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Water stress effects on leaf elongation, leaf water potential, transpiration, and nutrient uptake of rice, maize, and soybean

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Abstract

A pot experiment was conducted in the greenhouse to determine and compare the responses of rice (*Oryza sativa* L. var. IR36), maize (*Zea mays* L. var. DMR-2), and soybean (*Glycine max* [L.] Merr. var. Clark 63) to soil water stress. Leaf elongation, dawn leaf water potential, transpiration rate, and nutrient uptake in stressed rice declined earlier than in maize and soybean. Maize and soybean, compared with rice, maintained high dawn leaf water potential for a longer period of water stress before leaf elongation significantly declined. Rice transpired more than soybean and maize at the same dawn leaf water potential. Nutrient uptake under water stress conditions was influenced more by the capacity of the roots to absorb nutrients than by transpiration. Transport of nutrients to the shoots may occur even at reduced transpiration rate It is concluded that the ability of maize and soybean to grow better than rice under water stress conditions may be due to their ability to maintain turgor as a result of the slow decline in leaf water potential brought about by low transpiration rate and continued uptake of nutrient, especially K, which must have allowed osmotic adjustment to occur.

Introduction

It is well-established that water stress impairs numerous metabolic and physiological processes in plants (Begg and Turner, 1976; Hsiao, 1973; Levitt, 1980; Sullivan and Eastin, 1974; Turner and Kramer, 1980). Increasing resistance to transpiration, osmotic adjustment, and other adaptive mechanisms leading to xerophytism enables the plants to tolerate water stress.

Nutrient uptake by plants is decreased under water stress conditions due to reduced transpiration (Greenway and Klepper, 1969; O'Toole and Baldia, 1982; Yambao and O'Toole, 1984) and impaired active transport and membrane permeability (Hsiao, 1973) resulting in reduced root absorbing power. Nutrient uptake from the soil solution is also closely linked to soil water status. A decline in soil moisture is associated with a decrease in diffusion rate of nutrients from the soil matrix to the absorbing root surface (Barber, 1962; Marais and Weirsma, 1975; Viets, 1972). Thus, to fully explain the adverse effects of water stress on nutrient uptake, research should focus more on nutrient movement in the soil and plant response to applied nutrient and water stress.

Plant response to water stress varies with species and is modified by environmental and physiological factors. The different plant responses explain why one species survives or yields better than another under a limited water supply. This study sought to determine and compare the response of rice, maize, and soybean to soil water stress, specifically the leaf elongation, leaf water potential, transpiration, and nutrient uptake of each crop as water stress develops.

Materials and methods

Plant material, culture, and experimental design

Seeds of rice (IR36), maize (DMR-2), and soybean (Clark 63) were pregerminated in petri dishes. Planting was timed such that a uniform leaf area among species was attained when irrigation ceased.

Six pregerminated seeds of each crop were planted in plastic trays (32 × 24 × 10 cm) containing 6.5 kg of air-dried and sifted Maahas clay soil (isothermic clayey mixed typic tropaquept). Seedlings were thinned to a single plant after establishment.

Plants were grown under well-watered conditions until their leaf areas were $2\,\mathrm{dm}^2$. Twelve days after planting (DAP), 90-13-25 kg NPK ha^{-1} were applied in rice and soybean; maize was fertilized at 5 DAP.

Water was withheld on the same day; this was at 19 DAP in rice, 12 DAP in maize, and 15 DAP in soybean. The day before, all containers were covered with polyethylene sheets to minimize soil water evaporation.

A split-plot experimental design with five replications was used with crop species as the main plot, and water regime (control and stress) and sampling date as subplots in a factorial experiment.

Plant and soil sampling

Destructive sampling was employed to assess the crop's response to water stress. The first of 10 sampling dates was 2 days after water was withheld. Succeeding samplings were done 5, 8, 9, 10, 11, 12, 13, 16, and 17 days after water was withheld.

Leaf length was measured with a ruler every day at 0430 h. The difference between the initial and final measurement is expressed as the leaf elongation rate (cm day^{-1}). In rice, this was measured on any tiller with growing leaves 10–15 cm long; in maize, from the uppermost visible collar to the tip of either the youngest or the second growing leaf; and in soybean, from the middle leaflet of the youngest open trifoliate.

Transpiration rate was determined as the weight difference per plant over a 24-hour period. Weight loss was measured with a high capacity beam balance (OHAUS, 0.1 g sensitivity) and expressed on a leaf area and plant basis.

Dawn leaf water potential of the crops was measured at 0430 h with a pressure chamber following the procedures of Yambao and O'Toole (1984).

In rice, measurements were made on the second youngest leaf, excised about 2cm below the collar. Maize measurements were made on the youngest fully expanded leaf with exposed collar; sample leaves were excised at the collar. Measurements in soybean were made on either the 3rd or 4th leaf from the developing apex. The petiole was excised immediately after the pulvinus adjacent to the stem. After measuring leaf water potential, leaf area was measured using a Hayashi Denko AAM-7 leaf area meter.

Soil moisture content was determined gravimetrically at midday (1200 h) and expressed in percentage on an oven-dry weight basis. A hygrothermograph recorded the relative humidity and temperature. The atmospheric vapor pressure deficit (VPD) was calculated as a mean of 12-hour day (0600–1800 h) measurements.

Roots and shoots were separated from each other. Roots were removed from the soil by washing them gently with water. These were then dried at 80°C for 2–3 days to determine dry weight.

Nitrogen, phosphorus, and potassium contents of roots and shoots were estimated following the procedures of O'Toole and Baldia (1982) which is a modification of Varley's (1966). Nitrogen uptake

Table 1. Number of days after withholding water when characteristics of stressed plants began to differ significantly from those of the control

Plant character	Rice	Maize	Soybean
Dawn leaf water potential	11**	12*	16**
Midday leaf water potential	9*	12**	16**
Leaf elongation rate	7**	11**	11*
Transpiration rate	9*	11**	10**
Shoot dry weight	11**	13**	16**
Root dry weight	9**	17**	16**
Total shoot N uptake	9*	12**	11**
Total root N uptake	9**	Not affected	16**
Total shoot P uptake	9**	12*	13**
Total root P uptake	9**	13*	13*
Total shoot K uptake	9*	Not affected	16**
Total root K uptake	9**	Not affected	16**

* Significant at 5% level by LSD. ** Significant at 1% level by LSD.

