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Article

Plant Traits Associated with Stagnant Flooding Tolerance in Rice (*Oryza sativa* L.)

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Abstract: Stagnant flooding (SF) causes severe damage to modern rice varieties. This study was designed to evaluate morpho-physiological traits associated with tolerance of rice under SF. Ten aman rice varieties were tested under control and SF conditions. In SF treatment, 2-3 cm water depth was maintained upto 10 days after transplanting (DAT), than water depth increased gradually upto 50 cm that was maintained for 14 days. Although plants were not fully submerged, the yield was reduced by 25% across genotypes compared with those grown under control condition. This reduction was mainly attributed to the reduction in biomass caused by water height that reduced light interception under water. Stagnant flooding also affect chlorophyll content, spikelet and panicle production. The panicle number per unit area reduced by 55 % because of reduced tillering. Shoot elongation rate kept pace with rising floodwater and biomass production. Shoot elongation rate strongly and positively correlated with relative grain yield under SF. Principle component analysis suggest that to dry matter production and shoot elongation were the key determinant of SF tolerance in rice. Fine-tuning for optimum dry matter production and shoot elongation with rising floodwater is, therefore, a priority for future work.

Key words: Dry matter, grain yield, principle component analysis, rice, shoot elongation

1. Introduction

Rainfed and irrigated are the two major rice ecosystem and about half of the rice growing area of the world is irrigated, while the reminder half is rainfed. The rainfed rice ecosystem further classified into upland, lowland and flood-prone. The rice plant cultivated under rainfed condition facing both shortage as well as excess of water. The shortage of water occurs due to erratic rainfall, while poor drainage causes complete or partial submergence or stagnant flooding (SF). About 9% of the rainfed rice growing area of the world is flood-prone.

Rice (*Oryza sativa* L.) is the main staple food in Bangladesh. It occupies nearly 80% of the total net cropped area and aus (cultivated from March to July), aman (cultivated from July to November) and boro (cultivated from December to May) are the three major rice crops here [1]. Boro rice grows in the dry winter and the hot summer; thus, it is completely irrigated [2]. Only 5% of Aman rice and 8% of Aus rice are irrigated [3]. Aman is almost completely rainfed rice, although it requires supplementary irrigation during planting and sometimes in the flowering stage depending on the availability of rainfall. The growing season of aman rice is harmonised with monsoon season (July–October), when heavy rain fall occur through the growing season in Bangladesh. Therefore, aman rice suffer from complete submergence or SF every year in many parts of the country. The submergence or SF may occurs for a day to as long as few weeks. However, SF is often about 25 to 50 cm deep only partially submerges of the shoot [4]. Water stagnation are caused by heavy or excessive rainfall in a short period over a relatively small area. Flash floods are most common from April to July and from September to October. During flash flooding, water levels rise and fall rapidly with little or no advance warning. Typically, they occur in areas where the upstream basin topography is relatively steep and the time needed for the water to flow from the most remote point in a watershed to the watershed outlet is relatively short. The most affected areas are in the northern, as well as the southeast of Bangladesh.

Flooding seriously affects plant survival and complete submergence is highly damaging to most plant species, including rice. Yield loss due to floods ranges from10 to 100 % depending on flood duration, depth and floodwater conditions [5]. So far, a limited number of high yielding varieties tolerant of submergence have been developed and commercialized while even fewer high yielding genotypes have been identified which tolerate SF [6]. Traditional varieties still predominate in flood-prone lowland farms and rice yield is low, ranging from 0.5 to 2.0 t ha^{-1}, less than half that of irrigated rice [7]. Quiescence or escape are two contrasting strategies that enable rice to cope with different types of floods [8, 9, 10, 11]. To date, mechanisms bringing about quiescence or escape that involve genetic, molecular and physiological aspects have been intensively studied [5, 11, 12].

Submergence-tolerant, low-yielding landraces such as FR13A from eastern India have been identified as early as 1950s [13, 12]. These adopt the quiescence strategy and a major QTL controlling submergence tolerance of this genotype, named SUB1, has been located on chromosome 9 and cloned [14]. SUB1 induces quiescence by suppressing the ethylene-activated shoot elongation under submergence, reducing carbohydrate consumption and enhancing survival [15, 16]. Bangladesh Rice Research Institute (BRRI) has developed two submergence-tolerant varieties (BRRI dhan51 and BRRI dhan52) though interrogation of *Sub1* genes [1]. These two varieties are claimed to tolerate submergence for two weeks. *Sub1* gene is an ethylene-response-factor that enhances submergence tolerance of rice. BRRI dhan33, BRRI dhan56 and BRRI dhan57 performed better under submerged condition as reported by Islam et al. [17] and Abedin et al. [18].

