Chapter 8

Rice Straighthead Disease – Prevention, Germplasm, Gene Mapping and DNA Markers for Breeding

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Additional information is available at the end of the chapter

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1. Introduction

Straighthead is a physiological disorder of rice that results in sterile florets with distorted lemma and palea, and in extreme cases, the panicles or heads do not form at all (Atkins, 1974). As a result, heads remain upright at maturity due to lack of grain development: hence, the name 'straighthead'. The diseased panicles may not emerge from the flag leaf sheath when the disease is severe. Either the lemma or palea or both may be lacking, even if they are present they are distorted and crescent-shaped, particularly in long grain cultivars, forming a characteristic symptom of straighthead called 'parrot beak' (Rasamivelona et al., 1995). Other symptoms include unusually vigorous dark green leaves in mature plants and strikingly abnormal root systems with large, shallow roots with few branches and root hairs (Atkins, 1974; Bollich et al., 1989).

Figure 1. Straighthead symptoms in rice field of the United States (US) (left and middle) and Argentina (right).

Straighthead can cause a complete loss of grain yield in rice when sever (Fig. 1). In a study conducted by Wilson et al. (2001), grain yield reduction due to straighthead was up to 94% for a popular cultivar Cocodrie (Table 1). Yan et al. (2005) concluded that US cultivar Cocodore, Mars, Kaybonnet and Bengal were highly susceptible to straighthead, indicated by a yield reduction from 80% for Bengal to 96% for Mars in a study conducted in 1999 and 2000 (Fig. 2). Similarly, in a study conducted in 2001, Cocodrie and Mars suffered a yield reduction of 97% and 95%, respectively from straighthead (Table 2). Cocodrie, Cypress and Wells were grown on 73% of rice hectares in the southern US in 2001 (RTWG, 2002). The susceptibility of these widely grown cultivars to straighthead represents a potentially serious threat to southern US rice production, especially for Arkansas where about 50% of the US rice is produced (Wilson et al., 2010a). Therefore, the prevention of straighthead is not only an important target in the DD50 Computerized Rice Management Program http://dd50.uaex.edu/dd50Logon.asp (Slaton, 2001), but also is reminded to rice growers each year when the time of its prevention is getting close by Cooperative Extension Agents http://www.uaex.edu (Wilson et al., 2010b; 2010c).

Cultivar	Continuous flood	Drain and dry	10 days delay flood	20 days delay flood	Yield loss %*
Bengal	1210	5695	3629	4435	79
Cocodrie	353	6048	1361	1865	94
Cypress	3427	6250	6602	6300	45
Drew	4032	6905	5292	6451	42
Jefferson	5695	6854	6653	6048	17
Madison	3478	6149	4536	4990	43
Priscilla	5594	7510	7358	5443	26
Wells	5695	7913	6250	7459	28
LSD 0.05	2923 for comparing water managements within a cultivar				
LSD 0.05	1663 for comparing cultivars within a water management				

*Yield loss (%) for each cultivar was calculated by: [(Drain and dry yield – Continuous flood yield) / Drain and dry yield] x 100.

Table 1. Grain yield (kg/ha) of rice cultivars affected by straighthead disease under different water managements at the Rice Research and Extension Center, University of Arkansas near Stuttgart during 1999 (Wilson et al., 2001).

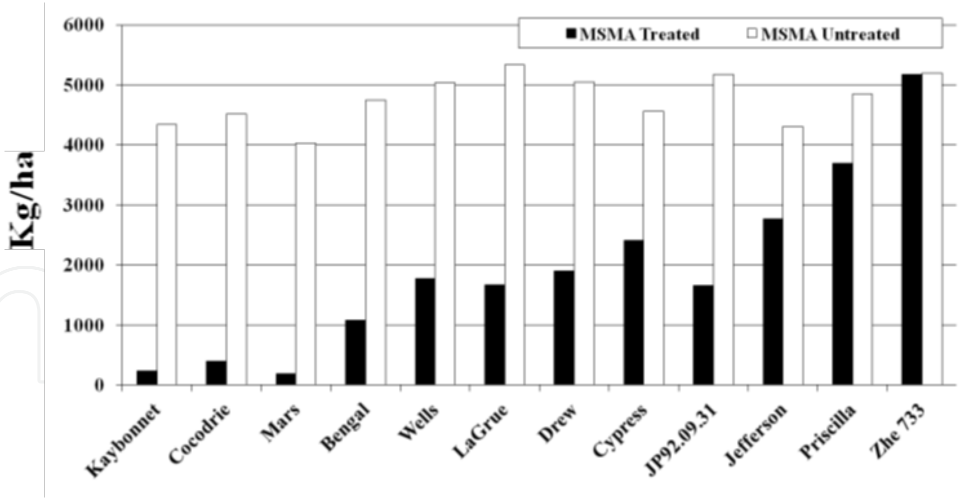


Figure 2. Comparison of grain yield between straighthead affected (MSMA Treated) and un-affected (MSMA Untreated) cultivars at the Dale Bumpers National Rice Research Center near Stuttgart, Arkansas in 1999 and 2000, where straighthead was induced by soil incorporation of 6.7 kg of monosodium methanearsonate (MSMA) per hectare (Yan et al., 2005).

2. Global threat from straighthead and its causal factors

Straighthead was first reported to dramatically affect grain yield in the US by Hewitt (1912). In the early 1900s, Collier (1912) estimated that approximately 20% of the US rice acreage suffered significant yield reductions by 12 to 15% due to straighthead. Afterwards, straighthead researches were published in Japan (Iwamoto, 1969), Portugal (called 'branca') (Cunha and Baptista, 1958), Australia (Dunn et al., 2006), Thailand (Weerapat, 1979), and Argentina (Yan et al., 2010a) (Fig. 1).

No pathogen has been identified to be associated with straighthead, so it is regarded as a physiological disease. The occurrence and severity of straighthead have been associated with soil organic matter (Editor's Note, 1946), low pH and low free iron (Baba and Harada, 1954), thiol compounds (Iwamoto, 1969), sandy to silt loam soil textures (Rasamivelona et al., 1995; Slaton et al., 2000), continuous flooding (Wilson et al., 2001), high soil As (Gilmour and Wells, 1980), N fertilization (Dilday et al., 1984; Dunn et al., 2006), and soil Cu availability (Ricardo and Cunha, 1968). A recent work suggested possible roles of magnesium but not As in naturally-occurring straighthead by chemical analyses of rice plant (node, internode, stem, leaf and root) and seed (brown and milled seed and hull) (Belefant-Miller and Beaty, 2007). Soil aeration is believed to speed the decay of soil organic matter (Editor's Note, 1946) and help oxidize arsenic (As) into arsenate, which is biologically inactive (Marin et al., 1992). Arsenic is toxic to many plant species including snap bean (*Phaseolus vulgaris* L.) (Sachs and Michael, 1971), soybean (*Glycine max* L.), potato (*Solanumtuberosum*L.), cotton (*Gossypiumhirsutum* L.), and rice (Baker et al., 1976).

In a straighthead study conducted by Yan et al. (2008) using resistant and susceptible cultivars in 2004 and 2005, minerals in flag leaves of heading panicles were measured because the susceptible cultivars could not produce seeds and direct measurement on seeds is not feasible. Straighthead was correlated negatively with grain yield (r=-0.89), plant height (r=-0.60) and flag leaf contents of Ca (r=-0.51), Mn (r=-0.31) and S (r=-0.26) and positively with days to head (r=0.63). Leaf Ca was associated positively with grain yield (r=0.60), leaf Mn (r=0.81), Fe (r=0.42), S (r=0.40) and Cu (r=0.38) and negatively with days to 50% heading (r=-0.64). The increased Mn in the flag leaves was associated with the increased leaf Ca (r=0.81), Fe (r=0.49), Cu (r=0.48), S (r=0.40) and As (r=0.29), but with the decreased days to 50% head (r=-0.56). Flag leaf S concentration was correlated positively with plant height (r=0.37), grain yield (r=0.35) and leaf P (r=0.59), K (r=0.49) and Mn (r=0.40) and negatively with days to head (r=-0.64) and leaf Na (r=-0.41) and Zn (r=-0.41). Leaf As concentration was correlated with the leaf Cu (r=0.65), Na (r=0.58), Fe (r=0.51) and Mn (r=0.29), but negatively with leaf K (r=-0.49) and B (r=-0.42). However, the exact causal factors of naturally occurring straighthead are still unknown.

