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The uptake and use of nitrogen by paddy rice in fallow, cereal, and legume cropping systems

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Abstract. In a previous paper, we reported that prior crops either increased or decreased the yield of paddy rice (*Oryza sativa* L.) and altered its response to fertiliser N. We considered that rice yield responses to prior crop might have reflected the uptake of crop residue N and the efficiency of its use to produce grain. Experiments consisted of dry-season grain or legume crops, or fallow, followed by wet-season rice (cv. Lemont); and wet-season grain or legume crops, or fallow, followed by dry-season rice. Urea at one-third of the rate required for optimum rice yield was applied at 3 stages of rice crop growth: sowing, permanent flood, and/or panicle initiation. Soil N supplied 4.1 to 6.5 g N/m^2 to the rice crop, depending on the season. Rice also recovered 0 to 0.25 of the N in the residue of a prior maize crop and 0.23 to 0.57 of the N in grain legume residues or a legume green manure crop; the fraction was greater if fertiliser N was not applied. Increased N uptake was the major contributor to heavier yield. The relationship between grain yield and crop N content was mostly linear, and thus physiological efficiency of N use for rice grain production was essentially constant across the range of environments provided by fertiliser N and cropping system treatments in this study. In experiments where fertiliser N was applied, there were small effects of prior cereal and legume cropping treatments on physiological efficiency. In contrast, without fertiliser N application, physiological efficiency was increased by prior cereal and legume crops, which likely resulted from a greater congruence between the N demand of the rice crop, and the N supply from the soil and incorporated residue, when compared with a fallow treatment.

Additional keywords: fertiliser, nitrogen recovery, nitrogen use efficiency, *Oryza sativa*, prior crop.

Introduction

The aim of this paper is to analyse how the nitrogen (N) in the soil and in the residue of cereal or legume crops affects the growth and yield of rice. A framework is used in which rice yield responses to N are expressed in terms of N absorption or recovery efficiency (RE, the uptake of crop N per unit of N applied in residue or fertiliser), and physiological efficiency (PE_{grain}, the grain yield produced per unit of crop N content) (Novoa and Loomis 1981; Moll *et al.* 1982). Using this approach, Cassman *et al.* (1993) showed an excellent relationship (PE_{grain} = –435 + 96 N content – 0.24 N content^2, r^2 = 0.97) for the rice variety IR72 grown in experiments in the Philippines. This relationship suggests that rice yield increases, in response to prior crops, may likely be a response to the uptake of residue N, especially in unfertilised rice grown in environments where solar radiation and water are not limiting. We also define a PE for crop production (PE_{crop}) as the above-ground crop dry weight per unit of crop N content.

Rice is a determinate species and both the amount and timing of N uptake may affect yield. In a concurrent paper, Ockerby *et al.* (1999) reported that the responses of rice dry weight, yield, and harvest index to fertiliser N were modified by prior fallow and crop treatments. Other work by Buresh and De Datta (1991) and Buresh *et al.* (1993) also suggested that rice yield responses to the time when fertiliser N is applied may be dependent on whether crop residues were incorporated before transplanting. The analyses used in this paper assess whether the rice responses to prior fallow and crop treatments (reported by Ockerby *et al.* 1999) occurred because of a change in N uptake by the rice crop and/or a change in the efficiency of N use to produce grain.

Materials and methods

Treatments and experimental design

The data in this paper were obtained from 3 experiments conducted between 1988 and 1990 at Millaroo Research Station, Queensland Department of Primary Industries (20°03′S, 147°17′E), in northern Queensland, Australia. Full details of the experimental procedures are

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Table 1. Chronology of the cultural and phenological events in the prior crop treatments and rice crops for three experiments grown in the Burdekin River Irrigation Area, 1988–90

