



How water stress impacts soybean grain yield and quality through canopy and root system adaptation

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Abstract

Soybean is the most widely grown legume species in the world. Nevertheless, the influence of irrigation on the morphological traits associated with grain productivity is not fully understood. In a field experiment, we investigated the effects of irrigation during the vegetative and flowering periods on the root system, canopy structure, grain yield, grain yield components, and grain quality of the soybean cultivar *Gallec* (MG000, Agroscope), as well as the relationship between these traits. Plants were collected to analyse root systems at R3–R4, biomass allocation within the canopy was analysed at R3–R4, R6–R7, and R7–R8, and the grain yield and grain protein were quantified. Irrigation augmented thousand kernel weight, grain per m² and grain protein content and modulated biomass allocation within the canopy and root systems. It also caused a delay in the developmental stages and increased the nodule number and biomass. Different relationships between canopy traits and root traits were observed for rain-fed and irrigated treatments. This suggests that irrigation before pod maturation can sufficiently drive morphological adaptations that could subsequently increase soybean productivity until harvest. Root system adaptation is crucial for optimizing soybean performance following irrigation and should be investigated in future plant breeding or variety evaluation studies.

Keywords plant traits · nodule · protein · root traits · soja · leguminous

Introduction

Legume crops are of primary importance for food security and sustainable farming development (Okumu et al. 2023). Soybean is the protein crop most widely grown worldwide (Van Ittersum et al. 2023), and the number of trading countries is still increasing (Ma et al. 2023). Soybean production is expanding in Switzerland and irrigated Mediterranean cropping systems (Klaiss et al. 2020; Simon-Miquel et al. 2023). Currently, breeding programs are in progress in many countries, including Switzerland (Klaiss et al. 2020; Nair et al. 2023; Singh et al. 2023). However, climate change

is expected to increase the frequency of drought events in many regions, including Europe (Tripathy et al. 2023; Zhang et al. 2023), which threaten soybean productivity (Fatima and Jan 2023). Drought can also influence grain quality, although its effects remain unclear, given conflicting reports of increases, decreases, and no significant changes in the protein concentration of soybean grains (Dornbos and Mullen 1992; Borrmann et al. 2009; Ghassemi-Golezani and Farshbaf-Jafari 2012). To adapt farming practices and crop breeding to these changing conditions, a good understanding of the soil moisture effect on soybean development and productivity is crucial.

Punctual water shortage of high intensity drastically reduces grain yield regardless of the plant developmental stage at which it occurred (Cui et al. 2019). Although water shortages during flowering and pod filling are generally expected to have a more drastic influence on yield compared to vegetative developmental stages (De Souza et al. 1997; Vadez 2014; Wei et al. 2018; Cui et al. 2019; Nadeem et al. 2019), other studies have reported earlier developmental stages as the most critical (Kadhem et al. 1985). In addition, irrigation during vegetative stages can provide advantages,

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such as the improvement of nodulation or the increase of early soil coverage, strengthening weed competitiveness (Mahler and Wollum 1981, p. 1; Place et al. 2011). Field experiments with different water supplies are needed to show whether adaptation of canopy and root systems at the first developmental stages can be maintained throughout the cultivation period (Dayoub et al. 2021).

Variations in soil water availability result in a reorganisation of biomass allocation within soybean and thus influence plant traits. Water status has a prominent influence on canopy traits (e.g. leaf area and plant height) and, in turn, grain yield components (Sadeghipour and Abbasi 2012; Jumrani and Bhatia 2018; Cui et al. 2019). However, the soil moisture effect on the relationships between canopy traits that govern grain yield components has rarely been investigated (Gao et al. 2020; Poudel et al. 2023) and remains unclear.

Adaptations for drought tolerance are expected to be more pronounced for soybean root systems than for the canopy (Yan et al. 2020). Soybean hydraulic characteristics are associated with root system architecture (Vadez 2014) that governs the efficiency of water uptake according to soil moisture conditions (Tron et al. 2015). Drought has been reported to stimulate lateral root development (Vadez 2014; Kunert et al. 2016) and can result in smaller fine root diameters (Henry et al. 2012). Across various soybean varieties, the root surface area of various soybean cultivars has been positively correlated with the thousand kernel weight and negatively correlated with water use efficiency (Kim et al. 2022). Nevertheless, opposite assumptions have also been drawn, highlighting an unfilled knowledge gap. For instance, root length and surface area can increase with soil moisture (Chun et al. 2021), whereas root length growth has also been reported to increase with drought (Hoogenboom et al. 1987, p. 1). In addition, a decrease in root length density has been proposed as a drought tolerance indicator that prevents rapid soil water consumption (He et al. 2017). By contrast, high root length density is reportedly one of the most efficient root traits for coping with drought, allowing plants to exploit soil moisture more efficiently (Turner et al. 2001; Tron et al. 2015). Overall, only a few studies have investigated soybean root system adaptations to water stress (Kunert et al. 2016).

