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HERITABILITY PATTERNS OF SOME AGRO-BOTANICAL CHARACTERS RELATED TO YIELD AND DROUGHT TOLERANCE IN TWO LANDRACES OF RICE

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Abstract

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Two landraces of rice, AWGUII-04 and IJ-124, were characterised and assessed for phenotypic variability, heritability, genetic advance and modes of inheritance of some primary yield and drought-tolerance traits. The target traits for yield were a percentage of filled spikelets, plant form, tillering, and for drought tolerance, leaf rolling, ratooning and maturity. This study was carried out to help both breeders and farmers make a wise choice when carrying out hybridisation and on the field. Hybridisation produced three F_1 hybrids that were advanced to F_2 generation. Quantitative and qualitative vegetative and reproductive data were taken from each F_2 population. The results obtained showed high heritability (62–100%) in all the thirty-eight vegetative and reproductive traits. The genetic advance was high (> 20%) in all the target traits except for leaf rolling. The traits segregated in the following ratio: plant growth form – 9:6:1; the percentage of filled spikelets – 13:3; ratooning – 3:1; maturity – 15:1; the number of tillers – 15:1 and leaf rolling – 15:1. The high heritability of the above traits makes them highly dependable for rice crop improvement.

Keywords: breeding, drought-tolerance, fertility, genetic inheritance, hybridisation, rice, yield.

INTRODUCTION

Rice, *Oryza sativa* Linn., is one of the most widely-consumed food crops next to maize. Its cultivation and production have, however, been reported to be declining due to climate changes through drought, heatwaves, flooding, pests and diseases (Rosenzweig et al., 2000). The yield loses recorded ranged from 15–50% (Pandey & Bhandari, 2009; Srividhya et al., 2011).

Landraces of rice have been reported to benefit from several introgressive hybridisation of locally-produced rice with their wild relatives, which occur on the fields of local farmers who unconsciously harvest the resulting hybrids and carry them into advanced generations (Faluyi & Nwokeocha, 1993). According to Faluyi & Nwokeocha (1993), most of the times, farmers recognise these hybrids as off-types, which they leave on the field without harvesting. These off-types eventually introgress with cultivated rice the next season, and the resulting hybrids may become harvested along with the cultivated rice, with their genomes redefined. This has helped to increase the genetic base of locally-produced rice, making them especially fit into local agro-ecologies coupled with the fact that local farmers have some basic knowledge of the biology of these different landraces. It is, therefore, not surprising that rice landraces are better adapted and have acceptable yield potentials compared to newly-introduced improved varieties, when cultivated under minimal cultural regimens (Faluyi & Nwokeocha, 1993; Zeven, 1998). Hybridisation has been shown to play an important role in the evolution of *Oryza* species over the ages as hybrid swarms have been reported by researchers in different parts of the world (Oka & Chu, 1970; Sano et al., 1984; Ghesquiere, 1986; Bolaji & Nwokeocha, 2013).

The cultivated rice is an annual plant with desirable agro-botanical characters such as hardiness, high yield and drought-tolerance. At the same time, the wild species are perennial, mainly because they can ratoon profusely even after they have completed their normal life cycle. The Nigerian landraces have been reported by some researchers as having perennial habit by the production of new shoots from the rootstock after completing their life cycle (Nwokeocha et al., 2007), and sometimes, they ratoon at the nodes just above the ground level. This ability of the landraces has made it possible for farmers to harvest grains beyond the standard, harvesting period, as long as water and other favourable environmental conditions prevail.

Productivity or yield of rice is determined by many factors, including the availability of light, water, nutrients and planting density (Baloch et al., 2002; Fageria et al., 2011). Also, the plant architecture (tillering pattern and plant morphology, plant height, leaf shape and arrangement) and panicle architecture (number and length of primary, secondary and tertiary branches, number of spikelets per branch, length and breadth of spikelets) play significant roles in the overall grain production of the rice plant. Yield can also be measured by the total number or weight of grains, as it has been established by Abraham et al. (2017) that rice show trade-offs between the number and weight of grains.

