

## ROOT-MEDIATED WATER TRANSPORT TO THE SHOOT IN RICE

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### ABSTRACT

Rice leaf rolled quickly and its water potential and relative water content decreased immediately following excision of a well-watered plant even though the excised plant stood in water. Externally applied pressure to force entry of water into the excised plant resulted in unrolling of leaf with concomitant elevation of leaf water status as did the supply of water to the root system of a previously stressed intact plant. Thus, in intact rice plant, roots appear to possess the capacity of pushing water up in the shoot. However, in the absence of seminal or basal root system, the function of bulk water uptake and transport is taken over by nodal roots. It is suggested that the bulk of the water in rice plants is essentially propelled upward by roots alone, not by water potential gradient between the top and bottom of the plant. To accomplish this the intact rice plant seems to generate pressure in the root.

### INTRODUCTION

THERE is a continuum of liquid water from the soil through root and stem to the leaves, and a continuum of water vapour from the intercellular spaces in the leaves, across leaf epidermis, and through the air boundary layer to the atmosphere<sup>1,2</sup>. The liquid continuum, which is maintained by continuous absorption and transport of water, constitutes the transpiration stream<sup>3</sup>. It is generally accepted that the absorption and transport of water are passive movement, downhill in terms of the free energy status of the water or water potential<sup>4,5</sup>. It then follows that leaf and shoot water potentials must be lower than root and soil water potentials for absorption and transport of water to the shoot, which in fact do occur, at least during the daytime, because transpiration often exceeds absorption<sup>6</sup>. Most workers agree that transpiration, by reducing leaf water content and water potential, gives rise to the water potential gradient for uptake<sup>7</sup>. Thus water uptake is considered as the consequence of water loss<sup>8</sup>.

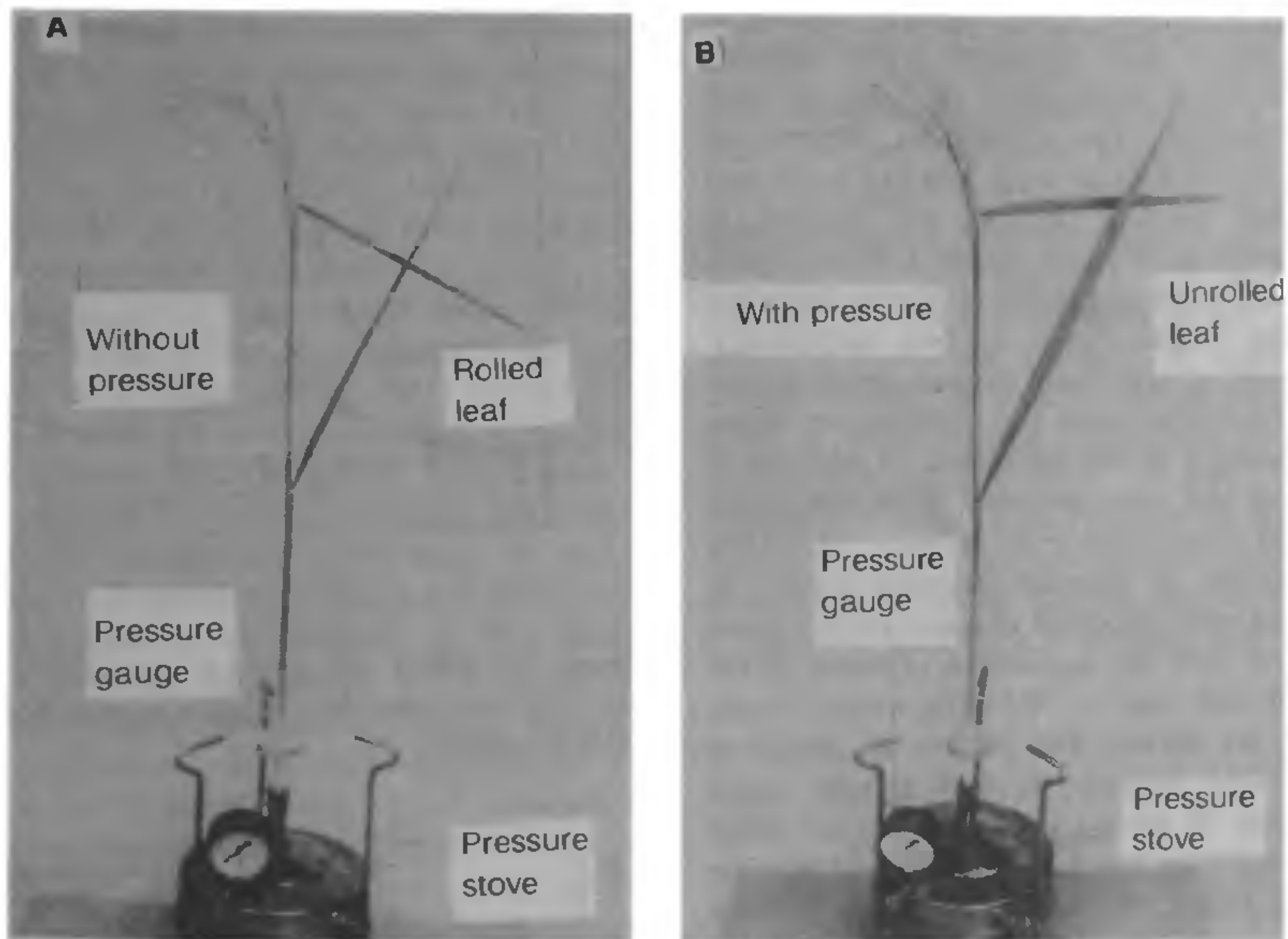
In this communication we present evidence which demonstrates that the bulk of water in rice is propelled upward in the shoot by some mechanism located in the roots and not by water potential gradient existing between the top and bottom of the plant.

