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# Interspecific interactions regulate plant reproductive allometry in cereal-legume intercropping systems

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## Abstract

1. Calling for ecological principles in agriculture has gained momentum. Intercropping systems have long been designed with the objective of optimizing resource use efficiency by growing two, or more, annual crop species in the same field. However, optimization criteria for their design are lacking. Notably, it is still unknown whether and how species performances are maximized during both the vegetative and reproductive phases given the sensitivity of reproductive allocation rules to resource limitation. Interestingly, ecological theory provides expectations regarding putative invariance of plant reproductive allometry (PRA) under non-limiting conditions for plant growth. Here we examined whether and how PRA changes in response to plant-plant interactions in intercropping systems, which represents a major inquiry for both ecological theory and the understanding of the functioning of intercropping systems.

2. We built and analyzed a unique dataset of 28 field cereal-legume intercropping trials from various climatic and management conditions across Western Europe. PRA were quantified in both mixing and single-species situations.

3. Management conditions significantly influenced PRA of the different components of the cropping systems. Deviations to PRA expectations were greater for legumes when grown in mixture, which explains their success in mixtures. The response for cereals was similar in direction but less pronounced in magnitude, and was more significant under limiting resource conditions.

4. Synthesis and applications. PRA matters in crop species in the same way as it does in wild species, suggesting the existence of universal biophysical constraints that cannot be broken by artificial selection. However, contrary to theoretical expectations about an overall invariance of PRA, our meta-analysis highlighted taxon-specific and context-dependent effects of plant-plant interactions on PRA. A systematic exploration of deviation to PRA expectations appears as a relevant tool to assist the management of intercropping systems through the choice of species and genotypes to use and the type of agricultural practices to apply. In turn, such a dialog between agronomy and ecology is a unique opportunity to challenge the validity domain and robustness of major ecological laws.

## Keywords

Biomass allocation; Intercropping; Metabolic scaling theory; Plant reproductive allometry

# Introduction

Intercropping, i.e. combining at least two annual crop species in the same field for most part of their growing periods (Willey, 1979), is a promising way to move towards more sustainable agriculture (Li-li et al., 2015; Lin, 2011). Intercropped species are expected to use resources differently and more efficiently (e.g. Malézieux et al., 2009; Beillouin, Ben-Ari, & Makowski, 2019; Jensen, Carlsson, & Hauggaard-Nielsen, 2020). Many intercrops mix a cereal and a legume, with the underlying assumption that the cereal will benefit from the legume's atmospheric nitrogen (N) fixation, thus decreasing the need for exogenous N fertilization (Gaba et al., 2018; Malézieux, 2012; Thorsted, Weiner, & Olesen, 2006). The performance of intercropping systems has been studied from an agronomic perspective, focusing mainly on yield and N use (e.g. Bedoussac & Justes, 2010b; Hauggaard-Nielsen, Gooding, Ambus, Corre-Hellou, Crozat, Dahlmann, Dahlmann, et al., 2009; Naudin, Corre-Hellou, Pineau, Crozat, & Jeuffroy, 2010; Pelzer et al., 2012). While introducing species diversity into cropping systems could appear promising under low-input conditions, specific recommendations for the management of intercrops is in its infancy (Litrico & Violle, 2015). One reason for this is that the underlying mechanisms of the positive effect of the intercropping remain elusive, which makes it challenging to choose species and cultivars for these systems accurately. One key unsolved issue for identifying these mechanisms is how vegetative biomass translates into reproductive biomass and how reproductive allocation differs between sole cropping and intercropping situations. Bridging ecology and agronomy could help resolve this issue.

In ecology, the plant allometry literature has extensively analyzed the change in many key plant features as a function of size. Notably, a large body of theory indicates that plant reproductive output (grain yield for annual cropping systems) is a function of plant size (Weiner, Campbell, Pino, & Echarte, 2009). It is based on metabolic optimization criteria, in which regulation processes and selection forces have similar influence on size-related traits across taxa (Enquist, West, Charnov, & Brown, 1999). It forms the basis of metabolic scaling theory (MST), which provides first principles of plant allometry laws (West, Brown, & Enquist, 1997, 1999). As a macroecological law, MST explains trait variation across several orders of magnitude of taxa, scales and body size. This body of theory attracts interest for the design and management of intercropping systems given the predictive power of universal scaling equations of MST (Deng et al., 2012).

