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Grain yield and physiological traits of rice lines with the drought yield QTL *qDTY*$_{12.1}$ showed different responses to drought and soil characteristics in upland environments

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Abstract. To improve yield in upland conditions, near-isogenic lines (NILs) of the major-effect drought yield quantitative trait locus *qDTY*$_{12.1}$ in rice (*Oryza sativa* L.) were developed in the background of the upland variety Vandana. These NILs have shown greater water uptake a larger proportion of lateral roots, and higher transpiration efficiency under drought than Vandana, and one NIL (481-B) was selected as having the highest yield. In this study, the NILs were assessed in two greenhouse and 18 upland field trials for their response to drought and different soil textures. Performance of *qDTY*$_{12.1}$ NILs was not affected by soil texture but showed a notable response to drought stress severity. The yield advantage of 481-B over Vandana was highest in field trials with intermittent drought stress, in which the mean trial yield was greater than 0.5 t ha^{-1}, and in the least favourable well watered trial. The effects of *qDTY*$_{12.1}$ on water uptake were most apparent under mild to moderate stress but not in very severe drought or well watered treatments, whereas the lateral root and transpiration efficiency responses were observed under a range of conditions. These results highlight the varying response of *qDTY*$_{12.1}$ across upland environments and the complexity of multiple mechanisms acting together to confer an effect on rice yield under drought.

Additional keywords: carbon isotope discrimination, environment, *Oryza sativa* L., root.

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Introduction

Higher grain yield and increased yield stability across a range of environments are needed for rice (*Oryza sativa* L.) farmers, who typically harvest yields of 0.9–2.4 t ha^{-1} in rainfed lowland fields and 0.6–1.5 t ha^{-1} in upland fields (Singh and Singh 2000). In an effort to improve rice yield under drought in upland environments, the major-effect drought yield quantitative trait locus (QTL) *qDTY*$_{12.1}$ was identified through simultaneous selection for yield under drought and under well watered conditions in the background of the upland rice variety Vandana (Bernier *et al*. 2007). This QTL has been observed to confer an average yield advantage of up to 0.5 t ha^{-1} under severe upland drought through increased water uptake, lateral root growth and transpiration efficiency under drought (Bernier *et al*. 2009*a*, Dixit *et al*. pers. comm.). Bernier *et al*. (2009*b*) reported an increasing effect of *qDTY*$_{12.1}$ with increasing stress severity (classified according to average grain yield) across environments in India and the Philippines, and near-isogenic lines (NILs) with *qDTY*$_{12.1}$ were subsequently developed. A large genotype × environment interaction is commonly cited in studies on rainfed rice (Wade *et al*. 1999, Cooper *et al*. 1999, Acuña *et al*. 2008) and varietal differences have been reported to become smaller in increasingly unfavourable environments (Mandal *et al*. 2010). The present study aimed to evaluate the environmental response of *qDTY*$_{12.1}$ NILs in terms of grain yield and at a mechanistic level, given the related traits that have been identified.

In NILs of *qDTY*$_{12.1}$, increased lateral root growth was observed at certain depths in field drought studies and an increased number of branches was observed in the roots at seedling stage under drought stress (Dixit *et al.* pers. comm.). Lateral root growth may be an important trait for stabilising yield in upland rice environments, which are typically drought-prone and are characterised by low soil fertility (Widawsky and O'Toole 1996). Lateral roots have been found to increase phosphorus uptake in common bean (*Phaseolus vulgaris*) (Lynch and Van Beem 1993) and in maize (*Zea mays* L.) (Zhu and Lynch 2004), and have been attributed to increased water uptake in rice under drought (Suralta *et al*. 2008, 2010). Furthermore, this trait has shown variation by genotype and environment in rice (Bañoc

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et al. 2000; Suralta *et al*. 2008 and 2010; Henry *et al*. 2011). A high degree of variability has been reported for rice root traits in general under upland conditions (as reviewed by Gowda *et al*. 2011). Genetic improvement of rice for root traits may be limited by soil conditions (Kondo *et al*. 2003), as some environments may not be favourable for expression of root traits. We therefore hypothesised that since $qDTY_{12.1}$ has been found to affect lateral root response, the effectiveness of this QTL for water uptake in different soil types and textures may vary.

In addition to the lateral root phenotype, $qDTY_{12.1}$ was observed to affect transpiration efficiency, as evidenced by leaf carbon isotope discrimination ($\Delta^{13}C$), gas exchange, and soil water uptake patterns in the field and gravimetrically in the greenhouse under drought stress but not under well watered conditions (Dixit *et al*. pers. comm.). In rice leaves, $\Delta^{13}C$ varies among genotypes (Dingkuhn *et al*. 1991; Impa *et al*. 2005) and has been reported to be affected by both drought and soil fertility (N application; Kondo *et al*. 2004). The different component traits for transpiration efficiency may be differentially affected by environmental conditions, including by the severity of drought stress and the vapour pressure deficit (Sinclair 2012). Therefore, environmental factors may play an important part in the increased transpiration efficiency as conferred by $qDTY_{12.1}$. Evaluation of this trait across environments was another objective of this study.

As part of research programs to improve drought tolerance in rice, varieties improved with $qDTY_{12.1}$ will be targeted to a range of upland environments. Although many stress tolerance genes and QTLs have recently been identified, little is known about their interactions with environmental factors (Fukao and Xiong 2013). Based on the physiological traits that have been found to be associated with $qDTY_{12.1}$, we hypothesised that the effectiveness of $qDTY_{12.1}$ on yield may vary with different soil characteristics. In this study, we evaluated the effects of $qDTY_{12.1}$ on grain yield and on physiological traits across a range of environments, in both greenhouse lysimeter and field studies, with emphasis on the response to differences in soil texture and drought severity. Our aim was to better define the responsiveness of $qDTY_{12.1}$ across different drought environments and to characterise the relative contribution of the related physiological traits to grain yield under drought.

Materials and methods

Genetic material

Four $qDTY_{12.1}$ NILs ($BC_2F_{3:4}$ and $BC_3F_{3:7}$) were developed at the International Rice Research Institute (IRRI) by marker-assisted backcrossing IR84984–83–15–481-B (481-B), IR849 84–21–19–78-B, IR90020:22–283-B-1 and IR90020:22–283-B-4. These were grown in the two greenhouse studies and in field trials (Trials 4–10 and 14–16), along with the parents Vandana (the drought-tolerant recipient parent) and Way Rarem (the drought-susceptible parent and $qDTY_{12.1}$ donor). As this physiological and environmental characterisation of $qDTY_{12.1}$ was conducted concurrently with NIL development, earlier-generation genotypes were evaluated in Trials 1–3 and 13, which were comparisons of BC_2- and BC_3-derived +QTL and –QTL lines; and in Trials 11, 12, 17 and 18, which included six BC_2 and BC_3 lines in addition to 481-B and Vandana (Table S1, available as Supplementary Material to this paper).

Experimental conditions

Greenhouse studies: effects of drought and soil texture on $qDTY_{12.1}$ NILs

Two greenhouse experiments in lysimeters constructed from PVC pipes were conducted to evaluate the effects of soil texture and drought severity on $qDTY_{12.1}$ NILs. Experiment 1 (Exp1) was conducted from July to October 2011 in large lysimeters, as described by Kijoji *et al*. (2013); and Experiment 2 (Exp2) in smaller lysimeters in the greenhouse from November 2011 to January 2012. Exp2 was conducted using smaller lysimeters and with earlier initiation of the drought stress treatment in an attempt to apply a severe drought stress treatment, which was not achieved in Exp1. Temperature and relative humidity averaged 29.8°C and 66.6% in Exp1, and 28.6°C and 77.4% in Exp2 (Fig. S1). Light levels at midday averaged 950 µmol m^{-2} s^{-1} in Exp1 and were not measured inside the greenhouse in Exp2 but averaged 800 µmol m^{-2} s^{-1} outside the greenhouse.

