Comparative morpho-physiological and biochemical responses of lentil and grass pea genotypes under water stress

Abstract

Background: Both lentil (Lens culinaris Medik.) and grass pea (Lathyrus sativus L.) in the family Fabaceae are two important cool-season food legumes, often experiencing water stress conditions during growth and maturity. Objective: The present study was undertaken to ascertain the response of these two crops under different water stress regimes. Materials and Methods: Different morpho-physiological and biochemical parameters were studied in a pot experiment under controlled environmental conditions. Along with control (proper irrigation, 0 stress), three sets of plants were subjected to mild (6 d), moderate (13 d) and severe (20 d) water stress by withholding irrigation at the appropriate time. Results: Compared with control, plant growth traits and seed yield components reduced significantly in both crops with increasing period of water stress, resulting in lowering of dry mass with more severe effect on lentil compared with grass pea. Foliar Relative Water Content (RWC) (%), K+/Na+ ratio, chlorophyll (chl) a, chl a/b ratio, stomatal conductance and net photosynthetic rate declined considerably in both crops under water stress. Leaf-free proline level increased significantly in both crops, but it decreased markedly in nodules of lentil and remained unchanged in grass pea. Nodulation was also affected due to water stress. The impairment in growth traits and physio-biochemical parameters under water stress was manifested in reduction of drought tolerance efficiency of both crops. Conclusion: Impact of water stress was more severe on lentil compared with grass pea, and modulation of growth traits signified necessity of a detailed strategy in breeding of food legumes under water stress.

Key words: Food legumes, growth, nodulation, water stress, yield

INTRODUCTION

The adaptability and productivity of cool-season food legumes such as lentil (Lens culinaris Medik.) and grass pea (Lathyrus sativus L.) are limited by major abiotic stresses, including drought, heat, frost, chilling, water logging, salinity, and mineral toxicities. The severity of these stresses is unpredictable in field experiments; therefore, field trials are increasingly supplemented with controlled environment testing and physiological screening. Both leguminous species are grown in arid and semi-arid regions of West Asia and North Africa, and parts of South Asia, where yield loss due to water stress is very high.[1] The identification of adaptive mechanisms to drought is of considerable importance, especially for legumes, as they play significant ecological and economic roles.[2] Both lentil (L. culinaris Medik) and grass pea (L. sativus L.) are considered valuable plant resources for diverse types of biological studies, including cytogenetic, mutation genetic, and genomic research.[3-5] Lentil is one of the predominant winter pulse crops in India, which is extensively cultivated (1.4 m ha) in northern, east-central and eastern parts of the country, being the largest lentil-growing country in the world.[6] The contribution of India to global lentil area and production is 39.52% and 42.42%, respectively.[6] However, the productivity of lentil in India is very low (619 kg/ha) in comparison with the world average of 887 kg/ha because it is normally grown
under rain-fed conditions by resource-poor farmers with
dearth of potential high-yielding cultivars. Among the
diseases, lentil breeding is one of the important approaches
to enhance yield and nutritional quality and several
molecular markers have been developed in this crop. Like lentil, grass pea (L. sativus L.) has been cultivated as a
winter grain crop since time immemorial. Both the crops
have narrow genetic variability and often face mid-way as
well as terminal drought stress during the growth
period. In recent times, number of desirable mutations,
including growth habit, flower and seed coat color, stipule
and leaf characteristics, etc., have been isolated through
induced mutagenesis. Both the crops, however, experience different types of abiotic stresses, although
both, especially grass pea, have remarkable capacity to
withstand extreme environmental conditions. In lentil,
cadmium-induced oxidative stress and its amelioration
by calcium has been studied, while two flavonoid-deficient
mutants, one glutathione-deficient and one overproducing
mutant, and one ascorbate-deficient semi-dwarf mutant
have recently been characterized in grass pea. These
valuable biochemical mutations are now giving vital clues
about the intrinsic tolerant mechanism of legume crops
and are now being mapped using the arrays of
cytological tester stocks such as aneuploids, translocations, and
polyploids. Gene action for some biometrical traits in
L. culinaris Medik. was carried out under mid-hill conditions
of the northwestern Himalayas.

