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17 February 1988

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My dear S.K.

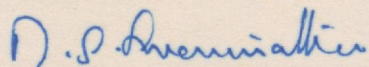
I thank you very much for your letter of February 12th.

I have read the papers you have sent with great interest. Your findings should help us to improve nutrient use efficiency. I wish you and Michael Dingkuhn success in your further work.

I am sorry I am unable to come to Cairo in the last week of March.

With warm regards to you and Vijjie and best wishes to Raj.

Yours sincerely



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MSS/am

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February 12, 1988

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Dear Dr. Swaminathan:

By this time you must have returned to India from your extended trip to Washington and Costa Rica. I hope your trip went on well. I still have not gotten adjusted to your not being here as I have taken advice from you for a number of difficult issues that confronted our department's success to fulfill our mandate. For example, we still have not gotten the additional funds that you approved subject to funding for purchasing essential equipment. I hope the situation will improve in the near future.

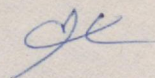
The main purpose of writing you this note is to advise you on the status of our project on measurement of nitrogen losses to improve fertilizer use efficiency in both transplanted and broadcast seeded flooded rice. Thus far, no one has quantitatively measured the extent of losses and avenues of minimizing these losses in broadcast seeded flooded rice which is becoming an important system of stand establishment in the region. Michael Dingkuhn is measuring the canopy photosynthesis rate by which we will be able to monitor what is happening in the crop. We have a total of five hectares rented with several objectives to be covered in a single experiment.

Attached please find three of our recent research reprints for your information and file.

In the end of March I understand you are invited to go to Egypt. If you would attend their annual meeting, I shall be seeing you there.

With my best personal regards to you and Mrs. Swaminathan.

Sincerely,



S.K. De Datta
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/raf
Att. (3 reprints)

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

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Key words: leaf elongation rate, leaf water potential, maize, nitrogen, nutrient uptake, phosphorus, potassium, rice, soybean, transpiration rate, water stress

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 Weirsmas, 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 dm². 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 bal-

ance (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 2 cm 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.

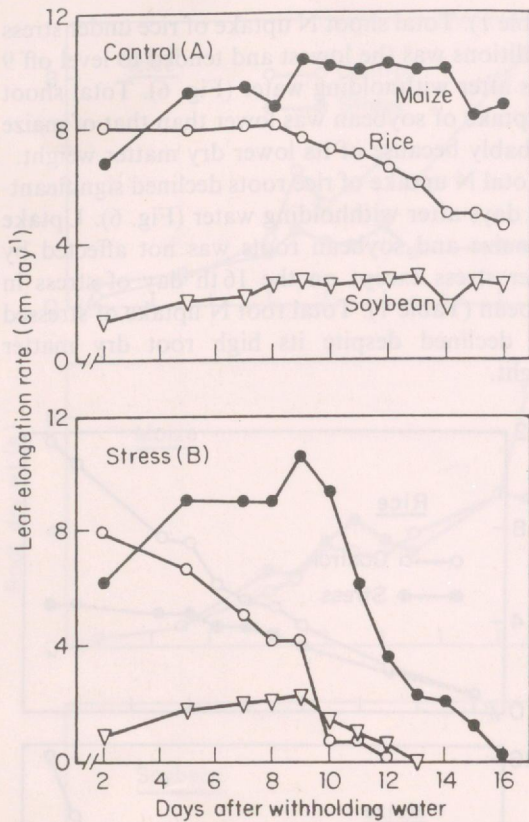


Fig. 1. Leaf elongation rate of rice, maize, and soybean under well-watered (A) and water-stressed conditions (B).

of root and shoot tissues was determined by the microkjeldahl method and by the colorimetric estimation of ammonia as indophenol blue using a

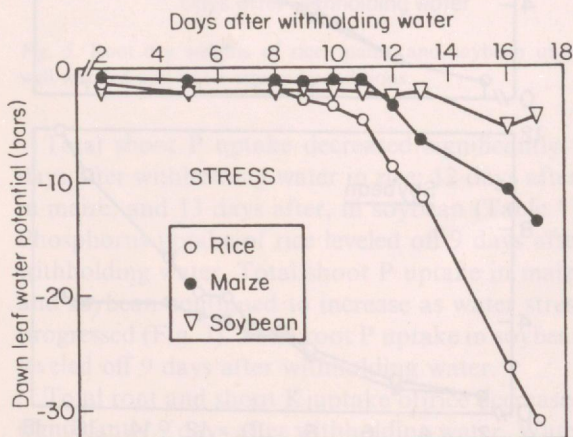


Fig. 2. Dawn leaf water potentials of rice, maize, and soybean during the 17-day stress period.

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 m μ . Potassium from the ash solution was determined using flame emission on a Perkin Elmer Model 2380 Atomic Absorption Spectrophotometer.

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 transpiration 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-

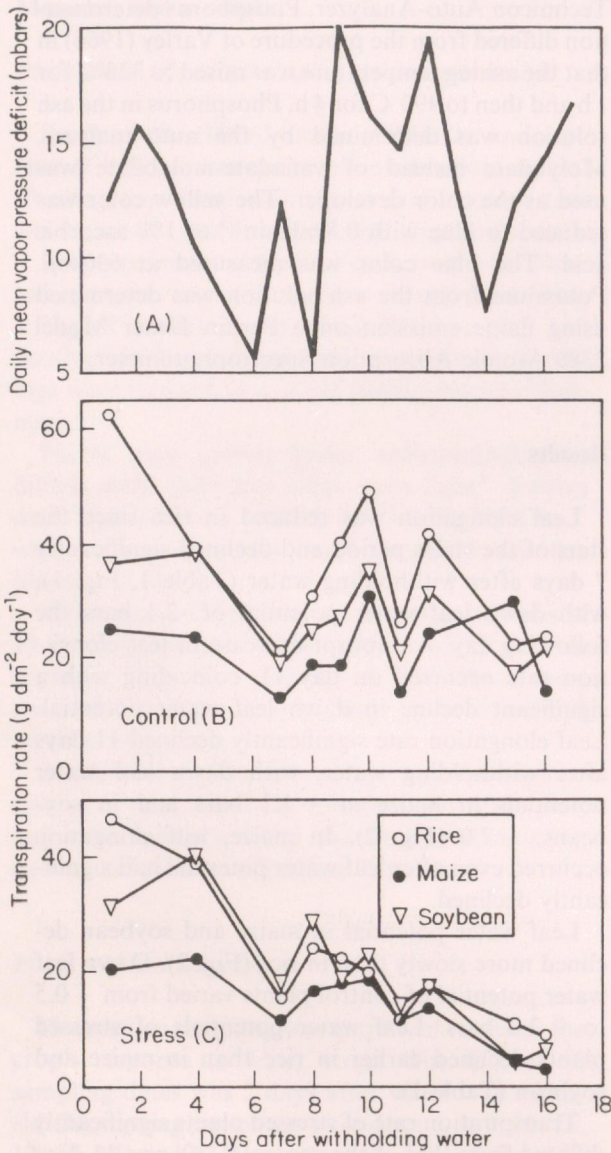


Fig. 13. Vapor pressure deficit (A) and transpiration rates of control (B) and stressed (C) rice, maize, and soybean plants during the 17-day stress period.

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.

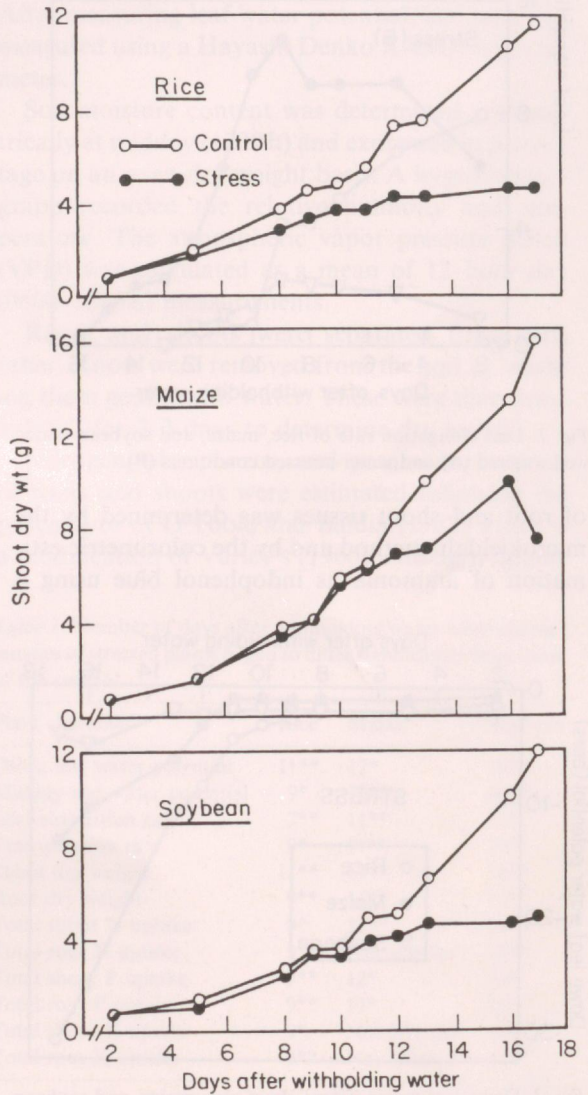


Fig. 4. Shoot dry weights of rice, maize, and soybean under well-watered and water-stressed conditions.

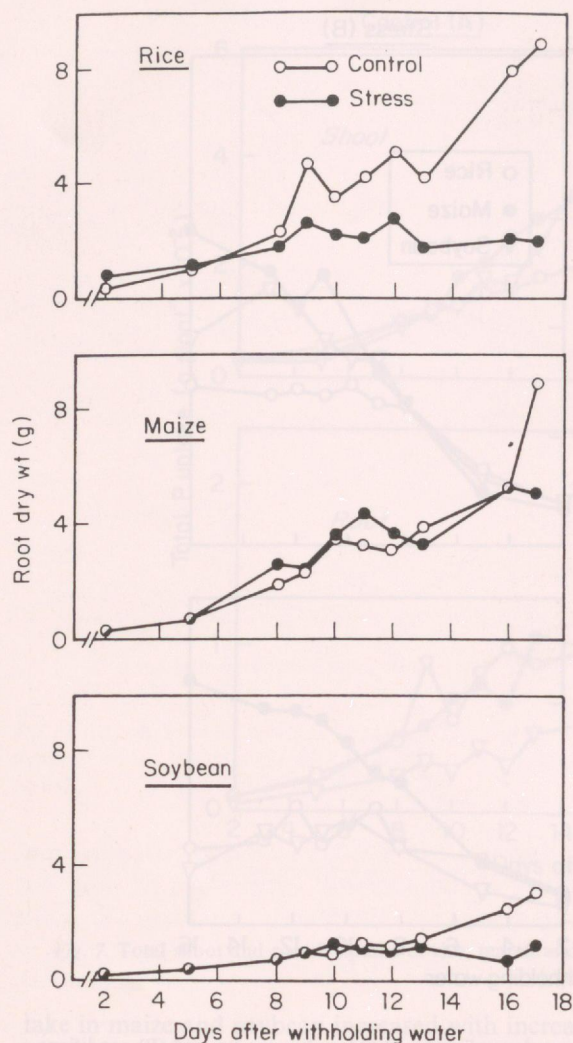


Fig. 5. Root dry weights of rice, maize, and soybean under well-watered and water-stressed conditions.

