECIES INTERCROP ADVANTAGE RESPONDS TO WATER STRESS: A YIELD-COMPONENT ECOLOGICAL FRAMEWORK AND ITS EXPERIMENTAL APPLICATION

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## KEYWORDS

agroecosystem sustainability, crop overyielding, intercrop drought resistance, overyield ecological components

## HIGHLIGHTS

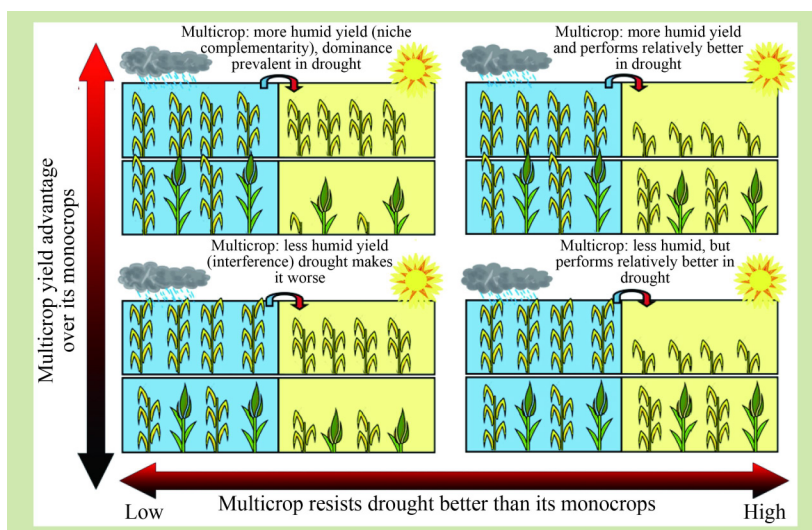
- A framework for multicrop advantage under varying watering conditions is provided.
- This framework clarifies the relation between multicrop overyielding and land use efficiency.
- A novel experimental setup was used to evaluate these theoretical developments.
- Theory and experiment conveyed precise understanding of overyielding scenarios.

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## GRAPHICAL ABSTRACT



## ABSTRACT

Absolute yield and land use efficiency can be higher in multicrops. Though this phenomenon is common, it is not always the case. Also, these two benefits are frequently confused and do not necessarily occur together. Cropping choices become more complex when considering that multicrops are subject to strong spatial and temporal variation in average soil moisture, which will worsen with climate change. Intercropping in agroecosystems is expected to buffer this impact by favoring resistance to reduced humidity, but there are few empirical/experimental studies to validate this claim. It is not clear if relatively higher multicrop yield and land use efficiency will persist in the face of reduced soil moisture, and how the relation between these benefits might change. Here, we present a relatively simple framework for analyzing this situation. We propose a relative multicrop resistance (RMR) index that captures all possible scenarios of absolute and relative multicrop overyield under water stress. We

dissect the ecological components of RMR to understand the relation between higher multicrop yield and land use efficiency and the ecological causes of different overyield scenarios. We demonstrate the use of this framework with data from a 128 microplot greenhouse experiment with small annual crops, arranged as seven-species multicrops and their corresponding monocrops, all under two contrasting watering regimes. We applied simple but robust statistical procedures to resulting data (based on bootstrap methods) to compare RMR, and its components, between different plants/plant parts. We also provide simple graphical tools to analyze the data.

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## 1 INTRODUCTION

Industrial agriculture has reduced biological diversity at the field and landscape level, worldwide<sup>[1]</sup>. Fortunately, there is a renewed interest among farmers, scientists and other stakeholders in preserving and promoting agrobiodiversity. They are recognizing that crop diversity is important to sustain production, reduce the impact of climate change, conserve biodiversity and preserve ecosystem services<sup>[2-4]</sup>. When such practices are tried in specific localities, stakeholders need to remember that the comparative advantages of species-rich agroecosystems are not always conspicuous, and can vary strongly with environmental conditions<sup>[5]</sup>, and can imply tradeoffs which need to be considered<sup>[6-8]</sup>.

Multispecies intercropping systems (i.e., more than two crops mixed in the same field) are still practiced by smallholders around the world. Their primary productivity serves both the short-term economic purposes of farmers (e.g., food, fiber and fuel yields) and the long-term need for preserving ecosystem services (e.g., soil and water conservation, and habitat for wildlife)<sup>[4]</sup>. Descriptive field studies claim that these systems have higher yields, use land more efficiently and are more capable of buffering spatial and temporal environmental variation than monocrop-based systems<sup>[9]</sup>. Experimental work has confirmed these notions in a lot of cases but also found situations where they do not hold or where results are ambiguous<sup>[10]</sup>.

Irregular rainfall and increasing water constraints are predicted to occur in the subhumid and semiarid tropics because of climate change and increasingly intensive land use<sup>[11]</sup>.

Several effects on multispecies intercropping systems are expected. Here we focus on how reduced soil moisture can modify multicrop yield performance and land use efficiency (LUE), as compared to the corresponding set of monocrops.

We also study the effects of reduced soil moisture on the tradeoff that in some cases occurs between absolute yield performance and LUE in the multicrop. Loss of LUE and yield performance advantages over the monocrops under these new conditions would only add to the current strains on multispecies systems.

Since the 1960s, agronomists have been experimentally comparing yields of two-species intercrops with their respective monocrops<sup>[12]</sup>. The most common basis for this comparison has been the relative yield total (RYT)<sup>[12]</sup>. RYT is the sum of the relative yields of both species (i.e.,  $RY_1 + RY_2$ ), where  $RY_i = (\text{intercrop yield } i / \text{monocrop yield } i)$ . A  $RYT > 1$  means that more monocrop land would be necessary to obtain the two intercrop yields. It has been found that higher LUE stems from ecological complementarity (which includes intraspecific < interspecific competition and facilitation) and that  $RYT > 1$  is common<sup>[13]</sup>.

Experimental and theoretical work has focused on comparing and explaining the coefficient of variation of intercrop and monocrop yields<sup>[14,15]</sup>; but few have explicitly studied the effects of reduced rainfall<sup>[15]</sup> or reduced soil moisture<sup>[16]</sup> on RYT. These studies have been done on sorghum-pigeon pea mixtures, and few other dryland crops<sup>[17]</sup>. Results suggest that LUE advantage is reduced or even lost in some cases but can remain the same or even increase in others.

Over the past decade, ecologists have generated theoretical arguments and obtained important evidence from experimental communities of herbaceous plants which suggest that aboveground primary production increases with plant species richness<sup>[3]</sup>, and that this relation becomes asymptotic in human-established experimental communities of about 7 to 10 species<sup>[2]</sup>. More in-depth research has looked at how much this overyield (compared to the average yield of the monocrops involved) depends on species richness or species specific

composition<sup>[18]</sup>, or traits of particular species<sup>[3]</sup>. As a result of intense debate over the causes of overyielding, this metric has been dissected<sup>[19–21]</sup> to show that it can be produced by a combination of complementarity and dominance effects which, as we will show later, imply that  $RYT > 1$  does not necessarily mean overyielding and vice versa. The relation between species richness and different measures of stability (including temporal stability, the inverse of the coefficient of variation of yield) has also been a matter of intense theoretical research and debate in ecology<sup>[22]</sup>. However, few experiments can explicitly relate species richness and resistance to changes in water availability. The most comprehensive one<sup>[23]</sup> suggests that species richness increases temporal stability, while others find that, under certain circumstances, multicrop gains are reduced under water stress<sup>[24]</sup>.

Developing a thorough and all-encompassing framework to understand changes in multicrop yield performance caused by soil moisture change offers several theoretical, experimental, logistic and statistical challenges which need to be fully addressed<sup>[25,26]</sup>. We build upon existing research to develop a relatively simple framework that helps to analyze and understand the response of multispecies intercrop overyielding to reduced soil moisture. This framework: (1) Reviews the concept of overyield components<sup>[20,21,27]</sup>, which clearly leads to understand why multicrop overyielding does not necessarily imply  $RYT > 1$  and vice versa; (2) Defines RMR; (3) Classifies all qualitatively different RMR outcomes; (4) Provides a simple graphical tool for comparing these outcomes among different multicrops (or different yield fractions of a single multicrop, e.g., shoot, fruit and total aboveground dry matter); (5) Explains why soil moisture changes can modify overyield components (as defined by Fox<sup>[21]</sup>) and, in consequence, the relation between land use efficiency and overyielding; and (6) Analyzes the contribution of each species in multicrop to changes in overyield and LUE.

We demonstrate the use of this framework with data from a 128 microplot experiment performed in a greenhouse with cultivated small annual species, arranged as seven-species multicrops and their corresponding monocrops, all under two contrasting watering regimes.

