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Short Communication

Is the relationship between grain number and spike dry weight linear? Insights from larger spikes in wheat

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ABSTRACT

Grain yield variation has been associated to variation in grain number per unit area (GN). It has been shown in the last about 40 years that GN is linearly associated to the spike dry weight (SDW) at anthesis in wheat, fact that has been useful to understand mechanistically potential grain yield. Fruiting efficiency (FE, grains per gram of spike dry weight), the slope between GN and SDW relationship, has been proposed as a possible trait to improve wheat yield potential. The linear relationship between GN and SDW implies a constant increase in GN per unit increase in spike growth and, then a constant FE. However, there are empirical and theoretical elements suggesting that this relationship would not be linear. In this study, we hypothesised and showed that the linearity of the relationship between GN and SDW would be non-linear for extreme values of SDW, implying that the FE would be noticeably reduced at these extreme cases of dry matter allocation to the juvenile spikes. These results have implications for both, genetic and management improvements in grain yield.

1. Introduction

Wheat grain yield can be explained by its numerical components: grain number per unit area (GN) and average grain weight (GW). While both components theoretically have the potential to enhance yield, extensive literature has demonstrated that GN is completely dominant [1–5] and step changes in grain yield would be only possible by increasing GN ([6] and several references quoted therein). This behaviour is not just based on correlations between grain yield and GN but also on solid theoretical evolutionary bases indicating that the crop evolved a conservative grain size [7–9] setting a higher source- than sink-strength during grain filling [10–12]. Therefore, to achieve further increases in grain yield, it is imperative to focus on increasing GN [13,14]. To understand the mechanisms underlying GN, it is possible to dissect it into its numerical (i.e., spikes number per unit area (SN) and grain number per spike (GNS)) and physiological determinants (i.e., spike dry weight (SDW) and fruiting efficiency (FE)). Although analysing the numerical determinants has been far more popular [5,15], there has been a growing interest in the physiological determinants of GN, particularly FE [13,14], when considering the possibility of exploiting genotypic differences both in wheat [5] and barley [16].

FE reflects in part the balance between two processes occurring simultaneously during stem elongation: growth of the juvenile spikes and floret development. The number of fertile florets per spike is a key determinant of GNS and is the result of an organogenesis process characterized by a massive initiation of floret primordia followed by a phase of substantial mortality when many of them die [17]. Although the initiation of floret primordia appears to be a purely developmental process, the survival of primordia to produce fertile florets (which ultimately become grains and determine yield) seems to be strongly related to dry matter accumulation in the juvenile spikes [18–22] occurring approximately 20–30 d before anthesis [23]. Indeed, the triggering of the phase of floret primordia mortality seems to be linked with the initiation of active growth of juvenile spikes [24–26]. Therefore, the relationship between GN and SDW, which has been frequently

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Abbreviations: GN, grain number per unit area; SDW, spike dry weight; FE, fruiting efficiency; Fem, fruiting efficiency at maturity; GW, average grain weight; SN, spikes number per unit area; GNS, grain number per spike.

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reported in the literature (Table S1), is strongly mechanistic. The slope of that relationship is FE (i.e., GN per each gram of SDW) which seems relevant for future breeding as it frequently explains differences in GN between genotypes of elite germplasm [3,27–29].

Normally, FE is estimated as the ratio between GN and SDW at anthesis (or chaff dry weight at maturity, as a surrogate of SDW at anthesis; [14]), both either per unit area or per spike. In general, studies report for any particular treatment the average of the FE across spikes of plants and replicates, which naturally tends to reduce the visualization of extreme values of GN and SDW. The fact that most literature reports a relationship between GN and SDW that is strongly linear (which is the basis for accepting a single value of FE to estimate GN during critical period, as in most of the simulation models) may well be because using averages excludes the extremely large and small spikes being considered (Table S1). This linearity implies a constant increase in GN per unit increase in spike growth and, then a constant FE. However, there are empirical and theoretical elements suggesting that this relationship would not be linear, should the range of SDW explored be larger. Assuming the linearity of the relationship between GN and SDW may overestimate the GN that might result from reducing or increasing noticeably the allocation of resources to the growing juvenile spikes (in response to severe stresses or exceptionally good growing conditions, respectively).