Irrigation increases nodulation, especially under strong water-limiting conditions (Matheny and Hunt 1983, p. 1). Root system architecture and nodulation are closely related, and synergy can occur. For instance, the GmEXPB2 gene is involved in both nodulation and root architecture regulation (Yang et al. 2017). Furthermore, both can compete for C and nutrients, as nodule development can reduce root growth (Reich et al. 2006; Aleman et al. 2010; Li et al. 2016). The positive effect of nodulation on plant biomass production and grain yield is expected (Moretti et al. 2018) but is not

systematic. Thus, a positive balance is necessary between the indirect effects of fixed N for improved photosynthesis (i.e. C uptake) and the C sink due to the nodules demand for photosynthate (Tamagno et al. 2018). More studies are necessary to unravel the interactions between root architecture and nodulation (Yang et al. 2017).

The plasticity of the root system in response to drought stress in field conditions is a key parameter to consider in soybean breeding, taking into account environmental conditions (Tron et al. 2015). It has been claimed that root traits and nodulation are important in breeding programs seeking to develop elite genotypes, according to a study indicating that nodulation and yields are better for genotypes with shallow-root parents than for those with deep-root parent (Yang et al. 2017). Therefore, being able to anticipate the effects of drought on soybean root systems would be pivotal, even though current knowledge provides only a limited understanding of the interactions between soil moisture and the root system (including nodulation). On the whole, identifying the relationships between nodulation and root, shoot, and seed traits should ease the cultivar phenotyping and contribute to determining a soybean ideotype (Dayoub et al. 2021).

In a field experiment, we tested the effects of irrigation during vegetative stages and flowering on the well-known soybean cultivar ‘*Gallec*’. We investigated how biomass allocation is reorganised and adapted at the R3–R4 development stage (8 days after the sixth and last irrigation event) by characterizing the plasticity of canopy structure, root traits, and nodulation. We further quantified the linear relationships between plant traits (canopy and root system) separately for rain-fed and irrigated treatment to improve understanding of soybean plant functioning and to seek the “stable” relationships (i.e. not affected by irrigation) that may be useful for future breeding programs. Our findings highlight how grain yield, grain yield components, and grain quality are affected at harvest time.

Materials and methods

Field trial

A field trial was established in Switzerland at Agroscope, Changins (46°23′55.72″N, 06°14′24.72″E; altitude 432 m) to test the effects of irrigation and weed competition on different soybean cultivars. The soil showed a fine soil texture with a high NO₃ soil content of 14.3 mg soil g⁻¹. In 2023, a widely cultivated old soybean variety (‘*Gallec*’, registered in Switzerland in 2000, maturity group 000) was sown at a density of 55 seeds per m², in 116 buffer plots (2 m × 6.7 m with 0.5 m of inter-row spacing) to separate the different

treatments (i.e. varieties $\times$ artificial weed $\times$ irrigation). Five plots irrigated (6 times using an irrigation ramp on May 30, June 6, June 12, June 28, July 7, and July 19, 2023, with 30 mm, Fig. 1) and rain-fed were selected for sampling (i.e. plots on the border of the trial and those close to the “irrigation limit” were avoided). Mechanical weeding was carried out twice during vegetative growth. Water (rainfall and irrigation) and temperature conditions are presented in Fig. 1.

Soybean sampling and field measurements

On July 27, 2023, (i.e. 84 days after sowing [DAS] at the R3–R4 development stage, Fig. 1), 10 soil clods (i.e. two for each of the five selected plots) containing at least 3 soybean root systems were carefully collected using a spade for both irrigated and rain-fed treatments. This sampling campaign was thereafter entitled “root and canopy sampling”. In the same plots, soybean density was quantified by counting plants in five linear meters. For each linear meter selected, the plant height (at the connection point between leaflets of the highest leaf) and collar diameter of five healthy plants were measured. These measurements will be hereafter referred to as “field measurements”.

On August 21 and 27, 2023, (i.e. 109 and 119 DAS), aboveground biomass of one linear meter (i.e. 2 transects of 50 cm) and three linear meters (i.e. 6 transects of 50 cm), respectively, were sampled for each treatment. On August 27, pod filling was observed to be nearly over for the rain-fed treatment, as the few remaining leaves were yellow/brown, whereas the pods and leaves were still green for the irrigated treatment. For each transect sampled, the grain

number per pod was quantified for one hundred pods. These sampling campaigns are thereafter entitled “canopy samplings”. On September 13, 2023, (i.e. 137 DAS), grain yield was measured by harvesting three soybean rows (6.7 m $\times$ 1.5) using a plot combine (Zürn 150, Germany) for five plots of irrigated and rain-fed treatments.

Grain analysis

At harvest, grain samples ($\approx$ 500 g) were collected, weighted before and after oven drying at 55 °C for 72 h to determine water content, and the thousand kernel weight was determined. In addition, grains were grounded to analyse protein content using near-infrared spectroscopy (Büchi, Flawil, Switzerland).

Analyses of root and canopy sampling

Just after field sampling, the soil clods were placed in a water bucket to remove the main part of the soil. We assumed that the root system biomass was nearly entirely recovered and that root loss was negligible. Root systems appeared to be constrained in the top 20 cm due to the hardpan that was obvious during the clod extraction. The root systems included in the clods were then washed, and the soybean plants were carefully separated (Fig. 2). From this, 10 healthy plants with robust root systems were selected for each treatment (i.e. irrigated and rain-fed).

