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Water Deficit at the Anthesis Stage Induces Early Leaf Senescence and Affects Dry Matter Accumulation and Remobilization Efficiency in Black Gram (*P. mungo*, L.)

Gunjan Garg[1*], Sanjay Kataria[2]

[1*] School of Biotechnology, Gautam Buddha University, Greater Noida (NCR) 201308, India.

[2] Department of Botany, BSA College, Dr. B.R.A University, Agra (U.P), India.

*Corresponding author: Gunjan Garg, Mo. No.: +91-9717968020, Fax no. +91-120-2344245, E-mail: gunjan@gbu.ac.in

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ABSTRACT

To investigate the effects of two levels of irrigation regimes (full irrigation [FI], i.e., normal water supply; and limited irrigation [LI], i.e., limited water supply) on growth and grain yield of two varieties of *Phaseolus mungo* (PU 19 and Type 9), a greenhouse experiment with three replicates was conducted from February to May in 2005. Results showed that pots in which water-deficit stress was introduced at the anthesis stage induced early senescence in both varieties (PU 19 and Type 9). Leaf chlorophyll content declined more quickly as leaves approached maturity for LI plants than for FI plants. The experiment demonstrated that var. PU 19 was a superior variety under both normal and limited irrigation conditions, compared with Type 9. It maintained high relative water content (RWC_L) and net assimilation rate (NAR_L) in leaves under LI. PU 19 had the highest amount of remobilized dry matter (ARDM), remobilization efficiency (REE), remobilization efficiency percentage (REP), seed weight and grain yield (GY) under LI. We therefore conclude that senescence and remobilization are apparently promoted by a limited water supply or drought stress, and they are coupled processes. Studying RWC, NAR and leaf senescence can be used as indirect selection criteria for grain yield. This would be a beneficial for understanding of the many physiological mechanisms that confer water-deficit tolerance, leading to the development of leguminous plant species better adapted to such environments.

Keywords: leaf senescence, net assimilation rate, remobilized dry matter, grain yield.

INTRODUCTION

Drought is among the most common abiotic stresses. It is a major constraint affecting crop production in arid and semi-arid climates. According to Wu [1], two types of drought resistance exit: (i) drought escape, which is the ability of a plant to complete its life cycle before a serious water-deficit develops; (ii) drought tolerance with high tissue water potential, which is the ability of a plant to endure dry periods by maintaining a high plant water status. The identification of adaptation mechanisms to drought is of considerable importance, especially for pulses, because they play significant ecological and economic roles [2]. Legumes exhibit high growth potential in substrates poor in nitrogen; they increase soil fertility and can resist high levels of disturbance [3]. Pulses are considered valuable for re-vegetation. Even though legumes seem to have a significant and multi-functional role, their hydrodynamic responses to impending environmental drought remain little known [4]. Among the environmental cues, limited water and nutrient availability (especially nitrogen) are major factors that adversely affect plant life in many ecosystems.

Plants have evolved mechanisms by which leaf senescence can be induced by these stresses to reallocate nutrients to the young leaves, fruits or flowers (reproductive organs), allowing the plant to complete its life cycle under stressful conditions [5, 6]. Thus resorption of nutrients from senescenced leaves is an important nutrient conservation mechanism for plants. The initiation of senescence also depends on the growth phase in which the stress was imposed. During leaf senescence, cell constituents such as proteins and chlorophyll are degraded and transported to younger leaves for building up of new structures [7, 8]. This process is called nutrient resorption, and is a form of adaptation in low nutrient environments or under stress conditions. Thus, leaf senescence is a part of the developmental program of plants; through senescence, plants are adapted for growth in disturbed environments and have evolved traits that are compatible with the high mortality risks from the environment. *Phaseolus mungo* (L.) is a warm season crop. It is normally grown in areas with an average annual temperature of 25–35°C and an average annual rainfall of 600–1000 mm. Temperature is an important physical parameter of the environment that determines the success or failure of a plant variety in a particular locality, which in turn depends mostly on germination ability. The present work investigates the response of two varieties of *P. mungo* that, were grown under two moisture regimes.

The aim of this work was to identify early events in the sequence of morphological and biochemical events associated with leaf senescence of plants experiencing water deficiency after the anthesis growth phase. We tested whether these sequences of events differed under control (FI) and water-deficit (LI) conditions. We simultaneously analyzed changes in remobilization of assimilates by measuring remobilized dry matter (ARDM), remobilization efficiency (REE), relative water content of leaves (RWC_L), net assimilation rate (NAR_L), chlorophyll contents of leaves of *P. mungo*, L. (var. PU 19 and var. Type 9).