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

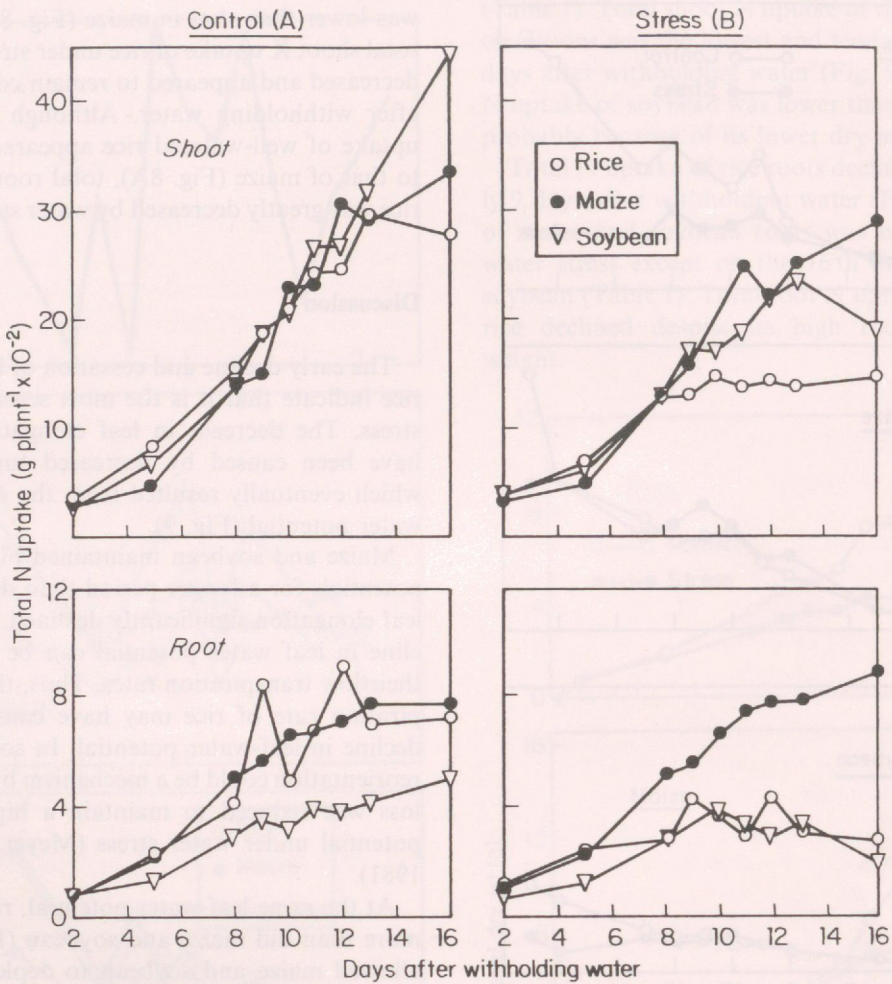


Fig. 6. Total shoot and root N uptake of rice, maize, and soybean under well-watered (A) and water-stressed (B) conditions.

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-

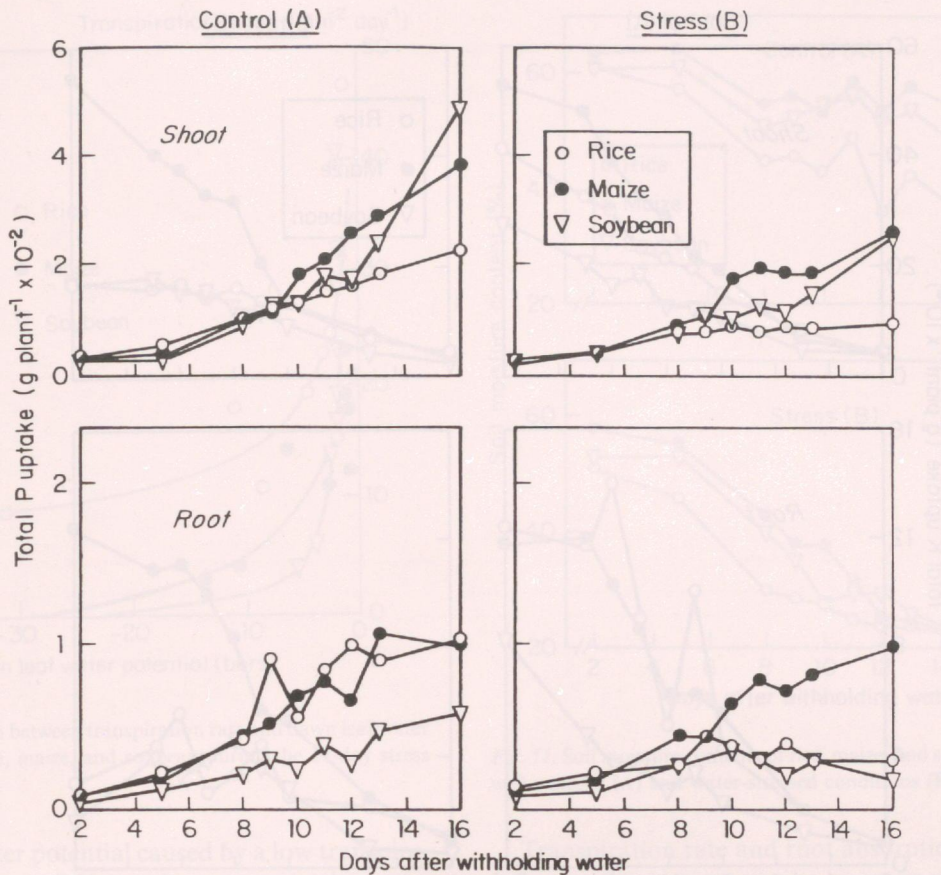


Fig. 7. Total shoot and root P uptake of rice, maize, and soybean under well-watered (A) and water-stressed (B) conditions.

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

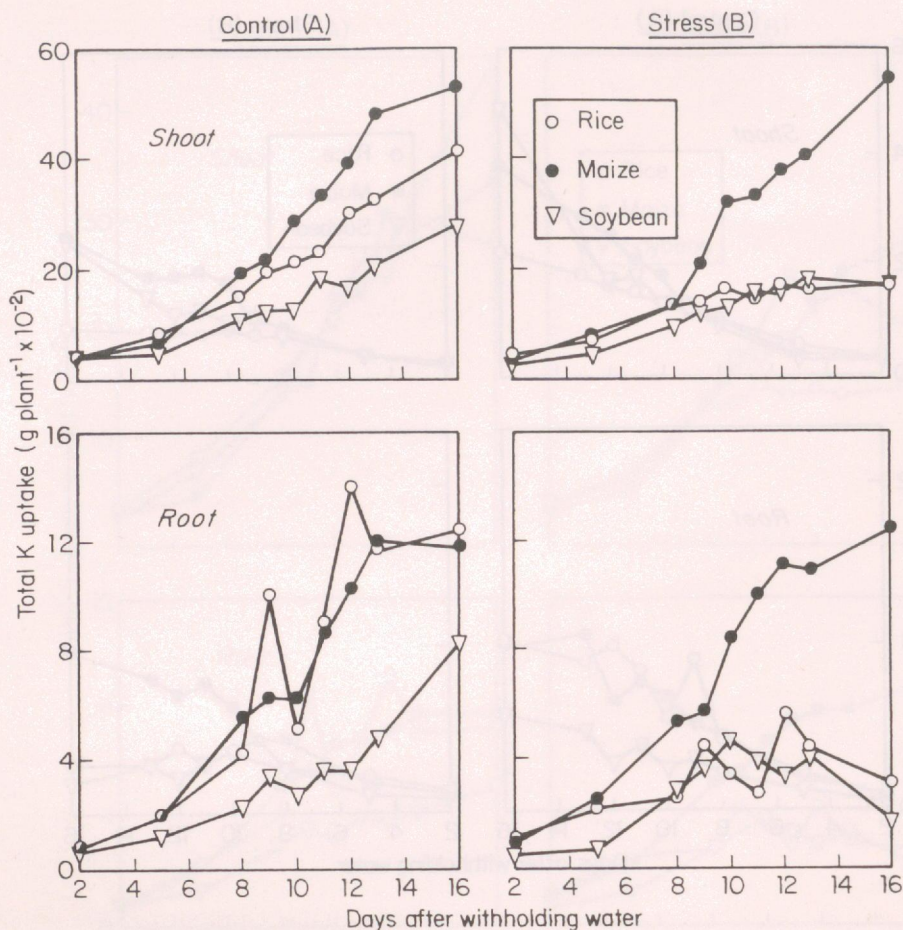


Fig. 8. Total shoot and root K uptake of rice, maize, and soybean under well-watered (A) and water-stressed (B) conditions.

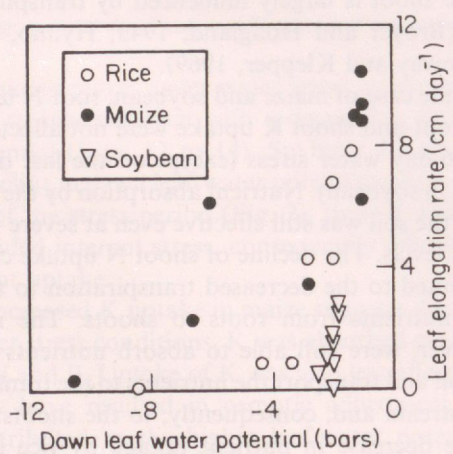


Fig. 9. Relation between leaf elongation and dawn leaf water potential of rice, maize, and soybean during the 17-day stress period.

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

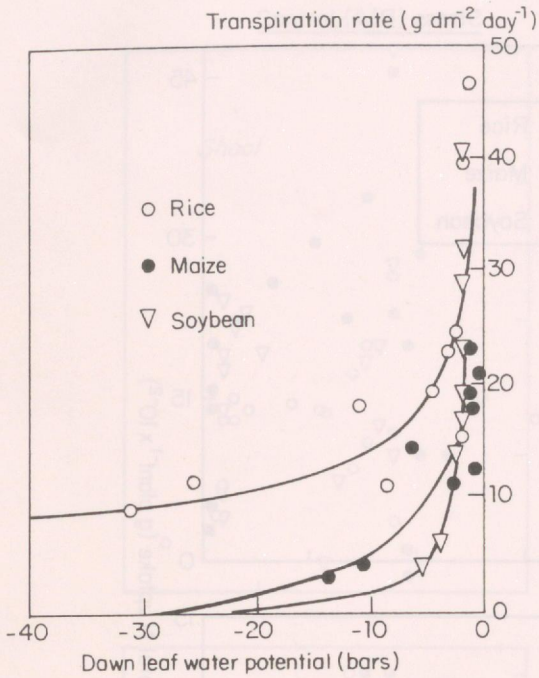


Fig. 10. Relation between transpiration rate and dawn leaf water potential of rice, maize, and soybean during the 17-day stress period.

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.

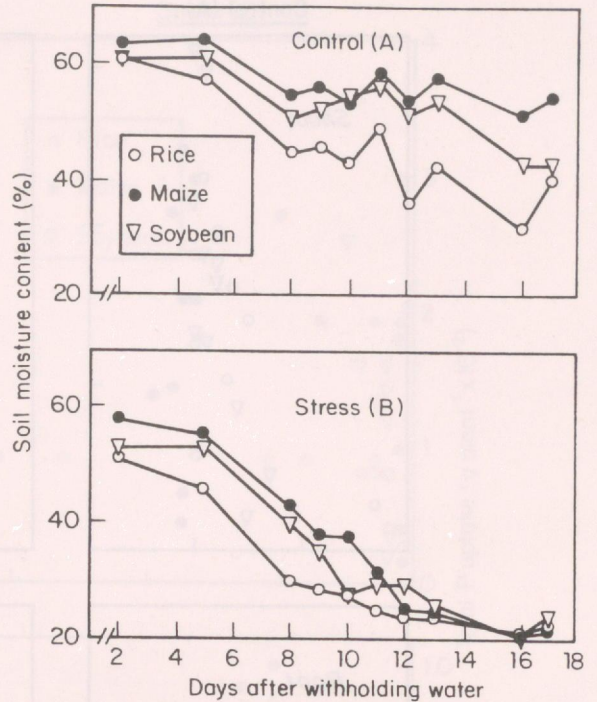


Fig. 11. Soil moisture contents of rice, maize, and soybean under well-watered (A) and water-stressed conditions (B).

