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Development of a New Cultivation Technology for Cold Stress Escape through Flowering Time Manipulation by Water Management in the Highlands of East Africa

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Abstract. Cold stress is a major abiotic factor limiting rice production by reducing spikelet fertility. Under field conditions, cold stress varies with years and seasons in terms of its intensity, duration, and timing of occurrence. To reduce the risk of cold damage because of its unpredictable nature, crop adaptation strategies, such as management practices, that complement breeding are required. Flowering time (heading time) is a key trait that can be used to adapt rice to changing climatic conditions. Therefore, we screened a rice mutant line (T6-16) that has very shallow root system and exhibits delayed heading time under moderate drought stress conditions. This mutant line was used in breeding and development of a new cultivation technology for cold stress escape by introgression of its genetic segments into the background of a recurrent parent of New Rice for Africa (NERICA), WAB56-104. The mutant-type F_2 plants grown under moderate drought stress conditions showed delayed heading by an average of 11 days. Three F_2 plants that showed delay of heading by 11−17 days and maintained over 95% grain weight under the stress conditions were identified. These F_2 plants could be useful in breeding for cold stress escape. These results suggest that the utilization of rice plants introgressed with the mutation gene and proper water management practices for rice cultivation based on the predicted length of cold periods could escape the cold stress through delaying heading time.

Key words: Kenya, Rice, New cultivation technology, Cold stress escape, Flowering time manipulation

Introduction

Cold stress is a major abiotic factor affecting rice cultivation in high latitude and altitude areas[1–3]. In rice growth stages, the booting stage, especially the early pollen microspore stage that occurs approximately 10–12 days before flowering time (heading time), is the most sensitive to cold injury[4]. Low temperature at the booting stage reduces spikelet fertility and, in turn, reduces grain yields[1].

In cold-prone highlands of East Africa, such as Mwea in Kenya (Fig. 1), cold stress exhibits yearly and seasonal variations in terms of its intensity, duration and timing of

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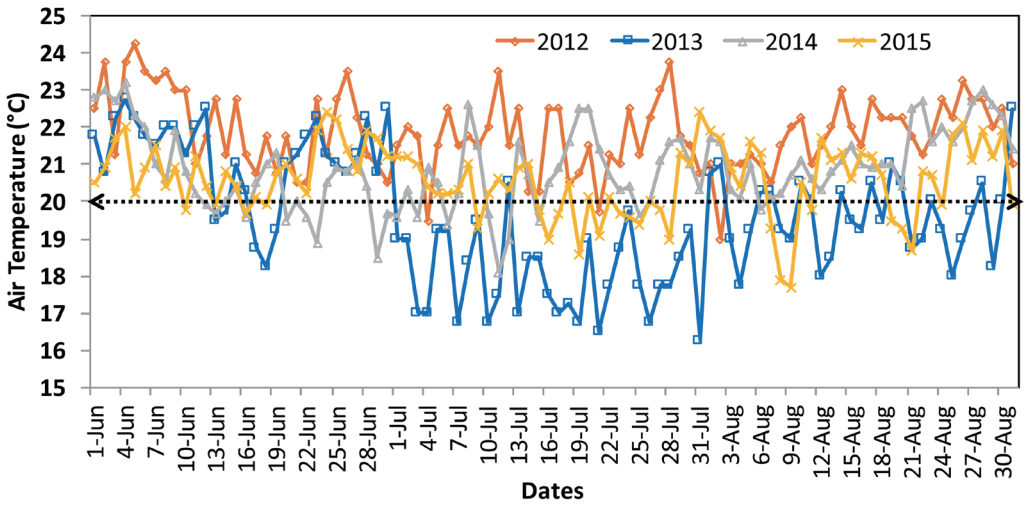

Fig. 1. Daily average air temperature in June to August in Mwea, Kenya between 2012 and 2015. Dotted arrow indicates minimum threshold temperature for normal rice growth and development.

occurrence[5]. In these locations, temperatures can reach below 18°C (i.e., during severe stressful years or seasons) thereby increasing the risk of yield loss due to cold damage, resulting in yield losses of up to 100%. Due to the unpredictable nature of cold stress under field conditions, breeding efforts for cold tolerance based on genetic improvement alone will not be enough to reduce the risk of cold damage. Improved crop adaptation strategies, such as new management practices, that would complement breeding for stress tolerant varieties are needed. Thus, exploration of key traits and management practices for adapting rice to variable low temperature environments will play a major role in sustaining rice yields.

