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REVIEW

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Opportunities to improve the seasonal dynamics of water use in lentil (*Lens culinaris* Medik.) to enhance yield increase in water-limited environments

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Abstract

Lentil (*Lens culinaris* Medikus) is one of the most important annual food legumes that plays an important role in the food and nutritional security of millions in the world. Lentil is mainly grown under rainfed environments, where drought is one of the most challenging abiotic stresses that negatively impacts lentil production in the arid and semi-arid areas. Therefore, development of drought-adapted cultivars is one of the major objectives of national and international lentil breeding programs. The goal of this review is to provide a report on the current status of traits of lentil that might result in yield increases in water-limited environments and identify opportunities for research on other traits. Lately, traits that are either related to developmental plasticity and/or altered rooting and shoot characteristics have received considerable attention in the efforts to increase lentil yield in water-limited environments. However, two traits that have recently been proven to be especially useful in other legumes are still missing in lentil drought research: early partial stomatal closure under soil drying, and limited-transpiration under high atmospheric vapor pressure deficit. This review provides suggestions for further exploitation of these two soil–water-conservation traits in lentil.

Keywords: Lentil, Drought, Limited transpiration, Vapor pressure deficit, Soil drying, Root

Introduction

Cultivated lentil (*Lens culinaris* Medikus) is an important cool-season legume, particularly within countries in North America, Australia, South Asia, West Asia, and North Africa [9]. The seeds are a cheap source of protein with a high vitamin and mineral content, thus contributing to the fight against hidden hunger. However, lentil yields are generally low. The most recent available data show that globally in 2014, 4.5 million tons of lentils was produced on 4.8 million hectares of land [10] for an average yield of 0.94 tons ha^{-1}. This average yield is comparable to chickpea (*Cicer arietinum* L.), which has a global average yield of 0.96 tons ha^{-1}. On the other hand, legumes like soybean [*Glycine max* (L.) Merr.] have average yields that can reach 3 tons ha^{-1} or more, highlighting an apparent potential for lentil yield improvement.

In addition to the nutritional benefits of lentil, lentil can be useful in improved cropping systems due to its symbiotic nitrogen fixation capability. It has been estimated that lentils reduce dependency on inorganic nitrogen fertilizer and improve soil health because they fix nitrogen at an average rate of 80 kg N ha^{-1} year^{-1} [8, 35]. Moreover, with its ability for nitrogen fixation and carbon sequestration in soils, lentil helps in enhancing the sustainability of the cereal-based farming when it is included as a rotation crop. Lastly, the lentil straw is valued as animal feed in developing countries [6].

Lentil, however, is commonly grown in developing countries on marginal lands with poor soil in rain-fed environments [14]. Like many other crops that grow in

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the Mediterranean and semi-arid zones, lentil often faces terminal drought stress during the reproductive phase as a consequence of diminishing rainfall or plant available water and rising temperatures. In such cases, what is usually called "drought tolerance" could be, in part, the consequence of plant constitutive traits that affect how soil water is used earlier in the growing season when water is non-limiting to plant transpiration [66]. The present yield of lentil in India is reported to be low [25] due to terminal drought and high temperatures, particularly during flowering and seed growth [32]. Climate change is expected to increase temperatures and an increase in extremes of rainfall as well as an increased risk of drought in many areas where lentil is grown [5]. Therefore, development of drought-adapted cultivars is one of the major objectives of national and international lentil breeding programs [8].

This paper reviews the current status of research on traits that can alter the pattern of crop water use resulting in the possibility of yield increase of lentil under water-deficit conditions. For decades, two main topics have received much attention in that area that are developmental plasticity, and altered rooting and shoot characteristics. This review will briefly highlight investigations on individual traits that are either related to developmental plasticity (phenology) or below ground traits. Two additional water-conservation traits considered in this review that have been missing in lentil drought studies are initiation of partial stomatal closure early in the soil drying cycle, and partial stomatal closure at elevated atmospheric vapor pressure deficit. This review considers the opportunities for lentil yield increase in water-limited environments by addressing these two traits linked to temporal dynamics of water use.