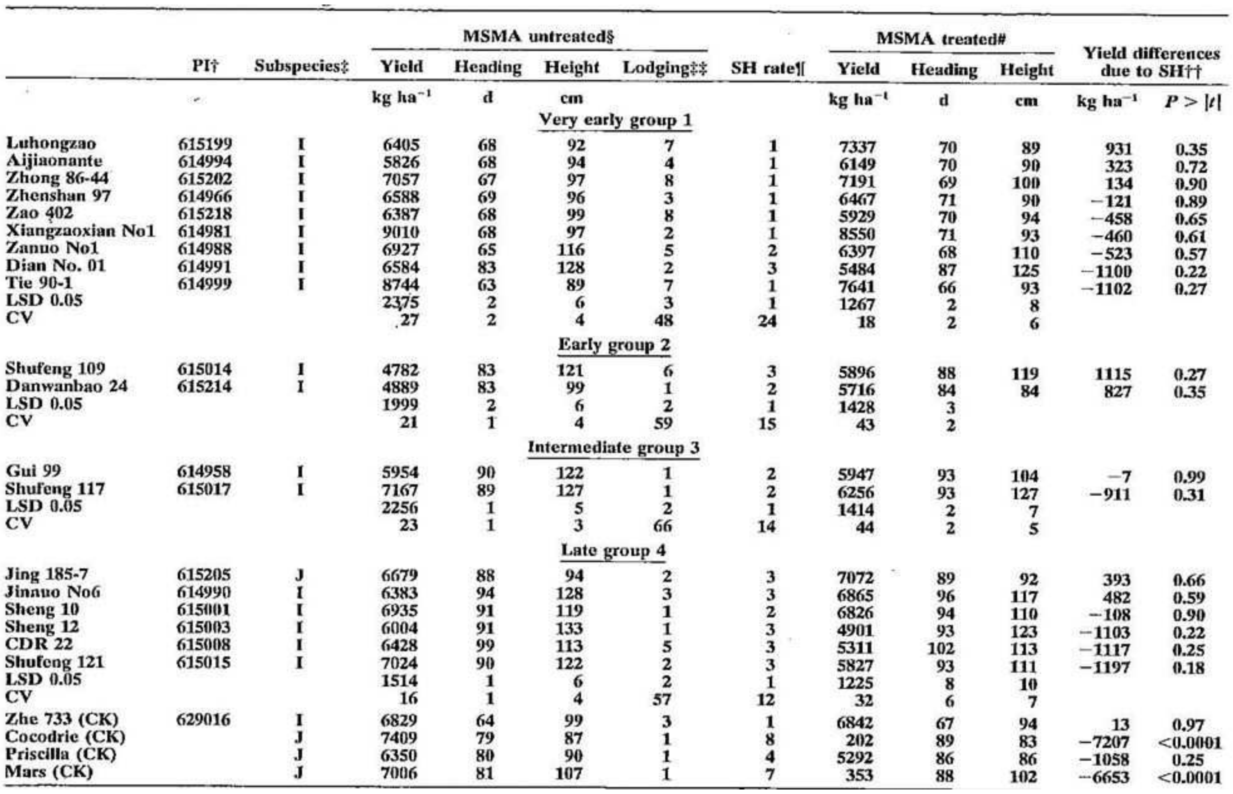
3. Methods for straighthead evaluation and prevention

3.1. Evaluation methods for straighthead

Because the symptoms of As injury are similar to straighthead of rice, incorporation of As in a form of monosodium methanearsonate (MSMA) has become the common and only practice for evaluating rice susceptibility to straighthead in research and breeding programs up to present (Horton et al., 1983; Frans et al., 1988; Wilson et al., 2001; Dunn et al., 2006; Pan et al., 2012).

A special field has been designated for straighthead research and breeding with MSMA amendment for more than 20 years (Somenahally et al., 2011) at the University of Arkansas, Division of Agriculture, Rice Research and Extension Center (RREC) jointly located with the United States Department of Agriculture (USDA), Agricultural Research Service (ARS), Dale Bumpers National Rice Research Center near Stuttgart, Arkansas. Usually, the MSMA as a solution in a spray volume of 85 L ha^{-1} at a rate of 6.7 kg MSMA ha^{-1} is directly applied to the soil surface with a calibrate CO_2-backpack sprayer and incorporated into the soil before planting the seeds (Yan et al., 2008).

At maturity of growth stage R9 (Counce et al., 2000), straighthead is visually rated in the center of a plot based on floret fertility or sterility and panicle emergence from the flag leaf sheath. The rating scale ranged from 1 to 9, 1 = no apparent sterility (more than 80% grains developed) and 100% of the panicles completely emerged; 2 = 71 to 80% of the grains developed and 96 to 100% of the panicles completely emerged; 3 = 61 to 70% of the grains developed and 91 to 95% of the panicles completely emerged; 4 = 41 to 60% of the grains developed and 85 to 90% of the panicles completely emerged; 5 = 21 to 40% of the grains developed and 75 to 80% of the panicles completely emerged (at this stage distorted and parrot-beak grains initially appear); 6 = 11 to 20% of the grains developed and 65 to 70% of the panicles completely emerged; 7 = 0 to 10% of the grains developed and most of the panicles emerged but remained totally erect; 8 = no grains developed and 0 to 10% of the panicles emerged from the flag leaf sheath but erect; and 9 = short stunted plants with no panicle emergence. Indicated by Table 2, at rate 1 straighthead, cultivars have either no numerical reduction of yield or slightly numerical reductions which are far from statistical significance (p>0.60). The yield reduction is not statistically significant at the rate 4 or below, but highly significant (p<0.0001) at the rate 7 with a reduction of 95% or above.



			MSMA untreated§					MSMA treated#			Yield differences due to SH††	
	PI†	Subspecies‡	Yield	Heading	Height	Lodging‡‡	SH rate¶	Yield	Heading	Height		
			kg ha⁻¹	d	cm			kg ha⁻¹	d	cm	kg ha⁻¹	$P > \|t\|$
					Very early group 1							
Luhongzao	615199	I	6405	68	92	7	1	7337	70	89	931	0.35
Aijiaonante	614994	I	5826	68	94	4	1	6149	70	90	323	0.72
Zhong 86-44	615202	I	7057	67	97	8	1	7191	69	100	134	0.90
Zhenshan 97	614966	I	6588	69	96	3	1	6467	71	90	−121	0.89
Zao 402	615218	I	6387	68	99	8	1	5929	70	94	−458	0.65
Xiangzaoxian No1	614981	I	9010	68	97	2	1	8550	71	93	−460	0.61
Zanuo No1	614988	I	6927	65	116	5	2	6397	68	110	−523	0.57
Dian No. 01	614991	I	6584	83	128	2	3	5484	87	125	−1100	0.22
Tie 90-1	614999	I	8744	63	89	7	1	7641	66	93	−1102	0.27
LSD 0.05			2375	2	6	3	1	1267	2	8		
CV			27	2	4	48	24	18	2	6		
					Early group 2							
Shufeng 109	615014	I	4782	83	121	6	3	5896	88	119	1115	0.27
Danwanbao 24	615214	I	4889	83	99	1	2	5716	84	84	827	0.35
LSD 0.05			1999	2	6	2	1	1428	3			
CV			21	1	4	59	15	43	2			
					Intermediate group 3							
Gui 99	614958	I	5954	90	122	1	2	5947	93	104	−7	0.99
Shufeng 117	615017	I	7167	89	127	1	2	6256	93	127	−911	0.31
LSD 0.05			2256	1	5	2	1	1414	2	7		
CV			23	1	3	66	14	44	2	5		
					Late group 4							
Jing 185-7	615205	J	6679	88	94	2	3	7072	89	92	393	0.66
Jinnuo No6	614990	I	6383	94	128	3	3	6865	96	117	482	0.59
Sheng 10	615001	I	6935	91	119	1	2	6826	94	110	−108	0.90
Sheng 12	615003	I	6004	91	133	1	3	4901	93	123	−1103	0.22
CDR 22	615008	I	6428	99	113	5	3	5311	102	113	−1117	0.25
Shufeng 121	615015	I	7024	90	122	2	3	5827	93	111	−1197	0.18
LSD 0.05			1514	1	6	2	1	1225	8	10		
CV			16	1	4	57	12	32	6	7		
Zhe 733 (CK)	629016	I	6829	64	99	3	1	6842	67	94	13	0.97
Cocodrie (CK)		J	7409	79	87	1	8	202	89	83	−7207	<0.0001
Priscilla (CK)		J	6350	80	90	1	4	5292	86	86	−1058	0.25
Mars (CK)		J	7006	81	107	1	7	353	88	102	−6653	<0.0001

† PI: Plant Introduction number in the U.S. germplasm system.