The hypothesis of invariance at the origin of allometric scaling laws has been challenged. Poorter et al. (2015) highlighted that allometric scaling exponents differ among species. Vasseur, Violle, Enquist, Granier, & Vile (2012) and Vasseur et al. (2018) highlighted variability in these exponents within the model species *Arabidopsis thaliana*, and demonstrated that this variability was genetically determined and environmentally regulated due to natural selection. Further, the influence of artificial selection on allometric constraints is not well understood due to the lack of comparisons of allometric relationships in crop species (Milla, Osborne, Turcotte, & Violle, 2015). The initial MST framework was designed along with plant observations in optimal conditions, i.e. where growth is not strongly limited by unfavorable abiotic or biotic conditions. Consequently, the influence of plant-plant interactions and soil resource limitations on deviations from MST expectations remains unknown (but see Coomes, Lines, & Allen, 2011; Vasseur et al., 2018). Intercropping systems represent a unique opportunity to challenge allometric laws, in order to fine-tune them and assess the validity of their most basic assumptions. Understanding the influence of plant-plant interactions on reproductive strategies of intercropped species would improve the understanding, modeling and ultimately management of intercrops (Gaudio et al., 2019), particularly to drive each species to its potential reproductive output in relation to the other species and the cropping conditions. In this study, we analyzed how plant allometry is related to the performance of intercropped species and how this relationship is influenced by varying cropping conditions. Crop scientists and stakeholders, including farmers, are primarily interested in yield, often assessed in intercropping systems by the land equivalent ratio in order to calculate land-use efficiency (e.g. Yu, Stomph, Makowski, Zhang, & Werf, 2016). Finer analysis of intercrop performance would improve our understanding of the mechanisms underlying intercrop performance.

We examined the influence of plant-plant interactions on the allometric relationship between grain yield production and plant biomass in annual cereal-legume intercrops grown under a variety of climatic and cropping conditions in Western Europe, with the underlying objective to test the MST under non-optimal conditions, characterized here by the plant-plant interactions and soil nutrient limitations. Our analysis was based on 28 field experiments. The main objective of this study was to investigate how the reproductive allometric relationships of both plant families (cereals and legumes) changed depending on whether they were grown in a sole crop or with another crop. We also focused on the influence of N fertilization within each plant family and crop type (sole crop *vs.* intercrop). The strength of allometric relationships can indicate that the ratio of yield to plant size does not vary, as the relationship between these two variables is supposed to be invariant (Nee, Colegrave, West, & Grafen, 2005). This ratio is called “reproductive effort” in ecology (Cheplick, 2005) and “harvest index” in agronomy (Echarte & Andrade, 2003; Vega, Sadras, Andrade, & Uhart, 2000). It is often used to focus on allocation of biomass to reproductive organs and to differentiate performances of species and cultivars (Hay, 1995), which is a framework that is complementary to MST. Thus, we also assessed the influence of crop management on reproductive efforts of the two plant families.

# Materials and methods

## Field experiments

We collected a set of experiments that compared different species and cultivars under intercropping and sole-cropping conditions under a variety of management practices in 9 locations in five European countries (France, Denmark, Italy, Germany, and the United Kingdom) (Fig. 1). The experiments covered 28 environments (location x year), of which 15 were managed as organic farming and 13 as conventional farming, with a total of 34 intercropping situations (environment x species) and 62 sole-cropping situations. Since the experiments were not completely factorial, i.e. not all factors (cultivars, N fertilization, sowing density) were combined, we analyzed a total of 159 and 219 experimental units under intercropping and sole-cropping situations, respectively. In the experiments, 53% and 47% of the intercropped species were winter and spring crops, respectively. The mean temperature over the crop cycle (from sowing to harvest) ranged from 6.8-11.3 °C for winter crops and 12.3-15.1 °C for spring crops. Cumulative rainfall ranged from 278-713 mm for winter crops and 60-366 mm for spring crops.

Additional details on experimental designs and management practices are reported in Supplementary Material S1 and in the reference publications for 22 of the 28 experiments (Bedoussac & Justes, 2010a, 2010b; Corre-Hellou, Fustec, & Crozat, 2006; Hauggaard-Nielsen, Gooding, Ambus, Corre-Hellou, Crozat, Dahlmann, Dahlmann, et al., 2009a; Hauggaard-Nielsen, Gooding, Ambus, Corre-Hellou, Crozat, Dahlmann, Dibet, et al., 2009b; Hauggaard-Nielsen, Jørnsgaard, Kinane, & Jensen, 2008; Knudsen, Hauggaard-Nielsen, Jornsgard, & Jensen, 2004; Launay et al., 2009; Naudin et al., 2010; Naudin, Werf, Jeuffroy, & Corre-Hellou, 2014; Pelzer, Bazot, Guichard, & Jeuffroy, 2016; Tang et al., 2016).