At the other extreme, fast submergence induced shoot elongation (escape strategy) is a characteristic of rice and wild-plant species that grow in flood-prone ecosystems [9]. Escape is only of major benefit to submerged terrestrial species if it leads to emergence from the water surface. In rice, at least both the quiescence and escape strategies are initiated by the accumulation of the volatile hormone ethylene inside submerged plant tissues [19]. However, neither strategy on its own leads to successful tolerance of SF. Fast elongation underwater gives very tall and spindly plants that suffer from severe lodging [13] and subsequent mortality [20]. On the other hand, underwater quiescence is also inappropriate because plants are not usually completely submerged. Clearly, an additional adaptive strategy is needed. Some recent studies showing that neither quiescence nor fast elongation growth is, by themselves, compatible with achieving high yields under SF [6]. While rice varieties that can respond to the slowly rising water of SF by elongating their stems or leaves (escape) are probably needed, the desirability of a quiescence component is less clear. The objective of the present study is to evaluate morpho-physiological traits associated with tolerance of rice under SF.

2. Materials and Methods

An experiment was conducted in the submergence tank of the Research Field of Bangabandhu Sheikh Mujibur Rahman Agricultural University (24°09′ N latitude, 90°26′ E longitudes), Gazipur-1706 from July to December, 2019. The site is located under the Agro Ecological Zone-28 named Madhupur Tract with an elevation of 8.4 m above the mean sea level. The site is situated in the sub-tropical region characterized by heavy rainfall during monsoon at the months from May to September and scanty rainfall in the rest of the year.

Ten aman rice varieties were tested against two treatments viz. (i) No submergence or control (C), ii) partial submerge/stagnant flooding (SF) for 14 days. In the control plot, 2–3 cm water depth was maintained from transplanting until 7 days before harvest when the field was drained. For the SF treatment, water depth was maintained at 2–3 cm from 0 to 10 days after transplanting (DAT), then increased gradually. Then, a water depth of 50 cm was maintained from 12 DAT to 26 DAT. This gradual increase in water depth is typical of the long-term stagnant floods in some areas of tropical Asia [20]. The experiment was laid out in a split plot design with three replications. Aman rice varieties included BU dhan1, BU dhan2, BRRI dhan57, BRRI dhan87, BRRI dhan49, Kanihati1, Kanihati6, AZ6007, BINA dhan7 and Ganzia.

Seeds are sown in seedbed on 10 July 2019. Seedlings were transplanted in the main field on 08 August 2019. The seedling age was 28 days. About 2-3 seedlings per hill were transplanted maintaining 25 × 15 cm spacing. The experimental plots were fertilized with triple super phosphate, murate of potash, gypsum, and zinc sulphate at 50, 45, 40, and 5 kg ha^{-1}, respectively, during the final land preparation. Urea was applied at 150 kg ha^{-1} in three equal splits at 10, 25, and 40 DAT. Gap filling was done at 5 days after transplanting. The crop was kept weed free throughout the growing period. Three hand weedings were done at 20, 35, and 45 DAT to prevent weed infestation. Irrigation and other cultural practices have been done whenever necessary.

Data collected on survival (Sur), lodging (Lod), plant height (PH), shoot elongation rate (SER), chlorophyll (Chl), shoot dry matter before submergence (SDMBS) and after de-submergence (SDMAS) were determined 1 day after de-submergence. During sample collection border-line was avoided to maintain data accuracy. To record shoot dry matter, plant shhots were dried in an oven at 70 °C for 72 hours and weighed. Seedling Sur rate was estimated after 14 day of submergence treatment followed by de-submergence for 7 day. At the same time, plant height and SER were measured [21]. Plant Sur were calculated as

$$\text{Sur (\%)} = \frac{\text{No. of plant survive of a variety}}{\text{Total no. of plants transplant of same the variety}} \times 100$$

$$\text{SER (\%)} = \frac{\text{Plant height before submergence - Plant height after de-submergence}}{\text{14 days}}$$

The intensity of Lod of plants were recorded after recession of flood water based on visual observation according to IRRI [22].

Relative growth index (RGI) was calculated according to Bhattacharjee [23] as follows:

$$\text{RGI (\%)} \quad \frac{\text{Dry weight of submerged plant}}{\text{Dry weight of control plant}} \times 100$$

Leaf chl was measured by taking 100 mg fresh leaves in a 25 mL capped-measuring tube containing 10 mL of 80% cold acetone. After extractions for 48 h in a refrigerator (4 ºC), chl was measured spectro-photometrically as absorbance at 663 and 645 nm. Days to flowering (DF) and growth duration (GD) were recorded. The crop was harvested at full maturity. Threshing, cleaning, and drying of grain were done separately variety by variety. Panicles (Pan) number m^{-2}, filled grains (FG) and unfilled grains (UFG) $panicle^{-1}$, 1000-grain weight (TGW), grain yield (GY) and straw yield (SY) and harvest index (HI) were determined at harvest. The grain was cleaned and sun dried to a moisture content of 14% and converted to ton ha^{-1}.