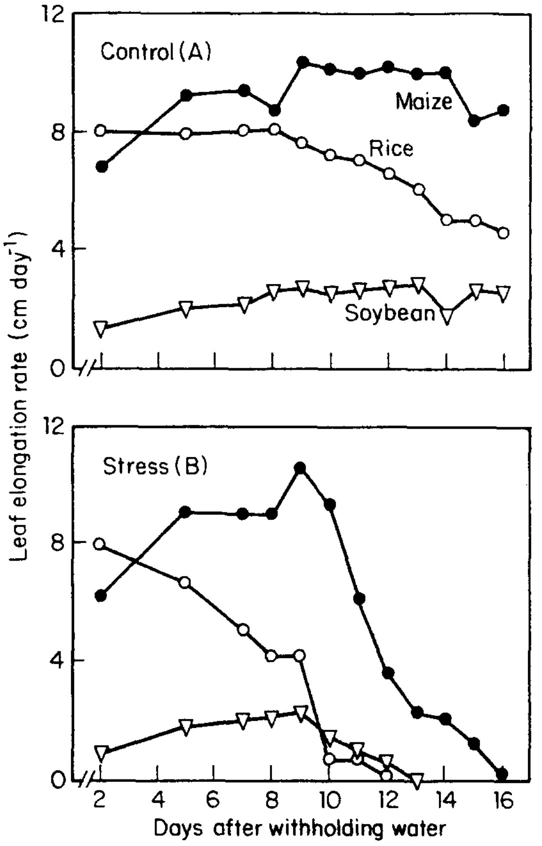

Fig. 1. Leaf elongation rate of rice, maize, and soybean under well-watered (A) and water-stressed conditions (B).

of root and shoot tissues was determined by the microkjeldahl method and by the colorimetric estimation of ammonia as indophenol blue using a Technicon Auto-Analyzer. Phosphorus determination differed from the procedure of Varley (1966) in that the ashing temperature was raised to 325°C for 1 h and then to 490°C for 4 h. Phosphorus in the ash solution was determined by the auto-analyzer. Molybdate instead of vanadate-molybdate was used as the color developer. The yellow color was reduced to blue with 0.8 ml min^{-1} of 1% ascorbic acid. The blue color was measured at 630 mμ. Potassium from the ash solution was determined using flame emission on a Perkin Elmer Model 2380 Atomic Absorption Spectrophotometer.

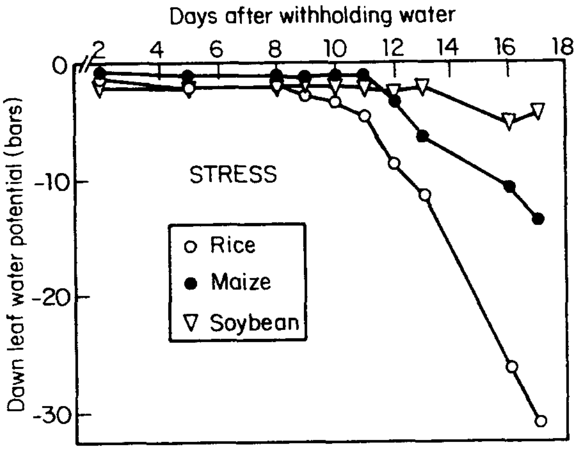

Fig. 2. Dawn leaf water potentials of rice, maize, and soybean during the 17-day stress period.

Results

Leaf elongation was reduced in rice since the start of the stress period and declined significantly 7 days after withholding water (Table 1, Fig. 1), with dawn leaf water potential of -2.1 bars the following day. An abrupt decrease in leaf elongation rate occurred on day 11, coinciding with a significant decline in dawn leaf water potential. Leaf elongation rate significantly declined 11 days after withholding water, with dawn leaf water potentials in maize at −1.1 bars and in soybeans, −2.0 (Fig. 2). In maize, leaf elongation occurred even after leaf water potential had significantly declined.

Leaf water potential in maize and soybean declined more slowly than in rice (Fig. 2). Dawn leaf water potential of control plants varied from −0.5 to −2.0 bars. Leaf water potentials of stressed plants declined earlier in rice than in maize and soybean (Table 1).

Transpiration rate of stressed plants significantly differed from that of the control 9, 10, and 11 days after withholding water in rice, soybean, and maize, respectively (Table 1). It declined significantly in rice at dawn leaf water potential of −2.7 bars; in soybean, at −2.0; and in maize, at −1.1. The trend can thus be described as rice > soybean > maize.

The VPD of the atmosphere greatly affected tranpiration rate in control plants (Fig. 3B), but only slightly at severe water stress levels (Fig. 3C) when all crops had minimum transpiration. Rice leaves were tightly rolled; maize leaves were wilted and slightly rolled; soybean leaves appeared thick, succulent, dark green, and some leaflets were re-

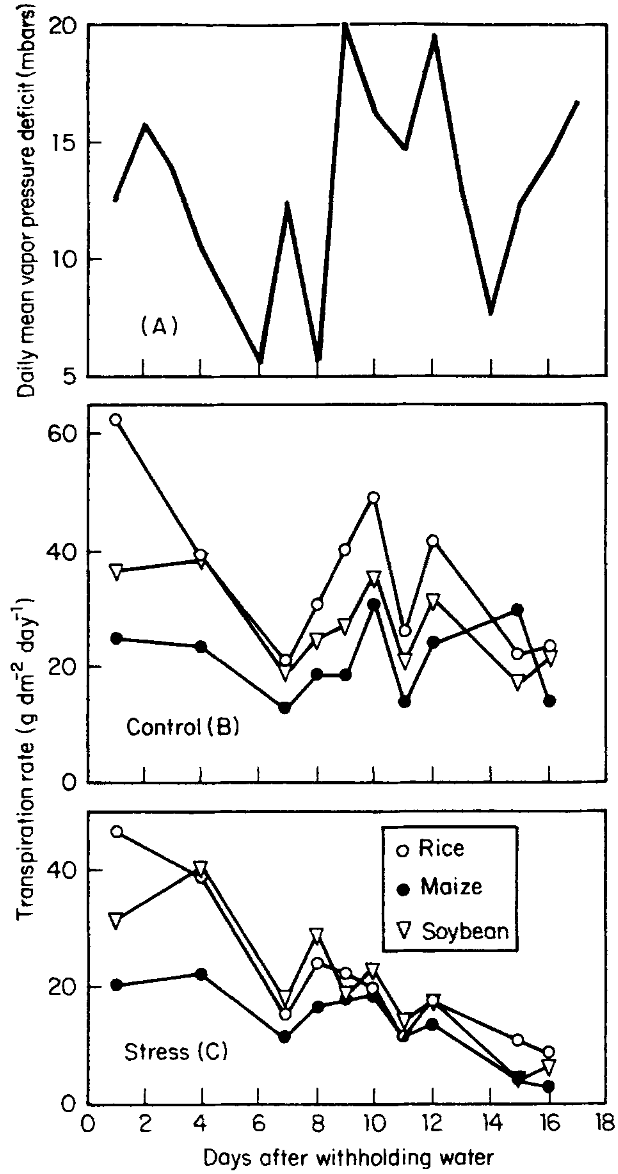

Fig. 13. Vapor pressure deficit (**A**) and transpiration rates of control (**B**) and stressed (**C**) rice, maize, and soybean plants during the 17-day stress period.

oriented exposing the abaxial surface to solar radiation.

