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ORIGINAL PAPER

QTLs associated with root traits increase yield in upland rice when transferred through marker-assisted selection

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Abstract Altering root morphology of rice (*Oryza sativa* L.) cultivars could improve yields in drought-prone upland ecosystems. Marker-assisted backcross breeding was used to introgress four QTLs for root traits into an upland rice cultivar. The QTLs had previously been identified under experimental conditions in a different genetic background. The introgressed lines and the recurrent parent were grown for 6 years by resource-poor farmers in upland sites in Eastern India and yields recorded. In combination the QTLs significantly increased yield by 1 t ha^{-1} under relatively favourable field conditions. In less favourable trials, the QTL effects were not detected due to greater heterogeneity in soil–water availability in very low yielding environments and consequent yield variability. Root studies under controlled conditions showed that lines with the introgressions had longer roots throughout tillering than the recurrent parent (14 cm longer 2 weeks after sowing). Therefore, both improved roots and increased yield can be attributed to the introgression of QTLs. This is the first demonstration that marker-assisted backcross breeding (MABC) to introgress multiple root QTLs identified under controlled conditions is an effective strategy to improve farmers' yields of upland rice. The strategy was used to breed a novel upland rice cultivar that has been released in India as Birsa Vikas Dhan 111.

Introduction

The development of crop cultivars with thicker and deeper roots is expected to increase yield under drought. Drought is frequent in Eastern India where more than 25 million people depend on the rainfed upland agricultural ecosystem for their staple food. Approximately 3.6 million ha of drought-prone upland rice is cultivated in the Indian states of Jharkhand, Odisha and West Bengal by resource-poor farmers, who have a limited choice of suitable cultivars.

Marker-assisted selection of QTLs for secondary traits such as roots has not yet been demonstrated as an effective strategy for improving grain yield (Vikram et al. 2011). Whole plant selection for yield under both drought and non-stress conditions has successfully identified rice genotypes with high yield in upland conditions (Verulkar et al. 2010), and has identified associations between roots and yield in other species (Ehdaie et al. 2003). Marker-assisted selection for QTLs for yield under drought has been effective in rice (Bernier et al. 2009, Vikram et al. 2011). However, none of these studies have examined the effects of root QTLs introgressed by marker-assisted backcrossing on yield.

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A rice breeding programme, targeting the rainfed uplands of Eastern India, used marker-assisted backcrossing (MABC) to incorporate root quantitative trait loci (QTLs) from the donor cultivar Azucena. The four QTLs (numbered here according to the chromosome location) were first identified in Bala/Azucena RILs for the following traits: QTL 2 increased root penetration, and deep root weight and thickness under well-watered conditions; QTL 7 increased root weight parameters and maximum root length; QTL 9 increased deep root thickness under both well-watered and droughted conditions; QTL 11 increased root length and root penetration. Subsequent meta-analysis of 12 populations confirmed that all four targets were meta-QTLs for root traits (Courtois et al. 2009; Khowaja et al. 2009), and analysis for QTL × environment interaction showed that expression of root traits at three of the targets (on chromosomes 7, 9 and 11) was influenced by the environment (MacMillan et al. 2006). Following MABC, participatory varietal selection (PVS) (Joshi and Witcombe 1996) was used to compare lines with different combinations of root QTLs in farmers' fields and they were assessed for traits including maturity, yield and grain shape. The most successful line from this breeding programme was PY 84 (Steele et al. 2007). PY 84 (released in Jharkhand state as Birsa Vikas Dhan 111) has been recognised as the first released rice cultivar bred through marker-assisted selection for improved roots (Ashraf 2010; Coudert et al. 2010), and is a good example of introgression of multiple QTLs for roots into a novel genetic background (Collard and Mackill 2008; Tuberosa and Salvi 2006).

