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Competitive interactions between wheat (Triticum aestivum L.) and rigid brome (Bromus rigidus Roth): a replacement series study

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Bromus rigidus is increasingly recognized as a problematic weed species in cereal production of Mediterranean areas, especially under conservation agriculture practices. A better understanding of its interaction with wheat may provide new options for sustainable management. To this end, this study aims to evaluate the competitive interactions between this weed and four soft wheat varieties (Remax, Faiza, Bandera and Guadalette) in a controlled pot experiment using a replacement series design. Results showed clear differences in morphological and ecophysiological traits between the two species and among wheat cultivars. In fact, wheat exhibited a superior competitive advantage, based on relative yield and competitiveness ratio values. This performance may be explained by specific growth and physiological parameters, particularly plant height, leaf area, stomatal conductance, chlorophyll and nitrogen content. This clear competitive superiority is more remarkable for the Remax and Faiza varieties than for Bandera or Guadalette. Indeed, while Faiza and Remax showed a suppressive profile towards *B. rigidus*, the other two varieties showed a less aggressive but more tolerant character, which allowed them to maintain their yield without necessarily affecting the weed growth. Overall, these findings provide the opportunity to choose these aggressive wheat genotypes as a cost-effective strategy, especially under high infestation of brome or areas of herbicide resistance cases.

Keywords: Wheat, rigid brome, competition, replacement series

INTRODUCTION

Wheat (Triticum aestivum) is one of the world’s most vital staple foods, thanks to its nutritional qualities and its ability to grow in different agro-climatic zones (Briak and Kebede, 2021). Indeed, wheat is the main growing crop in the Middle East and North Africa region, with more than 16.8 million hectares in 21 countries, including more than 2.8 million hectares in Morocco alone (FAOSTAT, 2024). However, in arid and semi-arid regions, as is the case in most of Morocco’s rainfed agricultural zones, wheat-based cropping systems are subject to a range of limitations that impact production and farmers' incomes, and ultimately national food security (Mamassi et al., 2023). Among these challenges, weed management appears to be a critical task since weeds are considered to be the most aggressive enemies of wheat worldwide (Oerke, 2006). They compete with wheat crops for resources (water, nutrients, light and space), leading to average yield losses of 24% (Xu et al., 2023).

In Morocco, research has shown that Bromus rigidus alone can cause yield losses exceeding 90% (Bouhache, 2020). It is an indigenous Mediterranean species with a winter annual life cycle that has been a serious weed concern worldwide, especially in areas with more than 250 mm of annual rainfall (Kon and Blacklow, 1990). Hamal et al., (2005) reported that across 100 cereal fields belonging to 18 regions in Morocco, 83.3% were found to be moderately to highly infested with ripgut brome. This weed has become even more abundant with the introduction and implementation of conservation tillage (Borger et al., 2021). Practically, B. rigidus germination pattern (longer dormancy and light inhibition) allows it to proliferate under no-till systems, where seeds are exposed to complete darkness following burial after the sowing operation (Kleemann and Gill, 2006). Indeed, Hajjaj (2018) reported that in Chaouia region of Morocco, rigid brome is the most troublesome and problematic weed among farmers who practice no-till technique. Besides that, the complexity of control of this weed, has been intensified with the emergence of herbicide resistance to seven active ingredients, particularly in Australia, where resistance has been documented in wheat, canola, lupin, and other cropping systems (Heap, 2025).

Nevertheless, some results showed that management strategies that combine effective herbicide treatments and crop competition could provide effective control of this troublesome weed (Kleemann and Gill, 2009). Actually, the choice of varieties with a higher capacity to tolerate and/or compete with weeds is an interesting way to reduce herbicide reliance without generating additional costs for farmers (Chhokar et al., 2012). In short, if wheat cultivars differ in their competitive abilities towards B. rigidus, it would be interesting to choose the more competitive ones. Despite this, and unlike other aspects such as chemical or mechanical control, studies on varietal competitiveness remain limited, with inconclusive results (Lever et al., 2022).

In this context arises the present work, which focuses on the evaluation of the competitiveness of four soft wheat varieties against B. rigidus. Its objective is to (i) analyze the competitive interactions between wheat and brome using a replacement series approach and (ii) assess the intraspecific variability among the selected wheat cultivars in their ability to suppress or tolerate this weed.