### MATERIALS AND METHODS

Rice plants (cv. Sarjoo-52) were grown in earthen pots of 15 kg capacity with adequate fertilizers and

water under open-air greenhouse conditions. When the plants were 3 months old some of them were subjected to water stress by withholding supply of water until leaf water potential fell to  $-2.7$  MPa. At this stage some pots were shifted to the laboratory and similar-looking tillers from well-watered pots were excised at the base under water, with panicle and only the top two leaves intact. Approximately 8 cm of the base of the excised tiller was gently inserted into the neck of a laboratory pressure stove through a rubber cork and the arrangement was made fully air-tight (see figure 1). These operations were carried out under water contained in a large tub. The tank of the stove was filled with water and fitted with a pressure gauge to monitor the pressure applied to force entry of water into the excised tiller through the cut end. Concurrently stress on plants previously subjected to water stress was released by supplying water to the root medium. Immediately after supplying water some pre-stressed tillers were also excised at the base under water in the pot and held in that position to allow recovery from the water stress. Observations of second leaf unrolling<sup>9</sup>, and measurements of water potential<sup>6</sup> and relative water content<sup>10</sup> were made between short intervals after applying a pressure of  $+0.25$  MPa in the case of excised watered plants and from the time of stress relief in intact stressed as well as excised stressed plants. By the time pressure was applied the leaf water potential had declined to  $-2.7$  MPa.

In another set of experiments a few healthy and uniform tillers from well-watered pots were excised and the panicle and all the leaves except the top two



**Figure 1.** Effect of applied pressure on water transport in excised shoot of rice as evidenced by (A) leaf rolling before pressure application, and (B) leaf unrolling after pressure application.

were removed. The excised tillers were then incubated, keeping them upright under low evaporative demand conditions in the laboratory (ambient temperature 24°C, RH 96% vapour pressure 19.9 mm, wind velocity zero—no air movement), with about 10 cm of the basal portion submerged in water contained in a beaker such that a node remained about 5 cm deep in water. The water was changed every alternate day. Profuse roots, measuring about 10 cm in length, developed at the node submerged under water by day 18. The nodally rooted excised tillers were then taken out and subjected to three types of treatment. In one case all the roots were cut at the point of their origin at the node and the basal cut ends of the rootless tillers were immediately placed in test tubes (15×2 cm), which were then filled with water up to the node such that the point of origin of the roots also remained submerged under water. In the second case the roots were left intact but kept out of water by pressing them against the inner wall of the test tube using a thin glass rod. In the third case, the roots were left intact and were fully submerged in water; this served as

control. In every case the cut end of the stem remained under water during experimentation. Every test tube was thickly lined with moist white cloth to prevent the nodal roots from overheating in the sun. The entire assembly was then transferred outside the laboratory to the open-air high evaporative demand conditions with ambient temperature 32°C, RH 88%, vapour pressure 21.4 mm and wind velocity 3.4 km per hour. Observations of second leaf rolling<sup>9</sup> were recorded between short intervals.

