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Gaudio, Noémie; Violle, Cyrille; Gendre, Xavier; Fort, Florian; Mahmoud, Rémi; Pelzer, Elise; Médiène, Safia; Hauggaard-Nielsen, Henrik; Bedoussac, Laurent; Bonnet, Catherine; Corre-Hellou, Guénaëlle; Couëdel, Antoine; Hinsinger, Philippe; Jensen, Erik Steen; Journet, Etienne-Pascal; Justes, Eric; Kammoun, Bochra; Litrico, Isabelle; Moutier, Nathalie; Naudin, Christophe; Casadebaig, Pierre

Published in:
Journal of Applied Ecology

DOI:
[10.1111/1365-2664.13979](https://doi.org/10.1111/1365-2664.13979)

Publication date:
2021

Document Version
Early version, also known as pre-print

Citation for published version (APA):
Gaudio, N., Violle, C., Gendre, X., Fort, F., Mahmoud, R., Pelzer, E., Médiène, S., Hauggaard-Nielsen, H., Bedoussac, L., Bonnet, C., Corre-Hellou, G., Couëdel, A., Hinsinger, P., Jensen, E. S., Journet, E-P., Justes, E., Kammoun, B., Litrico, I., Moutier, N., ... Casadebaig, P. (2021). Interspecific interactions regulate plant reproductive allometry in cereal-legume intercropping systems. *Journal of Applied Ecology*, 58(11), 2579-2589. <https://doi.org/10.1111/1365-2664.13979>

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1 **Interspecific interactions regulate plant reproductive allometry in cereal-legume intercropping**
2 **systems**

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22

23 **Abstract**

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

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

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

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

48 **Keywords**

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

50 **Introduction**

51 Intercropping, i.e. combining at least two annual crop species in the same field for most part of their growing
52 periods (Willey, 1979), is a promising way to move towards more sustainable agriculture (Li-li et al., 2015;
53 Lin, 2011). Intercropped species are expected to use resources differently and more efficiently (e.g.
54 Malézieux et al., 2009; Beillouin, Ben-Ari, & Makowski, 2019; Jensen, Carlsson, & Hauggaard-Nielsen, 2020).
55 Many intercrops mix a cereal and a legume, with the underlying assumption that the cereal will benefit from
56 the legume's atmospheric nitrogen (N) fixation, thus decreasing the need for exogenous N fertilization (Gaba
57 et al., 2018; Malézieux, 2012; Thorsted, Weiner, & Olesen, 2006). The performance of intercropping systems
58 has been studied from an agronomic perspective, focusing mainly on yield and N use (e.g. Bedoussac & Justes,
59 2010b; Hauggaard-Nielsen, Gooding, Ambus, Corre-Hellou, Crozat, Dahlmann, Dahlmann, et al., 2009;
60 Naudin, Corre-Hellou, Pineau, Crozat, & Jeuffroy, 2010; Pelzer et al., 2012). While introducing species
61 diversity into cropping systems could appear promising under low-input conditions, specific
62 recommendations for the management of intercrops is in its infancy (Litraco & Violle, 2015). One reason for
63 this is that the underlying mechanisms of the positive effect of the intercropping remain elusive, which makes
64 it challenging to choose species and cultivars for these systems accurately. One key unsolved issue for
65 identifying these mechanisms is how vegetative biomass translates into reproductive biomass and how
66 reproductive allocation differs between sole cropping and intercropping situations. Bridging ecology and
67 agronomy could help resolve this issue.

