Weed competitiveness and yielding ability of aerobic rice genotypes

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Abstract

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Aerobic rice, grown under aerobic soil conditions like maize or wheat, is an innovative way to cope with the growing demand for rice and the increasing water scarcity. Weeds are the most severe constraint to aerobic rice. The use of herbicides causes environmental pollution and induces the proliferation of resistant weed biotypes. These risks and the costs of labor for weeding prompt research on environment-friendly and labour-efficient methods of weed control. The adoption of weed-competitive genotypes is regarded as an effective tool in integrated weed management. The main objectives of this study were to explore the feasibility of breeding for weed competitiveness, to develop an indirect selection index for the trait, and to test the efficacy of a weed-competitive genotype in weed management.

Field experiments were carried out at the International Rice Research Institute in the Philippines. Aerobic and upland genotypes were grown under aerobic conditions to study their performance under both weed-free and weedy environments.

A large genetic variability within *Oryza sativa* both in weed-suppressive ability (WSA) and yielding ability under weed competition was detected. These two traits were moderately heritable and closely associated. Yield and early crop vigour investigated under weed-free conditions accounted for 87% of genotypic variation in yield under weed competition and for 40% of the variation in weed biomass; thus, weed-free yield and early crop vigour should both be included in an indirect selection index for breeding high-yielding, weed-competitive genotypes. Fast early vegetative growth rather than plant erectness was crucial to strong WSA.

Indica germplasm in both yielding ability and WSA, and *aus* germplasm in WSA were both superior to tropical *japonica* germplasm and the progenies of *indica*/tropical *japonica*; thus, *indica* and *aus* germplasm may be used as gene donors for breeding for strong WSA in the tropics. The effects of genotype and seeding rate on suppressing weeds were additive; it was shown that a strongly weed-competitive genotype at an appropriate seeding rate (300 viable seeds m^{-2}) suppresses weeds effectively. These findings indicate that weed-competitive genotypes may contribute greatly to weed management in aerobic rice agro-ecosystems.

Keywords: Broad-sense heritability; Crop vigour; Genetic correlation; Indirect selection index; Plant erectness; Rice germplasm; Seeding rate; Vegetative growth; Weed-suppressive ability.

Preface

Upon the recommendation by Dr. Ren Wang, DDG for Research of the International Rice Research Institute (IRRI), and with the arrangements by Prof. Ming Zhao from China Agricultural University (CAU), Prof. Martin Kropff from Wageningen University (WU), and Drs. Bas Bouman and Gary Atlin from IRRI, I was granted a Sandwich-PhD fellowship by WU under the agreement between IRRI and the C.T. de Wit Graduate School of Production Ecology and Resource Conversation (PE&RC) of WU. I am very grateful to all of them for their support to initiate my PhD programme. I started my Sandwich-PhD programme in July 2001 at IRRI, followed by my first 9-month stay in the Group Crop and Weed Ecology (CWE), Department of Plant Sciences of Wageningen in 2002.

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This thesis is dedicated to, and in memory of my mother and father, who passed away at the start and during my PhD program, respectively. Their profound love and encouragement were always a strong power driving me to go forward for my PhD, and I believe, for the rest of my life as well.

Dule Zhao Wageningen, May 2006

Contents

Abbreviations

AWD	alternate wetting and drying
CB	crop biomass
E	plant erectness
GC	ground cover of canopy
H	broad-sense heritability
HI	harvest index
HR	height growth rate
HT	plant height
IRRI	International Rice Research Institute
ISE	indirect selection efficiency
ISI	indirect selection index
IWM	integrated weed management
LAI	leaf area index
SLA	specific leaf area
SR	seeding rate
TN	tillers per plant
VV	crop vigour
WAS	weeks after sowing
WB_W	mean for weed biomass across three years
WC	weed competitiveness
WR_W	mean for weed rating across three years
WSA	weed-suppressive ability
WT	weed tolerance
Y_F	weed-free yield (rice yield under weed-free conditions)
Y_W	weedy yield (rice yield under weedy conditions)
YLD	mean for grain yield under weed-free conditions over three replicates in 2003
YLD_W	mean for grain yield under weedy conditions across three years

CHAPTER 1

General introduction

Introduction

Rice is life: it is the staple food for more than three billion people, over half the world's population. It provides 27% of dietary energy and 20% of dietary protein in the developing world, and is the primary source of income and employment for more than 100 million households in Asia and Africa (FAO, 2004). Rice production had continuously increased in the past three decades beginning with the Green Revolution, but has stagnated since 1999 (USDA, 2004). Rice demand is projected to increase by 25% from 2001 to 2025 to keep pace with population growth (Maclean et al., 2002). However, land for agriculture is decreasing because of urbanization and industrialization, especially in the rice-producing nations (FAO, 1992); water availability is declining resulting from population growth, over-consumption and pollution (Duda and El-Ashry, 2000). With such constraints, producing more rice in the future to feed additional population is a great challenge. To fulfil the increased rice demand with shrinking resources, it will be necessary to increase yield in a unit area with less water.

Rice ecosystems

Rice is produced in a wide range of locations and under a variety of climatic conditions ranging in temperature (growing season average) from 17 to 33°C, in rainfall (annual average) from 100 to 5100 mm, in altitude from sea level to 2600 m, and in solar radiation from 25 to 95% of potential during the main rice season. At least 114 countries produce rice. Asian nations, however, produce 92% of the world's (Maclean et al., 2002). Rice production is classified into four ecosystems based on water supply during cultivation (Khush, 1997) as illustrated in Figure 1:

- Irrigated rice: grown in well levelled, bunded fields, transplanted or direct seeded in puddled soil, with a shallow flood maintained during crop growth, and thus grown in anaerobic conditions.
- Rainfed lowland rice: grown in level to slightly sloping bunded fields, transplanted in puddled soil or direct seeded on puddled or ploughed dry soil, supplied with no irrigation water but submerged in rainfall water shallower than 50 cm for more than 10 consecutive days during crop growth, and thus grown in alternating aerobic to anaerobic conditions.
- Upland rice: grown in sloping, nonbunded, well drained fields, direct seeded in dry or wet soil, supplied with no irrigation and thus grown in completely aerobic conditions.
- Flood-prone rice: similar to rainfed lowland rice, but grown in deep water (>50 cm) from rainfall for a month or longer during late growth stage; thus its early growth may be under alternate aerobic and anaerobic conditions, but late growth is usually under anaerobic conditions.

Among the four rice ecosystems, irrigated rice is the main production system, occupying more than 50% of world rice area (Figure 1), producing the highest yields (Table 1) and supplying more than 75% of world rice at present. Irrigated rice is a profligate user of water. Water consumption for per kg of rice ranges from 1000 – 5000 liters depending on rice ecosystem, soil conditions and crop management, which is about two to three times more than is needed to produce other cereals such as wheat or maize (Bouman and Tuong, 2000; Cantrell and Hettel, 2005). In Asia, 90% of the total diverted freshwater is used for irrigated agriculture, and more than 50% of this is used to irrigate rice (Barker et al., 1998). There is a growing scarcity of water worldwide, which has already started to influence conventional irrigated rice production (Tuong and Bouman, 2003). By 2025, a 'physical water scarcity' is projected for more than 2 million ha of irrigated dry-season rice and 13 million ha of irrigated wet-season rice in Asia, and an 'economic water scarcity' is expected to hamper most of Asia's 22 million ha of irrigated dry-season rice (Tuong and Bouman, 2003). Obviously, the most important irrigated rice ecosystem for human beings is being increasingly threatened by water scarcity. The increasing water scarcity for agriculture, and competition for water from non-agricultural sectors, point to an urgent

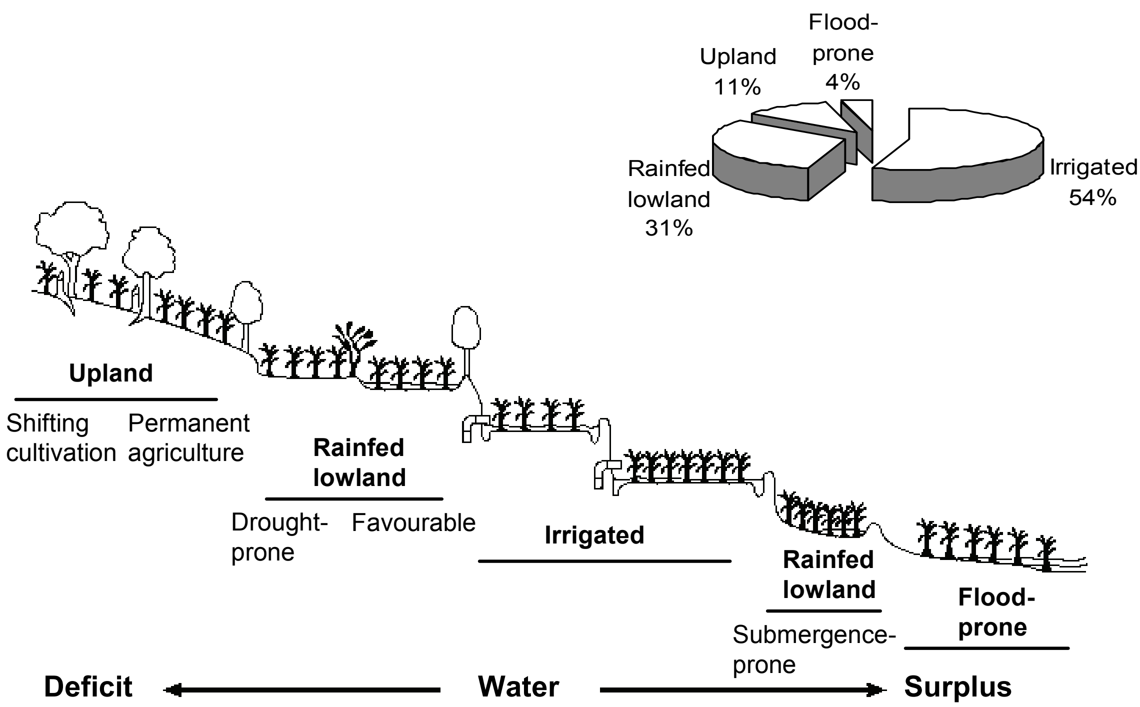

Figure 1. Rice ecosystems and their percentage of world area (source: IRRI, 2001, derived from FAO data).

Table 1. Average yield (Mg ha^{-1}) of four rice ecosystems worldwide.

Region	Irrigated	Rainfed	Upland	Flood-prone
Asia	4.9	2.3	1.1	1.5
Latin America	5.0	2.4	1.6	1.8
Africa	5.0	2.1	1.0	1.3
USA	6.3	-	-	-
Australia	8.2	-	-	-
Rest of World	4.9	-	1.0	-
Average	4.9	2.3	1.2	1.5

(Source: Anon, 1993).

need to improve crop water productivity to ensure adequate food for future generations with the same or less water than is presently available to agriculture. Two types of water-saving systems may be used to replace the traditional irrigated rice production schemes that are now under threat (Cantrell and Hettel, 2005):

- Alternate wetting and drying (AWD). In this system, the field is irrigated with enough water to flood the paddy for three to five days, and, as the water soaks into the soil, the surface is then allowed to dry for a few days (usually from two to four) before getting re-flooded. Genotypes suited to this system are same as irrigated rice (Atlin and Lafitte, 2002).
- Aerobic rice. In this system, rice is sown directly into dry soil, like wheat or maize, and irrigation is applied to keep the soil sufficiently moist for good plant growth, but the soil is never saturated.

Alternate wetting and drying is a promising rice system. Studies with this system have shown that it can maintain yield while saving water from 15 to 50% (Shi et al., 2002; Uphoff and Randriamiharisoa, 2002; Belder et al., 2004). The aerobic rice system was pioneered in China and Brazil, where breeders developed some new genotypes with high yield potential and strong drought tolerance, termed ‘Han Dao’ in Chinese or ‘aerobic rice’ at the International Rice Research Institute (IRRI) (Bouman, 2003), by crossing irrigated rice with upland rice germplasm. in northern China, such new genotypes can produce high yields (up to 6 to 7 Mg ha^{-1}) with limited water supply (irrigation + rainfall = 500 to 600 mm), resulting in water productivity of about twice that of conventional irrigated lowland rice (Wang et al., 2002; Bouman et al., 2002). Studies in tropical regions also showed a significant water saving and high water productivity of tropical aerobic rice (Bouman et al., 2005). Water saving in the aerobic rice system compared with the conventionally irrigated lowland rice results mainly from (1) no water losses during land preparation, (2) less percolation and seepage due to the elimination of the ‘pressure head’ of the ponded water layer normally maintained in an irrigated field, and (3) less evaporation (Bouman et al., 2005). ‘Aerobic rice’ and ‘upland rice’ are both grown under aerobic conditions. However, the former is under controlled water management, but the latter is not. Although the technology of growing rice with the new AWD and aerobic rice systems need to be further refined or developed, a broad adoption of these systems is expected to ensure rice production in water-short areas, and result in significant water saving (Cantrell and Hettel, 2005).

Weed problems in aerobic rice

In traditional irrigated lowland rice systems, rice has a two- to three-week ‘head start’ over weeds, which favors rice in competition against weeds that have not emerged yet at transplanting, and the water layer after transplanting effectively suppresses the emergence and growth of most weed flora, including upland and semi-aquatic weeds. Therefore, irrigated lowland rice is a good system in terms of ease and cost of weed control (De Datta and Baltazar, 1996). In aerobic and upland rice, the crop is directly sown in nonpuddled, nonflooded soil, where weeds and rice germinate simultaneously. The lack of ‘head start’ and the absence of floodwater make aerobic and upland rice more weed-infested than irrigated lowland rice (De Datta and Llagas, 1984). Among rice ecosystems, therefore, the greatest weed pressure and competition occurs in upland and aerobic rice, and the least in transplanted irrigated and rainfed lowland rice (De Datta and Baltazar, 1996; Moody, 1996). Generally, for water saving purposes in rice production, changing the establishment system from transplanting to direct seeding, and soil hydrological conditions from flooding to alternate wetting and drying or aerobic conditions will bring more severe weed problems. Weeds are the greatest constraint to yield in upland or aerobic rice systems, resulting in yield losses between 30 and 98% (De Datta and Llagas, 1984; Oerke and Dehne, 2004). Losses due to weeds are more severe than those caused by N deficiency, pests, or diseases (WARDA, 1996). Successful aerobic rice and AWD systems will largely depend on effective weed control.

Weed management of aerobic rice

Direct control

Chemical control Herbicides have been increasingly and broadly applied in agriculture since the 1940s. Both pre-emergence herbicides, applied before crop emergence, and post-emergence herbicides, applied after crop emergence, can be used in aerobic rice fields, and are effective if they are properly used (De Datta and Baltazar, 1996). In China, aerobic rice growing is completely dependent on herbicides (Wang et al., 2002). However, intensive and repeated use of herbicide causes problems of environment pollution and resistant weed biotypes, which have aroused increasing concerns. Since the first resistant weed biotype, spreading dayflower (C*ommelina diffusa*), was found in the USA in 1957, 304 resistant biotypes of 182 species (109 bicots and 73 monocots) have been found in 58 countries (Heap, 2006). Reports of herbicide-resistant biotypes have increased rapidly in recent years due to widespread adoption of herbicides (Figure 2). Weed resistant biotypes have appeared in the major rice producing nations including China, India, Thailand and the Philippines. In the USA, farmers in some areas have no herbicide options to control the grasses in their rice fields due to herbicide resistance (Hill and Hawkins, 1996; Fischer et al., 2000). Agronomists, weed scientists and environmentalists all agree that herbicides must be used judiciously, and when possible, should be replaced by other weed control techniques.

Physical control Direct physical control methods include removal of weeds by hand, with weeding tools (hoe, scythe and spade), or with mechanical implements. These were the only weeding methods in early ages before the discovery of herbicides. Hand-pulling, simple-tool-aided weeding, or hand- or animal-drawn-implement weeding is still common on small farms growing upland or aerobic rice in tropical Asia and Africa (De Datta and Baltazar, 1996). These methods are safe for the environment but

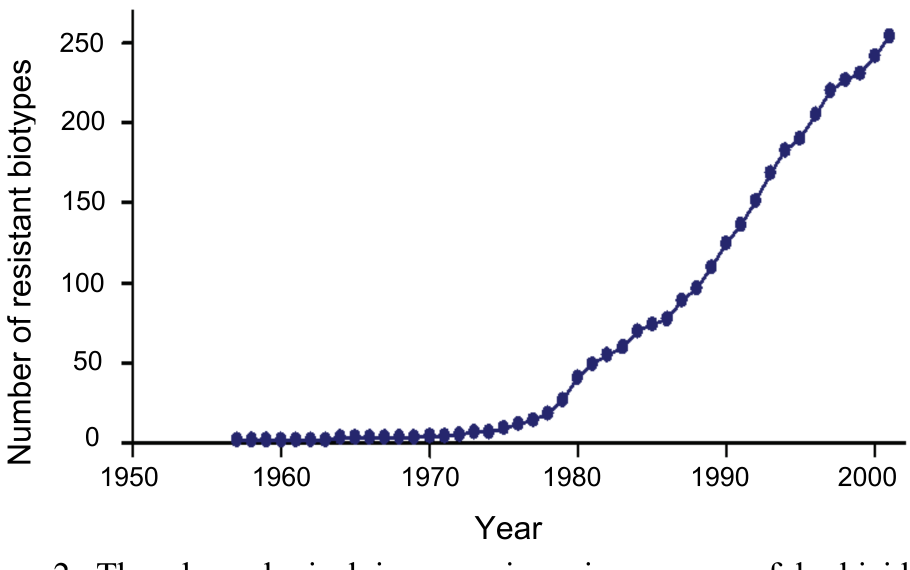

Figure 2. The chronological increase in unique cases of herbicide-resistant weeds worldwide (Source: Heap, 2006).

labour-intensive. The labour input per ha is up to 190 person-days for two to three weeding operations (Roder and Keobulapha, 1997). Quite often, weeding is delayed or cancelled due to the lack of availability of labour or the expensive labour costs (Johnson, 1996). Other problems with manual weeding include damage to the rice crop when weeders move through the field, and mistaken removal of rice instead of weeds because of the difficulty in distinguishing grassy weeds from rice (Moody and Cordova, 1985). Engine-powered rotary weeders are currently used to control perennial weeds (escapes from herbicide application) in Japan (Shibayama, 1992), and may be modified to fit aerobic rice production and extended to other regions to reduce labour costs.

Biological control Biological weed control is the use of biological agents such as animals, insects, or pathogens as enemies of weeds, but not rice and other crops, to kill weeds or inhibit weed growth. Herbivores of weeds such as fish, tadpoles, shrimps, shellfish and ducks are used to control weeds in irrigated lowland rice in a few countries (Smith, 1992; Shibayama, 1992), but these can not be used in aerobic rice where there is no standing water. A mycoherbicide (fungal pathogen inoculum) Collego® was reported to be successfully used in lowland rice in the USA to control broadleaf weed, northern jointwetch (*Aeschynomene virginica* L.) (Smith, 1986). It is, however, unlikely to be used in aerobic rice, because such fungal pathogen requires flooded field conditions. Mycoherbicides are still under research. However, the high specificity to a special weed of each mycoherbicide limits their potential use, because it will not help the total weed control much if only one or a few weed species are completely controlled in a natural environment.

Indirect control

Crop rotation The weed species that prevail in a particular field are closely associated with the agro-ecosystem and control practices. Repeated cropping on the same land could lead to a build-up of weed populations not easily controlled by existing methods. Such a build-up may be managed by rotating with another crop in which different weed control measures are used. Crop rotation is helpful not only for weed control but also for maintaining crop yield. Continuously growing aerobic rice on the same land for three to four years has been found to result in declining yields in Brazil (Guimarães and Stone, 2000) and in the Philippines (George et al., 2002), which may be caused by a buildup of soil pathogens or by micronutrient disorders. Crop rotation can be done in shift of aerobic rice - broadleaf crops, or aerobic rice - other upland monocot crops, or aerobic rice - vegetables. Although many crop rotation options exist for aerobic rice, rotation with broad leaf crops, which have different selective herbicides, is likely to be the most effective way to maintain a low weed population.

Weed prevention Preventive methods aiming at preventing weed dispersal and build-up of seed reserves in the soil include: (1) using weed-free seeds; (2) maintaining clean fields, borders, levees and irrigation canals, and (3) cleaning farm equipment to prevent weed transfer from one field to another (De Datta and Baltazar, 1996).

Land preparation and irrigation Good tillage and land levelling can (1) remove weed vegetation at sowing and suppress perennial weeds; (2) provide fine soil to allow uniform and early rice establishment; and (3) permit uniform and easy irrigation and drainage (De Datta and Baltazar, 1996). Sowing should be done immediately following the last tillage operation to give rice an equal start with weeds, and irrigation should not be performed immediately following sowing if soil moisture is high enough for rice emergence. When rice emergence and seedling growth is not influenced by drought stress, keeping dry soil surface as long as possible will largely suppress weed emergence and give rice a ‘head start’ over weeds. However, if a pre-emergence herbicide is applied, an irrigation following sowing is necessary to create a wet soil surface to ensure herbicide efficacy.

Fertilizer management Fertilizer management should aim at benefiting crop only, or if not possible, benefiting crop more than weeds. N-fertilizer is usually applied three times, at seeding, tillering, and panicle initiation, respectively, with a total amount from 75 (Ampong-Nyarko and De Datta, 1991) up to 200 kg N ha^{-1} (Yang et al., 2002) split as ⅓, ⅓, ⅓ or ½, ¼, ¼ to synchronize with the demand of rice growth (De Datta, 1981). Weeds must be removed before N application, otherwise a greater weed growth and competition would be created, and rice yield would be even lower than when there is no N application (Ampong-Nyarko and De Datta, 1989), because many weeds have greater ability than the crop to compete for N (Ampong-Nyarko and S.K. De Datta, 1993, Blackshaw et al., 2003). Deep placement (10 cm) of N fertilizer in irrigated rice (De Datta, 1981) is found to benefit crop more than weeds, thus enhance crop’s ability to compete against weeds.

Cultivar The cultivar itself must be able to compete against weeds to get the greatest benefit from other control measures. The ideal cultivar would be both high yielding and strongly weed-competitive, which may minimize weeding operations while maximizing rice production. Rice cultivar differences in ability to compete with weeds were initially reported several decades ago. Tall, droopy-leafed and vigorous traditional cultivars were reported to be more weed-competitive but lower in yield potential than short-statured, erect modern ones (Jennings and Aquino, 1968; Jennings and Jesus, 1968; Jennings and Herrera, 1968; Kawano et al., 1974; De Datta, 1980). The negative correlation between weed competitiveness and yield, and the successful application of herbicides in weed control reduced breeders' interest in breeding weed-competitive cultivars. Recently, increasing concerns about the environmental and health effects of, and resistant biotypes induced by herbicide application have motivated scientists to search for more environment-friendly approaches to dealing with weed problems. Weed-competitive cultivars are an important element of these approaches. Information from recent studies with wheat, irrigated rice and barley (Cousens and Mohktari, 1998; Ni et al., 2000; Didon and Boström, 2003; Gibson et al., 2003) suggests that it is possible to combine high yield potential with strong weed competitiveness.

Before initiating breeding for weed competitiveness, the following questions must be answered:

- Is the genetic variation in weed competitiveness among parents large enough for breeding?
- Are weed competitiveness and its related traits heritable?
- Is it possible to combine high yield potential with strong weed competitiveness in aerobic rice?
- Is it feasible to use indirect selection in breeding weed-competitive cultivars, rather than selecting for yield under competition, and, if so, what traits can be used?
- What kind of germplasm should be used as parents?

The research reported in this thesis aimed at answering these questions.

Seeding rate and row spacing Seeding rate and row spacing determine rice stands per unit area. This in turn determines the amount of canopy created to help rice shade and compete with weeds, especially during the critical early growing stages. Increased spacing between or within rows increases light penetration into the canopy, which enhances weed growth. A study with upland rice (Tosh et al., 1981) showed that within a range from 70 to 110 kg ha^{-1} weed infestation decreased with increased seeding rate. Similar results were reported with irrigated rice (Phuong et al., 2005). However, seeding rate effects in aerobic rice have rarely been reported, probably because it is a new crop. In China, farmers grow aerobic rice at a seeding rate from 120 to 150 kg ha^{-1} in rows spaced 20 to 30 cm apart (Wang, personal communication). Seeding rate effect on weeds in aerobic rice was also studied in the research reported in this thesis.

Research approach and objectives

Crop-weed competition parameters

Competition occurs in communities when two or more plants seek a common resource within a limited space, such as mineral nutrients, light, and water. It is called ‘intraspecific competition’ if the competition happens between individuals of the same species, and ‘interspecific competition’ if between individuals of different species (Lemerle et al., 2001b). A crop plant experiences intraspecific competition from its neighbour crop plants in a weed-free field, but experiences both intraspecific and interspecific competition from its neighbour crop and weed plants, respectively, in a weedy field. Weed-competitive ability (WC) of a crop includes two components: one is ‘weed-suppressive ability’ (WSA), or the ability of a crop to suppress weeds, also referred to as ‘weed suppression’; another is ‘weed tolerance’ (WT), or the ability to maintain yield of a crop with weed interference. ‘Interference’ describes an induced effect by an individual on a neighbour through changes in the environment and brought about by the proximity of neighbours. Cultivar differences in WSA are assessed by measuring weed biomass or weed seeds; the less the weed biomass or weed seeds produced in a plot occupied by a cultivar, the stronger is the WSA of that cultivar. WT, describing the yielding ability of a cultivar under a certain weed pressure, is difficult to determine. Because yield under weed competition, also referred to as weedy yield, of a cultivar is determined by the yield potential of the cultivar, the weed pressure imposed on the cultivar, and the ability of the cultivar to tolerate the weed pressure under a defined environment, WT can only be assessed among cultivars with the same yield potential and same WSA (Gibson and Fischer, 2004). In this research, WSA, weed-free yield (yield in the absence of weeds), weedy yield and their related traits were addressed.

Environment and experiments

Field experiments were conducted on the upland farm of IRRI, Los Baños, Philippines from 2001 to 2004. The Philippines is a tropical country with dry (January – April) and wet (May – December) seasons. The two seasons are similar in temperature, which permits rice growing year-round. An average total rainfall of 160 and 1900 mm are received during the dry and wet seasons, respectively. The IRRI upland farm was well levelled and equipped with irrigation and drainage facilities. The soil type was a Maahas clay loam (isohyperthermic mixed Typic Tropudalf).

Forty aerobic and upland rice cultivars (*Oryza sativa* L.), belonging to *indica*, tropical *japonica,* and *aus* germplasm groups and their progenies, were used in two field experiments. One experiment was conducted in three consecutive wet seasons to study weed-competitive abilities, and another was conducted in one wet season to study tillering abilities of cultivars and relate these to weed competitiveness. The third field experiment, using three of the forty cultivars, was conducted in one wet and one dry season, respectively, to study interactions of genotype × seeding rate × seed priming in crop-weed competition. The series field experiments did not experience natural or artificial disasters.

Research objectives

The main objectives of the research were to:

- assess genetic variation for weed suppression and yield of aerobic and upland rice cultivars;
- determine the heritability for crop weedy yield and weed suppression to estimate the potential gain that could result from breeding for weed competitiveness;
- explore useful traits which are heritable, closely correlated with both weedy yield and weed suppression, and easily used in breeding practices;
- develop an indirect selection index for use in practical selection for weed competitiveness under weed-free conditions;
- select elite germplasm and cultivars that can be used as parents in IRRI's aerobic rice breeding programme; and
- determine the interaction of genotype × seeding rate in terms of yield and weed suppression, with the objective of developing an environment-friendly and less labour-intensive integrated weed management system.

The whole research programme aimed at providing breeders with tools to help them in developing strongly weed-suppressive, high-yielding aerobic rice cultivars, and associated cultivation techniques to cope with the increasing water crisis threatening the current conventional irrigated lowland rice production system.

Thesis outline

This thesis consists of an introduction (Chapter 1), four research papers (Chapters 2-5), and a general discussion (Chapter 6).

Chapter 2 presents the genetic variation among 40 aerobic and upland genotypes, heritabilities of yield and weed biomass and their related traits, and a developed selection index for breeding for weed competitiveness.

In Chapter 3, vegetative traits of rice under weed-free conditions which may be used in indirect selection were screened by determining their heritabilities, and their correlations with, indirect selection efficiencies for, and regression coefficients for both weedy yield and weed biomass. Another indirect selection index for breeding for weed competitiveness was developed.

In Chapter 4, six cultivar groups within *Oryza sativa* L. classified on germplasm group and plant height were assessed in terms of usefulness as potential parents in breeding weed-competitive aerobic rice cultivars. The relationship of plant type (erectness) with weed suppression was discussed.

In Chapter 5, the effects of genotype, seeding rate and their interaction on crop vegetative growth, yield, and weed suppression under both weed-free and weedy conditions were assessed. The mechanism of rice-weed competition was explored by calculating competition-related parameters for genotypes and canopies, and by correlation analysis. The efficacy of a combination of genotype with seeding rate in weed control was discussed.

CHAPTER 2

Cultivar weed-competitiveness in aerobic rice: Heritability, correlated traits, and the potential for indirect selection in weed-free environments[1]

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Abstract

Forty rice (*Oryza sativa* L.) cultivars and breeding lines used in the International Rice Research Institute (IRRI) aerobic and upland rice breeding programme were evaluated in adjacent weed-free and weedy trials in aerobic soil conditions during the wet seasons of 2001, 2002 and 2003. The objectives of this study were to investigate genetic variability in weed suppression and yield and to identify traits that could be used as selection criteria for improved weed competitiveness. Correlations among and broad-sense heritability (*H*) of agronomic traits and early vigour were estimated in weedy and weed-free trials. Regression analysis was performed to predict weedy yield and weed biomass. Cultivars differed widely in the growth of weed biomass they permitted (126 – 296 g m^{-2}) and in yield under competition (0.5 – 2.5 Mg ha^{-1}). Cultivar yield, duration, biomass, harvest index, height, and vegetative vigour under weed-free conditions were closely correlated with the same traits measured under weedy conditions. Weedy yield and weed biomass were both moderately heritable (H = 0.55 and 0.38 for means estimated from single-year, three replicate trial, respectively) and genetically correlated with each other (r = –0.84). Weed-free yield and vigour at two weeks after sowing (WAS) were moderately heritable (H = 0.68 and 0.38 for means estimated from a single-year, three replicate trial, respectively) and were highly genetically correlated with weedy yield (r = 1.00 and 0.88, respectively) and weed biomass (r = –0.67 and –0.89, respectively). Vegetative vigour at two WAS and grain yield measured under weed-free conditions together explained 87% of cultivar variation in weedy yield and 40% in weed biomass. Indirect selection on these two traits was predicted to be efficient for improving yield under weed competition and weed-suppressive ability of aerobic rice.

Keywords: Broad-sense heritability; Genetic correlation; Indirect selection index; Vigour; Weed-suppressive ability; Yield

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INTRODUCTION

Aerobic or upland rice is direct seeded in nonpuddled, nonflooded fields (De Datta and Ross, 1975). Aerobic rice can require less water and labour than flooded rice established via transplanting, but is usually subject to much higher weed pressure (Balasubramanian and Hill, 2002), because direct-seeded rice germinates together with weeds, eliminating the 'head start' of transplanted seedlings (Moody, 1983). Weeds are the greatest yield-limiting constraint to aerobic rice, contributing about 50% to yield gaps, followed in importance by nitrogen deficiency, pests, and diseases (WARDA, 1996). Weeds are estimated to cause rice yield losses of 35% in the tropics (Oerke and Dehne, 2004), but losses can be much greater in aerobic rice crops (Balasubramanian and Hill, 2002). Weeding rice is labour-intensive; upland rice growers usually hand-weed their crops two or three times per season, investing up to 190 person-days ha^{-1} (Roder, 2001). Hand-weeding is complicated by the morphological similarity of rice and grassy weed seedlings (Moody, 1983). Herbicides have been proven effective in many cases (De Datta and Llagas, 1984), but intensive herbicide use can cause environmental contamination and the development of herbicide resistance (Fischer et al., 1993; Carey et al., 1995; Lemerle et al, 2001b). Using competitive varieties to suppress weeds might substantially reduce herbicide use and labour costs, permitting weeds to be controlled with a single herbicide application or hand-weeding. Competitive cultivars may therefore be an important component of integrated weed management strategies (Pester et al., 1999; Fischer et al., 2001; Lemerle et al., 2001b).

Cultivar weed-competitiveness is a function of weed tolerance, or the ability to maintain high yields despite weed competition, and weed-suppressive ability, or the ability to reduce weed growth through competition (Jannink et al., 2000). Cultivar differences in weed-suppressive ability are determined by assessing variation in weed biomass in plots under weed competition. Jannink et al. (2000) and Jordan (1993) advocated breeding for weed-suppressive ability over weed tolerance because suppressing weeds reduces weed seed production and benefits weed management in the future, while tolerating weeds only benefits the current growing season, and may result in increased weed pressure from unsuppressed weeds. The extent to which weed suppression and weed tolerance are independent traits is unclear.

Cultivar differences in weed competitiveness have been documented in wheat (*Triticum aestivum* L.) (Challaiah et al., 1986; Blackshaw, 1994; Lemerle et al., 1996), barley (*Hordeum vulgare* L.) (Christensen, 1995), soybean [*Glycine max* (L.) Merr.] (Jannink et al., 2000) and rice (Quintero, 1986; Chavez, 1989; Garrity et al., 1992; Fischer et al., 2001; Haefele et al., 2004). Rice cultivars that compete well against weeds are often thought to be tall, rapid in early growth, and have droopy leaves and high specific leaf area. These traits have been linked to low yield potential in some studies (Jennings and Aquino, 1968; Jennings and Jesus, 1968; Jennings and Herrera, 1968; Kawano et al., 1974), but not in others (Garrity et al., 1992; Ni et al., 2000; Fischer et al., 2001). Evidence that there may be no trade-off between yield and weed competitiveness has aroused interest in breeding for cultivars that combine high yield and weed-suppressive ability.

Selection for weed competitiveness can be done directly in the presence of weeds, or indirectly, under non-competitive conditions for secondary traits related to weed competitiveness. Direct selection for weed competitiveness can be conducted only in the later stages of a breeding program when sufficient seed is available (Wall, 1983). The labour requirements and high residual variance of yield and biomass measurements in weedy trials make direct selection for weed competitiveness impractical for most breeding programmes. Indirect selection under weed-free conditions for traits associated with weed competitiveness is likely to be easier and less expensive, and may permit selection to be started earlier in the breeding programme. Following Falconer (1989), traits measured under weedy and weed-free conditions can be thought of as correlated traits, expressed by a single genotype in separate environments. Correlated response under weed competition to selection under weed-free conditions is a function of the heritability (*H*) of the selection criterion under weed-free conditions, its genetic correlation with the target trait under weed competition, and selection intensity (Atlin et al., 2001).

The predicted correlated response under weed competition to indirect selection under weed-free conditions, expressed as a proportion of response to direct selection under weedy conditions, is referred to as indirect selection efficiency (ISE). Indirect selection under weed-free conditions is preferable to direct selection when ISE is close to or greater than 1 and indirect selection is less expensive than direct selection. Traits that are potentially useful indirect selection criteria for weed competitiveness should be heritable under weed-free conditions and highly correlated with both weed biomass and yield in weedy conditions. They should also be practical for use in large breeding populations to achieve adequate selection intensity (Atlin et al., 2001). There are few reports in the literature of the *H* of weed competitiveness and its component traits. Fischer et al. (1995, 1997) and Haefele et al. (2004) reported that some vegetative traits measured in weed-free rice variety trials, including leaf area index (LAI) and tiller number, were uncorrelated with weed growth or competition-induced yield loss, and they thus suggested that only direct selection for weed competitiveness would be effective. However, the work of Jannink et al. (2000) on seedling height of soybean, Ni et al. (2000) on rice seedling biomass, and Gibson et al. (2003) on rice LAI and root growth during the vegetative stages suggests that some seedling traits measured in weed-free conditions are highly correlated with weed growth, and thus that indirect selection for weed-suppressive ability may be feasible.

The purpose of this study was to assess the potential for selecting aerobic rice cultivars with improved weed-suppressive ability and yield under weed competition. Specific objectives were: (1) to examine the magnitude of genotype variation for weed-suppressive ability and yield under moderate weed competition and (2) to identify agronomic and vegetative traits strongly correlated with weed biomass and yield under weed competition.

MATERIALS AND METHODS

Germplasm

A broad collection of 40 aerobic and upland rice cultivars, used as parents in the aerobic rice breeding programme of the International Rice Research Institute (IRRI), was evaluated in this study. The genotypes have a wide range in height, duration, and plant type, and belong to six germplasm groups (*indica,* tropical *japonica*, *indica*/tropical *japonica*, *aus*, *aus*/tropical *japonica* and *indica*/tropical *japonica*/*aus*) (Glazsmann, 1987). Both traditional and improved varieties were included.

Trial management and data collection

The trials were grown on the IRRI upland farm (14°13' N, 121°15' E, 23 m elevation), Los Baños, Philippines, in the wet season in 2001, 2002 and 2003. The soil type was a Maahas clay loam (isohyperthermic mixed Typic Tropudalf). Fields were fallowed during the dry seasons, allowing weeds to grow before land preparation for planting. Before sowing, the field was ploughed, harrowed, levelled and furrowed. Two adjacent trials, weed-free and weedy, arranged in α-lattice design with three replications each, were planted in the same field within each year.

Cultivars were manually drilled in plots sized 4.5 m^2 with six 3 m-long rows and row spacing of 25 cm on 12 July 2001, 5 July 2002, and 8 July 2003, respectively. The seeding rate for each cultivar was 300 viable seeds m^{-2}. The weed-free trial was treated with pre-emergence herbicide Ronstar (oxadiazon) at the recommended rate just after sowing and immediate sprinkler irrigation, and was kept weed-free during the whole growing season by hand as needed. The weedy trial was completely hand-weeded once at 3 weeks after sowing (WAS) in 2001 and 2002, or treated with post-emergence herbicide Nominee (bispyribac sodium) once at 2 WAS instead of hand-weeding in 2003; weeds were allowed to grow thereafter.