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.

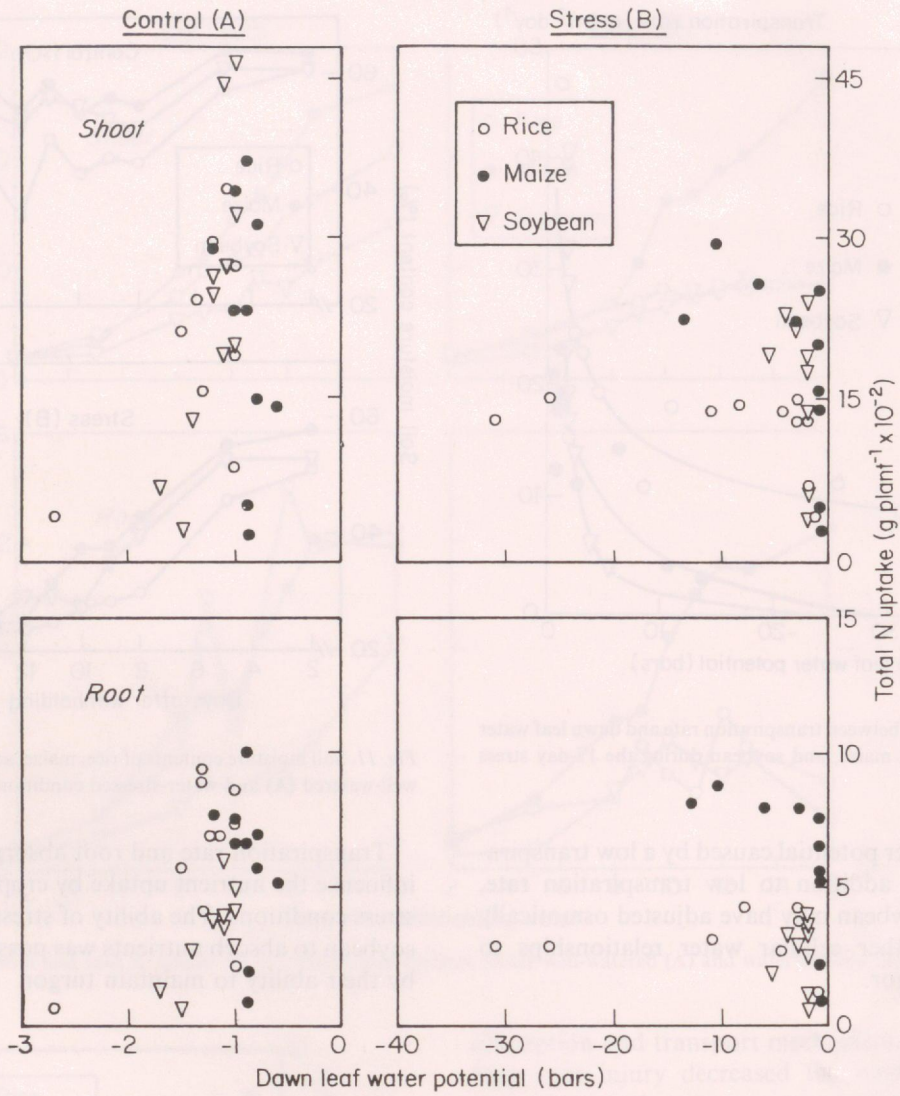


Fig. 12. Relationship between total shoot and root N uptake and dawn leaf water potential of well-watered (A) and water-stressed (B) rice, maize, and soybean.

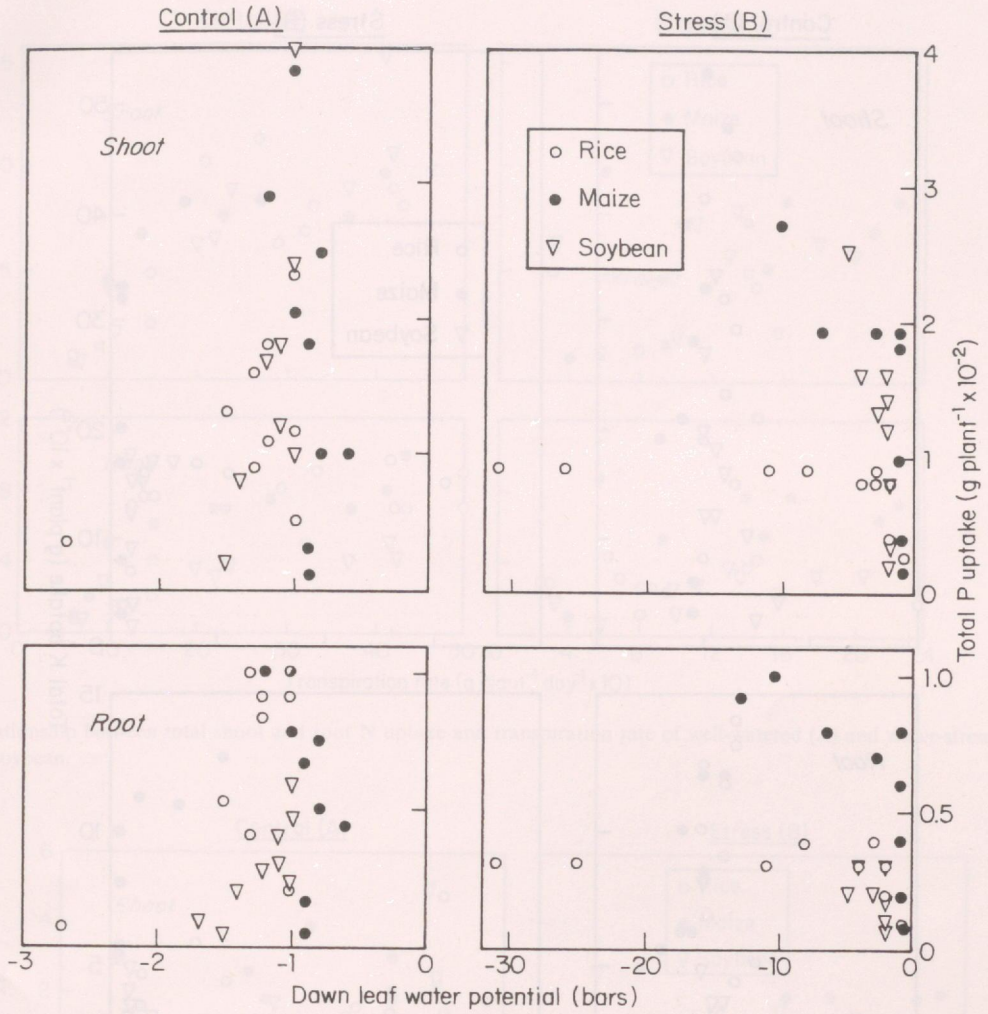


Fig. 13. Relationship between total shoot and root P uptake and dawn leaf water potential of well-watered (A) and water-stressed (B) rice, maize, and soybean.

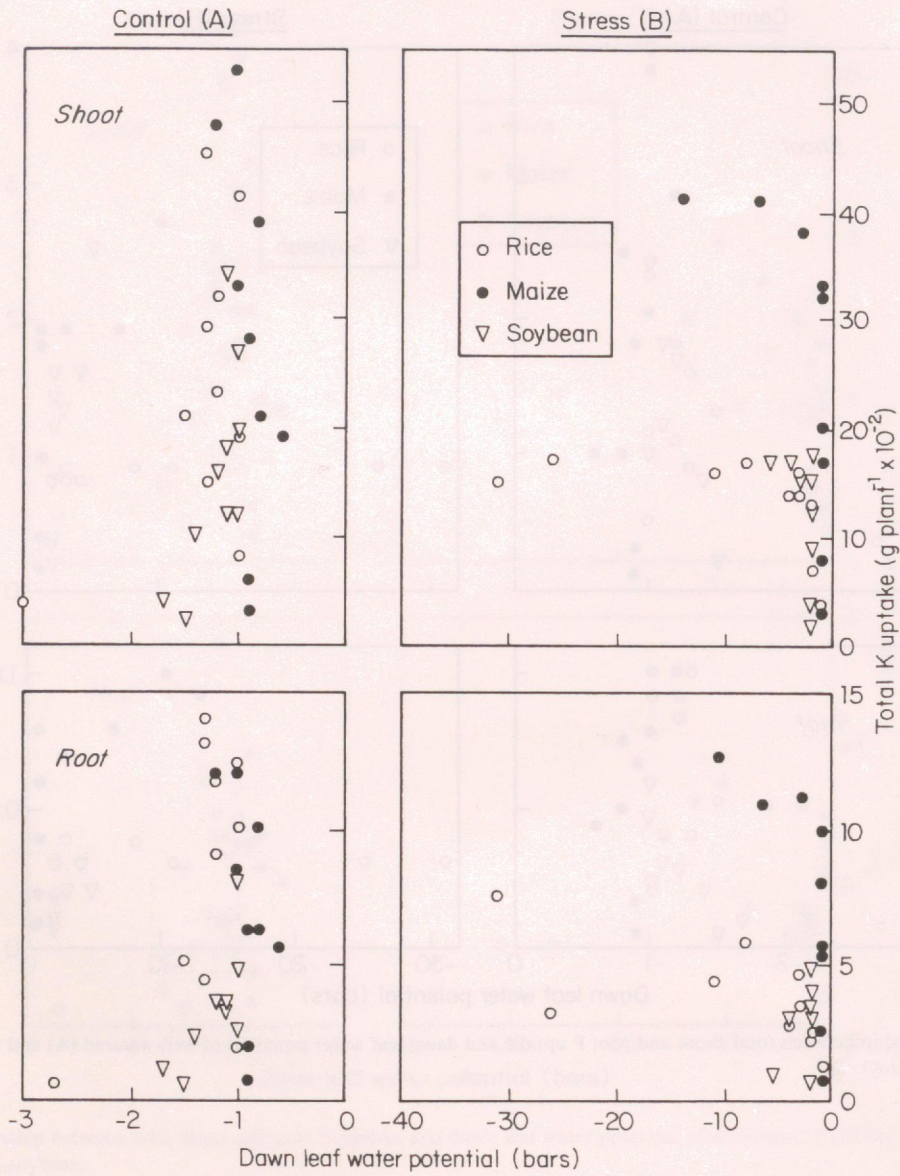


Fig. 14. Relationship between total shoot and root K uptake and dawn leaf water potential of well-watered (A) and water-stressed (B) rice, maize, and soybean.

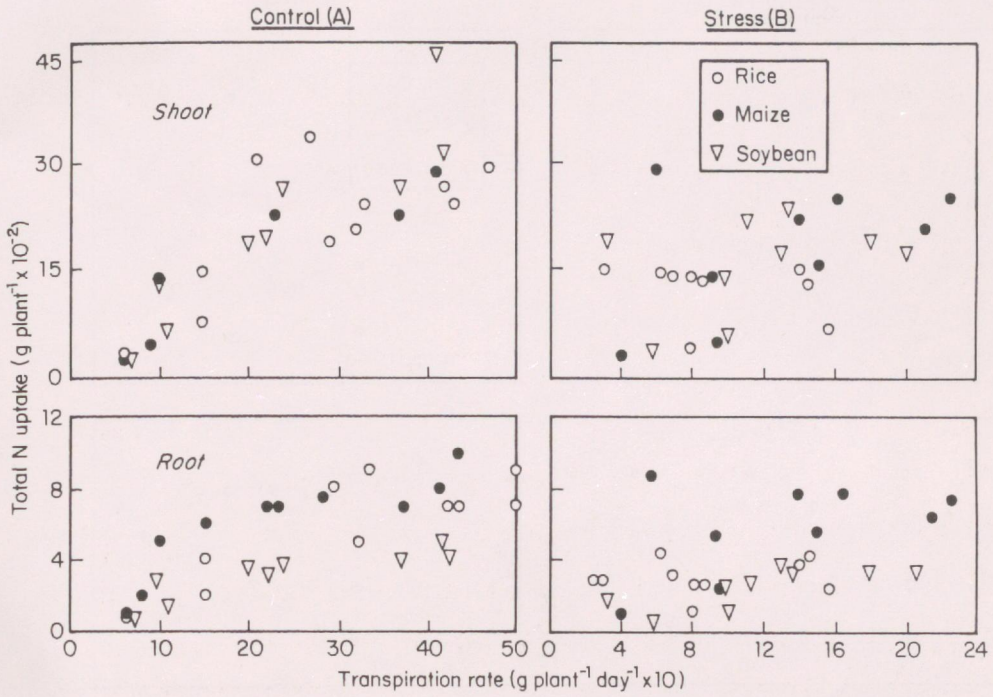


Fig. 15. Relationship between total shoot and root N uptake and transpiration rate of well-watered (A) and water-stressed (B) rice, maize, and soybean.

