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Influence of the Root System on Grain Yield and Related Characters in Rainfed Lowland Rice (*Oryza sativa* L.)

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Abstract: In this study canonical correlation analysis has been used in order to better understand the relationship between and among root morphological characters and yield components, under non-stress and stress conditions in rainfed lowland rice. This study revealed that maximum root length was the root morphological character that had the largest effect on plant height, panicle length and panicle number under non-stress conditions. Under low-moisture stress, root volume was also important in addition to maximum root length. *In toto*, the results of this study has shown that maximum root length and root: shoot dry weight are the characters of choice for improving grain yield under well-irrigated conditions, while maximum root length and root volume are a better combination under low moisture stress conditions.

Key words: Canonical correlation, drought resistance, rice-root traits, yield components

INTRODUCTION

Drought has been recognized as the primary constraint limiting the grain yield level of upland and rainfed lowland rice (Toorchi *et al*., 2002). The complex inheritance of drought resistance, encouraged breeders to adopt alternative strategies for improving stress resistance (Ludlow and Muchow, 1990). Fukai and Cooper (1995) believed that under low-moisture stress, traits that help the plant gain access to additional reserves were more important than traits associated with reducing moisture losses. Among the several factors contributing to enhanced drought resistance, root characters are believed to be vital components in the mechanisms of dehydration postponement since they contribute to regulation of plant growth, extraction of water and nutrients from deeper unexplored soil layers (Price *et al*., 1997; Thanh *et al*., 1999). Plants with a large root system could thus maintain a high rate of water uptake from the soil when faced with a progressively depleted water soil profile and could therefore maintain higher leaf water potential (Hirasawa, 1995). This implies that exist a strong associations between root morphological characters and yield components. The complexities of these interrelationships have not been unfolded so far. Little research has been carried out, especially in rainfed lowlands, to understand underlying root traits responsible for drought resistance.

Studies on the relationship between root characters and yield components under field conditions are limited. Also studies intending to assess the influence of components of drought resistance on grain yield have produced contrasting results. Several studies have documented very small or no influence of the primary or secondary components of drought resistance, including the root system, on grain yield and its attributes. While the effects under well-watered conditions were small, they were minuscule under moisture stress conditions (Blum *et al*., 1999; Zhang *et al*., 1999). Sarkarung and Pantuwan (1999) reported a minor role of rooting depth and root thickness in determining drought tolerance of rice varieties under rainfed lowland condition, in comparison to well-drained upland fields and suggested further research in order to determine the traits responsible for drought tolerance. In experiments simulating rainfed lowland conditions using pot-plants, genotypes differed in patterns of water extraction and these patterns were related to changes in root distribution under drought (Wade, 1999). Enhanced drought resistance in crop plants is gaining importance as more food is to be produced with limited land resources and dwindling water resources.

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The investigations that have been reported on drought tolerance during the past two decades does not gives clear picture of the association between root morphological characters and grain yield components. This is mainly because most of the studies have employed simple correlation coefficients to analyze the relationships. Simple correlations are inadequate to address this complex issue since root and yield components are neither independent from each other nor among themselves. Therefore one has to consider the correlation between these two sets of variables simultaneously. Canonical correlation, a well-known multivariate technique, has been developed for situations where one would like to measure the relationship between two sets of interrelated variables. Prior to the advent of computers, the calculations in this technique were too complex (Gittins, 1985). We have adopted canonical correlation analysis to study the strength of association between root morphological characters and grain yield components under low-moisture stress and non-stress conditions. Further, we intend to find the root morphological characters that have the largest influence on grain yield and its components under the two situations. Choice of the most important root characters based on their magnitude of influence on grain yield will help in developing marker assisted-selection strategies.

MATERIALS AND METHODS

Plant materials and phenotyping methodology: Twenty-five entries including ten crosses, their parents and four checks (Moroberekan, IR20, CO30 and Jaya), constituted the plant material for this study. The crosses were conducted by crossing Azucena and nine doubled haploid (DH) lines from IR64/Azucena mapping population with IR64 as the common male parent.

