벼와 雜草의 乾物生産 및 種子生産 特性에 따른 環境適應 戰略

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Adaptation Strategy in Dry Matter and Seed Production of Rice and Weed Species

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ABSTRACT

An experiment was conducted at the greenhouse of the International Rice Research Institute in 1987 to find out the character of dry matter production, the potential seed production ability and the ecological and physiological strategies to adaptation. For these, two rice cultivars, IR64(lowland rice) and UPLRi-5(upland rice), and seven weed species were used ; *Echinochloa glabrescens* Munro ex Hook. f., *E. crus-galli* ssp. *hispidula* (Retz.) Honda, *E. colona* (L.) Link, *Monochoria vaginalis* (Burm. f.), *Ludwigia octovalvis* Jacq.) Raven, *Fimbristylis miliacea* Vahl. and *Cyperus difformis* L.

Adaptation strategies of weed species varied by species. However, they had efficient seed production strategy through different ways. In general, sedge weed species (*F. miliacea* and *C. difformis*) produced great amount of seeds at the expense of seed size through greater ratooning ability and low relative dry weight for flowering. For broadleaved weed species, greater number of descendants were obtained through high plasticity and low relative dry weight for flowering (*M. vaginalis*) or greater growth ability through effective photosynthetic efficiency (*L. octovalvis*). Grass weed species, on the other hand, produced their seeds through effective growth (net assimilation rate and relative growth rate), high ratooning ability (except *E. crus-galli* ssp. *hispidula*) or low relative dry weight to maximum dry weight for flowering (*E. glabrescens*).

The harvest indices of the weed species were considerably lower than those of rice. *Fimbristylis miliacea* had the greatest ratooning ability followed by *C. difformis*, *E. colona* and *E. glabrescens*. The greatest seed productivity was recorded by *C. difformis* (279,000) and *L. octovalvis* (268,000) while rice produced the least number of seeds (1300-6100). Log seed weight had a negative linear relationship with log seed number ($y=6.30-1.48X$, $R=-0.965^{**}$).

For all species plant plasticity response was not directly correlated with mortality response.

摘 要

1987年 國際 米作硏究所(IRRI)에서 벼와 雜草의 乾物生産 및 種子 生産特性을 調査하여 이들 特性이 環境適應 戰略과의 關係를 究明하기 위해 벼 2品種과 논雜草 7種을 供試하여 試驗하였던 結果를 要約하면 다음과 같다.

環境適應 戰略은 雜草에 따라 다르게 나타났으며, 大體로 種子生産 戰略이 가장 重要한 適應 戰略이었다. 방동산이 科 雜草인 바람하늘직이와 알방동산이는 높은 再生力(Ratooning ability)과 낮

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은 相對開花 乾物重(첫 開花時 乾物重/一生中 最大 乾物重x100)으로 大斷히 많은 種子를 效率的으로 生產하였으며, 廣葉雜草인 물달개비와 여뀌바늘의 경우 높은 造形力(Plasticity)과 낮은 相對開花乾物重(물달개비), 또는 매우 높은 光合成 效率(여뀌바늘)을 通하여 많은 種子를 效率的으로 生產하였고, 禾本科 雜草인 피 種類는 效率的인 生長(純同化率, 相對 生長率)과 높은 Ratooning ability(*Echinochloa glabrescens*, 강피일종 및 *Echinochloa colona*, 돌피 일종) 또는 낮은 相對開花乾物重(*E. glabrescens*)을 通하여 效率的인 種子生產을 하였다.

收穫指數(Harvest index)는 벼에 比해 雜草가 全般的으로 낮았고, 再生力(Ratooning ability)은 바람하늘직이가 가장 높았고, 다음으로는 알방동산이, *E. colona*, *E. glabrescens* 順이였다.

種子生產力은 알방동산이(株當 約279,000個)와 여뀌바늘(268,000個/株)이 가장 높았고, 벼는 가장 낮은 種子生產力을 보였다(1,300~6,100個/株). 그러나 種子 무게는 種子數와는 負의 相關關係를 보였다(對數關係式).

INTRODUCTION

Weeds usually emerge faster than crop plants, absorb the available nutrients earlier, perpetuate their independent growth earlier and thus establish good seedling stand ahead of the crop resulting in suppression of crop growth (Mercado, 1979). A very small advantage to one species during seedling establishment results in a very significant vested right to this species in later competition with other species.

This aspect has not been emphasized in competition studies and thus there is not much information available on this subject. Furthermore, many plant physiologists have focused their research on the crop itself rather than on weed species which have tended to be neglected. In recent years, however, many weed species have gradually been recognized as important research materials due to their efficient adaptative mechanisms and good productivity with high stability. *Echinochloa* species and *Amaranthus* species are examples of this (Wang and Yan, 1984; Tyagi et al, 1985; Saunders and Becker, 1984).

Reproduction allocation which is the proportion of a plant's assimilated resources allocated to reproduction varies from 25-50% for cereal crops to 15-28% for wild annuals (Harper, 1977). Artificial selection has maximized reproduction allocation while natural selection has maximized reproduction allocation while natural selection has generally increased seed number at the expense of seed size. In other words in the wild, fitness may not always be maximized by maximum reproduction allocation because successful reproduction often depends a plant competing successfully with its neighbours before it can produce any seeds. Therefore, in dense, natural populations, it may be advantageous to divert extra resources into roots and leaves.

The potential growth and development of plants are largely determined by carbon metabolism within the plant. Photosynthesis provides the carbon that is incorporated into plants, and respiration makes the fixed chemical energy available for the formation and maintenance of the organs and tissues.

The photosynthetic efficiency which is the ration of the chemical energy captured by a crop to the solar energy received varies with the growth stage, plant organ and plant species. The photosynthetic efficiency usually increases with time until optimum leaf area is reached and is generally greater for C_4 species than for C_3 species (Murata et al, 1968; Rajendrudu et al, 1987). Many lowland rice weed species such as *Echinochloa* species, *Cyperus serotinus* Rottb., *C. iria* L., *Leptochloa chinensis* (L.) Nees. and *Fimbristylis miliacea* (L.) Vahl are C_4 species while rice is a C_3 species (Yamasue et al, 1983; Matsunaka, 1983).

The maximum photosynthetic efficiency reported for rice was 3.7% (Murata et al, 1968) and that for maize was 4.5% (Kanda, 1975) while the maximum achieveable value is 5.3% (Loomis and Williams, 1963).

Few papers are available on growth analysis of weed species in competition studies. Recently, Denvendra et al. (1986) reported the comparative growth pattern of *Echinochloa* species and rice. Similar research has been carried out for wheat (Gautam and Singh, 1983) and for soybean (Hagood et al, 1980).

The experiment was conducted to determine the character of dry matter production, quantify the potential seed production ability and clarify the ecological and physiological strategies to adaptation of rice and seven weed species.

MATERIALS AND METHODS

Experiments were conducted in a greenhouse at the International Rice Research Institute in 1987 using a randomized complete block design with six replications. Details of the species used in this experiment are given in Table 1. Seedlings of these species (4-5 days after germination) were transplanted on June 9 for rice and *Echinochloa* species and June 30 for the other species into plastic pots (30cm in diameter and 35cm in height) and there were three different fertilizer levels, 0, 90 and 180 kg N, P, K ai/ha. Initially three seedlings were transplanted per pot. Upon establishment the seedlings were reduced to one per pot.

Fifty percent of the fertilizer was applied basally and the remainder was applied in three top dressings, 20% at maximum tillering, 20% at panicle initiation, and 10% at flowering. IR64 was used as the reference species for fertilizer application due to variations in growth duration and growth stage among the species.