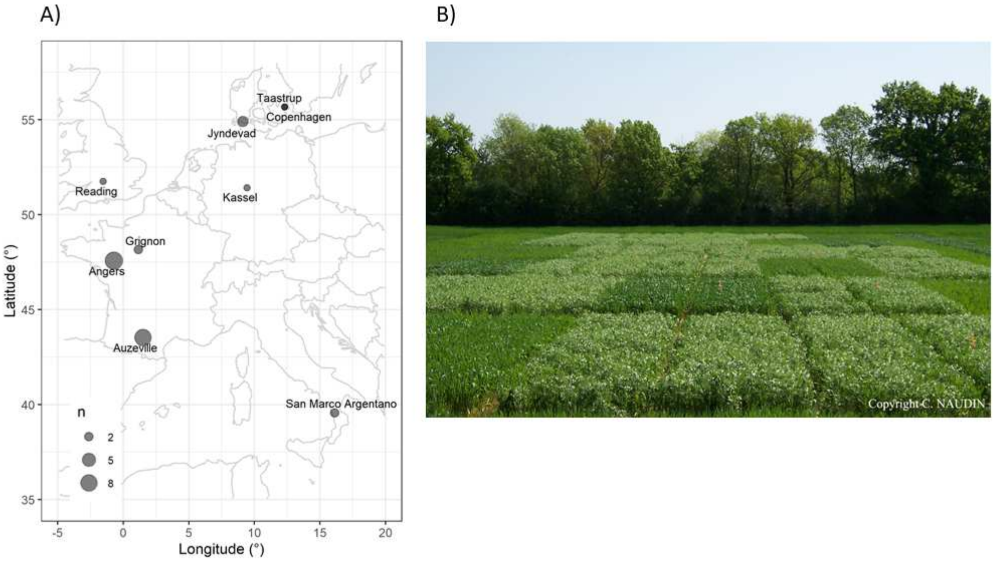

Fig. 1. (A) Number of field experiments (size of the circle) conducted at each location and (B) example of a field experiment of winter wheat-pea intercrops (and their corresponding sole crops) conducted at the ARVALIS experimental station, near Angers, France (Source: C. Naudin).

The set of experiments included annual cereal-grain legume intercrops and their corresponding sole crops, with i) barley (*Hordeum vulgare* L.), durum wheat (*Triticum turgidum* L.) and soft wheat (*Triticum aestivum* L.) as the cereals (only Poaceae), and ii) faba bean (*Vicia faba* L.) and pea (*Pisum sativum* L.) as the legumes (Fabaceae). The cross between crop species and cropping seasons resulted in five intercropping combinations: two spring intercrops (barley-faba bean and barley-pea) and three winter intercrops (durum wheat-faba bean, durum wheat-pea and soft wheat-pea). In all experiments, the two intercropped species were sown and harvested at the same time, with sowing dates ranging from March 11 to May 03 for spring crops and October 25 to December 15 for winter crops.

Within a given cropping situation, variations were related mainly to i) the number of cultivars tested per crop species (ranging from 1-5); ii) the relative sowing density of each species (actual:reference sowing density ratio, 1.0 and 0.5 for sole crops and 0.3 - 0.7 for each of the two intercropped species) and iii) the N fertilization, with non-fertilized and N-fertilized situations, the latter ranging from 30-200 kg N.ha$^{-1}$ (mean (± SD) = 95 ± 44 kg N.ha$^{-1}$) (Table 1).

To assess reproductive effort and allometry, all experiments measured at least three variables: grain yield (t.ha$^{-1}$), total aboveground biomass (t.ha$^{-1}$, including grains, flowers, pods and ears) at maturity, and actual plant density (plant.m$^{-2}$). Plant density was used to convert per-ha variables into per-capita variables (i.e. g.plant$^{-1}$; Table 1).

Table 1. Cropping situations pooled in the database by plant family (Poaceae *vs.* Fabaceae), crop type (sole crop *vs.* intercrop) and nitrogen (N) fertilization (non-fertilized N0 *vs.* N-fertilized). Several cultivars and crop species densities (relative proportions) were represented for each factor combination (family x crop type x N fertilization). Mean (± SD) total plant aboveground dry biomass and grain yield were calculated for each factor combination.

| Plant family | Crop type | N fertilization | No. cropping situations | No. cultivars | No. densities | Biomass (g.plant$^{-1}$) | Yield (g.plant$^{-1}$) |
|---|---|---|---|---|---|---|---|
| Cereal (Poaceae) | Sole crop | N0 | 57 | 12 | 2 | 3.8 ± 1.8 | 1.5 ± 0.6 |
| | | N | 57 | 11 | 2 | 6.8 ± 3.0 | 2.7 ± 1.1 |
| | Intercrop | N0 | 103 | 12 | 5 | 3.5 ± 1.7 | 1.5 ± 0.8 |
| | | N | 56 | 9 | 6 | 6.8 ± 2.1 | 2.8 ± 0.9 |
| Legume (Fabaceae) | Sole crop | N0 | 87 | 18 | 2 | 20.9 ± 16.7 | 9.0 ± 5.9 |
| | | N | 18 | 8 | 2 | 35.3 ± 25.5 | 16.0 ± 12.5 |
| | Intercrop | N0 | 103 | 18 | 5 | 15.2 ± 11.4 | 7.8 ± 5.8 |
| | | N | 56 | 8 | 6 | 16.0 ± 12.5 | 7.4 ± 5.7 |

## Data processing and analysis

Reproductive effort was calculated as the ratio of grain yield to total aboveground biomass at maturity, rather than final biomass, to avoid the influence of leaves that dropped before maturity (Unkovich, Baldock, & Forbes, 2010). Analysis of variance (ANOVA) was performed using the *aov* function of the stats package of R software (R Core Team, 2019). When relevant ($p < 0.05$), means were separated using a Tukey or, when ANOVA assumptions were not met, Kruskal-Wallis test. We performed one-way ANOVAs within each plant family (Poaceae *vs.* Fabaceae) to test the influence of crop type (sole crop *vs.* intercrop) and N fertilization (non-fertilized *vs.* N-fertilized) on reproductive effort and its components (i.e. plant aboveground biomass and plant yield). The influence of N fertilization could not be assessed for legumes in sole crops due to unequal sample sizes (18 situations fertilized, 87 non-fertilized) (Table 1). For the same reason, differences between sole crops and intercrops for legumes could be assessed only under non-fertilized conditions.