‡ Subspecies: I = *indica* and J = *japonica.*

§ No MSMA (monosodium methanearsonate) was applied as check conditions.

Stralghthead (SH) raling 1-9: 1 as normal and 9 as the worst SH.

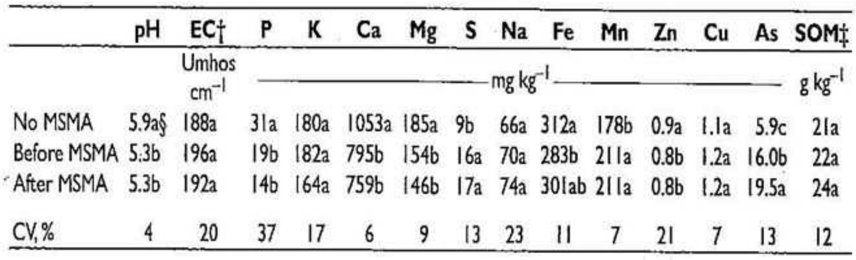
Soil was treated with 6.7 kg MSMA ha^{-1} to induce straighthead.

†† Yield difference = Treated yield - Untreated yield, and *P* is probability of *t* test for the difference.

‡‡ Lodging 1-9 scale: 1 as no plants lodged and 9 as over 80% plants lodged.

Table 2. Nineteen Chinese rice germplasm accessions had no significant yield reductions from straighthead induced by MSMA (monosodium methanearsonate) at 6.7 kg hn^{-1} in 2001 (Yan et al., 2005).

The soil to induce straighthead by application of MSMA for research purposes was studied by Yan et al. (2008) (Table 3). In the straighthead evaluation soil amended by MSMA, pH and Mehlich-3 extractable P, Ca, Mg, Fe, Zn and As concentrations are significantly lower, while S, Mn and As are higher than those in the native soil where MSMA has never been applied. However, soil electronic conductivity, organic matter and K, Na and Cu concentrations are not affected by the amendment of MSMA. Decreased soil pH resulted from the MSMA is significantly associated with decreased Ca (r=0.92), Mg (r=0.78), and P (r=0.41), but increased As (r=-0.87), S (r=-0.73), and Mn (r=-0.59) concentrations in the soil.



	pH	EC†	P	K	Ca	Mg	S	Na	Fe	Mn	Zn	Cu	As	SOM‡
		Umhos cm^{-1}	mg kg^{-1}											g kg^{-1}
No MSMA	5.9a§	188a	31a	180a	1053a	185a	9b	66a	312a	178b	0.9a	1.1a	5.9c	21a
Before MSMA	5.3b	196a	19b	182a	795b	154b	16a	70a	283b	211a	0.8b	1.2a	16.0b	22a
After MSMA	5.3b	192a	14b	164a	759b	146b	17a	74a	301ab	211a	0.8b	1.2a	19.5a	24a
CV, %	4	20	37	17	6	9	13	23	11	7	21	7	13	12

† EC, soil electrical conductivity.

‡ SOM, soil organic matter.

§ Means in each column with the same letter are not significantly different at the 0.05 probability level

Table 3. Soil properties and minerals for samples collected from the straighthead designated field before (Before MSMA) and after (After MSMA) the application of 6.7 kg MSMA ha^{-1} in comparison with native soil sample which never receives MSMA application (No MSMA) in 2004 and 2005. (Before MSMA soil received MSMA application previously for straighthead studies) (Yan et al., 2008).

3.2. Prevention methods in rice production

The sporadic nature of straighthead and the lack of a specific and definite causal factor have made straighthead difficult to be prevented. Since 1950s, rice researchers had tried to prevent straighthead using chemical application. Evatt and Atkins (1957) applied Feralum, a mixture of ferric and aluminum sulfates to soil for controlling straighthead. In Portugal, Cu deficiency was found to be associated with straighthead (Karim and Vlamis, 1962), and application of copper sulfate to the soil when seedlings were transplanted was reported to prevent or greatly reduce straighthead (Cunha and Baptista, 1958). Ricardo and Cunha (1968) studied copper sulfate as a supplier of Cu for straighthead control since soil organic matter may bind Cu and reduce its availability for uptake by plants. However, chemical prevention never reaches applicable scale because an effective chemical has never been developed, so the control effects are not stable.

A water management practice that is called 'Draining and Drying' was developed by farmers in the early 1900s (Atkins et al., 1957; Slaton, 2001), and is currently used as the only recommended method to prevent straighthead in rice through DD50 Computerized Program and agricultural extension system in the USA (Wilson et al., 2010b; 2010c). Rice fields are drained about 2 weeks after a permanent flood, dried thoroughly until cracks appear in the soil and rice leaves begin to curl and exhibit yellowing as drought stress symptoms, and then re-flooded for the remainder of season. The drying must be completed about 10 to 14 days before the internode elongation starts (Wells and Gilmour, 1977), and the best timing could be predicted by the online DD50 Program http://dd50.uaex.edu/dd50Logon.asp. Fields that favor straighthead are permanent, which means each time when rice is planted, straighthead will develop at some level to cause yield losses if the flood is not drained for the soil to be aerated at appropriate time (Wilson et al., 2010c). Soil aeration is believed to speed the decay of soil organic matter (Editor's Note, 1946) and help oxidize arsenic (As) into arsenate, which is biologically inactive (Marin et al., 1992). Therefore, once straighthead occurs in a field, growers will keep using the Draining and Drying method permanently because of unaffordable consequences.

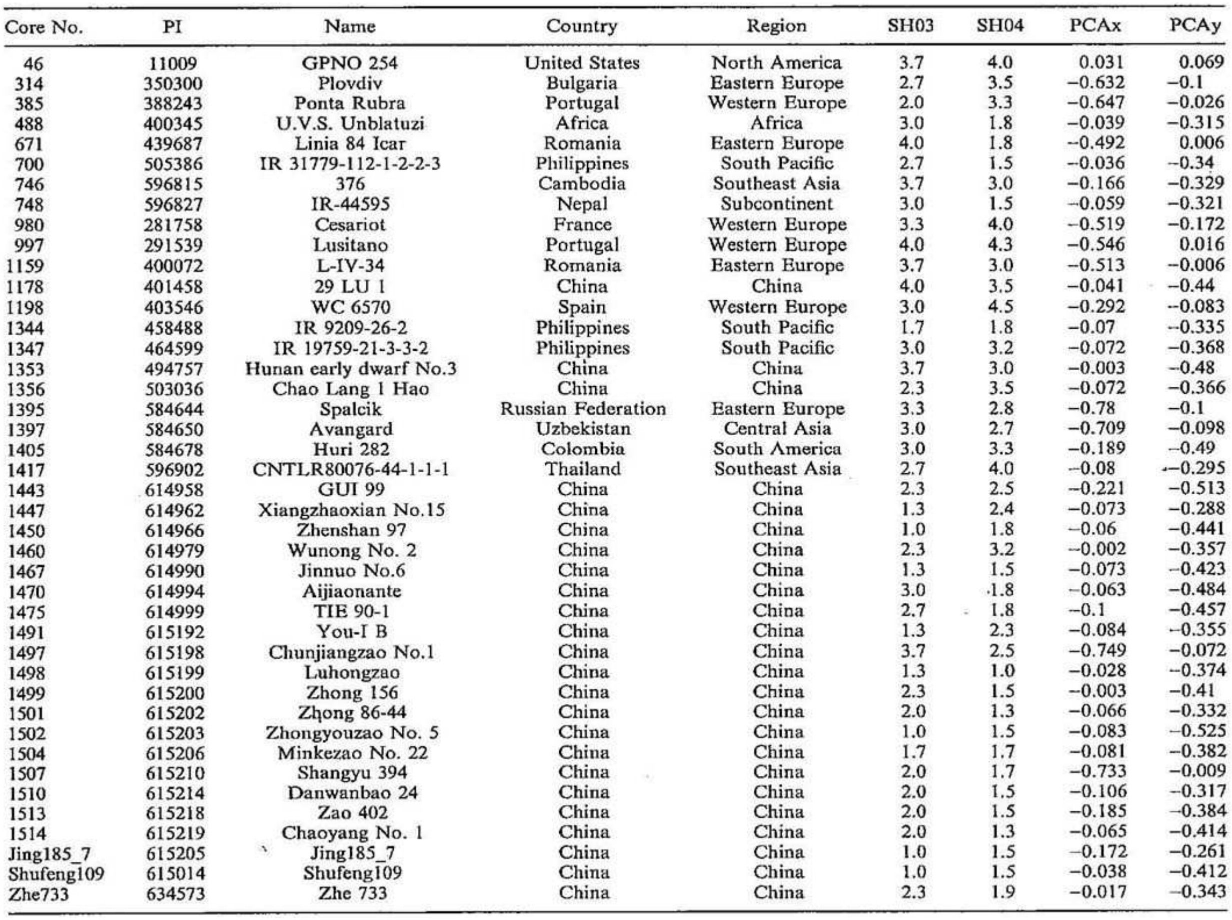
Table 1 shows cultivar variation on yield recovery of the Draining and Drying from the traditional-continuous flood. Long grain type cultivar Cocodrie and medium Bengal are high recovery cultivars with about 80% of the recovered yield. Cypress, Drew and Madison are the intermediate recovery cultivars with more than 40% of the yield to be recovered by the Draining and Drying. Jefferson, Priscilla and Wells are the low recovery cultivars because they display certain resistance to straighthead.