Four replicates of four treatments contrasting in soil texture (+sand and –sand) and moisture conditions (well watered (WW) and dry-down (DD)) were included in each experiment in a completely randomised design: –sand/WW, –sand/DD, +sand/WW and +sand/DD. In Exp2, eight replicates of the –sand treatments were included. The lysimeters were 95 cm tall × 20 cm in diameter in Exp1 and 36 cm tall × 20 cm diameter in Exp2. In the –sand treatment, the lysimeters were filled with 27.5 kg (Exp1) and 10.45 kg (Exp2) of dried sieved soil from the IRRI Experiment Station (1.1 mEq 100 g^{-1} K, 8.5 mEq 100 g^{-1} Mg, 15.2 mEq 100 g^{-1} Ca and 43.2 mg kg^{-1} P; and 36.2%, 22.5% and 41.5% clay, sand and silt, respectively) to a height of 90 cm (Exp1) and 31 cm (Exp2), with a bulk density of ~1.0 g cm^{-2}. In the +sand treatment, lysimeters were filled with 27.5 kg (Exp1) and 10.45 kg (Exp2) of a mixture of equal volumes of dried sieved soil and silica sand (Ava Construction, Quezon City, Philippines; ~11.5 L in Exp1 and 4.4 L in Exp2 of each component). In all lysimeters, the equivalent of 200 : 100 : 100 (N : P : K) kg fertiliser ha^{-1} (assuming a soil weight of 2000 t ha^{-1} per furrow slice) was added by thoroughly mixing the soil and the soil–sand mixture with 9.8 g and 3.7 g of complete fertiliser containing 14 : 14 : 14 (N : P : K) in Exp1 and Exp2, respectively, and 6.9 g and 2.6 g ammonium sulphate containing 20 : 0 : 0 (N : P : K) in Exp1 and Exp 2, respectively, before filling the lysimeters with the mixture.

Seeds were germinated in Petri dishes on filter paper moistened with tap water, then planted (three seedlings per lysimeter) after 4 days. Seedlings were planted into the lysimeters at field capacity, which was achieved by saturating the soil and then allowing the water to drain freely through holes drilled at the bottom of each lysimeter. The average total volume of water per lysimeter at field capacity was ~5.4 L (Exp1) and 2.6 L (Exp2) in the +sand treatment, and 7.0 L (Exp1) and 3.0 L (Exp2) in the –sand treatment, as determined by weighing before and after addition of water to the lysimeters. Plants were thinned to one per lysimeter before the start of the DD treatments. Lysimeters were covered with a plastic sheet around the base of each plant to reduce nontranspirational loss of water, and

water was withheld in the DD treatment starting at 35 days after planting (DAP) in Exp1 and at 25 DAP in Exp2.

Field studies: effects of drought and soil characteristics on yield and traits related to qDTY$_{12.1}$

Eighteen field trials that included soil characterisation were conducted (Table 1) under drought and well watered control treatments in India at the Central Rainfed Upland Rice Research Station (23°57′39.30″N, 85°22′5.07″E) in Hazaribag, Jharkand, and in the Philippines at IRRI (14°10′11.81″N, 121°15′39.22″E), Los Baños, Laguna, in 2010–12. All trials were established by direct seeding under aerobic conditions in levelled upland fields at a density of 2.0–2.5 g m^{-1} in 1.25–2.25 m^2 plots (2–6 rows of 1.25–5 m length), with three to five replicates per genotype in a randomised complete block design.

Fertiliser and crop management practices were followed as described by Bernier *et al*. (2007): typically one basal application of 40 : 40 : 40 (N : P : K) kg ha^{-1} using complete fertiliser containing 14 : 14 : 14 (N : P : K) followed by a topdressing of 40 kg N ha^{-1} using ammonium sulfate containing 21 : 0 : 0 (N : P : K) once in the stress treatment (except for Trials 4–8, which received the topdressing twice) and twice in the control treatments.. The control treatments were irrigated two or three times per week throughout the trials. All stress treatments were irrigated two or three times per week during establishment and early vegetative growth. The drought stress treatment was initiated by withholding irrigation at ~35 days after sowing (DAS), which was just before the time of panicle initiation.

Physiological measurements

Greenhouse lysimeters

To determine water uptake rates, lysimeters in both experiments were weighed three times per week after initiation of the drought stress treatment. In Exp1, weighing was done using an electric hoist (Shopstar Electric Chain Hoist, Columbus McKinon Corp., Amherst, NY, USA) attached to a custom-built gantry crane that lifted the lysimeters onto a weighing balance (KERN SCE-3.0, Kern and Sohn GmbH, Balingen, Germany) as described by Kijoji *et al*. (2013). In Exp2, the lysimeters were lifted onto the balance manually. Digital images of the shoot of each plant were acquired with a digital camera (Canon Powershot S90, Canon Inc., Tokyo, Japan) at the time of weighing to normalise water uptake rates for plant size according to the method used by Kijoji *et al*. (2013), in which water uptake between two weighing dates (g day^{-1}) was divided by the apparent leaf area (cm^2). On each weighing date, plants in the WW treatments were rewatered to a target weight to reach field capacity. In Exp2, plants in the DD treatment were rewatered on each weighing date as necessary to maintain soil moisture above 20% of field capacity. To allow recovery from severe drought stress, plants in the DD treatment of Exp2 were rewatered at 45 DAP by plugging the drainage holes with rubber stoppers and keeping the soil saturated for two days before re-initiating the DD treatment. Plants were harvested at 97 DAP (Exp1) and 75 DAP (Exp2). Shoots were dried at 70°C and weighed to determine shoot biomass. In Exp1, shoots (all aboveground parts) were then ground and analysed for nutrient

Table 1. Field experiments and descriptive soil parameters measured. Experiments were conducted in the dry seasons (DS) and wet seasons (WS)
IRRI, International Rice Research Institute. For 'Location' ROS indicates a rainout shelter trial; B2M, D24, J8, UN, UO, and UR are field codes. –, information not available

Trial	Season	Location	Nutrient				Soil			Bulk density	Bulk density	Minimum soil water potential	Initial slope of dry-down	Length of initial dry-down
			P (Olsen) mg kg^{-1}	K	Mg	Ca	Clay	Sand	Silt	5–10 cm	25–30 cm	at 30 cm	–kPa day^{-1}	days
				mEq 100 g^{-1}				%		g cm^{-3}		–kPa		
Stress														
1	2010 DS	IRRI J8b ROS	26	–	–	–	50	32	18	0.88	0.86	74	2.8	27
2	2010 WS	IRRI J8 ROS	28	–	–	–	48	37	15	0.88		42	1.5	27
3	2012 DS	IRRI UR	26	1.17	6.81	11.5	24	35	41	1.34	1.30	60	4.1	18
4	2012 DS	IRRI UN-A	33	1.33	8.39	15.6	39	15	46	1.36	1.39	83	3.8	21
5	2012 DS	IRRI UN-B	35	1.3	8.68	15.8	40	15	45	1.36	1.39	20	0.7	16
6	2012 DS	IRRI UN-C	33	1.48	8.81	15.9	40	16	44	1.36	1.39	24	0.6	13
7	2012 DS	IRRI UN-17	21	1.12	9.41	17.3	36	20	44	1.28	0.83	86	4.3	14
8	2012 DS	IRRI UN-18	23	1.34	9.26	17	36	19	45	1.30	1.32	83	1.6	10
9	2012 DS	IRRI D24 ROS1	27	–	–	–	39	–	–	1.10	1.13	67	2.6	23
10	2012 WS	IRRI D24 ROS1	27	–	–	–	39	–	–	1.10	–	32	0.5	30
11	2011	India ROS	12.6	0.93	–	–	28	38	34	1.50[B]	–	48[A]	1.3	35
12	2012	India ROS	12.6	0.93	–	–	28	38	34	1.50[B]	–	48	1.5	30
Control														
13	2012 DS	IRRI UR	22	1.11	5.72	9.92	24	36	40	–	–	–	–	–
14	2012 DS	IRRI UO	37	1.53	6.68	11.6	36	20	44	1.38	1.23	–	–	–
15	2012 DS	IRRI UR	22	1.11	5.72	9.92	24	36	40	1.27	1.24	–	–	–
16	2012 WS	IRRI UR	22	1.11	5.72	9.92	24	36	40	–	–	–	–	–
17	2011	India B2M	9.2	0.24	–	–	29.2	24	46.8	–	–	–	–	–
18	2012	India B2M	9.2	0.24	–	–	29.2	24	46.8	–	–	–	–	–