Data gathered on different parameters were statistically analyzed using computer software package Crop Stat, version 7.2. Treatment means were separated with Duncan's Multiple Range Test (DMRT) at the 5% level of probability. Graphical analyses were done using Excel software (Microsoft Corporation, Redmond, WA, USA). Principal component analysis (PCA) and cluster analysis were carried out using different morpho-physiological traits using SPSS version 16.2 software.

3. Results

Significant ($P < 0.01$) variation of Sur and Lod were observed among the testing rice varieties after 14 days of SF (Table 1). Sur rate varied from 65 to 100% while Lod 5 to 66%. Variety AZ6007 showed 100% plant Sur with 5% of Lod and this variety was therefore treated as tolerant one. However, BRRI dhan49, BRRI dhan57 and BRRI dhan87 were especially tolerant, showing higher Sur rate (93 to 97%) and 20% Lod. Moreover, BU dhan1, Kanihati1, Kanihati6 and BINA dhan7 were categorized as moderately tolerant and moderately susceptible to SF, respectively. Two varieties, BU dhan2 and Ganzia showed poor Sur rate (65 to 70%) and higher Lod (53 to 66%) and they were classified as susceptible to SF. The plant height of all varieties measured after 14 days of SF followed by de-submergence for 7 days. The plant height increased considerably under SF (Table 2). Genotypic difference in plant or shoot elongation in response to SF were obvious. In BRRI dhan57, shoots elongated little in response to SF (108 % of the control) but in BRRI dhan49 elongation in SF was much faster (122 % of control), even though both varieties are considered tolerant of SF. Constitutive (inherent) and adaptive (facultative) elongation are the two types of shoot elongation under SF stress. Ganziz was inherently tall and showed higher SF-induced elongation (121% of control). However, BU dhan1, BRRI dhan87, AZ6007 and BINA dhan7 had intermediate stature with faster (> 3.0 cm day^{-1}) flooding-induced (facultative) elongation. Moreover, BU dhan2, BRRI dhan57, Kanihati and Kanihati6 were semidwarf with the slow flooded-induced facultative elongation rate (< 3.0cm day^{-1}).

Table 1. Mean sum of square from the analysis of variance of rice varieties subjected to stagnation.

Parameters	**Sources of variation**		
	Variety (V) (*df* = 9)	Treatment (T) (*df* = 1)	V × T (*df* = 9)
Sur (%)	201.70**	2432.07**	201.70**
Lod (%)	504.12**	16500.4**	504.12**
Plant height (cm)	212.18**	2506.48**	25.72*
SER (cm day^{-1})	0.38*	8.28**	0.083
Chl (mg g^{-1})	0.26**	2.51**	0.17**
SDMAS (g m^{-2})	3556.33**	242775.0**	1649.90**
Days to flowering	379.48**	487.35**	20.68**
Growth duration (days)	115.15	228.15	9.15
Panicle (no. m^{-2})	3068.21**	35929.3**	882.34**
Filled grains (no. panicle^{-1})	2878.50**	3114.72**	186.30*
Unfilled grains (no. panicle^{-1})	620.13	37.77	482.18
1000-grain weight (g)	77.98**	62.23**	5.06**
Grain yield (t ha^{-1})	0.964**	17.51**	0.24**
Straw yield (t ha^{-1})	1.42**	4.54**	0.11

* and ** indicate significant at 0.05 and 0.01 level, respectively. Sur = Survival, Lod = Lodging, SER = Shoot elongation rate, Chl = Chlorophyll, SDMAS = Shoot dry matter after de-submergence.

Table 2. Effect of stagnant flooding on Sur, Lod and SER of rice.

