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Studying of genetic diversity for root traits in durum wheat

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BEFORE THE JURY

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TO MY PARENTS AND MY FAMILLY

Scientific publications related to thesis

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ملخص

تنوع السمات الجذرية له أهمية كبيرة في تحسين تحمل الجفاف. هدفت هذه الدراسة إلى تقييم تنوع السمات الجذرية وعلاقتها بأداء النبات في الحقل لمجموعة من اصناف القمح الصلب المحسنة والمحلية في الجزائر. في المجموع اجريت خمس تجارب، باستعمال طرق تقييمية مختلفة خلال النمو المبكر (تجربة اطباق البيتري و المجذر) والنباتات البالغة (تجربة الانابيب و المجرفة) والتقييم في الحقل .عموما، أظهرت النتائج تنوعًا كبيرًا لمجموعة معتبرة من السمات. لوحظ تفوق السلالات المحلية في تحمل الجفاف المبكرعلى حساب الأصناف المحسنة، حيث يظهرتدخل طول غمد الريشة في تحمل الجفاف. تم تحديد أربعة أنماط جذرية للشتلات، حيث تم اظهار انخفاض في طول الجذر ($R^2 = 0.28$) وتزايد في زاوية النمو ($R^2 = 0.19$) عبرالسنين. كان الوزن الجاف للجذور البالغة أكبر في الجزء العلوي، اين أظهرت الاصناف المحلية نموًا أكبر للجذر من الأصناف المحسنة. نمط التوزيع العمودي للكتلة الحيوية الجذرية كان متماثلاً بغض النظر عن نوع الاصناف. على عكس مرحلة الشتلات، في النباتات البالغة اختفى الفرق في زاوية النمو بين الأصناف المحسنة والمحلية. ظهرت بعض الارتباطات المهمة بين طوري النمومثل الكتلة الحيوية ($R^2=0.32$) ، وطول الجذور ($R^2 = 0.19$) ولكن لا توجد في زاوية النمو (MRA). الشتلات ذات TRL أطول مرتبطة بانخفاض المردود الحبي (GY)، والشتلات ذات زواية جذرية (MRA) أوسع مرتبطة بزيادة GY، ويرتبط ارتفاع الكتلة الحيوية في الجذور البالغة بانخفاظ في مؤشر الحصاد. في الحقل الجفاف كان اكثرحدة فى إنقاص الكتلة الحيوية ومردود الحبوب 76.14 و67.06٪ على التوالي. عدد الحب في المتر المربع ووزن الالف حبة ساهمو بالقدرالاكبر (< 99٪) في تفسيرالتغيرفي محصول الحبوب في السنة الرطبة والجافة. الاصناف المحلية كانت الاكثر انتاجا للكتلة الحية في الجفاف بينما الاصناف المحسنة اعطت اعلى مردود في الموسم الممطر. كشفت هذه الدراسة عن فائدة الاصناف المستعملة في تحسين القمح الصلب بناءً على سمات الجذور، الاصناف المحلية تشكل مصدراً هاماً لتحسين قوة النمو و امكانية تحمل الجفاف المبكر. التهجين بين الاصناف المحلية والمحسنة قد يسمح بالحصول على أنماط وراثية ذات محصول عالي ومستقرتحت الظروف المناخية شبه الجافة.

الكلمات المفتاحية: المناخ المتوسطي ، عمق الجذر، نمو الجذر، المرونة ،.برنامج SmartRoot

Abstract

Root diversity is of great importance in breeding for drought tolerance. This study aimed to evaluate root trait diversity and their relevance to field performance of a set of durum wheat cultivars and local landraces in Algeria. In total, five experiments were carried-out with different phenotyping root systems at seedling stage (Petri dishes and rhizo-slides), at adult stage (pipe-pots and shovelomics), and agronomic field trials. Overall, our results showed sizeable diversity for a wide array of traits. Differences in early traits were observd between landraces and cultivars, with the former presenting longer coleoptiles, a trait related to drought tolerance. Four seminal root patterns were identified in seedlings, with landraces showing overall steeper root angle (MRA) and higher root length (TRL), in comparison with cultivars. Several trends of change in traits over time were revealed, like a reduced TRL (R^2=0.28) and increased MRA (R^2=0.19). Biomass of mature roots was highest in the topsoil, and landraces showed higher overall root development than cultivars. The vertical root biomass distribution pattern was similar regardless of variety type. Unlike at seedling stage, in adult plants the difference of MRA between cultivars and landraces disappeared. Some appreciable correlations were found between seedlings and adult plants, like for shoot biomass (R^2=0.32), and root length (R^2=0.19), but not for root angle (MRA). In seedlings, longer TRL tended to be associated with lower grain yield (GY), wider MRA appeared associated to increased GY, and higher biomass of adult roots was related to lower harvest index. In the field trials, drought reduced markedly both the biomass and grain yield (GY), 76.14 and 67.06%, respectively. Grain number per area and thousand kernel weight explained the most variation (>99%) of GY in both the wet and drought years. Landraces had higher biomass under drought and cultivars out-yielded landraces under wet year. This study revealed the usefulness of the current germplasm in wheat breeding based on root traits. Landraces are an important source for shoot and root growth vigor and, potentially, early drought tolerance. Crosses between landraces and cultivars could result in genotypes with stable and enhanced grain yield across a wide range of semiarid conditions.

Keywords: Mediterranean environment, root depth, root growth, resilience, SmartRoot.

Résumé

La diversité des racines est d'une grande importance dans l'amélioration génétique à la tolérance à la sécheresse. Cette étude visait à évaluer la diversité des caractères racinaires et leur pertinence à la performance au champ d'un ensemble des cultivars et variétés locales de blé dur en Algérie. Au total, cinq expérimentations ont été réalisées avec différent systèmes de phenotypage des racines au stade précoce (boite de Petri et rhizo-slide) et adulte (pipe-pots et shovelomics) et essais agronomiques. En général, nos résultats ont montré une grande diversité pour l'ensemble des traits. Une meilleure tolérance précoce à la sécheresse a été observée chez les variétés locales, où la longueur des coléoptiles a été avantageuse. Quatre ideotypes des racines séminales ont été identifiés, en général, les variétés locales montrant des racines à angle (MRA) plus aigu et à longueur (TRL) plus elevée que les cultivars. Des tendances de changement de traits ont été revelée au fil des années comme la reduction de TRL (R^2=0.28) et l'augmentation de MRA (R^2=0.19). La biomasse des racines adultes a été plus élevée dans la couche arable, où les variétés locales disposaient de biomasse racinaire plus élevée que celle des cultivars. Le profil de distribution vertical de la biomasse racinaire a été similaire quel que soit le type de variété. Contrairement au stade précoce, au stade adulte, la différence d'angle de croissance des racines entre les cultivars et les variétés locales a disparu. Queleques corrélations appréciables ont été trouvées entre les deux stades de croissance comme la biomasse (R^2 = 0,32), et longuer des racines (R^2 = 0,19), mais non pour l'angle de croissance racinaire MRA. Au stade plantule, une TRL plus longue a été associée avec un rendement reduit (GY) et un angle obtus est associé avec un GY elevé, et une grande biomasse des racines adultes est liée à un indice de récolte réduit. Au champ, la sécheresse a réduit plus la biomasse et le rendement en grains (GY), 76,14 et 67,06%, respectivement. Le nombre de grains par m^2 et le poids de mille grains expliquent la plus grande variation (> 99%) du GY pendant l'année pluvieuse et de sécheresse. Les variétés locales ont produit une biomasse plus élevée sous la sécheresse, et les cultivars ont excellée les variétés locales en GY pendant l'année pluvieuse. Cette étude a révélé l'utilité du germoplasme actuel dans l'amélioration de blé dur sur la base des racines, dont les variétés locales constituent une source importante pour la vigueur de la croissance et potentialememnt une tolerance de sechresse précoce. Le croisement entre les variétés locales et les cultivars aboutirait à des génotypes avec un rendement en grain amélioré et stable sous conditions semi-arides.

Mots clé : environnement Méditerranéen, profondeur racinaire, croissance racinaire, résilience, SmartRoot.

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Liste of abbreviations

Ach	Area of the convex hull
Biomass	Total biomass
C	Control
CL	Coleoptile length
CT	Canopy temperature
Cv	Coefficient of variation
Depth	Root depth
Diameter	Mean root diameter
DSI	Drought susceptibility index
DTA	Days to anthesis
DTH	Days to heading
Emg	Emergence
Ff	Filling factor
FGP	Final germination percentage
FLA	Flag leaf area
FLDW	Flag leaf dry weight
FLFW	Flag leaf fresh weight
FLL	Flag leaf length
FLW	Flag leaf width
GNM^2	Grain number per area
GNS	Grain number per spike
GY	Grain yield
h^2	Broad heritability
HGY	Harvested grain yield
HI	Harvest index
LRM	Leaf rolling in morning
LRN	Leaf rolling at noon
LVA	Least vertical angle
mFD	Mean fractal dimension
mGZ	Median gap size
MRA	Mean root angle
MRL	Maximum root length
mSW	Median structure width.
MVA	Maximum vertical angle
mW	Maximum width
NaOCl	Sodium hypochlorite
NoG	Number of gaps
NRN	Nodal root number
ns	Not significant
PC	Principal component
PEG	Ploy ethylene glycol
PH	Plant height
PRL	Primary root length
RA	Root area
RDW	Root dry weight

RDW>60	Root dry weight for depth more than 60 cm
RDW30	Root dry weight up to 30 cm of depth
RDW60	Root dry weight between 30 and 60 cm
Redu	Reduction
REML	Restricted maximum likelihood
REST	Root estimator shovelomics traits (software)
RN	Root number
RoA	Root opening angle
RoA_f	Root opening angle measured by protractor
RoA_i	Root opening angle measure by imag j
RS	Root system
RSA	Root system architecture
RSL	Root to shoot length
RSR	Root to shoot ratio
RSW	Root to shoot weight
RWC	Relative water content
S	Stress
SDW	Shoot dry weight
SE	Standard error
SGY	Sample grain yield
SL	Shoot length
SLA	Specific leaf area
SN	Spike number
SNM^2	Spike number per area
Spkbio	Spike biomass
SpkDW	Spike dry weight
SRN	Seminal root number
StmDW	Stem dry weight
Surface	Total root surface area
SVI_l	Seedling vigor index based on seedling length
SVIw	Seedling vigor index based on seedling weight
SWM^2	Spike weight
T	Type
t50	Time needed to reach 50 % of germinated seeds
TKW	Thousand kernel weight
TN	Tiller number
TPB	Total plant biomass
tpSL	Total projected structure length
TRL	Total root length
TRN	Total root number
Trt	Treatment
TSP	Triple superphosphate
Volume	Total root volume

1. General introduction

1.1. Context and objectives of the study

Climate change is predicted to increase challenging environmental conditions for agriculture, such as drought and heat stress. This will be coupled with an expanding global population demanding more food, thus improving crop productivity and yield stability is crucial (Lobell *et al.* 2011; Tilman *et al.* 2011; Dai 2013; Asseng *et al.* 2015; Lobell *et al.* 2015). Durum wheat is one of the main sources of daily caloric intake and a major staple crop in the Mediterranean region. It is known for its unique quality characteristics, in particular high protein content and hard kernels that make it ideal for pasta, couscous, and bourghul manufacturing (Able and Atienza 2014; Habash *et al.* 2014; Kezih *et al.* 2014; Stuknytė *et al.* 2014). Wheat is prevalently grown under rainfed conditions in regions where drought is the major environmental factor limiting productivity. Furthermore, the Mediterranean region is predicted to lose 30% of its in-season rainfall in the next decades, which contribute to worsening the growth conditions of crops in this region (Christensen *et al.* 2007). Drought affects wheat at all vegetative stages. Early drought restricts germination (Misra *et al.* 2002), emergence and early seedling growth (Al-Karaki 1998), which may lead to crop failure, particularly in the West Asia and North Africa (WANA) region (Abdel-Ghani *et al.* 2015). Drought occurring late in the season, coincident with flowering and grain filling periods, is the most frequent in the Mediterranean region; it can dramatically affect yield and grain quality (Loss and Siddique 1994; Belaid 2000; Mohammadi *et al.* 2011; Bassi and Sanchez-Garcia 2017).

Root system architecture (RSA) plays a pivotal role in crop performance, particularly for cultivation under non-optimal water and nutritional supply conditions (Ludlow and Muchow 1990; de Dorlodot *et al.* 2007; Paez-Garcia *et al.* 2015). In the past decade, RSA has received increasing attention in cereals (Hochholdinger and Tuberosa 2009; Wasson *et al.* 2012, 2014; Bishopp and Lynch 2015), leading to the development of detailed RSA ideotypes (King *et al.* 2003; Lynch 2013; Meister *et al.* 2014). In rice, a narrow and deep root ideotype for enhancing drought resistance has been successfully pursued based on direct field observation of root distribution (Steele *et al.* 2013; Uga *et al.* 2013) and root growth angle (RGA) measurements in rhizotrons (Kitomi *et al.* 2015). In sorghum, stay-green genotypes have contributed additional evidence for the positive role on yield of narrow RGA quantitative trait loci (QTLs) under drought conditions (Borrell *et al.* 2014). In wheat, narrow root growth angle was associated to enhanced grain yield under water-limited environments (El Hassouni *et al.* 2018).

On the other hand, a root system well-developed at shallow depths is also important for the acquisition of phosphorus, a low-mobility nutrient usually more abundant in the upper soil layer (Miguel *et al.* 2015).

During the last years, the advancement in root research was made possible due to the development of several phenotyping methods, which were designed to discover the hidden part of the plant, which has been neglected for too long. The search for potential useful root traits in landraces is an important issue since they are well adapted to the regions where they were grown, and contain large genetic diversity useful to improve crops, like durum wheat (Nazco *et al.* 2012). These landraces were replaced (partly or totally, depending on the region) by high yielding semi-dwarf cultivars, better adapted to modern agriculture. However, scientists are convinced that local landraces still constitute a genetic resource useful to improve commercially valuable traits (Lopez *et al.* 2015). As a proof, they are still preferred over modern wheats in several parts of the world, mainly for their stable yields in low input conditions, prized end-use qualities, and high straw yield. Farm size, lack of machinery, and lack of fertilizer are also important constraints in growing modern wheats (Karagöz 2014).

Despite the increasing interest in the study of roots, few studies have been devoted to roots in Algeria, with a limited number of genotypes, mostly in studies without connection to plant performance in the field. The current thesis addresses the study of root system features in a large set of durum wheat genotypes, including local landraces and cultivars of different origins that have been cultivated over the Algerian agricultural history. Five experiments were carried out under controlled and field conditions to achieve the following objectives:

- Studying the early drought tolerance of durum wheat seedlings
- Evaluation of the diversity of seminal root traits
- Evaluation of root traits at adult plants in controlled and field conditions
- Evaluation of the performance of genotypes under rainfall contrasting conditions
- Testing the relation of root traits with field plant performance

1.2. Origin and spread of durum wheat

Tetraploid wheat domestication took place about 12,000 years ago in the Fertile Crescent. The process began by selecting emmer naked type (*Triticum turgidum* ssp. dicoccum) that was easy to thresh (MacKey 2005; Tanno and Willcox 2006; Zohary *et al.* 2012), grown among cultivated forms of wild of emmer (*Triticum turgidum ssp.* dicoccoides). Approximately 2,000 years after this event, the cultivation of naked emmer started spreading throughout Europe and Asia during the human migration and the spread of agriculture from the Fertile Crescent. During the same period, durum wheat (*Triticum turgidum ssp.* durum) appeared in the Fertile Crescent, as result of further selection and domestication of naked emmer (Zohary *et al*. 2012). Durum wheat progressively replaced its ancestor to become, by the second millennium BC, the major cultivated form of tetraploid wheat, due to its larger grains and higher productivity (Maier 1996; Nesbitt and Samuel 1998; Zohary *et al.* 2012). Therefore, durum wheat origin is the result of two successful domestication events by ancient farmers, first from wild emmer to domesticated emmer, and second from cultivated naked forms of emmer to durum (Gioia *et al,* 2015).

The Levant is considered to be the center of origin of this crop (Vavilov 1951; Feldman 2001). From there, it spread throughout the Mediterranean basin, probably via trading by Phoenician merchants, by the caravans' routes along the Sahara desert or the North African coasts (Bozzini 1988), and the Silk Road to Asia (Waugh 2010). Reports suggested, that durum wheat was also domesticated a third time (Mengistu *et al.* 2015, 2016) to derive *Triticum aethiopicum* Jakubz. (syn. *Tritium durum subsp.* abyssinicum Vavilov), which is mainly found today under cultivation in Ethiopia and neighboring countries. It remains yet unclear if this additional domestication was the result of further modification by farmers of a durum landrace population originated in the Levant, or rather if it represented a novel origin of durum by a separate domestication of naked emmer. What is clear is that the abyssinicum subspecies is morphologically very different, with uncompact spikes and small dark seeds (Sakamoto and Fukui, 1972; Porceddu *et al.* 1973; Pecetti *et al.* 1992; Mengistu *et al.* 2015).

1.3. Wheat landraces

An autochthonous wheat landrace is defined as a traditional variety with a high capacity to tolerate biotic and abiotic stresses, resulting in high yield stability and an intermediate yield level under a low input agricultural system (Zeven 1998). Wheat landraces were established during the process of domestication and spread of wheat from the East to the West of the Mediterranean, where natural and human selection favored new adaptive traits suitable for new environments (Mercer and Perales 2010; Charmet 2011; Peng *et al.* 2011). Traits related to easy harvest as large seed, no shattering plants (Fuller 2007), or flowering time fit to the prevailing environmental conditions of the region (Cockram *et al.* 2009), were probably primarily targeted by farmers. It has also been suggested that many other traits, such as plant height, number, and weight of spikes and grains, were co-selected by ancient farmers (Peng *et al.* 2011).

Consequently, these landraces were specifically adapted to their region of origin, representing a diversity of agro-ecological zones, and are considered the most important sources of biodiversity within the species (Nazco *et al.* 2012). Landraces were largely cultivated before the early 1970s, where progressively abandoned and replaced with improved, genetically uniform semi-dwarf cultivars as consequence of the Green Revolution (Ortiz *et al.* 2007). However, scientists still believe that local landraces represent an important group of genetic resources for the improvement of commercially valuable traits (Lopes *et al.* 2015). Durum wheat Mediterranean landraces are considered as resources for contemporary agriculture to increase the genetic diversity of modern cultivated varieties and to improve their adaptation to regions affected by biotic and abiotic constraints (Soriano *et al.* 2018).

1.4. Wheat production

Durum wheat (*Triticum durum* Desf.) is an important food crop, with an estimated 36 million tons of annual global production (Chris 2017). The largest producing countries are Turkey and Canada with estimated 2 million ha^{-1} each (Statistic Canada; USDA Foreign Agricultural Service 2017), followed by Algeria, Italy and India, each cultivating over 1.5 million ha^{-1} (Nagarajan *et al.* 2006; Le lamer *et al.* 2011; Bonjean *et al.* 2016). Syria belonged to this group of large producers but the recent unrest has strongly reduced its crop production. France, Greece, Morocco, Pakistan, Portugal, Kazakhstan, Russia, Spain and Tunisia, each cultivate durum wheat on between 0.5 and 0.8 million ha^{-1} annually (USDA Foreign Agricultural Service 2017). Azerbaijan, Iraq and Iran combined grow durum wheat on over 0.7 million ha^{-1} (Bonjean *et al.* 2016). In addition, Egypt, Jordan and Lebanon grow it on relatively large areas (Al Aissa *et al,* 2006; Karam *et al.* 2009; El-Areed *et al.* 2014). The Sonora desert and other small areas of Mexico also target the production of this crop for the export market on approximately 0.2 million ha^{-1} (Juarez *et al.* 2015). Australia is similarly exploring the cultivation of this crop with 0.1 million ha^{-1} allocated annually to its production (John *et al.* 2013). In sub-Saharan Africa (SSA), Ethiopia is the largest producer of durum wheat, with approximately 0.6 million ha^{-1} (Evan School Policy Analysis and Research 2012).

1.5. Wheat growth and development

Wheat is a cool season crop, widely grown between the latitudes 67° N and 45° S (Gustafson *et al.* 2009) in diverse environments from temperate to tropical and from sea level to high altitude under irrigated or rainfed cropping systems (Curtis *et al.* 2002). Temperature is among the factors mostly controlling growth and development of wheat (Porter and Gawith 1999). Each developmental stage requires a sum of daily temperature to be accomplished, where only temperatures between the two thresholds of base and optimum temperature (cardinal temperatures), are accounted. There is variation in the requirements of cardinal temperature between phenological stages and genotypes; however it raises steadily with plant development. Accordingly, base values increase from less than 0° to more than to 7°C during grain filling, while optimum values rise from less than 22° to more than 25°C (Slafer and Rawson 1995; Porter and Gawith 1999; Salazar-Gutierrez *et al.* 2013).

Vernalization is the acquisition of the competence to flower, accelerating development, by the exposure of sensitive cultivars to cool temperatures during the early stages of crop ontogeny (Slafer *et al.* 2015). Qualitatively, wheat cultivars are classified as two general types: winter wheat, with a variable low-temperature requirement to reach a proper flowering time (vernalization requirements) and thus successful grain reproduction, and spring wheat, without this requirement (Chouard 1960; Pugsley 1971; Amasino 2004). Quantitatively, winter wheat cultivars are classified as three types according to the low temperature duration required to reach the vernalization saturation point or to achieve the maximum vernalization effect: a weak winter type that is stimulated to flower by brief exposure to low temperature (for <2 weeks); a semi-winter type that requires 2–4 weeks of cold exposure for flowering; and a strong winter type that requires more than 4 weeks of cold exposure for timely flowering (Crofts 1989). Maximum vernalization usually occurs from 0° to 8°C (Chouard 1960; Pugsley 1971; Crofts 1989; Amasino 2004), although the exact interval of temperatures is disputed (Monneveux *et al.* 2012). Thus, winter wheat is sown in autumn, in mild weather to foster germination and early development. Young plants then experience decreased temperature and reduced growth over winter, and growth is resumed in the early spring. In contrast, spring wheat does not require vernalization and it can be planted in spring. However, it can also be sown in autumn in countries with mild winters, such as in South Asia, North Africa, and the Middle East (Monneveux *et al.* 2012). In wheat, the transition from vegetative to reproductive phase is coincident with ceasing of tillering (Baker and Gallagher 1983) and beginning of stem elongation, in which spikes and culms concurrently grow and compete for assimilates supply (Miralles *et al.* 2000).

After vernalization is completed, genotypes, which are sensitive to photoperiod, require a certain day-length to flower. Sensitivity to photoperiod differs among genotypes. Most cultivated wheats, however, are quantitative long-day plants. They flower faster as the day-length increases, but they do not require a particular length of day to induce flowering (Evans *et al.* 1975; Major and Kiniry 1991). The development of the inflorescence after induction occurs at a rate that is also dependent on day length in those genotypes sensitive to photoperiod (Stefany 1993). The shorter the day is, the longer the phase is from double ridge to terminal spikelet, increasing the period to terminal spikelet and the number of spikelets per spike. Changes in day length after the terminal spikelet have no effect on floret initiation or anthesis date (Acevedo *et al.* 2002).

1.6. Drought in the Mediterranean

1.6.1 Drought effect

Drought stress can be defined as a shortage of water, which induces dramatic morphological, biochemical, physiological, and molecular changes. All of these changes reduce plant growth and crop production (Sallam *et al.* 2019). The progress achieved by plant breeding in Mediterranean environments has been slower than in other regions (Slafer *et al.* 1993), probably because of the limitations that the Mediterranean environment places on plant growth, in particular, water stress. In Mediterranean environments, rainfall is unpredictable, water shortage can occur at any growth stage; sowing time, early spring, during flowering time and may extend up to grain filling. Therefore, drought tolerance for genotypes should be tested at various growth stages because tolerant genotype at early growth does not mean that it is also tolerant at final stages and *vice versa* (Sallam *et al.* 2019).

In wheat and barley, germination and seedling growth are drought sensitive stages (Srivastava *et al.* 2003). In Mediterranean-type environments, sowing is typically practiced when soil moisture is ensured by the first rain (Rebetzke *et al.* 2008a), where the rainfall after emergence is an uncertain event (El Hafid *et al.* 1998). Therefore, the germination and seedling growth can be negatively affected, which subsequently compromises later stages and, ultimately, grain yield (Gallagher *et al.* 1976). In such cases, drought (early drought) exerts even stronger negative effects on yield, impacting yield potential at the sink level, for example by decreasing the number of fertile spikes per unit area at the crop establishment and tillering phases, as well as the number of grains per spike (Garcia del Moral *et al.* 2003; Annicchiarico *et al.* 2005; Alvaro *et al.* 2008).

Terminal drought is the most frequent factor curtailing durum wheat yield in the Mediterranean basin, and is due to limited soil moisture availability during heading and grain filling periods, which are the most critical phases for grain yield and quality (El Hafid *et al.* 1998; Araus *et al.* 2003a,b; Garcia del Moral *et al*. 2003; Royo *et al.* 2006). This yield reduction occurs mostly through the negative effect on grain weight and grain volume (Araus *et al.* 2003a, b; Slafer *et al.* 2005). Usually, terminal drought is paired with heat stress as a trademark of the Mediterranean region (Loss and Siddique 1994; Acevedo *et al.* 1999).

1.6.2. Adaptive drought strategies

There are three main responses of plants to water stress: escape, avoidance (or resistance) and tolerance (Levitt 1972). Yield improvement by breeding for drought resistance mechanisms depends strongly on the drought regime i.e. drought duration, severity and time of occurrence (van Ginkel *et al.* 1998; Farooq *et al.* 2009, Blum 2011a).

Escape is mainly related to the adjustment of plant phenology, to avoid heat and drought stress period. Thus, the focus of this strategy is developing early maturing wheat genotypes as an adaptive mechanism for environments in which terminal heat and drought stress prevail (Motzo and Giunta 2007; Mondal *et al.* 2016). Most modern wheat genotypes incorporated vernalization and photoperiod insensitive genes to promote early flowering and maturity (Chen *et al.* 2016). Breeding strategies to replace the winter-type alleles, especially *Vrn-A1* and *Vrn-D1* loci associated with late heading times (Zhang *et al.* 2008), has been recommended to develop early-flowering cultivars for water-limited environments. Nevertheless, in some cases, yield increase was not associated with earlier flowering in wheat (Chairi *et al.* 2018; Flohr *et al.* 2018). The limited genetic gains incorporating early maturity may be due to reduced time available for assimilate partitioning required for high grain yield development (Royo *et al.* 2007), partly explained by the negative association between kernel weight per spike and heading date (Zhou *et al.* 2007).

Dehydration avoidance involves the changes by which plants maintain high tissue water potential. For example, closure of stomata, to reduce gas exchange, and avoid water loss through evapotranspiration, is a response often seen in leaves of water savers genotypes under stress. However, closing stomata under water stress also implies lower respiration rates and reduced assimilation of carbon dioxide. It can lead to uncoupling of photosynthesis and carbon fixation rates, and over-heating of the photosynthetic apparatus, especially when drought turns up along with heat, which is very common in the field (Ceccarelli and Grando 1996). Alternatively, water spenders genotypes can maintain high tissue water through reducing water loss and/or improving water uptake (Farooq *et al.* 2009), thus they maintain their photosynthetic activity active even under water stress.

Drought tolerance is the ability to withstand water-deficit with low tissue water potential. Osmotic adjustment (Moinuddin *et al.* 2005) and effective use of water (Blum 2009) are often associated to drought tolerance. Osmotic adjustment is achieved through accumulation of solutes (Serraj and Sinclair 2002; Nguyen *et al.* 2004). It enables plants to maintain water absorption and cell turgor pressure, leading to sustained photosynthetic rate, and expansion growth (Ali *et al.* 1999). The presence of water-soluble carbohydrates (WSC), of stems and leaf sheaths, significantly improved yield gains in wheat (Shearman *et al.* 2005; Foulkes *et al.* 2007). In addition, significant correlation has been reported between grain yield and preanthesis radiation-use efficiency in wheat (Shearman *et al.* 2005), which suggested that genetic gain in wheat yield is driven by improved growth rate due to increased accumulation of WSC (Shearman *et al.* 2005). Genotypes with high WSC are commonly shorter, flower and mature earlier, and produce significantly fewer tillers than those with low WSC (Rebetzke *et al.* 2008b).

Effective use of water, a concept different from water-use efficiency (WUE), implies enhanced moisture conservation and acquisition, to be used for transpiration. It involves improved water uptake, provided by both osmotic adjustment and deep root systems (Blum 2009), combining the two avoidance mechanisms of water savers and water spenders genotypes. Deep roots are especially useful with terminal drought (Mitchell *et al.* 1996; Kirkegaard *et al.* 2007), and thus it is an interesting mechanism for winter cereals in the Mediterranean region.

1.7. Agronomic traits in wheat breeding

Agronomic traits can be used as indirect selection criteria during breeding and cultivar development (Chen *et al.* 2012; Abdolshahi *et al.* 2015; Liu *et al.* 2015; Gao *et al.* 2017), due to their higher heritability than, and correlation with, grain yield. It has been suggested that genetic progress in yield can be achieved if several traits conferring better agronomic and physiological performance with biotic and abiotic stress tolerance are simultaneously selected and introgressed in a single variety (Lopes *et al.* 2012). Some of these traits are presented below:

1.7.1. Early flowering and maturity

The development of early maturing wheat genotypes can be an adaptive mechanism for environments experiencing terminal heat and drought stress (Motzo and Giunta, 2007; Mondal *et al.* 2016). The early flowering and maturity genotypes was achieved by the incorporation of vernalization and photoperiod insensitive genes in most modern wheat genotypes (Chen *et al.* 2016). The negative and significant correlations between days to flowering and grain yield potential suggests that breeding for high yielding and early maturing wheat genotypes can further be achieved by manipulating wheat phenology (Kamran *et al.* 2013; Mondal *et al.* 2016). Therefore, to increase grain yield potential, such earlier genotypes should have faster growth rates and accumulate sufficient biomass production in shorter times, is a difficult goal.

1.7.2. Plant Height

Breeding novel wheat genotypes with reduced plant height has increased genetic gains in wheat and significantly contributed to increased wheat productivity globally (Beche *et al.* 2014; Gummadov *et al.* 2015; Würschum *et al.* 2015; Zhang *et al.* 2016). The dwarfing/height reducing genes have been used in many breeding programs to develop genotypes with reduced plant height (Zheng *et al.* 2011; Green *et al.* 2012; Lopes *et al.* 2012; Joudi *et al.* 2014; Zhang *et al.* 2016; Chairi *et al.* 2018). By reducing coleoptile and internode length, and plant height (Rebetzke *et al.* 2011; Rebetzke *et al.* 2012 a,b), these genes increase assimilate partitioning to the ear (Grover *et al.* 2018), resulting in higher harvest index (HI) and lodging resistance (Divashuk *et al.* 2013). Different range of plant height reductions were reported when replacing old by recent and short plant height wheat cultivars, from 130 to 60 cm in China (Gao *et al.* 2017), 120 to 57 cm in Italy (De Vita *et al.* 2007), and from 125 to 65 cm in Spain (Royo *et al.* 2007).

1.7.3. Biomass production

The increased of biomass has resulted in grain yield improvement in wheat. It has been suggested that further improvements in grain yield can be achieved by increasing photosynthetic capacity by optimizing biomass production while maintaining lodging resistance (Beche *et al.* 2014). While several studies showed the positive effect of biomass on grain yield (Shearman *et al.* 2005; Xiao *et al.* 2012; Bustos *et al.* 2013; Aisawi *et al.* 2015; Gao *et al.* 2017), others studies indicated very little contribution of this trait (Royo *et al.* 2007; Tian *et al.* 2011; Zheng *et al.* 2011; Sun *et al.* 2014; Zhang *et al.* 2016). Reynolds *et al.* (2017) reported that crossing complementary genotypes exhibiting high biomass and HI may improve gains yield in wheat than crossing only high yielding genotypes.

1.7.4. Kernel weight

Grain yield improvement has been significantly associated with increased thousand kernel weight (TKW) (Zhou *et al.* 2007; Morgounov *et al.* 2010; Tian *et al.* 2011; Zheng *et al.* 2011; Lopes *et al.* 2012; Aisawi *et al.* 2015). However, non-significant contribution of TKW were reported in other studies (Shearman *et al.* 2005; Royo *et al.* 2007; Acreche *et al.* 2008; Brisson *et al.* 2010; Xiao *et al.* 2012), especially under heat stress condition limiting the selection response for this trait under low-yielding environments (Lopes *et al.* 2012; Sharma *et al.* 2012). Breeding for high grain number and TKW has been reported to be difficult due to trade-offs. Gaju *et al.* (2009) suggested to minimize the trade-off effect by selecting genotypes with higher number of spikelets per spike, which resulted in spikes with higher grain number and heavier TKW. Bustos *et al.* (2013) proposed crossing genotypes with contrasting grain number and grain weight to combine both traits in the progeny.

1.7.5. Number of grains per spike

Many studies reported the increased grain yield as result of higher grain number (Tian *et al.* 2011; Flohr *et al.* 2018; Liu *et al.* 2018), whereas in some instances it was not associated with genetic progress in grain yield (Zhou *et al.* 2007; Xiao *et al.* 2012; Gao *et al.* 2017). Grain number was reported to be higher in wheat cultivars than landraces in USA (Green *et al.* 2012) and China (Zhang *et al.* 2016). The relationship between grain yield and grain number is reportedly curvilinear in some instances suggesting that the strategy for increasing grain yield through higher grain number could be less efficient (Sadras and Lawson 2011; Bustos *et al.* 2013). On the contrary, the linear relationship reported between grain number per spike and grain yield suggests the possibility of using this trait for improving grain yield potential in some instances (Tian *et al.* 2011; Qin *et al.* 2015).

1.8. Root system architecture

Root system architecture (RSA) is a term that describes the pattern of distribution of roots within the soil profile through space and time (Lynch 1995). The importance of RSA in plant productivity lies in the fact that major soil resources are heterogeneously distributed in the soil, so that the spatial deployment of roots will substantially determine the ability of a plant to secure edaphic resources (Lynch *et al.* 1995).

1.8.1. Root system architecture in wheat

Cereal root systems are composed of axes arising first from primordia in the seed (the seminal or primary roots) and subsequently from the nodes of the main stem and tillers (the nodal, adventitious or crown roots) (Chochois *et al.* 2015; Sinha *et al.* 2018). Both types of roots play a crucial role for plant growth and are active throughout the whole plant life. Seminal roots include one primary root, two pairs of symmetric roots at each side (Figure 1.1), and, at times, a sixth central root (Esau 1965). The number of seminal axes is mainly determined genetically, although seed size can have an effect, and generally from 3 to 6 seminal axes are produced (Figure 1). The number of nodal axes depends largely on environmental conditions and can be up to 100 or more per plant, but under field conditions 10-25 per plant is more usual (Gregory *et al.* 1978; MacKey 1973). According to Krassovsky (1926), the seminal roots served principally the main stem whereas the nodal roots served the tillers.

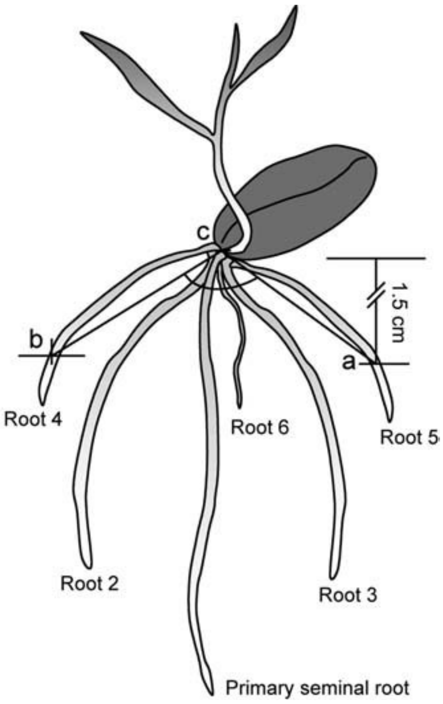

Figure 1.1. A schematic representation of the seminal root apparatus in wheat. Besides the primary seminal root, the two symmetric different root pairs (roots 2–3 and roots 4–5) are represented; the additional sixth seminal root has also been represented. The figure also depicts the spread angle of the seminal roots, a trait measured as the angle between the intersections of root 4 and root 5 as indicated in the scheme (Sanguineti et al. 2007).

1.8.2. Importance of root system in drought tolerance

The central importance of root systems in the acquisition of water and nutrients by plants has meant that they have become a focus of plant breeders and crop improvement programs (Del Bianco and Kepinski 2018). Accordingly, there has been a growing interest in the study of plant root systems, with much attention devoted to the adaptation to water stress (Manschadi *et al.* 2006; Christopher *et al.* 2008; Gregory *et al.* 2009; Asif and Kamran 2011, Wasson *et al.* 2014; Boudiar *et al.* 2020). Root length, root density and root depth are known as the major root system traits for the extraction of the deep stored water (King *et al.* 2003; Asif and Kamran 2011; Carvalho *et al.* 2014). In addition, other potential traits were also highlighted including increased root distribution at depth to improve deep water capture (O'Brien 1979; Manske and Vlek 2002), fast root elongation rates for deep water capture (Hurd 1974; O'Brien 1979), reducing the diameter of the xylem vessel in the seminal roots to conserve soil water (Richards and Passioura 1989), acute angle of seminal roots for extracting water from full soil depth (Nakamoto and Oyanagi 1994; Manschadi *et al.* 2006) and improve the root:shoot dry matter ratio to improve water capture across the soil profile (Siddique *et al.* 1990; Reynolds *et al.* 2007).

Special attention is being given to traits such as branching and growth angle, which determine the distribution of root surface area within the soil profile where nutrients and water are unevenly distributed (Nakamoto *et al.* 1991; Oyanagi *et al.* 1993; Oyanagi 1994; Lynch 2011; Borrell *et al.* 2014). Therefore, in terms of selection and breeding, the target environment and dominant pattern of moisture stress needs to be defined and understood before an appropriate root morphology can be considered (Palta *et al.* 2011). For instance, El Hassouni *et al.* (2018) showed that deep-rooted genotypes could increase grain yield by 37 to 38 % in environments with limited moisture compared to shallow rooted genotypes, but that it also causes a yield loss of 20 to 40 % in moisture-rich environments, compared to shallower root types. Under Mediterranean environments where the stored water is the main source during the filling grain period (Manschadi *et al.* 2006; Wasson *et al.* 2012), root depth is the trait most relevant. Based on modelling studies, 55 kg ha^{-1} would be gained in wheat yield because of 1 millimeter of extracted water during the post-anthesis period (Manschadi *et al.* 2006; Christopher *et al.* 2013). Therefore, breeding for deep-rooted varieties was proposed as a promising strategy to address drought tolerance (Manschadi *et al.* 2006; Wasson *et al.* 2012).

A large root system in wheat is described as having large biomass, long roots and high root length density (Hamblin and Tennant 1987). A major finding of Aamodt and Johnston (1936) was that the large root system of the wheat cultivar Pelissier was important in the avoidance of damage by drought in a dry season on the Canadian prairies. It has been suggested that a deep, wide-spreading and much-branched root system is essential in the design of drought-tolerant crops (Kramer 1969; Hurd 1974; Jackson *et al.* 2000). In another interesting hypothesis, Passioura (1983) suggested that small root systems could provide benefits in water-limited situations through improved water use efficiency. He argued that there would be an optimum root:shoot ratio above which further increases in root size would provide limited benefits but would also impose a cost on shoot growth by consuming biomass, and this suggestion was validated by Ma *et al.* (2008). In fact, the usefulness of great or reduced root system biomass in adapting wheat to water stress, greatly depending on the environment type in which root system is grown. The usefulness of a vigorous root system in increasing wheat yields under water-limited conditions maybe greater in environments where crops rely largely on seasonal rainfall, such as the Mediterranean-type environments. However, in such environments, a vigorous root system increases the risk of depleting soil water before completion of grain filling (Palta *et al.* 2011).

1.8.3. Effect of breeding on the root system architecture

Changes in root system architecture traits have occurred as a consequence of domestication and breeding and have led to contrasting spatial arrangements of roots (Sanguineti *et al.* 2006; Tardieu *et al.* 2018). The selection and breeding outcomes were driven by the effect of prevailing environmental conditions on the genetic material, which served as reference for breeding. Accordingly, the comparison between landraces from contrasting environmental conditions showed different patterns of seminal root traits. Turkish landraces, originated from drought-prone stress environment, tended to have a larger root size and wider root angle in contrast to those coming from eastern Balkan and Western Mediterranean (Roselló *et al.* 2019). The effect of breeding on the evolution of seminal RSA was also revealed during a study of bread wheat germplasm historically grown in the semi-arid northwestern of China (Zhu *et al.* 2019). In this study, breeding narrowed the seminal root angle, reduced root number, and increase of primary seminal root length. The hypothesis of weakening of “selfish” traits of Weiner *et al.* (2017) attempted to explain the reasons of different pattern of RSA reliant on the adaptation to plant density as the main driver. Under this hypothesis, fewer, longer seminal roots with narrower root angle is a result of group selection. When plants were cultivated at a higher density, only homogeneous individuals were kept, excluding those with selfish traits, which compete for space (higher root angle), water and nutrient. This suggestion was in contrast to the natural selection, which encourages RSA with wider angle. However, this hypothesis is not in line with other findings, where landraces were found to have steeper RSA (Ruiz *et al.* 2018; Roselló *et al.* 2019).

Several studies in wheat and barley showed that the root systems of 'green revolution' genotypes were smaller than earlier genotypes and landraces (Grando and Ceccarelli 1995; Wahbi and Gregory 1995; Waines and Ehdaie 2007; Ashe *et al.* 2017; Boudiar *et al.* 2020). The dwarfing genes seemed to have greatly affected the root growth over the breeding history. A number of Rht genes were shown to have a significant effect on root growth (Wojciechowski *et al.* 2009). These genes are known to have a large effect on plant height variation, indicating their importance in differentiating durum wheat cultivars released before and after the green revolution (Royo *et al.* 2007, 2008; Graybosch and Paterson 2010). Moreover, according to Subira *et al.* (2016), in relative terms, the dwarfing alleles had a greater effect on reducing the dry matter of roots than on reducing that of aerial organs. Zhu and Zhang (2013) suggested that the selection of cultivars with higher yield and other suitable traits during the 20th century also led to an unintentional selection of those with a reduced investment in root biomass. In Europe, wheat breeding has indeed played a role in the exclusion of higher root biomass (Voss-Fels *et al.* 2017). Nevertheless, previous studies found no consistent association between height genes and root growth and function (Blum 2011). It has been proposed that the enlargement of the root system and its penetration ability might not be under the control of dwarfing genes (Miralles *et al.* 1997; Kubo *et al.* 2005). Furthermore, negative relationships have been identified between root dry weight and plant height in bread wheat (Miralles *et al.* 1997), and a lower root:shoot ratio has been found in dwarf cultivars (Siddique *et al.* 1990).

1.9. Phenotyping of root traits

Given that molecular breeding populations can include up to 5000 lines, the ability to, accurately, characterize all lines simultaneously is challenging (McMullen *et al.* 2009). Advances in phenotyping are likely to be essential to capitalize on developments in conventional, molecular, and transgenic breeding and ensure genetic improvement of crops for future food security (Araus and Cairns 2014). Crop breeders and researchers are showing increased interest in phenotyping for root architecture traits as part of their breeding programs (Chen *et al.* 2015). This area of study was neglected for a long time, for practical reasons (Zhu *et al.* 2011). In recent years, increasing studies are being carried out related to root phenotyping; however, most of effort revolved about root phenotyping of seedling due to the practical constraints involving root phenotyping in the field (Araus and Cairns 2014).

1.9.1. Root phenotyping at early growth stage

A large numbers of phenotyping methods targeting roots at early stages have been developed. Simple screens, using Petri dishes where seeds germinated on damp papers, were used in several studies (Bai *et al.* 2013; Abdel-Ghani *et al.* 2014; Atkinson *et al.* 2015; Ramshini *et al.* 2016). Recording of number of axes and morphological characters, such as presence or absence of root hairs, are possible for large numbers of accessions using photographs after a short growth time (White *et al.* 2008). Such approaches have the advantage that replicated measurements of large numbers of lines can be achieved quickly, but information about root architecture is not rich. The orientation of seeds in Petri dishes can affect growth profoundly, thereby limiting the usefulness of any root architectural measures (Gregory *et al.* 2009). Another set of methods was devised to allow the acquisition of root architecture traits in aeroponic, hydroponic, agar plate systems, and gel chambers (Zobel *et al.* 1976; Vincent and Gregory 1986; Bengough *et al.* 2004; Manschadi *et al.* 2008; Armengaud *et al.* 2009), and rhizo-slide system (González *et al.* 2016; Ruiz *et al.* 2018). In these phenotyping methods, roots are grown in a narrow gap between plates, these screens have been useful to reveal a range of root architectural studies related evolution of these traits in barley during domestication and subsequent breeding (Bengough *et al.* 2004; de Dorlodot *et al.* 2007), and the relationship with eco-geographical and agronomic features in a core collection of tetraploid wheat landraces (Ruiz *et al.* 2018). Further traits such as diameter, surface length could be acquired when the images of root system were processed by root software, like *SmartRoot* (Lobet *et al.* 2011). Other methods, addressing specifically the root angle, like clear pot method, using transparent pots and growing seeds between the soil and the pot wall (Richard *et al.* 2015), were developed. The clear pot method can be coupled with other methods in which the root angle cannot properly assessed, like the rolled paper method, as done by Rosello *et al* (2019). All these previous methods are low-cost. There are also costly phenotyping platforms, in which the phenotyping can be done more thoroughly. An example of this is the high throughput phenotyping platform GrowScreen-Rhizo (Nagel *et al.* 2012), was designed to assess shoot and root traits in early growth stages. The advantage of this platform is its automation, linked to the use of an imaging cabinet, allowing daily sequential measurements of root growth traits, and in addition allows to measure secondary root traits. The GrowScreen-Rhizo has been tested in a number of studies, like the assessement of drought tolerance in bean (Belachew *et al.* 2019) and barley (Boudiar *et al.* 2020), and the combined effect water and nitrogen on wheat (Gioia *et al.* 2015).

The above phenotyping techniques of RSA have been performed on two-dimensional images of roots. Since roots grow and branch in a three-dimensional space, RSA information is necessarily lost when compressed to two dimensions (Zhu *et al.* 2011). Several approaches are currently being developed to phenotype RSA in 3D in both soil and gel-based growth systems. X-ray computed tomography (CT) is a promising technique for non-invasive 3D of the RSA imaging in soil. CT imaging was originally developed for medical uses, and results in 3D models based on 2D cross-sectional x-ray images taken around an axis of rotation. The images reflect x-ray attenuation based on sample composition. CT imaging of roots continues to be improved and has been applied to numerous species including barley, maize, Arabidopsis, wheat, and chickpea (Lontoc-Roy *et al.* 2006; Hargreaves *et al.* 2009; Lucas *et al.* 2011). The primary disadvantages of CT are high cost and scanning times. Additionally, the composition of the soil and its water content can affect the ability to distinguish roots from the surrounding substrate (Tracy *et al.* 2010). In this regard, multiple energy CT methods have been developed to improve discrimination between materials (Granton *et al.* 2008; Graser *et al.* 2009) and may be useful in addressing this problem. Magnetic resonance imaging (MRI) is another medical imaging technology that has been applied to soil-grown roots (van Dusschoten *et al.* 2016). MRI is essentially spatially resolved nuclear magnetic resonance (NMR), and images water protons based on their local magnetic environment. Like CT, MRI is expensive and requires long scan times. Additionally, imaging can be affected by paramagnetic components and water present in the soil. Currently, CT appears superior to MRI for imaging RSA. However, MRI is useful in specific applications like measuring water flow (Van As 2007) or, when coupled to positron emission tomography, to monitor photoassimilate transport (Jahnke 2009). At this moment, these 3D technologies are useful for basic plant physiology and morphology studies, but their use for the scale of experiments needed in plant genetics is still complicated.

Even though laboratory/glasshouse phenotyping methods provide controlled environments, allow increased throughput and require fewer resources, and may reveal real rooting differences among genotypes, they may not accurately reflect plant performance under field conditions. Nevertheless, this has been achieved in some cases. For instance, significant associations between root traits of the seedlings grown under controlled conditions and those of the plants grown in the field could be found species like wheat (Mian *et al.* 1994; Richards 1996) and maize (Landi *et al.* 1998; Tuberosa *et al.* 2002).

1.9.2. Phenotyping roots at mature plant

Screening the root system at later stages plant growth is more challenging that at early stages, thus fewer methods were comparatively developed. Root depth is the most relevant root trait under late drought, where the stored-water is the main source (Wasson *et al.* 2014). In this respect, a number of methods were designed based on the use of long tubes (pipe-pots). Blum (2011) proposed a tube method, using PVC tubes of 10.2 cm width and 120 cm long. This method was employed in wheat to evaluate the root depth and the root biomass at different depths (Subira *et al.* 2016), as affected by the dwarfing genes. Elazab *et al.* (2016) tested durum wheat genotypes in longer tubes (lysimeters), using PVC tubes of 14 cm width and 150 cm long, to assess water and nitrogen effects on root traits. A more sophisticated tube-based method was used recently by Friedli *et al.* (2019), the Deep Root Observation Platform (DROP), in which wheat roots were grown in acrylic plastic columns (1.6 m in height, 11 cm in width), which could be weighted to monitor the water balance. This platform is able to hold up to 144 plants with common field plant density of 375 plants per m^2. The methods mentioned above grow roots in artificial substrates. These soil-like-mediums in tube setups are not perfect, either. They can overestimate the rooting depth due to higher soil temperatures, a lower soil bulk density and border effects between the soil and the surface of the column wall (Friedli *et al.* 2019). In fact, the depth penetration rate of roots in tube rhizotrons was reported to be twice as high as those observed in the field (Ytting *et al.* 2014).

To overcome the artifacts of controlled experiments and to obtain realistic results, some methods were designed to screen the root system directly in the field, such as the soil-coring method implemented by Wasson *et al* (2014). Thanks to this method, these authors were able to explore the variation of root wheat traits at 1.8 m depth. Core-break method using an automatic sampler is effective in sampling high number of genotypes (Wasson *et al.* 2012). However, washing roots from soil cores and subsequent image analysis for a detailed picture of root morphology is time consuming, and not amenable to a large number of genotypes (Himmelbauer *et al.* 2004; Benjamin and Nielsen 2005). *Shovelomics*, an emerging term for a high-throughput phenotyping method using field root excavation, was used firstly for visual scoring of excavated root crowns to assess different root architecture traits of field-grown maize around flowering time (Trachsel *et al.* 2011, 2013), and has been shown as useful tool for quantifying genetic variation (Trashel *et al.* 2011). Recently, it has been used for wheat

(Maccaferri *et al.* 2016; Slack *et al.* 2018; York *et al.* 2018). Shovelomics involves the excavation and visual scoring of root crowns extracted from around 20 cm of depth. The former studies could quantify various traits like angle, nodal root number and root system width. More root traits data could be acquired thanks to root crown images analysis tools like Root Estimator for Shovelomics Traits (REST) (Colombi *et al.* 2015). Results in maize have been shown to be well correlated with root depth and root system total length (Trachsel *et al.* 2011). Recently, this method was used to demonstrate a positive influence of nodal root number and growth angle on both root depth and yield of wheat in the field (Slack *et al.* 2018).

Although of proven utility, excavation approaches are labor-intensive, they destroy much of the RSA information including that of fine roots, and they do not allow repeated observations of the same plant. To overcome some of the limitations of excavation methods, transparent tubes called minirhizotrons have been developed that are installed vertically, horizontally, or at various angles in the field (or in mesocosms) (Bates 1937). Roots that grow around the outside walls of the tubes can be imaged with cameras inserted down the tube length. Minirhizotrons allow the observation of root traits such as elongation rate, density, surface area, number, and length at different soil depths throughout the growing season (Taylor *et al.* 1987; Hendrick *et al.* 1992; Johnson *et al.* 2001; Ao *et al.* 2010). Because repeated observations can be made over time, minirhizotrons are particularly well suited for estimating root production and turnover (Johnson *et al.* 2001). Additionally, minirhizotron data can be used to estimate root biomass per unit of soil. To automate the analysis of root traits in minirhizotron images, several software packages have been developed including WinRhizoTRON (www. regentinstruments.com), RootView (www.mv.helsinki.fi/ aphalo/RootView.html), RooTracker (www.biology. duke.edu/rootracker), and MR-RIPL (http://rootimage. msu.edu). One limitation to minirhizotrons is that space may be created around the soil-tube interface that could influence root growth if the tubes are not installed properly. Furthermore, minirhizotrons only capture a fraction of the total RSA. In this regard, they are better suited for measuring fine roots than coarse roots because fine roots are sampled more frequently and are more likely to be fully captured in images. Traditional soil coring and trench profiling can be used as complementary techniques to minirhizotrons (Bohm 1979; Achat *et al.* 2008; Zhu *et al.* 2010). Like minirhizotrons, however, neither of these methods provides a full description of RSA, and both are tedious and time-consuming, and not amenable to large populations. Ground-penetrating radar (GPR) and electrical resistivity imaging are low-resolution geophysical techniques that have been adapted for non-invasive imaging of roots in field-grown plants and trees. GPR uses pulses of high frequency radio waves to image subsurface structures based on differences in their dielectric constants. GPR is rapid, but detection is generally limited to thick roots (at least 0.5 cm) present in relatively shallow depths, depending on the soil type (e.g. dry, sandy soils are optimal). These limitations make GPR primarily useful for measuring root biomass of woody species (Stover *et al.* 2007; Zenone *et al.* 2008).

Although the ultimate target is the ability to monitor RSA in the field, current methods for phenotyping RSA in field-grown plants lack resolution and throughput. According to Zhu *et al.* (2011), the most promising approaches for high resolution, high throughput RSA phenotyping are CT imaging and gel-based imaging platforms (Figure 1.2). While CT imaging has the advantage of being applicable to soil-grown plants, gel-based methods are more economical and allow for higher throughput. Concurrent with the advances in 3D imaging, advances in image analysis are needed to capture important spatial characteristics of RSA.

Collectively, from all the above-mentioned root phenotyping methods, no one of them was perfect; each has advantages and disadvantages. It is obvious that combining various methods at early and adult growth stages would give a complete insight on the root system phenotyping much better than using only one method.

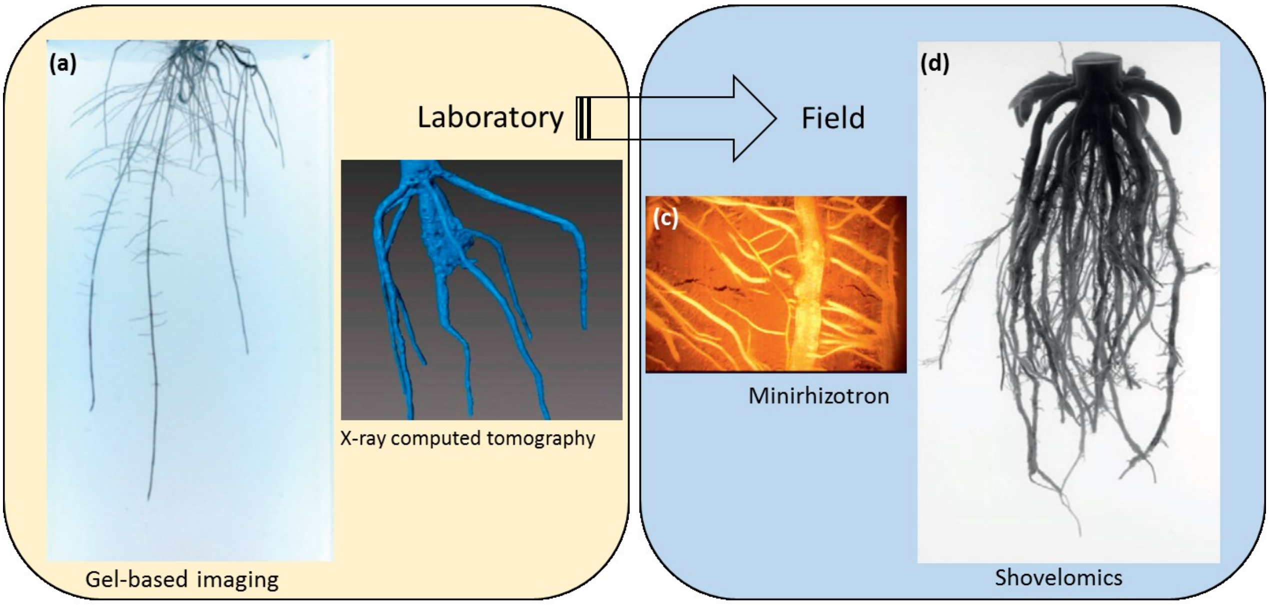

Figure 1.2. Approaches for phenotyping root system architecture in the lab and the field. (a) Digital image of the root system of an 11-day-old Sorghum bicolor plant grown in a 2 l transparent glass cylinder containing nutrient media solidified with 0.2% Gelzan CM. (b) Root architecture of a 3-week-old Zea mays (L.) plant grown in a soil column and imaged by x-ray computed tomography. (c) Frame of a minirhizotron image from a 6-week-old Zea mays (L.) plant grown in the field. (d) Excavated root crown of an 8-week-old Zea mays (L.) plant grown in field with low phosphorus availability (Zhu et al. 2011).

1.10. References

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2. Assessment of early drought tolerance of Algerian durum wheat reveals superiority of landraces

2.1. Abstract

Vigorous seedling growth is important for good crop establishment, particularly under drought conditions. Our study was set out to identify useful traits and genotypes to enhance early drought tolerance of durum wheat. Two experiments were carried out. In the first one, thirty-five genotypes (landraces and improved) were tested in a phytotron at germination and early seedling stages, subjected to three osmotic stress levels induced by polyethylene glycol PEG 6000 (0, -3, -6 bar). The second experiment was conducted in the field, with 27 out of the 35 genotypes. Root and shoot traits were measured at seedling stage in both experiments. High PEG 6000 treatment decreased final germination percentage (FGP) by 2.7 % and delayed the time to reach 50 % germination (t50) by 2.9 h. Shoot length was the trait most affected by drought (40 % reduction) as compared with other root traits, which even increased under drought, like root to shoot length ratio, root to shoot weight ratio, root dry weight and root number. Coleoptile length (CL) showed a contrasting relationship with other traits, it was negatively correlated in general under no stress, but with positive correlations under stress. Based on drought susceptibility index (DSI), Algerian wheat landraces were the most tolerant compared to modern genotypes. Correlations between traits measured in field and controlled conditions were low. CL could be a potential trait for screening drought tolerant genotypes. Algerian wheat landraces presented a clearly distinct ability for early drought tolerance, and could be a good resource for breeding programs.

2.2. Introduction

In Mediterranean-type environments, sowing is typically practiced when soil moisture is ensured by the first rain (Rebetzke *et al.* 2008). Early growth vigor has been proposed as a trait that could enhance crop water-use efficiency and yield in these environments (López-Castañeda and Richards 1994; Coleman *et al.* 2001). One of its possible benefits could occur through increased root growth early in the season (Liao *et al.* 2004). Early drought restricts germination (Misra *et al.* 1990), emergence and early seedling growth (Al-Karaki 1998), which may lead to crop failure in the West Asia and North Africa region(WANA) (Abdel-Ghani *et al.* 2015). In regions characterized by short periods of appropriate soil moisture, seeds with high germination percentage may be advantageous for ensuring a good plant establishment (Brar *et al.* 1991). Drought stress is a stage specific phenomenon, as it has been described that tolerance at plant establishment phase is poorly correlated with tolerance at other stages (Mano *et al*. 1996; González *et al.* 2008; Szira *et al.* 2008). Selection for drought tolerance at early growth stage has been frequently attempted using PEG 6000 to induce water stress, without causing significant physiological damage to crop plants (Carpita *et al.* 1979; Rauf *et al.* 2007).

Despite the importance of root system for acquisition of water and nutrients (Blum 1997; Blum 2009; Ehdaie *et al.* 2012), plant breeding focused for a long time almost solely on the above-ground traits, while root traits were relatively neglected because of the practical difficulties of phenotyping at a scale useful to perform selection (Waines and Ehdaie 2007). In the last decade, more attention has been paid to root phenotyping (Bengough *et al.* 2004; Nagel *et al.* 2012; Richard *et al.* 2015; York *et al.* 2018) thanks to novel phenotyping methods. Among these, root attributes at seedling stage are important for screening genotypes for early drought tolerance (Chloupek *et al.* 2010; Sayed 2011). Some breeders propose to select genotypes with higher root volume combined with maximum length of seminal and adventitious roots (Richards and Passioura 1981; Grando and Ceccarelli 1995). Jia *et al.* (2019) indicated that root system depth and root spread angle are valuable candidate traits for increasing grain yield. Root to shoot ratio and root length at early stages of plant development could also be valuable attributes for improving yield under arid and semi-arid conditions (Dhanda *et al.* 2004; Shahbazi *et al.* 2012). Coleoptile length (CL) has also been proposed as an important trait for drought tolerance at plant seedling stage: long coleoptiles allow deep sowing, which is an adequate practice in water-limited environments in which topsoil dries up fast (Mahdi *et al.* 1998; Schillinger *et al.* 1998), enabling growers a longer time window to perform sowing with optimum soil moisture (Gan *et al.* 1992).

