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A rapid method of measuring shoot hydraulic resistance of rice: implications for efficient water use

The capacity for better moisture storage and its retention by the soil is a key factor for avoiding crop failures in drought-prone and water-limited environments[1,2]. Such properties of soils are mainly dependent upon their texture and structure, which can be improved by adopting moisture-conserving practices like addition of organic matter, deep ploughing, field bunding, mulching, weed control, low crop density, etc.[3,4] However, in the chain of these events there still exists a factor, namely plant factor and more precisely plant hydraulic resistance, i.e. the ease or difficulty with which water is transported up in the plant, which could be of prime significance in agriculture. This morpho-physiological plant factor might be important in minimizing water consumption, hence saving the stored soil moisture by virtue of its slow transport in the plant due to greater shoot hydraulic resistance, thereby increasing the water-use efficiency[5,6]. This, in turn, would make the residual moisture available to plants for an extended period of time[7,8] and may eventually enable the crops to grow and yield satisfactorily under depleted water-supply conditions in water-limited environments[9–11]. But, in spite of its significance, this aspect of plant characteristics has attracted little attention of plant biologists, agronomists and plant breeders owing mainly to the lack of a reliable laboratory test for easy and quick measurement of hydraulic resistance of crop plants. In the recent past, however, some efforts have been made to measure the hydraulic resistance of tree plants[12], tomato plants[13] and the roots of wheat[6], but they are too laborious, costly, cumbersome and time-consuming techniques, rendering them unfit for large-scale testing, as required by plant breeders, of plant hydraulic resistance. Here we present a technique for measuring the hydraulic resistance of rice shoot, which is easy, simple, reliable and quick to perform in the laboratory.

Since the rolling and unrolling of rice leaves are the most visible and quickest physiological response to water deficit and its alleviation respectively[14], it was decided to use the duration of time-lapse between these two responses as a measure of shoot hydraulic resistance under externally applied pressure, to force entry and transport of water through the cut ends of the excised stems up to the leaves, reversing the phenomenon of natural leaf rolling upon plant excision back to unrolling[15]. Accordingly, plants of hybrid rice cultivar, NDRH-2 were grown in earthen pots of 10 kg capacity, each using soil as growth medium with normal supply of water and fertilizers till booting stage. The main tillers were then excised at 5 cm below the second node from the top with only flag leaf and the panicle wrapped inside the sheath intact and keeping the plant straight upright was inserted about 8 cm of one's base touching the floor of the tank, into the neck of an ordinary laboratory stove through rubber cork and made it fully air-tight. The tank of the stove was then filled with water through the side opening and subsequently a pressure gauge was fitted for monitoring the external pressure applied by hand power, similar to that of a kerosene oil stove. After preparing the experimental set-up in this manner, a pressure of 0.2 MPa was applied to unroll the leaves, which were already in the rolled state after plant excision. The unrolled leaves rolled back again *in situ* once the pressure was released. The process of pressure application and its release was repeated thrice with the observations recorded intermittently on the time taken for complete unrolling reaching a steady state. The duration of time thus taken for leaf unrolling was presumed to be proportional to the hydraulic resistance of the stem. The relative water content (RWC) of the experimental leaves was determined[16] at the beginning (score 5) and end of leaf unrolling (score 1) to find out whether pressure-induced leaf unrolling was due either to increased turgidity or simply to applied physical pressure per se. For the logical interpretation and useful conclusion of the findings, the observations were analysed statistically[17].

The time course of pressure-induced leaf unrolling is presented in Figure 1, wherein it can be seen clearly that the leaves took about 10 min before any signs of unrolling became visible (score slightly <5), but within the next 20 min (total time 30 min) the leaves completely unrolled (score 1) and remained so, thereafter resembling that of a normal, turgid leaf. On the other hand, the leaves remained completely rolled (score 5) with 65% RWC in the absence of applied pressure, suggesting that the pressure-induced leaf unrolling was indeed due to concurrent increase in the contents of water (RWC being 95%) having been forced to enter and travel up to the leaves through the stem against various magnitudes of forces offered within the stem itself. This firmly established that the pressure-induced leaf unrolling was not due to the physical pressure per se, rather it was due to increased turgidity of the leaf under externally applied pressure.