For growth analysis, plant height, tiller number, leaf area and dry weight were measured at weekly intervals during the entire growth period. For these, twenty plants were selected at random at weekly intervals to determine the average tiller or branch number. From these plants, three that had tiller or branch numbers closest to the mean value of twenty plants were selected for further growth analysis.

All the growth analysis computed both long-term period (average of whole life cycle) and short-term period (the maximum value among 1 week intervals).

CO_2 assimilation by intect leaves in light was measured at the flowering stage of each species using a portable leaf chamber analyser (LCA-2 from Analytical Development Company Ltd. Hoddesdon, Herts, England). There were 10 replicates and the procedures used were those described by the Analytical Development Co. Ltd (1985).

For all the fertilizer levels, the photosynthetic rate of the flag leaf was determined for rice and *Echinochloa* species. The effect of different leaf positions on the photosynthetic rate was measured only at the 180 kg/ha fertilizer level.

Photosynthetic efficiency which is directly

Table 1. Plant species used in the experiments

Species	Family	Photosynthetic pathway	Group	Habitat
Rice				
IR 64	Poaceae	C_3	Grass	Lowland
UPLRi-5	〃	C_3	〃	Upland
Weeds				
Echinochloa glabrescens	〃	C_4	Grass	Lowland
E. crus-galli ssp. *hispidula*	〃	C_4	〃	〃
E. colona	〃	C_4	〃	Upland
Monochoria vaginalis	Pontederiacease	C_3	Broadleaf (Monocot)	Lowland
Ludwigia octovalvis	Onagraceae	C_3	Broadleaf (Dicot)	
Fimbristylis miliacea	Cyperaceae	C_4	Sedge	〃
Cyperus difformis	〃	C_3	〃	〃

related to dry matter production was computed weekly using a heat of combustion value of 3750 cal/g (Yoshida, 1981).

The following equations were used for growth analysis (Harper, 1977; Hunt et al, 1984; Hardwick, 1984; Wilson, 1980; Yoshida, 1981).

Leaf volume density(LVD) =

$$\frac{\text{leaf area per unit area (cm}^2\text{)}}{\text{unit area (cm}^2\text{)} \times \text{plant height (cm)}}$$

Leaf area ratio(LAR) $= \frac{LA}{W}$

Net assimilation rate(NAR) =

$$\frac{W_2 - W_1}{t_2 - t_1} - \frac{\text{In } L_2 - \text{In } L_1}{L_2 - L_1}$$

Relative growth rate(RGR) $= \frac{\text{In } W_2 - \text{In } W_1}{t_2 - t_1}$

Crop growth rate(CGR) $= \frac{W_2 - W_1}{t_2 - t_1}$

Leaf area duration(LAD) $= \frac{(L_2 + L_1)\ (t_2 - t_1)}{2}$

where LA = mean leaf area,

W = mean dry weight,

L_1, L_2 = leaf area index at time t_1 and t_2, and

W_1, W_2 = dry weight at time t_1 and t_2

Harvest index(HI) =

$$\frac{\text{dry weight of grain or fruit}}{\text{total biomass}} \times 100$$

Photosynthetic efficiency($E\mu$) $= \frac{K \times \triangle W}{(S) \times T} \times 10^{-4}$

where K = heat of combustion(3750 cal $\cdot$ g^{-1})

$\triangle W$ = dry matter increase($g \cdot m^{-2}$) between two time intervals

S = average daily incident solar radiation(cal $\cdot$ $cm^{-2} \cdot dry^{-1}$), and

T = number of days

After harvesting the reproductive organs, the remaining plants were clipped at 20cm intervals from ground level to compare the ratooning ability of each species. From the ratoon culture panicles (rice and *Echinochloa* species), fruits, (*L. octovalvis*), racemes (*M. vaginalis*), or corymbs (*F. miliacea* and *C. difformis*) were counted. Uncut plants were included for comparison purposes. Fertilizer-dependent plasticity of 11 agronomic characters was computed using the following equation.

Fertilizer-dependent plasticity =

$$\left(1 - \frac{\text{minimum value across fertilizer levels for a given character}}{\text{maximum value across fertilizer levels for a given character}}\right) \times 100\%$$

Eleven agronomic traits used for fertilizer-dependent plasticity were growth duration (days from seeding to heading or flowering), plant height, biomass, leaf area index, maximum leaf area, number of tillers or branches, number of panicles, corymbs, racemes or fruit, length of panicle or fruit, number of seeds per panicle, raceme, head or spikelet, seed number per plant and seed weight. Measurement of these traits were done at heading (or flowering) or maturity depending on the traits with 5 replicates. All the techniques for measurement were followed by rice (Gomez, 1972) as a reference species.

To compare with fertilizer-dependent plasticity density-dependent plasticity was computed using two density levels, 1 and 22 seedlings per pot (8 cm in diameter and 9cm in height) and used the following equation.

Density-dependent plasticity =

$$\left(1 - \frac{\text{lower value between two densities for a given character}}{\text{higher value between two densities for a given character}}\right) \times 100\%$$

The similarity coefficient (Brower and Zar, 1977), diversity index (Simpson, 1949) and two-dimensional ordination analysis (Newsome and Dix, 1968; Barbour et al., 1980) were computed using 22 agronomic traits or characters which included general growth response, growth analysis, plasticity and seed production strategies. Twentytwo agronomic traits or characters used for these analysis were plant height, growth duration, biomass, leaf area, harvest index, seed weight, seed number per plant, flowering period, relative biomass for flowering, reatooning ability, density-dependent plasticity, fertilizer-dependent plasticity, mortality, crop growth rate, net assimilation rate, relative growth rate, specific leaf area, leaf volume density, leaf area duration, photosynthetic activity, average photosynthetic efficiency and maximum photosynthetic efficiency.

RESULTS AND DISCUSSION

Plant height at maturity increased by an average of 26% for all species as a result of fertilizer application (Table 2). Among the species, *Echinochloa crus-galli* ssp. *hispidula* was tallest having a plant height of 218cm when 180 kg/ha fertilizer was applied. *Ludwigia prostrata* was the next tallest (164cm) while *Monochoria vaginalis* was the shortest (58cm). The plastic response to fertilizer (or fertilizer responsiveness) was greatest for *M. vaginalis* (43%) and least for *E. colona* (4%).

Total biomass was 141% greater at the 180 kg/ha fertilizer level than when no fertilizer was applied (Table 3). IR64 had the greatest biomass followed by *L. octovalvis* and *E. crus-galli* ssp. *hispidula*. Again, *M. vaginalis* had the greatest plasticity (87%) to fertilizer even though it had the least biomass (364 g/m^2). *Echinochloa colona* and *E. glabrescens* had the least plasticity to fertilizer having values of 31 and 41%, respectively.

Table 2. Height of different plant species as affected by fertilizer level

Species	Plant height(cm)			Plasticity
	F0[a]	F90	F180	(%)
RICE				
IR 64	112	125	130	14
UPLRi-5	82	99	111	26
WEEDS				
Echinochloa glabrescens	103	117	118	13
E. crus-galli ssp. hispidula	159	200	218	27
E. colona	125	130	130	4
Monochoria vaginalis	33	49	58	43
Ludwigia octovalvis	117	150	164	29
Cyperus difformis	105	113	115	9
Fimbristylis miliacea	72	85	90	20
Mean	101[b] (100)	119 (118)	126 (125)	21

[a] F ; fertilizer level, kg/ha.