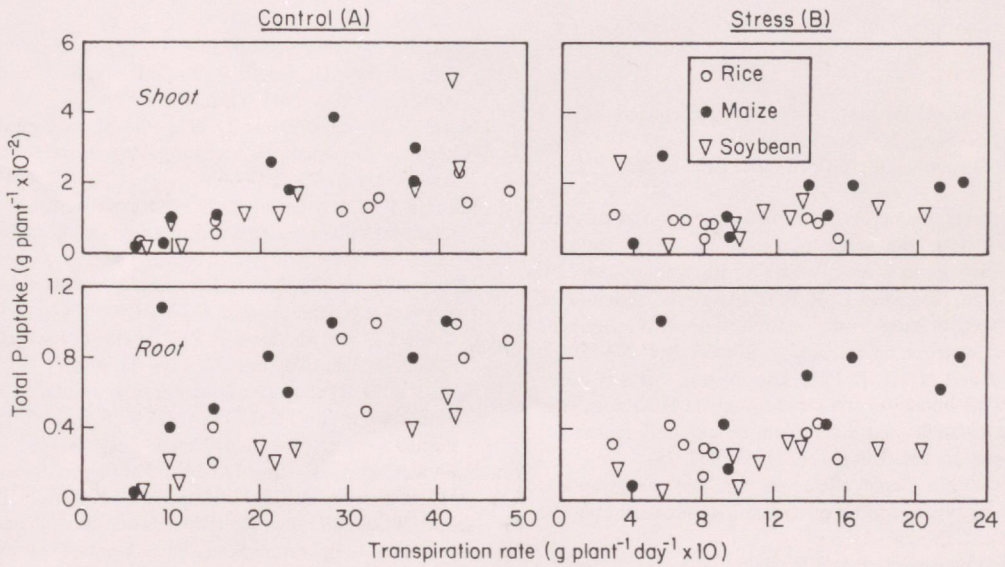


Fig. 16. Relationship between total shoot and root P uptake and transpiration rate of well-watered (A) and water-stressed (B) rice, maize, and soybean.

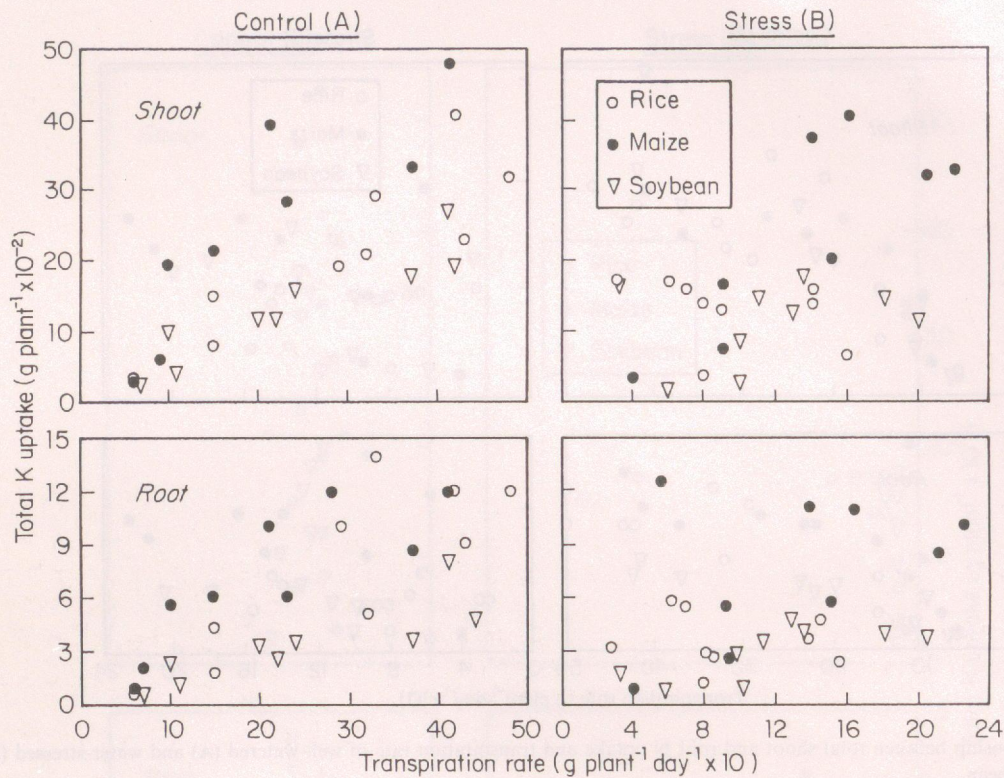


Fig. 17. Relationship between total shoot and root K uptake and transpiration rate of well-watered (A) and water-stressed (B) rice, maize, and soybean.

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Dynamics of ^{15}N -labeled ammonium sulfate in various inorganic and organic soil fractions of wetland rice soils

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Summary. The dynamics of basally applied ^{15}N -labeled ammonium sulfate in inorganic and organic soil fractions of five wetland rice soils of the Philippines was studied in a greenhouse experiment. Soil and plant samples were collected and analyzed for ^{15}N at various growth stages. Exchangeable NH_4^+ depletion continued after 40 days after transplanting (DAT) and corresponded with increased nitrogen uptake by rice plants. Part of the applied fertilizer was fixed by 2:1 clay minerals, especially in Maligaya silty clay loam, which contained beidellite as the dominant clay mineral. After the initial fixation, nonexchangeable ^{15}N was released from 20 DAT in Maligaya silty clay loam, but fixation delayed fertilizer N uptake from the soil. Part of the applied N was immobilized into the organic fraction. In Guadalupe clay and Maligaya silty clay loam, immobilization increased with time while the three other soils showed significant release of fertilizer N from the organic fraction during crop growth. Most of the immobilized fertilizer N was recovered in the nondistillable acid soluble (alpha-amino acid + hydrolyzable unknown-N) fraction at crop maturity. Between 61% and 66% of applied N was recovered from the plant in four soils while 52% of fertilizer N was recovered from the plant in Maligaya silty loam. Only 20%–30% of the total N uptake at maturity was derived from fertilizer N. N_{min} (mineral N) content of the soil before transplanting significantly correlated with N uptake. Twenty-two to 34% of applied N was unaccounted for possibly due to denitrification and ammonia volatilization.

Key words: ^{15}N balance – Ammonium fixation – Fertilizer N transformation – Soil organic nitrogen – Plant N uptake

Since plant uptake of applied nitrogen is a prime concern in crop production, it is important to determine the magnitude of reactions which utilize added N in other ways, such as ammonium fixation, NH_3 volatilization, denitrification, and biological immobilization. Although immobilization does not present N loss from soil, it competes with plant uptake. It is of great interest then to determine the rate at which it occurs. Almost no information is available indicating how long fertilizer N, once immobilized, remains unavailable to the rice crop.

Nitrogen transformations in wetland rice soils were reviewed recently (Savant and de Datta 1982). However, mainly the single N transformation process was discussed sequentially. Most studies conducted on N fertilizer efficiency were restricted to balance sheets at 30 days after transplanting (DAT) and at crop maturity.

In this study, N fertilizer dynamics in various soil fractions during the entire rice growth period is emphasized.

Materials and methods

A pot experiment was conducted in the greenhouse with five representative wetland rice soils from the Philippines, namely, Pili loam (Typic Pelludert), Guadalupe clay (Typic Pellustert), Maahas clay (Andaqueptic Haplaquoll), Sta. Rita clay (Typic Pelludert), and Maligaya silty clay loam (Vertic Tropaquept). Table 1 shows the characteristics of these soils.

Table 1. Chemical and physical properties of wetland soils from five experimental sites in the Philippines

Soil property	Pili loam	Guadalupe clay	Sta. Rita clay	Maahas clay	Maligaya silty clay loam
pH (1:1, H_2O)	5.9	7.0	6.7	7.1	6.2
pH (0.01M CaCl_2)	4.5	6.5	6.0	6.5	5.4
Organic C (%)	1.6	3.1	2.4	1.5	1.4
Total N (%)	0.16	0.27	0.20	0.16	0.11
CEC ($\text{mEq} \times 100 \text{ g}^{-1}$)	34	44	53	47	30
Exchangeable bases ($\text{mEq} \times 100 \text{ g}^{-1}$)					
K	0.31	1.42	0.62	1.52	0.15
Na	0.30	1.00	0.60	1.45	0.46
Mg	6	10	19	16	9
Ca	18	30	31	28	19
Nonexchangeable					
NH_4^+ (mg kg^{-1})	78	82	185	72	55
P (Olsen) $\text{mg (kg}^{-1})$	5	60	8	11	4
Clay (%)	56.9	59.2	71.4	66.8	45.2
Silt (%)	31.8	36.4	25.9	27.7	50.0
Sand (%)	11.3	4.4	2.7	5.6	4.8
Clay mineralogy	Montmorillonite	Montmorillonite	Montmorillonite Kaolinite	Montmorillonite	Beidellite Vermiculite
Soil series	Pili	Guadalupe	Sta. Rita	Maahas	Maligaya
Soil orders	Vertisol	Vertisol	Vertisol	Mollisol	Inceptisol

Equivalent amounts of 6 kg dry soil (oven-dry basis) were incubated in plastic pots with a total of 18 pots per soil sample. Soils were pre-flooded for 6 weeks before conducting the experiment.

Nitrogen fertilizer as ^{15}N -labeled (5% atom excess) ammonium sulfate solution was added to each pot at 100 mg N kg^{-1} soil, P fertilizer as $\text{Ca}(\text{H}_2\text{PO}_4)_2$ at 20–25 mg available P kg^{-1} , and K as KCl at 150 mg available K kg^{-1} . Fertilizers were thoroughly mixed with wet soil. For each soil sample, each of the 15 pots was planted with three IR36 rice seedlings dipped in 2% zinc oxide suspension.

After transplanting, the pots were flooded with deionized water to a depth of 7.5 cm, then covered with black cotton cloth, leaving a center hole for the plants, to prevent algae growth on the flood-water surface. Soils of the remaining three pots were also incubated with the same fertilizer rate and served as a zero-time check for ^{15}N recovery.

Soil and plant (shoot) samples were taken at 10, 20, 40, and 60 DAT and at crop maturity. Plant samples were analyzed for total N and ^{15}N content. Soil samples were analyzed for exchangeable NH_4^+ , nonexchangeable NH_4^+ , hydrolyzable organic N (and subfractions), and nonhydrolyzable organic N. Floodwater samples were taken at 2, 7, 10, and 20 DAT then analyzed for total NH_4^+ and ^{15}N .

Analytical procedure. All soil samples were analyzed for inorganic and organic N fractions according to a scheme assessing all fractions from a soil sample. KCl extraction (Bremner 1965) was done on fresh soil samples immediately after sampling. Nonexchangeable NH_4^+ -N was determined according to the method of Silva and Bremner (1966). Fractionation and determination of organic N fractions were carried out according to the method of Fleige et al. (1971a). Floodwater ammonium N was determined by steam distillation. Plant N was analyzed by the semi-micro-Kjeldahl method.