RI, residue incorporation; F, permanent flood; I, panicle initiation

	Prior crop treatments			Rice crops				
	Sowing	Harvest	RI	Sowing	F	I	Anthesis	Maturity
			Expt 1 (1988–89)					
Maize	1.vi	14.xi	16.xi	9.xii	7.i	20.i	24.ii	12.iv
Chickpea 'early'	1.vi	28.x	31.x					
Chickpea 'late'	1.vi	28.x	6.xii					
			Expt 2 (1988–89)					
Maize	27.xii	26.vi	28.vi	20.viii	12.ix	18.x	15.xi	14.xii
Soybean	27.xii	26.vi	28.vi					
			Expt 3 (1990)					
Maize	13.i	3.vii	4.vii	3.viii	14.ix	—	—	18.xii
Soybean	13.i	25.v	4.vii					
Lablab	13.i	—	4.vii					

reported by Ockerby *et al.* (1999). The experiments measured the uptake and use of N by wet-season (December–April) or dry-season (July–December) rice (cv. Lemont) in response to prior fallow or crop (cereal, grain legume, or legume green manure) treatments and the timing of fertiliser N application to rice. Chronologies of prior treatments are given in Table 1. Urea (46% N) was banded (0.17 m apart at a soil depth of 0.12 m) at sowing, broadcast onto the dry soil surface immediately before permanent flood, or broadcast into the floodwater at panicle initiation.

Expt 1 was a randomised complete block with 3 replications. The treatments were arranged as a 4 × 2 × 2 × 2 complete factorial and consisted of 4 dry-season treatments: fallow, maize (*Zea mays* L. cv. Pioneer 6875), chickpea 'early' (*Cicer arietinum* L. cv. Tyson) with residue incorporated immediately after harvest, and chickpea 'late' with residue incorporated immediately before rice sowing; 2 levels of fertiliser N applied at sowing to the wet-season rice crop; 2 levels of fertiliser N applied at permanent flood; and 2 levels of fertiliser N applied at panicle initiation. The levels of fertiliser N were 0 and 25 kg/ha (2.5 g/m^2), the latter rate being one-third of the fertiliser N needed for optimal yield of wet-season rice crops in the Burdekin River Irrigation Area (BRIA). Thus, fertiliser N was applied in 8 factorial combinations, and a range from nil to the optimum rate was achieved.

Expt 2 was a randomised complete block with 3 replications. The treatments were arranged as a 3 × 2 × 2 × 2 complete factorial and consisted of 3 wet-season treatments: fallow, maize (cv. Pioneer 6875), and soybean (*Glycine max* L. cv. Cannapolis); 2 levels of fertiliser N applied at sowing to the dry-season rice crop; 2 levels of fertiliser N applied at permanent flood; and 2 levels of fertiliser N applied at panicle initiation. The levels of fertiliser N were 0 and 60 kg/ha (6.0 g/m^2), the latter rate being one-third of the fertiliser N needed for optimal yield of dry-season rice crops in the BRIA.

Expt 3 was a randomised complete block with 3 replications. There were 4 wet-season treatments: fallow, maize (cv. Pioneer 6875), soybean (cv. Cannapolis), and lablab (*Lablab purpurea* cv. Rongai). Fertiliser N was not applied. Rice was grown during the dry season.

Measurements

Prior crops

Methods for determining the dry weight, N concentration, and N content of prior crops are described by Ockerby *et al.* (1999). Data are shown in Table 2.

Table 2. Mean dry weight (g/m^2), N concentration (g/kg), and N content (g/m^2) of the residue of maize, chickpea, soybean, and lablab prior crops at or near physiological maturity

The results are means of 24 samples with the standard deviation of means shown in parentheses

Prior crop treatment	Plant component	Dry weight	N conc.	N content
		Expt 1 (Dry-season treatments)		
Maize	Above-ground	880 (111)	4.1 (0.8)	3.6
	Roots	63 (26)	4.6 (2.0)	0.3
Chickpea	Above-ground	273 (62)	14.1 (1.8)	3.9
	Roots	28 (12)	17.7 (3.3)	0.5
		Expt 2 (Wet-season treatments)		
Maize	Above-ground	706 (89)	6.4 (1.6)	4.7
	Roots	100 (18)	3.8 (0.9)	0.4
Soybean	Above-ground	279 (71)	26.2 (2.3)	7.2
	Roots	33 (5)	12.9 (2.6)	0.4
		Expt 3 (Wet-season treatments)		
Maize	Above-ground	886 (217)	7.2 (1.7)	6.4
	Roots	41 (10)	5.2 (1.0)	0.2
Soybean	Above-ground	253 (56)	15.2 (3.9)	3.8
	Roots	15 (3)	9.2 (2.1)	0.4
Lablab	Above-ground	611 (282)	14.5 (2.4)	8.9
	Roots	24 (4)	16.5 (2.3)	0.4

