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Elana Dayoub, Jay Ram Lamichhane, Philippe Debaeke, Pierre Maury. Genotypic differences in root traits to design drought-avoiding soybean ideotypes. *OCLE Oilseeds and fats crops and lipids*, 2022, 29 (26), 10.1051/ocle/2022021 . hal-03726450

HAL Id: hal-03726450

<https://hal.inrae.fr/hal-03726450>

Submitted on 18 Jul 2022

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Genotypic differences in root traits to design drought-avoiding soybean ideotypes[☆]

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Received 8 December 2021 – Accepted 17 May 2022

Abstract – Soybean (*Glycine max* (L.) Merr.) may contribute to the agro-ecological transition of cropping systems in Europe, but its productivity is severely affected by summer drought. The crop is mainly grown in southern and continental parts of Europe, whereby increasing drought and heat waves are expected in the near future. Agronomic strategies, such as early sowing, require cultivars with enhanced early plant growth traits under suboptimal conditions. Moreover, efficient water uptake by root delays dehydration and promotes drought avoidance. In general, changes in root morphology and root architecture are important pathways for plant adaptation to water stress conditions. This paper reviews the cultivar differences in soybean for root morphological and architectural traits especially during early growth stage. Previous works reported cultivar differences for root traits in soybean but they did not deal with cultivars commonly grown in Europe on which little information is available to date. Genotypic differences in available early-stage root traits can be used as a framework to design soybean ideotypes less vulnerable to drought. To this aim, high-throughput phenotyping supported by digital methods and crop modelling offer new avenues for the exploration of target root traits involved in drought avoidance.

Keywords: early growth / ideotype / root traits / soybean cultivars / water deficit

Résumé – Différences génotypiques dans les caractéristiques des racines de soja pour concevoir des idéotypes évitant la sécheresse. Le soja (*Glycine max* (L.) Merr.) peut contribuer à la transition agro-écologique des systèmes de culture en Europe. Cependant, sa productivité est fortement impactée par la sécheresse estivale. Cette culture est principalement pratiquée en Europe du Sud et continentale, où sécheresse et vagues de chaleur plus fréquentes et plus intenses sont attendues à l'avenir. Les stratégies agronomiques, telles que le semis précoce, nécessitent des cultivars ayant une croissance précoce accrue en conditions sous-optimales. De plus, une absorption efficace de l'eau par les racines retarde la déshydratation et participe à l'évitement de la sécheresse. En général, les changements dans la morphologie et l'architecture des racines sont des voies importantes d'adaptation de la plante au stress hydrique. S'appuyant sur une revue bibliographique, cet article vise à examiner les différences génotypiques chez le soja pour ce qui concerne les traits morphologiques et architecturaux des racines, en particulier au stade précoce. Des travaux précédents ont mis en évidence des différences entre cultivars pour les traits racinaires du soja, mais ils ne se rapportaient pas à ceux couramment cultivés en Europe, pour lesquels peu d'informations sont disponibles à ce jour. Les différences génotypiques pour les traits racinaires observées au stade précoce peuvent être exploitées pour concevoir des idéotypes de soja moins vulnérables à la sécheresse. Dans ce but, le phénotypage à haut débit soutenu par des méthodes numériques et la modélisation des cultures offrent de nouvelles pistes pour l'exploration des traits racinaires cibles impliqués dans l'évitement de la sécheresse.

Mots clés : phase précoce / idéotype / traits racinaires / cultivars de soja / déficit hydrique

[☆] Contribution to the Topical Issue “Soybean / Soja”.

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Highlights

- A wide genetic variability exists for root architectural traits among soybean cultivars.
- Deep taproot, numerous lateral roots and wide root angle are components of drought avoiding ideotype.
- Phenotyping methods at early growth provide proxy for more advanced growth stages.
- Complementarity between structural and functional root traits should be considered in future research.

1 Introduction

The global soybean production in 2019 reached 334 million tons of which 80% were achieved in Brazil, USA and Argentina only (FAOstat, 2021). In the European Union, soybean production has increased progressively over the last 5 years, reaching 2,8 million tons on 933,000 ha in 2021 (European Commission, 2021). However, this production is still not sufficient to satisfy the increasing needs of the European market for food and feed requiring importation of soybean from the American continent. Indeed, out of 17 million tons of crude proteins imported annually in the European Union, 13 million tons come from soybean, corresponding to 30 million tons of equivalent grains (European Commission, 2018). In France, the strategic plan of the oil–protein sector aims at increasing the soybean acreage with an objective of 300,000 ha by 2030 (*versus* 186,000 ha in 2020). An increasing interest in this crop derives from the quality of its grain (~41% proteins) as well as from the agronomic and environmental benefits of this crop (diversification of crop rotation, lower need for pesticides, low greenhouse gas emissions, biological nitrogen fixation, etc.) (Jouffret *et al.*, 2015).

In Europe, soybean is mainly grown in southern and continental parts, where increasing drought and heat waves are expected in the near future (Dai, 2013; Rojas *et al.*, 2019). Soybean yield and its stability are constrained by drought, which is the most important limiting abiotic stress causing yield losses (up to 40%), particularly when it occurs during both the vegetative and the reproductive stages (Specht *et al.*, 1999). However, the most critical period of water stress in this crop occurs from flowering stage (Meckel *et al.*, 1984). Several agronomic practices and adaptive strategies could be planned to counteract crop losses due to water stress and to promote the soybean acreage (Maury *et al.*, 2015). One of these strategies is the choice of cultivars adapted to water-limited environments through drought escape, dehydration tolerance and drought avoidance (Turner *et al.*, 2001). Drought escape is an agronomic practice corresponding to the introduction of early-maturing cultivars or shifting sowing dates earlier. Dehydration tolerance is the ability of plant cells to continue the metabolic process at low leaf water status by various physiological adaptations such as osmotic adjustment. On the other hand, drought avoidance (or dehydration postponement) occurs when plants are able to keep a favourable water status under drought either by limiting water loss from leaves through

reduced stomatal conductance, by reducing leaf absorption of radiation or by enhancing the root water uptake through a deeper rooting system. Deepening rooting system could be a major adaptation trait to climate change for both increasing soybean yield and decreasing annual yield variability (Battisti and Sentelhas, 2017). This literature review explores genotypic differences in soybean root system with a particular focus on drought avoidance.