We analyzed reproductive allometric relationships between plant grain yield and plant aboveground biomass thanks to standardized major axis analysis (SMA; Warton, Wright, Falster, & Westoby, 2006; Poorter & Sack, 2012) using the R *smatr* package (Warton, Duursma, Falster, & Taskinen, 2012), through the power relation $y = ax^b$, where $y$ and $x$ are plant yield and aboveground biomass, respectively. This method enables geometrical interpretations that lead to statistical testing procedures to compare slope, offset and shift along the allometric line (Taskinen & Warton, 2013; Warton et al., 2012). More specifically, we assessed the effect of plant family and, within each family, the effect of crop type and N fertilization, on the position of individual plants along the main reproductive allometric line. Because of the unequal sample sizes, allometric lines for legumes were compared only i) under non-fertilized conditions, to compare the effect of crop type, and ii) in intercrops, to compare the effect of N fertilization.

When two groups had significantly different slopes of allometric lines, we determined the aboveground biomass for which the two allometric lines intersect, thus defining the plant-size threshold above which a plant had a proportionally higher yield. For example, this threshold equaled the abscissa $X_0$ of the intersection of the allometric relationships for an intercrop (IC) and sole crop (SC), calculated as $X_0 = \frac{a_{IC}-a_{SC}}{b_{SC}-b_{IC}}$, where $a_{IC}$ and $a_{SC}$ are the estimated intercept, and $b_{IC}$ and $b_{SC}$ are the least square estimate of the slope of the allometric relationship for an intercrop and sole crop, respectively. We calculated 95% confidence intervals (CI0.95) of this threshold using the procedure of Filliben & McKinney (1972).

To assess the dominance of the focal species in intercrop, we calculated a distance index based on biomass difference (i.e. fitness distance, Mayfield & Levine, 2010; Cadotte, 2017) between the two intercropped species within each of the 159 experimental units in intercropping situations. We first normalized plant yield and biomass values within species x fertilization groups to account for major plant size differences between intercropped species (unity-based normalization, $x' = \frac{x-x_{max}}{x_{max-}x_{min}}$). Then, considering an intercrop mixing two species *i* and *j*, the biomass distance index for the focal species *i* was defined as $x'_{j-}x'_i$, and respectively for species *j*. This index ranges from -1 (i.e. focal species is dominant) to +1 (i.e. focal species is dominated). We used a linear model to analyze change in plant yield as a function of the biomass distance index.

The allometric relationships led to centered residuals as the differences between the observed yield and the predicted one from associated biomass. A natural question arose about the impact of the conditions of each experiment on these results. Considering an ANOVA or a mixed model would be unsatisfying due to the unbalanced sizes of each experimental group in the dataset. Thus, an alternative approach was proposed to tackle such a question. The residual values were plotted separately for each subset of data obtained in the same conditions. Moreover, the p-th quantiles for p=2.5% and p=97.5% were drawn to bounds 95% of residual values to visualize possible outliers (Supplementary Material S2). The results indicated that no extreme value appeared as remarkable. Some variability is revealed but its order of magnitude remains below the dispersal of the residuals. The role of the experimental factors appears then as neglectable with respect to the residual variations of the allometric relationships.

Data were analyzed with R software version 3.6.0 with the packages *dplyr* (data processing; Wickham, François, Henry, & Müller, 2019), *ggplot2* (visualization; Wickham, 2016) and *knitr* (reporting; Xie, 2015).

# Results

## Reproductive allometry in cereals and legumes

The reproductive allometric relationship between plant yield and biomass was significant and robust ($R^2 = 0.94$) across all experimental units, indicating that size is a predominant driver of crop yield. Allometric relationships of legumes and cereals displayed a similar slope close to 1 (1.03 ± 0.02), indicating an overall isometric relationship between plant yield and biomass. However, legumes generally had larger biomass and grain yield than cereals (significant shift along the main relationship, Fig. 2A). Moreover, legumes generally had higher yield than cereals for a given biomass (significant offset along the y-axis). The relationships between reproductive effort and plant biomass were weak for both cereals and legumes ($R^2 = 0.104$ and 0.049, respectively), with reproductive effort decreasing slightly as plant biomass increased ($p < 0.0001$,

Fig. 2B). Legumes had slightly but significantly higher reproductive effort (0.48 ± 0.10, ranging from 0.19-0.73) than cereals (0.43 ± 0.08, ranging from 0.22-0.67), although it varied greatly.