The root systems and aboveground biomass of all soybean plants collected in the field were separated with pruning shears at the collar (Fig. 2). The main stem, branches (lateral shoots), pods, and leaves were separated, oven dried (48 h at 45 °C), and weighed for each selected plant. The main stem plus branches were thereafter referred to as “total stems”. The root systems remained in water in a plastic bucket for 2 h. The root system was then gently removed from the plastic bucket in which the soil around the roots remained. The root systems were gently washed with a shower above a sieve of 0.5 mm mesh size to avoid root and nodule loss, although root pieces or nodules were rarely found in the sieve. To analyse the root systems, nodules were first removed, counted, oven dried (48 h at 45 °C), and weighed. Before scanning, the root systems were stored in a cold chamber in plastic water pans, arranged in such a way as to avoid root overlapping as much as possible. The root systems were divided into two to four parts, and one image was acquired for each root system part (Fig. 2). Each scan image acquired was analysed using WinRHIZO software (WinRHIZO Pro, Regent Instruments, Canada) to quantify root length, root surface, and root volume for various root class diameters (i.e. by intervals of 0.5 mm). Finally, the root systems were oven dried (48 h at 45 °C) and weighed.

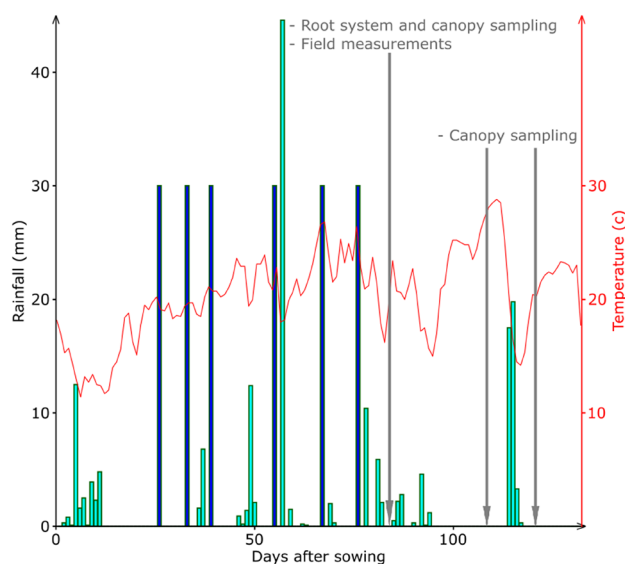


Fig. 1 Daily rainfall (cyan bars), irrigation (blue bars), and mean temperature (red line) at Agroscope Changins from the first day after sowing to the harvest. Soybean plant sampling is indicated with grey arrows

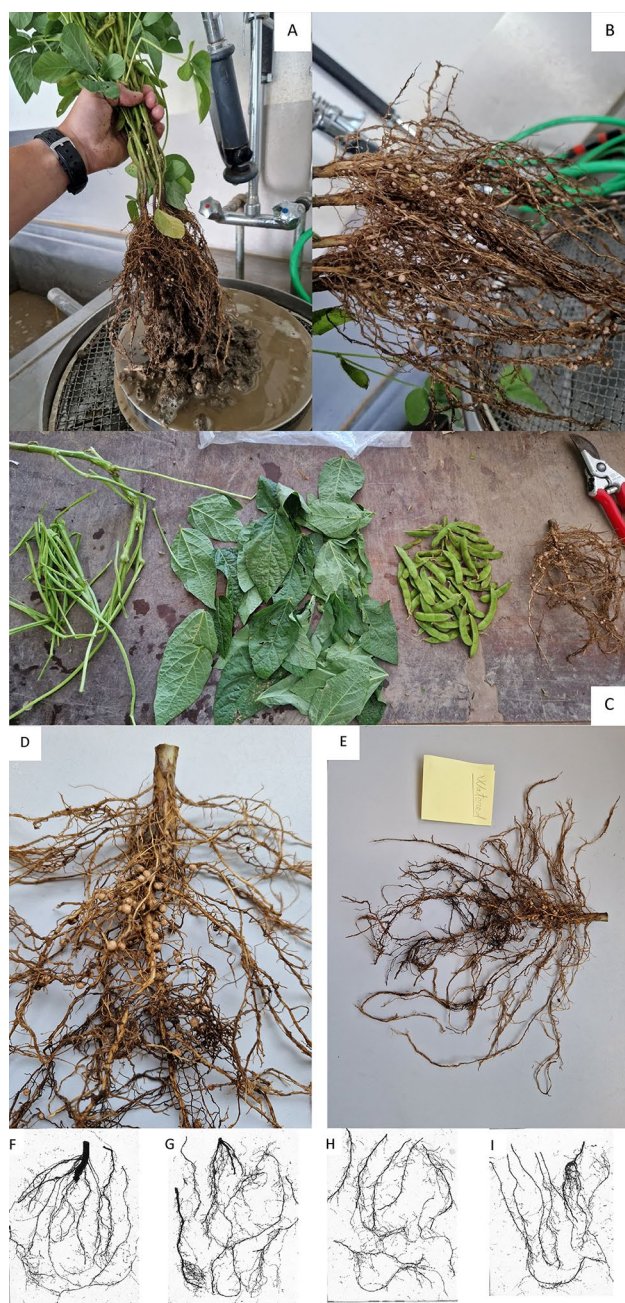


Fig. 2 Protocol for “root and canopy sampling”: root washing (A, B), separation of canopy parts and root system (C), root system before scanning analysis (D, E), and scans of sections of an entire root system (F, G, H, I)