Even though legumes seem to have a significant and
multi-functional role, their hydrodynamic responses to
impended environmental drought remain little known. Given that the ecophysiological mechanisms, triggered
by water shortage, differ among plants, an attempt to
indicate that legumes are sensitive to water deficit becomes
significant. Degree of salt tolerance of some lentil and
grass pea genotypes is known, but no reports are
available regarding their relative drought tolerance. Thus,
one of the primary objectives of the present study was to
assess the relative tolerance of the two potential legumes
to water stress.

MATERIALS AND METHODS

Plant materials and experimental design
Fresh and healthy seeds of lentil (L. culinaris cv. PL 4) and
glass pea (L. sativus L. cv. BioR-231) were surface sterilized
in 70% ethanol for 2 min, rinsed twice in deionized water
and then placed on water-moistened filter papers in 9 cm
diameter Petri dishes in an incubator at 25°C with 12 h light.
Germinated seeds were immediately transferred to 12-in
earthen pots containing a mixture of fine soil, vermiculite,
and farm yard manure (1:1:1). Seedlings were thinned to
one per pot after emergence and watered evenly for their
uniform growth until 7 days after first emergence. Then,
the pots were kept under controlled growth conditions
(temperature 27°C, 12 h photoperiod and relative humidity
75 ± 7%, PPFD-200 μmol/m²/s) in a randomized block
design. The water stress treatment commenced on
9-day-old seedlings. The experiment was carried out in a
factory design with four treatments (non-stress and stress
at 6, 13 and 20 d) with three replications during 2010-2011
at a research farm, Kalyani (22°59’ N/88°29’ E), Nadia,
West Bengal, India. The control plants were maintained
with proper irrigation (0 stress), while the other set of
plants were subjected to mild (6 d), moderate (13 d) and
severe (20 d) water stress by withholding irrigation at the
appropriate time. Pots were covered with aluminum foil
and plastic sheets to avoid evaporation during the stressed
period.

After the end of the respective duration of stress treatment,
plants were irrigated again (drought recovery) till maturity.
Different morpho-physiological and growth parameters
enlisted in Tables 1 and 2 are studied at harvest. After harvest,
root, pods, and shoots were separated, cleaned thoroughly
with de-ionized water and oven dried at 72°C for 48 h.
Dry weight (DW) of both parts were measured. The leaf RWC
was then measured and calculated according to Talukdar
as: RWC (%) = [(FW − DW)/(TW − DW)] × 100, where
FW = fresh weight and TW-total weight Leaf Na+ and
K+ contents were estimated following earlier methods
adopted in grass pea. Stomatal conductance was
measured according to Costa Franca et al. Measurements
were taken between 10.00 AM and 13.00 PM local time on
fully expanded leaves of three tagged plants per treatment
per replication. Drought tolerance efficiency (DTE) was
measured as follows:

\[
\text{DTE} = \frac{\text{Yield under stress}}{\text{Yield under no stress}} \times 100
\]

Biochemical parameters
Chlorophyll (chl) and carotenoid contents were determined
by the method of Lichtenhaler. Leaf tissue (50 mg)
was homogenized in 10 ml chilled acetone (80%). The
homogenate was centrifuged at 4000 g for 12 min.
Absorbance of the supernatant was recorded at 663, 647,
and 470 nm for chl a, chl b and carotenoids, respectively.
Leaf and nodule proline content was measured following
Bates et al.

Statistical analysis
The results presented here are mean values ± standard
errors (SE) for at least three replications. Statistical
significance between mean values was measured by
ANOVA using Statistical Package for the Social Sciences
(v 10, Statistical Package for the Social Sciences Inc.,
USA) software and means were separated by the Duncan's Multiple Range Test. A probability of \( P < 0.05 \) was considered significant.