Empirical evidence against the linearity includes the cases of: (i) Abbate [30] who focused on the linear relationship but noticed a GN much lower than expected in one case with SDW 7 d after anthesis much lighter than the rest of the data points, implying that very small spikes would decrease FE and (ii) Fischer [31], Gianmarco [32] and Gonzalez [25] who showed a relationship between fertile florets and SDW per spike with a strong linear component but losing the linearity when exploring high values of SDW, implying a decline in FE for the largest spikes. Similar behavior is generally reported for summer crops, such as maize and sunflower, in which GN per plant is curvilinearly related to individual plant growth rates during the critical period for yield determination [36].

A theoretical approach does not support a linear relationship either (Fig. S1A). At very low and very high SDW ranges, it might not be possible to maintain the linearity that can be expected in the wide, though intermediate, range of SDW, because:

i. at very low SDW there would necessarily be a lower FE as the very limited resources allocated to the juvenile spikes would chiefly be used to build up a minimum ‘vegetative’ spike structure (e.g., rachis, glumes) where florets develop before anthesis grains set afterward; and
ii. at very high SDW, FE would tend to be lower again because the youngest and most distal floret primordia within the spikelet may not reach the fertile floret stage at anthesis (these distal primordia do not have the time to develop fertile florets even if resources were available in excess, [21], or the fertile florets they may develop possess a rather small ovary, resulting in an increased likelihood of grain abortion [33]; while
iii. at intermediate values of SDW, when more resources are allocated to juvenile spikes, labile florets (e.g., floret 3 to 5 of central spikelets), that otherwise would have died, continue their development to produce more fertile florets at anthesis setting normal growing grains and supporting the well-known linear relationship.

We aimed to test, with empiric data from a field experiment, the hypothesis that the linearity of the relationship between GNS and SDW would be lost for extreme values of SDW, implying that FE would be noticeably reduced at these extreme cases of dry matter allocation to the juvenile spikes.

2. Materials and methods

2.1. General conditions, experimental design, and treatments

An irrigated field experiment was sown at Sucs, Lleida, Spain (41°38′N, 00°22′E, 260 m a.s.l.) on 8 December 2021 (for temperature and rainfall during the crop cycle, see Fig. S2). Before sowing, P and K were applied to reach 30 kg P ha^{-1} and 160 kg K ha^{-1} in the form of diammonium phosphate ($(NH_4)_2HPO_4$) and potassium chloride (KCL 60%).

Treatments consisted of the factorial combination of 3 cultivars and 5 sowing densities: (i) 3 commercial well-adapted and high-yielding cultivars of bread wheat selected according to their contrasting tillering ability resulting in consistent differences in spikes m^{-2} (Bologna > Marcopolo > Hondia), as observed in previous experiments under different environmental conditions (M. Lopes, Comm. pers.) and (ii) 5 plant densities including from almost isolated plants to populations much higher than those use commercially (30, 60, 120, 240, and 480 seeds m^{-2}), generating contrasting canopy structures that modified profoundly the number of tiller spikes and the size of main shoot spikes through affecting the availability of resources per plant for reproductive growth (and therefore generating a very wide range in spike sizes within each of the contrasting cultivars).

2.2. Measurements and analysis

Samples of 1 m of a central row of each plot were taken at physiological maturity. Although plots were sown with experimental machinery ensuring uniformity, soon after seedling emergence we identified and labelled sectors of the plots with the exact number of plants expected for each density that were also uniformly distributed. The sampling was limited to these marked sectors to ensure the reliability of the results. In the lab, the samples were partitioned into main shoots and tillers. The spike dry weight was determined individually: each spike was cut from the samples, oven-dried for 72 h at 60 °C, and weighed. The spike was ‘mapped’ to determine the number of grains along the different spikelets of the spikes. Then, we calculated FE at maturity (FEm) as the ratio between grain number and chaff dry weight (spike minus grains) for each of the individual spikes of main shoots and tillers in each of the 15 combinations of cultivars and densities (to allow exploring FEm of spikes actually representing the average size of the canopy as well as those representing extremes in size). We assumed chaff dry weight at physiological maturity to represent SDW at anthesis (as commonly done in the literature [14]).

The relationships between GNS and SDW were modelled using linear and bi-linear regressions, and the distribution of the residuals was analysed to identify appropriate models to fit these relationships across different levels of integration; from the whole dataset to different selected conditions (e.g., for each particular cultivar, for each particular plant density and for each particular spike hierarchy). Model selection was based on the analysis of the residuals of the regressions (i.e., assuming the correct model is that resulting in a random distribution of residuals [34]).