A compound N-P-K fertilizer (14:14:14) was broadcast before furrowing at the rate of 200 kg ha^{-1}; two additional splits of urea were top-dressed each at the rate of 60 kg ha^{-1} at 4 and 8 WAS, respectively. Total N fertilizer application was 82 kg ha^{-1}. The field was kept under nonsaturated aerobic condition through the whole growing season. Trials were primarily rainfed, but supplemental surface irrigation was applied on a few occasions when crop leaves started to roll due to drought stress, and drainage was conducted whenever heavy rains resulted in ponding. Insecticide and fungicide were applied following standard practices as required.

Weed species and their densities were investigated at 10 WAS in the weedy trials. Weed biomass was clipped at the soil surface from a random area of 0.5 m^2 in each plot in the weedy trials at 13 WAS, oven dried at 70°C for 5 days and weighed. Weed biomass was also visually rated for each plot just before sampling. The weed rating was expressed on a 1-to-9 scale, where 9 was defined as the highest weed growth and 1 as the least. Crop growth (total seedling biomass) was visually rated at 2 WAS for each plot. This rating, referred to as early vigour, was also expressed on a 1-to-9 scale, where 9 was the most growth and 1 was the least. Flowering date was recorded when 50% of the plants in a plot started to flower. Final plant height was measured as the distance from the ground to the panicle tip of three random plants from each plot. For harvest index (HI) and final crop biomass, a 0.25-m^2 sample from each plot was randomly chosen, clipped at ground level, threshed, dried as for weed biomass, and weighed. Crop biomass was expressed as the dry weight of above-ground plant per square meter of ground area. Harvest index was the proportion (percentage) of filled grain to the whole above-ground biomass sample in weight. Grain yield from each plot was harvested, dried (50°C, 3 days), weighed, and adjusted to a moisture content of 14%. In the 2002 wet season, productive tillers in the sample for HI measurement were counted; 10 random panicles from each plot were harvested, threshed, dried as for yield, and separated into filled and unfilled grains, which were then counted and weighed.

Statistical analysis

To test for the presence of genotype × weed management interaction, a combined analysis over years and weed management treatments was conducted using SAS Release 8.2 (TS2M0) (SAS Institute Inc., 1999 – 2001). For this analysis, genotypes and weed management treatments and their interaction were considered fixed, while years, replicates nested within year × weed management combinations, and blocks within replicates were considered random. Random effects for interactions between year and the fixed effects were also added to the model. Preliminary analysis proved that residual error terms within individual trials were heterogeneous for all characters except HI. The combined analyses were therefore conducted using a mixed model that did not assume equal within-trial residuals. Using the REML option of the SAS

MIXED procedure, nonhomogeneous within-trial variances were specified by the REPEATED/GROUP statement. Scaled Wald tests of fixed effects, distributed approximately as F, were done using the DDFM = KR option of the MODEL statement, which uses the Kenward-Rogers version of the Satterthwaite approximation to estimate degrees of freedom. Separate analyses of weedy and weed-free trials across years were conducted (also with the REML option of the MIXED procedure) to estimate cultivar least square means within weed management treatments. Variance components were estimated separately for weedy and weed-free trials using the REML option of the VARCOMP procedure, which considers all factors to be random. These variance component estimates were used in calculating predicted *H* for traits measured under weedy and weed-free managements, and genetic correlations among them. The reference population for these estimates is the set of parental materials used in recent years in IRRI's upland and aerobic rice breeding programmes. The estimates are meant to provide information about relationships among traits and the extent of replication needed to achieve adequate *H* for traits related to weed competitiveness. Inferences should be applicable to the screening of advanced breeding lines at IRRI, but may also be of wider use to rice breeders at other locations.

Broad-sense heritability

Predicted *H* for selection based on means estimated from a single three-replicate trial or over three years was calculated from variance components, after Nyquist (1991), as:

$$H = \frac{\sigma^2{}_G}{\sigma^2{}_G + \frac{\sigma^2{}_{GY}}{y} + \frac{\sigma^2{}_E}{ry}} \tag{1}$$

where $\sigma^2{}_G$, $\sigma^2{}_{GY}$, $\sigma^2{}_E$, y, and r are the genotype, genotype × year, and within-trial error variances, and the number of years and replicates of testing, respectively.

Phenotypic and genetic correlations

Phenotypic correlations among traits were calculated on the basis of cultivar means over years, within or between weed management treatments. Genetic correlations among traits from the same weed management treatment across years were estimated (Bernardo, 2002) as:

$$r_{G\,12} = \frac{Cov_{12}}{\sqrt{\sigma^2{}_{G\,1} \times \sigma^2{}_{G\,2}}} \tag{2}$$

where r_{G12}, Cov_{12}, $\sigma^2{}_{G\,1}$ and $\sigma^2{}_{G\,2}$ are the genetic correlation coefficient between traits 1 and 2 within the same weed management treatment, genetic covariance of traits 1 and 2, and the genotypic variances of traits 1 and 2, respectively.

Genetic correlations between traits measured in different weed management treatments were computed (Cooper et al., 1996) as:

$$r_{G12} = \frac{r_{P12}}{\sqrt{H_1 \times H_2}} \qquad (3)$$

where r_{G12}, r_{P12}, H_1 and H_2 are genotypic correlation coefficient between traits 1 and 2, phenotypic correlation coefficient between the same trait pair, and the H of traits 1 and 2, respectively. In this estimation method, it is assumed that the covariance between line means estimated in different experimental units (in this case, between means estimated in weedy and weed-free trials) is entirely genetic in causation, and that there is no environmental covariance.

Indirect Selection Efficiency

The ISEs of traits measured under weed-free conditions for the target traits yield under competition, weed biomass and weed rating across three years were calculated (Falconer, 1989) as:

$$\text{ISE} = r_G \sqrt{H_{WF} / H_{WC}} \qquad (4)$$

where r_G is the genotypic correlation between the selection criterion measured in the weed-free selection environments and the target trait in the weedy environments, and H_{WF} and H_{WC} are broad-sense heritabilities of the selection criterion and target trait, respectively. H_{WF} and H_{WC} were estimated on the basis of means from trials over three years. The model assumes that selection intensity is constant for the two traits.

Regression analysis

Means from the combined analysis over years for target traits weedy yield and weed biomass were regressed on the overall cultivar means for weed-free yield or the overall means for weed-free vigour rating at 2 WAS, or both. For the multiple regression models, an F test of the significance of the reduction in the residual mean square resulting from adding the second predictor variable to the regression model was computed.

Definitions and calculations

In this chapter, the following definitions are used:

- Weed-free trait: trait measured under weed-free conditions;
- Weedy trait: trait measured under weedy conditions;

- Weed-free yield: rice grain yield at 14% moisture content from trials grown under weed-free conditions;
- Weedy yield: rice grain yield at 14% moisture content from trials grown under weedy conditions;
- Absolute yield loss (Mg ha^{-1}) = weed-free yield (Mg ha^{-1}) – weedy yield (Mg ha^{-1});
- Relative yield loss (%) = 100[(weed-free yield – weedy yield) / weed-free yield].

RESULTS AND DISCUSSION

Weed flora and weed pressure

Twenty-two weed species were found in the experimental fields (data not shown). The prevalent species common in the three years were *Digitaria ciliaris* Retz.*, Eleusine indica* L.*, Echinochloa colona* L.*, Leptochloa chinensis* L.*, Dactyloctenium aegyptium* L. and *Portulaca oleracea* L. In 2001, *Rottboellia cochinchinensis* Lour. was also one of the predominant weed species. Weed pressure in the weedy trials varied substantially among the three years, ranging from 305 g m^{-2} in 2001 to 73 g m^{-2} in 2003 (Table 1). The differences in weed pressure were probably caused by different weed seedbanks in the experimental fields used in the three years, and the residual herbicide effect in 2003. Weather in the three years differed little (Table 2); it thus was not likely a factor influencing weed pressure.

Effects of weed management treatments

For the agronomic traits evaluated in this study, the effect of weed management treatment reached significance at α = 0.05 only for crop biomass (Table 3). Failure to detect a main effect of weed management for yield and HI was mainly due to the fact that there were only 2 error degrees of freedom for this stratum, the experiment having been designed primarily to detect genotype and genotype × weed management effects. Nevertheless, the negative effects of weeds on yield and its components, HI and crop biomass occurred in every year (Table 1). Harvest index reduction with weed competition was 66, 23 and 3% in 2001, 2002 and 2003, respectively, and 30% on average across three years; crop biomass reduction was 65, 44, and 15% in the three years, respectively, and 43% on average. Consequently, the yield reduction was 77, 35 and 18% in the three years, respectively, and 43% on average. Thousand-grain weight was not affected by weeds (data not shown), but productive tiller number, panicle size and filled grain ratio all decreased with weed competition (Table 1). Plant height decreased by about 20 cm in 2001 and 10 cm in 2002 when weed biomass was over 170 g m^{-2}, but weeds had no effect on days to flowering, days to maturity and early vigour (Table 1).

Table 1. Means and standard errors for traits of aerobic and upland rice evaluated under weed-free (F) or weedy (W) conditions in the wet seasons of 2001–2003 at Los Baños, Philippines.

Year	Weed management	Early vigour (score)	Height (cm)	Crop biomass (g m^{-2})	Days to flowering (d)	Duration (d)	Harvest index (%)	Yield (Mg ha^{-1})	Weed biomass (g m^{-2})	Productive tillers m^{-2}	Spikelets panicle^{-1}	Filled grain (%)
2001	F	4.9±1.2	121.7±3.1	1215±110	76±1	104±1	29±3	2.43±0.22				
	W	4.5±0.8	101.9±3.7	423±55	78±1	104±0	10±3	0.56±0.17	305±48			
2002	F	6.1±1.3	117.5±3.7	987±164	83±1	111±2	31±3	1.81±0.23		233±30	134±17	72±5
	W	6.1±1.0	106.5±4.3	548±107	81±1	110±2	24±3	1.18±0.20	172±34	170±24	77±13	65±7
2003	F	4.8±0.9	116.6±4.8	1020±96	71±1	99±2	29±3	2.66±0.23				
	W	4.6±0.8	117.0±4.7	867±114	72±1	99±1	28±2	2.18±0.28	73±23			
Mean	F	5.3±0.8	118.6±3.9	1074±103	77±4	105±4	30±2	2.30±0.38				
	W	5.0±0.8	108.4±5.4	613±146	77±3	104±3	21±6	1.31±0.54	183±72			

Table 2. Climate factors† during the growing seasons (July – November) of 2001 – 2003 at Los Baños, Philippines.

Year	Rainfall (mm)	Rainy days (d month^{-1})	Radiation (MJ m^{-2}d^{-1})	T_{Max} (°C)	T_{Min} (°C)	T_{Avg} (°C)
2001	1071.7	9.6	16.6	31.5	23.9	27.7
2002	1364.0	9.8	17.0	31.8	23.9	27.9
2003	1211.6	10.4	17.4	32.1	24.1	28.1

† rainfall was accumulated over July to November; rainy days indicates the days per month in which rainfall was over 5 mm; T_{Max}, T_{Min} and T_{Avg} indicate the means for the highest, lowest and average temperature across the five growing months in a year.

Genotype performance and genotype × weed management interaction

Cultivars differed significantly in all the traits studied (Table 3). The range in cultivar crop biomass was about two-fold under both the weed-free (800 – 1500 g m^{-2}) and weedy (400 – 900 g m^{-2}) conditions (Table 4). Equivalent ranges for grain yield were about three-fold (1.25 – 3.96 Mg ha^{-1}) in weed-free and five-fold (0.54 – 2.50 Mg ha^{-1}) in weedy conditions (Table 4). The weed biomass of the least suppressive cultivar was 2.4 times that for the most suppressive one, ranging from 126 to 296 g m^{-2} (Table 4). The absolute yield losses of cultivars with weed competition ranged from about 0.2 to 1.6 Mg ha^{-1}, and the relative yield losses from 11 to 63% (Table 4). These results indicate that the test cultivars, which are extensively used as parents in IRRI's aerobic rice breeding programme, have a wide range in both weed-suppressive ability and yield under weed competition. It was noteworthy that UPLRi-7, IR55423-01, and B6144F-MR-6-0-0 were the highest-yielding cultivars under both weedy and weed-free conditions, and had lower than average weed biomass (Table 4). These elite cultivars are likely to be useful as parents in breeding weed-competitive cultivars for the Asian tropics.

Variance components and broad-sense heritability (H) estimates

All the traits under both weed-free and weedy conditions had smaller variances for genotype × year interactions than for genotype effects (Table 5). This indicates that genotype performance for traits including weed growth (weed biomass or weed rating) were relatively consistent across years, supporting other reports showing that weed-suppressive ability is consistent across environments (Fischer et al., 1997, 2001; Jannink et al., 2000; Gibson et al., 2003).

Predicted *H* for yield, HI, and crop biomass differed only slightly under weed-free and weedy conditions, and the magnitude of the estimates appears to permit reasonable

Table 3. Wald tests of weed management and cultivar effects on early vigour and harvest traits of aerobic and upland rice from the combined analysis of weedy and weed-free trials over three years at Los Baños, Philippines.

ANOVA Effect	Early vigour		Height		Crop biomass		Days to flowering		Duration		Harvest index		Yield		Weed biomass		Weed rating	
	F†	P > F	F	P > F	F	P > F	F	P > F	F	P > F	F	P > F	F	P > F	F	P > F	F	P > F
Weed management (W)	0.47	0.502	4.67	0.097	9.42	0.037	0.00	0.958	0.29	0.644	2.96	0.227	5.11	0.152				
Genotype (G)	6.00	0.001	23.20	0.001	8.21	0.001	147.88	0.001	31.83	0.001	5.56	0.001	8.44	0.001	2.46	0.001	3.61	0.001
W × G	1.31	0.158	1.08	0.380	1.04	0.443	1.35	0.133	0.73	0.865	1.66	0.031	1.42	0.093				

† F, P > F indicate F value and probability, respectively.

Table 4. Means for 40 aerobic and upland rice cultivars evaluated under weed-free (F) or weedy (W) conditions in the wet seasons of 2001–2003 at Los Baños, Philippines.

Cultivar	Early vigour (score ‡)		Height (cm)		Crop biomass (g m^{-2})		Harvest index (%)		Yield (Mg ha^{-1})		Yield loss		Weed biomass (g m^{-2})	Weed rating (score)
	F	W	F	W	F	W	F	W	F	W	Mg ha^{-1}	%	W	W
UPLRi-7	6.4	6.4	108.5	102.8	1184.2	747.9	35.5	28.8	3.96	2.50	1.46*	36.9	135.5	2.0
IR55423-01	6.1	5.8	107.2	104.4	1192.3	774.1	36.1	28.2	3.84	2.42	1.42†	36.9	142.7	1.6
C22	6.2	6.5	125.7	111.4	1348.4	892.9	32.0	23.0	3.53	2.27	1.26†	35.6	151.1	1.8
CT6510-24-1-2	6.7	7.3	115.2	101.5	1273.3	750.6	35.0	25.7	3.50	2.34	1.15†	32.9	156.4	1.6
IR47686-30-3-2	6.5	6.8	119.1	110.5	1509.5	922.7	30.6	19.8	3.49	2.11	1.38†	39.4	155.7	3.4
IR55419-04	6.5	7.0	113.6	108.3	1114.9	671.2	38.5	25.4	3.34	1.88	1.46*	43.7	139.9	1.6
UPLRi-5	5.1	4.4	121.6	108.3	1287.9	790.6	27.8	24.7	3.30	1.83	1.48*	44.7	172.5	3.5
B6144F-MR-6-0-0	7.2	8.0	122.6	113.5	1192.1	784.4	36.5	27.9	3.28	2.36	0.92	28.1	128.2	2.3
Way Rarem	7.1	7.6	121.9	114.0	1166.7	663.8	30.6	27.6	3.04	1.71	1.32†	43.5	128.9	2.8
IR71524-44-1-1	5.0	4.7	123.8	114.6	1287.9	701.8	30.8	21.3	2.99	1.37	1.62*	54.2	186.2	4.3
IR60080-46A	5.2	4.5	123.6	113.2	1198.4	673.1	32.8	22.2	2.81	1.51	1.31†	46.5	183.3	3.8
IR68702-072-1-4-B	5.0	3.6	128.5	120.8	1022.3	565.1	32.4	21.8	2.73	1.30	1.43*	52.4	204.6	4.6
IR71525-19-1-1	5.1	3.9	122.9	112.2	1120.4	551.4	35.1	23.3	2.47	1.27	1.21†	48.8	161.6	4.5
IR72768-15-1-1	4.0	3.8	109.4	98.4	1109.9	573.7	33.4	19.8	2.43	1.05	1.38†	56.7	218.4	4.3
IR66424-1-2-1-5	6.6	7.8	108.5	104.5	987.9	633.5	33.2	20.2	2.40	1.27	1.13†	47.0	199.6	3.1
AUS 196	6.3	6.9	122.7	114.5	998.4	603.8	31.8	22.0	2.39	1.66	0.73	30.6	130.7	2.7
IR70360-38-1-B-1	5.1	5.2	114.3	111.2	1224.5	663.3	25.7	20.9	2.35	1.64	0.71	30.4	125.7	2.4
CT6516-24-3-2	6.1	4.6	116.4	102.3	1028.1	511.7	27.3	18.3	2.29	0.91	1.37†	60.1	210.3	6.0
CT13377-4-2-M	2.9	2.3	106.1	93.5	1054.2	453.8	35.8	18.9	2.25	0.82	1.42†	63.4	198.4	5.5
IR65907-116-1-B	4.3	2.3	107.7	104.9	843.6	544.9	28.0	18.8	2.17	0.97	1.21†	55.5	229.6	5.8
IR65261-09-1-B	5.6	5.1	127.9	118.0	1208.0	609.8	30.7	18.5	2.09	1.11	0.98	46.9	203.5	2.9

Table 4. Continued.

Cultivar	Early vigour (score ‡)		Height (cm)		Crop biomass (g m^{-2})		Harvest index (%)		Yield (Mg ha^{-1})		Yield loss		Weed biomass (g m^{-2})	Weed rating (score)
	F	W	F	W	F	W	F	W	F	W	Mg ha^{-1}	%	W	W
IR66421-062-1-1-2	3.4	3.4	109.7	94.1	1102.8	657.0	28.5	17.9	2.04	1.13	0.90	44.3	235.9	5.6
Azucena	5.1	3.8	156.2	139.7	1081.0	607.7	23.7	17.7	2.02	1.21	0.81	40.0	169.9	4.0
IRAT 170	5.5	4.1	118.9	101.9	1135.6	483.8	28.7	21.4	2.02	1.05	0.97	48.2	210.0	5.2
Vandana	6.9	7.6	122.2	115.2	930.7	624.5	28.1	24.0	1.92	1.72	0.20	10.5	129.0	1.9
IRAT 177	5.3	5.0	121.1	110.1	1107.3	596.5	24.3	13.8	1.85	0.94	0.90	48.8	191.1	4.3
Maravilha	4.1	3.6	120.0	111.0	834.8	426.9	35.3	20.9	1.84	0.91	0.93	50.5	171.1	4.9
Palawan	5.4	4.7	139.9	128.8	1055.2	579.3	23.9	19.0	1.76	1.27	0.49	28.1	173.5	2.4
CT13382-8-3-M	4.3	3.4	105.5	91.1	866.2	432.6	32.1	17.2	1.72	0.73	0.99	57.7	296.4	6.0
Dinorado	5.6	5.9	146.6	128.5	1008.0	739.0	21.5	20.0	1.71	1.22	0.50	29.1	143.1	2.5
IR66417-18-1-1-1	4.1	3.8	119.8	107.2	1191.5	666.6	21.4	11.6	1.71	0.75	0.96	56.3	224.4	5.6
IRAT 216	3.5	3.3	102.0	90.7	998.2	574.1	26.1	15.9	1.71	0.76	0.95	55.4	247.1	5.8
WAB638-1	3.5	3.9	138.5	118.5	1110.3	585.8	22.7	13.4	1.56	0.74	0.82	52.4	175.2	4.8
Primavera	2.9	4.0	120.4	108.3	882.5	496.3	30.3	23.8	1.53	1.01	0.52	33.9	184.9	4.4
WAB96-1-1	4.9	5.8	125.6	114.7	1038.9	617.0	27.2	17.2	1.49	0.80	0.69	46.2	189.0	3.4
WAB56-125	5.9	4.6	106.4	101.6	901.8	443.7	25.4	18.9	1.33	0.71	0.61	46.3	216.8	5.8
IRAT 212	5.6	5.9	91.6	85.5	805.2	408.9	27.0	17.0	1.30	0.66	0.64	49.4	219.7	4.3
WAB181-18	5.3	3.0	115.6	100.1	804.5	399.6	28.3	20.2	1.30	0.79	0.50	38.9	209.0	6.2
IR70358-84-1-1	5.9	6.6	108.6	103.9	841.3	596.7	23.2	18.6	1.27	0.98	0.29	22.7	137.9	2.4
CT13370-12-2-M	5.0	4.6	109.4	103.3	909.9	501.2	24.6	13.7	1.25	0.54	0.71	56.6	233.9	6.7
Grand mean	5.3	5.0	118.6	108.4	1074.0	613.0	29.5	20.5	2.30	1.31	0.99	43.7	183.0	3.9
$LSD_{0.05}$	1.9	1.7	10.2	8.7	210.9	177.8	6.1	6.0	0.81	0.73			61.9	2.2

*, † indicate a yield loss (weed-free yield - weedy yield) significantly different from 0 at $P < 0.05$, $P < 0.10$, respectively;

‡ early vigour and weed biomass rating scores were given as 1 = least biomass, 9 = most biomass.

Table 5. Variance components[†] estimated from the combined analysis over three years (2001–2003) within weed management regimes, and predicted heritabilities for selection units consisting of means estimated from three-replicate trials conducted in one ($H_{1,3}$) or three ($H_{3,3}$) years for aerobic and upland rice at Los Baños, Philippines.

	Weedy trials					Weed-free trials				
Trait	σ_G^2	σ_{GY}^2	σ_E^2	$H_{3,3}$	$H_{1,3}$	σ_G^2	σ_{GY}^2	σ_E^2	$H_{3,3}$	$H_{1,3}$
Early vigour	2.09	0.37	2.22	0.85	0.65	0.82	0.45	2.65	0.65	0.38
Height	104.79	12.06	45.58	0.92	0.79	136.38	24.65	40.86	0.91	0.78
Crop biomass	11858	3621	22572	0.76	0.52	20809	799	45825	0.80	0.56
Days to flowering	54.64	1.03	2.62	0.99	0.97	61.74	1.27	2.67	0.99	0.97
Duration	40.00	5.73	2.85	0.95	0.86	49.25	5.21	6.60	0.95	0.87
Harvest index	12.42	7.79	15.34	0.74	0.49	16.31	7.21	19.48	0.78	0.54
Yield	0.24	0.16	0.10	0.79	0.55	0.52	0.20	0.13	0.87	0.68
Weed biomass	986	609	3074	0.64	0.38	-	-	-	-	-
Weed rating	1.71	0.56	3.56	0.75	0.50	-	-	-	-	-

† σ_G^2, σ_{GY}^2, and σ_E^2 indicate genotype, genotype × year, and error variances, respectively.

gains from selection (Table 5). Predicted *H* for vigour rating was higher in weedy than in weed-free trials. Weedy yield and weed biomass, the two target traits, had predicted *H* of 0.79 and 0.64 estimated on the basis of means over three years and 0.55 and 0.38 estimated on the basis of means from a single three-replicate trial, respectively. Weed-free early vigour and weed-free yield had predicted *H* of 0.65 and 0.87 estimated on the basis of three-year means, and 0.38 and 0.68 for means estimated from a single three-replicate trial, respectively (Table 5). These results indicate that weed-suppressive ability and yield under competition were both moderately heritable traits, and that indirect selection for weed competitiveness based on vegetative vigour and yield under weed-free conditions may be feasible, if these weed-free traits are highly correlated with weed growth and yield under competition.

Correlations among traits under the same weed management regime

Under weedy conditions, estimates of genetic correlations of yield with weed biomass and weed rating were highly negative (Table 6), indicating that there was no trade-off between yield and weed-suppressive ability. Rather, these results indicate that weed-suppressive ability is an important determinant of yield under competition. There are conflicting reports on the association between yield and weed-suppressive ability. Early studies with lowland rice (Jennings and Jesus, 1968; Jennings and Herrera, 1968; Jennings and Aquino, 1968; Kawano et al., 1974) strongly suggested a trade-off between the two traits. Some recent work with lowland or upland rice (Garrity et al., 1992; Fischer at al., 1997, 2001; Dingkuhn et al., 1999; Fofana and Rauber, 2000; Ni et al., 2000; Gibson et al., 2003) suggests they may be combined.

Crop biomass and HI were positively correlated with yield under both weedy and weed-free conditions, but negatively with weed biomass (Table 6). Plant height was not associated with yield under either weedy or weed-free conditions, but was weakly negatively correlated with weed biomass. The modest positive effect of plant height on weed suppression was in agreement with some previous studies (Jennings and Jesus, 1968; Jennings and Herrera, 1968; Jennings and Aquino, 1968; Garrity et al., 1992). However, Fischer et al. (1997, 2001) reported no clear association between plant height and weed-suppressive ability in irrigated and upland rice. Duration and flowering date were not associated with weed suppression in our study. In contrast, Dingkuhn et al. (1999) observed a strong association of weed competitiveness in African rice (*O. glaberrima* Steud.) with long duration, while Jannink et al. (2000) linked strong weed-suppressive ability of soybean with short duration. Early vigour was closely related to weed growth and moderately associated with yield under both weed regimes, and thus appears to be an important component of both weed-suppressive ability and yield (Table 6).

Table 6. Genetic correlations among traits of aerobic and upland rice evaluated in weed-free (above the diagonal) or weedy conditions (below the diagonal) in the wet seasons of 2001–2003 at Los Baños, Philippines.

Trait	Early vigour	Height	Crop biomass	Days to flowering	Duration	Harvest index	Yield	Weed biomass
Early vigour		0.05^{ns}	0.33^{ns}	–0.03^{ns}	0.06^{ns}	0.32^{ns}	0.43**	
Height	0.16^{ns}		0.31^{ns}	0.53**	0.44**	–0.37^{ns}	0.02^{ns}	
Crop biomass	0.58**	0.32**		0.82**	0.85**	0.28^{ns}	0.85**	
Days to flowering	–0.09^{ns}	0.38**	0.67**		0.99**	–0.25^{ns}	0.41*	
Duration	0.01^{ns}	0.27^{ns}	0.74**	0.98**		–0.23^{ns}	0.46**	
Harvest index	0.56**	0.06^{ns}	0.45**	–0.12^{ns}	–0.04^{ns}		0.71**	
Yield	0.55**	0.20^{ns}	0.94**	0.44^{ns}	0.64*	0.88**		
Weed biomass	–0.82**	–0.56**	–0.61**	–0.10^{ns}	–0.16^{ns}	–0.70**	–0.84**	
Weed rating	–0.91**	–0.41*	–0.67**	–0.09^{ns}	–0.18^{ns}	–0.73**	–0.99**	0.97**

*, **, and ns indicate significance at $P < 0.05$, $P < 0.01$, $P > 0.05$ for the corresponding phenotypic correlation, respectively.

The close correlation between weed rating and weed biomass (Table 6) and the similar relationships of these two traits with the other traits (Tables 6 – 8) suggest that visual ratings of weed biomass could be a good substitute for destructive sampling in determining weed-suppressive ability. Directly measuring weed biomass is expensive and laborious, but visually rating weed biomass is nondestructive, quick, and more heritable (Table 5), perhaps due to the integration of visual information from the larger sampling area (the whole plot) on which scores are given, rather than the small quadrat directly sampled for weed biomass. This result is supported by Garrity et al. (1992), although the rating scales used were different.

Relationships of traits under weed-free versus weedy conditions

All the traits investigated under weed-free conditions were closely genetically correlated with the same traits measured in weedy conditions (Table 7), indicating that cultivar performance was relatively consistent across different weed managements, a result confirmed by the fact that no significant genotype × weed management interactions were observed for any of the traits measured in this study except HI (Table 3). These high correlations indicate the feasibility of selecting for traits related to weed competitiveness under weed-free conditions. This result is supported by Gibson et al. (2003), who found that there was no genotype × weed management interaction for yield in lowland rice. Fischer et al. (1997, 2001), however, found significant genotype × weed management interactions for plant height, crop biomass and grain yield in lowland and upland rice.

Of the weed-free traits evaluated in this study, only early vigour, yield and crop biomass had both high positive genetic correlations with weedy yield, and high negative correlations with weed biomass and weed ratings (Table 7). Of the three traits, the ISEs of weed-free early vigour and yield for the target traits weedy yield and weed biomass were highest (0.77 or greater) (Table 7), indicating that indirect selection for these traits under weed-free conditions should improve both yield in competition and weed-suppressive ability. Predicted ISEs for weed-free crop biomass were much lower than those for the other two traits (Table 7) because of its lower H (Table 5). Therefore, of these three weed-free traits, yield and early vigour appear to be the most promising indirect selection criteria.

Yield under weed competition is a function of yield potential without competition and relative yield loss caused by weed competition; breeding programmes designed to produce weed-competitive cultivars thus need to focus on both yield potential and weed-suppressive ability. Our data confirm the feasibility of this strategy. The positive correlation of weedy and weed-free yield (Table 7) suggests that high-yielding cultivars under weed-free conditions are relatively high yielding under weed

Table 7. Genetic correlations (r_G), between traits of aerobic and upland rice evaluated under weed-free (footnoted with F) and weedy (footnoted with W) conditions, and indirect selection efficiency (ISE) of weed-free traits for the target traits weedy yield, weed biomass and weed rating, estimated over three years (2001–2003) at Los Baños, Philippines.

Trait	$V2_W$ †	HT_W	CB_W	FLW_W	DUR_W	HI_W	YLD_W		WB		WR	
	----------	----------	----------	r_G	----------	----------	r_G	ISE	r_G	ISE	r_G	ISE
$V2_F$	1.00^{**}	0.28^{ns}	0.64^{**}	-0.09^{ns}	0.02^{ns}	0.77^{**}	0.88^{**}	0.80	-0.89^{**}	0.89	-0.92^{**}	0.85
HT_F	0.03^{ns}	1.00^{**}	0.32^{ns}	0.53^{**}	0.40^{*}	-0.02^{ns}	0.12^{ns}	0.13	-0.47^{*}	0.57	-0.30^{ns}	0.33
CB_F	0.37^{ns}	0.29^{ns}	1.00^{**}	0.79^{**}	0.81^{**}	0.39^{ns}	0.83^{**}	0.83	-0.53^{*}	0.59	-0.57^{**}	0.58
FLW_F	-0.04^{ns}	0.39^{*}	0.70^{**}	1.00^{**}	0.99^{**}	-0.11^{ns}	0.30^{ns}	0.34	-0.12^{ns}	0.15	-0.15^{ns}	0.17
DUR_F	0.02^{ns}	0.32^{ns}	0.75^{**}	0.99^{**}	1.00^{**}	-0.02^{ns}	0.39^{*}	0.43	-0.18^{ns}	0.22	-0.20^{ns}	0.23
HI_F	0.27^{ns}	-0.27^{ns}	0.21^{ns}	-0.29^{ns}	-0.26^{ns}	0.91^{**}	0.69^{**}	0.69	-0.30^{ns}	0.33	-0.39^{ns}	0.40
YLD_F	0.50^{**}	0.10^{ns}	0.92^{**}	0.35^{*}	0.42^{*}	0.93^{**}	1.00^{**}	1.05	-0.67^{**}	0.77	-0.72^{**}	0.77

*, ** and ns indicate significance at $P < 0.05$, $P < 0.01$ and $P > 0.05$ for the corresponding phenotypic correlation, respectively;

† V2, HT, CB, FLW, DUR, HI, YLD, WB, and WR indicate early seedling vigour at two weeks after sowing, plant height, crop biomass, days to flowering, duration, harvest index, yield, weed biomass and weed rating, respectively.

Table 8. Phenotypic correlations between yield losses and traits of aerobic and upland rice measured under weed-free (F) or weedy (W) conditions over three years (2001–2003) at Los Baños, Philippines.

Trait	Early vigour		Height		Duration		Crop biomass		Harvest index		Yield		Weed biomass	Weed rating
	F	W	F	W	F	W	F	W	F	W	F	W	W	W
Absolute yield loss	0.04^{ns}	-0.07^{ns}	-0.15^{ns}	-0.14^{ns}	0.37*	0.35*	0.58**	0.37*	0.60**	0.34*	0.75**	0.40*	0.03^{ns}	-0.03^{ns}
Relative yield loss	–0.53**	–0.63**	-0.28^{ns}	–0.38*	0.08^{ns}	0.11^{ns}	-0.06^{ns}	–0.40*	0.05^{ns}	–0.48**	-0.14^{ns}	–0.54**	0.72**	0.73**

*, **, ns indicate $P < 0.05$, $P < 0.01$ and $P > 0.05$, respectively.

competition although they might lose more absolute yield due to competition than some low-yielding ones (Table 8). There was a strong positive correlation between weed biomass and the relative yield reduction due to weed competition (Table 8). This supports the hypothesis that enhancing weed-suppressive ability is necessary when the goal is to decrease relative yield reduction. However, selection for weed-suppressive ability alone may not result in improvements in yield under competition. This is illustrated by the cases of the cultivars IR70358-84-1-1 and Vandana. These were among the most weed-suppressive cultivars, having similar weed biomass to the high-yield cultivar UPLRi-7, but their yields with and without weed competition were much lower (Table 4). Such cultivars combining low yield but strong weed-suppressive ability, are usually very short-duration genotypes with rapid early growth but relatively low final biomass accumulation and HI.

Predicting weedy yield and weed biomass with weed-free traits

Based on the correlations estimated across three years, weed-free traits early vigour and yield appeared to be the most promising predictors of weedy yield and weed biomass. We therefore regressed weedy yield and weed biomass on them singly and in combination (Table 9). Weedy yield was well predicted by weed-free yield alone, with R^2 = 0.81; by adding weed-free early vigour to weed-free yield, the prediction was slightly but significantly improved (R^2 = 0.87). However, only 40% of variation in

Table 9. Regression models for predicting aerobic and upland rice cultivar means for weedy yield and weed biomass using means for weed-free yield and weed-free early vigour scored at 2 weeks after sowing, estimated over three years (2001 – 2003) at Los Baños, Philippines.

Dependent variable	Regression coefficients for independent variables		Intercept	R^2
	Weed-free yield (Mg ha^{-1})	Weed-free early vigour (score)		
Weedy yield (Mg ha^{-1})	0.64 ± 0.05**†	-	−0.17 ± 0.12^{ns}	0.81
Weedy yield (Mg ha^{-1})	-	0.31 ± 0.06**	−0.32 ± 0.33^{ns}	0.40
Weedy yield (Mg ha^{-1})	0.56 ± 0.05**	0.13 ± 0.03**	−0.65 ± 0.16**	0.87
Weed biomass (g m^{-2})	−25.40 ± 7.19**	-	241.42 ± 17.43**	0.25
Weed biomass (g m^{-2})	-	−20.12 ± 4.64**	289.36 ± 25.06**	0.33
Weed biomass (g m^{-2})	−14.85 ± 7.39^{ns}	−15.33 ± 5.06**	298.22 ± 24.51**	0.40

*, **, and ns indicate P < 0.05, P < 0.01 and P > 0.05, respectively; in the case of multiple regression the test is for each independent variable added last.

† regression coefficient and its standard error.

weedy yield could be explained by cultivar differences in weed-free early vigour alone. This result confirms that both yield potential and rapid early crop growth are important determinants of yield under the moderate weed competition experienced in this study, and indicates that indirect selection for weedy yield by selecting for yield and early vigour under weed-free conditions is likely to be efficient. The regression coefficients for weed-free yield and early vigour could be used as weights for a selection index designed to maximize gains for yield under competition. However, it may be more cost-effective to apply independent culling levels (Bernardo, 2002), selecting for vegetative vigour early in a season, then evaluating yield only in those entries exhibiting a high rate of early growth.

Weed biomass was predicted by weed-free early vigour alone with R^2 = 0.33, and by weed-free yield alone with R^2 = 0.25 (Table 9). Adding weed-free yield to weed-free early vigour did not improve the prediction (Table 9). The much lower R^2 values observed for predictions of weed biomass than for weedy yield indicate that indirect selection for weed suppression via improved vigour is less efficient than indirect selection for grain yield under competition using both weed-free yield and early vigour as selection criteria. However, if the objective is to improve weed-suppressive ability, then selection based on early vigour alone under weed-free conditions is likely to be as efficient as selection based on both early vigour and yield.

The importance of seedling vigour rated at 2 WAS in determining yield and weed biomass observed in the present study is supported by Cousens et al. (2003), who found that the species achieving the greater biomass early in the cropping period remains the better competitor throughout growth. However, other vegetative traits, such as seedling vigour or biomass measured later during the vegetative period, seedling height, ground cover, and early tillering may be similarly correlated with weed biomass and yield under competition, and thus may also serve as useful indirect selection criteria. Ni et al. (2000) found that weed-free crop biomass at tillering (5 WAS) was predictive of weed-suppressive ability for irrigated rice. Jannink et al. (2000) reported that selection on plant height at seven weeks after emergence was efficient for improving weed suppression in soybean. Gibson et al. (2003) reported the importance of early leaf area growth as a predictor of weed biomass for irrigated rice. Lemerle et al. (1996) found that weed-free morphological traits such as early tillering, height at anthesis and leaf habit were predictive of yield reduction and weed biomass for wheat.

The *H* estimates, and correlations among traits reported in this study are most applicable to short- and medium-duration germplasm evaluated in tropical aerobic environments with moderate weedy conditions (weed pressure: 70 – 300 g m^{-2}) in the Philippines. Whether or not these relationships would change markedly in different environments is unknown. But because genotype × weed management and genotype × year interactions were limited, it seems that our results are likely to be widely applicable to aerobic rice target environments in the tropics. Whether or not they can be extrapolated to transplanted lowland systems remains unknown.

CONCLUSIONS

We observed that a wide range in weed suppression as well as yielding ability under moderate competition exists among cultivars of aerobic and upland rice used as parents in IRRI's breeding programmes, and that yields under moderately weedy and weed-free conditions are highly correlated. This strongly indicates that the development of cultivars combining high yield potential under weed-free conditions with good performance under moderate competition is feasible.