The root system characterization is commonly based on structural (morphological and architectural) and functional traits (*e.g.*, water uptake and nutrients acquisition). A trait is defined as a morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization (Violle *et al.*, 2007). Root morphology refers to the surface features of a single root axis as an organ, including characteristics of the epidermis such as number and length of roots hairs, root diameter, root length, root surface area, root volume and specific root length (Lynch, 1995). Root system architecture (RSA), defined as the spatial configuration of a root system in the soil, is used to describe the shape and structure of roots such as width, depth, ratio of roots width to depth (De Dorlodot *et al.*, 2007), and root growth angle between lateral roots and soil surface (Zhao *et al.*, 2004). In addition, RSA is determined by the interactions between genetic and environmental factors making it highly plastic and able to respond to rapid environmental changes such as water stress (Xiong *et al.*, 2020) or waterlogging. On the other hand, functional traits are defined as morpho-physio-phenological characteristics, which impact plant fitness indirectly *via* their effects on plant performance (*e.g.*, root traits involved in water uptake efficiency) (Violle *et al.*, 2007). However, the correlation between structural and functional traits is not straightforward and depends on plant growth environment.

Identifying ideotypes for root structural traits (morphology and architecture) involved in drought avoidance is useful in guiding the development of soybean cultivars to enhance soil exploration and thus water acquisition under water-limited conditions. Many efforts in plant breeding have been made to improve drought avoidance and resource acquisition. Several studies highlighted the interaction between structural and functional root traits. Crops characterized by a large root diameter could have an increased ability to penetrate the hard soil (Bengough *et al.*, 2011). Lynch (2013) showed that roots growing vertically at low metabolic cost (steep, cheap and deep) contribute to build an interesting ideotype in maize since root system with rapid exploitation of deep soil could optimize both water and N uptake. However, in the case of phosphorus (immobile resource), soybean cultivars with root phenes, such as shallower root growth angle of basal roots and long root hairs, have been a good choice to enhance P acquisition in low-P soils (Lynch, 2011; Lynch and Brown, 2001; Richardson *et al.*, 2011; Wang *et al.*, 2010). In addition, a relationship was observed between root architecture and arbuscular mycorrhizal fungi colonisation in soybean. The deep root genotype had greater colonisation by these fungi at low P compared to the shallow root genotype (Wang *et al.*, 2011). Previous studies reported some specific soybean root traits involved in water uptake particularly under drought (Boote, 2011; Valliyodan *et al.*, 2017). On the other hand, functional traits, such as N₂ fixation, are related to root nodulation ability (Prudent *et al.*, 2016) that could

Table 1. Main growth environments and associated root system phenotyping methods for soybean.

Growth environment	Phenotyping method	Advantages	Disadvantages	Reference
Field	Root excavation	Real conditions, early and advanced stages	Heavy extraction, challenge of visualizing of roots, destructive, labour-intensive	Allmaras <i>et al.</i> (1975); Pantalone <i>et al.</i> (1996a, 1996b); Zhao <i>et al.</i> (2004); Benjamin and Nielsen (2006); Ao <i>et al.</i> (2010); Matsuo <i>et al.</i> (2013); Fenta <i>et al.</i> (2014); Wijewardana <i>et al.</i> (2019)
Semi-field	Root excavation/rhizotrons		Visualisation of RSA in 2 dimensions	Kaspar <i>et al.</i> (1978); Kaspar <i>et al.</i> (1984)
	Pots/tubes	Close to the field conditions (the medium used may be soil or sand)		Gao <i>et al.</i> (2020)
	Lysimeters/minirhizotrons or pots			Matsuo <i>et al.</i> (2013)
Greenhouse	Plastic tubes (mesocosms)	Easy root extraction, easily repeatable	Only for early stages	Fried <i>et al.</i> (2018); Thu <i>et al.</i> (2014)
	Rhizotubes	Non-destructive method	No visualisation of RSA in 3 dimensions	Maslard <i>et al.</i> (2021)
	Rhizotrons	Visualisation of RSA in 2 dimensions		Dayoub <i>et al.</i> (2017)
	Pots	Rapid and low-cost		Mwamlima <i>et al.</i> (2019)
Growth chamber	Minirhizotrons			Dayoub <i>et al.</i> (2021)
	Germination paper			Falk <i>et al.</i> (2020)
	Cones/tubes			Manavalan <i>et al.</i> (2010)

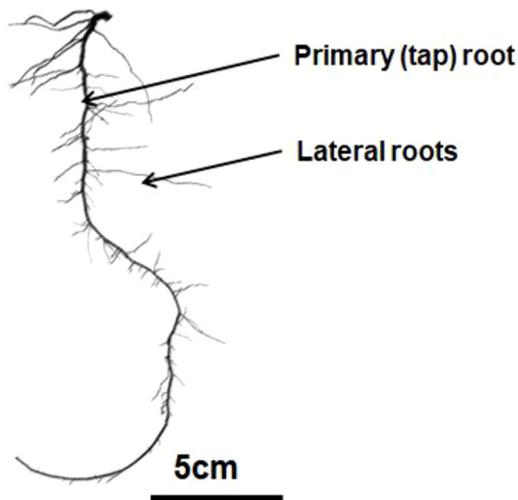


Fig. 1. A characteristic allorhizic root system architecture of soybean (cv. Isidor) at cotyledon stage (VC) (source: E. Dayoub, unpublished).

occur in interaction with structural root traits (morphology and architecture) and may thus be involved in drought avoidance (Pantalone *et al.*, 1996a, 1996b).

For instance, the ability of roots to colonize the soil quickly and effectively during crop establishment could be a major trait related to the competitiveness for resources. However, to date, only little is known on root traits involved in drought avoidance in commonly grown soybean cultivars in Europe.