## RESULTS AND DISCUSSION

One of the most immediate effects of plant excision was quick leaf rolling (figure 1,A) accompanied by significant fall in leaf water potential and relative water content even though the cut end of the excised plant remained under water in the pressure stove. Excising the stem and keeping the cut end under water should have enhanced water uptake and transport, preventing leaf rolling, on account of the removal of roots, if, according to Kramer<sup>6</sup>, the roots

were a major site of resistance to water movement. The inability of excised plants, though standing in water, to absorb and transport water strongly suggests the direct involvement of roots in these processes. However, the application of external pressure of +0.25 MPa to force entry of water into excised plants through the cut end resulted in complete unrolling of leaves (figure 1, B) and rapid increase in leaf water status within 30 min, including a 10-min lag period (figure 2). Not surprisingly, supply of water to previously stressed, intact potted plants also resulted in quick leaf unrolling, i.e. within 35 min including a 20 min lag period. In addition to leaf unrolling, leaf water potential of excised plants also increased sharply from -2.7 MPa to -0.36 MPa after application of external pressure (figure 3). Similarly, leaf water potential of intact potted plants also increased with the application of water to the root medium and rose to -0.5 MPa within 40 min, including a lag period. The pattern of change in pressure-induced increase in leaf relative water content (figure 4) agreed with that of leaf water potential, suggesting that leaf unrolling and increase in leaf water status were not merely due to increase in physical pressure *per se* in the leaf but in fact due to concurrent increase in leaf water content. Clearly, the case of pressure-induced unrolling of leaf and elevation of leaf water status of excised plants is analogous to the results obtained upon direct water application to intact plants. The reason for the relatively longer lag period (20 min) for leaf