Rice crops

The rice crops were sampled at permanent flood, panicle initiation, anthesis, and physiological maturity. The above-ground biomass of each crop was harvested from randomly selected 0.9-m^2 quadrats, and partitioned into vegetative and grain components. Samples were dried, weighed, and ground to pass through a 1-mm sieve. The N concentration of the plant components was determined by Kjeldahl digestion and colorimetric analysis (O'Neill and Webb 1970). The N content of the vegetative and grain components was calculated as the product of the dry weight and N concentration.

Recovery efficiency of N was calculated as the uptake of crop N at maturity (after subtracting the N content of rice grown with a prior

Table 3. Temporal responses of the vegetative and grain N content (g/m^2) of wet-season (Expt 1) and dry-season (Expts 2 and 3) rice to the main-effects of prior crop treatments

Rice was sampled at permanent flood, panicle initiation, anthesis, and maturity. Data for Expts 1 and 2 are the main-effects of prior crop treatments across eight fertiliser N treatments. Fertiliser N was not applied in Expt 3

Prior fallow and crop treatment	N content of rice shoots and straw: Permanent flood	Panicle initiation	Anthesis	Maturity	N content of rice grain	Rice N content at maturity
			Expt 1 (Wet-season rice)			
Fallow	1.52	2.7	5.3	3.9	4.6	8.5
Maize	0.74	1.5	4.3	3.6	4.4	8.0
Chickpea 'early'	0.36	2.9	6.4	3.9	4.9	8.8
Chickpea 'late'	1.65	3.4	7.3	4.3	5.0	9.3
l.s.d. (P = 0.05)	0.27	0.6	1.2	0.4	0.4	—
			Expt 2 (Dry-season rice)			
Fallow	0.33	5.4	8.7	3.8	6.9	10.7
Maize	0.22	4.6	8.5	3.7	7.2	10.9
Soybean	0.32	5.3	9.4	4.4	7.7	12.1
l.s.d. (P = 0.05)	0/06	0.5	n.s.	0.4	0.5	—
			Expt 3 (Dry-season rice)			
Fallow	0.35	1.0	2.7	1.7	2.4	4.1
Maize	0.17	1.9	3.9	2.4	3.9	6.3
Soybean	0.51	2.2	4.7	2.6	3.9	6.5
Lablab	0.45	2.0	4.7	2.7	4.0	6.7
l.s.d. (P = 0.05)	0.13	0.6	0.9	0.5	0.7	—

n.s., Not significant.

fallow) per unit of N applied in prior crop residues or fertiliser. Physiological efficiencies of crop (PE_{crop}) and grain (PE_{grain}) production were calculated as the dry weight of the above-ground crop, or grain, respectively, produced per unit of crop N content at maturity.

Statistical methods

Treatment effects were tested by analysis of variance using Biometry Statistical Software (Anon. 1992). Pairwise testing of means for main effects and interactions was done using the protected least significant difference procedure (l.s.d.) at P = 0.05. Linear or non-linear curves of best fit were used to describe the relationships between grain yield and the above-ground crop dry weight, and the N content of the rice crop at maturity.

Results

Nitrogen content of rice

In all experiments, prior cropping with maize, compared with fallow, reduced the N content of rice at permanent flood and/or panicle initiation (Table 3). When fertiliser N was not applied in Expt 3, however, maize increased the N content of rice after panicle initiation. In contrast, prior legume cropping increased the N content of rice in all experiments. The apparent N gain from a previous legume crop was enhanced when chickpea residue was incorporated 'late' (immediately before sowing the rice crop) in Expt 1. Incorporating the chickpea residue 'early' (immediately after the chickpea harvest) resulted in a large loss of residue N (1.5 g nitrate-N/m^2), probably to denitrification when the rice crop was permanently flooded (Ockerby *et al*. 1999).