In the ongoing context of climate change, and with the perspective of restrictive irrigation programs, new candidates (ideotypes) are required in relation to root traits in soybean cultivars under water-limited environments of Europe. The objectives of this paper were three-fold:

- to briefly report the main features of the soybean root system and root phenotyping methods;
- to review the genetic variability of root traits in soybean in relation to drought avoidance;
- to highlight how the cultivar differences for these traits could be used to design soybean ideotypes avoiding drought stress.

2 Root system phenotyping tools and methods

We have updated the list of root phenotyping methods, recently reviewed by Zhu *et al.* (2011) and Wasaya *et al.* (2018), by integrating newly published studies in the literature (Tab. 1). These studies proposed different methods for identifying root traits (morphology and architecture) under laboratory and field conditions. Phenotyping techniques under controlled environments (growth chamber, greenhouse) are much easier than those under field conditions due mainly to the easier extraction of roots. Several methods and approaches could be proposed based on the nature of growth medium (gel, liquid, or filter paper), which allow to measure a wide range of plants and root traits, mainly during early growth. Although

these techniques may not accurately reflect rooting system morphology and architecture under field conditions, they can be proposed as complementary approaches to overcome field limitations. Under greenhouse environment, new image analysis approaches were also implemented to characterize soybean root architectural traits at high throughput (Maslard *et al.*, 2021). Although root phenotyping under controlled conditions is a rapid, low-cost and adaptable method, further experiments are required under field conditions to evaluate the performance of cultivars and to show how shoot and root traits are affected by various soil, climate and management conditions.

3 Soybean root growth

Soybean has a simple rooting system named allorhizic (Fig. 1), consisting of a taproot and lateral roots (Ao *et al.*, 2010; Fenta *et al.*, 2011, 2014). The taproot may reach a depth of 200 cm and most lateral roots emerge from the upper 10 to 15 cm of the taproot (Lersten and Carlson, 2004). More than 50% of the roots are localised in the first 20 cm of soil layer (Hoogenboom *et al.*, 1987). Moreover, 95–97% of the total root weight and 85–70% of the total root surface area have been found in the upper 23 cm of soil (Benjamin and Nielsen, 2006; Mitchell and Russell, 2010).

The soybean root consists of a simple architecture and morphology, which is similar to that of oilseed rape (Louvieaux *et al.*, 2020). However, there is paucity of information on the soybean rooting system compared to other crop species such as cereals (*e.g.*, maize) or other leguminous species (*e.g.*, common bean). Indeed, maize is characterized by a complex rooting system composed of different root types *viz.* primary, crown, brace and seminal roots. Moreover, since lateral roots in maize are more metabolically demanding per gram of tissue than axial roots, a balance is required between the need of soil exploration and the metabolic need (Lynch, 2013).

During the vegetative phase, soybean rooting can reach 30 and 40 cm depth at 23 (second unrolled trifoliolate leaf: V2) and 30 (third unrolled trifoliolate leaf: V3) days after sowing, respectively (Fenta *et al.*, 2014; Torrión *et al.*, 2012). At the beginning of flowering stage (R1), rooting depth may vary from 50 to 70 cm (Böhm *et al.*, 1977; Manavalan *et al.*, 2010; Matsuo *et al.*, 2013). The maximum rooting depth in soybean differs between cultivars and could reach from 70 to 200 cm (Lersten and Carlson, 2004). An in-depth growth of rooting system could end between R1 to R3 (Kaspar *et al.*, 1978), or could continue until full seed stage (R6) (Torrión *et al.*, 2012). On cultivars with indeterminate growth habit, the taproot extension follows a linear model with a progression of 1,3 cm per day (Torrión *et al.*, 2012). Soybean root system could continue to grow after the beginning of pod filling but with no further increase in root weight from the late bloom to mid-pod fill growth stages (Mitchell and Russell, 2010). However, the root surface area increased between these two latter stages under both dryland and irrigated conditions (Benjamin and Nielsen, 2006). Therefore, there are contradictory information in the literature about soybean root growth in relation to cultivars and environmental conditions.

4 Genetic variability for root traits in soybean

A number of previous studies reported a variability in root traits among soybean cultivars. This variability was observed during early growth (Allmaras *et al.*, 1975; Kaspar *et al.*, 1978, 1984; Zhao, 2004; Ao *et al.*, 2010; Manavalan *et al.*, 2010; Matsuo *et al.*, 2013; Fenta *et al.*, 2014; Thu *et al.*, 2014; Fried *et al.*, 2018, 2019; Mwamlima *et al.*, 2019; Falk *et al.*, 2020; Gao *et al.*, 2020; Dayoub *et al.*, 2021; Maslard *et al.*, 2021), at flowering stage (Zhao *et al.*, 2004; Mwamlima *et al.*, 2019) or at maturity (Ao *et al.*, 2010). Phenotypic differences among soybean cultivars for root traits have been well documented under different conditions (drought, phosphorus availability) across many locations worldwide (Tabs. 2 and 3). In contrast, only a few studies focused on soybean cultivars commonly grown in Europe (Dayoub *et al.*, 2021; Maslard *et al.*, 2021). For most investigated root traits in the literature (Tabs. 2 and 3), the extent of variation seems to be different as a function of cultivar, phenology and growth environment.

4.1 Genetic variability in early growth

A wide genetic variability has been reported for most investigated architectural and morphological root traits during early growth (~stage V3) regardless of water regime or soil status. Architectural root traits such as rooting depth, root angle and root width were significantly different among cultivars, irrespective of the water regime and growth environment (Matsuo *et al.*, 2013; Fenta *et al.*, 2014; Falk *et al.*, 2020; Maslard *et al.*, 2021). Root morphological traits as root surface, root volume, taproot length, root tips number and total root length were also different among cultivars (Fenta *et al.*, 2014; Fried *et al.*, 2018, 2019; Falk *et al.*, 2020; Dayoub *et al.*, 2021). However, this variability was less noticeable for average root diameter (Manavalan *et al.*, 2010; Fenta *et al.*, 2014; Fried *et al.*, 2018). Because the cultivars used so far belonged to a wide range of maturity groups and were tested across different environments, the information presented in Tables 2 and 3 could help target root traits involved in drought avoidance mainly during early growth.