MATERIALS AND METHODS

Plant material

Seeds from five different varieties of the legume *Phaseolus mungo* (family: fabaceae) were procured from local National Seed Corporation (NSC) shops and were tested for seed vigor. The varieties with the best germination rates and vigor var. PU 19 and var. Type 9, were selected for further study.

Growing conditions and irrigation treatments

The seeds were mechanically scarified prior to germination and the experiment was conducted at the crop pavilion, Department of Botany, Chaudhary Charan Singh University, Meerut, India, from February-May, 2005. Each experimental unit was a 1.5 liter pot filled with top soil (pH 6.7 - 7.2) obtained from the farmland adjacent to the crop pavilion and planted with 10 seeds of each variety. When the seedlings were approximately 10 cm in height above the soil surface, they were thinned to five seedlings per pot. Prior too newly flowering buds appearing on both *P. mungo* varieties (i.e., anthesis); the experimental pots were grown under similar conditions and were supplied with control levels of water (full irrigation, hereafter (FI'). At 8 WAP, when newly flowering buds were apparent, the experimental pots of each variety were divided into two irrigation regime groups: full irrigation (FI), (i.e., control); and limited irrigation (LI), (i.e., water-deficit). Control plants were watered manually every day, whereas water was withheld from plants in the water-deficit treatment until soil water potential reached approximately -70 kPa. Air temperature and relative humidity during plant growth were recorded with the use of a microclimatic poly sensor (Novasima MS 1, Novasima AG, Zurich, Switzerland). Two plants were tagged in each experimental unit and these were used for the measurement of non-destructive data, which included leaf production, plant height, and number of pods (i.e., number of full pods or number of pod abortions). These two plants were harvested at maturity (harvesting stage, or HS) for yield components and grain yield (GY) determination. The remaining plants in each pot were harvested at the anthesis stage (AS) [i.e., 0 DAA (days after anthesis)/55 DAP (days after planting)/8 WAP (weeks after planting)] and at HS [i.e., 42 DAA/6WAA (weeks after anthesis)/96 DAP/14 WAP)], for estimating dry matter production in terms of remobilized dry matter (ARDM), remobilization efficiency (REE) and remobilization efficiency percentage (REP). To determine above ground dry matter of plant parts, three plants were randomly taken from each pot of both treatments; that is, control (FI) and water-deficit (LI). The plants were separated into stem and leaves and were oven- dried at 80 $^{\circ}$C for 48 hrs.

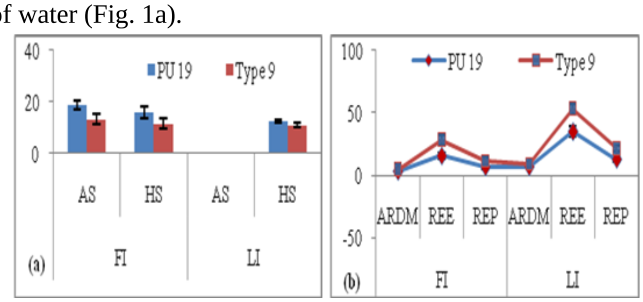
To measure the amount of remobilized dry matter in above ground plant parts, the following equations were used respectively: ARDM (g/plant) = AGDM (AS) – AGDM (HS); REE (%) = ARDM (g/plant) / AGDM (AS) x 100; REP (%) = ARDM (g/plant) / GY (g/plant) x 100, where ARDM is amount of remobilized dry matter (g/plant); AGDM (AS) is above ground dry matter of plant parts at the anthesis stage (g); AGDM (HS) is above-ground dry matter of plant parts at harvesting stage (g) except grain weight; REE is remobilization efficiency (%); REP is remobilization percentage (%); and Gy is grain yield (g/plant) [9, 10, 11]. To determined the leaf relative water content (RWC), net assimilation rate (NAR_L), remobilisation of photosynthetic assimilates and other physio-biochemical analyses, newly formed young leaves (4 - 5 days old) were tagged just at the date of anthesis and were analyzed at 0 DAA; that is, the date of tagging and after that they were analyzed at 2, 4 and 6 WAA until the leaves had not senesced completely. To evaluate water status during normal (unstressed) and water-deficit (stressed) periods, relative water content (RWC) was used, according to [12]. For the calculation of RWC, incised leaves were weighed (fresh weight, FW), then left in water for 8 hrs at 12 $^{\circ}$C for saturation. After saturation, leaves were blotted properly and weighed (turgid weight, TW). Leaf samples were then dried in an oven at 70 $^{\circ}$C for 48 hrs and weighed (dry weight, DW). The relative water content (%) was determined as: RWC= (FW-DW/ TW-DW) X 100. Net assimilation rate of photosynthetic assimilate (NAR_L) was calculated [13] as: NAR_L (g $cm^{-2}d^{-1}$) = $W_2 - W_1$ / $T_2 - T_1$ x $\ln LA_2 - \ln LA_1$/ $LA_2 - LA_1$, where, W1 is the= dry weight of first harvest, W2 is the= dry weight of second harvest, ln is the = natural logarithm, LA1 is the= leaf area at first harvest, LA2 is the= leaf area at second harvest and T2 - T1 is the= time interval between two harvests). [LA is expressed in cm^2 $plant^{-1}$ and was estimated with a LICOR photoelectric area meter (model 41-3100, USA)].