MATERIALS AND METHODS

The experiment was conducted in pots under shelter at the National School of Agriculture of Meknes, Morocco (33.841007, -5.477759), from December 2024 to June 2025, with a natural photoperiod. Indoor maximum temperatures ranged between 28 ºC and 36 ºC and minimum temperatures between 15 ºC and 21 ºC. For each pot (surface area: 201 cm^2; depth: 15 cm) used in this study, 3 cm layer of gravel was placed at the bottom, followed by 3 kg of air-dried sieved soil with a silty-clay texture. The chemical properties of the soil were: mineral nitrogen = 5.5 mg kg^{-1}, available phosphorus = 104 mg kg^{-1}, exchangeable potassium = 699 mg kg^{-1}, electrical conductivity = 0.195 dS m^{-1}, and exchangeable sodium = 42.0 mg kg^{-1}. Given that soil phosphorus and potassium levels were sufficient, only nitrogen was supplemented by fertigation. A total of 1 g of ammonium nitrate per pot was applied, split equally at sowing and during stem elongation (BBCH 31-33). Pots were irrigated with tap water to maintain soil moisture at field capacity. Additionally, any other weed that emerged from the soil was immediately removed.

Treatments and experimental design

The study included four soft wheat varieties: Bandera, Guadalette, Faiza and Remax; these varieties were chosen for their excellent agronomic performance in terms of grain yield in a no-till system within the Fes-Meknes region in Morocco (Ramdani et al., 2023). All these varieties are characterized by a good specific weight, high productivity, average to good tolerance to Septoria and rust diseases and a medium to precocious cycle. Mature seeds of B. rigidus were collected on June 10th, 2024, from a local field to ensure homogeneity of origin.

Prior to establishing the main experiment, a preliminary trial was carried out to determine the optimal plant density to induce competition. A range of planting densities (1, 2, 4, 8, 10, 16, and 24 plants per pot, equivalent to 50, 100, 199, 398, 498, 796, and 1,194 plants m^{-2}, respectively) was tested. The results showed that shoot dry matter showed no further increase beyond a density of 4 plants per pot, fulfilling the condition of the Law of Constant Final Yield (Radosevich et al., 2007) (data not shown). Accordingly, all treatments in the main experiment were conducted using a total of 4 plants per pot. For each wheat variety, five planting ratios of wheat to B. rigidus were tested: 100:0, 75:25, 50:50, 25:75, and 0:100 (4:0, 3:1, 2:2, 1:3, and 0:4 plants per pot, respectively) (Figure 1). For the two species, sowing was carried out at a depth of 2 cm on December 11th, 2024. The experimental setup consisted of a randomized complete block design with three replicates.

Observations and measurements

Each experimental unit consisted of two identical pots. One was sampled destructively at the booting stage (Feekes 10), while the other was maintained until physiological maturity for final yield evaluation. Measurements in the booting stage focused on four morphological parameters: plant height (cm), leaf area (cm^2 $plant^{-1}$), number of tillers, shoot dry matter (g pot^{-1}). Also, six ecophysiological measurements were taken from fully expanded upper leaves of plants within each treatment in that stage. Stomatal conductance (mmol m^{-2} s^{-1}) using an AP4 porometer (Delta-T Devices). Proline levels, a biochemical marker for plant stress, were quantified following the protocol of Bates et al., (1973). Mineral nitrogen was extracted from leaves by the Kjeldahl method. Chlorophyll (µg cm^{-2}), flavonoid index (range: 0-3) and anthocyanin contents (range: 0-1.5), were assessed using a Dualex Scientific sensor (Force-A). At maturity, relative yield was calculated as: and where Ywb and Ybw represent the yield of wheat and brome grown in mixture, respectively, and Yww and Ybb correspond to their yields in monoculture. Total relative yield (TRY) was obtained as the sum of both relative yields in mixture. In addition, competitive ability was assessed using the Competitive Ratio index (CR), calculated as: ; where Zw and Zb denote the respective proportions of wheat and B. rigidus in the mixture (Singh et al., 2013).