Heading time is mainly influenced by environmental factors such as day length (photoperiod) and temperature, but is also affected by abiotic stresses such as cold, drought and nutrient deficiency which can cause delay in heading time of rice[6–8]. The shifting of heading time is a key strategy that can be used to better adapt rice to changing climatic conditions, and is a major goal for plant breeders[9]. Delaying heading time in rice (i.e., lengthening the vegetative growth during the cold period and switching to floral transition when temperatures are optimum) is a potential option to adapt rice to cold-prone regions. Shifting of the reproductive phase in rice may maintain the yield potential in cold-prone environments through preserving spikelet fertility and grain filling.

In this study, we newly screened a rice mutant line, T6-16, that has a shallow root system and exhibits delayed heading time when subjected to moderate drought stress. We explore the possibility of using mutant traits for breeding rice lines that can escape cold periods by delaying heading time while sustaining yield or with minimal yield loss.

Materials and Methods

Plant materials

The plant materials (rice genotypes) used included a newly screened rice mutant line, T6-16, WAB56-104, and an F_2 population (115 individuals) derived from a cross between the T6-16 mutant and WAB56-104. The mutant parental variety is Taichung 65 (TC65), a Taiwanese lowland rice variety. WAB56-104 is an upland improved variety and parent of NERICA 1 to NERICA 11[10].

Seed germination and transplanting

Pre-germinated seeds were sown in seedling trays in mid-October, 2015. Each pre-germinated seed was sown in a cell measuring 5 cm × 5 cm × 5 cm and N fertilizer (ammonium sulfate) was applied 7 days after emergence as a nutrient solution (5 g/20 L) to enhance rapid tiller production. At day 40, the seedlings were transplanted in the field (on November 27, 2015) in single rows, 10 plants per row at a spacing of 30 cm × 15 cm between rows or plants. Each hill had 6 tillers by the transplanting time and was split into two parts, one with the main tiller (main-stem plant) was transplanted in an alternate wetting and drying (AWD) paddy field and the other (split-tiller plant) in a continuously waterlogged (CWL) paddy field.

Field evaluation

The F_2 population and the parent genotypes were evaluated in a paddy field at Kenya Agricultural and Livestock Research Organization-Mwea Centre, Kenya (KALRO-Mwea research farm (0°40'35"S, 37°18'06"E, and 1168 m a.s.l) from October 2015 to March 2016. The plant materials were evaluated under two water management practices:

AWD and CWL. The AWD field was kept flooded during the first two weeks after transplanting and then re-irrigated by surface irrigation up to 5 cm ponded water depth when the soil water potential reached –30 kPa at 20 cm soil depth. The threshold of –30 kPa was considered a moderate water stress condition[11]. Soil water potential in AWD field was measured every day at two points in the paddy field using tensiometers installed at 20-cm soil depth. Fertilizer was applied as basal fertilizer at a rate of 25 kg N/ha, 25 kg P_20_5/ha, and 25 kg K_2O/ha at transplanting time. Top-dressing fertilizer was applied in two splits at a rate of 25 kg N/ha (ammonium sulfate) at 21 and 45 days after transplanting (DAT) (Total N rate = 75 kg N/ha). The fields were regularly weeded, and other crop management practices were carried out following recommended farmer practices[12].

Measurements

Heading time was determined as the date of 50% heading, during which the number of panicles per plant was counted. The panicles were hand-threshed and the filled spikelets were separated from the unfilled ones by floatation in water. These were then dried in the sun for a few hours and weighed separately. The moisture content of the filled spikelets was measured using a grain moisture tester (Riceter f, Kett Electric Laboratory, Tokyo). Grain weight per plant, adjusted to 14% moisture content, was calculated using the weights of filled spikelets in each hill and the measured moisture values. The total number of filled and unfilled spikelets was counted. The percent spikelet fertility was calculated by multiplying the number of fertile spikelets by 100 then dividing by the total number of spikelets. The number of spikelets per panicle was also calculated.