[A]Extrapolated from measurements at depths of 15 and 45 cm.
[B]Estimated based on particle density.

content by inductively coupled plasma-optical emission spectrometry at the IRRI Analytical Service Laboratory (ASL).

Roots were sampled at depths of 40–60 cm and 60–90 cm in all treatments, as well as at 20–40 cm in the DD treatment in Exp1 and from the whole lysimeter in Exp2. This was achieved by pulling the plastic liner out of the lysimeters and, in Exp1, by cutting the soil column into four sections. Roots were gently washed, scanned and analysed using WinRhizo ver. 2007 (Regent Instruments, Québec, QC, Canada) to determine root length and the proportion of lateral roots (% root length in diameter classes <0.2 mm).

Field studies

Soil water potential was monitored in all stress trials using three tensiometers installed at a depth of 30 cm (Soilmoisture Equipment Corp., Santa Barbara, CA, USA), except in Trials 1 and 2 (20 cm), and 11 (15 and 45 cm). Plots were irrigated only when plants showed severe stress symptoms and when soil water tension fell below –50 to –65 kPa. A line-source sprinkler was used to create a soil moisture gradient with three distinct treatments in Trials 4–6, according to the method used by Puckridge and O'Toole (1980). Rain was excluded from the experimental fields using a rolling rainout shelter in all trials under drought stress treatments, except in Trials 3–8, which received ~148 mm of rain across the stress treatment period.

Analysis of soil physical properties was conducted on soil sampled from a depth of 0–15 cm at the IRRI ASL for trials in the Philippines and at the IRRI-India laboratory (Modipuram) for trials in India. For trials conducted at the same location in subsequent years, soil analysis was performed only once. Carbon isotope discrimination ($\Delta^{13}C$) was measured on the youngest leaves sampled mid-season (21–83 das) in Trials 3, 4–6, 10, 13 and 16; on flag leaves sampled at 76–81 DAP in Trials 1, 9 and 15; and on grain samples from Trials 1, 3, 9, 13 and 15. Tissue was dried at 70°C, ground in a Mini Wiley Mill (#20 mesh; Thomas Scientific, Swedesboro, NJ, USA), analysed by mass spectrometry (at the IRRI ASL for samples in the Philippines and at University of Agricultural Sciences Bangalore for samples in India), and $\Delta^{13}C$ was calculated as shown in Eqn 1 according to Farquhar *et al.* (1989):

$$\Delta^{13}C = \frac{-8 - [^{13}C]}{1 + \frac{\text{leaf}[^{13}C]}{1000}}. \quad (1)$$

Leaf samples were collected at 81 DAS (at the start of flowering) in Trials 9 and 15, and at 49 DAS (around panicle initiation) in Trials 10 and 16, dried at 70°C, and then ground and analysed for nutrient content as described above.

Shoot growth and groundcover dynamics were monitored according to normalised difference vegetation index (NDVI) measured around midday using a GreenSeeker Handheld Sensor (NTech Industries, Ukiah, CA, USA) that was carried through the field (Trials 1, 3, 9 and 10) or mounted ~1 m above the plant canopy from a rack that rolled along the tracks of the rainout shelter (Trial 2). A range of instruments were used to determine canopy temperature, which was measured at midday throughout the seasons in the stress treatments from a 3-m ladder by infrared thermography using an NEC TH7800 infrared camera (NEC Avio Infrared Technologies Co. Ltd, Tokyo, Japan) in Trials 1, 3 and 10; and with a FLIR Thermacam A320 Infrared Camera (FLIR Systems Co., Boston, MA, USA) from ~6 m above the ground in Trial 2. Infrared images were analysed with the software appropriate for the respective infrared cameras (Report Generator ver. 1.7 software, NEC Avio Infrared Technologies Co. Ltd; and TherMonitor, Thermoteknix Systems Inc., Cambridge, UK) by drawing a line along the planted rows in the thermal images in order to select pixels associated only with plant temperature and to avoid sections of soil. In Trial 10, a data-logging infrared sensor (three locations per plot; Apogee Instruments, Logan, UT, USA) was used to measure canopy temperature throughout the season; an infrared gun (IR Thermometer 8872 Spectrum Technologies Inc., Plainfield, IL, USA) was used in Trials 4–6 at 99 DAS, and an Agri-Therm III infrared sensor (Everest Interscience Inc., Tucson, AZ, USA) was used in Trial 12 at 59 DAS.

Stomatal conductance was measured at midday on two or three leaves per plot with an AP4 porometer (Delta-T Devices, Cambridge, UK) in Trials 1, 2, 3, 9 and 10; and three times at 67 DAS in Trial 12. Stomatal density was determined from images of leaf epidermal peels sampled at 30–120 DAS in Trials 1, 3 and 9 in order to sample a range of leaf ages under drought stress conditions, under which the leaves were formed. Samples were observed at 10× magnification and the number of stomata in a given area between leaf veins was counted.

Root samples were taken 2–3 days after rewatering following severe stress symptoms at 58–85 DAP in Trials 1, 3, 9, 10, 15 and 16, using a core sampler 4 cm in diameter (fabricated at IRRI, Los Baños, Philippines) to a depth of 60 cm. Soil cores were divided into 15-cm segments and roots were washed by repeatedly mixing the soil with water in a container and pouring the root–water suspension over a 1-mm plastic sieve. Only living rice roots were retained for analysis. All samples were stored in 50% ethanol until scanning. Root samples were scanned at 600 dots per inch (Epson V700, Epson, Suwa, Japan) and scanned images were analysed using WinRhizo ver. 2007d (Régent Instruments) as described above.

Data analysis

Statistical analyses were performed in R ver. 2.8.0 (R Foundation for Statistical Computing, Vienna, Austria). A Pearson correlation (*correlation* script) was run to compare trends among soil parameters with grain yield from the field studies. ANOVA (*aov* script) was used for single parameters in an individual trial with genotype and replication as fixed variables, and LSD mean comparisons were used as the *post hoc* test. For all field trials, the ANOVA included all genotypes in the trial, except for $\Delta^{13}C$ in Trial 6 and stomatal density in Trial 1, from which only selected genotypes were sampled. For the greenhouse lysimeter experiments and for canopy temperature and NDVI measurements from the field, a repeated-measures analysis was conducted with the mixed model ASREML using Wald's test in R, with genotype and days after sowing as fixed variables, and replicate as a random variable.