Shoot and root dry weights of stressed rice significantly decreased earlier than in maize and soybean (Table 1, Figs. 4 and 5). Root dry weight of stressed maize increased, although not significantly, 5 to 12 days after withholding water (Fig. 5).

Total shoot N uptake of stressed plants decreased earlier in rice than in soybean and maize (Table 1). Total shoot N uptake of rice under stress conditions was the lowest and tended to level off 9 days after withholding water (Fig. 6). Total shoot N uptake of soybean was lower than that of maize probably because of its lower dry matter weight.

Total N uptake of rice roots declined significantly 9 days after withholding water (Fig. 6). Uptake of maize and soybean roots was not affected by water stress except on the 16th day of stress in soybean (Table 1). Total root N uptake of stressed rice declined despite its high root dry matter weight.

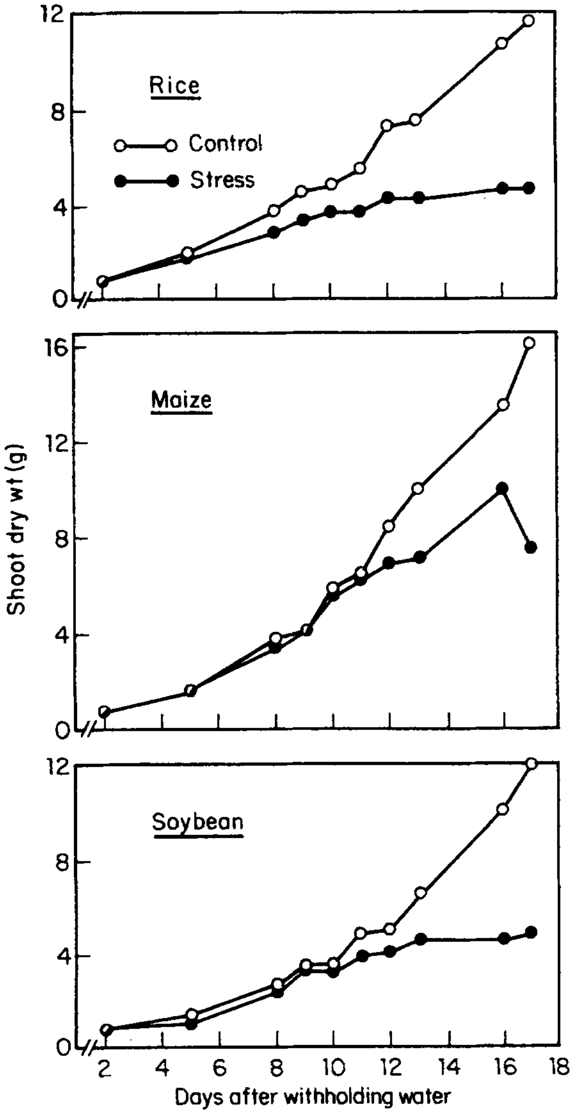

Fig. 4. Shoot dry weights of rice, maize, and soybean under well-watered and water-stressed conditions.

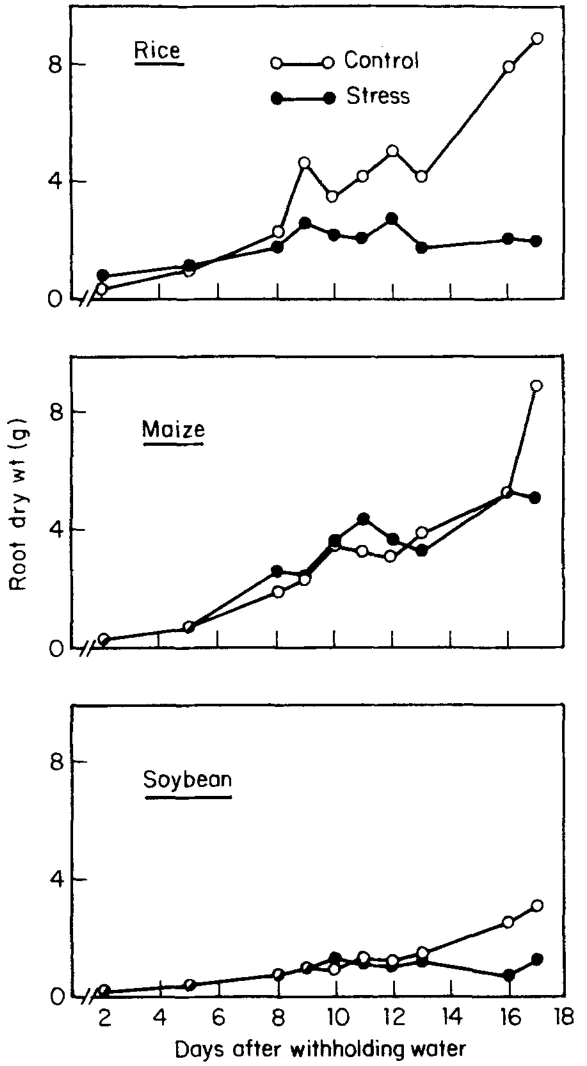

Fig. 5. Root dry weights of rice, maize, and soybean under well-watered and water-stressed conditions.

Total shoot P uptake decreased significantly 9 days after withholding water in rice; 12 days after, in maize; and 13 days after, in soybean (Table 1). Phosphorus uptake of rice leveled off 9 days after withholding water. Total shoot P uptake in maize and soybean continued to increase as water stress progressed (Fig. 7). Total root P uptake in soybean leveled off 9 days after withholding water.

Total root and shoot K uptake of rice decreased significantly 9 days after withholding water. Water stress did not affect the total K uptake of maize and soybean roots and shoots, except on the 16th day of stress in soybean (Table 1).

In the control plants, total shoot K uptake in rice was lower than that in maize (Fig. 8A). However, total shoot K uptake of rice under stress conditions decreased and appeared to remain constant 9 days after withholding water. Although total root K uptake of well-watered rice appeared comparable to that of maize (Fig. 8A), total root K uptake of rice was greatly decreased by water stress (Fig. 8B).

Discussion

The early decline and cessation of leaf growth in rice indicate that it is the most sensitive to water stress. The decrease in leaf elongation rate may have been caused by decreased turgor pressure which eventually resulted from the decline in leaf water potential (Fig. 9).

Maize and soybean maintained high leaf-water potentials for a longer period than did rice before leaf elongation significantly declined. The slow decline in leaf water potential can be attributed to their low transpiration rates. Thus, the high transpiration rate of rice may have caused the rapid decline in leaf-water potential. In soybean, leaflet reorientation could be a mechanism by which water loss was reduced to maintain a high leaf water potential under water stress (Meyer and Walker, 1981).

At the same leaf-water potential, rice transpired more than did maize and soybean (Fig. 10). This allowed maize and soybean to deplete soil water slowly and to conserve more water to survive longer under water stress. This was shown by the slower decrease in their soil moisture content (Fig. 11).