Statistical analysis

Relative yield (RY) and total relative yield (TRY) were assessed using the graphical method proposed for replacement series studies. Competitive interactions were interpreted based on the shape of the curves: a concave curve indicates a stronger competitor, while a convex one reflects a weaker competitor. To assess whether observed RY and TRY values deviated significantly from the expected values under the assumption of no interaction, a t-test was applied. For the competition index, pairwise comparisons were also evaluated using the t-test. Morphological and physiological data were subjected to analysis of variance (ANOVA) using the F-test. When significant, means were separated using the Tukey test. All statistical analyses were conducted using SPSS Statistics 27 software, at a significance level of $p \leq 0.05$.

RESULTS AND DISCUSSION

Relative yield

Graphical results of the relative yield (RY) for shoot dry matter and grain yield demonstrate a clear pattern of competitive interaction between the four wheat varieties and B. rigidus under varying plant proportions (Figure 2). Indeed, the observed total relative yield (TRY) values remained close to one in all combinations, without detecting any significant differences with the expected values, indicating that the species competed for shared limiting resources. Additionally, wheat varieties showed a contrasting response toward the interference with the weed species. Remax and Faiza were the strongest competitive ones. Their values consistently exceeded the expected values in mixtures, while B. rigidus RY values were significantly suppressed across most proportions, suggesting a clear dominance of those genotypes over brome. Moreover, the occurrence of the intersection point between RY curves of these two cultivars and brome to the right of the equivalence point (0.5), demonstrates clearly their competitive superiority. However, the other two, Guadalette and Bandera, have shown a more balanced interaction profile, translated by small deviations from expected values. Despite that, wheat maintained a slight advantage overall, the differences were not statistically significant in most ratios.

These results are typical of most crop-weed interactions, especially when the two species belong to the same botanical family (grasses in our case), which implies that they depend largely on similar growth factors and resources while at the same time, sharing comparable shoot and root architecture (Singh et al., 2013).

Indeed, this pattern of wheat superiority, especially observed for Remax and Faiza, is aligned with other findings from several replacement series studies, which often report that cultivated crops exhibit a stronger competitive ability than associated weed species. For instance, Agostinetto et al., (2017) reported that wheat consistently outperformed Italian ryegrass (Lolium multiflorum) across diverse nitrogen levels. In the same way, Wenda-Piesik et al., (2022) have shown that wheat held a clear advantage over both resistant and susceptible biotypes of blackgrass (Alopecurus myosuroides) in a wide range of substitution series experiments under multiple environmental conditions. Also, similar evidence exists in other cereals. Dunan and Zimdahl (1991) reported that barley was more competitive than wild oats (Avena fatua), while Fontana et al., (2015) found it to dominate wild radish (Raphanus raphanistrum). In rice systems, a strong competitiveness of this crop against alexandergrass (Brachiaria plantaginea) and barnyardgrass (Echinochloa crus-galli) was also documented (Galon et al., 2014; Rezaeieh et al., 2015).

These results could be explained by the fact that weed pressure is more influenced by how heavily the field is infested (weed density), rather than the superiority of individual competitors can be (Vilà et al., 2004; Agostinetto et al., 2013). Furthermore, uniform sowing patterns, as used in replacement series studies, can enhance crop performance, whereas the linear row arrangements typical of field conditions often reduce this advantage and intensify weed pressure (Weiner et al., 2001; Olsen et al., 2006; Zhao et al., 2024).

Another major contributing factor to the competitive advantage of wheat over B. rigidus in this study was the difference in emergence timing. In fact, competition between wheat and B. rigidus was preceded by a marked difference in emergence timing. While wheat seedlings had a synchronized emergence within two days after sowing (DAS), brome did not emerge until 10 DAS. Although both were sown simultaneously, wheat emerged nearly eight days earlier, enabling it to establish growth before the weed appeared. This delay related to emergence timing is well known as a key parameter that determines crop-weed interaction outcomes, as the plants that emerge early are better able to effectively secure essential resources, and thereby reduce weed growth and subsequent competition (Kropff et al., 1992; Kaur et al., 2018; Synowiec et al., 2021; Wenda-Piesik et al., 2022). This advantage played likely a central role in reinforcing wheat superiority, which was demonstrated in its RY results.

Competitive ratio

Competitive ratio (CR) results show that wheat exhibited a stronger competitive advantage over B. rigidus, as indicated by its higher values. However, the magnitude of this superiority differs from one variety to another. In fact, for all three ratios of mixtures, Remax and Faiza recorded values well above 1.0, indicating much more strong performance across proportions. In contrast, Bandera and Guadalette cultivars presented CR values close to 1.0, with minimal variability across proportions (Table 1).