Currently, the Draining and Drying method is applied to more than one third of the rice acreage in Arkansas as a preventative measure (Wilson, per. Comm.). Using Arkansas rice harvested area of 723,000 hectares in 2010, K.B. Watkins, agricultural economics professor in the University of Arkansas, Rice Research and Extension Center, made the following estimates: $ 9.21/ha for additional labor cost to open levee gates for the draining, $ 20.93/ha for power cost to water the dried fields afterwards, and $ 56.77/ha for additional application of fungicide to control blast since blast disease is known to be more severe in fields or parts of fields in which the water in paddies falls below recommended levels (TeBeest et al., 2007). As a result, straighthead prevention added either $ 7.264 million for the draining and reflooding only or $ 20.945 million for the draining, reflooding and blast control to rice growers in Arkansas. Furthermore, an additional 308.4 m^3 of water are required to re-flood each hectare after drying, which resulted in an extra 74.324 million m^3 of water utilized for straighthead prevention in Arkansas in 2010. Wasting water is becoming a public concern because Lonoke, Prairie, Arkansas, and Jefferson counties with 150,317 hectares of rice in 2010 have been designated as having critical levels of groundwater (Riley, pers. comm.). Thus, preserving the natural resource of water is important for the long term economic viability of these counties. Therefore, the Draining and Drying method for straighthead prevention is costly for rice growers and wasteful of natural resources, and results in drought-related yield loss.

3.3. Resistant germplasm for straighthead breeding

Varietal resistance is regarded as the most efficient, economical, and environmentally friendly strategy for straighthead prevention (Wilson et al., 2001; Yan et al., 2005; Dunn et al., 2006). The earliest attempt at breeding for straighthead resistance in the USA started in 1950s (Atkins et al., 1957), but little progress had been made because the inheritance of straighthead resistance had not been well understood because of limited resistant germplasm until 2002 (Yan et al., 2002).

In 2001, 124 accessions of germplasm including 109 *indica*and 15 *japonica* cultivars introduced from China were evaluated for straighthead resistance, and 19 showed resistance to straighthead (Table 2) (Yan et al., 2005). Seven had increases of grain yield from 134 to 1115 kg ha^{-1} under the influence of straighthead, and the other 12 had reductions from 7 to 1197 kg ha^{-1}, but all the increases and decreases due to straighthead were not significant. Their straighthead



Core No.	PI	Name	Country	Region	SH03	SH04	PCAx	PCAy
46	11009	GPNO 254	United States	North America	3.7	4.0	0.031	0.069
314	350300	Plovdiv	Bulgaria	Eastern Europe	2.7	3.5	−0.632	−0.1
385	388243	Ponta Rubra	Portugal	Western Europe	2.0	3.3	−0.647	−0.026
488	400345	U.V.S. Unblatuzi	Africa	Africa	3.0	1.8	−0.039	−0.315
671	439687	Linia 84 Icar	Romania	Eastern Europe	4.0	1.8	−0.492	0.006
700	505386	IR 31779-112-1-2-2-3	Philippines	South Pacific	2.7	1.5	−0.036	−0.34
746	596815	376	Cambodia	Southeast Asia	3.7	3.0	−0.166	−0.329
748	596827	IR-44595	Nepal	Subcontinent	3.0	1.5	−0.059	−0.321
980	281758	Cesariot	France	Western Europe	3.3	4.0	−0.519	−0.172
997	291539	Lusitano	Portugal	Western Europe	4.0	4.3	−0.546	0.016
1159	400072	L-IV-34	Romania	Eastern Europe	3.7	3.0	−0.513	−0.006
1178	401458	29 LU 1	China	China	4.0	3.5	−0.041	−0.44
1198	403546	WC 6570	Spain	Western Europe	3.0	4.5	−0.292	−0.083
1344	458488	IR 9209-26-2	Philippines	South Pacific	1.7	1.8	−0.07	−0.335
1347	464599	IR 19759-21-3-3-2	Philippines	South Pacific	3.0	3.2	−0.072	−0.368
1353	494757	Hunan early dwarf No.3	China	China	3.7	3.0	−0.003	−0.48
1356	503036	Chao Lang 1 Hao	China	China	2.3	3.5	−0.072	−0.366
1395	584644	Spalcik	Russian Federation	Eastern Europe	3.3	2.8	−0.78	−0.1
1397	584650	Avangard	Uzbekistan	Central Asia	3.0	2.7	−0.709	−0.098
1405	584678	Huri 282	Colombia	South America	3.0	3.3	−0.189	−0.49
1417	596902	CNTLR80076-44-1-1-1	Thailand	Southeast Asia	2.7	4.0	−0.08	−0.295
1443	614958	GUI 99	China	China	2.3	2.5	−0.221	−0.513
1447	614962	Xiangzhaoxian No.15	China	China	1.3	2.4	−0.073	−0.288
1450	614966	Zhenshan 97	China	China	1.0	1.8	−0.06	−0.441
1460	614979	Wunong No. 2	China	China	2.3	3.2	−0.002	−0.357
1467	614990	Jinnuo No.6	China	China	1.3	1.5	−0.073	−0.423
1470	614994	Aijiaonante	China	China	3.0	1.8	−0.063	−0.484
1475	614999	TIE 90-1	China	China	2.7	1.8	−0.1	−0.457
1491	615192	You-I B	China	China	1.3	2.3	−0.084	−0.355
1497	615198	Chunjiangzao No.1	China	China	3.7	2.5	−0.749	−0.072
1498	615199	Luhongzao	China	China	1.3	1.0	−0.028	−0.374
1499	615200	Zhong 156	China	China	2.3	1.5	−0.003	−0.41
1501	615202	Zhong 86-44	China	China	2.0	1.3	−0.066	−0.332
1502	615203	Zhongyouzao No. 5	China	China	1.0	1.5	−0.083	−0.525
1504	615206	Minkezao No. 22	China	China	1.7	1.7	−0.081	−0.382
1507	615210	Shangyu 394	China	China	2.0	1.7	−0.733	−0.009
1510	615214	Danwanbao 24	China	China	2.0	1.5	−0.106	−0.317
1513	615218	Zao 402	China	China	2.0	1.5	−0.185	−0.384
1514	615219	Chaoyang No. 1	China	China	2.0	1.3	−0.065	−0.414
Jing185_7	615205	Jing185_7	China	China	1.0	1.5	−0.172	−0.261
Shufeng109	615014	Shufeng109	China	China	1.0	1.5	−0.038	−0.412
Zhe733	634573	Zhe 733	China	China	2.3	1.9	−0.017	−0.343

Table 4. USDA core collection number, plant introduction (PI), cultivar name and country of origin, average rate of straighthead in 2003 (SH03) and 2004 (SH04) for resistant accessions rated 4 or less on a 1-9 scale and their positions in principal component analysis (PCA) (Agrama and Yan, 2010).

ratings ranged from 1 to 3 while susceptible check Cocodrie and Mars were rated 8 and 7, respectively.