Wheat landraces have been widely replaced by modern varieties (Khlestkina *et al.* 2004; Reif *et al.* 2005; Bonnin *et al.* 2014). Nevertheless, they are still preferred over modern wheats in several parts of the world, mainly for their stable yields in low input conditions, prized end-use qualities, and high straw yield. Farm size, lack of machinery, and lack of fertilizer are also important constraints in growing modern wheats (Karagöz 2014). Varietal substitution has led to reduction of germination-related traits like shoot, coleoptile and root length and seedling vigor in Iranian modern varieties, compared to landraces (Ramshini *et al.* 2016). Bektas *et al.* (2016) found that shoot biomass, shallow and deep root weight, number of tillers per plant and plant height were significantly greater in landraces than in modern varieties. In several cases, winter cereal landraces have shown better performances than modern varieties, usually under challenging environmental conditions (Yahiaoui *et al.* 2014, Erice *et al.* 2019). When root systems were compared, an Algerian wheat landrace (Pelissier) had more root growth than a widely grown modern variety (Ashe *et al*. 2017).

All these evidences highlight the importance of early drought tolerance, and the potential of landraces to contribute favorable traits in this respect. The aim of our research was to identify traits and genotypes of importance in early stress tolerance, and to explore the potential of Algerian landraces for drought tolerance breeding.

2.3. Material and Methods

2.3.1. Plant material

Thirty-five durum wheat genotypes (landraces and modern cultivars) from different countries (Algeria, France, Italy, Spain, Tunisia), and international breeding programs addressing semi-arid areas, namely the International Maize and Wheat Improvement Center (CYMMIT), the International Center for Agricultural Research in the Dry Area (ICARDA) and the Arab Center for the Studies of Arid zones and Dry lands (ACSAD), were chosen for this study (Table 2.1). Most of these genotypes have been widely cultivated in Algeria. There are reports of cultivation of the oldest genotype Hedba3 in 1921, whereas the newest ones (Boutaleb and Oued El Berd) were released by the Technical Institute of Field Crops (ITGC, Sétif, Algeria) in 2013, thus this set of genotypes is spanning more than 8 decades (Table 2.1).

2.3.2. Phytotron experiment

The experiment was conducted at the Biotechnology Research Center (CRBt), Constantine, Algeria. Fifteen apparently healthy seeds of the same size of each genotype, were weighted, surface sterilized with 0.5 % of sodium hypochlorite (NaClO) and rinsed for six times with distilled water. They were then germinated on Whatman (type1) filter paper soaked with 10 ml of PEG 6000 solutions in Petri dishes. PEG 6000 was used to induce osmotic stress at two levels, -3 and -6 bar, following the method suggested by Michel and Kaufmann (1973), while distilled water without PEG 6000 was used as control treatment. Petri dishes were transferred to a phytotron for 8 days, in darkness, at constant 25C° and 70 % relative humidity. The experimental design was a split plot design with two replications (each consisting of 15 seeds of a genotype in a Petri dish), where the whole plot was PEG treatment and the sub-plot was the genotype.

Germination date was recorded when the radicle reached at least 2 mm in length. Germinated seeds were counted every 24 hours for 8 days.

Final germination percentage (FGP) and the time needed to reach 50%-germinated seeds (t50) were recorded. Time to reach 50 % germination was calculated based on the following formula proposed by Coolbear *et al*. (1984) and modified by Farooq *et al*. (2005):

$t50 = ti + [((N / 2) - ni) (tj - ti)] / nj – ni,$

where N is the final number of seeds that germinated and ni and nj were the cumulative number of seeds germinated by adjacent counts at times ti and tj when ni < N/2 < nj

Table 2.1. Type, Origin and date of release information's of the 35 genotypes of durum wheat used in this study.

Genotype	**Abv**	**Type**	**Origin**	**Year of release**	**Phytotron**	**Field**
Beliouni	Bel	Landrace	Algeria	1958	×	
Bidi 17	Bid	Landrace	Algeria	1930	×	×
Djenah Khotifa	Dje	Landrace	North Africa	1955	×	
Gloire de Montgolfier	Glo	Landrace	Algeria	1960	×	×
Guemgoum R'khem	Gue	Landrace	Algeria	1960	×	×
Hedba 3	Hed	Landrace	Algeria	1921	×	×
Mohammed Ben Bachir	MBB	Landrace	Algeria	1930	×	×
Montpellier	Mon	Landrace	Algeria	1965	×	×
Oued Zenati 368	OZ	Landrace	Algeria	1936	×	×
Langlois	Lan	Landrace	Algeria	1930	×	×
Sbaa Aldjia	Sba	Landrace	Tunisia	-	×	
Acsad 65	Acs	Improved	ACSAD	1984	×	×
Altar 84	Alt	Improved	CYMMIT	1984	×	×
Aures	Aur	Improved	Algeria	2013	×	
Boutaleb	Bot	Improved	Algeria	2013	×	
Capeiti	Cap	Improved	Italy	1940	×	×
Cirta	Cir	Improved	Algeria	2000	×	×
El Maather	ELM	Improved	Algeria	-	×	
GTA Dur	GTA	Improved	CIMMYT	1972	×	×
INRAT 69	INR	Improved	Tunisia	1969	×	×
Korifla	Kor	Improved	ICARDA	1987	×	×
Mansourah	Man	Improved	Algeria	2012	×	×
Massinissa	Mas	Improved	Algeria	2012	×	×
Megress	Mgs	Improved	Algeria	2007	×	×
Mexicali 75	Mex	Improved	CIMMYT	1975	×	×
Miki-2	Mik	Improved	ICARDA	2008	×	
Ofanto	Ofa	Improved	Italy	1990	×	×
Oued El Berd	OEB	Improved	Algeria	2013	×	×
Polonicum	Pol	Improved	France	1973	×	×
Simeto	Sim	Improved	Italy	1988	×	×
Sitifis	Sit	Improved	Algeria	2011	×	×
Tejdid	Tej	Improved	Algeria	-	×	
Vitron	Vit	Improved	Spain	1987	×	×
Waha	Wah	Improved	ICARDA	1986	×	×
ZB × Fg	ZBF	Improved	Algeria	1983	×	×

×: indicate the presence of the corresponding genotype in the experiment.

At the end of the experiment, seedlings were preserved in a 30% ethanol solution until the rest of the traits were recorded in five representative seedlings chosen from each Petri dish: mean value of shoot length (SL), coleoptile length (CL), root number (RN), total root length (TRL), maximum root length (MRL), root dry weight and shoot dry weight (RDW and SDW, respectively), and total plant biomass (TPB). Additionally, several indices were calculated: root to shoot ratio for weight and length (RSW and RSL, respectively), seedling vigor index (SVI) and drought susceptibility index (DSI). The drought susceptibility index (DSI) for TPB was calculated according to Fischer and Maurer (1978) using the following formula, originally developed for yield:

$DSI = (1-Y_D/Y_P)) / (1-X_D/X_P))$

where, YD corresponds to the genotypic mean of TPB under stress, YP corresponds to the TPB mean of control for each genotype, XD is the TPB mean of all genotypes under stress, and XP is the TPB mean of all genotypes under control conditions.

The SVI based on seedling weight (hereafter, SVI_W) was obtained using the following formula: $SVI_W = (RDW + SDW) \times FGP$

The SVI based on seedling length (hereafter, SVI_L was calculated using the following formula (Abdul-Baki and Anderson, 1973) : $SVI_L = (MRL + SL) \times FGP$, where, MRL: maximum root length, SL: shoot length, FGP: Final germination percentage

2.3.3. Field experiment

Twenty-seven out of the 35 wheat genotypes were sown on 28 Nov 2016 in a randomized complete block design with two replications under rainfed conditions. The rainfall throughout Nov was 29.7 l/m^2 for 7 days, so soil humidity was appropriate for seed germination. Sowing density was 300 seeds/m^2 in six row plots of 1.2 m width and 2.5 m long (3 m^2), at the Technical Institute of Field Crops (ITGC), Sétif, Algeria. Five seedlings per replicate were carefully harvested 10 days after emergence; roots were gently cleaned from soil by washing with tap water. The same traits measured in phytotron experiment were recorded in the field, except t50, SVI and DSI.

2.3.4. Data analyses

The analyses of variance were carried out by REML (Restricted Maximun Likelihood) procedure of Genstat 18 (Payne *et al*. 2009), taking replications as random factor, and genotype, treatment, genotype by treatment and the comparison of landraces vs. improved varieties (named ‘type’ effect), as fixed factors. Multiple means comparison was carried out using an LSD at 0.05 level of significance.

Broad-sense heritability (h^2) was calculated on entry mean basis using the REML procedure in Genstat 18, as follows: $h^2 = \sigma^2 g/(\sigma^2 g + (\sigma^2 e/r))$, where $\sigma^2 g$ is the genotypic variance, $\sigma^2 e$ is the error variance and r is the number of replications.

2.4. Results

2.4.1. Effect of PEG-induced drought stress on the assessed traits

The differences between treatments were significant for t50 (time to reach 50 % germination), due to the slower germination at -6 bar, but not for FGP. Genotypes were significantly different for both t50 and FGP. However, interactions between genotypes and treatments were found only for t50 (Table 2.2). Both drought treatments increased t50 (Table 2.2), but only significantly at the high drought stress level (2.9 h, 7.4% at -6 bar). As the high treatment (-6 bar) effect was more pronounced on germination traits, from here on we will only report its results, referred to as the ‘drought stress treatment’, unless stated otherwise.

Table 2.2. Summary statistics and means comparison for the 35 wheat genotypes under PEG treatments (0, -3 and -6 bar) for final germination percentage (FGP) and time to reach 50% germination (t50).

	Min	Max	Mean (SE)	CV%	Reduction
FGP					
Control, 0 bar	53.3	100.0	89.1a (7.09)	14.2	
PEG -3 bar	33.3	100.0	90.1a (9.03)	14.6	-1.1
PEG -6 bar	20.0	100.0	86.7a (11.68)	16.8	2.7
t50					
Control 0 bar	0.7	3.5	1.6b (0.32)	27.5	
PEG -3 bar	0.8	2.5	1.6b (0.24)	17.7	-1.2
PEG -6 bar	1.4	3.5	1.7a (0.18)	18.7	-7.4

Under drought conditions, 24 genotypes showed a decrease in FGP while 11 genotypes showed no change or even increased their FGP (Table 2.S1). The opposite occurred for t50, 24 genotypes increased the time to 50% germination, and 11 showed accelerated germination under drought, or no change (Table 2.S1).

Drought had a significant effect on all of seedling traits, except for CL, RDW and TPB. Genotypes were significantly different for CL, MRL, RSL, RSW, SVI_W and SVI_L. It is remarkable that there was no significant interaction between genotypes and treatment (Table 2.3).

Table 2.3. Ranges, means, standard error (SE), coefficient of variation (CV) and significance of the analysis of variance for 35 wheat genotypes evaluated under optimum (non-tress) and drought stress conditions (-6 bar), for seedling traits.

	Control				Drought stress (-6 bars)						Combined ANOVA (control and stress)		
	Min	Max	Mean	CV	Min	Max	Mean	CV	SE	Reduction %	Genotype (Geno)	Treatment (Treat)	Geno×Treat
CL (cm)	1.84	5.42	3.92	18.23	1.45	5.85	3.83	22.01	0.66	2.26	***	ns	ns
SL (cm)	3.78	17.36	11.97	23.45	1.14	10.86	7.15	24.27	2.51	40.26	ns	***	ns
MRL (cm)	2.90	20.48	12.50	35.06	3.90	16.46	10.93	21.69	3.15	12.62	**	**	ns
TRL (cm)	7.02	71.26	39.88	40.74	9.06	57.06	34.62	25.61	26.9	13.19	ns	*	ns
RN	3.40	5.80	4.71	10.99	2.80	6.00	5.06	10.66	0.51	-7.46	ns	***	ns
SDW (mg)	0.60	15.10	8.00	36.50	1.40	9.90	6.50	24.92	0.0022	19.26	ns	***	ns
RDW (mg)	1.60	10.90	5.80	40.47	2.10	9.70	6.30	20.73	0.0017	-8.62	ns	ns	ns
TPB (mg)	3.90	21.70	13.90	34.74	3.50	19.30	12.80	21.01	0.0037	8.25	ns	ns	ns
RSL	0.50	1.84	1.07	30.80	0.71	3.42	1.58	23.00	0.32	-47.53	**	***	ns
RSW	0.27	1.08	0.73	26.34	0.49	1.55	1.00	19.53	0.18	-38.66	*	***	ns
SVI_W	0.29	2.16	1.26	39.56	0.22	1.56	1.11	26.70	0.35	11.64	**	*	ns
SVI_L	251	3188	2193	33	307	2312	1586	28	502.99	27.00	***	***	ns

CL: coleoptile length, SL: shoot length, MRL: maximum root length, TRL: total root length, RN: root number, SDW: shoot dry weight, RDW: root dry weight, TPB: total plant biomass, RSL: root to shoot length, RSW: root to shoot weight, SVI_w: seedling vigor index based on seedling weight, SVI_L: seedling vigor index based on seedling length. *, ** and ***: significant difference at 0.5, 0.01 and 0.001 level respectively.

Phenotypic mean values of seedling traits were higher under control than under stress conditions (-6 bar) except for RN, RDW, RSL and RSW. In general, the ranges of values were wider under control conditions, except for CL, RN, RSL and RSW (Table 2.3). The highest reduction due to PEG stress was observed for the mean value of SL (40.26%) followed by SDW (19.26%), TRL (13.19%) and MRL (12.62%), whereas mean of TPB (8.25%) and CL (2.26%) were reduced the least. In contrast, RSL, RSW, RDW and RN means were increased under PEG treatment by 47.53, 38.66, 8.62 and 7.46% respectively. For root to shoot length ratio (RSL) and root to shoot weight ratio (RSW), the mean values were greatly increased under PEG treatment, which was a consequence of the great reduction of SL and SDW respectively. In general, the coefficient of variation values (CV) were similar between traits under both conditions except for RN, which was the smallest one (10.99 and 10.66 for non-stress and stress conditions, respectively). CV values were greater under control than under stress conditions; only SL and CL had slightly higher CV values under stress conditions (Table 2.3).

The DSI based on TPB showed negative and positive values. Genotypes with negative values were considered drought tolerant, and genotypes having positive values were considered as drought susceptible. Wheat genotypes presenting the lowest negative DSI values were almost all landraces, whereas modern ones presented positive DSI values (Table 2.4).

2.4.2. Effect of field compared to phytotron conditions

Under field conditions, ANOVA analyses showed a significant difference (0.05) for CL, highly significant difference (0.001) for RSW and very highly significant difference (<0.001) for RN and RDW (Table 2.5). The comparison between the mean values for seedling traits recorded in the field and under phytotron non-stress and stress conditions, showed lower mean values in the field for all measured traits, except for SDW which was superior under field compared to both controlled conditions (stress and non-stress) and also for SL and TPB where the phenotypic mean values in the field were superior but only to those of stress (Table 2.5). The ranges of variation for seedling traits observed in the field were smaller than those found under stress and non-stress conditions for all traits, for example TRL (cm): field = (8.14 – 26.90), control = (7.02 – 71.26), stress = (9.06 – 57.06), MRL (cm): field = (3.4 – 8.04), control = (2.90 – 20.48), stress = (3.90 – 15.16), CL (cm): field = (1.56 – 4.70), control = (1.84 – 5.42), stress = (2.26 – 5.85), and for RN: field = (3.2-5.4), control = (3.4 – 5.8), stress = (2.8 – 6) (Table 2.5).

Table 2.4. Thirty-five wheat genotypes ranked on drought susceptibility index (DSI), calculated from total plant dry biomass (TPB, mg per seedling).

Genotype	Type	TBP/Control	TBP/Stress	DSI
Langlois	**Landrace**	8.70	16.00	-10.17
Djenah Khoteifa	**Landrace**	7.72	13.14	-8.51
Sbaa Aldjia	**Landrace**	6.75	11.32	-8.20
Gloire de Montgolfier	**Landrace**	11.68	17.52	-6.06
Guemgoum	**Landrace**	11.46	16.25	-5.06
MBB	**Landrace**	10.95	14.31	-3.72
Oued Znatie	**Landrace**	11.09	13.57	-2.71
Polonicum	Cultivar	10.56	12.62	-2.36
Hedba 03	**Landrace**	10.26	11.97	-2.02
INRAT 69	Cultivar	14.09	16.19	-1.81
Aures	Cultivar	13.55	14.75	-1.07
Mexicalli 75	Cultivar	10.41	11.19	-0.91
Megress	Cultivar	11.94	12.60	-0.67
Waha	Cultivar	12.65	13.23	-0.56
Beliouni	**Landrace**	10.18	10.29	-0.13
Vitron	Cultivar	13.73	12.69	0.92
Altar 84	Cultivar	11.73	10.73	1.03
Bidi 17	**Landrace**	14.62	13.15	1.22
Acsad 65	Cultivar	15.28	13.72	1.24
Miki-2	Cultivar	13.51	12.03	1.33
Tejdid	Cultivar	15.21	12.73	1.98
ZB/Fg	Cultivar	13.78	11.36	2.13
Gta Dur	Cultivar	14.32	11.41	2.46
Oued El Berd	Cultivar	16.19	12.70	2.61
Wahbi	Cultivar	19.81	14.60	3.19
Stitfis	Cultivar	17.42	12.61	3.35
Montpellier	**Landrace**	17.68	12.56	3.51
Cirta	Cultivar	17.24	12.09	3.62
Ofanto	Cultivar	18.07	12.64	3.64
Mansourah	Cultivar	15.38	10.49	3.85
Korifla	Cultivar	20.30	13.62	3.99
El Maather	Cultivar	19.96	12.31	4.64
Massinissa	Cultivar	20.19	11.93	4.96
Capeiti	Cultivar	13.46	7.79	5.10
Semito	Cultivar	19.21	11.09	5.12

Table 2.5. Ranges, means, coefficient of variation (CV) and analysis of variance for 27 wheat genotypes under control, stress and field conditions, with ANOVA analysis of field data for seedling traits.

	Non-stress				Stress				Field							
Trait	Mean	Min	Max	CV	Mean	Min	Max	CV	Mean	Min	Max	SE	CV	Redu% C	Redu% S	ANOVA
CL	3.92	1.84	5.42	19.59	3.87	2.26	5.85	22.01	3.19	1.56	4.70	0.55	19.82	18.64	17.39	*
SL	12.03	4.04	17.36	21.77	7.13	1.14	10.36	24.03	8.23	5.80	11.38	1.18	15.57	31.56	-9.20	ns
MRL	12.86	2.90	20.48	33.21	10.80	3.90	15.16	20.34	5.27	3.40	8.04	0.97	18.11	59.00	43.00	ns
TRL	40.64	7.02	71.26	39.47	34.46	9.06	57.06	25.54	16.29	8.14	26.90	3.88	25.08	59.91	44.69	ns
RN	4.67	3.40	5.80	11.08	5.05	2.80	6.00	10.18	4.33	3.20	5.40	0.38	11.84	7.22	15.42	***
SDW	8.00	0.60	15.10	35.74	6.50	1.40	9.90	25.18	9.30	6.40	11.70	0.0012	13.37	-16.08	-34.84	ns
RDW	6.00	1.60	10.90	37.62	6.30	2.10	9.70	20.67	4.60	2.50	7.90	0.0008	23.34	22.54	28.44	***
TPB	14.1	4.80	21.70	32.78	12.8	3.50	19.30	20.95	14.00	10.90	17.60	0.0016	11.52	0.95	-8.18	ns
RSL	1.10	0.53	1.83	30.21	1.57	0.71	3.42	24.22	0.64	0.45	0.88	0.12	18.53	41.51	83.78	ns
RSW	0.74	0.27	1.07	24.98	1.00	0.49	1.55	20.42	0.50	0.28	0.76	0.09	20.57	31.68	67.02	**
SVI$_W$	1.28	0.29	2.16	35.80	1.12	0.22	1.56	26.25	0.88	0.51	1.43	0.20	22.34	31.08	18.92	ns
SVI$_L$	2247.13	251.33	3188.00	30.47	1593.45	307.00	2312.00	27.20	868.81	523.71	1547.36	225.58	24.69	61.34	32.25	ns

CL: coleoptile length, SL: shoot length, MRL: maximum root length, TRL: total root length, RN: root number, SDW: shoot dry weight, RDW: root dry weight, TPB: total plant biomass, RSL: root to shoot length, RSW: root to shoot weight, SVI$_w$: seedling vigor index based on seedling weight, SVI$_L$: seedling vigor index based on seedling length. Redu% C: Mean value reduction compared to control. Redu% S: Mean value reduction compared to stress. *, **, ***: significant difference at 0.05, 0.01 and 0.001, respectively.

2.4.3. Landraces vs. improved genotypes

ANOVA analyses revealed a significant effect of type (landrace vs. improved) and type by treatment interaction on most traits measured except SL, RN, SDW for type effect (Table 2.6). Landraces showed higher coleoptile length than improved genotypes under control and stress conditions. For all other traits improved genotypes were superior or equal to landraces under control but the opposite was observed under stress (Table 2.6). Across treatment, landraces tended to increase all traits under stress except SL and CL, which were reduced by 40.44 and 8.85 % respectively. RDW of landraces was the most increased trait (traits per se) under stress (69.26 %) (Table 2.6, Figure 1). On the other hand, improved genotypes showed the largest decreases for most traits under stress. SL and SDW were the most affected by stress (reduced by 38.99 and 28.38 %, respectively), but a slight increase was observed for CL (0.96 %). Root number was increased for both improved genotypes and landraces under stress by 6.66 and 9.57 %, respectively (Table 2.6). Under stress, landraces and improved genotypes increased their root length and root biomass compared to shoot part (increase in RSL and RSW) (Fig. 1). Seedling vigor index based on seedling length (SVI_L) or on seedling weight (SVI_W), were significantly higher for improved cultivars under control conditions but not under stress conditions. Landraces tended to have a higher SVI_W under stress, compared to improved genotypes (Table 2.6).

The comparison between landraces and improved genotypes in field revealed significant differences only for SDW and RSW. Landraces presented higher SDW values and improved genotypes had a better RSW ratio (Table 2.S2).

2.4.4. Broad heritability in the field compared to controlled conditions

Overall, heritability calculated from field data was inferior to that obtained under control conditions and was higher than under stress. Under control conditions, broad heritability was higher than under drought stress for most traits (Table 2.S3). MRL presented appreciable heritability under stress (0.98) and field conditions (0.99). CL was more heritable (0.65) under control than other conditions (0.25). RDW had higher heritability values under all conditions than SDW. RSW displayed very high heritability value under control (0.98) followed by field (0.50) and stress (0.17) (Table 2.S3).

2.4.5. Traits relationship

Pearson correlation coefficients between seedling traits measured in both control and drought stress conditions ranged from very weak correlation (0.07) for TRL and SVI_W to highly

Table 2.6. Ranges, means, percentage of reduction (%redu) and analysis of variance for landraces and cultivar genotypes under control and stress (PEG, -6) conditions.

		Control			**Stress**				**ANOVA**		
Trait	Type	Min	Max	Mean	Min	Max	Mean	%redu	T	Trt	T × Trt
t50 (day)	Improved	0.70	2.38	1.49	1.46	2.10	1.66	-11.28	***	*	ns
	Landrace	1.00	3.50	1.90	1.44	3.50	1.90	-0.39			
FGP %	Improved	60.00	100.00	92.32	20.00	100.00	88.11	4.56	**	ns	ns
	Landrace	53.33	100.00	81.11	46.67	100.00	83.21	-2.60			
CL (cm)	Improved	1.84	5.20	3.68	2.26	5.85	3.72	-0.96	***	ns	ns
	Landrace	3.28	5.42	4.50	1.45	5.42	4.11	8.85			
SL (cm)	Improved	3.78	17.36	11.81	1.14	10.86	7.20	38.99	ns	***	ns
	Landrace	4.94	15.44	12.23	2.83	12.08	7.28	40.44			
MRL (cm)	Improved	2.90	20.48	13.57	3.90	16.46	10.83	20.25	**	**	**
	Landrace	3.90	16.76	9.83	6.20	13.76	11.18	-13.73			
TRL (cm)	Improved	7.02	71.26	44.08	9.06	57.06	33.84	23.22	*	*	***
	Landrace	13.20	56.72	29.38	15.20	48.04	36.56	-24.43			
RN	Improved	3.40	5.80	4.78	2.80	6.00	5.10	-6.66	ns	***	ns
	Landrace	3.40	5.60	4.55	3.30	5.80	4.98	-9.57			
SDW (mg)	Improved	0.58	15.05	8.62	1.38	9.48	6.17	28.3	ns	***	***
	Landrace	2.34	11.82	6.46	2.27	9.94	7.18	-11.18			
RDW (mg)	Improved	2.36	10.90	6.59	2.14	9.72	6.20	5.91	***	ns	***
	Landrace	1.60	6.84	3.88	2.55	9.40	6.56	-69.29			
TPB (mg)	Improved	4.78	21.67	15.38	3.52	17.94	12.38	19.51	**	ns	***
	Landrace	3.94	17.84	10.34	4.82	19.34	13.75	-32.98			
RSL	Improved	0.54	1.84	1.15	0.72	3.42	1.60	-39.78	*	***	ns
	Landrace	0.50	1.57	0.90	0.96	2.19	1.54	-71.68			
RSW	Improved	0.32	1.08	0.76	0.49	1.55	1.03	-35.48	**	***	ns
	Landrace	0.27	1.04	0.64	0.72	1.45	0.94	-47.76			
SVI$_W$	Improved	0.29	2.16	1.43	0.22	1.47	1.09	24.05	***	*	***
	Landrace	0.32	1.44	0.83	0.23	1.56	1.17	-41.02			
SVI$_L$	Improved	251.33	3188.00	2380.32	307.00	2312.00	1583.95	33.46	**	***	**
	Landrace	614.40	2850.00	1726.13	421.17	2290.00	1591.56	7.80			

t50: time to reach 50% germination, FGP: final germination percentage, CL: coleoptile length, SL: shoot length, MRL: maximum root length, TRL: total root length, RN: root number, SDW: shoot dry weight, RDW: root dry weight, TPB: total plant biomass, RSL: root to shoot length, RSW: root to shoot weight, SVI$_w$: seedling vigor index based on seedling weight, SVI$_L$: seedling vigor index based on seedling length. *, ** and ***: significant difference at 0.5, 0.01 and 0.001 level respectively. T: Type, Trt: Treatment.

significant ones (0.30-0.50) for FGP, t50, CL, RSL, and SVI_L (values in the diagonal, Table 2.7).

In the control treatment, many significant correlations were found, TPB was positively correlated with all traits, except RSW and t50, and was greatly influenced by SDW and RDW. A high correlation was also found between TRL and MRL. Negative correlations were observed for t50 and CL with all other traits, indicating that genotypes with earlier germination and/or shorter coleoptile tended to have higher seedling traits values. RDW had a positive correlation with SDW (0.76).

Under stress, a high correlation was found between TPB and SL (0.75). Correlation between TPB with TRL and MRL (0.74 and 0.63, respectively) was less pronounced under stress conditions than under non-stress. RN, SDW and RDW had a similar correlation with TPB as found in non-stress. Remarkably, CL had a positive correlation with all seedling traits except RSW and RSL, whereas these correlations were negative at the control conditions, which means that seedlings having a longer coleoptile tended to be more tolerant (vigorous) under stress by producing more TPB. In addition, TPB under stress was negatively correlated with RSL (-0.44) and RSW (-0.43), whereas these correlations were positive under control conditions, indicating that, under no stress, seedlings invested more in root growth, and under stress they invested more in shoot growth (Table 2.7).

Correlation coefficients calculated between traits measured in field showed a high correlation of TPB with SDW (0.75), a positive moderate correlation between TPB and RDW, TRL and MRL (0.70, 0.52 and 0.50 respectively), and a weak correlation with RN (0.30). RDW was highly correlated with TRL (0.57), moderately correlated with RN, MRL (0.57, 0.53 respectively) and weakly correlated with SL (0.29), RSW (-29) and RSL (-35). CL presented strong correlation with SL (0.72) and a weak correlation with RN and TRL (0.42 and 0.34, respectively) (Table 2.S4).

The correlation between traits measured in the field and under controlled conditions showed low and non-significant correlations among traits, except a weak significant correlation was observed between field and stress for SDW (0.33) (Table 2.S5)

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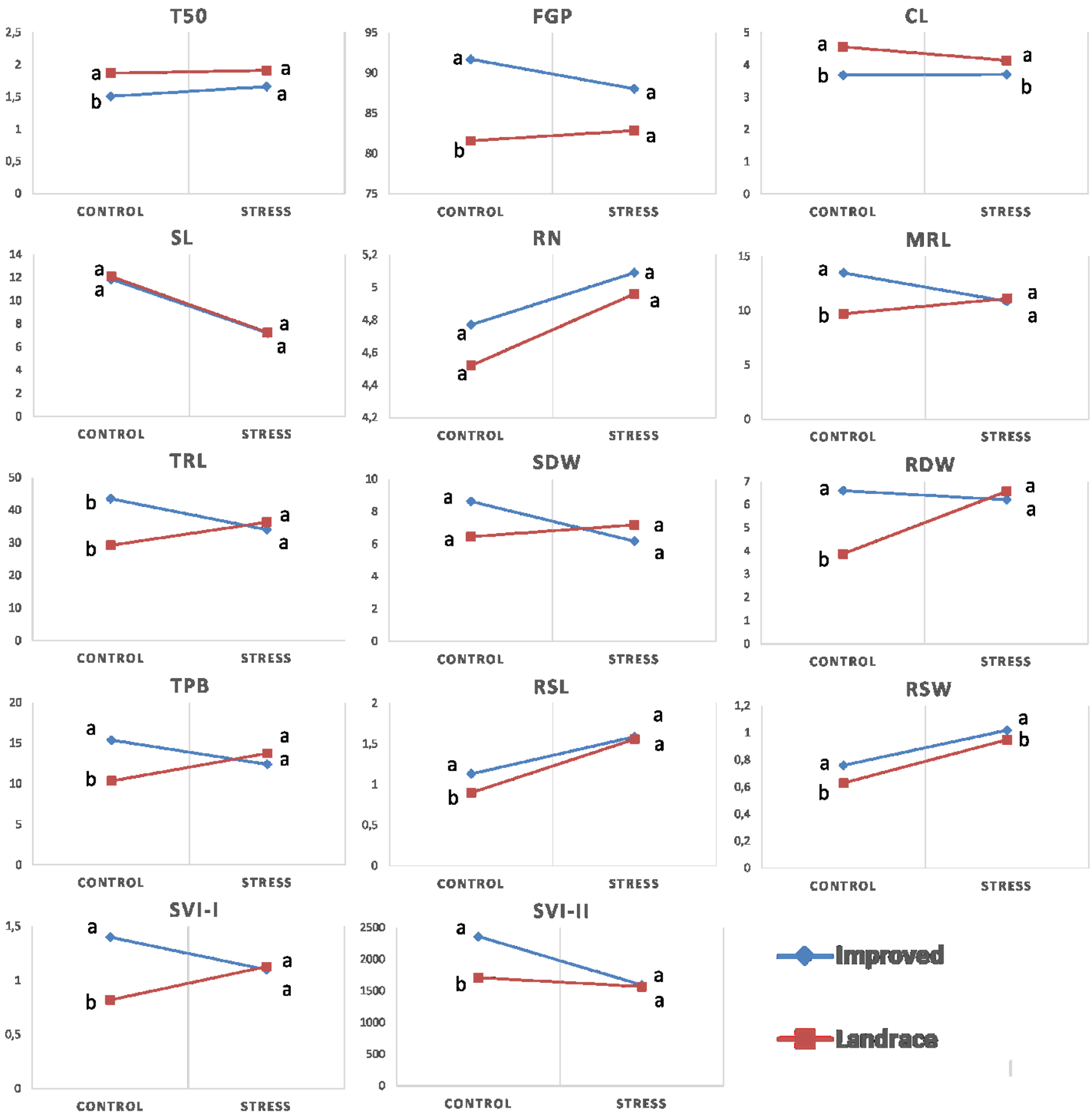

Figure 2.1. Seedling traits variation across stress and control conditions for landraces (red line) and improved genotypes (blue line). Different letters are indicating significant differenrence between control and stress for the corresponding trait.

Table 2.7. Pearson correlation coefficients of the assessed seedling traits under non-stress (below diagonal) and stress conditions (-6 bars) (above diagonal) and between the two conditions (cells with gray color).

		Stress													
		t50	FGP	SL	CL	RN	TRL	MRL	SDW	RDW	RSW	RSL	TPB	SVI$_W$	SVI$_L$
Non-Stress	t50	0.45***	**-0.51**	**-0.24**	**-0.27**	-0.02	**-0.31**	**-0.36**	-0.16	-0.22	-0.03	-0.03	-0.20	**-0.39**	**-0.46**
	FGP	**-0.53**	0.50***	0.21	0.23	0.12	**0.27**	**0.43**	0.11	0.22	0.07	0.09	0.17	**0.62**	**0.73**
	SL	-0.06	0.06	-0.02	**0.37**	**0.35**	**0.69**	**0.70**	**0.79**	**0.58**	**-0.57**	**-0.65**	**0.75**	**0.67**	**0.74**
	CL	0.08	0.05	-0.06	0.42***	**0.32**	**0.40**	**0.34**	**0.40**	0.19	**-0.42**	**-0.24**	**0.34**	**0.39**	**0.37**
	RN	-0.10	0.02	**0.40**	**-0.34**	-0.13	**0.40**	**0.25**	**0.40**	**0.52**	-0.16	**-0.43**	**0.49**	**0.40**	**0.25**
	TRL	**-0.36**	**0.45**	**0.47**	**-0.35**	**0.53**	0.07	**0.86**	**0.64**	**0.76**	-0.16	-0.14	**0.74**	**0.71**	**0.73**
	MRL	**-0.36**	**0.47**	**0.47**	**-0.28**	**0.43**	**0.96**	0.15	**0.56**	**0.62**	-0.20	-0.04	**0.63**	**0.71**	**0.89**
	SDW	-0.05	0.11	**0.65**	**-0.41**	**0.53**	**0.70**	**0.68**	-0.14	**0.73**	**-0.68**	**-0.53**	**0.95**	**0.79**	**0.54**
	RDW	**-0.34**	**0.35**	**0.39**	**-0.45**	**0.54**	**0.88**	**0.87**	**0.76**	0.10	-0.04	**-0.26**	**0.91**	**0.81**	**0.53**
	RSW	**-0.39**	**0.31**	**-0.34**	-0.16	0.13	**0.34**	**0.34**	-0.17	**0.47**	0.20	**0.63**	**-0.43**	**-0.30**	**-0.25**
	RSL	**-0.34**	**0.47**	**-0.24**	**-0.25**	0.13	**0.67**	**0.73**	**0.25**	**0.64**	**0.64**	0.32**	**-0.44**	**-0.27**	-0.18
	TPB	-0.20	**0.24**	**0.57**	**-0.45**	**0.57**	**0.83**	**0.81**	**0.95**	**0.93**	0.13	**0.46**	-0.20	**0.85**	**0.57**
	SVI$_W$	**-0.35**	**0.52**	**0.48**	**-0.39**	**0.51**	**0.88**	**0.87**	**0.85**	**0.93**	**0.24**	**0.58**	**0.95**	-0.07	**0.81**
	SVI$_L$	**-0.45**	**0.68**	**0.61**	-0.16	**0.39**	**0.88**	**0.91**	**0.64**	**0.76**	0.22	**0.52**	**0.74**	**0.86**	0.30**

t50: time to reach 50% germination, FGP: final germination percentage, CL: coleoptile length, SL: shoot length, MRL: maximum root length, TRL: total root length, RN: root number, SDW: shoot dry weight, RDW: root dry weight, TPB: total plant biomass, RSL: root to shoot length, RSW: root to shoot weight, SVI$_w$: seedling vigor index based on seedling weight, SVI$_L$: seedling vigor index based on seedling length.

*, ** and ***: significant difference at 0.5, 0.01 and 0.001 level respectively. Values in bold and with asterisks are different from 0 with a significance level alpha=0,05. Cells with grey color are correlations between stress and non-stress for the same trait.

2.5. Discussion

Drought stress at an early growth stage is a major limiting factor of wheat production in many parts of the world (Dhanda *et al*. 2004). Rebetzke *et al*. (2007) demonstrated that a good seedling emergence is important for achieving high wheat yields. Final germination percentage and time to reach 50% of germination are two important traits for plant establishment, especially under early drought conditions.

In this study, wheat genotypes behaved similarly under control and stress conditions for FGP but not for t50. The significant effect of treatment by genotype interaction in this last variable indicated that the genotypes responded differently across treatments, suggesting that the selection for this trait should be performed under target conditions (either under control or PEG stress), same as concluded by Abdel-Ghani *et al.* (2015).

Genotypes presenting a better FGP under stress were not necessarily the same genotypes having better t50 and *vice versa*. Only 4 (Beliouni, Capeiti, Gloire de Montgolfier and Miki-2) of the 9 most tolerant genotypes were considered tolerant for both FGP and t50, and these could be the best candidates to become drought-tolerant parents in a breeding program. Despite their results for other traits showed large variation, they could still have good breeding potential due to their ability to perform better under stress than under the control treatment. Gloire de Montgolfier could be singled out as the most promising genotype when taking into account all its rankings. It was particularly good under PEG stress regarding biomass related traits like SDW, RDW, TPB and SVI_W (Table 2.S6), and was the fourth most tolerant genotype regarding DSI (Table 2.4). Many genotypes decreased their FGP and delayed their t50 under drought stress, as expected for PEG-induced drought, which is reported to affect seed germination by reducing water availability (Al-Karaki 1998, Kaya *et al*. 2006). Conversely, some genotypes improved their FGP and t50 under drought stress, which could be explained by an already described osmo-priming effect of PEG (Al-Karaki 1998; Kaya *et al*. 2006). Some varieties widely grown under Algerian conditions, like Waha and Vitron, were among the most susceptible cultivars based on FGP and t50, indicating room for improvement for these two traits.

No interactive effect was found for all seedling growth traits, wheat genotypes ranked similarly under control and stress conditions for all seedling traits. SL was the most sensitive to drought stress (reduction 40.26%) while CL was the least affected trait. Our results differ from those of

Zarei *et al.* (2007), who found that root length was the most sensitive trait to drought stress induced by PEG in wheat.

In our experiment, genotypes tended to invest more resources in growing roots than shoots under stress conditions, compared to the control. Dhanda *et al.* (2004), in a similar study, found that root to shoot length ratio increased by 40 % under stress conditions. In some cases, the absolute root biomass of plants in drying soil may increase relative to well-watered conditions (Sharp and Davies 1985). The possible causes of increased root to shoot length ratio under water stress may be the limited supply of water and nutrients to the shoot, and changes in resource allocation due to changes in hormone messages induced in roots when they encounter drought stress (Davies and Zhang 1991).

Heritability, trait range and coefficient of variation, all decreased under stress conditions for most traits, as also found by Dhanda *et al.* (2004), indicating a reduction of expression or variation under stress conditions. More gain from selection might be expected for FGP, t50, CL and RSL (under control conditions), for FGP and t50 (under stress conditions) and for RDW, RSW and CL (in the field).

Seedling vigor index based on either length or weight of seedling are useful traits as they are correlated with other seedling traits. Time to reach 50% of germination (t50) correlated negatively with other traits, reflecting the importance of faster germination rate, indicating that faster germinating genotypes will be more vigorous. Remarkably, under non-stress, CL displayed negative correlations with all traits whereas they were positive under stress conditions, except for RSL and RSW ratio. This finding indicates that plants with longer coleoptile tended to be more tolerant by promoting more biomass under stress, contrarily to plants with shorter coleoptiles, which were yielding more biomass under optimal conditions. In our study, most landraces were ranked ahead of modern ones for CL (Table 2.S6), also manifested as the significant higher CL mean observed in landraces (as a group). Furthermore, CL expresses consistently across treatments, suggesting that this trait could be a potential target for indirect selection under either condition. An advantage for its use in breeding is its high narrow-sense heritability, as found by Shahbazi *et al*. (2012). Genotypes with longer coleoptile are appropriate for deep sowing to reach soil moisture in semi-arid regions, something which was often avoided by growers of dwarfing gene cultivars (Rebetzke *et al.* 2007). Currently, alternative dwarfing genes (e.g. *Rht8*), which reduce plant height without affecting coleoptile length, are available for use in wheat breeding (Rebetzke *et al.* 2007).

A positive correlation was found between root length (total and maximum) and shoot length under both conditions, indicating that increase in root length will increase shoot length, and *vice versa*, confirming results reported by Kan *et al*. (2002) and Baalbaki *et al.* (1999). Based on the drought susceptibility index (DSI), genotypes could be clearly separated into landraces and modern cultivars, with landraces showing increased drought tolerance. Six widely grown Algerian landraces were listed among the most tolerant genotypes (Beliouni, Djenah Khoteifa, MBB, Bidi 17, Oued Znatie and Guemgoum R'khem), which suggest their potential as donors of early drought tolerance. The importance of this difference, according to breeding history of the accessions, led us to focus on the comparison between landraces and improved cultivars, which is discussed next.

2.5.1. Type effect

One of the most interesting findings of this study was the clear differences between landraces and improved genotypes for several traits (Figure 1). Landraces had longer coleoptiles than improved cultivars, which is an advantageous trait for deep sowing practice. Ramshini *et al.* (2016) found that coleoptile length was significantly decreased in improved cultivars compared to old ones. They also found a significant difference between these two groups, with higher means observed in old cultivars for SL, RSL, SDW, TPB and SVI_L, whereas shoot length was significantly higher in modern cultivars. This effect could be influenced by the use of semi-dwarf alleles in modern cultivars, which has been shown to reduce early growth root length (Wojciechowski *et al*. 2009). Other studies found an overall reduction of root size in modern cultivars, compared to landraces (Waines and Ehdaie 2007). Some reports hypothesized that lower root to shoot ratio of improved cultivars early in the growing season may explain their increased harvest index, due to the reduced investment in root growth (Siddique *et al.* 1990). However, the optimum root size for grain yield has not been thoroughly investigated in wheat or most crop plants (Waines and Ehdaie 2007).

For most other traits, improved cultivars showed higher values than landraces only under control conditions. Landraces seemed to be more tolerant than improved cultivars since they increased trait performances under stress, as confirmed by the DSI result (Table 2.4, Figure 1). Several researches have already noted an outstanding performance of landraces. For instance, Ash *et al.*

(2017) found that durum wheat variety Strong field produced only about half of the root biomass of the wheat landrace Pelissier, at maturity in greenhouse trials under well-watered conditions. Bektas *et al*. (2016) found that wheat landraces were superior for root biomass, shallow root weight, deep root weight, number of tillers and plant height compared to improved cultivars. Some Spanish barley landraces also outperformed modern cultivars under low site productions (Yahiaoui *et al.* 2014).

2.5.2. Field conditions effect

Closing the gap between field and controlled experiment conditions is a current trend, which aims at extrapolating results obtained under artificial conditions to real (field) conditions. In this study, the ranges of variation and mean values of seedling traits in the field were less than what those observed under controlled conditions, except for SDW and TPB. This could be partly explained by the effect of soil impedance, which hampers root growth, and the effect of temperature and humidity of the soil as well. This suggestion is supported by that the SDW values obtained in field were superior to under controlled conditions, which may be explained by more space dedicated in field than in Petri dishes. Correlations established between traits in field and controlled experiment showed no interesting results and the two conditions of experiment were too different for all traits. The only weak correlation was found for SDW (Table 2.S5).

2.6. Conclusion and perspectives

- A good range of variation was observed for most seedling traits under controlled conditions, which could be useful in wheat breeding programs. Longer coleoptile length could be a potential trait for selection of drought tolerant genotypes especially at early growth stage in semi-arid environments, although pleiotropic effects on final shoot and root development and grain yield should be studied in parallel.
- After these results, Algerian wheat landraces, which have been cultivated for a long time in the region, could be introduced in durum wheat breeding programs to breed for drought tolerance at the early growth stage. Some widely cultivated modern varieties were listed among the most susceptible genotypes like Waha, Vitron and Wahbi. These varieties, which already have good agronomic performance overall, could be further improved by enhancing their FGP and/or t50.

- Further work is required to correlate root traits at seedling stage and root/agronomic traits at adult stage, to find proxy traits, which allow performing selection at early plant stage. Crosses between tolerant genotypes and susceptible genotypes identified in this study can generate populations appropriate for QTL mapping to identify genomic regions related to interesting seedling traits, and with good breeding potential.

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3. Durum wheat seminal root traits within modern and landrace germplasm in Algeria

3.1. Abstract

Seminal roots are known to play an important role in crop performance, particularly under drought conditions. A set of 37 durum wheat cultivars and local landraces was screened for variation in architecture and size of seminal roots using a laboratory setting, with a filter paper method combined with image processing by SmartRoot software. Significant genetic variability was detected for all root and shoot traits assessed. Four rooting patterns were identified, with landraces showing overall steeper angle and higher root length, in comparison with cultivars, which presented wider root angle and shorter root length. Some traits revealed trends dependent on the genotypes' year of release, like increased seminal root angle and reduced root size (length, surface and volume) over time. We confirm the presence of a remarkable diversity of root traits in durum wheat whose relationship with adult root features and agronomic performance should be explored.

3.2. Introduction

The root system of wheat includes two main types, seminal (embryonic) and nodal roots, also known as crown or adventitious roots (Chochois *et al.* 2015; Sinha *et al.* 2018). Both types of roots play a crucial role for plant growth and are active throughout the whole plant life. Seminal roots, however, could be more important under specific circumstances, like drought conditions, as they penetrate deeper into the soil layers than nodal roots, making water in deep layers accessible to the plant (Araki *et al.* 2001; Manske *et al*. 2002; Maccaferri *et al.* 2016). Seminal roots also play a capital role during crop establishment, as they are the only roots existing before the emergence of the fourth leaf. Seminal roots include one primary root, two pairs of symmetric roots at each side, and, at times, a sixth central root (Esau 1965).

The main features of root systems are encompassed under two categories, root system architecture (RSA) and morphology. RSA is related to the whole, or a large subset, of the root system, and may be described as topological or geometric measures of the root shape. Root morphology, as defined by J. Lynch, refers to "the surface features of a single root axis as an organ, including characteristics of the epidermis such as root hairs, root diameter, the root cap, the pattern of appearance of daughter roots, undulations of the root axis, and cortical senescence" (Lynch 1995). The traits often used to describe wheat roots are total root length, root surface area, root volume, root angle, number of roots and root diameter (Ahmadi *et al.* 2018; York *et al.* 2018; Nguyen *et al.* 2019).

Roots are difficult to measure readily in natural conditions. Root trait determination has become accessible through the development of phenotyping methods in artificial systems, for instance gel chambers (Bengough *et al.* 2004), rolled germination paper (Watt *et al.* 2013), clear pots and growth pouches (Richard *et al.* 2015), ‘Termita’ chamber and Whatman paper system (González *et al.* 2016), or growth pouches system (Adeleke *et al.* 2020). Seminal roots can be phenotyped early and easily compared to the root system of mature plants (El Hassouni *et al.* 2018; Richard *et al.* 2018), and for this reason they have been proposed as good candidates to act as proxy traits in wheat (Bai *et al.* 2013) and maize (Tuberosa *et al.* 2002a; Tuberosa *et al.* 2002b). Nevertheless, phenotyping these traits could be of interest only if they are useful to predict root growth and functioning in adult plants (Manschadi *et al.* 2006; Paez-Garcia *et al.* 2015). Indeed, several studies have found useful associations with traits in adult plants of wheat species (Løes *et al.* 2004; Manschadi *et al.* 2008; Ruiz *et al.* 2018; Li *et al.* 2020). For instance, seminal root angle was correlated with nodal root angle (Maccaferri *et al.* 2016; Alahmad *et al.* 2019), and with grain yield under drought conditions (Ali *et al.* 2015). Seminal root number was correlated with thousand kernel weight (TKW) under stress, while primary root length at seedling stage was correlated with TKW under wetter conditions (Ruiz *et al.* 2018). A steeper angle between the outermost roots, and a higher root number in wheat seedlings have been linked to a more compact root system with more roots at depth in wheat (Nakamoto and Oyanagi 1994; Bengough *et al.* 2004; Manschadi *et al.* 2008).

Genotypic variation in root architecture has been reported within genotypes of different crop species (Masi *et al.* 1998; Liao *et al.* 2001; Lynch *et al.* 2001), including wheat (Richard *et al.* 2015; Manschadi *et al.* 2006; Ruiz *et al.* 2018; Roselló *et al.* 2019). The presence of variation for the trait of interest is an essential requirement to improve the adaptability of agricultural crops under changing environmental conditions (El-Beltagy and Madkour 2012).

Local landraces are considered well adapted to the region where they were grown and contain large genetic diversity useful to improve crops like durum wheat (Nazco *et al.* 2015). These landraces were replaced by high yielding but more uniform semi-dwarf cultivars, better adapted to modern agriculture. However, scientists are convinced that local landraces still constitute a genetic resource useful to improve commercially valuable traits (Lopes *et al.* 2015). It is assumed that root traits enhance response to drought stress (Araujo *et al.* 2015), but the realization of their contribution into superior grain yield depends on the type of drought and the agro-ecological conditions (Rao *et al.* 2017). A deep rooting ideotype ("steep, cheap and deep") was proposed by Lynch (2013) to optimize water and N acquisition, building on the assumption that deeper rooting genotypes will use water that is beyond reach for shallower rooting genotypes. Modern breeding has caused some shifts in root system architecture of durum wheat, from shallower and densely rooted systems in landraces of Mediterranean origin to deeper and more evenly distributed systems throughout the soil depth in cultivars worldwide (Maccaferri *et al.* 2016).

The current study aims at evaluating the diversity of seminal root traits, including root angle and depth, during early growth of a set of durum wheat genotypes, consisting of modern cultivars and local landraces which are representative of the germplasm adapted to the mostly semi-arid conditions of Algerian cereal-growing regions before and after the advent of modern breeding. The study aims to reveal morphological diversity that could have agronomic relevance and, therefore, interest breeders.

3.3. Materials and Methods

3.3.1. Plant material

We studied thirty-seven genotypes (landraces and modern cultivars), representative of durum wheat (*Triticum turgidum ssp. durum* Desf.) grown in Algeria. Geographical origins were varied (Algeria, France, Italy, Spain, Tunisia), and included genotypes produced at international breeding programs addressing semi-arid areas, namely the International Maize and Wheat Improvement Center (CYMMIT), the International Center for Agricultural Research in the Dry Area (ICARDA) and the Arab Center for the Studies of Arid zones and Dry lands (ACSAD). These genotypes are representative of different periods of agriculture in Algeria, before and after the Green Revolution (Table 3.1).

3.3.2. Root phenotyping

3.3.2.1. Preparation of seeds

Twelve seeds of uniform size and healthy aspect were visually selected from each genotype and surface sterilized in a sodium hypochlorite solution (1.25% + one detergent drop, Mistol Henkel

Iberica®). Seeds of each genotype were soaked and shaken in the solution for 15 - 20 minutes. Then, they were rinsed four times with sterile deionized water, in sterile conditions.

Twelve seeds of each genotype were placed in Petri dishes, each with two filter papers soaked with 4 ml of sterile water. Then the Petri dishes were placed in a dark room at 4°C for four days, and then at 22°C/18°C in a growth chamber with a 12 h light/darkness photoperiod for about 16 hours.

Finally, the pre-germinated grains were transferred to the rhizo-slide system, described in detail in the next section and in Figure 3.S1. The experiment was carried out at the Laboratory of Cellular Biology and Genetics, Department of Biomedicine and Biotechnology of the University of Alcalá, Spain.

3.3.2.2. The Rhizo-Slide system

The rhizo-slide system was constructed as a sandwich made with glass plate, black cardboard, filter paper and a black plastic sheet. Sheets of A4-size black cardboard (180 g/m2, www.liderpapel.com) and filter papers were previously sterilized in an autoclave, and then soaked in the nutritive solution Aniol (Aniol 1984). The nutritive solution was prepared by dissolving 0.5550 g of CaCl2, 0.8215 g of KNO3, 0.6352 g of MgCl2.6H2O, 0.0165 g of (NH4)2SO, 0.0400 g of NH4NO3 in 100 ml of distilled water, to which 500 µl/l of Plant Preservative Mixture (PPMTM, Plant Cell Technology) at pH 5.8 was added. Each 8 ml was used to prepare 1 liter of nutritive solution. A black cardboard with a nick made at the top center, was placed on a glass plate with the same dimensions, then the pre-germinated grain (with embryonic part downward) was positioned just below the nick and covered by a filter paper. A black plastic sheet was used to cover the filter paper to ensure obscurity for roots, shifted ~2 cm upwards to allow better contact of the cardboard and filter paper sheets with the nutritive solution. Two rhizo-slides were confronted to each other by the glass plate side, and the set was placed vertically in a glass box (internal dimensions of 32.2, 22, and 16 cm, length, width and height) with two liters of the nutritive solution at the bottom, and then secured with two paper clips. Each glass box held 6 glass plates with two rhizoslides each, for a total of 12 seedlings, consisting of two genotypes, 6 seedlings for each (Figures 3.S1). In total, each genotype was replicated 12 times. More details on the system are found in Ruiz *et al.* (2018).

Once placed in the rhizo-slides and the glass boxes, the seedlings were grown in a growth chamber for 7 days at 22/18 °C and 12/12 h photoperiod, day/night. The 37 genotypes were processed in batches of 6.

Pre-germinated seeds of each 6 genotypes were placed into six glass boxes, holding each 6 seeds of two different genotypes. A complete batch comprised six boxes, three glass boxes prepared each Monday, and three each Thursday, every week. In total, 7 batches (14 runs) were performed

Table 3.1. Name, type of cultivar, origin and year of release of 37 genotypes of durum wheat used in the experiment.

Nº	**Genotype**	**Type/Pedigree**	**Origin**	**Year of Release**
1	Beliouni	Landrace	Algeria	1958
2	Bidi 17	Landrace	Algeria	1930
3	Djenah Khotifa	Landrace	North Africa	1955
4	Gloire de Montgolfier	Landrace	Algeria	1960
5	Guemgoum R’ khem	Landrace	Algeria	1960
6	Hedba 3	Landrace	Algeria	1921
7	Langlois	Landrace	Algeria	1930
8	Mohammed Ben Bachir	Landrace	Algeria	1930
9	Montpellier	Landrace	Algeria	1965
10	Oued Zenati 368	Landrace	Algeria	1936
11	Acsad 65	Gerardo-vz-469/3/Jori-1//Nd-61-	ACSAD	1984
12	Altar 84	Ruff/Flamingo,mex//Mexicali-	CYMMIT	1984
13	Ammar 6	Lgt3/4/Bicre/3/Ch1//Gaviota/Starke	ICARDA	2010
14	Bousselem	Heider//Martes/Huevos de oro	ICARDA	2007
15	Boutaleb	Hedba 3/Ofanto	Algeria	2013
16	Capeiti	Eiti*6/Senatore-Cappelli	Italy	1940
17	Chen’s	Shearwater(sib)/(sib)Yavaros-79	CYMMIT	1983
18	Ciccio	Appulo/Valnova(f6)//(f5)Valforte/Patrizi	Italy	1996
19	Cirta	Hedba-3/Gerardo-vz-619	Algeria	2000
20	Core	Platani/Gianni	Italy	2008
21	GTA Dur	Crane/4/Polonicum PI185309//T.glutin	CIMMYT	1972
22	INRAT 69	Mahmoudi/(bd-2777)Kyperounda	Tunisia	1969
23	Korifla	Durum-dwarf-s-15/Crane//Geier	ICARDA	1987
24	Mansourah	Bread wheat/MBB	Algeria	2012
25	Massinissa	Ofanto/Bousselem	Algeria	2012
26	Megress	Ofanto/Waha//MBB	Algeria	2007
27	Mexicali 75	Gerardo-vz-469/3/Jori(sib)//Nd-61-	CIMMYT	1975
28	Ofanto	Ademelio/Appulo	Italy	1990
29	Oued El Berd	Gta dur/Ofanto	Algeria	2013
30	Polonicum	Triticum polinicum/Zenati boulette	France	1973
31	Sahell	Cit”s”/4/Tace/4*tc//2*zb/wls/3/aa”s’’/5/	CYMMIT	1977
32	Simeto	Capeiti-8/Valnova	Italy	1988
33	Sitifis	Bousselam/Ofanto	Algeria	2011
34	Vitron	Turkey77/3/Jori/Anhinga//Flamingo	Spain	1987
35	Waha	Plc/Ruff//Gta’s/3/Rolette	ICARDA	1986
36	Wahbi	Bidi 17/Waha//Bidi 17	Algeria	2002
37	ZB × Fg	Zb/fg‘‘s’’ lk/3/ko 120/4/Ward cs 10604	Algeria	1983

*: Backcross

until the experiment was completed (accounting for some seedlings that had to be replicated for various reasons). The set of genotypes for each run was selected randomly.

During the experiment, the boxes were replenished with distilled water every two days, to refill to the initial solution level. At the same time, to minimize seedling failure, each single seedling received 10 ml of the nutritive solution, applied with a pipette, near each seed. On the eighth day, the rhizo-slides were opened, and shoots were immediately collected. The fresh roots were scanned using a Canon 'LiDE210' scanner at 300 ppi to capture the first image then overlapped roots were manually separated and a second scan was done. The individual plant shoot dry weight (SDW) was obtained after oven-drying at 80°C for six hours.

3.3.2.3. Image analysis

The two images of a rhizo-slide were analyzed using SmartRoot software v.3.32 (Lobet *et al.* 2011) plugin for ImageJ1.46R (http://imagej.nih.gov/ij/download.html). The first image was used to measure only root angles and the second one to assess the other root traits using manual and semi-automatic SmartRoot procedures. Each single root of the seedling was traced, semi-automatically, and then SmartRoot automatically generated the corresponding traits. In total, ten variables from the SmartRoot output were recorded for each single seedling: total root length (TRL), primary root length (PRL), mean length of the other seminal roots (MRL), total root surface area (Surface), mean root diameter (Diameter), total root volume (Volume), root number (RN), and shoot dry weight (SDW). Root angle was determined for each single root with respect to the vertical (90°). From this determination, we extracted the maximum vertical angle (MVA) represented by the root growing with steepest angle, the least vertical angle (LVA) represented by the root growing with the widest angle, and mean vertical angle (MRA) of all the roots, for each seedling.

3.3.3. Statistical analysis

The experiment was considered a completely randomized design, with 12 replicates per genotype. Statistical analyses were performed using the REML (Restricted maximum likelihood) procedure with Genstat 18 (Payne 2009). Genotypes were considered as fixed factors and replications were considered as a random factor. The "Genotype" factor (n-1 degrees of freedom) was broken down into a single degree of freedom comparison of landraces vs. cultivars (named "Type" effect), and a "within type" factor (n-2) which corresponds to the variation of genotypes within each type. Multiple means separation was carried out using LSD at 0.05 level, for variables in which the F-value for "Genotypes" was significant. A principal component analysis (PCA) and a hierarchical cluster analysis (HC) were performed using the R package FactoMineR (Le *et al.* 2008). The hcut function was used for tree cutting levels truncation. The R package Factoextra (Kassambara and Mundt 2017) was employed for extracting and visualizing the results. Broad-sense heritability (h^2) was calculated on entry mean basis using the REML procedure, as follows: $h^2 = \sigma^2_g / (\sigma^2_g + (\sigma^2_e/r))$, where σ^2_g is the genotypic variance, σ^2_e is the error variance and r is the number of replications.

3.4. Results

3.4.1. Genotypic variability

We found remarkable genetic variability for all measured traits, as revealed by the highly significant differences among genotypes in the analyses of variance (Table 3.2). Significant differences were also found in the "type" comparison for most traits, except for Diameter and RN (Table 3.2). For the other traits, the mean squares for type were 4 to 12 times larger than those for genotypes.

The means of landraces showed higher or equal mean values compared to cultivars for all traits, except root angle (MRA, LVA and MVA), which was higher in cultivars (Figure 3.1). It is worth mentioning that the landrace group presented higher root depth (PRL) than the cultivars.

All traits but SDW were root-related traits so, henceforward all the traits will be referred to generally as root traits unless stated otherwise. All traits (except RN) showed a near normal distribution (Figure 3.1) which denotes their polygenic control. A wide range of phenotypic values was observed for most traits (Table 3.2). The landrace group showed a larger range of variation for TRL, Surface, Volume and SDW than the cultivars. For the other traits, the cultivars had higher ranges of variation (Tables 3.S1, S2).

The coefficients of variation (CV) ranged from small values like 5.19 (Diameter) to 24.60 (MRA, Table 3.2). The exception was the large CV found for MVA, 59.82. When calculated separately for landraces and cultivars, slightly higher CV for most traits were found in landraces compared to cultivars (Table 3.S2). All the traits exhibited high broad sense heritability (h^2), ranging from 0.80 for MVA to 0.98 for MRA (Table 3.2).

