

**Proceedings of the
Fourth Temperate Rice
Conference**

Edited by S. Bocchi, A. Ferrero and A. Porro

25 - 28 June 2007, Novara - Italy

Printed by
Tipografia Fiordo s.r.l., Galliate (No), Italy

The views expressed herein are those of the Authors and do not necessarily represent those of the organizers of the of the Fourth Temperate Rice Conference.

Suggested citation:

Bocchi S, Ferrero A., Porro A, editors 2007. Fourth Temperate rice Conference. Proceedings of the Fourth Temperate Rice Conference, 25-28 June 2007, Novara, Italy. 384 p.

ISBN 978-88-95616-01-8
ISBN editor: SIRFI

Quantitative trait loci and path analysis of vegetative traits in rice (*Oryza sativa* L).

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ABSTRACT - Feasibility of breeding competitiveness requires identification of plant traits involved as well as understanding of their genetic control. Working with a set of 137 recombinant inbred lines from a japonica*indica cross, we identify about forty QTLs explaining between 7 to 46% of variation of seedling and vegetative morphological traits associated to rice competitiveness.

KEY WORDS - QTL analysis; path analysis; rice competitiveness..

I. INTRODUCTION

RICE competitiveness and plant vegetative vigor are quantitative traits that could impact crop production, yield stability and environment conservation by reduced use of herbicides. Stability of a variety's yield is a desirable characteristic as important as yield potential [1]. However, enhanced crop competitiveness could imply some restriction on yield potential [2]. Breeding for crop competitiveness needs the identification of rice plant traits involved in its expression and their genetic control; which, should be accomplished under an eco-physiological framework. Direct selection for crop interference has practical difficulties. Breeders would prefer an indirect selection procedure through traits expressed in the absence of weeds. Molecular markers have facilitated the identification of chromosomal regions associated with many complex traits in rice [3], allowing for marker-aided selection (MAS) [4], even though in the absence of a particular stress [5]. Our results [2] corroborated that the expression of many rice traits, in particular those measured at an early vegetative stage, were well correlated between competition and monoculture conditions. We have already identified that light-capture traits (LA, shoot length) expressed in young rice plants and early biomass accumulation contribute significantly towards competitiveness without necessarily affecting crop yielding ability [2]. Previous research has also identified plant traits for competitiveness against weeds, such as early plant vigor, seedling elongation, plant height and the ability for light capture, early seedling emergence, leaf area and specific leaf area, LAI and tiller production, biomass partitioning to leaves, and total vegetative biomass. See [2] for a review. The major objective

of this research was to locate genetic loci associated with rice vegetative traits related to plant vigor and competitiveness. Thus using a japonica × indica RIL mapping population [6] we: (a) generated a genetic map of microsatellite markers and identified putative QTL responsible for the expression of seedling and early vegetative traits; and (b) formulated causal relationships among main plant morphological traits at seedling and vegetative stages.

II. MATERIALS AND METHODS

A mapping population of 137 RILs (at F₇ generation) derived from a cross between the temperate japonica cv.M-202 and the tropical indica cv.IR50 [6] was evaluated for traits associated to seedling and vegetative vigor. Phenotyping studies were conducted under monoculture in 2003 and 2004 in a rice field at the Rice Experiment Station (RES) near Biggs, CA. Seeding dates were June 2, 2003 and May 19, 2004. By correcting for 1000-grain weight and germination, seeding rates of all recombinant inbred lines (RIL) were set to approximate 200 plants m⁻². Samplings were performed at 20, 30 and 60 days after seeding (DAS). At 20DAS (4-5-leaf stage of rice) we determined seedling length and stand. Tiller number per 50 cm of row, length of the main culm from the soil surface to the tip of the youngest fully extended leaf (shoot length, SL), leaf area per 10 tillers (LA), leaf dry weight (LW), sheath dry weight (ShW), and total aboveground dry weight (STW) were measured at 30DAS (early tillering) and 60 DAS (mid to late tillering). Dry weight was determined by cutting plants at ground level and oven-drying them at 60 C until constant weight. Leaf area was measured using a LI-3100¹ leaf area meter. Leaf area index (LAI, cm² cm⁻²), specific leaf area (SLA, cm² g⁻¹), leaf area ratio (LAR, cm² g⁻¹) leaf weight ratio (LWR, gr. gr⁻¹), biomass per tiller and leaves to sheaths biomass ratio (L:ShWR) were calculated.. The microsatellite marker framework map developed [24] for this RIL population is useful in examining vegetative traits. The genetic linkage map was comparable in terms of total length, marker distribution and detected regions having marker segregation distortion to other maps and populations used in QTL detection for several rice traits.

III. RESULTS AND DISCUSSION

After two years of field studies, we identified about 40 putative QTLs (Table I) related to quantitative variation of vegetative traits in a japonica x indica rice population.