Nitrogen-isotope ratio analysis. To determine ^{15}N , the distillates after acid filtration were collected, acidified with $1 \text{ N H}_2\text{SO}_4$, and evaporated to dryness in glass vials. Plant and soil ^{15}N were determined by mass spectrometry using a VG micromass M 622 after converting (NH_4^+) to molecular N_2 with lithium.

Results

Exchangeable ammonium

The exchangeable $^{15}\text{NH}_4^+$ concentration in the soil decreased rapidly during the first 40 days. It became less than 10% of the initial value at transplanting and decreased only slightly until maturity. Unlike in other soils, unlabeled exchangeable NH_4^+ in Pili loam and Guadalupe clay pronouncedly increased between 10 and 20 DAT (Fig. 1).

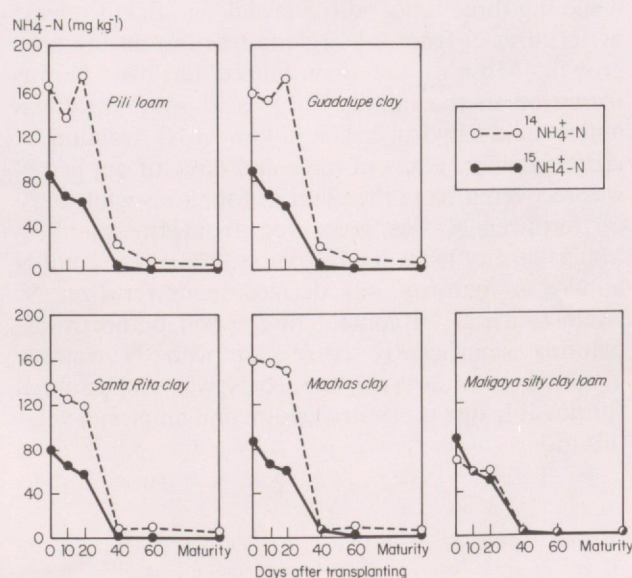


Fig. 1. Labeled (^{15}N) and nonlabeled (^{14}N) exchangeable NH_4^+ at various growth stages of IR36 in five Philippine soils

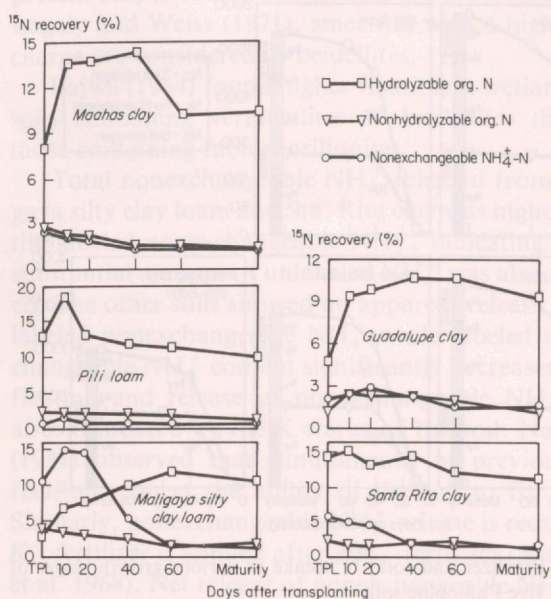


Fig. 2. ^{15}N fertilizer recovery from three soil N fractions at various growth stages of IR36 in five Philippine soils

Nonexchangeable ammonium

Immediately after applying the fertilizer, ^{15}N was fixed in the nonexchangeable fraction only up to 6% in all soils, except in Maligaya soil, which fixed up to 15% during the first 10 DAT (Fig. 2). Fixed $^{15}\text{NH}_4^+$ was steadily released during the growth period (Fig. 2). This was particularly evident in Maligaya soil at 20–60 DAT. In Sta. Rita clay and Maligaya silty clay loam, the nonexchangeable fraction released a considerable amount of untagged ammonium, i.e., 35 mg N kg^{-1} soil in Maligaya and 20 mg N kg^{-1} soil in Sta. Rita clay.

Organic soil nitrogen

The immobilization and remineralization patterns of fertilizer N of the hydrolyzable organic fraction were not similar (Fig. 2). In Maligaya silty clay loam and Guadalupe clay, ammonium immobilization into organic fraction increased with time; whereas in Pili loam and Maahas clay, initial immobilization was followed by a significant fertilizer N release after 20 and 40 DAT, respectively. Remineralized fertilizer in Maahas clay was 23%, and in Pili loam, 46% of the initially immobilized nitrogen. In all soils, about 10% of applied fertilizer remained in the hydrolyzable organic fraction at maturity.

Hexosamine nitrogen was not separated from amide N because its portion of hydrolyzate is comparatively small and does not show considerable variations (Fleige and Capelle 1975).

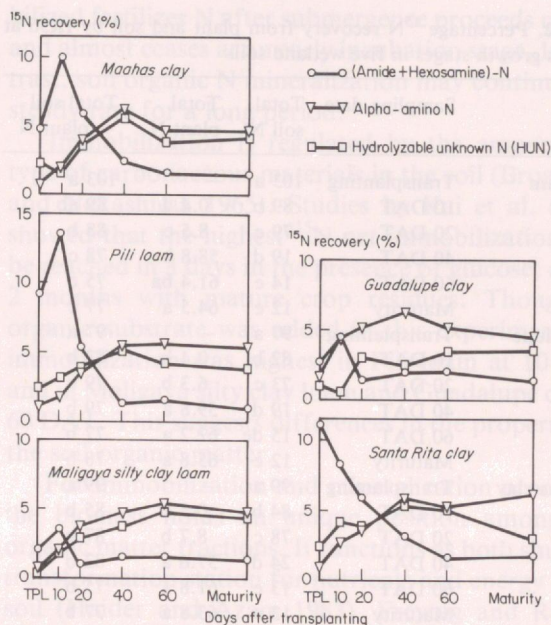


Fig. 3. ^{15}N fertilizer recovery from three organic soil N fractions at various growth stages of IR36 in five Philippine soils

In Pili loam, up to 14% ^{15}N was found in the amide+hexosamine N fraction shortly after applying fertilizer. Its rapid release followed. Only 0.40%–2.00% ^{15}N remained in this fraction at maturity (Fig. 3).

In the alpha-amino N fraction, ^{15}N recovery was up to 6.3% and it increased until 40 or 60 DAT. This fraction accounted for up to 55% of the total hydrolyzable organic N at maturity. Only in Maahas clay and Guadalupe clay were small amounts of ^{15}N released (Fig. 3).

Recovery of ^{15}N in the hydrolyzable unknown N (HUN) fraction was generally less but followed a similar pattern as that in the alpha-amino fraction (Fig. 3). It accounted for 27%–42% of total hydrolyzable organic N at maturity.

Fertilizer N recovered in the nonhydrolyzable organic fraction varied between 2.3% and 4.0%, although a significant ^{15}N release after initial fixation was observed in all soils (Fig. 2).

Floodwater nitrogen

^{15}N Nitrogen in floodwater was highest in Maligaya soil with 7% of applied fertilizer at 2 DAT. It decreased to undetectable concentrations in all soils, 20 DAT. Table 2 shows the highest N losses (largest decrease in recovery percentage) during the first 10 DAT, where concentration of fertilizer N in the soil solution was high and the plant-root system has not yet developed a large sink strength for N.

Table 2. Percentage ^{15}N recovery from plant and soil by IR36 at various growth stages in five wetland soils

Soil	Sampling date	Total soil N	Total plant N	Total soil N + plant N
Pili loam	Transplanting	103 a	—	103 a
	10 DAT	89 b	0.4 d	89 ab
	20 DAT	79 c	8.5 c	88 b
	40 DAT	19 d	58.8 b	78 c
	60 DAT	14 e	61.4 ba	75 c
	Maturity	12 e	64.5 a	77 c
Guadalupe clay	Transplanting	97 a	—	97 a
	10 DAT	82 b	0.4 b	82 b
	20 DAT	73 c	6.3 b	79 b
	40 DAT	19 d	59.8 a	79 b
	60 DAT	15 de	62.2 a	77 b
	Maturity	12 e	65.8 a	78 b
Maahas clay	Transplanting	99 a	—	99 a
	10 DAT	84 b	0.5 c	85 b
	20 DAT	78 c	8.7 b	87 b
	40 DAT	24 d	57.6 a	82 b
	60 DAT	13 e	61.8 a	75 b
	Maturity	13 e	63.8 a	77 b
Sta. Rita clay	Transplanting	103 a	—	103 a
	10 DAT	88 b	0.6 c	89 b
	20 DAT	78 b	8.3 b	86 b
	40 DAT	20 c	58.0 a	78 b
	60 DAT	16 c	60.2 a	76 b
	Maturity	14 c	60.7 a	75 b
Maligaya silty clay loam	Transplanting	102 a	—	102 a
	10 DAT	83 b	0.4 b	83 b
	20 DAT	74 c	6.9 b	81 b
	40 DAT	21 d	44.3 a	65 c
	60 DAT	15 de	49.4 a	64 c
	Maturity	14 e	52.7	67 c

In a column, means followed by a common letter are not significantly different at the 5% level by DMRT

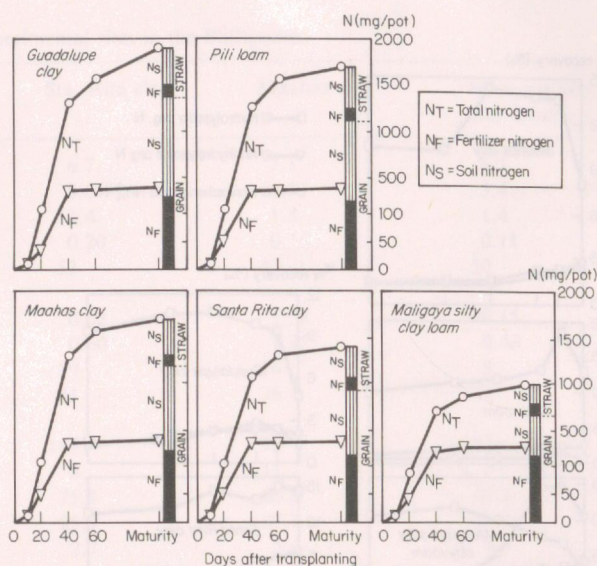
Table 3. Dry matter yield (g pot^{-1}) of IR36 at various growth stages in five different soils. IRRI, 1983

Soil	Sampling date				
	10 DAT	20 DAT	40 DAT	60 DAT	Harvest
Pili loam	0.15	3.0	37	124	175
Guadalupe clay	0.17	3.2	39	139	217
Sta. Rita clay	0.19	2.7	35	107	163
Maahas clay	0.19	3.9	42	149	202
Maligaya silty clay loam	0.13	1.7	31	81	123

Plant nitrogen

Dry matter yields of rice plants are presented in Table 3. Total N uptake of plants was positively correlated with N_{min} (exchangeable NH_4^+) content of soils before transplanting ($R^2 = 0.87$).

Figure 4 shows the N uptake patterns of the rice plant. Highest uptake rate occurred between 20 and

**Fig. 4.** Fertilizer and total N uptake at various growth stages of IR36 in five Philippine soils

40 DAT, after which fertilizer N uptake was no longer significant. Eighty to ninety percent of fertilizer N in the plant was taken up until 40 DAT. Only 20%–30% of fertilizer contributed to total N uptake of mature plants.