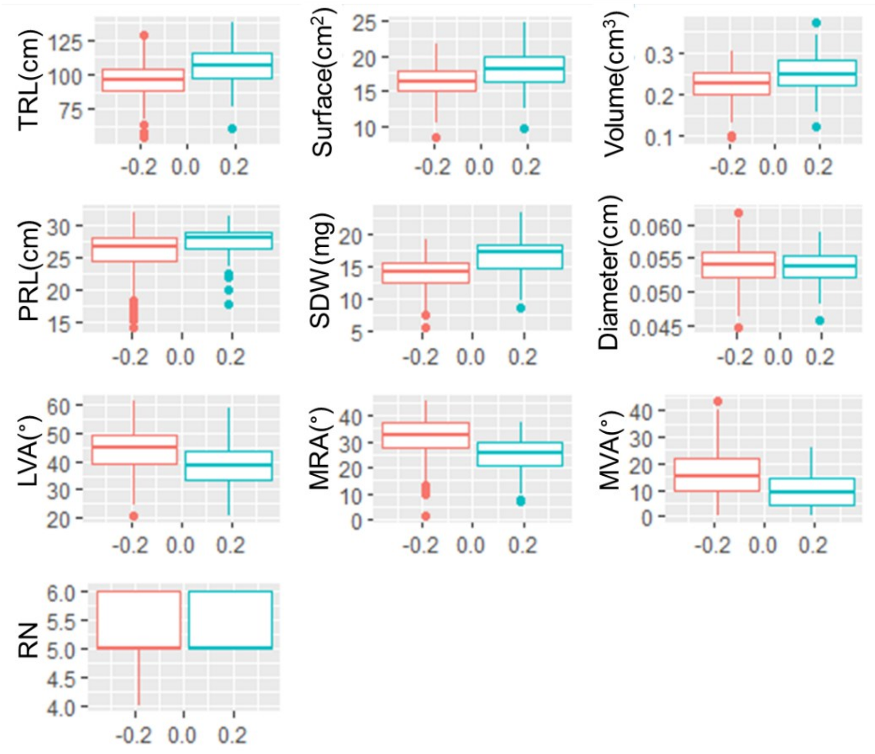

Figure 3.1. Boxplots for root traits for the cultivar (red) and landrace (blue) groups. Horizontal lines splitting the boxes indicate the median values, box limits indicate the 25th and 75th percentiles, whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles, whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles, outliers are represented by dots. Variable names coded as in Table 3.2. Genotypes mean values are in Table 3.S1.

3.4.2. Relationships between traits

Highly significant correlations were found between most traits (Table 3.2). TRL, Surface and Volume were highly and positively correlated among them. There were moderate positive correlations between TRL, Surface, and Volume, with PRL, SDW, RN and negative ones with root angle variables (seedlings with higher TRL, Surface and Volume tended to have steeper root angles). Seedlings with higher RN tended to have roots with thinner root diameter, indicating that there could be some kind of compensation between these traits (more roots with finer diameter and vice versa). Interestingly, seedlings with higher primary root length produced more shoot biomass. Performing correlations between traits within each group (cultivars and landraces) showed, in general, similar patterns to the correlations performed for the entire dataset (Table 3.S2). The moderate relationship of PRL with MVA and RN disappeared in the landrace group, compared to the cultivars and the whole dataset (Table 3.S2).

Table 3.2. Descriptive statistics, broad sense heritability (h^2), ANOVA summary and correlation coefficients for the root traits assessed in 37 durum wheat cultivars.

	Descriptive statistics					**ANOVA**		**Correlation**									
Traits	**Min**	**Mean**	**Max**	**CV**	**h^2**	**Genotype**	**Type**	**TRL**	**Surface**	**Volume**	**Diameter**	**PRL**	**SDW**	**MRA**	**LVA**	**MVA**	**RN**
TRL (cm)	54.28	98.49	137.22	13.51	0.90	***	***	1	***	***	ns	***	***	***	**	***	***
Surface (cm^2)	8.25	16.77	24.82	14.74	0.90	***	***	0.95	1	***	***	***	***	***	ns	***	***
Volume (cm^3)	0.0962	0.2326	0.3721	17.03	0.90	***	***	0.83	0.97	1	***	***	***	***	ns	**	***
Diameter (cm)	0.0447	0.0538	0.0620	5.19	0.87	***	ns	0.08	0.38	0.59	1	***	***	***	*	**	***
PRL (cm)	14.32	26.51	32.06	10.76	0.90	***	***	0.55	0.55	0.52	0.17	1	***	ns	**	***	ns
SDW (g)	5.70	14.72	23.50	18.66	0.94	***	***	0.55	0.63	0.64	0.40	0.58	1	ns	**	*	ns
MRA (°)	1.20	30.36	45.69	24.60	0.98	***	***	-0.39	-0.32	-0.23	0.20	-0.01	0.00	1	***	***	ns
LVA (°)	20.40	42.71	61.47	17.81	0.92	***	***	-0.28	-0.23	-0.18	0.12	0.08	0.01	0.76	1	***	ns
MVA (°)	0.00	14.10	43.49	59.82	0.80	***	***	-0.25	-0.20	-0.15	0.12	-0.27	-0.13	0.62	0.25	1	**
RN (no.)	4.00	5.32	6.00	9.13	0.87	***	ns	0.37	0.32	0.26	-0.22	-0.01	0.06	-0.09	0.02	-0.14	1

*, **, ***: sources of variation in the analyses of variance or correlation coefficients significant at $P<0.05$, 0.01 and 0.001, respectively. TRL: Total root length, Surface: total root surface area, Volume: Total root volume, Diameter: mean root diameter, PRL: Primary root length, SDW: Shoot dry weight, MRA: Mean root angle, LVA: Least vertical angle, MVA: Maximum vertical angle, RN: Root number.

3.4.3. Time trends of root traits

When the genotypic means were plotted against year of release of the genotypes, different trends were observed (Figure 3.2, Figure 3.S2), in which, all the traits presented significant regression coefficients except Diameter, RN and PRL (Table 3.S3). This trend was largely influenced by the comparison of landraces vs. cultivars, because landraces are older. The trend was positive or negative depending on the trait. Overall, cultivars reduced their seminal root length and developed a shallower root angle compared to landraces (Figure 3.2). Root surface and volume of root presented the same trend as root length, as they were highly correlated, as mentioned above. MVA and LVA showed the same trend as MRA. No substantial variation was observed for RN, Diameter and PRL. Regarding the shoot, a remarkable and steady reduction in SDW over the years was detected (Figures 3.1, 3.S2).

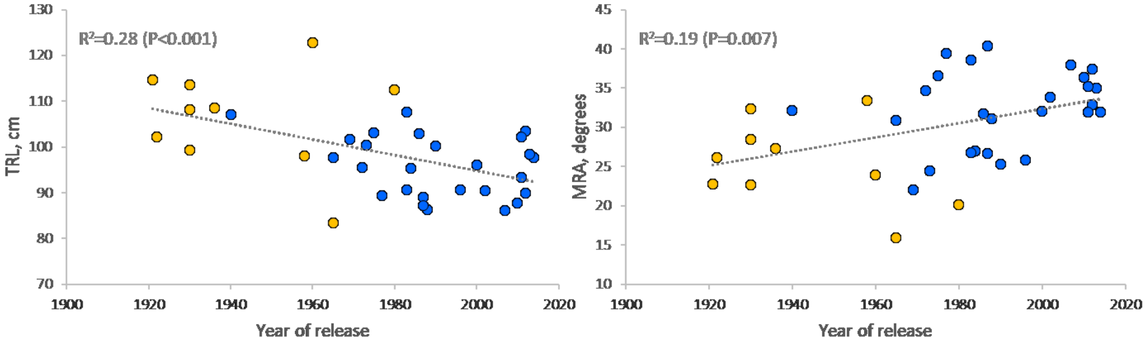

Figure 3.2. Time trends for root length and root angle in seedlings of 37 durum wheat varieties. Yellow symbols correspond to landraces, blue symbols correspond to cultivars. The coefficients of determination (R^2) of the regression lines are indicated in each graph.

3.4.4. Grouping of genotypes according to root traits

The first two principal components explained 69.63 % of the total variation (Figure 3.3A). The first component (46 %) was most related to Surface, TRL, Volume and SDW, with the respective contributions of 20.19, 19.04, 18.16 and 11.51 (Table 3.S4). MRA, LVA and Diameter had the highest loadings for the second component (PC2). Correlations between these traits are discussed above (Table 3.2). Thus, the first axis (PC1) was related to root size traits and the second one to root architecture traits.

Genotypes were better distributed along the first component, as a result of the contrasting position between landraces, many with large positive scores on PC1 (due to their higher root size

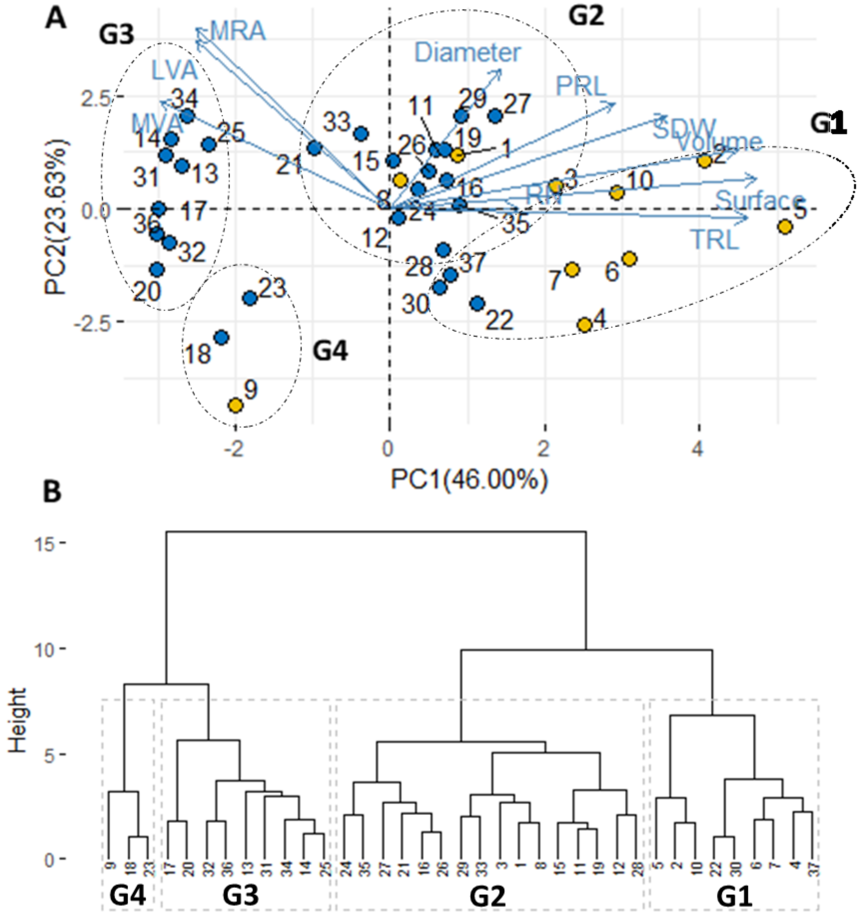

Figure 3.3. Biplot of first two principal components (A) and dendrogram resulting from hierarchical clustering (B) based on seedling traits for 37 durum wheat genotypes. Ellipses in (A) encompass the individuals according to the clustering presented in (B). Yellow symbols correspond to landraces, blue symbols correspond to cultivars. Genotypes coded with numbers as in Table 3.1.

and shoot weight) and the cultivars, with lower positive or negative scores in PC1, so the discrimination between these two groups was clear (Figure 3.3B). From the hierarchical classification, which was carried out based on the original data, four groups were created (G1 to G4) (Figure 3.3B). G1 was mostly formed by landraces. G2 was the largest one and was constituted by cultivars, and two landraces. This group was at a central position in the biplot graph (Figure 3.3B), presenting close to average values for most traits. G3 was located on the negative side of PC1, contrasting with G1 by having relative smaller root size. Finally, the last group (G4) was formed by only three genotypes depicted on the negative quadrant, for both PC1 and PC2, having smaller values for both classes of root traits, fine, steeper root angle and reduced root traits related to biomass. This group included landrace Montpellier (genotype 9), which showed a special root system architecture compared to other landraces, with steeper root angle, and lower SDW, closer to two cultivars from Italy and ICARDA.

3.5. Discussion

The durum wheat collection used in this study was assembled to explore the seminal root variability present in a set of genotypes cultivated in Algeria, with a historical perspective on the possible changes caused by modern breeding. The method chosen enabled data acquisition and processing of 444 single plants, by one person, in two months. Its performance could be easily expanded by increasing the number of boxes and operators. Therefore, it is amenable to the scale needed for the type of studies carried out in plant genetics and breeding. Root number together with root length, the main results of this type of experiment, describe how extensively the seminal axes can potentially explore the rooting volume. These easily measurable traits at early stage can have agronomic implications. For example, root spread angle is an additional feature whose variation can influence how crops cope with water-limited conditions and/or other environmental constraints, such as high pH, toxic ions, or low nutrient availability (Devaiah *et al.* 2007; da Silva *et al.* 2016). The root angular spread at an early growth stage can be used to predict the partitioning of root biomass in the soil profile at the adult plant stage (Maccaferri *et al.* 2016; Alahmad *et al.* 2019; Ali *et al.* 2015), a feature relevant for water use efficiency in wheat (Manschadi *et al.* 2006; Sanguineti *et al.* 2007). Therefore, artificial systems are efficient at revealing phenotypic (and presumably genetic) variability, but its implications on agronomic performance must be validated later under field conditions.

3.5.1. Large genotypic variation for seminal root traits

An overview of the results found in different studies sheds more light on the actual genetic variation available for seminal root traits, better than any single study. Differences among studies may be partly due to slight differences in the experimental methods, but also to the size and scope of the genetic material used. Nevertheless, some meaningful conclusions can be derived.

We found significant genetic variation for all traits. We found a range of values for the least vertical root angle (LVA) from 20.40° to 61.47°. Multiplying these values by two (range from 40.80° to 122.94°) allows the comparison of our study with others, in which the values of total opening of the angle of root system was reported. Our range was superior to those found by others in durum (Sanguineti *et al.* 2007) and bread wheat (Nakamoto and Oyanagi 1994; Manschadi *et al.* 2006) . Our wheat genotypes displayed similar low ranges of variation in mean root number as in similar studies in durum (Sanguineti *et al.* 2007; Cane *et al.* 2014), with a slightly higher mean. In our genotypes, the sixth root was present in about a third of all genotypes, with no significant differences between landraces and cultivars. This is a similar proportion than found in a study of Mediterranean and North-American elite material (Sanguineti *et al.* 2007), with the striking difference that in the former study they reported almost absence of the sixth seminal root in native Mediterranean materials (Sanguineti *et al.* 2007). Neither sample of landrace materials was large enough to derive definitive conclusions from these studies, but at least we can say that Algerian landraces are not more likely to lack the sixth seminal root than modern cultivars.

Based on the coefficients of variation, overall, landraces showed higher slightly variability for most traits, especially for root angle, even though the sample size was lower than for cultivars. Previous reports indicate that native Mediterranean landraces are likely to provide additional genetic variability for root architecture (da Silva *et al.* 2016), particularly in wheat accessions that experienced long-term natural selection in drought-prone environments (Robertson *et al.* 1979), and in barley (Grando and Ceccarelli 1995). Overall, the Algerian landraces showed sizeable genetic variation for most traits, indicating that they harbor relevant root morphology variation that should be further investigated by geneticists and breeders.

3.5.2. Classification of durum wheat genotypes according to root morphology

Overall, genotypes with higher root length tended to have larger root number, as found in a previous study (Sanguineti *et al.* 2007), and a narrower root angle. Other authors (O'Brien 1979; Manschadi *et al.* 2008) found no correlation between root angle and root number. Sanguineti *et al.* (2007) also found no correlation of root angle with other traits and suggested that root angle was controlled by an independent set of genes. In our study, however, given the negative correlation between MRA and root size traits, we cannot rule out that these two traits are controlled by the same set of genes.

We found that higher root length and Diameter were associated with higher SDW (r of 0.55 and 0.40, respectively, Table 3.2), suggesting a size effect that affected the whole plant. Rather similar observations were done in the Spanish core collection of tetraploid wheats, but the plant size effect was visible for subsp. *dicoccon* and *turgidum*, but not for *durum* (Ruiz *et al.* 2018). Correlation between root length and volume, and SDW was also found in hexaploid wheat (Narayanan *et al.* 2014). We found no correlation between RN and MRA, in agreement with previous studies (O'Brien 1979; Manschadi *et al.* 2008). It seems that an overall plant size effect that affects harmonically roots and shoots is common in wheat species.

Our genotypes displayed different seminal root system patterns, from vigorous and steep to a small and shallow root system. These root patterns may be related to phylogenetic relationships, regional origin, and functional plant adaptation to different environments, as indicated in previous studies (Bodner *et al.* 2013). There were differences in the length of seminal roots of single plants. This was made evident by calculating the difference between the length of the primary root (PRL), and the average of the rest (MRL). G2 and G3 had a higher difference between PRL and the mean length of other roots (MRL), compared to groups G1 and G4, which had roots with more similar lengths (Table 3.S5). G2 genotypes combined a significantly longer primary root (Table 3.S5) with the largest difference between it and the other seminal roots (together with G3). This rooting pattern, based on dissimilar growth of the roots, could have an impact on overall soil exploring capacity that should be explored further, particularly its usefulness in semi-arid environments, to access to stored water at deep layers at critical periods (flowering and grain filling), while keeping enough shallow roots to take advantage of in-season precipitations.

Two groups (G1 and G3) showed the highest contrast in the multivariate analysis (Figure 3.3). G1, with a majority of landraces, displayed a vigorous seminal root system, in contrast with G3, formed entirely by cultivars with small root systems. Our finding was in agreement with the study of a collection of 160-durum wheat landraces (Roseló *et al.* 2019) in terms of larger seminal root size. This study found that landraces coming from the eastern Mediterranean region (Turkey), the driest and warmest areas considered in the study, showed the largest seminal root size and widest root angle compared to landraces from eastern Balkan countries. The authors claimed that these differences were due to the adaptations of landraces to the contrasting environmental conditions of these two regions. The larger root size and wider root angle from Turkish landraces would allow better exploration of the full soil profile and better water capture. Among the four groups found in this study, no one combined the highest MRA and TRL, comparable to Turkish landraces. Therefore, there could be room for improvement for the root systems of durum wheat for Algeria. Crosses to combine these traits in a single genotype should be devised, and Turkish landraces could be tested in Algerian conditions, to assess their potential.

In our germplasm, the landraces showed on average narrower angle and higher root size. Previous studies on Mediterranean durum wheats (Roselló *et al.* 2019) found that the genotypes with the narrowest angle came from the western Mediterranean region, and that they also had heavier grains (Royo *et al.* 2014; Soriano *et al.* 2016). Additionally, it was reported that *Triticum turgidum* subsp. *dicoccon* landraces coming from cooler and wetter zones had shallower seminal root systems than those from warmer and drier areas (Ruiz *et al.* 2018). The subsp. *durum* landraces, developed in warmer and drier areas, tended to have larger and steeper root patterns than landraces coming from cooler and wetter zones. Accordingly, the root system architecture of the Algerian landraces would indicate adaptation to a warm and dry environment. Other studies have found different root morphologies in apparent adaptation to stressful conditions. For instance, the drought tolerant bread wheat cv. SeriM82 has a compact root system (Manschadi *et al.* 2006), associated to a limited water use early in the season, facilitating access to stored water later in the reproductive phase. Contrary to our landraces, SeriM82 exhibited less vigorous shoot growth. Also in contrast with our findings, a study of bread wheat germplasm grown historically in the semi-arid northwestern of China (Zhu *et al.* 2019) found that breeding caused narrowing of the seminal root angle, reduced root number, and increase of primary seminal root length. In that study "newer cultivars produced higher yields than older ones only at the higher sowing density, showing that increased yield results from changes in competitive behavior". This view was confirmed and expanded later (Song *et al.* 2010), confirming that the advantage of new Chinese wheat cultivars came from the attenuation of inter-plant competition and increased plasticity in root morphology. A seminal root architecture with fewer, longer seminal roots with narrower root angle, would overlap less with neighbors, leading to less competition between individuals (De Parseval *et al.* 2017), and these trends agree with the hypothesis of weakening of "selfish" traits (Weiner *et al.* 2017).

The shift in root morphology observed in Algeria in the step from landraces to modern cultivars does not conform to the scenario described in those works. There was a reduction of overall root length and volume after the advent of modern breeding, which could be consistent with the reduction of inter-plant competition, but combined with widening of root angle, which does not bode well with that hypothesis. It seems that wheat breeding may have resulted in different trends for root morphology in different parts of the world. This could be the result of adaptation of Algerian landraces to agronomic conditions different from current agriculture. The difference in rooting pattern between landraces from different geographical areas and cultivars may lie in the agronomic environments in which they were developed. In general, modern durum wheat cultivars were bred under high plant densities (Song *et al.* 2010), whereas landraces were grown in stands with density adapted to the environment. The morphology of Algerian landraces (long seminal roots growing in steep angles) conforms to the "steep, cheap and deep root ideotype" (Kembel and Cahill 2011) and could be the result of adaptation to accessing water in deep soil layers. Further studies with adult plants are needed to evaluate if root features of seedlings are maintained when the competition between individuals for root growth is increased (as the seminal and nodal roots require more space and resources than just the seminal roots of the seedlings). A shovelomics experiment is being carried out with the same genotypes, which could elucidate this issue at least for some measurable traits like root angle.

The high SDW of our durum landraces compared to cultivars could be related with the lack of dwarfing genes in the landraces. This hypothesis was already put forward previously for bread and durum wheat for some height reducing genes (Ellis *et al.* 2004), which reduced the first seedling leaf growth in *Rht* genotypes compared with the corresponding tall wheat lines.

3.6. Conclusion and perspectives

- We have found wide genetic variability in a collection of durum wheat genotypes cultivated in Algeria and unraveled a possible historic trend that sheds light on the outcomes of modern breeding. An important issue is to what extent this variability found at seedling stage can reflect the variability in the field with the same genetic material, more precisely, which traits can be consistent across plant phases (seedling and adult plant), enabling the selection at early seedling stage. If this relationship is not found, then the room for testing of seminal root traits is very limited. Experiments to evaluate this relationship are ongoing.
- Overall, landraces showed larger root size and steeper root angle. These two traits could be involved in the adaptation of landraces to water stressed environments. The dwarfing genes seem to influence biomass partitioning, screening the current germplasm for these genes would elucidate this issue. The root size and shape in our data indicated some

independence that would open opportunities to design cultivars with the desired combinations of traits.

- Overall, the current genotypes present a diverse root system architecture, from compact deep rooting to wide shallow one. This opens the opportunity to test the four different root ideotypes found (G1-G4) for functional implications under water and nutrient limited environments. Based on the above results, we hypothesize that root architecture difference between cultivars and landraces (or shallow vs. steep deep root systems, respectively) may result in different strategies of adaptation to the availability of water and nutrients over the soil profile.

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4. Vigorous shoot and root of Algerian durum wheat landraces over modern cultivars

4.1. Abstract

The characterization of root traits in wheat germplasm paves the way for their use in wheat breeding to obtain varieties adapted to target environments. We evaluated a set of forty genotypes (cultivars and landraces) at seedling and plant adult. Adult plants were studied with bespoke pipe-pots in a greenhouse trial, and following the *shovelomics* procedure in the field. The results were compared with root traits measured in a previous experiment carried out in seedlings, using a filter paper-based method. Root image processing was performed by SmartRoot and REST softwares at seedlings and at adult plants, respectively. A wide array of traits were assessed; like biomass, height, date to heading and tiller number (for shoots); growth angle, length, diameter and number (seminal roots); and growth angle, biomass, root number, fractal dimension, number and gap size and root area (for roots of adult plants). Root dry weight was highest in the upper section (0-30 cm) in the pipe-pot experiment, where landraces showed higher root development than cultivars. The root biomass distribution pattern along the tubes was similar regardless of variety type. Landrace group had higher shoot and root vigor at seedling and at plant as well. The set of traits measured in the field separated landraces from cultivars, especially for shoot and root vigor. Root growth angle was steeper at adult plant stage, compared to seedlings. Landraces presented a steeper root angle than cultivars at seedling stage, but this difference disappeared at adult plants. Interesting correlations were found between root dry weight and several root traits in field. No correlation was detected between seedling traits and adult plants for root angle, while appreciable ones were found for SDW at seedling and adult plant (R^2=0.32), and between total root length of seedlings and total projected structure length of excavated root systems (R^2=0.19). We concluded that seedling traits were influenced by an overall plant size factor, possibly related to early vigor, but the traits related to root architecture indicated specific features of the genotypes. Our results indicate that landraces show distinct root features and, therefore, constitute a potential genetic resource not only for shoot vigor, as previously acknowledged, but also for root traits at seedling and adult plant stages. Overall, the results of this study suggest that cultivars grow deeper roots, while landraces produce higher and shallower root biomass.

4.2. Introduction

Root system architecture (RSA) plays a key role for determining access to soil resources, which ultimately affects plant performance and yield (Coque and Gallais 2006). Durum wheat (*Triticum* *durum* Desf.), one of the main staple crops in the Mediterranean region (Shewry and Hey 2015), is typically cultivated under rainfed conditions. Under such conditions, yield is affected mostly by late drought, which coincides with the periods of flowering and grain filling (Loss and Siddique 1994; Belaid 2000; Mohammadi *et al*. 2011; Bassi and Sanchez-Garcia 2017). Besides, the in-season rainfall is predicted to decrease in the near future by up to 30 % because of climate change, which would lead to an increased drought severity (Christensen *et al*. 2007).

Several studies highlighted the great interest of root traits for water stress adaptation (Manschadi *et al*. 2006; Christopher *et al*. 2008; Gregory *et al*. 2009; Asif and Kamran 2011). However, these traits have been not considered in plant breeding due to practical difficulties, and selection focused almost solely on above-ground traits. In the last decades, more attention has been paid to the underground traits (Bengough *et al*. 2004; Nagel *et al*. 2012; Richard *et al*. 2015; York *et al*. 2018 and friedli *et al*. 2019). These traits are particularly important in water stressed environments. Root length, root density and root depth are the most important root features determining the ability for extraction of soil water (King *et al*. 2003; Asif and Kamran 2011; Carvalho *et al*. 2014). El Hassouni *et al.* (2018) showed that deep-rooted genotypes could increase grain yield by 37 to 38 % in environments with limited moisture, but that it also causes a yield loss of 20 to 40 % in moisture-rich environments, in both cases compared to shallower root types. Based on modelling studies, it has been proposed that wheat yield would increase by 55 kg ha^{-1} for each additional millimeter of water extracted during the post-anthesis period (Manschadi *et al*. 2006; Christopher *et al*. 2013). Therefore, breeding for deep-rooted varieties was proposed as a promising strategy to address drought tolerance for environments where the stored water is the main source during the filling grain period (Manschadi *et al*. 2006, Wasson *et al*. 2012). The root growth angle controls the overall root system architecture, driving the distribution of roots along the soil profile (Nakamoto *et al*. 1991; Oyanagi *et al*. 1993; Oyanagi 1994; Borrell *et al*. 2014). When the root system grows in a narrow angle, roots can go deeper down into the soil, which would be advantageous under terminal drought conditions (Manschadi *et al*. 2006; Reynolds *et al*. 2007; Christopher *et al*. 2008; Acuña and Wade 2012; Hamada *et al*. 2012). On the contrary, if grown in a shallow root angle, roots explore the more superficial layers of the soil, which also could be beneficial for capturing the superficial soil moisture and in-season rainfall (Alahmad *et al*. 2019).

Wheat landraces, developed during the last ten thousand years, were locally adapted to the region where they have been grown (Ehdaie and Waines 1989; Harlan 1992; Jaradat 2011). There is a general agreement that high yielding modern wheat varieties are more adapted to favorable environments, whereas old cultivars and landraces have better yield stability under water stress conditions (Ceccarelli *et al.* 1991; Blum 1996). Genetic heterogeneity and continuous evolution enabled landraces to cope with the changing conditions and evolve adaptive features to survive under the predominant environmental challenges (Harlan 1992; Zeven 2000, 2002; Jaradat 2013). For developing high yielding varieties, breeders did not focus on root features, but it is possible that these traits have been inadvertently altered because of the selection for higher yield. Great grain yield increases were achieved in modern breeding by the introduction of dwarfing genes during the Green Revolution. These genes were incorporated in tall durum wheat by crossing with semi-dwarf bread wheats (Borlaug 2007). Several studies showed that root length and biomass were reduced in modern varieties compared to old ones (Waines and Ehdaie 2007; Wojciechowski *et al*. 2009; Elazab *et al*. 2016; Aziz *et al*. 2017). The biomass of roots at profound layers was similar or increased (Hurd *et al*. 1974; Chloupek *et al*. 2006), whereas no change was observed in other studies (Lupton *et al.* 1974; Cholick *et al*. 1977).

Several phenotyping methods and platforms have been dedicated to characterize root system architecture at different stages, and under various conditions. At seedling stage, seminal roots were evaluated through, among others, filter paper systems (González *et al.* 2016), gel-filled chambers (Manschadi *et al*. 2006) and clear pots (Richard *et al*. 2015). Other methods were employed to assess root traits at the adult stage, with special regards to root depth, like PVC pipes systems in greenhouses (Blum 2011, Subira *et al.* 2016), and in the field (Wasson *et al*. 2014), and more recently in bespoke facilities like the Deep Root Observation Platform (DROP) (Friedli *et al*. 2019). Recently, a modified *shovelomics* method developed in maize (Trachsel *et al*. 2011) was employed in wheat (Maccaferri *et al.* 2016; York *et al*. 2018). This method targets the features related to the roots at superficial soil layers (root angle, number of nodal and seminal root, root dry weight…), and more traits (like fractal dimension, gap size, total projected structure length…) were accessible through the root imaging process using Root Estimator for Shovelomics Traits (REST) (Colombi *et al*. 2015).

In the present study, we combined various methods at seedling and adult plant stages to describe root traits diversity and their dynamics. The relationships among experiments within a representative set cultivars and landraces was used to assess i) the usefulness of these methods to depict root characteristics and ii) the genotypic diversity present in durum wheat in relation with its potential use to address plant breeding challenges for water-limited environments.

4.3. Materials and Methods

4.3.1. Plant material

A diverse set of durum wheat genotypes was selected aiming to include genotypes from different periods of Algerian agriculture. This set was formed by local landraces and cultivars of different countries (Algeria, France, Italy, Spain, and Tunisia) and international breeding programs addressing semi-arid areas, namely the International Maize and Wheat Improvement Center (CYMMIT), the International Center for Agricultural Research in the Dry Area (ICARDA) and the Arab Center for the Studies of Arid zones and Dry lands (ACSAD). A total of 40 genotypes were used, from which 37 genotypes were screened through both filter paper and shovelomics methods, and 27 genotypes (17 cultivars and 10 landraces) were tested in bespoke pipe-pots. A set of 24 genotypes (14 cultivars and 10 landraces) was common between the two experiments (Table 4.S1).

4.3.2. Growth chamber experiment

This experiment was already described in the chapter 3.

4.3.3. Greenhouse experiment

4.3.3.1. Experimental conditions

The experiment was conducted under greenhouse conditions, starting on May 20, 2018, at the Research Center for Biotechnology (CRBt), Constantine, Algeria. The greenhouse was set at ambient temperature 22 °C. Plants were grown in pots made of PVC pipes of 120 cm height and 11 cm width (Figure 4.S1), filled with a mixture of sand and agricultural soil from the experimental fields at Constantine at 3:1 ratio, sealed at the bottom with a hole for drainage. Each tube was fertilized with 3.0 g and 0.5 g of triple superphosphate (TSP). The urea was provided in two fractions, the first at four leaves, and the second at jointing stage. The triple superphosphate (TSP) was provided once during the preparation of substrate at the first 30 cm. The experiment consisted of 81 tubes (27 genotypes) arranged in a randomized complete block design with three replications. Seeds were germinated and kept in a growth chamber for three days, and then transferred directly to the soil-filled tubes. Four seedlings were transplanted to each tube, which were later thinned to two seedlings per tube. Irrigation was provided periodically each two days to prevent water limitation.

4.3.3.2. Trait phenotyping

In total, eleven traits were recorded/calculated: days to heading (DTH), recorded when the spike was completely emerged at the main stem, number of spikes per plant (SN), plant height (PH), measured from the soil to the top of the spike (barbs excluded), root depth (Depth), root dry weight of upper, middle and lower section (RDW30, RDW60, RDW>60, respectively), total root dry weight (RDW), shoot dry weight (SDW), root to shoot ratio (RSR) and growth habit (winter or facultative).

For the genotypes that did not reach heading, the overall plant height to the tip of the most developed leaf, in upright position, was recorded. At the termination of the experiment, the pipes were longitudinally opened, and roots were carefully washed with tap water (Figure 4.S2). The total root depth was determined and then the root system was cut at two depths, 30 cm and 60 cm, to obtain three sections: upper (0-30 cm), middle (31 to 60 cm) and lower (>60cm). The shoot and the three root sections of each tube were oven dried at 80 °C for three days. Then the root and shoot dry weight (RDW and SDW, respectively) were obtained. The plants, which did not reach heading, were harvested last. The trait values were expressed as the mean of the two plants per pipe-pot due to the overlap of their root systems.

4.3.4. Shovelomics experiment

4.3.4.1. Experimental conditions

The experiment was planted on November 2018 at the Aula Dei Experimental Station (EEAD, CSIC), Zaragoza, Spain, following a randomized complete block design with four replications, on loamy soil. Genotypes were grown in 36 cm-long single rows with seeds spaced 2 cm apart. Each target row was surrounded by two rows of a check durum wheat variety (Claudio). The rows were spaced 20 cm, resulted in a sowing density of 250 seeds/m^2, similar to a commercial stand. Sowing was carried out manually, using a custom-built sowing frame for one plot size (one target row and two neighboring rows). Seeds were placed at ~ 3 cm of depth. Watering was supplied by drip irrigation (Figure 4.S3) once per week for 4 hours from mid-February, provided by tubes placed alongside the rows, with emitters every 20 cm, each one providing 0.6 l/h of water. One flood irrigation was provided after jointing, after which drip irrigation was halted for

30 days, to allow root growing in depth, and drip irrigation was resumed after that, until the end of the experiment.

4.3.4.2. Trait phenotyping

4.3.4.2.1. Traits measured in the field

Heading and anthesis time were recorded for each single row when 50% of stems reached Zadocks stages 55 and 65, respectively (Zadocks *et al.* 1974). Roots were excavated two weeks after anthesis for each row. One day before plant excavation, rows were watered when it was necessary, to keep the soil at favorable humidity for root excavation. Two straight-edged spades with a width of 15 cm were inserted up to 20 cm directly adjacent to the neighboring rows on both sides of the focal row with the width of the blade parallel to the row (Figure 4.S4A). The target plants and attached soil were lifted from the ground on the spade and then plants were gently shaken to remove the big part of the attached soil. Four plants were picked up from each row based on their root size and tiller number. Plants with tiller number representative of the row were chosen. The direction of root extension (towards the space between rows) was marked on the stem of the selected plants with a permanent marker and attaching the stems with a ribbon. Thereafter, this served for determining the position for root angle measurement, orthogonal to the direction of the row.

The chosen plants were transferred to the laboratory, where the data were taken considering each single plant as the experimental unit. Images of the crown and roots of non-washed plants were acquired (image 1) using an RGB camera mounted on a tripod at a fixed distance of 30 cm (Figure 4.S4B, C). The root opening angle (RoA) was determined for each single plant using a protractor originally developed for maize shovelomics (Trachsel *et al.* 2011). The left and right angles of the outermost root from the horizontal was recorded. Then, the sum of both angles was subtracted from 180°. The plant height (PH), from the soil to the top of the main spike, without awns, was determined, and the number of spikes per plant were counted. Thereafter, the plants were soaked in water for a couple of hours, shaken, allowed to dry and then the roots were imaged again (Image 2). The root system was manually split into single roots, to count the nodal and seminal root number (NRN and SRN, respectively). The number of tillers per plant was counted (TN). Fine washing was carried out by leaving the separated roots soaked in vinegar with degree of acidity 6%, and then they were shaken and filtered after 24 hours. Shoot and root dry weight per plant were determined after oven drying at 60 °C for one week.

4.3.4.2.2. Root traits measured by REST software

The acquired images of clean roots (Image 2) were analyzed using the software REST, Root Estimator for Shovelomics Traits (Colambi *et al*. 2015). The root system (RS) images were corrected: The outermost 2.5% of root pixels at the right and left side each, and 5% of outermost pixels at the bottom were excluded from the analysis. Therefore 90 % of the root pixels were considered and included in the box area, from which the depth was determined (95 % quantile depth, corresponding to the depth of the 90% of the region of interest, ROI) and maximum width (mW) (Colombi *et al*, 2015). The area of the convex hull (AcH) is the smallest convex set of pixels that contains 90% of roots and indicates the size of the entire system.

The maximum width (mW) was derived from the width of the region of interest (ROI, in blue) (Figure 4.S4) to estimate the lateral spatial extension of the root system. The root opening angle (RoA) measured by REST was not considered because it was not properly measured in numerous images: the RoA could be measured correctly only if the length of the two outermost roots reaches at least 10 cm of length. Alternatively, we used RoA_I of non-washed roots (Image 1), which was evaluated with the open source image analysis package Image J (Schneider *et al.* 2012). The angle of the two outermost roots of the excavated root system was measured at the same distance by drawing triangle and then the sum of them was subtracted from 180°.

The following parameters were generated to characterize the inner structure of the RS: total projected structure length (tpSL), calculated as the sum, in cm, of the weighted length of root derived structures and the number of background patches within the AcH. Mean fractal dimension (mFD), derived from a box-count algorithm, which indicates the root system complexity (Grift *et al.* 2011), and how the root system fills the rooting space. Root area (RA) (cm^2), area of all root derived pixels within the convex hull. Fill factor (Ff), number of root derived pixels within convex hull divided by number of pixels within convex hull, which gives an idea on the root density. Number of gaps (NoG) is the total number of gaps enclosed by root-derived pixels. Gaps size (mGZ) within the root crown explains lateral branching patterns and the apparent density of lateral roots (Colombi *et al*. 2015). Median structure width (mSW), which is the distance from root crown derived structure to the background which provides information about the diameters of root clusters.

4.3.4.3. Data analyses

Statistical analyses were performed using General ANOVA procedure with Genstat 18 (Payne 2009), to compare between genotypes and between cultivar and landrace groups as “Type” effect. The tiller number per plant was used as co-varaiate for ANOVA analyses. Multiple means separation was carried out using LSD at 0.05 level, for variables in which the F-value for “Genotypes” and “type effect” was significant. A principal component analysis (PCA) and a hierarchical cluster analysis (HC) were performed using the R package FactoMineR (Le *et al.* 2008). The hcut function was used for tree cutting levels truncation. The R package Factoextra (Kassambara and Mundt 2017) was employed for extracting and visualizing the results. Broad-sense heritability (h^2) was calculated on entry mean basis using the REML procedure (genotype as random factors and replication as fixed factor), as follows: $h^2 = \sigma^2_g / (\sigma^2_g + (\sigma^2_e/r))$, where σ^2_g is the genotypic variance, σ^2_e is the error variance and r is the number of replications.

4.4. Results

4.4.1. Greenhouse experiment

The genotypes were exposed to essentially warm conditions during the whole experiment, and behaved differently in their progress towards flowering, probably because of differences in the vernalization requirement. The transition from vegetative to reproductive phase was successful in nineteen of the twenty-seven genotypes. This set of genotypes, which succeeded to progress to the reproductive stage without vernalization, are supposed to have a spring or facultative growth habit. There were 15 cultivars and 4 landraces in this group. Among the genotypes that failed to pass to the reproductive phase, there were six landraces and two cultivars. These genotypes have a winter habit, requiring a period of cold temperature to be able to reach the reproductive stage (Table 4.S1).

4.4.1.1. Trait variation

The analyses of variance showed significant genotypic differences for DTH, RDW30, SDW and RSR, but no difference was found for RDW below 30 cm and total RDW. The Landrace vs. cultivar contrast was significant for DTH, PH, RDW30 and total RDW. When genotypes were divided based on vernalization requirements (winter vs. facultative type), a significant difference was detected for root depth, RDW30, total RDW and RSR. Within the genotypes with facultative or spring habit, the comparison of landrace vs. cultivar indicated significant differences for DTH, PH, RDW30 and RSR, whereas within the winter genotypes, the difference was only significant for RDW30 (Table 4.1, Table 4.S2).

The coefficient of variation (CV) was higher for root dry weight (61.11-98.14%) than for the other traits. The lowest one was observed for SN and DTH (12.80 and 14.17, respectively). The earliest plant reached heading in one month and 11 days and the last one in two months and 11 days, spanning an interval of one month. PH varied from 10 cm in plants, which stayed at the vegetative growth stage to 80.5 cm in plants which reached reproductive stage, while the root depth varied from 30 cm in winter wheat plants to 170 cm in spring wheat plants (Table 4.1).

4.4.1.2. Landraces yielded more RDW at the shallow depth

Similar distribution for RDW was observed along the soil profiles for all genotype groups (Figure 4.1A) and for the individual genotypes (Figure 4.1B). The upper part of the root system was much more developed than the two other sections (RDW60, RDW>60), resulting in higher RDW30.

The difference between landraces and cultivars, when all genotypes were included or just within the non-winter genotypes, showed that the landrace group had higher RDW, in general, and particularly at the first 30 cm, higher PH and needed more days to reach heading (Table 4.1, Figure 4.1A).

Within the non-winter group, the overall trends were the same, with a significant difference in root-to-shoot ratio (RSR), indicating that landraces invested relatively more in roots than in shoots. However, within the winter genotypes (which stayed at the vegetative phase), cultivars showed more RDW30 than landraces. This result contrasted with the overall result. However, this might be due to the low numbers of cultivars (2 genotypes) which was not representative of all the cultivars (19 genotypes). The comparison between the winter and non-winter genotypes was not balanced. However, the higher RDW of winter cultivars was remarkable. Plants that reached heading later produced more SDW and RDW especially at the upper part of the root.

The RDW up to 30 cm was positively correlated with the middle RDW sections (at 60 cm) and with SDW. Genotypes with higher DTH, tended to have more root than shoot biomass. Tall genotypes produced more SDW and RDW as well, especially at the two upper sections (Table 4.2).

Table 4.1. Summary statistics and means comparison for the assessed traits within the habit and type group.

		Genotype number	DTH	SN	PH	Depth	RDW30	RDW60	RDW>60	RDW	SDW	RSR
Growth habit	Non-winter*	19	56.35	1	48.82	116.55 **a**	0.107 **b**	0.038	0.036	0.185 **b**	1.17 **a**	0.15
	Winter	8	-	1	46.07	95.93 **b**	0.172 **a**	0.048	0.041	0.260 **a**	1.15 **b**	0.22
Type	Cultivar	17	55.45 **b**	1	45.03 **b**	114.50	0.106 **b**	0.037	0.037	0.182 **b**	1.137	0.16
	Landrace	10	60.00 **a**	1	53.27 **a**	104.68	0.161 **a**	0.048	0.039	0.250 **a**	1.220	0.20
Non-winter* habit	Cultivar	15	55.45 **b**	1	45.84 **b**	117.03	0.095 **b**	0.037	0.036	0.172	1.134	0.15 **b**
	Landrace	4	59.91 **a**	1	59.50 **a**	114.79	0.151 **a**	0.041	0.040	0.235	1.314	0.17 **a**
Winter habit	Cultivar	2	-	1	38.00	92.20	0.186 **a**	0.033	0.046	0.266	1.160	0.22
	Landrace	6	-	1	48.59	97.09	0.167 **b**	0.053	0.039	0.259	1.157	0.22
Summary statistics	Min	-	41	1	10	30	0.007	0.000	0.000	0.013	0.107	0.04
	Max	-	71	2	80.5	170	0.465	0.156	0.161	0.539	2.332	0.44
	Mean	-	56.49	1.00	48.06	110.93	0.127	0.041	0.038	0.207	1.168	0.18
	CV%	-	14.17	12.80	29.85	28.36	71.50	80.33	98.14	61.11	44.42	47.58

*Non winter means facultative or spring

DTH: days to heading, SN: spike number, PH: plant height, Depth: root depth. RDW30: root dry weight up to 30 cm of depth, RDW60: root dry weight between 30 and 60 cm, RDW>60: root dry weight for depth more than 60 cm. RDW: total root dry weight. SDW: shoot dry weight, RSR: root to shoot ratio. Values with different letters are significantly different at 0.05 level of significance.

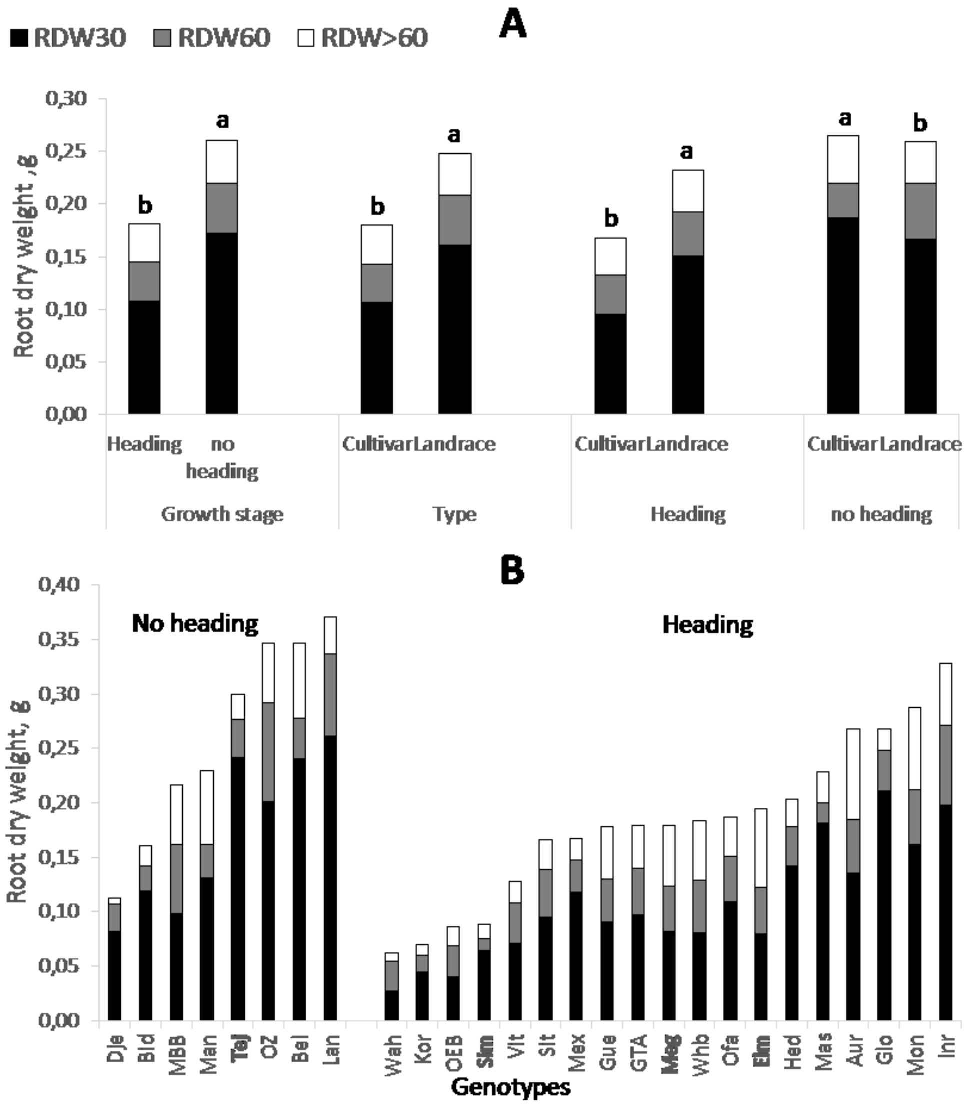

Figure 4.1. The distribution of root dry weight over the three root sections. The colors black, grey and white indicate the upper section (RDW30), middle section (RDW60) and lower section (RDW>60), respectively.

Table 4.2. Correlations between the traits measured in greenhouse experiment, performed with genotypes at adult stage.

	DTH	PH	Depth	RDW30	RDW60	RDW>60	RDW	SDW	RSR
DTH	*								
PH	0.33	*							
Depth	-0.02	-0.05	*						
RDW30	**0.64**	**0.53**	-0.26	*					
RDW60	0.29	**0.47**	0.05	**0.55**	*				
RDW>60	0.30	0.35	0.29	0.44	**0.72**	*			
RDW	**0.65**	**0.50**	-0.01	**0.91**	**0.73**	**0.71**	*		
SDW	**0.51**	**0.64**	0.17	**0.58**	**0.70**	**0.78**	**0.73**	*	
RSR	0.44	0.00	0.04	**0.65**	0.26	0.36	**0.67**	0.08	*

DTH: days to heading, PH: plant height, Depth: root depth. RDW30: root dry weight up 30 cm of depth, RDW60: root dry weight between 30 and 60 cm, RDW>60: root dry weight for depth more than 60 cm. RDW: total root dry weight. SDW: shoot dry weight, RSR: root to shoot ratio.

4.4.2. Shovelomics experiment

Significant differences between genotypes were found for all traits. Landrace vs. cultivar differences were significant for all traits except SpkDW, RSR and SRN (Table 4.3). Landraces needed more days to reach heading and anthesis (10 and 7 days, respectively) than cultivars. Landraces also showed more growth in general for biomass related traits (PH, TDW, SDW and TPB) than cultivars, whereas no difference was observed for SpkDW, likely because the spikes were sampled at the beginning of grain filling. On the contrary, cultivars produced more tillers and spikes (Table 4.4). For root traits, landraces root system presented larger spatial distribution than cultivars (expressed by RoA_F), and had more nodal roots (NRN), total number of roots (TRN) and root dry weight (RDW), but no difference was found for seminal root number (SRN) and root to shoot ratio (RSR) (Table 4.4).

A considerable range of variation was observed for most traits, except for SN, TN and SRN (Table 4.3). In general, a higher range of variation was observed in cultivars compared to landraces, especially for the time to reach heading and anthesis. The coefficients of variation (CV) ranged from 3.49 % in anthesis to 44.20 % in RDW for the complete dataset (Table 4.3). In general, similar CVs were found in landraces and cultivars separately, and compared with the

complete dataset. The only exception was PH, which had a much higher CV in the complete dataset (Table 4.3, Table 4.4). Broad sense heritability (h^2) was very high for PH, heading, anthesis and plant height. Lesser h^2 values were observed for number of roots (SRN, NRN and TRN). The other traits had moderate h^2 values, ranging from 0.44 to 0.73 (Table 4.3).
Regarding the traits measured with the REST software, genotypes and type (cultivar vs. landrace) presented significant differences for most traits, except for RoA$_I$ and structure width (mSW) for genotype, and RoA$_{I,}$ depth, mW and mSW for type (Table 4.3).

Landrace vs. cultivar comparison showed that landraces presented a significantly larger soil volume occupied by the root system (AcH), accompanied by a higher RA. The higher size of the root system in landraces also was characterized by higher values for Ff (root density), tpSL, mFD, NoG and mGZ, compared to cultivars, all variables related to the structure of the root system (Table 4.4).

Overall, a lower heritability was found in traits generated with the REST software, compared to the other traits recorded in this experiment. RA expressed the highest h^2 (0.61), followed by tpSL (0.55), and the lowest ones were observed in structure width (0) and RoA$_I$ (0.04). CVs ranged from 3.73 in mFD to 56.37 in mGZ (Table 4.3). CVs of cultivars were higher than those of landraces for most traits (Table 4.3).

4.4.2. Relationships among traits and clustering of varieties

Among the traits measured in the field experiment, high correlations were found between TPB and its components like SDW, RDW, SpkDW, and with TRN and NRN (0.54). RDW had significant correlations with shoot biomass traits like SDW, SpkDW, and TDW, indicating that there was a positive relationship between shoot and root biomass (R^2=0.55). RDW was mostly determined by TRN (R^2=0.41) (Figure 4.2). Taller varieties tended to need more time to heading (0.70) and *vice versa*. Nodal root growth angle was positively correlated with anthesis (0.43) and heading (0.42). NRN was well correlated with plant biomass traits (Table 4.5).

For the root traits measured using the REST software (Table 4.S3), a high positive correlation was observed between AcH and mW (0.81) and both had negative correlations with Ff and mFD. Root area was highly correlated with tpSL (0.85) and NoG (0.63). NoG was negatively correlated with mGZ and mSW indicating that root systems with higher NoG, were characterized

Table 4.3. Minimum, maximum, mean, CV%, broad heritability (h^2) and ANOVA analysis of genotype and type effect for the field and REST measured traits.

						ANOVA	
Traits	Min	Max	Mean	CV%	h^2	Genotype	Type
Field traits							
DTH (day)	104.00	125.00	112.72	4.68	0.95	***	***
DTA (day)	111.00	134.00	122.25	3.49	0.93	***	***
PH (cm)	70.00	165.00	104.89	17.11	0.97	***	***
SDW (g)	2.60	22.50	10.15	31.39	0.65	***	***
SpkDW (g)	0.20	6.60	2.63	34.71	0.57	***	ns
SN	1.00	5.00	2.58	24.86	0.52	***	***
StmDW (g)	1.40	17.40	7.52	34.64	0.72	***	***
TN	1.00	5.00	2.74	25.95	0.44	***	***
TPB (g)	2.63	23.01	10.39	31.32	0.66	***	***
RDW (g)	0.031	0.789	0.240	44.20	0.66	***	***
RSR	0.004	0.073	0.024	35.19	0.53	***	ns
RoAF (°)	35.00	130.00	86.03	20.83	0.47	***	***
SRN	1.00	6.00	4.87	17.63	0.29	***	ns
NRN	8.00	46.00	25.17	23.65	0.38	***	***
TRN	11.00	51.00	30.10	20.05	0.37	***	***
REST traits							
RoAI (°)	13.42	114.99	54.19	29.79	0.04	ns	ns
RA (cm^2)	3.86	36.73	16.66	28.80	0.61	***	***
AcH (cm^2)	22.18	257.00	93.47	37.94	0.31	***	*
tpSL (cm)	70.62	573.55	278.0	28.77	0.55	***	***
Depth (cm)	5.52	20.03	11.71	20.31	0.18	**	ns
mW (cm)	3.66	20.17	9.02	28.30	0.24	***	ns
Ff	0.06	0.49	0.20	36.68	0.37	***	***
mFD	1.42	1.81	1.64	3.73	0.36	***	***
NoG	52.00	900.00	383.80	42.57	0.47	***	***
mGZ (cm)	7.85-E05	0.011	0.0018	56.37	0.27	***	***
mSW (cm)	0.039	0.214	0.0603	27.26	0.00	ns	ns

DTH: days to heading, DTA: days to anthesis, PH: plant height, SDW: shoot dry weight, SpkDW: spike dry weight, SN: spike number, StmDW: stem dry weight, TN: tiller number, TPB: total plant biomass, RDW: root dry weight, RSR: root to shoot ratio.RoAF: root opening angle measured by protractor, SRN: seminal root number, NRN: nodal root number, TRN: total root number. RoAI: root opening angle measure by Imag J, RA: root area, AcH: area of the convex hull, tpSL: total projected structure length, mW: maximum width, Ff: filling factor, mFD: mean fractal dimension, NoG: number of gaps, mGZ: median gap size, mSW: median structure width.

Table 4.4. Minimum, maximum, CV % and mean comparison between cultivar and landrace for all assessed traits.

	Cultivar				Landrace			
	Min	Max	Mean	CV%	Min	Max	Mean	CV%
Field traits								
DTH (day)	104.00	123.00	109.93^{b}	3.02	115.00	125.00	120.03^{a}	1.81
DTA (day)	111.00	130.00	120.26^{b}	2.82	124.00	134.00	127.30^{a}	1.63
PH (cm)	70.00	127.00	95.48^{b}	9.23	108.00	165.00	130.07^{a}	8.98
SDW (g)	3.60	19.00	9.74^{b}	28.55	5.00	22.50	12.28^{a}	26.32
SpkDW (g)	0.20	6.60	2.71^{a}	33.85	0.60	5.30	2.61^{a}	33.68
SN	1.00	5.00	2.67^{a}	24.50	1.00	4.00	2.40^{b}	22.51
StmDW (g)	1.40	15.50	7.03^{b}	31.00	3.90	17.40	9.66^{a}	26.41
TN	1.00	5.00	2.85^{a}	25.76	1.00	4.00	2.54^{b}	23.34
TPB (g)	3.67	19.79	9.96^{b}	28.42	5.12	23.01	12.59^{a}	26.35
RDW (g)	0.034	0.789	0.221^{b}	40.63	0.051	0.754	0.301^{a}	43.60
RSR	0.004	0.074	0.023^{a}	34.81	0.007	0.053	0.024^{a}	34.24
RoA$_F$ (°)	35.00	130.00	82.92^{b}	21.03	40.00	130.00	96.03^{a}	17.23
SRN	1.00	6.00	4.90^{a}	16.92	2.00	6.00	4.89^{a}	18.04
NRN	9.00	43.00	25.22^{b}	23.38	10.00	46.00	25.98^{a}	23.51
TRN	12.00	49.00	30.14^{b}	19.92	16.00	51.00	31.01^{a}	19.53
REST traits								
RoA$_I$ (°)	13.42	114.99	54.01^{a}	28.98	21.00	109.32	54.68^{a}	31.89
RA (cm^2)	3.86	27.92	15.57^{b}	26.33	7.48	36.73	19.62^{a}	27.04
AcH (cm^2)	22.18	257.00	91.65^{b}	40.18	39.29	172.78	98.51^{a}	31.43
Ff	0.06	0.49	0.19^{b}	39.25	0.08	0.41	0.21^{a}	28.89
Depth (cm)	5.52	20.03	11.64^{a}	21.33	6.50	17.86	11.91^{a}	17.29
Width (cm)	3.66	17.11	8.55^{a}	31.18	4.31	15.70	8.95^{a}	26.27
mW (cm)	3.66	20.17	8.95^{a}	32.95	4.31	16.42	9.21^{a}	26.65
tpSL (cm)	70.62	485.71	263.55^{b}	27.54	87.10	573.55	317.90^{a}	27.04
mFD	1.43	1.82	1.64^{b}	3.83	1.54	1.81	1.66^{a}	3.28
NoG	52.00	896.00	369.62^{b}	44.19	61.00	900.00	422.45^{a}	37.33
mGZ (cm)	7.85-E05	0.0114	0.0018^{b}	62.37	0.0003	0.0081	0.0022^{a}	39.35
mSW (cm)	0.0396	0.2149	0.0604^{a}	29.36	0.0458	0.1276	0.0607^{a}	20.47

DTH: days to heading, DTA: days to anthesis, PH: plant height, SDW: shoot dry weight, SpkDW: spike dry weight, SN: spike number, StmDW: stem dry weight, TN: tiller number, TPB: total plant biomass, RDW: root dry weight, RSR: root to shoot ratio. RoA$_F$: root opening angle measured by protractor, SRN: seminal root number, NRN: nodal root number, TRN: total root number. RoA$_I$: root opening angle measure by Imag J, RA: root area, AcH: area of the convex hull, tpSL: total projected structure length, mW: maximum width, Ff: filling factor, mFD: mean fractal dimension, NoG: number of gaps, mGZ: median gap size, mSW: median structure width.

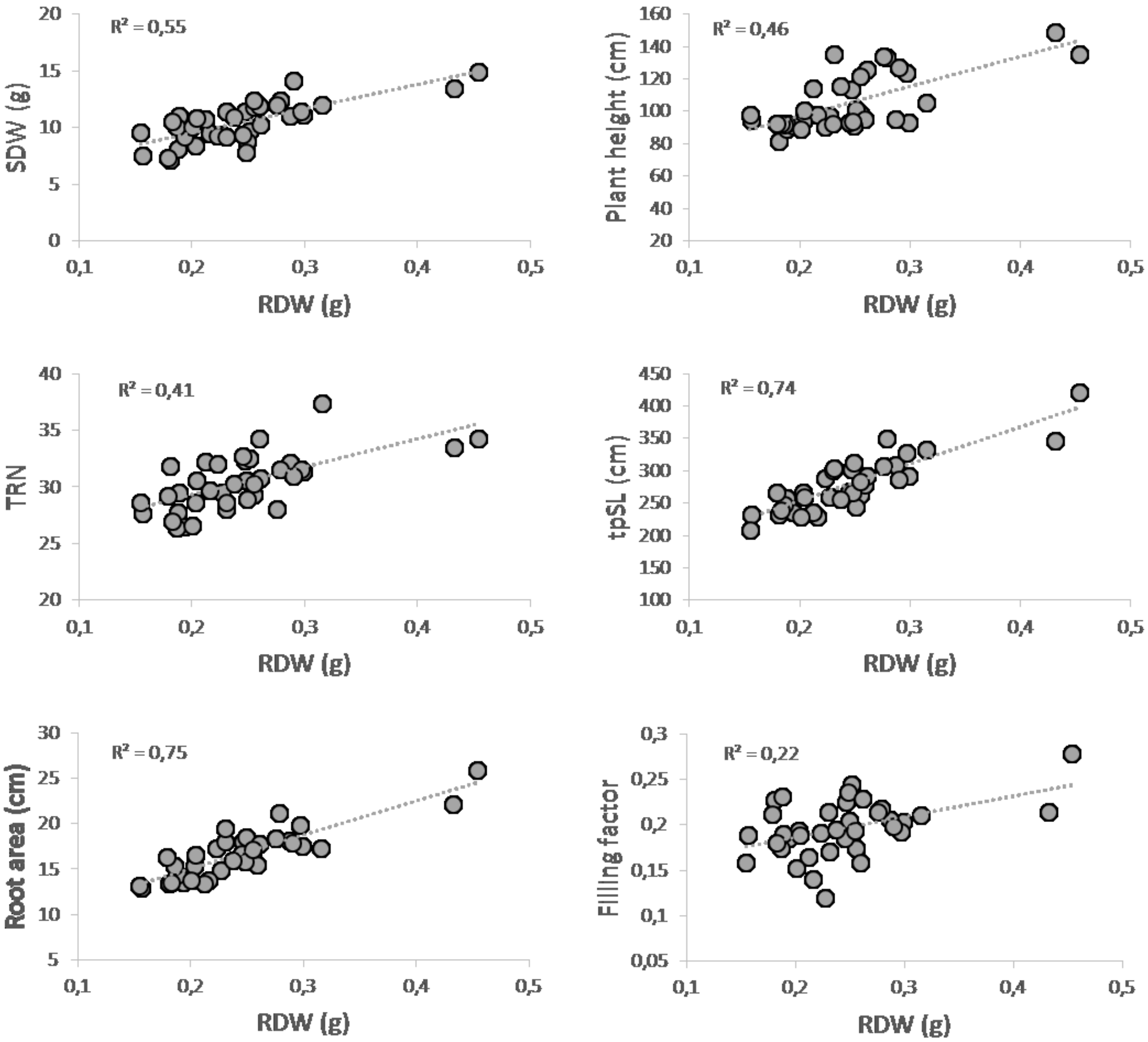

Figure 4.2. Root dry weight (RDW) relationship with shoot dry weight (SDW), plant height (PH), total root number (TRN), total projected structure length (tpSL), root area (RA) and Filling factor (Ff).

by smaller mGZ and mSW. Mean fractal dimension showed appreciable correlation with Ff (0.76) and negative correlation with outer dimensions features of RS (AcH, mW, and depth).