Early growth is a critical phase of the crop cycle, which spans from sowing until the beginning of competition among plants (crops or weeds) for the acquisition of trophic resources (Boiffin *et al.*, 1992; Fayaud *et al.*, 2014). This phasic sensitivity depends on species traits and sowing conditions, including seedbed moisture. The latter, for example, is a key factor for soybean establishment in southwestern France, affecting both seed germination and seedling emergence (Lamichhane *et al.*, 2020a, 2020b). Therefore, species or cultivars characterized by an early and prompt ability to uptake resources during the first phase could show a higher competitive ability for the acquisition of the same resources later in the crop cycle (Fig. 2). Early seedling establishment of soybean *via* an increased shoot and root vigour could thus be one of the most important traits for genotype selection in order to improve crop production under water-limited environments (Manavalan *et al.*, 2009; Thu *et al.*, 2014). Since water is a mobile resource, it may be advantageous to have a primary root (taproot) and a network of lateral roots penetrating deeper into

the soil layers since the early development of seedling growth. However, soybean cultivars differ for early seedling growth and vigour. A significant variability between cultivars was noticed early in the crop cycle from 21 days after sowing (~stage V3) for roots traits as taproot depth and root biomass (Manavalan *et al.*, 2010; Matsuo *et al.*, 2013). Differences among cultivars were also found as early as 12 days after sowing for taproot progression in depth (Manavalan *et al.*, 2010; Matsuo *et al.*, 2013).

4.2 Rooting plasticity in early growth

Unfavourable conditions during early growth may lead to yield losses due to reduced root growth. Flooding conditions during two weeks after emergence caused yield damage even if water conditions were optimal later in the crop cycle (Bajgain *et al.*, 2015) because of the inhibition of the rooting growth in depth (Matsuo *et al.*, 2013). Water stress during the vegetative phase in soybean or at the beginning of reproductive phase (R1–R2) induced a significant increase in root system growth (Manavalan *et al.*, 2009). However, soybean undergoing water stress before the flowering stage could be able to produce higher yield than the crop undergoing water stress in post-flowering thanks to early plasticity of rooting system (taproot length and rooting density) (Hirasawa *et al.*, 1994). Soil water uptake during early season may differ among soybean cultivars because of differences in root expansion and early plant growth. However, few studies focused to date on the variability for early stage plant development among soybean cultivars grown in Europe under contrasted soil water regimes (Dayoub *et al.*, 2021)

5 Interactions between root growth and root nodulation

During early growth, symbiosis establishment and the varietal difference for root nodulation traits in soybean were poorly highlighted in the literature, which might be due to either the absence of nodulation (Dayoub, unpublished) or to the insignificant role of N₂ fixation at early stage (Dayoub *et al.*, 2017). For example, although root nodulation was established, more than 90% of the plant N was derived from both seed N and soil N uptake at 35 days after sowing (stage V3) under low N soil condition (Dayoub *et al.*, 2017). This result illustrates that the complementarity between structural (root nodule) and functional root traits (biological N₂ fixation) is not relevant during early growth. However, a large variation in nodule number and size was found among soybean cultivars during later growth stages (Serraj *et al.*, 1998; Fenta *et al.*, 2014).

Little is known to date on how symbiosis modifies root growth and architecture in soybean (Concha and Doerner, 2020; Maslard *et al.*, 2021). Moreover, the correlations between the frequency and intensity of nodulation and root growth are still poorly understood, particularly the factors that control nodule density per unit root length in the absence or presence of stress (Kunert *et al.*, 2016). The cultivar, which was characterized by a great root length, surface, volume and tips number under drought, showed an increase in nodule number and size (Fenta *et al.*, 2014). Similarly, a positive

Table 2. Intraspecific variability in soybean cultivars for investigated morphological root traits.

Root traits (per plant)	Cultivar range	Mean	Genotype or cultivar effect	Water regime	Water regime effect	Other condition	Plant stage, days after sowing (DAS) or days after germination (DAG)	Growth environment/phenotyping method	Cultivar or genotype number	Maturity group	Location	Reference
Average root diameter (mm)	0.50–0.56	0.53	*	Well-watered (volumetric soil water content 28%) Water stress (volumetric soil water content 16.5%)	*		10 DAS	Growth chamber/minirhizotrons	10	From 000 to II	France	Dayoub <i>et al.</i> (2021)
	0.49–0.61	0.55	*									
	0.32–0.49	0.41	NS				42 DAS	Greenhouse/mesocosms	49	From IV to VIII	USA	Fried <i>et al.</i> (2018)
	0.43–0.49	0.46	NS		NS		60 DAS (V3)	Field/root excavation	3	NA	South Africa	Fenta <i>et al.</i> (2014)
	0.40–0.54	0.47	**	Well-watered (volumetric soil water content 14%) Water stress from V3 (volumetric soil water content)								
	0.66–0.90	0.78	NS	Well-watered (soil moisture 80% at field capacity)	**		Flowering	Greenhouse/pots	6	From 00 to II	Kenya	Mwamlima <i>et al.</i> (2019)
	0.52–0.62	0.57	NS	Water stress (soil moisture 20% at field capacity)	**							
Root biomass (dry weight, g)	0.01–0.26	0.135	***				6 DAG	Growth chamber/germination paper	292	II and III	USA	Falk <i>et al.</i> (2020)
	0.01–0.26	0.135	***				9 DAG					
	0.01–0.26	0.135	***				12 DAG					
	0.02–0.04	0.03	***	Well-watered (volumetric soil water content 28%) Water stress (volumetric soil water content 16.5%)	NS		10 DAS	Growth chamber/minirhizotrons	10	From 000 to II	France	Dayoub <i>et al.</i> (2021)
	0.02–0.03	0.025	***									
	0.36–0.52	0.44	*				23 DAS (V1)	Greenhouse/rhizotubes/throughput	9	I	France	Maslard <i>et al.</i> (2021)
	0.54–0.70	0.62	NS				40 DAS	Greenhouse/mesocosms	10	From V to VIII	USA	Fried <i>et al.</i> (2019)
	2.09–3.61	2.85	***	Well-watered (soil moisture 80% at field capacity) Water stress (soil moisture 20% at field capacity)	***		Flowering	Greenhouse/pots	6	From 00 to II	Kenya	Mwamlima <i>et al.</i> (2019)
	0.40–0.84	0.62	***									
Root length density (cm cm⁻³)	0.06–0.16	0.11	***	Well-watered (volumetric soil water content 28%) Water stress (volumetric soil water content 16.5%)	NS		10 DAS	Growth chamber/minirhizotrons	10	From 000 to II	France	Dayoub <i>et al.</i> (2021)
	0.07–0.16	0.115	***									
	0.92–1.84	1.38	NS				21 DAS	Field	2	NA	Japan	Matsuo <i>et al.</i> (2013)
	0.59–1.30	0.945	NS				41 DAS (R1)					
	0.54–1.18	0.86	*				62 DAS (R4)					
	0.84–1.21	1.025	NS				85 DAS (R6)					
	0.03–0.19	0.11	*				21 DAS					