Rice	Sur (%)		Lod (%)		Plant height (cm)			SER (cm day^{-1})		
varieties	C	SF	C	SF	C	SF	SF/C	C	SF	SF/C
BU dhan1	100	90 ^{ab}	0.0	40 ^{bc}	85.67 ^{ab}	98.50 ^{b}	115	2.83 ^{a}	3.59 ^{ab}	127
BU dhan2	100	70 ^{cd}	0.0	53 ^{ab}	78.75 ^{bcd}	92.33 ^{cd}	117	2.08 ^{b}	2.73 ^{e}	131
BRRI dhan57	100	97 ^{ab}	0.0	20 ^{de}	77.42 ^{cd}	83.33 ^{f}	108	2.51 ^{ab}	2.83 ^{de}	113
BRRI dhan87	100	93 ^{ab}	0.0	20 ^{de}	84.08 ^{abc}	95.92 ^{bc}	114	2.55 ^{ab}	3.29 $^{a\text{-}d}$	129
BRRI dhan49	100	95 ^{ab}	0.0	20 ^{de}	75.25 ^{d}	91.91 ^{cde}	122	2.40 ^{ab}	3.38 ^{abc}	141
Kanihati1	100	84 ^{bc}	0.0	40 ^{bc}	74.58 ^{d}	90.10 ^{de}	121	2.09 ^{b}	3.05 $^{b\text{-}e}$	146
Kanihati6	100	92 ^{ab}	0.0	26 ^{cd}	80.33 ^{bcd}	88.33 ^{e}	110	2.51 ^{ab}	2.95 ^{cde}	118
AZ6007	100	100 ^{a}	0.0	5 ^{e}	79.33 ^{bcd}	89.00 ^{de}	112	2.54 ^{ab}	3.19 $^{a\text{-}d}$	126
BINA dhan7	100	84 ^{bc}	0.0	40 ^{bc}	82.00 ^{bc}	98.25 ^{b}	120	2.73 ^{a}	3.64 ^{a}	133
Ganzia	100	65 ^{d}	0.0	66 ^{a}	90.91 ^{a}	109.92 ^{a}	121	2.25 ^{ab}	3.27 $^{a\text{-}d}$	145

C = Control, SF = Stagnant flooding

Chl content was significantly ($P < 0.01$) inhibited by SF and a significant ($P < 0.01$) varietal difference was also observed (Table 3). Among the tested varieties, chl content ranged from 1.06 to 1.81 mg g^{-1}, after SF. For this parameter, the main cause of variance was the treatment, followed by variety and variety × treatment interaction. The SDMAS production was significantly decreased by SF (Table 3). The range of SDMAS varied from 177.71 to 292.0 g m^{-2} and 56.47 to 133.13 g m^{-2} in control and SF, respectively. The SDMAS of SF was 25 to 57% of control and the reduction varied among the varieties. In particular, the susceptible variety (BU dhan2) exhibited a sharp reduction in SDMAS under SF compared with the control, whereas tolerant varieties exhibited higher SDMAS compared to BU dhan2. This parameter was greatly affected by treatment, which accounted for major variance, followed by variance attributable due to variety and their interaction.

Plant growth in terms of RGI was significantly varied among rice varieties. Under SF, RGI varied from 25 to 57% of control across the rice varieties. Flowering and maturity were delayed in all genotypes exposed to SF (Table 3). Flowering was delayed by about 1 to 10 days, and maturity delayed by about 1 to 7 days under SF across genotypes. Evidently, the interactions between genotype and treatment were highly significant for days to flowering, which is mainly because BRRI dhan57 experienced much less delay in flowering than the other genotypes.

Table 3. Effect of partial flooding on chl content, SDMAS and growth duration of rice.

Rice	**Chl (mg g^{-1})**		**SDMAS (g m^{-2})**			**Flowering (days)**		**Maturity (days)**	
varieties	C	SF	C	SF	RGI	C	SF	C	SF
BU dhan1	2.25 ^{a}	1.44 ^{ab}	234.42 ^{bc}	133.13 ^{a}	57	90 ^{cd}	100 ^{bc}	114 d	119 ^{e}
BU dhan2	1.36 ^{cd}	1.32 ^{b}	230.33 ^{bcd}	56.47 ^{d}	25	91 ^{bc}	101 ^{bc}	113 ^{de}	121 ^{d}
BRRI dhan57	1.55 ^{bcd}	1.49 ^{ab}	218.29 ^{cd}	64.17 ^{d}	29	90 ^{cd}	91 ^{d}	118 ^{bc}	119 ^{e}
BRRI dhan87	1.83 ^{abc}	1.81 ^{a}	292.00 ^{a}	114.13 ^{b}	39	94 ^{b}	100 ^{bc}	120 ^{b}	123 ^{c}
BRRI dhan49	1.86 ^{abc}	1.50 ^{ab}	214.08 ^{cd}	108.50 ^{bc}	51	100 ^{a}	109 ^{a}	120 ^{b}	125 ^{b}
Kanihati1	2.00 ^{ab}	1.10 ^{b}	193.17 ^{cd}	99.63 ^{bc}	52	79 ^{d}	83 ^{e}	111 ^{e}	112 ^{f}
Kanihati6	2.01 ^{ab}	1.22 ^{b}	177.71 ^{d}	95.29 ^{c}	54	79 ^{d}	83 ^{e}	111 ^{e}	112 ^{f}
AZ6007	1.94 ^{ab}	1.48 ^{ab}	244.58 ^{abc}	113.66 ^{b}	46	93 ^{bc}	102 ^{bc}	113 ^{de}	120 ^{de}
BINA dhan7	1.77 $^{a-d}$	1.31 ^{b}	266.00 ^{ab}	131.46 ^{a}	49	94 ^{b}	97 ^{c}	117 ^{c}	121 ^{d}
Ganzia	1.25 ^{d}	1.06 ^{b}	225.71 ^{bcd}	107.67 ^{bc}	48	101 ^{a}	104 ^{ab}	123 ^{a}	127 ^{a}