Results

Greenhouse studies: differences between qDTY$_{12.1}$ *NILs and Vandana*

The degree of drought stress applied in the lysimeter experiments was, in general, moderate in Exp1 (less leaf-rolling or drying; biomass was reduced by 36.0% and 42.1% from the –sand and +sand treatments, respectively, compared with the WW control) and severe in Exp2 (a high degree of leaf-rolling or drying; biomass was reduced by 60.3% and 59.6% from the –sand and +sand treatments, respectively, compared with the WW control). In Exp1 (large lysimeters), genotypic differences between the $qDTY_{12.1}$ NILs and the parents were most evident in the +sand/DD treatment, where the NILs had greater leaf area and lower water uptake rates per leaf area in the early stages of the drought stress treatment (Fig. 1, Table S2). In Exp2 (small lysimeters), differences among the NILs and the parents were less distinct, but some genotypic differences in water uptake rates were observed in the –sand/DD treatment after rewatering. These trends between the NILs and the parents were not evident in the other treatments. No consistently significant differences in root growth were observed in the lysimeter experiments (Figs S2, S3). In Exp1, the NILs showed the highest proportions of lateral roots in the +sand/WW treatment, whereas Way Rarem showed the greatest root length in the –sand/DD treatment (Fig. S2). In Exp2, Vandana showed the greatest total root length across treatments, which was significant in the +sand/DD treatment (Fig. S3).

Field studies

Environmental response of grain yield

The yield advantage of 481-B over Vandana was not consistent across environments (Table 2). Based on differences

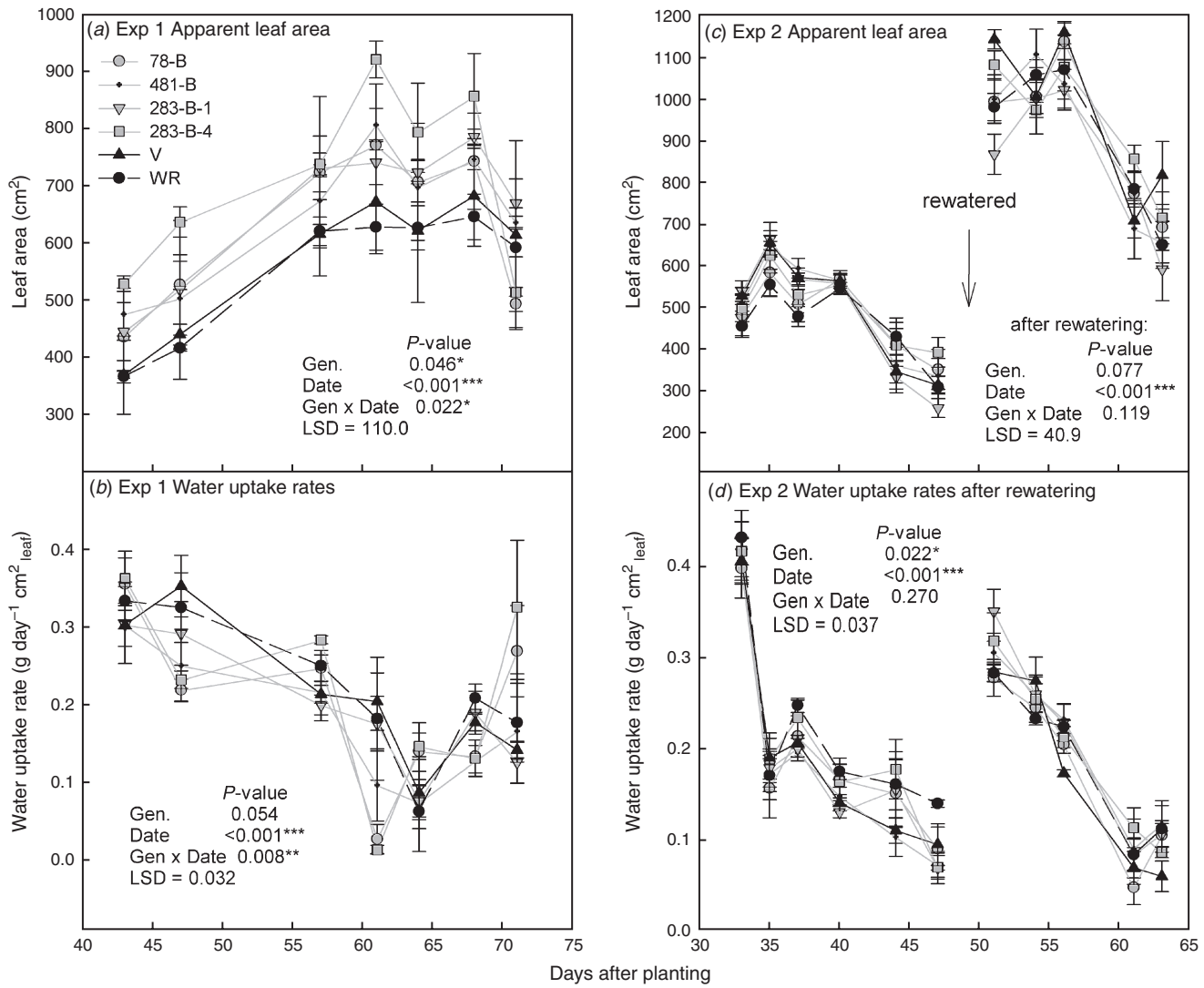

Fig. 1. (*a*) Apparent leaf area and (*b*) water uptake rates normalised for leaf area for rice plants in the DD treatment with sand (+sand/DD) in Experiment 1 (Exp1) (large lysimeters); (*c*) apparent leaf area and (*d*) water uptake rates normalised for leaf area in the DD treatment without sand in Experiment 2 (Exp2) (small lysimeters). Values shown are means ± s.e. Significance levels are indicated as follows: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Gen, genotype.

in mean yield and significance values, 481-B showed the most distinct advantage over Vandana in Trials 3, 6, 8 and 13. In contrast, 481-B showed no advantage over Vandana in Trials 2, 10, 12 and 14. In the group of trials in which 481-B showed a yield advantage over Vandana, the drought stress treatments all showed a mean trial yield above 50 g m^{-2} (0.5 t ha^{-1}). In the group of trials under drought stress treatments in which 481-B did not have a yield advantage over Vandana, the drought stress treatments all showed a mean trial yield of less than 30 g m^{-2} (0.3 t ha^{-1}; Table 2).

The soil water potential patterns varied widely across trials, but Trials 3 and 8, in which 481-B had a yield advantage over Vandana, tended to show more fluctuations in soil water potential than Trials 2, 10 and 12, in which 481-B had no yield advantage over Vandana (Fig. 2). The trials (Trials 3, 6 and 8) in which 481-B had a yield advantage over Vandana all had shorter initial dry-down periods than those (Trials 2, 10 and 12) in which 481-B had no yield advantage over Vandana (Table 1; Fig. 2).

Across the 18 field trials in this study, soil parameters that were significantly correlated with the yield of different genotypes (Table 3) were the percentage clay in the soil, which was negatively correlated with the yield of Vandana, and the minimum soil water potential reached across the drought stress treatments, which was negatively correlated with the yield of Way Rarem. No effects of bulk density, the slope of the initial dry-down or soil phosphorus levels were observed on yield. The yield advantage of 481-B over Vandana was not significantly correlated with any soil parameter measured.