The experiment was carried out at Hebbal campus of the University of Agricultural Sciences, Bangalore, India in summer 1999. Twenty-five genotypes were grown in light-gray polyvinyl chloride cylinders (100 cm long and 18 cm diameter) filled with clayish soil and farmyard manure as described in an earlier study (Shashidhar *et al*., 1999), in RCBD with 4 replications each under well watered (WW) and water stress (WS) conditions. In the WW experiment, plants were watered daily throughout the cropping period, while in the WS experiment, low moisture stress was created from 65 days after sowing (DAS) to 80 DAS by withholding irrigation and preventing rainwater using a rain out shelter. Sampling for root characters, as well as yield components, in both WW and WS conditions was done at maturity as described below.

Cylinders with soil and plants were thoroughly soaked in water over-night and prepared for sampling the next day. Sampling was done with care to retain roots, root hairs and branches. Observations on seven root morphological characters viz., Maximum Root Length (MRL) in cm, Number of Roots (RN), Root Dry Weight (RDW) in g, root: Shoot Dry Weight Ratio (RDW/ SDW), Root Volume (RV) in cc, Root Thickness (RT) in mm and Root: Shoot Length Ratio (MRL/PH) were recorded or computed. Roots about three centimeters below the crown region were used to study thickness. Root thickness was measured using a standardized ocular micrometer at 100X magnification using a microscope. Grain yield per plant (GY) in g, Panicle Length (PL) in cm, Panicle Number (PN), Tiller Number (TN), 200 Seed Weight (SW) in g, Plant Height (PH) in cm, Days to 50% Flowering (DF), chaffiness (CH) and Harvest Index (HI) in percent were recorded/computed as yield related characters.

Statistical analysis: The data based on mean over replications were subjected to simple and canonical correlation analysis using PROC CORR and PROC CANCORR procedure in the SAS program (SAS Institute, 1998). Root morphological characters and yield related characters were considered as independent (X) and dependent (Y) sets of variables, respectively. An overall test for statistical significance of all the seven possible canonical correlations from zero was performed using Wilk's Lambda (Gittins, 1985). The Wilk's Lambda (Λ) was computed using the formula

$$\Lambda = \prod_{i=1}^{p} (1 - C_i^2)$$

where, C_i is the ith canonical correlation and p is the number of root traits studied. Approximate F-tests (as per SAS default) were used for assessing the statistical significance of the Wilk's Lambda. The structure correlations (Johnson and Wichern, 1992) were calculated using the formulae

$$S_{i(j)k} = \frac{e_{ki(j)}\sqrt{\lambda_{i(j)}}}{\sqrt{\sigma_{kk}}}$$

where, I (j), k = 1,2,...p (q) depends on the number of characters studied in the root and yield related sets of variables, respectively; σ_{KK} is the variance of the kth variable and ($\lambda_{i(j)} e_{i(j)}$) are the eigen value-eigenvector pairs of the corresponding covariance matrices.

The practical importance of the canonical correlations was obtained by calculating the Redundancy Measure (RM) as per Sharma (1996) using the formula

$$RM_{Vi\backslash Wi} = AV(Y/V_i)\times C_i^2$$

where, $AV(Y/V_i)$, variance extracted, is the average variance in Y variables that is accounted for by the canonical variate Vi (ith linear combination of the yield related characters) and was calculated as

$$AV(Y/V_i) = \sum_{i=1}^{q} S_{jk}^2 / q$$

where, S_{jk}^2 is the Loading of the k^{th} Y variable on the canonical variate V_i and q is the number of yield related characters studied. Total redundancy for the Y variables ($RM_{Y/X}$) was computed as

$$RM_{Y/X} = \sum_{i=1}^{p} RM_{V_i/W_i}$$

where, $RM_{vi/wi}$ is the redundancy measure as explained above.

RESULTS

The simple correlation among the yield related characters showed that GY has positive correlation (0.95) with HI but negatively correlated with CH (-0.73) and DF (-0.66). PH was highly and positively correlated with PL (0.55) and negatively correlated with PN (-0.62). Among the root morphological characters MRL showed positive correlation with MRL/PH (0.77) followed by RV (0.46). As expected RDW showed high positive correlation with RDW/SDW (0.70). The interrelationships between yield components and root morphological characters revealed that PH has positive correlation with MRL (0.56). HI showed negative correlation with RDW (-0.54). Although there were high correlations among and between the two sets of variables, it would be more informative if the linear functions of the correlated variables of the two sets were considered. This would enhance the interpretation of the results since the characters themselves are correlated. Hence, the canonical analysis was carried out as described below.

