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 severe (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 for comparing water managements within a cultivar: 2923

LSD 0.05 for comparing cultivars within a water management: 1663

*Yield loss (%) for each cultivar was calculated by: \[ \frac{(\text{Drain and dry yield} - \text{Continuous flood yield})}{\text{Drain and dry yield}} \times 100. \]

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).
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 95% 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 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.

Table 2. Nineteen Chinese rice germplasm accessions had no significant yield reductions from straighthead induced by MSMA (monosodium methanearsonate) at 6.7 kg ha\(^{-1}\) 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‡ |
|----------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| No MSMA        | 5.9f | 188a | 31a | 180a| 1053a| 185a| 9b  | 66a | 312a| 176b| 0.9a| 1.1a| 5.9c| 21a  |
| Before MSMA    | 5.3b | 196a | 19b | 102a| 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
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).

**Table 4.** USDA core collection number, plant introduction (Pl), 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).

| 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 |
| 336      | 350000 | Plovdiv           | Bulgaria      | Eastern Europe | 2.7  | 3.5  | -0.632 | -0.1 |
| 385      | 882243 | Ponta Rubra       | Portugal      | Western Europe | 2.0  | 3.3  | -0.647 | -0.026 |
| 488      | 490344 | U.V.S. Unbleiuti  | 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      | 503385 | IR 31779-122-2-2-3 | Philippines | South Pacific | 2.7  | 1.5  | -0.036 | -0.34 |
| 746      | 596215 | 776               | Cambodia      | Southeast Asia | 3.7  | 3.0  | -0.166 | -0.329 |
| 748      | 596227 | IRA-1932          | Nepal         | Subcontinent | 3.0  | 1.5  | -0.059 | -0.321 |
| 980      | 235757 | Cesarot           | France        | Western Europe | 3.3  | 4.0  | -0.519 | -0.172 |
| 979      | 381539 | Luniziano         | 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 | LL 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     | 458449 | IR 9207-26-2      | Philippines   | South Pacific | 1.7  | 1.8  | -0.07  | -0.335 |
| 1347     | 464599 | IR 19759-21-3-2-2 | Philippines | South Pacific | 3.0  | 3.2  | -0.072 | -0.368 |
| 1353     | 494757 | Huacao early dwarf No.3 | China   | China      | 3.7  | 3.0  | -0.003 | -0.48 |
| 1356     | 509368 | Chao Ang 1 Hao    | China         | China      | 2.3  | 3.5  | -0.072 | -0.366 |
| 1395     | 594444 | Spalick           | Russian Federation | Eastern Europe | 3.2  | 2.8  | -0.709 | -0.098 |
| 1397     | 594450 | Avangard          | Uzbekistan    | Central Asia | 3.0  | 2.7  | -0.009 | -0.49 |
| 1405     | 384678 | Huri 282          | Colombia      | South America | 3.0  | 3.3  | -0.189 | -0.49 |
| 1417     | 599070 | CNTLR8007-66-4-1-1-1 | Thailand | Northeast Asia | 2.7  | 4.0  | -0.038 | -0.295 |
| 1443     | 614938 | GIU 99            | China         | China      | 2.3  | 2.5  | -0.231 | -0.513 |
| 1447     | 614962 | Xianghai No. 15   | China         | China      | 1.3  | 2.4  | -0.073 | -0.288 |
| 1450     | 614966 | Zhaoxian 97       | China         | China      | 1.0  | 1.8  | -0.06  | -0.441 |
| 1460     | 614979 | Wuchong No. 2     | China         | China      | 2.3  | 3.2  | -0.002 | -0.327 |
| 1467     | 614990 | Jinluo 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 | THB 90-1          | China         | China      | 2.7  | 1.8  | -0.1  | -0.457 |
| 1510     | 615192 | You-1 B           | China         | China      | 1.3  | 2.3  | -0.084 | -0.355 |
| 1497     | 615198 | Chuanlijiangzao No. 1 | China     | China      | 3.7  | 2.5  | -0.749 | -0.072 |
| 1498     | 615199 | Lahougaozao       | China         | China      | 1.3  | 1.0  | -0.028 | -0.374 |
| 1499     | 615200 | Zong 156          | China         | China      | 2.3  | 1.5  | -0.003 | -0.41 |
| 1501     | 615202 | Zong 86-44        | China         | China      | 2.0  | 1.3  | -0.056 | -0.332 |
| 1502     | 615203 | Zhongyouzi 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 | Shaoyou 394       | China         | China      | 2.0  | 1.7  | -0.733 | -0.059 |
| 1510     | 615214 | Dazhanbao 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 | Chyang 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 |
| Zhewei13 | 634873 | Zhe 733           | China         | China      | 2.3  | 1.9  | -0.017 | -0.343 |
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 ($p < 9.83 \times 10^{-9}$, $q < 1.31 \times 10^{-6}$). 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 $-\log_{10}q = 4$ 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 recombinant 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 \( q_{SH-8} \) (Fig. 5a for Zhe733/R312 and 5d for Cocodrie/Jing185).