Previously, we have shown that the multiple introgressed root QTLs increased root penetration, root thickness and nodal root apex stiffness (Clark et al. 2008) and we estimated that QTL 9 increases root length by 9.6 cm under both drought and well-watered conditions (Steele et al. 2006). Field testing over 2 years indicated that the introgression lines increased straw and grain yield (Steele et al. 2007); however, we were not able to directly associate the presence of root QTLs with increases in grain yield. Here, we present data from 6 years of testing in drought-prone upland field conditions to show how the improvement of root traits has directly increased yield in the cultivar PY 84. We discuss how our experiments have contributed knowledge on the effects of introgressed root trait QTLs under field conditions.

Materials and methods

Plant materials

Near isogenic lines (NILs) of Kalinga III (*Oryza sativa* L. spp. *indica*) upland rice that were developed through marker-assisted backcrossing to transfer Azucena QTLs were compared with each other and to Kalinga III (Tables 1, 2). The Philippines cultivar Azucena (*Oryza sativa* L. spp. *japonica*) was the donor of the positive effect QTLs, and the steps for introgression were described by Steele et al. (2006), including details of the target loci (Fig. 2 and Table 2 in Steele et al. 2006). Azucena alleles were selected at marker loci within, and flanking, all target QTLs. Background selection for Kalinga III alleles was made at a sample of marker loci across the rest of the genome. A set of NILs was produced which contained different combinations of the four target regions in a predominantly Kalinga III genetic background, these are the same NILs described in Steele et al. 2006 and Steele et al. 2007. Seed of the NILs selected with markers in Bangor, UK, was sent to India in 2001 for on-farm trials and seed of the same NILs multiplied in Bangor was sent to Aberdeen for the rhizotron experiment. In India, the NILs were selected for agronomic traits in farmers' fields and at Birsa Agricultural University (BAU)'s upland research station. From hereon they are identified as PY 81, PY 82, PY 83 and PY 84. PY 84 resulted from a cross between two BC_3F_2 lines and it had all four target introgressions (QTL 2, QTL 7, QTL 9 and QTL 11). PY 81 had none of the target QTLs, PY 82 had two (QTL 2 and QTL 11) and PY 83 had three (QTL 2, QTL 9 and QTL 11) (Table 1).

On-farm trials in Eastern India (2003-2008)

Trials were conducted in farmers' fields in the main (*kharif*) growing season as described by Steele et al. (2007). The farmers were subsistence farmers living in 32 villages participating in development programmes coordinated across Jharkhand, Odisha and West Bengal by the Gramin Vikas Trust. All plots were directly seeded (without transplantation). They followed the basic mother-baby trial design of Snapp (1999). In the mother trials lines were tested in single replicates, whereas only two lines were compared in baby trials. Farmers grew the lines following their own preferred management and most plots experienced terminal drought—none of the trials could be described as "well watered". No attempt was made to record rainfall or soil type in the farmers' fields, which were located in clusters throughout an area of approximately 70,000 km^2. In Ranchi, the mean rainfall during the *kharif* season (June–October) in the 10 years 1991–2000 was 1,424 mm (recorded at BAU) and in the 5 years 2007–2011 it was 1,186 mm (http://www.imd.gov.in), with a minimum of 652 mm (in 2010) and a maximum of 1,186 mm (in 2011). Similar levels were recorded in Ranchi in 2002–2007 (Steele et al. 2007; Verulkar et al., 2010) and in 2007–2011 in Keonjhargarh, Odisha and Purulia, West Bengal (http://www.imd.gov.in).

Table 1 Kalinga III and its near isogenic lines tested in field trials in India and the corresponding introgressed root QTLs

Line	Year and state where first released in India	Pedigree	Equivalent near isogenic line selected in MABC at Bangor	MAS generation in 2001 sent to India	Azucena root QTLs present on chromosome
Kalinga III	1983 Odisha	Ac 540/Ratna			None
PY 81		Kalinga III/ Azucena/// Kalinga III	23-01-06-06	BC_3F_2	None
PY 82		Kalinga III/ Azucena/// Kalinga III	21-01-03-11-17	BC_3F_3	2, 11
PY 83		Kalinga III/ Azucena/// Kalinga III	21-01-03-11-07	BC_3F_3	2, 9,11
PY 84[a]	2009 Jharkhand	Kalinga III/ Azucena/// Kalinga III	3-26-5-18	$BC_3F_2/BC_3F_2//BC_3F_3$	2, 7, 9, 11