In all experiments and treatments, the N content of rice straw at maturity was less than that of the rice crop at anthesis, showing that some pre-anthesis N was remobilised to the grain (Table 3). The amount of remobilised N was largest in Expt 2, when up to 18 g fertiliser N/m^2 was applied. The N content of rice grain at maturity was also largest in Expt 2, and was larger with prior soybean cropping compared with a prior fallow. In the latter case, however, the extra grain N was acquired from N uptake during grain-filling, as N remobilisation was similar for maize, soybean, and fallow treatments (Table 3). Remobilisation of N was also important with prior chickpea cropping in Expt 1, contributing more than half of the grain N content.

When no fertiliser N was applied in Expt 3, both N remobilisation and N uptake after anthesis contributed to the N content of rice grain. With a previous fallow, only a small amount of soil N was taken up during grain-filling and a similar small amount was remobilised. With prior legume cropping, increases in grain N content were due to enhanced N uptake and remobilisation during grain-filling. With previous maize cropping, the increase in grain N content was due mostly to N uptake.

Fertiliser N applied at sowing, permanent flood, or panicle initiation also increased the N content of rice (Table 4). The effect was largest when fertiliser N was applied at permanent flood in Expt 2. For all fertiliser N treatments, there was a large decrement between the N content of rice shoots at anthesis and the straw at maturity. In all cases, the decrement

Table 4. Effects of the time of application of fertiliser N on the vegetative and grain N content (g/m^2) of wet-season (Expt 1) and dry-season (Expt 2) rice

Fertiliser N was applied (+) or not applied (–) at sowing (S), permanent flood (F), or panicle initiation (I) in factorial combination. The rate of fertiliser was 2.5 g N/m^2 in the wet season and 6.0 g N/m^2 in the dry season. In Expt 1, only the treatment with a single N application at each time was sampled; the four-way interactions at maturity were never significant. In Expt 2, all plots were sampled and the data are for the main-effect of the N application at that time in complete factorial with prior crops and other N application treatments

Time of fertiliser N application	N content of rice shoots and straw: Permanent flood	Panicle initiation	Anthesis	Maturity	N content of rice grain	Rice N content at maturity
			Expt 1 (Wet-season rice)			
–S,–F,–I	0.97	1.40	4.09	3.61	3.70	7.31
+S	1.53	—	—	3.63	4.05	7.68
+F	—	2.73	—	3.95	4.50	8.45
+I	—	—	5.23	3.52	4.38	7.90
+S,+F,+I	1.56	3.69	8.16	4.38	6.18	10.56
l.s.d. (P = 0.05)	0.24	0.48	1.02	n.s.	n.s.	—
			Expt 2 (Dry-season rice)			
–S	0.23	4.2	7.7	3.6	6.7	9.3
+S	0.35	5.9	10.0	4.3	7.9	12.2
–F	—	2.1	5.7	2.9	5.3	8.2
+F	—	8.1	12.0	5.1	9.2	14.3
–I	—	—	7.5	3.7	6.3	11.0
+I	—	—	10.2	4.3	8.2	12.5
l.s.d. (P = 0.05)	0.05	0.4	0.9	0.3	0.4	—

n.s., not significant.

was less than the N content of the grain, indicating net N uptake by the crop between anthesis and maturity. The N uptake by the crop during this period ranged from 2.2 to 2.6 g/m^2. The N content of the rice grain increased in response to fertiliser N applied at all application times, but the response was largest for N applied at permanent flood and least for N applied at sowing. In Expt 1, increases in the N content of rice were smaller than in Expt 2 reflecting the reduced rate of fertiliser N applied.