All the resistant cultivars are *indica*. In terms of the cultivar 'Jing 185-7', ('Jing' means *japonica* in Chinese), a study has indicated that Jing185-7 is an *indica*(Agrama and Yan, 2010). Nine accessions of the resistant germplasm are in the very early group having 63 - 69 days to heading except Dian No. 01, two in the early group having 83 days to heading, two in the intermediate group having 89 - 90 days to heading, and all six in the late group having 90 or more days to heading except Jing 185-7. Preliminary observation of days to heading had incorrectly classified Dian No. 01 in the very early group. Plant heights vary from 89 cm for Tie 90-1 in the very early group to 133 cm for Sheng 12 in the late group. Two accessions, Zanuo No1 and Jinnuo No6, are waxy endosperm type containing no amylose, and the other seventeen non-waxy accessions have amyloses ranging from 14.8% for Shufeng 121 to 27.0% for Shufeng 109 in their endosperms. Aijiaonante is the first semi-dwarf cultivar bred in 1956 in China (Qian and Liu, 1993), and Zhenshan 97 is a popular maintainer line of hybrid rice in China (Virmani, 1994).

In 2002, 1002 accessions selected from 1794 accessions of the USDA Rice Core Collection (Yan et al., 2007; 2010b; Agrama et al., 2010) were evaluated for straighthead resistance in Arkansas (Agrama and Yan, 2010). These selections have proper maturities ranged from 48-110 days and plant heights ranged from 65-150 cm because the maturity and height largely affect the assessment of panicle fertility, which is essential for straighthead infestation. Those rated 4 or less in the 2003 straighthead evaluation were verified in larger plots and more replications in 2004. In total, 42 accessions (4.2%) displayed resistance (Table 4).

The 42 resistant cultivars originate from 15 countries in ten geographic regions worldwide, with the most (24 or 57%) from China, are classified into 5 clusters (Fig. 3) (Agrama and Yan, 2010). Cluster K1 includes three references, indicating none of the resistant cultivars belong to *Deep water*, *Australian* and *Aromatic* type. K2 includes 13 *indica* cultivars referenced by Zhe733, all from China except entry 488 from an unknown country in Africa. Referenced by IR64, K3 consists of another group of 12 *indica* cultivars originated from six countries of five regions: China, South America, South Pacific, Southeast Asia and the Subcontinent. Four Chinese cultivars, entry 1467, 1475, 1502 and Shufeng109, are positioned between K2 and K3. K4 has two *Tropical Japonica* references only and K5 contains 11 *Temperate Japonica* cultivars originating from seven countries of four regions: Centeral Asia, China, and Eastern and Western Europe. Two cultivars are positioned between K4 and K5: entry 46 (GPNO 254) developed in Louisiana, U.S.A. and entered in the germplasm collection in 1977; and entry 1198 (WC 6570) developed in Spain and entered the collection in 1975.

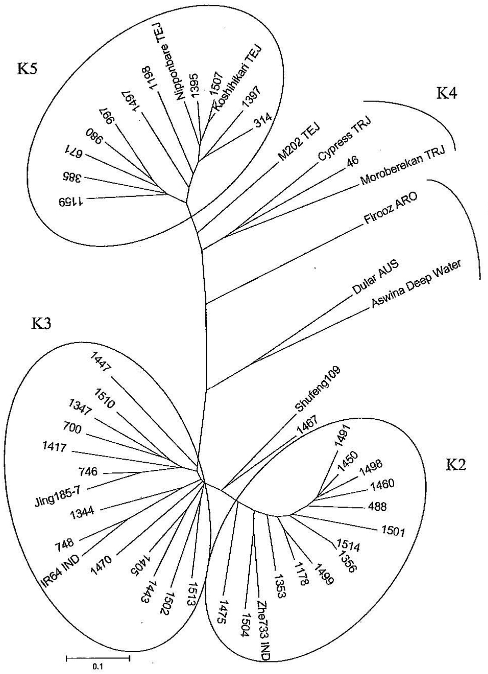


Figure 3. Unrooted neighbor-joining tree based on C.S. Chord (Cavalli-Sforza and Edwards, 1967) for 42 accessions resistant to straighthead rated 4 or less in a 1-9 scale and derived from the USDA rice core collection (Core entry number used in the chart) and reference cultivars (McNally et al. 2006) (AUS-Australia, ARO-Aromatic, IND-Indica, TRJ-Tropical Japonica, TEJ-Temperate Japonica) genotyped with 72 molecular markers (Agrama and Yan, 2010).

4. Gene mapping and development of DNA markers for breeding

4.1. Association mapping of quantitative trait loci (QTL) for straighthead

Because of the sporadic nature of straighthead and its unidentified causes, molecular marker assisted selection is essential for improvement of resistance in breeding programs. To take advantage of recent advances in gene-mapping technology, we executed a genome-wide association mapping study to identify genetic markers associated with straighthead using 547 accessions of germplasm from the USDA rice core collection and 75 simple sequence repeat (SSR) markers covering the entire rice genome (Agrama and Yan, 2009). A mixed-model approach combining the principal component assignments with kinship estimates proved to be particularly promising for association mapping. The extent of linkage disequilibrium was described among the markers. Seven marker loci are highly-significantly associated with straighthead at a significance level of 0.0001 = 4.0 value of $-\log_{10}q$ (Fig. 4).

The SSR markers RM263, RM105 and RM277 on chromosomes (chr) 2, 9 and 12, respectively, show very strong association with straighthead ($p < 9.83\text{x}10^{-8}$, $q < 1.31\text{x}10^{-6}$). Four other loci, RM490, RM413, RM116 and RM224 are highly associated with the disorder ($p < 0.0001$). Three alleles, each of marker RM490 (87 bp), RM413 (105 bp) and RM277 (122 bp), and two alleles (182 bp and 183 bp) of RM263 show significantly low straighthead rates of resistance. Only three accessions (core entry 748, 1344 and 1402) carrying allele 105 bp of RM413 have the lowest straighthead rate with the average of 3.9. Nine accessions with the allele 122 at RM277 on chr 12 (57.2 cM) have a significantly low straighthead rate (4.1). The rates of 15 accessions with allele 182 at RM263 (chr 2) are lower (4.6), on average, than the accessions with other alleles. Moderate straighthead rates are associated with alleles 87 bp at RM490 (23 accessions), 183 bp at RM263 (15 accessions) and 137 bp at RM105 (59 accessions).

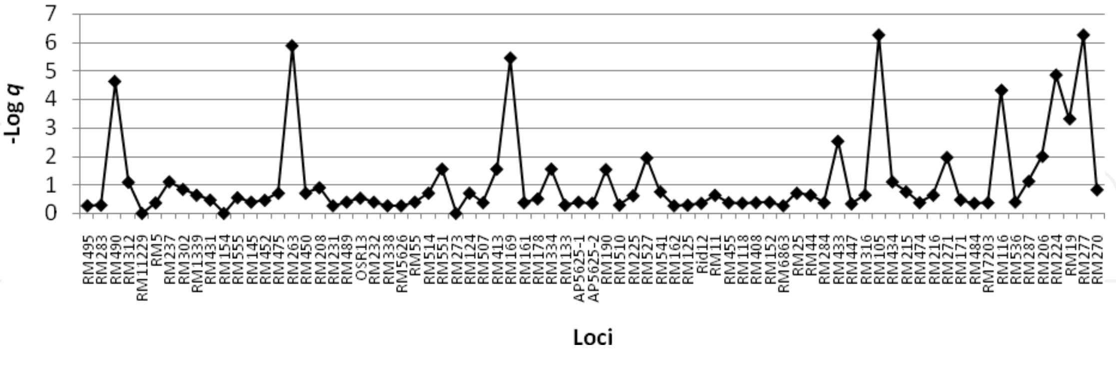


Figure 4. Marker loci significantly associated with straighthead disease with a value of - Log *q* = 4 which indicates a correlation probability 0.0001 among 547 accessions of germplasm in the USDA rice core collection, which were phenotyped in Arkansas and genotyped with 75 genome-wide SSR markers (Agrama and Yan, 2009).

4.2. Identification of a major QTL for straighthead resistance

We mapped the QTLs for straighthead using two recombined inbred line (RIL) F9 populations, one with 170 lines genotyped with 136 SSRs and another with 91 lines genotyped with 159

SSRs (Pan et al., 2012). These lines were evaluated for straighthead in both 2008 and 2009 with three replicates per year.