[a] Released as Birsa Vikas Dhan 111

Table 2 Comparisons between genotypes to test QTL effects

Effect tested	Comparison	Lines compared
Non-target Azucena alleles	1	PY 81 with Kalinga III
Two or more QTLs	2	PY 82, PY 83 and PY 84 with PY 81
QTL 7	3	PY 84 with PY 83
QTL 9	4	PY 83 with PY 82
All four target QTLs	5	PY 84 with PY 81

Forty-one mother trials were conducted between 2003 and 2008. Each mother trial was managed by one farmer. The control cultivars (tested alongside the five lines listed in Table 1) were Vandana, Ashoka 228 (Birsa Vikas Dhan 110), Ashoka 200F (Birsa Vikas Dhan 109), Varanideep, Birsa Gora 102 and one local cultivar chosen by the farmer. Baby trials were carried out in 2007 and 2006, where a single PY line was tested alongside either Kalinga III, Ashoka 228 or Vandana. Time to maturity was recorded in 39 baby trials containing one or both of the test lines as follows: PY 81 (8 farmers), PY 82 (10 farmers), PY 83 (8 farmers), PY 84 (7 farmers) and Kalinga III (10 farmers).

Rhizotron trials

Root and shoot traits were measured in plants grown in glass-sided rhizotrons in a glasshouse in Aberdeen, UK, in 2009. The method followed that of Price et al. (2002) except that the plants were grown for 42 days under aerobic conditions, well watered throughout. Shoot and root length were measured weekly for 6 weeks and water uptake was calculated by weighing the rhizotrons. The final root harvest was split into three sections: 0–40, 40–80 and 80–120 cm. Four replicates of each line were grown, and a total of 40 lines were included in the experiment in a fully randomised layout. Here, data from four lines (Azucena, Kallinga III, PY 83 and PY 84) are presented.

Statistical analysis

Mean trial yield across all lines was used to divide the trials into those conducted under favourable and unfavourable conditions. Trial yield and time to maturity for Kalinga III, PY 81, PY 82, PY 83 and PY 84 were estimated using a linear mixed effect model (Pinheiro and Bates 2004) in R (R Development Core Team 2012) with line, trial condition and trial type (mother/baby) as fixed effect and trial as random effect. Linear hypotheses comparing genotypes (Table 2) were tested using the R *multcomp* package (Hothorn et al. 2008). The rhizotron data were analysed using one-way ANOVA in Minitab 15.

Results

On-farm trials in Eastern India

There was no significant difference in yield between mother and baby trials (mixed effects model $P > 0.05$), so this factor was dropped from subsequent analysis. Based on graphical inspection (Fig. 1 inset) trials were divided into "favourable" and "unfavourable" conditions, where "favourable" trials were defined as trials with means exceeding 1.7 t ha^{-1}. There was a significant effect of line, conditions and a significant line conditions interaction on yield (all $P < 0.001$; Fig. 2). Similarly there was a significant effect of line and conditions on time to maturity, but