Correlations of REST with field traits showed interesting relationships between root area (RA) and TPB (0.52), SDW (0.50) and NRN (0.49). Similar correlations with the former field traits were found with tpSL and NoG (Table 4.S4). RDW was positively correlated with some REST traits like RA, tpSL and Ff with moderate to large coefficients of determination (Figure 4.2, Table 4.S4).

The principal component analysis based on traits measured in field showed that PC1 and PC2 explained together 51.55 % of the total variation (34.97 % and 16.57%, respectively). PC1 was influenced mostly by traits related to root and shoot biomass and plant height and, at lesser importance, by traits related to root architecture (root opening angle) and phenological traits (heading and anthesis) (Figure 4.3A). Therefore, this principal component was represented by traits related to shoot and root size. The distribution of genotypes on this axe showed clear distinction of genotypes based on their type (cultivar vs. landrace), where landrace showed higher values for all the biomass traits, being more vigorous compared to cultivars. TN, SN and SpkDW, mW and AcH contributed more to the second principal component (PC2) on the positive side, whereas Ff was the trait contributing most on the negative side (Figure 4.3A). These traits are related to plant fertility, size, and density of roots.

Three genotype groups were identified based on hierarchical classification at 88% of level of similarity (Figure 4.3B); the landrace group which presented higher vigor and most of them tended to have denser and complicated root system (G1), the second group included only cultivars (G2), which was formed by 7 genotypes and presented lower values for traits related to fertility and small and denser root system, and the third group (G3) formed by 20 cultivars characterized mainly by lower shoot and root size, high plant fertility and big scattered root system(Figure4.3B).

4.4.3. Root opening angle (RoA) in seedling and adult plants

ANOVA analyses revealed highly significant effects of all sources of variation on RoA: growth stage, genotype, type and the interactions (Table 4.6). Seedlings had a wider root angle than adult plants. The landrace group developed steeper root angles at the seedling stage than cultivar group but, as adult plants, this difference disappeared.

Table 4.5. Pearson correlations between traits assessed in the field.

	DTH	DTA	RoA$_F$	SN	TN	PH	SRN	NRN	TRN	SDW	StmDW	SpkDW	RDW	RSR	TPB
DTH	*														
DTA	**0.91**	*													
RoA$_F$	**0.42**	**0.43**	*												
SN	**-0.17**	**-0.17**	-0.08	*											
TN	**-0.25**	**-0.27**	**-0.14**	**0.84**	*										
PH	**0.70**	**0.57**	**0.26**	**-0.11**	**-0.12**	*									
SRN	**-0.07**	**-0.12**	**-0.16**	0.05	**0.08**	0.02	*								
NRN	-0.03	-0.08	-0.04	**0.49**	**0.50**	**0.14**	0.07	*							
TRN	-0.03	**-0.08**	-0.07	**0.49**	**0.50**	**0.15**	**0.21**	**0.99**	*						
SDW	**0.25**	**0.16**	0.06	**0.49**	**0.42**	**0.50**	0.06	**0.53**	**0.53**	*					
StmDW	**0.28**	**0.16**	0.07	**0.44**	**0.40**	**0.58**	0.09	**0.51**	**0.51**	**0.97**	*				
SpkDW	0.06	**0.11**	0.02	**0.46**	**0.33**	0.06	-0.05	**0.40**	**0.38**	**0.70**	**0.50**	*			
RDW	**0.21**	**0.13**	0.01	**0.24**	**0.24**	**0.40**	0.02	**0.63**	**0.62**	**0.62**	**0.63**	**0.36**	*		
RSR	0.02	-0.01	-0.07	**-0.11**	-0.04	0.03	-0.02	**0.34**	**0.32**	**-0.11**	-0.08	**-0.16**	**0.67**	*	
TPB	**0.25**	**0.16**	0.06	**0.49**	**0.42**	**0.50**	0.06	**0.54**	**0.54**	**1.00**	**0.97**	**0.70**	**0.64**	-0.09	*

DTH: days to heading, DTA: days to anthesis, RoA$_F$: root opening angle measured by protractor. SN: spike number. TN; tiller number, PH: plant height, SRN: seminal root number, NRN: nodal root number, TRN: total root number, SDW: shoot dry weight, StmDW: stem dry weight, SpkDW: spike dry weight, RDW: root dry weight, RSR: root to shoot ratio, TPB: total plant biomass.

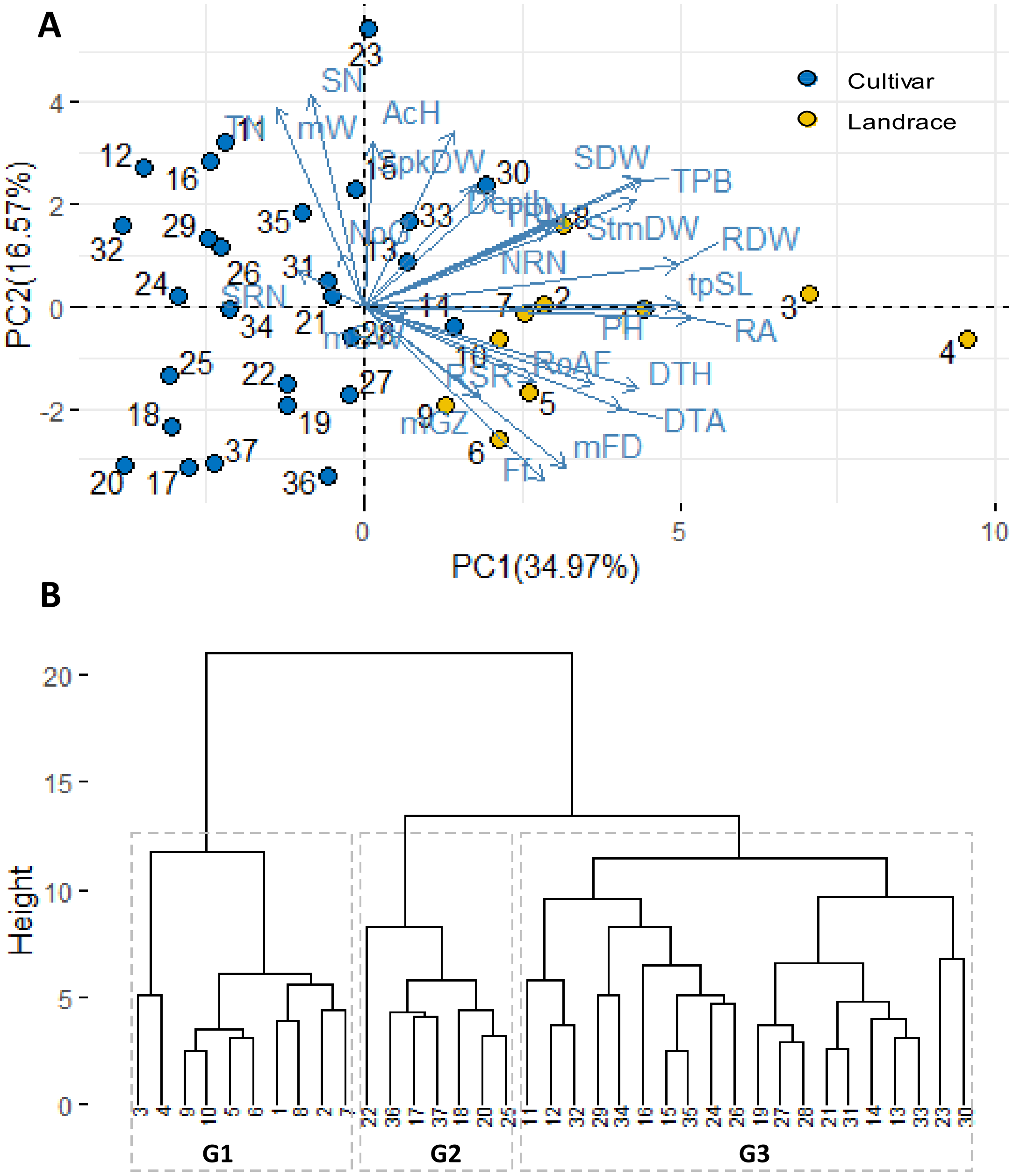

Figure 4.3. Biplot of the principal component (A) and hierarchical analysis (B) of shoot and root traits recorded in shovelomics experiment.

Both landraces and cultivars developed an adult plant root angle steeper than those of seedlings did, but this reduction of the adult plants' angle was larger for cultivars (Figure 4.4).

Table 4.6. Combined ANOVA analysis for root opening angle in seedlings and adult plants (RoA_I) for 37 genotypes and type of genotypes (cultivar vs. landrace).

Source of variation	d.f	s.s	m.s	v.r	F pr
Growth stage	1	131075.4	131075.4	362.18	<.001
Genotype	36	43706.0	1214.1	4.94	<.001
Type	1	4014.2	4014.2	16.34	<.001
Growth stage × Genotype	36	43879.7	1218.9	4.96	<.001
Growth stage × Type	1	7094.2	7094.2	28.88	<.001
Residual	958	235285.7	245.6		
Total	1035	455394.4			

At genotype level, genotypes ranked differently depending on growth stage (Table 4.6). Change of RoA from seedling (RoA_I) to adult plants ranged from -10.47 ° in Montpellier to 42.73 ° in Mansourah. Only three of the 37 genotypes showed larger or no difference of RoA in adult plants compared to seedlings: Ofanto (0.65 °), Langlois (0.97 °) and Montpellier (10.47 °) (Table 4.S5).

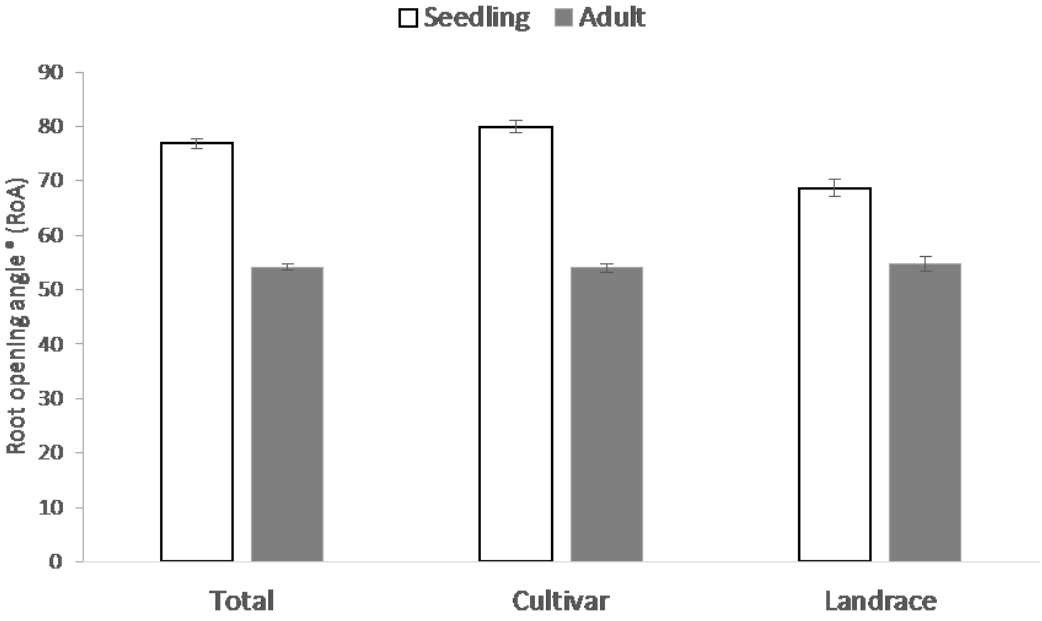

Figure 4.4. Root opening angle in cultivars and landraces at seedling and adult plant stages (RoA_I). Bars are the standard error of the mean (SEM).

4.4.4. Relationships of traits between experiments and growth stages

4.4.4.1. Correlation of seedling traits with greenhouse traits

Few correlations were detected between the two experiments. Seedlings with higher TRL tended to have higher PH but less depth in mature plants. Seminal root system with greater angle was negatively correlated with PH, RDW30 and RDW. Remarkedly, higher root number at seedling was associated with shallower root depth at plant adult (Table 4.S6).

4.4.4.2. Correlation of seedling traits with shovelomics traits

It is worth to note that, overall, the seedlings with higher root size tended to have positive correlations with all biomass traits assessed in the field (shoot and root), except with SN, TN and SpkDW. In contrast, root growth angle was only positively correlated with SN, TN and SpkDW.

All the seedling traits, except RN and Diameter were significantly correlated with root area (RA) whereas only root growth angles had negative correlations with RA. Seedlings with higher TRL and Surface had tendency to reach heading later in the field, with higher PH, RA, tpSL and with shallower root angle. Seminal root angle had significant negative correlations especially with DTH, PH, shoot biomass and RA. PRL had significant correlations only with RA and tpSL. No correlations were found with Diameter and only one significant correlation was found between RN (seedling) and SRN (plant) (Table 4.S7).

Correlations between similar traits at seedling and in field showed the highest correlation for SDW (r= 0.57). Total plant structure length (tpSL) had medium but significant correlation with total root length (r= 0.44), pointing out that TRL at seedling could, partly, predict for tpSL in plant adult. Root number had relatively weak correlation r = 0. 37. Regarding root opening angle, there was no relationship between seedling and adult plant measurements (Table 4.S7, Figure 4.5).

4.4.4.3. Correlation of greenhouse traits with shovelomics traits

In general, the same trends were evident for the same traits measured at the two experiments, PH, DTH, and RDW, but not for SDW. It is worth noting that genotypes, which produced high SDW in the field were more likely to have shallow rooting in the greenhouse (Figure 4.6C). Also, a high correlation was found between PH in tubes and mean fractal dimension (Figure 4.6D), and filling factor with the respective correlations 0.79, 0.77 (Table 4.S8). Genotypes with higher PH in the field, tended to yield more root biomass especially at the upper layer (30 cm). These genotypes apparently invested more biomass in the roots, but not in growth in depth

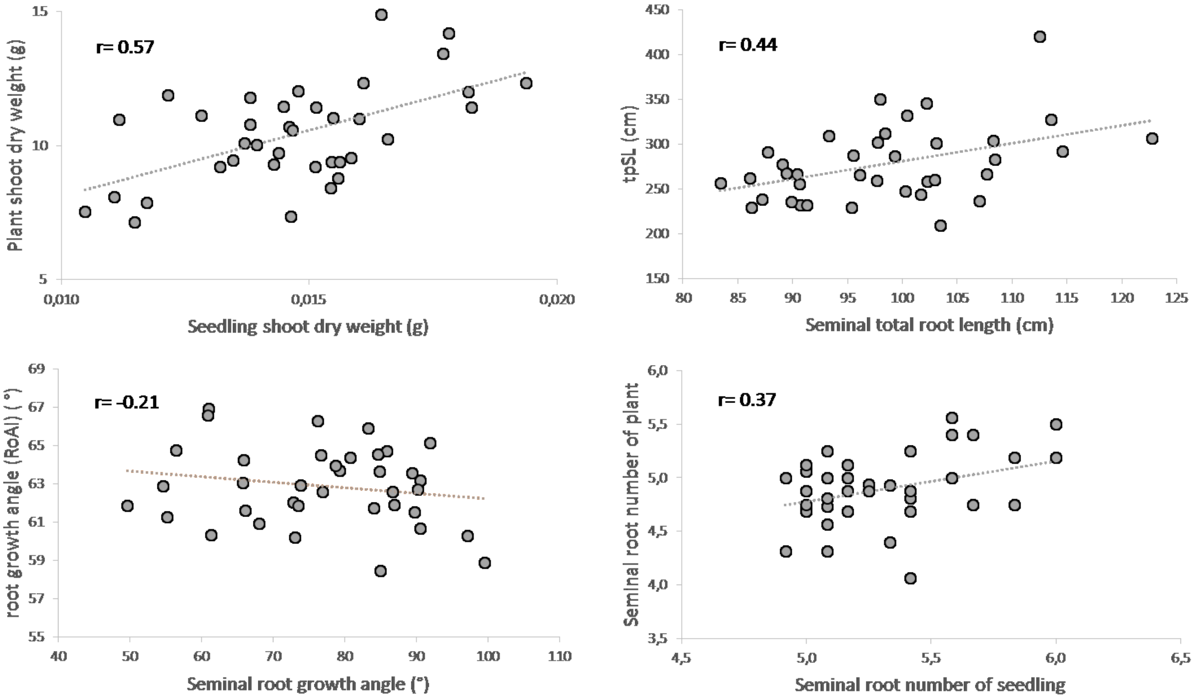

Figure 4.5. Relationships between the similar traits measured at seedlings and plant adult (Shovelomics).

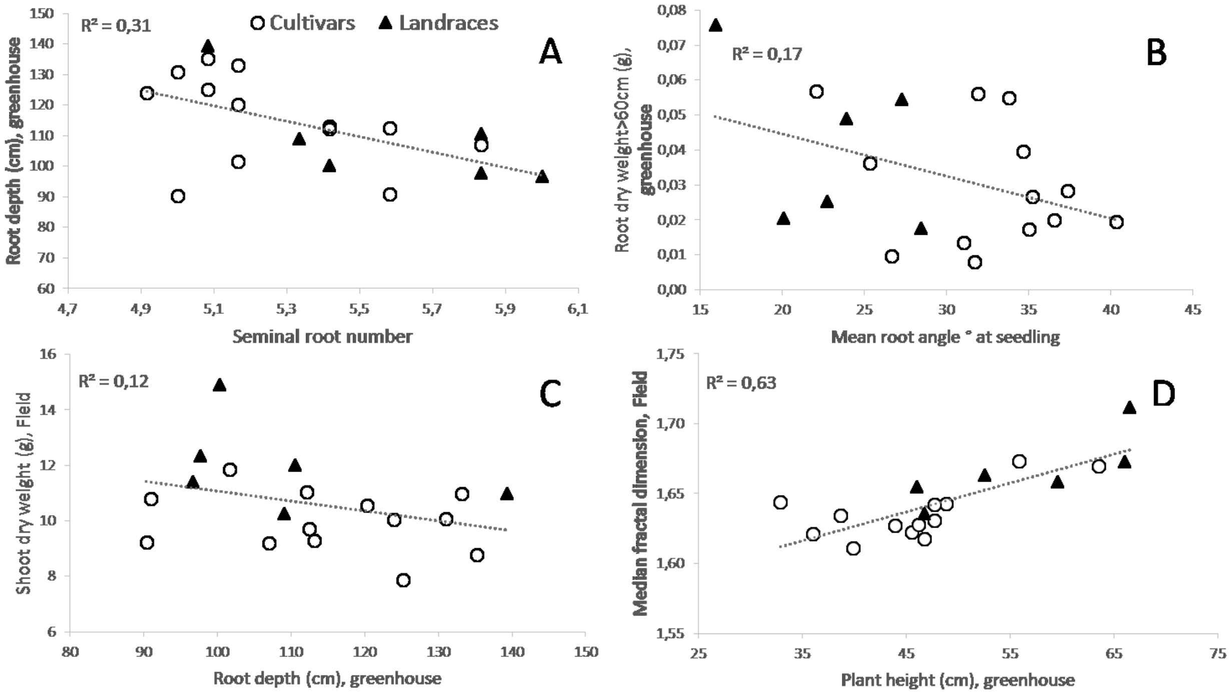

Figure 4.6. Relationships between some traits from different experiments. Only adult genotypes were considered in greenhouse experiment. Dotted line (Tendency) and r square correspond to the all dataset.

(no significant correlation with RDW>60). In general, the correlation of RDW in the upper section with the field traits was more pronounced than the correlations with root present at deeper sections. The number and dry weight of spikes in the field presented negative correlations with all the traits assessed in the greenhouse. Interesting, these two traits were negatively related to RDW of the lower section (RDW>60cm), and the genotypes with higher fertility (TN, SN, SpkDW) in the field allocated more biomass in shoot than in roots in the greenhouse (Table 4.S8). Genotypes, which reached later to heading under greenhouse, tended to be less fertile. Root system with higher size (higher AcH and mW) would produce less RDW at depth (RDW>60 cm) (Table 4.S8).

4.5. Discussion

The greenhouse experiment lasted up to seventy-one days (ten weeks); the first plant reached heading (harvest date) in only 41 days. The explanation for this short duration is that our experiment was set up in late spring - early summer, characterized by warm temperatures and long photoperiods. Although the temperature was controlled, this control was not complete, and it fluctuated between 22° and 35° C. Only nineteen of the twenty-seven genotypes, reached the reproductive phase (heading), including six landraces. Most landraces were reported as spring varieties in some database (i.e. GRIS: Genetic Resources Information System for Wheat and Triticale) whereas in the present study four of them previously described as spring types (Gloire de Montgolfier, Guemgoum R'khem, Hedba 03, Montpellier) behaved as winter genotypes.

4.5.1. Landraces had larger shallow root biomass, and similar root depth compared to cultivars

There were some differences in root and shoot development along the germplasm group dividing lines. Root depth differed between winter and facultative/spring habit, with winter plants presenting deeper roots, but not between landraces and cultivars. Landraces, however were 14 cm taller than cultivars. The difference in PH did not reflect that of root system depth. However, it was positively correlated with root biomass, overall, and for the two upper sections separately. It is supposed that most modern cultivars carry semi-dwarfing mutations that shorten dramatically plant height (Subira *et al.* 2016). Our results suggest that the dwarfing genes reduced plant height and root biomass at the upper section, but affected less, if anything, root depth and root biomass at lower sections. Recently, Friedli *et al.* (2019) showed that modern varieties decreased root depth under normal conditions, but they increased root depth under drought. In addition, they found that plant height was correlated with root depth under well-watered conditions, but not under early water stress conditions in agreement with the results of Carvalho *et al.* (2014) and Elazab *et al.* (2016). The latter authors reported a stronger reduction of above-ground biomass compared to the root biomass and an increased root-shoot ratio under drought.

In the current work, we found that root depth evaluated in pipe-pots was negatively correlated with the plant height and SDW of the shovelomics experiment, suggesting that modern genotypes (semi-dwarf) tended to grow deeper roots than landraces (tall), although the difference was not significant. This result is in agreement with the report of Dib *et al.* (1992) on two Algerian landraces (Hedba 3 and Oued Znatie 368) and three modern cultivars, they found that the cultivar Hourani presented higher root depth compared to the two landraces which presented a root volume much higher than that of cultivars. The negative relationship (R^2=0.31) between root number at the seedling experiment and root depth in the pipe-pots is a consequence of most landraces having higher seminal RN and less root depth compared to cultivars. The combined findings confirm that landraces invested more root biomass at the upper sections while cultivars favored root depth. In other words, cultivars had more homogeneous distribution of root biomass along the soil profile that landraces. These observations are supported by the results of the shovelomics experiment, in which landraces presented a significantly higher nodal root number than cultivars, which would explain the larger shallow root mass of the former. Several studies found that modern varieties reduced root length and root biomass weights compared to their taller ancestors (Waines and Ehdaie 2007; Wojciechowski *et al*. 2009; Elazab *et al*. 2016; Aziz *et al*. 2017).

Our results with respect to the differences in shoot and root biomass between cultivars and landraces were not in agreement with the results of Subira *et al.* (2016), obtained in another pipe-pot experiment, which found that both aerial biomass and each section of root biomass was reduced by the presence of *Rht-B1 b*, being the deepest section the one most altered by the dwarfing genes. Our landraces are very likely to have *Rht-B1a,* given their superior height, as observed in the shovelomics experiment. Unexpectedly, the difference in SDW was not found under greenhouse, when landraces were compared to cultivars. It is known that the Algerian landraces are more vigorous in shoot biomass, which was also clearly observed in the shovelomics experiment. On another hand, our landraces yielded more root biomass than cultivars; therefore, the dwarfing genes could also reduce root biomass, contrary to what was reported by previous studies where the reduction was only observed in aboveground biomass (Brancourt-Hulmel *et al.* 2003; Royo *et al*. 2007; Álvaro *et al*. 2008).

The most remarkable finding of the greenhouse study was that only at the upper root section, there was a reduction of cultivar biomass, compared to the landraces, and the RDW of upper section was much higher than the other sections. It is worth noting that this distribution was consistent for all categories; heading, non-heading, cultivar, landrace, and additionally at the single genotype level, indicating that neither the transitions to the reproductive stage nor the presence of dwarfing genes affected this root distribution over depth. A likely reason could be fertilizer distribution. The triple superphosphate applied was only provided in the first 30 cm of depth, which could favor root growth at this section. The effect of phosphorus on root: shoot ratio, was mentioned by De Souza Campos *et al*. (2019), in addition Kang *et al*. (2014), showed that deep placement of phosphorus could increase root biomass at deep layers in bread wheat. Other soil factors could drive the root distribution. For instance, Elazab *et al*. 2016, showed that the water regime did not affect the root weight density (RWD) in any of the soil layers, while a nitrogen level significantly increased the RWD in all soil layers except for the upper one (0-30 cm), compared to a high N level. We do not expect that the nitrogen would have any effect in our study since it was provided in fractions with assimilable form (urea) and on sandy soil with periodic watering. Additionally, we cannot exclude a possible effect of temperature on the higher RDW30, because the temperature has an important effect root growth. Hodgkinson *et al.* (2017) suggested that the greater thermal temperature might be the reason for the greater amount of surface rooting. The upper section of the pipe-pot profile in the current experiment could be exposed to higher ambient temperature than the lowers sections, given the height of tubes and the gradient of water level (more towards the bottom). In addition, the pipe-pots were tightly arranged in square (9 × 9), only 32 surrounding pots were directly exposed to the ambient temperature. A temperature effect like this was observed in a study of barley potted-plants, where root growth was exposed to a vertical temperature gradient (20–10 °C from top to bottom). The roots were concentrated in the upper 10 cm, in contrast to plants grown at uniform temperature 20 °C (Füllner *et al.* 2012). As with soil, there is variation in temperature among roots at different depths, but plants in pots have a different profile, with stronger and faster changes than plant roots experience in the field (Poorter *et al.* 2016).

4.5.2. Sowing density adopted in the shovelomics experiment

The plants in this experiment were grown at commercial sowing density (250 seeds/m^2) in order to assess root traits under real agronomic conditions. Therefore, wheat plants had, on average, 10 cm (half of the inter-row distance) on both sides to extend their roots towards the neighboring rows, and just 2 cm within the row. Therefore, most growth occurred in a soil volume close to a bidimensional plane. This experimental setting undoubtedly affected the results of the experiment, as seed density modifies root system architecture in barley (Hecht *et al.* 2019), at least by decreasing nodal root number per plant. Besides, seed density has large effect on aboveground traits, like reducing tiller number per plant (Soleymani *et al*. 2011) and shoot dry weight per plant (Harper 1977), while increasing tillers per area (Darwinkel 1978), leaf number per area (Khalil *et al*. 2011; Moosavi *et al*. 2012) and leaf area index (Olsen and Weiner 2007; Moosavi *et al*. 2012). Additionally, it can change biomass allocation and fine root distribution (Hecht *et al.* 2016). Our genotypes had a small range of variation and mean for NRN, ranging from 8 to 46 roots per plant, with an average of 25.2, compared to the bread wheat study carried out by York *et al.* (2018): 12 to 142 with an average of 38.8, although they had a lower plant density (200 plants m^{-2}).

4.5.3. Variability and relationships of traits

The shovelomics approach involves a large investment in labor that should pay off with the collection of a commensurate amount of biologically and agronomically meaningful data. For this reason, we first examine the quality of the data collected.

In this study, the heritability of root REST-traits ranged from very low to moderate, 0 in mSW to 0.61 in RA, and were mostly lower than those found in a maize study conducted by Le Marié *et al.* (2019). They found that the highest h^2 was observed for mW (0.77-0.80) and Ff (0.70), while in our case these two traits showed low h^2 (0.26 and 0.37, respectively). Only the h^2 of RA and tpSL could be comparable to the above studies. For aboveground traits, plant height in this study showed very high h^2 (0.97) compared to the former study (0.56 and 0.69). The h^2 of the root angle recorded using the protractor was 0.47 superior to that found by York *el al.* (2018) (0.37), and the h^2 of RA was very low (0.04). Some studies, like Canè *et al.* (2014) and Maccaferri *et al.* (2016) found genomic regions determining root angle and number, which overlapped with QTLs for yield in a wheat mapping population, so these root traits may have a true agronomic effect. However, in our field study we found only weak correlations between root angle and biomass of the aboveground traits. Our results indicate that the collection of data using the “shovelomics” approach at commercial stands is challenging. Higher heritability is desirable to get meaningful results, and we propose to increase the number of plants sampled to achieve this goal.

The relationship of root system architecture to crop performance in wheat is partially established, but many gaps in knowledge remain (York *et al*. 2016). Colombi and Walter

(2017) demonstrated that a high root number enhanced bread wheat growth in compacted soil. The nodal root number presented considerable and significant correlation with most aboveground biomass related traits.

There is general agreement that shoot biomass is positively correlated with root biomass (Weaver and Himmel 1929). Our results revealed positive correlations between the below and the aboveground biomass traits where the highest correlations were found between RDW and SDW (0.62) and StmDW (0.63) in shovelomics experiment, this result was confirmed by the pipe-pot experiment showing positive correlation of RDW and SDW (0.73), suggesting that direct selection for dry root weight would be effective for better aboveground vigor under favorable conditions and *vice versa*. This result agreed with previous results found in seedlings (Cai *et al*. 2012; Abdel-Ghani *et al.* 2015, Boudiar *et al*. 2019 (Chapter 2)) and in mature plants (Ehdaie *et al.* 2016; Bektas *et al.* 2016; El Hassouni *et al*. 2018). Based on the above previous findings, overall, it seems that under normal conditions root biomass was positively related to shoot biomass. However, some studies found that the ratio shoot to root biomass varies depending on growing conditions. Ruggiero and Angelino (2007) found that nitrogen starvation increased root to shoot ratio of durum wheat and barley plants. According to Gargallo-Garriga *et al*. (2014), drought induced opposite metabolic responses of shoot and root in some grass species. Growth dynamics of shoot and root showed different patterns between barley genotypes under drought (Boudiar *et al.* 2020). Therefore, efforts to use root traits for breeding should be performed in conditions as close as possible to the target conditions.

4.5.4. Is a large root system useful for environment adaptation?

Based on the results of the three experiments on root growth patterns, reported here and in chapter 3, the set of durum wheat genotypes presented various root system architectures. Compared to cultivars, landraces have steeper root angle at seedlings but, interestingly, this difference was lost at the adult stage, possibly influenced by differences of plant density between the experimental systems. Higher root dry weight was observed at topsoil for landraces compared to cultivars, in the two soil-based experiments. Landraces had steeper seminal root angle, which usually is taken as an indication of ability to reach higher depths. However, the greenhouse results indicated no difference in root depth between cultivars and landraces. Overall, there was appreciable genotypic variability for most traits, with the main driver of variability being the differences between cultivars and landraces. This last group had a larger/vigorous root system both at seedling and adult plant stages, expressed as total root length, root dry weight, area of convex hull, root area, total projected structure length and nodal root number. In conclusion, landraces had larger root systems than modern cultivars, at least when grown under good water availability conditions. The immediate question is if this feature is the result of adaptation to the predominantly dry conditions of Algeria.

The usefulness of a large root system in dry environments is a controversial issue. Several authors (for instance, Kramer 1969; Hurd 1974; Jackson *et al*. 2000) suggested that deep, wide spreading and profusely branched root system were essential traits to target in breeding for drought tolerant crops. This view was partially challenged by Passioura (1983) who shifted the focus to anatomical features, suggesting that a root system with reduced xylem vessel diameter was a the most beneficial trait in water stress environments, through increased water use efficiency. Plants should have a root to shoot ratio that would not exceed an optimum, above which further increase in root size would not only be useless, but also would impose a cost on shoot growth by wasting biomass. In Mediterranean-type environments, like in Algeria, the often-occurring final drought affects the rainfed crops during grain filling. In such situation, deep-rooted cultivars would be advantageous for exploiting the deep-stored water. Nevertheless, this deep rooting system would not be beneficious anymore if it depletes completely this stored water early in the season before the grain filling, otherwise it could cost plants a useless biomass. Therefore, a non-vigorous root system that progresses in depth slowly, and exploits the stored water during the grain filling would be the most advantageous ideotype (Kirkegaard *et al*. 2007; Palta *et al*. 2011). El Hassouni *et al*. (2018) revealed that genotypes with deep root system could increase grain yield by 37 to 38% under low moisture conditions, but the yield of these genotypes was reduced by 20 to 40% compared to shallow rooting genotypes under favorable moisture conditions. Therefore, the decision on which root characteristics are best to each environment should be supported by a quantitative assessment of the probability of occurrence of drought stress. Alternatively, in environments where the rainfall distribution is uniform, the ability to capture water and use it quickly may be beneficial (Turner and Nicolas 1987; Moeller *et al*. 2009).

The acquisition of nutrients is another important role of the root system. A large shallow root system becomes important under nutrient deficiency and especially around grain filling (Mattsson *et al*. 1993; Manske and Vlek 2002). In wheat, the shallow root system type, which forages the topsoil, would be beneficial in capturing nutrients with low mobility like phosphorus (Manske *et al*. 2000). This root pattern was found in our landraces consistently across both experiments (pipe-pot and shovelomics), which would allow to landraces exploiting water and nutrients in the topsoil better than cultivars. The topsoil foraging can be achieved through greater production of axial roots, shallower axial root growth angles, greater lateral root density, reduced root metabolic cost, and greater root hair length and density (Lynch 2019). For instance, root systems with greater production of nodal roots enabled higher growth and yield in maize (*Z. mays*) on soil with low phosphorus (Sun *et al*. 2018). Similarly, common bean (*Phaseolus vulgaris*) genotypes with more basal roots had greater P capture, growth, and yield under P stress than lines with fewer basal roots, in silico (Walk *et al*. 2006; Rangarajan *et al*. 2018).

There is no general conclusion for this section. The optimum root system depends on the prevalent soil, climate and management conditions (Palta *et al.* 2011). The fact that the root system features have changed markedly in Algeria due to modern breeding, indicates the presence of these interactions and, also, that there is more than one good outcome for a common environment.

4.5.5. Why do landraces have large root systems?

We have seen that larger root systems are not an automatic indication of better performance in dry environments. Then, why do landraces show higher root size at seedling and adult plant stages in our study? This seems an indication of a reduction of root system size due to modern breeding. This trend was first detected in bread wheat when cultivar differences for root biomass in bread wheat were reported by Troughton and Whittington (1968) and Monyo and Whittington (1970), who observed that landrace ‘Chinese Spring’ had twice as much root biomass as cultivar ‘Hope’ (released in 1930). Recently, this result was confirmed by Ashe *et al*. (2017). Later, several studies confirmed the superior root system biomass of bread wheat landraces compared to cultivars (Siddique *et al*. 1990; Crowley *et al*. 2005, 2006; Waines and Ehdaie 2007; Bektas *et al*. 2016). Some studies indicate that the root system of wheat genotypes post green revolution is smaller than those carried by earlier cultivars and landraces (Waines and Ehdaie 2007). The suite of Rht (reduced height) genes, which are at the core of the green revolution suite of new cultivars, had a demonstrated pleiotropic effect on root growth (Wojciechowski *et al*. 2009; Bektas *et al.* 2016; Subira *et al*. 2016).

There is abundant evidence on the effect of dwarfing alleles on plant morphology, including root development. Differences between *Rht-B1* alleles explained more than 81% of plant height genotypic variability, thus supporting the importance of plant height in differentiating durum wheat cultivars released before and after the green revolution (Royo *et al*. 2007, 2008; Graybosch and Paterson 2010). In previous studies, the dwarfing alleles were widely reported to reduce the aerial and root biomass (Brancourt-Hulmel *et al*. 2003; Royo *et al*. 2007; Álvaro *et al*. 2008). Moreover, the relative change in the root/aerial biomass ratio was more than twice that recorded for aerial or total biomass, showing that, in relative terms the dwarfing allele had a greater effect on reducing the dry matter of roots than on reducing that of aerial organs (Subira *et al*. 2016). MacKey (1973) noted that tall cultivars had larger root dry weights than their F1 descendants resulted from the cross with Norin 10 and Tom Thumb, the source of the Rht1, Rht2 and Rht3 alleles used by Borlaug (1968) in his Mexican semi-dwarf wheat-breeding program. He concluded that ‘a tall wheat plant tends to have a deep, and a short wheat plant a shallow root system’.

Our landraces were very tall, with an average of 130 cm, compared to cultivars (95 cm), in the field experiment. This difference of plant height could partly explain the larger root systems developed by landraces, supported by the positive significant correlation between RDW and PH (0.40). The lack of information about the presence of dwarfing genes in our materials, prevent us from confirming this assumption. However, the pleiotropic effect of root reduction due to the Rht genes seems the most plausible explanation for the difference in root system size between landraces and cultivars. The agronomic disadvantages of this size reduction, overall, seem negligible.

According to Hurd (1974) and Blum (1996), in the case of a landrace grown under rainfed conditions and faced with frequent water stress, the preferred root system should be large enough and well distributed throughout the soil profile in order to capture nutrients and water effectively throughout the season. This kind of root system may also be important to capture precipitation from light rains at the end of the growing season, and may help to reach non-mobile nutrients (Bektas *et al*. 2016). Therefore, the trend to reduce plant height and root size may have improved yields globally, but could be detrimental in some drought prone areas.

4.5.6. Root system traits at different plant stages

One of the important objectives of root traits phenotyping at seedling stage is to predict these traits at mature plants. Although there are examples in which the early stage root phenotype has some predictive value for later developmental stages (Tuberosa *et al*. 2002), the seedling root phenotype may not always be representative of the mature plant (Watt *et al*. 2013).

In our study, we found that mature plants displayed significant differences in terms of root growth angle. Similar results were found by York *et al*. (2015); Maccaferri *et al*. (2016); El Hassouni *et al* (2018). The growth angle based on root images of adult root systems in commercial field density is narrower than the RGA of seminal roots screened in rhizo-slides. It is worth noting that the genotypes behaved differently for root growth angle across growth stages expressed by the significant interaction genotype by growth stage. Adult plants narrowed its root angle by an average of 22.73° compared to seedlings (54.19° vs. 76.92°, respectively); this finding agrees with the results of Maccaferri *et al.* (2016). The relationship of root angle with yield varies between studies. According to Xie *et al.* (2017), there was a positive correlation between juvenile root length traits and grain yield of wheat genotypes grown under normal soil field conditions. In opposite, Atkinson *et al*. (2015) and Khokhar *et al.* (2019) did not find these associations. Based on the comparison of individual genotypes, Khokhar *et al.* (2019) reported that a wheat genotype with narrow root angle showed greater grain yield than a genotype that had wider root angle. Ruiz *et al.* (2018) showed that larger size and steeper root growth was associated with a lower number of spikelets per spike, whereas deeper primary roots were associated with earlier maturity.

Our attempts to find relationship between root angle of seedlings and mature plants was largely unsuccessful. However, this relationship was established in the study of Ali *et al.* (2015) and Maccaferri *et al.* (2016) (R^2=0.22), and was recently found by Alahmad *et al.* (2019). The lack of correlation between seedling and mature plants root angle could reflect factors not captured in the laboratory screen such as time, soil properties, climate variation and plant phenology (Watt *et al*. 2013). The extrapolation of seedlings screens results to field performance for mature plant should be made with caution due to the quite different process, which could related to the growth stage (Bai *et al*. 2013). For instance, some traits present at adult stage are not present in seedlings (Thorup-Kristensen *et al*. 2009). In our case, seedlings were grown in a medium with no competition from neighboring plants, and root angle spread had no limitations. In the shovelomics experiment, the situation was very different, with plants growing very close to each other within each row, and with a competitor row growing only 20 cm away. This large difference in the rooting environment may be behind the low correlations found, and raises a question on the predictability provided by systems based on seedlings.

The comparison of landraces vs. cultivars varied over growth stage. Compared to seminal root growth angle, landraces reduced less its nodal root angles 14° versus 26° in cultivar. On another hand, we found a positive correlation (R^2=0.32) between SDW at seedling and mature plants. Furthermore, root number and total root length (tpSL in mature plant) showed significant positive correlations.

4.6. Conclusion and perspectives

- The relationships between seedling and mature plant were established for traits related to biomass but not for those related to root architecture (root angle).
- The current results indicate a clear higher shoot and root biomass for landraces over cultivars, where the plant height seems to have a substantial effect, probably due to the asymmetrical distribution of dwarfing alleles in those germplasm groups.
- Lack or uncertain information about dwarfing, vernalization and photoperiod genes of the employed set of genotypes impeded us to confirm some assumptions; therefore, a screening for dwarfing genes would elucidate their implication in the shoot and root difference between tall and short genotypes. The same can be said for the vernalization and photoperiod genes, which will affirm the growth habit of this genotype collection.
- Relating root traits at seedling and at mature plant with grain yield of favorable and unfavorable cropping seasons would identify root traits implicated to drought tolerance.
- The root biomass distribution could be driven using phosphorus fertilization, induced higher root biomass at depth deserves attempt for enhanced drought tolerance.

4.7. References

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5. Assessment of yield and yield related traits of old and modern durum wheat varieties grown under contrasting rainfall conditions

5.1. Abstract

Breeding of drought-adapted genotypes is one of the main issues in Mediterranean environment. We studied thirty-durum wheat varieties, including moderns and local landraces widely gown in Algeria, during two successive contrasting rainfall conditions (2016/2017 and 2017/2018). Grain yield and its components were evaluated, in addition to some morpho-physiological traits. Overall, genotypic variation was found for the measured traits under both conditions. Drought affected most of traits; biomass and grain yield were the most decreased ones, whereas increase was observed only in harvest index and emergence (41.41 and 10.52%, respectively). Stepwise regression revealed that the grain number per area and thousand-kernel weight together explained the most variation of the grain yield (> 99%) under both conditions. The type of variety (cultivar vs. landrace) showed a significant effect on the studied traits. It is worth to mention that landraces showed higher biomass only under drought while cultivars out-yielded landrace only under non-drought conditions. Drought susceptibility index based on grain yield showed that overall landraces were more tolerant than modern cultivars. To conclude, our results pointed out to a different behavior for landraces and cultivar depending to water availability conditions, the combination of higher grain yield and higher biomass in one genotype would further enhance the grain yield under water limited conditions.

5.2. Introduction

Durum wheat is widely cultivated in the Mediterranean region, representing 75 % world's durum wheat area (Graziani *et al*. 2014). The grain yield of durum wheat in Algeria remains low, even when compared to the neighboring countries (Annicchiarico *et al.* 2002; Bahlouli *et al.* 2005). One of the main factors limiting yield is the water stress imposed by the insufficient rainfall and its irregular seasonal distribution (Bouzerzour *et al.* 1994; Annicchiarico *et al.* 2005; Chennafi *et al*. 2006; Mekhlouf et *al*., 2006). Chennafi et *al*. (2006) reported a highly variable rainfall during a 13 seasons of wheat cultivation in Algeria, ranging from 168.7 to 517.3 mm, from October to March, of which 56 to 88% fell in the cold period. These variable conditions are partly responsible for the a large genotype by environment interaction and high grain yield variation ranging from 1.8 to 3.6 t ha^{-1} at the same site in successive cropping years found in another durum wheat study in Algeria (Bahlouli *et al*. 2005).

Breeding directly for grain yield is feasible, but it is hindered by the low heritability of the trait, particularly if the genotype by environment interaction is large. Grain yield in wheat is related to several agronomic, morphological and physiological traits (Hsu and Walton 1971; García del Moral *et al.* 2003; Chen *et al.* 2012; Liu *et al.* 2015), which have been widely explored in wheat improvement programs to accelerate cultivar development. The high heritability of these traits and its correlation with grain yield make them useful indirect selection criteria during breeding and cultivar development (Chen *et al.* 2012; Abdolshahi *et al.* 2015; Liu *et al.* 2015; Gao *et al.* 2017). Moreover, it has been suggested that genetic progress in yield can be achieved if several traits conferring better agronomic and physiological performance with stress tolerance are simultaneously selected and introduced in a single variety (Lopes *et al.* 2012a). A number of studies showed the usefulness of agronomic traits in yield improvement. For instance early flowering and maturity (Chen *et al.* 2016; Mondal *et al.* 2016), harvest index (Giunta *et al.* 2007; Royo *et al.* 2007; Gummadov *et al.* 2015; Flohr *et al.* 2018), biomass (Shearman *et al.* 2005; Xiao *et al.* 2012; Bustos *et al.* 2013; Aisawi *et al.* 2015; Gao *et al.* 2017), thousand kernel weight (Zhou *et al.* 2007; Morgounov *et al.* 2010; Tian *et al.* 2011; Zheng *et al.* 2011; Lopes *et al.* 2012a; Aisawi *et al.* 2015), number of grains per spike (Yu *et al.* 2014; Alonso *et al.* 2018; Liu et *al.* 2018a; Würschum *et al.* 2018). Other studies highlighted the importance of some morpho-physiological features in yield formation like traits related to flag leaf (Fan *et al.* 2015; Wu *et al.* 2016; Liu *et al.* 2018b; Liu *et al.* 2018c; Zhao *et al.* 2018) and canopy temperature (Lopes and Reynolds 2010; Lopes *et al.* 2012b; Gao *et al.* 2017).

Variation for agronomic and physiological traits and discovering of new alleles for improving grain yield potential were assessed in durum and bread wheat genetic resources (Ruiz *et al.* 2012; Mohammadi *et al.* 2015; Zhang *et al.* 2016; Reynolds *et al.* 2017; Liu *et al.* 2018a). Wheat genetic resources including landrace varieties, synthetic cultivars, and wild relatives are potential sources of alleles for enhancing drought tolerance and improving yield and its component traits (Gororo *et al.* 2002; Moeller *et al.* 2014; Cossani and Reynolds 2015; Gaju *et al.* 2016; Merchuk-Ovnat *et al.* 2016; Pinto *et al.* 2017; Reynolds *et al.* 2017; Liu *et al.* 2018a). Wheat genotypes with drought and heat tolerance; that incorporated genes from landraces, have been developed for cultivation in arid and semi-arid environments to boost grain yield potential (Lopes *et al.* 2012a; Cossani and Reynolds 2015; Mondal *et al.* 2016; Pinto *et al.* 2017; Crespo-Herrera *et al.* 2018).

The current study sought to i) quantify the phenotypic plasticity of a set of traits in response to drought and their relation to grain yield ii) to classify the studied varieties according to their performance under drought and favorable conditions, iii) to determine how landraces and cultivars behave under contrasting rainfall conditions.

5.3. Materials and Methods

5.3.1. Plant material and experimental conditions

This study was conducted on two successive rainfed cropping seasons (2016/17 and 2017/2018) on the eastern highland of Algeria, at the experimental station of the Technical Institute for Field Crops (ITGC), Sétif, Algeria. This site is representative of a large agricultural semi-arid region where the dominant farming system is based on cereal and sheep production (Bahlouli *et al.* 2005). Thirty durum wheat varieties grown in Algeria (currently or historically) were evaluated, including local landraces and cultivars from different geographical origins (Table 5.S1).

Seeds were sown on November 28, 2016 and December 11, 2017, both with a sowing density of 300 seeds/m^2. The trial was arranged in a randomized complete block design with three replications of plots 2.5 m long and 1.2 m wide, resulting in plots of 3 m^2 (6 rows, 20 cm apart). Fertilization was applied twice; the first delivery was supplied during soil preparation using triple superphosphate (0.46.0) at a rate of 45 kg ha^{-1}, and the second delivery was supplied at tillering stage with urea (46 %) at a rate of 100 kg ha^{-1}. Weeds were controlled with herbicides (Grand Star®) at the rate of 12 g ha^{-1} applied at jointing stage.

5.3.2. Traits

The following traits were recorded in the two experiments, on a plot basis, or in samples, as indicated.

- Emergence (Emg, plant/m^2): Estimated based on counting of seedlings, which emerged until February along 1.4 m and 2 m linear for 2017 and 2018, respectively, then converted to meter squares.
- Days to heading (DTH, day): was recorded when 50 % of the spikes were halfway out of the flag leaf.
- Plant height (PH, cm): was recorded as average plot values at maturity, from the soil surface up to the top of spikes (awns were excluded).
- Harvested grain yield (HGY, g/m^2) was mechanically harvested from the whole plot (3 m^2).
- Drought susceptibility index (DSI) calculated according to Fischer and Maurer (1978) using the following formula: $DSI = (1-Y_D/Y_P)) / (1-X_D/X_P))$, where, Y_D and Y_P are

the genotype yields under drought and favorable conditions, respectively, and X_D and X_P are the mean yields over all genotypes under drought and favorable conditions, respectively.

The following traits were recorded as indicated at specific time points:

- Leaf rolling (LR): was scored around heading using a visual scale from 1 to 5 (1 = no-leaf rolling, 2 = leaf rim starts to roll, 3 = leaf is shaped like a V, 4 = 60 % dead leaf area, 5 = leaf is rolled like an onion). The scoring was done during heading stage on 20 April in the first (drought) season, in early morning (LRM) referred to non-stress, and at noon (LRN) referred to stress (Bellon and Reeves 2002).
- Canopy temperature (CT, °C): was recorded at heading at noon by using infrared thermometer (Model FLUKE 62 MAX) pointed to a healthy flag leaf.
- Flag leaf area (FLA, mm^2): was assessed towards the end of heading and was estimated based on ten flag leaves, which were randomly sampled from each plot, sum of length (FLL, cm) of 10 flag leaves and its mean width (FLW, cm) were recorded then leaf area was calculated by following the formula according to Spagnoletti-Zeuli and Qualset (1990): $FLA = FLL \times FLW \times 0.749$
- Relative water content (RWC, %): one flag leaf per plot was sampled; then the fresh weight (FLFW, mg) was recorded, leaves were submerged into distilled water to obtain the turgid weight of leaves (TW, mg). The samples were oven dried at 80 °C for 72 hours to obtain the dry weight (FLDW, mg) and finally the following formula (Barrs and Weartherly 1962) was used to calculate RWC: $RWC\ \% = \frac{FLFW - FLDW}{TW - FLDW}$.
- Specific leaf area (SLA, mm^2/mg) was calculated according to the following formula: Leaf area / leaf dry weight.

All the following traits were estimated based on vegetative sample harvested from one representative row of 1.4 m and 2 m for 2016/2017 and 2017/2018 cropping season, respectively:

- Spike number (SN).
- Spike weight (SW, g/m^2).
- Total biomass (Biomass, g/m^2).
- Sample grain yield (SGY, g/m^2).
- Grain number per spike (GNS): was calculated following the formula $GNS = (1000\ SGY) / (TKW \times SN)$.

- GNM²: calculated by multiplying GNS and spike number per meter squares (SNM²).
- Harvest index (HI): was derived as 100 times the ratio of grain yield to total biomass.
- Spike biomass (SpkBio, g/m²): was derived from sample grain yield and spike weight.
- Thousand-kernel weight (TKW, g): was estimated based on the weight of 250 grains.

5.3.3. Data analyses

Analyses of variance (ANOVA) were performed using the REML procedure where all factors, genotype, type (landrace vs. cultivar) and year were considered fixed effects, except replications that were considered random effect. Multiple means comparison was carried out using an LSD at 0.05 level of significance. Stepwise regression was performed separately for each conditions (year) using adjusted R squared as a selection criterion to generate the final model. All the statistical analyses were performed using Genstat software, version 18 (Payne *et al*. 2009).

5.4. Results

5.4.1. Growing conditions

The temperatures registered during the two cropping seasons were typical, with a warm autumn, cold winter, and warm to hot spring. The average temperature in 2016/2017 (13.39 °C) was higher than that recorded in 2017/2018 (11.9 °C), and this pattern was seen at each single month, except in January where the 2017/2018 season showed higher temperature (Figure 5.1).

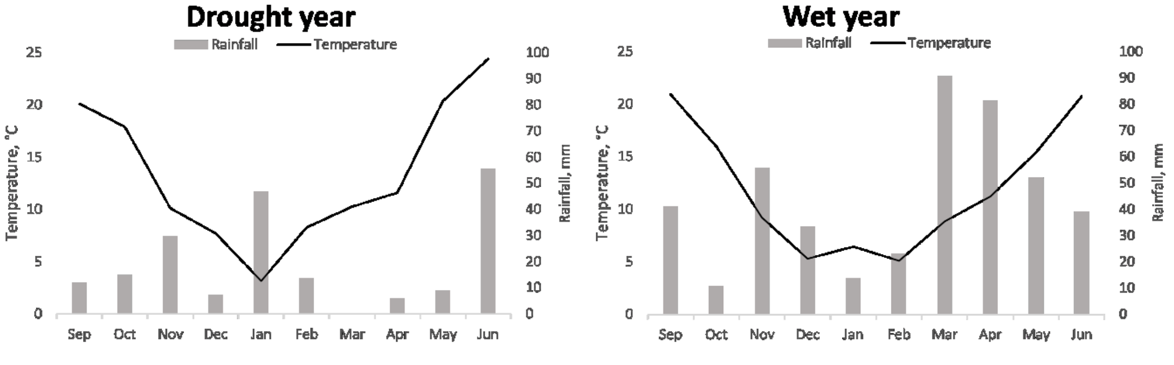

Figure 5.1. Accumulated monthly rainfall and mean monthly temperature recorded during the cropping seasons 2016/2017 and 2017/2018 referred to as drought and wet year, respectively.

For rainfall, the cropping season 2017/2018 accumulated a total of rainfall much higher than that of 2016/2017 (440.7 mm vs. 195.12 mm, respectively). The most significant difference was observed during the months of the active vegetative growth (Mars, April and May) with rainfall differences of 90.4, 75.4 and 42.7 mm, respectively, between the three months at the two seasons. Rainfall recorded in the two current seasons were very different of the historical rainfall season mean of the region, 315.7mm (https://en.wikipedia.org/wiki/S%C3%A9tif) According to the difference of rainfall and temperature recorded for both seasons, hereinafter 2016/2017 and 2017/2018 are referred to as drought/unfavorable and wet/favorable year, respectively, unless stated otherwise.

5.4.2. Genotypic variability and the effect of drought on the traits

The analyses of variance indicated that the genotypes behaved significantly different for most traits during the two cropping seasons, however genotypic differences were detected for SNM, GNS only in drought year (Table 5.1). The combined ANOVA of the two cropping seasons highlighted the strong effect of year (drought) on the totality of the traits except LRM and LRN. Significant interaction between genotypes and year was detected for Emg, PH, DTH, TKW, FLL, FLW, FLA, FLDW and RWC (Table 5.1).

Drought caused a drastic reduction for all traits, except emergence and HI, which were increased (by 10.52 and 41.41%, respectively) compared to favorable conditions (Table 5.2). Grain yield and biomass were the traits most affected by drought (reductions of 67.06 and 76.14 %, respectively) followed by the number of grains (49.83 %) and spikes (27.48%). The traits related to the flag leaf were relatively the least affected. No drought effect was observed for LRM and LRN. Drought induced an overall earliness by about 13 days (Table 5.2) compared to wet year.

The range of variation observed in wet year was higher for most traits compared to drought, exception was found for FLDW, FLFW, FLL and HI; these traits had higher range of variation under drought. Similar range of variation was found for LRM and LRN between the two conditions (Table 5.2).

5.4.3. Relationships between traits

Under non-drought conditions, grain yield showed positive and significant correlations with yield components, both biomass and fertility related traits, of which the correlation between GY and SWM^2 was very high (0.98). No correlation was detected between grain yield and DTH or PH. DTH and PH showed significant correlation between each other (0.80) and with biomass, and they did not showed correlations with fertility traits (SNM^2, GNS and GNM^2). Only DTH showed a weak significant correlation with TKW. The fertility traits were positively correlated with biomass. For the HI, positive correlations were found with GNS, GNM^2, SWM^2 and GY, but negative ones were found with PH, DTH. Morphological traits related to flag leaf (FLM) showed significant positive correlations in particular with PH, DTH. Emergence showed no or negative correlations with the other traits especially with those related to flag leaf, only one significant positive correlation was detected with SNM^2 (Table 5.S2).

Table 5. 1. Analyses of variance for the measured traits.

	2017	2018	2017 & 2018		
Traits	Genotype	Genotype	Genotype	Year	Genotype*Year
Emg	*	*	ns	***	*
DTH	ns	***	***	***	***
PH	***	***	***	***	***
HGY	*	***	***	***	**
LRM	***	***	***	ns	ns
LRN	***	***	***	ns	ns
CT	ns	ns	ns	***	ns
FLA	***	***	***	***	**
FLL	***	***	***	***	*
FLW	***	***	***	***	*
FLFW	***	**	***	***	**
FLDW	***	***	***	***	ns
RWC	ns	ns	ns	***	*
SLA	*	*	***	***	ns
SNM^2	*	ns	*	***	ns
SWM^2	ns	ns	ns	***	ns
Biomass	ns	ns	ns	***	ns
SGY	ns	ns	*	***	ns
GNS	*	ns	***	***	ns
GNM^2	ns	ns	ns	***	ns
HI	*	**	***	***	ns
SpkBio	ns	ns	ns	***	ns
TKW	***	***	***	***	***

Emg (plant/m^2): Emergence, DTH (day): Days to heading, PH (cm): Plant height, HGY (g/m^2): Harvested grain yield, LRM: Leaf rolling in morning, LRN: Leaf rolling at noon, CT (°C): Canopy temperature, FLA (mm^2): Flag leaf area, FLL (cm): Flag leaf length, FLW (cm): Flag leaf width, FLFW (mg): Flag leaf fresh weight, FLDW (mg): Flag leaf dry weight, RWC (%): Relative water content, SLA (mm^2/mg): Specific leaf area, SNM^2: Spike number per area, SWM^2 (g/m^2): Spike weight, Biomass (g/m^2): Total biomass, SGY (g/m^2): Sample grain yield, GNS: Grain number per spike, GNM^2: Grain number per area, HI: Harvest index, SpkBio (g/m^2): Spike biomass, TKW (g): Thousand kernel weight. Significance of sources of variation in single year analyses of variance (columns headed 2016 and 2017), and in a joint analysis of the two years (column 2017&2018). *, **, and ***: significant differences at 0.05, 0.01, and 0.001, respectively. ns: mean difference are not statistically significant.

Compared to non-drought, high positive correlation was found between sample grain yield and spike biomass under drought year, but this correlation did not appear under favorable conditions. The HI was negatively correlated with biomass only in the wet year. Emergence presented positive and negative correlations with SN and TKW, respectively, only under drought conditions. Overall, biomass traits presented more correlations with yield components under drought conditions. For flag leaf related traits, FLL was negatively correlated with spike number, spike biomass and spike weight only under wet conditions. Canopy temperature presented significant correlation with FLM only under drought conditions, plants with higher PH, flag leaf size and RWC tended to have lower canopy temperature (Table 5.S2). When correlations were tested between the two series of values of the same traits of both conditions, significant and positive correlations were detected whose the highest correlations were observed for DTH (0.71) and PH (0.70) while the lowest significant ones were found for GNS (0.24), SLA (0.29) and FLFW, HYLD (0.30) (Table 5.S2). Most traits recorded at the flag leaf had significant correlations. Significant correlation found for TKW (0.36), but not for GNM^2 nor biomass and grain yield (Table 5.S2).

Table 5.2. Minimum, maximum, mean comparison and reduction (Redu%) for the recorded traits.