The strong association observed in this study between early vigour (a visual seedling biomass rating) and yield under both weedy and weed-free conditions, as well as the high negative correlation of the trait with weed biomass, indicates that early vigour can be a useful selection criterion in aerobic rice breeding programmes. Early vigour has been incorporated as a selection criterion at the initial replicated yield trial stage in the IRRI aerobic rice breeding programme, where the target is to develop cultivars that can produce economically acceptable yields with a single hand weeding soon after sowing. Development of such cultivars could substantially reduce the labour requirements for aerobic and upland rice production in much of South and Southeast Asia.

It should be noted that these results apply only to the population of genotypes evaluated and the location at which they were evaluated. They may not be applicable to other germplasm or locations. We feel they are likely to be robust with respect to photoperiod insensitive upland or aerobic rice genotypes in the Asian tropics, but they may not extend to transplanted environments or long-duration, photoperiod-sensitive germplasm, where other characteristics may have a greater role in explaining differences in cultivar weed competitiveness.

CHAPTER 3

Developing selection protocols for weed competitiveness in aerobic rice[1]

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Abstract

Aerobic rice production systems, wherein rice is dry-sown in nonpuddled soil and grown as an upland crop, offer large water savings but are subject to severe weed infestation. Weed-competitive cultivars will be critical to the adoption of aerobic rice production by farmers. Breeding weed-competitive cultivars requires an easily-used selection protocol, preferably based on traits that can be measured under weed-free conditions. To develop such an indirect selection index for weed competitiveness, forty rice cultivars were evaluated in aerobic soil conditions in a weed-free environment in 2003 and in weedy environments over three years (2001 – 2003). Broad-sense heritabilities (*H*) of vegetative and harvest traits and their genetic correlation with weed biomass and yield under weed competition were estimated. All the traits measured under weed-free conditions were closely correlated with the same traits measured under weedy conditions. Crop vigour ratings at 2, 4, and 6 weeks after sowing (WAS), canopy ground cover at 6 WAS, height at 3 and 4 WAS, tillers per plant at 4 and 8 WAS, vegetative crop biomass at 4 and 9 WAS and plant erectness at 3 WAS under weed-free conditions in 2003 were all positively correlated with means for yield under weed competition and negatively with means for weed biomass across three years. In general, traits associated with rapid seedling biomass accumulation were also strongly associated with weed suppression and yield under weed competition. Regression analysis revealed that yield and early vigour under weed-free conditions in a single three-replicate trial could be used together in an indirect selection index, explaining 89% and 48% of variation for yield under weed competition and weed biomass, respectively. The predicted indirect selection efficiencies of weed-free yield and vigour ratings as selection criteria for yield under weed competition and weed biomass were high. Visual vigour rating at 4 WAS is the best vegetative trait as an indirect selection criterion for use together with weed-free yield, but it could be replaced by plant height at 4 WAS without loss in selection effectiveness.

Keywords: Aerobic rice; Canopy ground cover; Crop vigour; Plant erectness; Indirect selection index; Vegetative growth; Weed competitiveness

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INTRODUCTION

Water shortage in many rice-growing areas is prompting a search for production systems that use less water to produce rice. Aerobic rice systems, wherein the crop is established via direct seeding in nonpuddled, nonflooded fields and managed intensively as an upland crop, are among the most promising approaches to water-saving (Tuong and Bouman, 2003). Aerobic rice systems can reduce water requirements for rice production by over 44% relative to conventionally transplanted systems, by reducing percolation, seepage, and evaporation losses, while maintaining yield at an acceptable level (6 Mg ha^{-1}) (Bouman et al., 2005). However, aerobic rice systems are subject to greater weed pressure than conventional production systems, in which weeds are suppressed by standing water and transplanted rice seedlings have a 'head start' over germinating weed seedlings. Weeds are perceived to be the most severe constraint to upland and aerobic rice production (Moody, 1983; WARDA, 1996; Balasubramanian and Hill, 2002). Most upland and aerobic rice growers in Asia mechanically weed their crops two or three times per season, investing up to190 person-days ha^{-1} in hand-weeding (Roder, 2001). The labour requirement for weeding is a major impediment to the adoption of water-saving aerobic rice, and to increasing the productivity of traditional upland rice-based cropping systems. Breeding aerobic rice cultivars combining both high yield and strong weed competitiveness (WC), with a reduced requirement for weeding, is therefore critical to the development of aerobic rice systems. Moreover, the adoption of weed-competitive cultivars will decrease environment pollution and development of herbicide-resistant biotypes by reduced herbicide application. Weed-competitive cultivars are a low-cost and safe tool for integrated weed management (Pester et al., 1999; Fischer et al., 2001; Gibson and Fischer, 2004).

Weed competitiveness of crops has two components: weed tolerance (WT), the ability to maintain high yields despite weed competition, and weed-suppressive ability (WSA), the ability to reduce weed growth through competition (Jannink et al., 2000). Differences in WSA among cultivars can be directly determined by assessing weed biomass in plots under weed competition, but differences in WT can only be compared in terms of crop grain yield under weed competition among cultivars with the same yield potential and WSA (Jordan, 1992; Gibson and Fischer, 2004). The effects of yield potential, WSA and WT on grain yield under weed competition are usually confounded. Jannink et al. (2000) and Jordan (1993) advocate breeding for WSA over WT because suppressing weeds reduces weed seed production and benefits weed management in the future while tolerating weeds only benefits the current growing season. Weed pressure from unsuppressed weeds increases the likelihood of crop yield loss, irrespective of the crop's tolerance. However, strong WSA does not guarantee high yield under weed competition if the yield potential is low (Zhao et al., 2006a; Chapter 2). Therefore, selection for both WSA and yield potential are needed to develop cultivars that produce economically acceptable yields under competition.

Studies in wheat (Lemerle et al., 1996), corn (Lindquist and Mortensen, 1998), soybean (Jannink et al., 2000) and rice (Garrity et al., 1992) have reported extensive genetic variation for WC. Weed competitiveness is often linked to plant height (Garrity et al., 1992), tiller number (Fischer et al., 1997), early height growth rate (Caton et al., 2003), early crop biomass (Ni et al., 2000), leaf area index (LAI) (Dingkuhn et al., 1999), specific leaf area (SLA) (Audebert et al., 1999), canopy ground cover (GC) (Lotz et al., 1995) and early vigour (Zhao et al., 2006a). However, despite many years of research and considerable evidence of varietal differences in WC, there have been limited efforts to breed for improved WC (Zimdahl, 2004). Gibson and Fischer (2004) attributed the limited progress in breeding for WC to: (1) the successful chemical control of weeds, which has led researchers to focus on herbicide use with less emphasis on other control methods and (2) the trade-off between yield and WC suggested by earlier researchers (e.g., Jennings and Jesus, 1968; Kawano et al., 1974). Recent research has shown that WC and yield potential can be compatible (Garrity et al., 1992; Ni et al., 2000; Fischer et al., 2001; Gibson et al., 2003; Zhao et al., 2006a).

Selection for WC may be done directly in the presence of weeds, or indirectly, under non-competitive conditions for secondary traits related to WC. Direct selection for WC entails growing each genotype in the presence of weeds to measure weed biomass and crop yield as selection criteria (Wall, 1983). High labour requirements make direct selection impractical for most breeding programmes. Indirect selection, which can be carried out in the absence of weeds and may permit selection to be started earlier in a breeding programme, is likely to be easier and less expensive. Indirect selection efficiency (ISE) of a trait as a selection criterion is a function of the heritability (H) of the selection criterion under weed-free conditions and of the target trait under weed competition, and their genetic correlation (see Eqn. 5, page 42) (Falconer, 1989). Traits that are potentially useful indirect selection criteria for WC should be heritable under weed-free conditions and highly correlated with both weed biomass and yield in weedy conditions. They should also be practical for use in large breeding populations to achieve adequate selection intensity (Atlin et al., 2001). Indirect selection under weed-free conditions is preferable to direct selection when ISE is close to or greater than 1, and indirect selection is less expensive than direct selection. There are few reports in the literature of the heritability of WC and its component traits. Fischer et al. (1995, 1997) and Haefele et al. (2004) reported that some vegetative traits measured in weed-free rice variety trials, including LAI and tiller number, were uncorrelated with weed growth or competition-induced yield loss, and suggested that only direct selection for WC would be effective. However, the work of Jannink et al. (2000) on seedling height of soybean, Ni et al. (2000) on rice seedling biomass, and Gibson et al. (2003) on rice LAI and root growth during the vegetative stages suggests that some seedling traits measured in weed-free conditions are highly correlated with weed growth. Therefore, indirect selection for WSA, an important component of WC, may be feasible. However, destructively measured traits may be impractical selection criteria because of time, seed or land required when hundreds or thousands of lines must be assessed. If an easily-used selection protocol can be developed based on non-destructive measurements or ratings, breeding protocols for WC will be greatly simplified. Zhao et al. (2006a) reported that visual rating of crop seedling vigour at 2 weeks after sowing (WAS) may serve as an indirect selection criterion in breeding programmes aiming to improve both yield in competition and WSA. However, other nondestructive traits such as seedling height, tillering, and GC may also be useful.

The objectives of the present study were to identify traits that: (1) can be measured in weed-free environments, (2) are heritable, and (3) are highly correlated with both WSA and yield under weed competition; and to develop indirect selection protocols based on these traits for use in practical breeding programmes aiming at developing cultivars that can be profitably produced with a single hand-weeding or herbicide application.

MATERIALS AND METHODS

Experiments

Weed competition trials

Forty cultivars of upland and aerobic rice (*O. sativa* L.), belonging to six germplasm groups (*indica,* tropical *japonica, indica/*tropical *japonica, aus, aus/*tropical *japonica, indica/*tropical *japonica/aus*) (Glazsmann, 1987) and two variety types (traditional and improved), with a wide range in plant height (91 – 156 cm), duration (89 – 117 d), and plant type (erect and droopy), were grown on the upland farm of the International Rice Research Institute (IRRI) (14°13’ N, 121°15’ W, 23 m elevation), Los Baños, Philippines, in the wet seasons of 2001 – 2003. The field conditions and management of these trials were described in detail by Zhao et al. (2006a). Briefly, fields were ploughed, harrowed, levelled and furrowed before sowing. Two adjacent trials, weed-free and weedy, arranged in α-lattice design with three replications each, were direct-seeded in dry, nonpuddled soil in the same field within each year.

Cultivars were manually sown in 4.5 m^2 plots with six rows 3 m in length and spaced 0.25 m apart on 12, 5 and 8 July 2001, 2002 and 2003, respectively and immediately sprinkler-irrigated to insure uniform establishment. The seeding rate for each cultivar was 300 viable seeds m^{-2}. The weed-free trial was treated with pre-emergence herbicide Ronstar (oxadiazon) at the recommended rate one day after irrigation, and was maintained weed-free throughout the growing season by hand. The weedy trial was completely hand-weeded once at 3 WAS in 2001 and 2002, or treated with post-emergence herbicide Nominee (bispyribac sodium) once at 2 WAS instead of hand-weeding in 2003; weeds were allowed to grow thereafter.

A compound N-P-K fertilizer ($N:P_2O_5:K_2O$ = 14:14:14) was broadcast before furrowing at the rate of 200 kg ha^{-1}; two additional splits of urea were top-dressed at the rate of 60 kg ha^{-1} at 4 and 8 WAS, respectively. Total N, P and K fertilizer application were 82, 12 and 23 kg ha^{-1}, respectively. The field was maintained under nonsaturated aerobic conditions through the growing season. Trials were primarily rainfed, but supplemental surface irrigation was applied on a few occasions when crop leaves started to roll due to drought stress, and drainage was conducted whenever heavy rains resulted in ponding.

Weed species in the weedy trials were recorded as reported in Zhao et al. (2006a). The predominant weeds common in the three years were *Digitaria ciliaris* Retz., *Eleusine indica* L., *Echinochloa colona* L., *Leptochloa chinensis* L., *Dactyloctenium aegyptium* L. and *Portulaca oleracea* L. The weed pressures were 305, 172 and 73 g m^{-2} in 2001, 2002 and 2003, respectively. The weed populations in the three years appeared uniform throughout the fields. The grasses were as tall as or taller than the cultivars. Weed growth (WR) was visually rated on a 1-to-9 scale (9 for the most weed growth, 1 for the least) and biomass (WB) was clipped at the soil surface from a random area of 0.5 m^2 in each plot in weedy trials at 13 WAS, oven dried at 70°C for 5 days and weighed.

Days to flowering, days to maturity, final plant height, harvest index (HI), final crop biomass and grain yield (14% moisture basis) in weed-free and weedy treatments were measured as reported in Zhao et al. (2006a).

In order to identify useful traits for indirect selection, several vegetative traits were investigated in greater detail in 2003. Plant height (HT) was measured as the distance from soil surface to the tip of the longest extended leaf of 6 random plants in each plot of weed-free and weedy trials at 3, 4, 6, and 9 WAS (HT3, HT4, HT6, and HT9, respectively). Height growth rates (HR), the increase of plant height per day (cm d^{-1}), were calculated based on the height measurements to study cultivar growth patterns related to WC. HR3, HR4, HR6 and HR9 represent height growth rate during emergence – 3, 3 – 4, 4 – 6 and 6 – 9 WAS, respectively. Crop biomass on a per-plot basis in both trials, referred to herein as crop vigour (VV), was visually rated on a 1-to-9 scale at 2, 4, and 6 WAS (VV2, VV4, and VV6, respectively), with 1 as the least and 9 as the greatest. Plant erectness (E) also was rated on a 1-to-9 scale at 3 (both trials) and 6 (weed-free trial) WAS (E3 and E6, respectively), where 9, 7, 5, 3 and 1 represent plots in which >80%, 50 – 80%, 50%, 30 – 50% and <30% of leaves were nearly perpendicular to the ground, respectively. Canopy ground cover was measured with a digital canopy camera (First Growth, Model +1G, Decagon Devices, Inc.) at 6 WAS (GC6) in the weed-free trial only. It was expressed as the proportion (percentage) of the green area to total area in a photograph taken at a distance of 1.5 m vertically and 1 m horizontally from the closer edge of the shooting area covering 6 rows of a plot. Vegetative crop biomass was harvested by clipping at soil surface from a random area of 0.5 m^2 in each plot at 4 (weed-free trial) and 9 (both trials) WAS (CB4 and CB9, respectively).

Tillering trial

A separate trial with the same cultivar set and experimental design was sown in the same field as the weed competition trials on 8 July 2003 to study cultivar tillering ability and its correlation with the components of WC. Each cultivar was sown in a single 3 m row and thinned at 2 WAS to a single plant per hill. Hills were spaced 5 cm apart within rows; row spacing was 25 cm. The experimental management, including weed control, fertilization, irrigation and insecticide application was the same as in the weed-free competition trial. Tiller number (TN) was determined for 20 plants within a randomly selected 1 m of row in each plot at 4 and 8 WAS. Tillers per plant at 4 (TN4) and 8 (TN8) WAS were used to indicate cultivar tillering ability.

Data analysis

Combined data analysis

The common data (yield, weed biomass and weed rating) collected from weedy trials over three years were subjected to a combined analysis using SAS Release 8.02 (TS2M0) (SAS Institute Inc., 1999-2001) as reported in detail in Zhao et al. (2006a). Briefly, least square means for the three traits over three years were estimated using the REML option of the MIXED procedure, where years and replicates were defined as random factors and cultivars as fixed factors. Because a preliminary analysis showed that the data among years were heterogeneous, the option of REPEATED/GROUP = year to deal with the heterogeneity was employed. Variance components across years were estimated using the REML option of the VARCOMP procedure, which considers all factors to be random. These variance component estimates were used in calculating *H* estimated over three years (Nyquist, 1991) as:

$$H = \frac{\sigma^2{}_G}{\sigma^2{}_G + \frac{\sigma^2{}_{GY}}{y} + \frac{\sigma^2{}_E}{ry}} \tag{1}$$

where $\sigma^2{}_G$, $\sigma^2{}_{GY}$, $\sigma^2{}_E$, *y,* and *r* are the genotype, genotype × year and within-trial error variances, and the number of years and replicates of testing, respectively. The least square means from the combined analysis and those from separate analysis of 2003 data described below were used to calculate the phenotypic and genetic correlations of the target traits weedy yield (YLD_W), weed biomass (WB_W) and weed rating (WR_W) with the weed-free traits studied in 2003, and to evaluate indirect selection protocols by regression analysis. The *H* estimates were used in calculating the ISE for all the single-year weed-free traits to identify those that would be useful as indirect selection criteria.

Analysis of 2003 data

The data collected for the detailed investigations of vegetative growth in weed competition and tillering trials in 2003 were separately analysed using the appropriate mixed model for α-lattice designs to estimate cultivar means and variance components. *H* for traits within these trials was calculated (Nyquist, 1991) as:

$$H = \frac{\sigma^2{}_G}{\sigma^2{}_G + \frac{\sigma^2{}_E}{r}} \tag{2}$$

where $\sigma^2{}_G$, $\sigma^2{}_E$ and *r* are the genotype, within-trial error variances and the number of replicates of testing, respectively. This estimator of *H* is biased upward by confounding of the genotype and genotype × environment variances, but is useful in approximately comparing the precision with which cultivar means are estimated for different potential target traits for indirect selection.

Phenotypic and genetic correlations

Phenotypic correlations among traits were calculated on the basis of cultivar means over replicates for traits measured in 2003 (estimated by separate analyses), or over years for traits measured within the weedy treatment (estimated by combined analysis over three years). Genetic correlations among traits from the same trial in 2003 were estimated (Bernardo, 2002) as:

$$r_{G\,12} = \frac{Cov_{12}}{\sqrt{\sigma^2{}_{G_1} \times \sigma^2{}_{G_2}}} \tag{3}$$

where, r_{G12}, Cov_{12}, $\sigma^2_{G\,1}$ and $\sigma^2_{G\,2}$ are genetic correlation coefficient between traits 1 and 2 within a trial, genetic covariance of traits 1 and 2, and the genotypic variances of traits 1 and 2, respectively. Genetic correlations between traits measured in different experimental units were computed using (Cooper et al., 1996):

$$r_{G12} = \frac{r_{P\,12}}{\sqrt{H_1 \times H_2}} \tag{4}$$

where r_{G12}, $r_{P12,}$ H_1 and H_2 are genotypic correlation coefficient between traits 1 and 2, phenotypic correlation coefficient between the same trait pair, and the heritabilities of traits 1 and 2, respectively. This estimator is biased downward when the H estimates in the denominator are from a single trial, and when there is substantial genotype × year interaction for the paired traits. This estimator was used for genetic correlations between traits measured in:

- the weed-free versus weedy trial in 2003;
- the weed-free trial in 2003 versus weedy trials over the three years;
- the tillering trial versus the weed-free or weedy trial in 2003, or weedy trials over the three years.

The relationships among traits measured in the same or different weed regimes were assessed with these correlations. The genetic correlation was also used in estimating ISE for traits measured in the weed-free trial in 2003.

Indirect selection efficiency

The indirect selection efficiencies of traits measured under weed-free conditions in 2003 for the target traits YLD_W, WB_W, and WR_W under weedy conditions over three years were calculated (Falconer, 1989) as:

$$\text{ISE} = r_G \sqrt{H_F / H_W} \tag{5}$$

where r_G is the genotypic correlation between a selection criterion measured in the weed-free selection environment and a target trait in the weedy environments, and H_F and H_W are heritabilities of the selection criterion and the target trait, respectively. H_F was estimated within the weed-free trial or tillering trial in 2003, and H_W for a single year of testing was predicted using variance components estimated from weedy trials over three years. The model assumes that selection intensity is constant for the two traits.

As noted above, it is likely that there is upward bias in the H_F estimates and downward bias in the r_G estimates. These biases are only expected to be large if there is substantial genotype × year interaction for the trait being used as an indirect selection criterion. They are unlikely to affect comparisons of the efficiencies of different indirect selection criteria.

Regressions

Means from the combined analysis over three years for the target traits YLD_W and WB_W were assumed to represent the true yielding and weed-suppressive abilities of cultivars under weed competition, respectively. They were used as dependent variables in regression analyses that evaluated the effectiveness of weed-free traits measured in a single season as indirect selection criteria. Preliminary stepwise regression analysis showed that weed-free yield (YLD) and VV4 were the only two variables necessary to predict YLD_W, and that weed-free VV4 and HT4 were the two most important variables to predict WB_W. Therefore, we regressed the means for YLD_W and WB_W on the means for YLD, VV4 and HT4 individually or in combination using the MAXR option of REG procedure of SAS. The resulting models were used to compare the predicted effectiveness of different selection procedures. The improvement in prediction following the addition of a second independent variable to a model was deemed significant if both regression coefficients differed significantly from 0 and the reduction in the error sum of squares resulting from the addition was significant by F-test.

RESULTS AND DISCUSSION

Genetic variation and relationships among traits

Genetic variation in vegetative traits under weed-free or weedy conditions

Zhao et al. (2006a) previously showed that there were differences among the 40 cultivars in all the harvest traits including yield and WSA over three years of evaluation. In the present study, F-tests (not shown) demonstrated that the 40 cultivars also differed ($P < 0.01$) in all the vegetative traits (listed in Table 1) studied in 2003 under weed-free and weedy conditions. Genotype differences in early vegetative traits included in our study (seedling height, height growth rate, crop biomass and tiller number) as well as others (LAI, SLA, crop growth rate, and relative leaf area growth rate) have been reported elsewhere (Bastiaans et al., 1997; Johnson et al., 1998; Dingkuhn et al., 1999; Reinke et al., 2002; Caton et al., 2003; Haefele et al., 2004). The substantial variation in vegetative growth parameters existing among rice genotypes indicates that selection based on these differences is likely to be effective.

Vegetative growth under weed-free versus weedy conditions

All the vegetative traits measured under weed-free conditions from 2 to 9 WAS in 2003 were strongly genetically correlated with the same traits measured under weedy conditions (Table 2), indicating that cultivar growth and plant architecture during the

Table 1. Broad-sense heritability (H)[†] and indirect selection efficiency (ISE) of, and phenotypic (r_P) and genetic (r_G) correlations between, traits from 2003 weed-free trials and weedy yield (YLD_W), weed biomass (WB_W) and weed rating (WR_W) estimated across three years (2001 – 2003), IRRI, Los Baños, Philippines.

Trait	H	YLD_W (H = 0.55±0.06)			WB_W (H = 0.38±0.10)			WR_W (H = 0.50±0.07)		
		r_P	r_G	ISE	r_P	r_G	ISE	r_P	r_G	ISE
VV2[‡]	0.81±0.05	0.54**	*0.67*	0.81	–0.52**	*–0.72*	1.06	–0.55**	*–0.70*	0.90
VV4	0.88±0.03	0.75**	*0.91*	1.14	–0.68**	*–0.90*	1.38	–0.82**	*–1.00*	1.35
VV6	0.83±0.05	0.67**	*0.83*	1.02	–0.63**	*–0.86*	1.27	–0.74**	*–0.95*	1.22
E3	0.92±0.02	0.60**	*0.71*	0.91	–0.52**	*–0.68*	1.06	–0.54**	*–0.65*	0.89
E6	0.93±0.02	0.57**	*0.67*	0.87	–0.30^{ns}	*–0.39*	0.62	–0.40*	*–0.48*	0.66
GC6	0.67±0.09	0.55**	*0.75*	0.83	–0.53**	*–0.81*	1.07	–0.61**	*–0.87*	1.00
HT3	0.79±0.06	0.40*	*0.51*	0.61	–0.56**	*–0.78*	1.13	–0.58**	*–0.75*	0.95
HT4	0.81±0.05	0.47**	*0.59*	0.71	–0.66**	*–0.91*	1.34	–0.70**	*–0.89*	1.14
HT6	0.90±0.03	–0.09^{ns}	*–0.10*	0.13	–0.13^{ns}	*–0.17*	0.26	–0.19^{ns}	*–0.24*	0.32
HT9	0.79±0.06	–0.02^{ns}	*–0.02*	0.03	–0.27^{ns}	*–0.38*	0.55	–0.21^{ns}	*–0.27*	0.34
HTF	0.83±0.05	0.03^{ns}	*0.04*	0.04	–0.24^{ns}	*–0.32*	0.48	–0.18^{ns}	*–0.23*	0.29
HR3	0.79±0.06	0.40*	*0.51*	0.61	–0.56**	*–0.78*	1.13	–0.58**	*–0.75*	0.95
HR4	0.50±0.14	0.41**	*0.66*	0.63	–0.57**	*–1.00*	1.16	–0.62**	*–1.00*	1.01
HR6	0.83±0.05	–0.45**	*–0.56*	0.68	0.30^{ns}	*0.42*	0.62	0.25^{ns}	*0.32*	0.41
HR9	0.63±0.11	0.06^{ns}	*0.09*	0.10	–0.21^{ns}	*–0.33*	0.42	–0.07^{ns}	*–0.10*	0.11
CB4	0.69±0.09	0.67**	*0.90*	1.01	–0.54**	*–0.82*	1.10	–0.70**	*–0.98*	1.15
CB9	0.63±0.11	0.51**	*0.73*	0.78	–0.51**	*–0.81*	1.04	–0.63**	*–0.91*	1.03
CBF	0.62±0.11	0.68**	*0.97*	1.02	–0.33*	*–0.52*	0.67	–0.43**	*–0.63*	0.70
FLW	0.98±0.01	0.20^{ns}	*0.24*	0.32	–0.06^{ns}	*–0.07*	0.12	–0.09^{ns}	*–0.11*	0.15
DUR	0.93±0.02	0.39*	*0.46*	0.59	–0.15^{ns}	*–0.20*	0.31	–0.19^{ns}	*–0.23*	0.31
HI	0.78±0.06	0.58**	*0.74*	0.88	–0.30^{ns}	*–0.42*	0.61	–0.44**	*–0.58*	0.72
YLD	0.96±0.01	0.92**	*1.00*	1.40	–0.55**	*–0.69*	1.11	–0.64**	*–0.76*	1.06
TN4	0.89±0.03	0.45**	*0.54*	0.68	–0.41**	*–0.55*	0.84	–0.43**	*–0.53*	0.71
TN8	0.95±0.02	0.74**	*0.86*	1.13	–0.58**	*–0.74*	1.18	–0.64**	*–0.76*	1.05

*, **, and ns indicate significance at $P < 0.05$, $P < 0.01$ and $P > 0.05$, respectively, for phenotypic correlations (r_P);

† Heritability and standard error; H values in parentheses in the first row are for a single year of testing and predicted using variance components estimated from weedy trials over three years (2001 – 2003); H values in the second column were estimated within a single weed-free competition or tillering trial in 2003;

‡ VV2, VV4 and VV6 indicate crop vigour at 2, 4 and 6 weeks after sowing (WAS), respectively; E3, E6 and GC6 indicate plant erectness at 3, 6 WAS and ground cover at 6 WAS, respectively; HT3, HT4, HT6, HT9 and HTF indicate plant height at 3, 4, 6, 9 WAS and harvest, respectively; HR3 , HR4, HR6 and HR9 indicate height growth rate during emergence – 3, 3 – 4 , 4 – 6 and 6 – 9 WAS, respectively; CB4, CB9 and CBF indicate crop biomass at 4, 9 WAS and harvest, respectively; FLW, DUR, HI and YLD indicate days to flowering, duration, harvest index and yield, respectively; TN4 and TN8 indicate tillers per plant at 4 and 8 WAS, respectively, in 2003.

Table 2. Genetic correlations (r_G) of vegetative traits of 40 aerobic and upland rice cultivars across weed-free (F03) and weedy (W03) management regimes in the 2003 wet season, IRRI, Los Baños, Philippines.

Trait	$VV4_{W03}$†	$E3_{W03}$	$HT4_{W03}$	$HT6_{W03}$	$HT9_{W03}$	$HR4_{W03}$	$HR6_{W03}$	$HR9_{W03}$	$CB9_{W03}$
$VV4_{F03}$	1.00**	0.85**	0.84**	0.37^{ns}	0.21^{ns}	0.69**	–0.64**	$–0.05^{ns}$	0.92**
$E3_{F03}$	0.73**	0.99**	0.53**	0.13^{ns}	$–0.01^{ns}$	0.42*	–0.58**	$–0.17^{ns}$	0.63**
$HT4_{F03}$	0.77**	0.52**	0.97**	0.77**	0.57**	0.81**	$–0.22^{ns}$	0.10^{ns}	0.68**
$HT6_{F03}$	0.11^{ns}	$–0.12^{ns}$	0.53**	0.85**	0.74**	0.50**	0.51*	0.28^{ns}	0.07^{ns}
$HT9_{F03}$	0.12^{ns}	0.03^{ns}	0.56**	0.82**	0.96**	0.62**	0.46^{ns}	0.70**	0.10^{ns}
$HR4_{F03}$	0.83**	0.53*	1.00**	0.86**	0.75**	1.00**	$–0.21^{ns}$	0.32^{ns}	0.74**
$HR6_{F03}$	–0.41*	–0.53**	0.02^{ns}	0.60**	0.58**	0.09^{ns}	0.85**	0.30^{ns}	–0.40*
$HR9_{F03}$	0.05^{ns}	0.17^{ns}	0.16^{ns}	0.14^{ns}	0.49*	0.30^{ns}	0.02^{ns}	0.66*	0.08^{ns}
$CB9_{F03}$	0.96**	0.79**	0.86**	0.57*	0.26^{ns}	0.68**	$–0.41^{ns}$	$–0.16^{ns}$	1.00**

*, **, and ns indicate $P < 0.05$, $P < 0.01$ and $P > 0.05$ for the corresponding phenotypic correlation (r_P), respectively;

† VV4 and E3 indicate crop vigour at 4 weeks after sowing (WAS) and plant erectness at 3 WAS, respectively; HT4, HT6 and HT9 indicate plant height at 4, 6 and 9 WAS, respectively; HR4, HR6, HR9 indicate height growth rate during 3 – 4, 4 – 6 and 6 – 9 WAS, respectively; CB9 indicates crop biomass at 9 WAS.

vegetative stage were relatively consistent across weed management regimes. A similar relationship was reported for harvest traits (Zhao et al., 2006a). Gibson et al. (2003) also found a lack of genotype × weed management interaction for yield in lowland rice. Lemerle et al. (2001a) reported a positive correlation between weed-free and weedy yield. Caton et al. (2003) reported that some early traits of aerobic rice under intraspecific competition (rice against rice) were closely correlated with the same traits under interspecific competition (rice against weeds) in the greenhouse. The consistency of crop performance across competition levels indicates that intra- and interspecific competition within an environment may differ in degree but not in kind; thus cultivars performing better in weed-free conditions (intraspecific competition) are likely to perform relatively better under weedy conditions (intra- and interspecific competition). Goldberg and Landa (1991) also found that the suppressive ability of a species does not change with changes in its surrounding species in natural environments. The relatively consistent expression in both vegetative and harvest traits of cultivars over different weed regimes indicates that indirect selection for traits related to WC under weed-free conditions may be effective.

Relationships among traits and their usefulness as indirect selection criteria for weed competitiveness

Crop vigour Cultivar means for VV2, VV4 and VV6 were closely intercorrelated, and had similar correlation with the other traits under weed-free or weedy conditions (data not shown), indicating that vigour evaluations for cultivars conducted from 2 to 6 WAS are likely to be consistent. VV4 was highly correlated with CB4, HT4 and TN4 under weed-free conditions (Table 3); 74% of the variation in VV4 could be explained by linear regression on HT4 and TN4, indicating that the visual crop vigour rating, even though subjective, was a reliable estimator of crop biomass, and integrated information on both seedling height and tiller number. VV2, VV4, and VV6 under weed-free conditions all were highly heritable, had a high positive genetic correlation with YLD_W, and high negative genetic correlations with both WB_W and WR_W (Table 1), indicating that early vigour could have considerable predictive power for both yield under competition and WSA. *H* for VV4 was greater than for VV2 and VV6, as were its correlations with YLD_W, WB_W and WR_W (Table 1). Consequently, the ISE of VV4, being greater than 1.10 for YLD_W, WB_W and $WR_{W,}$ was the highest among the three vigour scores. Therefore, VV4 appears to be a suitable trait on which indirect selection for WC can be practiced. Because vigour rating is nondestructive, quick, and inexpensive, its use in breeding weed-competitive cultivars appears promising and feasible. Early vigour has been suggested as a selection criterion in wheat (Rebetzke et al., 1999), and breeders may be inadvertently selecting for WC when selecting for early vigour (Lemerle et al., 2001a).

Canopy ground cover Canopy ground cover at 6 WAS was positively correlated with plant height before 9 WAS, tillers per plant at 4 and 8 WAS, vigour ratings at all three rating times and crop biomass at 4 and 9 WAS (Table 3), indicating that GC6 is also a good descriptor of overall vegetative crop growth. GC6 was moderately heritable (although less so than vigour), positively correlated with YLD_W, and negatively with WB_W and WR_W (Table 1), and thus may be used as an indirect selection criterion for WC. This result is supported by Lotz et al. (1995), Audebert et al. (1999) and Dingkuhn et al. (1999). However, although GC measurement is nondestructive, photographs need to cover a relatively large area, limiting selection on GC to multi-row plots, which is impractical for early generation progenies. Because both *H* of GC6 and its genetic correlation with weedy yield and weed biomass were lower than the equivalent parameters for VV4, ISEs of GC6 were lower than those of VV4. Therefore, GC does not seem to have any practical advantage over VV4 as an indirect selection criterion.

Table 3. Phenotypic (above the diagonal) and genetic (below the diagonal) correlations among traits of 40 aerobic and upland rice cultivars measured under weed-free conditions only in the 2003 wet season, IRRI, Los Baños, Philippines.

Trait	VV4†	E3	GC6	HT4	HT6	HT9	HTF	HR4	HR6	HR9	CB4	CB9	CBF	DUR	YLD	TN4	TN8
VV4		0.72**	0.68**	0.73**	0.19^{ns}	0.24^{ns}	0.04^{ns}	0.64**	–0.28^{ns}	0.12^{ns}	0.88**	0.76**	0.47**	0.07^{ns}	0.67**	0.70**	0.78**
E3	*0.82*		0.21^{ns}	0.42**	–0.11^{ns}	–0.01^{ns}	–0.30^{ns}	0.36*	–0.45**	0.10^{ns}	0.65**	0.58**	0.31^{ns}	0.08^{ns}	0.51**	0.66**	0.75**
GC6	*0.85*	*0.30*		0.72**	0.44**	0.34*	0.27^{ns}	0.55**	0.05^{ns}	–0.01^{ns}	0.65**	0.58**	0.43**	0.09^{ns}	0.49**	0.43**	0.49**
HT4	*0.78*	*0.51*	*0.81*		0.65**	0.58**	0.25^{ns}	0.86**	0.12^{ns}	0.09^{ns}	0.67**	0.75**	0.21^{ns}	–0.01^{ns}	0.33*	0.37*	0.43**
HT6	*0.22*	*–0.13*	*0.41*	*0.70*		0.64**	0.50**	0.56**	0.83**	–0.20^{ns}	0.10^{ns}	0.40*	–0.17^{ns}	–0.23^{ns}	–0.18^{ns}	–0.11^{ns}	–0.11^{ns}
HT9	*0.27*	*0.01*	*0.38*	*0.64*	*0.74*		0.39*	0.56**	0.41**	0.63**	0.13^{ns}	0.31^{ns}	0.03^{ns}	–0.05^{ns}	–0.07^{ns}	–0.08^{ns}	–0.08^{ns}
HTF	*0.04*	*–0.34*	*0.31*	*0.34*	*0.60*	*0.50*		0.28^{ns}	0.48**	–0.02^{ns}	–0.15^{ns}	0.00^{ns}	–0.11^{ns}	0.05^{ns}	0.00^{ns}	–0.34*	–0.24^{ns}
HR4	*0.87*	*0.61*	*0.73*	*0.99*	*0.75*	*0.88*	*0.40*		0.10^{ns}	0.14^{ns}	0.50**	0.72**	0.19^{ns}	0.03^{ns}	0.30^{ns}	0.27^{ns}	0.40*
HR6	*–0.30*	*–0.54*	*0.02*	*0.22*	*0.85*	*0.50*	*0.56*	*0.32*		–0.32*	–0.36*	–0.03^{ns}	–0.37*	–0.28^{ns}	–0.47**	–0.41**	–0.45**
HR9	*0.14*	*0.16*	*0.04*	*0.12*	*–0.18*	*0.56*	*–0.12*	*0.38*	*–0.32*		0.07^{ns}	–0.01^{ns}	0.21^{ns}	0.17^{ns}	0.09^{ns}	0.01^{ns}	0.01^{ns}
CB4	*1.00*	*0.85*	*1.00*	*0.80*	*0.08*	*0.14*	*–0.21*	*0.85*	*–0.51*	*0.17*		0.75**	0.47**	–0.01^{ns}	0.62**	0.64**	0.71**
CB9	*0.95*	*0.77*	*0.70*	*0.88*	*0.38*	*0.48*	*0.00*	*1.00*	*–0.10*	*0.21*	*1.00*		0.16^{ns}	–0.24^{ns}	0.39*	0.51**	0.57**
CBF	*0.60*	*0.42*	*0.62*	*0.31*	*–0.24*	*0.05*	*–0.15*	*0.23*	*–0.54*	*0.36*	*0.72*	*0.12*		0.63**	0.74**	0.35*	0.62**
DUR	*0.07*	*0.09*	*0.11*	*–0.01*	*–0.26*	*–0.07*	*0.09*	*0.05*	*–0.31*	*0.19*	*–0.03*	*–0.30*	*0.87*		0.44**	–0.10^{ns}	0.25^{ns}
YLD	*0.71*	*0.56*	*0.59*	*0.35*	*–0.24*	*–0.09*	*–0.02*	*0.33*	*–0.58*	*0.15*	*0.79*	*0.47*	*0.93*	*0.46*		0.40**	0.70**
TN4	*0.79*	*0.73*	*0.55*	*0.44*	*–0.12*	*–0.10*	*–0.40*	*0.40*	*–0.48*	*0.01*	*0.82*	*0.68*	*0.47*	*–0.11*	*0.44*		0.78**
TN8	*0.86*	*0.80*	*0.62*	*0.49*	*–0.12*	*–0.09*	*–0.27*	*0.58*	*–0.51*	*0.02*	*0.88*	*0.74*	*0.81*	*0.26*	*0.73*	*0.86*	

*, **, and ns indicate significance at $P < 0.05$, $P < 0.01$ and $P > 0.05$, respectively, for phenotypic correlations.