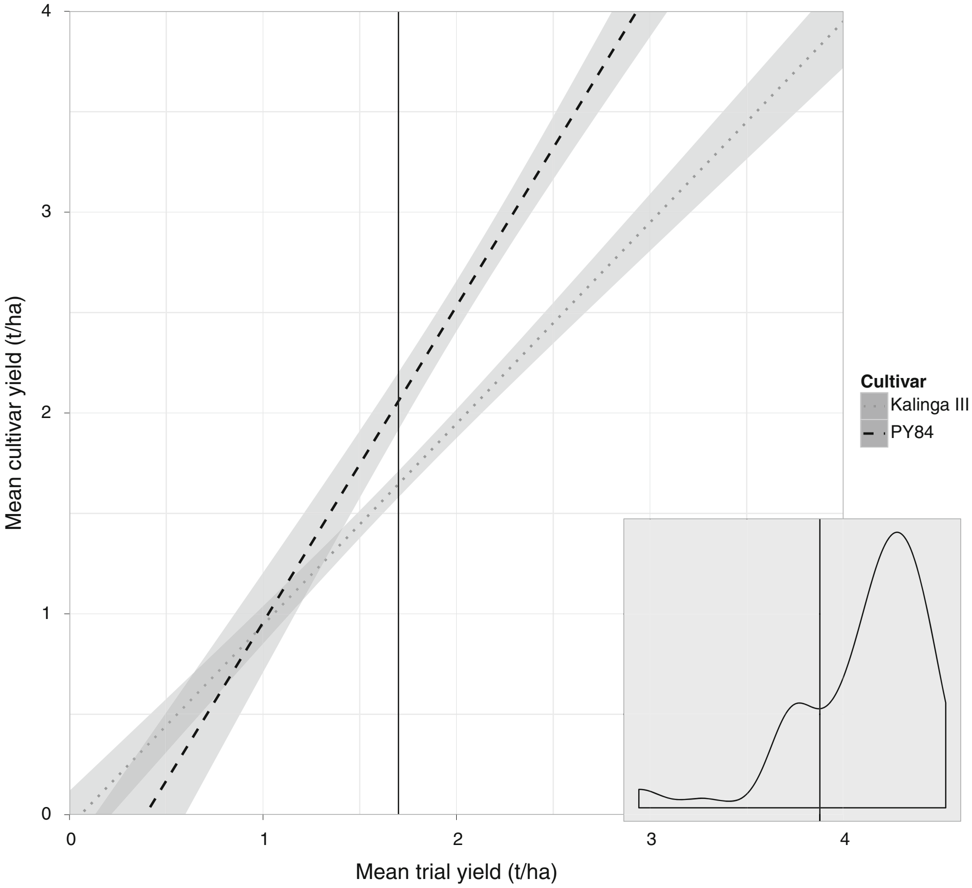

Fig. 1 Regression analysis of mean grain yield of PY 84 (Birsa Vikas Dhan 111) and Kalinga III on trial mean grain yield, from 42 mother and 15 baby trials in farmers' fields in Eastern India (Jharkhand, Odisha and West Bengal), 2003 to 2008. 95 % confidence intervals are indicated by shading. *Vertical line* indicates the division between favourable and unfavourable trials (1.7 t ha^{-1}). Lines of best fit are estimated by quadratic linear regression. *Inset plot*, *density plot* of distribution of mean trial yield across all cultivars

no significant interaction between conditions and line. In favourable conditions the mean grain yield of PY 84 was 46 % higher ($P < 0.001$) than that of Kalinga III and in unfavourable conditions it was 18 % higher (but not significant) (Fig. 2). There were no significant differences between any of the lines for yield or maturity in unfavourable conditions. PY 84 had the highest average yield in farmers' fields in the three eastern Indian states from 2002 to 2008 (Fig. 1).

Effect of QTLs on grain yield

Under favourable conditions there were significant differences for grain yield between lines with introgressed root QTLs and other lines (Fig. 3). Non-target Azucena alleles had no significant effect on yield as indicated by the lack of difference between PY 81 and Kalinga III, which differed only for a few non-target introgressions (comparison 1, Table 2). Lines with two or more Azucena alleles at root QTLs had a mean increase of 0.4 t ha^{-1} (comparison 2, Table 2). QTL 7 was associated with a mean increase of 0.9 t ha^{-1} in combination with the other QTLs (comparison 3, Table 2). QTL 9 (which has a demonstrated effect on increasing root length) had a significant effect of 0.2 t ha^{-1} on grain yield (comparison 4, Table 2). The combination of all four QTLs in PY 84 led to an increased grain yield of 1.0 t ha^{-1} (comparison 5, Table 2).