### 4.3. Fine mapping of \( q_{SH-8} \), a Major QTL for straighthead resistance

Within the putative region of \( q_{SH-8} \), 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, \( q_{SH-8} \) 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 cosegregate with \( q_{SH-8} \) 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 cosegregation exists between \( q_{SH-8} \) 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 \( q_{SH-8} \) 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
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. \( \chi^2 \) 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 \( \chi^2 \) 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

Figure 7. Fine mapping of \( qSH-8 \) using Zhe733/R312 (a-c) and Cocodrie/Jing185 (d-f) \( F_9 \) RIL populations. (a) \( qSH-8 \) region of 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) \( qSH-8 \) region of 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).
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*** | ACN | Name | Country of Origin | Allele Size | Genotype | Straighthead rating***** |
|---------|-----|------|-------------------|-------------|----------|-------------------------|
| 629016**** | PI  | Zhe733* | China | 151 | a**** | 1.2±0.5 |
| 5715205 | 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 | Clo | PR 433 | Puerto Rico | 145 | b | 8.7±0.5 |
| 242804 | PI  | Mojito Colorado | Bolivia | 145 | b | 9.0±0.0 |
| 505386 | PI  | IR 31779-1121-2-2-3 | Philippines | 145/151 | h | 2.7±0.9 |
| 596813 | PI  | 376 | Cambodia | 145/151 | h | 3.7±2.1 |
| 596827 | PI  | IR-44595 | Nepal | 151 | a | 3.0±0.9 |
| 281758 | PI  | Cesarlot | 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 |
| 392086 | PI  | Blakka Tere Theuma | Suriname | 145 | b | 8.7±0.5 |
| 392883 | PI  | Five Months | Mexico | 148 | 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  | IR 5418-PN-58-5-3-1 | Indonesia | 148 | b | 8.7±0.5 |
| 464599 | PI  | IR 19759-21-3-2 | Philippines | 151 | a | 3.0±0.8 |
| 584688 | PI  | CT9091-1-7-M | Colombia | 145 | b | 9.0±0.0 |
| 608418 | PI  | IR 54055-1422-2-1-2-3 | 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  | Chanyang 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 | CL161 | United States | 145 | b | 6.8±1.0 |
| 634572 | PI  | KBNT 1p1-1 | 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  | Shufang 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 C1 or No, PVP as Plant Variety Protection.
***** A total of 42 accessions display parental allele screened by InDel 11. The 32 accessions listed above are those whose genotypes match with phenotype, but there are other 10 accessions whose 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).
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 38 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.

| Population         | Marker name | Resistant lines | Susceptible lines | Percent match between phenotype and genotype | \( \chi^2 \) | P Value |
|--------------------|-------------|----------------|-------------------|--------------------------------------------|-------------|---------|
|                    |             | No of resistant genotype | No of susceptible genotype | No of resistant genotype | No of susceptible genotype | No. of total accessions used for verification |
| Global germplasm collection* | AP3858-1 | 7 | 9 | 0 | 18 | 24 | 73.3% | 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 | 80.3% | 58.02 | <0.0001 |
|                     | InDel 11    | 60 | 9 | 23 | 65 | 157 | 79.0% | 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 38 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.

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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