Ecology of deepwater rice-fields in Bangladesh
5. Mineral composition of the rice plant and other aquatic macrophytes

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Abstract

The mineral composition of deepwater rice (cultivar Kartik Sail) was studied during 1986 in a field near Sonargaon, Bangladesh, which is flooded by water from R. Meghna. Samples were taken four times, once prior to flooding and three times during the flood season. On two of the latter days (10 August = end of first flood peak, 23 September = second flood peak) the study was extended to other components of the ecosystem (sediments + soil, water, other aquatic macrophytes). On 23 September, 32% of the mass of the plant was out of water, 65% in water and 3% in sediment/soil. There were marked differences between elements in their pattern of accumulation by deepwater rice through the season. In comparison with the final totals for each element, about 48% of N, but only 11% of P and 10% of Na had been accumulated by the time the floodwater had arrived. The aquatic roots doubled in mass between the times of the two flood peaks and it is suggested that much of the P taken up by the plant may reach the plant via its aquatic roots after having becoming mobilized and released to the water when sediments become anaerobic. In comparison with other parts of the plant, Na was always much higher in the stem and Zn in the basal roots.

Other aquatic macrophytes ('weeds') increased from 0.40% of the mass (dry weight) of deepwater rice on 10 August to 4.0% on 23 September. However their content of each element (% dry weight) was considerably higher than that in deepwater rice, so they may at times compete effectively with the rice for nutrients. During the flood period (to 23 September) weeds accumulated 16% of the N accumulated by rice during the same period.

Introduction

The areas in Bangladesh where deepwater rice (DWR) is grown and which have been described in earlier papers in this series are mostly heterogeneous and ill-defined during the flood season (Whitton *et al.*, 1988a). The relative contributions of the various sources of nutrient input and loss are poorly understood (Rother *et al.*, 1988) and probably vary considerably from year to year. There have been a number of studies made to test the possible influence of fertilizer on deepwater rice grain yields, whether added to soil prior to flooding, or as granules to the water during the flood. These have mostly failed to give unambiguous answers concerning the possible influence of added nitrogen (see Vergara, 1985), though Roy (1975) reported that some soils responded to phosphorus and even more to mixed phosphorus and potassium. DWR on an area of acid sulphate soil in Thailand could not survive in deeper water without added P, even when N was added at a high level (Jugsujinda *et al.*, 1982). The experimental design of these agronomic studies on an aquatic crop has sometimes been little changed from that which would be used for a terrestrial crop, neglecting, for instance, to consider the possibility that nutrients may move from one field to another. Judging by Vergara's (1985) review, very little information exists about the mineral composition of DWR, although a considerable amount is known about the distribution of nitrogen in other types of rice (Mae, 1986). For all these reasons it seemed essential to obtain a more detailed understanding of the distribution of the major nutrient elements in the ecosystem. The present paper reports a study of changes taking place during the 1986 growth season in a DWR field near Sonargaon.

Methods

Site

Details of the Sonargaon location and DWR field used as study site are given in Whitton *et al.* (1988a). The field, which is termed 86-I here, is the same as 85-I, whose chemical features are described by Whitton *et al.* (1988b), while the 'weed' flora of fields at Sonargaon is described by Whitton *et al.* (1988c). The DWR cultivar in 1986 was Kartik Sail.

Sampling

Samples of DWR were collected for analysis in 1986 before flooding (19 June) and three times during the flood season. These were: 17 July, towards the end of a period when the water had been rising at a moderate speed c) 3 cm day^{-1}); 10 August, towards the end of the first flood peak; 23 September, on the fourth day of a rapid rise towards the second flood peak. Other aquatic macrophytes (weeds), water and sediments plus underlying soil were also collected from the same field on the last two days). Underwater samples were collected by swimming aided by a mask.

The standing crop of DWR was determined as follows. Tiller counts were made in 10 randomly selected 0.5 m^{-2} quadrats. The position of each quadrat was marked and the one which was considered the most representative of the whole field was selected for sampling. (Tillers were removed from only one quadrat in order to minimize damage to the field.) Choice of quadrat was based on tiller density (a value close to the mean) and criteria such as rat damage and weed content. All tillers within the quadrat, together with basal roots, were removed carefully, cleaned from sediments and other plants by washing in a channel, washed again in deionized water on return to the laboratory. Five plants were selected at random from the bulked sample and one typical tiller taken from each. (Mean and SD for tillers per plant on the first two surveys was 7.0 + 1.58 and 3.8 + 0.83, respectively.) Basal roots were subdivided according to the number of tillers. On 10 August and 23 September the tillers were separated into fractions based on the following criteria:

i) vertical position: above water, below water, sediments;

ii) fraction of plant: lamina, sheath, stem, aquatic roots, basal roots;

iii) healthy versus dead.