Rhizotron experiments

Roots of PY 83 and PY 84 were significantly longer than roots of Kalinga III on day 14, and they followed the same trend throughout tillering until day 35 (but not significant, Fig. 4). On day 14 the effect of Azucena alleles at multiple root QTLs was to increase root length by a mean of 14 cm. The experiment was harvested on day 42 when the roots reached the bottom of the rhizotron. PY 83 and PY 84 took up significantly more water than Kalinga III over the last 4 days (days 39–42). On day 42 PY 84 had thinner roots below 80 cm than Kalinga III, but there was no significant difference for mean root thickness at other depths sampled (Table 3).

Discussion

Data from more than 60 field trials in farmers' fields in Eastern India over 6 years have shown that the

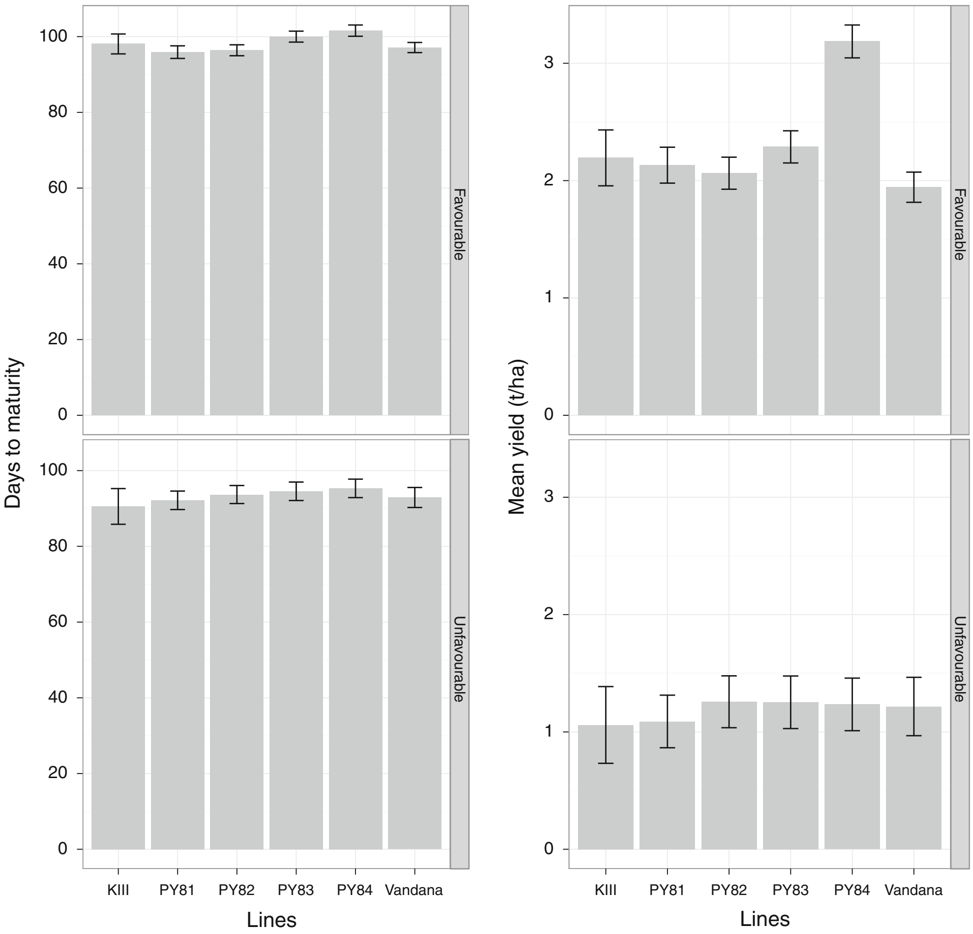

Fig. 2 Mean days to maturity (*left-hand panel*) and mean yield (*right-hand panel*) for genotypes in favourable and unfavourable trials (best linear unbiased predictors estimated by mixed effects models). *Error bars* are 95 % confidence intervals