[b] relative value.

Table 3. Biomass of different plant species as affected by fertilizer level

Species	Biomass(g/m^2)			Plasticity
	F0[a]	F90	F180	(%)
RICE				
IR 64	835	999	1445	42
UPLRi-5	175	400	778	78
WEEDS				
Echinochloa glabrescens	240	350	405	41
E. crus-galli ssp. hispidula	308	713	754	59
E. colona	305	437	444	31
Monochoria vaginalis	48	162	364	87
Ludwigia octovalvis	343	855	1147	70
Cyperus difformis	147	255	389	62
Fimbristylis miliacea	147	321	415	65
Mean	283[b] (100)	499 (176)	682 (241)	59

[a] F ; fertilizer level, kg/ha.

[b] relative value.

Table 4. Relative dry weight at flowering compared to maximum dry weight of different plant species as affected by fertilizer level

Species	Relative dry weight(%)			
	F0[a]	F90	F180	Mean
Rice				
IR 64	54	65	66	62
UPLRi-5	97	93	40	77
Weeds				
Echinochloa glabrescens	4	9	15	9
E. crus-galli ssp. *hispidula*	40	21	21	27
E. colona	33	22	22	26
Monochoria vaginalis	4	3	2	3
Ludwigia octovalvis	50	29	35	38
Cyperus difformis	4	4	10	6
Fimbristylis miliacea	9	9	11	10
Mean	33[b] (100)	28 (85)	25 (76)	29

[a] F ; fertilizer level, kg/ha.
[b] relative value.

The weed species produced seeds more efficiently than rice. They produced the first flower when the relative dry weight was less than 40% of their maximum dry weight while rice produced the first flower when the relative dry weight was greater than 60% (Table 4). *Monochoria vaginalis*, *C. difformis*, *F. miliacea* and *E. glabrescens* needed less than 10% of their relative dry weight to produce the first flower while UPLRi-5 required 77%. Greater variation among weed species might be due to the resultant of differential adaptation strategy during the evolutionary process.

Among the rice cultivars, UPLRi-5 had a greater relative dry weight when the first flower was produced at the 0 and 90 kg/ha fertilizer levels. This phenomenon might possibly be related to the selection process under different environmental conditions ; lowland conditions are more stable than upland conditions.

Another important aspect in seed production is the length of the flowering period. *Monochoria vaginalis*, *C. difformis*, *F. miliacea*, *E. colona* and *E. glabrescens* prolonged their seed production more than 4 months which was about twice that for the rice (Fig. 1).

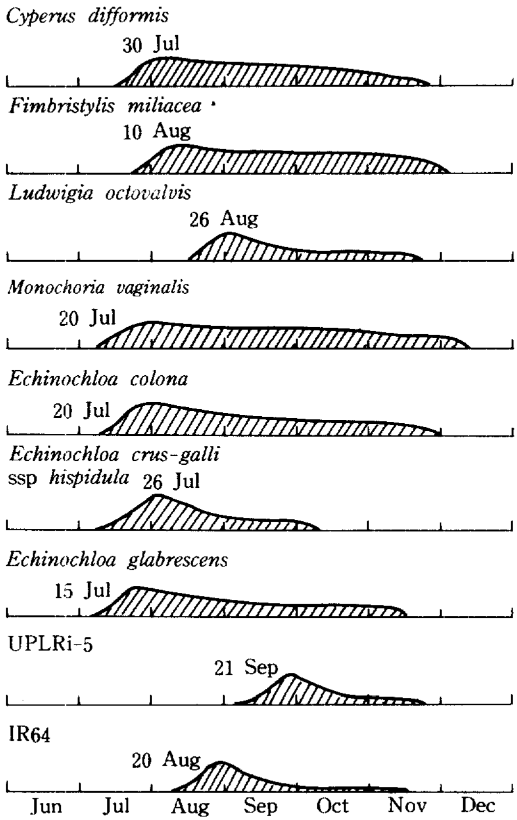

Fig. 1. Duration of seed production for several species.

For the long-term period analysis (whole life span) the leaf area indices were increased significantly with increase in fertilizer levels being greatest responsiveness to *M. vaginalis* followed by UPLRi-5. The leaf area indices of IR64 and *L. octovalvis* were higher (1.2-3.5) than those of the other species. *Monochoria vaginalis* and *E. glabrescens* had the lowest leaf area indices (0.1-1.0) (Table 5). The greatest crop growth rates were recorded by IR64, *L. octovalvis* and *E. crus-galli* ssp. *hispidula* at the fertilizer applied plots showing values of greater into 10 g/m²/day (Table 5). *M. vaginalis* had the lowest value among the species. Crop growth rates also increased with increase in fertilizer levels for all species. The greatest fertilizer responsiveness was recorded by *M. vaginalis* and UPLRi-5 (Table 5).

The net assimilation rates of the *Echinochloa* species were greater than those for the other species. Net assimilation rates for the *Echinochloa* species ranged from 13.35 to 25.38 (g/m²/day) while the values of UPLRi-5, *L. octovalvis* and *C. difformis* which were the lowest were less than 7.32 (Table 5). *Echinochloa* species also had high values for relative growth rate (0.135-0.166 g/g/day) followed by *L. octovalvis*, *F. miliacea* and IR64 while UPLRi-5 and *M. vaginalis* had the lowest values (0.066-0.085 g/g/day), respectively (Table 5).

Ludwigia octovalvis had the highest specific leaf area (502-594 cm²/g) while *C. difformis* and *F. miliacea* had the lowest values of 117 to 189 (cm²/g), respectively (Table 5). Leaf volume density was highest for IR64 (0.0183-0.0311 cm²/cm³) and *L. octovalvis* (0.0136-0.0239) while *E. glabrescens* and *E. crus-galli* ssp. *hispidula* had the lowest values (0.0048-0.0081 cm²/cm³). Leaf volume densities were increased significantly with increase in fertilizer levels for all species. However, fertilizer effect for specific leaf area were insignificant for Rice and *Echinochloa* species or exhibited negative effects for *M. vaginalis*, *L. octovalvis* and *C. difformis* (Table 5). The trends for photosynthetic efficiency were similar to those for leaf area index (Table 5).

For the short-term period analysis (1 week interval) *E. crus-galli* ssp. *hispidula* had the greatest values for crop growth rate (47.3 g/m²/day), net assimilation rate (69.0 g/m²/day), relative growth rate (0.730 g/g/day) and photosynthetic efficiency (5.3%). The other *Echinochloa* species also had high values for net assimilation rate and crop growth rate (Table 6).

IR64 had the highest value for leaf volume density (0.0718 cm²/cm³) because it had the greatest leaf area index (8.3). *Ludwigia octovalvis* had the second greatest values for leaf area index (6.8), crop growth rate (45.5 g/m²/day) and photosynthetic efficiency (4.4%).

The photosynthetic activities of *E. glabrescens* and *E. colona* were significantly higher than those of the other species but they did not differ significantly from each other (Table 7). Among the *Echinochloa* species, *E. crus-galli* ssp. *hispidula* exhibited the least photosynthetic activity but it had the largest flag leaf. However, *E. crus-galli* ssp. *hispidula* had greater photosynthetic efficiency among *Echinochloa* species for both short-term and long-term periods even though this had relatively low photosynthetic activity in flag leaf which was compensated by larger size. These results imply that *E. crus-galli* ssp. *hispidula* had greater potential to produce dry matter and thus adaptation strategy of this species might have different from other two *Echinochloa* species. In general, C_4 species exhibited high photosynthetic activity compared to C_3 species (Table 7) while photosynthetic efficiency was not apparent trend (Tables 5 and 6).