Statistical analysis

To assess the differences in agronomic traits between genotypes, analysis of variance (ANOVA) was performed using GLM procedure in SAS program (SAS version 9.1, SAS Institute Inc., Cary, NC, USA, 2002). The data for mean spikelet fertility was arcsine-transformed and the means were reported after back-transformation. The means were separated using the least significant difference (LSD) test at $P < 0.05$.

Results

Root distribution of T6-16 mutant line and parental variety TC65

The differences in root distribution between T6-16 mutant line and the parental variety (TC65) were evaluated in a rootbox experiment using a pinboard[13]. The mutant exhibited horizontal root distribution, while TC65 exhibited vertical root distribution (Fig. 2a). The mutant distributed 62% of its roots in the 0–60° root growth angle region whereas TC65 distributed only 36% of its roots in the same root growth angle region (Fig. 2b). These results reveal a clear variation in root distribution patterns between the mutant and the wild type.

Soil water potential and rainfall in the experiment site

The AWD paddy field experienced 4 wetting and drying cycles during the growing season (Fig. 3b). Even though the AWD practice was started at 14 DAT, the first cycle was reached at 58 DAT owing to the high rainfall in December and January (Fig. 3a) that resulted in the ponding of water depth, high soil water moisture, and a rise in the ground water table.

Agronomic and yield traits

Heading time: WAB56-104 and the T6-16 mutant significantly differed in heading time, with the heading occurring at 58 DAT and 90 DAT, respectively, under the AWD practice (Fig. 3b; Table 1). Under the CWL practice, the heading time of WAB56-104 and the mutant was 58 and 75 DAT, respectively (Table 1). The heading time of the wild-type F_2 plants ranged from 45 to 87 DAT, with a mean of 66 DAT under the AWD practice (Table 1; Fig. 4a), compared to 45 to 85 DAT, with a mean of 62 DAT under the CWL practice (Table 1; Fig. 4a). The heading time of the mutant-type F_2 plants ranged from 51 to 102 DAT, with a mean of 79 DAT under the AWD practice (Table 1; Fig. 4b) compared to 46 to 92 DAT and a mean of 68 DAT under the CWL practice (Table 1; Fig. 4b). For WAB56-104, the heading time was not affected by the AWD practice, whereas the heading time of T6-16 mutant was delayed by 15 days under the same practice (Table 1). For the F_2 plants, wild-type plants delayed heading by an average of 4 days (0–9 days), whereas the mutant-type plants delayed by 11 days (4–18 days) (Table 1). Over 86% of wild-type F_2 plants reached heading time earlier than 80 DAT (Fig. 4a and b) under both water management practices, which was similar to mutant-type F_2 plants under the CWL practice (Fig. 4b). When mutant-type F_2 plants were grown under AWD practice, over 65% of the plants reached heading time after 80 DAT (Fig. 4a).

Spikelet fertility: Spikelet fertility of WAB56-104 and T6-16 mutant was 87.1% and 44.5%, respectively, under the AWD practice (Table 1). Under the CWL practice, spikelet fertility of WAB56-104 and T6-16 mutant was 90.4% and 75.6%, respectively (Table 1). Spikelet fertility of wild-type F_2 plants ranged from 0.9 to 82.2%, with a mean of 38.6% under the AWD practice (Table 1; Fig. 4c), compared to 0.3 to 82.3%, with a mean of 40.6% under