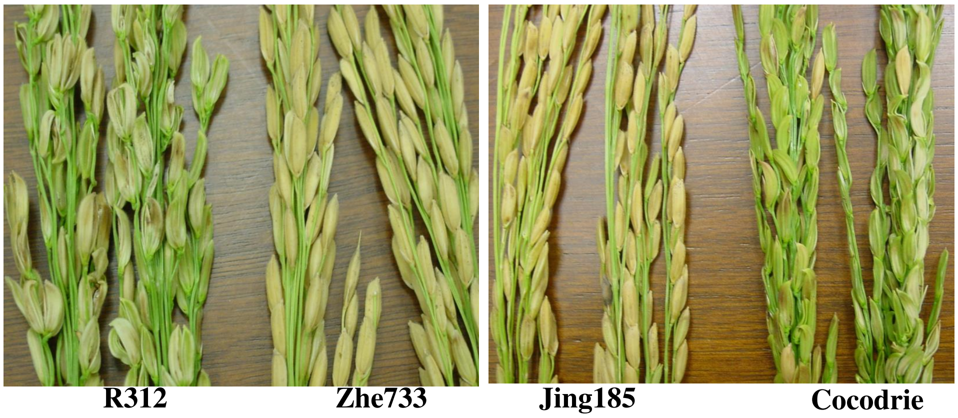


Figure 5. Straighthead phenotypes in parents of mapping populations,resistant parents Zhe733 and Jing185 with fully developed panicles while susceptible parents R312 and Cocodrie with severely distorted spikelets (Pan et al., 2012).

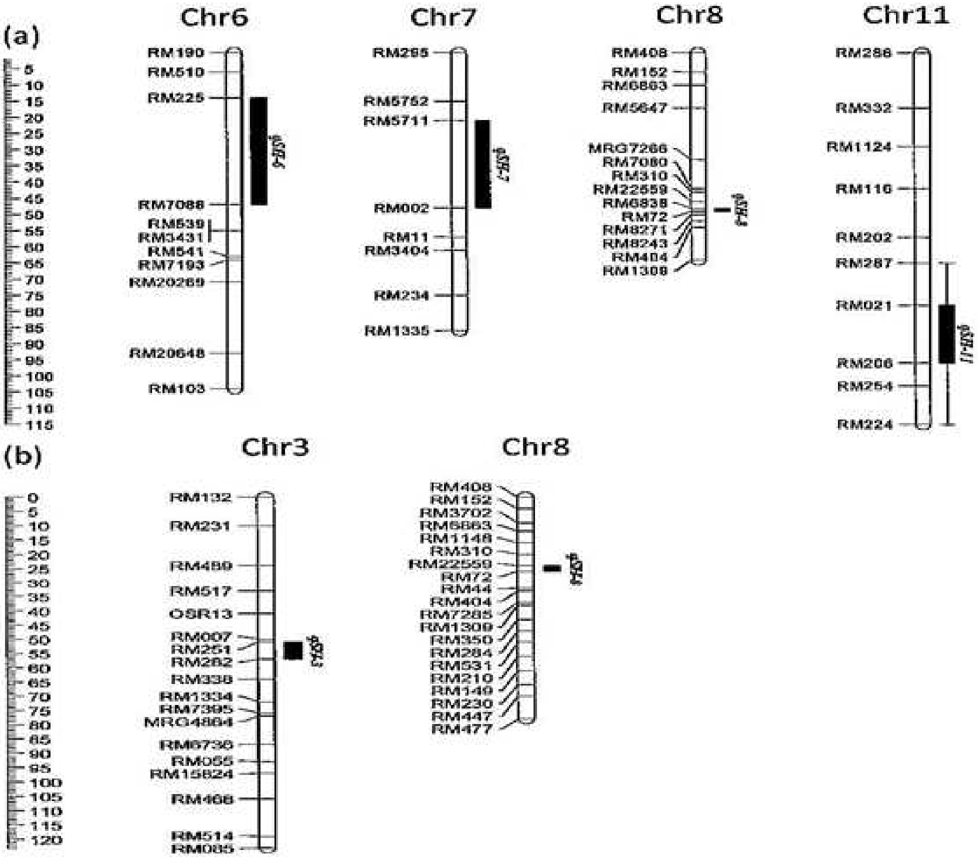


Figure 6. Four QTLs for straighthead resistance are identified from RIL F9 population of Zhe733/R312 (a) and two QTLs from RIL F9 population of Cocodrie/Jing185, are marked by black bar (Pan et al., 2012).

Four QTLs were identified to be associated with straighthead resistance in the Zhe733/R312 population on chr6, 7, 8 and 11 (Fig. 6a). The QTL on chr8 had the largest LOD (23.0), highest additive effect (-2.1) and smallest marker interval (1.0 cM) between RM6838 and RM72, and explained the most total variation (46%) for straighthead among the identified QTLs. From the Cocodrie/Jing185 population, two QTLs were identified (Fig. 6b), one on chr3 (LOD=3.8), and another on chr.8 (LOD= 27.0). The chr.8 QTL is within a 1.9 cM interval between RM22559 and RM 72, has a -2.1 additive effect, and explained 67% of total variation. RM72 at 6.76 Mb is the most distal marker of the chr8 QTL identified in both populations. RM6838 in Zhe733/R312 and RM22559 in Cocodrie/Jing185 are physically located very close to each other at 5.85 Mb and 5.70 Mb, respectively. The overlapping intervals on chr.8 identified in both populations indicate the presence of a major QTL at this location, designated as *qSH-8* (Fig. 5a for Zhe733/R312 and 5d for Cocodrie/Jing185).

4.3. Fine mapping of *qSH-8*, a Major QTL for straighthead resistance

Within the putative region of *qSH-8*, four recombinants (RIL12, 112, 174, and 306) are identified in Zhe733/R312 and four recombinants (RIL418, 423, 480, and 533) are identified in Cocodrie/Jing185 population for fine mapping according to the substitution strategy described by Paterson et al. (1990). Using an additional 16 SSR markers derived from the Gramene database http://www.gramene.org/, and 9 InDel markers designed from the MSU rice genome browser http://rice.plantbiology.msu.edu/cgi-bin/gbrowse/rice/to compare the sequence of Nipponbare with 93-11 in the targeted region,qSH-8 is fine mapped in a 290 kb interval between RM22573 and InDel 27 in the Zhe733/R312 population, and a 690 kb region between InDel 11 and RM22613 in the Cocodrie/Jing185 population (Fig. 7).

Three markers, SSR AP3858-1, InDel 11 and InDel 5 are in the 290 kb interval, and should co-segregate with *qSH-8* to predict either resistance or susceptibility of a rice line to straighthead. Both RIL 12 and 306 in the Zhe733/R312 population have the R312 genotype at AP3858-1, InDel 11 and InDel 5 loci, which matched up with the R312 phenotype, susceptible to straighthead with high ratings (8.7±0.5 for RIL 12 and 6.8±1.3 for RIL 306). Conversely, both RIL 112 and 174 have the Zhe733 resistant genotype at these loci, and have low straighthead ratings (1.6±0.9 for RIL 112 and 1.3±0.5 for RIL 174) as well. These results prove the hypothesis that co-segregation exists between *qSH-8* genotype and straighthead phenotype.

4.4. Marker development for marker-assisted breeding of straighthead resistance

We have tested 72 accessions of global germplasm for a match between straighthead phenotype and *qSH-8* genotype indicated by the markers AP3858-1 and InDel 11. The 72 accessions originated from 28 countries, and a large portion of them (22 accessions) were from China, followed by the Philippines and the USA. Forty of the tested accessions are resistant to straighthead with ratings of 4 or less, and the remaining 32 are susceptible with straighthead ratings of 6 or more based on previous studies by Yan et al. (2002; 2005) and Agrama and Yan (2009; 2010). For InDel 11, 30 accessions have either no alleles of or alleles different from parental Zhe733, R312, Cocodrie and Jing185. The remaining 42 have the parental alleles for InDel 11, where 32 genotypes have a good match with the expected phenotype (Table 5). For