Data analysis

Statistical analyses were performed using R 3.01 software (Team, 2013). The irrigation effect was tested for all the data measured using a t-test. Whenever normality and homoscedasticity conditions were not fulfilled, a permutational t-test was used using the function *perm.t.test*. For the root system and canopy sampling, the concatenation of the root diametral

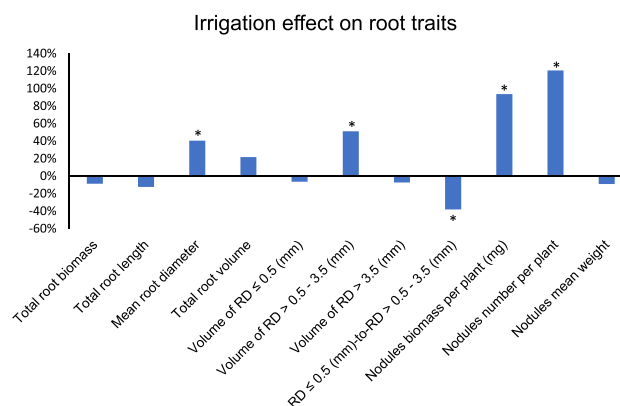


Fig. 3 Irrigation effect on nodules and root systems at the R3–R4 developmental stages (i.e. 84 DAS) using the data from “root and canopy sampling”. RD ≤ 0.5 mm, RD > 0.5–3.5 mm, and RD > 3.5 mm refer to root diameters of 0–0.5 mm, 0.5–3.5 mm, and larger than 3.5 mm, respectively. Stars indicate a significant difference ($p < 0.05$) between irrigated and rain-fed treatments (t-test)

classes (i.e. ≤ 0.5 mm, 0.5–3.5 mm, and > 3.5 mm) was set to best highlight the differences observed with and without irrigation. Similar irrigation effects were observed for root diameter classes ranging between 0.5 mm and 3.5 mm, so they were pooled to constitute the RD 0.5–3.5 mm variable. Thereafter, root diameter classes are hereafter: RD ≤ 0.5 mm, RD 0.5–3.5 mm, and RD > 3.5 mm (which are differently influenced by the irrigated and rain-fed treatments). In terms of functionality for root diametral classes, we considered that RD ≤ 0.5 mm was remarkably more related to water and nutrient uptake compared to RD > 0.5–3.5 mm, which was more involved in resource transport (Freschet et al. 2021).

To highlight the potential linear relationships between canopy traits and root traits at 84 DAS, correlations were carried out separately for irrigation and rain-fed treatments. Linear relationships (r Pearson) were tested, and p values were indicated.

Results

Irrigation effect on root systems

For plants subjected to irrigation, the root system weight and total root length were marginally lower, total root surface was unaffected, and total root volume tended to increase compared to the rain-fed treatment (Fig. 3). In the RD > 0.5–3.5 mm class, irrigation increased the mean root diameter, root surface, and root volume. Furthermore, the ratio of root volumes RD ≤ 0.5 mm-to-RD > 0.5–3.5 mm classes decreased with irrigation. Irrigation increased the number and the biomass of nodules compared to rain-fed soybean, while weight per nodule was unchanged. The RD ≤ 0.5 mm (mainly ascribed to water and nutrient uptake)

class represented around 75% of the total root length, with the remaining 25% constituting the RD>0.5–3.5 mm class, which are more related to resource transport (Table S1).

Irrigation effect on aboveground biomass

At the R3–R4 developmental stages, the height of the soybean plants measured in situ increased by more than 13 cm for the irrigation treatment, and the collar diameter increased by more than 1 mm (Table S2). Plant density was similar with or without irrigation (Fig. 4). For the healthy soybean plants collected in the field, no difference in the weight of leaves and total stems was observed with or without irrigation (Fig. 4), showing that the total aboveground biomass was similar, regardless of irrigation treatment. However, irrigation was found to increase the main stem biomass and the main stem-to-total stems ratio, indicating that irrigation influenced aboveground biomass partitioning. Pod biomass and pod number per plant tended to be higher without irrigation at 84 DAS.

The mean pod weight was higher at first sampling (84 DAS) in the rain-fed treatment (Fig. 5). However, mean pod weight kept increasing until the third sampling date (119 DAS) in the irrigated treatment, whereas it stabilised in the rain-fed treatment, and finally reached a lower total pod weight than in the irrigated plants.