† VV4, E3 and GC6 indicate crop vigour at 4 weeks after sowing (WAS), plant erectness at 3 WAS and ground cover at 6 WAS, respectively; HT4, HT6, HT9 and HTF indicate height at 4, 6, 9 WAS and harvest, respectively; HR4 , HR6 and HR9 indicate height growth rate during 3 – 4, 4 – 6 and 6 – 9 WAS, respectively; CB4, CB9, and CBF indicate crop biomass at 4, 9 WAS and harvest, respectively; DUR, YLD, TN4 and TN8 indicate duration, yield, and tillers per plant at 4 and 8 WAS, respectively.

Table 4. Phenotypic (above the diagonal) and genetic (below the diagonal) correlations among traits of 40 aerobic and upland rice cultivars measured under weedy conditions only in 2003 wet season, IRRI, Los Baños, Philippines.

	VV4†	E3	HT4	HT6	HT9	HTF	HR4	HR6	HR9	CB9	CBF	WB	WR	DUR	YLD
VV4		0.67**	0.77**	0.28^{ns}	0.02^{ns}	0.00^{ns}	0.59**	–0.50**	–0.24^{ns}	0.89**	0.46**	–0.59**	–0.80**	–0.04^{ns}	0.76**
E3	*0.74*		0.45**	0.16^{ns}	0.02^{ns}	–0.10^{ns}	0.31*	–0.32*	–0.12^{ns}	0.58**	0.11^{ns}	–0.33*	–0.44**	–0.02^{ns}	0.54**
HT4	*0.82*	*0.53*		0.70**	0.41**	0.31^{ns}	0.90**	–0.17^{ns}	–0.14^{ns}	0.65**	0.26^{ns}	–0.55**	–0.69**	–0.17^{ns}	0.43**
HT6	*0.28*	*0.21*	*0.77*		0.67**	0.46**	0.68**	0.57**	–0.06^{ns}	0.27^{ns}	–0.05^{ns}	–0.27^{ns}	–0.38*	–0.35*	–0.05^{ns}
HT9	*0.00*	*0.04*	*0.47*	*0.81*		0.58**	0.49**	0.44**	0.70**	0.03^{ns}	0.03^{ns}	–0.19^{ns}	–0.14^{ns}	–0.23^{ns}	–0.06^{ns}
HTF	*–0.01*	*–0.13*	*0.34*	*0.55*	*0.70*		0.35*	0.29^{ns}	0.33*	–0.07^{ns}	0.17^{ns}	–0.26^{ns}	–0.14^{ns}	0.19^{ns}	0.10^{ns}
HR4	*0.66*	*0.41*	*0.91*	*0.78*	*0.59*	*0.42*		–0.08^{ns}	–0.02^{ns}	0.47**	0.20^{ns}	–0.39*	–0.53**	–0.08^{ns}	0.31^{ns}
HR6	*–0.79*	*–0.49*	*–0.24*	*0.43*	*0.57*	*0.34*	*–0.09*		0.05^{ns}	–0.37*	–0.36*	0.27^{ns}	0.25^{ns}	–0.30^{ns}	–0.58**
HR9	*–0.35*	*–0.21*	*–0.11*	*0.20*	*0.75*	*0.52*	*0.10*	*0.50*		–0.21^{ns}	0.09^{ns}	0.00^{ns}	0.16^{ns}	0.01^{ns}	–0.02^{ns}
CB9	*0.98*	*0.69*	*0.70*	*0.15*	*–0.06*	*–0.12*	*0.52*	*–0.80*	*–0.28*		0.32*	–0.59**	–0.71**	–0.22^{ns}	0.65**
CBF	*0.66*	*0.09*	*0.37*	*–0.17*	*–0.17*	*0.24*	*0.32*	*–0.81*	*–0.09*	*0.45*		–0.29^{ns}	–0.56**	0.40**	0.60**
WB9	*–0.95*	*–0.55*	*–0.93*	*–0.28*	*–0.21*	*–0.44*	*–0.69*	*0.91*	*–0.04*	*–0.92*	*–0.33*		0.61**	0.02^{ns}	–0.60**
WR9	*–0.94*	*–0.59*	*–0.79*	*–0.31*	*–0.09*	*–0.06*	*–0.60*	*0.73*	*0.20*	*–0.86*	*–0.69*	*0.73*		–0.02^{ns}	–0.69**
DUR	*–0.04*	*–0.03*	*–0.18*	*–0.42*	*–0.29*	*0.20*	*–0.08*	*–0.41*	*0.00*	*–0.24*	*0.59*	*0.06*	*0.00*		0.27^{ns}
YLD	*0.79*	*0.56*	*0.49*	*–0.08*	*–0.09*	*0.06*	*0.38*	*–0.89*	*–0.10*	*0.73*	*0.85*	*–0.81*	*–0.82*	*0.24*	

*, **, and ns indicate significance at $P < 0.05$, $P < 0.01$ and $P > 0.05$, respectively, for phenotypic correlations.

† VV4 and E3 indicate crop vigour at 4 weeks after sowing (WAS) and plant erectness at 3 WAS, respectively; HT4, HT6, HT9 and HTF indicate height at 4, 6, 9 WAS and harvest, respectively; HR4, HR6 and HR9 indicate height growth rate during 3 – 4, 4 – 6 and 6 – 9 WAS, respectively; CB9 and CBF indicate crop biomass at 9 WAS and harvest, respectively; WB and WR indicate weed biomass and weed rating at 13 WAS, respectively; DUR and YLD indicate duration and yield, respectively.

Plant height and height growth rate Early plant height (HT3 and HT4) and early height growth rates (HR3 and HR4) all were positively correlated with vegetative crop biomass measures CB4 and CB9 under weed-free and weedy conditions (Tables 3 and 4; HT3 and HR3 not shown), but plant height measurements taken later than 6 WAS and their corresponding height growth rates were generally not. This finding indicates that the early height growth (≤ 4 WAS) is more useful than late height growth (after the initiation of reproductive growth) in describing vegetative growth patterns associated with genotypic differences in WC. Moreover, early height and early height growth rates (≤ 4 WAS) were all moderately to highly heritable and correlated with YLD_W, WB_W and WR_W (Table 1), but later measures (≥ 6 WAS) were not. This indicates that only the early height and height growth rates (≤ 4 WAS) may serve as useful selection criteria for WC. HT4 and HR4 appeared to be slightly better parameters than HT3 and HR3 in terms of ISE for YLD_W and WB_W (Table 1). Although measuring seedling height is not as easy as vigour rating and ISEs of HT4 and HR4 were less than those of VV4 (Table 1), it is nondestructive, and only requires measurement of a few seedlings, so early height measurement may be a useful option as an indirect selection criterion, particularly when stands are too poor for reliable vigour ratings. The importance of early height and early height growth rates in determining WC shown in this study is supported by studies with rice (Bastiaans et al., 1997; Caton et al., 1999, 2003; Gibson et al., 2001; Reinke, 2001), wheat (Ogg and Seefeldt, 1999) and soybean (Jannink et al., 2000). However, Fischer et al. (2001) and Dingkuhn et al. (1999) reported little association of early weed-free height with WC.

Tiller number per plant Tiller number per plant at 4 and 8 WAS (TN4 and TN8), recorded in a separate trial without weed competition, was also correlated with weed-free vegetative crop biomass (Table 3), indicating that the tillering ability of a cultivar, expressed when grown sparsely (40 seedlings m^{-2}), was predictive of vegetative crop biomass when planted more densely (300 viable seeds m^{-2}). Like vigour ratings, GC6, early height and height growth rates (≤ 4 WAS), TN4 and TN8 were both highly heritable and moderately correlated with YLD_W, WB_W and WR_W (Table 1). However, because tiller counts are laborious, vigour rating, which integrates tillering ability and plant height, is superior as an indirect selection criterion. High tillering ability is regarded as a desirable character for weed-competitive cultivars (Moody, 1979; Dingkuhn et al., 2001). This was confirmed by our study and other reports (Lemerle et al., 1996; Fischer et al., 1997, 2001; Johnson et al., 1998; WARDA, 1998; Dingkuhn et al., 1999; Caton et al., 2003). However, Garrity et al. (1992) and Ni et al. (2000) reported little correlation between tillering and WSA.

TN4 and TN8 were both positively correlated with weed-free yield (Table 3) and weedy yield (Table 1), indicating the benefit of tillering to yield with or without competition under aerobic conditions. The yield potential of modern lowland rice cultivars is reached with a relatively small number of tillers, but a trade-off between tillering and yield potential may not exist in aerobic rice.

Erectness The positive correlations of plant erectness rated at 3 and 6 WAS (not shown) with CB4, CB9, VV4, HT4, HR4, TN4 and TN8 under both weed-free and weedy conditions (Table 3 and 4) indicate that the erect type was more vigorous, grew more quickly in height during early vegetative development (≤ 4 WAS), and produced more tillers than the droopy type. The association between plant erectness and HT4 indicates that droopiness of the cultivars in this study was a feature of seedling architecture rather than simply a result of having long leaves. HT4, which was assessed before stem elongation, was primarily a measure of the length of longest leaf at 4 WAS; thus, cultivars with the longest seedling leaves were also the most erect. Surprisingly, plant erectness was not strongly correlated with GC6 (Table 3). Plants with droopy leaves are thought to cover the ground more than erect types, but in the context of a crop stand, GC is also influenced by crop density, tillering ability and height. Audebert et al. (1999) found that *O. glaberrima* Steud. cultivars achieved greater GC and LAI not through characteristics of individual leaves, but due to a rapid increase in the number of leaves through high tillering. In the present study, the supposed inferiority of erect-leaf types in generating GC appears to be offset by generating more tillers. Surprisingly, plant erectness were positively correlated with YLD_W and negatively with weed growth (Table 1), indicating that erect plant types that produce many tillers are more likely to combine high-yielding ability with strong WSA. This result is supported by Wang et al. (2004), who showed that erect cowpea genotypes are more effective in suppressing weeds than semi-erect or prostrate types, and by Fischer et al. (1997), who reported that erect types of irrigated rice can be both high yielding and competitive. However, other studies with rice (Dingkuhn et al., 1999) and wheat (Lemerle et al., 1996) suggested that more erect cultivars are less weed-competitive. Our result might be due to the fact that the *indica* cultivars in our study were both higher yielding and more suppressive than the tropical *japonica*s, and all the *indicas* were more erect than most of the tropical *japonica*s (data not shown). In a population stand, droopiness *per se* may be less important for weed suppression than fast early growth in height and tillering. Similarly, Johnson et al. (1998) linked WSA of *glaberrima* over *japonica* cultivars to early tiller production and early biomass accumulation. Further study using cultivars with contrasting plant types from the same germplasm group is needed to resolve the question of the relationship between plant erectness and WSA.

Vegetative crop biomass Vegetative crop biomass (CB4, CB9) was closely correlated with early height (≤ 4 WAS), tiller number, vigour ratings, and GC6 (Table 3), supporting the greenhouse study by Caton et al. (2003). Weed-free CB4 and CB9 were positively correlated with YLD_W, and negatively with weed growth (Table 1), indicating their predictive power and usefulness as indirect selection criteria for WC. Other studies also have shown the importance of vegetative crop biomass in determining WC in rice (Pons, 1979; Ni et al., 2000) and wheat (Lemerle et al., 1996; Cousens et al., 2003). However, the *H*, genetic correlation and ISE for CB4 and CB9 were all smaller than for VV4, indicating that the accuracy of biomass sampling is lower than that of visual biomass rating. This was probably due to the smaller area (0.5 m^2) sampled for crop biomass measurements than for visual vigour ratings, which were scored based on the entire plot (4.5 m^2). Additionally, sampling biomass is destructive and labour-intensive and cannot be done when plot size is small (e.g., a single row). Therefore, visual biomass rating (vigour) appears to be superior to biomass sampling as selection criterion for WC in aerobic rice.

Flowering, duration, and harvest traits Flowering and duration estimated in the 2003 weed-free trial were seldom correlated with YLD_W and weed growth (Table 1). This result is similar to the results of multi-year trials reported by Zhao et al. (2006a), and indicates the low predictive ability of these traits with respect to WC. Although the yield, HI and final crop biomass measured in the weed-free environment in 2003 all were related to YLD_W, WB_W, and WR_W (genetic correlation of HI with WB_W was not significant), weed-free yield was more heritable, more closely correlated with YLD_W and weed growth, and had greater ISE. Thus, weed-free yield seems to be more suitable than weed-free final crop biomass or HI as an indirect selection criterion for WC.

Cultivar duration, ranging from 89 to 117 days in this study, was not associated with vegetative traits under either weed-free or weedy conditions (except for a small correlation with HT6 under weedy conditions) (Tables 3 and 4), indicating that effectiveness of indirect selection on vegetative traits for WC may not be influenced by the duration of lines.

Relationship between weed competitiveness and growth patterns There were positive correlations of CB4 with HR4, TN4, and TN8 and negative correlations of CB4 with HR6 under weed-free conditions (Table 3). These relationships indicate that there were two main patterns of early growth among the cultivars used in this study. Some cultivars had greater HR4 and accumulated greater crop biomass at 4 WAS, resulting from both greater height and more tillers, but they decreased their height growth rate during 4 – 6 WAS while continuing to tiller. Other cultivars had greater HR6, produced less crop biomass by 4 WAS, and tended to produce taller plants with fewer tillers (correlations of HR6 with TN4 and TN8 were −0.41 and −0.45, respectively) (Table 3). These results indicate that more vigorous cultivars grew faster both in height and tillering during ≤ 4 WAS, but slowed their height growth rate to enhance their tillering during 4 – 6 WAS (the period of maximum tiller production), and consequently produced greater biomass and yield while suppressing weeds more (Tables 3 and 4). Relationships of HR with YLD_W, WB_W and WR_W further indicate that greater HR during ≤ 4 WAS was closely related to both greater yield and less weed growth, while greater HR6 was associated with lower yield and more weed growth (although not significantly) (Table 1). The correlations, positive between E3 and HR4 but negative between E3 and HR6 under both weed regimes (Tables 3 and 4) indicate that erect cultivars (mainly *indica*) in this study belong to the first group. In summary, there may be two contrasting growth patterns relating to WSA and yield for aerobic rice: (1) a competitive pattern, characterized by rapid early growth in both height and tillering before 4 WAS, relatively slow growth in height but fast growth in tillering during the maximum tillering stage (4 – 6 WAS) and (2) an uncompetitive pattern, characterized by slow growth in both height and tillering before 4 WAS, relatively fast growth in height but slow growth in tillering during the maximum tillering stage.

Predicting weedy yield and weed biomass with single-year weed-free traits

To predict YLD_W with a single weed-free independent variable, model Y1, using YLD alone, was the best (R^2 = 0.86), followed by model Y2 with VV4 alone (R^2 = 0.57); HT4 alone was a poor predictor of YLD_W (Table 5). By adding a second independent variable VV4 or HT4 to YLD, prediction of YLD_W was slightly but significantly improved (R^2 = 0.89, models Y4 and Y5). The model including all the three independent variables did not further improve prediction of YLD_W (data not shown) These results indicate that weed-free yield alone, measured from a single three-replicate trial, was effective in predicting weedy yield estimated over three years; adding early vigour (VV4) or early height (HT4) to weed-free yield slightly but significantly enhanced the prediction in about the same degree.

To predict WB_W, the models with weed-free independent variable VV4 alone (R^2 = 0.46, model W2) and HT4 alone (R^2 = 0.43, model W3), respectively, were the best two single-parameter models; YLD was poorer in predicting WB_W (Table 5). Adding YLD to HT4 improved the prediction of WB_W (R^2 = 0.55, model W5), but adding YLD to VV4 did not (model W4). The model including all the three independent variables did not further improve the prediction of WB_W (data not shown). These models indicate that the combination of YLD and HT4 was the most effective way to predict weed biomass, and that using VV4 or HT4 alone could predict weed growth fairly well. However, predicting weed biomass was much less efficient than predicting yield under weed competition.

This research shows that single-year estimates of vegetative traits and grain yield from weed-free trials were efficient in predicting the multi-year means of the target traits YLD_W and WB_W, indicating that selection for WC on a single-year basis may be effective. To achieve the goal of improving both yielding ability and WSA under moderate weed competition, YLD and HT4, or YLD and VV4 may be used in combination for indirect selection. For easy use, the latter combination may be a more practical option without much loss in selection efficiency for WSA (Table 5) because visual vigour rating is much cheaper and quicker than height measurement. However, in case of failure to take appropriate vigour ratings (e.g., due to emergence problems), height measurements at the early seedling stage may be substituted. A selection strategy based on independent culling levels (Bernardo, 2002) for early vegetative vigour

Table 5. Regression models for predicting cultivar means for weedy yield (YLD_W) and weed biomass (WB_W) estimated over three years (2001 – 2003) using means for weed-free traits from 2003 trials, IRRI, Los Baños, Philippines.

Model	Dependent variable	Regression coefficient and standard error for independent variable			Intercept	R^2
		YLD† (Mg ha^{-1})	VV4 (score)	HT4 (cm)		
Y1	YLD_W (Mg ha^{-1})	0.47 ± 0.03**	-	-	0.06 ± 0.09^{ns}	0.86
Y2	YLD_W (Mg ha^{-1})	-	0.19 ± 0.03**	-	0.45 ± 0.13**	0.57
Y3	YLD_W (Mg ha^{-1})	-	-	0.06 ± 0.02**	–1.12 ± 0.75^{ns}	0.22
Y4	YLD_W (Mg ha^{-1})	0.38 ± 0.04**	0.06 ± 0.02**	-	0.01 ± 0.08^{ns}	0.89
Y5	YLD_W (Mg ha^{-1})	0.44 ± 0.03**	-	0.03 ± 0.01**	–0.82 ± 0.29**	0.89
W1	WB_W (g m^{-2})	–19.69 ± 4.91**	-	-	235.45 ± 14.12**	0.30
W2	WB_W (g m^{-2})	-	–12.49 ± 2.19**	-	237.96 ± 10.71**	0.46
W3	WB_W (g m^{-2})	-	-	–6.50 ± 1.21**	426.47 ± 45.51**	0.43
W4	WB_W (g m^{-2})	–5.92 ± 5.79^{ns}	–10.47 ± 2.95**	-	244.84 ± 12.64**	0.48
W5	WB_W (g m^{-2})	–13.34 ± 4.20**	-	–5.31 ± 1.15**	417.16 ± 40.98**	0.55

*, **, and ns indicate significance at $P < 0.05$, $P < 0.01$ and $P > 0.05$, respectively, for regression coefficients; in case of multiple regression the test is for each independent variable added last.

† YLD, VV4 and HT4 indicate weed-free yield, crop vigour and plant height at 4 weeks after sowing, respectively.

and yield may be efficient. Selection may first be conducted for vegetative vigour or height early in the season, followed by yield evaluation only of those entries exhibiting a high rate of early growth. This strategy has been adopted by the IRRI aerobic rice breeding programme in its preliminary replicated evaluation of new breeding lines.

Because crop development is influenced by many factors such as temperature, fertilization, water, light etc., it should be noted that the time to measure the vegetative trait VV4 or HT4 may not be fixed at 4 WAS. According to the present study, VV4 or HT4 correspond to the early tillering stage, i.e., when there are three tillers per plant including the main stem. This appears to be the appropriate stage for vigour ratings and height measurements.

It must also be noted that the selection protocols developed for aerobic rice in the present study apply to a population of diverse genotypes, with clear differences in traits among cultivars. Their applicability in a narrower population of progenies from crosses among parents with similar growth characters is not known and requires further study. However, in wheat, significant genetic variation among lines within an F_3 population was detected in a number of aspects of plant growth including weed-free yield, and selection for WC in the F_3 generation was demonstrated to be effective (Mokhtari et al., 2002). Our conclusions apply to a tropical aerobic environment with moderate weed pressure. Whether or not they will change with changes in abiotic or biotic factors is unknown. However, because weed management × genotype interactions are reported to be limited (Gibson et al., 2003; Zhao et al., 2006a), it seems likely that our results will be widely applicable to aerobic rice target environments.

Several studies also reported the effective prediction of WSA using weed-free vegetative traits, including crop biomass at 5 WAS for lowland rice (Ni et al., 2000), early leaf area for lowland rice (Gibson et al., 2003), plant height at seven weeks after emergence for soybean (Jannink et al., 2000) and early tillering and height for wheat (Lemerle et al., 1996). However, the present study found that the nondestructive early vigour rating together with weed-free yield may serve as indirect selection criteria for selecting lines with both great yielding ability under competition and WSA simultaneously. The importance of early traits (vigour, height and height growth rate) in determining the final harvest traits (yield and weed biomass) shown in these studies is supported by Cousens et al. (2003), who found that the species achieving the greater biomass early on remains the better competitor throughout growth.

CONCLUSIONS

This study aimed to provide breeders with practical information on how to select efficiently for weed-competitive aerobic rice. We found that aerobic and upland rice upland cultivars perform relatively consistently across different weed regimes in both vegetative and harvest traits. Therefore, indirect selection based on traits under weed-free conditions for yield under competition and WSA is feasible. Selection on vegetative traits such as early crop vigour, early height, height growth rate, tiller number, crop biomass and canopy ground cover under weed-free conditions should all be effective in improving both yielding ability and WSA under weedy conditions, because all of these traits were positively correlated with yield under competition and negatively with weed biomass, and all were moderately or highly heritable. However, selection based on weed-free yield together with one vegetative trait, VV4 or HT4, is likely to be the best option for most breeding programmes. Each of these combinations explained 89% of the variation in yield under weed competition and above 48% of the variation in weed biomass. Using crop vigour as an indirect selection criterion may make selection for WC simple and practical because visual vigour rating can be done easily, quickly, and inexpensively, and does not require a large plot for measurement. Early height is also a useful criterion, particularly when visual vigour rating is not possible. Weed-free yield is the most important selection criterion for yielding ability under competition.

A noteworthy finding in this study was that erect genotypes had greater vigour, quicker early growth, greater yield under competition, and stronger WSA than droopier genotypes. The erectness differences among cultivars were associated with two distinct growth patterns that may help breeders to distinguish between strong and weak competitive cultivars/lines. Strongly competitive cultivars tend to be erect and grow faster in height and tiller number before 4 WAS; weakly competitive cultivars tend to be droopy and grow faster in height but not in tiller number during maximum tiller stage.

CHAPTER 4

Comparing rice germplasm groups for growth, grain yield, and weed-suppressive ability under aerobic soil conditions[1]

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Abstract

Germplasm and cultivars need to be selected as parents for breeding weed-competitive aerobic rice in the tropics. Forty rice (*Oryza sativa* L.) cultivars belonging to the *aus*, *indica* and tropical *japonica* germplasm groups, or derived from crosses among them, were evaluated in adjacent weed-free and weedy trials in aerobic soil conditions during the wet seasons of 2001 – 2003. The objectives of this study were to assess vegetative growth, grain yield under weed-free (Y_F) and weedy (Y_W) conditions, and weed-suppressive ability (WSA) of different germplasm groups. In the first four weeks after sowing, *indica* cultivars had fast growth in height, tillering and crop biomass. They also had high Y_F, Y_W, and strong WSA. *Aus* cultivars were similar to the *indica* types in early growth and WSA, but were poor in Y_F. Tropical *japonica* groups, and the group derived from *indica/*tropical *japonica* crosses, were generally inferior to *aus* and *indica* groups in early growth and WSA, and both of their Y_F and Y_W were lower than that of the *indica* group. Therefore, *indica* germplasm seemed to be most suitable for breeding high-yielding, weed-suppressive aerobic rice for the tropics. The relationship of WSA with various traits within tropical *japonica* germplasm revealed that fast early growth rather than plant erectness is crucial to WSA.

Keywords: Crop vigour; Weed competition; Plant erectness; Rice germplasm; Vegetative growth; Yield

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INTRODUCTION

The present food security of Asia depends largely on the irrigated rice production system, which supplies more than 75% of the rice production (Tuong et al., 2004). This rice system requires two to three times more water to produce the same amount of grain than those producing other cereals. In Asia, the amount of water used to irrigate rice fields accounts for about 50% of all diverted freshwater (Barker et al., 1998). There is evidence that water scarcity is already widespread in rice-growing areas, where rice farmers need technologies to cope with water shortage and ways must be sought to grow rice with less water (Tuong and Bouman, 2003). One approach to reducing water inputs in rice is to grow the crop as an upland crop such as wheat or maize, on nonpuddled aerobic soil without standing water. Traditional upland rice cultivars are grown this way, but their yield potential is low. High-yielding lowland cultivars show a severe yield penalty when grown under aerobic conditions (Tuong et al., 2004). New cultivars with high yield and responsiveness to inputs in aerobic conditions, termed ‘aerobic rice’ at the International Rice Research Institute (IRRI) (Bouman, 2003), need to be developed. Evidence for the feasibility of breeding for such aerobic rice comes from China and Brazil (Bouman, 2003), where the improved rice cultivars yield moderately high (6 – 7 Mg ha^{-1}) (Wang et al., 2002) under favourable aerobic conditions.

Upland or aerobic rice systems are subject to much higher weed pressure than lowland rice because direct-seeded rice sown under aerobic conditions germinates together with weeds, eliminating the ‘head start’ of transplanted seedlings, and because, in contrast to lowland systems, aerobic rice systems have no standing water layer to suppress weeds (Moody, 1983; Balasubramanian and Hill, 2002). Weeds are perceived to be the greatest yield-limiting constraint to aerobic and upland rice, contributing about 50% to yield gaps, followed in importance by nitrogen deficiency, pests, and diseases (WARDA, 1996). Hand-pulling or tool-aided weeding is labour-intensive and thus expensive (Roder, 2001). Many rice farmers rely on herbicides to control weeds, but intensive herbicide use can cause environmental contamination and the development of herbicide resistance (Fischer et al., 1993; Carey et al., 1995; Lemerle et al., 2001b). Solving severe weed problem in aerobic rice fields while alleviating environment and labour cost concerns may be achieved by adopting strong weed-competitive cultivars, which is regarded as a promising approach to weed management (Pester et al., 1999; Fischer et al., 2001; Lemerle et al., 2001b).

Weed competitiveness (WC) is defined as the ability of a crop to suppress (WSA) and tolerate weeds (WT) (Jannink et al., 2000). Cultivar WSA is determined by measuring weed biomass in a weedy environment, however, cultivar WT can only be assessed by comparing grain yields of cultivars with the same yield potential and WSA in a weedy environment (Gibson and Fischer, 2004). Jannink et al. (2000) and Jordan (1993) advocated breeding for WSA over WT because suppressing weeds reduces weed seed production and benefits weed management in the long term, while tolerating weeds only benefits yield in the current growing season, and may result in increased weed pressure from unsuppressed weeds in consecutive seasons. However, strong WSA does not guarantee high yield under weed competition if the yield potential is low (Zhao et al., 2006a; Chapter 2). Therefore, aerobic rice breeding should aim to improve both yielding ability and WSA under aerobic conditions. A trade-off between yield and WC was reported by earlier researchers (Jennings and Aquino, 1968; Jennings and Jesus, 1968; Jennings and Herrera, 1968; Kawano et al., 1974), but recent studies suggest that high yield and strong WC may be combined (Garrity et al., 1992; Ni et al., 2000; Fischer et al., 2001; Gibson et al., 2003; Zhao et al., 2006a).

A large genetic variation in WC has been found in aerobic and upland (Garrity et al., 1992; Zhao et al., 2006a) and lowland rice (Fischer et al., 1997; Gibson et al., 2003; Haefele et al., 2004), between *indica* and *japonica* (Oka, 1960), and between *O. glaberrima* and *O. sativa* (Johnson et al., 1998; Dingkuhn et al., 1999; Fofana and Rauber, 2000). These studies suggest that differences in WC exist between and within rice subspecies or ecotypes. Asian cultivated rice (*O. sativa*) is classified using isozymes by Glaszmann (1987) into six varietal groups I – VI, sequentially correspondent to *indica*, *aus*, *ashina*, *rayada*, *aromatic* and *japonica* varietal groups, respectively. Recently, it is differentiated using simple sequence repeats and chloroplast sequences by Garris et al. (2005) into *indica*, *aus*, *aromatic*, temperate *japonica*, and tropical *japonica* groups. These studies demonstrate the genetic diversity within *O. sativa* subspecies. However, knowledge on WC for these germplasm groups is very limited, especially for the *indica*, tropical *japonica*, *aus* and their progenies which are extensively used in aerobic and upland rice breeding programmes for the tropics. Research on their WC would give guidance to plan crosses aimed at aerobic systems.

Weed competitiveness is often linked to plant height (Garrity et al., 1992), tiller number (Fischer et al., 1997), early height growth (Caton et al., 2003), early crop biomass (Ni et al., 2000), leaf area index (Dingkuhn et al., 1999), specific leaf area (Audebert et al., 1999), canopy ground cover (Lotz et al., 1995), and early vigour (Zhao et al., 2006a, b; Chapters 2 and 3). There are conflicting reports on the effect of plant type (droopy or erect) on WC. In a study of a mixed population including *O. sativa indica*, *japonica*, *O. glaberrima* and the progenies of *O. sativa* × *O. glaberrima*, Dingkuhn et al. (1999) reported that the droopy plant type was more weed-suppressive. However, Zhao et al. (2006b) studied another mixed population composed of *indica*, tropical *japonica*, *aus* and their progenies, and concluded that erect plant type tended to be more weed-suppressive. To separate the effect of plant type on

WSA from germplasm, research using cultivars with contrasting plant types within the same germplasm group is necessary.

The objectives of this study were (1) to evaluate and characterize different germplasm groups with respect to yield, WSA and other relevant vegetative traits, using cultivars and breeding lines that have been used in IRRI's aerobic rice breeding programmes, and (2) to elucidate the relationship between plant type and WSA. The current study presents a detailed analysis of germplasm group differences, and of the relationships of vegetative traits with WC-related traits within the tropical *japonica* germplasm group.

MATERIALS AND METHODS

Germplasm and groups

Forty aerobic and upland rice cultivars, used as parents in IRRI's aerobic rice breeding programme, was evaluated in this study. The genotypes have a wide range in height, duration, and plant type, and belong to different germplasm groups (*indica,* tropical *japonica, indica*/tropical *japonica, aus, indica*/tropical *japonica*/*aus* and *aus*/tropical *japonica*) according to the Glazsmann (1987) classification. Both traditional and improved cultivars were included. For data analysis, we combined all the genotypes into six germplasm groups based on germplasm and plant height, as shown in Table 1. The *aus* group included three cultivars containing *aus* germplasm in their pedigree: Aus 196, Vandana (C22/ Kalakeri) and IR70358-84-1-1 (IRAT 216/ Vandana) being of 100, 50 and 25% *aus* pedigree, respectively. The *indica* group included seven predominantly *indica* cultivars. The *indica*/tropical *japonica* group included seven cultivars derived from *indica* × tropical *japonica* crosses at the African Rice Center, the International Center for Tropical Agriculture and IRRI. Three *japonica* groups, classified based on plant height, were the tall, medium and short groups including six, ten and seven tropical *japonica* cultivars, respectively.

Trial management and data collection

Weed competition trials

The trials were carried out on the IRRI upland farm (14°13' N, 121°15' E, 23m elevation), Los Baños, Philippines, in the wet seasons of 2001 – 2003. The soil type was a Maahas clay loam. The field conditions and management of these trials were described in detail in Zhao et al. (2006a). Briefly, fields were fallowed during the dry seasons allowing the natural weeds to grow before land preparation, and ploughed, harrowed, levelled and furrowed before sowing. Two adjacent trials, weed-free and

Table 1. Means under weed-free conditions in 2003 for traits of aerobic rice cultivars (*O. sativa*) classified according to Glaszmann (1987) germplasm classification and final plant height.

Group	Cultivar	Variety type	E3† (1-to-9 score)	V4 (1-to-9 score)	CB4 (g m^{-2})	HT4 (cm)	HR4 (cm d^{-1})	TN4 ($plant^{-1}$)	TN8 ($plant^{-1}$)
Aus	AUS 196	traditional	5.0	5.6	50.2	38.6	1.1	2.8	5.7
(> 25% *aus*	IR70358-84-1-1	improved	5.0	7.7	59.8	43.7	1.3	4.7	9.6
pedigree)‡	Vandana	improved	7.7	7.8	59.9	43.2	1.4	3.8	10.0
(110–120 cm) §									
Indica	B6144F-MR-6-0-0	improved	5.0	6.4	52.5	43.3	1.3	3.7	11.5
(predominantly	CT6510-24-1-2	improved	7.0	8.3	68.0	41.5	1.2	3.7	10.9
indica pedigree)	IR55419-04	improved	7.7	7.0	51.2	38.5	1.0	4.0	10.3
(110–120 cm)	IR55423-01	improved	9.0	6.8	55.8	37.9	0.9	3.8	9.1
	UPLRi-5	improved	5.7	6.3	51.2	36.0	1.2	3.6	11.2
	UPLRi-7	improved	7.0	6.5	56.2	37.5	0.8	3.9	10.7
	Way Rarem	improved	7.0	7.0	69.4	44.5	1.3	3.5	8.7
Indica/japonica	CT13370-12-2-M	improved	2.3	2.3	38.2	33.3	0.4	3.0	5.6
(derived from	CT13382-8-3-M	improved	4.3	2.3	32.2	29.8	0.6	3.0	5.2
indica ×	CT6516-24-3-2	improved	4.3	4.4	47.3	36.5	0.7	3.1	6.2
tropical	IR65907-116-1-B	improved	1.7	2.4	31.8	31.9	0.8	2.8	5.8
japonica)	IR66421-062-1-1-2	improved	1.0	1.7	24.0	32.4	0.6	2.4	5.8
(105–120 cm)	IR66424-1-2-1-5	improved	7.7	7.7	56.8	40.1	0.9	4.7	10.9
	IR71525-19-1-1	improved	1.7	2.3	38.6	34.7	0.5	3.7	6.3
Tall *japonica*	Azucena	traditional	1.0	4.4	30.9	39.1	1.2	2.7	5.6
(tropical	Dinorado	traditional	1.7	5.1	29.2	40.7	1.2	2.5	5.5
japonica)	IR65261-09-1-B	improved	3.0	5.0	56.7	46.1	1.5	2.5	6.0
(130–155 cm)	IR68702-072-1-4-E	improved	3.0	2.9	35.3	33.3	0.7	2.1	5.3
	Palawan	traditional	2.3	4.4	37.7	38.4	0.9	2.4	5.6
	WAB638-1	improved	5.0	1.6	19.8	36.8	1.0	2.5	6.3
Medium	C22	improved	5.7	7.6	65.3	41.6	1.1	3.4	9.9
japonica	IR47686-30-3-2	improved	8.3	7.7	59.3	42.3	1.2	4.3	13.3
(tropical	IR60080-46A	improved	1.0	3.5	35.3	36.6	0.8	3.2	5.9
japonica)	IR66417-18-1-1-1	improved	3.7	1.7	31.8	30.6	0.6	2.7	6.8
(120–125 cm)	IR71524-44-1-1	improved	3.0	3.1	34.0	35.8	0.7	2.8	6.6
	IRAT 170	improved	1.7	2.3	27.1	31.4	0.7	3.0	6.2
	IRAT 177	improved	2.3	4.1	42.4	37.4	1.1	3.8	8.0
	Maravilha	improved	3.7	2.9	30.1	35.6	0.8	2.6	5.1
	Primavera	improved	3.0	1.7	32.5	41.9	1.2	2.6	5.0
	WAB96-1-1	improved	4.3	3.7	41.0	39.1	0.8	2.9	5.7
Short	CT13377-4-2-M	improved	3.0	1.0	30.6	33.5	0.8	2.8	7.4
japonica	IR70360-38-1-B-1	improved	8.3	5.0	41.9	35.2	0.7	3.8	11.3
(tropical	IR72768-15-1-1	improved	1.0	3.1	40.4	35.6	0.6	2.7	5.9
japonica)	IRAT 212	improved	1.7	3.0	51.0	34.1	0.7	3.0	6.5
(90–115 cm)	IRAT 216	improved	3.0	3.1	29.5	35.3	0.8	3.4	6.3
	WAB181-18	improved	5.0	3.1	34.3	36.2	0.7	3.0	4.8
	WAB56-125	improved	5.7	3.7	36.6	37.3	1.0	3.6	5.6

† E3 and V4 indicate plant erectness at 3 week after sowing (WAS) and crop vigour at 4 WAS, respectively, both rated on a 1-to-9 scale (1 = droopiest (least for V4), 9 = most erect (greatest for V4)); CB4, HT4 and HR4 indicate crop biomass, plant height and height growth rate at 4 WAS, respectively; TN4 and TN8 indicate tiller number per plant at 4 and 8 WAS, respectively;

‡ pedigree of germplasm;

§ final plant height range of cultivars under weed-free environments within a germplasm group.

weedy, arranged in α-lattice design with three replications each, were direct-seeded in dry, nonpuddled soil on the same field within each year. Cultivars were manually drilled in plots sized 4.5 m^2 with six 3 m-long rows spaced 25 cm apart. Sowing dates were 12 July 2001, 5 July 2002 and 8 July 2003, respectively. The seeding rate for each cultivar was 300 viable seeds m^{-2}. Immediate sprinkler-irrigation after sowing was conducted to insure uniform establishment. The weed-free trial was treated with pre-emergence herbicide Ronstar (oxadiazon) at the recommended rate one day after irrigation, and was kept weed-free throughout the growing season by hand. The weedy trial was completely hand-weeded once at 3 weeks after sowing (WAS) in 2001 and 2002, respectively, or treated with post-emergence herbicide Nominee (bispyribac sodium) once at 2 WAS instead of hand-weeding in 2003. Weeds were allowed to grow thereafter.

A compound N-P-K fertilizer (14:14:14) was broadcast before furrowing at the rate of 200 kg ha^{-1}; additionally two applications of urea were top-dressed each at the rate of 60 kg ha^{-1} at 4 and 8 WAS, respectively. Total N-, P_2O_5- and K_2O- fertilizer applications were 82, 28 and 28 kg ha^{-1}, respectively. The field was kept under nonsaturated aerobic conditions throughout the growing season. Trials were primarily rainfed, but supplemental surface-irrigation was applied on a few occasions when crop leaves started to roll due to drought stress. Drainage was conducted whenever heavy rains resulted in ponding. Insecticide and fungicide were applied following standard practices as required.