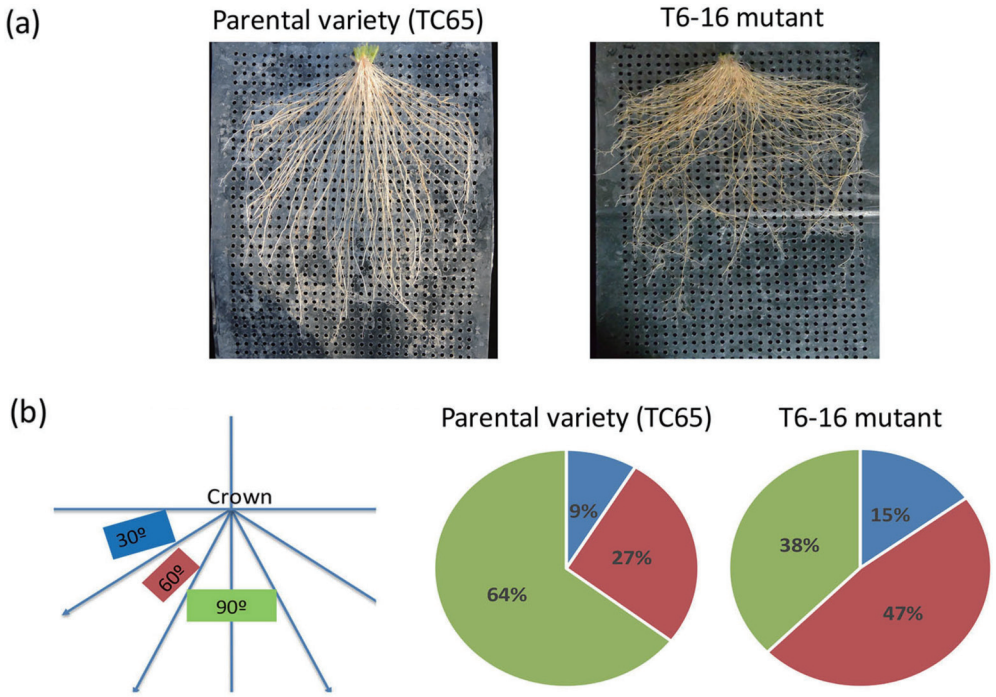

Fig. 2. Differences in root distribution between wild- and mutant-type plants and proportion of root distribution by root growth angle at 35 days after sowing. Root growth angle regions are 0–30° (blue shaded), 30-60° (red shaded) and 60–90° (green shaded).