Unusual weather conditions were observed in 2023 (the year of the experiment) at Changins compared to weather patterns over the previous decade. Therefore, irrigation increased mean pod weight until at least 119 DAS (Fig. 5), which corresponds to 1685 degree days (base 6 °C), slightly beyond the mean of degree days estimated for grain maturity from 2015 to 2023 for *Gallec* at Agroscope Changins in the irrigated field (i.e. 1667 degree days, unpublished data). At the final sampling, water content of stems and pods were higher for the irrigation treatment compared to in the rain-fed soybean (Table 1).

Relationships between plant parts

For plants subjected to the irrigation treatment, pod biomass was significantly ($p < 0.05$) related to all canopy traits except the main stem biomass, whereas the linear relationships between the pod biomass and canopy traits were weaker for the rain-fed treatment (Table 2). Mean pod weight was positively related to the harvest index for both treatments. Leaf biomass was related to the main stem and branch biomass for the irrigated treatment but only to branches for the rain-fed treatment.

Main stem, leaf and pod biomass were related to the root volume of RD>3.5 mm for the irrigation treatment

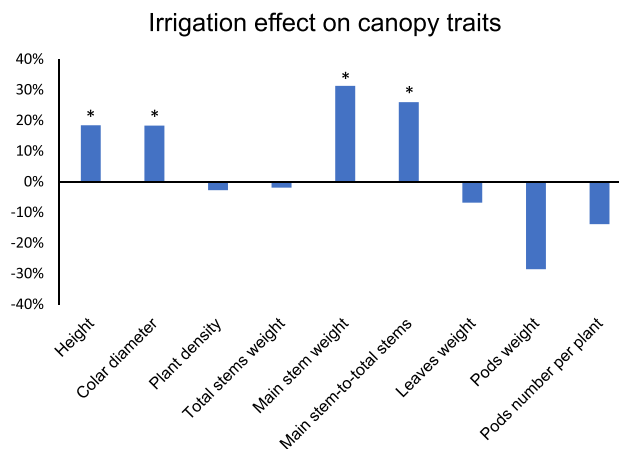


Fig. 4 Irrigation effect on aboveground biomass at 84 DAS (i.e. 27/07 at R3–R4 developmental stages). Stars indicate a significant difference ($p < 0.05$) between irrigated and rain-fed treatments (t-test)

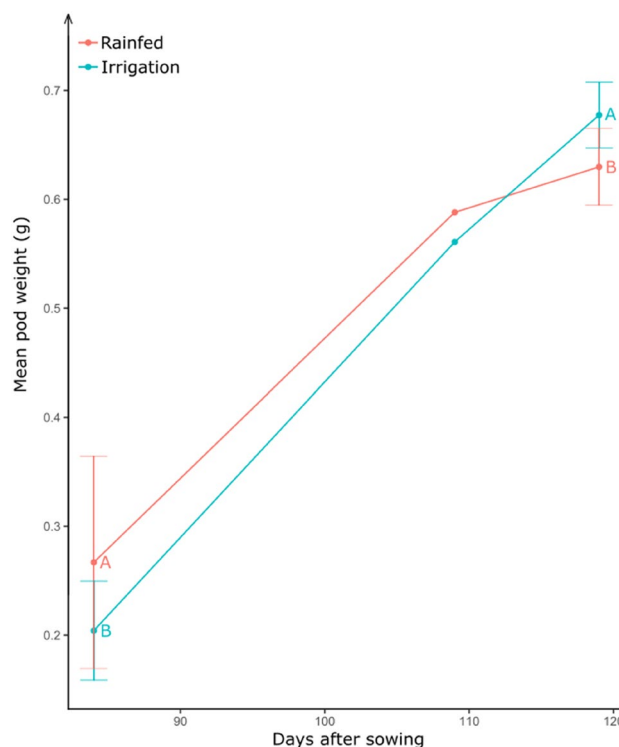


Fig. 5 Mean pod weights at 84, 109, and 119 DAS for irrigated and rain-fed treatments. At 109 DAS, the number of pods was too low for a t-test. Significant differences ($p < 0.05$) are indicated by different letters

Table 1 Irrigation effects on water content of stem and pod at the end of pod filling (%) using the data from “canopy samplings” on August 21 and 31, 2023

Plant part	Days after sowing	Irrigation	Rain-fed
Stems	109 [†]	63	47
	119	58 A	19 B
Pods	109 [†]	54	17
	119	12 A	9 B

[†]n was too low to carry out a t-test

Significant difference ($p < 0.05$) is indicated by different letters

Table 2 Correlations between canopy traits (total pod biomass, mean pod weight (M.W.), total leaf biomass, total stem biomass, main stem biomass, branch (Br.) biomass, and harvest index (Harv. Ind.) at 84 DAS. The significance of linear relationships is indicated at $p < 0.05$ (*), $p < 0.01$ (**) or $p < 0.001$ (***)