## 1.1 Multicrop overyield and its resistance to reduced soil moisture: an analysis of overyield and its ecological components

### 1.1.1 Multicrop overyield

Consider the hypothetical case of a farmer who decides to establish  $n$  annual monocrops in  $N$  contiguous and equally sized plots. We will call it the monocrop set. To keep things

simple, we will assume that all species are sown at an equal density of  $M$  plants  $m^{-2}$ . Alternatively, he could establish the same  $N$  plots such that all species were present in each plot, all in equal proportions, to preserve the same global density as in the monocrops ( $M/N$  plants of each species  $m^{-2}$ ; a substitutive multicrop). We will call this the multicrop set. (The multicrop set could be further diversified by using this same number of seed and land to establish  $N$  multicrops with different species compositions, but we will not consider that situation here).

Given that the same amount of land, species and plants per species are used in both cases, different comparisons could be made. Here we will focus on yield and LUE.

Even though the total population of each species is the same in monocrop and multicrop sets, the farmer should not expect the same production per species in both sets. At the same global density, the average individual plant of some species would perform better in the multispecies community than in their monospecific stands; others would perform equally in both sets; others still would perform worse. All species performing equally per individual in both sets would be very unlikely.

Each species has a relative yield ( $RY_i$ ):

$$RY_i = \frac{Y_{i \text{ multicrop}}}{Y_{i \text{ monocrop}}} \quad (1)$$

where  $Y_{i \text{ monocrop}}$  is  $M \times$  weight of the average individual plant of species  $i$  in the monocrop and  $Y_{i \text{ multicrop}}$  is  $(M/N) \times$  weight of the average individual plant of species  $i$  in the monocrop (see Table S1 in supplementary materials).

When the average individual performs equally in the monocrop and multicrop, then:

$$RY_i = RYE_i = \frac{1}{N} \quad (2)$$

where  $RYE_i$  is the relative yield to be expected if intra and interspecific net interactions are equal<sup>[20]</sup>. The net interaction is the compound effect of various factors including competition, facilitation, allelopathy, and others.

The first and most common agronomic notion of overyielding results from computing the relative yield total ( $RYT$ ) of the multicrop and monocrop sets, in this case:

$$RYT = \sum RY_i \quad (3)$$

It is important to keep in mind that  $RYT$  is not a sum of yields

but rather a sum of ratios. As stated above,  $RYT > 1$  implies that more monocrop land would be necessary to produce the exact combination of per-species yields obtained in the multicrop; a  $RYT < 1$  means the opposite.

A second definition of overyielding results from summing up all the production in the multicrop set and comparing it to the production in the monocrop set, assuming that both sets occupy the same amount of land (which is the case in our example). For this and all other cases it is better to express yield as weight per unit area ( $\text{g}\cdot\text{m}^{-2}$ ). This implies comparing the aggregate yield ( $\text{g}\cdot\text{m}^{-2}$ ) of all species in the multicrop ( $Mu$ ) with the average yield ( $\text{g}\cdot\text{m}^{-2}$ ) of the  $N$  monocrops ( $Mo$ ). We can write:

$$\Delta Y = Mu - Mo \quad (4)$$

where  $Mu$  is  $\sum Y_i$  in multicrop and  $Mo$  is  $(\sum Y_i \text{ in monocrop})/N$  for  $i = 1, 2, \dots, N$ .  $\Delta Y$  ( $\text{g}\cdot\text{m}^{-2}$ ) is positive when the multicrop overyields the average monocrop and negative in the opposite case.

### 1.1.2 Overyield ecological components

A  $\Delta Y > 0$  can be associated with a  $RYT > 1$ , and a  $\Delta Y < 0$  with a  $RYT < 1$ , but the opposite can also be true (see supplementary materials—hypothetical examples of tradeoffs between  $RYT$  and  $\Delta Y$ ). To understand this better, it is useful to consider the ecological components of  $\Delta Y$ . In the context of ecological research, Loreau and Hector<sup>[20]</sup> dissected  $\Delta Y$  into two components: trait-independent complementarity (TIC) and trait-dependent selection (TDS). Fox<sup>[21]</sup> further dissected TDS into dominance (DOM) and trait-dependent complementarity (TDC). Both authors assume that the multicrop is substitutive, that facilitation is part of complementarity, and that the species trait to consider is its monocrop yield:

$$\Delta Y = TIC + TDC + DOM \quad (5)$$

Fox<sup>[21]</sup> defines these terms as follows: TIC quantifies the extent to which species observed yields in mixture deviate from a zero-sum game, but in a way that is independent of species traits. Ecologically, we would expect this term to be large and positive, if species occupy different niches and/or facilitate each other, and negative when interspecific interference competition (when competition between species is direct and they suppress each other in the mix) or some other process(es) with the same effect occurs. DOM quantifies the extent to which relative yields in mixture resemble a zero-sum game. It indicates niche similarity. Large positive values mean that species with high monocultural yields dominate the mixture at the expense of species with low monocultural yields; negative values indicate

that it is the latter that dominate at the expense of the former. TDC quantifies the extent to which species observed yields in mixture deviate from a zero-sum game in a way that depends on species traits. Large positive values mean that species with high monocultural yields dominate the mixture but not at the expense of species with low monocultural yields; negative values indicate that it is the latter that dominate but not at the expense of the former.

$$TIC = N \times Mo \times \frac{\sum RY_i - RYE_i}{N} \quad (6)$$

$$DOM = N \times \text{Cov}\left(M_i, \left(\frac{RY_i}{RYT}\right) - RYE_i\right) \quad (7)$$

$$TDC = N \times \text{Cov}\left(M_i, RY_i - \left(\frac{Y_i}{RYT}\right)\right) \quad (8)$$

where  $i = 1, 2, \dots, N$  species, and  $M_i$  is the monocrop yield of species  $i$ .

A detailed development and explanation of these formulas can be found in the literature cited above. Here we will only analyze them to derive some consequences for our framework. From Eq. (4), it follows that:

$$Mu = Mo + \Delta Y \quad (9)$$

Now,  $\Delta Y$  can also be expressed as a function of  $Mo$  so that:

$$Mu = Mo + (p \times Mo) \quad (10)$$

where  $p$  can be positive or negative. We can also rewrite Eq. (6) as:

$$TIC = q \times Mo \quad (11)$$

where,

$$q = N \times \frac{\sum RY_i - RYE_i}{N} \quad (12)$$

$$= N \times \frac{1}{N} \times \sum RY_i - RYE_i \quad (13)$$

$$= \sum RY_i - \sum RYE_i \quad (14)$$

$$= RYT - 1 \quad (15)$$

so that:

$$TIC = Mo \times \sum RY_i - RYE_i = Mo \times (RYT - 1) \quad (16)$$

The relation between TIC and RYT has been previously presented by Loreau<sup>[28]</sup>. Given that Mo is always positive, Eq. (16) has two implications. (1) TIC does not contribute to ΔY (TIC = 0) when the relative performances of all species deviate from their expected performances, as defined above, in such a way that all deviations (RY<sub>i</sub> - RYE<sub>i</sub>) are zero or they cancel each other out. This happens when RYT = 1. (2) TIC explains all ΔY (i.e., TIC = ΔY) when q = p, which implies that:

$$\sum RY_i - RYE_i = \frac{\Delta Y}{Mo} \tag{17}$$

or, in other terms,

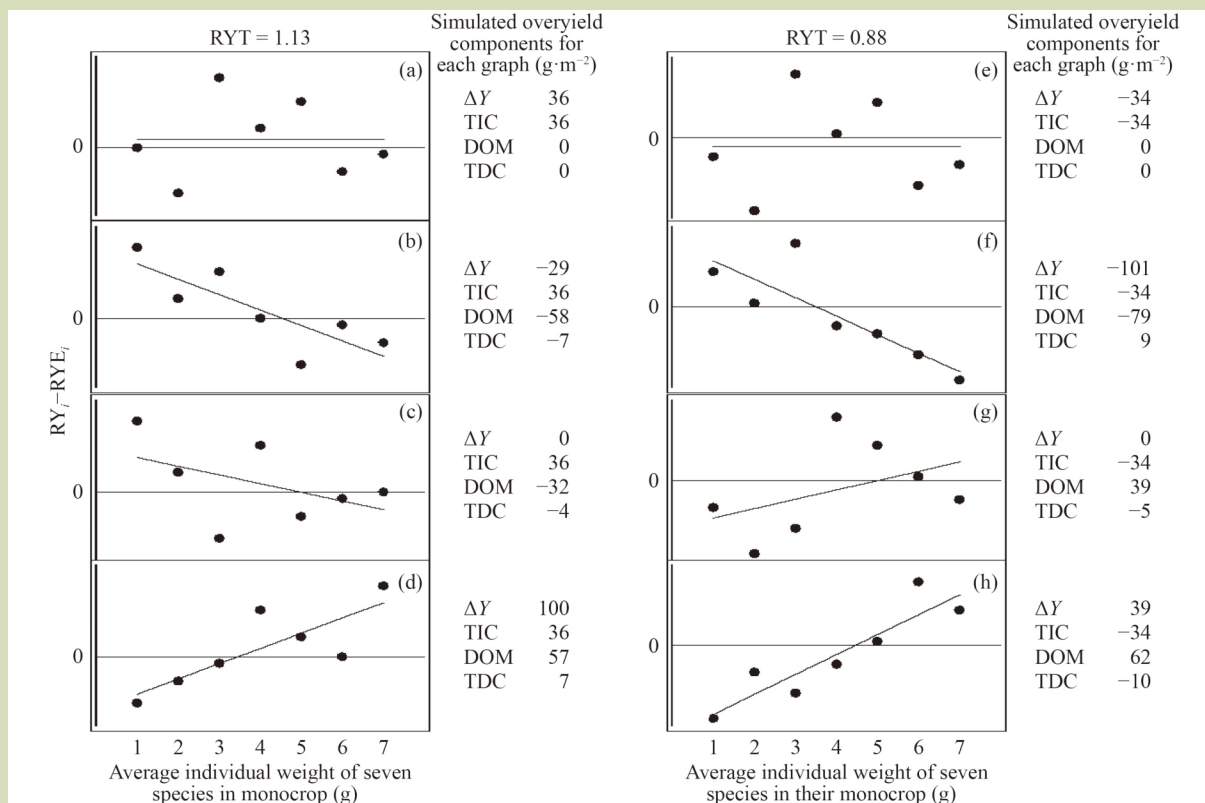
$$RYT = 1 + \frac{\Delta Y}{Mo} \tag{18}$$

where ΔY can be positive or negative.

Positive TIC and RYT > 1 values can translate into large, small or even negative ΔYs depending on the values of TDC and DOM. Simulations shown in Fig. 1 illustrate this situation. They also show graphically the meaning of TDC and DOM: a fixed set of (RY<sub>i</sub> - RYE<sub>i</sub>) relative performance values will always produce the same TIC and RYT value irrespective of how these relative performances are matched to each species. However, ΔY cannot be the same if, say, it is the low monocrop-yielding species rather than the high monocrop-yielding species that are overperforming. In the first case, TDC + DOM are negative, as (RY<sub>i</sub> - RYE<sub>i</sub>) is negatively correlated with species yield in monocrop. In the second case the correlation, as well as TDC + DOM, are positive. When the correlation is exactly zero, TIC = ΔY and, by definition, DOM and TDC = 0.

### 1.1.3 Relative multicrop resistance to reduced soil moisture

We want to define multicrop resistance to low humidity in



**Fig. 1** Simulated examples of overyielding scenarios: monocrop individual plant weights (species 1 weighed 1 g per individual on average, while species 7 weighed 7 g per individual on average) of a set of seven species and their relative individual performances (in relation to monocrop weight) in the seven-species multicrop (The dots (•) in each graph represent species 1–7 from left to right, respectively). In parts (a–d), RYT = 1.33; in (e–h), RYT = 0.8. The same RYT (relative yield total) value can be related to a positive, zero or negative ΔY (overyield) value, depending on the correlation between monocrop productivity of a set of species and their relative performances (RY<sub>i</sub> - RYE<sub>i</sub>) in multicrop, which can vary due to complementarity or selection effects. In part (h), for example, there is a strong positive correlation between plant size and its competitive capacity when in multicrop, a selection effect which leads to overyielding even when RYT < 1.

relation to the performance of the average monocrop. We have found that a convenient way to do this is by constructing a RMR index. RMR is the change observed in the relative multicrop overyield when soil moisture is reduced:

$$\text{RMR} = \frac{\Delta Y_L}{\text{Mo}_L} - \frac{\Delta Y_H}{\text{Mo}_H} = \text{R}\Delta Y_L - \text{R}\Delta Y_H \quad (19)$$

where  $\Delta Y$  is  $(\text{Mu} - \text{Mo})$ ,  $\text{Mu}$  is multicrop yield,  $\text{Mo}$  is average monocrop yield,  $\Delta Y/\text{Mo} = \text{R}\Delta Y$  is relative multicrop overyield, and H and L suffixes indicate high and low moisture conditions, respectively.

RMR as a relative measure of yield resistance in three ways:

(1) It uses the corresponding average monocrop performance as a reference point; (2) It scales  $\Delta Y$  to its respective average monocrop yield; and (3) high and low soil moisture conditions are arbitrary. This last point requires further comment: a researcher might want to establish standard high and low soil moisture conditions for calculating RMR values that can be compared across many soil types, climates and crops. This is possible in some cases but will not work in all situations. There might not be a universal measure of multicrop resistance to reduced soil moisture. Thus, RMR should be used to compare multicrops established under the same soil type, using high and low soil moisture conditions that are relevant to the case. Interpolation of RMR values should be avoided as yield responses to water availability are frequently nonlinear.

RMR is also a convenient measure of multicrop resistance because it can be decomposed to analyze relative changes in overyield components. Recall that  $\Delta Y = \text{TIC} + \text{DOM} + \text{TDC}$ , so:

$$\text{R}\Delta Y = \frac{\text{TIC}}{\text{Mo}} + \frac{\text{DOM}}{\text{Mo}} + \frac{\text{TDC}}{\text{Mo}} \quad (20)$$

and according to Eq. (16):

$$\text{R}\Delta Y = (\text{RYT} - 1) + \frac{\text{DOM}}{\text{Mo}} + \frac{\text{TDC}}{\text{Mo}} \quad (21)$$

It follows that:

$$\begin{aligned} \text{RMR} = & (\text{RYT}_L - 1) - (\text{RYT}_H - 1) + \left( \frac{\text{DOM}_L}{\text{Mo}_L} \right) \\ & - \left( \frac{\text{DOM}_H}{\text{Mo}_H} \right) + \left( \frac{\text{TDC}_L}{\text{Mo}_L} \right) - \left( \frac{\text{TDC}_H}{\text{Mo}_H} \right) \end{aligned} \quad (22)$$

We can simplify terms by making:

$$\left( \frac{\text{DOM}_L}{\text{Mo}_L} \right) - \left( \frac{\text{DOM}_H}{\text{Mo}_H} \right) = \Delta \text{RDOM} \quad (23)$$

$$\left( \frac{\text{TDC}_L}{\text{Mo}_L} \right) - \left( \frac{\text{TDC}_H}{\text{Mo}_H} \right) = \Delta \text{RTDC} \quad (24)$$

R stands for relative in both cases. We can then establish:

$$\Delta \text{RSEL} = \Delta \text{RDOM} + \Delta \text{RTDC} \quad (25)$$

SEL as defined by Loreau and Hector<sup>[20]</sup>, so that:

$$\text{RMR} = \Delta \text{RYT} + \Delta \text{RDOM} + \Delta \text{RTDC} \quad (26)$$

DOM and TDC as defined by Fox<sup>[21]</sup>. And then:

$$\text{RMR} = \Delta \text{RYT} + \Delta \text{RSEL} \quad (27)$$

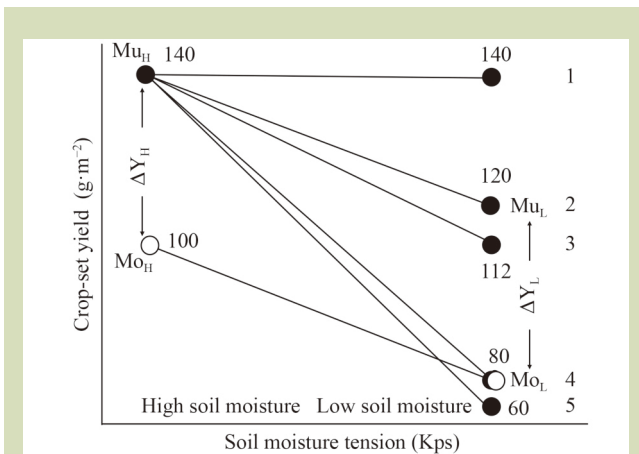
These last two equations allow us to relate the change in relative overyield (RMR) with the change in LUE in an analytical and a graphical way, respectively. This will show how much the change in relative overyield is due to a change in LUE, and if both change in the same or opposite directions. It is also important to note that it would be confusing to compare absolute changes in overyield components as, say, a reduced DOM value could result from a smaller  $\Delta Y$  and/or from a smaller contribution of DOM to  $\Delta Y$ . This ambiguity is solved when overyield components are scaled by their  $\text{Mo}$  value.

#### 1.1.4 Classification of relative multicrop resistance scenarios

We now classify qualitatively different multicrop resistance outcomes and their corresponding RMR indices. Let us first consider the case where the multicrop overyields in the reference (high) soil moisture condition, so that  $\Delta Y_H > 0$ . Figure 2 shows five relevant outcomes when soil moisture is significantly reduced. Scenarios are ordered from the most favorable to the most restrictive multicrop strategy, where soil moisture reduction becomes an issue.