The harvest indices of the weed species were considerably lower than those of rice (Table 8). This might be due to the differential evolutionary process : artificial selection (rice) has maximized reproduction allocation while natural selection (weeds) has increased seed number at the expense of seed size. Among the weed species, *L. octovalvis*, *E. colona* and *M. vaginalis* had the lowest harvest indices having values of 6.2, 9.3 and 10.8%, respectively.

Fimbristylis miliacea had the greatest ratooning ability followed by *C. difformis*, *E. colona* and *E. glabrescens* having values of 138, 58, 45 and 30 (corymbs or panicles per plant), respectively (Table 9). Ratooning ability increased by 74% when 180 kg/ha fertilizer compared to when no

Table 5. Average values for important growth factors throughout the growing season (long term period).

Species and fertilizer level (kg ai/ha)	Leaf area index	Crop growth rate (g/m²/day)	Net assimilation rate (g/m²/day)	Relative growth rate (g/g/day)	Specific leaf area (cm²/g)	Leaf volume density (cm²/cm³)	Leaf area duration (day)	Photosynthetic efficiency (%)	Photosynthetic pathway
*IR*64									
F_0	1.4	9.16	9.04	0.100	311	0.0183	9.9	1.02	
F_{90}	2.3	10.96	9.23	0.102	300	0.0224	16.3	1.22	C_3
F_{180}	3.5	16.09	9.92	0.107	316	0.0311	24.9	1.82	
Mean	2.4	12.07	9.40	0.103	309	0.0239	17.0	1.35	
UPLRi-5									
F_0	0.3	1.71	5.99	0.071	340	0.0039	1.9	0.03	
F_{90}	0.6	3.84	6.12	0.078	329	0.0075	4.7	0.07	C_3
F_{180}	1.2	7.37	6.55	0.085	323	0.0130	8.9	0.29	
Mean	0.7	4.31	6.22	0.078	331	0.0081	5.2	0.13	
Echinochloa glabrescens									
F_0	0.4	3.14	17.11	0.135	329	0.0048	3.0	0.36	
F_{90}	0.5	4.68	16.00	0.140	351	0.0061	4.1	0.54	C_4
F_{180}	0.8	5.25	16.06	0.142	345	0.0075	5.8	0.63	
Mean	0.6	4.36	16.39	0.139	342	0.0061	4.3	0.51	
E. crus-galli ssp. *hispidula*									
F_0	0.5	4.44	19.36	0.157	245	0.0035	3.4	0.49	
F_{90}	1.1	10.26	25.38	0.166	278	0.0067	8.4	1.10	C_4
F_{180}	1.3	11.02	20.32	0.165	276	0.0081	10.0	1.29	
Mean	1.0	8.57	21.68	0.163	277	0.0061	7.3	0.96	
E. colona									
F_0	0.7	4.83	13.35	0.143	354	0.0067	5.1	0.46	
F_{90}	1.0	7.10	14.20	0.137	368	0.0094	7.9	0.74	C_4
F_{180}	1.5	7.39	16.68	0.139	343	0.0135	11.7	0.76	
Mean	1.1	6.44	14.74	0.140	355	0.0099	8.2	0.65	
Monochoria vaginalis									
F_0	0.1	0.78	6.05	0.066	452	0.0044	1.0	0.07	
F_{90}	0.4	2.88	8.08	0.073	366	0.0083	2.9	0.24	C_3
F_{180}	1.0	6.55	10.35	0.079	297	0.0172	7.0	0.49	
Mean	0.5	3.40	8.16	0.073	371	0.0100	3.6	0.27	
Ludwigia octovalvis									
F_0	1.2	5.16	5.33	0.126	594	0.0136	8.6	0.46	
F_{90}	2.4	11.54	6.47	0.141	547	0.0196	17.3	1.12	C_3
F_{180}	3.1	14.45	7.32	0.138	502	0.0239	22.4	1.60	
Mean	2.3	10.38	6.38	0.135	547	0.0190	16.1	1.10	
Cyperus difformis									
F_0	0.5	2.43	4.54	0.094	189	0.0049	4.1	0.27	
F_{90}	1.1	4.05	6.89	0.091	177	0.0097	9.1	0.42	C_3
F_{180}	1.4	6.24	6.66	0.092	168	0.0129	11.3	0.64	
Mean	1.0	4.24	6.03	0.092	178	0.0092	8.2	0.44	
Fimbristylis miliacea									
F_0	0.5	2.36	8.42	0.118	117	0.0062	4.0	0.27	
F_{90}	0.9	5.54	9.07	0.129	134	0.0107	7.4	0.54	C_4
F_{180}	1.5	6.55	7.74	0.101	143	0.0170	11.9	0.67	
Mean	1.0	4.82	8.41	0.116	131	0.0113	7.8	0.49	

* Time interval : 7 days.

Table 6. Maximum values for important growth factors during maximum short term period(7 days).

Species and fertilizer level (kg ai/ha)	Leaf area index	Crop growth rate (g/m²/day)	Net assimilation rate (g/m²/day)	Relative growth rate (g/g/day)	Specific leaf area (cm²/g)	Leaf volume density (cm²/cm³)	Leaf area duration (day)	Photosynthetic efficiency (%)	Photosynthetic pathway
IR 64									
F_0	3.0	27.7	23.0	0.304	656	0.0291	20.9	2.6	
F_{90}	5.7	33.5	23.6	0.312	639	0.0499	38.6	2.7	C_3
F_{180}	8.3	36.5	24.9	0.335	745	0.0718	54.9	3.6	
Mean	5.7	32.6	23.8	0.317	680	0.0503	38.1	3.0	
UPLRi-5									
F_0	0.8	7.0	14.4	0.244	776	0.0109	5.1	0.1	
F_{90}	1.6	10.7	14.7	0.257	755	0.0179	10.4	0.1	C_3
F_{180}	3.1	17.2	14.5	0.231	700	0.0328	21.4	1.9	
Mean	1.8	11.6	14.5	0.244	744	0.0205	12.3	0.7	
Echinochloa glabrescens									
F_0	1.0	9.5	42.0	0.329	544	0.0096	7.7	1.0	
F_{90}	1.3	16.0	44.3	0.421	505	0.0119	8.1	1.3	C_4
F_{180}	1.5	18.8	54.5	0.535	508	0.0137	10.8	2.1	
Mean	1.3	14.8	46.9	0.428	519	0.0117	8.9	1.5	
E. crus-galli ssp. *hispidula*									
F_z	1.1	20.2	47.1	0.517	356	0.0088	7.5	2.3	
F_{90}	2.7	33.9	75.3	0.641	444	0.0157	17.4	3.8	C_4
F_{180}	3.0	47.3	69.0	0.730	390	0.0182	18.2	5.3	
Mean	2.3	33.8	63.8	0.629	397	0.0142	14.4	3.8	
E. colona									
F_0	1.8	14.9	31.1	0.350	495	0.0142	11.6	1.4	
F_{90}	2.5	41.7	43.2	0.459	529	0.0193	16.4	3.7	C_4
F_{180}	3.4	40.2	78.4	0.510	527	0.0265	23.3	4.3	
Mean	2.6	32.3	50.9	0.440	517	0.0200	17.1	3.1	
Monochoria vaginalis									
F_0	0.2	2.1	13.7	0.159	689	0.0073	1.6	0.2	
F_{90}	0.7	88.4	14.5	0.182	576	0.0136	4.6	0.6	C_3
F_{180}	2.3	31.2	26.4	0.160	373	0.0393	13.8	2.0	
Mean	1.1	13.9	18.2	0.167	546	0.0201	6.7	0.9	
Ludwigia octovalvis									
F_0	3.6	16.4	14.5	0.215	860	0.0306	21.9	1.3	
F_{90}	5.6	36.1	10.5	0.271	835	0.0375	35.6	3.7	C_3
F_{180}	6.8	45.5	16.3	0.368	1076	0.0413	45.2	4.4	
Mean	5.3	32.7	13.8	0.285	924	0.0365	34.2	3.1	
Cyperus difformis									
F_0	0.9	9.0	8.1	0.209	345	0.0086	6.13	1.0	
F_{90}	2.3	14.2	12.2	0.191	330	0.0209	15.86	1.0	C_3
F_{180}	2.7	24.9	18.4	0.306	269	0.0234	17.78	1.8	
Mean	2.0	16.0	12.9	0.235	315	0.0176	13.26	1.3	
Fimbristylis miliacea									
F_0	0.9	8.1	16.0	0.372	256	0.0104	5.99	0.9	
F_{90}	1.6	14.9	15.4	0.445	264	0.0188	11.38	1.1	C_4
F_{180}	2.6	30.7	17.4	0.243	281	0.0298	18.38	1.7	
Mean	1.7	17.9	16.3	0.353	267	0.0197	11.92	1.2	