		Watered	Pods		Total leaf biomass	Stems		
			Total	M.W.		Total	Main	Br.
M.W.	Yes		0.69*					
	No		0.28					
Total leaf biomass	Yes		0.75*	0.13				
	No		0.52	-0.57				
Stems	Total	Yes	0.71*	0.13	0.97***			
		No	0.65*	-0.46	0.94***			
	Main	Yes	0.56	-0.03	0.93***	0.97***		
		No	0.37	-0.39	0.42	0.65		
	Br.	Yes	0.82**	0.31	0.95***	0.96***	0.85**	
		No	0.63	-0.39	0.96***	0.94***	0.36	
Harv. Ind.	Yes		0.70*	0.91***	0.07	0.01	-0.15	0.19
	No		0.60	0.90***	-0.29	0.00	-0.18	-0.14

Table 3 Correlations between canopy traits (total pod biomass, mean pod weight (M.W.), total leaf biomass, total stem biomass, main stem biomass, branch (Br.) biomass and harvest index (Harv. Ind.) and root traits (volumes of $RD \leq 0.5$ mm, $RD > 0.5-3.5$ mm, $RD > 3.5$ mm, total volume, total nodules biomass per plant, number of nodules per plant, and nodule mean weight (M.W.) at 84 DAS. The significance of linear relationships is indicated at $p < 0.05$ (*), $p < 0.01$ (**) or $p < 0.001$ (***)

		Watered	Pods		Total leaf biomass	Stems			Harv. Ind.
			Total	M.W.		Total	Main	Br.	
Volumes (cm ³)	RD≤0.5 mm	Yes	-0.34	-0.33	-0.10	0.01	0.06	-0.05	-0.47
		No	-0.05	-0.60	0.60	0.41	-0.18	0.59	-0.54
	RD>0.5–3.5 mm	Yes	-0.10	-0.34	0.18	0.18	0.23	0.10	-0.36
		No	0.22	-0.62	0.84**	0.70*	0.15	0.79**	-0.41
	RD>3.5 mm	Yes	0.70*	0.24	0.78**	0.72*	0.75*	0.63	0.30
		No	0.76**	0.34	0.15	0.34	0.35	0.26	0.52
	Total	Yes	-0.26	-0.34	0.00	0.02	0.08	-0.06	-0.41
		No	0.00	-0.68*	0.74*	0.53	-0.04	0.67*	-0.54
Nodules	Total	Yes	0.41	0.05	0.75*	0.86**	0.90***	0.75*	-0.21
		No	0.43	0.02	0.19	0.47	0.66*	0.29	0.11
	Number	Yes	-0.03	-0.57	0.47	0.46	0.56	0.32	-0.52
		No	0.72*	0.14	0.31	0.54	0.50	0.44	0.35
	M.W.	Yes	0.35	0.40	0.38	0.54	0.55	0.48	0.07
		No	-0.09	-0.16	-0.05	0.15	0.53	-0.05	-0.23

(Table 3). Moreover, leaf and stem biomass were related to the total nodule biomass. In contrast, the leaf and branch biomass were closely related to root volume of $RD > 0.5-3.5$ mm, while root volume of $RD > 3.5$ mm was related to the pod biomass for the rain-fed treatment. Pod biomass was also related to the number of nodules.

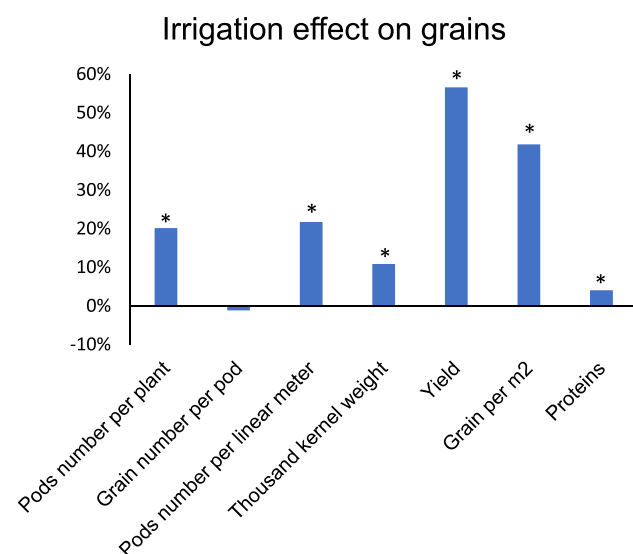
For both treatments, root volumes of $RD > 0.5-3.5$ mm and $RD \leq 0.5$ mm were related (and both were related to the total root volume), whereas root volumes of $RD > 3.5$ mm were related to canopy traits, nodule biomass, and number of rain-fed treatments only (Table 4).

Irrigation effect on grain yields and grain yield components

Irrigation increased pod number per plant and pod number per linear meter at 119 DAS, whereas grain number per pod was not affected (Fig. 6 and Table S3). Therefore, irrigation increased grain yield (+58%) due to an increase in both the thousand kernel weight (+11%) and the number of grain m⁻² (+42%). Considering the total amount of water received by each treatment, the rain-fed treatment (i.e. accumulated rainfall=204.5 mm) produced 11.7 kg of grains per mm of water, while the irrigation treatment (i.e. accumulated rainfall+irrigation=204.5 mm+180 mm) produced 9.9 kg of grains per mm of water. Finally, irrigation also increased the grain protein concentration (Fig. 6 and Table S3).