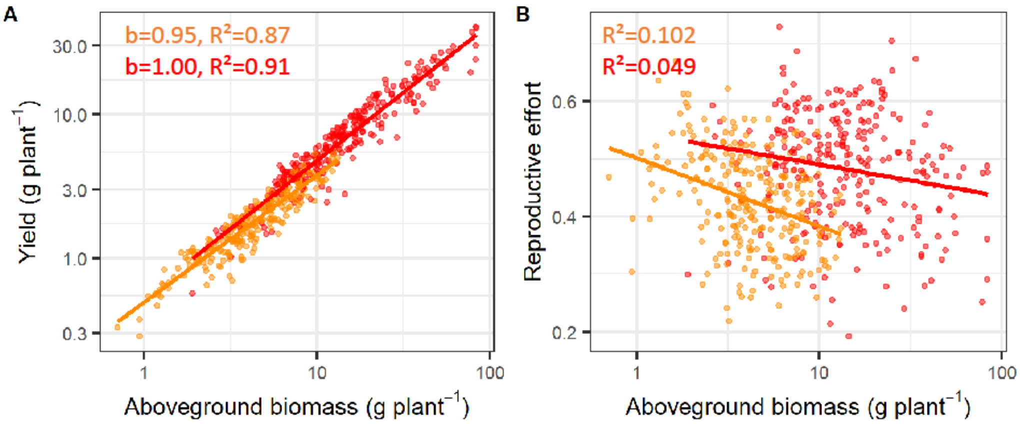

Fig. 2. (A) Reproductive allometric relationship (log-log scale) between plant yield (g.plant$^{-1}$) and plant biomass (g.plant$^{-1}$) and (B) relationship between reproductive effort (=yield:biomass) and plant biomass (g.plant$^{-1}$) for cereals (orange) and legumes (red) for all experimental units in intercropping and sole-cropping situations.

## Crop management impacted the plant reproductive allometry, especially for legumes

The slopes of allometric relationships were steeper under intercropping than sole-cropping conditions (Fig. 3A-C). The intercropping effect was stronger in non-fertilized conditions (legumes, $p < 10^{-6}$; then cereals $p = 0.004$) than in fertilized conditions (cereals, $p = 0.03$). For legumes under non-fertilized conditions, intercrops had significantly higher reproductive effort than sole crops. Although allometric differences were observed for cereals, ANOVAs indicated that intercropping had no significant effect on reproductive effort or its components (plant yield and biomass) whether in fertilized or non-fertilized conditions (Table 2).

We calculated the plant size threshold corresponding to the intersection of allometric lines in intercrop and sole crop conditions to identify the minimum plant size corresponding to a positive intercropping effect on biomass allocation (increased yield for a same plant size). The plant size threshold above which a legume under non-fertilized conditions (Fig. 3A) benefited from intercropping was 10.3 g.plant$^{-1}$ (CI0.95 = [6.7-13.5 g.plant$^{-1}$]), with biomass ranging from 1.9-83.2 g.plant$^{-1}$. For a cereal under non-fertilized conditions (Fig. 3B), the threshold was 3.5 g.plant$^{-1}$ (CI0.95 = [2.0-5.9 g.plant$^{-1}$]), with biomass ranging from 0.7-9.9 g.plant$^{-1}$. For a cereal under N-fertilized conditions (Fig. 3C), the threshold was 6.3 g.plant$^{-1}$, with biomass ranging from

2.6-13.2 g.plant$^{-1}$. We could not derive CI0.95 for this situation because the allometric relationships of the two datasets had high collinearity and widely scattered points.