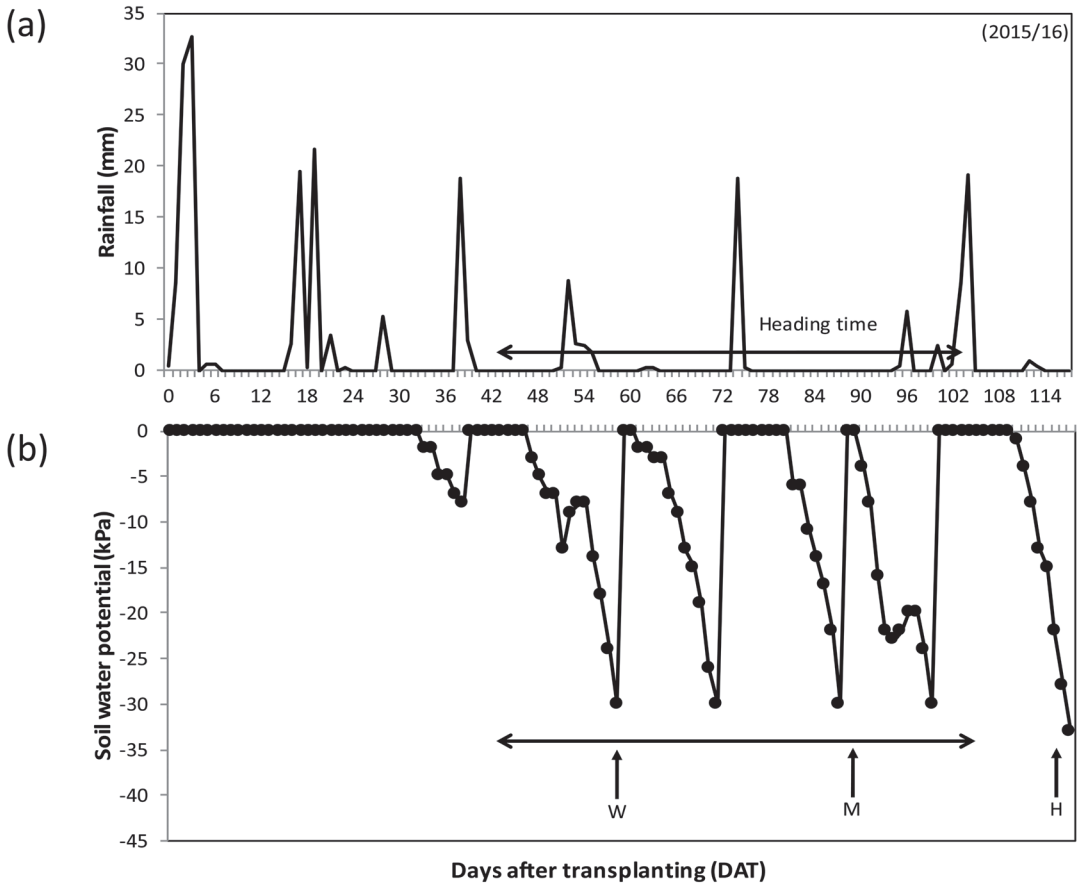

Fig. 3. Rainfall (a) and soil water potential at 20 cm (b) depth in the AWD paddy field in 2015–2016. W and M indicate heading time of WAB56-104 and T6-16 mutant respectively, under AWD conditions; H indicate harvesting time.

Table 1. Performance of agronomic characteristics in F_2 population and their parental varieties grown under AWD and CWL conditions

	Parents						F_2 population					
	WAB56-104			T6-16 mutant			wild-type			mutant-type		
Trait	CWL	AWD		CWL	AWD		CWL	AWD		CWL	AWD	
Heading time (DAT)	58.0	58.0	(0 d) ns	75.0	90.0	(15 d) ***	62.0	66.0	(4 d) ns	68.0	79.0	(11 d) *
Spikelet fertility (%)	90.4	87.1	(96.4%) **	75.6	44.5	(58.9%) ***	40.6	38.6	(95.1%) ns	40.4	36.0	(89.1%) ns
Panicle number	13.1	11.5	(87.8%) ns	19.8	11.5	(58.1%) ***	17.3	20.2	(116.8%) ns	15.0	16.0	(106.7%) ns
Spikelet number per panicle	154.2	108.3	(70.2%) ***	78.1	36.9	(47.2%) ***	99.1	96.7	(97.6%) ns	81.7	73.9	(90.5%) ns
Grain weight (g/plant)	46.6	29.2	(62.7%) **	31.0	5.1	(16.5%) ***	16.4	16.5	(100.6%) ns	14.4	13.4	(93.1%) ns

*$P < 0.05$, **$P < 0.01$, *** $P < 0.001$. ns, not significant.

Values in parenthesis indicate heading delay in days (d) or percent proportion (%) of the trait in AWD relative to that under CWL.

AWD, Alternate wetting and drying; CWL, Continously waterlogged.

the CWL practice (Table 1; Fig. 4c). Spikelet fertility of mutant-type F_2 plants ranged from 2.1 to 81.1% (a mean of 36%) under the AWD practice (Table 1; Fig. 4d) compared to 1.3 to 90.6% (a mean of 40.4%) under CWL practice (Table 1; Fig. 4d). WAB56-104 maintained 96.3% of its spikelet fertility under AWD practice, whereas that of the T6-16 mutant was greatly reduced (i.e., by 41.2%) (Table 1). For F_2 plants, the wild-type plants maintained 95.1% of their spikelet fertility whereas the mutant-type plants maintained 89.1% of their spikelet fertility (Table 1). However, the mean spikelet fertility in the F_2 population was low (< 50%) under both water management practices, suggesting that there were other causes of F_2 sterility, such as male sterility.

Panicle number: WAB56-104 and the T6-16 mutant produced almost the same number of panicles under the AWD practice (Table 1). Under the CWL practice, panicle numbers of WAB56-104 and T6-16 mutant were 13.1 and 19.8, respectively (Table 1). Panicle numbers of wild-type F_2 plants ranged from 7 to 35 (a mean of 20.2) under the AWD practice (Table 1; Fig. 4e), compared to 4 to 30 (a mean of 17.3) under the CWL practice (Table 1; Fig. 4f). Panicle numbers of mutant-type F_2 plants ranged from 7 to 30, with a mean of 16, under the AWD practice (Table 1; Fig. 4e), compared to 8 to 23, with a mean of 15, under the CWL practice (Table 1; Fig. 4f). WAB56-104 maintained 87.8% of its panicle numbers under the AWD practice, whereas in the mutant the number of panicles greatly reduced (i.e., by 41.9%) under the same practice (Table 1). For the F_2 plants, the panicle numbers of both wild-type and mutant-type plants were not affected by moderate water stress.