* Time interval : 7 days.

Table 7. Photosynthetic activity of different plant species at the flowering stage when 180 kg/ha fertilizer was applied.

Species	Photosynthesis (CO_2 mg/dm²/hr)	Flag leaf size (cm²)	Photosynthetic pathway
RICE			
IR64	23.0 b	26.34 a	C_3
UPLRi-5	25.1 b	26.37 a	C_3
WEEDS			
Echinochloa glabrescens	33.0 a	14.96 d	C_4
E. crus-galli ssp. *hispidula*	26.3 b	21.39 b	C_4
E. colona	35.8 a	17.47 c	C_4
Monochoria vaginalis	22.5 b	-	C_3
Ludwigia octovalvis	25.0 b	-	C_3

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

Table 8. Harvest index of different plant species as affected by fertilizer level

Species	Harvest index (%)			Mean
	F0[a]	F90	F180	
RICE				
IR 64	48.9	46.0	48.0	47.6
UPLRi-5	21.9	20.3	20.7	21.0
WEEDS				
Echinochloa glabrescens	17.1	17.3	16.6	17.0
E. crus-galli ssp. *hispidula*	25.1	19.3	7.7	17.4
E. colona	10.1	9.1	8.7	9.3
Monochoria vaginalis	12.0	10.5	9.8	10.8
Ludwigia octovalvis	4.6	5.7	8.4	6.2
Cyperus difformis	10.1	14.3	13.0	12.5
Fimbristylis miliacea	9.0	14.8	17.0	13.6
Mean	17.6[b] (100)	17.5 (99)	16.7 (95)	17.3

[a] F ; fertilizer level, kg/ha.
[b] relative value.

Table 9. Ratooning ability of different plant species as affected by fertilizer level

Species	Number of panicles, racemes, corymbs or fruits			Mean
	F0[a]	F90	F180	
RICE				
IR 64	11	14	14	13
UPLRi-5	3	6	10	6
WEEDS				
Echinochloa glabrescens	24	23	42	30
E. crus-galli ssp. *hispidula*	9	15	27	17
E. colona	41	44	50	45
Monochoria vaginalis	20	25	26	24
Ludwigia octovalvis	0	0	0	0
Cyperus difformis	49	55	70	58
Fimbristylis miliacea	89	144	182	138
Mean	27[b] (100)	36 (133)	47 (174)	37

[a] F ; fertilizer level, kg/ha.
[b] relative value.

Table 10. Seed productivity of different plant species as affected by fertilizer level

Species	Seed number per plant			Plasticity
	F0[a]	F90	F180	(%)
RICE				
IR 64	2,200	3,400	6,100	64
UPLRi-5	200	900	1,300	85
WEEDS				
Echinochloa glabrescens	2,900	7,000	11,300	74
E. crus-galli ssp. *hispidula*	2,100	7,100	16,600	87
E. colona	4,900	11,100	15,100	68
Monochoria vaginalis	12,400	38,700	119,000	90
Ludwigia octovalvis	94,400	184,800	268,000	65
Cyperus difformis	100,100	179,800	278,500	64
Fimbristylis miliacea	50,500	114,100	146,700	66
Mean	29,967[b] (100)	60,767 (203)	95,844 (320)	74

[a] F ; fertilizer level, kg/ha.
[b] relative value.

fertilizer was applied.

The seed productivity of the weed species was greater than for the rice crop. In general, sedge species (*C. difformis* and *F. miliacea*) produced the greatest number of seeds for both zero and highest fertilizer levels followed by broad leaved weeds (*M. vaginalis* and *L. octovalvis*) while grass species (rice and *Echinochloa* species) produced the least number of seeds (Table 10). The greatest seed productivity was recorded for *C. difformis* and *L. octovalvis* having values of 278,500 and 268,000 when 180 kg/ha fertilizer was applied while rice produced the least number of seeds (1,300-6,100) (Table 10). Seed number increased drastically by 320% as the amount of fertilizer applied increased from 0 to 180 kg/ha.

Log seed weight had a negative linear relationship with log seed number (Fig 2). Seed weight responded little to fertilizer addition. *Ludwigia octovalvis* had the lowest seed weight while rice had the highest (Table 11).

The summed plastic response to fertilizer of all traits was greatest with *M. vaginalis* (558%) followed by UPLRi-5 (526%) and *E. crus-galli* spp. *hispidula* (469%) and least with *E. glabrescens* (285%) (Fig 3). In general, biomass, leaf area index, seed number per plant and tiller or branch number exhibited the greatest plasticity while growth duration and seed weight exhibited the least plasticity.

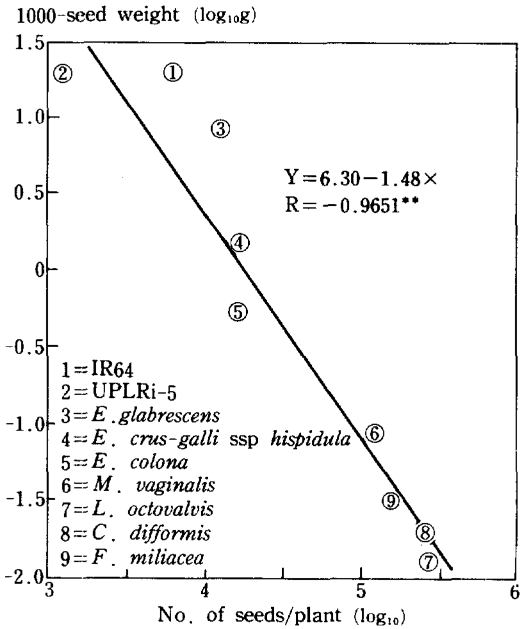

Fig. 2. Relationship between seed weight(log) and seed number per plant(log) for different plant species.

Cyperus difformis had the greatest dissimilarity coefficient for both fertilizer levels while *E. colona* had the least (Table 12). The greatest dissimilarity coefficient was between UPLRi-5 and *C. difformis* (77% at 180 kg/ha and 82% at 0 kg/ha) while the least was between *E. glabrescens* and *E. colona* (10-19%).