Also, many studies have pointed to the efficiency of some traits such as days to booting and maturity as well as percentage fertility as highly heritable and responsive to selection in hybrid populations (Kumar et al., 2018; Tripathy et al., 2018). Afiukwa et al. (2016) have assessed some landraces in conjunction with improved varieties of rice for DNA polymorphism using SSR markers for drought-tolerance. The promising landraces in their investigation were IJsllw-09, IJsllw-02, IKPh$^+$-PS and IKPh$^+$-FS, which have been extensively characterised by Umunnakwe (2015) and Abraham (2016). These landraces have unique alleles with FARO-11 (an established drought-tolerant variety) and even performed better under drought conditions (Afiukwa et al., 2016).

However, there is a scarcity of information on the inheritance pattern of the significant agro-botanical characters that determine rice yield and drought tolerance, making it difficult for breeders and farmers to follow or plan hybridisation adequately. The present study, therefore, exploited the rich genetic base of the landraces by involving them in a hybridisation experiment to determine the heritability of some of these traits as well as their modes of inheritance in hybrid populations.

MATERIALS AND METHODS

The study commenced with planting and hybridisation in April 2016. The parents (IJ-124 and AWGUII-04) were selected from accessions previously characterised by Afiukwa et al. (2016) and Abraham et al. (2017) based on yield and drought-tolerance traits. Landrace IJ-124 exhibit the same morphological characteristics as IJsllw-09, which had been earlier identified as a drought-tolerant accession by Afiukwa et al. (2016), and AWGUII-04 is not drought tolerant, but is a high-tillering plant with high yield (Table 1). Both parents (IJ-124 and AWGUII-04) were crossed, and three F_1 hybrids were obtained.

The F_2 seeds obtained from the F_1 plants were advanced to the F_2 generation in August 2017. The seeds were directly sown in the open field under rainfed conditions. They were planted one plant per hill at a spacing of 25 × 25 cm between rows and 50 cm between block, where a block represented a single F_2 population. Data included twenty-four vegetative and fourteen reproductive characters. Each character was classified according to the Biodiversity International et al. (2007) or using the authors' discretion, when the characters were not well-defined. The characters investigated are listed below:

a) culm angle: erect, intermediate, open, spreading or procumbent;
b) colour of the leaf sheath, flower, collar, auricle, hull and caryopsis;
c) leaf pubescence: glabrous, intermediate or pubescent;
d) days to booting (days from seeding to boot);
e) maturity (days from seeding to when more than 85% of the grains are fully ripened);
f) culm height (measured from the soil level to the

ciliate ring);

g) leaf length and breadth (for the flag and the penultimate leaves of the main culm);
h) length of ligule (average of 5 ligules on the same level on the plant);
i) leaf rolling (for drought tolerance);
j) ratooning (stay-green or new tiller production after plant death);
k) panicle characters (length, exertion).

Panicle parameters were measured for further characterisation, according to Futsuhara et al. (1979a, b). They were the following:

i. length of panicle (from the ciliate ring to the tip of the last grain; awns excluded);
ii. rachis length (from the ciliate ring to the base of the last primary branch);
iii. number and length of primary, secondary and tertiary (where present) branches;
iv. number of spikelets (taking into account the number of filled and unfilled ones.).

The percentage of fertility was calculated using the following formula:

$$Fertility\ (\%) = \frac{Number\ of\ filled\ spikelets}{Total\ number\ of\ spikelets} \times 100$$

Broad-sense heritability, genotypic and phenotypic coefficients of variation (GCV and PCV) and percentage genetic advance (GA) were calculated according to the formula provided by Ahmad et al. (2016).

$$\text{Heritablity}\,(H^2) = \left(\frac{Vg}{Vp}\right)\times 100 = \left(\frac{Vg}{Vg + Ve}\right)\times 100$$

Vg (genetic variance) = VF_2 – Ve,

$$\text{Ve}\,(\text{environmental variance}) = \frac{VP_1 + VP_2 + VF_1}{3},$$

VP_1 = variance of parent 1, VP_2 = variance of parent 2, VF_1 = variance of F_1, and VF_2 = variance of F_2. GCV and PCV were calculated using the following formulas:

$$\text{GCV} = \frac{\sqrt{Vg}}{\bar{X}_{F_2}}$$

$$\text{PCV} = \frac{\sqrt{Vp}}{\bar{X}_{F_2}}$$

where $\bar{X}_{F_2}$= grand mean of F_2.