C = Control, SF = Stagnant flooding, RGI = Relative growth index

Among the yield components, panicles m^{-2} is the most important one and associated with grain yield under both control and SF condition across the varieties. The panicle production reduced under SF condition by 24% (average) (Table 4). Reduction in panicles m^{-2} under SF stress was least in Ganzia and greatest in Kanihati6 (37 %). The difference in spikelets panicle^{-1} between the control and SF was significant, it was reduced by SF in seven varieties. However, the difference in filled grain percentage between the control and SF was not significant, although it was reduced by SF in all varieties except BINA dhan7. Filled-grain percentage in BINA dhan7 was significantly higher under SF than the control because of the compensatory effect of reduced spikelets m^{-2}. Grain weight was slightly reduced by SF stress in all varieties (Table 4). On average, SF reduced grain yield by 25 %, with a varietal range of 19–37% (Table 5). BRRI dhan49 (high-yielding variety bred for irrigated rice ecosystem) had the highest yield under SF, with the 22% yield reduction. On the other hand, BU dhan2 showed the highest yield in the control but the highest yield reduction under SF. Although yield reduction from SF was lower in the variety Ganzia and BINA dhan57, these varieties yielded by far the least grain, under control and SF conditions than the other more modern varieties. The straw yield was the lowest in BINA dhan7 under SF.

Table 4. Effect of partial flooding on yield attributes of rice.

Rice	Panicles (no. m^{-2})			Spikelets (no. panicle^{-1})			Grain fertility (%)		
varieties	C	SF	SF/C (%)	C	SF	SF/C (%)	C	SF	SF/C (%)
BU dhan1	177 ^{cd}	130 ^{cd}	73	113 ^{d}	97 ^{ef}	86	81	80	99
BU dhan2	227 ^{a}	152 ^{bc}	67	145 ^{b}	117 ^{cd}	81	86	79	92
BRRI dhan57	223 ^{ab}	147 ^{c}	66	142 ^{b}	111 ^{de}	78	88	87	99
BRRI dhan87	217 ^{ab}	180 ^{a}	83	160 ^{a}	136 ^{ab}	85	88	85	97
BRRI dhan49	218 ^{ab}	175 ^{ab}	80	142 ^{b}	142 ^{a}	101	89	88	99
Kanihati1	200 ^{bc}	148 ^{c}	74	81 ^{e}	75 ^{g}	93	86	79	92
Kanihati6	190 ^{c}	119 ^{d}	63	88 ^{e}	92 ^{fg}	105	93	78	84
AZ6007	225 ^{ab}	155 ^{abc}	69	132 ^{b}	132 ^{ab}	100	89	86	97
BINA dhan7	158 ^{de}	137 ^{cd}	87	162 ^{a}	109 ^{de}	67	56	80	143
Ganzia	138 ^{e}	138 ^{cd}	100	132 ^{b}	126 ^{bc}	95	95	85	89

C = Control, SF = Stagnant flooding

Table 5. Effect of partial flooding on 1000-grain weight and yield of rice.