Discussion

Nonexchangeable ammonium

Fixation and release of nonexchangeable NH_4^+ were not related to either the total amount of nonexchangeable NH_4^+ or the cation exchange capacities of soils (Table 1). Sta. Rita clay soil had about threefold more nonexchangeable NH_4^+ than Maligaya silty clay loam but fixation and release of nonexchangeable NH_4^+ in this soil were much lower than in Maligaya (Table 1) in line with results obtained by Keerthisinghe et al. (1984). They presumed that the fixing capacity of Maligaya silty clay loam was related to the vermiculites present as its major clay mineral in the soil. On the other hand, montmorillonite was presumed to be the dominant clay of other soils. Reexamination of clay minerals by Ca + glycerol diagrams showed that the major clay mineral in all soils was the smectites (peak at 18 Å). The assumption about vermiculites being a major clay mineral (peak at 14 Å) was not confirmed. But since vermiculites in the clay fraction (0.1 μm) were also able to expand to 17.6 Å upon Ca + glycerol saturation, occurrence of vermiculites in Maligaya soil is still possible.

The contraction test, upon K saturation to 10 Å, proved that smectites with high layer charge were

present only in Maligaya silty clay loam. According to Lagaly and Weiss (1971), smectites with a high layer charge are considered as beidellites.

Bajwa (1984) found higher fixation in wetland rice soils containing vermiculites or beidellites than in those containing montmorillonites.

Total nonexchangeable NH_4^+ released from Maligaya silty clay loam and Sta. Rita clay was higher than the labeled nonexchangeable NH_4^+ , indicating that a substantial amount of unlabeled NH_4^+ was also released. The other soils showed no apparent release of unlabeled nonexchangeable NH_4^+ while labeled nonexchangeable NH_4^+ content significantly decreased. The fixation and release of nonexchangeable NH_4^+ was also influenced by the K status of the soil. Nommik (1957) observed that simultaneous or previous K^+ fixation reduces the ability of the soil to fix NH_4^+ . Similarly, nonexchangeable NH_4^+ release is reduced if K^+ fertilizer is applied after NH_4^+ fertilizer (Atanasiu et al. 1968). Net release of nonexchangeable NH_4^+ occurs when plant uptake progressively reduces both NH_4^+ and K^+ in the soil solution.

NH^+ refixation may occur especially in soils with high mineralization rate (Mengel and Scherer 1981). Refixation likely took place in Pili, Guadalupe, and Maahas soils.

Organic soil nitrogen

Organic soil nitrogen supplied 70% – 80% of N taken up by the crop. Considerable amounts of added N were rapidly immobilized and incorporated into the hydrolyzable organic N fractions of the soil. However, immobilization and mineralization patterns differed markedly among soils.

Fertilizer N immobilized into the organic fraction in Maligaya silty clay loam and Guadalupe clay increased with time. In Pili loam and Maahas clays, significant amounts of initial immobilized N were remobilized. Increase in unlabeled exchangeable NH_4^+ in Pili loam between 10 and 20 DAT, despite plant uptake, indicates high mineralized native soil organic N. These results are similar to Schoen's (1982), which showed that exchangeable NH_4^+ remained at a constant level for a longer period after transplanting in Pili loam than in other soils. Its relationship to soil biomass is also discussed in this paper.

Fertilizer nitrogen was remobilized only at the early growth stages (Pili loam and Maahas clay). At the late growth stages, remineralization was negligible. Tyler and Broadbent (1958) noted that immobilized N seems progressively less available because the nitrogenous compounds are constantly converted into more biologically stable compounds. Kai and Kawaguchi (1977) observed that remineralization of immo-

bilized fertilizer N after submergence proceeds rapidly and almost ceases at an early incubation stage. In contrast, soil organic N mineralization may continue at a steady rate for a long period.

Immobilization is regulated by the amount and type of carbonaceous materials in the soil (Broadbent and Nakashima 1965). Studies by Kai et al. (1973) showed that the highest ^{15}N net immobilization may be reached in 3 days in the presence of glucose, and in 2 months with mature crop residues. Though no organic substrate was added in this experiment, net immobilization was highest in Pili loam at 10 DAT and in Maligaya silty clay loam and Guadalupe clay at 60 DAT. This suggests differences in the properties of the soil organic matter.

For immobilization and mineralization processes, the biomass holds an unique position among soil organic matter fractions. It functions as both sink and transformation station for nutrients and energy in the soil (Haider and Azam 1983). Freytag and Rausch (1982) observed that N present in living cells of biomass seems to be less important for N availability than N turnover, which is significant in alternating synthesis-autolysis cycles. Further, Marumoto et al. (1982) reported the N turnover from dead microbial cells to be about 5 times faster than that from native soil organic N. Beck (1983) found mineralization rate to be well correlated to the biomass of the soils ($r = 0.96$). The different immobilization-mineralization patterns of the soils may be closely correlated to soil biomass rather than to soil organic matter or other soil properties. In this respect, Pili loam was expected to have the highest soil biomass production.

Soil N fractionation supports this hypothesis because the major part of the immobilized fertilizer was incorporated in organic, microbially synthesized N compounds. According to Marumoto et al. (1982), organic N compounds of microorganisms are hydrolyzable to a greater extent than the native organic soil N. Therefore, microbially immobilized N enriches the hydrolyzable organic compounds. The hydrolyzable organic matter, especially the easily hydrolyzable fraction, plays a dominant role in N mineralization although this fraction contains only 7% of total C and 16% of total N (Campbell 1978).

Subfractions of organic soil nitrogen

Fertilizer N was first incorporated mainly into the amide-hexosamine fraction until 10 DAT. High ^{15}N recovery in this fraction was found in Pili loam, Sta. Rita clay, and Maahas clay. Decrease in ^{15}N in the amide-hexosamine fraction was accompanied by an increase in the alpha-amino and HUN fractions, an agreement with results obtained by Fleige et al. (1971b).

Fleige et al. (1971b) also reported that amides asparagine and glutamine have a storage function in microorganisms. Similar to higher plants, they probably buffer an oversupply of inorganic N. Hexosamines are mainly located in microbial cell walls. It is possible that they are particularly prone to decomposition.

Distinctive net mineralization of immobilized fertilizer N in Pili loam between 10 and 20 DAT seems to be due to rapid decomposition of the amide-hexosamine fraction. However, Stewart et al. (1963) confirmed that the alpha-amino and HUN fractions likely decomposed later. Voelker and Asmus (1981) further noted that alpha-amino N plays a major role in the N supplying capacity of the soil.

Since the ^{15}N pattern in the HUN fraction is similar to that in the alpha-amino fraction, a close correlation to amino acid metabolism and microbial N turnover should exist as reported by Kai et al. (1973) and Marumoto et al. (1982). The nonhydrolyzable organic N fraction is considered to consist of heterocyclic N compounds (Fleige et al. 1971a), i.e., mainly the "nucleus-N" of the humic acids and, thus, regarded as being generally very stable.

The small but significant ^{15}N decrease in this fraction, however, is not consistent with the assumed stability. In a ^{15}N field experiment (without straw), Fleige and Capelle (1975) reported an initial ^{15}N increase and later on an almost complete disappearance of ^{15}N in this fraction. They associated this with a short and apparently weak chemical fertilizer NH_4 fixation by organic substances (Lindbeck and Young 1965). Laboratory experiments proved that heterocyclic N compounds are decomposed by fungi and bacteria (Ivarson and Schnitzer 1979). This might also be valid for wetland soil though it contains mainly bacteria.

Uptake of fertilizer and soil nitrogen by the rice plant

Fertilizer nitrogen recovery in the rice plant ranged from 61% to 66% in four soils. In Maligaya silty clay loam, however, plant recovery accounted for only 52% of applied fertilizer N. Uptake of basally applied N was almost completed at 40 DAT and derived mainly from the exchangeable NH_4^+ pool. This confirms the results of Keerthisinghe et al. (1985). Nitrogen taken up until the maximum tillering period critically influences yield potential (Vlek and Craswell 1979). This was apparent in Maligaya silty clay loam, where fertilizer N uptake at 40 DAT was significantly low. Low ^{15}N uptake from the soil was partly due to high ammonium fixation (Keerthisinghe et al. 1985) and ammonia volatilization losses during the first 20 days

as suggested by the high percentage (7%) of flood-water ^{15}N at 2 DAT. Though fertilizer N in the nonexchangeable fraction was released during the later growth period, its uptake was delayed and it negatively affected plant growth. Atanasiu et al. (1968) similarly observed that ammonium fixation not only delayed N uptake but also increased total fertilizer N loss from the soil-plant system.

Unlike fertilizer N uptake, soil N uptake by rice continued until maturity in all soils, but the amounts taken up differed markedly among soils. These differences represent the various N supplying capacities of the soils as reflected by their N_{min} contents at transplanting.

N_{min} content and soil N uptake were neither related to total organic C content nor to total N content of the soils. Thus, soil N uptake in Pili loam and Maahas clay were much higher than in Sta. Rita clay even though the organic C content of Sta. Rita clay was higher (2.4%) than in Pili loam (1.6%) and Maahas clay (1.5%).

Poor correlation between total soil N and N uptake were also reported by Fox and Piekielek (1978). Total soil N and organic matter seem to be reliable parameters only for N uptake if biomass is proportional.

Results of this study suggest that parts of the soil N rather than the total N content are important for N-supplying capability. Although fertilizer N uptake was high (60% – 65% recovery), soil N accounted for 70% – 80% of the total N in the plants at maturity, indicating that the rice plant largely depends on available soil N.

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Measurement of Nitrogen Utilization Efficiency in Rice Genotypes¹

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ABSTRACT

Recent research suggests that there is considerable potential for exploiting genotypic differences in N utilization efficiency by crops. Our research attempted to identify traits associated with rice (*Oryza sativa* L.) genotypes that support maximum grain production with a minimum input of fertilizer. From field experiments on an Andaqueptic Haplaquoll in three consecutive seasons we identified a group of plant parameters associated with efficiency of N utilization to determine if the different genotypes exhibited consistent and significant variations in these parameters. A group of nine parameters was selected, and rankings based upon different combinations of these parameters were developed and compared. Statistically significant differences among genotypes were observed, and reasonably consistent rankings were obtained from season to season. For example, IR183429-3-2-1-2 ranked first in two seasons and third in the other. IR18349-135-2-3-2-1 ranked second, third, and fifth in the three seasons. These are medium maturity rices. IR42, which is known to perform well on low N soils, ranked between ninth and 17th. The consistency of performance of outstanding genotypes demonstrated in these experiments suggests that the methodology is feasible and practical for use in research on genetic improvement of N utilization efficiency.

Additional index words: Nitrogen utilization efficiency, Genetic selection, Nitrogen-15-depleted materials, Parameter selection, Associative N₂ fixation.

IN MANY of the rice (*Oryza sativa* L.) growing areas of the world the cost of N fertilizer constitutes a major fraction of the total cost of production. According to Prasad and De Datta (1979) the low recovery of fertilizer-N applied to rice in South and Southeast Asia, coupled with the high cost of fertilizer in relation to the price of rice, is an important constraint to fertilizer use by farmers with small holdings. In addition to economic considerations, inefficient N utilization by the rice plant represents a significant energy loss. These conditions arise in part because rice is grown in an environment conducive to N losses by denitrification, ammonia volatilization, and runoff. Even well-fertilized rice obtains 50 to 80% or more of its N from indigenous soil sources (Reddy and Patrick, 1977). In uniform rice fertility trials conducted in eight countries under the auspices of the International Atomic Energy Agency (1970), the proportion of total N in the crop furnished by mineralization of soil N varied from

60 to 74%, even though 100 kg/ha of fertilizer-N was supplied. Clearly, these values indicate that there is scope for improvement.

A great deal of work has been done in the direction of improving N utilization through fertilizer, soil, and water management. Practices receiving attention include adjusting fertilizer rates and timing to take advantage of efficient uptake during the maximum tillering and flowering stages of growth (Tanaka et al., 1959; Misra et al., 1972; Modgal et al., 1974). Various methods of application have also improved N utilization efficiency (De Datta et al., 1968). Recent progress in these areas has been reviewed by Prasad and De Datta (1979), De Datta and Craswell (1982), Savant and De Datta (1982), and De Datta and Patrick (1986).