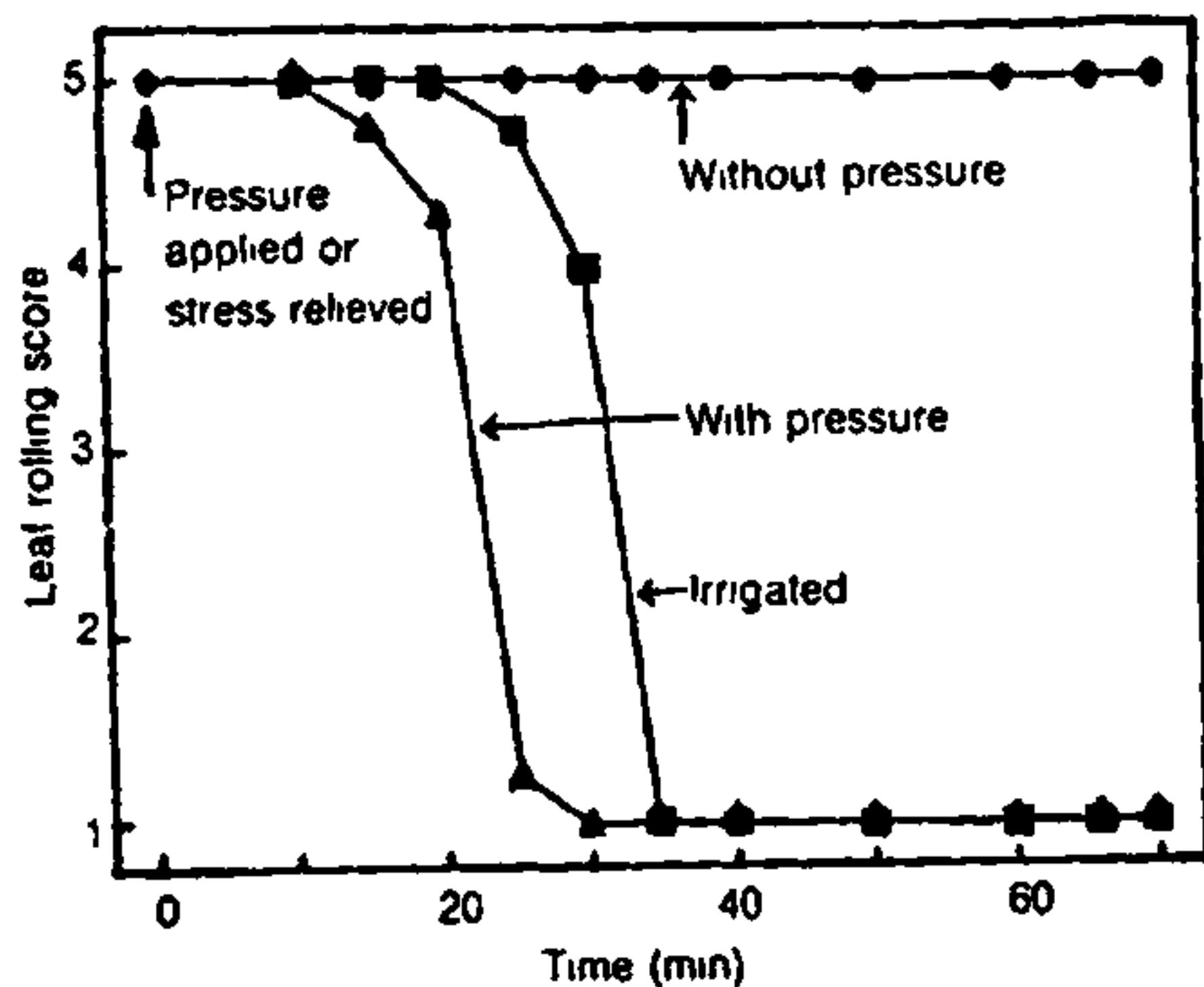


Figure 2. Effect of applied pressure on water transport in excised shoot of rice as evidenced by leaf unrolling. (Score 1, unrolled; score 3, partially rolled; score 5, rolled.)