Rice	1000-grain weight (g)			Grain yield (t ha^{-1})			Straw yield (t ha^{-1})		
varieties	C	SF	SF/C (%)	C	SF	SF/C (%)	C	SF	SF/C (%)
BU dhan1	27.15 ^{c}	25.82 ^{bcd}	95	3.85 ^{ef}	3.03 ^{bcd}	79	6.06 ^{a}	5.08 ^{bcd}	84
BU dhan2	29.37 ^{b}	27.25 ^{b}	93	5.18 ^{a}	3.28 ^{ab}	63	6.29 ^{a}	5.61 ^{abc}	89
BRRI dhan57	25.53 ^{de}	25.09 ^{cd}	98	4.73 ^{b}	3.11 ^{bc}	66	6.47 ^{a}	6.01 ^{ab}	93
BRRI dhan87	26.74 ^{cd}	26.51 ^{bc}	99	4.54 ^{bc}	3.44 ^{a}	76	5.81 ^{ab}	5.45 $^{a-d}$	94
BRRI dhan49	21.84 ^{g}	18.55 ^{g}	85	4.51 ^{bc}	3.53 ^{a}	78	6.02 ^{a}	5.53 $^{a-d}$	92
Kanihati1	30.71 ^{a}	28.98 ^{a}	94	4.05 ^{de}	3.09 ^{bcd}	76	5.17 ^{b}	4.96 ^{cd}	96
Kanihati6	26.01 ^{cde}	23.44 ^{e}	90	3.70 ^{fg}	2.66 ^{e}	72	5.28 ^{b}	4.58 ^{d}	87
AZ6007	25.38 ^{f}	24.56 ^{de}	97	4.39 ^{cd}	3.31 ^{ab}	75	6.46 ^{a}	6.27 ^{a}	97

BINA dhan7	27.05^{c}	20.53^{f}	76	3.55^{fg}	2.88^{cde}	81	6.06^{a}	5.13^{bcd}	85
Ganzia	18.37^{h}	17.04^{h}	93	3.44^{g}	2.78^{de}	81	5.34^{b}	4.84^{cd}	91

C = Control, SF = Stagnant flooding

RGY showed a strong and positive correlation with RGI (r = 0.808**), SER (r = 0.890**) and SDMAS (r = 0.921**) (Table 6). RGY also showed poor but positive with Lod (r = 0.122^{ns}), negative with Chl (r = -0.114^{ns}) and Sur (r = 0.019^{ns}). However, RGI had significant and positive correlation with SER (r = 0.685*) and SDMAS (r = 0.812**). In addition, RGI also showed poor correlation with Sur (r = 0.197^{ns}), Lod (r = -0.043^{ns}) and Chl (r = -0.287^{ns}). In contrast, Lod had strong negative correlation with Sur (r = -0.954**) and Chl (r = -0.660*). Moreover, SDMAS showed strong and positive correlation with SER (r = 0.942**).

The genotypic variation under SF among the rice varieties was examined by multivariate analysis including PCA. The PCA was performed to identify trends in morpho-physiological responses to SF in rice plants based on Lod, SER, SDMBS and SDMAS under SF. The first three axes of PCA captured 98.61% of the total variation. This suggests a wide variability among the studied landraces (Table 7). PC1, with an eigenvalue of 2.029, accounted for 50.721% of the variation among the parameters measured. In PC1, SDMAS exhibited the highest positive loading followed by SER and SDMBS, whereas, in PC2, Lod was constituted mainly of positive and SDMBS constituted negative effects. Based on the result, SDMAS and SER were the major determinants of diversity (Figure 1).

Table 6. Relationship between different morpho-physiological parameters of rice under SF.

	RGY	Sur	Lod	SDMAS	RGI	SER	Chl	Pan	FG	UFG	TGW
RGY	1										
Sur	-0.019	1									
Lod	0.122	-0.954**	1								
SDMAS	0.921**	0.201	-0.084	1							
RGI	0.808**	0.197	-0.043	0.812**	1						
SER	0.890**	0.115	0.023	0.942**	0.685*	1					
Chl	-0.114	0.624	-0.660*	0.110	-0.287	0.160	1				
Pan	-0.036	0.243	-0.389	-0.057	-0.366	0.013	0.661*	1			
FG	0.098	0.172	-0.329	0.054	-0.270	0.155	0.578	0.705*	1		
UFG	-0.027	-0.442	0.368	0.098	-0.086	0.150	0.008	-0.104	-0.007	1	
TGW	-0.526	0.212	-0.202	-0.317	-0.321	-0.426	0.208	0.061	-0.495	-0.056	1

RGY = Relative grain yield, Sur = Survival (%), Lod = Lodging (%), SDMAS = Shoot dry matter after de-submergence (g m^{-2}), RGI = Relative growth index, SER = Shoot elongation rate (cm day^{-1}), Chl = Chlorophyll (mg g^{-1}), Pan = Panicle (no. m^{-2}), FG = Filled grains (no. $panicle^{-1}$), UFG = Unfilled grains (no. $panicle^{-1}$), TGW = 1000-grain weight (g). * and ** significant at 0.05 and 0.01 level, respectively.

Table 7. Correlation between initial values with principle component and component loading.