Each fraction was washed in four changes of deionized water, air-dried and stored in glass snap-cap vials. A different sampling programme was used for other macrophytes in the same field. Plants were harvested from five randomly selected 1 m^2 quadrats, separated into species, washed in the channel and then four changes of deionized water, air-dried and stored in glass snap-cap vials. (This sampling programme was the maximum which could be done without excessive damage to the field.)

Water samples were collected at seven different depths and analyzed as described by Whitton *et al.* (1988a); the mean values were used for estimates in Table 1. Sediments were collected using a coring device made from PVC pipe. The cores, 2 cm in diameter and 5 cm deep, were divided into two layers: upper 1 cm and 1 cm to 5 cm. Preparation, digestion and analysis were as described by Whitton *et al.* (1988a).

Digestion and analysis of plant material

On return to the U. K. all plant samples were oven-dried at 105 °C, thoroughly broken up and mixed (using Glen-Creston mill for samples > 5 g dry weight, otherwise by cutting with small stainless steel scissors), redried and subsampled for digestion. Concentrated HNO_3 was used for metals (Na, K, Mg, Ca, Mn, Fe, Zn: Rother & Whitton, 1976) and Kjeldahl digestion (Yoshida *et al.*, 1976) for N and P. Metals were analyzed by atomic absorption spectrophotometry (Perkin-Elmer 5000), N by distillation into boric acid and titration against HCl and P colourimetrically after neutralizing the digest (Eisenreich *et al.*, 1975). Replicate digestions were made of bulked material from 10 August and 23 September (n = 5 on both days) to establish the variability of the digestion/analytical procedure. The coefficient of variation was 0.05 or less for all elements except Ca (0.06 on both days) and Zn (0.14) on both days).

Results

Partitioning of mineral nutrients in the DWR field ecosystem

The amounts of various elements in different components of the DWR field are shown in Table 1. The DWR standing crop increased by a factor of 7.1 between 19 June (just before flooding) and 10 August, but there was little change between then and 23 September. There were marked differences between the increases for the various elements between 19 June and 10 August: Mg, × 2.47; Ca, × 2.42; N, × 2.58; Mn, × 2.76; K, × 4.44; P, × 7.17; Fe, × 10.6; Na, × 14.3. In every case the uppermost 5 cm of sediment/soil contained more than the water or the plants, although the former was the amount extracted with concentrated HNO_3, not that potentially availability to roots. Sodium is the element with the lowest ratio between sediment/soil and water or DWR. Weeds were only 0.40% of the DWR standing crop on 10 August, but had increased to 4.05% on 23 September. Most elements in the weeds also showed an approximately tenfold increase, but K and Zn were about 18 times higher.

The distribution of elements in DWR between air, water and sediment/soil shows marked differences (Table 2); but, by the time of the first measurement under flood conditions (17 July), the highest percentage for any particular element almost always occurred in the part of the plant in the water and the lowest in sediment/soil. (The fraction of the plant above water is not exactly comparable on each day, because of the influence of a sudden rise in the water). The N : P ratio of the above-water part of the plant increased during the season. Standing crops of the various weed species are expressed only as dry weight (Table 3), but values for individual elements may be obtained by combining these data with concentrations for each species.

The concentrations of some elements in the tiller showed marked changes between the period just before flooding and a month later (Table 4), with Na doubled and K, Mg, Ca and N approximately halved. The N concentration progressively decreased through the season, whereas P showed no obvious pattern. Na was always much higher in that part of the tiller in the water and Zn much higher in basal roots in the sediment/soil.

The mean tiller density, dry weight per tiller (and hence tonnes dry matter per hectare) and concentrations of the major elements are given in Table 1. In this summary table the tillers are divided into three major fractions; above water (mainly leaf blade and sheath), below water (stem and aquatic routs plus some, generally moribund, leaves and sheaths) and the basal roots (in the sediment). During the season the weight per tiller increases but less rapidly once the peak flood is reached. Tiller density decreased throughout, probably due to damage by rats and insect pests. In contrast, the concentration of all the elements analyzed, and in all three fractions, fell during the season or, such as P, showed little change. The difference was most marked between the first two samples, reflecting the sharp change in the environment at the onset of flooding.