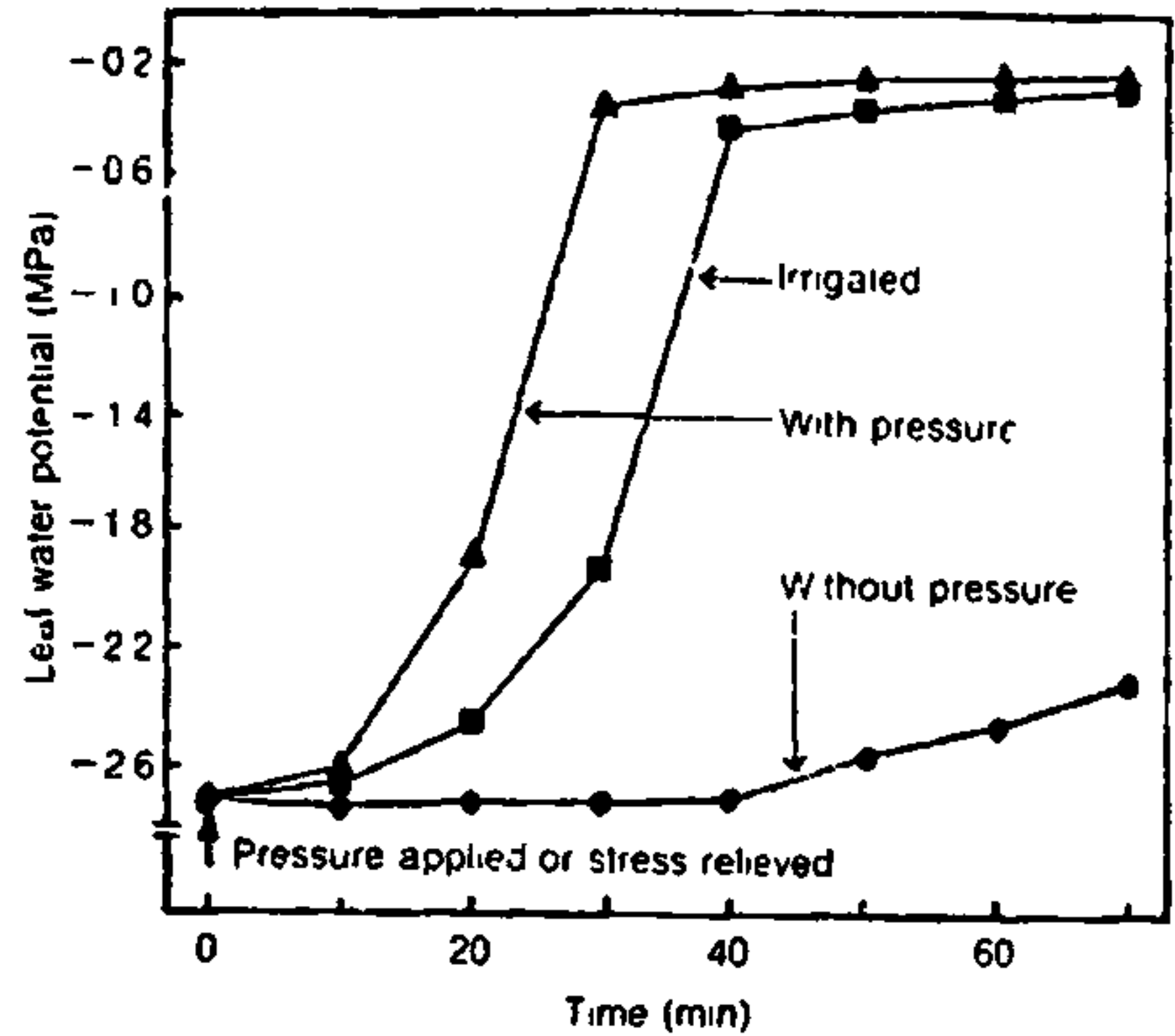


Figure 3. Effect of applied pressure on water transport in excised shoot of rice as evidenced by leaf water potential.