### RESULTS AND DISCUSSION

#### Changes in growth parameters

Significant \((P < 0.05)\) differences were observed in response of lentil and grass pea cultivars to periodic exposure (6, 13, and 20 d) to water stress. Among the growth traits, plant height, number of primary branches, and leaves per plant reduced markedly in lentil seedlings subjected to 13 d water stress conditions, and further reductions were observed in plants exposed to 20 d water stress [Table 1]. Compared with controls, the reduction was 2-3-fold for plant height, 2-7-fold for number of primary branches and nearly 2-5-fold for leaves per plant in the lentil cultivar. Dry weights of shoots, roots and pods also reduced significantly at the 13 d treatment period, and the lowest values were recorded in plants under 20 d water stress conditions [Table 1]. Pod DW decreased by about 1.4-fold, whereas DW of shoots reduced by about 2-3.3-fold across the treatments. Root DW declined by about 2-5-folds in lentil under stress.

In contrast to lentil, significant reductions in the above-said growth traits were found only in plants subjected to 20 d water stress conditions for the grass pea cultivar [Table 2]. However, pod DW in grass pea genotype remained unchanged throughout the treatment regimes. Compared with control, no marked changes were observed in both crops under 6 d stressed conditions, and this was extended to the 13 d period in case of grass pea.

#### DW of plants

DW of plants is one of the realistic criteria in determining plant responses to diverse types of stresses, like water stress, salinity, and metal toxicity.\[^{17,18,28,39,34}\] Decrease in height, primary branches and leaf number might be attributed to reduced shoot DW in both crops, but the effect was more severe on lentil cultivar. Therefore, low tolerance to water stress was found to be associated with reduced plant DW, which was reduced by negative contributions from other components markedly affected by water stress in sensitive genotypes. In grass pea, superior performance under salinity stress was indicated by normal plant DW, while low plant biomass accumulation was associated with symptoms of increased salt sensitivity.\[^{28,29}\] Reduction in DW under water stress was reported in different crops, including legumes.\[^{25,36}\]
Table 2: Changes in morpho-physiological and yield parameters in *Lathyrus sativus* L. cv. BioR-231 under non-stressed (control), 6 d, 13 d, and 20 d durations of water stress conditions