Genetic advance was calculated according to the formula:

$$GA = \frac{i\sigma p}{\bar{X}_{F_2}} \times 100$$

i is a constant – 2.06, σp – phenotypic standard deviation.

The goodness-of-fit test was used to determine the conformity of six yield and drought-tolerance related traits to classical segregation ratios. Chi-square was calculated according to the following formula:

$$Chi\text{-}square = \frac{(o^2 - e^2)^{\,2}}{e^2}.$$

RESULTS AND DISCUSSION

Heritability, genotypic and phenotypic coefficients of variation, and genetic advance

The results displayed that all the vegetative and reproductive characters had high heritability (Table 2 and 3). The broad-sense heritability (H^2) has been characterised by Robinson (1966) into high (> 75%), medium (50–75%) and low (< 50%), while GA > 20% was considered high (Kumar et al., 2018). Among the thirty-eight vegetative traits studied, only the breadth of flag leaf had heritability lower than 50% (38%), while the heritability of the other traits was well above 60% (Table 2). The number of days to maturity had the least GCV and PCV (7.26 and 7.53%, respectively), while the total number of tillers had the highest GCV and PCV (46.6 and 52.41%, respectively). Despite the low GCV and PCV of the number of days to maturity, it, however, had high heritability of 93%. The results from this study support the previous findings (Suman et al., 2005; Singh et al., 2007; Singh et al., 2008; Sarangui et al., 2009; Akinwale et al., 2011; Kumar et al., 2018; Tripathy et al., 2018).

The number and total length of tertiary branches had negative heritability stemming from the fact that the high parent for both traits (AWGUII-04) had very high variance, thereby making the Vg for both traits negative values. However, both (number and length of tertiary branches) had the highest PCV and GCV (Table 3).

In this study, six characters were associated with yield and drought tolerance, that is, percentage of filled spikelets, culm length, number of days to maturity, number of tillers, leaf coiling and ratooning had high percentages of heritability (94, 79, 93, 79, 100

Table 1. Parental materials used in the study

S/N	Name	Location	Status	Remarks	Collector(s)
1.	IJsllw-09/IJ-124	Ekiti State	Landrace	Tall, early, perennial, drought-tolerant, long white grains, long panicle	Faluyi & Nwokeocha (1985)
2.	AWGUII-04	Enugu State	Landrace	Short, annual, high tillering, compact, moderate maturity, high spikelet number, short dense panicle	Umunnakwe (2013)

Table 2. Estimates of variance and genetic parameters for twenty-four vegetative traits of rice landraces

Traits	IJ-124 variance	AWGUII-04 variance	F_1 Variance	Vp	Ve	Vg	H^2 (%)	F_2 mean	PCV (%)	GCV (%)	GA (%)
Leaf pubescence	0.00	0.00	0.00	0.69	0.00	0.69	100	1.96	42.35	42.35	72.55
Pigmentation of outer leaf sheath	0.00	0.00	0.00	0.13	0.00	0.13	100	1.12	32.81	32.81	24.75
Pigmentation of inner leaf sheath	0.00	0.00	0.00	0.14	0.00	0.14	100	1.12	33.13	33.13	25.27
Days to booting	7.44	1.04	1.56	74.33	3.35	70.99	95.0	83.47	10.33	10.09	175.20
Days to maturity	1.36	6.96	8.00	78.22	5.44	72.78	93.0	117.48	7.53	7.26	127.62
Panicle synchronization	0.00	0.00	0.00	0.22	0.00	0.22	100	1.34	35.35	35.35	34.48
Stigma colour	0.00	0.00	0.00	0.01	0.00	0.01	100	1.01	10.23	10.23	2.17
Flag leaf angle	0.00	0.00	0.00	0.93	0.00	0.93	100	2.00	48.31	48.31	96.16
Panicle type	0.00	0.00	0.00	0.09	0.00	0.09	100	1.90	15.82	15.82	9.80
Panicle exsertion	0.00	0.00	0.00	0.71	0.00	0.71	100	2.91	28.93	28.93	50.20
Plant form	0.00	0.00	0.00	0.33	0.00	0.33	100	1.66	34.66	34.66	41.12
Culm length	136.72	12.57	0.20	239.85	49.83	190.02	79.0	56.79	27.27	24.27	689.23
Number of tillers	0.16	0.64	0.22	1.63	0.34	1.29	79.0	2.44	52.41	46.61	109.01
Apiculus pigmentation	0.00	0.00	0.00	0.03	0.00	0.03	100	1.03	17.79	17.79	6.71
Awning	0.00	0.00	0.00	0.09	0.00	0.09	100	1.89	16.26	16.26	10.31
Hull colour	0.00	0.00	0.00	0.50	0.00	0.50	100	2.55	27.68	27.68	40.32
Length of penultimate leaf	37.48	3.85	131.23	164.44	57.52	106.93	65.0	53.02	24.19	19.50	415.46
Breadth of penultimate leaf	0.02	0.01	0.00	0.09	0.01	0.08	89.0	1.31	23.61	22.24	13.30
Length of flag leaf	52.68	9.53	52.92	99.18	38.37	60.80	61.0	38.11	26.13	20.46	328.64
Breadth of flag leaf	0.02	0.01	0.16	0.10	0.06	0.04	38.0	1.56	20.51	12.71	5.20
Mean ligule length	0.08	0.04	0.07	0.16	0.06	0.10	63.0	1.80	22.61	17.95	11.92
Pigmentation at maturity	0.00	0.00	0.00	0.05	0.00	0.05	100	1.05	21.13	21.13	9.68
Leaf coiling	0.00	0.00	0.00	0.07	0.00	0.07	100	1.07	25.01	25.01	13.82
Ratooning	0.00	0.00	0.00	0.21	0.00	0.21	100	1.71	26.54	26.54	24.82