Parameters	PC1	PC2	PC3	PC4
SDMBS (g m^{-2})	0.417	-0.700	0.119	0.134
SDMAS (g m^{-2})	0.967	0.166	0.085	-0.020
SER (cm day^{-1})	0.951	0.242	0.239	-0.230
Lod (%)	-0.118	0.841	0.258	0.085
Eigen value	2.029	1.283	0.633	0.055
Variance (%)	50.721	32.070	15.824	1.384

SDMBS = Shoot dry matter before submergence (g m^{-2}), SDMAS = Shoot dry matter after de-submergence (g m^{-2}), SER = Shoot elongation rate (cm day^{-1}), Lod = Lodging.

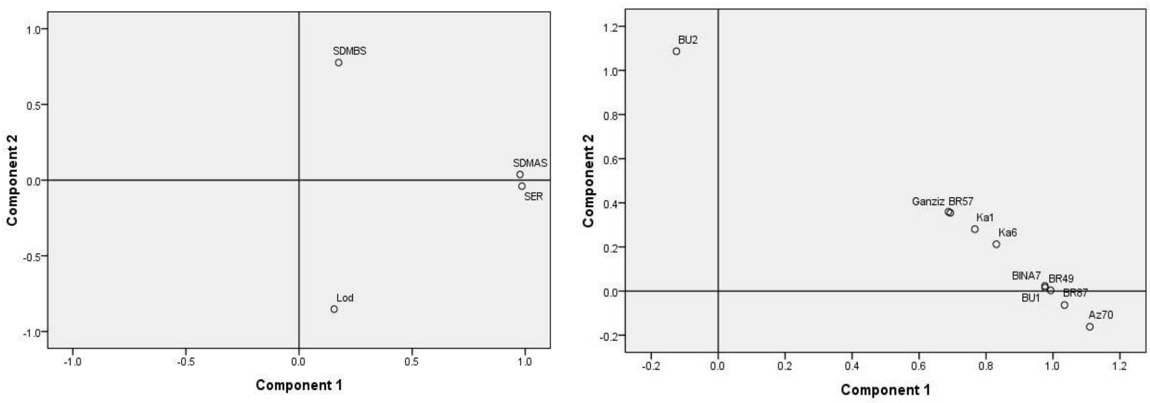

Figure 1. Principle component analysis of different parameters linked to tolerance of SF.

SER = Shoot elongation rate, SDMBS = Shoot dry matter before stagnation, Lod = Lodging, SDMAS = Shoot dry matter after stagnation.

4. Discussion

Stagnant flooding adversely affect all the parameters studied except plant height of rice. All the tested varieties elongate their shoot during stagnation. Elongation of shoots is one of the most important escape strategies for adaptation under water logging either partial or complete submergence [24]. The rate of shoot elongation under flooding depends on genetic character of the cultivars and controlled by ethylene. The interaction of ethylene with abscisic acid, gibberellins and auxin also control the shoot elongation under flooding [19]. Shoot elongation is an inhibitory factor for plant growth under complete submergence because shoot elongation during submergence uses energy and consumed carbohydrate. The results of this experiment showed that shoot dry matter and its shoot elongation have major role in SF tolerance.

However, dry matter increased with the elongation of shoot due to partial submergence. It is well established that control of shoot elongation is important for tolerance of complete submergence both during germination and early establishment as well as during vegetative stage [25]. Kato et al. [4] stated that the desirable elongation response to flood is dependent on the flood type and growth stage of the crop. The Sur percent and Chl content of the rice plant is less affected by SF in this study. This indicates that degradation of Chl in leaves above the water surface is not evident under SF. Thus, leaf photoassimilation capacity is much less affected by stress from SF. Degradation of leaf Chl under flash floods is triggered by ethylene accumulation, which the

SUB1 gene can effectively prevent [26, 27]. The effects of SF stress on photoinhibition and on the generation and deactivation of reactive oxygen species in leaves at different positions on stems await further investigation. However, flowering and maturity were delayed due to SF in all varieties except BRRI dhan57 which need similar time both under control and SF. Of the yield components we examined, panicles m^{-2} was the most affected by SF stress (Table 4), agreeing with our previous studies [20]. The average reduction in plant survival under SF was less than 20% in all varieties except Ganzia (Table 2), whereas panicles per m^{-2} were reduced by 23%. Dynamic changes in relative tiller number (Table 4) suggest that varietal differences in tillering ability and biomass production under SF are largely attributable to reduced light interception and concurrent lowering of photoassimilation. However, tillering was inhibited by SF, even in BU dhan1 where biomass accumulation during the vegetative stage was higher (Table 3). These observations suggest that the suppression of tiller growth under SF happens irrespective of the availability of concurrent assimilation at the onset of rising floodwater and that these tiller buds would not recover at later stages. This is supported by previous study on tillering dynamics under SF [28]. Since reduction in tiller number directly affects rice yield under SF, anatomical, biochemical and molecular studies on this temporal tiller suppression should be considered in future studies.