These findings encouraged us to extend our studies further and test the possibility of using the variation in duration of the time taken for unrolling of the leaf upon pressure application as a yardstick for indirectly measuring and comparing the genotypic variability in shoot resistance to water transport in rice. For this, we chose six rice cultivars, developed by N.D. University of Agriculture and Technology, Faizabad, two each representing three distinct ecological habitats, i.e. N-22 and Baranideep, reputed for adaptability to drought-prone environments, Jal-priya and Jal-lahari adapted to lowland situation with 50–100 cm deep water, and NDRH-2 and NDR-359 suited to irrigated ecosystem. Plants of these cultivars were grown in a manner described earlier, excepting that for the sake of uniformity their sowing dates were so adjusted that all of them came into heading more or less the same time. However, it is not necessary to stagger the sowing dates of various genotypes to be tested; rather the test is to be performed on plants of similar phenological growth stage, i.e. whenever they come, having well-developed stems, into jointing or booting or heading stage. All other operations for the experimental set-up and the recording of observations were done much the same way as for the experiment described earlier, selecting again the main tillers from each of the six cultivars after they had attained complete heading. This time the numbers of stoves were increased to three, one each for the three ecological groups of varieties. Interestingly, a striking genotypic variability, typical of their habitat, with respect to the duration of time taken for leaf unrolling was evident among three ecological groups of rice cultivars (Figure 2). The cultivars Baranideep and N-22, reputed for their adaptability to upland and drought-prone environments, were identified as having the greatest shoot hydraulic resistance, taking 64–67 min for leaf unrolling followed by those of NDR-359 and NDRH-2 suited to irrigated ecosystem which took 48–52 min for leaf unrolling. The lowland cultivars Jal-lahari and Jal-priya, adapted to medium deep to shallow water depth of 50–100 cm, offered the least resistance to water transport, taking only 36–38 min for leaf unrolling. Thus, the duration of time taken by the leaves for pressure-induced unrolling was presumed to be proportional to the magnitude of the shoot hydraulic

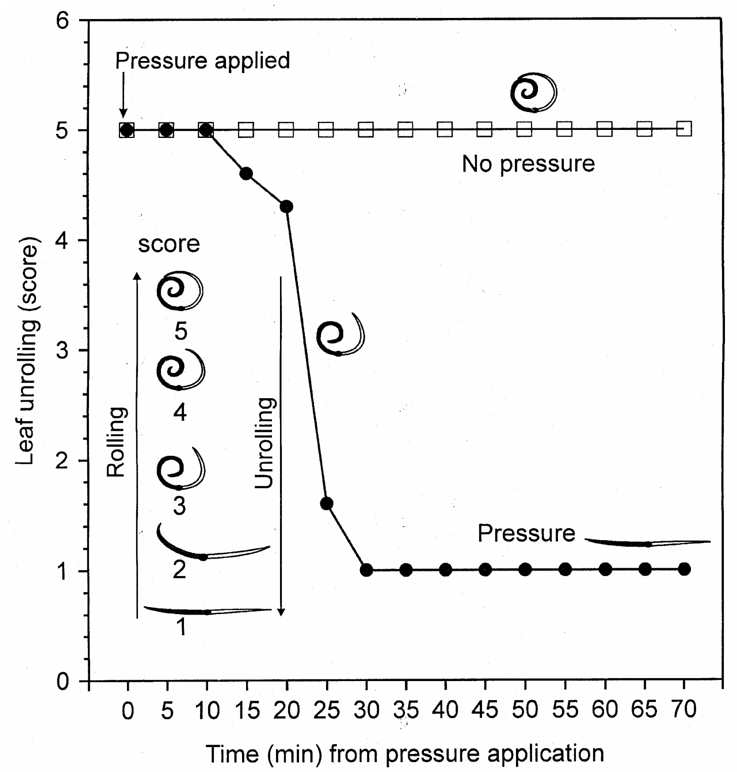

Figure 1. Effect of applied pressure on leaf unrolling (reverse of rolling) of excised rice plant of cv. NDRH-2. The main tillers at booting stage were excised at 5 cm below the second node from the top with only flag leaf and the panicle intact and inserted about 8 cm of the base with cut end dipped under water of the tank, into the neck of an ordinary laboratory stove through rubber cork and made it fully air-tight. A pressure of 0.2 MPa was applied by hand power, resulting in the unrolling of leaf with the duration depending upon the magnitude of shoot hydraulic resistance of the genotype. LSD ($P = 0.05$) = 0.3.