IJ-124 and AWGUII-04 – landraces, Vp – phenotypic variance, Vg – genetic variance, Ve – environmental variance, H^2 – broad-sense heritability, PCV – phenotypic coefficient of variation, GCV – genotypic coefficient of variation, GA – genetic advance.

and 100%, respectively). All these above-mentioned traits had high genetic advance except leaf coiling and ratooning, which was 13.82 and 24.82%, respectively. The traits mentioned above were, therefore, subjected to tests of goodness-of-fit to classical genetic ratios, as presented in Table 4 to determine their modes of inheritance.

The goodness-of-fit test

According to Tripathy et al. (2018), the nature of gene action and its heritability determines its selection success for a plant or crop improvement. The goodness-of-fit test for the six characters earlier mentioned was used to determine the gene action through conformity to classical segregation ratios and is explained below (Table 4).

Table 3. Estimates of variance and genetic parameters of fourteen panicle traits of two landraces of rice

Traits	IJ-124 variance	AWGUII-04 variance	F$_1$ variance	Vp	Ve	Vg	H^2 (%)	F$_2$ mean	PCV (%)	GCV (%)	GA (%)
Panicle length	1.39	0.64	2.42	12.92	1.48	11.44	89.0	23.80	15.10	14.21	98.98
Rachis length	2.62	2.17	3.56	10.06	2.78	7.28	72.0	12.45	25.49	21.68	120.52
Number of filled spikelets	452.40	1685.76	90.89	1940.00	743.02	1196.99	62.0	67.40	65.35	51.33	3658.61
Number of unfilled spikelets	346.64	78.24	164.67	1767.31	196.52	1570.79	89.0	58.32	72.09	67.96	5548.78
Total number of spikelets	85.44	2353.04	472.89	3299.34	970.46	2328.88	71.0	129.10	44.49	37.38	3716.02
Caryopsis colour	0.00	0.00	0.00	0.57	0.00	0.57	100	2.24	33.83	33.83	52.73
Threshability	0.00	0.00	0.00	0.26	0.00	0.26	100	2.07	24.77	24.77	26.19
Number of primary branches	0.24	0.64	0.00	6.58	0.29	6.29	96.0	9.37	27.39	26.77	138.28
Total length of primary branches	193.96	149.08	49.67	1022.87	130.90	891.97	87.0	94.42	33.87	31.63	1945.98
Number of secondary branches	34.16	71.20	22.89	119.05	42.75	76.30	64.0	21.03	51.89	41.54	747.45
Total length of secondary branches	432.38	674.50	364.63	1030.09	490.51	539.58	52.0	57.61	55.71	40.32	1929.42
Number of tertiary branches	0.00	10.16	0.00	0.05	3.39	-3.34	-6895	0.02	897.78	7454.52	-28057.31
Total length of tertiary branches	0.00	36.91	0.00	0.17	12.30	-12.13	-7030	0.04	931.26	7808.35	-56026.91
Percentage of filled spikelets	94.42	4.07	6.53	593.60	35.01	558.59	94.0	52.35	46.54	45.15	2198.10