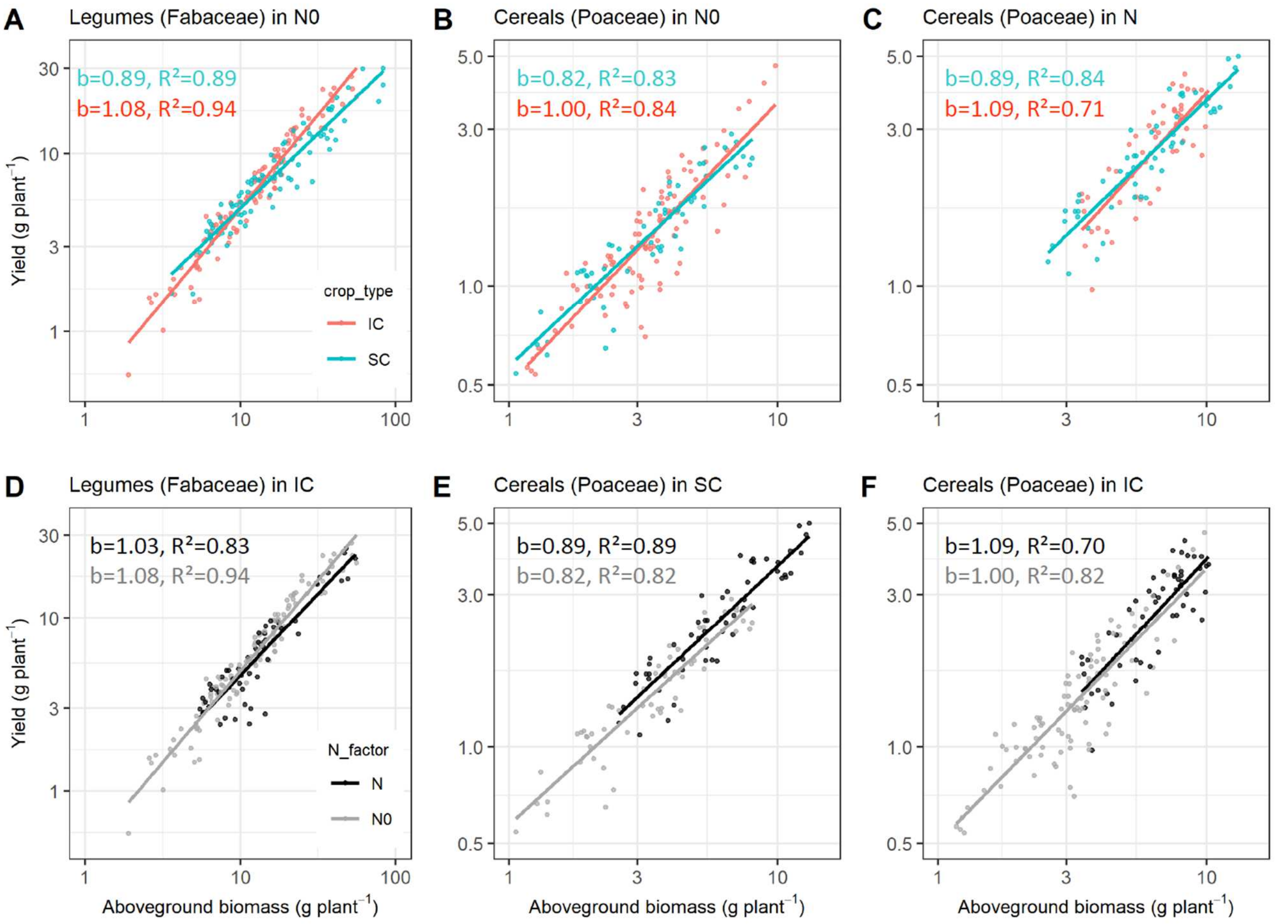

Fig. 3. Reproductive allometric relationship (log-log scale) between plant yield (g.plant$^{-1}$) and plant biomass (g.plant$^{-1}$) by i) crop type (i.e. sole crop (SC) *vs.* intercrop (IC)), for (A) legumes (Fabaceae) under non-fertilized conditions (N0), (B) cereals (Poaceae) under N0 and (C) cereals under N-fertilized conditions (N), and by ii) N fertilization, for (D) legumes grown under IC, (E) cereals under SC and (F) cereals under IC. b represents the allometric scaling exponent of the studied relationships.

In intercropping conditions, for a given species, we analyzed how variation in its yields depends on biomass distance between the two intercropped species. This distance index strongly explained yield variation (Fig. 4), with a decreasing slope (lesser sensitivity to the other species) from non-fertilized legumes (a = -0.52, r2 = 0.68), non-fertilized cereals (a = -0.45, r2 = 0.65), and fertilized cereals (a = -0.39, r2 = 0.47).