The maintenance of high leaf-water potential in maize and soybean was considered responsible for dry matter accumulation. The increased root dry weight in maize (Fig. 5) was also an adaptive mechanism to resist water stress. In wheat, Blum *et al.* (1983) considered high root mass production to be associated with drought resistance.

Water stress reduced nutrient uptake by crops due to decreased transpiration and impaired active nutrient absorption and transport mechanisms of the roots. Furthermore, water stress reduced dry matter, thereby decreasing the demand for nutrients.

Nutrient uptake by the crops may have been influenced by leaf water potential. Total nutrient

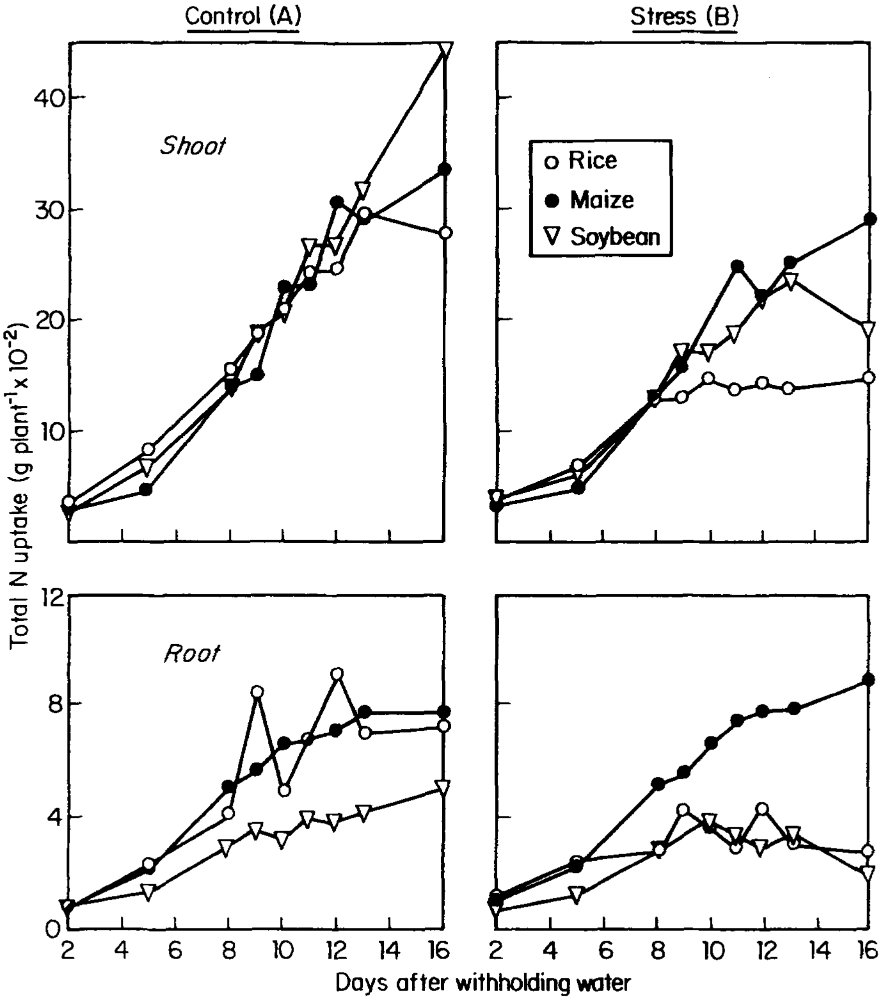

Fig. 6. Total shoot and root N uptake of rice, maize, and soybean under well-watered (A) and water-stressed (B) conditions.

uptake in maize under water stress conditions tended to increase even with a decreasing leaf-water potential (Figs. 12 to 14). Soybean did not show a decline in dawn leaf-water potential except on day 16 of the stress period (Fig. 2); thus, it must have avoided internal stress, consequently affecting nutrient uptake.

Increased K uptake in maize suggests that under water stress conditions, K was absorbed preferably to N and P. Uptake of K was also less affected and may have resulted in osmotic adjustment which contributed to the higher leaf-water potential in maize and soybean crops (Gerakis *et al.*, 1975).

Sinha (1978) observed that drought-tolerant wheat varieties can accumulate more K than do the susceptible varieties and that plants well supplied with K had higher stomatal resistance which resulted in low transpiration rate. Further, Maurya and Gupta (1984) observed increased water potential of wheat plants with increased K fertilization. Such increase in water potential was postulated as an adaptation to plant water stress.

Nutrient uptake was highly related to transpiration rate under well-watered conditions (Figs. 15 to 17). The higher the transpiration rate, the greater the nutrient uptake. Under water stress conditions, however, nutrient uptake did not appear to be significantly related to transpiration rate except for total N (Fig. 15B) and K (Fig. 17B) uptake by soybean roots. Apparently, however, nutrient up-

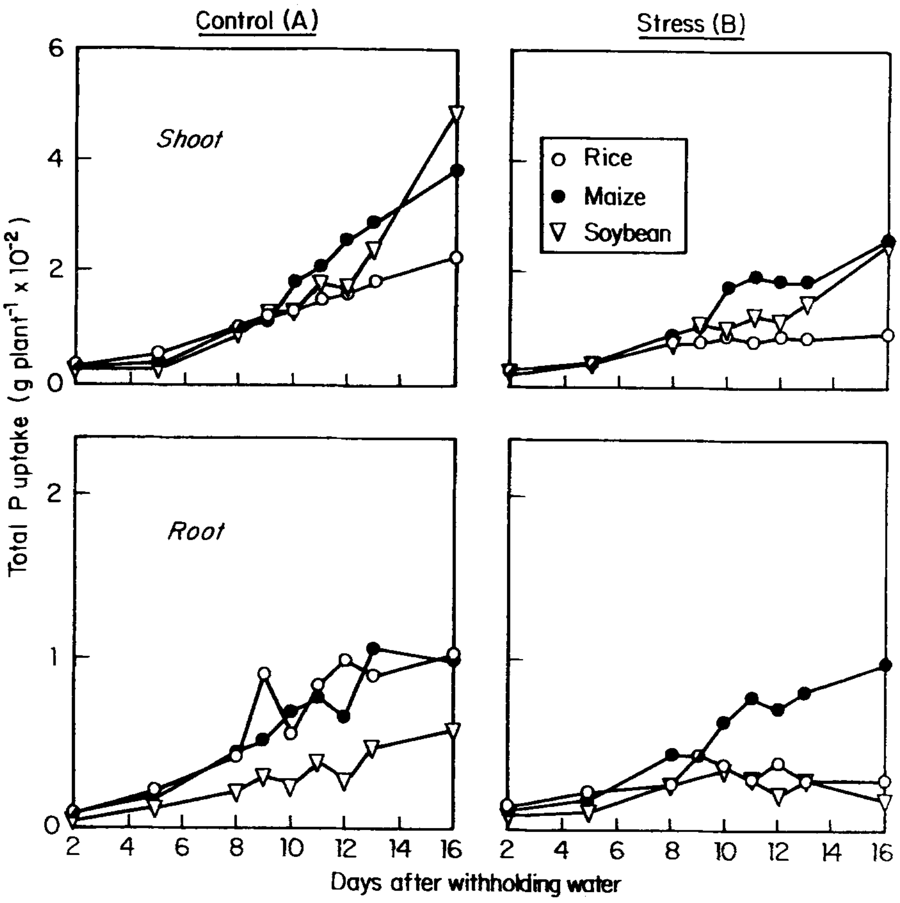

Fig. 7. Total shoot and root P uptake of rice, maize, and soybean under well-watered (A) and water-stressed (B) conditions.

take in maize and soybean increased with increasing transpiration rate (Figs. 15B to 17B).