introgression into Kalinga III of four root QTLs has improved grain yield by 1.0 t ha$-^{1}$ in these environments. QTL9 increased yield by 0.2 t ha^{-1}. This QTL was originally detected as influencing root thickness and has previously been shown to lengthen roots in the Kalinga III background (Steele et al. 2006). QTL7 was originally detected as influencing root depth and weight and it increased yield by 0.9 t ha^{-1}. It was found to have a stable effect on roots across environments by MacMillan et al. (2006). The high effect for yield detected here for QTL7 might be influenced by favourable interactions with QTLs 2, 9 and 11 that were common to the lines used for this comparison.

Compared to above-ground organs, roots have undergone very little direct selection during cereal domestication, so most modern cultivars have insufficient root systems for optimum uptake of water and nutrients for maximum grain yield (Waines and Ehdaie 2007). The introgression of genes for increased root size should enable the plant to take up more water and nutrients, and thereby increase photosynthesis and carbohydrate synthesis and mobilize assimilates to grain yield. Our research supports the hypotheses that diverting photosynthates to develop the root system does not reduce from grain yield, but presumably increases water/nutrient uptake in the field with consequent yield increases.

Associations between root traits and yield have been found in cereals. In QTL studies in maize (*Zea mays* L.) a root QTL was associated with yield (Landi et al. 2010). In wheat (*Triticum aestivum* L.), translocations of the rye (*Secale cereale* L.) chromosome 1RS increased root dry matter and also increased grain yield by 7 % (Ehdaie et al. 2003). However, the root-improving rye 1RS translocations offered no greater yield advantage under drought than under optimal conditions in the UK environment (Foulkes et al. 2007). In rice, the evidence for the effect of root traits is mixed (see review by Gowda et al. 2011). A study of pairs of rice NILs differing for root growth loci (Venuprasad et al. 2011) found that large differences in root phenotypes were not associated with yield differences, whereas large differences in yield were associated with higher transpiration rates. In our experiments, the benefit of the introgressed Azucena root QTLs was clearer in the higher yielding trials than the lower yielding ones. The errors detected in the unfavourable conditions were large (Fig. 1), so this limited our ability to detect genotypic