Physiological response of qDTY$_{12.1}$ *NIL 481-B and Vandana under different field conditions*

To understand the mechanistic responses related to the yield advantage of *qDTY$_{12.1}$* NIL 481-B over Vandana that was observed in some trials (significant in Trials 6 and 8; higher trends but not significant in Trials 1, 3, 4, 5, 7, 9 and 11), the types of drought stress and the physiological responses from available data for the two most contrasting groups of trials (those with and without a yield advantage) were compared. Higher transpiration efficiency trends in 481-B were evident in both groups of trials that were under drought stress treatment (Trials 3, 10 and 12 (not significant); Fig. 3), but not in the two trials that received regular irrigation (Fig. 3; Trial 6 (mild stress treatment in the line-source experiment) and in Trial 13 (well watered treatment)). However, $\Delta^{13}C$ in the grain was higher in 481-B across trials in both drought and well watered treatments, and in trials in which 481-B did or did not have a yield advantage over Vandana (Fig. 4). Canopy temperature did not differ between 481-B and Vandana in any measurement across the various trials (Fig. 5). Stomatal conductance as measured by a porometer did not show consistent differences between 481-B and Vandana (Fig. S4). No differences in stomatal density were observed (Table S3). Increased lateral root formation was observed at multiple depths in Trial 15 (Fig. 6) and in Trial 9 in which the yields of 481-B and Vandana did not differ; and in Trial 1 (Dixit *et al.* pers. comm.) in which 481-B had a yield advantage over Vandana. NDVI did not differ among genotypes (Fig. 7) and no differences in phosphorus uptake were observed between 481-B and Vandana (Table S4).

Table 2. Grain yield values and statistics for each trial based on ANOVAs on all rice genotypes in each trial.
Yield values shown are means ± s.e. *, significant at $P < 0.05$; **, significant at $P < 0.01$; ***, significant at $P < 0.001$; df. degrees of freedom

Trial	Mean trial yield (g m^{-2})	LSD	*P*-value (all entries)	*F*	df	481-B yield (g m^{-2})	Vandana yield (g m^{-2})
Stress							
1	32.0	20	0.009**	3.923	8	57.9 ± 13.8	41.6 ± 16.8
2	30.3	49	0.347	1.482	3	23.0 ± 14.7	30.1 ± 19.4
3	56.3	119	<0.001***	2.431	5	204.2 ± 48.2	178.2 ± 36.3
4	16.6	142	0.073	2.709	5	202.5 ± 66.5	156.7 ± 60.0
5	156.6	47	0.0247*	3.907	5	183.2 ± 19.2	149.0 ± 25.0
6	192.5	47	<0.001***	16.083	5	246.7 ± 17.7	139.4 ± 13.9
7	77.4	31	0.060	2.902	5	84.5 ± 12.6	78.3 ± 11.0
8	176.3	52	<0.001***	26.815	5	229.8 ± 17.5	177.2 ± 14.0
9	1.7	5	0.357	1.356	5	4.17 ± 4.17	0.339 ± 0.339
10	16.9	7	<0.001***	24.86	5	19.0 ± 6.1	30.0 ± 5.5
11	133.2	72	0.0178*	4.58	8	168.7 ± 22.5	132.7 ± 9.0
12	1.8	22	0.389	1.256	5	8.3 ± 1.6	18.7 ± 8.0
Control							
13	248.2	64	0.00322**	8.298	4	324.3 ± 33.5	269.7 ± 20.3
14	243.6	61	0.400	0.943	5	226.4 ± 18.0	230.9 ± 15.4
15	176.6	106	0.058	4.092	5	210.3 ± 18.2	201.3 ± 31.5
16	177.5	68	0.0172*	4.352	5	192.0 ± 24.6	172.8 ± 13.1
17	198.5	72	0.023*	4.178	8	245.6 ± 40.8	191.1 ± 42.2
18	197.9	38	0.121	2.808	5	200.5 ± 6.9	171.9 ± 9.0

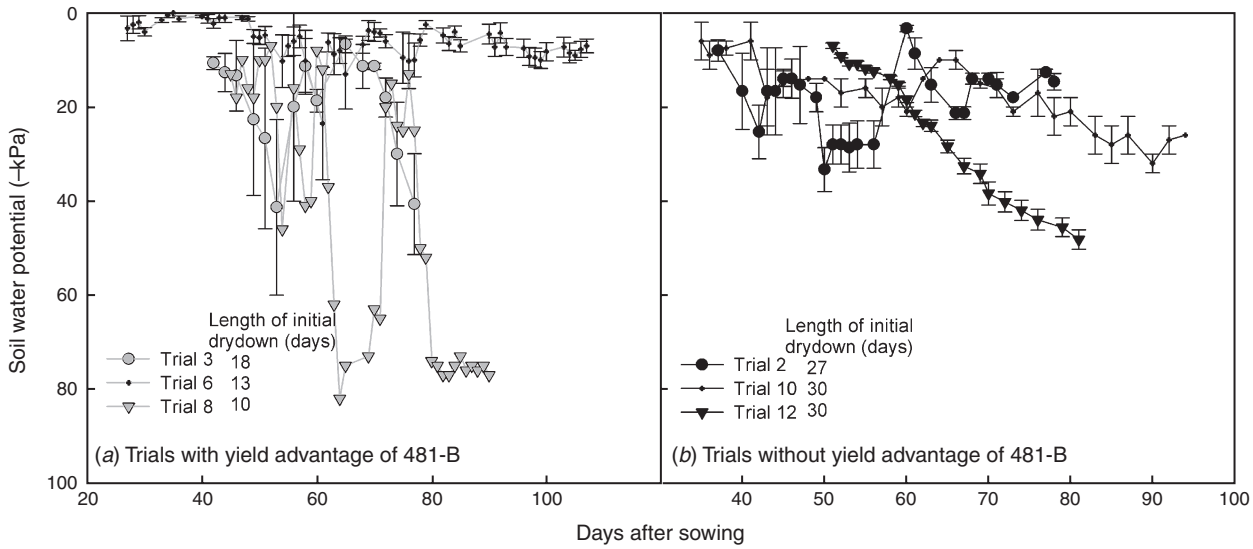

Fig. 2. Soil water potential readings from tensiometers installed at a depth of 30 cm in (*a*) trials in which the rice line 481-B had a yield advantage over the cultivar Vandana, and (*b*) trials in which 481-B had no yield advantage over Vandana. Values shown are means ± s.e.

Table 3. Correlation matrix of physical soil characteristics, soil water potential dynamics in the stress treatment and rice grain yield across the 18 field trials in this study *, significant at $P < 0.05$; **, significant at $P < 0.01$; ***, significant at $P < 0.001$

	Available P	% Clay	Bulk density 5–10 cm	Minimum soil water potential at 30 cm	Slope of initial dry-down	Length of initial dry-down	Vandana yield	Way Rarem yield	481-B yield	283-B-1 yield
% Clay	0.53*	–	–	–	–	–	–	–	–	–
Bulk density 5–10 cm	–0.22	–0.72**	–	–	–	–	–	–	–	–
Minimum soil water potential at 30 cm	–0.23	–0.03	–0.1	–	–	–	–	–	–	–
Slope of initial dry-down	–0.03	–0.17	–0.05	0.79**	–	–	–	–	–	–
Length of initial dry-down	–0.49	–0.04	–0.15	–0.21	–0.23	–	–	–	–	–
Vandana yield	–0.13	–0.52*	0.38	–0.13	–0.26	–0.52	–	–	–	–
Way Rarem yield	0.41	–0.01	0.32	–0.6*	–0.41	–0.46	0.58*	–	–	–
481-B yield	–0.13	–0.46	0.42	–0.23	–0.35	–0.54	0.96***	0.6*	–	–
283-B-1 yield	–0.05	–0.29	0.29	–0.25	–0.41	–0.55	0.94***	0.6*	0.99***	–
Yield difference (481-B – Vandana)	–0.09	–0.08	0.28	–0.34	–0.42	–0.45	0.43	0.34	0.66**	0.59*

Discussion

In this study, the effect of $qDTY_{12.1}$ was more related to the level of drought severity than to the characteristics of the soil in which the trials were conducted. In the field, $qDTY_{12.1}$ NIL 481-B showed a yield advantage over Vandana in trials with more fluctuating soil water potential and shorter initial dry-down periods, but not in response to different soil parameters. The effect of $qDTY_{12.1}$ on different physiological traits was also lowest under very severe and under well watered field conditions, but did not follow the same trends as grain yield in all trials. These results highlight that the effects of $qDTY_{12.1}$ vary across environments and that the physiological traits associated with $qDTY_{12.1}$ show a distinct environmental response to that of grain yield.