Table 1. Standing crop of DWR and weeds (dry wt) and mineral nutrients (kg ha^{-1} element) in major components of DWR field (86-I) at Sonargaon. Values for sediment/soil refer to total in uppormost 5-cm layer; aqueous N based on inorganic only, whereas aqueous P includes organic fraction

Date	Tiller density (no. m^{-2})	Component	Standing crop (kg ha^{-1})									
			d. wt	Na	K	Mg	Ca	Mn	Fe	Zn	N	P
19.6	314	DWR	1804	3.10	56.0	8.20	8.83	0.507	1.69	0.195	43.14	2.99
17.7	326	DWR	7973	28.0	141.9	12.93	16.6	2.065	9.87	0.564	88.11	9.649
10.8	287	water	–	34.35	13.6	34.5	57.0	0.237	7.09	0.130	1.32	0.900
		sed/soil	7.9×10^5	104.2	1377	5017	1769	214.9	17040	52.8	1124	395.0
		DWR	12830	44.5	248.5	20.26	21.4	1.399	17.92	1.829	124.1	21.44
		weeds	50.89	0.387	2.13	0.38	0.748	0.047	0.19	0.0099	1.35	0.156
23.9	215	water	–	31.3	12.0	28.02	51.2	0.310	9.93	0.222	2.34	1.86
		sed/soil	7.9×10^5	97.2	1323	4869	1662	210.9	16320	50.4	1130	361.0
		DWR	12900	32.0	197.1	16.92	19.65	1.092	10.98	0.607	89.6	26.10
		weeds	522.2	3.61	37.6	3.14	6.31	0.263	1.15	0.178	11.20	1.48

Table 2. Distribution of dry weight and elements (expressed as %) in DWR between fractions of the plants in the three different environments (air, water, soil and or sediment/soil).

Date	Environment	d. wt (kg ha^{-1})	% component									
			d. wt	Na	K	Mg	Ca	Mn	Fe	Zn	N	P
19.6	air	1657	91.9	71.7	98.1	95.9	96.2	97.4	73.2	74.7	96.3	97.2
	soil	146	8.1	28.3	1.9	4.1	3.8	2.6	26.8	25.3	3.7	2.8
17.7	air	3069	38.5	3.1	46.3	41.4	52.8	16.2	5.1	16.6	47.9	44.6
	water	4521	56.7	93.9	52.5	53.8	43.4	81.7	78.8	57.4	47.8	53.0
	sed/soil	383	4.8	3.6	1.5	4.8	3.8	2.1	16.1	26.0	4.3	2.4
10.8	air	2859	22.6	0.6	21.7	27.8	46.0	14.6	2.8	6.3	36.7	22.4
	water	8949	70.5	96.5	77.4	64.4	45.9	77.8	53.1	46.0	54.3	74.6
	sed/soil	1026	6.9	2.9	0.9	7.8	8.1	7.6	44.1	47.7	9.0	3.0
23.9	air	4114	31.9	5.2	33.2	45.6	56.8	41.5	12.6	26.0	47.9	29.1
	water	8421	65.3	94.0	66.5	51.4	39.6	52.0	65.0	52.1	48.5	69.7
	sed/soil	361	2.8	0.8	0.3	3.0	3.6	6.5	22.4	21.9	3.6	1.2

Table 3. Concentrations of elements ($\mu g\ g^{-1}$) in vascular plants present in DWR field (86-I) on two days during 1986 flood season. Five 1-m^2 quadrats sampled for weeds on each date. (For DWR, see Methods) A = 10 August; S = 23 September.