Table 2. (continued).

Root traits (per plant)	Cultivar range	Mean	Genotype or cultivar effect	Water regime	Water regime effect	Other condition	Plant stage, days after sowing (DAS) or days after germination (DAG)	Growth environment/phenotyping method	Cultivar or genotype number	Maturity group	Location	Reference
Root surface area (cm²)	0.07–0.24	0.155	*				40 DAS	Lysimeter/minirhizotrons				
	0.01–0.22	0.115	*				61 DAS					
	1.48–1.52	1.5	*				21 DAS	Pots				
	4.26–4.88	4.57	NS				42 DAS					
	8.30–8.68	8.49	NS				56 DAS					
	0.50–2.50	1.5	*	Water stress			R2	Semi field/pots/tubes	8	NA	China	Gao <i>et al.</i> (2020)
	0.0–27.5	13.75	***				6 DAG	Growth chamber/germination paper	292		USA	Falk <i>et al.</i> (2020)
	0.0–59.0	29.5	***				9 DAG					
	0.0–122.7	61.35	***				12 DAG					
	15.8–38.1	26.95	***	Well-watered (volumetric soil water content 28%) Water stress (volumetric soil water content 16.5%)	NS		10 DAS	Growth chamber/minirhizotrons	10	From 000 to II	France	Dayoub <i>et al.</i> (2021)
20.0–37.2	28.6	***										
Root tips number	59.0–271.0	165	***				42 DAS	Greenhouse/mesocosms	49	From IV to VIII	USA	Fried <i>et al.</i> (2018)
	406.0–622.0	514	NS				40 DAS	Greenhouse/mesocosms R7	10	From V to VIII	USA	Fried <i>et al.</i> (2019)
	277.0–548.0	412.5	***		*		60 DAS (V3)	Field/root excavation	Field 3	NA	South Africa	Fenta <i>et al.</i> (2014)
	6.5–8.3	7.4	NS	Well-watered (volumetric soil water content 14%) Water stress from V3 (volumetric soil water content)								
	4.7–15.4	10.05	**									
	86–204.3	145.2	***	Well-watered (volumetric soil water content 28%) Water stress (volumetric soil water content 16.5%)			10 DAS	Growth chamber/minirhizotrons	10	From 000 to II	France	Dayoub <i>et al.</i> (2021)
	103.8–217.6	160.7	***									
	168.7–190.5	179.6	NS	Well-watered (volumetric soil water content 14%) Water stress from V3 (volumetric soil water content)	*		60 DAS (V3)	Field/root excavation	3	NA	South Africa	Fenta <i>et al.</i> (2014)
	177.8–377.8	277.8	*									
	0.10–0.54	0.32	***				6 DAG	Growth chamber/germination paper	292	II and III	USA	Falk <i>et al.</i> (2020)
Root volume and primary root volume (cm³)	0.10–0.71	0.405	***				9 DAG					
	1.14–1.20	1.17	***				12 DAG					
	0.22–0.47	0.345	***	Well-watered (volumetric soil water content 28%) Water stress (volumetric soil water content 16.5%)	NS		10 DAS	Growth chamber/minirhizotrons	10	From 000 to II	France	Dayoub <i>et al.</i> (2021)
	0.27–0.46	0.365	***									

Table 2. (continued).