Developmental plasticity

Lentil is an annual herbaceous plant with indeterminate growth exhibiting high variation in its growth habit: single stem, erect, semi-erect, compact growth or much-branched low bushy forms [13, 14, 31, 42]. Developmental plasticity can involve one or all of these plant characteristics. In particular, the ability of plants to adjust the duration of different growth phases in response to the availability of soil water during the growing season enables a plant to produce higher yields when the growing period is longer [52]. Such plasticity is an important mechanism in unpredictable climates and under unfavorable soil water regimes. Studies have shown that drought escape (early flowering and pod setting) is a common drought strategy for lentil in environments where water deficits and high temperatures at the reproductive stage induce senescence and early maturity [7, 51, 54, 64, 69].

Siddique et al. [54] have shown that while early flowering and accelerated phenological development gave higher seed yields and higher yield stability than late flowering under terminal drought. Thus, drought-induced early maturity could be advantageous in some dry seasons, but achieving a higher yield under well-watered conditions is often associated with longer growth duration, late flowering and greater water use [51]. Therefore, drought escape is not always a viable breeding strategy for lentil if increasing yield under a range of water conditions is the objective.

Root and shoot characteristics

The value of root and shoot characteristics for drought adaption in lentil has often been judged based on the sole criterion of yield increase. Although yield is definitely the ultimate criterion for any breeding effort, yield itself cannot be considered as a trait since it is an integrated parameter, which involves many different traits at totally different organization levels of a plant: subcellular-, cellular-, tissue-, organ-, whole plant-, and stand-level [17]. Therefore, data on "yield phenotypes" alone are inappropriate in efforts to advance specific traits that can ultimately contribute to yield under defined environments [17].

The root system of lentil is characterized by a slender taproot with a mass of fibrous lateral roots that may be shallow, intermediate or deep [43]. High genetic variation has been reported for root traits such as taproot length, lateral root number, total root length, and total root weight for lentil germplasm from different origins [13, 14, 25, 26, 31, 42]. The high heritability estimates that were reported by these authors indicate the feasibility of making use of this genetic variability for the development of drought-adapted cultivars. Deep, well-developed roots and vigorous shoots at early-seedling stage were associated with drought escape and tolerance in lentil [21, 42] as a way to ensure uptake of water and nutrients. Sarker et al. [42] reported high correlations between stem length, taproot length, and lateral root number with lentil grain yield under drought.

Given the complexity of drought, it is not surprising that root and shoot traits have been found to interact in the expression of tolerance. Kumar et al. [25] assessed genetic variability for 12 attributes including root and shoot traits among lentil genotypes originating from rainfed areas adapted to short-season environments. They found correlations between the individual traits and achieving a higher yield under drought conditions. More recently, Mishra et al. [32] found correlations between chlorophyll content and stability, increased accumulation of osmotically active solutes, soluble sugars and proline, lower H_2O_2 and malondialdehyde (MDA) contents, and lower carbon isotope discrimination (ΔC_{13}) values and drought resistance in lentil. This study was conducted on a very limited number of genotypes (two) and drought was imposed at three different phenological stages (vegetative, flowering initiation and pod development). It is likely that the results cannot be extrapolated since the reported correlations are most probably related to the particular conditions of the study.

The above-mentioned studies remain descriptive and correlative and allow limited mechanistic explanation of the underlying functional processes, especially in terms of water uptake and water-use dynamics. For instance, although the selection for deeper rooting to access water at depth could be potentially interesting, it might lead to faster soil water depletion, which would be a problem for crops depending on stored soil moisture. Likewise, rapid development of leaf area is likely to result in more rapid depletion of soil water. This functional aspect of the changes in root and shoot and root characteristics on the temporal dynamics of water use have been overlooked. Thus, it is not possible to obtain a clear and univocal indication of root and shoot functionality when just relying on structural features.

A better integration of different, yet interactive, traits in their role in the plant's adaptation to water limitation is highly needed by having a better understanding of the dynamics of plant water use under both under well-watered conditions and upon exposure to water deficits [66].

Early transpiration decrease with soil drying

Studies indicate that sufficient amounts of water at key times during the plant cycle may be more important than total water availability across the whole cycle [30, 37, 66]. One plant trait to achieve conservative water use to increase water availability during reproductive develop is partial stomatal closure at a higher soil water content during the soil drying cycle than normally occurs in most plants [28, 57]. If there is a late-season water deficit, genotypes with a conservative water behavior have the possibility of using the conserved soil water to sustain physiological activity during seed fill and generate a greater yield than genotypes that do not have the trait [56].