Estimation of chlorophylls

Chlorophyll a (Chl. a), chlorophyll b (Chl. b), and total chlorophyll (t Chl.) were estimated by the Arnon method [14]. Experiments were conducted with three replications. The significance of differences between means (for control and stressed) for different parameters was measured using Student's t-test, and differences were considered significant at $p \leq 0.05$. All of the statistical calculations were performed using the computer software Microsoft Excel 2000.

RESULTS

The results of this study showed significant effects of water-deficit stress on above-ground dry matter (AGDM), amount of remobilized dry matter (ARDM), resorption efficiency (REE), resorption efficiency percentage (REP) and grain yield (GY). AGDM at anthesis (AS) and harvesting stage (HS) was significantly affected by water-deficit conditions ($p \leq 0.05$). AGDM significantly increased by 23.27% and 8.69% in var. PU 19 and var. Type 9, respectively, under a limited supply of water (Fig. 1a).



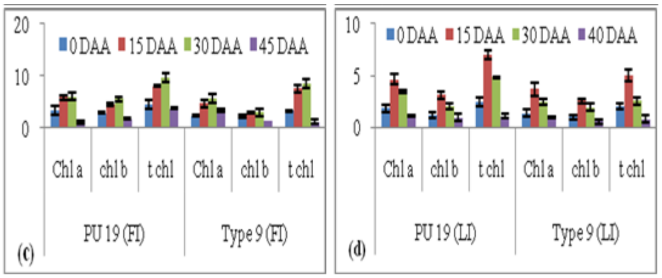


Figure: 1 Effect of two levels of moisture regimes [full irrigation (FI) and limited irrigation (LI)] on (a) aboveground dry matter (AGDM)(g); (b) amount of remobilized dry matter (ARDM)(g/ plant), remobilization efficiency (REE) (%) and remobilization percentage (REP) (%) at the anthesis stage (AS) and harvesting stage (HS); (c) Chlorophyll content (mg g-1 FW) in leaves at full irrigation (FI), and (d) limited irrigation (LI) of two varieties of P. mungo (var. PU 19 and var. Type 9). Vertical bars represent mean ± SE; *significant at p≤ 0.05.

Table1. Effect of two levels of moisture regimes [full irrigation (FI) and limted irrigation (LI)] on: (A) number of pods/plant, number of seeds/pod, seed weight (g) and grain yield (GY) (g) at harvesting stage (HS); (B) leaf weight (mg) and leaf area (cm^2) at different days (days after anthesis, DAA) in two varieties of *P. mungo* (var. PU 19 and var. Type 9).

Condition(s)	Full irrigation (FI)		Limited irrigation (LI)	
Parameter (s)	PU 19	Type 9	PU 19	Type 9
Number of Pods	10	8	8	6
Number of seeds/pod	5-6	4-5	5-6	4-5
Seed weight (g)	0.91	0.83	1.3	0.92
Grain yield (GY) (g/yield)	45.5	33.2	52.0	27.6

Leaf weight (mg)					
Days after anthesis (DAA)	Full irrigation (FI)		Days after anthesis (DAA)	Limited irrigation (LI)	
	PU 19	Type 9		PU 19	Type 9
0 DAA	16	12	0 DAA	11	8
15 DAA	22	19	15 DAA	15	11
30 DAA	26	20	30 DAA	16	9
45 DAA	17	16	40 DAA	11	7
Leaf area (cm^2)					
0 DAA	2.5	1.9	0 DAA	1.6	0.88
15 DAA	3.5	3.2	15 DAA	2.2	1.68
30 DAA	4.75	3.9	30 DAA	3.0	1.92
45 DAA	4.1	4.1	40 DAA	3.2	1.96

Drought stress occurring at the anthesis stage significantly reduced dry matter production at the harvesting stage. Variety PU 19 had 2.6-fold higher AGDM compared to var. Type 9 under LI conditions.