(1) The monocrop with water limitation fails but the multicrop does not. An ideal situation in which perfect compensation occurs. Drought tolerant species (suppressed by drought-intolerant species in the high moisture condition) now become dominant and compensate for the losses of drought-intolerant species. In this case  $\text{RMR} = (\text{Mu}_L/\text{Mo}_L) - (\text{Mu}_H/\text{Mo}_H)$  (see supplementary materials—derivation of RMR formulas).

(2)  $\text{R}\Delta Y_L > \text{R}\Delta Y_H$  and  $\Delta Y_L = \Delta Y_H$ . The monocrop and multicrop sets lose the same amount of yield, but the multicrop is more resistant in relative terms. Imperfect compensation occurs.  $\text{RMR} = (\text{Mu}_L/\text{Mo}_L) - ((\text{Mu}_L - \text{Mo}_L)/\text{Mo}_H) - 1$ .



**Fig. 2** Five hypothetical multicrop-resistance scenarios. The x-axis is qualitative. Empty circles, average monocrop yield; filled circles, multicrop yield;  $Mo_H$ , monocrop yield in high moisture conditions;  $Mo_L$ , monocrop yield in low moisture conditions;  $Mu_H$ , Multicrop yield in high moisture;  $Mu_L$ , multicrop yield in low moisture;  $\Delta Y_H$ , multicrop overyield in high moisture; and  $\Delta Y_L$ , multicrop overyield in low moisture. In scenario 3, for example, the relative yield is the same  $((140 - 100)/100) = 0.4$  and  $((112 - 80)/80) = 0.4$  in both high and low moisture. Each scenario is explained in detail in the main text (Section 1.1.4).  $\Delta Y_H$  is fixed and  $\Delta Y_L = Mu_L - Mo_L$ ;  $\Delta Y_L$  is exemplified for scenario 2.

(3)  $R\Delta Y_L = R\Delta Y_H$ . The monocrop and multicrop sets are equally resistant in relative terms (e.g., they both fall by 20%). We call this neutral resistance because a simple scale reduction occurs, and the relation between monocrop and multicrop is not modified. Consequently,  $RMR = 0$ . Observing Eq. (26), we see this outcome can occur when  $\Delta RYT$ ,  $\Delta DOM$  and  $\Delta TDC$  are all zero (strict neutrality) or when they sum up to zero (overall neutrality).

(4)  $R\Delta Y_L = 0$ . All multicrop overyield is lost. In this case,  $RMR$  is negative, and its value is  $(Mu_H - Mo_H)/Mo_H$ .

(5)  $R\Delta Y_L < 0$ . The high moisture soil outcome is reversed: the monocrop set now has a higher yield than the multicrop set because of reduced moisture.  $RMR < (Mu_H - Mo_H)/Mo_H$

When we calculate an  $RMR$  value for a specific multicrop/monocrop set that has a  $\Delta Y_H > 0$ , we can statistically compare this value with the  $RMR$  values that correspond to each of the five scenarios and decide which fits the case best. We can also compare  $RMR$  values among different multicrops (or plant parts within a multicrop).  $RMR$  is a random variable that does not necessarily conform to assumptions of normality, heteroscedasticity and independence. It is nevertheless possible

to construct the distribution and confidence limits of the difference between average  $RMR$  values using bootstrap methods<sup>[29,30]</sup> and to make inferences from them. We will develop this further in the next section.

Another set of scenarios are possible when  $\Delta Y_H < 0$ . These are of little interest, as the multicrop underyields in high soil moisture conditions, but we will look at them for the sake of completeness. We can understand these by a graphical analysis of all possible outcomes in the  $RMR$  vs.  $R\Delta Y_H$  plane.

In Fig. 3, we give scenarios on this plane, and smaller plots showing how  $\Delta Y_H$  and  $\Delta Y_L$  relate in each case. In the upper section we show scenarios 5 and 3, and a case intermediate between scenarios 1 and 2. In the lower part we show scenarios with the same  $RMR$  values as the previous, but with  $\Delta Y_H < 0$ . All cases falling in the gray area have  $\Delta Y_L > 0$ . The monocrop line is fixed; only the multicrop line varies. Any number of different multicrops can be represented in this plane and compared statistically. For this latter purpose, the joint distribution and joint confidence limits of average  $RMR$  and average  $R\Delta Y_H$  values can be constructed for each case using bootstrap methods.

1.1.5 Ecological components of the relative multicrop resistance index

For a specific multicrop,  $RMR$  can be tracked down to the relative change in each of the overyield components. Recall Eq. (26):  $RMR = \Delta RYT + \Delta RDOM + \Delta RTDC$

For example, we could find that high multicrop resistance (positive  $RMR$ ) was derived from an increase in complementarity or from an increase in dominance, or from a synergistic or antagonistic combination of both.

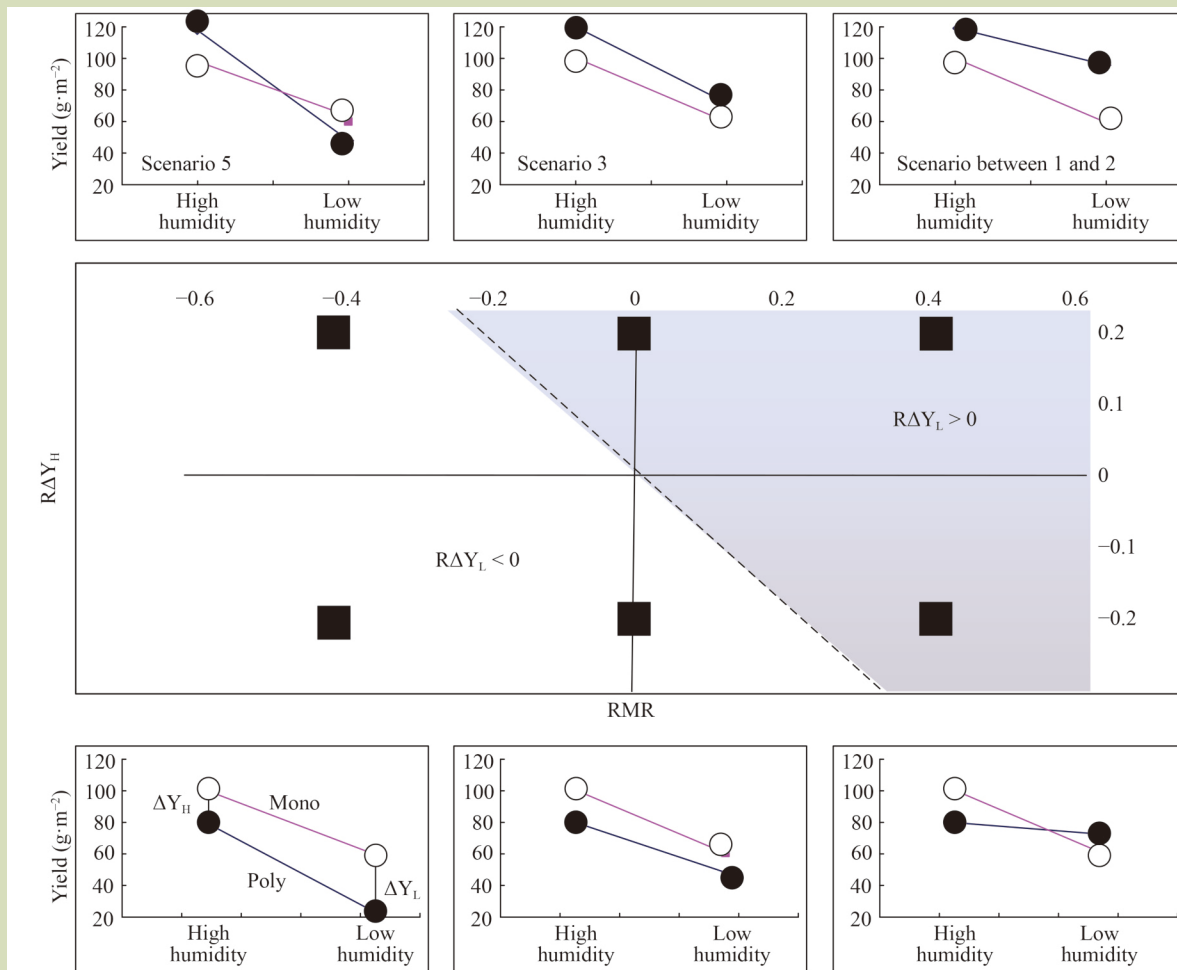
We can extend this analysis to graphically compare any number of multicrops (or multicrop plant parts) in these terms. For this purpose:

(1) Eq. (27) was rearranged as:

$$\Delta RYT = RMR - \Delta SEL \tag{28}$$

(2) The joint distribution and joint confidence limits of average  $RMR$  and average  $\Delta RYT$  values for each multicrop were calculated, and

(3) these distributions graphed in the  $\Delta RYT$  vs  $RMR$  plane and analyze their positions and overlap (Fig. 4).