Taxon	Month	Quadrats present	d. wt (kg ha^{-1})	Na	K	Mg	Ca	Mn	Fe	Zn	N	P
Alternanthera phyloxeroides	A	0	–	–	–	–	–	–	–	–	–	–
	S	3	395.72	7243	79470	5507	10990	195	1012	93.7	19330	2751
Aponogeton	A	3	1.35	35970	48260	6513	8301	599	3159	96.9	31280	2634
	S	0	–	–	–	–	–	–	–	–	–	–
Azolla pinnata	A	5	8.95	13640	16910	5754	7542	333	1508	39.9	44660	1910
	S	0	11.14	13160	19610	5639	7394	347	1534	46.1	42700	2548
Ceratopteris thalictroides	A	4	1.99	2969	54010	4962	12390	905	3789	145.1	27120	3469
	S	1	15.42	3878	86390	5830	14760	1195	9468	2481	39070	3274
Eichhornia crassipes	A	2	28.50	2671	46100	9139	18570	1181	4500	246.4	19270	3446
	S	2	43.02	3496	60570	11060	19130	1098	3815	671	16760	2989
Lemna	A	5	0.67	5618	40720	3999	10060	3000	3146	1115	64430	5833
	S	5	1.37	5143	39910	3627	9948	2968	2945	1142	57270	3769
Limnophilum	A	0	–	–	–	–	–	–	–	–	–	–
	S	3	3.96	4982	27110	7707	18050	765	3617	350.1	22200	3757
Myriophyllum sp.	A	5	2.47	8214	60510	6328	16420	842	4294	177.0	31300	2875
	S	0	–	–	–	–	–	–	–	–	–	–
Najas indica	A	4	0.45	6127	33070	6452	7880	526	2289	96.2	21750	3385
	S	1	10.44	6368	11450	4792	10500	2244	8212	378	30380	2784
Nechamandra	A	5	1.85	6693	61330	5736	13750	613	3267	162.6	23150	3400
	S	2	10.22	3326	70950	11570	28400	749	4035	233	31070	3902
Nymphaea nouchali	A	5	3.07	25040	38660	3686	6922	416	3183	110.4	26670	2221
	S	1	4.42	15070	22070	4059	6738	329	1026	68.3	35510	3272
Pistia stratiotes	A	0	–	–	–	–	–	–	–	–	–	–
	S	2	2.42	11150	43540	9514	26830	1352	5141	565.5	24540	3242
Salvinia cucullata	A	1	0.19	2778	39750	5068	8934	1284	5875	206.5	31530	5303
	S	5	19.93	6085	35420	4582	10930	3436	12370	29065	30450	3347
Utricularia stellaris	A	1	1.40	13100	43510	3932	7992	904	7129	175.6	32750	2582
	S	1	4.18	11780	29850	2976	9495	1410	7378	1102	29370	2842
DWR	A		12830	3573	19670	1573	1669	107	1320	129.7	9613	1693
	S		12900	2613	16650	1329	1497	87.6	943	52.1	7722	2028

Table 4. Changes in mean dry weight of individual DWR tillers and element composition between fractions of the tiller in the three different environments (air, water, soil and/or sediment/soil).

Date	Environment	d. wt	Mean concentration ($\mu g\ g^{-1}$)								
			Na	K	Mg	Ca	Mn	Fe	Zn	N	P
19.6	air (above soil)	0.528	1345	31980	4748	5128	298.1	746.5	88.07	25060	1753
	soil	0.046	6013	7059	2301	2264	89.28	3108	338.5	10860	589.3
	whole tiller	0.574	1723	31440	4550	4896	281.28	937.6	108.3	23910	1658
17.7	air	0.941	283.7	21700	1744	2872	109.48	164.6	30.55	13760	1403
	water	1.386	5796	16410	1541	1605	373.18	1722	71.66	9313	1132
	sed/soil	0.119	2605	5374	1603	1623	111.8	4107	378.8	9816	595.2
	whole tiller	2.446	3520	17910	1622	2093	258.9	1238	70.76	11050	1210
10.8	air	0.9964	91.70	18980	1950	3360	74.03	148.6	26.70	15516	1740
	water	3.118	4873	21740	1424	1088	116.7	976.1	99.92	7358	1796
	sed/soil	0.3574	1784	2338	1757	1971	119.9	8652	787.6	12510	754.8
	whole tiller	4.472	3573	19670	1573	1669	107.4	1320	129.7	9613	1693
23.9	air	1.914	475.2	17790	1998	2672	123.4	410.9	38.72	11960	1894
	water	4.470	3609	17270	1057	963	70.0	967.1	39.60	6014	2092
	sed/soil	0.2029	596.6	1753	1398	1686	194.1	6698	373.3	9532	829.5
	whole tiller	6.767	2613	16650	1329	1497	87.6	943.0	52.14	7722	2028

Distributions of mass and mineral nutrients within the DWR plant

The distribution of tiller weight in each fraction (leaf, stem etc) on the last two sampling days is shown in Table 5. Most of the increase in mass between the two days in the stem, both in and out of the water, and there was a slight decrease in total live leaf tissue (1.44 v 1.20 g). Aquatic roots had doubled in mass on 23 September, and by then exceeded the basal roots.