Several studies suggest that the simple designation of “competitive advantage” to describe a trait could be ambiguous, since it may imply both the ability to suppress weeds and/or the ability to tolerate their presence. In fact, the suppressive ability describes the extent to which a crop can reduce weed growth and reproduction, while on the other hand, tolerance describes the crop’s capacity to maintain its production potential despite the pressure exerted by the weed. In this context, competitive indices represent a useful and powerful tool for researchers to make the distinction and reinforce the relative yield analysis. Indeed, in this study, the highest CR values of Remax and Faiza indicate strong suppressive capacity. More notably, at the 2:2 ratio, where CR values exceeded 2, it meant that they were more than twice as competitive as B. rigidus. Conversely, Bandera and Guadalette are suggested to have a more tolerant than suppressive profile, as reflected by their respective CR values close to unity.

Morphological traits

Results indicate clear morphological differences between wheat and B. rigidus and among wheat genotypes (Figure 3). Under equal proportion, the greatest plant height and canopy cover were observed for Remax and Faiza, indicating their capacity to sustain vertical growth and comparatively large foliage expansion under interspecific pressure conditions. Bandera, although significantly shorter, outperformed the others by exhibiting the widest leaf area and the highest number of tillers, demonstrating a strategy of compensatory growth based on canopy cover rather than stature and vertical development. Guadalette, in contrast, displayed moderate height values but relatively limited tillering capacity, which may have induced its reduced competitiveness. For B. rigidus, results reveal that for most of its morphological traits, its growth remained significantly constrained, except for tiller number where it notably surpassed Remax, Guadalette and Faiza.

Growth habit contrasts among wheat varieties are known to play a decisive and central role in their ability to suppress weed plants. Height, for example, has been widely recognized as a key determinant of crop-weed interaction outcomes. Challaiah et al. (1986) found that wheat height is more strongly correlated with reductions in Bromus tectorum yield than canopy area or tiller number, while Ogg and Seefeldt (1999) reported that cultivars presenting faster height development were more competitive when severe field infestations by Aegilops cylindrica occurred. Such findings are also aligned with the conclusions drawn by Vandeleur and Gill (2004), who identified plant height as a key contributor to the fitness and aggressivity of wheat cultivars. This advantage can be simply explained by enhanced interception of photosynthetically active radiation (PAR), which limits the light availability to weeds and negatively affects their growth (Lemerle et al., 1996). In the present study, the superior height recorded for Faiza and Remax appears to have provided a clear competitive edge over the weed.

Furthermore, leaf area also proved to be a major determinant of wheat competitiveness in this study. In fact, since wheat maintained a substantially greater leaf area than B. rigidus, it contributed to reinforcing its advantage through enhanced canopy development and light interception. Among the cultivars, Bandera recorded the highest values of leaf area, a trait that appears to have compensated its reduced stature and contributed to its ability to compete with brome, supporting the conclusion that strong early vigor can counterbalance limitations in terms of plant height (Zerner et al., 2008). Previous studies have demonstrated that traits such as leaf size, specific leaf area, and rate of leaf production are closely correlated with crops’ suppressive capacity (Vandeleur and Gill, 2004; Zerner et al., 2008). Consistent with these findings, studies on wheat showed that higher values of leaf area index (LAI), especially at early stages, and greater interception of photosynthetically active radiation (PAR) explain a good part of the variation in weed suppression between varieties (Reiss et al., 2018; Mwendwa et al., 2020). Nevertheless, the exact role that tillering plays in crop-weed interaction remains largely debated in the literature.

While some studies suggest a positive relationship between tiller number and weed suppression (Challaiah et al., 1986; Lemerle et al., 1996), others report that its effect is limited or inconsistent (Champion et al., 1998; Didon and Boström, 2003). In our study, B. rigidus remained consistently less competitive than the crop, although it displayed high tillering capacity, which may indicate that tillering alone was not sufficient to confer any dominance. Similarly, despite producing the highest number of tillers among wheat cultivars, Bandera did not surpass Remax or Faiza, whose competitive edge appeared to rely more on height and canopy traits, which reinforce the idea that high tillering production ability may be more a complementary trait than a key factor in competitiveness.