In rice, nutrient uptake did not increase with increasing transpiration rate, suggesting that nutrient uptake of stressed rice was influenced more by the capacity of the roots to absorb nutrients than by transpiration. Transport of nutrients to the shoots occurred even at reduced transpiration rate.

Undoubtedly, reduced transpiration also had a major effect on the nutrient uptake process shown by the decline in transpiration rate coinciding with the decrease in nutrient accumulation in rice roots and shoots (Table 1). Thus, the amount of nutrients that can be transported to the shoots depends on the capability of the roots to absorb nutrients from the soil and transport them to the transpiration stream. The subsequent translocation of nutrients to the shoot is largely influenced by transpiration rate (Broyer and Hoagland, 1943; Hylmo, 1953; Greenway and Klepper, 1969).

In the case of maize and soybean, root N uptake and root-and shoot K uptake were not affected by the 16-day water stress (except on the last day of stress in soybean). Nutrient absorption by the roots from the soil was still effective even at severe water stress levels. The decline of shoot N uptake can be attributed to the decreased transpiration to transport nutrients from roots to shoots. The roots, however, were still able to absorb nutrients from the soil and transport the nutrients to the transpiration stream and, consequently, to the shoots.

The decrease in nutrient uptake by rice under water stress conditions was primarily caused by the physiological impairment of the active nutrient

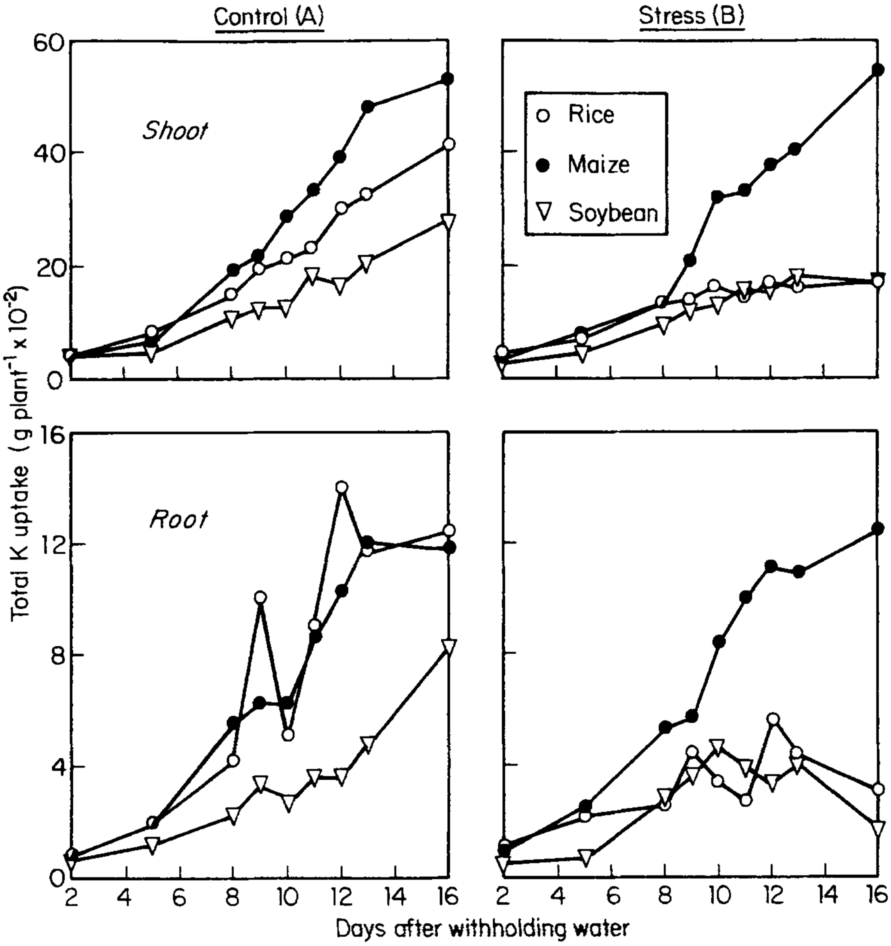

Fig. 8. Total shoot and root K uptake of rice, maize, and soybean under well-watered (A) and water-stressed (B) conditions.

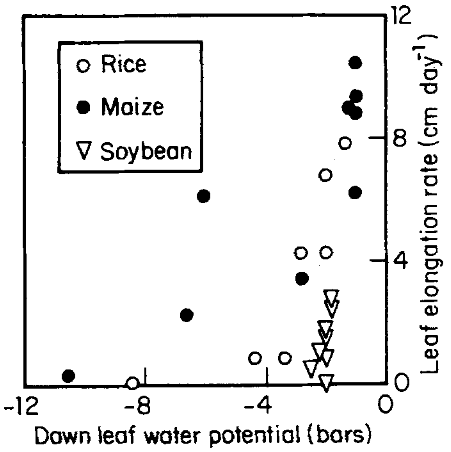

Fig. 9. Relation between leaf elongation and dawn leaf water potential of rice, maize, and soybean during the 17-day stress period.

absorption and transport mechanism of the roots. Rice root injury decreased the roots' ability to absorb nutrients as water stress progressed.

Erlandsson (1975) showed that a change in the water potential of plants caused by water stress has an effect on the active-ion-uptake mechanism. Evidence of a decreased ion absorption due to reduced root absorption power as affected by water stress was also reported by Dunham and Nye (1976). Similarly, O'Toole and Baldia (1982) observed that stressed rice plants continued taking up nutrients but the uptake rates were not as responsive to evaporative demand and transpiration rate as in the control plants.