IJ-124 and AWGUII-04 – landraces, Vp – phenotypic variance, Vg – genetic variance, Ve – environmental variance, H^2 – broad-sense heritability, PCV – phenotypic coefficient of variation, GCV – genotypic coefficient of variation, GA – genetic advance.

Fertility

In the F$_2$ generation, segregation was distinguished, and it corresponded to the classical F$_2$ ratio: 13 (low to moderately fertile): 3 (highly fertile) plants (Table 4 (a)). The ratio suggests that the gene responsible for fertility can be inhibited by the dominant state of another independent gene. Long et al. (2008) have determined that genes *SaF* and *SaM*$^+$ control male fertility, but the action of these two genes is suppressed, when *SaM*$^-$ is present, because it affects the protein structure. In essence, it suggests that the gene *SaM*$^-$ inhibits fertility and, thus, supports the segregation pattern observed for spikelet fertility in our study.

Tillering

Tillering is a significant agronomic character of rice in that it determines panicle number and, therefore, grain yield (Li et al., 2003). The number of tillers segregated into the ratio 15 (moderate to low tillering): 1 (high tillering) plants (Table 4 (b)). Even though the individual populations did not fit this ratio, the sub-total as presented under the full-sibs category conformed to the 15:1 ratio. It is important to note here that the high tillering plants have reduced height across the three F$_2$ populations. The segregating ratio (15:1) suggests that tillering is conditioned by the action of duplicate genes without cumulative effect. Nwokeocha & Faluyi (1998) have reported the association of the dwarfing gene with high tillering, and it was confirmed in this study as tall plants tiller less than the shorter or dwarf plants. This is in agreement with Li et al. (2003), who have found that a gene *MOC1* affects tillering, and plant height in these plants decreases. Li et al. (2003) have also found that the genes *OSH1* and *OsTB1*, which con-

Table 4. Test of goodness-of-fit of six agro-botanical traits to classical segregating ratios

Populations	IJ-124 x AWGUII-04 (1)			IJ-124 x AWGUII-04 (3)			IJ-124 x AWGUII-04 (4)			Full-sibs		
Character state	Observed	Expected	(χ^2cal)	Observed	Expected	(χ^2cal)	Observed	Expected	(χ^2cal)	Observed	Expected	(χ^2cal)
a. Fertility (3:13)*												
Low	171	166.5625	0.12	112	109.6875	0.05	55	56.875	0.06	338	33.125	0.07
High	34	38.4375	0.51	23	25.3125	0.21	15	13.125	0.27	72	76.875	0.31
Total	205	205	0.63	135	135	0.26	70	70	0.33	410	410	0.38
b. Number of tillers (15:1)												
Low	224	212.8125	0.59	131	140.625	0.66	74	78.75	0.29	429	432.1875	0.02
High	3	14.1875	8.82	19	9.375	9.88	10	5.25	4.29	32	28.8125	0.35
Total	227	227	9.41	150	150	10.54	84	84	4.58	461	461	0.37
c. Plant growth form (9:6:1)												
Intermediate	69	84.9375	2.99	77	76.5	0.0033	59	46.6875	3.24	205	208.125	0.05
Compact	75	56.6250	5.96	48	51.0	0.1765	22	31.1250	2.67	145	138.75	0.28
Open	7	9.4375	0.63	11	8.5	0.7353	2	5.1875	1.95	20	23.125	0.42
Total	151	151	9.58	136	136	0.9151	83	83	7.86	370	370	0.75
d. Maturity (15:1)												
Late	216	216.5625	0.0015	141	140.625	0.001	80	81.5625	0.03	447	448.125	0.0028
Early	15	14.4375	0.0219	9	9.375	0.015	7	5.4375	0.45	31	29.875	0.0423
Total	231	231	0.0234	150	150	0.016	87	87	0.48	478	478	0.0451
e. Ratooning (3:1).												
Ratooned	207	220.5	0.83	169	174.75	0.19	79	85.5	0.49	455	480.75	1.37
No ratoon	87	73.5	0.57	64	58.25	0.57	35	28.5	1.48	186	160.25	4.14
Total	294	294	3.31	233	233	0.76	114	114	2.97	641	641	5.51
f. Leaf coiling (15:1)												
No coiling	201	205.3125	0.09	133	134.0625	0.0084	75	73.125	0.048	409	412.5	0.03
Coiled	18	13.6875	1.36	10	8.9375	0.1263	3	4.875	0.721	31	27.5	0.45
Total	219	219	1.45	143	143	0.1347	78	78	0.769	440	440	0.48