**Fig. 3** A graphical tool for representing with ordered pairs (RMR, relative multicrop resistance; and  $R\Delta Y_H$ , relative multicrop overyield under humid conditions) all drought resistance outcomes of a multicrop and its associated monocrops. The small outer plots show the soil moisture tension vs yield for each of the six points in the central plot. The upper plots with  $R\Delta Y_H > 0$  are scenarios 5 and 3 from Fig. 2, and an intermediate scenario between scenarios 1 and 2, also from Fig. 2. The three lower plots (not considered in Fig. 2) have the same RMR values but  $R\Delta Y_H < 0$ . Empty circles, average monocrop yield; filled circles, multicrop yield; and in the gray area,  $R\Delta Y_L > 0$ .

This reveals the tradeoffs implied in choosing among multicrops when the contribution of  $\Delta RYT$  to RMR differs strongly among them.

1.1.6 Individual species contribution to  $\Delta Y$ ,  $RYT$ ,  $RMR$  and  $\Delta RYT$

Finally, for a given multicrop, it is possible to establish the contribution of each crop species to its  $\Delta Y$ ,  $RYT$ ,  $RMR$  and  $\Delta RYT$  values. This is because all these terms are simple sums of species partial contributions. Thus:

$$R\Delta Y_{iH} = Y_{iH} \text{ monocrop} - Y_{iH} \text{ multicrop} \quad (29)$$

$i$  = species  $i$ ; H = high moisture

$$R\Delta Y_{iL} = Y_{iL} \text{ monocrop} - Y_{iL} \text{ multicrop} \quad (30)$$

L = low moisture

$$R\Delta Y_{iH} = \frac{Y_{iH} \text{ multicrop}}{Y_{iH} \text{ monocrop}} \quad (31)$$

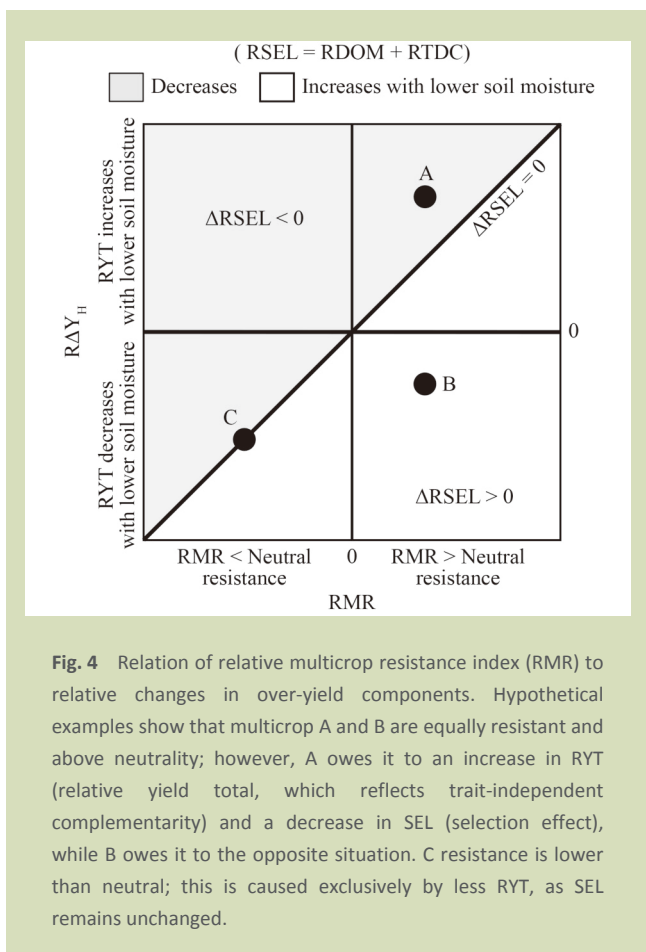
$$R\Delta Y_{iL} = \frac{Y_{iL} \text{ multicrop}}{Y_{iL} \text{ monocrop}} \quad (32)$$

$$\Delta RYT_i = \Delta RY_i = RY_{iL} - R\Delta Y_{iH} \quad (33)$$

$RYT_i$  is equivalent to  $RY_i$  defined in Eq. (1)

$$RMR = R\Delta Y_{iL} - R\Delta Y_{iH} \quad (34)$$





## 2 MATERIALS AND METHODS

### 2.1 Experimental database

To test the framework, we performed a greenhouse experiment starting June 20, 2001, at El Colegio de la Frontera Sur, a research center in the highlands of Chiapas, México (tropical-temperate subhumid climate; 2100 m.a.s.l.). The experiment included eight annual crops and a total of 128 (1 × 0.93 m with a depth of 0.285) microplots arranged in four beds in a greenhouse. Crop species, from smallest to largest, were finger millet (*Eleusine coracana*), pea (*Pisum sativum*), lentil (*Lens culinaris*), chickpea (*Cicer arietinum*), canarygrass (*Phalaris canariensis*), flax (*Linum usitatissimum*), wheat (*Triticum aestivum*) and vetch (*Vicia villosa*). These species were selected on grounds of being small and rapid growing, with similar sizes and similar life cycles, implying growing individuals competed more-or-less symmetrically between themselves during their main growth phase.

A set of the eight monocrop microplots, randomly distributed in a monocrop set was established to the side of a set of eight

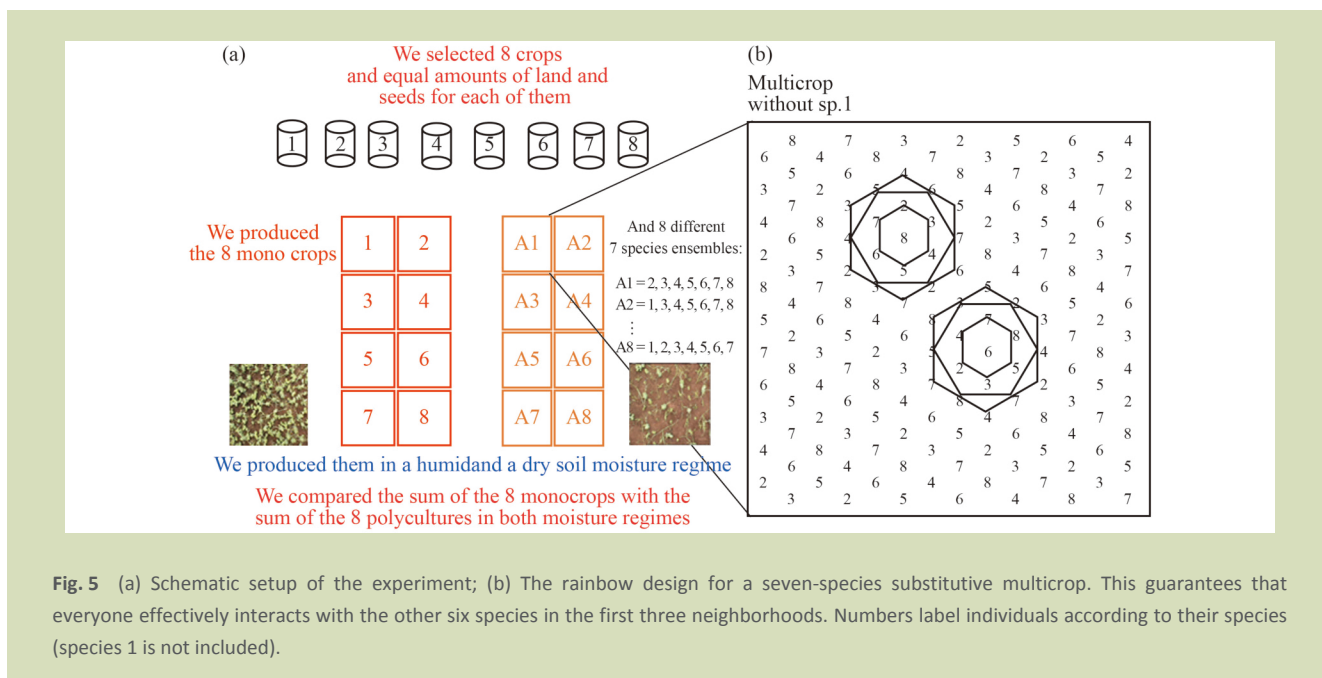
multicrop plots, randomly distributed in a multicrop set (Fig. 5(a)). This pair of sets was established under high and low soil watering conditions and replicated four times. Watering treatments were randomized within replicates, and crop sets within watering treatments. All monocrop and multicrop microplots were sown at the same overall density of 180 plants per square meter, according to reported optimum monocrop densities for most species. The eight multicrops represented the eight possible combinations of eight crops into seven-species multicrops. Each multicrop microplot was sown in a novel hexagonal arrangement (which we call a rainbow design). In this design every target plant experiences all other six species in each of its first, second and third level neighborhood (Fig. 5(b)). The radial distance between plants was 8 cm. Monocrops were established using the same spatial arrangement.