The following crop data were collected from both the weed-free and weedy trials over three years:

- crop vigour, recorded as visually rated crop biomass at 2 WAS on a per-plot basis on a 1-to-9 scale, where 9 was the greatest crop biomass and 1 was the least;
- date of flowering, measured as the date at which 50% of plants in a plot started to flower;
- date of maturity;
- final plant height, measured at harvest as the distance from soil surface to the panicle tip of three random plants;
- final crop biomass, expressed as the dry weight (70°C for 5 d) of above-ground plant per square meter of ground area, extrapolated from a random sample of 0.25 m^2 harvested at soil surface at maturity in each plot;
- harvest index (HI), measured as the proportion (percentage) of filled grain to the total above-ground biomass sample in dry weight; and
- grain yield, harvested from each plot, dried (50°C for 3 d) and adjusted to a moisture content of 14%.

The following data were collected from weedy trials over three years:

- weed species;
- weed biomass, clipped at the soil surface from a random area of 0.5 m^2 in each plot at 13 WAS, dried (70°C for 5 d) and weighed; and
- weed rating, visually rated weed biomass before weed biomass sampling on the same scale as crop vigour rating.

In 2003, more plant traits were measured from weed-free and weedy trials:

- crop seedling height, measured from soil surface to the tip of the longest extended leaf of six random plants in each plot at 3, 4, 6, and 9 WAS;
- height growth rate, the increase of plant height per day (cm d^{-1}), based on the height measurements with an assumption that emergence of all tested cultivars occurred at 5 days after sowing;
- crop vigour, visually rated crop biomass at 4 and 6 WAS, respectively, on a 1-to-9 scale as described above;
- plant erectness, visually rated also on a scale of 1-to-9 with 9 as the most erect and 1 as the most droopy type (9, 7, 5, 3 and 1 represent > 80%, 50 – 80%, 50%, 30 – 50% and < 30% nearly vertical leaves of plants, respectively), at 3 (both trials), and 6 (weed-free trial only) WAS;
- canopy ground cover, the proportion (percentage) of the green area to total area in a photograph taken using a canopy digital camera (First Growth, Model +1G, Decagon Devices, Inc.) at a distance of 1.5 m vertically and 1 m horizontally from the closer edge of the shooting area at 6 WAS in the weed-free trial only; and
- crop biomass, dry weight of a random sample of 0.5 m^2 harvested at soil surface in each plot at 4 (weed-free trial) and 9 (both trials) WAS.

Tillering trial

A separate trial with the same cultivar set and experimental design was carried out adjacent to the weed competition trials to study cultivar tillering ability. Sowing date was 8 July 2003. Each cultivar was drilled in a single 3-m row and thinned at 2 WAS to a single plant per hill. Hills were spaced 5 cm apart within rows; row spacing was 25 cm. The experimental management including weed control, fertilization, irrigation and insecticide application was the same as the weed-free competition trial. Tiller number was determined for 20 plants from a random 1 m row at 4 and 8 WAS, respectively. Tiller number per plant at 4 and 8 WAS was used to indicate cultivar tillering ability.

Data analysis

Combined data analysis

To test for the presence of germplasm group × weed management interaction, a combined analysis for the traits collected over three years and weed management treatments was conducted using SAS Release 8.2 (TS2M0) (SAS Institute Inc. 1999-2001). For this analysis, groups, genotypes within groups and weed management treatments and their interaction were considered fixed, while years, replicates nested within year × weed management combinations, and blocks within replicates were considered random. Random effects for interactions between year and the fixed effects were also added to the model. Preliminary analysis proved that residual error terms within individual trials were heterogeneous for all characters except HI. The combined analysis was therefore conducted using a mixed model that does not assume equal within-trial residuals. Using the METHOD = REML option of the MIXED procedure, non-homogeneous within-trial variances were specified by the REPEATED/GROUP statement. Scaled Wald tests of fixed effects, distributed approximately as F, were done using the DDFM = KR option of the MODEL statement, which uses the Kenward-Rogers version of the Satterthwaite approximation to estimate degrees of freedom. Least square means of germplasm groups within and between weed management treatments were compared by using PDIFF option in the LSMEANS statement. Although the multi-year trials were heterogeneous, variance components analysis showed that variances for year × germplasm group and year × germplasm group × weed management were small relative to those for group (data not shown). Therefore, it is reasonable to compare the multi-year means of germplasm groups.

To gain insight of the relationships of vegetative traits with weedy yield and weed growth within a germplasm, a separate analysis for the subset of tropical *japonica* was conducted. Variance components were estimated for all the 23 *japonica* cultivars within weedy environments over three years using the REML option of the VARCOMP procedure, which considers all factors to be random. These variance component estimates were used in estimating predicted heritability (not shown) for weedy yield, weed biomass and weed rating following Nyquist (1991), The heritabilities estimated here together with those estimated for the single-year traits as below were used to estimate the genetic correlations described later.

Analysis of 2003 data

The data collected in 2003 for the plant traits from the weed competition and tillering trials were separately analysed using the appropriate MIXED model for α-lattice designs to estimate group and cultivar means. Variance components for the vegetative traits for the *japonica* subset from the weed-free and tillering trials were also estimated using the REML option of the VARCOMP procedure. Heritabilities (not shown) of these traits were calculated following Nyquist (1991).

Phenotypic and genetic correlations

To determine the relationships of plant erectness and other vegetative traits with WSA and yield under competition within a germplasm, phenotypic correlations of the vegetative traits measured on the tropical *japonica* subset in the weed-free environment in 2003, with yield, weed biomass and weed rating measured in the weedy environment, were calculated on the basis of cultivar means over replicates for the vegetative traits, and over years for the latter three weedy traits. Their corresponding genetic correlations were estimated (Cooper et al., 1996) as:

$$r_{G12} = \frac{r_{P12}}{\sqrt{H_1 \times H_2}} \tag{1}$$

where r_{G12}, r_{P12}, H_1 and H_2 are genotypic correlation between traits 1 and 2 , phenotypic correlation between the same trait pair, and the heritabilities of traits 1 and 2, respectively.

RESULTS AND DISCUSSION

Weed pressure and effects of weed competition

Twenty-two weed species, out of which six were predominant over years, were found in the experimental fields as reported earlier (Zhao et al., 2006a). The weed biomass in weedy trials varied among the three years, being 305 g m^{-2} in 2001, 172 g m^{-2} in 2002 and 73 g m^{-2} in 2003, due to different weed seedbanks among fields or after-effects of herbicide residues (Zhao et al., 2006a). Weed competition reduced the final crop biomass by 35 to 49%, HI by 21 to 38%, and yield by 22 to 52% among the tested groups averaged over three years (Table 2). However, because the experimental design aimed to study the germplasm group and the germplasm group × weed management effects, but not weed management effect, degrees of freedom for testing weed management effect were only 2, the substantial differences between weed-free and weedy managements in HI and yield for all the groups were not significant at a confidence level of α = 0.05, although they were for crop biomass (Table 3). The effect of weed management on the final plant height was relatively small, decreasing plant height by 8% on average across the six groups over three years, but a significant effect was detected for the tall *japonica* group (Table 2). Early vigour rating at 2 WAS, days to flowering and duration were not affected by weed competition (Tables 2

Table 2. Germplasm group means for traits measured over three years (2001 – 2003) under weed-free (F) or weedy (W) environment, the absolute (Diff) and percent (%) reduction due to weed competition.

Trait		*Aus*	*Indica*	*Indica/ japonica*	Tall *japonica*	Medium *japonica*	Short *japonica*
Vigour at 2 WAS[†]	F	6.4a[‡]	6.4a	5.0b	5.0b	5.0b	4.6b
(1-to-9 score:	W	7.1a	6.6a	4.3bc	4.5bc	4.9b	4.0c
1=least, 9=greatest)	Diff	–0.7^{ns}	–0.2^{ns}	0.7^{ns}	0.5^{ns}	0.1^{ns}	0.7^{ns}
Duration	F	93.7d	108.9a	102.7c	109.2a	106.1b	100.7c
(d)	W	94.3d	107.8ab	102.4c	108.6a	105.5b	101.7c
	Diff	–0.7^{ns}	1.1^{ns}	0.3^{ns}	0.6^{ns}	0.6^{ns}	–1.0^{ns}
Final plant height	F	117.8bc	115.8c	111.4d	139.6a	121.8b	106.5e
(cm)	W	111.2b	107.5b	101.8c	125.7a	110.3b	97.3d
	Diff	6.6^{ns}	8.2^{ns}	9.7^{ns}	13.8*	11.5^{ns}	9.2^{ns}
	%	5.6	7.1	8.7	9.9	9.4	8.6
Final crop biomass	F	925c	1203a	980c	1081b	1154ab	983c
($g\ m^{-2}$)	W	603bcd	740a	545cd	613bc	649b	505d
	Diff	322^{ns}	463*	436*	468*	505*	478*
	%	34.8	38.5	44.5	43.3	43.8	48.6
Harvest index	F	27.8bc	34.2a	29.8b	25.8c	29.4bc	28.8bc
(%)	W	21.4b	26.9a	18.5b	18.4b	19.5b	18.9b
	Diff	6.3^{ns}	7.3^{ns}	11.3^{ns}	7.4^{ns}	9.9^{ns}	10.0^{ns}
	%	22.7	21.3	37.9	28.7	33.7	34.7
Grain yield	F	1.86bc	3.47a	2.05bc	1.98bc	2.33b	1.81c
($Mg\ ha^{-1}$)	W	1.45b	2.15a	0.97b	1.14b	1.27b	0.92b
	Diff	0.41^{ns}	1.32^{ns}	1.07^{ns}	0.84^{ns}	1.05^{ns}	0.89^{ns}
	%	22.0	38.0	52.2	42.4	45.1	49.2
Weed biomass ($g\ m^{-2}$)	W	132.5c	143.3c	223.8a	178.4bc	184.7b	205.3ab
Weed rating (1-to-9 score; 1=least, 9-greatest)	W	2.4c	2.2c	5.4a	3.5bc	4.1ab	4.9ab

*, ns indicate significance at $P < 0.05$ and $P > 0.05$ for the difference (weed-free minus weedy), respectively;

† WAS indicates weeks after sowing;

‡ multi-comparisons among germplasm groups under the same weed management regime; terms with one or more common lowercase letter(s) in the same row were not significantly different at $P < 0.05$.

Table 3. Mixed-model analysis of the effects of weed management regime (W), germplasm group (G) and cultivars within groups [C(G)] on traits combined over three years: 2001 – 2003, IRRI, Philippines.

Source of variation	Vigour at 2 WAS†		Days to flowering		Duration		Final plant height		Final crop biomass		Harvest index		Yield		Weed biomass		Weed rating	
	F‡	P > F	F	P > F	F	P > F	F	P > F	F	P > F	F	P > F	F	P > F	F	P > F	F	P > F
Weed management (W)	0.29	0.600	0.00	0.955	0.09	0.768	4.38	0.105	8.88	0.041	2.91	0.230	4.93	0.156				
Group (G)	12.72	0.001	350.29	0.001	61.25	0.001	81.98	0.001	13.66	0.001	8.37	0.007	13.89	0.001	7.67	0.008	7.55	0.003
W×G	1.87	0.104	0.85	0.536	0.41	0.833	1.30	0.337	1.84	0.108	1.47	0.288	1.49	0.277				
Cultivar within G [C(G)]	5.76	0.001	121.45	0.001	34.72	0.001	7.63	0.001	5.88	0.001	5.24	0.001	7.62	0.001	1.49	0.084	2.31	0.002
W×C(G)	0.82	0.740	0.97	0.517	0.61	0.952	0.80	0.777	0.75	0.840	1.36	0.116	0.85	0.702				

† WAS indicates weeks after sowing;

‡ F, P > F indicate F value and probability, respectively.

and 3). Weed effects were very limited for all the vegetative traits except vegetative crop biomass measured at 9 WAS (Table 4). This may be due to the comparatively low weed pressure in 2003.

Interaction of germplasm group × weed management

There was no germplasm group × weed management interaction for any trait studied over three years (Table 3). For the vegetative traits studied in 2003, the ranks of germplasm groups changed very little across weed regimes for all the traits. Zhao et al. (2006a) reported earlier that there was little genotype × weed management interaction for agronomic traits, a conclusion drawn from the same experimental units, but without considering germplasm groups. Gibson et al. (2003) also drew a similar conclusion in lowland rice. These results suggest that it is feasible to assess, select and use elite germplasm under weed-free conditions for breeding weed-competitive aerobic rice.

Characterizing different germplasm groups

Germplasm groups differed ($P < 0.01$) in all the traits studied over three years (Table 3) and those studied in one year (F-test not shown). The germplasm groups are characterized as follows:

Aus The *aus* group was less erect than the *indica* group, but more erect than all the *japonica* and *indica*/*japonica* groups (Table 4). It had the greatest early crop vigour ratings (Table 2, Table 4), early height growth (both height and height growth rate) and early tillering during ≤ 4 WAS, vegetative crop biomass during ≤ 9 WAS and canopy ground cover (Table 4). It was the most weed-suppressive (i.e., least weed biomass) germplasm group with the shortest duration (< 95 d) (Table 2), and medium height (110 – 120 cm) (Table 1), and showed the least yield and yield components (i.e. final crop biomass and HI) reductions due to weed competition among all the groups (Table 2). However, its weed-free (Y_F) and weedy yield (Y_W) were lower than those of the *indica* group due to its low final crop biomass combined with its low HI. This germplasm may be used as a donor of early maturity and strong WSA in aerobic rice cultivar development.

Indica The *indica* group was most erect (Table 4). Very similar to the *aus* group in early vegetative growth, it also had high early crop vigour ratings (Table 2, Table 4), early height growth during ≤ 4 WAS, tillering ability at early or later stages, vegetative crop biomass during ≤ 9 WAS and canopy ground cover (Table 4). Consequently, it was as weed-suppressive as the *aus* group (Table 2). It had the greatest Y_F and Y_W due to both high crop biomass and HI under both weed regimes (Table 2). Its duration was about 110 d, two weeks longer than the *aus* group (Table 2), and height was medium (110 – 120 cm) (Table 1). This germplasm appeared to be most suitable for breeding both high-yielding and strongly weed-suppressive aerobic rice for the tropics.

Japonica The three *japonica* groups were generally inferior to both the *aus* and *indica* groups in vegetative growth (Table 4) and in WSA (Table 2), and were the same as *aus* group in Y_F and Y_W (Table 2). They were droopier, produced fewer tillers and less vegetative crop biomass and canopy ground cover (Table 4). However, the tall *japonica* group was close to *aus* or *indica* groups in early height growth during ≤ 4 WAS (Table 4) and in weed suppression (Table 2). In comparison among the three *japonica* groups, the tall *japonica* group was droopiest, and least productive in tillering (Table 4); the medium *japonica* group seemed to be most productive in Y_F while the short *japonica* group appeared to be least weed-suppressive (although not always statistically detected) (Table 2). Generally, because of the inferiority of the tropical *japonica* cultivars to *indica* in both yield and WSA, they may be less useful for breeding weed-competitive aerobic rice for the tropics.

Indica/japonica The *indica/japonica* germplasm group was similar to the short *japonica* group in vegetative growth (Table 4), and in yield and WSA (Table 2). Therefore, this germplasm may not be useful too.

Our study clearly demonstrates that the relationship between WSA and Y_F was germplasm-specific (summarized in Figure 1): the *aus* group showed strong WSA but low Y_F; the *indica* group showed both strong WSA and high Y_F; the *japonica* and *indica/japonica* groups showed both weak WSA and low Y_F. This observation suggests that there may be no trade-off between yield potential and weed competitiveness, contrary to the opinions of many authors (Jennings and Aquino, 1968; Jennings and Jesus, 1968; Jennings and Herrera, 1968; Kawano et al., 1974). Y_W seemed to be a function of Y_F and WSA: the *indica* group produced the highest Y_W might be due to its high Y_F and relatively low yield reduction caused by weeds; the *aus* group showed lower Y_W than *indica* only because of its lower Y_F, its yield reduction by weeds was the least among the groups resulting from its strong WSA; the low Y_W for the three *japonica*, and the *indica/japonica* groups, may result from both the low Y_F and weak WSA (Table 2). The stronger WSA of the *indica* group than of *japonica* is in line with Oka (1960) in lowland rice, and with Dingkuhn et al. (1999) in upland rice.

Table 4. Germplasm group means over replicates in 2003 for vegetative traits under weed-free or weedy environment.

Group	E3† (score)	V4 (score)	V6 (score)	HT3 (cm)	HT4 (cm)	HT6 (cm)	HT9 (cm)	HR3 ($cm\ d^{-1}$)	HR4 ($cm\ d^{-1}$)	HR6 ($cm\ d^{-1}$)	HR9 ($cm\ d^{-1}$)	TN4 (tillers $plant^{-1}$)	TN8 (tillers $plant^{-1}$)	CB4 ($g\ m^{-2}$)	CB9 ($g\ m^{-2}$)	GC6 (%)
	Weed-free environment															
Aus	5.9b‡	7.0a	6.4a	29.8ab	41.8a	69.3b	113.4a	1.99ab	1.29a	1.95bc	1.93a	3.8a	8.4b	57a	596a	89.6ab
Indica	6.9a	6.9a	6.4a	30.4a	39.9ab	63.4cd	97.7c	2.02a	1.08ab	1.68d	1.49b	3.7a	10.3a	58a	529a	90.0a
Indica/japonica	3.3cd	3.3b	2.9b	28.1c	34.1c	61.2d	98.1c	1.88b	0.64d	1.94c	1.60b	3.3b	6.5d	38b	409b	83.6c
Tall *japonica*	2.7d	3.9b	3.8b	29.2bc	39.1b	74.2a	109.7a	1.95b	1.09ab	2.51a	1.54b	2.4c	5.7e	35b	433b	86.3bc
Medium *japonica*	3.7c	3.8b	3.4b	29.2bc	37.2c	67.4b	104.8b	1.95b	0.91bc	2.15b	1.63b	3.1b	7.2c	40b	446b	86.7bc
Short *japonica*	4.0c	3.1b	2.9b	28.4bc	35.3d	64.0c	98.4c	1.89b	0.76cd	2.05bc	1.50b	3.2b	6.8cd	38b	450b	84.7c
	Weedy environment															
Aus	6.0b	7.6a	8.3a	29.9a	47.8a	72.9a	116.0a	1.99a	1.99a	1.80ab	1.89a	ND§	ND	ND	625a	ND
Indica	7.1a	7.3a	6.3b	30.2a	44.6b	65.1b	99.9c	2.01a	1.61b	1.46c	1.51b	ND	ND	ND	512b	ND
Indica/japonica	3.6cd	3.3b	3.6c	27.0c	37.9d	63.2b	99.9c	1.80c	1.21d	1.82ab	1.59b	ND	ND	ND	356cd	ND
Tall *japonica*	2.7e	3.6b	4.4c	27.6bc	43.7b	70.9a	113.1a	1.84bc	1.79ab	1.93a	1.84a	ND	ND	ND	321d	ND
Medium *japonica*	3.3de	3.6b	3.5c	27.9b	39.1cd	63.3b	105.4b	1.86b	1.25cd	1.73b	1.84a	ND	ND	ND	372cd	ND
Short *japonica*	4.0c	3.5b	3.8c	27.3bc	40.1c	63.1b	100.7c	1.82bc	1.42c	1.65bc	1.63b	ND	ND	ND	401c	ND

† E3 indicates plant erectness rated on a 1-to-9 scale with 1 as most droopy, 9 as most erect at 3 weeks of sowing (WAS); V4 and V6 indicate crop vigour rated on a 1-to-9 scale with 1 as lowest biomass, 9 as highest biomass at 4 and 6 WAS, respectively; HT3, HT4, HT6 and HT9 indicate plant height measured at 3, 4, 6 and 9 WAS, respectively; HR3, HR4, HR6 and HR9 indicate plant height growth rate during emergence – 3, 3 – 4, 4 – 6 and 6 – 9 WAS, respectively; TN4 and TN8 indicate tillers per plant at 4 and 9 WAS, respectively; CB4 and CB9 indicate crop biomass measured at 4 and 9 WAS, respectively; GC6 indicates canopy ground cover measured at 6 WAS;

‡ multi-comparisons among germplasm groups under the same weed regime, not significant at $P < 0.05$ between terms with one or more common lowercase letter(s) in the same column (within the same weed regime);

§ ND indicates no data.

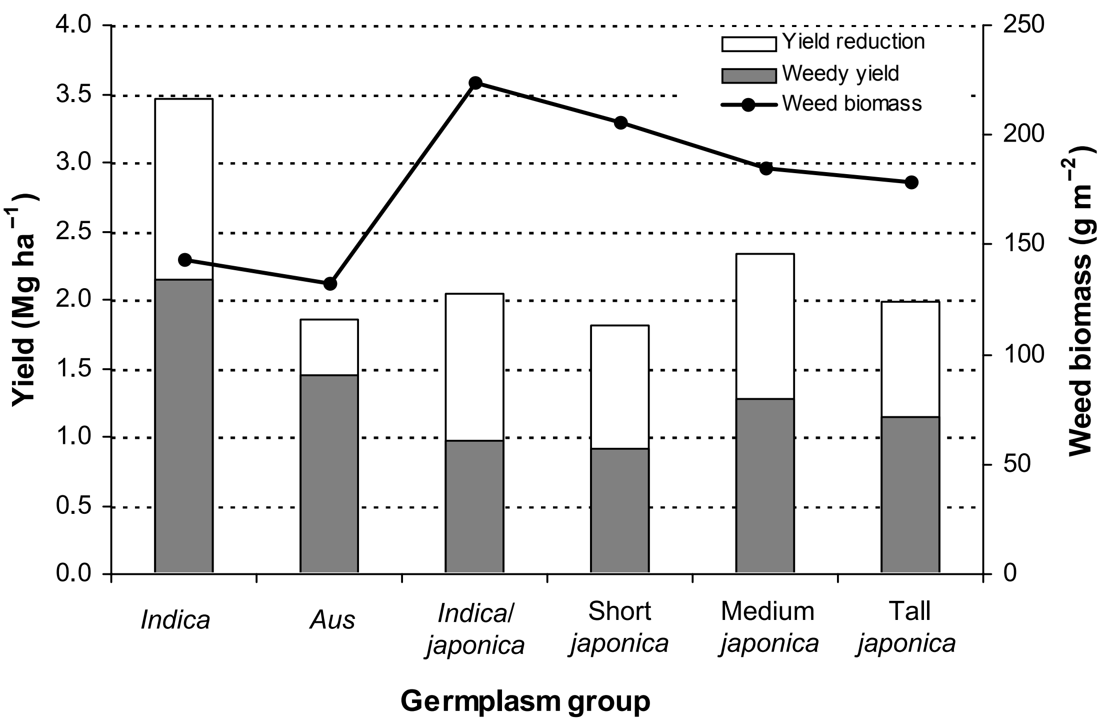

Figure 1. Weed-free yield (the whole bar), weedy yield (the shaded bar), and weed biomass (the curve) for the six germplasm groups evaluated over three wet seasons of 2001 – 2003 at IRRI, Los Baños, Philippines. LSD$_{YF}$ (0.54 Mg ha^{-1}), LSD$_{YW}$ (0.54 Mg ha^{-1}) and LSD$_{W}$ (39 g m^{-1}) are least square differences at P < 0.05 for comparisons among groups in weed-free yield, weedy yield, and weed biomass, respectively.

It should be noted that a few exceptions to the observation that *indica* lines are usually more weed-suppressive and productive than tropical *japonicas* were found in this study. C22 and IR47686-30-3-2 from the medium *japonica* group, and IR66424-1-2-1-5 from *indica/japonica* group all were similar to *aus* and *indica* groups in vegetative growth (Table 1), and had moderate to high Y_F and WSA (Zhao et al., 2006a). It also should be noted that the population tested in this study was relatively small for the *aus* and *indica* germplasm groups. Whether or not the conclusion that both *aus* and *indica* in WSA, and the latter also in yield, were superior to the other germplasm can be extended to a larger population remains unclear. However, Janiya et al. (1996) used a larger population and found that both *aus* and *indica* were superior to *japonica* in some early growth traits including height, leaf area index, tiller number and biomass, suggesting that the applicability of our results may be extended to a larger population.

Relationship of plant erectness with weed-suppressive ability and yielding ability

Within the subset of tropical *japonica* genotypes, plant erectness rated at two stages was weakly ($P < 0.10$) but negatively correlated with weed biomass and positively with weedy yield (Table 5), indicating that erect plant type tended to be more productive and weed-suppressive. This supports the conclusion drawn from the whole dataset containing different germplasm (Zhao et al., 2006b). The lack of or weak negative correlations between plant erectness and weed biomass indicate that, at the least, erect plant type is not a characteristic that negatively impacts WSA, and in fact it may enhance WSA. The fact that the *aus* and *indica* groups were both erect and superior to the droopy groups in suppressing weed growth strongly supports this point. The close relationships of early vigour ratings, early height growth and tillering, positive with weedy yield and negative with weed biomass (and weed rating) (Table 5), indicate that fast early growth, rather than plant erectness, is crucial for a cultivar to suppress weeds and sustain yield.

The droopy plant type is thought to enable a crop to cover more ground, thus suppress weed growth more than the erect type. However, crop density, row spacing, tillering ability, tiller angle, height and plant erectness may determine ground cover together. Therefore, the contribution of droopy leaves to ground cover may be very limited. Dingkuhn et al. (1999) reported that the canopies of droopy *japonica* and *O. glaberrima* did not provide more shade to weeds than those of erect *indicas* at 4.5 WAS. Audebert et al. (1999) found that the greater ground cover of *O. glaberrima* cultivars is achieved by rapid increase in the number of leaves through high tillering, but not through characteristics of individual leaves. Moreover, Gibson and Fischer (2001) found that shade alone of a crop may not prevent the weed growth due to the morphological plasticity and dry-matter allocation of weeds expressed under shading stress, and speculated that early nutrient deprivation of weeds by rice roots may be more crucial to a crop's WSA. In the present study, the erect *aus* and *indica* groups had a greater ground cover than the droopier groups, probably due to their faster early growth including stronger tillering ability (Table 4). Their faster early growth may allow them to compete more effectively for nutrients and water. These may explain why fast early growth, not plant erectness, is essential to WSA. Early root biomass also contributes to WSA (Gibson et al., 2003). Such below-ground traits were not included in our study.

Conflicting results have been reported about the relationship between plant erectness and WSA. Dingkuhn et al. (1999) in upland rice and Lemerle et al. (1996) in wheat suggested that more erect cultivars are less weed-suppressive. In contrast, Wang et al. (2004) found that erect cowpea genotypes are more weed-suppressive than semi-erect or prostrate types, and Fischer et al. (1997) reported that erect irrigated rice could

Table 5. Phenotypic (r_P) and genotypic (r_G) correlations for *japonica* cultivars (*O. sativa*) of plant traits under weed-free conditions in 2003 with grain yield, weed biomass, and weed rating under weedy conditions over three years of 2001 – 2003, IRRI, Philippines.

Trait	Yield under Competition		Weed biomass		Weed rating	
	r_P	r_G	r_P	r_G	r_P	r_G
E3‡	0.39†	0.50	–0.41†	–0.64	–0.14ns	–0.19
E6	0.27ns	0.35	–0.09ns	–0.15	–0.05ns	–0.07
V2	0.59**	0.84	–0.30ns	–0.52	–0.45*	–0.69
V4	0.80**	1.00	–0.58**	–0.97	–0.73**	–1.00
V6	0.72**	1.00	–0.47*	–0.87	–0.59**	–0.97
HT3	0.49*	0.76	–0.47*	–0.89	–0.70**	–1.00
HT4	0.46*	0.65	–0.45*	–0.77	–0.62**	–0.94
HT6	0ns	0.01	–0.06ns	–0.10	–0.25ns	–0.36
HT9	0.14ns	0.20	–0.27ns	–0.45	–0.34ns	–0.52
HR3	0.49*	0.76	–0.47*	–0.89	–0.70**	–1.00
HR4	0.32ns	0.67	–0.34ns	–0.85	–0.40†	–0.90
HR6	–0.30ns	–0.41	0.22ns	0.36	0.06ns	0.09
HR9	0.20ns	0.35	–0.29ns	–0.61	–0.22ns	–0.41
TN4	0.37†	0.49	–0.19ns	–0.30	–0.06ns	–0.08
TN8	0.69**	0.88	–0.50*	–0.77	–0.41†	–0.56
CB4	0.60**	0.89	–0.21ns	–0.38	–0.57**	–0.92
GC6	0.59**	1.00	–0.22ns	–0.45	–0.52*	–0.95

*, **, †, ns indicate significance at $P < 0.05$, 0.01, 0.10 and not significant, respectively;

‡ E3 and E6 indicate plant erectness rated on a 1-to-9 scale with 1 as most droopy and 9 as most erect at 3 and 6 week after sowing (WAS), respectively; V2, V4 and V6 indicate crop vigour rated on a 1-to-9 scale with 1 as the lowest and 9 as the greatest biomass at 2, 4 and 6 WAS, respectively; HT3, HT4, HT6 and HT9 indicate plant height measured at 3, 4, 6 and 9 WAS, respectively; HR3, HR4, HR6 and HR9 indicate plant height growth rate during emergence − 3, 3 − 4, 4 − 6 and 6 − 9 WAS, respectively; TN4 and TN8 indicate tillers per plant at 4 and 9 WAS, respectively; CB4 and GC6 indicate crop biomass and canopy ground cover measured at 4 and 6 WAS, respectively.

be strongly weed-suppressive. The different conclusions may result from the different tested crops. In our study, both fast early growth and erect plant type were closely linked to strong WSA in the *aus* and *indica* germplasm, but only fast early growth appeared important to strong WSA in the tropical *japonica* germplasm. Therefore, we assume that cultivars with fast early growth characteristics, regardless of being erect or droopy, should be weed-suppressive. The importance of fast early growth in determining WSA found in this study was also observed by others (Lemerle et al., 1996; Bastiaans et al., 1997; Fischer et al., 1997, 2001; Audebert et al., 1999; Dingkuhn et al., 1999; Jannink et al., 2000; Ni et al., 2000; Reinke, 2001; Caton et al., 2003; Gibson et al., 2003; Zhao et al., 2006b). However, a few studies on early height (Fischer et al., 1997, 2001; Dingkuhn et al., 1999) and early tillering (Garrity et al., 1992) did not show close relationships between these vegetative traits and WC.

CONCLUSIONS

High-yielding and weed-competitive aerobic rice is a promising option for coping with the increasing water scarcity in the rice-growing areas. We found that, within *Oryza sativa*, the cultivars sampled from the *aus*, *indica*, tropical *japonica* and *indica*/tropical *japonica* germplasm groups in this study differ in Y_F, Y_W, WSA, and vegetative characteristics, and that the relative performance of the germplasm groups is consistent across different weed infestation levels. This finding may assist breeders in designing crosses more effectively by selecting elite germplasm as parents, and confirms that indirect selection under weed-free environments for breeding weed-competitive cultivars is feasible.

Among the germplasm groups tested, *indica* cultivars are recommended for breeding weed-competitive aerobic rice for the tropics, because they were found to be of high Y_F and strongly weed-suppressive. Cultivars containing *aus* germplasm had short duration and strong WSA, but low Y_F. They thus may be used as donors of short duration and strong WSA. The tropical *japonica* cultivars, and the progenies of *indica* × tropical *japonica* were generally low in Y_F and WSA, so their usefulness as parents for tropical aerobic rice seems low. These results indicate that special emphasis on selection for early vegetative vigour may need to be applied in programmes that make extensive use of tropical *japonica* genotypes as parents.

One interesting finding in this study was that erect plant type is not a factor that negatively affected WSA. Plant type appeared to have much less effect than early growth on WSA. Fast early growth seems to be the most essential character of weed-suppressive cultivars.

CHAPTER 5

Effects of genotype and management on early crop vigour and weed suppression of aerobic rice

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Abstract

Water shortage in drought-prone rice-growing areas of the world is threatening conventional irrigated rice production systems, in which rice is transplanted into fields where standing water is maintained until harvest. Aerobic rice production systems, in which rice is grown as a direct-seeded upland crop without flooding, require less water than conventional systems, but the transition to aerobic rice systems is impeded by severe weed infestation. An environmentally friendly and less labour-intensive weed control method needs to be introduced to aerobic rice farmers. A study was conducted at the International Rice Research Institute in the 2003 wet season and 2004 dry season to evaluate the effects of genotype, seeding rate, seed priming and their interaction on yield and weed suppression. Three contrasting aerobic rice genotypes differing in yield and vigour were grown at three seeding rates (100, 300 and 500 viable seeds m^{-2}) with or without seed priming under two weed management treatments (weed-free and weedy) in a split-plot design. In 2004, the overall weed pressure was higher than in 2003, and consequently treatment effects in this year were more distinct than in 2003. No significant interactions among the experimental factors were found for crop yield, weed biomass, leaf area index, tiller number and vegetative crop biomass. A rise in seeding rate from 100 to 300 viable seeds m^{-2} resulted in a significant increase in yield and a significant decrease in weed biomass, whereas a further increase from 300 to 500 viable seeds m^{-2} did not result in a further improvement in both yield and weed suppression. Genotype APO had a stronger weed-suppressive ability than genotypes IR60080-46A and IRAT 216, which was related to a stronger competitive ability of individual plants and a faster canopy closure (0.5 – 6 days earlier). The weed-suppressive ability of weakly competitive genotypes could partially be compensated by a higher seeding rate. Seed priming, which was only evaluated in 2003, accelerated emergence by two days and slightly enhanced early crop growth, but had no significant effect on yield and weed suppression. The present study suggests that combining a weed-suppressive genotype with an optimum seeding rate can serve as a tool to manage weeds.

Keywords: Seeding rate; Seed priming; Vegetative growth; Weed suppression; Yield

INTRODUCTION

Water shortage is becoming severe in many rice-growing areas in the world, prompting the introduction of water-saving aerobic rice, which is direct-seeded in nonpuddled, nonflooded aerobic soil; aerobic rice systems can reduce water use in rice production by as much as 50% (Tuong and Bouman, 2003). However, direct-seeded aerobic rice is subject to more severe weed infestation than transplanted lowland rice, because in aerobic rice systems weeds germinate simultaneously with rice, and there is no water layer to suppress weed growth (Moody, 1983; Balasubramanian and Hill, 2002). Weeds in direct-seeded rice may cause yield losses up to 35% (Oerke and Dehne, 2004); they are a major hurdle to broad adoption of aerobic rice. Pre- and post-emergence herbicide may satisfactorily control weeds in rice fields (Moody, 1992), but concerns about environmental pollution and the development of resistant biotypes of weeds resulting from extensive use of selective herbicides are rising (Fischer et al., 2000; Lemerle et al., 2001b). In some rice-growing regions in the USA, where herbicides have been intensively used, herbicides are no longer effective against rice field grasses (e.g., *Echinochloa oryzoides* and *E. phyllopogon*) because of herbicide resistance (Hill and Hawkins, 1996; Fischer et al., 2000). Hand-weeding is the main technique used by traditional upland rice farmers in Asia to control weeds, but is extremely labour-intensive; upland rice farmers usually weed their fields two to three times, investing as much as 190 person-days ha^{-1} (Roder, 2001). It is not uncommon for farmers to leave their rice fields infested with weeds because of unavailability or high cost of labour (Johnson, 1996). A less chemical-dependent and less labour-intensive weed control technology is needed to enhance aerobic rice adoption while protecting the environment.

Many studies have shown that rice genotypes differ significantly in weed competitiveness, and cultivars with strong weed-competitive ability are often suggested to be a useful tool in integrated weed management (Garrity et al., 1992; Ni et al., 2000; Fischer et al., 2001; Gibson and Fischer, 2004; Zhao et al., 2006a). Studies with wheat (Blackshaw et al., 1999, 2000; Roberts et al., 2001; Mennan and Zandstra, 2005; Olsen et al., 2005), barley (O'Donovan et al., 2001), soybean (Norsworthy and Oliver, 2001), canola (Harker et al., 2003) and lowland rice (Ni et al., 2004; Phuong et al., 2005) have shown that increased seeding rates also strengthen the ability of crops to suppress weeds while increasing crop yield under weedy conditions. However, Kirkland et al. (2000) reported that at a seeding rate 50% higher than that recommended for wheat, barley, and lentil, crop yields and crop weed-suppression were not affected. Gibson et al. (2001) also reported that seeding rates for direct-seeded lowland rice had no effects on weed growth. Reports on effects of seeding rate in aerobic rice have been rarely seen. Though most of the aforementioned studies speculate that a combination of genotype and seeding rate will improve weed suppression of crop to a high extent, few studies have actually focused on genotype × seeding rate effects on grain yield and weed growth. Seed priming with water was reported to lead to early emergence, more uniform and vigorous stands, and higher grain yield in corn (Harris et al., 1999), chickpea (Harris et al., 1999; Musa et al., 2001), wheat (Harris et al., 2001), barley (Ajouri et al., 2004), and upland rice (Harris et al., 1999, 2000; Bakare et al., 2005). Therefore, seed priming may also be a practice favourable to weed management. However, to our knowledge, there have been few studies on the effect of seed priming on crop-weed competition.

It was hypothesized that combining the inherent weed-suppressive ability of rice genotypes with an appropriate seeding rate and seed priming practice could contribute to the control of weeds in aerobic rice systems. The objective of this study was to (1) assess how genotype, seeding rate, seed priming and their interactions affect weed suppression and crop yield, and (2) explore the mechanism of crop-weed competition by evaluating vegetative crop growth, including crop biomass, leaf area index (LAI) and tillering, which were assumed to be closely related to genotype, seeding rate, seed priming and weed interference.

MATERIALS AND METHODS

Field experiment

A two-year field experiment was conducted on the upland farm of International Rice Research Institute (IRRI), Los Baños (14°13’ N, 121°15’E, 23 m elevation), Philippines in the wet season of 2003 and dry season of 2004. The soil type was a Maahas clay loam (isohyperthermic mixed Typic Tropudalf). Fields were ploughed, harrowed, levelled and furrowed before sowing.