A comparison of mean grain yield under water stress conditions showed that it improved 12.5% in var. PU 19, whereas in var. Type 9 it declined by 16.86%. The number of pods at the harvesting stage (HS) declined in both varieties of P. mungo under LI conditions (Table 1A). Hence, a water deficit occurring at the anthesis stage caused abortion of pods in both varieties. Similarly it reduced the number of seeds per pod. By contrast, the weight of var. PU 19 seeds increased by 30% under stress conditions (LI) compared to control conditions (FI). This may be due to the accumulation of photosynthetic assimilates that remobilized from senesced vegetative tissues to developing grains under stress full conditions. ARDM, REE and REP improved in both PU 19 and Type 9 variety of *P. mungo* under LI. In var. PU 19, drought condition (LI) caused

56.06, 56.06 and 49.8% increases in ARDM, REE and REP, respectively, compared to FI conditions. ARDM, REE and REP were 1.5 - 2.0 fold higher in var. PU 19 compared to var. Type 9 under LI (Fig. 1b). Water deficit exerted a negative effect on relative water content (RWC_L), causing both varieties to lose much more water than under FI conditions. Results showed that although both varieties lost water under LI, but var. PU 19 retained 25.7% more water compared to var. Type 9 under LI (Fig. 2a, b). Variation in water contents (i.e., FI and LI) caused large differences in leaf duration (leaf life span).

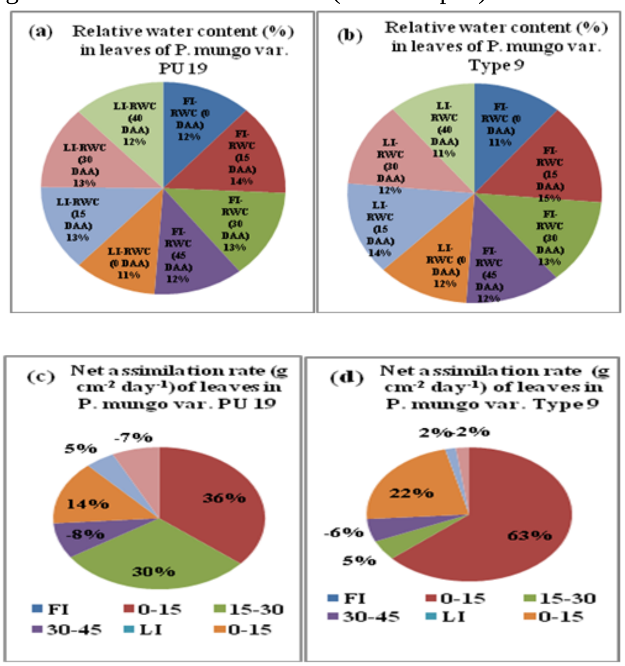


Figure: 2 Effect of two levels of moisture regimes [full irrigation (FI) and limited irrigation (LI)] on (a, b) relative water content (RWCL) (%), and (c, d) net assimilation rate (NARL) (g cm-2d-1) of two varieties of P. mungo (var. PU 19 and var. Type 9).

Leaf unfolding occurred synchronously in both FI and LI treatments. In contrast, the duration of leaf unfolding to yellowing differed greatly between treatments (Fig. 3a-f). In PU 19 and Type 9 varieties, it was 42 - 45 d and 36 - 40 d, respectively, under LI conditions. As a consequence, the lifespan of var. PU 19 exceeded by 5 - 8 days that of var. Type 9, thereby demonstrating more drought-tolerant capacity. These differences were consistent with the measurements of leaf area (LA), where a limited supply of water reduced leaf area (Table 1B). It was also evident from the results that net assimilation rate (NAR_L) of leaves reduced linearly in both varieties when they passed from one growth phase to another under FI and LI conditions. Water-deficit conditions significantly reduced NAR_L compared to the control. NAR_L was reduced by 60.0 - 64.8% in both varieties of *P. mungo* under FI and LI conditions. Results showed that var. PU 19 had comparatively high values of NAR_L under water stress (LI) compared to var. Type 9 (Fig. 2c, d). The decline in chlorophyll content always began shortly before visible yellowing. It lasted about 30 d in all cases under LI conditions. Chl. a, b and total (a+b) decreased significantly to a similar extent between 55 and 61% under FI conditions, and between 77 and 83% under LI conditions, in var. PU 19 and var. Type 9, respectively (Fig. 1c, d).