Table 11. Seed weight of different plant species as affected by fertilizer level

Species	1000-Seed weight (g)				Plasticity (%)	Mean number of seeds per gram
	F0[a]	F90	F180	Mean		
RICE						
IR 64	21.8	21.9	22.3	22.0	2	45
UPLRi-5	21.7	21.9	22.5	22.0	4	45
WEEDS						
Echinochloa glabrescens	1.93	1.94	1.92	1.93	1	518
E. crus-galli ssp. *hispidula*	1.39	1.41	1.38	1.39	2	719
E. colona	0.47	0.49	0.49	0.48	4	2,083
Monochoria vaginalis	0.0895	0.0897	0.0896	0.0896	0.2	11,161
Ludwigia octovalvis	0.0126	0.0127	0.0127	0.0127	0.7	78,740
Cyperus difformis	0.0212	0.0215	0.0215	0.0214	1.4	46,729
Fimbristylis miliacea	0.0289	0.0291	0.0289	0.0290	0.7	34,483
Mean	5.27[b] (100)	5.310 (101)	5.416 (103)	5.328	1.8	19,391

[a] F ; fertilizer level, kg/ha
[b] relative value.

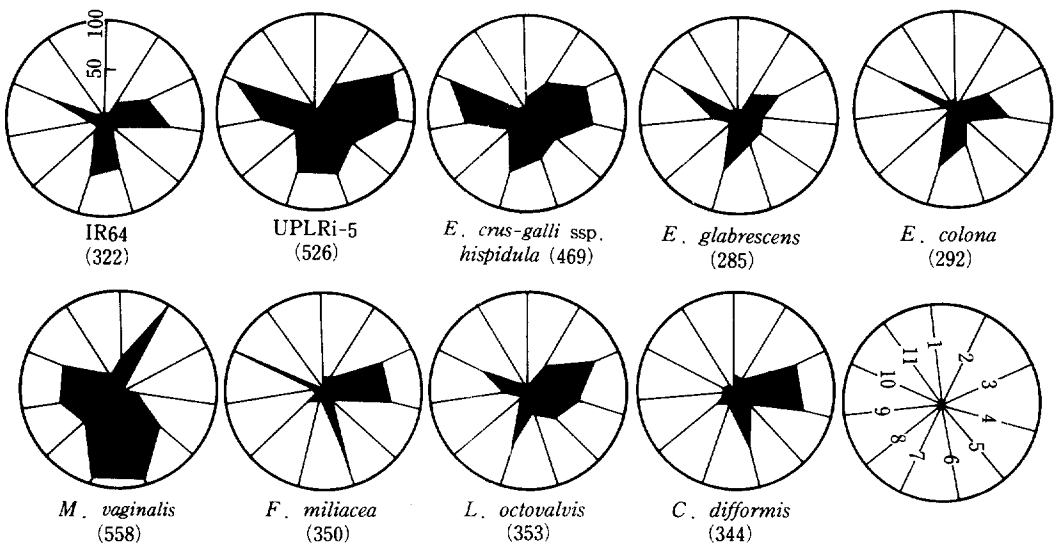

Fig. 3. Fertilizer-dependent plasticity of 11 agronomic traits for each species. (The sum of plasticity is given in parenthesis)

1=growth duration
2=plant height
3=biomass
4=LAI
5=maximum leaf area
6=tiller number
7=panicle number
8=panicle length
9=seed no./panicle
10=seed no./plant
11=seed weight

Several implications could be concluded based on the above results discussed so far. Weed species generally evolved toward effective production of their descendants in terms of the number not by the weight. During the evolutionary process weed species might developed their strategy differently to arrive their final target, increase in descendants. These strategies will be high plasticity (*M. vaginalis*), high photosynthetic efficiency and high growth rate (*Echinochloa*

Table 12. Dissimilarity coefficients between species at two fertilizer levels.

Species	IR64	UPLRi-5	*Echinochloa glabrescens*	*E. crus-galli* ssp. *hispidula*	*E. colona*	*Monochoria vaginalis*	*Ludwigia octovalvis*	*Cyperus difformis*	*Fimbristylis miliacea*	Total
IR 64		31	33	28	36	53	62	77	65	385
UPLRi-5	24		38	36	47	53	70	82	72	429
Echinochloa glabrescens	35	31		18	19	35	64	68	53	328
E. crus-galli ssp *hispidula*	29	34	21	*F0*	22	42	61	75	57	339
E. colona	32	36	10	16 *F180*		26	58	63	43	314
Monochoria vaginalis	55	57	45	43	42		60	64	45	378
Ludwigia octovalvis	59	68	65	58	60	36		12	34	421
Cyperus difformis	75	77	65	68	62	35	12		28	496
Fimbristylis miliacea	65	69	56	57	51	23	37	29		397
Total	374	396	328	326	309	336	395	423	387	

* F ; fertilizer level (kg/ha).

species and *L. octovalvis*), high ratooning ability (*F. miliacea* and *C. difformis*) and combined strategies (*E. glabrescens* and *E. colona*). The difference between two rice cultivars might be due to different growing environment : IR64 was grown under more stable condition (flooded) than UPLRi-5 (upland) and thus growth rate and fertilizer utilization will differ from each other.

In the ordination analysis, there was a pattern of relatedness in terms of species order and the location of each species (Fig 4). This was justified by the relationship between the direct distance between two species and the dissimilarity coefficient given in Fig 5. Theoretically the dissimilarity between two species become greater when the direct distance between these species increased under statistical significance. The order of the species was exactly the same for both fertilizer levels. However, the location of *M. vaginalis* moved towards the upper left side when the fertilizer level increased from 0 to 180 kg/ha. This implies that *M. vaginalis* had the greatest responsiveness to fertilizer.

The locations of all the species in the diagram did not overlap which implies that each species has its own peculiar strategy to survive. In other words, the degree of difference in survival strategy will become greater when the direct distance between two species becomes greater. However, this analysis only helps us to quickly determine trends and indicates how much a particular species differs from another species. Therefore, the original data needed to be examined to find out the particular characters which determine the species location.

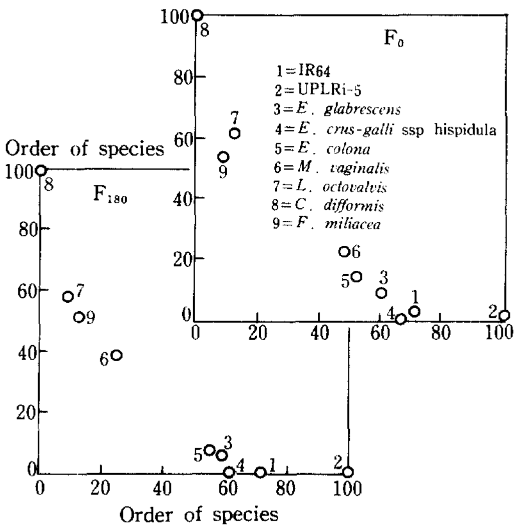

Fig. 4. Distribution of species based on 22 agronomic characters using a two-dimensional ordination diagram. The order of species refers to their positions along the X-and Y-axes. (F ; fertilizer level, kg/ha).