In Expt 2, the prior fallow and crop treatments interacted with fertiliser N treatments applied at planting and permanent flood to affect the N content of the rice crop. At permanent flood, rice which was not fertilised with N at planting had less N content (g/m^2) if it was grown after maize (0.13) than after either fallow (0.25) or soybean (0.32). Rice that was fertilised with N at planting contained more N if it was grown after a fallow (0.42) than after either soybean (0.33) or maize (0.30) (l.s.d. at P = 0.05, 0.08). At panicle initiation, rice that was not fertilised with N at planting had a similar N content (4.2 g/m^2) for all prior fallow and crop treatments, whereas, with fertiliser N at planting, the rice N content was less when grown after maize (5.1) than after either fallow (6.5) or soybean (6.3) (l.s.d. at P = 0.05, 0.8).

A prior crop treatment also modified the effect of fertiliser N applied at permanent flood on the N content of rice grain. Without fertiliser N at permanent flood, the N content (g/m^2) of grain was less when grown after fallow (4.6) than after either maize (5.4) or soybean (5.9), but with fertiliser N at permanent flood, the N content of grain was similar for all prior fallow and crop treatments (9.2) (l.s.d. at P = 0.05, 0.7).

Recovery efficiency

In Expt 1, unfertilised wet-season rice grown after a fallow took up 6.5 g/m^2 of soil N. Prior cropping with maize did not change the N content of unfertilised rice, thus there was no apparent recovery of maize residue N. For prior cropping with chickpea, however, the RE was 0.23 when residues were incorporated ‘early’ and 0.54 when incorporated ‘late’. When fertiliser N was applied to wet-season rice, the RE of N from incorporated residues of previous crops decreased. For example, with the maximum application of fertiliser N (7.5 g/m^2), there was a negative RE of the N in maize residue (–0.4) and the RE of N in chickpea residue was negligible. The RE of fertiliser N was 0.35 when applied at planting or panicle initiation and 0.65 when applied at permanent flood.

In Expt 2, unfertilised dry-season rice grown after a fallow took up 4.4 g/m^2 of soil N. The RE of maize residue N was 0.25 and of soybean residue N was 0.39. As occurred in Expt 1, fertiliser N reduced the RE of residue N. With the maximum application of fertiliser N (18 g/m^2), the N content of rice when grown after maize was less than if it was grown after a fallow giving a negative RE of maize residue N (–0.25). The RE of soybean residue N was 0.23, although this may be underestimated since 2.5 g nitrate-N/m^2 in the

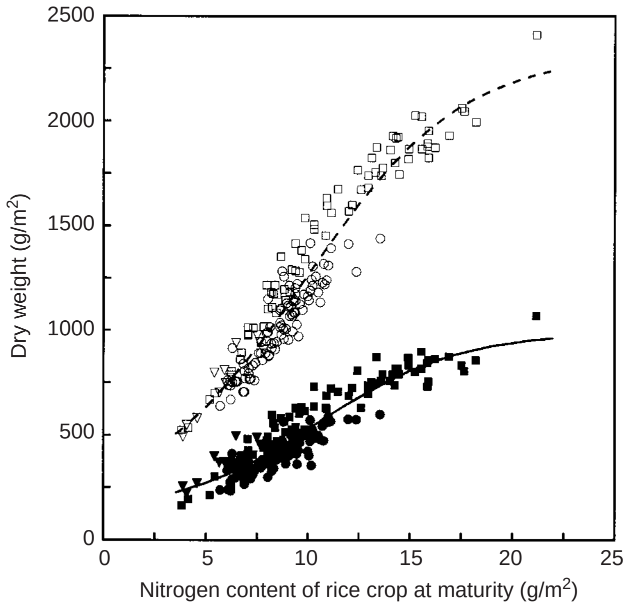

Fig. 1. Relationships between grain yield and total above-ground dry weight (crop), and the N content of the rice crop at maturity. Data are from experiments in 3 seasons with different prior crop and fertiliser nitrogen treatments. Linear or non-linear curves of best fit were:
1988 wet-season:

● grain, $y = 180.2+481.2/(1+\exp[-0.4631*(x-8.836)])$ ($R^2 = 0.76$)
○ crop, $y = 573+856/(1+\exp[-0.65*(x-8.486)])$ ($R^2 = 0.85$)