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Table 1. Total number of QTLs identified in 2003 and 2004 Biggs, CA

Trait	20DAS ¹	30DAS	60DAS
SL	1 ² (46) ²	2 ² (34)	2(14.5)
Tiller number	1 ³ (6.5)	0	3(13.3)
LA	0	0	1(11)
LAI		1 ² (16.1)	1(7)
LW		1(16.4)	4(10)
ShW		1 ² (9)	3(14.5)
STW		0	2(7.7)
Biom/tiller		0	3(11)
L:Sh WR		1(8)	1(9)
LWR		2(9)	7(12)
LAR		0	3(20.6)
SLA		0	0

¹ number of consistent QTLs across both years or,

² QTL(s) identified in separate analyses for each year when RIL x Y was significant ($P < 0.05$).

³ QTL(s) identified in a combined two-year analysis in absence of significant ($P < 0.05$) RIL x Y.

⁴ Values in parentheses are R^2 for a QTL or the larger value when more than one QTL is found for a given trait.

A few of these QTLs are pleiotropic to more than one trait which represent rather similar characteristics, i.e. QTLs coding for biomass per tiller were also identified for sheath and for leaf weight. Also one QTL was involved in controlling both late vegetative aboveground biomass and tiller number (close to RM288 at chrom. 9). A major QTL was found for seedling length (RM235 at chrom 12), which has no effect on late vegetative plant height. Increasing early plant vigor would result in both taller seedlings and abundant early tillering. However, in our set of RILs, tiller number by 60DAS and seedling height (20DAS) were negatively correlated ($r = -0.30$, $P < 0.01$), indicating a payoff between both traits. Marker RM235 was significantly associated to both, increasing tiller number at 60 DAS ($I = 381.3$, $M = 376.1$) (Fig. 1) and having shorter seedlings. Path analysis at Fig. 1 clarifies that RM288 has the strongest direct effect on tillering while not affect plant height; so, it could be possible to increase tillering through IR50 alleles at RM288 without renouncing seedling length, which would occur if M-202 alleles were incorporated at RM235 position. We also found QTLs explaining late vegetative growth; tillering ability and individual tiller biomass have both significant path coefficients to total biomass. However, the former was negatively correlated with plant height. Therefore, compared to other growth traits, enhancing tillering would be less likely to result in excessive plant height and the associated yield penalty. Conversely, increasing biomass of individual tillers would increase leaf and sheath weight, which were positively correlated with plant height. For enhancing crop vegetative vigor we could take advantage of tillering ability, explained mostly by one QTL (i.e. RM 288, Fig. 1). Nevertheless, promoting excessive tillering may also detract from high yielding ability [7]. Increased leaf expansion would contribute to light capture and competition by shading weeds. Our study identified four QTLs contributing to 29.5% of the variability in dry matter allocation to leaves. For the specific cross used in this study, early development was mostly due to alleles from the *japonica* progenitor M-202 with QTLs located on chromosomes 2, 4

and 12, while late tillering ability was contributed by the *indica* parent IR50 through QTLs in chromosome 9 that were uncorrelated to the previous ones. Previous research [8-11] agrees with our study in that different genetic control can be found for early vs. late-season vegetative traits involved in crop competitiveness, such that breeding can manipulate them separately. The evidence we have presented of differential genetic control between seedling vigor and components of late biomass growth, as well as the insight on the interrelationships among these components clearly suggests that an opportunity exists for increasing early weed competitiveness, while minimizing undesired excess plant height and biomass accumulation at later stages to preserve rice productivity.

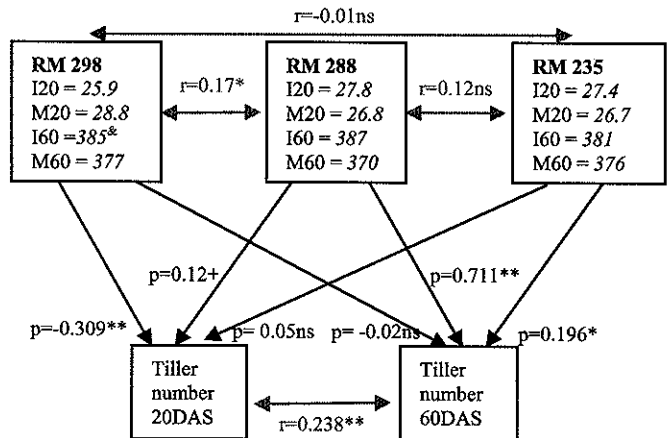


Figure 1. Path (p values, in single-headed arrows) and correlation (r values, in double-headed arrows) coefficients among independent (RM molecular markers' scores) and dependent (tiller number at 20 and 60 DAS) variables in a cause-effect model. Numbers in italics within boxes are mean phenotypic values of tiller number from the parent's alleles ($I =$ IR50 allele, $M =$ M-202 allele) at two sampling times (20=20DAS and 60=60DAS). & = transformed data by $\text{Log}(\ln 60\text{DAS})^* 94.5335316099419$; (data transformation generated by JMPin). $^{**} = P < 0.01$, $^* = P < 0.05$, $^{ns} =$ non significant.

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