The yield ranges in this study (0.01–2.5 t ha^{-1}) were similar with those reported in the evaluation of $qDTY_{12.1}$ by Bernier *et al*. (2009*b*). The mean trial yield was lowest in the trials conducted in rainout shelters, which were characterised by tensiometer readings that showed long initial dry-down periods, little fluctuation due to continuous dry-down and infrequent irrigation (Table 1, Fig. 2). The trials in rainout shelters were those in which 481-B showed the least or no yield advantage over Vandana. $qDTY_{12.1}$ NIL 481-B showed a yield advantage over Vandana in trials with more fluctuating soil water potential and shorter initial dry-down periods. No yield advantage was seen in drought stress trials that had a mean yield of 0.3 t ha^{-1} or less, which falls under the classification of 'very severe stress', in which yield is reduced by more than 85% compared with the well watered control (Kumar *et al*. 2009). In the well watered treatments, there appeared to be more yield advantage in trials conducted on soil with lower fertility (Trial 13 compared with Trial 14, for example) than in trials conducted in more favourable conditions. All trials were conducted on research station fields, which are

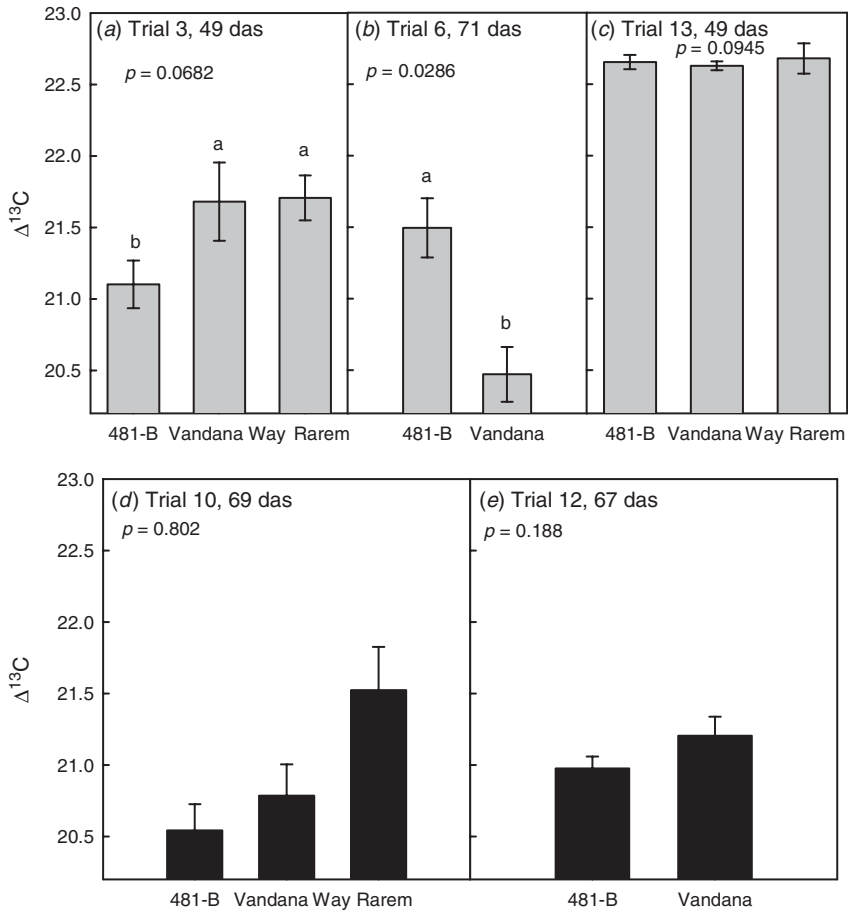

Fig. 3. Transpiration efficiency based on carbon isotope discrimination in the youngest leaves on selected dates in (*a*, *b*, *c*) trials in which the rice line 481-B had a yield advantage over the cultivar Vandana and (*d*, *e*) trials in which 481-B had no yield advantage over Vandana. (*a*), Trial 1; (*b*) Trial 6; (*c*) Trial 13; (*d*) Trial 10; (*e*) Trial 12. Values shown are means ± s.e., and letters indicate significant differences among genotypes as determined by LSD comparison ($P < 0.05$). *P*-values shown are for genotype effects on the whole trial (including genotypes not shown). DAS, days after sowing.

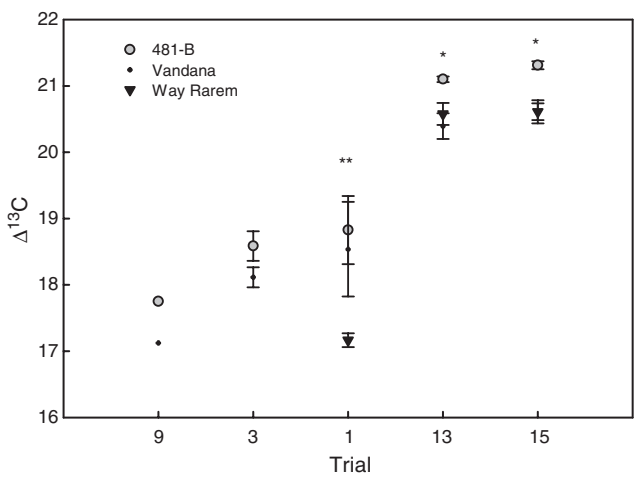

Fig. 4. Carbon isotope discrimination ($\Delta^{13}C$) as measured in harvested rice grains. Values shown are means ± s.e. Significance levels shown are for the whole trial (including genotypes not shown) and *, $P < 0.05$; **, $P < 0.01$.

typically highly fertile; as such, the effects of $qDTY_{12.1}$ on nutrient deficiency were not assessed.

In contrast with grain yield, physiological traits related to $qDTY_{12.1}$ showed less consistent groupings across different environments. Trends in physiological differences in lateral root growth and leaf $\Delta^{13}C$ (although nonsignificant in some cases) were observed even in trials where 481-B showed no yield advantage over Vandana. In Trial 15, it is possible that mild drought stress developed in the WW treatment between days on which the field was irrigated during the dry season, thereby inducing a lateral root response in 481-B but not affecting yield. In the greenhouse lysimeter experiments, differences among genotypes were observed in the DD treatment (leaf area and water uptake rates; Exp1), but not in the WW treatment. The differences in traits observed between the well watered and drought stress treatment in the field and greenhouse highlight the drought-specific response of $qDTY_{12.1}$.