Spikelet numbers per panicle: Spikelet numbers per panicle of WAB56-104 and T6-16 mutant were 108.3 and 36.9, respectively, under the AWD practice. Under the CWL practice, spikelet numbers per panicle of WAB56-104 and T6-16 mutant were 154.2 and 78.1, respectively (Table 1). Spikelet numbers per panicle of wild-type F_2 plants ranged from 25.2 to 178.4, with a mean of 96.7, under the AWD practice (Table 1; Fig. 4g) compared to 30.7 to 183.1, with a mean of 99.1, under the CWL practice (Table 1; Fig. 4g). Spikelet numbers per panicle of mutant-type F_2 plants ranged from 29.5 to 134.2, with a mean of 73.9, under the AWD practice (Table 1; Fig. 4h) compared to 45.2 to 133.1, with a mean of 81.7, under the CWL practice (Table 1; Fig. 4h). Under the AWD practice, WAB56-104 maintained 70.2% of its spikelet numbers per panicle, whereas the T6-16 mutant had a reduced number (i.e., 52.8%) (Table 1). For the F_2 plants, wild-type plants maintained 97.6% of their spikelet numbers per panicle whereas the mutant-type plants maintained 90.5% of their spikelet numbers per panicle (Table 1).

Grain weights: Grain weight of WAB56-104 and T6-16 mutant was 29.2 g/plant and 5.1 g/plant, respectively, under the AWD practice. Under the CWL practice, grain weight of WAB56-104 and T6-16 mutant was 46.6 g/plant and 31 g/plant, respectively (Table 1). Grain weight of wild-type F_2 plants ranged from 0.7 to 35.4 g/plant, with a mean of 16.5 g/plant, under the AWD practice (Table 1; Fig. 4i), compared to 0.1 to 41.2 g/plant, with a mean of 16.4 g/plant, under the CWL practice (Table 1; Fig. 4i). Grain weight of mutant-type F_2 plants ranged from 0.4 to 43.5 g/plant, with a mean of 13.4 g/plant, under the AWD practice (Table 1; Fig. 4j), compared to 0.1 to 50.6 g/plant, with a mean of 14.4 g/plant, under the CWL practice (Table 1; Fig. 4j). Under the AWD practice, WAB56-104 maintained 62.7% of its grain weight, whereas the grain weight of T6-16 mutant was greatly reduced, by 83.5% (Table 1). For the F_2 plants, wild-type plants were not affected by the AWD practice whereas mutant-type plants maintained 93.1% of their grain weights (Table 1) under the same treatment.

