Relationship of root cone angle with key physiological traits and grain yield of rice grown in aerobic production systems

Vinarao R[1], Proud C[1], Snell P[2], Fukai S[1], and Mitchell J[1]

[1] The University of Queensland, School of Agriculture and Food Sciences, Brisbane, QLD 4072, Australia
[2] Department of Primary Industries, Yanco Agricultural Institute, Yanco, NSW 2703, Australia

Abstract
Rice crops are one of the world's major consumers of irrigation water. With water becoming more limited, aerobic production (AP) systems, which use less water, may provide an alternative to traditional flooded culture. Development of genotypes with narrow root cone angle (RCA) and subsequently deeper rooting systems is a key AP adaptation trait ensuring water uptake at depth. Using a recombinant inbred line population derived from IRAT109, two experiments were conducted in well-watered (WW) and intermittent water stressed (IWS) conditions to characterise the relationship of RCA with grain yield (GY) and key physiological traits. Strong positive genetic correlation existed for RCA between experiments (r = 0.98) indicating stability and consistency of the trait measured. In WW in which most physiological traits and GY were determined, significant genotypic variation existed for GY and related traits. GY was found to be mostly influenced by phenology, plant height, and lodging resistance. Narrow RCA promoted cooler canopy temperatures, minimised leaf death due to heat, and increased the number and proportion of deep roots in WW conditions. Evaluation of contrasting genotypes in terms of RCA in intermittent water stress conditions might reveal the advantage of narrow angled genotypes in this environment. This work provides improved physiological understanding of RCA and will be valuable for the development of AP-adapted, sustainably produced rice.

Keywords
root depth, narrow root angle, lodging resistance, aerobic rice

Introduction
The negative effects of climate change in agricultural production systems are clear, with water scarcity as major consequence. The aerobic rice production (AP) system is a promising technology which may provide solutions for this imminent problem. The AP system uses less water compared with conventional flooded systems through the reduction of water used in land preparation, seepage, percolation, and evaporation. Since the AP system is relatively new and less widely adopted, the knowledge base relevant and specific to AP adaptation is still limited. Development of improved root system architecture with narrower/steeper root angle should result in a deeper rooting system and greater water uptake at depth. In upland drought conditions, Uga et al. (2013) were able to show that deeper, narrow angled rooting genotypes produced higher grain yield compared to shallower, wider angled genotypes. Moreover, stable and environment-specific genomic regions associated with narrow root cone angle (RCA) have been identified in AP systems (Vinarao et al. 2021). Investigation on the variation and relationships of these traits in an AP system will prove to be useful in increasing the knowledge base for AP. Physiological dissection of key traits such as RCA is important to gain further understanding of underlying mechanisms for aerobic adaptation. By utilising a recombinant inbred line (RIL) population derived from Sherpa and IRAT109, a cross between two contrasting genotypes in terms of RCA, this study aims to investigate the physiological traits contributing to aerobic adaptation specifically RCA and related traits.

Methods
Plant materials and experimental design
Progeny (252 RILs) between Sherpa and IRAT109 were produced by the NSW Department of Primary Industries (DPI). Two experiments (well-watered (WW) and intermittent water stress (IWS)) were set-up and utilised a total of 248 genotypes which was comprised of 236 RILs derived from

Sherpa/IRAT109 along with 12 checks including the parents. These checks included: IRAT109, Kinandang Patong, Langi, Reiziq, Sherpa, and YUE15=V038. These were planted in two locations with two replications using a resolvable column design using the R package DiGGer (Coombes 2009) on two soil types (dermosol for WW and vertosol for IWS) at the University of Queensland Gatton campus (27.5551° S, 152.3369° E). These two locations were managed similarly with the exception that WW was irrigated thrice a week while IWS was irrigated only twice a week with approximately 24 mm on each occasion, with a total of 263.4 mm of rainfall received over the experimental period.