1989 dry-season:
■ grain, $y = -4023+5076/(1+\exp[-0.1325*(x+7.715)])$ ($R^2 = 0.85$)
□ crop, $y = -1042+3366/(1+\exp[-0.1931*(x-4.967)])$ ($R^2 = 0.97$)

1990 dry-season:
▼ grain, $y = 1.7+62x$ ($R^2 = 0.81$)
▽ crop, $y = 75+116x$ ($R^2 = 0.90$)

Combined:
— grain: $127.3+863/(1+\exp[-0.2899*(x-10.497)])$ ($R^2 = 0.85$)
- - - crop: $158+2169/(1+\exp[-0.2616*(x-9.855)])$ ($R^2 = 0.92$)

soybean residue was lost at permanent flood (Ockerby *et al.* 1999). If it is accounted for, the RE of soybean residue N was 0.57 without fertiliser N and 0.33 with fertiliser N. The RE of fertiliser N was 0.42 when applied at planting or panicle initiation, and 1.06 when it was applied at permanent flood.

In Expt 3, unfertilised dry-season rice grown after a fallow took up 4.1 g soil N. Prior cropping with maize, soybean, or lablab increased the N content of the rice crop at maturity. The REs were 0.35 of soybean residue N, 0.33 of maize residue N, and 0.28 of lablab green manure N.

Physiological efficiency

In each experiment, PE_{crop} and PE_{grain} were essentially constants, since the relationships between grain yield and total above-ground dry weight, and crop nitrogen content, were mostly linear (Fig. 1). In expts 1 and 2, non-linear curves best described the data, but in neither experiment was the grain or the above-ground dry weight function maximised. It is possible that PE_{crop} and PE_{grain} might have decreased when the crop N content exceeded 12 g/m^2 in the wet season and 15 g/m^2 in the dry season.

Analysing the data for PE using ANOVA indicated differences between prior fallow and crop, and fertiliser treatments. In Expt 1, PE_{crop} decreased in order when rice was grown after chickpea 'early', fallow, chickpea 'late', and maize, respectively, although there were no effects on PE_{grain} (Table 5). Fertiliser N applied at permanent flood increased PE_{crop}, whereas fertiliser N applied at planting or panicle initiation increased PE_{grain} (Table 6).

In Expt 2, PE_{crop} was greater when rice was grown after a fallow than after maize or soybean (Table 5). Fertiliser N applied at permanent flood and panicle initiation reduced PE_{crop}. PE_{grain} was greater when rice was grown after maize than after soybean or fallow. PE_{grain} was reduced by fertiliser N applied at permanent flood and increased by fertiliser N applied at panicle initiation.

In Expt 3, prior crop treatment did not significantly ($P = 0.05$) affect PE_{crop}, although a trend was apparent for more efficient N use for lablab green manure, maize, and fallow treatments than for the soybean treatment. PE_{grain} was more efficient ($P = 0.064$) for maize and lablab than for soybean and fallow treatments.

Discussion

Recovery efficiency

The uptake of more soil N by the unfertilised, wet-season rice crop compared with the dry-season crop suggested that soil N was mineralised more rapidly during the wet-season. Whereas maximum temperatures were similar during both seasons, minimum temperatures were warmer during the wet-season, particularly during the early stages of the crop (Ockerby *et al.* 1999). It is known that warmer temperatures promote soil N mineralisation (Cassman and Munns 1980; Westcott and Mikkelsen 1985). The amounts of soil N mineralised in the current experiments were consistent with other estimates of N mineralisation during tropical rice crops (Morris *et al.* 1986; Furoc and Morris 1989; John *et al.* 1989*b*).