* – trait segregation ratio, IJ-124xAWGUII-04 (1), (2) and (3) – F_2 populations, χ^2cal – calculated chi-square.

trol the initiation and regulation of meristem production and growth, have reduced effect when the gene *MOC1* is present in rice. It has been suggested that the gene *MOC1* regulates the actions of both *OSH1* and *OsTB1*. Thus, it was concluded that the dominant gene *MOC1* reduces tillering, hence, resulting in fewer tillers in tall plants.

Plant growth form

Plant growth form is a trait that affects the efficiency of photosynthesis and ultimately grains yield for rice (Fang et al., 2009; Abraham, 2016). The plant growth form and tillering ability of a rice plant determine its architecture. Fang et al. (2009) have recognised the action of a single gene *tac2*, which controls tiller angle in rice and have suggested that tiller angle is a monogenic character because the segregation ratio of 3:1 is observed when a *tac2* mutant (open plant) is crossed with Xinong 1A (a compact plant). Fang et al. (2009), however, have concluded that since this gene, *tac2*, may be an allelic form of *tac1* gene, which has a similar phenotypic expression as *tac2* plants, it is possible that plant form is controlled by these two allelic genes.

The plant form segregation pattern was as follows: 9 (intermediate): 6 (compact): 1 (open) plants (Table 4 (c)). The open or procumbent plants were categorised together, because plants with open plant form sometimes approach the procumbent form after grain-filling depending on the weight of the panicles. This ratio suggests the effect of a duplicate gene with cumulative effect. The results obtained, as stated above, agreed with Fang et al. (2009) in that the intermediate plant form is dominant over the compact and open plant form especially since all F_1 hybrids had the intermediate plant form.

Maturity

Drought tolerance in rice involves some array of traits, which includes ratooning, leaf rolling, days to maturity and stay-green. The segregation ratio for the number of days to maturity was: 15 (moderate to late maturing): 1 (early maturing) plants (Table 4 (d)). It was observed on the field that the early maturing plants were tall and produced fewer tillers than the late maturing ones. The segregating ratio suggested the action of a duplicate gene without cumulative effect. The implication of this is that it is the recessive state of these genes that will engender early maturity in rice. Early maturity has been identified as an attempt by a plant to escape terminal drought (Yoshida, 1981). Hence, earliness in rice can be considered a drought-escape mechanism.

However, maturity can also be a yield-related trait. It has been earlier stated that the early maturing hybrids use the early maturity to escape a drought that may occur later in the planting season. Hence, they spend less time accumulating biomass to reach the reproduction stage quickly. This, in essence, will reduce the number of tillers produced and ultimately reduce yield.

Ratooning

Ratooning, which is the ability of the rice plant to maintain vegetative and reproductive growth or die and rejuvenate from the rootstock, was found in our study to be a dominant character in the F_1. It segregated into 3 (ratooning/perennial): 1 (non-ratooning/annual) plants in the F_2, also confirming the dominant character of the ratooning gene (Table 4 (e)). Both types of ratooning were categorised together as opposed to the work of Oloyede et al. (1999). Our study, however, supports their findings in that perennial habit is dominant over annual although they found the rejuvenating from rootstock after dying back to be a recessive trait. Ratooning is of importance especially in an early maturing variety as the ratoons take less time to mature (usually less than two months). This stems from the fact that the ratoons' age starts from the age of the primordial cells from which they are developed.