Crop establishment and management

Both locations utilised in this study had an oaten hay crop prior to the experiment which was incorporated in 6-7 weeks before the start of the experiment. Basal fertiliser was applied five days prior to sowing at a rate of 400 kg/ha using Incitec Pivot's CK140S (23-2-18-4) fertiliser and nitrogen topdressing was carried out 42 and 54 days after sowing (DAS) in WW and IWS, respectively. Prior to sowing, 15 kg/ha of zinc sulphate monohydrate was also applied and lightly incorporated. Seeds were drill sown to a depth of 3-4 cm at a rate of 130 kg/ha which is considered as industry recommendation. Plots were 2 m in length with seven rows and an inter-row spacing of 22 cm, resulting in a 3.08 m^2 plot size.

Phenotypic measurements and analysis

The WW experiment was phenotyped for the following traits: leaf death (LD), canopy temperature differential (CTD), days to heading (DTH), plant height (PH), lodging score (LG) scored as 1, where no lodging occurred to 5, where 100% of the plot lodged, and grain yield (GY). Root crowns were manually sampled from each plot at 99 DAS, after the majority of the genotypes had reached the heading stage (WW), and maturity (IWS). The plants were lifted from the ground along with soil attached. Soil particles were manually removed from the roots to facilitate the measurement of root cone angle (RCA) using a protractor, by measuring the cone angle from the two most external nodal roots. Using the same plants, the pulling resistance score (PS) was also recorded by noting the degree of difficulty in pulling the plants out from the ground with 1 being the easiest to pull and 5 considered the hardest. Soil cores (5 cm diameter x 100 cm deep) utilising a hydraulic soil coring rig mounted on the back of a trailer were taken to determine root number at depth from each plot after the maturity harvest, in WW. The soil cores were processed as described by Mitchell et al. (2019) by quantifying the proportion of deep roots below 20 cm (DR20B) and the total number of core break counts below 20 cm (TR20B). Establishment in IWS was poor and hence data was only collected for RCA and PS.

Statistical analysis on a resolvable row-column design was carried out on all phenotypic traits collected using ASReml package in R (VSNi, UK). Best linear unbiased predictors (BLUPs) and heritability of traits were computed using a model with genotype as a random effect. Significant genotypic variation among genotypes tested were considered at $P < 0.05$, unless stated otherwise. Correlation between significant traits were determined using correlations on the BLUPs.

Results and Discussion

GY and related traits in WW

Significant genotypic variation ($P < 0.001$) existed for GY and related traits such as PH, DTH, and LG, with heritability ranging from 0.53-0.98 (Table 1) when grown under WW conditions. GY of RILs ranged from 4.96 – 11.64 t/ha with a mean of 8.55 t/ha, and a heritability of 0.73. Sherpa produced higher yield than IRAT109 with 11.82 t/ha and 7.57 t/ha, respectively. On the other hand, Reiziq had the highest GY among the checks under WW, with 12.30 t/ha, followed by Sherpa, and then YUE15=V038 with 11.13 t/ha, while Kinandang Patong produced the lowest yield at 3.12 t/ha. Of the RILs, the top 25 genotypes with the highest GY had an average yield of 10.89 t/ha, while the lowest produced 5.97 t/ha. Similar with these results, previous experiments in the subtropics and temperate climates have demonstrated that high-yielding aerobic production is possible (Boonjung and Fukai 1996; Kato et al. 2009).

Table 1. Grain yield (GY), days to heading (DTH), plant height (PH), lodging score (LG), root cone angle (RCA), proportion of deep roots below 20 cm (DR20B), and maximum root depth (DEPTH) and the respective p values and heritability of RILs derived from Sherpa/IRAT109 and checks, under well-watered experiment at Gatton during 2019-2020 cropping season.