The RE of legume residue N ranged from 0.23 to 0.57, which is comparable with other studies (Morris *et al.* 1986; Westcott and Mikkelsen 1987; Furoc and Morris 1989; John *et al.* 1989*a*, 1989*b*). The late incorporation of chickpea residue increased the RE because there was less time for residue N to be mineralised to nitrate and subsequently lost to denitrification when the rice crop was permanently flooded. The RE of N in legume crop residues was similar for each experiment; however, the RE of N in maize residues varied between seasons. Negative RE of the maize residue N by the unfertilised, wet-season rice crop may have been caused by the dilute concentration of N in the maize residue (Table 2), which, in turn, promoted the microbial immobili-

Table 5. Effects of prior fallow and crop treatments on the physiological efficiencies (g dry weight/g crop N content) of crop (PE_{crop}) and grain (PE_{grain}) production for wet-season (Expt 1) and dry-season (Expts 2 and 3) rice

Prior fallow and	Expt 1		Expt 2		Expt 3	
crop treatment	PE_{crop}	PE_{grain}	PE_{crop}	PE_{grain}	PE_{crop}	PE_{grain}
Fallow	119	48	137	56	130	60
Maize	114	47	131	59	131	66
Chickpea 'early'	121	49	—	—	—	—
Chickpea 'late'	116	46	—	—	—	—
Soybean	—	—	131	56	126	61
Lablab	—	—	—	—	132	66
l.s.d. (P = 0.05)	5	n.s.	4	2	n.s.	5.4^{A}

n.s., not significant. ^{A}P = 0.64.

Table 6. Change in the physiological efficiencies (g dry weight/g crop N content) of crop (ΔPE_{crop}) and grain (ΔPE_{grain}) production of wet-season (Expt 1) and dry-season (Expt 2) rice due to the application of fertiliser N at planting, permanent flood, or panicle initiation

The rate of fertiliser N was 2.5 g/m^2 in Expt 1 and 6.0 g/m^2 in Expt 2

Time of fertiliser	Expt 1		Expt 2	
N application	ΔPE_{crop}	ΔPE_{grain}	ΔPE_{crop}	ΔPE_{grain}
Planting	0.3	2.5	–1.4	0.0
Permanent flood	5.7	0.4	–7.2	–4.8
Panicle initiation	2.1	4.7	–4.2	3.4
l.s.d. (P = 0.05)	3.4	2.0	3.6	1.7

sation of soil N (Vigil and Kissel 1991). The recovery of up to a third of the maize residue N by unfertilised, dry-season rice is an unusual result normally achieved only for legumes (Chapman and Myers 1987; Norman *et al* 1990). It is suggested that this cropping sequence, maize followed by dry-season rice, minimises N loss and aligns N mineralisation with the N demand of the rice crop.

The RE of legume residue N was similar to the RE of fertiliser N applied at planting and panicle initiation, but less than the RE of fertiliser N applied at permanent flood. The uptake of fertiliser N was similar to other studies for the applications at planting (Patrick *et al.* 1984) and panicle initiation (Humphreys *et al.* 1987); however, the uptake of fertiliser N applied at permanent flood in these studies was greater than that obtained by Humphreys *et al.* (1987) in a temperate environment. The RE of the fertiliser N applied at permanent flood in Expt 2 was >1.0, suggesting that fertiliser N may have 'primed' the release of additional soil N (Kawaguchi *et al.* 1986). In general, the uptake of fertiliser N was consistent (0.3–0.5) with that measured for a range of N strategies used in other studies in the tropics (Morris *et al.* 1986; Furoc and Morris 1989; John *et al.*1989*b*).

The RE of residue N was greater when fertiliser N was not applied. Furoc and Morris (1989) reported that the marginal rate of N uptake from a green manure decreased as the rate of N fertiliser increased. Reduced uptake of residue N, with increased fertiliser N, may partly be due to the uptake of more soil N when organic and inorganic N fertilisers are applied (Patrick *et al.* 1984; Humphreys *et al.* 1987; Azam 1990). Another contributing cause may be that rice will not take up all the N that is available if the N supply from the soil, residues, and fertiliser occurs simultaneously. The N not taken up by the crop may be lost, resulting in inefficient N recovery from any or all of the sources.