A study conducted on chickpea (*Cicer arietinum* L.), a crop that is grown in similar regions as lentil, showed that plants that exhibit early stomatal closure to reduce transpiration rates (TR) when soil water deficit occurs, save water for more critical plant stages like reproduction and grain-filling under rain-fed environments [68]. Transpiration does not decrease immediately after water is withheld, but rather there is a threshold soil water content at which transpiration rate declines [34]. The initiation of a decline in transpiration rate with soil drying occurs at certain fraction of transpirable soil water (FTSW) thresholds [2], which indicates a significant and exploitable water-saving trait. Figure 1a illustrates the changes in transpiration as soil water content decreases and shows a plot of transpiration rate of plants subjected to soil drying relative to well-watered plants versus the FTSW remaining in the soil for three different cultivars displaying early, normal, and delayed transpiration decrease with soil drying [41].

The soil water is represented by a reservoir characterized by its total transpirable soil water (TTSW), representing the difference between maximum and minimum (extractable) water content, the actual transpirable soil water (ATSW) and the fraction of transpirable soil water

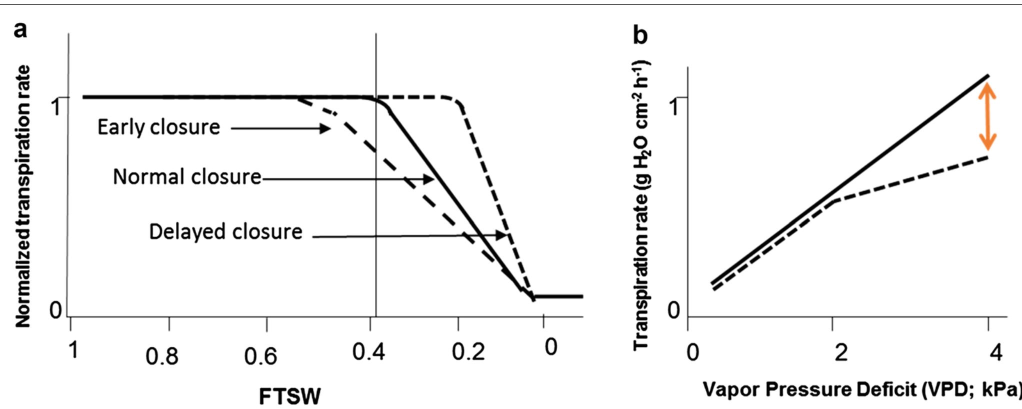

Fig. 1 **a** Plot of transpiration rate of plant subjected to soil drying relative to well-watered plants versus the fraction of transpirable soil water (FTSW) remaining in the soil (adapted from Sadok and Sinclair 2011). **b** Plot of transpiration rate versus vapor pressure deficit (VPD) for two genotypes with contrasting response to VPD: on where transpiration rate increases linearly with increasing VPD (*continuous line*) and the other showing the limited transpiration rate (*dotted line*) (adapted from [61]

FTSW is calculated as the ratio of ATSW to the TTSW remaining at any time during the season [58]. For example, in chickpea (*Cicer arietinum* L.), a conservative transpiration decline, occurring at a high FTSW when the soil is still relatively wet distinguished drought-adapted and drought-sensitive genotypes [68].

In lentil, experiments conducted in Western Australia, with a Mediterranean-type climate, showed that seed yield was not correlated with total water use or with water use before flowering [27], but was positively correlated with post-flowering water use [53]. Evidence in groundnut (*Arachis hypogaea* L.) [37], pearl millet (*Pennisetum glaucum* L.) [22, 23], and wheat (*Triticum aestivum* L.) [11] indicates that lower vegetative rates of water use leave more water available for grain filling. Under rainfed environments in Nepal and Jordan, early-sown lentils produced greater yield as a result of adequate vegetative mass, longer grain-filling periods, and higher pod number [32, 35, 49]. It is, however, surprising that these findings have not been extended to study seasonal dynamics of water use in regard to early-season soil water conservation and increased water availability to complete seed filling under drought conditions [28, 59].