Root traits (per plant)	Cultivar range	Mean	Genotype or cultivar effect	Water regime	Water regime effect	Water regime Other condition	Plant stage, days after sowing (DAS) or days after germination (DAG)	Growth environment/phenotyping method	Cultivar or genotype number	Maturity group	Location	Reference
	0.45–3.52	1.985	*				42 DAS	Greenhouse/mesocosms	49	From IV to VIII	USA	Fried <i>et al.</i> (2018)
	4.56–7.79	6.175	*				40 DAS	Greenhouse/mesocosms	10	From V to VIII	USA	Fried <i>et al.</i> (2019)
	5.90–16.30	11.1	***				R7	Field	10			
	0.07–0.10	0.085	NS	Well-watered (volumetric soil water content 14%)	*		60 DAS (V3)	Field/root excavation	3	NA	South Africa	Fenta <i>et al.</i> (2014)
	0.05–0.16	0.105	**	Water stress from V3 (volumetric soil water content)								
Taproot length (cm)	0.2–38.2	19.2	***				6 DAG	Growth chamber/germination paper	292	II and III	USA	Falk <i>et al.</i> (2020)
	1.7–54.4	28.05	***				9 DAG					
	1.2–68.3	34.75	***				12 DAG					
	18.0–30.5	24.25	*				12 DAS	Greenhouse/plastic tubes	13	NA	Vietnam	Thu <i>et al.</i> (2014)
	36.2–59.3	47.75	*				21 DAS (V3)					
	9.4–30.2	19.8	***				12 DAS	Growth chamber/cones	34	From III to VI	USA	Manavalan <i>et al.</i> (2010)
	20.0–50.0	35	***				21 DAS (V3)	Growth chamber/tubes	8			
	50.0–70.0	60	***				35 DAS					
Total root length (cm)	290.2–227.2	113.7	***				6 DAG	Growth chamber/germination paper		II and III	USA	Falk <i>et al.</i> (2020)
	2.8–566.5	284.65	***				9 DAG					
	0.6–923.3	461.95	***				12 DAG					
	93.9–247.6	170.75	***	Well-watered (volumetric soil water content 28%)	NS		10 DAS	Growth chamber/minirhizotrons	10	From 000 to II	France	Dayoub <i>et al.</i> (2021)
	106.2–241.9	174.05	***	Water stress (volumetric soil water content 16.5%)								
	2942–4107	3524.5	NS				40 DAS	Greenhouse/Mesocosms	10	From V to VIII	USA	Fried <i>et al.</i> (2019)
	646–1949	1297.5	***				42 DAS	Greenhouse/mesocosms	49	From IV to VIII	USA	Fried <i>et al.</i> (2018)
	51.5–56.9	54.2	NS	Irrigated (volumetric soil water content 14%)	*		60 DAS (V3)	Field/root excavation	3	NA	South Africa	Fenta <i>et al.</i> (2014)
	41.0–120.5	80.75	**	Not irrigated from V3 (volumetric soil water content)								
	60.4–110.4	85.4	***				100 DAS	Field	8		China	Zhao <i>et al.</i> (2004)
	70.8–110.4	90.6	***				China					
	132.8–416.6	274.7	***	High phosphorus			Maturity	Field	2	NA	China	Ao <i>et al.</i> (2010)
	81.71–199.1	140.405	***	Low phosphorus								

NS: non-significant, NA: not available.

Table 3. Intraspecific variability in soybean cultivars for investigated architectural root traits.

Root traits (per plant)	Cultivar range	Mean	Genotype or cultivar effect	Water regime	Water regime effect	Other condition	Plant stage, days after sowing (DAS) or days after germination (DAG)	Growth environment/phenotyping method	Cultivar or genotype number	Maturity group	Location	Reference
Rooting depth (cm)	0.2–37	18.6	***				6 DAG	Growth chamber/germination paper	292	II and III	USA	Falk <i>et al.</i> (2020)
	0.3–49	24.65	***				9 DAG					
	0–56	28	***				12 DAG					
	43–56	49.5	*				35 DAS	Field	2	NA	Japan	Matsuo <i>et al.</i> (2013)
	62–93	77.5	*				R1	Field/excavation of rhizotrons to 217 cm deep	7	NA	USA	Kaspar <i>et al.</i> (1978)
	122–167	144.5	*				R3					
	170–208	189	*				R4					
	111–142	126.5	**				54 DAS (R2 to R3)	Field/excavation of rhizotrons compartments	105	From I to III	USA	Kaspar <i>et al.</i> (1984)
	159–186	172.5	**				75 DAS (R5)					
	16–27	21.5	**			High phosphorus	Maturity	Field	2	NA	China	Ao <i>et al.</i> (2010)
21–25	23	**			Low phosphorus							
2.0–90.0	46	***				6 DAG	Growth chamber/germination paper	292	II and III	USA	Falk <i>et al.</i> (2020)	
2.0–90.0	46	***				9 DAG						
2.0–90.0	46	***				12 DAG						
42.9–57.4	50.15	NS		Well-watered	***	10 DAS	Growth chamber/minirhizotrons	10	From 000 to II	France	Dayoub <i>et al.</i> (2021)	
57.7–71.4	64.55	NS		Water stress								
23.3–64.2	43.75	**		Well-watered	NS	60 DAS (V3)	Field/root excavation	3	NA	South Africa	Fenta <i>et al.</i> (2014)	
28.8–68.3	48.55	**		Water stress								
0.1–22.4	11.25	***				6 DAG	Growth chamber/germination paper	292	II and III	USA	Falk <i>et al.</i> (2020)	
0.1–33.8	16.95	***				9 DAG						
0.3–34.3	17.3	***				12 DAG						
15.3–24.6	19.95	*				23 DAS (V1)	Greenhouse/rhizotubes/throughput	9	I	France	Maslard <i>et al.</i> (2021)	
4.8–26.7	15.75	***		High phosphorus		Maturity	Field	2	NA	China	Ao <i>et al.</i> (2010)	
1.33–18.33	9.83	***		Low phosphorus								

NS: non-significant, NA: not available.

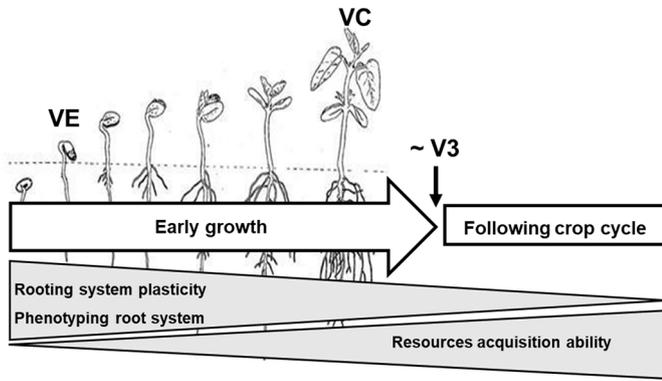


Fig. 2. Schematic representation of the importance of early growth period for resource acquisition, rooting system plasticity and root phenotyping ability (VE, VC and V3 indicates emergence, cotyledon and third-node stage, respectively (Fehr and Caviness, 1977).

correlation was observed between an increase in the length and surface of fibrous roots and nodule number (Pantalone *et al.*, 1996a). In contrast, the number of lateral roots was negatively correlated to the rate of nodulation 23 days after transplanting for a range of soybean cultivars (Maslard *et al.*, 2021). A previous study investigating the potential correlation between root architecture and nodulation found that the deep root genotype had better nodulation than the shallow root genotype but only under high P soil 60 days after planting (Wang *et al.*, 2011). This trade-off between nodulation and root growth, which is due mainly to the competition for carbon (Voisin *et al.*, 2003), needs to be investigated under various growing environments.