3. Results

When data from all cultivars and plant densities were analysed together, there was high variability in GNS and SDW, ranging from 10 to 107 grains per spike and from about 20 to about 1500 mg per spike for the smallest to the largest spikes (Fig. 1A, B). GNS was significantly related to SDW. Although both coefficients of determination were highly significant, the bi-linear relationship resulted more appropriate than the simplest linear relationship, often

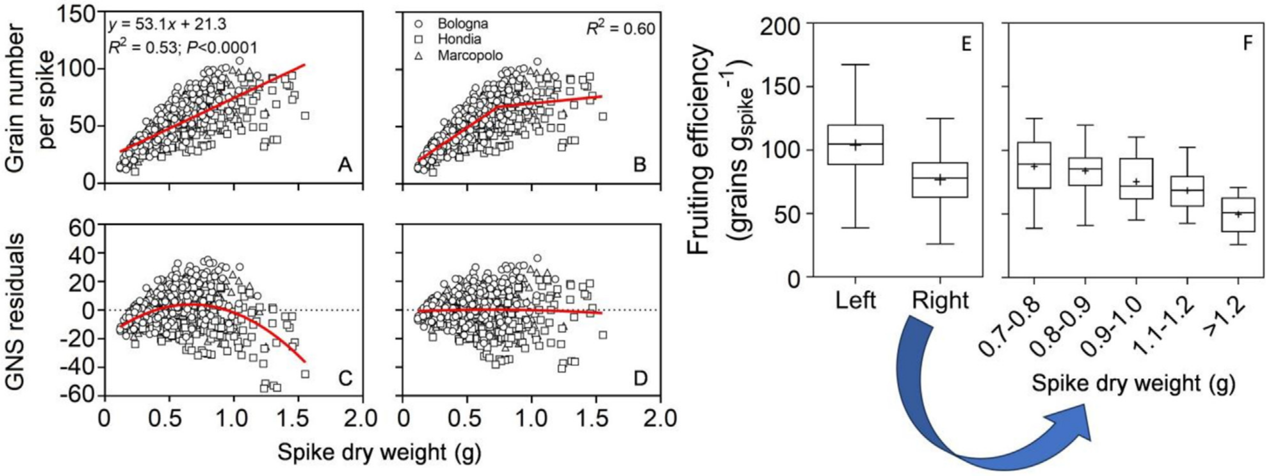

Fig. 1. Relationships between: (i) grain number per spike (GNS) and spike dry weight fitted with a linear (A) or bi-linear regression (B), and (ii) the residuals of GNS from the linear (C) or bi-linear (D) regression and spike dry weight. Panels (E) and (F) show box plots for fruiting efficiency (FEm) for the cases with a spike dry weight lower (left) and higher (right) than the breaking point in the bi-linear model (as shown in panel (B)), as well as a detail of FEm for data higher (right) than the breaking point in the bi-linear model discriminated for different spike dry weight categories (F).

reported in the literature. The residuals from the bi-linear relationship were randomly distributed around zero (with a coefficient of determination close to zero; $R^2 < 0.001$), showing any discernible pattern (Fig. 1D). On the other hand, residuals from the linear model exhibited a curvilinear trend (explaining a significant proportion of the distributions of residuals along the SDW; $R^2 = 0.15$; $P < 0.001$), depicting negative values for the smallest and largest spikes (Fig. 1C).

Therefore, FEm was clearly different between larger and smaller spikes (Fig. 1B). Considering the actual ratio of GNS and SDW of each individual spike, FEm was higher for the relatively small spikes (103.9 ± 0.9 grains per gram of spike) compared to that corresponding to relatively large spikes (76.6 ± 1.6 grains per gram of spike) (Fig. 1E). Indeed, decomposing the FEm corresponding to the larger spikes it is clear that the higher the SDW the lower the FEm (Fig. 1F).

The general evidence for a lower FEm of the very large spikes considering the entire data set was also appropriate to each of the three genotypes when evaluated independently. Even though these cultivars exhibited important differences in average FEm (113.7 ± 1.3, 75.3 ± 1.2, and 102.9 ± 1.2 grains per gram of SDW for Bologna, Hondia, and Marcopolo, respectively), the relationship between GNS and SDW was bi-linear for each of them individually analysed (Table 1). Alike the description for the whole dataset, the linear regression was also statistically highly significant, but the residuals were not randomly distributed, therefore the bi-linear model was the one appropriately fitting the data (Table 1). Consequently, the lower FEm of the larger spikes compared to that of the smaller ones reported for the whole dataset is maintained for each of the individual cultivars (Fig. S2), regardless of the genotypic differences in average FEm among them.