Sowing beds were filled with a sandy loam soil (43% sand, 36% clay and 21% silt; with apparent density of 0.95; field capacity of 42%; and permanent wilting point of 24%) and were watered near field capacity 5 days before sowing. All species were sown as seeds from June 20 to 22. Fifteen days later, seedlings were cleared to one individual per sowing point and transplants from a contiguous nursery were established where plants were missing. Plots were kept free of weeds during the experiment.

Microplots were watered weekly (10 L per microplot) during the first 28 days to assure proper establishment (more than 99.5% of individuals successfully established). From there on, microplots under high-watering treatment were watered with this same amount every 7 days, and those under low-watering treatment every 21 days. During active vegetative growth (AVG) the amount of water per event was doubled. Contrasting soil water content conditions were checked using the gravimetric method from 63 to 84 days after sowing (during the AVG period). A sample of the soil profile was taken from each microplot a day before and a day after every watering event and the average soil moisture content was calculated for the whole period. Soil moisture conditions were compared between crop sets and watering levels with a split-plot minimum significant difference (MSD) test, given the spatial arrangement of treatments, which resemble a split-plot design<sup>[31]</sup>. To have a general idea of stress experienced by crops, average soil moisture (%) per crop set and watering treatment were transformed into soil moisture tension (atmospheres) with the model<sup>[32]</sup>:

$$\text{Soil moisture tension} = \frac{5 \times 10^{10}}{\% \text{ Soil moisture}^{6.8635}} \quad (35)$$

Model parameters of this soil water characteristic curve were estimated in the laboratory for a compound soil sample, using



**Fig. 5** (a) Schematic setup of the experiment; (b) The rainbow design for a seven-species substitutive multicrop. This guarantees that everyone effectively interacts with the other six species in the first three neighborhoods. Numbers label individuals according to their species (species 1 is not included).

the pressure and membrane method<sup>[33]</sup>.

On day 150, 49 plants per monocrop microplot and seven plants per species per multicrop microplot were harvested. Each species per plot sample was separated into shoot and fruit, dried to constant weight in convection ovens, and weighed to 0.01 g. Fruit (whole fruit, since it was cumbersome to separate the seed), shoot and aboveground dry matter average weights (ADM, g) per plant were calculated for each species in each plot. Species averages were compared (Tukey HSD,  $P = 0.05$ ).

Within each of the four replicates and each watering treatment,  $Mo_H$ ,  $Mu_H$ ,  $Mo_L$ ,  $Mu_L$ ,  $R\Delta Y_H$ ,  $R\Delta Y_L$ ,  $RMR$ ,  $\Delta RYT$ ,  $\Delta TDOM$ ,  $\Delta RTDC$  and  $\Delta RSEL$  were calculated separately for each multicrop plot. We decided to pool multicrop composition within watering levels, so each of the former variables in the end had 32 data which were used to construct bootstrap distributions of their averages. This was done separately for fruit, shoot and total ADM. A similar procedure was followed to calculate bootstrap distributions of  $RMR_i$  and  $\Delta RYT_i$  averages for each species. The framework was tested by characterizing and comparing multicrop resistance between different plant parts and between different multicropped species. Multicrops within each watering treatment were pooled for the following four reasons. (1) The 2001 experiment was originally set up to explore the effects of subtle changes in multicrop composition on the  $\Delta Y$ s but composition effects were not significant (fruit  $F_{7,42} = 1.14$ ,  $P = 0.35$ ; shoot  $F_{7,42} = 0.46$ ,  $P = 0.85$ ; total ADM  $F_{7,42} = 0.66$ ,  $P = 0.7$ ). Also, species performance in multicrop was not significantly affected by

multicrop composition; i.e.,  $F_{6,18}$  varied from 2.01; ( $P = 0.12$ ) to 0.42; ( $P = 0.86$ ). (2) The sample distribution of the compound variables considered in this framework have not been previously described in the literature and do not necessarily conform to conditions of normality, heteroscedasticity and independence. Most compound variables (and their log and square-root transformation) did not satisfy the Kolmogorov-Smirnoff and the Levene tests of normality and homoscedasticity, respectively. (3) The distribution of the averages of these compound variables should approximate normality and heteroscedasticity for big samples ( $n > 100$ ) but such sample sizes are impractical. (4) With  $n > 30$ , bootstrap univariate or bivariate distributions of means can be constructed and used to infer if any two distributions differ significantly (without making any assumptions about these distributions)<sup>[29,30,34]</sup>.

## 2.2 Statistical analysis

Univariate bootstrap distributions were obtained using Resample Stats for Excel software<sup>[34]</sup>. Matrix 1 was constructed in Microsoft Excel, with the 32 replicates as rows and resistance-analysis variables as columns. Matrix rows were resampled with replacement 32 times, taking each row as a unit to preserve the correlation between its variables. This produced matrix 2 from which the average of each column was calculated. Procedure b was repeated 1000 times to produce matrix 3 which contains in each column 1000 estimates of the average of a variable. Percentiles 0.025 and 0.975 are the 95% confidence limits of this average.

Distributions of average differences were obtained by pairwise subtraction of bootstrapped averages [34]; their 95% confidence limits were established as previously explained. Bivariate distributions, i.e., (RMR, RΔYh) and (RMR, ΔRYT), were plotted after eliminating cases beyond their 95% confidence limits.

### 3 RESULTS

During active vegetative growth, soil moisture in the average monocrop changed significantly from 34.9% (131.7 kPa) to 25.1% (1246.3 kPa) when watering frequency was reduced. In the average multicrop it changed from 31.1% (283.7 kPa) to 23.7% (1824 kPa); (split-plot MSD for both comparisons = 8.1%;  $P < 0.05$ ). The multicrop consumed more water than the monocrop in the high-watering treatment but not in the low one (split-plot MSD for both comparisons = -3.2%;  $P < 0.05$ ).

In monocrop and high-watering level, the smallest species (millet) and the largest (vetch) differed more than threefold in

total ADM. Millet, pea and lentil formed a small-size group of species while canarygrass, flax, wheat and vetch formed a large-size group; chickpea stood in between. Millet and pea had significantly lower shoot yield than vetch, flax and canarygrass. Lentil, canarygrass and millet had significantly lower fruit yield than wheat. Applying the framework revealed the following.

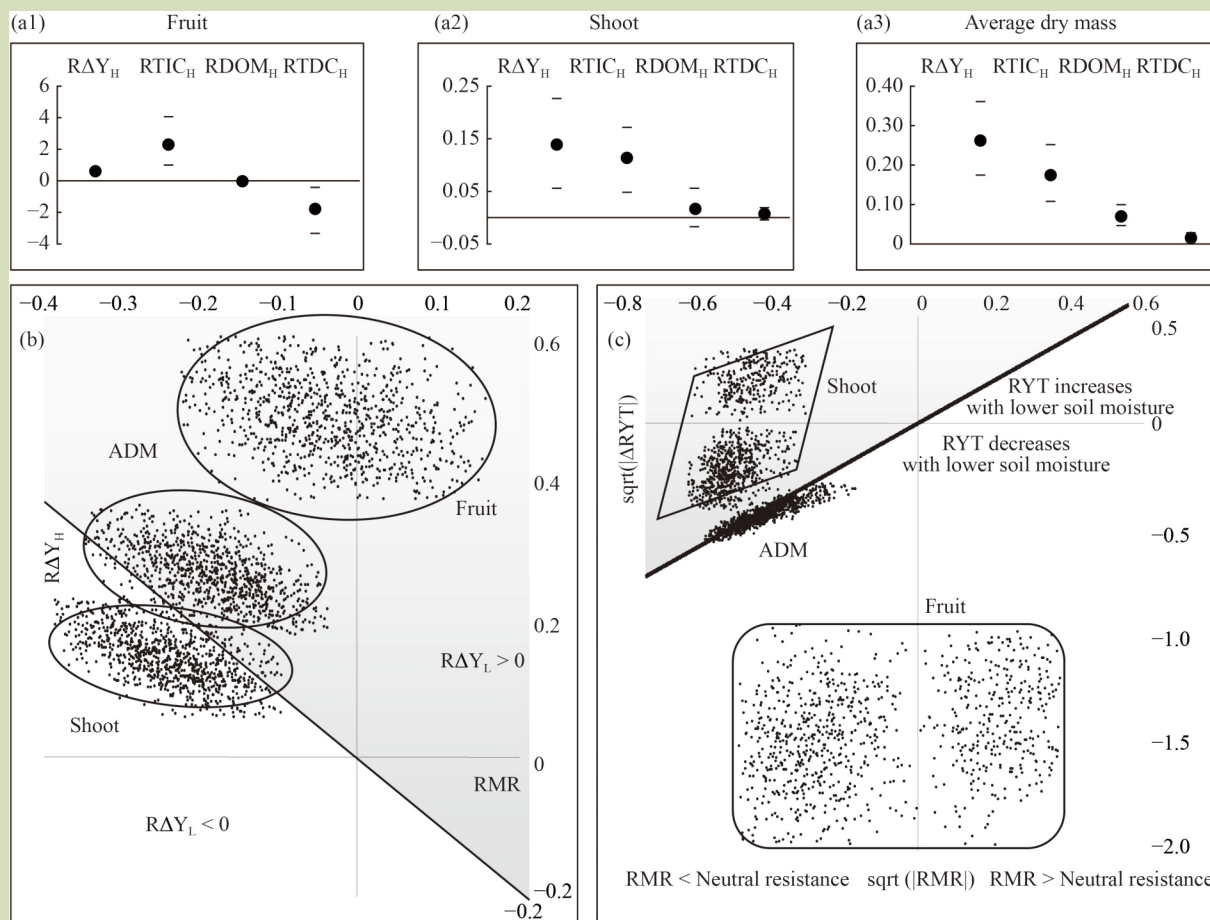
Fruit, shoot and total ADM overyielded in multicrop in moist soil. Fruit had significantly higher relative overyield than shoot and ADM. RYT values were also higher than unity. Fruit RYT was unusually high because some species had very low monocrop fruit yields in moist soil (Table 1).