Slow shoot elongation (quiescence strategy) is an important mechanism of flood tolerance in rice especially advantageous in flashflood prone areas where the whole shoot is submerged at a depth too great for vigorous shoot elongation to return leaves to the air, or the flooding duration is short (less than 2 weeks). On the other hand, the escape strategy with its characteristic fast underwater elongation is crucial for survival in deepwater rice areas where floodwater deepens rapidly in the field [9, 11]. In the present study, we found that relying on either strategy alone would not be adaptive for SF. Faster shoot elongation contributed to establishing a larger aerial leaf area and higher light interception, biomass production and plant survival compared with slower elongating plants.

Associated penalties was severe lodging and reduced harvest index. Although BU dhan1 produced

a high biomass under SF, the demand for assimilates to support fast elongation seemingly did not match the supply. Young panicles compete with stems for assimilates during reproductive development [29], suggesting that BU dhan1 and similar deepwater varieties could potentially suffer from carbohydrate shortage for panicle and grain formation.

Two patterns of shoot elongation that are potentially adaptive to SF stress in modern rice varieties as suggested by Kato et al. [4]. In this study, varieties with intermediate height, such as BRRI dhan57, Kanihati1 and AZ7007 which are semi-dwarf and with little additional elongation capacity in response to rising floodwater. Rice genotypes (Ganzia) with plant heights of 110 cm under SF conditions lodge under SF.

The other pattern is seen in the inherently semidwarf genotypes, such as BRRI dhan49, BINA dhan7 and Kanihati1, where a higher elongation response with rising floodwater holds adaptive value. Any of the semidwarf rice varieties that are suitable for SF conditions can, therefore, be expected to elongate relatively quickly and maintain sufficient leaf area above the water surface to generate adequate biomass, while avoiding excessive height that would cause lodging.

Vergara et al. [6] reported that elongation rate that maintains about 50% of the shoot height above the water surface is likely to be optimum for higher yields under SF. Relying on the quiescence strategy in taller genotypes would in contrast increase the probability of complete submergence when flooding depth exceeds the inherent height. But, similarly in semi-dwarf lines there is an enhanced risk of complete submergence at the seedling stage compared with genotypes with intermediate height.

PCA was performed based on (a) shoot dry matter from 1 day before stagnation (SDMBS) (b) shoot dry matter from 1 days after de-submergence of stagnant water (SDMAS), (c) lodging from 1 days after de-submergence of stagnant water (Lod) and (d) shoot elongation rate during stagnation. Figure 1 shows the patterns of character correlations projected in the plane of the first and second factor axes. Mathematically transformed data with greatest variance are projected to lie on the first co-ordinate (so-called first principal component), those with second greatest variance are projected to lie on the second co-ordinate.

For the first principal component, increases in SDMAS and SDMBS showed positive values, while those of lodging and shoot elongation showed negative values. From these positions it is inferred that the increase in SDMBS confers an increase in SDMAS, but Lod and SER adversely affect the increase in SDMAS. For the second principal component, the increase in SDMAS and SER showed higher positive coefficient value than other characters, meaning that cultivars with high shoot elongation or high increase in SDMAS during stagnation are plotted on the positive PC2.

SF tolerant cultivars plotted to the negative portion of PC1, suggesting that the physiological characteristics of SF tolerant varieties are low shoot elongation during submergence, minimal lodging after de-submergence, and higher increase in SDMBS and after de-submergence. On the other hand, most of the varieties plotted in the positive portion of PC1 and PC2. In particular, most of the susceptible varieties plotted to the opposite portion to that of SF tolerant varieties on PC1. The physiological characteristics of susceptible varieties are high shoot elongation under SF, high lodging after de-submergence, and lower increase in SDMBS and after de-submergence.

Inherent stature and elongation response to rising floodwater determine shoot elongation rate and optimum height under SF stress. Shoot elongation is closely related to enhanced leaf area and light interception as determinants of photoassimilation under SF stress. The results presented in this study could assist breeders to screen or select breeding material with tolerance to SF for targeted breeding for flood-prone environments.

5. Conclusion

In this study, a wide range of variation for SF tolerance was observed among the studies rice varieties. Shoot elongation and dry matter accumulation during and after submergence are the key determinants SF tolerance in rice. AZ7006 and BRRI dhan87 exhibited the highest survival rate and minimum lodging that are associated with greater shoot elongation and dry matter production under SF. These varieties may be beneficial for lowland rice growing area that is affected by both flash flood and SF. Molecular genotyping study was needed to confirm the gene associated with SF tolerance of these varieties. These varieties may be useful for developing new rice varieties with high level of submergence as well as SF.

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