When limiting the dataset to the top quartile of GNS for each interval of SDW (i.e., focusing only on the spikes with the highest FEm within each category of SDW, Fig. S3), the linear model was again inadequate whereas the bi-linear model proved to be highly robust (Table S3). Thus, limiting the analysis to the population of the spikes with highest FEm within each category of SDW also revealed a constitutive reduction in FEm for the most fertile spikes within each category of SDW (Fig. S4).

There were no clear differences in the relationship between GNS and SDW from main shoots or tillers spikes (Fig. S5). Although, in general, the clouds of data points of the main shoot and tiller spikes were mostly overlapped, the data points of the latter tended to populate more conspicuously the bottom part of the cloud (Fig. S5A). Thus, FEm of main shoot and tiller spikes was rather similar, with the main shoot spikes showing only slightly higher FEm than the tiller spikes (Fig. S5B, C). In other words, GNS was mainly dependent upon the resources allocated to the spikes, with only a rather minor influence on the hierarchy within the canopy. Naturally, the difference in FEm among relatively small and relatively large spikes was evident across main shoots and tillers, with clearly higher FEm for the relatively small spikes (Fig. S5B) than for the relatively large spikes (Fig. S5C).

Table 1

Model type (linear or bi-linear) and its associated parameters for grain number per spike (GNS) and spike dry weight (SDW) relationship for Bologna, Hondia, and Marcopolo. The correlation coefficient and the residuals of the GNS-SDW relationship are also indicated.

Cultivar	Relationship	Model type	GNS vs. SDW				Residuals GNS vs. SDW[#]
			Y intercept (GN per spike)	Slope 1 (grains per gram)	Slope 2 (grains per gram)	Correlatation coefficient (*r*)	Correlatation coefficient (*r*)
Bologna	GNS-SDW	Linear	11.0	87.4		0.885 ***	0.267 ***
		Bi-linear	8.4	93.8	3.5	0.894 ***	0.031 ^{ns}
Hondia	GNS-SDW	Linear	17.0	45.0		0.775 ***	0.247 ***
		Bi-linear	10.8	57.1	23.4	0.791 ***	0.007 ^{ns}
Marcopolo	GNS-SDW	Linear	16.9	66.0		0.851 ***	0.318 ***
		Bi-linear	9.1	86.1	45.4	0.865 ***	0.024 ^{ns}

[#] the residuals of the GNS vs. SDW were adjusted with a second order polynomial (quadratic). ***, $P < 0.001$.

On the other hand, plant density regulated spike size within the entire population of spikes. In general, the clouds of the data points corresponding to the different plant densities overlapped substantially. However, the range of spike sizes was inversely related to the density and all densities produced spikes of relatively small size, but only the lower densities allowed us to explore larger spikes (Fig. S6, left panels). Therefore, the proportion of large spikes in the population increased when plant density decreased (Fig. S6, right panels). The median of SDW increased from about 0.36 g per spike at 480 plants m^{-2} to about 60 g per spike at 30 plants m^{-2} (Fig. S6, right panels). In contrast, FEm tended to explore lower values when densities decreased (Fig. S6, center panels), precisely because at these densities larger spikes were reachable. The median of FEm was increased from about 94 grains per gram of spike at 30 plants m^{-2} to about 117 grains per gram at 480 plants m^{-2} (Fig. S6, central panels). Thus, across plant densities, the average FEm was negatively related to the average SDW (Fig. S7).

4. Discussion

We carried out this study to test the hypothesis that the well-known linear relationship between GNS and SDW might not be truly linear if extremes of SDW are considered, and that FEm would be clearly penalized for very large and very small spikes. We profited from a field experiment combining cultivars with contrasting tillering capacities and plant densities ranging from isolated plants to overcrowded populations, altering dramatically the number and size of spikes that each plant may produce. The most important finding of our work consistently provided support to the hypothesis for the larger spikes, which exhibited clearly lower FEm than the smaller ones. This observation was consistent across contrasting cultivars and regardless of whether main shoot or tiller spikes were considered. On the other hand, we did not find evidence supporting that very small spikes would also possess lower FEm.