Treatments consisted of three aerobic rice genotypes (APO, IRAT 216, IR60080-46A (*Oryza sativa* L.)) sown at three seeding rates (100, 300, and 500 viable seeds m^{-2} (SR100, SR300 and SR500, respectively)) under two weed management treatments (weed-free and weedy). Seed priming (presoaked and non-presoaked) was only included in 2003. APO is a high-yielding *indica* cultivar with vigorous vegetative growth, medium stature (107 cm) and medium maturity (104 d); IRAT 216 is a low-yielding tropical *japonica,* and is less vigorous, with shorter stature (97 cm) and early maturity (98 d); IR60080-46A is a medium-yielding *japonica* with tall stature (116 cm) and medium maturity (104 d). The experimental design was a split-plot in a randomized complete block arrangement with three replications. Main plots were weed management (weed-free and weedy) and subplots were genotype × seeding rate

× priming in 2003, resulting in 108 plots, or genotype × seeding rate in 2004, resulting in 54 plots. The seed quantity for each plot was adjusted to the target seeding rates according to germination percentage (tested in Petri dishes), thousand-grain weight, and moisture content. For seed priming seeds were submerged in water for 24 hours in separate net bags, and incubated at 25ºC for another 24 hours after surface drying. About 50% of the presoaked seeds began to extrude their radicles at sowing.

Each genotype was sown (for SR100, seeds in each row were equally spaced using marked stick because of the small seed quantity) in 6 m^2 plots with eight 3 m rows spaced 25 cm apart on 28 June 2003 and 15 January 2004, respectively, and immediately sprinkler-irrigated to protect the presoaked seeds from drought and ensure uniform emergence. The 'weed-free' plots were weed-controlled throughout the growing season by an application of pre-emergence herbicide Ronstar (oxadiazon) one day after irrigation and later on by hand-weeding (in 2003), or by hand-weeding only (in 2004). The 'weedy' plots were hand-weeded once at 3 weeks after sowing (WAS) in 2003, or at 2 WAS in 2004, and weeds were allowed to grow thereafter. Hand-weeding was advanced in 2004 to create a heavier weed pressure.

A compound N-P-K fertilizer ($N:P_2O_5:K_2O$ = 14:14:14) was applied before soil tillage at a rate of 200 kg ha^{-1}; two additional splits of urea were top-dressed each at the rate of 60 kg ha^{-1} at 4 and 8 WAS, respectively. Total N, P and K applied were 82, 12 and 23 kg ha^{-1}, respectively. In 2003 wet season, as rainfall was frequent and heavy (Table 1), only occasional surface-irrigations were conducted as a supplement when leaves started to roll due to drought stress, and the field was drained whenever heavy rains resulted in ponding. In 2004 dry season, as rainfall was scarce, the experiment was surface-irrigated once a week after emergence until harvest. Insecticide and fungicide were applied following standard practices as required.

Measurements

Plant number, tiller number, leaf area and above-ground crop biomass were measured from a random 0.5 m^2 area (i.e., two rows by 1 m) in each plot at 2, 5 and 8 WAS, respectively, in both years. Plants with crown roots were collected with a shovel, washed, and counted (both main shoots and tillers). The blades of all expanded leaves were separated from the shoot, and immediately measured with a Li-3100 Area Meter (Li-COR, inc., Lincoln Nebraska USA). About 2000 cm^2 leaf area was measured for each sample (less than 2000 cm^2 leaf area for the samples taken at 2 WAS because of small seedlings). The leaf blades and stems were separately dried at 70ºC to a constant weight before weighing. The remaining plants in a sample were root-removed, dried and weighed. Plant number m^{-2}, tiller number m^{-2}, leaf area index (LAI, m^2 m^{-2}), and crop biomass (g m^{-2}) were calculated from these measurements.

Table 1. Weather conditions during the growing seasons (June – October 2003, and January – May 2004) at IRRI, Los Baños, Philippines.

	Rainfall† (mm)	Rainy days‡ ($d\ mo^{-1}$)	Radiation ($MJ\ m^{-2}d^{-1}$)	T_{Max}§ (°C)	T_{Min} (°C)	T_{Avg} (°C)
2003 wet season	1092	9.6	18.1	32.4	24.0	28.2
2004 dry season	113	1.3	20.1	31.4	23.2	27.3

† Rainfall accumulated from June to October in 2003, and January to May in 2004;

‡ Rainy days indicates the days per month in which rainfall was more than 5 mm;

§ T_{Max}, T_{Min} and T_{Avg} indicate the means for the highest, lowest, and average temperature.

Weeds were collected by clipping at soil surface from the 0.5 m^2 sampling area at 8 WAS (the same sampling area as for crop biomass) in each weedy plot in both years, and from another 0.5 m^2 random area at 12 WAS in 2004. Weed species were identified and weed biomass was dried at 70ºC to a constant weight before weighing.

Panicle number m^{-2}, harvest index (HI), and final crop biomass were measured from a 0.25 m^2 random area (i.e., 1 linear m row) harvested at soil surface in each plot in both years. The remaining area of each plot (4.25 m^2) was panicle-harvested for grain yield, which was adjusted to 14% moisture basis.

In 2003 at sowing, a randomly selected 0.5 m^2 area covering two rows in each plot was marked with sticks. Seedling counting within the marked area was conducted at 3, 5, 7, 10 and 12 days after sowing, respectively, to determine the rate of emergence and the final fraction of emerged plants.

In 2004 at harvest, 10 panicles were randomly collected from each plot and threshed separately. Filled and unfilled grains from each panicle were separated with a vertical blower and counted with a seed counter to calculate average grain number per panicle (including filled and unfilled grains) and filled grain ratio (%). Thousand-grain weight was measured and adjusted to 14% moisture basis.

Data analysis

An analysis of variance for data collected each year was conducted separately using the restricted maximum likelihood (REML) option of the MIXED Procedure of SAS (SAS Inst. Inc., 2002 – 2003). Weed management, genotype, seeding rate and seed priming (2003) and their interactions were fixed factors; replication was random. Scaled Wald tests of fixed effects were done using the DDFM = KR (Kenward-Roger version of the Satterthwaite approximation) option of the MODEL statement. Comparisons among treatment means were performed using the PDIFF option of the LSMEANS statement. Filled grain ratio (%) data were square root transformed, and emergence (%) data arcsine transformed before analysis according to Gomez and Gomez (1984).

For each genotype, crop biomass under weed-free conditions at 2, 5 and 8 WAS was fitted to the expolinear growth equation (Goudriaan and Monteith, 1990) using GENSTAT (VSN Int. Ltd., 2005) as:

$$CB_{\mathrm{t,s}} = (c_{\mathrm{m}} / r_{\mathrm{m}}) \times \ln(1 + e^{r_{\mathrm{m}} \times (t - t_{\mathrm{b,s}})}) \tag{1}$$

where $CB_{\mathrm{t,s}}$ is the crop biomass at time t (expressed as days after sowing (d)), for a crop sown at a seeding rate s (seeds m^{-2}), r_{m} is the maximum relative growth rate (g g^{-1} d^{-1}), c_{m} is the maximum absolute growth rate (g m^{-2} d^{-1}), $t_{\mathrm{b,s}}$ is the time at which the stand, sown at the seeding rate s, effectively passes from exponential to linear growth, also referred to as lost time (Montheith, 1981). Non-linear regression using GENSTAT (VSN Int. Ltd., 2005) was conducted after logarithmic transformation of crop biomass. For each genotype, data were simultaneously fitted, implicitly assuming that c_{m} and r_{m} are genotype based and not influenced by seeding rate, whereas t_{b} is seeding rate specific. Differences in t_{b} between seeding rates reflect the differences in time required to obtain a closed canopy.

Weed biomass at 8 WAS was fitted to a rectangular hyperbola describing the relation between weed biomass (WB, g m^{-2}) and the densities of weeds (N_{w}, m^{-2}) and crop (N_{c}, m^{-2}), according to Spitters (1983):

$$WB = \frac{N_{\mathrm{w}}}{a_0 + b_{\mathrm{wc}_1} N_{\mathrm{c}_1} + b_{\mathrm{wc}_2} N_{\mathrm{c}_2} + b_{wc_3} N_{\mathrm{c}_3}} \tag{2}$$

In this function, the effect of interspecific competition of the rice genotypes on the weeds is expressed as the product of an interspecific competition coefficient (b_{wc}, m^2 g^{-1}) and crop plant density. Parameter a_0 represents the reciprocal of the average weight per weed plant at density N_{w} in the absence of rice plants and consequently, the weed biomass in the absence of a rice crop is represented by (N_{w}/a_0, g m^{-2}). Data of weed biomass for all genotype × seeding rate combinations within one year were simultaneously fitted to the actual number of established crop plants (Table 2), using the non-linear regression option of GENSTAT (VSN Int. Ltd., 2005). The analysis was conducted under the assumption that weed density and weed species composition were uniformly distributed throughout the experimental field. As weed number was not counted, N_{w} was set to 1000 plants m^{-2}. This analysis provides quantitative information on the relative competitive abilities of the rice genotypes against the weeds, as expressed in parameter b_{wc}.

Table 2. Mean plant densities† (plants m^{-2}) at three seeding rates, and mean emergence‡ of genotypes in 2003 wet season and 2004 dry season, respectively.

	Seeding rate (viable seeds m^{-2})			Emergence (%)
	100	300	500	
	-----------------------2003 wet season----------------------			
APO	90	242	421	83.6
IR60080-46A	92	258	392	82.4
IRAT 216	92	251	363	78.4
	-----------------------2004 dry season-----------------------			
APO	102	251	406	84.4
IR60080-46A	88	298	383	85.5
IRAT 216	92	182	370	71.6

† averaged over seed priming (2003) and sampling (2, 5 and 8 weeks after sowing) in weedy plots.

‡ mean percent value of plant number m^{-2} to viable seeds m^{-2} sown over seeding rate, seed priming (2003), and sampling (2, 5 and 8 weeks after sowing) in weedy plots.

RESULTS

Weed pressure and crop establishment

Twenty-two weed species were found in the experimental fields (data not shown). The prevalent species common in both years were *Digitaria ciliaris* Retz., *Eleusine indica* L., *Echinochloa colona* L., *Leptochloa chinensis* L., *Dactyloctenium aegyptium* L., and *Portulaca oleracea* L. In both years, distribution of weed species and weed density seemed to be uniform throughout the experimental field. However, the weed pressures imposed on the crops in both years were different: low in 2003 (weed biomass was 84 g m^{-2} at 8 WAS averaged over all weedy plots) and high in 2004 (weed biomass was 222 g m^{-2} at 8 WAS averaged over all weedy plots) (Table 3). The low weed pressure in 2003 was most likely due to the relatively late weeding operation (at 3 WAS compared to 2 WAS in 2004). However, this provided us an opportunity to evaluate the performance of genotypes and their interactions with seeding rate and weed management under different weed pressures.

Rice crops were uniformly established in both years. On average, the plant densities observed were about 14 – 18% lower than the target seeding rates for APO and IR60080-46A, and 22 – 28% lower for IRAT 216 (Table 2). The emergence ability of IRAT 216 appeared to be weak compared to the other two genotypes.

Table 3. Means for genotypes over seeding rates, and for seeding rates (viable seeds m^{-2}) over genotypes under weed-free (F) and weedy (W) conditions for weed biomass, yield, and yield components in 2003 and 2004, respectively.

	Rice yield			Harvest index		Final crop biomass			Panicle number			Weed biomass 8 WAS†	Weed biomass 12 WAS
	---- Mg ha^{-1}----		%	%		-------- g m^{-2}--------		%	---- panicle m^{-2}-----		%	--------- g m^{-2}---------	
	F	W	F-W‡	F	W	F	W	F-W	F	W	F-W	W	W
	2003 wet season												
Genotype													
APO	4.16	4.12	1.1	30.6	30.6	1264.3	1297.7	–2.6	333.1	316.9	4.9	51.6	ND§
IR60080-46A	2.65	2.27	14.1	24.6	22.7	1179.1	1041.2	11.7	269.8	261.3	3.1	99.5	ND
IRAT 216	1.60	1.40	12.4	16.6	16.5	991.7	934.9	5.7	273.8	275.6	–0.7	99.3	ND
Seeding rate													
100	2.86	2.52	12.2	27.2	25.5	1163.5	937.3	19.4	249.6	202.4	18.9	151.0	ND
300	2.83	2.69	5.0	23.0	22.8	1082.1	1109.7	–2.5	291.1	305.3	–4.9	67.4	ND
500	2.71	2.59	4.6	21.5	21.5	1189.5	1226.8	–3.1	336.0	346.0	–3.0	32.0	ND
Overall mean	2.80	2.60	7.3	23.9	23.3	1145.0	1091.3	4.7	292.2	284.6	2.6	83.5	ND
LSD¶	0.23	0.23		2.4	2.4	147.8	147.9		38.2	38.2		63.8	ND
LSD_{FW}#	0.47			3.9		147.9			44.0				

Table 3. Continued.

	Rice yield			Harvest index		Final crop biomass			Panicle number			Weed biomass 8 WAS†	Weed biomass 12 WAS
	---- $Mg\ ha^{-1}$----		%	%		------- $g\ m^{-2}$--------		%	---- panicle m^{-2}-----		%	-------- $g\ m^{-2}$	----------
	F	W	F-W‡	F	W	F	W	F-W	F	W	F-W	W	W
	------------------------ 2004 dry season ------------------------												
Genotype													
APO	4.93	3.11	37.0	30.8	31.5	1738.0	1135.5	34.7	474.2	364.2	23.2	176.6	231.6
IR60080-46A	3.16	2.00	36.8	24.7	28.1	1425.7	1129.3	20.8	276.0	298.7	−8.2	226.7	305.9
IRAT 216	2.21	0.94	57.6	24.3	25.5	1171.5	762.1	34.9	319.1	202.5	36.6	262.4	467.3
Seeding rate													
100	3.11	1.31	57.9	26.4	30.9	1421.0	732.8	48.4	298.7	180.0	39.7	314.8	477.0
300	3.53	2.34	33.5	28.0	28.8	1453.1	1099.0	24.4	372.4	310.5	16.6	199.2	296.3
500	3.67	2.39	34.9	25.5	25.5	1461.2	1195.2	18.2	398.2	374.9	5.9	151.5	231.5
Overall mean	3.43	2.01	41.4	26.6	28.4	1445.1	1009.0	30.2	356.4	288.5	19.1	221.9	335.0
LSD	0.54	0.63		5.9	6.8	232.4	268.3		57.6	66.5		71.6	130.7
LSD_{FW}	0.95			9.7		251.0			72.3				

† WAS indicates weeks after sowing;

‡ F-W indicates percent reduction under weedy conditions compared to that under weed-free conditions;

§ ND indicates no data;

¶ LSD is least square difference at $P < 0.05$ for comparison among means for the genotypes or seeding rates within a year;

LSD_{FW} is least square difference at $P < 0.05$ for comparison between means for genotypes or seeding rates under weed-free and weedy conditions within a year.

Rice yield and yield components

Genotype effect

Average grain yields of genotypes were significantly different, ranging from 1.6 to 4.2 Mg ha^{-1} under weed-free and from 1.4 to 4.1 Mg ha^{-1} under weedy conditions in 2003, and from 2.2 to 4.9 Mg ha^{-1} under weed-free and from 0.9 to 3.1 Mg ha^{-1} under weedy conditions in 2004 (Table 3). The ranking of genotypes in both weed-free and weedy yields was always APO > IR60080-46A > IRAT 216 in either year, and this ranking did not change with seeding rate (Figure 1). All the genotypes showed a higher grain yield under weed-free conditions in 2004 than in 2003 (Table 3), most likely resulting from the more intense radiation in the dry season of 2004 than in the wet season of 2003 (Table 1).

Seeding rate effect

Under weed-free conditions, grain yield for each genotype did not differ with seeding rate in either year (Figure 1). Under weedy conditions, yield for SR100 was less than that for SR500 for IRAT 216 in 2003, and yield for SR100 was less than those for SR300 and SR500 for both IR60080-46A and IRAT 216 in 2004. No yield differences among the three seeding rates for APO were observed in either year (Figure 1). Average yield over genotypes under the high weed pressure in 2004 was increased by

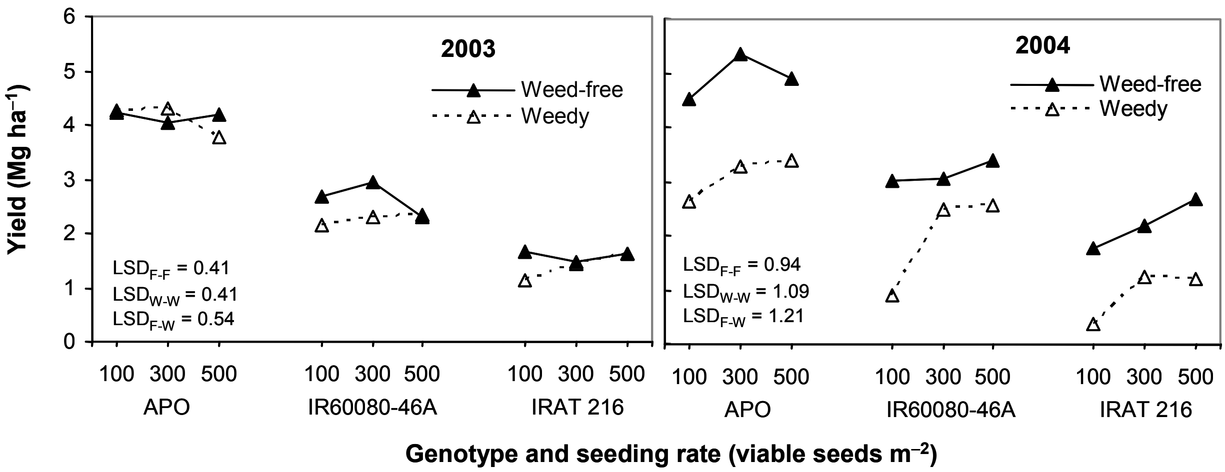

Figure 1. Grain yields for three genotypes at three seeding rates under weed-free and weedy conditions in 2003 and 2004, respectively. $LSD_{F\text{-}F}$, $LSD_{W\text{-}W}$ and $LSD_{F\text{-}W}$ are least square differences at $P < 0.05$ significance level for comparisons among means for genotype × seeding rate under weed-free conditions, under weedy conditions, and between weed-free and weedy conditions, respectively.

1.0 Mg ha^{-1} with increased seeding rate from SR100 to SR300, but not from SR300 to SR500 (Table 3). There was little difference in average yield among the seeding rates under the light weed pressure in 2003. Reduced yields for SR100 under weedy conditions resulted from lower final crop biomass and panicle number, whereas HI (Table 3), panicle size (total grains in a panicle), filled grain ratio and thousand-grain weight (data not shown) were not significantly affected compared with values obtained at higher seeding rates.

Weed effect

The low weed pressure in 2003 did not cause a detectable yield loss (Table 4). Under the high weed pressure in 2004, the negative effect of weeds on grain yield was clear (Table 5). Yield loss over seeding rates due to weed competition was significant for each genotype in 2004, but more for IRAT 216 (58%) than for APO (37%) and

Table 4. ANOVA† for weed management, genotype, seeding rate, and seed priming effects on rice traits studied in 2003 wet season, at IRRI, Los Baños, Philippines.

		Rice yield		Harvest index		Panicle number		Final crop biom.	
Effect	DF	F§	P#	F	P	F	P	F	P
Weed management (W)	1	1.45	0.295	0.24	0.653	0.30	0.615	1.56	0.216
Genotype (G)	2	518.22	<.0001	138.57	<.0001	11.14	<.0001	18.03	<.0001
Seeding rate (R)	2	0.89	0.414	17.10	<.0001	36.73	<.0001	4.63	0.013
Seed priming	1	0.48	0.489	0.00	0.973	2.19	0.144	1.31	0.257
W × G	2	1.96	0.149	0.86	0.428	0.22	0.802	1.36	0.265
W × R	2	1.11	0.336	0.60	0.551	3.19	0.047	4.13	0.021
G × R	4	2.25	0.073	1.54	0.202	1.30	0.279	0.13	0.973
W × G × R	4	3.43	0.013	2.17	0.082	0.34	0.848	0.59	0.673
		Crop biomass at 8 WAS		LAI at 8 WAS‡		Tiller number at 8 WAS		Weed biomass at 8 WAS	
		F	P	F	P	F	P	F	P
Weed management (W)	1	0.22	0.664	0.00	0.952	0.57	0.529	-	-
Genotype (G)	2	43.96	<.0001	40.12	<.0001	39.96	<.0001	1.54	0.228
Seeding rate (R)	2	100.79	<.0001	56.83	<.0001	81.73	<.0001	7.57	0.002
Seed priming	1	9.92	0.002	1.10	0.299	0.29	0.594	0.44	0.511
W × G	2	2.27	0.111	0.17	0.847	3.05	0.054	-	-
W × R	2	1.70	0.191	2.20	0.119	4.57	0.014	-	-
G × R	4	0.48	0.753	0.17	0.954	1.86	0.127	0.63	0.644
W × G × R	4	0.63	0.641	0.67	0.617	1.32	0.272	-	-

† Interactions of seed priming with other factors were not significant for any trait, they are thus not presented;

‡ WAS indicates weeks after sowing; § F indicates F value; # P indicates probability.

Table 5. ANOVA for weed management, genotype, and seeding rate effects on rice traits studied in 2004 dry season, at IRRI, Los Baños, Philippines.

Effect	DF	Rice yield F‡	Rice yield P§	Harvest index F	Harvest index P	Panicle number F	Panicle number P	Final crop biomass F	Final crop biomass P	Crop biomass at 8 WAS† F	Crop biomass at 8 WAS† P	LAI at 8 WAS F	LAI at 8 WAS P	Tiller number at 8 WAS F	Tiller number at 8 WAS P	Weed biomass at 8 WAS F	Weed biomass at 8 WAS P	Weed biomass at 12 WAS F	Weed biomass at 12 WAS P
Weed management (W)	1	18.85	0.011	0.36	0.612	9.91	0.078	37.77	<.0001	33.41	0.005	37.07	0.004	8.19	0.008	-	-	-	-
Genotype (G)	2	73.62	<.0001	4.37	0.023	32.08	<.0001	15.55	<.0001	9.12	0.001	8.48	0.001	11.81	0.000	3.70	0.056	8.45	0.005
Seeding rate (R)	2	9.64	0.001	1.16	0.328	24.82	<.0001	4.66	0.017	19.71	<.0001	27.03	<.0001	12.19	0.000	13.06	0.001	8.99	0.004
W × G	2	1.46	0.251	0.21	0.812	6.35	0.006	1.61	0.217	1.36	0.273	1.67	0.207	0.71	0.501	-	-	-	-
W × R	2	1.52	0.238	0.71	0.500	2.51	0.100	3.28	0.051	0.06	0.941	0.32	0.732	0.71	0.502	-	-	-	-
G × R	4	0.21	0.928	1.22	0.326	0.37	0.828	0.31	0.867	1.05	0.399	1.37	0.271	1.13	0.364	0.89	0.501	1.39	0.295
W × G × R	4	0.99	0.431	0.55	0.703	3.46	0.021	1.00	0.424	0.41	0.799	0.58	0.678	0.20	0.937	-	-	-	-

† WAS indicates weeks after sowing;
‡ F indicates F value;
§ P indicates probability.

IR60080-46A (37%) (Table 3). The responses in yield to weed competition also differed among seeding rates. Genotypes at SR100 had a larger average yield loss (58%) than at SR300 (34%) and SR500 (35%) (Table 3). This result indicates that in a weedy environment a relatively high seeding rate (300 viable seeds m^{-2}) is required to reduce yield losses. Weed competition caused yield loss mainly through reducing final crop biomass, panicle number (but panicle number for IR60080-46A was not reduced in 2004) (Table 3) and panicle size (not shown). Harvest index (Table 3), filled grain ratio and thousand-grain weight (not shown) were not affected.

Interactions

No genotype × seeding rate, and weed management × genotype interactions for grain yield were detected in either year (Tables 4 and 5), indicating that the yields of genotypes were relatively consistent over weed management and seeding rates. Grain yield under weed-free and weedy conditions were positively correlated, and this relationship did not change with seeding rate (Table 6).

Weed-suppressive ability

Genotype effect

Genotype differences in weed suppression were obvious only in 2004, when weed pressure was high (Tables 4 and 5). With APO the weed biomass at 8 WAS was lower than with IRAT 216. The weed biomass in plots with IR60080-46A was intermediate and did not differ significantly from that of the other two genotypes at 8 WAS, but was significantly lower than that for IRAT 216 at 12 WAS (Table 3). An analysis in which weed biomass at 8 WAS was fitted to crop plant density (Eqn. 2) resulted in an adequate description of observed data for all three genotypes in both years (percentage of variance accounted for > 82%) (Figure 2). The analysis demonstrated that in both years APO was about 1.9 times as competitive as the other two genotypes (Table 7), confirming that APO was superior to the other two genotypes in weed suppression.

Table 6. Correlations between weed-free and weedy yield in 2003 wet season (N = 18) and 2004 dry season (N = 9) at three seeding rates, respectively.

Seeding rate (viable seeds m^{-2})	2003 wet season	2004 dry season
100	0.88**	0.74**
300	0.91**	0.61**
500	0.81**	0.70**

** significant at P < 0.01.

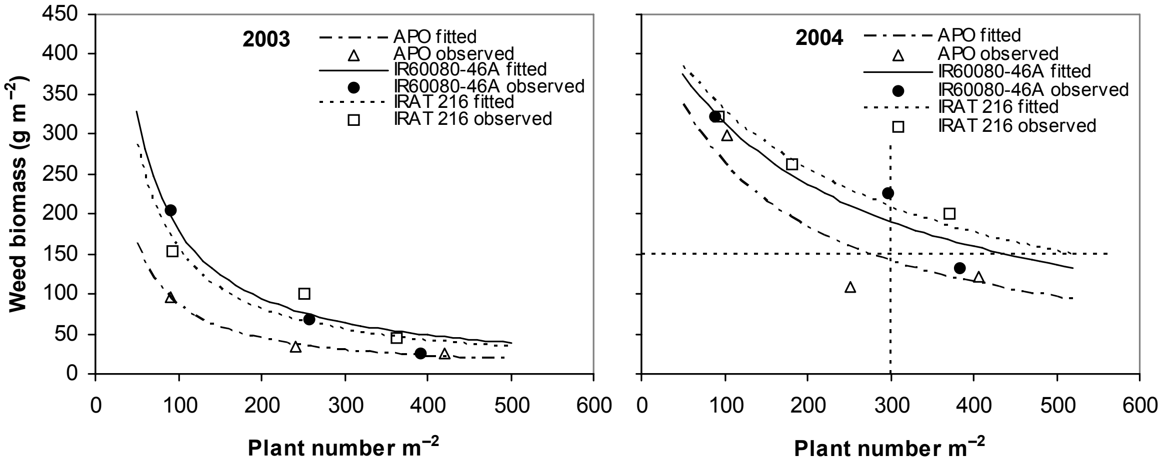

Figure 2. Relationship between weed biomass and plant density for three genotypes in 2003 and 2004, respectively. The markers indicate the observed data. Lines were obtained by fitting the data to Eqn. 2. See also text.

Table 7. Estimates† of weed-suppression parameters for each genotype in 2003 wet season and 2004 dry season.

	a_0‡ (weed g^{-1})	b_{wc}§ (m^2 g^{-1})		
		APO	IR60080-46A	IRAT 216
2003 wet season	0.530±1.390#	0.111±0.027	0.050±0.014	0.059±0.015
2004 dry season	2.151±0.366	0.017±0.004	0.010±0.003	0.009±0.003

† in the estimation, percentage of variance accounted for 89% and 82% in 2003 and 2004, respectively;

‡ a_0 is the reciprocal of the average weight per weed plant in the absence of rice, under the assumption of a constant weed density of 1000 plants m^{-2};

§ b_{wc}, weed competition coefficient of crop, represents the competitive effect of crop on weeds;

\# parameter value and stand error.

Seeding rate effect

Seeding rate had a significant effect on weed biomass in both years. Average weed biomass over genotypes for SR100 was always significantly higher than that for SR300 and SR500, both in 2003 and 2004 (at 8 and 12 WAS) (Table 3). Differences between SR300 and SR500 were not significant. These results indicate that, as is also demonstrated in Figures 2 and 3, at SR100 the ability of the crop to compete against

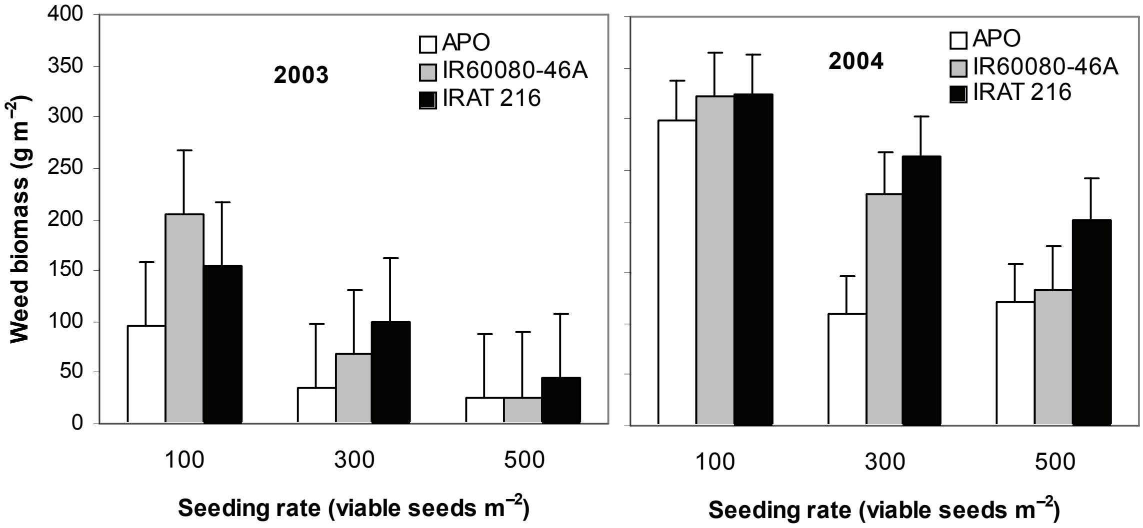

Figure 3. Weed biomass at 8 weeks after sowing in plots with three genotypes at three seeding rates in 2003 wet and 2004 dry seasons, respectively. The vertical bars indicate standard error of mean.

weeds is relatively weak; by increasing the seeding rate to SR300 weed suppression of the crop is enhanced, but a further increase over SR300 has limited effects on improvement in weed suppression. The effect of seeding rate on weed biomass was in line with its effect on grain yield.

Genotype × seeding rate

Analysis of variance did not reveal any interaction between genotype and seeding rate in weed growth. Weed biomass responded to crop density hyperbolically for any genotype (Figure 2), indicating that weed growth increased in a more than proportional way with decreased seeding rate. The fitted curves demonstrate that a strongly weed-suppressive genotype at a lower seeding rate could be equivalent in weed suppression to a weakly weed-suppressive genotype at a higher seeding rate. For example as demonstrated in Figure 2, APO at a density of 270 plant m^{-2}, IR60080-46A at 440 plant m^{-2} and IRAT 216 at 510 plant m^{-2} all could suppress weed growth to 150 g m^{-2} at 8 WAS in 2004. From another viewpoint, at an identical plant density of for instance 300 plants m^{-2}, APO is expected to have a lower weed biomass (140 g m^{-2}) than IR60080-46A (190 g m^{-2}) and IRAT 216 (208 g m^{-2}) at 8 WAS in 2004 (Figure 2). Generally, a higher seeding rate is required for weakly weed-suppressive genotypes under weedy conditions in order to effectively suppress weeds.

Vegetative crop growth

Relationship between vegetative crop growth with yield and weed growth

Vegetative crop growth traits at 8 WAS including LAI, crop biomass, and tiller number under weed-free or weedy conditions were all correlated positively with weedy yield and negatively with weed biomass in both years (Table 8), indicating that vegetative crop growth was predictive of weed growth and weedy yield, and suggesting that fast vegetative growth should be focused on in breeding efforts. Weedy yield and weed biomass were negatively correlated in both years, but not significantly in 2003 probably due to the low weed pressure.

Analysis of variance demonstrated that only main effects were important in vegetative crop growth including LAI, crop biomass, and tiller number (Tables 4 and 5, data at 2 and 5 WAS are not shown). Few interactions were significant, but their F values were relatively small. Therefore, only the main effects in each year are presented. Since weed management effects on vegetative crop growth in 2003 were not significant, they were not presented.

Seed priming effect

Seed presoaking accelerated emergence by about 2 days (50% emergence occurred at 4.5 and 6.5 days after sowing for presoaked and non-presoaked seeds, respectively)

Table 8. Correlations among weedy yield (YLD_W), weed biomass at 8 weeks after sowing (WAS) ($WB8_W$), and leaf area index (LAI), crop biomass (CB) and tiller number (TN) at 8 WAS under weed-free (8_F) or weedy (8_W) conditions in 2003 wet season (N = 18) (above the diagonal) and 2004 dry season (N = 9) (below the diagonal).

	YLD_W	$WB8_W$	$CB8_W$	$LAI8_W$	$TN8_W$	$CB8_F$	$LAI8_F$	$TN8_F$
YLD_W		-0.39^{ns}	0.47*	0.57*	0.59**	0.55*	0.63**	0.45^{ns}
$WB8_W$	−0.76*		−0.85**	−0.84**	−0.76**	−0.79**	−0.76**	−0.76**
$CB8_W$	0.77*	−0.93**		0.96**	0.93**	0.84**	0.83**	0.86**
$LAI8_W$	0.74*	−0.91**	0.99**		0.92**	0.87**	0.88**	0.86**
$TN8_W$	0.76*	−0.88**	0.91**	0.90**		0.79**	0.81**	0.82**
$CB8_F$	0.90**	−0.87**	0.88**	0.88**	0.87**		0.98**	0.79**
$LAI8_F$	0.82**	−0.84**	0.89**	0.91**	0.84**	0.98**		0.81**
$TN8_F$	0.81**	−0.68*	0.69*	0.67*	0.88**	0.82**	0.76*	

* indicates significant at P < 0.05;

** indicates significant at P < 0.01;

ns indicates not significant at P < 0.05.

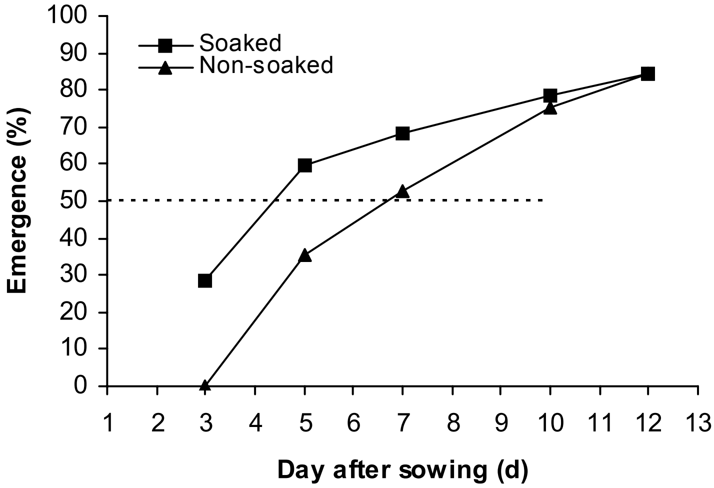

Figure 4. The effect of seed priming on emergence in the wet season of 2003, Los Baños, Philippines. Data points represent means over weed management, genotypes and seeding rates.

(Figure 4). As a consequence of earlier emergence, crop biomass at 2, 5 and 8 WAS (Figure 5B) and LAI 2 and 5 WAS (Figure 5A) were slightly but significantly increased. Seed priming had no effect on grain yield and weed biomass (Table 4), nor did it have interactions with other factors (data not shown).

Weed effect

Weed effect on vegetative crop growth was only significant in 2004 when the weed pressure was relatively high (Tables 4 and 5). Weeds decreased LAI and crop biomass detectably from 5 WAS onward and tiller number at 8 WAS. The reductions due to weeds became larger with crop development (Figures 6A, B and C).

Genotype effect

Genotypes differed in vegetative growth. APO had a higher LAI, crop biomass and tiller number than IRAT 216, and the differences between the two genotypes were detectable from 2 WAS in either year (but from 5 WAS for LAI and crop biomass in 2003) (Figures 5D, E, F; Figures 6D, E, F). IR60080-46A was similar to IRAT 216 in tillering, but greater than IRAT 216 and less than APO in LAI and crop biomass (although not always significantly so). Tiller number increased from 5 to 8 WAS for APO, but not for IR60080-46A and IRAT 216, indicating the stronger tillering ability of APO. The genotype differences in vegetative growth were in line with their performances in weed suppression and yield.