| Parameters (at harvest) | Control (0 stress) | 6 d | 13 d | 20 d |
|-------------------------|--------------------|-----|------|------|
| Plant height (cm)       | 52.34±0.10         | 50.45±0.13 | 47.11±0.17 | 30.87±0.18 |
| Primary branches/plant  | 12.56±0.17         | 12.11±0.09 | 11.88±0.10 | 7.87±0.11  |
| Leaves/plant            | 128.0±0.10         | 122.6±0.13 | 117.6±0.11 | 100.9±0.09 |
| Days to flowering       | 45.6±0.23          | 50.1±0.20  | 45.8±0.19  | 49.7±0.23  |
| Days to 50% flowering   | 76.8±0.28          | 71.6±0.13  | 55.8±0.20  | 30.1±0.09  |
| Days to maturity        | 134.6±0.30         | 133.9±0.29 | 119.8±0.43 | 100.8±0.10 |
| Pods/plant              | 88.87±0.09         | 86.54±0.10 | 85.5±0.08  | 80.6±0.08  |
| Seeds/pod               | 3.6±0.11           | 3.5±0.13   | 2.9±0.11   | 0.22±0.11  |
| 100 seed weight (g)     | 4.6±0.08           | 4.5±0.11   | 3.2±0.08   | 0.67±0.06  |
| Seed yield/plant (g)    | 16.67±0.33         | 16.06±0.30 | 14.3±0.27  | 3.76±0.13  |
| Pod DW/plant (g)        | 2.02±0.28          | 2.00±0.23  | 1.99±0.19  | 0.82±0.10  |
| Shoot DW (g/plant)      | 1.19±0.20          | 1.18±0.23  | 0.99±0.09  | 0.82±0.10  |
| Root DW (g/plant)       | 0.23±0.10          | 0.23±0.13  | 0.19±0.10  | 0.08±0.06  |
| Biological yield (g/plant) | 18.6±0.41      | 20.65±0.39 | 20.07±0.38 | 7.49±0.29  |
| Harvest index %         |                   |         |       |       |
| RWC %/plant             | 81.15±0.23         | 80.74±0.29 | 63.76±0.22 | 40.49±0.17 |
| Leaf K*/Na* ratio       | 1.59±0.20          | 1.62±0.18  | 1.59±0.13  | 1.56±0.16  |
| Leaf chl a (mg/g FW)    | 4.29±0.08          | 4.21±0.11  | 4.07±0.08  | 2.14±0.07  |
| Leaf chl b              | 1.69±0.11          | 1.51±0.19  | 1.50±0.20  | 1.08±0.09  |
| Leaf chl a/b ratio      | 1.22±0.16          | 1.22±0.12  | 1.19±0.36  | 1.20±0.06  |
| Carotenoids (mg/g FW)   | 1.09±0.09          | 0.997±0.11 | 0.987±0.10 | 0.572±0.07 |
| Net photosynthetic rate (mg CO₂/m²/s) | 1.66±0.22 | 1.59±0.23 | 1.65±0.27 | 0.49±0.12 |
| Stomatal conductance (cm/s) | 16.6±0.21 | 17.5±0.20 | 15.0±0.18 | 5.15±0.10 |
| Nodules/plant           | 14.36±0.12         | 14.56±0.13 | 13.11±0.09 | 5.43±0.08 |
| Nodule DW (mg/plant)    | 2.01±0.18          | 3.99±0.10  | 4.17±0.20  | 5.28±0.20  |
| Leaf proline content (µ mol/g FW) | 83.4±0.15 | 87.0±0.13 | 80.3±0.16 | 79.9±0.14 |
| Total seed protein content % | 27.4±0.17 | 27.7±0.20 | 20.8±0.13 | 14.8±0.09 |
| DTE %                   | 100.0±0.01         | 96.0±0.07  | 85.8±0.18  | 22.5±0.10  |

Data are means±standard error of at least three replicates, Means followed by the common letters are not significantly different at P<0.05, DTE=Drought tolerance efficiency; chl=Chlorophyll; FW=Fresh weight; DW=Dry weight; RWC=Relative Water Content

Flowering, seed yield, and harvest index (%)

Onset of flowering in lentil cultivar was advanced by about 17-27 days depending on the duration of plants’ exposure to water stress for 13 d and 20 d periods, as increasing durations led to greater earliness in flowering. On the other hand, days to 50% flowering was advanced by 30-75 days, while maturity was earlier by about 70-95 days in the treated seedlings in comparison with the controls [Table 1]. Number of pods per plant and 100 seed weight decreased 2-5-fold, resulting in a significant decline of seed yield per plant, although the per pod seed number changed marginally under water stress conditions. By contrast to lentil, onset of flowering was marginally changed in the grass pea cultivar across the treatment regimes. However, 50% flowering stage appeared nearly 20-40 days earlier than control. Under 13 d and 20 d stress periods, maturity was advanced by 20-34 days from the control value [Table 2]. Unlike lentil, there was no reduction in the number of pods per plant, but the per pod seed number and seed yield per plant reduced significantly in grass pea seedlings exposed to 20 d stress period [Table 2]. In both crops, 100 seed weight and harvest index value declined to a considerable extent. The results suggested that the per plant seed yield reduced in both crops under water stress, but the reduction in lentil was mainly due to a decrease in pod number, while in grass pea it can be attributed to the low number of seeds per pod. It is also clear that water stress impeded normal grain filling, resulting in a decrease in the 100 seed weight in both crops. The results indicated that grass pea was relatively more tolerant than lentil to water stress conditions.