It is concluded that compared with rice, maize and soybean can thrive better under water stress conditions. This is probably due to their ability to maintain turgor as a result of the slow decline in

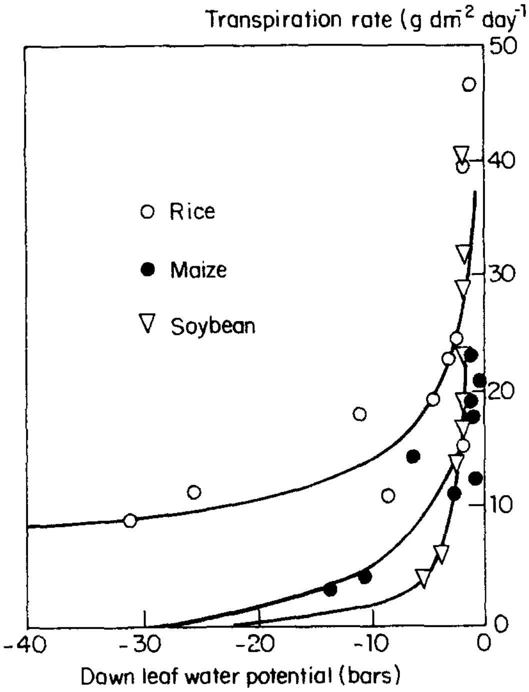

Fig. 10. Relation between transpiration rate and dawn leaf water potential of rice, maize, and soybean during the 17-day stress period.

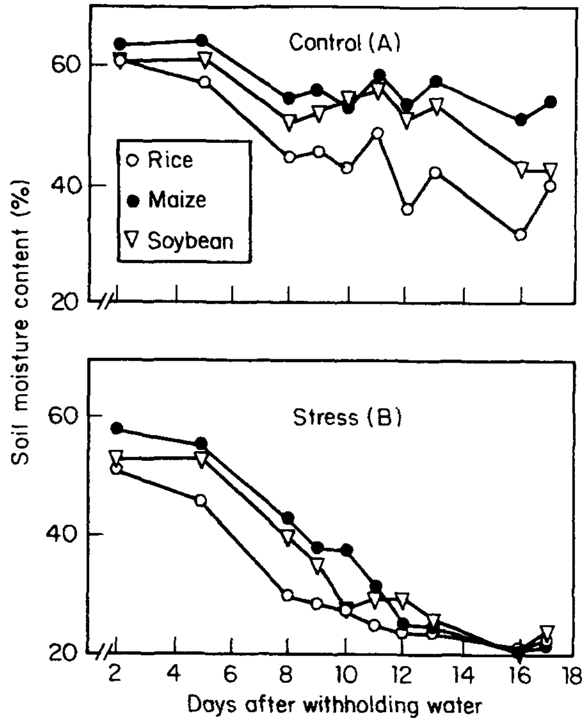

Fig. 11. Soil moisture contents of rice, maize, and soybean under well-watered (**A**) and water-stressed conditions (**B**).

their leaf water potential caused by a low transpiration rate. In addition to low transpiration rate, maize and soybean may have adjusted osmotically or altered other cellular water relationships to maintain turgor.

Transpiration rate and root absorption capacity influence the nutrient uptake by crops under water stress conditions. The ability of stressed maize and soybean to absorb nutrients was possibly enhanced by their ability to maintain turgor.

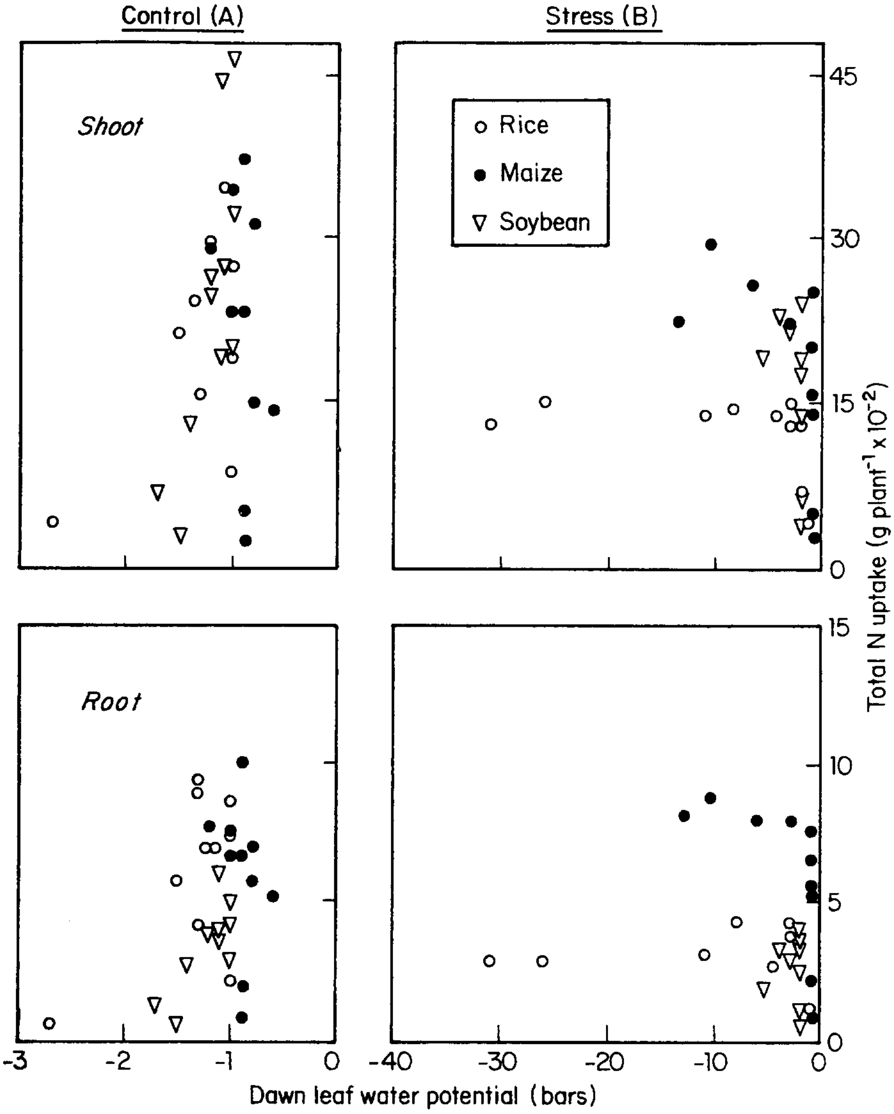

Fig. 12. Relationship between total shoot and root N uptake and dawn leaf water potential of well-watered **(A)** and water-stressed **(B)** rice, maize, and soybean.