Canonical correlation: The statistical test using Wilk's lambda criteria has shown that the first two canonical correlations were significant under both WW and WS environments. The first canonical correlation coefficient was 0.99 under both conditions and the second was 0.95 and 0.89 under WW and WS conditions, respectively. This implies that the linear functions of the yield related characters and that of root morphological characters have strong association as they together explained nearly 98% of the variation for the first components under both WW and WS conditions. The contributions of these linear composites for the second canonical variates were 90 and 80% under WW and WS conditions, respectively. The first two canonical variates explained 48 and 52% of the total variability, whereas the first five canonical variates explained about 93 and 90% of the total variability present in the two sets of variables (Table 1).

Contribution of variable to variate: Since structural correlations are helpful in identifying variables and their contribution to canonical variate, the first five canonical variates under the two conditions were considered. The intra-set structured correlations which give the magnitude and direction of the variable contribution to the variate are presented in Table 2 and 3 for yield and root morphological characters, respectively. It is evident that among the root morphological characters MRL (0.716) has a high contribution to the first variate followed by RDW/SDW (-0.612) and RDW (0.218) under WW condition. RV (0.436), RN (0.424) and RDW (0.421) have shown almost an equal contribution to the second canonical variate of root characters. Under WS condition, apart from MRL (-0.592), RV (-0.317) and RDW (-0.300) also contribute to the variability and were important in plant development followed by RDW/SDW (0.285). RV (0.734) was the most influential character in forming the second canonical variate followed by MRL/PH (0.507) and MRL (0.394). The relationships of the root morphological characters with the first canonical variates clearly identified that MRL, RDW and RDW/SDW were highly contributing characters under WW condition and MRL, RV, RDW and RDW/SDW under WS condition which, in turn, influence the grain yield and its components.

Among the yield related characters (Table 3) PH had the maximum contribution (0.944) to the first canonical variate in the WW condition followed by PL (0.630), PN (-0.567) and HI (-0.485). Under WS condition, PH was still the highest contributing character but in the opposite direction (-0.977) followed by PN (0.695) and TN (0.569). In formation of the second canonical variate TN (0.546) and PN (0.479) were the highest contributors. The relationships among the variables clearly showed that PH, PL, PN and TN were the most influential characters in the intra variable domain of the yield components.

Interrelationships between root morphological characters and yield related characters: There are two types of contributions that define the relationship between the two variable domains. One is the linear function of root morphological characters and their importance in the expression of the individual yield characters and the other is the individual contribution of

Table 1: The first five canonical correlations between root morphological and yield related characters, approximate F, significance level, squared canonical correlation and cumulative proportion under Well- Watered (WW) and Water Stress (WS) conditions

Canonical correlation		Approximate F		Pr>F		Squared canonical correlation		Cumulative canonical	
WW	WS	WW	WS	WW	WS	WW	WS	WW	WS
0.990	0.987	3.82	2.49	0.0001	0.0003	0.981	0.974	0.252	0.284
0.949	0.892	2.19	1.30	0.0029	0.1773	0.901	0.796	0.483	0.516
0.838	0.789	1.48	<1	0.1034	0.5371	0.702	0.623	0.663	0.698
0.791	0.633	1.24	<1	0.2646	0.7537	0.626	0.401	0.823	0.815
0.663	0.550	<1	<1	0.6023	0.7378	0.439	0.303	0.935	0.903

Table 2: Structural correlations between the grain yield related characters and their (first five) canonical variates under well-watered and water stress conditions

	Well-watered					Water stress				
Trait	V_1[#]	V_2	V_3	V_4	V_5	V_1	V_2	V_3	V_4	V_5
GY	-0.328	-0.065	0.182	-0.680	0.607	0.274	0.126	-0.172	-0.338	-0.194
PL	0.630	-0.040	0.342	-0.128	0.254	-0.429	0.104	0.485	-0.222	0.180
PN	-0.567	0.479	0.071	-0.180	0.226	0.695	-0.118	-0.357	0.372	-0.077
PH	0.944	-0.264	0.121	0.010	0.061	-0.977	-0.155	0.083	0.028	0.041
TN	-0.430	0.546	0.371	-0.230	0.110	0.569	-0.107	-0.368	0.383	0.365
DF	0.410	0.187	0.001	0.685	0.045	-0.372	0.138	0.028	0.353	0.570
HI	-0.485	-0.234	0.195	-0.639	0.501	0.403	-0.107	-0.115	-0.513	-0.235
CH	0.309	0.281	0.021	0.690	-0.370	-0.211	0.107	0.056	0.635	0.218
SW	0.275	-0.195	-0.755	0.181	0.280	-0.101	-0.083	0.787	-0.194	-0.222