Table 4 Correlations between root traits (volumes of $RD \leq 0.5$ mm, $RD > 0.5-3.5$ mm, $RD > 3.5$ mm, total volume, total nodules biomass per plant, number of nodules per plant, and nodule mean weight (M.W.) at 84 DAS. Significance of linear relationships is indicated at $p < 0.05$ (*), $p < 0.01$ (**) or $p < 0.001$ (***)

	Watered	$RD \leq 0.5$ mm	$RD > 0.5-3.5$ mm	$RD > 3.5$ mm	Root volume	Nodules biomass	Nodules number
$RD > 0.5-3.5$ mm	Yes	0.76*					
	No	0.83**					
$RD > 3.5$ mm	Yes	-0.23	0.10				
	No	-0.13	-0.05				
Root volume	Yes	0.84**	0.97***	-0.06			
	No	0.92***	0.96***	-0.19			
Nodules biomass	Yes	0.26	0.25	0.51	0.16		
	No	-0.07	0.03	0.67*	-0.12		
Nodules number	Yes	0.24	0.29	0.21	0.20	0.44	
	No	0.07	0.20	0.83**	0.02	0.84**	
M.W.	Yes	0.22	0.12	0.32	0.12	0.81**	-0.10
	No	-0.18	-0.25	0.25	-0.26	0.75*	0.30

**Fig. 6** Pod number per plant and grain number per pod at the R7–R8 developmental stages (at 119 DAS) with and without irrigation for the second canopy sampling campaign. Grain yield, grain number per m², thousand kernel weight, and protein concentration at harvest time are also shown. Stars indicate a significant difference ($p < 0.05$) between irrigated and rain-fed treatments (t-test).

Discussion

Root system adaptation to water conditions

In our field trial, the plough pan apparently constrained the root system in the 0–20 cm soil layer (personal observation), as previously observed for soybean in a black soil of China (Dong et al. 2017). Generally, the root distribution along the soil profile is very likely influenced by site conditions, as observed for other species (Tron et al. 2015; Fontana et al. 2020; van der Bom et al. 2020). Soybean tends to maintain a higher part of its root system close to the soil surface compared to other legumes, including in drought conditions

(Benjamin and Nielsen 2006). We therefore assumed that root biomass in the deeper soil layer was negligible and that root systems were collected almost entirely. Moreover, very few materials were found in the sieve during the root system washing step, representing a negligible fraction of the total root biomass, so we assume that the loss in root pieces or nodules was negligible.

In this study, irrigation of soybean during vegetative growth and flowering influenced root traits. The observed decrease in mean root diameter (Fig. 3), which is common for soybean (Fenta et al. 2014; Yang et al. 2021), was previously reported as a water shortage adaptation (Henry et al. 2012), suggesting that water condition was limiting for soybean grown with rain-fed treatment. Although irrigation was reported to increase the total root length and root biomass of soybean (Fenta et al. 2014; Thu et al. 2014; Chun et al. 2021), in this study, the opposite was observed (Fig. 3), suggesting that the irrigation effect on root production is context specific. The sandy soil in Fenta et al. (2014) compared to the fine soil texture in this study, or the pot experiments in Chun et al. (2021) and Thu et al. (2014) compared to the in situ conditions of this study, could explain the differences in the responses to irrigation. In our study, irrigation likely modified the carbon allocation strategy within the root system, considering the root length distribution across the root diameter classes (Table 1). The higher root length $RD \leq 0.5$ mm-to- $RD > 0.5-3.5$ mm ratio in the rain-fed treatment group suggests a root system strategy more focused on resource acquisition compared to the irrigated treatment. In addition, this study suggests that irrigation can modify the interactions between the root system and the canopy. For instance, leaves, branches, and stems biomass were linearly related to different root diameter classes according to the treatment (i.e. $RD > 3.5$ mm for irrigated vs. $RD > 0.5-3.5$ mm for rain-fed, Table 3). The strong linear relationship between nodule biomass and canopy traits

for irrigated treatment suggests that the higher nodulation favoured the aboveground biomass production compared to rain-fed treatment, whose nodule biomass was related to root volume $RD > 3.5$ mm and weakly related to canopy traits. Noteworthy, a common linear relationship between pod biomass and the root volume of $RD > 3.5$ mm emerged. These coarse roots drive the highest resource fluxes in the root system and could be an interesting root trait to test in future soybean breeding studies.

The positive effect of irrigation on nodulation (Fig. 3) was previously observed (Sinclair et al. 1988; Sulieman et al. 2015). Nodule biomass of the ‘*Gallec*’ soybean cultivar increased by more than 100% (Table 1), which was higher than what was observed in other studies, with different soybean cultivars, ‘*Jackson*’ (drought tolerant for N_2 fixation) and ‘*Flint*’ (Serraj and Sinclair 1998; Streeter 2003). In our study, the likely increased investment in photosynthate necessary for the higher nodule biomass of irrigated treatment may have led to an important increase in fixed N, despite the relatively high soil NO_3 content in our field trial (14.3 mg g^{-1} , data not shown), which could potentially limit nodulation and its efficiency (Chen et al. 1992; Ferguson et al. 2010). This assumption is supported by the higher grain protein concentration (i.e. harvest at 132 DAS) combined with an increase of both grain per m^2 and thousand kernel weight (which, in addition, is expected to dilute grain protein concentration) for irrigated compared to rain-fed soybean. Indeed, a more efficient N fixation can lead to a higher grain protein concentration (Zimmer et al. 2016). This shows that irrigation during vegetative growth and flowering can be crucial to favour nodulation, grain protein content, and grain yield, even in the absence of irrigation during grain ripening (Fig. 6).