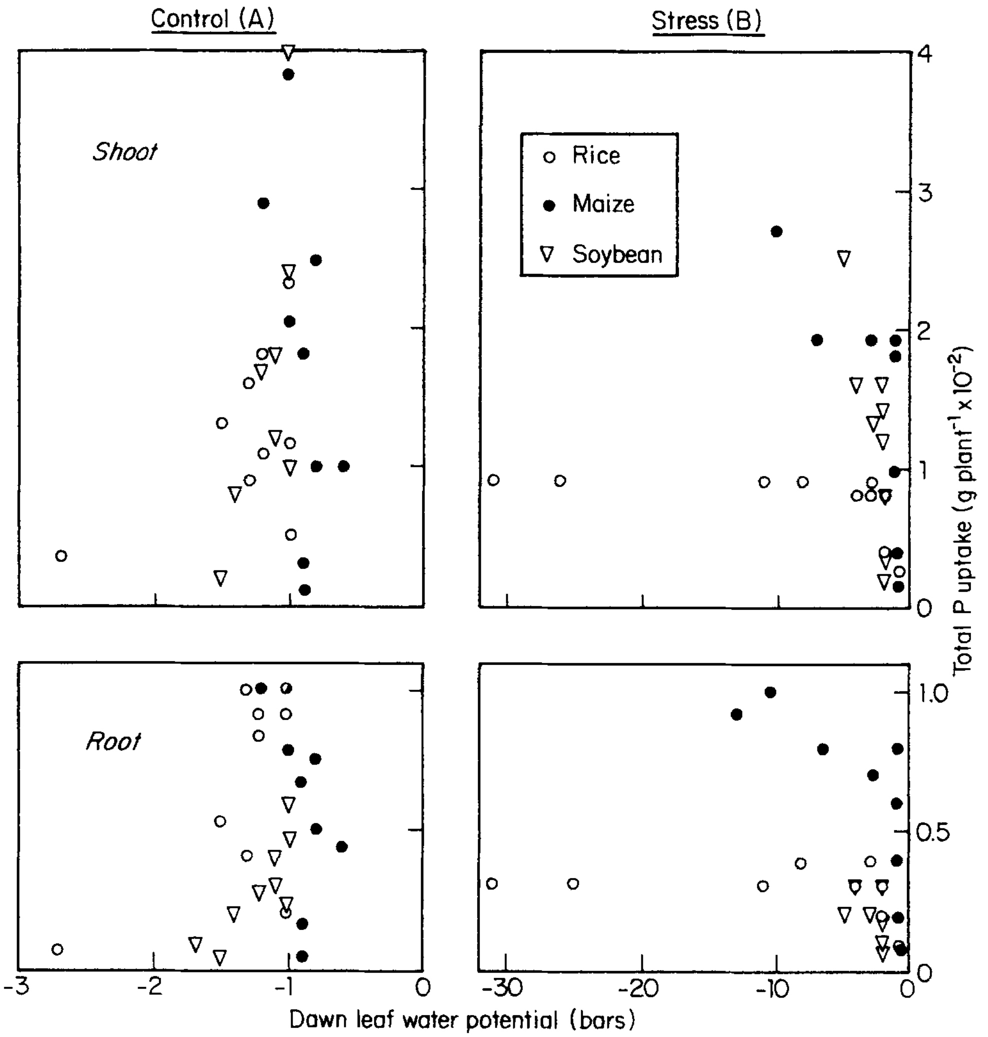

Fig. 13. Relationship between total shoot and root P uptake and dawn leaf water potential of well-watered (**A**) and water-stressed (**B**) rice, maize, and soybean.

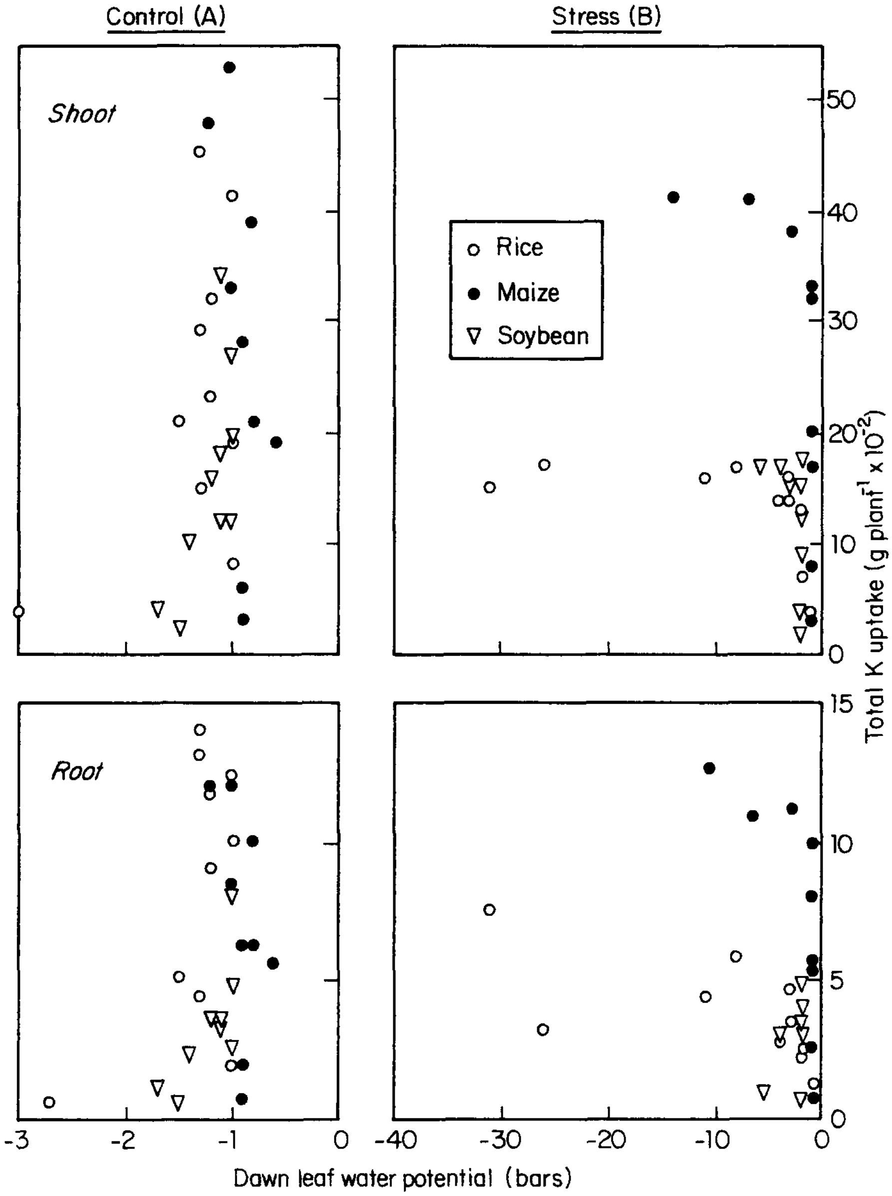

Fig. 14. Relationship between total shoot and root K uptake and dawn leaf water potential of well-watered (A) and water-stressed (B) rice, maize, and soybean.