	Drought season			Non-drought season			
Traits	Min	Max	Mean	Min	Max	Mean	Redu%
Emg	121.43	310.71	204.09^{a}	128.57	332.14	184.66^{b}	-10.52
DTH	106.00	118.00	109.53^{b}	115.00	130.00	122.51^{a}	10.59
PH	40.00	95.00	65.00^{b}	75.20	143.56	97.95^{a}	33.64
HGY	77.30	235.63	164.29^{b}	247.19	709.06	470.86^{a}	65.11
LRM	1.00	4.00	2.18^{a}	1.00	4.00	2.17^{a}	-0.61
LRN	1.00	5.00	2.84^{a}	1.00	5.00	2.84^{a}	0.06
CT	23.00	31.00	26.48^{b}	24.00	38.60	28.97^{a}	8.58
FLA	938.86	2455.29	1476.31^{b}	1421.65	3809.67	2081.65^{a}	29.08
FLL	11.52	23.24	17.15^{b}	16.15	24.78	20.63^{a}	16.87
FLW	0.96	1.49	1.20^{b}	1.13	1.75	1.40^{a}	14.50
FLFW	165.66	472.68	273.70^{b}	211.21	511.79	348.88^{a}	21.55
FLDW	69.73	183.59	122.08^{b}	94.73	192.44	143.68^{a}	15.03
RWC	72.58	92.14	80.83^{b}	77.45	99.79	89.67^{a}	9.86
SLA	10.01	14.22	12.13^{b}	11.66	17.30	14.37^{a}	15.61
SNM^2	150.00	335.71	230.54^{b}	170.00	472.50	317.90^{a}	27.48
SWM^2	145.39	417.35	259.36^{b}	446.67	1462.50	857.17^{a}	69.74
Biomass	83.82	548.57	380.46^{b}	753.80	2812.10	1594.50^{a}	76.14
SGY	66.14	283.85	158.81^{b}	105.18	713.65	482.05^{a}	67.06
GNS	9.24	29.64	19.80^{b}	8.70	40.86	28.58^{a}	30.72
GNM^2	2077.35	8194.28	4553.71^{b}	2022.60	15323.97	9077.36^{a}	49.83
HI	0.25	1.01	0.57^{a}	0.11	0.65	0.40^{b}	-41.41
SpkBio	53.54	140.79	100.55^{b}	126.94	979.94	386.11^{a}	73.96
TKW	27.60	50.60	35.00^{b}	44.68	68.60	53.41^{a}	34.47

Emg (plant/m^2): Emergence, DTH (day): Days to heading, PH (cm): Plant height, HGY (g/m^2): Harvested grain yield, LRM: Leaf rolling in morning, LRN: Leaf rolling at noon, CT (°C): Canopy temperature, FLA (mm^2): Flag leaf area, FLL (cm): Flag leaf length, FLW (cm): Flag leaf width, FLFW (mg): Flag leaf fresh weight, FLDW (mg): Flag leaf dry weight, RWC (%): Relative water content, SLA (mm^2/mg): Specific leaf area, SNM^2: Spike number per area, SWM^2 (g/m^2): Spike weight, Biomass (g/m^2): Total biomass, SGY (g/m^2): Sample grain yield, GNS: Grain number per spike, GNM^2: Grain number per area, HI: Harvest index, SpkBio (g/m^2): Spike biomass, TKW (g): Thousand kernel weight. Different letters indicate that means of cultivars and landraces were significantly different at 0.05 level of significance.

5.4.4. Classification of genotypes

The ranking of the 30 genotypes was performed based on HGY for each condition (drought and non-drought), from the highest-yielding variety (scored as 1) to the lowest yield one (scored as 30). Then the genotypes were plotted on the plan ranking drought vs. ranking non-drought and the ranking 15 was used as baseline to discriminate between good (<15) and bad

(>15) genotypes (Figure 5.2). Therefore, in terms of grain yield, the baseline was set at 167.86 g/m^2 for drought and 474.41 g/m^2 for non-drought (Table 5.S3).

Accordingly, four groups were identified. The First group was always good, including genotypes, which performed well under both conditions, this group; included 10 genotypes were all cultivars. The second group performed well in non-drought and bad in drought and included five genotypes, they were all cultivars except one was landrace. The third group was good in drought and bad in non-drought, 3 cultivars and 2 landraces. The last group, which performed bad under both conditions, was formed by 5 cultivars and 5 landraces (Figure 5.2).

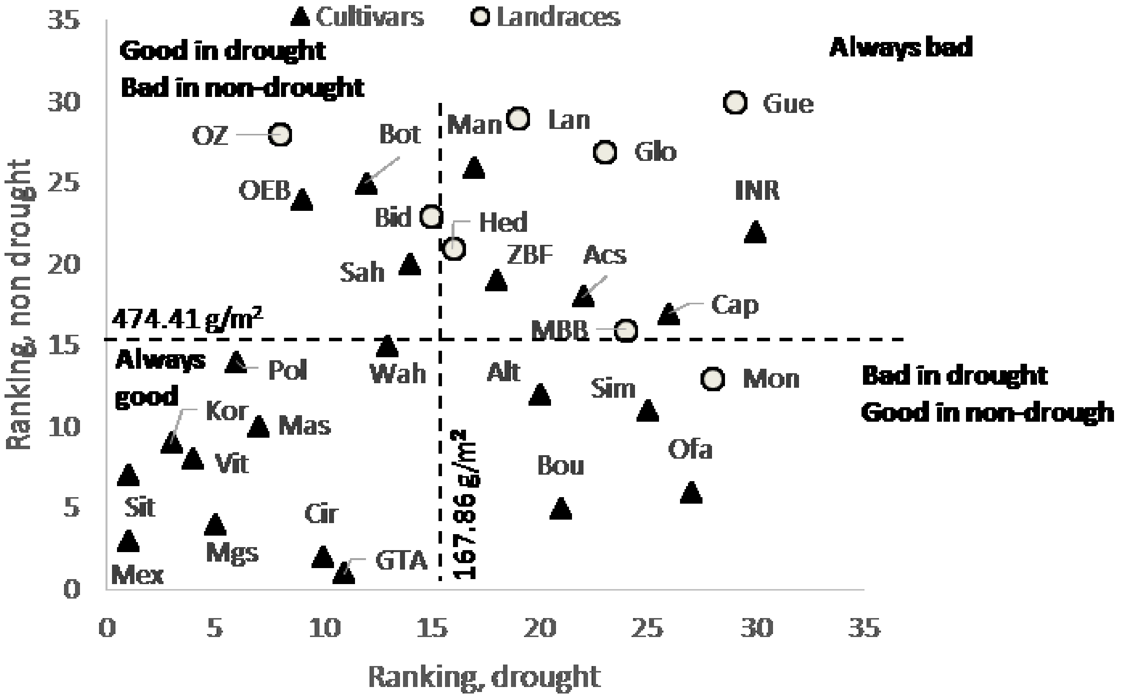

Figure 5.2. Varieties classification according to their grain yield-based ranking under drought and non-drought conditions.

5.4.5. GNM^2 and TKW explained the most variation of grain yield under both conditions

Stepwise regression analyses, using adjusted R-squared as the selection criterion, showed that the traits GNM^2, TKW, DTH, emergence, PF, Leaf length, HI and CT, were retained in the final model under favorable conditions (Table 5.3). These traits explained together 99.46 % of the grain yield variation. The GNM^2 alone explained most of the grain yield variation, 93.27 %, and together with the TKW explained the quasi-totality of the grain yield variation (99.25%) and all the remaining variables added only 0.21 % of explained variation (Table 5.S4). Both traits were significantly higher under wet conditions compared to drought (Figure 5.3).

Under the drought conditions, the GNM^2 and TKW still explaining most of the grain yield variation (99.29), but this time the GNM^2 explained less variation than under wet conditions (86.37% vs. 93.27%, respectively) in contrast to TKW which explained more variation under stressful conditions (Table 5.S4). Similar number of variables (7 to 8) were included in the model to explain the grain yield under both conditions, however only three of them were in common (GNM^2, TKW and HI). Biomass was included in the model only under drought, in contrast to days to heading and emergence, which contributed to explain the grain yield only under favorable environment (Table 5.3), however, except GNM^2 and TKW, other terms including Biomass retained in the final model had negligible variation (Table 5.S4).

Table 5.3. Stepwise regression of the sample grain yield (dependent variables) and other traits (independent variables) under drought and non-drought conditions.

Model	**Source**	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F pr.**
Non drought	Regression	9	1E+06	1E+05	1566	<.001
	Residual	68	6236	91.71		
	Total	77	1E+06	16871		
	Final Model	GY= -345.1 + 0.05 (GNM) + 7.57 (TKW) - 0.72 (DTH) + 0.07(Emg) + 0.08 (FLFW) - 1.59 (FLL) + 34.2 (HI) + 0.45 (CT) + 0.87(SLA)				
drought	Regression	7	146171	20882	2183	<.001
	Residual	75	717.5	9.566		
	Total	82	146889	1791		
	Final Model	GY= -136.02 + 0.03(GNM) + 3.53(TKW) + 0.06 (Biomass) + 28.32 (HI)-1.17(SLA) +0.98 (LRM) + 0.08 (RWC)				

Abbreviations of traits are mentioned in Table 5.1, 5.2.

5.4.6. Cultivars vs. landraces comparison under contrasting water conditions

The type of variety had a significant effect on almost traits and the interaction type by year was found significant only for some traits like GY, GNM^2, SNM^2, and PH (Table 5.4).

In the wet year, the landraces still had higher values for DTH and for the traits related to the flag leaf; however, the significant difference for biomass and RWC, found under drought, disappeared in the non-drought year. In contrast, yield and its components (SNM, GNM^2 and SWM^2), which showed significant differences under favorable conditions, became insignificant under drought (Table 5.4, Figure 5.3).

The GNM^2 was the trait that explained most of the yield variation, clearly discriminating between the two groups (cultivars vs. landraces) in the wet year (Figure 5.4). The TKW, which also explained a part of the variation, did not differentiate between the two varieties groups under both conditions. Similar patterns for GMN^2 and TKW were observed for the two groups (cultivars and landraces), with higher values in the favorable conditions compared to drought (Figure 5.4).

The drought susceptibility index (DSI) based on grain yield, overall, ranked landraces as more tolerant than cultivars (Table 5.S5). However, at the single variety level, five landraces ranked among the first six ones with one cultivar (Vitron) which ranked the fourth (Table 5.S5). The other five landraces were distributed randomly among the other cultivars.

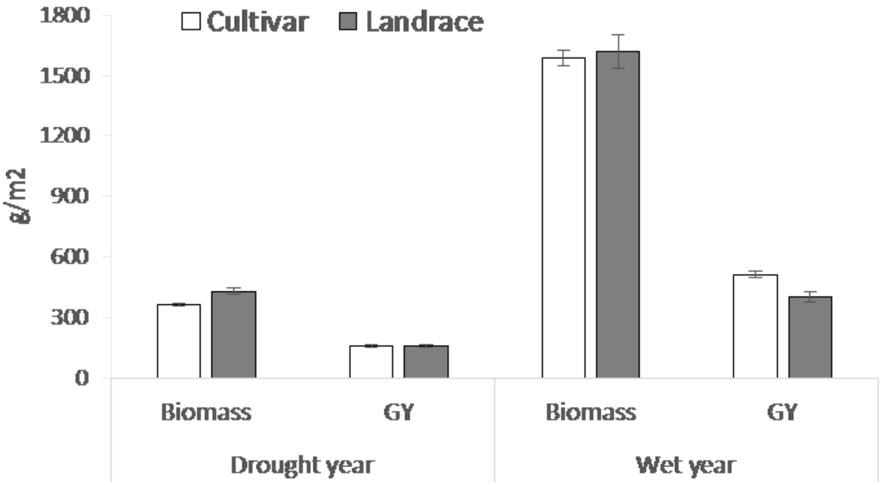

Figure 5.3. Biomass and grain yield (GY) of cultivar and landrace groups across drought and wet years. Bars represent standard error of the means (±SEM).

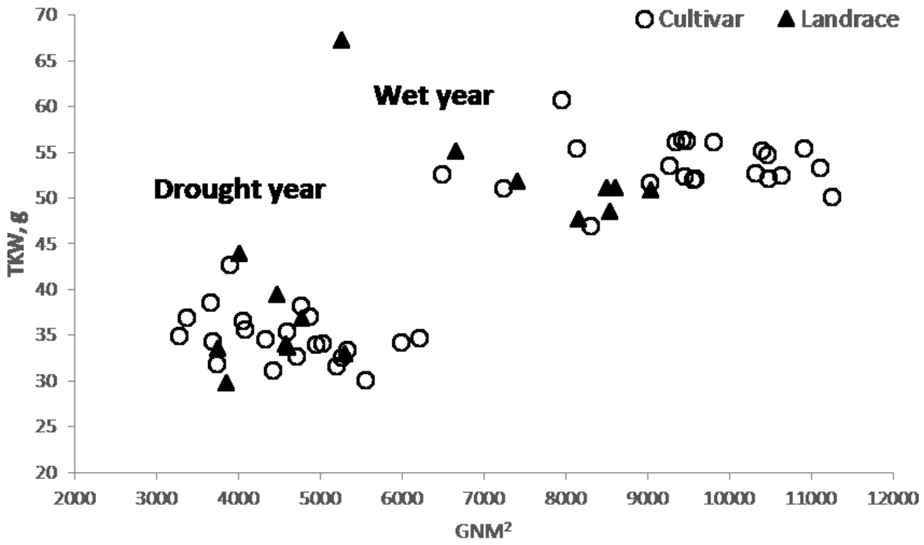

Figure 5.4. Relationship between the number of grains per squared meter (GNM^2) and thousand-kernel weight (TKW) of cultivars and landraces under drought and wet conditions.

Table 5.4. Analyses of variance (ANOVA) and means comparison of landrace vs. cultivar group (type effect) for the assessed traits across drought (2017) and wet (2018) years.

	Type		2017 & 2018			2017		2018	
Traits	2017	2018	Type (T)	Year (Y)	T x Y	Cultivar	Landrace	Cultivar	Landrace
Emg	ns	ns	ns	***	ns	206.65^{a}	197.17^{a}	183.90^{a}	186.80^{a}
DTH	***	***	***	***	ns	107.74^{b}	114.38^{a}	120.69^{b}	127.42^{a}
PH	***	***	***	***	***	61.14^{b}	75.46^{a}	88.66^{b}	123.50^{a}
HGY	ns	***	***	***	***	167.97^{a}	154.31^{a}	498.55^{a}	395.88^{b}
LRM	ns	ns	ns	ns	ns	2.12^{a}	2.33^{a}	2.11^{a}	2.33^{a}
LRN	*	*	**	ns	ns	2.71^{b}	3.21^{a}	2.71^{b}	3.21^{a}
CT	ns	ns	ns	***	ns	26.69^{a}	25.92^{a}	28.95^{a}	29.01^{a}
FLA	***	***	***	***	ns	1372.82^{b}	1756.59^{a}	1996.87^{b}	2307.71^{a}
FLL	***	***	***	***	ns	16.42^{b}	19.13^{a}	20.02^{b}	22.27^{a}
FLW	**	*	***	***	ns	1.16^{b}	1.28^{a}	1.38^{b}	1.45^{a}
FLFW	***	*	***	***	**	252.56^{b}	330.93^{a}	341.81^{b}	368.03^{a}
FLDW	***	**	***	***	ns	115.03^{b}	140.87^{a}	139.70^{b}	154.46^{a}
RWC	***	ns	ns	***	**	80.00^{b}	83.07^{a}	89.86^{a}	89.15^{a}
SLA	*	***	***	***	ns	12.00^{b}	12.49^{a}	14.14^{b}	14.99^{a}
SNM^{2}	ns	***	**	***	*	232.67^{a}	224.85^{a}	330.92^{a}	281.09^{b}
SWM^{2}	ns	*	*	***	*	258.27^{a}	262.29^{a}	885.94^{a}	775.87^{b}
Biomass	***	ns	ns	***	ns	363.11^{b}	427.46^{a}	1586.24^{a}	1617.13^{a}
SGY	ns	***	***	***	***	159.32^{a}	157.42^{a}	512.88^{a}	401.13^{b}
GNS	ns	ns	ns	***	ns	19.87^{a}	19.62^{a}	28.75^{a}	28.13^{a}
GNM^{2}	ns	*	**	***	*	4604.87^{a}	4417.27^{a}	9529.31^{a}	7878.71^{b}
HI	***	***	***	***	ns	0.60^{a}	0.49^{b}	0.43^{a}	0.32^{b}
SpkBio	ns	ns	ns	***	ns	98.95^{a}	104.86^{a}	394.96^{a}	361.87^{a}
TKW	ns	ns	ns	***	ns	34.80^{a}	35.55^{a}	53.82^{a}	52.32^{a}

Abbreviations of traits are mentioned in table 5.2. Different letters indicate significant difference at 0.05 level.

5.5. Discussion

5.5.1. Effect of drought on the agronomic traits

In the current study, we assumed that the observed environmental variation in grain yield and other evaluated traits was mainly due to differences in rainfall amount and distribution rather than to any variation in temperature or other environmental factors between years. The drought occurred during this experiment was typical of the Algerian cereal growing regions (Annichiarico *et al*. 2005; Mekhlouf *et al.* 2006), which coincided around the flowering phase of the plant. The eastern high plateaus of Algeria have a variable rainfall conditions ranging from 168.7 to 517.3 mm (Chennafi *et al.* 2006), this range was similar to that found in our study where the rainfall accumulated during the drought and wet years in our study was 195.12 and 440.7 mm, respectively. Accordingly, in the current study the grain average yield achieved under drought year (1.58 tons/ha) falls slightly below the Algerian average wheat yield (1.9 tons/ha) (FAO 2018), in the contrary to the wet year where the grain yield (4.82 tons/ha) was much higher. Bahlouli *et al.* (2005) reported range of yield from 1.79 to 3.58 tons/ha during six successive cropping seasons (1997/1998 to 2002/2003) on the same region where our experiment was conducted. Therefore, we were fortunate to have two highly contrasting seasons within the natural range of the region. This circumstance has allowed a meaningful comparison of the genotypes, despite being tested in just two seasons.

It is well known that drought causes reductions in agronomic traits during the plant cycle (Zhang *et al*. 2018). The growth period between double ridge to anthesis, is the most sensitive to drought stress with respect to grain yield (Shpiler and Blum 1986, 1991; Huang *et al.* 2020), it affects wheat head size (i.e., the number of spikelets per spike) and might be irreversible since late-emerging tillers would not contribute to yield (Guan *et al.* (2010). Furthermore, drought stress over anthesis and maturity reduces grain yield by penalizing the grain-filling period in terms of rate and duration (Sofield *et al.* 1977; Al-Khatib and Paulsen 1984), this drought timing was more critical compared to other stages (Pinheiro *et al.* 2000; Matiu *et al.* 2017). Therefore, that results in poor assimilation, reduced translocation of photosynthates to the grain and higher respiratory losses (Al-Khatib and Paulsen 1984; Acevedo 1990; Shpiler and Blum 1986, 1991). In contrary to the findings of Ehdaie *et al.* (2006) and Ahmadi *et al.* (2009), when drought stress was applied at the post-anthesis period, grain number and TKW were not affected. This is probably because of the potential of these components could be formed before spike initiation, so post-anthesis water stress had no significant influence on them (Araus *et al.* 2002). In our study, the drought seemed to be prolonged one, thus these circumstances caused a drastic differences in most traits, including grain yield, between the two seasons. The higher reduction was observed in grain yield and biomass (67.06 and 76.14%, respectively), while the harvest index was the most increased trait (40%), the increase of harvest index under the effect of drought was a consequence of the higher reduction in biomass compared to grain yield. These findings agree with the results of Bidinger *et al*. (1977), but they contrast with those of Aggarwal *et al*. (1986) and Giunta *et al*. (1993). These contrasting findings could be a result of differences in the drought scenario encountered (severity, timing and duration).

Most likely that the drought stress started earlier in the pre-anthesis period (over March). This assumption was based on traits affected and climatic data. Difference of rainfall was observed between the two years since March and extended to May (Figure 5.1). Furthermore, biomass was the most affected by drought, which confirms that severe drought penalized the active growth period (Biomass) before reproductive stage (flowering) where biomass growth should be almost completed. We believe also that drought was extended over the grain-filling period, which negatively affected the TKW.

5.5.2. Traits contributing to grain yield formation

The increased grain yield was attributed to various set of traits depending to the environments. For example, in Mexico genetic gains in grain yield were associated with fewer days to heading, cooler, and reduced canopy temperature at grain filling, increased stay-green, and thousand kernel weight (Lopes *et al*. 2012b). Similarly, significant yield increases in China resulted from increased grain number per spike, thousand kernel weight, HI, and plant height (Zhang *et al*. 2018). Genetic gains among CIMMYT's spring wheat cultivars developed between 1966 and 2009 in Mexico were associated with increased aboveground dry matter and increased seed weight (Lopes *et al*. 2012a; Aisawi *et al*. 2015). The higher number of grains per unit area has been the yield component most associated with yield gains in bread wheat (McCaig and Clarke 1995) and barley (Jedel and Helm 1994). Nevertheless, changes in grain weight have been null (McCaig and Clarke 1995) or even negative (Perry and D'Antuono 1989; Brancourt-Hulmel *et al*. 2003). According to Benbelkacem and Kellou (2000), the TKW, is not quite controllable, because this trait is highly affected by environment during grain filling. The lack of water after flowering, combined with elevated temperature (usually observed in Algeria conditions) results in a decrease of TKW by alteration of the rate of grain filling and/or the grain filling time. During this phase, the lack of water results in a reduction of the grain size (scalding) thus reducing yield (Megherbi-Benali *et al*. 2014).

In the current study, grain number per unit area and TKW were the traits predominantly explaining grain yield variation under drought and well-watered conditions (99.29 and 99.25 %, respectively). Our results were in line with several studies (Shpiler and Blum, 1986; 1991; Ma *et al*. 2017; Zhang *et al.* 2018), however they were in contrast to the findings of Zhong-hu and Rajaram (1994) who found that the grain yield, kernels per spike, biomass and plant height were more drought sensitive compared with spike number and thousand-kernel weight. The huge variation of grain yield that was explained by GNM^2 and TKW under the current contrasting rainfall conditions pointing out the importance of these two traits under wide range of Algerian semi-arid conditions. Thus, focus should be further given to enhance these traits through breeding programs or agricultural managements. GNM^2 seemed to be more amenable for breeding according the correlations found in our study with its components (SNM^2 and GNS) and biomass however, TKW did not present correlations with other traits, which make it hard for indirect selection. This lead to think to integrate other traits in further studies to attempt dissecting TKW, like grain filling duration and timing. Supplement irrigation during grain filling under drought could be of great interest to improve grain filling. The non-relationship found between these two traits within this germplasm indicate possible improvement one trait without penalizing the other.

5.5.3. Different patterns of biomass partitioning of cultivars and landraces

The increase in biomass has been largely attributed to higher photosynthetic rate, stomatal conductance, leaf chlorophyll content and improved radiation-use efficiency (Bustos *et al.* 2013). It has been suggested that further improvements in grain yield can be achieved by increasing photosynthetic capacity by optimizing biomass production while maintaining lodging resistance (Beche *et al.* 2014). Several studies showed that biomass contributed significantly to increased grain yield (Shearman *et al.* 2005; Xiao *et al.* 2012; Bustos *et al.* 2013; Aisawi *et al.* 2015; Gao *et al.* 2017), whereas others studies indicated very little contribution of this trait in yield achievement (Royo *et al.* 2007; Tian *et al.* 2011; Zheng *et al.* 2011; Sun *et al.* 2014; Zhang *et al.* 2016).

There is a lack of consensus on differences in crop dry matter between landraces and modern cultivars. Ayadi *et al.* (2015) and Carranza-Gallego *et al.* (2019) found that landraces produced more dry matter than modern cultivars, in contrast to De Vita *et al*. (2007) and Royo *et al*. (2007) who found no significant difference. Notably, our study showed a higher biomass of landraces over cultivars only under drought conditions, but under favorable conditions no significant difference was detected. Similar results for biological yield were found in the study conducted by Siddique *et al*. (1989) under rainfed conditions (273.1 mm accumulated from January to December). Several researches agreed that high biomass at anthesis minimizes yield reduction under terminal heat and drought stress (Roseille and Hamblin, 1981; Simane *et al*. 1993; Fellah *et al*. 2002, Bahlouli *et al.* 2005). Our findings highlight the importance of landraces under low-input semiarid agro-ecosystem, where water scarcity reduces the residues incorporations, which have a negative impact on the soil organic matter (Bista *et al*. 2017). Likewise, landraces could lead to higher soil organic carbon sequestration (Aguilera *et al*. 2013), thus, high-residue-yielding varieties could contribute to reduce soil organic content (SOC) depletion vulnerability under these climate conditions (Iglesias *et al*. 2011). Moreover, SOC increases can offset a relevant share of agricultural greenhouse gases (Parton *et al*. 2015), contributing to climate change mitigation. Algerian landraces have been utilized for dual purpose in cereal livestock farming system in semi-arid environment, simultaneously for human consumption and for animal feed for higher straw yield (Ben Amar 1997). Although, simultaneous improvement for drought tolerance and C sequestration has not been pursued in crop breeding programs (Paustian *et al.* 2016), particularly in cereals such as wheat where breeding for high grain yield is the primary objective. The biomass plasticity found in the current study was found also by Mathew *et al.* (2019), where biomass accumulation in roots, shoot and grains was significantly reduced by 32, 30 and 48%, respectively, under drought stress confirming that biomass accumulation has phenotypic plasticity. This plasticity could be exploited in drought tolerance breeding of wheat to mitigate water scarcity (Dalal *et al.* 2017).

In contrast to the results observed for the biomass, the difference in grain yield between landraces and cultivars was not significant under drought while under favorable conditions the cultivars out-yielded the landraces. The higher yield of cultivars over landraces under non-drought was due in part to increased spike and grain number per area. These two traits followed the same pattern of grain yield across years; they were significantly different between cultivars and landraces under non-drought and similar under drought conditions. The cultivars could also have better ability of tillering than landraces under favorable conditions (as observed in chapter 4), along with the higher floret fertility. According to Royo *et al.* (2007), the increased grain number could be attributed to a higher number of fertile florets per spikelet in the modern varieties compared to the old ones, because of a higher assimilate partitioning to the spike during the pre-flowering critical period (Miralles *et al*. 2000). The number of grains per unit land area is being formed throughout the whole pre-flowering period (Slafer and Rawson 1994) as a consequence of a rather complex process through which structures (florets), which might later be able to bear grains, are first generated and then a rather large proportion of them degenerate. According to Vahamidis *et al*. (2019), modern genotypes produced a higher number of initiated floret primordia compared to the old ones. Additionally, cultivars and landraces followed different strategy to determine the number of fertile florets per spikelet (NFFS). In cultivars, NFFS was mainly explained by the variation in the degeneration rate, however in landraces, it was best explained by the variation in the duration of terminal spikelets to anthesis.

Under drought, grain and spike number were not significantly different between the two groups of genotypes, however under favorable conditions these two traits were higher in cultivars. Furthermore, grain number per spike were similar under both conditions, therefore the number of spikes remains the strongest explanation for this difference. The higher spike number was proposed by Bouzerzour and Benmahammed (2009) among the favored traits for the high plateaus of eastern Algeria.

Although our landraces produced higher biomass under drought but they were not able to convert the assimilates into grain, which resulted in lower harvest index compared to cultivars. The lower HI could be due to higher tillers without spikes compared to cultivars, which had higher spikes (fertile tillers), led to increase the biomass without increasing the grain yield. This assumption is still to be confirmed, as the vegetative tillers were not recorded in the current study. Although other biomass components could also explain this result, like plant height and leaf area which were higher in landraces. Landraces seemed to have a limited potential of production even under favorable conditions, but they are a useful genetic resource of higher biomass even under drought conditions.

5.5.4. The importance of flag leaf related traits in drought tolerance

Flag leaves are the main photosynthetic organ and contribute about 41–43% of the carbohydrates required for grain filling (Duncan 1971; Khaliq *et al.* 2008; Xu and Zhao 1995 in Ma *et al.* 2020). Accordingly, a large flag leaf should be desirable under favorable conditions, but under unfavorable ones, it would be difficult to set the optimum leaf size (Lefi *et al*. 2004). The morphological attributes of flag leaves, such as FLL, FLW and FLA, falg leaf posture and flag leaf opening angle are therefore critical factors in determining a desirable plant type (Tsukaya *et al*. 2006; Ma *et al.* 2020).

In our study, all the traits related to flag leaf (width, length, surface, weight) were reduced as a response to drought, this finding agreed with that of Yang *et al.* (2016). This indicated that flag leaves keep smaller sizes and erect postures when adapting to drought stress, in agreement with previous studies (Innes *et al*. 1980; Qian *et al.* 2009). Most traits related to flag leaf morphology were correlated with each other under both field conditions, similar as found by Yang *et al*. (2016). Flag leaf related traits showed positive correlations mainly with PH and DTH, pointing out that these traits were larger in taller and late genotypes, which characterized our landraces. In addition, these results were confirmed by ANOVA when landraces were compared to cultivars. Nevertheless, the current results did not show any correlation between FLM and grain yield and TKW unlike to the results of Yang *et al*. (2016).

Schonfeld *et al.* (1988) showed that wheat cultivars having high RWC are more resistant against drought stress. We found that RWC was, slightly reduced in the drought year. This trait was not significantly different between genotypes, unlike to type effect, which was significantly affected the RWC where landraces showed higher RWC mean values, but only under drought. This suggested that landraces could be more physiologically tolerant to drought stress than cultivars; however, this suggestion was based on unique measurement of RWC, which is very sensitive trait to instantaneous conditions. According to Dong *et al.* (2008) and Khakwani *et al*. (2011), leaf relative water content (RWC) was found to be correlated to the drought resistance and water saving of wheat cultivars. The higher value observed in landraces compared to cultivars could be ascribed to the flag leaf morphology change during the high evaporative demand, this suggestion is confirmed by the results of leaf rolling recorded at noon showing greater values for landraces under both conditions (the higher the rolling leaf index higher, the more enrolled leaves were). Moreover, a significant correlation was detected between these two traits (LR and RWC) only under drought. Leaf rolling has been demonstrated in various rice genotypes to facilitate a more efficient water utilization during photosynthesis, which undoubtedly indicates a certain resistance of plants with rolled leaves to drought and high temperature (Dingkuhn *et al*. 1989). In addition, a high degree of leaf rolling in cv. Otan protects chlorophyll against degradation during short-term treatment with high temperature (Sarieva *et al*. 2010). According to Clarke (1986), leaf rolling is unlikely to be of adaptive significance to wheat in environments where stress develops rapidly but could be of potential use where stress develops gradually or is of short duration. Canopy temperature was negatively correlated with FLM traits and RWC indicating that genotypes with larger leaves (landrace) tended to have cooler leaves, which implicates higher transpiration.

5.6. Conclusion and perspectives

- Grain number per area was the yield component with greater effect on the grain yield in any condition. Therefore, further increases in this trait would improve yield under drought and favorable conditions. The cross between genotypes of higher biomass and high-yielding ones (particularly with high HI) could provide genotypes with enhanced yield under stressful conditions.
- Ten cultivars: Cirta, GTA dur, Korifla, Massinissa, Megress, Mexilcalli 75, Sitifis, Polonicum, Vitron and Waha have shown appreciable grain yield under both conditions. Those varieties are recommended for semi-arid regions.
- Landraces have a limited grain yield potential compared to cultivars under drought and wet conditions, although they could be an interesting resource for vigorous biomass production, which revealed a positive effect on GY under drought. Their HI must be improved to attain the grain yield potential of modern cultivars. Therefore, they can be directly used or introduced in breeding program addressing sustainable agriculture systems, particularly if biomass and grain yield increases are sought.
- Biomass showed positive correlation with yield under both conditions, this arises the question about the implication of this biomass plasticity on root biomass and then on grain yield.
- Various performance patterns were identified within landraces and cultivars, which indicates the suitability of the current germplasm for studying the different strategies of drought adaptation in durum wheat.

5.7. References

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6. General Discussion and General Conclusion

The previous chapters included each its own discussion. The current section will be devoted to connect the results on the evaluation of root traits in different experimental systems (Table 6.1) with field performance, mainly grain yield, to evaluate the agronomic relevance of root traits. Also, I will discuss some points based on the experience gained during this thesis and on my own reflections.

6.1. Relevance of root traits regarded to agronomic traits

The ultimate objective of this study was to assess how root traits are involved in grain yield formation, particularly under drought. More importantly, if significant root traits can be identified at the seedling stage, which would allow early selection, and acceleration of decision making in breeding programs for developing drought-adapted varieties.

6.1.1. Seminal root traits could help to predict some agronomic traits

The correlations established between the results of seedling traits assessed in the rhizo-slide system and the agronomic traits showed that the total length of seminal roots (TRL), along with seminal shoot dry weight (SDW), had a negative correlation with grain yield under favorable conditions (Table 6.2), but these correlations were disappeared under drought. In contrast to our findings, Xie *et al.* (2017) found that seminal root number and total root length were both positively associated with grain number and grain yield. In opposite to total root length, seminal root angle (MRA) was positively correlated with GY under both conditions. The positive effect of wider root angle on grain yield was not in line with previous results, which associated the compact root system to higher grain yields, as an adaptation to drought conditions (Manschadi *et al.* 2006; El Hassouni *et al.* 2018). MRA seemed to be higher in short and early genotypes with small flag leaves (which were mainly cultivars). The effect of root angle seemed to be more consistent across the two years in relation to GY than total root length, which might have greater negative effect on GY under drought conditions (Table 6.2). Primary root length (PRL) showed more pronounced correlations in the wet year (Table 6.2). It is worth noting that PRL did not have the same pattern of the correlation as total root length (TRL) with agronomic traits, and especially with the traits related to flag leaf, it (PRL) tends to have negative correlations with flag leaf morphology traits (FLM). Genotypes with shorter PRL would have more GNS in the wet year and rolled less their leaves under both conditions. Root diameter did not expressed any significant correlation with traits assessed in field under both years, in contrast to the findings of Ruiz *et al.* (2018) who reported significant correlations of root diameter with plant height and test weight in durum wheat.

Despite the non-significant correlations of primary root length (PRL) with GY under both

Table 6. 1. Genotypes evaluated across the set of experimental phenotyping systems (row) carried-out in the current work.

Nº	Genotype	Petri dishes	Rhizo-slide	Pot-pipe	Shovelomics	Agronomic	
1	Acsad 65	×	×		×	×	
2	Altar 84	×	×		×	×	
3	Ammar 6		×		×		
4	Aures	×		×			
5	Beliouni	×	×	×	×		
6	Bidi 17	×	×	×	×	×	•
7	Bousselem		×		×	×	
8	Boutaleb	×	×		×	×	
9	Capeiti	×	×		×	×	
10	Chen's		×		×		
11	Ciccio		×		×		
12	Cirta	×	×		×	×	
13	Core		×		×		
14	Djenah Khotifa	×	×	×	×		
15	El maather	×		×			
16	Gloire de Montgolfier	×	×	×	×	×	•
17	GTA Dur	×	×	×	×	×	•
18	Guemgoum R'khem	×	×	×	×	×	•
19	Hedba 3	×	×	×	×	×	•
20	INRAT 69	×	×	×	×	×	•
21	Korifla	×	×	×	×	×	•
22	Langlois	×	×	×	×	×	•
23	Mansourah	×	×	×	×	×	•
24	Massinissa	×	×	×	×	×	•
25	Megress	×	×	×	×	×	•
26	Mexicali 75	×	×	×	×	×	•
27	Miki-02	×					
28	Mohammed Ben Bachir	×	×	×	×	×	•
29	Montpellier	×	×	×	×	×	•
30	Ofanto	×	×	×	×	×	•
31	Oued El Berd	×	×	×	×	×	•
32	Oued Zenati 368	×	×	×	×	×	•
33	Polonicum	×	×		×	×	
34	Sahell		×		×	×	
35	Sbaa Aldjia	×	-		-		
36	Simeto	×	×	×	×	×	•
37	Sitifis	×	×	×	×	×	•
38	Tejdid	×		×			
39	Vitron	×	×	×	×	×	•
40	Waha	×	×	×	×	×	•
41	Wahbi		×	×	×		
42	ZB × Fg	×	×		×	×	
	Number of genotypes	35	37	27	37	30	21

×: Presence of the corresponding genotype (row) in the corresponding experiments (column).

•: Genotypes, which were present in all experiments.

conditions, the changing of sign of correlations, negative under wet year (-0.26) and positive under drought (0.19), could point out to contrasting implication of PRL in GY formation (Table 6.2). This finding suggests that PRL contributed to reduced GY under non drought and to increased it (GY) under drought, which was in line with the results of El Hassouni *et al.* (2018) who found that a shallower root system in wheat was advantageous under well-watered conditions while steeper root system sustained better GY under drought. Therefore, our results suggest that higher PRL of seedlings most likely resulted in higher root depth at adult plant, thus it permitted to extract more stored water later in the drought season and to sustain the grain yield. In contrast, under favorable conditions, a long primary root was of no help for grain yield. Furthermore, negative and significant correlations (-0.42, -0.43) were observed between PRL and leaf rolling index (LRM) under both conditions pointing out that increased PRL seems to play positive role in maintaining higher leaf water status, however these correlations did not reach to significant values with leaf rolling at noon (LRN) (-0.33) (Table 6.2). Relative water content (RWC) was significantly correlated only with seminal root angle (-0.41) and root number (0.49) under drought, the sign of these correlations was changed under wet year 0.28 and -31 for MRA and RN, respectively, TRL also had the same correlations pattern across years as RN. Accordingly, RWC would be higher in plants with higher seminal root length and steeper root angle (landraces) but only under drought.

Seminal total root length, overall, tended to be higher in tall and late genotypes with higher flag leaf size (landraces). Genotypes with higher seminal root number rolled more their leaves under both conditions (Table 6.2). There is no logical physiological explanation for that and could be a feature of the specific genotypes tested in our panel. MRA was positively correlated with GY (Figure 6.1) and negatively correlated with TRL, which was negatively correlated to GY. This result could indicate that genotypes having greater MRA were also associated with slow growth of seminal roots. This would be in line with the hypothesis, which was put forward by Manschadi *et al.* (2006), about the usefulness of slow root growth in water-limited environments, where crops relied on soil-stored water, to complete the post-anthesis stages. Thereby, vigorous root growth may cause the depletion of the stored water before the grain-filling period leading to reduced grain yield.

Field biomass was more related to seminal SDW under drought than in the favorable year (Table 6.2). Overall, RN presented negative correlations with many traits assessed during the favorable year, in contrast to the drought year. Remarkably, there was a change of the sign of correlations of RN with GY and biomass, indicating that more RN likely tended to reduce

Table 6.2. Relationships between seedling traits in rhizo-slide system (row) and traits assessed in field under wet and drought year (column).

	TRL	D	PRL	SDW	MRA	RN	TRL	D	PRL	SDW	MRA	RN
			Wet year						**Drought**			
FLA	0.28	-0.10	-0.33	0.10	**-0.45**	0.17	**0.41**	-0.14	-0.23	0.34	**-0.46**	**0.59**
LRM	0.12	0.08	**-0.43**	0.01	-0.26	**0.50**	0.12	0.08	**-0.42**	0.01	-0.26	**0.51**
LRN	0.18	0.17	-0.33	0.06	-0.33	**0.54**	0.18	0.17	-0.33	0.06	-0.33	**0.53**
RWC	-0.16	0.04	0.24	0.11	0.28	-0.31	0.33	-0.20	-0.05	0.32	**-0.41**	**0.49**
DTH	**0.43**	-0.13	**0.36**	**0.56**	-0.17	0.15	**0.66**	-0.21	0.23	**0.66**	**-0.36**	**0.40**
PH	**0.68**	-0.14	0.18	**0.55**	**-0.51**	0.35	**0.54**	-0.01	0.14	**0.48**	**-0.38**	0.26
Biomass	0.11	-0.12	0.22	0.22	-0.05	-0.19	0.30	0.01	0.08	**0.38**	-0.08	0.36
SNM²	-0.15	-0.09	0.23	-0.04	0.34	-0.14	-0.05	0.14	0.12	0.04	**0.39**	0.15
GNS	-0.26	-0.21	**-0.40**	**-0.38**	-0.03	-0.05	-0.16	0.16	-0.15	-0.17	0.07	-0.06
GNM²	**-0.39**	-0.14	-0.16	**-0.50**	0.20	-0.19	-0.16	0.21	-0.03	-0.12	0.31	0.04
TKW	0.18	0.33	0.06	0.10	0.05	0.09	0.24	0.10	0.06	0.34	0.07	0.19
HGY	**-0.62**	0.23	-0.26	**-0.44**	**0.45**	-0.26	-0.21	0.33	0.19	-0.01	**0.53**	0.05
HI	**-0.51**	0.15	-0.23	**-0.54**	**0.45**	-0.15	-0.35	0.34	-0.07	-0.29	**0.41**	-0.28

TRL (cm): Total root length, D: mean root diameter (cm), PRL: Primary root length (cm), SDW (g): Shoot dry weight, MRA (°): Mean root angle, RN: Root number. FLA (mm^2): Flag leaf area, LRM: Leaf rolling in morning, LRN: Leaf rolling at noon, RWC (%): Relative water content, DTH (day): Days to heading, PH (cm): Plant height, Biomass (g/m^2): Total biomass, SNM^2: Spike number per meter square, GNS: Grain number per spike, GNM^2: Grain number per meter square, TKW (g): Thousand kernel weight, HGY(g/m^2): Harvest grain yield, HI: Harvest index. Values in bold are different from 0 with a significance level alpha=0,05.

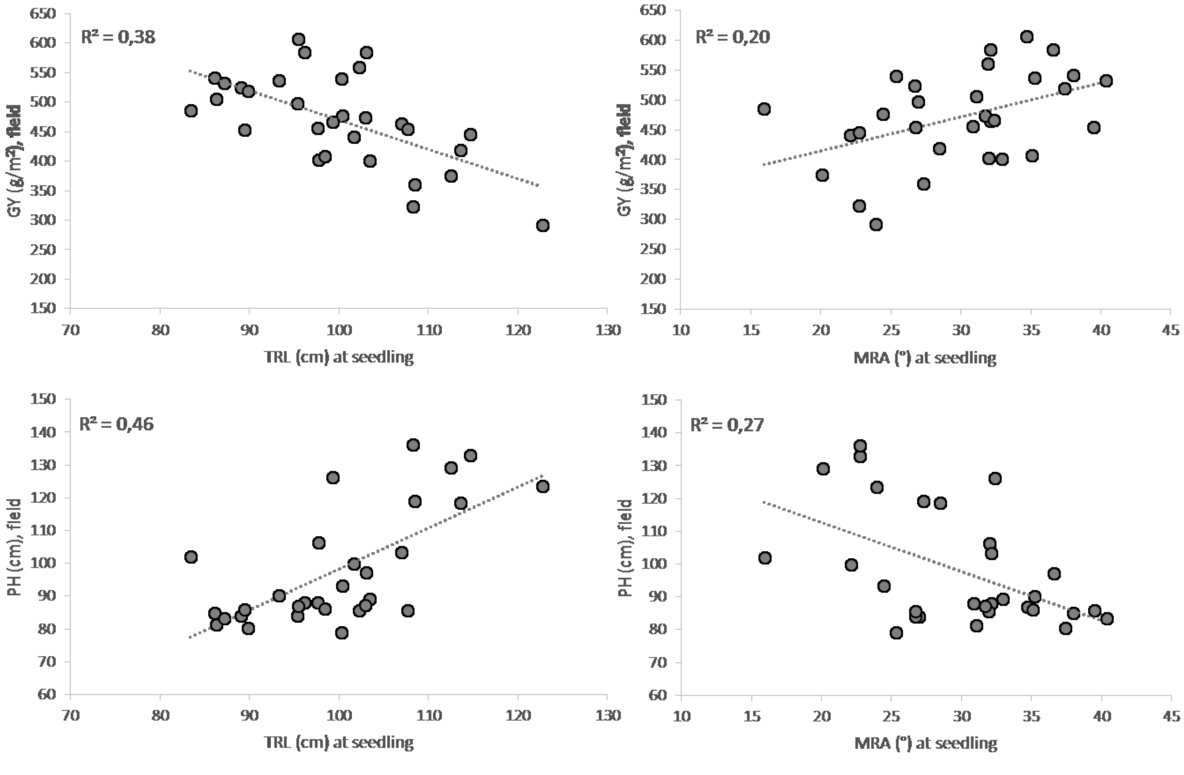

Figure 6. 1. Relationships of total root length (TRL) and root angle (MRA) with plant height (PH) and grain yield (GY) assessed at field during the wet year.

yield and biomass in the wet conditions (Table 6.2), and to increase biomass under drought conditions (Table 6.2), similar to the results of Xie *et al.* (2017). Atkinson *et al.* (2015) found no correlation between seedling root traits and grain yield and PH measured in field experiment with low and high nitrogen treatments.

6.1.2. Higher root biomass tends to reduce harvest index under drought

The correlation of the traits of excavated roots ("shovelomics experiment", chapter 4) with the field agronomic evaluation under droughted and wet years, showed only a significant negative correlation of root angle with harvest index (HI) under favorable conditions (Table 6.3).

Table 6.3. Relationships between traits assessed in shovelomics experiment (row) and traits assessed under wet and drought field conditions (column).

Traits	DTH	TN	PH	TRN	SDW	RDW	RoAI	RA	HcA	Ff	tpSL
Wet year											
FLA	**0.43**	**-0.50**	**0.51**	0.34	0.24	**0.49**	0.16	**0.55**	-0.20	**0.60**	**0.53**
LRM	0.17	-0.28	0.07	0.22	-0.19	-0.01	0.10	-0.04	-0.23	0.17	0.04
LRN	0.23	-0.29	0.18	0.12	-0.06	0.04	0.18	0.01	-0.09	0.11	0.09
RWC	-0.05	-0.01	-0.22	-0.13	-0.33	-0.15	-0.19	-0.05	0.23	-0.17	-0.11
DTH	**0.85**	**-0.51**	**0.69**	-0.05	**0.46**	**0.40**	0.35	**0.62**	0.11	0.34	**0.48**
PH	**0.78**	**-0.44**	**0.96**	0.21	**0.61**	**0.56**	**0.50**	**0.64**	0.02	**0.45**	**0.55**
Biomass	0.13	-0.23	0.11	-0.19	0.06	-0.09	**0.36**	-0.04	-0.20	0.13	-0.07
SNM^2	**-0.37**	0.15	**-0.43**	-0.04	-0.22	-0.28	-0.12	-0.23	**-0.42**	0.17	-0.21
GNS	-0.08	0.32	-0.06	0.30	0.10	0.17	0.01	0.06	0.16	-0.13	0.12
GNM^2	**-0.54**	**0.43**	**-0.48**	0.20	-0.22	-0.14	-0.15	-0.27	-0.10	-0.13	-0.20
TKW	-0.06	-0.15	0.01	-0.34	-0.09	-0.20	-0.12	-0.15	-0.06	-0.07	-0.09
HGY	**-0.45**	0.34	**-0.73**	-0.05	**-0.41**	-0.28	-0.27	-0.36	-0.14	-0.17	-0.25
HI	**-0.62**	**0.52**	**-0.65**	0.10	-0.36	-0.25	**-0.42**	-0.35	-0.05	-0.25	-0.26
Drought											
FLA	**0.57**	-0.35	**0.56**	0.30	0.32	**0.43**	0.31	**0.37**	-0.14	**0.39**	**0.38**
LRM	0.16	-0.28	0.06	0.22	-0.19	-0.02	0.11	-0.05	-0.25	0.17	0.03
LRN	0.23	-0.29	0.19	0.12	-0.06	0.05	0.17	0.02	-0.08	0.11	0.09
RWC	**0.43**	-0.28	**0.56**	0.15	**0.50**	**0.40**	0.23	0.29	-0.18	**0.38**	0.24
Biomass	**0.51**	**-0.36**	**0.55**	0.08	**0.43**	0.30	0.19	0.33	-0.05	0.25	0.32
DTH	**0.70**	-0.36	**0.84**	0.25	**0.65**	**0.56**	**0.45**	**0.61**	0.11	0.36	**0.60**
PH	**0.59**	-0.29	**0.79**	0.20	**0.50**	**0.52**	**0.41**	**0.55**	0.27	0.22	**0.53**
SNM^2	-0.07	0.03	-0.06	-0.04	-0.14	-0.24	-0.18	-0.17	-0.09	-0.10	-0.21
GNS	-0.04	0.16	-0.10	0.23	0.05	0.17	-0.06	0.10	0.16	-0.03	0.21
GNM^2	-0.07	0.15	-0.11	0.16	-0.06	-0.03	-0.16	-0.02	0.05	-0.08	0.03
TKW	-0.01	-0.15	0.07	-0.36	0.12	-0.12	0.05	-0.15	-0.02	-0.13	-0.06
HGY	-0.11	0.11	**-0.37**	-0.01	-0.08	-0.19	0.00	-0.13	0.03	-0.13	0.04
HI	**-0.51**	0.35	**-0.62**	-0.15	**-0.41**	-0.35	-0.27	**-0.37**	0.12	**-0.37**	-0.24

DTH (day): days to heading, TN: tiller number, PH (cm): plant height, TRN: total root number, SDW (mg): shoot dry weight (mg), RDW (mg): root dry weight, RoA$_I$ (°): root opening angle measure by Imag J, RA (cm^2): root area, AcH (cm^2): area of the convex hull, Ff: filling factor, tpSL (cm): total projected structure length. Traits agronomic abbreviations are explained in the table 6.2.

In general, higher root growth seemed to be linked to higher shoot biomass as found in the fourth chapter, 0.62 and 0.78 in shovelomics and pipe-pot experiments, respectively, however this results was not obtained when correlating those experiments to the agronomic experiment under both conditions (Table 6.3, Table 6.4). Increases in root area (RA) and root density (Ff), were related to a decrease in field harvest index, only under drought conditions (Table 6.3), indicating that a big shallow root system was not beneficial to attain good grain filling under drought.

Table 6.4. Relationships between traits assessed in tubes (row) and traits assessed under wet and drought field conditions (column).

	DTH	PH	Depth	RDW30	RDW60	RDW>60	RDW	SDW	RSR
Wet year									
FLA	**0.65**	**0.51**	-0.20	**0.81**	0.35	0.38	**0.75**	0.41	**0.67**
LRM	0.43	0.09	0.03	0.41	**0.49**	**0.61**	**0.54**	0.33	**0.62**
LRN	0.40	-0.05	0.08	0.17	0.29	0.42	0.32	0.14	**0.47**
RWC	-0.38	0.03	0.18	-0.29	-0.27	-0.28	-0.40	-0.27	-0.21
DTH	0.22	**0.50**	-0.19	0.32	0.18	-0.02	0.21	0.04	0.21
PH	0.43	**0.71**	-0.29	**0.54**	0.33	0.19	0.45	0.32	0.27
Biomass	0.41	0.15	0.27	0.24	0.03	0.11	0.24	0.43	-0.01
SNM^2	-0.14	-0.18	0.21	-0.13	0.11	-0.03	-0.11	0.20	-0.38
GNS	-0.09	-0.44	-0.18	0.08	-0.43	-0.15	-0.02	-0.26	0.34
GNM^2	-0.11	-0.42	0.04	0.00	-0.18	-0.06	-0.05	0.03	-0.04
TKW	0.25	-0.07	-0.01	-0.22	0.04	0.23	-0.07	0.06	-0.19
HGY	-0.22	**-0.64**	0.19	-0.29	-0.29	-0.14	-0.29	-0.19	-0.08
HI	-0.33	**-0.63**	0.01	-0.30	-0.24	-0.12	-0.32	-0.19	-0.22
Drought									
FLA	**0.58**	**0.53**	-0.18	**0.59**	**0.50**	0.42	**0.63**	0.38	**0.53**
LRM	0.43	0.09	0.03	0.40	**0.50**	**0.66**	**0.54**	0.38	**0.59**
LRN	0.40	-0.04	0.08	0.18	0.28	0.39	0.32	0.10	**0.49**
RWC	0.37	0.44	-0.14	0.41	0.31	0.14	0.42	0.23	0.26
DTH	0.28	**0.60**	-0.32	0.30	0.20	0.05	0.21	0.12	0.11
PH	0.28	**0.60**	-0.24	0.24	0.06	-0.16	0.11	0.00	0.07
Biomass	0.40	0.14	-0.36	0.40	0.18	0.05	0.30	0.07	0.36
SNM^2	0.08	-0.24	-0.27	-0.07	0.07	-0.17	-0.12	-0.09	-0.18
GNS	-0.37	-0.21	-0.40	-0.06	-0.36	-0.32	-0.24	-0.42	0.10
GNM^2	-0.24	-0.31	**-0.49**	-0.10	-0.24	-0.36	-0.26	-0.38	-0.05
TKW	0.30	0.02	0.06	-0.20	-0.06	0.02	-0.08	0.01	-0.07
HGY	-0.46	**-0.50**	-0.16	-0.38	-0.27	-0.43	**-0.49**	-0.39	-0.28
HI	-0.40	**-0.50**	-0.14	**-0.56**	-0.44	-0.39	**-0.59**	**-0.48**	-0.37

DTH (day): days to heading, PH (cm): Plant height, Depth (cm): Root depth, RDW30 (mg): root dry weight at 30 cm, RDW60 (mg): root dry weight at 60 cm , RDW>60 (mg): root dry weight beyond 60 cm, RDW (mg): total root dry weight, SDW (mg): shoot dry weight (mg), FLA (mm^2): Flag leaf area, LRM: Leaf rolling in morning, LRN: Leaf rolling at noon, RWC (%): Relative water content, Biomass (g/m^2): Total biomass, SNM^2: Spike number per meter square, GNS: Grain number per spike, GNM^2: Grain number per meter square, TKW (g): Thousand kernel weight, HGY(g/m^2): Harvest grain yield, HI: Harvest index. Values in bold are different from 0 with a significance level alpha=0.05.

Root dry weight obtained in tubes were positively correlated with biomass traits in the field but, in general, tended to reduce yield and its components (Table 6.4). The same results were observed with leaf rolling, i.e., the higher the root biomass, the more the leaves tended to roll. Increased RDW in tubes was significantly associated with a reduction of HI, which is a ratio of GY to biomass, thus increased biomass with respect to GY (Figure 6.2), but only under drought. This finding point out that higher RDW promotes more shoot biomass under drought but fails to convert it into grain (Table 6.4). Unexpectedly, the root depth (in tubes) was associated with a reduction in grain number per area, which was a major component of GY formation, under drought conditions. Few significant correlations were found with root depth, although this might be due to the limited variation in root depth imposed by the limited depth of the tubes (1.20 m) since roots in wheat can reach up to 1.8 m depth (Wasson *et al.* 2014).

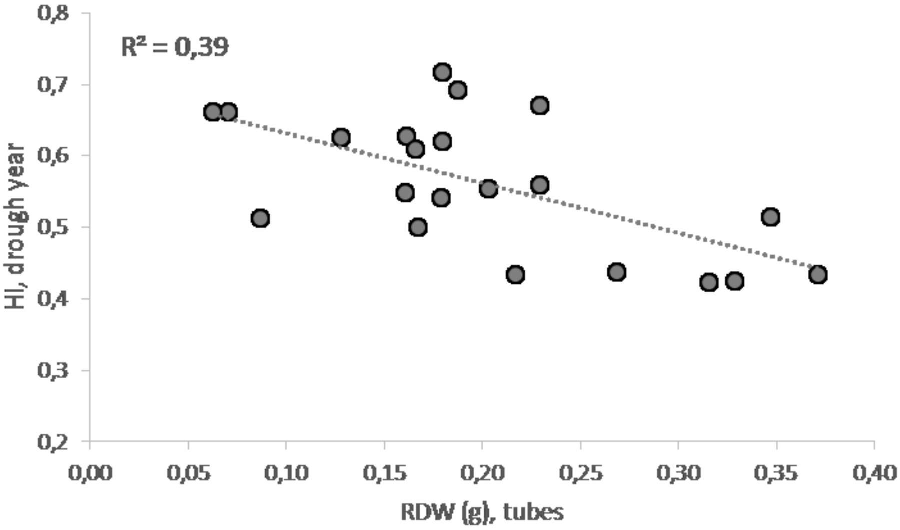

Figure 6.2. Relationships of root dry weight of adult durum wheat plants in tube with harvest index under drought conditions.

The negative effect of increased RDW on the grain yield was already reported by Subira *et al.* (2016). This fact could be related to the presence of two type of varieties, cultivars and landraces. Landraces promote the production of more biomass, both of root and shoot. However, under field conditions, the cultivar group had higher GY overall. The effect of RDW on GY could be the result of the introduction of dwarfing genes, which has reduced the aerial and root biomass of wheat (Subira *et al.* 2016), leading to the increased grain yield in the varieties of post-green revolution. This result was also confirmed by Ma *et al.* (2008), Waines and Ehdaie (2005) and Wojciechowski *et al.* (2009). Our findings confirm the views expressed in previous studies for arid zones, stating that modern cultivars in Australia were confirmed to have smaller roots, reduced root redundancies, more roots in deep soil, and reduced root/shoot ratios, which resulted in more reasonable root configurations that were conducive to the improvement of agricultural production on dry land (Siddique *et al.* 1990; Aziz *et al.* 2017).

The presence of two varieties types, landraces and cultivars, in the germplasm explored largely influenced the results. On one hand, landraces characterized by vigorous growth at seedling and at adult plant, but less productive under field conditions and the opposite was found in cultivars. On the other hand, seminal root growth angle was steeper in the landrace group than in the cultivar one. Collectively, steeper seminal root angle resulted in reduced grain yield; the explanation could be partly due to the effect of root growth on the amount and the timing of soil water uptake (Passioura 1983; Monteith 1986), than in the growth in depth *per se*.

6.2. Personal reflections

A range of root phenotyping systems at seedling stage have been developed and have generated abundant results for different species for several traits. One message is that there is no perfect method, but their combination is feasible for researchers, and their features are complementary, so the disadvantages of one method can be offset by the advantages of another one. These systems are easy, rapid, cost effective and amenable to automation. From a breeding point of view that opens the possibility to phenotype populations for genetic and breeding studies. This notwithstanding, the reliability of these results is undoubtedly affected by the lack of realistic conditions and repetition over different planting years. This is not only because of the artificial media where roots were grown but also because roots are very plastic organs, and the soil is very heterogenous system, which increases the interactions of roots with the soil environment. In the literature, there are numerous attempts to associate these early root phenotyping results to the performance of adult plants under field conditions. Some of them were unsuccessful, others found some associations, although showing sometimes contradictory outcomes between different studies. Anyway, to my knowledge, so far, there are no varieties released based on the selection of roots at early stage. Consequently, some researchers addressed the characterization of the root system directly in the field to acquire reliable results, and to go further in their breeding programs with more confidence, although the several limitations due to the hidden nature of the roots still pose big practical challenges.

Shovelomics is a promising method for field root phenotyping. It was largely developed in studies for various species like maize, wheat and bean. Here I will discuss some details about the implementation of this method. Given the hard labour needed to carry out this method, the choice of experimental site becomes important, to facilitate the sampling procedure and the subsequent root manipulation. Light soil with little organic debris would be the best in terms of sampling effort, excavating intact roots, and root cleaning. However, this may not be always possible, especially when our target region does not have this type of soil. In this case, focus should be placed on the sampling and the cleaning procedure. I have noticed that sampling at favorable humidity allowed excavating better intact and homogeneous root systems. Given that the soil is under continuous wetting-drying cycles during the period of sampling, according to the natural precipitations, sampling at similar soil humidity for all samples is a challenging task, especially when dealing with high number of samples over many days. Thus, moistening the soil surrounding the roots with an appropriate amount of water the day before sampling is highly recommended. The excavation of roots more complete allows the subsequent root analysis with image-analysis software, especially in case of working with software like REST, which requires roots at least 10 cm long. Another important consideration is the choice of sowing density, which has a proven influence on root architectural traits. This decision should be taken according to the objectives. Working with commercial density could difficult the separation of individual plants after excavation but, in fact, this point did not show any problem in our case. Separation was done easily with careful manipulation by hand. If spaced plants are grown, more genetic variation could be expressed for the assessed traits, but this will not represent the actual field conditions with commercial sowing density. Although the commercial sowing density (250 seeds/m^2) was used in the shovelomics experiment in this this thesis, sizeable genetic variation was still found for many traits, so these conditions are amenable to carry out germplasm evaluation and its results should be more similar to those of commercial agriculture. A third consideration is the cleaning procedure of the sampled roots; if the soil is heavy and rich in organic debris, the cleaning becomes increasingly difficult. I think no single reference that I have consulted provides an optimum cleaning protocol. Therefore, there is clearly room for improvement in this issue, in order to obtain clean roots that will facilitate further processing. Importantly, after the roots have been excavated, some roots tended to stretch out of the overall root system, this may imply an overestimation of some parameters of root like root maximum width by the software. Accordingly, it would be better acquiring the images after excavation as soon as possible.

The root growth angle measured by using scoreboard method revealed wider angle in landraces compared to cultivars, however when using ImageJ software this difference disappeared. I still believe that landraces had shallower root system than cultivars and the different results might be due to the manner of measurement in each case. With scoreboard method, more focus could be placed on the uppermost roots whereas with ImageJ on the average set of roots, so the two uppermost roots seemed to be slightly separated. These two uppermost roots in landraces were likely for anchoring the plant to avoid the lodging which is more frequent in landraces because of the higher biomass and plant height they have. Anyway, two root patterns related to the growth stages have existed, which could be the main reason of not finding consistent results for root growth angle when searching for relationships between seedling and adult plants.