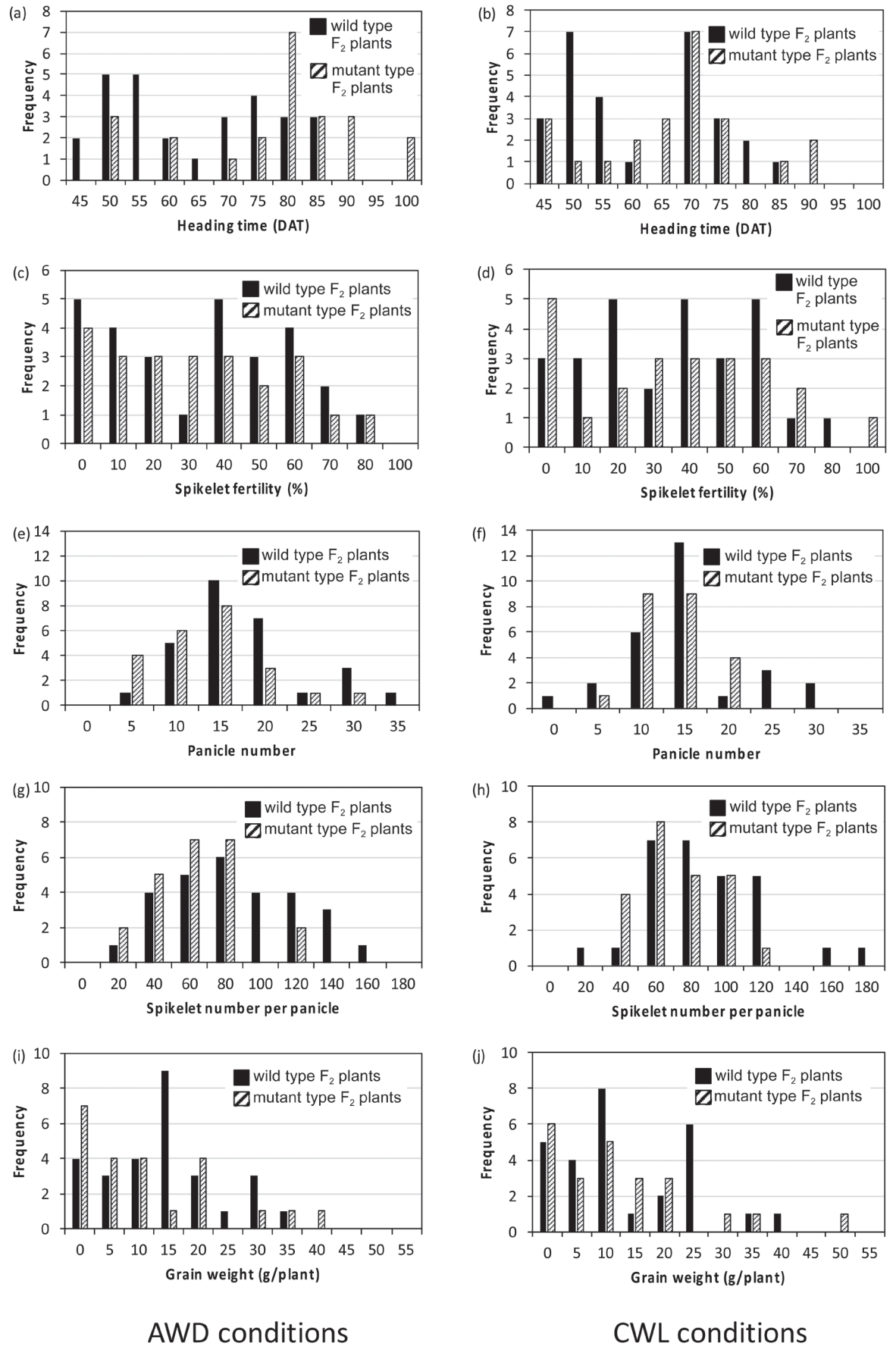

Fig. 4. Distribution of heading time (a, b), spikelet fertility (c, d), panicle number (e, f), spikelet numbers per panicle (g, h) and grain weights (i, j) in F_2 population under AWD and CWL conditions. Closed squares indicate Wild-type F_2 plants and stripped squares indicate mutant-type F_2 plants.

Table 2. Trait mean values in selected mutant-type F_2 plants

F2 plants	Water treatment	Heading time (DAT)	Spikelet fertility (%)	Panicle number	Spikelet number per panicle	Grain weight (g/plant)
1	CWL	75.0	72.1	17.0	133.1	36.8
	AWD	86.0	61.2 (85%)	19.0 (112%)	134.2 (101%)	35.0 (95%)
	Difference	11.0	15.0	–2.0	–1.2	1.8
2	CWL	71.0	66.9	10.0	103.4	21.0
	AWD	82.0	68.5 (102%)	23.0 (230%)	98.5 (95%)	43.5 (207%)
	Difference	11.0	–2.4	–13.0	4.9	–22.5
3	CWL	73.0	70.0	15.0	54.1	20.8
	AWD	90.0	62.9 (90%)	30.0 (200%)	61.4 (113%)	39.9 (192%)
	Difference	17.0	10.0	–15.0	–7.3	–19.1

Negative value indicate not affected by moderate water stress.
Values in parenthesis indicate percent proportion of the trait in AWD relative to that under CWL.