The unfertilised rice crop (Expt 3) recovered N from cereal and legume residues both prior to and after anthesis. When fertiliser N was applied in Expts 1 and 2, however, N contribution from maize residues occurred only after anthesis. When the yield of rice was greatest (Expt 2, and Expt 1 after chickpea: Ockerby *et al.* 1999) and the N content of the rice grain was generally large (Table 3), a significant amount of grain N was remobilised from the vegetative rice biomass. Bufogle *et al.* (1997) found that late-season N demand by maturing rice grain was satisfied by native soil N and remobilisation of N from straw to grain. The present data show that both the uptake and remobilisation of residue N can supply the maturing grain.

Physiological efficiency

In the experiments reported here, PE_{crop} and PE_{grain} were essentially constant across the range of crop N content. Some data may indicate that PE may have decreased when the crop N content exceeded 12 g/m^2 in the wet season and 15 g/m^2 in the dry season, but there were few data with a large crop N content in each experiment. For example, in Expt 2, there was only one datum point with a crop N content >20 g/m^2 (Fig. 1), and this treatment tended to increase the slopes of the relationships, thus promoting PE_{crop} and PE_{grain}. This result may also reflect the way in which soybean residue N tended to increase PE.

In other studies conducted in the tropics (Morris *et al.* 1986; John *et al.* 1989*a*; Buresh *et al.* 1993), PE_{grain} decreased as the N content of the rice crop increased, and quadratic or cubic models were appropriate. These studies were conducted in environments where yield was limited by insufficient solar radiation, and maximum rice yields ranged between 480 and 570 g/m^2 with maximum crop N contents of 10–15 g/m^2. In a temperate climate, Westcott and Mikkelsen (1987) used a quadratic relationship to describe the relationship between PE_{grain} and the crop N content of rice but the maximum yield was greater at 1200 g/m^2 with 18 g crop N/m^2. In the current experiments, maximum yield was 600 g/m^2 for 14 g crop N/m^2 in the wet season, and 1000 g/m^2 for 22 g crop N/m^2 in the dry season. Working in the tropics, Schnier *et al.* (1990) also reported the N content of dry-season rice crops up to 22 g/m^2 with grain yield of 900 g/m^2. These comparisons suggest that the PE_{grain} in our experiments demonstrates the potential response of rice to N in this environment, despite the possibility that PE_{grain} may have decreased at larger crop N contents in the first dry-season rice crop. Importantly, despite the application of recommended amounts of fertiliser N in some treatments, an asymptote for the relationship between grain yield and crop N content was not recorded in either the wet- or dry-season crops: a greater yield potential for rice in these environments was indicated.

The average PE_{grain} in the 3 experiments was 53 g/g. For the range 4–12 g crop N/m^2, PE_{grain} was comparable to the 46–48 g/g reported by John *et al.* (1989*a*) but greater than the 20–22 g/g reported by Morris *et al.* (1986) and Furoc and Morris (1989). The latter studies were conducted during tropical wet-seasons and concluded that rice yield was limited by insufficient solar radiation and hot temperatures, but not limited by N.

Although in the current experiments, non-linear and linear curves reasonably described the growth and yield relationships of the rice crop to the combined uptake of soil, residue, and fertiliser sources of N (Fig. 1), the use of a factorial experimental design permitted the effect of each N source to be examined separately. In each experiment, the source and timing of N application affected PE_{crop} and PE_{grain}. For rice, PE_{crop} was greatest after a fallow and PE_{grain} was greatest after maize. Morris *et al.* (1986), in a comparison of green manure and fertiliser N effects on rice, previously reported differential N use; however, most studies (Furoc and Morris 1989; John *et al.* 1989*a*) have reported that PE_{grain} was independent of the N source. In the current experiments, PE_{crop} and PE_{grain} were different for the soil, residue, and fertiliser sources of N.

Rice growth and grain yield are affected by N supply at critical growth stages (Yoshida 1981) and this knowledge has been used to apply fertiliser N efficiently. For example, fertiliser N applied at permanent flood and panicle initiation increased crop growth and the crop N content at panicle initiation and heading when most yield components were determined (Akita 1989). With more knowledge of the RE and PE_{grain} of the N in different crop residues it should be possible to devise new fertiliser strategies that improve N use efficiency in rice cropping systems.

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