Physiological parameters

Foliar RWC (%), K⁺/Na⁺ ratio, chl a, chl a/b ratio, stomatal conductance and net photosynthetic rate decreased significantly in lentil seedlings under 13 d stress, and further reduced at 20 d period. The measurement of RWC under low soil moisture is of importance as high RWC appears to be a common trait in drought-resistant species, as species that exhibit restricted changes in RWC per unit reduction in water potential are often considered to be relatively drought resistant.[34] In grass pea, RWC decreased significantly only at the 20 d stressed period, indicating that the plant experienced low water status only at the late vegetative and early reproductive stages, while lentil seedlings experienced it much earlier at the vegetative stage, and continued it to the reproductive stage. Similar results were found in *Vigna subterranea* (bombara groundnut).[35]
and in Medicago sativa.\textsuperscript{[34]} The decrease in K\textsuperscript+ /Na\textsuperscript+ ratio was mainly due to lowering of K\textsuperscript+ content and concomitant rise in Na\textsuperscript+ level under water stress. Similarly, reduction in chl a led to a decrease in the chl a/chl b ratio, although the chl b content increased in 13 d-treated plants but decreased marginally under 20 d stress period [Table 1]. The lowering of pigment composition along with impairment in stomatal conductance might be responsible for the reduction of the net photosynthetic rate in lentil cultivar under 13 d and 20 d water stress conditions. Stomatal conductance has long been considered an important selection criterion for drought resistance. Higher stomatal conductance in plants increases the CO\textsubscript{2} diffusion into the leaf thereby, favoring higher photosynthetic rates. Higher net CO\textsubscript{2} assimilation rates can in turn favor a higher biomass and higher crop yields.\textsuperscript{[30]} Photosynthetic rate and stomatal conductance of the two leguminous species showed a positive relationship ($r = 0.78$, $n = 8$, $P < 0.05$), and both variables declined considerably under water-deficit conditions, with a more severe effect on lentil, which is in agreement with earlier reports in crop legume, Phaseolus vulgaris and forage legume, Sesbania aculeata.\textsuperscript{[17]} In grass pea, leaf RWC decreased markedly but the K\textsuperscript+ /Na\textsuperscript+ ratio was largely unaffected even at elevated duration of water stress [Table 2]. Excessive accumulation of Na\textsuperscript+ and Cl\textsuperscript− in the leaves has been considered highly harmful for normal metabolism of plants, and tolerant genotypes have the capacity of successful salt exclusion.\textsuperscript{[38]} The K\textsuperscript+:Na\textsuperscript+ ratio has been used as a discriminating factor between tolerant and sensitive genotypes, with a greater capacity of the former to block or reduce the uptake or exclude the excess amount of Na\textsuperscript+ and associated increase in K\textsuperscript+ content.\textsuperscript{[39]} There was no significant change in chl b and carotenoid contents, but a 2-fold reduction of chl a content under 20 d stress period resulted in a decline in the chl a/chl b ratio, and concomitantly on the net photosynthetic rate in grass pea [Table 2]. Disruption in pigment composition may be due to severe impairment in pigment synthesis, structure and function, which is mainly orchestrated through stress-induced membrane damage, as reported in different crop plants.\textsuperscript{[29,39,40]} However, this phenomenon is not universal.\textsuperscript{[37]}