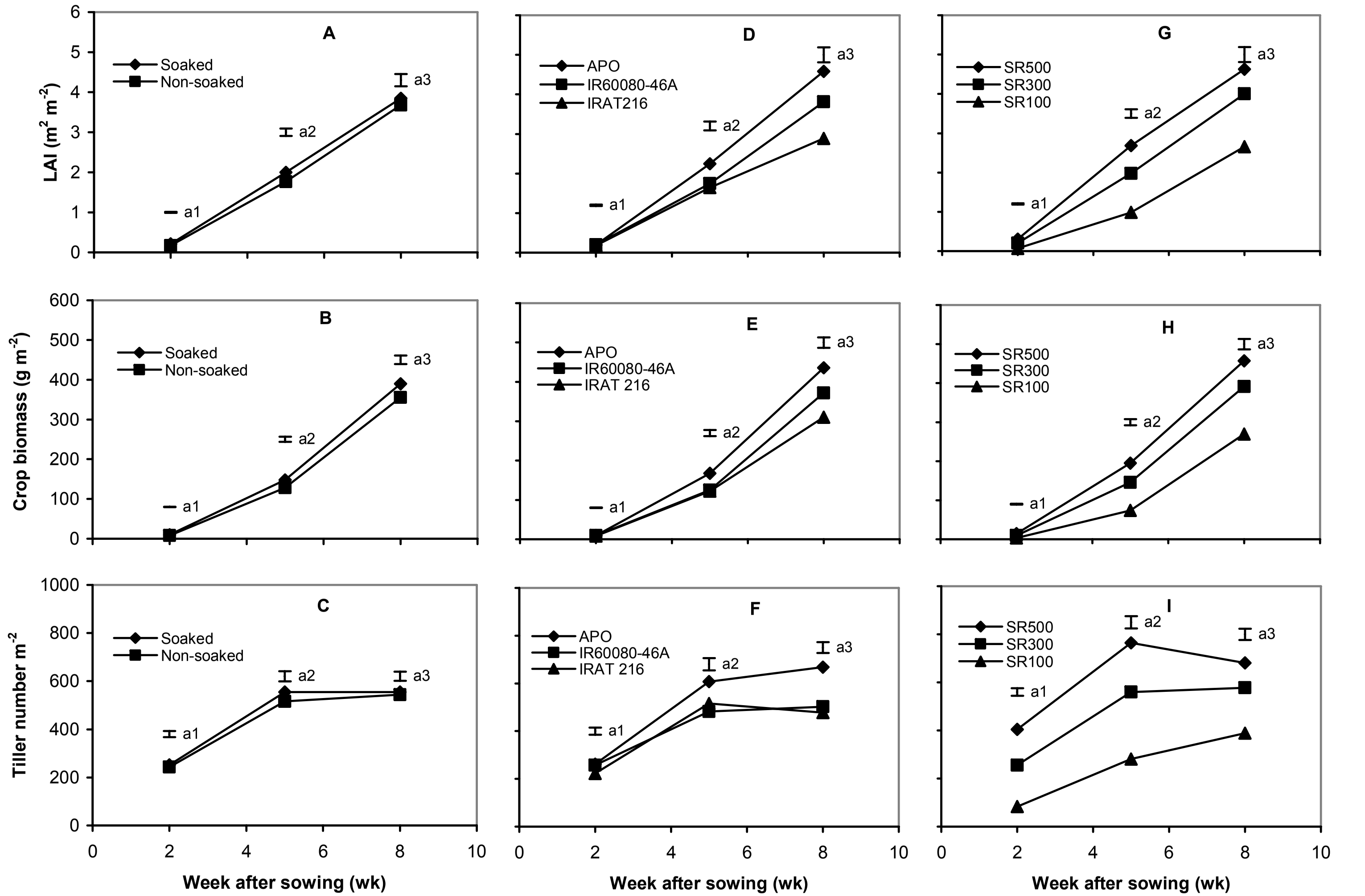

Figure 5. Differences among seed priming treatments (A – C), genotypes (D – F) and seeding rates (SR, viable seeds m^{-2}) (G – I) in leaf area index (LAI), vegetative crop biomass and tiller number in the wet season of 2003, Los Baños, Philippines. a1, a2 and a3 are least significant difference (LSD) at $P < 0.05$ significance level for comparison between means at 2, 5 and 8 weeks after sowing, respectively.

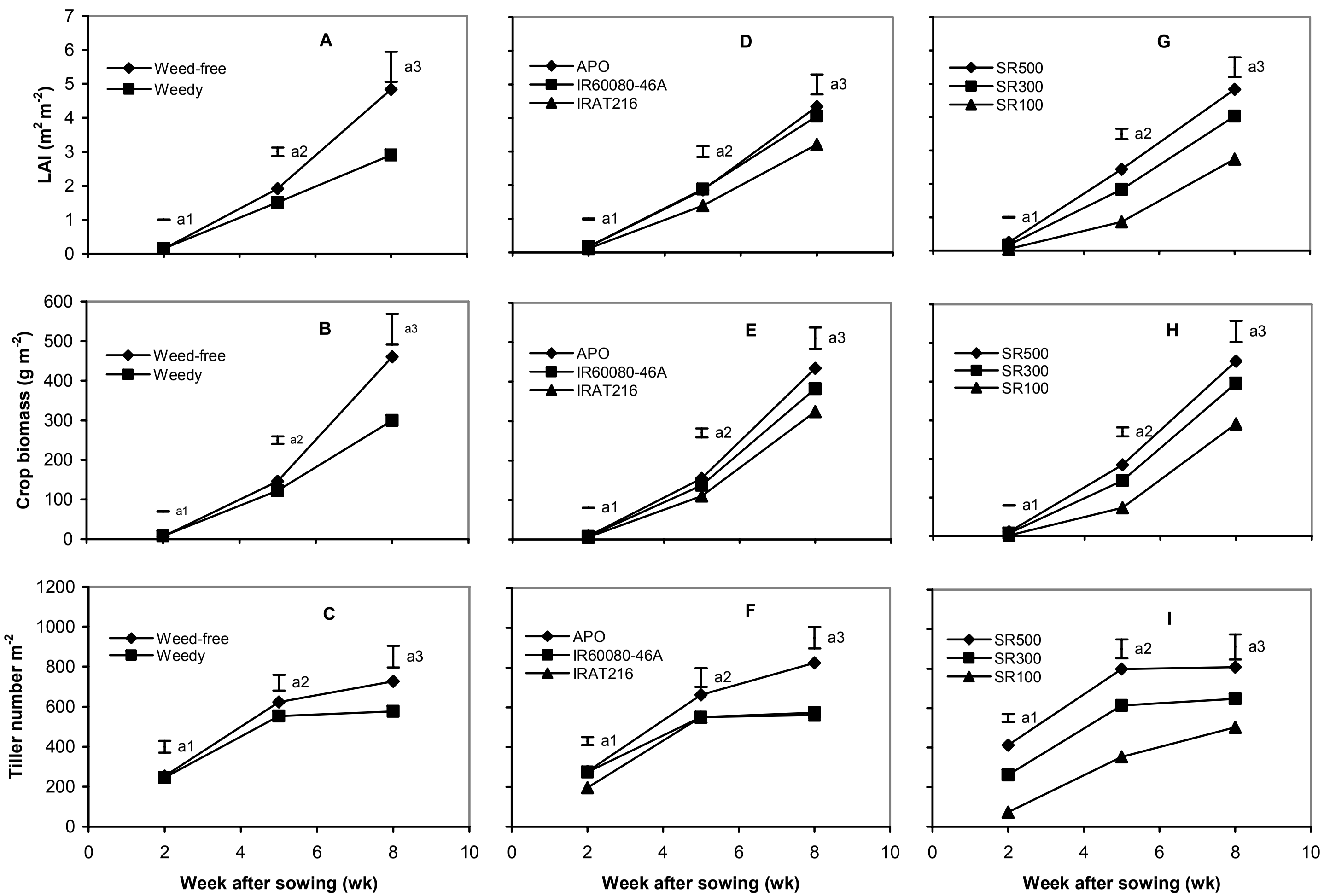

Figure 6. Differences among weed management treatments (A – C), genotypes (D – F) and seeding rates (SR; viable seeds m^{-2}) (G – I) in leaf area index (LAI), vegetative crop biomass and tiller number in the dry season of 2004, Los Baños, Philippines. a1, a2 and a3 are least significant difference (LSD) at $P < 0.05$ significance level for comparisons between means at 2, 5 and 8 weeks after sowing, respectively.

Table 9. Estimates† of maximum growth rate (c_m), maximum relative growth rate (r_m), and the moment that linear growth effectively begins for the genotypes at seeding rate of 100 (t_{b1}), 300 (t_{b2}) and 500 (t_{b3}) viable seeds per square meter ground area in 2003 and 2004, respectively.

	c_m (g m^{-2} d^{-1})	r_m (g g^{-1} d^{-1})	t_{b1} (d)	t_{b2} (d)	t_{b3} (d)
			2003 wet season		
APO	14.32±0.93‡	0.19±0.01	30.64±1.08	23.69±1.02	20.79±0.97
IR60080-46A	14.67±0.80	0.15±0.00	36.50±0.93	29.19±0.91	26.22±0.89
IRAT 216	10.71±1.55	0.16±0.01	34.94±2.52	26.55±2.45	23.88±2.38
			2004 dry season		
APO	19.97±1.95	0.18±0.01	33.52±1.49	28.51±1.47	25.05±1.42
IR60080-46A	18.94±3.77	0.16±0.01	36.62±3.11	28.85±3.07	25.77±2.98
IRAT 216	15.43±3.75	0.17±0.02	36.38±3.75	28.96±3.76	25.64±3.65

† in the estimation of expolinear growth parameters, percentage of variance accounted for > 99% for each genotype in either year;

‡ parameter value and standard error.

Seeding rate effect

The differences in vegetative LAI, crop biomass and tiller number among the three seeding rates were very clear: SR500 > SR300 > SR100 (Figures 5G, H, I; Figures 6G, H, I). This was not surprising because seeding rate determines crop density. However, crop growth was obviously not proportional to seeding rate. Due to intraspecific competition, the differences between SR500 and SR300 were less than those between SR300 and SR100. Seeding rate effects on vegetative crop growth were in line with their effects on weed growth and crop yield. These observations were confirmed by the analysis using the expolinear growth equation (Eqn. 1). The moment of canopy closure is closely related to the time (t_b) at which linear growth effectively begins (graphically demonstrated in Figure 7). The moment of canopy closure was 5 – 8 days later for SR100 than for SR300, and 3 days later for SR300 than for SR500 (Table 9), indicating that crop canopy needs a longer time to close at a lower seeding rate regardless of genotype, and that the difference in t_b between SR100 and SR300 was about twice the difference between SR300 and SR500. This may explain why there was a greater weed growth at a lower seeding rate, and why the difference in weed growth was larger between SR100 and SR300 than between SR300 and SR500. In comparison with IR60080-46A and IRAT 216, t_b for APO was 3 – 6 days less in 2003, and 0.5 – 3 days less in 2004 at all seeding rates (Table 9). It may result from its higher

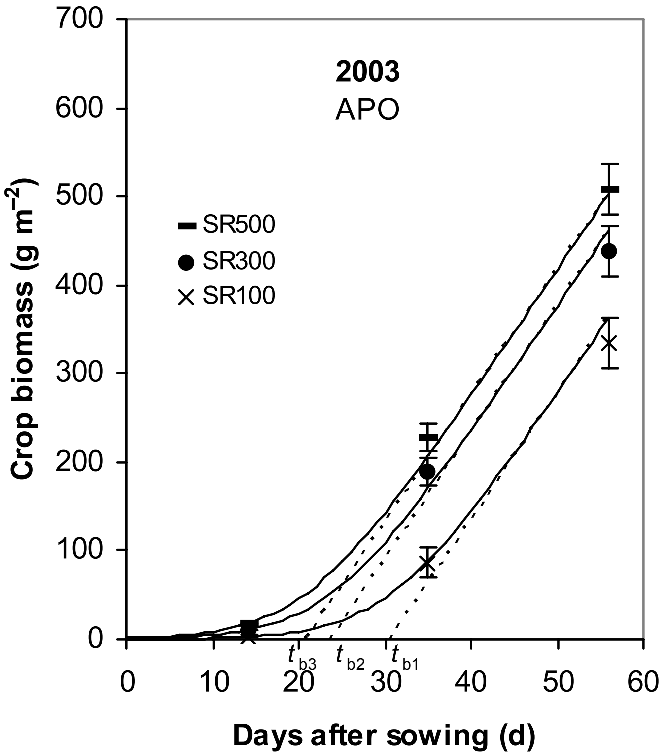

Figure 7. Expolinear growth of APO at seeding rate 100 (SR100), 300 (SR300) and 500 (SR500) viable seeds m^{-2} in the wet season of 2003, Los Baños, Philippines. Parameters t_{b1}, t_{b2} and t_{b3} represent the times at which linear growth effectively starts for SR100, SR300 and SR500, respectively. The markers with vertical bars represent observed data and standard errors of means. The solid lines were obtained by fitting the data to Eqn. 1.

maximum relative growth rate (r_m) together with a high maximum growth rate (c_m) (Table 9). This result may explain why APO was more weed-suppressive than the other two genotypes.

Interactions

There were no interactions among genotype, seeding rate, seed priming and weed management that were important for vegetative crop growth, although some small F values showed significant interactions (Tables 4 and 5, interactions of seed priming not shown because of no significance). The lack of interactions with regard to vegetative crop growth indicates that early growth of a genotype, such as grain yield, was relatively consistent across weed management, seeding rate and seed priming treatments, and that the contributions of genotype and seeding rate to early growth were additive.

DISCUSSION

Our study with three genotypes differing in yield potential showed that the highest yielding genotype in the absence of weeds was also highly weed-suppressive and highest yielding in the presence of weeds. In contrast, the low-yielding genotype in the absence of weeds was also low yielding in the presence of weeds and was weakly weed-suppressive. Therefore, weed-free yield and weedy yield were positively correlated, whereas weedy yield and weed biomass were negatively correlated (Tables 6 and 8). These results strongly support the studies with aerobic rice by Zhao et al. (2006a, b) and with lowland rice by Gibson et al. (2003). The implications of these findings are that high yield potential and strongly weed-suppressive ability are compatible and consequently breeding for a combination of high yield and strongly weed-suppressive ability is feasible. Furthermore, the results confirm that weed-suppressive genotypes are useful for weed management. However, these findings do not imply that strong weed-suppressive ability is always linked to high-yielding ability. Evidence of strong weed suppression but low yield potential was earlier reported (Zhao et al., 2006a).

Seeding rates within the range of 100 – 500 viable seeds m^{-2} had little effect on grain yield for any genotype when grown in the absence of weeds, indicating that seeding rates as low as 100 viable seeds m^{-2} can be used for aerobic rice when weeds can be completely controlled. If, however, weed pressure is expected to be high, a seeding rate of 300 viable seeds is needed to avoid a large yield loss, because decreasing the seeding rate from SR300 to SR100 increased weed biomass significantly (Figures 2 and 3) and consequently reduced grain yield (Table 3). However, a seeding rate as high as SR500 seems not to be necessary. Both weedy yield and weed biomass averaged over genotypes were nearly identical for SR500 and SR300 (Table 3). The conclusion of our study that an increased seeding rate can increase crop yield while decreasing weed growth supports studies with wheat (Blackshaw et al., 1999, 2000; Roberts et al., 2001; Mennan and Zandstra, 2005; Olsen et al., 2005), barley (O'Donovan et al., 2001) and lowland rice (Ni et al., 2004; Phuong et al., 2005). The small difference between SR300 (= 80 kg ha^{-1}) and SR500 (= 130 kg ha^{-1}) in weed biomass was in line with the observation in direct-seeded lowland rice by Gibson et al. (2001), who found that increasing seeding rate from 84 to 168 kg ha^{-1} had no effect on weed growth. However, in direct-seeded lowland rice, Phuong et al. (2005) found that yield loss due to weed competition was significantly decreased when seeding rate was increased from 80 to 160 kg ha^{-1}. The different 'thresholds' of seeding rate at which yield losses are minimized in the various studies may result from the different weed pressures created in these studies. In the study of Phuong et al.

(2005) the weeds in the weedy plots remained growing throughout the growing season, whereas in our study weeds were completely removed at either 2 (2004) or 3 (2003) WAS. Consequently the weed pressure in our study was much lower. If weed pressure is the only causation of different 'thresholds', growing aerobic rice without any or with a very limited weeding practice probably requires a seeding rate higher than 300 viable seeds m^{-2} to minimize yield loss.

The lack of a genotype × seeding rate interaction for yield and weed suppression as found in our study supports the results of a study on wheat by Korres and Froud-Williams (2002). In our study it was found that the weed-suppressive APO at a low seeding rate was as effective in weed suppression as the other two genotypes (IR60080-46A and IRAT 216) at a higher seeding rate (Figure 2). This result is confirmed by the analysis based on Eqn. 2. In this equation the weed-suppressive effect of each genotype at the crop level is represented as the product of a competition coefficient (b_{wc}) and crop density. In both years, the competition coefficient of APO was about twice that of the other genotypes, indicating that for APO only half of the plant density was required to obtain an identical level of weed suppression. These findings suggest that genotype and seeding rate affect crop-weed competition in an additive way. Therefore, using a strong weed-suppressive genotype with an optimum seeding rate can effectively suppress weed growth and benefit crop yield. These findings also have an important implication for experiments in which differences in weed-suppressive ability among genotypes are studied, that is, genotype differences will be biased with differences in plant density, particularly so if conducted at low seeding rates where the effect of plant density is relatively strong (Figure 2).

One important finding in the present study was that genotype differences appeared already during early growth stages. Although different genotypes had no differences in time of emergence (data now shown), the differences between strong and weak genotypes in LAI, crop biomass and tillering ability were detected as early as 2 WAS, the earliest sampling date. At that time the strongly weed-suppressive genotype APO already outperformed the weakly weed-suppressive genotype IRAT 216 in all the studied traits. These observations confirm the strong link between fast vegetative growth and strong weed-suppressive ability. Correlation analysis further proved that genotype-dependent weed-suppressive ability was positively linked to fast early growth. All these results suggest that fast early growth may be the fundamental attribute of weed-suppressive genotypes. This finding supports studies with lowland rice (Ni et al., 2000; Gibson et al., 2003) and aerobic rice (Caton et al., 2003; Zhao et al., 2006a, b), where vegetative growth were found to be important in determining weed-suppressive ability. Faster vegetative growth may allow a crop to outcompete weeds for nutrients and water, to close its canopy earlier to reduce the light availability more for weeds down in the canopy. Vegetative crop biomass and LAI were greatly increased, and the crop canopy was closed earlier by increasing seeding rate from SR100 to SR300, and from SR300 to SR500. Clearly, an increased seeding rate is another contribution to the ability of a crop to suppress weeds.

Differences between SR100 and SR300 were larger than those between SR300 and SR500 in most studied traits, including vegetative crop biomass, LAI, weed biomass and weedy yield. These may result from different intensities of intraspecific competition of crops sown at different seeding rates. At the lower seeding rates of 100 and 300 viable seeds m^{-2}, individual plants initially experience less intraspecific competition and grow relatively faster than at a higher seeding rate of 500 viable seeds m^{-2}. Consequently, differences between SR300 and SR500 become smaller, while differences between SR100 and SR300 are maintained. Under weed-free conditions, this compensatory growth of individual plants in crops sown at a low density results in comparable grain yields for a range of high densities, a phenomenon commonly known as the law of constant final yield (Counce, 1987; Bond et al., 2005) (e.g., Figure 1). However, under weedy conditions, the advantage of a lower intraspecific competition of individual plants at a low seeding rate is eliminated by an increased interspecific competition from weeds, and consequently the compensatory growth largely disappears. As a consequence, weedy yield for SR100 was much lower than that for higher seeding rates for IR60080-46A and IRAT 216 (Figure 1). The comparable weedy yield for APO at SR100 to those at SR300 and SR500 likely resulted from its fast early growth in tillering and biomass, which resulted in comparable weed suppression to those at higher rates. Although increasing seeding rate from SR300 to SR500 may slightly improve weed control further, other problems that harm crop yield like lodging (Bond et al., 2005), rat damage (Castin and Moody, 1989), and insect and diseases infection (Tan et al. 2000) might be exacerbated by higher seeding rates. In this study, only very slight lodging occurred during maturity in plots of SR500 for APO and IR60080-46A (data not shown).

Our study revealed that presoaking seeds before sowing shortened emergence by 2 days and slightly enhanced vegetative crop growth. The effect of presoaking is thus slightly less than a further increase in seeding rate from 300 to 500 viable seeds m^{-2}. This finding confirms the positive effects of seed priming on emergence and crop growth reported by previous studies (Harris et al., 1999, 2000; Bakare et al., 2005). However, these positive effects of priming were not translated to grain yield and weed suppression. This is not unexpected, as the further increase in seeding rate from SR300 to SR500 advanced crop development by about 3 days and also in this case no significant differences in yield and weed suppression were obtained. Furthermore, seed priming was only studied in 2003 when a complete hand-weeding was conducted at 3

WAS, resulting in low weed pressure which might have reduced the effect of seed soaking on weed growth as the newly germinated weeds might have been suppressed to the same extent by the crops from either presoaked or non-presoaked seeds. The effect of seed priming might be more significant in relatively dry environments in which non-presoaked seeds need a relatively long time to imbibe enough water from the soil to germinate. In our study, immediate irrigation after sowing may have further reduced the effects of priming. Evidence of no positive, or even negative effects of seed priming on emergence and vegetative crop growth were found in wheat (Giri and Schillinger, 2003), corn (Subedi and Ma, 2005) and cotton (Murungu et al., 2004), suggesting that seed priming in these cases is unlikely to improve crops' weed-suppressive ability. Further study seems to be necessary to define the effects of priming on weed control in aerobic rice under farm conditions.

CONCLUSIONS

Weeds are the main impediment to aerobic rice production systems. Therefore, it is critical to search for easily used weed management methods that require little labour and are not dependent on herbicide. The present study showed that both weed-suppressive genotypes and increased seeding rates can decrease both weed growth and yield loss. A combination of a weed-suppressive genotype with an appropriate seeding rate (300 viable seeds m^{-2}) may substantially reduce weed growth, and restrict the need for weeding operations to once in a growing season. A high seeding rate of 500 viable seeds m^{-2} resulted in little reduction in weed growth or increase in crop yield compared to a seeding rate of 300 viable seeds m^{-2}. Compared to genotype and seeding rate, seed priming appeared not to be important under the experimental conditions.

Fast early plant growth and an increased seeding rate both contribute to an early crop canopy closure and better weed suppression. Genetic improvement for weed competitiveness should focus on early traits.

CHAPTER 6

General discussion

Introduction

This research on weed competitiveness of aerobic rice aimed at answering three questions:

- Is it feasible to breed weed-suppressive, high-yielding genotypes?
- What is the best way to select such genotypes?
- How effective is a weed-suppressive genotype as a weed management tool?

The main findings in this research include a large genetic variability in weed-suppressive ability (WSA), the close association between yielding ability and WSA, the close association between crop vegetative growth and WSA, and the significant effect of weed-suppressive genotypes on weed control. In addition, two indirect selection indices, each including weed-free yield and early vigour, were developed for selection for both WSA and yielding ability under weed competition. In this section, these main findings together with the relationship between plant type and WSA are comprehensively discussed.

Genetic variability in WSA in aerobic and upland rice

The potential gain through breeding for weed competitiveness of aerobic rice depends on the genetic variability of rice in weed competitiveness. The results of our experiments using 40 aerobic and upland genotypes including *indica*, *japonica*, *aus*, and mixed types within *Oryza sativa*, grown under weed pressures (expressed as weed biomass averaged over all weedy plots within a year) ranging from 73 to 305 g m^{-2} among three years, showed that a large genetic variability in weed suppression exists among the tested genotypes. The mean weed biomass over three years (ranging from 126 to 296 g m^{-2} among genotypes) was 2.4 times higher for the least weed-suppressive genotype than for the most weed-suppressive one (Chapter 2, Table 4). The large genetic variability of the rices in weed suppression suggests that genetic improvement in WSA is likely to be effective. Genetic variability in WSA of aerobic and upland rice was also reported elsewhere (Moody, 1979; Garrity et al., 1992).

Genetic variability in WSA among germplasm groups was also found in this study. *Indica* and *aus* germplasm appeared to be more weed-suppressive than tropical *japonica* germplasm or the lines with mixed *indica* and *japonica* pedigrees (Chapter 4, Table 2). This finding indicates that *indica* and *aus* can be good gene donors for improvement of WSA in aerobic rice grown in tropical regions. The superiority of *indica* and *aus* over *japonica* found in this research was reported in earlier studies with lowland (Oka, 1960) and upland rice (Janiya et al, 1996; Dingkuhn et al., 1999). However, since a very limited number of genotypes from *indica* and *aus* were tested in the experiment, it is still unknown whether or not this finding can be extended to a larger population. To get more insight on *O. sativa* germplasm differences in WSA, a study using larger and random germplasm populations will be necessary. Our research did not include *O. glaberrima*, another cultivated subspecies grown in Africa. Studies with this germplasm showed that it is even more weed-suppressive than both *indica* and *japonica* (Johnson et al., 1998; Dingkuhn et al., 1999; Fofana and Rauber, 2000). The genetic variability in WSA may be much larger than reported in this thesis.

Compatibility of yielding ability with WSA

Breeding for weed competitiveness should not result in a trade-off for yield, because farmers are unlikely to adopt weed-competitive but low-yielding cultivars. Therefore, compatibility of yielding ability with WSA is a prerequisite for breeding weed-competitive aerobic rice. In this research, high-yielding ability with or without weed competition was found to be associated with low weed biomass, both in the studies with 40 genotypes (Chapter 2, Tables 6 and 7) and with three genotypes (Chapter 5, Table 8, correlation for weed-free yield was not included), indicating that high-yielding ability under weed competition (or high yield potential) and strong WSA are compatible, and may be combined in one genotype.

Controversial conclusions have been drawn on the compatibility of yield potential and WSA. During 1960s to 1970s, the Green Revolution brought high-yielding cultivars with short, sturdy-strawed culms (about 100 cm) and erect leaves. These cultivars were high tillering, fertilizer-responsive, lodging resistant, and had high harvest index (HI) (Peng et al., 1999). However, such cultivars were less vigorous during early vegetative growth and not as weed-suppressive as the traditional cultivars, which were tall, droopy, and vigorous in early growth, but were also susceptible to lodging, unresponsive to fertilizer, low tillering, low yielding and had low HI. Studies with these contrasting cultivar types led researchers to the conclusion that there was a trade-off between yield potential and weed competitiveness (Jennings and Aquino, 1968; Jenings and Jesus, 1968; Jenings and Herrera, 1968; Kawano et al., 1974). Because of the supposed trade-off and the successful control of weeds by herbicides, breeding for weed competitiveness was neglected for many years. However, more recent studies with lowland (Ni et al., 2000; Gibson et al., 2003) and upland rice (Garrity et al., 1992; Fofana and Rauber, 2000) showed that yield potential and weed competitiveness may not be conflicting.

In this thesis, two independent experiments showed that yielding ability and WSA are not only compatible, but also closely associated in aerobic and upland rice. The close relationship between them found among the existing genotypes implies that WSA may have been inadvertently improved with the improvement in yield in aerobic rice. However, as discussed later (see section *indirect selection index*, pp. 106–108), selecting for yield only has limited positive effect on improvement in WSA.

Consistency of crop performance across weed management regimes, years and locations

Weed management

No weed management × genotype (or germplasm) interaction was found in the experiment with 40 (Chapters 2, 3 and 4), and with three (Chapter 5) aerobic and upland genotypes for almost all the studied traits (a few exceptions with relatively small F values were HI (Chapter 2) and panicle number (Chapter 5)), including harvest traits yield and final crop biomass, and vegetative traits crop vigour, early plant height, height growth rate, vegetative crop biomass, tiller number, leaf area index (LAI), plant erectness, and ground cover (GC). The high positive correlations for every trait expressed under weed-free and weedy environments further confirmed the observations above. All these results indicate that performance of a genotype at any growing stage is relatively consistent across weed management regimes. This finding implies that selection under weed-free conditions will result in a corresponding response under weedy conditions. In agreement with this result, Gibson et al. (2003) also found a lack of weed management × genotype interaction for yield in lowland rice. Lemerle et al. (2001a) reported a positive correlation between weed-free and weedy yield in wheat, and Caton et al. (2003) a close correlation for vegetative traits of aerobic rice under intra- and interspecific competition. Our findings and the results reported in the literature suggest that intra- and interspecific competition may differ in degree but not in kind. Therefore, cultivars performing better under weed-free conditions (intraspecific competition) are likely to perform relatively better under weedy conditions (both intra- and interspecific competition). This conclusion is supported by Goldberg and Landa (1991), who found that suppressive ability of a species does not change with changes in its surrounding species in natural environments. However, Fischer et al. (1997, 2001) found significant weed management × genotype interactions for plant height, crop biomass, and yield in lowland and upland rice.

Years

An analysis of variance showed that variances for genotype × year for traits including yield, final crop biomass, weed biomass and early vigour were all smaller than those for genotype (Chapter 2, Table 5), indicating that genotype performance is also relatively consistent across years. In another study over two years (also two seasons: dry and wet), the three genotypes showed relative consistency in all the studied traits including yield, weed biomass, LAI, tiller number and vegetative crop biomass (Chapter 5). These results from different studies indicate that genotype-yielding ability and its WSA will not change greatly from year to year. This finding is supported by a number of studies with upland rice (Garrity et al. 1992; Fischer et al., 2001), lowland rice (Fischer et al., 1997; Gibson et al., 2003) and soybean (Jannink et al., 2000). Cousens and Mokhtari (1998) reported that some of the tested wheat cultivars were also consistent over years.

Agro-ecological zone

The experiments in this research were conducted at the International Rice Research Institute (IRRI) in the Philippines. However, whether or not the ranking of genotypes in yield and WSA will change with locations varying markedly remains unknown. A study with wheat (Cousens and Mokhtari, 1998) showed that some cultivars performed consistently well or poorly at different sites, but some not.

Relatively consistent WSA and yielding ability under weed competition across years within a target environment is very important for breeding for weed competitiveness. If relative genotype performance changes markedly from year to year, or place to place (or, in other words, if heritability is low), breeding efforts for these traits will be of little value.

Heritability for yield, WSA and their related traits

The estimated broad-sense heritability (*H*) for weedy yield and weed biomass, the two target traits in breeding for weed competitiveness, amounted to 0.79 and 0.64 on a three-year basis, and 0.55 and 0.38 on a single-year basis, respectively (Chapter 2, Table 5). The magnitude of the estimates appears to permit reasonable gains from selection. The estimated *H* for weed-free yield and weed-free crop vigour at 2 weeks after sowing (WAS) were 0.87 and 0.65 on a three-year basis, and 0.68 and 0.38 on single-year basis (Chapter 2, Table 5), and 0.96 and 0.81 estimated on the basis of means from the weed-free trial in 2003 (Chapter 3, Table 1), respectively. The other weed-free traits including crop vigour at 4 and 6 WAS, and plant height at 4 WAS had *H* values all greater than 0.80 estimated on the 2003 weed-free trials (Chapter 3, Table 1). The magnitude of the *H* values for all the weed-free traits indicates that they may serve as indirect selection criteria if they are genetically correlated with the target traits. Heritability for weed competitiveness-related traits in rice is rarely studied. A study with soybean by Jannink et al. (2000) showed that early plant height and WSA are both heritable.

Association of yielding ability in competition and WSA with weed-free vegetative traits

Among the weed-free traits studied in three experiments in this thesis, yield, vigour ratings (2 – 6 WAS), early crop biomass (≤ 9 WAS), early plant height (≤ 4 WAS), early tillering (4, 8 WAS) and LAI (8 WAS) were all phenotypically and/or genetically correlated positively with weedy yield but negatively with weed biomass (Chapter 2, Table 7; Chapter 3, Table 1; Chapter 5, Table 8). These results indicate:

- Fast early growth of a crop is an attribute of strong weed-suppressive genotypes;
- Weed-free vegetative traits of a crop are predictive of WSA and yielding ability under weed competition.

A number of vegetative traits were found to be related to WSA elsewhere: vegetative crop biomass in lowland rice (Ni et al., 2000); LAI in lowland (Gibson et al., 2003) and upland rice (Dingkuhn et al., 1999); SLA in upland rice (Dingkuhn et al., 1999); early tillering in upland rice (Dingkuhn et al., 1999) and wheat (Lemerle et al., 1996); early plant height in upland rice (Caton et al., 2003), lowland rice (Gibson et al., 2001) and soybean (Jannink et al., 2000); early vigour in wheat and barley (Bertholdsson, 2005); GC in upland rice (Dingkuhn et al., 1999); early root length in upland rice (Fofana and Rauber, 2000). All of these studies support our findings and link rapid early growth to WSA. However, a few traits were reported to have a weak association with WSA: early height (Fischer et al., 2001) and early tillering (Garrity et al., 1992) in upland rice.

Indirect selection for yielding ability in competition and WSA

Indirect selection efficiency (ISE)

Among all the investigated weed-free traits, crop vigour and yield were found to have high estimated ISE for both weedy yield and weed biomass. On a multi-year basis, the ISE of crop vigour at 2 WAS was 0.80 for weedy yield and 0.89 for weed biomass, while the ISE of weed-free yield was 1.05 and 0.77, respectively (Chapter 2, Table 7). On a single-year basis, the ISE of crop vigour at 4 WAS was 1.14 for weedy yield and 1.38 for weed biomass, while the ISE of weed-free yield was 1.40 and 1.11, respectively (Chapter 3, Table 1). Because of the high ISEs of weed-free yield and early vigour resulting from their high H and genetic correlations with the two target weedy traits, they are identified as the most promising weed-free traits that can be used as indirect selection criteria. The relatively higher ISEs on a single year basis than those on a multi-year basis were probably from their higher predicted Hs which were biased upward because of the confounding of genotype and genotype × year variances. However, the degree of bias is similar across traits, and therefore is unlikely to affect the comparisons among traits for inclusion in indirect selection indices.

Indirect selection index (ISI)

Two indirect selection indices were developed in this research. One was developed on a multi-year basis where data used for independent variables (weed-free traits) were means over three years (Chapter 2, Table 9), while another was developed on a single-year basis where data used for independent variables were means from one season trials (Chapter 3, Table 5). Both were developed by using the same data (means over three years) for dependent variables weedy yield and weed biomass. The multi-year based ISI was developed by firstly choosing weed-free traits on ISE, and secondly regressing weedy yield and weed biomass, respectively, on the chosen weed-free traits alone or in combinations. The single-year based ISI was developed by firstly stepwise regression analysis to select the most important traits predicting weedy yield and weed biomass, respectively, and secondly following the regression procedure for the former ISI. These two methods resulted in similar ISIs: both weed-free yield and early crop vigour (rated at 2 or 4 WAS) were included in each ISI. In both ISIs, weed-free yield and crop vigour together explained > 87% of variation in weedy yield and > 40% of variation in weed biomass. Therefore, selecting for both yielding ability and WSA is effective, although more effective for yielding ability. Since selection is usually performed in each growing season, the ISI developed on the single-year basis is more practical.

Within an ISI, weed-free yield is more important than weed-free crop vigour in predicting weedy yield, while weed-free crop vigour is more important than weed-free yield in predicting weed biomass, as was discussed in Chapters 2 and 3. Thus, selecting on both yield and crop vigour under weed-free conditions is necessary to simultaneously improve yielding ability under weed competition and WSA. The positive correlation between weed-free yield and early vigour found in this research implies that there is no trade-off between the two selection criteria. A selection strategy based on independent culling levels (Bernardo, 2002) may be effective. Within one season, selection may first be conducted on early vigour, followed by selection based on yield only of those entries exhibiting high vigour. Since early plant height (at 4 WAS) was found to be as good as vigour in predicting weed biomass (Chapter 3), vigour evaluation may be replaced by height measurement for the early season selection in case poor crop establishment does not allow a proper vigour rating.

Indirect selection has the following advantages over direct selection with respect to weed competitiveness:

- Indirect selection avoids the need to grow genotypes with weeds, thus permitting the growing area for each line to be decreased, because 2 to 4 rows may be large enough for vigour rating and yield evaluation.
- Indirect selection eliminates the need for weed biomass measurement, which is a selection criterion in direct selection, and which has a large error variance.

- Indirect selection permits selection to be conducted in early generations when only a small amount of seeds available, thus accelerating the breeding process.
- Indirect selection simplifies the selection process since rating crop vigour is easy and fast, thus allowing large breeding populations to be managed. Further, since the first selection will be done early in the season (at about 4 WAS), before yield sampling, no further data need to be collected from plots which are not selected.
- Indirect selection saves breeding costs of seed, field and labour because of decreased plot size and seed amount, and the simplified selection process.

The ISIs were developed based on a large population of diverse genotypes, with clear differences in traits among cultivars. Its applicability in a narrower population of progenies from crosses among parents with similar growth characters is not known and requires further study. However, since weed-competitive aerobic rice breeding will mainly aim at improving drought tolerance, yield and WSA, crosses made will be between genotypes which are drought-tolerant and weed-suppressive (upland or aerobic rice), and genotypes which are high yielding (lowland rice); the genetic variability within the segregating populations derived from the crosses is expected to be large enough to permit effective selection. A study in wheat (Mokhtari et al., 2002) showed also that variability in plant growth and yield within an F_3 population is large enough for selecting promising lines with respect to weed competitiveness. Jannink et al. (2000) reported that selection on early height can be effective for improving WSA in soybean, but he argued that gains for yield from selection may be difficult while improving WSA because of a negative correlation between early height and yield. However, this is unlikely to happen in aerobic rice because of the positive association between the two target traits yielding ability and WSA, and between the two selection criteria and the two target traits, as discussed earlier.

Relationship between plant erectness and WSA

One interesting finding in our research is that the droopy plant type tends to be less weed-suppressive than the erect one. This conclusion is based on the following findings derived from the experiments reported in the thesis:

- In the population of 40 diverse genotypes, visual ratings of plant erectness (9 = most erect, 1 = most droopy) were negatively correlated with weed biomass, but positively correlated with crop vigour, vegetative crop biomass and yield, which were also negatively correlated with weed biomass (Chapter 3).
- *Indica* and *aus* germplasm groups were both erect and more weed-suppressive than the relatively droopy *japonica* germplasm groups (Chapter 4).

- Within *japonica* germplasm, plant erectness was also negatively but not significantly correlated with weed biomass (Chapter 4).
- In an independent experiment with three genotypes, the erect genotype APO was more weed-suppressive than the other two relatively droopy genotypes IR60080-46A and IRAT 216 (Chapter 5).

The droopy plant type was hypothesized to provide larger GC, thus enabling it to suppress weeds more than the erect plant type, but this research showed that there was no close relationship between GC and plant erectness (Chapter 3, Table 3), and that the erect *indica* and *aus* germplasm groups even had a somewhat larger GC than the droopy *japonica* groups (Chapter 4, Table 4). These results indicate that the above-mentioned hypothesis may be not true. Under field conditions, with constant planting density and row spacing, GCs of cultivars are determined by their growth rates, LAIs, tillering, tiller angles, plant height, and leaf erectness. Therefore, the contribution of droopy leaves to GC may be very limited. Audebert et al. (1999) reported that the greater GC of *O. glaberrima* cultivars relative to *O. sativa japonica* cultivars is achieved by rapid increase in the number of leaves through high tillering, but not through characteristics of individual leaves. Dingkuhn et al. (1999) observed the same light extinction coefficients at 4.5 WAS for *O. glaberrima* and *O. sativa* cultivars with contrasting plant types. These studies indicate that effects of plant erectness on GC are small. However, the observed negative effect of droopy plant type on WSA may not result from the droopy plant *per se*. The weak association between erectness and weed biomass within *japonica* germplasm suggests that droopy plant *per se* is a trait that is unrelated to WSA. The negative association between droopy plant type and WSA observed in the diverse 40-cultivar population and among the germplasm groups may result from the fact that all the cultivars belonging to *indica* and *aus* germplasm groups used in this research are erect and have fast early growth. It may have been a chance occurrence that the *japonica* materials included in this study did not have fast early growth, in which case, droopy plant type *per se* may be not detrimental to WSA. However, as discussed earlier, fast early growth is the most important attribute of a strongly weed-suppressive genotype. This viewpoint is supported by Gibson and Fischer (2001), who found that shade alone does not prevent the weed growth due to the morphological plasticity and dry matter allocation of weeds expressed under shading stress, and speculated that fast nutrient deprivation of weeds by rice is more crucial to weed suppression. Similarly, Johnson et al. (1998) linked the advantage in WSA of *glaberrima* over *japonica* cultivars to early tiller production and early biomass accumulation. In contrast, however, studies with rice (Dingkuhn et al., 1999) and wheat (Lemerle et al., 1996) suggest that droopier cultivars are more weed-suppressive.