[#]: The 1st caninical variate of grain yield related characters

Table 3: Structural correlations between the root morphological characters and their (first five) canonical variates under well-watered and water stress conditions

	Well-watered					Water stress				
Trait	W_1[#]	W_2	W_3	W_4	W_5	W_1	W_2	W_3	W_4	W_5
MRL	0.716	-0.250	-0.112	0.001	0.624	-0.592	0.394	0.484	-0.096	0.384
RN	-0.152	0.424	0.655	-0.276	0.326	0.032	0.062	-0.827	0.201	0.366
RV	0.078	0.436	-0.191	0.277	0.025	-0.317	0.734	-0.167	0.154	0.024
RDW	0.218	0.421	0.201	0.721	-0.079	-0.300	0.112	0.380	0.801	0.038
RDW/SDW	-0.612	-0.058	0.264	0.551	-0.007	0.285	-0.115	0.192	0.422	-0.445
MRL/PH	0.086	-0.010	-0.363	-0.102	0.898	0.007	0.507	0.621	-0.087	0.551
RT	0.159	0.031	-0.797	-0.205	-0.322	-0.212	-0.165	0.702	-0.155	0.186

[#]: The 1st caninical variate of root morphological characters

each of the root characters on the expression of the yield related characters. The contribution of the linear function of all the root morphological characters to the expression of PH under WW condition was 87% from the first canonical variate and 94% from the first two linear functions (Table 4). Interset-structured correlations have also showed the same result (data not shown), where pH showed the highest correlation (0.935) with the first canonical variate of root characters. This was followed by a contribution of the first two canonical variates of about 52% for PN, 45% for TN and 39% for PL (Table 4). Under WS condition, the contribution of the root morphological characters for the development of yield related characters was similar, as we found that the contribution from the first two linear functions was 95% for PH, 48% for PN and 32% for TN. Interset-structured correlation has also identified PH as the most important character contributing to the first canonical variate of root morphological characters (data not shown).

Similarly, contribution of the individual root characters to the first two linear functions of the yield related characters showed that about 56 and 37% of the variability was explained by MRL and RDW/SDW, respectively, under WW condition (Table 5). This contribution increased to 57% from MRL, 49% from RN and 42% from RDW/SDW for the first three linear functions of the yield related characters. Under WS condition, however, the cumulative contribution from RDW/SDW was as small as 10% even up to the first three linear functions, whereas it was the contribution from RV (53% for the first two and 54% for the first three canonical variates) that had the highest relation with yield characters followed by MRL (46 and 61% for the first two and first three components, respectively).

The redundancy measures for a given set of variables gives the average squared multiple correlation which explains the amount of total variability in one domain accounted for by the second domain. The result showed that about 60% of the total variability in grain yield related characters is accounted for by the root morphological characters under WW condition. Under WS condition, however, the total variability in yield

Table 4: Cumulative proportion of the grain yield related traits contributing to the first five canonical variates of the root morphological characters under well-watered and water stress conditions

	Well-watered					Water stress				
Trait	1	2	3	4	5	1	2	3	4	5
GY	0.105	0.109	0.132	0.422	0.584	0.073	0.086	0.104	0.150	0.161
PL	0.389	0.391	0.473	0.483	0.511	0.179	0.188	0.334	0.354	0.364
PN	0.315	0.522	0.526	0.546	0.568	0.471	0.482	0.561	0.617	0.619
PH	0.875	0.938	0.948	0.948	0.950	0.930	0.949	0.953	0.954	0.954
TN	0.181	0.450	0.546	0.579	0.585	0.315	0.325	0.409	0.468	0.508
DF	0.165	0.197	0.197	0.491	0.492	0.135	0.150	0.151	0.201	0.299
HI	0.231	0.280	0.307	0.562	0.672	0.158	0.167	0.176	0.281	0.298
CH	0.094	0.165	0.165	0.464	0.524	0.043	0.053	0.054	0.216	0.231
SW	0.074	0.109	0.509	0.529	0.563	0.010	0.015	0.401	0.416	0.431