6 Root traits involved in drought avoidance

Soybean root traits play a key role for soil resource acquisition and for improved crop performance under abiotic stress including drought or low soil phosphorus availability (Zhao *et al.*, 2004; Ao *et al.*, 2010). The literature (Tabs. 2 and 3) shows that some root traits were modified by the water regime applied but this modification began mainly after early growth period (from V3). An important increase in root tips number, root volume and root length was observed (Fenta *et al.*, 2014; Mwamlima *et al.*, 2019; Dayoub *et al.*, 2021). However, root diameter was decreased under water stress (Mwamlima *et al.*, 2019).

Previous studies found significant correlations in soybean between drought avoidance and root traits such as root biomass, total root length, root volume and number of lateral roots (Liu *et al.*, 2005; Read and Bartlett, 2006). Since soybean yield under drought depends highly on both root depth and root density, deeper rooting system may improve soybean yield. Some soybean cultivars are able to adapt to water stress conditions by developing a deeper taproot and a large and fibrous rooting system and by increasing the root/shoot biomass ratio, which enable to reach deeper soil layers with available water (Manavalan *et al.*, 2009; Boote, 2011). It is well established that root length is one of the main traits that support plants to tolerate the limited water condition during early crop growth stage (Shao *et al.*, 2008).

On the other hand, root nodules are known to be crucial sensors of drought, but their responses and their drought tolerance features remain poorly characterized in the literature for soybean. Root nodule number and size were reduced 60 days after sowing for soybean cultivars under drought (Fenta *et al.*, 2014). Decreased N₂ fixation in response to drought leads to soybean yield losses (King and Purcell, 2001; Sinclair *et al.*, 2010). However, differences exist among cultivars in sensitivity of N₂ fixation to drought (King and Purcell, 2001; Fenta *et al.*, 2014). Some cultivars can maintain more nodules under drought conditions, thus the ability to form and sustain root nodules may also be an important trait underpinning shoot productivity under drought (Fenta *et al.*, 2014). Previous studies showed that a sustained nitrogen fixation is a major trait associated to drought tolerance in some soybean cultivars, which was due mainly to greater nodule size (Pantalone *et al.*, 1996b; King and Purcell, 2001).

Soybean root traits involved in increased water acquisition were defined by:

- deeper rooting (and faster root growth in depth);
- improved distribution of root length density into deeper soil layers;
- increased length per unit root mass;
- increased assimilate partitioning to roots at the expense of shoot growth (constitutive);
- increased biomass partitioning to roots to increase root length density but only when induced by onset of water deficit (adaptive) and delayed onset of seedling growth to increase assimilate to roots (Boote, 2011).

A deeper taproot associated with a high density of lateral roots leads to an increased total root surface area and thus water absorption from soil (Garay and Wilhelm, 1983; Hufstetler *et al.*, 2007; Matsuo *et al.*, 2013). When subject to water stress, soybean cultivars with a shallow root architecture (root angle <60°) tend to decrease the total root length, root surface area and root volume. In contrast, water stress tolerant cultivars show a deep or an intermediate root architecture (root angle >60°) (Fenta *et al.*, 2014). Identifying root traits in soybean cultivars will thus allow to find candidates able to avoid drought that could be an essential step in cultivar adaptations.

7 Potential soybean ideotype for drought avoidance

A recent study investigating a range of soybean cultivars (Fig. 3) commonly grown in France and Europe has proposed an ideotype (Fig. 4) in order to avoid drought represented by a number of traits (morphology and architecture) (Dayoub *et al.*, 2021). This study showed that cultivars characterized by high root depth and length, high root density and narrow root angle could be considered as good candidates to cope with water stress *via* better soil exploration. This study identified cultivar differences at the beginning of crop cycle (10 days after sowing); that will require a further validation later during the crop cycle and under different environments.

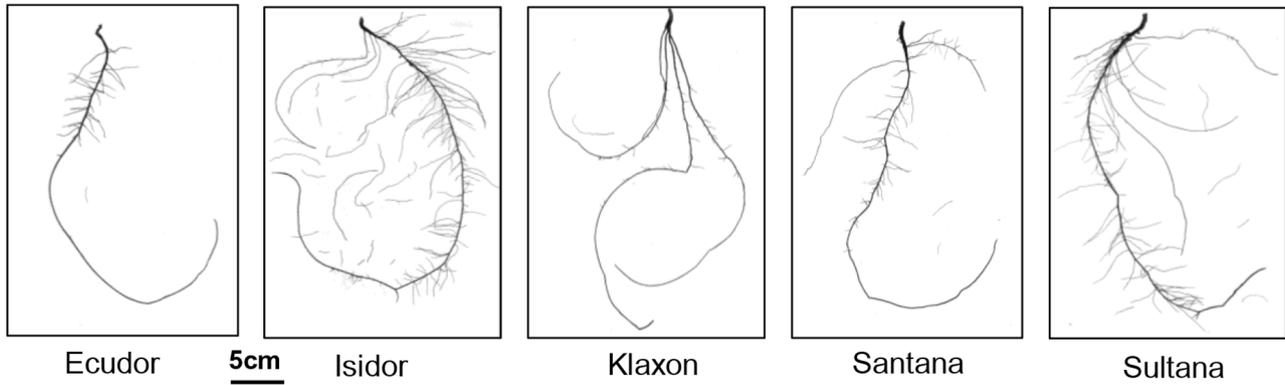


Fig. 3. Overview of different root system morphologies for a range of soybean cultivars at cotyledon stage (VC) (Fehr and Caviness, 1977) (credit: E. Dayoub).