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

77 The hypothesis of invariance at the origin of allometric scaling laws has been challenged. Poorter et al. (2015)
78 highlighted that allometric scaling exponents differ among species. Vasseur, Violle, Enquist, Granier, & Vile
79 (2012) and Vasseur et al. (2018) highlighted variability in these exponents within the model species
80 *Arabidopsis thaliana*, and demonstrated that this variability was genetically determined and environmentally
81 regulated due to natural selection. Further, the influence of artificial selection on allometric constraints is
82 not well understood due to the lack of comparisons of allometric relationships in crop species (Milla,
83 Osborne, Turcotte, & Violle, 2015). The initial MST framework was designed along with plant observations in
84 optimal conditions, i.e. where growth is not strongly limited by unfavorable abiotic or biotic conditions.
85 Consequently, the influence of plant-plant interactions and soil resource limitations on deviations from MST
86 expectations remains unknown (but see Coomes, Lines, & Allen, 2011; Vasseur et al., 2018). Intercropping
87 systems represent a unique opportunity to challenge allometric laws, in order to fine-tune them and assess
88 the validity of their most basic assumptions. Understanding the influence of plant-plant interactions on
89 reproductive strategies of intercropped species would improve the understanding, modeling and ultimately
90 management of intercrops (Gaudio et al., 2019), particularly to drive each species to its potential
91 reproductive output in relation to the other species and the cropping conditions. In this study, we analyzed
92 how plant allometry is related to the performance of intercropped species and how this relationship is
93 influenced by varying cropping conditions. Crop scientists and stakeholders, including farmers, are primarily
94 interested in yield, often assessed in intercropping systems by the land equivalent ratio in order to calculate
95 land-use efficiency (e.g. Yu, Stomph, Makowski, Zhang, & Werf, 2016). Finer analysis of intercrop
96 performance would improve our understanding of the mechanisms underlying intercrop performance.

97 We examined the influence of plant-plant interactions on the allometric relationship between grain yield
98 production and plant biomass in annual cereal-legume intercrops grown under a variety of climatic and
99 cropping conditions in Western Europe, with the underlying objective to test the MST under non-optimal
100 conditions, characterized here by the plant-plant interactions and soil nutrient limitations. Our analysis was
101 based on 28 field experiments. The main objective of this study was to investigate how the reproductive
102 allometric relationships of both plant families (cereals and legumes) changed depending on whether they
103 were grown in a sole crop or with another crop. We also focused on the influence of N fertilization within
104 each plant family and crop type (sole crop vs. intercrop). The strength of allometric relationships can indicate

105 that the ratio of yield to plant size does not vary, as the relationship between these two variables is supposed
106 to be invariant (Nee, Colegrave, West, & Grafen, 2005). This ratio is called “reproductive effort” in ecology
107 (Cheplick, 2005) and “harvest index” in agronomy (Echarte & Andrade, 2003; Vega, Sadras, Andrade, & Uhart,
108 2000). It is often used to focus on allocation of biomass to reproductive organs and to differentiate
109 performances of species and cultivars (Hay, 1995), which is a framework that is complementary to MST. Thus,
110 we also assessed the influence of crop management on reproductive efforts of the two plant families.

111 **Materials and methods**

112 **Field experiments**

113 We collected a set of experiments that compared different species and cultivars under intercropping and
114 sole-cropping conditions under a variety of management practices in 9 locations in five European countries
115 (France, Denmark, Italy, Germany, and the United Kingdom) (Fig. 1). The experiments covered 28
116 environments (location x year), of which 15 were managed as organic farming and 13 as conventional
117 farming, with a total of 34 intercropping situations (environment x species) and 62 sole-cropping situations.
118 Since the experiments were not completely factorial, i.e. not all factors (cultivars, N fertilization, sowing
119 density) were combined, we analyzed a total of 159 and 219 experimental units under intercropping and
120 sole-cropping situations, respectively. In the experiments, 53% and 47% of the intercropped species were
121 winter and spring crops, respectively. The mean temperature over the crop cycle (from sowing to harvest)
122 ranged from 6.8-11.3 °C for winter crops and 12.3-15.1 °C for spring crops. Cumulative rainfall ranged from
123 278-713 mm for winter crops and 60-366 mm for spring crops.

124 Additional details on experimental designs and management practices are reported in Supplementary
125 Material S1 and in the reference publications for 22 of the 28 experiments (Bedoussac & Justes, 2010a,
126 2010b; Corre-Hellou, Fustec, & Crozat, 2006; Hauggaard-Nielsen, Gooding, Ambus, Corre-Hellou, Crozat,
127 Dahlmann, Dahlmann, et al., 2009a; Hauggaard-Nielsen, Gooding, Ambus, Corre-Hellou, Crozat, Dahlmann,
128 Dibet, et al., 2009b; Hauggaard-Nielsen, Jørnsgaard, Kinane, & Jensen, 2008; Knudsen, Hauggaard-Nielsen,
129 Jørnsgaard, & Jensen, 2004; Launay et al., 2009; Naudin et al., 2010; Naudin, Werf, Jeuffroy, & Corre-Hellou,
130 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 ($\pm$ SD) = 95 $\pm$ 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

150 plant density (plant.m⁻²). Plant density was used to convert per-ha variables into per-capita variables (i.e.
 151 g.plant⁻¹; Table 1).