Through the set of experiments carried out during this thesis, interesting results have been recurrently found when the comparison was performed between cultivars and landraces. Landraces showed distinctive characteristics, vigorous growth for root and shoot, at seedling and adult plants, but this growth vigor was at the expense of grain yield, compared to cultivars, through a reduced harvest index. Although a smaller root system was observed in cultivars compared to landraces, it seemed to be more efficient to acquire water at critical periods of the plants. This advantage was most likely due to the rate of growth and distribution of roots over soil profile rather than higher root size. In our work, further improvement of yield seemed to be achievable through reducing root biomass under well-watered and stressed conditions. We observed that a standard root system distribution pattern was observed in tubes for all genotypes, with most root biomass at the surface (30 cm), and then little biomass was found beyond this depth. The alteration of this root pattern certainly could have a great effect on plant performance. If root biomass at depth could be increased, more water would be acquired from deeper layers under drought conditions. Water might not be the only driver of this root distribution pattern, otherwise roots would be more abundant at depth under semi-arid conditions where topsoil is often drier that deeper layers. Instead, this pattern is likely to be adapted to the agricultural practices; topsoil usually ploughed and enriched with potassium and phosphorus fertilizers. It is sensible to think that extending this practice deeper in the soil, together with deep placement of fertilizer would contribute to modify this pattern, promote deeper root growth and consequently the acquisition of water. Accordingly, landraces, which had heavier root system at topsoil, could also have it (heavier root system) at deeper layer if these practices are extended deeper in the soil, so possibly they could be able to acquire more water than cultivars. Therefore, the abovementioned hypothesis should take in consideration the interaction of genotypes by environment. Alternatively, the breeding for such root pattern would be advantageous over the agricultural practices in terms of the preservation of the environment from the chemical fertilizers and avoiding the cost of these practices (deep plough and fertilization). However, much work and time is needed to reach this goal given the difficulties of phenotyping for deep roots, which is impractical in breeding programs. In this respect Passioura *et al.* (1983), proposed to search for parents with deep rooting and introduce them, without further explicit selection, into a breeding program. Here, using long tubes made of PVC seems to be appropriate method to search for parents. The plasticity of roots is tightly linked to the soil context, which is very complicated system and can be very variable at small scales. The characterization of the target region of the breeding program should pay great attention to the soils present, before the embarking on any breeding program addressing root-traits based selection. The temporal and spatial variation of humidity of the soil is one the main factors that should be taken into account especially in breeding for drought-adapted varieties. Questions like when water is available, which amount and at which depth, should be addressed before designing the root system ideotype.

6.3. Conclusions

- Sizeable genetic variation of root and shoot traits assessed at seedling and adult plant stages were found, suggesting the potential of their use for wheat breeding using the tested germplasm.
- At least at early stage, a longer coleoptile length could be a potential trait for selection of drought tolerant genotypes under semi-arid environments. This trait was found in the Algerian wheat landraces, which represent a potential genetic resource for breeding for early drought tolerant genotypes, using some widely cultivated modern varieties which were listed among the most susceptible genotypes like Waha, Vitron and Wahbi.
- Breeding and anthropic effect seemed to have shaped seminal root system architectural, reducing root length and increasing root angle. Various seminal root patterns were found in the current germplasm, particularly when landraces and cultivars were compared (steep deep vs. shallow root systems), suggesting different strategies to drought adaptation. Overall, wider and reduced seminal root length seemed to be linked to higher grain yield.

- Vigorous shoot of Algerian landraces was already acknowledged. In the current results, vigorous root system was also found in landraces compared to cultivars at early and late growth stages.
- Both the vigor of shoot and root were related and tended to reduce grain yield in the field.
- The similarities between root systems at different growth stages and systems were not high, especially when grown in different conditions.
- Given that seedling root angle has received a lot of attention lately, as a predictor of adult root behaviour, the lack of correlation found in our study puts a question mark on the usefulness of assessment of root traits in seedlings.
- Cross between landraces with higher biomass (source) and high yielding cultivars (sink) could result in genotypes with enhanced grain yield resilient to large environmental variation occurring in semiarid conditions.
- The cultivars: Cirta, GTA dur, Korifla, Massinissa, Megress, Mexilcalli 75, Sitifis, Polonicum, Vitron and Waha are recommended for cultivation in a wide range of rainfall conditions in semiarid regions of Algeria and regions with similar environmental features.

6.4. References

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7. Supplementary Materials

Table 2.S1. Genotypes ranked from the most tolerant to the most susceptible based on the final germination percentage (FGP %, left-hand side columns) and on the time to reach 50 % germination (t50, days, right-hand side columns).

FGP				t50			
Genotype	FGP C	FGP S	Reduction%	Genotype	t50 C	t50 S	Reduction%
GTA Dur	76.67	93.33	-21.74	Oued Zenati 368	5.00	3.35	32.92
Djenah Khoteifa	70.00	82.86	-18.37	Capeiti	4.38	3.54	18.98
Beliouni	53.33	62.62	-17.41	Beliouni	5.50	4.62	16.02
Bidi 17	77.75	89.52	-15.15	Gloire de Mongolfier	4.25	3.69	13.24
Gloire de Mongolfier	76.67	86.43	-12.73	Tejdid	3.50	3.08	11.90
Miki-2	90.00	96.15	-6.84	Simeto	3.60	3.21	10.71
MBB	96.67	100.00	-3.45	Guemgoum R'khem	4.10	3.67	10.57
Altar 84	76.67	79.29	-3.42	Korifla	3.52	3.30	6.27
Capeiti	74.62	76.67	-2.75	Miki-2	3.65	3.45	5.48
Korifla	86.67	86.67	0.00	MBB	3.07	3.00	2.33
Sitifis	96.67	96.67	0.00	Megress	3.11	3.08	1.18
Langloise	96.67	96.43	0.25	Langloise	3.43	3.44	-0.36
Mexicali 75	93.33	92.86	0.51	Djenah Khoteifa	3.75	3.83	-2.22
Oued Zenati 368	70.00	67.86	3.06	Aures	3.10	3.20	-3.08
Massinissa	100.00	96.67	3.33	Mexicali 75	3.11	3.25	-4.53
Megress	100.00	96.67	3.33	INRAT 69	3.10	3.29	-6.15
Aures	96.67	93.33	3.45	Montpellier	3.04	3.25	-6.77
Waha	96.67	93.33	3.45	Hedba 3	2.83	3.04	-7.62
INRAT 69	93.33	90.00	3.57	Oued El Berd	2.89	3.13	-8.23
Hedba 3	100.00	96.43	3.57	Acsad 65	3.38	3.75	-11.11
Ofanto	100.00	96.43	3.57	Polonicum	2.94	3.33	-12.92
ZB/Fg	100.00	96.43	3.57	Mansourah	3.14	3.56	-13.07
Cirta	93.33	90.00	3.57	El Maather	2.97	3.37	-13.61
Acsad 65	86.67	83.33	3.85	Ofanto	2.81	3.25	-15.56
Montpellier	100.00	95.83	4.17	Cirta	2.87	3.32	-15.95
Mansourah	100.00	93.33	6.67	Massinissa	2.79	3.32	-18.86
Oued El Berd	96.67	90.21	6.68	Altar14	2.69	3.29	-22.19
Tejdid	100.00	92.82	7.18	Sitifis	2.50	3.08	-23.08
Vitron	96.67	89.29	7.64	Bidi 17	2.30	3.11	-35.27
Guemgoum R'khem	90.00	80.00	11.11	Vitron	2.48	3.45	-39.32
Polonicum	90.00	80.00	11.11	Wahbi	2.30	3.21	-39.67
Sbaa Aldjia	80.00	70.00	12.50	Waha	2.14	3.14	-46.73
El Maather	100.00	86.67	13.33	GTA Dur	2.70	4.10	-51.85
Wahbi	90.00	73.33	18.52	ZB/Fg	1.82	2.99	-64.38
Simeto	73.33	43.33	40.91	Sbaa Aldjia	3.71	6.33	-70.51

FGP C and FGP S: final germination percentage under control and under stress respectively. t50 C and t50 S: time that takes the genotype to reach 50 % of germination under control and under stress respectively.

Table 2.S2. Cultivar and landrace mean separation and ANOVA analysis for seedling traits of the 27 genotypes and type effect under field conditions.

	Mean values		ANOVA	
Traits	Cultivar	Landrace	Genotype	Type
FGP	64.99	61.56	ns	ns
SL	8.10	8.60	ns	ns
CL	3.18	3.22	*	ns
RN	4.34	4.33	***	ns
TRL	16.03	17.02	ns	ns
MRL	5.25	5.34	ns	ns
SDW	9.07 **b**	9.92 **a**	ns	*
RDW	4.71	4.37	***	ns
TPB	13.85	14.32	ns	ns
RSW	0.53 **a**	0.46 **b**	**	*
RSL	0.66	0.63	ns	ns
SVI$_{W}$	0.89	0.87	ns	ns
SVI$_{L}$	871.77	860.54	ns	ns

FGP: final germination percentage, CL: coleoptile length, SL: shoot length, MRL: maximum root length, TRL: total root length, RN: root number, SDW: shoot dry weight, RDW: root dry weight, TPB: total plant biomass, RSL: root to shoot length, RSW: root to shoot weight, SVI$_{w}$: seedling vigor index based on seedling weight, SVI$_{L}$: seedling vigor index based on seedling length.
*, ** and ***: significant difference at 0.5, 0.01 and 0.001 level respectively.

Table 2.S3. Variance components and broad heritability (h^2) calculated for control, stress and field data.

	Control (n=35)			Stress (n=35)			Field (n=27)		
	Geno	Error	h^2	Geno	Error	h^2	Geno	Error	h^2
t50	0.0972	0.101	0.66	0.0749	0.0329	0.82	/	/	/
FGP	112.56	50.26	0.82	75	136.5	0.52	7.2	115.8	0.11
CL	0.2455	0.262	0.65	0.1037	0.62	0.25	0.0576	0.326	0.26
SL	0.153	7.808	0.04	0	3.456	0	0.174	1.387	0.20
MRL	4.47	14.33	0.38	125.732	4.895	0.98	33.131	0.876	0.99
TRL	39.8	218.6	0.27	0	92.64	0	2.01	14.86	0.21
RN	0.0111	0.257	0.08	0.0358	0.247	0.22	0.1238	0.143	0.63
SDW	9.61E-07	7.18E-06	0.21	0	2.64E-06	0	0	1.6E-06	0
RDW	1.181E-06	4.31E-06	0.35	1.65E-07	1.55E-06	0.18	4.57E-07	7.2E-07	0.56
TPB	3.63E-06	1.91E-05	0.28	0	7.58E-06	0	6E-08	2.6E-06	0.04
RSL	0.054	0.0549	0.66	0	0.153	0	0	0.0155	0
RSW	0.57864	0.0273	0.98	0.00349	0.0346	0.17	0.003694	0.00737	0.50
SVI$_{W}$	0.0792	0.163	0.49	0.01783	0.0703	0.34	0	0.0398	0
SVI$_{L}$	176139	346980	0.50	54975	150709	0.42	0	51736	0

T50: time to reach 50% germination, FGP: final germination percentage, CL: coleoptile length, SL: shoot length, MRL: maximum root length, TRL: total root length, RN: root number, SDW: shoot dry weight, RDW: root dry weight, TPB: total plant biomass, RSL: root to shoot length, RSW: root to shoot weight, SVI$_{w}$: seedling vigor index based on seedling weight, SVI$_{L}$: seedling vigor index based on seedling length.

Table 2. S4. Pearson correlation of germination and seedling traits in field conditions.

Variables	FGP	SL	CL	RN	TRL	MRL	SDW	RDW	TPB	RSW	RSL	SVI_W	SVI_L
FGP	**1.00**												
SL	0.16	**1.00**											
CL	0.08	**0.72**	**1.00**										
RN	-0.17	**0.49**	**0.42**	**1.00**									
TRL	-0.04	**0.57**	**0.34**	**0.67**	**1.00**								
MRL	0.11	**0.41**	0.22	0.19	**0.79**	**1.00**							
SDW	0.24	0.10	0.07	-0.11	0.04	0.21	**1.00**						
RDW	-0.07	**0.29**	0.01	**0.57**	**0.74**	**0.53**	0.05	**1.00**					
TPB	0.13	0.26	0.06	**0.30**	**0.52**	**0.50**	**0.75**	**0.70**	**1.00**				
RSW	-0.09	-0.19	**-0.29**	**0.29**	**0.43**	**0.33**	0.00	**0.78**	**0.52**	**1.00**			
RSL	-0.03	**-0.42**	**-0.35**	-0.20	**0.32**	**0.64**	0.14	0.28	**0.28**	**0.51**	**1.00**		
SVI_W	**0.75**	**0.51**	0.21	**0.28**	**0.46**	**0.41**	0.25	**0.51**	**0.52**	0.18	-0.04	**1.00**	
SVI_L	**0.83**	**0.61**	**0.38**	0.10	**0.41**	**0.53**	**0.29**	0.20	**0.34**	-0.04	0.02	**0.86**	**1.00**

T50: time to reach 50% germination, FGP: final germination percentage, CL: coleoptile length, SL: shoot length, MRL: maximum root length, TRL: total root length, RN: root number, SDW: shoot dry weight, RDW: root dry weight, TPB: total plant biomass, RSL: root to shoot length, RSW: root to shoot weight, SVI_w: seedling vigor index based on seedling weight, SVI_L: seedling vigor index based on seedling length. Values in bold are different from 0 with a significance level alpha=0,05.

Table 2.S5. Pearson correlation of measured traits beween field, no stress and stress.

Trait	Field vs Control	Field vs Stress
FGP	0.13	0.10
SL	-0.16	0.01
CL	0.07	-0.01
RN	0.02	0.13
TRL	-0.16	-0.04
MRL	-0.06	-0.08
SDW	0.02	**0.33**
RDW	0.08	-0.12
TPB	-0.05	0.14
RSW	0.05	0.02
RSL	0.05	-0.04
SVI_W	0.06	-0.04
SVI_L	0.06	0.12

Values in bold are different from 0 with a significance level alpha=0,05.
Traits abbreviations are mentioned in Table 2.S4.

Table 2.S6. Mean values for measured seedling traits in control, stress and field conditions.

Genotype (n=27)	SL (cm)	CL (cm)	RN	TRL (cm)	MRL (cm)	SDW (mg)	RDW (mg)	TPB (mg)	RSW	RSL	SVI_W	SVI_L
Control												
Acs	12.37	2.92	4.80	37.98	11.68	9.03	6.25	15.28	0.70	0.96	1.32	2084.33
Alt	7.32	3.03	4.50	34.49	10.84	6.79	4.94	11.73	0.87	1.39	1.02	1548.27
Bid	12.84	4.55	4.90	42.12	13.60	8.57	6.05	14.62	0.71	1.13	1.14	2056.48
Cap	13.47	3.84	4.90	30.05	9.57	8.44	5.02	13.46	0.59	0.70	1.03	1743.58
Cir	14.14	3.22	4.10	23.46	8.52	4.51	8.80	13.31	1.04	1.00	1.72	1539.67
Glo	13.43	3.97	4.70	30.42	10.97	7.12	4.56	11.68	0.68	0.82	0.89	1879.60
GTA	11.12	3.11	5.40	40.96	12.16	7.34	6.98	14.32	0.96	1.11	1.09	1772.67
Gue	11.15	4.86	4.00	35.89	11.25	7.42	4.04	11.46	0.60	1.06	0.97	1898.80
Hed	14.72	5.00	4.60	42.16	13.61	5.95	4.31	10.26	0.73	0.92	1.03	2833.00
INR	12.54	3.78	5.00	48.24	14.37	7.60	6.49	14.09	0.86	1.15	1.32	2511.60
Kor	14.08	3.57	4.80	44.35	13.45	12.73	7.58	20.30	0.60	0.97	1.76	2386.15
Lan	8.95	4.78	4.60	28.31	10.29	5.00	3.70	8.70	0.82	1.23	0.83	1840.47
Man	12.64	4.05	5.00	54.91	16.90	9.06	6.32	15.38	0.70	1.34	1.54	2954.00
Mas	11.62	3.00	4.90	64.30	19.71	10.68	9.51	20.19	0.89	1.70	2.02	3133.00
MBB	13.52	5.15	4.70	33.60	11.07	7.29	3.66	10.95	0.47	0.81	1.07	2390.07
Mgs	8.31	3.61	4.30	41.80	12.64	6.33	5.61	11.94	0.91	1.44	1.19	2095.00
Mex	12.12	4.01	4.80	34.04	10.68	5.74	4.67	10.41	0.80	0.88	0.98	2137.87
Mon	9.35	4.36	4.50	45.96	16.73	9.38	8.30	17.68	0.89	1.79	1.77	2608.00
Ofan	12.13	3.38	5.00	55.59	16.89	10.21	7.86	18.07	0.77	1.39	1.81	2902.00
OEB	12.56	3.90	4.60	44.05	14.38	9.00	7.19	16.19	0.79	1.14	1.55	2592.27
OZ	11.08	4.01	3.90	23.69	8.28	7.57	3.52	11.09	0.47	0.76	0.78	1349.33
Pol	11.31	5.01	4.40	25.78	8.86	6.49	4.07	10.56	0.62	0.76	0.96	1830.13
Sim	13.96	2.88	5.05	39.68	12.17	12.15	7.06	19.21	0.63	0.88	1.43	1907.00
Sit	12.96	4.02	5.10	65.36	18.79	8.99	8.43	17.42	0.94	1.45	1.67	3063.73
Vit	13.14	3.72	5.00	44.17	12.60	7.90	5.83	13.73	0.72	0.95	1.32	2478.33
Wah	13.09	4.06	4.20	39.05	13.14	6.62	6.03	12.65	0.88	1.00	1.23	2542.13
ZBF	11.86	4.00	4.40	46.97	14.09	8.00	5.78	13.78	0.68	1.17	1.38	2595.00
Stress												
Acs	7.91	2.79	5.00	28.55	10.28	7.35	6.37	13.72	0.87	1.32	1.13	1556.67
Alt	4.73	2.86	4.30	30.40	8.00	5.43	5.30	10.73	1.22	2.44	0.85	1003.81
Bid	7.64	4.46	5.00	36.64	11.02	6.61	6.54	13.15	1.00	1.44	1.18	1665.03
Cap	4.24	3.61	4.90	19.08	6.08	3.63	4.16	7.79	1.13	1.44	0.61	799.93
Cir	5.07	4.40	5.80	29.48	9.11	5.92	6.17	12.09	1.04	1.83	1.10	1277.40
Glo	8.99	3.79	5.10	38.46	11.81	9.39	8.13	17.52	0.86	1.32	1.50	1783.44
GTA	6.06	2.99	5.40	32.64	10.28	5.30	6.11	11.41	1.16	1.73	0.88	1518.13
Gue	7.57	4.28	5.50	42.81	12.11	8.36	7.89	16.25	0.95	1.62	1.30	1574.40
Hed	7.96	4.56	5.00	40.29	13.10	6.01	5.96	11.97	1.00	1.67	1.15	2037.36
INR	8.26	3.49	5.60	45.10	11.14	7.14	9.05	16.19	1.27	1.41	1.44	1715.40
Kor	7.56	3.39	5.00	30.21	10.71	6.94	6.68	13.62	1.00	1.45	1.18	1583.40
Lang	8.39	4.25	4.70	34.78	11.59	9.19	6.81	16.00	0.74	1.40	1.54	1920.64
Man	6.24	3.54	4.90	37.39	12.39	5.02	5.47	10.49	1.16	1.99	0.98	1738.80

Continued Table 2S6

Genotypes	SL (cm)	CL (cm)	RN	TRL (cm)	MRL (cm)	SDW (mg)	RDW (mg)	TPB (mg)	RSW	RSL	SVI_W	SVI_L
Stress												
Mas	6.10	2.96	4.80	34.45	11.61	5.58	6.35	11.93	1.15	1.92	1.15	1712.73
MBB	8.11	4.98	5.00	43.20	12.66	7.78	6.53	14.31	0.84	1.59	1.43	2077.00
Mgs	6.16	3.09	5.00	33.99	10.49	5.93	6.67	12.60	1.16	1.73	1.22	1606.60
Mex	6.99	3.59	4.90	29.05	10.26	5.66	5.53	11.19	0.98	1.47	1.04	1612.43
Mon	6.56	5.21	5.00	31.56	10.03	6.18	6.38	12.56	1.05	1.53	1.21	1589.08
Ofa	7.49	3.39	4.90	38.13	12.63	6.34	6.30	12.64	1.00	1.71	1.22	1947.57
OEB	7.81	4.10	4.70	36.02	11.32	6.64	6.06	12.70	0.91	1.45	1.14	1718.57
OZ	7.24	4.61	5.10	36.37	10.14	7.14	6.43	13.57	0.91	1.44	0.94	1223.07
Pol	7.89	4.91	5.60	33.21	10.99	7.26	5.36	12.62	0.74	1.39	1.01	1532.00
Sim	8.09	4.07	4.50	23.36	7.67	6.67	4.42	11.09	0.68	0.98	0.48	692.17
Sit	7.53	4.39	4.70	37.34	12.69	6.30	6.31	12.61	1.01	1.69	1.22	1951.13
Vit	6.14	3.25	5.10	28.89	9.33	6.00	6.69	12.69	1.12	1.53	1.13	1388.36
Wah	8.79	3.28	5.40	36.93	12.45	6.36	6.87	13.23	1.08	1.42	1.24	1994.93
ZBF	6.86	4.24	5.60	42.05	11.79	5.25	6.11	11.36	1.19	1.72	1.10	1803.00
Field												
Acs	8.17	2.99	3.80	11.60	4.29	8.66	4.10	12.76	0.45	0.52	1.06	994.24
Alt	10.10	3.93	4.65	22.18	6.98	9.73	7.10	16.83	0.62	0.69	1.18	1087.29
Bid	9.02	3.45	4.70	18.97	5.48	10.27	4.87	15.14	0.46	0.61	0.79	742.40
Cap	8.17	3.32	5.00	17.87	4.79	8.96	5.06	14.02	0.56	0.58	1.01	932.71
Cir	7.68	3.07	4.60	18.72	5.17	8.62	5.52	14.14	0.54	0.68	0.87	715.48
Glo	8.54	4.52	4.40	16.46	4.79	10.18	3.63	13.81	0.34	0.58	0.94	885.79
GTA	7.96	3.19	5.20	20.04	5.09	8.38	5.99	14.37	0.66	0.64	1.00	855.93
Gue	8.49	3.50	4.40	18.37	5.58	8.75	4.58	13.33	0.51	0.66	0.61	630.92
Hed	9.18	3.39	4.60	17.14	5.75	9.15	3.71	12.86	0.39	0.64	0.75	846.45
INR	8.52	3.13	4.60	17.60	5.47	9.60	5.46	15.06	0.60	0.64	0.85	820.89
Kor	8.79	3.00	4.00	16.35	5.80	9.03	4.22	13.25	0.45	0.67	0.81	901.74
Lan	9.04	3.06	4.40	16.62	4.96	9.48	4.91	15.20	0.50	0.56	1.03	966.67
Mans	8.24	3.34	4.20	14.34	5.07	8.85	3.69	12.54	0.40	0.62	0.85	885.89
Mas	8.80	3.42	4.10	14.48	4.98	8.94	3.95	12.89	0.45	0.57	0.88	949.82
MBB	8.14	2.70	3.40	14.48	5.71	10.70	4.03	14.73	0.48	0.71	1.03	1130.65
Mgs	7.64	3.14	4.00	15.40	5.68	7.00	4.40	12.00	0.52	0.74	0.64	666.00
Mex	8.02	3.56	4.50	16.70	5.64	10.13	3.94	14.07	0.49	0.69	0.90	1037.26
Mon	5.92	2.96	3.50	09.71	4.17	8.95	3.01	11.96	0.40	0.70	0.74	708.70
Ofa	8.89	2.89	4.50	21.66	6.73	9.27	5.85	15.12	0.62	0.76	1.04	1055.77
OEB	7.35	2.93	3.70	12.61	5.08	10.00	4.55	14.55	0.56	0.70	0.78	771.11
OZ	7.76	2.56	4.40	17.10	5.14	10.69	4.89	15.58	0.51	0.67	0.92	820.88
Pol	7.29	3.52	4.50	15.70	5.59	10.78	4.85	15.63	0.60	0.79	0.82	806.76
Sim	6.58	1.80	4.20	17.71	5.70	8.32	5.09	13.41	0.65	0.87	0.69	673.50
Sit	7.07	3.05	3.90	10.14	4.00	8.82	4.13	12.95	0.56	0.57	0.71	682.02
Vit	10.00	4.08	4.93	18.44	5.18	8.94	4.97	13.91	0.52	0.52	0.94	985.57
Wah	8.52	3.28	4.00	14.04	4.82	9.48	3.23	12.71	0.38	0.57	0.83	944.62
ZBF	8.07	2.94	4.70	15.05	4.92	9.03	4.98	14.01	0.54	0.64	0.94	857.30

CL: coleoptile length, SL: shoot length, MRL: maximum root length, TRL: total root length, RN: root number, SDW: shoot dry weight, RDW: root dry weight, TPB: total plant biomass, RSL: root to shoot length, RSW: root to shoot weight, SVI_w: seedling vigor index based on seedling weight, SVI_L: seedling vigor index based on seedling length.

Table 3.S1**.** Mean values and standard errors (12 replications) of the assessed seminal root traits for the 37 durum wheat genotypes.

Genotypes	TRL	Surface	Volume	Diameter	PRL	SDW	MRA	MVA	LVA	RN
Beliouni	97.96±4.67	16.36±0.94	0.2241±0.02	0.0536±0.00	29.87±0.93	19.37±2.26	33.45±2.43	9.40±4.44	44.60±4.04	5.00±0.00
Bidi 17	113.55±10.12	20.31±2.17	0.2954±0.04	0.0558±0.00	26.95±1.61	18.28±1.75	28.44±5.10	12.76±6.50	40.46±8.13	6.00±0.00
Djenah Khotifa	102.22±7.56	17.76±1.60	0.2518±0.03	0.0552±0.00	29.57±1.11	17.70±1.32	26.17±2.89	9.14±5.16	41.27±4.90	5.00±0.00
Gloire de Montgolfier	112.47±8.20	18.13±1.40	0.2371±0.02	0.0504±0.00	27.58±1.64	16.45±2.01	20.10±6.69	9.76±4.39	31.38±7.63	5.42±0.51
Guemgoum R'khem	122.73±8.13	20.80±1.24	0.2857±0.02	0.0534±0.00	28.52±1.47	18.21±1.44	23.90±3.94	6.79±5.04	37.41±5.61	5.83±0.39
Hedba 3	114.61±12.68	19.31±2.50	0.2650±0.04	0.0536±0.00	26.63±1.87	16.58±2.09	22.73±3.22	12.90±4.31	33.14±4.62	5.33±0.49
Langlois	108.24±5.08	18.49±1.20	0.2560±0.02	0.0539±0.00	28.06±0.96	14.48±1.90	22.71±4.77	9.25±7.69	34.22±5.93	5.08±0.29
Mohammed Ben Bachir	99.30±6.90	16.50±1.36	0.2230±0.03	0.0527±0.00	27.53±1.01	17.81±1.81	32.37±4.24	12.88±6.53	45.91±6.77	5.08±0.29
Montpellier	83.41±8.48	13.90±1.90	0.1895±0.03	0.0516±0.00	23.43±2.50	11.17±1.38	15.94±6.51	3.69±6.97	36.82±4.05¥	5.08±0.29
Oued Zenati 368	108.45±13.56	19.17±2.80	0.2767±0.05	0.0555±0.00	27.03±2.35	16.08±3.07	27.29±3.19	9.83±7.05	41.75±7.26	5.83±0.39
Acsad 65	97.63±9.59	17.33±1.66	0.2495±0.03	0.0568±0.00	26.88±1.25	15.45±1.84	30.87±4.10	10.02±5.53	48.62±7.33	5.00±0.00
Altar 84	95.35±15.76	16.63±2.67	0.2370±0.04	0.0553±0.00	27.01±1.34	13.46±1.76	26.96±10.03	10.70±7.27	43.24±6.86¥	5.17±0.39
Ammar 6	87.73±10.83	15.38±1.84	0.2205±0.03	0.0559±0.00	22.74±2.59	12.83±2.07	36.33±3.18	23.27±4.00	45.70±4.96	5.33±0.49
Bousselem	86.07±11.72	14.81±1.86	0.2071±0.02	0.0548±0.00	26.17±3.51	13.81±1.42	38.00±4.84	20.09±3.74	49.73±8.38	4.92±0.51
Boutaleb	97.70±6.09	17.23±1.42	0.2476±0.03	0.0560±0.00	25.97±1.73	15.13±1.25	31.97±5.79	16.58±5.96	44.19±7.33	5.00±0.00
Capeiti	107.02±10.62	18.17±2.10	0.2517±0.04	0.0536±0.00	25.91±1.64	14.59±1.69	32.13±3.15	17.12±6.59	45.61±8.66	5.58±0.51
Chen’s	90.66±9.14	14.72±1.47	0.1964±0.02	0.0515±0.00	24.30±2.72	11.47±1.34	38.62±4.24	16.19±5.64	50.74±9.66¥	6.00±0.00
Ciccio	90.64±11.32	14.79±1.94	0.1972±0.03	0.0517±0.00	23.43±3.00	11.07±2.54	25.84±6.93	11.29±10.19	37.30±6.31¥	5.08±0.29
Cirta	96.13±9.98	17.48±1.62	0.2588±0.02	0.0577±0.00	25.73±2.42	15.43±1.39	32.10±4.19	12.31±4.68	44.79±8.70	5.25±0.45
Core	91.27±14.74	14.66±2.53	0.1935±0.04	0.0512±0.00	23.42±3.53	10.48±1.41	31.92±6.32	15.49±6.51	47.13±11.86	5.67±0.65
GTA Dur	95.48±12.76	16.62±2.17	0.2338±0.03	0.0548±0.00	25.92±2.76	14.28±1.56	34.70±4.65	21.05±8.56	47.01±8.27	5.42±0.51
INRAT 69	101.69±11.29	17.26±2.20	0.2378±0.04	0.0534±0.00	25.18±1.60	14.38±2.38	22.08±7.41	11.83±6.10	32.91±8.84	5.58±0.51
Korifla	89.04±15.74	15.05±3.48	0.2077±0.06	0.0528±0.00	24.03±4.17	12.14±3.90	26.70±2.58	13.01±4.25	38.18±4.67	5.17±0.39
Mansourah	103.44±9.07	16.86±1.56	0.2240±0.03	0.0514±0.00	28.71±0.97	15.85±1.44	32.92±4.07	10.12±2.99	48.97±6.02	5.42±0.51

Continued Table S1										
Massinissa	89.84±5.11	15.63±0.96	0.2207±0.02	0.0547±0.00	25.92±1.34	13.19±1.12	37.40±4.05	22.90±5.24	46.97±5.24	5.00±0.00
Megress	102.24±12.84	17.45±2.06	0.2423±0.03	0.0538±0.00	27.36±1.97	15.48±1.50	31.92±5.69	16.42±5.33	44.91±8.14	5.42±0.51
Mexicali 75	103.04±7.96	18.30±1.47	0.2637±0.02	0.0559±0.00	28.50±1.12	15.12±1.62	36.60±3.83	16.72±4.22	45.00±6.22¥	5.83±0.39
Ofanto	100.23±8.07	17.37±1.37	0.2443±0.02	0.0543±0.00	26.88±1.23	13.94±1.82	25.35±5.25	14.56±5.34	35.40±7.77	4.92±0.29
Oued El Berd	98.40±10.28	17.48±1.70	0.2518±0.02	0.0564±0.00	29.82±1.10	15.58±1.34	35.04±3.46	12.16±3.66	46.79±6.77	5.08±0.29
Polonicum	100.42±8.40	17.05±1.88	0.2357±0.03	0.0534±0.00	23.86±1.84	14.78±2.46	24.44±5.71	12.26±4.56	36.27±9.04	5.67±0.49
Sahell	89.40±9.39	14.63±1.84	0.1952±0.03	0.0517±0.00	25.59±2.45	15.62±1.41	39.46±3.97	24.08±4.18	48.25±5.61	5.42±0.51
Simeto	86.25±7.57	14.40±1.45	0.1954±0.03	0.0526±0.00	24.40±1.63	13.69±1.46	31.07±4.87	20.35±3.79	40.81±7.49	5.00±0.00
Sitifis	93.31±8.46	16.06±1.68	0.2242±0.03	0.0542±0.00	29.97±2.18	16.00±2.46	35.23±5.94	15.66±2.66	46.63±6.35	5.17±0.39
Vitron	87.21±5.56	14.77±1.08	0.2039±0.02	0.0541±0.00	27.10±1.53	14.67±1.13	40.34±2.54	18.65±4.68	52.95±5.78	5.17±0.39
Waha	102.90±7.49	17.42±1.59	0.2403±0.03	0.0534±0.00	28.65±2.36	13.80±1.31	31.71±2.99	11.15±3.50	42.29±8.57	5.58±0.51
Wahbi	90.39±14.41	14.63±2.67	0.1933±0.04	0.0514±0.00	25.49±4.58	11.73±1.84	33.84±5.84	18.01±4.54	45.80±10.42	5.08±0.29
ZB × Fg	107.64±10.22	17.41±1.41	0.2296±0.02	0.0513±0.00	26.66±1.81	14.63±1.14	26.73±4.16	13.41±4.34	37.05±8.63	5.25±0.45

TRL: total root length, Surface: total root surface area, Volume: total root volume, Diameter: mean root diameter, PRL: primary root length, SDW: shoot dry weight, MRA: mean root angle, MVA: maximal vertical angle; LVA, least vertical angle, RN: root number.

Values in the table represent mean ± standard deviation.

Coefficient of variation (CV%) can be calculated following the formula (standard error/mean) *100.

¥: Mean and standard error of LVA were calculated based on 11 replications for the corresponding genotypes.

Table 3.S2. Descriptive statistics and correlation coefficients for seedling traits, calculated separately for the cultivar and landrace groups.

	Traits	**Min**	**Mean**	**Max**	**CV**	**TRL**	**Surface**	**Volume**	**Diameter**	**PRL**	**SDW**	**MRA**	**LVA**	**MVA**	**RN**
Cultivar (n=27)	TRL (cm)	54.28	95.60	128.75	12.54	1	***	***	ns	***	***	***	**	**	***
	Surface (cm^2)	8.25	16.28	21.69	13.70	0.83	1	***	***	***	***	***	*	*	***
	Volume (cm^3)	0.0962	0.2260	0.3034	16.02	0.80	0.96	1	***	***	***	*	ns	ns	**
	Diameter (cm)	0.0447	0.0538	0.0620	5.28	0.06	0.39	0.61	1	***	***	***	ns	**	***
	PRL (cm)	14.32	26.13	32.06	11.26	0.55	0.56	0.51	0.16	1	***	ns	**	***	ns
	SDW (g)	5.70	14.02	19.10	16.52	0.45	0.58	0.63	0.49	0.53	1	***	**	ns	ns
	MRA (°)	1.20	32.23	45.69	21.24	-0.38	-0.31	-0.23	0.15	0.01	0.10	1	***	***	ns
	LVA (°)	20.40	44.20	61.47	16.19	-0.14	-0.16	-0.12	0.08	0.14	0.12	0.73	1	***	ns
	MVA (°)	0.00	15.75	43.49	53.91	-0.19	-0.18	-0.13	0.11	-0.26	0.02	0.57	0.18	1	ns
	RN (no.)	4.00	5.30	6.00	9.17	0.24	0.22	0.15	-0.29	0.02	-0.03	-0.04	0.06	-0.16	1
Landrace (n=10)	TRL (cm)	90.40	106.29	137.22	12.80	1	***	***	ns	ns	**	***	**	ns	***
	Surface (cm^2)	14.18	18.07	24.82	14.50	0.95	1	***	***	*	***	**	ns	ns	***
	Volume (cm^3)	0.1710	0.2504	0.3721	17.16	0.85	0.97	1	***	*	***	ns	ns	ns	***
	Diameter (cm)	0.0481	0.0536	0.0588	4.95	0.24	0.51	0.67	1	ns	***	**	*	ns	ns
	PRL (cm)	21.98	27.52	31.38	8.45	0.49	0.48	0.46	0.28	1	***	ns	**	*	*
	SDW (g)	11.00	16.61	23.50	17.67	0.54	0.58	0.39	0.43	0.68	1	**	**	ns	ns
	MRA (°)	9.69	25.31	37.45	26.56	-0.02	0.05	0.57	0.35	0.34	0.47	1	***	***	ns
	LVA (°)	22.91	38.71	59.01	19.03	-0.17	-0.10	0.11	0.22	0.23	0.28	0.70	1	ns	ns
	MVA (°)	0.14	9.64	26.03	66.87	0.11	0.13	-0.04	0.16	0.01	0.14	0.53	0.09	1	ns
	RN (no.)	5.00	5.37	6.00	9.02	0.53	0.52	0.49	0.03	-0.03	0.20	-0.05	-0.01	-0.01	1

TRL: total root length, Surface: total root surface area, Volume: total root volume, Diameter: mean root diameter, PRL: primary root length

SDW: shoot dry weight, MRA: mean root angle, LVA: least vertical angle, MVA: maximal vertical angle, RN: root number.

*, **, ***, ns, indicate P-values lower than 0.05, 0.01, 0.001, and non-significant, respectively.

Table 3.S3. Results of linear regressions of traits over years of release. Positive slopes indicate increase of the trait with year of release; negative slopes indicate decrease of the traits over years of release. Other columns show the standard errors (s.e.) of the slopes, variance ratio tests (F) and the probability of the slope being different from 0 (F pr.). Traits abbreviations are explained in Table 3S.1

Traits	**slope**	**s.e.**	**F**	**F pr.**
Diameter	0.0000023	0.0000108	0.04	0.836
LVA	0.0724	0.0313	2.31	0.020
MRA	0.0896	0.0313	8.18	0.007
MVA	0.0687	0.0256	7.18	0.011
PRL	-0.0140	0.0114	1.50	0.228
RN	-0.00249	0.00183	1.85	0.182
SDW	-0.0355	0.0110	10.39	0.003
Surface	-0.03094	0.00869	12.67	0.001
TRL	-0.1728	0.0462	14.00	<0.001
Volume	-0.000447	0.000144	9.66	0.004

Table 3.S4. Contribution (%) and coordinates of the traits to the first four principal components (PC1, PC2, PC3, PC4). Traits abbreviations as in Table 3.S1.

	Contributions				Coordinates			
Traits	**PC1**	**PC2**	**PC3**	**PC4**	**PC1**	**PC2**	**PC3**	**PC4**
TRL	19.04	0.08	3.44	2.42	0.93	-0.04	0.20	0.14
Surface	20.19	0.77	1.96	0.97	0.96	0.13	0.15	-0.09
Volume	18.16	2.91	1.03	8.39	0.91	0.26	0.11	-0.27
Diameter	1.82	16.8	2.44	50.19	0.29	0.63	-0.17	-0.67
PRL	7.53	9.63	12.80	20.43	0.59	0.47	-0.39	0.43
SDW	11.51	7.35	3.46	7.91	0.72	0.41	-0.20	0.26
MRA	5.65	28.16	2.34	2.76	-0.51	0.81	0.17	0.16
MVA	7.97	9.89	7.46	1.63	-0.60	0.48	0.30	-0.12
LVA	5.65	24.30	0.49	3.23	-0.51	0.75	0.07	0.17
RN	2.44	0.00	64.53	2.03	0.33	-0.00	0.89	0.13

Table 3.S5. Means comparison between groups formed by hierarchical clustering for the traits assessed.

Groups	**TRL**	**Surface**	**Volume**	**Diameter**	**PRL**	**RN**	**SDW**	**LVA**	**MRA**	**MVA**	**MRL**	**PRL-MRL**
G1	109.98 a	18.66 a	0.26 a	0.0534 b	26.72 b	5.56 a	15.98 a	36.07 c	24.27 c	10.97 c	18.43 a	8.29 b
G2	98.74 b	17.01 b	0.24 b	0.0546 a	27.57 a	5.21 b	15.43 a	44.93 b	31.98 b	13.93 b	16.97 b	10.60 a
G3	90.15 c	15.16 c	0.21 c	0.0533 b	25.37 c	5.34 b	13.28 c	47.14 a	36.10 a	19.13 a	15.00 c	10.37 a
G4	87.70 c	14.58 c	0.20 c	0.0520 c	23.63 d	5.11 c	11.46 d	37.45 c	22.83 c	9.33 c	15.69 c	7.94 b
Significance	***	***	***	***	***	***	***	***	***	***	***	***

TRL: total root length, Surface: total root surface area, Volume: total root volume, Diameter: mean root diameter, PRL: primary root length, RN: root number, SDW: shoot dry weight, LVA: least vertical angle, MRA: mean root angle, MVA: maximal vertical angle, RL: mean root length was calculated based on the length of roots, (primary root was not included), PRL-MRL: difference between length of the primary root and mean length of the other roots.

At each column, means followed by the same letter indicate that they did not differ significantly for P=0.05.

***, difference between groups was significant at P<0.001.

Figure 3.S1. A) One-week-old durum wheat seedlings in the rhizoslide system; B) pictures of two genotypes contrating for root angle, landrace Gloire de Montgolfier (left) and cultivar Oued El Berd (right); C) schematic representation of a glass box, holding 6 glass plates, each holding two rhizoslides.

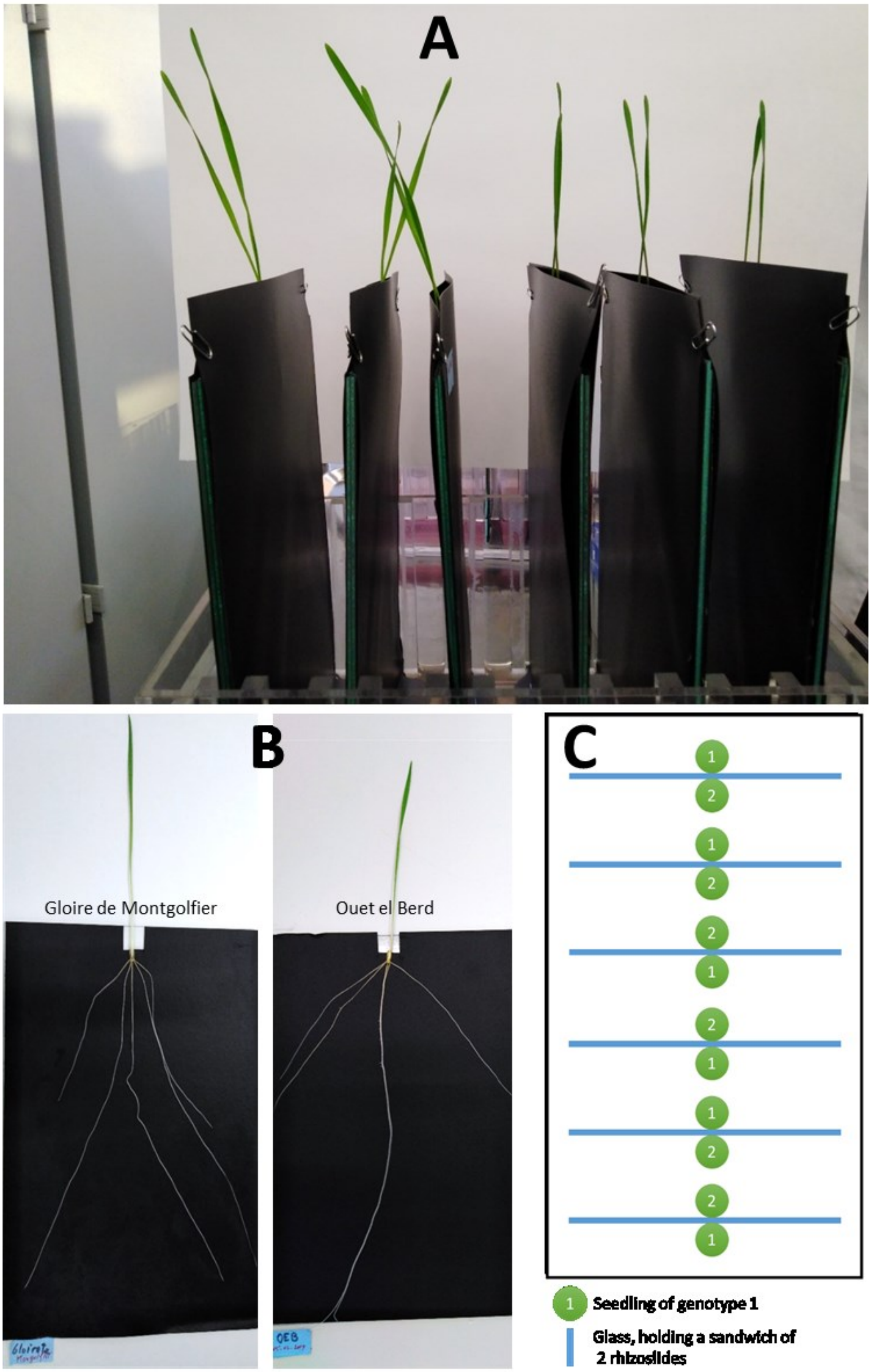

Figure 3.S2. Time trends of seminal root traits over years of release of the varieties. The coefficients of determination of the regression lines are indicated in each graph. Landraces are indicated with yellow symbols; modern cultivars are indicated with blue symbols.

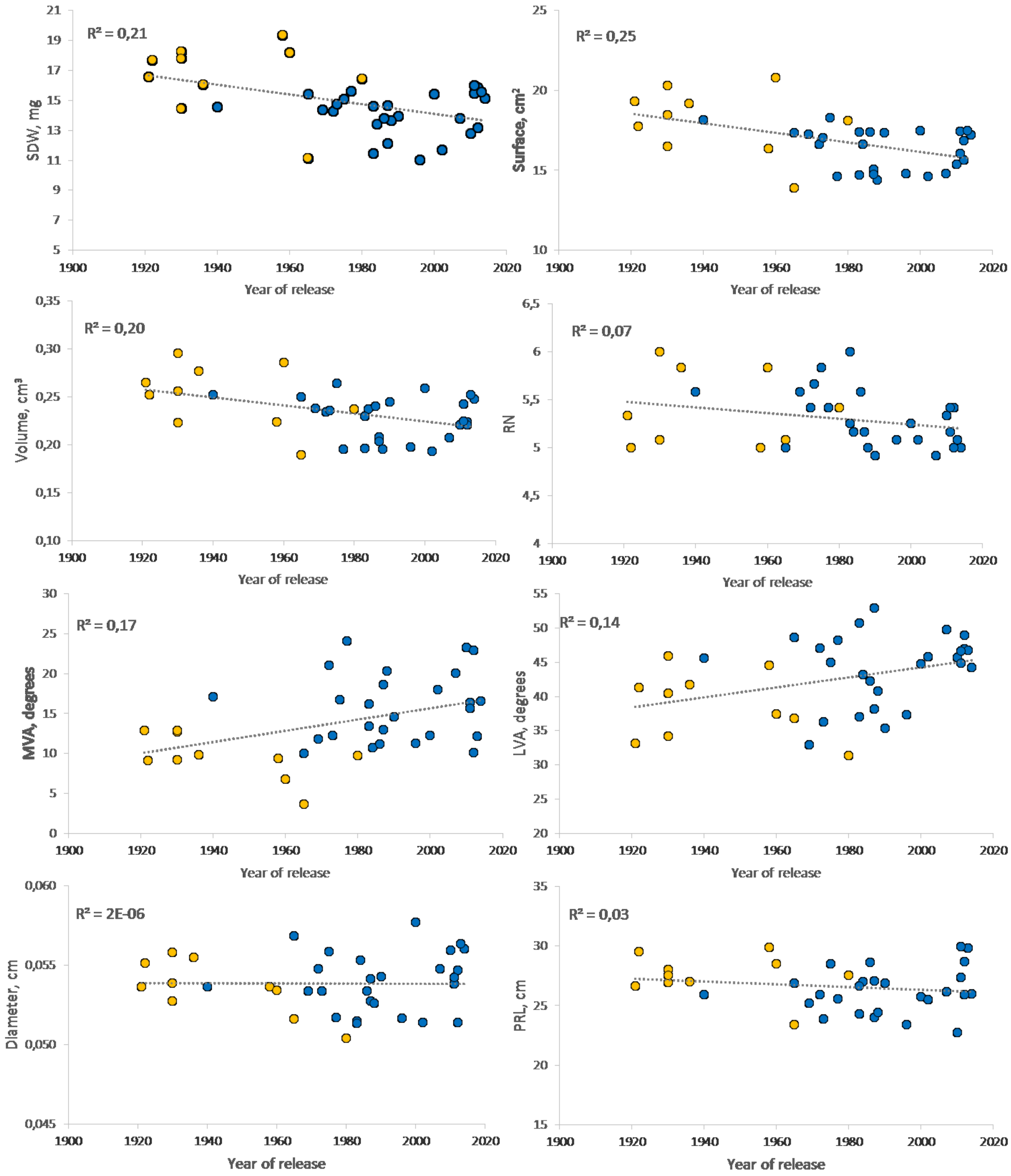

Table 4.S1. Type, origin and year of release of the evaluated genotypes, and the growth habit of some genotypes based on the current greenhouse experimental conditions.

Nº	**Genotype**	**Abbreviation**	**Type**	**Origin**	**Released Year**		**Growth Habit**
1	Beliouni	Bel	Landrace	Algeria	1958	×	Winter
2	Bidi 17	Bid	Landrace	Algeria	1930	×	Winter
3	Djenah Khotifa	Dje	Landrace	North Africa	1955	×	Winter
4	Gloire de Montgolfier	Glo	Landrace	Algeria	1960	×	Facultative
5	Guemgoum R'khem	Gue	Landrace	Algeria	1960	×	Facultative
6	Hedba 3	Hed	Landrace	Algeria	1921	×	Facultative
7	Langloise	Lan	Landrace	Algeria	1930	×	Winter
8	Mohammed Ben Bachir	MBB	Landrace	Algeria	1930	×	Winter
9	Montpellier	Mon	Landrace	France	1965	×	Facultative
10	Oued Zenati 368	OZ	Landrace	Algeria	1936	×	Winter
11	Acsad 65	Acs	Cultivar	ACSAD	1984		
12	Altar 84	Alt	Cultivar	CYMMIT	1984		
13	Ammar 6	Amm	Cultivar	ICARDA	2010		
14	Bousselem	Bou	Cultivar	ICARDA	2007		
15	Boutaleb	Bot	Cultivar	Algeria	2013		
16	Capeiti	Cap	Cultivar	Italy	1940		
17	Chen’s	Che	Cultivar	CYMMIT	1983		
18	Ciccio	Cic	Cultivar	Italy	1996		
19	Cirta	Cir	Cultivar	Algeria	2000		
20	Core	Cor	Cultivar	Italy	-		
21	GTA Dur	GTA	Cultivar	CIMMYT	1972	×	Facultative
22	INRAT 69	INR	Cultivar	Tunisia	1969	×	Facultative
23	Korifla	Kor	Cultivar	ICARDA	1987	×	Facultative
24	Mansourah	Man	Cultivar	Algeria	2012	×	Winter
25	Massinissa	Mas	Cultivar	Algeria	2012	×	Facultative
26	Megress	Mgs	Cultivar	Algeria	2007	×	Facultative
27	Mexicali 75	Mex	Cultivar	CIMMYT	1975	×	Facultative
28	Ofanto	Ofa	Cultivar	Italy	1990	×	Facultative
29	Oued El Berd	OEB	Cultivar	Algeria	2013	×	Facultative
30	Polonicum	Pol	Cultivar	France	1973		
31	Sahell	Sah	Cultivar	CYMMIT	1977		
32	Simeto	Sim	Cultivar	Italy	1988	×	Facultative
33	Sitifis	Sit	Cultivar	Algeria	2011	×	Facultative
34	Vitron	Vit	Cultivar	Spain	1987	×	Facultative
35	Waha	Wah	Cultivar	ICARDA	1986	×	Facultative
36	Wahbi	Wah	Cultivar	Algeria	1995	×	Facultative
37	ZB × Fg	ZBF	Cultivar	Algeria	1983		
38	Aures	Au	Cultivar	Algeria	-	①	Facultative
39	El maather	Elm	Cultivar	Algeria	-	①	Facultative
40	Tejdid	Tej	Cultivar	Algeria	-	①	Winter

Up to the genotype Nº 37, all were evaluated in growth chamber (Seedlings) and in field (Plants).

×: Genotypes evaluated in all experiments. ①: Genotypes evaluated only under greenhouse.

Table 4.S2. ANOVA analysis for the assessed traits under greenhouse experiment.

	DF	DTH	PH	Depth	RDW30	RDW60	RDW>60	RDW	SDW	RSR
Genotype	26	***	ns	ns	*	ns	ns	ns	*	*
Type										
(Landrace vs. cultivar)	1	*	*	ns	*	ns	ns	*	ns	ns
Growth habit										
(Facultative vs. winter)	1	-	ns	*	**	ns	ns	**	ns	**
Facultative habit										
(Landrace vs. cultivar)	1	***	**	ns	**	ns	ns	0,07	ns	***
Winter habit										
(Landrace vs. cultivar)	1	-	ns	ns	*	ns	ns	ns	ns	ns

DTH: days to heading, PH: plant height, Depth: root depth, RDW30: root dry weight up 30 cm of depth, RDW60: root dry weight between 30 and 60 cm, RDW>60: root dry weight for depth more than 60 cm. RDW: total root dry weight. SDW: shoot dry weight, RSR: root to shoot ratio.

*,** and ***: differences are significant, high significant and very high significant at 0.05 level.

Table 4.S3. Pearson correlations between traits assessed with the REST software.

	RoA$_{I}$	RA	AcH	Ff	depth	mW	tpSL	mFD	NoG	mGZ	mSW
RoA$_{I}$	*										
RA	0.00	*									
AcH	0.01	**0.36**	*								
Ff	-0.02	**0.32**	**-0.67**	*							
Depth	0.05	**0.35**	**0.55**	**-0.29**	*						
mW	-0.01	**0.21**	**0.81**	**-0.64**	0.03	*					
tpSL	0.01	**0.85**	**0.38**	**0.18**	**0.41**	**0.20**	*				
mFD	0.00	**0.32**	**-0.51**	**0.76**	**-0.28**	**-0.46**	**0.24**	*			
NoG	0.00	**0.63**	**0.19**	**0.25**	**0.31**	0.03	**0.89**	**0.26**	*		
mGZ	-0.02	0.05	-0.03	0.06	-0.05	0.00	**-0.11**	0.02	**-0.29**	*	
mSW	-0.01	0.27	**-0.11**	**0.34**	**-0.12**	-0.06	**-0.17**	**0.24**	**-0.26**	**0.13**	*

RoA$_{I}$: root opening angle measure by Image J, RA: root area, AcH: area of the convex hul, Ff: filling factor, Depth: root depth, mW: maximum width, tpSL: total projected structure length, mFD: mean fractal dimension, NoG: number of gaps, mGZ: median gap size, mSW: median structure width.

Table 4.S4. Pearson correlations between traits assessed in field and traits measured with the REST software.

	DTH	DTA	RoA$_F$	SN	TN	PH	SRN	NRN	TRN	SDW	StmDW	Spk-DW	RDW	RSR	TPB
RoA$_I$	**0.10**	**0.11**	**-0.10**	-0.08	**-0.10**	0.09	-0.05	-0.02	-0.01	0.02	0.03	-0.02	0.01	-0.02	0.02
RA	**0.31**	**0.23**	0.08	**0.12**	**0.11**	**0.41**	0.02	**0.50**	**0.48**	**0.50**	**0.50**	**0.32**	**0.72**	**0.46**	**0.52**
AcH	0.00	-0.05	-0.06	0.02	0.04	**0.12**	0.05	**0.09**	**0.08**	**0.10**	**0.12**	0.00	**0.17**	**0.13**	**0.10**
Ff	**0.14**	**0.15**	0.07	0.04	0.03	**0.11**	-0.05	**0.25**	**0.23**	**0.19**	**0.16**	**0.18**	**0.31**	**0.23**	**0.19**
Depth	-0.02	-0.05	**-0.08**	0.03	0.06	**0.08**	0.07	**0.13**	**0.13**	0.08	0.08	0.04	**0.20**	**0.19**	0.09
mW	0.01	-0.04	-0.03	0.01	0.03	**0.09**	0.03	0.03	0.02	0.07	**0.09**	-0.03	**0.08**	0.04	0.07
tpSL	**0.21**	**0.15**	**0.08**	0.05	0.04	**0.33**	0.04	**0.42**	**0.41**	**0.40**	**0.40**	**0.24**	**0.64**	**0.45**	**0.41**
mFD	**0.18**	**0.17**	0.06	0.02	0.00	**0.14**	-0.01	**0.24**	**0.24**	**0.19**	**0.18**	**0.14**	**0.29**	**0.19**	**0.20**
NoG	0.04	-0.02	0.02	0.02	0.04	**0.18**	0.07	**0.39**	**0.37**	**0.27**	**0.28**	**0.16**	**0.52**	**0.40**	**0.29**
mGZ	**0.25**	**0.25**	**0.15**	-0.06	-0.03	**0.12**	-0.02	**-0.11**	**-0.12**	0.03	0.01	0.06	**-0.10**	**-0.15**	0.02
mSW	0.01	-0.04	-0.07	**0.19**	**0.21**	0.06	0.01	**0.23**	**0.24**	**0.18**	**0.18**	**0.14**	**0.21**	**0.12**	**0.19**

DTH: days to heading, DTA: days to anthesis, RoA$_F$: root opening angle measured by protractor, SN: spike number, TN: tiller number, PH: plant height, SRN: seminal root number. NRN: nodal root number, TRN: total root number, SDW: shoot dry weight, StmDW: tiller dry weight, SpkDW: spike dry weight, RDW: root dry weight, RSR: root to shoot ratio, TPB: total plant biomass, RoA$_I$: root opening angle measure by Image J, RA: root area, AcH: area of the convex hul, Ff: filling factor, Depth: root depth, mW: maximum width, tpSL: total projected structure length, mFD: mean fractal dimension, NoG: number of gaps, mGZ: median gap size, mSW: median structure width.

Table 4.S5. Root opening angle (RoA$_I$) (°) at seedling and adult plant (field) for the 37 genotypes.

Genotype	Seedling	Adult	Change
Chen's	97.13	54.40	42.73
Mansourah	91.91	49.37	42.53
Vitron	99.52	59.11	40.41
Ammar 6	86.64	48.61	38.03
MBB	84.62	47.24	37.38
Oued El Berd	89.77	52.69	37.09
Mexicalli75	84.81	51.18	33.63
Sahell 77	86.86	53.40	33.46
Megress	78.67	45.78	32.90
Waha	90.58	57.75	32.83
Bousselem	90.23	58.48	31.75
Beliouni	84.06	52.45	31.61
Cirta	83.25	51.70	31.55
Sitifis	85.87	55.12	30.75
Acsad 65	90.58	60.15	30.43
GTA dur	84.92	55.44	29.48
Massinissa	89.34	61.44	27.90
Capeiti	79.26	52.02	27.24
Oued Znatie 368	76.68	52.74	23.93
Boutaleb	76.84	53.25	23.59
Altar 84	72.80	49.39	23.41
Wahbi	80.71	58.53	22.18
Bidi 17	76.17	55.56	20.60
Korifla	68.00	51.61	16.39
Polonicum	65.84	49.71	16.13
ZB/FG	66.05	50.36	15.69
Simeto	73.46	60.38	13.08
INRAT 69	55.16	42.66	12.50
Hedba 3	61.00	48.92	12.08
Djenah Kotifa	73.87	62.25	11.62
Guemguoum R'khem	65.76	54.73	11.03
Ciccio	61.28	51.39	9.89
Core	72.98	67.33	5.65
Gloire de Mongolfier	54.58	50.98	3.59
Ofanto	56.42	57.08	-0.65
Langloise	60.84	61.82	-0.97
Montpellier	49.66	60.12	-10.47

Table 4.S6. Correlations between traits at seedlings and under greenhouse experiment (genotypes at adult stage).

	TRL	Surface	Volume	Diameter	PRL	SDW	MRA	MVA	LVA	RN
DTH	0.32	0.31	0.28	0.04	-0.17	0.28	-0.25	0.06	-0.35	0.24
PH	**0.52**	0.38	0.24	-0.35	0.05	0.37	**-0.51**	-0.38	**-0.52**	0.12
Depth	**-0.48**	**-0.48**	**-0.47**	-0.14	-0.07	-0.28	-0.02	-0.04	0.14	**-0.56**
RDW30	0.26	0.22	0.19	-0.13	-0.22	0.15	**-0.48**	-0.22	**-0.46**	0.22
RDW60	0.19	0.19	0.18	0.01	0.00	0.07	-0.31	-0.37	-0.16	0.29
RDW>60	-0.02	-0.06	-0.08	-0.22	-0.32	-0.20	-0.41	-0.33	-0.16	0.04
RDW	0.13	0.09	0.06	-0.21	-0.33	0.01	**-0.54**	-0.30	-0.42	0.16
SDW	0.15	0.07	0.00	-0.23	-0.16	-0.01	-0.35	-0.16	-0.29	-0.01
RSR	-0.07	-0.01	0.04	0.03	-0.41	-0.01	-0.37	-0.18	-0.21	0.15

DTH: days to heading, PH: plant height, Depth: root depth, RDW30: root dry weight up 30 cm of depth, RDW60: root dry weight between 30 and 60 cm, RDW>60: root dry weight at depth more than 60 cm. RDW: total root dry weight. RSR: root to shoot ratio. TRL: total root length, Surface: root surface, Volume: root volume, Diameter, PRL, SDW: shoot dry weight, MRA: mean root angle, MVA: maximum vertical angle, LVA: least vertical angle, RN: root number. Values in bold are significant correlations at 0.05 level.

Table 4.S7. Pearson correlations between traits recorded at seedlings and traits recorded at shovelomics experiment.