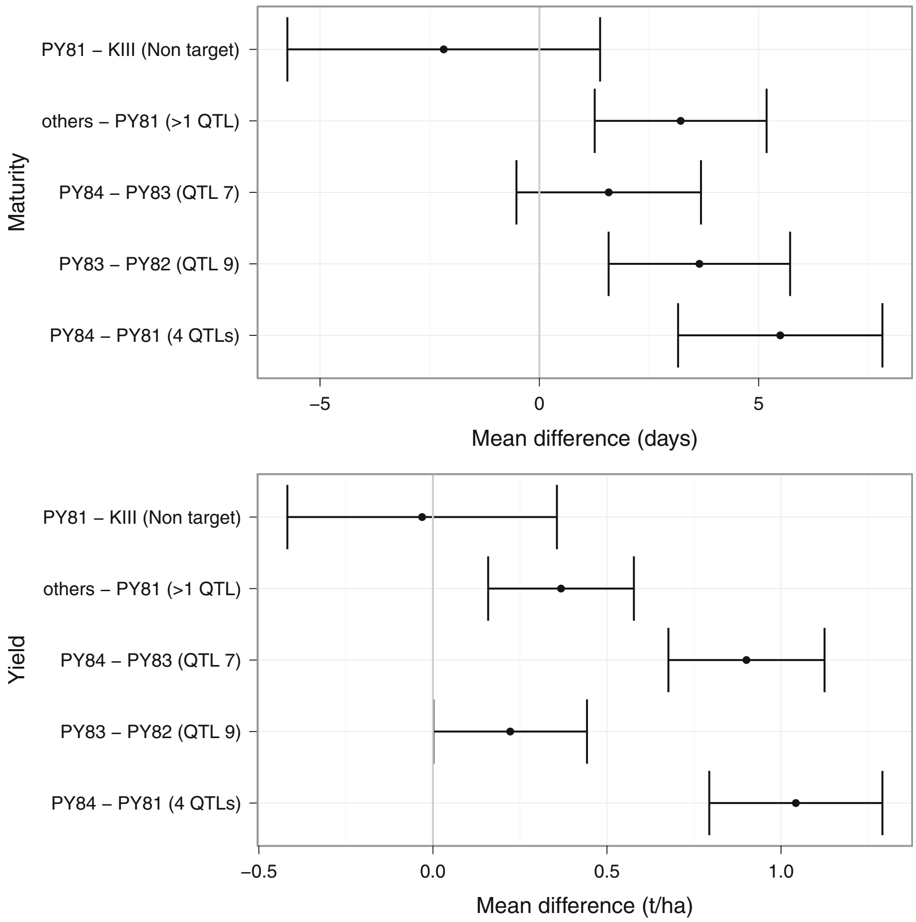

Fig. 3 Linear hypothesis tests of differences between genotypes for mean time to maturity (*upper panel*) and mean yield (*lower panel*) in favourable conditions. The others—PY 81 comparison compares the mean of PY 82, PY 83 & PY 84 with PY 81. Points are mean estimates of difference, *error bars* are 95 % confidence intervals. Where the error bars do not overlap with zero (*grey vertical line*), there is evidence of significant difference between genotypes. The effects tested are summarised in Table 2

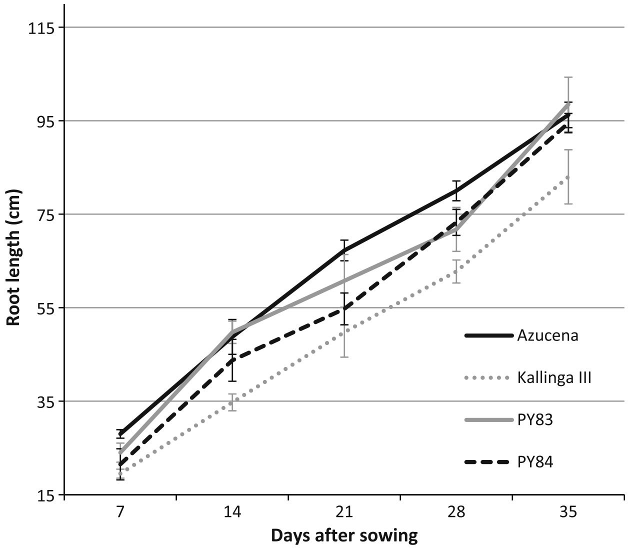

Fig. 4 Root growth in rhizotrons for four rice genotypes

differences in the unfavourable conditions. The reason for this could be heterogeneity in soil water holding capacity that is concealed in well-watered conditions. When genotypes are compared at increasing levels of drought stress, small variations in soil properties have increasingly large effects on within-cultivar variability (Ceccarelli and Grando 1996). In drying soils, competition between plants for limiting recourses increases as parts of the soil dry out (Hinsinger et al. 2009).

The trials we conducted in Eastern India were under drought-stressed conditions where the trial mean yields were $\leq$2.7 t ha^{-1}. The same four PY lines and Kalinga III were tested at IRRI in the Philippines (Amelia Henry, IRRI, pers. comm.) in four non-stressed (two upland rainfed and two irrigated lowland; trial mean yields $\geq$2.7 t ha^{-1}) and one upland trial with drought stress (trial mean yield = 0.5 t ha^{-1}). No significant differences were found for grain yield, indicating that there was no yield penalty attributable to the introgressed QTLs under these higher production environments, although in the stressed trial PY 84 had the lowest canopy temperature and the greatest root length density at depth (Amelia Henry, IRRI, pers. comm.).