152 Table 1. Cropping situations pooled in the database by plant family (Poaceae vs. Fabaceae), crop type (sole crop vs.
 153 intercrop) and nitrogen (N) fertilization (non-fertilized N0 vs. N-fertilized). Several cultivars and crop species densities
 154 (relative proportions) were represented for each factor combination (family x crop type x N fertilization). Mean (± SD)
 155 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

156

157 **Data processing and analysis**

158 Reproductive effort was calculated as the ratio of grain yield to total aboveground biomass at maturity, rather
 159 than final biomass, to avoid the influence of leaves that dropped before maturity (Unkovich, Baldock, &
 160 Forbes, 2010). Analysis of variance (ANOVA) was performed using the *aov* function of the stats package of R
 161 software (R Core Team, 2019). When relevant (*p* < 0.05), means were separated using a Tukey or, when
 162 ANOVA assumptions were not met, Kruskal-Wallis test. We performed one-way ANOVAs within each plant
 163 family (Poaceae vs. Fabaceae) to test the influence of crop type (sole crop vs. intercrop) and N fertilization
 164 (non-fertilized vs. N-fertilized) on reproductive effort and its components (i.e. plant aboveground biomass
 165 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

191 species *j*. This index ranges from -1 (i.e. focal species is dominant) to +1 (i.e. focal species is dominated). We
192 used a linear model to analyze change in plant yield as a function of the biomass distance index.

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

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

205

206 **Results**

207 **Reproductive allometry in cereals and legumes**

208 The reproductive allometric relationship between plant yield and biomass was significant and robust
209 ($R^2 = 0.94$) across all experimental units, indicating that size is a predominant driver of crop yield. Allometric
210 relationships of legumes and cereals displayed a similar slope close to 1 (1.03 ± 0.02), indicating an overall
211 isometric relationship between plant yield and biomass. However, legumes generally had larger biomass and
212 grain yield than cereals (significant shift along the main relationship, Fig. 2A). Moreover, legumes generally
213 had higher yield than cereals for a given biomass (significant offset along the y-axis). The relationships
214 between reproductive effort and plant biomass were weak for both cereals and legumes ($R^2 = 0.104$ and
215 0.049 , respectively), with reproductive effort decreasing slightly as plant biomass increased ($p < 0.0001$,

216 Fig. 2B). Legumes had slightly but significantly higher reproductive effort (0.48 ± 0.10 , ranging from 0.19-
 217 0.73) than cereals (0.43 ± 0.08 , ranging from 0.22-0.67), although it varied greatly.

218
 219 Fig. 2. (A) Reproductive allometric relationship (log-log scale) between plant yield (g.plant^{-1}) and plant biomass
 220 (g.plant^{-1}) and (B) relationship between reproductive effort ($=\text{yield:biomass}$) and plant biomass (g.plant^{-1}) for cereals
 221 (orange) and legumes (red) for all experimental units in intercropping and sole-cropping situations.

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

224 The slopes of allometric relationships were steeper under intercropping than sole-cropping conditions
 225 (Fig. 3A-C). The intercropping effect was stronger in non-fertilized conditions (legumes, $p < 10^{-6}$; then cereals
 226 $p = 0.004$) than in fertilized conditions (cereals, $p = 0.03$). For legumes under non-fertilized conditions,
 227 intercrops had significantly higher reproductive effort than sole crops. Although allometric differences were
 228 observed for cereals, ANOVAs indicated that intercropping had no significant effect on reproductive effort or
 229 its components (plant yield and biomass) whether in fertilized or non-fertilized conditions (Table 2).