The ecological causes of overyield in moist soil (Fig. 6(a)) were different in each case. Average fruit yield was 37% to 61% higher in multicrop. This resulted from a positive RTIC that overcompensated a negative RTDC. This means that the less productive species did exceedingly better in multicrops compared to their monocrops. Consequently, their high relative contribution to multicrop yield overcompensated their lower capacity to contribute to yield in absolute terms. Average

Table 1 Framework parameters for fruit, shoot and total ADM (average dry mass)

Plant part	Mu <sub>H</sub>	Mo <sub>H</sub>	Mu <sub>L</sub>	Mo <sub>L</sub>	RΔY <sub>H</sub>	RYT <sub>H</sub>	RΔY <sub>L</sub>	RYT <sub>L</sub>	RTIC <sub>H</sub>	RDOM <sub>H</sub>	RTDC <sub>H</sub>	RMR	ΔRYT	ΔRDOM	ΔRTDC
<b>Fruit</b>															
Average of avgs	254	172	141	100	0.49	3.34	0.45	1.14	2.34	-0.12	-1.73	-0.04	-2.20	0.42	1.74
Percentil 2.5%	232	165	125	94	0.37	1.94	0.28	1.00	0.93	-0.26	-3.31	-0.22	-3.87	0.29	0.49
Percentil 97.5%	276	179	158	106	0.61	5.02	0.63	1.29	4.02	0.02	-0.48	0.16	-0.78	0.54	3.33
<b>Shoot</b>															
Average of avgs	348	305	180	199	0.14	1.11	-0.09	1.09	0.11	0.02	0.01	-0.23	-0.03	-0.15	-0.06
Percentil 2.5%	318	293	155	182	0.06	1.05	-0.19	1.00	0.05	-0.02	0.00	-0.37	-0.17	-0.23	-0.11
Percentil 97.5%	381	316	206	216	0.23	1.17	0.02	1.20	0.17	0.06	0.02	-0.09	0.12	-0.06	-0.01
<b>Total ADM</b>															
Average of avgs	603	476	320	298	0.26	1.18	0.08	0.98	0.18	0.07	0.01	-0.18	-0.19	0.02	-0.01
Percentil 2.5%	557	466	284	280	0.17	1.11	-0.03	0.89	0.11	0.05	0.00	-0.33	-0.32	-0.03	-0.02
Percentil 97.5%	652	488	360	317	0.36	1.25	0.19	0.07	0.25	0.10	0.03	-0.04	-0.08	0.07	0.01

Note: Values estimate the 95% limits and median of the bootstrap distribution of averages. Mu<sub>H</sub>, multicrop yield in high moisture conditions; Mo<sub>H</sub>, monocrop yield in high moisture conditions; Mu<sub>L</sub>, multicrop yield in low moisture; Mo<sub>L</sub>, monocrop yield in low moisture; RΔY<sub>H</sub>, relative overyield with respect to monocrop in high moisture; RYT<sub>H</sub>, relative yield total with respect to average monocrop yield in high moisture; RΔY<sub>L</sub>, relative overyield with respect to monocrop in low moisture; RYT<sub>L</sub>, relative yield total with respect to average monocrop yield in low moisture; RTIC<sub>H</sub>, relative trait-independent complementarity in high moisture; RDOM<sub>H</sub>, relative dominance effect in high moisture; RTDC<sub>H</sub>, relative trait-dependent complementarity effect under high moisture; RMR, relative multicrop resistance index; ΔRYT, relative total yield change; ΔRDOM, relative change in dominance effect; and ΔRTDC, relative change in trait-dependent complementarity effect.



**Fig. 6** Relative overyield in moist soil ( $R\Delta Y_H$ ) and its three ecological components. Bootstrap distributions of average values are represented by their medians and 95% confidence limits: (a1) fruit; (a2) shoot; (a3) total ADM. (b) Covariate bootstrap distributions of shoot, fruit and total ADM averages in the RMR vs  $R\Delta Y_H$  (RMR, relative multicrop resistance index; and  $R\Delta Y_H$ , relative multicrop overyield in humid conditions) plane. Points beyond 95% confidence limits not included. Distributions differ significantly. In all cases,  $R\Delta Y_H > 0$ , but average fruit RMR is not significantly different from zero (scenario 3), while average shoot  $R\Delta Y_L$  is lower than zero (scenarios 4 and 5). Total  $R\Delta Y_L$  is higher than zero (scenarios 4 and 5). (c) Observed covariate bootstrap distributions of shoot, fruit and total ADM average in the  $\sqrt{|\Delta RYT|}$  vs.  $\sqrt{|\Delta RMR|}$  plane (where,  $\Delta RYT$  is change in relative yield total). Points are scaled to the square roots of their absolute values for visual purposes.

shoot yield was 6% to 23% higher in the multicrop. This was almost entirely due to a positive RTIC, as RDOM and RTDC were not significantly different from zero. Average total ADM yield was 17% to 36% higher in the multicrop. All relative overyield components were positive but RTIC explained most of the overyield. For all three plant parts,  $\Delta Y$  was positive and  $RYT > 1$ .

Table 1 shows that when soil moisture was reduced: fruit,  $\Delta Y$  remained positive and  $RYT > 1$ ; shoot,  $\Delta Y$  most probably became negative while  $RYT$  remained  $> 1$ ; and total ADM,  $\Delta Y$  most probably became zero while  $RYT$  most probably became unity. Table 2 shows that fruit displayed neutral multicrop resistance (scenario 3;  $RMR = 0$ ) while shoot multicrop most

probably underyielded or, at best, equaled the average monocrop yield (scenarios 5 and 4). Consequently, total ADM most probably lost all multicrop overyield in low moisture (scenario 4) or might have even underyielded (scenario 5). Figure 6(b) shows that the relation between multicrop overyield in moist soil ( $R\Delta Y_H$ ) and multicrop resistance (RMR) was significantly negative within all bivariate distributions ( $P < 0.01$ ), implying a tradeoff between overyield and resistance.

The position of the distributions of averages in Fig. 6(c) shows the following. (1) Fruit: neutral multicrop resistance ( $x$ -axis) resulted because a reduction in  $RYT$  (negative  $y$ -axis) was compensated for by a more positive relative selection ( $\Delta RSEL > 0$ ; white semiplane). This means that when soil moisture was reduced, smaller crops lost their ability to contribute much

**Table 2 RMR (relative multicrop resistance) scenarios for fruit, shoot and total ADM (average dry mass)**

Plant part	Scenario 1 ( $\mu_{L} = \mu_{H}$ )	Scenario between 1 and 2	Scenario 2 ( $\Delta Y_{L} = \Delta Y_{H}$ )	Scenario between 2 and 3	Scenario 3 ( $R\Delta Y_{L} = R\Delta Y_{H}$ )	Scenario between 3 and 4	Scenario 4 ( $R\Delta Y_{L} = 0$ )	Scenario 5 ( $R\Delta Y_{L} < 0$ )
Fruit								
Shoot								
Total ADM								

Note: A filled cell indicates that the observed RMR distribution did not significantly differ from the RMR distribution expected for that scenario;  $P < 0.05$ . Dark gray indicates where the median of the distribution lays. Blank columns indicate intermediate scenarios.  $\mu_{L}$ , multicrop yield in low moisture conditions;  $\mu_{H}$ , multicrop yield in high moisture conditions;  $\Delta Y_{L}$ , overyield in low moisture;  $\Delta Y_{H}$ , overyield in high moisture;  $R\Delta Y_{L}$ , relative overyield (with respect to monocrop) in low moisture; and  $R\Delta Y_{H}$ , relative overyield in high moisture.