A parallel study on the distribution of individual elements in different fractions of the tiller (Table 6) showed that the highest concentrations of K, Ca and N were in the laminae. For the 10 August sample, this was particularly so for those laminae above water. None of the tillers collected in the samples had healthy leaves below water, and inspection elsewhere in the field on this date showed that submerged healthy leaves were rare. Basal roots had the highest concentrations of Fe and Zn and, among the underwater fractions, the aquatic roots generally had the highest concentrations of K, Mn, Fe and N. There was little consistent difference between the two dates although the concentrations of some elements, for example Na, K and Mg, were variable. This may be due to losses during harvesting and washing. Decaying leaf sheaths generally had lower concentrations of K and Mg than healthy ones (Table 7); N and P were also frequently lower but the results were more variable. Ca and Mn did not show any obvious trend, whereas Fe and Zn generally increased in concentration. This increase was more marked in the underwater parts of the plant.

Mineral nutrients in the weeds

Because the distribution of weeds was patchy, most species were not found in all five quadrats sampled on each date, so only the mean values for dry weight and concentrations are given in Table 3. *Azolla* and *Lemna* did occur in all ten samples, but, since their density was low, samples for each date were bulked to produce sufficient material for analysis. *Myriophyllum*, *Nechamandra* and *Nymphaea* were found in all quadrats on 10 August, and *Salvinia* on 23 September.

Almost without exception the concentrations of all the elements were higher than those in any part of the DWR (cf Table 1). This was true even if the comparison was made with leafy material before flooding, when the concentrations of most elements in DWR were at their highest. Only where decaying tissue, or aquatic and basal roots were analyzed are comparable concentrations of Fe and Zn found (cf Table 2). The weeds with perhaps the closest similarity were *Nymphaea* and *Azolla* (for K, M, Zn and P). However, it is difficult to make direct comparisons between species, because of their differing life forms (see

Table 5. Comparison of mass (dry weight) of various fractions of tillers at Sonargaon on 10 August and 23 September.

Environment	Fraction	10 Aug		23 Sep	
		x̄	SD	x̄	SD
air	lamina live	0.731	0.0803	0.641	0.418
	decaying	<0.001	–	0.195	0.175
	sheath live	0.146	0.0674	0.387	0.280
	decaying	<0.001	–	0.241	0.153
	stem	0.120	0.0279	0.609	0.378
water	lamina live	0.164	0.132	<0.001	–
	decaying	0.197	–	0.206	0.120
	sheath live	0.408	0.202	0.175	0.0904
	decaying	0.585	0.233	0.608	0.296
	aquatic roots	0.123	0.0292	0.243	0.115
	stem	1.891	0.254	3.026	1.644
sediment/soil	basal roots	0.357	0.245	0.203	0.0927

Table 6. Distribution of dry weight and elements (expressed as %) in DWR between various fractions (stem, roots etc) on 10 August and 23 September.