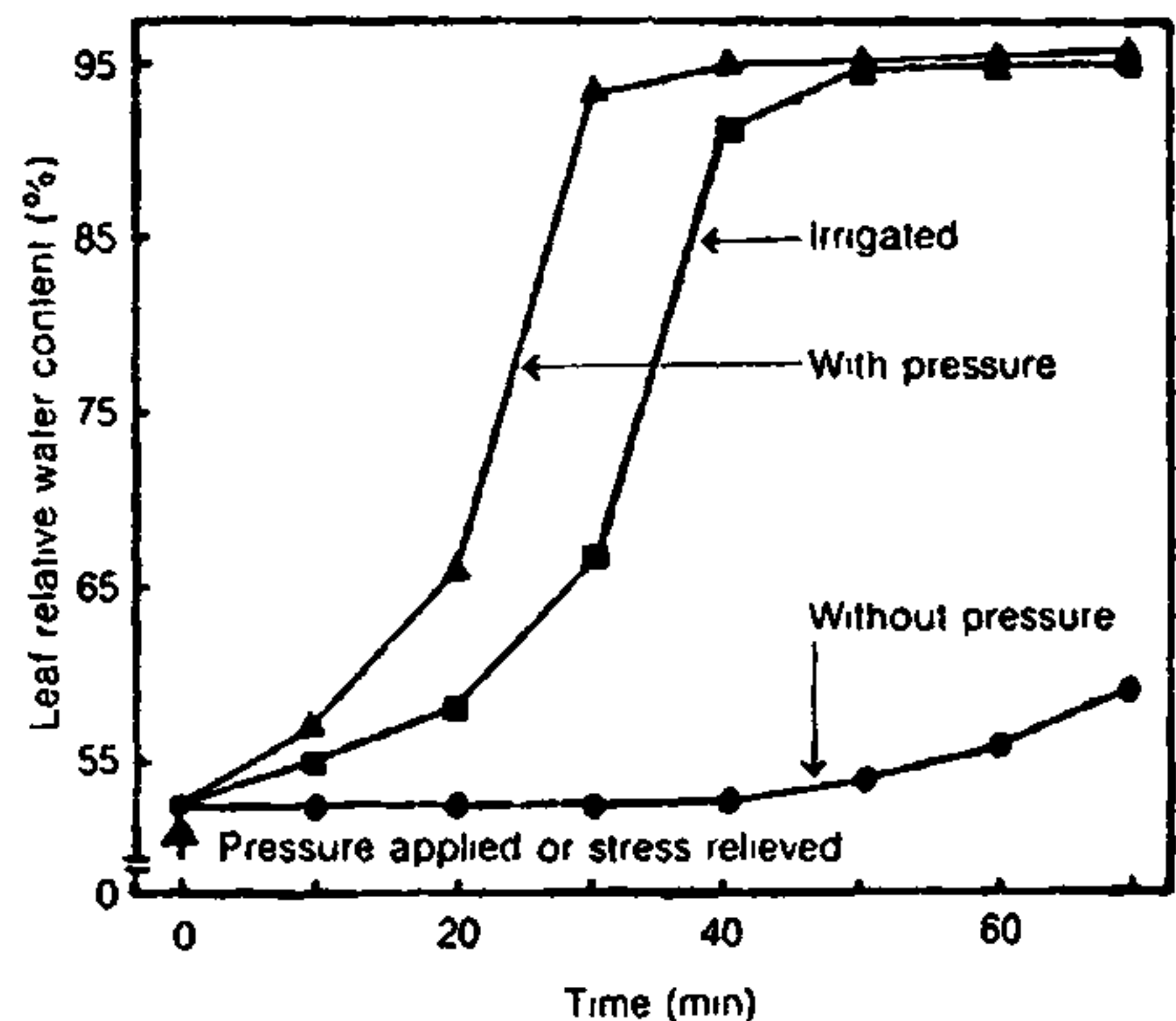


Figure 4. Effect of applied pressure on water transport in excised shoot of rice as evidenced by leaf relative water content.

unrolling and recovery of leaf water status in the case of intact potted plants could be, partly the resistance to water movement offered by the soil and the plant and partly the adjustment of root metabolic activity to the changed circumstances upon water supply<sup>5</sup>. Ignoring the lag, intact plants took only 15 min for complete unrolling of leaf whereas excised plants under external positive pressure of 0.25 MPa took about 20 min. One of the reasons for rapid uptake and transport of water in

intact plants could be increased root permeability on account of abscisic acid accumulation<sup>11</sup>, generating a pressure in the roots that is greater than the externally applied pressure to excised plants. Generally, root pressure of about +0.1 MPa, and rarely, +0.2 MPa, has been registered in detopped plants, but in intact rice plants it appears to be more than the values reported for other crops<sup>12</sup>.

The effects of nodal roots on leaf water relations provide additional evidence in support of roots functioning as a major site of water uptake and generation of force for upward transport of water in rice. Root removal or keeping water out of reach of the roots resulted in almost immediate leaf rolling (only 2–6 min) though the plant stood in water, whereas leaf rolling took 65 min when roots were intact and dipped in water (figure 5). This clearly indicates that roots are essential for water uptake and upward transport of water in the shoot and play an important role in overall water economy of rice plants. Rolling of leaves even in the presence of nodal roots under high evaporative demand conditions simply indicates that the supply of water by the roots was perhaps not enough to cope with loss from the leaves, probably because ascending water has to encounter enormous resistance in the shoot, which has at least 30% aerenchymatous tissues and air cavities<sup>13</sup>.

In rice plants, like in other intact transpiring plants, it appears as if water is transported upward on account of water potential gradient between leaves and roots. But the present findings suggest that water reaches the top of rice plants on account of some kind of 'water pump' essentially located in the roots. However, in intact plants it becomes