Leaf rolling

Leaf coiling/rolling segregated into 15 (non-coiling): 1 (coiled) plants (Table 4 (f)). This suggests the action of a duplicate gene without cumulative effect. In the F_3 (data not presented), this character was found to segregate with the stay-green character, i.e. the plants continually produced tillers or ratoons even while the original tillers were maturing. It was also observed on the field that plants with rolling leaves have stay-green characteristic, i.e. they produce tillers continually without necessarily dying to regenerate from the rootstock. Chandra Babu et al. (2003) have found leaf rolling/coiling to be characterised by QTLs located primarily on chromosomes 1 and secondarily on chromosomes 8 and 11. During water stress, leaf rolling reduces the leaf area exposed to sunlight, thereby, reducing evapotranspiration (Naleem et al., 2017).

Leaf rolling, in addition to leaf angle, has been identified as an adaptive character to conserve water during drought (Pandey and Shukla, 2015). The observations made in this study support the findings of the above researchers in that leaf rolling was found in plants with upright leaves and stay-green characters. The upright-leaf trait is much coveted in rice breeding as plants possessing this trait utilise solar radiation more efficiently than those with lax leaves (Long et al., 2006; Sarvestani et al., 2008). Horizontal leaves have been reported to waste energy because, at midday, the surface exposed to light absorbs radiation that is three times more than the amount required for the saturation of photosynthesis (Long et al., 2006). Due to this, cultivars of rice with a lower canopy of lax leaves and top canopies of erect leaves have been designed so that when the upper layer of leaves have intercepted minimal amount of energy, the remaining can be used by the lower canopy, leading to efficiency in the usage of energy by plants (Long et al., 2006; Evans, 2013).

CONCLUSIONS

It was established that high fertility occurs when gene *SaM*$^-$ is absent, and gene *SaF* is dominant in at least one locus. The high tillering and the dwarfing genes are in an adaptive gene complex and are thus inherited together. Plant form and leaf-rolling are each controlled by two dominant genes with cumulative effects. Early maturity in rice is an escape mechanism with the trade-off being lower biomass accumulation, hence, lower yield. Ratooning is, however, the desired trait in this regard as farmers can harvest at least twice in a single planting season with the advantage that the ratoons grow and nurse spikelets to maturity in a short period. Leaf-rolling and upright leaf angle were found to be associated with stay-green plants in the present study. However, further research should be conducted to understand the relationships amongst these traits.

Our study has, thus, been able to confirm that the six agro-botanical characters (fertility, tillering, plant form, maturity, ratooning and leaf-rolling) that are associated with yield and drought tolerance have high heritability and genetic advance. They can, therefore, be used as selection indices for hybridisation purposes. The goodness-of-fit test provided information on the segregation patterns of the traits mentioned above that will be useful for breeders in breeding programmes.

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DVIEJŲ RYŽIŲ VEISLIŲ AGROBOTANINIŲ DERLINGUMO IR TOLERANCIJOS SAUSRAI POŽYMIŲ PAVELDIMUMAS

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Santrauka

Tyrimas buvo atliktas siekiant padėti selekcininkams ir ūkininkams racionaliau vykdyti ryžių hibridizaciją ir jų auginimą. Buvo aprašyta ir įvertinta dviejų vietinių ryžių veislių, AWGUII-04 ir IJ-124, požymių, susijusių su derliumi ir sausros tolerancija, fenotipinis įvairavimas, paveldimumas ir genetinis kintamumas. Tirti agrobotaniniai požymiai, susiję su derliumi, buvo pilnų varpučių dalis, augalo forma, krūmijimasis, o su sausros tolerancija – lapų susisukimas, augalų atželimas ir jų branda. Hibridizacijos dėka buvo sukurti trys F1 hibridai, kurie pasiekė F2 kartą. Kiekybiniai ir kokybiniai morfologinių bei reprodukcinių požymių duomenys buvo surinkti tirtose F2 populiacijose. Gauti rezultatai parodė, kad visi tirti požymiai buvo paveldimi (62–100%) F2 kartoje. Visų tikslinių savybių, išskyrus lapų susisukimą, genetinis kintamumas buvo didesnis nei 20 %. Dėl aukšto tirtų požymių paveldimumo jie gali būti traktuojami kaip patikimi tolesnėje ryžių derliaus gerinimo strategijoje.