Agronomic performance of selected F_2 plants

Three F_2 plants that showed good agronomic performance, in terms of delayed heading time and maintenance of spikelet fertility, panicle numbers, spikelet number per panicle, and grain weights, under water stress were identified (Table 2). Heading time delayed by 11-17 days. The F_2 lines maintained 85% or more of their spikelet fertility. Their panicle numbers were not affected by moderate water stress. Similarly, the spikelet number per panicle was almost maintained under moderate water stress (relative to continuously waterlogged conditions). The three F_2 lines also maintained 95% or higher grain weight under moderate water stress. However, two of the three F_2 plants produced 2-fold higher grain weight, which was attributed to the production of high number of panicles under moderate water stress (Table 2).

Discussion

Flowering in rice is delayed under environmental stresses, such as under drought stress imposed at different developmental stages [8, 14–21]. In this study, we demonstrated the effectiveness of a mutation gene in causing delay in heading time of rice under moderate water stress. Past studies have reported the genes and pathways involved in the control of flowering in rice based on the photoperiodic response[22–29]. Under floral inductive period, exposure to drought delays flowering through reduction in transcription of primary integrators of day length signals which include *EARLY HEADING DATE 1* (*Ehd1*), *HEADING DATE 1* (*Hd1*), *Hd3a* and *RICE FLOWERING LOCUS T 1* (*RFT1*) [30].

The parental cultivar of the mutant line (T6-16), Taichung 65, contains non-functional alleles of both *Hd1* and *Ehd1*, and flowers relatively late regardless of the natural photoperiod[26]. In this study, the variation of delayed heading time among the mutant-type F_2 plants was very wide under the AWD practice (4-18 days), indicating that a set of genes regulating heading time was very different between the T6-16 mutant and WAB56-104. Therefore, there is potential to identify optimal lines for the mutation gene's effect by selecting genotypes that have effective genetic basis for delayed heading time. Indeed, heading time of the three F_2 plants was delayed by 11–17 days, and their spikelet fertility and grain weight were minimally or not affected by moderate water stress. These three plants have been selected as potential genotypes to be improved and further tested for use as a strategy for cold stress adaptation to reduce yield losses. Work is underway to evaluate the selected plants' descendants (F_3 lines) during the long-rains season (in June and July) when a cold spell is likely to be experienced.

In this study, AWD was applied from 14 DAT as recommended by other researchers[31]. However, the first cycle of drying was reached late in the vegetative stage of the F_2 plants (at 58 DAT) due to the frequent rainfall during the 2015/16 short-rains season in Mwea, Kenya. Water stress imposed at this stage resulted in heading delay by a mean of 11 days in mutant-type F_2 plants. We speculate that cumulative moderate water stress from early stages of plant growth may result to a more prolonged delay in heading of rice with minimal yield losses. As such, there is need to evaluate the effect of cumulative water stress from early vegetative stage to maturity. In addition, there is need to assess the effect of moderate water stress imposed at specific growth stages on heading delay and yield performance using the advanced generations produced from this cross of mutant-type rice. This information would be helpful for determining the best timing of water management practices as a cold stress adaptation strategy based on weather forecasts.

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Working Paper

東アフリカ高地を対象とした水管理による開花期の制御を通して低温ストレスを回避させうるイネ新栽培技術の開発

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要約

低温ストレスは、種子稔性の低下を通してイネの収量を大きく低下させる。低温の程度や継続期間は年や季節によって異なるため、最も気温が低下する時期を回避して開花させうる新技術の開発が求められる。一般に、乾燥ストレスは出穂を遅延させる傾向があり、また根が浅く張る浅根性品種は軽微な乾燥ストレスに敏感に反応することが知られている。そこで本研究では、軽微な乾燥ストレス下で出穂期の遅延を示す突然変異体（T6-16）を選抜し、アフリカで有望視されているネリカ品種の反復親の1つであるWAB56-104と交配することで、本変異遺伝子の有用性を評価した。F_2個体群のうち、変異体型個体の出穂日は軽微な乾燥ストレス下で平均11日間遅延する傾向を示した。特に3つのF_2個体では、11 ～ 17日間出穂日が遅延したが収量の低下は見られなかった。これらの結果は、浅根性に関わる遺伝子座の利用と軽微な灌水量の制限により、収量の減少を伴うことなく、最も厳しい低温期を回避して開花させうる新技術確立の可能性を示している。