Many of our trials experienced late season drought in conditions equivalent to the unfavourable sites in India used by Mandal et al. (2010) to test a wide range of rice lines. Their trials included two of our lines, Richa 5 and Richa 6, developed from the same cross as PY 84. Instead

Table 3 Mean (±standard error) of root traits recorded on day 42 in the rhizotron experiment, University of Aberdeen, 2009

	Mean root thickness (mm)	Root thickness at 80 cm depth (mm)	Root mass (%)	Proportion of roots at top (%)	Proportion of roots at middle (%)	Proportion of roots at bottom (%)	Proportion of roots to total plant mass (%)	Water uptake days 39–42 (ml)	Plant height (cm)
Kallinga III	1.00 ± 0.11	1.00 ± 0.09	25 ± 2.7	84.4 ± 2.56	14.24 ± 2.22	1.4 ± 0.37	25.0 ± 1.85	275 ± 15.4	90 ± 1.78
PY 83	1.01 ± 0.04	1.00 ± 0.09	32 ± 2.7	79.6 ± 1.41	17.38 ± 1.21	3.1 ± 0.44	31.8 ± 1.00	362 ± 15.4**	83.25 ± 6.28
PY 84	0.96 ± 0.04	0.90 ± 0.11*	32 ± 3.1	82.2 ± 2.04	13.88 ± 2.01	3.9 ± 1.71	32.6 ± 1.43	350 ± 15.4*	82.5 ± 2.33
Azucena	1.11 ± 0.04	1.13 ± 0.09	30 ± 2.7	73.7 ± 3.86	23.33 ± 3.56	3.0 ± 0.36	30.1 ± 4.59	345 ± 17.8*	103.5 ± 3.23

*, ** Significantly different from Kalinga III at 0.05 and 0.01 probability levels

of marker-assisted backcrossing, single large scale marker-assisted selection was used for the same target root QTLs in the BC_2 generation to produce bulk lines with target QTLs in either a fixed or heterozygous state (Steele et al. 2002). The bulks were selected for yield and other desired traits by farmers in their own fields following client-oriented breeding protocols (Steele et al. 2002; Joshi et al. 2007). Richa 5 and Richa 6, that had combinations of the same four root QTLs as PY 84, were reported by Mandal et al. (2010) to yield more than Kalinga III under low and moderate-input conditions, a finding consistent with the results we have obtained here with PY 84.

Impact of PY 84 on resource-poor farmers in Eastern India

Verulkar et al. (2010) have shown that the mega-cultivars of rice, i.e. those grown on millions of hectares in Eastern India, are highly drought susceptible. New cultivars with good-quality grain are required that can be grown successfully by upland farmers where drought is a common problem. Recent breeding efforts have produced several drought-resistant cultivars released in India with very high degree of drought resistance (Verulkar et al. 2010; Gowda et al. 2011). Some of the most promising lines described by Verulkar et al. (2010) had yields "on par with Vandana" under severe drought stress. We have shown that PY 84 has a higher average yield in three eastern Indian states than Vandana and Kalinga III (Fig. 2) and better adaptation for yield (Fig. 1). Many farmers in Jharkhand preferred Kalinga III to Vandana because it has fine, slender grains (Virk et al. 2003; Witcombe et al. 2011), a trait shared by PY 84 (and potentially conferring a higher market price).

Large-scale seed production and dissemination is required if seed of PY 84 is to reach the millions of farmers who could benefit. State subsidies for seed production of drought-tolerant cultivars could help the spread of drought tolerant cultivars (Pray et al. 2011), but PY 84 distribution has not yet been subsidised in India. It has been produced on a small scale by the Jaganath Crop Producer Company (JCPC) in Odisha in the Research Into Use programme funded by the UK's Department for International Development (DFID) and was distributed to 390 farmers in Jharkhand in 2011.

Conclusions

The combined evidence from previous studies and the field and experimental trials reported here supports the hypothesis that the four introgressed root QTLs from Azucena are associated with phenotypes with longer roots, as predicted when the MABC programme was initiated. Here, we have demonstrated that the introgressed QTLs are also associated with higher grain yield in farmers' fields. Therefore, introgression of four root QTLs using marker-assisted selection has successfully increased grain yield in upland, drought-prone environments.

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