DISCUSSION

Anthesis is the most sensitive stage to water-deficit stress in pulses and other cereals. Drought occurrence at the anthesis stage causes a drastic reduction in yield and yield component [15]. Crops rely on remobilization of stored carbohydrates from the pre-anthesis stage when drought stress occurs [16, 17]. This becomes more important under terminal drought stress that is coincident with the grain filling period and inhibits current photosynthesis. The more rapid and severe the senescence, the more rapidly carbon and nitrogen are allocated from leaves to grains.

It may be postulated that when *P. mungo* varieties are subjected to water-deficit conditions at the anthesis stage, although yield is decreased compared to full irrigation conditions, the rate of above-ground remobilized dry matter (ARDM), resorption efficiency (REE) and resorption efficiency percentage (REP) increases. This result may be due to disturbance in photosynthesis. Disturbance in photosynthesis increases ARDM, REE and REP. These traits could be selected to screen varieties of *P. mungo* for yield potential under water-deficit conditions. This indicates that when crops are exposed to drought stress during grain filling, and current photosynthesis is not adequately able to support the sink, they tend to utilize stored assimilates of the plant parts. In our experiment we observe that var. PU 19 had the highest yield compared with var. Type 9 in drought stress conditions, indicating that var. PU 19 could be considered a drought-resistant cultivar and cultivated under water-deficit conditions. Bonnett and Incoll [18] also reported that both pre-anthesis and grain filling stages in barley are affected by water-deficit conditions. Leaf senescence is accelerated by decreases in leaf relative water content (RWC) caused by limited water supply. Our finding shows that limited supply of water reduced leave relative water content (RWC_L) and affected net assimilation rate (NAR_L), which ultimately reduced grain yield. The leaf relative water content data indicated that plants in the maturation stage were the most sensitive to drought stress, probably due to their higher transpiration rate. In addition, plants began leaf senescence in this stage, contributing to a reduction of water content in plant tissues. A limited supply of water in the maturation stage is linked to the process of senescence, in which it promotes a decrease of water and nutrient absorption and cell death in plant tissues. Reduced leaf area resulted in less interception of light, which caused a decrease in photosynthetic efficiency and hence decreased relative growth rate and net assimilation rate (NAR_L). The reduction in leaf area observed under LI conditions (Table 1B) can be attributed to changes in plant-water relations with water deficits, which cause a reduction in meristem activity as well as cell elongation. Reduced leaf area significantly affected the net assimilation rate (NAR_L) of leaves. We observed a 60 - 65% reduction in NAR_L under LI conditions.

According to Datta [19] the low net assimilation rate might be due to restricted availability of essential nutrients and decreased photosynthetic efficiency. Comparatively high net assimilation rate of var. PU 19 under water-deficit conditions showed that this variety can tolerate low water supplies up to a certain limit (Fig. 2c, d), because in drought stress, net photosynthetic rate declines due to poor or limited availability of water that reduces NAR. In addition, water restriction during the anthesis stage accelerated the degradation of photosynthetic pigments [20]. Water restriction promoted reduction in the levels of pigments due to the metabolic changes in the plants. It increased the production of ethanol and lactate, which consequently reduced chlorophyll synthesis [21]. In addition, water restriction during the anthesis stage accelerated the degradation of photosynthetic pigments [16]. Ultimately, the leaf reaches a compensation point at which carbon assimilation and respiration are equal. At this point, the leaf will no longer contribute as a photosynthetic organ to the assimilatory needs of the rest of the plant and it turns yellow as it senesces.

Figure: 3(a, d) 55 days old plants; i.e., 8 WAP (weeks after planting); (b, e) exhibiting flowering and pod formation; and (c, f) 96 day old senesced plants with ripped pods, ready for harvesting, for PU 19 and Type 9 varieties of P. mungo, respectively, under full irrigation (FI) and limited irrigation (LI).

CONCLUSION

We found that water deficiency at the anthesis stage induces early senescence in both varieties of *P. mungo* compared to full irrigation. Variety PU 19 appears more tolerant to water stress during the grain filling period due to its ability to maintain high relative water content, NAR, under LI. It also showed high ARDM, REE and REP, seed weight and grain yield (GY) under LI. We therefore conclude that senescence and remobilization are apparently promoted by a limited supply of water and are coupled processes. Studying RWC, NAR and leaf senescence used as indirect selection criteria for grain yield (known as “analytical breeding”) is an interesting approach, because those traits are easily and rapidly screened and are relatively inexpensive. Furthermore, this can help us gain a potential understanding of the many physiological mechanisms that confer water-deficit tolerance, leading to the development of leguminous plant species better adapted to such environments.

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