	Field traits													
	DTH	DTA	TN	SN	PH	SRN	NRN	TRN	SDW	StmDW	SpkDW	RDW	RSR	TPB
Seedling														
TRL	**0,43**	0.33	**-0,42**	-0.37	**0,60**	0,11	0,09	0,12	0,32	**0,39**	-0,14	0,30	0,09	0,32
Surface	**0,40**	0.31	**-0,41**	-0.35	**0,56**	0,18	0,05	0,08	0,32	0,38	-0,07	0,29	0,08	0,33
Volume	0,36	0.28	**-0,39**	-0.32	**0,49**	0,23	0,01	0,05	0,30	0,34	-0,03	0,27	0,06	0,30
Diameter	-0,01	0.02	-0,10	-0.04	0,01	0,18	-0,15	-0,11	0,07	0,03	0,17	0,06	0,00	0,07
PRL	0,42	0.34	-0,19	-0.11	0,40	-0,10	-0,08	-0,09	0,31	0,29	0,20	0,24	0,08	0,31
SDW	**0,52**	0.42	-0,25	-0.22	**0,63**	0,06	0,19	0,20	**0,57**	**0,57**	0,19	**0,49**	0,14	**0,57**
MRA	**-0,38**	-0.23	0,25	0.27	**-0,53**	-0,09	-0,19	-0,20	**-0,32**	**-0,45**	0,35	-0,32	-0,11	**-0,32**
MVA	**-0,51**	**-0.40**	0,32	0.30	**-0,57**	-0,18	-0,09	-0,10	**-0,29**	**-0,40**	0,26	-0,24	-0,04	**-0,29**
LVA	-0,30	-0.19	0,20	0.21	**-0,45**	0,06	-0,21	-0,21	-0,30	**-0,39**	0,21	-0,36	-0,18	-0,30
RN	0,02	0.05	-0,19	-0.21	0,03	**0,37**	0,20	0,23	-0,08	-0,06	-0,09	-0,01	0,06	-0,08

	REST traits										Root angle	
	AcH	RA	Ff	Depth	mW	tpSL	mFD	NoG	mGZ	mSW	RoAi	RoAF
TRL	0,18	**0,47**	**0,25**	0,22	0,14	**0,44**	0,26	0,30	0,22	0,16	**0,48**	0,16
Surface	0,31	**0,45**	0,13	**0,34**	0,23	**0,43**	0,12	0,27	0,18	0,09	**0,53**	0,14
Volume	0,39	**0,41**	0,03	0,41	0,28	0,40	0,01	0,22	0,14	0,02	**0,54**	0,11
Diameter	0,45	0,08	-0,30	0,46	0,31	0,10	-0,36	-0,05	-0,08	-0,20	0,25	-0,01
PRL	0,38	**0,46**	0,01	**0,37**	0,34	**0,38**	-0,06	0,11	0,38	0,08	0,27	0,21
SDW	0,39	**0,61**	0,12	0,39	0,33	**0,57**	0,14	**0,39**	0,21	0,12	0,42	0,27
MRA	-0,15	**-0,32**	-0,21	-0,04	-0,14	-0,28	**-0,32**	-0,27	0,00	-0,17	-0,24	-0,21
MVA	-0,28	**-0,32**	-0,10	-0,18	-0,24	-0,28	-0,17	-0,15	**-0,16**	0,01	-0,20	-0,37
LVA	-0,07	**-0,42**	-0,37	-0,02	-0,06	-0,38	**-0,44**	-0,41	0,01	-0,29	-0,27	-0,12
RN	-0,26	0,00	0,23	-0,22	-0,17	0,05	0,23	0,13	0,11	0,03	0,02	-0,13

TRL: total root length, Surface: root surface, Volume: root volume, Diameter, PRL, SDW: shoot dry weight, MRA: mean root angle, MVA: maximum vertical angle, LVA: least vertical angle, RN: root number. DTH: days to heading, DTA: days to anthesis, TN: tiller number, SN: spike number, PH: plant height, SRN: seminal root number, NRN: nodal root number, TRN: total root number, SDW: shoot dry weight, TDW: tiller dry weight. SpkDW: spike dry weight, RDW: root dry weight, RSR: root to shoot ratio, TPB: total plant biomass, AcH: area of the convex hul, RA: root area, Ff: filling factor, Depth: root depth. mW: maximum width, tpSL: total projected structure length, mFD: mean fractal dimension, NoG: number of gaps, mGZ: median gap size, mSW: median structure width. RoAI: root opening angle measure by Imag J. RoAF: root opening angle measured by protractor, Values in bold are significant correlations at 0.05 level.

Table 4.S8. Correlations performed with adult genotypes under greenhouse for traits recorded under greenhouse and in shovelomics experiment.

	Field traits													
	DTH	DTA	TN	SN	PH	SRN	NRN	TRN	SDW	StmDW	SpkDW	RDW	RSR	TPB
Greenhouse														
DTH	0.19	0.12	**-0.66**	**-0.79**	0.29	0.02	-0.33	-0.32	-0.05	0.13	**-0.64**	0.07	0.08	-0.05
PH	**0.46**	**0.46**	-0.33	-0.45	**0.64**	-0.10	0.35	0.35	0.30	0.40	-0.28	**0.57**	**0.51**	0.32
Depth	-0.08	-0.09	0.07	-0.00	-0.31	-0.10	-0.17	-0.21	-0.35	-0.28	-0.28	-0.17	0.12	-0.34
RDW30	0.41	0.38	**-0.58**	**-0.68**	**0.49**	0.12	0.15	0.19	0.33	0.45	-0.35	0.43	0.25	0.34
RDW60	0.28	0.25	-0.24	-0.38	0.26	0.32	0.20	0.22	0.12	0.19	-0.25	0.09	0.12	0.12
RDW>60	0.26	0.20	-0.34	**-0.45**	0.18	0.28	-0.01	0.01	-0.08	0.06	**-0.50**	-0.10	0.01	-0.08
RDW	0.38	0.31	**-0.53**	**-0.68**	0.42	0.23	0.08	0.12	0.23	0.39	**-0.52**	0.26	0.15	0.23
SDW	0.17	0.15	-0.32	**-0.48**	0.18	0.11	0.05	0.06	-0.07	0.06	-0.45	0.07	0.18	-0.07
RSR	0.37	0.30	**-0.52**	**-0.57**	0.31	0.31	0.01	0.06	0.18	0.33	**-0.47**	0.20	0.07	0.19

	REST traits										**Root angle**	
	AcH	RA	Ff	Depth	mW	tpSL	mFD	NoG	mGZ	mSW	$\mathrm{RoA_i}$	$\mathrm{RA_F}$
DTH	-0.28	0.07	0.31	-0.34	-0.09	-0.01	0.38	0.08	-0.01	0.30	0.38	-0.02
PH	-0.39	**0.46**	**0.77**	-0.14	-0.44	0.41	**0.79**	0.45	0.09	0.26	0.29	0.33
Depth	-0.06	-0.20	-0.09	-0.26	0.09	-0.20	-0.05	-0.10	-0.12	-0.01	-0.12	-0.14
RDW30	-0.27	0.33	**0.53**	-0.14	-0.31	0.25	**0.59**	0.29	0.04	0.28	0.32	0.29
RDW60	-0.38	0.07	0.37	-0.31	-0.32	-0.02	**0.47**	0.01	0.21	0.25	0.08	-0.04
RDW>60	**-0.53**	-0.17	0.24	-0.36	**-0.49**	-0.22	0.30	-0.13	0.01	0.13	0.10	-0.02
RDW	-0.38	0.15	0.43	-0.36	-0.30	0.05	**0.55**	0.11	0.05	0.30	0.24	0.15
SDW	**-0.70**	-0.05	**0.53**	-0.33	**-0.68**	-0.09	**0.53**	0.10	-0.24	0.26	0.28	-0.13
RSR	0.16	0.17	0.00	-0.15	0.24	0.10	0.14	0.07	0.20	0.10	0.13	0.30

DTH: days to heading, PH: plant height, Depth: root depth, RDW30: root dry weight up 30 cm of depth. RDW60: root dry weight between 30 and 60 cm, RDW>60: root dry weight for depth more than 60 cm. RDW: total root dry weight, SDW: shoot dry weight. RSR: root to shoot ratio. DTA: days to anthesis, TN: tiller number, SN: spike number, SRN: seminal root number, NRN: nodal root number, TRN: total root number, TDW: tiller dry weight. SpkDW: spike dry weight. RDW: root dry weight. RSR: root to shoot ratio. TPB: total plant biomass. RA: root area, AcH: area of the convex hul, Ff: filling factor. mW: maximum width. tpSL: total projected structure length. mFD: mean fractal dimension. NoG: number of gaps. mGZ: median gap size. mSW: median structure width, $\mathrm{RoA_I}$: root opening angle measure by Imag J, $\mathrm{RoA_F}$: root opening angle measured by protractor, Values in bold are significant correlations at 0.05 level.

Figure 4.S1. General view of durum wheat plants grown in pipe-pots.

Figure 4.S2. Washed root system of durum wheat plant in an open pipe-pot.

Figure 4.S3. Drip irrigation system installed during durum wheat shovelomics experiment.

Figure 4.S4. Root system of excavated rows (A) and individual durum wheat plants for cultivar, Simeto (B) and landrace, Djenah Khotifa (C).

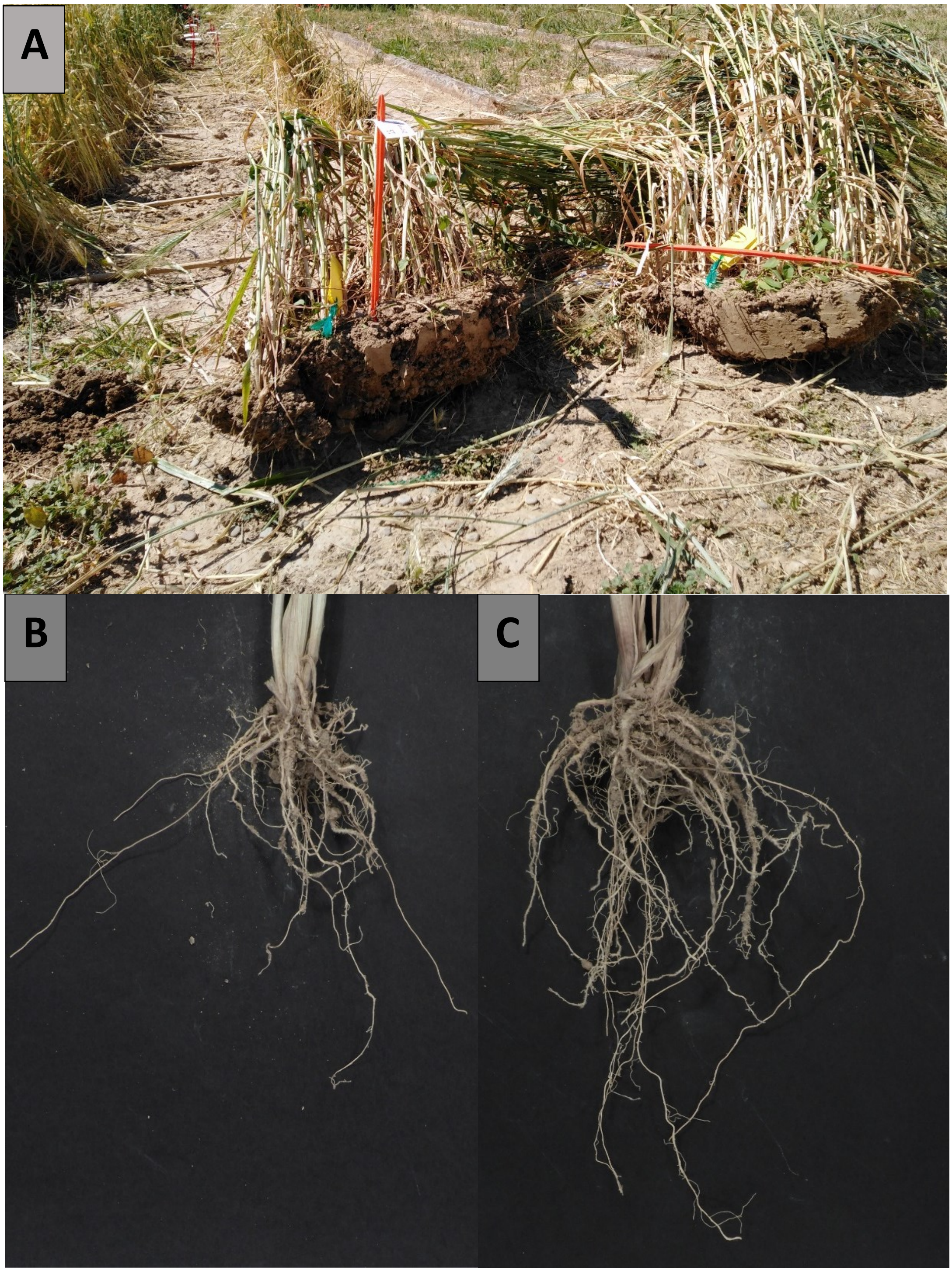

Figure 4.S5. REST output image showing the original image (left) and its segmented (binary) form (right) with the arc where the outermost angle is determined (in red) and the values for the angle form the horizontal to the left (here 37.5°) and the right arm (here 52.2°), the opening angle (here 90.3°) and the 90% region of interest (in blue).

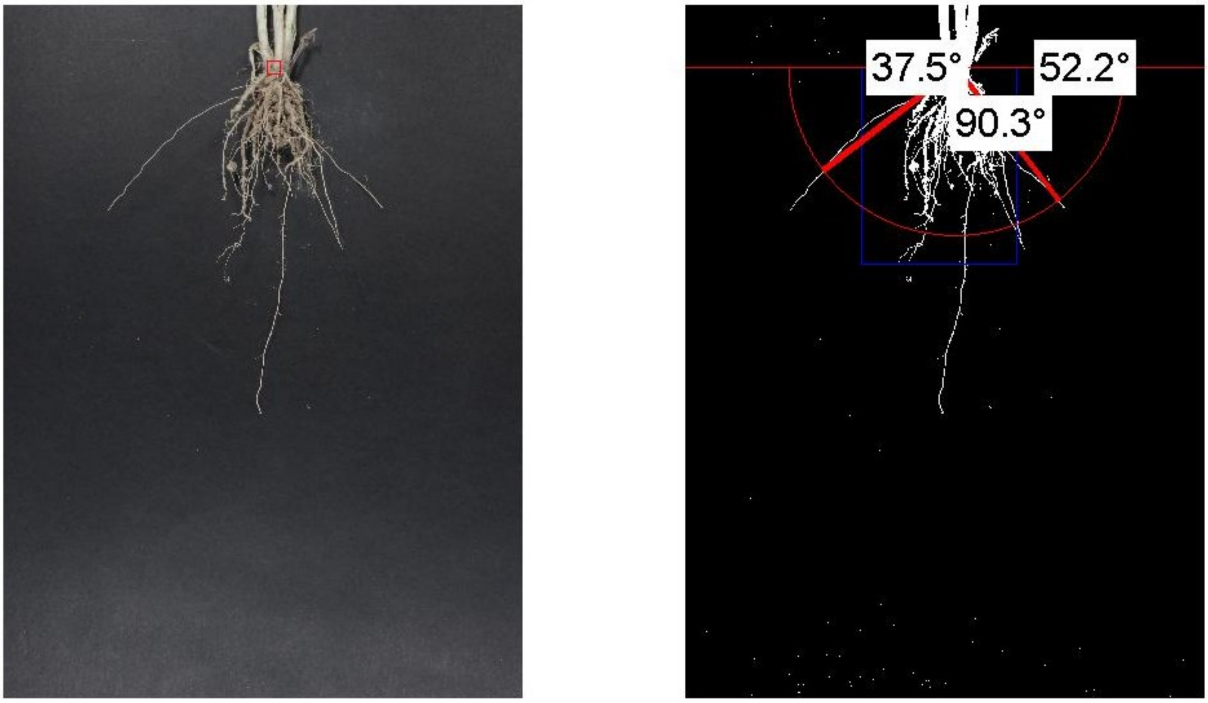

Table 5.S1. List of the 30 varieties of durum wheat evaluated during the two cropping seasons.

Nº	**Genotype**	**Abbreviation**	**Type/Pedigree**	**Origin**	**Year of release**
1	Bidi 17	Bid	Landrace	Algeria	1930
2	Gloire de Montgolfier	Glo	Landrace	Algeria	1960
3	Guemgoum R'khem	Gue	Landrace	Algeria	1960
4	Hedba 3	Hed	Landrace	Algeria	1921
5	Langlois	Lan	Landrace	Algeria	1930
6	Mohammed Ben Bachir	MBB	Landrace	Algeria	1930
7	Montpellier	Mon	Landrace	Algeria	1965
8	Oued Zenati 368	OZ	Landrace	Algeria	1936
9	Acsad 65	Acs	Gerardo-vz-469/3/Jori-1//Nd-61-130/Leeds	ACSAD	1984
10	Altar 84	Alt	Ruff/Flamingo,mex//Mexicali-75/3/Shearwater	CYMMIT	1984
11	Bousselem	Bou	Heider//Martes/Huevos de oro	ICARDA	2007
12	Boutaleb	Bot	Hedba 3/Ofanto	Algeria	2013
13	Capeiti	Cap	Eiti*6/Senatore-Cappelli	Italy	1940
14	Cirta	Cir	Hedba-3/Gerardo-vz-619	Algeria	2000
15	GTA Dur	GTA	Crane/4/Polonicum PI185309//T.glutin enano/2* Tc60/3/Gll	CIMMYT	1972
16	INRAT 69	INR	Mahmoudi/(bd-2777)Kyperounda	Tunisia	1969
17	Korifla	Kor	Durum-dwarf-s-15/Crane//Geier	ICARDA	1987
18	Mansourah	Man	Bread wheat/MBB	Algeria	2012
19	Massinissa	Mas	Ofanto/Bousselem	Algeria	2012
20	Megress	Mgs	Ofanto/Waha//MBB	Algeria	2007
21	Mexicali 75	Mex	Gerardo-vz-469/3/Jori(sib)//Nd-61-130/Leeds	CIMMYT	1975
22	Ofanto	Ofa	Ademelio/Appulo	Italy	1990
23	Oued El Berd	OEB	Gta dur/Ofanto	Algeria	2013
24	Polonicum	Pol	Triticum polinicum/Zenati boulette 1953-58	France	1973
25	Sahell	Sah	Cit"s"/4/Tace/4*tc//2*zb/wls/3/aa"s''/5/Ruff"s"/Albe"s"	CYMMIT	1977
26	Simeto	Sim	Capeiti-8/Valnova	Italy	1988
27	Sitifis	Sit	Bousselam/Ofanto	Algeria	2011
28	Vitron	Vit	Turkey77/3/Jori/Anhinga//Flamingo	Spain	1987
29	Waha	Wah	Plc/Ruff//Gta's/3/Rolette	ICARDA	1986
30	ZB×Fg	ZBF	Zb/fg''s'' lk/3/ko 120/4/Ward cs 10604	Algeria	1983

*: Backross

Table 5.S2. Pearson coefficients for the assessed traits under the cropping season 2016/2017 and 2017/2018, unfavorable and favorable environment, respectively.

Non-drought

Drought	Emrg	PH	SNM^2	GNS	GNM^2	DTH	TKW	StemBio	SpkBio	TotBio	SWM^2	SYLD	HYLD	HI	FLL	FLW	SF	FLFW	FLDW	SLA	RWC %	LRM	LRN	CT
Emrg	-0.07	-0.08	-0.18	-0.17	**-0.27**	-0.03	0.01	**-0.31**	**-0.32**	**-0.36**	**-0.37**	**-0.25**	-0.14	-0.02	0.12	0.14	0.16	0.04	0.13	0.07	0.03	0.13	0.19	0.13
PH	-0.18	**0.70**	-0.18	-0.02	-0.15	**0.71**	-0.19	**0.29**	0.01	0.22	-0.15	**-0.24**	**-0.38**	**-0.55**	**0.55**	0.14	**0.47**	**0.31**	**0.27**	**0.44**	-0.19	0.04	0.15	-0.07
SNM^2	**0.45**	0.01	0.06	-0.20	**0.65**	**-0.24**	-0.07	**0.63**	**0.59**	**0.71**	**0.82**	**0.65**	**0.45**	0.18	**-0.27**	-0.09	**-0.24**	-0.12	**-0.25**	-0.01	**-0.29**	-0.13	**-0.24**	0.03
GNS	-0.19	0.13	-0.08	**0.24**	**0.60**	-0.08	**-0.23**	0.18	**-0.40**	-0.03	0.08	**0.55**	**0.30**	**0.54**	0.13	-0.03	0.05	0.11	0.10	-0.08	0.02	0.20	0.12	-0.01
GNM^2	0.17	0.11	**0.60**	**0.74**	0.09	**-0.24**	-0.23	**0.66**	0.17	**0.56**	**0.73**	**0.96**	**0.61**	**0.55**	-0.12	-0.11	-0.16	-0.03	-0.14	-0.07	-0.21	0.05	-0.10	0.03
DTH	-0.09	**0.80**	-0.03	0.01	-0.01	**0.71**	-0.07	0.06	0.04	0.06	-0.16	**-0.30**	**-0.38**	**-0.38**	**0.35**	-0.01	**0.24**	0.11	0.11	**0.28**	0.03	-0.03	0.03	-0.06
TKW	**-0.28**	0.19	-0.20	0.07	-0.08	**0.24**	**0.36**	-0.14	-0.03	-0.12	0.00	0.04	-0.06	0.18	-0.04	-0.07	-0.09	-0.06	0.07	**-0.30**	-0.02	0.10	0.08	0.07
StmBio	0.17	**0.48**	**0.51**	**0.23**	**0.52**	**0.50**	**0.30**	0.13	**0.45**	**0.93**	**0.70**	**0.62**	**0.42**	-0.20	0.05	0.12	0.10	0.15	0.02	0.16	**-0.33**	-0.06	-0.13	-0.05
SpkBio	0.16	**0.25**	**0.64**	**0.42**	**0.75**	0.20	0.12	**0.81**	-0.01	**0.75**	**0.77**	0.14	**0.32**	**-0.25**	**-0.26**	0.08	-0.11	-0.06	-0.16	0.08	0.00	**-0.25**	**-0.30**	-0.08
TotBio	0.17	**0.44**	**0.56**	**0.28**	**0.60**	**0.44**	**0.26**	**0.99**	**0.89**	0.05	**0.84**	**0.52**	**0.44**	**-0.25**	-0.07	0.12	0.03	0.08	-0.05	0.15	**-0.25**	-0.15	-0.22	-0.07
SWM^2	0.09	**0.22**	**0.57**	**0.67**	**0.92**	0.13	**0.26**	**0.72**	**0.88**	**0.78**	0.03	**0.74**	**0.62**	**0.24**	**-0.27**	-0.02	-0.20	-0.07	-0.19	-0.05	-0.14	-0.12	**-0.26**	-0.02
SGY	0.06	0.19	**0.50**	**0.73**	**0.92**	0.09	**0.30**	**0.63**	**0.77**	**0.68**	**0.98**	0.06	**0.62**	**0.64**	-0.14	-0.11	-0.19	-0.03	-0.12	-0.16	-0.22	0.08	-0.08	0.07
HGY	0.02	0.01	0.21	**0.37**	**0.42**	-0.07	0.12	**0.28**	**0.43**	**0.33**	**0.46**	**0.45**	**0.30**	**0.37**	**-0.23**	0.04	-0.15	-0.03	-0.10	-0.11	-0.11	0.01	-0.17	-0.04
HI	-0.09	**-0.22**	0.06	**0.65**	**0.56**	**-0.33**	0.09	**-0.26**	0.09	-0.18	**0.44**	**0.56**	**0.26**	0.17	-0.19	**-0.28**	**-0.32**	-0.20	-0.17	**-0.33**	0.04	0.14	0.02	0.13
FLL	**-0.41**	**0.51**	-0.15	0.06	-0.05	**0.52**	0.20	0.20	0.13	0.19	0.07	0.05	-0.06	-0.18	**0.64**	0.20	**0.79**	**0.63**	**0.72**	**0.25**	-0.12	**0.38**	**0.39**	-0.09
FLW	-0.16	**0.28**	-0.13	0.13	0.02	**0.35**	0.09	**0.25**	0.11	**0.22**	0.08	0.06	-0.05	-0.15	**0.54**	**0.40**	**0.76**	**0.67**	**0.64**	**0.32**	-0.16	0.04	-0.02	-0.13
SF	**-0.35**	**0.47**	-0.17	0.10	-0.03	**0.51**	0.18	**0.25**	0.13	**0.23**	0.08	0.06	-0.05	-0.20	**0.92**	**0.82**	**0.43**	**0.84**	**0.87**	**0.39**	-0.16	**0.26**	**0.23**	-0.15
FLFW	**-0.36**	**0.45**	-0.17	0.10	-0.02	**0.47**	0.14	**0.22**	0.09	0.19	0.06	0.04	-0.07	-0.20	**0.89**	**0.72**	**0.94**	**0.30**	**0.83**	0.12	-0.18	0.06	0.06	-0.20
FLDW	**-0.39**	**0.39**	-0.20	0.15	-0.01	**0.42**	**0.26**	**0.24**	0.17	**0.23**	0.14	0.11	-0.04	-0.13	**0.89**	**0.74**	**0.94**	**0.92**	**0.46**	-0.12	-0.19	**0.24**	0.17	-0.10
SLA	0.13	**0.24**	0.10	-0.16	-0.07	**0.25**	-0.18	0.04	-0.11	0.01	-0.14	-0.15	-0.05	-0.17	0.10	**0.25**	0.19	0.05	-0.16	**0.29**	0.02	0.11	0.17	-0.12
RWC	**-0.26**	**0.30**	-0.02	-0.02	-0.05	**0.35**	0.10	**0.22**	0.13	0.21	0.04	0.00	0.07	**-0.24**	**0.43**	**0.28**	**0.42**	**0.39**	**0.33**	**0.24**	-0.08	-0.08	-0.08	-0.16
LRM	**-0.28**	0.12	-0.09	0.02	-0.05	0.14	0.12	0.13	0.07	0.12	0.03	0.01	0.08	-0.12	**0.44**	**0.45**	**0.51**	**0.48**	**0.48**	0.09	**0.25**		**0.74**	0.07
LRN	-0.18	0.19	0.05	-0.01	0.02	0.21	0.15	**0.21**	0.11	0.20	0.10	0.09	-0.09	-0.13	**0.37**	**0.48**	**0.47**	**0.50**	**0.46**	0.03	**0.29**	**0.71**		-0.06
CT	0.09	**-0.22**	-0.08	0.10	0.05	-0.17	0.00	-0.09	-0.10	-0.10	0.00	0.04	0.07	0.16	**-0.25**	**-0.25**	**-0.29**	**-0.29**	**-0.31**	0.04	**-0.26**	-0.14	-0.15	0.01

Emg (plant/m2): Emergence, PH (cm): Plant height, SNM^2: Spike number per area, GNS: Grain number per spike, GNM^2: Grain number per area, DTH (day): Days to heading, TKW (g): Thousand kernel weight, HI: Harvest index, SpkBio (g/m2): Spike biomass, Biomass (g/m2): Straw biomass, SWM^2 (g/m2): Spike weight, GY (g/m2): Grain yield, HGY (g/m2): Harvested grain yield, HI: Harvest index, FLA (mm2): Flag leaf area, FLL (cm): Flag leaf length, FLW (cm): Flag leaf width, FLFW (mg): Flag leaf fresh weight, FLDW (mg): Flag leaf dry weight, SLA (mm2/mg): Specific leaf area, LRM: Leaf rolling in morning, LRN: Leaf rolling at noon, RWC (%): Relative water content, , CT (°C): Canopy temperature,
Values in bold are different from 0 with a significance level alpha=0.05. Cells in grey are the correlations between drought and wet conditions for the corresponding trait.

Table 5.S3. Harvested grain yield for drought and non-drought cropping season for 30 durum wheat varieties including cultivars and landraces.

Varieties	Type	HGY, g/m^2 (drought)	HGY, g/m^2 (non-drought)
Gloire de Montgolfier	Landrace	147.86 bcdef	374.97 fghij
Guemgoum R’khem	Landrace	130.63 ef	291.63 j
Langlois	Landrace	155.08 abcde	322.75 ij
Bidi 17	Landrace	167.86 abcde	419.41 defghij
Hedba 3	Landrace	165.63 abcde	445.52 bcdefghi
Mohammed Ben Bachir	Landrace	147.30 bcdef	466.70 abcdefgh
Montpellier	Landrace	138.97 def	486.08 abcdefg
Oued Znatie 368	Landrace	181.19abcd	359.97 ghij
INRAT 69	Cultivar	105.63 f	441.08 cdefghi
Acsad 65	Cultivar	150.08 abcdef	456.08 bcdefghi
Altar 84	Cultivar	154.52 abcde	498.02 hij
Bousselem	Cultivar	151.74 abcde	541.08 abcde
Boutaleb	Cultivar	173.41 abcde	402.75 efghij
Capeiti	Cultivar	145.63 cdef	464.38 abcdefghi
Mansourah	Cultivar	163.41 abcde	401.63 efghij
Ofanto	Cultivar	145.08 def	539.97 abcde
Oued El Berd	Cultivar	181.19 abcd	407.75 efghij
Sahel	Cultivar	168.41 abcde	453.86 bcdefghi
Simeto	Cultivar	146.74 bcdef	505.52 abcdef
Waha	Cultivar	170.63 abcde	474.41 abcdefgh
ZB×Fg	Cultivar	158.97 abcde	454.41 bcdefghi
Cirta	Cultivar	181.19 abcd	584.97 ab
GTA Dur	Cultivar	178.97 abcd	606.63 a
Korifla	Cultivar	191.74 ab	524.41 abcde
Massinissa	Cultivar	182.30 abcd	519.41 abcde
Megress	Cultivar	189.80 abcd	559.97 abcd
Mexicali 75	Cultivar	194.52 a	584.41 abc
Polonicum	Cultivar	182.86 abcd	477.19 abcdefg
Sitifis	Cultivar	194.52 a	537.19 abcde
Vitron	Cultivar	191.19 abc	532.75 abcde

Different letters indicate that means are significantly different at 0.05 level of significance.

Table 5.S4. Result of stepwise regression analysis for sample grain yield in durum wheat genotypes under normal and stress conditions.

Normal	**Parameters**					**Traits**								
	Estimate	**s.e.**	**t (68)**	**t pr.**	**R aduj**	**GNM**	**TKW**	**DTH**	**Emg**	**FLFW**	**FLL**	**HI**	**CT**	**SLA**
Constant	-345.1	44.400	-7.78	<.001										
GNM (X1)	0.05	0.001	76.77	<.001	93.27	x								
TKW (X2)	7.57	0.304	24.90	<.001	99.25	x	x							
DTH (X3)	-0.72	0.303	-2.38	0.02	99.35	x	x	x						
Emg (X4)	0.07	0.029	2.31	0.024	99.41	x	x	x	x					
FLFW (X5)	0.08	0.026	3.01	0.004	99.42	x	x	x	x	x				
FLL (X6)	-1.59	0.691	-2.30	0.025	99.44	x	x	x	x	x	x			
HI (X7)	34.20	18.300	1.86	0.067	99.46	x	x	x	x	x	x	x		
CT (X8)	0.45	0.424	1.05	0.298	99.46	x	x	x	x	x	x	x	x	
SLA (X9)	0.87	1.090	0.80	0.426	99.46	x	x	x	x	x	x	x	x	x
Final model	**Y= -345.1 + 0.05 (X1) + 7.57 (X2) - 0.72 (X3) + 0.07(X4) + 0.08 (X5) - 1.59 (X6) + 34.2 (X7) + 0.45 (X8) + 0.87(X9)**													
Stress						**GNM**	**TKW**	**Biomass**	**HI**	**SLA**	**LRM**	**RWC**		
Constant	-136.02	8.950	-15.20	<.001										
GNM (X1)	0.03	0.001	26.40	<.001	86.37	x								
TKW (X2)	3.53	0.161	21.96	<.001	99.29	x	x							
Biomass (X3)	0.06	0.016	3.97	<.001	99.33	x	x	x						
HI (X4)	28.32	8.540	3.32	0.001	99.40	x	x	x	x					
SLA (X5)	-1.17	0.399	-2.94	0.004	99.44	x	x	x	x	x				
LRM (X6)	0.98	0.429	2.27	0.026	99.46	x	x	x	x	x	x			
RWC (X7)	0.08	0.079	1.07	0.289	99.47	x	x	x	x	x	x	x		
Final model	**Y= -136.02 + 0.03(X1) + 3.53(X2) + 0.06 (X3) + 28.32 (X4)-1.17(X5) +0.98 (X6) + 0.08 (X7)**													

Table 5.S5. Drought susceptibility index (DSI) of 30 durum wheat genotypes and their type ranked from the most tolerant to the most susceptible ones.

Genotype	**Type**	**DSI**
Guemgoum R'khem	Landrace	0,70
Oued Zenatie 368	Landrace	0,77
Bidi 17	Landrace	0,80
Vitron	Cultivar	0,88
Hedba 3	Landrace	0,90
MBB	Landrace	0,91
Cirta	Cultivar	0,91
Altar 84	Cultivar	0,93
GTA Dur	Cultivar	0,93
Korifla	Cultivar	0,94
Boutaleb	Cultivar	0,96
Langlois	Landrace	0,96
Massinissa	Cultivar	0,97
Waha	Cultivar	0,98
Oued El Berd	Cultivar	1,00
Polonicum	Cultivar	1,00
Gloire de Montgolfier	Landrace	1,01
ZB×Fg	Cultivar	1,01
Simeto	Cultivar	1,02
Mansourah	Cultivar	1,03
Bousselem	Cultivar	1,05
Sitifis	Cultivar	1,06
Acsad 65	Cultivar	1,06
Mexicali 75	Cultivar	1,06
Sahel	Cultivar	1,08
Montpellier	Landrace	1,12
Megress	Cultivar	1,12
INRAT 69	Cultivar	1,16
Capeiti	Cultivar	1,17
Ofanto	Cultivar	1,17
Group	Cultivar	1,02
Group	Landrace	0,90

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Assessment of Early Drought Tolerance of Algerian Durum Wheat Reveals Superiority of Landraces

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VIGOROUS seedling growth is important for good crop establishment, particularly under drought conditions. Our study was set out to identify useful traits and genotypes to enhance early drought tolerance of durum wheat. Two experiments were carried out. In the first one, thirty-five genotypes (Landrace and improved) were tested in a phytotron at germination and early seedling stages, subjected to three osmotic stress levels induced by polyethylene glycol PEG 6000 (0, -3, -6 bar). The second experiment was conducted in the field, with 27 out of the 35 genotypes. Root and shoot traits were measured at seedling stage in both experiments. High PEG 6000 treatment decreased final germination percentage (FGP) by 2.7% and delayed the time to reach 50% germination (t50) by 2.9h. Shoot length was the trait most affected by drought (40% reduction) as compared with other root traits, which even increased under drought, like root to shoot length ratio, root to shoot weight ratio, root dry weight and root number. Coleoptile length (CL) showed a contrasting relationship with other traits, it was negatively correlated in general under no stress, but with positive correlations under stress. Based on drought susceptibility index (DSI), Algerian wheat landraces were the most tolerant compared to modern genotypes. Correlations between traits measured in field and controlled conditions were low. CL could be a potential trait for screening drought tolerant genotypes. Algerian wheat landraces presented a clearly distinct ability for early drought tolerance, and could be a good resource for breeding programs.

Keywords: Early growth, Polyethylene glycol, Durum wheat seedlings, Drought susceptibly index.

Introduction

In Mediterranean-type environments, sowing is typically practiced when soil moisture is ensured by the first rain (Rebetzke et al., 2008). Early growth vigor has been proposed as a trait that could enhance crop water-use efficiency and yield in these environments (López-Castañeda & Richards, 1994; Coleman et al., 2001). One of its possible benefits could occur through increased root growth early in the season (Liao et al., 2004). Early drought restricts germination (Misra et al., 1990), emergence and early seedling growth (Al-Karaki, 1998), which may lead to crop failure in the West Asia and North Africa (WANA)-region (Abdel-Ghani et al., 2015). In regions characterized by short periods of appropriate soil moisture, seeds with high germination percentage may be advantageous for ensuring a good plant establishment (Brar et al., 1991). Drought stress is a stage specific phenomenon, as it has been described that tolerance at plant establishment phase is poorly correlated with tolerance at other stages (Mano et al, 1996; González et al., 2008;

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Szira et al., 2008). Selection for drought tolerance at early growth stage has been frequently attempted using PEG 6000 to induce water stress, without causing significant physiological damage to crop plants (Carpita et al., 1979; Rauf et al., 2007).

Despite the importance of root system for acquisition of water and nutrients (Blum, 1997; Blum, 2009; Ehdaie et al., 2012), plant breeding focused for a long time almost solely on the above-ground traits, while root traits were relatively neglected because of the practical difficulties of phenotyping at a scale useful to perform selection (Waines & Ehdaie, 2007). In the last decade, more attention has been paid to root phenotyping (Bengough et al., 2004; Nagel et al., 2012; Richard et al., 2015; York et al., 2018), thanks to novel phenotyping methods. Among these, root attributes at seedling stage are important for screening genotypes for early drought tolerance (Chloupek et al., 2010; Sayed, 2011). Some breeders propose to select genotypes with higher root volume combined with maximum length of seminal and adventitious roots (Richards & Passioura, 1981; Grando & Ceccarelli, 1995). Jia et al. (2019) indicated that root system depth and root spread angle are valuable candidate traits for increasing grain yield. Root to shoot ratio and root length at early stages of plant development could also be valuable attributes for improving yield under arid and semi-arid conditions (Dhanda et al., 2004; Shahbazi et al., 2012). Coleoptile length (CL) has also been proposed as an important trait for drought tolerance at plant seedling stage: Long coleoptiles allow deep sowing, which is an adequate practice in water-limited environments in which topsoil dries up fast (Mahdi et al., 1998; Schillinger et al., 1998), enabling growers a longer time window to perform sowing with optimum soil moisture (Gan et al., 1992).

Wheat landraces have been widely replaced by modern varieties (Khlestkina et al., 2004; Reif et al., 2005; Bonnin et al., 2014). Nevertheless, they are still preferred over modern wheats in several parts of the world, mainly for their stable yields in low input conditions, prized end-use qualities, and high straw yield. Farm size, lack of machinery, and lack of fertilizer are also important constraints in growing modern wheats (Karagöz, 2014). Varietal substitution has led to reduction of germination-related traits like shoot, coleoptile and root length and seedling vigor in Iranian modern varieties, compared to landraces (Ramshini et al., 2016). Bektas et al. (2016) found that shoot biomass, shallow and deep root weight, number of tillers per plant and plant height were significantly greater in landraces than in modern varieties. In several cases, winter cereal landraces have shown better performances than modern varieties, usually under challenging environmental conditions (Yahiaoui et al., 2014; Erice et al., 2019). When root systems were compared, an Algerian wheat landrace (Pelissier) had more root growth than a widely grown modern variety (Ashe et al., 2017).

All these evidences highlight the importance of early drought tolerance, and the potential of landraces to contribute favorable traits in this respect. The aim of our research was to identify traits and genotypes of importance in early stress tolerance, and to explore the potential of Algerian landraces for drought tolerance breeding.

Materials and Methods

Plant material

Thirty-five durum wheat genotypes (landraces and modern cultivars) from different countries (Algeria, France, Italy, Spain, Tunisia), and international breeding programs addressing semi-arid areas, namely the International Maize and Wheat Improvement Center (CYMMIT), the International Center for Agricultural Research in the Dry Area (ICARDA) and the Arab Center for the Studies of Arid zones and Dry lands (ACSAD), were chosen for this study (Table 1). Most of these genotypes have been widely cultivated in Algeria. There are reports of cultivation of the oldest genotype Hedba3 in 1921, whereas the newest ones (Boutaleb and Oued El Berd) were released by the Technical Institute of Field Crops (ITGC, Sétif, Algeria) in 2013, thus this set of genotypes is spanning more than 8 decades (Table 1).

Phytotron experiment

The experiment was conducted at the Biotechnology Research Center (CRBt), Constantine, Algeria. Fifteen healthy seeds of the same size of each genotype, were weighted, surface sterilized with 0.5 % of sodium hypochlorite (NaClO) and rinsed for six times with distilled water. They were then germinated on Whatman (type1) filter paper soaked with 10 ml of PEG 6000 solutions in Petri dishes. PEG 6000 was used to induce osmotic stress at two levels, -3 and -6 bar, following the method suggested by Michel & Kaufmann (1973), while distilled water without PEG 6000 was used as control treatment. Petri dishes were transferred to a phytotron for 8 days, in darkness, at constant 25°C and 70% relative humidity. The experimental design was a split plot design with two replications (each consisting of 15 seeds of a genotype in a Petri dish), where the whole plot was PEG treatment and the sub-plot was the genotype.

TABLE 1. Type, origin and date of release information's of the 35 genotypes of durum wheat used in this study.

Genotype	Abv	Type	Origin	Year of release	Phytotron	Field
Beliouni	Bel	Landrace	Algeria	1958	×	
Bidi 17	Bid	Landrace	Algeria	1930	×	×
Djenah Khotifa	Dje	Landrace	North Africa	1955	×	
Gloire de Mongolfier	Glo	Landrace	Algeria	1960	×	×
Guemgoum R'khem	Gue	Landrace	Algeria	1960	×	×
Hedba 3	Hed	Landrace	Algeria	1921	×	×
Mohammed Ben Bachir	MBB	Landrace	Algeria	1930	×	×
Oued Zenati 368	OZ	Landrace	Algeria	1936	×	×
Langloise	Lan	Landrace	Algeria	1930	×	×
Sbaa Aldjia	Sba	Landrace	Tunisia	-	×	
Acsad 65	Acs	Improved	ACSAD	1984	×	×
Altar	Alt	Improved	CYMMIT	1984	×	×
Aures	Aur	Improved	Algeria	2013	×	
Boutaleb	Bot	Improved	Algeria	2013	×	
Capeiti	Cap	Improved	Italy	1940	×	×
Cirta	Cir	Improved	Algeria	2000	×	×
El Maather	ELM	Improved	Algeria	-	×	
GTA Dur	GTA	Improved	CIMMYT	1972	×	×
INRAT 69	INR	Improved	Tunisia	1969	×	×
Korifla	Kor	Improved	ICARDA	1987	×	×
Mansourah	Man	Improved	Algeria	2012	×	×
Massinissa	Mas	Improved	Algeria	2012	×	×
Megress	Mgs	Improved	Algeria	2007	×	×
Mexicali 75	Mex	Improved	CIMMYT	1975	×	×
Miki-2	Mik	Improved	ICARDA	2008	×	
Montpellier	Mon	Improved	France	1965	×	×
Ofanto	Ofa	Improved	Italy	1990	×	×
Oued El Berd	OEB	Improved	Algeria	2013	×	×
Polonicum	Pol	Improved	France	1973	×	×
Simeto	Sim	Improved	Italy	1988	×	×
Sitifis	Sit	Improved	Algeria	2011	×	×
Tejdid	Tej	Improved	Algeria	-	×	
Vitron	Vit	Improved	Spain	1987	×	×
Waha	Wah	Improved	ICARDA	1986	×	×
ZB × Fg	ZBF	Improved	Algeria	1983	×	×

×: Indicate the presence of the corresponding genotype in the experiment.

Germination date was recorded when the radicle reached at least 2mm in length. Germinated seeds were counted every 24h for 8 days. Final germination percentage (FGP) and the time needed to reach 50 % germinated seeds (t50) were recorded. Time to reach 50% germination was calculated based on the following formula proposed by Coolbear et al. (1984) and modified by Farooq et al. (2005):

$$t50= ti + [((N/ 2)-ni)\ (tj-ti)]/\ nj – ni$$

where N is the final number of seeds that germinated and ni and nj were the cumulative number of seeds germinated by adjacent counts at times ti and tj when ni < N/2 < nj

At the end of the experiment, seedlings were preserved in a 30% ethanol solution until the rest of the traits were recorded in five representative seedlings chosen from each Petri dish: mean value of shoot length (SL), coleoptile length (CL), root number (RN), total root length (TRL), maximum root length (MRL), root dry weight and shoot dry weight (RDW and SDW, respectively), and total plant biomass (TPB). Additionally, several indices were calculated: root to shoot ratio for weight and length (RSW and RSL respectively), seedling vigor index (SVI) and drought susceptibly index (DSI). The drought susceptibly index (DSI) for TPB was calculated according to Fischer & Maurer (1978) using the following formula, originally developed for yield:

$$DSI= (1-Y_D/Y_P))/\ (1-X_D/X_P))$$

where, YD corresponds to the mean genotypic TPB under stress, YP corresponds to the mean control TPB for each genotype, XD is the TPB mean of all genotypes under stress, and XP is the mean TPB of all genotypes under control conditions.

The SVI based on seedling weight (hereafter, SVI_W) was obtained using the following formula:

$$SVI_W= (RDW + SDW) \times FGP$$

The SVI based on seedling length (hereafter, SVI_L was calculated using the following formula (Abdul-Baki & Anderson, 1973):

$$SVI_L= (MRL + SL) \times FGP.$$

where, MRL: Maximum root length, SL: Shoot length, FGP: Final germination percentage

Field experiment

Twenty-seven out of the 35 wheat genotypes were sown on 28 Nov 2016 in a randomized complete block design with two replications under rainfed conditions. The rainfall throughout Nov was 29.7 l/m^2 for 7 days, so soil humidity was appropriate for seed germination. Sowing density was 300 seeds/m² in six row plots of 1.2m width and 2.5m long (3m²), at the Technical Institute of Field Crops (ITGC), Sétif, Algeria. Five seedlings per replicate were carefully harvested 10 days after emergence; roots were gently cleaned from soil by washing with tap water. The same traits measured in phytotron experiment were recorded in the field, except t50, SVI and DSI.

Data analyses

The analyses of variance were carried out by REML (Restricted Maximun Likelihood) procedure of Genstat 18 (Payne et al., 2009), taking replications as random factor, and genotype, treatment, genotype by treatment and the comparison of landraces vs. improved varieties (named 'type' effect), as fixed factors. Multiple means comparison was carried out using an LSD at 0.05 level of significance.

Broad-sense heritability (h^2) was calculated on entry mean basis using the REML procedure in Genstat 18, as follows:

$$h^2= \sigma^2\, g/(\sigma^2 g + (\sigma^2 e/r))$$

where is the genotypic variance, is the error variance and r is the number of replications.

Results

Effect of PEG-induced drought stress on the assessed traits

The differences between treatments were significant for t50 (Time to reach 50% germination), due to the slower germination at -6 bar, but not for FGP. Genotypes were significantly different for both t50 and FGP. However, interactions between genotypes and treatments were found only for t50 (Table 2).

Both drought treatments increased t50 (Table 2), but only significantly at the high drought stress level (2.9h, 7.4% at -6 bar). As the high treatment (-6 bar) effect was more pronounced on germination traits, from here on we will only report its results, referred to as the ‘drought stress treatment’, unless stated otherwise.

Under drought conditions, 24 genotypes showed a decrease in FGP while 11 genotypes showed no change or even increased their FGP (Supplementary Table 1). The opposite occurred for t50, 24 genotypes increased the time to 50% germination, and 11 showed accelerated germination under drought, or no change (Suppl. Table 1).

Drought had a significant effect on all of seedling traits, except for CL, RDW and TPB. Genotypes were significantly different for CL, MRL, RSL, RSW, SVI_W and SVI_L. It is remarkable that there was no significant interaction between genotypes and treatment (Table 3).

Phenotypic mean values of seedling traits were higher under control than under stress conditions (-6 bar) except for RN, RDW, RSL and RSW. In general, the ranges of values were wider under control conditions, except for CL, RN, RSL and RSW (Table 3). The highest reduction due to PEG stress was observed for the mean value of SL (40.26%) followed by SDW (19.26%), TRL (13.19%) and MRL (12.62%), whereas mean of TBP (8.25%) and CL (2.26%) were reduced the least. In contrast, RSL, RSW, RDW and RN means were increased under PEG treatment by 47.53, 38.66, 8.62 and 7.46%, respectively. For root to shoot length ratio (RSL) and root to shoot weight ratio (RSW), the mean values were greatly increased under PEG treatment, which was a consequence of the great reduction of SL and SDW respectively. In general, the coefficient of variation values (CV) were similar between traits under both conditions except for RN which was the smallest one (10.99 and 10.66 for non-stress and stress conditions, respectively). CV values were greater under control than under stress conditions; only SL and CL had slightly higher CV values under stress conditions (Table 3). The DSI based on TPB showed negative and positive values. Genotypes with negative values were considered drought tolerant, and genotypes having positive values were considered as drought susceptible. Wheat genotypes presenting the lowest negative DSI values were almost all landraces, whereas modern ones presented positive DSI values (Table 4).

Effect of field compared to phytotron conditions

Under field conditions, ANOVA analyses showed a significant difference (0.05) for Cl, highly significant difference (0.001) for RSW and very highly significant difference (<0.001) for RN and RDW (Table 5).

The comparison between the mean values for seedling traits recorded in the field and under phytotron non-stress and stress conditions, showed lower mean values in the field for all measured traits, except for SDW which was superior under field compared to both controlled conditions (stress and non-stress) and also for SL and TPB where the phenotypic mean values in the field were superior but only to those of stress (Table 5).

TABLE 2. Summary statistics and means comparison for the 35 wheat genotypes under PEG treatments (0, -3 and -6 bar) for final germination percentage (FGP) and time to reach 50% germination (t50).

	Min	Max	Mean (SE)	CV%	Reduction %
FGP					
Control, 0 bar	53.3	100.0	89.1a (7.09)	14.2	
PEG -3 bar	33.3	100.0	90.1a (9.03)	14.6	-1.1
PEG -6 bar	20.0	100.0	86.7a (11.68)	16.8	2.7
t50					
Control 0 bar	0.7	3.5	1.6b (0.32)	27.5	
PEG -3 bar	0.8	2.5	1.6b (0.24)	17.7	-1.2
PEG -6 bar	1.4	3.5	1.7a (0.18)	18.7	-7.4

TABLE 3. Ranges, means, standard error (SE), coefficient of variation (CV) and significance of the analysis of variance for 35 wheat genotypes evaluated under optimum (non-tress) and drought stress conditions (-6 bar), for seedling traits.

	Control				Drought stress (-6 bars)						Combined ANOVA (control and stress)		
	Min	**Max**	**Mean**	**CV**	**Min**	**Max**	**Mean**	**CV**	**SE**	**Reduction%**	**Genotype (Geno)**	**Treatment (Treat)**	**Geno×Treat**
CL (cm)	1.84	5.42	3.92	18.23	1.45	5.85	3.83	22.01	0.66	2.26	***	ns	ns
SL (cm)	3.78	17.36	11.97	23.45	1.14	10.86	7.15	24.27	2.51	40.26	ns	***	ns
MRL (cm)	2.90	20.48	12.50	35.06	3.90	16.46	10.93	21.69	3.15	12.62	**	**	ns
TRL (cm)	7.02	71.26	39.88	40.74	9.06	57.06	34.62	25.61	26.9	13.19	ns	*	ns
RN	3.40	5.80	4.71	10.99	2.80	6.00	5.06	10.66	0.51	-7.46	ns	***	ns
SDW (mg)	0.60	15.10	8.00	36.50	1.40	9.90	6.50	24.92	0.0022	19.26	ns	***	ns
RDW (mg)	1.60	10.90	5.80	40.47	2.10	9.70	6.30	20.73	0.0017	-8.62	ns	ns	ns
TPB (mg)	3.90	21.70	13.90	34.74	3.50	19.30	12.80	21.01	0.0037	8.25	ns	ns	ns
RSL	0.50	1.84	1.07	30.80	0.71	3.42	1.58	23.00	0.32	-47.53	**	***	ns
RSW	0.27	1.08	0.73	26.34	0.49	1.55	1.00	19.53	0.18	-38.66	*	***	ns
SVI_W	0.29	2.16	1.26	39.56	0.22	1.56	1.11	26.70	0.35	11.64	**	*	ns
SVI_L	251	3188	2193	33	307	2312	1586	28	502.99	27.00	***	***	ns

- CL: Coleoptile length, SL: Shoot length, MRL: Maximum root length, TRL: Total root length, RN: Root number, SDW: Shoot dry weight, RDW: Root dry weight, TPB: Total plant biomass, RSL: Root to shoot length, RSW: Root to shoot weight, SVIw: Seedling vigor index based on seedling weight, SVIL: Seedling vigor index based on seedling length.
- *, ** and ***: Significant difference at 0.5, 0.01 and 0.001 level, respectively.

TABLE 4. Thirty five wheat genotypes ranked on drought susceptibility index (DSI), calculated from total plant dry biomass (TPB, mg per seedling).

Genotype	Type	TBP/control	TBP/stress	DSI
Langloise	**Landrace**	8.70	16.00	-10.17
Djenah Khoteifa	**Landrace**	7.72	13.14	-8.51
Sbaa Aldjia	**Landrace**	6.75	11.32	-8.20
Gloire de Mongolfier	**Landrace**	11.68	17.52	-6.06
Guemgoum	**Landrace**	11.46	16.25	-5.06
MBB	**Landrace**	10.95	14.31	-3.72
Oued Znatie	**Landrace**	11.09	13.57	-2.71
Polonicum	Improved	10.56	12.62	-2.36
Hedba 03	**Landrace**	10.26	11.97	-2.02
INRAT 69	Improved	14.09	16.19	-1.81
Aures	Improved	13.55	14.75	-1.07
Mexicalli 75	Improved	10.41	11.19	-0.91
Megress	Improved	11.94	12.60	-0.67
Waha	Improved	12.65	13.23	-0.56
Beliouni	**Landrace**	10.18	10.29	-0.13
Vitron	Improved	13.73	12.69	0.92
Altar 14	Improved	11.73	10.73	1.03
Bidi 17	**Landrace**	14.62	13.15	1.22
Acsad 65	Improved	15.28	13.72	1.24
Miki-2	Improved	13.51	12.03	1.33
Tejdid	Improved	15.21	12.73	1.98
ZB/Fg	Improved	13.78	11.36	2.13
Gta Dur	Improved	14.32	11.41	2.46
Oued El Berd	Improved	16.19	12.70	2.61
Wahbi	Improved	19.81	14.60	3.19
Stitfis	Improved	17.42	12.61	3.35
Montpellier	Improved	17.68	12.56	3.51
Cirta	Improved	17.24	12.09	3.62
Ofanto	Improved	18.07	12.64	3.64
Mansourah	Improved	15.38	10.49	3.85
Korifla	Improved	20.30	13.62	3.99
El Maather	Improved	19.96	12.31	4.64
Massinissa	Improved	20.19	11.93	4.96
Capeiti	Improved	13.46	7.79	5.10
Semito	Improved	19.21	11.09	5.12

TABLE 5. Ranges, means, coefficient of variation (CV) and analysis of variance for 27 wheat genotypes under control, stress and field conditions, with ANOVA analysis of field data for seedling traits.

	Non-stress				Stress				Field							
Trait	**Mean**	**Min**	**Max**	**CV**	**Mean**	**Min**	**Max**	**CV**	**Mean**	**Min**	**Max**	**SE**	**CV**	**Redu. % C**	**Redu.% S**	**ANOVA**
CL	3.92	1.84	5.42	19.59	3.87	2.26	5.85	22.01	3.19	1.56	4.70	0.55	19.82	18.64	17.39	*
SL	12.03	4.04	17.36	21.77	7.13	1.14	10.36	24.03	8.23	5.80	11.38	1.18	15.57	31.56	-9.20	ns
MRL	12.86	2.90	20.48	33.21	10.80	3.90	15.16	20.34	5.27	3.40	8.04	0.97	18.11	59.00	43.00	ns
TRL	40.64	7.02	71.26	39.47	34.46	9.06	57.06	25.54	16.29	8.14	26.90	3.88	25.08	59.91	44.69	ns
RN	4.67	3.40	5.80	11.08	5.05	2.80	6.00	10.18	4.33	3.20	5.40	0.38	11.84	7.22	15.42	***
SDW	8.00	0.60	15.10	35.74	6.50	1.40	9.90	25.18	9.30	6.40	11.70	0.0012	13.37	-16.08	-34.84	ns
RDW	6.00	1.60	10.90	37.62	6.30	2.10	9.70	20.67	4.60	2.50	7.90	0.0008	23.34	22.54	28.44	***
TPB	14.1	4.80	21.70	32.78	12.8	3.50	19.30	20.95	14.00	10.90	17.60	0.0016	11.52	0.95	-8.18	ns
RSL	1.10	0.53	1.83	30.21	1.57	0.71	3.42	24.22	0.64	0.45	0.88	0.12	18.53	41.51	83.78	ns
RSW	0.74	0.27	1.07	24.98	1.00	0.49	1.55	20.42	0.50	0.28	0.76	0.09	20.57	31.68	67.02	**
SVI_W	1.28	0.29	2.16	35.80	1.12	0.22	1.56	26.25	0.88	0.51	1.43	0.20	22.34	31.08	18.92	ns
SVI_L	2247.13	251.33	3188.00	30.47	1593.45	307.00	2312.00	27.20	868.81	523.71	1547.36	225.58	24.69	61.34	32.25	ns

- CL: Coleoptile length, SL: Shoot length, MRL: Maximum root length, TRL: Total root length, RN: Root number, SDW: Shoot dry weight, RDW: Root dry weight, TPB: Total plant biomass, RSL: Root to shoot length, RSW: Root to shoot weight, SVIw: Seedling vigor index based on seedling weight, SVIL: Seedling vigor index based on seedling length. Redu. % C: Mean value reduction compared to control. Redu. % S: Mean value reduction compared to stress.
- *, **, ***: Significant difference at 0.5, 0.01 and 0.001 level, respectively.

The ranges of variation for seedling traits observed in the field were smaller than those found under stress and non-stress conditions for all traits, for example TRL (cm): field= (8.14– 26.90), control= (7.02– 71.26), stress= (9.06– 57.06), MRL (cm): field= (3.4– 8.04), control= (2.90– 20.48), stress= (3.90– 15.16), CL (cm): field= (1.56– 4.70), control= (1.84– 5.42), stress= (2.26– 5.85) and for RN: field= (3.2-5.4), control= (3.4– 5.8), stress= (2.8– 6) (Table 5).

Landraces vs. improved genotypes

ANOVA analyses revealed a significant effect of type (landrace vs. improved) and type by treatment interaction on most traits measured except SL, RN, SDW for type effect (Table 6). Landraces showed higher coleoptile length than improved genotypes under control and stress conditions. For all other traits improved genotypes were superior or equal to landraces under control but the opposite was observed under stress (Table 6). Across treatment, landraces tended to increase all traits under stress except SL and CL, which were reduced by 40.44 and 8.85%, respectively. RDW of landraces was the most increased trait (traits per se) under stress (69.26%) (Table 6, Fig. 1). On the other hand, improved genotypes showed the largest decreases for most traits under stress. SL and SDW were the most affected by stress (reduced by 38.99 and 28.38%, respectively), but a slight increase was observed for CL (0.96%). Root number was increased for both improved genotypes and landraces under stress by 6.66 and 9.57%, respectively (Table 6). Under stress, landraces and improved cultivars increased their root length and root biomass compared to shoot part (increase in RSL and RSW) (Fig. 1). Seedling vigor index, based on seedling length (SVI_L) or on seedling weight (SVI_W), were significantly higher for improved cultivars under control conditions but not under stress conditions. Landraces tended to have a higher SVI_W under stress, compared to improved genotypes (Table 6).

The comparison between landraces and improved genotypes in field revealed significant differences only for SDW and RSW. Landraces presented higher SDW values and improved genotypes had a better RSW ratio (Suppl. Table 2).

Broad heritability in the field compared to controlled conditions

Overall, heritability calculated from field data was inferior than that obtained under control conditions and was higher than under stress. Under control conditions, broad heritability was higher than under drought stress for most traits (Suppl. Table 3). MRL presented appreciable heritability under stress (0.98) and field conditions (0.99). Cl was more heritable (0.65) under control than other conditions (0.25). RDW had higher heritability values under all conditions than SDW. RSW displayed very high heritability value under control (0.98) followed by field (0.50) and stress (0.17) (Suppl. Table 3).

Traits relationship

Pearson correlation coefficients between seedling traits measured in both control and drought stress conditions ranged from very weak correlation (0.07) for TRL and SVI_W to highly significant ones (0.30-0.50) for FGP, t50, CL, RSL, and SVI_L (values in the diagonal, Table 7).

In the control treatment, many significant correlations were found, TPB was positively correlated with all traits, except RSW and t50, and was greatly influenced by SDW and RDW. A high correlation was also found between TRL and MRL. Negative correlations were observed for t50 and CL with all other traits, indicating that genotypes with earlier germination and/or shorter coleoptile tended to have higher seedling traits values. RDW had a positive correlation with SDW (0.76).

Under stress, a high correlation was found between TPB and SL (0.75). Correlation between TPB with TRL and MRL (0.74 and 0.63 respectively) was less pronounced under stress conditions than under non-stress. RN, SDW and RDW had a similar correlation with TPB as found in non-stress. Remarkably, CL had a positive correlation with all seedling traits except RSW and RSL, whereas these correlations were negative at the control conditions, which means that seedlings having a longer coleoptile tended to be more tolerant (vigorous) under stress by producing more TPB. In addition, TPB under stress was negatively correlated with RSL (-0.44) and RSW (-0.43), whereas these correlations were positive under control conditions, indicating that, under no stress, seedlings invested more in root growth, and under stress they invested more in shoot growth (Table 7).