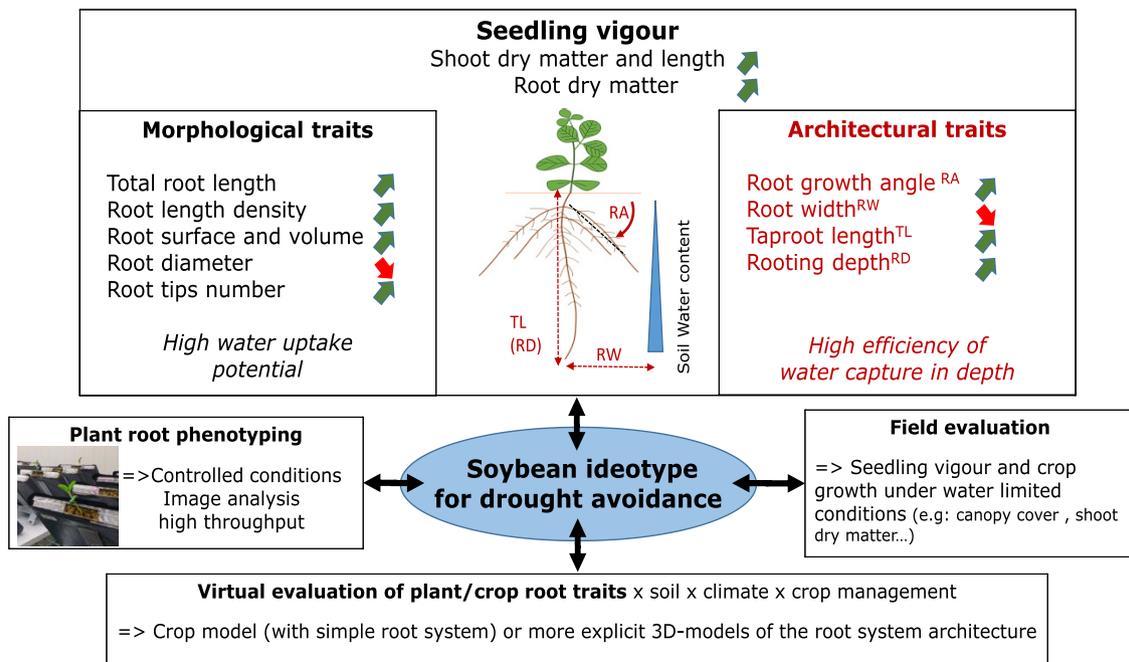


Fig. 4. A framework to designing of a potential soybean ideotype for drought avoidance during early growth. The ideotype is characterized by a high (green arrow) or low (red arrow) value depending on the considered trait.

8 Concluding remarks and perspectives

Wide genetic variability for soybean root traits has been reported in the literature, particularly for root system architecture traits involved in drought avoidance. The cultivars studied were mainly those grown outside Europe and they belonged to later maturity groups than those grown in Europe, the latter ranging from 000(0) to II (III) from North to South of Europe. Soybean cultivars characterized by deeper taproot associated with a high contribution of lateral roots and wide root angle could be considered as good candidates to cope with water stress *via* a better soil exploration. On the other hand, cultivars characterized by shallow rooting system with many lateral roots could be adapted for environments with low soil phosphorus availability (Lynch, 2011; Lynch and Brown,

2001; He *et al.*, 2017, 2021). Future studies should consider these different soil situations in order to find a compromise for root traits adapted for different growing environments.

Root phenotyping techniques are still tedious to study differences in soybean cultivars under field conditions. Consequently, little attention has been paid to date in analysing the phenotypic differences in terms of root morphological, architectural and nodulation traits among European soybean cultivars. Furthermore, the complementarity between structural (morphological and architecture) and functional (water uptake and nutrients acquisition) traits of the root system should be considered in future studies under different conditions. Identifying root traits and classifying soybean cultivars according to these traits could be useful in the selection of cultivars adapted to water-limited environments. Phenotyping methods at early growth stages in the laboratory provide

opportunities for high throughput phenotyping and may explain differences in vigour between soybean cultivars under water-limited field conditions (Dayoub *et al.*, 2021). Screening root traits at early stages in plant development can provide proxy for more advanced stages but such evaluation is needed on a case-by-case basis in order to verify that early traits are related to increased crop productivity under drought conditions (Comas *et al.*, 2013). Research aiming at the design of ideotypes should be encouraged for European soybean cultivars to increase the market availability of soybean cultivars adapted for different sowing conditions. Cultivar differences in root traits reported at early stages could be used as a reference framework for ideotype designing. To this aim, simple trait phenotyping methods under laboratory conditions should be developed and evaluated to assist the selection of drought avoiding soybean cultivars.

Crop growth models could be suitable tools for evaluating and designing ideotypes adapted to a range of environments (Sinclair *et al.*, 2010; Rötter *et al.*, 2015). In most of the 1D field crop models, a limited number of parameters are required for describing the growth of the rooting system and its dynamics under ideal and water-limited conditions (Jones *et al.*, 1991; Calmon *et al.*, 1999; Brisson *et al.*, 2009): *e.g.*, maximum root depth, root front velocity, root length density distribution with depth, fraction of biomass partitioned into roots. However, the parameterization of these models is generally only achievable at species level (*e.g.*, soybean) and seldom at the cultivar level. Due to the progress in phenotyping methods, one can expect to have an easier future access to both above- and below-ground plant parameters with an increased accuracy, a high throughput and for a wide range of inbred lines and cultivars. The evaluation of root traits in young plants (*e.g.*, root angle) could bring useful information for predicting the final development of the rooting system, and thus could be used for the parameterization of crop models at the cultivar level. This will facilitate the virtual evaluation of soybean cultivars across a wider range of environments under current and future climates.

Acknowledgments. The authors thank all partners of the “Sojamip” research project and the UMT Pactole. Special thanks to Béatrice Quinquary, to the other technicians of the Vasco research team (UMR AGIR), and to Terres Inovia, LIDEA, and RAGT 2n for their kind support during this study.

Conflicts of interest. The authors declare that they have no conflicts of interest in relation to this article.

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Cite this article as: Dayoub E, Lamichhane JR, Debaeke P, Maury P. 2022. Genotypic differences in root traits to design drought-avoiding soybean ideotypes. *OCL* 29: 26.