Ecophysiological traits

According to statistical analysis, ecophysiological responses varied considerably between wheat genotypes and among wheat and brome. In general, B. rigidus accumulated more proline and anthocyanins, whereas wheat maintained higher stomatal conductance, chlorophyll, and nitrogen content. However, there were only slight varietal variations in the flavonoid content for each species (Figure 4).

These physiological findings further clarify the underlying mechanisms that account for wheat's superiority over B. rigidus. Particularly in Bandera, wheat continuously showed higher levels of chlorophyll content, suggesting a more stable photosynthetic status and, consequently, improved energy capture under interference from the other species. Such observations are consistent with prior findings from many studies linking higher chlorophyll content with increased grain yield and resilience in wheat (Alaei, 2011; Sallam et al., 2019). Similarly, stomatal conductance patterns revealed that the two competitive varieties, Remax and Faiza, maintained the highest means, which is in accordance with several literature reports indicating that this trait is positively correlated with high yield expression under stress, as it reflects the crop's ability to maintain gas exchange and transpiration processes under competitive or drought-prone conditions (Suneja et al., 2019; Pantha et al., 2025). Meanwhile, reduced stomatal conductance in B. rigidus could be interpreted as a consequence of stress induced by competition.

Similar patterns were also observed for nitrogen content, where wheat maintained higher levels, especially in Bandera, whereas B. rigidus recorded lower values across most combinations. This is in line with findings suggesting that sensitive plants often exhibit reduced nutrient uptake under stress conditions (Sallam et al., 2019). In contrast, B. rigidus accumulated more proline and anthocyanins across mixtures, compounds that are widely recognized as osmoprotectants and antioxidants, and whose accumulation has been repeatedly observed under stress (Wahid, 2007; Ma et al., 2014; Brunetti et al., 2015). Their presence, though, is typically associated with stress mitigation rather than competitive vigor. In fact, the enhanced anthocyanin levels in B. rigidus, associated with its lower chlorophyll content, may suggest a reactive, rather than proactive, stress adaptive response. Flavonoid values remained substantially comparable between species and across varieties, though their role as reactive oxygen species (ROS) scavengers and signaling molecules under biotic interference is well established in the literature (Sytar et al., 2018; Wang et al., 2024).

These physiological insights present a further confirmation of morphological results, where wheat is more competitive than the weed. In fact, Faiza and Remax varieties demonstrated an enhanced photosynthetic efficiency related to a good water regulation in the presence of weeds. Bandera in contrast, showed a compensatory mechanism through its elevated chlorophyll and nitrogen levels that made it capable to maintain its yield despite its structural disadvantage. This observed pattern shows that in cereals, traits like plant height and early vigor are the primary factors that determine competition outcomes. Therefore, taller varieties that ensure quicker growth especially of their canopy can get greater amounts of light and make it harder for brome to get the resources it needs. In these cases, physiological traits alone cannot compensate for limitations in structural characteristics. Indeed, Hamal (2022) reported that results from comparative studies are indicating that genotypes exhibiting favorable morphological traits, are more likely to be stronger and more aggressive towards weeds.

CONCLUSION

In a context of increasing concerns about the use of chemical herbicides as the main tool to control weeds in arable fields, agroecological levers are of major importance. This study highlights the great potential of cultivar choice as a key factor in this ecological, eco-efficient vision. Indeed, wheat varieties such as Faiza and Remax presented highly competitive morphological and physiological traits that allowed them to outcompete brome, which was clearly demonstrated in replacement series diagrams. Meanwhile, Bandera and Guadalette showed a moderate competitive profile by tolerating the pressure of competition without necessarily affecting weed growth and reproductive potential. It is noteworthy to affirm that staggered emergence timing gave wheat a clear competitive advantage since it allowed it to grow rapidly and colonize the surrounding environment and therefore capture resources more efficiently than B. rigidus. Therefore, the appropriate varietal choice can be a very interesting tool that could significantly enhance crop competitiveness, reduce reliance on synthetic herbicides, and minimize weed seedbank inputs, especially in conservation agriculture systems where brome infestations can be particularly severe. Field-based studies, where genotype-environment interactions are more complex, are necessary in order to validate the outcomes of this work.

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