230 We calculated the plant size threshold corresponding to the intersection of allometric lines in intercrop and
 231 sole crop conditions to identify the minimum plant size corresponding to a positive intercropping effect on
 232 biomass allocation (increased yield for a same plant size). The plant size threshold above which a legume
 233 under non-fertilized conditions (Fig. 3A) benefited from intercropping was $10.3 \text{ g.plant}^{-1}$ ($\text{CI}_{0.95} = [6.7\text{-}13.5$
 234 $\text{g.plant}^{-1}]$), with biomass ranging from $1.9\text{-}83.2 \text{ g.plant}^{-1}$. For a cereal under non-fertilized conditions (Fig. 3B),
 235 the threshold was 3.5 g.plant^{-1} ($\text{CI}_{0.95} = [2.0\text{-}5.9 \text{ g.plant}^{-1}]$), with biomass ranging from $0.7\text{-}9.9 \text{ g.plant}^{-1}$. For
 236 a cereal under N-fertilized conditions (Fig. 3C), the threshold was 6.3 g.plant^{-1} , with biomass ranging from

237 2.6-13.2 g.plant⁻¹. We could not derive CI0.95 for this situation because the allometric relationships of the
 238 two datasets had high collinearity and widely scattered points.

239
 240 Fig. 3. Reproductive allometric relationship (log-log scale) between plant yield (g.plant⁻¹) and plant biomass (g.plant⁻¹)
 241 by i) crop type (i.e. sole crop (SC) vs. intercrop (IC)), for (A) legumes (Fabaceae) under non-fertilized conditions (N0), (B)
 242 cereals (Poaceae) under N0 and (C) cereals under N-fertilized conditions (N), and by ii) N fertilization, for (D) legumes
 243 grown under IC, (E) cereals under SC and (F) cereals under IC. b represents the allometric scaling exponent of the studied
 244 relationships.

245 In intercropping conditions, for a given species, we analyzed how variation in its yields depends on biomass
 246 distance between the two intercropped species. This distance index strongly explained yield variation (Fig. 4),
 247 with a decreasing slope (lesser sensitivity to the other species) from non-fertilized legumes (a = -0.52,
 248 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	*** (NO < N)	*** (NO < N)	ns	ns	***
		Intercrop	ns	*** (NO < N)	*** (NO < N)	ns	ns	***
Legume (Fabaceae)	Crop type	Non-fertilized	* (SC < IC)	** (SC > IC)	ns	***	-	-
	N fertilization	Intercrop	* (NO > N)	ns	ns	ns	*	ns

269

270 Discussion

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

281 In addition to the strong size-dependence of grain yield production, which was predicted by allometric
282 relationships and highlighted in other studies (Liu, Wang, Wei, & Wang, 2008; Qin, Weiner, Qi, Xiong, & Li,
283 2013; Sugiyama & Bazzaz, 1998; Vega et al., 2000; Weiner, 2004), we observed that species grown in
284 intercrops had a greater increase in yield for a given increase in plant size than species grown in sole crops
285 through the threshold analysis (x-coordinate of the intersection of allometric lines between sole cropping
286 and intercropping conditions). This highlights a better spatial and temporal resource use efficiency in a field
287 situation, which is a pillar of ecological intensification (Li-li et al., 2015).

288 This effect depends on plant family and the relative dominance of the two intercropped species. When
289 ranking this effect among cropping conditions, intercropping benefited legumes under non-fertilized
290 conditions the most, followed by cereals under non-fertilized conditions and then cereals under N-fertilized

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

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

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

328

329 **Pathway to applications**

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

338 We found that plant-plant interactions were a strong driver of yield variation in crop mixtures. In this case,
339 an agronomic action on one species can readily influence the other even under relatively variable climate
340 conditions, which is an important observation for designing and managing intercrops. For instance, if the goal
341 of the farmer is to promote legume yield, using the cereal mainly to limit legume disease and lodging (e.g.
342 Viguir, 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.

Acknowledgements

The authors thank all the technical staff who helped to acquire this vast dataset, and Michael and Michelle Corson for their helpful comments and English revision. This study was supported by the French National Research Agency under the Investments for the Future Program (ANR-16-CONV-0004) and by the INRA Environment and Agronomy Division through the project IDEA (Intra- and interspecific diversity mixture in agriculture). CV was supported by the European Research Council (ERC) Starting Grant Project 'ecophysiological and biophysical constraints on domestication in crop plants' (grant ERC-StG-2014-639706-CONSTRAINTS).

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