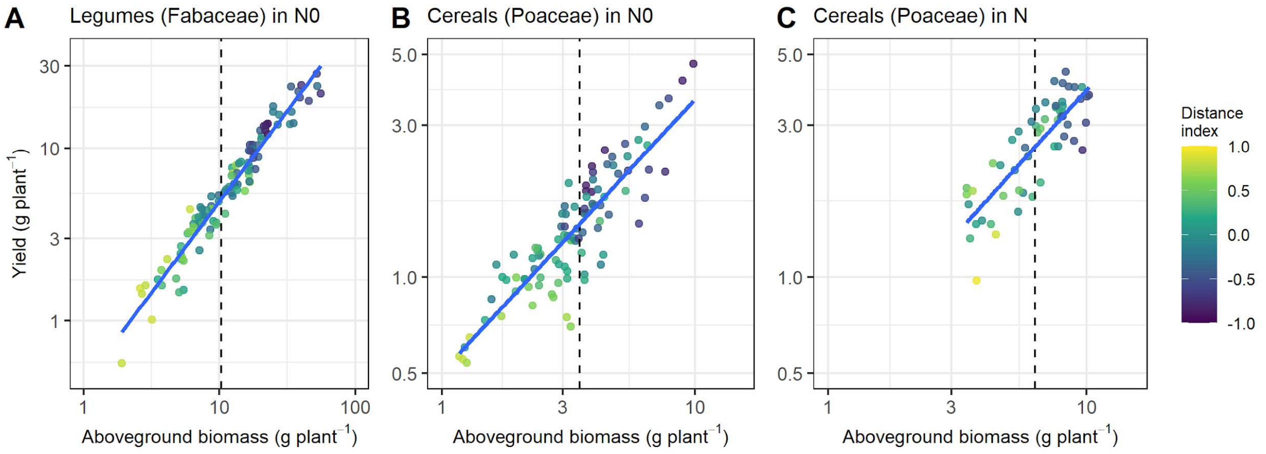

Fig. 4. Reproductive allometric relationship (log-log scale) between plant yield (g.plant$^{-1}$) and plant biomass (g.plant$^{-1}$) in intercrops, for (A) legumes (Fabaceae) under non-fertilized conditions (N0), (B) cereals (Poaceae) under N0 and (C) cereals under N-fertilized conditions (N). The biomass distance between the focal species and its associated species is encoded by the color gradient. Vertical dotted lines correspond to the intersection of allometric lines between sole crops and intercrops in Fig. 3.

N fertilization also influenced allometric relationships (Fig 3D-F). For a given plant biomass, intercropped legumes had higher yield without N fertilization than with it (significant offset, Fig. 3D). The analysis of the reproductive effort confirmed this result, with significantly higher biomass allocation for legumes under non-fertilized (0.51 ± 0.09) than N-fertilized (0.47 ± 0.11) conditions. However, we could not determine whether biomass or yield caused this difference. For cereals, N fertilization did not influence the allometric relationship: N-fertilized plants had proportionally larger biomass and yield, regardless of the crop type (significant shift, Fig. 3E-F). This result was confirmed by both crop types having a similar reproductive effort: both ratio components (plant biomass and yield) were higher under N-fertilized conditions than non-fertilized conditions, regardless of the crop type.

Table 2. Effect of crop type (sole crop SC *vs.* intercrop IC) and nitrogen (N) fertilization (non-fertilized N0 *vs.* fertilized N) by plant family (Poaceae *vs.* Fabaceae) on i) reproductive effort, plant biomass (g.plant$^{-1}$) and plant yield (g.plant$^{-1}$) using analysis of variance and ii) allometric relationships (slope, offset and shift along the relationship) using standardized major axis (SMA) analysis (*** <0.0001, ** <0.001, * <0.05, ns non-significant).

|  |  |  | Analysis of variance |  |  | SMA analysis |  |  |
|---|---|---|---|---|---|---|---|---|
| Plant family | Factor | Condition | Reproductive effort | Biomass | Yield | Slope | Offset | Shift |
| Cereal (Poaceae) | Crop type | Non-fertilized | ns | ns | ns | * | - | - |
|  |  | N-fertilized | ns | ns | ns | * | - | - |
|  | N fertilization | Sole crop | ns | *** (N0 < N) | *** (N0 < N) | ns | ns | *** |
|  |  | Intercrop | ns | *** (N0 < N) | *** (N0 < N) | ns | ns | *** |
| Legume (Fabaceae) | Crop type | Non-fertilized | * (SC < IC) | ** (SC > IC) | ns | *** | - | - |
|  | N fertilization | Intercrop | * (N0 > N) | ns | ns | ns | * | ns |

# Discussion

Intercrop design aims to improve resource-use efficiency, especially crop N use (yield per unit of N absorbed) in cereal-legume intercrops (Jensen et al., 2020). In the experiments examined, plant-plant interactions in intercropping conditions influenced reproductive allometry. These results increase knowledge about the factors that influence plant allometry while the allometric rules are usually considered invariant across species and ecological situations, notably as expected from the metabolic scaling theory (MST; Niklas & Enquist, 2001). Moreover MST appears as a new and promising conceptual framework to improve intercrop management. The allometric approach improves our understanding of which intercropping situation favors one species or the other, and provides some guidelines to identify putative trade-offs depending on the agronomic objective assigned to the intercrop (e.g. focus on the legume, or having both intercropped species reaching a suitable yield without one species strongly dominating the other).

In addition to the strong size-dependence of grain yield production, which was predicted by allometric relationships and highlighted in other studies (Liu, Wang, Wei, & Wang, 2008; Qin, Weiner, Qi, Xiong, & Li, 2013; Sugiyama & Bazzaz, 1998; Vega et al., 2000; Weiner, 2004), we observed that species grown in intercrops had a greater increase in yield for a given increase in plant size than species grown in sole crops through the threshold analysis (x-coordinate of the intersection of allometric lines between sole cropping and intercropping conditions). This highlights a better spatial and temporal resource use efficiency in a field situation, which is a pillar of ecological intensification (Li-li et al., 2015).