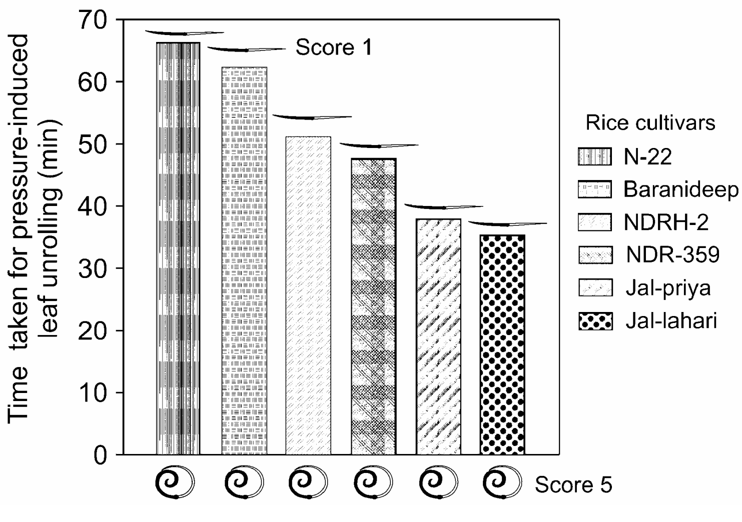

Figure 2. Genotypic variability in shoot hydraulic resistance of six rice cultivars as revealed by variation in duration of time taken for pressure-induced unrolling of leaves (from score-5 to score-1) of excised plant. For details see the legend of Figure 1. LSD ($P = 0.05$) = 1.2.

resistance of varieties belonging to distinct ecological habitats. The actual cause of the observed genotypic variability in the shoot hydraulic resistance is not known immediately. However, it could be due to variation in stem tissue density, strength and anatomical structures[18,19] accompanied by variation in the form, function and gating properties of aquaporins as well[20,21].

Taken all together it implies then that the cultivars having a high degree of resistance to water transport in the stem may be expected to exhaust a given amount of stored water or moisture in the soil slowly than those having less of such resistance[6]. Therefore, this trait may be advantageous for rice cultivars, enabling them to complete their growth cycle, vegetative and reproductive, satisfactorily under limited-water supply conditions in drought-prone areas[5–7]. It is, therefore, suggested that by adopting this technique one can screen at least 50 genotypes per day from the breeding materials for shoot hydraulic resistance cutting down the duration of time enormously, thereby enabling the selection of desirable genotypes; for example, setting a time limit of 55 min for leaf unrolling in this case and discarding all those exhibiting time period less than this cut-off point, much faster than those obtained by field trials often ill-defined for yielding capacity under drought[22]. The duration of time taken for leaf unrolling can further be proportionately shortened by increasing the magnitude of external pressure proposed to be applied. To make this technique more efficient, we are currently designing and preparing a prototype of this apparatus with a view to interlinking a series of simple pressure chamber-like structures made of steel pipes, of workable length and diameter for connecting the whole set-up to a computer assembly for operations such as pressure application, observation recording and presentation of results and their interpretation automatically.

In view of world climate change and global warming signifying an alarming situation of water scarcity in most parts of our sub-continent and elsewhere in the world[11], it is hoped that these findings could be useful for dryland agriculture in general and aerobic rice in particular, as the development of crops and varieties thereof with greater shoot hydraulic resistance would help reduce the consumption of water[6,23]. Further, the genes controlling this trait in the genotypes so identified and selected may be mapped and used for creating transgenic rice with altered genetic make-up for higher shoot hydraulic resistance, with a view to increasing the rice productivity, particularly under water-limited environments, well above its present level to make the world food security mission a success[23–25].

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