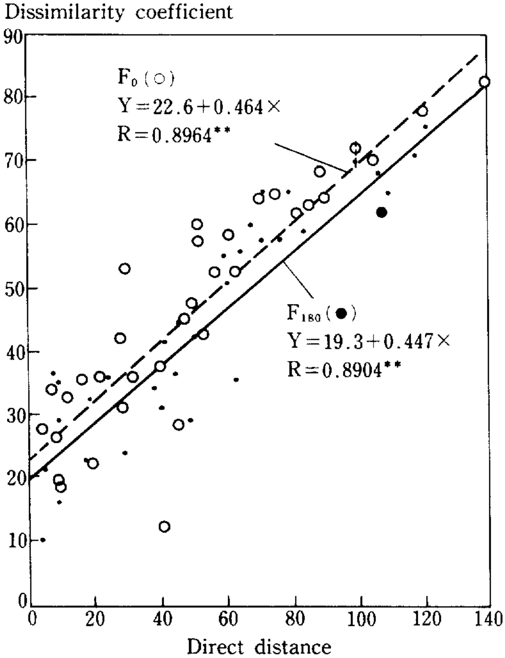

Fig. 5. Relationship between direct distance and the dissimilarity coefficients for two species for two fertilizer levels. (F; fertilizer level, kg/ha).

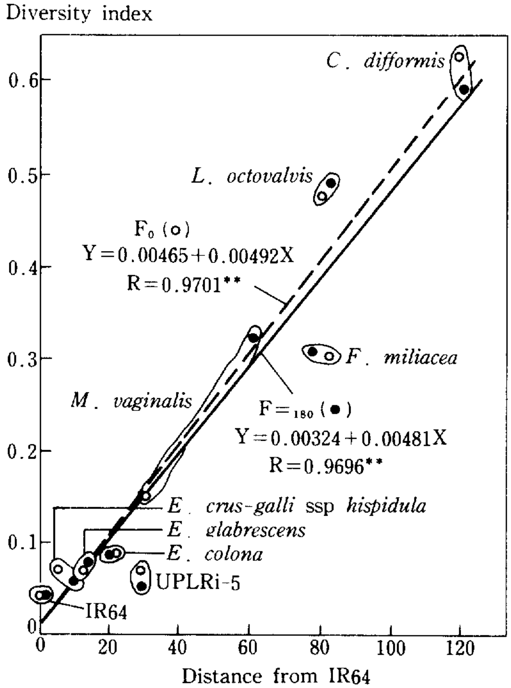

Fig. 6. Relationship between direct distance from IR64 and diversity index for two fertilizer levels. (F; fertilizer level, kg/ha).

There was also a good positive correlation between direct distance from IR64 (reference species) and the diversity index for 22 traits. The diversity index increased when the distance from IR64 increased (Fig 6). Diversity index indicates the degree of concentration of dominance: diversity index of 1 imply that only one species is grown in a particular community while lower diversity value indicates either more species are coexist or dominance was shared by several species with similar degree. Based on this idea it can be concluded that when the distance from IR64 becomes greater fewer characters or particular characters are important in the survival strategy of the species. This relationship also helps us to imagine quickly how many characters are related in their survival strategies even though the exact number of characters could not determined.

Figures 7 and 8 indicate the relative importance of 22 morphological, physiological and ecological characters against IR64 (reference species) at the 0 and 180 kg/ha fertilizer levels, respectively. As the zero fertilizer level compared with the reference species, UPLRi-5 had slightly different strategies in terms of growth duration, flowering period and fertilizer plasticity. *Echinochloa* species, on the other hand, had characters of ratooning ability, flowering period, seed number, net assimilation rate, relative growth rate, mortality and photosynthetic activity which were different from those of IR64 even though there were some variations within the *Echinochloa* species. For *M. vaginalis* seed number, mortality and flowering period were the important characters for survival while for *F. miliacea* seed number and ratooning ability were imporant. For *L. octovalvis* and *C. difformis* seed number was the most important character for survival. A similar trend was recorded at the 180 kg/ha fertilizer level.

For all species plant plasticity response was not correlated with mortality response (Fig 9).

For the density regime, the plant species could

Table 13. Summary table of adaptation strategy of rice and weed species

Character	IR64	UPLRi-5	*Echinochloa glabrescens*	*Echinochloa crus-galli* ssp. *hispidula*	*Echinochloa colona*	*Monochoria vaginalis*	*Ludwigia octovalvis*	*Cyperus difformis*	*Fimbristylis miliacea*
A. *Germination* and *Seedling Establishment*									
. Dormancy (day)	absent	absent	present (40-50)	present (60-70)	absent	absent	present (10-20)	absent	absent
. Germinability (%)	> 95	> 95	60-70	20-40	65-75	40-50	60-70	65-75	60-70
. Morphology of the first leaf	leaf blade and chlorophyll absent		leaf blade like expanded leaf present with chlorophyll			-	-	-	-
B. *Vegetative Growth*									
. Relative root weight during frist 30 days (%)	18	13	33	25	30	15	13	9	10
. Crop growth rate (g/m²/day)									
-Mean (whole season)	12.1	4.3	4.4	8.6	6.4	3.4	10.4	4.2	4.8
-Maximum (one week)	36.5	17.2	18.8	47.3	40.2	31.2	45.5	24.9	30.7
. Net assimilation rate (g/m²/day)									
-Mean	9.4	6.2	16.4	21.7	14.7	8.2	6.4	6.0	8.4
-Maximum (one week)	24.9	14.5	54.5	69.0	78.4	26.4	16.3	18.4	17.4
. Relative growth rate (g/g/day)									
-Mean	0.103	0.078	0.139	0.163	0.140	0.073	0.135	0.092	0.116
-Maximum	0.335	0.231	0.535	0.730	0.510	0.160	0.368	0.306	0.243
. Photosynthetic efficiency (%)									
-Mean	1.35	0.13	0.51	0.96	0.65	0.27	1.10	0.44	0.49
-Maximum	3.6	1.9	2.1	5.3	4.3	2.0	4.4	1.8	1.7
C. *Reproductive growth*									
. Reduction of reproductive organ bearing probability due to									
-Density stress	24	48	52	87	49	93	50	40	54
-Fertilizer stress	13	76	34	78	27	11	26	53	69
. Productivity of secondary and tertiary panicle (no./plant)	9	12	17	11	23	-	-	-	-
. Relative dry weight to produce the first flower (%)	62	77	9	27	26	3	38	6	10
. Harvest index (%)	47.6	21.0	17.0	17.4	9.3	10.8	6.2	12.5	13.6
. Ratooning ability (no./plant)	13	6	30	17	45	24	0	58	138
. Seed producing duration (month)	2.7	2.3	4.5	3.0	4.7	5.0	3.2	4.6	4.5
. Uniformity of the seed maturing within panicle or fruit	relatively uniform	uneven	extremely uneven	extremely uneven	extremely uneven	extremely uneven	extremely uneven	uneven	uneven
. Seed productivity (no./plant)	6,100	1,300	11,300	16,600	15,100	119,000	268,000	278,000	146,700
D. *Mortality* and *Plasticity*									
. Mortality (%)									
-Density	24	3	6	41	11	54	40	35	48
-Fertilizer	40	3	10	25	28	3	5	8	4
. Plasticity (%)									
-Density (10traits)	55	57	58	58	59	51	57	45	41
-Fertilizer (11traits)	29	48	26	43	27	51	32	31	32
E. Total Dissimilarity with IR64 (%)	0	24	35	29	32	55	59	75	65