Canopy adaptation to irrigation

We tested the response of the soybean canopy structure to contrasting water regimes. Irrigation increased plant height at 84 DAS, likely because the internode length (Desclaux et al. 2000) and/or cell elongation (Yang et al. 2021) were increased. Although irrigation was expected to increase soybean aboveground biomass (Fenta et al. 2014; Du et al. 2020), this was not observed in our study (Fig. 4). This shows that forecasting the irrigation effect on the basic morphological traits of soybean aboveground biomass is not straightforward and likely depends on the site and/or cultivar and/or annual weather conditions and/or irrigation intensity. In this study, irrigation favoured biomass allocation in the main stem compared to the rain-fed treatment (Fig. 4), possibly because the branches demanded less water than the main stem (Gao et al. 2020). Overall, this study suggests that soybean can rearrange biomass allocation in

the canopy to adopt a water-saving strategy while keeping a similar total biomass.

Irrigation effect on developmental stages and grain yield components

We reported numerous indicators showing that irrigation delayed the developmental stages of soybean. Accordingly, increasing soil water content is expected to slow down the initiation of the orderly process of senescence (Nathanson et al. 1984). Indeed, the causal relationship between developmental stage duration and soil water conditions is well-known (Desclaux and Roumet 1996; De Souza et al. 1997). Considering that pod water content decreases continuously during maturation (Saab and Obendorf 1989), the higher water content of pods from at least the R3–R4 to R7–R8 developmental stages for irrigation treatment (Fig. 5) suggests an extension of developmental stage periods. This higher pod water content for irrigated treatment is not due to a higher soil water content, which was very likely similar for both irrigation and rain-fed treatments at the “canopy sampling” times, which occurred 33 and 43 days after the last irrigation, respectively (Fig. 1). Furthermore, the mean pod weight at 84 (i.e. at R3–R4), 109 (i.e. at R6–R7), and 119 (i.e. at R7–R8) DAS, which were lower, similar, and higher, respectively, than the rain-fed treatment (Fig. 5), suggests that irrigation during vegetative growth and flowering delayed and extended the grain filling period. The higher mean pod weight with irrigation was only due to an increase in the thousand kernel weight, rather than an increase in seed number per pod (Fig. 6). In this case, our results seem to contradict a report of a decrease in seed number per pod (Desclaux et al. 2000) following water shortages during the vegetative and flowering developmental stages. However, our results suggest a lower pod abortion during pod maturation for irrigated treatment compared to rain-fed treatment (i.e. Figure 4 vs. Figure 6), which could explain the higher grain per m^2 observed for the irrigation treatment.

Overall, we suppose that the positive effect of irrigation on grain yield is due to an extended pod maturation period combined with changes in canopy and root system architecture, rather than a higher soil water content during pod maturation. For instance, we assume that changes in root traits of irrigated treatment may allow the pods to take full advantage of the last rainfall (i.e. from 114 to 116 DAS, Figs. 1 and 3). In fact, the positive influence of irrigation on fixed N and grain yield depends on rainfall patterns (Matheny and Hunt 1983; Purcell and Specht 2004). We assume that if there had been less rainfall in August (i.e. during pod filling), the difference in soybean performance between treatments would have dropped. Conversely, more rainfall during this period could have led to a greater difference between

treatments, and this assumption should be formally tested in future studies. Nevertheless, our findings suggest that adaptation acquired during the vegetation developmental stages resulting from irrigation can have a positive impact until grain harvest, even if irrigation is stopped during pod filling. Although several studies in greenhouse conditions have highlighted that water limitations can negatively affect grain yield, especially during pod maturation (De Souza et al. 1997; Vadez 2014; Wei et al. 2018; Cui et al. 2019; Nadeem et al. 2019), our field study suggests a considerable influence of irrigation during the soybean vegetative and flowering developmental stages.

Conclusion

This study highlights the influence of irrigation carried out only during vegetative growth and flowering. The positive effects of irrigation on grain yield components and grain protein content occurred along with (i) a modification of the biomass allocation within the canopy and root system, (ii) an extension of the following pod maturation period, and (iii) an increase in nodule number and biomass. From a practical point of view, this study shows the importance of irrigation during the first weeks/months of growth. From a breeding perspective, this study underlines the importance of morphological plasticity, which should be investigated further regarding comparisons between varieties. The linear relationship between biomass allocation to the coarsest roots and pod production should be confirmed in future studies. Indeed, our study was conducted only on one site-year and one soybean variety. Therefore, future investigations should clarify the extent to which our findings on site and soybean variety adaptation to irrigation can be generalised across genotypes $\times$ environment $\times$ management practices.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors have no conflicts of interest to disclose.

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