Genetic selection and plant breeding techniques have long been effectively used for development of disease and insect resistance in rice, and more recently, for tolerance of adverse environmental conditions such as drought (Chang et al., 1982), zinc deficiency (Cayton et al., 1984), iron toxicity (Gunawardena et al., 1982), and salinity (Ponnamperuma, 1984). However, these techniques appear not to have been applied specifically to the objective of improving N utilization by rice. Some work has been done in maize (*Zea mays* L.), which indicates that there is considerable potential for exploiting genotypic differences in N utilization by that crop (Balko and Russell, 1980; Kamprath et al., 1982).

Efficiency of uptake of available N by plants is an important component of overall utilization efficiency. The use of ¹⁵N-labeled fertilizer provides a method for readily measuring N uptake efficiency in a growing

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crop, and makes it possible to discriminate between applied N and that derived from the soil or atmosphere, or both. In this connection, ^{15}N -depleted materials are particularly suited to field-scale research (Broadbent and Carlton, 1980). The availability of such material, combined with the wide range of rice genotypes available at the International Rice Research Institute, provided an excellent opportunity to determine if genetic lines differ in their N utilization efficiency and to identify plant characteristics that contribute to it. The fundamental objective of the experiments was to identify genotypes that produce the maximum amount of grain with a minimum input of fertilizer N. This required development of suitable criteria for evaluating plant performance in this respect.

EXPERIMENTAL PROCEDURE

Field Experiments

In the 1983 wet season and during the 1984 dry and wet seasons, field experiments were conducted at the International Rice Research Institute farm at Los Baños, where the soil is a fine, mixed, isohyperthermic Andaqueptic Haplaquoll (Maahas series) containing about 0.2% total N. A split-plot design was used, with N level as main plots (no N and added N) and 24 different genotypes as subplots with six replications. The latter included eight genotypes of 100-day relative maturity, eight of 110-day, and eight of 120- to 135-day relative maturity. An area of about 5 m² was fertilized with ^{15}N -depleted ammonium sulfate at the rate of 30 kg N/ha in the wet seasons and 60 kg N/ha in the dry season. Use of the labeled fertilizer made it possible to determine how much of the N in the rice plant was derived from the applied fertilizer. At 30 days after transplanting, at panicle initiation, and at maturity, six plant samples representing an area of 0.24 m² were collected for analysis. Leaf and culm samples from the first two sampling periods were analyzed separately, and at harvest, straw, panicles, and roots were analyzed separately. Grain yields were obtained on a plot area of 9.3 m² that was fertilized with unlabeled fertilizer at the same rate as the subplots receiving labeled N. Dry weight, total N, and percent ^{15}N were determined for all samples collected from plots given labeled fertilizer. Total N was determined by the Kjeldahl procedure and N-isotope ratio analysis by methods similar to those described by Hauck (1982).

Parameter Selection

In developing criteria for genotype evaluation, it was necessary to select a plant parameter or group of parameters associated with efficiency of N utilization, and to determine if the different genotypes exhibited significant and consistent differences in these parameters. Several parameters were considered, including dry matter production (DM), total N uptake (N_t), uptake of soil N (N_s), uptake of fertilizer N (N_f), percent N derived from fertilizer, and the ratios DM/N_t , DM/N_s , and DM/N_f at all three sampling periods. Additional parameters based on harvest data included weight of panicle (WP), grain yield (Y), harvest index, and N-harvest indices for total, soil, and fertilizer N calculated separately. From these an initial selection of nine parameters was made, including two measures of yield, WP and Y; three reflecting the ratio of panicle production per unit of total-, soil-, or fertilizer-N; three reflecting the ratio of dry matter produced per unit of total-, soil-, or fertilizer-N; and one based on grain yield per unit of total N assimilated by the whole plant. The criteria for selection of these parameters were that they should reflect either plant productivity or efficiency of N utilization, or both. It was considered necessary for the parameters to be reasonably well correlated with each other so that an evaluation based on multiple parameters would represent cumulative values rather than a situation in which one parameter cancels out the effects of another.

Parameters such as root weight, harvest index, and tiller number were excluded because of a lack of a consistent relationship to the parameters essential to a measure of N utilization efficiency. Although grain yield was based on a larger sample than that used for panicle weight, the latter was used in calculating the ratio parameters for soil- and fertilizer-N since total N and ^{15}N were measured in the same sample as that for panicle weight, thus permitting statistical treatment of values from individual replicates, which could not be done otherwise.

RESULTS AND DISCUSSION

Correlations among the nine selected parameters can be examined in Tables 1 to 3. In the 1983 wet season there were 63 positive and significant correlations among these parameters out of 72 possible, 24 in the 1984 dry season, and 42 in the 1984 wet season. Considering individual parameters over the three seasons,

Table 1. Correlation matrix for nine crop parameters, 1983 wet season.

	WP/ N_f	WP/ N_s	WP	DM/ N_f	DM/ N_s	WP/ N_t	DM/ N_t	Y
WP/ N_s	0.645**							
WP	0.573**	0.586**						
DM/ N_f	0.916**	0.438*	0.442*					
DM/ N_s	0.475*	0.630**	0.281	0.610**				
WP/ N_t	0.739**	0.990**	0.610**	0.537**	0.623**			
DM/ N_t	0.593**	0.642**	0.329	0.723**	0.987**	0.657**		
Y	0.622**	0.554**	0.581**	0.500*	0.353	0.582**	-0.207	
Y/ N_t	0.595**	0.702**	0.165	0.452*	0.505**	0.713**	0.525**	0.777**

*,** Significant at the 0.05 and 0.01 levels, respectively.

Table 2. Correlation matrix for nine crop parameters, 1984 dry season.

	WP/ N_f	WP/ N_s	WP	DM/ N_f	DM/ N_s	WP/ N_t	DM/ N_t	Y
WP/ N_s	0.042							
WP	0.722**	0.248						
DM/ N_f	0.948**	-0.218	0.584**					
DM/ N_s	0.009	0.896**	0.071	-0.147				
WP/ N_t	0.380	0.935**	0.468*	0.118	0.825**			
DM/ N_t	0.484*	0.751**	0.360	0.346	0.865**	0.865**		
Y	0.412*	0.236	0.736**	0.309	0.136	0.352	0.279	
Y/ N_t	-0.130	0.737**	-0.099	-0.296	0.747**	0.649**	0.583**	0.382

*,** Significant at the 0.05 and 0.01 levels, respectively.

Table 3. Correlation matrix for nine crop parameters, 1984 wet season.

	WP/N _f	WP/N _s	WP	DM/N _f	DM/N _s	WP/N _t	DM/N _t	Y
WP/N _s	0.387							
WP	0.564**	0.766**						
DM/N _f	0.951*	0.199	0.446*					
DM/N _s	0.368	0.484*	0.481*	0.491*				
WP/N _t	0.529**	0.982**	0.815**	0.360	0.542**			
DM/N _t	0.491*	0.432*	0.499*	0.623**	0.982**	0.522**		
Y	0.334	0.427*	0.418*	0.223	0.131	0.417*	0.112	
Y/N _t	0.091	0.309	-0.124	0.018	0.098	0.281	0.062	0.690**

*,** Significant at the 0.05 and 0.01 levels, respectively.

Table 4. Seasonal correlations for nine plant parameters.

Parameter	1983 wet season	1983 wet season	1984 dry season
	vs.	vs.	vs.
	1984 wet season	1984 dry season	1984 wet season
WP/N _f	0.660**	0.686**	0.543**
WP/N _s	0.493*	0.024	0.476*
WP	0.672**	0.659**	0.618**
DM/N _f	0.683**	0.729**	0.585**
DM/N _s	0.879**	-0.193	-0.092
WP/N _t	0.576**	0.218	0.543**
DM/N _t	0.910**	0.201	0.230
Y	0.649**	0.437*	0.519**
T/N _t	0.388	0.068	0.527**

*** Significant at the 0.05 and 0.01 levels, respectively.

the range was from 12 out of a possible 24 significant correlations for Y/N_t to 19 for WP/N_f. Parameters WP/N_f, WP/N_s, and WP were all well correlated with the other parameters. Those parameters based on plant samples collected at 30 days after transplanting and at panicle initiation were not utilized for our present purposes, since plant performance over the entire season was of primary interest.

Seasonal correlations among the plant parameters (Table 4) were all statistically significant for the two wet seasons, with the exception of Y/N_t. In several instances the wet-versus-dry season correlations were not significant, which is not surprising in view of sub-

Table 5. Range and variability statistics for genotype and relative maturity means, 1983 wet season.

Parameter	Genotype means			Relative maturity				CV
	Minimum	Maximum	F-values	100 days	110 days	120+ days	F-values	
WP/N _f	424	866	3.07**	494	687	695	21.3**	27.4
WP/N _s	51.6	70.6	3.79**	56.3	61.8	63.0	12.6**	11.6
WP, Mg/ha	4.15	6.49	2.98**	5.05	5.58	5.61	6.95**	15.5
DM/N _f	818	1578	3.25**	904	1203	1327	24.6**	26.6
DM/N _s	94.2	132	4.80**	103	108	120	31.1**	9.64
WP/N _t	45.7	64.3	4.48**	50.3	56.4	57.5	19.0**	11.3
DM/N _t	86.0	117	6.30**	92.2	98.7	109	47.0**	8.70
Y, Mg/ha	3.31	5.67	9.29**	4.00	4.78	4.28	37.4**	10.4

** Significant at the 0.01 level.

Table 6. Range and variability statistics for genotype and relative maturity means, 1984 dry season.

Parameter	Genotype means			Relative maturity				CV
	Minimum	Maximum	F-values	100 days	110 days	120+ days	F-values	
WP/N _f	265	474	2.79**	313	371	412	14.8**	24.6
WP/N _s	60.6	91.6	5.76**	81.6	78.4	73.6	10.8**	10.9
WP, Mg/ha	4.86	7.60	2.88**	5.30	6.34	6.36	15.4**	17.8
DM/N _f	459	819	2.67**	537	625	723	15.8**	25.8
DM/N _s	111	154	3.97**	140	132	128	11.7**	9.27
WP/N _t	52.3	74.8	10.6**	63.7	63.6	61.7	2.97	7.41
DM/N _t	96.2	126	8.20**	109	107	108	2.12	5.94
Y, Mg/ha	4.39	6.66	7.84**	5.27	5.59	5.54	6.38**	8.71

** Significant at the 0.01 level.

Table 7. Range and variability statistics for genotype and relative maturity means, 1984 wet season.

Parameter	Genotype means			Relative maturity				CV
	Minimum	Maximum	F-values	100 days	110 days	120+ days	F-values	
WP/N _f	557	1530	2.54**	635	1105	936	17.4**	44.3
WP/N _s	52.7	74.0	3.92**	59.9	63.1	61.7	2.67	11.0
WP, Mg/ha	4.15	5.88	3.58**	4.48	4.99	4.94	7.49**	14.9
DM/N _f	957	2477	2.79**	1089	1890	1757	21.0**	41.1
DM/N _s	96.1	122	3.33**	102	109	115	16.1**	9.83
WP/N _t	48.2	67.9	4.43**	54.5	59.2	57.6	7.66**	10.5
DM/N _t	87.8	114	4.53**	93.2	102	107	28.2**	9.28
Y, Mg/ha	3.55	4.63	2.67	3.89	4.05	3.80	4.74*	10.5

*** Significant at the 0.05 and 0.01 levels, respectively.

stantially different environmental conditions under which rice is grown in the different seasons. However, all the seasonal correlations were positive and significant for four of the nine parameters.

Tables 5 to 7 show the ranges for the 24 genotype means with respect to eight of the nine parameters for the three growing seasons, together with corresponding *F*-values for differences among means. The parameter Y/N_t is excluded because Y and N_t were measured on separate samples. Also shown are relative maturity means, *F*-values for differences among these means, and coefficients of variation for the individual parameters. All of the genotype means exhibited differences that are significant at the 99% level of probability or higher in all three seasons, suggesting that these might provide a basis for selecting genotypes for their efficiency in N utilization. With three exceptions, relative maturity means showed statistically significant differences. With few exceptions, parameter values increased with increasing relative maturity, as might be expected. Parameters involving fertilizer-N tended to be more variable than the others, particularly in the wet seasons (Tables 5 and 7) when the uptake of fertilizer-N was a relatively small fraction of the total. In these experiments the range of values of percent N derived from fertilizer was from 5.4 to 11.5% in the wet seasons and from 13.4 to 23.7% in the dry seasons.