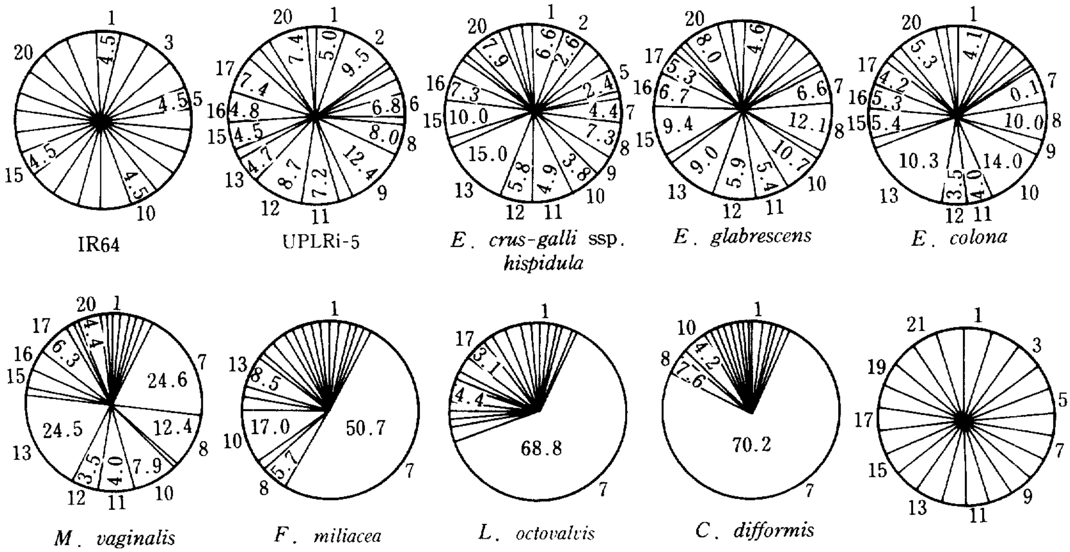

Fig. 7. Comparison of the relative importance of 22 morphological, physiological and ecological characters against IR64 at the zero fertilizer level

1=plant height
2=growth duration
3=biomass
4=leaf area
5=harvest index
6=seed weight
7=seed number
8=flowering period
9=relative biomass for flowering
10=ratooning ability
11=density-dependent plasticity
12=fertilizer-dependent plasticity
13=mortality
14=crop growth rate
15=net assimilation rate
16=relative growth rate
17=specific leaf area
18=leaf volume density
19=leaf area duration
20=photosynthetic activity
21=average photosynthetic efficiency
22=maximum photosynthetic efficiency

be divided into three groups; UPLRi-5, *E. colona*, and *E. glabrescens* which had high plasticity with low mortality, IR64 which had high plasticity with intermediate mortality and *E. crus-galli* ssp. *hispidula*, *L. octovalvis*, *C. difformis*, *F. miliacea* and *M. vaginalis* which exhibited high plasticity with high mortality.

For the fertilizer regime, the plant species could be also categorized into three groups; *L. octovalvis*, *F. miliacea*, *C. difformis* and *E. glabrescens* that had intermediate plasticity response with low mortality, *M. vaginalis* and UPLRi-5 that had high plasticity with low mortality and *E. crus-galli* ssp. *hispidula*, *E. colona* and IR64 which had intermediate to high plasticity with high mortality.

The research results can not be generalized by one or few sentences for the adaptation strategies of the species. The adaptation strategy is rather diverse and no two species has exact same strategy. However, weed species had a tendency of greater number of seed production through effective but various ways. In general, sedge weed species (*F. miliacea* and *C. difformis*) produced greater number of seeds at the expense of seed size through greater ratooning ability and low relative dry weight to maximum dry weight for flowering. Broadleaved weed species (*M. vaginalis* and *L. octovalvis*) obtained their greater number of descendants through high plasticity and low relative dry weight for flowering (*M. vaginalis*) or greater growth rate through effective photosynthetic efficiency (*L. octovalvis*). Grass weed species (*Echinochloa* species), on the other hand, achieved their final goal through effective growth (NAR, RGR), high ratooning ability (except *E. crus-galli* ssp. *hispidula*) or low relative dry weight for flowering (*E. glabrescens*). The difference between two rice cultivars was mainly due to different habitat: IR64 (lowland

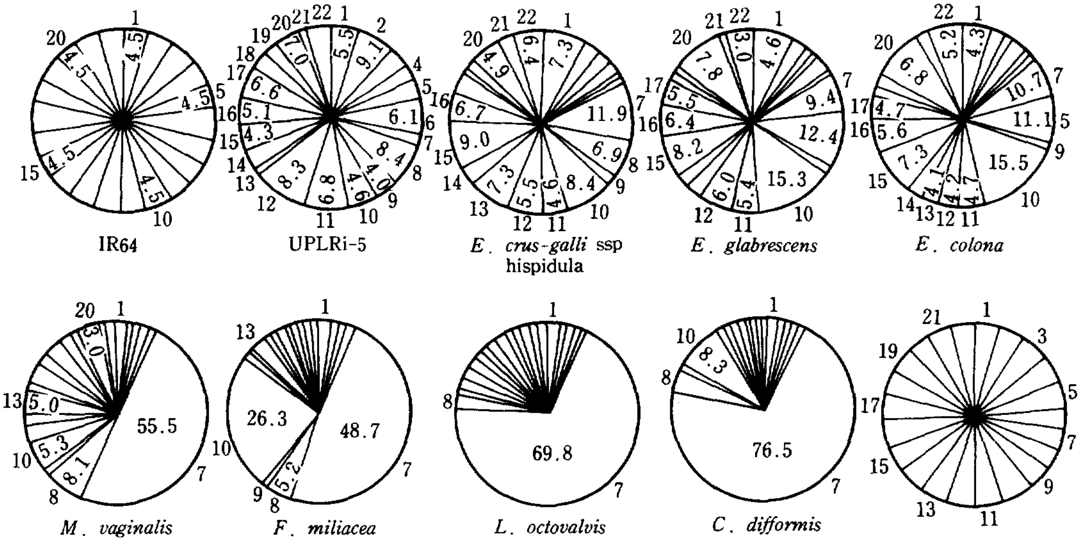

Fig. 8. Comparision of the relative importance of 22 morphological, physiological and ecological characters against IR64 at the 180kg/ha fertilizer level.

1=plant height	9=relative biomass for flowering	17=specific leaf area
2=growth duration	10=ratooning ability	18=leaf volume density
3=biomass	11=density-dependent plasticity	19=leaf area duration
4=leaf area	12=fertilizer-dependent plasticity	20=photosynthetic activity
5=harvest index	13=mortality	21=average photosynthetic efficiency
6=seed weight	14=crop growth rate	22=maximum photosynthetic efficiency
7=seed number	15=net assimilation rate	
8=flowering period	16=relative growth rate	

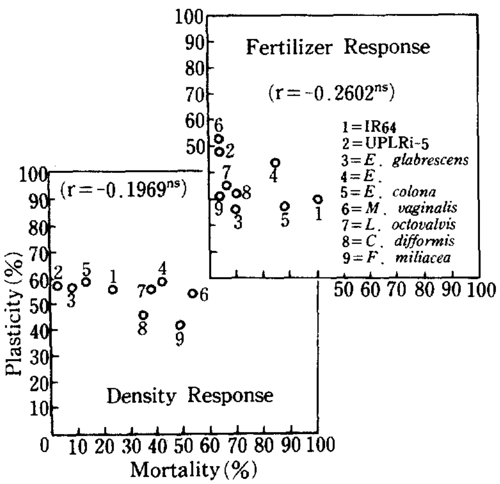

Fig. 9. Relationship between mortality response and plasticity response as affected by density and fertilizer regimes(Average of three replications).

type) was grown under flooded condition while this for UPLRi-5 was upland condition and thus the growth rate, fertilizer utilization and some other growth factors will be differed from each other.

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