Integrated weed management (IWM)

Integrated weed management is an approach combining two or more direct or indirect weed control methods aiming to keep weed infestation levels below the economic threshold (De Datta and Baltazar, 1996). The economic threshold is a weed infestation level at which weeds must be controlled otherwise it would result in economic loss. IWM is largely a decision-making process involving (1) what combinations can provide best control at greatest profits, and (2) when to apply control measures with use of critical thresholds. Although the principle of IWM is the same, i.e. combining control methods economically in a given field situation, IWM practices vary among countries and regions with various socio-economic conditions. Chemical control is still an important component of IWM. However, since chemical herbicides can pollute the environment and cause the proliferation of resistant biotypes, herbicide application should be reduced as far as possible.

In this thesis, a combination of genotype and seeding rate was evaluated. The result was very positive: the effects on weed suppression of genotype and seeding rate were additive, and the weed-suppressive genotype combined with an appropriate seeding rate (300 viable seeds m^{-2}) could effectively suppress the growth of naturally-germinating weeds. Therefore, this strategy may minimize weeding operations in aerobic rice field to one time a season, freeing labour from onerous weeding practices and reducing dependence on herbicides. The application of this technology relies on the availability of weed-suppressive, high-yielding cultivars. The technology of increasing seeding rate to decrease weeds infestation is not unfamiliar with farmers. It is, however, often misused by planting extremely large amounts of seed. In our direct-seeded aerobic rice experiments, a seeding rate over 300 viable seeds m^{-2} was found to have little effect on weeds. An excessive seeding rate which results in severe intra-specific competition may reduce grain setting of the crop, cause lodging (Bond et al., 2005), more severe rat damage (Casin and Moody, 1989) and increased insect and disease damage (Tan et al., 2000), and consequently reduce final yield.

Outlook

Aerobic rice breeding in Asia has aimed mainly at high yield and drought tolerance, and a relatively high yield of 6 – 7 Mg ha^{-1} under good farming practices has been achieved (Wang et al., 2002). According to this research, weed competitiveness can be included among the main breeding goals because of its positive association with yield. IRRI has recently started an aerobic rice breeding programme aiming at improving both yield and WSA using the indirect selection method developed in this research. However, other emerging technologies such as marker-assisted breeding and genetic engineering may be incorporated into this method. Recently, scientists incorporated genes from *O. glaberrima* into *O. sativa japonica* through backcrossing and doubled haploid breeding aiming to combine weed-suppressive traits from *O. glaberrima* with agronomic traits from *O. sativa* into new genotypes (Jones et al., 1997). These interspecific hybrid genotypes with improved WSA, called NERICA rices, can yield from 1.5 to 3.5 Mg ha^{-1} and are now grown in 17 African countries (Harsch, 2004).

With the challenge of feeding more people in the decades ahead with rice under increasing water scarcity, a breakthrough in yield and WSA in aerobic rice breeding would provide benefits in water saving while increasing rice production. This goal is achievable according to our study. With the expected high-yielding weed-competitive aerobic rice cultivars, irrigated lowland rice may be partly replaced by direct-seeded aerobic rice, especially in water scarce areas in Asia. Traditional low-yielding upland rice may also be replaced with high-yielding aerobic rice in areas where rainfall is uniform and frequent during the growing season. Our results indicate that these changes may occur without dependence on herbicides. Rice production may, therefore, go on in a more resource-saving, environment-friendly and development-sustainable way.

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Summary

Rice is the staple food for over half the world's population. Demand for rice in 2025 is projected to increase by 25% compared with that in 2001. However, rice production is threatened by a decline of arable land caused by continuous urbanization and industrialization, and by water scarcity resulting from increased urban and industrial use, depletion of ground water resources, and pollution. Irrigated lowland rice systems, where 75% of world rice is currently produced, will be most hampered by water scarcity in the near future. To ensure rice production with less water, two promising water-saving rice systems, alternate wetting and drying (AWD) and aerobic rice, need to be further developed. Aerobic rice is direct-seeded in nonpuddled, nonflooded fields, and is ideally grown in soils where the water content can be maintained at field capacity. It may produce moderately high yield (6 – 7 Mg ha^{-1}) while saving more than 50% water compared with conventional lowland irrigated rice. Both aerobic and upland rice grow under aerobic conditions for the entire life cycle. However, the latter is less input-responsive, and completely dependent on rainfall, thus produces much lower yield (1.0 – 1.5 Mg ha^{-1}) than the former.

In aerobic rice systems where rice and weeds germinate simultaneously, the lack of 'head start' of rice seedlings over weeds and the absence of a water layer that suppress weeds, in contrast to irrigated lowland rice, result in more severe weed infestation. Weeds in aerobic rice may cause a yield loss from 30 to 100%, and thus are the greatest constraint to aerobic rice production. Chemical weed control is mostly effective; however, the intensive use of herbicides results in environmental pollution and herbicide resistance in weed biotypes. Weeding by hand or with simple tools is labour intensive, and is often not done properly due to high cost or unavailability of labour. A more environment-friendly and less labour-intensive weed control method is needed. Weed-competitive genotypes may be an effective tool for weed management.

This study mainly aimed at exploring the feasibility of breeding for weed-competitiveness in aerobic rice, developing an indirect selection index for the trait, and testing the efficacy of the combination of weed-competitive genotype with seeding rate in weed management. With these objectives, three experiments were conducted under aerobic conditions at the experimental station of the International Rice Research Institute in the Philippines:

Experiment 1 Forty aerobic and upland genotypes (*O. sativa* L.) including *aus*, *indica*, tropical *japonica,* and *indica/japonica* germplasm, were grown under weed-free and weedy conditions, respectively, in the

	wet seasons of 2001, 2002 and 2003. Yield, yield components and weed biomass (weedy conditions only), and crop vigour at 2 weeks after sowing (WAS) were investigated in each season. In 2003, more detailed vegetative traits including crop vigour, seedling height, plant erectness, crop biomass and crop ground cover were studied.
Experiment 2	The same set of genotypes was grown in one row each with the design as described in Experiment 1 under weed-free conditions, plants in rows were thinned to one plant per hill spaced 5 cm apart. In this experiment, tiller number per plant was measured twice during the vegetative growth stage to relate tillering ability with weed competitiveness.
Experiment 3	Three contrasting aerobic rice genotypes differing in yield and vigour were grown at three seeding rates (100, 300 and 500 viable seeds m^{-2}) with or without seed priming under two weed management regimes (weed-free and weedy) in 2003 wet season and 2004 dry season. In this experiment, emergence, yield, weed biomass and vegetative traits including tiller number, crop biomass and leaf area index (LAI) at 2, 5 and 8 WAS were investigated.

Genetic variability in weed-suppressive ability (WSA) and in yielding ability under weedy conditions among the 40 tested genotypes was large. Mean weed biomass over three years ranged from 126 to 296 g m^{-2}, whereas the mean weedy yield (yield under weed competition) varied from 0.5 to 2.5 Mg ha^{-1}. The four germplasm groups differed in WSA and weedy yield too. Both *aus* and *indica* appeared to be more weed-suppressive than tropical *japonica* and the progenies of *indica*/*japonica* crosses, and the *indica* appeared to be more productive than the other germplasm. These results indicate that gain in WSA from breeding efforts can be expected, and that *aus* and *indica* can be used as gene donors for improving WSA in the tropics.

Yield under weedy conditions and weed biomass were both moderately heritable. Their broad-sense heritabilities were 0.79 and 0.64 estimated on a three-year basis and 0.55 and 0.38 estimated on a single year basis, respectively. Moreover, these two traits were genetically negatively correlated. These results indicate that yielding ability under weed competition and WSA are compatible and may be simultaneously improved.

Relative performance of genotypes was quite consistent across weed management regimes and years. Both harvest traits, including yield, final crop biomass, harvest index and final plant height, and vegetative traits, including crop vigour, plant height, plant erectness, vegetative crop biomass, LAI and tiller number, investigated under weed-free conditions, were all genetically or phenotypically correlated with the same traits investigated under weedy conditions. Traits associated with rapid biomass accumulation of rice seedlings were also strongly associated positively with weedy yield and negatively with weed biomass, indicating that fast early growth is crucial to WSA and yielding ability under weed competition, and that they may be used as components of indirect selection indices. These traits include crop vigour (2, 4 and 6 WAS), ground cover (6 WAS), early plant height (3 and 4 WAS), vegetative crop biomass (4, 8 and 9 WAS), tiller number (4, 8 WAS), and LAI (8 WAS). All the vegetative traits for which heritability was estimated were found to be moderately to highly heritable.

Two indirect selection indices (ISI) for selection for the two target traits, weedy yield and weed biomass, were developed on a three-year and single-year mean basis, respectively. The three-year based ISI was developed through (i) choosing the weed-free traits that had high indirect selection efficiencies for the target traits, and (ii) regressing the target traits on the chosen traits, while the single-year based ISI was developed through regression analysis only. In each indirect selection index, both weed-free yield and early crop vigour were included, and they together explained more than 87% of genotype variation in weedy yield, and 40% in weed biomass. This result indicates that selection on both weed-free yield and weed-free early vigour can improve yielding ability under weed competition and WSA simultaneously. By evaluating the linear regression models with either weed-free yield or early crop vigour or both as independent variable(s), it was found that weed-free yield is important in predicting weedy yield, while crop vigour is important in predicting weed biomass. Therefore, selection on both weed-free yield and crop vigour is necessary. Furthermore, plant height at 4 WAS was found to be a replacement of early crop vigour without loss in selection effectiveness. Weed-free yield and early crop vigour may be combined as criteria in an indirect selection index, or selection may be carried out using independent culling levels, with early season selection on crop vigour (or plant height) followed by late season selection on yield.

Plant erectness was positively associated with WSA within the population of 40 genotypes, which was highly diverse in terms of the germplasm groups and plant types represented. However, when this relationship was tested within *japonica* germplasm, it was not significant. These results indicate that the droopy plant type within *O. sativa* is not a trait contributing to strong WSA, and may indeed be detrimental to WSA. On the other hand, the results show clearly that the erect plant type is not unfavourable to WSA.

Increasing seeding rate from 100 to 300 viable seeds m^{-2} resulted in a significant increase in weedy yield and decrease in weed biomass. However, increasing seeding rate from 300 to 500 viable seeds m^{-2} did not result in a further improvement in either weedy yield or weed suppression. Stronger WSA was related to faster early growth and thus an earlier canopy closure (0.5 – 6 days). Effects of genotype and seeding rate on weed growth were additive. Weaker inherent weed competitiveness of a genotype could be partially compensated by a higher seeding rate in suppressing weeds. Using weed-competitive genotypes at a seeding rate of 300 viable seeds m^{-2} may effectively suppress weed growth and reduce the need for weeding to once per growing season.

The main findings in this research are:

- A large genetic variability in WSA exists in aerobic and upland rice; thus breeding for weed competitiveness should be effective.
- *Indica* genotypes are higher yielding and more weed-suppressive than either tropical *japonica* or *indica/japonica* genotypes; *aus* genotypes are low yielding but are as weed-suppressive as *indicas*. Both *indica* and *aus* genotypes may be used as gene donors for improving WSA.
- Yielding ability under weed competition and WSA are both heritable traits, and compatible to each other; breeding for new genotypes combining both is feasible.
- Vegetative traits and final yield under weed-free conditions are highly correlated with weedy yield and weed biomass, indicating that indirect selection under weed-free conditions is effective. The traits that can be used most effectively in indirect selection are weed-free yield and early vigour (or early height at 4 WAS). Indirect selection on both weed-free traits may improve yielding ability and WSA simultaneously.
- Early vigorous growth of a crop rather than plant erectness is critical to weed suppression; droopy plant type is not a trait contributing to strong WSA within *O. sativa*.
- Using weed-suppressive genotypes together with an optimum seeding rate can be effective in weed management. This strategy may limit the need for direct weed control to once in a growing season.

To produce more rice with less water to ensure food security, aerobic rice may play an important role. Since weed-competitive genotypes are effective in suppressing weed growth, and it is feasible to improve both yielding ability and WSA simultaneously in aerobic rice, weed competitiveness should be included among the main breeding goals together with drought tolerance and yield.

Samenvatting

Rijst is het belangrijkste voedsel voor meer dan de helft van de wereldbevolking. Men verwacht dat de vraag naar rijst de komende jaren flink zal toenemen en in 2025 ongeveer 25% hoger zal zijn dan in 2001. Daarentegen staat de rijstproductie flink onder druk; enerzijds door de onttrekking van landbouwgrond voor stedelijke bebouwing en industriële doeleinden, anderzijds door een tekort aan irrigatiewater vanwege een toenemend gebruik van water door huishoudens en industrie, uitputting van grondwatervoorraden en verontreiniging. Geïrrigeerde laagland rijst omvat momenteel 75% van de totale rijstproductie; in de toekomst zullen deze rijstsystemen het meest getroffen worden door een tekort aan water. Om met minder water toch voldoende rijst te kunnen blijven produceren zullen veelbelovende waterbesparende rijstproductiesystemen verder moeten worden ontwikkeld. Het gaat hierbij met name om een geïrrigeerd rijstsysteem dat afwisselend bevloeid en onbevloeid wordt en om 'aërobe' rijst, waarbij er gedurende het gehele seizoen geen water op het veld staat. De rijst wordt niet overgeplant maar direct gezaaid, en wordt onder ideale omstandigheden geteeld op gronden waar het vochtgehalte in de bodem op veldcapaciteit gehandhaafd kan worden. Onder dergelijke omstandigheden kan een redelijk hoge opbrengst (6 – 7 Mg ha^{-1}) worden behaald, terwijl er meer dan 50% water bespaard wordt in vergelijking met traditionele geïrrigeerde rijstsystemen. Ook 'upland' rijst groeit gedurende het gehele seizoen onder aërobe bodemomstandigheden. Echter traditionele 'upland' rijstrassen zijn voor de watervoorziening volledig afhankelijk van regenval en reageren minder op externe inputs. Daardoor blijft de gemiddelde opbrengst steken op 1,0 – 1,5 Mg ha^{-1}.

In aërobe rijstsystemen, waar rijst en onkruiden gelijktijdig kiemen, is er sprake van een grote onkruiddruk, doordat in tegenstelling tot de geïrrigeerde laaglandsystemen met overgeplante rijst het gewas geen voorsprong heeft en er bovendien geen waterlaag is die de kieming van onkruiden onderdrukt. In aërobe systemen vormen onkruiden vaak de grootste beperking van de rijstteelt en opbrengstverliezen kunnen oplopen van 30 tot wel 100%. Onkruidbestrijding met herbiciden is meestal effectief, maar intensief gebruik van deze middelen leidt tot milieuvervuiling en bevordert het ontstaan van herbicide resistente biotypes van het onkruid. Handmatige verwijdering van onkruiden of eenvoudige mechanische bestrijding is vaak onvolledig in verband met de hoge kosten en het gebrek aan arbeidskrachten. Om die redenen is er behoefte aan een milieuvriendelijke en weinig arbeidsintensieve methode van onkruidbeheer. Concurrentiekrachtige rassen vormen wellicht een goed alternatief.

Het in dit proefschrift beschreven onderzoek was er op gericht de mogelijkheden

voor het veredelen op onkruidonderdrukking te verkennen, een indirecte selectie-index voor deze eigenschap te ontwikkelen en na te gaan of het gebruik van onkruid-onderdrukkende genotypes in combinatie met een optimale zaaidichtheid wezenlijk kan bijdragen aan het onkruidbeheer. Op basis van deze doelstellingen werden, onder aërobe omstandigheden, drie experimenten uitgevoerd op het Internationale Rijst Onderzoek Instituut (IRRI) in de Filippijnen.

Experiment 1 Veertig aërobe/upland genotypes (*Oryza sativa* L.), waaronder uitgangsmateriaal van uiteenlopende herkomst zoals *aus*, *indica*, tropische *japonica* en *indica/japonica* kruisingen, werden in de natte seizoenen van 2001, 2002 en 2003 geteeld in zowel aanwezigheid als afwezigheid van onkruiden. Opbrengst en de gerelateerde opbrengst-componenten, biomassa van het onkruid en groeikracht van het gewas geschat op 2 weken na zaai (WAS) werden elk seizoen bepaald. In 2003 werd bovendien een uitgebreide reeks vegetatieve eigenschappen bepaald, waaronder groeikracht, zaailinghoogte, bladstand, biomassa van het gewas en bodembedekking.

Experiment 2 In een proef met een vergelijkbare opzet als in Experiment 1 werd dezelfde set genotypes met één rij per genotype onder onkruidvrije omstandigheden geteeld. De planten werden gedund tot één plant per plaats en een onderlinge afstand binnen de rij van 5 cm. In dit experiment werd het aantal spruiten per plant twee keer geteld gedurende de vegetatieve groeifase om het uitstoelend vermogen te relateren aan de mate van onkruidonderdrukking.

Experiment 3 Drie uiteenlopende aërobe rijstgenotypen, met verschillen in opbrengend vermogen en vroege groeikracht werden geteeld bij drie zaaidichtheden (100, 300 en 500 levenskrachtige zaden m^{-2}) met zaden, die al of niet waren voorgekiemd. In het natte seizoen van 2003 en het droge seizoen van 2004 werden de genotypen zowel met als zonder onkruiden geteeld. In dit experiment werden opkomst, op-brengst, biomassa van het onkruid en vegetatieve kenmerken zoals aantal spruiten, biomassa van het gewas en bebladeringsindex (LAI) op 2, 5 en 8 WAS vastgesteld.

De genetische variatie in onkruidonderdrukkend vermogen (WSA) en opbrengend vermogen van de 40 geteste genotypen was in aanwezigheid van onkruiden bijzonder groot. De gemiddelde onkruidbiomassa over de drie jaren van onderzoek varieerde van 126 tot 296 g m^{-2}, terwijl de gemiddelde rijstopbrengst in aanwezigheid van onkruid varieerde van 0,5 tot 2,5 Mg ha^{-1}. Ook de vier onderscheiden herkomsten varieerden in WSA en opbrengst onder onkruiddruk. Zowel *aus* als *indica* toonden zich duidelijk meer onkruidonderdrukkend dan de tropische *japonica* en de kruisingen van *indica/japonica*, terwijl de *indica* duidelijk hogere opbrengsten liet zien dan de overige herkomsten. Deze resultaten duiden erop dat het onkruidonderdrukkende vermogen door veredeling kan worden verhoogd, en dat *aus* en *indica* als geschikte donoren kunnen worden ingezet voor genetische verbetering op het gebied van onkruid-onderdrukking.

Opbrengst bij aanwezigheid van onkruiden en biomassa van het onkruid bleken redelijk goed overerfbaar. De ververvinggraad in bredere zin werd respectievelijk geschat op 0,79 en 0,64, op basis van drie jaar onderzoek, en op 0,55 en 0,38, indien geschat op basis van één jaar. Bovendien bleken beide eigenschappen (negatief) genetisch gecorreleerd. Deze resultaten wijzen erop dat opbrengend vermogen in de aanwezigheid van onkruiden en onkruidonderdrukkend vermogen goed verenigbaar zijn en gelijktijdig kunnen worden verbeterd.

De relatieve prestaties van genotypen in verschillende onkruidbeheerregimes en jaren was vrij consistent. Eigenschappen bepaald onder onkruidvrije omstandigheden bij de oogst, zoals opbrengst en biomassa van het gewas, oogstindex en planthoogte; en de eigenschappen in de vegetatieve fase waaronder vroege groeikracht, planthoogte, bladstand, vegetatieve biomassa, LAI en aantal spruiten, waren alle genetisch of fenotypisch gecorreleerd met dezelfde eigenschappen als bij aanwezigheid van onkruiden. Eigenschappen geassocieerd met een snelle vegetatieve groei van zaailingen waren ook in sterke mate positief gecorreleerd met de opbrengst in aanwezigheid van onkruiden en negatief met onkruidbiomassa. Dit duidt erop dat snelle begingroei uiterst belangrijk is voor het onkruidonderdrukkend en opbrengend vermogen bij aanwezigheid van onkruiden en dat de gemeten kenmerken gebruikt kunnen worden als onderdeel van indirecte selectie indices. Het gaat dan met name om vroege groeikracht (geschat op 2, 4 en 6 WAS), bodembedekking (6 WAS), vroege planthoogte (3 en 4 WAS), vegetatieve biomassa van het gewas (4, 8 en 9 WAS), aantal spruiten (4, 8 WAS) en LAI (8 WAS). Voor die eigenschappen waarvan de overerfbaarheid werd vastgesteld, werden matige tot hoge waarden gevonden.

Twee indirecte selectie indices (ISI) voor selectie op opbrengst in aanwezigheid van onkruiden en onkruidbiomassa, de twee gewenste eigenschappen, werden ontwikkeld op basis van zowel gemiddelden van drie jaren als van één jaar. De ISI, op basis van drie jaren, werd ontwikkeld door in eerste instantie individuele kenmerken te kiezen met hoge indirecte selectie-efficiënties voor de gewenste eigenschappen onder onkruidvrije omstandigheden en vervolgens een regressie-analyse van deze gewenste eigenschappen op de gekozen kenmerken uit te voeren. Echter, de ISI gebaseerd op individuele experimenten werd enkel ontwikkeld door middel van een regressie-analyse. Zowel opbrengst in afwezigheid van onkruiden als vroege groeikracht maakte deel uit van alle indirecte selectie-indices; samen verklaarden deze twee kenmerken meer dan 87% van de genotypische variatie in opbrengst bij aanwezigheid van onkruiden en 40% van de variatie in onkruidbiomassa. Dit resultaat duidt erop dat het selecteren op zowel opbrengst als vroege groeikracht bij afwezigheid van onkruid kan resulteren in een verhoging van zowel het onkruidonderdrukkend als het opbrengend vermogen bij aanwezigheid van onkruiden. Nadere analyse van de lineaire regressiemodellen maakte duidelijk, dat de rijstopbrengst van genotypen in afwezigheid van onkruiden belangrijk is voor het voorspellen van de opbrengst in aanwezigheid van onkruiden, terwijl vroege groeikracht belangrijk is voor het voorspellen van onkruidbiomassa. Om die reden is selectie op zowel onkruidvrije opbrengst als vroege groeikracht noodzakelijk. Planthoogte, gemeten op 4 WAS, bleek een goede vervanger van vroege groeikracht zonder enig verlies in effectiviteit van selectie. Naast het combineren van opbrengst bij afwezigheid van onkruiden en vroege groeikracht in een indirecte selectie-index is het ook mogelijk de selectie in twee stappen uit te voeren. Vroeg in het seizoen wordt dan een selectie gemaakt op basis van vroege groeikracht (of planthoogte), waarna later in het seizoen in de resterende populatie geselecteerd wordt op opbrengst.

In de populatie van de 40 genotypen bleek een verticale bladstand positief geassocieerd te zijn met WSA. Getoetst binnen de *japonica* lijnen bleek dit verband echter niet statistisch significant te zijn. Deze resultaten duiden erop dat binnen *O. sativa* een horizontale bladstand niet een eigenschap is die in sterke mate bijdraagt aan een hoge WSA, of wellicht zelfs een negatieve bijdrage levert aan dit vermogen.

Een toename in zaaidichtheid van 100 naar 300 kiemkrachtige zaden m^{-2} resulteerde in een significante toename van de opbrengst in aanwezigheid van onkruiden en een afname in onkruidbiomassa. Een verdere toename van 300 naar 500 zaden m^{-2} liet geen verdere verbetering zien in opbrengst of onkruidonderdrukking. Een beter onkruidonderdrukkend vermogen was gerelateerd aan een snellere vroege groei en daarmee een vervroegde gewassluiting (0,5 – 6,0 dagen). De effecten van genotype en zaaidichtheid op de groei van het onkruid bleken additief. Een zwakker inherente onkruidonderdrukking van een genotype kan dan ook gedeeltelijk worden gecompenseerd door een hogere zaaidichtheid. Het gebruik van een onkruidonderdrukkend genotype, gecombineerd met een zaaidichtheid van 300 kiemkrachtige zaden m^{-2}, levert een goede onkruidonderdrukking en kan daarmee de noodzaak tot onkruidbestrijding terugdringen tot één ingreep per groeiseizoen.

De belangrijkste bevindingen van dit onderzoek zijn:

- Er bestaat een grote genetische variatie in onkruidonderdrukkend vermogen in aërobe/upland rijstgenotypen en daarmee is er een goede basis voor het veredelen op deze eigenschap.

- *Indica* genotypes zijn hoger opbrengend en meer onkruidonderdrukkend dan zowel tropische *japonica* als *indica/japonica* genotypes. *Aus* genotypen zijn laagopbrengend, maar even onkruidonderdrukkend als *indica*. Zowel *indica* als *aus* genotypen kunnen gebruikt worden als gendonoren voor het verbeteren van het onkruidonderdrukkend vermogen.
- Opbrengendvermogen in de aanwezigheid van onkruiden en WSA zijn beide overerfbare eigenschappen en bovendien goed verenigbaar. Het veredelen op nieuwe genotypen die beide eigenschappen in zich dragen is goed mogelijk.
- Vegetatieve gewaseigenschappen en opbrengst onder onkruidvrije omstandigheden zijn hoog gecorreleerd met opbrengst in aanwezigheid van onkruiden en de onkruidbiomassa. Zodoende is indirecte selectie onder onkruidvrije omstandigheden goed mogelijk. De eigenschappen die hiervoor het meest in aanmerking komen zijn opbrengst en vroege groeikracht (of planthoogte op 4 WAS). Indirecte selectie op de combinatie van beide eigenschappen kan leiden tot een gelijktijdig verbeteren van opbrengend en onkruidonderdrukkend vermogen.
- Meer dan bladstand is groeikracht gedurende de eerste ontwikkelingsstadia de eigenschap, die bepalend is voor onkruidonderdrukking. Voor rijst geldt dat een horizontale bladstand niet bijdraagt aan een sterke WSA.
- Het gebruik van onkruidonderdrukkende genotypen in combinatie met een optimale zaaidichtheid vormt een relevant onderdeel van het onkruidbeheer. Met deze strategie kan de noodzaak van onkruidbestrijding tot één ingreep per seizoen worden beperkt.

Aërobe rijstteelt kan een belangrijke rol spelen in het waarborgen van voedselzekerheid, door de bijdrage aan het realiseren van een verhoogde rijstproductie met minder water. Aangezien concurrentiekrachtige genotypen op een effectieve manier de groei van onkruiden weten te onderdrukken en het bij de veredeling van 'aërobe' rijst bovendien mogelijk is opbrengend vermogen en WSA gelijktijdig te verbeteren, zou selectie op onkruidonderdrukkend vermogen, naast droogteresistentie en opbrengst, moeten behoren tot de belangrijkste veredelingsdoelen bij 'aërobe' rijst.

摘要

世界上超过一半的人口以稻谷为主食。2025年世界稻谷需求量预计比2001年增长25%。然而, 由于城市化和工业化导致耕地面积持续减少, 由于城市和工业用水增加、地下水枯竭、污染等造成水资源短缺, 稻谷生产正面临威胁。灌溉水稻目前占世界总稻产量的75%, 然而亚洲大部分地区的水稻种植预计不久即会受到水资源短缺的严重影响。“干湿交替水稻种植 (AWD)” 和 “改良旱稻” (简称旱稻,下同)这两种节水系统需要进一步发展以确保在水源减少情况下的总稻产量。旱稻可直播在旱地上, 并在土壤达到或低于最大持水量的情况下良好生长。旱稻产量可达到每公顷6～7 吨, 并比水稻节水50% 以上。“改良旱稻” 与 “传统旱稻” 都种植在旱田条件下, 但传统旱稻不耐高肥并完全依靠降雨, 因此产量较低 (1～1.5 吨/公顷)。

旱稻播种后稻子和杂草同时萌发, 由于不象水稻那样在插秧时即对杂草有苗龄上的优势, 也没有水层抑制杂草的萌发和生长, 旱稻田较水稻田草害严重。旱稻田杂草可导致 30～100% 的产量损失, 因此杂草是旱稻生产的最大限制因子。化学除草剂可有效除草, 但大量施用化学除草剂带来环境污染并导致抗除草剂杂草的产生; 人工除草则劳力投入巨大, 且常因人工费高或缺少劳力而不能做到除草及时彻底。因此一种对环境有益且节省人工的除草方法对旱稻生产十分必要, 而强杂草竞争力品种被认为是治理旱稻草害的有效工具。

本研究旨在探索强杂草竞争力旱稻育种的可行性, 确立杂草竞争力育种的间接选择指标, 并测定强杂草竞争品种结合播种量对杂草控制的有效性。为实现上述研究目标, 我们在菲律宾国际水稻所（IRRI）试验基地旱田上进行了下述三个试验:

试验 1　在 2001、2002 和 2003 年三个雨季将 40 个（*O. sativa* L. ）包括 aus 稻、籼稻、热带粳稻及籼粳杂交后代（简称籼/粳, 下同）的改良及传统旱稻品种分别种植在有草和无草环境下, 调查作物籽粒产量、产量组成、杂草干重及播后两周稻苗活力。在 2003 年雨季, 调查了更多作物早期生长性状包括稻苗活力、苗高、植株直立度、苗干重和地面覆盖率。

试验 2　材料和试验方案同试验 1, 但只种植在无草环境下, 每品种一行, 株距 5 厘米, 营养生长期间调查单株分蘖数两次以研究分蘖力与作物杂草竞争力的关系。

试验 3　在 2003 年雨季和 2004 年旱季, 将三个产量及苗活力差异明显的品种种植在三个密度（每平米 100、300、500 个 具有发芽力的种子）, 两种预处理（浸种、非浸种）和两种草处理（有草、无草）下, 调查出苗率、籽粒产量、草干重以及播种 2、5、8 周后的单株分蘖、苗干重及叶面积指数（LAI）。

40 个品种在杂草抑制力（简称 WSA, 下同）及杂草环境下作物籽粒产量能力（简称草下产量, 下同） 方面存在较大变异, 三年平均草干重变异幅度为 126～296 克/平方米, 而平均草下产量变异幅度为 0.5～2.5 吨/公顷。4 种稻类型的 WSA 和草下产量也不同, aus 稻和籼稻比热带粳稻及籼/粳的 WSA 强, 籼稻比其它稻类型草下产量高。以上结果表明, 旱稻的 WAS 具有遗传改良空间, 且 aus 稻和籼稻可作为热带地区改良旱稻 WSA 的基因供体。

旱稻品种在不同年份间以及在有草竞争和无草环境下表现相对一致。收获期性状包括籽粒产量、地上部分干重、收获指数、株高, 营养生长期性状包括苗活力、苗高、植株直立度、苗干重、LAI、分蘖数等在有草和无草两种环境下高度自相关。与稻苗干重快速积累相关的性状与草下产量高度正相关, 与草干重高度负相关。该结果表明, 苗期快速生长对旱稻的 WSA 和草下产量至关重要, 与苗期快速生长相关的性状可作为抑制杂草旱稻育种的间接选择指标。这些指标包括: 苗活力（播后 2、4、6 周）、地面覆盖率（播后 6 周）、苗期株高（播后 3、4 周）、苗干重（播后 4、8、9 周）、分蘖数（播后 4、8 周）及 LAI（播后 8 周）。这些性状都具有较高的遗传力。

本研究确立了对草下产量和 WSA 两个目标性状进行间接选择的两组指标（简称 ISI, 下同）, 第一组 ISI 的确立是基于 3 年平均值: 首先根据无草竞争下作物性状的间接选择效率筛选出可作为选择指标的性状, 然后用选中的性状对两个目标性状分别进行回归分析; 第二组 ISI 是基于一年平均值（但两个目标性状均使用 3 年平均值）通过回归分析确立。每一组选择指标都仅包含无草下的作物籽粒产量和苗活力, 这两个无草环境下的作物性状在任何一组选择指标中都可共同解释 87%以上的草下产量变异和 40%以上的草干重变异。该结果表明, 对无草下的作物籽粒产量和苗活力进行选择可同时提高草下产量和 WSA。通过评价用单一无草下作物籽粒产量或苗活力或两者组合对目标性状进行线性回归而建立的数学模型发现, 无草产量对预测草下产量很重要, 而苗活力对预测 WSA 很重要。因此, 对两者进行双重选择很必要。此外, 苗期株高（播后 4 周）可替代苗活力而不会影响选择效率。无草下籽粒产量和苗活力可以组合在一起实施选择, 也可以按独立选择法实施选择: 早期对苗活力进行选择, 后期在第一次选择基础上再对产量进行选择。

在稻类型及株型极为多样的 40 个品种的群体中, 植株直立度与 WSA 呈正相关, 而在热带粳稻群体中, 两者间相关不显著。这些结果表明, 在 *O. sativa* 亚种中披散株型对 WSA 不是个有利性状, 也许是个有害性状 。另一方面, 试验结果清楚地显示直立株型对 WSA 并非不利。

播种量从 100 增至 300（发芽力种子/平方米）可使草下产量显著增加而草干重显著减少, 然而播量从 300 增至 500, 草下产量没有提高, 且作物对杂草生长的抑制能力也

未增强。作物较强的 WSA 与其较快的早期生长及较早的冠层关闭（提前 0.5 ~ 6 天）相关连。基因型与播种量对杂草抑制的效果是加性的, 弱竞争力品种相对强竞争力品种对杂草抑制的不足可通过增加播量得以部分祢补。强竞争力品种配合 300 的播量可有效抑制杂草生长因而或可将人工除草减至每生长季一次。

本研究的主要发现包括:

- 旱稻品种间在抑制杂草生长方面存在较大变异, 因此旱稻杂草竞争力育种应该是有效的。
- 籼稻比热带粳稻及其两者的后代产量高且杂草抑制力强; aus 稻虽产量低但杂草抑制力强。 籼稻和 aus 稻可作为改良旱稻 WSA 的基因供体。
- 草下产量和 WSA 两个性状都可遗传且互容; 通过育种实现两者结合是可行的。
- 无草环境下营养生长性状及籽粒产量与草下产量及草干重高度相关; 对无草产量和苗活力（或早期苗高, 播后 4 周）进行选择可同时改良草下产量及 WSA。
- 作物早期的快速生长特性是决定抑制杂草生长能力的关键因素; 披散株型在 O. sativa 亚种内对 WSA 并非有利。
- 强杂草竞争品种结合适宜播量可有效控制杂草, 该技术可减少人工除草作业至每季一次。

旱稻在水资源日益短缺情况下保证世界粮食安全具有重要作用。鉴于杂草抑制基因型对杂草控制作用显著, 而且同时提高产量及 WSA 是可行的, 抑制杂草力应与抗旱及高产同时列为旱稻育种的主要目标。

Publications of the author

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Non-peer reviewed publications

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Wang, H.Q. and D.L. Zhao, 1999. Aerobic rice – a new rice type for sustainable agriculture. Science Daily.

Zhao, D.L., 1998. Case studies in seed physiology. China Agricultural University, Beijing, China.

PE&RC PhD Education Statement Form

With the educational activities listed below, the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 22 credits (= 32 ECTS = 22 weeks of activities).

Review of Literature (3 credits)
- Crop weed competitiveness (2002)

Writing of Project Proposal (4 credits)
- Weed competitiveness and yielding ability of rice under aerobic conditions (2002)

Post-Graduate Courses (3 credits)
- Rice breeding (2003)
- ORYZA2000 modelling course (2003)

Deficiency, Refresh, Brush-up and General Courses (12 credits)
- Simulation of ecological processes (2002)
- Ecophysiology of crop products (2002)
- English (2002)
- Simulation of crop growth (2003)
- SAS version 8.0 (2003)

PhD Discussion Groups (3 credits)
- Plant and crop ecology (2002)
- IRRI seminars (2002-2005)

PE&RC Annual Meetings, Seminars and Introduction Days (1 credit)
- 12^{th} EWRS (European Weed Research Society) symposium, Wageningen University (2002)
- PE&RC 10-years anniversary (2005)
- PE&RC annual meeting: 'The truth of science'(2005)

International Symposia, Workshops and Conferences (5 credits)
- National aerobic rice workshop 2000, Beijing, China. Oral presentation: Traits used to screen aerobic rice for drought tolerance (2000)
- IRRI seminar, plant breeding genetics and biotechnology. Oral presentation: Traits related to cultivar weed-competitiveness in aerobic rice (2004)
- International Frontis Workshop: Gene-plant-crop relations, scale and complexity in plant system research, Wageningen. Poster: Weed competitiveness and yielding ability of aerobic rice (2006)
- International workshop: Aerobic Rice: Progress and Prospects, IRRI, Philippines. Oral presentation: Weed competitiveness – a goal of breeding aerobic rice (2006)

Curriculum vitae

Dule Zhao was born in Changle county, Shandong province, China on September 18, 1963. He graduated from China Agricultural University (CAU) and received a BSc degree majoring in Agronomy and Crop Genetics and Breeding in 1985. He worked at CAU from 1985 to 2001 subsequently as a teaching assistant, lecturer and associate professor. He taught courses on seed physiology, seed testing and seed storage, and carried out research on physiology of wheat seed development, aerobic rice breeding and cultivation. In 1988, he enrolled in CAU as a part-time MSc-student, and gained his MSc-degree majoring in Agronomy and Crop Genetics and Breeding in 1995. He worked as a visiting scientist at Kestely Agricultural University, Hungary for 2 months in 1997 on seed science. In 2001, he started a Sandwich-PhD programme in the Group Crop and Weed Ecology (CWE) of the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC). The research in this thesis was carried out under the frame-work of the strategic co-operation between Wageningen University, the International Rice Research Institute (IRRI) and CAU. Since 2001 he has travelled several times between the Philippines, China and The Netherlands for attending courses and carrying out the research activities.

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