Ranking System

A system for ranking individual rice genotypes for N utilization efficiency was thought to be more dependable if based on more than one plant parameter. The absolute values of the various parameters cover a wide range of magnitude. In order to give approximately equal weight to the different parameters, their values were normalized by expressing them as a fraction of the genotype mean for a particular season. Thus, a genotype having a parametric value equal to the mean would be assigned a value of 1.0. In general, the ratio WP/N_f covered the widest range, with normalized values from 0.68 to 1.38 in the 1983 wet season, from 0.73 to 1.30 in the 1984 dry season, and from 0.62 to 1.71 in the 1984 wet season. The least variable parameter, DM/N_t , had normalized values from 0.86 to 1.17 in the 1983 wet season, from 0.89 to 1.17 in the 1984 dry season, and from 0.87 to 1.13 in the 1984 wet season. Transformed values in a particular group of parameters were summed and the sums then sorted, with the highest sum assigned a rank of 1 and the lowest a rank of 24. The first ranking was based on all nine parameters, although a ranking based on this many parameters is cumbersome to deal with. A second ranking was based on the parameters WP/N_f , WP/N_s , and WP . These three are well-correlated with the others (Tables 1-3) and represent three independent measurements. From a practical standpoint it would be advantageous to use a single parameter for ranking rice genotypes. Three that might be used are WP/N_f , WP/N_t , and Y/N_t . The latter two have the advantage of not requiring the use of isotopically labeled fertilizer. Rankings based on nine parameters, three parameters, and on each of the three single parameters mentioned above are presented in Tables 8 to 10. The rankings

according to the nine parameters agree quite well with those based on only three, indicating little advantage in using the larger number. Table 11 shows correlations of rankings based on three single parameters, and correlations of rankings based on a three-parameter combination with the nine-parameter rankings. Cor-

Table 8. Rankings of genotypes according to different individual or sets of parameters, 1983 wet season.

Genotype	Parameter(s)				
	1-9	1-3	WP/N_f	WP/N_t	Y/N_t
100-day maturity					
IR8455-78-1-3-3	20	24	22	23	13
IR8608-167-1-2	24	21	23	21	24
IR9729-67-3	17	15	21	16	17
IR9752-1-2-1	23	23	24	24	22
IR19729-5-1-1-3-2	21	19	15	20	23
IR15429-268-1-2-1	22	22	20	18	16
IR19728-9-3-2-3-3	16	16	19	12	12
IR19735-2-3-2-1	15	18	17	14	8
110-day maturity					
IR36	14	11	12	11	19
IR50	19	20	18	22	15
IR13429-150-3-2-1-2	4	3	7	4	5
IR13427-40-2-3-3-3-3	18	14	14	17	18
IR13240-82-2-3-2-3-1	6	5	3	8	7
IR25588-32-2	11	13	11	13	4
IR18349-135-2-3-2-1	1	2	1	5	1
IR21912-56-3-1-2-2	3	4	4	1	2
120-135-day maturity					
IR13540-56-3-2-1	7	6	10	2	9
IR21912-131-3-3-2-2	2	1	2	3	11
IR26	10	8	5	7	6
IR2863-38-1	13	9	13	9	20
IR42	8	17	16	10	3
IR8192-200-3-3-2-2	12	10	9	15	21
IR11248-148-3-2-3-3	5	7	8	5	10
IR15323-78-1-3-1	9	12	6	19	14

Table 9. Rankings of genotypes according to different individual or sets of parameters, 1984 dry season.

Genotype	Parameter(s)				
	1-9	1-3	WP/N_f	WP/N_t	Y/N_t
100-day maturity					
IR8455-78-1-3-3	19	22	19	14	9
IR8608-167-1-2	21	23	24	18	11
IR9729-67-3	10	12	16	5	4
IR9752-1-2-1	22	21	23	17	15
IR19729-5-1-1-3-2	14	17	21	9	7
IR15429-268-1-2-1	13	19	22	10	2
IR19728-9-3-2-3-3	2	4	6	1	1
IR19735-2-3-2-1	15	20	17	20	3
110-day maturity					
IR36	18	13	14	21	22
IR50	16	14	13	13	20
IR13429-150-3-2-1-2	1	1	1	3	6
IR13427-40-2-3-3-3-3	14	24	20	22	21
IR13240-82-2-3-2-3-1	17	15	15	12	16
IR25588-32-2	12	11	18	7	5
IR18349-135-2-3-2-1	4	5	4	6	13
IR21912-56-3-1-2-2	5	7	10	8	10
120-135-day maturity					
IR13540-56-3-2-1	9	9	7	11	18
IR21912-131-3-3-2-2	6	3	6	4	8
IR26	23	18	8	24	23
IR2863-38-1	20	16	12	23	24
IR42	11	10	9	16	14
IR8192-200-3-3-2-2	3	2	3	2	12
IR11248-148-3-2-3-3	8	8	2	15	19
IR15323-78-1-3-1	7	6	5	19	17

Table 10. Rankings of genotypes according to different individual or sets of parameters, 1984 wet season.

Genotype	Parameter(s)				Y/N _t
	1-9	1-3	WP/N _f	WP/N _t	
100-day maturity					
IR8455-78-1-3-3	20	21	19	15	11
IR8608-167-1-2	24	24	23	24	19
IR9729-67-3	16	19	22	5	1
IR9752-1-2-1	22	23	24	20	21
IR19729-5-1-1-3-2	23	22	20	21	20
IR15429-268-1-2-1	19	18	17	12	9
IR19728-9-3-2-3-3	18	17	18	14	3
IR19735-2-3-2-1	21	20	21	18	14
110-day maturity					
IR36	13	10	14	9	8
IR50	8	6	3	8	10
IR13429-150-3-2-1-2	1	1	2	2	5
IR13427-40-2-3-3-3-3	17	16	9	23	17
IR13240-82-2-3-2-3-1	2	2	1	6	6
IR25588-32-2	12	15	16	11	4
IR18349-135-2-3-2-1	3	3	4	4	12
IR21912-56-3-1-2-2	9	8	13	7	7
120-135-day maturity					
IR13540-56-3-2-1	4	5	5	3	16
IR21912-131-3-3-2-2	7	4	10	1	22
IR26	15	11	7	22	23
IR2863-38-1	14	9	15	19	24
IR42	6	13	11	16	2
IR8192-200-3-3-2-2	11	14	8	17	15
IR11248-148-3-2-3-3	10	12	12	13	13
IR15323-78-1-3-1	5	7	6	10	18

relation coefficients for the three-parameter combination are higher in all seasons than those for any single parameter. Of the single parameters, WP/N_f had the best correlations overall. Reference to Tables 8 to 10 shows that in a few instances there was a considerable difference between the rankings obtained with the single rankings and those based on three or nine parameters, e.g., IR26 in the 1984 dry season and IR13427-40-2-3-3-3-3 in the 1984 wet season. Because of the greater possibility of obtaining a nonrepresentative value with a single parameter, the three-parameter rankings are regarded as more dependable, and the discussion that follows is based on these.

Genotype Performance

Similar performance in the wet and dry seasons would not necessarily be expected because of substantial differences in environmental conditions. Thus, according to the three-parameter criteria, IR19728-9-3-2-3-3 ranked much higher during the single dry season than during either wet season, while IR13240-82-2-3-2-3-1 had a high ranking only during the wet seasons. Nevertheless, many genotypes did exhibit consistent performance during the three seasons. For example, IR13429-150-3-2-1-2 ranked third in the 1983 wet season and first in both 1984 seasons. IR18349-135-2-3-2-1 ranked second in the 1983 wet season, fifth in the 1984 dry season, and third in the 1984 wet season. Rankings for IR21912-131-3-3-2-2 were first, third, and fourth for the three seasons. At the other end of the scale, IR8608-167-1-2 ranked 21st in the 1983 wet season, and 23rd and 24th in the 1984 seasons. IR42, an established cultivar with a reputation for good performance on poor soils, ranked between ninth and 17th.

Table 11. Correlations of rankings based on three single parameters and on a three-parameter combination with those based on nine parameters.

Parameter(s)	1-3	WP/N _f	WP/N _t	Y/N _t
1983 wet season	0.915**	0.896**	0.886**	0.770**
1984 dry season	0.872**	0.687**	0.759**	0.440*
1984 wet season	0.932**	0.872**	0.746**	0.275

*,** Significant at the 0.05 and 0.01 levels, respectively.

In general the short duration genotypes ranked below the median, the only exception being IR19728-9-3-2-3-3 in the 1984 dry season. These rice genotypes are more dependent on fertilizer N over their short growing season than are those able to take advantage of a longer period of soil N mineralization. However, the two best performing genotypes, IR13429-150-3-2-1-2 and IR18349-135-2-3-2-1, were both of medium duration. The mean ranking for 100-day genotypes based on the three-parameter combination was 19. The mean ranking was 9 for 110-day genotypes and 9 for 120- to 135-day genotypes. It appears that although growth duration affects N utilization efficiency up to a point, long duration genotypes are not superior to those of medium duration in this respect.

Rice genotypes selected for N utilization efficiency should be capable of performing well over a range of environmental conditions. Most of those included in our experiment performed similarly in the differing environments of the dry and wet seasons, although there were a few exceptions as noted above. The experiments reported here were conducted on a soil quite well supplied with N. Similar experiments with the same 24 genotypes are currently underway on soil of low N fertility to determine their efficiency in a contrasting environment.

Optional Methods

We have examined optional methods of evaluating N utilization efficiency that do not require the use of isotopically labeled fertilizer. One such method that measures N uptake efficiency, though not necessarily efficiency of N utilization, is given by the expression:

$$\frac{(\text{N in fertilized crop}) - (\text{N in unfertilized crop})}{(\text{fertilizer N applied})}$$

This method assumes that the contribution of soil N to growth of the plant is the same whether or not the crop is fertilized. This assumption is frequently invalid, and measurements of N uptake efficiency compared with the isotope method show large discrepancies, some of which have been documented by Broadbent (1979). Application of this method to our experimental data yielded many negative values, which have no physical meaning. The correlation coefficient for values obtained by this method and the isotope method was 0.059 for the 1983 wet season data, for example. Another approach is to use the ratio, (grain yield of fertilized crop)/(grain yield of unfertilized crop). Rankings obtained by this method were not correlated with the rankings of Tables 8 to 10. Of the several methods and parameters that we have investigated and that do not require isotopic data, the ratio WP/N_f appears to offer the most advantages. It is well correlated

with the other parameters and, with a few exceptions, provides rankings that do not differ greatly from the multiple-parameter rankings we have used.

Relation to N_2 Fixation

A factor that may contribute to the N utilization efficiency of a given genotype is the association of the rice plant with soil microorganisms capable of N_2 fixation. App et al. (1986) have recently reported differences among rice genotypes in their contribution to N balance of flooded soil. Since the isotope method does not differentiate between unlabeled N from soil and that from the atmosphere, genotypes that exhibit high N utilization efficiency as measured by Y/N_f and related parameters may in fact obtain a significant part of their total N from N_2 fixation. Studies by Ladha et al. (1986a,b) suggest that distinct genotypic differences exist in rice plant-associated N_2 fixation. However, quantitative data on the actual amount fixed by different genotypes are not available owing to the lack of suitable measurement techniques.

Although it is not yet clear what factors contribute to N utilization efficiency in addition to associative N_2 fixation, the consistency of performance of outstanding genotypes demonstrated in these experiments suggests that genetic improvement in this characteristic is both feasible and practical.

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