Different water uptake patterns of $qDTY_{12.1}$ NILs and Vandana were evident in the lysimeters of Exp1 (Fig. 1), in

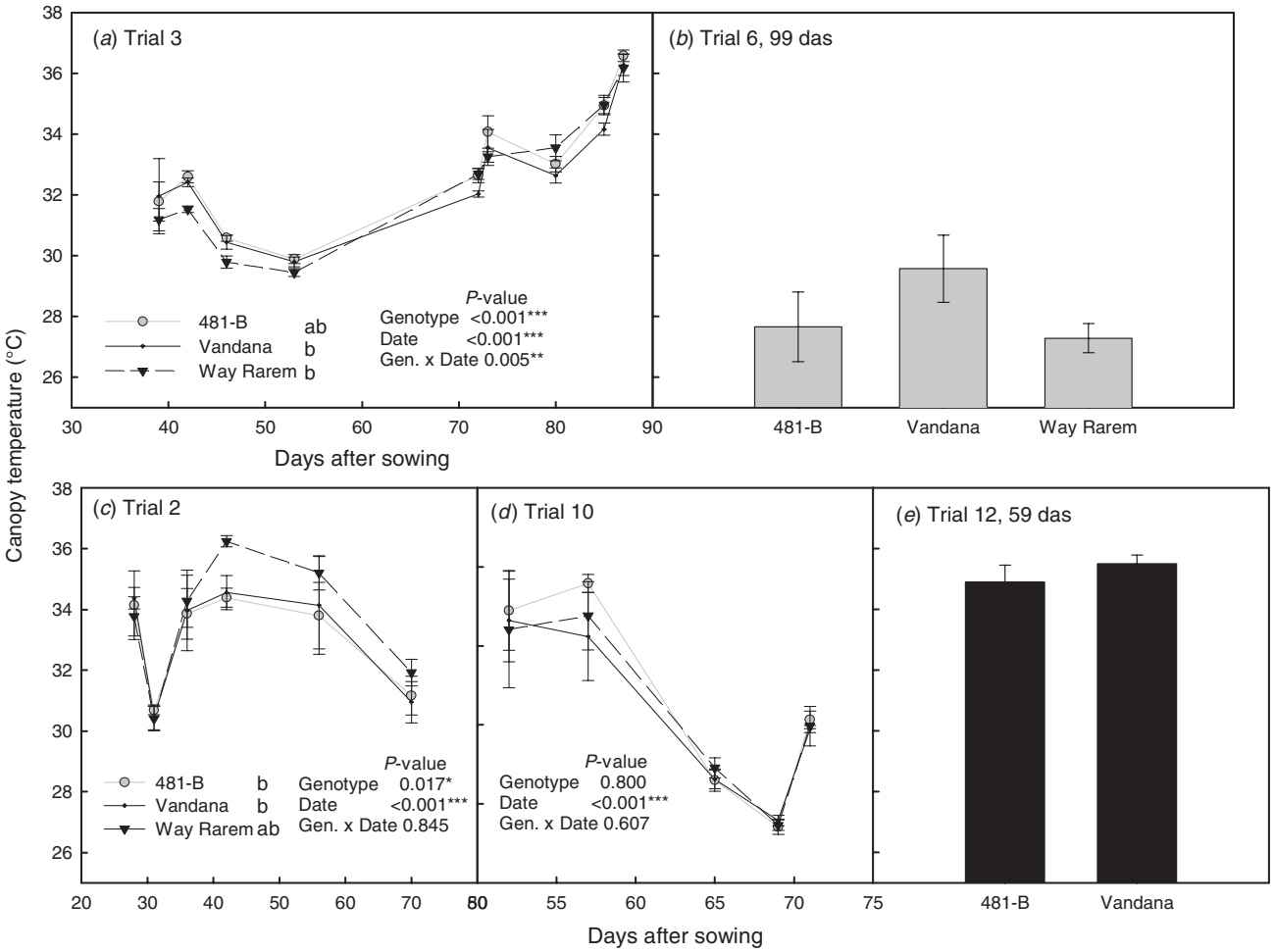

Fig. 5. Canopy temperature across the season or on selected dates in (*a*, *b*, *c*) trials in which the line 481-B had a yield advantage over the cultivar Vandana, and (*d*, *e*) trials in which 481-B had no yield advantage over Vandana. (*a*) Trial 3; (*b*) Trial 6; (*c*) Trial 2; (*d*) Trial 10; (*e*) Trial 12. Values shown are means ± s.e. Significance levels shown are for the whole trial (including genotypes not shown). *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; DAS, days after sowing.

which the NILs showed more conservative water uptake early in the drought stress period (despite having similar or greater shoot biomass) and greater water uptake later in the drought stress treatment. This conservative water uptake early in the drought stress was also observed through monitoring soil moisture levels in the field in Trials 9 and 10 (Dixit *et al*. pers. comm.). A conservative water uptake pattern has been previously reported in dryland crop lysimeter studies (e.g. Zaman-Allah *et al*. 2011) but was not observed in previous lowland rice experiments conducted in the same lysimeter facilities (Gowda *et al*. 2012; Kijoji *et al*. 2013). In previous lowland rice lysimeter studies that were initiated under flooded conditions, soil drying occurred slowly and the genotypes with the highest water uptake rates were typically those that had the greatest root length at depth. In contrast, the soil dried more rapidly in the upland conditions of the present lysimeter study, especially in the +sand treatment, and genotypes showed little differences in root length at depth. This suggests that mechanisms that provide a more rapid response (such as stomatal regulation) may be more important in upland conditions, where soil dries more rapidly, than in lowland drought conditions in which soil dries more slowly and thus may be more conducive to the plastic drought response of increasing root growth at depth.

The conservative water uptake observed in $qDTY_{12.1}$ NILs early in the stress period in the lysimeters (i.e. in the +sand/DD treatment of Exp1) and in the field (Trials 1 and 9; Dixit *et al*. pers. comm.) are in agreement with the higher transpiration efficiency, according to lower $\Delta^{13}C$, in multiple trials (Fig. 3; Dixit *et al*. pers. comm.). The different trends in $\Delta^{13}C$ between drought stress treatments and those in which irrigation was applied is further evidence that this mechanism behind $qDTY_{12.1}$ is drought-specific, which is in contrast to the results of Kondo *et al*. (2004), who reported consistent genotype rankings for $\Delta^{13}C$ across environments. Despite this evidence of reduced transpiration early in the stress treatment, no canopy temperature differences were detected in any field study (Fig. 5), and stomatal conductance as measured by porometer showed little differences in early in the stress periods (Fig S4). Furthermore, $\Delta^{13}C$ in the grain was consistently higher in 481-B across trials, which did not agree with the leaf $\Delta^{13}C$ results.