This effect depends on plant family and the relative dominance of the two intercropped species. When ranking this effect among cropping conditions, intercropping benefited legumes under non-fertilized conditions the most, followed by cereals under non-fertilized conditions and then cereals under N-fertilized conditions. For example, a cereal plant in a sole crop is surrounded by other cereal plants. Since cereal plants generally compete strongly for soil resources, they experience strong intra-specific competition under non-fertilized conditions. If this cereal plant is intercropped with legume plants, however, some of its close neighbors are legumes, which compete less for soil N than cereals (Mariotti, Masoni, Ercoli, & Arduini, 2009; Satorre & Snaydon, 1992) and can fix atmospheric N. This decreases the competition experienced by the cereal plant due to functional complementarity in N acquisition strategy (Duchene, Vian, & Celette, 2017; Hinsinger et al., 2011). However, when the intercrop is fertilized with N, cereals have a competitive advantage over legumes and complementarity for resource use is replaced with strong interspecific competition from the cereal over the legume. Thus, intercrop design should focus on three key points: i) plant family, characterized by their competitive ability (Goldberg, 1990); ii) characteristics of the two intercropped species, to consider the plant neighborhood (Gaudio et al., 2019; Stoll & Weiner, 2000); and iii) abiotic resource availability.

The relaxation of competitive interaction in intercropping situations is highlighted by the strong effect of biomass differences between the two intercropped species on grain yield production (also called fitness distance in the ecological literature; Cadotte 2017). This reflects the difference in dominance between the two intercropped species (Mayfield & Levine, 2010), which is one key driver for competitive exclusion. Then, in intercrops, yield of cereals in N-fertilized conditions is hardly influenced by the biomass of the legume, whereas cereals in non-fertilized and then legumes in non-fertilized were much more influenced. When the biomass difference between the two intercropped species is high, there is an obvious imbalance between the two species, leading to strong differences in competitive ability of the two components of the mixture: the greater the biomass difference, the more intense hierarchical competition (Kunstler et al., 2016). Therefore, around the size threshold corresponding to the intersection between allometric lines in sole- and intercropping conditions identified for each cropping situation, the two intercropped species do not reach their maximal size and associated yield but an equilibrium exists between them. When we move away from this threshold, one intercrop component becomes highly dominant or conversely dominated due to hierarchical competition.

For legumes, we showed that fertilization decreases the reproductive effort (i.e. lower yield for a given biomass) compared to that under non-fertilized intercropping situations, as highlighted in other studies (e.g. Corre-Hellou, Brisson, Launay, Fustec, & Crozat, 2007 for spring barley-pea). This is probably because when strong competition limits a resource, plants tend to allocate more biomass to structures associated with acquiring it, potentially to the detriment of reproductive organs (Bonser, 2013; Poorter & Nagel, 2000). In contrast, cereals in intercrops had similar reproductive effort whatever the fertilization condition, but a given reproductive effort was reached with proportionally higher biomass and yield in fertilized plots. In these cropping conditions, cereals are larger and compete more for aboveground and soil resources. Understanding the causal processes for such a modified allocation would require targeted experiments that measure key functional traits of legumes that reflect plant behavior for light (e.g. specific leaf area) and N availability (e.g. leaf N content) (Freschet, Violle, Bourget, Scherer-Lorenzen, & Fort, 2018).

# Pathway to applications

Weiner et al. (2009) described the reproductive-vegetative allometric relationship as a relatively fixed-boundary condition, meaning that a plant cannot increase its reproductive output without growing more first. Our findings highlight that, in a crop mixture, the interaction between the two intercropped species makes this boundary more complex given that the reproductive output of one component also depends on the performance of the other. From a practical viewpoint, the analysis of the intersection of allometric relationships enables the identification of plant biomass thresholds for each component of the mixture. We propose to use these thresholds as management criteria to cultivate each species up to its reproductive output maximum while accounting for the performance of the other.

We found that plant-plant interactions were a strong driver of yield variation in crop mixtures. In this case, an agronomic action on one species can readily influence the other even under relatively variable climate conditions, which is an important observation for designing and managing intercrops. For instance, if the goal of the farmer is to promote legume yield, using the cereal mainly to limit legume disease and lodging (e.g. Viguier, Bedoussac, Journet, & Justes, 2018 for spring wheat-lentil intercrops), then we should identify plant size level of the target legume above which higher growth means higher yield, accounting for the interaction with the cereal. Conversely, if the goal is to promote both intercropped species, then trade-offs should be managed to be close to the threshold in order to avoid a strong dominance of one of the two species.

Moreover, results at the family rank are particularly interesting because intercrops are grown to meet a variety of objectives. While intercrop systems are often designed to achieve a balance in the yield of both species harvested (Hauggaard-Nielsen et al., 2008; Pelzer, Hombert, Jeuffroy, & Makowski, 2014), they can also help to increase legume acreage, which is a major issue in the current agronomic context in order to decrease greenhouse gas emissions - through decreased use of synthetic N fertilizer and increased production of plant protein for human consumption (Magrini et al., 2018; Zander et al., 2016).

# Authors' contributions

NG, PC, CV, FF designed and planned the study;

LB, GCH, AC, HHN, PH, ESJ, EPJ, EJ, BK, CN, EP provided data;

NG, PC, CB, RM designed, formatted and homogenized the database;

NG, PC, XG, RM analyzed the data;

NG, PC, CV, FF, EP, SM, XG, RM, HHN, LB, AC, CN, NM participated in the writing and editing.

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