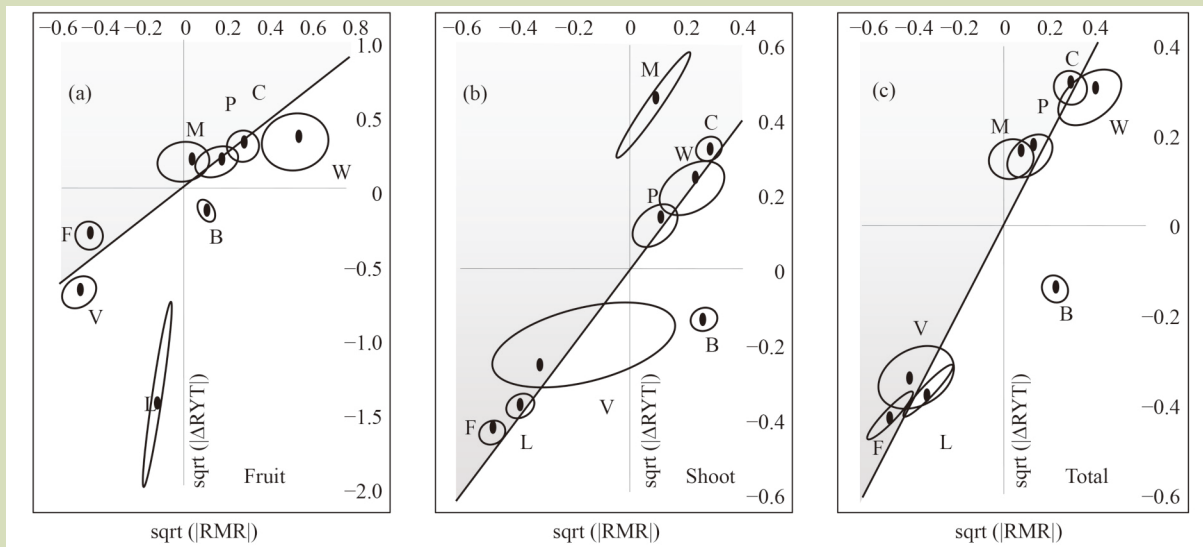
more than expected to multicrop fruit yield. (2) Shoot: the loss of multicrop overyield was not due to a change in RYT but rather to a more negative relative selection ( $R\Delta SEL < 0$ ; gray semiplane); (3) Total ADM: the loss of multicrop overyield was due exclusively to a reduction in RYT; ( $\Delta RSEL = 0$ ; diagonal). Thus, the balance between overyield components was modified by reduced soil moisture, but differently among plant parts. Overall, LUE decreases with this environmental change.

The position of the distributions of averages in Fig. 7 shows that species and their plant parts contributed in contrasting ways to RMR and its components. (1) Fruit: While wheat, pea, chickpea and canarygrass contributed to increase resistance, flax, vetch and lentil did the opposite. This occurred mostly through changes in  $RYT_i$  and less so in  $RSEL_i$ ; (2) Shoot: idem, but millet also contributed to RMR mainly by increasing RYT

and decreasing RSEL, while canarygrass contributed to RMR by doing the opposite; (3) Total ADM: an intermediate combination of the previous cases.

### 4 DISCUSSION

Overyield ( $\Delta Y > 0$ ) and higher land use efficiency ( $RYT > 1$ ) have been major arguments for practicing and supporting mixtures of two or more crops. Recent debate over the meaning and causes of overyield has led ecologists to dissect the ecological components of overyield. The framework presented here extends this research to multicrops, stresses the fact that  $\Delta Y > 0$  does not necessarily imply  $RYT > 1$  and vice versa, and explains in a simple, graphical way how the complex interactions of a suit of many crop species can produce this situation.



**Fig. 7** Observed covariate bootstrap distributions of species average RMR<sub>i</sub> and  $\Delta RYT_i$  values for fruit (a), shoot (b) and total ADM (c). M, millet; P, pea; L, lentil; C, chickpea; Y, canarygrass; F, flax; W, wheat; and V, vetch.

In rainfed agricultural areas in the subhumid tropics, water availability and soil moisture can be highly variable and unpredictable. Soil moisture is expected to diminish and its variability in space and time to increase with global climate change. In theory, species richness in agroecosystems is expected to buffer this impact on yield quantity and yield stability by favoring system resistance to reduced soil moisture. However, few empirical/experimental studies have documented this topic, and results are varied and debated. Different measures of absolute and relative overyield resistance are frequently considered. Together with the different definitions of overyield, this adds to the inherent difficulty of interpretation and consensus.

We proposed the index, RMR, that captures all possible scenarios of absolute and relative multicrop overyield resistance to drought. We dissected the ecological components of RMR (defined as the relative change in  $\Delta Y$  components) to track changes in the relation between  $\Delta Y$  and RYT and to better understand the causes of different overyield resistance scenarios. We provided simple graphical tools and applied simple but robust statistical procedures to these compound variables (based on bootstrap methods) to compare performance of different multicrops, plant parts and multicropped species. It will be important to explore the need for more analytical approaches to statistical inferences about RMR and its components.

The experiment used was appropriate because: (1) contrasting soil moisture conditions were achieved; (2) multispecies interactions were carefully controlled with a novel rainbow design and a greenhouse environment; (3) species monocrop yields followed a gradient that allowed for calculating significant DOM and TDC values; and (4) statistical dispersion of variables was increased by pooling multicrop composition treatments but with no significant difference; yet the contrasting performance between plant parts and between species allowed interesting comparisons.

The experiment showed the following. (1)  $\Delta Y$  and RYT can both be positive (under high moisture conditions) but they can also have different signs (under dry conditions). (2) Fruit displayed neutral resistance (scenario 3) but spanned all the range between scenarios 2 and 4 due to high RMR dispersion. This is in line with the data of Natarajan and Willey<sup>[16]</sup>, for which we infer scenarios 2 and 3 would apply. Dispersion of

experimental fruit RMR average values can partly explain the high variability found by Rao and Wiley<sup>[15]</sup> in their meta-analysis of intercrop yield sensitivity to a rainfall gradient. (3) Shoot and Total ADM had lower than neutral resistance, spanning values above and below scenario 4 ( $\Delta RYI = 0$ ). This was commonly associated with a drop in RYT. This is a less favorable scenario than those from the results of Tilman<sup>[23]</sup> (above neutral resistance), Pfisterer and Schmid<sup>[24]</sup> (neutral resistance) and Kahmen et al.<sup>[11]</sup> (at or below neutral resistance), and more similar to the results of van Peer et al.<sup>[35]</sup> (below neutral resistance) for wild annual species ensembles. (4) The relation between RMR and  $\Delta RYT$  can differ strongly among plant parts and multicropped species, meaning that the relation between absolute overyield ( $\Delta Y$ ) and land use efficiency can be affected by reduced soil moisture.

This framework can help identify the components of multicrop overyield, the potential tradeoffs between productivity and LUE, the consequences derived from environmental change and the complex plant-plant interaction patterns that explain these phenomena in a multicrop ensemble. It could be useful for comparing several multicrops, identifying the contribution of different plant parts and/or crop species to RMR. It might also be used to study RMR in natural multispecies ensembles and can be adapted for studying other resource gradients.

## 5 CONCLUSIONS

Analysis of relative overyielding in contrasting humidity environments using the proposed framework gives us understanding on how the ecological components of overyield (trait-independent complementarity, trait-dependent complementarity and dominance) interplay to produce diverse results. Data from our experiment revealed that the balance between overyield components was modified by reduced soil moisture differently among species and plant parts. Less productive species did better in multicrops compared to their monocrops. High complementarity can be balanced by selection effects and as a result, the resulting change in overyield can be negative, but the contrary can also happen, when overcompensation of losses by complementarity effects emerges. Data also suggested a tradeoff between multicrop overyield and resistance. Further research on how these effects relate to characteristics of species could shed light on how to assemble multispecies intercrops that resist environmental stress.

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### Supplementary materials

The online version of this article at <https://doi.org/10.15302/J-FASE-2021412> contains supplementary materials.

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### Compliance with ethics guidelines

Luis García-Barrios and Yanus A. Dechnik-Vazquez declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any study with human or animal subjects performed by any of the authors.

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