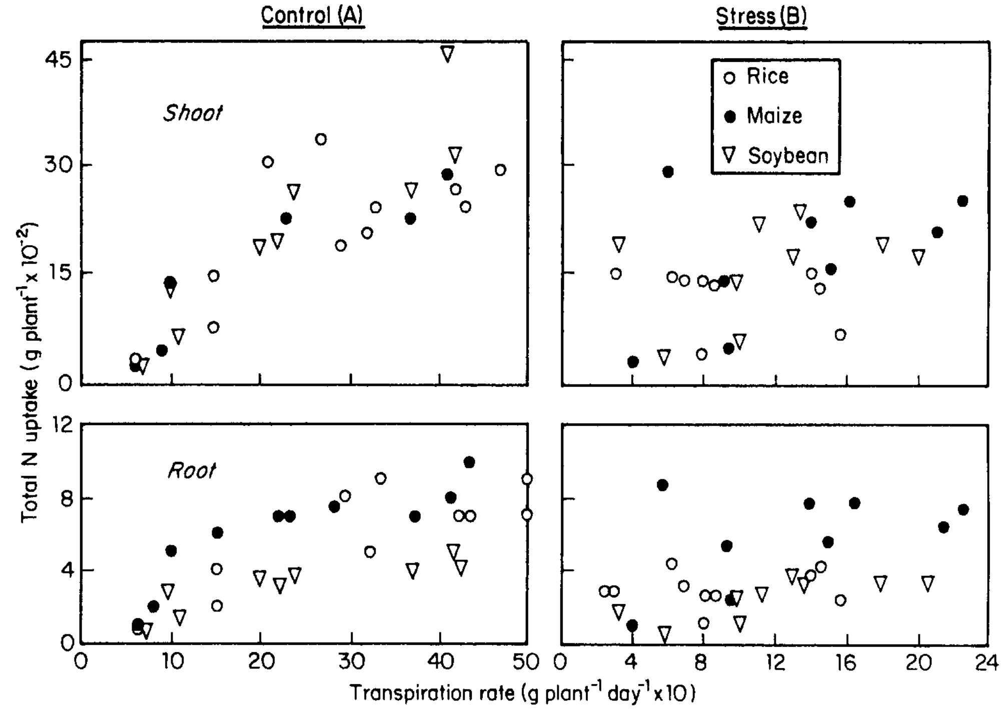

Fig. 15. Relationship between total shoot and root N uptake and transpiration rate of well-watered (A) and water-stressed (B) rice, maize, and soybean.

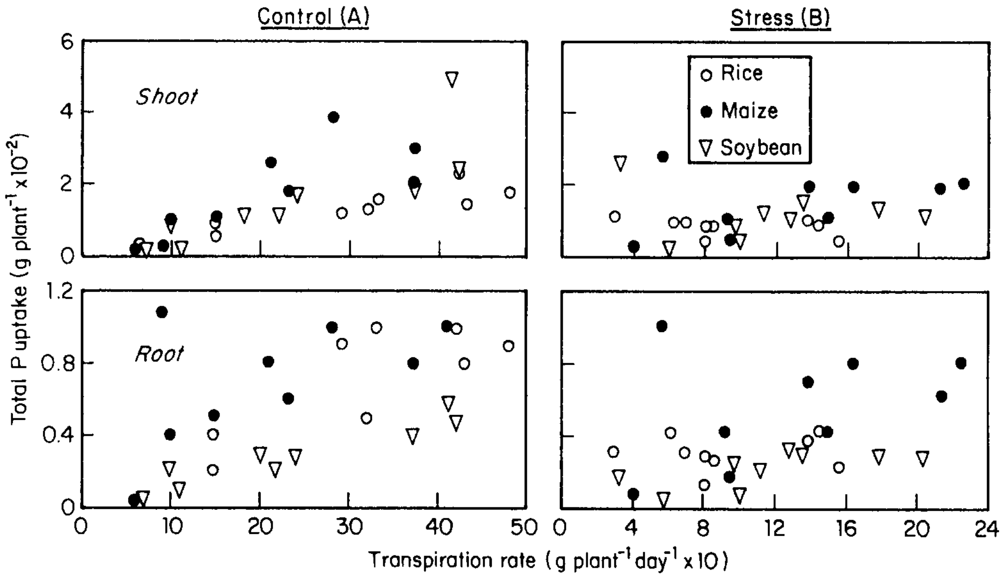

Fig. 16. Relationship between total shoot and root P uptake and transpiration rate of well-watered (A) and water-stressed (B) rice, maize, and soybean.

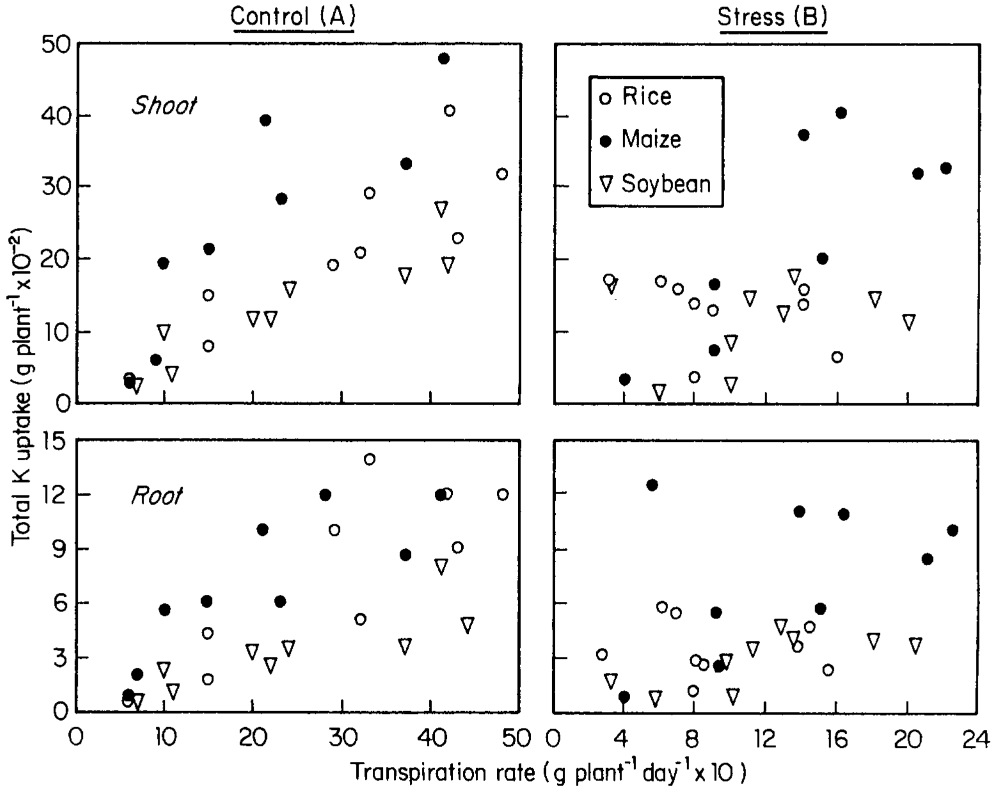

Fig. 17. Relationship between total shoot and root K uptake and transpiration rate of well-watered (**A**) and water-stressed (**B**) rice, maize, and soybean.

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