Environment	fraction	Month	% component									
			d. wt	Na	K	Mg	Ca	Mn	Fe	Zn	N	P
air	lamina live	A	15.47	0.30	16.30	18.51	33.75	10.41	1.74	3.12	28.86	15.17
		S	9.81	0.97	7.94	16.89	33.45	14.49	6.81	10.19	22.53	7.71
	decaying	A	–	–	–	–	–	–	–	–	–	–
		S	2.99	1.71	1.10	3.28	8.26	4.28	2.90	1.98	4.30	1.89
	sheath live	A	3.09	0.15	4.37	3.74	2.00	2.14	0.23	0.61	2.58	3.60
		S	5.92	1.99	7.47	10.24	4.73	9.42	2.09	3.46	6.20	5.55
	decaying	A	–	–	–	–	–	–	–	–	–	–
		S	3.69	0.55	2.46	3.88	4.72	4.30	2.50	3.08	4.33	2.66
	stem	A	2.52	0.14	3.68	2.69	1.45	1.41	0.16	0.48	2.71	3.11
		S	9.32	2.90	13.08	12.66	5.04	10.56	1.48	6.17	11.09	12.26
water	lamina live	A	3.46	0.66	2.50	5.18	5.90	3.67	1.90	0.62	3.00	2.80
		S	–	–	–	–	–	–	–	–	–	–
	decaying	A	4.17	1.00	1.68	5.05	13.13	9.01	3.80	1.15	3.40	2.06
		S	3.16	0.36	0.25	1.88	8.99	3.96	4.74	1.68	2.76	1.17
	sheath live	A	8.65	4.42	9.49	11.87	7.00	12.52	2.70	1.91	6.54	4.83
		S	2.67	2.10	3.07	3.90	2.34	4.41	1.01	2.06	1.61	1.80
	decaying	A	12.39	1.47	0.73	12.20	14.31	20.22	26.78	32.94	8.02	3.17
		S	9.30	1.61	1.02	5.50	10.16	8.66	18.36	16.21	9.03	3.49
	aquatic roots	A	2.61	1.70	0.65	2.97	1.98	5.38	11.78	5.79	3.10	1.64
		S	3.71	1.59	0.73	3.25	3.32	6.27	16.84	4.47	5.96	2.71
	stem	A	40.06	86.10	62.34	29.89	12.65	27.29	6.75	8.81	31.85	60.07
		S	46.33	85.47	62.56	35.32	15.75	26.92	20.00	26.85	28.31	59.52
sediment/	basal roots	A	7.57	4.08	0.96	7.90	7.83	7.95	44.16	44.57	9.94	3.55
soil		0	3.10	0.75	0.32	3.20	3.24	6.73	23.27	23.85	3.88	1.34

Table 7. Comparison of element composition ($\mu g\ g^{-1}$) of live versus dead sheaths, in air or water, on 23 September.

Environment	Fraction	Statistics	Concentration ($\mu\ g^{-1}$)								
			Na	K	Mg	Ca	Mn	Fe	Zn	N	P
air	sheath live	$\bar{x}$	833	21190	2343	1289	145.2	315.6	28.34	7914	1805
		SD	633	1922	412.3	166.6	58.5	176.9	6.70	2526	661.2
	decaying	$\bar{x}$	369	11190	1425	2066	104.3	604.6	40.50	8937	1388
		SD	192	8074	229.8	500.2	27.0	141.8	19.33	2350	691.1
water	sheath live	$\bar{x}$	1949	19310	1978	1414	147.9	338.2	37.51	4583	1300
		SD	848	2029	246.6	212.6	44.7	41.2	8.88	831.9	194.1
	decaying	$\bar{x}$	429	1845	801.3	1765	83.4	1764	84.63	7395	722.0
		SD	293	1551	214.4	158.9	18.1	358.1	112.5	1063	98.7

Whitton *et al.*, 1988c) and the range of habitants (eg totally submerged versus emergent); neither wild rice nor other weed rices were found in the quadrats, which might have been compared with DWR, although these were present elsewhere at Sonargaon. It was found, for example, that depending on the fraction and age of rice plant which was analyzed, a wide range of concentrations of most elements can be found. As with DWR during the flood period, there was little apparent change between the two dates.

Discussion

There were marked differences in the extent to which the DWR plant has accumulated mass (as dry weight) or individual elements by the various sampling dates (Table 1). If comparison is made between the amounts just prior to the flood (19 June) and those towards the end of the first flood peak (10 August), the plant shows the least increase for Mg, Ca and N. Alternatively, it may be considered that the plant has gone further with these three elements towards achieving its final requirement than for the other elements. It will take further study to establish to what extent this is because the plant has a greater requirement for these elements at this stage and to what extent it is a reflection of their greater availability to the plant then.

Whereas N tended to be accumulated early in the season, most of the P accumulation occurred while the plant was flooded and P and Mn were the only two elements whose totals were higher on 23 September than 10 August. The amounts of P provided by the incoming water and the sediments deposited by this water (Whitton *et al.*, 1988a) are much less than required by the plant. Most of the P must come from the soil beneath the newly deposited sediments. The increased availability of P which probably occurs when sediments and parts of the water column become anoxic (Whitton *et al.*, 1988b) may provide the explanation. A key question is whether this comes via the basal roots or via the aquatic roots, but in view of the deterioration of the basal root system later in the flood season, it is suggested that the aquatic roots may become the main site of P uptake. If this is so, the water column has an important role in providing the pathway from the soil to the site of uptake.