TABLE 6. Ranges, means, percentage of reduction (Redu. %) and analysis of variance for landraces and improved genotypes under control and stress (PEG, -6) conditions.

		Control			Stress				ANOVA		
Trait	**Type**	**Min**	**Max**	**Mean**	**Min**	**Max**	**Mean**	**Redu. %**	**T**	**Trt**	**T × Trt**
t50 (day)	Improved	0.70	2.38	1.49	1.46	2.10	1.66	-11.28	***	*	ns
	Landrace	1.00	3.50	1.90	1.44	3.50	1.90	-0.39			
FGP %	Improved	60.00	100.00	92.32	20.00	100.00	88.11	4.56	**	ns	ns
	Landrace	53.33	100.00	81.11	46.67	100.00	83.21	-2.60			
CL (cm)	Improved	1.84	5.20	3.68	2.26	5.85	3.72	-0.96	***	ns	ns
	Landrace	3.28	5.42	4.50	1.45	5.42	4.11	8.85			
SL (cm)	Improved	3.78	17.36	11.81	1.14	10.86	7.20	38.99	ns	***	ns
	Landrace	4.94	15.44	12.23	2.83	12.08	7.28	40.44			
MRL (cm)	Improved	2.90	20.48	13.57	3.90	16.46	10.83	20.25	**	**	**
	Landrace	3.90	16.76	9.83	6.20	13.76	11.18	-13.73			
TRL (cm)	Improved	7.02	71.26	44.08	9.06	57.06	33.84	23.22	*	*	***
	Landrace	13.20	56.72	29.38	15.20	48.04	36.56	-24.43			
RN	Improved	3.40	5.80	4.78	2.80	6.00	5.10	-6.66	ns	***	ns
	Landrace	3.40	5.60	4.55	3.30	5.80	4.98	-9.57			
SDW (mg)	Improved	0.58	15.05	8.62	1.38	9.48	6.17	28.38	ns	***	***
	Landrace	2.34	11.82	6.46	2.27	9.94	7.18	-11.18			
RDW (mg)	Improved	2.36	10.90	6.59	2.14	9.72	6.20	5.91	***	ns	***
	Landrace	1.60	6.84	3.88	2.55	9.40	6.56	-69.29			
TPB (mg)	Improved	4.78	21.67	15.38	3.52	17.94	12.38	19.51	**	ns	***
	Landrace	3.94	17.84	10.34	4.82	19.34	13.75	-32.98			
RSL	Improved	0.54	1.84	1.15	0.72	3.42	1.60	-39.78	*	***	ns
	Landrace	0.50	1.57	0.90	0.96	2.19	1.54	-71.68			
RSW	Improved	0.32	1.08	0.76	0.49	1.55	1.03	-35.48	**	***	ns
	Landrace	0.27	1.04	0.64	0.72	1.45	0.94	-47.76			
SVI$_W$	Improved	0.29	2.16	1.43	0.22	1.47	1.09	24.05	***	*	***
	Landrace	0.32	1.44	0.83	0.23	1.56	1.17	-41.02			
SVI$_L$	Improved	251.33	3188.00	2380.32	307.00	2312.00	1583.95	33.46	**	***	**
	Landrace	614.40	2850.00	1726.13	421.17	2290.00	1591.56	7.80			

- T50: Time to reach 50% germination, FGP: Final germination percentage, CL: Coleoptile length, SL: Shoot length, MRL: Maximum root length, TRL: Total root length, RN: Root number, SDW: Shoot dry weight, RDW: Root dry weight, TPB: Total plant biomass, RSL: Root to shoot length, RSW: Root to shoot weight, SVIw: Seedling vigor index based on seedling weight, SVIL: Seedling vigor index based on seedling length.
- *, ** and ***: Significant difference at 0.5, 0.01 and 0.001 level respectively.
- T: Type, Trt: Treatment.

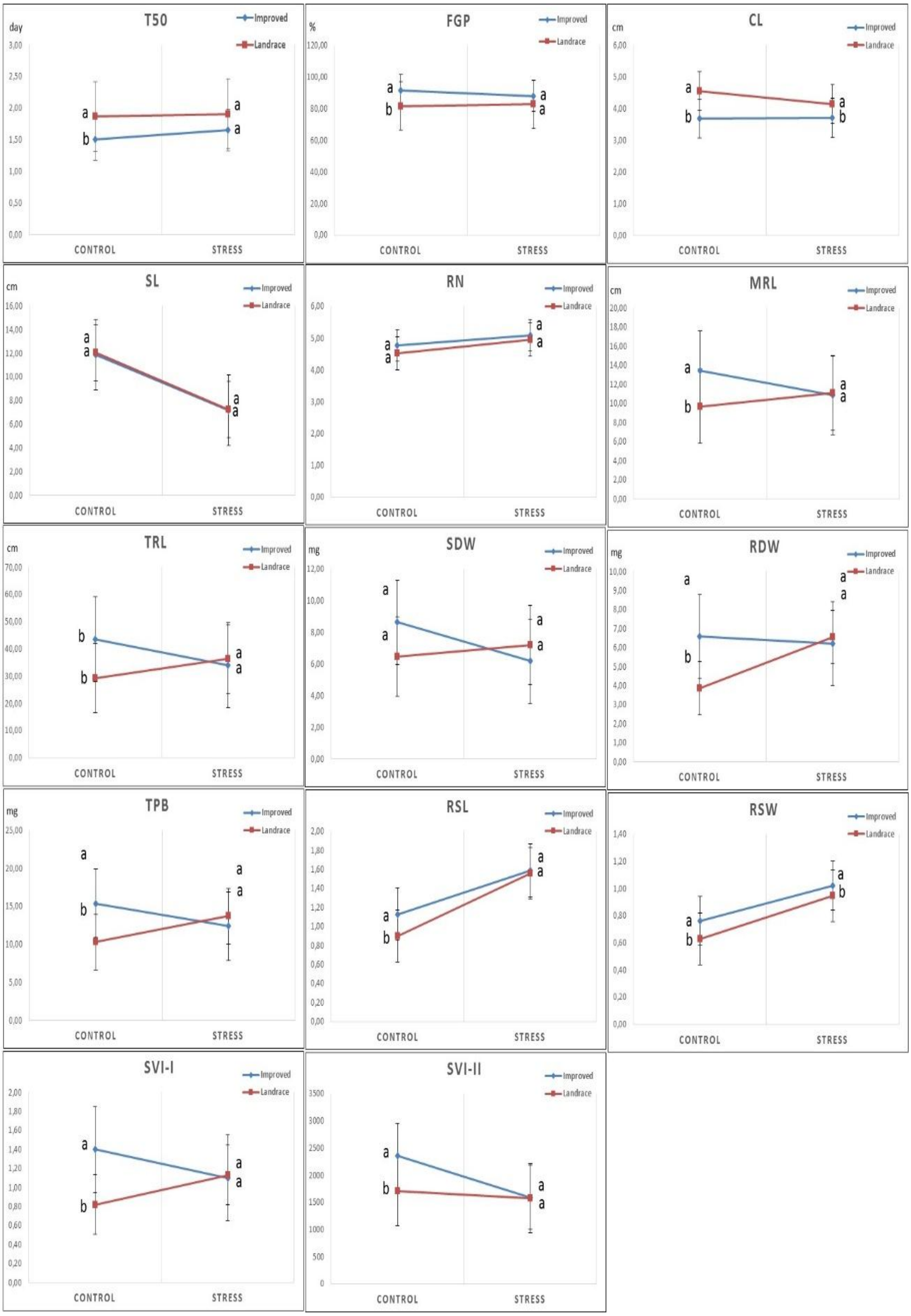

Fig. 1. Seedling traits variation across stress and control conditions for landraces (red line) and improved genotypes (blue line) (Bars represent ± standard error).

TABLE 7. Pearson correlation coefficients of the assessed seedling traits under non-stress (below diagonal) and stress conditions (-6 bars) (above diagonal) and between the two conditions (cells with gray color).

		Stress													
		t50	**FGP**	**SL**	**CL**	**RN**	**TRL**	**MRL**	**SDW**	**RDW**	**RSW**	**RSL**	**TPB**	**SVI_W**	**SVI_L**
Non-Stress	t50	0.45***	**-0.51**	**-0.24**	**-0.27**	-0.02	**-0.31**	**-0.36**	-0.16	-0.22	-0.03	-0.03	-0.20	**-0.39**	**-0.46**
	FGP	**-0.53**	0.50***	0.21	0.23	0.12	**0.27**	**0.43**	0.11	0.22	0.07	0.09	0.17	**0.62**	**0.73**
	SL	-0.06	0.06	-0.02	**0.37**	**0.35**	**0.69**	**0.70**	**0.79**	**0.58**	**-0.57**	**-0.65**	**0.75**	**0.67**	**0.74**
	CL	0.08	0.05	-0.06	0.42***	**0.32**	**0.40**	**0.34**	**0.40**	0.19	**-0.42**	**-0.24**	**0.34**	**0.39**	**0.37**
	RN	-0.10	0.02	**0.40**	**-0.34**	-0.13	**0.40**	**0.25**	**0.40**	**0.52**	-0.16	**-0.43**	**0.49**	**0.40**	**0.25**
	TRL	**-0.36**	**0.45**	**0.47**	**-0.35**	**0.53**	0.07	**0.86**	**0.64**	**0.76**	-0.16	-0.14	**0.74**	**0.71**	**0.73**
	MRL	**-0.36**	**0.47**	**0.47**	**-0.28**	**0.43**	**0.96**	0.15	**0.56**	**0.62**	-0.20	-0.04	**0.63**	**0.71**	**0.89**
	SDW	-0.05	0.11	**0.65**	**-0.41**	**0.53**	**0.70**	**0.68**	-0.14	**0.73**	**-0.68**	**-0.53**	**0.95**	**0.79**	**0.54**
	RDW	**-0.34**	**0.35**	**0.39**	**-0.45**	**0.54**	**0.88**	**0.87**	**0.76**	0.10	-0.04	**-0.26**	**0.91**	**0.81**	**0.53**
	RSW	**-0.39**	**0.31**	**-0.34**	-0.16	0.13	**0.34**	**0.34**	-0.17	**0.47**	0.20	**0.63**	**-0.43**	**-0.30**	**-0.25**
	RSL	**-0.34**	**0.47**	**-0.24**	**-0.25**	0.13	**0.67**	**0.73**	**0.25**	**0.64**	**0.64**	0.32**	**-0.44**	**-0.27**	-0.18
	TPB	-0.20	**0.24**	**0.57**	**-0.45**	**0.57**	**0.83**	**0.81**	**0.95**	**0.93**	0.13	**0.46**	-0.20	**0.85**	**0.57**
	SVI_W	**-0.35**	**0.52**	**0.48**	**-0.39**	**0.51**	**0.88**	**0.87**	**0.85**	**0.93**	**0.24**	**0.58**	**0.95**	-0.07	**0.81**
	SVI_L	**-0.45**	**0.68**	**0.61**	-0.16	**0.39**	**0.88**	**0.91**	**0.64**	**0.76**	0.22	**0.52**	**0.74**	**0.86**	0.30**

- T50: Time to reach 50% germination, FGP: Final germination percentage, CL: Coleoptile length, SL: Shoot length, MRL: Maximum root length, TRL: Total root length, RN: Root number, SDW: Shoot dry weight, RDW: Root dry weight, TPB: Total plant biomass, RSL: Root to shoot length, RSW: Root to shoot weight, SVIw: Seedling vigor index based on seedling weight, SVIL: Seedling vigor index based on seedling length.

- *, ** and ***: Significant difference at 0.5, 0.01 and 0.001 level. respectively.
- Values in bold and with asterisks are different from 0 with a significance level alpha=0,05. Cells with grey color are correlations between stress and non-stress for the same trait.

Correlation coefficients calculated between traits measured in field showed a high correlation of TPB with SDW (0.75), a positive moderate correlation between TPB and RDW, TRL and MRL (0.70, 0.52 and 0.50, respectively), and a weak correlation with RN (0.30). RDW was highly correlated with TRL (0.57), moderately correlated with RN, MRL (0.57, 0.53, respectively) and weakly correlated with SL (0.29), RSW (-29) and RSL (-35). CL presented strong correlation with SL (0.72) and a weak correlation with RN and TRL (0.42 and 0.34, respectively) (Suppl. Table 4).

The correlation between traits measured in the field and under controlled conditions showed low and non-significant correlations among traits, except a weak significant correlation was observed between field and stress for SDW (0.33) (Suppl. Table 5).

Discussion

Drought stress at an early growth stage is a major limiting factor of wheat production in many parts of the world (Dhanda et al., 2004). Rebetzke et al. (2007) demonstrated that a good seedling emergence is important for achieving high wheat yields. Final germination percentage and time to reach 50% of germination are two important traits for plant establishment, especially under early drought conditions.

In this study, wheat genotypes behaved similarly under control and stress conditions for FGP but not for t50. The significant effect of treatment by genotype interaction in this last variable indicated that the genotypes responded differently across treatments, suggesting that the selection for this trait should be performed under target conditions (either under control or PEG stress), same as concluded by Abdel-Ghani et al. (2015).

Genotypes presenting a better FGP under stress were not necessarily the same genotypes having better t50 and vice versa. Only 4 (Belliouni, Capeiti, Gloire de Mongolfier and Miki-2) of the 9 most tolerant genotypes were considered tolerant for both FGP and t50, and these could be the best candidates to become drought-tolerant parents in a breeding program. Despite their results for other traits showed large variation, they could still have good breeding potential due to their ability to perform better under stress than under the control treatment. Gloire de Mongolfier could be singled out as the most promising genotype when taking into account all its rankings. It was particularly good under PEG stress regarding biomass related traits like SDW, RDW, TPB and SVI_W (Suppl. Table 6), and was the fourth most tolerant genotype regarding DSI (Table 4). Many genotypes decreased their FGP and delayed their t50 under drought stress, as expected for PEG-induced drought, which is reported to affect seed germination by reducing water availability (Al-Karaki, 1998; Kaya et al., 2006). Conversely, some genotypes improved their FGP and t50 under drought stress, which could be explained by an already described osmo-priming effect of PEG (Al-Karaki, 1998; Kaya et al., 2006). Some varieties widely grown under Algerian conditions, like Waha and Vitron, were among the most susceptible cultivars based on FGP and t50, indicating room for improvement for these two traits.

No interactive effect was found for all seedling growth traits, wheat genotypes ranked similarly under control and stress conditions for all seedling traits. SL was the most sensitive to drought stress (reduction 40.26%) while CL was the least affected trait. Our results differ from those of Zarei et al. (2007), who found that root length was the most sensitive trait to drought stress induced by PEG in wheat.

In our experiment, genotypes tended to invest more resources in growing roots than shoots under stress conditions, compared to the control. Dhanda et al. (2004), in a similar study, found that root to shoot length ratio increased by 40% under stress conditions. In some cases, the absolute root biomass of plants in drying soil may increase relative to well-watered conditions (Sharp & Davies, 1985). The possible causes of increased root to shoot length ratio under water stress may be the limited supply of water and nutrients to the shoot, and changes in resource allocation due to changes in hormone messages induced in roots when they encounter drought stress (Davies & Zhang, 1991).

Heritability, trait range and coefficient of variation, all decreased under stress conditions for most traits, as also found by Dhanda et al. (2004), indicating a reduction of expression or variation under stress conditions. More gain from selection might be expected for FGP, t50, CL and RSL (under control conditions), for FGP and t50 (under stress conditions) and for RDW, RSW and CL (in the field).

Seedling vigor index based on either length or weight of seedling are useful traits as they are correlated with other seedling traits. Time to reach 50% of germination (t50) correlated negatively with other traits, reflecting the importance of faster germination rate, indicating that faster germinating genotypes will be more vigorous. Remarkably, under non-stress, CL displayed negative correlations with all traits whereas they were positive under stress conditions, except for RSL and RSW ratio. This finding indicates that plants with longer coleoptile tended to be more tolerant by promoting more biomass under stress, contrarily to plants with shorter coleoptiles, which were yielding more biomass under optimal conditions. In our study, most landraces were ranked ahead of modern ones for CL (Suppl. Table 6), also manifested as the significant higher CL mean observed in landraces (as a group). Furthermore, CL expresses consistently across treatments, suggesting that this trait could be a potential target for indirect selection under either condition. An advantage for its use in breeding is its high narrow-sense heritability, as found by Shahbazi et al. (2012). Genotypes with longer coleoptile are appropriate for deep sowing to reach soil moisture in semi-arid regions, something which was often avoided by growers of dwarfing gene cultivars (Rebetzke et al., 2007). Currently, alternative dwarfing genes (e.g. Rht8), which reduce plant height without affecting coleoptile length, are available for use in wheat breeding (Rebetzke et al., 2007).

A positive correlation was found between root length (total and maximum) and shoot length under both conditions, indicating that increase in root length will increase shoot length, and *vice versa*, confirming results reported by Kan et al. (2002) and Baalbaki et al. (1999). Based on the drought susceptibility index (DSI), genotypes could be clearly separated into landraces and modern cultivars, with landraces showing increased drought tolerance. Six widely grown Algerian landraces were listed among the most tolerant genotypes (Beliouni, Djenah Khoteifa, MBB, Bidi 17, Oued Znatie,and Guemgoum R'khem), which suggest their potential as donors of early drought tolerance. The importance of this difference, according to breeding history of the accessions, led us to focus on the comparison between landraces and improved cultivars, which is discussed next.

Type effect

One of the most interesting findings of this study was the clear differences between landraces and improved genotypes for several traits (Fig. 1). Landraces had longer coleoptiles than improved cultivars, which is an advantageous trait for deep sowing practice. Ramshini et al. (2016) found that coleoptile length was significantly decreased in improved cultivars compared to old ones. They also found a significant difference between these two groups, with higher means observed in old cultivars for SL, RSL, SDW, TPB and SVI_L, where as shoot length was significantly higher in modern cultivars. This effect could be influenced by the use of semi-dwarf alleles in modern cultivars, which has been shown to reduce early growth root length (Wojciechowski et al., 2009). Other studies found an overall reduction of root size in modern cultivars, compared to landraces (Waines & Ehdaie, 2007). Some reports hypothesized that lower root to shoot ratio of improved cultivars early in the growing season may explain their increased harvest index, due to the reduced investment in root growth (Siddique et al., 1990). However, the optimum root size for grain yield has not been thoroughly investigated in wheat or most crop plants (Waines & Ehdaie, 2007).

For most other traits, improved cultivars showed higher values than landraces only under control conditions. Landraces seemed to be more tolerant than improved cultivars since they increased trait performances under stress, as confirmed by the DSI result (Table 4, Fig. 1). Several researches have already noted an outstanding performance of landraces. For instance, Ash et al. (2017) found that durum wheat variety Strong field produced only about half of the root biomass of the wheat landrace Pelissier, at maturity in greenhouse trials under well-watered conditions. Bektas et al. (2016) found that wheat landraces were superior for root biomass, shallow root weight, deep root weight, number of tillers and plant height compared to improved cultivars. Some Spanish barley landraces also outperformed modern cultivars under low site productions (Yahiaoui et al., 2014).

Field conditions effect

Closing the gap between field and controlled experiment conditions is a current trend which aims at extrapolating results obtained under artificial conditions to real (field) conditions. In this study, the ranges of variation and mean values of seedling traits in the field were less than what those observed under controlled conditions, except for SDW and TPB. This could be partly explained by the effect of soil impedance, which hampers root growth, and the effect of temperature and humidity of the soil as well. This suggestion is supported by that the SDW values obtained in field were superior to under controlled conditions which may be explained by more space dedicated in field than in Petri dishes. Correlations established between traits in field and controlled experiment showed no interesting results and the two conditions of experiment were too different for all traits. The only weak correlation was found for SDW (Suppl. Table 5).

Conclusion and Perspective

A good range of variation was observed for most seedling traits under controlled conditions, which could be useful in wheat breeding programs. Longer coleoptile length could be a potential trait for selection of drought tolerant genotypes especially at early growth stage in semi-arid environments, although pleiotropic effects on final shoot and root development and grain yield should be studied in parallel.

After these results, Algerian wheat landraces, which have been cultivated for a long time in the region, could be introduced in durum wheat breeding programs to breed for drought tolerance at the early growth stage. Some widely cultivated modern varieties were listed among the most susceptible genotypes like Waha, Vitron and Wahbi. These varieties, which already have good agronomic performance overall, could be further improved by enhancing their FGP and/or t50.

Further work is required to correlate root traits at seedling stage and root/agronomic traits at adult stage, to find proxy traits, which allow performing selection at early plant stage. Crosses between tolerant genotypes and susceptible genotypes identified in this study can generate populations appropriate for QTL mapping to identify genomic regions related to interesting seedling traits, and with good breeding potential.

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تقييم التحمل المبكر للجفاف لسلالات من قمح الديورم الجزائرية

قوة نمو البادرات مهمه للحصول على محصول جيد، خاصة تحت ظروف الجفاف. لذلك تم إجراء هذه الدراسه لتحديد صفات وتراكيب وراثية مفيدة في تعزيز التحمل المبكر للجفاف في قمح المكرونة (القمح الصلب). تم إجراء تجربتين، التجربة الأولى تمت في الصوبة لإختبار 35 تركيب وراثي (أصناف قديمه وحديثه) في مرحلة الإنبات والمراحل المبكرة للبادره، حيث تم تعريض التركيب الوراثية لثلاثة مستويات من الإجهاد الأسموزي استحدثت بإستخدام مادة البولي إيثيلين جليكول (PEG 6000) بتركيزات؛ صفر، -3 و -6 بار. أما التجربة الثانية تم إجراءها في الحقل بإستخدام 27 تركيب وراثي من الخمسة و الثلاثين. في كلتا التجربتين تم تقدير صفات الجذر والسويقة في عمر البادره.

أظهرت النتائج أن المعاملة العالية من البولي إيثيلين جليكول أدت إلى إنخفاض نسبة الإنبات النهائي بنسبة 2.7% وكذلك تأخر وقت الوصول إلى 50% من الإنبات 2.9 ساعة. وكانت صفة طول السويقة (Shoot length) الأكثر تأثرًا بالجفاف (إنخفضت بنسبة 40%) على عكس بعض صفات الجذر التي زادت حتى تحت الجفاف، مثل نسبة طول الجذر إلى طول السويقة، نسبة وزن الجذر إلى وزن السويقة، الوزن الجاف للجذر، وعدد الجذور. وأظهرت صفة طول غمد الريشة (Coleoptile length) علاقة متغيرة مع الصفات الأخرى، حيث كان مرتبطا سلبيا بشكل عام تحت عدم الإجهاد، ولكن كان مرتبطا إيجابيا تحت الإجهاد. بناءً على دليل الحساسية للجفاف، كانت أصناف القمح الجزائرية القديمة أكثر تحملا للجفاف مقارنة بالأصناف الحديثة. الإرتباط بين الصفات التي تم تقديرها تحت ظروف الحقل والصوبة كان منخفض. صفة طول غمد الريشة (Coleoptile length) يمكن أن تكون صفة مهمه لتحديد التركيب الوراثية المتحملة للجفاف. أصناف القمح الجزائرية القديمة أظهرت قدرة مميزة وبشكل واضح على تحمل الجفاف المبكر، لذلك يمكن أن تكون مصدر جيدا لبرامج التربية.

agronomy

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Article

Durum Wheat Seminal Root Traits within Modern and Landrace Germplasm in Algeria

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Abstract: Seminal roots are known to play an important role in crop performance, particularly under drought conditions. A set of 37 durum wheat cultivars and local landraces was screened for variation in architecture and size of seminal roots using a laboratory setting, with a filter paper method combined with image processing by SmartRoot software. Significant genetic variability was detected for all root and shoot traits assessed. Four rooting patterns were identified, with landraces showing overall steeper angle and higher root length, in comparison with cultivars, which presented a wider root angle and shorter root length. Some traits revealed trends dependent on the genotypes' year of release, like increased seminal root angle and reduced root size (length, surface, and volume) over time. We confirm the presence of a remarkable diversity of root traits in durum wheat whose relationship with adult root features and agronomic performance should be explored.

Keywords: proxy traits; genetic resources; root screening; root architecture

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1. Introduction

The root system of wheat includes two main types, seminal (embryonic) and nodal roots, also known as the crown or adventitious roots [1,2]. Both types of roots play a crucial role in plant growth and are active throughout the whole plant life. Seminal roots, however, could be more important under specific circumstances, like drought conditions, as they penetrate deeper into the soil layers than nodal roots, making water in deep layers accessible to the plant [3–5]. Seminal roots also play a capital role during crop establishment, as they are the only roots existing before the emergence of the fourth leaf. Seminal roots include one primary root, two pairs of symmetric roots at each side, and, at times, a sixth central root [6].

The main features of root systems are encompassed under two categories, root system architecture (RSA) and morphology. RSA is related to the whole, or a large subset, of the root system, and may be described as topological or geometric measures of the root shape. Root morphology, as defined by J. Lynch, refers to "the surface features of a single root axis as an organ, including characteristics of the epidermis such as root hairs, root diameter, the root cap, the pattern of appearance of daughter roots, undulations of the root axis, and cortical senescence" [7]. The traits often used to describe wheat roots are total root length, root surface area, root volume, root angle, number of roots, and root diameter [8–10].

Roots are difficult to measure readily in natural conditions. Root trait determination has become accessible through the development of phenotyping methods in artificial systems, for instance, gel chambers [11], rolled germination paper [12], clear pots and growth pouches [13], "Termita" chamber and Whatman paper system [14], or growth pouches system [15]. Seminal roots can be phenotyped early and easily compared to the root system of mature plants [16,17], and for this reason, they have been proposed as good candidates to act as proxy traits in wheat [18] and maize [19,20]. Nevertheless, phenotyping these traits could be of interest only if they are useful to predict root growth and functioning in adult plants [21,22]. Indeed, several studies have found useful associations with traits in adult plants of wheat species [23–26]. For instance, the seminal root angle was correlated with nodal root angle [5,27], and with grain yield under drought conditions [28]. The seminal root number was correlated with thousand kernel weight (TKW) under stress, while the primary root length at the seedling stage was correlated with TKW under wetter conditions [25]. A steeper angle between the outermost roots and a higher root number in wheat seedlings have been linked to a more compact root system with more roots at depth in wheat [11,24,29].

Genotypic variation in root architecture has been reported within genotypes of different crop species [30–32], including wheat [13,21,25,33]. The presence of variation for the trait of interest is an essential requirement to improve the adaptability of crops under changing environmental conditions [34].

Local landraces are considered well adapted to the region where they were grown and contain large genetic diversity useful to improve crops like durum wheat [35]. These landraces were replaced by high yielding but more uniform semi-dwarf cultivars, better adapted to modern agriculture. However, scientists are convinced that local landraces still constitute a genetic resource useful to improve commercially valuable traits [36]. It is assumed that root traits enhance response to drought stress [37], but the realization of their contribution to superior grain yield depends on the type of drought and the agro-ecological conditions [38]. A deep rooting ideotype ("steep, cheap, and deep") was proposed by [39] to optimize water and N acquisition, building on the assumption that deeper rooting genotypes will use water that is beyond reach for shallower rooting genotypes. Modern breeding has caused some shifts in the root system architecture of durum wheat, from shallower and densely rooted systems in landraces of Mediterranean origin to deeper and more evenly distributed systems throughout the soil depth in cultivars worldwide [5].

The current study aims at evaluating the diversity of seminal root traits, including root angle and depth, during early growth of a set of durum wheat genotypes, consisting of modern cultivars and local landraces which are representative of the germplasm adapted to the mostly semi-arid conditions of Algerian cereal-growing regions before and after the advent of modern breeding. The study aims to reveal morphological diversity that could have agronomic relevance and, therefore, interest breeders.

2. Materials and Methods

2.1. Plant Material

We studied thirty-seven genotypes (landraces and modern cultivars), representative of durum wheat (*Triticum turgidum* ssp. *durum* Desf.) grown in Algeria. Geographical origins were varied (Algeria, France, Italy, Spain, Tunisia), and included genotypes produced at international breeding programs addressing semi-arid areas, namely the International Maize and Wheat Improvement Center (CYMMIT), the International Center for Agricultural Research in the Dry Area (ICARDA) and the Arab Center for the Studies of Arid zones and Drylands (ACSAD). These genotypes are representative of different periods of agriculture in Algeria, before and after the Green Revolution (Table 1).

Table 1. Name, type of cultivar, origin, and year of release of 37 genotypes of durum wheat used in the experiment.

N°	Genotype	Type/Pedigree	Origin	Year of Release
1	Beliouni	Landrace	Algeria	1958
2	Bidi 17	Landrace	Algeria	1930
3	Djenah Khotifa	Landrace	North Africa	1955
4	Gloire de Montgolfier	Landrace	Algeria	1960
5	Guemgoum R′ khem	Landrace	Algeria	1960
6	Hedba 3	Landrace	Algeria	1921
7	Langlois	Landrace	Algeria	1930
8	Mohammed Ben Bachir (MBB)	Landrace	Algeria	1930
9	Montpellier	Landrace	Algeria	1965
10	Oued Zenati 368	Landrace	Algeria	1936
11	Acsad 65	Gerardo-vz-469/3/Jori-1//Nd-61-130/Leeds	ACSAD	1984
12	Altar 84	Ruff/Flamingo,mex//Mexicali-75/3/Shearwater	CYMMIT	1984
13	Ammar 6	Lgt3/4/Bicre/3/Ch1// Gaviota/Starke	ICARDA	2010
14	Bousselem	Heider//Martes/ Huevos de oro	ICARDA	2007
15	Boutaleb	Hedba 3/Ofanto	Algeria	2013
16	Capeiti	Eiti*6/Senatore-Cappelli	Italy	1940
17	Chen′s	Shearwater(sib)/(sib)Yavaros-79	CYMMIT	1983
18	Ciccio	Appulo/Valnova(f6)//(f5)Valforte/Patrizio	Italy	1996
19	Cirta	Hedba-3/Gerardo-vz-619	Algeria	2000
20	Core	Platani/Gianni	Italy	2008
21	GTA Dur	Crane/4/Polonicum PI185309//T.glutin enano/2* Tc60/3/Gll	CIMMYT	1972
22	INRAT 69	Mahmoudi/(bd-2777)Kyperounda	Tunisia	1969
23	Korifla	Durum-dwarf-s-15/Crane//Geier	ICARDA	1987
24	Mansourah	Bread wheat/MBB	Algeria	2012
25	Massinissa	Ofanto/Bousselem	Algeria	2012
26	Megress	Ofanto/Waha//MBB	Algeria	2007
27	Mexicali 75	Gerardo-vz-469/3/Jori(sib)//Nd-61-130/Leeds	CIMMYT	1975
28	Ofanto	Ademelio/Appulo	Italy	1990
29	Oued El Berd	Gta dur/Ofanto	Algeria	2013
30	Polonicum	Triticum polinicum/Zenati boulette 1953-58	France	1973
31	Sahell	Cit″s″/4/Tace/4*tc//2*zb/wls/3/aa″s″/5/Ruff″s″/Albe″s″	CYMMIT	1977
32	Simeto	Capeiti-8/Valnova	Italy	1988
33	Sitifis	Bousselam/Ofanto	Algeria	2011
34	Vitron	Turkey77/3/Jori/Anhinga//Flamingo	Spain	1987
35	Waha	Plc/Ruff//Gta′s/3/ Rolette	ICARDA	1986
36	Wahbi	Bidi 17/Waha//Bidi 17	Algeria	2002
37	ZB × Fg	Zb/fg“s″ lk/3/ko 120/4/Ward cs 10604	Algeria	1983

*: Backcross.

2.2. Root Phenotyping

2.2.1. Preparation of Seeds

Twelve seeds of uniform size and healthy aspects were visually selected from each genotype and surface sterilized in a sodium hypochlorite solution (1.25% + one detergent drop, Mistol Henkel Iberica®). Seeds of each genotype were soaked and shaken in the solution for 15–20 min. Then, they were rinsed four times with sterile deionized water, in sterile conditions. Twelve seeds of each genotype were placed in Petri dishes, each with two filter papers soaked with 4 mL of sterile water. Then the Petri dishes were placed in a dark room at 4 °C for four days, and then at 22 °C/18 °C in a growth chamber with a 12 h light/darkness photoperiod for about 16 h.

Finally, the pre-germinated grains were transferred to the rhizo-slide system, described in detail in the next section and Figure S1. The experiment was carried out at the Laboratory of Cellular Biology and Genetics, Department of Biomedicine and Biotechnology of the University of Alcalá, Spain.

2.2.2. The Rhizo-Slide System

The rhizo-slide system was constructed as a sandwich made with glass plate, black cardboard, filter paper, and a black plastic sheet. Sheets of A4-size black cardboard (180 g/m^2, www.liderpapel.com) and filter papers were previously sterilized in an autoclave and then soaked in the nutritive solution Aniol [40]. The nutritive solution was prepared by dissolving 0.5550 g of $CaCl_2$, 0.8215 g of KNO_3, 0.6352 g of $MgCl_2 \cdot 6H_2O$, 0.0165 g of $(NH_4)_2SO$, 0.0400 g of NH_4NO_3 in 100 mL of distilled water, to which 500 µL/L of Plant Preservative Mixture (PPM^{TM}, Plant Cell Technology) at pH 5.8 was added. Each 8 mL was used to prepare 1 L of nutritive solution. Black cardboard with a nick made at the top center was placed on a glass plate with the same dimensions; then the pre-germinated grain (with embryonic part downward) was positioned just below the nick and covered by a filter paper. A black plastic sheet was used to cover the filter paper to ensure obscurity for roots, shifted ~2 cm upwards to allow better contact of the cardboard, and filter paper sheets with the nutritive solution. Two rhizo-slides were confronted to each other by the glass plate side, and the set was placed vertically in a glass box (internal dimensions of 32.2, 22, and 16 cm, length, width, and height) with two liters of the nutritive solution at the bottom, and then secured with two paper clips. Each glass box held 6 glass plates with two rhizoslides each, for a total of 12 seedlings, consisting of two genotypes, 6 seedlings for each (Figure S1). In total, each genotype was replicated 12 times. More details on the system are found in Ruiz et al. (2018) [25].

Once placed in the rhizoslides and the glass boxes, the seedlings were grown in a growth chamber for 7 days at 22/18 °C and 12/12 h photoperiod, day/night. The 37 genotypes were processed in batches of 6. Pre-germinated seeds of each 6 genotypes were placed into six glass boxes, each holding 6 seeds of two different genotypes. A complete batch comprised six boxes, three glass boxes prepared each Monday, and three each Thursday, every week. In total, 7 batches (14 runs) were performed until the experiment was completed (accounting for some seedlings that had to be replicated for various reasons). The set of genotypes for each run was selected randomly.

During the experiment, the boxes were replenished with distilled water every two days, to refill to the initial solution level. At the same time, to minimize seedling failure, each single seedling received 10 mL of the nutritive solution, applied with a pipette, near each seed. On the eighth day, the rhizo-slides were opened and shoots were immediately collected. The fresh roots were scanned using a Canon "LiDE210" scanner at 300 ppi to capture the first image then overlapped roots were manually separated and a second scan was done. The individual plant shoot dry weight (SDW) was obtained after oven-drying at 80 °C for six hours.

2.2.3. Image Analysis

The two images of a rhizo-slide were analyzed using SmartRoot software v.3.32 [41] plugin for ImageJ1.46R (http://imagej.nih.gov/ij/download.html). The first image was used to measure only root angles and the second one to assess the other root traits using manual and semi-automatic SmartRoot procedures. Each root of the seedling was traced, semi-automatically, and then SmartRoot automatically generated the corresponding traits. In total, ten variables from the Smartroot output were recorded for each seedling: total root length (TRL), primary root length (PRL), mean length of the other seminal roots (MRL), total root surface area (Surface), mean root diameter (Diameter), total root volume (Volume), root number (RN), and shoot dry weight (SDW). The root angle was determined for each root with respect to the vertical (90°). From this determination, we extracted the maximum vertical angle (MVA) represented by the root growing with the steepest angle, the least vertical angle (LVA) represented by the root growing with the widest angle, and mean vertical angle (MRA) of all the roots, for each seedling.

2.3. Statistical Analysis

The experiment was considered a completely randomized design, with 12 replicates per genotype. Statistical analyses were performed using the REML (Restricted maximum likelihood) procedure with Genstat 18 [42]. Genotypes were considered as fixed factors and replications were considered as a random factor. The "Genotype" factor (n-1 degrees of freedom) was broken down into a single degree of freedom comparison of landraces vs. cultivars (named "Type" effect), and a "within type" factor (n-2) which corresponds to the variation of genotypes within each type. Multiple means separation was carried out using LSD at 0.05 level, for variables in which the F-value for "Genotypes" was significant. A principal component analysis (PCA) and a hierarchical cluster analysis (HC) were performed using the R package FactoMineR [43]. The hcut function was used for tree cutting levels truncation. The R package Factoextra [44] was employed for extracting and visualizing the results. Broad-sense heritability (h^2) was calculated on an entry mean basis using the REML procedure, as follows:

$$h^2 = \sigma^2{}_g/(\sigma^2{}_g + {}_{(}\sigma^2{}_e/r)) \qquad (1)$$

where $\sigma^2{}_g$ is the genotypic variance, $\sigma^2{}_e$ is the error variance and r is the number of replications.

3. Results

3.1. Genotypic Variability

We found remarkable genetic variability for all measured traits, as revealed by the highly significant differences among genotypes in the analyses of variance (Table 2). Significant differences were also found in the "type" comparison for most traits, except for Diameter and RN (Table 2). For the other traits, the mean squares for type were 4 to 12 times larger than those for genotypes.

The means of landraces showed higher or equal mean values compared to cultivars for all traits, except root angle (MRA, LVA, and MVA), which was higher in cultivars (Figure 1). It is worth mentioning that the landrace group presented higher root depth (PRL) than the cultivars.

All traits but SDW were root-related traits so, henceforward all the traits will be referred to generally as root traits unless stated otherwise. All traits (except RN) showed a near-normal distribution (Figure 1) which denotes their polygenic control. A wide range of phenotypic values was observed for most traits (Table 2). The landrace group showed a larger range of variation for TRL, Surface, Volume, and SDW than the cultivars. For the other traits, the cultivars had higher ranges of variation (Tables S1 and S2).

The coefficients of variation (CV) ranged from small values like 5.19 (Diameter) to 24.60 (MRA, Table 2). The exception was the large CV found for MVA, 59.82. When calculated separately for landraces and cultivars, slightly higher CV for most traits were found in landraces compared to cultivars (Table S2). All the traits exhibited high broad sense heritability (h^2), ranging from 0.80 for MVA to 0.98 for MRA (Table 2).

Table 2. Descriptive statistics, broad sense heritability (h^2), ANOVA summary, and correlation coefficients for the root traits assessed in 37 durum wheat cultivars.

	Descriptive Statistics					**ANOVA**		**Correlation**									
Traits	**Min**	**Mean**	**Max**	**CV**	**h^2**	**Genotype**	**Type**	**TRL**	**Surface**	**Volume**	**Diameter**	**PRL**	**SDW**	**MRA**	**LVA**	**MVA**	**RN**
TRL (cm)	54.28	98.49	137.22	13.51	0.90	***	***	1	***	***	ns	***	***	***	**	***	***
Surface (cm^2)	8.25	16.77	24.82	14.74	0.90	***	***	0.95	1	***	***	***	***	***	ns	***	***
Volume (cm^3)	0.0962	0.2326	0.3721	17.03	0.90	***	***	0.83	0.97	1	***	***	***	***	ns	**	***
Diameter (cm)	0.0447	0.0538	0.0620	5.19	0.87	***	ns	0.08	0.38	0.59	1	***	***	***	*	**	***
PRL (cm)	14.32	26.51	32.06	10.76	0.90	***	***	0.55	0.55	0.52	0.17	1	***	ns	**	***	ns
SDW (g)	5.70	14.72	23.50	18.66	0.94	***	***	0.55	0.63	0.64	0.40	0.58	1	ns	**	*	ns
MRA (°)	1.20	30.36	45.69	24.60	0.98	***	***	−0.39	−0.32	−0.23	0.20	−0.01	0.00	1	***	***	ns
LVA (°)	20.40	42.71	61.47	17.81	0.92	***	***	−0.28	−0.23	−0.18	0.12	0.08	0.01	0.76	1	***	ns
MVA (°)	0.00	14.10	43.49	59.82	0.80	***	***	−0.25	−0.20	−0.15	0.12	−0.27	−0.13	0.62	0.25	1	**
RN (no.)	4.00	5.32	6.00	9.13	0.87	***	ns	0.37	0.32	0.26	−0.22	−0.01	0.06	−0.09	0.02	−0.14	1

*, **, ***: sources of variation in the analyses of variance or correlation coefficients significant at $p < 0.05$, 0.01, and 0.001, respectively. TRL: Total root length, Surface: total root surface area, Volume: Total root volume, Diameter: mean root diameter, PRL: Primary root length, SDW: Shoot dry weight, MRA: Mean root angle, LVA: Least vertical angle, MVA: Maximum vertical angle, RN: Root number.

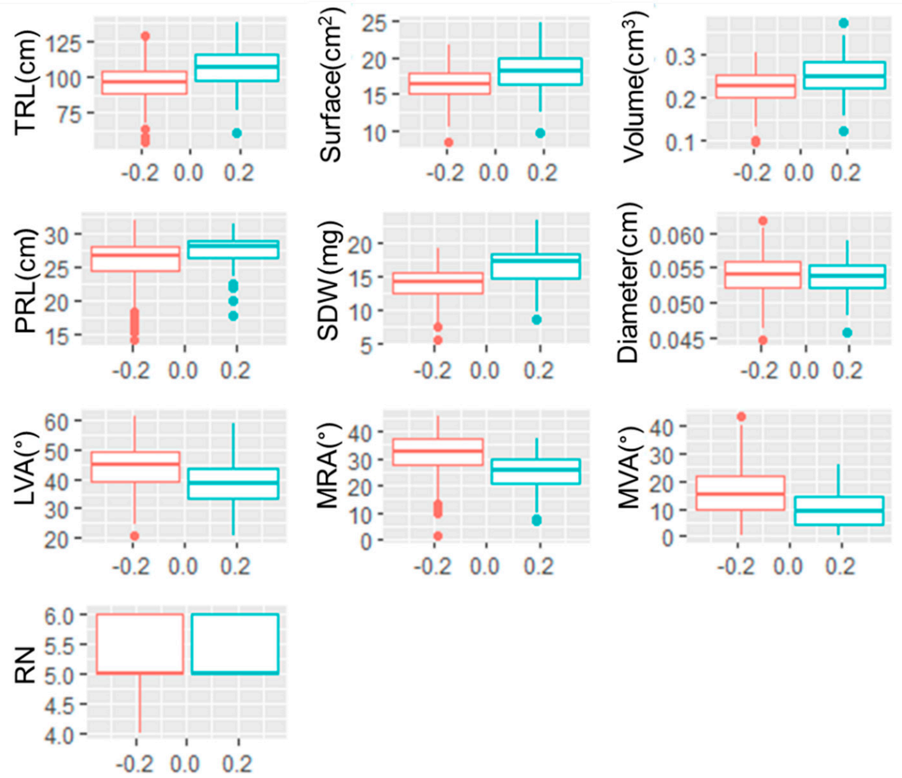

Figure 1. Boxplots for root traits for the cultivar (red) and landrace (blue) groups. Horizontal lines splitting the boxes indicate the median values; box limits indicate the 25th and 75th percentiles; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles; outliers are represented by dots. Variable names coded as in Table 2. Genotype mean values are in Table S1.

3.2. Relationships between Traits

Highly significant correlations were found between most traits (Table 2). TRL, Surface and Volume were highly and positively correlated among them. There were moderate positive correlations between TRL, surface, and Volume, with PRL, SDW, RN, and negative ones with root angle variables (seedlings with higher TRL, Surface, and Volume tended to have steeper root angles). Seedlings with higher RN tended to have roots with thinner root diameter, indicating that there could be some kind of compensation between these traits (more roots with a finer diameter and vice versa). Interestingly, seedlings with higher primary root length produced more shoot biomass. Performing correlations between traits within each group (cultivars and landraces) showed, in general, similar patterns to the correlations performed for the entire dataset (Table S2). The moderate relationship of PRL with MVA and RN disappeared in the landrace group, compared to the cultivars and the whole dataset (Table S2).

3.3. Time Trends of Root Traits

When the genotypic means were plotted against year of release of the genotypes, different trends were observed (Figure 2 and Figure S2), in which, all the traits presented significant regression coefficients except Diameter, RN and PRL (Table S3). This trend was largely influenced by the comparison of landraces vs. cultivars because landraces are older. The trend was positive or negative depending on the trait. Overall, cultivars reduced their seminal root length and developed a shallower root angle compared to landraces (Figure 2). The root surface and volume of root presented the same trend as root length, as they were highly correlated, as mentioned above. MVA and LVA showed the same trend as MRA. No substantial variation was observed for RN, Diameter, and PRL. Regarding the shoot, a remarkable and steady reduction in SDW over the years was detected (Figure 1 and Figure S2).

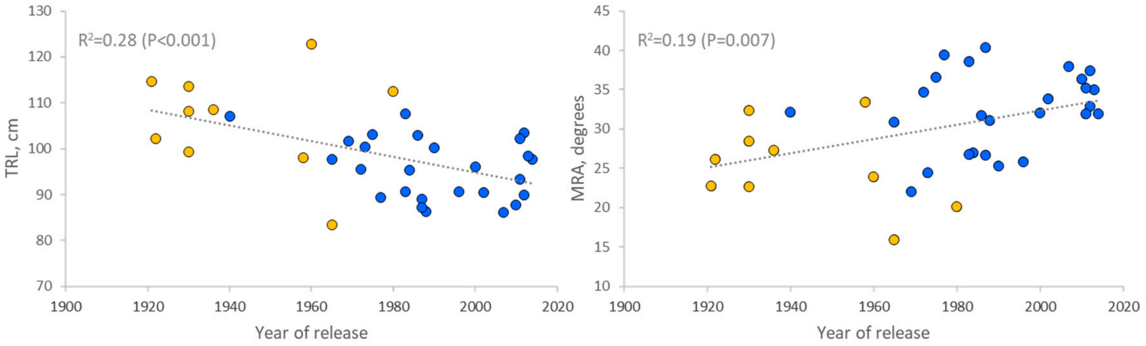

Figure 2. Time trends for total root length (TRL) and mean root angle (MRA) in seedlings of 37 durum wheat varieties. Yellow symbols correspond to landraces; blue symbols correspond to cultivars. The coefficients of determination (R^2) of the regression lines are indicated in each graph.

3.4. Grouping of Genotypes According to Root Traits

The first two principal components explained 69.63% of the total variation (Figure 3A). The first component (46%) was most related to Surface, TRL, Volume, and SDW, with the respective contributions of 20.19, 19.04, 18.16, and 11.51 (Table S4). MRA, LVA, and Diameter had the highest loadings for the second component (PC2). Correlations between these traits are discussed above (Table 2). Thus, the first axis (PC1) was related to root size traits and the second one to root architecture traits.

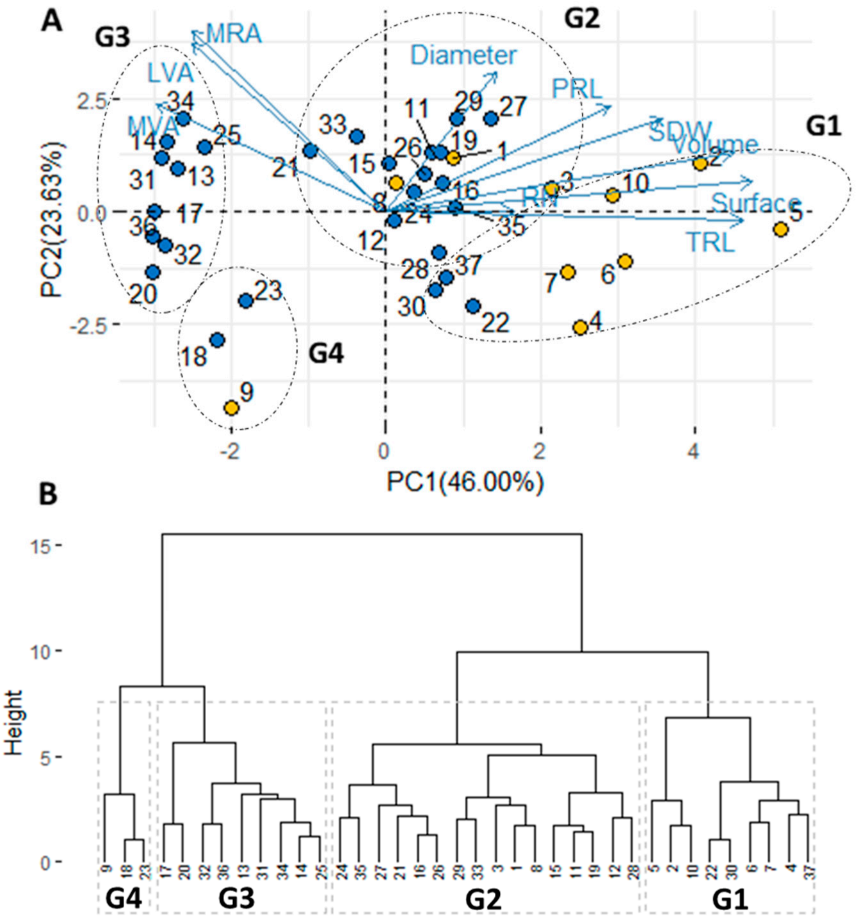

Figure 3. Biplot of the first two principal components (**A**) and dendrogram resulting from hierarchical clustering (**B**) based on seedling traits for 37 durum wheat genotypes. Ellipses in (**A**) encompass the individuals according to the clustering presented in (**B**). Yellow symbols correspond to landraces; blue symbols correspond to cultivars. Genotypes coded with numbers as in Table 1.

Genotypes were better distributed along with the first component, as a result of the contrasting position between landraces, many with large positive scores on PC1 (due to their higher root size and shoot weight) and the cultivars, with lower positive or negative scores in PC1, so the discrimination between these two groups was clear (Figure 3B). From the hierarchical classification, which was carried out based on the original data, four groups were created (G1 to G4) (Figure 3B). G1 was mostly formed by landraces. G2 was the largest one and was constituted by cultivars, and two landraces. This group was at a central position in the biplot graph (Figure 3B), presenting close to average values for most traits. G3 was located on the negative side of PC1, contrasting with G1 by having a relative smaller root size. Finally, the last group (G4) was formed by only three genotypes depicted on the negative quadrant, for both PC1 and PC2, having smaller values for both classes of root traits; fine, steeper root angle and reduced root traits related to biomass. This group included landrace Montpellier (genotype 9), which showed a special root system architecture compared to other landraces, with steeper root angle, and lower SDW, closer to two cultivars from Italy and ICARDA.

4. Discussion

The durum wheat collection used in this study was assembled to explore the seminal root variability present in a set of genotypes cultivated in Algeria, with a historical perspective on the possible changes caused by modern breeding. The method chosen enabled data acquisition and processing of 444 single plants, by one person, in two months. Its performance could be easily expanded by increasing the number of boxes and operators. Therefore, it is amenable to the scale needed for the type of studies carried out in plant genetics and breeding. Root number together with root length, the main results of this type of experiment, describe how extensively the seminal axes can potentially explore the rooting volume. These easily measurable traits at an early stage can have agronomic implications. For example, root spread angle is an additional feature whose variation can influence how crops cope with water-limited conditions and/or other environmental constraints, such as high pH, toxic ions, or low nutrient availability [45,46]. The root angular spread at an early growth stage can be used to predict the partitioning of root biomass in the soil profile at the adult plant stage [5,27,28], a feature relevant for water use efficiency in wheat [21,47]. Therefore, artificial systems are efficient at revealing phenotypic (and presumably genetic) variability, but its implications on agronomic performance must be validated later under field conditions.

4.1. Large Genotypic Variation for Seminal Root Traits

An overview of the results found in different studies sheds more light on the actual genetic variation available for seminal root traits, better than any single study. Differences among studies may be partly due to slight differences in the experimental methods, but also to the size and scope of the genetic material used. Nevertheless, some meaningful conclusions can be derived.

We found significant genetic variation for all traits. We found a range of values for the least vertical root angle (LVA) from 20.40° to 61.47°. Multiplying these values by two (range from 40.80° to 122.94°) allows the comparison of our study with others, in which the values of the total opening of the angle of the root system was reported. Our range was superior to those found by others in durum [47] and bread wheat [24,29]. Our wheat genotypes displayed similar low ranges of variation in mean root number as in similar studies in durum [47,48], with a slightly higher mean. In our genotypes, the sixth root was present in about a third of all genotypes, with no significant differences between landraces and cultivars. This is a similar proportion than found in a study of Mediterranean and North-American elite material [47], with the striking difference that in the former study they reported almost absence of the sixth seminal root in native Mediterranean materials [47]. Neither sample of landrace materials was large enough to derive definitive conclusions from these studies, but at least we can say that Algerian landraces are not more likely to lack the sixth seminal root than modern cultivars.

Based on the coefficients of variation, overall, landraces showed higher slightly variability for most traits, especially for root angle, even though the sample size was lower than for cultivars. Previous reports indicate that native Mediterranean landraces are likely to provide additional genetic variability for root architecture [46], particularly in wheat accessions that experienced long-term natural selection in drought-prone environments [49], and in barley [50]. Overall, the Algerian landraces showed sizeable genetic variation for most traits, indicating that they harbor relevant root morphology variation that should be further investigated by geneticists and breeders.

4.2. Classification of Durum Wheat Genotypes According to Root Morphology

Overall, genotypes with higher root length tended to have larger root number, as found in a previous study [47], and a narrower root angle. Other authors [24,51] found no correlation between root angle and root number. Sanguinetti et al. [47] also found no correlation of root angle with other traits and suggested that the root angle was controlled by an independent set of genes. In our study, however, given the negative correlation between MRA and root size traits, we cannot rule out that these two traits are controlled by the same set of genes.

We found that higher root length and Diameter were associated with higher SDW (r of 0.55 and 0.40, respectively, Table 2), suggesting a size effect that affected the whole plant. Rather similar observations were done in the Spanish core collection of tetraploid wheat, but the plant size effect was visible for subsp. *dicoccon* and *turgidum*, but not for *durum* [25]. Correlation between root length and volume and SDW was also found in hexaploid wheat [52]. We found no correlation between RN and MRA, in agreement with previous studies [24,51]. It seems that an overall plant size effect that affects harmonically roots and shoots is common in wheat species.

Our genotypes displayed different seminal root system patterns, from vigorous and steep to a small and shallow root system. These root patterns may be related to phylogenetic relationships, regional origin, and functional plant adaptation to different environments, as indicated in previous studies [53]. There were differences in the length of the seminal roots of single plants. This was made evident by calculating the difference between the length of the primary root (PRL), and the average of the rest (MRL). G2 and G3 had a higher difference between PRL and the mean length of other roots (MRL), compared to groups G1 and G4, which had roots with more similar lengths (Table S5). G2 genotypes combined a significantly longer primary root (Table S5) with the largest difference between it and the other seminal roots (together with G3). This rooting pattern, based on dissimilar growth of the roots, could have an impact on overall soil exploring capacity that should be explored further, particularly its usefulness in semi-arid environments, to access to stored water at deep layers at critical periods (flowering and grain filling), while keeping enough shallow roots to take advantage of in-season precipitations.

Two groups (G1 and G3) showed the highest contrast in the multivariate analysis (Figure 3). G1, with a majority of landraces, displayed a vigorous seminal root system, in contrast with G3, formed entirely by cultivars with small root systems. Our finding was in agreement with the study of a collection of 160-durum wheat landraces [33] in terms of larger seminal root size. This study found that landraces coming from the eastern Mediterranean region (Turkey), the driest and warmest areas considered in the study, showed the largest seminal root size and widest root angle compared to landraces from eastern Balkan countries. The authors claimed that these differences were due to the adaptations of landraces to the contrasting environmental conditions of these two regions. The larger root size and wider root angle from Turkish landraces would allow better exploration of the full soil profile and better water capture. Among the four groups found in this study, no one combined the highest MRA and TRL, comparable to Turkish landraces. Therefore, there could be room for improvement for the root systems of durum wheat for Algeria. Crosses to combine these traits in a single genotype should be devised, and Turkish landraces could be tested in Algerian conditions, to assess their potential.

In our germplasm, the landraces showed on an average narrower angle and higher root size. Previous studies on Mediterranean durum wheat [33] found that the genotypes with the narrowest angle came from the western Mediterranean region and that they also had heavier grains [54,55].

Additionally, it was reported that *Triticum turgidum* subsp. *dicoccon* landraces coming from cooler and wetter zones had shallower seminal root systems than those from warmer and drier areas [25]. The subsp. *durum* landraces, developed in warmer and drier areas, tended to have larger and steeper root patterns than landraces coming from cooler and wetter zones. Accordingly, the root system architecture of the Algerian landraces would indicate adaptation to a warm and dry environment. Other studies have found different root morphologies in apparent adaptation to stressful conditions. For instance, the drought-tolerant bread wheat cv. SeriM82 has a compact root system [21], associated with a limited water use early in the season, facilitating access to stored water later in the reproductive phase. Contrary to our landraces, SeriM82 exhibited less vigorous shoot growth. In contrast with our findings, a study of bread wheat germplasm grown historically in the semi-arid northwestern of China [56] found that breeding caused a narrowing of the seminal root angle, reduced root number, and increase of primary seminal root length. In that study "newer cultivars produced higher yields than older ones only at the higher sowing density, showing that increased yield results from changes in competitive behavior." This view was confirmed and expanded later [57], confirming that the advantage of new Chinese wheat cultivars came from the attenuation of inter-plant competition and increased plasticity in root morphology. A seminal root architecture with fewer, longer seminal roots with narrower root angle, would overlap less with neighbors, leading to less competition between individuals [58], and these trends agree with the hypothesis of weakening of "selfish" traits [59].

The shift in root morphology observed in Algeria in the step from landraces to modern cultivars does not conform to the scenario described in those works. There was a reduction of overall root length and volume after the advent of modern breeding, which could be consistent with the reduction of inter-plant competition but combined with the widening of the root angle, which does not bode well with that hypothesis. It seems that wheat breeding may have resulted in different trends for root morphology in different parts of the world. This could be the result of the adaptation of Algerian landraces to agronomic conditions different from current agriculture. The difference in rooting patterns between landraces from different geographical areas and cultivars may lie in the agronomic environments in which they were developed. In general, modern durum wheat cultivars were bred under high plant densities [57], whereas landraces were grown in stands with density adapted to the environment. The morphology of Algerian landraces (long seminal roots growing in steep angles) conforms to the "steep, cheap, and deep root ideotype" [60], and could be the result of adaptation to accessing water in deep soil layers. Further studies with adult plants are needed to evaluate if root features of seedlings are maintained when the competition between individuals for root growth is increased (as the seminal and nodal roots require more space and resources than just the seminal roots of the seedlings). A shovelomics experiment is being carried out with the same genotypes, which could elucidate this issue at least for some measurable traits like root angle.

The high SDW of our durum landraces compared to cultivars could be related to the lack of dwarfing genes in the landraces. This hypothesis was already confirmed previously for bread and durum wheat for some height reducing genes [61], which reduced the first seedling leaf growth in *Rht* genotypes compared with the corresponding tall wheat lines.

4.3. Conclusions and Perspectives

We have found wide genetic variability in a collection of durum wheat genotypes cultivated in Algeria and unraveled a possible historic trend that sheds light on the outcomes of modern breeding. An important issue is to what extent this variability found at the seedling stage can reflect the variability in the field with the same genetic material, more precisely, which traits can be consistent across plant phases (seedling and adult plant), enabling the selection at the early seedling stage. If this relationship is not found, then the room for the testing of seminal root traits is very limited. Experiments to evaluate this relationship are ongoing.

Overall, landraces showed a larger root size and steeper root angle. These two traits could be involved in the adaptation of landraces to water-stressed environments. The dwarfing genes seem to influence biomass partitioning; screening the current germplasm for these genes would elucidate this issue. The root size and shape in our data indicated some independence that would open opportunities to design cultivars with the desired combinations of traits.

Overall, the current genotypes present a diverse root system architecture, from compact deep-rooting to wide shallow one. This opens the opportunity to test the four different root ideotypes found (G1–G4) for functional implications under water and nutrient-limited environments. Based on the above results, we hypothesize that root architecture difference between cultivars, landraces (or steep deep vs. shallow root systems) may result in different strategies of adaptation to the availability of water and nutrients over the soil profile.

Supplementary Materials: The following are available online at http://www.mdpi.com/2073-4395/10/5/713/s1, Table S1. Mean values and standard errors (12 replications) of the seminal root traits for the 37 durum wheat genotypes. Table S2: Descriptive statistics and correlation coefficients for seedling traits, calculated separately for the cultivar and landrace groups. Table S3: Results of linear regressions of traits over years of release. Table S4: Contribution (%) of the traits to the first two principal components (PC1, PC2), as represented in Figure 3A. Table S5: Means comparison between groups formed by hierarchical clustering for the traits assessed. Figure S1. (A) One-week-old durum wheat seedlings in the rhizoslide system; (B) pictures of two genotypes contrasting for root angle, landrace Gloire de Montgolfier (left) and cultivar Oued El Berd (right); (C) schematic representation of a glass box, holding 6 glass plates, each holding two rhizoslides. Figure S2: Time trend of seminal root traits over the year of release.

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