The nitrogen-fixing ability of root nodules in leguminous plants is generally influenced by the availability of water to the host plant. If drought stress persists for long, this activity is reduced, and is often lost completely.\textsuperscript{[41,42]} In the present study, number of root nodules and DW of nodule decreased in both crops with increasing intensity of water stress. But, the effect was more severe on lentil crops than that on grass pea. No nodule was formed in lentil seedlings under 20 d stress period, while nodule was formed at this stage in grass pea, but in the lowest frequency [Tables 1 and 2]. Similar results due to water deficit have earlier been reported in common bean\textsuperscript{[41]} and soybean.\textsuperscript{[43]} Ashraf and Iram\textsuperscript{[47]} observed that the effect of water stress was more severe on Phaseolus than that on Sesbania, and attributed the phenomenon to the size of the nodules, with larger-sized nodules having a relatively greater proportion of N\textsubscript{2}-fixing tissue and providing a greater sink for phloem-derived unloading of photoassimilates and water than small nodules providing better protection to plants under water stress.\textsuperscript{[17]}

Among the parameters responding to stress treatment, rapid accumulation of free proline content is one of the significant events in plants. The accumulation of cytosolutes, particularly proline, should avoid the detrimental effects of a low osmotic potential of the cells without interfering with protein synthesis.\textsuperscript{[43]} Proline content took reverse directions in the leaves and nodules of lentil; it increased significantly in the leaf but decreased markedly in nodules at 13 d and 20 d stress durations as compared with the control. In grass pea, on the other hand, leaf proline content increased with increasing exposure to stress, while in nodule the content remained unchanged [Table 2]. Increase in proline level was also reported in leaves of tolerant grass pea genotypes under salinity stress.\textsuperscript{[39]} However, the exact role of proline in abiotic stress tolerance is being debated. Presumably, increased amounts of free proline could be associated with more effective dehydration and drought avoidance mechanisms, as explained earlier.\textsuperscript{[37]} A positive correlation between proline overaccumulation and increasing salinity/drought tolerance has also been found in different crop plants, including transgenics that were engineered for overproduction of proline.\textsuperscript{[37,43]} In fact, proline synthesis has been associated with protein hydrolysis induced by water deficit.\textsuperscript{[43]} A marked increase in proline content in the roots and nodules of S. aculeata was reported as an indicator of its high drought tolerance. Contrasting response of proline level to uniform exposure to water stress in lentil and grass pea and, furthermore, in leaves and nodules indicated differential responses of plant parts to water-deficit conditions through osmotic adjustment mediated by proline accumulation.

The cumulative effect of reduction in growth stage and physiological parameters under water stress was ultimately manifested in total dry mass accumulation and DTE of plants. Total DW (root + shoot) was reduced 1.5-fold in lentil under 13 d stresses and 1.9-fold under 20 d growth period. TDW in grass pea was relatively stable except at 20 d stress treatment, where it reduced by about 1.2-fold in comparison with control [Table 2]. The retardation of growth usually comes as a cumulative effect of low water relation, stomatal nature, low photosynthesis and mineral nutrition, and other morpho-physiological features related to root and shoot growth as reviewed in different legumes,
including groundnut, black gram, and mung bean. All these ultimately manifested in retardation of grain yield under water stress in the present crops with more severe effect on lentil than that on grass pea, as was evidenced by the lower DTE value in the former than in the latter.

The data presented here were recorded at harvest. Obviously, following recovery of water stress (irrigation resumed after a stipulated period of withholding of irrigation), lentil seedlings exposed to 6 d-stressed conditions exhibited marginal variations of all the parameters studied in comparison with the control values, but plants under 13 d and 20 d water stress conditions exhibited significant deviations from control, as explained above. By contrast, grass pea seedlings exhibited normal performances under 6 d- and 13 d-stressed conditions, but significant deviations from control for most of the traits were observed only in plants subjected to 20 d water stress. The results confirmed the effect of water stress on vital physiological and biochemical parameters, which was reversed in both crops but in different magnitudes following recovery of drought.

For the first time, responses of two important grain legumes have been compared under different water stress regimes. Plant growth was reduced with increasing durations of water-deficit conditions. Compared with grass pea, lentil showed more sensitivity to water stress. With increasing demand for pulse food security in the backdrop of diverse types of abiotic stresses the legumes are facing in a changing natural environment, the present investigation may give vital input in the biology and breeding of food legumes under water stress conditions.

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