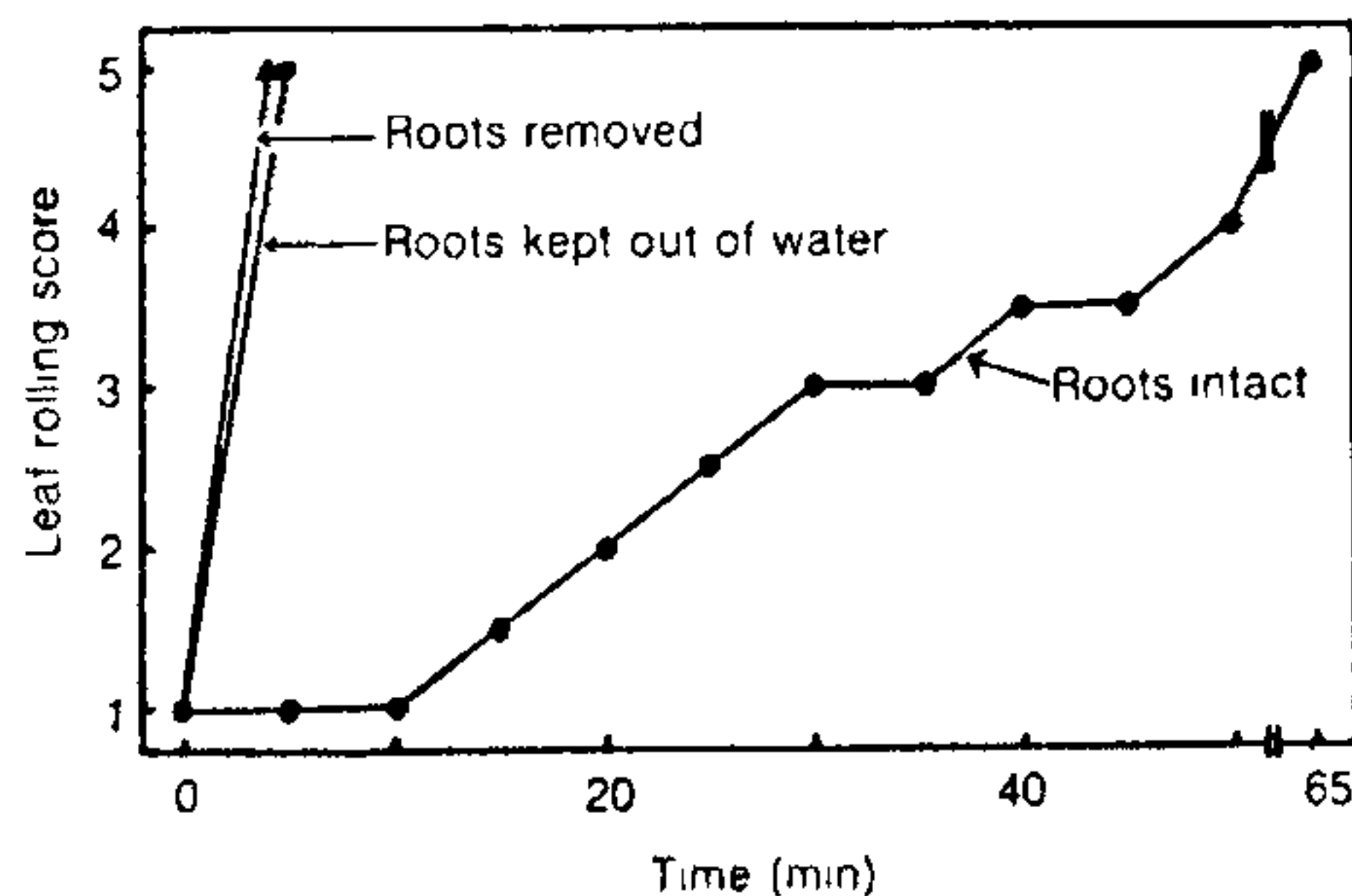


Figure 5. Role of roots in water transport to the shoot as evidenced by leaf rolling in rice.

difficult to ascertain the role of roots as a 'pushing force' and therefore the pressure developed by roots *in situ* is not obvious. The analogy between pressure-induced transport of water in the excised plant and root-mediated transport in the intact plant strongly suggests the possibility of roots functioning as a pumping machine and not merely as wicks for water supply to the shoot<sup>14,15</sup>. The existence of such a mechanism in rice roots as the sole source of bulk transport of water is further strengthened by the evidence of the inability of rice plants to make osmotic adjustments for leaf turgor maintenance in the event of water deficit<sup>16,17</sup>. Though it is difficult to evaluate the magnitude of such root pressure in intact plants *in situ*, in the light of the present findings it is tempting to estimate that it is at least +0.3 MPa in irrigated rice.

#### ACKNOWLEDGEMENT

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## ANNOUNCEMENT

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### Airway Hyperreactivity—Is it Really Important for Asthma?

Date: 26–27 February 1990  
Place: London

Airway hyperreactivity is a characteristic feature of asthma which is generally thought to be a consequence of chronic airway inflammation. Over the past five years dramatic changes have occurred in the approach adopted by the preclinical groups working in asthma. New models of airway hyperreactivity have been set up in an attempt to analyse the basic underlying mechanism(s) and to identify

new therapeutic agents. Asthma therapy is increasingly being directed to the earlier alleviation of airway hyperreactivity by the treatment of the underlying inflammation using prophylactic and anti-inflammatory drugs.

This meeting will review the preclinical and clinical developments in this exciting new field. It will be of benefit to scientists and physicians alike with an interest in this area, as well as those individuals who require an up-to-date overview.

For details contact: Renata Duke, IBC Technical Services Ltd., Bath House (3rd Floor), 56, Holborn Viaduct, UK.

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