Table 5: Cumulative redundancy and cumulative proportion of the root morphological traits contributing to the first five canonical variates of the grain yield related characters under well watered and water stress conditions

	Well-watered					Water stress				
Trait	1	2	3	4	5	1	2	3	4	5
MRL	0.503	0.560	0.569	0.569	0.740	0.341	0.464	0.610	0.614	0.659
RN	0.023	0.185	0.486	0.534	0.580	0.001	0.004	0.430	0.446	0.487
RV	0.006	0.177	0.203	0.251	0.251	0.098	0.527	0.544	0.554	0.554
RDW	0.047	0.206	0.235	0.561	0.564	0.088	0.098	0.187	0.444	0.445
RDW/SDW	0.368	0.371	0.420	0.610	0.610	0.079	0.090	0.112	0.184	0.244
MRL/PH	0.007	0.007	0.100	0.106	0.461	0.000	0.205	0.445	0.448	0.540
RT	0.025	0.026	0.472	0.498	0.544	0.044	0.066	0.372	0.382	0.392
Cumulative Redundancy	0.270	0.351	0.422	0.558	0.605	0.257	0.268	0.349	0.406	0.429

related characters explained by root morphological traits was about 43% (Table 5). The redundancy measures for individual canonical variates under the two conditions indicated that about 27 and 26% of the variability in the first linear function of the yield related characters is explained by root morphological characters under WW and WS conditions, respectively. When these results are expressed as percentage of the total redundancy, the total variability in yield related characters that is accounted for by the root morphological characters was about 44 and 55% for the first canonical variate under WW and WS conditions, respectively.

DISCUSSION

The purpose of this study was to investigate how the root morphological characters influence the characters of economic importance particularly the grain yield under both well-irrigated and low-moisture stress conditions. The result suggests that MRL was the most important character for plant standing followed by RDW/SDW under WW condition. The longer the roots are, the better will the plants be standing and this is important in shaping plant characters like PN and PL, which in turn will enhance the grain output. Studies on physiological aspects of the root system in rice have shown that water extraction was related to root length density under upland conditions and deep root systems seem to be advantageous under those conditions (Toorchi *et al*., 2003). Hirasawa *et al*. (1994) and Hirasawa (1995) have also reported a smaller reduction in leaf water potential in plants with a deeper root system compared with plants with a shallow root system. This interrelationship indicate that the root morphological characters MRL, RDW/SDW and RDW would be the characters of choice in order to improve the yield production under well-irrigated situations.

When the plants are subjected to stress, apart from MRL, the relative importance of RV and RN have been observed in this study. In order to extract more water, a well-established root system is necessary and under stress condition the plants naturally exhibits this quality by increasing the root volume. It has also been found that the contribution of MRL/PH to the total variability was substantial. This means that in order to extract more water from deeper layers, MRL automatically increases and because of limitation in the source of carbohydrates the plants become stunted. Therefore RV and RN would be the best combination of root characters, in addition to MRL, in order to increase the grain yield under water stress conditions. Positive correlations between plant height and maximum root length have often been observed (Champoux *et al*., 1995) and this study also show that they are the most important characters in each of the variable sets. Toorchi *et al*. (2003) has also reported a positive simple phenotypic correlation between plant height and root characters of rice in hydroponics' study.

The inter-relationships between root morphological characters and yield related traits clearly identified the importance of MRL and RDW/SDW under WW conditions and MRL, RV and RN under WS conditions. This study also demonstrate the importance of root morphological characters under WS condition as compared to WW conditions by looking at the redundancy measures for the first canonical variate (55% under WS as compared to 45% under WW). Hence, judged from the most important canonical variate, the contribution of root characters on grain yield under stress conditions is more important than well-irrigated conditions. These results do indicate that identification and characterization of Quantitative Trait Loci (QTLs) for MRL, RV and RN could be used to improve grain yield production of rice, especially under drought conditions.

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