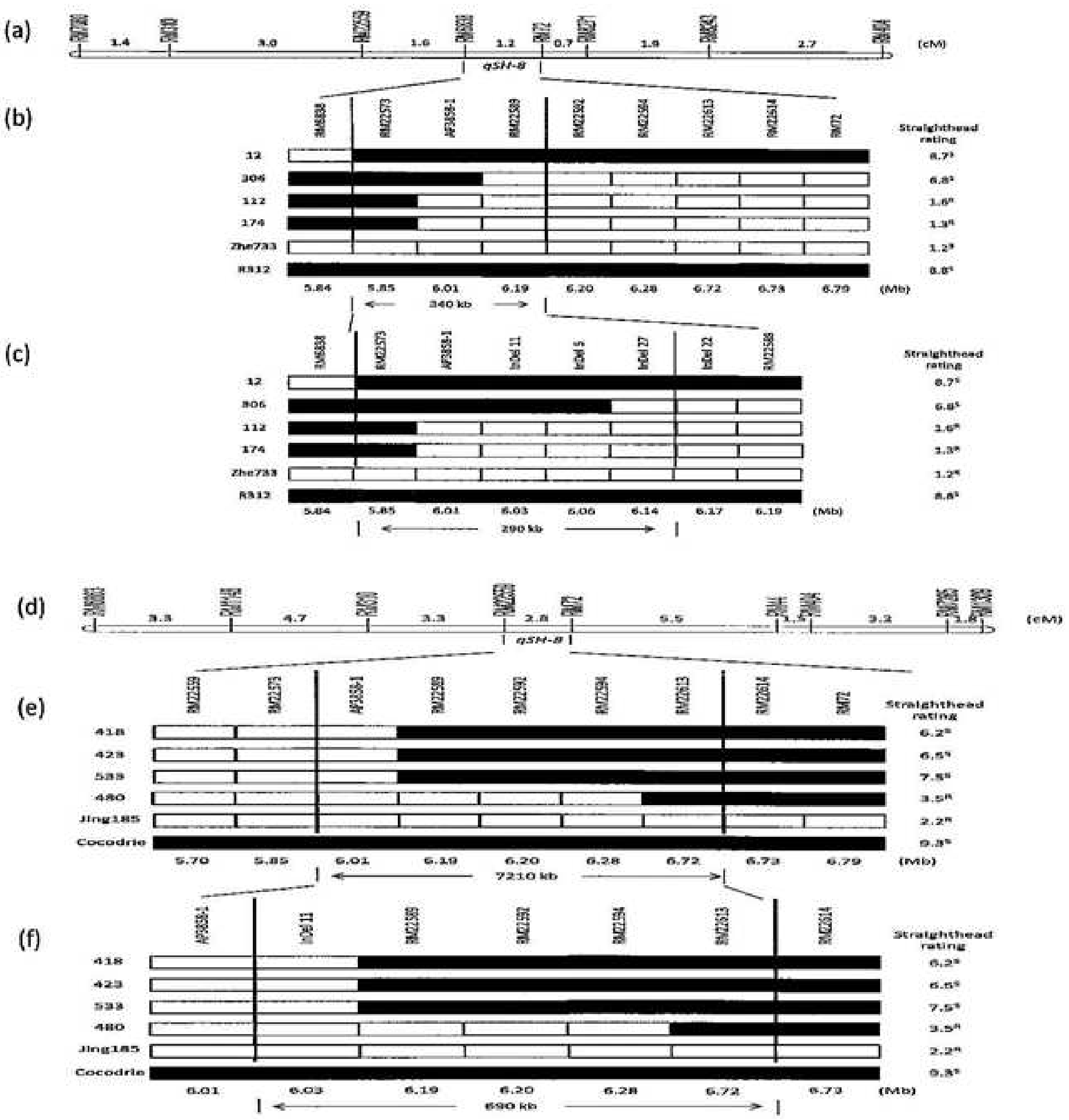
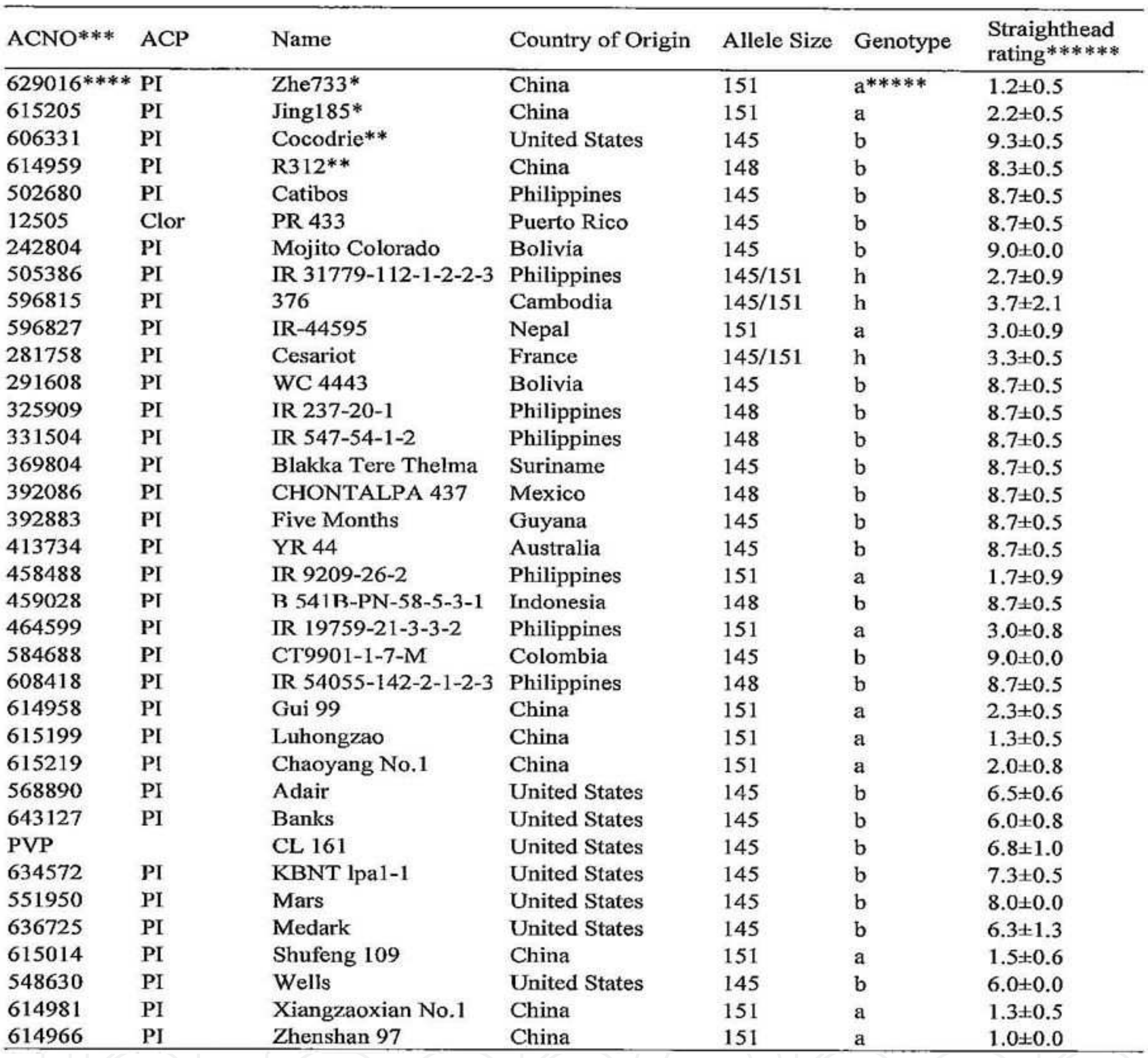


Figure 7. Fine mapping of *qSH-8* using Zhe733/R312 (a-c) and Cocodrie/Jing185 (d-f) F_9 RIL populations. (a) *qSH-8* regionof 1.2 cM between RM6838 and RM72, (b) a 340 kb region between RM22573 and RM22589, (c) a 290 kb region between RM22573 and InDel 27; (d) *qSH-8* regionof 2.8 cM between RM22559 and RM72, (e) a 710 kb region between AP3858-1 and RM22613 and (f) a 690 kb region between InDel 11 and RM22613 (Pan et al., 2012).

marker AP3858-1, 38 accessions do not have the parental alleles, and 25 out of the remaining 34 accessions have a good match between the genotype and phenotype. Because InDel 5 is monomorphic in the Cocodrie/Jing185 population, it is not desirable for screening the global germplasm collection. χ^2 test indicates a high association of InDel 11 with straighthead (P=0.0014), with 76.2% of the genotypes matching the phenotypes among those global accessions (Table 6). Similarly, AP3858-1 is highly associated with straighthead (P=0.0004) with a match of 73.5%. In the Zhe733/R312 population, all three markers (InDel 5, InDel 11, and AP3858-1) are verified by χ^2 test at the P<0.0001 level of significance for all where AP3858-1 has a slightly higher ratio of co-segregation (80.0%) than InDel 11 (79.6%) and InDel 5 (78.5%). InDel 5 is not polymorphic in the Cocodrie/Jing185 population, and the remaining two markers are verified at the $P<0.0001$ level of significance for both. InDel 11 has slightly higher ratio of co-segregation (85.1%) than AP3858-1 (81.2%) in the Cocodrie/Jing185 population.