Partial stomatal closure under high atmospheric vapor pressure deficit (VPD)

A specific trait that is especially promising for allowing conservative soil water use is one in which transpiration rate is limited under high, midday vapor pressure deficit (VPD). Figure 1b shows a plot of transpiration rate versus vapor pressure deficit for two genotypes with contrasting responses to high VPD: a linear increase in transpiration rate with increasing VPD and a limited-transpiration rate above a certain VPD breakpoint. The partial restriction of transpiration rate under high VPD limits the rate of soil water use, and raises the transpiration efficiency, allowing the crop to conserve water to support plant growth later in the season when drought develops [4, 62].

Sinclair et al. [59] examined the possible benefits for sorghum (*Sorghum bicolor* L.) from limiting transpiration rate to a constant, maximum transpiration rate value under high levels of air VPD even when soil moisture contents were high. Using a crop model that simulated sorghum growth in Australia, they reported the possibility of a yield increase in about 75% of the seasons over 100 years at four different locations.

Considerable evidence has confirmed that the limited-transpiration trait, assessed under well-watered conditions, is expressed in selected genotypes of several crop species, including soybean [12, 20, 40, 45, 60], peanut (*Arachis hypogaea* L.) [3, 47], sorghum [19, 24, 39, 48], chickpea (*Cicer arietinum* L.) [68], pearl millet [22], cowpea (*Vigna unguiculata* L.) [1], maize (*Zea mays* L.) [18, 67], and wheat [38, 44]. With regard to lentil, no information is available to date on diversity among lentil genotypes in the transpiration response to vapor pressure deficit (VPD). Since lentil is grown in environments with high VPD conditions (hot and dry areas) in the post-rainy season (South-Asia) where scanty rainfall is frequently observed, the limited-transpiration trait might be especially important in this particular region.

Model assessment of water conservation traits

The impact of water-conservation traits on lentil productivity is likely to vary across growing seasons with geography, environment type, and level of expression of the trait. The positive consequence of partial stomatal closure with soil drying or under high VPD is that transpiration rate is decreased early in the growing season so that there is conservation of soil water for use later in the season to complete reproductive growth. The initiation of soil water conservation will have the double benefit of increasing transpiration water use efficiency, and conserving soil water for use later in the growing season as drought develops in comparison with those plants that delay their stomatal closure [62]. If the period of water-deficit is sufficiently long, the plant genotype with partial stomatal closure with soil drying will be better position to sustain CO_2 assimilation and to produce greater yield. However, if there is late-season rainfall or if the decrease of photosynthetic rate due to partial stomatal closure is too high, the benefit of conserved water would not be obtained, thus, lines with water-conservation traits lead to equal or lower yield than line that does not express these traits [62]. Considering the breadth of geographical area and environments in which lentil is grown, the assessment of the potential benefits of the water-saving traits on lentil yield can only be done effectively by using crop simulation modeling.

Not only is there no information among lentil genotypes about the expression of limited-transpiration traits, there is no indication of the possible yield benefit of developing genotypes that express these traits. The complexity associated with genotype × environment × management interactions can be explored in a quantitative assessment using a mechanistic simulation model [30, 63]. Simulation studies have proved useful to evaluate the impact of a limited-transpiration rate at high VPD in sorghum [59], soybean [61, Sinclair et al. 2014] and maize [30]. Simulations of chickpea—another cool-season legume—have shown that the limited-transpiration trait can result in 3–7% increased grain yield in Iran depending on location and soil depth [63].

Therefore, simulation modeling efforts are also needed to do a geospatial assessment of the likely effect of genotypic variation in the limited-transpiration traits on yield performance [61, 63] of lentil at a regional scale. A lentil version of the SSM-Legumes model was developed and proven robust in evaluating variation in phenological development and yield of lentil in a range of environments, with different rainfall patterns, in the Middle East [15], and investigating the roles of changing phenology and sowing dates on the possible expansion of lentil culture in East Africa [16]. This model needs to be applied to assessing the potential values of these traits on water-limited lentil.

Conclusion

Two water-conservation traits seem to be especially promising in increasing lentil yield in water—(1) limited environments early partial stomatal closure under soil drying, resulting in soil water conservation and (2) limited-transpiration under high atmospheric vapor pressure deficit. A multi-level, multi-faceted approach needs to be applied to study these traits in lentil involving simulation studies using a mechanistic crop simulation modeling and physiological screenings.

Authors' contributions

MEG, TRS conceived the paper. MEG, TRS, FK, and JG wrote the paper. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Consent for publication

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