DESC	GY (t/ha)	DTH (days)	PH (cm)	LG	RCA (°)	DRB20B	DEPTH (cm)
IRAT109	7.57	96	124	2.47	129	0.51	72
Kinandang Patong	3.12	123	154	3.22	126	0.49	73
Langi	10.31	97	111	2.94	147	0.43	64
Reiziq	12.30	90	89	1.29	146	0.40	57
Sherpa	11.82	88	93	1.22	140	0.43	59
YUE15=V038	11.13	84	83	1.29	174	0.41	62
Overall Mean (RILs)	8.55	94	107	2.19	139	0.40	59
Top 25 RILs	10.89	108	127	3.44	125	0.46	67
Lowest 25 RILs	5.97	80	89	1.80	150	0.33	52
P value (RILs)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0001	0.0002
Heritability	0.73	0.98	0.90	0.53	0.49	0.39	0.37

RCA and related traits

Significant genotypic variation was also observed in root traits such as RCA, DR20B, and depth (Table 1) in WW. In terms of RCA, RILs registered the narrowest RCA of 120° while the widest had 155°, with a mean of 139°. Sherpa had a wide RCA of 140° while IRAT109 and Kinandang Patong showed narrow RCA, 129° and 126° respectively, consistent with previously reported results (Lou et al. 2015; Uga et al. 2013). In terms of the IWS experiment, significant genotypic variation also existed for RCA, with a heritability of 0.27. Genetic correlations between the WW and IWS RCA showed strong positive relationship (r = 0.98), suggesting consistency of the trait measured, however, selection in a well-watered environment appears more favourable due to a higher heritability.

Relationship of GY, RCA, and key traits in WW

GY was found to be related to several traits measured such as DTH, PH, and LG in the WW experiment. GY was negatively related to DTH (r = -0.35***), PH (r = -0.31***), and LG (r = -0.25***). This trend was largely explained by the association between PH and LG, where tall genotypes tended to have greater lodging, and consequently, resulted in reduced GY. A more detailed analysis of the relationship of LG and DTH also showed that genotypes with DTH ranging from 85-102 days had higher incidence of lodging as a result of significant rainfall and storms during this period. While significant relationships existed between RCA and other physiological traits, they were relatively weak relationships in which narrow RCA tended to have higher PS (r = -0.27***), cooler canopy temperatures (r = 0.21**), lower lodging incidence (r = 0.21**), and minimal LD (r = 0.18**). Nor was there a significant association between RCA and GY, which is largely due to the nature of the WW environment with minimal to no water deficit. It is anticipated that in the current season, where an intermittent water deficit environment has been generated, that genotypes with narrow RCA may result in higher GY compared to those with wide RCA as was found by Mitchell et al. (2019) when evaluating 20 diverse varieties. In addition, RCA was also found to be weakly related with DR20B (r = -0.14*) and TR20B (r = -0.14*). Weak relationship between RCA and rooting depth may have been due to WW environment and other factors such as plant density similar to the results shown by Abe and Morita (1994), where rooting angle was affected by external factors such as plant density and nitrogen application in addition to varietal differences. All things considered, the result above suggest that narrow angled roots had a tendency to develop deeper rooting systems. This also meant that these genotypes had more access to water, which in turn resulted in better plant water

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relations and ultimately, in cooler canopies and lower leaf damage, in congruence with previous reports (Kato and Okami 2010).

Conclusion

This work dissected the underlying physiological traits associated with AP adaptation in rice using a recombinant inbred population. Analysis revealed that yield in AP systems in WW environment was related with DTH, PH, and resistance to lodging. Furthermore, extending the analysis on root related traits, it was shown that in AP systems, a narrow RCA promoted cooler canopy temperatures, minimised leaf death due to heat, and increased the number and proportion of deep roots. Evaluation of contrasting genotypes in terms of RCA in intermittent waters stress conditions in future experiments might reveal the advantage of narrow angled genotypes in this environment. This study provided key results in the physiological understanding of AP-related traits and with genomics-based breeding, could hasten the development of AP-adapted varieties for a more sustainable rice production system.

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