ACNO***	ACP	Name	Country of Origin	Allele Size	Genotype	Straighthead rating******
629016****	PI	Zhe733*	China	151	a*****	1.2±0.5
615205	PI	Jing185*	China	151	a	2.2±0.5
606331	PI	Cocodrie**	United States	145	b	9.3±0.5
614959	PI	R312**	China	148	b	8.3±0.5
502680	PI	Catibos	Philippines	145	b	8.7±0.5
12505	Clor	PR 433	Puerto Rico	145	b	8.7±0.5
242804	PI	Mojito Colorado	Bolivia	145	b	9.0±0.0
505386	PI	IR 31779-112-1-2-2-3	Philippines	145/151	h	2.7±0.9
596815	PI	376	Cambodia	145/151	h	3.7±2.1
596827	PI	IR-44595	Nepal	151	a	3.0±0.9
281758	PI	Cesariot	France	145/151	h	3.3±0.5
291608	PI	WC 4443	Bolivia	145	b	8.7±0.5
325909	PI	IR 237-20-1	Philippines	148	b	8.7±0.5
331504	PI	IR 547-54-1-2	Philippines	148	b	8.7±0.5
369804	PI	Blakka Tere Thelma	Suriname	145	b	8.7±0.5
392086	PI	CHONTALPA 437	Mexico	148	b	8.7±0.5
392883	PI	Five Months	Guyana	145	b	8.7±0.5
413734	PI	YR 44	Australia	145	b	8.7±0.5
458488	PI	IR 9209-26-2	Philippines	151	a	1.7±0.9
459028	PI	B 541B-PN-58-5-3-1	Indonesia	148	b	8.7±0.5
464599	PI	IR 19759-21-3-3-2	Philippines	151	a	3.0±0.8
584688	PI	CT9901-1-7-M	Colombia	145	b	9.0±0.0
608418	PI	IR 54055-142-2-1-2-3	Philippines	148	b	8.7±0.5
614958	PI	Gui 99	China	151	a	2.3±0.5
615199	PI	Luhongzao	China	151	a	1.3±0.5
615219	PI	Chaoyang No.1	China	151	a	2.0±0.8
568890	PI	Adair	United States	145	b	6.5±0.6
643127	PI	Banks	United States	145	b	6.0±0.8
PVP		CL 161	United States	145	b	6.8±1.0
634572	PI	KBNT lpa1-1	United States	145	b	7.3±0.5
551950	PI	Mars	United States	145	b	8.0±0.0
636725	PI	Medark	United States	145	b	6.3±1.3
615014	PI	Shufeng 109	China	151	a	1.5±0.6
548630	PI	Wells	United States	145	b	6.0±0.0
614981	PI	Xiangzaoxian No.1	China	151	a	1.3±0.5
614966	PI	Zhenshan 97	China	151	a	1.0±0.0

* Zhe733 and Jingl85 as the straighthead resistant parents for the RIL populations while

** Cocodrie and R312 as the susceptible parents.

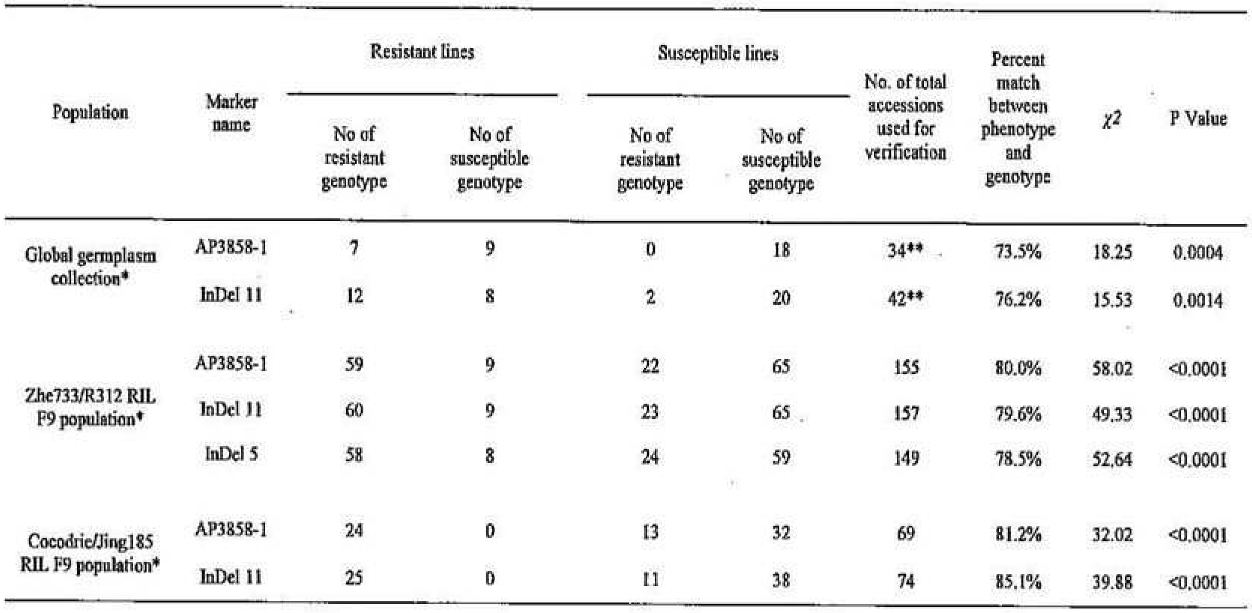
*** Core collection accessions with PI No. and C1or No, PVP as Plant Variety Protection.

***** A total of 42 accessions display parental allele screened by In Del 11. The 32 accessions listed above are those have genotype matched with phenotype, but there are other I 0 accessions which genotypes do not match with phenotypes.

**** 'a' as resistant, 'b' as susceptible, and 'h' as heterozygote genotype but still considered as resistant because straighthead is a dominant trait.

****** Straighthead rating using a 1-9 scale, with 4 or below being resistant and 6 or above being susceptible.

Table 5. Association of marker InDel 11 genotype with straighthead phenotype in a global germplasm collection (Pan et al., 2012).



Population	Marker name	Resistant lines		Susceptible lines		No. of total accessions used for verification	Percent match between phenotype and genotype	χ^2	P Value
		No of resistant genotype	No of susceptible genotype	No of resistant genotype	No of susceptible genotype				
Global germplasm collection*	AP3858-1	7	9	0	18	34**	73.5%	18.25	0.0004
	InDel 11	12	8	2	20	42**	76.2%	15.53	0.0014
Zhe733/R312 RIL F9 population*	AP3858-1	59	9	22	65	155	80.0%	58.02	<0.0001
	InDel 11	60	9	23	65	157	79.6%	49.33	<0.0001
	InDel 5	58	8	24	59	149	78.5%	52.64	<0.0001
Cocodrie/Jing185 RIL F9 population*	AP3858-1	24	0	13	32	69	81.2%	32.02	<0.0001
	InDel 11	25	0	11	38	74	85.1%	39.88	<0.0001

*The accessions or RILs selected for marker verification were either the resistance with straighthead rating 4 or below or the susceptibility with rating 6 or above in global germplasm collection and two F9 populations.

**A total of 34 accessions were selected for verification of AP3 858-1 because remaining 3 8 had either no alleles of or different from parental Zhe733, R312, Cocodrie and Jingl85, and for the same reason, 42 accessions were applied for verification of lnDell 11.

Table 6. Association analysis between marker genotypes and straighthead phenotype (Pan et al., 2012).

4.5. Bridge germplasm for cultivar development

Since the susceptible parent Cocodrie is a widely grown cultivar in the USA (Linscombe et al., 2000), it will be important to improve Cocodrie for straighthead resistance. Among 162 SSRs used for mapping and fine mapping in Cocodrie/Jing185 population, 101 are monomorphic between parent Cocodrie and resistant line RIL506 which is resistant with straighthead rating 2.3. Thus, the genetic similarity between Cocodrie and RIL506 is 62%. In other word, 62% of marker loci are same between Cocodrie and RIL506 in the whole genome. Four other resistant RIL lines 404, 407, 479 and 480 have a genetic similarity of more than 50% with Cocodrie. These resistant lines can be used for improving straighthead resistance in long grain *tropical japonica* cultivars like Cocodrie in the southern US. However, the susceptible R312 is not a commercial cultivar in the USA, so the improvement of straighthead resistance for R312 is not important in the USA.

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