Haque (1975) reported that DWR may have two types of nodal (aquatic) root, upper ones and a later set of lower ones that are longer and unbranched. Our own observations at various locations in Bangladesh, including Sonargaon, have shown that these lower roots are often well-developed, though less branched than roots nearer the surface of the water, and frequently stained brown, presumably with Mn and/or Fe. It may be speculated that these roots are adapted especially for the alternating microaerobic and anoxic conditions occurring in this part of the water column and where there may be a surge of P every time the water becomes anoxic. Observations in Bangladesh and Thailand (by B. A. W.) indicate that there are marked differences between DWR at various locations in the extent to which they develop aquatic roots. It would be useful to establish to what extent this feature is genetic or environmental and whether it is correlated with the frequency of anoxic conditions at the sites where the plants are growing.

Although the DWR standing crop expressed as dry weight increased between 10 August and 23 September, the values for most elements, and especially N, decreased. One reason was the lack of healthy submerged leaves on the second day, but this can not be the full cause. The field suffered damage from rats (*Bandicota* spp.) during the period and this may have been another factor, though it is not clear quite how this might have had a selective effect on the various elements. P showed a considerable increase during the period, largely associated with the increased amount of stem above and below the water. However the 6-week period between the first and second floods appears relatively unimportant for the growth and mineral nutrition of the DWR plant. This suggests that if the flood season was shorter, there might not be much impact on DWR biology, although grain formation can not take place sooner because panicle initiation is photosensitive. However grain yield at this location in 1986 was low (B. P. Jupp, pers. comm.), so perhaps the lack of nutrient accumulation during the six weeks was because the plant was growing under unfavourable conditions.

Judging by their biomass, weeds were a relatively minor part of the ecosystem during the flood season, because the inoculum had been kept to a minimum by weeding before the arrival of the water. Nevertheless the fact that their mineral concentration was higher than that of DWR means that they might have some impact on the cycling of nutrients inside the field. N in weeds on

23 September was 10% of that in DWR; however as the DWR had already accumulated about 40% of its N by the time the floodwater had arrived, N accumulated by weeds during the flood period was probably about 16% of that accumulated by DWR over the same period, suggesting that competition with DWR may occur. However the weeds may have a valuable role in trapping nutrients which would otherwise be lost from the field at the end of the flood season. The higher concentrations of nutrients in weeds also emphasizes their importance in fallow fields for the subsequent winter crop after the flood water has gone.

Several detailed studies of the composition of aquatic macrophytes have been reported in the literature (Dykjova, 1973; Cowgill, 1974; Howard-Williams & Junk, 1977) and many on *Eichhornia* (e.g. Parra & Hortenstine, 1974) and it is possible to make a few general comments. The ranges at Sonargaon for the various elements mostly appear comparable to those found in the central Amazonian region by Howard-Williams and Junk. Their list include *Oryza perennis*, a wild species with some resemblance to DWR (a variety of *O. sativa*). Comparison of mean values for Sonargaon DWR on 10 August and 23 September versus *O. perennis* shows (as% dry weight); Na, 0.31 v 0.07; K, 1.73 v 2.02; Mg, 0.14 v 0.10; Ca, 0.15 v 0.15; N, 0.83 v 1.29; P, 0.18 v 0.11. In comparison with the wild grass, DWR has relatively high Na and P and relatively low N. Within DWR these are all features of the stem, emphasizing that production of stem material is a key aspect of the biology of this plant. This suggests that DWR in the deepest waters may have the highest requirements for Na and P, which may explain why Roy (1975) got a clear-cut response to P in fertilizer trials at Habiganj, where the water is deeper and even softer than at Sonargaon (Whitton *et al.*, 1988a). Although there is no evidence that the high Na concentration in the stem is essential, the fact that it is higher here than elsewhere in the plant suggests that it may be so.

Howard-Williams and Junk (1977) regarded species with 3.0% N or more as exceptional and listed five species (of 27 analyzed). Half the 'weed' species at Sonargaon (Table 3) had N contents over 3.0%, which may be a reflection of the less woody nature of plants there associated with the short growing season. However where it is possible to compare species within the same genus, such as *Azolla*, *Ceratopteris*, *Eichhornia*, *Salvinia* and *Utricularia*, N concentrations are again higher in the Sonargaon material for all except *Eichhornia*, where they are similar.

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