The number of fertile florets per spike (one of the components of FE) is the result of the massive initiation process of floret primordia followed by an important mortality of many of them [17]. While the initiation process is particularly independent of the dry matter accumulation on juvenile spikes during stem elongation phase, the survival of primordia seems to be linked with the crop growth rate (and particularly with the spike growth rate) during the last part of the stem elongation phase [18–22]. Within this context, a paradox emerges whereby larger spikes (with no limitation in the growing conditions) had lower FEm than the smaller ones. Although in this work we did not directly measure the floret primordia development, the inability of most distal floret primordia within the spikelets to develop fertile florets even with no resource limitations could be the reason for the lower FEm in larger spikes. It is possible to speculate that proximal florets (florets 1–3 from the rachis in central spikelets) become fertile florets in practically all cases (smaller and larger spikes), the intermediate florets (florets 4–5) become fertile only in a proportion of the spikes and that proportion could be higher in the larger spikes; and finally, distal florets (florets 6–9) develop more in very large spikes, but even in those cases they never reach the stage of fertile floret. This behaviour could explain the increase in GNS less than proportional compared to the increase in spike growth when large spikes are considered. Although the normal development of labile floret primordia to become fertile florets is responsive to spike growth (see references above), there is evidence that the most distal florets, that are considerably delayed in their development, cannot reach the stage of fertile florets even when development is not restricted by lack of assimilates [6,20,35].

On the other hand, our results showed no conclusive evidence to support the hypothesis of the lack of linearity when including in the analysis very small spikes. When few resources are allocated to the juvenile spikes, we hypothesized that they would be primarily used for the essential vegetative structure formation (e.g., rachis and glumes), which provides the physical structure where florets develop and eventually set grains. However, the minimum growth of spikes needed to support the survival of floret primordia (as was commonly found in maize for example, [36]) was not found in our study, even when the relationships explored considered 3 different well-adapted cultivars (i.e., Bologna, Hondia, and Marcopolo) and 5 contrasting sowing densities ranging from virtually isolated plants (30 plants m^{-2}) to populations much higher than those use commercially (480 plants m^{-2}). Probably, more efforts will be necessary to explore conditions where even smaller spikes will be incorporated into the relationships between GNS and SDW.

Within a wheat plant, there are spikes of different hierarchies, with the spikes of main shoots and first tiller being dominants in terms of development [37]. As was shown in our results, plant density regulated spike size within the entire population of spikes, being the range of spike sizes inversely related to sowing density. Thus, all densities (from virtually isolated plants to sowing densities that practically doubled the normal ones) produced spikes of relatively small size, but only the lower densities allowed us to explore larger spikes. In this context, GNS was mostly dependent upon the allocation of resources to the spikes (indicated by the higher FE observed in smaller spikes compared to the larger ones), whereas the hierarchical structure inside the plant (main shoots or tillers) had very little impact. This fact may be directly linked to the asymptotic relationship between grain yield and sowing density commonly found for wheat and for many other small crops [38,39]. The spike number necessary to maximize grain yield can be achieved almost certainly using any of the sowing densities included in our experiments, but FEm can only be maximized at intermediate and higher sowing densities and never at the lowest sowing densities (30 seeds m^{-2}). Under this condition, the proportion of larger spikes in the total spike population increases with the consequent FEm reduction.

This work allowed us to explore one of the main mechanistic relationships within wheat physiology [6]. We were able to determine that when the variability in spike size is explored in detail (here through working on an individual basis), the relationship between GN and SDW is not linear, but bi-linear where larger spikes have a lower FEm than smaller ones. These results have implications for both, genetic and management improvements. Regarding genetic improvement, it would seem that a limitation exists considering the size of the spike to optimize the FEm. With respect to crop management, even though in our experiment an ultra-low density was used (which can hardly be extrapolated to real crop production), crops with a very high proportion of large spikes could present reduction in the average FEm. The strategies that propose very low densities in environments without noticeable growing restrictions would not be appropriate.

CRediT authorship contribution statement

Román A. Serrago: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Writing – original draft, Writing – review & editing. **Constanza S. Carrera:** Data curation, Investigation, Writing – review & editing. **Roxana Savin:** Funding acquisition, Project administration, Supervision, Writing – review & editing. **Gustavo A. Slafer:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing.

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Appendix A. Supplementary data

Supplementary data for this article can be found online at https://doi.org/10.1016/j.cj.2024.12.007.

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