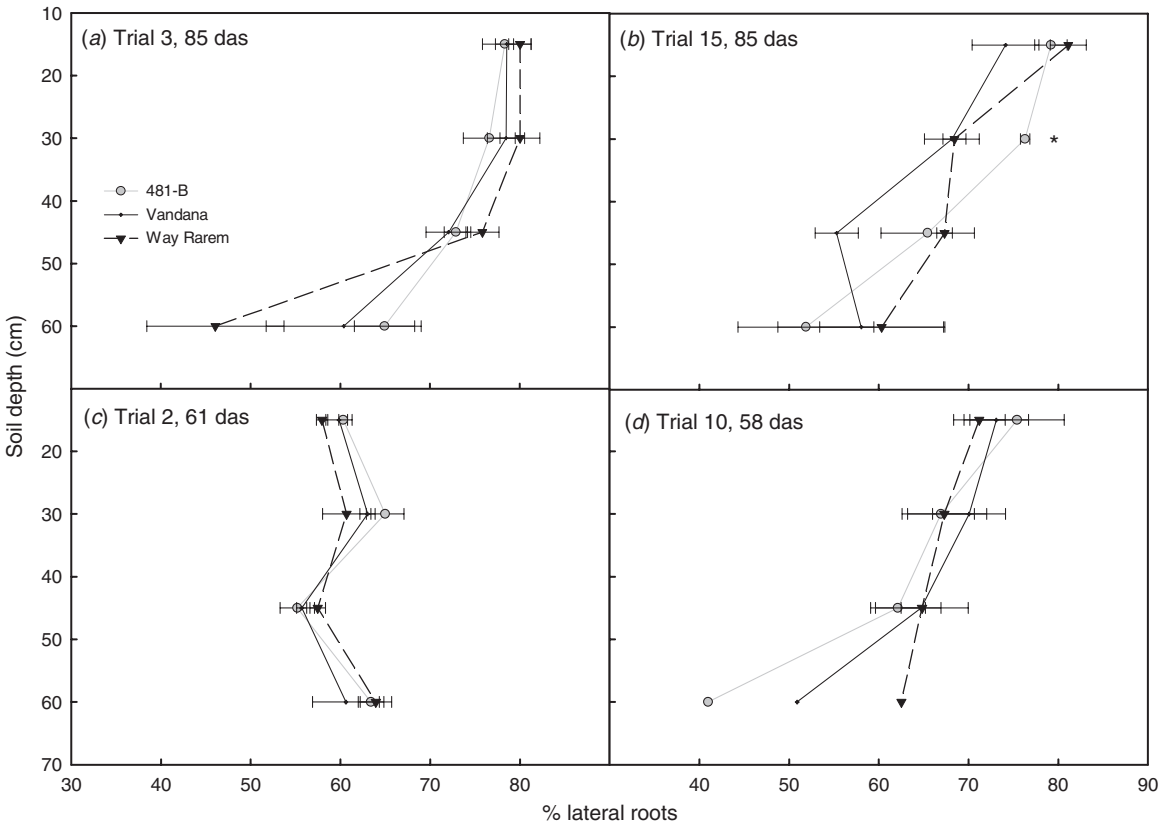

Fig. 6. Lateral root growth at four depth increments in (*a*, *b*) trials in which the rice near isogenic line 481-B had a yield advantage over the cultivar Vandana, and (*c*, *d*) trials in which 481-B had no yield advantage over Vandana. (*a*) Trial 3; (*b*) Trial 15; (*c*) Trial 2; (*d*) Trial 10. Values shown are means ± s.e. Significance levels shown are for the whole trial (including genotypes not shown). *, $P < 0.05$; DAS, days after sowing.

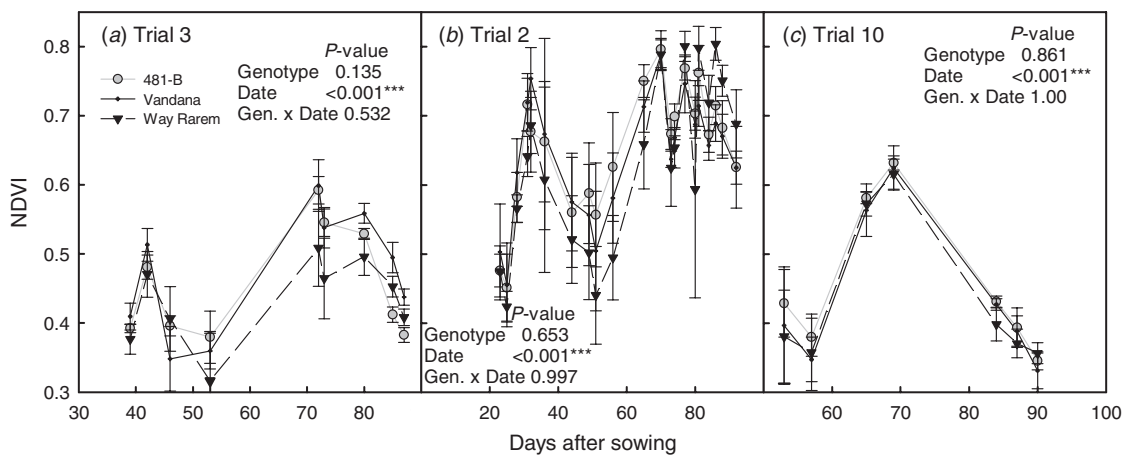

Fig. 7. Normalised difference vegetation index (NDVI) in (*a*) trials in which the rice near isogenic line 481-B had a yield advantage over the cultivar Vandana (Trial 3), and (*b*, *c*) trials in which 481-B had no yield advantage over Vandana. (*b*) Trial 2; (*c*) Trial 10. Values shown are means ± s.e. Genotypes did not differ significantly for NDVI across dates in the three trials shown.

More research is needed to understand these results as well as the details behind the conservative water use of $qDTY_{12.1}$ NILs.

The timing and severity of drought stress was previously reported to affect root growth in upland rice field studies (Boonjung and Fukai 1996). In general, the differences seen in lateral root growth were more apparent in trials in which 481-B had a yield advantage, particularly in the trials that were not conducted in a rainout shelter. The lateral root phenotype was not observed in the lysimeter studies, which may have been a result of the late root sampling date or of the restricted soil

volume in those experiments. These results suggest that a lateral root growth response, although induced by drought stress in $qDTY_{12.1}$ NILs, may require a certain level of residual soil water or a slightly more gradual onset of drought stress in order to be expressed. Furthermore, the conservative water uptake observed early in the drought stress treatment, followed by increased lateral root growth later in the drought stress treatment (which probably increased water uptake), may cause a complex effect on the net water uptake and leaf water status of $qDTY_{12.1}$ NILs. A more detailed understanding of the multiple mechanisms associated with $qDTY_{12.1}$ and their interactions is necessary.

It is likely that the combination of multiple physiological mechanisms (lateral root growth and transpiration efficiency) conferred by $qDTY_{12.1}$ helps explain the strong effect this single major-effect QTL has on grain yield under drought and on its stability across environments. Given the unexplained physiology results reported here (e.g. no differences found in canopy temperature despite significant differences in water uptake, and consistently higher $\Delta^{13}C$ in the grain of 481-B), it is likely that additional mechanisms also contribute to the yield advantage conferred by $qDTY_{12.1}$. More sensitive measurements and additional research is necessary to address the questions that arise from these results and to continue improving rice yield under drought in unfavourable upland environments.

The approach used in this evaluation of environmental effects differs slightly from those previously reported (Wade *et al*. 1999; Cooper *et al*. 1999, Acuña *et al*. 2008). In this study, rice NILs that were more than 95% genetically similar (except for Way Rarem) were used, rather than a set of genotypes with a range of maturity duration, plant height and yield. The environments in which the NILs were evaluated here included only upland fields rather than a range of agroecosystems (such as flood-prone lowland conditions) and emphasis was given on the physiological mechanisms associated with drought response. Trials were confined to only upland conditions because the recipient parent Vandana is not a lowland-adapted variety. However, $qDTY_{12.1}$ has since been introgressed into the background of the lowland-adapted Nepalese variety Sabitri and has also showed increased yield under drought (Mishra *et al*. 2013), although the physiological mechanisms behind the Sabitri–$qDTY_{12.1}$ lines have not been evaluated.

In summary, this study contributes to understanding the mechanistic response of $qDTY_{12.1}$ and the limits to which it is likely to be effective by evaluating the grain yield and physiological responses of $qDTY_{12.1}$ across multiple experiments in upland conditions. The release of improved varieties over the last two decades has helped increase yield in upland rice ecosystems (Sinha *et al*. 1994) but yield levels are still very low. The effect of $qDTY_{12.1}$ under a range of conditions is expected to help improve the yield of upland genotypes under moderate to severe drought.

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